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Pascal Laffaille, Sébastien Brosse, Eric Feunteun, Aurore Baisez, Jean-Claude Lefeuvre. Role of fish communities in particulate organic matter fluxes between salt marshes and coastal marine waters in the Mont Saint-Michel bay.. *Hydrobiologia*, 1998, vol. 373-374, pp. 121-133. 10.1023/A:1017079823670 . hal-00780260

HAL Id: hal-00780260

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Eprints ID: 6074

To link to this article: DOI: 10.1023/A:1017079823670

URL: <http://dx.doi.org/10.1023/A:1017079823670>

To cite this version: Laffaille, Pascal and Brosse, Sébastien and Feunteun, Eric and Baisez, Aurore and Lefevre, Jean-Claude *Role of fish communities in particulate organic matter fluxes between salt marshes and coastal marine waters in the Mont Saint-Michel bay.* (1998) *Hydrobiologia*, vol. 373-374 (n°0). pp. 121-133. ISSN 0018-8158

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Role of fish communities in particulate organic matter fluxes between salt marshes and coastal marine waters in the Mont Saint-Michel Bay

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Key words: salt marsh, outwelling, organic matter fluxes, fish community, nursery, mullets

Abstract

Among the 90 fish species censused in the Mont Saint-Michel Bay (France), 23 colonise and forage in the salt marshes during flood. Therefore, this environment may play an important trophic and nursery role for these species. This community is largely dominated by mullets (81% of the biomass), *Liza ramada* and secondarily *L. aurata*. But gobies (mainly *Pomatoschistus minutus* and *P. lozanoi*) and sea bass (*Dicentrarchus labrax*) are also present; they represent respectively 11% and 4% of the biomass. During the tide cycles, mullets export from salt marshes about 7% of their body weight (FW) containing a mixture of sediment (43%), organic matter (24%) and water (33%). Gobies and sea bass mainly feed on dwelling macro-invertebrates, and they export respectively 4.5% and 10% of their body weight during a tide cycle. Thus, we estimated that 50 tonnes year⁻¹ of particulate organic matter (dry weight POM) are exported from the 4000 ha of salt marshes to the marine coastal waters. These fish communities appear to be POM transporters and could play a significant role in the global energy budgets of coastal environments such as Mont Saint-Michel Bay. According to the seasons and the years, the energy exported by fish communities is assumed to range between 0 and 10% of the total POM output.

Introduction

Salt marshes are complex ecotones between terrestrial and marine systems, regularly flooded by tides. Fluxes of particulate organic matter (POM), dissolved organic matter (DOM) and inorganic nutrients occur between salt marshes and coastal environments. Research on these fluxes and the global functioning of these systems were undertaken by Odum (1968) in the development of outwelling hypothesis. According to this concept, up to 45% of organic matter produced in salt marshes may be exported to the coastal ocean that benefits from this fertilisation to support secondary production (Teal, 1962). However, several studies have shown that this concept should not be applied to all salt marshes, and that nutrient and or-

ganic matter fluxes between adjacent systems ought to be systematically measured (i.e. Pomeroy & Wiegert, 1981; Lefeuvre & Dame, 1994). Many authors thus have quantified these fluxes by abiotic vectors such the tidal currents and the drainage, between various salt marshes and adjacent marine coastal waters (e.i., Teal, loc. cit.; Valiela & Teal, 1979; Nixon, 1980; Dame et al., 1986; Chambers et al., 1992), and more specific to this study in the Mont Saint-Michel Bay (e.i., Lefeuvre et al., 1994; Troccaz et al., 1994; Bouchard, 1996; Troccaz, 1996; Troccaz & Giraud, 1996).

Functioning of salt marshes of Mont Saint-Michel Bay have been studied for 10 years (Lefeuvre et al., 1994). The salt marshes provide high primary productivity. Some vascular plants (e.g. *Atriplex portula-*

coides and *Elytrigia aetherica*) produce up to 3600 g DW m² y⁻¹ (Lefevre et al., loc. cit.), among which less than 1% is exported to the sea as macrodetritus during spring tide (Bouchard, 1996). The remaining is decayed rapidly (Bouchard, loc. cit.) and exported as dissolved organic matter to the open sea by abiotic vectors (tidal currents and especially drainage) (Troccaz, 1996; Troccaz & Giraud, 1996). This contributes to sustain a high biodiversity in Mont Saint-Michel Bay, especially in fish and mollusks (Legendre, 1984; Feunteun & Laffaille, 1997). On the other hand, salt marshes globally trap sediment and particulate organic matter imported by marine waters (Troccaz, loc. cit.; Troccaz & Giraud, loc. cit.). Although significant fluxes of N and C occur between salt marshes, marine waters and atmosphere by rain and evapotranspiration (Hemond & Fifield, 1981), they had not been measured in Mont Saint-Michel Bay.

Beside these biogeochemical and physical processes, the role played by fauna, as biotic vector of organic matter fluxes, in the global functioning of estuarine systems has received scant attention (Bildstein et al., 1992). For instance, animals are able to export organic matter from salt marshes, where they forage, to other ecosystems where they rest or breed (i.e. 6% of phosphorus inputs were due to birds in a lake of western France (Marion et al., 1994; Feunteun & Marion, 1994)).

This role of animals in energy fluxes had not been studied in Mont Saint-Michel Bay either. However, the high primary productivity of Mont Saint-Michel Bay contributes to an exceptional invertebrate and vertebrate biodiversity. In particular, its fish community is very rich (Legendre, 1984; Feunteun & Laffaille, in press). Moreover, the Bay's mud flats represent one of the main nurseries of the French coast of the English Channel for many species such as sea bass, fishes and clupeids (Beillois et al., 1979; Legendre, loc. cit.). Many adult fishes also utilise the marshes and sustain a traditional fishery (Legendre, loc. cit.).

The objective of this study was thus assess the role of fishes in transferring particulate organic matter (POM) between salt marshes and marine waters in the Mont Saint-Michel Bay. Fish communities were studied in order to determine which species are most involved in these fluxes of organic matter, and to quantify and compare these fluxes with those due to abiotic vectors.

