



REVIEW

# Intensification of contaminants, hydrology, and pollution of hyporheic zone: the liver of river ecology—a review

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## Abstract

The ecological activities within the hyporheic zone (HZ) heavily rely on water flow dynamics. The arrangement of the hyporheic community is influenced significantly by the hydrological fluxes occurring within the zone, particularly driven by the dynamics of watercourse surface flow. While there is an ongoing debate, it is suggested that benthic organisms may utilize the HZ as a sanctuary. The ability of stream organisms to colonize the HZ is influenced by their biological characteristics. Lower oxygen levels and reduced pore space in deeper sediment layers restrict the presence of macroinvertebrates while favoring meiofauna and protists. Limited research has been conducted on the overall role of hyporheos in the assembly of entire ecosystems, with most studies focusing on larger species. The metabolism of the hyporheos facilitates the transformation of pollutants and nutrients within the HZ through the action of biofilms that degrade dissolved substances, including contaminants. Lastly, the community that feeds on biofilms and participates in hyporheic exchange flow indirectly contributes to these processes. The aim of this review article is to highlight the critical role of water flow dynamics in the hyporheic zone and its influence on the arrangement of the ecological community within. It emphasizes the potential sanctuary function of the hyporheic zone for benthic organisms, shaped by their biological characteristics.

**Keywords** Hyporheic exchange · Hydrological fluxes · Benthic · Biofilms · Environmental pollution

## Introduction

The hyporheic zone (HZ) represents a critical interface where surface water and groundwater intermingle, playing a pivotal role in the nutrient cycling and contaminant attenuation processes within river ecosystems (Biehler et al. 2020). Within this zone, sediment filters can act as a means of removing contaminants from rivers or groundwater, while microbial communities carry out direct or indirect activities to metabolize and transform these substances (Yang et al. 2020). In freshwater ecosystems, the sediments at the bottom serve as a connection between the water near the surface of the open channel and the underground water table (Biehler et al. 2020). Consequently, there exists a bidirectional flow along the stream and river continuum, where groundwater is absorbed into the surface water system and vice versa (Bencala et al. 2011). The convergence points of surface and groundwater are referred to as the HZ (Costanzo et al. 2005). Researchers from diverse fields have looked at how the HZ functions within the larger river ecosystem, resulting in the absence of a singular, all-encompassing definition for

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the HZ. The study of hyporheic processes has long served as a defining characteristic of the field as shown in Table 1 (Gomes and Wai 2019). Various definitions of the HZ exist depending on the discipline: in geochemistry, it pertains to the sediment area containing a proportion of water on the surface, while in biological science, it refers to the capacity of sediments harbouring a given population of the aquatic community (Buffington and Tonina 2009). These definitional and scope-related differences have significant implications. However, a more comprehensive and interdisciplinary definition has been recommended by Ward (2016) (Table 1). From this description of the HZ, it becomes evident that the timescale at which these events occur is crucial. Indeed, the dynamics of the surface water flow greatly influence the flow direction and exchange rate with HZ, with seasonal changes having a particularly pronounced effect. Seasonality can induce a cascade of dramatic shifts in water flow conditions, independent of river dynamics (Gasith and Resh 1999), ultimately determining the position and size of the HZ (Singer et al. 2013). Nonetheless, the HZ mitigates

the severity of this variations, making it a more favourable habitat for riverine biota during challenging time (Yu et al. 2020). These seasonal fluctuations have profound implications for shifts in species diversity and abundance (Stubington 2012). The rich and dynamic populations within the HZ are significantly influenced by the whirling and quantitative possessions of hydrological flows in both position and configuration (Boulton et al. 1998). These hyporheic communities, also known as hyporheos, comprises microorganisms (primarily fungi and bacteria) that form biofilms, and protists, and invertebrates. Biodiversity and colonisation have a direct impact on the secondary production budget and biomass of the HZ. The HZ is both a biogeochemical and mechanical filter, regulated by water flow and sediment pore space (Boulton 2000; Ren et al. 2023). This zone possesses remarkable self-purification capabilities purification (Lewandowski and Nützmann 2010), ensuring the protection of aquifers (Huang and Yang 2022). Aquifers are vital for providing humans with safe drinking water. Consequently, the headwater zone of rivers and streams plays a vital role

