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Tidal freshwater habitat restoration through controlled reduced tide system: a multi-level assessment

Herstel van getijhabitat in de zoetwaterzone door middel van gecontroleerd gereduceerd getij: een evaluatie op meerdere niveaus

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AVANT-PROPOS

Ce travail fut réalisé au sein du groupe de recherche « Gestion des écosystèmes » (ECOBE) de l'université d'Anvers. Il a bénéficié du soutien de ladite université et de l'administration flamande « Voies d'eau et affaires maritimes » dans le cadre du programme de recherche sur les effets environnementaux du plan SIGMA (OMES) appliqué à l'estuaire de l'Escaut. Ce large programme offre de remarquables opportunités en couvrant les champs de recherche aussi bien fondamentale qu'appliquée au sein d'une problématique environnementale de portée internationale. C'est dans ce contexte que ce travail se concentre sur la restauration des habitats estuairiens.

Je dois mes premiers pas en recherche au très regretté Réjean Fortin de l'Université du Québec à Montréal ; je ne l'oublierai jamais. Quelques années plus tard, j'ai rencontré sa « doublure belge », Patrick Meire, avec qui il aurait bien passé d'interminables moments à converser de cadre environnemental et société. Malgré son emploi du temps de ministre, qui cependant ne connaît pas la crise de la créativité, j'ai bien apprécié le soutien de Patrick et de multiples moments avec ce dernier. On pourrait énumérer les discussions plus ou moins centrées sur l'écologie, très riches, fondamentales ou autres, je n'oublierai pas son plus seyant commentaire quand il s'agit d'application environnementale, voir de désarroi… Nous étions en train « d'ausculter » notre terrain un dimanche de printemps, et en contemplant une surface naturellement végétée et richement colorée, il dit : « comment allons nous faire comprendre aux gens qu'un vrai jardin, c'est ça !! ». Les consciences ne se gèrent pas comme un écosystème; simplement, attendons, ils viendront, et ils verront.

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CONTENTS

CHAPTER 4

SEDIMENT MACROINVERTEBRATE COMMUNITY FUNCTIONING
IN IMPACTED AND NEWLY-CREATED TIDAL FRESHWATER HABITATS

CHAPTER 5

SPATIOTEMPORAL BIOTURBATION PATTERNS
IN A TIDAL FRESHWATER MARSH

CHAPTER 1

INTRODUCTION

ESTUARIES

Estuaries are transitional zones between continental and marine ecosystems. They exhibit a complex ecological functioning regulated by the concomitant influence of river inputs and the tidal regime imposed by coastal water bodies. For that reason, estuaries experience strong spatiotemporal variations blurring the limits of these ecosystems, unlike more discernible ecosystems such as lakes or forests (Elliott and McLusky 2002). Although landward salt intrusion has been a prominent criterion to delimit an estuary for a long time (Pritchard 1967), other parameters are now recognized to be strongly characteristic along multiple gradients (McLusky 1993). The pulsing tidal regime, daily exposing the sediments to the air, is the most characteristic estuarine feature never encountered in other ecosystems (Odum et al. 1995). It conditions the nature of the living forms from the intertidal zone, periodically flooded, to the subtidal one, permanently submerged. Hence, the pulsing tidal regime, exposing daily the sediments to the air, is the most characteristic estuarine feature never encountered in other ecosystems (Odum et al. 1995).

Under continuous fluxes of inputs from the whole river catchment, estuaries accumulate large amounts of organic matter and nutrients. These substances reside in the estuary for a variable time, depending on the longitudinal oscillations of water volumes induced by the complex interactions between the tides and the freshwater discharges. This results in physical and chemical reactions between water and sediments, whereby suspended matter and nutrients are sequestrated and/or recycled (Middelburg and Herman 2007). As a consequence, estuaries are biogeochemical transformers which strongly alter the properties of water before it reaches the marine environment and significantly contribute to coastal water qualities (Billen et al. 1991; Jickells 1998; Billen et al. 2005).

Such fundamental properties engender a high biological productivity in estuaries. Despite the fact that the production is operated by a relatively lower number of species when compared to other highly productive ecosystems, estuaries exhibit complex food-webs based on phytoplankton. From water to air-breathing organisms as well as from micro-organisms to top predators, different functional groups across multiple trophic guilds can occupy a same intertidal habitat over a single tide.

These ecological components are subject to different temporal variations. The combined effects of tide-driven erosion and sedimentation determine habitat morphology, particularly habitat succession on the long term, giving rise to flooding frequency-specific biota (Baldwin et al. 2009). This organization is regulated by hydrological forces which shape estuarine river bed and shores. Within an entire estuary, the spatiotemporal variability of such forces maintains a mosaic of geomorphologic structures and characteristic biota. This environmental diversity exhibits different nutrient transfer and cycling, and provides refuge, foraging, reproduction and nursery grounds to different kind of resident and migratory organisms across seasons.

TIDAL FRESHWATER ZONES

Situated at the upstream part of estuaries, the tidal freshwater section is conventionally considered as a very low salinity zone never exceeding 0.5 psu (salt concentration approximating 0.5 g.L^{-1}; Fig. 1). Much less studied than their brackish counterparts, tidal freshwater zones have been neglected for a long time in the bulk of estuarine research, mainly because marine ecologists
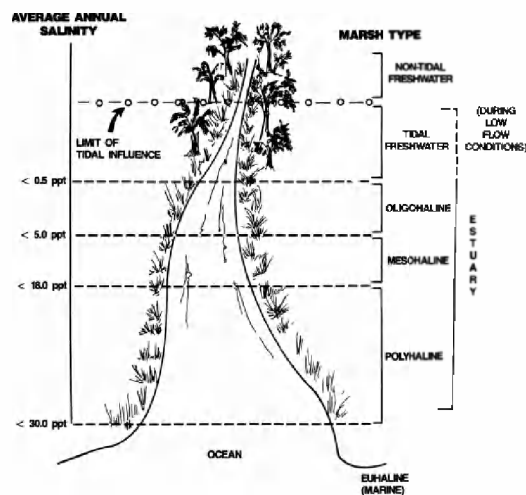

Fig. 1. Longitudinal zonation along an estuary; from Odum et al. (1988).

exclude freshwaters from their studies and stream ecologists consider tidal zones beyond their research scope due to the estuarine aspect (Barendregt et al. 2006). The geographic extent of such environments also explains this lack of interest. They have been considered as rare ecosystems as regards to their a priori limited spatial extent (Reinicke 2000). In spite of the absence of global inventory, they nevertheless are known to occur in estuaries from most of the largest river drainages (Baldwin et al. 2009). Given the importance of ecological processes that this suggests, much more attention should be given to tidal freshwater ecology. Indeed, biogeochemical research has been neglected since a Web of Science search from 1980 to 2008 shows that less than 5 % of all tidal wetland literature concerns tidal freshwater wetlands, whereas these latter can represent 20 % of the estuary surface area (Megonigal and Neubauer 2009).

Morris et al. (1978) highlighted their prominent physicochemical role in estuaries, particularly at the freshwater-saltwater interface where the salinity does not exceed a few tenths of units. There, water turbidity strongly increases as a consequent of organic matter accumulation. The upstream allochthonous organic matter is very labile since it is mainly composed of undegraded dying freshwater algae and bacteria (Soetaert et al. 1994; Soetaert and Herman 1995). A steep salinity change at the freshwater-saltwater interface generally prevents spontaneous water mixing, resulting in an intense bacterial activity which engenders a sharp downstream drop in oxygen concentration. As regard to this process, tidal freshwater zones undeniably constitute an essential component within the ecocline that an estuary represents between continental and marine ecosystems (Schuchardt et al. 1993).

Tidal freshwater wetlands have been most inventoried and described in United-States, particularly along the East coast where they encompass more than 500 000 ha (Simpson et al. 1983). During the last two decades, they have been subject to more attention, particularly along the North Sea coast where the largest tidal freshwater systems occur in Europe. Tidal freshwater habitats occur under diverse forms such as tidal flats, forested or herbaceous swamps and marshes (Leck et al. 2009; Struyf et al. 2009). Most of the time, intertidal freshwater habitats are organized along progressive continuums, from pioneer stages consisting in mudflats and helophytes, to climax dominated by forested assemblages. These successions are conditioned by accretion over decades and the consequent elevation determines the flooding frequency (Fig. 2). They are drained by creek networks of which the density depends on the local hydrological dynamics and where permanent pools occasionally form.
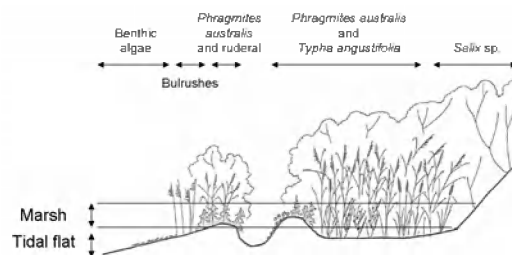
Fig. 2. General aspect of an intertidal freshwater habitat gradient. From Van Allemeersch et al. (2000).

Odum (1988) realized the first review on the comparative ecology of tidal freshwater and salt marshes. Although most of organic matter mineralization in estuaries occurs anaerobically in both wetland types, methanogenesis predominates in tidal freshwater whereas sulphur reduction is more characteristic of salt marshes. Besides, salinity stress was argued to be the main feature accounting for the difference between ecological processes in the two wetland types. Compared to tidal salt marshes, the reduced stress in tidal freshwater wetlands promotes plant species richness, decomposition rates and net primary production of vascular plants, and ultimately organic matter accumulation, as confirmed by several studies (Doumlele 1981; Więski et al. 2010). By contrast, animal communities show different patterns. Although intertidal freshwater zones exhibit higher invertebrate species richness than mesohaline zones due to a reduced salinity stress (Remane 1934; Attrill 2002), species richness remain lower than in adjacent non-tidal freshwater zones (Swarth and Kiviat 2009; Barendregt et al. 2009). This was partly attributed to the ephemeral nature of estuaries which experience a long term disturbance regime maintained by the successive Pleistocene glaciations (Remane 1958). This instability was hypothesized to prevent a specific adaptation to the tidal regime, as supported by the quasi absence of tidal-specific and endemic species (Wolff 1973). On the contrary, tidal freshwater wetlands display a higher diversity in more mobile faunistic groups such as fishes, terrestrial insects, reptiles, mammals and especially birds (Barendregt et al. 2009).

HUMAN PRESSURES
AND RESTORATION ECOLOGY
IN ESTUARIES

In Western Europe, humans are known to have settled and used natural resources in estuarine areas at the latest during the Neolithic (Baldwin et al. 2009). These areas were propitious to hunting and fishing, and later to agriculture after drying marshes which offered highly fertile grounds. The civilization led to trade and exchanges through water bodies where ports provided access from the sea to rivers. This resulted in an expansion of cities and port facilities, and concomitant land reclamation along estuaries. Reclamation consists in enclosing an intertidal area by dikes; such a construction, lying below the mean high water level, is commonly called "polder". Since the beginning of the first millennium, 15 000 km² of marshes have been polderized in Europe (Goeldner-Gianella 2007). Although land reclamation for agriculture and residential extension stopped during the twentieth century, coastal landscapes have been profoundly modified since. The intensification of economic exchanges engenders a still growing industrialization and denaturation of estuaries. Additionally to land reclamation for industry, navigation and flood protection have required estuarine channel deepening and dike reinforcement. This results in narrowing and deepening of the estuarine corridor within which the floodwater volume, called tidal prism, engenders an increased tidal energy. Nowadays, this funnel effect is exacerbated by see level rise consequent from climate changes giving rise to further coastal squeeze (Pethick 1993; Doody 2004): rising seas narrow shorelines and increase pressures in areas where sea walls protect agricultural and residential areas.

Strong alterations of estuarine ecosystems arise from such pressures and dramatic consequences from a human perspective. Indeed, more than one third of the world's human population resides on the world's coasts, which account for only 4 % of the land surface (United Nations Environment Programme, 2006) since coastal ecosystems provide more services to human populations than any other environment (Costanza et al. 1997). In the most anthropized estuaries, human impacts have depleted a large part of formerly important species and have directly and indirectly degraded water quality by release of agricultural and industrial toxicants (Lotze et al. 2006). Whereas these estuaries used to provide a wide panel of essential resources such as food even a century ago, they became the theatre of an unsustainable economy pervasively globalized (Vitousek et al. 1997), where physical and chemical impacts prevent to benefit from natural estuarine potentials.

Facing an increasing cost of these adverse pressures, irreplaceable services remain present in estuaries (Barbier et al. 2011). By reworking and recycling the large amounts of sediments and associated nutrients from riverine inputs, a natural estuarine functioning ensures one of the most valuable services to human populations occupying coastal areas. Estuaries regulate excess nitrogen and phosphorus and buffer their pervasive effects such as toxic algal blooms and eutrophication (Jickells 1998). The quality of released waters to coastal seas conditions productivity and sustainability of fisheries and associated economical activities in marine environments. In this context, restoring and preserving estuarine environments is especially justified since concentrations of major nutrients such as nitrogen and phosphorus have been doubled by human activities. Physically, a preserved estuarine morphology and habitats ensures storage capacity, reduces wave energy and mitigates storm surges (Townend and Pethick 2002), as particularly evidenced after recent human disasters in coastal zones (King and Lester 1995; Adger et al. 2005; Danielsen et al. 2005). More widely, estuarine habitats offer resources to numerous plant and animal species which stabilize and regulate material fluxes, contribute to water purification, and among which many exhibit economic or conservation value. Therefore, estuaries are particularly important for integrating sound ecological management with sustainable economics (Meire et al. 1995). In recent years, different studies provided baselines on the extent of historical degradation and vision for regenerating essential functions of estuaries with regard to international preoccupations and directives which emerged at the end of the twentieth century (Neckles et al. 2002; Cooper et al. 2004; Lotze et al. 2006; Gedan et al. 2009; Barbier et al. 2011).

THE SCHELDE ESTUARY

In northwestern Europe, the Schelde estuary is one of the largest riverine openings on the North Sea coast. At the continental scale, despite a small river catchment of 21 863 km², the estuary extends on a relatively large surface area of 3 872 km² stretched along 235 km of the main river and its tributaries, encompassing 44 km² of tidal freshwater surface. Combined with a macrotidal regime, this induces a long residence time ranging

from 2 to 3 months (Soetaert and Herman 1995). The estuary is particularly characterized by the length of the tidal wave which propagates over 160 km of the main river which runs along 335 km from France to The Netherlands where its average discharge is about 120 $m^3.s^{-1}$ (Meire et al. 2005). Situated in a temperate zone, it is a rain-fed system.

The Schelde estuary was 2000 years ago a part of the Helinium, a large estuarine delta where intersected the Schelde, Maas and Rhine rivers. Over the centuries, the morphology of the area has been progressively modified by storm surges, giving rise to three distinct estuaries. Since the 13th century, the morphology of the Schelde estuary has been continuously reshaped by about 30 storm surges (Coen 2008). Ten centuries ago, the tidal amplitude in the oligohaline zone did not exceed a half meter. The progressive isolation of the estuary induced by storm disturbances conducted to a 4 m rise and a concomitant upstream extension of the tidal zone. Although these changes are thought to be also consequent from embankment, a 1 m rise during the twentieth century was mainly attributable to human activities (Fig. 3). Indeed, like all large European estuaries, sea walls as flood protection, industrial land reclamation and navigation channel deepening in response to growing economic exchanges have strongly affected the estuarine morphology. This is a typical feature of impacted estuaries whereby human settlements lie below a raised mean high water level.
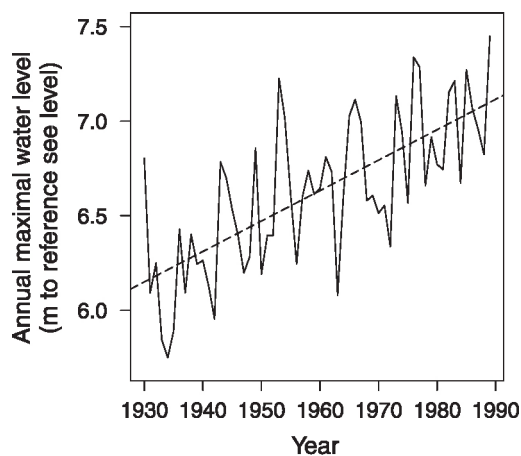
Fig. 3. Evolution of the annual water level maxima in the Schelde estuary. Source: Coen (2008).

Within one century, 16 % of the total tidal surface area has been lost, particularly among tidal flats (Fig. 4). The narrow nature of the estuarine channel sustains a hydrological stress characteristic of coastal squeeze. The remaining intertidal habitats

experience erosive forces which limit their extent and prevent the formation of mudflats and marshes in many parts of the estuary. The current intertidal habitats strongly contrast to those a century ago (Fig. 5). Given the essential nature of the water-sediment processes in the whole ecosystem functioning, the restoration of intertidal habitats is imperative. Such an achievement could benefit from the implementation of a flooding frequency gradient, since intertidal habitats ensure specific biogeochemical functions (Van Damme 2010).
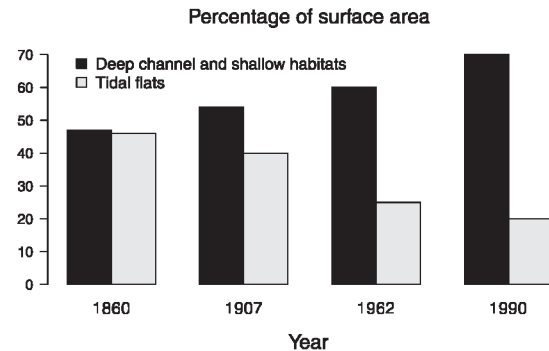
Fig. 4. Evolution of habitat surface area in Schelde estuary. Source: Meire et al. (2005).

TIDAL WETLAND RESTORATION IN THE SCHELDE ESTUARY

Nowadays, in an area where the population density is about 500 inhabitants per km^2, human pressures in the Schelde estuary have never been so huge (Meire et al. 2005). These pressures interact with flood risk which may increase fivefold when an average sea level rise of 60 cm by 2100 is considered according to the IPCC predictions (Broekx et al. 2010). Additionally, expansion of Antwerp's harbour infrastructures is still ongoing and implies habitat compensations (Van den Bergh et al. 2005). Indeed, in compliance with the conservation goals defined by several European directives, water and habitat qualities have to warrant the long term self-sustainability of organism communities (Elliott et al. 1999; Van Damme 2010). Moreover, several waterbird species have been shown to encounter the 1% level criterion of the Ramsar convention, conferring an international importance and a high conservation priority level to the Schelde estuary.

After the last storm flood in 1976, a safety plan was envisaged in the Belgium part of the estuary. Through the SIGMA plan, different options have been developed in order to combine safety against floods, port accessibility and restoration ecology (Jacobs 2009). In 2004, an

Fig. 5. A) Typical habitat gradient in the freshwater zone of the Schelde estuary; photograph from Jean Massart, 1904. B) Contemporary degradation of intertidal habitats in the same river section one century after.

optimal combination was adopted so that the European conservation goals for the Schelde estuary to be fulfilled (Adriaensen et al. 2005). A long-term vision for the Schelde estuary was determined as the development of a healthy and multifunctional estuarine water system that can be utilized in a sustainable way for human needs (Van den Bergh et al. 2005). As part of this plan, a new technique for tidal marsh restoration, the controlled reduced tide system (CRT), was implemented through a pilot project aiming to combine flood control and intertidal habitat creation (Maris et al. 2007).

THIS WORK

Associated to a strong anthropisation characteristic of impacted estuaries, the remarkable extent of the freshwater section of the Schelde estuary offers a double interest as part of ecosystem restoration. The CRT system was proposed and hypothezised to successfully restore tidal freshwater wetlands in embanked areas (Cox et al. 2006; Maris et al. 2007). To this aim, an experimental area in the freshwater zone of the Schelde estuary was equipped with the CRT system, and the monitoring of different ecosystem compartments was defined in an interdisciplinary context. Ecosystem functions can be defined as the activities or processes that characterize an ecosystem. Four general categories have been used for wetlands: hydrologic, biogeochemical and organism community maintenance (Brinson et al. 1994).

Among specific contributions to sedimentology (Vandenbruaene 2011) and biogeochemistry (Jacobs 2009), this work focuses on different ecosystem compartments and interactions in order to assess the coherence between abiotic and biotic components. This is a necessary task to appraise the relevance of further wide applications in tidal wetland restoration. After this introductory review of the restoration problematics in estuaries (Chapter 1), each of the following chapters relates the outcomes of research on an ecological facet emerging from the CRT system. Chapter 2 presents a brief review of existing habitat restoration techniques in estuaries, and former predictions on the ability of the CRT system in generating a tidal regime in an embanked area are tested; the flooding gradient is expected to warrant the development of complete ecological gradients. Chapter 3 provides an exploration of the development of the estuarine substrate; the sediment physicochemical characteristics are supposed to be conditioned by the flooding frequency; a comparative analysis confronts reference and CRT sediment functioning; fundamental processes involving water, granulometry and nutrients are described. Chapter 4 focuses on the spatiotemporal dynamics of sediment macroinvertebrate community; taxonomic and functional aspects are linked to environmental properties of current estuarine and CRT habitats. Chapter 5 links the former two chapters and deals with bioturbation; the relation between invertebrates and sediment mixing is explored by an in situ experiment to study the dispersal modes of sediment particles along a flooding gradient. Chapter 6 focuses on the upper trophic levels and brings an overview on bird species distributions among the newly-created habitats; CRT habitat value is discussed in the functional and conservational contexts. Chapter 7 synthesizes the main findings of this work; ecological features of current estuarine and CRT habitats are compared in the light of tidal wetland restoration.

CHAPTER 2

A NEW TECHNIQUE FOR TIDAL HABITAT RESTORATION: EVALUATION OF ITS HYDROLOGICAL POTENTIALS

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Abstract. The inability to create an adequate tidal regime in embanked areas is a major problem for restoring estuarine habitats. The Controlled Reduced Tide system (CRT) was previously hypothesized to overcome this constraint. As part of an estuarine management plan which combines flood protection and tidal habitat restoration, the first CRT system was implemented in the freshwater zone of the Schelde estuary (Belgium). Based on four years of high-frequency monitoring on the first CRT and the adjacent estuary, this study demonstrates the hydrological functionality of CRT. The tidal characteristics generated by this technique were suitable on the short and on the long term, with a reproduction of the spring-neap tidal cycle. In both CRT and estuary, the spatial and temporal variability of several hydrological descriptors were comparatively analysed. In spite of some hydrological deviations from the estuarine pattern, nothing precluded a suitable ecosystem features in CRT. The potential influences of CRT-specific hydrology on ecology and estuarine restoration are discussed. The restoration potential of the CRT system is shown to be particularly relevant for tidal marshes in early succession stage, habitats which are often lacking in embanked estuaries. Additionally, it offers a more robust and adaptable alternative to other systems. Conclusively, the CRT system should be more advocated in estuarine restoration.

INTRODUCTION

The worldwide extent of tidal marshes has greatly decreased, primarily due to large scale embankments for agriculture, industrial and urban developments. More recently, the combination of increasing sea level and the maintenance of hard defences has caused coastal squeeze (Doody 2004): tidal marshes, that would normally retreat landwards to maintain overall extent, encounter solid structures and are eroded, while marsh reformation is prevented, leading to further habitat loss. In the Schelde estuary (Belgium), coastal squeeze has resulted in a typical morphological profile of intertidal marshes: climax marshes boarded by eroded cliffs and non-vegetated sand- or mudflats. Over the last century, this engendered a loss of 16 % of the total surface of tidal marshes (Meire et al. 2005; Van den Bergh et al. 2005), and the remaining ones remain subject to erosion.

Managed realignment is a technique which is increasingly used to restore tidal habitats (Burd 1995). This technique, which consists of the removal or breaching of dikes to restore tidal influence to formerly reclaimed land, is extensively reviewed in French (2006). Elevation is a key factor for selecting suitable site and planning managed realignment as it relates directly to frequency, height and duration of tidal inundation, which are the main drivers of sedimentation pattern and vegetation development (e.g. Brooke 1991; Cundy et al. 2002; Teal and Weinstein 2002). However, many embanked sites have a lower elevation than tidal marshes in the adjacent estuary, on the one hand due to subsidence by compaction of the sediments and mineralization of peat layers, on the other hand due to continued sedimentation in the estuarine marshes, following sea level rise (Temmerman et al. 2003; Teal and Weishar 2005). This typically leaves them below the levels of contemporary marshes and rules out many potential sites for realignment. Indeed, realignment would result in a complete flooding of the site at every tide, leading to bare flats. Hence, it is not certain whether and how fast they could evolve to a vegetated marsh system. Vegetated tidal marshes, in particular the natural succession gradient from pioneer herbs to

forest climax habitats, are the main goal for tidal restoration in the Schelde estuary, and this is consolidated through legislation. Moreover, replacement of agricultural land by only tidal flats is undesirable for the public. The risk of creating a long-term unvegetated mudflat is a major drawback for realignment as a restoration technique.

This problem was firstly countered by acting directly on marsh elevation. In the UK, convenient sites which approximate the suitable level are selected and natural processes are allowed to proceed (French 2006). In the US, it is common to increase site elevation prior to dike breaching (Brooke 1992). However, artificial site elevation has been a common reason for project failure (Quammen 1986; Perry et al. 2001).

Nowadays, other options are offered by regulated tidal exchange systems (RTE; Hirons et al. 2002; Lamberth and Haycock 2002). RTE covers a wide range of engineered structures such as spillway, simple culverts, sluices, tide-gates or artesian wells, and has been implemented in the US, Canada, UK, France, Belgium, Germany and Netherlands (Giannico and Souder 2005; Wolters et al. 2005). To solve the problem of elevation, simple culvert presents the advantage of lowering the average flooding height to a water level adapted to the site, but the technique cuts out spring-neap variation and compromises the restoration of a whole intertidal habitat gradient. Buoyant tide-gates, such as self-regulating tide system, could allow to restore a spring-neap cycle, but, the reproduction of the natural tidal variability (e.g. variation in water height from one spring tide to

another) has not been proven yet. Moreover, the system exhibits mechanical flaws and implies high maintenance costs (Giannico and Souder 2005), which decreases the application potential.

In 2006, a more robust RTE technique was proposed to restore tidal marshes on lower sites in the Belgian part of the Schelde estuary (Cox et al. 2006). The controlled reduced tide system (hereafter called CRT) allows the implementation of an adaptable restricted tidal regime with neap and spring tides by the use of high inlet culverts and low outlet valves, as well as storm flood protection (see Methods for a complete description). As part of a project combining flood protection and ecological development, over 1500 ha of tidal marsh along the whole Schelde estuary are being created through CRT system. Cox et al. (2006) and Maris et al. (2007) hypothesised that the CRT-technique could successfully restore tidal marsh habitats on a lower rural site. Therefore, a pilot CRT was built in the freshwater tidal zone of the Schelde estuary to verify this hypothesis.

The pulsing tidal regime has been recognized as the key to estuarine habitat function and structure (Odum et al. 1995), but the hydrological characteristics of tidal wetlands in the context of marsh restoration still need better documentation (Montalto and Steenhuis 2004). So far, CRT's hydrological characteristics have only been modelled (Cox et al. 2006) and no empirical evidence has been available to verify the CRT hydrological functionality on both short and long term. This study documents and analyzes long term observations of water levels in this pilot CRT
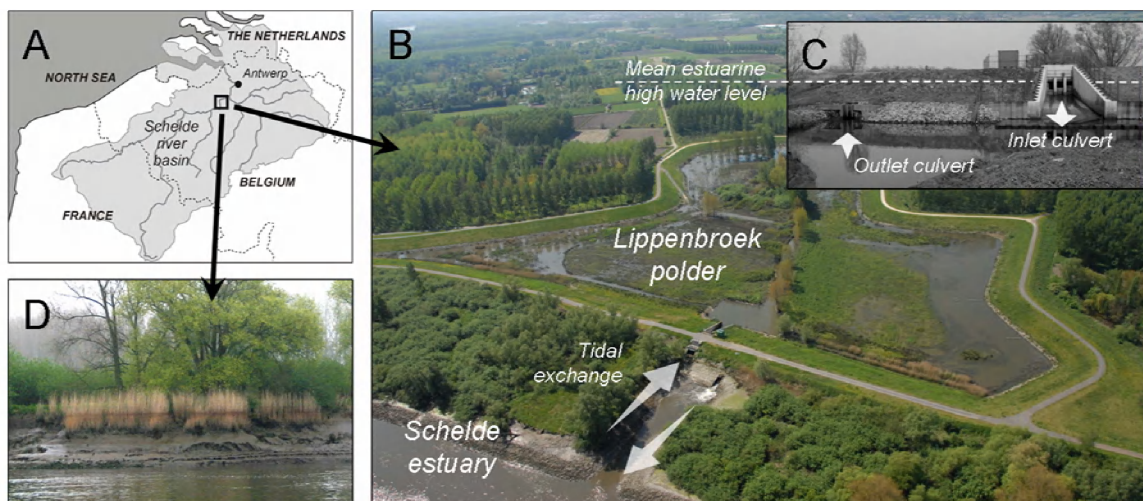
Fig. 1. A) Study area. B) The polder of the pilot project. C) View of the water exchange system, from inside the polder towards the estuary. D) Typical intertidal gradient in the freshwater zone of the Schelde estuary; the severe erosion limits pioneer marsh development.

and compares its characteristics to an estuarine reference. We argue that unlike existing tidal marsh restoration techniques, the CRT system provides a tidal regime suitable for efficient restoration of a complete intertidal habitat gradient, confirming Cox et al.'s hypothesis (2006).

METHODS

1. Study area

The study took place in the freshwater zone of the Schelde estuary, Belgium (Fig. 1; 51.086 °N; 4.171 °E). At the study location, the estuary is strongly confined and the average tidal amplitude is about 5.2 m. Typically, marshes exhibit a steep profile where erosion sheers form (Fig. 1D). The first CRT system was implemented in the Lippenbroek polder (Fig. 1B), where crops were grown until 2000.

The CRT technique is based on a system of culverts specifically designed to connect the flood area to the estuary, and is described in Figure 2. Depending on the site elevation relative to the mean high water level in the estuary and the within-site topographical gradient, the thresholds of several inlet culverts are vertically and independently adjustable (Fig. 1C). This allows to modulate the tidal height and amplitude, creating an adequate flooded surface distribution according to the restoration goal (i.e. the whole area is flooded each tide at the lowest threshold, and the flooded surface decreases when heightening the threshold). Near the site location, mean high water level in the estuary is approximately 5.6 m above the Belgian sea level reference. The whole surface of the polder is below this level (mean elevation: 2.8 m; see Fig. 1C). The polder was subjected to the tidal influence by means of CRT system on March 1st, 2006. It has been connected to the estuary by means of inlet and outlet culverts allowing water exchange. For four years, research and observations have focused on tidal habitat creation and ecosystem functioning.

2. Monitoring and data analyses

The study period extended from March 2006 to March 2010. In the estuary (at a location nearby the CRT), water levels were recorded by Flanders Hydraulics Research every minute with a radar sonde. In the CRT, water levels were recorded at 9 permanent locations every five minutes with pressure transducers corrected for atmospheric pressure.

First, recordings from the CRT's locations were used to compare observed flooding frequencies with earlier model predictions (Cox et

al. 2006); flooding frequencies were computed by taking observed accretion into account. Additionally, as sedimentation was supposed to influence hydrology in the CRT (Cox et al. 2006; Vandenbruwaene et al. 2010), the significance of
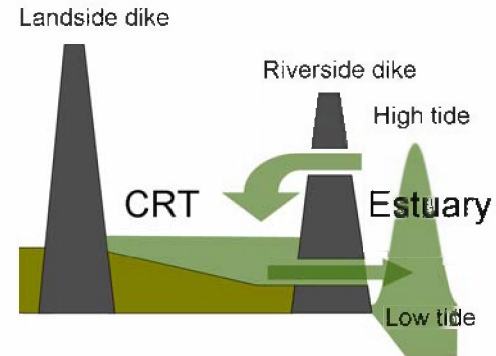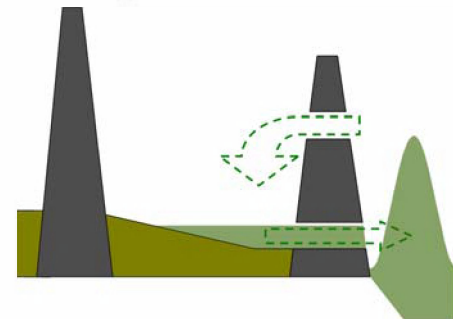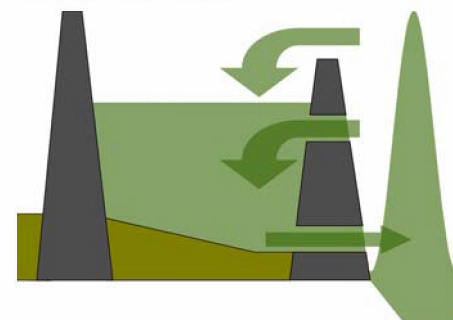
Fig. 2. CRT system. A) Water (mainly at mid and spring tide) enters in the polder uniquely during the maximal flood through an upper culvert. Then, water evacuates through a lower culvert (equipped with an outlet valve) during the ebb once the level in the river matches the level inside the polder. B) Around neap tide, the lower flood levels reduce the amount of incoming water. C) A spillway on the riverside dike ensures maximum water storage during a storm tide.
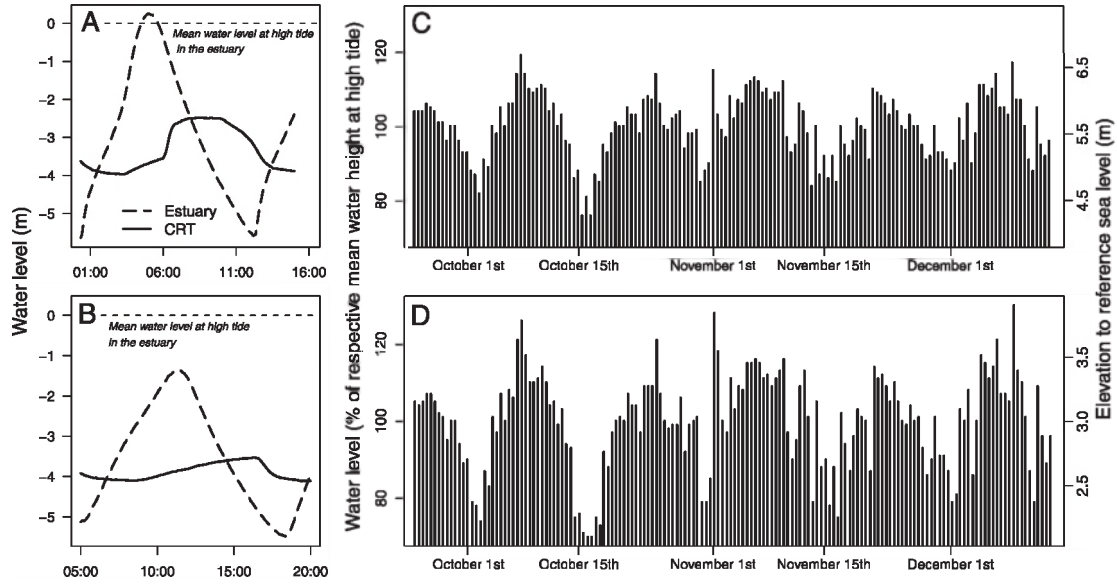
Fig. 3. Comparative illustration of time series. A) A tidal cycle on September 25th, 2006 (spring tide); values on y axis are absolute. B) A tidal cycle on October 16th, 2006 (neap tide). C and D) Water heights at high tide over the autumn 2006 in respectively the estuary and the CRT; water heights were divided by their respective mean value in order to reflect the extent of the extremes water levels.

flooding frequency evolutions was therefore verified. A reference site in the high marsh adjacent to the CRT was considered in order to cope with possible inter-seasonal or annual variations.

Then, in order to compare the tidal characteristics in the CRT and in the estuary, we used the continuous recordings at one location in the CRT. This allowed calculation of flooding frequencies associated with different elevations in the CRT. Surface proportions corresponding to 10 flooding frequency classes (10, 20,…, 100 %) were calculated based on a digital terrain model. In the estuary, this model was computed by a radar altimeter and an acoustic tide gauge, and in the CRT, by a total station. The mean high and low water levels were based on classic mechanical or pneumatic altimeter measurements (Taverniers and Mostaert 2009). Different hydrological descriptors (see below) were computed over this period. This was done for the same flooding frequency classes in each of the two systems to ensure the comparison of two perfectly paired spatiotemporal patterns. Season was considered as the temporal unit, during approximately three months (calendar-based seasons of temperate Europe). In order to balance the amount of water varying between spring and neap tide, each season extended from an initial spring tide to a final neap tide. The following hydrological descriptors were computed for each season:
– actual flooding frequency (number of inundating tides as a percentage of the total number of tides);
– mean water height at high tide;
– mean flooding duration;
– longest flooding duration;
– longest drought duration.

Analyses of variance (ANOVA) on paired data were applied on each of these descriptors. Null hypothesis was tested for system effect (difference estuary-CRT) as well as its interactions with elevation and season. Seasonal effect within and between the two systems was explored by multiple pairwise t-tests. Temporal variability of each descriptor was quantified by the coefficient of variation at each flooding frequency, and system effect was assessed by Wilcoxon signed-rank tests on paired data.

Computations and associated graphical representations were realised with R software (R Development Core Team 2009). Commands available in the package "Tide" (Cox 2010) were used to extract the flooding events and lengths of dry periods in order to compute hydrological descriptors.

