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European salt marshes diversity and functioning: The case study of the Mont Saint-Michel bay, France

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Key words: ecosystem development, exchange, food webs, human activities, organic matter, outwelling

Abstract

The macrotidal Mont Saint-Michel bay has been studied intensively since 1990. The objectives of this study, supported by the European Union, was to understand various processes underlying the functioning of this hydrosystem with a special focus on organic matter and nutrient fluxes between saltmarshes and marine waters. This paper presents a synopsis of these studies. The tidal flats are unvegetated and primary production is exclusively due to microphytobenthos communities dominated by diatoms. Halophile plant communities colonize the top parts of the tidal flats. Their composition and production vary according to a maturity gradient and sheep grazing. In ungrazed saltmashes, production ranged from 1080 gDW $m^{-2}\cdot yr^{-1}$ in the lower marsh to 1990 gDW $m^{-2}\cdot yr^{-1}$ in the upper marsh whereas it was only 200 to 500 gDW $m^{-2}\cdot yr^{-1}$ in *Salicornia* spp. dominated pioneer zones and sheep grazed areas. Most of this organic matter (OM) was trapped *in situ*, processed by fungi and bacteria, and then released seaward via tidal fluxes, groundwater and runoff as particulate OM and nutrients: –497 kg N, –1200/–1000 kg P-PO_4 and –9900/–4200 kg inorganic carbon). A small amount of OM was exported to the bay as macrodetritus. Fatty acids and stable isotopes, used as markers, showed that OM produced by the marsh halophytes contributed to the diet of all the tidal flats invertebrates that were studied. Transient fish species were shown to colonize the saltmarshes to forage or graze, exporting about 50 tons POM (DW)$\cdot y^{-1}$. Therefore, it is assumed that the saltmarsh production enhances the production of the whole bay. But the functioning is still poorly known because the nutrient sinks have not all been identified. Part of the nutrients input was provided by precipitation (+327 kg y^{-1}), but the contribution of the catchments was not quantified despite the fact that their influence was shown by the presence of lindane in all the compartments of the system. Dynamics of saltmarshes are mainly influenced by natural sedimentation (1.5 million $m^3\cdot y^{-1}$ in the bay), plant community succession, and management (i.e., reclamation and agricultural activities).

Introduction

Bays and estuaries, and their surrounding salt marshes and mudflats, are among the most productive systems of the biosphere. Because they provide valuable functions, considerable effort has been spent to understand individual as well as holistic processes which occur in these complex systems. In the early 1960s, a set of research projects was undertaken in salt marshes of North American Atlantic coasts to assess their role in the functioning of coastal systems. In 1968, Odum, using the findings of Teal (1962) and Odum and de la Cruz (1967), developed the outwelling paradigm which stated that salt marshes export organic matter, therefore enhancing the whole food-web of the adjacent coastal waters. During the following decades, a wide range of papers described process models based on the outwelling paradigm (see reviews by: Nixon, 1980; Wiegert and Pomeroy, 1981; Long and Mason, 1983; Adam, 1990; Vernberg, 1993). It appeared that the outwelling paradigm should not be taken for granted worldwide and that organic matter (OM) and nutrient budgets depend on latitude, tidal amplitude, plant communities and geomorphologic characteristics of each individual system (e.g., Nixon, 1980; Dame and Gardner, 1993; Lefeuvre and Dame, 1994).

Saltmarshes constitute dynamic environments that present characteristics of both marine and terrestrial systems. The physical features of tides, sediments, freshwater inputs and shoreline structure determine the development and extent of salt marshes within their geographical range (Vernberg, 1993). Such conditions occur behind spits, offshore bars and islands, in protected bays or on the shores of estuaries where river sediments deposit (Chapman, 1974). Along the north east coast of North America, the salt marsh plants occupy the major part of the intertidal area and are immersed at each tide (McKee and Patrick, 1988). But in most European bays and estuaries, salt marsh plants are confined to the uppermost part of the intertidal zone where they are immersed only periodically by spring high tides (Morley, 1973; Beeftink, 1977). Indeed, plants that occur in European salt marshes are able to tolerate being covered occasionally by saline estuarine water, but not twice a day such as *Spartina alterniflora* the dominant species of North American marshes.

It is still unclear whether generalizations can be made for *Spartina alterniflora* salt marshes, and both differences in floristic composition and in flooding regime between American and European marshes, make it more difficult to compare results. During the 1960s and 1970s, European salt marshes were not studied as part of a complex estuarine-marsh system, but as isolated areas where research focused principally on individuals, populations and communities in these stressed environments (Beeftink, 1977; Adam, 1990). Because of the lack of information concerning European saltmarsh functioning, the Research Directorate (DG XII) of the European Union has encouraged and supported research on the functioning of diverse coastal wetlands along European coasts. Since 1990, salt marsh studies have been carried out in parallel in the Netherlands, England, Portugal and France (Lefeuvre, 1993; Lefeuvre, 1996; Lefeuvre et al., 1998). In each country, salt marshes were selected for detailed studies in order to test the outwelling hypothesis.

In France, research has been conducted since 1979 in the Mont Saint-Michel bay (Lefeuvre et al., 1994). The objective was to focus on this ‘workshop site’ in order to understand its complexity and diversity, and to maintain long-term studies, such as those developed on Sapelo Island on the east coast of North America by the University of Georgia. The Mont Saint-Michel bay presents the opportunity to gather information on a variety of coastal wetlands, including natural and grazed salt marshes, reclaimed marshes and mudflats. The contribution of these different systems, together with the rivers, to the functioning of the bay should be taken into account.

The first results from the French team have been presented by Lefeuvre et al. (1994). Since 1994, classical approaches – such as studies of primary production and OM fluxes – have been maintained to collect information on spatial (influence of human activities and marsh maturation) and temporal (seasonally and long-term) variations (Bouchard, 1996; Troccaz, 1996; Vivier, 1997). At the same time, new research was developed on various components of the system: the influence of biotic transfers between salt marshes and coastal waters on the OM budget (Laffaille et al., 1998); the role of grazing on salt marsh structure and functioning (Vivier, 1997); the understanding of the marsh detrital food web through the study of detritus pathway (Bouchard, 1996), the use of molecular markers such as stable isotopes (Créach, 1995; Créach et al., 1997), osmotica (Bessière, 1998), and fatty acids (Meziane, 1997) and the measurement of bacterial activity in sediment (Créach, 1995; Lucas, 1997; Bessières, 1998); the evaluation of extent of mudflats influenced by river input using pesticides as markers (Grare, 1996); the evaluation of system dynamics by assessing sedimentation rates (Jigorel, 1996) and salt marsh vegetation changes (Bouchard et al., 1995).

The present paper is an attempt to provide a synopsis of all these studies which have been conducted by our inter-disciplinary team for more than 10 years. The functioning and the interactions between the various ecological compartments of this complex coastal ecosystem (natural and grazed salt marshes, reclaimed marshes, mudflats and rivers) are presented and discussed. References are made to other published papers for more detailed methods and results.