**Table 1** Various definitions of the hyporheic zone exist depending on the discipline

Term	Definition	Source
HZ-Original definition	The space between a stream's surface water and its actual groundwater, where various forms of life can thrive	Buffington and Tonina (2009)
HZ-Geological view	Quantity of surface-water-bearing sediments inside a given volume	
HZ-Hydrological view	The area of a streambed that allows water to move from the open channel to the groundwater below it because of pressure differences and water's ability to flow	
HZ-Biological view	The area of a streambed that allows water to move from the open channel to the groundwater below it as a result of pressure gradients and hydraulic conductivity	
HZ-Integrative definition	Anyplace that satisfies these four requirements; To completely saturate the surface, The existence of a flow channel that begins in surface water and terminates back there is required for the timescales at which processes of interest Interact with the stream are those that are important to those studies From the subsoil to the groundwater continuum, interesting processes occur continually	Ward (2016)
Hyporheos	Biological communities found in a stream's saturating interstitial areas (benthic zone)	Stanley and Boulton (1993)
Upwelling (UW) zone	Some parts of the riverbed have more pressure than others, and this is where the surface water leaves the HZ and flows into the open channel	Franken et al. (2001)
Downwelling (DW) zone	Those low spots in the riverbed where the HZ meets the surface water	
Hyporheic exchange flows	The HZ's water mass that permeates the sediment pore spaces is amplified and steered by the alternating UW and DW zones	
Micropollutants	Trace amounts of numerous new contaminants (such as medications, personal care items, steroid hormones, industrial chemicals, and pesticides) are widespread in our waters. These quantities can range from a few nanograms per litre to several 114 milligrammes per litre	Luo et al. (2022)
Hyporheic bioreactor	To put it simply, hyporheic systems are biologically active systems in which chemical molecules are altered as a result of the actions of hyporheic organisms or the active chemicals they produce	Lewandowski and Nützmann (2010)
Residence time	Solutes dissolved in water are subject to biogeochemical transformations during the period of their hydrodynamic retention in the HZ	Biehler et al. (2020)

in biomass and energy redistribution, nutrient recovery, and pollution prevention (Tewari et al. 2022). The headwater zone of rivers and streams reduces concentrations of nitrogen, phosphorus, and organic carbon (Akhtar et al. 2022). The fate and elimination rates of emerging micropollutants in lotic systems (Table 1) remain largely unknown (Zhou and Endreny 2013), making it unclear how these molecules interact with the bioreactor. This unresolved subject is of fundamental importance in ecology. One can draw parallels between the hyporheic bioreactor and the “liver” of a river (Krause et al. 2009; Krause et al. 2009). Besides its role in the creation, exchange, metabolism, and modification of dissolved chemicals, the HZ also significantly impacts the overall ecosystem condition. This paper examines the interrelationships among hyporheic exchange flow, community ecosystem, and the reduction of contaminants in the HZ (Zhou and Endreny 2013). While distinct research projects have investigated these questions and concerns individually, it is essential for all of them to be interconnected for the effective functioning of the hyporheic bioreactor.

## Methodology for literature survey

The initial stepS involved defining the research question and determining the scope of the literature review. In this case, the research question is “How does the HZ attenuate contaminants, and what role do hydrology, community ecology, and pollution play in this process?” Subsequently, a list of keywords and search terms relevant to the research question were developed. Examples of these search terms include “HZ”, “contaminants”, “pollution”, “hydrology”, “community ecology”, and “attenuation”. Using these search terms, we conducted comprehensive literature searches utilizing academic databases, such as Web of Science, Google Scholar, and Scopus. Additionally, reviewing the bibliographies of relevant articles provided further sources. Upon compiling a list of pertinent studies, we shortlisted the titles and abstracts that were relevant to the topic and discarded irrelevant ones. Relevant information from the selected articles was carefully noted and comprehensively analyzed. Finally, a conclusion was drawn, and a flowchart representing future research prospects in the field was created (Fig. 1).

## Features of hypophoric zone

### Hydrology

In most cases, the majority of baseflow in streams is derived from subterranean water sources although there are exceptions (Son et al. 2022). The HZ acts as the interface between groundwater and surface water, facilitating

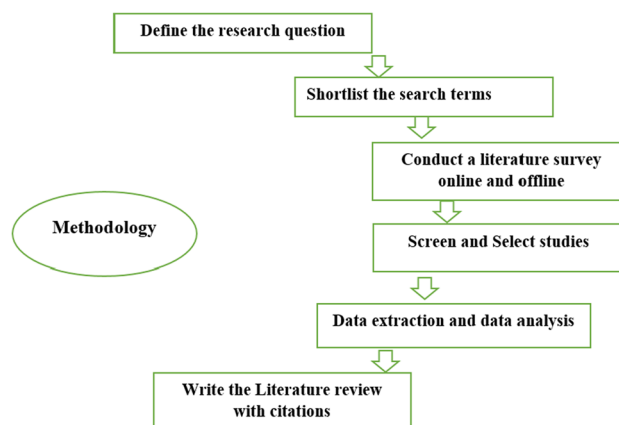


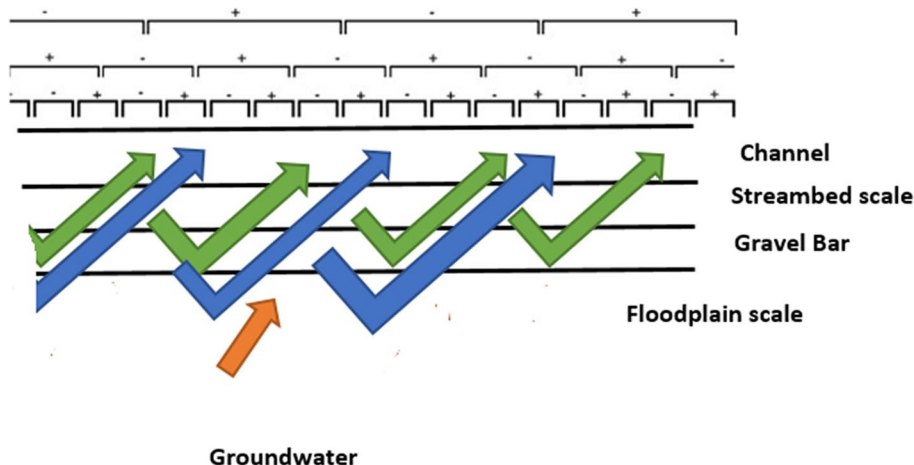
Fig. 1 Methodology followed for literature survey

