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A mega-nourishment creates novel habitat for intertidal macroinvertebrates by enhancing habitat relief of the sandy beach

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ABSTRACT

Globally, sandy beaches are subject to coastal squeeze due to erosion. Soft-sediment strategies, such as sand nourishment, are increasingly applied to mitigate effects of erosion, but have long-term negative impacts on beach flora and fauna. As a more ecologically and sustainable alternative to regular beach nourishments, a mega-nourishment has been constructed along the Dutch coast by depositing 21.5 Mm³ of sand, from which sand is gradually redistributed along the coast by natural physical processes. The 'Sand Motor' mega-nourishment was constructed as a long-term management alternative for coastal protection and is the first large-scale experiment of its kind. We evaluated the development of intertidal macroinvertebrate communities in relation to this mega-nourishment, and compared it to species composition of beaches subject to regular beach or no nourishment. We found that a mega-nourishment resulted initially in a higher macroinvertebrate richness, but a lower macroinvertebrate abundance, compared to regular beach nourishment. As there was no effect of year after nourishment, this finding suggests that colonization and/or local extinction were not limiting macroinvertebrate richness at the mega-nourishment. In addition, a mega-nourishment does not converge to an intertidal macroinvertebrate community similar to those on unnourished beaches within a time scale of four years. Beach areas at the mega-nourishment sheltered from waves harbored a distinct macroinvertebrate community compared to typical wave-exposed sandy beach communities. Thus, a mega-nourishment temporally creates new habitat for intertidal macroinvertebrates by enhancing habitat relief of the sandy beach. We conclude that a mega-nourishment may be a promising coastal defense strategy for sandy shores in terms of the macroinvertebrate community of the intertidal beach.

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1. Introduction

Sandy beaches are among the most prevalent coastal ecosystems on the planet, harboring unique ecological communities that provide a wide variety of ecosystem functions and services (McLachlan and Brown, 2006). Globally, sandy beach ecosystems are subject to coastal squeeze, where beaches are negatively affected by both the rising sea level and storm events on the sea

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https://doi.org/10.1016/j.ecss.2018.03.003 0272-7714/© 2018 Elsevier Ltd. All rights reserved. side and static anthropogenic structures on the land side (Schlacher et al., 2007). This combination of factors causes severe erosion of the sandy beach, threatening local ecological communities by leaving only a narrow strip of beach habitat as the sea advances inland.

A common management strategy to combat coastal squeeze is to replenish eroded sandy beaches by frequently adding a large volume of sand either in the upper beach zones or in the nearshore, thus increasing coastal sediment budgets and widening the beach (Cooke et al., 2012). Although sand nourishment has been considered as an ecologically friendly alternative to hard coastal defense

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structures (Hanley et al., 2014), it generally causes temporal local extinction of sandy beach flora and fauna (Speybroeck et al., 2006; Leewis et al., 2012). During regular beach nourishment, a thick laver of sand (up to a few meters) is deposited on the beach, causing burial and mortality of primary vegetation and invertebrates of the intertidal and supratidal zones (Speybroeck et al., 2006; Schlacher et al., 2012). Additional indirect effects of regular beach nourishment include constraining macroinvertebrate colonization when there is a mismatch in sediment characteristics (e.g. median grain size) between the fill sediment used for nourishment and the original sediment of the eroded beach (Speybroeck et al., 2006; Vanden Eede et al., 2014). This potentially leads to long-term negative impacts of sand nourishment on the macroinvertebrate community (Speybroeck et al., 2008), even though intertidal macroinvertebrate species are well adapted to the highly dynamic environment of the intertidal zone and can guickly colonize bare sands (McLachlan and Brown, 2006). Intertidal macroinvertebrate species can recolonize a beach that has received regular beach nourishment within one year after disturbance, though community composition does differ from beaches without nourishment (Leewis et al., 2012). Therefore, alternative nourishment strategies are called for to constrain negative effects on these intertidal macroinvertebrate communities on the sandy beach.

As a more ecologically and sustainable alternative to current beach and foreshore nourishment practices, a mega-nourishment has been proposed. To test the economical, anthropogenic and environmental implications of this novel approach, the so-called 'Sand Motor' pilot experiment was started in 2011 along the Dutch main coast (Stive et al., 2013). Instead of regularly applying smaller-scale beach nourishments every three to five years as is the current practice in the Netherlands, this mega-nourishment has an expected life time of about twenty years, thus decreasing the number of local pulse disturbances to intertidal organisms as a very large volume of sand is nourished at one single occasion. After construction, the mega-nourishment continuously changes in shape over time as deposited sand is gradually transported by wind and waves and nourishes up-stream beaches. On these beaches, intertidal and supratidal macroinvertebrate communities potentially experience limited disturbance by sand deposition. Another envisioned advantage of a mega-nourishment is that the large volume of sand allows for the construction of certain geomorphological shapes, which gives the possibility to increase the habitat diversity, for example by creating sheltered intertidal zones, attracting a wider variety of species. An enhanced habitat relief generally leads to an increase in species diversity (Stein et al., 2014; Tamme et al., 2010).

