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Effects of spates on interstitial assemblages of the Rhône River. Importance of spatial heterogeneity

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Abstract

The dynamics of interstitial assemblages, after a spate and during low discharge, was studied in a regulated channel (Miribel Canal) of the Upper Rhône River, France. Using a Bou-Rouch pump, three stations were samples: 1) Station IIA, a site fed by superficial water infiltrations, 2) Station IIC, a site fed by riparian phreatic water, and 3) Station IA, a site fed by both surface and phreatic waters. The spate greatly influenced the interstitial assemblages, their dynamics were different according to the hydrology of the given site. At Station IIA, the spate had a wash-out effect on the assemblages (reduction in abundance and diversity), whereas during low discharge the interstitial layer received a continuous influx of epigean organisms (benthic and limnophilous). At Stations IIC and IA, the spate introduced numerous limnophilous and benthic invertebrates into the interstices, which function as an organismic trap. However, these sites appear to be more isolated from surface waters during low discharge. Stygobites decreased or disappeared after the spate. They appear highly sensitive to hydrologic perturbations in the surface waters.

Introduction

Disturbance in stream ecosystems was recently redefined by Resh *et al.* (1988) as 'any relative discrete event in time that is characterized by a frequency, intensity, and severity outside a predictable range, and changes resources or physical environment'. Rapid variation of discharge such as spates and drought are amongst the more typical disturbances observed in unpolluted temperate streams (Resh *et al.*, op. cit.). Seasonal flooding in desert stream, for example, greatly disturbs the nutrient dynamics and energy cycling of the ecosystem (Fisher *et al.*, 1982; Grimm & Fisher, 1982; Grimm, 1987). The effect of spates on benthic assemblages has been well documented (Barton & Wallace, 1979; Gray & Fisher, 1981; Gaschignard, 1984; Gaschignard-Fossati, 1986; Prevot & Prevot, 1986; Badri *et al.*, 1987; Scrimgeour *et al.*, 1988: Giberson & Hall, 1988), but similar studies on interstitial assemblages are scarce (Poole & Stewart, 1976; Williams & Hynes, 1974; Danielopol, 1976; Marmonier & Dole, 1986). The purpose of this present paper is to evaluate the effect of a spring spate on the composition and structure of the interstitial assemblages, and the recolonisation of the interstitial layer during the subsequent aestival period of low discharge.

Study area, materials & methods

Three sampling sites were studied in a regulated arm (Miribel Canal) of the Upper Rhône River, 20 km upstream of Lyon, France (Fig. 1), because this channel is subjected to great hydrological fluctuations – periods of constant low discharge alternating with intermittent strong spates. Regulated in 1938 by a dam, which diverts most of the river discharge to an adjacent hydroelectric power station, Miribel Canal receives a minimum low water discharge of 30 $m^3 s^{-1}$. During the low discharge, the channel drains phreatic water from the alluvial plain, whereas during spates or floods, Miribel Canal serves as a spillway for the adjacent hydroelectric facility, and its discharge can increase very rapidly within a few days. The surface sediments of the channel are coarse (gravel from 0.4 to 5 cm, and pebbles from 5 to 20 cm; Poinsart *et al.*, 1989) with a poor developed sandy matrix and a high porosity.

Previous studies have demonstrated that the spatial distribution of interstitial fauna in Miribel Canal is linked to the origin of the interstitial water (Marmonier & Dole, 1986; Marmonier, 1988; Creuzé des Châtelliers, in press). Thus, three stations were chosen according to their hydrology (Fig. 1): Station IIA, which is fed by surface water infiltrations; Station IIC, is fed by groundwater; and Station IA, which receives a mixture of both surface and underground waters. The hydrological characteristics of these stations have been defined according to a previous chemical study of the interstitial water (Marmonier & Dole, 1986; Marmonier, 1988).

