



Trait-based structure of invertebrates along a gradient of sediment colmation: Benthos versus hyporheos responses

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HIGHLIGHTS

- We studied the effects of colmation on the biological attributes of invertebrates of three rivers.
- A higher number of traits were significantly modified with colmation in the benthic vs. hyporheic assemblages.
- Most of the biological attributes impaired were different in the two zones.
- A potential indicator of river colmation may be based on the functional traits of benthic communities.

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ABSTRACT

Streambed colmation by fine sediment, e.g. the deposition, accumulation and storage of fines in the substrate, is known to have severe effects on invertebrate assemblages in both the benthic and hyporheic zones but the changes in biological attributes of invertebrate assemblages related to colmation have never been considered simultaneously for these two zones. We studied the effects of colmation on the invertebrate assemblages of three rivers, testing a priori hypotheses on the biological attributes that should be more selected in communities subjected to different levels of colmation in both zones. Only the proportion of organisms with high fecundity increased and the proportion of small-sized organisms decreased along the colmation gradient in both zones simultaneously. As expected, a higher number of traits were significantly modified with colmation in the benthic vs. hyporheic assemblages. Most of the biological attributes impaired were different in the two zones. In the benthic zone, colmation mainly selected particular physiological or trophic characteristics of species and features related to their resistance or resilience capacities. In contrast, the morphological attributes of species were much more impaired by colmation in the hyporheic zone than in the benthic zone. In clogged benthic habitats, traits seemed to be more impaired by an increase in physico-chemical constraints (e.g. the reduction of oxygen availability) and a reduction of potential exchanges (including exchanges of food resources) due to a decline in stream bed conductivity. The morphological attributes of the hyporheic species were probably more influenced by changes in interstitial space characteristics. A potential indicator of the effects of colmation on river health may be based on the functional traits of benthic communities because they (i) satisfy the WFD recommendations, (ii) respond consistently along a colmation gradient and (iii) are comparable among assemblages even across ecoregions that differ in their taxonomic composition.

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1. Introduction

Human activities including agriculture and forestry accelerate land erosion and increase fine sediment inputs into aquatic ecosystems (Waters, 1995; Hancock, 2002). This problem is widespread worldwide

and, in addition to flow perturbations (e.g. damming, withdrawal), often leads to the clogging of substrate interstitial spaces with fine sediments (i.e. colmation), reducing hydrological exchanges between surface and ground waters, then impairing the availability of dissolved oxygen, nutrients and organic matter within the streambed (Petts et al., 1989; Waters, 1995; Matthaei et al., 2006; Boulton, 2007). As a result, colmation could have severe negative consequences on the structure and function of aquatic assemblages which may be impaired in terms of both taxonomic and functional trait structure (Gayraud and Philippe, 2001).

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Trait structure refers to the combination of traits present in a given community. These traits are considered as 'functional' because they can affect ecosystem functioning by influencing organismal performance (McGill et al., 2006). The combination of traits in a community results from adaptive pressures (Usseglio-Polatera et al., 2000a, 2001). Indeed, the 'habitat filtering hypothesis' considers that the characteristics of habitats, in particular those related to disturbance regime and habitat diversity, provide the evolutionary conditions from which life history traits and community properties are derived (Southwood, 1977, 1988; Townsend and Hildrew, 1994). Numerous workers have confirmed predictions from habitat templet theory (Menezes et al., 2010; Statzner and Bêche, 2010), giving evidence that the functional trait approach can provide a direct link between organisms and ecosystems (Petchey and Gaston, 2006). Therefore, using species traits as response variables should facilitate the successful explanation of the mechanisms structuring communities, including human-induced disturbances such as toxic contamination (Archambault et al., 2010), salinity (Piscart et al., 2006), waste water discharge (Charvet et al., 2000); agricultural pressure and/or hydrological disturbance (Lecerf et al., 2006; Townsend et al., 2008); land use in the watershed (Dolédec et al., 2006), hydrological connectivity alteration (Paillex et al., 2009) or multiple stressors (Gayraud et al., 2003; Dolédec and Statzner, 2008).