Study site

The Mont Saint-Michel bay is located in France, in the south of the gulf of Normandy, between Brittany and Cotentin (lat. 48°40′N, long. 1°35′W). The Abbey of the Mont Saint-Michel, often named the eighth won-

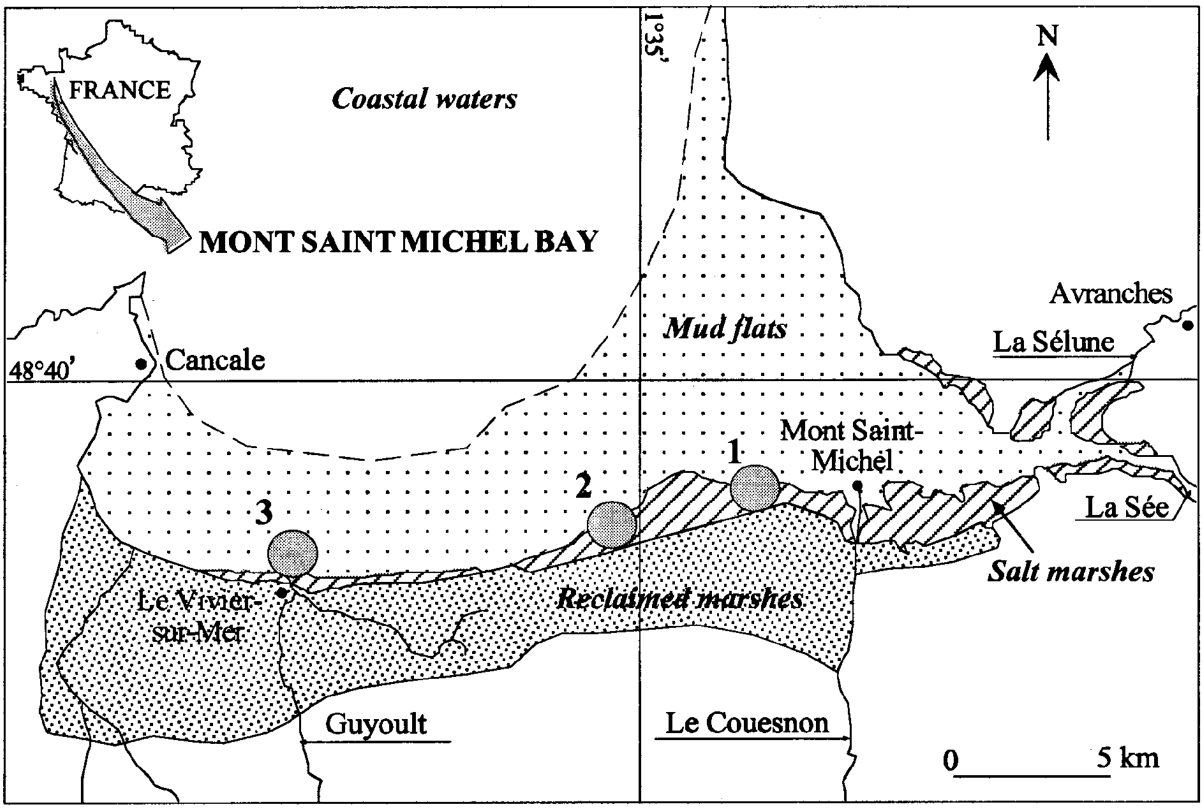

Figure 1. Map of the Mont Saint Michel Bay with the location of the three sites studied: 1 – non-grazed saltmarsh, 2 – grazed saltmarsh and 3 – mudflats.

der of the world, is perched atop a promontory in the middle of the bay. The choice of such a prestigious site appeared relevant to develop long-term studies on the functioning of inter-dependent systems and, particularly, the exchanges of energy between terrestrial and marine systems. Some of the most extensive salt marshes of Europe are found in the area. The bay ecosystem complex comprises four inter-related subunits. Three belong or have belonged to the coastal marine system: mudflats, salt marshes and reclaimed marshes (Figure 1). The fourth entity is continental and is composed of four main river catchments (Rivers See, Selune, Couesnon, Guyoult) and several minor ones which altogether cover 3250 km^2.

The Mont Saint-Michel bay is a macrotidal system with the second highest tidal range in Europe (average: 10–11 m and up to 16 m). The intertidal zone covers 240 km^2, comprising 200 km^2 of mudflats and 40 km^2 of salt marshes. Most of the saltmarshes are used by local agriculture for sheep production. Since the 11th century, 133 km^2 of salt marshes have been reclaimed, isolated from tidal events and converted to more or less intensive agricultural lands.

During the past ten years, most of the research conducted in the Mont Saint-Michel bay have taken place in a non-grazed salt marsh, located approximately 5 km west from the Mont Saint-Michel (Figure 1). This saltmarsh is 1.8 km wide, with a well-developed creek system and clear zonation of plant communities. Depending on flooding frequency and vegetation zonation, the salt marsh can be divided in four areas: the pioneer marsh (10 ha), the lower marsh (20 ha), the middle marsh (37 ha) and the high marsh (47 ha). Across the elevation gradient, flooding frequency decreased from 25 to less than 0.2%. Studies of OM fluxes have been conducted in a tidal creek flooded by 43% of the tides and draining a 5.7 ha catchments (Troccaz et al., 1994). The grazed site is located approximately 10 km west from the natural marsh site (Figure 1). Under the influence of sheep grazing, a low marsh community dominated by *Puccinellia maritima* is maintained (Guillon, 1984; Vivier, 1997). The third site, selected to evaluate the transfer of energy from

Table 1. Summary of techniques and methods used by our multidisciplinary team at each of the three sites (1 – non-grazed salt marsh; 2 – grazed salt marsh and 3 – mudflats).

Site	Compartment studied	Methods	References
1	Source of OM from for halophytes and microphytobenthos	Harvesting methods, nutrient content, communities structure	Bouchard (1996), Brosse(1996); Bouchard and Lefeuvre (1996); Bessière (1998)
	Fate of OM inside the marsh	Macrodetritus fluxes; decomposition studies	Bouchard (1996), Bouchard et al. (1998)
	Fluxes and budgets of material	Water budget estimation	Troccaz et al. (1994)
		OM and nutrients fluxes through biotic and abiotic processes	Bouchard (1996); Troccaz (1996); Laffaille et al. (1998)
	Transfer of organic matter to detrital and consumers food-web	Communities sampling and guts content analysis	Créach et al. (1996); Laffaille et al. (1998)
		Molecular markers (stable isotops, osmoticum, fatty acids)	Créach (1995); Créach et al. (1996); Meziane (1997); Bessière (1998); Lucas (1997)
	Fish communities	Community sampling, fishery surveys	Feunteun and Laffaille (1997); Laffaille et al. (1998)
	Dynamic of vegetation communities, sedimentation	Vegetation surveys, GIS, sediment trap and sedimentation table	Bouchard et al. (1995); Gigorel (1996).
2	Source of organic matter from halophytes	Harvesting methods, nutrient content	Vivier (1997)
	Fate of organic matter inside the marsh	Mineralization studies	Vivier (1997)
	Transfer of nutrient between systems	Soil and groundwater studies	Vivier (1997)
	Dynamic of vegetation communities	Vegetation surveys, GIS, enclosure experiment	Bouchard et al. (1995), Vivier (1997)
3	Source of OM from microphytobenthos	Microphytobenthos determination	Grare (1996), Savouré and Radureau (1996)
	Fluxes of OM	Use of pesticides as molecular markers	Grare (1996)
	Consumer and bacterial foodchains	Microbial activity, Molecular markers (fatty acids)	Lucas (1997); Meziane (1997)

reclaimed salt marshes to coastal waters, is located in the western area of the bay in front of the Vivier-sur-Mer (Figure 1). This site is the outlet of three canals and one river (Guyoult) which, all combined together, drains a 212 km^2 watershed comprising agricultural polder.

