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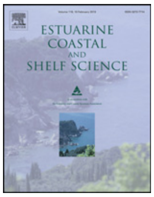

Sediment macroinvertebrate community functioning in impacted and newly-created tidal freshwater habitats

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ABSTRACT

Although experiencing strong anthropogenic pressures in many estuaries, the ecology of tidal freshwater areas remains largely undocumented. As part of a restoration project in the freshwater zone of the Schelde estuary (Belgium), a new tidal habitat restoration technique (Controlled Reduced Tide system, CRT) was hypothesised to successfully compensate for the impairment of contemporary habitats. The suitability of this newly-created habitat (CRT) and the estuary was investigated over a period of three years for its macroinvertebrate community development. In both the estuary and the CRT, habitats along a flooding gradient were monitored. Differences between the CRT and reference sites in community functioning were explored according to environmental characteristics and organism biological attributes using the RLQ ordination analysis together with the fourth-corner method. Frequently flooded reference sites exhibited environmental characteristics resulting from a hydrological shear stress. In the CRT, after a rapid removal of the terrestrial fauna at low and mid elevations, the low-energy hydrology led to taxonomic and functional enrichment. The RLQ analysis produced significant environmental filtering of biological attributes mainly related to the terrestrial–aquatic transition and to the environmental stressors. This provides an example of life history modification via estuarine ecosystem management.

1. Introduction

Tidal freshwater wetlands are relatively rare but known to occur in the estuaries of the largest river drainages (Baldwin et al., 2009) but to date they have been mainly studied in North America. In Europe, most of them are found along the North Sea coast, in the Schelde, Maas and Elbe estuaries; almost 10% of them occur in the Belgian part of the Schelde estuary (Struyf et al., 2009). This estuary has been hugely impacted by human activities (industry and navigation), and embankments have led to a large-scale loss of 36% of the total surface of tidal habitats during the last century, while the remaining ones are under severe stress of changing hydrodynamic conditions (Meire et al., 2005).

Typically, tidal freshwater marshes bordering river channels consist of continua which extend over mudflat, helophyte and woody plant habitats where the daily flood interacts with elevation (Baldwin et al., 2009; Struyf et al., 2009). As low marshes in the Schelde estuary have now become rare through embankments, entire habitat gradients have also become rare (Struyf et al., 2009). In order to accommodate both ecological and economical problems, a long-term vision for the Schelde estuary was agreed to be the development of a healthy and multifunctional estuarine water system that can be used in a sustainable way for human needs (Van den Bergh et al., 2005). This vision includes the restoration of the intertidal habitats throughout the estuary, including the freshwater zone. In many coastal zones, restoration and creation of natural habitats are constrained by historic embankments and soil subsidence where mean high water level prevents a complete flooding gradient which in turn conditions habitat diversity (Beauchard et al., 2011). However, using a system of inlet and outlet culverts, controlled reduced tide (CRT) engineering is a new restoration technique to overcome this constraint. CRT was hypothesized to successfully restore intertidal habitats (Maris et al., 2007), and a pilot CRT was implemented in the freshwater zone of the Schelde estuary in 2006.

The ecological importance of tidal freshwater wetlands has been mainly attributed to the biogeochemical processes that they ensure in estuaries (Megonigal and Neubauer, 2009). However, the lack of knowledge of tidal freshwater ecology is well-recognized, particularly in invertebrate studies (Rundle et al., 1998; Reinicke, 2000;

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Sousa et al., 2005); invertebrates represent a key ecosystem compartment as they cycle energy between autotrophic and heterotrophic components. The many roles of sediment invertebrates include organic matter decomposition and mineralization, humification, sediment mixing, soil/sediment oxygenation and irrigation (Wallace and Webster, 1996; Herman et al., 1999; Lavelle et al., 2006), whereas the loss of functional groups may impair ecosystem performance (Thrush et al., 2006). In tidal freshwater and brackish zone, invertebrate biomass and density increase in response to nutrient enrichment (Oviatt et al., 1993; Frost et al., 2009); this underlines another crucial role of invertebrates in impacted estuaries by mineralising excess nutrients which otherwise cause adverse effects such as eutrophication (Jickells, 1998).

In the Schelde estuary, only a few studies, focussing mainly on the whole salinity gradient, reported invertebrate data from the freshwater zone (Ysebaert et al., 1993, 1998; Seys et al., 1999); locally, none of them took the flooding gradient into account, leading to incomplete description of intertidal communities. Furthermore, Ysebaert et al. (1998) advocated the need to focus on the functional role of organisms in the ecosystem and especially the relationships between species communities, environmental features and habitat use. This is typically interrogated using methods coupling sites × variables and sites × species matrices (Dray et al., 2003). However, the taxonomic nature of such investigations limits our understanding of the mechanistic processes explaining species occurrences along a gradient. Recent methodological advances (Dolédec et al., 1996; Legendre et al., 1997; Dray and Legendre, 2008) have allowed us to identify biological properties which determine species occurrences in a given environment, but there are still few published applications in estuaries. Therefore, this study aims: (1) to describe the current macroinvertebrate communities along a flooding gradient in the estuary, (2) to verify the suitability of CRT for invertebrate community development among the newly-created tidal habitats and (3) to compare the community functioning in CRT and reference adjacent estuarine habitats.

2. Methods

2.1. Study area

This study took place in the freshwater zone of the Schelde estuary, Belgium (51.086 °N; 4.171 °E; Fig. 1). The estuary is particularly characterized by the length of the tidal wave which influences the river and some tributaries, 235 km in total, encompassing 44 km^2 of tidal freshwater surface. At the study location, the estuary is a narrow tidal channel bordered with mudflats and high marshes, and the average tidal amplitude is ca.5.2 m. The first CRT system was implemented in the Lippenbroek polder (8.2 ha; Fig. 1B), where agriculture was practiced until 2000, whereas now it supports a pilot project for intertidal habitat restoration together with protection against flooding by storm surges and high tides. It is connected to the estuary by an inlet culvert and an outlet valve allowing water exchanges between the two systems (see Maris et al. (2007) and Beauchard et al. (2011) for technical details). The polder has been under the CRT tidal influence since March 1st, 2006.

2.2. Sampling site description

Eight field samplings were carried out from April 2006 to February 2008 (once each season) plus an additional one in summer 2009. In the CRT, the monitoring was conducted at four sites covering the whole gradient (Fig. 1B) with 3 sites covering the entire elevation range, giving rise to three flooding frequencies (Fig. 2): site H (high elevation, low flooding frequency), site M (mid elevation, moderate flooding frequency) and site L (low elevation, high flooding frequency). In general, site L is flooded on most days (87% of the tides) whereas site H is flooded less-frequently around spring tides (24% of the tides). Since a part of the CRT is permanently filled with water, the fourth site was considered as representative of this tidal pool (site P). Sediment deposition was rapid and elevation-dependent, with higher accretion rates in frequently flooded sites (Vandenbruwaene et al., 2011, Fig. 2). The soil at site L was covered by more than 15 cm of river sediments within a year.

Site H was covered with remnant terrestrial vegetation, mainly represented by *Urtica dioica*, and did not change notably. In contrast, site M was progressively colonized by wetland species such as *Epilobium hirsutum* and *Lythrum salicaria* (Jacobs et al., 2009). At site L, plant species turnover was complete after one season, where *Lythrum salicaria* and especially *Phragmites australis* replaced the terrestrial community.