The method of Bou and Rouch has been used here (Bou & Rouch, 1967; Bou, 1974); the metal pipe has a perforated stretch of 13 cm length situated at 4 cm of the distal end of the pipe, with holes of 5 mm diameter (9 raws). Samples were collected in the emerged sediment at 50 cm depth under the piezometric level at each of the three sites, with a plastic hand pump. Sampling occurred about every 10 days from June 1984 (9 days after a spring spate of 340 $m^3 s^{-1}$) to September 1984 (Fig. 2). Each sample consisted of 10 liters of fine sediments and water, which was filtered through a 160 μm mesh net; the fauna was preserved in 5% formaldehyde.

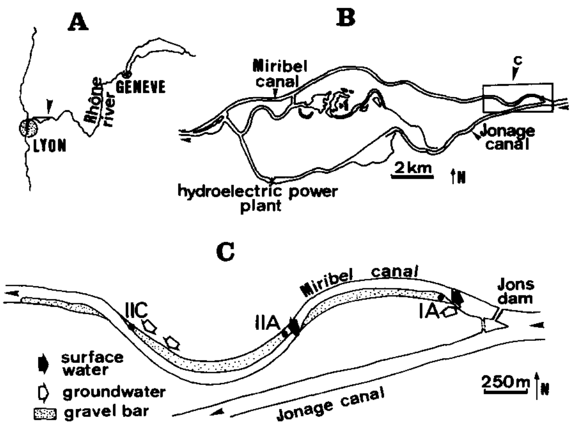

Fig. 1. Sampling site. A – The Rhône River upstream from Lyon. B – Location of the study area at the upstream end of the Miribel canal. C – Study area with sampling stations (IA, IIA and IIC) and origin of the interstitial water (surface water infiltrations and groundwater outflow).

Results

61 taxa were identified and used in this study, but Oligochaeta, Nematoda, Cyclopoidae and Harpacticoidae (except the genus *Parastenocaris*) were not identified and not considered here. To evaluate the temporal distribution dynamics of the other taxa, the fauna was divided in three

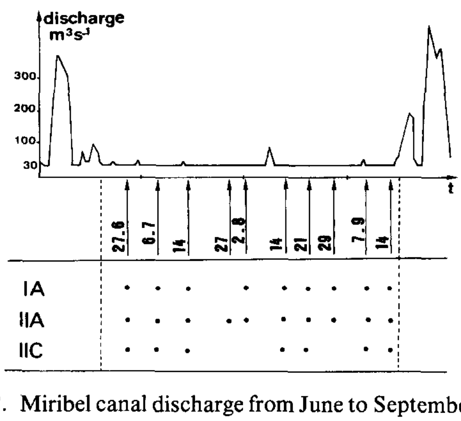

Fig. 2. Miribel canal discharge from June to September 1984 (end of the spate on the 19 june 1984). Sampling frequency during this period at the three stations.

groups for each station: 1) animals present just after the spate, 2) animals establishing permanent population in the sediments during the subsequent period of low discharge, and 3) occasional animals sampled one or two times during this latter period (Tables 2, 3 and 4).

In the period just after the spate, the faunal composition in the three stations differed markedly. At Station IIA (fed by surface water infiltrations), the spate displaced the sediment and induced a wash-out of the fauna, which more or less disappeared of the interstitial layer (only five taxa are sampled at −50 cm depth, Table 1). Many taxa generally abundant at this station were absent (Planarians, Ostracoda, Isopoda and stygobite Amphipoda, Table 2). The five taxa collected (Table 2) are epigean dwellers frequently found in the benthic layers of Miribel Canal (*Gammarus* sp., Empididae and juveniles of Ephemeroptera; Gaschignard & Berly, 1987; Gashignard-Fossati, 1986) and a Cladocera normally living in stagnant water such as dead arms of the river (*Leydigia leydigi*: Amoros, 1980).

At the two other stations (IA & IIC; Tables 3 and 4), which are fed mainly by groundwater, species richness was higher just after the spate (16 and 13 taxa, respectively, Table 1). Some of these taxa (Planarians, Ephemeroptera, Plecoptera, Trichoptera) belong to the usual benthic fauna of Miribel Canal and disappeared rapidly in the subsequent period of low discharge. Considering the shallow sampling depth (50 cm in sediment), it is probable that some of these organisms actively removed themselves from the sediment or passively drift through it via the groundwater flow. The sediments of areas fed predominantly by groundwater can be considered as storage areas for benthic organisms during high water periods.