bidirectional water flow between the stream and sediment at the stream-sediment boundary, provided that porous sediments allow fluid albeit with dispersed flow patterns (DeIvecchia et al. 2022).

Slight pressure differentials between subsurface and surface water give rise to upwelling and downwelling zones, where groundwater flows into the stream and surface water enters the HZ (Arora and Misra 2022). The size of these zones can vary from a few square centimetres to kilometres (Reidy and Clinton 2004), although they are typically small (Dole-Olivier et al. 2022). Due to the steady-state nature of stream discharge, hyporheic flow is more likely to occur in the central part of the streambed. Within the subsurface, the residency time is shorter along the stream’s edges and longer in its middle (Kaiser 2022). Discharging zones typically dominate most stream reaches, however, continuous up and down flows become more frequent downstream (Conant Jr 2004). Stream flows can also occur longitudinally or laterally along the bankside. Slight differences in elevation above the groundwater level in a stream create flows in one direction (Marciniak et al. 2022). Groundwater discharges and head-driven inflows are often observed near the head of pools and the foot of riffles, which are characteristic of steady-state flows shown in Fig. 2. However, transient changes in the water environment, such as rainfall, snowmelt, major floods, and dam releases, can generate significant spatial variations (Boano et al. 2009).

Longitudinal flows can be initiated by advective pumping, where groundwater meets surface water at the upstream faces of bedforms due to flow-driven pressure differences (Liang et al. 2022). This phenomenon, initially described analytically by Vaux (1968) is known to enhance exchange rates without altering the head differences between surface and subsurface water (Mendoza-Lera et al. 2019). In the absence of bedform relief, turbulence can potentially induce hyporheic exchange (Packman et al. 2004). However,

**Fig. 2** Subsurface flow paths vary from seconds to minutes to months to years (modified from Poole et al. 2008). Subsurface pathways are longer when temporally longer. Groundwater directs flow



bedform conditions may be transient due to the constant reshaping of the bed sediment (Stubbington 2012).

Lateral flows within HZs can be attributed to various factors, including temporary water level fluctuations (bank storage), paleochannels across floodplains, meandering with varying degrees of head, riffle-pool sequences, and channel sinuosity (Bruno et al. 2009). While less attention has been given to lateral flows compared to longitudinal flows, studies have demonstrated that meander-driven flows are the most significant (Torgeson et al. 2022) with the highest flows occurring at hinge points and persisting even under high groundwater discharge rates. Asymmetrical point bar drifts are initiated by channel sinuosity (Cardenas 2008), and horizontal flow rates can range from 1 cm per day to 43 m per day. Poole et al. (2008) have observed substantial flow parallel to stream channels in alluvial aquifers.

## Geochemistry

Surface-subsurface interactions have a profound impact on stream characteristics, particularly in terms of geochemistry (Fang et al. 2020). Redox reactions, involving the reduction and oxidation of molecules, play a critical role in these interactions. In biologically active systems, these reactions often involve carbon (C) (Iepure et al. 2022). Oxygen ( $O_2$ ) is the most common electron acceptor in the environment, while other compounds lacking  $O_2$  serve as terminal electron donors. As the redox potential decreases, electron acceptors are thermodynamically favored in the following order: nitrate to dinitrogen/ammonia; manganese valence state declines from 4 to 2, and iron valence state decreases from 3 to 2; sulfates to sulfides; and carbon dioxide to methane (Yan et al. 2022). Groundwater in surface flow systems generally contains insufficient dissolved organic C to sustain significant metabolism that consumes large amounts of  $O_2$  over short periods. Therefore, groundwater is typically well-oxygenated (Poole et al. 2022).