In the adjacent estuary, three sites, as the most representative habitats of the area, distributed along the flooding gradient, were also monitored (Figs. 1 and 2): willow (site W, high marsh, mainly characterized by *Salix* sp.), reed (site R, monospecific coverage of *Phragmites australis*) and bare tidal flat (site F). As the result of tidal

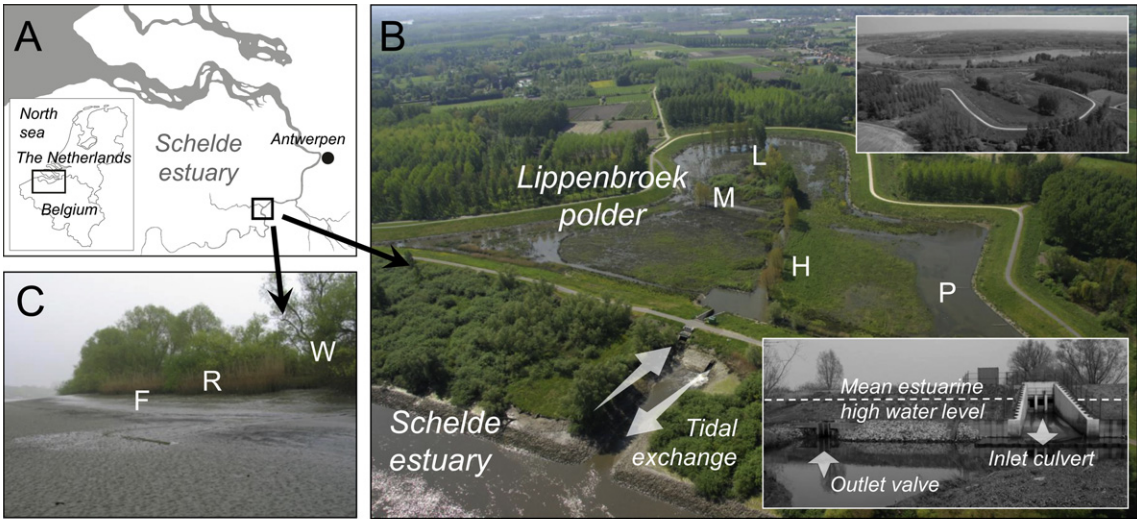

Fig. 1. A) Location map of the study area. B) Photograph of the experimental CRT; H, L, M and P for respectively high, mid, low elevation and pool; upper insert, global view of the location area; lower insert, water exchange system. C) Reference sites located 600 m upstream the polder: W, R and F for respectively willow, reed, flat.

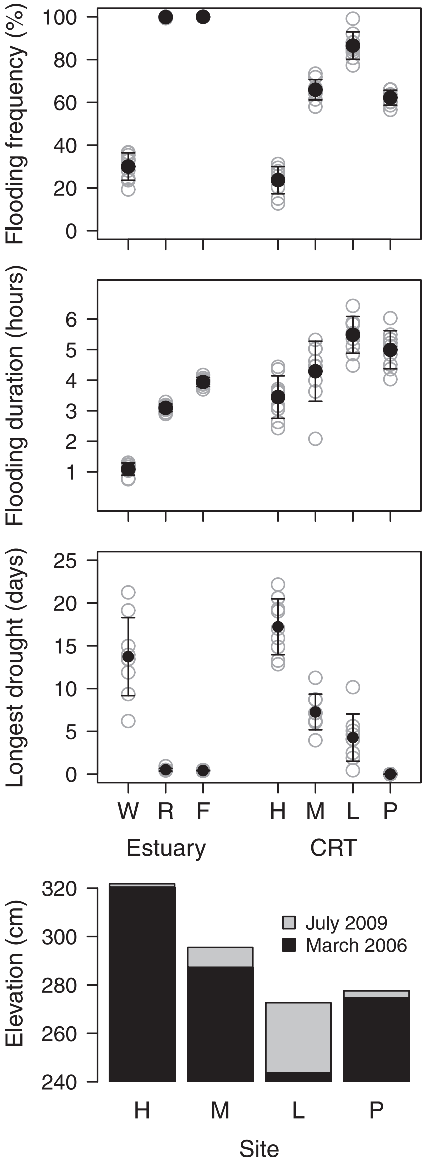

Fig. 2. Hydrotopographical context of the study. Top error bars: mean values (±S.D.) were calculated based on the 9 seasonal means from March 2006 to July 2009 (grey points). Bottom diagram: sediment accumulation is represented in grey.

squeeze, a marsh cliff developed through erosion and shear stress prevents natural sedimentation at the low elevation (Meire et al., 2005; Van den Bergh et al., 2005; Beauchard et al., 2011). Therefore, R and F habitats were considered as impacted reference sites in order to assess the ability of the CRT system to counteract tidal squeeze.

2.3. Sampling design and laboratory analyses

A core sampler (4.6 cm Ø) was used to sample invertebrates from the top sediment to 15 cm deep. Six replicates were stored in 5% formalin, then sieved in the laboratory though a 500 μm mesh. After sorting, worms were stored in 5% formalin and arthropods in norvanol and then identified to highest taxonomic separation (see Appendix 1). The sediment physical nature was characterized after sampling with a core-sampler (1 cm Ø and 15 cm deep). Each sample was based on 10 to 15 mixed cores spread over the whole site surface (25 m^2). Samples were stored at 4 °C and processed within 24 h. Sediment water content (WC) was determined by measuring sediment weight after drying for 5 days at 70 °C. Organic matter (OM) content was estimated after weight loss-on-ignition between oven dried sediment (105 °C) and incineration at 550 °C after 6 h. The remaining dry sediment was used to quantify several granulometric aspects by means of a laser diffraction particle size analyzer: mean grain size (MGS) and clay/silt/sand percentages (respectively as the <4, 4–63 and >63 μm fractions). In the field, sediment resistance was quantified with a penetrometer (Resistance, in N/m^2); a cone of 5.0 cm^2 was used on the softest sediments, whereas a cone of 3.3 cm^2 was occasionally used on dry summer sediments.

2.4. Sediment characteristics and faunistic descriptions

Sediment characteristics were explored by a standardized Principal Component Analysis (PCA) on the 7 sediment descriptors. Taxa were described, and the occurrences were displayed per site and per date.

2.5. Community functioning: relationships between environmental descriptors, taxa occurrences and taxa biological traits

RLQ analysis (Dolédec et al., 1996) was conducted to explore the biological mechanisms that determine the taxa occurrences along environmental gradients. Three tables were considered: environmental descriptors (table **R**; date-site × descriptors; the 7 sediment characteristics plus flooding frequency and longest drought), taxa occurrences (table **L**; date-site × taxa; log-transformed densities, pooled replicates), and taxa biological traits (table **Q**; taxa × biological traits; qualitative attributes, see Table 1). This method allows the simultaneous ordination of the three tables based on the singular value derived from the crossed matrix $\mathbf{R}^t\mathbf{LQ}$. **L** (Link) is processed by a correspondence analysis (CA) which reciprocally relates date-site and taxa weighted by sums of densities in lines and columns of **L** (Thioulouse and Chessel, 1992). The variances of CA axes (eigenvalues) provide explained variances in the reciprocal taxa *vs.* samples relationship.

Before analysing their relationships, tables **R** and **Q** were separately processed by an appropriate ordination. A standardized PCA and a Multiple Correspondence Analysis (MCA; Tenenhaus and Young, 1985) were performed respectively on tables **R** and **Q**. To justify a simultaneous ordination of the three tables, the significance of the links between **R** and **L** on the one hand, and tables $\mathbf{L}^t$ and **Q** on the other hand, have to be tested (Dray and Legendre, 2008). Therefore, co-inertia analyses (Dolédec and Chessel, 1994) were performed on the two pairs of analyses (PCA *vs.* CA, **R** and **L** matched by date-site; CA *vs.* MCA, $\mathbf{L}^t$ and **Q** matched by taxa). The *Rv* coefficient (Escoufier, 1973), an equivalent of a simple Pearson correlation coefficient between two variables), was computed in each co-inertia analysis; its significance was tested by a Monte-Carlo procedure based on 9999 random permutations of the lines of **R** and **Q** (Heo and Gabriel, 1998). In RLQ analysis, the test statistic is the total co-inertia of the RLQ analysis (the squared covariance between tables **R** and **Q**), and its significance is tested by 9999 random permutations of the lines of **R** and **Q** (Dolédec et al., 1996). The traits contributing most to the axes were identified by their correlation ratios (CR); a CR returns the proportion of explained variance of the axis species scores by the discrimination of the trait modalities (species groups).