RESULTS

1. Tidal characteristics in the CRT

Direct comparison of one tidal cycle in the CRT and in the estuary shows the reduction of tidal amplitude (Fig. 3A). The tidal pattern is characterized by reduced amplitude and a prolonged period of high water, reaching two

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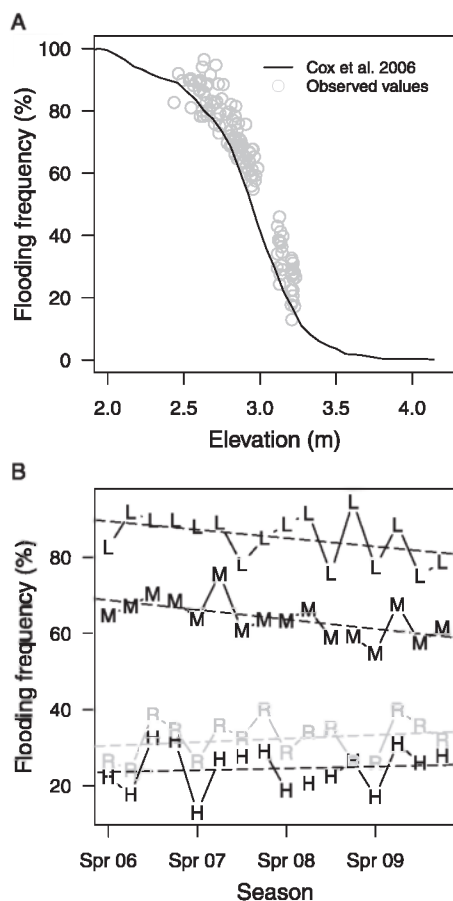
Fig. 4. A) Comparison between predicted (Cox et al. 2006) and observed flooding frequencies (grey points, mean seasonal values) over the four-year follow-up. B) Evolution of the flooding frequency at three of the 9 locations and at a reference one; "Spr" for spring season, from 2006 to 2009; H, M and L for respectively high, mid and low elevation; R for estuarine reference.

hours and a half at spring tide, and a delayed flooding at the lowest CRT elevations (due to the higher inlet culvert elevation; Fig. 2). On a longer term, high water levels along spring-neap period were more distant from the mean (100 %) in the CRT (Fig. 3C and 3D). As such the CRT system reproduces the targeted spring-neap cycle, despite the lower elevation of the site.

Observed flooding frequencies were in good accordance with earlier model predictions, although these predictions are at the lower end of the observed seasonally specific flooding frequencies (Fig. 4A). Flooding frequencies show a slight long term trend, with a decrease at low and mid elevations, and an increase at high elevation (Fig. 4B). High inter-season and inter-annual variations are superimposed on the long term trends. None of the long-term relationships were significant, except at mid elevation ($r = -0.57$; $p = 0.022$). This

showed that the accretion effect on the flooding frequency pattern was negligible over the four first years.

2. Comparative analysis – spatial pattern

Surface-elevation distributions clearly differed between estuary and CRT (Fig. 5, top left). A Kolmogorov-Smirnov test indicated a significant shift of the CRT distribution to higher values ($D^- = 0.36$; $p < 0.001$). About one third of the freshwater intertidal area consists of young pioneer marshes (flooding frequency > 70 %). These young marshes are mainly composed of partly unconsolidated mudflats with pioneer species as *Lythrum salicaria*, *Polygonum lapathafolium*, and in later stages *Typha latifolia* and *Phragmites australis* (Struyf et al. 2009). In this CRT, these habitats cover more than two thirds of the surface (see Jacobs et al. 2009 for details). Trends of hydrological descriptors along the flooding gradient exhibited some contrasts when comparing the two systems. A significant system effect was found on some descriptors (Tab. 1); in addition, significant interactive effects were found with elevation. CRT generates:
– a lower mean water height at high tide, mainly at the most frequently flooded sites;
– a longer mean flooding duration, to a lesser extend at the highest flooding frequency;
– longer extreme flooding events, especially at high flooding frequencies.

Particularly for the latter, there was a different order of magnitude between the CRT and the estuary. In the estuary, longest flooding events were comprised between 2 hours (at high elevation) and 5 hours (at low elevation) in the estuary, whereas in the CRT they ranged between 9 and more than 30 hours. System effect was the strongest for mean flooding duration. Mean flooding duration in the CRT was approximately twice the estuarine value at low elevation, and three times at high elevation (from 1 to 3 hours in the estuary; from 3.5 to 6 hours in the CRT; Fig. 5).

3. Comparative analysis – temporal pattern

The pairwise t-test detected significant seasonal differences within and between the two systems (Fig. 6). This was particularly the case for flooding duration and longest flooding. These values were lower in summer time than in winter time. Differences were stronger in the CRT than in the estuary, as confirmed by a significant interaction between system and season (Tab. 1).
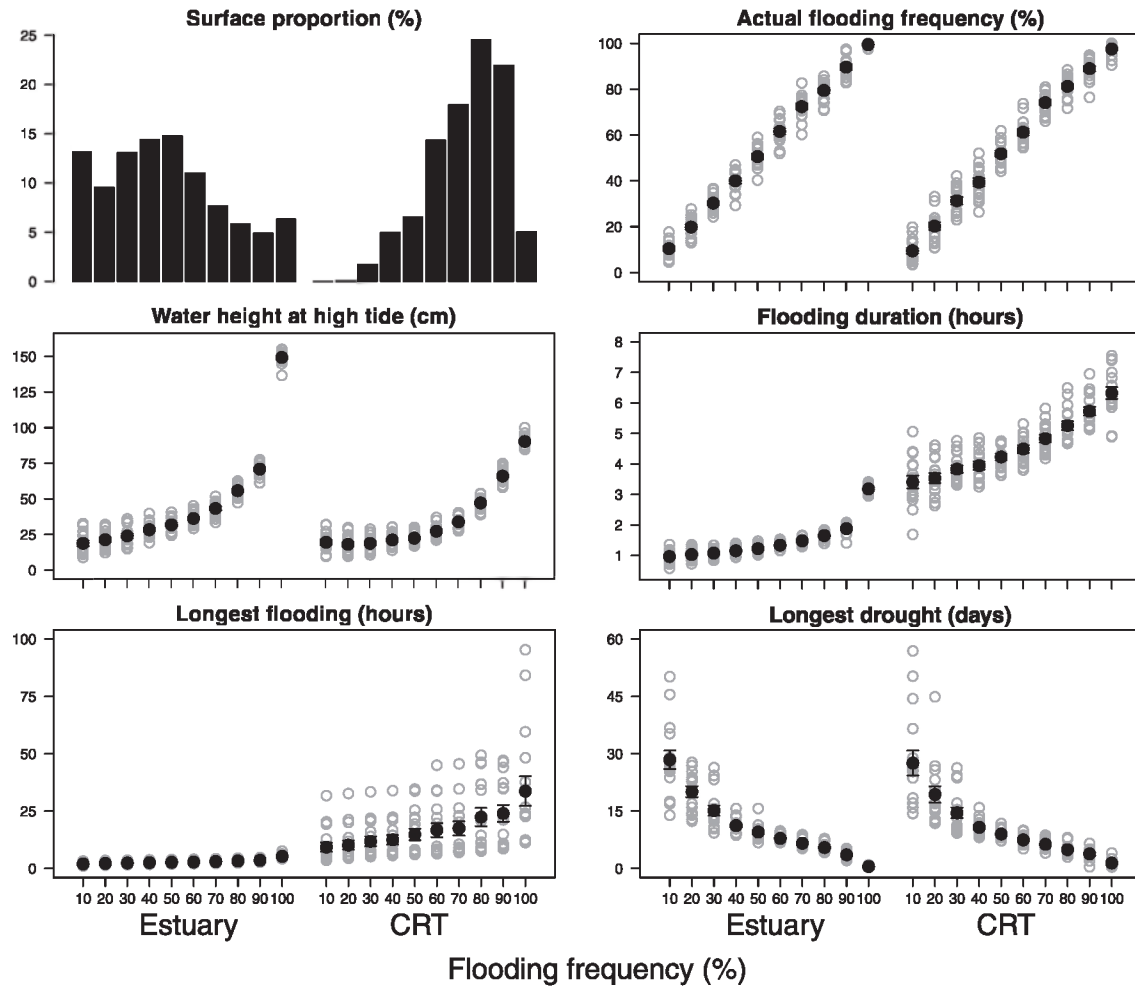
Fig. 5. Spatial comparison between estuary and CRT along the flooding gradient. Top left: surface-elevation distributions; surface proportion takes account for the main part of the freshwater zone of the Schelde estuary. Hydrological descriptors: y-values are grouped per interval of 10 %. Black points indicate mean value (± S.E.) and grey points represent the 16 seasonal intervals.

Tab. 1. Systems effect on hydrological descriptors (ANOVA). Numbers indicate Fisher's F. Rejection level: *, 0.05; ** 0.01; ***, 0.001. "×" for interaction.

		Actual flooding frequency (%)	High water level (cm)	Flooding duration (hours)	Longest flooding (hours)	Longest drought (days)
Mean ± SE	Estuary	55.362 ± 0.182	47.995 ± 0.235	1.498 ± 0.004	2.963 ± 0.006	10.832 ± 0.056
	CRT	55.539 ± 0.182	36.467 ± 0.148	4.556 ± 0.006	17.280 ± 0.093	10.507 ± 0.058
Effect	System	0.2	78.0 ***	3538.2 ***	164.8 ***	1.2
	System × Elevation	1.3	650.0 ***	33.0 ***	14.4 ***	0.3
	System × Season	4.4 **	2.9 *	25.3 ***	24.5 ***	2.1

Despite these partial differences, the seasonal dynamics between summer and winter (amount of water) was consistently reproduced in the CRT. High water level and longest drought were also sensitive to season, with reduced water levels; interactions were weak or null.

Additionally, temporal variability of all hydrological descriptors was found to be function
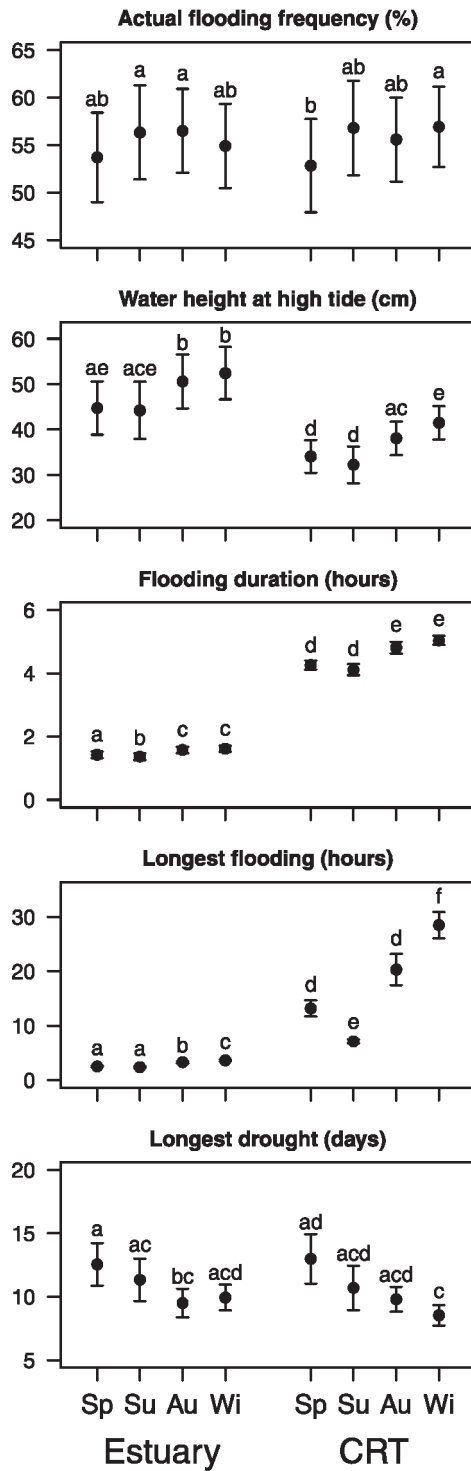
Fig. 6. Temporal comparison between estuary and CRT among the four seasons (mean ± S.E.). Abbreviation: "Sp" to "Wi" for spring to winter. Absence of common letter (a, b, c and d) between two seasons indicates an absence of statistical significance at the level $\alpha = 0.05$.
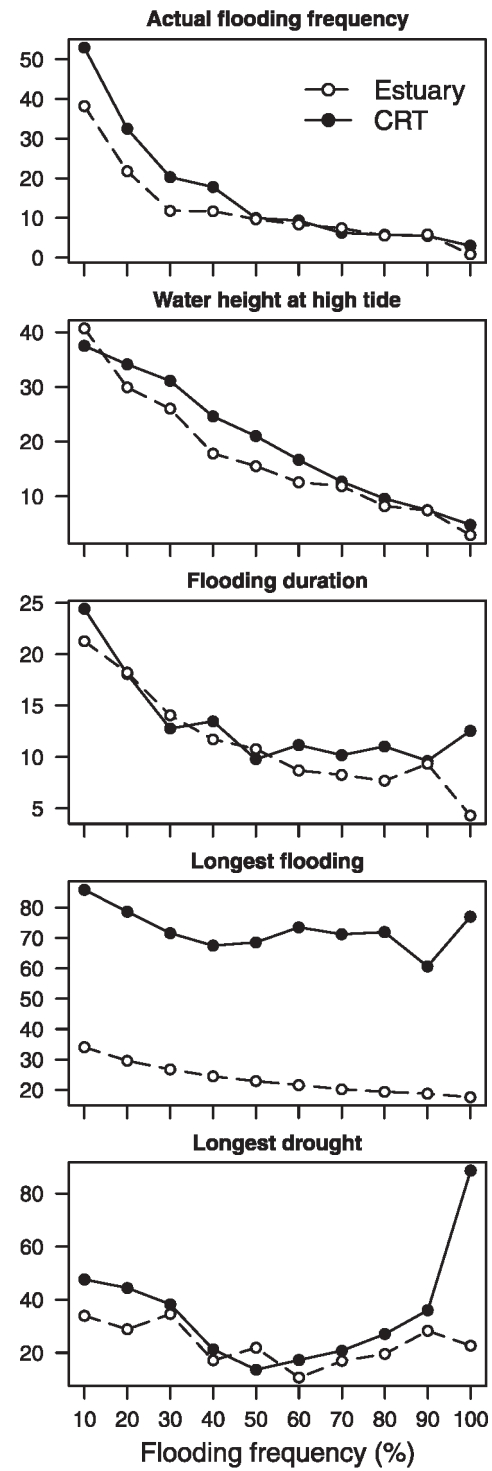
Fig. 7. Temporal variability along the flooding gradient. Points indicate the coefficients of variation (standard deviation in percentage of the mean) of the series per flooding frequency in Fig. 4 (grey points).

13

Tab. 2. Wilcoxon signed-rank tests on the paired coefficients of variation of each hydrological descriptor. Wilcoxon V is computed based on the difference of the ranks in estuary minus the ranks in CRT. *, $p < 0.05$; **, $p < 0.01$.

		Actual flooding frequency	High water level	Tide duration	Longest flooding	Longest drought
Mean coefficient of variation	Estuary	12.1	17.3	11.4	23.5	23.5
	CRT	16.3	20.0	20.0	72.6	35.5
Wilcoxon V		8 *	5 *	8 *	0 **	7 *

of the flooding frequency in both systems (Fig. 7). On the average, Wilcoxon tests revealed significantly higher coefficients of variation in the CRT (Tab. 2). Except for the longest drought, all coefficients of variation decreased along the gradient. Longest drought was more stable at mid flooding frequencies and more unpredictable at the extremes of the gradient. Whereas it varied within a couple of hours in the estuary at low elevation, it could reach 1.5 day in the CRT. At high elevation, it ranged between circa 15 and 60 days.

A higher variability in actual flooding frequency occurred at high elevation in the CRT, whereas flooding duration was more variable in the CRT at low elevation. Indeed, low elevations experience all the range of tides unlike high elevations which are flooded only around spring tides. This explains the nature of CRT in amplifying the spring-neap cycle as previously observed (Fig. 3C and 3D). This amplification is frequency-dominated at high elevation (flooded only at spring tide) and duration-dominated at low elevation (all tides from neap to spring).

DISCUSSION

After four years of hydrological monitoring, empirical evidence confirms that the CRT system ensures an adequate tidal regime for tidal marsh restoration in lower areas adjacent to the estuary. Additionally, the flexible adjustment of the inlet culverts demonstrates the capacity of this system in restoring a complete flooding gradient, despite the overall lower elevation and the limited elevational amplitude of the flood area (1.2 m here). However, some deviances from references were observed which might constrain ecological functioning. Ecological relevance of such a success and potential constraints are discussed below.

1. Successful introduction of a tidal regime

Our observations demonstrate that a relatively simple model, as presented by Cox et al. (2006), can provide sufficient guidance in the design of a

CRT. This modelling study predicted tidal characteristics based on water flow through culverts and on a relationship between water volume and water depth in the polder. These two ingredients allowed simulations of the water level dynamics in the CRT. This led to a well-informed design of the inlet and outlet culverts of the CRT, in order to maximize the potential for vegetation development.

The introduction of a spring-neap cycle is particularly important, as it drives many ecological processes covering all ecosystem compartments. Indeed, among other processes, the successive wetting and drying phases over a spring-neap cycle were demonstrated to pulse biogeochemical cycles in gas emissions (Nuttle and Hemond 1988) and in nutrients dynamics (Vörösmarty and Loder 1994; Hou et al. 2005), to facilitate plant colonization and persistence (Fiot and Gratiot 2006), and even to regulate processes at the highest trophic levels such as fish and birds (Davidson and Evans 1986; Rosa et al. 2006; Krumme et al. 2008). In addition, the delayed high tide in the CRT (Fig. 3A) may offer temporally extended habitat availability for birds, as already highlighted in restored wetlands adjacent to an estuary (Davidson and Evans 1986).

Water velocity is another important hydrological aspect, but it was not considered in this study because of its high variability and its complex interactions with sediment morphology from flats to creeks. In the estuary, the water current speeds can reach 1 m/s (Flanders Hydraulics Research, June 2009) whereas they never exceed a couple of cm/s on the CRT flats (field observations). Embankment and dredging sustain a chronic shear stress in the remaining intertidal flats of the freshwater zone where the benthic communities cannot evolve beyond a pioneer stage (Seys et al. 1999). In CRT, the reduced shear stress may increase the food quantity and quality for the benthos at the sediment surface, as already shown under low water velocity in intertidal flats (Bock and Miller 1995). The formation of tidal flats and pioneer

marshes in CRT provides the estuarine system with rejuvenation processes which have been missing (Meire et al. 2005). As such, CRTs can offer opportunities to tackle hydromorphological impacts of coastal squeeze in the estuary, which is now degraded by sustained erosion of climax marshes and prevented new marsh formation or landward extension.

2. Sources of hydrological deviance

So far, CRT has been the sole technique which has been proven to create a complete intertidal gradient on a lowered area. Although the seasonal dynamics are well reproduced, the tidal characteristics in the CRT system significantly differ in different ways from the estuary. The ebb phase is relatively prolonged by the limited size of the outlet culvert which limits the discharge. The same holds for the longest flooding events and their increased variability, which, in winter time, result from storm tides when the polder is filled through the spillway at critical tidal levels. Hence, after a storm event at spring tide (Fig. 2C), complete emptying of the polder is prevented for a few successive tides, resulting in inundations of up to four days at low elevation.

At a given flooding frequency, hydrological variability consists in seasonal variations and also, to a lesser extent, in annual variations (see yearly dephasings for each of the four seasons in Fig. 4B). In winter, the extended water retention effect due to storm tide is higher at low than at high elevation in both systems. This explains the higher variability in tide duration in the CRT at low elevations which ranges from short residence time of small and rapidly drained amounts of water (neap tide) to long winter inundations (storm tide). In contrast, the brevity of the flooding events at high elevation is more constant in both systems. In the CRT, it is accompanied by a higher variability of actual flooding frequency due to reduced summer water volumes, underlined by the seasonal variation in water height. This induces scarcer and extended flooding events (because of retention) during winter storm tides. As a consequence, these complex interplays between the hydrological descriptors engender more variable durations of dry events at the extremes of the flooding gradient in the CRT.

3. An ecologically negative deviance?

The described differences in hydrological characteristics between the CRT and the estuary (in mean and in variance) do not seem to inhibit the development of intertidal habitats. Indeed, the plant community development in this CRT was shown to be consistent with existing reference tidal freshwater marshes (Jacobs et al. 2009). Moreover, wetland plants are known to be adapted to anoxic stress (e.g. rhizomes, storage organs, adventitious roots) and to overcome submergence, from a few days to several weeks (Drew 1997; Vartapetian and Jackson 1997). Some direct observations support the innocuousness of long submergence since some less tolerant species such as *Alisma plantago* or *Lycopus europaeus* (Vartapetian and Jackson 1997) abundantly occur in this CRT (Jacobs et al. 2009). Although the occurrences of reference species have confirmed the potential for successful habitat creation at the community level (Jacobs et al. 2009), one cannot exclude an effect of prolonged flooding duration at the population scale (Krauss et al. 2006). For instance, this could be hypothesized concerning the Himalayan Balsam (*Impatiens glandulifera*) which is abundantly present in the estuarine references, but still rare in the CRT.

Additionally, ongoing faunistic studies (under review and in preparation) strengthen the relative innocuousness of the prolonged inundations in the CRT. In a nutshell, during the study period, estuarine invertebrate communities successfully developed in the CRT reaching higher densities and taxa richness than in estuarine reference sites (range in seasonal taxa richness: estuary, 4 − 9; CRT, 12 − 19). Most of macroinvertebrates living in frequently flooded zones (mainly aquatic worms, aquatic insects and gastropods) are adapted to aquatic conditions with branchial and tegumentary respiration. In non-frequently flooded zones, no significant change was observed in the initial community, since most of the organisms occurring here (i.e. earthworms, potworms, myriapods, isopods, beetles) have various physiological adaptations to 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). Comparatively, these taxa are typical for high marshes in freshwater tidal zones of the North Sea coast estuaries (Barendregt 2005). Complementarily, 103 bird species have been encountered, among which 55 are wetland specialists.

Spatiotemporal heterogeneity of environmental features is an ecological determinant often neglected. Indeed, from disturbance (rare event, high order of magnitude) to stress (frequent event, low to high order of magnitude), environmental unpredictability is recognized to regulate the functional diversity of

Fig. 8. Aerial view of an actual CRT construction along the Schelde estuary. Photograph shows outlet (left) and inlet (right) construction which will allow implementation of CRT on several hundreds of hectares of lower agricultural land.

organism communities in stream ecology (Resh et al. 1994). Despite established facts dealing with regenerative effect of storm tides (May 1981), such information remains scarce in estuarine studies. In a CRT, the slackened water currents limit water velocity-induced disturbances which could set back community succession. In contrast, drought variability which is characterized by higher order of magnitude in the CRT may be a more influential parameter. The higher variability can engender different sediment states at low tide, from constant moisture in winter to mud cracks (Allen 1987) during extended summer droughts. Such formations were observed in the CRT but not in the estuary. These macropores assure important ecosystem functions such as modulation of gas emission (Hemond and Chen 1990) or plant seed trapping (Fiot and Gratiot 2006). CRTs are being constructed along the salinity gradient of the Schelde estuary. Also, tidal salt marshes are known to be more stressing environments than tidal freshwater ones (Odum 1988). This is an important point as salinity and droughts were shown to interact, for instance on marsh vegetation mortality (Brinson et al. 1985). Hence, the higher variability

of dry events in a CRT might increase the environmental heterogeneity when implemented in the brackish zone.

Conclusively, the extended flooding duration in the CRT do not seem to impair the development of the faunistic and floristic components. More generally, most estuarine organisms are known to encompass different types of tides (e.g. with diurnal, semidiurnal, or mixed tides) within their biogeographical area. The prolonged inundations during storm tides either do not seem to be influential since they happen only once or twice a year, and specifically during the period of reduced biological activity (in winter). Although we found no indications of impaired marsh development in this pilot project, we cannot exclude the possibility that some specific ecosystem functions might differ from the estuarine system.

4. CRT in estuarine management strategies

The CRT system increases the number of potential sites for tidal marsh restoration, and thus enhances chances for tidal restoration in estuarine management policy. This technique – in contrast

16

to other realignment techniques – is flexible. The design of the culverts is robust, straightforward and very similar to the construction of classic evacuation culverts. Adapting culvert thresholds or day to day functioning does not require complex mechanical or electrical automation, which avoids malfunctions and decreases maintenance costs compared to alternative systems with buoys or water level detectors (Giannico and Souder 2005). Depending on the local tidal characteristics, site elevation and within-site topography, the inlet culvert thresholds are fine-tuned to obtain desired surfaces of mudflat, pioneer tidal marsh, or climax tidal marsh, an aspect which has not been adequately addressed (Hammersmark et al. 2005). In the context of management, this system offers the possibility to set back ecosystem succession by a total flushing of the CRT with a complete opening of the culverts. In order to avoid excessive water accumulation during a storm in newly constructed CRT's, outlet culverts are dimensioned so that no retention effect is possible and the whole water volume evacuates within one low tide (Fig. 8). This provides a leeway to adapt more specifically the hydrological regime if necessary for optimizing ecosystem functions or changing conservation goals while fulfilling the essential flood protection measures (Meire et al. 2005; Broekx et al. 2010).

5. Conclusion

In accordance with earlier predictions, this study demonstrates the functionality of the CRT system in assuring a tidal regime on an area lower than the adjacent estuary. This system generates the essential tidal periodicity required for estuarine habitat creation. The combination of the morphology and hydrology of the area offers a physical templet suitable for marsh development, particularly in an estuary undergoing coastal squeeze. The few hydrological differences highlighted in the CRT do not seem to impede the development of a functional marsh as the development of ecological aspects was previously shown to be successful (Jacobs et al. 2008; Jacobs et al. 2009).

Embankments have profoundly modified the natural hydrology of estuaries, so that this impaired integrity blurs the exact hydrological requirements for marsh creation. The lack of documented effects of hydroperiod heterogeneity on intertidal habitats needs particularly to be addressed in order to minimize restoration uncertainties. Nevertheless, the design of the CRT system offers the advantage of a hydrological adaptability to different ecological objectives.

CHAPTER 3

SEDIMENT ABIOTIC PATTERNS IN CURRENT AND NEWLY-CREATED INTERTIDAL HABITATS FROM AN IMPACTED ESTUARY

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Abstract. Controlled Reduced Tide system (CRT) is a new technique for restoring tidal marsh, and is being applied in the Schelde estuary (Belgium). Biogeochemical services of CRT were hypothesized to support and improve several estuarine functions such as sediment trapping and nutrient burial. In 2006, the first pilot CRT was implemented in the freshwater zone of the estuary. 15 sediment physicochemical descriptors were intensively monitored over three years in the newly-created CRT and reference habitats from the adjacent estuary. Strong soil transformations appeared in the CRT: the formation of a nutrient rich estuarine sedimentary substrate in the most frequently flooded zones contrasted with the estuarine sand flats where a shear stress is sustained by coastal squeeze. In a comparative way, the temporal dynamics of the sediment descriptors was explored in order to identify key processes engendered by the flooding of the CRT sediment. Although processes were found inherent to the CRT, reference and CRT sediment characteristics experienced long-term oscillations, whereby both systems fluctuated in a similar way. However, despite such variations, successful nutrient trapping and fine particles burial were demonstrated in the partly independent evolution of the CRT sediment. This study proves that the CRT system, in accordance with restoration goals, can compensate some deficient ecological functions in impacted estuaries. Besides, the results highlight the complex temporality of abiotic patterns in intertidal sediments.

INTRODUCTION

Estuaries are known to play a crucial role in biogeochemical cycles by reworking riverine inputs and trapping contaminants (Billen et al. 1991; Jickells 1998), but they are among the most threatened ecosystems by human activities (Vitousek et al. 1997; McLusky and Elliot 2004; Long 2000). Densely populated and industrialized, the Schelde Estuary (Belgium) has been strongly impacted for a long time. Embankments, dredging and pollution have severely modified the estuary integrity. These pressures have led to a drastic reduction of mudflats and shallow subtidal habitats, while the remaining ones undergo a strong physical stress sustained by coastal squeeze (Meire et al. 2005). However, large projects aiming at restoring wetlands and estuarine habitats are ongoing since, at the scale of an estuary, tidal marsh restoration may increase the economical value of biogeochemical services (Andrews et al. 2006).

Although marsh restoration by land reclamation has become frequent through different coastal management practices, concomitant biogeochemical processes have received little attention (French 2006). Questions arise concerning the functional success of marsh restoration projects since tidal marshes are known to be nutrient sinks and transformers (Billen et al. 1991; Megonigal and Neubauer 2009). Their important role in nutrient cycling has been pointed out for a long time (Morris et al. 1978; Odum 1988), and recent mass-balance studies clearly showed their nature of water quality filters (Gribsholt et al. 2005; Van Damme et al. 2009; Struyf et al. 2006; Jacobs et al. 2008). Among different functions they assure, tidal marshes reduce the transfer of riverine material to the coastal ocean (Middelburg and Herman 2007). Balance between excess nutrient importation and exportation has been debated (Nowicki and Oviatt 1990), but most of studies today agree on the fact that they trap nutrients (Jickells 1998). However, information is extremely variable given the diversity of estuaries over the world (Heip et al. 1995), and temporal patterns can exhibit either seasonal or non-seasonal trends (see Nowicki and Oviatt 1990 for review).

Especially freshwater tidal zones have been for a long time recognized to need greater

attention (Morris et al. 1978), but knowledge still remains scarce, particularly concerning sediment biogeochemistry (Blackwell et al. 2004; Megonigal and Neubauer 2009). Even in the Schelde estuary, one of the most studied in the world, no reference data series concerning sediment abiotic descriptors is available at a yearly scale. Such a lack is critical since it is not possible to value an ecosystem when its structure and functioning are not fully understood (Jickells 1998). Hence, this points to the importance of studying long-term sedimentary processes in tidal marshes.

So far, managed realignment has been the main technique to restore tidal marshes (French 2006). It consists in dike breaching or removal in order to increase estuarine surface area from reclaimed land. However, most embanked areas adjacent to estuaries lie lower than the mean high water level so that dike opening conducts to a unique flooding frequency. Hence, this prevents the creation of a whole intertidal gradient which ensures a diversity of habitats and subsequent functions in accordance with non-impacted tidal marshes (Baldwin et al. 2009). A few years ago, a new restoration technique, the controlled reduced tide system (CRT), was hypothesized to overcome this constraint (Cox et al. 2006; Maris et al. 2007). Recently, CRT was proved to successfully restore a complete flooding gradient (Beauchard et al. 2011b), along which plant species communities were found to be highly specific (Jacobs et al.

2009). In parallel, a sediment physicochemical gradient is expected.

Increasing shear stress due to an increasing tidal amplitude (more than 1 m in 100 years), leads to a severe degradation of current estuarine habitats (Van den Bergh et al. 2005). As the shear stress is reduced in CRT, CRT is hypothesized to compensate for the functional deficiencies of current estuarine habitats such as sediment trapping and nutrient burial. Hence, a structural divergence between estuarine and CRT sediment characteristics is expected. Besides, since long-term sediment physicochemical patterns are still poorly documented in estuarine restoration (Blackwell et al. 2004), a mechanistic description of sediment flooding may provide new insights. Therefore, additionally to its applied objective, this study provides more fundamental investigations of the temporal dynamics of intertidal sediment characteristics.

METHODS

1. Study area and monitoring design

This experimental area ("Lippenbroek polder"; 8.2 ha) is situated in the freshwater zone of the Schelde estuary, Belgium (51.086 °N; 4.171 °E; Fig. 1). It concerns a large pilot project of intertidal habitat restoration by means of controlled reduced tide system (CRT) in
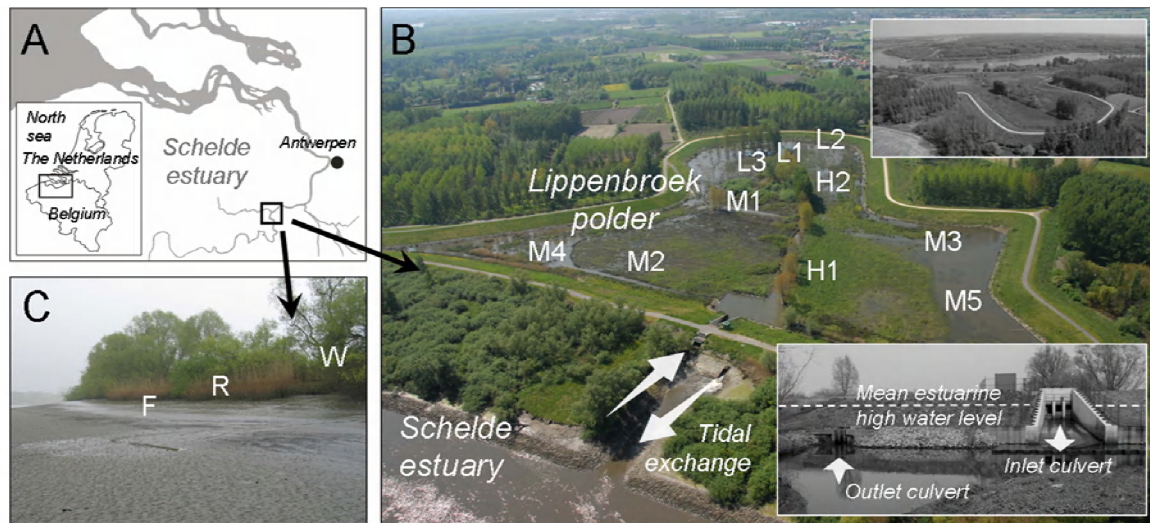
Fig. 1. A) Location map of the study area. B) Photograph of the CRT; H, M and L for respectively highly, moderately and lowly elevated sites (see Figure 2 for a complementary description); upper insert, global view of the study area; lower insert, exchange culvert system in the CRT. C) Reference sites located 600 m upstream the polder: W, R and F for respectively willow, reed and flat.
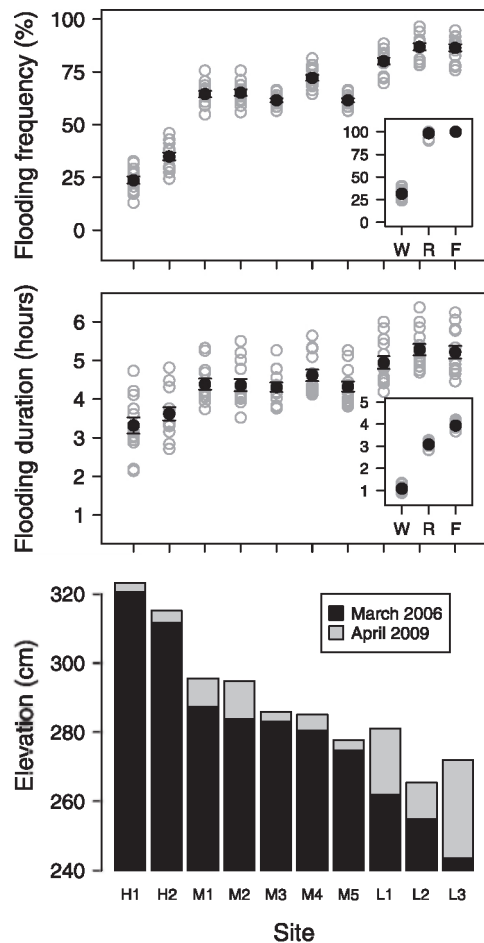
Fig. 2. Hydrological and topographical aspects of the monitoring sites. Black points represent mean values (± S.E.) of the 13 mean seasonal values (grey points).

combination with a safety function (protection against storm tides). The polder was formerly an arable land, and now is connected to the estuary by means of inlet and outlet culverts allowing water exchanges between the two systems (see Maris et al. (2007) and Beauchard et al. (2011b) for details). The polder has been under tidal influence by means of CRT system since March 1st, 2006. Adjacent to the polder, a gradient of intertidal habitats was selected as the most representative intertidal habitats in the estuary.

A spatiotemporal sampling framework was carried out through thirteen field samplings from April 2006 to April 2009 (once every three months, calendar-based seasons). In the CRT, ten permanent sites (20 m² each) covering the whole intertidal range were monitored, and in the estuary, three reference sites distributed within a comparable range of flooding frequency: tidal flat (F), reeds (R) and willow (W). Figure 2 displays the topographical and hydrological characteristics of

the sites. In the CRT, sediment deposition was rapid and elevation-dependent, with higher accretion rates in frequently flooded sites (Vandenbruwaene et al. 2011). Soil of lowly-elevated sites was almost entirely covered by 15 cm of river sediment in less than two years. At each site, three sediment strata were considered: 0 − 5 cm, 5 − 10 cm and 10 − 15 cm. A core-sampler (1 cm Ø) was used for soil extraction and strata were separated in three mixed samples based on 10 to 15 cores for each.

2. Abiotic descriptors and laboratory analyses

Sediment samples were stored at 4 °C and processed within 24 h. Extractable N and P were analysed in a sub-sample using 1 M KCl for N and ammonium acetate EDTA for P. After centrifugation, ammonium associated N (NH_4^+), nitrite and nitrate associated N ($NO2^- - NO3^-$), and phosphate associated P (PO_4^{3-}) concentrations were determined by colorimetric measurement with a segmented flow analyser. Soil pH (pH-H₂O and pH-KCl) were measured in the supernatant solution from soil extraction with distilled water (Houba et al. 1989); then, delta pH was calculated from pH-KCl minus pH-H₂O. Total nitrogen and total phosphorous concentrations were determined by acid digestion followed by colorimetric analysis, and particulate N and P were deduced by subtracting the total concentration from ionic concentrations. Amorphous silica concentration (ASi) was quantified on a thermo-inductively coupled plasmaspectrophotometer after sequential alkaline extraction for 3, 4 and 5 hours in 1 M Na₂CO₃ at 80 °C. Sediment water content was determined by measuring sediment weight after drying for 5 days at 70 °C. Organic matter concentration (OM) was estimated after loss on ignition. For this purpose, weight difference between oven dried sediment (105 °C) and sediment incinerated at 550 °C after 6 h was determined. Then, the remaining dry sediment was used to quantify several granulometric aspects by means of a laser diffraction particle size analyzer: mean grain size and clays/silts/sands percentages (respectively as the < 4, 4–63 and > 63 μm fractions). In the field, sediment resistance was quantified with a penetrometer.

