Comparative analysis of the food webs of two intertidal mudflats during two seasons using inverse modelling: Aiguillon Cove and Brouage Mudflat, France

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Abstract

Inverse analysis was used to model the food webs of two intertidal mudflat ecosystems: Aiguillon Cove (AC) and Brouage Mudflat (BM) (south-western Atlantic coast, France). The aim of the present study is to describe and compare the functioning of these two ecosystems. The method of inverse analysis has been adapted in order to take into account, in a single calculation, two seasons: spring/summer (mid-March to mid-October) and autumn/winter (the rest of the year). Gathering all available data on the two sites, the most important gaps in knowledge were identified with the help of sensitivity analyses: they concerned mainly the exports of material by grazing fish (such as mullet *Liza ramada*), resuspension of microphytobenthos, and fluxes linked to microfauna which is poorly known for the two systems. The two sites presented the same overall type of functioning (net import of detritus, export of living organic material and higher faunal activity during spring/summer). In both ecosystems, primary production was dominated by the microphytobenthic production, of which a great part was exported via water-column advection and biotic vectors (grazing fish), while many secondary producers also used detritus as a food resource. Each system also had its own characteristics, one BM being much more seasonally driven than the other AC. It appeared essential to take the seasons into account, as variations in microphytobenthos production and in meiofauna, macrofauna and biotic vectors led to great differences in the food-web organisation.
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1. Introduction

European intertidal mudflats are considered as one amongst the most biologically productive areas in the world (Mc Lusky, 1989). Along the French Atlantic coast, Aiguillon Cove and Brouage Mudflat are both known for their shellfish culture (Goulletquer and Héral, 1997; Goulletquer and Le Moine, 2002), their role as nursery for juvenile fish within the Bay of Biscay (Le Pape et al., 2003a,b), and feeding ground for shorebirds (Triplet et al., 2001). Each of those two areas is composed mainly of intertidal mudflats (Verger, 1968; Gouleau et al., 2000). The purpose of the present paper is to describe and compare the functioning of these two close intertidal areas, addressing questions about their similarities and differences and about their seasonal dynamics.

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In coastal management, it is necessary to describe holistically the ecosystem functioning (Jørgensen and Müller, 2000a). A good way to gather all the information on an ecosystem's biocenosis and assess the relationships between its various components is to build its food-web model (Winemiller and Polis, 1996). Inverse analysis (Vézina and Platt, 1988) allows complete food-web models to be constructed from ecological data too sparse to allow other means. However, these models generally describe balanced food webs and all temporal variations are erased by an annual average. This is a drawback for European mudflats, which vary seasonally. The wintering season, when migratory shorebirds are the more numerous (Yésou, 1992), is characterised by lower primary production (Cariou-Le Gall and Blanchard, 1995; Blanchard et al., 1997; Guarini et al., 1998) and reduced secondary production (Bachelet, 1982; Essink et al., 1991). One way to represent such seasonal changes is to model separately the mean food web of each season, and then compare the functioning of the two periods (Baird and Ulanowicz, 1989; Donali et al., 1999). The problem of such a method is that the seasons are totally independent one from the other, and it is necessary to allow variation of the different compartments' biomass between the two seasons, even though the system will be at steady-state at the annual scale. Computing one season with a possible imbalance and then using it to constrain the other is not a satisfying solution either, because then, the computation of the first season takes the lead over the second one. It was thus decided to compute both seasons by a simultaneous calculation. Inverse analysis was adapted to take into account two seasons in an annual-balanced model which would include all the current knowledge about the two sites. The classical matrix calculation (Vézina, 1989) was modified by coupling matrices bearing information on the two seasons or general information. This inverse-analysis modelling allows: (1) evaluation of fluxes between the trophic components about which there exists the least information, (2) investigation of whose relationships between the trophic components are dominant and (3) demonstration, with the help of sensitivity analyses, of those components which are needed to improve our knowledge.