Only older groundwater with deeper and longer flow paths could be anoxic and support redox reactions with terminal electron acceptors other than  $O_2$  (Huang and Yang 2022). Surface water is typically oxygen rich (Robertson and Wood 2010a). However, areas with reduced dissolved oxygen (DO) can occur in surface water behind dams or in channels and backwaters where organic matter accumulates and water advection is limited (Michaelis et al. 2022). Hyporheic flow pathways encounter sufficient C to support respiration, leading to a decrease in subsurface oxygen (Dwivedi 2019), and oxygen levels decline with residence time in the HZ (Ahmed and Srinivasa Rao 2015). Upwelling water has much lower DO than downwelling water due to increased groundwater intrusion. The nutrient dynamics of streams are primarily influenced by the HZ due to its location (Lapham et al. 2021). The HZ serves as a transitional area between open water and sediment conditions. It is characterized by fluctuating electron donors and acceptors within a patchy mosaic, creating the impression of water cycling in and out of the zone. Baker (2000) found that these parameters significantly affected the chemical composition of streams. Due to the occurrence of a redox gradient linked with DO depletion, the HZ is considered a geochemical hotspot. This gradient promotes chemical transformations, particularly denitrification (Yan et al. 2022). The production of carbon dioxide as a byproduct of respiration leads to pH values in the HZ that differ from those of the groundwater and the stream. Other interactions, many of which are amplified by the connection between sediment and water, can also alter the surrounding pH (Runkel 2007). According to the research conducted by Cooper et al. (2022), reaction sites shift in response to changes in subsurface flows caused by groundwater or stream movements. If flow alterations are driven by seasonal patterns, such as floods, droughts, or precipitation, then these changes are likely to be predictable (Nelson et al. 2019).

## Biology

Biological factors, such as populations of hyporheic-dependent invertebrates, are often given high priority by stream remediation project managers. The HZ is renowned for its significant biological characteristics, serving as a refuge for disturbed invertebrates and a prime incubation site for stream fauna (Milner et al. 2022). Stream invertebrates seek shelter in the HZ, which provides a more stable environment compared to open waters, thanks to reduced water velocity and more constant temperatures. Temperature, as indicated by Banks et al. (2019) plays a crucial role in HZ processes. Deeper waters exhibit less temperature variability than surface waters. Over short time scales, night-time lows increase and daytime highs decrease, while over mitigating daily or seasonal temperature fluctuations, hyporheic flows equilibrate with groundwater temperatures, and longer flow paths, (Poole et al. 2008). Consequently, the intermittent pulses of water from HZ help regulate stream water temperatures. Researchers have utilized temperature variations in the stream to measure hyporheic exchange rates (Hübner et al. 2020). The presence of stable subsurface temperatures in upwelling zones is beneficial for the spawning of salmonids (van Grinsven et al. 2015).

Recovery of benthic populations takes longer after major floods (Maier and Howard 2011), primarily because organisms seeking refuge in downwelling areas assist in the rapid recovery of benthic dwellers (Guo and Jiang 2020). According to Stubbington (2012), determining which organisms seek refuge where and when is possible is not consistent. The efficacy of the refuge depends on sediment type, taxa, type of disturbance, and whether the response to the disturbance is passive or active (Lorenzo et al. 2021). Robertson and Wood (2010a) suggest that certain disturbance events have the potential to alter the hyporheic environment and refuge functions. The HZ is composed of a patchwork of various small habitats due to sediments, water flows, and prevailing conditions (Sackett et al. 2019). Upwelling groundwater in close proximity (possibly associated with finer sediments of the pool) and other sediments and flows related to meander erosion all contribute to the benthic sediment pattern of a river (Boulton 2007). Benthic sediment patterns can also be associated with meander erosion (Langenhoff et al. 2013).

Microbes, meiofauna, and macrofauna are all organisms that can be found in the HZ (Mermillod-Blondin et al. 2013). Faunal characterizations of the HZ are dominated by insect instars, which are transient members of ecosystem (Boulton et al. 2010). The HZ is known to harbor aquatic insect juveniles, water mites, flatworms, rotifers, segmented worms, and, hyporheos crabs, as identified by various biologists (Graham et al. 2022). Management programs for the HZ often focus on salmonid fish eggs and alevin, which inhabit

excavated redds that are subsequently refilled by adults. DO affects the overall distribution of hyporheos organisms (Kasahara et al. 2022), along with grain proportions and vertical flow arrangements (Olsen and Townsend 2003).

Biofilms in the HZ are formed by HZ bacteria. According to Storey et al. (2003) biofilms create microenvironments, which are small anaerobic zones within oxygenated environments. These zones are crucial for denitrification. However, the supply of nutrients and waste in biofilms is controlled by advected waters (Sobczak and Findlay 2002). This is due to the presence of expressed enzymes and limited pore space, which create highly specialized environments within biofilms.

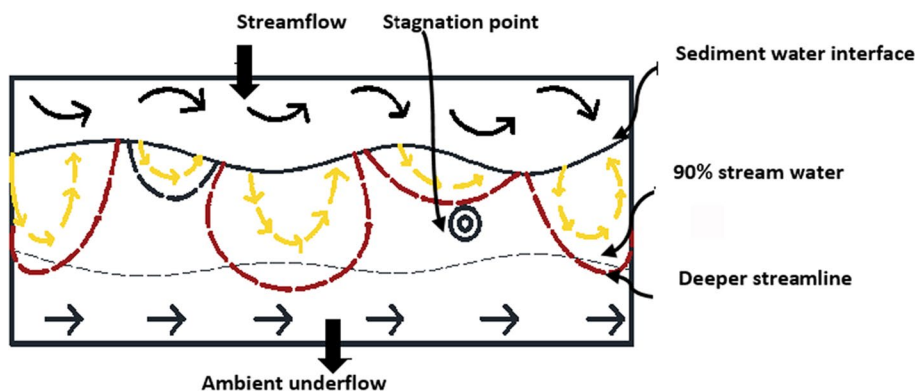
## Hyporheic hydrodynamics drives hyporheic zone ecology

