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Adaptation of benthic invertebrates to food sources along marine-terrestrial boundaries as indicated by carbon and nitrogen stable isotopes

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ABSTRACT

Frequent environmental changes and abiotic gradients of the Wadden Sea require appropriate adaptations of the local organisms and make it suitable for investigations on functional structure of macrozoobenthic communities from marine to terrestrial boundaries. To investigate community patterns and food use of the macrozoobenthos, a transect of 11 stations was sampled for species number, abundance and stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of macrozoobenthos and for stable isotope values of potential food resources. The transect was located in the back-barrier system of the island of Spiekeroog (southern North Sea, Germany). Our results show that surface and subsurface deposit feeders, such as *Peringia ulvae* and different oligochaete species, dominated the community, which was poor in species, while species present at the transect stations reached high abundance. The only exception was the upper salt marsh with low abundances but higher species richness because of the presence of specialized semi-terrestrial and terrestrial taxa. The macrozoobenthos relied predominantly on marine resources irrespective of the locality in the intertidal zone, although $\delta^{13}C$ values of the consumers decreased from -14.1 ± 1.6‰ (tidal flats) to -21.5 ± 2.4‰ (salt marsh). However, the ubiquitous polychaete *Hediste diversicolor* showed a $\delta^{15}N$ enrichment of 2.8‰ (an increase of about one trophic level) from bare sediments to the first vegetated transect station, presumably due to switching from suspension or deposit feeding to predation on smaller invertebrates. Hence, we conclude that changes in feeding mode represent an important mechanism of adaptation to different Wadden Sea habitats.

1. Introduction

The Wadden Sea ecosystem of the southern North Sea is one of the world's largest intertidal regions and represents a transition zone between marine and terrestrial boundaries (Dittmann and Grimm, 1999). This environment is subjected to semidiurnal tides, creating highly dynamic conditions with regard to hydrography, morphology and sedimentology (Hild, 1999). Intertidal soft-bottom shores are often associated with salt marshes that cover large parts of higher altitudes of the mainland coasts and back-barrier systems of the barrier islands (Dijkema, 1991; Eggers, 2006).

Within these sheltered shores, substratum differs greatly, showing vertical zonation from bare tidal flats with microbial mats, to coverage with macroalgae patches, to salt marshes vegetated by halophytes close to the mean high-water level. Thus, there is a shift from marine to terrestrial resources depending on shore height. Varying food availability and formation of microhabitats provide different niches for the intertidal benthic fauna resulting in a distinct community structure from the tidal flats to the salt marsh zones (Vöge et al., 2008).

In particular, marine macrozoobenthos is very abundant and represents an important link between sedimentary organic matter and higher trophic levels, such as fishes and birds (Doi et al., 2005; Kurata et al., 2001). Furthermore, it has a strong impact on intertidal areas because it determines sediment structure through its bioturbation (Birchenough et al., 2012; Braeckman et al., 2014; Lohrer et al., 2004; Queirós et al., 2013). It limits the biomass of primary producers, especially microphytobenthos, and promotes nutrient cycling (Doi et al., 2005; Galván et al., 2008; Kang et al., 2003).

Macrobenthic consumers comprise different feeding types using diverse food resources (Dubois et al., 2014), including surface and

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subsurface deposit feeding as well as suspension feeding. However, the diet of marine invertebrates can change in space (Galván et al., 2008) and many benthic invertebrates are not restricted to only one feeding type (Fauchald and Jumars, 1979; Jumars et al., 2015; Ólafsson, 1986; Reise, 1978). This enables them to deal with changing environmental factors by adapting their feeding mode according to resource availability.

For instance, the common ragworm *Hediste diversicolor* is an omnivorous polychaete, acting as a facultative suspension feeder (Fauchald and Jumars, 1979; Scaps, 2002), deposit feeder, scavenger and active predator (Reise, 1978). The species is able to settle in non-vegetated and vegetated habitats, where it uses various food resources and even changes its trophic level, an effect detected for two different habitats, where *H. diversicolor* rises one trophic position in the eelgrass meadow compared to bare sediments (Rossi et al., 2015). Because not all taxonomic groups are capable of opportunistic feeding, mud content as well as total organic carbon content (TOC), and chlorophyll *a* content alter the composition of benthic communities (Schückel et al., 2013).

To date, studies on benthic Wadden Sea communities considered structuring factors focused on eutrophication, climate change and species interactions (Beukema, 1991; Reise, 1978; Schückel and Kröncke, 2013). Because food supply and trophic interactions play an important role in sea-land transition habitats, other studies aimed at detecting spatial food use and trophic structure of invertebrates in coastal environments (Lautenschlager et al., 2014; Rossi et al., 2015; Schückel et al., 2015; Winter et al., 2017) and terrestrial ecosystems (Albers et al., 2006; Pollierer et al., 2007; Pollierer et al., 2009). However, small-scale variations in trophic niches of macrozoobenthic species across marine-terrestrial boundaries of tidal soft bottoms remain poorly understood.

The δ^{15}N and δ^{13}C stable isotope ratios of animal tissue reflect those of their diet. The δ^{15}N values enable assignment to trophic groups because these values are enriched by about 3 ± 1‰ per trophic level (Martínez del Rio et al., 2009; Minagawa and Wada, 1984; Peterson and Fry, 1987; Vanderklift and Ponsard, 2003). Carbon isotopic composition shows a slight enrichment per trophic level of ≤ 1‰ (DeNiro and Epstein, 1978; Martínez del Rio et al., 2009; Vanderklift and Ponsard, 2003) and is more suited to trace potential food resources of consumers with differing δ^{13}C values, enabling marine inputs, C_4 salt marsh vegetation and terrestrial C_3 plants to be distinguished (Peterson, 1999; Tiunov, 2007).