3. Data analyses

3.1. Overall spatiotemporal pattern

Data were organized in a table composed of 13 dates × 13 sites × 3 strata in lines and the 15

sediment descriptors in columns. This dataset was explored in a synthetic way by means of a standardized principal component analysis (PCA) in order to derive the main gradients organizing the whole spatial and temporal information. PCA axis scores were used as synthetic descriptors to test differences between reference and CRT over time by means of Wilcoxon signed-rank tests and a non-parametric multiple test procedures (Behrens-Fisher type; Munzel and Hothorn 2001).

3.2. Temporal dynamics

Although estuarine water was likely to engender changes in soil CRT characteristics, the nature of temporal trends among sediment descriptors remained uncertain. For each descriptor, temporal profiles were computed respectively for estuary and CRT by averaging values per date and stratum. Common trends to estuary and CRT were identified by Pearson's correlation coefficients in order to detect processes inherent to the CRT sediment.

In a synthetic way, a last analysis consisted in testing the independence of temporal processes occurring in the CRT sediments. A multivariate procedure involving the 13 monitoring dates and the three sediment strata was applied i) to test the relationship between the estuary and the CRT temporal trajectories, and ii) to eventually explore the similarities between the trajectories and the stability of this relationship through depth. Numerically, each system was composed of the corresponding strata at the same dates for each descriptor. Three pairs of data tables (each representative of a sediment stratum) sharing the same lines (dates) and the same columns (sediment descriptors) were therefore considered; values were averages per system and date. This data set was analysed by applying the STATICO procedure (Thioulouse et al. 2004), which is based on the principle of co-inertia (Dray et al. 2003); axes are constructed so that they maximize the covariances between the descriptors of estuary and CRT sediments. The similarity between temporal trajectories (i.e. multidimensional structures consisting of two clouds of 13 paired points) was assessed by the Rv coefficient which is a multidimensional correlation index between two tables, equivalent to a simple Pearson's correlation coefficient between two variables (Escoufier 1973); its significance was tested by a Monte-Carlo procedure based on 999 random permutations of the lines of the two tables (Heo and Gabriel 1997). The STATICO analysis has been successfully applied in several estuarine and marine studies; see Simier et al. (2006), Carassou and Ponton (2007) and

Mendes et al. (2009) for further documentation.

Computations and graphical representations were realized using R software (R Development Core Team 2009); non-parametric multiple comparison and multivariate analyses were conducted respectively under the "npmc" and "ade4" packages available in R.

RESULTS

1. Overall spatiotemporal pattern

The PCA highlighted a strongly structured pattern along two components encompassing 68 % of the total information (Fig. 3A); correlation matrices are provided in Appendices 1, 2 and 3. The first axis characterized the particulate nature of the soil/sediment. It opposed particulate nutrients and silty elements to sands percentage and mean grain size. These descriptors positioned the sites along a flooding gradient, form site W to site F in the estuary, and reversely from lowly to highly elevated sites in the CRT (Fig. 3B and 3C). Both reference and CRT PCA axis scores were significantly correlated to flooding frequency (estuary, $N = 117$, $r = 0.72$, $p < 0.001$; CRT, $N = 390$, $r = -0.44$, $p < 0.001$). The most frequently flooded CRT sites exhibited the highest concentrations in particulate nutrients (see Appendix 4 for detailed values). Silts and ASi contents, which could reach respectively more than 70 % and 15 mg/g of dry material (DM) at low elevation, exceeded by far the values encountered in the reference sites. Site R and F were particularly marked by their high sand content (more than 40 %) and their low nutrient concentrations. Particulate N and OM concentrations were also highest at low elevation in the CRT (more than respectively 5 mg/g DM and 120 mg/g DM) whereas they peaked at respectively 4 mg/g DM and 120 mg/g DM in site W in the estuary. Particulate P ranged between 3 and 4 mg/g DM at the most (site W; in the CRT, mid and high elevations) and were lower elsewhere.

The second axis was also correlated to flooding frequency in both estuary and CRT (estuary, $N = 117$, $r = -0.93$, $p < 0.001$; CRT, $N = 390$, $r = -0.49$, $p < 0.001$). In both systems, this gradient was commonly related to a wetting process. It opposed dry, clayey and resistant sediment at high elevation to wet and ion rich sediment (PO_4^{3-} and NH_4^+) at low elevation.

Temporal changes were observed in the CRT over the three years along both axes (Fig. 3D). They consisted in a switch from the initial arable
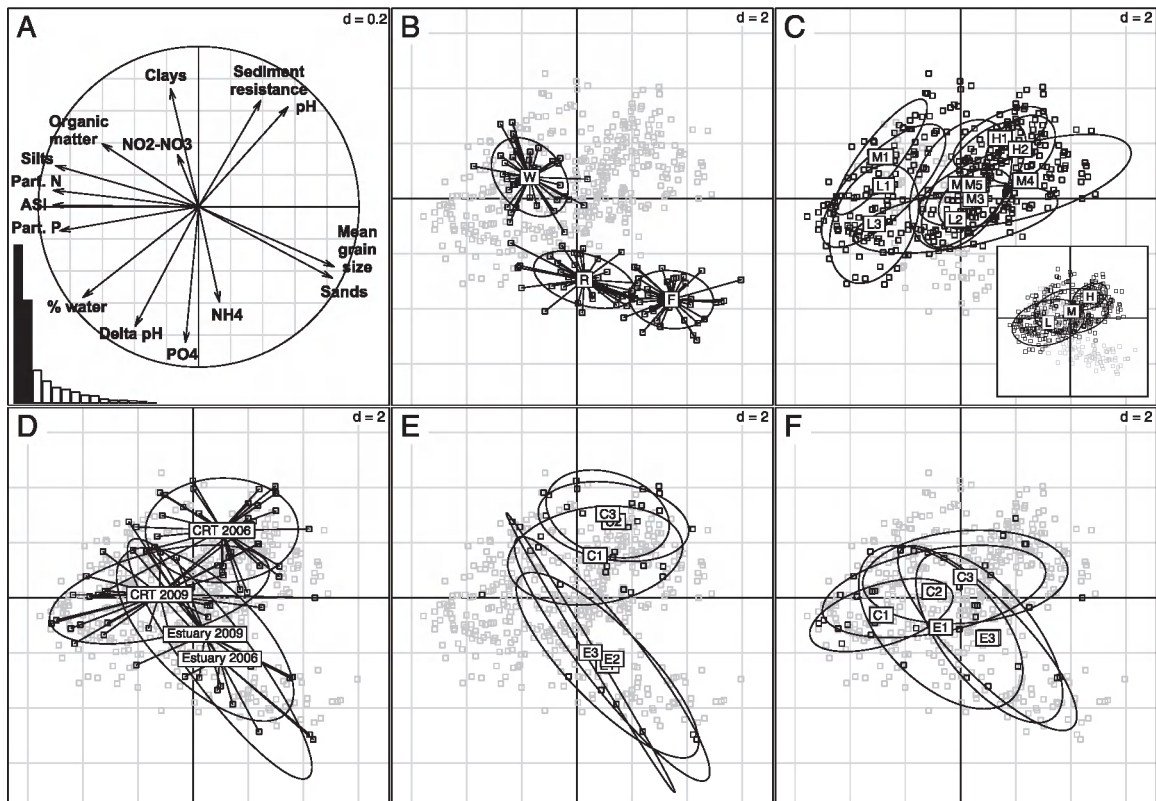
Fig. 3. PCA, overall spatiotemporal pattern. A) Correlations circle and eigenvalue diagram; axis 1 (horizontal), 41 %; axis 2 (vertical), 27 %. B) Reference sites. C) CRT sites; insert, CRT sites grouped per elevational category; see Figures 1 and 2 for codes. D) Sites grouped per system the first and last samplings (spring season). E) Strata grouped per system in spring 2006 ("E", estuary; "C", CRT; 1, 0 − 5 cm; 2, 5 − 10 cm; 3, 10 − 15 cm). F) Strata grouped per system in spring 2009. "d" indicates the grid scale.

Tab. 1. Pearson's correlation coefficients and significances between sediment descriptors and PCA axis scores (N = 507). Significance level: *, 0.05; **, 0.01; ***, 0.001.

Descriptor	PCA axis 1	PCA axis 2
Mean grain size	0.84 ***	-0.37 ***
Clays	-0.18 ***	0.74 ***
Silts	-0.91 ***	0.10 *
Sands	0.83 ***	-0.44 ***
Sediment resistance	0.39 ***	0.66 ***
% water	-0.72 ***	-0.57 ***
PO4	-0.08	-0.84 ***
Particulate P	-0.60 ***	0.39 ***
NH4	0.13 **	-0.59 ***
NO2-NO3	-0.13 **	0.33 ***
Particulate N	-0.91 ***	0.01
ASi	-0.86 ***	-0.15 **
OM	-0.89 ***	0.26 ***
pH	0.56 ***	0.62 ***
Delta pH	-0.40 ***	-0.75 ***

soil in spring 2006 to a silty and wet estuarine sediment in spring 2009 (Fig. 3D). To test the significance of these changes, PCA axes scores were used as synthetic surrogates of the sediment descriptors since they were strongly correlated to their most characteristic descriptors (Tab. 1). Wilcoxon signed-rank tests confirmed highly significant differences between April 2006 and April 2009 scores on both PCA axes ($p < 0.0001$); no significant difference was detected in the estuary ($p > 0.05$). Changes were particularly significant at mid and low elevations along the first axis (Tab. 2). Relative to estuarine elevation scores, mid and low CRT elevation scores switched from the right to the left of the axis over the three years. To a lesser extent, changes were also significant along the second axis, from top to bottom.

In parallel, a stratification developed in the CRT (Fig. 3E and 3F), suggesting a top-down building of an estuarine sediment through accretion (see Fig. 2). This interaction between

Tab. 2. Non-parametric multiple comparison tests between reference sites and CRT elevations scores on the PCA axes. "−" and "+" indicate respectively lower and greater mean axis score for CRT elevations. Significance level: *, 0.05; **, 0.01; ***, 0.001. See Figure 1 for codes.

		First year			Second year			Third year		
		W	R	F	W	R	F	W	R	F
First PCA axis score	H	+ ***	+ ***	− *	+ ***	+ ***	− ***	+ ***	+ *	− ***
	M	+ ***	+	− ***	+ ***	+	− ***	+ **	− *	− ***
	L	+	−	− ***	−	− ***	− ***	−	− ***	− ***
Second PCA axis score	H	+ **	+ ***	+ ***	+ ***	+ ***	+ ***	+ **	+ ***	+ ***
	M	+	+ ***	+ ***	+	+ ***	+ ***	−	+ ***	+ ***
	L	−	+ ***	+ ***	− **	+ ***	+ ***	− ***	+ ***	+ ***
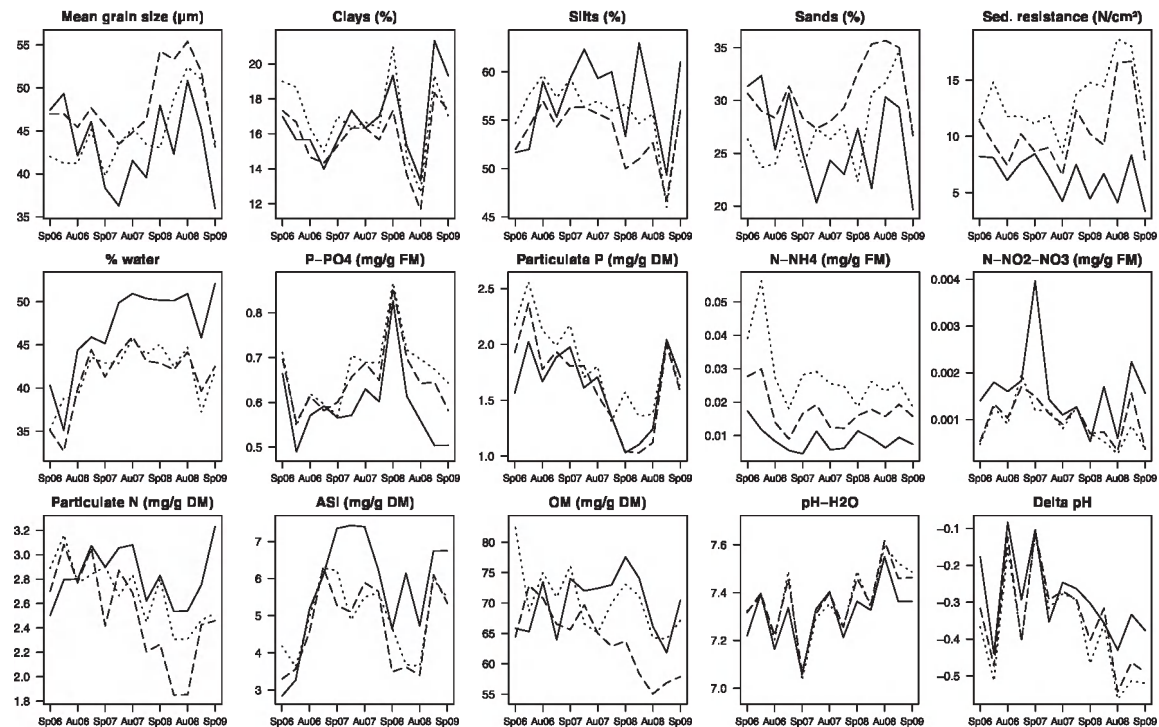
Fig. 4. Temporal profiles of the physicochemical descriptors in the estuary. In abscissa, seasons from spring 2006 (Sp06) to spring 2009 (Sp09). Continuous, dotted and finely dotted lines corresponding to respectively 0 − 5, 5 − 10, and 10 − 15 cm strata. FM: fresh material; DM: dry material.

elevation and accretion led to a more homogeneous top sediment at low elevation.

2. Temporal profiles

In both systems, average values of sediment characteristics exhibited non-seasonal variations, except $NO_2^- - NO_3^-$ concentrations in the CRT which were maximal in winter and minimal in summer (Fig. 4, Fig. 5). Additionally, several temporal series were highly similar and significantly correlated (Tab. 3). This suggests that processes occurred in a similar way in both the estuary and the CRT sediments. Series were strongly synchronous for mean grain size, clays, water content, particulate P, PO_4^{3-}, ASi and surface particulate N. Some descriptors exhibited a noticeable stratification; whereas PO_4^{3-} concentration increased with depth in the estuary, the gradient was reversed in the CRT sediment. On the long-term, reversible trends of particulate P, PO_4^{3-}, ASi and particulate N were observed from the second to the third year.

These results could not exclude possible independent processes in the CRT given the quantitative changes previously highlighted in the PCA. Therefore, differences between estuary and CRT (subtraction of the first from the second)
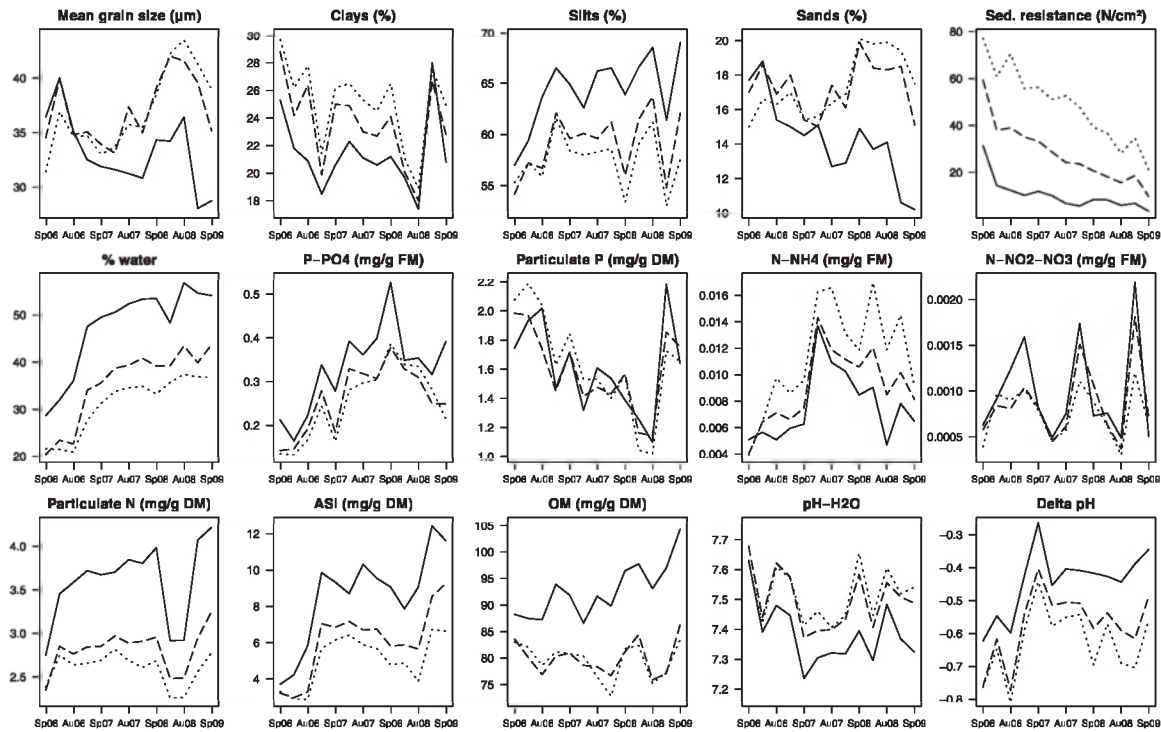
Fig. 5. Temporal profiles of the physicochemical descriptors in the CRT. In abscissa, seasons from spring 2006 (Sp06) to spring 2009 (Sp09). Continuous, dotted and finely dotted lines corresponding to respectively $0 - 5$, $5 - 10$, and $10 - 15$ cm strata. FM: fresh material; DM: dry material.

Tab. 3. Pearson's correlation coefficients between estuary and CRT temporal series (N = 13 dates). Significance level: *, 0.05; **, 0.01; ***, 0.001.

Descriptor	$0 - 5$ cm	$5 - 10$ cm	$10 - 15$ cm
Mean grain size	0.67 *	0.82 ***	0.82 ***
Clays	0.75 **	0.74 **	0.80 **
Silts	0.62 *	0.41	0.43
Sands	0.54	0.73 ***	0.48
Sediment resistance	0.50	-0.19	-0.47
% water	0.85 ***	0.77 **	0.58 *
PO4	0.54	0.59 *	0.74 **
Particulate P	0.72 **	0.75 **	0.90 ***
NH4	-0.04	-0.34	-0.42
NO2-NO3	0.23	0.59 *	0.60 *
Particulate N	0.74 **	0.29	0.54
ASi	0.78 **	0.69 **	0.71 **
OM	0.03	-0.13	0.44
pH	0.14	0.30	0.46
Delta pH	-0.09	0.02	0.26

were computed in order to identify the nature of such changes (Fig. 6). Clear trends of different natures revealed independent changes of the CRT soil. Differences in sediment resistance, water content, PO_4^{3-}, NH_4^+, pH and delta pH decreased over time. $NO_2^- – NO_3^-$ concentrations did not exhibit particular changes, but differences were lower in the top sediment, where a seasonality was

marked by winter maxima. Growing differences in particulate N, ASi and OM concentrations (for the 2 first strata concerning this latter) confirmed increase in these concentrations independently of possible common processes occurring in both estuary and CRT sediments. ASi enrichment in the top sediment exhibited a notable seasonal pattern, with maxima in winter and minima in summer. Hence, the difference between estuary and CRT values tended to disappear in some parameters, whereas it became greater in some others, especially particulate N, ASi and OM.

3. System trajectory

Correlations between estuarine and CRT data tables were highly significant ($0 - 5$ cm, Rv = 0.49, $p < 0.001$; $5 - 10$ cm, Rv = 0.38, $p < 0.001$; $10 - 15$ cm, Rv = 0.37, $p < 0.001$). Positioned in a common system of axes by the STATICO analysis, the temporal trajectories conserved a strong link on two main axes encompassing more than 80 % of the total co-inertia (Fig. 7A to 7C). The relationships among the three co-structures were also significant, but their strength decreased when confronting extreme strata ($0 - 5$ cm vs. $5 - 10$ cm, Rv = 0.51, $p < 0.001$; $5 - 10$ cm vs. $10 - 15$ cm, Rv = 0.85, $p < 0.001$; $0 - 5$ cm vs. $10 - 15$ cm,
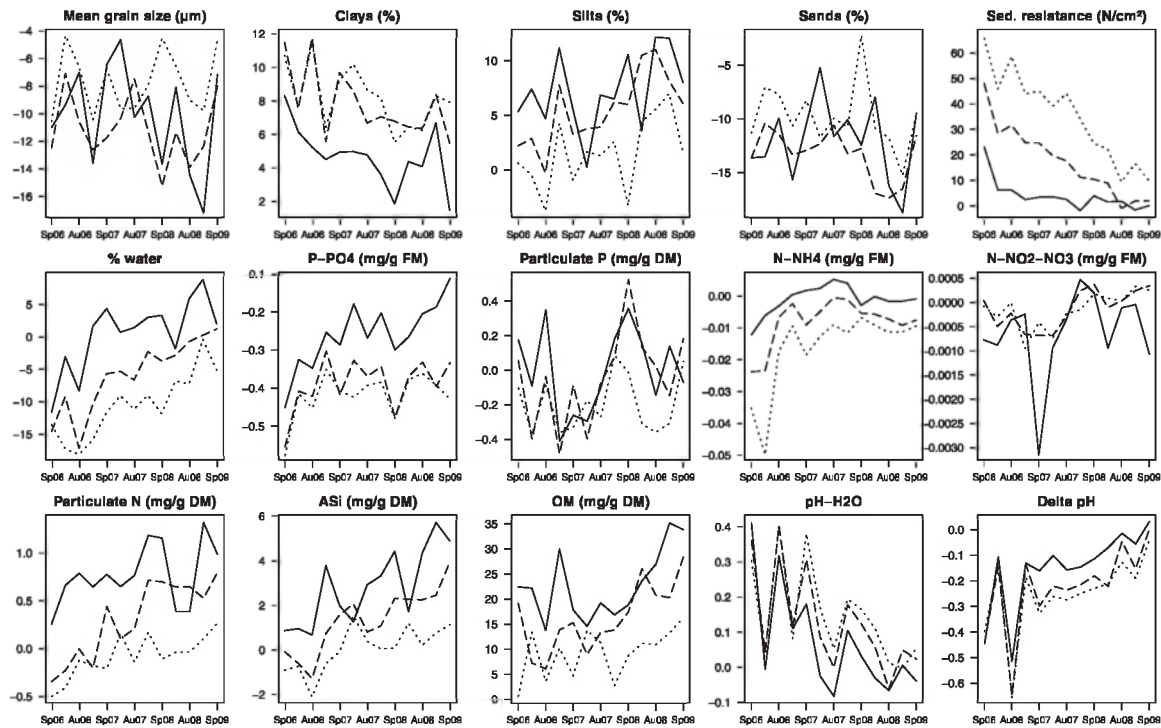
Fig. 6. Temporal profiles of physicochemical descriptor differences between CRT and estuary (values in Figure 5 minus values in Figure 4). In abscissa, seasons from spring 2006 (Sp06) to spring 2009 (Sp09). Continuous, dotted and finely dotted lines correspond to respectively the 0 − 5 cm, 5 − 10 cm and 10 − 15 cm strata. FM: fresh material; DM: dry material.

Rv = 0.27, p < 0.002). This means that common processes to estuary and CRT patterns were slightly different from top to bottom sediment. Indeed, processes were more variable along the second axis in the top sediment (Fig. 7D, Fig. 7G, Fig. 7J, Fig. 7M), albeit the estuary trajectory was more distorted (Fig. 7D). Although both systems temporally oscillated in a very similar way (Fig. 7D to 7I), the interplays between descriptors slightly changed from the first to the two other strata (Fig. 7J to 7O). In opposition to sands and mean grain size, increases in ASi, silts and water contents were the main drivers of the trajectory of both systems during a first phase (from spring 2006 to autumn 2007); this was also the case for particulate N, but only in the top sediment whereas its concentrations decreased in the two other strata. A second phase (from autumn 2007 to autumn 2008) was characterized by a partly reversed trend. During this phase, the association between mean grain size and sands, pointing to increase in these contents, was relatively constant through depth and mainly opposed to particulate P, particulate N and ASi, especially in the two deepest strata. In the CRT, ASi was constantly associated to silts, whereas this was less notable in the estuary were silts occupied an intermediate position between ASi and

particulate N. A last phase (from autumn 2008 to spring 2009) consisted of a return toward the state in autumn 2007.

DISCUSSION

1. Hydrological effects of the CRT system on sediment characteristics

Since sediments were shown to accrete up to several centimetres over the first year (Vandenbruwaene et al. 2011), the former agricultural soil gradually developed to a typical estuarine sediment. As demonstrated here, the CRT system mitigates tidal energy and rapidly engenders the development of a complete intertidal gradient, from high marsh to mudflat unlike in the estuary where eroded sheer cliffs form (Beauchard et al. 2011b). Accretion of a fine-grained and soft estuarine substrate at mid and low elevations, confirms the compensation potential of the CRT system for habitat impairment in the Schelde Estuary (Meire et al. 2005; Van den Bergh et al. 2005). On estuarine tidal flats and reed beds, the water current speed can reach 1 m/s (Flanders Hydraulics Research, June 2009, personal communication) whereas it
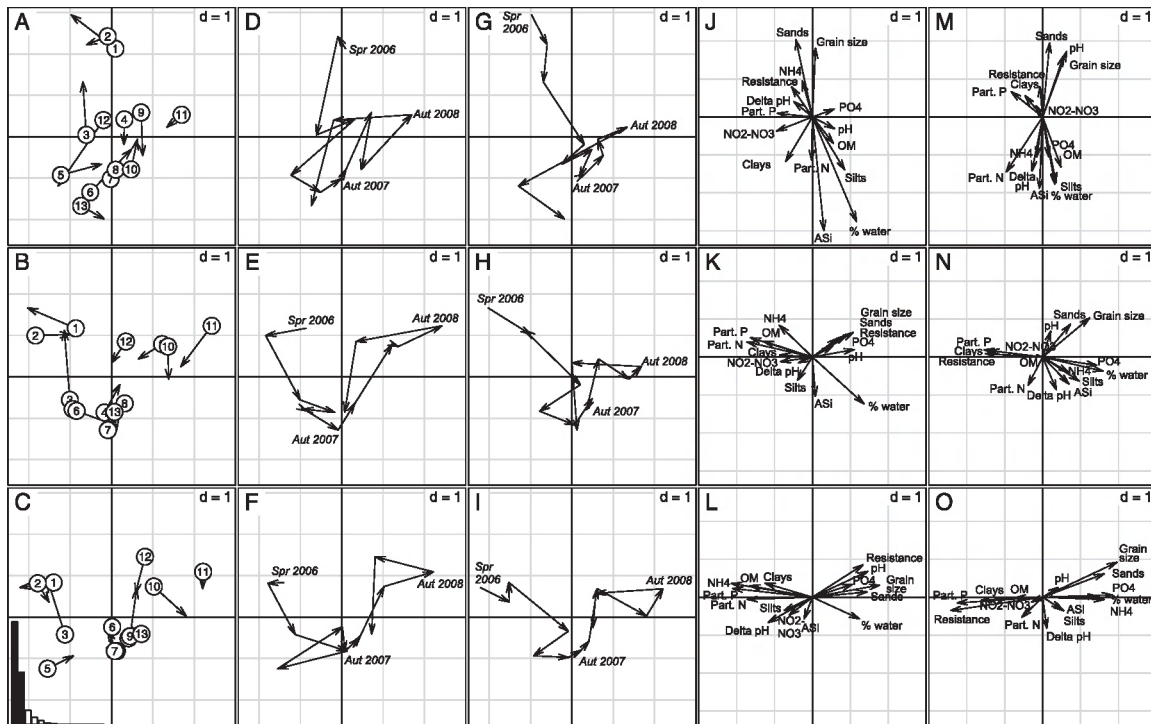
Fig. 7. STATICO analysis. Bottom-left corner, eigenvalue diagram: axis 1 (horizontal), 57 %; axis 2 (vertical), 29 %. The first, second and third row of graphs correspond to respectively the 0 − 5 cm, 5 − 10 cm and 10 − 15 cm sediment strata. A − C) Co-structure between the trajectories of estuary (circle) and CRT (arrow tip); arrow length indicates the lack of fitting. D − F) Estuary trajectory alone. G − I) CRT trajectory alone. J − L) Covariances of sediment descriptors in the estuary. M − O) Covariances of sediment descriptors in the CRT.

never exceeds a couple of cm/s on the CRT flats (field observations). This shear stress on the estuarine tidal flats (absolute weekly variations in elevation over one year: 16 ± 11 mm; maximum cumulated erosion = 43 mm; maximum cumulated deposition = 53 mm; O. Beauchard, unpublished data) is clearly illustrated here by the high sand content. Here, the high flow velocities limits the accumulation of fine sediments, hence explaining the lowest nutrient concentrations encountered in site F and R; sediment disturbances such as shear stress and dredging are known to engender a release of nutrients in the water column (Lohrer and Jarrell Wetz 2003; Nayar et al. 2007). This contrasts with the inversed nutrient concentration gradient in the CRT, from high elevation (low concentrations) to low elevation (high concentrations). The deposition of fine sediment fractions in the CRT confirms the enhanced capacity of CRT in trapping nutrients, usually adsorbed onto fine sediment fractions (Forstner et al. 1982; Nayar et al. 2007). Concomitant mass-balance measurements support these conclusions since the CRT acts as a sink for nitrogen (Maris et al. 2008) and heavy metals (J. Teuchies, unpublished data). Moreover, the physical properties of this newly-created substrate

offers important opportunities for ecological development such as the substrate quality for benthic invertebrates (Bock and Miller 1995), vegetation development as already shown in this CRT by Jacobs et al. (2009).

2. Organic matter and nutrient dynamics

Freshwater tidal marshes are detritus-based systems, hence explaining the strong organic nature of their sediments (Odum 1988; Findlay et al. 1990). The temporal trends of OM content of both CRT and estuary were independent (Tab. 3). This suggests that different processes governed the dynamics of organic carbon in the CRT. In the top sediment, the observed increase could be attributed to vegetation development and litter formation. Firstly, large amounts of organic matter are produced by plants which contribute to its accumulation in the sediment (Rooth et al. 2003). Secondly, the vegetation development was shown to exceed the reference sites production (S. Jacobs, personal communication). Plant and litter represent an important compartment in sediment carbon storage when buried in tidal freshwater marshes (Findlay et al. 1990; Megonigal and

Neubauer 2009). This supports the importance of autotrophy next to estuarine import in explaining organic matter accumulation.

Like particulate P, particulate N was strongly correlated to OM in both systems (Appendices 1, 2 and 3), hence supporting its organic origin. As expected, particulate N accumulated in the CRT sediment, hence ensuring an excess nutrient removal from the water. However, this nitrogen sink may have not accounted for the whole nitrogen removal since other pathways exist, such as denitrification of nitrate to gaseous dinitrogen or nitrous oxide. In the Schelde estuary, depending on habitat, nitrogen removal under gaseous form ranges from 2.4 % in freshwater marsh (Gribsholt et al. 2006) to 55 % in brackish intertidal flats (Middelburg et al. 1995).

On average, particulate P concentrations were similar in both systems, and no clear accumulation was observed in the CRT sediment despite tidal freshwater marshes are recognized to efficiently retain phosphorus (Hartzell et al. 2010). Increasing particulate P concentrations should have been expected in the CRT given its higher capability in trapping fine sediments. The absence of trend might suggest an immediate ionic P release (e.g. decomposition of the organic fraction) following deposition in the CRT sediment.

CRT NH_4^+ concentration was not or weakly correlated to OM and particulate N concentrations, whereas the relationships were significant in the estuary (Appendices 2 and 3). In the CRT, a greater OM accumulation rate than OM decomposition rate might explain this discordance. However, the decreasing trend of the difference between estuary and CRT NH_4^+ temporal profiles (Fig. 6) suggests an additional hypothesis related to floodwater. The increase in delta pH following the introduction of the flooding regime indicates an increase in ionic charge of the sediment particles, possibly enhancing desorption of cations, particularly in the top sediment. However, the link between NH_4^+ and delta pH in the CRT was found to be poorly significant (Appendix 2). In both systems, concentrations were found to increase with depth, whereas the reverse was observed in the difference, with a faster stabilisation in the CRT top sediment. Hence, this relative NH_4^+ enrichment in the CRT may have originated directly from simple top-down diffusion from the floodwater. Indeed, in a ^{15}N labelling study in a nearby tidal marsh (Gribsholt et al. 2005), NH_4^+ was shown to be partially retained by the marsh. The estuarine nature of the deposited sediments in the CRT may have also contributed to this stabilisation.

$NO2^--NO3^-$ and NH_4^+ concentrations were negatively correlated in both systems (Appendix 2 and 3) with concentrations of NH_4^+ increasing with depth. This suggests a conversion from the second to the first by nitrification following a hypoxia gradient from top to bottom sediment, and supported by recent field measurements. At high elevation, redox potential ranged from + 50 mV in the top sediment to –230 mV at 15 cm depth, and from –140 mV to –230 mV at a low elevation (J. Teuchies and O. Beauchard, April 2011). However, the marked seasonality of $NO_2^--NO_3^-$ CRT concentration contrasted with the estuary concentrations. The lower CRT concentrations were probably attributable to the seasonal vegetation dynamics, as the CRT has been colonized mainly by annual plants species exhibiting a clear seasonal pattern (Jacobs et al. 2009). This might result from a preference of plants and microorganisms for NO_2^- and NO_3^- to cope with NH_4^+ toxicity at high uptake rates (Stevens et al. 2011). The maximal summer vegetation development concurs with the minimal summer concentrations here, which suggests a plant uptake regulation. In the estuary, such a variation could have only been suggested in site R, since no plant occurs in site F, and pluriannual plants dominate in site W (*Salix* sp.).

When sediments are flooded, it is largely recognized that the subsequent hypoxia engenders a reduction of Fe^{3+} which then could release iron bounded PO_4^{3-} (Baldwin et al. 1997). The relative increase in PO_4^{3-} concentrations in the CRT sediments could have resulted from a release of PO_4^{3-} ions in deeper sediment layers and a subsequent bottom-up migration of ions, possibly re-adsorbed in the top sediment. This could additionally be attributed to a direct import from the estuary. Indeed, CRT concentrations were decreasing from top to bottom sediment contrary to those in the estuary, organized in an inverted way with highest concentrations in the deepest stratum (Fig. 4, Fig. 5). Since top sediments are generally more oxic, the release in PO_4^{3-} should have been expected lower in the top sediment. Since the concentration tended to stabilize in the top sediment when compared to the estuarine one (Fig. 6), as for NH_4^+ concentration, this might have resulted from the setting of an equilibrium between CRT sediment and floodwater concentrations. This assumption is supported by the positive correlation between PO_4^{3-} and water content in the CRT sediment, non-significant in the estuary sediment (Appendices 2 and 3). Moreover, in the estuary, OM and particulate P were positively correlated and both negatively correlated to PO_4^{3-}, but no significant correlation

was found between particulate P and PO_4^{3-} in the CRT. Hence, the negative relationship between particulate P and PO_4^{3-} in the estuary might have been explained by OM decomposition. In the CRT, imported PO_4^{3-} in the top sediment might have blurred the same process, at least at mid and high elevations (particulate P *vs.* PO_4^{3-} relationships; low elevation (L sites), $r = -0.35$, $p < 0.001$; mid elevation (M sites), $r = -0.02$, $p = 0.712$; high elevation (H sites), $r = 0.41$, $p < 0.001$).

The ASi accumulation is of importance as re-dissolved silica was shown to be released in high concentrations in interstitial water of this CRT (Jacobs et al. 2008). This dissolved silica is released to the flood water, providing a buffer function for silica limitation in the estuary. Such a limitation can engender harmful algal blooms and subsequently eutrophication (Van Spaendonk et al. 1993). Recent measurements showed that 80 % of ASi content in the Schelde marsh sediments originate from diatoms (Conley and Guo, unpublished data). The seasonal pattern in differential ASi concentration (Fig. 6) was interestingly linked to the seasonality of accretion rate in the CRT which was shown to be maximal in winter (Temmerman et al. 2003; Struyf et al. 2007; Vandenbruwaene et al. 2011). The differential ASi accumulation between CRT and estuary supports, once again, an impaired accretion capability of the tidal flats and reed beds.

3. Long-term system oscillation

In the estuary, no predictable pattern arose at the scale of a single year. The lack of a clear seasonality justifies the need for continuous measurements in order to detect comprehensive patterns. Indeed, the estuarine sediment characteristic patterns were subject to variations over the whole monitoring period. Starting from completely different states in 2006 (Fig. 3D), both systems oscillated in a same way as confirmed by the STATICO analysis. Hence, this covariation suggests the implication of processes common to both systems.

In the top stratum, the first phase of the trajectory was mainly driven by increases in water content, silt content, particulate N and ASi concentrations, while no change in flooding frequency or duration were registered during the study period (Beauchard et al. 2011b). As underlined by the concomitant opposition between these fractions in the STATICO analysis, silts replaced sands which could have increased ASi and particulate N concentrations as they were positively correlated to silt content (Appendix 1).

During the two last phases, degradation of some organic fractions rich in particulate N, particulate P and ASi, followed by a recovery, could be speculated. Indeed, conversion of particulate P to PO_4^{3-} could have taken place given their clear opposite patterns and the strong affinity between particulate P and OM. Also, resuspension of particulate material during the flood is possible (Kemp and Boynton 1984), but release from 15 cm depth has never been documented.

Overall, the three-year oscillation is difficult to interpret. Whereas seasonality was shown to govern the temporal pattern of water properties in estuaries from temperate zones (Livingston et al. 1997; Van Damme et al. 2005), the temporal patterns of the sediment characteristics were clearly non-seasonal. These patterns strongly contrast with the seasonality of most water characteristics in this part of the estuary according to a concomitant water quality monitoring in the same zone of the estuary (Van Damme et al. 2005). During the study period, not a single water descriptor exhibited the observed temporal trend observed here. The important influence of sediment dynamics (erosion / deposition) could be hypothesized, since they are relatively independent from the main water properties such as temperature and oxygen. Indeed, the stronger distortions of the estuary top sediment trajectory (Fig. 7D) probably highlighted the sediment instability induced by the shear stress. However, erosion or accretion of sediment from one season to another could not have completely driven the trajectories of both systems. Firstly, the sediment accretion in the CRT was constant over the whole study period (Vandenbruwaene et al. 2011). Secondly, the physicochemical variations observed here concerned the whole 15 cm horizon of the sediment. Also, bioturbation cannot explain this temporal pattern given its superficiality and seasonality (Beauchard et al. 2011a). Another hypothesis could support the implication of microorganisms. In estuarine sediments, organic nutrient dynamics are mainly controlled by the activity of microorganisms, and recent studies on marine sediments showed that bacterial community dynamics exhibit rather pluriannual than seasonal trends (Böer et al. 2009; Thiyagarajan et al. 2010). Moreover, Dale (1974), highlighted strongly significant relationships between bacterial numbers, nitrogen and granulometry in intertidal sediments. Hence, the influence of microorganisms could be hypothesized to explain the long-term variation in nutrient concentrations.