According to Gomez-Velez and Harvey (2014) there is a continuous, bidirectional interchange of energy and water between the primary channel of the river and the surrounding sediments at the sediment water interface (SWI). This interchange plays a significant role in biogeochemical cycling, stream heat regulation, and ecological functioning along river corridors (Hannah et al. 2009; Harvey and Gooseff 2015; Vonk et al. 2019). A comprehensive understanding of dynamic hyporheic processes requires insights of the interactions among drivers and controls of exchange (see Fig. 3; Gomez-Velez and Harvey 2014). These interactions include dynamic forces in sediment transport, sediment hydraulic conductivity and porosity, morphometry, and slope. The complex interactions and exchange mechanisms not only affect the scale of hyporheic exchange flux (HEF), but also influence the residence time of water and solutes on the streambed and the formation of stagnation zones. Singh et al. (2020) found that the extent and depth of streambed exposed to these processes are also impacted. Hyporheic exchange occurs across a wide array of temporal and spatial scales, which are determined by factors such as channel geometry, slope, and landscape characteristics of the streambed (Boano et al. 2009). Additionally, sediment hydraulic properties and their heterogeneity, along with ambient groundwater flow, influence the exchange process (Cardenas et al. 2004; Gomez-Velez and Harvey 2014).

## The influence of seasonal fluctuations in river flow on the communities

There have been extensive studies on the HZ over the last three decades, particularly focusing on steady-state flow conditions (Buffington and Tonina 2009). However, researchers are only just beginning to comprehend the significance of ephemerality in-stream flow (Boano et al.

**Fig. 3** Hyporheic hydrodynamics driving hyporheic zone ecology



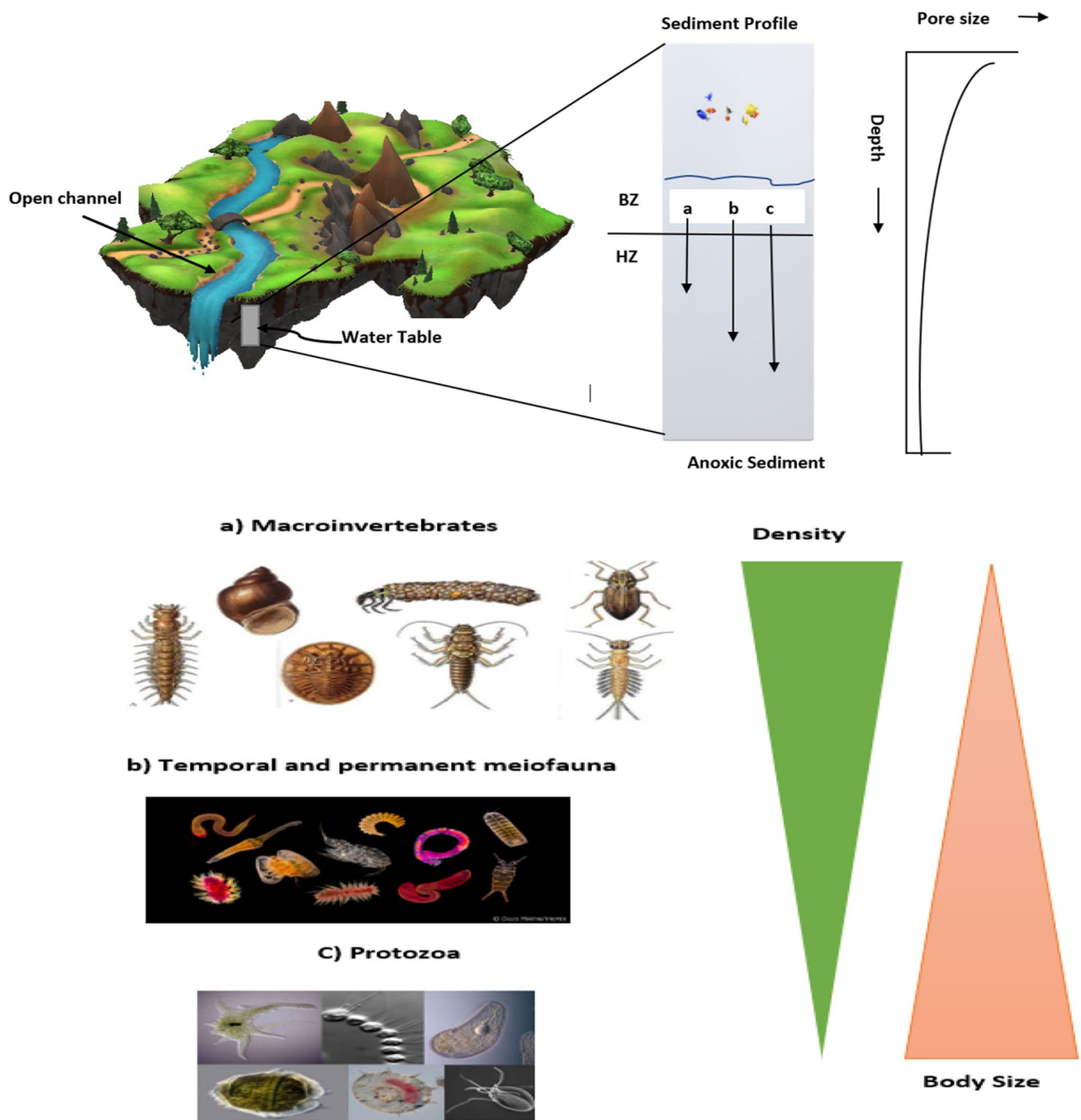
2007; Gomez-Velez et al. 2017). Hydropeaking and thermal peaking can occur due to regular variations in rainfall, evapotranspiration, and snowmelt, as well as human activities, like wastewater treatment and dam operations. Peak flow events lead to increased downwelling surface water, which is richer in essential nutrients and oxygen, consequently impacting biogeochemical processes in the streambed, including denitrification, nitrification, anaerobic and aerobic carbon respiration (Fritz et al. 2008; Trauth and Fleckenstein 2017). These effects can potentially extend to greater depths and larger streambed areas (Bruno et al. 2009). Therefore, stream stage and flow have significant implications for hyporheic and benthic invertebrates, thermal conditions, and nutrient cycling (Bruno et al. 2020).

