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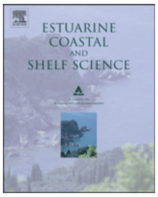

Spatiotemporal bioturbation patterns in a tidal freshwater marsh

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ABSTRACT

Bioturbation has been hypothesized to exhibit different forms of sediment mixing in aquatic systems, but few in situ tests have been conducted in estuaries, and anyone along a flooding gradient which is the main feature characterizing intertidal areas. The relationships between bioturbation and macroinvertebrate communities were studied as part of a restoration project in the tidal freshwater zone of the Schelde estuary, and highlighted specific sediment mixing patterns along a tidal gradient. Three permanent sites, evenly distributed along the flooding gradient, were monitored over a period of one year. Tidal influence engendered a clear gradient opposing newly-established aquatic communities (low elevation and strong disturbance) to remnant terrestrial communities (high elevation and low disturbance). Different bioturbative modes were identified along this gradient. Biodiffusion (random spreading of sediment particles) was the dominant mode at high and mid elevations. Low elevation was characterized by bioadvection (vertical movement of sediment particles) and higher bioturbative intensities. Maximum bioturbative intensities were observed in summer. This is the first bioturbation study, conducted along a flooding gradient, and which characterizes the bioturbative modes and intensities among tidal habitats and confirms the key role of disturbance. These findings underline the significance of the multiplicity of bioturbation modes in estuarine habitats, and the potential implications in estuarine biogeochemistry in general.

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1. Introduction

Bioturbation induced by soil and sediments macrofauna is now recognized as a fundamental ecological engineering process involving physicochemistry, organisms and food webs in both terrestrial and aquatic ecosystems (Meysman et al., 2006). Bioturbation is the source of key biogeochemical processes occurring at the sediment–water interface, and its contribution to diagenetic processes is far from negligible (Aller, 1994; Boudreau, 1997). Different modes of bioturbation are known to differently rework the sediments (Rhoads, 1974; Gerino et al., 2003). These physical processes have been shown to influence specifically water fluxes and oxygen concentration, and thus microbial activity (Mermillod-Blondin and Rosenberg, 2006). In wetlands and aquatic systems, these close relations between fauna and sediments contribute to increased water-sediment exchanges and enhance biogeochemical processes (Nickell et al., 2003; Lohrer et al., 2004; Nogaro et al., 2009). Also, specific bioturbative modes at the community level were found to be determinant in ecosystem functioning (Biles et al., 2002).

Multiple evidences now support relations between bioturbation and ecosystem functioning. For instance, human activities in estuaries have been shown to impact community structure and/or bioturbative mode via effects on functional richness (Pearson and Rosenberg, 1978; Mazik and Elliott, 2000; Wheatcroft, 2006; Gerino et al., 2007). However, while changes in benthic community structure are obvious along a gradient of disturbance (Rhoads, 1974; Voshell and Simmons, 1984; Solimini et al., 2003), there is still a lack of examples supporting a general pattern of bioturbative mode and intensity along such a gradient. Furthermore, since association and interaction between faunal communities and abiotic features are well recognized (Ricklefs, 1990), spatiotemporal gradients such as ecosystem recovery or ecosystem development offer opportunities to describe and quantify the sediment bioreworking at different levels of disturbance and to assess its involvement in ecological successions (Pearson and Rosenberg, 1976).

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In Belgium, the Schelde estuary has been impacted for a long time by human activities, resulting in severe physical and chemical stress. Estuarine habitats have been drastically reduced and their functionality critically impaired (Meire et al., 2005). Despite a clear improvement in oxygen concentration the last fifteen years, embankment sustains a severe physical stress, particularly on tidal flats. Nevertheless, restoration projects aiming at the ecological rehabilitation of the estuary through land reclamation are ongoing (Van den Bergh et al., 2005), and thus offer the opportunity to investigate different aspects of tidal ecosystem development. Among the different techniques used in estuarine restoration, Controlled Reduced Tide (CRT) is until now the only one proved to restore a neap-spring cycle in lowered embankments (Beauchard et al., 2011), which are a typical feature of historically embanked estuaries. The CRT system was hypothesized to successfully restore intertidal marshes in combination with safety function against storm tides (Maris et al., 2007). A recent study highlighted the high restoration potential for tidal freshwater vegetation in CRT (Jacobs et al., 2009).

However, it is difficult to value an ecosystem when its structure and functioning are not fully understood (Jickells, 1998). There is still a lack of information dealing with ecosystem development for rehabilitation and/or compensation in estuaries, particularly in the scope of biogeochemistry (French, 2006). Although freshwater tidal zones have been pointed to need greater attention given the important chemical and biological reaction occurring there (Morris et al., 1978), knowledge remains scarce, particularly concerning sediment biogeochemistry (Megonigal and Neubauer, 2009). Despite the absence of clear quantification of their spatial extent, tidal freshwater wetlands nevertheless are known to occur in the estuaries of most of the world largest river basins (Baldwin et al., 2009).

Recent works in the experimental CRT of the Schelde estuary showed that a clear flooding frequency gradient is implemented (Beauchard et al., 2011) and conditions sediment depositions (Vandenbruaene et al., 2011). Hence, similarly to vegetation, macroinvertebrate development is hypothesized to result from these typical estuarine determinants, and to generate different habitat specific bioturbation modes (Mermillod-Blondin and Rosenberg, 2006) possibly changing over season (Teal et al., 2008). For the first time, bioturbation was studied in situ along a flooding gradient in a newly-created tidal freshwater environment. Beyond the restoration success assessment of the project, this study aims to explore the spatiotemporal pattern of bioturbative modes and intensities, and to provide interpretations of faunal features evidencing soil sediment processes. As previously demonstrated for tidal freshwater vegetation (Jacobs et al., 2009), this gradient generates different levels of community disturbance and ecological succession by water submersion.

2. Methods

2.1. Study area

The study took place in the “Lippenbroek polder” (51°05′10′′N; 4°10′20′′E) located in the freshwater tidal zone of the Schelde estuary near the city of Antwerp (Fig. 1). There, the salinity can reach exceptionally 1.0 psu during periods of reduced river discharge in summer, but remains most of the time below 0.5 psu. Since 2006, this formerly agricultural area (8 ha, crops) has been the focus of a pilot project dealing with tidal habitat restoration in combination with flood protection. It is connected to the estuary by means of entrance and exit floodgates allowing water exchange between the two systems (see Maris et al. (2007) for technical details). The definitive hydrological regime was set in March 2006.

2.2. Field monitoring and environmental context

A spatiotemporal sampling framework was carried out over five seasons from February 2007 to February 2008 as part of the interdisciplinary Lippenbroek project focusing on different ecological compartments (hydrology, soil physicochemistry and soil macrofauna among others). Spatially, three sites evenly distributed along the elevation range were selected for this study: high elevation (H; low flooding frequency), mid elevation (M; moderate flooding frequency) and low elevation (L; high flooding frequency) (Fig. 2). Site H is flooded only during spring tides whereas site L is daily flooded except sometimes at neap tide.

From the initial restoration of tidal influence in March 2006 to the beginning of this study (February 2007), important abiotic changes occurred, mainly driven by an increased estuarine sediment deposition at low elevation (Vandenbruwaene et al., 2011, Fig. 2), giving rise to a clear physical gradient opposing silty- and water-rich (high flooding frequency) to sandy- and water-poor (low flooding frequency) environments. After the first drastic environmental modifications, changes in soil physics remained moderate (Fig. 3).

2.3. Soil macrofauna and bioturbation follow-up

Macrofauna was considered as part of the long term monitoring. Six replicate cores were sampled (46 mm Ø, 150 mm long) and stored in 5% formalin, and sieved through a 500 μm mesh size before organism sorting and taxonomic identification.