Methods

The integrative study developed in the Mont Saint-Michel bay used different approaches and methodologies (Table 1). At each of the three sites, we developed similar or specific methodologies to estimate the distribution and fluxes of OM between salt-marshes, creeks and coastal marine waters. Sampling methodologies, and field and laboratory techniques are described in details in the literature references listed in Table 1.

The first step aimed to assess the production of OM and its fate inside the salt marshes. The net aerial primary production (NAPP) of halophytes was estimated with plant harvesting methods and expressed in dry weight (DW), carbon, nitrogen and diverse osmotica such as glycine betaine (GB), soluble sugars (SS) and proline (PRO) (Bouchard, 1996; Bouchard and Lefeuvre, 1996; Vivier, 1997; Bessières, 1998). The primary production of the mud flats was approached through the study of microphytobenthos in tidal creeks (Brosse, 1996; Savouré and Radureau, 1996). The detrital pathway (i.e., detritus production, litter fall and export to coastal waters) was studied using litter traps, detrital turn-over estimations, nets collecting floating material in tidal creeks and drift lines surveys (Bouchard, 1996). Further decomposition and mineralization processes were analyzed in relation with grazing activity by sheep by using the litter bag and soil incubation techniques (Bouchard, 1996; Vivier, 1997).

The second step aimed to measure fluxes of live (fish communities) and inert material (sediment, water, OM, carbon, nitrogen, phosphorus and silica) during and between tide cycles. An experimental gauging station was placed across the main creek (15 m wide). Automatic samplers were used to acquire flux data over several years and to relate them to environmental parameters such as temperature, salinity, winds, rainfall, tidal range, etc. Ground water was studied with piezometers settled following transversal (parallel to the shore line) and longitudinal (perpendicular) transects (Troccaz et al., 1994; Troccaz, 1996). The data were used to develop an existing model, Drainmod (Troccaz, 1996), in order to estimate the water balance and discharge (upwards and downwards) according to the tidal range, seasonal and climatic conditions. This hydrodynamic model was validated and used to assess the global budgets of OM and nutrients. The contribution of transient fish communities in OM matter fluxes between salt marshes and marine coastal waters during their trophic displacements was also assessed by identifying gut content and estimating their carbon and nitrogen concentration (Laffaille et al, 1998; Lefeuvre et al., in press).

The third step aimed to follow the integration of OM into the food web and was studied through trace elements (i.e., fatty acids) and stable isotope ratios (Créach, 1995; Créach et al, 1997; Meziane, 1997). The fate of osmoprotectors (glycin betain, soluble sugars and prolin) produced by halophytes and their role on the dynamics of micro-organisms in mudflats was also studied (Bessières, 1998; Lucas, 1997). The influence of the catchment outputs on the functioning of the bay of Mont Saint Michel was studied by using markers such as residual pesticides in sediment and animals (Grare, 1996).

Finally, the fourth step was the study of the evolution of the salt marsh coastline and vegetation communities during the past decade in the Mont Saint-Michel bay. A first vegetation map of the 4,000 ha salt marsh was prepared in 1984 (Guillon, 1984). This map has been actualized in 1995, and changes analyzed with GIS (Bouchard et al., 1995). These two maps were established with the same methodology: salt marshes coast lines and vegetation types were observed on the field and noted on aerial photographs. Vegetation types were described according to dominant species (Guillon, 1984; Bouchard et al., 1995). The sedimentation dynamic was estimated with sediment traps and sedimentation table at 3 different sites (Jigorel, 1996).

Results

Plant diversity and production of OM

Phytoplancton production has not been studied thoroughly in the bay, but the available data show low abundance which was certainly due to the high turbidity in the water column. Therefor, the high chlorophyll a concentration (7.8 mg m^{-3}) and the important primary production (52 mgC m^{-3} h^{-1}) (Anon., 1982) was assumed to be due to microphytobenthos produced on the mudflats rather than microphytoplankton of the water column. This assumption relied on the exclusive presence of benthic diatoms in the gut contents of mussels, *Mytilus edulis* (Savouré and Radureau, 1996), whose production averages 10 000 metric tons per year in the bay (Lefeuvre, 1996). The biomass, production and composition of the mudflats microphytobenthos community is ongoing (Brosse, 1996).

In salt marshes, the plant diversity and NAPP varied according to marsh maturity and influence of sheep grazing (Table 2). In the non-grazed salt marsh, where the vegetation cover was dense, the diversity tended to decrease from the low marsh (community dominated by 4 or 5 species) to the high marsh community (dominated by 2 species), whereas NAPP followed an opposite pattern (from 1080 gDW $m^{-2}\cdot yr^{-1}$ in the lower marsh to 1990 gDW $m^{-2}\cdot yr^{-1}$ in the high marsh). In the pioneer zone, the plant colonization was scarce, dominated by 2 species (*Salicornia* spp. and *Spartina anglica*), and NAPP was low (200 to 500 gDW $m^{-2}\cdot yr^{-1}$). In grazed saltmarshes, the vegetation community was dominated by *Puccinellia maritima.* Therefore, the whole marsh became like a non-grazed low marsh from where the primary production (NAPP: 360 to 550 g DW $m^{-2}\cdot yr^{-1}$) was consumed by sheep and partly released into the marsh as feces.

Production of carbon and nitrogen by the salt marsh vegetation followed the same pattern as the DW production, i.e., the main production occurred in the middle and high non-grazed salt marshes whereas carbon and nitrogen pools were much lower in the vegetation communities dominated by *Puccinellia maritima*. In the non-grazed salt marsh, the production of three species (*Puccinellia maritima, Suaeda maritima* and *Atriplex portulacoides*) was also evaluated in term of soluble compounds, namely compatible solutes or osmotica, and produced by halophytes to resist salinity. *Puccinellia maritima* produced up to 13 gPRO $m^{-2}\cdot yr^{-1}$ in the lower marsh and only 7

Table 2. Community diversity according to Braun-Blanquet abundance index (Braun-Blanquet, 1965), vegetation cover, community structure and NAPP (expressed in gDW·m^{-2}·yr^{-1}) at each marsh area of both non-grazed and grazed salt marshes.

