Living on the edge

van Egmond, E.M.

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Chapter 6

General discussion

6.1 General findings

This thesis addressed the following two main aims: 1) to improve our understanding of the effect of resource availability on species interactions and community assembly of the macroinvertebrate community on sandy beaches, and how this influences ecosystem functioning, and 2) to investigate the effect of sand nourishment on the macroinvertebrate community of the sandy beach and identify implications for future sand nourishments. For this purpose, both the intertidal and supratidal zone were studied and a mix of field studies (both monitoring and experimental) and mesocosm studies was used. Below, I give a brief summary of the research questions and main findings for each chapter, followed by bringing together the outcomes of each chapter and indicating how they contributed to the overall thesis aims. Finally, I present ideas and recommendations for future ecological research and coastal management respectively and I finish with the main conclusions of this thesis.

How does the intertidal macroinvertebrate community develop after a mega-nourishment?

In **Chapter 2** we assessed the spatial and temporal effects on the intertidal macroinvertebrate community after placement of a mega-nourishment and compared these to the communities present on beaches subject to regular beach nourishment and unnourished beaches. There were strong spatial effects within the mega-nourishment, where a distinct intertidal macroinvertebrate community was present in the lagoon as compared to the wave-exposed locations. Temporal effects on the macroinvertebrate community within the mega-nourishment, up to four years after construction, were limited. 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 unnourished beaches.

How does resource availability affect the non-additive effects of consumption between intertidal macroinvertebrate species?

In **Chapter 3** we studied the effect of diatom availability on the non-additive effects of consumption by a simple intertidal macroinvertebrate community. Of the three macroinvertebrate species, *Bathyporeia pilosa* was the most successful competitor in terms of consumption at both high and low diatom availability, while *Haustorius arenarius* and *Scolelepis squamata* consumed less in community than in their respective monocultures. Non-additive effects of consumption were present and were larger than mere additive effects, which were similar across diatom availabilities. Complementary effects related to niche-partitioning were the main driver of the non-additive effects of consumption, with a slightly increasing contribution of selection effects related to competition with decreasing diatom availability.

Is the supratidal macroinvertebrate community a driver of wrack mineralisation and does this differ between drift lines and seasons?

In **Chapter 4** we addressed the question whether the supratidal macroinvertebrate community, in terms of abundance, richness and diversity, is a driver of N and P mineralisation of wrack. In addition, temporal (seasonal) and spatial (young and old drift lines) effects were included in this litter bag experiment. 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 or 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 P mineralisation was additionally to some extent positively affected by macroinvertebrate richness and diversity.

What is the effect of wrack burial and supratidal macroinvertebrate presence on nutrient availability and beach pioneer plant growth?

In **Chapter 5** we assessed the effect of wrack burial and supratidal macroinvertebrate presence on decomposition-driven nutrient availability and beach pioneer plant growth. Buried wrack had a strong positive effect on plant dry mass and both N and P content of *Cakile maritima* compared to surface wrack, while effects for *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.

6.2 Resource availability effects on the macroinvertebrate community

Resource availability is key for the survival, growth and reproduction of species in any given environment and hence drives the outcome of biological interactions, shaping final community composition (e.g. Chapin III et al. 2000). Sandy beach communities have traditionally been considered to be primarily structured by physical control, i.e. the environmental filter, while biological interactions such as competition, i.e. the limiting similarity filter, are considered to be less influential (Defeo and McLachlan 2005, McLachlan and Brown 2006). This is in contrast to rocky shore communities, where biological interactions, including resource competition, have been widely shown to play an additional role to the influence of the physical environment in macroinvertebrate community assembly (e.g. Menge 2000, Liess and Hillebrand 2004, Guerry and Menge 2017). Recently, however, evidence has been accumulating that resource availability and related biological interactions may be more important in structuring intertidal macroinvertebrate communities on sandy beaches as well (e.g. Schlacher and Hartwig 2013, Bergamino et al. 2016). The findings of **Chapter 3** strongly support this idea by identifying the importance of resource availability for species interactions and consumption between intertidal macroinvertebrates of sandy beaches. Also, the findings of **Chapter 4** show that wrack attracts a diverse supratidal macroinvertebrate community, where a change in wrack quality during decay is suggested to support a succession of supratidal macroinvertebrate species.

On sandy beaches, resource availability is highly variable in time and space, both in the intertidal (Shanks et al. 2017, Morgan et al. 2018) and supratidal (Liebowitz et al. 2016) zone, and macroinvertebrates are expected to respond strongly to these changes as resources can temporally or locally be scarce. At the same time, macroinvertebrate species may be well adapted to this low food environment. In **Chapter 3** it became evident that resource availability is a driver of the outcome of biological interactions between intertidal macroinvertebrates, with complementary effects (i.e. niche segregation) being dominant at high diatom availability, but with a larger role for negative species interactions (i.e. competition) when diatom availability was low. Nevertheless, positive non-additive effects of consumption were maintained across diatom availabilities, regardless of a shift in species interactions. This finding emphasises the flexibility of intertidal macroinvertebrates to the availability of food. When diatom availability is low, less successful competitors for diatoms in the community may have shifted their diet towards other food sources if these would have been available. Intertidal macroinvertebrate species indeed exhibit plasticity in resource use and have been shown to adjust their consumption pattern based on the presence of surf diatoms with a higher nutritional quality, consuming more POM and zooplankton when diatoms were absent (Bergamino et al. 2016). This suggests that if abundant lower nutritional quality food sources are available, macroinvertebrate species can cope with a decreased availability of high nutritional quality food sources by strong competition. Hence, co-existence is promoted between intertidal macroinvertebrates and overall non-additive effects of consumption may be maintained over a longer period of time. Furthermore, we have shown in **Chapter 2** that intertidal macroinvertebrate densities can locally be high (see also Leewis et al. 2012), indicating that biological interactions may potentially be important in driving intertidal macroinvertebrate community composition on sandy beaches. Biological interactions should therefore not be disregarded when trying to understand macroinvertebrate community patterns of the intertidal zone and from the above, it can be stated that the importance of biological interactions likely depends on a combination of resource availability, macroinvertebrate density and macroinvertebrate diversity.

