50 YEARS WITH IMPACT
Journal of Applied Ecology
1913 British Ecological Society 2013
CELEBRATING 100 YEARS

Journal of Applied Ecology 2014, **51**, 1304–1313 doi: 10.1111/1365-2664.12314

Assessing the impact of beach nourishment on the intertidal food web through the development of a mechanistic-envelope model

Sarah Vanden Eede[1]*†, Joke Van Tomme[1]†, Charlotte De Busschere[2], Martijn L. Vandegehuchte[3], Koen Sabbe[4], Eric W.M. Stienen[5], Steven Degraer[6], Magda Vincx[1] and Dries Bonte[2]

[1]Marine Biology Section, Department of Biology, Ghent University, Krijgslaan 281/S8, 9000 Ghent, Belgium; [2]Terrestrial Ecology Unit, Department of Biology, Ghent University, K. L. Ledeganckstraat 35, 9000 Ghent, Belgium; [3]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Research Unit Community Ecology, Subunit Plant-Animal Interactions, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland; [4]Department of Biology, Protistology & Aquatic Ecology, Ghent University, Krijgslaan 281/S8, 9000 Ghent, Belgium; [5]Research Institute for Nature and Forest, Kliniekstraat 25, 1070 Brussels, Belgium; and [6]Marine Ecosystem Management Section, Management Unit of the Mathematical Model of the North Sea, Royal Belgian Institute of Natural Sciences, Gulledelle 100, 1200 Brussels, Belgium

Summary

1. Beach nourishment, the placement of sand onto a sediment-starved stretch of coast, is widely applied as a soft coastal protection measure because of its reduced ecological impact relative to hard coastal protection. In order to predict effects on the intertidal sandy beach ecosystem, we developed a simulation model that integrates species envelope-based projections for the dominant macrobenthos species and mechanistic food web modules for higher trophic levels.

2. Species envelopes were estimated by using Bayesian inference of species' biomass relationships according to the three determining abiotic variables: intertidal elevation, median grain size and total organic matter, obtained from multiple sampling campaigns along the Belgian coast. Maximum potential abundance of higher trophic levels represented by birds, shrimp and flatfish were estimated based on their derived trophic relationship with macrobenthos.

3. After validation, we demonstrated that unlike nourishment slope, sediment grain size strongly determines beach-level species richness and production, with strong deterioration in species richness after nourishment with coarse sediment (>300 μm). Patterns for higher trophic levels do not follow the changes in macrobenthos abundance and biomass.

4. *Synthesis and applications*. The optimal grain size range for nourishment of fine-grained beaches is 200–300 μm. This modelling approach shows that the impact assessment of beach nourishment needs to include the evaluation of different species richness and biomass variables. Focusing solely on the potential abundance of species from higher trophic levels might lead to deceptive conclusions due to the dominance of opportunistic prey species.

Key-words: beach profile, birds, flatfish, grain size, intertidal beach, macrobenthos, shrimp, species envelope modelling

Introduction

Coastal ecosystems are severely threatened by climate change due to changes in sea level, storm and wave regimes, flooding, altered sediment budgets and the loss of coastal habitat (Harley *et al.* 2006; Jones, Gladstone & Hacking 2007). In the last hundred years, the global average sea level has risen by 0·1–0·2 m (Houghton *et al.* 2001), while 70% of all beaches are receding, 20–30% remain stable and 10% or less are accreting (Bird 2000), making coastal erosion a pressing issue on sandy beaches.

Sandy beaches form the single largest coastal ecosystem on earth, covering 70% of all continental margins

---

*Correspondence author. E-mail: vanden.eede.sarah@gmail.com
†These authors contributed equally.

© 2014 The Authors. *Journal of Applied Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society. This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

(McLachlan & Brown 2006). They have a multitude of ecosystem functions as they are an important habitat for a variety of flora and fauna and are concurrently of immense social and cultural importance to humans as main food source and prime recreational assets (McLachlan & Brown 2006; Schlacher *et al.* 2008; Speybroeck *et al.* 2008; Defeo *et al.* 2009). Sandy beaches also play an important role in coastal defence by functioning as a natural buffer between sea and land, thus protecting landward sea defences from scour and wave erosion (Brampton 1992; Riddell & Young 1992).

The construction of hard coastal defence structures continues to enhance beach erosion while destroying important ecosystem functions (Defeo *et al.* 2009). Current widely applied defence approaches use beach nourishment to counteract coastal erosion and protect the hinterland from flooding. This is particularly the case on the West European beaches of Belgium and the Netherlands, as these countries are vulnerable to sea level rise and storms due to their low elevation. Until now, technical considerations, for example easy access to sand with coarse grain size and a preference for steep, more stable beach slopes (Chen 2002), dominated management decisions regarding beach nourishment projects. Although beach nourishment is generally considered a less harmful beach management option than the construction of hard structures (Hamm *et al.* 2002; Hanson *et al.* 2002), it does put severe pressure on the habitat and the biota living on, in and around sandy beaches regardless of the sophistication of its deployment (Speybroeck *et al.* 2006a). Most research documents negative direct and indirect effects on the intertidal fauna due to changes in sediment grade, burial and the engineering process itself (e.g. Peterson, Hickerson & Johnson 2000; Peterson *et al.* 2006; Jones *et al.* 2008). However, well-conceived impact studies are scarce (Schlacher *et al.* 2008; Leewis *et al.* 2012), and adequate information to predict the direct and indirect impact of nourishment on the beach ecosystem over local and regional spatial scales is especially lacking. Since the ecological characteristics of the beach fauna and flora are very much determined by morphodynamic beach characteristics such as beach slope and grain size (McLachlan & Jaramillo 1995; McLachlan, De Ruyck & Hacking 1996; Defeo & McLachlan 2005), optimizing these technical aspects of nourishment projects is indispensable to maintain ecologically healthy beach ecosystems.

As detailed information on the morphodynamics and the food web (Fig. 1) of Belgian sandy beaches is available (Degraer, Volckaert & Vincx 2003; Speybroeck *et al.* 2004), this beach ecosystem was used to develop a combined mechanistic-niche envelope model to predict the impact of beach nourishment on species richness, abundance and biomass at different trophic levels. The model builds further on the well-established insight that the realized niche of lower trophic levels can be predicted based on three beach parameters, that is elevation, median grain size and total organic matter, which are correlated under equilibrium conditions (Degraer, Volckaert & Vincx 2003; Speybroeck *et al.* 2006a). Microphytobenthos and macrobenthos species composition are well documented along the Belgian coast, and the importance of macrobenthos as food for birds and fish has also been illustrated and quantified (Beyst, Cattrijsse & Mees 1999; Vanermen *et al.* 2009). As clarified further, we assume the absence of dispersal limitation for macrobenthos. Our prediction for higher trophic levels is only based on the lower trophic level biomass availability, thereby neglecting possible additional external disturbances such as recreation and/or the vicinity of refugia, nurseries and resting places.

The general objective of this study was to develop a nourishment simulation model for the Belgian beach ecosystem that (i) predicts short-term changes in beach macrobenthos community composition in response to changes in beach profile and median grain size following beach nourishment and (ii) elucidates how these changes in community composition feed back to the maximum potential abundance of dominant species of higher trophic levels (birds, flatfish and shrimp).

