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ECOLOGY OF MACROBENTHOS AS A BASELINE FOR AN ECOLOGICAL ADJUSTMENT OF BEACH NOURISHMENT

ECOLOGIE VAN MACROBENTHOS ALS EEN BASIS VOOR EEN ECOLOGISCHE BIJSTURING VAN STRANDSUPPLETIES

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Dankwoord

Met groot risico op een melige epiloog, aan het einde van de rit nog even dit.

Men vertelt mij dat dit onderdeel het enige is dat echt gelezen wordt. Daarom dacht ik misschien te moeten beginnen met een of ander smakelijk grapje of een opmerkelijke anekdote. Gezien mijn dissidente aard, doe ik dit echter niet en verwijs ik de lezer door naar de overvloedige prozaïsche praat die ongetwijfeld zal te horen zijn tijdens mijn doctoraatsreceptie.

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Summary

This thesis investigates the macrobenthic infauna from Belgian beaches and the impact of beach nourishment on unique sandy beach species of the upper intertidal *Scolelepis squamata-Eurydice pulchra* community (Van Hoey *et al.*, 2004). Whereas diversity and zonation describing research on this community is partially available (Elliott *et al.*, 1997; Degraer *et al.,* 1999a; Degraer *et al.*, 2003a), population studies of the key species are lacking. Furthermore, a process-directed approach of the impact of beach nourishment is lacking, as most studies present 'just another case study', often with methodological imperfections (Parr *et al.*, 1978; Dankers *et al.*, 1983; Reilly and Bellis, 1983; McLachlan, 1996; Rakocinski *et al.*, 1996; Nordstrom, 2005; Peterson *et al.*, 2006).

Nowadays, beach nourishment is widely applied for coastal protection. Though it is believed to result in less severe ecological changes than the construction of hard structures, a detrimental impact has been observed. In order to investigate the impact of beach nourishment on the ecosystem, we need knowledge on the overall sandy beach ecosystem (Chapter 1), on the known impact of beach nourishment (Chapter 2), on the life cycle and small-scale distribution (zonation) of key species (Chapters 3 and 4) and on the species-dependent impact to be expected (Chapters 5 and 6). This information allows us to build up a methodology for pre-impact assessment of effects, rather than to record the impact of a single nourishment project in 'just another case study' (Chapter 7).

The thesis consists of four major parts. The first part serves as introduction to the thesis' theme (Chapter 1 and 2). The second part presents field research on population dynamics, life cycle and intertidal zonation patterns (Chapter 3 and 4). The third part presents an experimental approach of habitat-related processes relevant to beach nourishment (Chapter 5 and 6). The final part uses the output of all previous parts to build a methodology for the study of the ecological impact of beach nourishment (Chapter 7). This final part of the thesis uses the outcome of those chapters to build up a discussion *ad rem*.

Each chapter has been conceived as a stand-alone paper. To allow separate reading of each chapter, some content overlap was unavoidable. The cited literature has, however, been compiled in a single list at the end of the thesis. The author's list of publications is provided in appendix.

A need for background information

A literature review was conducted on the Belgian sandy beach ecosystem (Chapter 1). Available knowledge on sedimentology and hydrodynamics and five major ecosystem components - microphytobenthos, vascular plants, terrestrial arthropods, zoobenthos (macrobenthos, meiobenthos, hyperbenthos and epibenthos) and avifauna - was summarised. Belgian beaches are characterised by highly adapted organisms. Even a highly recreational and heavily populated coastline like the Belgian coast provides valuable yet threatened habitats to several beach-dependent species, which may reach high numbers. Short-lived and thalassochorous vascular plants inhabit the drift line, dry beach and embryonic dunes. Terrestrial arthropods inhabiting the same general area are highly diverse, comprising halobiontic, halophilous and haloxene species, with sandhopper (*Talitrus saltator*) and

dipterans (flies) as prominent members. Very little is known about the microphytobenthos as an important primary producer on Belgian beaches, mainly consisting of diatoms. Belgian beaches also have a specific zoobenthic fauna in both meiofauna and macrofauna, e.g. the typical upper intertidal *Scolelepis squamata-Eurydice pulchra* community. Also epi- and hyperbenthic animals are depending on the beach, e.g. as nursery grounds. Birds do not nest nowadays on Belgian beaches, yet they are important for resting and foraging (e.g. sanderling *Calidris alba*). Little is know about biological interactions on Belgian beaches. Conclusively, it is stressed how human actions associated with several aspects of recreation, beach management and fisheries, endanger the biota.

A second step was to investigate what is known on the impact of beach nourishment all over the world (Chapter 2). From literature, negative, ecosystem-component specific effects of beach nourishment dominate on a short to medium term, with the size of the impact being determined by (1) activities during construction phase, (2) quality and (3) quantity of the nourishment sand, (4) timing, place and size of project, and (5) the nourishment technique and strategy applied. On a long term, the speed and degree of ecological recovery largely depend on the physical characteristics of the beach habitat, mainly determined by (1) sediment quality and quantity, (2) the nourishment technique and strategy applied, (3) place and size of nourishment, and (4) the physical environment prior to nourishment. The limited information available on indirect and cumulative ecological effects indicates that these effects cannot be neglected in an overall impact assessment. Hence, for ecologically good practice of beach nourishment, it is advised (1) to choose nourishment sands with a sediment composition comparable to that of the natural sediment, (2) to avoid short term compaction by ploughing immediately after construction, (3) to execute the nourishment in a period of low beach use by birds and other mobile organisms, (4) to choose a number of smaller projects rather than a single large nourishment project and (5) to select the nourishment technique with respect to the local natural values. A major outcome of this review is the need for elucidation of the biological processes behind impact and recovery of all ecosystem components through experimental research, which gave rise to the research as presented in Chapters 5 and 6.

A need for in-depth knowledge on key species

We focused on the unique *Scolelepis squamata-Eurydice pulchra* community and investigated life cycle, demography, somatic production and zonation of three key species within this community. Eight beach transects on Belgian sandy beaches were monthly sampled from October 2003 until October 2004, in order to investigate seasonal trends in abundance, biomass, secondary production, and patterns in reproduction and zonation.

