BIOTIC INTERACTIONS WITHIN SANDY BEACH ECOSYSTEMS, WITH IMPLICATIONS FOR AN ECOLOGICALLY-SOUND BEACH NOURISHMENT

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Biotic interactions within sandy beach ecosystems, with implications for an ecologically-sound beach nourishment

Biotische interacties in zandstrandecosystemen, met zijn implicaties voor ecologisch onderbouwde strandopspuitingen

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Summary

Sandy beaches are the largest coastal ecosystem on earth, covering 70% of all continental margins. As more people interact directly with beaches than with any other type of shoreline worldwide, beaches are of huge social and cultural importance. Sandy beaches have a multitude of ecological but also economic functions: they are important nursery areas for a variety of marine species and function as natural coastal defence. Beaches are also highly valuable as socio-economic areas since they are key components of many tourist destinations and are important for coastal fisheries. These activities are causing a direct anthropogenic impact and put, together with natural impacts such as sea level rise and beach erosion, a severe pressure on the sandy beach ecosystem. To preserve beaches and their important ecosystem functions, management and conservation have become critical issues, especially in the light of burgeoning global population growth, demographic shifts towards the coast, and economic prosperity. However, to develop a valuable management strategy, sound knowledge of all the aspects of the beach ecosystem is important. As studies on sandy beaches are however poorly represented in scientific literature, there are some critical gaps in basic ecological information. Although patterns on sandy beaches are well-studied, the functional beach ecosystem is largely unknown. Food web dynamics, species interactions and energetic linkages on sandy beaches are barely studied and ecosystem-wide processes as nutrient cycling, cross-system nutrient fluxes, productivity and connectivity among metapopulations on different sandy beaches are undescribed.

An overview of the current knowledge on the sandy beach ecosystem is presented in **chapter 1**. Both the physical characteristics and biological features of sandy beaches are reviewed. In addition, important beach functions and threats are discussed and an overview of current beach management is given.

In **chapter 2**, a modelling approach is applied to examine the role of abiotic and biotic factors in clarifying the distribution and zonation patterns of sandy beach macrobenthos in Western Europe.

The seven most important and abundant species were selected, including the amphipods *Bathyporeia pilosa* and *B. sarsi*, the isopods *Eurydice pulchra* and *E. affinis* and the polychaetes *Scolelepis squamata*, *Nephtys cirrosa* and *Eteone longa.* Species-specific regression models were developed, taking into account abiotic and biotic factors as explanatory variables and the selected species' distribution as response variable. The variance in the model could in part be explained by the abiotic factors and in part by the biotic factors. The two abiotic variables used (median grain size of the sediment and emersion time) did not exclusively explain the variance in species distribution and biotic interactions were suggested to explain up to one third of the variance in species distribution

accounted for by the model. Both predator-prey interactions and competition were suggested as likely biotic interactions. Although the modelling approach could not unravel the true processes and implications of biotic interactions, this study gave indications for the importance of biotic interactions on sandy beaches. Moreover, it allowed us to select the most appropriate potential cause-effect relationships to be tackled subsequently.

The first hypothesis that was experimentally tested was competition between the congeneric amphipods *Bathyporeia pilosa* and *B. sarsi* **(chapter 3)**. These two amphipods co-occur on West European sandy beaches, are morphologically very similar but show a segregated zonation pattern on the beach. A mesocosm experiment was set up to elucidate the role of competition in explaining this zonation pattern. Nine treatments, combining several densities of the two species multiplied with three food level treatments were combined and replicated five times. After a period of three weeks, the experiment was finished and the population parameters (mortality, recruitment, injuries) of the two amphipod species were determined. Results show that the two amphipods attacked each other by biting off appendages. This encounter competition was more pronounced when food was scarce and densities were high. Intraspecific competition could be significantly shown in the *B. sarsi*-population, while intraspecific competition could not be observed in the *B. pilosa*-population. Interspecific competition between both amphipods could not be demonstrated significantly based on the results of this study. Conclusively, our observations of encounter competition in *B. sarsi*, especially under lowered food conditions, suggest that intraspecific competition contributes to this species' upper distribution limit and peak density in the mid-intertidal zone. As no indications of competition effects in *B. pilosa* populations were detected, we suggest that the high abundance of this species in the high-intertidal zone is independent from *B. sarsi* occurrence lower on the beach and primarily relates to lower predation pressure by epi- and hyperbenthic organisms in the high-intertidal zone, as was further studied in the following chapter.

Hyperbenthic and epibenthic predators are known to be of great structuring importance for the communities on soft-bottom intertidal sediments but the great majority of the studies concentrated on tidal flats. On sandy beaches, the importance of predation by epi- and hyperbenthic predators and the trophic relationships between these predators and the macrobenthos community are far less studied and information on predation pressure is lacking. Therefore, the value of top-down regulation on the macrobenthic community of intertidal sandy beaches by brown shrimp and juvenile flatfish predators is studied in **chapter 4.** Two mesocosm experiments were carried out to answer general questions on predation pressure and prey selectivity. The results confirmed the role of *Crangon crangon* as an opportunistic omnivore on dissipative intertidal sandy beaches, similar as in other intertidal habitats. The consumption results of juvenile flatfish acknowledged *S. squamata* as being the most important prey for this predator group. *Bathyporeia pilosa* also was a substantial prey in the predator's diet and this amphipod was significantly preferred over *B. sarsi.* Prey selectivity between both amphipods was assumed to be specifically based on the general size of *B. pilosa* and *B. sarsi. Bathyporeia sarsi* is larger than *B. pilosa* and this may be an adaptation against predation by intertidal predators of intermediate size. Furthermore, the estimated predation pressure of shrimp and juvenile flatfish was found to be extensive and the combination of substantial predation pressure with significant prey selectivity suggests that predation may be an important structuring factor for macrobenthos communities on sandy beaches.

An important abiotic habitat characteristic for macrobenthos on sandy beaches is the beach sediment, as infaunal organisms live in close relation with this sediment and greatly rely on it for their food and survival. In the light of current beach nourishments, we conducted mesocosm sediment selection experiments **(chapter 5)** with four dominant macrobenthic species, both in allotopic and in syntopic conditions. These experiments indicated the sediment preference of these dominant species and could therefore contribute to the ecological adjustment of beach nourishments. Furthermore, the experiments in syntopic conditions showed whether interactions (competition and predation) changed the sediment preferences. As such, the latter experiments could show if species interactions are important structuring factors on the beach. The frequency distribution of sediment choices was tested with a log-likelihood test (G-test) against the null hypothesis that choices were equally distributed among the four sediment types presented. Results indicated that *B. pilosa* and *E. pulchra* preferred the finest sediment, while *B. sarsi* had a broader preference and also occurred in medium-coarse sediments. The polychaete *S. squamata* had the broadest preference and even showed a high occurrence in very coarse sediments that are not naturally occurring on sandy beaches where the animals were caught. While the preferences of the amphipods were supported by other studies, the preference of *E. pulchra* for fine sediments did not correspond to the results in former studies and this contrast deserves further study. The obtained preference for the polychaete was not surprising as *S. squamata* is a cosmopolitan polychaete, occurring both on fine-grained as well as coarse-grained beaches. These preferences imply that beach nourishment with coarse sediment will have a negative effect on *B. pilosa*; effects of coarser sediments on *S. squamata* will be rather positive. Finally, interspecific competition with the syntopically occurring amphipod *B. sarsi* was found to change the sediment selection of the amphipod *B. pilosa* towards the coarser sediments where *B. sarsi* occurred in lower frequencies.

In **chapter 6**, a combined envelope-mechanistic food web model is developed, predicting the response of the beach ecosystem on beach nourishment, with emphasis on the impact of several scenarios of beach nourishment on the dominant macrobenthic species (cf. previous chapters) as well. The model consists of three major modules, one determining the abiotic conditions of the beach, a second modelling expected changes in densities and biomass of lower trophic levels (microphytobenthos and macrobenthos) and a third one predicting the maximal abundance of the most important species from higher trophic levels. Three abiotic variables determine the abundances and densities of microphytobenthos and macrobenthos along soft-sanded beaches: median grain size, total organic matter and elevation relative to the lowest tide. The model is stochastic with parameters for species envelopes and beach characteristics estimated from prior statistical distributions. The input data for these envelope models were derived from 23 beaches sampled in the period 1997-2011 along the Belgian coast. The obtained regression coefficients are used to estimate species abundances according to implemented beach characteristics in the main simulation model. In this simulation model, abundances of higher trophic levels including birds and flatfish are estimated based on their relationships with macrobenthos. The simulation model was validated by sampling two beaches from which densities of the dominant species, total AFDW and species richness were subsequently compared with simulated data according to the sample location. In general, observed species densities and total biomass matched the expected values. To illustrate the ecological value of this beach nourishment simulation model, different scenarios were tested. All model simulations indicate that the used nourishment sediment is the dominant factor in determining the effect on the ecosystem, with deterioration of the beach ecosystem after nourishment with too coarse sediment (e.g. >> than 300 µm). Based on these results, a gradient of sediment grain size could be recommended for nourishment of natural, fine-grained beaches: 200-300 µm and generally, it is advised to use sediment that resembles natural beach conditions. Furthermore, it is advised to evaluate the beach ecosystem health by a combination of different variables (biodiversity, macrobenthos biomass) since focusing on one variable can be deceptive as opportunistic species can become very abundant on a beach impacted by nourishment.

In conclusion, this thesis showed that biotic interactions are present within the sandy beach ecosystem and that these interactions can have a structuring role in community patterns, as discussed more profoundly in **chapter 7**. In addition, the better ecosystem knowledge obtained in this study, is essential for ecologically-sound beach nourishment and sandy beach management.

Samenvatting

Zandstranden vormen het grootste kustecosysteem op aarde aangezien 70 % van alle continentale grenzen wordt afgebakend door deze stranden. Stranden zijn erg belangrijk voor de mens in zowel sociaal als cultureel opzicht: wereldwijd hebben meer mensen een directe link met stranden dan met elk ander type van kustlijn. Zandstranden hebben heel wat ecologische maar ook economische functies. Ze zijn belangrijk als voedselgebieden voor een variëteit aan mariene organismen en hebben een belangrijke functie als natuurlijke kustverdediging. Stranden zijn ook erg waardevol als socio-economische gebieden aangezien ze essentieel zijn als toeristische bestemming en bovendien ook belangrijk zijn voor de (kust)visserij. Deze activiteiten zorgen voor een antropogene impact, die, gecombineerd met natuurlijke invloeden zoals de stijging van het zeeniveau en stranderosie, een ernstige druk op het ecosysteem van zandstranden veroorzaakt. Om stranden en hun belangrijke functies te vrijwaren zijn management en bescherming daarom erg belangrijke kwesties geworden, zeker in de huidige context van globale bevolkingstoename, demografische verschuivingen richting de kust en economische vooruitzichten. Om een waardevolle managementstrategie op te stellen, is een goede kennis van alle aspecten van het strandecosysteem essentieel. Aangezien studies over zandstranden echter ondervertegenwoordigd zijn in de wetenschappelijke literatuur, zijn er enkele kritische tekorten in de huidige ecologische kennis. Hoewel patronen op zandstranden goed bestudeerd zijn, ontbreekt een goede kennis over het functionele aspect van het strandecosysteem. Voedselwebdynamiek, interacties tussen soorten en energetische relaties op zandstranden zijn nauwelijks bestudeerd en ecosysteemprocessen zoals nutriëntenrecyclage, nutriëntfluxen, productiviteit en connectiviteit tussen metapopulaties op verschillende zandstranden zijn niet beschreven.

Een overzicht van de huidige kennis over het zandstrandecosysteem wordt gegeven in **hoofdstuk 1**. Zowel de fysische kenmerken als de biologische karakteristieken van zandstranden worden besproken. Verder worden ook de belangrijke strandfuncties en bedreigingen bediscussieerd en een overzicht van de huidige stand van zaken wat betreft strandmanagement wordt gegeven. Ten slotte wordt ook een overzicht geboden van de belangrijkste hiaten in de kennis over het zandstrandecosysteem.

In **hoofdstuk 2** wordt een modelbenadering gebruikt om de rol van abiotische en biotische factoren te verduidelijken bij het verklaren van distrubutie- en zonatiepatronen van zandstrandmacrobenthos in West-Europa. De zeven meest dominante en abundante soorten werden geselecteerd. Dit zijn de amfipoden *Bathyporeia pilosa* en *B. sarsi*, de isopoden *Eurydice pulchra* en *E. affinis* en de polychaeten *Scolelepis squamata*, *Nephtys cirrosa* en *Eteone longa*. Soortspecifieke

regressiemodellen werden ontwikkeld, met de geselecteerde soortsdistributie als responsvariabele en zowel abiotische als biotische factoren als verklarende variabelen. De meest geschikte modellen met significante abiotische en biotische factoren werden vervolgens geselecteerd via de AIC methode (Akaike's Information Criterium). De variantie in het model kon gedeeltelijk worden verklaard door de abiotische factoren en ook deels door de biotische factoren. De twee abiotische variabelen die in beschouwing werden genomen (mediane korrelgrootte en emersietijd) verklaarden de variantie in de soortdistributies niet volledig en biotische interacties werden gesuggereerd ook een bijdrage te leveren, tot zelfs één derde van de totale variantie in soortdistributie verklaard door het model. Zowel predator-prooi interacties als competitie werden gesuggereerd als mogelijke biotische interacties. Hoewel de modelaanpak niet voldoende was om de achterliggende biotische processen volledig te ontrafelen, gaf deze studie indicaties voor het belang van biotische interacties op zandstranden. Verder lieten deze modellen ons toe om de meest belangrijke potentiële relaties te selecteren en deze te onderzoeken in een volgende stap.

De eerste hypothese die experimenteel wordt getest, is de competitie-hypothese tussen de syntoop voorkomende amfipoden *Bathyporeia pilosa* en *B. sarsi* **(hoofdstuk 3)**. Deze twee amfipoden komen samen voor op West-Europese zandstranden, zijn morfologisch sterk gelijkend maar vertonen een gescheiden zonatiepatroon op het strand. Er werd een mesocosm experiment opgesteld om de rol van competitie, als verklaring voor dit zonatiepatroon, te onderzoeken. Negen treatments, die verschillende densiteiten van de twee soorten combineerden, vermenigvuldigd met drie voedselniveaus, werden getest voor vijf replicaten. Na een periode van drie weken werd het experiment beëindigd en werden de populatieparameters (mortaliteit, rekrutering, verwondingen) van de twee amfipode-soorten bepaald. De resultaten toonden aan dat de twee amfipoden elkaar aanvielen en elkaars lichaamsaanhangsels beschadigden en zelfs afbeten. Deze encounter competitie was meer uitgesproken wanneer voedsel schaars en densiteiten hoog waren. Intraspecifieke competitie kon op een significante manier worden aangetoond in de *B. sarsi*-populatie, terwijl intraspecifieke competitie niet kon worden aangetoond in de *B. pilosa*-populatie. Interspecifieke competitie tussen de twee soorten amfipoden kon niet op een significante manier worden aangeduid. Onze observaties van encounter competitie bij *B. sarsi*, en dan vooral onder verlaagde voedselcondities, suggereren dat intraspecifieke competitie bijdraagt tot zowel de bovenste distributie-limiet van de soort maar ook tot de piekdensiteiten in de mid-intertidale zone. Aangezien er geen indicaties waren voor het voorkomen van intraspecifieke competitie in de *B. pilosa*-populatie, opperen we dat de hoge abundanties van deze soort in de hoog-intertidale strandzone onafhankelijk zijn van het voorkomen van *B. sarsi* lager op het strand, maar in de eerste plaats gerelateerd zijn aan de lagere predatiedruk van epi- en hyperbenthische predatoren in de hoog-intertidale zone, wat in het hieropvolgende hoofdstuk verder werd onderzocht.

Hyperbenthische en epibenthische predatoren zijn gekend voor hun belangrijke structurerende rol in gemeenschappen van intertidale zachte sedimenten maar de grote meerderheid van de studies hieromtrent concentreren zich op intergetijdengebieden zoals slikken. Op zandstranden zijn zowel het belang van predatie door epi- en hyperbenthos als de trofische relaties tussen deze predatoren en de macrobenthosgemeenschap heel wat minder bestudeerd en is informatie over predatiedruk helemaal afwezig. Daarom wordt het belang van top-downregulatie door garnalen en juveniele platvissen op de macrobenthosgemeenschap van intertidale zandstranden bestudeerd in **hoofdstuk 4**. Er werden twee laboratoriumexperimenten uitgevoerd om een antwoord te vinden op de vragen rond predatiedruk en prooiselectiviteit. De resultaten bevestigden de rol van *Crangon crangon* (grijze garnaal) als opportunistische omnivoor op dissipatieve zandstranden, analoog aan zijn rol in andere intertidale habitats. De consumptieresultaten van de juveniele platvis bevestigden *S. squamata* als de belangrijkste prooisoort voor jonge platvissen. *Bathyporeia pilosa* was ook een belangrijke prooisoort in het dieet van juveniele platvissen en deze amfipode werd verkozen boven *B. sarsi.* Prooiselectiviteit tussen beide amfipoden werd verondersteld gebaseerd te zijn op de grootte van *B. pilosa* en *B. sarsi. Bathyporeia sarsi* is groter dan *B. pilosa* en dit kan een adaptatie zijn aan de aanwezigheid van intertidale predatoren van intermediaire grootte in de habitat van de soort. De combinatie van een aanzienlijke predatiedruk en een significante prooiselectiviteit suggereerde bovendien dat predatie een belangrijke structurerende factor is voor macrobenthos-gemeenschappen op zandstranden.

Een belangrijk abiotisch habitatkenmerk voor macrobenthos van zandstranden is het strandsediment, aangezien benthische organismen in nauwe relatie leven met dit sediment en erg afhankelijk zijn van het sediment voor hun voedsel en overleving. In de context van de huidige strandopspuitingen, voerden we sedimentselectie-experimenten uit **(hoofdstuk 5)** met vier dominante macrobenthossoorten, zowel in allotope als syntope omstandigheden. Deze experimenten toonden de sedimentpreferentie van de dominante soorten aan en deze kennis kan bijdragen tot het ecologisch aanpassen van strandopspuitingen. Verder toonden de experimenten in syntope condities aan of soorteninteracties (competitie en predatie) al dan niet deze voorkeur veranderen. Daarom kunnen deze laatste experimenten aanduiden of soorteninteracties belangrijke structurerende factoren zijn op zandstranden. De frequentiedistributie van de sedimentkeuzes werd getest met een log-likelihood test (G-test). De nulhypothese hierbij veronderstelde dat de testorganismen gelijk verdeeld zouden zijn over de vier aangeboden sedimenttypes. Resultaten toonden aan dat *B. pilosa* en *E. pulchra* het fijnste sediment verkozen, terwijl *B. sarsi* een bredere preferentie had en dus ook in grovere sedimenten voorkwam. De polychaet *S. squamata* had de breedste voorkeur en kwam zelfs in aanzienlijke abundanties voor in grove sedimenten die van nature niet voorkomen op de zandstranden waar de organismen werden verzameld. Terwijl de preferenties van amfipoden werden ondersteund door andere studies, kwam de preferentie van *E. pulchra* voor fijne sedimenten niet overeen met de resultaten van vorige studies. Aangezien *S. squamata* een kosmopoliete polychaet is, die zowel voorkomt op stranden met fijn en grof sediment, was de bekomen preferentie van de polychaet niet verrassend. Al deze preferenties impliceren dat strandopspuitingen met grof sediment een negatief effect zullen hebben op *B. pilosa*, terwijl effecten van grof sediment eerder positief zullen zijn voor *S. squamata.* Ten slotte werd aangetoond dat interspecifieke competitie met de syntoop voorkomende amfipode *B. sarsi*, de sedimentpreferentie van *B. pilosa* veranderde in de richting van grovere sedimenten waar *B. sarsi* voorkwam in lagere densiteiten.

In **hoofdstuk 6** wordt een mechanistisch-envelope model ontwikkeld, dat de respons van het strandecosysteem na strandopspuiting kan voorspellen. Het model bestaat uit drie grote modules, een eerste module die de abiotische condities van het strand bepaalt, een tweede module die de verwachte veranderingen in densiteit en biomassa van lagere trofische niveaus (microfytobenthos en macrobenthos) modelleert en een derde module die de maximale abundanties van de meest belangrijke soorten van hogere trofische niveaus voorspelt. Drie abiotische variabelen bepalen de abundanties van microfytobenthos en macrobenthos op zandstranden: mediane korrelgrootte *(MKG)*, totaal organisch materiaal *(TOM)* en de positie relatief t.o.v. het laagste getijniveau *(h).* Het model is stochastisch en parameters voor soortenenvelopes en strandkenmerken werden geschat op basis van voorgaande statistische distributies. De input data voor deze envelopemodellen was afkomstig van 23 stranden, bemonsterd langs de Belgische kust in de periode 1997-2011. De bekomen regressie-coëfficiënten werden gebruikt om soortenabundanties te schatten in overeenstemming met de geïmplementeerde strandkarakteristieken in het basis-simulatiemodel. In dit simulatiemodel werden abundanties van hogere trofische niveaus zoals vogels en platvissen geschat op basis van hun relaties met het macrobenthos. Het simulatiemodel werd gevalideerd door twee stranden te bemonsteren waarbij densiteiten van de dominante soorten, totaal asvrij drooggewicht (AFDW) en soortenrijkdom achtereenvolgens vergeleken werden met de gesimuleerde data in overeenstemming met de staalnameplaats. De waargenomen soortendensiteiten en totale biomassa kwamen goed overeen met de verwachte waarden. Om de ecologische waarde van dit strandsuppletie-simulatiemodel te illustreren, werden verschillende scenario's getest. Alle modelsimulaties toonden aan dat het gebruikte suppletiesediment de dominante factor is in het bepalen van de effecten op het ecosysteem, met een degradatie van het strandecosysteem na een opspuiting met té grof zand (d.w.z. >> 300 µm). De aanbevolen gradiënt voor mediane korrelgrootte van het suppletiesediment werd daarom gelegd op 200-300 µm voor fijnkorrelige stranden en algemeen wordt aangeraden zand te gebruiken dat qua karakteristieken overeenkomt met de natuurlijke condities op een strand. Verder is het aangeraden de gezondheid van het strandecosysteem te evalueren a.d.h.v. een combinatie van verschillende variabelen (biodiversiteit, biomassa van het macrobenthos), aangezien de focus op één variabele misleidend kan zijn. Opportunistische soorten kunnen immers erg abundant worden op een strand dat geïmpacteerd werd door een opspuiting.

Deze doctoraatsstudie toont aan dat biotische interacties aanwezig zijn binnen het strandecosysteem en dat deze interacties bovendien een structurerende rol kunnen hebben voor gemeenschapspatronen op het strand, zoals in detail wordt besproken in **hoofdstuk 7**. Daarenboven is de betere kennis omtrent het strandecosysteem, bekomen via deze studie, essentieel voor ecologisch verantwoorde strandopspuitingen en management van zandstranden.

1

Chapter 1: General introduction

In this introductory chapter, the following general physical and biological features of sandy beaches, the focus habitat of this PhD study, are documented: the dominant ecosystem components, the complex food web and current knowledge on biotic interactions. Subsequently, sandy beach functions and threats are documented and current difficulties in sandy beach management are discussed. Finally, the aims of this PhD study are formulated and the thesis outline is presented.

1. Physical features of sandy beaches

1.1 General

Sandy beaches are the largest coastal ecosystems on earth, covering 70% of all continental margins (McLachlan and Brown, 2006). They are very dynamic environments due to the wave and wind driven transport of sediment between the dunes and the sea. Their morphology is determined by the interaction among sand, waves and tides (Masselink and Short, 1993; McLachlan and Brown, 2006) and these features characterize different beach types, described by beach indices such as the Relative Tidal Range (RTR). RTR is a dimensionless index that measures the relative importance of waves and tides in influencing beach morphology. Low values (< 3) indicate wave-dominated beaches, values in the range 3 to 12 indicate tide-modified beaches, and values > 12 indicate tide-dominated beaches fronted by sand flats (McLachlan and Brown, 2006). When the tidal range is smaller than 2 m, beaches are called microtidal, while beaches with a tidal range larger than 4 m are considered macrotidal. Beaches with intermediate tidal range are called meso-tidal. Wave-dominated microtidal beaches can generally appear in three beach states: reflective, intermediate and dissipative. On reflective beaches, sediment is generally coarse, cusps or short longshore undulations caused by edge waves are present, the slope is steep and there is no surf zone (figure 1 (a)). Dissipative beaches are characterized by a broad surf zone, fine sediment and the presence of multiple bars, parallel to the beach (figure 1 (b)). Relatively, the conditions on these latter beaches are more benign compared to the conditions on reflective beaches. Intermediate beaches are typically defined by intermediate characteristics such as medium-coarse sediment, a medium slope and the presence of a medium-large surf-zone (Defeo and McLachlan, 2005).

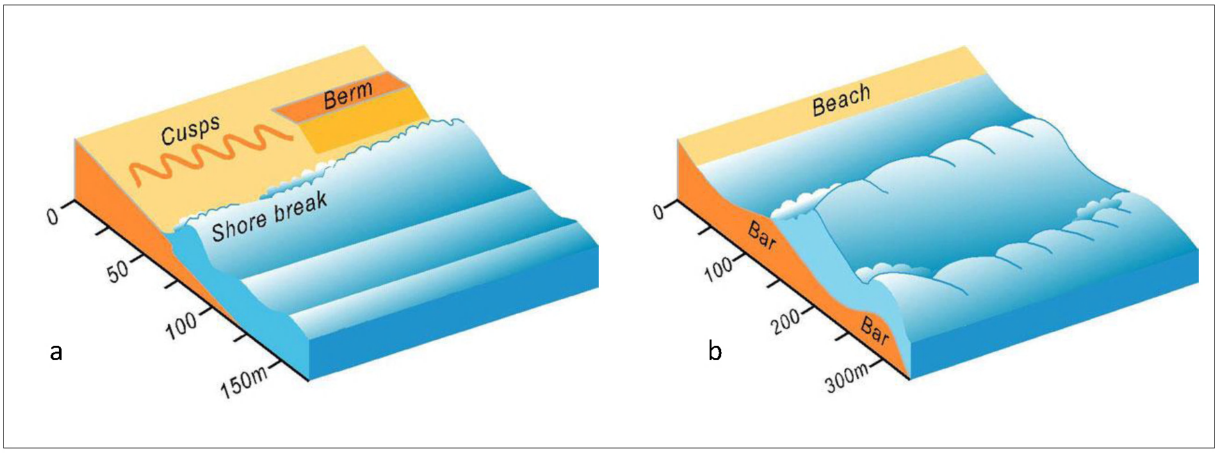

Figure 1: schematic presentation of (a) a reflective and (b) dissipative beach (Short, 2012).

On tide-modified macrotidal beaches, the picture becomes more complex and the three beach states described, being the reflective type with a low-tide terrace, the low-tide bar/rip type and the ultra-dissipative type, differ from the beach states on microtidal beaches. The reflective type with low-tide terrace is characterized by a steep beach face and a low-tide terrace that may be continuous or cut by rips (figure 2 (a)). The low-tide bar/rip beach type can be distinguished by its high-tide reflective beach face fronted by a wide low gradient intertidal zone, which may contain a low swash bar (ridge and runnel) at low tide (figure 2 (b)). Finally, ultra-dissipative beaches are typified by the flat and relatively featureless intertidal zone (figure 2 (c)).

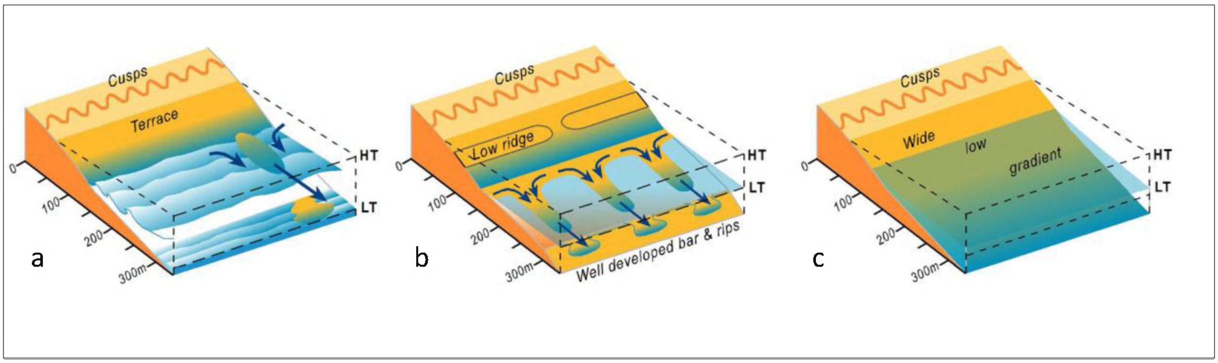

Figure 2: schematic presentation of (a) a reflective beach with low-tide terrace, (b) a low-tide bar/rip beach and (c) an ultra-dissipative beach (Short, 2012).

1.2 Belgian beaches

Belgian beaches are characterized by a large tidal range and are classified from ultra-dissipative in the west to low-tide bar/rip in the east (Degraer et al., 2003; Speybroeck et al., 2008a). Most important physical features of Belgian dissipative beaches are the average spring tide range of 4.3-5 m (Fremout, 2002), an intertidal zone between 200 m and 500 m, an average sediment grain size ranging from 200 to 220 µm with a cross-shore variation in median grain size of 160–380 µm (De Moor, 2006) and a gentle beach slope of 0.8 % to 2.5 % (Speybroeck et al., 2008a).

2. Biological features of sandy beaches

2.1 Species communities on Belgian dissipative beaches

Although sandy beaches seem devoid of life at first sight, a relative high species diversity and density is present. Flora and fauna is represented in and on the sandy beach sediment as well as in the water, flooding the intertidal sandy beach at incoming tide. Furthermore, a continuum is formed from dunes over the intertidal beach to the subtidal coastal zone, making the sandy beach ecosystem extremely complex (Schlacher et al., 2008).

Primary producers

On dissipative sandy beaches, diatoms dominate the microphytobenthos of the intertidal sediment, but dense populations of cyanobacteria, dinoflagellates, euglenoids, crypto- and chrysophytes may also occur (MacIntyre et al., 1996; Noffke and Krumbein, 1999). A total of 120 species of microphytobenthos have been reported for Belgian beaches (van der Ben, 1973; Blondeel, 1996).

Vascular plants are restricted to the supralittoral near the drift line, the upper dry beach, and the embryonic dunes. The most common species along the Belgian coast is sea rocket (*Cakile maritima*), often accompanied by prickly saltwort (*Salsola kali* subsp. *kali*) and sea sandwort (*Honckenya peploides*) (Speybroeck et al., 2008a).

Consumers

The sandhopper *Talitrus saltator* (Amphipoda, Talitridae) is a dominant species of the arthropod fauna living along the Belgian strand line (Speybroeck et al., 2008a). Furthermore, beetles and spiders occur in the dunes and on the beach while Diptera (flies and mosquitoes), comprising the most abundant group of beach insects, are restricted to the supralittoral zone at high tide, while at low tide, Diptera also occur in the intertidal (Ardö, 1957; Tsacas, 1959).

Although sandy beach meiofaunal research has focused mainly on the higher taxon level (Gray and Rieger, 1971; Harris, 1972; McIntyre and Murison, 1973; McLachlan, 1977; Olafsson, 1991; Rodriguez et al., 2001; Menn, 2002), nematodes as being the largest group within the meiofauna, have been studied at species level on Belgian sandy beaches (Gheskiere et al., 2004). In general, fifteen meiofauna taxa have been recorded on Belgian dissipative beaches, with Nematoda, Harpacticoida and Turbellaria being dominant (Gheskiere et al., 2004; Kotwicki et al., 2005; Gheskiere, 2006).

Several nematode communities can be found on the Belgian intertidal beach, showing an increase in species diversity from the upper-intertidal to the mid-intertidal zone and remaining more or less constant towards the low-intertidal (Gheskiere et al., 2004). However, nematode densities are showing a slightly different pattern, with the highest densities being present at the lower beach. In addition, microhabitat heterogeneity such as the ridge-and-runnel system on Belgian beaches is strongly influencing more small-scaled nematode zonation patterns on sandy beaches (Maria, 2011).

A high dominance of the brackish-water nematode *Pellioditis marina* is found above the drift line (Gheskiere et al., 2004) while a drift-line specific meiobenthic community is present around the drift line. In both the mid-intertidal and the low-intertidal, nematodes such as *Monoposthia mirabilis*, *Odontophora* sp. and *Paracanthonchus* sp. are dominant (Gheskiere et al., 2004).

Similar to the different meiofauna communities, diverse macrobenthos communities can be distinguished along the cross-shore intertidal beach gradient (Degraer et al., 2003). The community in the high intertidal zone is species-poor but shows high densities and is dominated by the polychaete *Scolelepis squamata*, the isopod *Eurydice pulchra* and the amphipod *Bathyporeia pilosa* (Degraer et al., 2003; Van Hoey et al., 2004), while the lower intertidal has a higher species richness but lower species densities and is characterized by *Nephtys cirrosa, Donax vittatus* and several smaller polychaete species such as *Spio* sp. and *Spiophanes bombyx*. This sandy beach macrobenthos typically shows a distinct zonation pattern in the intertidal (figure 3).

Besides the fauna permanently present on the beach, a lot of species are only temporarily residents of the sandy beach during high tide (marine epi- and hyperbenthos), but also during low tide (birds). Juveniles of marine hyper- and epibenthos inhabit intertidal habitats, including sandy beaches, during some phases of their life cycle (Miller et al., 1984; Gibson, 1994; Beck et al., 2003; Peterson, 2003) to feed and to hide from subtidal predators (Laffaille et al., 1998; Beyst et al., 1999; Lefeuvre et al., 1999; Le Pape et al., 2007; Nicolas et al., 2007). Beyst et al. (1999) studied epi- and hyperbenthic communities on the Belgian intertidal sandy beach and found a rich hyperbenthic fauna as well as a diverse epibenthic assemblage, with mysids, the shore crab *Carcinus maenas*, the brown shrimp *Crangon crangon*, postlarval fish such as gobies and clupeids, juvenile flatfish such as plaice *Pleuronectes platessa* and early life stages of a variety of other marine species such as polychaetes and amphipods to be present at the beach. At high tide, these species are occurring in the surf zone on the intertidal beach, while at receding tide some species (e.g. juvenile shrimp and juvenile flatfish) stay behind in runnels and pools on hydrodynamically benign beaches.

While the supralittoral zone of Belgian beaches has become less important as a nesting area for birds due to the high anthropogenic pressures, destroying and disturbing nesting habitat (Stienen and Van Waeyenberge, 2002), Kentish plover *Charadrius alexandrinus,* Common ringed plover, *Charadrius* *hiaticula,* and little tern *Sternula albifrons* are breeding on the Belgian beach, in newly created habitats near ports where natural processes are mimicked and therefore attract large numbers of coastal breeders (Stienen and Van Waeyenberge, 2002; Stienen and Van Waeyenberge, 2004; Stienen et al., 2005) or in adjacent nature reserves (Courtens and Stienen, 2004; Stienen et al., 2005). Furthermore, Belgian sandy beaches are also important as resting and foraging areas. The supralittoral area is used as resting area at high tide by gulls and waders. While gulls and foraging wading birds (e.g. Oystercatcher *Haematopus ostralegus* and Dunlin *Calidris alpina*, Grey plover *Pluvialis squatarola*, Common ringed plover *Charadrius hiaticula* and Common redshank *Tringa totanus* (Speybroeck et al., 2005a)) rather reside on tidal flats, Ruddy turnstone *Arenaria interpres*, Purple sandpiper *Calidris maritima* and Sanderling *Calidris alba* preferably rest on groins along the the central part of the Belgian coastline (Engledow et al., 2001; Becuwe et al., 2006).

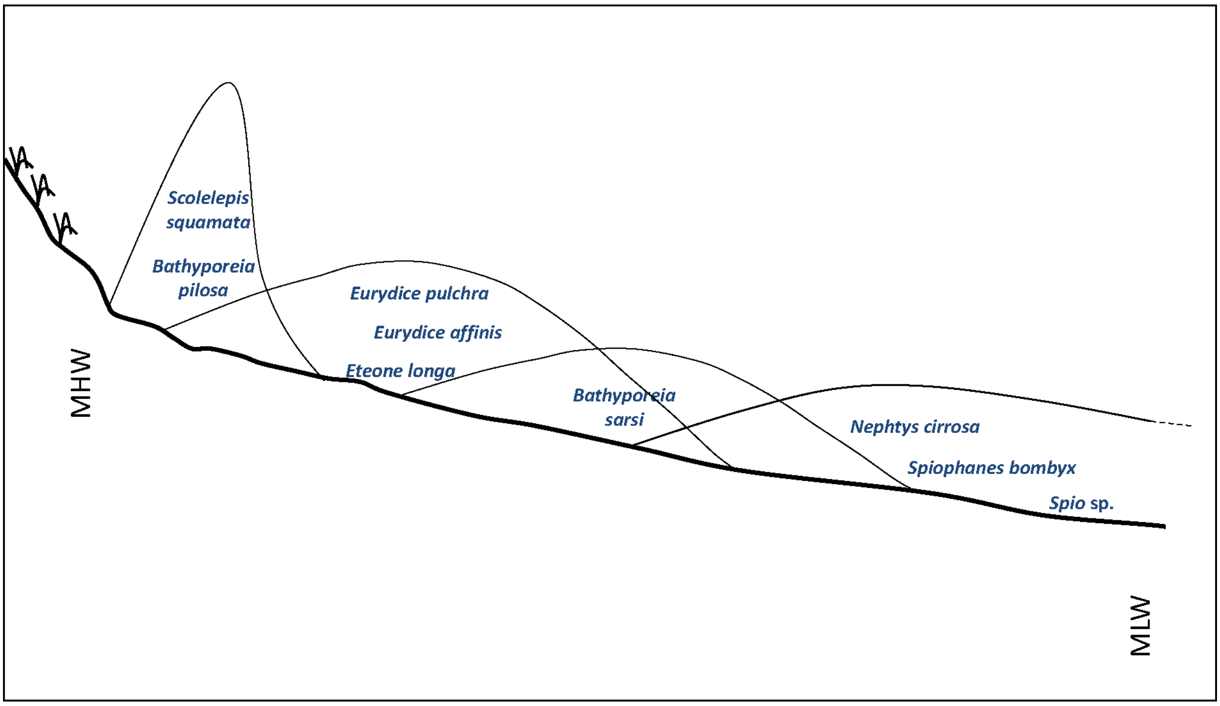

Figure 3: macrobenthos zonation pattern (based on Degraer, 2003); MHW: Mean High Water level; MLW: Mean Low Water level.

2.2 Food web on intertidal dissipative sandy beaches

Food webs of sandy beaches, recently studied by stable isotope analyses (Schlacher and Connolly, 2009; Bergamino et al., 2011; Colombini et al., 2011) are generally thought to be based on marine sources such as phytoplankton, stranded algae and plants, marine detritus and carrion (Defeo and McLachlan, 2005; McLachlan and Brown, 2006; Schlacher et al., 2008; Bergamino et al., 2011) due to the low *in situ* primary production (Inglis, 1989; McLachlan and Brown, 2006). However, Maria et al. (2011), Bergamino (2011) and Kostecki (2010) demonstrated that food webs of (ultra)dissipative sandy beaches depend partly on *in situ* benthic primary production, as there is a high retention of autochthonous phytoplankton and microphytobenthos on the hydrodynamically less harsh dissipative beaches. Furthermore, several authors (Darnaude et al., 2004; Leakey et al., 2008; Pasquaud et al., 2008; Vinagre et al., 2008; Bănaru and Harmelin-Vivien, 2009; Schlacher and Connolly, 2009; Kostecki, 2010) showed that marine systems can also be energetically linked to terrestrial systems, especially in the vicinity of river plumes.

The higher primary production of the dissipative beach compared to more reflective beaches, provides a large amount of food available for higher trophic levels and could therefore explain the significantly higher biomass on dissipative systems worldwide (reviewed in Defeo and McLachlan, 2005). Generally, the dissipative beach supports a more complex food web compared to reflective beaches, with more trophic levels and more trophic links, as a response to a combination of environmental (e.g. favourable hydrodynamic regime and benign swashes) and biotic (e.g. high diversity of food sources) features (Bergamino et al., 2011).

Although three more or less distinct food webs have been previously described on sandy beaches including (1) a discrete food web constituted by **interstitial** organisms; (2) a **microbial food web** in the surf zone and (3) a **macroscopic food web** structured by macrofauna, zooplankton, fishes and birds (Heymans and McLachlan, 1996; McLachlan and Brown, 2006; Bergamino et al., 2011), recent studies highlight the connectivity between functional groups in these food webs, suggesting one overall sandy beach food web, characterized by a variety of trophic links (Maria et al., 2012).

Both interstitial bacteria as well as protozoans are consuming dissolved and particulate organic material, while protozoans also prey on bacteria (McLachlan and Brown, 2006). Interstitial meiofauna feeds on a variety of food sources: epistratum feeders, predators and omnivores form a driftline-specific meiobenthic community while deposit-feeding nematodes, living on organic material, are dominant in the mid- and the low-intertidal (Gheskiere et al., 2004). Recently, Maria et al. (2011) showed a preference for *in situ* benthic primary production over pelagic production for all meiofauna organisms, confirming the importance of *in situ* benthic production for dissipative sandy beach food webs. Deposit-feeding oligochaetes can also reach high abundances on sandy beaches due to the substantial amount of organic material present on dissipative beaches. Overall, the interstitial community functions as a huge natural filter, cleansing and purifying the surf waters, mineralizing the organic materials and finally returning the nutrients to the sea (Pearse et al., 1942; McLachlan and Brown, 2006).

Although micro-organisms in the surf-zone can reach high abundances (McLachlan and Brown, 2006), the surf-zone community is not well-studied. However, it has a very important role in the sandy beach food web as it consumes a major part of the primary production in marine ecosystems. This surf-zone community is trophically connected with higher trophic levels as flagellates and micro-zooplankton are consumed by filter-feeders (McLachlan and Brown, 2006).

Terrestrial arthropods living associated with the drift line of sandy beaches, depend on wrack deposits and stranded material as a food source (Backlund, 1945; Ardö, 1957; Tsacas, 1959; Egglishaw, 1960; Remmert, 1964; Caussanel, 1970; Cheng, 1976; Louis, 1977; Bergerard, 1989). This wrack consists mostly of kelp and other brown algae that support detritivores (mainly flies) and their predators (mainly beetles and spiders) and parasites (Bergerard, 1989). Arthropod larvae on the other hand are feeding on the organic matter of the strand line (Ardö, 1957; Tsacas, 1959).

In the intertidal marine environment most macrofaunal species are generalistic feeders (Zacharias and Roff, 2001). Although decapods, bivalves and crustaceans have been identified as consumers, while gastropods and polychaetes are generally considered predators (Bergamino et al., 2011), all these taxa are typically enclosing a variety of feeding types. On (ultra)dissipative beaches, the amphipods *B. pilosa* and *B. sarsi* mainly consume benthic and recently settled pelagic diatoms (Nicolaisen and Kanneworff, 1969; Herman et al., 2000; Maria et al., 2011), while the polychaete *S. squamata* collects a wide range of suspended food (organic matter, planktonic animals, fragments of algae, …) with its sticky palps (Dauer, 1983; Pardo and Amaral, 2004). The predacious isopod *E. pulchra* and predacious polychaetes *E. longa* and *N. cirrosa* prey on a variety of prey species including *B. pilosa*, *B. sarsi* and *S. squamata* (Jones, 1968; Hartmann-Schröder, 1996; Michaelis and Vennemann, 2005). The high species richness and abundances of macrofauna on dissipative beaches provide a quite complete range of nutritional resources (Duffy et al., 2007) and increase the overall system energy acquisition from basal food sources (Bergamino et al., 2011). Moreover, this high biomass of suspension and detritus feeders in (ultra)dissipative beaches plays a key role in recycling nutrients through the excretion of nitrogen and phosphorous in inorganic form, which enhances the availability of nutrients to phytoplankton cells (McLachlan, 1983).

The intertidal meio- and macrobenthos of dissipative sandy beaches is an important food source for birds, large crustaceans and epibenthic fishes (Le Drean-Quenec'h Du et al., 1995; Beyst et al., 1999), being temporarily present at the beach. Although it is generally accepted that intertidal sandy beaches function as nursery areas, essential to marine species and birds, the detailed trophic linkages between predators and prey remain largely unknown (but see Laffaille et al., 1998; Beyst et al., 1999; Lefeuvre et al., 1999; Le Pape et al., 2007; Nicolas et al., 2007) as studies on sandy beach food web interactions are scarce. The few studies examining the diet of marine sandy beach predators including juvenile fish and shrimp, generally use stable isotopes or gut analyses approaches (Beyst et al., 1999; Kostecki, 2010) but these approaches have limitations, especially concerning results up to species level, and do not result into a detailed view on the relations in the food web (Hyslop, 1980; Amara et al., 2001). Both meio- and macrofauna are known to constitute the food supply for young stages of hyper- and epibenthos in nursery grounds (Beyst et al., 1999; Howell et al., 1999; McConnaughey and Smith, 2000; Phelan et al., 2001; Beyst et al., 2002; Le Pape et al., 2007), confirming the connectivity and existence of several links in the sandy beach food web. Indeed, young juvenile epibenthic species such as small shrimp and fish are known to feed on meiofauna at early juvenile stages (Aarnio et al., 1996; Beyst et al., 1999) while switching their diet to macrofauna as they grow (Phelan et al., 2001). Furthermore, since the trophic role of juvenile fish and juvenile crustaceans varies according to their size and life cycle stadium and these predators even consume early stages of each other (Wennhage and Gibson, 1998), the dissipative sandy beach food web can become highly complex.

