Living on the edge

van Egmond, E.M.

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Summary

Sandy beaches are among the most prevalent coastal ecosystems in the world, harbouring unique ecological communities and providing many ecosystem functions, including the buffering of wave energy and nutrient cycling. Due to the highly dynamic nature of sandy beaches, the *in situ* primary production is low and the availability of marine exogeneous organic matter, in the form of phytoplankton (intertidal zone) and beach-cast macroalgae (supratidal zone), are highly heterogenous in time and space. The sandy beach food web is, therefore, heavily dependent on this marine exogeneous organic matter and is thus primarily bottom-up controlled. In particular, the macroinvertebrate communities of the intertidal and supratidal zone together form the link between marine primary production and higher trophic levels, via microalgae consumption, wrack decomposition and as food for predators, thereby connecting the marine and terrestrial food webs. The macroinvertebrate community mainly includes polychaete worms, amphipods, isopods and insects, which reside either a few centimetres in the sand or in piles of beach-cast macroalgae (termed wrack). A relatively clear separation between the intertidal and supratidal zone exists on sandy beaches. Twice a day, intertidal sands alternate between being either dry or saturated by sea water due to the lunar tidal cycle. Macroinvertebrate species living in the intertidal zone are well adapted to this dynamic environment. This is reflected by most species being filter or deposit feeders that catch organic particles floating in the water column or laying on the bottom. In contrast to the intertidal zone, the supratidal zone is very rarely submerged by the sea during the tidal cycle, as it is located between the high water line and the dune foot, and the sand remains dry for a large part of the time. Wrack is important for supratidal invertebrates by serving both as a source of food and refuge (e.g. protection from desiccation and predation by birds). However, it remains unclear how resource availability influences species interactions and community assembly of the macroinvertebrate community on sandy beaches, and how this influences ecosystem functioning.

While of critical ecological importance, sandy beach ecosystems are globally under threat. Due to coastal squeeze, sandy beaches are trapped between the rising sea level and an increase in storm events due to climate change on the sea side on the one hand, and static anthropogenic structures on the land side on the other hand. On a global scale, the coastal zone, including sandy beaches, is usually densely populated by humans and coastal populations are only expected to further increase. This combination of factors causes severe erosion of the sandy beach, threatening the human population and livelihood as the sea advances inland, leaving only a narrow strip of beach for ecological communities to reside. To mitigate the effects of erosion, sand nourishment has been widely applied, but recently a mega-nourishment (the Sand Motor pilot project) was proposed as a more ecological and sustainable alternative to regular sand nourishment. A mega-nourishment is created by placing a large volume of sand concentrated on a small stretch of coast, which then gradually nourishes up-stream beaches over a long period of time. This lowers the number of pulse disturbances to the sandy beach ecosystem compared to regular sand nourishment. As the macroinvertebrate community is a key component of the sandy beach ecosystem, it is crucial to understand what drives assembly of macroinvertebrate communities on sandy beaches in general and after nourishments in particular. After application of a mega-nourishment, macroinvertebrate communities have to re-assemble, but community assembly may be directly or indirectly influenced by the

characteristics of the mega-nourishment. Altered local hydrodynamics around a mega-nourishment may, for example, change macroinvertebrate dispersal patterns and resource availability. This, in turn, may influence species interactions and drive community assembly, resulting in the actual macroinvertebrate community composition present on a sandy beach. So far, the effect of a mega-nourishment on the macroinvertebrate communities and how this compares to regular sand nourishment has not been studied.

The main aims of this thesis were, therefore, to 1) improve our understanding of the effect of resource availability on macroinvertebrate community dynamics and ecosystem functioning on sandy beaches, and 2) investigate the effect of a mega-nourishment on the macroinvertebrate community of the sandy beach. For these purposes, I conducted both laboratory experiments and field work in the Netherlands and worked both in the intertidal and supratidal zone to cover the entire beach.

In Chapter 2 the spatial and temporal effects on the intertidal macroinvertebrate community after placement of a mega-nourishment were assessed. In addition, the intertidal community composition at the mega-nourishment was compared to communities present on beaches subject to regular beach nourishment and unnourished beaches. To do this, we obtained, combined and analysed macroinvertebrate field data from three different data sets, one data set contained data for the Sand Motor mega-nourishment, while the other two data sets contained data on both beaches subject to regular beach nourishment and unnourished beaches, all along the Dutch coast. There were strong spatial effects within the mega-nourishment, where a distinct intertidal macroinvertebrate community, consisting of species commonly encountered on intertidal mudflats, was present in the lagoon as compared to the wave-exposed locations of the mega-nourishment. The mega-nourishment thus locally gives rise to a habitat that attracts a different intertidal macroinvertebrate community as compared to wave-exposed beaches. Wave-exposed locations at the mega-nourishment had a higher macroinvertebrate richness, lower macroinvertebrate abundance and did not converge into a macroinvertebrate community composition similar to those on regularly nourished and unnourished beaches. A mega-nourishment may thus result in an altered intertidal macroinvertebrate community with potential cascading effects within the sandy beach food web.