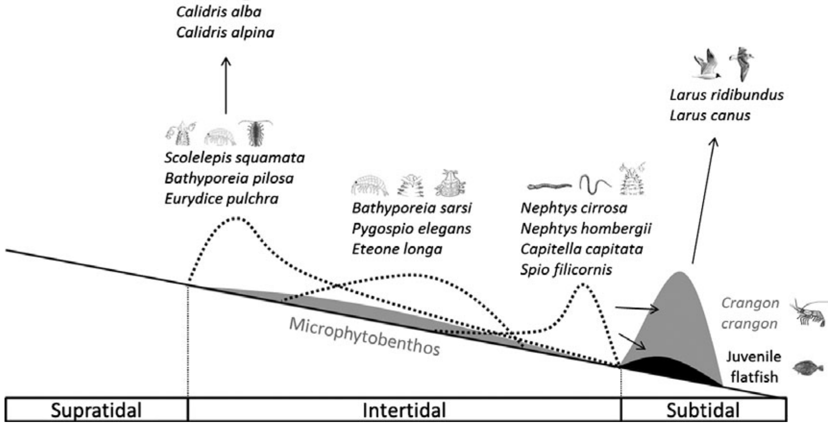

Fig. 1. Diagram of the modelled sandy beach food web (density patterns: light grey shaded area: microphytobenthos; dotted lines: macrobenthos; grey shaded area: *Crangon crangon*; and black shaded area: juvenile flatfish).

Materials and methods

NICHE ENVELOPES

We estimated niche envelopes for eleven dominant macrobenthos species in relation to three abiotic input variables, that is median grain size (*MGS*), total organic matter (*TOM*) and elevation (*h*) relative to the lowest tide, being 0 m TAW (TAW denotes the vertical level of reference in Belgium). The macrobenthos species comprised the polychaetes *Nephtys cirrosa* (Ehlers), *Nephtys hombergii* (Savigny in Lamarck), *Capitella capitata* (Fabricius), *Spio filicornis* (Müller), *Pygospio elegans* (Claparède), *Eteone longa* (Fabricius) and *Scolelepis (Scolelepis) squamata* (O.F. Muller), the amphipods *Bathyporeia pilosa* (Lindström) and *Bathyporeia sarsi* (Watkin) and the isopods *Eurydice pulchra* (Leach) and *Eurydice affinis* (Hansen) (Fig. 1). All species envelopes were based on intertidal data collected on 23 intensively sampled beaches along the Belgian coast, during different seasons within the period 1997–2011 (Degraer, Volckaert & Vincx 2003; Speybroeck, Degraer & Vincx 2003; Speybroeck *et al.* 2005; Welvaert 2005; Van Ginderdeuren *et al.* 2007; Vanden Eede, Vincx & Degraer 2008; Vanden Eede & Vincx 2010, 2011) (see Appendix S1, Supporting Information). The envelopes were modelled by second-order polynomial Poisson regression models because prior information evidenced both linear and quadratic responses according to the abiotic input variables (Degraer, Volckaert & Vincx 2003). Parameter estimates were obtained by Bayesian estimation using a Monte Carlo Markov Chain (MCMC) procedure in WinBugs v.1.4 (Spiegelhalter *et al.* 2003). The obtained regression coefficients (see Appendix S2, Supporting Information) were used to estimate species abundances according to implemented beach characteristics in the main simulation model. Parameters were sampled from the obtained Gaussian regression distribution kernels but constrained within the 95% credibility interval. The resulting abundance estimates were converted to biomass using earlier determined conversion factors (Speybroeck *et al.* 2006a; see Appendix S3, Supporting Information).

ENTITIES, STATE VARIABLES AND SCALES OF THE SIMULATION MODEL

The model consists of three major modules: one determining the abiotic conditions of the beach, a second module predicting (changes in) abundance, species richness and biomass of eleven dominant macrobenthos species according to their envelopes, and a third module predicting the maximum potential abundance of dominant species of higher trophic levels, being the gulls *Larus canus* (Linnaeus) and *Larus ridibundus* (Linnaeus), the waders *Calidris alba* (Pallas) and *Calidris alpina* (Linnaeus), the shrimp *Crangon crangon* (Linnaeus) and juvenile flatfish, mainly *Pleuronectes platessa* (Linnaeus) (Speybroeck *et al.* 2008; Fig. 1). The model predictions are always at the scale of 1 m^2, according to the local conditions of the beach state variables, namely *MGS*, *TOM* and *h*. When predictions are made at the beach level, all estimates are integrated along a beach transect, assuming a width of 1 m. The available biomass of species belonging to the lower trophic levels are input variables for estimating abundance of species from higher trophic levels, while the beach slope (α) determines the submergence area and thus the availability of prey for higher trophic levels (Fig. 2).

PROCESS OVERVIEW AND SCHEDULING

Beach nourishment results in changes in *h* and *MGS*. The simulation model first estimates the local *TOM* based on its relationship with *MGS* because the direct correlation with *h* is weak. For reference situations (non-impacted beaches), *MGS* was estimated as a function of *h* since earlier work has demonstrated and confirmed the prevalence of such grain sorting mechanisms (Short 1991, 1999). Based on the beach state variables and input data (see Appendix S1, Supporting Information) on macrobenthos niche properties, local abundance (number of individuals m^{-2}) of macrobenthos is estimated and subsequently converted to biomass (g AFDW m^{-2}). Total availability of chlorophyll-a (mg m^{-2}), which is a measure for microphytobenthos, is estimated without conversion. In a second phase, estimated macrobenthos biomass is integrated into functions to determine the maximum potential abundance of higher trophic levels, according to available biomass of prey species and tidal frequency. The model is stochastic with parameters for species envelopes and beach characteristics estimated from prior statistical distributions. For each beach condition, 10 000 simulations are performed to estimate mean values and variance of species and predation pressure from higher trophic levels. Performance of the model was successfully validated for macrobenthos (see Appendix S1, Supporting Information). As recolonisation is shown to be fast for some benthos species (Gmelig Meyling & De Bruyne 1994; Slim & Löffler 2007), no lag effects are incorporated in the model. The predicted state of the beach subsequently assumes equilibrium in species dynamics according to the envelope. Emerging abundances and biomass of prey items will eventually impact higher trophic levels, but no implicit interactions due to predation and interspecific competition are modelled. The input data for the prey species are derived from non-disturbed beaches, so niche properties are assumed to reflect realized niche dimensions.

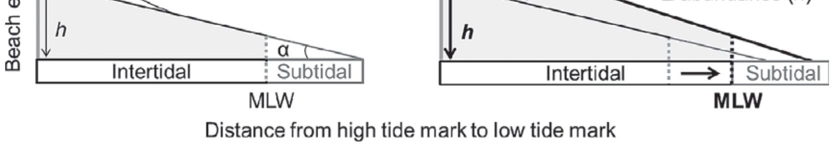

Fig. 2. Schematic overview of the principal state variables on a reference beach (a) and on a nourished beach (b), where the position of mean low water level (MLW; 0 m TAW) changed (black bold dotted lines instead of grey bold dotted lines), creating a higher and wider beach (grey shaded area).