Besides epi- and hyperbenthos, avifauna is also using the intertidal sandy beach as foraging area. Turnstones feed in the supralittoral zone on strand line material (Smit and Wolff, 1981; Becuwe et al., 2006), while several wading birds forage and feed in the intertidal zone (Engledow et al., 2001; Stuer, 2002; De Groote, 2003; Speybroeck et al., 2005a) and around the strand line (Smit and Wolff, 1981). Especially gulls and wading birds, the latter being mainly Oystercatcher, Dunlin and Sanderling, are known to feed on intertidal macrofauna and shellfish (Engledow et al., 2001; Stuer, 2002; Speybroeck et al., 2005a). Several birds are known to show prey selectivity, with Oystercatchers feeding nearly exclusively on shellfish during winter (Camphuysen et al., 1996; Hulscher, 1996; Zwarts et al., 1996), whereas Dunlin typically feeds on oligochaetes and polychaetes (Kelsey and Hassall, 1989; Mouritsen and Jensen, 1992; Nehls and Tiedemann, 1993). Sanderling feeds in the swash zone and is partly depending on the presence of the polychaete *Scolelepis squamata* as prey, but also on various other prey washed ashore (Smit and Wolff, 1981; Mooij, 1982; Dankers et al., 1983; McLachlan, 1983; Glutz von Blotzheim et al., 1984; De Meulenaer, 2006; Vanermen et al., 2009). Common gull *Larus canus* and Black-headed gull *Larus ridibundus* frequently forage for worms and shrimps in the littoral zone, around the high tide mark and in puddles and pools of stagnant water, whereas other species of gulls (like Great black-backed gull *Larus marinus*) depend much more on infralittoral food (Spanoghe, 1999; Engledow et al., 2001; Stuer, 2002). Finally, gulls also feed on stranded dead animals and on food left behind by man (Engledow et al., 2001; Stuer, 2002).

3. Biotic interactions in the macrobenthos community of intertidal dissipative beaches

As sandy beaches have long been considered physically controlled (Noy-Meir, 1979), the distribution and zonation of infaunal sandy beach organisms have been typically related to morphodynamical factors such as slope, wave energy, tidal range and sediment characteristics (e.g. McLachlan and Jaramillo, 1995; McLachlan, 1996; Defeo and McLachlan, 2005) while biological interactions were considered of minor importance in structuring benthos zonation patterns (McLachlan, 1983; McLachlan et al., 1993; McLachlan, 1996, 2001). This is in contrast to rocky shore ecosystems where biotic interactions were demonstrated to play an additional role besides the dominant structuring influence of the physical environment. For example, Ragnarsson & Raffaelli (1999) and Benedetti-Cecchi (2001) showed that species interactions significantly influenced community structure and species densities in the latter intertidal habitat. Since species interactions often contribute largely to the organization and conservation of rocky shore communities, it is currently stated that biotic interactions are instrumental to both habitat selection and habitat specialization, as well as to niche segregation and niche overlap of organisms on rocky shores (e.g. McPeek, 1996; Iken et al., 2001; Schluter, 2001; Liess and Hillebrand, 2004).

Over the last decade, food web dynamics of the sandy beach ecosystem are more intensively studied (Lastra et al., 2006; Ince et al., 2007; Bergamino et al., 2011) and biotic factors as predation and competition were also indicated to play a role in structuring patterns on dissipative beaches (Dugan et al., 2004; Janssen and Mulder, 2005; McLachlan and Dorvlo, 2005; Janssen et al., 2007), but empirical evidence from this intertidal habitat is still very limited. Birds are known to be opportunistic feeders (McLachlan and Brown, 2006), consuming wrack associated macrofauna (Dugan et al., 2003) and intertidal invertebrates but estimates on the predator impact of the avifauna on intertidal invertebrates are strongly varying from 2 % to even 65 % removal of invertebrate standing stock (Hockey, 1983; McLachlan and Brown, 2006). Several bird species are showing specific preferences, with sanderling *Calidris alba* preferring *S. squamata* (Dankers et al., 1983; De Gee, 1984; Glutz von Blotzheim et al., 1984; De Meulenaer, 2006; Vanermen et al., 2009). Furthermore, some prey species also show anti-predator behaviour like the adjustment of the tidal rhythm of vertical migration in molluscs (Roberts et al., 1989) or the nocturnal emergence of several crustaceans as a result of predator avoidance (McLachlan and Brown, 2006). Despite their ecological importance during the life cycle of many marine organisms (e.g. Gibson, 1973; Beyst et al., 2001), the nursery function of sandy beaches for epibenthic species and especially the coupled predator-prey interactions have not been intensively studied compared to shallow water and estuarine habitats (Amara and Paul, 2003).

Since predation pressure by marine predators is known to decrease towards the upper intertidal (Reise, 1978), this allows the prediction that competitive interactions between benthic species are likely to occur more landwards, but this hypothesis needs to be elaborated as only limited evidence is available and terrestrial predation is hereby not taken into account. Defeo et al. (1997) studied two congeneric sandy beach isopods (*Excirolana*) and indicated that competition might play a role in structuring their field distribution. Furthermore, both Jaramillo et al. (2003) and Lastra et al. (2010) studied upper shore arthropods and showed that the niches of these arthropods showed both space and time partitioning, probably as a result of avoiding negative interspecific interactions. Croker & Hatfield (1980) found direct evidence of competition between two sandy beach amphipods based on lab experiments. Both survival of adults and reproductive output decreased significantly for the first amphipod when the second amphipod was present. However, further and more direct experimental evidence on the presence of competition on sandy beaches is absent and the structuring effect of competition has not yet been demonstrated in the field.

Since general theories on the structuring role of both abiotic and biotic factors are absent for sandy beaches, this PhD study aimed at completing part of the missing knowledge, important to explain the distribution and zonation patterns of sandy beach macrobenthos.

4. Functions and services of dissipative sandy beaches

Coastal zones are densely populated areas and the human population is increasing exponentially, so many of existing and future human pressures on global ecosystems are directed at sandy beaches, which have a variety of important functions and fulfill important services, both ecological as well as socio-economic (Schlacher et al., 2008). In the next paragraphs the most important beach functions and beach services are given, both on a global scale as well as with specific attention for Belgian beaches.

The high productivity in dissipative sandy beach surf zones can support high densities of phytoplankton, micro-organisms, zooplankton and macrofauna. Therefore, the sandy beach serves as an important nursery and foraging area for juvenile fish and higher crustaceans (McLachlan and Brown, 2006). On Belgian beaches, this function is highly important as Beyst et al. (1999; 2002) studied fish and macro-crustaceans on these beaches and found significant densities and a clear trophic link with beach fauna. Beaches are also important nesting, resting and foraging areas for marine turtles, seals and shorebirds (Schlacher et al., 2008). Belgian beaches are especially important for foraging birds (De Meulenaer, 2006; Vanermen et al., 2009). Some dissipative beaches are also populated by huge bivalve populations that support commercial, artisanal or recreational fisheries. Furthermore, shrimps and flatfishes, using sandy beaches as nursery areas, can also be exploited (Defeo, 2003; Defeo et al., 2009).

Beach ecosystems and its porous sand body are important in processing large quantities of organic material and recycling nutrients back to coastal waters. Bioturbation of the sediment by macrofauna enhances microbial processes and stimulates degradation of organic material and pollutants

(Schlacher et al., 2008). Along the Belgian coast these processes were recently studied by Braeckman et al. (2010), who found a significant role of macrofauna in stimulating biogeochemical fluxes.

Sandy beaches play an important role in coastal defence by functioning as a buffer between sea and land (Brampton, 1992; Riddell and Young, 1992). Finally, they also have great socio-economic value as recreational resources and are key components of many tourist destinations (Schlacher et al., 2008).

5. Management and protection of sandy beach ecosystems

Beaches are of social and cultural importance to humans as prime recreational assets: more people interact directly with beaches than with any other type of shoreline worldwide (Schlacher et al., 2008). As sandy beaches have a multitude of ecological but also economic functions, this causes a severe pressure on the ecosystem. To preserve beaches and their important ecosystem functions, management and conservation have become critical and pressing issues (Borja et al., 2008; Schlacher et al., 2008) especially in the light of burgeoning global population growth, demographic shifts towards the coast, and economic prosperity (Brown and McLachlan, 2002; Schlacher et al., 2006; Schlacher et al., 2007). Management of beaches has traditionally focused almost exclusively on maintaining and restoring physical and geomorphological features important for coastal defence and tourism while ecological aspects have been rarely considered (James, 2000; Micallef and Williams, 2002; Schlacher et al., 2008). Although coastal biologists are now recognizing the ecological significance of beaches (Schlacher et al., 2006; Schlacher et al., 2007), this is not always the case within the broader scientific and coastal management community. Consequently, the impacts on ecosystems are rarely included in current impact assessments. Furthermore, as a wide range of stakeholders have active, but not necessarily compatible interests in sandy beach systems, management of sandy coasts is a multi-faceted and complex endeavour that encompasses environmental, economic, social and cultural dimensions as a minimum set (Bird, 1996; Micallef and Williams, 2002; Schlacher et al., 2008). Therefore, sandy beach management will have to operate increasingly within the framework of Integrated Coastal Zone Management (ICZM) to achieve a sustainable outcome (Schlacher et al., 2008). The main objective of the ICZM is to protect and restore marine ecosystems by ensuring that human activities are carried out in a sustainable manner to provide safe, clean, healthy and productive marine waters.

Hereafter, I give an overview of legislation aiming at protecting intertidal areas, I describe beach nourishment as a frequent management approach on sandy beaches and finally I describe the gaps in knowledge that hamper good management decisions for sandy beaches.

5.1 Legislation

Over the last decades, legislation to protect marine environments was developed at different levels. Although a multitude of international and European legislation exists concerning the protection of marine environments, it is not always clear what legislation is applicable for the intertidal environment. Here we try to give an overview of the most important international, European and Belgian legislation concerning the protection of intertidal beaches.

The international Ramsar Convention ('Wetlands of international importance') is an inter-governmental treaty which provides the framework for national action and international cooperation for the conservation and wise use of wetlands and their resources (ICIMOD, 2004).

The European Habitats Directive (1992) on the conservation of natural habitats and of wild fauna and flora aims at establishing a coherent ecological network of special conservation zones. This network, Natura 2000 (including both terrestrial and marine areas), is designed to guarantee the conservation of a minimum level of biodiversity in Europe. The types of habitat that take priority include, amongst others habitat 1110 defined as "sand banks with only a shallow covering of seawater (rarely more than 20 m below MLLWS)" and habitat 1140 defined as "sands and mud of the coasts of the oceans, their connected seas and associated lagoons, not covered by sea water at low tide, devoid of vascular plants, usually coated by blue algae and diatoms". The Habitats Directive recognizes that conserving habitats of great value and the diversity of landscapes makes it possible to conserve marine diversity (European Commission, 1992).

The European Birds Directive states that the Member States need to take protection measures for the sea, coastal and terrestrial areas where birds, described in Annex I (of Directive 79/409/EEC of 2 April 1979) on the conservation of wild birds, are living, so that they can continue to exist and reproduce in these places (European Commission, 2009). The areas, protected under the European Birds Directive are also integrated in the Natura 2000 network.

All international and European legislation needs implementation in the national context. In Belgium, sustainable coastal management is integrated through the Marine Protection Law of January 20th, 1999. However, as the institutions responsible for coastal management in Belgium are highly fragmented and jurisdiction is often shared between Flemish Government and State (Cliquet, 2001; De Ruyck et al., 2001), the implementation of European and international policy is delayed.

Concerning management of beaches, the progress is even less compared with the subtidal environment. As beaches and dikes do not fall under the Federal but under the Flemish Authority, the legislation for spatial planning on land is applicable on beaches and dikes. Furthermore, local authorities have a lot of power concerning coastal development and have tolerated and approved a lot of constructions in the past. Nevertheless, 16 % of the Belgian intertidal zone falls under the protection of habitat 1140 areas within the Natura 2000 framework (European Habitats & Birds Directive). In addition, there are two protected intertidal beach areas, the “Baai van Heist” in Knokke-Heist and “the Ijzermonding reserve” in Lombardsijde.

Besides these aspects concerning the protection of beach areas, a Coastal Safety Plan was also created by the Flemish authorities after consultation and deliberation with local authorities. Maritieme Dienstverlening & Kust (MDK) is the competent (Flemish) authority in Belgium for coastal safety and this safety has priority over possible other conflicting functions along the coast. In this Coastal Safety plan, an overview of all coastal areas threatened by storms and sea level rise are listed and measures are proposed for enhancing the safety in these areas. Among these management measures, beach nourishment is mostly applied for enhancing coastal safety along the Belgian coast.

5.2 Beach nourishment

Since the construction of hard structures as seawalls and groins has been proven to be inefficient against structural erosion (Pilkey and Dixon, 1998) and even detrimental for the sandy beach ecosystem (Greene, 2002), the generally considered less harmful beach nourishment is gaining popularity as a measure in coastal defence. Beach nourishment has become a general strategy to protect beaches and lower lying lands against erosion and sea level rise, since it has a number of advantages over hard coastal defence. Some of these advantages associated with beach nourishment include a wider recreational beach, protection to shoreline structures, possible beneficial use for dredged material from nearby sources and the ability to switch to other beach management methods in the future (as long as increased coastal development does not preclude this) (Board, 1995). Beach nourishment can also protect threatened or endangered plants in the dune area and restore habitat for sea turtles, shore birds and other transient or permanent beach organisms (LeBuff and Haverfield, 1990; Melvin et al., 1991; Spadoni, 1991). Unfortunately, there are still many uncertainties concerning effects on the marine and beach environment as monitoring studies are often characterized by a lack of replication and the absence of peer review (Greene, 2002).

Speybroeck et al. (2006a) described the impact of beach nourishment as a coastal defence strategy.

During the construction phase of the nourishment, the sandy beach flora and fauna is directly disturbed, while the long-term damage to the ecosystem is depending on the exact nourishment strategy and techniques and the resilience of the ecosystem. The sandy beach ecosystem is closely related to the sediment (McLachlan and Brown, 2006), so the quantity and quality of the nourished sediment is one of the key factors in determining nourishment impact on the sandy beach ecosystem. The effects will be minimal when morphodynamic features of the nourished beach resemble the initial conditions, but since reliable and peer-reviewed information on the recovery of beach ecosystems after nourishment is lacking, it is difficult to predict if and at what timescale the ecological balance of the system will be restored (Speybroeck et al., 2006a). Some studies mention a recovery period for the benthic life of three to five years (Gmelig Meyling and De Bruyne, 1994; Slim and Löffler, 2007) but the impact of beach nourishment on higher trophic levels such as fish is still poorly understood and cumulative effects of repeated beach nourishments are inadequately addressed (Greene, 2002).

5.3 Knowledge gaps hampering sound beach management

Studies on sandy beaches are poorly represented in scientific literature (Dugan et al., 2010). Hence, more beach research is essential in filling the critical gaps in basic ecological information required for beach management and conservation. Although patterns on sandy beaches are well-studied (e.g. Degraer et al., 2003; McLachlan and Dorvlo, 2005; Rodil et al., 2006), the functional beach ecosystem is largely unknown (Schlacher et al., 2008). Food web dynamics, species interactions and energetic linkages on sandy beaches are barely studied and ecosystem-wide processes as nutrient cycling, cross-system nutrient fluxes, productivity and connectivity among metapopulations on different sandy beaches are undescribed (McLachlan and Brown, 2006; Schlacher et al., 2008). However, knowledge on these processes is of crucial importance to achieve an ecosystem-based management approach (EBM) (Sainsbury and Sumaila, 2003; Pikitch et al., 2004; Jennings, 2006; Dahl et al., 2009). An ecosystem-based management approach is defined as an approach where ecological, economic and social goals and objectives are balanced towards a sustainable development (Dahl et al., 2009). Since beaches interact closely with coastal dunes both physically and biologically, sandy coasts, including surf zones, beaches and dunes, must be managed as functional units (Schlacher et al., 2008). However, as mostly only short-term projects are funded, studying the complete sandy beach ecosystem in all its aspects is difficult (Elliott et al., 1999).

While ecological knowledge on several separate sandy beach ecosystem components is present, a good translation of this scientific information into environmental management strategies is a delicate exercise (Elliott et al., 1999). Spatial information on ecological values of beaches, available in user-friendly formats, can therefore be essential in integrating ecological knowledge in management decisions (Derous et al., 2007; Schlacher et al., 2008; Laporta, 2012). Furthermore, an integrated framework, encompassing both the economic and ecological values of the sandy beach, expressed at the same scale, is ideal. Unfortunately, environmental benefits are difficult or even impossible to quantify in economic terms (Elliott et al., 1999), making an integrated sandy beach management a complex task.

Models, predicting the evolution and ecological responses of ecosystems following changing environmental conditions or human interventions, are of high importance for good management decisions, since different strategies can be tested and compared (Schlacher et al., 2008). Although global climate change models, predicting environmental changes of coastal zones as a result of climate change have been developed over the last decades, more detailed models predicting local and small-scale responses of sandy beaches, following altered environmental conditions or changes due to management decisions, are far less available (Borja, 2006; Borja et al., 2008).

Finally, beach management lacks ecological dimensions. Communication between scientists, managers and the general public therefore should be crucial to achieve sustainable conservation outcomes for beaches and coastal zones (Schlacher et al., 2008).

In this PhD study, these knowledge gaps concerning the sandy beach ecosystem are tackled. The next paragraph describes the specific aims of this thesis.

6. Aims of the PhD thesis

The overall aim of this PhD thesis is twofold: (1) to complement the knowledge on sandy beach ecosystem functioning with emphasis on the biotic interactions between sandy beach species and (2) to use this knowledge in order to provide practical tools for managing these beach ecosystems in a sustainable way.

- **Examining the structuring role of biotic interactions on dissipative sandy beaches**

The structuring role of biotic interactions needs profound examination to give a better quantification of the processes which are at the basis of the structural biological characteristics of the sandy beach. On intertidal rocky shores, biotic interactions such as competition and predation were shown to be responsible for processes and patterns of niche differentiation, niche specialisation, habitat selection and ecological adaptation (Rosenzweig, 1987; Menge, 1995; McPeek, 1996; Bertness and Leonard, 1997). However, on sandy beaches the role of these ecological processes has not been examined or related to observed patterns. We hypothesized that biotic interactions such as competition or predation will not have a structuring effect on dissipative sandy beaches and tested this hypothesis by means of mesocosm experiments. In chapter 7, the findings of the experiments were discussed more profoundly in the context of ecological and evolutionary theories and hypotheses were given concerning the historical and current processes responsible for observed distribution patterns on sandy beaches.

- **Contributing to sandy beach food web dynamics**

Sandy beach food web dynamics were investigated by mesocosm experiments determining predator-prey relationships in and between macrofauna and epifauna communities. So far, isotopic studies on the sandy beach food web do not provide a complete and profound description of the trophic relationships nor determine accurate trophic levels for the species in the food web (Hesslein et al., 1993; MacAvoy et al., 2001; Guelinckx et al., 2008).

- **Ecologically adjusting beach nourishment**

Beach nourishment has become a generally applicable coastal defence method on Belgian sandy beaches, so information on optimizing technical aspects of these nourishments is essential. Benthic populations are highly impacted so experimental information and model predictions on their responses to varying environmental conditions and different beach nourishment aspects can help in ecologically adjusting these projects. Furthermore, model predictions are valuable tools for stakeholders as they represent the consequences of different management decisions in an illustrative way.

- **Formulating management guidelines**

Since European legislation needs to be implemented for Belgian coastal zones and sandy beaches, management decisions have to be taken in spatial planning and demand good baseline information. Therefore, policy guidelines were formulated to simplify the multi-faceted management decision process.

7. Outline of the PhD thesis

Apart from the general introduction and discussion, this thesis is a compilation of research articles (published or submitted). For that reason, the outline and output of the chapters resembles almost exactly the published or submitted papers. Each chapter is therefore intended to be an autonomous part, which can be read separately from the other chapters. Inevitably, there is some overlap between the introduction and discussion sections of the different chapters. Cited literature is compiled in a single list at the end of the thesis. Chapter 6 has shared first authorship with Drs. Sarah Vanden Eede; all other chapters have the candidate as first author.

Chapter 1 (general introduction) describes the sandy beach ecosystem. Both the physical, biological and functional characteristics of the sandy beach are considered, with a special emphasis on the features of dissipative sandy beaches. Furthermore, the current knowledge on the dissipative sandy beach food web and on species interactions of dissipative sandy beaches is reviewed. In addition, management and protection of beaches was discussed. To get a first indication on the presence and importance of biotic interactions on sandy beaches, **Chapter 2: "The structuring role of abiotic factors and species densities in distribution patterns of macrobenthos along European Atlantic sandy beaches."** discusses a modelling study of macrobenthos on West European sandy beaches. The aim of the modelling study was to detect macrobenthos patterns that were likely to be structured via biotic interactions. Based on the obtained hypotheses on the structuring role of biotic interactions, experiments were developed and tested in the following two chapters.

Chapter 3: "**Encounter competition partly explains the segregation of the sandy beach amphipods *Bathyporeia pilosa* and *Bathyporeia sarsi.* A mesocosm experiment"** describes a competition experiment between two morphologically similar amphipods, living segregated on intertidal dissipative sandy beaches. Both intra- and interspecific competition were experimentally tested in a mesocosm experiment.

The structuring role of predation on sandy beaches was described in **chapter 4**: "**Role of predation on sandy beaches: predation pressure and prey selectivity estimated by mesocosm experiments."** Prey selectivity, prey consumption and predation pressure of the two most abundant epibenthos species, present on the beach at high tide, were examined through lab experiments.

The second part of this PhD study is more management-oriented and aims at providing guidelines for ecologically sound beach management. As beach nourishment is one of the most important threats that alters the environment for all sandy beach organisms, but especially impacts the benthic species, the sediment preferences of Belgian sandy beach macrofauna were examined both in single-species and combined-species conditions in **chapter 5**, titled "**Macrofaunal sediment selectivity**

considerations for beach nourishment programmes". This information can help in adjusting the technical beach nourishment aspects to minimize ecological impact. The study additionally examined whether biotic interactions influenced sediment preferences of macrofauna. Although being an indirect approach, it can give valuable information on the presence and role of biotic interactions on sandy beaches.

Since beach nourishments have become generally applicable on Belgian beaches, and an ecosystem based management is indispensable, information on the response of the complete sandy beach ecosystem to the altered physical environment is needed. Therefore a model was developed in **chapter 6: "Assessing the impact of beach nourishment on the intertidal food web through the development of a mechanistic-envelope model"**, predicting responses of all ecosystem components after nourishment using both the available knowledge and knowledge obtained in this PhD study. As different scenarios can be tested in this model, optimizing various technical aspects of beach nourishment will be one of the main advantages of the model.

In the last chapter, **chapter 7** (General discussion), biotic interactions on sandy beaches are discussed in a broader context. Hypotheses on how current patterns of habitat segregation and –specialisation have been established, are proposed. Finally, a translation of obtained knowledge towards beach nourishment recommendations and policy guidelines for an ecosystem based, integrated sandy beach management is given.

1

Chapter 2: The structuring role of abiotic factors and species densities in distribution patterns of macrobenthos along European Atlantic sandy beaches

Joke Van Tomme, Steven Degraer, Wouter Willems, Jean-Claude Dauvin, Lionel Denis, Rosario de la Huz, Gerard Janssen, Iris Menn, Ivan Rodil and Magda Vincx. The structuring role of abiotic factors and biotic interactions in distribution patterns of macrobenthos along European Atlantic sandy beaches.

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Abstract

In this study, the relative importance of abiotic factors and species densities (as a proxy for possible biotic interactions) in influencing the distribution patterns of seven common macrobenthic species of 45 beaches in Western Europe was investigated. Following species were taken into account: *Bathyporeia pilosa, B. sarsi, Scolelepis squamata, Eurydice pulchra, E. affinis, Nephtys cirrosa* and *Eteone longa.* Based on regression models (GLMs), including bot abiotic factors and species densities, the distribution of these dominant species was analysed. The most appropriate models were selected using the AIC (Akaike's Information Criterium) method and the contributions of the abiotic variables and species densities were determined. Mean grain size of the sediment and emersion time, two abiotic variables generally considered as important structuring factors on sandy beaches, only partially explained the variability in species distribution. In the majority of the models created, species densities also had a significant contribution in explaining species distributions. Both predator-prey and competitive correlations were found, especially for some specific species associations. Although abiotic factors have the most important structuring role on sandy beaches, biotic factors could thus also have a significant contribution in explaining species distribution patterns although experimental work will be indispensable to confirm the causal role of biotic factors in this context.

Key words: beach, benthos, biotic interactions, distribution, modelling.

1. Introduction

In intertidal ecosystems, the role of abiotic factors and biotic interactions is well-studied in macrofaunal communities on rocky shores (Paine, 1966; Dayton, 1971; Paine, 1974; Connell, 1975; Menge and Sutherland, 1987; Bertness and Callaway, 1994). These studies suggest that both the influence of the physical environment and biotic interactions can play an important role in explaining the structure of these communities (Menge and Olson, 1990). Biotic interactions are also considered as an important factor for the community structure of macrobenthos on intertidal mudflats (Le Pape et al., 2003). However, species interactions and their influence on the structure of macrofaunal biological communities have not yet been thoroughly studied on sandy beaches, since it is stated that the intertidal community structure on these beaches is mainly physically controlled (McLachlan and Jaramillo, 1995; Degraer et al., 2003; Veloso et al., 2003; Fernandes and Soares-Gomes, 2006). In this respect, following autecological hypothesis assumed that macrofaunal communities in physically controlled, variable and stressful environments are structured by the response of the individual species to the physical environment (Noy-Meir, 1979). Physical processes such as the movement of waves and tides, the swash climate and the retention and circulation of interstitial water are considered to be the most dominant abiotic factors structuring the macrofaunal communities on sandy beaches (Salvat, 1964, 1967; McArdle and McLachlan, 1991, 1992).

Despite the importance of physical processes, more recent studies emphasize the potential role of biotic interactions as structuring factors in intertidal distribution and zonation of macrobenthos (Dugan et al., 2004; Defeo and McLachlan, 2005; McLachlan and Dorvlo, 2005). On a wide scale (between morphodynamic beach types) physical factors are considered to be dominant, while on a smaller scale (within one beach type) and especially on dissipative beaches, biotic interactions are suggested to play a role (Defeo and McLachlan, 2005; Janssen and Mulder, 2005; McLachlan and Dorvlo, 2005; Janssen et al., 2007). However, experimental data supporting this hypothesis are very limited and sometimes contradictory (Croker and Hatfield, 1980; Defeo and de Alava, 1995; Defeo et al., 1997; Speybroeck, 2007).

West European sandy beaches can generally be divided in dissipative beaches in the north and reflective beaches in the south (McLachlan et al., 1981; McLachlan and Dorvlo, 2005). Along the northern European Atlantic coastline, the macrotidal and mesotidal beaches (e.g. in Belgium, The Netherlands and Germany) are generally described as dissipative to ultra-dissipative (Menn, 2002; Degraer et al., 2003; Janssen and Mulder, 2005). These dissipative to ultra-dissipative beaches with a broad surf zone generally have a higher macrobenthos density and diversity than the reflective beaches (Defeo and McLachlan, 2005). Along these macrotidal sandy beaches, the polychaete *S.*

squamata, two amphipods *B. sarsi*, *B. pilosa* and the isopod *E. pulchra* (figure 1) are the dominant species (Menn, 2002; Degraer et al., 2003; Janssen and Mulder, 2005). Along the more southern French and Spanish Atlantic coastline, the beaches are reflective to intermediate (Rodil and Lastra, 2004; Lastra et al., 2006) and do not have the same distinct intertidal zonation pattern as the dissipative ones. On these reflective beaches, species such as *B. pelagica* but also *S. squamata* and *Eurydice* spp. (Dauvin, unpublished data; Rodil et al., 2006) are more common. In figure 1, the zonation pattern of the common macrobenthic species is given, based on information described in Dauvin, unpublished data; Degraer, 2003; Janssen and Mulder, 2005; Lastra et al., 2006; Menn, 2002 & Rodil and Lastra, 2004.

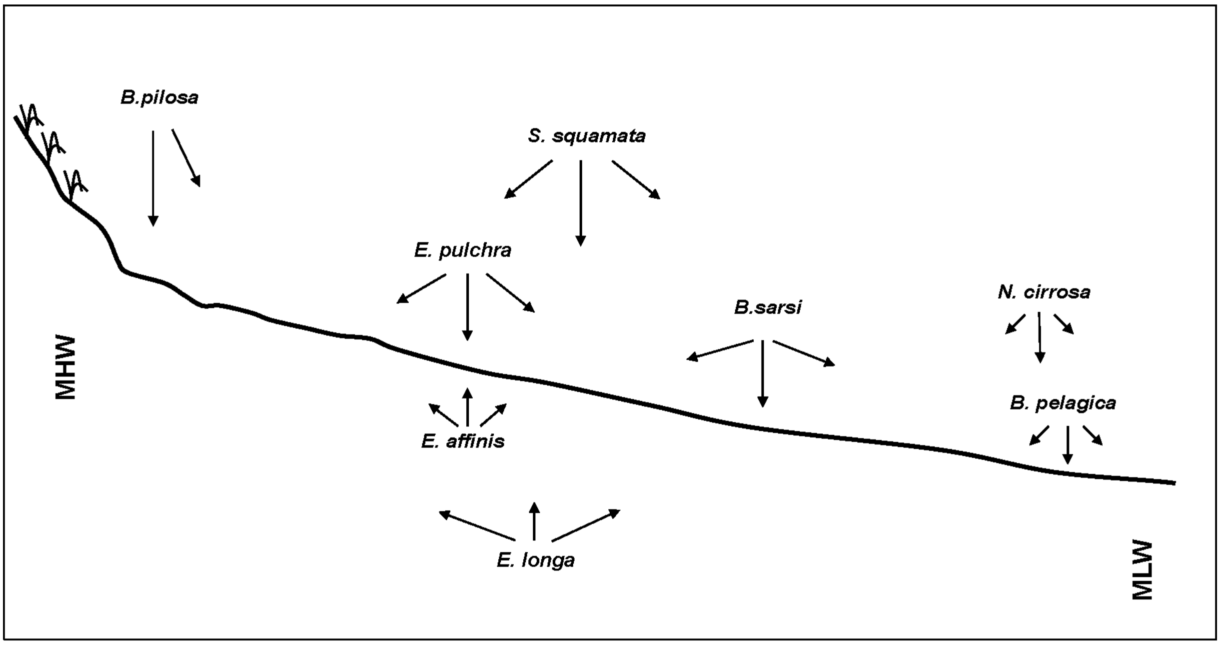

Figure 1: schematic presentation of the general zonation pattern of the most important macrobenthic species on sandy beaches along the Atlantic European coastline. MHW: Mean High Water level, MLW: Mean Low Water level (Adapted from: Dauvin, unpublished data; Degraer, 2003; Janssen and Mulder, 2005; Lastra et al., 2006; Menn, 2002 & Rodil and Lastra, 2004).

As biotic interactions are known to have a structuring role on intertidal rocky shores (Menge, 2000), but are only barely studied on sandy beaches, the main objective of this research was to examine whether biotic variables alongside abiotic variables had a structuring role in clarifying the distribution patterns of sandy beach macrobenthos. As no data on biotic interactions are however currently available, species densities were used as a proxy for biotic interactions. Although this approach would not expose causal relations between species, correlations between the distribution of the considered species and other species' densities can give a first idea on the potential presence of biotic interactions. In subsequent steps, the correlations found by this approach have to be verified by experimental work.

The relative contribution of abiotic variables and species densities will be determined by performing a modelling study, using regression analysis. The null hypothesis stated that the species densities, used as a proxy for biotic interactions, did not exert a significant role in explaining distribution patterns of macrobenthos on the sandy beaches of the European Atlantic coastline.

2. Material and methods

2.1 Data collection

For the objectives of this study, the raw intertidal macrobenthos data (species distribution and species densities (per square meter)) from published and unpublished studies on 45 West European macrotidal and mesotidal sandy beaches were re-analysed (table 1). Since the analysis was performed on data gathered in separate case studies, we organized the data in a country-based approach.

The amount of detail in the data regarding the abiotic variables was very different per country and per sample location; therefore (only) two abiotic variables which were commonly measured for all data points could be considered in our modelling approach: height on the beach and sediment characteristics. These abiotic variables are thought to be very important in order to explain distribution of sandy beach species (McLachlan and Jaramillo, 1995; Veloso et al., 2003).

Table 1: origin of the macrobenthos data. Limited sampling was defined as transect sampling where only a limited number of samples was taken along a transect (typically on three beach heights).

country	number of beaches	date of sampling	method
Belgium	9	1997	transect sampling (Degraer et al., 2003)
The Netherlands	8	2002	transect sampling (Janssen and Mulder, 2005)
Germany	2	1999	limited sampling (Menn, 2002)
France	2	2006	limited sampling (Dauvin, unpublished data)
Spain	24	1999-2000	transect sampling (Rodil and Lastra, 2004; Lastra et al., 2006)

2.2 General strategy

The sampling strategy was not completely standardized between countries, therefore analysing the data with standard methods like multivariate analyses would misrepresent reality. Indeed, taxonomical identification was not completely comparable between the different countries considered. Furthermore, the sandy beaches in Belgium, The Netherlands and Spain were sampled from high to low intertidal level (transect sampling), while the sampling occurred only on specific beach heights in Germany and France (table 1). Therefore, it was decided to focus on individual species present on all sampled beaches, and apply a modelling approach that described the distribution of these dominant species, taking into account the specific beach height sampled (cf. further in section 2.2.2).

To test the null hypothesis, the following procedure was used in which two sub null hypotheses were formulated (as explained in Araujo and Luoto, 2007): (1) The model selection procedure did not select species densities as significant variables into the model. (2) There would be no difference in model performance between the models only including abiotic variables and the models including both abiotic variables and species densities.

To test these hypotheses and thus to examine the role of abiotic variables and species densities in explaining the distribution of the dominant macrobenthic species along Atlantic European sandy beaches, the following strategy, consisting of 4 subsequent steps, was set up:

(1) species selection
(2) abiotic variable selection
(3) creating regression models with abiotic variables and species densities
(4) calculation and comparison of model performances

2.2.1 Species selection and species densities as explanatory variables

In this study, seven dominant macrobenthos species were selected based on their prominent abundance on West European sandy beaches. These selected species were the amphipods *B. pilosa* and *B. sarsi*, the isopods *E. pulchra* and *E. affinis* and the polychaetes *S. squamata*, *N. cirrosa* and *Eteone longa* (Menn, 2002; Degraer et al., 2003; Janssen and Mulder, 2005; Rodil et al., 2006). Data from *B. pelagica* (figure 1) were too scarce to be included in the analyses. As the macrobenthos community on sandy beaches is very species-poor, these seven dominant species are representing the great majority of the community. For each of these seven species, regression models were developed, in which the other six species' densities were added as possible explanatory variables.

2.2.2 Abiotic variable selection

The most important abiotic variables, globally determining biodiversity and biomass on sandy beaches, are sediment characteristics, swash climate and tidal regime (Veloso et al., 2003; McLachlan and Dorvlo, 2005). Therefore, two abiotic variables were added in the regression models: mean grain size (MEAN) of the sediment and emersion time (ET). The first variable (MEAN) was considered as a proxy for the physical conditions on the beach (Veloso et al., 2003; McLachlan and Dorvlo, 2005) and the latter variable (ET) was assumed to reflect the occurrence of the species along the intertidal transect (cf. zonation pattern). Emersion time (ET) was calculated based on the beach height of the sample and the tidal graph for that location (Colijn and Dijkema, 1981). Reliable and especially complete data on other variables like beach slope, the retention and circulation of interstitial water and organic matter or productivity were not available so unfortunately, these factors could not be included in the models.

2.2.3 Regression models

Generalized linear models (GLMs) were used to examine the relation between the distribution patterns of each of the seven dominant macrobenthos species (functioning as response variables) and the selected abiotic variables and remaining six other species densities (as explanatory variables). Graphical correlation analysis was conducted to identify important relations between the variables added in the model. To include both linear and eventual non-linear relationships, both the regular (ET and MEAN) as well as the quadratic terms (ET^2 and $MEAN^2$) of the two abiotic variables were considered. By adding the density of the six remaining dominant macrobenthos species as biotic variables in the regression model, the potential effect of biotic interactions was included (Guisan and Zimmermann, 2000).

As a first examination of the distribution data of the seven selected macrobenthos species showed a substantial amount of zero values, both a binomial sub-model (1 and 3) for the presence-absence of every species and a Poisson distributed sub-model (2 and 4) for the positive density values of every species – expressed as $ind.m^{-2}$ – were created as described by Le Pape et al. (2005).

Due to the differences in sampling strategy for the different case studies, which were comparable only at a country level, country specific models (CS) (1 and 2) were created for every selected species. But because of the advantage of a model based on a broader range of data (including all the data of the 45 beaches), global models (G) (3 and 4) were created for the selected species as well. However, since not all seven selected species were present in all countries, one global model including all potentially-interacting species as biotic variables could not be created. An alternative approach could be to use functional groups of species, but by doing so, a lot of detailed information is lost since sandy beaches are relatively species-poor and the information of the seven species would be reduced to only two functional groups (Van Hoey et al., 2004). Therefore, six global models were created for each selected response species, every time with a single other species as interacting species (3a to 3f and 4a to 4f). Since in these global models only one interacting species was added each time, it was possible to additionally calculate the contribution of the "interaction terms" between biotic and abiotic variables (3a to 3f and 4a to 4f). These "interaction terms" have too often been omitted from regression models (Austin, 2002), although frequently improving the fit when included (Guisan et al., 1999; Thuiller et al., 2003). A practical reason for this frequent omission is that they greatly increase the number of parameters in the model, because each interaction term requires its own parameter. That's also the reason for the omission of the interaction terms in the country specific models in this study (where four abiotic and six biotic variables would lead to an excess of interaction terms).

Country specific model:

Binomial sub -model

Response $species_{0/1}$ *= ET + MEAN +* ET^2 *+* $MEAN^2$ *+ presence/absence interacting species1 + presence/absence interacting species2+ …+ presence/absence interacting species 6.* (1)

Poisson sub-model

Response $species_{+}$ *= ET + MEAN +* ET^2 *+* $MEAN^2$ *+ density interacting species1 + density interacting species2+ …+ density interacting species 6.* (2)

Global model:

Binomial sub-models

Response $species_{0/1}$ *= ET + MEAN +* ET^2 *+* $MEAN^2$ *+ presence/absence interacting species1 + interaction term (ET- presence/absence interacting species1) + interaction term (MEAN - presence/absence interacting species1) + interaction term (*ET^2*- presence/absence interacting species1) + interaction term (*$MEAN^2$ *- presence/absence interacting species1) .* (3a)

…

Response $species_{0/1}$ *= ET + MEAN +* ET^2 *+* $MEAN^2$ *+ presence/absence interacting species6 + interaction term (ET- presence/absence interacting species6) + interaction term (MEAN - presence/absence interacting species6) + interaction term (*ET^2*- presence/absence interacting species6) + interaction term (*$MEAN^2$ *- presence/absence interacting species6) .* (3f)

Poisson sub-models

Response species$_+$ *= ET + MEAN +* ET^2 *+* $MEAN^2$ *+ density interacting species1+ interaction term (ET-density interacting species1) + interaction term (MEAN-density interacting species1) + interaction term (*ET^2*-density interacting species1) + interaction term (*$MEAN^2$ *-density interacting species1).*

(4a)

•••

Response species$_+$ *= ET + MEAN +* ET^2 *+* $MEAN^2$ *+ density interacting species6+ interaction term (ET-density interacting species6) + interaction term (MEAN-density interacting species6) + interaction term (*ET^2*-density interacting species6) + interaction term (*$MEAN^2$ *-density interacting species6).*

(4f)

All statistical analyses were performed by using the statistical package R (version 2.8.1, R Foundation for Statistical Computing). If the residual variability in the created models exceeded the degrees of freedom, the data were “overdispersed”, and one of the assumptions of GLMs was violated. In that case, a compensation method was included in the models. For the binomial sub-model, the approach of Williams (1982) was applied while for the Poisson sub-model, the method of Breslow (1984) was used.

The most appropriate models with significant abiotic variables and species densities were selected based on AIC (Akaike’s Information Criterion; (Akaike, 1974)) since this is a well-known approach, widely used in modelling studies (e.g. Heikkinen et al., 2007; Godbold et al., 2009).

2.2.4 Model performance

The approach reported by Weisberg (2005) and Guisan & Zimmerman (2000) was applied to assign the relative importance of abiotic factors and species densities. The adjusted D^2 value was used as a measure of model performance to compare models that include different combinations of variables and interaction terms. The adjusted D^2 is a measure - equivalent to the adjusted R^2 in LS models (Guisan and Zimmermann, 2000) - that resembles the fit of the model and increases with an increasing number of observations (n) or a decreasing number of parameters (p) in the model (Guisan and Zimmermann, 2000). Weak and possibly erroneous conclusions are frequently caused by statistically significant models only explaining a low proportion of the variability (Mac Nally, 2002; Guisan and Thuiller, 2005). Therefore, abiotic models, explaining less than 20 % of the variability, were considered unreliable in this study, since these models had a severe risk that including species densities as predictor variables alongside the abiotic variables might not truly reflect a biotic interaction but rather the absence of important environmental predictors in the model (Guisan and

Thuiller, 2005). The contributions of the abiotic variables, the species densities and the interactions between these two in explaining the variability in species distribution were calculated by partitioning the total explained variability in these three components (Legendre and Legendre, 1998).

2.3 Missing models

In several cases (especially for the binomial sub-models), it was impossible to create a regression model. The reason for this was twofold: either the AIC method could not develop a model based on the given data, or the model could not be created after compensation for overdispersion. As the latter is an important assumption for the validity of the model and therefore could not be left aside, no conclusions were drawn from these cases. All created models can be found in the tables in appendix A (tables A.1-A.4), while an overview of the missing models was given in tables 2 & 3. Averagely, one third of the models could not be created.

Table 2: country specific missing models. response species no regression model could be created for.

	Poisson sub-model	**Binomial sub-model**
Belgium		*Scolelepis squamata*
France	*Bathyporeia sarsi*	
		Eurydice pulchra
Germany		*Bathyporeia* spp
		Scolelepis squamata
		Eteone longa
	Eurydice pulchra	*Eurydice pulchra*
The Netherlands		*Bathyporeia pilosa*
	Bathyporeia sarsi	*Bathyporeia sarsi*
	Nephtys cirrosa	
		Scolelepis squamata
Spain	*Eteone longa*	

Table 3: global missing models. combinations of species (first: response species, second: potentially-interacting species) no regression model could be created for.

Poisson sub-model	**Binomial sub-model**
Scolelepis squamata - *Nephtys cirrosa*	*Bathyporeia sarsi* - *Bathyporeia pilosa*
Scolelepis squamata - *Eteone longa*	*Bathyporeia sarsi* - *Nephtys cirrosa*
Scolelepis squamata - *Eurydice affinis*	*Bathyporeia sarsi* - *Eurydice affinis*
Scolelepis squamata - *Eurydice pulchra*	*Bathyporeia sarsi* - *Eurydice pulchra*
	Bathyporeia pilosa - *Nephtys cirrosa*
	Bathyporeia pilosa - *Eurydice affinis*
	Bathyporeia sp - *Eurydice affinis*
	Bathyporeia sp - *Nephtys cirrosa*
	Scolelepis squamata - *Eurydice pulchra*

	Scolelepis squamata - Eteone longa
	Scolelepis squamata - Nephtys cirrosa
	Scolelepis squamata - Eurydice affinis
	Nephtys cirrosa - Bathyporeia pilosa
	Nephtys cirrosa - Bathyporeia sarsi
	Nephtys cirrosa - Scolelepis squamata
	Eurydice pulchra - Bathyporeia sarsi
	Eurydice pulchra - Bathyporeia pilosa
	Eurydice affinis - Scolelepis squamata
	Eurydice affinis - Bathyporeia sarsi
	Eurydice affinis - Bathyporeia pilosa
	Eurydice affinis - Bathyporeia sp
	Eteone longa - Bathyporeia pilosa
	Eteone longa - Bathyporeia sarsi

3. Results

The used predictor variables were not highly correlated (graphically examined for all data), so multicollinearity, a regular source of model unreliability, could be excluded (Guisan and Thuiller, 2005).