Although a significant RLQ co-inertia can be expected under the null hypothesis, this does not imply that biological attributes are all correlated with environmental descriptors (Legendre et al., 1997). Therefore, the fourth-corner method (see Dray and Legendre, 2008 for further information) was applied on the dataset in order to identify the significant associations between biological attributes and environmental descriptors. Model 1 of Legendre et al. (1997)

Table 1

Taxa's occurrences and biological attributes. % indicates the relative abundance in each system over the whole study period. HS and nHS nominates Tubificidae respectively with and without hair seta. See Table A.1 for bibliographical sources of biological attributes. Life duration: sort, <1 year; long >1 year. Voltinism: univoltin, ≤1 generation/year, multivoltine, >1 generation/year.

Group	Taxon	Estuary				CRT					Size	Respiration	Trophic status	Foraging mode	Life duration	Voltinism	Regeneration potential	Burrowing ability	Swimming ability	Resistance
		W	R	F	%	H	M	L	P	%										
Insects	Bibionidae	X			0.33						Medium	Trachea	Detritivore	Endobenthic	Short	Multivoltine	None	Weak	None	Flood
Insects	Chrysomelidae					X				0.02	Medium	Trachea	Herbivore	Endobenthic	Long	Univoltine	None	Weak	None	Flood
Insects	Curculionidae					X				0.02	Medium	Trachea	Herbivore	Endobenthic	Long	Univoltine	None	Weak	None	Flood
Diplopods	Diplopoda					X				0.34	Large	Trachea	Detritivore	Both	Long	Univoltine	None	Weak	None	None
Insects	Limoniini					X				0.02	Medium	Trachea	Omnivore	Epibenthic	Short	Univoltine	None	Medium	None	None
Gastropods	Radix					X				0.02	Large	Tegument	Herbivore	Epibenthic	Long	Univoltine	None	Weak	Strong	None
Isopods	Trichoniscidae					X				0.32	Medium	Trachea	Detritivore	Both	Long	Multivoltine	None	Weak	None	None
Insects	Carabidae	X			0.06	X				0.06	Large	Trachea	Predator	Both	Long	Univoltine	None	Medium	None	Flood
Insects	Elateridae	X			0.04	X				0.15	Large	Trachea	Herbivore	Both	Long	Univoltine	None	Medium	None	Flood
Insects	Ephydridae	X			0.04	X	X			0.06	Medium	Trachea	Omnivore	Epibenthic	Short	Univoltine	None	Weak	None	Flood
Insects	Tipulidae	X			0.02	X	X			0.15	Large	Trachea	Omnivore	Endobenthic	Long	Univoltine	None	Medium	None	Desiccation
Chilopods	Geophilus					X	X			0.26	Large	Trachea	Predator	Both	Long	Univoltine	None	Weak	None	None
Gastropods	Gyraulus					X		X		0.06	Small	Tegument	Herbivore	Epibenthic	Short	Univoltine	None	Weak	Strong	Desiccation
Annelids	Enchytraeidae	X			1.80	X	X	X		7.00	Medium	Tegument	Detritivore	Both	Long	Multivoltine	None	Strong	None	Flood
Insects	Eriopterini	X			0.27	X	X	X		0.17	Medium	Trachea	Detritivore	Epibenthic	Short	Univoltine	None	Weak	None	None
Annelids	Lumbricidae	X			2.13	X	X	X		3.32	Large	Tegument	Detritivore	Both	Long	Univoltine	None	Strong	None	Flood
Leeches	Erpobdella					X	X	X		0.06	Medium	Tegument	Predator	Epibenthic	Long	Univoltine	None	Weak	Weak	None
Insects	Psychodidae	X			0.02		X	X		0.13	Medium	Trachea	Detritivore	Both	Short	Multivoltine	None	Medium	None	None
Insects	Dolichopodidae	X	X		0.08	X				0.02	Medium	Trachea	Predator	Endobenthic	Long	Univoltine	None	Weak	None	Flood
Insects	Phalacrocera						X			0.02	Medium	Trachea	Detritivore	Epibenthic	Long	Univoltine	None	Weak	None	None
Insects	Staphylinidae						X			0.02	Medium	Trachea	Predator	Epibenthic	Long	Multivoltine	None	Weak	None	Flood
Insects	Rhagionidae	X	X		0.12	X	X	X		0.84	Medium	Trachea	Predator	Both	Short	Univoltine	None	Weak	None	Flood
Gastropods	Galba						X	X		0.36	Medium	Tegument	Detritivore	Epibenthic	Short	Multivoltine	None	Weak	Strong	Desiccation
Insects	Sciomyzidae						X	X		0.13	Medium	Tegument	Predator	Epibenthic	Short	Multivoltine	None	Medium	None	Flood
Insects	Ceratopogoninae					X	X	X	X	2.83	Medium	Gill	Predator	Epibenthic	Short	Multivoltine	None	Weak	None	None
Collembols	Anurida maritima							X		0.02	Small	Plastron	Detritivore	Epibenthic	Short	Univoltine	None	Weak	Weak	Flood
Insects	Tanypodinae						X	X	X	3.81	Small	Tegument	Predator	Endobenthic	Short	Univoltine	None	Medium	None	None
Nematods	Nematoda	X	X	X	1.48			X	X	5.10	Small	Tegument	Omnivore	Both	Short	Univoltine	None	Medium	Weak	None
Gastropods	Physa							X	X	0.04	Medium	Tegument	Detritivore	Epibenthic	Short	Univoltine	None	Weak	Strong	Desiccation
Annelids	Tubificidae HS		X	X	52.85		X	X	X	8.63	Medium	Tegument	Detritivore	Epibenthic	Long	Multivoltine	Fragmentation	Strong	Strong	None
Annelids	Tubificidae nHS		X	X	40.60		X	X	X	60.58	Medium	Tegument	Detritivore	Epibenthic	Long	Multivoltine	Fragmentation	Strong	Strong	None
Annelids	Nais		X	X	0.12						Small	Tegument	Detritivore	Epibenthic	Long	Univoltine	Fragmentation	Strong	Strong	None
Insects	Chironominae								X	4.76	Medium	Tegument	Detritivore	Epibenthic	Short	Multivoltine	None	Medium	None	None
Annelids	Dero								X	0.28	Small	Gill	Detritivore	Epibenthic	Long	Multivoltine	Fragmentation	Strong	None	None
Insects	Micronecta								X	0.32	Small	Plastron	Omnivore	Epibenthic	Short	Multivoltine	None	Weak	Strong	Desiccation
Insects	Sigara								X	0.04	Medium	Plastron	Omnivore	Epibenthic	Short	Multivoltine	None	Weak	Strong	Desiccation
Amphipods	Gammarus			X	0.02						Medium	Gill	Omnivore	Epibenthic	Long	Multivoltine	None	Weak	Strong	None
Annelids	Paranais			X	0.02					0.00	Small	Tegument	Detritivore	Epibenthic	Long	Multivoltine	Fragmentation	Strong	Strong	None

was used to test the null hypothesis according to which individuals of a species are randomly distributed with respect to site characteristics which do not offer optimal living conditions.

Finally, the functional potentials of estuary and CRT were compared by computing functional richness following the framework of Villéger et al. (2008). The main MCA axes were used as synthetic biological descriptors. The numerical analyses were performed using R software (R Development Core Team, 2010); multivariate analyses were run on the "ade4" package available in R.