In the supratidal zone, macroinvertebrates respond strongly to wrack in terms of abundance and richness (e.g. Olabarria et al. 2007, Colombini et al. 2009, **Chapter 4**). Wrack is deposited over a restricted area on the beach and as supratidal macroinvertebrate species essentially use the same type of resource (i.e. wrack) for food and habitat (Ince et al. 2007, Ruiz-Delgado et al. 2015), there is a potential for resource competition (Lastra et al. 2010). At the same time, macroinvertebrates are expected to exhibit niche segregation in time and space to allow for co-existence on wrack patches (Lastra et al. 2010). The availability of wrack to the supratidal macroinvertebrate community may differ between macroinvertebrate species within a single drift line, as wrack traits that influence its resource use (e.g. nutritional quality and moisture content) differ between wrack species and decomposition stages (Orr et al. 2005, Liebowitz et al. 2016). In **Chapter 4**, a locally high abundance of Diptera larvae in wrack was observed while few *T. saltator* individuals were found, indicating a later successional stage of wrack was sampled. Early succession macroinvertebrate species such as *T. saltator* may indirectly facilitate late succession macroinvertebrate species such as Diptera larvae (e.g. Olabarria et al. 2007). This suggests that resource availability (in terms of e.g. resource quality) changes with decomposition stage of wrack, therefore supporting different macroinvertebrate species at different moments in time. This is supported by the result that mineralisation of wrack is not uniform and depends on both abiotic and biotic factors (**Chapter 4 and 5**), which changes wrack availability to (subsequent) supratidal macroinvertebrate species.

In conclusion, this thesis showed a clear effect of resource availability on macroinvertebrate species interactions and subsequent consumption in the intertidal zone, which may indirectly affect community composition and ecosystem functioning (primarily nutrient cycling). 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 thus need be taken into account in future studies on macroinvertebrate community assembly on sandy beaches.

Take home message: *Resource availability affects species interactions and community composition of macroinvertebrates on sandy beaches*

6.3 Macroinvertebrate community effects on ecosystem functioning

The macroinvertebrate community of sandy beaches contributes to two main ecosystem functions: 1) nutrient cycling and 2) food to support higher trophic levels, while adding to a unique biodiversity exclusively associated with sandy beaches (Schlacher et al. 2007). Changes in community composition alter ecosystem functioning when species are lost or added with specific functional traits or when abundances of a functionally important species significantly increase or decrease (Hooper et al. 2005, Cardinale et al. 2006, Hillebrand et al. 2008). We have shown in **Chapter 4** that supratidal macroinvertebrate community abundance, richness and diversity were drivers of N and P mineralisation of wrack. Changes in supratidal macroinvertebrate community composition may therefore alter nutrient cycling and thus ecosystem functioning, which has been shown on sandy beaches (Costa et al. 2017) and is in line with general ecological theory (Hooper et al. 2005). Densities of supratidal macroinvertebrates can, in addition, be locally high (Van Colen et al. 2005, Ruiz-Delgado et al. 2016), hence creating the potential to have a significant effect on ecosystem functioning (Hillebrand et al. 2008). Also in **Chapter 4**, Diptera larvae densities in wrack were similar to for example Jędrzejczak (2002b), with on average 92 ± 15 (SE) *Fucellia* sp. larvae per litter bag (**Chapter 4**) against approximately 90 *Fucellia tergina* larvae per litter bag (Jędrzejczak 2002b), in both studies after two weeks of field incubation, and thus relatively high. Furthermore, I aimed in **Chapter 5** to test the effect of the presence of *T. saltator* on the decomposition-driven nutrient availability for beach pioneer plants, where macroinvertebrates were indeed found to enhance decomposition and mineralisation of wrack, but the effect of *T. saltator* presence on final nutrient uptake by *C. maritima* appeared to be potentially influenced by the competitive ability of both the microbial community and the individual plant for these nutrients. In addition, early succession species, such as *T. saltator* may indirectly facilitate late succession macroinvertebrate species e.g. due to their feeding activities on wrack and its biofilm (e.g. Olabarria et al. 2007). *Talitrus saltator* is in that case also indirectly responsible for an increase in wrack decomposition and mineralisation. To summarise, the supratidal macroinvertebrate community appears to be an important driver of nutrient cycling on sandy beaches.