Table 1. Characteristics of the 12 tides sampled for fish in Mont Saint-Michel Bay, November 1995 to September 1996.

Dates	Tide amplitude (m)	Duration of submersions (min)	Sampling during	
			flood tide	ebb tide
07/11/95	11.60	100	Yes	Yes
23/11/95	12.45	155	Yes	Yes
07/03/96	12.00	125	No	Yes
18/03/96	12.25	150	Yes	Yes
05/04/96	12.30	130	No	Yes
17/04/96	12.20	120	No	Yes
03/05/96	12.15	125	No	Yes
17/05/96	11.80	100	Yes	Yes
02/06/96	12.05	120	No	Yes
01/07/96	12.55	140	No	Yes
31/07/96	12.65	160	No	Yes
01/09/96	12.60	155	No	Yes

Study site

The Mont Saint-Michel Bay (France) is a wide littoral zone situated in the Normano-Breton Gulf (lat. 48°40' N, long 1°40' W) and which extends over 500 km² (Figure 1). The tidal marshes cover 220 km², including 180 km² of mud flats and 40 km² of salt marshes. This Bay is characterised by strong tidal ranges which reach up to 16 m. Salt marshes are incised by a more or less dense creek network where sea water comes in during a number of tidal cycles. The study site is located in accreting salt marshes (30–50 ha per year) west of Mont Saint-Michel (Lefevre et al., 1994), dominated by *Halimione portulacoides* (Bouchard, 1996). It is situated at 2.5 km from the coastline on a 10 m wide creek which drains a 5.7 ha watershed. The water only reaches this canal in 43% of the tides when the water level is > 11.25 m, (Troccaz et al., 1994).

Materials and methods

Sampling fish community of the salt marsh

Fishes were caught in the creek between November 1995 and September 1996 during a total of 12 spring tides (Table 1). The samplings were made during ebb or ebb and flood tide in order to compare gut contents before and after residence in the salt marsh. Sampling selectivity was reduced by combining fyke net (4 mm

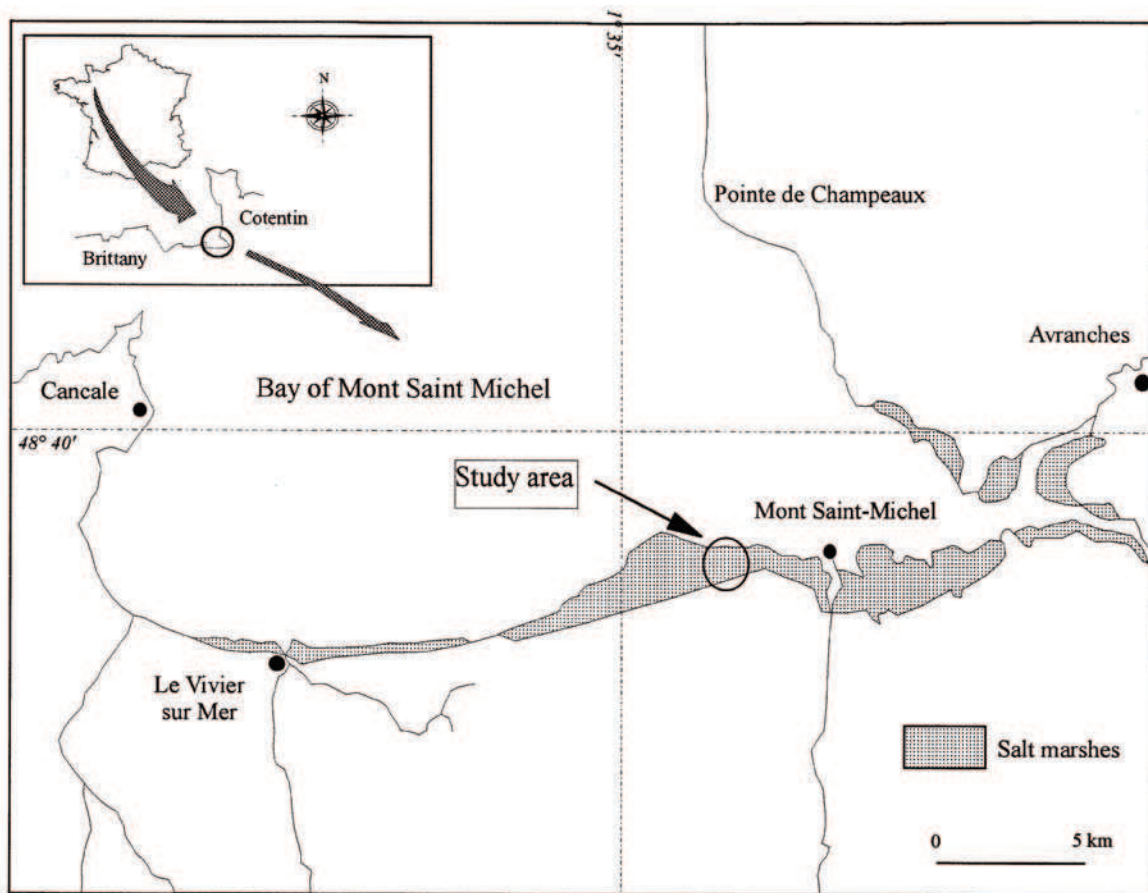


Figure 1. Location of the Mont Saint Michel Bay and study site.

mesh size, 5 m deep, 1.80 m high, 20 m long) to catch small fishes and trammel net (30 to 70 mm mesh size, 2 m high and 30 m long) to capture bigger fishes, especially mugilids, that could escape by avoiding the fyke net. Both devices were set in the canal to catch every fish that accessed the salt marsh during flood or left it during ebb. Sampling was conducted in order to quantify the fish which colonised the marsh and to analyse the variation of population and community structure during the tidal cycle. Every 15 min, a fyke and two trammel nets were set simultaneously. After five minutes, the fyke net was emptied. The trammel nets were taken up after 10 min. Thus, seven to 10 samples were collected depending upon the duration of the tidal cycle. Large fish were sampled during 66% of the time (10 min of fishing every 15 min) with trammel nets and fyke net. Small individuals such as larvae and juvenile, but also small species (i.e. gobies,

gasterosteids, etc.), were caught 33% of the time (5 min of fishing every 15 min) with the fyke net.

