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## Living on the edge

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## **Chapter 1**

### General introduction

Sandy beaches are among the most prevalent coastal ecosystems in the world and are estimated to cover up to 70% of the ice-free coasts (McLachlan and Brown 2006). They harbour unique ecological communities with many species only found on sandy beaches and provide a wide variety of ecosystem functions, including nutrient cycling (McLachlan and Brown 2006). Due to the very dynamic character of sandy beaches, the *in situ* primary production is low and resource availability in the form of phytoplankton (intertidal zone) and wrack (supratidal zone) is spatially and temporally highly heterogeneous (Colombini and Chelazzi 2003, Liebowitz et al. 2016). The sandy beach food web heavily depends on this input of marine exogenous organic matter (Polis et al. 1997, Liebowitz et al. 2016). In particular, the macroinvertebrate community of the intertidal and supratidal zone together form the link between marine primary production and higher trophic levels, connecting the marine and terrestrial food webs (Speybroeck et al. 2008a). It remains unclear, however, how resource availability influences species interactions and community assembly of the macroinvertebrate community on sandy beaches, and how this influences ecosystem functioning.

While of critical importance, on a global scale, sandy beach ecosystems are subject to coastal squeeze: beaches are trapped between the rising sea level and an increase in storm events due to climate change on the sea side, and static anthropogenic structures on the land side (Schlacher et al. 2007). The coastal zone, sandy beaches included, is densely populated by humans (Small and Nicholls 2003) and coastal populations are only expected to further increase (Neumann et al. 2015). This combination of factors causes severe erosion of the sandy beach, threatening the human population and livelihood as the sea advances inland and leaving only a narrow strip for ecological communities to reside. Sand nourishment has been applied to mitigate the effects of beach erosion, but recently a mega-nourishment has been proposed as a more ecologically and sustainable alternative (Stive et al. 2013). A mega-nourishment is created by placing a very large volume of sand in a concentrated location along the coast, which is intended to gradually nourish up-stream beaches over a long period of time. This lowers the number of pulse disturbances to the sandy beach ecosystem compared to regular sand nourishment practices. After application of a mega-nourishment, ecological communities have to re-assemble, but community assembly may be directly or indirectly influenced by the characteristics of the mega-nourishment. The effect of a mega-nourishment on the macroinvertebrate community and how this compares to regular sand nourishment thus remains unknown.

Below, I will first explain the physical characteristics of the beach and its effect on resource availability, followed by a description of the sandy beach food web and its components. I will give a definition of the macroinvertebrate community and indicate the main drivers of community assembly in general and of the macroinvertebrate community on the sandy beach in particular, with a focus on resource competition. I will explain how sand nourishment has been applied and what the ecological impacts have been thus far, followed by a description of a mega-nourishment and its expected effects on the macroinvertebrate community. Finally, the aims, research questions and outline of this thesis are given.

## **1.1 The sandy beach ecosystem on the interface between sea and land**

### *1.1.1 Physical environment of sandy beaches*

In its essence, sandy beaches are enormous aggregations of sand particles on the interface between sea and land. These ecosystems are highly dynamic, as sandy beaches are subject to the interaction between wind, waves and tides that continuously change the abiotic environment and beach profile (McLachlan and Brown 2006). The perpetual movement of sand particles and water across the beach results in a range of beach types (Short and Wright 1983, Wright and Short 1984). This distinction among beach types can be made based on their morphodynamical features: reflective beaches are narrow and steep with waves braking directly on the beach, while dissipative beaches are wide and flat with waves being broken by an extensive surf zone before reaching the beach. Moreover, fine sand and a large tidal range are found on dissipative beaches as opposed to reflective beaches with coarse sand and a small tidal range. Intermediate beaches are found between these two extremes (Short and Wright 1983, Short 1996). A beach can furthermore be categorised based on the degree of wave exposure, being either exposed, where the beach is subject to a high wave energy regime, sheltered, where the beach is more protected and subject to a low wave energy regime (such as in a lagoon), or in between (McLachlan and Brown 2006).

Perpendicular to the coast, the sandy beach is generally divided into two main zones divided by the water line as a dynamic border: the intertidal and the supratidal zone (McLachlan and Jaramillo 1995, Dugan et al. 2013; see Figure 1.1). The intertidal zone is defined as the zone between the mean high water line at spring tide (MHWS) and the mean low water line at spring tide (MLWS). Twice a day, this part of the beach is submerged by the sea under influence of the lunar tidal cycle, moving the water line up and down along the beach. The water column overlaying the intertidal zone during high tide is also termed the surf zone (Morgan et al. 2018). Intertidal systems therefore alternate between being either dry or moist, or fully saturated by sea water (McArdle and McLachlan 1991). The supratidal zone of the sandy beach is defined as the part of the beach above MHWS up to the dune foot where primary and secondary dunes begin to emerge. In contrast to the intertidal zone, this zone is not submerged by the sea during the tidal cycle and the sand remains dry, except for heavy storms creating high waves passing the MHWS and occasional precipitation. Thus, the abiotic environment, including water, salinity and oxygen content, differs notably between these two beach zones. The intertidal zone borders the subtidal zone (below MLWS) which is permanently submerged by the sea (Figure 1.1).

### *1.1.2 Effect of the physical environment on resource availability*

Sandy beaches provide a unique coastal interface between sea and land linking marine and terrestrial ecosystems (Polis et al. 1997, Liebowitz et al. 2016). The ecosystem boundaries of sandy beaches are continually crossed by (in)organic matter, nutrients and, where biologically possible, organisms (Barrett et al. 2005, Heck et al. 2008). Sandy beaches are considered to be primarily recipient ecosystems, because they receive large amounts of exogenous organic matter that has been produced by primary and secondary producers in the sea (Liebowitz et al. 2016). Marine exogenous organic matter mainly enters the sandy beach ecosystem in the

form of organic matter particles and plankton in intertidal waters or beach-cast sea weed and sea grass, collectively termed wrack (Colombini and Chelazzi 2003). Due to the dynamic character of sandy beaches, the input of marine exogenous organic matter and thus resource availability to the sandy beach ecosystem is spatially and temporally highly heterogeneous.

Within the surf zone, a diverse mixture of dissolved and particulate organic matter, phytoplankton and zooplankton is present. Once these organic matter particles and plankton have entered the surf zone, their distribution is strongly driven by hydrodynamic processes which are related to the coastal morphology of a certain beach (Shanks et al. 2017, Morgan et al. 2018). For example, the abundance of phytoplankton in the surf zone is dependent on along-shore variation in hydrodynamics, with a higher abundance in dissipative than in reflective surf zones (Shanks et al. 2017). The same pattern has been observed for zooplankton (Morgan et al. 2018). Phytoplankton community composition may also be affected by hydrodynamic processes. Only a small number of species are adapted to the high wave energy conditions at certain beaches and considered as surf diatoms (e.g. *Thalassiosira* sp. Cleve), while other phytoplankton species mainly occur outside the surf zone (Odebrecht et al. 2014). Offshore phytoplankton is transported by waves and currents to the surf zone where it is an important component of phytoplankton communities, as surf diatom taxa may only compose 1% of the phytoplankton community (Morgan et al. 2018). Unlike phytoplankton communities, zooplankton community composition may be further determined by the interaction between hydrodynamic processes and the ability of most zooplankton to actively move in the water column (Morgan et al. 2018).