3.1 Important abiotic variables

Both abiotic variables ET and MEAN (either the single or the quadratic expression) were included in the majority of the CS and global models for every species (tables A.1, A.2, A.3 & A.4). Although the influence of the abiotic variables on the abundance (Poisson sub-model) of the species was not significant each time, the influence of the abiotic variables on the presence or absence of these species (binomial sub-model) was significant in the majority of those cases or vice versa. Thus, the Poisson sub-model and the binomial sub-model complemented each other: the abiotic variables gave a contribution in explaining either the presence or the density distribution of the response species. The greater part of the models only containing abiotic variables explained > 20 % of the variability in species abundance (in detail: 62.5 % of the CS models and 75 % of the global models). However, less than a quarter of these models explained more than 50% (in detail: 16.6 % of the CS models and 22.7% of the global models), indicating that other variables were important in determining species distributions.

3.2 Important biotic variables

In 75% of the CS models created, the density of other species was found to contribute significantly to the model (tables A.1 & A.2). In nearly all of these models, the model performance was higher compared to the models only containing abiotic variables.

In 33.3 % of the global models created, a significant species density factor was found. Similar to the CS models, the model performance generally increased when species densities were admitted to these models. Both the species densities and the interaction between abiotic factors and species densities had a contribution to the model performance (tables A.3 & A.4).

Specific species correlations could also be derived from the obtained country specific and global models including significant species densities as biotic factors. In the French model, *B. sarsi* was showing a significant negative relation with *B. pilosa* (tables A.1 and A.2). A significant amount of the distribution (17 % of the variance) of *B. pilosa* could be explained by *B. sarsi* density and the interaction between abiotic variables and *B. sarsi* density in the global model (figure 2 & tables A.3 and A.4).

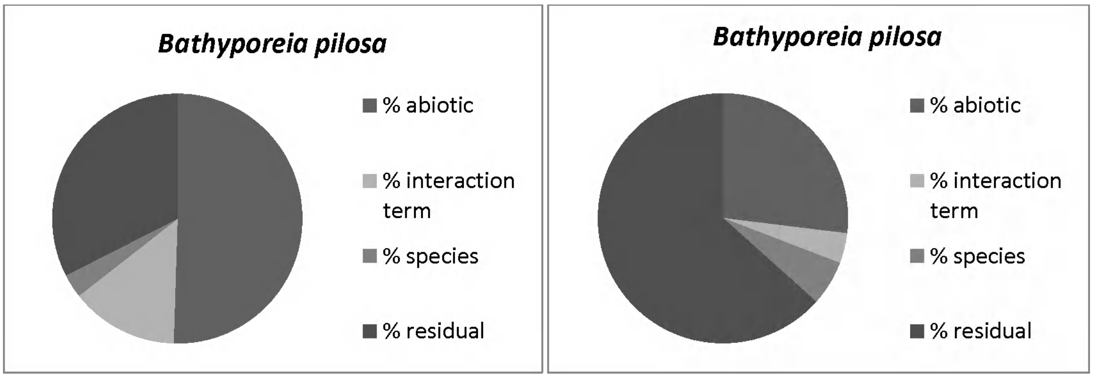

Figure 2: variability in the global *Bathyporeia pilosa (-B. sarsi)*-distribution explained by the Poisson (left) and binomial (right) sub-model. % abiotic: percentage of the variability explained by the abiotic variables. % species: percentage of the variability explained by the interacting species. % interaction terms: percentage of the variability explained by the interaction terms between species and abiotic variables. % residual: percentage of the variability that could not be explained by the regression model.

In addition to these results, a significant mutual interaction was observed as the global Poisson sub-model showed that the distribution of *B. sarsi* was negatively correlated with the density of *B. pilosa*. However, the increase in model performance was rather low and completely attributed to the interaction between abiotic variables and the *B. pilosa* density (table A.3). *Eteone longa* acted as a significant density factor in both the *B. pilosa* and *B. sarsi* models, increasing the model performances of both models. The same pattern was found for *E. pulchra* density, increasing the model performances of the *B. pilosa* and *B. sarsi* models, in the latter even with 15 %, one third of the total variability explained by the model (table A.3 & A.4).

3.3 Relative importance of abiotic variables versus species densities

The inclusion of significant species densities in the models increased the predictive power but this increase was very species-specific and generally ranged from 0 up to a maximum of 24% (= 48% of the total variability explained by the model) of additional predictive power (e.g. *Nephtys cirrosa)* (figure 3 and tables A.1- A.4). It should however be noticed that the total variability explained by models including both abiotic factors and species densities, never exceeded 70 % (tables A.1- A.4).

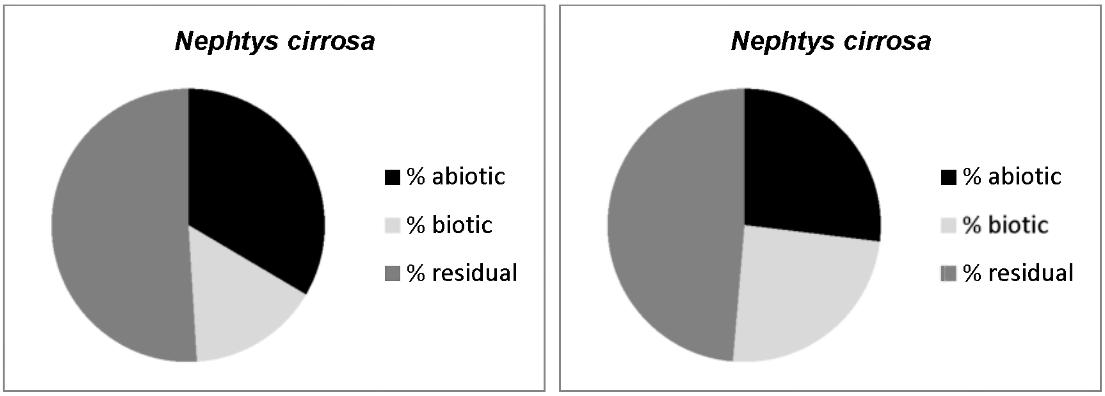

Figure 3: variability in the Belgian *N. cirrosa*-distribution explained by the Poisson (left) and binomial (right) sub-model. % abiotic: percentage of the variability explained by the abiotic variables. % biotic: percentage of the variability explained by the biotic variables (= species densities). % residual: percentage of the variability that could not be explained by the regression model.

4. Discussion

The role of abiotic variables and species densities in clarifying the distribution patterns of sandy beach macrobenthos was examined by the creation of regression models, describing the distribution of seven dominant species. The value of analyzing such ecological questions by modelling techniques has been underlined by Schoeman & Richardson (2002).

4.1 Role of abiotic variables and species densities

Macrobenthos species on sandy beaches are known to show a specific zonation and distribution pattern (e.g. Degraer et al., 2003; Rodil and Lastra, 2004). As these sandy beaches are physically defined habitats where harsh environmental conditions play a prominent role, abiotic variables like median grain size (MEAN) and emersion time (ET) are thought to be important structuring factors on the intertidal sandy beach (McLachlan and Jaramillo, 1995; Veloso et al., 2003). Although no other abiotic variables were taken into account in this study and this lack of a broader range of abiotic variables definitely had its implications, the results do support the structuring role of MEAN and ET. Emersion time (ET) was a significant factor in the models of all studied macrobenthos species (except for the model of *Bathyporeia* as a genus)), clearly corresponding to the typical zonation pattern of macrobenthos on sandy beaches (Degraer et al., 2003; Janssen and Mulder, 2005; Rodil et al., 2006) and underlining that each species shows a specific niche on the beach, while MEAN was significant in the majority of the models. However, the model performances of the abiotic models were on average only moderate (in most of the models less than 50 % of the variability was explained by the abiotic variables).

These results are similar to a previous study, wherein was shown that there is generally a residual part of the variability of the distribution of sandy beach species that cannot be explained by models including the typical sandy beach abiotic variables, indicating that additional explanatory variables exist and should have been considered in the models (Schoeman and Richardson, 2002). Natural systems are complex and a lot of factors and variables interact and cause the final distribution pattern. Emersion time and sediment characteristics were initially assumed to be important variables but other abiotic variables like swash climate, waves, beach slope, water retention and water circulation may have a structuring influence as well, especially on species level (Salvat, 1964, 1967; Defeo et al., 1992; Veloso et al., 2003). Latitude has been found to be an important explanatory variable in several studies on species distributions (Defeo and McLachlan, 2005; McLachlan and Brown, 2006; Leewis et al., 2012). Primary production, although generally correlated with sediment characteristics and emersion time, could play a substantial role in steering species distributions as well (Brazeiro and Defeo, 1996; Gimenez and Yannicelli, 1997). Unfortunately, complete data for the afore-mentioned variables were not available and could therefore not be taken into account in this study.

Moreover, as suggested by Defeo & McLachlan (2005) and Honkoop et al. (2006), biotic variables could also “fill this gap” in explaining the variability in distribution of the macrobenthos. These authors stated that biotic interactions may be particularly meaningful on dissipative beaches with relative high species richness, high densities, and relatively stable substrate.

The null hypothesis in this study, formulated to investigate the idea that intertidal species densities as a proxy for biotic interactions do not play a significant role in explaining distribution patterns of macrobenthos, was falsified by a significant part of our model results. Hence, it was suggested that biotic interactions may play a more important role on sandy beaches than generally accepted. Although interactions were not expected between all species, an approach deliberately avoiding an *a* *priori* selection for some combinations of species was used and as a result all possible species associations were analysed. In one third of the global models created, a significant species density variable was shown, implying that the interacting species density added indeed had a significant contribution in explaining the distribution of the response species. However, the average additional explanation of the variability in species distribution by this explanatory species density was relatively low. Conversely, at least one significant species density was found in 75 % of the country specific models created. The average additional explanation of the species distribution by the explanatory species densities was generally higher than in the global models. This was due to the difference in species densities offered to the stepwise selection procedure of the two types of models. In the country specific models, all species densities were added to the model at once while in the global models only one species density at the time was added, explaining the lower average model performance of the global models. However, both the global and especially the country specific models are supporting the importance of other species densities in determining species distributions on sandy beaches, especially for some specific species associations. Hence, biotic interactions were suggested to play a role on these beaches.

Exploitation competition is known to appear when intertidal systems become less wave-dominated and more influenced by tidal factors (Norkko et al., 2006). Specific habitats on beaches (such as small water pools and runnel systems) are more benign and thus far more suitable for macrobenthos since they have a constant supply of water and food (Brazeiro and Defeo, 1996; Hartmann-Schröder, 1996; Gimenez and Yannicelli, 1997). Consequently, species aggregate in these locations and competition for food or space can be strongly increased here. Additionally, predation and recruitment may exert an even greater influence on sandy beach community structure (Reise, 1985). Nevertheless, biotic interactions in the sandy beach macrobenthos community have only rarely been investigated by experimental studies, partially because of the difficulty of conducting standard exclosure/enclosure experiments in this dynamic habitat (Peterson, 1991). The few previous studies actually investigating the potential importance of biotic interactions on sandy beaches gave no univocal results but some of them indicated biotic interactions to be important (Croker and Hatfield, 1980; Defeo et al., 1997; Dugan et al., 2004; Speybroeck, 2007). Especially competition between congeneric amphipods and isopods was found to be present on sandy beaches (Croker and Hatfield, 1980; Defeo et al., 1997).

Moreover, the critical issue is not whether species densities matter in explaining distribution patterns of sandy beach macrobenthos. The relevant question is: how much do these densities contribute to the model performance, so how vital are they in explaining distribution patterns? The average contribution of species densities to the models is difficult to consider in a general way since the significance of these densities is species-specific and the interaction terms between abiotic variables and species densities are difficult to interpret. When a substantial part of the variability was explained by the interaction term, this can be interpreted as one species switching its preferences for the abiotic variables under the influence of the presence of the other species. This mechanism clearly illustrates the structuring role of biotic interactions. For some species, densities of other species seemed to steer the distribution pattern far more than for others, as was expected in advance. Significant density correlations were suggested between species of different trophic groups (predator-prey interactions) and between congeneric species (competition) as was observed in other aquatic systems (e.g. Connell, 1961; Rius and McQuaid, 2006; Fortino and Creed, 2007).

4.2 *Bathyporeia pilosa* and *B. sarsi*

An indication for competition was given by the global models created for *B. pilosa*, whose distribution was negatively correlated with *B. sarsi* and vice versa. Although the abiotic factors explained the majority of the variance in species distribution, the density of *B. sarsi* also contributed significantly to the model performance of *B. pilosa*. *Bathyporeia pilosa* and *B. sarsi* are two closely related amphipods, living segregated on ultra-dissipative beaches (Degraer et al., 2003) (figure 4). Since the food supply on sandy beaches is relatively small due to low primary production (Brown and McLachlan, 2002), niche partitioning caused by competition for food could be suggested, as seen in terrestrial habitats (Voeten and Prins, 1999). However, physicochemical constraints could also play a role as it is known that *B. pilosa* and *B. sarsi* have different tolerances for salinity and temperature (Fish and Preece, 1970; Preece, 1970). Since former experiments on these congeneric species did not demonstrate competition (Speybroeck, 2007), additional experimental work is necessary to support the competition hypothesis, suggested by these modelling results.

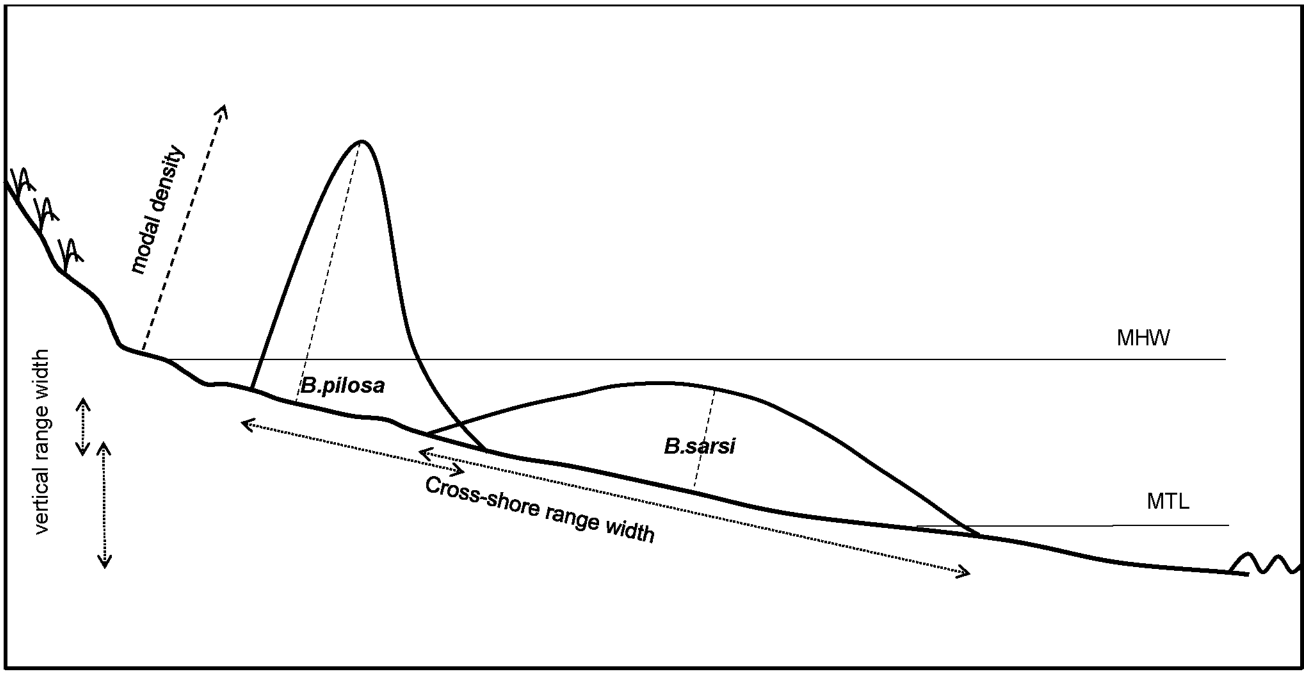

Figure 4: schematic overview of cross-shore distribution of *Bathyporeia pilosa* and *B. sarsi* across the intertidal gradient, based on data of Degraer et al. (2003). MHW = Mean High Water level; MTL = mid-tidal level.

4.3 *Eteone longa* and *Eurydice pulchra*

Potential interactions between predator and prey species on sandy beaches were also indicated by the results of this study. Negative interaction effects of *E. longa* and *E. pulchra* were detected on the prey species *B. pilosa* and *B. sarsi*. *Eteone longa* is known to pursue prey species during low tide (Michaelis and Vennemann, 2005) and *E. pulchra* is an aggressive predator consuming polychaetes, amphipods and other isopods (Jones, 1968). The negative relation between the densities of these predators and prey is thus probably caused by predator-prey interactions and can be explained twofold. The prey species could avoid or leave locations where these predators occur (Dill, 1987; Mittelbach and Chesson, 1987; Sih, 1987), creating a distinct distribution pattern between prey and predators, while on the other hand, predation pressure itself may reduce the prey densities on locations where predators occur (Holt, 1977).

4.4 Limitations of this study

One of the main limitations in this study is the afore-mentioned lack of available abiotic variables. As a result, the overall model performances were low. Hence, there is a risk that including species densities as predictor variables in a model of another species might not truly indicate a biotic interaction but rather the absence of important environmental predictors in the model (Guisan and Thuiller, 2005). Although an *a priori* knowledge on the biology of the modeled species leads to a robust mechanistic basis for interpreting biotic interaction predictors such as densities of potential interacting species (Araujo and Luoto, 2007), models explaining less than 20% of the variability only by the abiotic variables were therefore ignored. However, this decision adversely had a risk of underestimating the importance of biotic interactions since in the disregarded models the distribution of the response species could actually be poorly structured by abiotic variables and more influenced by other species' densities and consequently by biotic interactions.

Biotic processes can be important on a relatively small scale on the beach. In this study, variables were considered in the beach context, but abiotic variables and biotic interactions could also steer more small-scaled patterns on the beach. Runnel systems on the beach can be important as these micro-habitats contain a permanent supply of water and food and harbour more dense populations of detritus feeding macrobenthos (Brazeiro and Defeo, 1996; Hartmann-Schröder, 1996; Gimenez and Yannicelli, 1997). As species aggregate in these locations, competition for food or space can be strongly increased here. Nevertheless, the current abiotic information was not detailed enough to identify and characterize runnel systems on the beach, so these small-scaled patterns could not be considered in this study.

Finally, species-specific explanations could clarify the rather low model performance for some of the considered species. *Eteone longa* and *B. sar*si inhabit a broad zone in the mid-intertidal of the beach (Degraer et al., 2003) and *S. squamata* is a cosmopolitan species (Eleftheriou and McIntyre, 1976; McDermott, 1987; Rakocinski et al., 1993; Souza and Gianuca, 1995), being able to live both higher and lower in the intertidal zone (Degraer et al., 2003; Janssen and Mulder, 2005; Rodil et al., 2006). Moreover, the sediment preference of *E. pulchra* lies in a broad range (Jones, 1969). Since the habitat preferences of all these species are clearly wide, a strong correlation between the abiotic variables and the species could not be found and the distribution could not be defined precisely by the selected abiotic variables. Species with a more precisely defined habitat and hence a better correlation with the abiotic variables, like *B. pilosa* and *N. cirrosa* (Salvat, 1967; Degraer et al., 2003), showed a higher abiotic model performance. *Bathyporeia pilosa* is an amphipod only living in the high-intertidal on dissipative beaches, while *N. cirrosa* is a polychaete only living in the low-intertidal on the beach (although also occurring in several habitats in the subtidal but in this study, the subtidal habitat was not taken into account) (Salvat, 1967; Degraer et al., 2003).

5. Conclusions

Notwithstanding its limitations, this study explicitly addresses the consequences of incorporating both abiotic variables and species densities, the latter as a proxy for biotic interactions, in modelling distribution patterns of sandy beach macrobenthos. The abiotic variables emersion time and mean grain size are key structuring variables in explaining distribution patterns of macrobenthos inhabiting sandy beaches. However, biotic interactions may additionally play a substantial role in explaining these distribution patterns.

Further research should focus on enlarging and broadening this technique. Models using more extensive and standardized data (including a broader range of abiotic variables), resulting in more accurate model performances and giving a reliable idea on the relative significance of abiotic and biotic variables in explaining species distribution patterns, should be created. This chapter however gives a first indication on the importance of biotic interactions. Hence, in the context of this PhD research, it has appeared to be a valuable exercise. The experimental studies necessary to verify the suggested biotic interactions and to fully understand the underlying processes and the structuring role of biotic interactions on sandy beaches, are subsequently described in the following chapters of this PhD.

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Chapter 3: Encounter competition partly explains the segregation of the sandy beach amphipods *Bathyporeia pilosa* and *Bathyporeia sarsi.* A mesocosm experiment

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Abstract

Biotic interactions, such as competition and predation are known to play an important role in structuring communities. In this study, the intra- and interspecific competition between two congeneric sandy beach amphipods *Bathyporeia pilosa* and *B. sarsi* was examined by means of a two-way factorial mesocosm experiment. The amount of natural food resources as well as population densities of *B. pilosa* and *B. sarsi* were manipulated in order to investigate whether firstly, the species compete for food, and secondly, whether crowding effects, such as damaging encounter competition are present within and between both *Bathyporeia* species. The absence of food negatively influenced survival and recruitment and enhanced aggressive behaviour in the *B. sarsi* population, while there was no influence of the absence of food in the *B. pilosa* population. In the field, *B. pilosa* is occurring high in the intertidal where food supply is low, while *B. sarsi* is occurring in the mid-intertidal where food supply is higher. Hence, *B. pilosa* is more adapted to low food conditions than *B. sarsi.* Although an increased intraspecific density stimulated encounter competition within the *B. sarsi* population, no evidence of interspecific competition was found in this study. This first report on encounter competition for the deposit-feeding amphipod *Bathyporeia sarsi* suggests that zonation patterns of the two amphipods may be the result of the combined influence of species-specific physiological restrictions and biotic interactions within the *B. sarsi* population, indicating that on dissipative beaches, biotic interactions may be more common than generally considered.

Key words: sandy beach, encounter competition, biotic interactions, mesocosm, amphipods, distribution.

1. Introduction

Sandy beaches are harsh environments that are dominated by winds and waves (McLachlan, 1983; McArdle and McLachlan, 1991, 1992). Consequently, the distribution and zonation of infaunal sandy beach organisms have been typically related to beach morphodynamical factors such as slope, wave energy, tidal range and sediment characteristics (McLachlan and Jaramillo, 1995; McLachlan, 1996; Defeo and McLachlan, 2005). Moreover, food supply has been shown to be even more important for structuring communities on sandy beaches (Dugan et al., 2003; Lastra et al., 2006; Rodil et al., 2012). Studies on sandy beach food web dynamics indicate that besides allochthonous wrack material (Dugan et al., 2003; Ince et al., 2007; Lastra et al., 2008), also primary production in the water column (Lastra et al., 2006) and on dissipative beaches even *in situ* primary production (Bergamino et al., 2011; Schlacher and Hartwig, 2012) are supporting the beach food web and are structuring meio- and macrofaunal communities. Yet, biological interactions, in particular competition, are considered of minor importance in structuring benthos zonation patterns (McLachlan, 1983; McLachlan et al., 1993; McLachlan, 1996, 2001). This is in contrast to rocky shore ecosystems where biotic interactions often play an additional role to the dominant structuring influence of the physical environment. For example Ragnarsson & Raffaelli (1999) and Benedetti-Cecchi (2001) showed that species interactions significantly influenced community structure and species densities in this habitat. Consequently, it is currently stated that biotic interactions are instrumental to habitat selection, niche segregation and -overlap of benthic organisms on rocky shores (e.g. McPeek, 1996; Iken et al., 2001; Schluter, 2001; Liess and Hillebrand, 2004). Dugan et al. (2004) and McLachlan & Dorvlo (2005) have postulated that biotic interactions do play a role in structuring the distribution of macrofaunal communities on sandy beaches as well, especially on more benign dissipative beaches (Defeo and McLachlan, 2005; Janssen and Mulder, 2005; McLachlan and Dorvlo, 2005; Janssen et al., 2007). Empirical evidence about this structuring role of biotic interactions on sandy beach macrobenthos distribution is however scarce (but see Croker and Hatfield, 1980; Defeo et al., 1997; Dugan et al., 2004) and to our knowledge only one of these studies has focused on congeneric species so far. Defeo et al. (1997) demonstrated that congeneric isopods (*Excirolana)* changed their sediment preference in syntopic conditions.

The congeneric amphipods, *Bathyporeia pilosa* and *Bathyporeia sarsi,* show a segregated zonation pattern on intertidal sandy beaches with only a restricted overlap along the Northwest European coast: i.e. *Bathyporeia pilosa* inhabits a narrow zone between MHWS and mid-tide level (Fish and Preece, 1970), while *Bathyporeia sarsi* inhabits a broader zone in the mid-intertidal, between MHWN and MLWS (Toulmond, 1964; Nicolaisen and Kanneworff, 1983). On Belgian beaches, peak abundances of *B. pilosa* were found at 436 ± 25 SD cm above MLWS, while those of *B. sarsi* were found at 357 ± 40 SD cm above MLWS, corresponding (depending on beach slope) to a 40–62 m cross-shore distance (Speybroeck et al., 2008b). It remains, however, unclear why these two closely related and morphologically highly similar species perform this cross-shore spatial segregation. The mouthparts of *B. pilosa* and *B. sarsi* are very similar and their feeding strategy is very alike (Nicolaisen and Kanneworff, 1969). Based on their similar feeding behaviour we hypothesize that competition for food may govern the cross-shore spatial segregation of both congeneric species across sandy beaches.

Here we report on a mesocosm experiment where both natural food resources; i.e. diatoms, and population densities of *B. pilosa* and *B. sarsi* were manipulated in order to investigate whether firstly, the species compete for food, and secondly, whether crowding effects, such as damaging encounter competition (Schoener, 1983) are present within and between both *Bathyporeia* species. This information should allow understanding of whether biotic interactions, such as competition for food and encounter competition, contribute to the cross-shore spatial segregation of both *Bathyporeia* species.

2. Material & Methods

2.1 Experimental design

A two-way factorial experiment was designed in order to investigate competitive interactions between and within the amphipods *B. pilosa* and *B. sarsi.* Both amphipod species were mixed together in seven different density combinations, crossed with three dissimilar food levels: no food, ambient food conditions and double the amount of ambient food available. As natural population densities of *B. pilosa* and *B. sarsi* are unequal and can differ substantially between beaches, experimental densities had to be chosen carefully. Too low densities would underestimate competition effects, while too high densities on the other hand would overestimate the effects. Therefore, two different total densities were used, each one reflecting existing field densities of *B. pilosa* or *B. sarsi.* The first density (20 ind.treatment^{-1} = 3000 ind. m^{-2}) was observed in natural *B. sarsi* populations, while the second density (40 ind.treatment^{-1} = 6000 ind. m^{-2}) was observed in natural *B. pilosa* populations (Speybroeck et al., 2008b).

The experimental set-up consists of four sub-units: (1) intraspecific effects within the *B. pilosa* population; (2) intraspecific effects within the *B. sarsi* population; (3) interspecific effects of *B. sarsi* on *B. pilosa* and (4) interspecific effects of *B. pilosa* on *B. sarsi* (table 1). If competition for food exists within and between amphipod populations we would expect less survival and less recruitment at high amphipod densities and in the treatments with less food. If encounter competition is a dominant biotic interaction within and between both amphipod populations we would expect higher interaction rates at higher densities and lower food conditions.

Table 1: experimental design to test for intraspecific effects within and interspecific effects between *Bathyporeia pilosa* and *Bathyporeia sarsi* at three different food levels. five replicates implied 105 treatments in total.

treatment	Density *B. pilosa*	Density *B. sarsi*	total density	food level
1	20	0	20	no food
2	20	0	20	ambient food
3	20	0	20	enhanced
4	40	0	40	no food
5	40	0	40	ambient food
6	40	0	40	enhanced
7	0	20	20	no food
8	0	20	20	ambient food
9	0	20	20	enhanced
10	0	40	40	no food
11	0	40	40	ambient food
12	0	40	40	enhanced
13	10	10	20	no food
14	10	10	20	ambient food
15	10	10	20	enhanced
16	10	30	40	no food
17	10	30	40	ambient food
18	10	30	40	enhanced
19	30	10	40	no food
20	30	10	40	ambient food
21	30	10	40	enhanced

2.2 Collection of study organisms and experimental conditions

Adults of *B. pilosa* and *B. sarsi* were collected from two sandy beaches along the Belgian coast: *Bathyporeia pilosa* was collected on the high-intertidal beach in Ostend (2°55’43” E 51°14’17” N), while *B. sarsi* was collected at the mid-intertidal in De Panne (2°33’24” E 51°05’42” N). Study organisms were kept in the lab for 24 h before initiation of the experiment which allowed adaptation to laboratory conditions and removal of accidentally injured organisms during processing. Sediment was collected in the mid-intertidal beach zone of De Panne and subsequently sieved over a 0.5 mm sieve and decanted to remove all benthos and detritus. Sediment composition did not differ among both sites where organisms were collected (Two Sample Wilcoxon test: W: 12; p: 0.34), indicating that the obtained results and posed conclusions regarding governing factors of field distribution are not compromised by the sediment used. Decantation did not remove the epipsammon attached to the sand grains but only the epipelon and the detritus from the interstitial spaces between the sand grains (cf. Moss and Round, 1967; Baird and Wetzel, 1968). Sediment for the treatments without food was heated for 4 hours (450°C) to eliminate all organic matter. Enhanced food supply treatments were achieved by stimulation of epipsammic microphytobenthos growth during incubation for 14 days with f2 culture medium (Guillard, 1975) in a climate-controlled room at 19 °C prior to the experiment. At the start of the experiment, the chlorophyll a contents were 0 µg/g, 0.78 ± 0.05 SD $\mu g.g^{-1}$ and 1.64 ± 0.14 SD $\mu g.g^{-1}$, respectively for the treatments with no food, ambient food and enhanced food supply. Natural sea water was filtered over a 45 µm filter.

PVC cylinders (Ø 8 cm, 30 cm height) were filled for one third with the collected sediment and placed in an aquarium (120 cm x 120 cm x 40 cm). Two rows of little permeable holes (covered with 250 µm gauze), one under and one above the sediment-water interface, allowed refreshment of seawater in the cylinders during each tidal cycle, keeping the sediment and organisms inside, while the sea water could flow in and out of the cylinders. Circulation pumps and timers were used to imitate the tidal cycle, enabling conditions as similar as possible to the field situation, which ensured a good survival of the test organisms. A total of 105 cylinders were used to permit 21 treatments (7 density treatments x 3 food levels) in 5 replicate aquaria each, arranged in a randomized design. Each replicate aquarium had its own independent maintenance system and its own sea water tank of 120 l where water was pumped in and out according to the tidal cycle. The experiment was carried out in a temperature-controlled room at 19 °C with a 11:13-h dark/light regime, i.e. the natural dark/light regime during late summer at the beach were the study organisms were retrieved. The experiment was started at high tide on the 3th of September 2009 and was terminated three weeks later, at low tide on the 24th of September 2009. The amphipods that were alive at the end of the experiment, were extracted from the sediment, counted and preserved in a 70% ethanol solution. Additionally, a sediment sample of 2 ml was collected from each of the 105 cylinders to analyse the final food concentration.

2.3 Data analysis

The following population characteristics of *B. pilosa* and *B. sarsi* were determined for each treatment: (i) survival, (ii) recruitment and (iii) the amount of injury free organisms.

(i) Survival was expressed as the ratio between the number of adult organisms alive at the end of the experiment and the number of organisms added at the start of the experiment. Average body size of adult amphipods was 5.4 ± 0.6 SD mm and 6.1 ± 0.7 SD mm for *B. pilosa* and *B. sarsi* respectively.

(ii) Recruitment was calculated likewise for the number of recruits alive at the end of the experiment, so this ratio actually reflects the average recruitment per individual. The recruits were small juvenile amphipods that freshly hatched during the experiment (average size juvenile *B. pilosa*: 3.0 ± 0.05 SD mm; juvenile *B. sarsi*: 4.0 ± 0.08 SD mm).

(iii) Encounter competition was assessed by calculation of the ratio between the number of organisms without injuries at the end of the experiment and the number of organisms added at the start of the experiment. Injuries were only taken into account when black scar tissue was present on the wound, amphipods having wounds without scar tissue were assumed to have been damaged during sample processing at the end of the experiment (Halcrow and Smith, 1986; Halcrow, 1988; Sheader, 1998). Amphipods with regenerated body parts were likewise not considered to be wounded during the experiment, taken into account that regeneration time is generally longer than the experimental time, i.e. 11 weeks (Wilhelm et al., 2003).

Statistical analyses were performed by using PRIMER v6 (Primer-E Ltd, UK) in conjunction with PERMANOVA add-on software (Clarke and Gorley, 2006; Anderson et al., 2008) and the statistical package R (version 2.10.1, R Foundation for Statistical Computing).

For each of the four sub-units, a two-factor design was performed in PERMANOVA (Permutational multivariate analysis of variance (Anderson, 2001)) to separate the effects of density and food and test for an interaction, using Euclidian distance dissimilarities. PERMANOVA allows to perform univariate ANOVAs with p-values obtained by permutation (Anderson and Millar, 2004), thus avoiding the assumption of normality. Homogeneity of dispersion was tested with PERMDISP, using distances among centroids in order to check whether obtained results could be attributed to the factors examined. Factors were considered significant at $p < 0.05$ in all analyses. The PERMDISP-test was never significant for the analysis of *B. pilosa*, indicating equally dispersed distances to centroids, hence a difference due to location.

However, for *B. sarsi*, the PERMDISP-test was significant for some factors. If both PERMDISP and PERMANOVA tests are significant, dispersion effects occur but the presence of location effects is uncertain (Anderson et al., 2008). Therefore, prudence is advised when interpreting these results and the relative sizes of the within and between-group resemblances deserve further attention (Anderson et al., 2008).

In case of significant single factor effects, pair-wise tests within each factor were carried out to distinguish what treatments differed exactly. Because of the restricted number of possible permutations in pair-wise tests, p-values were obtained from Monte Carlo samplings (Anderson and Robinson, 2003).

3. Results

3.1 *Bathyporeia pilosa*: intraspecific competition

Survival, recruitment and the ratio of injury free *B. pilosa* organisms varied between 6.7 % and 85.0 %, 0.0 % and 100.0 %, and 10.0 % to 100.0 % respectively. However, none of the population characteristics differed significantly among density - and food levels (table 2 & figure 1).

Table 2: permanova results on intraspecific effects in the *Bathyporeia pilosa*-population.

survival	df	SS	Pseudo-F	p
density	1	33,333	1.70E+02	0,901
food	2	382,92	0,97922	0,3907
density x food	2	362,92	0,92808	0,415
Res	24	4692,5		
Total	29	5441,7		
recruitment	df	SS	Pseudo-F	p
density	1	541,88	21,876	0,1579
food	2	992,92	20,042	0,1566
density x food	2	71,25	0,14382	0,8724
Res	24	5945		
Total	29	7551		
injury free	df	SS	Pseudo-F	p
density	1	130,21	0,79365	0,3797
food	2	593,75	18,095	0,181
density x food	2	165,42	0,50413	0,6063
Res	24	3937,5		
Total	29	4826,9		

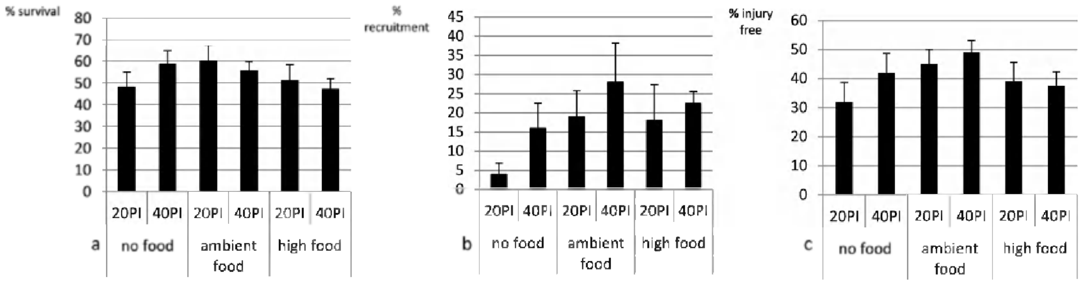

Figure 1: survival (a), recruitment (b) and injury free (c) ratio (%; mean ± SE) of *Bathyporeia pilosa*. 20Pl: low-density treatment of *Bathyporeia pilosa*, 40Pl: high-density treatment of *Bathyporeia pilosa*.

3.2 *Bathyporeia sarsi*: intraspecific competition

Survival, recruitment and the ratio of injury free *B. sarsi* organisms did not differ significantly among density levels (density: $p > 0.1$; table 3). However, all population characteristics varied significantly among food levels ($p < 0.05$; table 3). In sediments without food the survival was on average 15.5 ± 4.7 SE %, while survival was 40.0 ± 8.5 SE % and 40.5 ± 4.2 SE % in the sediments with ambient food supply and enhanced food supply, respectively. The recruitment showed a similar pattern with no recruitment in the treatments without food, 13.8 ± 4.2 SE % of recruitment in the treatments with ambient food and 12.3 ± 6.2 SE % of recruitment in the treatments with enhanced food.

Although not significantly at the 0.05 level, aggressive attacks (leading to injuries or even mortality) increased with density (injury free: $p = 0.069$ and survival: $p = 0.071$; table 3), independent of the amount of food available. The amount of injury free organisms was lowest in sediments which contained high densities and no food (figure 2).

Table 3: permanova results on intraspecific effects in the *Bathyporeia sarsi*-population.

survival	df	SS	Pseudo-F	p
density	1	676,88	35,703	0,0713
food	2	3721,2	98,143	0,0014
density x food	2	16,25	4.29E+02	0,9632
Res	24	4550		
Total	29	8964,4		
recruitment				
density	1	163,33	18,127	0,1933
food	2	1137,9	63,145	0,006
density x food	2	182,92	1,015	0,375
Res	24	2162,5		
Total	29	3646,7		
injury free				
density	1	676,88	35,703	0,0694
food	2	3721,2	98,143	0,0017
density x food	2	16,25	4.29E+02	0,9555
Res	24	4550		
Total	29	8964,4		

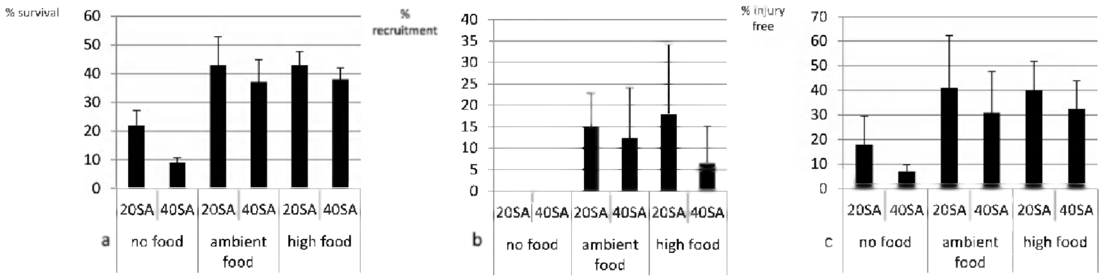

Figure 2: survival (a), recruitment (b) and injury free (c) ratio (%; mean ± SE) of *Bathyporeia sarsi*. 20SA: low-density treatment of *Bathyporeia sarsi*, 40SA: high-density treatment of *Bathyporeia sarsi*.

3.3 *Bathyporeia pilosa*: interspecific effects of *B. sarsi*

Survival, recruitment and the ratio of injury free *B. pilosa* organisms did not differ significantly among levels of *B. sarsi* density or food (p > 0.1; table 4 & figure 3).

Table 4: permanova results on interspecific effects on the *Bathyporeia pilosa*-population.

survival	df	SS	Pseudo-F	p
density	3	1341,3	11,575	0,3337
food	2	110,83	0,14347	0,8669
density x food	6	1932,5	0,83387	0,5494
Res	48	18540		
Total	59	21925		
recruitment				
density	3	1521,2	0,94561	0,4345
food	2	965,83	0,90054	0,4203
density x food	6	3537,5	10,995	0,3718
Res	48	25740		
Total	59	31765		
injury free				
density	3	293,33	0,28053	0,841
food	2	395,83	0,56784	0,5737
density x food	6	1374,2	0,6571	0,689
Res	48	16730		
Total	59	18793		

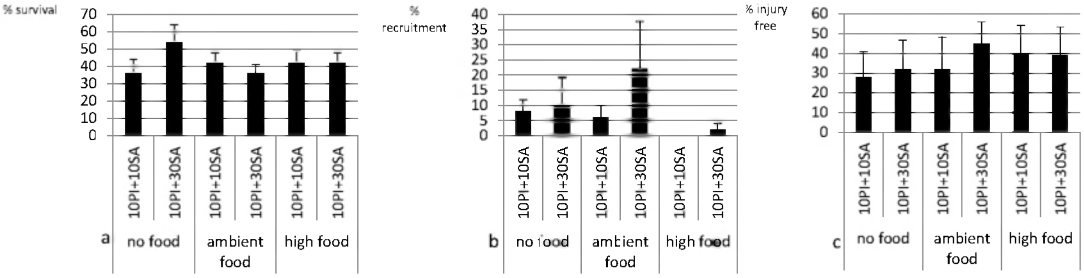

Figure 3: survival (a), recruitment (b) and injury free (c) ratio (%; mean ± SE) of *Bathyporeia pilosa*. 10PI+10SA: treatment with 10 individuals of *Bathyporeia pilosa* and 10 individuals of *Bathyporeia sarsi*, 10PI+30SA: treatment with 10 individuals of *Bathyporeia pilosa* and 30 individuals of *Bathyporeia sarsi*.

3.4 *Bathyporeia sarsi*: interspecific effects of *B. pilosa*

Survival, recruitment and the ratio of injury free *B. sarsi* organisms did not differ significantly among *B. pilosa* density levels (density: $p > 0.1$; table 5). However, all population characteristics varied significantly among food levels (food: $p < 0.05$; table 5). In sediments without food the survival was on average 25.0 ± 7.06 SE %. In the sediments with ambient food supply average survival rates were 39.0 ± 8.75 SE % whereas in the sediments with enhanced food supply survival increased even up to 41.0 ± 7.86 SE %. The ratio of injury free organisms showed a similar pattern with the lowest ratio in the no food treatments (20.0 ± 5.83 SE %), 32.0 ± 8.26 SE % of injury-free organisms in the ambient food treatments and the highest ratio of injury-free organisms (39.0 ± 6.84 SE %) in the enhanced food treatments (figure 4).

Table 5: permanova results on interspecific effects on the *Bathyporeia sarsi*-population.

survival	df	SS	Pseudo-F	p
density	1	563,33	20,994	0,1662
food	2	6806,7	12,683	0,0004
density x food	2	526,67	0,98137	0,3862
Res	24	6440		
Total	29	14337		
recruitment				
density	1	83,333	0,37313	0,5355
food	2	2286,7	51,194	0,0147
density x food	2	886,67	19,851	0,1588
Res	24	5360		
Total	29	8616,7		
injury free				
density	1	213,33	0,84211	0,3614
food	2	5180	10,224	0,0011
density x food	2	126,67	0,25	0,7811
Res	24	6080		
Total	29	11600		

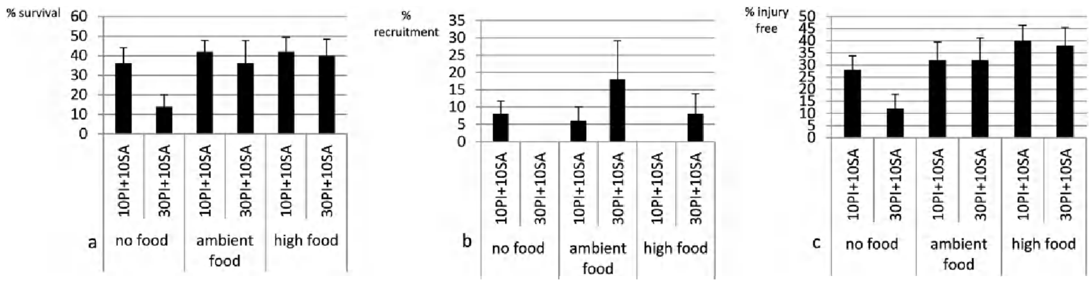

Figure 4: survival (a), recruitment (b) and injury free (c) ratio (%; mean ± SE) of *Bathyporeia sarsi*. 10PI+10SA: treatment with 10 individuals of *Bathyporeia pilosa* and 10 individuals of *Bathyporeia sarsi*, 30PI+10SA: treatment with 30 individuals of *Bathyporeia pilosa* and 10 individuals of *Bathyporeia sarsi*.

4. Discussion

Relatively few experiments have been designed to directly infer whether resources of any sort are ever limiting to soft-sediment species or whether competition for limited resources is a structuring factor for soft-sediment communities (although see Woodin, 1974; Levinton and Lopez, 1977; Peterson, 1977; Peterson and Andre, 1980). However, competitive interactions among individuals cannot be fully understood without manipulations of the resources that are subject to competition.