Here, we focus on species of the macroinvertebrate community of the intertidal sandy beach. The intertidal macroinvertebrate community is essential for the functioning of the sandy beach ecosystem, including nutrient cycling and the provision of prey species to support predator biodiversity (Defeo et al., 2009). Hence, the intertidal macroinvertebrate community is at the core of the sandy beach food web, linking primary production by e.g. microalgae to higher trophic levels such as shore birds (Lercari et al., 2010; Bergamino et al., 2011). It thereby also connects marine and terrestrial food webs and promotes the flow of nutrients across the coastal boundary (Polis and Hurd, 1996; Catenazzi and Donnelly, 2007). It is, however, unknown what the spatiotemporal effects of a mega-nourishment are on the intertidal macroinvertebrate community and, ultimately, whether a meganourishment can be considered a promising coastal defense strategy in terms of sandy beach ecology.

In this study, we aimed to assess 1) the spatial and temporal effects within a mega-nourishment on the intertidal macroinvertebrate community up to four years after establishment, and 2) whether the intertidal macroinvertebrate community of waveexposed beaches of mega-nourishments differs from those with regular beach nourishments or without nourishment. We hypothesize that 1) the most common intertidal macroinvertebrate species are present at the mega-nourishment within one year after establishment; 2) enhanced habitat relief within the meganourishment will attract other macroinvertebrate species than those encountered on wave-exposed sandy beaches alone, thus locally enhancing species richness; 3) the wave-exposed locations at the mega-nourishment will have a similar macroinvertebrate community composition as those subject to regular beach nourishment, and 4) beaches subject to no nourishment are expected to have a community composition most dissimilar from the meganourishment and beaches subject to regular beach nourishment.

2. Methods

2.1. Data collection and description

Our focus was on the macroinvertebrate community, which comprises all sandy beach invertebrates that are obtained by sieving sand over a 1 mm mesh. Unnourished beaches were considered those that had not received any nourishment from the year 1990 onwards, when sand nourishment became an active management strategy in the Netherlands (Van Dalfsen and Aarninkhof, 2009). In light of our study aims, we compiled and analyzed data originating from three data sets. Macroinvertebrates were identified to species level if possible.

2.1.1. Data set 1; the Sand Motor experiment

The 'Sand Motor' is a mega-nourishment created along the coast near Den Haag, the Netherlands (52.05 N, 4.19 E) as a hook-shaped peninsula attached to the original coast line (Stive et al., 2013). Sand nourishment started in 2010 and was completed in 2011. Data on the intertidal macroinvertebrate community was collected in five years, 2010 (prior to establishment), 2012 (t = 1), 2013 (t = 2), 2014 (t = 3) and 2015 (t = 4), in September or October to reduce seasonal effects. Twelve transects were directed perpendicular to the coast and span from the high water line (HWL, 1 m above mean sea level) to the low water line (LWL, 0.6 m below mean sea level). Transect length varied according to the slope of the beach at each transect. Four transects were positioned north (down-stream), south (upstream; 1000 m between transects) and in the center (800 m between transects) of the mega-nourishment (Fig. 1). With this setup, a full spatial range of impacts on the macroinvertebrate communities adjacent to the mega-nourishment could be monitored. The sampling points on the central transects were, after placement of the mega-nourishment, re-positioned on the outside of the hook as the original sampling points were now covered by sand. These transects are further referred to as the transects at the hook. In 2012, a transect was positioned in the lagoon of the meganourishment and in 2013 a second transect was added to the lagoon, resulting in two transects at the lagoon that were sampled in 2013, 2014 and 2015. Moreover, from 2013 onwards, one transect was added south and the most northern of the four initial southern transects was dropped. This was done to track the effect of more sand moving southwards than was anticipated. To create a robust design, despite the changes made while accounting for expected differences in the intertidal macroinvertebrate community across the mega-nourishment, the beach was divided into four locations for analysis: North (four (or three) transects), South (four (or five) transects), Hook (four transects) and Lagoon (two transects) (Fig. 1).

With receding tide starting at the HWL, every 75 min one sample was taken around the water line with the last sample taken at the LWL, ensuring that sediment moisture levels were similar for

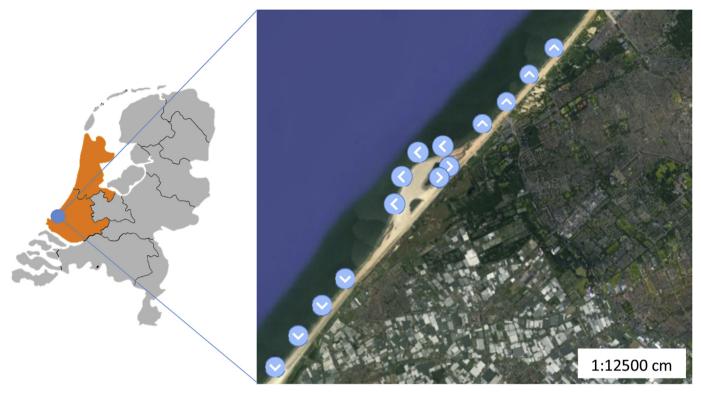


Fig. 1. Map of the Netherlands with the position of the 'Sand Motor' mega-nourishment (blue dot) and the region in which all other beaches of the combined data set were located (orange provinces). A satellite image of the mega-nourishment area (right) with the transects at the hook (arrow left), north (arrow up), south (arrow down) and in the lagoon (arrow right) of the mega-nourishment indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

each sample. This resulted in a total of five sampled zones per transect for the intertidal region. With a GPS tracking device, the transects as established in 2012 were located each year to standardize transects over time. As the shape of the mega-nourishment changed over time, corresponding samples were taken at slightly different positions each year. Each sample was taken with a steel rectangular corer of 27 by 37 cm (surface area 999 cm²) until a depth of 15 cm. Sediment was sieved and upon collection macroinvertebrates were transferred to a 4% formalin solution and later stored in 70% ethanol. Abundance and richness were determined for each of the five zones separately within each meganourishment location, treating all transects within a location as replicates. We thus assumed that variation in the intertidal macroinvertebrate community between zones is greater than between adjacent transects within a mega-nourishment location (c.f. Schlacher et al., 2008).