SUBMODEL STRUCTURE AND MODELLING TROPHIC RELATIONSHIPS

Epibenthos

Previous work has demonstrated the importance of intertidal habitat for residing epibenthos foraging on macrobenthos (Kuipers & Dapper 1984; del Norte-Campos & Temming 1994; Beyst, Cattrijsse & Mees 1999; Koot 2009). Along Belgian beaches, epibenthos is dominated by *C. crangon* (95%) and to a much lesser extent by juvenile flatfish (5%), mainly *P. platessa* (Beyst, Hostens & Mees 2001). The maximum proportion of prey consumed by either *C. crangon* or juvenile flatfish was experimentally quantified (predation pressure in equation 1; Van Tomme, Degraer & Vincx 2014). These values are used to estimate the maximum local predation pressure by epibenthos based on the available macrobenthos abundance. Predation pressure is time constrained and only possible under submergence; therefore, the total available biomass (g AFDW m^{-2}) at a certain elevation along the beach *(h)* for higher trophic levels is described by the following function with x as the macrobenthos prey species and h_{max} as the elevation on the beach at high tide:

$$\text{Biomass}_{\text{available}}(h) = \sum\nolimits_{x \to i}\left[\text{biomass}(h) * \left(1 - \frac{h}{h_{\max}}\right) * \text{predation pressure}_x\right] \qquad \text{eqn 1}$$

The caloric value of macrobenthos equals 23 kJ g AFDW^{-1} (Beukema 1997), so the available energy (kJ) for higher tropic levels is described as:

$$E_{\text{available}}(h) = \text{biomass}_{\text{available}}(h) * 23 \qquad \text{eqn 2}$$

From this available source of energy, the maximum number of *C. crangon*, able to feed on this biomass at *h*, is based on their daily energetic needs (NEI), being 16% of their total body mass (del Norte-Campos & Temming 1994). Based on the average biomass of a single *C. crangon* of 0·0175 g AFDW (Beukema 1992) and a mean average caloric value of 4·768 cal mg $\text{AFDW}^{-1} \approx$ 20 kJ g AFDW^{-1} (Szaniawska 1983; Zwarts, Wanink & Ens 1996), $\text{NEI}_{\text{crangon}}$ is 0·056 kJ per individual. The maximum abundance of *C. crangon* at *h* can be calculated as follows:

$$\text{Crangon}_{\max}(h) = \frac{E_{\text{available}}(h) * 0 \cdot 95}{\text{NEI}_{\text{crangon}}} \qquad \text{eqn 3}$$

Similarly, the NEI for juvenile flatfish is estimated to be 10% of the body mass (Lockwood 1984), so the maximum abundance of flatfish at *h* can be calculated as follows with $\text{NEI}_{\text{flatfish}}$ being 0·188 kJ per individual:

$$\text{Flatfish}_{\max}(h) = \frac{E_{\text{available}}(h) * 0 \cdot 05}{\text{NEI}_{\text{flatfish}}} \qquad \text{eqn 4}$$

These estimates should be regarded as ceiling values for higher trophic levels, since it assumes immediate consumption under laboratory conditions, mimicking natural prey abundances.

Wading birds

Two wader species, *C. alba* and *C. alpina*, feed predominantly on macrobenthos along Belgian beaches. Despite some differences in foraging behaviour, both species were found to forage about 25% of their total residential time within one tidal cycle on all macrobenthos species (Beyst, Cattrijsse & Mees 1999; Speybroeck *et al.* 2006a; Vanermen *et al.* 2009). They are therefore treated as one functional group. According to Vanermen *et al.* (2009), waders along soft sandy beaches only forage from 2 h before to 4 h after low tide. This implies that foraging is not possible at the higher intertidal zone. At the low intertidal zone, each location receives a predation pressure of 2 × 0·25 (two tidal cycles). With increasing *h*, this pressure decreases gradually to zero at the upper third of the beach. This leads to a maximum foraging pressure at *h*, with h_{rel} being the relative proximity to the low water level (being 1 at 0 m TAW and 0 at high tide), as follows:

$$\text{Foraging Pressure}(h) = -0 \cdot 25 + 0 \cdot 75 * h_{\text{rel}} \qquad \text{eqn 5}$$

When equation 5 yields values <0, foraging Pressure (*h*) equals 0. The availability of prey is additionally dependent on the beach slope (α) since this affects the depth of the prey burrowing into the sediment, with prey unavailable for waders when the water-table exceeds 40 cm beneath the surface (Stienen, personal communication). Foraging possibilities are theoretically highest on flat beaches and lowest when beach slopes exceed 21° (which produces a zone of less than 1 m available at the water line). Taking into account continuous changes in biomass availability (related to foraging time) for the central and lower intertidal zone, a caloric value of macrobenthos of 23 kJ g AFDW^{-1} and a daily energy uptake for small waders ($\text{NEI}_{\text{waders}}$) of on average 224 kJ per individual per day (Kersten & Piersma 1987; Castro, Myers & Place 1989; Speybroeck *et al.* 2006b), potential wader pressure can be calculated as follows:

$$\text{Daily wader pressure}(h) = \text{foraging pressure}(h) * \text{biomass}(h) * \left(1 - \frac{\alpha}{21^\circ}\right) * \frac{23}{\text{NEI}_{\text{waders}}} \qquad \text{eqn 6}$$

Small-sized gulls

Larus canus and *L. ridibundus* are the principle foraging gulls on Belgian beaches. They feed on polychaetes and *C. crangon* (Speybroeck *et al.* 2006a). Prey availability within the intertidal food web peaks at low tide and is concentrated in beach pools. Because of the lack of any insights into this pool formation and temporal patterns in gulls' foraging behaviour, we assume polychaetes and *C. crangon* biomass to be available after submergence, with x being polychaetes and *C. crangon*:

$$\text{Biomass}_{\text{available}(h)} = \text{biomass}_{\text{polychaeta}} + \text{biomass}_{\text{crangon}} = \sum\nolimits_{x \to i} \text{biomass}(h) * \left(\frac{h}{h_{\max}}\right) \qquad \text{eqn 7}$$

Given caloric (cal) values for polychaetes and *C. crangon* of, respectively, 23 and 20 kJ g AFDW^{-1}, the average daily energy need of small *Larus* species ($\text{NEI}_{\text{gulls}}$) of 607 kJ per individual per day (Ysebaert & Meire 1989) and x being, respectively, polychaetes and *C. crangon*, the potential maximum number of foraging gulls is:

$$\text{Gulls}(h) = \frac{\sum_{x \to i}(\text{Biomass}_{\text{avilable}})_x * Cal_x}{\text{NEI}_{\text{gulls}}} \qquad \text{eqn 8}$$

Although several bird species are also known to feed on stranded wrack material, this trophic link was not incorporated in this model due to the difficulties of quantifying stranded wrack on beaches.

