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Effects of bottom sediment restoration on interstitial habitat characteristics and benthic macroinvertebrate assemblages in a headwater stream

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The restoration of in-stream habitats by structural improvement of stream beds is more and more frequent, but the ecological consequences of such works are still little known. We have examined the influence of the deposit of a 15 cm gravel layer over the stream bottom on the chemical characteristics of the interstitial water, the sediment grain size and the composition of the benthic assemblages. We have compared a restored reach to an upstream control over three years and at three seasons each year. Dissolved oxygen, ammonium, nitrite and nitrate contents were measured in both surface and interstitial (–15 cm deep) waters, together with the depth of anoxia estimated using wooden stakes and fine sediment content at the surface. During the same period and seasons, benthic invertebrates were sampled at five points in each reach. The restoration induced an increase in vertical exchanges of water between surface and interstitial habitats, with an increase in the depth of hypoxia. Changes were observed in the composition of invertebrate communities, but not in the density or in the taxonomic richness of assemblages. These changes in assemblages were fragile: a local disturbance (such as a drying period) diminished the beneficial effect of the restoration with the disappearance of several organisms. The viability of such restoration works may be associated with catchment management designed to reduce fine sediment inputs to the river.

KEY WORDS: river; agriculture; sediment clogging; hyporheic zone; drought

INTRODUCTION

The heterogeneity of in-stream habitats is one of the most important factors controlling aquatic communities (Hynes, 1968; Ward and Stanford, 1979; Sheldon, 1986; Townsend and Hildrew, 1994). Both anthropogenic and natural processes can generate patchiness across a wide range of spatial scales (Beisel *et al.*, 1998), and habitat characteristics can vary drastically over small distances (Jenkins *et al.*, 1984). Many authors have shown that a high degree of habitat heterogeneity favours biotic diversity, especially for invertebrate (Collier *et al.*, 1998; Palmer *et al.*, 2000) and fish communities (Jungwirth *et al.*, 1993; Jowett *et al.*, 1996). Heterogeneity increases the diversity of resources, such as specific substratum characteristics (Cummins and Lauff, 1969; Reice, 1980; Culp *et al.*, 1983; Erman and Erman, 1984), hydraulic conditions (Minshall and Minshall, 1977; Statzner *et al.*, 1988; Quinn and Hickey, 1994) or food availability (Hawkins *et al.*, 1982; Dobson and Hildrew, 1992). This spatial variation of resources has direct effects on aquatic assemblages, especially the grain size of the bottom sediments, which is one of the most important parameters determining the composition of benthic communities (Culp *et al.*, 1983; Rempel *et al.*, 2000).

The agriculture intensification of the 20th century has profoundly affected aquatic ecosystems and their assemblages (Harding *et al.*, 1998). Catchment disturbance by agriculture may affect invertebrates' assemblages through a range of mechanisms. (1) The high level of cereal cultures in catchments is associated with an increase in discharges of toxic agro-chemicals into streams, affecting directly aquatic fauna (Lenat, 1984; Quinn and Hickey, 1990; Liess *et al.*, 1999); (2) The increase in primary production, via nutrient enrichment and reduction in shading

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by riparian vegetation (Stone and Wallace, 1998; McKie and Cranston, 2001) has contrasting effects. It not only induces the development of aquatic macrophytes, which can provide suitable habitat for invertebrates (Humphries, 1996), but it also induces an increase in microbial activities and algal growth, which generates river eutrophication and local oxygen depletion (Mulholland *et al.*, 1984; Tuchman and King, 1993; Young and Huryn, 1999; Gulis and Suberkropp, 2003); (3) Changes in stream morphology (i.e. canalization and dredging) and hydrology (i.e. flow regulation) induce an alteration of habitats and changes in biotic and abiotic processes in streams (Junk *et al.*, 1989; Lancaster and Hildrew, 1993; Cellot *et al.*, 1994; Resh *et al.*, 1994) and (4) The increase in field size and the destruction of hedgerow networks and woody buffers heighten soil scouring and, consequently, fine sediment inputs into streams (Benfield *et al.*, 1991; Wood and Armitage, 1997; Stevens and Cummins, 1999; Hancock, 2002). Inorganic bed sediments are thus frequently dominated by fine material in streams draining agricultural catchments, which is considered unsuitable for many aquatic invertebrates (Quinn *et al.*, 1992; Jowett *et al.*, 1996; Mary and Marmonier, 2000). This induces a homogenization of stream-bed habitats, with potential stream-bed clogging (Hall *et al.*, 2001), which cause a reduction in density and diversity of most invertebrates (Quinn *et al.*, 1992) especially for invertebrates living inside sediment interstices (hyporheos; Boulton *et al.*, 1998; Brunke, 1999; Hancock, 2002).

For several years, many stream management policies have been developed by several parties (i.e. researchers, local authorities and associations) to improve water quality and preserve biodiversity in aquatic ecosystems (Gore *et al.*, 2001). Advice on the use of fertilizers and pesticides by farmers and for the reduction of runoff from agricultural areas is provided as one of the main management methods. The ban of some toxic products, such as Atrazine or Lindane, the regulation of field drainage and the protection of hedgerow networks act towards the decrease of toxic inputs (Liess and Schultz, 1999; Girling *et al.*, 2000; Haggard *et al.*, 2001). Another management method consists of buffer strip creation (Rabeni and Smale, 1995; Rawe *et al.*, 2002) which increases the distance separating fields from streams, physically reduces direct solute inputs into streams and favours the microbial processes in the river banks.

