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Hydrodynamic conditioning of diversity and functional traits in subtidal estuarine macrozoobenthic communities

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ABSTRACT

Variations in abundance and diversity of estuarine benthic macrofauna are typically described along the salinity gradient. The influence of gradients in water depth, hydrodynamic energy and sediment properties are less well known. We studied how these variables influence the distribution of subtidal macrofauna in the polyhaline zone of a temperate estuary (Westerschelde, SW Netherlands). Macrofauna density, biomass and species richness, combined in a so-called ecological richness, decreased with current velocities and median grain-size and increased with organic carbon of the sediment, in total explaining 39% of the variation. The macrofauna community composition was less well explained by the three environmental variables (approx. 12–15% in total, with current velocity explaining approx. 8%). Salinity, water depth and distance to the intertidal zone had a very limited effect on both ecological richness and the macrofauna community. The proportion of (surface) deposit feeders (including opportunistic species), decreased relative to that of omnivores and carnivores with increasing current velocity and sediment grain-size. In parallel, the proportion of burrowing sessile benthic species decreased relative to that of mobile benthic species that are able to swim. Correspondingly, spatial variations in hydrodynamics yielded distinct hotspots and coldspots in ecological richness. The findings highlight the importance of local hydrodynamic conditions for estuarine restoration and conservation. The study provides a tool based on a hydrodynamic model to assess and predict ecological richness in estuaries.

1. Introduction

Estuaries rank among the most productive natural ecosystems on earth (Costanza et al., 1997). They are generally characterized by a relatively limited number of species that are well adapted to cope with stress, but with abundant populations (Snelgrove and Butman, 1994; Elliott and Quintino, 2007). However, species do not contribute equally to ecosystem processes and services (Stuart-Smith et al., 2013). Their contribution depends on their biological traits, such as their feeding habit and behaviour (Bremner et al., 2006; Kristensen et al., 2014). Understanding spatial patterns in the communities, as well as their functional traits is essential for management and conservation measures in estuaries.

Variation in the spatial distribution of benthic macrofauna in estuaries has been described as a function of biotic and abiotic variables. Particularly, salinity has been identified as an important driver of large-scale distribution patterns (Ysebaert et al., 2003; Giberto et al., 2004; Bremner et al., 2006; van der Linden et al., 2012; Dutertre et al., 2013). An early work by Remane (1934) showed that species richness was minimal at salinities of 5–7, and increased at higher salinities in the Baltic Sea. More recent work in the Baltic Sea demonstrated that these trends were accompagnied by changes in abundance, diversity and functional composition of benthic assemblages (Darr et al., 2014b). The distribution of invertebrates along the salinity gradient in estuaries is

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further regulated by tidal variation and salinity fluctuations (Attrill, 2002; Whitfield et al., 2012; van der Linden et al., 2012). Statzner and Higler (1986) proposed to include flow as a driver for the zonation of benthos along the salinity gradient. Moreover, large local gradients in water depth and emersion duration, hydrodynamic energy, grain-size and mud content of the sediment may be present in estuaries, particularly in the intertidal zone. In the intertidal zone, these factors have been shown to drive changes in macrofauna community characteristics (Gray, 1974; Ysebaert and Herman, 2002; Ellis et al., 2006; van der Wal et al., 2008; van Colen et al., 2010; Compton et al., 2013; Robertson et al., 2015; Cozzoli et al., 2017).

Few studies have dealt with the gradient from intertidal to subtidal zones, in part due to sampling constraints (Heip et al., 1995; Ysebaert and Herman, 2002). In particular, the often narrow transition zone between the intertidal area and deeper channels is undersampled and understudied. This shallow subtidal zone is of considerable conservation and management interest as it is a potential disposal area for dredged material from navigation channels (where the dredged sediment is kept close to the source, while avoiding disposal on the more productive tidal flats). Ysebaert et al. (2003) found a clear decrease in macrozoobenthic biomass, density and diversity from the intertidal zone to the shallow subtidal zone of the Westerschelde estuary (southwest Netherlands). However, it is not clear whether this response is driven by depth sensu stricto, or by variables typically co-varying with depth (Lambert et al., 2011). Some potential influential variables could be proximity to tidal flats (benefiting from dispersal of animals or food supply from the richer adjacent intertidal flats), hydrodynamic forces and/or sediment grain-size.

Hydrological disturbance can impose strong selection forces on the biota (Rosenberg, 1995; Lytle and Poff, 2004; Hershkovitz and Gasith, 2013). Elliott and Whitfield (2011) argue that such strong selection applies to the estuary as a whole, and that hydrodynamics may therefore not pose a stress to the species adapted to such dynamic systems. Warwick and Uncles (1980) stated that hydrodynamics may impose a direct physical stress on infaunal communities. In addition, hydrodynamics may influence the food supply for benthic organisms (e.g., Riisgard et al., 2007), may regulate top-down control (i.e., Leonard et al., 1998) and may also regulate transport of (larval or juvenile) fauna (e.g., Snelgrove and Butman, 1994; Haase et al., 2012). We hypothesize that in areas with high current velocities, mobile macrofauna is best adapted.