MODEL APPLICATION AND RESEARCH STRATEGY

The technical aspects of nourishment projects that can be optimized are slope and grain size. However, the distribution of species is not directly related to the beach slope but to the elevation relative to the lowest tide, being 0 m TAW. The slope further determines the length of the beach between low and high tide levels and the surface of suitable habitat within elevation (m versus TAW) intervals. Slope is therefore, with median grain size, considered as the most important input parameter for the nourishment simulations. The relative importance of each parameter is tested under realistic conditions by keeping the other parameter constant. While maintaining the natural sediment grain size (ranging from 139 to 285 μm), three beach profiles were tested: the natural beach profile (t0, 15°), a nourishment profile of 15° (s1) and a nourishment profile of 30° (s2) (Fig. 3). We predicted the effects on chlorophyll-a levels, macrobenthos abundance per dominant species, total macrobenthos biomass, species richness and potential predation pressure of higher trophic levels including birds, flatfish and shrimp. Similarly, predictions were made of the effect of varying sediment grain size, from 200 to 500 μm with increments of 50 μm, on macrobenthos and on higher trophic levels. In this case, the nourishment profile did not deviate from the natural beach profile (t0, 15°).

The t0-situation, frequently depicted in figures and tables, encompasses the situation on a typical Belgian beach prior to nourishment when sediment is in equilibrium and well sorted across the shore, with coarser sediment on the upper shore and finer sediment on the lower shore. Conversely, the simulated situations (s1 and s2) are characterized by a uniform sediment grain size.

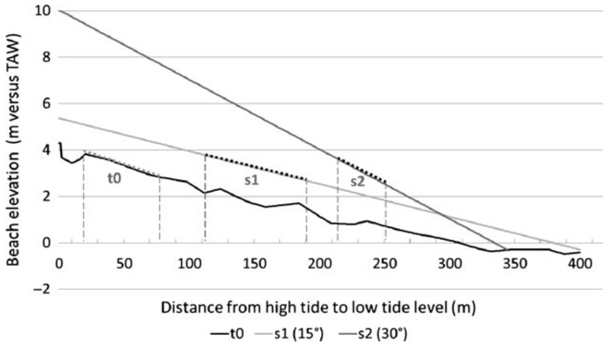

Fig. 3. Different nourishment profiles and the exemplary shift of habitat (dotted lines) on the beach due to nourishment, going from t0 (natural beach profile) to s1 or s2.

Results

INFLUENCE OF THE ALTERED BEACH PROFILE AND NOURISHMENT SLOPE

An important consequence of beach nourishment, coinciding with the steeper beach slope, is the shift in intertidal beach area (Fig. 3). When nourishment is applied, regardless of the slope, the chlorophyll-a levels, which are a measure for microphytobenthos, and the abundance of *B.pilosa* increase slightly while the abundance of *B. sarsi*, *E. pulchra*, *N. cirrosa* and *S. squamata* decreases (Table 1). Along the entire beach, no changes in species richness of all considered species are recorded, but the average species richness at each elevation is about 1 unit lower for the nourished beaches along the entire transect (Fig. 4). The nourishment profile does not impact the total macrobenthos biomass and the potential abundance of species from higher trophic levels (Fig. 5). However, the nourishment values are always lower relative to the t0-situation, except for waders. Moreover, a 20% decrease in macrobenthos biomass seems to produce a twofold decrease in predation pressure.

INFLUENCE OF THE MEDIAN SEDIMENT GRAIN SIZE

The average simulated abundance of the species after nourishment is similar to pre-nourishment conditions when the grain size of the used sediment resembles natural conditions (200–250 μm). However, when nourishment sediment differs in grain size from natural beach sediment, species abundances will respond profoundly to this habitat transformation. The microphytobenthos (chlorophyll-a), *B. pilosa* and *N. cirrosa* show a clear negative trend when beaches are nourished using sediment with a median grain size of 300 μm or coarser (Table 2). For *B. sarsi*, this negative trend starts from 350 μm onwards. *E. pulchra* and *S. squamata* are not negatively but positively influenced by nourishment using sediment with a medium grain size of >250 μm.

Figure 6 shows that after nourishment using sediment with a median grain size from 300 μm onwards, macrobenthos species richness on the beach decreases. Nourishment with sediment characterized by a median grain size of 350 μm will cause a decrease in macrobenthos species richness by 30% compared to the t0-situation. There

Table 1. Simulated chlorophyll-a (mg m^{-2}) and species abundance (number of individuals m^{-2}) on a typical Belgian beach for the pre-nourishment (t0, slope: 15°) and post-nourishment situation, using different slopes: s1 (15°) and s2 (30°); mean ± standard error (based on 10 000 simulations)

Slope	Chlorophyll-a (mg m^{-2})	*Bathyporeia pilosa*	*Bathyporeia sarsi*	*Eurydice pulchra*	*Nephtys cirrosa*	*Scolelepis squamata*
t0	2·03 ± 0·01	111·5 ± 9·3	323·8 ± 7·7	7·4 ± 1·0	47·0 ± 1·4	178·9 ± 10·2
s1 (15°)	3·05 ± 0·02	242·9 ± 15·4	283·0 ± 7·0	3·7 ± 0·4	26·1 ± 1·0	59·5 ± 5·2
s2 (30°)	3·07 ± 0·02	287·8 ± 16·1	263·5 ± 6·8	2·6 ± 0·5	34·4 ± 1·2	60·1 ± 5·4

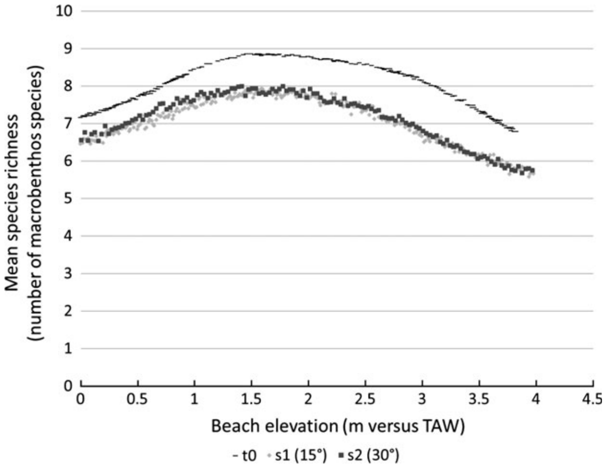

Fig. 4. Expected mean species richness (number of macrobenthos species) on a typical Belgian beach, according to beach elevation (m versus TAW), before (t0) and after nourishment with different nourished slopes (s1 and s2) (based on 10 000 simulations).

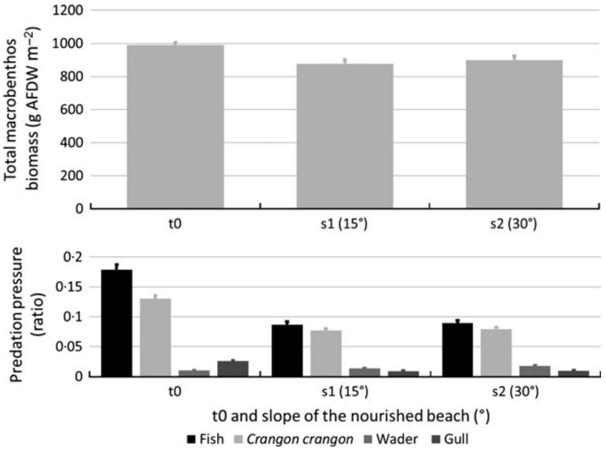

Fig. 5. Simulated total macrobenthos biomass (g AFDW m^{-2}) and potential predation pressure (ratio) of higher trophic levels on a typical Belgian beach before (t0) and after nourishment with different nourished slopes (s1 and s2); mean ± standard error (based on 10 000 simulations).

seems to be no apparent species richness loss when fine sediment is used (200 and 250 μm).

