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Do fish communities function as biotic vectors of organic matter between salt marshes and marine coastal waters?

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Abstract

The contribution of fish communities to organic matter (OM) fluxes, especially between salt marshes and adjacent marine coastal waters are reviewed. For this a data set from the bay of Mont Saint-Michel and literature is examined and discussed. In a range of macro-tidal coasts of Europe, salt marshes are only flooded at spring tides for a short time. Many animals, including fish, then invade the salt marshes through tidal creeks. They forage there for up to a few hours and swim back to sea at ebb. Meanwhile, organic matter is exported as gut content. In the 4000 ha of salt marshes of the bay of Mont Saint-Michel mullets were responsible for the export of about 8 kg of dry weight OM ha^{-1} in 1996 and of roughly 12 kg in 1997. Although spatio-temporally variable, the fish communities appear to play a more or less significant role, as 'biotic vectors' in the nutrient fluxes between salt marshes and coastal waters.

Introduction

The degradation of the planet's water resources and the disfunctioning observed in continental, estuarian and coastal hydrosystems (Lacaze, 1996) have induced a range of intensive research about the exchange between terrestrial and aquatic environments as well as in the transition zones between these wetlands. The concept of 'coupling system' (Hasler, 1974) was often used appropriately to initiate research focusing on terrestrial environments as source and on wetlands as transformation areas of various types of organic matter (OM), nutrients, and other chemicals. Major research has also been conducted on the effects of materials transformed in wetlands on adjacent aquatic ecosystems (Lefeuvre & Dame, 1994).

The high primary productivity of salt marshes sustains a high biomass of sedentary invertebrates, which are in their turn predated by a number of transient species, including mammals, waterbirds and fishes. Fish invade salt marshes during floods and forage there during the short submersion period (a few min to a few hrs according to the location on the marsh). When they leave the salt marshes at ebb, it is assumed that at least a part of the ingested food is exported and the non-assimilated OM is deposited in marine coastal waters as faeces. Therefore, these transient species participate in energy fluxes between adjacent systems: they act as biotic vectors of OM (sensu Forman, 1981). This aspect of salt marsh functioning has rarely been studied. The aim of this paper is to discuss and assess the role of fish communities as vectors of organic matter between various adjacent systems and mainly between salt marshes and marine coastal waters.

Exchange between salt marshes and coastal waters: the 'outwelling hypothesis'

Limnologists have played a major role in the development of the 'coupling system' concept since the 1920s when it was shown that the trophic status of lakes depended upon the structure and use of soil and of the matters transferred from the catchments to the lakes.

In the seventies, these ideas were adopted by scientists working on running waters. For example, Fisher & Likens (1973) demonstrated that more than 99% of the nutrients received by a forest stream is allochtonous. It is now accepted that water flow and composition of dissolved or particulate elements depend mainly on watershed structure and human activities (Décamps et al., 1979). Using this approach it is easy to consider that in littoral zones the concept of 'coupling system' is even better adapted to analyse the relation between salt marshes and marine coastal waters. Indeed, water flow between these two systems is a two-way process driven by tides and gravity which favour exchanges.

In the coastal zone, this concept has been one of the most dynamic and controversial issues since the last three decades (Dame, 1989). This type of research was initiated by Teal (1962), who studied the functioning of North American *Spartina alterniflora* dominated salt marshes. He concluded that 'the tides remove 45% of the production before the marsh consumers have a chance to use it and therefore enables the estuaries to support abundant and diversified animal communities'. This view was supported by Odum & De la Cruz (1967) for particulate organic detritus studies, and contributed to the origin of the 'outwelling hypothesis' (Odum, 1968, 1980). It states that salt marshes dominated by *Spartina alterniflora* produce more material than can be degraded or stored within the system and that the excess is exported to coastal waters where it supports ocean productivity.

Several steps in pursuit of the outwelling question may be identified. First, following Teal (1962) and Odum (1968, 1980), many authors have shown export of particulate OM: second, Haines (1977) showed that the carbon isotope value of the detritus in tidal creeks around Sapelo Island was not similar to the one of *Spartina*. The observed value was close to those of phytoplankton and chemosynthetic bacteria or a mixture of *Spartina* detritus and terrestrial material imported by river runoff. At the same time, Woodwell et al. (1977) and Hackney (1977) showed import of particulate OM in salt marshes. Third, the third step is a more general view of exchanges between salt marshes and estuaries and considers particulate OM as well as dissolved OM, nitrogen, phosphate and silica. For Dame (1989), the *Spartina* marshes can act as sinks not only for nutrients but also for heavy metals.