2.1.2. Data set 2; the Leewis data set

Leewis et al. (2012) collected data on the intertidal macroinvertebrate community at seventeen Dutch beaches in August 2007. Here, only the nine beaches (seven nourished and two unnourished) in the provinces North-Holland and South-Holland were used. We excluded sites from the Wadden Sea (in the north of the Netherlands) and the Zeeland Delta (in the south of the Netherlands), as these beaches were more dissimilar to the meganourishment for environmental conditions (e.g. tidal range and calcium and mud content). As the original study was designed as a chronosequence, the time since the last regular beach nourishment, ranged from 1 to 13 years and sampling occurred at a single moment in time. The intertidal region was randomly sampled between HWL and directly below the mean tidal level. At each beach, over a 25 m wide beach part parallel to the coast, a total of twenty samples was taken using a stratified random design. Perpendicular to the coast, the beach between HWL and directly below the mean tidal level was divided into four zones, each spanning 1/8 of the tidal height. With receding water starting at HWL, five samples were randomly taken from each of four zones (Leewis et al., 2012). Each sample was taken with a circular steel corer with a diameter of 20 cm (surface area 314 cm²) and depth of 20 cm. Macro-invertebrates were collected by sieving sediment and animals were stored in 10% formalin.

2.1.3. Data set 3; the Janssen dataset

Janssen and Mulder (2005) collected data on the intertidal macroinvertebrate community at nine Dutch beaches in June 2002, of which the five beaches from the provinces North-Holland and South-Holland were selected for this study. One beach had been subject to regular beach nourishment four years before sampling, while four beaches had not received any sand nourishment. On each beach, seven zones were marked perpendicular to the water line within a 25 m wide beach from 40 cm above HWL to 40 cm below LWL. Sampling was based on the predicted tidal curve, ensuring that each position at which a sample was taken received a similar flooding time and sediment moisture level for each zone within each beach. Five out of seven zones were randomly chosen and ten macroinvertebrate samples were taken in each selected zone (Janssen and Mulder, 2005). Samples were taken with a steel corer to a depth of 30 cm with a sampling surface of 78.5 cm^2 . Sediment was sieved and macroinvertebrates were collected and stored in 3.8% formalin.

In total, we had data available for eight nourished and six unnourished beaches to compare with the mega-nourishment and put the development of the mega-nourishment in a broader perspective.

2.2. Combining and preparing data

2.2.1. General considerations

Abundance data was standardized by calculating the macroinvertebrate abundance per m² for each sample based on the sample surface area. Richness was determined per zone and location (i.e. North, South, Hook or Lagoon) within the meganourishment or for each separate regularly nourished or unnourished beach. This amounted to an area sampled of $0.4 \text{ m}^2 (0.2 \text{ m}^2 \text{ for})$ Lagoon) (data set 1), 0.16 m² (data set 2) and 0.08 m² (data set 3). A difference in sampling area makes it difficult to directly compare richness, but further correction was not possible because the species-area relationship was not known. Richness in data set 3, and to a lesser extent data set 2, may therefore to a certain degree be an underestimation of actual richness. Only taxa that were representative of the intertidal macroinvertebrate community were included in the analysis. Macroinvertebrates belonging to the class Insecta were removed, because these are short-term visitors from the supratidal and the dunes (Defeo and McLachlan, 2013). In addition, the amphipod Talitrus saltator (two observations) and animals that could not be further identified in the order Amphipoda (two observations) were removed as these are considered to be supratidal inhabitants. Finally, three taxa (Schistomysis kervillei (Mysidae), Actiniaria and Hydrozoa) were removed as they were likely washed ashore after a storm.

2.2.2. Spatial and temporal effects within a mega-nourishment

To analyze spatial and temporal effects of a mega-nourishment on community composition, we further processed the data from data set 1. First, the average abundance per taxon was calculated per zone and location. Abundance was then summed over all taxa per zone and location to obtain total abundance, which was $log_{10}(n+1)$ -transformed. The number of taxa was counted per zone and location within each year to determine richness. For multivariate analysis within the mega-nourishment, 73 taxa were included.

2.2.3. Mega-nourishment versus beach- and no nourishment

To compare the intertidal macroinvertebrate community across nourishment types, the zone from which the sample was taken was standardized between HWL (1) and LWL (0), where all sampling locations were placed in between 0 and 1 based on emersion time during the tidal cycle. An intertidal position of 0.5 thus corresponds with being emersed for half of the time. Furthermore, in the comparison of nourishment types, the focus is on the intertidal macroinvertebrate community of the wave-exposed beaches, therefore excluding the lagoon at the mega-nourishment as it is sheltered from hydrodynamic forces. In addition, the data collected at the mega-nourishment in 2010 was not included as this sampling occurred prior to establishing the mega-nourishment. As a result of this selection, a total of 66 taxa were included in the analysis. For both data set 2 and 3, abundance and richness were calculated in analogy to the procedure applied to data set 1.