These two mudflats have not been previously studied with the same intensity from a species richness point of view (Montaudouin (de) and Sauriau, 2000) and only the trophic food web of the Brouage Mudflat has been modelled by Leguerrier et al. (2003, 2004). We propose here to go further in the comparison of the functioning of both intertidal areas by using more recent data obtained in the field and by improving the modelling method. Aiguillon Cove has never been the subject of a model and has been studied only for a shorter time but much data have been acquired on its population densities and dynamics, from primary producers to top predators.

2. Materials and methods

2.1. Study sites and sampling

Located on the south-western Atlantic coast of France, the Charentais Sounds (Pertuis) are situated between the latitude N 45°50′ and N 46°20′ and the longitude W 1°00′ and W 1°30′ (Fig. 1). The Brouage Mudflat (BM) and the Aiguillon Cove (AC) are protected from the direct ocean influence by Ile d'Oléron and Ile de Ré, respectively, and influenced by estuarine transport through the Charente and Sèvre Niortaise rivers. These extensive mudflats are similar to semi-enclosed macrotidal bays (Verger, 1968) and both of them are important international areas for wintering shorebirds (Joyeux, 2001).

2.1.1. Brouage Mudflat

The Marennes-Oléron Bay is situated between the Oléron Island and the mainland (Fig. 1). It covers 180 km² of which 60 km² are mudflats. The most extensive flat is the Brouage Mudflat (BM), situated in the eastern part of the bay that covers 40 km² (Gouleau et al., 2000). It has a relatively flat
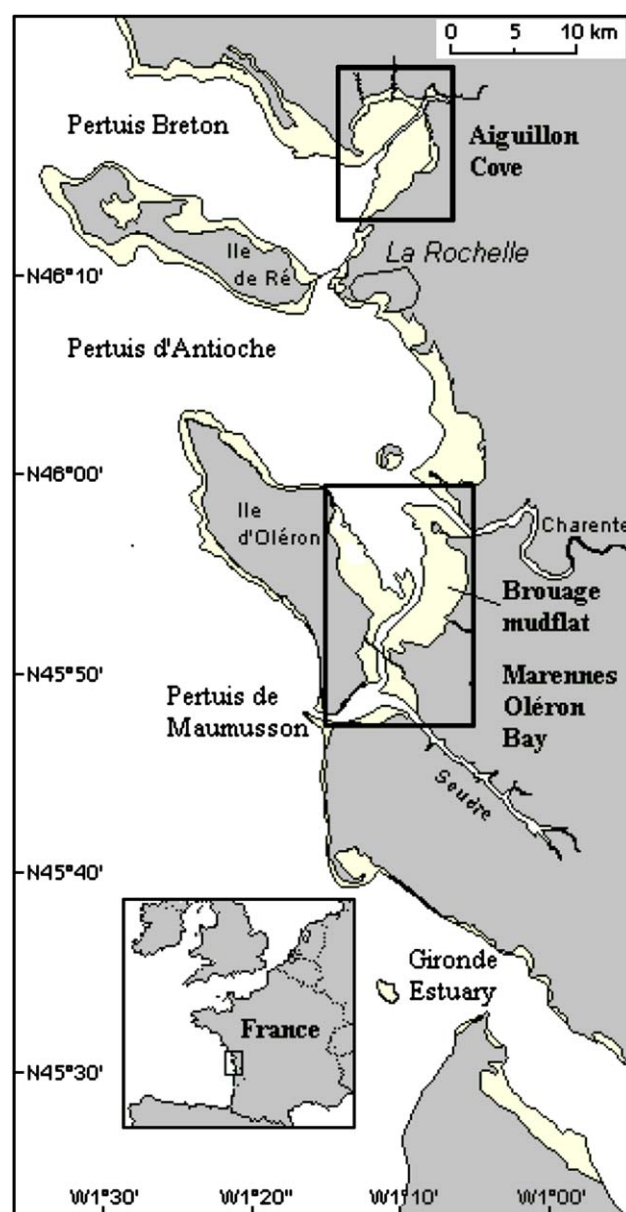

Fig. 1. Map of the Charentais Sounds (Pertuis) showing the location of the two study sites the Aiguillon Cove and the Brouage Mudflat.