Spatial and seasonal variability in ecosystem processes: quantifying the contribution of macrofauna to particle mixing and burrow ventilation in estuarine soft sediments

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This study quantified the relative importance of macrobenthic species population properties in mediating particle reworking and burrow ventilation activities present across the spatial and temporal gradients in the Schelde estuary. More specifically, 9 sites with varying sediment types and contrasting macrobenthic compositions were selected along the salinity gradient, for the quantification of different biogenic mixing processes (biodiffusive, bioadvective and regeneration) and bio-irrigation and identification of the relative contributions from the dominant macrofauna species.

Spatial and temporal variability in benthos activities were prevalent with generally low irrigation and particle mixing rates in the subtidal ecotopes. Bioturbation rates were generally highest in the low dynamic intertidal ecotopes, except for the polyhaline region where highest rates were found in the high dynamic intertidal ecotope in most seasons. Bio-irrigation peaked at high dynamic intertidal locations with maximal rates in wintertime in the polyhaline region. PERMANOVA analysis demonstrated most of the variability at spatial scale, as indicated by the significant interaction between the factors salinity and habitat (P=0.001). Significant salinity level by habitat interaction was detected in bioturbation and bio-irrigation, indicating that the effect of sediment types tended to vary along salinity gradient.

When multiple-linear regression model was run over seasonal cycle, the range of explained variation in bioturbation was from 22.3% to 81.2% and in bio-irrigation was from 21% to 90.7%. The best distance-based linear model explained 66.1% of total spatio-temporal variation of both bioturbation and bio-irrigation, yielding the same most important drivers as in the seasonal models: *Hediste diversicolor*, *Corophium arenarium*, *Bathyporeia pilosa*, Elonga and *Oligochaeta*.

The classification scheme of the integrated benthos activity at community level was assessed by principle component analysis, based on a wide array of measured variables for particle reworking and burrow ventilation, revealing the potential bioturbation-bio-irrigation link, thus the dual-identity of keystone species. It well described the total dataset (R2=77.8%) by four characterized principle components (PCs), which separated the fauna into different groups: the bulk quantity of particles that are relocated over time (PC1), the vertical distance particles are displaced (PC2), biodiffusion-enhanced bioirrigation (PC3) and bioadvection-enhanced bio-irrigation (PC4). The bioturbation-bio-irrigation linkage was revealed by PC 3 and PC 4, PC 3 showed the dual status of *Oligochaeta* and *Macoma balthica* as biodiffusor- bioirrigator, and PC 4 revealed the identity of *Hediste diversicolor* as dominant bioirrigator which generate bioadvection, and they perform reworking and ventilation simultaneously.

Keywords: macrobenthos; bioturbation; bio irrigation; Schelde estuary