In addition to the effect of macroinvertebrate community on wrack mineralisation, the effect of season, wrack burial by sand and drift line position were investigated (**Chapter 4 and 5**).

Even though the relative effect of wrack burial against macroinvertebrate community metrics, season and drift line remains unknown, since these were tested in two separate experiments, and two different macroalgae species (*Ulva lactuca* and *Fucus* sp. respectively) were used, a summary of the main drivers of wrack decomposition and mineralisation as assessed in this thesis is given (Figure 6.1).

Wrack patches found at drift lines higher up the supratidal zone are commonly buried by sand (Hammann and Zimmer 2014). Sand burial had a large, positive effect on wrack mineralisation and subsequent beach pioneer plant growth (**Chapter 5**). However, in the field, litter bags containing wrack were (partly) buried by sand in both young and old drift lines. This could have created similar environmental conditions compared to sand burial, potentially explaining why no difference in wrack mineralisation was found between drift line positions in **Chapter 4**. Nevertheless, when comparing mineralisation between **Chapter 4 and 5** (Table 6.1), mineralisation in the field was intermediate between mineralisation observed for shallow and deep buried wrack. It is important to note that the incubation period between experiments differed: two weeks in the litter bag experiment and four weeks in the mesocosm experiment. Since decomposition is a non-linear process which depends on a.o. macroalgae species (Jędrzejczak 2002a, Olabarria et al. 2007), we cannot calculate the exact mineralisation after two weeks in the mesocosm experiment, but it can be assumed that less material was decomposed than after four weeks of incubation. Mineralisation in the field, where a variety of factors affects wrack decomposition, may in that case actually be higher than in the mesocosm experiment. This suggests that sand burial of wrack was not the only factor influencing N and P mineralisation of wrack, supporting the results of **Chapter 4**. Indeed, mesocosm experiments may only capture a subset of possible mechanisms that occur under natural conditions in the field (e.g. Stachowicz et al. 2008).

As to the second main ecosystem function, the macroinvertebrate community is an important food source for higher trophic levels (e.g. birds), thereby connecting marine and terrestrial food webs (McLachlan and Brown 2006). Changes in macroinvertebrate community composition are therefore expected to propagate upwards in the sandy beach food web and finally alter ecosystem functioning. Lower macroinvertebrate abundance may attract fewer predators, both in the intertidal (Peterson et al. 2006, Costa et al. 2017) and supratidal zone (Dugan et al. 2003, Reyes-Martínez et al. 2015). These predators, especially birds, are however crucial in linking the intertidal and supratidal zone, together forming the sandy beach food web. As a lower intertidal macroinvertebrate abundance and a different intertidal macroinvertebrate community composition was observed at the Sand Motor mega-nourishment compared to other sandy beaches (**Chapter 2**), this may influence predators depending on these food sources (e.g. Linnartz 2012). Shore birds avoid sandy beaches where prey availability is low in the intertidal zone e.g. due to anthropogenic pressures (Peterson et al. 2006, Costa et al. 2017). For the supratidal macroinvertebrate community, we assessed the macroinvertebrate community composition associated with wrack (**Chapter 4)**, but how these findings relate to wrack communities on other Dutch sandy beaches and the subsequent effect on predators is unclear due to a lack of relevant studies. As indicated above, Diptera larvae abundance in wrack was similar compared to e.g. Jędrzejczak (2002b), suggesting predators such as birds may benefit from the availability of this prey source (Dugan et al. 2003).

Table 6.1. Summary of N and P mineralisation of wrack (standardised per g of initial wrack) in the experiments performed in Chapter 4 and 5. Incubation periods were two and four weeks in Chapter 4 and 5 respectively.

	Treatment	**N mineralisation (mg)**	**P mineralisation (mg)**
Litter bag experiment	Spring	9.4 (± 0.9)	1.1 (± 0.1)
(Chapter 4)	Summer	14.8 (± 2.6)	1.3 (± 0.1)
	Autumn	15.0 (± 2.6)	1.6 (± 0.1)
Mesocosm experiment	Shallow	5.8 (± 1.8)	0.8 (± 0.2)
(Chapter 5)	Deep	16.1 (± 2.8)	2.2 (± 0.4)