In Chapter 3, the polychaete *Scolelepis squamata* was investigated. This species constitutes an important food resource for juvenile flatfish and wading birds, thus playing an important role in sandy beach ecosystem functioning. Average density, modal density and modal biomass did not exhibit major seasonal changes, whereas average biomass and individuals and biomass per strip transect did, peaking in May 2004. P/B ratio was intermediate to moderately low compared to other polychaete species. Gravid females and fertile males were found from February until August and a single recruitment period was observed from July until September. Highest densities (> 200 ind/m²) were mostly found above 3 m above MLLWS and average modal or peak density along each transect was situated from 3.95 m up to 4.40 m above MLLWS, in contrast to some other studies where the species was restricted to mid-tidal levels. Significant differences in elevation of peak density were found between non-fertile and fertile animals, but not between fertile males and fertile females. Fertile males occupied a significantly wider range than fertile females, corresponding with a horizontal range difference of 6-9 m cross-shore. The observed zonation pattern, together with a trend in the difference of peak abundance elevation between males and females, are hypothesised to be a result of a strategy of fertile animals to ensure co-occurrence in a narrower zone during reproduction. Observed differences between Brazilian, Moroccan and Belgian populations (e.g. density, biomass, productivity, P/B, life span, body width, period of presence of fertile individuals and recruitment) do not seem to concur with differences in morphodynamics and might be attributed to latitude-associated gradients like climate.

Chapter 4 dealt with the amphipods *Bathyporeia pilosa* and *B. sarsi*. Their biomass and production were assessed for the first time. *Bathyporeia pilosa* could reach two times higher abundance and biomass and higher levels of production, while nearly absent along eastern transects. Continuous reproduction and recruitment with three relative peaks of the latter (February, July, October) were observed. Fecundity showed parallel temporal variation for both species, peaking in February and September-October. Interestingly, the July relative recruitment peak could not be explained by relative abundance of gravid females or fecundity, but is probably caused by adult mortality. Both species displayed comparable gonad production, but *B. pilosa* produced fewer yet larger embryos. Peak abundances were found at 436 ± 25 SD cm (*B. pilosa*) and 357 ± 40 SD cm (*B. sarsi*) above MLLWS, corresponding to a 40-62 m cross-shore distance between the peaks of both species. The occupied cross-shore range was larger for *B. sarsi* than for *B. pilosa,* for females than for males, and for adults than for juveniles of *B. pilosa*. Both species displayed many comparable life history features.

A need for species-dependent impact prediction

The importance of the sediment composition of the fill sediment was investigated through lab experiments with the same three key species.

Regarding *Scolelepis squamata*, its benthic habitat was investigated through lab experiments but also field data analysis, aiming at guidelines for impact mitigation of beach nourishment (Chapter 5). Survival, feeding frequency, burrowing time and grain size selection were investigated to assess tolerance and preference for sediment types varying in median grain size. Remarkable preference for very coarse sands contrasted with longer burrowing time. Feeding frequency was higher in coarser sands. Survival was total in all but very fine sands, where total mortality was observed. Data from five beaches were used to model *Scolelepis* abundance based on three environmental variables (elevation, median grain size and slope). The degree of overdispersion remained large across models. Experimentally observed grain size preference seems to conflict with in situ distribution. High levels of overdispersion in our field data analysis suggest other additional factors (additional physical variables, interspecific and intraspecific interactions) determine *Scolelepis* abundance and post-nourishment recovery. For swift recolonisation of nourished beaches, nourishment is advocated to be executed in winter by means of foreshore nourishment in sections with alternation of nourished and unnourished stretches of beach. Concerning the fill quality, very fine sands and high concentrations of fines should be avoided, while also very coarse sands may hamper *Scolelepis squamata* populations. Factors explaining cross-shore and long-shore distribution of the species are still poorly known, as apparent from the field data analysis.

Chapter 6 looked into the same issue with the co-occurring amphipods *Bathyporeia pilosa* and *B. sarsi* but also investigated the more fundamental causes for the observed cross-shore segregation of both species. Sediment preferences and tolerances were investigated through lab experiments. Preferences were investigated in both allotopic and syntopic conditions, in order to investigate possible avoidance (as a proxy for interspecific competition). Selection of grain size showed no significant differences between the species, nor did the presence of the other species affect the selection. Both species avoided the finest (63-125 µm) and coarsest (>500 µm) grain sizes. Potential niche width with regard to grain size, as established from our experiments, was larger than the occupied width, as observed from field data. Selection of level of fines did not show any difference between species or condition (allo- vs. syntopy) either, while the highest abundance of *B. pilosa* occurred in 5% fines, whereas that of *B. sarsi* occurred in the absence of fines. Mortality of animals forced to survive in a single given sediment, was significantly higher in *B. sarsi*, and both species had low mortality levels at a grain size best resembling natural beach sediment. Thus, whereas preferences of both species are largely comparable, tolerances are not. No evidence for interspecific competition, explaining cross-shore segregation, could be found.

Towards a pre-impact predictive and mitigative methodology for scientific research

In this conclusive section (Chapter 7), a methodological scheme was developed for pre-impact assessment of the ecological impact of beach nourishment. Data needs on the physical and biological environment were specified. Secondly, methodological aspects of data collection were presented and a distinction was made between indispensable and less essential types of data. Cost-benefit considerations were made and options to cut costs were raised. Thirdly and finally, we applied the scheme to our case study on intertidal macrobenthic fauna of Belgian beaches. Population studies and experiments characterising the habitat of three selected key species were conducted. For these taxa foreshore nourishment in winter (December-January) seems preferable. Fill sediment has to match the natural sand closely. The proposed framework is easily applicable to other taxa, ecosystems and impact studies.

This thesis first offers two valuable literature overviews, which resulted in focused research. This research provides important, previously unavailable data on the life and distribution of key species of the sandy beach ecosystem. The process-directed experimental research offers a novel approach towards the study of the ecological impact of beach nourishment and makes way for predictive research and mitigating measures prior to the impact. This approach can easily be translated to other ecosystem components and the study of other human impacts.