While the maximum macrobenthos species richness is found at a median grain size of 200–250 μm, the maximum total macrobenthos biomass is found at 300 μm (Fig. 7). The total biomass after nourishment with 350 and 400 μm is comparable to the total biomass, respectively, in the t0-situation and after nourishment with 200 μm. After nourishment with 400 μm and coarser, an increase in total macrobenthos biomass towards conditions comparable to the t0-situation appears. The effects of beach nourishment with different types of sediment on higher trophic levels can be linked to the evolution of total macrobenthos biomass, although higher trophic levels become relatively less abundant at lower grain sizes (Fig. 7). For shrimp, juvenile flatfish and birds, there is a maximum potential predation pressure (ratio) at 300 μm, followed by first a decrease and then again an increase in presence on the beach with increasing coarser grain sizes.

Discussion

Beach erosion combined with increasing economic and human development along the coast is resulting in coastal squeeze. To counteract this evolution, beach nourishment is aimed at coastal relaxation. However, this management measure has its own ecological implications for sandy beach ecosystems. By integrating data from the well-studied Belgian coast, we are able to provide guidance to local managers and stakeholders. Given the similarities to other species with respect to taxonomic position and trophic relationships (McLachlan, De Ruyck & Hacking 1996; Defeo & McLachlan 2005), the model insights should be applicable to sandy beach ecosystems worldwide.

The model simulations indicate a slight decrease in total macrobenthos biomass on the beach (Fig. 5) as a result of nourishment but virtually no response to the different nourishment profile types s1 (15°) and s2 (30°). Species richness across the entire beach profile is not affected because the niches remain available but are only shrinking with steeper slopes. Most of the modelled macrobenthos rather respond to the grain size of the nourished sediment

Table 2. Simulated chlorophyll-a (mg m^{-2}) and species abundance (number of individuals m^{-2}) on a typical Belgian beach for the pre-nourishment (t0, median grain size: 218·31 μm) and post-nourishment situation, using different sediment grain sizes; mean ± standard error (based on 10 000 simulations)

Median grain size (μm)	Chlorophyll-a (mg m^{-2})	*Bathyporeia pilosa*	*Bathyporeia sarsi*	*Eurydice pulchra*	*Nephtys cirrosa*	*Scolelepis squamata*
t0	2·03 ± 0·02	111·5 ± 9·3	323·8 ± 7·7	7·4 ± 1·0	47·0 ± 1·4	178·9 ± 10·2
200	3·05 ± 0·02	242·9 ± 15·4	283·0 ± 7·0	3·7 ± 0·4	26·1 ± 1·0	59·5 ± 5·2
250	2·32 ± 0·01	225·8 ± 14·8	311·2 ± 7·6	12·5 ± 1·4	12·7 ± 0·6	302·8 ± 13·7
300	1·59 ± 0·01	162·9 ± 12·1	309·4 ± 8·0	20·0 ± 2·5	4·7 ± 0·3	553·4 ± 19·1
350	0·98 ± 0·01	82·4 ± 7·3	125·4 ± 4·8	17·5 ± 2·8	1·7 ± 0·2	524·7 ± 19·0
400	0·82 ± 0·01	0·0 ± 0·0	117·0 ± 5·2	41·0 ± 4·8	0·7 ± 0·1	423·6 ± 17·6
450	0·55 ± 0·01	0·0 ± 0·1	30·9 ± 2·5	47·2 ± 5·5	1·4 ± 0·2	424·3 ± 18·8
500	0·42 ± 0·01	0·0 ± 0·2	79·8 ± 4·5	32·8 ± 4·5	1·8 ± 0·3	468·3 ± 20·4

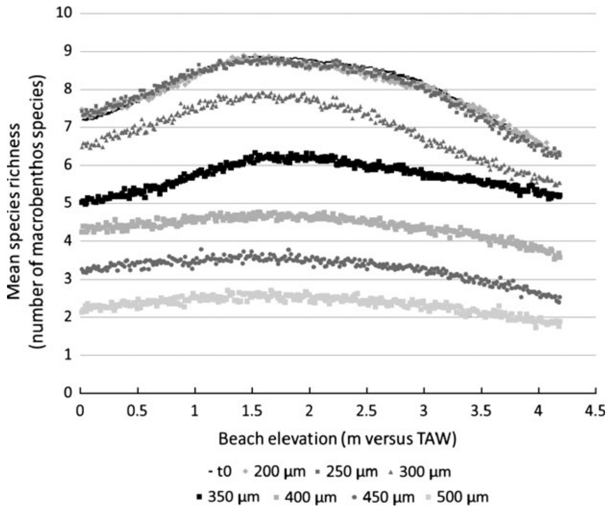

Fig. 6. Expected mean species richness (number of macrobenthos species) on a typical Belgian beach, according to beach elevation (m versus TAW), before (t0, median grain size: 218·31 µm) and after nourishment with different sediment grain sizes (µm) (based on 10 000 simulations).

(Fig. 6 and Fig. 7), confirming the findings of Speybroeck *et al.* (2006a). The nourishment sediment is indeed of vital importance to predict the nourishment effects on the beach ecosystem. Coarse sediments ($MGS \geq 300$ µm), not naturally occurring on Belgian beaches (Vanden Eede 2013), negatively influence the microphytobenthos, the amphipods *B. pilosa* and *B. sarsi* and the polychaete *N. cirrosa* (Table 2). However, these coarse sediments positively influence the omnivorous predatory isopod *E. pulchra* and the generalist and cosmopolitan polychaete *S. squamata*, resulting in an increase in total macrobenthos biomass and an increase of the trophically linked birds and flatfish present on the beach. With steeper slopes, the foraging time decreases, and this explains the twofold decrease in predation pressure while macrobenthos biomass drops slightly (Fig. 5). The impact of variation in macrobenthos biomass on higher trophic levels seems to be mainly driven by availability of prey rather than by their actual presence.

In contrast to the calculated abundance and biomass patterns, the simulated overall species richness declines when coarse sediment is used for beach nourishments. Nourishment with coarser sediment thus leads to species impoverished beach ecosystems. The contrasting abundance, biomass and species richness patterns clearly show that macrobenthos or avian biomass, as single descriptors for evaluating the health of an ecosystem, are insufficient and can lead to wrong conclusions. We therefore advise the use of a combination of species richness, abundance and biomass indices to monitor the ecological impact of nourishment on sandy beach ecosystems.

The model predicts whether the habitat after nourishment is suitable for the most dominant members of the sandy beach community. However, the predicted species richness, abundance and biomass may in practice be different because of natural temporal variability or other anthropogenic impacts, for example tourism (Brown & McLachlan 2002; Defeo *et al.* 2009). A complete ecosystem shift is also possible if invasive species recolonize the nourished and morphodynamically altered beach or if keystone species disappear (Schlacher *et al.* 2008; Mumby, Steneck & Hastings 2012; Perry *et al.* 2013). Furthermore, the post-nourishment evolution depends on several nourishment-specific (e.g. nourishment period, method and technique) and ecosystem-dependent features (e.g. erosion susceptibility of the beach ecosystem, recolonizing capabilities of the sandy beach species). As these factors surely complicate the predictions of the ecological consequences of nourishment, a more integrated data collection and research program are needed to unravel the structuring mechanisms and emerging biodiversity patterns.