Wrack supply on sandy beaches depends on the availability, transport and deposition of wrack (Liebowitz et al. 2016). Sea weeds and sea grasses are primary producers that grow attached to a substratum, but become detached as a result of severe hydrodynamic conditions, such as storm events (Suursaar et al. 2014). Detachment may be influenced by both abiotic factors, including substratum type and near-bed current velocity, and biotic factors, including strength of attachment and senescence (Liebowitz et al. 2016). The transportation and deposition of wrack subsequently depends on a complex interplay between factors such as wind, waves and currents in the surf zone, wrack traits related to buoyancy capacity, size and life form, and beach morpho-dynamic type (Orr et al. 2005, Liebowitz et al. 2016). Combined, these factors influence the amount, composition, location and nutritional quality of wrack present on a beach. As such, wrack input is highly variable. For example, wrack input ranged between 0.2 and 43.1 kg m<sup>-1</sup> y<sup>-1</sup> on Spanish beaches (measured as the wrack cover within a 1 m wide strip of beach along a transect running from the dune foot to the lowest swash level, adapted from Barreiro et al. 2011), but ranged between 1000 and 2000 kg m<sup>-1</sup> y<sup>-1</sup> on Californian beaches (Polis et al. 1997).

Several semi-continuous bands of wrack are usually formed parallel to the coast line. On a tide-dominated beach, multiple drift lines are formed as the water slowly recedes from spring to neap tide, allowing patches of wrack to deposit on the beach at different tidal heights (Hamman and Zimmer 2014). In contrast, tide-independent beaches mainly accumulate wrack just above the high water line and wrack may be redistributed by extreme high sea water levels or high wind speeds to form multiple drift lines (Hamman and Zimmer 2014).

Also, the location of wrack on the beach, i.e. the distance to mean sea level, is strongly determined by tidal amplitudes which change monthly to annually (e.g. Plag and Tsimplis 1999). Fresh wrack is primarily present in younger drift lines around the high water line (Orr et al. 2005). If fresh wrack is not resuspended into the sea, wrack may either remain in its current location or be transported further up-shore by wind until the material is buried in the sand, caught by other structures (e.g. plants) or has reached a wind-dead location (Hammann and Zimmer 2014). This older wrack is thus generally present in drift lines higher up the beach and closer to the dune foot than young drift lines consisting of fresh wrack. Old wrack is no longer directly influenced by sea water and decomposes through a variety of abiotic and biotic processes, further changing the nutritional quality of the wrack (Colombini and Chelazzi 2003). Abiotic processes that work on deposited wrack include drying by the sun, erosion of organic material by wind and coverage by a layer of sand, while biotic processes include the decomposition of wrack by microbes and detritivores (Colombini and Chelazzi 2003).

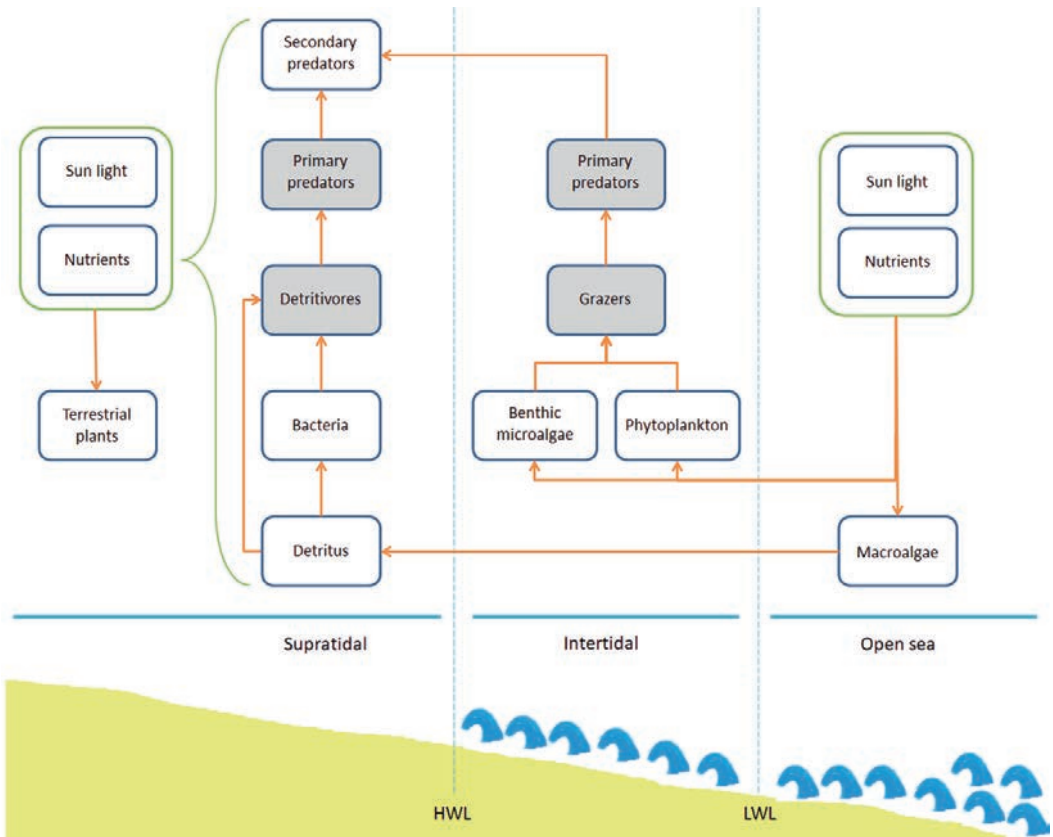
### *1.1.3 Sandy beach food web*

Although sandy beaches may appear void of life upon first glance, sandy beaches harbour unique ecological communities consisting of many species that are not found in any other ecosystem. On sandy beaches, three food webs that have traditionally been considered to show little connectivity, can be distinguished: 1) the interstitial food web in intertidal sands (benthic microalgae, bacteria, protozoa and meiofauna (including mites and spring tails)), 2) the microbial food web in the surf zone (phytoplankton, zooplankton, bacteria and protozoa) and 3) the macroscopic food web (including macrofauna, fish and birds) (McLachlan and Brown 2006). The macroscopic food web, however, has more recently been linked to the microbial food web via the consumption of phytoplankton by macrofauna and to the interstitial food web via the shared consumption of benthic microalgae by meio- and macrofauna (Lercari et al. 2010, Bergamino et al. 2011, Maria et al. 2011, Bergamino et al. 2013). In this thesis, the focus is on the macroscopic food web while including phytoplankton and benthic microalgae, and is here referred to as the sandy beach food web.