4. Conclusion

This study shows that the CRT system engenders a successful development of an estuarine sediment. The CRT sediment physicochemical characteristics strongly contrast with those encountered in the frequently flooded habitats of the adjacent estuary. The restoration technique was proved to counteract the shear stress exerted on estuarine tidal flats and reed beds where estuarine functions are deficient. Furthermore, on the long term, this study clearly shows that the CRT sediment reacts similarly to an estuarine sediment. More fundamentally, this suggests that the flooding process operates in a same way on both newly-created and reference habitats. However, some processes behind a long-term system oscillation remain to be elucidated. On a methodological point of view, these observations stress that investigations and predictive models on nutrient budget may dramatically be biased when conducted on the short term.

Conclusively, as part of the development of a healthy and multifunctional estuarine water system (Van den Bergh et al. 2005), the implementation of the CRT system on several hundreds ha along the Schelde estuary might have a significant influence on the biogeochemistry of the entire system. Other ecosystem compartments and trophic levels may react in an interactive way since concomitant studies reported the development of typical wetland organism communities among plant (Jacobs et al. 2009), invertebrates and birds (Beauchard et al., under review).

APPENDICES

Appendix 1. Pearson's correlation coefficients between sediment descriptors on the whole data set. MGS for mean grain size ($N = 507$). Significance level: *, 0.05; **, 0.01; ***, 0.001.

	MGS	Clays	Silts	Sands	Sed. resist.	% water	PO4	Part. P	NH4	NO2-NO3	Part. N	ASi	OM	pH
Clays	-0.48 ***													
Silts	-0.84 ***	0.10 *												
Sands	0.93 ***	-0.57 ***	-0.87 ***											
Sed resist.	-0.02	0.46 ***	-0.25 ***	-0.02										
% water	-0.37 ***	-0.30 ***	0.61 ***	-0.36 ***	-0.70 ***									
PO4	0.16 ***	-0.54 ***	-0.04	0.30 ***	-0.49 ***	0.51 ***								
Part. P	-0.59 ***	0.29 ***	0.45 ***	-0.52 ***	-0.02	0.11 *	-0.25 ***							
NH4	0.22 ***	-0.24 ***	-0.19 ***	0.28 ***	-0.14 **	0.17 ***	0.60 ***	-0.32 ***						
NO2-NO3	-0.17 ***	0.05	0.11 *	-0.11 *	0.07	-0.10 *	-0.24 ***	0.38 ***	-0.31 ***					
Part. N	-0.70 ***	0.15	0.76 ***	-0.70 ***	-0.34 ***	0.63 ***	0.08	0.64 ***	-0.08	0.11 **				
ASi	-0.65 ***	0.04	0.75 ***	-0.64 ***	-0.42 ***	0.77 ***	0.17 ***	0.35 ***	-0.07	0.07	0.78 ***			
OM	-0.82 ***	0.34 ***	0.82 ***	-0.84 ***	-0.18 ***	0.48 ***	-0.11 *	0.66 ***	-0.22 ***	0.16 ***	0.83 ***	0.68 ***		
pH	0.26 ***	0.20 ***	-0.38 ***	0.21 ***	0.52 ***	-0.65 ***	-0.51 ***	-0.14 **	-0.38 ***	0.17 ***	-0.47 ***	-0.47 ***	-0.33 ***	
Delta pH	-0.06	-0.48 ***	0.24 ***	0.04	-0.58 ***	0.63 ***	0.58 ***	0.02	0.24 ***	-0.06	0.30 ***	0.42 ***	0.11 *	-0.81 ***

Appendix 2. Pearson's correlation coefficients between sediment descriptors in the estuary. MGS for mean grain size ($N = 117$). Significance level: *, 0.05; **, 0.01; ***, 0.001.

	MGS	Clays	Silts	Sands	Sed. resist.	% water	PO4	Part. P	NH4	NO2-NO3	Part. N	ASi	OM	pH
Clays	1.00 ***													
Silts	0.72 ***	0.72 ***												
Sands	-0.85 ***	-0.85 ***	-0.98 ***											
Sed resist.	0.45 ***	0.45 ***	0.41 ***	-0.45 ***										
% water	0.37 ***	0.37 ***	0.57 ***	-0.54 ***	-0.26 **									
PO4	-0.53 ***	-0.53 ***	-0.62 ***	0.63 ***	-0.60 ***	-0.06								
Part. P	0.65 ***	0.65 ***	0.62 ***	-0.66 ***	0.69 ***	-0.02	-0.86 ***							
NH4	-0.38 ***	-0.38 ***	-0.50 ***	0.49 ***	-0.44 ***	-0.30	0.61 ***	-0.47 ***						
NO2-NO3	0.41 ***	0.41 ***	0.42 ***	-0.45 ***	0.50 ***	-0.07	-0.58 ***	0.53 ***	-0.39 ***					
Part. N	0.73 ***	0.73 ***	0.77 ***	-0.80 ***	0.43 ***	0.40 ***	-0.56 ***	0.79 ***	-0.39 ***	0.37 ***				
ASi	0.71 ***	0.71 ***	0.80 ***	-0.82 ***	0.31 **	0.60 ***	-0.52 ***	0.52 ***	-0.51 ***	0.46 ***	0.69 ***			
OM	0.81 ***	0.81 ***	0.91 ***	-0.94 ***	0.58 ***	0.38 ***	-0.71 ***	0.75 ***	-0.56 ***	0.45 ***	0.80 ***	0.75 ***		
pH	0.07	0.07	-0.03	0.00	0.43 ***	-0.13	-0.25 **	0.20 *	-0.28 **	0.01	0.02	-0.09	0.07	
Delta pH	-0.32 *	-0.32	-0.21 *	0.26 **	-0.52 ***	0.06	0.36 ***	-0.38 ***	0.25 **	-0.08	-0.25 **	-0.11	-0.30	-0.87 ***

Appendix 3. Pearson's correlation coefficients between sediment descriptors in the CRT. MGS for mean grain size ($N = 390$). Significance level: *, 0.05; **, 0.01; ***, 0.001.

	MGS	Clays	Silts	Sands	Sed. resist.	% water	PO4	Part. P	NH4	NO2-NO3	Part. N	ASi	OM	pH
Clays	-0.23 ***													
Silts	-0.77 ***	-0.34 ***												
Sands	0.92 ***	-0.21 ***	-0.85 ***											
Sed resist.	0.15 **	0.39 ***	-0.48 ***	0.27 ***										
% water	-0.47 ***	-0.36 ***	0.75 ***	-0.58 ***	-0.72 ***									
PO4	-0.42 ***	-0.24 ***	0.60 ***	-0.49 ***	-0.48 ***	0.74 ***								
Part. P	-0.61 ***	0.29	0.41 ***	-0.59 ***	-0.10 *	0.13 ***	0.01							
NH4	-0.05	0.02	0.10	-0.12 *	-0.01	0.26 ***	0.51 ***	-0.28						
NO2-NO3	-0.11 *	0.03	-0.01	0.00	0.06	-0.14 **	-0.23 ***	0.30 ***	-0.33 ***					
Part. N	-0.67 ***	-0.09	0.77 ***	-0.74 ***	-0.50 ***	0.72 ***	0.56 ***	0.60 ***	0.11 *	0.04				
ASi	-0.62 ***	-0.19 ***	0.77 ***	-0.70 ***	-0.54 ***	0.84 ***	0.61 ***	0.35 ***	0.10 *	0.01	0.80 ***			
OM	-0.75 ***	0.04	0.77 ***	-0.82 ***	-0.38 ***	0.60 ***	0.47 ***	0.68 ***	0.07	0.09	0.85 ***	0.68 ***		
pH	0.44 ***	0.10 *	-0.59 ***	0.56 ***	0.50 ***	-0.69 ***	-0.62 ***	-0.22 ***	-0.39 ***	0.26 ***	-0.63 ***	-0.58 ***	-0.54 ***	
Delta pH	-0.35 ***	-0.32 ***	0.58 ***	-0.42 ***	-0.55 ***	0.71 ***	0.53 ***	0.13 **	0.11 *	-0.13 **	0.55 ***	0.64 ***	0.41 ***	-0.81 ***

Appendix 4. PCA, spatiotemporal units and respective values of the considered physicochemical descriptor. FM: fresh material. DM: dry material.
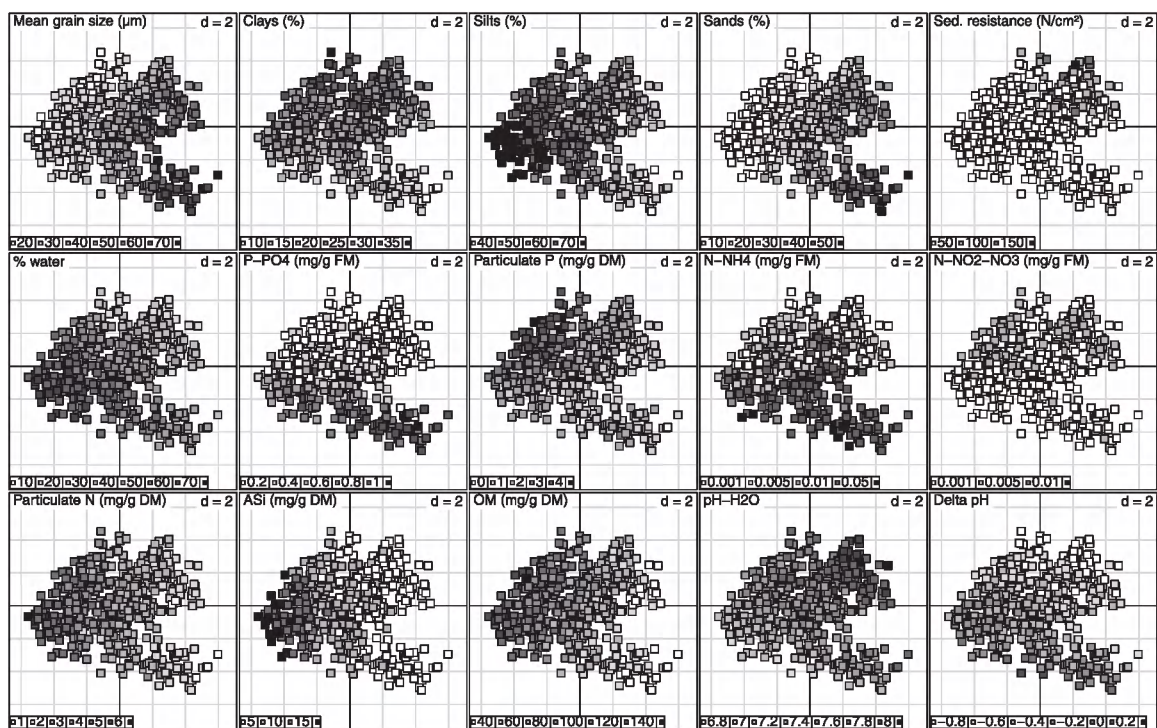
CHAPTER 4

SEDIMENT MACROINVERTEBRATE COMMUNITY FUNCTIONING IN IMPACTED AND NEWLY-CREATED TIDAL FRESHWATER HABITATS

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Abstract. Tidal freshwater ecology remains largely undocumented whereas related habitats experience strong anthropogenic pressures in many estuaries. Within 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. In newly-created habitats (CRT), which emerged from a former agricultural area, macroinvertebrate community development was investigated over a period of three years. In a comparative way, common estuarine habitats were monitored in order to verify the suitability of CRT in promoting invertebrate community development. In both systems, habitats were considered along a flooding gradient. Sediment characteristics were described and compared between CRT and reference sites. Differences were pointed out, and potential divergences in community functioning were explored by confronting environmental characteristics and organism' biological attributes. To this aim, a RLQ analysis was applied in combination with the fourth-corner method. Frequently flooded reference sites exhibited environmental characteristics consequent from a hydrological shear stress. On the contrary, the soft CRT hydrology engendered less stressed habitats at a comparable flooding frequency. After a phase of extirpation of the terrestrial fauna, this resulted in taxonomic and functional enrichment in the CRT. Macroinvertebrate communities were found to be strongly structured along the flooding gradient, and functional changes were dominantly conditioned by flooding frequency, with an immediate aquatic community development at low elevation. The RLQ analysis revealed significant environmental filtering of biological attributes mainly related to the terrestrial–aquatic transition and to the environmental adversity.

INTRODUCTION

Tidal freshwater wetlands offer special ecological interests as they are doubly confined: first, they lie at the end-point of the freshwater river continuum; second, the corresponding intertidal habitats mark the interface between aquatic and terrestrial biota. Typically, tidal freshwater marshes bordering river channels consist in progressive continuums, stretching over mudflat, helophyte and woody plant habitats where daily flood interacts with elevation (Baldwin et al. 2009; Struyf et al. 2009). The ecological importance of tidal freshwater wetlands has been mainly recognized according to the biogeochemical processes occurring in these systems (Morris et al. 1978; Odum 1988), hence conferring them a buffer role between upstream ecosystems and salt water zones.

Despite the fact that they are considered rare ecosystems, tidal freshwater wetlands nevertheless are known to occur in most of the largest river drainage estuaries (Baldwin et al. 2009). They have been mainly studied in North America where they are frequent, and also in Europe where most of them are found along the North Sea coast, in the Schelde, Maas and Elbe estuaries. In Europe, almost 10 % of the described tidal freshwater habitats are encompassed 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 several embankments have led to a drastic 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). Nowadays, since low marshes have been rendered rare by embankment, no more

pristine habitat gradient subsists (Struyf et al. 2009). To cope with both ecological and economical problems of the estuary, the Schelde is the fairway to the harbour of Antwerp, and a long-term vision for the Schelde estuary was determined as the development of a healthy and multifunctional estuarine water system that can be utilized in a sustainable way for human need (Van den Bergh et al. 2005). Part of the vision is the restoration of the intertidal habitats throughout the estuary, largely 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 prevent the implementation of a complete flooding gradient which conditions habitat diversity (Beauchard et al. 2011b). However, based on a system of inlet and outlet culverts, Controlled Reduced Tide system (CRT) is a new restoration technique to overcome this constraint. In 2006, a CRT was implemented in the freshwater zone of the Schelde estuary, and CRT was hypothesized to successfully restore intertidal habitats (Maris et al. 2007).

Facing an unjustified lack of interest, the paucity of knowledge in tidal freshwater ecology is unanimously recognized, particularly in invertebrate studies (Rundle et al. 1998; Reinicke 2000; Sousa et al. 2005). Paradoxically, invertebrates represent a key ecosystem compartment as they ensure energy transmission between autotrophic and heterotrophic components. Activities of soil and sediment invertebrates are multiple, such as organic matter decomposition and mineralization, humification, sediment mixing,

soil/sediment oxygenation and irrigation (Herman et al. 1999; Wallace and Webster 1996; Lavelle et al. 2006), whereas the loss of functional groups may cause impairments of ecosystem performance (Thrush et al. 2006). In tidal freshwater and brackish zones, increase in invertebrate biomass and density in response to nutrient enrichment were shown (Oviatt et al. 1993; Frost et al. 2009); this underlines another crucial role of invertebrates in impacted estuaries by neutralizing excess nutrients which often engender pervasive effects such as eutrophication (Jickells 1998).

In the Schelde estuary, only a few studies, focusing mainly on the whole salinity gradient, reported invertebrate data from the freshwater zone (Ysebaert et al. 1993; Ysebaert et al. 1998; Seys et al. 1999), and locally, none of them took the flooding gradient into account, leading to incomplete description of intertidal communities. Moreover, Ysebaert et al. (1998) advocated for studies focusing on the functional role of organisms in the ecosystem. Indeed, relationships between species communities and environmental features are generally investigated in order to explore habitat occupancy. This is typically processed by methods coupling sites × variables and sites × species matrices (Dray et al. 2003). However, the taxonomic nature of such kind of investigations limits the comprehension of the mechanistic processes explaining the species occurrences along a gradient. In recent years, methodological advents (Dolédec et al. 1996; Legendre et al. 1997; Dray and Legendre 2008) allowed some studies to identify biological
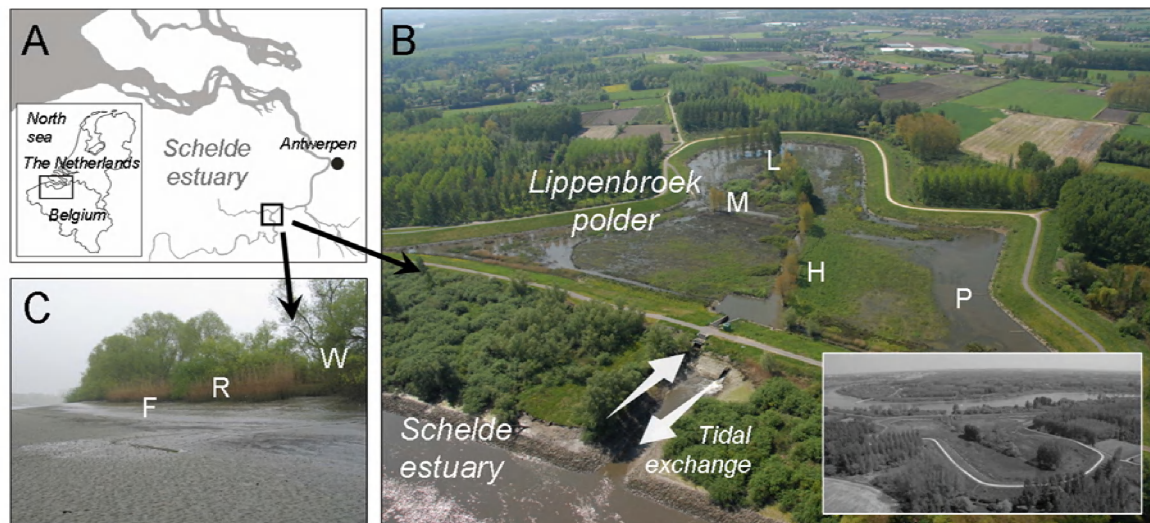
Fig. 1. A) Location map of the study area. B) Photograph of the experimental CRT; H, L, M and P for respectively high, mid, low elevation and pool; lower insert, global view of the location area. C) Reference sites located 600 m upstream the polder: W, R and F for respectively willow, reed, flat.

properties which determine species occurrences in a given environment, but there are still few published applications in estuaries (Dray and Legendre 2008).

Therefore, this study aims (i) to describe the current macroinvertebrate communities along a flooding gradient in the estuary, (ii) to verify the suitability of CRT in promoting invertebrate community development among the newly-created tidal habitats and (iii) to compare the community functioning between CRT and common reference habitats in the adjacent estuary using organism's biological attributes.

METHODS

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 Schelde River runs along 335 km from France to The Netherlands where its average discharge is about 120 m³/s, and its catchment area extend on 21 863 km². The estuary is particularly characterized by the length of the tidal wave which influences 235 km of the river and some downstream tributaries, encompassing 44 km² 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 about 5.2 m. The first CRT system was implemented in the Lippenbroek polder (8.2 ha; Fig. 1B), where agriculture was practiced until 2000. Now, it consists in a pilot project for intertidal habitat restoration in combination with safety function (protection against storm tides). It is connected to the estuary by means of inlet and outlet culverts allowing water exchanges between the two systems (see Maris et al. (2007) and Beauchard et al. (2011b) for technical details). The polder has been under tidal influence by means of CRT system since March 1ˢᵗ, 2006.

2. Sampling design and laboratory analyses

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 in four sites covering the whole gradients (Fig. 1B). Three of them cover the whole elevational range, giving rise to three flooding frequencies (see Fig. 2 for flooding frequencies and durations): 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 almost every day whereas site H is
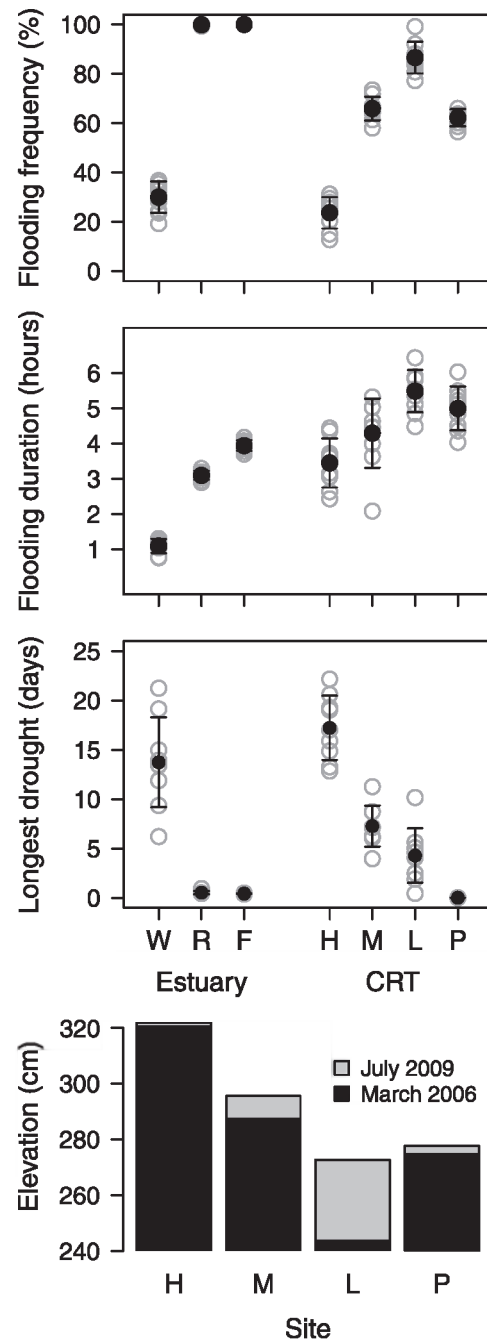
Fig. 2. Hydrotopographical context of the study. Top error bars: mean values (± S.D.) were calculated based on the 9 seasonal means from March 2006 to July 2009 (grey points). Bottom diagram: sediment accumulation is represented in grey.

flooded only during a couple of tides around spring tide. 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 of site L was cover by more than 15 cm of river sediments in less than one year. With respect to vegetation, whereas site H, mainly covered by *Urtica dioica*, did not exhibit noticeable changes, site M was progressively colonized by *Epilobium hirsutum* and *Lythrum salicaria* (Jacobs et al. 2009). In 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 concomitantly monitored (Fig. 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). Consequent from tidal squeeze, this gradient exhibits a steep profile where erosion sheers form and where a shear stress prevent a natural sedimentation at low elevation (Meire et al. 2005; Van den Bergh et al. 2005; Beauchard et al. 2011b). Therefore, R and F habitats were considered as deteriorated references in order to assess the capability of the CRT system to counteract the consequences of tidal squeeze.

A core sampler (4.6 cm Ø) was used to sample invertebrates from top sediment to 15 cm deep. Samples were based on six replicates and were stored in 5 % formalin. In the lab, the mineral part was removed though a 500 μm mesh size sieve. After sorting, worms were stored in 5 % formalin and arthropods in norvanol. Taxonomic identification was realized under microscope; different bibliographic sources were used (see Appendix 1).

Concomitantly, sediment was sampled with a core-sampler (1 cm Ø) in order to characterize the physicochemical environment of invertebrate communities in the same sediment layer (15 cm deep). Each sample was based on 10 to 15 mixed cores spread over the whole site surface (25 m²). Samples were stored at 4 °C and processed within 24 h. Sediment water content was determined by measuring sediment weight after drying for 5 days at 70 °C. Content in organic matter (OM) was estimated after loss on ignition. For this purpose, weight difference of oven dried sediment (105 °C) and sediment incinerated at 550 °C after 6 h was determined. Then, 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 clays/silts/sands percentages (respectively as the < 4, 4–63 and > 63 μm fractions). In the field, sediment resistance was quantified with a penetrometer.

3. Sediment characteristics and faunistic descriptions

Firstly, the main features of sediment and fauna were described. Sediment characteristics were explored by a standardized Principal Component Analysis (PCA) on the 7 sediment descriptors. Then, taxa and their main occurrences were presented, and the occurrences were displayed per site and per date.

4. Community functioning: relationships between environmental descriptors, taxa's occurrences and taxa's biological traits

RLQ analysis (Dolédec et al. 1996) was conducted to explore the biological mechanisms that determine the taxa occurrences on the environmental gradients. To this aim, three tables were considered: environmental descriptors (table **R**; date-site × descriptors; the 7 sediment characteristics plus flooding frequency and longest drought), taxa's occurrences (table **L**; date-site × taxa; log-transformed densities, pooled replicates), and taxa's biological traits (table **Q**; taxa × biological traits; qualitative attributes, see Tab. 1). This method allows the simultaneous ordination of the three tables based on the singular value decomposition of the matrix R^tLQ. Table **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 Correspondences Analysis (MCA; Tenenhaus and Young 1985) were performed respectively on tables **R** and **Q**. To justify a simultaneous ordination of the three tables, the significances of the links between table **R** and **L** on the one hand, and tables 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, L^t and **Q** matched by taxa). *Rv* coefficient (Escoufier 1973), an equivalent of a simple Pearson's correlation coefficient between two variables), was computed in each co-inertia analysis; its significance was tested by a Monte-
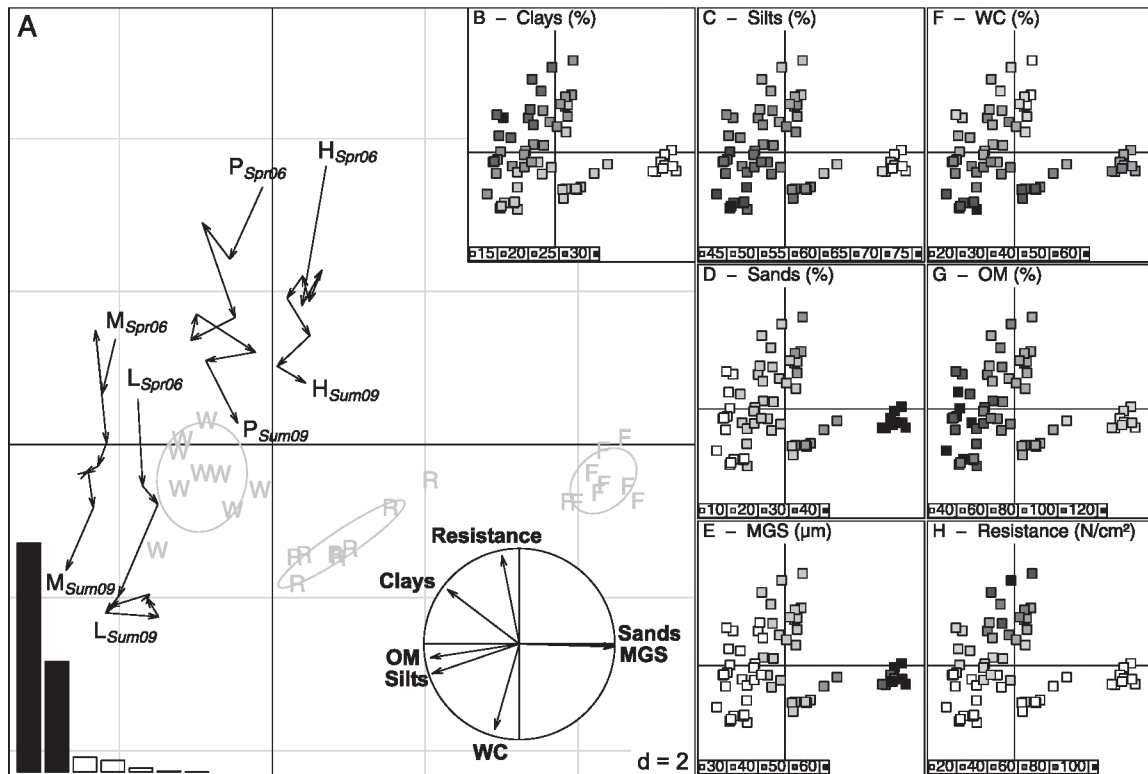
Fig. 3. PCA on sediment descriptors. A) Bottom left corner, eigenvalues diagram: first axis (horizontal), 62 %; second axis (vertical), 30 %; bottom right corner, correlation circle (OM, organic matter; WC, water content; MGS, mean grain size); grey letters, reference sites; black arrows, CRT sites represented 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).

Carlo procedure based on 9999 random permutations of the lines of **R** and **Q** (Heo and Gabriel 1997). 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).

Although a significant RLQ co-inertia can be expected under the null hypothesis, this does not imply that biological attributes are all correlated to environmental descriptors (Legendre et al. 1997). Therefore, the fourth-corner method (Dray and Legendre 2008) 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) was used to test the null hypothesis according to which individuals of a species are randomly distributed with respect to site characteristics which offer no optimal living conditions.

Computations and graphical representations were realized using R software (R Development Core Team 2010); multivariate analyses were run on the "ade4" package available in R.

RESULTS

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 substrate (> 40 % sands) and a lower organic matter content (< 80 mg/g dry material) in sites R and F by opposition to the higher silt content in CRT sites (% silts > 50 %). Within the CRT, sites L and M were globally composed of a finer substrate than sites H and P.

Axis 2 encompassed clear temporal changes in CRT sites, mainly driven by a water content enrichment, and leading to a softer sediment

Tab. 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 Appendix 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 W	Estuary R	Estuary F	Estuary %	CRT H	CRT M	CRT L	CRT P	CRT %	Size	Respiration	Trophic status	Foraging mode	Life duration	Voltinism	Regeneration potential	Burrowing ability	Swimming ability	Resistance
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	Limonini					X				0.02	Medium	Trachea	Omnivore	Epibenthic	Short	Univoltine	None	Medium	None	None
Gastropods	Radix					X				0.02	Large	Tegument	Herbivore	Epibenthic	Long	Multivoltine	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		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	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	Detritivore	Epibenthic	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	X	0.04	Medium	Tegument	Detritivore	Epibenthic	Long	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	Desiccation
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
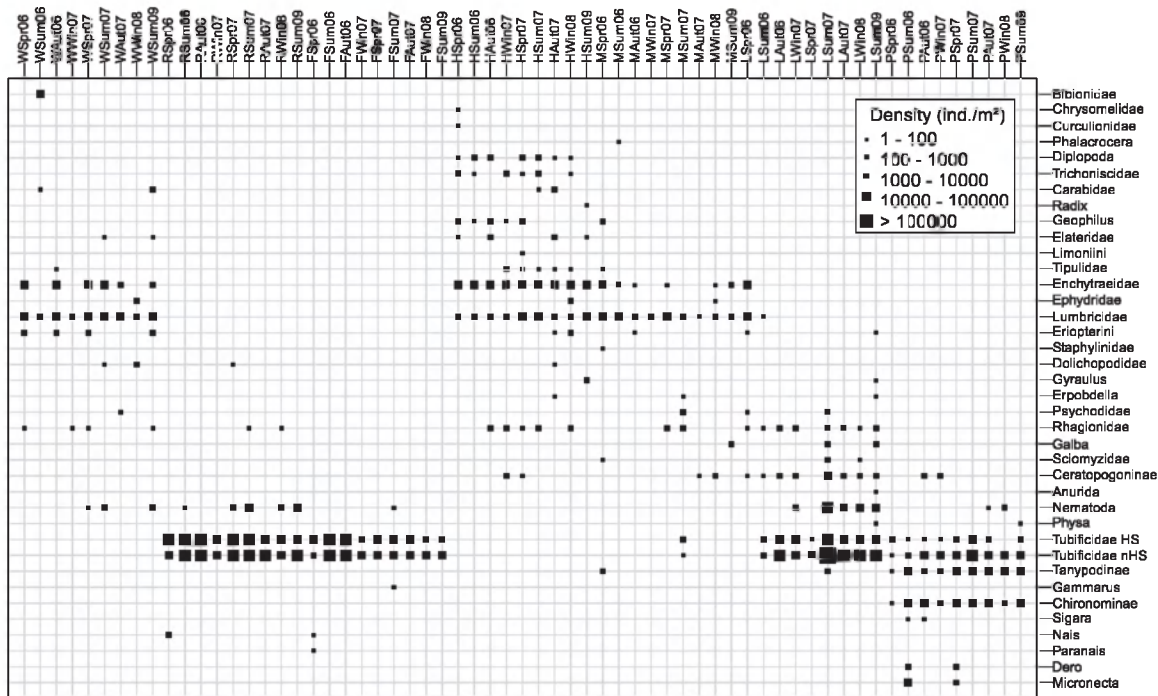
Fig. 4. Taxa densities per site (W to P, see text) over the study period ("Spr06" to "Sum09" for spring 2006 to summer 2009).

(decreasing sediment resistance). To a lesser extent, these changes were accompanied by a replacement of clays by silts, 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, no such stabilization appeared in site P and M (Fig. 3).

2. Faunistic description

A total of 38 taxa were encountered over the whole study period (Tab. 1; Fig. 4). Globally, taxa richness was higher in CRT sites (from 1 to 11 taxa) than in the adjacent reference sites (from 2 to 5 taxa; Appendix 2; Appendix 3). Site R and F were the most impoverished, with communities dominated by tubificids. Site W, H and P exhibited a more constant taxa richness over the study period, highest in sites H and P. Taxa richness was the most variable in sites M and L, with a clear decrease the first year in both sites, followed by an increase during the rest of the study period in 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 enriched site H; Tipulidae and

chilopods (*Geophilus* sp.) were encountered only the first season in 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 nematods, but enriched with different Diptera and gastropod species, particularly in summer 2009. Densities (individuals/m²) were clearly related to flooding frequency in the estuary, from several ten thousands in sites R and F (slightly lower in site F) to several hundreds to thousands ind./m² in 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 in site L than in reference sites R and F. Beside its lower taxa richness, site M contrasted with reduced densities never exceeding more than a few thousands ind./m². Site P, like site H, exhibited few changes and was mainly composed of chironomids and tubificids (several thousands ind./m²).

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 = 0.46, p < 0.0001), hence allowing carrying out a RLQ analysis, where the randomization test detected a significant co-inertia between

environment and organisms' biology ($p < 0.0001$). The amounts of projected variance on the RLQ axes are provided in Tab. 2. The fourth-corner method highlighted significant relationships between environmental descriptors and most of biological attributes (Tab. 3).

Three main axes emerged from the ordination (Fig. 5A and 5B). 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

Tab. 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

Tab. 3. Results of the fourth-corner analysis. Signs indicate whether relationships between biological attributes and environmental descriptors (Pearson's correlation coefficients) are positive (+) or negative (−). No sign, non-significant relationship; rejection level $\alpha = 0.05$.

		Flooding frequency	Drought	Clays	Silts	Sands	MGS	Water content	OM	Sediment resistance
Size	Small	+	−					+		
	Medium	+	−	−			+	+		−
	Large	−	+	+			−	−	+	+
Respiration	Trachea	−	+	+			−	−		+
	Tegument	+	−	−		+	+	+	−	−
	Gill						−	−		
	Plastron		−	+						+
Trophic status	Predator			+	+	−	−		+	
	Herbivore	−	+				−			
	Omnivore									
	Detritivore	+			−	−	+	+	−	
Foraging mode	Epibenthic	+	−	−	−	+	+	+	−	−
	Both	−	+	+	+	−	−	−	+	+
	Endobenthic	−	+							+
Life duration	Short		−	+	+	−	−		+	+
	Long	+	−	−		+	+		−	−
Voltinism	Univoltine	−	+	+	+	−	−	−	+	+
	Multivoltine	+	−	−	−	+	+	+	−	−
Regeneration	None	−	+	+	+	−	−	−	+	+
	Fragmentation	+	−	−	−	+	+	+	−	−
Burrowing ability	Weak	−	+	+	+	−	−		+	+
	Medium			−	+					+
	Strong	+	−	−	−		+	+	−	−
Swimming ability	None	−	+	+	+	−	−	−	+	+
	Weak	+	−		−	−		+		−
	Strong	+	−	−	−	+	+	+	−	−
Resistance	Desiccation				+	−	−			
	Flood	−	+	+	+	−	−	−	+	
	None	+	−	−	−	+	+	+	−	

opposition between flooding frequency and drought along the first axis underlined the elevational ordination common to both systems from high to low sites. From the biological point of view, this corresponded to decrease in body size (Fig. 5D), a transition from tracheal to tegumentary respiration (Fig. 5E), a switch to detritivory (Fig. 5F), an increased epibenthic foraging mode (Fig. 5G), a reproduction rather multivoltine (Fig. 5I), a regeneration capability (Fig. 5J) and a stronger swimming ability (Fig. 5L).

To a lesser extent, axis 2 also encompassed a part of this gradient, mainly in the CRT. However, the granulometric effect at low elevation, opposing site R and F to site L, was marked by divergent functional attributes. Between site F and L, the main biological responses were mainly driven by decreasing body size (Fig. 5D), life duration (Fig. 5H), and swimming ability (Fig. 5L); concomitantly, they were driven by increased branchial respiration (Fig. 5E), predation (Fig. 5F), and resistance to desiccation (Fig. 5M).

According to Figure 4, the communities in sites F and R were strongly represented by tubificids, similarly to site L. The specific sandy nature of sites R and F substrates induced a strong faunistic correspondence to these organisms (Fig. 5C, right side of the first axis). By contrast, the enriched fauna in site L was characteristic of a muddy substrate (silt rich).