All samples were stored in a refrigerated box and deep frozen at the laboratory (-18°C) until analysis. Later, they were identified to species using various guides (Wheeler, 1969; Russel, 1976; Farrugio, 1977; Reay & Cornell, 1988; Serventi et al., 1996). Individual fish was measured to the nearest 1 mm (fork length, FL) and weighed to the nearest 0.01 g (individual fresh body weight, BW). They were then weighed to the nearest 0.1 g for species (total fresh weight, TFW) to establish the biomass and numeric composition of the community during each sampling. The sampling design enabled us to assess the total numbers and biomass of fish that colonized the salt marsh at each tide studied by extrapolation with moving average of the samples: (i) relative number and biomass frequency of species at each tide and (ii) number and biomass of fish caught per min (CPUE). According to the sampling

design, two methods were based on the calculation of estimating the composition (number and biomass abundance of species caught, %NA and %BA) of the fish community during this study: When the sampling was only conducted during ebb,

$$N_j = \frac{\left(\frac{N_i}{t_i}\right) + \left(\frac{N_{i+1}}{t_{i+1}}\right)}{2} \times t_j, \quad (1)$$

$$\text{CPUE} = \frac{\sum N_j + \sum N_i}{\sum t_j + \sum t_i}, \quad (2)$$

with:

t_i = sampling time (mn) for each sample and each device,

t_j = time between sample i and $i + 1$;

N_i = quantity of fish (numbers or g) caught per sample and per species;

N_j = estimated quantity of fish (numbers or g) which entered in the canal between sample i and $i + 1$.

When the sample was conducted during ebb and flood:

$$\text{CPUE} = \frac{\sum N_j + \sum N_i + \sum N_k}{\sum t_i + \sum t_j} \quad (3)$$

with:

N_k = Quantity of fish (numbers or g) caught per species and per sampling device during the flood.

Gut contents analysis

After thawing, measuring and weighing fishes, the entire content of the digestive tract was removed from every thin-lipped mullet (*Liza ramada*, FL > 200 mm), 213 sand gobies (*Pomatoschistus minutus*, FL > 29 mm) caught in March 1996 and every sea bass (*Dicentrarchus labrax*, FL > 59 mm) caught in November. The percentage of empty stomachs was noted (vacuity index, V). Then, the gut contents were weighed to the nearest 0.01 g (gut content fresh weight, FW). To assess the relationship between FW and DW, for each studied species, we also measured the dry weights of gut contents to nearest 0.01 g (gut content dry weight, DW) after desiccation at 50 °C in a drying oven.

In *L. ramada*, the percentage of particulate organic matter (POM) in the gut of 30 specimens caught during ebb was determined by loss on ignition at 480 °C. In order to remove mineral carbon, 10 samples of gut contents of thin-lipped mullets caught during the ebb tide were decarbonated by HCl (1 N, pH 2.0),

rinsed with distilled water and lyophilized. The proportion of total organic carbon (%Ctot) and nitrogen (%Ntot) and the molar C/N ratio was determined with a CHN analyser (Carlo-Erba 1500). Diatoms were also identified in the stomach contents of 15 *L. ramada* specimens. These were separated from sediment by centrifugation and density gradient in a 40% silica gel: Ludox HS solution (Blanchard et al., 1988). Diatom identifications were made according to Peragallo & Peragallo (1897), Hustedt (1927–1933; 1937 & 1959), Hendey (1964), Patrick & Relmer (1966), Germain (1981) and Ricard (1987). The frequency of occurrence (%FO) was estimated and the diatoms classified into three categories (I); accidental: FO < 0.10, secondary: 0.10 < FO < 0.50 and preferential: FO > 0.50 (Albertini-Berhault, 1973).

In sand gobies and sea bass, the food items of 100 and 26 stomach contents were identified to lowest possible taxonomic level and counted. The frequency of occurrence (%FO) and numerical frequency (%N) of macroinvertebrates were estimated according to Hureau (1970).

Estimation of POM exported by fish community

The amount of particulate organic matter exported by a fish community is mainly related to three factors: quantity of POM exported by species, weather conditions (seasonal fluctuation of composition of fish community) and duration of submersion at each tide. These variables were measured automatically. During each tide and for each species, we assessed the abundance and composition of fishes that grazed in the salt marshes, and, thus we estimated the POM they carried. For each species studied, we calculated the instantaneous ration (Ir), ratio between gut contents weight (FW) and body weight (BW). The difference of Ir between ebb and flood tide was assumed to represent the POM budget of each species during a tide cycle. Assuming that the quantity of fish which exploited the salt marsh is proportional to the total duration of the submersion, it is possible to assess the quantity of POM transferred per tide cycle and hence per month ($Q(\text{POM})_m$), where:

$$Q(\text{POM})_m = \text{CPUE}_m \times t_m \times \delta (\text{Ir}) \quad (4)$$

where: CPUE_m = average CPUE per species (g/mn^{-1}) during the month m , t_m = total duration (mn) of the submersion during the month m , and $\delta (\text{Ir})$ = total dif-

Table 2. Composition of fish community caught in the canal between November 1995 and September 1996 during 12 tides. %Occ: percentage of samples in which the species was present, %BA: biomass abundance (%), %NA: numeric abundance (%), FL: fork length (mm), *n*: number of measured fish, *: no quantification of *A. anguilla*.