Chapter 3 focused on the effect of diatom availability on the non-additive effects of consumption by a three-species intertidal macroinvertebrate community. A mesocosm study was performed in which we quantified isotopically labelled diatom consumption by three macroinvertebrate species (*Bathyporeia pilosa*, *Haustorius arenarius* and *Scolelepis squamata*), kept in either monocultures or a three-species community at a range of diatom densities. The amphipod *B. pilosa* was the most successful competitor in terms of consumption at both high and low diatom availability, while the amphipod *H. arenarius* and the polychaete worm *S. squamata* consumed less in the community than in their respective monocultures. Non-additive effects of consumption were present and larger than mere additive effects, being similar across diatom availabilities. The drivers of the non-additive effects of consumption, however, did change with diatom availability. Complementary effects

related to niche-partitioning were the main drivers of the non-additive effects of consumption, with a slightly increasing contribution of selection effects related to competition with decreasing diatom availability. Hence, in macroinvertebrate communities with functionally different, and thus complementary, species, non-additive effects of consumption can arise even when food availability is low.

The question addressed in Chapter 4 was whether the supratidal community, in terms of abundance, species richness and diversity, was a driver of N and P mineralisation of wrack. In addition, temporal (seasonal) and spatial (young and old drift lines) effects were included. A litter bag experiment was performed on the beach, where litter bags filled with wrack were incubated for two weeks. Season was a strong driver of both N and P mineralisation and the supratidal macroinvertebrate community. Drift line did not have a strong effect on N and P mineralisation and the supratidal macroinvertebrate community, except for macroinvertebrate diversity which was higher in young than old drift lines. N and P mineralisation was mainly predicted by season and macroinvertebrate abundance, while macroinvertebrate richness and diversity were also, albeit less strong, predictors of P mineralisation. Season and the macroinvertebrate community thus have strong effects on wrack mineralisation, resulting in a positive effect on nutrient cycling on sandy beaches, thereby linking terrestrial and marine ecosystems.

In Chapter 5 the effects of wrack burial and supratidal macroinvertebrate presence on decomposition driven nutrient availability and beach pioneer plant growth were assessed. A mesocosm experiment was performed, where wrack was either buried or placed on the sand's surface and supratidal amphipods were either present or absent, with two beach pioneer plant species as phytometers. Buried wrack had a strong positive effect on plant mass and both N and P content of the annual plant *Cakile maritima* compared to surface wrack, while effects for the perennial grass *Elytrigia juncea* were largely absent. For *C. maritima*, an effect of macroinvertebrate presence on the N content of the total plant was observed, with a higher N content in the absence of macroinvertebrates. For buried wrack, P content was higher for both the total plant and total shoot in the presence of macroinvertebrates. Differences in N and P content of plants due to macroinvertebrate presence did however not result in differences in plant dry mass. Together, this suggests that macroinvertebrates enhance decomposition of wrack, but that released inorganic N is either taken up by the microbial community or forming complexes with phenolic compounds, resulting in immobilisation of N for plants. Excess P on the other hand was incorporated in *C. maritima*, which might have been P limited. We conclude that the burial of wrack is of paramount importance for *C. maritima* growth in support of embryo dune formation and possibly further ecological development of the sandy beach and dune ecosystems.

To conclude, this thesis showed a clear effect of resource availability on macroinvertebrate species interactions and subsequent consumption in the intertidal zone of sandy beaches, which may indirectly affect community composition. Resource availability had a direct effect on macroinvertebrate community composition in the supratidal zone as supratidal

macroinvertebrates colonised deposited wrack. Biological interactions related to resource availability, therefore, cannot be ignored when aiming to understand macroinvertebrate community assembly on sandy beaches. Both season and supratidal macroinvertebrate community composition, especially macroinvertebrate abundance, had a strong effect on mineralisation of wrack on sandy beaches. Released nutrients from wrack mineralisation are subsequently taken up by plants, where buried wrack supports beach pioneer plant growth. This emphasises the link between the marine and terrestrial ecosystems, with a central role for the macroinvertebrate community in sandy beach ecosystem functioning.

For the first time, the effect of a sand nourishment of this scale on the intertidal macroinvertebrate community has been quantified. Although the Sand Motor mega-nourishment may initially be beneficial for overall intertidal macroinvertebrate community richness and diversity, macroinvertebrate abundance was lower**.** It is therefore evident that a mega-nourishment can have both positive and negative effects on the intertidal macroinvertebrate community. It appears that the net effect of the Sand Motor mega-nourishment leans towards a positive effect, but it is important to note that this depends on the specific coastal management goals of the mega-nourishment. Thus, in terms of the intertidal macroinvertebrate community, a mega-nourishment appears to be a promising coastal defence strategy compared to regular beach nourishment, at least during the first years after construction. For both the supratidal macroinvertebrate community and sandy beach ecosystem functioning, it is crucial that wrack is maintained on both nourished and unnourished sandy beaches. Overall, this thesis highlights the need to include the effect of resource availability on both the intertidal and supratidal macroinvertebrate community and the sandy beach ecosystem as a whole, especially when designing and planning future coastal management practices.