Samenvatting

Deze scriptie onderzoekt de macrobenthische infauna van Belgische stranden en de impact van strandopspuitingen (of suppletie) op de unieke zandstrandsoorten van hoogintertidale *Scolelepis squamata-Eurydice pulchra*gemeenschap (Van Hoey *et al.*, 2004). Terwijl kennis over de diversiteit en zonatiepatronen van deze fauna reeds deels voorhanden is (Elliott *et al.*, 1997; Degraer *et al.,* 1999a; Degraer *et al.*, 2003a), ontbreken populatiestudies over de sleutelsoorten. Bovendien zijn de meeste beschikbare studies omtrent de impact van strandsuppletie slechts individuele gevalsstudies, veelal met methodologische gebreken (Parr *et al.*, 1978; Dankers *et al.*, 1983; Reilly and Bellis, 1983; McLachlan, 1996; Rakocinski *et al.*, 1996; Nordstrom, 2005; Peterson *et al.*, 2006). Een proces-gerichte benadering ontbreekt.

Strandsuppletie wordt tegenwoordig courant gebruikt als middel voor kustverdediging. Hoewel men aanneemt dat deze ingreep minder ernstige ecologische veranderingen veroorzaakt dan het bouwen van harde structuren, werden schadelijke effecten waargenomen. Om dit onderwerp te onderzoeken, is er nood aan kennis inzake het zandstrandecosysteem (Hoofdstuk 1), de gekende impact van strandsuppletie (Hoofdstuk 2), de levensgeschiedenis en kleinschalige verspreiding (zonatie) van sleutelsoorten (Hoofdstukken 3 and 4) en de te verwachten soortgebonden impact (Hoofdstukken 5 en 6). Deze informatie laat toe een methodologie op te stellen voor de pre-impact inschatting van effecten, in tegenstelling tot het vaststellen van de impact van afzonderlijke suppletieprojecten in verenkelde gevalsstudies (Hoofdstuk 7).

De tekst bestaat uit vier hoofdonderdelen. Het eerste deel dient als een inleiding op het thema van de thesis (Hoofdstukken 1 en 2). Het tweede deel bestaat uit de resultaten van velonderzoek naar de populatiedynamica, levenscyclus en intertidale zonatiepatronen van de geselecteerde studiesoorten (Hoofdstukken 3 en 4). Het derde deel biedt een experimentele benadering van habitat-gerelateerde processen, die relevant zijn bij suppletie (Hoofdstukken 5 en 6). Het finale onderdeel gebruikt de resultaten van alle voorgaande delen om te trachten een methodologie te ontwikkelen voor de studie van de ecologische impact van strandsuppletie (Hoofdstuk 7). Dit laatste deel wendt de output van deze hoofstukken aan om een discussion *ad rem* te voeren.

Elk hoofdstuk werd opgevat als een zelfstandig artikel. Om afzonderlijke lezing van elk hoofdstuk toe te laten, was enige overlap onvermijdelijk. De gerefereerde literatuur werd, echter, gecompileerd in een enkele lijst achterin the thesis. De publicatielijst van de auteur werd tenslotte in appendix toegevoegd.

Nood aan achtergrondinformatie

Een literatuurstudie werd uitgevoerd rond het Belgisch zandstrandecosysteem (Hoofdstuk 1). De beschikbare kennis inzake sedimentologie en hydrodynamiek alsook inzake vijf prominente ecosysteemcomponenten - microfytobenthos, vaatplanten, terrestrische arthropoden, zoöbenthos (macrobenthos, meiobenthos, hyperbenthos en epibenthos) en avifauna - werd samengevat. De Belgische zandstranden worden gekenmerkt door sterk aangepaste organismen. Zelfs een dicht bevolkte kustlijn met hoge graad aan recreatie biedt waardevolle doch bedreigde habitats voor verschillende strandafhankelijke soorten, die hoge aantallen kunnen bereiken. Kortlevende, thalassochore vaatplanten bewonen de vloedmerklijn, het droogstrand en de embryonale duinen. Een diverse fauna aan terrestrische arthropoden bewoont dezelfde zone. Ze omvat halobionte, halofiele en haloxene soorten, met de strandvlo (*Talitrus saltator*) en dipteren (vliegen) als prominente vertegenwoordigers. Over de primaire productie door het microfytobenthos (voornamelijk kiezelwieren) op Belgische stranden is bijna niks geweten. Belgische stranden herbergen ook een specifieke benthische fauna, zowel inzake meio- als macrofauna, bv. de typisch hoogintertidale *Scolelepis squamata-Eurydice pulchra* gemeenschap. Ook epi- en hyperbenthische dieren zijn gebonden aan het strand, bv. als broedkamer. Op heden broeden geen vogels op Belgische stranden. Toch zijn deze belangrijk als rust- en foerageergebied, bv. voor de drieteenstrandloper (*Calidris alba*). Er blijkt amper iets geweten over interacties tussen de biota op Belgische stranden. Tenslotte werd geduid hoe menselijke activiteiten geassocieerd met recreatie, kustzonebeheer en visserij de strandbiota bedreigen.

Een tweede stap was het verzamelen van de beschikbare kennis omtrent de ecologische impact van strandsuppleties wereldwijd (**Hoofdstuk** 2). Uit de literatuur blijken negatieve, ecosysteemcomponent-specifieke effecten te domineren op korte en middellange termijn. De omvang van de impact wordt hierbij bepaald door (1) activiteiten tijdens de aanlegfase, (2) kwaliteit en (3) kwantiteit van het suppletiezand, (4) timing, plaats en grootte van het project, en (5) de toegepaste opspuitingstechniek en -strategie. Op lange termijn hangen de snelheid en mate van ecologisch herstel grotendeels af van de fysische karateristieken van de strandhabitat, voornamelijk bepaald door (1) sedimentkwaliteit en -kwantiteit, (2) de toegepaste opspuitingstechniek en -strategie, (3) plaats en grootte van het project en (4) het fysisch milieu vóór de suppletie. De beperkte beschikbare informatie omtrent indirecte en cumulatieve ecologische effecten geeft aan dat deze niet verwaarloosd mogen worden in een globale impactinschatting. Uit de literatuur volgen een aantal adviezen voor een ecologisch goede praktijk voor strandsuppletie: (1) keuze van suppletiezand met een sedimentsamenstelling zoals het natuurlijke sediment, (2) ploegen kort na de aanleg, om kortetermijncompactie te vermijden, (3) timen van de werkzaamheden in functie van het strandgebruik door vogels en andere mobiele organismen, (4) liever enkele kleinere projecten dan één grote opspuiting en (5) keuze van de suppletietechniek in functie van de lokale natuurwaarden. Eén van de voornaamste besluiten van de literatuurstudie is de nood aan het bestuderen van de lopende biologische processen bij impact en herstel voor alle ecosysteemcomponenten door middel van experimenteel onderzoek. Hieruit volgde het onderzoek zoals besproken in de **Hoofdstukken 5 en 6**.