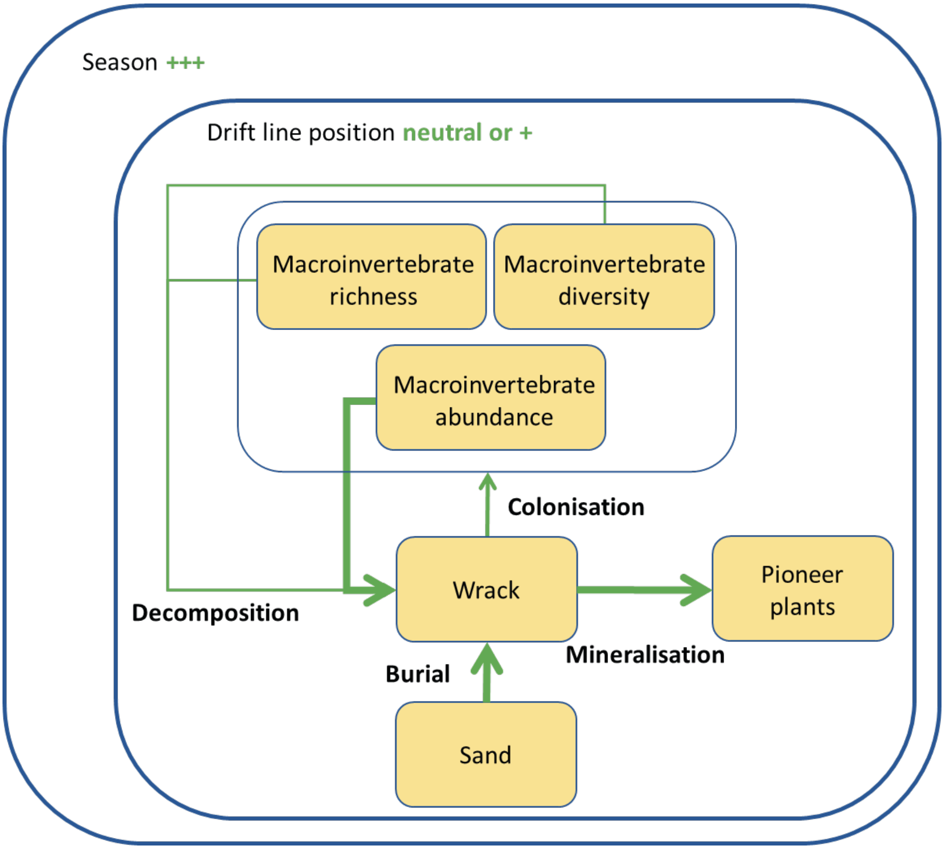

Figure 6.1 Summary of the drivers of wrack decomposition and mineralisation on sandy beaches. Arrows indicate processes (identified in bold text) between biotic and abiotic ecosystem components. Thickness of arrows indicate the strength of the relationship. All relationships are positive, except for the effect of drift line position which can be neutral (also indicated within the figure).

It is clear that both the intertidal and supratidal macroinvertebrate community are involved in the recycling of nutrients via both bottom-up (consumption and decomposition of organic matter) and top-down processes (being available as prey to predators) on sandy beaches. The results of this thesis thus strengthen the idea of a central role of the macroinvertebrate community within sandy beach ecosystem functioning. This is in line with observations in other ecosystems, such as salt marshes (Schrama et al. 2015), freshwater stream ecosystems (Wallace and Webster 1996, Covich 1999) and terrestrial soil ecosystems (e.g. Heemsbergen et al. 2004, Lavelle et al. 2006).

Take home message: *Mineralisation of wrack is mainly driven by season, wrack burial and supratidal macroinvertebrate abundance, and supports beach pioneer plant growth*

6.4 Mega-nourishment effects on the sandy beach ecosystem

Mega-nourishments are not fundamentally different from other sand nourishments, but do differ in shape, size and frequency. Consequently, a mega-nourishment can have direct (e.g. change in habitat characteristics) and indirect (e.g. change in dispersal and food availability) effects on the macroinvertebrate community and the sandy beach ecosystem that differ from other types of sand nourishment. The results of **Chapter 3** suggest that the Sand Motor mega-nourishment could have an indirect effect on the intertidal macroinvertebrate community by changing food availability. The hook-shape of the Sand Motor mega-nourishment resulted in significant changes in local hydrodynamics (Meirelles et al. 2017). This is expected to influence the distribution of organic particles (including diatoms), as these are strongly driven by hydrodynamic processes which are related to the coastal morphology of a certain beach (Shanks et al. 2017, Morgan et al. 2018). Phytoplankton may then become an important food source for the intertidal macroinvertebrate community in highly hydrodynamic environments (Menge 2000), for example around at the hook of the Sand Motor mega-nourishment. Indeed, intertidal macroinvertebrates do change their feeding behaviour, hence biological interactions, based on food availability in the field, with surf zone diatoms being a more important food source at dissipative than reflective beaches (Bergamino et al. 2016, Shanks et al. 2017). Measurements identifying the distribution of phytoplankton and relating this to the intertidal macroinvertebrate community in the field is necessary to establish this link directly. A relatively extensive system of tidal (sand) flats has been formed north and south of the Sand Motor mega-nourishment (from 2013 onwards) as a result of the distribution of sand originating from the hook of the Sand Motor mega-nourishment (Figure 1.3 in the General Introduction). A mosaic of intertidal micro-habitats with varying environmental conditions is created in this way, which may facilitate a higher intertidal macroinvertebrate abundance and richness as observed south of the Sand Motor mega-nourishment (**Chapter 2**). Interestingly, this result was not related solely to median grain size, supporting the growing notion that intertidal macroinvertebrate communities are assembled by a complex set of drivers including both abiotic factors and food availability (e.g. Rodil et al. 2012). Furthermore, the shape of the Sand Motor mega-nourishment created a hydrodynamically benign beach with a high mud and organic matter content (Wijsman 2016), resulting in the attraction of a distinct intertidal macroinvertebrate community typically associated with mud flats (**Chapter 2**). The Sand

Motor mega-nourishment therefore has a direct effect on the macroinvertebrate community by changing beach habitat characteristics. As different intertidal ecosystems (e.g. mud and sand flats) hold different species and show different food web characteristics, habitat diversity is likely important in maintaining overall ecosystem functioning (Horn et al. 2017).