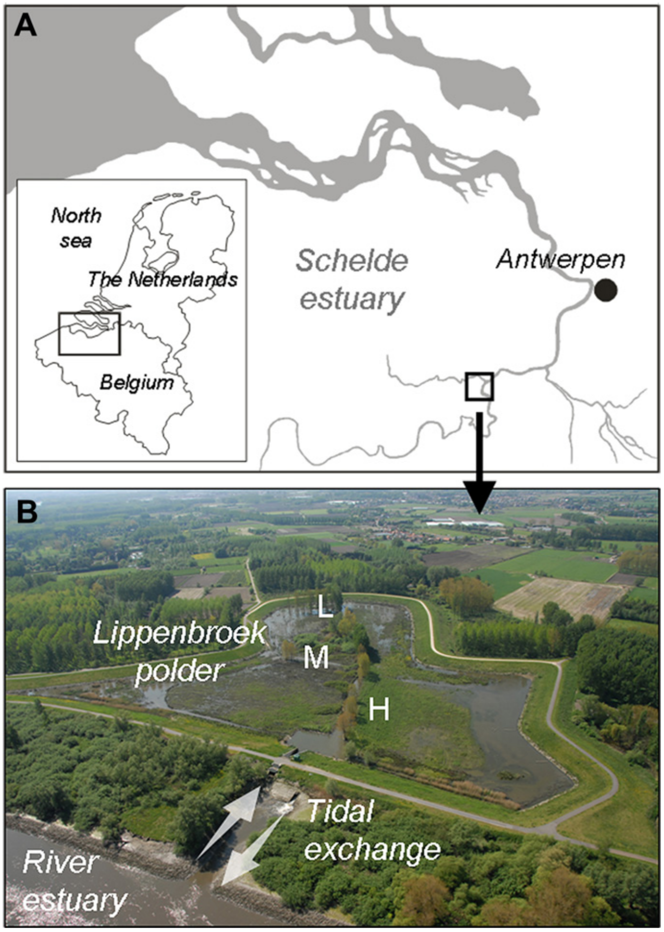

Fig. 1. Location map and photograph of the study area. H, M and L showing the locations of the three sites, respectively at high, mid and low elevation.

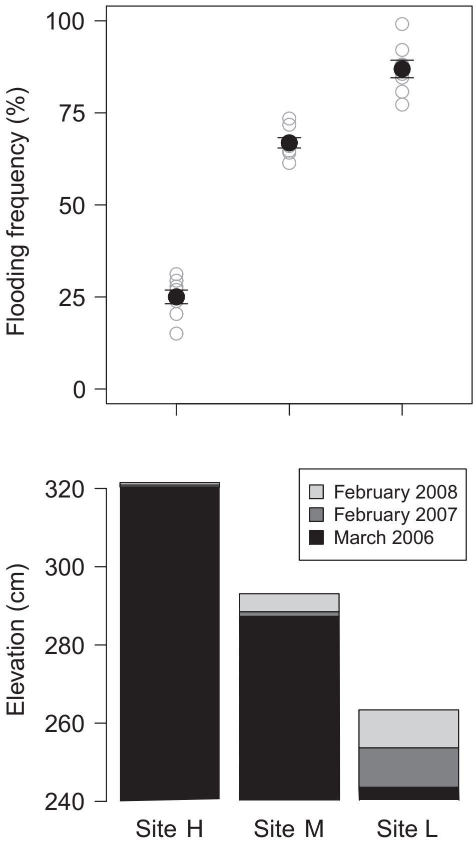

Fig. 2. Experimental setup: Flooding frequencies (top) versus site elevations (bottom) along the tidal gradient. Sediment accumulation is represented in grey. Flooding frequencies were averaged per season from March 2006 to February 2008 (upper graph, grey points).

Bioturbation was measured by applying the procedure described in Gerino et al. (1994) and Ciutat et al. (2005) with PVC tubes (76 mm Ø, 170 mm long). Each season, three replicates per site plus one control were considered. First, 15 cm control cores were extracted and dried at 70 °C during 24 h in order to eliminate living organisms. Then, control cores were reinserted in their respective site and replicate cores were similarly disposed (inserted to 15 cm deep). A frozen sediment layer containing tracers (1 μm Ø fluorescent spheres; 0.1 mL) was deposited at the surface of each tube. Tubes were extracted after fifteen days and cores were sliced in nine soil strata: 0–0.5, 0.5–1, 1–2, 2–3, 3–4, 4–5, 5–7, 7–10 and 10–15 cm. Sediments were dried and the tracers were counted in each layer with an epifluorescence microscope.

2.4. Data analysis

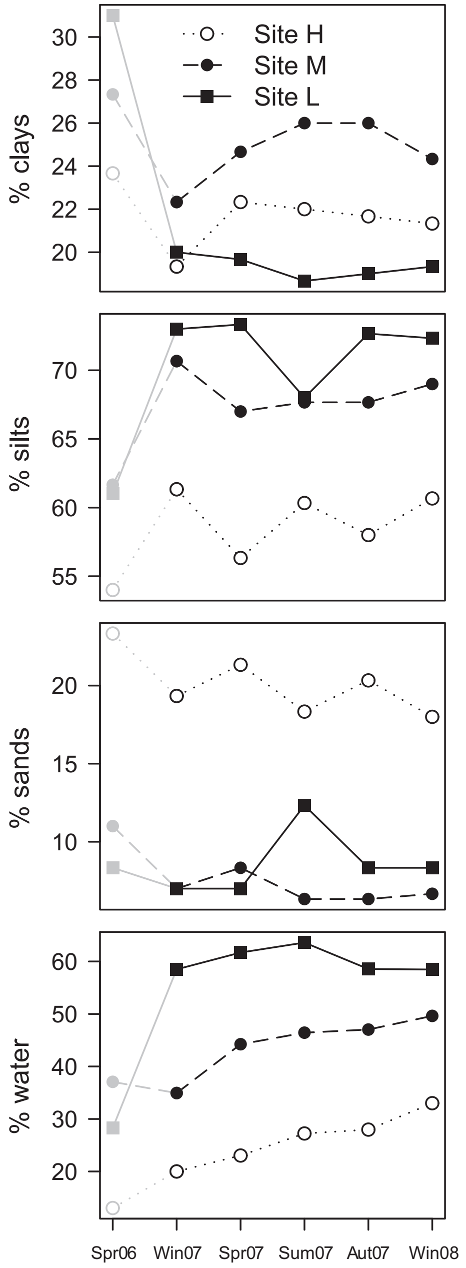

Fig. 3. Temporal profiles of the water content and granulometry. Grey: transition from spring 2006 to winter 2007.

First, a descriptive approach of community structure was done by performing a centred Principal Component Analysis (PCA) on the date-site × taxa table after log $(x + 1)$ transformation of organism densities (ind./m^2). Functional aspects were investigated by classifying organisms according to their living mode (terrestrial, amphibious and aquatic) and their locomotion and substrate relations which induced the consequent dispersal modes of sediment particles (Gerino et al., 2003); the considered abilities were crawling, burrowing, conveying (non-local transport by ingestion) and fixation to substrate. Despite the fact that these abilities may not engender specific bioturbative modes, their combination can be relevant to infer relationships between taxa occurrences and bioturbation pattern (François et al., 2002; Gerino et al., 2007). Biological information stemmed mainly from general handbooks (Merritt and Cummins, 1984; Tachet et al., 2000) and more specific literary sources (see discussion).

Bioturbation quantification was considered based on the three dispersal modes of particles which are engendered by organism activity (Gerino et al., 2003): bioadvection, biodiffusion and regeneration (Gerino et al., 1994). Three specific coefficients were calculated following the bioadvection-biodiffusion model of Officier and Lynch (1982) to which a component was added in order to take account for the regenerative mode (Delmotte et al., 2007):

$$\frac{dC_{(z,t)}}{dt} = D_b \frac{d^2C_{(z,t)}}{dz^2} - \frac{dW_{(z,t)}}{dz} + K_{(z,t)} - R_{(z,t)}$$

where the temporal variation (dt) of the tracer concentration C through depth (z) is decomposed into the three dispersal modes of sediment particles. *Db* (biodiffusion, local transport), *W* (bioadvection, active non-local transport) and *R* (regeneration, non-local transport) respectively refer to random dispersal (cm^2/year), vertical transport through the gut (cm/year) and burrows collapsing ($mg/cm^{-3}/y^{-1}$). *K* is the injection function of the non-local transport that simulates tracer inputs ($mg/cm^{-3}/y^{-1}$) into the injection zone of the sediment column.

