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Microorganism dynamics during a rising tide: Disentangling effects of resuspension and mixing with offshore waters above an intertidal mudflat

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ABSTRACT

Resuspension of microphytobenthic biomass that builds up during low tide has been acknowledged as a major driver of the highly productive food web of intertidal mudflats. Yet, little is known about the contribution to pelagic food web of the resuspension of other microorganisms such as viruses, picoeukaryotes, cyanobacteria, bacteria, nanoflagellates, and ciliates, living in biofilms associated with microphytobenthos and surficial sediment. In the present study, a novel approach that involves simultaneous Lagrangian and Eulerian surveys enabled to disentangle the effects of resuspension and mixing with offshore waters on the dynamics of water column microorganisms during a rising tide in the presence of waves. Temporal changes in the concentration of microorganisms present in the water column were recorded along a 3 km cross-shore transect and at a fixed subtidal location. In both surveys, physical and biological processes were separated by comparing the time-evolution of sedimentary particles and microorganism concentrations. During a rising tide, sediment erosion under wave action occurred over the lower and upper parts of the mudflat, where erodibility was highest. Although erosion was expected to enrich the water column with the most abundant benthic microorganisms, such as diatoms, bacteria and viruses, enrichment was only observed for nanoflagellates and ciliates. Grazing probably overwhelmed erosion transfer for diatoms and bacteria, while adsorption on clayed particles may have masked the expected water column enrichment in free viruses due to resuspension. Ciliate enrichment could not be attributed to resuspension as those organisms were absent from the sediment. Wave agitation during the water flow on the mudflat likely dispersed gregarious ciliates over the entire water column. During the rising tide, offshore waters imported more autotrophic, mainly cyanobacteria genus *Synechococcus* sp. than heterotrophic microorganisms, but this import was also heavily grazed. Finally, the water column became a less heterotrophic structure in the subtidal part of the semi-enclosed bay, where mixing with offshore waters occurs (50% decrease), compared to the intertidal mudflat, when resuspension occurs. The present study suggests that this differential evolution resulted predominantly from dilution with offshore waters less rich in heterotrophic microorganisms. Indeed, any input of microorganisms accompanying physical transfers due to bed erosion or offshore water mixing was immediately buffered, probably to the benefit of grazers.

1. Introduction

The productivity of coastal systems, especially intertidal mudflats, and their capacity to enrich adjacent terrestrial and marine zones through trophic pathways (i.e. export by mobile consumers) and hydrodynamic pathways (i.e. waves, wave-generated currents, estuarine currents and tides) is now common knowledge. The biological productivity of intertidal mudflats is due to the intense activity of benthic microorganism communities. During emersion, epipelic diatoms (microphytobenthos, MPB) form a biofilm (up to 20 mg chlorophyll *a* m^2) in the top centimeter layer of a mud surface (Blanchard and Cariou-Le Gall, 1994; Blanchard et al., 1997; Herlory et al., 2004). Prokaryote communities are associated with this biofilm, and bacterial production (secondary production) can be as high or even higher than MPB production (primary production) (Cammen, 1991; Garet, 1996; Van Duyl and Kop, 1994). Bacterial concentration is generally about 10^9 cells per cm^3 in a mudflat (Schmidt et al.,

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1998). Nanoflagellate concentrations range from 100 to several million cells per mL of sediment (Gasol, 1993), with greater concentrations in surficial sediment (Alongi, 1991). Conversely, ciliates are more abundant in fine sand (Epstein, 1997; Fenchel, 1969; Kemp, 1988) compared to muddy sediment enriched with organic matter (Giere, 1993). Viruses are also abundant in marine sediments (Danovaro et al., 2008).

Resuspension of microorganisms living either in the pore water of surficial sediment or attached to surficial sedimentary particles has been reported under tidal currents at subtidal sites (Shimeta et al., 2002). Large tidal currents in macrotidal bays are likely to induce unconsolidated sediment resuspension (Mehta et al., 1989). Yet, resuspension of sediment across intertidal mudflats, where recurrent desiccation promoted sediment consolidation (Anderson and Howell, 1984), generally requires higher shear stress than those induced by tidal current and has been mainly attributed to wave action (Bassoulet et al., 2000; French et al., 2008). However, sediment erodibility thresholds may be significantly reduced (bed friction velocity below 3 cm s^{-1}) due to macrofaunal bioturbation activity (Orvain et al., 2007).

Resuspended microorganisms may greatly affect pelagic and benthic food webs. Resuspended diatoms and autotrophic nanoflagellates may alter phytoplankton community structure, enhance phytoplankton biomass and modify the size structure of primary producers, ultimately modifying microbial food web function (Marquis et al., 2007; Ory et al., 2010). In addition, resuspended heterotrophic cells, such as nanoflagellates, prokaryotes (bacteria and archaea) and viruses, can affect the function of the food web, and favor the microbial loop or the viral shunt (Garstecki et al., 2002; Seymour et al., 2007; Wainwright 1987). Furthermore, some of these resuspended microorganisms may be used as food resources for mesozooplankton and benthic suspension feeders (Carlson et al., 1984), such as oysters (Dupuy et al., 2000) and bivalve mollusks (*Scrobicularia plana*) (Hughes, 1969).