2.3. Statistical analysis

Of all potentially important abiotic factors explaining macroinvertebrate community composition, we only had data available for median grain size for all data points, except for the meganourishment in 2014. When including median grain size in the analysis, median grain size alone did not have a significant effect on macroinvertebrate abundance and richness, even though there were differences in median grain size between locations and years at the mega-nourishment and between nourishment types (see Supplementary). This supports the recommendation to analyze the full suite of abiotic factors, but minimally include median grain, size, beach slope and tidal range (McLachlan and Brown, 2006; Schlacher et al., 2008). As this was not possible, we treat nourishment and year as factors instead to include all relevant abiotic factors in the analysis.

In light of the unbalanced number of replications, we ran a GAM to test the effect of intertidal position (continuous factor, fitted with a polynomial spline (k=5)) and mega-nourishment location (discontinuous factor, four locations) on intertidal macroinvertebrate abundance and richness. Another GAM was used to determine the effect of intertidal position (continuous factor, fitted with a polynomial spline (k = 5)) and year (discontinuous factor, five years) on intertidal macroinvertebrate abundance and richness over the five-year period prior and post application of the meganourishment. Macroinvertebrate community composition at the mega-nourishment was evaluated with NMDS ordination which was run for 100 iterations at k=3 (decreased number of dimensions). Similarities of macroinvertebrate communities between groups, either year (five levels) or location (four levels), were tested with ANOSIM. For this analysis of similarities, the nullhypothesis is that the similarity between groups is greater than or equal to the similarity within groups, and the test statistic R is constrained between -1 and 1 (Clark, 1993).

We also ran a GAM to test the effect of intertidal position (continuous factor, fitted with a polynomial spline (k=5)) and nourishment type (discontinuous factor; mega-nourishment, regular beach nourishment and unnourished beaches) on macroinvertebrate abundance and richness. Macroinvertebrate community composition for each nourishment type was plotted with NMDS ordination which was run for 100 iterations at k = 3(decreased number of dimensions). Similarities of macroinvertebrate communities between nourishment types were again tested with ANOSIM. As data set 2 was focused on the higher intertidal position an underestimation of the lower position community may exist, however, this underestimation is divided over both beaches subject to regular beach nourishment and no nourishment. All statistical analyses were done in R, version 3.2.3.

3. Results

3.1. Spatial and temporal effects on the macroinvertebrate community within a mega-nourishment

3.1.1. Abundance and species richness

Macroinvertebrate abundance varied significantly with intertidal position within the mega-nourishment (F=5.3, df=2.6, p=0.006) with a more than four times higher abundance close to LWL (78 ± 5 against 13 ± 12 individuals m⁻² at LWL and HWL, respectively; Fig. 2). Overall variation in abundance was large, ranging from 0 to 1580 individuals m⁻². South of the meganourishment, macroinvertebrate abundance was significantly higher compared to the other locations (t = 3.7, p < 0.001). In 2014, macroinvertebrate abundance was significantly lower than in any other year (t = -3.6, p < 0.001).

Macroinvertebrate species richness also varied significantly with intertidal position (F = 13.1, df = 1, p < 0.001) with a higher species richness close to LWL (5.9 ± 4.1 against 2.9 ± 3.5 species on average at zone LWL and HWL, respectively, Fig. 3). South of the mega-nourishment, species richness was significantly higher compared to the other mega-nourishment locations (t = 3.4, p = 0.001). There was strong variation in species richness among years with higher richness in 2012, 2013 and 2015 than in 2010 and 2014 (GAM, t = 2.6, p = 0.01; t = 2.8, p = 0.007; t = 3.5, p < 0.001, respectively).

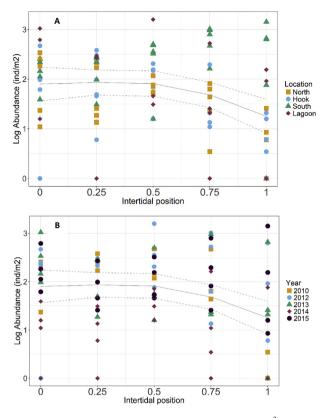


Fig. 2. Macroinvertebrate abundance (log-transformed; individuals m⁻²) at the meganourishment across the intertidal region grouped by A) location (North, Hook, South and Lagoon) and B) year (2010, 2012, 2013, 2014 and 2015). The continuous variable 'intertidal position' ranges from 0 being equal to the low water line (LWL) to 1 being equal to the high water line (HWL). Each dot represents the average of all transects within a location, grouped per year. Grey solid line shows the GAM estimate for the overall fit, with grey dashed lines indicating 95% confidence interval. Spline: k = 5.

3.1.2. Community composition

The macroinvertebrate communities North and at the Hook of the mega-nourishment were most similar (Fig. 4). South of the mega-nourishment, the beach harboured a more dissimilar macroinvertebrate community composition compared to locations North and at the Hook, with no overlap in group means (Fig. 4A). The most distinct macroinvertebrate community was found in the lagoon, with no overlap in group means and a larger variation in community composition than for any other location at the meganourishment (Fig. 4A). These differences in macroinvertebrate community composition between locations were significant (R = 0.31, p < 0.001), despite an overlap in community composition for individual sampling points at the mega-nourishment (Fig. 4A). There were significant differences in macroinvertebrate community composition and variation between years (R = 0.08, p < 0.001). In 2010, the macroinvertebrate community composition was least variable and showed overlap in group means with all the other years (Fig. 4B). The macroinvertebrate community composition showed the largest variability in 2012, followed by 2013 (Fig. 4B).