More recently, some management experiments have focused on the direct restoration of in-stream habitats, by structural improvement of stream bed (Fuselier and Edds, 1995; Shields *et al.*, 1995; Van Zyll de Jong *et al.*, 1997; Purcell *et al.*, 2002; Wheaton *et al.*, 2004; Merz and Ochikubo Chan, 2005). Gore *et al.* (1998) and Gortz (1998) used current deflectors and boulder placement in rivers to improve habitats for aquatic insects. Gravel and pebble deposits have also received increasing attention as a restoration tool to improve interstitial habitat and Salmonidae spawning area in regulated rivers (Scruton *et al.*, 1997; Nakamura, 1999).

This paper examines the influence of the deposit of a 15 cm gravel layer on the interstitial water characteristics, the sediment grain size dynamics and the composition of the benthic assemblages of a regulated river of North Brittany (the Tamoute River). We have compared over three years a restored reach and a control one and hypothesize that: (1) the gravel layer deposit will positively influence the vertical connectivity between the surface and the interstitial waters and consequently increase the oxygen content of the interstitial habitat (Lefebvre *et al.*, 2004), (2) these changes will decrease progressively through clogging, (3) the density and the species richness of invertebrate assemblages will be higher in the restored area than in control because of the clogging of interstices and the homogeneity of the substratum in the control site (Quinn *et al.*, 1992; Beisel *et al.*, 1998; Palmer *et al.*, 2000) and (4) the invertebrate assemblages of the restored reach will be more resistant to local disturbance (here a drying period) because of possible refuges in the restored bed sediments (Delucchi, 1988; Dole-Olivier *et al.*, 1997).

METHODS

Study site

The study site was located on the Tamoute River, in Northern Brittany (South of the Mont Saint Michel Bay, France), at a low altitude (55 m a.s.l.) and at 1.5 km downstream from the spring. This 1st order stream (0.5 m width) flows above Brioverian schist with a poor slope (0.12%). At this site, the Tamoute was straightened and channelized (without embankment) and drained a small agricultural catchment (1.3 km²) dominated by milk and cereal productions. Land use comprises of 70 agricultural fields (33% of corn, 27% of wheat and 30% of temporary meadows). Since 1999, agricultural land has been isolated from the river channel by a planted meadow buffer strip of 5–10 m width. In the summer of 2000, a 100 m long section was restored by the local fishing association and the

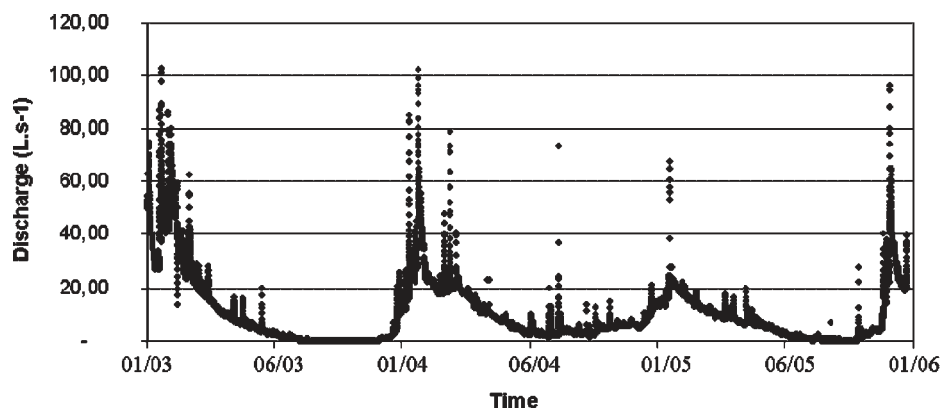


Figure 1. Daily discharges measured between January 2003 and January 2006 in the Tamoute River

State Fishing Council, with the deposit of a 15 cm gravel layer (1.5–3 cm mean diameter) on the bottom of the stream, without removing the natural substratum. The study site harboured few aquatic vegetation patches, because it was bordered by a dense riparian vegetation.

The mean daily discharge (Figure 1) was monitored from January 2003 to December 2005 (data from Arvalis-Vegetal Institute). The seasonal changes observed correspond to a classic Atlantic climate with high discharges during autumn and winter (more than 100 L s^{-1} during flood) followed by a gradual decrease from spring to the end of summer (from 20 L s^{-1} in March to only 2 L s^{-1} in September). During the autumn of 2003 (September to December), the river dried following the hottest summer of the decade, whereas discharges remained high during the summer of 2004 (up to 73.3 L s^{-1} in August), followed by a relatively dry winter in 2004–2005 (15.4 L s^{-1} on average).

The water quality of the Tamoute River was surveyed daily by a Cemagref unit (ADER unit) over 6 years. The river is characterized by a high level of nutrients (Table I), especially nitrates (generally above 10 mgNL^{-1} on average), ammonium (above 0.1 mgNL^{-1}), Soluble Reactive Phosphorus (SRP; above 0.02 mgPL^{-1}) and a high level of suspended matter (SM; above 150 mg L^{-1}) especially during the autumn floods. These nutrient and suspended material levels are representative of most of the rural streams in Brittany.