Significance of temporal and spatial effects of the bioturbative modes was tested by applying Kruskal–Wallis tests and a non-parametrical multiple test procedures (Behrens-Fisher type; Munzel and Hothorn, 2001). Then, taxa and functional groups densities *vs* bioturbation coefficients relationships were explored by Spearman's correlations. For this, based on 5 dates × 3 sites, averaged bioturbation coefficients and organism densities were defined as 15 statistical units.

Analyses were conducted under R version 2.10.1 (R Development Core Team, 2009) with "*ade4*", "*stats*" and "*npmc*" packages.

3. Results

3.1. Soil macrofauna

The PCA on faunal data (Fig. 4A) highlights two main axes. Axis one encompasses the flooding gradient opposing terrestrial taxa in site H (mainly terrestrial worms, woodlices and myriopods; see Table 1 for faunal description) to more aquatic ones in site L (mainly aquatic worms and nematods). Globally, the strong site effect over the study period (Fig. 4B, discrimination of the black characters) underlines a strong environmental specificity of the communities. A temporal change in community composition parallels the flooding gradient where the taxa turnover is enhanced by flooding frequency (Fig. 4B, from grey to black characters). In one year, site L experienced a total taxa turnover whereas site H did not exhibit change. The second axis is characterized by mostly positive covariances between taxa (Fig. 4A), and thus exhibits a density gradient. Also, from sites H and L to site M, the decrease in organism densities is accompanied by a taxa impoverishment (Fig. 4B, lower insert). Concomitantly to taxa turnover, seasonality induces an increase of the within-site variance on both axes. This seasonality involves taxa richness and is enhanced from site H to site L (Fig. 4B, upper insert).

Fig. 5 highlights contrasted total organism densities among the three sites. The highest densities were found in site L reaching more than 100000 ind./m^2 in summer (min = 401; max = 170883). Much lower were the densities in site H (around 5000 ind./m^2; min = 4111; max = 7020) and even less in site M (less than 2000 ind./m^2; min = 201; max = 1704). Extirpation of the terrestrial fauna was obvious the first year (from spring 2006 to spring 2007) in site L with a clear replacement by mostly aquatic organisms. Similar to taxa richness, densities reached their maxima in summer, and seasonality was more pronounced at higher flooding frequency.

Five groups were considered on the point of view of locomotion and substrate relations (Table 1): fixed organisms as non-bioturbator, crawler, crawler-burrower, burrower and conveyor. Conveyors, represented mainly by lumbricids and enchytraeids in sites H and M, and by tubificids in site L (from 2007), were dominant everywhere (circa 75%). From winter 2007, they constituted the main functional group in sites H and L, whereas crawlers-burrowers and conveyors were co-dominant in site M (reduction of lumbricids and particularly enchytraeids). Crawlers, crawler-burrower and burrowers were represented by woodlices, myriopods and ground beetles in site H (1000 ind./m^2), amphibious Diptera in site M (300 ind./m^2), and amphibious to aquatic Diptera and gastropods in site L (2500 ind./m^2). Non-bioturbators were marginally represented and composed of leeches found only once in site H and M (from 0 to 600 ind./m^2). Over the studied year, functional dominance accompanied the flooding frequency (Shannon index, mean *H* ± SE; site H, *H* = 0.78 ± 0.02; site M,

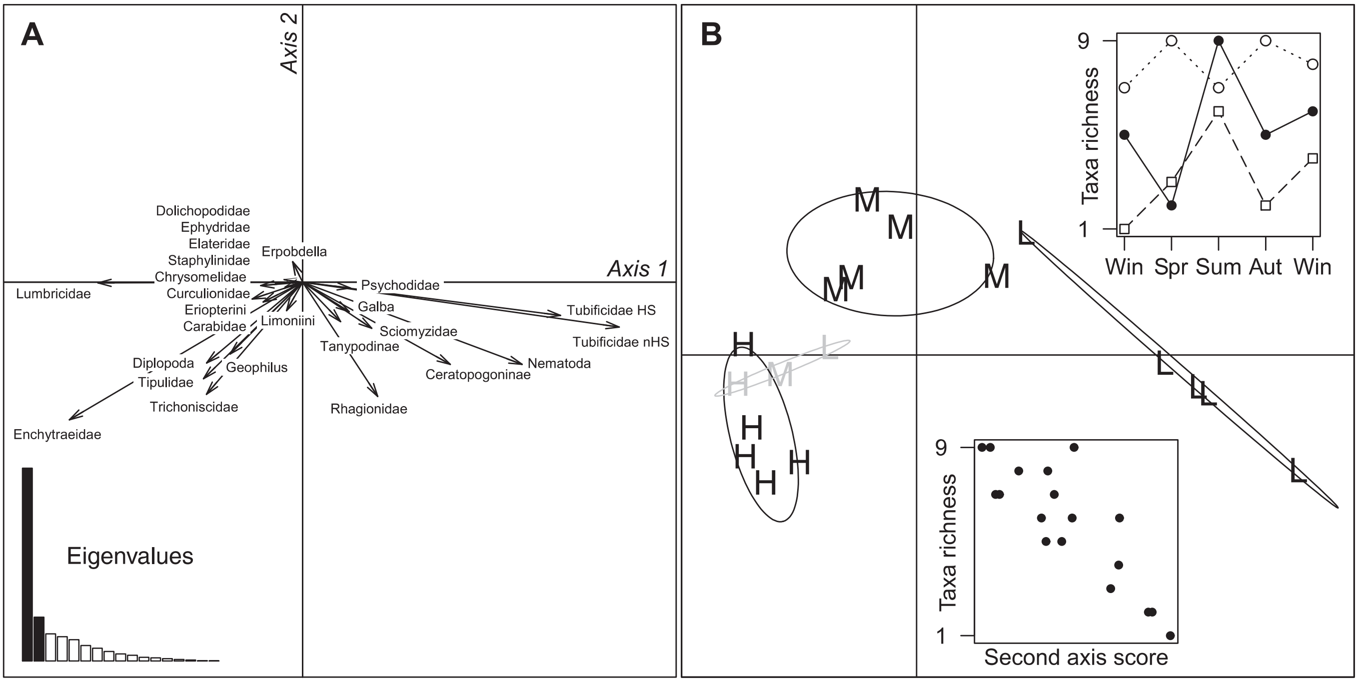

Fig. 4. Centred PCA on faunal data. A: taxa covariances and eigenvalues diagram; F1, 48%; F2, 11%. B: spatiotemporal units (date-site) grouped per site; in grey, positions of the three sites in April 2006; in black, positions from February 2007 to February 2008; upper inset: taxa richness over the study period (open dots, site H; filled dots, site M; squares, site L); lower inset: taxa richness versus second axis scores.

Table 1

Faunal characteristics and faunal relationships with bioturbation coefficients. Distribution: bold crosses indicate occurrences only from spring 2006. Locomotion and substrate relation: Cr, crawler; CB, crawler-burrower; Bu, burrower; Co, conveyor; Nb, non-bioturbator. HS and nHS refer respectively to Tubificidae with and without hair seta. Densities vs bioturbation coefficients relationship: Spearman's correlation coefficients; *, $p < 0.05$; **, $p < 0.01$.