The development of a beach with a high mud and organic matter content (Wijsman 2016), the formation of a microbial mat in the supratidal zone (personal observation, Figure 6.2) and the presence of wrack patches colonised by macroinvertebrates and support pioneer plants (**Chapter 4**, personal observation Figure 6.3) at the lagoon of the Sand Motor mega-nourishment, raises the question whether there is the potential for green beach development (Bakker et al. 2005, Esselink et al. 2009). Green beaches consist of a mosaic of salt marsh and dune vegetation in combination with microbial mats and develop on the seaward side of a dune ridge (De Groot et al. 2017a, Esselink et al. 2017). Salt marsh succession has been shown to be initiated by a decomposer-based food web, with a significant contributing role of microbial mats, rather than a terrestrial plant-based food web (Schrama et al. 2012). In particular, Diptera larvae of the species *Fucellia maritima* present on wrack deposits are a dominant detritivore group in the first years of salt marsh succession (Schrama et al. 2012). In **Chapter 4** we found that *Fucellia* sp. larvae were also the most abundant group on wrack adjacent to the lagoon. Thus, marine organic input plays an important role in initiating early succession of coastal ecosystems and facilitating pioneer plant establishment (**Chapter 4 and 5**). Another important factor for green beach development is the stabilization of the sand and provision of nutrients to pioneer plants via a microbial mat (Leewis 2017), which mainly consists of cyanobacteria and benthic microalgae that fix nitrogen (Severin and Stal 2008, Dijkman et al. 2010, Bolhuis and Stal 2011). Already in the first year after construction (2012) of the Sand Motor mega-nourishment, a microbial mat was present at the lagoon. However, up till now (2018, seven years after construction), no plants have established on this microbial

Figure 6.2 Microbial mat formation at the south-east side of the lagoon of the Sand Motor mega-nourishment (left: overview, lower right: detail). Directly below the surface of the microbial mat a black layer of sand is observed (upper right picture), indicating anoxic conditions due to the presence of iron sulphide (Pit et al. 2018, Bolhuis and Stal 2011).

mat. This may be due to a combination of factors including the lack of increased shelter by embryo dunes, high sand supply and low supply of fresh water (Bakker et al. 2005, van Puijenbroek 2018). Even mega-nourishments that were specifically designed to facilitate green beach succession did not develop as such to date (van Puijenbroek 2018). The lagoon at the Sand Motor mega-nourishment therefore seems unlikely to develop into a green beach or salt marsh, even though (parts of) the initial successional stage of a salt marsh ecosystem is present with a dominant role for the brown, decomposer-based food web (Schrama et al. 2012, Schrama et al. 2016).

In the general introduction, a conceptual scheme was proposed that indicated the expected effects of a change in coastal zone geomorphology (placement of a mega-nourishment) on niche-based community assembly and ecosystem functioning (Figure 1.4. Based on the outcomes of this thesis, I will indicate for which links evidence was found (Figure 6.4). For the intertidal macroinvertebrate community, we found that dispersal was not strongly limiting richness at the Sand Motor mega-nourishment as there was no effect of year after nourishment (**Chapter 2**), even though local hydrodynamic forces did change (Meirelles et al. 2017). No effect of median grain size was found on the intertidal macroinvertebrate community of the wave-exposed locations at the mega-nourishment, but the hook of the Sand Motor mega-nourishment did result in a change in beach environment and subsequent intertidal macroinvertebrate community composition (**Chapter 2**). The hook protected part of the beach from hydrodynamic forces thus enhancing habitat relief, which resulted in a benign lagoon which finally attracted a distinct intertidal macroinvertebrate community. The link between a change in coastal zone geomorphology and resource availability via a change in hydrodynamic forces was not explicitly studied, but the results of **Chapter 3** indicate that even though diatom availability to the intertidal macroinvertebrate community changes species interactions, co-existence can occur at least temporally. Whether this holds over a longer period of time remains the question. The presence of benthic microalgae as an additional food

Figure 6.3 Pioneer plant growth (left: *Honckenya peploides*, right: *Cakile maritima*) in a drift line on the beach of the Sand Motor mega-nourishment.