In Stations IA and IIC, some limnic invertebrates were also collected (Calanoida and Cladocera, i.e. *Bosmina longirostris*, *B. corregoni* and *Daphnia hyalina*, Tables 3 and 4), which are usually found amongst the planctonic fauna of Rhodanian side arms (Amoros, 1980) and perhaps in the macrophytes of the banks (Amoros, pers. comm.). It is possible that these invertebrates, which develop in stagnant or lentic waters, have been dislodged from lentic habitats by surface waters and drifted into the Miribel Canal. Thus, the interstitial layer at these two stations may also be considered as a trap for limnophilous animals. Finally, at Station IIC, two stygobite Crustacea, *Proasellus walteri* and *Salentinella* sp. (Table 4), were not present after the spate and thus appear to be highly sensitive to the hydrologic disturbances.

During the subsequent aestival period of low discharge, both recolonisation and decreased abundance occurred depending upon the site. At Station IIA, taxonomic richness increases (Table I), 39 taxa were collected during this period (Table 2), of which 22 were found frequently throughout the summer and appeared to be established for a long period in the interstitial habitats. Most these 22 taxa (e.g. Planarians, Mollusca and Isopoda) are typical of benthic fauna in Miribel Canal (Gaschignard-Fossati, 1986), or colonise the first centimeters of the sediment of the main river (e.g. Cladocera and Ostracoda), and are frequently found in the interstitial habitats of Miribel canal at least 50 cm depth (Dole, 1983). The remainder of these 22 are stygobite Crustacea (e.g. *Fabaeformiscandona wegelini*, *Niphargus rhenorhodanensis* and *Niphargopsis casparyi*), which are abundant in the main river (Ginet, 1982), even at 50 cm depths (Dole, 1983;

Table 1. Number of taxa identified in the samples at the three stations during the sampling period. Nematode, Oligochaeta, Cyclopoida and Harpacticoida, present in all the samples, are not identified and not considered here.

Dates	27/6	6/7	14/7	27/7	2/8	14/8	21/8	29/8	7/9	14/9
Station IIA	5	18	15	9	18	21	12	12	20	20
Station IA	16	11	11		6	6	9	5	11	10
Station IIC	13	4	10			6	6		7	7

Table 2. List and abundance of taxa sampled in station IIA. Nematoda, Oligochaeta, Cyclopoida and Harpacticoida are not identified and not considered here. First group: taxa sampled just after the spate. Second group: taxa sampled all along the low discharge period. Third group: occasional taxa.

Dates	27/6	6/7	14/7	27/7	2/8	14/8	21/8	29/8	7/9	14/9
Ephemeroptera (juv.)	2									
Gammarus sp.		17	2							
Leydigia leydigi		4								
Empididae	3								1	
Polycelis sp.		38	9	1	13	87	2	5	4	3
Planarians (juv.)		3	3	2	1	1	2	1	4	7
Gastropoda	2				14	2	4	4	1	12
Pisidium sp.	1	1			1			1	2	
Iliocryptus sordidus		9	1			8				2
Biapertura affinis		13	2			2			8	
Pseudocandona albicans	3	3	6	10	12	18	4	26	7	9
F. wegelini		1	1	2	9	10	34	15	3	5
Cypria opthalmica		3			3	3	1			
Candona candida		4		1	1	4	1			
Candona neglecta				2		3		1		
Ostracoda (juv.)			4		8	8		14	15	
Asellus aquaticus		3	2	1	4	2	2			1
Proasellus meridianus		3	5		1					3
Isopoda (juv.)					1	1				
N. rhenorhodanensis		5	8	2	3	8	3	160	40	53
N. casparyi			2		12	22	58	122	56	70
Dryops sp.		1							1	1
Tanypodinae		2			1	1				1
Orthocladiinae		2							6	1
Diamesinae			1	1			1			
Tanytarsini			4			1			4	1
Cladocera (juv.)		4							10	
Baetis sp.			4							1
Erpobdella sp.					1					
Cyclocypris ovum					1					
Pseudocandona marchica					1					
Prionocypris zenkeri						1				
Cypridopsis vidus						1				
Pseudocandona lopides							1	1		
Esolus parallelepipedus						1				1
Stenelmis sp.						1				
Hydracarina						2				4
Chironomidae (juv.)								1	7	
Disparalona rostrata									36	
Alona rectangula									4	
Macrothrix laticornis									8	2
Limoniidae									1	1
Proasellus walteri										6