Physico-chemical analyses

The Tamoute water was monitored for three years after restoration, in February, April and June 2003, 2004 and 2005 (except in June 2003 for technical reasons). At each period, surface water was sampled at three randomly chosen locations in a restored reach and a control unrestored reach (located 50 m upstream) and the interstitial water at

Table I. Seasonal changes (means \pm standard deviation) of suspended matter (SM), nitrate, ammonium, Soluble Reactive Phosphorus (SRP) and total phosphorus contents in surface water of the Tamoute River, from September 1998 to September 2004 (data from ADER Unit of the Cemagref)

	Seasons				1998–2004
	Spring	Summer	Autumn	Winter	
SM (mg L^{-1})	152.55 ± 310.67	174.52 ± 299.66	247.87 ± 459.43	170.16 ± 277.99	186.27
NO_3 (mgNL^{-1})	12.09 ± 3.24	13.61 ± 4.18	9.74 ± 3.06	10.29 ± 2.37	11.43
NH_4 (mgNL^{-1})	0.22 ± 0.63	0.14 ± 0.22	0.10 ± 0.10	0.13 ± 0.13	0.15
SRP (mgPL^{-1})	0.021 ± 0.019	0.036 ± 0.051	0.052 ± 0.073	0.032 ± 0.028	0.035
Total P (mgPL^{-1})	0.18 ± 0.29	0.20 ± 0.26	0.36 ± 0.70	0.19 ± 0.27	0.232

three locations in the restored reach. Interstitial water of the unrestored reach could not be sampled because of complete clogging of bottom sediment in this zone. Interstitial water was extracted using mini-piezometers (1.2 m long PVC pipes, 1.5 cm diameter and 5 cm screen length) inserted to a depth of 15 cm within sediments. Inside water was pumped using a syringe extended by a soft tube plunged into piezometers. Dissolved oxygen content (mg L^{-1} ; WTW OXY 92), temperature, electrical conductivity ($\mu\text{S cm}^{-1}$; WTW LF92) and pH (pH-meter: IQ, scientific Instrument) were measured directly on the field.

The depth of hypoxia inside the river sediment was evaluated in both unrestored and restored reaches using artificial substrates (30 cm pine wood stakes and 0.8 cm in square section) pushed into the bottom sediment. After four weeks of incubation, the change of colour (from brown to pale grey or black) indicates the depth of hypoxia (Marmonier *et al.*, 2004).

In the laboratory, water samples were filtered (Whatman GF/C, 1.2 μm pore size) before analysis by colorimetric methods: indophenol blue for ammonium (N-NH_4 ; Rossum and Villaruz, 1963), diazotation for nitrite (N-NO_2 ; Barnes and Kollard, 1951) and for nitrate (N-NO_3) after a reduction of nitrate to nitrite by activated cadmium followed by nitrite titration. Grain size was measured on 500 g samples taken directly from the river bed with a shovel (behind a current deflector to reduce as much as possible the loss of fine particles) and dried in the laboratory (48 h, 105°C). Results were expressed in percentage of fine ($<250 \mu\text{m}$), medium (between 0.25 and 1 mm) and coarse particles ($>1 \text{ mm}$).

Fauna

The study of aquatic invertebrates was restricted to the benthos because hyporheos was impossible to sample in the clogged sediment of the unrestored station. Five replicates of benthic fauna were sampled at each date in both restored and unrestored areas (three of them were taken at the same sites where water was sampled for chemistry). A mini Surber net was used (200 μm mesh size, 0.03 m^2 sampling surface and 5 cm thick) and samples were filtered and preserved in the field (5% formaldehyde solution). Invertebrates were sorted in the laboratory and identified to genus or species level when possible (Tachet *et al.*, 2000), except for most of the Diptera (Family level), Copepods (separated in Cycloids and Harpacticids) and Oligochaeta.

Statistical analyses

A total of 48 samples were collected for water chemistry, and 90 for fauna. Differences in fine sediment contents, depth of oxygenation, water characteristics, taxonomic richness and total abundance of invertebrates between restored and unrestored areas were tested with the Student T-test. Differences in the densities of each species between stations and between years were tested using Kruskal–Walis ANOVA of rank. The composition of the assemblages was studied using Correspondence Analyses (CA). All the statistical analyses were performed using Statistica software (Statsoft, INC.). Levels of probability are noted: $^+p < 0.1$, $^*p < 0.05$, $^{**}p < 0.01$ and $^{***}p < 0.001$.

RESULTS

Grain size and water chemistry

Significant differences can be observed between restored and unrestored reaches for fine sediment contents ($T = 5.18^{***}$, Figure 2). In the unrestored reach, fine sediment contents varied from 10 to 20% in 2003 and 2004 and increased to 60% in April and June 2005. In contrast, fine particle contents were always below 5% at the surface of the restored area.

The depth of hypoxia estimated by artificial substrates was clearly different between restored and unrestored reaches ($T = 12.39^{***}$, Figure 3). For the unrestored reach, the depth did not exceed -7 cm deep into sediments and often reached -2 cm below the surface. For the restored reach, hypoxic conditions appeared at -15 cm deep into the sediment from February 2003 to April 2004 and slightly decreased (close to -12 cm deep) in June 2004 and 2005.

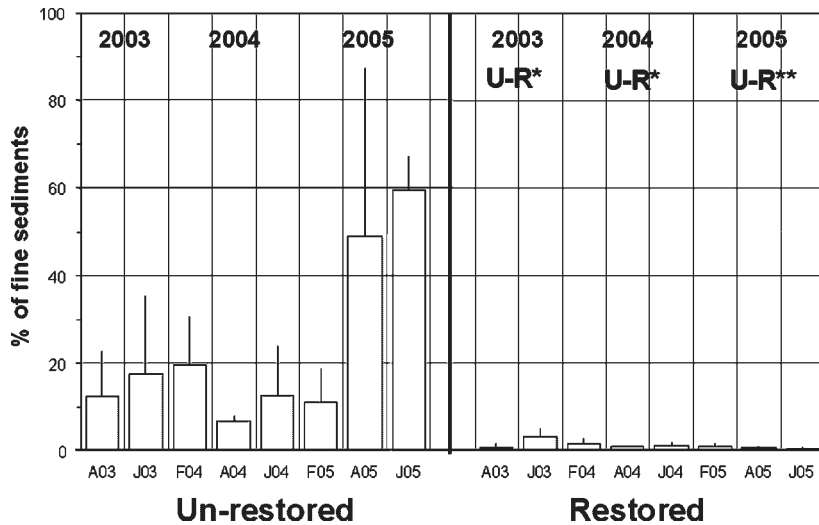


Figure 2. Percentage of fine sediments measured in the un-restored and restored reaches over the 3 years (mean \pm standard error; $n = 3$ for each season). The significant differences between restored and un-restored reaches are noted U-R. F: February; A: April; J: July