Generally, competition rate is known to be higher when food is scarce (Steinwascher, 1978; Kotrschal et al., 1993; Dolman, 1995; Moody and Ruxton, 1996). During this experiment, it was observed that some animals seemed to attack others while swimming in the water column. Detailed analyses of the surviving organisms confirmed these attacks by showing remarkable injuries on several amphipods. Generally, amphipods are known to perform aggressive attacks, both intra- and interspecific (Dick et al., 1995; van der Velde et al., 2009). However, aggression is mostly acknowledged for predator species like *Gammarus,* where cannibalism and intraguild predation is well-described (Polis et al., 1989; Dick et al., 1999; Dick and Platvoet, 2000). For the deposit feeding amphipod *Bathyporeia*, aggressive behaviour has never been observed yet. As *Bathyporeia* normally feeds by scraping organic material and diatoms from sand grains (Nicolaisen and Kanneworff, 1969), its mouth parts are not designed to attack other species. Nevertheless, the observed injuries during the experiment clearly confirm the presence of encounter competition (Schoener, 1983) in the non-predaceous amphipods *B. pilosa* and *B. sarsi.* Black scar tissue was covering the injured parts of the wounded amphipods and in several cases the start of regeneration of the lost appendage was observed. In crustaceans, wounds are known to be sealed rapidly by blood clotting and the damaged area is subsequently hardened by tanning (Halcrow and Smith, 1986; Halcrow, 1988). Depending on the extent of the damage, appendages or body parts can be regenerated over several moults (Skinner, 1985; Hopkins, 2001; Wilhelm et al., 2003). Although wounds resulting from encounter competition might thus not be directly lethal, wound healing and regeneration of lost limbs requires a reasonable energy investment decreasing overall organism fitness, enhancing its vulnerability to diseases and to subsequent attacks, and hence affect the outcome of competition (Wilhelm et al., 2003).

In this study, no intraspecific interaction among *B. pilosa* individuals was demonstrated, nor was there a distinct indication of damaging interference. Although wounded animals were occasionally observed in the allotopic treatments of *B. pilosa,* we did not notice a significant negative effect of higher density on the survival, the recruitment and the ratio of injury free organisms. Consequently, we conclude that intraspecific attacks might have occurred, but that the intensity was obviously too low to induce distinct effects on the population of *B. pilosa* and that this mechanism is thus most likely not a governing ecological interaction at the natural population densities of *B. pilosa* that were investigated in this experiment. This corroborates Wenngren & Olafsson (2002) who empirically demonstrated that crowding effects such as damaging interference were not important at common field densities of *Monoporeia affinis*, an amphipod which like *Bathyporeia* belongs to the family of Pontoporeiidae. Similarly, we did not find a significant effect of *B. sarsi* density on *B. sarsi* population characteristics, although survival, recruitment and amount of injury free organisms were always higher at the lowest density level. The results of this study show that under mesocosm conditions, *B.*

sarsi population characteristics are mediated by food availability. Survival, recruitment and the amount of injury free organisms were significantly diminished in sediments without food. Consequently, one would expect an increase of these characteristics from ambient to high food conditions. The amphipods did however not benefit from the high food conditions in this experiment suggesting that they were already satisfied by the ambient food conditions. The tested population characteristics did not significantly differ among density levels at the 95 % confidence level but the higher survival and the enhanced occurrence of injury free *B. sarsi* individuals in the low density treatments at all three food levels suggest that aggressive attacks might be enhanced at higher densities of this species (p = 0.07 for survival, p = 0.07 for injury-free ratio). In the treatments without food this pattern was best illustrated as the ratio of injury free organisms was 18.0 ± 12.0 SE % in the low density and 7.0 ± 2.7 SE % in the high density treatments.

Analysis of the syntopic treatment x food combinations did not reveal clear indications of the occurrence of interspecific competitive interactions. Moreover, syntopic species combinations further emphasized the dependence of *B. sarsi* on food to attain good fitness, characterized by high survival, recruitment and low rates of intraspecific attacks.

Extrapolation of experimental mesocosm results to natural systems should be considered with caution. However, the chosen experimental densities and conditions were carefully determined to mimic the field situation as good as possible. In addition to the available knowledge on species distribution and physiology, the obtained information deduced from this study should enable a better assessment of the processes structuring benthic communities on sandy beaches.

Speybroeck et al. (2008b) described spatially segregated populations of both amphipods along the Belgian coast with local densities of *B. sarsi* being two to even four times lower than *B. pilosa*-densities. The enhanced intraspecific attacks found under experimental low-food and high-density conditions for *B. sarsi*, are likely to occur in the field when food is scarce and amphipod densities high, resulting in a lower fitness under these conditions. Since the only resident primary producers on sandy beaches are epipsammic diatoms, the general food supply on beaches is limited (0 to 50 $gC \cdot m^{-2} \cdot y^{-1}$) (McLachlan and Brown, 2006). However, surf zone diatoms may also occur and locally enhance the food supply in the mid-intertidal zone (McLachlan and Brown, 2006) that *B. sarsi* inhabits. *B. sarsi* is known to be less tolerant for starvation compared to *B. pilosa,* since the physiology of *B. pilosa* can stand a substantial amount of dessication, deprivation and other stress (Preece, 1971). Therefore, unlike *B. sarsi*, *B. pilosa* is well adapted to the harsh environmental and food conditions high in the intertidal. Our observations of enhanced encounter competition in *B. sarsi*, especially under lowered food conditions, suggest that intraspecific competition contributes to this species' upper distribution limit and peak density in the mid-intertidal zone. No indications of competition effects on *B. pilosa* populations were detected. We therefore suggest that the high abundance in the high intertidal zone of this species is independent from *B. sarsi* occurrence lower on the beach and primarily relates to lower predation pressure by epi- and hyperbenthic organisms in the high intertidal zone.

5. Conclusions

This is the first study that indicates the presence of encounter competition in the deposit-feeding amphipod *Bathyporeia.* In the *B. sarsi* population, intraspecific encounter competition increased at lower food levels and higher densities, while intraspecific competition was not shown in the *B. pilosa* population. The occurrence of interspecific competition among both congeneric species could not be demonstrated. In general, this study shows that biotic interactions may have a more structuring role on benthic communities from dissipative sandy beaches than generally considered.

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Chapter 4: Role of predation on sandy beaches: predation pressure and prey selectivity estimated by laboratory experiments

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Abstract

Predation is known to play an important role in structuring communities. In rocky intertidal communities, both environmental variables and the structuring role of predation determine species zonation and distribution patterns. However, on intertidal sandy beaches, little is known on the presence and the role of predation. In this study, laboratory experiments were used to examine prey consumption, prey selectivity and predation pressure of the two main epibenthic predators, being shrimp and juvenile flatfish, present on the intertidal beach at high tide. Results show that macrobenthos is important in the diet of these epibenthic predators and that prey selectivity is present. As predation pressure on the intertidal beach is high, predation may be an important structuring factor for the sandy beach macrobenthos community. Hence, the macrobenthos zonation pattern is probably steered by the combination of abiotic and biotic factors: while the upper limit of a species zone is defined by the species' physiological response to abiotic environmental variables, the lower limit is defined by biotic factors such as predation pressure. Furthermore, the intertidal zone functions as an important nursery area for commercially important species like shrimp and flatfish.

Key words: sandy beach, macrobenthos, *Crangon crangon*, *Pleuronectes platessa*, predation pressure, prey selectivity.

1. Introduction

Predation is one of the major organizing forces within communities (e.g. Christensen and Pauly, 1998; Matson et al., 2011). The importance of predation in structuring communities has been well documented for terrestrial plant communities (e.g. Lau et al., 2008), freshwater zooplankton communities (e.g. Ibe et al., 2011) and rocky intertidal communities (e.g. Bonaviri et al., 2009; Brazão et al., 2009). The great majority of the marine predation studies concentrated on tidal flats, where the most important predators at high tide are juvenile flatfish and macro-crustaceans such as shrimps and crabs (Kuipers, 1977; Kuipers and Dapper, 1984; Koot, 2009). Epibenthic predators are known to be of structuring importance for the macrofauna communities on soft-bottom intertidal sediments (Reise, 1977; Kuipers and Dapper, 1981; Kuipers et al., 1981; Evans, 1984; Pihl and Rosenberg, 1984; Pihl, 1985).

Richards and colleagues (1999) showed that crab predation on an intertidal mudflat diminished the abundances of the bivalve *Macoma balthica* while Kuipers & Dapper (1984) demonstrated the importance of tidal flats as nursery areas for brown shrimp. Trush et al. (1994) showed that the negative effect of predation by birds and fish on soft bottom sediment communities was largely scale-dependent. Moreover, field enclosure or exclosure experiments are characterized by technical problems such as caging effects or scale-dependency (Thrush, 1999).

On sandy beaches, the importance of predation by epibenthic predators and the trophic relationship between these predators and the macrobenthos are far less studied. Biological interactions are believed to be of minor structuring importance in the mainly physically determined sandy beach ecosystems (McLachlan, 1983; Jaramillo and McLachlan, 1993; McLachlan et al., 1996; McLachlan, 2001; Schlacher et al., 2008). Despite their ecological importance during the life cycle of many marine organisms (e.g. Gibson, 1973; Beyst et al., 2001), the nursery function of sandy beaches for epibenthic species has not been intensively studied compared to shallow water and estuarine habitats (Amara and Paul, 2003). On dissipative intertidal beaches, epibenthic predators are abundant at high tide (Beyst et al., 2001) but it is not sure whether these predators can execute a significant predation pressure on the resident macrofauna of intertidal dissipative beaches as the only studies on epibenthic predators did not focus on the smaller juvenile species (due to the used sampling strategy where epibenthos was collected by using a fishing net with mesh sizes of 0.5 x 0.5 mm) that are known to consume macrobenthos the most (Beyst et al., 1999; Beyst et al., 2002). Furthermore, field experiments on intertidal sandy beaches are difficult to execute in the intertidal sandy beach environment as this environment is highly dynamic, especially in comparison with the more benign tidal flats (McLachlan & Brown, 2006).

The high- intertidal macrobenthos community on Belgian dissipative sandy beaches consists mainly of the polychaete *Scolelepis squamata*, the two amphipods *Bathyporeia pilosa* and *B. sarsi* and the isopod *E. pulchra* (Degraer et al., 2003). These species show a specific zonation pattern on the intertidal sandy beach (Degraer et al., 2003). The distribution and zonation of infaunal sandy beach organisms have been typically related to beach morphodynamical factors such as slope, wave energy, tidal range and sediment characteristics (McLachlan and Jaramillo, 1995; McLachlan, 1996; Defeo and McLachlan, 2005). Moreover, food supply has been shown to be important for structuring communities on sandy beaches (Dugan et al., 2003; Lastra et al., 2006; Rodil et al., 2012; Van Tomme et al., 2012) but detailed food web interactions between sandy beach species are not yet clarified.

The epibenthic community, being temporarily present on dissipative intertidal Belgian beaches is dominated by shrimp and juvenile flatfish (Beyst et al., 2001). Although these predators are known to have an important influence on macrofauna on intertidal flats, the detailed trophic relations between these epibenthic predators and sandy beach macrofauna on intertidal sandy beaches are not yet studied.

The aims of this study were therefore (1) to estimate the predation pressure of shrimp and juvenile flatfish on the dominant representatives of the intertidal dissipative macrobenthos community, (2) to determine the prey consumption of sandy beach macrobenthos by epibenthic predators present on intertidal dissipative beaches and (3) to examine whether predation can have a structuring role in the segregated zonation pattern of *B. pilosa* and *B. sarsi*. The null hypothesis, tested in this study, stated that the predators had no significant effect on the survival of the prey species.

2. Material and methods

2.1 Selection and origin of the species and specimens

Predation pressure was investigated for all dominant members of the high-intertidal dissipative macrobenthos community of the Belgian coast: the polychaete *Scolelepis squamata*, the two amphipods *Bathyporeia pilosa* and *B. sarsi* and the isopod *Eurydice pulchra.* As *E. pulchra* itself is a predator, who feeds on the other species, the predation impact of shrimps and flatfish on *E. pulchra* was tested separately from the other prey species (table 1).

On dissipative beaches, several runnels are situated where shrimps and juvenile flatfish stay behind with receding tide. *Crangon crangon* (brown shrimp), *Scophthalmus maximus* (turbot) and especially *Pleuronectes platessa* (plaice) are the most commonly caught epibenthic predators (Beyst et al., 1999). Predators and prey species for the laboratory experiments were collected on the Belgian dissipative beach of De Panne (2°33’24” E 51°05’42” N).

2.2 Experimental conditions

Laboratory experiments were conducted in June of 2010, in a climate-controlled room at 18 °C and with a day/night regime of 16:8 h, the natural summer photoperiod in Belgium. Predators and prey were added to aquaria provided with a constant oxygen supply. Similar aquaria of 18-9-13 (l-w-h) cm were used for both experiments. These aquaria were filled with 4 cm of natural Belgian beach sediment, sieved and decanted to remove all fauna, and with 1 l of Belgian coastal sea water, sieved over 64 µm mesh size to remove all larger fauna.

Predators were collected one day before the start of the experiment by dredging shallow water with a hand operated beam trawl. Before the start of the experiments, predators were starved and acclimatized in the lab for 24h (Hiddink et al., 2002). All prey species were collected by sieving the beach sediment over a 1 mm sieve.

The average total length of the shrimps used was 3 to 3.5 cm and the total length of the juvenile flatfish used was 3 to 5 cm (0-group flatfish) since predators of these sizes are known to feed on macrobenthos (Janssen and Kuipers, 1980; Beyst et al., 1999; Campos et al., 2008). Sex of the experimental predators was not determined but predators were divided randomly over the treatments and replicates. The effects of *C. crangon* and juvenile flatfish were studied in separate aquaria since the two types of predators might also have a mutual effect on each other (table 1) (Beyst et al., 1999). Although this probably resulted in a higher consumption estimation as compared to the field situation where predation by other predators probably decreased consumption, it was the aim of this experiment to determine potential consumption without inter-predator influences. In all flatfish-treatments the same two-predator combination of one larger *P. platessa* and one smaller *S. maximus* was used.

2.3 Set-up combined predator-prey experiment

The predator impact of juvenile flatfish and shrimps was investigated on four prey species: *B. pilosa*, *B. sarsi*, *S. squamata* and *E. pulchra* (table 1). Prey densities were chosen to be the naturally occurring, average densities of Belgian beaches (Speybroeck, 2007). Experimental densities of *B. pilosa* were 1708 ind.m^{-2} (= 40 ind.experimental treatment^{-1}), these of the related *B. sarsi* 427 ind.m^{-2} (= 10 ind.experimental treatment^{-1}), these of the polychaete *S. squamata* 213 ind.m^{-2} (= 5 ind.experimental treatment^{-1}), and finally these of the isopod *E. pulchra* 856 ind.m^{-2} (= 20 ind.experimental treatment^{-1}). The latter density is ten-fold higher compared to natural densities (Vandewalle, 2009) since at natural *Eurydice* abundances, the number of experimental isopods would be too low to guarantee a reliable estimation of the predator impact. However, the ten-fold higher density is likely to overestimate natural consumption of the isopod, something to keep in mind when interpreting the results. When extrapolations to field conditions were made based on the results of the laboratory consumption, the results were re-calculated, taken into account the lower effective field densities of *E. pulchra*. Although densities of predators are known to strongly fluctuate on the beach with every tidal cycle, a predator density of 85 ind.m^{-2} (= 2 ind.experimental treatment^{-1}) was used in the current study, based on observed densities in the study by Beukema (1992). The prey species were added in the aquaria prior to the predators in above-mentioned natural densities, to mimic the field situation at upcoming tide and give a reliable estimation of field predation pressure. The predator-prey experiment lasted for 72 hours and all treatments were replicated seven times. The tidal cycle was not imitated in the experiment, so predators had the opportunity to feed continuously.

Table 1: treatments predator-prey experiment (predators in bold)

1	***C. crangon*** + *B. pilosa* + *B. sarsi* + *S. squamata*
2	***C. crangon*** + ***E. pulchra***
3	**juvenile flatfish** + *B. pilosa* + *B. sarsi* + *S. squamata*
4	**juvenile flatfish** + ***E. pulchra***
5	Control *B. pilosa* + *B. sarsi* + *S. squamata*
6	Control *E. pulchra*

2.4 Set-up predator-amphipod experiment

The second experiment focused on the predator-prey relationships between epibenthic predators and the two congeneric amphipods *B. pilosa* and *B. sarsi.* As these two species differ in size, with *B. sarsi* being significantly larger than *B. pilosa* (5.4 ± 0.6 SD mm and 6.1 ± 0.7 SD mm for *B. pilosa* and *B. sarsi* respectively) (Speybroeck et al., 2008b), the aim of this second experiment was to study the role of prey size, prey identity and prey behaviour in the predators choice. A two-factorial experiment with the factors density (three levels) and species (two levels) was set up to study the impact of the predators on uniform populations of *B. pilosa* and *B. sarsi*. The three different densities of *B. pilosa* and *B. sarsi* were (1) the natural density of *B. pilosa* (1708 ind/m^2 = 40 ind.treatment^{-1}), (2) twice this density (3416 ind/m^2 = 80 ind.treatment^{-1}) and (3) half of this density (856 ind/m^2 = 20 ind.treatment^{-1}). Natural densities of both amphipods can vary substantially and the maximum observed densities can be quite high (Vader, 1965; Bamber, 1993). In this experiment, moderate natural densities were used to (1) avoid a surplus of prey species, overestimating consumption and

(2) to avoid an overestimation of *B. sarsi* abundance, generally occurring in lower field densities (per square meter) compared to *B. pilosa* (Bamber, 1993). Nevertheless, the densities of *B. sarsi* in this experiment were still higher than average field densities due to the substantial difference in field densities between the two amphipods. An overview of the treatments of this experiment is given in table 2. The predation effect on the two amphipod species was tested in separate treatments as these syntopic amphipods also show a segregated zonation pattern in the field. All treatments were simultaneously replicated five times except for the high-density treatments of *B. pilosa* (four replicates) and *B. sarsi* (two replicates) due to the lack of amphipods collected in the field. Densities of predators were similar to the predator densities used in the first experiment.

Table 2: treatments predator-amphipod experiment: low amphipod density = 20 ind.treatment^{-1}; natural amphipod density = 40 ind.treatment^{-1}; high amphipod density = 80 ind.treatment^{-1}; predators in bold

1	***C. crangon* +** *B. pilosa* (low)	10	**juvenile flatfish** + *B. sarsi* (low)
2	***C. crangon*** + *B. pilosa* (natural)	11	**juvenile flatfish +** *B. sarsi* (natural)
3	***C. crangon*** + *B. pilosa* (high)	12	**juvenile flatfish** + *B. sarsi* (high)
4	**juvenile flatfish** + *B. pilosa* (low)	13	control *B. pilosa* (low)
5	**juvenile flatfish** + *B. pilosa* (natural)	14	control *B. pilosa* (natural)
6	**juvenile flatfish** + *B. pilosa* (high)	15	control *B. pilosa* (high)
7	***C. crangon*** + *B. sarsi* (low)	16	control *B. sarsi* (low)
8	***C. crangon*** + *B. sarsi* (natural)	17	control *B. sarsi* (natural)
9	***C. crangon*** + *B. sarsi* (high)	18	control *B. sarsi* (high)

2.5 Statistical analysis prey selectivity

The second experiment was analysed using Permanova (Permutational multivariate analysis of variance, (Anderson, 2001)) in PRIMER-v6-PERMANOVA (Primer-E Ltd, UK) (Clarke and Gorley, 2006; Anderson et al., 2008) to separate the effects of density and species and test for an interaction, using Euclidian distance dissimilarities. PERMANOVA allows to perform univariate ANOVAs with p-values obtained by permutation (Anderson and Millar, 2004), thus avoiding the assumption of normality. Homogeneity of dispersion was tested with PERMDISP, using distances among centroids in order to check whether obtained results could be attributed to the factors examined. If both PERMDISP and PERMANOVA tests are significant, dispersion effects occur but the presence of location effects is uncertain (Anderson et al., 2008). As the analyses of this experiment showed both significant

PERMANOVA and PERMDISP (p = 0.03) results, prudence is advised when interpreting the results and the relative sizes of the within and between-group resemblances deserve further attention (Anderson et al., 2008). In case of significant single factor effects, pair-wise tests within each factor were carried out.

2.6 Calculating consumption and predation pressure

Average daily prey consumption was calculated as the average difference between prey numbers remaining in the control and in the experimental treatments, corrected for the duration of the experiment (Moens et al., 2000). Subsequently, the numbers of prey removed were converted to biomass using ash free dry weight (AFDW) values calculated by Speybroeck et al. (Speybroeck et al., 2007; 2008b) and Vandewalle (2009) (table 3). Based on this daily experimental consumption (g AFDW. Day^{-1}), both daily prey consumption as a percentage of the predators own body weight (also expressed as g AFDW - table 3) and average daily prey consumption in the field (expressed as mg biomass consumed.m^{-2}. Day^{-1}) could be determined. As two different flatfish species were used the average AFDW value of the larger *P. platessa* and smaller *S. maximus* was used for the calculations of the consumption (table 3). Average daily prey consumption in the field was determined by recalculating the experimentally consumed prey to biomass values.m^{-2} taken into account the size of the experimental set-up.

Table 3: average individual AFDW (mg) of experimental prey and predator species according to Speybroeck et al. (2008b), Vandewalle (2009), Beukema (1992) and Hostens (2003).

average AFDW (mg)/species	*B. pilosa*	0.27 mg
	B. sarsi	0.37 mg
	S. squamata	6.05 mg
	E. pulchra	0.72 mg
	C. crangon	17.5 mg
	P. platessa 5 cm	230.0 mg
	S. maximus 3.5 cm	81.0 mg

Daily predation pressure was calculated as the daily prey population decrease, expressed as a relative pressure. Since the experiment lasted for three days, total population decrease at the end of the experiment was corrected for the duration of the experiment to obtain the daily predation pressure (1). To determine field predation pressure on the high-intertidal macrobenthos, the experimental results need to be corrected for the time this macrobenthos is actually available for the epibenthic predators in the field since in our experiment prey were constantly available for predators. Therefore, the predation pressure obtained in the experiment was corrected by the time the location of the prey species in the intertidal is flooded. This immersion time is dependent on the cross-shore distribution of the prey populations on the beach. Since populations of macrobenthos species on sandy beaches generally show a unimodal distribution, the elevation of the modal density was taken as a proxy to estimate immersion time for the population (Speybroeck et al., 2007; Speybroeck et al., 2008b; Vandewalle, 2009). For the locations of *B. pilosa*, *S. squamata* and *E. pulchra*, daily immersion time was estimated 6 hours (correction factor ¼), while the *B. sarsi* location was calculated to be flooded 12 hours (correction factor ½) a day (1).

$$\text{Daily predation pressure (\% prey population removed.Day}^{-1}\text{)} =$$
$$100 * [((\text{\# prey consumed/duration experiment})/\text{\# ind}_{control}) \quad * \text{ factor}_{\text{ immersion}}] \ (1)$$

3. Results

3.1 Prey consumption and prey selectivity

Crangon crangon consumed on average 96.8 ± 1.2 % (mean ± SE) of the *B. pilosa* population, 90.0 ± 3.72 % of *B. sarsi* and 96.7 ± 2.0% of *E. pulchra* by the end of the three-day experiment. Regarding *S. squamata*, only 31.4 ± 7.4% of the polychaetes was eaten by *C. crangon*. Translation of these consumption results into daily biomass consumption is given in table 5 (b).

The Permanova analysis of the amphipod experiment for shrimp as a predator gave no significant results for either density of the amphipod species ($p > 0.1$) or amphipod species itself ($p > 0.1$) as the shrimps almost depleted all prey by the end of the experiment.

Juvenile flatfish consumed on average 83.8 ± 2.81 % (mean ± SE) of the experimental *B. pilosa* population, 67.6 ± 9.07 % of *B. sarsi*, 51.4 ± 5.95 % of *S. squamata* and 45.2 ± 17.49 % of *E. pulchra*. Translation of this consumption into daily biomass consumption is given in table 5 (b).

The Permanova analysis of the amphipod experiment for juvenile flatfish as predator showed that the factor amphipod species (pseudo-F: 10.02; df: 1; $p = 0.008$) and the interaction term amphipod species*density (pseudo-F: 3.86; df: 2; $p = 0.049$) were significant, indicating that the amphipod species effect varied according to the density. Although only significant at the 0.05 level, the pairwise tests showed that within the low-density treatments ($p = 0,049$) and the high-density treatments ($p= 0.026$), *Bathyporeia pilosa* was found to be more vulnerable for predation by juvenile flatfish than *B. sarsi* (figure 1), while for the medium-density treatment this pattern was not found ($p= 0.99$).

In total, shrimps ate 23.5 % of their own body weight a day while juvenile flatfish only ate 2.98 % of their own body weight a day, corresponding to 4.11 mg.day^{-1}.shrimp^{-1} and 4.64 mg.day^{-1}.fish^{-1} respectively (table 5, (a) & (b)).

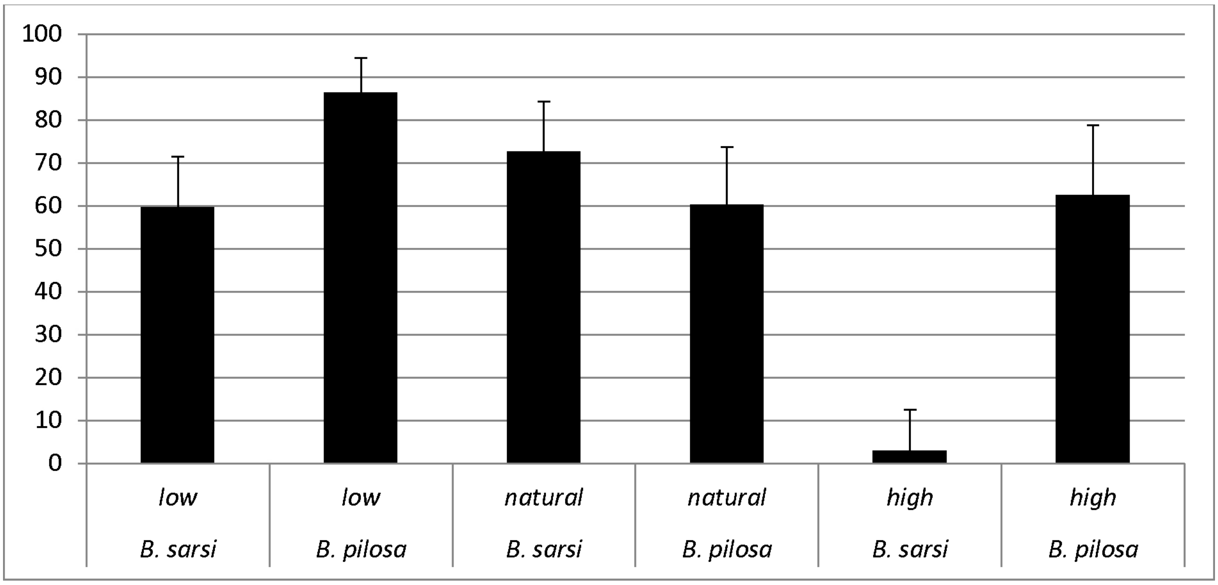

Figure 1: consumption of *B. pilosa* and *B. sarsi* by juvenile flatfish. X-axis: treatments (low-denstiy treatment = 20 prey. treatment^{-1}; natural-denstiy treatment = 40 prey. treatment^{-1}; high-denstiy treatment = 80 prey. treatment^{-1}); Y-axis: % of the experimental population consumed, mean ± SE.

Table 4: (a) daily prey consumption as a percentage of the predator's body weight (% of the predators body weight (AFDW) consumed. Day^{-1}), (b) daily prey consumption in the field (mg AFDW.m^{-2} consumed. Day^{-1}), (c) daily predation pressure in the lab (% of the prey population consumed. Day^{-1}), (d) daily predation pressure in the field (% of the prey population consumed. Day^{-1})

		(a) daily prey consumption	(b) daily prey consumption	(c) predation pressure	(d) predation pressure
C. crangon	*B. pilosa*	9,97%	148.31	32,31%	8.08%
	B. sarsi	3,19%	47.49	30,21%	15.11%
	S. squamata	9,05%	133.71	10,48%	2.62%
	E. pulchra	1,33%	19.89	3,23%	0.81%
juvenile flatfish	*B. pilosa*	0.97%	128.41	27,97%	7.00%
	B. sarsi	0,27%	36.01	22,92%	11.50%
	S. squamata	1.67 %	221.13	17,14%	4.30%
	E. pulchra	0.07%	8.57	1,41%	0.35%

3.2 Predation pressure

In table 5 (c) the predation pressure in the lab and (d) in the field were shown for both *C. crangon* and juvenile flatfish as predators. The field predation pressure of both *C. crangon* and juvenile flatfish was highest on *B. sarsi,* while *E. pulchra* experienced the lowest pressure from both predator species (table 5 (d)).

Since the epibenthos consists for 5% out of juvenile flatfish and for 95 % of *C. crangon* (Beyst et al., 1999) and field predation pressure on the macrobenthos is the result of the combined pressures of all predators present on the beach, overall field predation pressures were calculated taken into account these predator abundances (table 5). Based on the calculated field predation pressures and the average field biomass at the modal density, the population of *B. pilosa* would be eradicated after 12 to 13 days and the population of *B. sarsi* even after 6 to 7 days. For *S. squamata* and *E. pulchra*, extinction of the prey population would occur after 37 to 38 and 126 to 127 days respectively, due to predation of the two main epibenthic predators.

Table 5: estimated predation pressure in the field

predation pressure (%)		
C. crangon + juvenile flatfish	*B. pilosa*	8.03%
	B. sarsi	14.93%
	S. squamata	2.70%
	E. pulchra	0.79%

4. Discussion

All four macrobenthic prey species were consumed by the epibenthic predators in this experiment. Overall crustacean consumption was very high and selectivity, consumption and predation pressure varied according to the prey species.

4.1 Prey selectivity

4.1.1 Crangon crangon

While predation by *C. crangon* in other studies was found to be size-selective (Pihl and Rosenberg, 1984; Jensen and Jensen, 1985; Keus, 1986; Beukema et al., 1998; van der Veer et al., 1998), the size difference between *B. pilosa* and *B. sarsi* (Speybroeck et al., 2008b) did not seem to influence predation behaviour of *C. crangon* in this study. The relative size difference of predators and prey could be explanatory for this difference between our and former studies. Since size selectivity is more likely when the prey size is closer to the prey size limits of the shrimp, the use of smaller predators or a shorter experimental duration could potentially demonstrate selectivity. Nevertheless, shrimps are known to be opportunistic carnivores (Pihl, 1985) so the effect of prey size may be subordinate to consumption consistent with the relative occurrence of prey species in the field (Wilcox and Jeffries, 1974) at the experimental scale used.

4.1.2 Juvenile flatfish

A clear preference for *B. pilosa* over *B. sarsi* was shown (except in the medium density experiment). Hence, the selectivity of predators and vulnerability of prey organisms are likely to be influenced by relative body sizes (Werner and Gilliam, 1984; Van der Veer and Bergman, 1987; Fuiman, 1994; Ellis and Gibson, 1995; Gibson et al., 1995). Although larger prey are energetically more interesting (Ivlev, 1961; Werner and Gilliam, 1984; Harper and Blake, 1988; Scharf et al., 2000) it is also assumed that catchability decreases with increasing prey body size (Sissenwine, 1984; Folkvord and Hunter, 1986; Anderson, 1988; Blaxter and Fuiman, 1990; Sogard, 1997; Scharf et al., 2000), so a trade-off is made by predators between these advantages and disadvantages. The flatfish of the used size class showed a lower consumption of *B. sarsi* compared to *B. pilosa*, indicating that *B. sarsi* may have profited from its larger body size and therefore is more protected against predation from predators in this size range.

4.2 Prey consumption

4.2.1 Crangon crangon

Pihl & Rosenberg (1984) registered a daily food intake of 12.1 % and del Norte-Campos & Temming (1994) a daily food intake of 16.0 % of the shrimps body wet weight. When recalculating these wet weight results, obtained by stomach and gut analyses, to AFDW using conversion factors between wet weight and AFDW (Sistermans et al., 2005), our shrimp consumption results were double the ones from Pihl & Rosenberg (1984) and 1.5 times those of del Norte-Campos & Temming (1994). Furthermore, a deficit in experimental prey availability by the end of the experiment may have negatively influenced obtained prey consumption, so obtained results in the current study, may even underestimate field consumption. Although consumption is known to be season and temperature dependent (Pihl and Rosenberg, 1984), temperature only partially explains the higher prey consumption of shrimp in this study compared to other studies (Pihl and Rosenberg, 1984; del Norte-Campos and Temming, 1994) as the temperature used in the current study was higher compared to Pihl & Rosenberg (1984), but was the same as in the study of del Norte-Campos & Temming (1994). Nevertheless, physiology can also show regional-specific differences. The different methods to calculate consumption in both studies may be a second factor influencing the results. Pihl & Rosenberg (1984) used *in situ* stomach weight measurements and linear or exponential models estimating shrimp consumption, while in our study, consumption was determined based on mesocosm experiments where consumed prey could be counted straightforwardly. Moreover, the highly energetic environment and the tidal dynamics may hamper feeding, resulting in a lower field consumption compared to consumption in the laboratory. In addition, in this lab study starved predators were used, densities of *Eurydice* were ten-fold higher compared to natural densities, densities of *B. sarsi* were also somewhat higher than in the field and the used predator densities were also higher than in some other studies (Beyst et al., 2001) so these factors possibly overestimated total consumption. Conclusively, *C. crangon* is potentially capable of having a great impact in crustacean and polychaete prey populations but this potential may in the field be constrained by biological interactions or the dynamics of the tide.

4.2.2 Juvenile flatfish

Food consumption of juvenile flatfish is strongly dependent on temperature and development stage or species size (Lockwood, 1984; Fonds et al., 1992; Fuiman, 1994). Therefore, only comparisons between studies performed with species of the same size class and under comparable conditions are valuable. Lockwood (1984) found an average daily uptake between 1.5 and 10 % of the fish' body weight, so the results obtained in this study fall well within this consumption range.

The higher *Bathyporeia* consumption of flatfish in this study compared to the results in Beyst et al. (1999) can be explained by the set-up of the experiment. In our study, the number of potential prey species was limited while in Beyst et al. (1999), more prey species were available in the field. Although results of Beyst et al. (1999) suggested that *P. platessa* is preferably feeding in the high-intertidal, this study wanted to examine the consumption of juvenile flatfish in general (cfr. the use of two different flatfish species) and not related to a tidal gradient. At low tide, juvenile flatfish reside in the lower intertidal and subtidal where other prey species are part of the diet, thus lowering consumption of high-intertidal fauna (Beyst et al., 1999). Crustaceans including *B. pelagica* and mysids replace *B. pilosa* and *B. sarsi* in the low-intertidal while polychaetes including *Nephtys cirrosa* and to a lesser extent *N. hombergii* replace the spionid polychaete *S. squamata* lower on the beach (Beyst et al., 1999). As the individual biomass of these low-intertidal species does not differ substantially from the biomass of high-intertidal replacement species (Sistermans et al., 2005), obtained consumption results in this study are considered truthful.

4.3 Predation pressure

Since some of the prey populations would have been eradicated in a short time based on the calculated field predation pressures, caution is needed when extrapolating these laboratory results to the field where predators and prey experience more complex situations, which lower the field predation pressures. A complex web of interactions is present in the field among predators and prey, potentially enhancing (different predators consume the same prey species) or reducing (when predators compete for the same prey or use each other as prey) predation pressure. A food niche overlap between *C. crangon* and plaice *P. platessa* was found by Evans (1984) and Pihl (1985), suggesting that predation by *C. crangon* may be one of the factors affecting survival of newly settled fish (Van der Veer, 1986; Van der Veer and Bergman, 1987; Cushing et al., 1996; Ansell et al., 1999; Oh et al., 2001). Moreover, the intertidal sandy beach is an extremely complex, three-dimensional dynamic habitat and this may diminish predation and prevent the depletion of the prey populations since prey populations can hide in the sediment and can be replaced by other prey species when densities decrease (Beyst et al., 1999). Nevertheless, the high consumption and predation pressures found in this study, both endorse the important role of epibenthic predators on Belgian sandy beaches as well as suggest food limitation for shrimps and juvenile flatfish, confirming the results of Hufnagl et al. (2010) and Van der Veer et al. (2010) in the Wadden Sea.

5. Conclusions

The results of these mesocosm experiments showed a very high consumption and no prey selectivity for shrimp while juvenile flatfish showed a lower consumption and a preference for *S. squamata* and small amphipods. While our results may have been overestimated due to the absence of tidal beach dynamics, obtained consumption results were in the same range as results from other intertidal habitats. In addition, the predation pressure of shrimp and juvenile flatfish on the macrobenthos populations of sandy beaches was quantified for the first time. It was shown that this epibenthic predation pressure could have a structuring influence on the macrobenthos community but additional field exclosure experiments are advisable to elucidate this role more profoundly.

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Chapter 5: Macrofaunal sediment selectivity considerations for beach nourishment programmes

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Abstract

Nowadays, beach nourishment is widely considered as a better alternative compared to the construction of hard structures to protect a sandy coast against detrimental erosive effects, both from an ecological and an engineering perspective. The rare studies conducted on the ecological impact of beach nourishment are short-term, *post hoc* monitoring investigations of the benthic macrofauna. Little is known of the biological processes during and after nourishment. To allow swift recolonisation after nourishment, the characteristics of the nourished beach have to match the habitat demands of the benthic macrofauna. The sediment preference of the key intertidal species *Scolelepis squamata, Eurydice pulchra, Bathyporeia pilosa* and *B. sarsi*, which dominate many West European sandy beaches, was therefore investigated through laboratory experiments, both in single-species as well as combined-species treatments. While the former aimed at developing guidelines for impact mitigation of beach nourishment, the latter aimed at elucidating the role of biotic interactions in sediment preference. Results of the experiments indicated that *B. pilosa* and *E. pulchra* preferred the finest sediment, while *B. sarsi* had a broader preference and also occurred in medium-coarse sediments. However, the sediment preference of *E. pulchra* for fine sediments was not confirmed by other field and experimental studies. The polychaete *S. squamata* had the broadest preference and even showed a high occurrence in coarse sediments that are not naturally occurring on the sandy beaches where the animals were caught for this experiment. However, this polychaete is a cosmopolitan species, not only occurring on fine-grained beaches, but also on coarse-grained beaches worldwide. The preferences imply that beach nourishment with relative coarse sediment will have a major effect on *B. pilosa* while effects of coarse sediments on *S. squamata* will be minor. Finally, interspecific competition with the syntopically occurring amphipod *B. sarsi* was found to change the sediment selection of the amphipod *B. pilosa* towards the coarser sediments where *B. sarsi* occurred in lower frequencies.

Keywords: beaches, benthos, beach nourishment, environmental impact, sediment, macrobenthos, ecosystem management.

1. Introduction

Beach nourishment is an episodic, dramatic event for the sandy beach ecosystem with diverse impacts (Speybroeck et al., 2006a) both on organisms inhabiting the beach (Jones et al., 2008; Leewis et al., 2012; Schlacher et al., 2012) as well as on adjacent ecosystems (Jordan et al., 2010). However, effects depend on a variety of diverse characteristics of the specific nourishment programme. The choice between high-shore, foreshore or profile nourishment greatly determines what species communities on the beach are influenced while the frequency between different nourishments is essential for the recovery of the system. In addition, the timing of the nourishment deserves careful consideration to maximally avoid periods of breeding or recruitment of different sandy beach organisms (Melvin et al., 1991; Peterson et al., 2000a; Peterson and Manning, 2001). As beach nourishment, supplying several tons of sediment on the intertidal beach, does not allow any survival of macrobenthic infauna (Schlacher et al., 2012), attempts to bring the post-nourishment beach back to pre-nourishment ecosystem conditions, have to address post-impact restoration. Two major process-related elements seem to be of importance for swift recolonisation: (1) dispersal capacities and (2) habitat demands of the species. The first aspect is related to species-specific characteristics, albeit local geography and hydrodynamics of the area surrounding the nourished beach will play an important role. Large anthropogenic structures like harbour walls may hamper long-shore drift of pelagic larvae and water-column dispersal of sub-adult and adult organisms. Once the nourished beach has been reached, animals will have to be able to settle, burrow and survive. All this will depend on their specific tolerances and preferences, in relation to the encountered habitat. Although peer-reviewed studies on the effect of beach nourishment are scarce (Jones et al., 2008; Schlacher et al., 2012), several studies have investigated the effects after dredging (Somerfield et al., 1995; Radenac et al., 1997; Savage et al., 2001; Byrnes et al., 2004; Diaz et al., 2004; Witt et al., 2004; Powilleit et al., 2006), thereby demonstrating that benthic macrofauna frequently show changes in abundance, species richness and community structure. The negative effects may either be small, with a short period of recovery in some regions (Van Dolah et al., 1984; Radenac et al., 1997; Roberts and Forrest, 1999), since macrofauna of dynamic coastal zones is tolerant to disturbances (Newell et al., 1998), or may be highly important, permanently altering the macrobenthic association (Harvey et al., 1998). Structural damages on the macrofauna may occur due to changes in the granulometric characteristics, since the macrofauna composition is closely related to the sediment characteristics (McLachlan, 1996; Brazeiro, 2001; McLachlan and Brown, 2006). Indeed, sediment composition is a major controlling factor for changes in benthic associations within the constraints of the adjacent species pool as it is directly linked to the organic matter content (food availability) which is one of the important factors in determining trophic complexity and species abundances (Knox, 2001; Incera et al., 2006; Rodil et al., 2012). However, sediment organic matter is not the only structuring factor and other factors such as the beach morphodynamics also have an important role in structuring sandy beach communities (McLachlan and Jaramillo, 1995; McLachlan, 1996; Defeo and McLachlan, 2005). Recent studies show that both physical as well as nutritional variables are important for the sandy beach community structure (Incera et al., 2006; Cisneros et al., 2011). Therefore, information on the responses of macrobenthic species on changing sediment characteristics is one of the crucial elements to assess the impact of beach nourishment on the macrobenthic community. Unfortunately, experimental studies on sediment preferences of sandy beach species are scarce and existing studies only examine sediment selection of higher trophic species such as flatfish (Gibson and Robb, 2000; Nasir and Poxton, 2001; Carl et al., 2008) while studies on the preferences of macrobenthos are rare (Speybroeck, 2007).

Since profile beach nourishment mostly affects the high-intertidal beach as large amounts of sediment are first placed on the high shore and are than divided by bulldozers over the entire beach (Hanson et al., 2002), we examined the sediment preferences of the key macrobenthic species of the high-intertidal *Scolelepis squamata-Eurydice pulchra* community of the Belgian beach ecosystem (Van Hoey et al., 2004). Belgian beaches are characterized by gentle slopes and fine sediments and are thus generally considered to be dissipative (Degraer et al., 2003). The selected species of the high-intertidal community of these dissipative beaches were the polychaete *Scolelepis squamata*, the isopod *Eurydice pulchra* and the two amphipods *Bathyporeia pilosa* and *B. sarsi*. *Scolelepis squamata* is a suspension feeding polychaete (Dauer, 1983) while the amphipods feed on epipsammic diatoms attached to the sand grains (Nicolaisen and Kanneworff, 1969). The isopod *E. pulchra* is an aggressive and very mobile predator, feeding on polychaetes and crustaceans such as *B. pilosa*, *B. sarsi* and *S. squamata* and even showing kannibalism (Jones, 1968).

The aims of this study, investigating the sediment selection of sandy beach macrobenthos of dissipative sandy beaches, were (1) to examine the sediment preference of the four dominant macrobenthic species (*S. squamata, E. pulchra, B. pilosa* and *B. sarsi*) of these beaches to formulate valuable recommendations for the used sediment in beach nourishments and (2) to study the effect of interspecific interactions in influencing this choice.

2. Material and methods

2.1 Experimental design

Sediment preference was examined for the four species, both in single-species and combined-species conditions. Besides the single-species treatments, several two-, three- and four-species combinations were experimentally studied (table 1) during the summer of 2011. Due to the high number of two- and three-species combinations possible, only the two-species combinations between species with different trophic positions or between possible competitors were tested. As the polychaete and the amphipods are known to feed on different food sources (Nicolaisen and Kanneworff, 1969; Dauer, 1983), polychaete-amphipod combinations were thus not tested. Furthermore, only a limited number of three-species combinations were tested as the results of these treatments could not unequivocally indicate what species was the most influencing for possible preference changes. The experiment was conducted in a climate room at 19° C, the summer temperature on Belgian sandy beaches, in a natural summer dark/night regime (16:8 h light/dark).

Table 1: sediment preference treatments. single-species (column 1) and combined-species treatments (column 2-4) where sediment preferences were tested for.