The sandy beach food web spans across the intertidal and supratidal zones and is connected to the subtidal zone and dune foot (Speybroeck et al. 2008a). The spatially separate intertidal and supratidal food webs are connected at the higher trophic level by predators that consume from the lower trophic level in both beach zones, intertwining these food chains to create the sandy beach food web (Figure 1.1). Dissolved nutrients in the sea water and sunlight drive the production of phytoplankton, benthic microalgae, sea weed and sea grass, the so-called green web. In the intertidal zone, the benthic microalgae attached to sand grains and phytoplankton in the water column are consumed by grazers. In the supratidal zone, detached sea weed and sea grass cast upon the beach serve as a food source for bacteria and detritivores, the so-called brown web. Different primary predators in the intertidal and supratidal zone feed on these lower trophic levels and are in turn consumed by secondary predators. Together with solar energy, nutrients that become available at different trophic levels through decay of organic matter in the supratidal zone may finally flow to terrestrial plants. Below I will expand on the food web components of the sandy beach.

1.1.3.1 Primary producers

The *in situ* primary production of sandy beaches is low due to the intense and continuous reworking of sandy sediments, providing an unstable environment for primary producer establishment (McLachlan and Brown 2006). In the intertidal zone, benthic microalgae grow attached to sand grains and communities are dominated by diatoms (Speybroeck et al. 2008a). Benthic microalgae can be an important food source for deposit-feeders or, if resuspended in the water column, for filter-feeders (Miller et al. 1996). In temperate beaches, vascular plants are only present in the supratidal zone, where the drift line forms the lower boundary for plant settlement (Speybroeck et al. 2008a). Most plants are annuals and adapted to a dynamic environment, with *Cakile maritima* Scop. and *Honckenya peploides* (L.) Ehrh. as examples of common species on sandy beaches, growing in the neighbourhood of old wrack (Davy et al. 2006, Speybroeck et al. 2008a). Nutrient supply for these plants originates from decomposition of organic matter from the supratidal zone, primarily wrack (Williams and Feagin 2010, Del Vecchio et al. 2013).



**Figure 1.1** A schematic representation of the sandy beach food web, spanning across the open sea, the intertidal and supratidal zone. Grey boxes indicate the components of the macroinvertebrate community in both the intertidal and supratidal zone. HWL = high water line at spring tide, LWL = low water line at spring tide.



### 1.1.3.2 Consumers

Consumers of the intertidal zone are dominated by deposit- and filter-feeders (grazers) and depend on particulate organic matter, phytoplankton and benthic microalgae as food sources (McLachlan and Brown 2006; see Figure 1.2). Taxonomic groups mainly include polychaete worms and crustaceans (McLachlan and Jaramillo 1995, Degraer et al. 2003). Foraging occurs during high tide, when the water column containing food particles overlays the intertidal zone. For example, the polychaete worm *Scolelepis squamata* Müller remains in its burrow during high tide but protrudes its palps from the burrows opening and moves its palps to collect any organic particles floating in the water or deposited on the sediment surface (Dauer 1983). The amphipod *Bathyporeia pilosa* Lindström, on the other hand, feeds by scraping the organic material from sand grains using its mouth parts (Nicolaisen and Kannevorff 1969). Consumers of the supratidal zone are dominated by detritivores and depend on wrack and other drift line components, such as faeces and carrion (Colombini and Chelazzi 2003). In addition, it is suggested that some detritivores not (only) feed on wrack itself but on the wrack-associated biofilm (Porri et al. 2011). Taxonomic groups mainly include amphipods and insects of the orders Coleoptera and Diptera (Olabarria et al. 2007). The amphipod *Talitrus saltator* Montagu is an abundant species in wrack (Ruiz-Delgado et al. 2016) and is a key consumer on sandy beaches and may consume up to 11% of its dry body weight in wrack per day (Lastra et al. 2008). During the day, the amphipod remains in its burrows but emerges at night to feed on stranded wrack (Fallaci et al. 1999). Another abundant group of wrack consumers are Diptera larvae. After egg hatching, the emerged Diptera larvae bury themselves into the wrack and start feeding immediately, consuming up to 1.8 times their dry weight in wrack per day (Stenton-Dozey and Griffiths 1980).

### 1.1.3.3 Predators

Both primary and secondary predators occur in the sandy beach food web and predators include polychaete worms, isopods, crabs, shrimp, fish and birds in the intertidal zone (Van Tomme et al. 2014) and insects of the order Coleoptera and birds in the supratidal zone (Speybroeck et al. 2008a). In the intertidal zone, the common isopod *Eurydice pulchra* Leach predares actively during high tide but remains buried in the sand during low tide (Reid 1988).



**Figure 1.2** An individual of the macroinvertebrate species *Scolelepis squamata* from the intertidal zone (left) and *Talitrus saltator* from the supratidal zone (right).

*Eurydice pulchra* tries to feed on any animal that it encounters (Holdich 1981), including the co-occurring intertidal species *Bathyporeia sarsi* Watkin, *B. pilosa* and *S. squamata* (Van Tomme et al. 2014). It is a primary predator as it may be consumed by secondary predators. With incoming tide, fish, shrimp and crabs can access the intertidal zone to forage on the intertidal macroinvertebrates (Beyst et al. 2001). For example, juvenile flat fish (such as *Pleuronectes platessa* L. and *Scophthalmus maximus* L.) and the shrimp *Crangon crangon* L. consumed large and equal amounts of *S. squamata* and *B. pilosa* in a feeding experiment (Van Tomme et al. 2014). In the supratidal zone, shorebirds may feed on wrack-associated macroinvertebrates using visual and tactile cues. For example, a positive correlation was found between the abundance of two plover species (*Pluvialis squatarola* L. and *Charadrius alexandrinus nivosus* Cassin) and both wrack mass and macroinvertebrate abundance (Dugan et al. 2003). These species are expected to catch prey from the sand and wrack surface, while bird species that mainly use tactile cues (such as *Calidris alba* Pallas) are more efficient at capturing buried macroinvertebrates, also from the intertidal zone (Vanermen et al. 2009, Dugan et al. 2003).

#### 1.1.4 Key role for the macroinvertebrate community on sandy beaches

Within the sandy beach food web, grazers, detritivores and primary predators together form the macroinvertebrate community (see grey boxes in Figure 1.1). Macroinvertebrates are in this thesis defined as all invertebrate animals that are >1 mm as adults, thus being retained when sieved over a 1-mm sieve. A distinction is made between the macroinvertebrate community of the intertidal and supratidal zone (Mariani et al. 2017), because macroinvertebrates have specific adaptations to the environmental conditions of the zone they inhabit and seldomly move between these zones (Speybroeck et al. 2008a). This is especially true for macroinvertebrates in the intertidal zone, which are bound to a moist environment and bury into the sand to avoid being swept into the sea or desiccate during low tide (McLachlan and Brown 2006). In the supratidal zone, many macroinvertebrate species are air-breathers (e.g. insects) and may only visit the intertidal zone during low tide to forage. Since macroinvertebrate densities can locally be very high for certain species (e.g. *S. squamata*), the macroinvertebrate community holds the potential to have a significant effect on ecosystem functioning.