Tidal currents generally increase with water depth, while wave stress that reaches the bottom may be highest in the transition zone between the subtidal and lower intertidal area. Tidal currents and wave stress influence near-bed flow conditions for erosion, settling and deposition of sediments and hence the nature of the bottom substrate, including stability, sediment grain-size, organic matter, pore-water chemistry, and microbial content, with consequences for macrofauna (Wildish and Kristmanson, 1979; Snelgrove and Butman, 1994; Schaffner et al., 2001; Dolbeth et al., 2009).

Low current velocities facilitate the deposition of fine particles and organic material (Pearson and Rosenberg, 1978). With limited oxygenation (for example in deeper systems with stratification) this can yield anaerobic conditions in the sediment (e.g., Dauer et al., 2008). In areas with such large amounts of fine particles and organic material, only a few shallow living species can persist, but typically in high densities (Pearson and Rosenberg, 1978). In contrast, in more sandy sediments with little organic material, many species may co-exist, but often in much lower densities, and these species can also rework the sediment to considerable depths. A number of studies have classified the species of macrofauna in ecological groups, that are typical for a certain state of organic enrichment or disturbance (Pearson and Rosenberg, 1978; Borja et al., 2000; Robertson et al., 2015), although many of these studies were done in the context of pollution, rather than natural variations in disturbance or organic matter and sediment grain-size. We expect that the ecological group best adapted to organic enrichment is dominating fine, organic sediments (Pearson and Rosenberg, 1978; Robertson et al., 2015), but is also likely to be associated with lower current velocities.

As water depth, distance from tidal flats, hydrodynamic energy, and sediment grain-size vary locally in an estuary, depending on the configuration of tidal flats, shoals and channels, a patchy and heterogeneous distribution of macrofauna community characteristics may be expected, superimposed on gradual patterns of longitudinal variations in salinity, wave stress and tidal range. At a local scale, areas with relatively high abundance, species diversity or functional diversity may occur, even in estuaries that are typically characterized by relatively few species. Such local areas may be referred to as hotspots. Thus, in this paper, the term hotspot is loosely used as an area with a *relatively* rich macrofauna community, not to be confused with the term hotspot sensu Myers et al. (2000), used strictly for threathened biogeographic regions of extreme endemic biodiversity. Attrill et al. (1996) identified a local (relative) hotspot in the Thames estuary with over 200 invertebrate species in a heterogeneous subtidal substrate. Darr et al. (2014a) identified a number of hotspots of high bivalve biomass in the Baltic Sea, each related to specific environmental conditions. This suggests the potential importance of specific areas for estuarine functioning, e.g., for providing a habitat for macrofauna and fish, and more generally for increasing the health and resilience of the estuary. Their relevance for ecosystem functioning may likely depend on both the extent of the local hotspot and the magnitude and nature of biodiversity in macrofanua in the hotspot area.

We conducted a benthic survey targeting the shallow subtidal zone of the Westerschelde estuary (southwest Netherlands) to quantify the relationships between macrofauna and environmental variables using a spatially explicit approach. We aimed to establish (1) what environmental variables best explained the variation in density, biomass, richness, community composition and functional traits of macrofauna, and (2) whether this resulted in localised hotspots and coldspots or in gradients in ecological richness, within the estuary. We discuss how the results can be used to predict ecological richness within shallow waters.

2. Material and methods

2.1. Study area

The Westerschelde is a funnel-shaped estuary in the southwest of the Netherlands (Fig. 1), with ebb and flood channels surrounding intertidal flats. The estuary experiences a semi-diurnal tide, with a mean tidal range of 3.8 m at the mouth, and 5m at the Dutch-Belgian border (Eleveld et al., 2014). The estuary is turbid, well-mixed and river discharge is low, approx. 100 $m^3 s^{-1}$ (De Vriend et al., 2011; Eleveld et al., 2014).

The estuary provides entrance to a number of ports; the main navigation channel is subject to continuous maintenance dredging and occasional capital dredging. Dredged sediment is disposed at designated locations in secondary channels, in the deeper parts of the navigation channel and in the shallow subtidal zone adjacent to the tidal. The latter is aimed to reduce current velocities near the tidal flats and to enhance sediment transport towards the tidal flats, in order to sustain the ecologically productive multiple channel system and expand ecologically valuable habitat (Plancke et al., 2014). The Westerschelde is also part of the EU Natura 2000 network that is aimed to ensure the long-term survival of Europe's most valuable and threatened species and habitats.