Single-species treatment	2-species treatment	3-species treatment	4-species treatment
B. pilosa	*B. pilosa-B. sarsi*	*B. pilosa-B. sarsi-* *S. squamata*	*B. pilosa-B. sarsi-* *S. squamata-* *E. pulchra*
B. sarsi	*E. pulchra-B. pilosa*		
S. squamata	*E. pulchra-B. sarsi*		
E. pulchra	*E. pulchra-* *S. squamata*		

The experimental organisms were released into round-shaped aquaria (cross-section = 30 cm; h = 10 cm), subdivided into four quarters by metal partitions which prevented movement between sections via the sediment. Each section was covered with a layer of one of the four different sediment types, either naturally occurring on sandy beaches or used in current and future beach nourishment projects (fine: 125-180 µm; medium-fine: 180-250 µm; medium-coarse: 250-355 µm; coarse (outside the range of sediments naturally occurring on the beaches considered in this study): 355-500 µm). Each species treatment was replicated five times. Sediment depth was 4 cm and the seawater depth on top of the sediment was 5 cm. Sediments remained submerged throughout the experiments, ruling out desiccation of experimental specimens. During the 48 hour experiment, the aquaria were constantly aerated but no food was added since experimental time was limited. However, due to the predatory and even kannibalistic nature of *Eurydice*, this isopod was able to feed during the experiment. Experiments were started at low tide and animals were released at random into the aquarium by pouring the organisms (submerged in a small amount of sea water) in a circular movement over the four subdivisions. As the experiment started at low tide when most species stay buried, a time lag of 15 minutes was respected after addition of the first species before adding the next species to allow every species to bury in the sediment. The tidal cycle was however not imitated during the experiment, but due to the short experimental duration and the internal clock of the experimental species, they showed several swimming cycles during the experiment. After 48 hours (ensuring several swimming cycles of the species), the experiment was terminated and all living individuals were extracted from each section and counted. During several subsequent weeks from May to July 2011, all species combinations were examined each time using new experimental organisms.

2.2 Collection of organisms, sand and sea water

Beach sediment was collected at the beach of De Panne (Belgium; 2°33’24” E 51°05’42” N) and after removal of organic matter by heating the sediment up to 450°C, the sand was sieved over a sequence of sieves with mesh width of 125 µm, 180 µm, 250 µm, 355 µm and 500 µm. The sea water, originating from the same Belgian beach, was filtered over a 45 µm filter to remove all fauna from the water.

All organisms were collected by sieving the beach sediment on the high-intertidal beach in De Panne. In the experimental treatments, natural densities of the macrobenthic species were used that ensured enough encounters to force active selection between sediment types (Speybroeck, 2007): 150 individuals.treatment $^{-1}$ (=2125 ind.m^{-2}) for *B. pilosa*; 70 individuals.treatment $^{-1}$ (=991 ind.m^{-2}) for *B. sarsi;* 20 individuals.treatment $^{-1}$ (=284 ind.m^{-2}) for *S. squamata* and 10 individuals.treatment $^{-1}$ (=143 ind.m^{-2}) for *E. pulchra.*

In the multi-species treatments, total species densities were higher than in the single-species treatments, but as this actually reflects the field situation (where different species also occur toghether), this was expected to give valuable results. Indeed, the zonation patterns of the high-intertidal macrobenthos species show (partial) overlap (Degraer et al., 2003), resulting in a higher overall species abundance on the beach. Before the start of the experiment, species stocks were left overnight to allow acclimatization of the experimental organisms.

2.3 Data analysis

The distribution of species was tested with a replicated G-test of goodness-of-fit (Sokal and Rohlf, 1995; Stoner and Ottmar, 2003). This test was used to examine whether the species showed a random distribution over the four sediment types offered. The null hypothesis states that the number of observations in each sediment is equal to the expected distribution, i.e. as a random distribution is hypothesized, the number of observations in each sediment type should be equal. The replicated G-test of goodness-of-fit has the advantage that the null hypothesis can be tested for each individual experiment (partial G's) but also for the pooled data set (Sokal and Rohlf, 1995). Heterogeneity G(Gh) (with [no. of replicates – 1] × [no of sediment types – 1] degrees of freedom) was calculated to assess heterogeneity among replicate treatments. Pooled G (Gp) (with no. of sediment types – 1 degrees of freedom) tested the goodness of fit for the pooled data over all experimental replicates, and Gt, the sum of Gh and Gp (with [df Gh] + [df Gp] degrees of freedom) tested whether the data as a whole fitted the expected distribution. In the combined-species treatments, the same G- test was used against the null hypothesis that species distribution was similar to the species distribution in the single-species experiments.

The sediment selectivity was estimated by the Electivity index, E'. E' is calculated per sediment type as: $E' = (c_i - o_i)/(c_i + o_i)$ where c_i is the species abundance in one sediment type and o_i the expected abundance, in case of random distribution, for that sediment (Ivlev, 1961). Positive E' values indicate a preference, negative ones a rejection (Hiddink et al., 2002).

3. Results

3.1 Single species treatments

The results of the G-test showed a significant sediment preference for all tested species (table 2 & table 3). In detail, *Bathyporeia pilosa* clearly preferred the finer sediments since 87 % of the experimental population of this amphipod was found in the sediments with a grain size smaller than 250 µm (figure 1 (A) & table 2). As 42 % of the experimental population of the related amphipod *B. sarsi* was found in the sediment types with a grain size larger than 250 µm, *B. sarsi* had a broader preference (figure 1 (B) & table 2). *Scolelepis squamata* was more divided over finer and coarser sediments, 30 % of these polychaetes was even found in sediment with a grain size larger than 355 µm (figure 1 (C) & table 2), whereas for *E. pulchra* the sediment preference resembled the preference of *B. pilosa* (figure 1 (D) & table 2). The results of the G-tests for goodness of fit showed that replicates were heterogeneous for *B. pilosa* and *E. pulchra*. Nevertheless, the partial G's were highly significant (p < 0.001).

Table 2: G-test results of the single-species and combined-species treatments of *Bathyporeia pilosa, B. sarsi, Scolelepis squamata and Eurydice pulchra.*

B. pilosa	Gt *(df: 15)*	p(Gt)	Gh *(df: 12)*	p(Gh)	Gp *(df: 3)*	p(Gp)
B. pilosa (single species treatment)	435.31	< 0.001	56.85	< 0.001	378.47	< 0.001
B. pilosa-B. sarsi- S. squamata-E. pulchra	290.79	< 0.001	183.71	< 0.001	107.08	< 0.001
B. pilosa-B. sarsi-S. squamata	1008.08	< 0.001	883.89	< 0.001	124.18	< 0.001
B. pilosa-B. sarsi	128.87	< 0.001	57.14	< 0.001	71.73	< 0.001
E. pulchra-B. pilosa	108.01	< 0.001	84.06	< 0.001	23.95	< 0.001
B. sarsi	Gt *(df: 15)*	p(Gt)	Gh *(df: 12)*	p(Gh)	Gp *(df: 3)*	p(Gp)
B. sarsi (single species treatment)	24.71	0.054	7.59	0.82	17.13	< 0.001
B. pilosa-B. sarsi- S. squamata-E. pulchra	225.62	< 0.001	171.58	< 0.001	54.04	< 0.001
B. pilosa-B. sarsi-S. squamata	100.13	< 0.001	32.91	< 0.001	67.22	< 0.001
B. pilosa-B. sarsi	2331.39	< 0.001	59.79	< 0.001	2271.59	< 0.001
E. pulchra-B. sarsi	276.71	< 0.001	172.83	< 0.001	103.87	< 0.001
S. squamata	Gt *(df: 15)*	p(Gt)	Gh *(df: 12)*	p(Gh)	Gp *(df: 3)*	p(Gp)
S. squamata (single species treatment)	20.19	0.16	9.32	0.68	10.88	0.012
B. pilosa-B. sarsi- S. squamata-E. pulchra	107.22	< 0.001	77.93	< 0.001	29.29	< 0.001
B. pilosa-B. sarsi-S. squamata	92.04	< 0.001	39.83	< 0.001	52.21	< 0.001
E. pulchra	Gt *(df: 15)*	p(Gt)	Gh *(df: 12)*	p(Gh)	Gp *(df: 3)*	p(Gp)
E. pulchra (single species treatment)	61.23	< 0.001	47.26	< 0.001	13.97	0.0029
B. pilosa-B. sarsi- S. squamata-E. pulchra	88.11	< 0.001	64.13	< 0.001	23.98	< 0.001
B. pilosa-B. sarsi-E. pulchra	43.08	< 0.001	34.95	< 0.001	8.13	0.043

Table 3: sediment selectivity based on the Electivity index

	125-180 µm	180-250 µm	250-355 µm	355-500 µm
B. pilosa	+	+	-	-
B. sarsi	+	-	+	-
E. pulchra	+	+	-	-
S. squamata	-	+	+	+

3.2 Combined species treatments

Sediment preferences of all tested macrobenthic species differed significantly between single-species and combined species conditions (table 2). Although replicates were heterogeneous for all tested species, the partial G's were highly significant (p < 0.001). In the presence of *E. pulchra*, the *B. pilosa* frequency of occurrence in the fine and medium-fine sediment decreased, while the frequency of occurrence in the medium-coarse sediment increased from 11 ± 1 % to 22 ± 5 % (figure 1 (A)). In the presence of the related amphipod *B. sarsi*, the *B. pilosa* frequency of occurrence in the medium-fine sediment decreased from 45 ± 3 % to 25 ± 4 %, while the frequency of occurrence of *B. pilosa* in the two coarsest sediments increased (figure 1 (A)). In the 3-species treatment, the *B. pilosa* frequency of occurrence in the medium-fine sediment decreased to 28 ± 3 %, while the frequency of occurrence in the medium-coarse sediment increased (figure 1 (A)) and in the 4-species treatment, there was a decrease of *B. pilosa* frequency of occurrence in the fine sediment, while there was an increase in the medium-coarse and coarse sediments (figure 1 (A)).

In the presence of *E. pulchra*, a strong increase of *B. sarsi* from 18.94 ± 1.93 % to 42.05 ± 13.36 % was observed in the medium-fine sediment, while a decrease was found in the fine and coarse sediments (figure 1 (B)). In the presence of *B. pilosa*, the sediment preference of *B. sarsi* changed only slightly (figure 1 (B)).

The polychaete *S. squamata* showed a significant increase in the fine sediment from 13.33 ± 4.16 % in the single-species treatment to 29.23 ± 4.10 % in the 3-species treatment and even 34.16 ± 8.48 % in the 4-species treatment (figure 1 (C)).

Isopod frequency of occurrence increased in the coarse sediment from 13.11 ± 4.19 % to 27.56 ± 7.58 % and to 23.00 ± 10.20 % in the 3- and 4-species treatments respectively (figure 1 (D)).

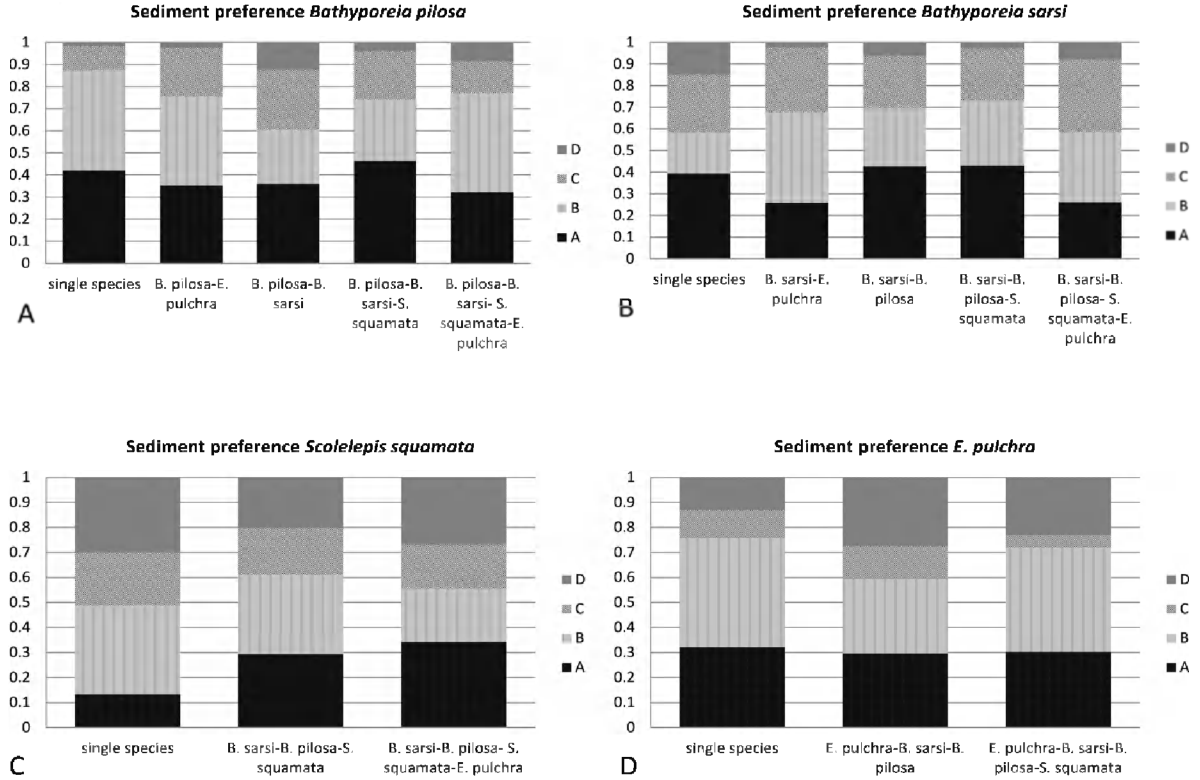

Figure 1: sediment preference of *Bathyporeia pilosa* (A), *Bathyporeia sarsi* (B), *Scolelepis squamata* (C) & *Eurydice pulchra* (D) in single-species- and combined-species conditions. X-axis: species treatments; Y-axis: average proportion of the experimental population in sediment types: A: 125-180 µm; B: 180-250 µm; C: 250-355 µm; D: 355-500 µm.

4. Discussion

4.1 Species sediment preference

The preference of *B. pilosa* for the two sediment types with a grain size smaller than 250 µm, is in line with observed field preferences of this amphipod for sediment with a median grain size smaller than 250 µm and even smaller than 210 µm (Vader, 1965; Vader, 1966; Khayrallah and Jones, 1980; Persson, 1982; Nicolaisen and Kanneworff, 1983). The field sediment preference of *B. sarsi* for somewhat coarser sediment (Vader, 1965) was also confirmed in this experimental study. While a previous study by Jones (1969) found a preference for coarser sediments, the isopod *E. pulchra* preferred fine sediment in the current study. Since the pattern was found both in combined-species as well as in single-species conditions, the presence of prey species in the finer sediments could not directly explain this behaviour. However, it is possible that isopods “know” that prey items are mostly present in this finer sediment. As *E. pulchra* is a highly energetic swimmer (Alheit and Naylor, 1976), the preference for the finer sediment is likely to have been an active choice. The differences between studies are remarkable and differing experimental conditions can be an important cause. However, a former experimental study in the same laboratory and under similar experimental conditions as the current study showed a preference for coarse sediment (Vandewalle, 2009). The only clear difference between these studies is the origin of the experimental organisms. While the species used in this study were gathered on the dissipative beach of De Panne, the used species in the study of Vandewalle (2009), were collected on the dissipative beach of Raversijde but sediment did not differ significantly between these two beaches. *Bathyporeia*-densities are however higher on the beach of De Panne, confirming that the indirect knowledge of where prey species are most present in the field, probably influenced the choice of the isopods in the laboratory experiment. The statistical analysis of this study did however indicate that replicates were heterogeneous and this can hamper a clear interpretation of the sediment preference. Hence, the sediment preference of *E. pulchra* might have been less specific than for other sandy beach species and a broad tolerance could be suggested for the isopod. This conclusion is supported by the cosmopolitan occurrence of *E. pulchra*, both on fine-grained dissipative beaches (Degraer et al., 2003) as well as on coarse-grained reflective beaches (Rodil et al., 2006).

The most striking result in this study was the preference of the polychaete *S. squamata* for both medium-fine as well as coarse sediment, also found by Speybroeck (2007). While this spionid polychaete inhabits fine to medium sediments on West European dissipative beaches (Degraer et al., 2003; Janssen and Mulder, 2005), it is a rather cosmopolitan species inhabiting both fine-grained as well as coarse-grained sediments (Dahl, 1971; Hartmann-Schröder, 1996; Van Hoey et al., 2004), which is in accordance with the results of our experiments.

4.2 Recommendations for beach nourishment of West European sandy beaches

Although differences were found between preferences in single-species and combined-species conditions, general recommendations for nourishment could be made based on the results of this study. All studied species preferred sediment with a median grain size smaller than 250 µm (figure 2). Sediment with a median grain size between 250 µm and 355 µm negatively influenced the presence of the amphipod *B. pilosa* and the isopod *E. pulchra*, while coarse sediment (355-500 µm) negatively influenced all species except the polychaete *S. squamata* (figure 2).

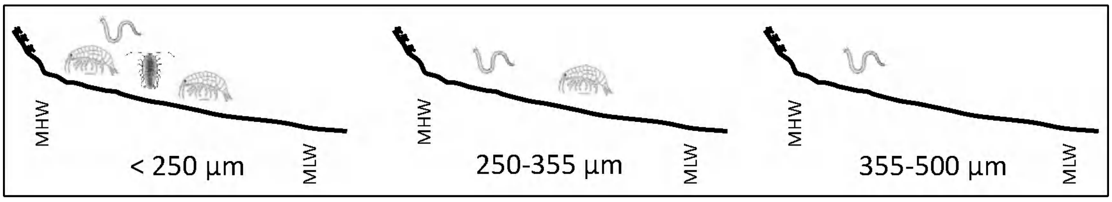

Figure 2: hypothetical high-intertidal macrobenthos community after beach nourishment using three sediment types. MHW: Mean High Water level; MLW: Mean Low Water level.

The results of this experimental study on sediment preferences of the most dominant species of dissipative sandy beaches do not immediately imply field mortality or a decrease in field recruitment when the habitat is altered due to nourishments. However, observations and monitoring after nourishments are showing that when the habitat of sandy beaches is altered towards less favourable conditions, some species do not recolonise the nourished beach or only recolonise the beach in lower abundances after several months (Schlacher et al., 2012). As the intertidal sandy beach environment is a dynamic habitat and sandy beach animals are very mobile, they are likely to avoid those habitats that do not satisfy their preferences.

While other factors like beach profile, inundation time and organic matter are also important in determining the outcome of nourishments, repeated beach nourishments with coarse sediments will inevitably lead to habitat loss for macrobenthos on dissipative beaches, especially for those species preferring fine sediments like *B. pilosa*. As a result, the macrobenthos diversity and abundance will decrease and beaches will in essence be inhabited by extremely opportunistic species like the polychaete *S. squamata* (figure 2) as was also found after dredging events (Rosa and Bemvenuti, 2006). This polychaete will probably suffer least from nourishment events as it can quickly recolonise nourished beaches due to its pelagic larvae (being present in the population from spring to autumn

(Speybroeck et al., 2007)), and will not suffer from the presence of coarse sediment. In addition, when nourishment projects are characterized by coarse sediment and steep slopes, there is a risk of not only decreasing biodiversity but also of causing entire community shifts. Indeed, macrobenthos communities in flat, fine-grained dissipative beaches differ greatly from communities in coarse-grained, steeper reflective beaches (McLachlan, 1990; Defeo et al., 1992; Defeo and McLachlan, 2011) and the alteration of the morphodynamics of a beach may thus lead to community shifts. For the West European dissipative beaches this evolution would cause an important loss of biomass and biodiversity since dissipative beaches are known to be richer than reflective ones (McLachlan et al., 1996).

4.3 Sediment preferences and species interactions on sandy beaches

Examining biotic interactions by sediment selection experiments is an indirect approach (Dugan et al., 2004), but previous research has shown its merit (Defeo et al., 1997). Hence, the results of this sediment selection experiment can give insights in the role of biotic interactions on dissipative sandy beaches.

Bathyporeia pilosa significantly changed its sediment preference towards the coarser sediments, where densities of the related amphipod *B. sarsi* were lower in combined-species conditions. These changes seemed to be steered by interspecific competition with *B. sarsi*. Adversely however, *B. sarsi* did not seem to actively avoid *B. pilosa* and was thus probably not affected by competition of *B. pilosa*. Since former experiments on competition between the co-occurring amphipods *B. pilosa* and *B. sarsi* were not decisive on the role of interspecific competition (Van Tomme et al., 2012), this sediment selection experiment could gain a better insight into their segregated zonation pattern on the intertidal beach (Speybroeck et al., 2008b). Interspecific competition usually has asymmetric effects (Connell, 1983; Schoener, 1983), especially in the marine intertidal zone, with larger species being competitively dominant (Paine, 1980; Schoener, 1983; Brown and Maurer, 1986; van Riel et al., 2007). In this study, the competitive superiority of the largest amphipod, *B. sarsi* (Speybroeck et al., 2008b), was indicated, suggesting that asymmetric interspecific competition can play a structuring role on dissipative sandy beaches.

Predation by the predator *E. pulchra* could also be hypothesized to be an important factor in influencing species distribution on sandy beaches. In combined-species treatments where the predator *E. pulchra* was present, a clear avoiding behaviour could be inferred from the data since the amphipods and especially *B. pilosa* moved to sediments with the lowest density of *E. pulchra*.

Finally, it was clear that the amphipod *B. pilosa* was suffering most from biotic interactions and this could explain its small realized niche on the high-intertidal sandy beach. Although the morphology of the co-occurring *B. sarsi* is not highly different at first sight, competition and predation did not seem to have a clear effect on the behaviour of this larger amphipod (Speybroeck et al., 2008b), as could be reflected in its occupancy of a wider zone on the beach compared to *B. pilosa* (Speybroeck et al., 2008b).

5. Conclusions

The results of this sediment selection experiment show that while the amphipods *Bathyporeia pilosa* and *B. sarsi* preferred fine to medium-fine sediment, the opportunistic polychaete *Scolelepis squamata* preferred coarse sediment. The isopod *Eurydice pulchra* preferred fine sediment but these results were not in accordance with former field and experimental studies. Additionally, interspecific competition with the syntopically occurring amphipod *B. sarsi* was found to change the sediment selection of the amphipod *B. pilosa* towards the coarser sediments where *B. sarsi* occurred in lower frequencies.

To mitigate the impact of beach nourishments on intertidal sandy beaches and to assure a swift recolonisation of the nourished beach by the original sandy beach community, the use of sediment that resembles the initial beach sediment, is therefore strongly encouraged (see also Janssen et al., 2011). The use of coarse sediments is likely to have a negative effect on some of the dominant macrobenthic species of the high-intertidal on fine-grained beaches. Therefore, both technical as well as ecological aspects of the sandy beach ecosystem should be considered in beach nourishment programmes to assure its highly valuable ecosystem role.

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Chapter 6: Assessing the impact of beach nourishment on the intertidal food web through the development of a mechanistic-envelope model

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Abstract

Beach nourishment is currently widely applied as a coastal protection measure because of its reduced ecological impact relative to hard coastal protection. In order to inform managers of the expected ecological impact on the sandy beach ecosystem, we developed a simulation model that integrates species envelope-based projections of the expected microphytobenthos and macrobenthos composition and mechanistic feedbacks on higher trophic levels. Species envelopes are estimated by using Bayesian inference of species' biomass relationships according to the three main determining abiotic variables, i.e. median grain size, total organic matter and the intertidal position. Data were obtained from multiple sampling campaigns along the Belgian coast. Abundances of higher trophic levels, being birds and flatfish, are estimated based on their functional and energetic relationships with macrobenthos as an important food item. We subsequently demonstrate the applicability of the model by assessing the ecological impact of different nourishment scenarios on a typical Belgian sandy beach with respect to beach profile and beach sediment grain size. Scenario testing indicates that the used nourishment sediment grain size is the dominant factor in determining the effect on the ecosystem, with deterioration of the beach ecosystem after nourishment with too coarse sediment (e.g. >> than 300 µm). Therefore the gradient in sediment grain sizes that is advised for nourishment of fine-grained beaches is defined as 200-300 µm. Although the effect of nourishment slope was less strong compared to the sediment, nourishment slope did also affect species zonation patterns. For a constant sediment, high-shore nourishment was found to positively influence the densities of high-shore species such as *Bathyporeia pilosa* compared to profile nourishment. Our simulations make clear that the assessment of ecosystem health after nourishment needs to include the evaluation of different diversity and biomass variables since focusing on for instance potential abundance of species from higher trophic levels might lead to deceptive conclusions due to the dominance of opportunistic prey species.

Key words: beach nourishment, species envelope modelling, macrobenthos, fish, birds

1. Introduction

Coastal ecosystems are strongly threatened by climate change due to expected changes in sea level rise, erosion, changes in storm and wave regimes, flooding, altered sediment budgets and the loss of coastal habitat (Harley et al., 2006; Jones et al., 2007). In the last hundred years global average sea level has risen by 0.1–0.2 m (Houghton et al., 2001). In the past, the adaptive management response for the soft-sediment ecosystems such as sandy beaches has been the enhancement of existing sea defences and retreat in areas of low-value land. Furthermore, coastal erosion has become an important issue on sandy beaches over the last decades as globally 70% of beaches are receding, while 20–30% remain stable and 10% or less are accreting (Bird, 2000).

Sandy beaches are the single largest coastal ecosystem on earth and they are covering 70% of all continental margins (McLachlan and 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 prime recreational assets. More people interact directly with beaches than with any other type of shoreline worldwide (Schlacher et al., 2008). Sandy beaches also play an important role in coastal defence by functioning as a natural buffer between sea and land (Brampton, 1992; Riddell and Young, 1992), thus protecting landward sea defences from scour and wave erosion (Brampton, 1992; Riddell and Young, 1992).

In the past, the construction of hard structures as a management strategy for coastal defence enhanced beach erosion and destroyed important ecosystem functions (Defeo et al., 2009). Current widely applied defence approaches use beach nourishment to counteract coastal erosion and protect the land 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. Up till now, technical aspects (e.g. easily available sand with coarse grain size and a rather steep and thus more stable beach slope (Finkl and Walker, 2002)) were dominant in taking management decisions for beach nourishment projects. In the light of international and European legislation, urging towards Integrated Coastal Zone Management (ICZM), attention for the functionality of the sandy beach ecosystem has increased (Schlacher et al., 2008). Although beach nourishment is generally considered as the less harmful beach management option (Hamm et al., 2002; Hanson et al., 2002), it does put a severe pressure on the biota living on, in and around sandy beaches (Speybroeck et al., 2006a). However, peer-reviewed impact studies are scarce (Jones et al., 2008; Leewis et al., 2012; Schlacher et al., 2012) and especially adequate information to predict the impact of nourishment on the beach ecosystem and to ecologically adjust nourishment projects, is lacking.

Optimizing technical aspects (e.g. characteristics of the sediment used, slope of the nourished beach, nourishment timing) of the nourishment projects is indispensable to maintain an ecologically healthy ecosystem on the beach. Indeed, the ecological characteristics of the beach fauna and flora are very much determined by morphodynamic beach characteristics such as grain size and beach slope (McLachlan and Jaramillo, 1995; McLachlan et al., 1996; Defeo and McLachlan, 2005). As management of beaches is a multi-faceted and complex endeavour, where the interests of several stakeholders need to be combined, coastal managers need to interact with ecologists to integrate ecological aspects in beach management. Hence, clear and user-friendly management tools are essential in taking interdisciplinary management decisions (Schlacher et al., 2008).

As a good knowledge on the morphodynamics of Belgian sandy beaches is present (Degraer et al., 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 biodiversity at different trophic levels. The model builds further on well-established insights that the realised niche of lower trophic levels can be predicted based on three beach parameters, i.e. slope, grain size and organic matter, that are correlated under equilibrium conditions (Degraer et al., 2003; Speybroeck et al., 2006b). For the Belgian beaches, the following ecosystem components are well described, taking into account the relationship with the abiotic environment: microphytobenthos and macrobenthos. The importance of macrobenthos as food for birds and fish is also illustrated and quantified (Beyst et al., 1999; Vanermen et al., 2009) and here mechanistically modelled by applying energy-based trophic interaction rules.

The general objective of this study was to develop a nourishment simulation model for the Belgian beach ecosystem. The simulation model had the aim (1) to predict short-term changes in beach microphytobenthos and macrobenthos biodiversity in response to changes in beach profile and grain size following beach nourishment and (2) to elucidate how these changes in community composition feedback on the abundance of dominant species of higher trophic levels (birds, fish and shrimp).

2. Material & methods

2.1 Model description

For the model description, the “Overview, Design concepts and Details” protocol (ODD) (Grimm et al., 2010) was followed.

2.2 Species envelopes

A species envelope is defined as the set of environmental conditions at locations where a species is known to occur, thereby assuming that on other locations with similar conditions, the species will also be present. This approach has been hugely successful in both applied and theoretical ecology (Guisan and Zimmermann, 2000). Earlier research elucidated either linear or quadratic relationships among the abundance or biomass of the main macrobenthos species and microphytobenthos with abiotic parameters (Beyst et al., 2002; Degraer et al., 2003; Speybroeck et al., 2004). Species envelopes for these taxa were derived from data collected on 23 intensively sampled beaches along the Belgian coast, during different seasons within the period 1997-2011 (Degraer et al., 2003; Speybroeck et al., 2004; Speybroeck et al., 2005b; Welvaert, 2005; Van Ginderdeuren et al., 2007; Vanden Eede and Vincx, 2010, 2011) (see also appendix B1).

2.3 Entities, state variables, and scales

Model entities

The model consists of three major modules, one determining the abiotic conditions of the beach, a second module modelling predicted (changes in) densities and biomass of microphytobenthos and macrobenthos according to their envelopes and a third one predicting the maximum abundance of the most important species from higher trophic levels. Chlorophyll a levels were used to represent microphytobenthos biomass, while for the macrobenthos, the density and biomass of the eleven most dominant species were taken into account. These dominant species comprised the polychaetes *Nephtys cirrosa* and *N. hombergii*, *Capitella capitata*, *Spio filicornis*, *Pygospio elegans*, *Eteone longa* & *Scolelepis squamata*, the amphipods *Bathyporeia pilosa* and *B. sarsi* and the isopods *Eurydice pulchra & E. affinis.* The most important species from higher trophic levels included the gulls *Larus canus* & *L. ridibundus*, the waders *Calidris alba* & *C. alpina*, the shrimp *Crangon crangon* and juvenile flatfish (mainly *Pleuronectes platessa*).

State variables

Three state variables determine the abundances and densities of microphytobenthos and macrobenthos along sandy beaches: median grain size (*MGS*), total organic matter (*TOM*) and position (h) relative to the lowest tide, being 0 m TAW, i.e. the vertical level of reference in Belgium (McLachlan and Jaramillo, 1995; Degraer et al., 2003; Veloso et al., 2003). The slope of the beach (α) determines the submergence area and availability of prey for higher trophic levels (see figure 1). The available biomass of species belonging to the lower trophic levels are input variables for estimating abundance of species from higher trophic levels and species richness (*S*).

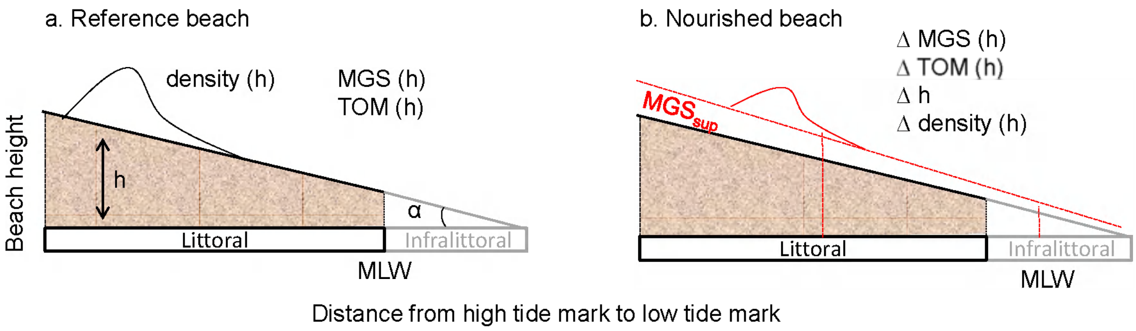

Figure 1: schematic overview of the principal state variables. MLW: Mean Low Water level.

Scales

The model predicts the biomass of microphytobenthos (chlorophyll a), biomass, densities and species richness of the macrobenthos and maximum carrying capacity for foraging predators at the scale of 1m^2, according to the local conditions of the beach state variables. These estimates are interpreted along the intertidal transect and, when summed, at the beach level.

2.4 Process overview and scheduling

According to the input data on the beach profile after beach nourishment (changes in height according to the distance from the low water mark and grain size of the nourished sand), the model first estimates the local *TOM.* Based on the beach state variables and input data on microphytobenthos and macrobenthos niche properties, local densities (number of individuals.m^{-2}) of macrobenthos are estimated and subsequently converted to biomass (g AFDW.m^{-2}) (appendix B1). Total availability of chlorophyll a (mg.m^{-2}) is estimated without conversion. More detailed information on the source of the input data and sampling strategies can be found in appendix B1.

This basic envelope modelling is used for both the reference situation, with *MGS* estimated according to *h* since earlier work has demonstrated the prevalence of such grain sorting mechanisms (Short, 1991) and for nourished beaches with a predefined *MGS.* These envelope models are subsequently projected on the supplemented beach profile (changes in *h*, *α* and *MGS*), with *TOM* inferred from its previously derived relationship with *MGS.* In a second phase, estimated macrobenthos biomass is integrated into functions to determine the maximum local abundance of higher trophic levels, according to available biomass of prey species and availability according to tidal frequency. The model is stochastic with parameters for species envelopes and beach characteristics estimated from prior statistical distributions. For each beach condition, 10000 simulations are performed to estimate mean values and variance of species and predation pressure from higher trophic levels.

The model has been successfully evaluated and validated by three data sets from two beaches (of which data were not used to create the envelope model) for the dominant macrobenthos species, that were sampled in an identical way as described in Degraer *et al.* (2003). Densities of the dominant species, total ash free dry weight (AFDW) and species richness from the samples were subsequently compared with simulated data (average values and 95% confidence intervals for 10 000 simulations) according to the sample location *h* and grain size *MGS* (see appendix B1).

2.5 Design concept

Basic principles

The model integrates envelope modelling approaches to estimate density and biomass of lower trophic levels into mechanistic modules to quantify maximum available biomass for higher trophic levels. The model allows a biotic evaluation of local beach nourishment impact on biodiversity by comparison of pre- and post-nourishment states. As currently, recolonisation processes are not well-known, no lag effects are incorporated in the model. Nevertheless, further examination of these processes based on a scientifically-based monitoring is of the utmost importance and can in the future extend and improve the predictions of the model. The predicted state of the beach subsequently assumes equilibrium in species dynamics according to the envelope.

Interactions

Sand grains are sorted according to their position and height on the beach (Short, 1991) with coarse grains deposited at higher locations. Total organic matter is positively correlated with the median grain size (correlation coefficient: $(0.13)^{1/2}$). Beach nourishment alters the height and the profile of the beach and it initially induces an unsorted, often coarser, sand grain distribution. 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 items in this model are derived from non-disturbed beaches, so niche properties are assumed to reflect realized niche dimensions.

2.6 Submodel structure

Microphytobenthos and macrobenthos envelopes

We estimated niche dimensions for eleven dominant macrobenthos species (appendix B2) in relation to three abiotic input variables. Total biomass of chlorophyll *a* was only modelled in function of *h* and *MGS* in order to avoid circular reasoning (microphytobenthos is part of TOM). As earlier work clearly indicated Gaussian niche dimensions, niche 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 et al., 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 Poisson error structure was found to generate the best convergence for all species, and was thus chosen because of its intrinsic simplicity relative to zero inflated Poisson and Negative Binomial regressions.

We subsequently expected the abundance of species y in sample i to follow a Poisson distribution $y_{(i)} \sim$ dpois $(\theta_{(i)})$ with expected abundance in sample i $\theta_{(i)} = e^{\eta}{}_{(i)}$.

η(i) is a mixed function with overall intercept β_0 and both linearly and quadratically dependent on the abiotic variables *MGS, TOM and h.* All variables were Z-transformed to guarantee standardized effect weights. We additionally incorporated variance estimates related to dependency within samples due to spatio-temporal homogeneity (*u)* and the overall residual variation (*v)* to account for possible over- or underdispersion among samples from transects (eq. 1). As such we modelled average densities across seasons among different beaches.

The full model formulation is:

$$\eta(i) = \beta_0 + \beta_1 \times \frac{MGS(i) - \overline{MGS}}{stdev(MGS)} + \beta_2 \times \left(\frac{MGS(i) - \overline{MGS}}{stdev(MGS)} \right)^2 + \beta_3 \times \frac{h(i) - \bar{h}}{stdev(h)} + \beta_4 \times \left(\frac{h(i) - \bar{h}}{stdev(h)} \right)^2$$

$$+ \beta_5 \times \frac{OM(i) - \overline{OM}}{stdev(OM)} + \beta_6 \times \left(\frac{OM(i) - \overline{OM}}{stdev(OM)} \right)^2 + u(beach(i)) + v(i) \qquad \text{(eq.1)}$$

Because we had no *a priori* information, flat priors for regression coefficients were drawn from a normal distribution with a mean of 0 and a standard deviation SD of 10^6. Priors for variance components were drawn from a positively constrained uniform distribution with a mean of 1 and SD 5. Three chains were modelled for each model. To assure accurate MCMC simulations from the prior distributions, an initial "burn in" of 10 000 iterations was performed and discarded from analysis. This was followed by 20 000 iterations for both analyses. After visual inspections for possible autocorrelation and assessing chain convergence Brooks-Gelman-Rubin diagnostics (Brooks and Gelman, 1998), the mean and SD of each posterior parameter, estimate regression coefficients and variance estimates were calculated, as well the 2.5th and 97.5th percentiles of the samples. These were used to describe the 95% Bayesian credibility interval of the posterior distributions of model parameters. An overview of all the estimated regression coefficients can be found in appendix B2.

Microphytobenthos and macrobenthos biomass

The obtained regression coefficients (appendix B2) are used to estimate species abundances according to implemented beach characteristics in the main simulation model. Parameters were sampled from the obtained regression distributions kernels N(,SD) but constrained within the 95% credibility interval. The eventual abundance estimates are subsequently transformed towards biomass (gram ash-free dry weight – g AFDW) by earlier determined conversion factors (Vanden Eede et al. unpub. data; Speybroeck et al. 2006a; see appendix B3).

Modelling trophic relationships

Macrobenthos – epibenthos

Previous work has demonstrated the importance of intertidal habitat for residing epibenthos foraging on macrobenthos (Kuipers and Dapper, 1984; del Norte-Campos and Temming, 1994; Beyst et al., 1999; Koot, 2009). Along Belgian beaches, epibenthos is dominated by *Crangon crangon* (95%), while the other 5% constitutes of juvenile flatfish, mainly *Pleuronectes platessa* (Beyst et al., 2001). We experimentally quantified the maximum proportion of prey consumed by either *C. crangon* or juvenile flatfish (chapter 4). These values are used to estimate the maximum local predation pressure by epibenthos based on the available macrobenthos abundance. Because predation pressure is additionally time constrained, and only possible under submergence, the total available biomass at a certain position along the beach *(h)* for higher trophic levels is described by the following function:

$$\text{Biomass}_{\text{available}}\,(h) = {}_{x\text{->}i}\sum \left[\text{biomass}(h)*(1-h/h_{max})*\text{Predation pressure}_x\right] \qquad \text{(eq.2)}$$

with x = preyed species from the macrobenthos,

h_{max} *the height of the beach at high tide* and [biomass] = g AFDW m^{-2}

The caloric value of macrobenthos equals 23 kJ/gAFDW (Beukema, 1997), so the available energy for higher tropic levels is

$E_{available}(h) = biomass_{available}(h) * 23$ with [energy] = kJ (eq.3)

From this available source of energy, the maximum number of *C. crangon* (constituting 95% of the epibenthos), able to feed on this biomass at height *h* is based on their daily energetic needs ($NEI_{crangon}$), being 16% of their total body mass (del Norte-Campos and 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 4.768cal/mg AFDW ≈ 20kJ/gAFDW (Szaniawska, 1983; Zwarts et al., 1996), $NEI_{crangon}$ = 0.056kJ; the maximum abundance of *C. crangon* at location *h* can be calculated as follows:

$Crangon_{max}(h) = (E_{available}(h)*0.95)/NEI_{crangon}$ (eq. 4)

Similarly, the *NEI* for juvenile flatfish is estimated to be 10% of the body mass (Lockwood, 1984), so the maximal abundance of flatfish at location *h* can be calculated as follows:

$Flatfish_{max}(h) = (E_{available}(h)*0.05)/NEI_{flatfish}$ (eq. 5)

with $NEI_{flatfish}$=0.188kJ

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

Waders

Two wader species, *Calidris alba* and *C. alpina*, feed predominantly on macrobenthos along Belgian beaches. Although both species show some differences in foraging behaviour, they both feed on the same prey and therefore we treat them as being one functional group. Both species were found to forage about 25% of their total residential time on all macrobenthos species (Speybroeck et al., 2006b; Vanermen et al., 2009). According to Vanermen et al. (2009), waders along soft sanded beaches only forage from two hours before till four hours after low tide. This implicates that foraging is not possible at the high littoral (upper quartile of the beach). At the low littoral, foraging is possible twice a day for six hours, resulting in a daily foraging time of 12 hours in the low littoral and thus a foraging time of 0.50 (eq. 6).

This leads to maximal foraging time at a certain height (*h*) as follows:

$Foraging\ Time(h) = -0.25+0.75*h_{rel}$ (eq.6) with h_{rel} the relative proximity to the low water level (being 1 when at 0 TAW, 0 at high water) and Foraging Time (h)=0 when eq.6 yields values <0.

The availability of prey is additionally dependent on the slope of the beach 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 maximal on flat beaches and minimal when beach slopes exceed 21° (a zone of less than 1 m available at the water line). Taking into account continuous changes in biomass availability (foraging time) for the central and lower littoral, a caloric value of macrobenthos of 23kJ/gAFDW and a daily energy uptake for small waders (NEI_{waders}) of on average 224kJ/dag (Kersten and Piersma, 1987; Castro et al., 1989; Speybroeck et al., 2006a), potential wader pressure can be calculated as follows:

$$\text{Wader pressure } (h) = \text{foraging time}^* \text{ biomass } (h)^*(1-\alpha/21°)^*23/NEI_{\mathrm{waders}} \qquad \text{(eq. 7)}$$

Small-sized gulls

Larus canus and *L. ridibundus* are the principle gull foragers on beaches. They feed on Polychaeta and *C. crangon* (Speybroeck et al., 2006a). Prey availability within the littoral food web is maximal at low tide and concentrated in beach pools. Because the lack of any insights into this pool formation and temporal patterns in gull foraging behaviour, we assume Polychaeta and *Crangon* biomass to be available after submergence.

$$\text{Biomass}_{\text{avialable}}\ (h) = \quad \text{biomass}_{\text{polychaeta}} + \text{biomass}_{\text{crangon}}$$

$$= \ _{x\text{->}i}\textstyle\sum \text{ biomass}_x\ (h)^*(h/h_{max})$$

with x = species Polychaeta and *C. Crangon* (eq.8)

Given caloric (cal) values for Polychaeta and *C. crangon* of respectively 23kJ/g AFDW and 20kJ/g AFDW, and the average daily energy need of small *Larus* species ($NEI_{\mathrm{gulls})}$ of 607 kj (Ysebaert and Meire, 1989), the potential maximal number of foraging gulls is:

Gulls (h)= $_{x\text{->}i}\sum ((\text{Biomass}_{\text{available}})_x * \text{cal}_x)/ NEI_{\mathrm{gulls}}$, with x respectively polychaeta and *C. crangon*

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.

2.7 Model application & research strategy

Four typical Belgian beaches that represent the prevalent variation in beach morphodynamics are shown in figure 2: De Panne, Lombardsijde, Mariakerke and Knokke-Zoute. Lombardsijde is a wide, gentle beach with minimal human impact (% TOM: 0.43 %; average median grain size: 252 µm); Mariakerke is a somewhat shorter and steeper touristic beach (% TOM: 0.62 %; average median grain size: 344 µm); the beach of De Panne is an ultra-dissipative beach on the western Belgian coast (% TOM: 0.61 %; average median grain size: 198 µm) and Knokke-Zoute is a low-tide bar/rip beach on the eastern Belgian coast (% TOM: 0.73 %; average median grain size: 325 µm) (figure 2).

