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Role of macrofauna on benthic oxygen consumption in sandy sediments of a high-energy tidal beach

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ABSTRACT

Sandy beaches exposed to tide and waves are characterized by low abundance and diversity of benthic macrofauna, because of high-energy conditions. This is the reason why there are few studies on benthic communities living in such highly dynamic environments. It has been shown recently that tidal sandy beaches may act as biogeochemical reactors. Marine organic matter that is supplied in the sand during each flood tide is efficiently mineralized through aerobic respiration. In order to quantify the role of macrofauna in the whole beach benthic respiration, we studied the macrofauna and the pore water oxygen content of an exposed sandy beach (Truc Vert, SW of France) during four seasons in 2011. The results showed that macrofauna was characterised by a low number of species of specialized organisms such as the crustaceans *Eurydice naylori* and *Gastrosaccus* spp. and the polychaetes *Ophelia bicornis* and *Scolelepis squamata*. The distribution and abundance of macrofauna were clearly affected by exposure degree and emersion time. The combined monitoring of benthic macrofauna and pore waters chemistry allowed us to estimate (1) the macrofauna oxygen uptake, calculated with a standard allometric relationship using biomass data, and (2) the total benthic oxygen uptake, calculated from the oxygen deficit measured in pore waters. This revealed that benthic macrofauna respiration represented a variable but low (< 10%) contribution to the total benthic oxygen consumption. This suggests that oxygen was mainly consumed by microbial respiration.

1. Introduction

Sandy beaches dominate exposed coastal zones in temperate and tropical areas (Davies, 1972). They provide habitats for a great variety of species including benthic macrofauna, fish, and birds (McLachlan, 1983; McLachlan and Brown, 2006): their biological functioning and their ecological state are well documented, and particularly the connection with human-induced stressors (Schlacher et al., 2007; Nel et al., 2014; Reyes-Martinez et al., 2015). Beyond the major role played by beach fauna in coastal ecosystems (McLachlan and Brown, 2006), it has been shown recently that tidal sandy beaches may act as biogeochemical reactors (Huettel and Webster, 2001; Anschutz et al., 2009) and can contribute significantly to nutrient fluxes in the coastal zone (Charbonnier et al., 2013).

Dissolved oxygen is the most efficient electron acceptor for organic matter respiration and the oxygen flux between sediment and water is a proxy commonly used for benthic carbon mineralization (Canfield et al., 1993; Glud, 2008). In permeable coastal sediments, wave action, flow characteristics, and bottom topography are continuously changing, inducing a very dynamic distribution of benthic oxygen (Cook et al., 2007). There are still only a very few investigations on benthic O_2 dynamics in such changing environments and it remains a challenge to quantitatively resolve the importance of sandy sediments for marine carbon cycling (Berg et al., 2013).

Fauna-mediated O_2 uptake can be quantitatively significant for the total benthic O_2 uptake in coastal areas (Glud, 2008). Macrofauna metabolism may represent up to 85% of the total oxygen uptake (e.g. Forster and Graf, 1995; Banta et al., 1999; Webb and Eyre, 2004), especially in cohesive sediments. Macrofauna oxygen uptake can also play a role in permeable sediments (Behrens et al., 2007; Huettel et al., 2014). Nevertheless, only a few studies investigated both pore water oxygen dynamics and benthic macrofauna in the intertidal zone of exposed sandy beaches (Jansson, 1967; Dye, 1981), because of the difficulty to study such a dynamic environment and the scarcity of benthic organisms in these

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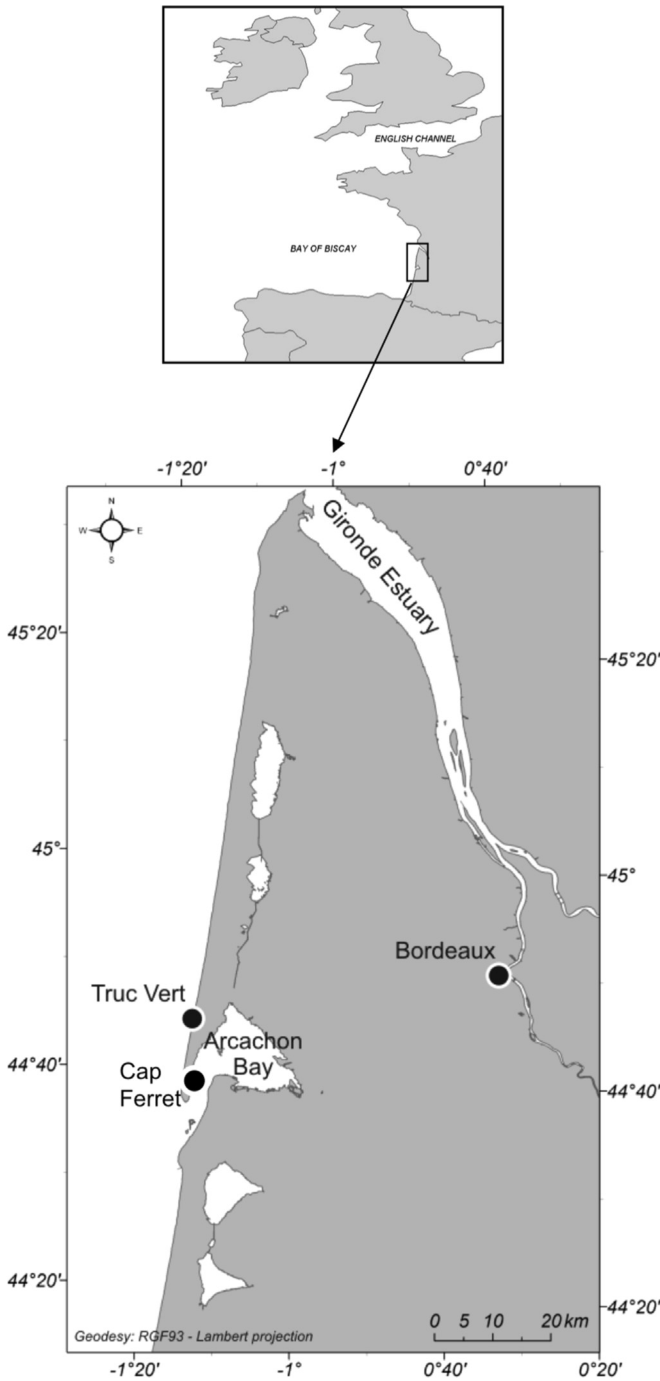