3. Results

3.1. Sediment characteristics

The PCA on sediment characteristics highlighted two main axes (Fig. 3). Axis 1 displayed a granulometric gradient reflecting the flooding gradient in the estuary, from high marsh (site W) to bare tidal flat (site F). CRT sites were inversely ordinated, from low and mid to high elevations. This divergence between the frequently flooded sites of the two systems was attributable to a coarse substratum (>40% sand) and a lower organic matter content (<80 mg/g dry material) at sites R and F in contrast to the higher silt content in the CRT sites (% silt > 50%). Within the CRT, sites L and M had a finer substratum than sites H and P.

Axis 2 showed clear temporal changes in the CRT sites, mainly driven by increased water content and leading to a softer sediment (decreasing sediment resistance). To a lesser extent, these changes were accompanied by replacing clay with silt, according to flooding frequency (from site H to L; see Fig. 2). Site H experienced a main change the first season (increase in water content), whereas site L seemed to stabilize after one year, reaching the highest silt content (>70%). After three years, sites P and M still had not stabilised (Fig. 3).

3.2. Faunistic description

A total of 38 taxa were encountered over the whole study period (Table 1; Fig. 4) and total taxa richness was higher in the CRT (from 1 to 11 taxa) than in the estuary (from 2 to 5 taxa; Fig. A.1 and Fig. A.2). Site R and F were the most impoverished, with communities dominated by tubificid oligochaetes. Site W, H and P exhibited a more constant taxa richness over the study period and was highest at sites H and P. Taxa richness was the most variable at sites M and L (from 1 to 11), with a clear decrease during the first year in both sites, followed by an increase during the rest of the study period at site L (maximum in summer 2009, the highest over the whole study). Terrestrial taxa mainly composed the communities in sites W, H and M, such as Lumbricidae and Enchytraeidae. Additional taxa such as diplopods, chilopods, isopods, Tipulidae and beetles increased taxa richness at site H; Tipulidae and chilopods (*Geophilus* sp.) were encountered only the first season at site M. Site L was dominated by Lumbricidae and Enchytraeidae the first season, after which these taxa disappeared, replaced by a community dominated by Tubificids and nematodes, but enriched with different Dipteran and gastropod species, particularly in summer 2009. Densities (individuals/m^2) were clearly related to flooding frequency in the estuary, from tens of thousands at sites R and F (slightly lower in site F) to hundreds to thousands ind./m^2 at site W. Similarly, densities exhibited the same order of magnitude from site L to site H. However, from the second summer, higher tubificids densities were encountered at site L than at reference sites R and F. In addition to its lower taxa richness, site M was in contrast with reduced densities never exceeding more than a few thousands ind./m^2. Site P, as with site H, exhibited few changes and its fauna was mainly composed of chironomids and tubificids (several thousands ind./m^2).

3.3. Relationships between environmental properties and taxa biological characteristics

The two relationships were highly significant (**R** *vs.* **L**, $Rv = 0.46$, $p < 0.0001$; and $\mathbf{L}^t$ *vs.* **Q**, $Rv = 0.50$, $p < 0.0001$), hence enabling a RLQ analysis, where the randomization test detected a significant co-inertia between environment and organism biology ($p < 0.0001$). The amounts of projected variance on the RLQ axes are given in

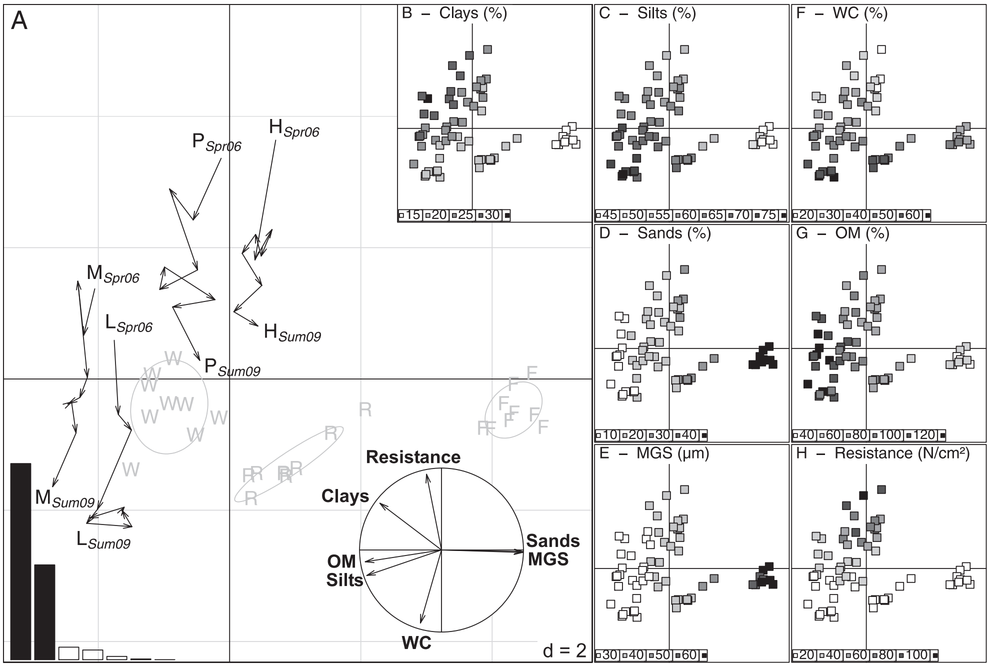

Fig. 3. PCA on sediment descriptors. A) Bottom left corner, eigenvalues diagram: first axis (horizontal), 62%; second axis (vertical), 30%; bottom right corner, correlation circle (OM, organic matter; WC, water content; MGS, mean grain size); grey letters, reference sites; black arrows, CRT sites represented according to their temporal trajectory, from spring 2006 (Spr06) to summer 2009 (Sum09); "d" indicates the grid scale. B – H) values of descriptors for each sample (date-site, grey letters and arrow intersections in A).