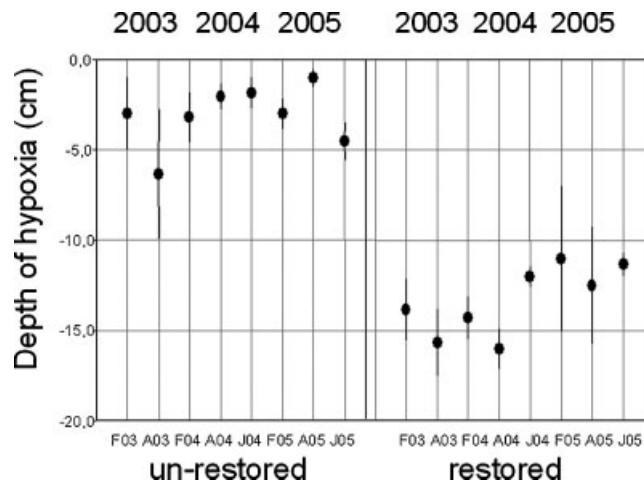


Figure 3. Depth of hypoxia evaluated over the 3 years using colour changes on artificial substrates (mean \pm standard error; $n = 3$ for each season). F, February; A, April; J, July

Oxygen contents of surface water were always above 8 mg L^{-1} (Figure 4), while interstitial water in the restored reach was relatively high for a rural stream (between 3 and 8 mg L^{-1}). Nitrite, nitrate and ammonium contents of interstitial water (Figure 4) were very similar to surface values and followed roughly the same temporal pattern, except in February 2003 and June 2005 when ammonium and nitrite of interstitial water reached higher values than in surface.

Taxonomic richness and abundances

A total of 41 721 individuals and 63 taxa were sampled in the river over the three years. The assemblages were dominated by Oligochaeta, the Molluscs *Ancylus fluviatilis* and *Pisidium* sp., the Amphipod *Gammarus pulex*, the Ephemeroptera *Serratella ignita* and by Chironomidae and Ceratopogonidae Diptera.

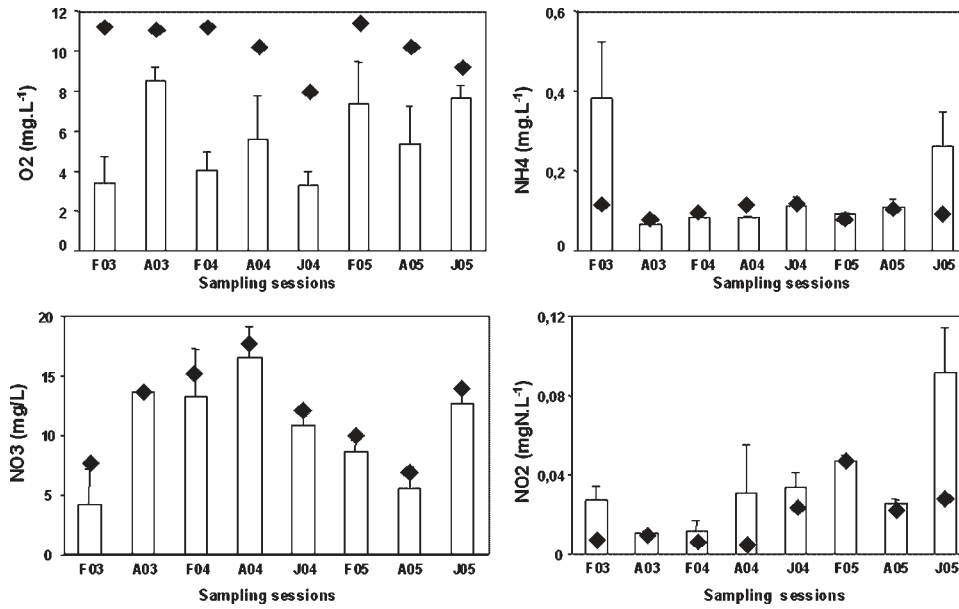


Figure 4. Comparison of water chemistry between the surface water (square) and the interstitial water (vertical bars) for dissolved oxygen, ammonium, nitrate and nitrite contents (mean \pm standard error; $n = 3$ for each season)