Colmation impairs vertical connectivity and could have severe effects on river ecosystem function (Stanford and Ward, 2001; Boulton, 2007). In the absence of scouring spates, the main direct physical effect is a reduction in habitat availability (Lenat et al., 1979; Maridet and Philippe, 1995). Colmation changes also the biogeochemical conditions of habitats, shifting from oxic to anoxic conditions and increasing toxicant concentrations (Minshall, 1984; Gayraud and Philippe, 2003). By reducing (i) interstitial pore size, (ii) habitat heterogeneity and (iii) hydrological disturbance effects, then increasing habitat stability (Petts et al., 1989; Ryan and Boufadel, 2007), colmation has the potential to modify community structure and major functional traits within both the benthic and hyporheic invertebrate assemblages. These modifications have been mainly studied for the benthic zone. A decrease in benthic invertebrate density and taxonomic diversity has been widely demonstrated by Lenat et al. (1979) and Richards and Bacon (1994). The percentage of the benthic Ephemeroptera, Plecoptera and Trichoptera (EPT) assemblage has been negatively correlated with an increase in fine sediment deposition (Bjornn et al., 1977; Lenat et al., 1979; Matthaei et al., 2006; Larsen et al., 2009; Larsen and Ormerod, 2010), while the abundance of other taxa, such as Oligochaeta, often increases with colmation (Lenat et al., 1979; Angradi, 1999; Zweig and Rabeni, 2001). The increase in fine sediment disadvantages organisms that need large interstitial spaces and high oxygen availability (James et al., 2008), potentially resulting in the selection of specific co-adapted traits within faunal assemblages. Gayraud and Philippe (2001) showed that the proportions of small-sized (<5 mm) and cylindrical or spherical organisms, were negatively correlated to interstitial space availability. The balance between the major feeding groups can also be modified, with a shift from filter-feeders and scrapers to deposit-feeders (Lemly, 1982; Waters, 1995; Relyea et al., 2000).

Very few studies on the impact of sediment colmation on hyporheic invertebrate communities exist, even though the functional role of the hyporheic zone and the importance of faunal exchanges between the epibenthic and hyporheic areas are well known. In particular, the hyporheic zone acts as a refugium and nursery for many benthic organisms (Marmonier et al., 1993; Ward et al., 1998). The densities of hyporheic invertebrate assemblages generally decrease with increasing fine sediment deposition (Richards and Bacon, 1994; Weigelhofer and Waringer, 2003; Descloux et al., in press), by reducing invertebrate dispersal within the substrate. However, the effects of colmation on the biological trait composition of hyporheic communities are poorly known, despite the strong

effects of colmation on the availability of habitats, their abiotic characteristics and biotic interactions within the resident community.

The objective of this study was to compare the effects of an increasing gradient of fine sediment proportion in mineral substrate on the trait profiles of both benthic and hyporheic invertebrate assemblages at the reach scale. We aimed to assess whether changes in community trait combinations could be used to evaluate the impact of colmation. First, we predicted that colmation should less drastically affect the traits of invertebrate communities of the hyporheic zone than of the benthic zone because, the hyporheic zone collecting fine particles that are less frequently washed away by floods than in surface sediments, might host an assemblage naturally more adapted to fine sediment (hypothesis H1). Second, for ten biological traits, we predicted differences in attributes selected by invertebrates along an increasing colmation gradient (Table 1, Appendix 1), taking into account four potential driving processes: (i) a size reduction of interstitial spaces (process 1 = 'proc 1' hereafter); (ii) a reduction of potential exchanges due to a decline in streambed hydraulic conductivity (proc 2); (iii) an increase in physico-chemical constraints (e.g. a reduction in oxygen availability; proc 3) and (iv) an increasing temporal stability of harsh habitat conditions generated by the three first processes (proc 4). We hypothesized an increasing proportion of organisms (i) small-sized (due to proc 1), (ii) burrowing (proc 1 and 2), (iii) monovoltine (proc 4) with (iv) asexual reproduction (proc 2), (v) medium to high fecundity (proc 3), (vi) no or few resistance stages (proc 4), (vii) mainly tegumental respiration (proc 2 and 3), (viii) cylindrical body (proc 1), (ix) being deposit-feeders (proc 2) and (x) consuming fine organic detritus and microorganisms (proc 2) along an increasing colmation gradient (Table 1, Appendix 1, hypothesis H2).

Table 1

Trait-based predictions in both benthic and hyporheic site assemblages along a colmation gradient described by three colmation classes. 'Intermediate' means a selection of adaptations 'intermediate' between the predictions of the heavily and lightly clogged reaches. Proc 1 = process 1, a size reduction of interstitial spaces; proc 2 = a reduction of potential exchanges due to a decline in streambed hydraulic conductivity; proc 3 = an increase in physico-chemical constraints and proc 4 = an increasing temporal stability of harsh habitat conditions.

No	Trait	Process involved	Colmation class		
			Lightly clogged (LC)	Moderately clogged (MC)	Heavily clogged (HC)
1	Maximal potential size	proc 1	Large/small	Large/small to small	Small
2	Number of reproductive cycles per year	proc 4	Low to high	Medium	Medium
3	Fecundity	proc 3	Low to high	Medium to high	Medium to high
4	Body form	proc 1	Varied	Varied/ mainly cylindrical	Mainly cylindrical
5	Reproduction Technique	proc 2	Varied	Intermediate	Asexual; free eggs and clutches
6	Resistance forms	proc 4	Present/absent	Present/absent	Absent
7	Respiration	proc 2 + 3	Varied	Intermediate	Mainly tegumental
8	Locomotion and substrate relation	proc 1 + 2	Varied	Intermediate	Crawlers; burrowers attached
9	Food	proc 2	Varied	Intermediate	mainly microorganisms in fine sediment; fine detritus
10	Feeding habits	proc 2	Varied	Intermediate	Mainly deposit-feeders and filterers reduced proportion of scrapers

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