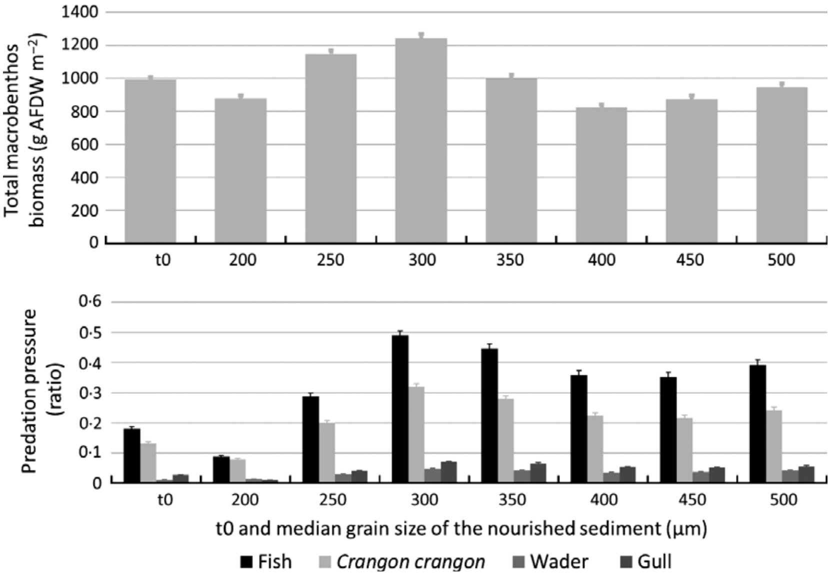

Fig. 7. Simulated total macrobenthos biomass (g AFDW m^{-2}) and potential predation pressure (ratio) of higher trophic levels on a typical Belgian beach before (t0, median grain size: 218·31 µm) and after nourishment with different sediment grain sizes (µm); mean ± standard error (based on 10 000 simulations).

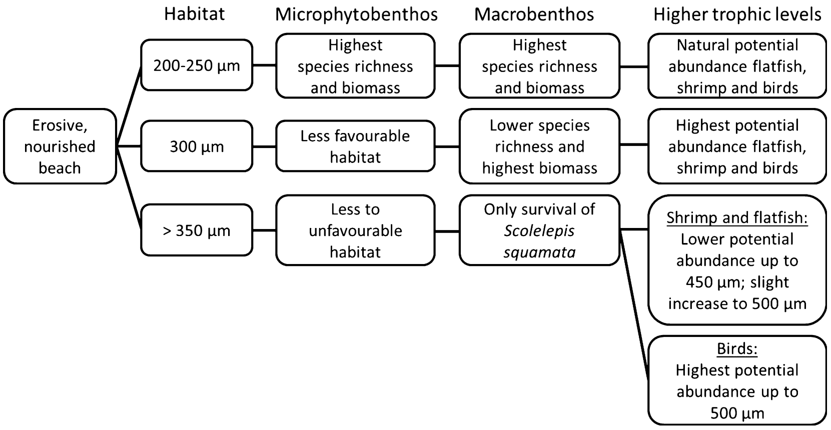
Habitat
Microphytobenthos
Macrobenthos
Higher trophic levels
Erosive, nourished beach
200-250 µm
Highest species richness and biomass
Highest species richness and biomass
Natural potential abundance flatfish, shrimp and birds
300 µm
Less favourable habitat
Lower species richness and highest biomass
Highest potential abundance flatfish, shrimp and birds
> 350 µm
Less to unfavourable habitat
Only survival of *Scolelepis squamata*
Shrimp and flatfish: Lower potential abundance up to 450 µm; slight increase to 500 µm
Birds: Highest potential abundance up to 500 µm

Fig. 8. Schematic overview of beach nourishment impact on the beach ecosystem, based on the model simulations.

As the sandy beach food web is complex and all species interactions are not yet elucidated, the predicted nourishment impact effect on higher trophic levels should be regarded as an assessment of the potential, based on macrobenthos productivity, rather than a realistic prediction. As outlined earlier, the maximum potential abundance of higher trophic levels might be additionally impacted by external disturbances like recreation or the vicinity of refugia, nurseries and resting grounds (Dugan & Davis 1993; Beyst *et al.* 2001; Goss-Custard *et al.* 2006; Rogers, Piersma & Hassell 2006). Furthermore, the predators incorporated in the model are strongly linked to *S. squamata*, their main food item. This link naturally simulates a relatively high potential presence for these predators. The latter result needs careful consideration as firstly, these predators also feed on other food sources that are currently not incorporated in the model (such as stranded wrack material (De Meulenaer 2006)) and secondly, the potential presence of predators is not yet linked to abiotic variables such as beach morphodynamics or hydrological conditions although they may affect the presence of epi- and hyperbenthos (Beyst *et al.* 2002).

SYNTHESIS AND APPLICATIONS

Based on the modelling results for the different ecosystem components, we distinguish three nourishment types, linked to *MGS*, with divergent impacts on the food web structure: (i) 200–250 µm, (ii) 300 µm and (iii) ≥350 µm (Fig. 8). As long as the used sediment resembles the sediment in pre-nourishment conditions, the ecosystem does not change. The use of coarse sediment ($MGS \geq 300$ µm) has a negative effect on macrobenthos species richness. Due to the differences in simulated patterns for abundance, species richness and biomass, the importance of these variables should be carefully considered. Based on the results of this model, it could be stated that beach nourishment with a sediment grain size of 300 µm is most favourable for higher trophic levels. However, this result is largely dependent on the strong correlation between the abundance of the predators included in the model and that of the generalist polychaete *S. squamata* and is likely to change when more predators and additional trophic and abiotic links are included in the model. Due to these uncertainties regarding the presence of higher trophic species, the gradient in sediment grain size that is advised to be used for nourishment of natural fine-grained beaches is established as 200–300 µm.

Acknowledgements

The first authors are grateful to the funding authorities AMINAL-Nature (Flemish administration responsible for environment, nature, land and water management, department Nature – BEST project, file number AN.GKB/2002/nr.2), AWK (Coastal Waterways Division – projects with file numbers 202.165, 202.290, 04/A2084-3, 205.240, 207.230, 208.245, 209.090, 211.095), ANB (Agentschap voor Natuur en Bos) and Ghent University and they acknowledge an aspirant grant provided by the Research Foundation – Flanders (FWO).

Data accessibility

Input data and model validation: uploaded as supporting information in Appendix S1.

Estimated regression coefficients: uploaded as supporting information in Appendix S2.

Average conversion factors converting abundance to biomass: uploaded as supporting information in Appendix S3.

Model syntax and results: DRYAD entry http://dx.doi.org/10.5061/dryad.vq76f (Vanden Eede *et al.* 2014).

References

Beukema, J.J. (1992) Dynamics of juvenile shrimp *Crangon crangon* in a tidal-flat nursery of the Wadden Sea after mild and cold winters. *Marine Ecology Progress Series*, **83**, 157–165.

Beukema, J.J. (1997) Caloric values of marine invertebrates with an emphasis on the soft parts of marine bivalves. *Oceanography and Marine Biology*, **35**, 387–414.