The present study aims at elucidating changes in the macrozoobenthic community composition and their dietary interrelationships along an intertidal marine-terrestrial gradient. We focused especially on three typical Wadden Sea consumers of different feeding types: the omnivorous polychaete *H. diversicolor*, the surface deposit feeding snail *Peringia ulvae* and the interface feeding bivalve *Limecola balthica*. We hypothesize (1) that the community changes along this gradient because of variations in food availability from the bare tidal flats to the upper salt marsh vegetation, (2) that changing resource use of macrozoobenthic consumers depends on their feeding types, and (3) the occurrence of habitat-related trophic shifts, which might function as a mechanism of adaptation to the tidal back-barrier environment.

2. Material and methods

2.1. Study area

The study was carried out at the barrier island of Spiekeroog (53°45′728″ N, 7°43′367″ E), which is located in the Wadden Sea National Park of Lower Saxony (southern North Sea), Germany (Fig. 1). The morphology of this coastal region is shaped by semidiurnal tides with a tidal amplitude of approximately 2.7 m (Hertweck, 1995) and relatively low current velocities from about 2 to 28 cm s^{-1}. Whereas dunes characterize the northern coast of Spiekeroog, tidal flats prevail in the south that faces the mainland. The sampling transect was located in the sheltered, southern part of Spiekeroog and comprised 11 stations from the tidal flats (53°45′ 38,63,790″ N, 7°43′17,91,206″ E) to the upper salt marsh (53°45′45,61,599″ N, 7°43′20,34,211″ E). Within the transect, inundation times decrease continuously from 5.6 h d^{-1} to 12 min d^{-1} going toward the upper salt marsh.

Sandy sediments (mud content < 10%) and mixed sediments (mud content 10–50%) predominate the tidal flats, which are characterized by marine resources (e.g. marine detritus and microphytobenthos) (Flemming and Davis, 1994; Flemming and Ziegler, 1995). Salt marsh sediments are dominated by mud contents > 70% (Flemming and Davis, 1994) and higher TOC contents compared to unvegetated sediments (Bouillon and Boschker, 2006).

In contrast to the bare tidal flats, the salt marsh site is characterized by three different vegetation zones based on differing shore heights and inundation frequencies and durations (Balke et al., 2016; Bockelmann et al., 2002; Eggers, 2006): the pioneer zone, the lower salt marsh and the upper salt marsh. The pioneer zone is colonized predominantly by halophytic plants such as *Salicornia europaea* and *Spartina anglica*, whereas the lower salt marsh is dominated by *Puccinellia maritima* and *Atriplex portulacoides* and the upper salt marsh by *Elytrigia atherica* (Bakker, 2014).

2.2. Sampling

In September 2014, 11 transect stations were sampled (Fig. 1). Stations 1–3 were located in the tidal flat habitat, stations 4–8 in the transition zone between the tidal flat and the pioneer zone, and stations 9–11 in the three vegetation zones of the salt marsh. To collect the macrozoobenthos, five replicates were taken with a hand corer at each sampling station, each 20 cm in length and 10 cm inner diameter, resulting in a surface area of 0.039 m^2 per station. In the field, cores were placed in 1-L containers and washed through a sieve with a mesh size of 500 μm. Benthic organisms on the mesh were collected and preserved in 70% ethanol.

Potential food resources for the benthic macrofauna were collected close to the transect stations and classified into marine and terrestrial resources. Marine resources comprised detritus/microphytobenthos (containing detritus of marine vascular plants, micro- and macroalgae); macroalgae species including *Fucus vesiculosus*, *Ceramium* spp., *Chaetomorpha linum*, *Rhizoclonium riparium, Ulva lactuca*, and *Ulva intestinalis*; and the C_4 grass *S. anglica* and C_3 halophyte *S. europaea*, which were defined as marine plants by previous authors (Davy et al., 2001; Hacker et al., 2001). Suspended particulate organic matter (sPOM) was not sampled during this study. However, to consider it as a potential marine food resource, we used data from Middelburg and Nieuwenhuize (1998), who investigated a comparable nearby coastal area. Terrestrial resources comprised vascular plants from the three salt marsh vegetation zones, including *E. atherica*, *A. portulacoides*, *P. maritima*, *Triglochin maritima*, *Spergularia salina*, *Suaeda maritima* and *Limonium vulgare* in addition to terrestrial detritus (containing detritus of terrestrial vascular plants) and meiofauna (comprising six Collembola species). Terrestrial detritus and marine detritus/microphytobenthos were sampled carefully with a spatula by scraping: (1) the litter layer for terrestrial detritus from the lower to the upper salt marsh, and (2) the algal mats for marine detritus/microphytobenthos from the tidal flat surface. Fresh vascular plants and macroalgae were sampled by hand. The samples were stored in plastic bags at − 10 °C until further processing. Sediment and soil organic matter (SOM) was also determined as a potential food resource. Samples from the tidal flats and the three salt marsh zones were taken of the surface in horizons (0–5 cm) using a core cutter with a diameter of 7 cm.

To analyze TOC and the mud content (fraction < 63 μm), surface sediment samples (< 2 cm depth) were taken from each transect station and frozen at − 20 °C until measurement.