Many studies have investigated the dynamics of the MPB biomass, including resuspension of these microorganisms (Guarini et al., 2008; Lucas et al., 2000; Shimeta et al., 2002). Some studies have qualitatively and quantitatively evaluated the resuspension of other microorganisms present in the intertidal mudflat. Protist and bacteria resuspension thresholds have been quantified at a subtidal coastal site with in situ flumes and sampling of the benthic boundary layer during tidal accelerations (Shimeta and Sisson, 1999; Shimeta et al., 2002). Shimeta et al. (2003) studied the resuspension of benthic protists at subtidal coastal sites with different sediment compositions. Other studies have explored the effects of sediment resuspension on a coastal planktonic microbial food web, either experimentally (Garstecki et al., 2002; Pusceddu et al., 2005; Wu et al., 2007) or in the field (Grémare et al., 2003). However, in field studies, resuspension is often accompanied by other physical processes, such as river flooding and tidal rise, which require adapted sampling strategies to separate the contribution of each process.

In the current study, we applied a novel approach based on two simultaneous Lagrangian and Eulerian field surveys to disentangle the effect of resuspension and mixing with offshore waters on the dynamics of water column microorganisms during a tidal flow. The time-evolution of microorganisms, including viruses, autotrophic protists, heterotrophic protists and prokaryotes present in the water column, was carried out at one fixed location (Eulerian) and one mobile station (Lagrangian) in the Marennes–Oléron bay (French Atlantic coast). In both surveys, physical and biological processes were separated by comparing the time-evolution of suspended sediment particles and microorganism concentrations.

2. Methods

2.1. Study site and sampling strategy

The study was carried out during the afternoon rising tide (tidal amplitude of 3.8 m) in the Bay of Marennes–Oléron (BMO) on 24 July, 2008. Located between the mainland French Atlantic coast and Oléron Island, BMO is a macrotidal bay with a tidal range up to 6 m during spring tides. This macrotidal system is influenced by continental inputs, mainly from the Charente River to the north of the BMO (monthly average discharge was 30 $m^3\ s^{-1}$ in July 2008, slightly less than the median value of 40 $m^3\ s^{-1}$ over the last ten years). The BMO covers 170 km^2, of which 60 km^2 are intertidal mudflats. The Brouage mudflat is >4 km wide, and its sediment consists of silt and clay particles (95% of <63 μm, median grain size d_{50} = 10 μm). Triplicate samples of the first 1 cm layer of sediment were taken at the end of low tide in the upper region of the mudflat (Fig. 1). Only concentrations of bacteria and viruses were assessed in surficial sediment. Two simultaneous field surveys (Lagrangian and Eulerian) were carried out to separate the effect on the dynamics of water column microorganisms of resuspension and mixing with offshore waters during tidal flow. Adopting a Lagrangian strategy avoided transport flux gradients that occur in a Eulerian survey. Such transport flux gradients occur as the water level changes in a Eulerian survey and pelagic concentrations are generally expected to be mixed (diluted or enriched) by offshore waters in proportion to water depth. Conversely, no mixing (especially dilution) is expected in a Lagrangian survey, where the water level remains constant. In both types of surveys, temporal changes in concentrations of a group of organisms, or particulate or dissolved matter that depart from these expectations indicate an imbalance between the many biogeochemical processes that potentially affect this group (Fig. 2). For particulate matter or living low-motility cells, an overall increase in concentration indicates that either benthic resuspension or population growth dominates, whereas a decrease indicates that either sedimentation mediated by sorption on matters or population decay (e.g. grazing) dominates.

Before organizing the field measurements, a 2D barotropic model was used to compute using a backward procedure the trajectory of a drifter reaching the shore in the northern part of the Brouage mudflat (Fig. 1) at the end of the rising tide (Nicolle and Karpytchev, 2007). The model used a high resolution, finite element grid and TELEMAC software to solve the depth integrated equations of Saint Venant (Hervouet, 2007; Hervouet and Van Haren, 1994). The Eulerian subtidal station was located at the origin of the drifter trajectory for the case of a no-wind tidal circulation in the BMO (Fig. 1).

The Lagrangian survey consisted of tracking a submerged buoy following the tidal front during the first 2 h 45 min of the rising tide over the intertidal Brouage mudflat, between 15:45 h and 18:30 h local time (Fig. 1). The tidal front traveled roughly at a speed of 30 cm s^{-1}. Cylindrical drifters (46 cm in diameter and 50 cm in height) were used to track the advancing tidal currents into the BMO. Drifter walls were made of plastic film wrapped around a thin metal rod armature and a 10 cm plastic spherical buoy was fixed on its top. The drifter was completely immersed to be directed by surface currents and the buoyant sphere which emerged from water was used to keep track of the drifter position. The drifter was tracked using a flatboat which engine was stopped and left drifting for at least 5 min before sampling in order to avoid bottom resuspension artifacts. Water samples were obtained at five different stations along the 3 km cross-shore transect (Fig. 1) on 24 July, 2008. Due to rapid drifting when the engine was stopped before sampling, the first Lagrangian station was already located 100 m away from the Eulerian station. Water depth varied little during the Lagrangian survey, ranging from 40 to 70 cm. One sample was collected in the middle of the water column at each station using a 1 L plastic bottle attached to a graduated stick. Short wave agitation combined with limited water depth during the Lagrangian survey did not allow sampling with an open-ended Nisking bottle, so a smaller closed-bottom bottle was used. However, sampling bias due to accumulation of settling particles in a closed-bottom bottle was reduced by a fast sampling lasting less than a few seconds and by introducing the bottle upside down. Since wavelength was greater than water depth,