Considering this great variability in results, Nixon (1980) stated that 'now, the prevailing view among this field work is that the chaos reigns and that we dare not make any statement at all what marshes are importing or exporting'. Since this statement, many studies tried to explain this apparent confusion. Many factors may be related to this variability either in primary production or in the import/export capacity of salt marshes. It is only since the 1980s that the Europeans have really participated in this debate (Wolff et al., 1979: Dankers et al., 1984). Since 1985, a number of research teams from the Netherlands, United Kingdom, Portugal and France have joined in an EC research (D.G. XII) funded programme: 'Comparative Studies on Salt marsh Processes'. These comparative approaches have shown that, in Europe, the eulittoral zone is partly covered by pioneer vegetation, while in the USA it is dominated by extensive surfaces of *Spartina alterniflora*. In fact, what we call salt marshes in Europe as those located between high water level and spring high water level. In the USA, the vegetation of the salt marshes is flooded twice a day while in Europe the salt marshes are only flooded occasionally – depending on the tidal amplitude of each tide cycle – their highest part being reached by sea water only during spring tides.

The variation of flooding frequency and time determine a zonation well marked by different plant species. For instance, in the bay of Mont Saint-Michel the dominant species are: *Salicorna* sp. in pioneer zones, *Puccinellia maritima* in lower marshes, *Halimione portulacoides* in middle marshes and *Elytrigia pungens* and *Festuca rubra* in upper marshes. The primary production is also variable according to species and position in the salt marsh. Bouchard (1996) has shown that the net aerial primary production (NAPP) can fluctuate between 107 ± 26 g dry weight (DW) m^{-2} y^{-1} for *Puccinellia maritima* and 1920 ± 470 g DW m^{-2} y^{-1} for *Halimione portulacoides*. NAPP varies within a species according to the localisation in the lower, middle or upper marsh (Bouchard & Lefeuvre, 1996).

All this dead OM coming from halophytes forms the macro-detritus which is transported floating in the water mass during tidal cycles. This macro-detritus is then transformed into particulate OM and dissolved OM during decomposition processes (Pieczynska, 1993). This pool of OM can be either trapped in the salt marsh as litter, or transferred by tidal currents (i) into the upper salt marsh or (ii) towards the coastal waters. Contrarily to many North American marshes, which export up to 45% of the produced OM (Teal, 1962), and even nearly 100% like in the Bay of Fundy (Gordon & Cranford, 1994), European salt marshes export only about 1% of the produced OM as macro-detritus. In fact, the low frequency of floods in European salt marshes favours the deposition of dead OM which forms litter which is later decomposed and mineralised. Therefore, at young and middle stages of maturity, European salt marshes export dissolved matter (dissolved organic carbon, nutrient, etc.) and import particulate matter principally as particles of sediment.

Invertebrate communities play key roles in these transfers: many small herbivores (i.e. gastropods) feed directly on epiphyte production, but most vascular plants are only grazed once they are dead, as macro-detritus by invertebrates like the amphipod *Orchestia gammarellus* (Fouillet, 1986). Such grazing eases mineralisation processes and litter is finally exported as dissolved organic carbon and nutrients by tidal currents or by runoff in the creeks and finally enriches the mud flats. This may favour the development of microphytobenthos (mainly diatoms). Both OM sources provide food for suspension feeding or saprophagous invertebrates and for grazing fish species like mullets, predators like gobies (*Pomatoschistus* spp) and juvenile sea bass (*Dicentrarchus labrax*) (Figure 1) (Feunteun & Laffaille, 1997; Laffaille et al., 1998), illustrating the importance of these coastal exchanges for fish populations.

It is well known that many commercial fish species spend a more or less long period of their life cycle in salt marshes and estuaries (e.g., McHugh, 1966; Weisberg et al., 1981; Boesch & Turner, 1984; Elie et al., 1990). The nursery function concerns young stages, larvae or very young juveniles of fish which are drifted to the salt marshes by tidal currents. The trophic function concerns older stages, either young of the year or adult fish which exploit the salt marshes for longer periods. They invade the marsh actively at flood and then graze either on the primary production (limnivorous species) or prey on invertebrates such as polychaetes, amphipods, isopods and mysids. On the other hand, the participation of fish communities to the general functioning of marine coastal systems has rarely been looked at.