Nood aan diepgaande kennis over sleutelsoorten

In deze scriptie spitsten we ons toe op de unieke *Scolelepis squamata-Eurydice pulchra*gemeenschap en onderzochten we de levensgeschiedenis, demografie, somatische productie en zonatie van drie sleutelsoorten binnen deze gemeenschap. Acht transecten op Belgische stranden werden maandelijks bemonsterd van oktober 2003 tot en met oktober 2004 om seizoenale trends in abundantie, biomassa, secondaire productie en reproductie- en zonatiepatronen te bestuderen.

In **Hoofdstuk 3** werd de polychaet *Scolelepis squamata* onderzocht. Deze soort vormt een belangrijke voedselbron voor juveniele platvissen en steltlopers en vertolkt aldus een sleutelrol in het functioneren van het zandstrandecosysteem. Gemiddelde en modale dichtheid en modale biomassa vertoonden geen seizoenale schommelingen, in tegenstelling tot gemiddelde biomassa en dichtheid en biomassa per transectstrook met pieken in mei 2004. De P/B-ratio was intermediair tot vrij laag in vergelijking met die van andere borstelwormsoorten. Fertiele individuen werden aangetroffen van februari tot augustus en een enkele rekruteringsperiode werd waargenomen van juli tot september. De hoogste dichtheden (> 200 ind/m²) werden veelal aangetroffen boven 3 m boven GLLWS en de gemiddelde piekdichtheid langsheen elk transect bevond zich op 3.95 m tot 4.40 m boven GLLWS, in contrast met een aantal studies waar de soort tot mid-intertidale niveaus beperkt was. Significante verschillen in de hoogteligging van de piekdichtheid werden gevonden tussen niet-fertiele en fertiele dieren maar niet tussen mannetjes en wijfjes. Fertiele mannetjes bezetten een significant bredere zone dan de wijfjes (horizontaal dwarsstrands verschil van 6-9 m). Het waargenomen zonatiepatroon en de trend in het verschil tussen mannetjes en wijfjes in de ligging van hun piekdichtheden zouden kunnen deel uitmaken van een strategie van fertiele dieren om gezamenlijk voorkomen ten tijde van de voortplanting te bevorderen. Verschillen tussen Braziliaanse, Marokkaanse en Belgische populaties (inzake o.m. dichtheid, biomassa, productiviteit, P/B-ratio, levensduur, lichaamsomvang, periode van aanwezigheid van fertiele dieren en rekrutering) lijken niet overeen te stemmen met verschillen in strandmorfodynamica en is mogelijk te wijten aan breedtegraad-gebonden gradiënten zoals het klimaat.

Hoofdstuk 4 behandelt de vlokreeftjes *Bathyporeia pilosa* en *B. sarsi*. Hun biomassa en productiviteit werden voor de eerste maal bepaald. *Bathyporeia pilosa* bereikte op bepaalde locaties twee maal hogere dichtheden en biomassa en hogere productiviteit, terwijl deze soort nagenoeg ontbrak op de meest oostelijk gelegen transecten. Continue reproductie en rekrutering met drie relatieve pieken (februari, juli en oktober) werden waargenomen. De fecunditeit vertoonde sterk parallelle temporele variatie van beide soorten, met pieken in februari en september-oktober. Interessant is dat de relatieve rekruteringspiek van juli niet verklaard kon worden op basis van de patronen in de relatieve dichtheid van graviede wijfjes of de fecunditeit, maar meer dan waarschijnlijk te wijten is aan adulte mortaliteit. Beide soorten vertoonden vergelijkbare waarden voor de gonadenproductie, terwijl *B. pilosa* minder doch grotere embryo's produceerde. Piekdichtheden werden aangetroffen op 436 ± 25 SD cm (*B. pilosa*) en 357 ± 40 SD cm (*B. sarsi*) boven GLLWS, wat overeenstemt met een dwarsstrandse afstand van 40-62 m tussen de pieken van beide soorten. De bezette dwarsstrandse zone was breder voor *B. sarsi* dan voor *B. pilosa,* voor wijfjes dan voor mannetjes en bij *B. pilosa* voor adulten dan voor juvenielen. Beide soorten vertoonden veel sterk gelijkaardige levensgeschiedeniskarakteristieken.

Nood aan soortafhankelijke impactvoorspelling

Het belang van de samenstelling van het op te spuiten zand werd onderzocht door middel van labo-experimenten met dezelfde drie sleutelsoorten.

De benthische habitat van *Scolelepis squamata* werd onderzocht door middel van zowel labo-experimenten als analyse van veldgegevens met het oog op richtlijnen voor impactreductie van strandsuppletie (**Hoofdstuk** 5). Overleving, voedingsfrequentie, graaftijd en korrelgrootteselectie werden onderzocht om de tolerantie en preferentie ten aanzien van verschillende sedimenttypes (variërend inzake mediane korrelgrootte) te bestuderen. Een opmerkelijke voorkeur voor zeer grof zand stond in contrast met een langere graaftijd in dat zelfde zandtype. De voedingsfrequentie was hoger in grover zand. Er werd totale overleving vastgesteld in alle sedimenttypes, behalve in het zeer fijn zand, waar dan weer totale mortaliteit werd waargenomen. Veldgegevens van vijf stranden werden gebruikt om de dichtheid van *Scolelepis* te modelleren op basis van drie omgevingsvariabelen (hoogteligging, mediane korrelgrootte en hellingsgraad). De graad van overdispersie bleef hoog in alle modellen. De experimenteel vastgesteld korrelgroottepreferentie leek in strijd met de verspreiding van de soort in het veld. Hoge niveaus van overdispersie in de velddata-analyse gaven aan dat ook andere factoren (overige fysische variabelen, inter- en intraspecifieke interacties) invloed moeten hebben op de dichtheid van de soort en het herstel van diens populaties na suppletie. Voor een vlotte rekolonisatie van opgespoten stranden wordt suppletie best 's winters uitgevoerd door middel van vooroeversuppletie en in secties met langsstrandse afwisseling van opgespoten en onopgespoten stukken strand. Inzake de zandkwaliteit worden zeer fijn zand en hoge slibconcentraties best vermeden, hoewel ook zeer grof zand nefast kan zijn voor de onderzochte soort. Uit de analyse van de veldgegevens blijkt dat de dwars- en langsstrandse verspreiding van de soort vooralsnog moeilijk verklaard kan worden.