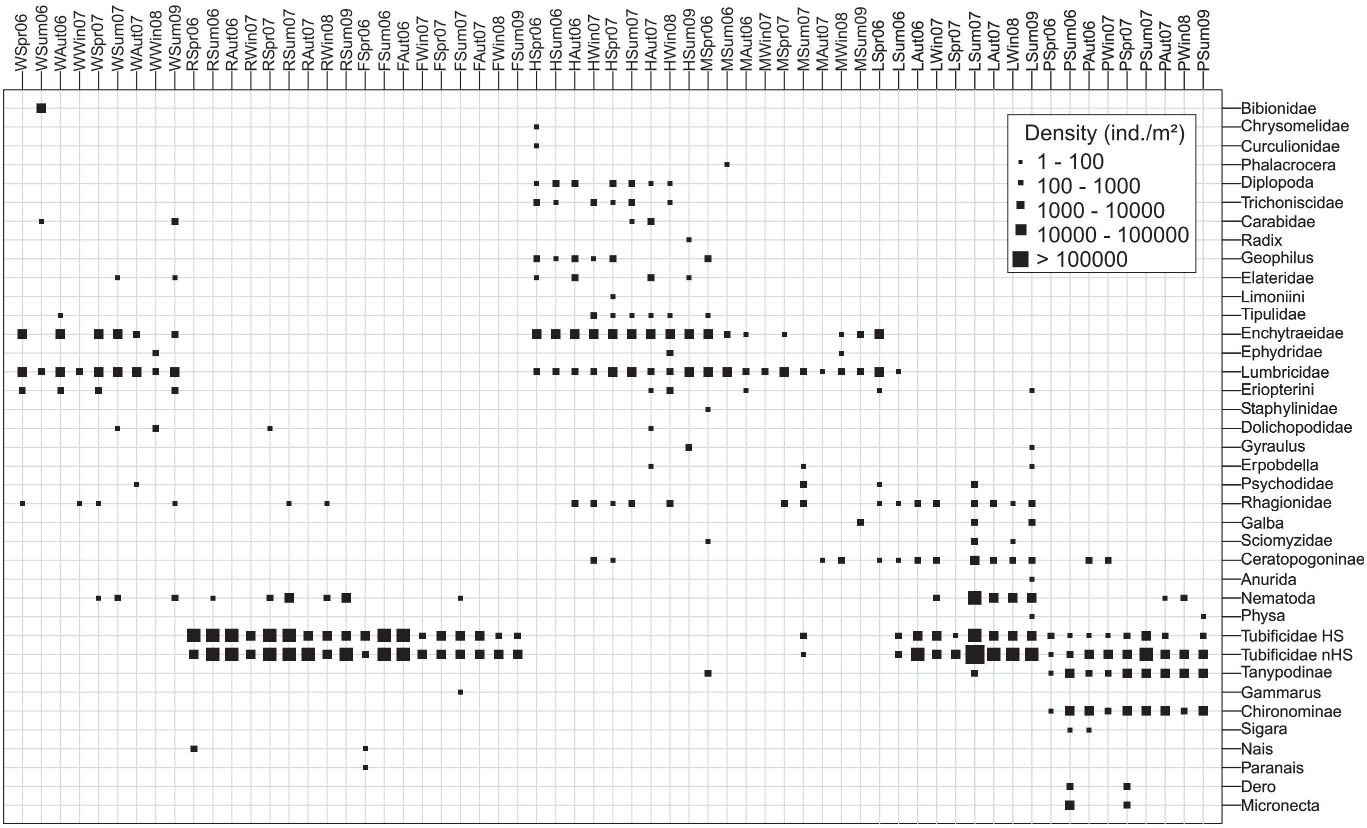

Fig. 4. Taxa densities per site (W to P, see text) over the study period ("Spr06" to "Sum09" for spring 2006 to summer 2009).

Table 2 and Table 3 gives the correlation ratios of the traits on the first RLQ axes. The fourth-corner method highlighted significant relationships between environmental descriptors and most of biological attributes (Table A.1).

Three main axes emerged from the ordination (Fig. 5A and B). The first factorial plane (axes 1 and 2) provided the sedimentary information highlighted in Fig. 3 (see also axis projections on correlation circle in Fig. 5). Additionally, an opposition between flooding frequency and drought along the first axis underlined the elevational gradient common to both systems from high to low sites, with a clear separation of sites R and F from the other sites. The biological responses contributing most were an increased regeneration capability (Fig. 5J), a stronger swimming ability (Fig. 5L), an increased epibenthic foraging mode (Fig. 5G), a rather multivoltine reproduction mode (Fig. 5I), and a form indicating an absence of resistance (Fig. 5M).

To a lesser extent, axis 2 also reflected part of this gradient, mainly in the CRT from high to low elevation (swimming ability and epibenthic foraging mode). In addition, the dominant biological responses were decreasing life duration (Fig. 5H), a switch from herbivory to predation (Fig. 5F), a decreased burrowing ability (Fig. 5K) and body size (Fig. 5D), and a tendency to aquatic respiration and resistance to desiccation (Fig. 5M). However, a granulometric effect at low elevation, show sites R and F in contrast to site L, hence the reverse of the gradient in the estuary. The dominance of tubificids at sites R and F induced characteristic longer lifespan and higher regeneration potential. The specific sandy nature of the substratum at sites R and F was strongly correlated to these organisms (Fig. 5C, right side of the first axis). By contrast, the enriched fauna at site L was characteristic of a muddy substratum (silt rich).

Two observations are apparent from the third axis, along which the ecological variability mainly reflects the CRT samples (Fig. 6). Firstly, it reflects the water permanency of site P, characterized by

Table 2
Summary of the RLQ analysis. Tables R (sediment descriptors; PCA) and Q (biological attributes; MCA): cumulated variance (%) from their respective three first axes onto each of the three RLQ axes. Table L: amount of explained faunistic variance on RLQ axes (% of CA axis variance explained by RLQ axis).

RLQ axes	Axis 1	Axis 2	Axis 3
	Axis 1	Axis 1, 2	Axis 1, 2 and 3
R/RLQ	81.8	91.6	98.7
Q/RLQ	88.2	86.6	77.3
L/RLQ	73.9	47.2	57.8

Table 3
Correlation ratios (CR) of the biological traits on the three first RLQ axes. CR is the proportion of explained variance of the species axis scores (total variance) by a trait (modalities, species groups). *p*-value returns the rejection level of the Fisher's *F* from the ANOVA.

Trait	Axis 1		Axis 2		Axis 3	
	CR	*p*-value	CR	*p*-value	CR	*p*-value
Size	0.319	0.001	0.483	<0.001	0.105	0.144
Respiration	0.392	0.001	0.213	0.041	0.092	0.344
Trophic status	0.306	0.006	0.563	<0.001	0.042	0.690
Foraging mode	0.630	<0.001	0.047	0.428	0.664	<0.001
Life duration	0.109	0.043	0.795	<0.001	0.038	0.242
Voltinism	0.557	<0.001	0.024	0.349	0.003	0.753
Regeneration	0.827	<0.001	0.169	0.010	0.001	0.875
Burrowing ability	0.371	<0.001	0.486	<0.001	0.210	0.016
Swimming ability	0.799	<0.001	0.314	0.001	0.084	0.215
Resistance	0.432	<0.001	0.080	0.231	0.224	0.012