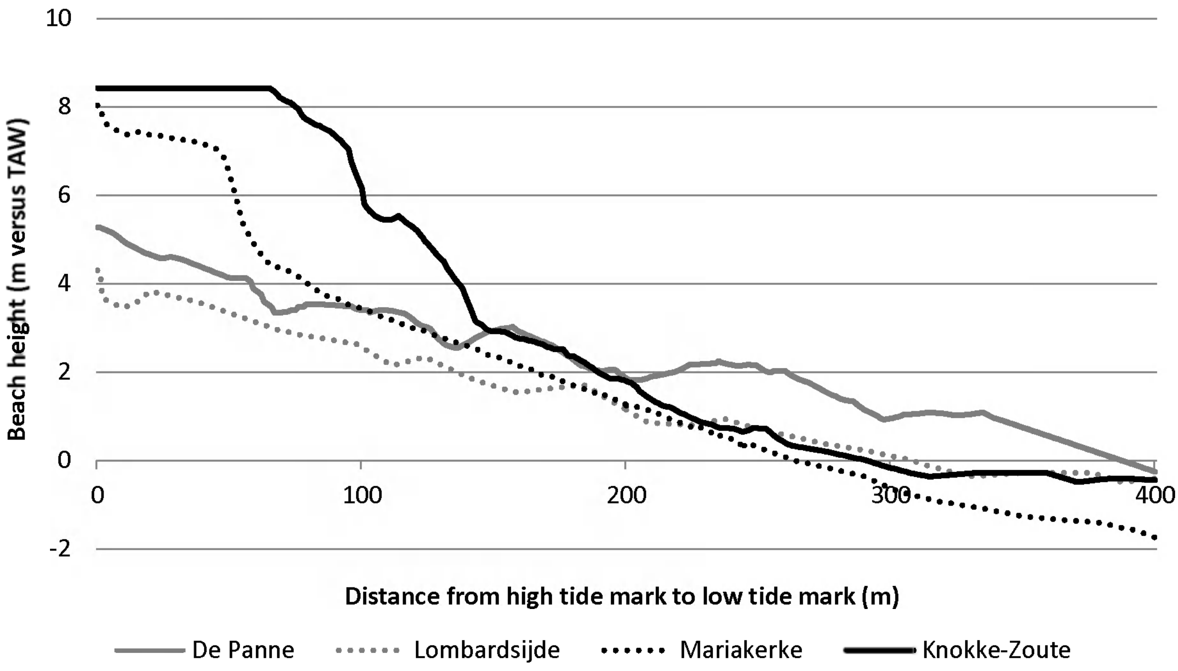

Figure 2: natural intertidal beach profiles of De Panne, Lombardsijde, Mariakerke and Knokke-Zoute). X-axis: distance from high tide mark to low tide mark (m); Y-axis: beach height (m versus TAW)

To illustrate the model functioning and to examine the effect of beach nourishment, we hereafter tested different scenario's on the beach profiles of figure 2. In the results, these scenario's will only be illustrated for the beach of Lombardsijde as obtained trends were similar for all tested beach profiles. Initially, the effect of different nourishment profiles and slopes was simulated for the lower and higher trophic levels on the beach. Subsequently, the effect of varying sediment grain sizes used for nourishment was tested.

3. Results

3.1 Influence of altered beach profile and nourishment slope

Due to beach nourishment with natural sediment (grain size ranging from 139 to 285 µm (Vanden Eede and Vincx, 2011)), the beach profile was altered (figure 3). As a result, the modeled zonation patterns of the macrobenthos shifted towards the low tide mark (as an example, the situation of *B. sarsi* is shown in figure 4) since the intertidal beach itself was shifted further from the dune foot towards the low water mark in absolute distance. Another important consequence of beach nourishment, coinciding with the steeper beach slope as a result of beach nourishment, is the loss of intertidal beach area and consequently the decrease in total biomass on the beach. This decrease is larger as the nourishment slope becomes steeper (figure 5).

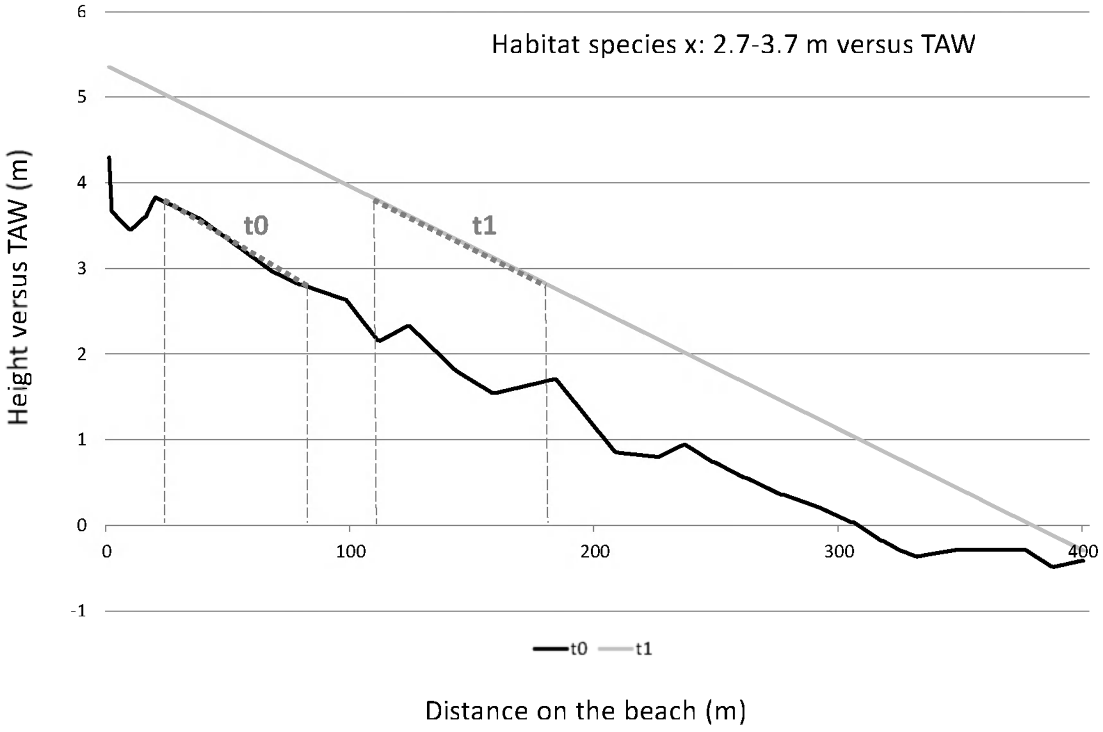

Figure 3: exemplary shift of habitat on the beach due to nourishment. t0: natural beach profile; t1: suppletion profile. X-axis: cross-shore beach distance from a fixed point above high tide mark (left) towards low tide mark (right). Y-axis: relative beach elevation (m versus TAW), calculated by the M2-reduction model (Coastal Division of the Agency of Maritime and Coastal Services).

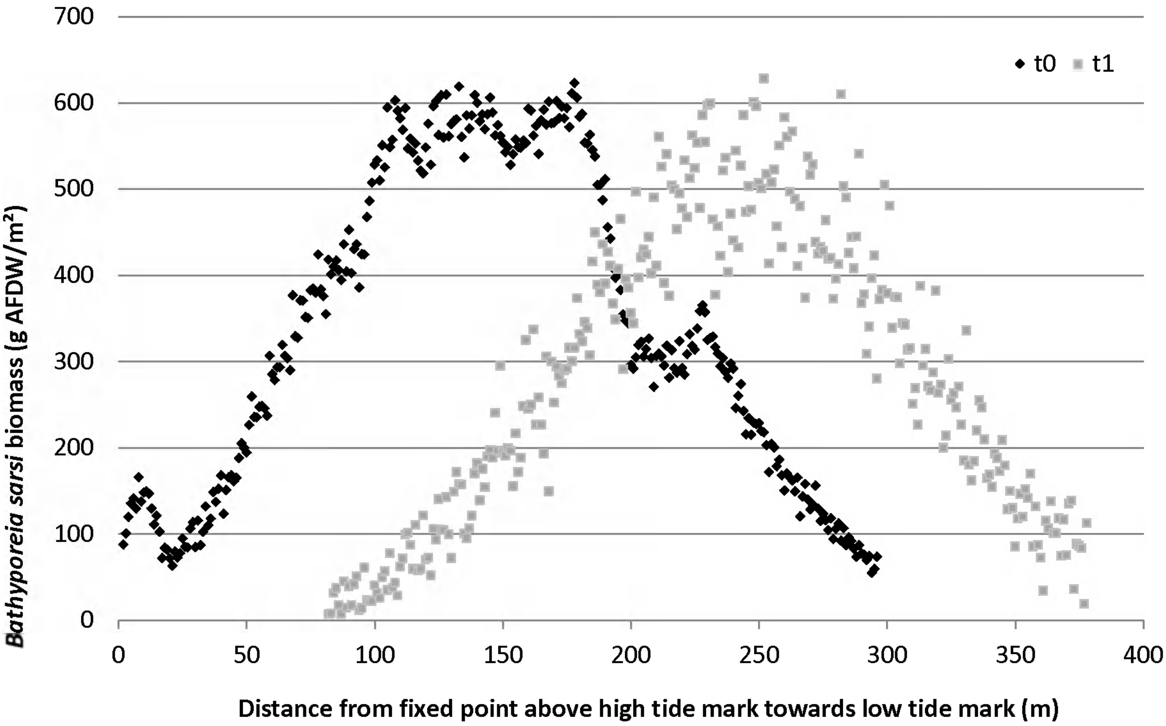

Figure 4: simulated zonation pattern of *B. sarsi* on Lombardsijde beach before (t0) and after nourishment using sediment with median grain size of 200 µm (t1). X-axis: distance from fixed point above high tide mark towards low tide mark (m); Y-axis: *B. sarsi* biomass (g AFDW.m^{-2})

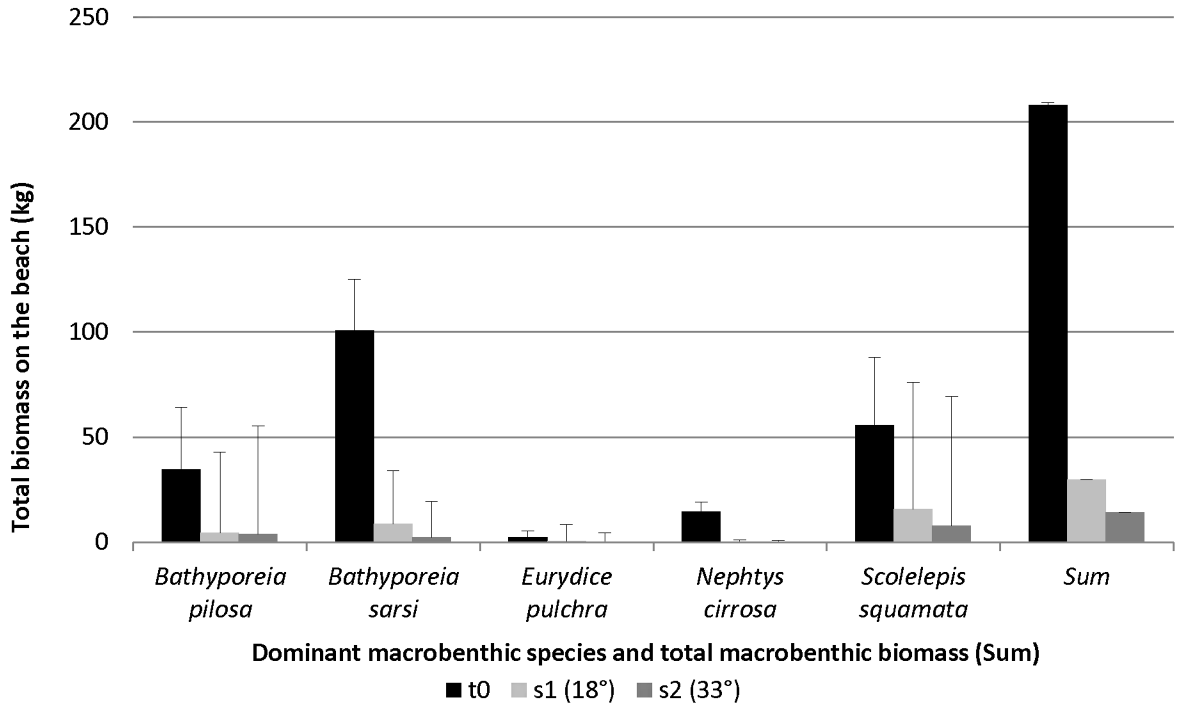

Figure 5: simulated total species biomass on a typical beach (Lombardsijde) in pre-nourishment conditions (t0) and after nourishment with a beach slope of 18° (s1) & 33° (s2). X-axis: dominant macrobenthic species and total macrobenthic biomass (Sum); Y-axis: total biomass on the beach (kg). mean ± SE (based on 1000 simulations)

Different nourishment slope types on a single beach were compared (figure 6): a first continuous slope typical for profile nourishment (s1), a second slope typical for high-shore nourishment (s2) and a third one typical for low-shore nourishment (s3). *Bathyporeia pilosa* shows higher densities after high-shore nourishment with sediment of 200-300 µm than after profile nourishment using the same sediment (figure 7). For the related *B. sarsi*, profile nourishment resulted in the highest densities when comparing different nourishment slopes and fixed sediment of 300 µm.

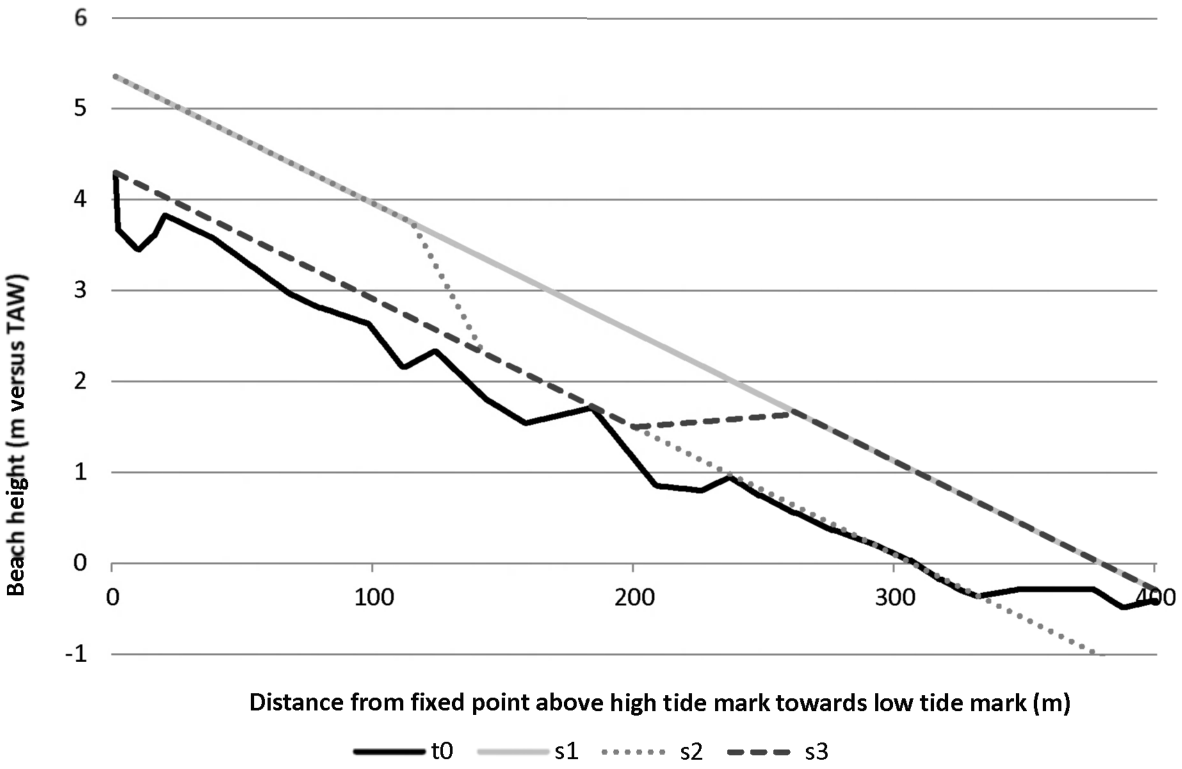

Figure 6: different nourishment slopes tested on a typical Belgian beach: t0: before nourishment, s1: profile nourishment; s2: high-shore nourishment & s3: low-shore nourishment. X-axis: distance from fixed point above high tide mark towards low tide mark (m); Y-axis: beach height (m versus TAW)

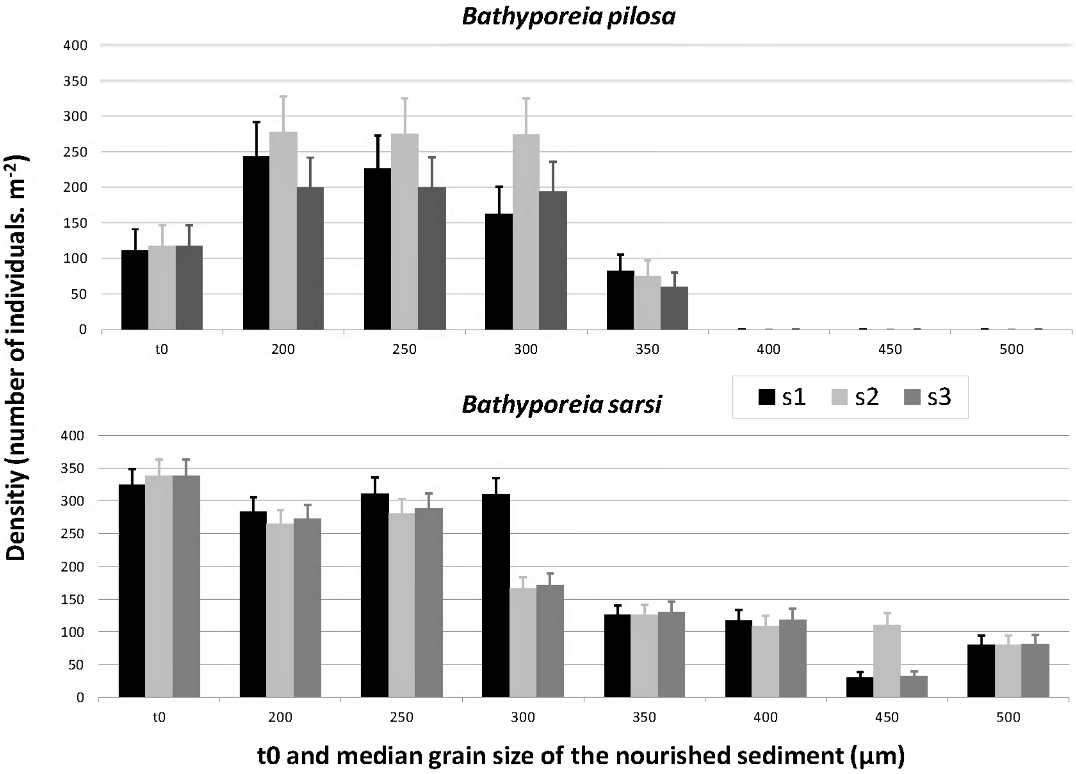

Figure 7: simulated *B. pilosa* and *B. sarsi* densities on Lombardsijde beach: t0: before nourishment; s1: profile nourishment; s2: high-shore nourishment; s3: low-shore nourishment. X-axis: t0 and median grain sizes of the nourished sediment (µm); Y-axis: species density (number of individuals.m^{-2}); mean ± SE (based on 1000 simulations)

3.2 Influence of the used sediment (grain size)

After nourishment, average microphytobenthos and macrobenthos densities can be higher, lower or equal to the densities before the nourishment and this response differs between species. The average simulated densities of the species after nourishment are similar to pre-nourishment conditions when the grain size of the used sediment resembles natural conditions. However, when nourishment sediment differs in grain size from natural beach sediment, species densities will respond more profoundly to this habitat transformation. The microphytobenthos biomass shows a general negative response towards an increasing sediment grain size after nourishment. The macrobenthos patterns are given in table 1. The amphipod *B. pilosa* and the polychaete *N. cirrosa* show a clear negative biomass trend when beaches are nourished using sediment with a median grain size of 300 µm or coarser (table 1). For the amphipod *B. sarsi*, this negative trend starts from 350 µm onwards (table 1). *Eurydice pulchra* and *S. squamata* are not negatively but positively influenced by nourishments using sediments with a medium grain size of (more than) 300 µm (table 1). However, this coarse sediment is not naturally occurring along the Belgian coastline (Vanden Eede and Vincx, 2011).

Table 1: simulated species biomass (g AFDW.m^{-2}) on Lombardsijde beach for the pre-nourishment (t0) and post-nourishment situation (using different sediment grain sizes); mean ± SE (based on 1000 simulations)

korrel (µm)	*Bathyporeia pilosa*	*Bathyporeia sarsi*	*Eurydice pulchra*	*Nephtys cirrosa*	*Scolelepis squamata*
t0	111,5 ± 29,4	323,8 ± 24,4	7,4 ± 3,2	46,9 ± 4,4	178,9 ± 32,3
200	242,9 ± 48,8	283,0 ± 22,2	3,7 ± 1,3	26,1 ± 3,0	59,5 ± 16,5
250	225,8 ± 46,9	311,2 ± 24,1	12,5 ± 4,3	12,7 ± 1,8	302,8 ± 43,3
300	162,9 ± 38,2	309,4 ± 25,4	19,9 ± 7,9	4,7 ± 0,9	553,4 ± 60,3
350	82,4 ± 23,1	125,4 ± 15,1	17,5 ± 8,7	1,7 ± 0,5	524,7 ± 60,0
400	0,0 ± 0,0	117,0 ± 16,5	41,0 ± 15,1	0,7 ± 0,3	423,6 ± 55,7
450	0,0 ± 0,0	30,9 ± 7,9	47,2 ± 17,4	1,4 ± 0,7	424,3 ± 59,4
500	0,0 ± 0,0	79,8 ± 14,4	32,8 ± 14,2	1,8 ± 0,9	468,3 ± 64,5

Figure 8 shows that after nourishment using sediment with a median grain size from 300 µm onwards, macrobenthos biodiversity on the beach decreases. Nourishment with sediment characterized by a median grain size of 350 µm will cause a decrease in macrobenthos biodiversity by 30 % compared to the t0 situation. There seems to be no apparent biodiversity loss when fine sediment is used (200 and 250 µm) (figure 8).

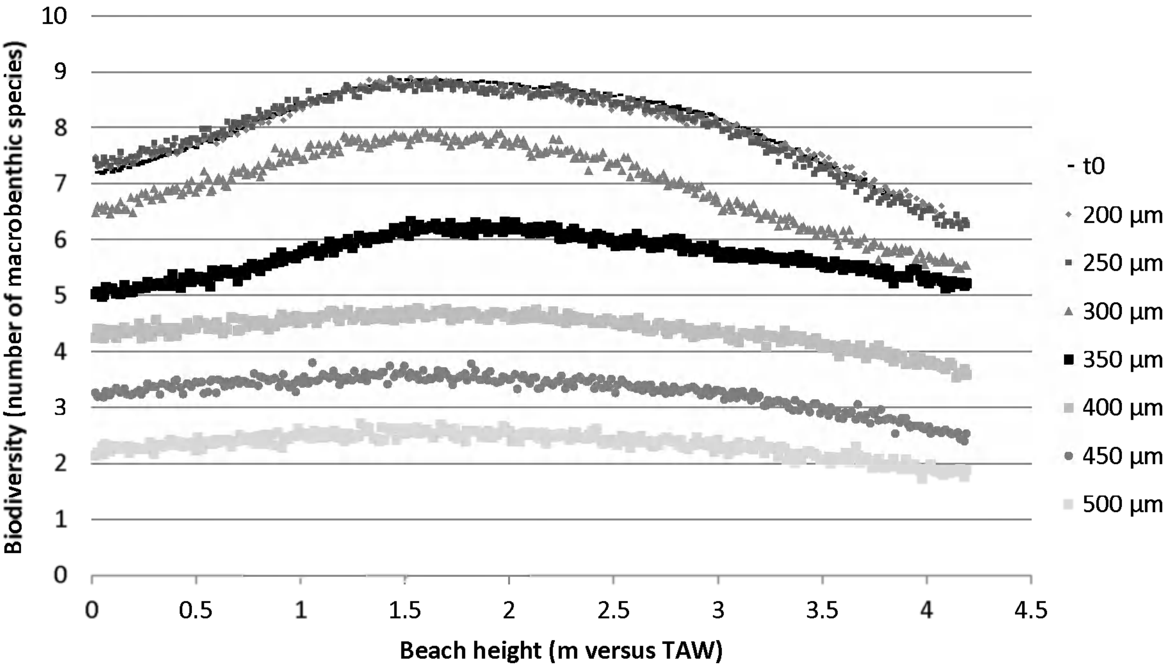

Figure 8: simulated biodiversity on Lombardsijde beach before (t0) and after nourishment with different sediment grain sizes (µm). X-axis: beach height (m versus TAW); Y-axis: mean biodiversity (number of macrobenthic species)

The biodiversity results (figure 8) are contrasted by the biomass results (figure 9). While the maximum macrobenthos biodiversity was found at a median grain size of 200-250 µm, the maximum total macrobenthos biomass was found at 300 µm. The total biomass after nourishment with 350 µm was comparable to the biomass in the t0-situation, but from 350 µm onwards, there was a decrease in total macrobenthic biomass. At 400 µm, total biomass was similar to the situation at 200 µm and from 400 µm onwards, there was again an increase in total macrobenthic biomass towards conditions comparable to the t0-situation (figure 9).

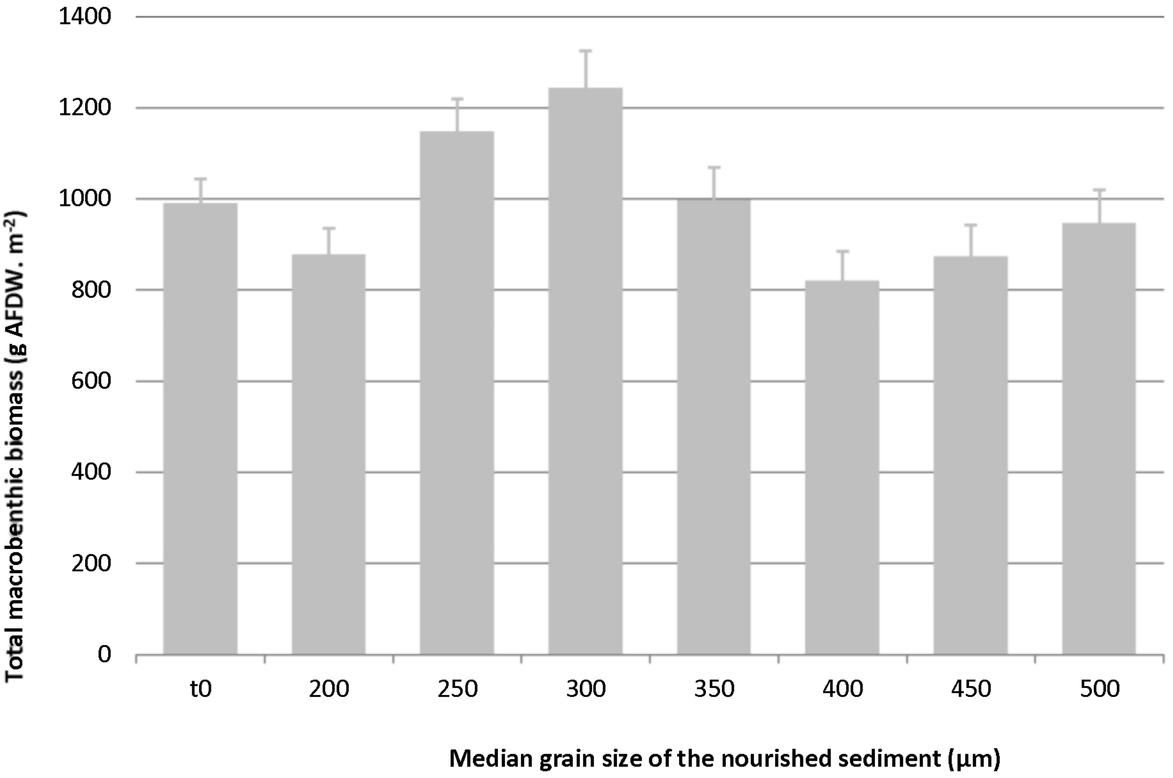

Figure 9: simulated macrobenthic biomass on Lombardsijde beach. X axis: median grain size of the nourished sediment (µm); Y-axis: total macrobenthic biomass (g AFDW.m^{-2}); mean ± SE (based on 1000 simulations)

3.3 Effects of beach nourishment on higher trophic levels

The trends for the higher trophic levels did not differ between nourishment profile types used on a single beach. The effects of beach nourishment on higher trophic levels can be completely linked to the evolution of total macrobenthic biomass after nourishment with different types of sediment (figure 9 & 10). For shrimp, juvenile flatfish and birds, there is a maximum potential predation pressure (number of individuals.m^{-2}) at 300 µm, followed by first a decrease and then again an increase in presence on the beach at increasing coarser grain sizes (figure 10).

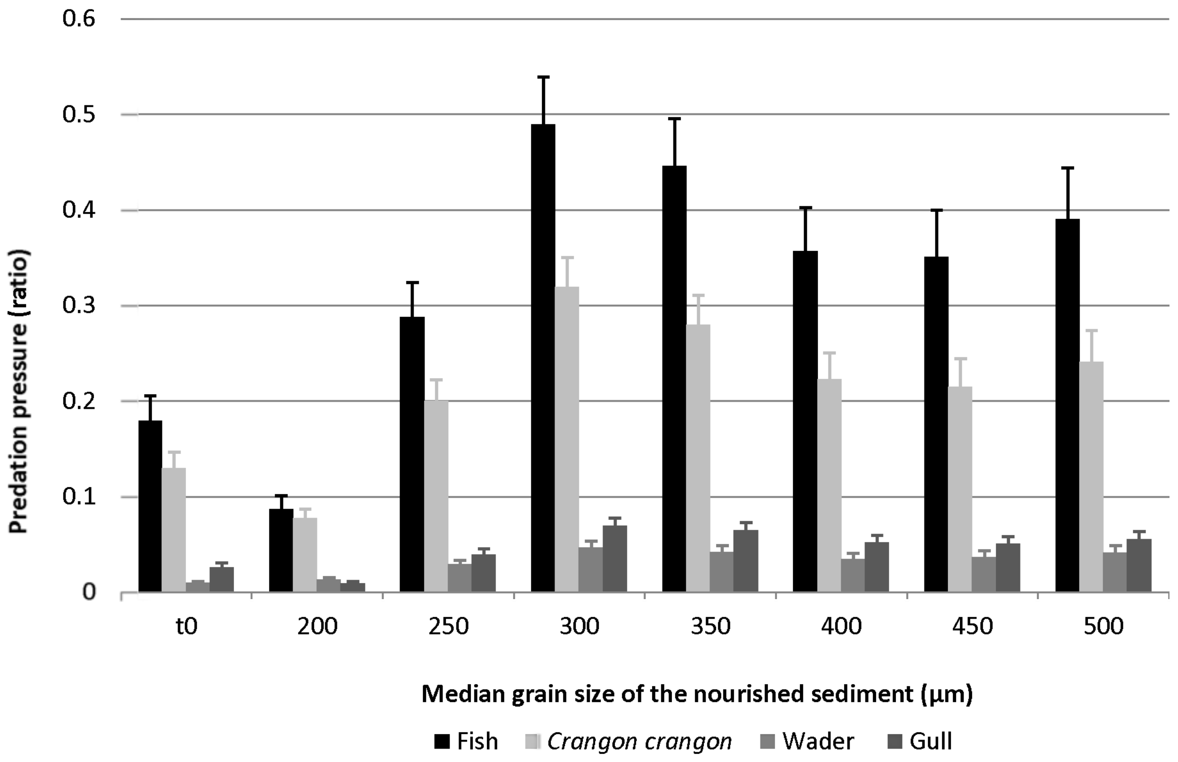

Figure 10: potential predation pressure of higher trophic levels on Lombardsijde beach. X axis: t0 and median grain size of the nourished sediment (µm); Y-axis: potential predation pressure (ind.m^{-2}); mean ± SE (based on 1000 simulations)

4. Discussion

Beach nourishment is known to alter the morphodynamic state of the beach due to the significant changes in beach slope and sediment. In the mechanistic-envelope model developed in this study, the changes in beach morphodynamics and the changes on the ecosystem (comprising the ecosystem components microphytobenthos, macrobenthos and higher trophic species) following beach nourishment are simulated.

4.1 Strengths and weaknesses of the model

Envelope models are widely used in ecological assessment studies. These models assume that species show no dispersal limitations and have constant niches. Moreover, biotic interactions are expected to be incorporated in the models as input data are gathered from field situations where these interactions determine the distribution patterns of species (Araújo and Peterson, 2012). In the nourishment context, envelope models are thus highly usable and have advantages over models predicting processes on a larger spatial scale (such as climate models). The nourishment model, developed in this study, is based on a large set of input data. Furthermore, validation of the model showed that predicted values adequately matched observed values, so distribution is well-balanced.

One of the major innovations in this model is the ecosystem-level approach. Up till now, an ecosystem vision was generally lacking in beach nourishment studies (Speybroeck, 2007). Here, the model integrates all important beach ecosystem components and predicts their evolution after nourishment. Since beach nourishment is nowadays widely applied for coastal protection, this model could be very valuable in making management decisions that minimize the impact on the ecosystem. By simulating the effect of different slopes and sediment grain sizes, ecological nourishment can be developed. An ecological nourishment tries to guarantee both a sustainable beach ecosystem together with solid coastal protection (Speybroeck et al., 2006a). However, ecological nourishment is not the best option on every location, and large-scale and radical nourishments can be necessary to guarantee a sound coastal protection. In these cases, the model can predict the severity of the (necessary) nourishment on the ecosystem parameters and can give a good estimation on the measures necessary for beach compensation.

As a result of nourishment with a steep(er) beach slope, the total intertidal beach area shrinks and consequently, the total species biomass on the beach decreases. Since the beach production is important for the coastal zone due to the nursery function of the intertidal beach (Beyst et al., 1999), this evolution can affect the complete coastal ecosystem. To maintain a healthy coastal ecosystem, the biomass on the beach has to persist at a certain level. Although this threshold value still has to be determined according to European legislation (that urges towards the determination of a good environmental status of the beach (European Commission, 2010)), the nourishment model developed in this study can be highly valuable to determine the minimum intertidal beach area necessary to maintain this threshold biomass value.

The model predicts if the habitat after nourishment is considered suitable for the most dominant members of the sandy beach community, although the predicted species may in practice be absent because of other anthropogenic impacts, such as tourism or natural temporal variability. Indeed, this model predicts the specific ecological potential of a habitat rather than the realized ecological structure, as the model is based on data of natural Belgian beaches (not located near major tourist locations) where human impact is not dominant (Degraer et al., 2003). Hence, the model is an ideal tool to evaluate the potential for nature restoration along the coast.

The model however gives a prediction without taking into account the nourishment period, the nourishment method and the techniques used. After a nourishment event, both the beach slope as well as the characteristics of the beach sediment will evolve towards pre-nourishment conditions (Speybroeck et al., 2006a). Due to the present uncertainties with regard to recolonisation processes, no lag effects are currently incorporated in the model. Although some data show that the macrobenthic life recovers completely within three to five years after nourishment (Gmelig Meyling and De Bruyne, 1994; Slim and Löffler, 2007), these statements are not based on peer-reviewed information or well-developed monitoring. In this context, it is also important to clearly define the term "recovery". Generally, full recovery is defined by long-term biological, ecological and physical processes controlling recolonisation and succession. Although the recolonisation of the beach by all species, present in pre-nourishment conditions, can be considered recovery in a way, full recovery is established if all ecosystem interactions are present and thus the complete ecosystem functioning has recovered. Furthermore, the post-nourishment evolution is depending on several nourishment-specific (e.g. high-shore versus profile nourishment) but also ecosystem-dependent features (erosion-susceptibility of the beach ecosystem, recolonising capabilities of the sandy beach species). A further examination of the temporal and spatial post-nourishment processes, based on a scientifically-based monitoring, is thus essential to extend and refine the predictions of the model for a longer time period. These predictions on the beach evolution after nourishment will also be highly important for the frequency of repeated nourishments and these repeated nourishments will in turn have an effect on the evolution of the beach after nourishment.

As the sandy beach food web is complex and all species interactions are not yet elucidated, the predictive effect of the nourishment impact on higher trophic levels can still be improved and should currently be interpreted with care. One of the main predictions of the model showed a positive effect on both the total macrobenthic biomass as well as on the potential presence of predators after nourishment using coarse sediment. However, it should be kept in mind that the model simulated the potential presence of higher trophic levels solely based on macrobenthos productivity. The increase in total macrobenthic biomass, following nourishment with coarse sediment, can be exclusively attributed to the increase of the opportunistic polychaete *S. squamata.* Furthermore, the predators incorporated in the model were strongly linked to this polychaete as main food item. As a result, the model also showed a high potential for the presence of these predators on the beach. Nevertheless, the latter result needs careful consideration, as firstly, these predators also feed on other sources that were currently not incorporated in the model (such as stranded wrack material (De Meulenaer, 2006)) and secondly, the potential presence of predators are not linked in the current model to abiotic variables such as beach morphodynamics or hydrological conditions. However, morphodynamic beach features and hydrological conditions are known to highly affect the presence of epi- and hyperbenthos on the beach (Beyst et al., 2001). Thirdly, *P. platessa*, being the most abundant juvenile flatfish on Belgian sandy beaches, was used as sole representative of juvenile flatfish, but in reality a variety of different flatfish is present on the beach. Beyst et al. (1999) studied the diet of these flatfish and showed that generally two groups of flatfish could be distinguished: a first, including *P. platessa*, feeding on benthic prey, and a second group, including flatfish as turbot (*Scophthalmus maximus*) and brill (*S. rhombus*), feeding on mobile crustaceans (Beyst et al., 1999). As amphipod biomass was found to be affected the most by beach nourishment, this second flatfish group would probably suffer more from beach nourishment compared to *P. platessa.* Hence, the incorporation of more flatfish species with different diets into the model could give better balanced results for the potential presence of higher trophic species on the beach.

While a decrease in some species abundances or a shift in the zonation pattern after nourishment with coarse sediment was indicated by the results of this study, a complete community shift is possible when environmental conditions, such as sediment grain size and beach slope, are changed dramatically. Currently, however, such shifts cannot be predicted by the model. When the modelled habitat becomes unfavourable for certain species, they will disappear from the model output without the possibility of replacement by (opportunistic) alien species. In the field however, such shifts are probable and it is likely that current species are then replaced by their counterpart species from morphodynamically opposite beaches (such as *Urothoe*, *Haustorius* but also *Eurydice* and *Scolelepis* from reflective beaches characterized by a steep slope and coarse sediment).

Despite the afore-mentioned suggestions to further improve the model, the general predictions that beach nourishment shortens the intertidal beach, thereby negatively affecting the foraging area and thus the overall food supply for higher trophic levels on the beach (Hall, 1998; Peterson et al., 2000b), are highly valuable.

4.2 Assessing ecological impact

Influence of the beach profile and slope

Beach erosion combined with increasing economic and human development along the coast, is resulting in coastal squeeze. To counteract this evolution, beach nourishment is aiming at coastal relaxation. This management measure however has ecological implications for the sandy beach ecosystem. The model simulations indicated a drastic decrease in total macrobenthos biomass on the beach (figure 5) as a result of the steeper nourishment slope leading to a narrower intertidal beach.

On a smaller scale, when different nourishment slope types were taken into account on one specific beach, the nourishment model showed that particular nourishment slopes could favour specific species. This possibility to compare species responses to different slopes makes this model especially useful for management purposes, aiming at protecting species or habitats. Indeed, by positively influencing biomass of macrobenthos, through the use of specific beach slopes enlarging the habitat of dominant prey species (such as high-shore nourishment, positively influencing *B. pilosa* in the high-intertidal), the presence and abundances of higher trophic levels such as birds or fish can also be positively influenced. In this context, the knowledge that intermediate beaches with steeper beach slopes are unfavourable for epi- and hyperbenthos (Beyst et al., 2001), should be taken into account when developing nourishment slopes.

Influence of the used sediment (grain size)

The nourishment sediment is of vital importance to predict the effects of nourishment on the beach ecosystem (Speybroeck et al., 2006a). The dominant role of sediment grain size was supported through the results obtained by testing different beach slopes and sediment grain sizes. Indeed, most of the tested macrobenthic species did not respond to the different slope type but only to the grain size of the sediment used. Coarse sediments, not naturally occurring on Belgian beaches, positively influenced the opportunistic polychaete *S. squamata*, resulting in an increase in total macrobenthic biomass and an increase of the trophically linked birds and fish present on the beach. The polychaete *S. squamata* is an opportunistic and cosmopolitan species both thriving on fine-grained as well as coarse-grained beaches (Dauer, 1983; Hartmann-Schröder, 1996). Hence, this could explain the high biomass of the polychaete after nourishment with coarse sediment. As the knowledge that intermediate beaches with steeper slopes harbour less epi- and hyperbenthos compared to dissipative beaches (Beyst et al., 2001), is currently not incorporated in the model, it remains at this moment unsure if the abundances of higher trophic levels would consequently increase in the field as a response to higher abundances of *S. squamata*.

Opposite to the calculated biomass patterns, the overall biodiversity was simulated to decline when coarse sediment was used for beach nourishments. The contrasting biomass and biodiversity patterns clearly show that macrobenthos or avian biomass, as single descriptors to evaluate the health of an ecosystem, are insufficient and can lead to wrong conclusions concerning ecosystem health. We therefore advise to use a combination of both biodiversity as well as biomass indices to monitor the ecological impact of nourishments on sandy beach ecosystems.

Furthermore, it is precarious to conclude that the effect of nourishment using coarse sediment is harmless for higher trophic levels in general, due to the afore-mentioned uncertainties in the model concerning these higher trophic levels.

4.3 Synthesis and applications

Beach nourishment in practice occurs with a sediment grain size from 200 µm onwards. Based on the results of the model, we distinguish three groups of beach habitat, based on the most important variable according to the model, grain size of the sediment: (1) 200-250 µm; (2) 300 µm and (3) ≥ 350 µm. In figure 11, an overview of the beach nourishment effects for these different habitats is given.

The different ecosystem components included in the model are evaluated. As long as the used sediment resembled the sediment in pre-nourishment conditions, the ecosystem did not change. The use of coarse sediment (sediment grain size ≥ 300 µm) for nourishments had a negative effect on macrobenthos biodiversity. Due to the differences between simulated patterns of total biomass and biodiversity, the importance of these variables should however be carefully considered.

Furthermore, it could be stated that beach nourishment with a sediment grain size of 300 µm is most favourable for higher trophic levels based on the results of this model. Nevertheless, this result is largely depending on the strong correlation of the used predators with the opportunistic 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 sizes that is advised to be used for nourishment of natural fine-grained beaches is established as 200-300 µm.

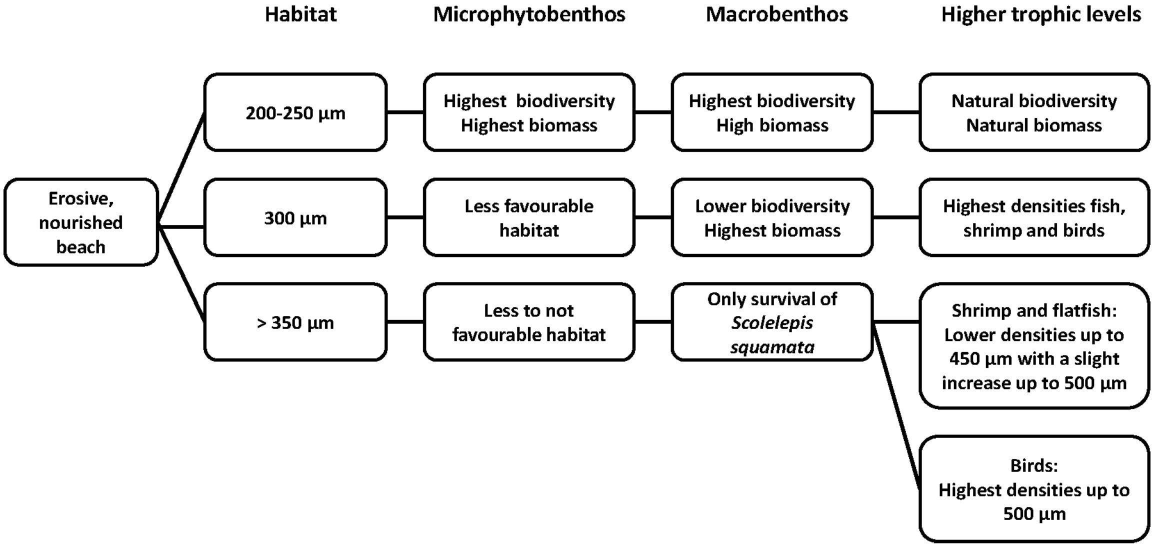

Figure 11: schematic overview of beach nourishment impact on the beach ecosystem, based on the nourishment model simulations

5. Conclusion

The simulations of the model indicate that the grain size of the sediment, used for beach nourishment, is the dominant factor in determining the effects on the ecosystem. The gradient for median grain size of nourishment sediment on dissipative West European beaches is advised to be 200-300 µm, in order to reduce the impact effects as much as possible.

The evaluation of the beach ecosystem health by total macrobenthic biomass or by the presence of socially or economically important species, like some birds and fish, can be deceptive as opportunistic species (cfr. *S. squamata*) can become very abundant on a beach impacted by nourishment. Hence, the combination of different variables (biodiversity, biomass) is advisable to estimate the effects of nourishment on the beach ecosystem. Finally, the development of the nourishment model in this study is only a first step and the refinement and enhancement of the model relationships, should greatly contribute to a better ecosystem-based nourishment approach in the future.

1

Chapter 7: General discussion, conclusions and future challenges

1. Goals of this PhD

Biotic interactions on sandy beaches and the processes structuring sandy beach ecological community patterns are not well documented in literature (Dugan et al., 2010). A better understanding of the functioning of an ecosystem is essential in obtaining an ecosystem approach for management purposes (Rubec et al., 1999; Beck et al., 2003). Therefore, the overall aim of this PhD study was to examine the important processes that structure the intertidal sandy beach community. We focused on the high-intertidal macrobenthos community of dissipative sandy beaches since macrobenthos patterns on these beaches are well-described and the relatively benign conditions on these beaches enable the presence of species interactions (Dugan et al., 2004; McLachlan and Dorvlo, 2005).