In **Hoofdstuk** 6 werden dezelfde elementen onderzocht voor de samen voorkomende vlokreeftjes *Bathyporeia pilosa* en *B. sarsi*, maar werd ook gezocht naar de meer fundamentele oorzaken van de waargenomen dwarsstrandse segregatie van beide soorten. Sedimentpreferenties en -toleranties werden onderzocht door middel van labo-experimenten. De preferenties werden onderzocht in zowel allotope als syntope condities, om zo mogelijk eenzijdig of wederzijds mijden te onderzoeken (als een benadering van interspecifieke competitie). De selectie van korrelgrootte onthulde geen significante verschillen tussen de soorten. De aanwezigheid van de andere soort oefende hier ook geen invloed op uit. Beide soorten meden het fijnste (63-125 µm) en grofste (>500 µm) zand. De experimenteel vastgestelde potentiële niche ten aanzien van korrelgrootte, bleek breder dan deze waargenomen in het veld. De selectie ten aanzien van slibgehalte vertoonde evenmin significante verschillen tussen de soorten en de condities (allo- vs. syntopie). De hoogste dichtheid van *B. pilosa* kwam echter voor in het sedimenttype met 5% slibgehalte, terwijl die van *B. sarsi* voorkwam in afwezigheid van slib (0 %). De sterfte van dieren die verplicht werden te overleven in één welbepaald sedimenttype was significant hoger bij *B. sarsi* en beide soorten vertoonden lage sterfte in een strandzand-benaderend sedimenttype. Hieruit volgde dat terwijl de preferenties van beide soorten sterk gelijkaardig zijn, de toleranties dat niet zijn. Er kon geen duidelijk bewijs voor interspecifieke competitie gevonden worden, zodat de waargenomen segregatie vooralsnog onverklaard blijft.

Nood aan een methodologisch kader voor pre-impact voorspelling en mitigatie

In dit conclusief luik (Hoofdstuk 7) werd een methodologisch schema ontwikkeld voor de pre-impact inschatting van de ecologische impact van strandopspuitingen. Ten eerste werden databehoeften inzake het fysisch en biologisch milieu geïdentificeerd. Ten tweede werden de methodologische aspecten van het verzamelen van deze data voorgesteld. Onderscheid werd gemaakt tussen onmisbare en minder essentiële datatypes. Kosten-batenbeschouwingen werden gemaakt en enkele kostenbesparende opties werden naar voor gebracht. Ten derde en ten laatste, werd het schema toegepast op onze gevalsstudie omtrent de intertidale macrobenthische fauna van Belgische stranden. Populatiestudies en habitat-karakteriserende experimenten werden uitgevoerd voor drie geselecteerde sleutelsoorten. Voor deze taxa lijkt vooroeversuppletie in de winter (december-januari) te verkiezen, waarbij onder meer het suppletiezand best het natuurlijke sediment maximaal benadert. Het voorgestelde kader is eenvoudig toepasbaar voor andere taxa, ecosystemen en impactstudies.

Deze scriptie levert eerst enkele waardevolle literatuuroverzichten, die vervolgens uitmondden in gericht onderzoek. Dit onderzoek verschaft in een eerste luik belangrijke, vooraf onbeschikbare gegevens over de levenswijze en verspreiding van sleutelsoorten van het zandstrandecosysteem. Het tweede luik omvat procesgericht experimenteel onderzoek, biedt een nieuwe benadering omtrent de studie van de ecologische impact van strandsuppleties en opent de weg voor voorspellend onderzoek en mitigerende maatregelen voorafgaandelijk aan de impact. Deze invalshoek kan eenvoudig vertaald worden naar andere ecosysteemcomponenten en onderzoek naar de impact van andere anthropogene ingrepen.

Outline

RATIONALE

This thesis investigates the macrobenthic infauna from Belgian beaches and the ecological impact of beach nourishment on unique sandy beach species of the upper intertidal *Scolelepis squamata-Eurydice pulchra* community (Van Hoey *et al.*, 2004). Whereas research output describing diversity and zonation of this community is partially available (Elliott *et al.*, 1997; Degraer *et al.,* 1999a; Degraer *et al.*, 2003a), population studies of the key species are lacking. Furthermore, a process-directed approach of the impact of beach nourishment is lacking, as most studies present 'just another case study', often with methodological imperfections (Parr *et al.*, 1978; Dankers *et al.*, 1983; Reilly and Bellis, 1983; McLachlan, 1996; Rakocinski *et al.*, 1996; Nordstrom, 2005; Peterson *et al.*, 2006).
The general objective is to allow *a priori* assessment on the ecological impact of beach nourishment. Often constrained in time and funding, research on the impact of nourishment has largely been confined to monitoring a specific beach nourishment project. In this thesis, the goal is to anticipate and mitigate the detrimental effects of nourishment, rather than recording damage and recovery *post hoc*. In order to achieve this, an ecosystem approach is advocated (see Chapters 1 and 2). In this thesis, we dealt with a single, pivotal component of this ecosystem -the intertidal macrobenthos- based on grounds discussed in Chapter 1. Our assessment methodology (as proposed in Chapter 7) desires, however, application to all ecosystem components. Nevertheless, macrobenthos is a key taxon in the sandy beach ecosystem and therefore an excellent first step.