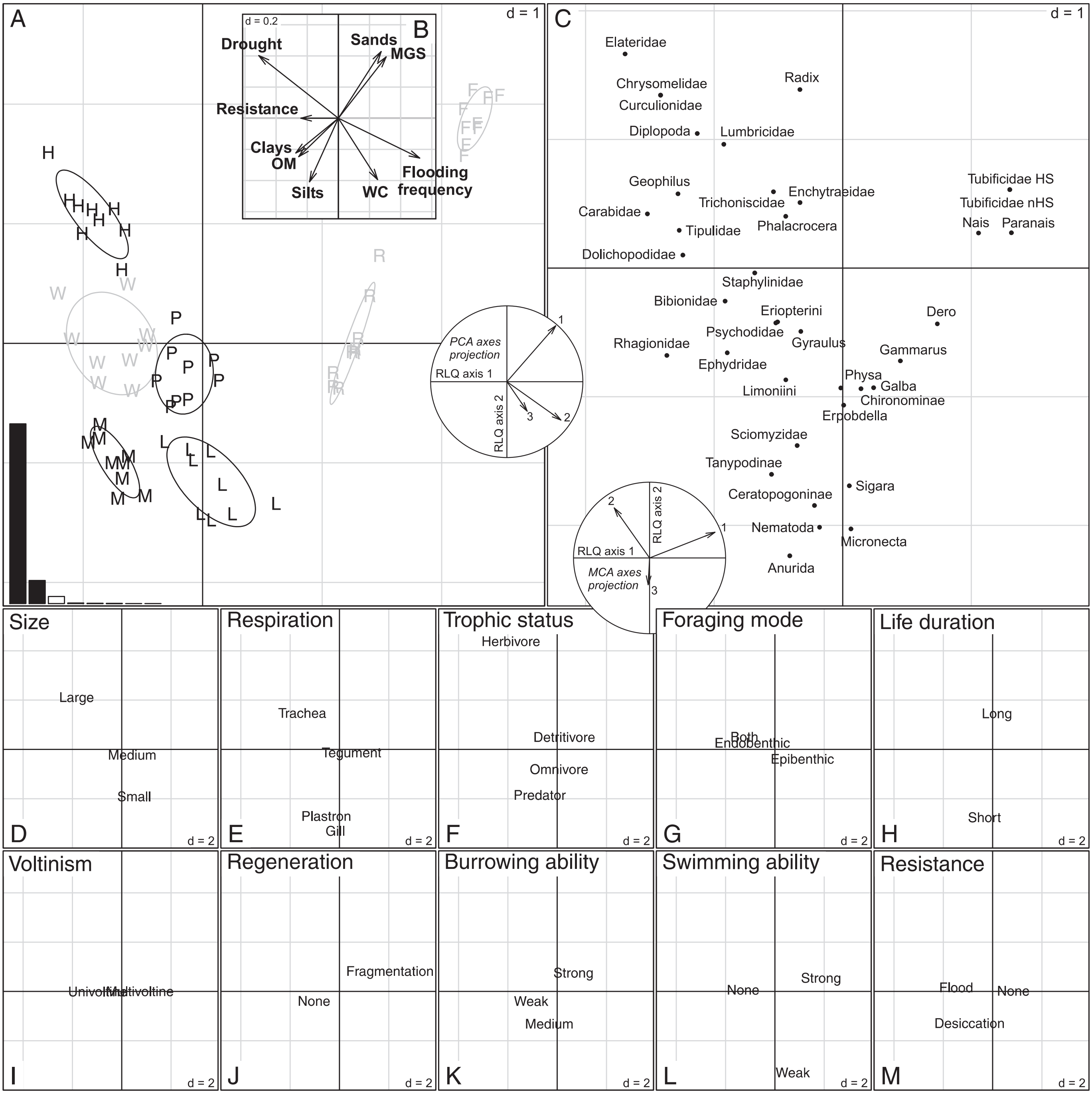

Fig. 5. RLQ analysis. A) Samples (grey and black letters) grouped per site and eigenvalues diagram; first axis (horizontal), 85%; second axis (vertical), 11%. B) Environmental descriptors. C) Positions of taxa. Correlation circles display the projections of the three first axes of the separate analyses on the RLQ axes. D-M) positions of biological attributes. "d" indicates the grid scale.

a resistance to desiccation (*Sigara* sp. and *Micronecta* sp.), in contrast to the intertidal sites. Secondly, within each site of the CRT, the third axis shows a temporal change characterized by increases in sediment silt and water content. The main detectable biological responses were a decrease in endobenthic foraging mode and a shift from medium to weak and strong burrowing ability, respectively for most of the colonizers and tubificids (Table 1). In addition to the rapid settlement of tubificids (epibenthic foraging mode, strong burrowing ability) since the second season (site L), the biological changes were particularly attributable to gastropods (epibenthic foraging mode, weak burrowing ability) over the whole flooding gradient (*Radix* sp. and *Gyraulus* sp. at site H; *Gyraulus* sp., *Galba* sp. and *Physa* sp. at sites M, L and P), mainly observed the last season (Fig. 4). However, only a part of MCA axes 2 and 3 was projected on to the third RLQ axis (Fig. 6; correlation circle), which accounted for environmental change with regard to the amount of projected PCA inertia.

In general, the rapid CRT community changes led to a more stable functional richness, higher than in the estuary (Fig. 7). Based on the purely intertidal part of the CRT (without site P), values increased through time and were higher after one year.

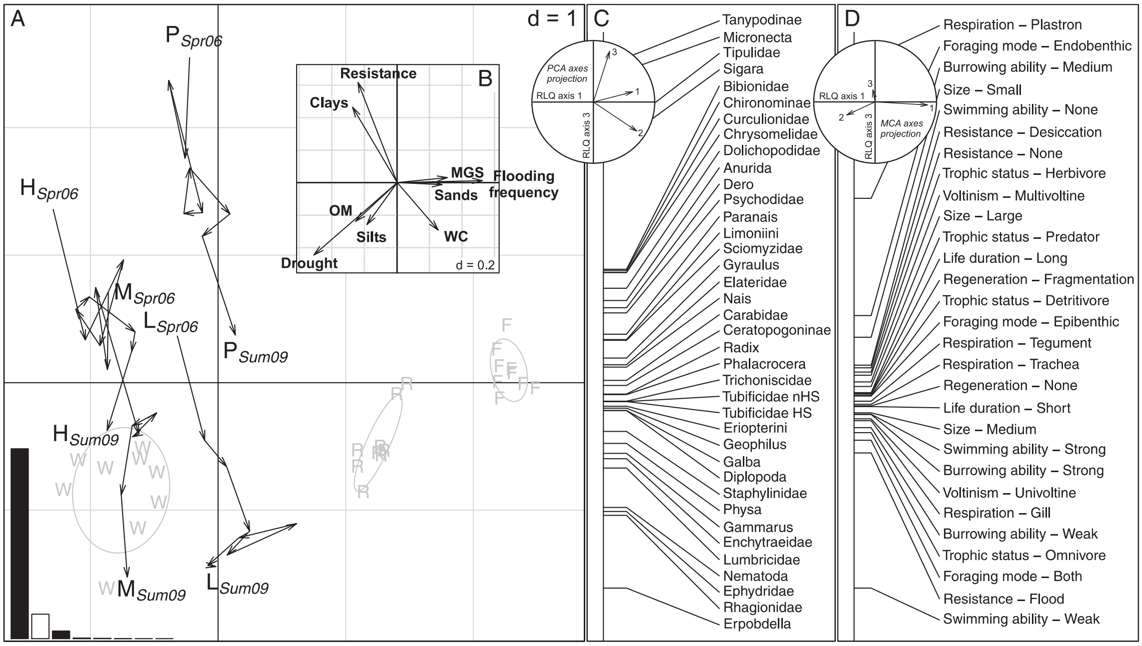

Fig. 6. RLQ analysis, axes 1 (horizontal) and 3 (vertical, 3.4%). A) Samples grouped per site (grey letters and arrow intersections); in grey, reference sites; in black, CRT sites represented according to their temporal trajectory, from spring 2006 (Spr06) to summer 2009 (Sum09). B) Environmental descriptors. C) Taxa's positions along the third axis. D) Biological attributes positions along the third axis. Correlations circles, axes projections of the separate analyses on RLQ axes. "d" indicates the grid scale.

4. Discussion

4.1. Potential methodological drawbacks

Given the variable nature of sediments among the sites, the sampling strategy might have been unsuitable for some faunistic groups. Although the core sampler diameter reflected that used in terrestrial arthropod studies, the presence or density of some groups such as terrestrial arthropods at high elevation (sites W and H) might have been underestimated; an additional method such as pitfall traps could have allowed us to detect the presence of other taxa at the adult stage (e.g. adult Coleoptera). However, core sampling was preferred in order to standardize the procedure and is shown to be more accurate than trapping for estimating a population (Briggs, 1961).

Despite the initial CRT communities (from site H to site L) being slightly different, both were mainly composed of terrestrial worms. The slight faunistic dissimilarity at site L (sampled in April) was probably attributable to a rapid flooding effect after only one and half months of strong tidal influence (implemented on March 1st, 2006), removing most air-breathing (tracheal) organisms still occurring at site H and M.

Depending on the flooding frequency, faunal changes were either slightly perceptible (site H) or immediate (site L) in contrast to sediment characteristics which continuously changed during the first three years (unpubl. results). The lack of agreement between environment and biological attributes on the third axis of the RLQ analysis may be attributable to a different vertical stratification between sediment characteristics and the fauna. Whereas most sediment descriptors showed stratification through the whole 15 cm core depth, the main part of the fauna was mainly distributed in the top 10 cm (0–5 cm: 75% of individuals; 5–10 cm: 20%; 10–15 cm: 5%). Thus, for a sediment descriptor, an average value representing the whole 15 cm may not necessarily represent the specific environmental requirements of the fauna. Given the migratory nature of some taxa such as Tubificidae, which actively forage in the top sediment at high tide and migrate downwards at low tide, no stratification was considered in this study.