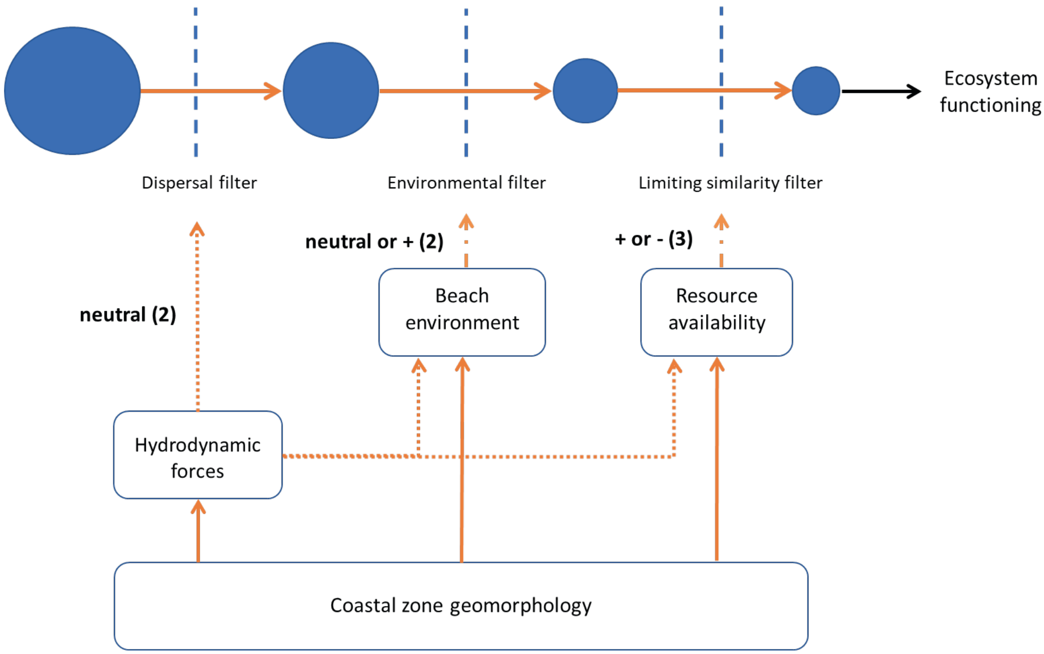

Figure 6.4 A model of niche-based community assembly and the impact of changes in coastal zone geomorphology (placement of a mega-nourishment) on the three filters: dispersal, environmental and limiting similarity, which are indicated above. A change in the coastal zone geomorphology can have both direct effects (continuous arrows in the lower part of the figure) and indirect effects (dotted arrows in the lower part of the figure) on the assembly filters. After each filter, fewer species remain in the species pool, finally resulting in a specific biological community (the far-right and smallest circle). This actual biological community then influences ecosystem functioning. Numbers in brackets correspond to the chapters in this thesis that provided evidence for specific links and whether these were found to have a neutral, positive or negative effect on the intertidal macroinvertebrate community.

source in the lagoon can furthermore support co-existence of intertidal macroinvertebrates. Finally, **Chapter 2** clearly showed that a mega-nourishment changes intertidal macroinvertebrate community composition, but subsequent effects on ecosystem functioning (e.g. nutrient cycling) have not been studied so far.

Adapting this model for the supratidal zone works less well, as links between changes in the coastal zone geomorphology and the supratidal macroinvertebrate community are expected to be less pronounced compared to the intertidal zone. These links have not been explicitly tested in this thesis. It is therefore more useful to implement knowledge on the relationship between supratidal macroinvertebrate community composition and wrack mineralisation (Figure 6.1) to apply to coastal management, e.g. after construction of a mega-nourishment.

Take home message: *A mega-nourishment creates novel habitat for intertidal macroinvertebrates, but abundance is lower than at regular beach nourishments*

6.5 Recommendations for future sand nourishments and coastal management

Based on the above, recommendations are given for the development of future mega-nourishments and coastal management to be applied on sandy beaches in general, to support the sandy beach ecosystem and macroinvertebrate communities in particular.

First, a future mega-nourishment should be highly heterogeneous in shape, creating a variety of habitats of exposed versus sheltered beach areas to temporally enhance intertidal macroinvertebrate diversity (**Chapter 2**). Sheltered habitats also lead to local concentrations of diatoms, promoting co-existence of intertidal macroinvertebrate species (**Chapter 3**) or potentially accumulate wrack of a different species composition and total mass (Orr et al. 2005, Liebowitz et al. 2016). This may initiate the early successional stage of green beach development (Schrama et al. 2012). Secondly, the beach should have a gentle slope to create a dissipative beach, which also reduces hydrodynamic stress on macroinvertebrate communities. A wider beach is then created with a wider intertidal zone, with a greater potential for nature to develop. The highest part of the Sand Motor mega-nourishment was 7.3 m above NAP (NAP being the Dutch datum at mean sea level (MSL)) directly after construction, creating a relatively steep increase from the low water line to the highest part of the beach (De Schipper et al. 2016). On the northern part of the hook, even 'sand cliffs' up to 1.5 m high were formed over the first years after construction as erosion occurred, resulting in an artificial break in the cross-shore beach profile (Linnartz 2012, personal observation). This is expected to have a negative effect on both the intertidal and supratidal macroinvertebrate community and should therefore be avoided, which potentially is achieved by reducing the total height above MSL and the beach slope. Thirdly, a future mega-nourishment is ideally designed as an island to minimise anthropogenic impacts on macroinvertebrate communities. An island is harder to reach for humans and results in less anthropogenic disturbance of macroinvertebrate communities. A wide variety of anthropogenic activities has been observed at the Sand Motor mega-nourishment on many occasions (personal observation), suggesting that these may have influenced macroinvertebrate communities negatively (Defeo et al. 2009, Schlacher et al. 2016). Alternatively, if the development of embryo dunes is desired, it is recommended to place the mega-nourishment attached to the coast line allowing for embryo dunes to become part of the current dune system. A future mega-nourishment is thus ideally heterogeneous in habitat, with both exposed and sheltered beach habitats, has a dissipative beach and is as much as possible protected from anthropogenic disturbances.