Fish communities as biotic vectors of organic matter

Organic matter transfer in general

Nutrient and OM fluxes, both in salt marshes of USA and Europe, have only been estimated by measurements of OM and nutrients transferred by water (Figure 2). OM and nutrients are analysed in terms of physical or chemical processes depending mainly upon tidal amplitude, current velocity and runoff, whereas the involvement of fish in these fluxes has rarely been studied. Yet, Krokhin (1975), Durbin et al. (1979), Northcote (1988) and Elliott et al. (1997) have shown that amphihaline species, e.g., salmonids, are responsible for major inputs of OM in oligotrophic riverine systems. Many anadromous salmonid breeders die after spawning. As a result, OM is introduced as dead organic matter which is decayed and finally mineralised. Elliott et al. (1997) estimated that in a catchment in Northeast England, adults import 26 to 40 metric tons y^{-1} of organic carbon and, simultaneously, smolts export 2 to 4.5 ton y^{-1}. Moreover, Krokhin (1975) showed that corpses of dead salmon spawners may be responsible for up to 40% of phosphorus input in lake Dalnee (Russia). In the same way, European and American eels (*Anguilla anguilla* and *A. rostrata*) export live OM from continental waters (brackish and fresh) in which they grow into the Sargasso Sea where they spawn and die (Laffaille et al., in press). Therefore, because spawning, nursery and growth areas are located in different systems, important amounts of nutrients and OM are transferred during the migrations. This is also the case in coastal and estuarine nurseries where larvae and juveniles spend their first few months before they migrate to offshore waters. For instance, menhaden (*Brevoortia patronus*), that support one of the main commercial fisheries in North America, grow and accumulate biomass in estuaries and constitute an important source of nutrients for coastal marine ecosystems of the gulf of Mexico (Deegan, 1993). During their seaward reproductive migration, menhaden export 5 to 10% of the total primary production of these estuarine areas. The incursions of fish into habitats such as salt marshes or subtidal grasslands are sometimes extremely brief. Nevertheless, important grazing pressure can occur, e.g., the herbivore sparid fish, *Salpa salpa*, consumes 24 g C m^{-2} y^{-1} of *Posidonia oceanica*, 4.8 g C m^{-2} y^{-1} of epiphytes and 13 g C m^{-2} y^{-1} of epipelic algae (Havelange et al., 1997). These examples show that fish transfer OM during their displacements and therefore act as biotic vectors of OM between adjacent systems. The extent of this still remains largely unknown.

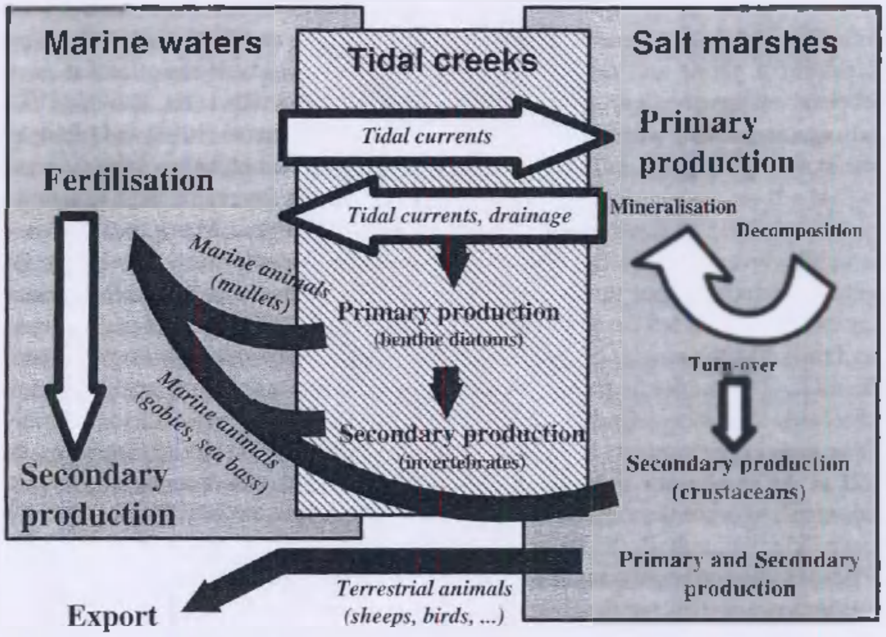

Figure 1. Exchanges of organic matter between saltmarsh and coastal marine water by abiotic and biotic vectors in the bay of Mont Saint-Michel.