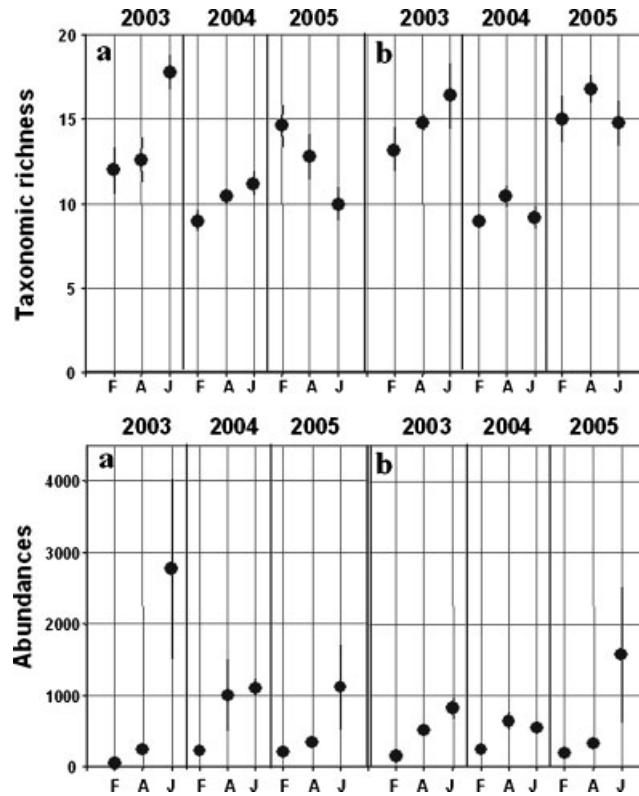


Figure 5. Taxonomic richness and abundances of invertebrate assemblages for restored (a) and unrestored (b) reaches over 3 years (mean \pm standard error; $n = 5$ for each season). F, February; A, April; J, July

The taxonomic richness of invertebrate assemblages in the unrestored and restored reaches were not significantly different ($T = -1.36$ n.s., Figure 5), except in 2005 ($T = -2.79^{**}$) when the taxonomic richness was higher in the restored reach than in the unrestored one. In 2004, three to six months after the drought, a significant decrease in the taxonomic richness was observed in both reaches ($H = 24.09^{***}$). The taxonomic richness increased in 2005 and reached values similar to those of 2003 in the restored reach ($H = 0.53$ n.s.). Similar observations were made for the total taxonomic richness that decreased from 51 taxa in 2003, to 30 and 32 taxa in 2004 and 2005, respectively. The abundances were not significantly different between the unrestored and the restored areas ($T = 1.46$ n.s., Figure 5) and between years ($T = 0.48$ n.s.). The only consistent difference observed was the high invertebrate abundance measured in June 2003 in the unrestored reach ($H = 9.90^{**}$), due to a large number of Chironomidae (more than 3700 individuals) sampled in one of the five replicate samples.

Macro-invertebrate assemblages

The CA performed on the invertebrate assemblages ascribed 11.20% of the variability on the first axis (F1), and 8.20% on the second axis (F2). The three years are roughly separated on the F1 × F2 plane (Figure 6). Samples taken in 2003 are located on the positive side of the first axis, while 2004 samples are located on the negative side of F1 and the 2005 samples have an intermediate location. This gradient on the F1 axis is due to strong changes after the 2003 drying: (1) 31 taxa disappeared between 2003 and 2004, most of them being strictly aquatic organisms such as Planaria (*Polycelis tenuis* and *Polycelis nigra*), Leeches (*Glossiphonia complanata* and *Erpobdella octoculata*), Ostracoda (*Pseudocandona* sp., *Cypria ophthalmica* and *Ilyocypris* sp.), Molluscs (*Galba* sp.) and the Amphipod *G. pulex*, which was one of the dominant taxa in 2003 (59.8 ± 68.1 ind/0.03 m²); (2) Three taxa significantly decreased in 2004 compared to 2003, either strict aquatic organisms (*Pisidium* sp. $H = 21.4^{***}$) or insects sensitive to drought (*Elmis* sp. $H = 13.8^{***}$; *Baetis* sp. $H = 15.4^{***}$); (3) Two taxa increased in 2004 compared to 2003, the Oligochaeta (from 26.1 ± 32.5 to 106.3 ± 90 , $H = 30^{***}$) and *S. ignita* (from 0.5 ± 0.7 to 7.4 ± 14.6 , $H = 8.6^*$).