Two observations arose from the third axis, along which the ecological variability was mainly encompassed by the CRT samples (Fig. 6). Firstly, it opposed the water permanency of site P, characterized by plastron respiration (*Sigara* sp. and *Micronecta* sp.), to drought, to which the weak swimming ability of *Erpobdella* sp. was the most characteristic attribute. Secondly, within each site of the CRT, the third axis encompassed a temporal change characterized by silt and water sediment enrichment. The main biological responses were an increase in density of organisms able to swim and a shift to a predatory status (Rhagionidae and *Erpobdella* sp.). However, only a limited part of MCA axes 2 and 3 was projected on the third RLQ axis (Fig. 6; correlation circle). Hence, this accounted rather for environmental change as regard to the amount of projected PCA inertia. Beside the rapid settlement of Tubificidae since the second season (site L), the biological changes were particularly attributable to gastropods (tegumentary respiration; herbivorous and detritivorous) over the whole flooding gradient (*Radix* sp. and *Gyraulus* sp. in site H; *Gyraulus* sp., *Galba* sp. and *Physa* sp. in
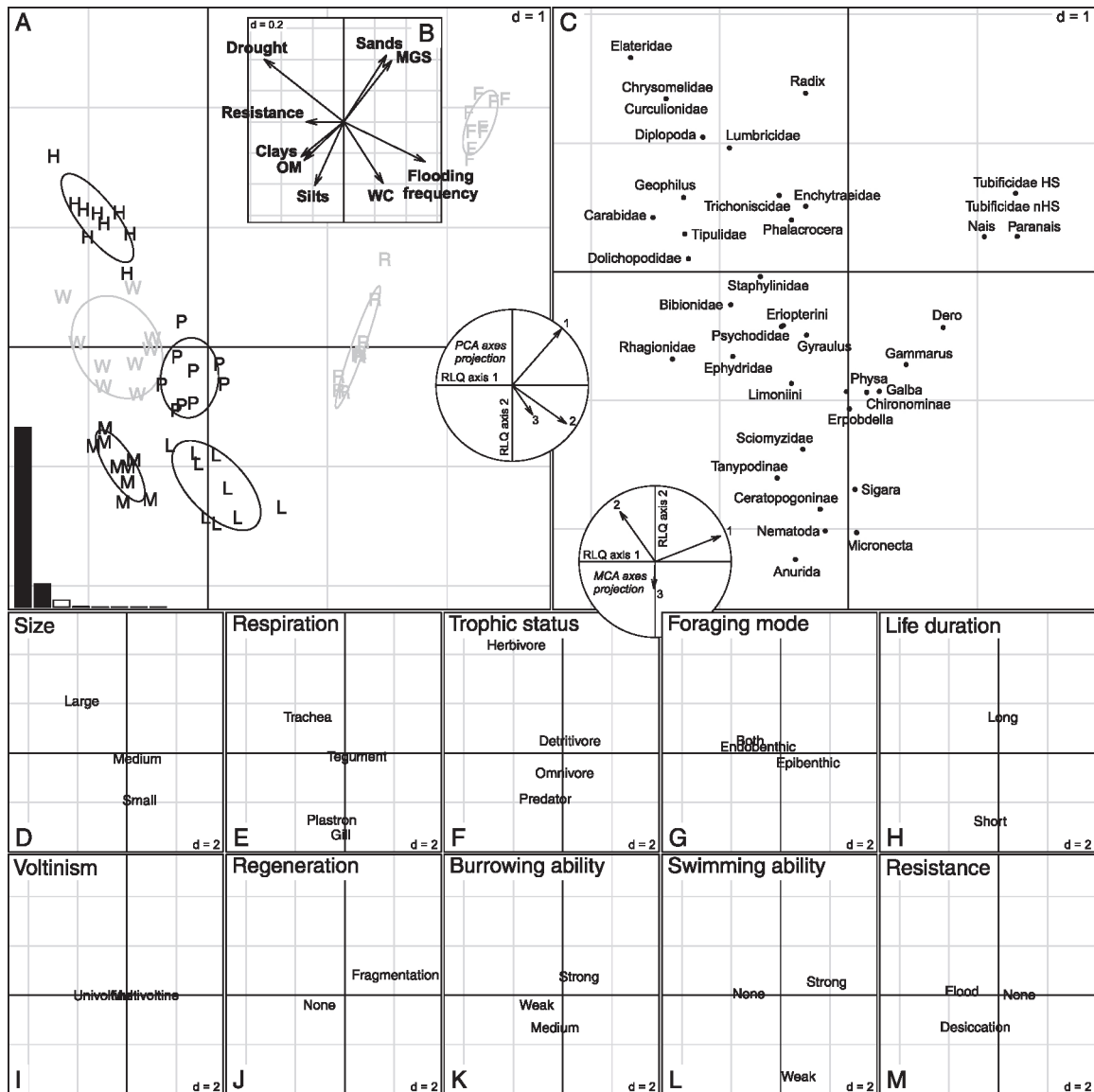
Fig. 5. RLQ analysis. A) Samples (grey and black letters) grouped per site and eigenvalues diagram; first axis (horizontal), 85 %; second axis (vertical), 11 %. B) Environmental descriptors. C) Positions of taxa. Correlation circles display the projections of the three first axes of the separate analyses on the RLQ axes. D-M) Positions of biological attributes. "d" indicates the grid scale.

sites M, L and P), mainly observed the last season (Fig. 4 and Fig. 5C).

DISCUSSION

1. Potential methodological drawbacks

Given the variable nature of sediments encountered among the sites, the sampling strategy might have been unsuitable for some faunistic groups. Although the core sampler diameter ranged within what it is 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 as additional method such as pitfall traps could have allowed 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 as sampling was shown to be more accurate than trapping for estimating a population (Briggs 1961).

Despite the initial CRT communities (from site H to site L) were not completely similar, they were mainly composed of terrestrial worms. The slight faunistic dissimilarity in site L (sampled
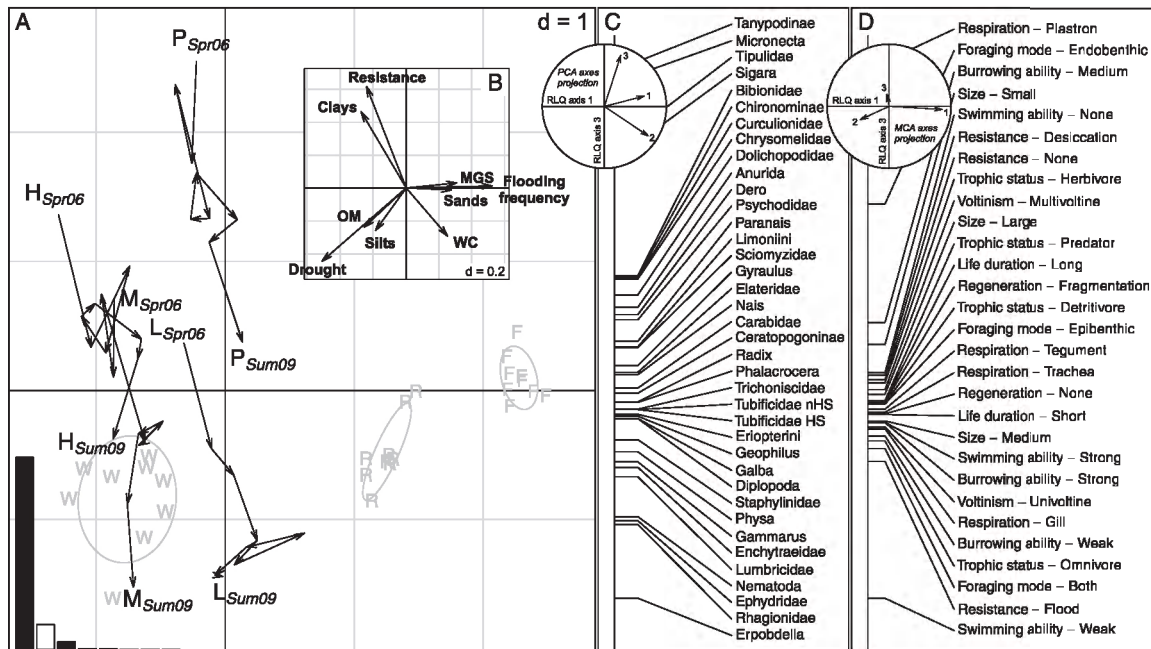
Fig. 6. RLQ analysis, axes 1 (horizontal) and 3 (vertical, 3.4 %). A) Samples grouped per site (grey letters and arrow intersections); in grey, reference sites; in black, CRT sites represented according to their temporal trajectory, from spring 2006 (Spr06) to summer 2009 (Sum09). B) Environmental descriptors. 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.

in April) was probably attributable to a rapid flooding effect after only one and half month of strong tidal influence (implemented on March 1st, 2006), extirpating most of tracheal organisms still occurring in site H and M.

Depending on the flooding frequency, faunistic changes were either slightly perceptible (site H) or immediate (site L), contrary to sediment characteristics which continuously changed during the first three years as shown in a concomitant study (O. Beauchard, unsubmitted manuscript). The lack of concordance between environment and biological attributes on the third axis of the RLQ analysis may be attributable to a differential vertical stratification between sediment characteristics and the fauna. Whereas a stratification was observed for most of sediment descriptors through the whole 15 cm, the main part of the fauna was mainly distributed in the 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 have not been sufficiently relevant to represent the specific environmental requirements of the fauna. But 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.

Analytically, the strong relationship between environmental and faunistic characteristics according to the co-inertia analysis supports the robustness of the adopted sampling strategy in comparing reference and CRT sites on a common basis. Moreover, the fourth-corner analysis confirmed the spatiotemporal specificity of organisms' biology.

2. General faunistic considerations

Situated at the end-point of the river continuum, the most aquatic tidal freshwater habitats exhibit impoverished communities highly dominated by collector/detritivorous organisms as generally encountered in lowland temperate rivers (Vannote et al. 1980; Statzner and Higler 1986). 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 strongest changes occurred, the settled aquatic taxa are generally encountered in non-impacted tidal freshwater marshes of North America (La Salle and Bishop 1987; Baldwin et al. 2009; Johnson 2010).

3. Common reference community state

Compared to the few observations in the freshwater part of the estuary (Ysebaert et al. 1993; Ysebaert et al. 1998; Seys et al. 1999; Hampel et al. 2009), no noticeable difference appeared in the composition of the macroinvertebrate communities occurring on the tidal flat and reed bed (sites F and R). These communities are still dominated by Tubificidae, and, to a lesser extent, Nematoda. Naididae were additionally found, but in a restricted abundance. At the scale of the 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 sole 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 concomitant study on sediment heavy metals in the CRT and the same reference sites highlighted higher concentrations in the CRT than the in reference sites (Teuchies et al. 2012), and according to which concentrations in both CRT and reference sites exceeded by several times contamination thresholds (Grumiaux et al. 1998). Although all concentrations exhibited a three-year decrease, they never reach lower concentrations than those encountered in the reference sites after three years. Moreover, recent sediment redox measurements (J. Teuchies and O. Beauchard, April 2011) revealed 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 in sites R, F, M and L; values were higher in the less frequently flooded sites W and H. Hence, these complementary observations support the preponderance of physical considerations such as shear stress in explaining the faunistic impoverishment in reference sites as regard to CRT sites. The granulometric characteristics and organic matter concentration clearly underline the different physical contexts between the lowest estuary and the CRT sites. In the estuary, the water current velocity can reach 1 m/s whereas they never exceed a couple of cm/s on the CRT flats (Beauchard et al. 2011b). Such conditions may engender dramatic consequences as 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 of sites R and F, where aquatic oligochaetes could maintain viable populations under shear stress. Associated to longevity and absence of resistance form, this support a process of A-strategy selection *sensu* Greenslade (1983), induced by the highly predictable adversity of these habitats from one tide to another. The physical implication of this adversity is also supported by the reduced abundances in site F which was more exposed to tidal energy (Appendix 3). 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) constraining sediment consumability by Tubificidae. These observations concur with the findings of Mellado Diàz et al. (2008) who observed an adversity gradient induced by anthropogenic activities 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 faunistic 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 transversal profile where erosion sheers form. This engenders a depletion of intermediate habitats (Beauchard et al. 2011b) and associated fauna.

4. Functional change in CRT communities

In the CRT, few changes were observed at high elevation (site H). Mainly terrestrial during at least the two first years, the remnant organisms did not seem to be sensitive to the imposed flooding regime and the few winter storm tides engendering prolonged inundations (Beauchard et al. 2011b). Indeed, most of the 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). Comparatively, 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, since 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 (O. Beauchard, unsubmitted manuscript).

At mid elevation (site M), the decrease in organism's densities and taxa richness was marked by the early extirpation of organisms with tracheal respiration. Only organisms with tegumentary respiration survived (Lumbricidae and Enchytraeidae) or replaced the extirpated fauna (Diptera, gastropods). This corresponds to the observations of 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. Here, the settlement of the gastropods *Galba* sp. and *Physa* sp., observed during the last summer, are in agreement with these observations. From non- to more frequently flooded zones, these taxa indicate a functional shift from a tracheal and herbivorous living mode toward a more amphibious one, characterized by tegumentary respiration and detritivory. Indeed, the high plant productivity in site M (S. Jacobs, personal communication) was accompanied by a high amount of decaying organic matter.

At low elevation (site L), changes engendered by the high flooding frequency were rapid and gave rise to strong functional specificities. The trophic functioning was enriched by the settlement of detritivores and small predators. At a comparable flooding frequency to those in sites R and F, this development 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 toward a successive stage.

The tidal pool (site P), characterized by water permanence, reacted as a freshwater reference by attracting typical freshwater taxa. The subtidal nature of this habitat, did not induce a faunistic overweight to the CRT intertidal fauna since only four taxa were specific to site P and six other were found elsewhere, testifying to a benthic continuum toward water intermittence. The presence of *Dero* sp. (Naididae), recorded for the first time in the Schelde estuary sediment, proves 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 observation 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, operated here on branchial respiration.

Most of additional taxa were insects which were almost absent in site R and F (where only 3 individuals were found over the study period). Their absences in sites R and F can be attributed to the adverse conditions previously pointed out. 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 leeches and gastropods (especially the last date) colonized the new estuarine substrate of the CRT whereas they were not found in the reference sites. Hence, although additional detritivores settled at low elevation, other taxa take advantage of the soft CRT hydrology and diversify the trophic structure.

Tidal freshwater habitats are detritus-based systems (Odum 1988; Findlay et al. 1990), and like 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, by opposition to high elevation where organisms were dominantly 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 was rather epibenthic at low elevation where organisms are recognized to feed on freshly deposited sediments. However, a possible oxygen limitation cannot be excluded to explain this epibenthic preference.

5. Tidal freshwater habitats as a life history interface?

In both estuary and CRT, from high to low elevation, the flooding frequency clearly conditions distinct living modes, from terrestrial to aquatic. Along this gradient, growth rate appears to be the dominant biological tendency where small size, short living duration and multivoltinism emerge from a forced hydrological regime. Moreover, a clear seasonality characterized the population turnover in frequently flooded sites compared to non-frequently flooded ones (Appendix 3, density). Despite the fact that differences between terrestrial and aquatic functioning are still debated (Chase 2000), these results are in accordance with current considerations since, in aquatic environment, reduced organisms' size and faster growth are recognized and attributed to a faster rate in replacing organisms' 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), more often denominated "fast–slow" continuum nowadays (Bielby et al. 2007). Early studies predicted that habitat spatiotemporal heterogeneity would condition organism's life history strategies (Southwood 1977; Geenslade 1983; Southwood 1988). Large size, long generation time and long life duration (*K*-selection), such as observed at high elevation, are typical traits predicted to occur in a spatiotemporally stable environment. By opposition, small size, short life duration and multivoltinism, as observed in site L, are representative of an *r*-selection expected at high temporal heterogeneity (i.e. disturbed regime, unpredictable events of high magnitude). As previously mentioned, the shear stress exerted on sites R and F sediments seems to select an *A*-strategy, generally encountered at low temporal heterogeneity in continuously harsh environments (Geenslade 1983). Indeed, along the flooding gradient, the temporal predictability of most of hydrological descriptors was found to decrease with increasing flooding frequency (see Beauchard et al. (2011b) for a complete description).

The main part of the fauna observed in 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. 2011b), thus invalidating the hypothesis according to which the flooding gradient generates an *r/K*-selection continuum. It could be suggested that other environmental factors, such as variability of sediment characteristics, exert a greater influence. According to Fig. 3, this does not seem likely in so far as site L trajectory, when 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 terrestrialized 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 end-points of converging gradients from terrestrial and aquatic templets, and possibly marked by a different magnitude of spatiotemporal heterogeneity.

6. Conclusion

This study demonstrates that sediment macroinvertebrate communities in tidal freshwater habitats are significantly structured according to their biological properties. The preponderance of a physical impact on the communities from the deteriorated reference was clearly supported, and comparatively, the CRT system was shown to successfully give rise to functionally richer aquatic communities, closer to what we could expect 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 (Cox et al. 2006; 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. 2011b). On a fundamental point of view, further long-term research should be encouraged since typical characteristics of intertidal freshwater habitats offer complementary insights in the scope of life history strategies, largely abandoned these last 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. 7). Whereas the elevation is intimately related to shear stress, this latter disappears after CRT implementation whereby the flooding frequency alone regulates community functioning.
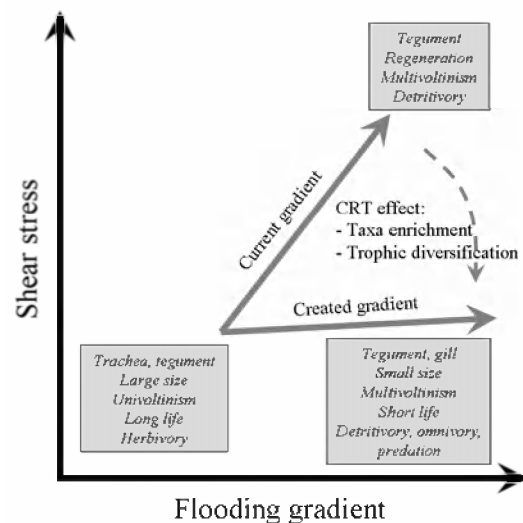
Fig. 7. Conceptual schema synthesizing the main functional changes operated by CRT.

Since several hundreds hectares of CRT are being constructed along the Schelde estuary, benthic community development 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, juvenile fish species have been massively encountered in the present CRT which effectively functions as a nursery. Additionally, regular bird surveys (Beauchard et al., under review) revealed that wetland invertivorous birds represented more than 45 % of the avifauna of which several bird populations are recognized of international importance in the Schelde estuary (e.g. Anatidae, Scolopacidae).

ACKNOWLEDGMENTS

APPENDICES

Appendix 1. Bibliographical sources from which biological attributes of taxa are derived.

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Appendix 2. Total number of taxa per site over the whole study period from spring 2006 (1) to summer 2009 (9).
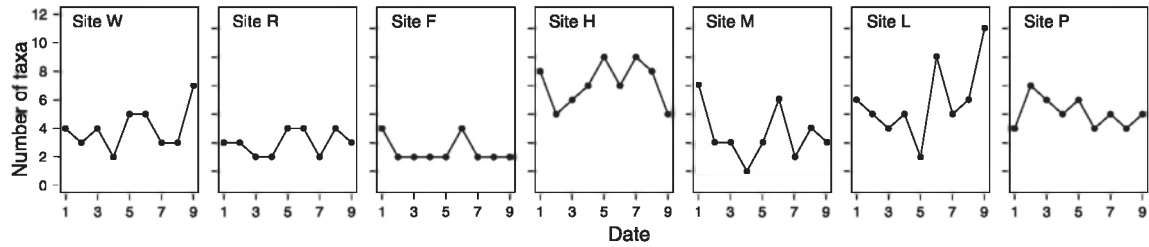
Appendix 3. Macroinvertebrate community characteristics per site and date over the whole study period from spring 2006 (1) to summer 2009 (9). Black points, mean values (± S.E.); grey points, replicates.
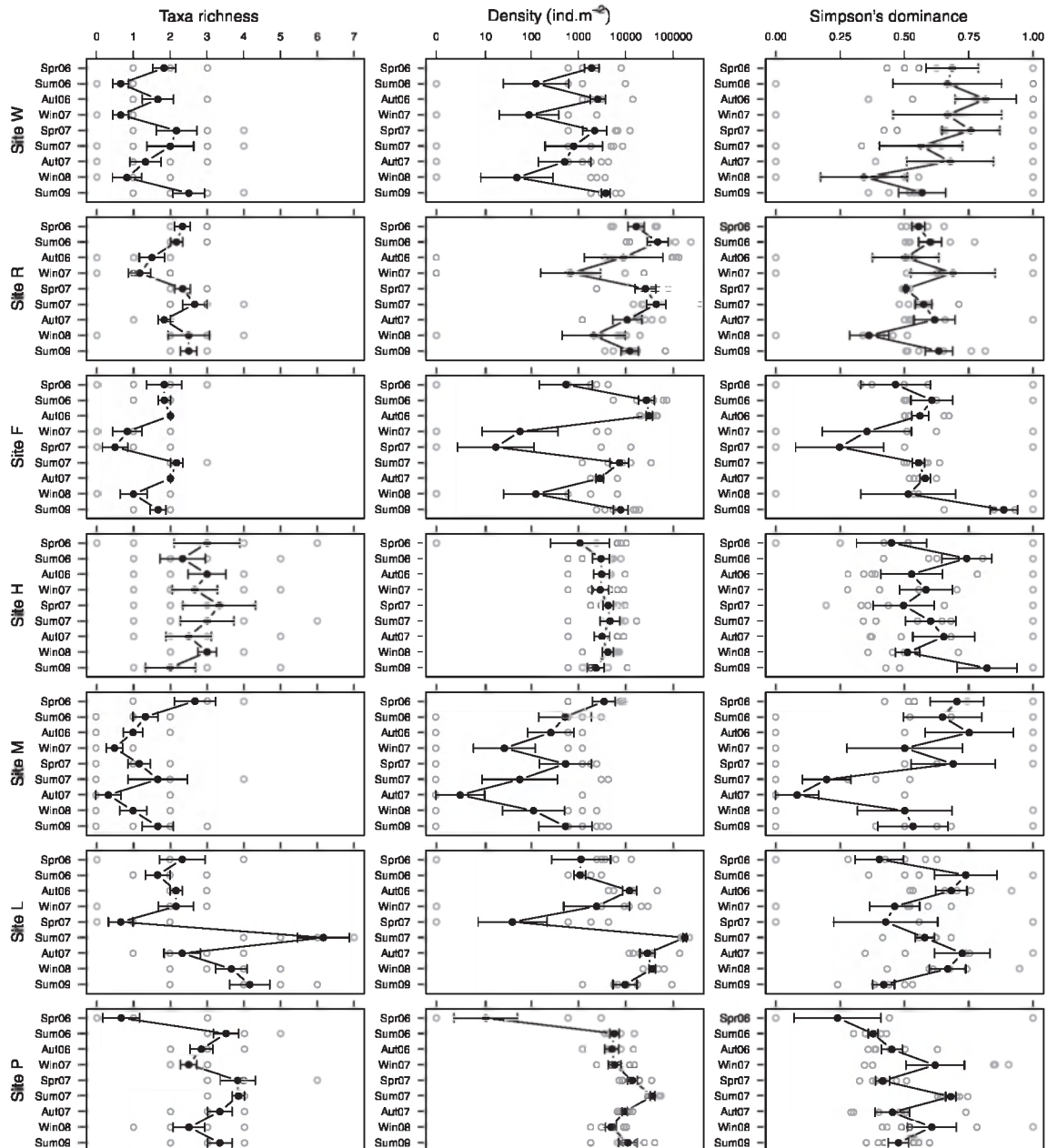
CHAPTER 5

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.

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).

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

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.

neap-spring cycle in lowered embankments (Beauchard et al. 2011b), 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. 2011b) 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.

METHODS

1. Study area

The study took place in the "Lippenbroek polder" (51.086 °N; 4.171 °E) located in the freshwater
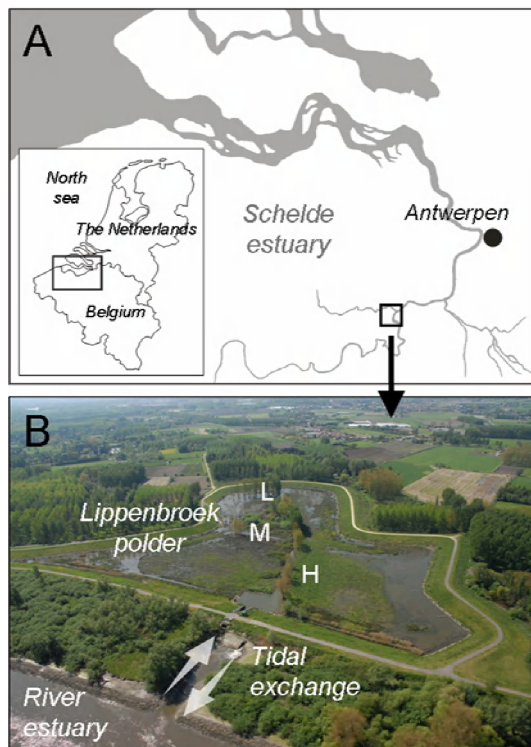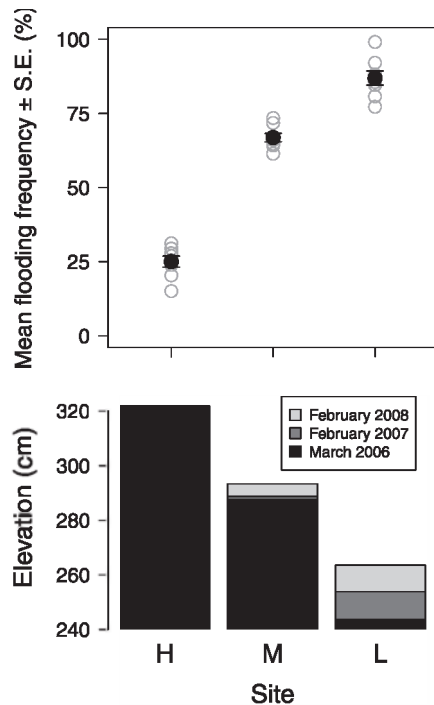
Fig. 2. Experimental setup: flooding frequencies (top) versus site elevations (bottom) along the tidal gradient. Sediment accumulation is represented in grey. Flooding frequencies were averaged per season from March 2006 to February 2008 (upper graph, grey points).

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 (8.2 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. 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).
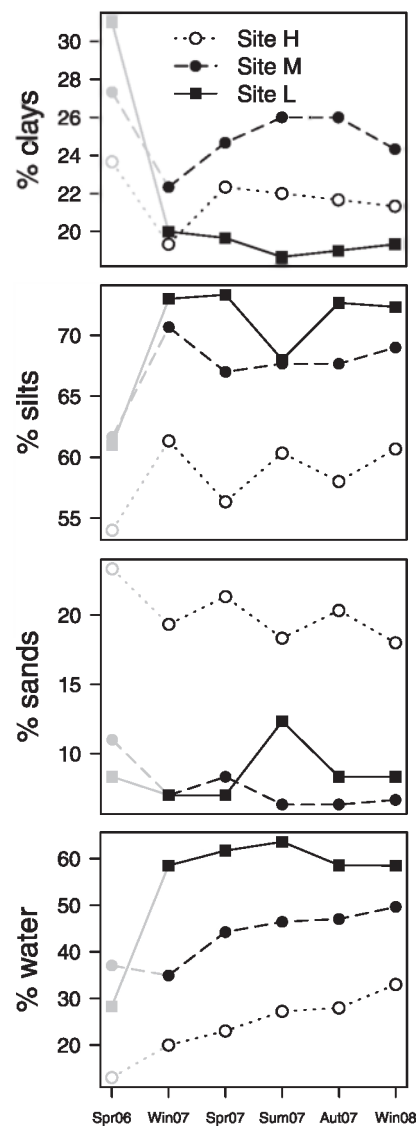
Fig. 3. Temporal profiles of the water content and granulometry. Grey: transition from spring 2006 (Spr06) to winter 2007 (Win2007).

51

3. Sediment 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.

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 hours 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.

4. Data analysis

Firstly, 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. / m²). 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):

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

where the temporal variation (*dt*) of the tracer concentration *C* through depth (*z*) is decomposed into the three dispersal modes of sediment particles. D_b (biodiffusion, local transport), *W* (bioadvection, active non-local transport) and *R* (regeneration, non-local transport) respectively refer to random dispersal (cm².y^{-1}), vertical transport through the gut (cm.y^{-1}) and burrow collapse (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.

RESULTS

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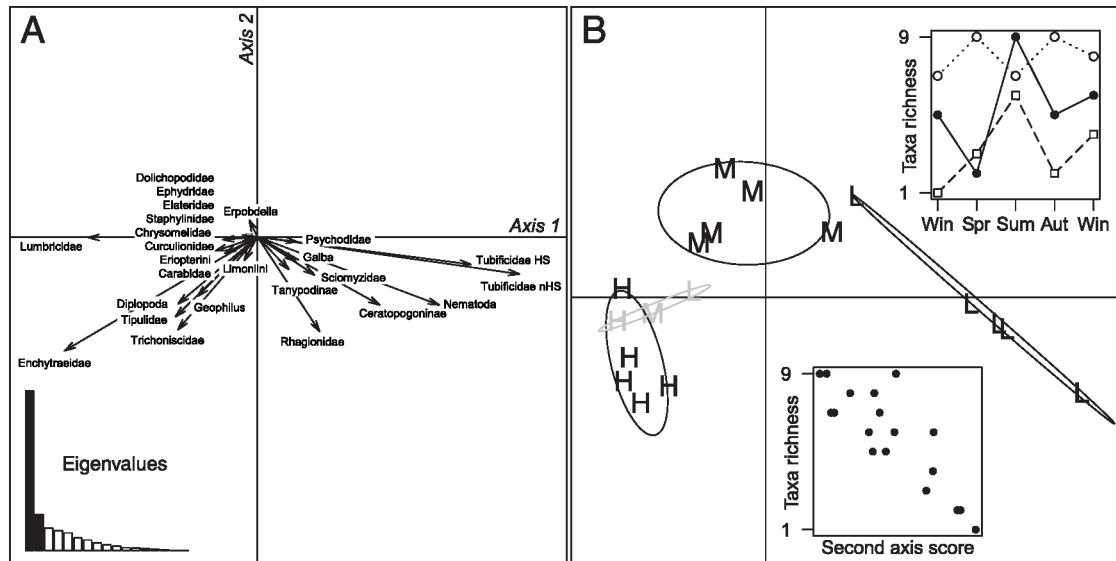
Fig. 4. Centred PCA on faunal data. A) Taxa covariances and eigenvalue diagram; F1, 48 %; F2, 11 %. B) Spatiotemporal units (date-site) grouped per site; in grey, positions of the three sites in April 2006; in black, positions from February 2007 to February 2008; upper inset: taxa richness over the study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

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).

Figure 5 highlights contrasted total organism densities among the three sites. The highest densities were found in site L reaching more than 100000 ind. / m² in summer (min = 401; max = 170883). Much lower were the densities in site H (around 5000 ind. / m²; min = 4111; max = 7020) and even less in site M (less than 2000 ind. / m²; 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 (Tab. 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. / m²), amphibious Diptera in site M (300 ind. / m²), and amphibious to aquatic Diptera and gastropods in site L (2500 ind. / m²). Non-bioturbators were marginally represented and composed of leeches found only once in site H and M (from 0 to 600 ind. / m²). Over the studied year, functional dominance accompanied the flooding frequency (Shannon index, mean H ± SE; site H, H = 0.78 ± 0.02; site M, H = 0.58 ± 0.20; site L, H = 0.33 ± 0.10; Kruskal-Wallis test, χ^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).

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.

Tab. 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; *, 0.05; **, 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			
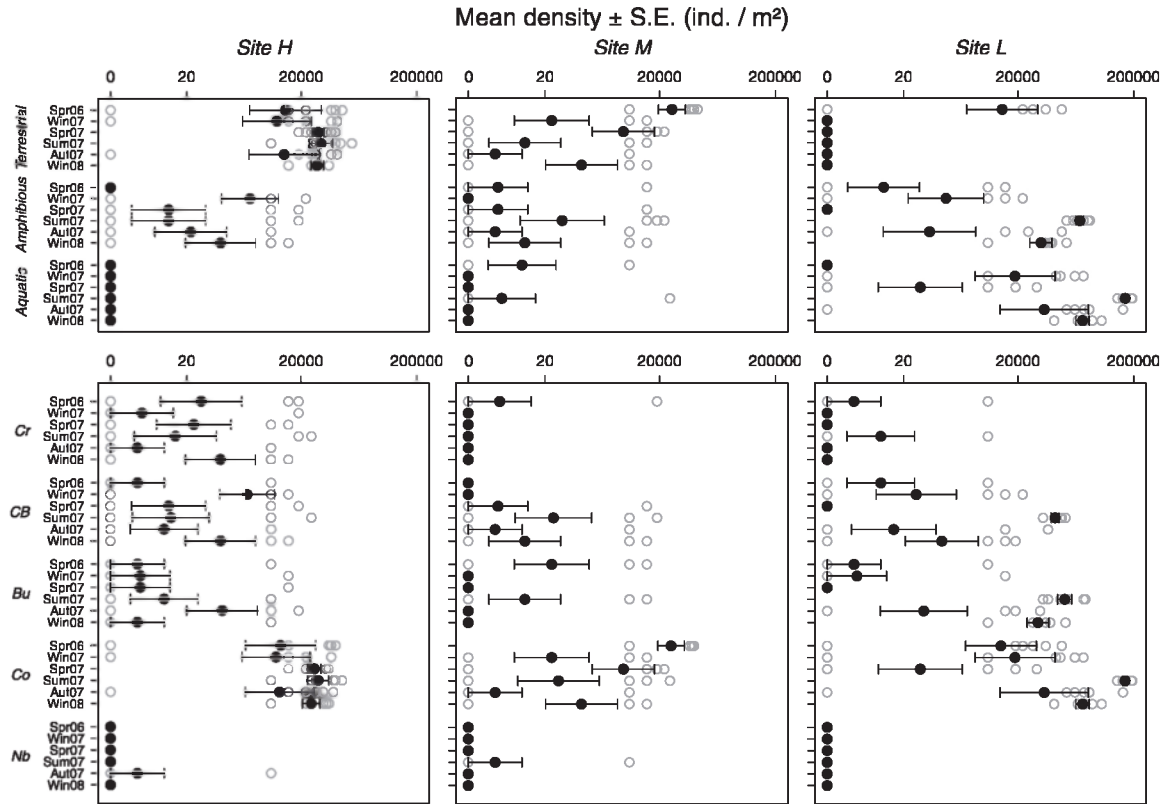
Fig. 5. Organism densities depending on functional characteristics from spring 2006 (Spr06) to winter 2008 (Win08); Cr, CB, Bu, Wo and Nb for respectively crawling, crawling-burrowing, burrowing, worm and non-bioturbator. Grey points: replicates.
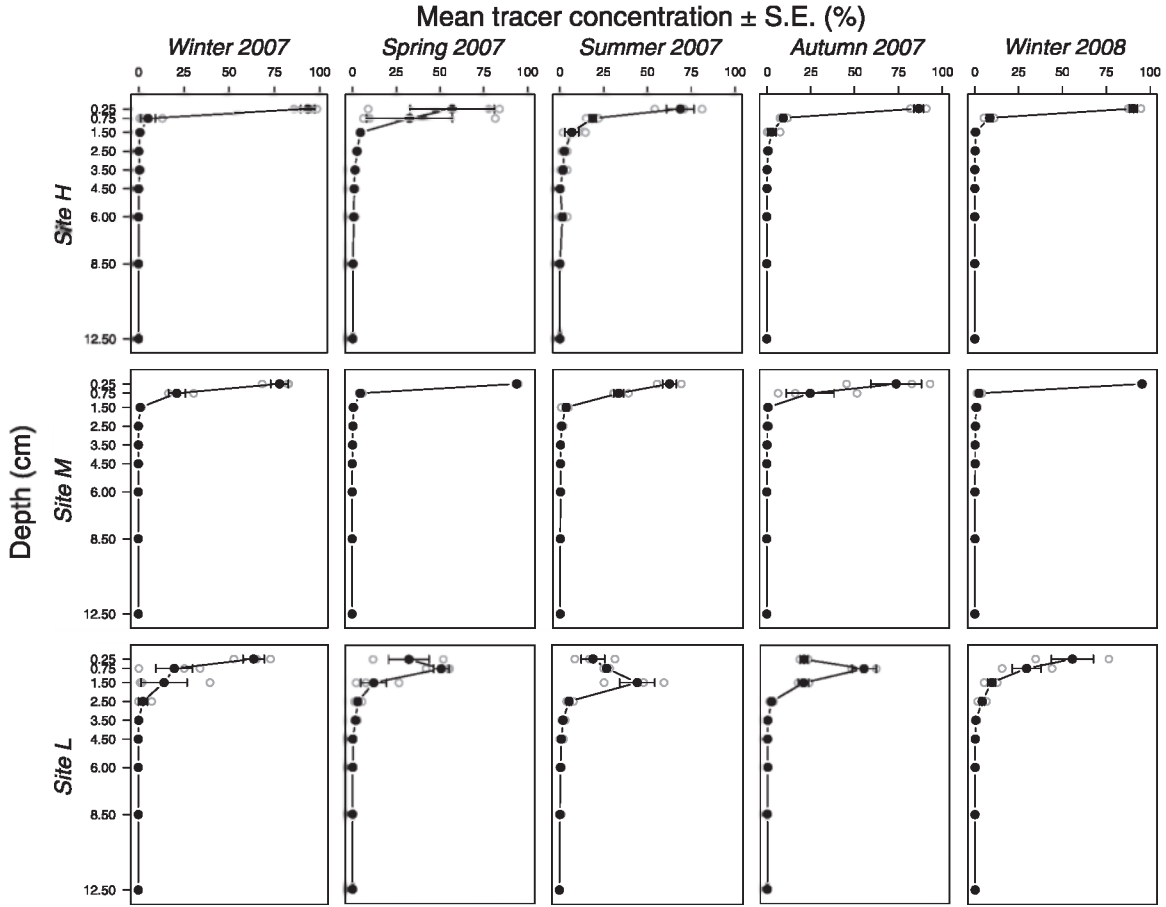
Fig. 6. Depth profiles of tracer concentrations over the studied year (percentage of the total amount of microspheres). Grey points: replicates.