Families	Species	%Occ	%BA	%NA	FL min (mm)	FL max (mm)	FL mean (<i>n</i>)
<i>Mugilidae</i>	<i>Mugil</i> sp.	100	0.5	3.1	19	60	25 (454)
	<i>Liza aurata</i> (Risso, 1810)	33	1.7	0.1	95	200	136 (16)
	<i>Liza ramada</i> (Risso, 1826)	50	78.9	0.3	285	494	408 (50)
<i>Gobiidae</i>	<i>Aphia minuta</i> (Risso, 1810)	8	0.0	0.0	21	55	45 (9)
	<i>Crystallogobius linearis</i> (Von Düben, 1845)	8	0.0	0.0	33	38	36 (6)
	<i>Pomatoschistus microps</i> (Kroyer, 1838)	8	0.1	0.7	42	53	49 (7)
	<i>Pomatoschistus minutus</i> (Pallas, 1770)	83	8.1	60.3	19	58	40 (610)
	<i>Pomatoschistus lozanoi</i> (de Buen, 1923)	75	2.4	12.2	19	70	34 (117)
<i>Serranidae</i>	<i>Dicentrarchus labrax</i> (Linnaeus, 1758)	67	3.9	0.8	60	260	85 (200)
<i>Atherinidae</i>	<i>Atherina presbyter</i> (Cuvier, 1829)	17	1.8	1.4	61	85	72 (118)
<i>Pleuronectidae</i>	<i>Limanda limanda</i> (Linnaeus, 1758)	25	0.0	2.3	9	15	12 (150)
	<i>Platichthys flesus</i> (Linnaeus, 1758)	17	0.9	0.0	195	210	202 (4)
	<i>P. flesus</i> (larvae)	33	0.0	3.1	8	21	14 (200)
	<i>Pleuronectes platessa</i> (Linnaeus, 1758)	17	0.7	0.0	222	232	227 (2)
	<i>P. platessa</i> (larvae)	50	0.0	7.0	8	20	13 (200)
<i>Clupeidae</i>	<i>Clupea harengus</i> (Linnaeus, 1758)	25	0.2	1.3	23	110	37 (165)
	<i>Sprattus sprattus</i> (Linnaeus, 1758)	75	0.8	6.3	26	86	39 (515)
<i>Gasterosteidae</i>	<i>Gasterosteus aculeatus</i> (Linnaeus, 1758)	67	0.1	0.3	21	68	39 (45)
<i>Ammodytidae</i>	<i>Ammodytes tobianus</i> (Linnaeus, 1758)	8	0.0	0.4	14	20	17 (62)
<i>Soleidae</i>	<i>Solea vulgaris</i> (Quensel, 1806)	33	0.0	0.2	9	27	15 (30)
<i>Syngnathidae</i>	<i>Hippocampus hippocampus</i> (Linnaeus, 1758)	8	0.0	0.0	/	/	120 (1)
	<i>Syngnathus abaster</i> (Risso, 1826)	8	0.0	0.0	/	/	82 (1)
	<i>Syngnathus rostellatus</i> (Nilson, 1855)	25	0.0	0.1	65	99	81 (18)
<i>Trachinidae</i>	<i>Echiichtys vipera</i> (Cuvier, 1829)	8	0.0	0.0	/	/	11 (1)
<i>Anguillidae</i>	<i>Anguilla anguilla</i> (Linnaeus, 1758)	50	*	*	60	79	69 (35)

ference of Ir between flood and ebb during month m.

Results

Composition of the fish community

We caught 23 species belonging to 12 families (Table 2). Among these, eight occurred frequently and could be regarded as permanent species, including three species of mullets (*L. aurata*, *L. ramada* and *Chelon labrosus* (Risso, 1826)), two gobies (*P. minutus* and *P. lozanoi*), sea bass, sprat (*Sprattus sprattus*) and three-spined stickleback (*Gasterosteus aculeatus*). Thus, the community's biomass was highly dominated by mullets (81.1%), especially by thin lipped grey mullet (78.9%) and secondarily by *Pomatoschistus* spp. (10.5%) and sea bass (3.9%). The community was

numerically dominated by gobies (73.2%), especially by sand gobies (60.3%), flatfish larvae (12.6%) but only 3.5% are mugilids. Glass eels (*Anguilla anguilla*) and flatfish larvae were not quantified because the fyke net was not considered an efficient sampler of these small fishes. Except for gobies, mullets, sea bass and three-spined stickleback, the fishes were mainly found as larvae and juveniles and they only occurred for short period, in particular during early spring. During these early stages, most fishes feed on microplankton (Russel, 1976) which is transported the water during the tide; therefore, we assumed that they were not significantly involved in POM fluxes.

The salt marsh was colonised by fish every time the tide reached the creek. Nevertheless, abundances were variable: CPUE varied between 2.8 g min⁻¹ (March 1996) and 400 g min⁻¹ (September 1996) (Figure 2a). The first abundance peak occurred in November 1995;