Modelling and experimental studies were developed to (1) examine the role of biotic interactions in structuring distribution and zonation patterns, and to (2) develop ecosystem-based guidelines for sandy beach management. In what follows, the findings of these studies are discussed in the light of evolutionary theories and are related to results obtained in other intertidal habitats.

2. Biotic interactions on dissipative sandy beaches

2.1 General zonation and distribution patterns

The distribution of macrobenthos on the intertidal sandy beach shows variability, both along the cross-shore gradient (zonation; figure 1) and the long-shore gradient (patchiness). These patterns have long been considered as mainly physically controlled (McLachlan et al., 1993; McLachlan and Jaramillo, 1995; McLachlan et al., 1996; McLachlan, 2001; Schlacher et al., 2008). This implies that abiotic factors are the most important structuring variables on the beach. However, when conditions are favourable, as they are on dissipative beaches or systems that are rather undisturbed by human activity, high abundance can cause intra- and interspecific interactions (Defeo and McLachlan, 2005) which structure the general distribution pattern of the species.

The results of the experimental studies in this PhD study (chapters 3, 4 and 5) contribute to the understanding of the underlying processes responsible for the observed patterns on sandy beaches. In chapter 2, the role of biotic interactions was suggested by regression models, describing the distribution of dominant macrobenthic species as a function of abiotic and biotic variables. A mesocosm experiment examining the role of competition both between the co-occurrent amphipods *B. pilosa* and *B. sarsi* (interspecific competition) and within each of the populations separately (intraspecific competition), was explained in chapter 3. Intraspecific competition was found to have an important role in distribution and abundance patterns of *B. sarsi*, while intraspecific competition could not be shown for *B. pilosa*. In chapter 4, prey consumption and predation pressure of juvenile shrimp and flatfish was examined. All macrobenthic species tested (the amphipods *B. pilosa* & *B. sarsi*, the polychaete *S. squamata* and the isopod *E. pulchra*) were found to be readily taken as prey by the tested predators. Furthermore, prey selectivity was found to be present and predation pressure by shrimp and flatfish was suggested to play an important structuring role. The sediment selectivity experiments in chapter 5 also indicated the structuring role of the predacious isopod *E. pulchra* in the macrobenthic community and suggested the presence of interspecific competition between *B. pilosa* and *B. sarsi*.

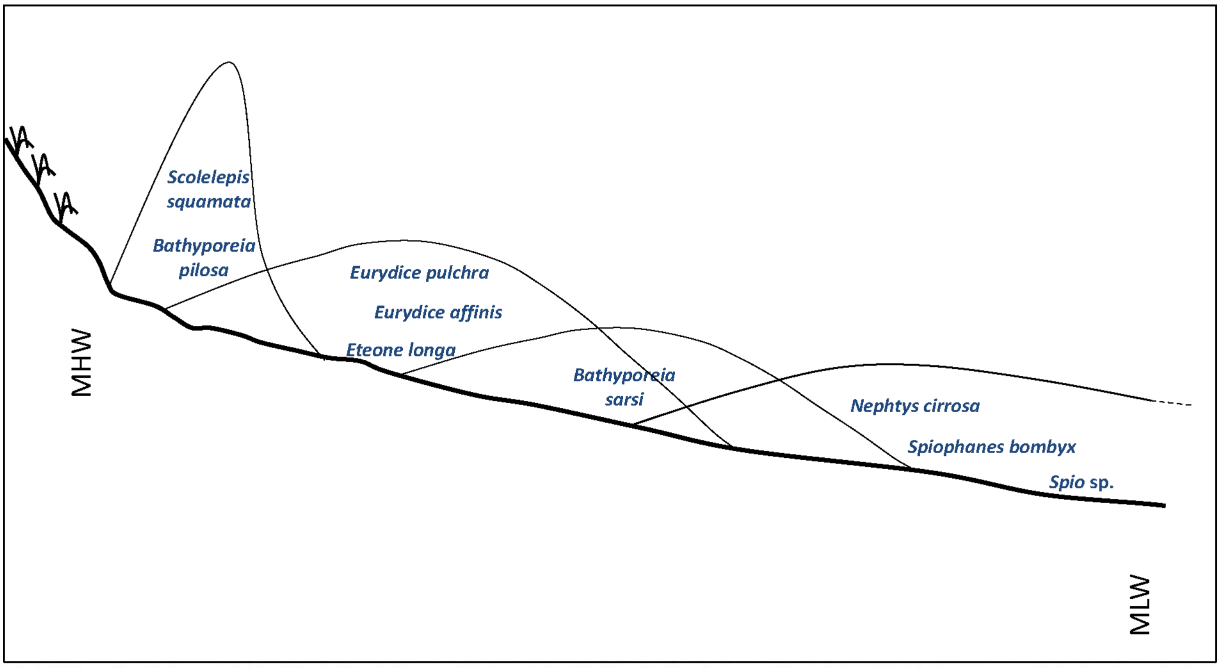

Figure 1: zonation pattern of the most abundant species of the intertidal macrobenthos community on NE Atlantic dissipative sandy based on info in Degraer et al. (2003). MHW: Mean High Water level; MLW: Mean Low Water level.

For the first time, evolutionary processes, possibly causing current zonation and distribution patterns, are considered and reconstructed for sandy beaches. In the following paragraphs, the distribution patterns of the dominant species of the high-intertidal macrobenthos community are discussed. As the congeneric amphipod species *B. pilosa* and *B. sarsi* are interesting from an evolutionary perspective due to their syntopic occurrence on dissipative beaches on the one hand and their different characteristics and zonation pattern on the other, these species are given most attention.

2.2 *Bathyporeia pilosa* and *B. sarsi*

Congeneric amphipods with dissimilar characteristics

Although *B. pilosa* and *B. sarsi* are two morphologically similar amphipods at first sight, they have several dissimilar characteristics. *Bathyporeia sarsi* is generally larger than *B. pilosa* (Speybroeck et al., 2008b), both amphipods have a different reproduction strategy with *B. sarsi* producing more but smaller eggs compared to *B. pilosa* (Speybroeck et al., 2008b) and *B. pilosa* is more tolerant for harsh environmental conditions (Preece, 1970, 1971). The amphipods show a segregated zonation pattern on the intertidal beach with very high densities of *B. pilosa* occurring in a small zone in the high-intertidal, while lower densities of *B. sarsi* are occurring in a broader zone in the mid-intertidal (figure 1) (Speybroeck et al., 2008b). This zonation pattern and the species characteristics are probably the result of evolutionary adaptation to environmental conditions. Both physical as well as biological factors, including competition and predation, are hypothesized to steer this pattern and are described in detail in the next paragraphs.

Based on results obtained in (chapter 2, 3, 4 & 5 of) this PhD study, the following hypotheses are formulated regarding the evolutionary development of the congeneric *B. pilosa* and *B. sarsi*, starting from a single ancestor phenotype (figure 2) (Brown and Vincent, 1992).

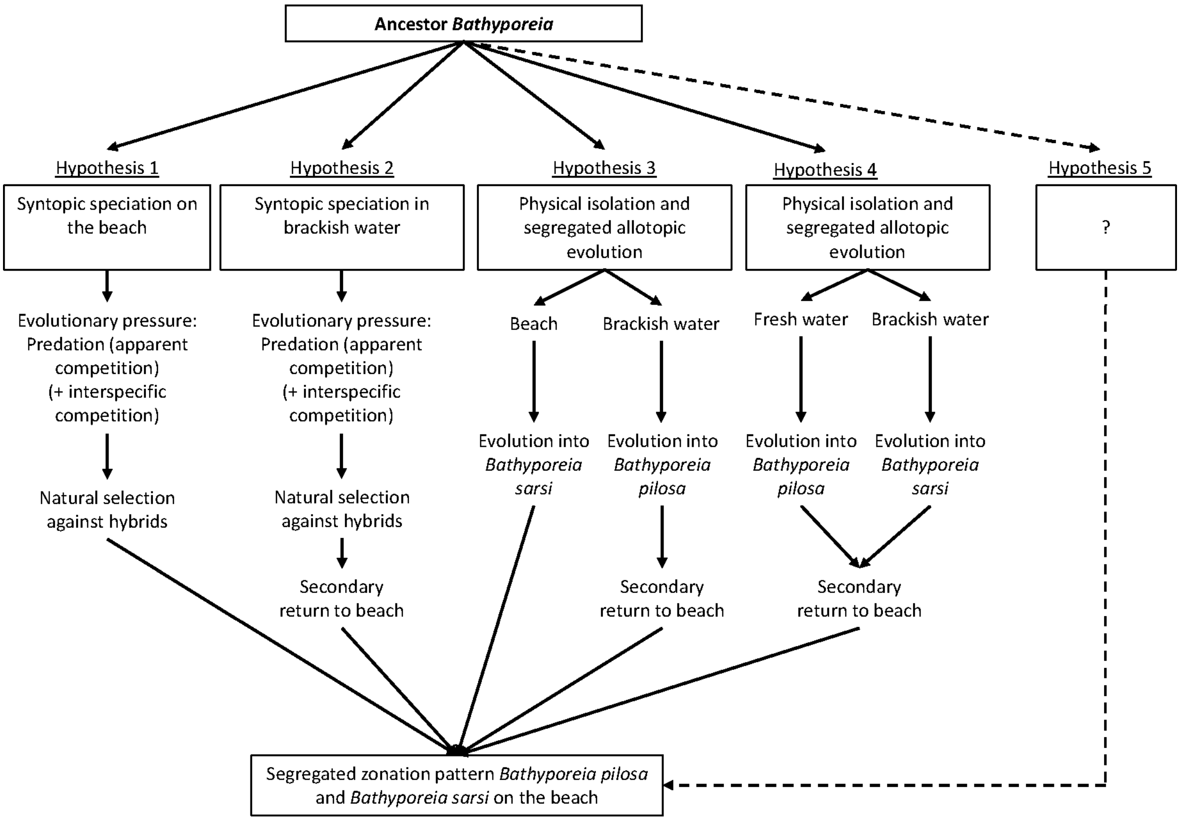

Figure 2: schematic overview of several hypotheses explaining the adaptive radiation into *Bathyporeia pilosa* and *Bathyporeia sarsi*

Hypothesis 1

In the past, the ancestor of *B. pilosa* and *B. sarsi* probably lived in the mid-intertidal (figure 2 (hypothesis 1) & 3 (a)) since a trade-off between physiological stress, increasing towards the upper-intertidal for marine species, and biological stress, increasing towards the low-intertidal where marine predators are abundant, would result in the selection of this zone as most favourable. However, as shown in chapter 4, predation pressure by juvenile shrimp and flatfish in the mid-intertidal is still strongly impacting prey populations living in this zone. Although studies on evolutionary adaptation and character shifts driven by shared predation as an evolutionary force are scarce (Abrams, 2000), it is possible that high predation pressure in the mid-intertidal may have been the driving force behind the adaptive radiation of the ancestor of these amphipods, resulting in the evolutionary divergence of anti-predator characteristics such as a larger body size or the development of spines on the body (Holt, 1977; Abrams, 2000). The indirect ecological effect as a result of this shared predation is called apparent competition or competition for enemy-free space (Holt, 1977; Abrams, 2000; Schluter, 2000). Apparent competition is defined as an indirect interaction between species, that reduces each other's abundances or leads to habitat segregation (Holt, 1977). The underlying cause is that the introduction of a second prey species increases the density of the predator. Consequently, the original prey suffers heavier levels of predation because of the increased density of predators and equilibrates at a lower density (Holt, 1977). Several ecologists have suggested that prey species "compete" for "escape space" and that this "competition" leads to gaps between species' characters or habitat segregation (Gilbert and Singer, 1975; Ricklefs and O'Rourke, 1975). As a result of this apparent competition, some members of the *Bathyporeia*-ancestor population, that by random mutations gained higher physiological tolerances, where relocated towards the higher intertidal (ancestors of *B. pilosa*). Due to other random mutations, some other members of the ancestor population acquired a larger body size (ancestors of *B. sarsi*), favourable in the mid-intertidal. As hybrids of these two species-lines were less fit in high-intertidal and mid-intertidal conditions, there was natural selection against these hybrids and as a result, homozygotes, further diverged syntopically by evolution of sexual selection and subsequent drift into *B. pilosa* and B. *sarsi* (figure 2 (hypothesis 1)). A lot of model evidence is available to endorse this theory (Doebeli, 2002; Bolnick and Fitzpatrick, 2007) and speciation in syntopic conditions was also shown by phylogeographic and population-genetic studies for cyclid fish (Shaw et al., 2000; Barluenga et al., 2006).

Bathyporeia sarsi in the mid-intertidal, with larger body size, can be seen as an ecological adaptation against the predation pressure by juvenile shrimp and flatfish in this habitat. The increasing body size can be considered character displacement (cf. also Abrams 2000). Character displacement is a genetic differentiation where syntopic species' characteristics are changed by natural selection in a specific habitat (Schluter, 2000). The smaller *B. pilosa* was highly vulnerable for the high predation pressure in the mid-intertidal and was therefore forced towards the high-intertidal. In the high intertidal, the predation pressure is lower (figure 3 (b)) but *B. pilosa* had to adapt to the severe physiological stress of this high-intertidal (niche adaptation). Indeed, the high-intertidal is characterized by high fluctuations in salinity, temperature, moisture and food availability due to the long periods of emersion, alternated with shorter periods of immersion. Hence, species living in this zone suffer from severe physiological stress. Due to natural selection, *B. pilosa* adjusted its physiology to cope with the harsh conditions on the high- intertidal beach. Although no specific information is available on the physiological differences between *B. pilosa* and *B. sarsi*, Preece (1970, 1971) showed that *B. pilosa* was far more tolerant for harsh conditions compared to *B. pelagica*, a related amphipod occurring in the low-intertidal (Preece, 1971). Furthermore, survival in lab conditions also showed the higher tolerance of *B. pilosa* compared to *B. sarsi* (Speybroeck, 2007).

Alongside the dominant structuring force of predation (Matson et al., 2011), resource competition between the two amphipods could also have influenced the adaptive radiation into *B. pilosa* and *B. sarsi.* Generally, (resource) competition is considered the most important driving force for adaptive radiation and character displacement but this is generally due to a lack of theory on predation as a driving force (Abrams, 2000). Although interspecific competition between *B. pilosa* and *B. sarsi* could not be significantly shown in chapter 3 of this PhD study, the sediment selection experiment (chapter 5) indicated that asymmetric competition was present with *B. sarsi,* the largest amphipod, acting as the strongest competitor (Schoener, 1983; Brown and Maurer, 1986). Furthermore, the studies of Croker (1967) and Jaramillo (1987) on other species pairs of peracarids living segregated in the intertidal zone, support the structuring role of competition for these congeneric species. The difficulties to clearly demonstrate the presence of interspecific competition between the two congeneric amphipods may be caused by the low current strength of the interaction due to the ghost of the competition past (Connell, 1980; Silvertown, 2004). This concept states that observed differentiation between species is the result of past competition and that due to the differentiation, the reason for competition disappears. As the general prediction of this concept is that interaction (competition) intensity, lying at the base of the character displacement or niche diversification, declines with time (and ultimately only remains a "ghost" of its former strength) (Schluter, 2000; Pritchard and Schluter, 2001), the difficulties of finding current interspecific competition can be explained by this concept. Conclusively, it is likely that *B. pilosa* was forced towards the upper-intertidal by the dominant structuring role of predation by juvenile flatfish and shrimp, possibly accompanied by the role of interspecific competition with *B. sarsi.*

Hypothesis 2

Besides the syntopic beach hypothesis for the divergent radiation into *B. pilosa* and *B. sarsi*, some other hypotheses could also be explanatory for the origin of both species. These were based on observations of *B. pilosa* (and sometimes even *B. sarsi)* in brackish water conditions and even observations of *B. pilosa* in (nearly) fresh water (Vader, 1966). In the second hypothesis considered here (figure 2), the two species both evolved syntopically in brackish water conditions due to divergent natural selection (analogous to hypothesis 1) and returned secondarily to the intertidal beach. However, as specific abiotic and biotic conditions in these brackish water conditions were not examined in this PhD study, the specific processes leading to radiation into *B. pilosa* and B. *sarsi* in the brackish water environment are not described here.

Hypothesis 3

Starting from a marine *Bathyporeia*-ancestor, a part of the population could also have been isolated in a more brackish water environment due to a physical obstacle (figure 2 (hypothesis 3)). This could have been the result of the silting up of a part of the beach and the subsequent arising of a lidded brackish water environment. In this brackish water environment, natural selection benefitted physiological characteristics, valuable in a brackish-water environment and ultimately, the brackish water amphipod *B. pilosa* arose. The population, staying behind at the beach, was also subject to natural selection but under typical beach environmental conditions. As a result, *B. sarsi*, characterized by a lower tolerance for fluctuating salinity and typified by adaptations to the biological stress on the mid-intertidal beach such as a larger body size, originated. The brackish-water amphipod *B. pilosa* then secondarily returned to the beach, where it settled in the physiologically stressful high-intertidal where conditions are similar to brackish water conditions.

Hypothesis 4

Starting from a brackish water *Bathyporeia*-ancestor, a part of the population could have been physically separated in a more fresh water environment, followed by different natural selection forces in both habitats (whereby *B. pilosa* evolved in ((nearly) fresh water). In this fourth hypothesis (figure 2), both *B. pilosa* and *B. sarsi* secondarily moved towards the higher beach.

In the two latter hypotheses, biotic interactions were of minor importance and since the presence and importance of these interactions were demonstrated in this PhD study, one could tend towards the first hypothesis, where biotic interactions played a more important role. However, as species populations and especially species interactions in brackish environments are hardly studied, further examination of *Bathyporeia*-populations in different environments is necessary to find a decisive and well-founded answer in this context.

Bathyporeia pilosa and B. sarsi patterns on the intertidal sandy beach

In the following section, the current zonation pattern and species characteristics of *B. pilosa* and *B. sarsi* will be discussed more profoundly in the intertidal beach context. In the high-intertidal beach environment, *B. pilosa* only occupies a small niche (figure 3 (b)). The lower limit of occurrence is probably defined by biotic interactions (predation and competition), while the higher limit is defined by the species' physiological tolerances for the abiotic environmental variables. Although *B. pilosa* is tolerant for harsh environmental conditions, it is still a non-terrestrial amphipod that needs water for its survival. Therefore, the average high-water line is the physiological upper boundary of the *B. pilosa* habitat and the species reaches its optimum just below MHWN (Mean High Water Neap tide). As shown in chapter 3, no intraspecific competition is present in the *B. pilosa* population so this specialist amphipod is able to reach very high densities in its small niche where biotic stress due to predation or competition is minimal.

In the mid-intertidal, *B. sarsi* occupies a broader cross-shore beach zone (figure 3 (b)). Similar to the occupied niche of *B. pilosa*, the lower limit can be defined by biotic factors mainly consisting of predation by bigger low-intertidal and subtidal predators, while the upper limit is set by the species' physiological restrictions towards the harsh environmental conditions on the upper-intertidal beach. In addition, the intraspecific competition found to be present in the mid-intertidal *B. sarsi* population (chapter 3), could also contribute to this species' upper distribution limit. Both the high predation pressure in the mid-intertidal as well as this intraspecific competition are probably delimitating the field densities of *B. sarsi.* Nevertheless, since the individual biomass of *B. sarsi* is higher than the one of *B. pilosa* and since *B. sarsi* is occurring in a broader zone on the beach, overall biomass of both amphipods on the entire beach is comparable.

The dissimilar reproduction strategies of the two amphipod species (Speybroeck et al., 2008b) are in correspondence with and adjusted to the afore-mentioned distribution patterns and processes causing these patterns. Hence, analogous to the dissimilar physiological and morphological characteristics of the amphipods, the different reproduction strategies are probably the result of ecological adaptation. *Bathyporeia pilosa* is investing more energy in larger but fewer eggs that have enough energy reserves to survive the harsh physiological conditions in the upper-intertidal, while *B. sarsi* is producing more but smaller eggs. Indeed, for several species from different environments, it was shown that species, living under higher physiological stress, produce less but larger eggs (Fischer et al., 2003; Bertrand et al., 2006). Physiological conditions in the mid-intertidal are moderate, so ample egg reserves are not necessarily to survive the physical conditions in this zone, while higher recruitment level in the *B. sarsi* population is favourable in the biologically stressful mid-intertidal where high predation pressure causes a substantial loss in the population. This higher recruitment level in biologically stressful environments was also recently suggested by Kotta (2010) for related amphipods (*Gammarus*).

Conclusively, the current zonation, distribution, abundance and species characteristic patterns of *B. pilosa* and *B. sarsi* are likely to be the result of both niche diversification and character displacement, driven by abiotic and biotic conditions in the field. Although abiotic factors are largely defining the upper zonation limits of both amphipod species on the beach, as has been generally accepted for sandy beaches (e.g. McLachlan, 1996, 2001), for the first time it was shown that the lower limits can only be explained by biotic forces: comparable findings are known on rocky shores (Connell, 1961; Paine, 1974).

The keystone species concept of rocky shore ecology can also be applied to intertidal beaches. Keystone species were first described by Paine (1969) but afterwards the concept was expanded (Brown and Vincent, 1992; Mills et al., 1993). In this intertidal sandy beach context, one could define the juvenile shrimp and juvenile flatfish predators on the beach as ecological keystone species since their presence is probably the dominant factor that structures the macrobenthos community. More evidence for this role could be gained from field enclosure or exclosure experiments. Unfortunately, such field experiments are hard to execute in the very dynamic intertidal sandy beach habitat. Nevertheless, further field and phylogenetic studies could give valuable information on the evolutionary processes lying at the base of current distribution patterns of *B. pilosa* and *B. sarsi.* Schluter (2000) predicted exaggerated divergence in syntopy, whereby phenotypic and genetic differences between two or more species are greater where the species coexist (syntopy) than where they occur separately (allotopy). As *B. pilosa* can also occur in allotopy (e.g. in subtidal brackish environments where *B. sarsi* is absent (Vader, 1966)), this prediction can be examined for field populations of the two amphipods *B. pilosa* and *B. sarsi*, both morphologically as well as genetically. Furthermore, it is important to determine the field predation pressure on amphipods living in syntopy and allotopy to examine the evolutionary role of predation.

Bathyporeia pilosa, B. sarsi & B. pelagica

Bathyporeia pelagica, another related amphipod species, living in the low-intertidal and subtidal, was not taken into account in this PhD study, since in our study area it was only present in low abundances. As adaptive radiation probably steered the development of *B. pilosa* and *B. sarsi*, *B. pelagica* could also be the result of extended adaptive radiation in the *Bathyporeia* genus. These three intertidal amphipods can occur in several combinations of syntopy and in varying abundances on different locations (Fish and Preece, 1970; Speybroeck et al., 2008b). In general, they show a distinct zonation pattern (figure 4). On Belgian beaches, all three amphipods occur but *B. pelagica* is only present on a limited number of beaches (Degraer et al., 2003). On French beaches, all three amphipod species occur in notable densities (personal observations) while on Dutch beaches, *B. sarsi* is the less abundant of the three amphipods and is absent from many beaches (Janssen and Mulder, 2005). As it was shown in this study that predation pressure can be an important structuring factor on intertidal beaches, a different predation pressure on beaches can be causing these different community patterns. On Belgian dissipative beaches, where predation pressure on the intertidal beach is high, small amphipods in the low-intertidal are under severe pressure. On other beaches (e.g. France), lower predation pressures can explain the higher densities of the low-intertidal amphipod *B. pelagica*. However, as information on predation pressure on French beaches is not available, it is impossible to test this hypothesis. In addition, *B. pelagica* is actually a subtidal amphipod, so the lower densities on the lower intertidal beach can also be the result of the occurrence of this amphipod in a sub-optimal environment. Probably, the hypotheses and ecological theories that were formulated in this study on *B. pilosa* and *B. sarsi* could be extended towards *B. pelagica*. Lower on the beach, the amphipods have a larger body size compared to related species living higher on the beach as a protection against predators, being present on this part of the beach for a longer time (Fish, 1975; Speybroeck et al., 2008b). Furthermore, the amphipods produce more but smaller eggs (Speybroeck et al., 2008b) and densities are in correspondence with higher predation pressure lower on the beach (Degraer et al., 2003; Speybroeck et al., 2008b). However, for the population of *B. pelagica* on the Belgian beaches, there is currently no information to verify these hypotheses.

Besides the structuring role of the shrimp and juvenile flatfish predators, the predacious isopod *E. pulchra*, being a member of the macrobenthic community, can also have a structuring effect on the amphipod patterns. However, as this isopod (1) is only occurring in low abundances and (2) has a broad distribution over the intertidal beach (Degraer et al., 2003), it was not expected to have a structuring role on the large-scale zonation and distribution patterns of the amphipods considered here. Nevertheless, as *E. pulchra* was shown to have an effect on prey species in mesocosm experiments (chapter 5), this role is further discussed in paragraph 2.4.

In this study, the structuring role of predation by birds on intertidal macrofauna was not taken into account. Generally, birds are known to feed on intertidal benthos (Speybroeck et al., 2006a;

Vanermen et al., 2009) but they are also very opportunistic feeders. Hence, stranded wrack material and subtidal mollusks are also an important part of the birds' diet (De Meulenaer, 2006). Some studies tried to quantify the importance of macrofauna in the diets of several bird species (De Meulenaer, 2006; Vanermen et al., 2009), but there are still huge uncertainties as it is difficult to closely observe the feeding behaviour of birds. The relative importance of bird predation on the one hand and marine predation on the other hand still needs further research. Although this study showed a significant predation pressure by marine predators, it is currently unclear whether this predation is more important than predation by avifauna.

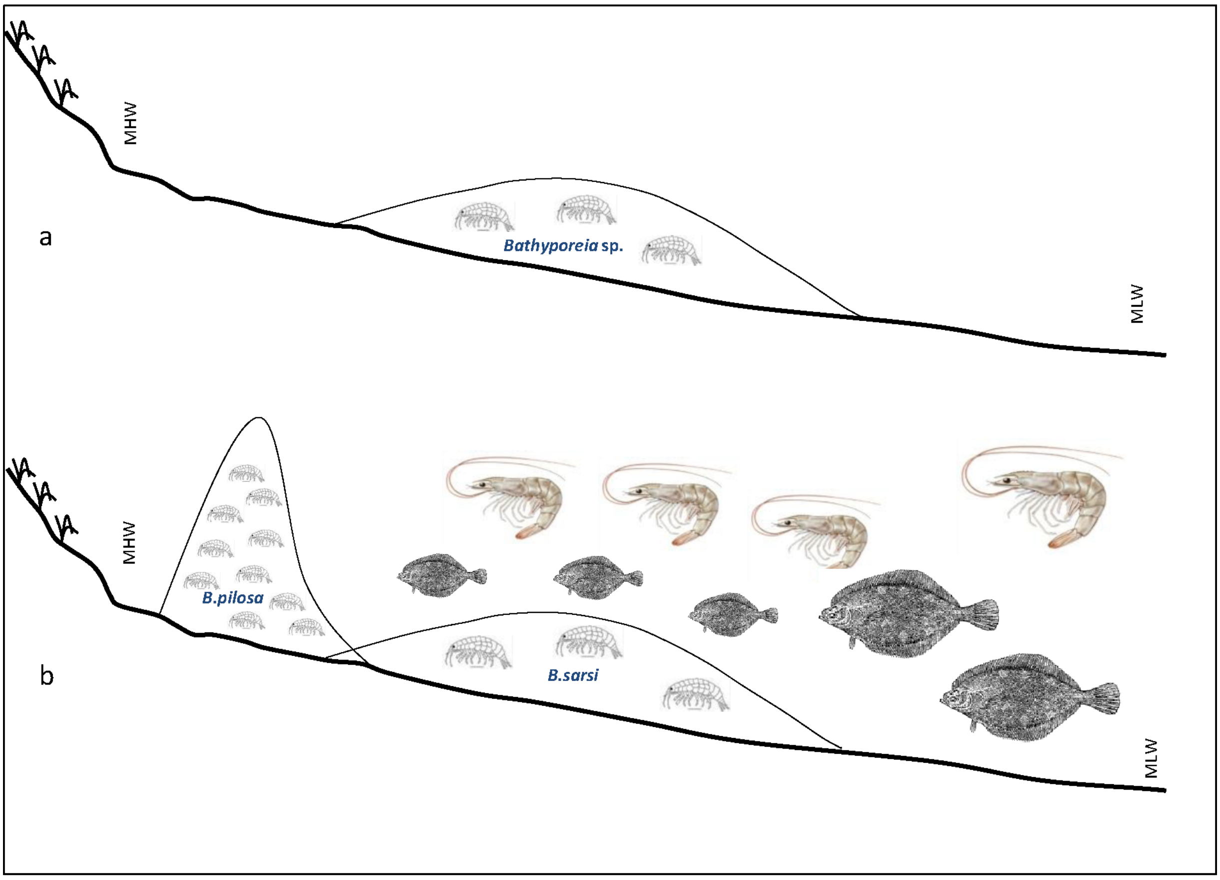

Figure 3: (a) zonation pattern of a hypothetical ancestor species of *B. pilosa* and *B. sarsi*; (b) current zonation pattern of *B. pilosa* and *B. sarsi*, along Belgian dissipative beaches. MHW: Mean High Water level; MLW: Mean Low Water level.

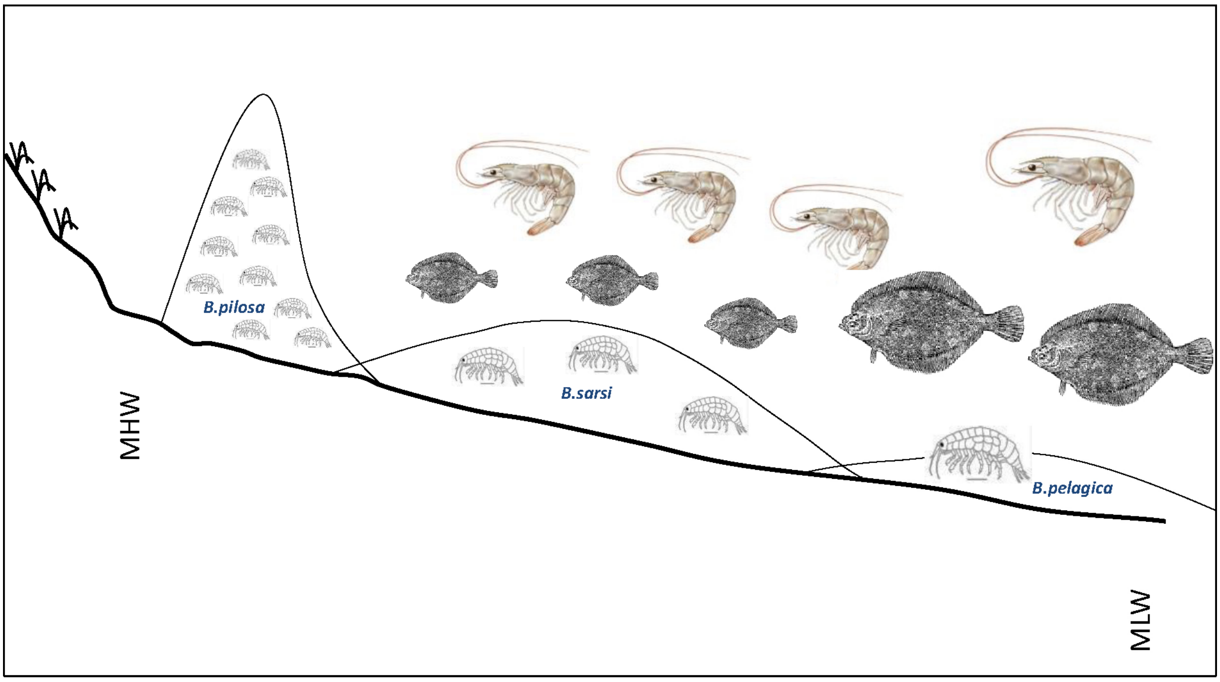

Figure 4: zonation pattern of the three syntopically occurring *Bathyporeia* species along the NE Atlantic dissipative sandy beaches. MHW: Mean High Water level; MLW: Mean Low Water level.

2.3 *Scolelepis squamata*

On Belgian dissipative beaches, the polychaete *S. squamata* lives in the high-intertidal (Speybroeck et al., 2007) (figure 5 (b)), while the same polychaete inhabits a much broader zone on morphodynamically similar Dutch beaches (Janssen and Mulder, 2005) (figure 5 (a)). Although striking at first sight, this difference can possibly be attributed to a difference in biotic interactions. As was shown in chapter 4 and in Beyst et al. (1999), the polychaete is a readily taken prey item for juvenile flatfish and shrimp that occur in high densities in the Belgian surf zone at high tides. The structuring influence of these predators is likely to force *S. squamata* towards the upper intertidal, where marine predation pressure is lower (figure 5 (b)). Furthermore, this effect will be most severe on juveniles and larvae of the polychaete. After reproduction, the pelagic larvae will be spread evenly over the entire beach, but due to the higher marine predation on the lower beach, larvae and juveniles of the polychaete will not be able to settle there and will only reach adult sizes on the upper beach (keystone effect of epibenthic predators). Due to the specific morphological characteristics of the Belgian coastal zone (characterized by an extensive shallow sandbank system in front of the western part of the Belgian coast and the Westerschelde estuary in the east), densities of epibenthos, temporarily feeding in the intertidal, could be higher than at neighbouring beaches (Dewicke et al., 2003). Indeed, in other coastal zones of the North Sea, the epi- and hyperbenthic densities are considered lower (Colman and Segrove, 1955; San Vicente and Sorbe, 1993; Munilla and Corrales, 1995). Nevertheless, since no exact epibenthos information is available from adjacent beaches of neighbouring countries, verifying this hypothesis is currently impossible. Other explanations for the different distribution patterns of the polychaete in the two countries could be related to differences in morphodynamic, hydrological, or food characteristics, but generally, the morphodynamics of Belgian and Dutch beaches are similar. Furthermore, avian predation pressure is not taken into consideration here (De Meulenaer, 2006; Vanermen et al., 2009). As overall bird predation is generally higher on the high-intertidal beach as a result of the longer emersion time of this zone, this predation pressure would moreover not explain the higher densities of the polychaete on this upper beach zone. In addition, the current zonation pattern of *S. squamata* on Belgian beaches suggests that marine predation is relatively more important for intertidal fauna compared to avian predation.

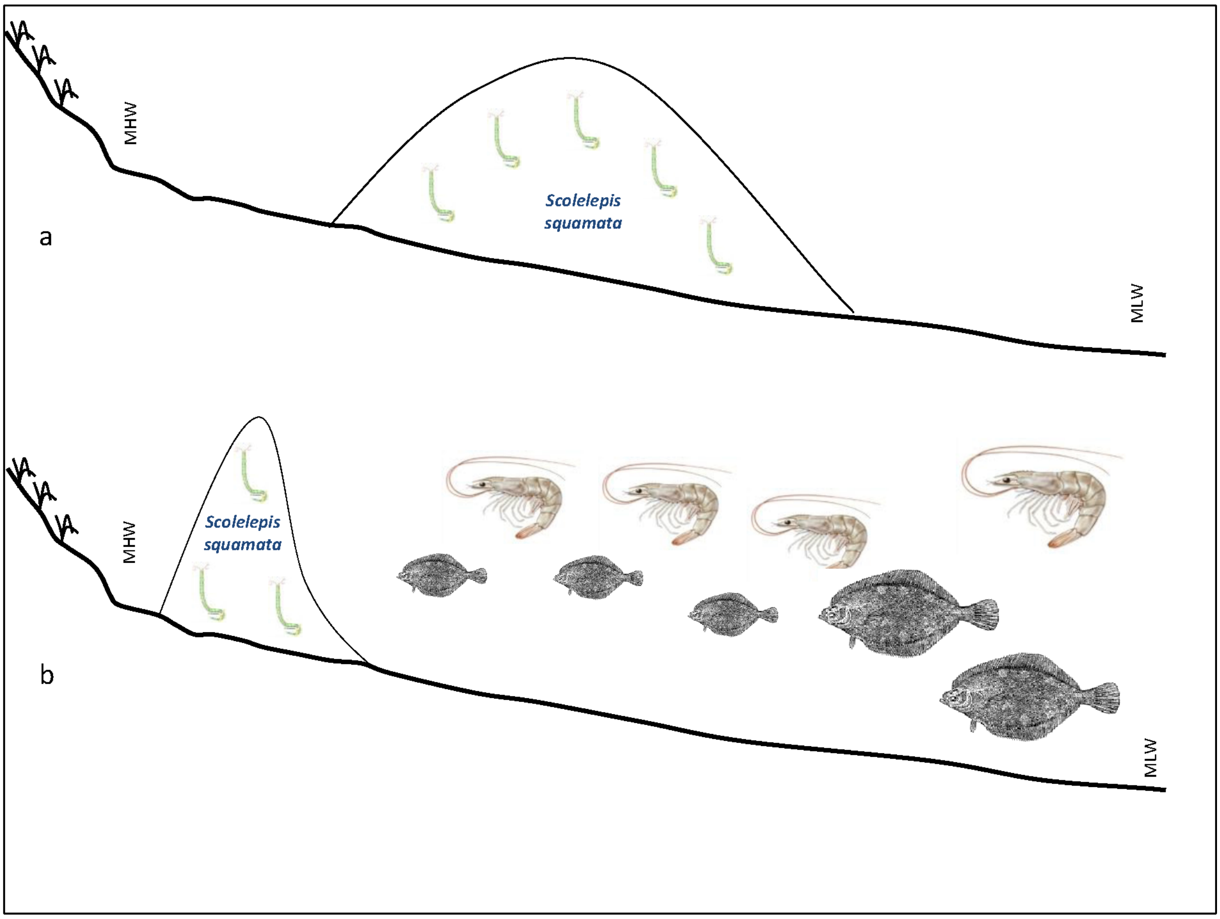

Figure 5: (a) zonation pattern of *Scolelepis squamata* without marine predation pressure; (b) zonation pressure of *S. squamata* with predation pressure of shrimp and flatfish. MHW: Mean High Water level; MLW: Mean Low Water level.

2.4 *Eurydice pulchra*

Although the macrobenthic predator *E. pulchra* only occurs in low densities on dissipative sandy beaches (Degraer et al., 2003), it might play an important role in the intertidal sandy beach ecosystem since *E. pulchra* is both prey for higher trophic levels as well as predator within the macrobenthos community itself (Jones, 1968). It is a very mobile predator, swimming and feeding in intertidal runnels and bars at low tide, while swimming in the surf zone at high tide.

In the sediment selectivity experiments in chapter 5, it was shown to have a negative effect on the prey species *B. pilosa*, *B. sarsi* and *S. squamata.* Hence, this predator could steer small-scaled patchiness patterns of these prey species on the beach. The role of prey size is crucial in determining the predation impact of this small isopod (Werner and Gilliam, 1984; Fuiman, 1994). Our study suggests that *B. pilosa* is more vulnerable to predation by *E. pulchra* than *B. sarsi,* probably due to its smaller body size (Speybroeck et al., 2008b). *Scolelepis squamata* also suffered from predation by *E. pulchra*, although this predation may be non-lethal due to the relative sizes of predator and prey (Michaelis and Vennemann, 2005). Furthermore, the isopod may predominantly affect larval and juvenile stages of the polychaete. Although the structuring role of this small predator may thus be confined on the overall beach scale, the isopod may have a unique role in determining small-scale patterns on dissipative beaches. However, to verify this role, further investigations including both mesocosm and field enclosure experiments are necessary.

In the predator-prey mesocosm experiments in chapter 4, *E. pulchra* was found to be a potential prey for epibenthic predators. Especially the shrimp were feeding on the highly mobile crustacean. Hence this isopod is an important member of the sandy beach food web but due to its low abundances (Degraer et al., 2003), it is not expected to be an essential link in terms of biomass.

3. Implications for sandy beach management in Belgium

Due to current and future processes steered by global climate change (sea level rise, flood risk by storms, beach erosion…), coastal countries (including Belgium-Flanders) have to take decisions in sandy beach management. One of the main challenges for a low-lying area like Flanders is coastal protection. Therefore a coastal safety plan (Mertens et al., 2008) has been developed including necessary management interventions such as the construction of hard defence structures and beach nourishment. However, all these management decisions, together with the multitude of other beach functions such as tourism and economic development, threaten the natural balance of the beach ecosystem. Similar to spatial planning on land, there is also a growing need for marine spatial planning due to the multitude of marine functions. Coastal safety is the most important priority in the decision making process concerning spatial planning for the Belgian coast. Maritieme Dienstverlening & Kust (MDK) is responsible for the execution of coastal defence projects.

A beach expert panel delivers advice on the possible significance of the proposed defence measures for the beach ecosystem. Based on these advices a MER- report (Environmental Impact Assessment) is worked out, in which the project is described and its consequences for the ecosystem are discussed. Currently, beach nourishment is the prefered defence measure along the Belgian coast, since previous hard defence measures enhanced structural erosion and the “softer” technique has no negative effect on tourism (Greene, 2002; Hamm et al., 2002; Hanson et al., 2002). In the MER report, necessary for every beach nourishment project, significant effects on the ecosystem are estimated and if a significant impact is expected, mitigation measures are proposed (such as the use of fine-grained nourishment sediment or the separation of one bigger nourishment in more smaller projects (Speybroeck, 2007)). In this context, well-founded and scientifically-based guidelines for ecological adjustment of beach nourishments, leading to a minimization of the impact on the beach ecosystem are indispensable nowadays. Speybroeck et al. (2006a) indicated that an ecosystem approach concerning nourishment effects is generally missing. Hence, extensive scientific information on the complete beach ecosystem is needed and good communication between scientists and management is essential.

Based on the knowledge obtained in this PhD study (chapter 5 & 6) and former knowledge we will, in this chapter, (1) formulate guidelines for the ecological adjustment of beach nourishments, (2) formulate some management and policy suggestions to optimize current processes in sandy beach management and finally, (3) indicate some future perspectives for sandy beach management.

3.1 Guidelines for ecological beach nourishment

In this section, a number of factors, important for beach nourishments are discussed. The recommendations are based on the results obtained in chapter 5 & 6 of this PhD study. As it was not the first aim of this PhD study to describe beach management in all its aspects, this list is not exhaustive. A complete overview of current and future issues in Belgian beach management will be given in the future, incorporating the recommendations formulated hereafter (PhD study Sarah Vanden Eede, in preparation).

Grain size of the sediment

Generally, it is advised to use sand that closely matches the grain size and chemical attributes of the natural beach sediment to minimize environmental impacts (Greene, 2002). As the most valuable Belgian beaches have an average sediment grain size of 200-220 µm (De Moor, 2006), it is advisable to use fine to medium-fine sand for beach nourishments. However, from a technical point of view, coarser grain sizes produce steeper, more stable and longer lived fill sizes (Finkl and Walker, 2002). Hence, a compromise between the technical aspects and ecology is necessary and it is of crucial importance to know the upper limit of sediment grain size that can be used, to affect the ecosystem minimally.

The recovery of the ecosystem after nourishment using sediment with a well-known grain size and a specific beach slope, can be predicted by the species envelope model designed in chapter 6. The model showed that the ecosystem after nourishment using sediment with a grain size of 300 µm changes towards a significantly "diversity-less" system (figure 6). However, total macrobenthic biomass was high when 300 µm was used for nourishment, but this was only attributed to the high densities of one opportunistic polychaete. At 350 µm, the species richness was already very strongly diminished and total biomass also started decreasing. Furthermore, the sediment selectivity experiments (chapter 5) showed that the four tested macrobenthic species all preferred sediment with a median grain size smaller than 250 µm, while coarser sediment was not preferred by two of the four tested species. Therefore, the gradient in sediment grain sizes that is advised to be used for nourishment of fine-grained Belgian beaches is 200-300 µm.