Two main clusters of taxa were identified, with species of exposed sandy beaches, such as the polychaete worm *Scolelepis squamata*, the amphipods *Bathyporeia pilosa* and *Haustorius arenarius* and the isopod *Eurydice pulchra* at the core of one cluster (Fig. 5, left) and typical mudflat species, such as the amphipod *Corophium volutator* and the polychaete worm *Heteromastus filiformis* at the core of the other cluster (Fig. 5, right). This coincides with the community clusters North, South and at the Hook of the mega-nourishment as wave-exposed sandy beaches and the

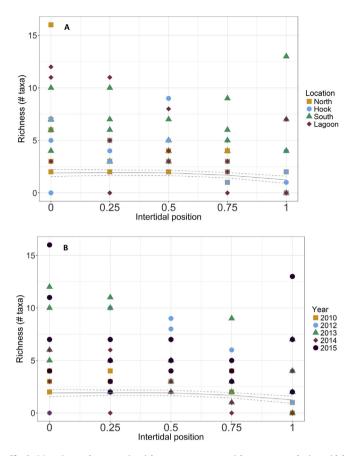


Fig. 3. Macroinvertebrate species richness at a mega-nourishment across the intertidal region grouped by A) location (North, Hook, South and Lagoon) and B) year (2010, 2012, 2013, 2014 and 2015). The continuous variable "intertidal position" ranges from 0 being equal to the low water line (LWL) to 1 being equal to the high water line (HWL). Each dot represents the sum of all taxa within a location, grouped per year. Grey solid lines show the GAM estimate for all dots combined, with grey dashed lines indicating 95% confidence interval. Spline: k = 5.

Lagoon as a sheltered beach (see Figs. 4A and 5A).

3.2. Effect of nourishment type on the macroinvertebrate community

3.2.1. Abundance and species richness

Macroinvertebrate abundance was similar between beaches subject to regular nourishment and no nourishment (t = -0.7, p = 0.5), while abundance was significantly lower at the meganourishment (t = -5.4, p < 0.0001; Fig. 6A). Overall, macro-invertebrate abundance varied significantly with intertidal position (F = 8.9, df = 3.1, p < 0.0001), with higher abundances in the mid and low intertidal positions (120 ± 5 against 25 ± 8 individuals m⁻² at LWL and HWL, respectively; Fig. 6A).

Macroinvertebrate species richness was significantly lower at the unnourished beaches than at beaches subject to regular nourishment and the mega-nourishment (F=3.5, df=2, p=0.03). Macroinvertebrate species richness varied significantly with intertidal position (F=18.6, df=1, p<0.0001), with a higher species richness close to the low water line (5.6 ± 3.5 against 3.0 ± 3.6 species at HWL, respectively, Fig. 6B).

3.2.2. Community composition

The macroinvertebrate communities at beaches subjected to regular nourishment and no nourishment were most similar in

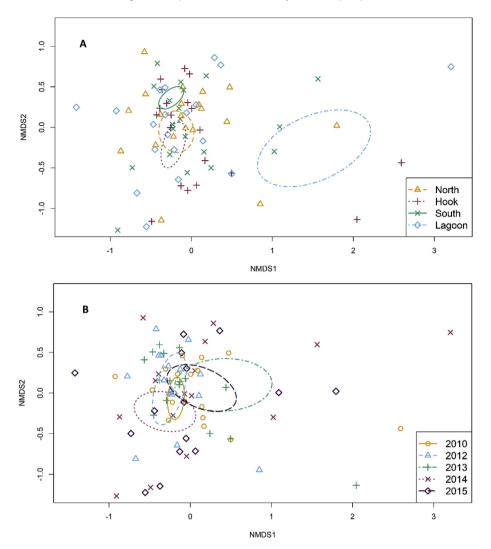


Fig. 4. NMDS ordination of the intertidal macroinvertebrate community at all locations at the mega-nourishment grouped by A) location (North, Hook, South and Lagoon), B) year (2010, 2012, 2013, 2014 and 2015). Group means are shown as centroids based on the average group rank and a 95% confidence interval. Points indicate the individual samples. Stress = 0.12, k = 3.

composition with a high overlap in group means (Fig. 7A). The community composition at the wave-exposed beach locations within the mega-nourishment was most distinct with no overlap in group means with unnourished beaches and a slight overlap with beaches subject to regular beach nourishment (Fig. 7A). The macroinvertebrate community composition and variation showed significant differences between nourishment types (R = 0.08, p = 0.002). Unnourished beaches harboured the greatest variation in community composition as indicated by a larger group centroid (Fig. 7A).

In unnourished beaches, the community composition was driven by the presence of carnivorous species, such as the crab *Carcinus maenas* (Fig. 7B). Species that were shared among the three nourishment types included the polychaete worm *Scolelepis squamata* and the amphipod *Haustorius arenarius* (Fig. 7B). At the mega-nourishment, macroinvertebrate community composition was strongly related to the presence of the amphipod *Bathyporeia elegans* and members of the crab family *Portunidae*, but also by the polychaete worm *Spio martinensis* (Fig. 7B).

4. Discussion

We found that a mega-nourishment can locally enhance

intertidal macroinvertebrate species richness by enhancing habitat relief through variations in sandy beach morphology at landscape level. In particular, a mega-nourishment provides a new beach habitat along the main coast in the form of a sheltered lagoon, which was inhabited by a distinct intertidal macroinvertebrate community that is commonly encountered on beach types with among others finer sands and a higher organic matter content (see McLachlan and Brown, 2006; Beukema et al., 1999). In addition, intertidal macroinvertebrate species richness and abundance were higher south of the mega-nourishment compared to the other locations, which may again be related to the shape of the meganourishment (see section 4.2).