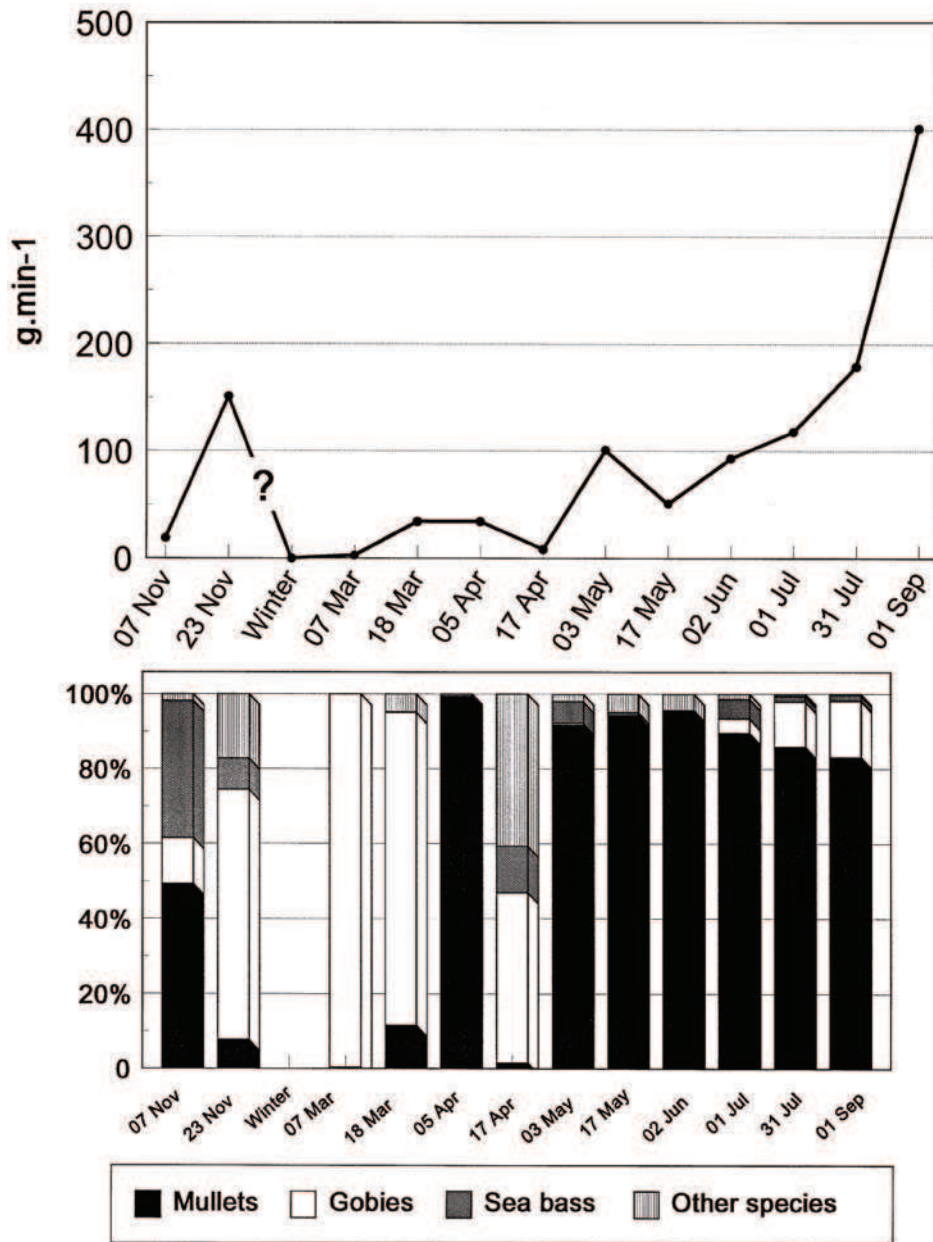


Figure 2. Seasonal fluctuations of the fish abundance. a. biomass (g) of fish caught per min (CPUE). b. biomass frequency (%).

it was mainly due to gobies (100 g.min⁻¹) (Figure 2b). No data was collected during winter but, considering the low water temperatures, we assume that abundances dropped and remained low in accordance with other sites (Feunteun, 1994) and in this creek in winter 1997 (Laffaille, unpublished data). The CPUE began to increase again at the beginning of March (2.8 g.min⁻¹) and in August (150 g.min⁻¹), when catches

were generally dominated by mullets between April and September.

Thus, only five species were able to export significantly organic matter produced in the salt marshes or on the mud flats: two species of mullets (*Liza ramada* and *L. aurata*), two species of gobies (*Pomatoschistus minutus*, *P. lozanoi*) and the sea bass (*Dicentrarchus labrax*).

Table 3. Diatoms identified in the gut contents of *L. ramada* caught during ebb tide. %FO: frequency of occurrence, I: food items importance (P: preferential, S: secondary, A: accidental).

Food items	%FO	I	Benthic	Planktonic
<i>Nitzschia sigma</i> (Kützing) Wm. Smith	1.00	P	*	
<i>Coscinodiscus excentricus</i> Ehrenberg	1.00	P	*	
<i>Scoliopleura tumida</i> de Brébisson	1.00	P	*	
<i>Podosira stelliger</i> (Bailey) Mann	0.93	P	*	*
<i>Surirella ovata</i> Kützing	0.93	P	*	
<i>Paralia sulcata</i> (Ehrenberg) Kützing	0.93	P	*	
<i>Actinoptychus undulatus</i> (Bailey) Ralfs	0.87	P	*	*
<i>Biddulphia rhombus</i> (Ehrenberg) Wm. Smith	0.87	P	*	
<i>Surirella gemma</i> Ehrenberg	0.87	P	*	*
<i>Raphoneis amphicerus</i> Ehrenberg	0.87	P	*	
<i>Navicula phyllepta</i> Kützing	0.73	P	*	*
<i>Auliscus sculptus</i> (Wm. Smith) Ralfs	0.47	S	*	
<i>Navicula palpebralis</i> de Brébisson ex Wm. Smith	0.47	S	*	
<i>Biddulphia mobiliensis</i> Bailey	0.27	S	*	*
<i>Navicula cincta</i> (Ehrenberg) Van Heurck	0.27	S	*	
<i>Melosira westii</i> Wm. Smith	0.27	S	*	*
<i>Gyrosigma obtusatum</i> A. Boyer	0.20	S	*	
<i>Navicula praetexta</i> Ehrenberg	0.20	S	*	
<i>Coscinodiscus rothii</i> var. <i>subsalsa</i> (Juhl-Dannf) Hustedt	0.13	S	*	
<i>Diploneis crabro</i> Ehrenberg	0.13	S	*	
<i>Navicula digito-radiata</i> (Gregory) Ralfs	0.13	S	*	

Contribution to organic matter budget

Mulletts

Mulletts colonised the salt marshes at different life stages during the whole year. Large mulletts (*L. ramada* and *L. aurata*) mainly occurred in November. Their abundances decreased in winter and started increasing again in April, reaching a peak in summer (Figure 2). This could be due to the fact that, in the northern hemisphere, mugilids graze more actively in spring and in summer (i.e., Hickling, 1970; Odum, 1970; De Silva & Witeryaratne, 1977; Albertini-Berhault, 1980). The scarceness of adult during winter could be related to the low temperatures, but also to a fasting period during gonad maturation between October and April (Cassifour, 1975).

Young mulletts exclusively feed on zooplankton, but their diet focuses on phytobenthos with increasing age (i.e., Hickling, loc. cit.; Odum, loc. cit.; Blaber & Whitfield, 1977; Albertini-Berhault, loc. cit.). Therefore, we assume that only large individuals contribute significantly to organic matter fluxes. We found that the diet of large mulletts was mainly composed of sediment, phytobenthos, zooplankton

Table 4. Comparison, between ebb tide and flow tide, of average instantaneous ration (%Ir) and vacuity index (%V) of *L. ramada*. sd: standard deviation, n: number of digestive contents analysed.