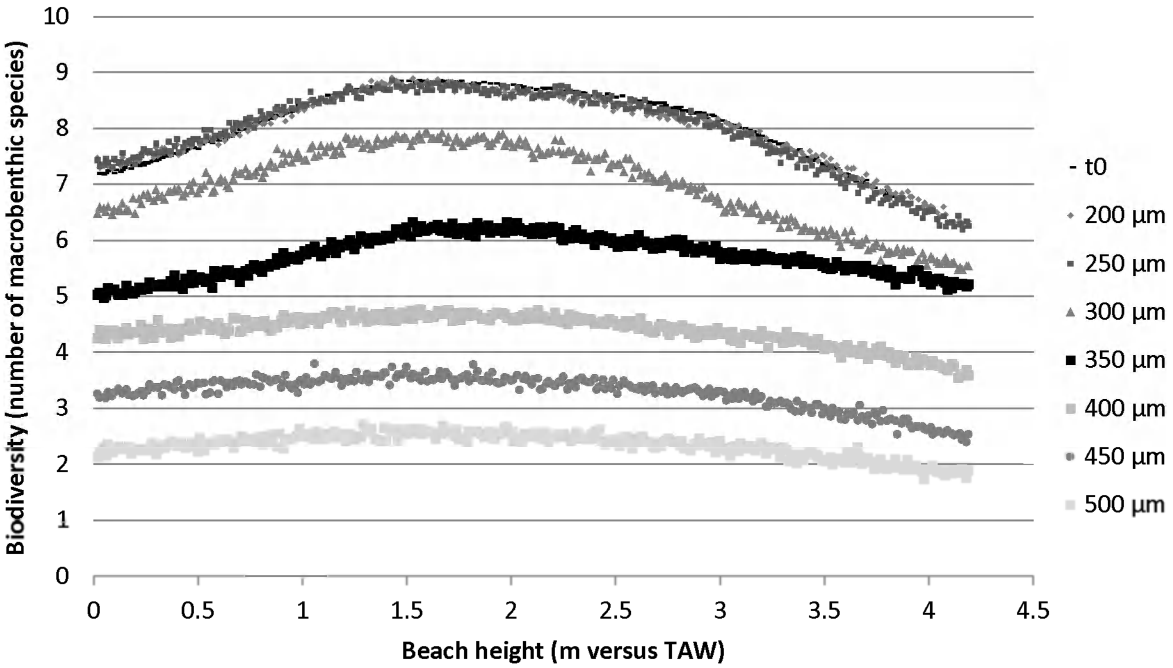

Figure 6: biodiversity on a typical Belgian beach before (t0) and after nourishment with different sediment grain sizes (µm). X-axis: beach height (m versus TAW); Y-axis: mean biodiversity (number of macrobenthic species)

Slope of the beach

Besides sediment grain size, the beach slope of the nourished beach is also an important variable. It influences the ecosystem and determines the efficiency and the lifetime of the nourishment. The model in chapter 6 indicated that the constructed beach slope in a nourishment project can favour specific species and their habitats. However, this positive effect will only be temporarily, as the slope will ultimately evolve towards the pre-nourishment conditions. Conversely, a very steep slope will negatively affect the total biomass of macrobenthos and trophically linked higher species as such a steep slope will reduce the intertidal habitat. Furthermore, a very steep slope will enhance the risk of a complete community shift on the intertidal beach. Belgian beaches are characterized by gentle slopes and fine sediment and harbour a relative species-rich community while beaches with steep slopes and coarse sediment are inhabited by a less species-rich community (Defeo and McLachlan, 2005). When the morphodynamic features of a dissipative beach are changed to such a degree that they resemble the features of a reflective beach, it is very likely that the (macrobenthos) community will also shift to the less species-rich alternative. Such a shift can be reversible, but taken into account community shifts in other habitats (Matsunaga et al., 1999), these shifts can also be irreversible. However, the latter irreversible shifts are typical for very species-rich ecosystems. Since sandy beaches are generally species-poor (McLachlan and Brown, 2006), possible shifts are considered to be reversible in sandy beach ecosystems. Nevertheless, to maintain ecologically valuable beaches, it is advisable to construct an intertidal beach slope that closely matches the initial beach slope, which will be in balance with the local hydrodynamic forces.

The use of predictive models to determine the best ecological nourishment approach

The species envelope model, developed in chapter 6, enables the user to compare the effects of nourishments with varying technical features. Both the slope of the nourishment project as well as the sediment can vary in the model, enabling the user to determine the combination with the lowest impact on the ecosystem. Therefore, this preliminary predicting model for nourishment effects is a valuable tool for management decisions concerning beach nourishment projects.

3.2 Policy suggestions concerning beach nourishment

Higher investment in the protection of the intrinsic nature value of valuable beaches while only focusing on coastal defence on touristic beaches

Highly touristic beaches with a high percentage of development along the coast are heavily threatened by coastal erosion and sea level rise and need the highest priority for protection against flooding. Hence, beach nourishments will be applied on these beaches and probably they will have to be repeated within short time intervals (years). Furthermore, to enlarge the “lifetime” of the nourishment, both steep slopes and coarse sediments will be used. Such repeated beach nourishments will have a negative impact on the ecosystem. However, the ecosystem of highly touristic beaches is already strongly impacted and consequently impoverished by beach cleaning, trampling, pollution and presence of coarse material due to previous nourishments (Speybroeck et al., 2008a). Therefore, it can be advisable to give a lower priority to these touristic beaches in the light of nature protection and to focus on the protection of less touristic and ecologically (or potentially) valuable beaches. That way, both the intrinsic value of the beach ecosystem could be protected on ecologically valuable beaches and the anthropogenic use of the beach can be kept on the touristic beaches. Nevertheless, a good connection between biologically valuable beaches is necessary to ascertain enough genetic exchange between populations of protected beaches and thus to maintain an overall valuable beach ecosystem.

Combination of different management measures

In some conditions, the best approach for coastal defence is a combination of management measures. Beach nourishment, foreshore nourishment, the construction of technically highly enhanced dykes that do not disturb the view, dune creation, reshaping, the plant of brushwood hedges and the construction of groins can all be combined to obtain a sound beach safety plan for each beach zone. A combination of these measures can minimize the costs, the work and the impact on the beach ecosystem as cheaper and more sustainable measures such as the growing of brushwood can positively influence the stability of the beach and lower the number of neccesary nourishments.

Determining recovery after nourishment

Although beach nourishment is considered a soft coastal defence measure, it still has a negative effect on the beach ecosystem (Speybroeck et al., 2006a). However, if no further nourishments or other pressures impact the beach, the system will evolve towards the pre-nourishment conditions. Not only the specific characteristics of the nourishment are determining factors, but also the specific features of the beach ecosystem influence the post-nourishment evolution. Ideally, this recovery time could be determined by yearly monitoring after nourishment. However, as management actions are constantly impacting beach systems, this post-nourishment monitoring is hard to execute in practice and currently no reliable post-nourishment monitoring data are available to give a good estimate on recovery time following beach nourishment. Nevertheless, this knowledge is essential to accurately predict the response of the ecosystem and give valuable management guidelines.

Ecosystem vision: effects of nourishment on higher trophic levels

The species envelope model (chapter 6) predicts the response of the beach ecosystem after nourishment and assesses the food potential for higher trophic species. Based on former information on sandy beach patterns and information on processes obtained in this PhD study (chapters 2-5), an ecosystem approach was incorporated in the model. As a result, the nourishment impact on the distribution and zonation of microphytobenthos, macrobenthos, birds and fish could be modelled. The necessity for a good ecosystem approach and a solid ecosystem interpretation was also illustrated by the model. The presence of a lot of birds or a high macrobenthos biomass on the beach can be deceiving indicators for the ecosystem health. Indeed, the model indicates that after nourishment with coarse sediment, both macrobenthos biomass as well as bird abundances are showing a higher potential presence. However, this is the result of the decrease in overall biodiversity and the increase in abundance of one opportunistic macrobenthos species (e.g. the polychaete *S. squamata*). As higher trophic levels in the model are strongly linked to this polychaete in the model functions, the higher trophic species are also estimated to be potentially present in high numbers. However, the food relations in the model still need refinement as firstly, macrobenthos is not the only food source and secondly, predators are in the current model not linked directly to morphodynamic or hydrological conditions. Nevertheless, the latter conditions are known to be important in influencing the presence of marine predators on the beach (Beyst et al., 2001). Hence, the observation and evaluation of a too limited selection of ecosystem features will hamper a good ecosystem approach. Conclusively, it could be stated that the combination of both biodiversity and biomass is advisable for assessing the quality of the intertidal beach ecosystem and that the model still needs refinement, especially concerning the relationships of higher trophic levels.

The intertidal sandy beach is an important nursery area for both marine fish as well as birds (Beyst et al., 1999; Vanermen et al., 2009). Hence, degradation of the intertidal beach will impact these higher trophic levels. When nourishment projects only affect beaches that are not important as feeding grounds for birds and fish, effects will be minor, while a nourishment impact on biologically valuable beaches (Laporta, 2012) will have an important effect on the populations of higher trophic species. Although different intertidal habitats (estuaries, mud flats, intertidal beaches) are important as nursery areas, the loss of sandy beach areas due to nourishment will have a major effect as sandy beaches are the most abundant intertidal habitats along the Belgian coast. Since Belgian beaches are hypothesized to have a higher nursery value than beaches of neighbouring countries (Janssen, personal communication), degradation of Belgian intertidal beaches will probably impact both economics and ecosystem health on a larger scale. At the moment, it is however impossible to quantify the minimum impact area of valuable beaches that will have a considerable effect on the higher trophic levels of the ecosystem. It is also unsure whether the 67 km of Belgian beaches will be crucial as nursery for marine species due to the uncertainties concerning nursery value of adjacent larger beach areas.

One of the proposed nourishment techniques, i.e. the combination of one major beach nourishment project, followed by foreshore nourishment for maintenance of the nourished beach, will probably be a bad option for juvenile epi- and hyperbenthos feeding in the Belgian coastal zone. Major beach nourishment, covering several km of beaches, known to have an important nursery function, will make this intertidal nursery area (temporarily) unusable for juvenile epi- and hyperbenthos. Moreover, the subsequent foreshore nourishment will negatively impact the subtidal and its fauna as alternative nursery area. As a result, the nursery function of the complete (intertidal & subtidal) Belgian coastal zone will be affected and juvenile epi- and hyperbenthos will no longer be able to feed in the area. Therefore it is important to carefully consider the combination of beach and foreshore nourishment along beaches with an important nursery value for juvenile epi- and hyperbenthos.

4. Conclusions

The overall aim of this PhD thesis was twofold: (1) to contribute to the general knowledge on sandy beach ecosystem functioning and (2) to provide practical tools for managing these beach ecosystems, especially in the light of beach nourishments. This was achieved by a combination of modelling studies and mesocosm experiments. The answers, obtained in this PhD study, are formulated as follows:

- **Examining the structuring role of biotic interactions on dissipative sandy beaches**

The structuring role of biotic interactions was indicated by the results of the regression modelling study. Although this was a rather indirect approach, the results were confirmed by subsequent mesocosm experiments. Intraspecific encounter competition was found to play an important role in the *Bathyporeia sarsi*-population. Especially under lowered food conditions, the encounter competition, expressed as intraspecific attacks, enhanced and was suggested to be responsible for the species' upper distribution limit as well as its peak density in the mid-intertidal beach zone. Interspecific competition between *B. pilosa* and *B. sarsi* could not be demonstrated significantly but was suggested by the sediment selectivity experiment.

The predation pressures of juvenile flatfish and shrimp, the two most dominant predator groups on sandy beaches, are likely to have a structuring effect on the infauna-communities on the beach. Shrimp was found to be an opportunistic predator, showing no prey selectivity between macrobenthic species, while juvenile flatfish did show a preference for *S. squamata* and small amphipods. The zonation pattern of the macrobenthos can thus be related to the predation pressure on the beach, increasing towards the low-intertidal. As a result of this gradient in predation pressure, high densities of the highly tolerant amphipod *B. pilosa* and the opportunistic polychaete *S. squamata* can only be reached on the high-intertidal, while lower densities of *B. sarsi* are present in the mid-intertidal.

- **Contributing to the sandy beach food web dynamics**

Intertidal macrobenthos was shown to be an important food source for economically important predators such as shrimp and juvenile flatfish. Hence, the sandy beach habitat, characterized by high benthic biomass, can be an essential component in the overall coastal habitat as it acts as an important nursery area for important marine species.

- **Ecologically adjusting beach nourishments**

Sediment selection experiments showed that species, typical for dissipative beaches such as *Bathyporeia pilosa* and *B. sarsi*, prefer fine-grained sediments while other species, such as the cosmopolitan polychaete *S. squamata*, had a broad sediment preference and even showed a high occurrence in coarse sediment, not naturally occurring on Belgian beaches. Additionally, the nourishment model confirmed these preferences and showed that beach nourishment with sediment, characterized by a median grain size of 300 µm and higher, significantly reduced macrobenthos biodiversity. Furthermore, the slope of the nourished beach was to a smaller extent found to influence species densities and zonation patterns. For the first time, it was distinctly shown that nourishment sediment should not deviate much from natural conditions to maintain a healthy and species rich community. Finally, the model is a valuable tool for management purposes as it can easily predict the ecosystem effects of nourishments with specific technical characteristics.

- **Formulating management guidelines**

Although the development of profound measures for beach management fell out of the scope of this PhD study, some specific guidelines for a more ecologically-sound beach management could be formulated. Thanks to the nourishment model, better recommendations could be given concerning ecological adjustment of the technical beach nourishment characteristics. In post-nourishment monitoring studies, a careful consideration of the observed parameters is essential to become a realistic view on the complete ecosystem health. In this context, it is advisable to monitor both species biomass as well as species biodiversity. Moreover, it may be advisable to make a distinction between ecologically valuable and less valuable beaches. While coastal defence can be the dominant objective on the latter beaches, the former ones could be primarily managed in the light of beach conservation.

Suggestions for further research

- To examine the biotic processes on sandy beaches more profoundly, detailed field surveys, studying population parameters (including size differences, reproductive output & genetic diversity) of *B. pilosa* and *B. sarsi* in syntopic and allotopic conditions, could elucidate the presence and role of interspecific competition between these amphipods. Indeed, in allotopic conditions, the population parameters are hypothesized to be more intermediate compared to syntopic populations. In these latter populations, interspecific competition could act as an important evolutionary pressure, leading to a larger radiation of population parameters. Furthermore, field and experimental studies in which the amphipod *B. pelagica* is included, can give a more general view on the beach patterns and processes. Moreover, field and experimental studies on the population parameters of these amphipods in brackish and even fresh water conditions, could elucidate the true origin of these tolerant amphipods. Finally, genetic analyses can play a significant role in this context, as was already shown in a preliminary study (Demaerel et al., 2008) that specific DNA markers are useful to elucidate phylogenetic patterns within the genus *Bathyporeia.*

- Although predation pressure was estimated in this study, the structuring role of this predation still needs further examination. Therefore, field exclusion experiments are preferable but will nevertheless need a sound preparation to obtain valuable results in the highly dynamic intertidal beach area. Both the structuring role of epi- and hyperbenthic predators as well as the structuring role of the small predacious isopod *E. pulchra* should be examined in field-exclosure experiments. The structuring role of the isopod can be studied in small-scaled field experiments, while the role of epi- and hyperbenthic predators will demand large-scaled field experiments. In addition, a good knowledge on both the avian and marine predation pressure is essential to determine their relative importance in structuring patterns on the beach.
- A field study on the zonation pattern of the polychaete *S. squamata* in Belgium and neighbouring countries using the same reference plane, could give a better view on potential differences in zonation. The simultaneous study of epi-and hyperbenthic populations on these beaches could furthermore be important to explain these differences in zonation patterns.
- The refinement of the nourishment model, developed in chapter 6, will contribute to more accurate predictions of nourishment effects and will lead to more concrete recommendations for an ecologically-sound nourishment approach. This refinement includes the incorporation of better food relationships, the addition of relationships between epibenthos and abiotic variables and the extension of the predictions for more than one year. In the current model the largest uncertainty is that only macrobenthos was added as a food source for higher trophic levels, but stranded wrack material and stranded subtidal

mollusks should also be taken into account to predict the presence of higher trophic species on the beach. Furthermore, the addition of relationships between epibenthos and beach morphodynamics can enhance the reliability of the model predictions for higher trophic species. Finally, when scientifically-sound and long-term post-nourishment data become available in the future, these can be incorporated in the model and consequently the model could predict recovery of the beach ecosystem in time.

- A science-based and well-developed monitoring programme for assessing post-nourishment effects should be developed. Constantly adjusting nourishment guidelines based on the results of post-nourishment monitoring and the predictions of the nourishment model as also earlier proposed by Janssen et al. (2011), will contribute to a valuable management approach for future beach nourishments. In this context, it is advisable to develop and use the same methodology in all monitoring projects.
- Concerning beach management, one of the most urging issues is the development of an integrated coastal and beach spatial plan. Therefore, a good cooperation and communication between all institutions and authorities involved will be essential.
- The good ecological status for beach ecosystems needs to be defined and conservation objectives need to be formulated in the light of European legislation. As marine scientific institutions are most experienced in marine research, they should play a predominant role in defining those aspects.

Appendices

Appendix A (to chapter 2): tables containing all country specific and global models created

Belgium	**poisson**	emersion time	emersion time2	mean	mean2	Euryaffi	Eurypulc	Bathypilo	Bathysp	Bathysars	Nephcirr	Scolsqua	Eteolong	adj D2	% abio	% biotic
	Bathpilo		*			**								**0.61**	**0.65**	**0**
	Bathsars	**		**	**								**	**0.45**	**0.34**	**0.11**
	Nephcirr	*	**					**					**	**0.49**	**0.33**	**0.16**
	Scolsqua						*				**		*	0.48	0.15	0.33
	Eteolong	**	**	**	*						**			**0.29**	**0.26**	**0.026**
	Euryaffi						**							**0.61**	**0.57**	**0.037**
	Eurypulc					**		**				**		**0.55**	**0.50**	**0.055**
France	**Bathpilo**			**	**					**				**0.62**	**0.46**	**0.15**
	Eurypulc							*						**0.32**	**0.32**	**0**
Germany	Bathsp													0.0042	0.027	0
	Scolsqua			*					*					**0.24**	**0.20**	**0.041**
	Eteolong			**	**		*		**					0.19	0.017	0.17
Netherlands	**Bathpilo**	**	**	**	**							**		**0.74**	**0.75**	**0**
	Scolsqua	*		**	**			**		**			**	**0.37**	**0.27**	**0.099**
	Eteolong													0.0071	0.15	0
	Eurypulc													0.0075	0.024	0
Spain	**Bathsp**					**								**0.36**	**0.22**	**0.14**
	Nephcirr													0.048	0.078	0
	Scolsqua			**		**	**							0.24	0.067	0.18
	Euryaffi	**	**				**		*				**	**0.52**	**0.38**	**0.14**
	Eurypulc			**	**	**						*	**	0.38	0.11	0.27

Table A.1: country specific models - Poisson sub-models: columns: regression model coefficients; "*": almost significant (0.05<p<0.08); "": significant; adj D2: variability explained by the total model; % abio: variability explained by the abiotic variables; % biotic: variability explained by the biotic variables; Bold: abiotic models explaining > 20 % of the variability.**

Belgium	**binomial**	emersion time	emersion time^2	mean	mean^2	Euryaffi	Eupulc	Bathpilo	Bathsp	Bathsars	Nephcirr	Scolsqua	Eteolong	adj D2	% abio	% biotic
	Bathpilo	**	*	**	**	**	**				**			0.24	0.075	0.17
	Bathsars	**	**	**	**						**		**	0.43	0.15	0.28
	Nephcirr		*	**			**	**		**		**		**0.51**	**0.27**	**0.24**
	Eteolong	**		**			*				**	**		0.26	0.026	0.23
	Euryaffi	**			*		**							**0.47**	**0.30**	**0.16**
	Eurypulc	**		**	**	*		*			**	*		**0.38**	**0.30**	**0.078**
France	Bathpilo													0.079	0.0036	0.076
	Bathsars		**					*						0.20	0.088	0.11
Netherlands	**Nephcirr**													**0.55**	**0.39**	**0.16**
	Eteolong	**	**		*							**		**0.49**	**0.34**	**0.14**
	Eurypulc		**	**				**				*		0.20	0.10	0.10
Spanje	Bathsp		**		**		*				**	**	*	0.26	0.11	0.16
	Nephcirr	**							**			*	**	0.27	0.13	0.14
	Scolsqua		**	**			**							**0.26**	**0.20**	**0.052**
	Eteolong	**	**	**	**									**0.36**	**0.22**	**0.14**
	Euryaffi	**			**				**					0.13	0.096	0.035
	Eurypulc										**			0.13	0.0030	0.13

Table A.2: country specific models - binomial sub-models: columns: regression model coefficients; "*": almost significant (0.05<p<0.08); "": significant; adj D2: variability explained by the total model; % abio: variability explained by the abiotic variables; % biotic: variability explained by the biotic variables; Bold: abiotic models explaining > 20 % of the variability.**

poisson model	emersion time	emersion time2	mean	mean2	biotic factor	adj D2	% abio	% interactions	% species	% species+ int
Bathpilo - Bathsars	**	**	**	**	**	**0.67**	**0.51**	**0.14**	**0.031**	**0.17**
Bathpilo - Nephcirr	**	**	**	**		**0.55**	**0.52**	**3.78E-05**	**0.028**	**0.028**
Bathpilo - Eteolong	**	**	**	**	**	**0.60**	**0.52**	**0.037**	**0.044**	**0.081**
Bathpilo - Euryaffi	**	**		*		**0.41**	**0.46**	**5.90E-04**	**0**	**0**
Bathpilo - Eurypulc	**	**		**		**0.50**	**0.45**	**2.40E-02**	**1.90E-02**	**4.20E-02**
Bathpilo - Scolsqua						**0.66**	**0.60**	**5.40E-02**	**5.00E-03**	**6.00E-02**
Bathsars -Bathpilo	**		**	**	**	**0.29**	**0.26**	**0.03**	**0**	**0.027**
Bathsars - Nephcirr	**		**	**		**0.33**	**0.26**	**0.077**	**0**	**0.07**
Bathsars - Eteolong	*		*	**		**0.36**	**0.26**	**0**	**0.1**	**0.1**
Bathsars - Eurypulc	**		**	**	**	**0.41**	**0.26**	**0.15**	**0**	**0.15**
Bathsars - Scolsqua	**				*	**0.41**	**0.36**	**6.30E-02**	**0**	**5.00E-02**
Bathsars - Euryaffi	*		*	**		**0.24**	**0.26**	**0**	**0**	**0**
Nephcirr - Bathsars	**	**	**	**	**	**0.55**	**0.52**	**0**	**0.025**	**0.022**
Nephcirr - Bathpilo	**	**	**	**	**	**0.53**	**0.52**	**1.30E-04**	**3.10E-03**	**0.0032**
Nephcirr - Scolsqua	**	**	**	**	**	**0.57**	**0.52**	**0.047**	**0**	**0.045**
Nephcirr - Bathsp	*	**	**	**		**0.53**	**0.52**	**5.60E-03**	**0**	**0.0043**
Nephcirr - Euryaffi			*			0.077	0.022	9.60E-03	0.046	0.055
Nephcirr - Eteolong		*	**	**		**0.55**	**0.52**	**0**	**0.028**	**0.027**
Nephcirr - Eurypulc	*	**	**	**	*	**0.55**	**0.52**	**2.10E-02**	**7.90E-03**	**2.90E-02**
Eteolong - Bathsars						0.23	0.18	0.057	0	0.053
Eteolong - Bathpilo		**	**	**		0.18	0.12	5.50E-03	0.057	0.063
Eteolong - Bathsp						0.23	0.18	0.055	0	0.051
Eteolong - Scolsqua						0.19	0.18	0.018	0	0.011
Eteolong - Euryaffi	**	**	**	**		**0.39**	**0.35**	**0.036**	**1.10E-03**	**0.037**
Eteolong - Eurypulc						0.16	0.18	0	3.50E-03	0
Eteolong - Nephcirr			**	*		**0.38**	**0.33**	**7.80E-03**	**0.043**	**0.051**
Euryaffi - Scolsqua	**	**	**			**0.36**	**0.36**	**0**	**4.00E-04**	**6.40E-05**
Euryaffi - Bathsars	**	**	**			**0.38**	**0.36**	**9.60E-03**	**5.60E-03**	**0.015**
Euryaffi - Bathpilo	**	**	**			**0.37**	**0.36**	**6.30E-03**	**0**	**0.0016**
Euryaffi - Bathsp	**	**	**		**	**0.41**	**0.36**	**0.051**	**0**	**0.047**
Euryaffi - Eurypulc	**	**	**		**	**0.40**	**0.36**	**2.80E-02**	**1.20E-02**	**4.00E-02**
Euryaffi - Nephcirr	**	**				0.12	0.10	1.10E-02	5.90E-03	1.70E-02

Euryaffi - Eteolong	**	**	**			**0.47**	**0.36**	**1.10E-01**	**0**	**1.00E-01**
Bathsp - Nephcirr						**0.44**	**0.40**	**0.045**	**0**	**0.042**
Bathsp - Eteolong					**	**0.42**	**0.40**	**0.018**	**4.80E-04**	**0.018**
Bathsp - Euryaffi				*	**	**0.44**	**0.35**	**1.00E-01**	**0**	**9.80E-02**
Bathsp - Eurypulc		*				**0.42**	**0.41**	**8.80E-03**	**0**	**5.10E-03**
Eurypulc - Euryaffi	**	**	*	*		**0.22**	**0.21**	**0**	**1.10E-02**	**9.50E-03**
Eurypulc - Scolsqua	**	**				0.22	0.19	0.023	6.80E-03	0.029
Eurypulc - Bathsars	**	**				0.20	0.19	0.01	3.50E-03	0.014
Eurypulc - Bathpilo	**	**				0.22	0.19	0.03	0	0.028
Eurypulc - Bathsp	**	**			*	0.23	0.18	0.053	4.10E-03	0.057
Scolsqua - Bathpilo	**	**	**	**		**0.24**	**0.26**	**0**	**6.10E-03**	**0**
Scolsqua - Bathsars	**	*	**	**		**0.43**	**0.26**	**1.60E-01**	**1.40E-02**	**1.70E-01**

Table A.3: global models - Poisson sub-models: columns: regression model coefficients; "*": almost significant (0.05<p<0.08); "": significant; adj D^2: variability explained by the total model; % abio: variability explained by the abiotic variables; % interactions: variability explained by the interaction term between abiotic variables and the biotic variables, % species: variability explained by the interacting species; % species + int: sum of % interactions and % species; Bold: abiotic models explaining > 20 % of the variability.**

binomial model	emersion time	emersion time2	mean	mean2	biotic factor	adj D2	% abio	% interactions	% species	% species+ int
Bathpilo - Bathsars	**		**		**	**0.37**	**0.27**	**0.039**	**0.058**	**0.097**
Eteolong - Eurypulc	**		**		**	**0.40**	**0.28**	**0.11**	**0.0066**	**0.12**
Bathsp - Eurypulc			**	**		**0.26**	**0.23**	**0.023**	**0.0011**	**0.024**
Scolsqua - Bathpilo			**	**		**0.23**	**0.23**	**0**	**0.0011**	**0.0011**

Table A.4: global models - binomial sub-models: columns: regression model coefficients; "": significant; adj D2: variability explained by the total model; % abio: variability explained by the abiotic variables; % interactions: variability explained by the interaction term between abiotic variables and the biotic variables, % species: variability explained by the interacting species; % species + int: sum of % interactions and % species; Bold: abiotic models explaining > 20 % of the variability.**

Appendix B (to chapter 6)

Appendix B1: Input data, sampling strategy and model validation

Input data

The research of the Belgian beach ecosystem started about a decade ago (1997 – present). The simulation model is based upon quantitative information on the littoral macrobenthos and microphytobenthos community along the Belgian coastline provided by two major research projects, financed by different branches of the Flemish government. Within the framework of the BEST project (financed by AMINAL-Nature; (Speybroeck et al., 2005b)) an inventory of the main ecosystem components (avifauna, benthos, dry beach plants and insects) was made for eleven selected beaches along the Belgian coastline both spatially and temporally (seasonal). These eleven beaches (De Westhoek (De Panne), Schipgatduinen, Zeebermduinen, Ijzermonding, Raversijde, Spinoladijk, Paelsteenpanne, de Fonteintjes, Zeebrugge, Baai van Heist, VNR “De Zwinduinen en –polders”) were considered rather natural at the time (2002-2004). Monitoring studies on beach nourishment (financed by the Flemish Coastal Waterways Division) have been carried out since 2002 (Speybroeck et al., 2004; Welvaert, 2005; Van Ginderdeuren et al., 2007; Vanden Eede and Vincx, 2010, 2011). In total, eight intertidal beaches have been sampled at different occasions and times (Ostend-Center, Ostend-East, Mariakerke, Wenduine, Bredene, Lombardsijde, Koksijde-Oostduinkerke, Nieuwpoort). These data provide a more realistic view of the current state of the Belgian beaches and as such enhance the simulating power of the model. The input data for the envelope models were derived from 300 beach samples in total, taken in the period 1997-2011 along the Belgian coast (Degraer *et. al.,* 2003; Vanden Eede, unpub. data). The biomass of chlorophyll a was assessed based on 72 samples from 9 locations (Speybroeck et al., 2008a).

Abiotic variables

Median grain size of the sediment (*MGS*) was determined by laser diffraction using a Coulter LS Particle Size Analyzer (or Coulter-counter).

The total organic matter (*TOM*, in mass percentage) of the sediment was determined by drying a subsample two days at 110°C, giving the dry weight of the sample. Afterwards the organic matter was removed by heating the sample for two hours at 450 °C, resulting in the ash weight. The difference between the former and the latter then gives the ash free dry weight that after division by the dry weight results in a measure for *TOM.*

Elevation of sampling stations and the entire beach profile were measured using a leveler. Afterwards, these readings were corroborated with the output of the M2-tidal reduction model (Coastal Division of the Agency of Maritime and Coastal Services).

Microphytobenthos

Microphytobenthos was sampled by collecting surface sediment samples through instantly freezing the upper 2 mm of the 27.3 cm Ø contact cores, using liquid nitrogen. For every sampling location, five cores were pooled together, resulting in a total sediment volume of 5.85 cm^3. Samples were stored in aluminium recipients in liquid nitrogen in the field and were transported to the lab where they were stored at -80°C until analysis.

Pigment analyses of the sediment samples determined total microphytobenthos biomass (= amount of chlorophyll a). Firstly, 5 cm^3 of the sample was lyophilized. Pigments were extracted using 5 ml 90% aceton solution and were then sonicated for 1 minute. The extract was filtered over 0.2 µm and was analysed using the High Performance Liquid Chromatography (HPLC) by the method of Wright et al. (Wright et al., 1991).

Macrobenthos

Macrobenthos (the infauna larger than 1 mm) was sampled by excavating a 0.1026 m^2 orthogonal frame to a depth of 15 cm. The sample was sieved alive in sea water, over a mesh size of 1 mm and afterwards fixated in 8 % formaldehyde solution. Samples were taken at the water line at equal time intervals, starting at high tide and following the receding tide until low tide. After staining the samples with Rose Bengal, the organisms were sorted out of the sample residue and all organisms were identified upon species level.

Beach profile

The beach profile with height above low tide along a transect of 400 m is used as basic input of the model because this length captures the intertidal region on Belgian beaches. *MGS* and *TOM* are estimated based on the following regressions, obtained from 23 beaches that served as input for the species envelope assessment (partly published in Degraer *et al.,* 2003). The eventual *MGS* and *TOM* estimates are non-deterministic and based on sampling from regression parameter distributions (mean ± SD).

$$MGS = 193.8\ (\pm 11.52) + 13.87\ (\pm 1.32) * h \qquad \text{(eq.1)}$$

$$TOM = 1.82\ (\pm 0.21) - 0.009\ (\pm 0.001) * MGS + 0.000016\ (\pm 0.000001) * MGS^2 \qquad \text{(eq. 2)}$$

Model validation

In order to validate the model, we sampled three transects along two beaches for the dominant macrobenthos species in an identical way as described in Degraer *et al.* (2003). Densities of the dominant species, total ash free dry weight (AFDW) and species richness from the samples were subsequently compared with simulated data (average values and 95% confidence intervals for 10 000 simulations) according to the sample location *h* and grain size *MGS.*

As evidenced from figure B1, observed densities and species richness fall within the confidence intervals of the model predictions. Note, however, that observed values are derived from samples with surface 0.1026m², while model estimates are always per m². This discrepancy in scale is responsible for the higher observed numbers of samples with zero individuals (on log-scale: 0.001) and higher estimates of species richness by the simulation model.

Unfortunately, we lack data on higher trophic levels. This was especially the case for birds, since they are additionally impacted by other factors like proximity to resting areas and disturbance, not allowing any validation.

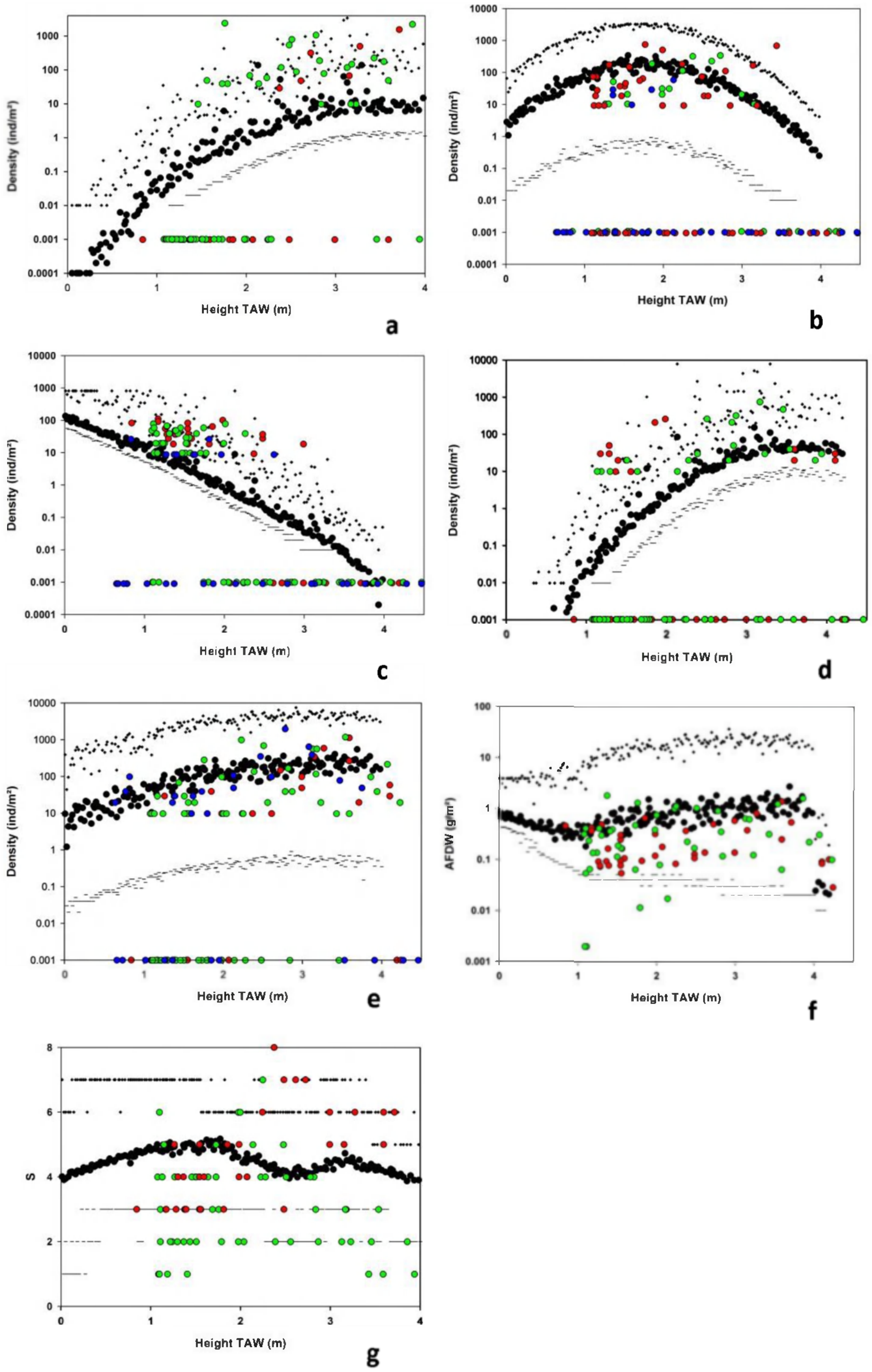

Figure B1: observed and expected densities for the main macrobenthos species (a: *Bathyporeia pilosa*; b: *B. sarsi*; c: *Eurydice pulchra*, d: *Nephtys cirrosa*, e: *Scolelepis squamata),* total macrobenthos biomass (f) and species richness (g). Note that for (a-f), y-values or on log scale. In figure (f), observed species richness comprises values within one sample (0.10 m²), while expected values are estimates per m². Observed values are depicted in coloured circles (green: Mariakerke, red: Lombardsijde transect 1, blue: Lombardsijde transect 2), average estimated values from the model are black filled circles, lower limits are (-), upper limits are (+).

Appendix B2: estimated regression coefficients by Bayesian modelling for the studied macrobenthos species and microphytobenthos (Chl a).

Mean estimates are provided with SD between brackets. The 95 % credibility intervals are depicted between square brackets in grey tones.

taxa	β_0	β_1 (MKG)	β_2 (MKG^2)	β_3 (h)	β_4 (h^2)	β_5 (OM)	β_6 (OM^2)
Chl a	0.16 (0.57)	-0.63 (0.25)	-0.1 (0.08)	-0.44 (0.1)	-0.1 (0.11)	-	-
	[-1.03,1.02]	[-1.15,-0.16]	[-0.05,0.25]	[-0.63,-0.24]	[-0.31,0.11]	-	-
P. elegans	3.2 (1.43)	-3.[illegible] (2.3[illegible]	-7.4 (3.38)	-1.13 (0.67)	-2.14 (0.6)	0.43 (0.74)	-1.06 (0.81)
	[0.49,5.9]	[-8.5,0.51]	[-14.5,-1.97]	[-2.68,0.07]	[-3.35,-1.07]	[-1.15,1.84]	[-2.68,0.47]
S. filicornis	-0.22 (2.04)	-2.82 (2.43)	-6.48(3.34)	-5.38 (1.06)	-1.69 (0.88)	0.8 (0.7)	-0.25 (0.68)
	[-4.64,3.35]	[-7.76,1.67]	[-13.39,-0.86]	[-7.65,-3.4]	[-3.85,-0.25]	[-0.52,2.34]	[-1.69,1.05]
E. longa	4.76 (0.95)	1.65 (0.75)	-1.27 (0.43)	-0.93 (0.34)	-1.28 (0.26)	1.04 (0.46)	-0.96 (0.34)
	[3.14,7.21]	[0.29,3.23]	[-2.18,-0.52]	[-1.59,-0.25]	[-1.82,-0.81]	[0.12,1.92]	[-1.66,-0.32]
C. capitata	0.93 (1.61)	-0.19 (1.31)	-0.28 (0.73)	-2.24 (0.57)	-0.14 (0.4)	0.68 (0.89)	0.15 (0.22)
	[-1.82,4.52]	[-2.54,2.22]	[-2.1,0.88]	[-3.63,-1.27]	[-0.95,0.65]	[-0.78,2.85]	[-0.26,0.62]
S. squamata	2.05 (2.28)	1.18 (0.51)	-0.46 (0.19)	0.49 (0.50)	-0.81 (0.31)	-0.50 (0.57)	0.15 (0.11)
	[-4.40,4.22]	[-0.39,1.94]	[-0.73,0.20]	[-0.90,1.2]	[-1.19,0.11]	[-1.93,0.24]	[-0.01,0.46]
N.hombergii	-13.22 (5.54)	-5.56 (5.68)	-5.89 (7.49)	-16.27 (9.2)	-6.94 (5.82)	1.27 (2.21)	0.82 (2.34)
	[-28.61,-5.17]	[-20.1,3.11]	[-27.92,2.94]	[-37.88,-4.63]	[-19.02,1.51]	[-2.85,6.02]	[-3.14,6.97]
N.cirrosa	-1.41 (0.69)	-1.03 (0.47)	-0.22 (0.31)	-3.51 (0.33)	-0.09 (0.28)	-0.29 (0.31)	-0.17 (0.19)
	[-2.76, -0.14]	[-2.15,-0.21]	[-0.85,0.36]	[-4.2,-2.89]	[-0.71,0.44]	[-0.93,0.30]	[-0.58,0.15]
B. pilosa	-1.18 (0.25)	-0.19 (0.65)	-0.15 (0.12)	3.54 (0.18)	-1.13 (0.13)	-0.15 (0.31)	0.17 (0.11)
	[-2.22,-1.30]	[-1.55,0.91]	[-0.42,0.07]	[3.05,3.87]	[-1.35,0.93]	[-0.83,0.35]	[-0.03,0.45]
E. pulchra	-0.04 (1.41)	0.52 (0.76)	-0.52 (0.25)	2.75 (0.67)	-1.61 (0.40)	-0.28 (0.46)	0.04 (0.13)
	[-4.15,1.48]	[-1.02,2.01]	[-0.98,0.02]	[0.99,3.72]	[-2.14,0.44]	[-1.16,0.62]	[-0.20,0.29]
E. affinis	0.26 (1.88)	-1.08 (0.68)	-0.25 (0.28)	-0.36 (0.39)	-1.68 (0.39)	0.24 (0.54)	-0.22 (0.28)
	[-5.48,2.48]	[-2.65,0.17]	[-0.77,0.43]	[-1.15,0.51]	[-2.31,0.43]	[-0.64,1.40]	[-0.92,0.22]
B. sarsi	4.02 (0.93)	-0.65 (0.82)	-0.63 (0.59)	-0.21 (0.48)	-2.51 (0.53)	-0.66 (0.79)	-0.15 (0.46)
	[2.37,5.75]	[-2.36,0.9]	[-1.76,0.54]	[-1.11,0.75]	[-3.66,-1.54]	[-2.52,0.65]	[-1.09,0.67]

Appendix B3: average conversion factors for abundance towards g ash-free dry weight (AFDW) (Vanden Eede, unpublished results)

	Species	**gAFDW**
Isopoda	*Eurydice pulchra*	0.00066
Isopoda	*Eurydice affinis*	0.00066
Amphipoda	*Bathyporeia pilosa*	0.00025
Amphipoda	*Bathyporeia sarsi*	0.00033
Annelida (Spionidae)	*Scolelepis squamata*	0.00479
Annelida (Spionidae)	*Pygospio elegans*	0.00016
Annelida (Spionidae)	*Spio filicornis*	0.00010
Annelida (Phyllodocidae)	*Eteone longa*	0.00016
Annelida (Capitellidae)	*Capitella capitata*	0.00007
Annelida (Nephtyidae)	*Nephtys cirrosa*	0.00434
Annelida (Nephtyidae)	*Nephtys hombergii*	0.00500

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Publication list

A1 - Peer reviewed articles

1. Speybroeck, J., Van Tomme, J., Vincx, M. and Degraer, S. In situ study of the autecology of two closely related, co-occurring sandy beach amphipods. 2008. Helgoland Marine Research 62(3): 257-268.

2. Van Tomme, J., Van Colen, C., Degraer, S. and Vincx. M. Encounter competition partly explains the segregation of the sandy beach amphipods *Bathyporeia pilosa* and *Bathyporeia sarsi*. 2012. Journal of Experimental Marine Biology and Ecology 438, 118–124.

3. Van Tomme, J., Vanden Eede, S. , Speybroeck, J. , Degraer, S. and Vincx, M. Macrofaunal sediment selectivity considerations for beach nourishment programmes. Marine Environmental Research 84, 10-16.

4. Van Tomme, J., Degraer, S., Willems, W., Dauvin, J.C., Denis, L., de la Huz, R., Janssen, G.M., Menn, I., Rodil I.F. and Vincx. M. The structuring role of biotic interactions in distribution and zonation patterns of macrobenthos on West European sandy beaches. Submitted in Estuarine, Coastal and Shelf Science.

5. Van Tomme, J., Degraer, S. and Vincx. M. Role of predation on sandy beaches: predation pressure and prey selectivity estimated by lab experiments. Submitted in Journal of Experimental Marine Biology and Ecology.

6. Van Tomme, J., Vanden Eede, S., De Busschere, C., Vandegehuchte, M., Sabbe, K., Stienen, E., Degraer, S., Vincx, M. and Bonte, D. Assessing the impact of beach nourishment on the intertidal food web through the development of a mechanistic-envelope model. In preparation.

Oral presentations

1. Van Tomme, J., Vincx, M., Degraer, S. “Biotic interactions on Sandy beaches?” Oral presentation Sixth Marine Biology Section Symposium, Ghent (Belgium), 2008.

2. Van Tomme, J., Degraer, S., Willems, W., Dauvin, J.C., Denis, L., de la Huz, R., Janssen, G.M., Menn, I., Rodi, I.F. and Vincx, M. "The structuring role of biotic interactions in distribution and zonation patterns of macrobenthos on West European sandy beaches." Oral presentation Sandy Beach Symposium, Rabat (Morocco), 2009.

3. Van Tomme, J., Vincx, M., Degraer, S. "Competition between *Bathyporeia pilosa* and *Bathyporeia sarsi*?" Oral presentation Eighth Marine Biology Section Symposium, Ghent (Belgium), 2010.

Poster presentations

1. Van Tomme, J., Degraer, S., Willems, W., Dauvin, J.C., Denis, L., de la Huz, R., Janssen, G.M., Menn, I., Rodi, I.F. and Vincx, M. "The structuring role of biotic interactions in distribution and zonation patterns of macrobenthos on West European sandy beaches." Poster presentation VLIZ young scientists' day, Ostend (Belgium), 2009.

Reports

1. Van Tomme, J., Vincx, M., Degraer, S. Biologische monitoring van de munitiestortplaats "Paardenmarkt". Eindrapport. 2007. FOD Volksgezondheid, Veiligheid van de voedselketen en Leefmilieu. 66 p.

2. Van Tomme, J., Vandewalle, S., Speybroeck, J., Bonte, D., Maelfait, J., Provoost, S., Degraer, S., Vincx, M. Studie over de impact van zandsuppleties op het ecosysteem – fase 4 – dossiernummer 207.260. 2009. Ministerie van de Vlaamse Gemeenschap, Departement Leefmilieu en Infrastructuur, Agentschap voor Maritieme Dienstverlening en Kust, Afdeling Kust. 87 p.