The strong relationship between environmental and faunistic characteristics according to the co-inertia analysis supports the robustness of the adopted sampling strategy in comparing

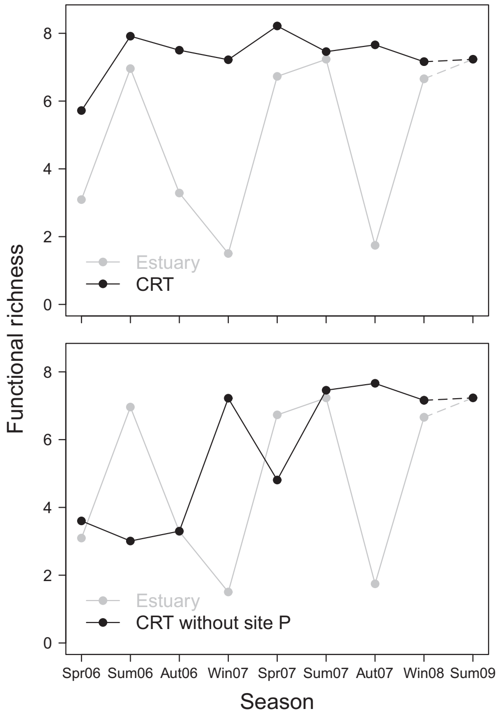

Fig. 7. Functional richness (adimentional) over time, from spring 2006 ("Spr06") to summer 2009 ("Sum09").

reference and CRT sites. Moreover, the fourth-corner analysis confirmed the spatio-temporal specificity of organism biology.

4.2. General faunistic considerations

The most frequently flooded tidal freshwater habitats exhibit impoverished communities highly dominated by collector/detritivorous organisms as generally encountered in lowland temperate rivers (Vannote et al., 1980). In both estuary and CRT, most of taxa are known to occur in other European tidal marshes (Rundle et al., 1998; Desender and Maelfait, 1999; Baldwin et al., 2009). In the CRT, at low elevation where the greatest changes occurred, the settled aquatic taxa are generally encountered in non-impacted tidal freshwater marshes (La Salle and Bishop, 1987; Baldwin et al., 2009; Johnson, 2010).

4.3. Common reference community state

Compared to the few observations in the freshwater part of the estuary (Ysebaert et al., 1993, 1998; Seys et al., 1999; Hampel et al., 2009), no notable difference appeared in the composition of the macroinvertebrate communities occurring on the tidal flat and reed bed (sites F and R). These communities were still dominated by Tubificidae, and, to a lesser extent, Nematoda. Naididae were also found but in a restricted abundance. At the scale of the whole estuary, this low taxa richness has been mainly attributed to pollutants, shear stress and also hypoxia (Ysebaert et al., 1998).

Although heavy metals are not the only potentially influencing pollutants, metal contamination has nevertheless been shown to strongly influence invertebrate community structure in different ecosystems (Gibert et al., 1995; Grumiaux et al., 1998; Courtney and Clements, 2002; Loayza-Muro et al., 2010). A related study on sediment heavy metals in the CRT and the same reference sites highlighted higher concentrations in the CRT (Teuchies et al., 2012), and concentrations in both CRT and reference sites exceeded contamination thresholds by several times (Grumiaux et al., 1998). Although all concentrations exhibited a decrease over the three-year period, they never reach concentrations lower than those encountered in the reference sites. Furthermore, sediment redox measurements (unpubl. obs. for April 2011) indicated that reference sites did not exhibit values lower than those measured in the CRT sites. From the top sediment to 10 cm deep, values ranged between −180 mV and −220 mV at sites R, F, M and L; values were higher at the less frequently flooded sites W and H. Hence, these complementary observations support conclusion that physical conditions such as shear stress explain the faunistic impoverishment in reference sites compared to CRT sites. The granulometric characteristics and organic matter concentration clearly underline the different physical conditions between the lowest estuary and CRT sites. In the estuary, the water current velocity can reach 1 m s^{-1} whereas they never exceed a few cm s^{-1} on the CRT flats (Beauchard et al., 2011). Such conditions may have large-scale consequences with regard to food quantity and quality for the benthos at the sediment surface, as already shown under high water velocity on intertidal flats (Bock and Miller, 1995).

Regeneration by fragmentation (asexual reproduction) was the most characteristic biological attribute at sites R and F, where aquatic oligochaetes could maintain viable populations under a high shear stress. Associated to longevity and absence of resistance form, this supports a process of *A*-strategy selection *sensu* Greenslade (1983), induced by the highly predictable adverse conditions in these habitats between tides. The implication of these adverse physical conditions is also supported by the reduced abundances at site F which was more exposed to tidal energy (Fig. A.2). As suggested by Seys et al. (1999), this reduction can be attributed to a limitation of organic matter concentration which was the lowest in this site, but also to grain size (highest here) limiting sediment consumption by Tubificidae. These observations agree with Mellado Diàz et al. (2008) who observed an adverse anthropogenic gradient on stream invertebrate communities, here represented by a coastal squeeze-induced shear stress.

The transition to a more terrestrial community at the upper end of the flooding gradient (site W) is marked by a strong faunal dissimilarity where only three taxa (two Diptera and Nematoda), in low density, were common to sites R or F. This disruption of the gradient parallels the habitat morphology as marshes typically exhibit a steep transverse profile where erosion sheers form. This depletes intermediate habitats (Beauchard et al., 2011) and the associated fauna.

4.4. Functional change in CRT communities

In the CRT, few changes were observed at high elevation (site H) where the remnant community was mainly terrestrial. During at least the two first years, it did not seem to be stressed by the imposed flooding regime or disturbed by the few winter storm tides where inundation was prolonged (Beauchard et al., 2011). Indeed, most organisms occurring there (i.e. earthworms, potworms, myriapods, isopods, beetles) display various physiological adaptations, and can overcome the lack of oxygen under water up to several days (Hoback and Stanley, 2001; Schmitz and Harrison, 2004; Plum, 2005; Plum and Filser, 2005). These taxa are typical of high marshes in the tidal freshwater zones of the North Sea coast estuaries (Barendregt, 2005). However, some regularly encountered taxa such as Diplopoda, Trichoniscidae and *Geophilus* sp. were not encountered the fourth year (summer 2009; Fig. 4) whereas gastropods appeared. This might indicate a slight environmentally-induced switch in community composition, as from spring 2006 to spring 2009, the water content increased from 15% to 38% in the top sediment and from 12% to 23% in the bottom sediment (unpubl. obs.).

At mid elevation (site M), the decrease in organism densities and taxa richness was marked by the early removal of organisms with tracheal respiration. Only organisms with tegumentary respiration survived (Lumbricidae and Enchytraeidae) or replaced the extirpated fauna (Diptera, gastropods). This corresponds to Barendregt (2005) who investigated a tidal freshwater marsh in the Rhine River, and who observed minimum above-ground species richness near the mean high water level where only gastropods survived. This agrees with the present study showing the settlement of the gastropods *Galba* sp. and *Physa* sp., observed during the last summer. From non- to more frequently flooded zones, these taxa indicate a functional shift from a tracheal and herbivorous living mode towards a more amphibious one, characterized by tegumentary respiration and detritivory. Indeed, the high plant productivity in site M (unpbl. obs.) was accompanied by much decaying organic matter.

At low elevation (site L), changes created by the high flooding frequency were rapid and gave rise to strong functional traits. The trophic functioning was increased by the settlement of detritivores and small predators. At a comparable flooding frequency to those at sites R and F, this confirms the environmental unsuitability of current estuarine tidal flats in sustaining a richer ecological functioning; the exerted shear stress prevents optimal living conditions for a richer fauna, where communities cannot evolve towards a climax stage.