	% Ir		%V	n
	average	sd		
Flood tide	5.86	1.43	0	11
Ebb tide	12.71	3.15	0	39
Difference	6.5			
T test	$p < 0,01\%$			

and various detritus. Most of the food items were diatoms. Among the 32 identified species, 11 dominant species were determined from the literature to be benthic forms (Table 3): *Nitzschia sigma*, *Coscinodiscus excentricus*, *Scoliopleura tumida*, *Podosira stelliger*, *Surirella ovata*, *Paralia sulcata*, *Actinoptychus undulatus*, *Biddulphia rhombus*, *Surirella gemma*, *Raphoneis amphicerus* and *Navicula phyllepta* (Peragallo & Peragallo, 1887; Hustdet, 1927–1933; 1937; 1959; Hendey, 1964; Patrick & Relmer, 1966; Germain,

Table 5. Proportion of total organic carbon (%Ctot) and nitrogen (%Ntot) and the molar C/N ratio determined in mullet's digestive contents. sd: standard deviation, *n*: number of digestive contents analysed.

	%Ctot	%Ntot	C/N
Average	5.74	0.78	8.69
sd	1.34	0.21	0.89
<i>n</i>	10	10	10

1981; Ricard, 1987). At the same period, these species were also present in the creeks sediment (Brosse et al., 1996). This suggests that *L. ramada* grazed the superficial sediment layer and confirms several former studies (i.e. Hickling, loc. cit.; Odum, loc. cit.; Fagade & Olaniyan, 1973; Brusle, 1981; Almeida et al., 1993). We found a confirmation of these observations in the occurrence of grazing marks in the silt of the channels after the passage of mullets. None of the sampled mullets had empty guts ($V=0$) during ebb or during flood (Table 4). This shows that the grazing started on the mud flats adjacent to the marsh during flood. However, the average repletion index increased from 5.9%, when the mullets arrived from the sea with the flood, to 12.7% when they left the marsh at ebb. Thus, on average, mullets swallowed about 6.9% of their body weight while they grazed on the salt marsh at high tide.

A significant regression correlation ($r=0.96$) was found between the dry weight and fresh weight of the gut contents of 30 mullets. On average, DW is 66.9% of FW (sd=7.44). However, no significant relation ($r=0.26$) was found between POM biomass and total gut contents (FW). The proportion of POM was comprised between 24.2% and 64.3% (average=36.3%, sd=13.1). Therefore, it was not possible to predict POM biomass from total ingested food biomass. This result was not surprising, because the proportion of organic matter depends on factors such as feeding behaviour, sediment composition, site, etc. For instance, Farrugio (1975) assessed that one third of the gut contents was composed of sediment, and Jacot (1920) showed that 40% of *Mugil* spp. stomach content were 'non digestible matter'. Tung (1971, in Brusle, 1981) showed that the proportion of organic matter varied from 65% of sediment when mullets fed on diatoms to only 35% when they fed on copepods. Moreover, the proportion of POM varies considerably according

to seasons and to trophic areas (Almeida et al., 1993). The proportion of total organic carbon and nitrogen contained in the digestive tract of ten mullets (Table 5) averaged 5.7% (sd = 1.34) and 0.8% (sd = 0.21). These proportions were low, certainly because sediment was important in the gut contents. The average C/N ratio is 8.7% (sd = 0.89). Thus, inter-individual differences appeared to be relatively low.

Gobies

Five species of *Gobiidae* were sampled in the creek. But, because of their commonness, only *Pomatoschistus minutus* and *P. lozanoi* were significantly involved in organic matter fluxes. Gobies were present in the salt marsh during the whole study period except at the end of May (Figure 2 b). At the beginning of May, only 7.1% of males were present whereas 39.4% were mature females full of oocytes. At the end of May, no gobies were caught and after this date high concentrations of larvae occurred (up to 125 gobies min^{-1}), but the biomass was low (3.6 g min^{-1}) which suggests that gobies did not participate significantly to organic matter flux at that period of year. A high abundance of adults occurred in autumn, when CPUE ranged between 60 and 100 g mn^{-1} .

Pomatoschistus minutus is considered as a generalist predator (Hamerlynck & Cattrijsse, 1994). But, with regard to the food items in the gut (Table 6), *Pomatoschistus* sp. can also be considered as an opportunist. They can either feed on microinvertebrates, but also on macroinvertebrates, and cases of cannibalism are occasionally observed. *Orchestia gammarellus* were the preferential food items in the canal (%OF=0.600 and %N=0.710). This amphipod is a resident species at Mont Saint-Michel salt marshes (Fouillet, 1986).

In *Pomatoschistus minutus*, *V* was low ($V=1.5\%$) during flood tides, but it dropped to 0% during ebb a few minutes later (Table 7). Meanwhile, *Ir* increased from 9.7% (flood tide) to 14.4% (ebb tide), indicating that these fishes fed actively while they colonised the salt marshes and that they exported on average 4.7% of their body weight during a tidal cycle. A significant correlation was found between dry weight and fresh weight of guts contents ($r=0.96$). On average, DW represents 59% (sd = 8.3) of gut contents.

Sea bass

Dicentrarchus labrax were present as juveniles stages, 0+ and 1+ (Table 2). They were absent in winter, but started arriving in the middle of spring (Figure 2). Un-

Table 6. Food items identified in the stomach contents of *D. labrax* ($n=26$) and *P. minutus* ($n=100$) caught during ebb tide. %FO: frequency of occurrence, %N: numeric frequency, n : number of stomach contents analysed.

Food items	Sea bass ($n=26$)		Sand gobies ($n=100$)	
	%FO	%N	%FO	%N
<i>Orchestia gammarellus</i> (Pallas)	0.923	0.666	0.600	0.710
<i>Sphaeroma rugicauda</i> (Leach)	0.538	0.244	0	0
<i>Eurydice pulchra</i> (Leach)	0.308	0.014	0.050	0.025
<i>Corophium volutator</i> (Pallas)	0.346	0.020	0	0
<i>Bathyporeia</i> sp.	0.192	0.028	0	0
<i>Neris diversicolor</i> (O.F. Müller)	0.269	0.011	0.180	0.076
Mysidacea n.i.	0	0	0.160	0.143
<i>Crangon crangon</i> (Linnaeus)	0.077	0.003	0	0
<i>Carcinus mancas</i> (Linnaeus)	0.115	0.003	0	0
Tellinidae sp.	0.038	0.001	0	0
Insect	0.115	0.005	0	0
Fish	0	0	0.050	0.025
Other	0.077	0.005	0.050	0.021

Table 7. Comparison, between ebb tide and flow tide, of average instantaneous ration (%Ir) and vacuity index (%V) of *P. minutus* caught the 18th March. sd: standard deviation, n : number of digestive contents analysed.