After careful study of the available knowledge on beach nourishment impacts (Chapter 2) and on the sandy beach ecosystem in our study area (i.e. Belgium – Chapter 1), two major areas of research were identified as instrumental to achieve our goal: (1) population studies (Chapters 3 and 4) and (2) experimental studies (Chapters 5 and 6). Because both areas of research involve a lot of research and time, we selected a limited number of key species to be studied. The studied species were chosen based on their (1) relative abundance, (2) established trophic role and (3) dependency on sandy beaches or uniqueness for the sandy beach ecosystem (observed by their absence from neighbouring ecosystems like dune areas and the shallow intertidal). Further information on these features and the general ecology of the studies species is provided in the introductory sections of chapter 3 and 4. The three studied species occur in the upper half of the Belgian intertidal zone: the bristleworm *Scolelepis squamata* (Fig. 1) and the amphipods *Bathyporeia pilosa* (Fig. 2) and *B. sarsi*.

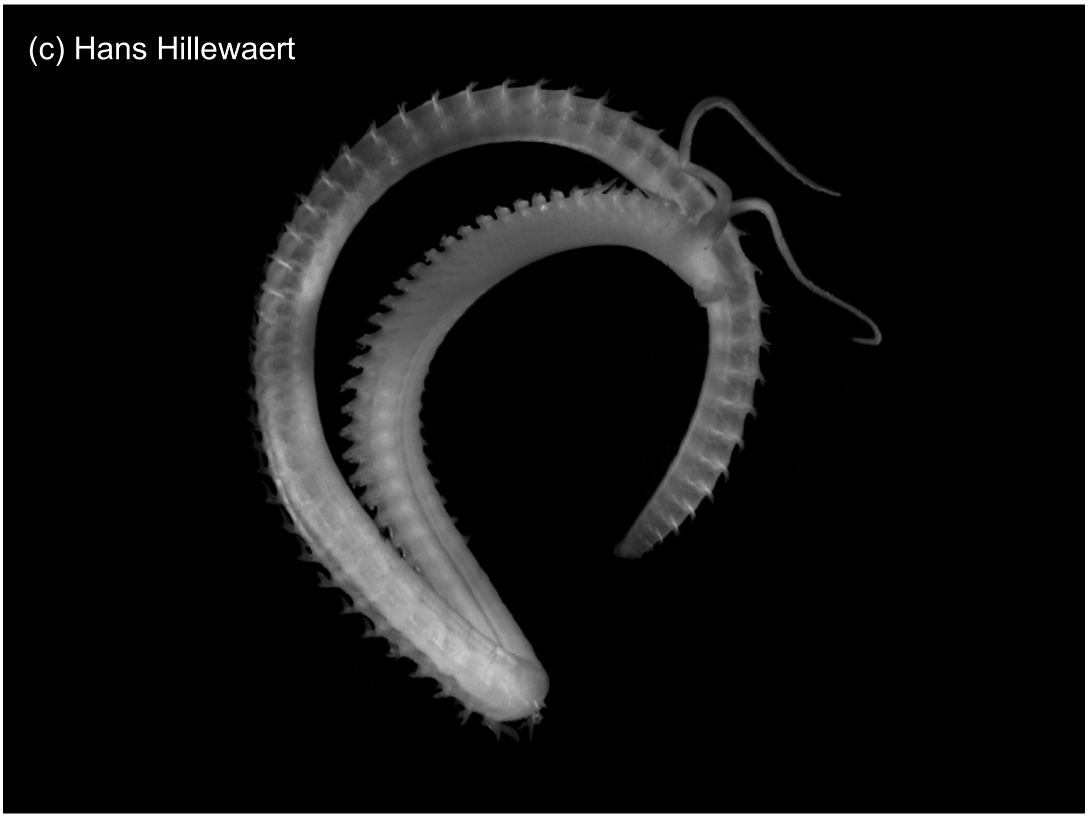


Figure 1. *Scolelepis squamata* – note typical pointed prostomium and two retractile palps. Actual body size: 6-8 cm.

Figure 2. Female *Bathyporeia pilosa* – the closely related *B. sarsi* differs a.o. in shape of first part of first antenna (= pseudorostrum), visible in this picture as an enlarged antennal segment in front of the eye. Actual body size: 0.6-1 cm.

Population studies on these species intended to provide information on the natural life cycle, production and zonation patterns of the animals on 'nourishment-free' beaches, as a pre-impact description. These data can be used in view of nourishment studies in several ways: life cycle knowledge serves ecology-friendly timing of nourishment activities, zonation patterns and their temporal variability can suggest a minimal detrimental place and time for nourishment, patterns of reproduction and recruitment can be compared later with those of nourished and possibly replenished beaches. Besides these applications, important fundamental ecological output is provided, enlarging knowledge on sandy beach ecology. The results of this research are presented in Chapters 3 and 4. Because of the nature of both studies, they have been submitted as fundamental ecological papers. However, their application to the ecological impact of beach nourishment has been made in Chapter 7.

Beach locations where the population studies have been executed were selected based on their known morphodynamic characteristics. These features have been discussed in detail and the investigated beaches have been placed within the framework of the entire Belgian coast (Chapter 1). Details on how sampling was done can be found in the material and methods sections of Chapters 3 and 4. Some minor deviations had to be made from the ideal sampling scheme, as described in Chapter 7. Sampling at spring tide would allow sampling of a maximal part of the intertidal beach. Due to practical restrictions related to sampling with a large number of people at night, this could not be achieved. To document recruitment in more detail, more frequent sampling and sieving over a 0.5 mm mesh are retrospective considerations for results of higher resolution.

Our experimental work has focused at the biological processes associated with beach nourishment and post-nourishment recolonisation and recovery of the sandy beach macrofauna. Only by investigating underlying processes such as those related to impact size and rate of recovery, the effects of future projects can be predicted and thus objective ecological adjustments in nourishment practice suggested.

As identified in Chapter 2, the relevant processes are essentially: (1) the process of disturbance and survival during nourishment and (2) the process of recolonisation after nourishment. Disturbance and survival are mainly determined by (1) species-dependent tolerances, while recolonisation is determined by (2) species specific dispersal and migration capacities and (3) species specific habitat demands and tolerances, including physical and biological elements. From these three major fields of experimental research, we focused on the latter. Considering macrobenthos, disturbance caused by nourishment is devastating and survival is believed to be quasi zero (Menn *et al.*, 2003). This makes this field of research rather trivial, and it is more relevant to focus on recovery than on survival. Burial experiments may seem highly relevant but they are not in the case of the selected taxa of the Belgian coast. The investigated species all live high up in the intertidal zone. After nourishment, the high water line and the zone occupied by each species will have moved offshore for 100-200 m. Therefore, any surviving individual will find itself on the newly created dry beach zone. As the species dealt with are clearly not adapted to terrestrial live, survival is impossible. This means that even if the species would be able to burrow upwards through the fill sediment, mortality would be close to 100%. Thus, we chose not to do this kind of experiments.