Beyst, B., Cattrijsse, A. & Mees, J. (1999) Feeding ecology of juvenile flatfishes of the surf zone of a sandy beach. *Journal of Fish Biology*, **55**, 1171–1186.

Beyst, B., Hostens, K. & Mees, J. (2001) Factors influencing fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium: temporal variation. *Journal of Sea Research*, **46**, 281–294.

Beyst, B., Buysse, D., Dewicke, A. & Mees, J. (2001) Surf zone hyperbenthos of Belgian sandy beaches: seasonal patterns. *Estuarine, Coastal and Shelf Science*, **53**, 877–895.

Beyst, B., Vanaverbeke, J., Vincx, M. & Mees, J. (2002) Tidal and diurnal periodicity in macrocrustaceans and demersal fish of an exposed sandy beach, with special emphasis on juvenile plaice Pleuronectes platessa. *Marine Ecology Progress Series*, **225**, 263–274.

Bird, E.C.F. (2000) *Coastal Geomorphology: An Introduction*. John Wiley, Chichester.

Brampton, A. (1992) *Beaches-the Natural Way to Coastal Defence*. Coastal Zone Planning and Management, ICE, 221–229.

Brown, A.C. & McLachlan, A. (2002) Sandy shore ecosystems and the threats facing them: some predictions for the year 2025. *Environmental Conservation*, **29**, 62–77.

Castro, G., Myers, J. & Place, A.R. (1989) Assimilation efficiency of sanderlings (*Calidris alba*) feeding on horseshoe crab (*Limulus polyphemus*) eggs. *Physiological Zoology*, **62**, 716–731.

De Meulenaer, B. (2006) Voedselecologie van strandvogels: Drieteenstrandloper (*Calidris alba*). M.Sc. University of Gent, 93.

Defeo, O. & McLachlan, A. (2005) Patterns, processes and regulatory mechanisms in sandy beach macrofauna: a multi-scale analysis. *Marine Ecology-Progress Series*, **295**, 1–20.

Defeo, O., McLachlan, A., Schoeman, D.S., Schlacher, T.A., Dugan, J., Jones, A., Lastra, M. & Scapini, F. (2009) Threats to sandy beach ecosystems: a review. *Estuarine Coastal and Shelf Science*, **81**, 1–12.

Degraer, S., Volckaert, A. & Vincx, M. (2003) Macrobenthic zonation patterns along a morphodynamical continuum of macrotidal, low tide bar/rip and ultra-dissipative sandy beaches. *Estuarine, Coastal and Shelf Science*, **56**, 10.

Dugan, J.E. & Davis, G.E. (1993) Applications of marine refugia to coastal fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 2029–2042.

Chen, J., Eisma, D., Hotta, K., Walker, H.J., Walker, H.J. & Finkl, C.W. (2002) Beach nourishment: case studies. *Engineered Coasts*, pp. 23–59. Springer, Netherlands.

Gmelig Meyling, A.W. & De Bruyne, A.W. (1994) Zicht op zee: waarnemingen van veranderingen in de nabije kustzone door strandmonitoring met 381 strandwachten. *Technical Report*, **79**, 79.

Goss-Custard, J.D., Triplet, P., Sueur, F. & West, A.D. (2006) Critical thresholds of disturbance by people and raptors in foraging wading birds. *Biological Conservation*, **127**, 88–97.

Hamm, L., Capobianco, M., Dette, H.H., Lechuga, A., Spanhoff, R. & Stive, M.J.F. (2002) A summary of European experience with shore nourishment. *Coastal engineering*, **47**, 237–264.

Hanson, H., Brampton, A., Capobianco, M., Dette, H.H., Hamm, L., Laustrup, C., Lechuga, A. & Spanhoff, R. (2002) Beach nourishment projects, practices, and objectives-a European overview. *Coastal engineering*, **47**, 81–111.

Harley, C.D.G., Randall Hughes, A., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L. & Williams, S.L. (2006) The impacts of climate change in coastal marine systems. *Ecology Letters*, **9**, 228–241.

Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der LINDEN, P.J., Dai, X., Maskell, K. & Johnson, C. (2001) *Climate Change 2001: The Scientific Basis*. Cambridge University Press, Cambridge.

Jones, A.R., Gladstone, W. & Hacking, N.J. (2007) Australian sandy-beach ecosystems and climate change: ecology and management. *Australian Zoologist*, **34**, 190–201.

Jones, A.R., Murray, A., Lasiak, T.A. & Marsh, R.E. (2008) The effects of beach nourishment on the sandy beach amphipod Exoediceros fossor: impact and recovery in Botany Bay, New South Wales, Australia. *Marine ecology*, **29**(S1), 28–36.

Kersten, M. & Piersma, T. (1987) High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea*, **75**, 175–187.

Koot, J. (2009) *Interannual patterns in predation pressure by juvenile plaice Pleuronectes platessa L. on intertidal macrobenthos in the Dutch Wadden Sea*. 21, Royal Netherlands Institute for Sea Research, 21.

Kuipers, B.R. & Dapper, R. (1984) Nursery function of Wadden Sea tidal flats for the brown shrimp *Crangon crangon*. *Marine Ecology Progress Series*, **17**, 171–181.

Leewis, L., van Bodegom, P.M., Rozema, J. & Janssen, G.M. (2012) Does beach nourishment have long-term effects on intertidal macroinvertebrate species abundance? *Estuarine, Coastal and Shelf Science*, **113**, 172–181.

Lockwood, S.J. (1984) The daily food intake of 0-group plaice (*Pleuronectes platessa* L.) under natural conditions: changes with size and season. *Journal du Conseil*, **41**, 181–193.

McLachlan, A. & Brown, A.C. (2006) *The Ecology of Sandy Shores*. Academic Press, Burlington, MA, USA, 373.

McLachlan, A., De Ruyck, A. & Hacking, N. (1996) Community structure on sandy beaches: patterns of richness and zonation in relation to tide range and latitude. *Revista Chilena de Historia Natural*, **69**, 451–467.

McLachlan, A. & Jaramillo, E. (1995) Zonation on sandy beaches. *Oceanography and Marine Biology - an Annual Review*, **33**, 305–335.

Mumby, P.J., Steneck, R.S. & Hastings, A. (2012) Evidence for and against the existence of alternate attractors on coral reefs. *Oikos*, **122**, 481–491.

del Norte-Campos, A.G.C. & Temming, A. (1994) Daily activity, feeding and rations in gobies and brown shrimp in the northern Wadden Sea. *Marine Ecology-Progress Series*, **115**, 41–53.

Perry, C.T., Murphy, G.N., Kench, P.S., Smithers, S.G., Edinger, E.N., Steneck, R.S. & Mumby, P.J. (2013) Caribbean-wide decline in carbonate production threatens coral reef growth. *Nature Communications*, **4**, 1402.

Peterson, C.H., Hickerson, D.H.M. & Johnson, G.G. (2000) Short-term consequences of nourishment and bulldozing on the dominant large invertebrates of a sandy beach. *Journal of Coastal Research*, **16**, 11.

Peterson, C.H., Bishop, M.J., Johnson, G.A., D'Anna, L.M. & Manning, L.M. (2006) Exploiting beach filling as an unaffordable experiment: benthic intertidal impacts propagating upwards to shorebirds. *Journal of Experimental Marine Biology and Ecology*, **338**, 205–221.