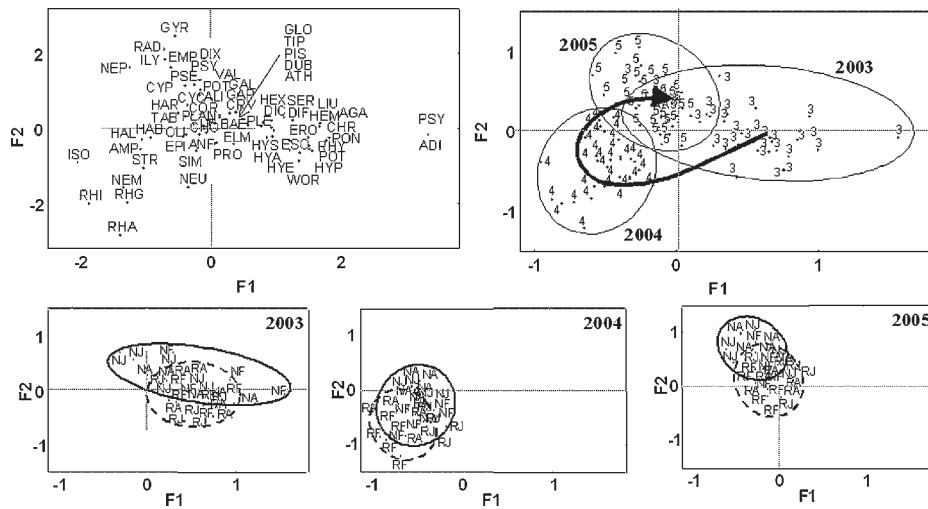


Figure 6. F1–F2 plane of the Correspondence Analysis (CA) for the benthos samples. (A) ordination of species; (B) ordination of the complete set of samples; (C) ordination of restored (R-dotted lines) and unrestored samples (N-solid line) for 2003; (D) the same for 2004 and (E) the same for 2005. F, February; A, April and J, July. Codes for organism names (A): ADI, *Adicella* sp.; AGA, *Agapetus* sp.; ALI, other Limoniidae; AMP, *Amphinemura* sp.; ANF, *Ancylus fluviatilis*; ATH, *Athripsodes* sp.; BAE, *Baetis* sp.; CER, *Ceratopogonidae*; CHO, *Chironomidae*; CHR, *Chrysopilus* sp.; COR, *Cordulegaster* sp.; CRY, *Cryptocandona vavrai*; CYC, Cyclopids; CYP, *Cypria ophthalmica*; DIC, *Dicranota* sp.; DIF, *Diplectrona felix*; DRY, *Dryops* sp.; DUB, *Dupophilus brevis*; ELM, *Elmis* sp.; EMP, Empididae; EPI, *Serratella (Ephemerella) ignita*; ERO, *Erpobdella octoculata*; ESO, *Esolus* sp.; GAL, *Galba* sp.; GAP, *Gammarus pulex*; GLO, *Glossiphonia* sp.; HAB, *Habrophlebia fusca*; HAL, *Haliplus* sp.; HAR, Harpacticidsl; HEM, Hemerodromiinae; HEP, *Habroleptoides* sp.; HEX, Hexatomini; HYD, Hydracarina; HYE, *Hydra* sp.; HYP, *Hyporhyacophila* sp.; HYS, *Hydropsyche siltalai*; ILY, *Ilyocypris* sp.; ISO, *Isoperla grammatica*; LAC, *Laccophilus* sp.; LIP, Limnephilinae; LIU, *Limnius* sp.; NEM, *Nemoura* sp.; NEU, *Neureclipsis* sp.; OLI, Oligochaeta; PIS, *Pisidium* sp.; PLE, *Plectrocnemia* sp.; PON, *Polycelis nigra*; POT, *Polycelis tenuis*; PRO, *Proasellus meridianus*; PSE, *Pseudocandona* sp.; PSY, Psychodidae; RHA, *Rhabdiopterix* sp.; RHG, Rhagionidae; RHI, *Rhithrogena* sp.; RHY, *Rhyacophila* sp.; SCI, Sciomyzidae; SER, *Sericostoma* sp.; SIM, Simuliidae; STR, Stratiomyidae; TAB, Tabanidae; TIP, Tipulidae; WOR, *Wormaldia* sp.

Surprisingly, the strictly aquatic Mollusc *A. fluviatilis* did not disappear after the drought: its density just slightly decreased in 2004 (13.2 ± 30.2) compared to 2003 (36.8 ± 102.8 , $H = 0.4$ n.s.) and (4) Only 10 taxa appeared between 2003 and 2004, with seven insects: two Ephemeroptera (*Rhithrogena* sp. and *Habrophlebia fusca*), four Plecoptera (*Isoperla grammatica*, *Amphinemura* sp., *Nemoura* sp. and *Rhabdiopteryx* sp.) and a Trichoptera (*Neureclipsis* sp.).

The intermediate location of the 2005 samples on the F1 axis is explained by a recovery of the assemblages after the drought. Nine taxa that were absent in 2004 reappeared in 2005 (e.g. *Galba* sp., *Cryptocandona vavrai*, *Hydropsyche siltalai*, *Plectrocnemia* sp., *Dupophilus brevis*, the Limoniidae Hexatomini and *G. pulex*). In 2005, *G. pulex* reached high densities (66.4 ± 65.5 ind/ 0.03 m^2) similar to those measured in 2003 (59.8 ± 68.1 ind/ 0.03 m^2 ; $p > 0.1$ between 2003 and 2005). Most of the taxa that appeared in the 2004 samples disappeared in 2005 (e.g. *Rhithrogena* sp., *I. grammatica* and *Rhabdiopteryx* sp.) and three organisms never collected before appeared in 2005, one insect (*Habroleptoides* sp.) and two Molluscs (*Potamopyrgus antipodarum* and *Radix* sp.).

The effect of restoration works on the composition of invertebrate assemblages is documented by the location of the samples on the F2 axis (Figure 6C–E). Samples from the unrestored reach have slightly more positive coordinates on the F2 axis than samples from the restored reach. This is particularly true in 2003: nine taxa were restricted to the unrestored reach (e.g. *P. nigra*, *Ilyocypris* sp. and *Limnius* sp.), and the Oligochaeta were significantly more abundant in the unrestored than in the restored reach (35.6 ± 33.5 and 16.5 ± 29.4 , respectively, $H = 6.76^{**}$). In contrast, five taxa were more abundant in the restored reach (*Elmis* sp. $H = 7.23^{**}$, *Baetis* sp. $H = 7.71^{**}$, *A. fluviatilis* $H = 5.26^*$, *Esolus* sp. $H = 2.73^+$ and *S. ignita* $H = 7.5^{**}$) and seven taxa were restricted to this reach (e.g. the Trichoptera *Hyporhyacophila* sp., *Wormaldia* sp. and *Plectrocnemia* sp.). All these organisms are coarse sediment dwellers. Very similar differences were observed in 2005 (Figure 6E), with seven taxa significantly more abundant in the restored station (*Baetis* sp. $H = 9.98^{***}$, *A. fluviatilis* $H = 16.85^{***}$, *S. ignita* $H = 4.16^*$, *Elmis* sp. $H = 8.72^{**}$, *Habroleptoides* sp. $H = 6.66^{**}$, the Chironomidae $H = 5.69^*$ and the Simuliidae $H = 3.33^+$) and seven taxa restricted to this station (e.g. *Cryptocandona vavrai*, *Amphinemura* sp. and *H. siltalai*).