	% Ir		%V	n
	average	sd		
Flood tide	9.71	3.84	1.45	72
Ebb tide	14.4	4.61	0	141
Difference	4.69			
<i>T</i> Test	$p < 0,01\%$			

Table 8. Comparison, between ebb tide and flow tide, of average instantaneous ration (%Ir) and vacuity index (%V) of *D. labrax* caught in November 1995. sd: standard deviation, n : number of digestive contents analysed.

	% Ir		%V	n
	average	sd		
Flood tide	0.96	1.84	61.8	99
Ebb tide	11.04	2.24	0	68
Difference	10.08			
<i>T</i> Test	$p < 0,01\%$			

til the beginning of summer, their abundances were generally low (0 to 5.1 g min⁻¹), and peaked at the end of summer and especially in autumn (7 to 13 g min⁻¹).

The diet was exclusively composed of macroinvertebrates (Table 6), mainly the amphipod *Orchestia gammarellus*, which occurred in 92% of the stomach, and secondarily the isopod *Sphaeroma rugicauda*, found in 54% of the stomach contents. These preferential food items (%N=0.910) are resident species in the Mont Saint-Michel salt marshes (Fouillet, 1986).

During flood, vacuity (Table 8) averaged 61.8% and dropped to 0% when the bass left the marsh at ebb. Ir (Table 8) increased from 0.96% at flood to 11.04% at ebb tide. The sea bass ingested about 10.08% of

their body weight while they were in the salt marshes. This organic matter was then transferred to the marine coastal waters. There was a significant correlation between DW and FW of the gut contents ($r=0.97$). Thus, it was possible to predict the DW from the FW as DW represented 62% (sd=6.6) of the FW.

Discussion – Conclusion

At least 90 fish species are present in the Bay of Mont Saint-Michel (Beillois et al., 1979; Legendre, 1984; Feunteun & Laffaille, 1997). Of these, 23 species colonise the salt marsh mainly during their early life stages. Other species are also known to frequent salt marshes, for instance shad *Alosa alosa*

(Linnaeus, 1758) and salmon *Salmo salar* (Linnaeus, 1758) are occasionally caught in traditional fisheries (Lefeuvre, unpublished data), and juveniles of *Belone belone* (Linnaeus, 1758) and *Lepadogaster lepadogaster* (Bonnaterre, 1788) have also been collected during recent samplings (Laffaille, unpublished data). Therefore, the intense productivity of this environment, that is known to be exploited by birds (Schricke, 1983; Lefeuvre et al., 1994), is also actively foraged by fish communities. The Bay of Mont Saint-Michel (Beillois et al., loc. cit.) as with comparable shallow marine coastal waters such as estuaries and lagoons (i.e. Costa, 1988; Elie et al. 1990), are known to play a nursery role for many fish species. This function is usually described as restricted to the mud flats of the midlittoral zones in Mont Saint-Michel Bay. The present study shows that the salt marshes of the supralittoral zone also play an important nursery role (i.e. Boesch & Turner, 1984). Salt marshes are believed to serve as nurseries for many fishes as a result of the high production of vascular plant detritus and diatoms. The refuge role generally described in shallow bays may not be as significant in Mont Saint-Michel Bay; despite scarce predators (a few seals, piscivorous birds and large fish), salt marshes are submerged for too short period (max. 2 h) and the currents are too strong (megatidal system) to represent a significant refuge role for young fish.

We found that a minimum of five fish species feed actively in the salt marshes of Mont Saint-Michel Bay during tidal floods: two species of mullets, two species of gobies and juvenile sea bass. These five seem to colonise marshes to exploit their high productivity. Mulletts exploit the primary productivity (mainly diatoms), whereas gobies and sea bass exploit the secondary productivity (especially *Orchestia gammarellus*). These resident species feed on diatoms and vascular plant detritus (Creach, 1995). Moreover, these fishes play a dominant role in the food web and in the fisheries of the Mont Saint-Michel Bay either as prey of other fishes and birds (gobies, and young mullets) or as valuable commercial species (sea bass) (Feunteun & Laffaille, 1997). Therefore, the primary productivity of salt marshes appears to play a fundamental role in the global functioning of Mont Saint-Michel Bay.

The magnitude of organic matter fluxes mainly depends on the biomass of fish that forage on the salt marsh during the tidal cycle. To summarise, during the tidal cycles, mullets export a mixture of sediment and organic matter from the salt marshes to the ma-

rine coastal waters of the Bay. During a given tide cycle, each fish exports about 6.9% of its fresh weight, comprising 42.6% of sediment, 24.3% of particulate organic matter and 33.1% of water. The dry gut contents POM averages 5.7% organic C and 0.8% organic N. Sand gobies and sea bass mainly feed and export respectively 4.5% and 10% of their body weight during a tide cycle. The difference of I_r takes into account excretion and gastric evacuation in the creek. Retention time of the ingested material is highly variable. For example, it ranges from 2 to 6 h for mullets (Brusle, 1981), which is much longer than the tidal submersion period of the creeks and the salt marsh. Therefore we assume that POM is low in the salt marsh and creeks during the tide cycle.