The tidal pool (site P), characterized by permanent water, reacted as a freshwater reference site by attracting typical freshwater taxa. The subtidal nature of this habitat did not create an excess to the CRT intertidal fauna since only four taxa were specific to site P and six other were found elsewhere, indicating a benthic tolerance for intermittent emersion. The presence of *Dero* sp. (Naididae), recorded for the first time in the Schelde estuary, shows that propagules occur in the estuary since this genus does not exhibit any aerial stage or capability facilitating settlement from nearby water bodies (unlike e.g. Chironomidae, Corixidae). This underlines the upstream origin of the main part of the fauna in intertidal freshwater habitats (Remane, 1958), and the absence of *Dero* sp. in intermittently flooded sites confirms the environmental selection as the result of branchial respiration.

Most additional taxa were insects which were almost absent at sites R and F (where only 3 individuals were found over the study period). Their absences at sites R and F can be attributed to the adverse conditions indicated above. This is supported by Diaz (1994) who observed that insects were the most sensitive organisms to recover from sediment disturbance in the tidal freshwater James River (USA). Other epibenthic taxa such as leeches and gastropods (especially during the last summer) colonized the new estuarine substratum of the CRT whereas they were absent at the reference sites. Hence, although additional detritivores settled at low elevation, other taxa take advantage of the soft CRT hydrology and so diversify the trophic structure.

Tidal freshwater habitats are detritus-based systems (Odum, 1988; Findlay et al., 1990) and, as with many aquatic systems, they receive more allochthonous detritus than their terrestrial counterparts (Shurin et al., 2006). This explains the strong detritivorous nature of the fauna at low elevation, in contrast to high elevation where organisms were predominantly herbivorous. The association of foraging mode points to the resource origin. Whereas the terrestrial fauna exhibited foraging capabilities from the top to the bottom sediment (e.g. Lumbricidae, Elateridae), the foraging mode at low elevation was rather epibenthic where organisms are recognized as feeding on freshly deposited sediments. However, a possible oxygen limitation cannot be excluded to explain this epibenthic preference.

In addition to the obvious shift to aquatic characteristics such as respiration (tegument and gill) and swimming ability, the main changes in organism biological properties at low CRT elevation were driven by the biological properties inherent to tubificids, which are dominantly encountered at low elevation in the estuary. However, other properties much more characteristic of the low CRT's elevation emerged – such as small size, short life duration, omnivory and predation – due to increased taxa and the consequent increase in functional richness. The increased number of small taxa might reflect a consequence of the less energetic CRT hydrology allowing establishment of organisms unable to resist to the hydrological stress exerted on the estuarine flat. Associated to trophic diversification, this also suggests development of other trophic pathways and an increased food web stability (Gross et al., 2009). In addition, the shift to an epibenthic foraging mode at low CRT elevation corroborates previous observations on bioturbation along the CRT flooding gradient (Beauchard et al., in press), where sediment mixing modes were found to be elevation-specific, especially at low elevation marked by a strong surface sediment activity.

4.5. Tidal freshwater habitats as a life history interface?

In both the estuary and CRT, from high to low elevation, the flooding frequency clearly encourages distinct living modes, from terrestrial to aquatic. Along this gradient, growth rate appears to be the dominant biological tendency where small size, short lifespan and multivoltinism emerge from a forced hydrological regime. Moreover, a clear seasonality characterized the population turnover in frequently flooded sites in contrast to non-frequently flooded ones (Fig. A.2, density). Despite the fact that differences between terrestrial and aquatic functioning are still debated (Chase, 2000), these results agree with current considerations since, in aquatic environment, reduced organism size and faster growth are recognized and attributed to a faster rate in replacing organism tissues by reducing carbon storage (Sabo et al., 2002; Shurin et al., 2006).

These functional features coincide with an *r*/*K*-selection trade-off (MacArthur and Wilson, 1967), now termed a 'fast–slow' continuum (Bielby et al., 2007). Early studies predicted that habitat spatio-temporal heterogeneity would condition organism life history strategies (Southwood, 1977, 1988; Greenslade, 1983). Large size, long generation time and long lifespan (*K*-selection), such as observed at high elevation, are typical traits predicted to occur in a spatio-temporally stable environment. In contrast, small size, short lifespan and multivoltinism, as observed at site L, are representative of an *r*-selection expected at high temporal heterogeneity (i.e. disturbed regime, unpredictable severe events). As indicated here, the shear stress exerted at sites R and F sediments appears to select an *A*-strategy, generally encountered at low temporal heterogeneity in continuously harsh environments (Greenslade, 1983). Indeed, along the flooding gradient, the temporal predictability of most of hydrological descriptors decreased with increasing flooding frequency (Beauchard et al., 2011).

Most of the fauna at site L is commonly found in temperate lowland streams and related floodplains of Western Europe (Tachet et al., 2000) where hydrological disturbances, such as floods and droughts, commonly occur. However, in the CRT, as in the estuary, the hydrological pattern was shown to be more stable at low elevation (Beauchard et al., 2011), thus invalidating the hypothesis according to which the flooding gradient generates an *r*/*K*-selection continuum. Other environmental factors, such as variability of sediment characteristics, may exert a greater influence. As shown on Fig. 3, this does not seem likely as the site L trajectory, which stabilized after one year of change, clearly points to a higher sediment homogeneity during the five following seasons. Another hypothesis could explain this theoretical mismatch. Aquatic and terrestrial habitats in ecotones such as wetlands and riparian systems undergo different disturbance regimes (Zaimes et al., 2010). Hence, the extremities of the intertidal gradient might be endpoints of converging gradients from terrestrial and aquatic systems, and possibly marked by a different magnitude of spatio-temporal heterogeneity.

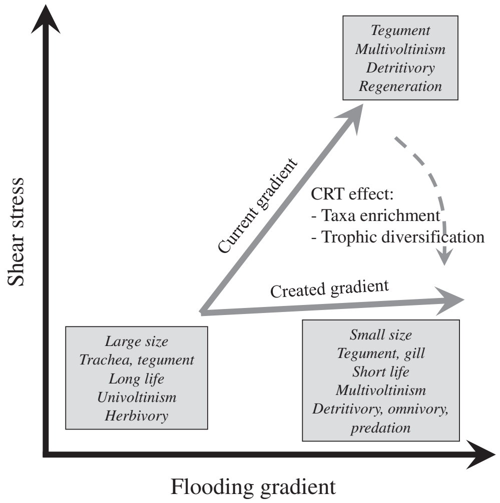

Fig. 8. Conceptual schema synthesizing the main functional changes operated by CRT.

5. Conclusions

Sediment macroinvertebrate communities in tidal freshwater habitats are significantly structured according to their biological properties. The effect of a physical impact on the communities from the deteriorated reference was clearly supported, and in comparison the CRT system successfully gave rise to functionally richer aquatic communities, closer to that expected from a natural marsh. On an applied point of view, depending on restoration objectives, this study supports the functionality of the CRT system previously hypothesized (Maris et al., 2007). Hence, restoration goals can be fulfilled by the hydrological flexibility of the system which allows an adapted ecological functioning (Beauchard et al., 2011). On a fundamental point of view, further long-term research should be encouraged since typical characteristics of intertidal freshwater habitats offer complementary insights on life history strategies, a topic less studied in recent years. Despite the lack of clear theoretical outcomes along the flooding gradient, this study nevertheless demonstrates that life history strategies are influenced through ecological management (Fig. 8). Whereas the elevation is linked to shear stress, this disappears after CRT implementation whereby the flooding frequency regulates community functioning.

Since several hundreds hectares of CRT are being constructed along the Schelde estuary, benthic community development in them may have a significant influence on the ecology of the whole estuary, not only on biogeochemistry, but also on higher trophic levels such as fishes and birds. Indeed, Van Liefferinge et al. (2012) showed that invertebrates provided a diet of a higher caloric value than those in the adjacent estuary. Additionally, a bird survey (unpubl. obs.) revealed that wetland invertebrate feeding birds represented >45% of an avifauna recognized of international importance in the Schelde estuary.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2013.01.013.

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