Recent findings have highlighted the significance of understanding the dynamic environment of river corridors (Dudley-Southern and Binley 2015; McCallum and Shanafield 2016; Malzone et al. 2016; Schmadel et al. 2016; Gomez-Velez et al. 2017; Trauth and Fleckenstein 2017; Bruno et al. 2020). Ward et al. (2018) have identified key drivers and controls of hyporheic exchange flows during transient stream flow conditions. Several studies have demonstrated the significance of hillslope lag, hillslope amplitude, cross-valley and down-valley slopes in determining hyporheic flow paths and residence times (Malzone et al. 2016; Schmadel et al. 2016). Graham et al. (2022) observed changes in inflow and outflow residence time patterns for various discharge events. Peak discharge and event duration play a crucial role in determining the mean age of water and solutes, which in turn affects rates of anaerobic and aerobic respiration. In a study, Gomez-Velez et al. (2017) employed a dimensionality-free framework to investigate the relationship between flow characteristics, the spatial and temporal progression of riverbank storage, and sinuosity-driven hyporheic exchange. However, hydrological and geomorphological controls on hyporheic exchange flows with biogeochemical implications have not been thoroughly addressed in previous dynamic studies.

### River budgeting, stream biota, and productivity utilising the hyporheic zone

Determining system limitations is crucial for analyzing ecological processes (Fudyma et al. 2021). When studying stream and river, the three classic spatial compartments considered are the benthic zone, the open channel, and the headwater zone (H–Z) or riparian zone. Measuring secondary production allows for the quantification of the flux of energy output (in the form of biomass) and its distribution in time and space for heterotrophic organisms (Yuan et al. 2022). However, only a few researches have demonstrated the relative importance of the HZ compartment in the overall system structure (Collier et al. 2004; Reynolds Jr and Benke 2012a; Wright-Stow and Wilcock 2017). Although initially defined biologically, the uppermost 0 to 5–10 cm of sediments have been labeled as the benthic zone (BZ), while the deeper depths are referred to as the hypoxic zone (Smock et al. 1992; Collier et al. 2004). Accurate delineation of the boundaries of the hyporheic zone compartment's requires a depth-gradient strategy on a microscopic scale, which considers centimetre-scale differences in assemblage structure, and maps the ranges of key species in both habitats.

Multiple studies have demonstrated that as one moves deeper into the water, the composition of invertebrate assemblages undergoes a shift. The control over these communities' changes from large individuals near the surface to a dominance of smaller-bodied species (Schmid-Araya 1994). This alteration in invertebrate communities becomes evident with increasing water depth. The ability of hyporheic taxa's to colonize the HZ varies among species due to several biological factors (Nogaro et al. 2009; Robertson and Wood 2010; Descloux et al. 2014). Sediment agglomeration (Fig. 4) leads to a reduction in oxygen concentration and pore size along the gravity gradient, restricting the dispersal of large macroinvertebrates with high metabolism (Maridet and Philippe 1995; Strayer et al. 2003). Consequently, meiofauna (microscopic metazoans) and protists tend to increase in abundance as one descends into the water (Fig. 4). Studies