Further coastal management should focus on allowing wrack to remain on the beach as it is the foundation of the sandy beach ecosystem. In **Chapter 5** we found that buried wrack was an important driver of beach pioneer plant growth, indicating the importance of leaving wrack untouched after deposition on the beach (i.e. at least up to several weeks). *Talitrus saltator* was found to be a driver of decomposition-driven nutrient availability for beach pioneer plants, affecting plant nutrient dynamics. The field experiment performed in **Chapter 4** showed that wrack attracted a variety of supratidal macroinvertebrate species, which likely had a positive effect on mineralisation of wrack. In particular, this experiment stressed the importance of leaving wrack undisturbed on nourished beaches (and elsewhere) to support a diverse supratidal macroinvertebrate community, especially in summer. Summer is however also the period when the pressure of recreation is high and beaches are intensively cleaned (McLachlan and Brown 2006). The Sand Motor mega-nourishment was positioned in an area with a high recreational pressure (Jonker and Janssen 2007) and was therefore expected to attract many beach visitors. In 2004, Scheveningen, the beach directly north of the Sand Motor mega-nourishment, is yearly visited by 560.000 people and Kijkduin, the beach directly south of the Sand Motor mega-nourishment, is visited by 428.000 people a year (Otto 2004 in Jonker and Janssen 2007). These numbers are not expected to have changed considerably over the years, as beach recreation remains to be popular and was an additional management goal of this mega-nourishment. High recreational pressure may, however, have a negative effect on both intertidal and supratidal macroinvertebrates, for example by trampling, high use of off-road vehicles and wrack removal during beach cleaning (Defeo et al. 2009, Schlacher et al. 2016). At the Sand Motor mega-nourishment itself, wrack was allowed to remain on the beach and beaches were cleaned by handpicking trash bi-monthly (John van Nierop, personal communication). Beaches directly adjacent to the Sand Motor mega-nourishment, however, were mechanically cleaned from all trash and organic material by a beach cleaner, either daily in summer (May-September) or as required outside this period (John van Nierop, personal communication). This is where the municipality border runs and Dutch municipalities are able to make their own decisions regarding beach cleaning management. The Sand Motor mega-nourishment may have acted as a 'refuge' for supratidal macroinvertebrates, where food and shelter in the form of wrack was available in contrast to adjacent beaches. Throughout the year, Dutch sandy beaches are irregularly cleaned among others depending on season, tourism activity and funds and equipment available. It is therefore unclear at what distance from the Sand Motor mega-nourishment the next 'refuge' was situated for supratidal macroinvertebrates, which may have influenced community assembly processes related to dispersal and migration.

It is advisable to indicate the importance of wrack for the sandy beach ecosystem to those responsible for beach cleaning management at the coastal municipalities. Measures worth considering to reduce the impact of beach cleaning on the sandy beach ecosystem include 1) reducing the frequency of beach cleaning (e.g. to monthly or every other week), 2) repositioning the collected wrack to decompose within the same beach, retaining the nutrients in the system, 3) clean only a part of the beach, where uncleaned beaches facilitate recolonisation by supratidal macroinvertebrates of freshly deposited wrack after beach cleaning, and 4) manually cleaning beaches where possible, removing trash only and leaving the structure of wrack intact (Dugan and Hubbard 2010, Morton et al. 2015). Ideally, an inventory is made of the entire sandy coast line of the Netherlands, indicating where, how and how often wrack is cleaned from sandy beaches. Adjacent coastal municipalities are then able to communicate and align their beach cleaning activities, allowing wrack to be maintained on the sandy beach as much as possible in support of the sandy beach ecosystem. It would be even more effective if beach cleaning activities are included in coastal management on a national level as part of the nature conservation policy. Surprisingly, the supratidal zone is currently not part of any Natura 2000 habitat type or only partly protected under the Birds and Habitat Directive (De Groot et al. 2017b). This calls for a nation and European wide change in policy related to sandy beach ecosystems by including the supratidal zone to protect wrack communities.

Sand nourishments are primarily designed to protect the hinterland against flooding, but may be intended to serve several other purposes. After a nourishment has been placed, coastal management thus continues. Beach management after placement of the nourishment can be based on the identification of two key factors: conservation value and recreational potential of the sandy beach (McLachlan et al. 2013). Beaches in urban areas such as in the Netherlands can be best managed for multiple-purpose use, covering both aspects of ecological conservation and recreation. Thus, a compromise has to be achieved between what ecologists suggest as optimal solutions and what local stakeholders will allow for the sandy beach in question.

Take home message: *A future mega-nourishment should be heterogeneous in habitats, have a dissipative beach and be protected from anthropogenic disturbances*

6.6 Research agenda

As with all research, while some questions received an answer in this thesis, new questions have emerged. New research avenues related to the findings of this thesis are hence identified below.

Resource availability showed to be important in changing species interactions and consumption by intertidal macroinvertebrates (**Chapter 3**), but it remains unclear exactly how this translates to changes in community composition and finally ecosystem functioning. Long-term mesocosm studies would allow for testing the effect of changing species interactions related to food availability and give further insight in intertidal macroinvertebrate community assembly processes over time, but may be hard to establish. In the field, a study to determine the link between the intertidal macroinvertebrate community composition and diatom availability would be interesting to perform, supplementing the results of the mesocosm experiment (**Chapter 3**). This study could then include the identification of both juveniles and adults in the intertidal macroinvertebrate community, linking species interactions and community composition via population dynamics of individual macroinvertebrate species. By also identifying abiotic factors that may structure the intertidal macroinvertebrate community (such as beach slope and median grain size), an assessment of the relative importance of abiotic and biotic factors in intertidal macroinvertebrate community assembly on sandy beaches can be made. Insights on this topic have recently started to emerge, but deserve further attention (HilleRisLambers et al. 2012, Schlacher et al. 2015).