The focus of this thesis will be on the macroinvertebrate community of the intertidal and supratidal zone, because these two communities form the link between marine primary production and higher trophic levels, connecting the marine and terrestrial food webs. As such, the macroinvertebrate community serves 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). Both functions are supported by the intertidal and the supratidal zone, where the latter has briefly been covered in section 1.3.3 and the former will be shortly discussed below.

##### 1.1.4.1 Macroinvertebrate community effects on nutrient cycling

Nutrient cycling is mainly driven by the activity of intertidal macroinvertebrates who assimilate and mineralise organic particles, resulting in a release of inorganic nutrients to the

surf zone, e.g. stimulating phytoplankton blooms (McLachlan 1980, McLachlan et al. 1981). For example, macroinvertebrates (including both macrobenthos and zooplankton (e.g. *Eurydice longicornis* Studer)) were estimated to recycle  $2990 \text{ g N m}^{-1} \text{ y}^{-1}$  (across the beach from the highest drift line to 10 m depth) or  $6.0 \text{ g N m}^{-2} \text{ y}^{-1}$ , producing 23% of N needed by the phytoplankton community on an exposed sandy beach in South Africa (adapted from Cockcroft and McLachlan 1993). Beach-specific estimates of the contribution of the macroinvertebrate community on total carbon and nitrogen budgets are, however, dependent on many factors, such as local species abundances and the functional diversity of the macroinvertebrate community, e.g. variation in excretion rates (Villéger et al. 2012). The effect of changes in community composition on nutrient cycling has, however, not been intensively studied. Processing of wrack by the supratidal macroinvertebrate community may also lead to a flow of nutrients back to the sea to support marine primary production, as nutrients leach from partly decomposed wrack around the high water line (Colombini and Chelazzi 2003). Alternatively, nutrient hot spots may be created in the supratidal zone, locally supporting terrestrial primary (Hemminga and Nieuwenhuize 1990, Del Vecchio et al. 2013) and secondary production (Polis and Hurd 1996, Schlacher et al. 2017). When these nutrients become available for plant uptake, this may facilitate pioneer beach plant species to establish on the sandy beach (Dugan et al. 2011). Finally, this could initiate embryo dune formation as pioneer plant species colonise the older, comprised of lots of decomposed material, and higher positioned drift lines (Hemminga and Nieuwenhuize 1990). Total carbon and nitrogen budgets of the supratidal zone that include wrack and its consumers are lacking from the literature, but supratidal macroinvertebrates are estimated to consume up to 80% (Griffiths and Stenton-Dozey 1981, Griffiths et al. 1983) and even 100% (Lastra et al. 2015) of the organic matter input entering the beach. Hence, the supratidal macroinvertebrate community potentially plays an important role in recycling nutrients from wrack deposits but needs to be studied further.

## **2.2 Drivers of macroinvertebrate community assembly on sandy beaches**

Since the macroinvertebrate community is a key component of the sandy beach ecosystem, it is crucial to understand what drives the assembly of macroinvertebrate communities on sandy beaches. As indicated above, after application of a mega-nourishment, the macroinvertebrate community has to re-assemble, but community assembly may be directly or indirectly influenced by the characteristics of the mega-nourishment. Altered local hydrodynamics around a mega-nourishment may for example change macroinvertebrate dispersal patterns and resource availability (by influencing the distribution of phytoplankton, benthic microalgae and wrack). This in turn may influence species interactions and drive community assembly, resulting in the actual macroinvertebrate community composition present on a sandy beach. Below, I will first discuss general community assembly theory, followed by the main drivers of macroinvertebrate community assembly on sandy beaches in particular, with a focus on resource competition.

### *2.2.1 Assembly theory*

Identifying the processes that drive and control community assembly are crucial to understand the actual composition of biological communities on sandy beaches. One way to

approach this is to determine the relative importance of abiotic and biotic drivers of the assembly process and if the factors can be captured in 'rules' (HilleRisLambers et al. 2012). Classical assembly rules are proposed by Diamond (1975) stating that interspecific interactions (mainly competition) lead to a non-random co-existence of species within a community. This view was expanded by Keddy (1992), proposing that both the biotic and abiotic environment act like a filter, or set of filters, selecting species based on their traits from the species pool (see Figure 1.4, upper part). Through the stochastic processes dispersal and migration, a set of species is selected from the regional species pool (dispersal filter). Then, species are filtered by local, deterministic processes from the environment (environmental filter) and via biological interactions, especially competition (limiting similarity filter). In the end, a community is assembled of which the composition depends on the influence of each filter present and what these filters comprise of in a specific ecosystem (Márquez and Kolasa 2013, Götzenberger et al. 2011). Contrasting thoughts on assembly rules are given by Hubbell (2001) who proposed the 'unified neutral theory of biodiversity and biogeography', which is based on the assumption that differences between individuals of the same trophic level are 'neutral', and therefore these differences are irrelevant for their success. It means that all individuals within a trophic level have the same chances for migration, birth and death. Communities are then assembled by dispersal limitation, speciation and ecological drift (Rosindell et al. 2011). Hubbell's theory basically states that by replacing one species for another or by eliminating all species but one, this will have no effect on the community functioning (e.g. nutrient cycling). To date, there is continuous debate about the importance of niche-based and neutral community assembly (Rosindell et al. 2011), but consensus is emerging that niche-based community assembly and stochastic processes may operate simultaneously to assemble biological communities (Weiher et al. 2011, Vellend et al. 2014, Conradi et al. 2017).

### *2.2.2 Assembly processes on sandy beaches*

In sandy beach ecology, the existing paradigm is that biological communities are 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). First, many intertidal macroinvertebrate species depend on local hydrodynamic forces for dispersal, i.e. the dispersal filter (Günther 1992, Van Tomme et al. 2013). 'Source' populations with a continuous age population structure may seed sandy beaches with harsh environmental conditions that harbour 'sink' populations containing few age classes, postulated as the source-sink hypothesis (Defeo and McLachlan 2005). The autecological hypothesis states that communities in a physically stressed environment, such as the intertidal zone of an exposed sandy beach, are structured by the independent responses of individual species to this environment, rendering biological interactions largely unimportant (Noy-Meir 1979, McLachlan 2001). More specifically, the swash exclusion hypothesis states that on reflective beaches the harsher swash climate excludes, or filters, species from the regional species pool (McLachlan et al. 1993). The combination of coarse sand and a turbulent swash make it difficult for species to burrow in the intertidal zone, leading to a lower abundance and species richness on reflective beaches (Defeo and McLachlan 2011). As a result, intertidal macroinvertebrates on reflective beaches must attribute more energy to maintenance, while less energy is available for reproduction and this

idea has been postulated as the habitat harshness hypothesis (Defeo et al. 2001). Towards more dissipative beaches, however, the physical environment becomes more benign and biological interactions may become more important as a driver of community assembly. Abundance and species richness increase towards these more dissipative beaches, leading to a greater potential for encounters between individuals and hence biological interactions (McLachlan and Brown 2006, Defeo and McLachlan 2011). This is not merely due to the effect of beach width itself, but a wide beach contains more areas that are less severely influenced by abiotic stress caused by the sea, allowing for more different species to inhabit this beach (McLachlan and Dorvlo 2007).