**Fig. 4** Box 1: shows a diagram showing the distribution of the streambed community along the depth profile in relation to pore size and redox potential. Large macroinvertebrate colonisation depth is represented by arrows in (a), (b), and (c) respectively. The hypothetical separation between the hyporheic zone (HZ) and benthic zone (BZ),

which serves as the cap on colonisation between benthos and hyporheos, is also depicted. The sediment profile's grey/black scale represents the redox potential, with deep black denoting extremely anoxic conditions. Box2: Body size and density distributions of different groups in the community structure. Organisms are not drawn to scale

of riverbank ecosystems have revealed a decline in the density of large species with depth (Marchant et al. 2000; Davy-Bowker et al. 2006; Pacioglu and Robertson 2017). Thus, the loss of riverbed biota and secondary production may be linked to the gravity gradient as a combination of

diverse physicochemical parameters. The meta-analysis of invertebrate communities from diverse river systems, based on information from Smock et al. (1992) and Reynolds Jr and Benke (2012) lends support to this hypothesis by demonstrating a significant and negative effect on secondary

production and depth of biomass. It should be noted that the studies included in this meta-analysis have primarily focused on large species, while the majority of meiofauna and protozoa have not been included in the analysis of differences along the depth gradient in terms of secondary production and biomass.

The variability in the ability to infiltrate the HZ is influenced by the characteristics of hyporheic species, and we expect there to be a significant interaction between depth and size. Future studies incorporating these groupings and their interactions with depth, sediment properties, and hydrology, could greatly enhance predictive modeling and compartment comparisons (Wohl 2021). This is particularly intriguing because it has been hypothesized that dynamic hyporheic communities play a crucial role in maintaining the bioreactor function of the HZ (Krause et al. 2014). Thus, areas with higher rates of biomass and secondary production may correspond to hotspots of nutrient and pollutant transformation.

It is also anticipated that the depth gradient would influence the functional behaviour of different organisms within the bioreactor. For instance, relatively large burrowing organisms like Oligochaeta, Ephemeridae nymphs, and Chironomidae larvae, would have a greater impact on the benthic zone and the upper layer of the HZ compared to the deeper layers. Their activities, including bioturbation and bioirrigation, have significant effects on water biogeochemistry by enhancing respiration, permeability, and bacterial activity (Hölker et al. 2015; Baranov et al. 2020).

## Hyporheic bioreactor

The health of ecosystems is often negatively affected when human activities alter the chemistry of pore water and flow exchange in the HZ (Peralta-Maraver et al. 2018). The influx of contaminated water from wastewater treatment plants (WWTPs) has led to the continuous or intermittent introduction of nutrients such as organic C, nitrate, phosphate and additional contaminants (such as insecticides) into many rivers worldwide (Rutere et al. 2020; Höhne et al. 2022). Once these molecules enter the sediments due to hydrological patterns, they may undergo metabolic processes facilitated by active and prolific hyporheic communities, resulting in the production of oxidised or reduced substances (Schaper et al. 2018).

Considering the crucial role of microbial biofilm in water purification within the HZ, it can be regarded as a bioreactor. Hyporheic biofilms exhibit highly diverse bacterial and archaeal populations that share a common polysaccharide matrix (Peter et al. 2019). As a result, numerous functional taxonomic units, metabolic capabilities, and sites with high enzymatic activity within these biofilms coexist (Peter et al. 2019). In-stream biofilms exert a significant impact on

biogeochemical fluxes of carbon, phosphorus and nitrogen (Rutere et al. 2020). One theory suggests that the physiology, activity, and biomass of microbial communities are constrained by the availability of nutrients (Albergamo et al. 2019). Consequently, increased intake of dissolved organic carbon (DOC) should lead to higher bacterial biomass and metabolic activity (Garcia-Becerra and Ortiz 2018). Water constantly flows into and out of the HZ and riparian zone (Li et al. 2022) due to water level fluctuations that creates significant hydraulic gradients and enhances mixing in regulated waterways. Daily variations in river level increase bacterial respiration and turnover of the organic carbon (Li et al. 2022).

## Micropollutants

The HZ refers to the space of the streambed where surface water infiltrates the sediment, leading to a subsurface flow of porewater and potential reemergence into the surface water, a process known as hyporheic exchange flow (Frei et al. 2019). These flows occur at various scales and create hotspots for biogeochemical activity, making the HZ akin to the “liver” of a river (Posselt et al. 2018). The conveyance of O<sub>2</sub>, nutrients, and bioavailable organic C to the sub-surface sediment creates an ecohydrological environment with steep redox gradients and increased biological activity (Posselt et al. 2018).

Research (by Lewandowski and Nützmann (2010), Bardini et al. (2012), and Maazouzi et al. (2017) indicates that organic C, phosphorus, and nitrogen, are the major contaminants in the HZ. However, a new class of chemicals called micropollutants poses an emerging threat to both surface water systems and their interactions with groundwater systems. Inputs from wastewater treatment plants (WWTPs) have significantly increased the concentration of micropollutants, including pharmacological and individual care items like ibuprofen or antibiotics, in waterways (Li et al. 2015; Kalekar et al. 2022). These micropollutants raise concern about their potential harmful impacts on environmental systems, such as bioaccumulation, and anthropological toxicity like aquifer contamination. Prolonged exposure to subtherapeutic levels of antibiotics in aquatic systems also acts as a selective mechanism for microbial populations (Hirsch et al. 1999; Yang and Carlson 2003; Schaper et al. 2018). Consequently, the capability of biofilms to provide ecosystem services may be altered due to variations in the bacterial population’s antibiotic resistance (composition, richness, density) (Roose-Amsaleg and Laverman 2016), which can negatively affect denitrifying bacteria subsequently decrease denitrification processes. Nonetheless, in various cases, micropollutants can be effectively reduced along flow pathways (Lewandowski and Nützmann 2010). Biofilms are