Fig. 1. Location of Truc Vert beach, on the French SW coast.

sediments.

High-energy tidal reflective sandy beaches are exposed to wave breaks that generate a turbulent swash zone. Such an environment generally presents a low biomass of benthic macrofauna, and macrofauna abundance is strongly influenced by physical parameters, especially wave exposure, sediment grain size (Dexter, 1990; McLachlan and Jaramillo, 1995), abrupt changes of sand moisture and temperature during tidal cycles, and strong water and sand movements. On exposed sandy beaches, benthic macrofauna usually consists of a few specialized species adapted to the harsh living conditions of these environments (McLachlan and Brown, 2006).

We present here a joint study of the seasonal evolution of pore water oxygen content and of benthic macrofauna in such an exposed sandy beach characterized by high-energy conditions and an intertidal zone strongly affected by wave breaking (Truc Vert beach, SW France; Fig. 1). Previous studies on this beach showed that considerable oxygen consumption through aerobic respiration took place in the upper saline plume formed by the hydraulic turnover of sea water driven by the tide and swash (Fig. 2) (Anschutz et al., 2009; Charbonnier et al., 2013). Indeed, hydrological models evidenced that sea water penetrated sandy sediments during floods, filling the pore space and bringing dissolved oxygen and marine organic matter in intertidal sediments. Sea water mixed with underlying saline or brackish pore waters and finally, these waters are expelled from the sand and are flushed to the ocean during ebb tide (Robinson et al., 2007; Bakhtyar et al., 2012; Chassagne et al., 2012; Abarca et al., 2013).

In Truc Vert beach, an appropriate monitoring of dissolved O_2 concentration along cross-shore profiles (Charbonnier et al., 2013, 2015) evidenced that waters seeping on the lower beach were depleted in oxygen as a result of benthic aerobic respiration processes (Fig. 2). The estimate of sea water fluxes due to tidal pumping permitted to calculate the annual whole-beach oxygen consumption and the associated nutrient fluxes due to either sea water circulation or terrestrial groundwater seepage (Buquet et al., 2015). These previous studies also revealed that the intensity of aerobic respiration processes mainly evolved at the seasonal scale and that respiration was induced by marine organic matter entering the pore space. However, the mechanisms of this benthic oxygen consumption, including macrofaunal, meiofaunal, and bacterial respiration, and chemical processes, such as oxidation of reduced compounds, still remained to be explored.

We proposed in this study to partially fill this gap by focusing on the role of macrofauna on the whole oxygen respiration. In each season of 2011, macro-organisms were sampled as an accompanying study of the monitoring of pore water chemistry in order to study the role of macrofauna on the total benthic oxygen uptake measured in Truc Vert beach, linking benthic macrofauna structure and pore water oxygenation state. To our knowledge, it was the first time that such a study was performed in a high-energy beach exposed to tide and waves.

2. Materials and methods

2.1. Study site

The Aquitanian coast (SW France) is a 240-km-long straight sandy coastline between the Gironde and the Adour estuaries, and is fringed by high aeolian dunes. This coast displays double bar beaches exposed to high-energy conditions (Castelle et al., 2007). Considered as being representative of the Aquitanian coast, and preserved from human disturbance, Truc Vert beach is located a few kilometres north of Cap Ferret sand spit (Fig. 1).

Sediment consists of medium quartz sand with a mean grain size of 435 μm, a mean $CaCO_3$ content of 1.2 wt%, and a mean organic carbon concentration of only 280 ppm. The porosity is 0.38–0.42 (Charbonnier et al., 2013). The tide is meso-macro-type with an average tidal range of 3.2 m, extending up to 5 m during spring tides. Truc Vert beach is also characterized by the occurrence of high-energy conditions, with a mean wave amplitude of 1.5 m that can reach up to 10 m during winter storms (Butel et al., 2002). These conditions can induce the presence of a ridge and runnel system, which is more or less developed depending on meteorological conditions. The beach morphology can move at a hour to weeks time scale (Michel and Howa, 1999; Castelle et al., 2007). Tidal regime, swell, and meteorology influence the cross-shore topography of the beach and huge sand movements can be observed. At a given position, more than 1 m sand accretion or