



## Habitat modification drives benthic trophic diversity in an intertidal soft-bottom ecosystem



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### ABSTRACT

In intertidal soft-bottom ecosystems, ecosystem engineers such as reef-building bivalves, can strongly affect the associated benthic community by providing structure and stabilizing the sediment. Although several engineering species have declined dramatically in the past centuries, the consequences of their loss for the trophic structure of intertidal benthic communities remain largely unclear. In this study, we experimentally test the hypothesis that above- and belowground habitat modifications by ecosystem engineers, facilitate distinctly different, but trophically more diverse benthic communities, using intertidal mussel and tube worm beds as model systems. We constructed a large-scale experiment at two intertidal mudflats in the Dutch Wadden Sea, with distinctly different environmental conditions. At both sites, we applied anti-erosion mats to simulate belowground structure and sediment stabilization by commonly found tube worm beds and crossed this with the addition of adult mussels to investigate effects of aboveground structure. The anti-erosion mats mainly enhanced species and trophic diversity (i.e., feeding guild richness and diversity) of the infaunal community, while the addition of mussels primarily enhanced species and trophic diversity of the epifaunal community, irrespective of location. The effect size of mussel addition was larger at the exposed site in the western Wadden Sea compared to the more sheltered eastern site, probably due to relatively stronger abiotic stress alleviation. We conclude that structure-providing and sediment-stabilizing species such as reef-building bivalves and tube worms, form the foundation for trophically diverse benthic communities. In intertidal soft-bottom ecosystems like the Wadden Sea, their conservation and restoration are therefore critical for overall ecosystem functioning.

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### 1. Introduction

Coastal ecosystems are of great importance to a multitude of marine species and provide crucial services to human society (Barbier et al., 2011; Beck et al., 2001; Costanza et al., 1997; Hodgson and Liebler, 2002). Ecosystem engineers, species that strongly modify their environment, such as reef-building bivalves, seagrasses and corals (Jones et al., 1994, 1997), typically play an important role within these ecosystems, because they diversify the landscape by forming complex structures and relieve environmental stress, for instance by attenuating currents and waves (Donadi et al., 2013a; Gutierrez et al., 2003; Koch et al., 2009). Due to these habitat modifications, ecosystem engineers

typically not only facilitate themselves (Donadi et al., 2014; Rietkerk et al., 2004; van de Koppel et al., 2005; van der Heide et al., 2007), but also provide a key-habitat for a wide variety of species that depend on them for settlement, refuge or food supply (e.g., Donadi et al., 2013b; Gutierrez et al., 2003; Nagelkerken et al., 2000; van der Heide et al., 2012; van der Zee et al., 2012).

Over the last decades, ecosystem engineer-dominated coastal ecosystems have become severely degraded worldwide, often due to anthropogenic impacts (Barbier et al., 2008; Lotze et al., 2006; van Gils et al., 2006; Waycott et al., 2009). Moreover, natural recovery of ecosystem engineers is typically slow, unpredictable or absent due to strong internal positive feedbacks, and even active restoration has proven difficult (Eriksson et al., 2010; Jackson et al., 2001; Schulte et al., 2009; van der Heide et al., 2007). The loss of ecosystem engineers and their lack of recovery often have dramatic implications for many associated species, especially in soft-bottom ecosystems, where solid substrate and

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aboveground structure are almost exclusively provided by engineering species such as seagrass, tube worms, mussel and oyster beds (Eriksson et al., 2010; Hodgson and Liebler, 2002; Lotze, 2005; Waycott et al., 2009). Although the importance of engineering species for overall biodiversity has been well established, there is little experimental evidence showing how ecosystem engineers affect the trophic structure (i.e., feeding guild richness and diversity) of the benthic community in intertidal soft-bottom ecosystems.

In this study, we empirically test the hypothesis that habitat modification by epi- and endobenthic habitat modifying species facilitates distinctly different, but trophically more diverse intertidal benthic communities, using intertidal mussel and tube worm beds as model systems. In the Dutch part of the Wadden Sea, one of the world's largest intertidal ecosystems (Compton et al., 2013; Wolff, 1983), intertidal mussels – ecosystem engineers that create hard substrate, reduce hydrodynamic stress, modify sediment conditions and increase the cohesiveness of the substrata (Donadi et al., 2013a; Gutierrez et al., 2003; Kröncke, 1996; Widdows and Brinsley, 2002) – covered an area of over 4000 ha at the end of the 1970s. In the beginning of the 1990s, however, intertidal mussel beds disappeared completely due to a combination of overfishing, storms and several years of recruitment failure (Beukema and Cadée, 1996; Dijkema, 1991). In addition to the direct physical removal of mussels, sand extraction and bottom trawling for shrimps (*Crangon crangon*) and edible cockles (*Cerastoderma edule*) also removed sediment-stabilizing species and resuspended the upper layer of the sediment (Kraan et al., 2007; Piersma et al., 2001; e.g., Riesen and Reise, 1982; van der veer et al., 1985). Despite a ban on mechanical dredging for intertidal mussels (1999) and cockles (2005), it took more than a decade for mussels to start to re-establish and even now their recovery is still mainly restricted to the eastern part of the Dutch Wadden Sea (Ens et al., 2009; Goudswaard et al., 2009).