Evidence indicating that biological interactions may be more important for intertidal community assembly on sandy beaches than previously recognised, is slowly accumulating. Previous studies have primarily focused on physical control of macroinvertebrate communities but did not include main drivers such as competition for resources or investigated the relative effect of the environment and biological interactions on final community composition (exceptions include Defeo et al. 1997, Dugan et al. 2004, Van Tomme et al. 2012). Studies that included biological interactions were mainly aimed at understanding zonation patterns of co-occurring species, instead of community responses. Ortega-Cisneros et al. (2011), however, found that the intertidal macroinvertebrate community composition of a South African sandy beach did not primarily respond to physical changes, but that these communities were assembled through a complex mixture of environmental factors and resource availability, including salinity, beach width and nutrient quality and availability. Moreover, Lastra et al. (2006) found on a Spanish sandy beach that in addition to an increase in intertidal species richness with a decrease in mean grain size and an increase in beach width, there was a positive relationship between food availability (measured as chlorophyll-a in the water column) and intertidal species richness. A recent global meta-analysis indicated that beach slope, tidal range and chlorophyll-a combined were the most important explanatory variables of intertidal macroinvertebrate richness, closely followed by grain size (Defeo et al. 2017). This suggests that environmental factors and biological interactions related to resource availability combined may alter intertidal macroinvertebrate community composition. It may be that physical factors on their own have a less powerful predictive ability of intertidal macroinvertebrate community composition, and that the changes in resource availability elicited by these physical factors and subsequent competition are more important drivers of community assembly. Finally, environmental factors may act on the macro-scale (between climate zones and morphodynamic beach types) and meso-scale (between beaches), while biological interactions may determine the final intertidal macroinvertebrate community composition on the micro-scale (within beaches) (Defeo and McLachlan 2005).

Less theory related to community assembly has been developed for the macroinvertebrate community of the supratidal zone. The habitat safety hypothesis states that microtidal, reflective beaches, due to their narrow swash and steep slope, provide a more stable habitat for supratidal macroinvertebrates, such as talitrids (Defeo and Gómez 2005). On these beaches, supratidal macroinvertebrates run a lower risk to be submerged by the sea as the supratidal zone is not frequently inundated and macroinvertebrates are not affected by the interaction between coarse sand and turbulent swash (Defeo and Gómez 2005). This results

in a less harsh environment and a less narrow environmental filter, allowing more supratidal macroinvertebrates to inhabit this sandy beach. Although abundance and species richness of crustaceans in the supratidal zone increased towards reflective beaches, supporting the habitat safety hypothesis, insects showed the opposite trend with higher species richness at more dissipative beaches (Defeo and McLachlan 2011). This difference may be related to their distribution, with crustaceans extending towards the sea and insects extending landwards into the dunes, but the drivers of insect communities in the supratidal zone remain largely unknown (Defeo and McLachlan 2011).

As the supratidal macroinvertebrate community is less directly influenced by the sea, resource availability such as wrack input has an important structuring effect on the supratidal macroinvertebrate community (Colombini and Chelazzi 2003). This is especially the case since supratidal macroinvertebrates associated with wrack are generally characterised by a limited dispersal ability and a direct larval development (e.g. talitrids), making them heavily dependent on this resource (Grantham et al. 2003, Dugan et al. 2000, Schooler et al. 2017). Wrack provides both food and habitat, e.g. refuge from severe environmental conditions and space for reproduction, to the supratidal macroinvertebrate community (Dugan et al. 2003, Ince et al. 2007). Freshly deposited wrack is swiftly colonised by supratidal macroinvertebrates after which a succession of macroinvertebrate species is initiated (Colombini et al. 2000, Olabarria et al. 2007). The spatial distribution, amount, identity (i.e. sea weed species), quality and microhabitat features of wrack on the beach all drive the supratidal macroinvertebrate composition (Colombini and Chelazzi 2003). For example, macroinvertebrate species richness is greater in wrack patches deposited higher on the beach than wrack patches lower on the beach, with a higher temperature and lower moisture content of wrack at high tidal levels (Ruiz-Delgado et al. 2015). Smaller patches of wrack harboured less macroinvertebrate species and individuals than larger wrack patches (Olabarria et al. 2007), following the rules of island biogeography (MacArthur and Wilson 1967). Native versus invasive sea weed species in wrack showed a different macroinvertebrate colonisation pattern, possibly related to differences in nutritional quality, temperature and humidity of wrack (Rodil et al. 2008). With an increase in wrack age, macroinvertebrate succession occurs and macroinvertebrate abundance, richness and community composition change over time (Colombini et al. 2000, Jędrzejczak 2002b, Olabarria et al. 2007). As the wrack is less fresh and more decomposed, the quality of the litter decreases and differences in wrack quality may attract a varied macroinvertebrate community (Olabarria et al. 2010). Thus, supratidal macroinvertebrate communities, as is the case for intertidal macroinvertebrate communities, appear to be structured by a complex interaction between environmental factors and biological interactions related to resource availability.

### *2.2.3 The role of resource competition on sandy beaches*

Biological interactions have long been proven to be a major driver of community assembly in a wide range of ecosystems. On sandy beaches, biological interactions, such as competition, have the potential to structure macroinvertebrate communities where macroinvertebrates are densely aggregated in a small area. Intertidal macroinvertebrate densities can locally be high and may be up to 13.000 individuals  $m^{-2}$  of surface area on Belgium beaches (Degraer et al. 2003), but have even been reported to exceed 280.000 individuals  $m^{-2}$  of surface area along

a North-American coast (McLachlan 1990). Supratidal macroinvertebrates may also reach high densities in wrack patches up to 455 individuals m<sup>-2</sup> on an Australian beach (adapted from Ince et al. 2007) and up to 6098 individuals m<sup>-2</sup> on a Baltic sandy beach (adapted from Jędrzejczak 2002b). These high densities enhance the chance to encounter and interact, which may lead to intra- and interspecific competition for space and resources, such as food. Food supply has been shown to be important for structuring both intertidal and supratidal communities on sandy beaches, in the form of phytoplankton in the water column (Lastra et al. 2006, Bergamino et al. 2016), *in situ* production by benthic microalgae (Schlacher and Hartwig 2013) and beach cast sea weed (e.g. Ince et al. 2007).