Our study also shows that a mega-nourishment has both positive and negative effects on the intertidal macroinvertebrate community when compared to beaches subject to regular beach or no nourishment. While macroinvertebrate species richness was higher at both the mega-nourishment and beaches subject to regular beach nourishment than at unnourished beaches, macroinvertebrate abundance was lower at the mega-nourishment. This suggests that intertidal macroinvertebrate species are able to establish on these sandy beaches, but a variety of abiotic nonoptimal habitat characteristics and/or biotic factors, such as post-

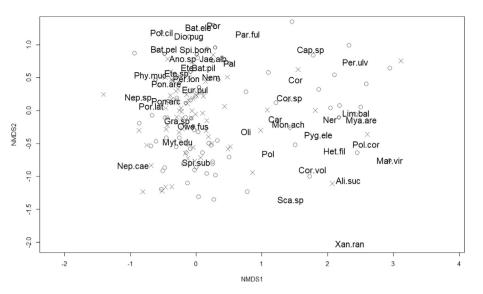
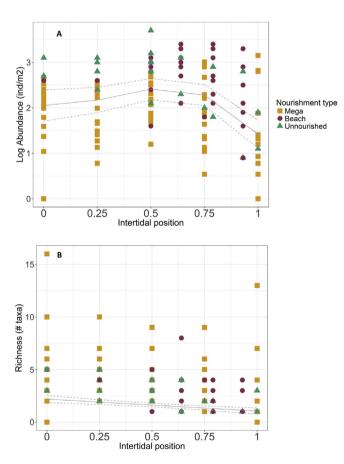


Fig. 5. NMDS ordination of the intertidal macroinvertebrate community at all locations at the mega-nourishment indicating taxa by code names. For readability, 63% of all code names are plotted due to the high number of taxa (see <u>Supplementary</u> for a legend of code names of plotted taxa). Open dots indicate each individual taxon and crosses indicate each individual sample. Stress = 0.12, k = 3.



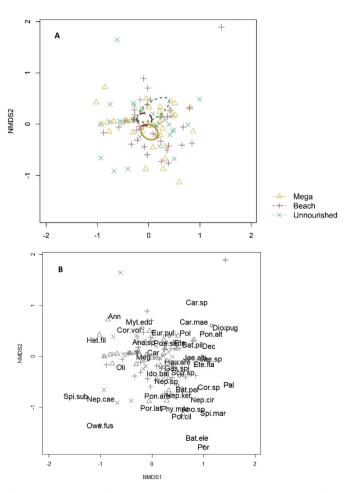


Fig. 6. Macroinvertebrate abundance (log-transformed) (A) and richness (B) across the intertidal region at three different nourishment types (Mega = mega-nourishment, Beach = regular beach nourishment and Unnourished = unnourished beaches). The continuous variable "intertidal position" ranges from 0 being equal to the low water line (LWL) to 1 being equal to the high water line (HWL). Each dot represents the average (abundance) or sum of taxa (richness) of all transects within a location (mega-nourishment) or beach (regular beach nourishment and no nourishment) at each position, grouped per year. Grey lines show the GAM estimate for the overall fit, with grey dashed lines indicating 95% confidence interval. Spline: k = 5.

Fig. 7. NMDS ordination of the intertidal macroinvertebrate community across three nourishment types (Mega = mega-nourishment, Beach = regular beach nourishment and Unnourished = unnourished beaches) showing group centroids (A) or indicating taxa (B). Group means are shown as centroids based on the average group rank and a 95% confidence interval. For both plots, stress = 0.13, k = 3. Crosses, plusses and triangles indicate the individual samples assigned to each of the three nourishment types. For readability, 88% of all code names are plotted due to the high number of taxa (see Supplementary for a legend of code names of plotted taxa).

settlement competition and predation, limit the abundance of these species (Todd, 1998). Furthermore, the wave-exposed beaches of a mega-nourishment harbored a different intertidal macroinvertebrate community compared to the species composition encountered on beaches subject to regular beach and no nourishment. A mega-nourishment thus does not result in a similar intertidal macroinvertebrate community as was found on unnourished beaches. Whether this should be regarded as a problem or not depends on the specific nature-related goals coinciding with the applied sand nourishment. Through its differences in shape, size and frequency of nourishing, a mega-nourishment changes the environment in a different way compared to regular beach nourishments by its shape, size and frequency, even though e.g. sediment characteristics not intended to be fundamentally different. These differences result in an altered intertidal macroinvertebrate community with potential cascading effects within the sandy beach food web.

4.1. Dispersal is not strongly limiting after a mega-nourishment

As expected, intertidal macroinvertebrate species common for wave-exposed sandy beaches were already encountered one year after establishment of the mega-nourishment. These common species included the polychaete worm *S. squamata*, the amphipods *H. arenarius* and *B. pilosa* and the isopod *E. pulchra* (Van Hoey et al., 2004). These findings are in accordance with Leewis et al. (2012). This rapid colonization of the bare sand associated with the hook of the mega-nourishment was especially successfully executed by *S. squamata* which reached the highest abundance of all taxa encountered at the mega-nourishment (data not shown). In the years following mega-nourishment, these common species were still present. These findings show that common intertidal macro-invertebrates successfully colonized the mega-nourishment, emphasizing their great dispersal ability (e.g. Speybroeck et al., 2007; Grantham et al., 2003).