Faunal description			Distribution					Locomotion and relations to substrate					Density vs bioturbation relationship		
Taxon	Group	Living mode	Site H	Site M	Site L	Frequency	Number of occurences	Fixed	Crawling	Burrowing	Conveying	Bioturbator type	Biodiffusion	Bioadvection	Regeneration
Curculionidae	Snout beetles	Ter	**X**			0.0	1		X			Cr			
Chrysomelidae	Leaf beetles	Ter	**X**			0.0	1		X			Cr			
Trichoniscidae	Woodlices	Ter	X			0.4	4		X			Cr			
Elateridae	Click beetles	Ter	X			0.1	1			X		Bu			
Dolichopodidae	Midges	Amp	X			0.0	1		X	X		CB			
Diplopoda	Myriapods	Ter	X			0.2	4		X	X		CB			
Carabidae	Ground beetles	Ter	X			0.1	2			X		Bu			
Limoniini	Midges	Amp	X			0.0	1			X		Bu			
Staphylinidae	Midges	Ter		**X**		0.0	1		X			Cr			
Geophilus	Myriapods	Ter	X	**X**		0.1	2		X			Cr			
Lumbricidae	Lumbricids	Ter	X	X	**X**	2.3	10		X	X	X	Co	-0.61^{*}	-0.57^{*}	−0.23
Enchytraeidae	Enchytraeids	Ter	X	X	**X**	5.3	7		X	X	X	Co	−0.56	-0.50^{*}	−0.13
Erpobdella	Leeches	Amp	X	X		0.1	2	X				Nb			
Tipulidae	Midges	Amp	X	X		0.2	5			X		Bu	−0.43	−0.30	−0.01
Ephydridae	Midges	Amp	X	X		0.1	2		X	X		CB			
Eriopterini	Midges	Ter	X		**X**	0.2	2		X			Cr			
Rhagionidae	Midges	Amp	X	X	X	1.0	10		X	X		CB	0.38	0.17	−0.16
Ceratopogoninae	Midges	Amp	X	X	X	3.9	8		X	X		CB	0.22	0.67^{**}	0.14
Psychodidae	Midges	Amp		X	X	0.2	2			X		Bu			
Tanypodinae	Midges	Aqu		**X**	X	0.2	1			X		Bu			
Sciomyzidae	Midges	Amp		X	X	0.2	2			X		Bu			
Tubificidae HS	Tubificids	Aqu		X	X	9.6	6		X	X	X	Co	0.72^{**}	0.61^{*}	0.31
Tubificidae nHS	Tubificids	Aqu		X	X	68.1	6		X	X	X	Co	0.73^{**}	0.68^{**}	0.29
Nematoda	Nematodes	Amp			X	7.6	4			X		Bu			
Galba	Gastropods	Amp			X	0.1	1		X			Cr			

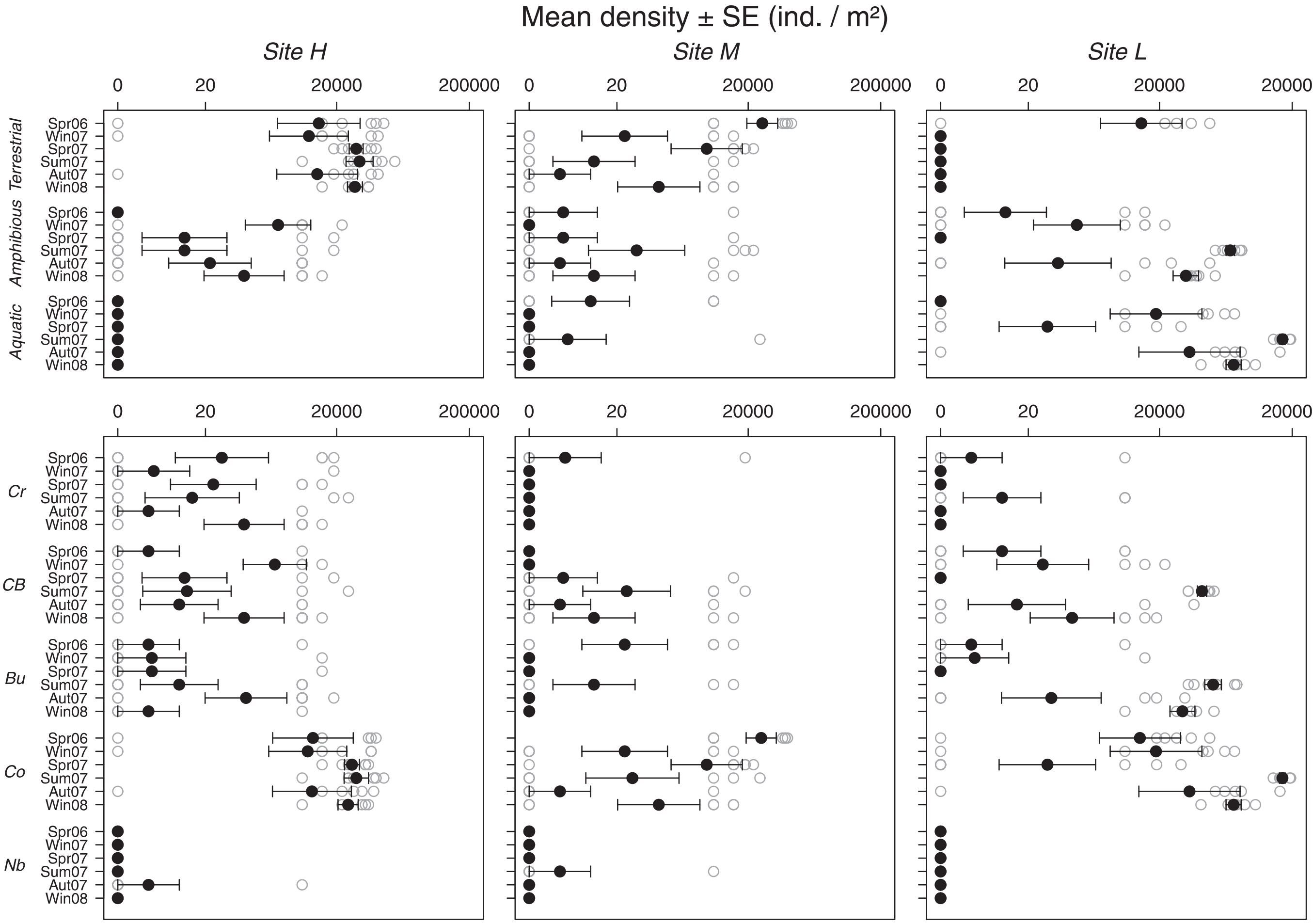

Fig. 5. Organism densities depending on functional characteristics from spring 2006 (Spr06) to winter 2008 (Win08); Cr, CB, Bu, Wo and Nb for respectively crawling, crawling-burrowing, burrowing, worm and non-bioturbator. Grey points: replicates.

$H = 0.58 \pm 0.20$; site L, $H = 0.33 \pm 0.10$; Kruskal–Wallis test, $\chi^2 = 7.458$, $p = 0.024$). Densities of functional groups in site H were significantly more even than those in site L (without significant distinction from site M after a multiple comparison test).

3.2. Bioturbation

Tracer penetration in soil deeper than 0.25 cm (microspheres injection zone) was noticeable at all three sites and deeper at low elevation (Fig. 6). A decreasing exponential trend with depth in tracer profiles attests of a typically biodiffusive mode. If the maximum tracer concentration is transferred in depth with a lower concentration in surface, bioadvection is the dominant mode. It is generated by conveyor belt species which continuously ingest sediments in depth and excrete in surface. Thus, these organisms create a top-down vertical migration of the tracers which is maximal in subsurface. A seasonal trend clearly appeared with a maximum penetration in summer, particularly in site L.

Table 2 summarizes the corresponding bioturbation coefficients. Among the three coefficients, biodiffusion was the most regular bioturbation mode among the three sites and over the studied period. This mode was more gradual along the flooding gradient where a significant difference was detected between sites H and L without distinction from site M (Table 3). Despite their more scattered values, bioadvection and regeneration also responded significantly to site effect, particularly due to the high bioturbative intensities in site L (Table 3; no significant difference between sites H and M).

A seasonal trend was confirmed by a significant date effect only for biodiffusion (Kruskal–Wallis test, Table 3) where the coefficients were significantly higher in summer (Table 2; Table 3, multiple comparisons; Fig. 7). Additionally, the summer bioturbation rate was much higher in site L where the biodiffusion coefficient was circa three to eight times higher compared to the other seasons, while it was circa twice higher in both sites H and M (Fig. 7). Despite a lack of seasonality in bioadvection on the whole flooding gradient, an interactive effect of date and site is suggested as a clear seasonal trend was observed in site L (Fig. 7).

Regeneration and bioadvection (in sites H and M for this latter), did not occur in controls. Bioadvection in controls L and biodiffusion in the three controls however were not null. Indeed, recolonization of some control cores was observed when sieving, particularly those from site L.