To test our hypotheses, we constructed a large-scale experiment, in which we used the application of anti-erosion mats with the addition of adult mussels to test for the effects of above and belowground habitat modification by ecosystem engineers. We applied anti-erosion mats to simulate belowground structure and sediment stabilization by commonly found tube worm beds (Friedrichs et al., 2000; Volkenborn et al., 2009) and crossed this with the addition of adult mussels to

investigate effects of aboveground structure. To investigate whether the treatment effects were consistent across our study system, the experiment was carried out at two different sites with distinctly different conditions and ambient benthic communities (Compton et al., 2013). The first site was located in the western part of the Dutch Wadden Sea, south of the island Terschelling, and the second was situated in the eastern part of the Dutch Wadden Sea, south of the island Schiermonnikoog (Fig. 1). After three months, we investigated treatment effects on the invertebrate community.

## 2. Methods

### 2.1. Study area

Large-scale experimental plots were established on the intertidal mudflats of two barrier islands in the Dutch Wadden Sea. The first site was located in the western part, south of the island of Terschelling (53°21'39.69"N, 5°18'29.18"E) and the second site was located in the eastern part, south of the island of Schiermonnikoog (53°28'3.43"N, 6°14'13.40"E) (Fig. 1). The site at Terschelling has a small tidal range (~0.9 m, based on mean high water levels), is exposed to waves from the southwest, and is typified by relatively clear water and sandy sediment (Table 1). The site at Schiermonnikoog has a somewhat larger tidal range (~1.2 m, based on mean high water levels), is situated in more sheltered conditions, and is characterized by very turbid water and more silty sediments (Table 1). Both sites were located at approximately the same tidal elevation (0.6 to 0.8 m below mean water level), which is similar to the elevation of natural intertidal mussel and oyster beds in the vicinity of the experimental plots (distance: ~1000–2000 m).

### 2.2. Experimental design

At each site, 12 plots of 20 × 20 m were established in a line parallel to the gully (distance from the gully ~100–150 m) and with a distance of ~20 m between plots. Plots were divided over three blocks. Within each block, we randomly assigned one replicate of each of the following treatments to the plots: (1) control, which represents the ambient bare sediment surface at each site, (2) addition of a coco-coir mat on the bare

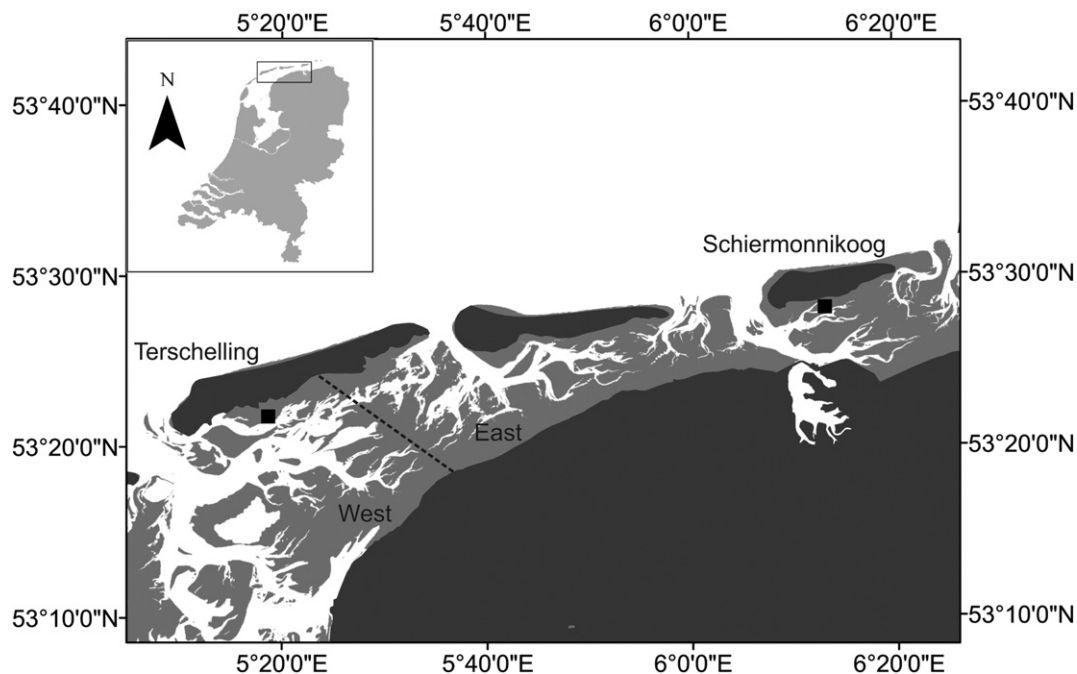


Fig. 1. Map with locations of the experimental plots in the western Dutch Wadden Sea at Terschelling and in the eastern Dutch Wadden Sea at Schiermonnikoog (black squares). White areas represent water, intermediate gray areas represent tidal flats exposed during low tide and land is represented by dark gray.

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