Table 3. List and abundance of taxa sampled in station IA. Nematoda, Oligochaeta, Cyclopoida and Harpacticoida (except the genus *Parastenocaris*) are not identified and not considered here. First group: taxa sampled just after the spate. Second group: taxa sampled all along the low discharge period. Third group: occasional taxa.

Dates	27/6	6/7	14/7	2/8	14/8	21/8	29/8	7/9	14/9
Bosmina longirostris	4								
Bosmina coregoni	68								
Daphnia hyalina	6								
Chloroperla sp.	1								
Hydropsyche sp.	1								
Gammarus sp.	1								
Calanoida	8	1							
Ephemeroptera (juv.)	2				1				
Gastropoda	4	1						2	1
Orthocladiinae	57	11	1			1		2	
Tanytarsini	9	2	9			1			
Hydra sp.			1	2	1	1			
Leuctra sp.	3	4	2	5	1	6	5	3	3
Hydracarina						12		21	9
Parastenocaris sp.	16	8	2	16	36	12	24	100	104
Alona phreatica	8	12	11	84	248	89	409	221	85
Niphargidae	44	37	37	157	179	51	19	58	74
Pseudorthocladius sp.		1							
Bidessus sp.		1							
E. parallelepipedus		1		1		1			
Chironomini			1						
Corynoneura sp.	1		1				1		
Baetis sp.			1					1	
Prosellus walteri			2					1	
Ceratopogonidae								1	
Pseudocandona albicans								1	2
Pseudocandona zschokkei									1
Iliocriptus sordidus									1
Ostracoda (juv.)									2

Marmonier & Dole, 1986). The other 17 taxa were found only occasionally in the samples, and did not establish for a long time in the sediments at Station IIA. Some of these 17 taxa are benthic invertebrates, which are usually found in Surber samples (e.g. *Erpobdella* sp., *Hydrachnellae*, *Pseudocandona marchica*, *Pseudocandona lobipes*, *Baetis* sp., *Esolus parallelepipedus*, *Stenelmis* sp., Chironomidae, Limoniidae). The rest are more limnophilous or phytophylous, and are usually collected in Rhodanian side arms or in aquatic macrophytes near the banks (e.g. *Alona rectangula*, *Macrothrix laticornis*, *Disparalona rostrata*, Amoros, 1980; *Cyclocypris ovum*, *Prionocypris zenkeri*, *Cypridopsis vidua*; Tetart, 1974; Scharf, 1976, 1988; Marmonier, 1988). Only one stygobiont (*Proasellus walteri*) belongs to this group and appeared at the end of the low water period.

The interstitial assemblage of Station IIA, which was fed by surface water infiltrations, was characterized by a high diversity. Large number of benthic invertebrates recolonised the sediments at this site during low discharge, and established stable, abundant and permanent populations (e.g. the occurrence of very young individuals of

Table 4. List and abundance of taxa sampled in station IIC. Nematoda, Oligochaeta, Cyclopoida and Harpacticoida (except the genus *Parastenocaris*) are not identified and not considered here. First group: taxa sampled just after the spate. Second group: taxa sampled all along the low discharge period. Third group: occasional taxa.