3.3. Relationship between bioturbation and fauna

The first PCA axis score was used as a synthetic descriptor encompassing faunal features expressed on the flooding gradient. Its Spearman's correlation coefficients were significantly positive with biodiffusion ($\rho = 0.63$; $p = 0.014$) and bioadvection ($\rho = 0.67$; $p = 0.007$) but not with regeneration ($p > 0.050$). Considering locomotion and substrate relations, one single significant

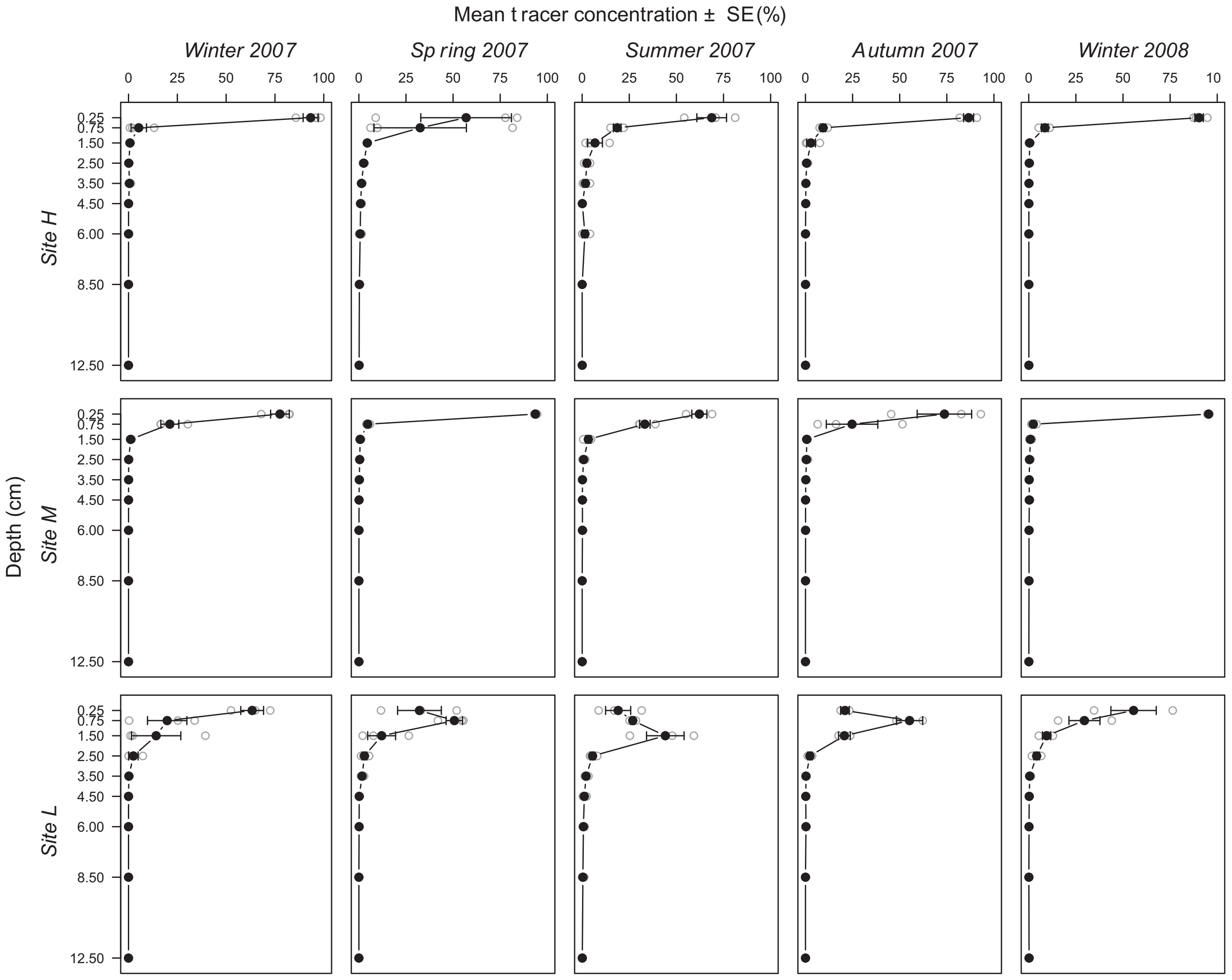

Fig. 6. Depth profiles of tracer concentrations over the studied year (percentage of the total amount of microspheres). Grey points: replicates.

Table 2
Bioturbation coefficients (mean ± standard error).

Date	Site	n	Biodiffusion (cm^2/year)	Bioadvection (cm/year)	Regeneration (mg/cm^2/year)
Winter 2007	H	3	1.07 ± 0.29	0.03 ± 0.03	0.00
	M	3	2.53 ± 0.60	0.00	0.00
	L	3	1.95 ± 0.97	1.40 ± 0.70	43.33 ± 43.33
Spring 2007	H	3	1.52 ± 0.20	6.77 ± 6.77	13.33 ± 6.67
	M	3	1.14 ± 0.04	0.03 ± 0.01	0.00
	L	3	2.20 ± 0.36	15.93 ± 3.80	10.00 ± 5.77
Summer 2007	H	2	2.58 ± 0.53	0.00	0.00
	M	3	5.33 ± 0.94	0.00	0.00
	L	3	16.23 ± 11.25	21.30 ± 10.72	0.00
Autumn 2007	H	3	1.53 ± 0.09	0.00	6.67 ±6.67
	M	3	1.70 ± 0.25	3.83 ± 3.83	0.00
	L	2	3.40 ± 1.00	19.60 ± 0.40	0.00
Winter 2008	H	3	1.42 ± 0.15	0.00	0.00
	M	3	0.96 ± 0.06	0.00	0.00
	L	3	4.60 ± 1.43	4.50 ± 4.50	16.67 ± 3.33
Whole period Replicates	H	14	1.56 ± 0.15	1.46 ± 1.45	4.29 ± 2.28
	M	15	2.33 ± 0.47	0.77 ± 0.77	0.00
	L	14	5.84 ± 2.57	12.04 ± 3.17	15.00 ± 9.12
Whole period Controls	H	5	1.18 ± 0.19	0.00	0.00
	M	5	1.66 ± 0.70	0.00	0.00
	L	5	2.16 ± 0.32	9.80 ± 3.82	0.00

relationship was found; burrower density was positively correlated to biodiffusion ($\rho = 0.63$; $p = 0.012$). Despite the lack of regularly encountered taxa over the study period (Table 1, Number of occurrences), the high faunal specificity along the flooding gradient

Table 3
Kruskal–Wallis tests and multiple comparisons (significance level $\alpha = 0.050$) of temporal and spatial effects. Multiple comparisons: Letters in common indicate an absence of significant difference.

Effect			Biodiffusion	Bioadvection	Regeneration
Site	Kruskal–Wallis test	df	2	2	2
		χ^2	10.894	14.504	7.584
		p	0.004	$<$0.001	0.023
	Multiple comparisons	Site H	a	a	a
		Site M	ab	a	a
		Site L	b	b	b
Date	Kruskal–Wallis test	df	4	4	4
		χ^2	13.778	5.482	5.965
		p	0.008	0.241	0.202
	Multiple comparisons	Winter 2007	a	a	a
		Spring 2007	a	a	a
		Summer 2007	b	a	a
		Autumn 2007	a	a	a
		Winter 2008	a	a	a

(Table 1, Distribution) strengthens the link between fauna and bioturbation. The taxa representing at least one percent of the total abundances over the studied year, and ensuring a minimum number of occurrences, were processed to Spearman's correlation tests with bioturbation coefficients (Table 1, Densities *vs.* bioturbation relationship). Mainly worms were found to be significantly correlated to biodiffusion and bioadvection whereas any significant relationship was found with regeneration. In opposition to Lumbricidae and Enchytraeidae, Tubificidae's density was positively linked to bioturbation; whereas Enchytraeidae were linked only to biodiffusion, Ceratopogonidae (crawler-burrower) were complementary linked to bioadvection. Significant correlations between living modes and bioturbation coefficients corroborated the importance of this fauna's environmental specificity: whereas no significant link was found between amphibious organism density and bioturbation coefficients ($p > 0.050$), terrestrial organism density was found to be negatively correlated to biodiffusion ($\rho = -0.54$; $p = 0.037$) and bioadvection ($\rho = -0.62$; $p = 0.014$), contrary to aquatic organism density (biodiffusion, $\rho = 0.73$ and $p = 0.002$; bioadvection, $\rho = 0.68$ and $p = 0.006$).