Dispersal and migratory capacities are important, if a species is to reach a post-impact beach. Longer stretches of nourished beach will take longer to become recolonised, varying according to the species-dependent differences in dispersal. We tried to obtain a rough, first estimate of *Bathyporeia* dispersal, as well as that of *Eurydice pulchra* (a fourth, less abundant member of the same community), by means of a capture-mark-recapture experiment. Dispersal of small, hard to tag and to track marine animals is difficult to assess, as obvious from the limited amount of literature available of dispersal of marine invertebrates (Günther, 1992; Dugan & McLachlan, 1999). While we successfully caught and marked over 500 specimens of *Bathyporeia pilosa*, not a single specimen was recaptured. We believed the chances of recapture are too limited in this case, because the captured amount of animals represents a too small portion of the total population to allow recapture.

Thus, our experiments were restricted to those associated with the intertidal habitat, trying to elucidate tolerances and preferences of our studied species towards a range of environmental variability that is relevant with regard to beach nourishment. We focused on median grain size of the sandy sediment and -in part- on the level of fines. The results of this research are presented in Chapters 5 and 6. Each chapter has been conceived as a separate paper. We did not make the application on beach nourishment in Chapter 6. In this chapter, we rather chose to elaborate on the syntopy of the *Bathyporeia* species and the fundamental ecological topic of niche segregation. Chapter 5, however, does include discussion and conclusions considering beach nourishment. The results of both chapters have been integrated in the general discussion, as provided in Chapter 7.

To conclude, it is crucial to bare in mind that an ecosystem approach is needed. All natural values of the beach to be nourished have to be considered, rather than a single ecosystem component. Our results specifically apply to the intertidal macrobenthos and should not be extrapolated too lightly. Although this component has a pivotal role on sandy beaches, we do not advocate the use of any component as a proxy for the entire ecosystem. Future research should focus on completing the puzzle by assessing the ecological impact of nourishment on avifauna, vascular plants, … . Challenging yet relevant fields for further study would also be invertebrate dispersal and biological interactions.

THESIS CONTENTS AND STRUCTURE

The thesis consists of four major parts. The first part serves as introduction to the thesis' theme (Chapter 1 and 2). The second part presents field research on population dynamics, life cycle and intertidal zonation patterns (Chapter 3 and 4). The third part presents an experimental approach of habitat-related processes relevant to beach nourishment (Chapter 5 and 6). The final part uses the output of all previous parts to build a methodology for the study of the ecological impact of beach nourishment (Chapter 7). This final part of the thesis uses the outcome of those chapters to build up a discussion *ad rem*.

Each chapter has been conceived as a stand-alone paper. To allow separate reading of each chapter, some content overlap was unavoidable. The **cited literature** has, however, been compiled in a single list at the end of the thesis. The author's **list of publications** is provided in appendix.

Chapter 1 presents a comprehensive overview of the available knowledge on the sandy beach ecosystem, from the foreshore up to the foredunes. Besides the macrobenthic infauna, as the focal organism group of this thesis, other major sandy beach ecosystem components are taken into account: microphytobenthos, semi-terrestrial arthropods, vascular plants, avifauna and the other benthic groups (epi-, hyper- and meiobenthos). Characteristics of the hydrodynamics and sedimentology of the Belgian shoreline are also incorporated. Anthropogenic threats faced by the sandy beach ecosystem are identified. This chapter has been accepted for publication as: Speybroeck, J.; Bonte, D.; Courtens, W.; Gheskiere, T.; Grootaert, P.; Maelfait, J.-P.; Provoost, S.; Sabbe, K.; Stienen, E.W.M.; Van Lancker, V.; Van Landuyt, W.; Vincx, M.; Degraer, S. (in press). The Belgian sandy beach ecosystem – a review. *Marine Ecology – An Evolutionary Perspective.*

Chapter 2 offers a comprehensive summary of what is known on the ecological impact of beach nourishment. Biological effects of beach nourishment are attributed to numerous habitat effects, whereas the latter are linked to the physical characteristics of beach nourishment in three major categories, resulting in impacts related to the fill quantity, impacts related to the fill quality and impacts directly related to activities during the construction phase of nourishment. The conclusive part of this chapter provides ecology-friendly nourishment practice alternatives and guidelines, points out shortcomings of impact assessment research, and offers some perspectives for future research that have been elaborated in part in the subsequent chapters. This chapter has been published as: Speybroeck, J.; Bonte, D.; Courtens, W.; Gheskiere, T.; Grootaert, P.; Maelfait, J.-P.; Mathys, M.; Provoost, S.; Sabbe, K.; Stienen, E.W.M.; Van Lancker, V.; Vincx, M.; Degraer, S. (2006). Beach nourishment: An ecologically sound coastal defence alternative? A review. *Aquatic Conservation: Marine and Freshwater Ecosystems* 16: 419-435.

Chapter 3 is dedicated to the population dynamics, life cycle and zonation patterns of *Scolelepis squamata*. Samples collected during a monthly sampling campaign of one year are used to investigate trends in traditional population characteristics: abundance and biomass, life cycle, demography, reproduction and recruitment, growth and mortality, mean annual biomass, secondary production and P/B ratios. Furthermore, cross-shore zonation and range width were studied. This chapter has been published as: Speybroeck, J.; Alsteens, L.; Vincx, M.; Degraer, S. (2007). Understanding the life of a sandy beach polychaete of functional importance - *Scolelepis squamata* (Polychaeta: Spionidae) on Belgian sandy beaches (northeastern Atlantic, North Sea). *Estuarine, Coastal and Shelf Science* 74: 109-118.