Site	Marsh area	Community diversity (abundance index)	Vegetation cover (%)	Community structure	NAPP (gDW·m^{-2}·yr^{-1})
Non-grazed	pioneer	*Spartina anglica* (3), *Salicornia* spp. (5)	10	short (10–30) herbaceous	200–500
	low	*Spartina anglica* (+), *Salicornia* spp. (2), *Suaeda maritima* (3), *Puccinellia maritima* (4), *Aster tripolium* (2), *Atriplex portulacoides* (1)	90	short (10–30 cm) herbaceous	1080
	middle	*Atriplex portulacoides* (5), *Suaeda maritima* (1), *Aster tripolium* (+), *Puccinellia maritima* (1)	100	tall (30–70 cm) dwarf shrub	1910
	high	*Elytrigia aetherica* (4), *Festuca rubra* (2), *Puccinellia maritima* (1), *Salicornia*	100	tall (50–130 cm) herbaceous	1990
Grazed salt	pioneer	*Spartina anglica* (3), *Salicornia* spp. (5)	10	short (10–30) herbaceous	nd
	low	*Spartina anglica* (+), *Salicornia* spp. (2), *Suaeda maritima* (3), *Puccinellia maritima* (4), *Aster tripolium* (2), *Atriplex portulacoides* (1)	80	short (5–10 cm) herbaceous	410
	middle	*Puccinellia maritima* (4), *Salicornia maritima* (3), *Spergularia maritima* (1)	80	short (5–10 cm) herbaceous	360
	high	*Puccinellia maritima* (4), *Salicornia* spp. (2), *Spergularia maritima* (1), *Triglochin maritima* (1), *Juncus gerardii* (1)	80	short (5–10 cm) herbaceous	550

nd: non determined.

gPRO m^{-2}·yr^{-1} in the middle marsh. *Atriplex portulacoides* produced relatively the same quantity of GB whatever was the flooding frequency (from 38 to 41 gGB m^{-2}·yr^{-1} according to the sampling site). Finally *Suaeda maritima* produced from 1 (lower populations) to 8 (higher populations) gGB m^{-2}·yr^{-1}.

Fate of OM in the saltmarsh system: macrodetritus budget, mineralization and detrital food webs

There was a net export of macro-detritus from salt marshes to coastal waters which may not be surprising considering the fact that tidal water entered a macrophyte-dominated system containing high amount of plant detritus throughout the year. However, this export represented less than 1% of the marsh production. The majority of the macro-detritus produced by the halophytic vegetation was trapped inside the ecosystem (Figure 2). The major part of the detritus pool produced in the lower marsh was removed by the tide energy, whereas most of the detritus produced in the middle and upper marsh decomposed at the site. Around 70% of the carbon and nitrogen in macro-detritus in the low marsh was exported from this site, and transferred to the high marsh where they accumulated in drift lines (Figure 2). This fraction decreased to approximately 20% and 12% for the middle and the high marshes, respectively. In the non-grazed marsh, detritus fluxes were not directly estimated but drift lines were observed in the high marsh, along the sea wall. These drift lines were composed of salt marsh vegetation debris and sheep's feces.

During plant development, the osmotica was released into the environment by exudation, diffusion or in dead material (leaves, shoots, etc.). The level of these ejections depended upon environmental forcing such as tide cycles, anoxia and salinity. When they were ejected, osmotica were released seawards and could therefore become available to the ecosystem, mainly in the sediments through root exudation and leaching of the litter. We demonstrated that the non-grazed site studied exported 15 metric tons y^{-1} of GB and 77 metric tons y^{-1} of SS with floating macrodetritus. A total of 72% of GB is produced by *Atriplex portulacoides*. Osmotica are also released in the environment by the litter: about 8 tons y^{-1} of GB and 12 tons y^{-1} of SS.

Research on macro-detritus dynamic demonstrated that the mineralization of halophyte-derived organic matter almost completely take place within the marsh itself. This evidence led to the conclusion that decay rates, coupled with the frequency of tidal flooding, may be one of the major controls of OM availability. Detritus decomposition was rapid in the low and middle non-grazed marshes with decay constants equal to 0.023 and 0.028 d^{-1}, respectively. Decay con-

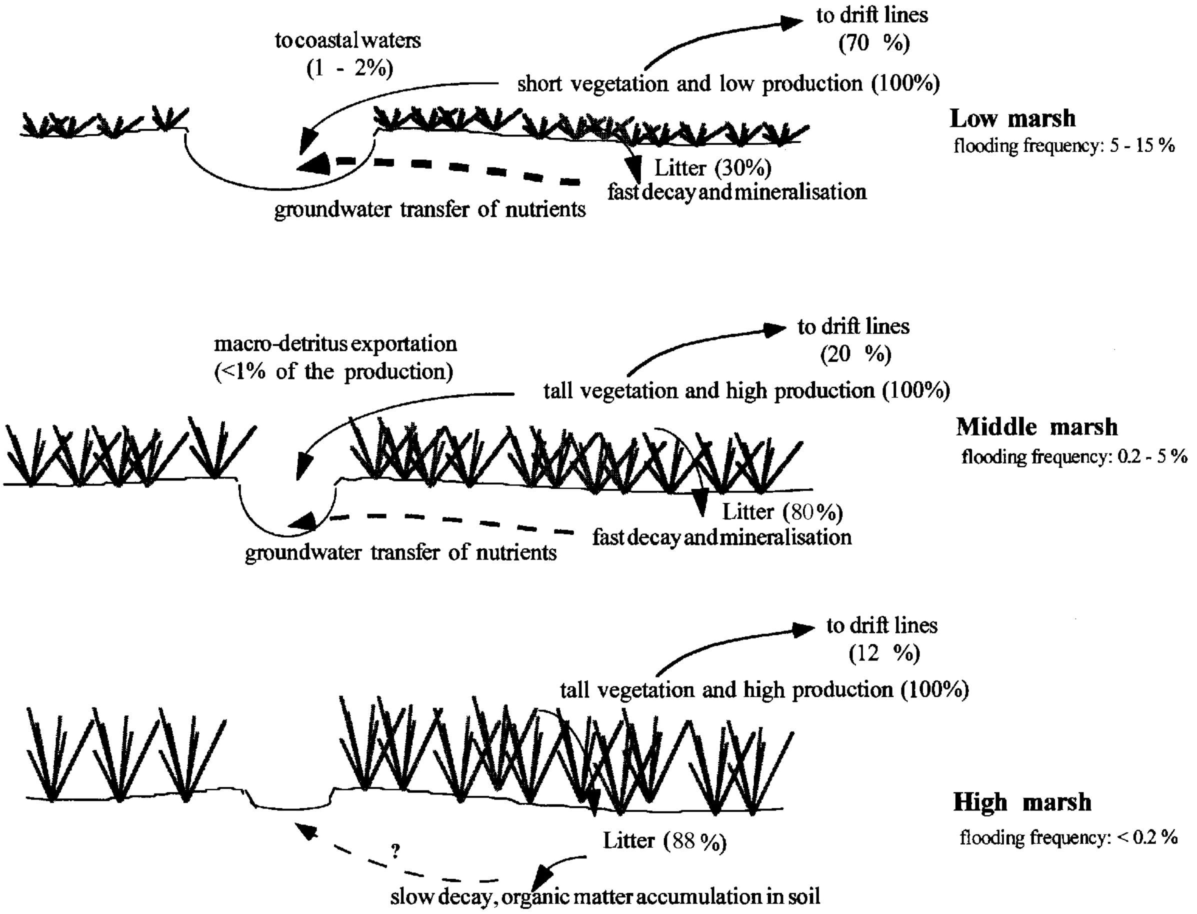

Figure 2. Schematic presentation of the macro-detritus dynamics in each of the three major marsh elevations (low, middle and high) in the non grazed site (from Bouchard, 1996).

stant was estimated to 0.0047 d^{-1} in the non grazed upper marsh. More rapid leaching of nitrogen from decaying litter were found in the low and the middle marshes than in the high marsh. At the end of the decomposition experiment (300 days), around 1–5% of nitrogen remained in litter the two lowest plant communities, whereas up to 60% remained in the high marsh. Part of the detritus was consumed by invertebrates which are known to accelerate organic matter decay. It is assumed that the OM was transformed into various forms of particulate, dissolved and mineralized material which leached into the ground water and was released seaward by runoff.