4. Discussion

4.1. Reliability of control cores

Tracer migration in control cores provides a quantitative measurement of tracer fluxes due to experimental manipulation. The slicing of cores is not exempt from non-biological microsphere penetration. In this sense, control coefficients should be taken into account for estimation of experimental coefficients measured under faunal effects. However, since organisms were found in control cores, tracer profiles in control cores are not mere experimental bias as they are also – at least partially – the result of biological participation. This was particularly the case for site L, characterized by the highest densities in the controls. In such an environment, a possible faunal recolonization of control cores may explain the bioadvective intensity (9.800 ± 3.820 cm/year in control against 12.042 ± 3.820 cm/year in experimental cores) as well as the biodiffusive intensity. In these conditions, the coefficients in experimental cores are probably slightly overestimated. Hence, real biologically induced coefficients in experimental cores are in a range of intensity between the recorded values reported in Table 2 and the values obtained by subtracting the coefficients of the experimental cores from the coefficients measured in the control cores. Nevertheless, the correspondence between the highest bioturbation coefficients and the highest faunal densities supports the hypothesis according to which microsphere penetration is induced by fauna as revealed in most studies using similar experimental design.

4.2. Functional restoration potential of CRT

In an estuarine lagoon, Duport et al. (2007) reported a maximum biodiffusion of 3.1 cm^2/year in summer. In a same environment, Gerino et al. (2007) reported maximum biodiffusion of 3.2 and 3.1 cm^2/year, and maximum bioadvection of 27.4 and 0.2 cm/year in respectively spring and autumn. Compared with maximum values observed in site L (biodiffusion of 16.2 cm^2/year and bioadvection of 21.3 cm/year), this strongly suggests that CRT habitats, after only one year, already exhibited estuarine bioturbative features. Thus, considering the ecological importance of bioturbation (Meysman et al., 2006), CRT can substantially increase the functional potential of the estuary. More qualitatively, the pattern in bioturbative modes along the flooding gradient strongly underlines the notion of bioturbation-induced functional gradient.

4.3. Intertidal gradient versus bioturbative functioning

The faunal specificity along the flooding gradient underlines the obvious link between abiotic and biotic components, and the clear effect of flooding frequency in space and time. The mean bioturbation coefficients observed in the most changed environment (site L; biodiffusion of 5.84 cm^2/year and bioadvection of 12.04 cm/year) strongly contrast in mode and intensity with maximum values observed in the most stable environment (site H; biodiffusion of 1.56 cm^2/year and bioadvection of 1.46 cm/year).

Despite a critical lack of quantitative information on bioturbation in terrestrial environments, biological activity in soil has been largely described (Bouché, 1972; Lavelle, 1988) because of its implication in stratigraphic artefacts (Balek, 2002; Van Nest, 2002) and soil persistence for natural and agricultural purposes (Brussaard et al., 1997; Johnson, 2002). In natural area, as well as in agricultural areas, earthworms are the dominant bioturbators of the terrestrial communities. These organisms directly or indirectly modulate the availability of resources (like physical space and food) to other species, by changing physical state in soil (Jones et al., 1994). Earthworms move soil particles either by ingestion (non-local transport) or by displacement (Barnett et al., 2009). The detected bioadvection in site H (still faunistically terrestrial) confirms the conclusion of Jarvis et al. (2010) who highlighted the importance both local and non-local transport to explain soil mixing in terrestrial grasslands. Hence, bioadvection and biodiffusion reflect the activities of respectively conveyors and all three crawling, burrowing and conveying organisms at this site.

Impoverishment in both taxa richness and densities in mid elevation might result from a long term extinction-recolonization process intermediate between the biweekly flooded terrestrial environment (no change) and the intensively flooded aquatic one (rapid change). It might also result from a chronic stress at intermediate flooding frequency which has been pointed out in freshwater tidal zones (Wolff, 1973). However, biodiffusion coefficient, non-significantly lower than in site H, contrasts with the lower organism density. This suggests that the fauna realizes a more effective biodiffusion in site M. In this site, changes conducted to a muddier substrate which could facilitate bioturbation. Controlled experiments would be necessary to verify if a given taxon can realize an increased biotransport in a modified environment.

In site L, on the contrary, the flooding effect erased all terrestrial characteristics and new aquatic conditions drove the settlement of aquatic organisms. The pioneer species, mainly tubificids, are tubicolous and live near the surface of the sediment. The strong increase in bioadvection from site H to site L (almost ten times) attests of the major effects of these organisms which vertically convey sediments (Fisher et al., 1980; Gerino et al., 2003; Ciutat et al., 2006). The concomitant increase in biodiffusion (more than three times) is probably engendered in part by a side effect of the conveying process as demonstrated by Ciutat et al. (2006) and Delmotte et al. (2007). The higher regeneration is consistent with the high densities of organisms with burrowing faculties (tubificids and ceratopogonids), and could additionally result as a side effect of the biodiffusive activity (François et al., 2002). The correspondence between the highest organism densities and the highest bioturbative intensities recorded at this site concur with several studies (Mazik and Elliott, 2000; Mermillod-Blondin et al., 2001; Duport et al., 2006).

The lack of a clear link between physical foraging mode and bioturbation is due to the wide distribution of crawling, burrowing and conveying abilities on the whole flooding gradient (Fig. 5). The preponderance of living mode suggests that other ecological attributes might explain the bioturbation pattern. Indeed, from terrestrial to aquatic environment, the main representative taxa (worms)

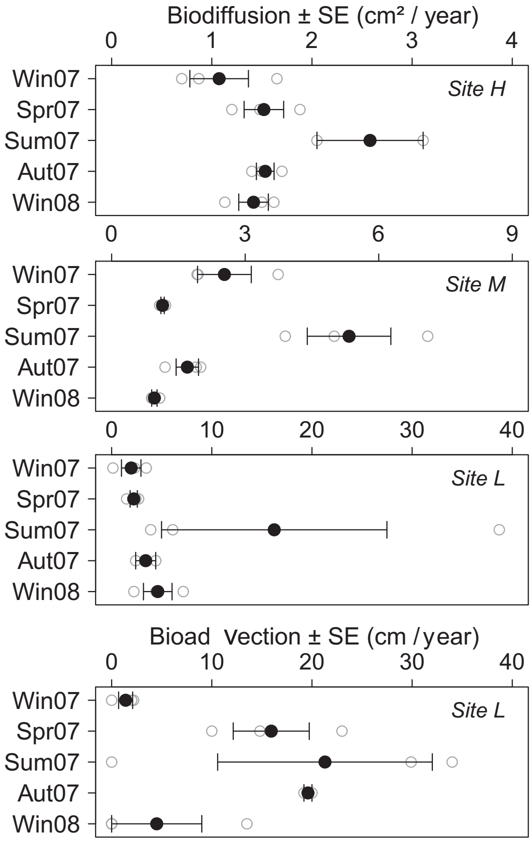

Fig. 7. Temporal profiles of biodiffusion in the three sites and of bioadvection at site L. These profiles show the clear seasonality in the three sites. Grey points: replicates.

differ in feeding mode. Earthworms forage from surface to deep soil where they ingest fine to coarse plant detritus (Shuster et al., 2001; Bastardie et al., 2005), and this could explain the absence of a dominant bioturbation mode in site H. On the contrary, tubificids, more specialized, are surface deposit-feeder at the water-sediment interface (Mermillod-Blondin et al., 2001), and synchronize their activity with the tide, thus generating a dominant bioadvective transport by vertically conveying freshly-deposited sediments. However, given the strong successional nature of site L, these findings cannot demonstrate a steady bioturbation pattern opposing the terrestrial to the aquatic bioturbative functioning.

4.4. Flooding effect as community disturbance

The faunal and bioturbative specificities on the flooding gradient may be attributed to a double effect: the environmental context (terrestrial/aquatic) giving rise to specific living modes and, also, the degree of disturbance engendered by flooding frequency. The present environmental context cannot be inferred as a unique determinant of the bioturbation pattern since the comparison between terrestrial and aquatic bioturbation is weakened by the lack of measurements of biotransport in terrestrial environments (Jarvis et al., 2010). On the contrary, since all bioturbation modes are largely documented in aquatic environments, a flooding-induced disturbance effect cannot be discarded. Indeed, opposed to the remnant community in site H, the functionally dominated community in site L has rapidly replaced the original one. It undergoes a primary succession with establishment of pioneers and dominant taxa as typically described in the development of faunal assemblages after a major disturbance (Rhoads, 1974; Rhoads and Germano, 1982). According to Rhoads (1974), in marine environments, bioturbation pattern evolves as a direct consequence of enrichment in biological functions.