Dates	27/6	6/7	14/7	14/8	21/8	7/9	14/9
Calanoida	2						
Bosmina coregoni	9						
Daphnia hyalina	1						
Planarians (juv.)	1						
Chironomidae (juv.)	2						
P. flavomaculatus	1						
Plecoptera (juv.)	1						
Baetis sp.	3						
Bosmina longirostris	4					1	
Orthocladiinae	22	5	1			2	2
Parastenocaris sp.	76	48	16	72	100	12	62
Pseudocandona zschokkei	2	5			2		2
N. rhenorhodanensis	3	3	15	1	2	1	6
Proasellus walteri			64	2	1		1
Salentinella sp.			2	4	3		7
Alona phreatica			2				
Corynoneura sp.			1				
Leuctra sp.			2				
Proasellus sp.			7				
Gastropoda			1	1	2		
Limoniidae				1			
Ostracoda (juv.)						1	
Pseudorthocladius sp.						1	
Chironomidae (juv.)						2	1

Planarians and Isopoda; Table 2). As well, surface water infiltrations continuously imported the occasional epigean organisms, species that normally develop permanent populations in lentic areas of the river (e.g. quiet side arms and vegetation of the banks).

At Station IA, which was supplied by both surface and underground waters, the taxonomic richness decrease during the time (Table 1), only 23 taxa were sampled during the period of low discharge (Table 3). Permanent populations were established in the interstitial layer by 10 taxa, of which 7 belong to the usual benthic fauna of Miribel Canal (i.e. *Hydra* sp., Gastropoda, Hydrachnella, Ephemeroptera, Plecoptera and Chironomidae), the remainder are stygobites (*Parastenocaris* sp., the Niphargidae and *Alona phreatica*; for this Cladoceran see Dumont, 1983; Sabater, 1987). Twelve other taxa appeared scarcely during the low water period, and constitute benthic fauna typical of Miribel canal (i.e. *Pseudocandona albicans*, *Baetis* sp., *Bidessus* sp., *Corynoneura* sp., Chironomini and Ceratopogonidae), or may be considered as stygophilous (*Esolus paralellepipedus* – Richoux & Forestier, in press; *Pseudorthocladius* sp. – Marmonier, 1988). The remaining taxa (Table 3) are stygobionts (i.e. *Proasellus walteri* and *Pseudocandona zschokkei*).

Similar decrease of taxonomic richness (Table 1) was observed at Station IIC, which was supplied by groundwater only. Of the 15 taxa sampled during low discharge (Table 4), only six colonised the sediment for a long period, most of them are stygobites (i.e. *Parastenocaris* sp., *Pseudocandona zschokkei*, *Niphargus rhenorhodanensis*, *Proasellus walteri* and *Salentinella* sp.) and the

Orthocladiinae is the only epigean organism which developed in the sediments during this period. Nine other taxa occurred intermittently in the samples; they are epigean dwellers of the Miribel Canal's benthos (i.e. Gastropoda, *Leuctra* sp. *Corynoneura* sp., Limoniidae and juveniles of Ostracoda and Chironomidae), stygophilous organisms (*Pseudorthocladius* sp.), or stygobites (*Proasellus* sp. and *Alona phreatica*).

The composition, structure and temporal dynamics of the interstitial assemblages of these two latter stations (entirely or partly fed by groundwater) were very similar during the summer period of low discharge. In comparison with the Station IIA, the assemblages were less diverse (with a low number of occasional taxa) and had a greater abundance of stygobites.

Table 5. Particulate organic matter content of samples mesured by loss in weight on ignition. Remainer sediment and organic matter (> 160 μm), after the fauna is removed, is dryed and ignited at 550 °C during 1.5 hour. x̄: arithmetic mean, Sd: Standard deviations, *n*: number of samples.

Stations	IIA	IA	IIC
Origin of interstitial water	Surface water infiltrations	Mixed origin	Groundwater outflows
P.O.M. ($mg\,l^{-1}$)			
x̄	167.2	33.8	47.6
Sd	59.9	13.7	29.1
n	10	9	7

Discussion

'The types of hydraulic aquifer/river relationships are induced by the relative position of the water table and the water level of the river' (Castany, 1985). During spates, surface water generally infiltrates within the river bed sediments and along the bank. In contrast, a greater diversity of exchanges between superficial and interstitial waters occurs during periods of low discharge. In Miribel Canal, the interstitial communities were strongly affected by the spring spate, but responded to hydrological fluctuations differently at the various sites.