After bacterial action in the low and middle marshes and fungi action in the high marsh, the plant material can also be assimilated by macro-invertebrates. Isotopes studies and gut analyses confirmed that the diet of *Orchestia gammarellus*, one of the main species which colonized the non-grazed salt marsh, consisted of more than 50% plant detritus (Créach et al., 1997). For other species studies such as *Corophium volutator* and *Ovatella bidenta*, benthic diatoms appeared to be the principal source of OM. Other evidence of the detrital food web was demonstrated with the use of osmotica as tracers. Many organisms are unable to synthesize osmotica and therefore, those produced by halophytes may be used as tracers. It has been shown that, in marine environment, the growth of bacteria of the rhizosphera was facilitated by the use of osmotica produced by halophytes. Fatty acids were also used to follow the plant detritus integration into the food web. Long fatty acids (carbon chains $>$ 22:0), and phytosterols are know to be exclusively produced by halophytes (*Salicornia* spp., *Atriplex portulacoides* and *Spartina anglica*). Their presence in lipids of various marine

Table 3. Fluxes (in kg·ha^{-1}) of dissolved organic matter (DOM) and Suspended matter (SM) budgets between the non-grazed saltmarsh watershed studied and coastal waters during tides and runoff. Negative values indicate exportation.

Year	DOM			SM		
	tides	runoff	total	tides	runoff	total
1991	–1.4	–1.2	–2.6	112.5	–0.8	111.7
1992	–0.8	–1.2	–2.0	58.3	–0.8	57.5
1993	–0.7	–1.1	–1.8	42.5	–0.8	41.7
1994	–0.7	–1.0	–1.8	–0.8	–1.3	–2.1

invertebrates dwelling the mudflats, such as *Nereis diversicolor*, gave an indication of the fate of OM produced in the saltmarsh. It was also shown that halophytes originated part of the organic matter found in sediments.

Abiotic transport of energy between saltmarshes and coastal waters

In the Mont Saint-Michel bay, salt marshes are only flooded a few days per year, during spring tides. Therefore, it seemed logical to assume that most of the exchanges occurred during such submersion events, especially when combined with storm driven surge. However, the results from an automatic sampling station sited on a tidal creek since 1991 demonstrated that this approach was not sufficient for a correct assessment of the exchanges. The part of runoff in the exchange budgets appeared more than significant (Table 3).

As already described above, there was a net export of macro-detritus even if this export represented a minor part of the OM available inside the salt marsh system. Annual budgets were in favor of dissolved OM (DOM) export and suspended matter (SM) import (Table 3). The major part of the OM exported was washed away by tides, but also during intercycles in runoff. During 1994, the nitrogen term obtained for tides, intercycles and precipitation were –224, –273 and 327 kg, respectively, revealing also the importance of rain in the system. In the same way, for other dissolved nutrients, the budget of the tidal intercycles were similar (–1200/–1000 kg for P-PO$_4$) or even greater (–9900/–4200 kg for inorganic carbon) than those from tides. The nutrient and OM budgets were closely linked to tidal range: we measured export at low and medium tidal amplitudes, import at high tidal amplitudes and budgets close to zero at exceptional tidal amplitudes. The study of four consecutive years (1991 to 1994) revealed a subsequent transformation of the marsh, with a progressive diminution of DOM export; on the contrary, imports of SM declined greatly from 1991 to 1993 and became export in 1994 (Table 3).

In the grazed salt marsh, the potential for OM export was investigated through the study of nitrogen availability and mineralization in the sediment. At the studied site, grazing intensity was higher than bearing capacities of the saltmarsh and caused excess vegetation treading and soil compaction. Mineral nitrogen availability was linked to the marsh elevation, i.e., marsh maturation. The lower marsh, placed under marine influence, was characterized by a fast organic nitrogen turnover rate, whereas in high marsh the organic nitrogen turnover rate decreased. The relationship between N-mineralization and N-leaching suggested that when organic nitrogen ratio increased, losses from the system increased. The high grazing pressure enhanced soil OM content. The OM was trapped in the sediment, and as a matter of fact, not available for export towards coastal waters. Grazing increased sediment compaction which definitively acted negatively on soil microbiological processes governing nitrogen and carbon cycling (low porosity and low nitrification). Grazing removed between 6.4 and 10.5 gN m^{-2}·yr^{-1} which represented between 70 and 100% of the nitrogen available from the vegetation primary production.

Role of salt marshes for fish communities and fish communities as OM tranporters

Among the 90 fish species censused in the Mont Saint Michel Bay, 23 colonized and foraged in the salt marshes during spring tide floods. The community was largely dominated by juvenile and adult mullets (81% of the biomass), *Liza ramada* and secondarily, *L. aurata*, both species being mud scrapers. Gobies (*Pomatoschistus minutus* and *P. lozanoi*) were also present at all stages (11% of the biomass). Sea-bass, *Dicentrarchus labrax* (4% of the biomass) occurred mainly at early stages (0+ and 1+). The 3 latter species mainly feed on amphipods such as *Orchestia gammarellus*, which are primary consumers of the halophytes. Therefore this environment is shown to play an important nursery role for these transient species, just like mudflats do for more stenohaline species such as flatfish, rays and clupeids (Beillois et al., 1979). Salt marshes are thought to play an key role