Intra- and interspecific competition affect the cross-shore zonation of intertidal macroinvertebrates, and hence community composition (Defeo and McLachlan 2005). Intraspecific encounter competition has for example been observed for *Bathyporeia sarsi*, especially under low food conditions, which may explain its limited distribution in the higher intertidal zone compared to the co-occurring *B. pilosa* (Van Tomme et al. 2012). In addition, higher up the intertidal zone environmental conditions are harsher and food availability lower than in the mid intertidal zone, to which *B. pilosa* is better adapted than *B. sarsi* (Van Tomme et al. 2012). Interspecific competition, for example, between two intertidal isopod species resulted in the displacement of *Excirolana braziliensis* Richardson to coarser sands and higher up the intertidal zone by *Excirolana armata* Dana (Defeo et al. 1997). Furthermore, interference competition for space has been recorded between a hippid crab and a bivalve at the moment of burrowing in the intertidal zone, resulting in longer burrowing times and greater exposure to the swash climate (Dugan et al. 2004). This could in turn affect both zonation and community composition of intertidal macroinvertebrates. Interspecific competition for food was suggested by a stable isotope study, revealing that intertidal macroinvertebrates had a high niche-overlap in a low-food environment, thus species are expected to compete strongly for these food sources (Ortega-Cisneros et al. 2017). In another study, the intertidal zonation of four amphipod species was related to differences in feeding habits and preferred food source, thereby avoiding food competition (Yu et al. 2002).

Biological interactions have also been documented for supratidal macroinvertebrates within wrack patches (Colombini and Chelazzi 2003). Both intra- and interspecific competition occurred at high densities of the Diptera larvae *Coelopa frigida* Fabricius and *Coelopa pilipes* Haliday in wrack, which was likely related to food limitations (Leggett et al. 1996). These Diptera larvae were able to co-exist within a wrack patch by inhabiting either cooler (*C. frigida*) or warmer (*C. pilipes*) parts, hence avoiding competition (Phillips et al. 1995). In addition, the larvae of *C. frigida*, *C. pilipes* and *Thoracochaeta zosterae* Haliday were found occupying wrack patches at the same time in high abundances, indicating a potential for competitive interactions (Hodge and Arthur 1997). This was confirmed in a laboratory experiment showing that of these three Diptera species, the larvae of *C. frigida* were the strongest competitor for food (Hodge and Arthur 1997). For two supratidal amphipod species (*Talitrus saltator* and *Talorchestia brito* Stebbing) and an isopod species (*Tylos europaeus* Arcangeli), a strong temporal effect on niche-partitioning was observed when foraging on freshly deposited wrack, reducing competition and promoting co-existence among these species (Lastra et al. 2010).

This finding was supported by a stable isotope study, showing that these co-occurring species adopt different feeding strategies when wrack availability is low (Bessa et al. 2014a).

### **2.3 Sand nourishment effects on the macroinvertebrate community**

#### *2.3.1 A history of sand nourishment and its ecological impacts*

Coastal squeeze, where beaches are trapped between the rising sea level and static anthropogenic structures on the land side (Defeo et al. 2009), causes severe erosion of the sandy beach, threatening the human population and livelihood as the sea advances inland and leaving only a narrow strip for ecological communities to reside. To mitigate the effects of beach erosion, effective coastal defence strategies are needed. Up until the second half of the 20<sup>th</sup> century, hard coastal defence structures, including seawalls, groynes and dykes, had been extensively employed to protect the coast (Hanley et al. 2014). The construction of hard coastal defence structures changes the coastal environment and directly impacts local biodiversity as soft-sediment habitat is replaced by artificial hard substrate (Airoldi et al. 2005). Indirect effects are the disruption of coastal hydrodynamics and reduction of habitat connectivity altering the flow of sand, nutrients and organisms between adjacent sandy beaches that are separated by hard coastal defence structures, which impact sandy beach communities (Hanley et al. 2014). Thus, even though hard coastal defence structures can locally be effective to protect against flooding, adjacent sandy beaches may suffer from low sediment supply and increased erosion (Hanley et al. 2014). This hampers coastal protection along a wider stretch of coast, as complementary measures to the hard coastal defence structures would be needed.

To account for the dynamic nature of the sandy coast and its biogeochemical linkages, soft-sediment strategies have become more common as a sustainable form of coastal defence (Hanson et al. 2002). A common soft-sediment strategy is sand nourishment, where eroded beaches are nourished by frequently applying a large volume of sand to increase coastal sediment budgets and to widen the beach (Cooke et al. 2012). Depending on the cross-shore placement of the sand, several types of sand nourishment are distinguished, including foreshore (placement in the shallow subtidal zone), backshore (placement in the dunes), and regular beach or profile nourishment (placement in the intertidal and supratidal zones) (Speybroeck et al. 2006). Sand nourishments were first employed in the 1950s and have been increasingly applied from the 1990s onwards within Europe (Hanson et al. 2002). In the Netherlands, the first sand nourishments were deployed in 1970, but from 1990 onwards sand nourishments have been used on a larger scale to prevent further coastal erosion and maintain the current coast line (Hanson et al. 2002; Baptist and Wiersinga 2012). In the beginning, mostly beach nourishments were used, but around 2000 foreshore nourishments became more common (Baptist and Wiersinga 2012).

Although sand nourishment has been considered as an ecologically friendly alternative to hard coastal defence 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 layer of sand (up to a few meters) is deposited on top of the beach, causing burial and mortality of primary vegetation and invertebrates of both the intertidal and



supratidal zones (Speybroeck et al. 2006, Schlacher et al. 2012). During foreshore nourishment, sand is usually deposited on the seaside part of the bar closest to the beach. This does prevent direct mortality of intertidal and supratidal organisms as sand is gradually deposited onto the beach, but local subtidal communities are heavily affected instead (Speybroeck et al. 2006). Sand nourishments typically have to be applied every three to five years to prevent beaches from further erosion and to maintain the coast line in position (van Dalssen and Aarninkhof 2009). As ecological communities need time to recover after a disturbance such as sand nourishment, the timing, frequency and size of the sand nourishment are crucial for its impact on the sandy beach food web (Speybroeck et al 2006). Even though intertidal macroinvertebrate species can recolonise a beach that has received regular beach nourishment within one year after disturbance, community composition does differ from beaches without nourishment (Leewis et al. 2012). Changes in the intertidal macroinvertebrate community due to beach nourishment may propagate upwards in the food web to e.g. birds, with fewer birds foraging on a nourished beach with a lower intertidal macroinvertebrate abundance (Peterson et al. 2006). This indicates that although macroinvertebrate species are well adapted to the highly dynamic environment of the intertidal zone and can quickly colonise bare sands (McLachlan and Brown 2006), there may nevertheless be long-term negative impacts of sand nourishment on the macroinvertebrate community and the sandy beach food web (Speybroeck et al. 2008a). Therefore, alternative nourishment strategies are called for to limit negative effects on these intertidal macroinvertebrate communities of the sandy beach.