As for ecosystem functioning, sandy beaches provide many ecosystem functions, including nutrient cycling, but this has rarely been quantified (Schlacher et al. 2008, Nel et al. 2014). The results of **Chapter 4 and 5** place emphasis on the importance of cross-boundary connectivity in the context of sandy beaches as a subsidised ecosystem (Polis and Hurd 1996, Schlacher et al. 2015; Gounand et al. 2018). Identifying nutrient cycling and performing food web analysis of the entire sandy beach ecosystem, thus including both the intertidal and supratidal zone, would in that light be a valuable research avenue, as such studies have previously focused on the intertidal zone alone (e.g. McLachlan et al. 1981). More generally, sandy beach studies now need to move from primarily trying to understand changes in community composition and food webs, but more specifically address the question how these changes alter ecosystem functioning (see Costa et al. 2017). For example, this question could be addressed by studying the effect of supratidal macroinvertebrate community composition on decomposition and nutrient mineralisation of wrack of different quality (e.g. macroalgae species) in a mesocosm experiment.

Follow-up studies on the intertidal macroinvertebrate community related to the Sand Motor mega-nourishment should focus on the spatial and temporal variations of the intertidal macroinvertebrate over a longer period of time, as the shape of the Sand Motor mega-nourishment will continue to change. Only the first four years of monitoring after construction of the Sand Motor mega-nourishment could be included in **Chapter 2**. Whether abundance would increase and community composition converges to or further deviates from regular beach nourishment over the coming years, requires continuous monitoring of the intertidal macroinvertebrate community. In particular, the intertidal macroinvertebrate community of the lagoon should be monitored more intensively, in concert with taking sediment and water samples to assess the relation between the intertidal community and food availability (primarily benthic microalgae). Together, this will provide more insight on the effects of a low frequency of sand nourishment on the intertidal macroinvertebrate community on a temporal and spatial scale. It is further interesting to study the relationship between wrack input and its supratidal macroinvertebrate community composition at a mega-nourishment in comparison to other types of sand nourishment. Since a mega-nourishment is expected to change the coastal zone geomorphology considerably, wrack input may subsequently change (Orr et al. 2005, Liebowitz et al. 2016, Reimer et al. 2018). Ideally, this would include studying wrack and its supratidal macroinvertebrate community at the sandy beach both before and after construction of the mega-nourishment, in the same time of year to account for seasonal differences in wrack input and supratidal macroinvertebrate community composition (as shown in **Chapter 4** for the latter). As an alternative, sandy beaches representing a range of potential changes in coastal zone geomorphology as a result of sand nourishment could be sampled. This will improve our understanding of how a change in coastal zone geomorphology changes wrack input to sandy beaches and subsequently supratidal macroinvertebrate community composition.

Finally, it is striking that sandy beach monitoring programs in the Netherlands are solely focused on the intertidal and subtidal macroinvertebrate communities or the dune ecosystem, but the supratidal zone is structurally being ignored. Few studies have focused on wrack and (succession of) the supratidal macroinvertebrate community in the Netherlands (but see Schrama et al. 2012, Leewis 2017), thus requiring more study in the Dutch context (Cadée 2014). Especially on the Wadden islands in the north of the Netherlands, wrack is allowed to accumulate and reach a higher macroinvertebrate abundance and richness than on sandy beaches along the Dutch coast (Schrama et al. 2012, Cadée 2014). This provides an interesting opportunity to study the relationship between wrack mineralisation and pioneer plant growth and the role of macroinvertebrates in this process, which will improve our understanding of how the marine and terrestrial ecosystems are connected and of the drivers of the first stage of salt marsh and/or dune succession (Schrama et al. 2012, Schrama et al. 2015).

***Take home message:** Future studies need to focus on linking community composition to ecosystem functioning on sandy beaches, especially for the largely neglected supratidal macroinvertebrate community associated with wrack*

6.7 Conclusions

This thesis showed a clear effect of resource availability on macroinvertebrate species interactions and subsequent consumption in the intertidal zone, which may indirectly affect community composition. Biological interactions related to resource availability therefore cannot be ignored when aiming to understand macroinvertebrate community assembly on sandy beaches. Also, it has been shown here that it is crucial for both the supratidal macroinvertebrate community and sandy beach ecosystem functioning that wrack is maintained on sandy beaches. The results of this thesis therefore emphasise the link between the marine and terrestrial ecosystems, with a central role for the macroinvertebrate community in sandy beach ecosystem functioning, in particular decomposition and nutrient cycling.

For the first time, the effect of a large-scale sand nourishment on the intertidal macroinvertebrate community has been studied. In terms of the intertidal macroinvertebrate community, it is concluded that a mega-nourishment appears to be a promising coastal defence strategy compared to regular beach nourishment, at least during the first years after construction. Overall, this thesis highlights the need to include the effect of resource availability on both the intertidal and macroinvertebrate community and the sandy beach ecosystem as a whole, especially when designing and planning future coastal management practices.