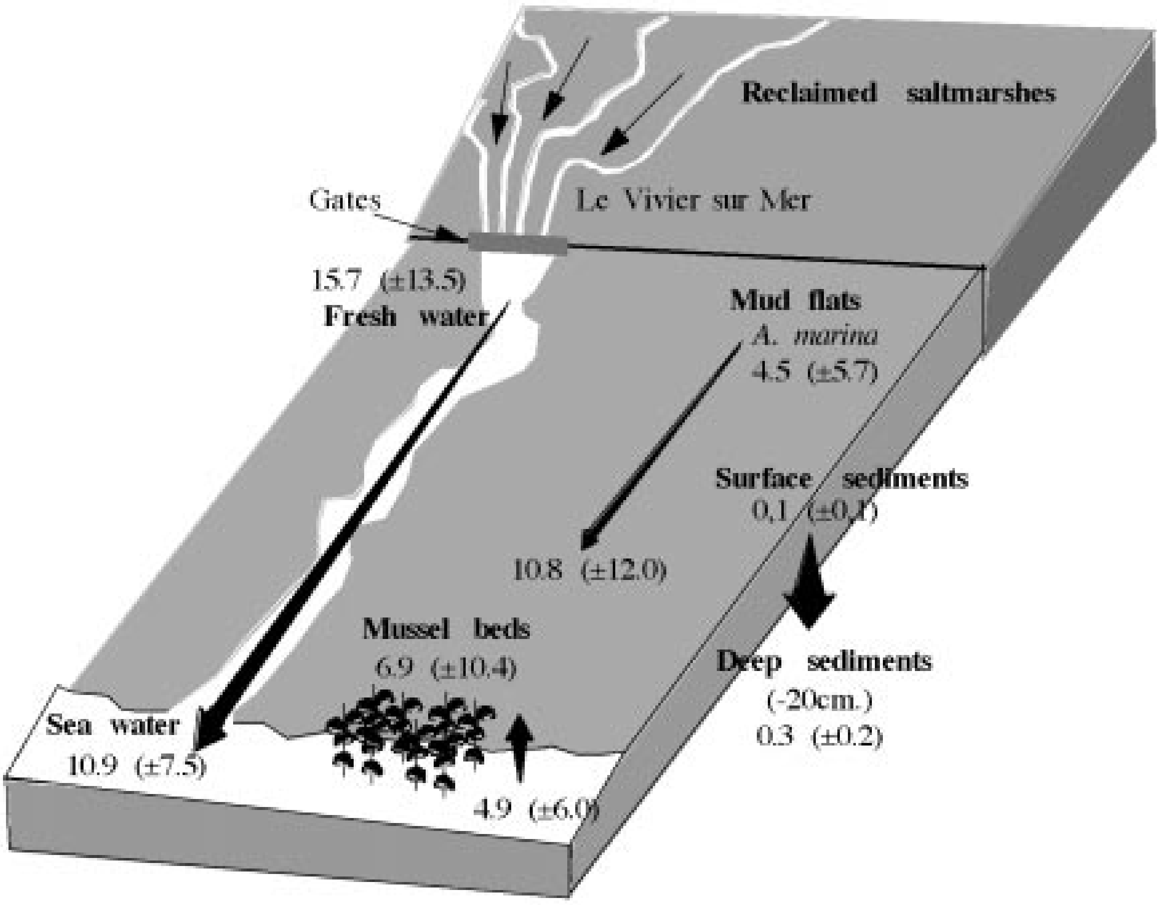

Figure 3. Distribution of lindane (concentrations in ng·l^{-1} or ng·g^{-1} DW) in the different components of the mudflats.

in the production of the sea bass commercial fishery of the region. When fish invaded the creeks and the salt marsh, most stomachs were empty and conversely when they swam away as the tide ebbed, around 100% of the stomachs are full, indicating that such displacements are oriented by feeding behaviors. Mullets swallowed about 7% of their body weight and exported a mixture of sediment (43%), organic matter (24%) and water (33%).

Similarly, gobies and sea bass exported respectively 4.5% and 10% of their body weight. This extrapolated to about 50 tons yr^{-1} of POM (dry weight) being exported seaward from the 4000 ha of salt marshes by the fish community. These values are highly variable since the size of the transient fish community varies tenfold among the years. Thus, fish communities are responsible for 0 to 10% of the yearly export of POM according to the season and the year.

Influence of catchements on the functioning of the bay

Pesticides were found in three intertidal component, i.e., water, sediment and benthos (Figure 3). In water, Lindane was present in every samples, suggesting continuous influence of the reclaimed saltmarshes (polders) on the adjacent marine environment. Pesticides accumulated in organisms such as *Arenicola marina* and in mussels, *Mytilus edulis* and *Cardium edule,* concentration levels being dependent on physiology, species (i.e., trophic level) and abiotic parameters (mainly seasonal). The exchanges between reclaimed salt marshes and coastal waters were continuous throughout the year, but presented seasonal and interannual variations mainly controlled by precipitation events. The use of pesticides as molecular markers illustrate the influence of catchments on the saltmarshes. This also indicates that components exported by terrestrial systems are transported into the bay by coastal currents. Such an approach is crucial to understand the fate and the role of nutrients produced by terrestrial sinks in saltmarshes and adjacent waters OM.

Spatial dynamic of coastal marshes

In the non-grazed saltmarsh, the vegetation communities had a significant effect on sedimentation rates. Sedimentation rates were around 12 kg $m^{-2} \cdot yr^{-1}$ in the lower marsh, then increased in the middle marsh (15 kg $m^{-2} \cdot yr^{-1}$) and decreased in the upper marsh (3 kg $m^{-2} \cdot yr^{-1}$). The dwarf shrub vegetation (*Atriplex portulacoides*) acted as a powerful sediment trap. In the grazed salt marsh, the short vegetation induced lower sedimentation rates (ranged between 2 and 6 kg $m^{-2} \cdot yr^{-1}$). This phenomenon is thought to be one of the processes involved in the regular extension of the salt marsh surface seaward. It has been shown that salt marshes increase by about 35 $ha \cdot yr^{-1}$.

This natural dynamic is perturbed by man's influence (mainly cattle grazing and reclamation). After they were destroyed by reclamation, these ecosystems have been progressing in the Mont Saint-Michel bay between the last embankment in 1934 and the early 1980s. However, during the last 10 years, the area of saltmarshes has stabilized with some in erosion at some locations, and at others in progression. For example, a local erosion close to the 'Pointe de la Roche-Torin' was directly due to the destruction of a dike in 1984 (Figure 4). This dike was built during the last century to continue saltmarsh reclamation between the 'Pointe de la Roche-Torin' and the Mont Saint-Michel. When the Mont Saint-Michel began to be threatened by silting-up, this dike was thought to be one of the principal cause of sedimentation rate increase. Therefore, it was destroyed in 1984. Ten years after this destruction, we continued to observe the progression of saltmarshes closer to the Mont Saint-Michel (Figure 4).

Two major processes were involved in the dynamism of salt marshes vegetation communities. The first one concerned sedimentation which amounts to 1.5 million $m^3 \cdot y^{-1}$ in the bay (Larsonneur and Walker, 1982) and the natural link to vegetation primary succession in European saltmarshes. The second process concerns a more complex link to human influence such as the destruction of dikes, tourism activities around the Mont or sheep grazing. The major evolution of vegetation communities concerned (i) the progression of middle marsh to lower marsh in area where grazing has been progressively abandoned, (ii) the progression of low marsh vegetation where grazing intensity was increased, and (iii) the fast progression of upper marshes with *Elytrigia aetherica* in non grazed areas (Figure 4).

Discussion

Despite their valuable functions, saltmarshes are threatened within the European community by a range of natural and mainly anthropogenic factors. To enable the European Community to pursue a sustainable policy on the conservation of these marshes it was necessary to develop intensive research on their general function with a quantification of the various processes sustaining their productivity. Studies were carried out in four countries (The Netherlands, UK, Portugal and France) in order to test the outwelling hypothesis and to propose new paradigms (Lefeuvre, 1996).

Diversity of saltmarsh functioning

Results presented in this study indicate that saltmarshes located in the macrotidal Mont Saint Michel bay do export OM and nutrients to coastal waters which enhance detrital and consumer foowebs (Figure 5). Like the *Spartina alterniflora* marshes, systems originally taken as models for the outwelling hypothesis (Teal, 1962; Odum, 1968), salt marshes in the Mont Saint Michel Bay are highly productive and dominated by detrital food chains. As in North American systems (Dame, 1982), the export of macrodetritus seems insignificant in the global OM budget. The mineralization of halophyte-derived organic matter almost completely takes place within the marsh itself. This evidence leads to the conclusion that decay rates, coupled with the frequency of tidal flooding, may be a control of export rates. The OM produced is subjected to *in situ* decomposition before being incorporated into the foodweb of detritivore communities (Figure 5). Comparison with other European sites indicate the same general characteristics even if some variability occurs (Lefeuvre, 1996). This variability is due *pro parte* (i) to tidal amplitude (less than 3 m in The Netherlands, almost 15 m in the Mont Saint Michel Bay in France), (ii) to the location of the salt marsh according to the mean sea level and (iii) to plant community structure. This variability is also sesonal and inter-annual (Lefeuvre et al., 1996). These results globally confirm previous European studies (Wolff et al., 1979; Dankers et al., 1984) except in Mira estuary (Portugal) (Lefeuvre, 1996).