Riddell, K.J. & Young, S.W. (1992) The management and creation of beaches for coastal defence. *Water and Environment Journal*, **6**, 588–597.

Rogers, D.I., Piersma, T. & Hassell, C.J. (2006) Roost availability may constrain shorebird distribution: exploring the energetic costs of roosting and disturbance around a tropical bay. *Biological Conservation*, **133**, 225–235.

Schlacher, T.A., Schoeman, D.S., Dugan, J., Lastra, M., Jones, A., Scapini, F. & McLachlan, A. (2008) Sandy beach ecosystems: key features, sampling issues, management challenges and climate change impacts. *Marine ecology*, **29**, 70–90.

Short, A.D. (1991) Macro-meso tidal beach morphodynamics: an overview. *Journal of Coastal Research*, **7**, 417–436.

Short, A.D.E. (1999) *Handbook of Beach and Shoreface Morphodynamics*. Wiley and Sons, Chichester, UK.

Slim, P. & Löffler, M. (2007) Kustveiligheid en natuur: een overzicht van kennis en kansen. *Alterra-Rapport*, **1485**, 1–92.

Speybroeck, J., Degraer, S. & Vincx, M. (2003) *Ecologische monitoring kustverdedigingsproject Oostende (t0 situatie, fase 1) – Dossiernummer 202.290*. 64, Ministerie van de Vlaamse Gemeenschap, Departement Leefmilieu en Infrastructuur, Administratie Waterwegen en Zeewezen, Afdeling Waterwegen Kust (AWK) 64.

Speybroeck, J., Bonte, D., Courtens, W., Gheskiere, T., Grootaert, P., Maelfait, J.P. *et al.* (2004) *Studie over de impact van zandsuppleties op het ecosysteem – fase 1 – Dossiernummer 202.165*. 203, Ministerie van de Vlaamse Gemeenschap Departement Leefmilieu en Infrastructuur Administratie Waterwegen en Zeewezen Afdeling Waterwegen, 203.

Speybroeck, J., Bonte, D., Dasseville, R., Gheskiere, T., Grootaert, P., Lionard, M. *et al.* (2005) *Biological evaluation of eleven beach zones along the Flemish coast-BEST: Final report* 181.

Speybroeck, J., Bonte, D., Courtens, W., Gheskiere, T., Grootaert, P., Maelfait, J.P. *et al.* (2006a) Beach nourishment: an ecologically sound coastal defence alternative? *A review Aquatic Conservation: Marine and Freshwater Ecosystems*, **16**, 419–435.

Speybroeck, J., Bonte, D., Grootaert, P., Maelfait, J.P., Stienen, E., Vandomme, V., Vanermen, N., Vincx, M. & Degraer, S. (2006b) *Studie over de impact van zandsuppleties op het ecosysteem – fase 2 – Dossiernummer 204.295* 118, Ministerie van de Vlaamse Gemeenschap Departement Leefmilieu en Infrastructuur Agentschap voor Maritieme Dienstverlening en Kust, Afdeling Kust 118.

Speybroeck, J., Bonte, D., Courtens, W., Gheskiere, T., Grootaert, P., Maelfait, J.P. *et al.* (2008) The Belgian sandy beach ecosystem: a review. *Marine Ecology - An Evolutionary Perspective*, **29**, 171–185.

Spiegelhalter, D., Thomas, A., Best, N. & Lunn, D. (2003) *WinBUGS User Manual*. MRC Biostatistics Unit, Cambridge.

Szaniawska, A. (1983) Seasonal changes in energy content of *Crangon crangon* L. (Crustacea, Decapoda). *Polskie Archiwum Hydrobiologii*, **30**, 45–56.

Van Ginderdeuren, K., Maene, S., Vincx, M. & Degraer, S. (2007) *Ecologische monitoring kustverdedigingsproject Oostende (t0 situatie, fase 3) – Dossiernummer 205.240*. 103, Ministerie van de Vlaamse Gemeenschap, Departement Leefmilieu en Infrastructuur, Agentschap voor Maritieme Dienstverlening en Kust (MD&K) 103.

Van Tomme, J., Degraer, S. & Vincx, M. (2014) Role of predation on sandy beaches: predation pressure and prey selectivity estimated by laboratory experiments. *Journal of Experimental Marine Biology and Ecology*, **451**, 115–121.

Vanden Eede, S. & Vincx, M. (2010) *Ecologische monitoring natuurinrichtingsproject Lombardsijde (t1 situatie, 2009) – Dossiernummer 209.090*. 71, Vlaamse Overheid, Agentschap voor Maritieme Dienstverlening en Kust, Afdeling Kust 71.

Vanden Eede, S. & Vincx, M. (2011) *Ecologische monitoring natuurinrichtingsproject Lombardsijde en OW-plan Oostende (t1 situatie, 2010) – Dossiernummer 209.090*. 91, Vlaamse Overheid, Agentschap voor Maritieme Dienstverlening en Kust, Afdeling Kust 91.

Vanden Eede, S. (2013) *Impact of beach nourishment on coastal ecosystems, with recommendations for coastal policy in Belgium*. PhD thesis, Universiteit Gent, Belgium.

Vanden Eede, S., Vincx, M. & Degraer, S. (2008) *Ecologische monitoring natuurinrichtingsproject Lombardsijde (t0 situatie, fase 4) – Dossiernummer 208.245*. 49, Vlaamse Overheid, Agentschap voor Maritieme Dienstverlening en Kust, Afdeling Kust 49.

Vanden Eede, S., Van Tomme, J., De Busschere, C., Vandegehuchte, M., Sabbe, K., Stienen, E., Degraer, S., Vincx, M. & Bonte, D. (2014) Data from: Assessing the impact of beach nourishment on the intertidal food web through the development of a mechanistic-envelope model. Dryad Digital Repository, doi:http://dx.doi.org/10.5061/dryad.vq76f.

Vanermen, N., Stienen, E.W.M., De Meulenaer, B., Van Ginderdeuren, K. & Degraer, S. (2009) Low dietary importance of polychaetes in opportunistic feeding Sanderlings *Calidris alba* on Belgian beaches. *ARDEA*, **97**, 81–87.

Welvaert, G. (2005) *Ecologische monitoring kustverdedigingsproject Oostende (t0 situatie, fase 2) – Rapportnummer 04/A2084-3*. 166, Ministerie van de Vlaamse Gemeenschap, Departement Leefmilieu en Infrastructuur, Administratie Waterwegen en Zeewezen, Afdeling Waterwegen Kust 166.

Ysebaert, T. & Meire, P. (1989) Uitkomstsukses en foerageergedrag van kokmeeuwen in drie kolonies gelegen langs de Westerschelde. *Rapport WWE*, **95**, 95.

Zwarts, L., Wanink, J.H. & Ens, B.J. (1996) Predicting seasonal and annual fluctuations in the local exploitation of different prey by Oystercatchers *Haematopus ostralegus*: a ten year study in the Wadden Sea. *Ardea*, **84A**, 401–440.

Received 21 March 2014; accepted 1 July 2014
Handling Editor: David Angeler

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Input data and model validation.

Appendix S2. Estimated regression coefficients.

Appendix S3. Average conversion factors converting abundance to biomass.