Tab. 2. Bioturbation coefficients (mean ± standard error).

Date	Site	n	Biodiffusion (cm² / year)	Bioadvection (cm / year)	Regeneration (mg / cm² / 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

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 (Tab. 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 (Tab. 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, Tab. 3) where the coefficients were significantly higher in summer (Tab. 2; Tab. 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. 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 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 (Tab. 1, Number of occurrences), the high faunal specificity along the flooding gradient (Tab. 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 (Tab. 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

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

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 $p = 0.006$).
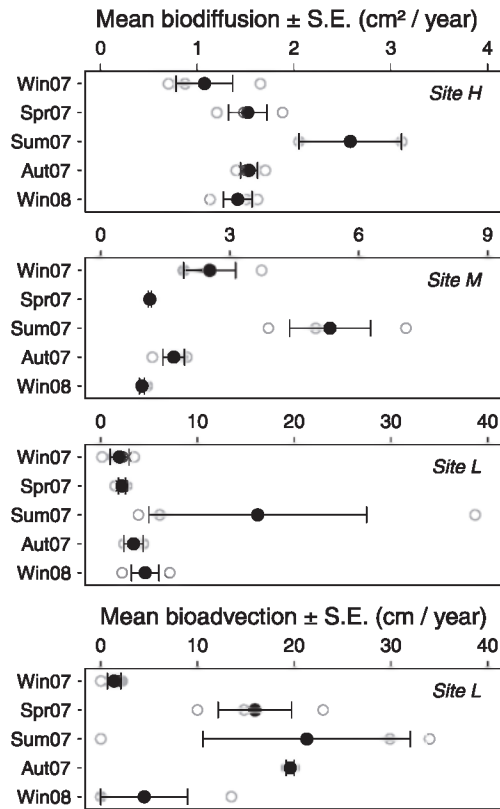
Fig. 7. Temporal profiles of biodiffusion in the three sites and of bioadvection at site L. These profiles show the clear seasonality in the three sites. Grey points: replicates.

DISCUSSION

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 Tab. 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.

2. Functional restoration potential of CRT

In an estuarine lagoon, Duport et al. (2007) reported a maximum biodiffusion of 3.1 cm² / year in summer. In a same environment, Gerino et al. (2007) reported maximum biodiffusion of 3.2 and 3.1 cm² / 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 cm² / 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.

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 cm² / 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 cm² / 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 areas, 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 concurs 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) 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. 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.

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 Figure 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* sp. and Tanypodinae (respectively biodiffusors and bioirrigators). 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).

6. 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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CHAPTER 6

AVIAN RESPONSE TO TIDAL FRESHWATER HABITAT CREATION BY CONTROLLED REDUCED TIDE SYSTEM

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Abstract. Human activities have caused extensive loss of estuarine wetlands, and the restoration of functional habitats remains a challenging task given several physical constraints in strongly embanked estuaries. In the Schelde estuary (Belgium), a new tidal marsh restoration technique, the controlled reduced tide system (CRT), is being experimented in the freshwater zone. This system was hypothesized to successfully create functional tidal wetland habitats adjacent to the estuary. Among different ecological compartments which have been studied for assessing the restoration success, avifauna was monitored over three years in order to evaluate the ecological potential of CRT habitats for the highest trophic level. The tidal regime conditioned by the system engendered the development of a succession of typical tidal freshwater habitats which were considered as spatial units. Over the three years, 103 bird species were inventoried, encompassing a dominant part of characteristic wetland species, among which 38 exhibited local and/or international concern. Communities were found to be strongly habitat specific and non-randomly organized across habitats. From ground to foliage, habitat occupancy was found to be consistent with species functional abilities over the whole seasonal cycle. Globally, the avifauna positively responded to CRT habitat creation since communities were composed of a large majority of generalist and specific birds typical of European freshwater wetlands. Hence, CRT implementation in tidal freshwater areas is recommended to compensate for losses in general freshwater wetland habitat availability.

INTRODUCTION

Several decades of intense human activities in estuaries have engendered an increasing need to remedy their adverse effects. Nowadays, regulations and international directives compel decision-makers to restore the ecological integrity of estuaries given the increasingly recognized value of ecosystem services they provide (Elliott et al. 1999; Van den Bergh et al. 2005; Barbier et al. 2010). As a consequence, restoration plans are being broadened, mainly in North America and western Europe. Within the context of managing ecological restoration projects, monitoring different ecosystem compartments is a necessary post-implementation task to evaluate the restoration success. Birds are generally recognized as strongly relevant indicators in habitat restoration, ecosystem assessment and conservation ability (Bernstein et al. 1991; Koskimies 1989; Johnson 2007; Latta and Faaborg 2008). Many wetland bird species are known to be habitat specific and sensitive to

hydrological variations (Roshier et al. 2002; Gonzáles-Gajardo et al. 2009). Functionally, as ecosystem regulators from upper trophic levels, bird abundance and community structure inform about habitat quality (Moreira 1997; Atkinson 2003; Johnson 2007; Mendonça et al. 2007; Xiong et al. 2010).

In Europe, the North Sea coast is a crucial region along the East Atlantic flyway of migrant bird species, where the Schelde estuary (The Netherlands and Belgium) is one of the important stopovers. The international importance of the Schelde estuary is evidenced since 21 waterbird species, depending mainly on the presence of tidal flats and marshes, exceed regularly the 1 % criterion of the Ramsar convention (Ysebaert et al. 2000). However, the Schelde estuary has been hugely impacted by expanding port facilities and embankments, and 16 % of the habitat surface was lost during the twentieth century, particularly low marshes and tidal flats which lost more than 50 % of their initial surface area (Meire et al. 2005).

Although the Schelde estuary is protected under the European Birds and Habitats directives (2009/147/EC and 92/43/EEC, being part of the network Natura 2000) and several national laws, expansion of harbour infrastructures is still ongoing and implies habitat compensations (Van den Bergh et al. 2005). This stresses the importance of tidal flat and marsh restoration in order to ensure a sound conservation of the international bird populations present.

In many cases, estuarine habitat restoration is operated by managed realignment which consists of dike retreat in order to increase estuarine surface area from reclaimed land (French 2006). However, these areas generally lie below the mean high water level due to subsidence after embankment combined with sea level rise. This prevents the restoration of a complete flooding frequency gradient which ensures a diversity of successive habitats. Different techniques have been implemented, but none of them has been reliable to overcome this constraint (Beauchard et al. 2011b). For instance, Atkinson et al. (2004) mentioned that despite the successful tidal flat bird community development following dike breaching in UK, the area lacked the full range of biodiversity found in the surrounding natural intertidal habitats. To solve this problem, a new technique, the controlled reduced tide system (CRT), has been experimented since 2006 in the freshwater zone of Schelde estuary and shown to generate a complete intertidal gradient (Beauchard et al. 2011b), along which vegetation developed as typically encountered in natural tidal freshwater marshes (Baldwin et al. 2009; Struyf et al. 2009). Hence, CRT is hypothesized to successfully promote bird community development among the newly created habitats.

It is difficult to measure accurately the success of wildlife community restoration in the absence of reference sites, at least in large areas (McCoy and Mushinsky 2002). Typically, tidal freshwater marshes border river channels and consist in progressive continuums stretching over mudflat, helophytes and woody plant habitats, where daily flood interacts with elevation (Odum 1988; Baldwin et al. 2009). In the Schelde estuary, most low marshes are lost due to embankments; no complete habitat gradient exists anymore (Struyf et al. 2009). This leaves the contemporary river shores as a homogeneously deteriorated reference and consequently an unsuitable restoration goal (Meire et al. 2005). Only sparse bird studies conducted on the tidal freshwater zones of the North Sea coast allow coarse comparisons. Nevertheless, in the absence of a reference marsh as a baseline,

approximating the evolutionary environment is likely the best approach for restoring wildlife populations (MacMahon and Jordan 1994; Moore et al. 1999). This does not preclude from inferring positive or negative habitat utilization by bird species for which ecology and consequent habitat requirements across seasons has been largely documented in the western Palearctic (Cramp 1977). Hence, the success of tidal wetland bird community restoration can be ensured by (i) the dominance of wetland-specific species, (ii) a functional concordance between the observed and regional reference species pools, and (iii) non-random functional habitat occupancy across seasons. Therefore, this study aims to explore the spatiotemporal dynamics of bird species community in the first CRT in order to appraise the avian response to the newly-created habitats and the relevance of further wide applications in tidal marsh restoration.

METHODS

1. Study area

The experimental area, the Lippenbroek polder, is located in the freshwater zone of the Schelde estuary (51.086 °N; 4.171 °E; Fig. 1). Equipped with the CRT system, the polder has been under tidal influence since March 1st, 2006. It covers an area of 8.2 ha, and is connected to the estuary by high inlet and low outlet culverts which allow the implementation of a controlled tidal regime (see Cox et al. (2005), Maris et al. (2006) and Beauchard et al. (2011b) for technical details); it is expected to successfully combine ecological functioning and storm flood protection. The polder is completely flooded every spring tide, with a mean water height of 40 cm, whereas either no water or a limited amount enters at neap tide.

The polder used to be an arable field like the adjacent ones where crops and poplar cultures are still grown. Typical bird species occurring there are represented by non-wetland specialist species such as *Buteo buteo, Columba palumbus, Corvus corone, Garrulus glandarius, Pica pica* and *Phasianus colchicus*; occasionally, duck species such as *Anas platyrhynchos* and *Tadorna tadorna* are encountered in fields and marginal ditches (own observations).

2. Habitats

Clearly distinct vegetation structures emerged after the first growing season, giving rise to seven habitats a priori subject to harbour different bird

Fig. 1. The experimental polder in the study area. Bottom-right insert: location map of the polder along the Schelde estuary. Top-left insert: census path. Top-right insert: habitat abbreviations; numbers in brackets indicate the surface area in ha. Photograph: Google Earth, 2009.

species communities (MacArthur and MacArthur 1961; Blondel 1973; Willson 1974). During the first year, vegetation surveys pointed to changes in composition, density and vegetation height (Jacobs et al. 2009). The three following years, other changes consisted only in plant species composition, with two exceptions. Firstly, dense monospecific Reed (*Phragmites australis*) and Cattail (*Typha latifolia*) patches extended, where mixed annual vegetation (but mostly reed/cattail dominated) was initially observed. However, in the second spring, these zones were sufficiently homogeneous and categorised "Reed" (abbreviated R in results) and "Cattail" (C). Secondly, in the third spring season, a patch of single shoots of willow (*Salix* sp.) formed a 4 m height shrub of which canopy dominated the remnant Forbs vegetation; this habitat was categorized "Shrub" (S).

The main portion of the study area remained occupied by Forbs. Species composition was mostly

dominated by *Epilobium hirsutum*, *Lythrum salicaria*, *Polygonum lapathafolium* or combinations of those. Height varies between 0.5 and 2 m, and generally these zones were very dense; this habitat was categorized "Forbs" (F). In the central part of the study area, a dense forest-type patch, already present for several decades and persisting, was categorized "Willow" (W). It consisted mainly of *Salix* sp., but some poplars (*Populus* sp.) also persisted. This habitat is about 7 m high, very hard to penetrate and strongly shaded with almost no annual understory. Scattered throughout the area, some Isolated trees (*Salix* sp. and *Populus* sp.) were categorized "Isolated tree" (I). All the foliated habitats remained constantly available for bird foliage specialists since the highest water level, encountered at spring tide, did not exceed 40 cm on the average.

Finally, in about 40 % of the area, only isolated plants can be found, but the general aspect is that of a bare ground. Recent studies pointed to

the high silty nature of deposited particles (O. Beauchard, unsubmitted manuscript), and this habitat was therefore categorized "Mudflat" (M). Although in recent years its total surface has declined due to *Phragmites australis* extension, the main zonation has remained generally unchanged during the study period.

3. Monitoring

The bird survey was seasonally conducted from autumn 2006 to winter 2010. Two types of records were distinguished: anecdotal observations during field trips specific to other purposes (invertebrates, vegetation, and sediment properties) since mid-autumn 2006, and a regular monitoring from December 21st, 2006 to March 18th, 2010, representing the core of this study. Bird censuses were conducted in four extreme tidal contexts: spring high tide, neap low tide, spring low tide and neap high tide. Over the whole study period, this resulted in 166 regular censuses preferably done in the morning, most of the time between 6:30 and 14:00 by the same observer (O. Beauchard) who was replaced six times by S. Jacobs in cases of indisposition.

Bird counts consisted of a combination of point counts (northernmost dike and central wood of the polder, Fig. 1) and transects covering the main area and across the main habitat patches in order to flush undetectable species; this active procedure is necessary since several marsh bird species stay concealed within the vegetation (Courtney and Gibbs 2005). Quantitative records comprised visual and auditory observations of resting, singing, foraging and escaping individuals. Census duration was variable given the habitat disturbance nature of the method, which nevertheless ensures inventories as exhaustive as possible; it ranged between 45 and 120 min depending on species richness and abundances.

4. Data analyses

4.1. Avifaunal description
and comparison to reference species pool

Bird species were described and functional information was considered based on habitat guild and residential status. Species were categorized according to their affinity for wetlands (W, specific; nW, non-specific) and their migratory affinity (P, permanent resident; S, summer resident; W, winter resident); information was derived from Cramp (1977). The CRT species pool was then compared to a reference species pool from the existing regional inventories conducted in tidal freshwater zones totalising more than 700 ha (Strucker 1992; Temmerman 1992; Van Waeyenberge 1999). Independence of functional group proportions were tested by chi-square and Fisher's exact tests.

4.2. Spatiotemporal determinants
of communities

Prior to structural community description, a quantitative approach was conducted to disentangle the effects of year, season and tide on community structure (composition and abundance). Based on habitat as an environmental entity, the relative influence of these factors on bird abundances were quantified by between-group analyses (Dolédec and Chessel 1987) applied to sample × species matrices (log-transformed abundances). Abundances in each sample were averaged following the combination of year × season × tide (last winter season excluded in order to balance the observation plan). Since shrub habitat was not present over the whole study period, analyses were done from spring 2008 to winter 2010. Each matrix (habitat) was column-centred so that the resulting principal component analysis (centred PCA) ordinates communities according to niche breadth (Dray et al. 2003). Between-group analysis returns the amount of explained inertia by the considered factor from the PCA. Then, the effect significance was tested by a randomization procedure based on 9999 random permutations on the matrix lines (Heo and Gabriel 1997). The same procedure was then applied on the whole dataset to identify the factors which dominantly structured the communities at the marsh scale.

4.3. General habitat community characteristics

General community characteristics such as number of species and dominance were computed and displayed per habitat and calendar-based season. Cumulative species richness curves were plotted over the whole study period in order to assess temporal community responses to the newly-created habitats. Seasonal effect on functional group proportions was tested by Kruskal-Wallis test.

4.4. Spatiotemporal dynamics
of marsh community composition

This study took place in a spatiotemporal context and gave rise to a complex dataset partitioned by at least two crossed factors, habitat in the one

hand, and time in the other hand. In such a case, exploration of species composition dynamics may be made difficult by interactive effects between factors when focusing only on a single one. Therefore, possible confounding effects were circumvented by applying Foucart's Correspondence Analyses (FCA; Foucart 1978; Pavoine et al. 2007) to the dataset in order to disentangle the effects of the most structuring factors. Then, data were arranged in a global sample × species matrix conrtaining mean abundances. Following FCA, this matrix is transformed by double avaraging prior to correspondence analysis (Thioulouse and Chessel 1992). Then, an average matrix (reference) is computed based on the modalities of the factor of interest (e.g. seasons or habitats), from which FCA constructs a reference system of axes. Finally, samples and species ordinations results from the projections of the sub-matrices (one per factor modality) of the global one. Despite the fact that FCA has been ignored so far, its first application in ecology was proved to be particularly relevant to spatiotemporal analyses (Pavoine et al. 2007). As a complement, the interpretation of the results was supported by Jaccard's similarity index.

Computations and graphical representations were performed on R software (R Development Core Team 2009) and multivariate analyses on "ade4" package available in R (Chessel et al. 2004; Dray et al. 2007).

RESULTS

1. Avifaunal description

Over the whole study period, a total of 13 013 individual birds were counted during the regular censuses (mean daily count = 78.4 ± 30.2 S.E., corresponding to 9.6 birds.ha^{-1} on average). With additional observations, this encompassed 103 species, among which 94 were encountered during the regular censuses (Tab. 1). Despite the disturbing nature of the counting (51 % of escapements), 81 species were observed at least once in foraging activity (27 % of the observations); resting and other activities (e.g. singing, territoriality and

breeding) accounted for 11 and 11 % of the observations respectively. Among the 21 bird species of international importance in the Schelde estuary (Ysebaert et al. 2000), 12 of them were observed to forage, and 4 (*Anas crecca, A. strepera, A. platyrhynchos,* and *T. tadorna*) were among the 10 dominant species and accounted for 50 % of the total abundance. Additionally, 14 species of concern listed by the European Bird Directive (1 % of all observations) and 21 species inscribed on the Flemish red list (17 % of all observations) were encountered.

Only one species (*Poecile palustris*) was not found in the reference pool which encompassed 228 species (Appendix 1). CRT and reference wetland species functional groups were in similar proportions (Tab. 2); neither proportions of wetland specialists nor migrant and foraging groups within wetland specialists were not significantly independent according to chi-square and Fisher's tests ($p > 0.05$).

2. Spatiotemporal determinants
of community structure

No significant year effect was detected on community structure, except in Cattail and Reed, albeit rather weak (Tab. 3). On the contrary, all habitats experienced a strongly significant seasonality. Tidal effect was more variable; whereas no effect was significant on Reed and Cattail communities, effects on Isolated tree and Willow communities were either not or weakly significant; by contrast, Forbs and Mudflat community structures seemed to be significantly influenced by tide. At the marsh scale, the community structure responded significantly to habitat and season effects. Habitat had a strongly dominant effect, followed by season. Year and tide engendered a non- or poorly significant effect. Hence, community structure was explored with respect to habitat and season.

3. General habitat community characteristics

Species richness patterns exhibited a stronger effect of habitat than season (Fig. 2A). Globally,

Tab. 1 (next page). Species characteristics and occurrences. Numbers represent the total amount of observations over the study period. Foraging status: A, air specialist; F, foliage specialist; FG, foliage and ground ubiquist; G, ground specialist. Trophic status: H, herbivore; G, granivore; SO, small omnivore; SC, small carnivore; LO, large omnivore; LC, large carnivore. Migratory status: P, permanent resident; S, summer (and spring); W, winter (and autumn). Ramsar status: X indicates international importance base on the Ramsar convention criterion applied to the Schelde estuary. EU status: X indicates listing in annex I of the European Directive 2009/147/EC. Flemish status (Devos et al. 2004): D, declining; R, rare; V, vulnerable; T, threatened; TE, threatened to extinction. Common names: * indicates species which were encountered outside the regular censuses; they were not considered in the analyses.

Common name	Latin name	Wetland status	Foraging status	Trophic status	Residential status	Ramsar status	EU status	Flemish status	Isolated tree	Willow	Shrub	Forbs	Reed	Cattail	Mudflat
Cuckoo	*Cuculus canorus*		F	SC	S			D	1						
Marsh Tit	*Poecile palustris*		F	SC	P				1						
Redwing	*Turdus iliacus*		FG	SO	W				10						
Sparrowhawk	*Accipiter nisus*		FG	LC	P				2	1					
Green Woodpecker	*Picus viridis*		FG	SO	P				11	4	2				
Jay	*Garrulus glandarius*		FG	LO	P				12	28					
Great spotted Woodpecker	*Dendrocopos major*		F	SC	P				7	16					
Greenfinch	*Carduelis chloris*		F	SO	P				11	12		1			
Goldfinch	*Carduelis carduelis*		F	G	P				14	3		2			
Garden Warbler	*Sylvia borin*		F	SO	S				4	22	1	1			
Short-toed Treecreeper	*Certhia brachydactyla*		F	SC	P					8					
Rock Dove	*Columba livia*		FG	G	P					2					
Willow Tit	*Poecile montanus*		F	SO	P			V		4					
Lesser spotted Woodpecker	*Dendrocopos minor*		F	SC	P					1					
Night Heron	*Nycticorax nycticorax*	X	G	LC	S		X	R		1					
Eurasian Golden Oriole	*Oriolus oriolus*		F	SO	S			T		1					
Eurasian Tree Sparrow	*Passer montanus*		F	SO	P			D		5					
Long-eared Owl*	*Asio otus*		FG	LC	P					1					
European Turtle-dove*	*Streptopelia turtur*		FG	G	S			T		1					
Rock Kestrel	*Falco tinnunculus*		FG	LC	P				12	7		9			
Great Tit	*Parus major*		F	SO	P				19	55	5	13	1		
Blackcap	*Sylvia atricapilla*		F	SO	S				3			3			
Chaffinch	*Fringilla coelebs*		FG	G	P				43	108		55	1		
Long-tailed Tit	*Aegithalos caudatus*		F	SC	P				55	182	44	49	28		
Dunnock	*Prunella modularis*		FG	SO	P				11	8	4	19	2		
Blackbird	*Turdus merula*		FG	SO	P				19	25	7	143			
Common Buzzard	*Buteo buteo*		FG	LC	P				2	6		9			
Common Whitethroat	*Sylvia communist*		F	SO	S				9	7	1	41		1	
European Robin	*Erithacus rubecula*		FG	SO	P				11	37	8	73	4	1	
Black-billed Magpie	*Pica pica*		FG	LO	P				13	24	1	1			1
Blue Tit	*Cyanistes caeruleus*		F	SO	P				11	40	11	15	30	4	
Linnet	*Carduelis cannabina*		F	G	P			D	2	8		40			
Song Thrush	*Turdus philomelos*		FG	SO	P				2	5	1	47			
Wren	*Troglodytes troglodytes*		F	SC	P				4	64	7	81	13	9	
Northern Chiffchaff	*Phylloscopus collybita*		F	SC	S					28	10	19	3	2	
Brambling	*Fringilla montifringilla*		FG	G	W					2		2			
Carrion Crow	*Corvus corone*		FG	LO	P				13	11		9			1
Mistle Thrush	*Turdus viscivorus*		FG	SO	P					2		3			
Marsh Warbler	*Acrocephalus palustris*	X	F	SC	S				2	1	15	123	7	3	
Reed Bunting	*Emberiza schoeniclus*	X	F	SO	W			T	3	20	7	522	172	6	
Goldcrest	*Regulus regulus*		F	SC	P					3		3		1	
Wood Pigeon	*Columba palumbus*		FG	G	P				16	65		33		1	2
Cetti's Warbler	*Cettia cetti*	X	F	SC	S			R			1	1	4		
Common Pheasant	*Phasianus colchicus*		G	LO	P					4		38	7		
Water Rail	*Rallus aquaticus*	X	G	SO	W					1	1	32	2		
Common Kingfisher	*Alcedo atthis*	X	G	SC	P		X		16	37	3	8	1		4
Sedge Warbler	*Acrocephalus schoenobaenus*	X	F	SC	S			T				1			
European Stonechat	*Saxicola torquata*		F	SC	S							3			
Meadow Pipit*	*Anthus pratensis*	X	G	SC	P			T				1			
Blue Throat	*Luscinia svecica*	X	F	SC	S		X				1	25	6	1	
Grasshopper Warbler	*Locustella naevia*	X	F	SC	S							3	1		
Bearded Reedling	*Panurus biarmicus*	X	F	SO	P			R				27	14	8	
Water Pipit	*Anthus spinoletta*	X	G	SC	W							3			
Common Swift	*Apus apus*		A	SC	S							3			
Western Marsh Harrier	*Circus aeruginosus*	X	FG	LC	P		X					3			
Eurasian Woodcock	*Scolopax rusticola*	X	G	SO	P							1			
Common Starling	*Sturnus vulgaris*		FG	SO	P							1			
Tufted Duck	*Aythya fuligula*	X	G	SO	W							2			
Hen Harrier	*Circus cyaneus*		FG	LC	P		X					4			
Jack Snipe	*Lymnocryptes minimus*	X	G	SO	W							2			
Red-crested Pochard	*Netta rufina*	X	G	SC	W							2			
Reed Warbler	*Acrocephalus scirpaceus*	X	F	SC	S					2	4	38	253	38	2
Common Moorhen	*Gallinula chloropus*	X	G	SO	P					102	5	263	38	26	264
Grey Heron	*Ardea cinerea*	X	G	LC	P				4	70		22	2		62
Common Snipe	*Gallinago gallinago*	X	G	SC	W			TE			33	894	262	5	163
Mallard	*Anas platyrhynchos*	X	G	SO	P	X				155	4	671	7	7	391
Common Teal	*Anas crecca*	X	G	SO	W	X				543		1135	39	10	1769
Coot	*Fulica atra*	X	G	SO	P					4		13	1	6	13
Gadwall	*Anas strepera*	X	G	H	S	X				43		495	2	5	473
Barn Swallow	*Hirundo rustica*		A	SC	S			D					5		5
Common Shelduck	*Tadorna tadorna*	X	G	SC	S	X				1		116			628
Great Cormorant	*Phalacrocorax carbo*	X	G	LC	P				2						10
Lapwing	*Vanellus vanellus*	X	G	SC	P							53			180
Common Sandpiper	*Actitis hypoleucos*	X	G	SC	S							3			12
Canada Goose	*Branta canadensis*	X	G	H	P							7			74
Common Greenshank	*Tringa nebularia*	X	G	SC	S							3			19
Common Redshank	*Tringa totanus*	X	G	SC	S	X		V				1			5
Green Sandpiper	*Tringa ochropus*	X	G	SC	P							3			112
Ringed Plover	*Charadrius hiaticula*	X	G	SC	S	X		R							5
Herring Gull	*Larus argentatus*	X	G	LO	P										5
Spotted Redshank*	*Tringa erythropus*	X	G	SC	S	X									5
Egyptian Goose	*Alopochen aegyptiacus*	X	G	H	P										30
Pintail	*Anas acuta*	X	G	H	W	X		R							1
Greylag Goose	*Anser anser*	X	G	H	W	X									3
Little Ringed Plover	*Charadrius dubius*	X	G	SC	S										1
Stock Dove	*Columba oenas*		FG	SO	P										1
House Martin	*Delichon urbicum*		A	SC	S			V							3
Little Egret	*Egretta garzetta*	X	G	LC	S	X		R							1
Eurasian Hobby	*Falco subbuteo*		F	LC	S										1
Eurasian Oystercatcher	*Haematopus ostralegus*	X	G	SC	S	X									15
Common black-headed Gull	*Larus ridibundus*	X	G	LO	P										199
Smew	*Mergellus albellus*	X	G	LC	W		X								1
White Wagtail	*Motacilla alba*	X	G	SC	S										7
Spoonbill	*Platalea leucorodia*	X	G	LC	S	X	X								2
Pied Avocet	*Recurvirostra avosetta*	X	G	SC	P	X	X	V							2
Common Tern	*Sterna hirundo*	X	G	LC	S	X		V							8
Little Grebe	*Tachybaptus ruficollis*	X	G	LC	P										2
Wood Sandpiper	*Tringa glareola*	X	G	SC	S	X									6
Northern Shoveler*	*Anas clypeata*	X	G	H	W										2
Great White Egret*	*Egretta alba*	X	G	LC	S		X								1
Osprey*	*Pandion haliaetus*	X	G	LC	P		X								1
Ruff*	*Philomachus pugnax*	X	G	SC	S		X								1
Great Crested Grebe*	*Podiceps cristatus*	X	G	LC	P										1

Tab. 2. Numbers and proportions of species per functional groups in CRT and reference species pools. Foraging status: A, air specialist; F, foliage specialist; FG, foliage and ground ubiquist; G, ground specialist.

| | | Non-wetland species | | | | | | | | Wetland species | | | | | | | |
| | | Permanent resident | | | | Migratory resident | | | | Permanent resident | | | | Migratory resident | | | |
		A	F	FG	G	A	F	FG	G	A	F	FG	G	A	F	FG	G
Number of species	Reference	0	20	24	9	6	20	21	9	0	2	1	30	1	11	1	73
	CRT	0	14	19	1	3	8	3	0	0	1	1	18	0	7	0	28
Proportion of species (%)	Reference	0.0	8.8	10.5	3.9	2.6	8.8	9.2	3.9	0.0	0.9	0.4	13.1	0.4	4.8	0.4	32.0
	CRT	0.0	13.6	18.4	1.0	2.9	7.8	2.9	0.0	0.0	1.0	1.0	17.5	0.0	6.8	0.0	27.2

Tab. 3. Effects of spatiotemporal factors on community structure.

Effect	Habitat	Explained inertia (%)	p
Year	Isolated tree	5.1	0.2055
	Wood	4.8	0.2762
	Shrub	4.4	0.1968
	Forbs	5.4	0.1629
	Reed	6.9	0.0430
	Cattail	6.6	0.0461
	Mudflat	4.3	0.4154
Season	Isolated tree	10.2	0.0101
	Wood	19.8	< 0.0001
	Shrub	22.0	0.0019
	Forbs	27.0	< 0.0001
	Reed	26.3	< 0.0001
	Cattail	14.5	< 0.0004
	Mudflat	21.0	< 0.0001
Tide	Isolated tree	8.5	0.0682
	Wood	8.9	0.0539
	Shrub	6.5	0.8976
	Forbs	12.7	0.0012
	Reed	3.2	0.9968
	Cattail	5.7	0.6576
	Mudflat	9.9	0.0214
Whole data set			
Year		< 1.0	0.2215
Season		5.5	< 0.0001
Tide		1.5	0.0218
Habitat		29.1	< 0.0001

Willow and Forbs were the richest habitats (circa 20 species), followed by Mudflat (circa 15 species) and Isolated tree(circa 10 species); the other habitats harboured less than 10 species. On average, species richness pattern was similar between Isolated tree, Willow and Shrub where number of species increased from spring to autumn, and reaching its minimum in winter. Forbs and Mudflat exhibited a seasonality marked by a higher number of species in spring and summer. The pattern was similar between Reed and Cattail where spring and autumn maxima opposed to summer and winter minima. Over the whole study period, the richest habitats and Shrub accumulated more than 75 % of

their species pool after one year, whereas Reed and Cattail required twice more time (Fig. 2B).

Across seasons, the seven habitat communities did not exhibit large differences in dominance (Fig. 3); in most of cases, 50 % of the most dominant species encompassed between 60 and 70 % of the bird abundance. Reed and Mudflat communities were more dominated in autumn when 50 % of the most dominant species accounted for circa 80 % of the abundances; this was attributed to massive populations of the migrant *Emberiza schoeniclus* in Reed and *A. crecca* in Mudflat.

Abundance was significantly correlated to species richness (r = 0.86; p < 0.001), and similarly less influenced by season than habitat. The number of wetland specific individuals reached 84 % of the total (Fig. 4). Non-wetland species proportions were dominant in Isolated tree, Willow and Shrub whereas the dominance switched to wetland species from Forbs along the vegetation succession. Whereas Isolated tree, Willow and Shrub were more characterized by ubiquists, birds with a ground affinity largely dominated from Forbs to Mudflat. Air foragers were omitted as they were encountered in a small proportion (3 species, 16 observations; not considered in the analyses). Proportions of migrants were clearly higher in wetland specialists, from Forbs to Mudflat (Fig. 4C and 4F).

A significant seasonal effect common to foliated habitats was found, whereby migrant foliage specialists were in higher proportions during spring and summer (Tab. 4; Appendix 2); in autumn and winter, foliage was dominated by permanent residents. In Mudflat and Forbs, a compositional stability on the ground was maintained by a switch from permanent resident in spring and summer to migrant in autumn and winter. Proportions of species responded similarly to proportions of individuals (Pearson's correlation coefficient; N = 86; $0.47 \leq r \leq 0.93$; p < 0.0001).
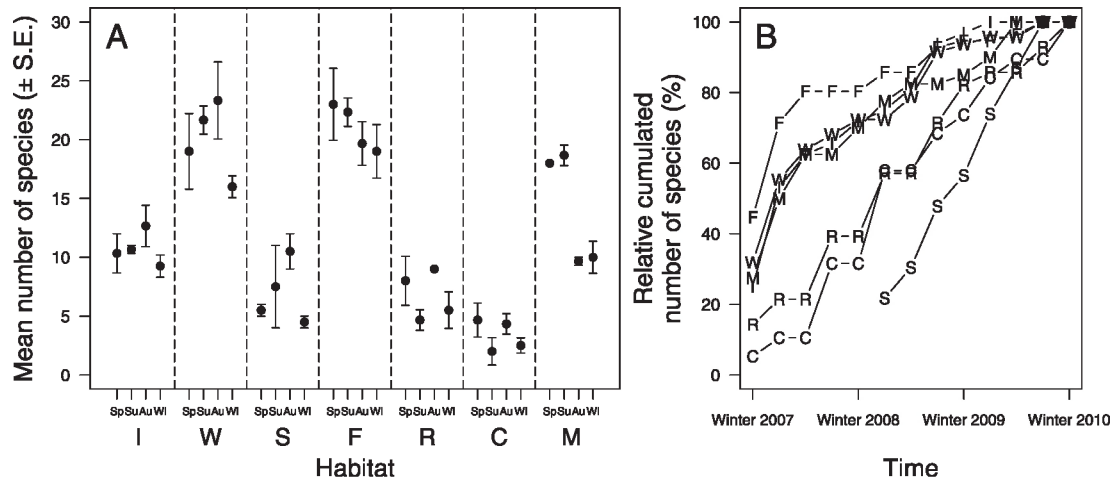
Fig. 2. Spatiotemporal pattern of species richness. A) Number of species per habitat from spring ("Sp") to winter ("Wi"); I, Isolated tree; W, Willow; S, Shrub; F, Forbs; R, Reed; C, Cattail; M, Mudflat. B) Relative species accumulation per habitat over the study period.
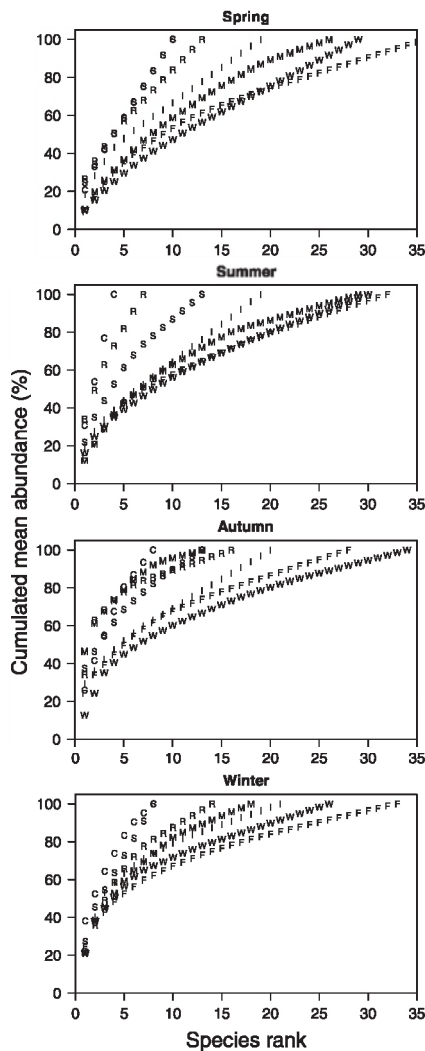

Fig. 3. Dominance curves per season and habitat. See Fig. 2 for habitat codes.

4. Spatiotemporal dynamics of marsh community composition

FCA underlined the clear habitat effect on the average (i.e. within season), and a remarkable spatial stability across seasons (Fig. 5) despite a strong seasonal species turnover in each habitat ranging between 10 and 60 % (Tab. 5); only Reed and Cattail communities were similar. This stability was characterized by relative constancy in configuration (environmental gradients) and amplitude (niche overlap). The first axis arranged three groups of habitats according to vegetation stages: Mudflat, helophytes (Cattail, Reed and Forbs) and tree-like habitats (Shrub, Willow and Isolated tree). The Mudflat community was characterized by benthivores such as gulls (e.g. *Larus ridibundus*), waders (e.g. *Tringa* spp., *Haematopus ostralegus*) and anatids (e.g. *Branta canadensis*, *Alopochen aegyptiacus*). Among the latter, *A. crecca* ensured a transition toward the successive vegetation stages by occupying also Forbs. In this habitat, *Gallinago gallinago* and *Panurus biarmicus* were characteristic, albeit frequently encountered in Reed and Cattail in which *Acrocephalus scirpaceus* was the most specific species. Communities in Isolated tree, Willow and Shrub were characterized by forest species (e.g. *G. glandarius*, *Aegithalos caudatus*) among which *A. caudatus*, as a foliage specialist, ensured a faunistic transition to helophyte habitats.