When comparing years after nourishment, both intertidal macroinvertebrate abundance and species richness were lower in 2014 compared to other post-nourishment years. It is not uncommon to find large differences in macroinvertebrate composition between individual years due to the highly dynamical environment of the sandy beach (Turner et al., 1995) for example causing local changes in mud content and chlorophyll a (Ysebaert and Herman, 2002). Also, there may be years in which the reproductive output of certain species is lower or when mortality is higher, which is related to the relatively long life-span of certain species and discontinuous reproduction throughout the year (which is e.g. the case for S. squamata (Speybroeck et al., 2007)). In the years after establishment, the intertidal macroinvertebrate community showed greater spatial variability in composition compared to the community encountered before the mega-nourishment was applied. Although this can again be attributed to between-year differences, the further development of the lagoon over the years likely had the greatest effect on the increased variability in intertidal macroinvertebrate community composition (see section 4.2).

4.2. Spatial variation by design facilitates species

Secondly, we hypothesized that the enhanced habitat relief in beach morphology within the mega-nourishment would result in a sheltered beach that attracts other macroinvertebrate species than those commonly encountered on wave-exposed sandy beaches, which was indeed observed. A distinct intertidal macroinvertebrate community composition was encountered in the lagoon, which included the amphipod *C. volutator* and the polychaete worms *H. filiformis, C. capitata* and *P. elegans* which are species commonly encountered on intertidal mudflats (Beukema et al., 1999). The species P. elegans and H. filiformis are characteristic for intermediate and late successional stages of mudflats, respectively (Van Colen et al., 2008), indicating that assembly of a mudflat macroinvertebrate community occurred in the lagoon. Where dredged material is used for the creation of a mudflat, colonization by typical mudflat species (including C. volutator and C. capitata) occurs within a year (Bolam and Whomersley, 2005), which is in accordance to our study. The mega-nourishment therefore represents a connection between sandy beach ecology and tidal flat ecology. The presence of this intertidal macroinvertebrate community coincides with the sediment composition of the lagoon which accumulates organic matter (Wijsman, 2016) as organic particles precipitate and benthic primary production prospers in this benign hydrodynamic environment (Hartwig, 1978). This community type is rarely encountered along the Dutch coast which is dominated by wave-exposed sandy beaches subject to high hydrodynamic forces. Some mudflats are present in the upper North (the Wadden sea) and the lower South (the Zeeland delta) of the Netherlands. The mega-nourishment thus locally gives rise to a habitat that attracts a different intertidal macroinvertebrate community.

Interestingly, both macroinvertebrate abundance and richness were higher south of the mega-nourishment compared to the other locations within the mega-nourishment. This finding may be related to the sea currents that move from South to North along this part of the Dutch coast and hence influence migration patterns of intertidal macroinvertebrate species. Many intertidal macro-invertebrate species have a planktonic period in their life cycle and depend on hydrodynamic forces for dispersal to establish on new beaches, either in their planktonic phase or as an adult (Grantham et al., 2003). As a result, the base of the sand hook potentially acts as a sink for migrating intertidal macroinvertebrate species, which may lead to an accumulation of a high number of macro-invertebrates but also of more species.

Moreover, the environmental conditions differ, e.g. in sediment characteristics and variation in dry and wet beach (micro-habitats), and may explain the higher intertidal macroinvertebrate abundance and richness south of the mega-nourishment. For example, Huisman et al. (2014) found that at the outer hook of the mega-nourishment the sediment was 20–30% coarser compared to other parts of the mega-nourishment. Coarse sediment is known to be associated to low macroinvertebrate abundance and richness (Speybroeck et al., 2006). In addition, the beach south of the mega-nourishment could be more dissipative, which is associated with finer sands and a higher macroinvertebrate abundance and richness (McLachlan and Brown, 2006). This suggests that intertidal macroinvertebrate colonization of less common species may depend on suitable environmental conditions around the mega-nourishment.

4.3. Comparing the post-recovery intertidal macroinvertebrate community to other types of nourishment

The intertidal macroinvertebrate community composition of wave-exposed beaches at the mega-nourishment were to a small degree dissimilar from beaches subject to regular beach and no nourishment, which is in contrast to our third hypothesis. Directly after construction of the mega-nourishment, the average median grain size was only slightly higher than at the original beach before construction (Huisman et al., 2014), which was expected to facilitate macroinvertebrate colonization. However, the sediment at the mega-nourishment became generally coarser over time (Huisman et al., 2014), which likely had an effect on macroinvertebrate community composition. In addition, a mega-nourishment may

give rise to a range of other environmental changes (i.e. variability in hydrodynamic forces, beach slope) which influence the prevalence of certain intertidal macroinvertebrate species. The taxa that drive the intertidal macroinvertebrate community composition at the mega-nourishment, such as *B. elegans*, Portunidae, *S. martinensis* and *P. ciliata*, were less common but still part of several transitional intertidal macroinvertebrate communities related to the *Eurydice pulchra* – *Scolelepis squamata* community (Van Hoey et al., 2004).