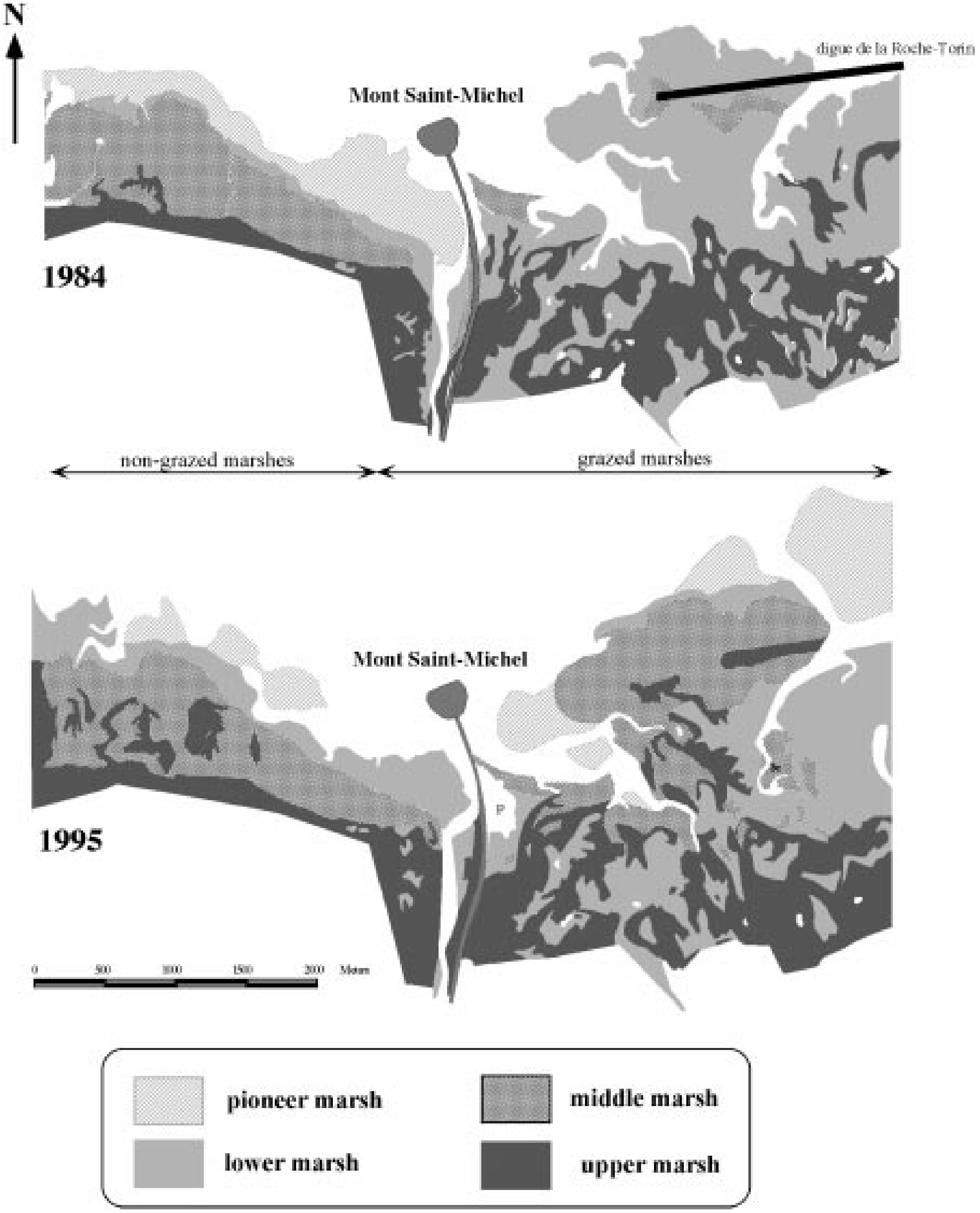

Figure 4. Evolution of saltmarsh coastline and vegetation communities between 1984 and 1995 around the Mont Saint Michel.

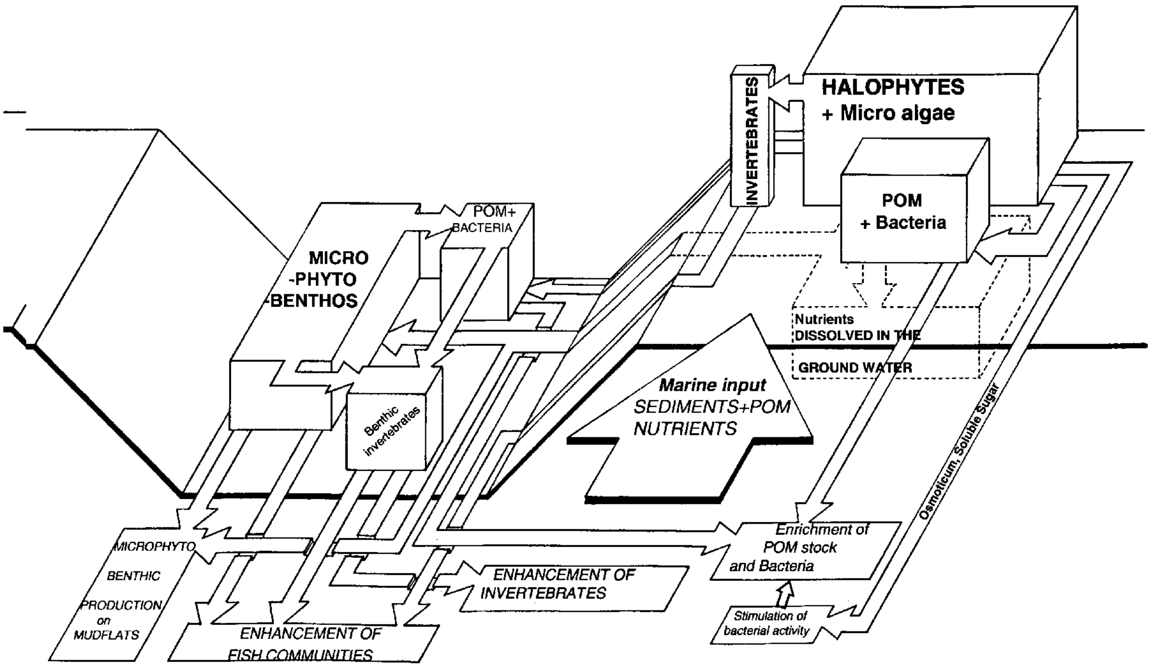

Figure 5. Schematic presentation of OM exchanges between vegetated ungrazed marshes, tidal creeks and coastal waters.