Second axis exhibited a similar pattern, however contrasted by the position of Mudflat, closer to tree-like habitats. *A. scirpaceus*, specific to Reed beds (narrow spatial niche), conferred a high foliage specificity to Reed and Cattails.
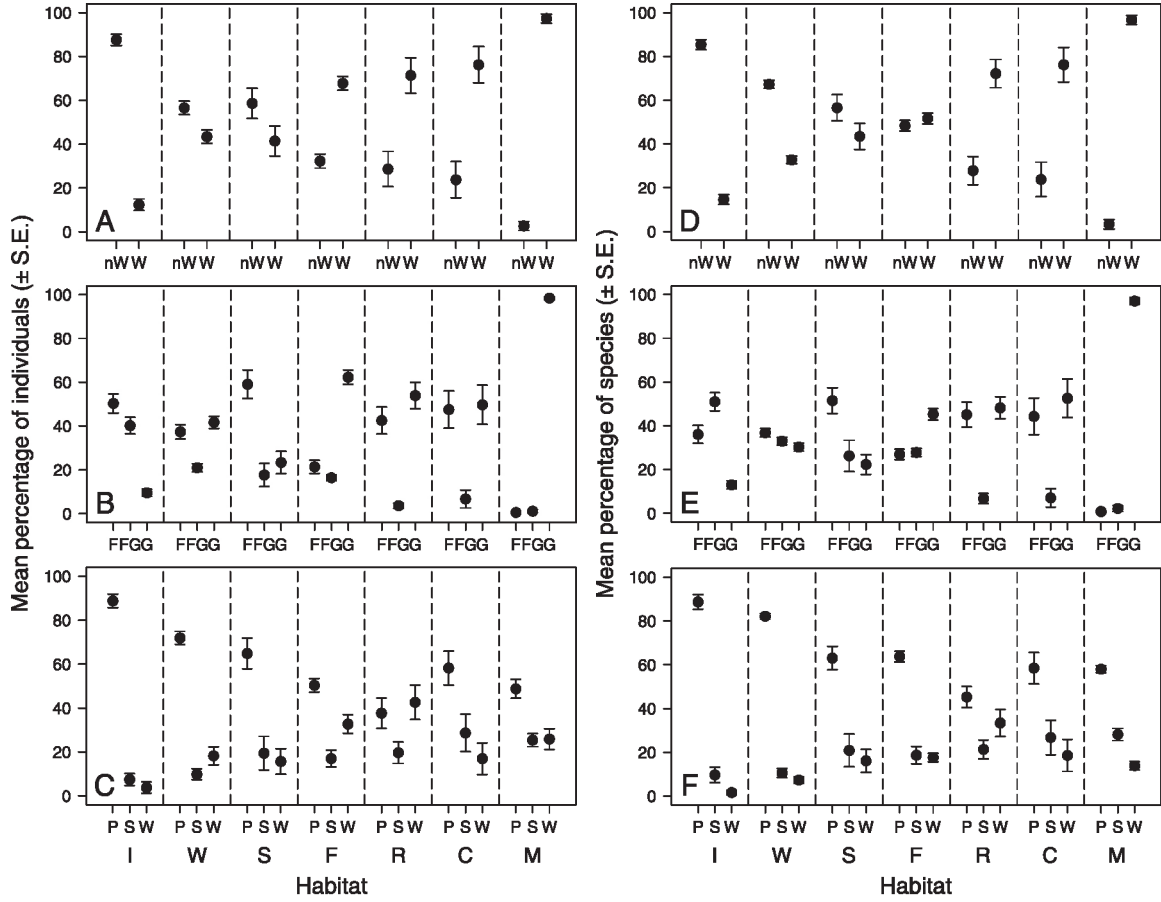
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Fig. 4. Mean proportion of birds and species per habitat and status. A and D) nW, non-wetland species; W, wetland species. B and E) F, foliage specialist; FG, foliage and ground ubiquist; G, ground specialist. C and F) P, permanent resident; S, summer resident; W, winter resident. See Fig. 2 for habitat codes.

Tab. 4. Kruskal-Wallis tests on the relationships between functional group proportions and season within each residential status. F, foliage specialist; FG, foliage and ground ubiquist; G, ground specialist. Underscore indicates absence of representative individuals.

| Descriptor	Habitat	Premanent resident						Migratory resident					
		F		FG		G		F		FG		G	
		χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Proportion of individuals	Isolated tree	1.2	0.763	4.4	0.224	0.4	0.949	12.4	0.006	2.3	0.522	_	_
	Wood	1.9	0.602	8.8	0.032	7.0	0.072	20.1	<0.001	6.8	0.079	9.7	0.021
	Shrub	10.0	0.018	6.0	0.112	2.3	0.515	6.5	0.089	_	_	13.4	0.004
	Forbs	24.4	<0.001	9.3	0.026	13.7	0.003	21.1	<0.001	3.3	0.343	1.6	0.654
	Reed	12.7	0.005	2.4	0.498	6.3	0.097	13.6	0.004	_	_	5.3	0.148
	Cattail	6.8	0.080	1.8	0.604	1.2	0.748	14.4	0.002	_	_	2.2	0.530
	Mudflat	_	_	5.8	0.119	9.8	0.020	2.9	0.412	_	_	11.0	0.012
Proportion of species	Isolated tree	0.5	0.924	5.8	0.123	0.4	0.948	13.4	0.004	2.3	0.522	_	_
	Wood	4.2	0.241	2.6	0.460	6.4	0.092	18.0	<0.001	6.8	0.079	6.8	0.079
	Shrub	8.4	0.039	6.8	0.079	2.4	0.495	6.4	0.094	_	_	12.9	0.005
	Forbs	24.7	<0.001	15.7	0.001	13.2	0.004	38.0	<0.001	3.3	0.343	0.9	0.827
	Reed	12.5	0.006	2.5	0.475	4.2	0.241	15.0	0.002	_	_	5.4	0.142
	Cattail	6.8	0.079	1.8	0.604	1.2	0.763	14.4	0.002	_	_	2.3	0.516
	Mudflat	_	_	5.8	0.119	4.5	0.215	2.9	0.412	_	_	5.8	0.120
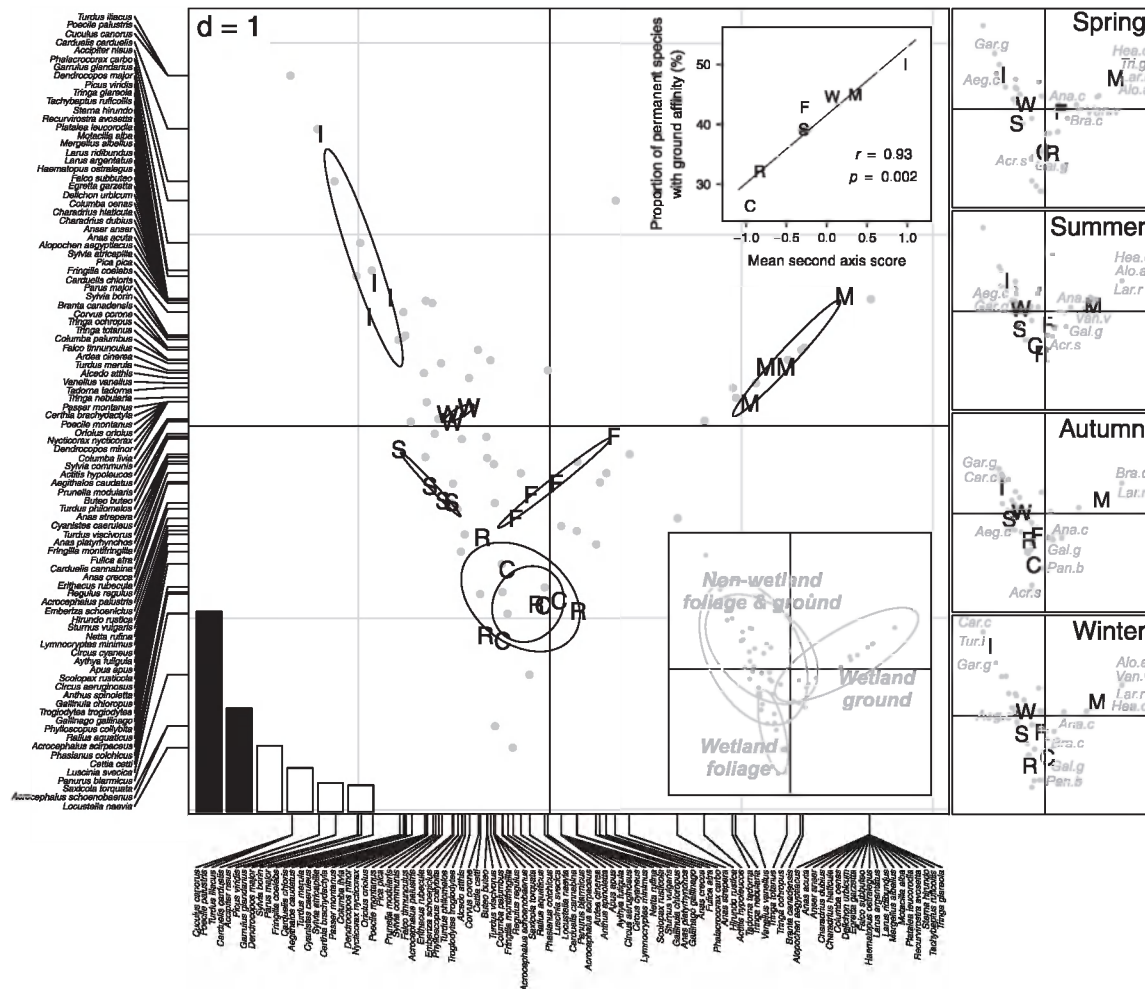
Fig. 5. Foucart's correspondence analysis on season tables. Axis 1 (horizontal), 43 %; axis 2 (vertical), 22 %. Left panel: average position of species (grey points); seasons grouped per habitat (black characters); "d" indicates the grid scale. Right panels: respective seasonal positions of species (grey points) and habitats (black characters). Abbreviations of the most contributing species (see Appendix 3 for absolute contributions): *Aeg.c*, *Aegithalos caudatus*; *Acr.s*, *Acrocephalus scirpaceus*; *Alo.a*, *Alopochen aegyptiacus*; *Ana.c*, *Anas crecca*; *Bra.c*, *Branta canadensis*; *Car.c*, *Carduelis carduelis*; *Gar.g*, *Garrulus glandarius*; *Hae.o*, *Haematopus ostralegus*; *Lar.r*, *Larus ridibendus*; *Pan.b*, *Panurus biarmicus*; *Tri.g*, *Tringa glareola*; *Tur.i*, *Turdus iliacus*; *Van.v*, *Vanellus vanellus*.

Conversely, Mudflat, Willow and Isolated tree were visited by permanent resident able to forage or roost in foliage and/or on the ground (i.e. large spatial niche): omnivores and carnivores such as *Ardea cinerea*, *C. corone*, *Phalacrocorax carbo* and *P. pica*; *C. palumbus* as ground and foliage opportunists; *Alcedo atthis* fishing in Willow as well as on Mudflat at high tide. Indeed, the strongest correlation to the second axis was obtained with the proportion of permanent species with affinity for ground (Fig. 5, upper insert). Concurrently, both axes clearly discriminated species foraging specificities (Fig. 5, lower insert).

The FCA performed on the habitat tables revealed that winter-spring and summer-autumn transitions along the first axis encompassed most of

the seasonal variation (Fig. 6). The second axis completed the seasonal cycle by expressing the spring-summer and winter-autumn transitions. Although assemblages globally differed between seasons, the seven habitats responded in a slightly different way to the seasonality.

Mainly composed of permanent species, Isolated tree and Willow communities were the most homogeneous, among which visits of *Carduelis* spp. and *Turdus iliacus* engendered a winter differentiation. Shrub and Forbs communities were enriched by foliage insectivorous species (e.g. *Acrocephalus* spp., *Sylvia* spp., *Phylloscopus collybita*) in spring and summer; whereas the species poor community in Shrub was slightly differentiated in winter by

Tab. 5. Mean faunistic similarity between seasons (Jaccard's similarity index). Values express percentages of common species.

		Spring	Summer	Autumn
overall	Summer	62		
	Autumn	45	47	
	Winter	48	45	62
Isolated tree	Summer	65		
	Autumn	44	39	
	Winter	43	43	64
Wood	Summer	64		
	Autumn	50	52	
	Winter	57	56	58
Shrub	Summer	28		
	Autumn	15	44	
	Winter	29	31	31
Forbs	Summer	58		
	Autumn	28	40	
	Winter	38	48	61
Reed	Summer	33		
	Autumn	21	35	
	Winter	23	24	43
Cattail	Summer	27		
	Autumn	12	9	
	Winter	12	9	45
Mudflat	Summer	49		
	Autumn	34	40	
	Winter	37	42	48

mainly permanent residents (*A. caudatus, Erithacus rubecula, Troglodytes troglodytes*), the Forbs community was enriched by wetland granivorous species (*E. schoeniclus, P. biarmicus*) in autumn and winter, replaced by insectivores in spring and summer (*Acrocephalus* spp., *Luscinia svecica*). From Reed to Mudflat, seasonality substantially inflated by higher proportions of migrants (see Fig. 3). In Reed and Cattail, a functional switch similar to the one in Forbs was characterized by *A. scirpaceus* and *Locustella naevia* in spring and summer, and *E. schoeniclus* and *P. biarmicus* in autumn and winter. In Mudflat, the seasonality mainly consisted in a switch from waders (e.g. *Tringa* spp., *H. ostralegus*) in summer to anatids (e.g. *A. crecca, B. canadensis*) in autumn and winter, although *A. strepera*, a herbivorous dabbling duck, was dominantly present in summer.

DISCUSSION

1. Potential experimental drawback

Observed species richness and abundances might have been constrained by the small surface area of the study site (8.2 ha). Surface area have been shown to be a limiting factor of species richness and abundance in marsh ecosystems (Brown and Dinsmore 1986; Craig and Beal 1992), where small

surface areas may increase adverse edge effects on sensitive species through increased risk of predation, and especially disturbance due to human presence (Benoit and Askins 2002). Influences on abundance and species richness seem likely since frequent walking and cycling passages occur along the surrounding dyke of the studied polder. Large marsh surface areas ensure buffer zones which minimize disturbance to sensitive birds such as waders for which flush distances can reach several tens meters (Burger 1981; Rodgers and Smith 1997).

Also, habitat species richness pattern could have been biased due to unequal habitat surface area and perimeter; however, these parameters were not significantly correlated to the number of species ($p > 0.05$). On the contrary, abundance was significantly correlated to surface area ($p < 0.001$); this proves that habitat occupancy kept constant in terms of bird density.

The number of species observed in the CRT was less than the compiled reference list, but all characteristic species of the natural tidal freshwater marshes of the North Sea coast were encountered in the CRT. Several reasons may explain the lower CRT species richness such as habitat size requirement and isolation, especially concerning colonial species (Platteeuw et al. 2010). However, most of reference species are derived from a study along a tidal river including habitats atypical of tidal marshes: river channel and residential zones, and managed habitats such as tidal coppices and meadows (Strucker 1996). Nevertheless, no difference was found between the functional structures of the two species pools. This demonstrates that the CRT surface area did not prevent to highlight the suitability of the CRT habitats with regard to the functional reference.

2. Community functioning

The rapid habitat development during the year preceding the bird monitoring (Jacobs et al. 2009) probably explains the weakness or the absence of a year effect on the bird communities in most habitats. As displayed by Figure 2, a large majority of species was already present the first monitoring year, particularly in the richest and the most populated habitats. In restored intertidal habitats through managed realignment in the UK, the main community changes were shown to occur within the first year (Atkinson et al. 2004; Mander et al. 2007). Generally, once habitats are created, benthic invertebrates and birds respond fairly quickly if conditions are suitable (Atkinson 2003; Ma et al. 2004). Habitat quality is most of the time
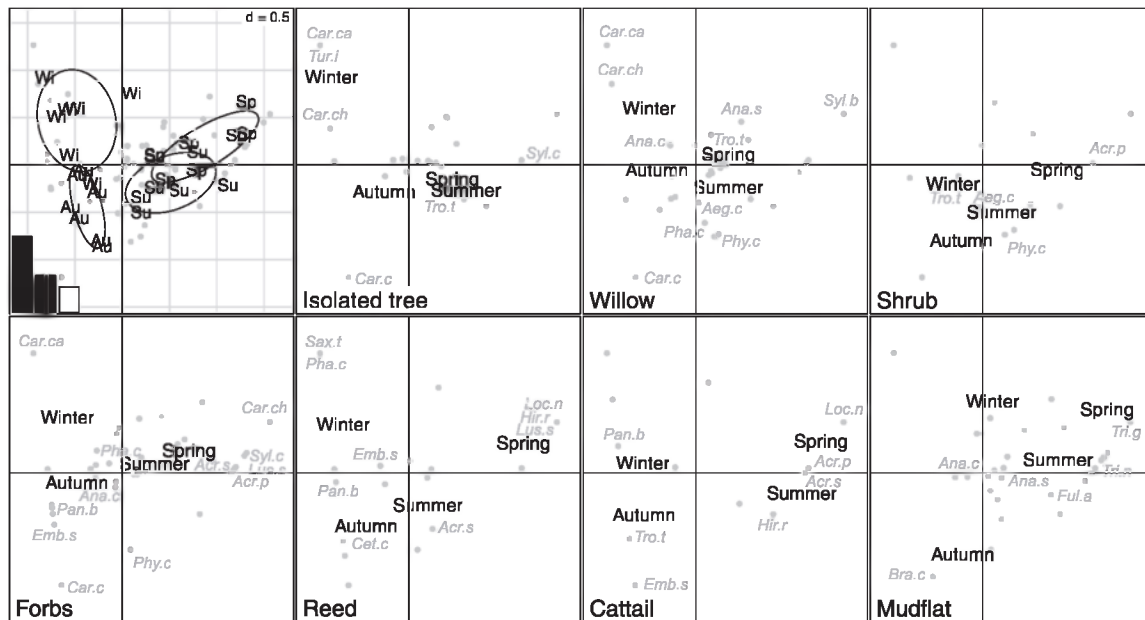
Fig. 6. Foucart's correspondence analysis on habitat tables. Axis 1 (horizontal), 55 %; axis 2 (vertical), 27 %. Top-left: average position of species (grey points); habitats grouped per season (black characters); "d" indicates the grid scale. Following panels: respective positions of species (grey points) and seasons (black characters) per habitat. Abbreviations of the most contributing species: *Aeg.c, Aegithalos caudatus; Acr.p, Acrocephalus palustris; Acr.s, Acrocephalus scirpaceus; Ana.c, Anas crecca; Ana.s, Anas strepera; Bra.c, Branta canadensis; Car.c, Carduelis carduelis; Car.ca, Carduelis cannabina; Car.ch, Carduelis chloris; Cet.c, Cettia cetti; Emb.s, Emberiza schoeniclus; Ful.a, Fulica atra; Hir.r, Hirundo rustica; Loc.n, Locustella naevia; Lus.s, Luscinia svecica; Pan.b, Panurus biarmicus; Pha.c, Phasianus colchicus; Phy.c, Phylloscopus collybita; Sax.t, Saxicola torquata; Syl.c, Sylvia communis; Syl.b, Sylvia borin; Tri.g, Tringa glareola; Tri.n, Tringa nebularia; Tur.i, Turdus iliacus; Tro.t, Troglodytes troglodytes.*

the leading criterion to ensure a successful restoration for foraging waterfowls (Atkinson 2003; West et al. 2005). Sediment characteristics play a key-role since they condition prey densities, and particle size distribution were shown to be a relevant predictor of shorebirds densities (Yates et al. 1993). In the CRT, the lowest locations received 15 cm of silty estuarine sediment after less than one year (Vandenbruwaene et al. 2010); higher macroinvertebrate densities were found compared to those encountered on the adjacent estuarine sandflats (O. Beauchar, unsubmitted manuscript). This could explain the absence or the weakness of year effect on the communities, at least in Mudflat, dominated by benthivorous birds.

However, at the species scale, Appendix 4 shows that the abundances of three species among the most frequent ones exhibited between-year growing tendencies, and their abundances required either one year (*A. crecca*) or more (*E. schoeniclus, A. scirpaceus*) to reach a pluriannual demographic stability. Positive covariations were found between abundances of these species and the amount of specific resources in the CRT: *A. crecca*, a wintering bird in the Schelde estuary, which feeds on tubificids on estuarine flats (Ysebaert et al.

2000), with winter tubificid densities; *A. scirpaceus*, a reed specialist, with Reed coverage, and probably explaining the slightly significant year effect on Reed community; massive populations of *E. schoeniclus* were observed to forage in Loosestrife foliage when seed reached maturation. This strongly points to a successful habitat uses by three migratory species, in the complement of their life cycle for overwintering or breeding (*A. scirpaceus*; see below).

The marsh communities were strongly habitat-specific, indicating non-random habitat occupancy. This is a typical feature of bird communities in natural ecosystems (MacArthur 1964; Block and Brennan 1993), and particularly in vegetation stages (Adams 1908; MacArthur and MacArthur 1961; Blondel 1973; Willson 1974). All foraging group distributions intersected in Forbs habitat (Fig. 5, lower insert) which articulated the two habitat gradients by offering resource to ground and foliage ubiquists and specialists. This probably explains the highest number of species encountered in this habitat. This also concurs with Weller (1978) who suggested that increased tidal freshwater habitat use by birds is promoted by plant community diversity as it is

the case in Forbs. Whereas bird species richness can exhibit monotonic or hump-shaped tendencies in terrestrial successions, no clear pattern arose here; this aspect seems to have never been mentioned in wetland bird community ecology. This suggests that, along the habitat succession, any resource offers a common environmental optimum to a majority of species, hence reflecting independent processes among habitats. Specific environmental characteristics or sub-gradient such as foliage complexity, below-ground space, tidal influence or prey availability might explain the observed pattern.

The remarkable stability of the spatial structure and the faunistic evenness over seasons was concordant with common seasonal effects on foraging group proportions or switches in dominance between permanent and migratory residents. Indeed, no significant distinction between positions of foraging groups arose from the two axes of the FCA on habitat tables (Tukey HSD test; $p > 0.05$). This is in contradiction with bird communities from non-tidal wetlands where community structure varies depending on seasonal water fluctuations (Elmberg et al. 1993; Froneman et al. 2001). Here, the relatively seasonal constancy of the tidal regime may have conditioned the permanence of the functional structure whereby the seasonal trajectories were consequent of taxonomic turnovers inherent to each habitat. Besides, the seasonal dynamics is an important feature which takes account for temporal habitat value as regard to species life cycle completion (Runge and Marra 2005; Wightman et al. 2007).

3. Tidal effect

The tide effect was more substantial on the Forbs and Mudflat communities. Three characteristic benthivores, among the most frequent species in both the CRT and the adjacent tidal flats where they forage at low tide (Ysebaert et al. 2000), *A. crecca*, *A. platyrhynchos* and *A. strepera*, were the most sensitive ones to the tidal effect (Appendices 5 and 6). In estuaries, waterbird movements are generally regulated by the tidal cycle, during which birds uses terrestrial resting or foraging grounds at high tide (Rogers 2003; Shepherd et al. 2003; Burton et al. 2004). As a consequence of the CRT system, the polder is flooded with a delay of nearly 1.5 hours on the adjacent river tidal flats (Beauchard et al. 2011b); moreover, almost no water enters the polder at neap tide. Hence, CRT offers extended feeding time for species that also forage on the adjacent tidal flats, especially when large areas are created. This could have explained the tide effect on Forbs and Mudflat communities when the adjacent

river flats were submerged at high tide and thus unavailable for birds, as already shown in wetlands adjacent to an estuary (Davidson and Evans 1986; Evans et al. 1998). This hypothesis was invalidated since abundances were not determined by the availability of the adjacent flats (Appendix 6). Besides, this does not prove a preference for river habitats in so far as the bird abundances in the CRT were not significantly lower when the adjacent tidal flats were available at low tide. This highlights complex behaviours, possibly in synchrony with hydrological conditions at a larger spatial scale, but such phenomenon does not seem to have been documented in dabbling ducks.

Dabbling duck nests (*A. platyrhynchos* and *A. strepera*) were observed every year in the Forbs habitat, but they were either abandoned during building or after spring tide events. Although this aspect is also poorly documented concerning dabbling ducks, tidal cycle may have acted as an ecological trap for these species, as already observed for other species in North America (Gjerdrum et al. 2005; Nordby et al. 2009). However, complete breeding was observed for several species: *Acrocephalus palustris*, *A. scirpaceus*, *A. atthis*, Fulica atra, *Gallinula chloropus* and *Sylvia communis*. Contrary to the statements of Barendregt et al. (2009), breeding below the mean high water level was possible; *Fulica atra* and *Gallinula chloropus* built floating nests to cope with inundation. Additionally, the CRT ensured a nursery function as chicks from ducks and other species were regularly observed (Appendix 7).

4. A positive avian response to CRT habitat creation?

This study clearly demonstrates a significant CRT habitat occupancy by avifauna, dominantly represented by wetland specialist species. The functional coherence observed and reference species pools on the one hand, and the strong correspondence between communities and habitats across seasons on the other hand, support the suitability of CRT habitats for marsh bird communities, at least for the completion of species life cycle. Moreover, the high diversity of species, among which one third exhibits ecological importance or concern at local and/or international scale, adds a strong conservation value to CRT habitats. More fundamentally, the seasonal constancy of the tidal regime points to the potential importance of tidal freshwater restoration for providing stable wetland habitats beneficial to

a large diversity of inland bird species. Further CRT implementation on larger surface areas – as planned along the Schelde estuary – may increase the restoration potential.

ACKNOWLEDGEMENTS

Spotted Redshank (Tringa erythropus), Lippenbroek polder, April 2007. Photograph: Paul Heerwegh.

APPENDICES

Appendix 1. Species of the reference pool not encountered in the CRT. Sources: 1, Strucker (1996); 2, Temmerman (1992); 3, Van Waeyenberge et al. (1999).

Common name	Latin name	Wetland status	Foraging status	Trophic status	Residential status
Northern Goshawk	*Accipiter gentilis*[1]		G	LC	P
Great Reed Warbler	*Acrocephalus arundinaceus*[1]	X	F	SC	S
Mandarin Duck	*Aix galericulata*[1]	X	G	SO	P
Alauda arvensis	*Alauda arvensis*[1]		G	SO	P
Eurasian Wigeon	*Anas penelope*[1]	X	G	SO	W
Garganey	*Anas querquedula*[1]	X	G	SO	S
Greater White-fronted Goose	*Anser albifrons*[1]	X	G	H	W
Pink-footed Goose	*Anser brachyrhynchus*[1]	X	G	H	W
Taiga Bean Goose	*Anser fabalis*[1]	X	G	H	W
Taiga Bean Goose	*Anthus campestris*[1]		FG	SO	S
Red-throated Pipit	*Anthus cervinus*[1]		FG	SO	S
Richard's Pipit	*Anthus richardi*[1]		G	SC	P
Tree Pipit	*Anthus trivialis*[1]		F	SC	S
Purple Heron	*Ardea purpurea*[1]	X	G	LC	P
Squacco Heron	*Ardeola ralloides*[1]	X	G	LC	S
Ruddy Turnstone	*Arenaria interpres*[1]	X	G	SO	S
Short-eared Owl	*Asio flammeus*[1]	X	FG	LC	W
Little Owl	*Athene noctua*[1]		G	LC	P
Common Pochard	*Aythya ferina*[1]	X	G	SO	W
Greater Scaup	*Aythya marila*[1]	X	G	SC	W
Bohemian Waxwing	*Bombycilla garrulus*[1]		F	SO	W
Eurasian Bittern	*Botaurus stellaris*[1]	X	G	LC	P
Brant Goose	*Branta bernicla*[1]	X	G	H	W
Barnacle Goose	*Branta leucopsis*[1]	X	G	H	W
Western Cattle Egret	*Bubulcus ibis*[1]	X	G	SC	P
Bufflehead	*Bucephala albeola*[1]	X	G	SC	W
Common Goldeneye	*Bucephala clangula*[1]	X	G	SC	W
Rough-legged Buzzard	*Buteo lagopus*[1]		G	LC	S
Lapland Longspur	*Calcarius lapponicus*[1]		FG	SO	S
Dunlin	*Calidris alpina*[1,2]	X	G	SC	W
Red Knot	*Calidris canutus*[1]	X	G	SC	W
Calidris ferruginea	*Calidris ferruginea*[1]	X	G	SC	W
Little Stint	*Calidris minuta*[1]	X	G	SC	W
Temminck's Stint	*Calidris temminckii*[1]	X	G	SC	S
European Nightjar	*Caprimulgus europaeus*[1]		A	SC	S
Common Redpoll	*Carduelis flammea*[1,2]		F	SC	W
Eurasian Siskin	*Carduelis spinus*[1,2]		F	SC	W
Eurasian Treecreeper	*Certhia familiaris*[1]		F	SC	P
White-winged Tern	*Chlidonias leucopterus*[1]	X	G	SC	S
Black Tern	*Chlidonias niger*[1]	X	G	SC	S
White Stork	*Ciconia ciconia*[1]		G	LC	S
Black Stork	*Ciconia nigra*[1]		G	LC	S
Montagu's Harrier	*Circus pygargus*[1]		FG	LC	S
Hawfinch	*Coccothraustes coccothraustes*[1]		F	G	S
Western Jackdaw	*Coloeus monedula*[1,2]		FG	LO	P
Rook	*Corvus frugilegus*[1,2]		FG	LO	P
Common Quail	*Coturnix coturnix*[1]		G	SO	S
Corn Crake	*Crex crex*[1]		G	SO	S
Black Swan	*Cygnus atratus*[1]	X	G	H	P
Tundra Swan	*Cygnus columbianus*[1]	X	G	H	S
Whooper Swan	*Cygnus cygnus*[1]	X	G	H	W
Mute Swan	*Cygnus olor*[1]	X	G	SC	S
Middle Spotted Woodpecke	*Dendrocopos medius*[1]		F	SC	P
Yellowhammer	*Emberiza citrinella*[1]		F	SO	S
Merlin	*Falco columbarius*[1]	X	F	LC	W
Peregrine Falcon	*Falco peregrinus*[1]		G	LC	P
Red-footed Falcon	*Falco vespertinus*[1]		FG	LC	S
European Pied Flycatcher	*Ficedula hypoleuca*[1]		A	SC	S
Red-throated Loon	*Gavia stellata*[1]	X	G	LC	P
Common Crane	*Grus grus*[1]	X	G	SO	S
White-tailed Eagle	*Haliaeetus albicilla*[1]	X	G	LC	W
Icterine Warbler	*Hippolais icterina*[1]	X	F	SC	S
Little Gull	*Hydrocoloeus minutus*[1]	X	G	SC	W

| Common name	Species	Wetland status	Foraging status	Trophic status	Residential status
Caspian Tern	*Hydroprogne caspia*[1]	X	G	LC	S
Mediterranean Gull	*Ichthyaetus melanocephalus*[1]	X	G	SC	S
Eurasian Wryneck	*Jynx torquilla*[1]		G	SC	S
Red-backed Shrike	*Lanius collurio*[1]		FG	SC	S
Great Grey Shrike	*Lanius excubitor*[1,2]		FG	LC	S
Mew Gull	*Larus canus*[1,2]	X	G	LC	P
Lesser Black-backed Gull	*Larus fuscus*[1,2]	X	G	LO	P
Great Black-backed Gull	*Larus marinus*[1,2]	X	G	LC	P
Yellow-legged Gull	*Larus michahellis*[1]	X	G	LC	P
Bar-tailed Godwit	*Limosa lapponica*[1]	X	G	SC	W
Black-tailed Godwit	*Limosa limosa*[1]	X	G	SC	W
Savi's Warbler	*Locustella luscinioides*[1]	X	F	SC	S
European Crested Tit	*Lophophanes cristatus*[1]		F	SC	P
Red Crossbill	*Loxia curvirostra*[1]		F	G	W
Woodlark	*Lullula arborea*[1]		FG	SO	P
Common Nightingale	*Luscinia megarhynchos*[1,2,3]		FG	SC	S
Common Merganser	*Mergus merganser*[1,2]	X	G	LC	W
Red-breasted Merganser	*Mergus serrator*[1]	X	G	LC	W
European Bee-eater	*Merops apiaster*[1]		F	SC	S
Black Kite	*Milvus migrans*[1]		G	LC	S
Red Kite	*Milvus milvus*[1]		G	LC	S
Grey Wagtail	*Motacilla cinerea*[1,2]	X	G	SC	S
Western Yellow Wagtail	*Motacilla flava*[1,2]	X	G	SC	S
Spotted Flycatcher	*Muscicapa striata*[1]		A	SC	S
Eurasian Curlew	*Numenius arquata*[1,2]	X	G	SC	S
Whimbrel	*Numenius phaeopus*[1]	X	G	SC	S
Northern Wheatear	*Oenanthe oenanthe*[1]		FG	SC	S
House Sparrow	*Passer domesticus*[1,2,3]		F	SO	P
Rosy Starling	*Pastor roseus*[1]		FG	SC	S
Rock Partridge	*Perdix perdix*[1,3]		G	SO	P
Coal Tit	*Periparus ater*[1]		F	SO	P
European Honey Buzzard	*Pernis apivorus*[1]		FG	LC	S
Black Redstart	*Phoenicurus ochruros*[1]		FG	SC	S
Common Redstart	*Phoenicurus phoenicurus*[1]		FG	SC	S
Yellow-browed Warbler	*Phylloscopus inornatus*[1]		F	SC	S
Wood Warbler	*Phylloscopus sibilatrix*[1]		F	SC	S
Greenish Warbler	*Phylloscopus trochiloides*[1,2,3]		F	SC	S
European Golden Plover	*Pluvialis apricaria*[1]	X	G	SC	W
Grey Plover	*Pluvialis squatarola*[1]	X	G	SC	W
Black-necked Grebe	*Podiceps nigricollis*[1]	X	G	LC	P
Spotted Crake	*Porzana porzana*[1]	X	G	SO	S
Rose-ringed Parakeet	*Psittacula krameri*[1]		FG	G	P
Eurasian Bullfinch	*Pyrrhula pyrrhula*[1,2]		FG	SO	P
Common Firecrest	*Regulus ignicapilla*[1]		F	SC	P
Eurasian Penduline Tit	*Remiz pendulinus*[3]	X	F	SO	P
Sand Martin	*Riparia riparia*[1,2]	X	A	SC	S
Whinchat	*Saxicola rubetra*[1]		FG	SC	S
European Serin	*Serinus serinus*[1]		FG	G	S
Eurasian Nuthatch	*Sitta europaea*[1]		F	SC	P
Long-tailed Jaeger	*Stercorarius longicaudus*[1]	X	G	LC	P
Great Skua	*Stercorarius skua*[1]	X	G	LC	S
Arctic Tern	*Sterna paradisaea*[1]	X	G	LC	S
Little Tern	*Sternula albifrons*[1]	X	G	SC	S
Eurasian Collared Dove	*Streptopelia decaocto*[1,2,3]		G	G	S
Tawny Owl	*Strix aluco*[1]		G	LC	P
Lesser Whitethroat	*Sylvia curruca*[1,2]		F	SC	S
Ruddy Shelduck	*Tadorna ferruginea*[1]	X	G	SO	S
Sandwich Tern	*Thalasseus sandvicensis*[1]	X	G	LC	S
Marsh Sandpiper	*Tringa stagnatilis*[1]	X	G	SC	S
Fieldfare	*Turdus pilaris*[1,2]		FG	SO	W
Ring Ouzel	*Turdus torquatus*[1]		FG	SO	S
Western Barn Owl	*Tyto alba*[1]		G	LC	P
Eurasian Hoopoe	*Upupa epops*[1]		FG	SC	S

Appendix 2. Mean percentages (± S.E.) of individual birds and species per habitat and season. Group: P, permanent resident; M, migrant; F, foliage specialist; FG, foliage and ground ubiquist; G, ground specialist.