As to our final hypothesis, unnourished beaches did have the most dissimilar macroinvertebrate community composition as compared to beaches subject to sand nourishment practices. The intertidal macroinvertebrate communities can further develop in the largely undisturbed unnourished beaches. For example, intertidal macroinvertebrate communities at beaches that received no nourishment included the carnivorous crab species C. maenas. These are attracted to beaches where sufficient prey species, consisting of primary consumers, are present (Wong and Dowd, 2013). Also, these beaches did not receive any sand nourishment because they are non-erosive. Unnourished beaches are therefore expected to have a lower temporal variability in beach slope and mean grain size, which may have affected the macroinvertebrate community composition (Brazeiro, 2001). Nevertheless, there may be many underlying and interrelated factors causing these differences in community patterns which will be difficult to quantify in future studies.

Furthermore, intertidal macroinvertebrate abundance was lower at the mega-nourishment compared to beaches subject to regular and no nourishment, which potentially has cascading effects on fish, crabs and shore birds that use these species as prey (McLachlan and Brown, 2006). For example, birds have been shown to choose their foraging sites based on prey density at the landscape scale along a sandy beach (Schlacher et al., 2014). These effects have not been explored in the current set-up. Therefore, it remains unknown whether this has significant consequences for higher trophic levels when compared to other nourishment types.

In our study, zonation patterns for intertidal macroinvertebrate abundance and richness were similar across locations within a mega-nourishment and over a five-year period. Both the meganourishment and the beaches subject to regular beach nourishment had similar zonation patterns as unnourished beaches. Abundance and richness were higher close to the low water line with abundance being more variable, which is in accordance to conceptual models proposed by McLachlan and Brown (2006). This suggests that the zonation of the macroinvertebrate community regarding abundance and richness was not disproportionally influenced by (different) environmental factors altering zonation patterns (Degraer et al., 2003).

It is finally important to note that we used three data sets with different experimental set-ups, which may have put constraints on the comparisons and interpretations we could make. For example, the intertidal macroinvertebrate community composition showed equal variability for the mega-nourishment at the wave-exposed locations as for beaches subject to regular beach nourishment. Drawing a conclusion from this finding is, however, difficult as the variability in community composition is obtained from within one beach for the mega-nourishment (North, Hook, South and Lagoon) but several beaches for both regular and no nourishment. The mega-nourishment data therefore probably display α -diversity, while the other beaches give an indication of β -diversity for the intertidal macroinvertebrate community. Moreover, we needed to combine transects that were up to 1000 m apart at the meganourishment to have replicate values within each location at the mega-nourishment, while sampling on all other beaches was concentrated on a much smaller beach part (25 m). Finally, there was great variability in time of collection as samples were collected between 2002 and 2015. In addition, only at the mega-nourishment samples were collected as a small time series, generating several data points for the same beach. Despite these limitations to our combined data set, we believe this study provides interesting and robust results on a novel sand nourishment strategy and its impact on the intertidal macroinvertebrate community compared to regular beach nourishments.

4.4. Implications for coastal management

We have shown that macroinvertebrate biodiversity can be temporally enhanced by creating a hook-shaped mega-nourishment. The shape is crucial, as it creates a lagoon sheltered from incoming waves, resulting in large-scale heterogeneity of the sandy beach morphology in terms of wave-exposure and accumulation of organic matter. Enhance habitat relief attracts a wider variety of species and new communities can be assembled (Stein et al., 2014; Tamme et al., 2010). Although depending on the exact ecological goals of a sand nourishment to be implemented, biodiversity is a widely valued and easy to measure characteristic within coastal management which supports the sandy beach food web and gives rise to a variety of ecosystem functions, such as production and nutrient cycling (Schlacher et al., 2007). This suggests that a meganourishment may constitute an attractive design for creating diverse intertidal macroinvertebrate communities. Continuous monitoring of the development of the 'Sand Motor' meganourishment and the intertidal macroinvertebrate community patterns over time will provide insight in the long-term dynamics. This is especially interesting as the mega-nourishment was designed to be completely incorporated with the original coast in twenty years (Stive et al., 2013), making the lagoon and its intertidal macroinvertebrate community a transient beach feature. On the other hand, intertidal macroinvertebrate abundance was overall lower at the mega-nourishment compared to beaches subject to regular beach and no nourishment. A lower intertidal macroinvertebrate abundance means a lower prey availability, with potentially cascading effects on the sandy beach food web (Vanden Eede et al., 2014; Peterson et al., 2006). We recommend that further research includes the effects of changes in intertidal macroinvertebrate community composition on higher trophic levels to obtain a more complete overview on the ecological effects of sand nourishment practices. Finally, an in-depth analysis of the underlying abiotic factors causing differences in the intertidal macroinvertebrate community between sand nourishment practices would yield critical information to facilitate future sand nourishment designs.

4.5. Conclusions

The 'Sand Motor' mega-nourishment was constructed as a longterm management alternative for coastal protection of sandy shores and is the first large-scale experiment of its kind. Local disturbance to ecological communities is reduced providing new, temporary habitat for nature development. We conclude that a mega-nourishment creates novel habitat for intertidal macroinvertebrates by enhancing habitat relief of the sandy beach. While coastal protection is the primary goal in the management of most Dutch sandy shores, well designed mega-nourishments seem to be a promising coastal defence strategy in terms of the macroinvertebrate community of the intertidal sandy beach.

Author contributions

EME, PMB, MPB and RA conceived and designed the study. LL,

JWMW and GMJ provided data. EME, PMB, MPB and RA analyzed the data. EME wrote the manuscript with all other authors providing editorial advice.

Data accessibility

Data can be obtained by contacting the corresponding author directly.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.ecss.2018.03.003.

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