However, several lines of evidence suggest that saltmarshes in the Mont Saint Michel Bay have quite different properties from north east North American saltmarshes which might affect their interaction with adjoining waters. In European saltmarshes, tidal water is confined to its narrow tidal creeks during most of the tides, and the vegetated marsh flats remain totally exposed. Even during spring tides, the high marsh is only occasionally flooded. Thus for most tides, and for all periods between tides, the marsh is exposed to the atmosphere facilitating exchanges of gaseous carbon and nitrogen with atmosphere rather than organic carbon and nutrients with the bay. Therefore, transient fish species can only colonize the saltmarshes for very short periods, and most often, they have to stay in the tidal creeks which act as transition zones between vegetated areas and bare mudflats. In European salt marshes fish forage for very short periods in the high marsh, but they have to leave the salt marsh as the tide ebbs, meanwhile exporting an important amount of OM as gut content. This creates a very strong difference with North American Atlantic salt marshes, where resident fish may stay for much longer periods therefore depositing *in situ* ingested food as feces. Only marine transient species such as menhaden are thought to export OM between estuaries and sea (Weinstein, 1981; Deegan, 1993).

Effects of human management on saltmarsh functionning

In order to provide for reliable and useful information for a sustainable management of these environments, it is also necessary to understand the interactions between human activity and functioning of these systems and the coastal waters to which they are linked. In the past, most saltmarshes have been exploited by agriculture in Europe. Haymaking has gradually decreased, but is still ongoing in some high marshes. Nowadays the most widespread use is livestock grazing. Seventy per cent of the north western European salt marshes are still exploited but, in many countries, area of abandoned salt marsh is increasing rapidly (Bakker, 1989). In the Mont Saint-Michel bay, grazing activity has been maintained and will be encouraged in a very near future by the development of a special label recognizing the quality of this production. However, different opinions exist about what kind of development is relevant for a marsh. From a biodiversity conservation point of view, grazing plays a management role. Grazing at moderate stocking density creates a pattern of closely grazed and lightly grazed patches, where plant diversity is increased (Bakker et al., 1993). Extensive grazing apparently induces higher structural diversity. Intensive grazing – which is the case in the salt marshes studied in the Mont Saint-Michel bay – may result in a low species number, due to the complete or partial destruction of vegetation and topsoil by trampling (Bakker, 1989). Intensive grazing also decreased the potentiality of OM and nutrient export to coastal waters by modifying totally the soil microbiological processes which affect nitrogen and carbon cycling (Vivier, 1997). It also probably reduces the trophic functions played by ungrazed marshes for fish communities. However, this human activity helps to maintain a structure of open and short vegetation. This vegetation induces a lower sedimentation rate than in 'natural' salt marshes. The low sedimentation, together with the direct effect of grazing, control the spread of *Elytrigia aetherica*, dominant species of non-grazed high marshes, almost disconnected from coastal waters.

The application of the marsh-estuarine theory

This study strengthens recent works of American scientists (Dame, 1989) on the causes of variability and questions the marsh-estuarine theory (Dame et al., 1992; Dame and Gardner, 1993). This theory states that saltmarshes tend to mature along a seaward – landward gradient; pioneer zones being located closest to the sea at the limit of mud flats and mature ones bordering the terrestrial systems. In estuaries, the gradient is organized differently probably because of the influence of fresh water: pioneering marshes developing upstream and mature marshes in downstream reaches influenced by marine waters. To Dame et al. (1992) and Dame and Gardner (1993), evidences to date indicate that mature American systems export all materials, mid-aged systems import particulate materials and immature systems import all forms of materials. Regarding the strong contrasts between North American and European salt marshes, it is not certain that this theory can provide for a clear vision of import-export budgets for the marshes of the western coast of Europe. Differences in tidal flooding and vegetation production and structure have to be considered. In North America, along the Atlantic coasts, low marshes are covered with a tall vegetation dominated by *Spartina alterniflora*, which act as trap for sediment and particulate OM. When, those marshes mature, this tall vegetation is replaced by a short *Spartina alterniflora*, and by other short species such as *Spartina patens*. In non-grazed European saltmarshes, we observe an opposite pattern: the vegetation is first dominated by a short prairie (*Puccinellia maritima*), and then replace by taller species (*Atriplex portulacoides* and *Elytrigia aetherica*). If sediment and macro-detritus accumulate under the tall vegetation as it has been demonstrated in this paper, particulate OM should also be trapped being unavailable for export. In the contrary, in grazed salt marshes, low and high marshes – both cover by the same short vegetation – are potential source of particulate OM. These structural aspects differences between American and European marshes, and between grazed and non-grazed marshes, must induce differences in the nutrient budgets and marsh-estuarine theory. Long-term studies (more than 4 years) appear definitively necessary to test this theory.

Study of OM fluxes at the bay or estuary scale

Whatever the processes involved, there is a general evidence that these saltmarshes, (i) use available nutrients to transform energy into OM, (ii) function, more or less directly, as OM and nutrient producers which enrich the coastal fringe and sustain the productivity of coastal marine biota. However, there is a crucial need to (i) understand better the processes underlying the organic matter fluxes between marshes and coastal waters, (ii) to identify the extent of coastal waters which functioning is influenced by the adjacent saltmarshes either by abiotic transport or by transient animal migrations and (iii) to quantify the respective influence of atmospheric, marine and terrestrial systems as original nutrient sources.

In this study, we start raising the question of OM transport from reclaimed marshes into the bay by rivers. Despite their very wide distribution among Europe and other continents, the role of these created systems on the functioning of coastal systems, regarding in particular the outwelling paradigm, is very badly known. Because reclaimed marshes have been disconnected from the sea, the intersystem exchanges of energy with coastal systems is reduced or, at the very least, modified. In fact, the connections with coastal waters are controlled by a set of water gates, which are managed mainly to reduce the admittance of sea water. Therefore fluxes are oriented mainly seaward and amounts of nutrients exported towards the coasts mainly depend upon agricultural activity. In fact reclaimed salt marshes have become similar to inland catchments.

Saltmarshes are only a part of the 'estuarine engine' and fluxes of OM in estuaries and bays should be assessed at large and relevant scales. What is the contribution of saltmarshes, compared to rivers, to the coastal OM budgets? Are saltmarshes sources or converters of OM? Such questions will need to be addressed in order to develop sustainable management policies.

Conclusion

Although much knowledge has been gained during the past two decades on European salt marshes, many lacunae still persist. In order to sort out and synthesize the complexities of biological, chemical and physical interactions in marshes and estuaries, ecologists have resorted to simplified models or simulations of marsh-estuarine systems. These simulation models provide important feedback indicating what kind of new data are needed to enhance understanding and managing these systems. Following two previous EU funded projects, the overall objective of our new project 'European salt marsh modeling' (Lefeuvre et al., 1998) is to develop a policy and management tool for the conservation and restoration of salt marshes.

This project aims are: (i) to improve and test a range of ecological processes and hydrodynamic models to predict the likely responses of various salt marsh ecosystems to environmental changes such as potential impacts of predicted rise of sea level or human activities on the functioning of salt marshes; (ii) to calibrate the process models with specific conditions encountered in various European salt marshes; and (iii) to link the process models and the hydrodynamic models in order to develop a decision support system (DSS) tool.

The evaluation and testing of various models under different marsh typologies will both increase our understanding of the processes controlling the salt marsh ecosystem, and will highlight areas where the processes are not well understood, and where more detailed research is needed.

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