### *2.3.2 A novel approach: The Sand Motor mega-nourishment*

As a more ecologically and sustainable alternative to current regular beach and foreshore nourishment, a mega-nourishment has been proposed. To test the economic, anthropogenic and environmental implications of this novel approach, the so-called 'Sand Motor' project was started in 2011 along the Dutch main coast (Stive et al. 2013; Figure 1.3). A very large volume of sand (approximately 20 Mm<sup>3</sup>) was strategically deposited in connection to the coast, forming a hook-shaped artificial peninsula initially extending 2 km along the coast and protruding 1 km into the sea (de Schipper et al. 2016). This mega-nourishment is a combination of regular beach and foreshore nourishment, but it is unique in its size and low frequency of placement. Instead of regularly applying smaller-scale sand 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 (van Dalssen and Aarninkhof 2009). After construction, the sand is gradually redistributed through hydrodynamics and aeolian transport, nourishing beaches further along the coast (de Schipper et al. 2016). This is in sharp contrast with regular beach nourishments, where a sandy beach is nourished directly and locally with the desired volume. A mega-nourishment thus decreases the number of local pulse disturbances to the sandy beach ecosystem over time, as a very large, concentrated volume of sand is placed at one single occasion. The primary management goal of the Sand Motor mega-nourishment is coastal protection, with increased space for recreation and nature as additional goals.

### 2.3.3 Potential mega-nourishment effects on the macroinvertebrate community

Sand nourishment can be viewed as a significant disturbance to the sandy beach ecosystem with various effects on its ecological communities (Speybroeck et al. 2006). As mentioned earlier, one direct effect is the burial and local extinction of ecological communities during application of the sand nourishment (Speybroeck et al. 2006, Schlacher et al. 2012). The same holds for a mega-nourishment, which may even have a larger initial impact on macroinvertebrate communities due to its large size. However, as the frequency of nourishment is much lower and along shore beaches are gradually nourished by the mega-nourishment, potentially limiting disturbance by sand deposition, it may finally have a lower combined impact on the macroinvertebrate community compared to regular beach and foreshore nourishment. Therefore, I will focus here on the potential effects of a mega-nourishment on the macroinvertebrate community after completion of sand deposition. Effects on macroinvertebrate community assembly processes can be both direct (change in habitat characteristics) and indirect (change in dispersal and food availability; Figure 1.4). After completion, the mega-nourishment itself will, as is the case with regular beach nourishments, initially provide a new beach that can be recolonised by organisms. Recovery by recolonisation can be assumed to be completed when the disturbed community is no longer significantly



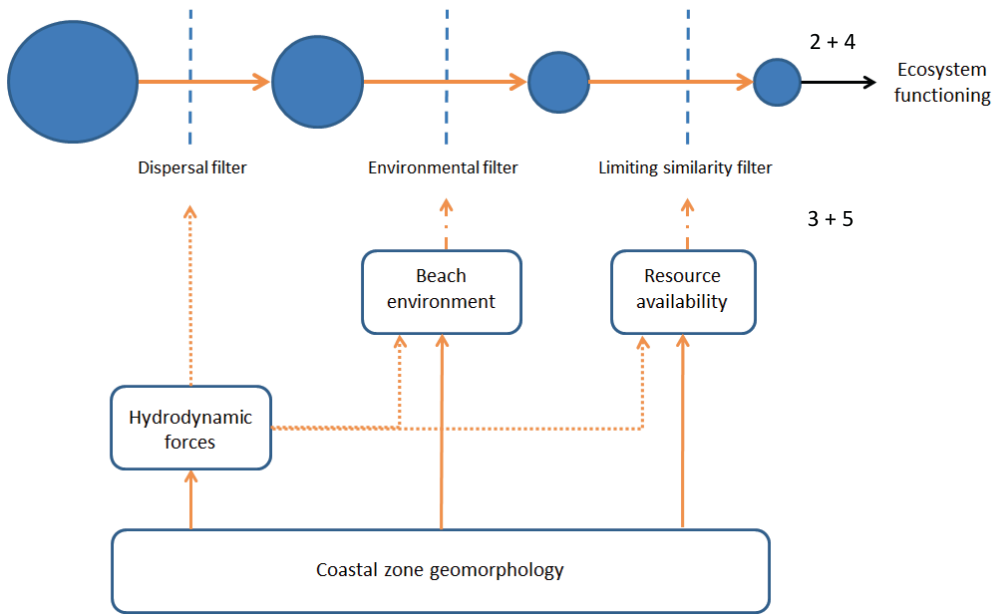
**Figure 1.3** Aerial pictures of the Sand Motor mega-nourishment along the Dutch coast. Left: Overall shape of the Sand Motor mega-nourishment, protruding from the relatively straight Dutch coast line into the sea. Upper right: Sand Motor mega-nourishment shortly after completion in July 2011. Lower right: Sand Motor mega-nourishment four years after completion in January 2015.

different from an undisturbed community in an adjacent area (Dernie et al. 2003). For the intertidal macroinvertebrate community, recovery primarily depends on the dispersal capacity of juveniles and adults, i.e. the dispersal filter, and their species-specific habitat requirements during and after settlement, i.e. the environmental filter (Van Tomme et al. 2013). Dispersal of intertidal macroinvertebrates can be either passive or active in the water column, at the sediment surface and within the sediment, which is affected by hydrodynamic forces (Günther 1992). The shape of the Sand Motor mega-nourishment is expected to change the strength and direction of local currents around the hook, especially during the first three years after completion when the hook-shape is most pronounced (Meirelles et al. 2017). This may influence the dispersal of intertidal macroinvertebrates and may be reflected in an impoverished macroinvertebrate community, with lower abundances and/or a subset of species from surrounding beaches. Beach geomorphology and local hydrodynamics can thus create either a barrier or an opportunity for successful dispersal (Van Tomme et al. 2013). After dispersal, the settlement of intertidal macroinvertebrates is determined by its interactions with the new habitat (Todd 1998). For a successful recovery, the individual species must match the specific habitat conditions and one factor for intertidal macroinvertebrates is the median grain size of the substrate (Speybroeck et al. 2006). The amphipod *B. sarsi* and the isopod *E. pulchra* have a preference for fine sediments, while the amphipod *B. pilosa* and to a greater extent the polychaete worm *S. squamata* prefer coarser sediments (Van Tomme et al. 2013). As the median grain size of the Sand Motor mega-nourishment is slightly coarser than the original beach and shows spatial heterogeneity in the years after completion, this may be one structuring factor of intertidal communities at the Sand Motor mega-nourishment (Huisman et al. 2014).

When macroinvertebrates have established in the intertidal zone, post-settlement processes such as competition, i.e. the limiting similarity filter, will finally shape the intertidal macroinvertebrate community present at a sandy beach (Todd 1998). The change of local hydrodynamics around the hook of the Sand Motor mega-nourishment is, in addition to macroinvertebrate dispersal, expected to change resource availability by influencing the distribution of phytoplankton and benthic microalgae. Phytoplankton may become an important food source in highly hydrodynamic environments (Menge 2000). Sediments that are continuously disturbed by waves and currents have a lower benthic microalgae biomass in comparison to sheltered, less disturbed beaches (Forehead et al. 2013). At the Sand Motor mega-nourishment, low hydrodynamic conditions are expected to be present in the lagoon which is sheltered from the high hydrodynamic forces of the open sea. These changes in the quantity and quality of food may impact the outcome of species interactions and community composition, as macroinvertebrate species exhibit differences in feeding preference. For example, *S. squamata* and *E. pulchra* did not make a clear choice between phytoplankton and benthic microalgae, where *B. sarsi* and *B. pilosa* did show a preference for benthic microalgae (Maria et al. 2011). When competition for food occurs for these intertidal macroinvertebrate species, species may focus on other food sources or relocate to an area where macroinvertebrate densities are lower.