In contrast, differences between unrestored and restored reaches were weak in 2004, just after the drought (Figure 6D). Only three taxa were restricted to the unrestored reach (i.e. *Cordulogaster annulatus*, the Coleoptera *Laccophilus* sp. and the Diptera Tipulidae), two taxa were significantly more abundant in this zone (*Pisidium* sp. $H = 11.84^{***}$ and the Harpacticids $H = 2.84^+$), a single taxon was significantly more abundant in the restored reach (the Simuliidae $H = 9.85^{***}$) and six taxa were restricted to this reach (i.e. *Rhithrogena* sp., *I. grammatica*, *Rhabdiopteryx* sp., *Neureclipsis* sp., the Diptera Rhagionidae and Stratiomyidae).

DISCUSSION

Effects of the restoration on the surface-sediment connectivity

The bottom sediment restoration with a deposit of a gravel layer strongly impacted the characteristics of the interstitial environment, as predicted. The restoration created a new interstitial habitat with strong exchanges with surface water. The solute contents were roughly similar between surface and interstitial waters, with similar temporal trends. The restoration also improved the quality of bottom sediments, with an increase in the depth of hypoxia, low nitrite and low ammonium contents inside sediments.

Vanek (1997) and Gayraud and Philippe (2003) have already observed that a decrease in fine sediment contents (and the resulting increase in gravel porosity) induced increasing exchanges between surface and interstitial waters and changes in biological processes (Hendricks and Rice, 2000). In agricultural areas, inputs of fine sediments and organic matter increase in rivers (Vitousek *et al.*, 1997), which induces a physical clogging of interstices and a biological colmation through excessive growth of biofilm (Dahm *et al.*, 1998; Brunke, 1999). Both types of clogging induce changes in water chemistry, with a decrease in oxygen and nitrate contents (through respiration and denitrification), while ammonia and nitrite contents increase (through ammonification and lack of nitrification, Boulton *et al.*, 1998; Lefebvre *et al.*, 2004). In our study, the restoration works changed the bottom sediment from a clogged layer (as observed in the unrestored reach) to a well-oxygenated gravel bed, where aerobic microbial processes were dominant.

Viability of the restoration works

The viability of restoration works is an important factor influencing its use at a larger scale (Gore *et al.*, 2001; Clarke *et al.*, 2003). Over the three years of our study, grain size, depth of anoxia and chemistry of interstitial water demonstrate that conditions inside bottom sediment in the restored reach remained acceptable in comparison to the unrestored reach. The percentage of fine sediments in the restored area remained extremely low over the three years in comparison with the unrestored one, even in 2005, when strong inputs of fine particles affected the stream (only observed in the unrestored reach). Furthermore, nitrite and ammonium contents in the interstitial water remained low over the three years, almost certainly because of a stimulation of nitrification by aerobic conditions (Chapelle, 1993). The depth of hypoxia remained about –15 cm deep inside sediment until 2004, but decreased to –12 cm in 2005 (i.e. when strong inputs of fine sediment were observed). It is difficult to predict how long this type of restoration work will be sufficient for oxygenation of the sediment interstices, because it is strongly linked to the flux of suspended fine sediments in the surface water. The fine particle flux to a river is governed by the catchment erosion (e.g. agriculture practices) and the efficiency of riparian buffer strips to stop it (landscape structure). It is thus important to combine the in-stream habitat restoration with an efficient landscape management at the catchment scale.

Effects of the restoration on invertebrate assemblages

It is well known that habitat characteristics and heterogeneity have a great impact on invertebrate assemblages (Hynes, 1968; Erman and Erman, 1984; Gerhard and Resh, 2000; Fowler and Death, 2001; Merz and Ochikubo Chan, 2005). In agricultural catchments, disturbances by human activities affect the aquatic fauna more or less directly through modifications of in-stream habitats, such as changes in the density of aquatic macrophytes (Humphries, 1996) or stream-bed clogging (Benfield *et al.*, 1991; Hall *et al.*, 2001). For a few years now, some experiments on the restoration of in-stream habitats have shown that the addition of coarse sediments on the stream bottom increases hydraulic exchanges between surface water and interstitial water, and thus has positive effects on aquatic invertebrates (Muotka *et al.*, 2002; Gayraud and Philippe, 2003) and fish egg survival in Salmonidae spawning habitats (Hamor and Garside, 1976; Witzel and MacCrimmon, 1981; Malcolm *et al.* 2003).

Our study only partially confirmed these assumptions. The predicted increase in the density and the species richness of invertebrate assemblages was not verified, with poor differences between unrestored and restored reaches. These poor differences may be explained by the very similar surface water chemistry of both reaches and the high organic matter content of the sediment of the unrestored reach. Culp *et al.* (1983) highlighted that the available organic matter content was more efficient than the grain size in explaining the composition and the density of invertebrate assemblages. Furthermore, the 2003 drought may overshadow the positive effects of the restoration on invertebrate assemblage.