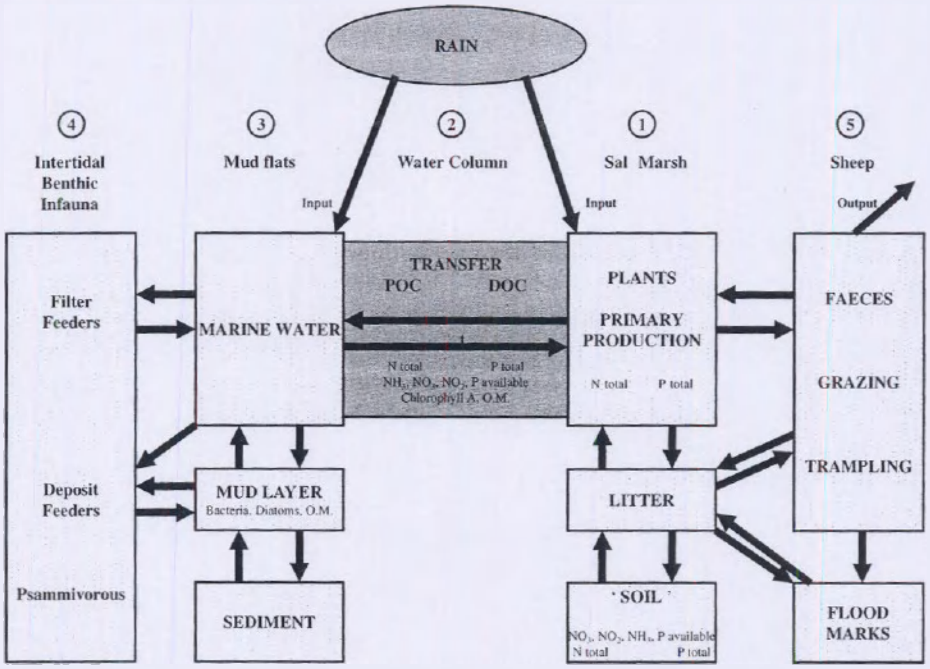

Figure 2. Schematic presentation of the compartment model used to study the saltmarsh functioning and exchanges between salt marsh and coastal marine systems. Example of the bay of Mont Saint-Michel (Lefeuvre et al., 1994).

Transfer between salt marshes and coastal waters

European salt marshes and their creeks are only flooded during spring tides. In the Bay of Mont Saint-Michel, a macrotidal system, the salt marshes and their creeks are flooded, and therefore accessible to fish, during only 40% of the tides, for one to two hours (Troccaz, 1996; Laffaille et al., 1998). During the rest of the time the salt marshes remain unflooded. The runoff water flows to the creeks that transfer organic material and nutrients to the bay (Troccaz, 1996). During spring tides, the flow is bi-directional in the creeks and the OM fluxes due to water flow (during flood and ebb) are balanced. Opposite to this, OM is exported by crustaceans and mainly by fish that feed in the marsh during the short time of flood. This OM is transferred to coastal waters in three different ways: (1) gross output corresponding to ingested OM; (2) net output due to excreted OM (non assimilated); and (3) potential output of assimilated OM transformed into body weight and metabolism.

Labourg et al. (1985) studied the fish community in a salt marsh of the Bay of Arcachon (Western France). It was colonised by juvenile transient species, mainly limnivorous grazers (Mugilids) and predators (*Dicentrarchus labrax* and *Sparus aurata*). At ebb, the fish remain in pools or tidal creeks. Despite high densities, these young fish grew rapidly thanks to the high primary productivity. At each tide, part of the population is renewed, and older stages invade the marshes to graze. Labourg et al. (1985) suggested that fish were responsible for the transfer of OM but without quantifying the amounts.