As in marine communities where they settle in association with polychaetes, the pioneer species in the freshwater community in site L are aquatic oligochaetes engendering bioadvection (Rhoads and Germano, 1982). Since the sediments have been reworked by these conveyors, the oxygen boundary gets lower in the sediment column and compactness decreases so that other species may colonise the sediment. In the latest stage of the succession, Rhoads (1974) describes deeper burrow systems and more different mixing types thus explaining the enhancement of biodiffusion and regeneration. The lower taxa richness in site L (ranging from 2 to 8 bioturbative taxa) compared to that of site H (ranging from 7 to 9 bioturbator taxa) underlines the pioneer stage of this community performing a dominant bioadvective transport.

4.5. Function and diversity over time

It was crucial to consider all seasons in order to detect a temporal effect in bioturbative activities. This agrees with Duport et al. (2007) who also found higher bioturbation coefficients in summer. In temperate environments, temperature governs biological rhythms and population's dynamics, thus explaining here the summer biodiffusion increase mediated by a faunal density effect. Beside this, an interaction with foraging intensity could be hypothesized, at least in site L. Indeed, foraging intensity was shown to be enhanced by summer-induced hypoxia in order to increase oxygen penetration in aquatic sediment (Hollertz and Duchêne, 2001; Mermillod-Blondin et al., 2001; Ouellette et al., 2004). Additionally, a spatial interaction is not excluded as Fig. 7, without ambiguity, displays a summer biodiffusive intensity enhanced by flooding frequency, and a clear seasonal cycle of bioadvection in site L, undetectable in sites H and M. However, the present sampling design cannot afford to statistically test for an interactive effect. This could enrich the comparison between terrestrial and aquatic environments and more precisely their seasonal nature.

Similar to organism density, taxa richness exhibited a seasonal cycle, particularly in site L with the addition of specific taxa such as Galba and Tanypodinae (respectively biodiffusors and bio-irrigators). On the short term, this could complement the explanation of the seasonality of bioturbative intensity. On the long term, a relative enrichment in these taxa could enrich compositional functions and a consequent diversification of biotransports (Pearson and Rosenberg, 1978).

5. Conclusions

This study demonstrates that all bioturbation modes can be detected in situ on a flooding gradient. From high to low elevation, the tidal gradient exhibits functional specificities linking faunal features and bioturbation. The double temporal implication of disturbance and succession conditions contrasted bioturbation patterns between terrestrial and aquatic environments, probably via life history traits (e.g. body size, feeding regime and mode, life span, oxygen availability). Evidences of different environmental features such as energy fluxes and food web structure from dry to wet habitats are reported, but these aspects are still poorly documented (Shurin et al., 2006).

Estuaries are recognized to play a crucial role in global biogeochemical cycles by trapping riverine inputs and contaminants (Jickells, 1998). This study brings functional gradients to prominence at the local scale in estuaries. Further research is necessary to explore the diversity of biogeochemical processes concentrated in tidal zones and eventually their role in large scale ecosystem processes (e.g. Vannote et al., 1980).

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References

Aller, R.C., 1994. Bioturbation and remineralization of sedimentary organic matter, effects of redox oscillation. Chemical Geology 114, 331–345.

Baldwin, A.H., Barendregt, A., Whigham, D.F., 2009. Tidal freshwater wetlands – An introduction to the ecosystem. In: Barendregt, A., Whigham, D.F., Baldwin, A.H. (Eds.), Tidal Freshwater Wetlands. Backhuys Publisher, Leiden, pp. 1–10.

Balek, C.L., 2002. Buried artefacts in stable upland sites and the role of bioturbation: a review. Geoarchaeology an International Journal 17, 41–51.

Barnett, C.M., Bengough, A.G., McKenzie, B.M., 2009. Quantitative image analysis of earthworm-mediated soil displacement. Biology, Fertility of Soils 45, 821–828.

Bastardie, F., Capowiez, Y., Cluzeau, D., 2005. 3D characterisation of earthworm burrow systems in natural soil cores collected from a 12-year-old pasture. Applied Soil Ecology 30, 34–46.

Beauchard, O., Jacobs, S., Cox, T., Maris, T., Vrebos, D., Van Braeckel, A., Meire, P., 2011. A new technique for tidal habitat restoration: evaluation of the long term hydrological pattern. Ecological Engineering 37, 1849–1858.

Biles, C.L., Paterson, D.M., Ford, R.B., Solan, M., Raffaelli, D.G., 2002. Bioturbation, ecosystem functioning and community structure. Hydrology and Earth System Sciences 6, 999–1005.

Bouché, M.B., 1972. Lombriciens de France. Ecologie et Systematique. Editions INRA, Paris, p. 671.

Boudreau, B.P., 1997. Diagenetic Models and Their Implementation, Modelling Transport and Reactions in Aquatic Sediments. Springer Verlag, Berlin, p. 414.

Brussaard, L., Behan-Pelletier, V.M., Bignell, D.E., Brown, V.K., Didden, W., Folgarait, P., Fragoso, C., Freckman, D.W., Gupta, V.V.S.R., Hattori, T., Hawksworth, D.L., Klopatek, C., Lavelle, P., Malloch, D.W., Rusek, J., Soderstrom, B., Tiedje, J.M., Virginia, R.A., 1997. Biodiversity and ecosystem functioning in soil. Ambio 26, 563–570.

Ciutat, A., Weber, O., Gerino, M., Boudou, A., 2006. Stratigraphic effects of Tubificids in freshwater sediments: a kinetic study based on X-Ray images and micro-granulometry. Acta Oecologica 30, 228–237.

Ciutat, A., Gerino, M., Mesmer-Dudons, N., Anschutz, P., Boudou, A., 2005. Cadmium bioaccumulation in Tubificidae from the overlying water source and effects on bioturbation. Ecotoxicology and Environmental Safety 60, 237–246.

Delmotte, S., Meysman, J.R., Ciutat, A., Boudou, A., Sauvage, S., Gerino, M., 2007. Cadmium transport in sediments by tubificid bioturbation, an assessment of model complexity. Geochimica et Cosmochimica Acta 71, 844–862.

Duport, E., Gilbert, F., Poggiale, J.C., Dedieu, K., Rabouille, C., Stora, G., 2007. Benthic macrofauna and sediment reworking quantification in contrasted environment in the Thau Lagoon. Estuarine, Coastal and Shelf Science 72, 522–533.

Duport, E., Gilbert, F., Trambley, P., Poggiale, J.C., Stora, G., 2006. Effects of population density on the sediment mixing induced by the gallery-diffusor Hediste (Nereis) diversicolor O.F. Müller, 1776. Journal of Experimental Marine Biology and Ecology 336, 33–41.

Fisher, J.B., Lick, W.L., Mc Call, P.L., Robbins, J.A., 1980. Vertical mixing of lake sediments by tubificid oligochaetes. Journal of Geophysical Research 85, 3997–4006.

François, F., Gerino, M., Stora, G., Durbec, J.P., Poggiale, J.C., 2002. Functional approach to sediment reworking by gallery-forming macrobenthic organisms, modelling and application with the polychaete *Nereis diversicolor*. Marine Ecology Progress Series 229, 127–136.

French, P.W., 2006. Managed realignment – The developing story of a comparatively new approach to soft engineering. Estuarine, Coastal and Shelf Science 59, 409–423.

Gerino, M., Frignani, M., Mugnai, C., Belluci, L.G., Prevedelli, D., Valentini, A., Castelli, A., Delmotte, S., Sauvage, S., 2007. Bioturbation in the Venice Lagoon, rates and relationship to organisms. Acta Oecologica 32, 14–25.

Gerino, M., Stora, G., Carcaillet, F., Gilbert, F., Poggiale, J.C., Mermillod-Blondin, F., Desrosiers, G., Vervier, P., 2003. Macro-invertebrate functional groups in freshwater and marine sediments, a common mechanistic classification. Life and Environment 53, 221–231.

Gerino, M., Stora, G., Durbec, J.P., 1994. Quantitative estimation of biodiffusive and bioadvective sediment mixing, in situ experimental approach. Oceanologica Acta 17, 547–554.