Habitat	Group	Proportion of individuals				Proportion of species			
		Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Isolated tree	PF	29.3 ± 7.9	24.5 ± 8.2	28.0 ± 8.0	35.6 ± 9.1	20.0 ± 4.7	22.4 ± 7.6	21.4 ± 5.4	27.1 ± 6.9
	PFG	51.7 ± 6.8	44.8 ± 9.6	64.6 ± 7.1	39.2 ± 8.8	57.7 ± 6.0	45.0 ± 9.4	70.4 ± 4.9	49.4 ± 7.6
	PG	5.6 ± 3.7	8.1 ± 3.1	7.4 ± 3.6	7.5 ± 3.6	5.6 ± 3.7	9.3 ± 3.4	8.1 ± 3.8	8.7 ± 3.8
	MF	13.3 ± 5.6	16.3 ± 6.8	0.0 ± 0.0	1.9 ± 1.9	16.6 ± 6.7	17.1 ± 6.7	0.0 ± 0.0	1.3 ± 1.3
	MFG	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	3.3 ± 3.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.0 ± 1.0
Willow	PF	22.2 ± 4.4	28.1 ± 4.8	33.3 ± 5.1	29.5 ± 6.1	22.5 ± 2.9	25.3 ± 3.2	31.7 ± 2.8	30.8 ± 3.7
	PFG	27.8 ± 4.0	24.2 ± 3.6	26.5 ± 3.2	14.7 ± 2.2	30.7 ± 3.2	28.3 ± 3.1	33.2 ± 2.7	26.0 ± 2.9
	PG	25.4 ± 3.6	28.5 ± 3.3	17.8 ± 2.8	19.5 ± 3.6	24.9 ± 2.9	29.5 ± 1.8	20.8 ± 1.7	28.4 ± 3.9
	MF	9.7 ± 1.2	9.1 ± 1.9	4.4 ± 1.6	1.3 ± 0.9	11.5 ± 1.5	11.4 ± 2.1	5.3 ± 1.6	2.2 ± 1.2
	MFG	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.1 ± 0.8	0.0 ± 0.0
	MG	14.9 ± 4.8	10.0 ± 3.7	17.4 ± 3.8	35.0 ± 7.0	10.4 ± 2.5	5.4 ± 1.7	7.8 ± 1.7	12.6 ± 2.5
Shrub	PF	0.0 ± 0.0	12.0 ± 7.0	37.1 ± 11.7	8.3 ± 8.3	0.0 ± 0.0	9.9 ± 5.6	24.1 ± 6.0	8.3 ± 8.3
	PFG	0.0 ± 0.0	17.5 ± 8.5	18.9 ± 6.4	12.5 ± 8.2	0.0 ± 0.0	21.5 ± 9.4	29.5 ± 6.0	12.5 ± 8.2
	PG	18.8 ± 12.0	10.4 ± 7.2	1.8 ± 1.8	16.7 ± 12.6	18.8 ± 12.0	8.9 ± 6.2	2.1 ± 2.1	16.7 ± 12.6
	MF	81.3 ± 12.0	40.1 ± 12.5	8.2 ± 2.6	31.3 ± 16.2	81.3 ± 12.0	41.0 ± 12.3	15.4 ± 4.7	31.3 ± 16.2
	MG	0.0 ± 0.0	3.3 ± 3.3	34.0 ± 12.7	6.3 ± 6.3	0.0 ± 0.0	2.1 ± 2.1	29.0 ± 11.6	6.3 ± 6.3
Forbs	PF	0.8 ± 0.8	3.5 ± 1.4	13.0 ± 2.7	21.7 ± 4.9	1.1 ± 1.1	5.3 ± 1.7	16.5 ± 2.2	19.5 ± 3.4
	PFG	17.2 ± 2.6	12.4 ± 2.9	25.5 ± 2.9	18.8 ± 3.3	21.9 ± 3.5	15.6 ± 3.1	32.3 ± 2.0	30.0 ± 3.5
	PG	24.7 ± 2.9	25.9 ± 3.2	13.2 ± 1.6	18.1 ± 2.1	27.2 ± 2.8	27.6 ± 2.2	16.5 ± 1.6	22.9 ± 2.1
	MF	17.2 ± 2.4	19.4 ± 2.8	15.5 ± 2.5	5.2 ± 1.4	25.0 ± 2.5	28.2 ± 2.3	12.3 ± 1.2	6.3 ± 1.4
	MFG	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 0.6	0.0 ± 0.0
	MG	40.1 ± 3.8	38.8 ± 3.5	32.4 ± 5.0	36.3 ± 5.5	24.8 ± 3.1	23.4 ± 1.6	21.8 ± 1.6	21.2 ± 2.9
Reed	PF	0.0 ± 0.0	8.8 ± 4.8	24.8 ± 6.3	24.0 ± 7.6	0.0 ± 0.0	9.2 ± 3.9	27.9 ± 5.2	22.7 ± 7.2
	PFG	1.8 ± 1.8	1.3 ± 1.3	1.5 ± 1.0	1.0 ± 1.0	2.1 ± 2.1	1.6 ± 1.6	4.1 ± 2.2	2.1 ± 2.1
	PG	23.4 ± 6.4	12.3 ± 3.6	4.9 ± 2.1	10.3 ± 4.5	26.9 ± 7.1	14.9 ± 4.0	9.3 ± 3.5	16.5 ± 5.3
	MF	62.1 ± 8.1	52.7 ± 7.7	34.3 ± 5.2	24.2 ± 5.3	59.6 ± 7.8	55.3 ± 7.2	34.3 ± 3.0	25.6 ± 5.2
	MG	12.7 ± 6.8	24.8 ± 6.2	34.5 ± 7.1	40.5 ± 9.3	11.5 ± 6.5	19.0 ± 4.5	24.4 ± 3.3	33.1 ± 7.3
Cattail	PF	0.0 ± 0.0	0.0 ± 0.0	16.2 ± 8.6	20.2 ± 9.4	0.0 ± 0.0	0.0 ± 0.0	12.5 ± 6.5	18.8 ± 9.0
	PFG	0.0 ± 0.0	1.8 ± 1.8	4.2 ± 4.2	0.0 ± 0.0	0.0 ± 0.0	2.1 ± 2.1	4.2 ± 4.2	0.0 ± 0.0
	PG	12.5 ± 8.8	21.5 ± 8.5	22.0 ± 9.7	15.9 ± 8.0	14.6 ± 9.7	23.6 ± 8.7	25.0 ± 9.7	16.7 ± 7.9
	MF	41.7 ± 17.5	50.4 ± 11.0	20.8 ± 11.4	0.0 ± 0.0	41.7 ± 17.5	48.0 ± 10.9	20.8 ± 11.4	0.0 ± 0.0
	MG	8.3 ± 8.3	1.3 ± 1.3	11.8 ± 6.7	13.9 ± 8.5	6.3 ± 6.3	1.3 ± 1.3	12.5 ± 6.5	14.6 ± 8.6
Mudflat	PFG	0.9 ± 0.6	1.1 ± 0.7	0.0 ± 0.0	0.0 ± 0.0	1.7 ± 1.1	1.7 ± 1.2	0.0 ± 0.0	0.0 ± 0.0
	PG	54.2 ± 3.6	48.2 ± 2.5	33.9 ± 4.3	38.1 ± 6.0	54.2 ± 3.9	58.3 ± 1.7	50.8 ± 2.1	56.7 ± 4.3
	MG	44.5 ± 3.4	50.3 ± 2.8	66.1 ± 4.3	61.9 ± 6.0	43.3 ± 3.6	39.5 ± 2.0	49.2 ± 2.1	43.3 ± 4.3

Appendix 3. Absolute contributions of species in the Foucart's correspondence analyses (in % of axis inertia).

| Species	Season tables		Habitat tables		Species	Season tables		Habitat tables	
	Axis 1	Axis 2	Axis 1	Axis 2		Axis 1	Axis 2	Axis 1	Axis 2
Accipiter nisus	0.5	1.3	0.5	0.1	Garrulus glandarius	1.5	2.8	0.1	0.2
Acrocephalus palustris	0.6	0.7	6.3	0.0	Haematopus ostralegus	2.9	0.9	0.2	0.4
Acrocephalus schoenobaenus	0.0	0.6	0.2	1.1	Hirundo rustica	0.9	0.9	4.8	0.3
Acrocephalus scirpaceus	0.0	3.9	3.4	1.0	Larus argentatus	1.7	0.5	0.9	0.1
Actitis hypoleucos	0.7	0.0	1.6	0.1	Larus ridibundus	5.2	1.6	0.1	0.0
Aegithalos caudatus	8.8	0.0	1.5	10.9	Locustella naevia	0.0	2.2	2.9	0.7
Alcedo atthis	0.6	0.4	0.2	0.5	Luscinia svecica	0.1	1.9	4.8	0.9
Alopochen aegyptiacus	4.9	1.5	1.2	0.8	Lymnocryptes minimus	0.0	0.1	0.1	0.5
Anas acuta	0.4	0.1	0.2	0.6	Mergellus albellus	0.4	0.1	0.2	0.6
Anas crecca	1.3	3.3	6.6	0.0	Motacilla alba	1.2	0.4	0.5	0.0
Anas platyrhynchos	0.2	0.6	0.0	1.2	Netta rufina	0.0	0.1	0.4	0.1
Anas strepera	1.1	0.3	2.9	1.0	Nycticorax nycticorax	0.1	0.0	0.5	0.1
Anser anser	1.3	0.4	0.5	1.8	Oriolus oriolus	0.1	0.0	0.5	0.1
Anthus spinoletta	0.0	0.1	0.2	0.6	Panurus biarmicus	0.0	6.6	4.2	0.2
Apus apus	0.0	0.2	0.2	0.1	Parus major	2.0	1.4	0.0	0.2
Ardea cinerea	0.0	0.5	0.0	0.1	Passer montanus	0.1	0.0	0.1	1.0
Aythya fuligula	0.0	0.2	0.8	0.2	Phalacrocorax carbo	0.1	2.4	0.3	0.0
Branta canadensis	10.8	2.0	0.7	9.8	Phasianus colchicus	0.1	3.3	1.3	4.5
Buteo buteo	0.2	0.0	0.1	0.0	Phylloscopus collybita	0.4	1.6	0.3	4.0
Carduelis cannabina	0.1	0.4	3.8	7.1	Pica pica	0.8	1.7	0.9	0.2
Carduelis carduelis	3.5	11.1	3.7	5.0	Picus viridis	1.5	1.8	0.0	1.6
Carduelis chloris	1.5	1.1	2.2	3.7	Platalea leucorodia	0.5	0.2	0.1	0.1
Certhia brachydactyla	0.2	0.0	0.0	0.5	Poecile montanus	0.3	0.0	0.7	2.6
Cettia cetti	0.1	0.6	0.5	3.2	Poecile palustris	0.4	1.2	0.2	0.1
Charadrius dubius	0.5	0.2	0.1	0.1	Prunella modularis	1.0	0.0	0.0	0.2
Charadrius hiaticula	1.0	0.3	0.7	0.2	Rallus aquaticus	0.1	1.1	1.0	0.3
Circus aeruginosus	0.0	0.2	0.0	0.1	Recurvirostra avosetta	1.1	0.3	0.9	0.2
Circus cyaneus	0.0	0.2	0.2	0.0	Regulus regulus	0.1	0.3	0.7	1.0
Columba livia	0.1	0.0	0.4	1.3	Saxicola torquata	0.0	2.1	1.0	3.6
Columba oenas	0.5	0.2	0.1	0.1	Scolopax rusticola	0.0	0.1	0.2	0.6
Columba palumbus	0.3	0.7	1.3	0.0	Sterna hirundo	2.6	0.8	1.0	0.0
Corvus corone	0.3	0.7	0.7	0.5	Sturnus vulgaris	0.0	0.1	0.4	0.1
Cuculus canorus	0.4	1.3	0.8	0.2	Sylvia atricapilla	0.3	0.7	1.4	0.0
Cyanistes caeruleus	1.9	0.2	0.0	0.0	Sylvia borin	0.8	0.5	3.3	0.2
Delichon urbicum	1.6	0.5	0.4	0.2	Sylvia communis	0.5	0.0	4.9	0.3
Dendrocopos major	1.1	1.7	0.2	0.2	Tachybaptus ruficollis	0.9	0.3	0.0	0.5
Dendrocopos minor	0.1	0.0	0.1	0.1	Tadorna tadorna	3.4	0.3	0.3	0.3
Egretta garzetta	0.6	0.2	0.4	0.1	Tringa glareola	3.4	1.0	2.7	0.6
Emberiza schoeniclus	0.7	1.1	3.0	0.6	Tringa nebularia	1.3	0.1	2.3	0.2
Erithacus rubecula	0.7	0.5	0.0	1.9	Tringa ochropus	3.0	0.5	0.3	0.1
Falco subbuteo	0.6	0.2	0.4	0.1	Tringa totanus	1.2	0.2	0.6	0.8
Falco tinnunculus	0.6	0.4	0.0	0.0	Troglodytes troglodytes	0.7	2.1	1.1	2.9
Fringilla coelebs	1.4	1.7	0.4	0.6	Turdus iliacus	2.7	9.6	2.8	10.2
Fringilla montifringilla	0.0	0.0	0.2	1.1	Turdus merula	1.2	0.4	0.1	0.0
Fulica atra	0.2	0.3	2.9	0.6	Turdus philomelos	0.3	0.0	0.4	0.0
Gallinago gallinago	0.4	5.0	0.1	0.6	Turdus viscivorus	0.1	0.0	0.4	0.1
Gallinula chloropus	0.1	3.1	0.0	0.1	Vanellus vanellus	5.1	0.4	0.8	1.4

Appendix 4. Daily counts of three species marked by increased yearly abundances. Grey bars indicate the density of resource for which each species has a strong affinity. Tubificid (monitored during the two first years, Chapter 4): winter sediment densities in a frequently flooded site (> 80 % of the tides). Loosestrife and Reed coverage: assessed on the overall surface area in spring and autumn 2007 and 2008, and in autumn 2009 (S. Jacobs, unpublished data).
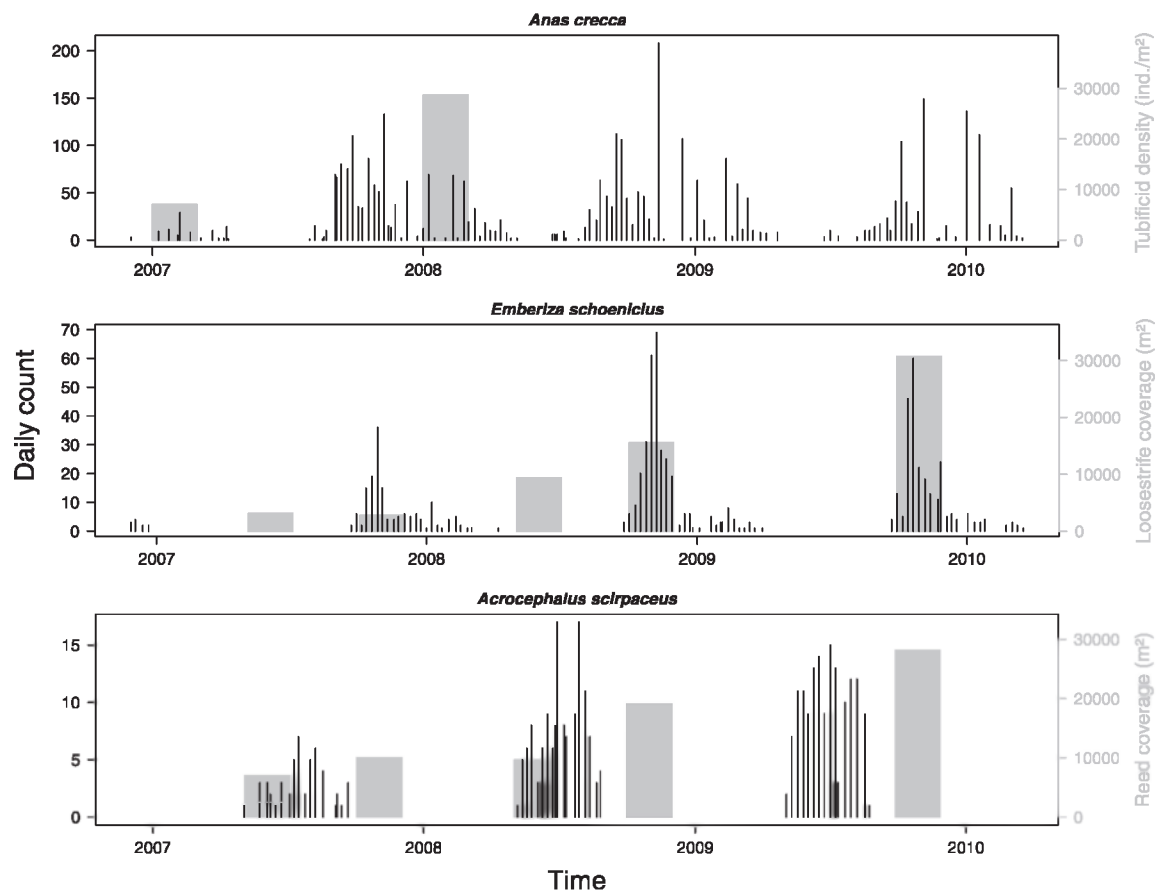
Appendix 5. Water level and tide effects on the daily abundances of the three main waterbird species processed to ANOVA. Number of observations: CRT reference, neap high (38), neap low (42), spring high (40), spring low (37); riverine tidal flats reference, neap high (33), neap low (15), spring high (13), spring low (45).

Water level reference	Effect	*Anas crecca*		*Anas platyrhynchos*		*Anas strepera*	
		F	p	F	p	F	p
CRT	Level	0.5	0.4655	5.7	0.0178	4.4	0.0369
	Tide	11.5	0.0008	18.4	< 0.0001	9.3	0.0027
	Level × Tide	4.3	0.0062	9.1	< 0.0001	4.8	0.0032
Riverine tidal flats	Level	9.5	0.0026	2.0	0.1562	0.3	0.5774
	Tide	12.0	< 0.0001	8.5	0.0044	4.2	0.0427
	Level × Tide	5.0	0.0027	2.9	0.0402	2.6	0.0568

Appendix 6. Average daily counts of the most sensitive species to tide effect in Forbs and Mudflat habitats. Tidal state: N, neap; S, spring; H, high; L, low. A-C) Water levels (H and L) in the CRT. D-F) Water levels according to the availability of riverine flats: H, high level when the floodwater excludes the availability of the tidal flats (> 4 m above the reference sea level); L, low level at low tide (< 2 m above the reference sea level). Absence of common letter indicates a significant difference according to a Tukey HSD test at the rejection level $\alpha = 0.05$.
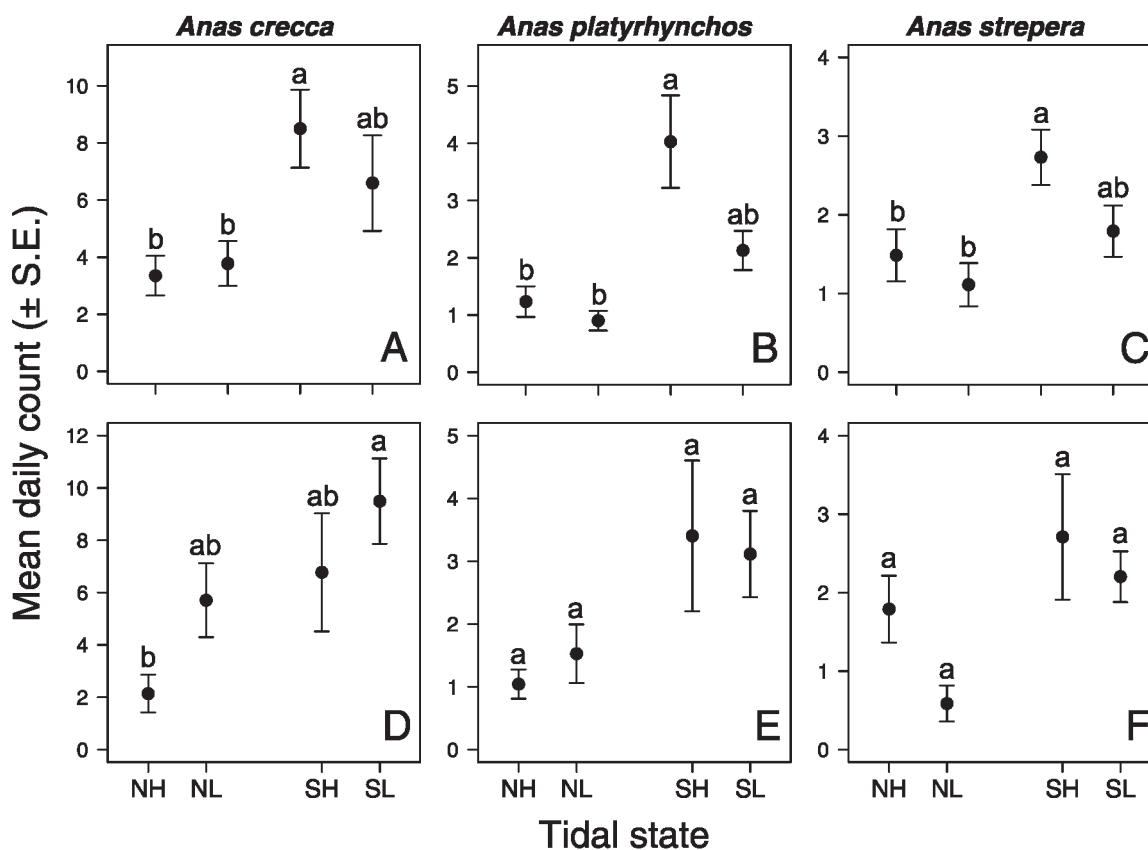
Appendix 7. Daily counts of the four most abundant chick species.
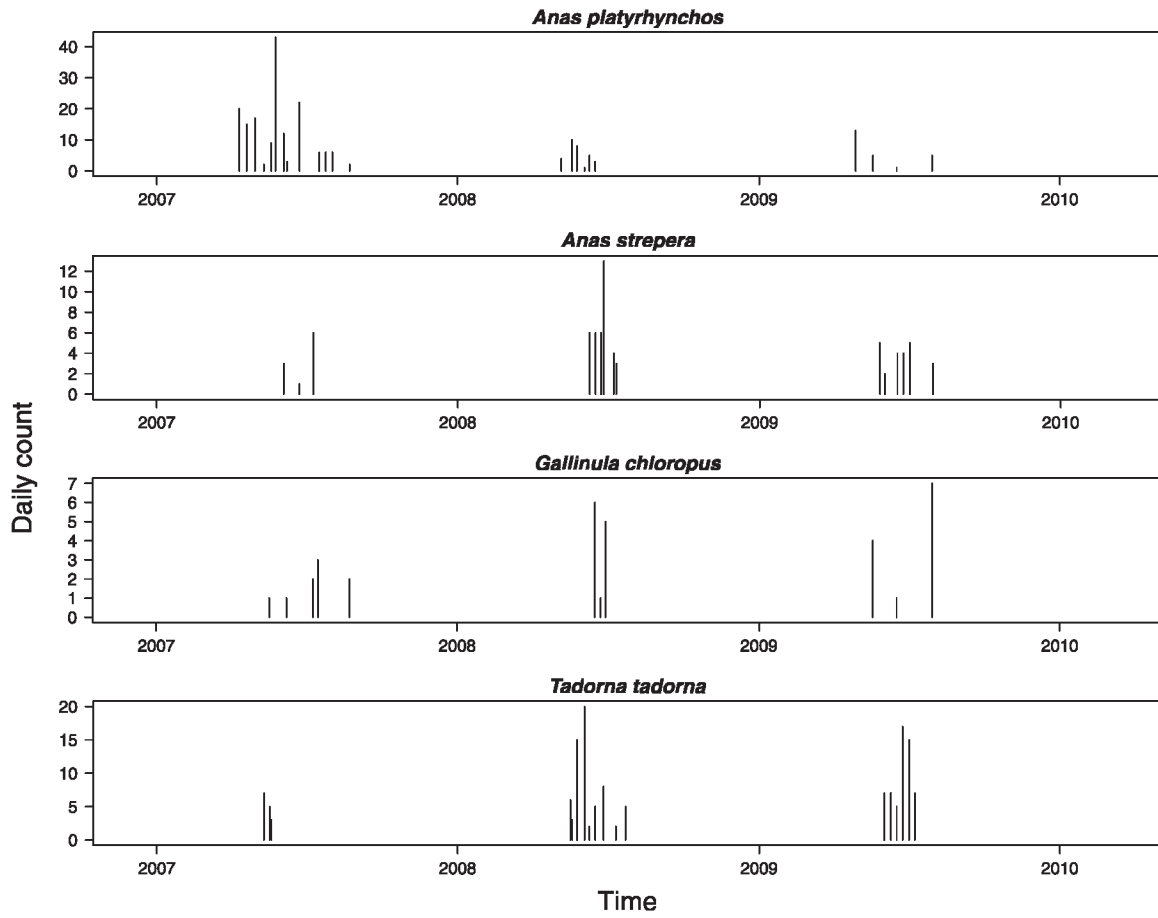
CHAPTER 7

SYNTHESIS

ECOSYSTEM PROCESSES

By combining abiotic and biotic compartments, this work provides one of the first overview of a multi-facetted investigation in the field of tidal freshwater wetland restoration. In a correlative way, abiotic and biotic features engendered by the controlled reduced tide system (CRT) were found to be concordant; organism communities were not randomly organized and functionally specific to environmental conditions.

CRT was supposed to be a key determinant for a suitable estuarine development in areas lowly elevated relative to the high water level. Several ecosystem compartments were monitored in order to account for spatiotemporal processes documented in natural tidal wetlands (Simpson et al. 1983; Odum 1988), and as suggested for tidal restoration assessment (Weinstein et al. 2001; Neckles et al. 2002; French 2006). From hydrology to high trophic levels, the CRT system was shown to rapidly generate diverse ecological conditions gradually structured; the main processes reported in this work are illustrated in Figure 1.

From physical to biological components, hydrological characteristics such as flooding frequency and hydroperiod are at the basis of wetland structure and functions (Odum et al. 1995; Mitsch and Gosselink 2002). In Chapter 2, the CRT

system was proved to successfully create a complete flooding gradient in an area where a simple realignment would have failed due to the elevational incompatibility between the flooded area and the mean high water level. The main gradients highlighted in the abiotic and invertebrate community patterns (Chapter 3 and Chapter 4) were consistently correlated to flooding frequency. Complementarily, the enriched biological functioning of the CRT invertebrate communities underlines the effect of the reduced hydrological stress ensured by the restoration technique. This corroborates the fundamental control of hydrology over other ecosystem compartments. Complementarily, Van Liefferinge et al. (2012) demonstrated in a concomitant study that invertebrates provided a diet of a higher caloric value than those in the adjacent estuary. Interactively, the elevation-specific sediment mixing types operated by invertebrates underline, from organism to environment, potential ecological feed-back and implications in estuarine biogeochemistry (Chapter 4).

Although accretion is expected to retroactively influence flooding frequency, the decreasing trend of the latter was not significant over the first four years (Chapter 2). This has maintained the development of pioneer invertebrate communities at low and mid
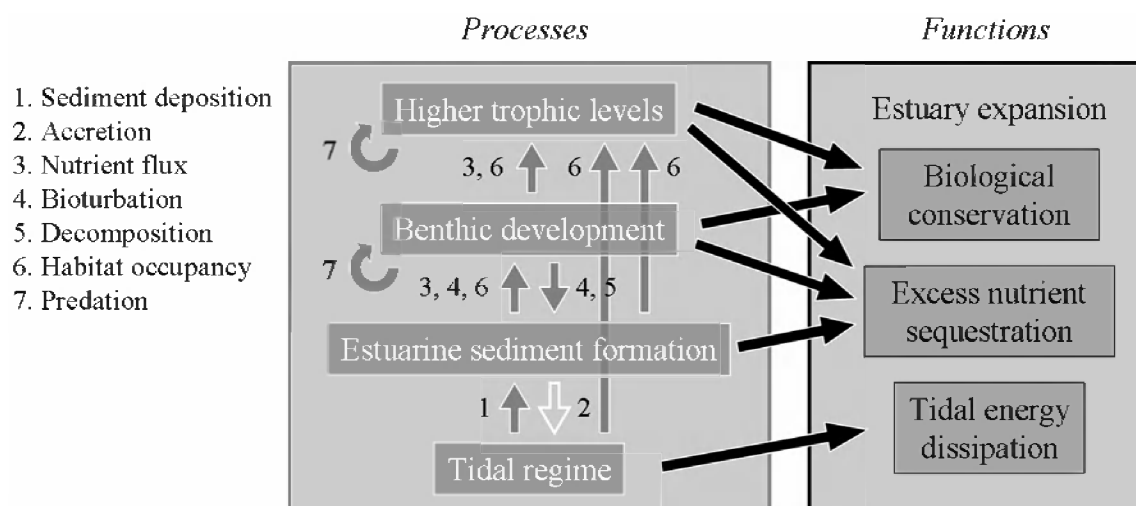

Fig. 1. Identified processes and functions following CRT implementation, independently of elevation. Open arrow (2), accretion without significant effect on flooding frequency.

elevations, at least during the three first years (Chapter 4). In the meantime, the newly-created tidal freshwater habitats were occupied by a large diversity of bird species, represented by a majority of wetland bird specialists (Chapter 6); the seasonal habitat-specific response of avifauna points to the importance of the richness and the permanence of the floristic and faunistic resources across multiple trophic levels provided by CRT. In spite of slight hydrological deviations from the estuarine reference (Chapter 2), the results stemmed from the accomplished monitoring did not infer negative consequences on the ecological development with regard to the wetland nature of the inventoried organism communities.

From a human perspective, these processes provide different functions of natural services set in the long-term vision for the Schelde estuary for the development of a healthy and multifunctional water system that can be utilized in a sustainable way (Van den Bergh et al. 2005). Through CRT development, the estuary expansion ensures a continuous tidal energy dissipation every tide, and an increased floodwater storage capacity during storm tides. So far, the system has fulfilled these functions without failure (Fig. 2).

The consequent import of dissolved and solid nutrients was stored and transferred to the food webs as illustrated in Figure 3. This seems to be particularly the case in vegetation development which was shown to typically reflect the high productivity of tidal freshwater marshes (Jacobs et al. 2009). To a lesser extent, consumers suggest other nutrient sequestration pathways. Indeed, compared to salt marsh vegetation, the high palatability and number of seed-bearing plants of tidal freshwater vegetation allows upper transfers to food webs via zoobenthos, adult insects and birds (Odum 1988). The high deposit feeder (Tubificidae;

Chapter 3), reed bunting (*Emberiza schoeniclus*; Chapter 6) and summer insectivorous bird densities encountered in the CRT are representative of such features. Other secondary consumers at the top of the food webs such as raptors give evidence of the ecological pyramid completion and the ecosystem performance (Estes et al. 2011). Besides, birds are recognized to ensure many ecosystem services and economical benefits (Şekercioğlu et al. 2004; Whelan et al. 2008); the high plant dispersal potential of waterfowls may contribute to a sustainable connectivity of freshwater wetlands at a regional scale (Rauling et al. 2011). Moreover, bird species of local or international concern largely observed (Chaper 6) indicate the high conservation value of the marsh as an additional function.

EVALUATION OF CRT HABITAT CREATION

It has been claimed that it is difficult to measure accurately the success of ecological restoration in the absence of reference sites (Brinson and Rheinhardt 1996; McCoy and Mushinsky 2002; Neckles et al. 2002). Non-impacted ecosystems obviously provide reference standards which typify regional sustainable conditions and make restoration goals more explicit. However, a perfect restoration cannot be proved given the natural spatiotemporal variations of natural habitats; hence, due to its inherently experimental nature, restoration requires approximations (White and Walker 1997). The debate becomes controversial when the use of reference information in restoration assessment is defended by opposite point of views, even in a same editorial board (McCoy and Mushinsky 2002; Kalies et al. 2012; Beauchard et al. 2011c). Nevertheless, restoring species communities in the absence of

Fig. 2. Tidal energy dissipation operated through CRT system. A) Spring tide, inlet culvert. B) Storm tide, spillway; photograph, Droge voeten association (March 2008).
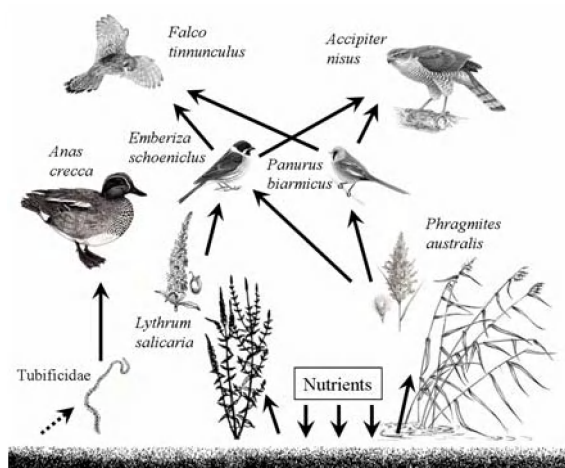
Fig. 3. Some highlighted trophic pathways from sediment (bottom) to the highest trophic levels in the studied CRT. Continuous arrows, direct observations; dotted arrow, supposed indirect link. Other links and pathways are not excluded.

reference marsh as a baseline can be achieved by approximating the habitat requirements of organisms which have been largely documented (MacMahon and Jordan 1994; Moore et al. 1999; Kalies et al. 2012).

In the Schelde estuary, ecological restoration is non-economically costly and the emergency to control floods allows a substantial increase of natural habitats (Broekx et al. 2011). Therefore, discarding habitat creation due to the absence of reference habitats is senseless. The literature on fundamental and applied estuarine sciences is growing and provides a baseline so that restoration measures to be efficient. In the Schelde estuary, key restoration goals were identified, and a conceptual rehabilitation model was developed, based on a problem analysis (Van den Bergh et al. 2005). This approach had been strengthened by the intensive OMES monitoring, launched in 1995 (Van Damme et al. 2005). It has largely contributed to the fundamental comprehension of the estuarine functioning so that restoration goals to be optimal.

So far, most of tidal restoration projects have been conducted in salt or brackish zones (Sinicrope et al. 1990; Simenstad and Thom 1996; Eertman et al. 2002; Havens et al. 2002; Wolters 2005; French 2006; Garbutt et al. 2006; Gallego Fernández and Novo 2007; Mazik et al. 2007; Mazik et al. 2010; van Proosdij et al. 2010). In most of studies, the main ecosystem development is achieved within the first five years following tidal regime implementation. Tanner et al. (2002) provided a study on a realignment site on the North-West pacific coast of the USA; although no elevation

gradient was reported, the area developed estuarine habitats within three years. Although fundamental differences occur between freshwater and salt marshes (Odum 1988), a rapid emergence of estuarine features was observed in the experimental CRT as soon as one year after the opening of the exchange culverts. This emphasizes the importance of hydrology as a common denominator in tidal freshwater and salt marsh restoration.

Neckles et al. (2002) developed a hierarchical approach to evaluate the performance of tidal marsh restoration. Although they advised a monitoring for a minimum of one year before restoration, this task was not necessary given the agricultural nature of the experimental area where crop rotation was practiced until three years before tidal regime implementation. The contrasting wetland nature of the area engendered by flooding is a strongly positive outcome of the project with regard to the restoration goal.

Like in most of tidal restoration studies, different ecological compartment were considered in order to cover several ecosystem levels and facets. As regard to previous studies, the low taxa richness in invertebrate communities from the freshwater zone of the Schelde estuary has been mainly attributed to organic and inorganic micro-pollutants (Ysebaert et al. 1993; Seys et al. 1999); so far, this consideration cannot be discarded as regard to the human pressures exerted on the estuary (Meire et al. 2005). However, the CRT system was shown to be experimentally efficient for disentangling the effects of physical and chemical constraints. Under the soft CRT hydrology, richer invertebrate communities developed compared to those in reference habitats which undergo a shear stress (Chapter 4). This strengthens the importance of multi-compartment approaches since such an impact could not have been revealed by limiting the tidal restoration assessment by avifauna alone.

Analytically, multivariate methods, which incorporate many of the useful features of the univariate methods simultaneously, were claimed and shown to offer good potential for measuring restoration success (Henry and Amoros 1996; Henry et al. 2002; Vecrin et al. 2007; Jacobs et al. 2009; Paillex et al. 2009). In a comparative study on assessment of restoration success, McCoy and Mushinsky (2002) concluded that these methods were unsuitable, but they ignored a wide panel of techniques allowing specific spatiotemporal investigations and statistical inferences (Chessel et al. 2004; Dray et al. 2007). Some of the analytical approaches used in this work clearly highlight

contrasts between the degraded references, as previously pointed out (Meire et al. 2005; Van den Bergh et al. 2005), and the newly-created habitats (Chapter 3 and 4).

PROSPECTS

The results emerging from this work provide evidence for the potential of the CRT technique in rapidly creating a diversified tidal freshwater ecosystem. Implementing the CRT system in brackish zones would likely result in rapid successful habitat creation given the apparent similar restoration delay in salt and freshwater zones. Since the restoration problematics in many embanked estuaries is commonly related to the constraint of elevation, a wider application of CRT is advocated.

On the long-term, the accretion should level the platform of the CRT area (Vandenbruwaene et al. 2011). This should engender an equalization of the flooding frequencies on the whole surface area, and a consequent functional homogenization of the present habitats, with the exception of the creeks. Without intervention, the area would be flooded at a high frequency since the floodwater volume is determined by the culverts and not by elevation. However, the opening of the inlet culvert is flexible and allows setting a desired flooding frequency (Cox et al. 2006; Jacobs 2009; Beauchard et al. 2011b). A low flooding frequency should conduct to a stable forested climax characterized by willow (*Salix* sp.) typical of the adjacent natural high marshes at any chosen elevation during accretion.

Although the CRT system was mainly designed for restoring high marshes more rapidly than managed retreat (Maris et al. 2007), a continuous monitoring will be necessary as part of an adaptive management of the ecosystem in so far as nothing rules out the possibility of maintaining a homogeneously diversified marsh during a certain time. This could be achieved by maintaining a suitable flooding frequency. Of course, such a scenario would have significant repercussions on the present highly-elevated habitats, such as the extirpation of the remnant terrestrial invertebrate (Chapter 4) and plant communities (Jacobs et al. 2009a); besides, every scenario would be accompanied of inevitable repercussions on biota's from an extremity of the flooding gradient. Also, this would maintain accretion whereas a water storage capacity has to be preserved to ensure a safety function against storm floods. Without intervention, Vandenbruwaene et al. (2011) predicted that accretion could not exceed 1 m within a century, and Broekx et al. (2011) suggested that the storage capacity would not be significantly affected in such a case. Moreover, the volume of imported sediments might be partly counterbalanced by the rapid channel formation which was not considered in the long term predictions (Fig. 4; Vandenbruwaene et al. 2012). Conclusively, since nothing excludes a long-term flexibility of the diversified ecosystem which has emerged so far, the CRT system opens the way to long-term sustainable management of estuarine functions while further enriching ecological understanding.

Fig. 4. Channel development in the Lippenbroek polder (April 2009).

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SUMMARY

The worldwide extent of tidal wetlands has greatly decreased, primarily due to large-scale embankments for agricultural, industrial and urban developments. Such pressures have resulted in narrowing estuarine corridors and in increasing shear stress on the remaining estuarine habitats. Concomitantly, the increased mean high water level has constrained ecological restoration in adjacent embanked areas. The inability to create an adequate tidal regime in embanked areas is a major problem for restoring estuarine habitats.

A new restoration technique, the controlled reduced tide system (CRT), was hypothesized to overcome this constraint. As part of a management plan combining flood protection and tidal habitat restoration, the first CRT system was implemented in polder from the freshwater zone of the Schelde estuary (Belgium). In an interdisciplinary context, this work focuses on different ecosystem compartments and interactions in order to assess the coherence between abiotic and biotic components and to appraise the relevance of further wide applications in tidal wetland restoration. Within four years following the connection of the polder to the estuary, different ecosystem compartments and processes were studied: hydrology, sediment physicochemical characteristics, and invertebrate and bird communities.

Despite some slight deviances from the reference, the tidal characteristics generated by the CRT technique were suitable with a clear reproduction of the spring-neap tidal cycle. This soft hydrology led to the formation of a fine-grained estuarine sedimentary substrate in the most frequently flooded zones, contrasting with estuarine sand flats. Biogeochemical services such as sediment trapping and nutrient burial were demonstrated.

These new environmental conditions were shown to be more suitable to sediment invertebrate community development than those encountered in reference sites from the adjacent estuary. CRT habitats displayed enriched communities, especially with epibenthic organisms. Divergence in community functioning was explored by confronting environmental characteristics and organism' biological attributes. In a comparative way, the shear stress exerted on the estuarine tidal flats was assumed to be the main explanation to the faunistic impoverishment at a high flooding frequency. Additionally, specific bioturbative modes were identified along the CRT flooding frequency gradient. From organism to environment, this underlines potential ecological feed-back and implications in estuarine biogeochemistry.

At higher trophic levels, 103 bird species were inventoried, encompassing a dominant part of characteristic wetland species, among which 38 exhibited local and/or international concern. Communities were found to be strongly habitat specific and non-randomly organized across habitats. From ground to foliage, habitat occupancy was found to be consistent with species functional abilities over the whole seasonal cycle. Globally, the avifauna positively responded to CRT habitat creation since communities were composed of a large majority of generalist and specific birds typical of European freshwater wetlands.

Significant relations were found among the different ecological compartments. Conclusively, the results emerging from this work provide evidence for the potential of the CRT technique in rapidly creating a diversified tidal freshwater ecosystem. The restoration potential of this restoration technique is shown to be particularly relevant for tidal marshes in early succession stage, habitats which often lack in embanked estuaries.