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 diversity of habitats, for example by creating sheltered intertidal zones, attracting a wider variety of species. An increase in environmental heterogeneity at landscape level generally leads to an increase in species diversity (Stein et al. 2014, Tammé et al. 2010). For coastal systems in particular, it is found that habitat heterogeneity on a larger scale, up to 1 km, is a driver of intertidal macroinvertebrate species richness (Archambault and Bourget 1996). Thus, the hook-shape of the Sand Motor mega-nourishment has the potential to increase species richness and diversity through a local increase in large-scale heterogeneity of the sandy beach. The potential effects of a mega-nourishment on the supratidal macroinvertebrate community are less clear. As wrack input may depend on beach type, hydrodynamic forces and buoyancy characteristics of wrack (Orr et al. 2005), wrack may be heterogeneously distributed around the hook-shaped Sand Motor mega-nourishment, potentially affecting macroinvertebrate community composition. Other effects may be related to the increase in beach width after application of the mega-nourishment, allowing for the formation of multiple drift lines and increasing the potential for embryo dune formation (van Puijenbroek et al. 2017). Since the major goal of sand nourishment is coastal protection and dune formation contributes to this goal, understanding the interactive effect of wrack and macroinvertebrate community composition on plant establishment on sandy beaches is highly



**Figure 1.4** 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. 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, less 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 correspond to the chapters in this thesis and indicate which part of the conceptual model was studied.

relevant. Finally, the Sand Motor mega-nourishment is expected to lead to an increase in recreational visitors, which is an additional management goal. High recreational pressure may, however, have a negative effect on supratidal macroinvertebrates, for example by human trampling, high use of off-road vehicles and wrack removal during beach cleaning (Defeo et al. 2009).

Overall, the Sand Motor mega-nourishment is expected to have a significant effect on various community assembly processes, hence altering macroinvertebrate community composition, food web dynamics and ecosystem functioning of the sandy beach.

#### **1.4 Thesis aims and outline**

Sandy beach ecology is a relatively new discipline and although progress has been made in broadening the scope and integrating general ecological theory, many research challenges remain (Nel et al. 2014). Sandy beaches are not expected to be conceptually different from other ecosystems, but there are some specific and strong physical forces acting on this ecosystem and the relative importance of community assembly filters may therefore be different compared to other marine and terrestrial ecosystems. In the field of community assembly, the importance of e.g. species interactions and colonisation rates needs to be studied in macroinvertebrate communities of sandy beaches to test the generality of community assembly theory from other ecosystems (Schlacher et al. 2015). In addition, macroinvertebrate communities of sandy beaches show widespread functional redundancy, especially in the intertidal zone (Schlacher et al. 2008), allowing for critical ecological testing. In the field of ecosystem functioning, sandy beaches as a whole provide many ecosystem functions, including nutrient cycling, but this has rarely been quantified (Schlacher et al. 2008, Nel et al. 2014). It also remains largely unknown what the effect is of changes in macroinvertebrate community composition on ecosystem functioning. Finally, more emphasis can be placed on general concepts regarding cross-boundary connectivity across an ecological interface in the context of sandy beaches, as they represent a wide-spread interface region in the coastal zone (Schlacher et al. 2015, Gounand et al. 2018). Many knowledge gaps related to the integration of ecological attributes in sandy beach management are also in need to be addressed (Jones et al. 2017). These include studying the effect of nourishment on ecological communities and their recovery trajectories, providing management information on the design of monitoring programs to track community changes over time and guiding the design and development of (nourished) beaches for specific (ecological) purposes (Schlacher et al. 2008).

It is clear from the above that many questions remain unanswered regarding the ecology of macroinvertebrate communities on sandy beaches, especially in the light of resource availability and biological interactions. Although abiotic drivers strongly determine macroinvertebrate community composition on sandy beaches, research endeavors indicating the importance of biological interactions are steadily increasing. However, detailed studies on the role of biological interactions, resource competition in particular, are needed to further understand the assembly and composition of macroinvertebrate communities and its effect on ecosystem functioning. The effect of marine organic matter crossing the land-ocean interface on terrestrial organisms (supratidal macroinvertebrates and plants) and nutrient

cycling also requires further attention. In addition, the effect of a novel mega-nourishment on the macroinvertebrate community, and how this relates to communities present on beaches subjected to regular beach nourishment, has not been studied before and requires an in-depth evaluation.

In this thesis, I will therefore address two main aims. First, I aim 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. Secondly, I aim to investigate the effect of a mega-nourishment on the macroinvertebrate community of the sandy beach and identify implications for future sand nourishments.

This thesis focusses on Dutch sandy beaches that are exposed to high hydrodynamics. The outline of the chapters in this thesis will briefly indicate which research questions are considered in relation to the thesis aims.

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

In **Chapter 2** I compare the macroinvertebrate community of the intertidal zone present at a mega-nourishment, beaches subject to regular beach nourishment and unnourished beaches along the Dutch sandy coast. To do this, I constructed a database by combining data from three different sources and performed analyses on macroinvertebrate abundance and richness across the intertidal zone. Macroinvertebrate community patterns at the mega-nourishment are compared before and after implementation (across years and between locations) and between nourishment types.

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

In **Chapter 3** I focus on the effect of a limiting resource, here diatom availability, on the non-additive effects of consumption by a simple intertidal macroinvertebrate community. Diatom consumption was determined in both species' monocultures and three-species communities based on stable isotope signatures to disentangle positive and negative species interactions at low and high diatom availabilities, driving potential non-additive effects of consumption.

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

In **Chapter 4** I address the question whether the supratidal macroinvertebrate community, in terms of abundance, richness and diversity, is a driver of N and P mineralisation of wrack. Also, I determine whether drift line position and season are drivers of mineralisation. A litter bag experiment was performed in the field for two weeks, where wrack was subjected to natural process to obtain a range of mineralisation and macroinvertebrate community compositions.

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

In **Chapter 5** I assess the effects of wrack burial and macroinvertebrate presence on decomposition-driven nutrient availability and subsequently beach pioneer plant growth,

using two contrasting plant species. Plant dry mass and N and P contents of the shoot and roots were determined to assess the effect of either buried or surface wrack and macroinvertebrate presence or absence on plant growth. This allows to experimentally study the link between beach-cast sea weed and terrestrial primary production, via macroinvertebrates.

In **Chapter 6** I synthesise and discuss the results of the previous chapters in order to address the main aims and research questions of this thesis. I discuss how resource availability and species interactions shape intertidal and supratidal macroinvertebrate communities on sandy beaches and how this influences ecosystem functioning. In the end I formulate an answer to the question whether a mega-nourishment can be considered a more ecological-friendly alternative than regular beach nourishment for the macroinvertebrate community and provide recommendations for future coastal management.