Hollertz, K., Duchêne, J.C., 2001. Burrowing behaviour and sediment reworking in the earth urchin Bissopsis lyrifera Forbes (Spatangida). Marine Biology 139, 951–957.

Jacobs, S., Beauchard, O., Struyf, E., Cox, T., Maris, T., Meire, P., 2009. Restoration of tidal freshwater vegetation using controlled reduced tide (CRT) along the Schelde Estuary (Belgium). Estuarine Coastal and Shelf Science 85, 368–376.

Jarvis, N.J., Taylor, A., Larsbo, M., Etana, A., Rosén, K., 2010. Modelling the effects of bioturbation on the re-distribution of ^{137}Cs in an undisturbed grassland soil. European Journal of Soil Science 61, 24–34.

Jickells, T.D., 1998. Nutrient biogeochemistry of the coastal zone. Science 281, 217–222.

Johnson, D.L., 2002. Darwin would be proud: bioturbation, dynamic denudation and the power of theory in science. Geoarchaeology: An International Journal 17, 7–40.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.

Lavelle, P., 1988. Earth worm activities and the soil system. Biology, Fertility of Soils 6, 237–261.

Lohrer, A.M., Thrush, S.F., Gibbs, M.M., 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. Nature 431, 1092–1095.

Maris, T., Cox, T., Temmerman, S., De Vleeschauwer, P., Van Damme, S., De Mulder, T., Van den Bergh, E., Meire, P., 2007. Tuning the tide, creating ecological conditions for tidal marsh development in a flood control area. Hydrobiologia 588, 31–43.

Mazik, K., Elliott, M., 2000. The effects of chemical pollution on the bioturbation potential of estuarine intertidal mudflats. Helgoland Marine Research 54, 99–109.

Megonigal, J.P., Neubauer, S.C., 2009. Biogeochemistry of tidal freshwater wetlands. In: Perillo, G.M.E., Wolanski, E., Cahoon, D.R., Brinson, M.M. (Eds.), Coastal Wetlands: An Integrated Ecosystem Approach. Elsevier, pp. 535–562.

Meire, P., Ysebaert, T., Van Damme, S., Van den Bergh, E., Maris, T., Struyf, E., 2005. The Scheldt estuary, a description of a changing ecosystem. Hydrobiologia 540, 1–11.

Mermillod-Blondin, F., Rosenberg, R., 2006. Ecosystem engineering, the impact of bioturbation on biogeochemical processes in marine and freshwater benthic habitats. Aquatic Science 68, 434–442.

Mermillod-Blondin, F., Gerino, M., Degrange, V., Lensi, R., Chassé, J.L., Rard, M., Creuzé des Châtelliers, M., 2001. Testing the functional redundancy of Limnodrilus and Tubifex (Oligochaeta, Tubificidae) in hyporheic sediments, an experimental study in microcosms. Canadian Journal of Fisheries and Aquatic Sciences 58, 1747–1759.

Merritt, R.W., Cummins, K.W., 1984. An Introduction to the Aquatic Insects of North America, second ed. Kendall/Hunt Publishing Company, Dubuque, Idaho, p. 722.

Meysman, J.R., Middelburg, J., Heip, C.H.R., 2006. Bioturbation, a fresh look at Darwin's last idea. Trends in Ecology and Evolution 21, 688–695.

Morris, A.W., Mantoura, R.F.C., Bale, A.J., Howland, R.J.M., 1978. Very low salinity regions of estuaries: important sites for chemical and biological reactions. Nature 274, 678–680.

Munzel, U., Hothorn, L.A., 2001. A unified approach to simultaneous rank test procedures in the unbalanced one-way layout. Biometrical Journal 43, 553–569.

Nickell, L.A., Black, K.D., Hughes, D.J., Overnell, J., Brand, T., Nickell, T.D., Breuer, E., Martyn, H.S., 2003. Bioturbation, sediment fluxes and benthic community structure around a salmon cage farm in Loch Creran, Scotland. Journal of Experimental Marine Biology and Ecology 285–286, 221–233.

Nogaro, G., Mermillod-Blondin, F., Valett, M.H., François-Carcaillet, F., Gaudet, J.P., Lafont, M., Gibert, J., 2009. Ecosystem engineering at the sediment-water interface, bioturbation and consumer-substrate interaction. Oecologia 161, 125–138.

Officier, C.B., Lynch, D.R., 1982. Interpretation procedures for the determination of sediment parameters from time-dependant flux inputs. Earth and Planetary Science Letters 61, 55–62.

Ouellette, D., Derosiers, G., Gagne, J.P., Gilbert, F., Poggiale, J.C., Blier, P.U., Stora, G., 2004. Effects of temperature on in vitro sediment reworking processes by a gallery biodiffusor, the Polychaete Neanthes virens. Marine Ecology Progress Series 266, 185–193.

Pearson, T.H., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology, An Annual Review 16, 229–311.

Pearson, T.H., Rosenberg, R., 1976. A comparative study of the effects on the marine environment of wastes from cellulose industries in Scotland and Sweden. Ambio 5, 77–79.

R Development Core Team, 2009. R, a Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Austria, Vienna. http://cran.at.r-project.org/index.html WWW Page.

Rhoads, D.C., Germano, J.D., 1982. Characterization of organism-sediment relations using sediment profile imaging: an efficient method of remote ecological monitoring of the seafloor (RemotsTM system). Marine Ecology Progress Series 8, 115–128.

Rhoads, D.C., 1974. Organism-sediment relations on the muddy sea floor. Oceanography and Marine Biology, An Annual Review 12, 263–300.

Ricklefs, R.E., 1990. Ecology, third ed. W.H. Freeman, New York, p. 896.

Shurin, J.B., Gruner, D.S., Hillebrand, H., 2006. All wet or dried up? Real Differences Between Aquatic and Terrestrial Food Webs. Proceedings of the Royal Society B 273, 1–9.

Shuster, W.D., Subler, S., McCoy, E.L., 2001. Deep-burrowing earthworm additions changed the distribution of soil organic carbon in a chisel-tilled soil. Soil Biology & Biochemistry 33, 983–996.

Solimini, A.G., Ruggiero, A., Bernardini, V., Carchini, G., 2003. Temporal pattern of macroinvertebrate diversity and production in a new man-made shallow lake. Hydrobiologia 506–509, 373–379.

Tachet, H., Richoux, P., Bournaud, M., Usseglio-Polatera, P., 2000. Invertébrés d'eau douce. Systématique, biologie, écologie. CNRS Editions, p. 588.

Teal, L.R., Bulling, M.T., Parker, E.R., Solan, M., 2008. Global patterns of bioturbation intensity and mixed depth of marine soft sediments. Aquatic Biology 2, 207–218.

Van den Bergh, E., Van Damme, S., Graveland, J., de Jong, D., Baten, I., Meire, P., 2005. Ecological rehabilitation of the Schelde Estuary (The Netherlands-Belgium; Northwest Europe), linking ecology, safety against floods, and accessibility for port development. Restoration Ecology 13, 204–214.

Van Nest, J., 2002. The good earthworm: how natural processes preserve upland archaic archaeological sites of western Illinois, USA. Geoarchaeology: An International Journal 17, 53–90.

Vandenbruwaene, W., Maris, T., Cox, T.J.S., Cahoon, D.R., Meire, P., Temmerman, S., 2011. Sedimentation and response to sea-level rise of a restored marsh with reduced tidal exchange: comparison with a natural tidal marsh. Geomorphology 130, 115–126.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The River Continuum Concept. Canadian Journal of Fisheries and Aquatic Sciences 37, 130–137.

Voshell, J.R., Simmons, G.M., 1984. Colonization and succession of benthic macroinvertebrates in a new reservoir. Hydrobiologia 112, 27–39.

Wheatcroft, R.A., 2006. Time-series measurements of macrobenthos abundance and sediment bioturbation intensity on a flood-dominated shelf. Progress in Oceanography 71, 88–122.

Wolff, W.J., 1973. The Estuary as a Habitat. An Analysis of Data on the Soft-bottom Macrofauna of the Estuarine Area of the Rivers Rhine, Meuse and Scheldt, vol. 126. Zoölogische Verhandelingen, Leiden, p. 242.