The role played by fish communities in OM output from salt marshes to adjacent waters was quantified in a part of Mont Saint-Michel bay and compared with fluxes of nutrients, particulate and dissolved OM (Laffaille et al., 1998). Among the 90 species present in the Bay of Mont Saint-Michel (Legendre, 1984; Feunteun and Laffaille, 1997), about one-third invade the saltmarsh at flood. When fish entered the marsh, more than 90% of the digestive tracts were empty, but when leaving the creek during ebb, almost 100% of the tracts contained ingested food. Thus fish export an important amount of OM: 7% of the body weight (FW) in mullets, 4.5% in gobies (*Pomatoschistus* spp) and 10% in sea bass. In mullets, benthic diatoms dominated the stomach content in 24% of cases. Predators, such as gobies and sea bass, mainly fed on crustaceans such as *Orchestia gammarellus* (Laffaille et al., 1998). These differences have to be taken into account when calculating energy budgets. In 1996, fish communities were responsible for the export of about 12.5 kg, of which about 8 kg by mullets, of particulate OM DW y^{-1} ha^{-1} from salt marshes to coastal waters of Mont Saint-Michel bay (Laffaille et al., loc. cit.). However, strong variations of OM export occur. For instance, in 1997, over 12 kg ha^{-1} DW of particulate OM was exported by mullets alone. Furthermore, the first data collected suggest that pioneer salt marshes are more intensively exploited by fish than mature ones. Fish communities of salt marshes appear to be biotic vectors of OM and may thus play a significant role in the energy budgets of coastal environments.

Starting in the past centuries, and up to the 1930s, many reclamation works have weakened the nursery function and affected the fisheries of many coastal areas (Elie et al., 1990; Feunteun & Laffaille, 1997). Moreover, in many reclaimed marshes, the dominant transient fish communities of the tidal marshes have been replaced by sedentary communities dominated by either freshwater or marine species, e.g., in the Breton Marsh (Feunteun et al., 1992, 1999; Feunteun, 1994). Biotic transfers of OM are only due to migratory species (mainly amphihaline species) during their catadromous and anadromous migrations (Laffaille et al., in press).

Comparison with abiotic vectors

Comparative studies on OM and nutrient fluxes (see Lefeuvre & Dame, 1994) show that most of the transfers are due to abiotic vectors such as tidal currents and runoff. Transfers due to fish communities are therefore quantitatively less important than those are due to abiotic vectors (see above). However, the quality of OM transported by both vectors is very different. In salt marshes abiotic vectors mainly transfer OM in dissolved, particulate and detritic form. Detritic OM has a low energetic value, which is rapidly deposited and mainly used by saprophagous species and decomposers (Nixon, 1980). Particulate OM is incorporated into the food web by primary consumers such as filter feeders (Créach, 1995; Créach et al., 1997; Meziane, 1997). Dissolved OM, however, is used directly by primary producers. Therefore, one can expect that most of the material exported by abiotic vectors is slowly integrated into the food web, assuming a slow turnover. Ingestion by fish accelerates the turnover of OM produced in the salt marshes, because the OM is digested and more directly returned to the coastal waters and finally integrated into the food web. Moreover, grazing by invertebrates is known to accelerate turnover of micro-algae communities (e.g., Colijn & de Jonge, 1984; Le Rouzic et al., 1995) and is, therefore, assumed to increase productivity. Thus, the involvement of fish communities in the functioning of salt marshes must be considered differently than a simple 'outwelling process'.

Conclusion

Tidal movements are thought to control fluxes of nutrients and organic matter (OM) between salt marshes and marine coastal waters. The role of fish as a means of transport for important quantities of OM between salt marshes and marine coastal waters has hardly been investigated. OM transport due to fish communities depends upon fish species and their migration behaviour. Amphihaline fish mainly transport OM as body weight when they migrate. Downstream migrations (smolt, silver eels, juvenile sturgeons and shads, etc.) involve export of OM from inland water systems to the sea, and opposite in upstream migrations (i.e., salmon or shad breeders that die on the spawning grounds). Other species, during their daily migrations also transfer OM as gut content from feeding zones. i.e., salt marshes, to marine coastal environment, where non assimilated food is released as faeces. Transient species, such as mullets, transfer OM both by exporting assimilated OM (growth, body weight), during their seasonal migrations between, coastal, marine and inland water systems, and by released OM (faeces) during their daily displacements between salt marshes and bays.

The approach which, in addition to air, water and soil, also considers organisms as vectors involved in OM fluxes between various environments, is important for a better understanding of the carbon and various nutrient cycling processes through terrestrial and aquatic environments.

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