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ECOSYSTEM ENGINEERING IN MARINE BENTHOS BY THE LUGWORM *ARENICOLA MARINA*: SHIFTING FROM DIFFUSIVE TO PERMEABLE SEDIMENT CHARACTERISTICS

Intertidal sands are highly active systems where organic material is degraded and nutrients are released into the overlying water. Sediment permeability is an important factor influencing exchange rates between the overlying water and the sediment. In permeable sediments, rates of organic matter degradation can be enhanced by advection, driven by waves, currents and the sediment surface topography. Processes in impermeable sediments, like intertidal mudflats, are often limited by molecular diffusion.

In this study, the influence of benthic macrofauna on the sediment was assessed by comparing an intertidal sandflat with high abundance of the lugworm *Arenicola marina* and a 400 m² sandflat where lugworms were removed experimentally two years before the present study. Former lugworm exclusion experiments on a smaller scale showed that large scale exclusion is necessary to reveal the full spectrum of potential effects due to lateral transport of surface sediment. In a multidisciplinary approach sediment properties (grain size, organic content, permeability, porosity, chlorophyll content), oxygen and sulphide dynamics (using a microsensor lander, a planar oxygen optode system and chamber incubation experiments), bacterial density and porewater nutrients were analysed.

Absence of *Arenicola marina* strongly decreased the permeability of the sediment (approx. 7-fold, from 2.2×10^{-12} to $0.35 \times 10^{-12} \text{m}^2$). A higher content of fine particles (<63µm) in the upper 5 cm and a higher organic content incorporated in the sand matrix and clogging the pore water space may be the main factors responsible for this observation. Additionally, higher microphytobenthos biomass in the *Arenicola*-free sediments may stabilize sediments and accumulate fine particles. Under calm conditions, both sites exhibited similar *in situ* oxygen penetration depths (5-10mm) and oxygen consumption rates (OCR) ($3\text{-}9 \text{mmol.m}^{-2}.\text{h}^{-1}$). However, when exposing sediment to different water pressures experimentally, oxygen could penetrate significantly deeper in the bioturbated site, suggesting that the areal OCR could increase significantly under more dynamic conditions (e.g. a storm). While low nutrients concentrations (NH_4 , PO_4 , SiO_2) in the *Arenicola* sediments indicate rapid flushing, nutrients are accumulating in the absence of the worm. Highest microbial density could be found in the exclusion area. The density of bacteria in the subsurface sediment was twofold in the lugworm exclusion area compared with the lugworm tidal flat. Sulphide concentrations were measured only on the exclusion area below 7 cm.

The experiment suggests that the lugworm influences the sediment by facilitating an efficient exchange of oxygen and nutrients between the sediment and the overlying water. This is done directly by pumping oxygenated water into its burrows, but also, and perhaps more importantly, indirectly by maintaining higher permeability of the sediment, thus shifting the sediment from diffusion-dominated towards a more advective one.