In order to assess the relative importance of POM fluxes from the salt marsh due to fish, we assume that respectively *Liza ramada* and *L. aurata*, and *Pomatoschistus minutus* and *P. lozanoi* export, on average, an equal quantity and assumable quality of organic matter. Since sea bass and gobies' diets were largely dominated by *Orchestia gammarellus*, we used the proportion of C_{tot} and N_{tot} assessed by Creach (1995) in the Mont Saint-Michel Bay: $C_{tot} = 50.9 \pm 4.13\%$ ($n=20$), $N_{tot} = 8.7 \pm 0.97$ ($n=20$) and $C/N = 9.7 \pm 0.9$ ($n=20$). On this basis, we estimated the organic matter fluxes due to these fish per tide cycle and per month (Figure 3). During the study, a total of 50 g ha^{-1} to 1700 g ha^{-1} of organic matter (DW) was exported monthly towards the marine coastal waters. On average, 67% of this organic matter is exported by mullets, 23% by gobies and 10% by sea bass. But during late autumn, gobies export more than 70% of the organic matter transported by fish. The study site has a central location among the salt marshes of the Bay of Mont Saint-Michel. Therefore, assuming such a geographical representativity, the extrapolation of our data set permits to assess that the fish communities export about 50 tons DW of organic matter per year from the salt marshes towards the sea, comprising 10.3 tons of organic C and 1.7 tons of N. Of course, part of the POM exported by fish is decayed and can be imported later by tidal currents as POM, DOM or dissolved nutrients. However, we assume that the POM output by fish was very low compared to other sources during the study period. More, recent samplings have shown that the biomass of mullets present in the creek may be at least 15 times higher (unpublished data) which suggests that important interannual variations of fish contribution to organic matter fluxes between salt marshes and marine coastal waters are expected.

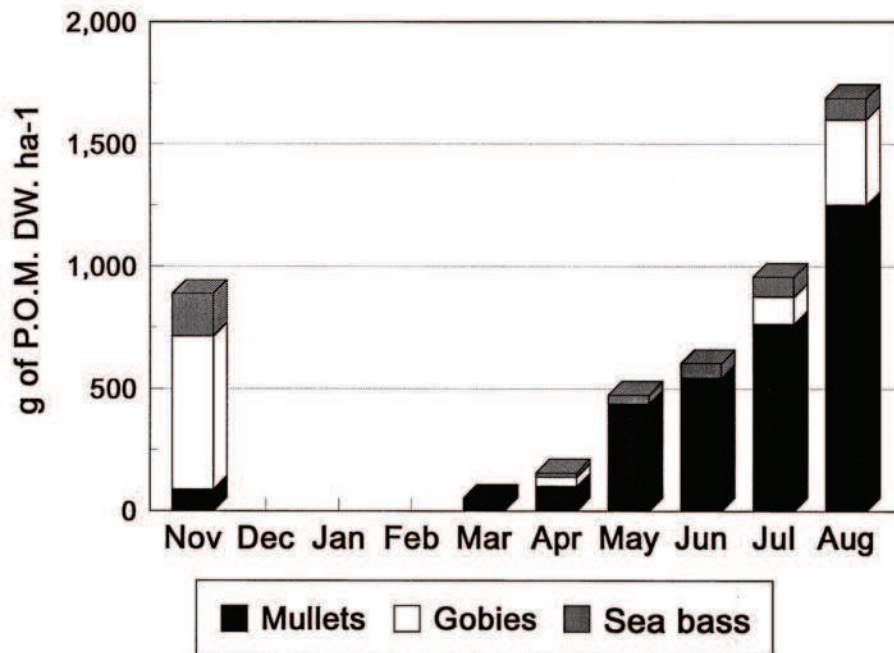


Figure 3. Monthly transfers of particulate organic matter by fishes between the studied salt marshes and marine coastal waters in the bay of Mont Saint Michel, between November 1995 and August 1996.

Even if the total input of OM to the Bay of Mont Saint-Michel has been estimated in the past years (Troccaz, 1996), we still do not know the proportion of this organic matter which is exported by fish. In order to improve the understanding of the coastal biogeochemical cycles, it is interesting to compare the POM budgets due to fish communities with those due to abiotic vectors (tidal currents, interstitial water, etc.). On a Bay-wide scale, the salt marsh traps POM during the tide cycles: for instance in 1991, the input was 2.9 kg m^{-2} (Troccaz, 1996; Troccaz & Giraud, 1996). In comparison, during the ebb tides between 1991 and 1994, Troccaz et al. (1994), Troccaz & Giraud, (loc. cit.) and Troccaz (loc. cit.) estimated that between $0.7 \text{ g m}^{-2} \text{ y}^{-1}$ and $5.8 \text{ g m}^{-2} \text{ y}^{-1}$ of total N, and $83.3 \text{ g m}^{-2} \text{ y}^{-1}$ to $114.2 \text{ g m}^{-2} \text{ y}^{-1}$ of total organic C was exported from these salt marshes. Of course, such comparison is difficult because of several uncertainties. Firstly, we noted an important temporal heterogeneity of the POM budgets due to fish transport and also to abiotic vectors. Therefore, a simultaneous survey of both POM fluxes vectors ought to be conducted a longer period. Secondly, the assumption that the study site is representative of the whole salt marsh will have to be verified because its productivity depends on several factors. For instance, in the parts of

the marsh which are grazed by sheep, the original vegetation cover, dominated by *Atriplex portulacoides*, is replaced by *Puccinellia maritima*. Thirdly, the 4000 ha of salt marshes have variable ages, the oldest have had about 60 y of existence, whereas the youngest are only a few years old: 30 ha of pioneer mud flat zones are colonised every year, especially by *Spartina* spp., and *Salicornia* spp. (Levasseur et al., 1995). It has been shown that salt marshes have a tendency to export more OM as they get older (Dame & Lefevre, 1994). Therefore, these variables add another variability source which has to be investigated in order to make accurate comparisons between the OM budgets due to fish communities and abiotic vectors. Nevertheless, as a preliminary approach, we assume that the fish community is responsible for part of the output of nitrogen and carbon from the salt marsh, which varies strongly according to years, and to characteristics of the salt marsh. We conclude that fish communities play an important role in the global functioning of the Bay and more generally of coastal environments, at least in terms of organic matter fluxes.

Acknowledgements

We are grateful to Dr M. T. Schricke and B. Savouré for identification of the macro-invertebrates and diatom species. We thank other members of Laboratoire d'Evolution des Systèmes Naturels et Modifiés for their laboratory and field assistance. We are indebted to V. Bouchard and two anonymous referees for their remarks and corrections of the manuscript.

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