more efficient at transforming several of these substances, such as diclofenac, bezafibrate, ibuprofen, and naproxen, in stream sediments compared to WWTPs (i.e., Schulz and Sherwood 2008; Radke et al. 2009). This efficacy can be attributed to the diverse microbial communities present in natural environments (Gan et al. 2023). Additionally, biodegradation processes are more efficient in the HZ due to the longer water residence time compared to the open channel (Lewandowski and Nützmann 2010).

Although the importance of biofilm in pollution mitigation is widely recognized, many unresolved concerns surround the underlying mechanisms of this ecological process, such as the role of the rest of the population (Zhu et al. 2020). When studying the degradation of pollutants and nutrients in the HZ, it is crucial to consider the hierarchical interplay between biogeochemical processes and hydrological patterns (Sophocleous 2002). Hydrodynamics can have two conflicting effects on solute responses in sediments. Higher inward water flows result in shorter residence periods for chemicals in the sediments, giving the hyporheic microbiota less time to undertake biogeochemical reactions (Krause et al. 2017) (Fig. 3a). When the potential influence of hyporheic organisms on hydraulic conductivity is taken into account, these pathways become more complex (Li et al. 2020). The growth of biofilm matrices in sediment pores reduces permeability and enhances water residence time in the HZ (Li et al. 2022). Furthermore, the thickness of the biofilm polysaccharide matrix is believed to be the limiting factor in solute uptake, according to biofilm theory (Gantzer et al. 1988). External mass transfer involves the movement of solutes from the pore water to the biofilm surface, followed by internal mass transfer via the biofilm matrix and into the cells (Battin et al. 2003). However, sediment permeability increases due to the ongoing reworking (Boulton 2000). HZ microfauna, acting as ecosystem engineers, create preferential flow paths, increase the surface area of biofilms, and enhance bacterial densities through burrowing, sediment removal, and biofilm foraging (Boulton 2000; Mermillod-Blondin et al. 2011). Thus, the balance between these competing forces ultimately determines the impact on breakdown rates (Cardenas and Tiedje 2008; Arnon et al. 2010; Bardini et al. 2012). Consequently, carefully planned experiments conducted under defined conditions and employing proper cultivation techniques are necessary to acquire a mechanistic knowledge of biofilm function (Singer et al. 2006).

## Future perspectives

Future studies on the attenuation of pollutants in the HZ are expected to focus on the interactions between pollution, hydrology, and community ecology (Kalekar et al. 2022).

Understanding how these variables interact is crucial for developing practical strategies to reduce pollution and maintain the health of the HZ (Zhou and Zhou 2023). One area of investigation could be the impact of hydrological variations on pollutant attenuation and transport. For instance, scientists could examine how changes to sediment dynamics, groundwater flow rates, and groundwater level affect the transport and fate of contaminants in the HZ (Dichgans et al. 2023). By understanding these dynamics, researchers could develop predictive models to identify the most vulnerable areas of the HZ to contamination. Another avenue of research could be to explore the role of community ecology in contaminant attenuation (Gan et al. 2023). Microbial communities in the HZ play a significant role in pollutant breakdown and toxicity reduction. Future studies could investigate how changes in the composition and diversity of these microbial communities influence contaminants attenuation. By gaining a better understanding of the factors that impact microbial communities in the HZ, researchers could develop strategies to promote the growth of microbial communities that are effective at breaking down pollutants (Ren et al. 2023). Furthermore, future research could assess the effectiveness of various remediation strategies in the HZ. For example, researchers could investigate the efficacy of using permeable reactive barriers or other engineered solutions to remove contaminants from groundwater before it enters the HZ (Feng et al. 2023). Additionally, natural processes like bioremediation or phytoremediation could be explored as potential methods to break down contaminants in the HZ.

## Conclusion

Still, there are several factors that pose challenges in ecological studies of the HZ. Not only are these factors interconnected in space and time, but they also exhibit a discernible hierarchy. The study of the HZ is emerging as a prominent field in freshwater science, primarily due to the availability of advanced technological methods. While HZ research is still in its early stages, it is poised to become a central focus and challenge for freshwater scientists in the future as they strive to comprehend how the HZ influences the provision and delivery of ecosystem services within the entire river system. Numerous intriguing and unresolved questions remain, such as the impact of hyporheic exchange on energy fluxes within these communities and the fate of pollutants and nutrients as they exit the HZ. The influence of river regulations on hyporheic exchange flow is another area that warrants exploration in future studies. Consequently, the most appropriate approach to address all these challenges is through a comprehensive and interdisciplinary framework at the interface of ecology and hydrology.

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## Declarations

**Conflict of interest** All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

**Ethical approval** This article does not contain any studies involving animals performed by any of the authors.

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