In the interstitial area continuously supplied by surface waters even during low discharge periods (i.e. Station IIA), an increased infiltration of surface waters during the spate induced a wash-out effect of organisms from the interstitial layer. As a result, the abundance of animals and the species richness of the assemblages decreased. The hydrological disturbance created by the spate, the wash-out effect, appears to be due to increased intra-sediment water movement as well as the deplacement of superficial alluvia, which decreases the 'physical stability' or interstitial habitats (sensu Dole & Chessel, 1986). During low discharge, such interstitial areas receive a regular influx of limnophilous organisms and organic matter via surface water infiltrations and are recolonised by abundant and diversified assemblages, including numerous benthic animals (Table 3). At Station IIA, the particulate organic matter content was 3.5 and 5 times higher than at the other stations (Table 5), this may explain the presence of numerous detritivorous animals (such as Isopoda and stagnant water Ostracoda) in the interstitial layer.

Areas supplied entirely or partially by groundwater during low discharge (i.e. Stations IA & IIC) are subjected to surface water infiltration during spates, which induce an input of limnophilous invertebrates: the bed sediments are acting as a trap for these organisms. The interstitial habitats also act as a storage zone for benthic invertebrates which subsequently recolonise the canal benthos after the spate and participate to the resilience of the surface system (Williams & Hynes, 1976). The abundance of these stored benthic invertebrates is weak (i.e. 77 individuals in the station IA and 30 individuals in IIC for a ten liters sample) but considering the volume of the river bed sediments, these stored organisms could represent an important source of fauna for future recolonisation of surface habitats. The limnophilous and some of the benthic invertebrates probably drift passively into the interstitial layer. But some benthic animals may also colonise actively the interstitial layer during spates or floods, in this case surface water infiltrations only facilitated the active colonisation. During low discharge, increased groundwater influxes, with little or no infiltrations or surface waters (e.g. Stations IA & IIC), resulted in a decrease in abundance and specific richness of the corresponding assemblages. The passive drift of lentic animals into bed sediments observed in Station IIA was thus highly reduced in Station IIC, and moderately reduced in Station IA. Therefore, the combination of increased groundwater influxes and the lack of surface water infiltrations can induce: 1) a decrease of inputs of surface animals into the bed sediments; and 2) a low particulated organic matter content in the sediments of these two stations (Table 5), which directly or indirectly limits the colonisation of interstitial habitats by surface fauna.

In this present study, two main characteristics could be observed in the dynamics of the eight species of stygobite Crustacea collected: 1) most stygobite decrease in abundance or disappear just after a spate (e.g. Station IIA, where no stygobites where collected immediately after the spate – the stygobite Ostracoda, *F. wegelini*, and Amphipoda, *N. rhenorhodanensis*, *N. casparyi*, which colonised Station IIA during low discharge and remain very sensitive to spates); and 2) during low discharge, stygobites are more abundant and diversified in the interstitial layer, especially in sediments supplied by groundwater (Marmonier & Dole, 1986; Creuzé des Châtelliers, in press). The occurrence of abundant and diversified stygofauna in areas supplied by groundwater (e.g. Station IIC) results from the active colonisation of sediments by animals coming from deeper layers. Two hypotheses can explain this: 1) the low variability of mesological conditions in such interstitial habitats induced by groundwater influxes, and 2) the reduced colonisation, and thus reduced competition, in the sediment by epigean dwellers.

In conclusion, the dynamics of animal assemblages in the interstitial layers of a river are strongly influenced by the hydrology of surface waters, with spates modifying the spatial distribution (Williams & Hynes, 1974; Poole & Stewart, 1976; Danielopol, 1976) and the composition and structure of invertebrate assemblages therein (Marmonier & Dole, 1986). But the interstitial habitats of a river show a great heterogeneity of reaction to spates: the magnitude of modification induced by spates depends on the origin of waters supplied to the area in question.

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