In contrast, several changes in the composition of invertebrate assemblages were observed between the restored and unrestored reaches. Some taxa living preferentially on coarse sediments were found only in the restored area. They were the Mollusc *A. fluviatilis*, some Trichoptera (e.g. *Wormaldia* sp. and *Plectronemia* sp.), some Ephemeroptera (e.g. *Baetis* sp. or *Habroleptoides* sp.) and some Plecoptera (e.g. *Amphinemura* sp. or *I. grammatica*). In contrast, taxa living in fine sediments (e.g. Oligochaeta, the Ostracoda *Ilyocypris* sp., the Odonata *Cordulegaster annulatus* and the Diptera Empididae) were sampled only in the unrestored area. The preference of organisms for sediment grain size was not the only ecological trait modified by the restoration. Some species restricted in the restored reach were sensitive to organic pollution (e.g. *I. grammatica*, *Rithrogena* sp. and *Rhabdopterix* sp.). Similar colonizations by clear water organisms were observed by Gortz (1998), but the high eutrophication of the Tamoute River certainly reduced the pool of sensitive species able to establish permanent populations in the restored reach (Liess *et al.*, 1999; Muotka *et al.*, 2002).

Drought impacts on invertebrate assemblages

The disturbance regime affects aquatic diversity mostly through modifications of hydrological conditions (Junk *et al.*, 1989; Cellot *et al.*, 1994). Hydrological disturbance predominantly consists of spates and droughts, which generate an alteration of the habitats (Smock *et al.*, 1994), changes in biotic processes (Williams, 1987; Smock *et al.*, 1994; Wright *et al.*, 2004) and aquatic communities (McElravy *et al.*, 1989; Boulton and Lake, 1992b;

Wright, 1992; Smock *et al.*, 1994; Miller and Golladay, 1996). Droughts generally induce decrease in densities, species richness of invertebrate assemblages (Cowx *et al.*, 1984; Wood and Petts, 1999; Meyer and Meyer, 2000; Boulton, 2003) and changes in the size or age structure of populations (Lake, 2003). These modifications vary according to the characteristics of the river (size, depth and slope; Boulton and Lake, 1992a; Lake, 2003) and could be buffered by groundwater discharge (Wood and Petts, 1999). Changes were also observed in behavioural and physiological conditions of invertebrates (Gore, 1994) and in their life cycle strategies (Sommerhäuser *et al.*, 1997). For example, Crichton (1971) highlights changes in various strategies and adaptations to a dry phase with extended flight period for some caddis flies, which could survive a summer drought as adults.

In our study, the summer drought induced a significant reduction in the taxonomic richness of invertebrates assemblages in both restored and unrestored reaches, with the disappearance of a large number of strictly aquatic species, such as Planaria (*P. tenuis* and *P. nigra*), leeches (*G. complanata* and *E. octoculata*), Ostracoda (*Pseudocandona* sp., *Cypria ophthalmica* and *Ilyocypris* sp.) and the Amphipod *G. pulex*. The resulting decrease in taxonomic richness observed in 2004 was certainly due to a high sensitivity to drought of the invertebrates of the Tamoute River, which is very rarely dry: most of the organisms present in the river do not have pre-established survival strategies (Meyer and Meyer, 2000).

Invertebrate recolonization after drought is generally rapid (Larimore *et al.*, 1959; Boulton, 2003) because of several processes (Humphries and Baldwin, 2003). In contrast with strictly aquatic fauna, species with aerial dispersal, such as the Ephemeroptera (*Rhitrogena* sp. and *H. fusca*), the Plecoptera (*I. grammatica*, *Nemoura* sp. and *Rhadiopterix* sp.) and the Trichoptera (*Neureclipsis* sp.) appeared early in 2004. Aerial dispersal is a key biological trait for colonization of headwater streams after the destruction of the assemblages. This rapid colonization highlights the high potential pool of immigrant species (MacArthur and Wilson, 1967) in this region rich in small streams.

Williams and Hynes (1976) showed that drift from upstream is the most important recolonization mechanism for temporary streams, but the river completely dried in 2003 and drift may not be a source of colonizers. The upstream migration represents another important pathway (Williams and Hynes, 1976). In our study, the Amphipod *G. pulex* reached in 2005 (i.e. 1 year after the drought) similar densities to those measured in 2003. Upstream migration represents the most probable mechanism of recolonization for this strictly aquatic species.

Finally, some aquatic organisms seem to survive inside dry sediment. The strictly aquatic Mollusc *A. fluviatilis* did not disappear after the 2003 drought. This species is known to survive as torpid adults inside gravel bed during droughts (Légier, 1977, 1979), resisting to drying by using the capillary water located just above the piezometric level. A different strategy is shown by the Ephemeroptera *Serratella ingnita* which is only present during spring in most of the rivers. Egg laying occurs in early summer and they hatch in the following winter (Tachet *et al.*, 2000). The eggs of this species can certainly survive inside dry sediment. For these two species significantly more abundant in the restored reach after the drought, the new gravel layer can be a refuge during this disturbance (Delucchi, 1988; Griffith and Perry, 1993; Dole-Olivier *et al.*, 1997).

In conclusion, this study supports our hypothesis that the restoration of the Tamoute River with a 15 cm gravel layer has induced an improvement in the quality of in-stream habitats, through an increase in vertical exchanges between surface and interstitial habitats and a reduction of sediment clogging. The impact of such restoration works on invertebrate assemblages was obvious for the composition of the assemblages, but poorly changed the density and the taxonomic richness. Furthermore, a local disturbance (such as a drying period) cancels the beneficial effect of the restoration with the disappearance of several organisms. This drought had a limited effect in time and the gravel layer may subsequently enable new habitats to be exploited by a greater range of species. We have observed the effects of the restoration over only three years, but the viability of such restoration may be strongly linked to long-term fluxes of fine sediments and solutes from the catchment and to other physical factors (e.g. channel structure and riparian habitats). It is thus obvious that any sediment restoration works (deposit of clean gravel and mechanical removal of fine particles) must be combined with catchment management (reduction in the use of fertilizers, creation of buffer strips, protection of hedgerow and riparian vegetation) to insure their viability.

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