In Chapter 4 a study similar to that of chapter 3 is conducted on *Bathyporeia pilosa* and *B. sarsi* populations from the same sampled beaches. Population characteristics and zonation are equally studied and thorough comparison is made between these congeneric, cross-shore segregated species. This chapter has been submitted for publication as: Speybroeck, J.; Van Tomme, J.; Vincx, M.; Degraer, S. (submitted). *In situ* study of the autecology of two closely related, co-occurring sandy beach amphipods. *Helgoland Marine Research.*

In **Chapter 5** both experimental and field data are used in order to characterise sediment-related demands of *Scolelepis squamata.* Sediment preferences of the species seemed to differ between what is observed *in situ* and experimental results. The role of other factors than sediment to explain habitat restrains of the species, is examined by analysing field data from Belgian beaches through predictive models for density as a function of three habitat characteristics (intertidal elevation, slope and median grain size). This chapter has been submitted for publication as: Speybroeck, J.; Hendrickx, F.; Vincx, M.; Degraer, S. (submitted). The ecological impact of beach nourishment and the restrained habitat of a key species – experiments insights and field data. *Biological Conservation.*

Chapter 6 investigates the role of interspecific competition and substrate preferences and tolerances in structuring and maintaining the observed cross-shore segregated zonation pattern of *Bathyporeia pilosa* and *B. sarsi.* Substrate selection over a range of grain sizes and levels of fines is investigated in both allotopic and syntopic conditions, thus allowing insight in preferences of each species, as well as investigating possible species interactions affecting selection. Mortality in a given sediment is used as an inverse quantifier for tolerance towards a certain sediment type. This chapter has been submitted for publication as: Speybroeck, J.; Pede, A.; Rivas Higuera, H.; Van Tomme, J.; Vincx, M.; Degraer, S. (submitted). Competition and sediment-related responses explaining segregated zonation of two closely related, co-occurring key species on sandy beaches? *Journal of Experimental Marine Biology and Ecology.*

General discussion is provided in **Chapter 7**, where a generally applicable methodology is developed for the assessment of the ecological impact of beach nourishment. Cost-benefit considerations are made and the proposed research scheme is applied to the results of all preceeding chapters. Because this chapter largely depends on the results of the previous chapters, this paper will be submitted for publication after those chapters have been published or at least accepted for publication. Until then it remains in preparation as: Speybroeck, J.; Vincx, M.; Degraer, S. (in prep.) Towards a methodological framework for the prediction and mitigation of the ecological impact of beach nourishment – a case study on intertidal benthic macrofauna.

CANDIDATE'S CONTRIBUTION TO THE DIFFERENT CHAPTERS

The candidate is the first author of all chapters in the thesis. The first two chapters (**Chapter 1 and 2**) were the joint effort of a consortium of beach scientists. This collaboration provided an important added value and resulted in one published paper and one in press. The PhD candidate is responsible for the general sections, the part on macrobenthos, and the compilation and integration of all contributions by the various authors. This integration involved thorough restructuring, rethinking and rewriting of original draft contributions, rightfully placing the candidate as the first author of both . The **Chapters 3, 4 and 6** were essentially entirely the work of the candidate. However, important parts of the practical work and to a lesser extent of the analyses, were executed within the framework of Master theses, as specified on the title page of each chapter. This was not the case for the remaining chapters (Chapter 5 and 7). While Steven Degraer and Magda Vincx acted as mentors and contributors on all chapters, Frederik Hendrickx helped with statistical analysis in Chapter 5.

CHAPTER 1

The Belgian sandy beach ecosystem – a review

Accepted for publication as:

Speybroeck, J.; Bonte, D.; Courtens, W.; Gheskiere, T.; Grootaert, P.; Maelfait, J.-P.; Provoost, S.; Sabbe, K.; Stienen, E.W.M.; Van Lancker, V.; Van Landuyt, W.; Vincx, M.; Degraer, S. (in press).
The Belgian sandy beach ecosystem – a review.
Marine Ecology: An Evolutionary Perspective.

Abstract

This paper provides a comprehensive overview of the available knowledge on sedimentology and hydrodynamics and five major ecosystem components - microphytobenthos, vascular plants, terrestrial arthropods, zoobenthos (macrobenthos, meiobenthos, hyperbenthos and epibenthos) and avifauna - of Belgian sandy beaches (from foredunes to foreshore). An ecosystem overview is presented for this specific geographically delimited shoreline, instead of dealing with a single component only.

Belgian beaches are (ultra-)dissipative, macrotidal and wide beaches with a cross-shore average median grain size of 160-380 µm. Sediment becomes coarser, slopes steeper, tidal range smaller towards the east. Especially eastern beaches have been reshaped frequently through human action (e.g. beach nourishment). Belgian beaches are characterised by the presence of highly adapted organisms. It is demonstrated that even a highly recreational and heavily populated coastline like the Belgian coast provides valuable yet threatened habitats to several beach-dependent species, which may reach high numbers. Vascular plants of the drift line, dry beach and embryonic dunes are mostly short-lived and thalassochorous. Most common species are sea rocket (*Cakile maritima*), prickly saltwort (*Salsola kali* subsp. *kali*) and sea sandwort (*Honckenya peploides*). Terrestrial arthropods inhabiting the same general area are highly diverse, comprising halobiontic, halophilous and haloxene species. Prominent members of this fauna are sandhopper (*Talitrus saltator*) and dipterans (flies). Microphytobenthos is an important primary producer on Belgian beaches, mainly consisting of diatoms. Very little is known about this group of organisms. Belgian beaches also have a specific zoobenthic fauna in both meiofauna and macrofauna, e.g. the typical upper intertidal *Scolelepis squamata-Eurydice pulchra* community. Also epi- and hyperbenthic animals depend on the beach, e.g. as nursery grounds. Nowadays no nesting of birds occurs on the beach itself. Nevertheless, Belgian beaches are important for resting and foraging (e.g. sanderling *Calidris alba*). Little is know about biological interactions on Belgian beaches. Human actions associated with several aspects of recreation, beach management and fisheries, are endangering all the discussed biota, and are specified.

Keywords: sandy beach ecosystem, microphytobenthos, vascular plants, terrestrial arthropods, zoobenthos, avifauna

Introduction

Belgian beaches are strongly developed for recreational needs and mostly have concrete dykes separating the littoral part of the beach from the adjacent dune areas. Thus, they may seem biologically poor and resistant to human activity. The ecosystem of Belgian beaches has been heavily impacted by human actions. Both negative and positive effects on the sandy beach ecosystem have been observed (Speybroeck *et al.,* 2005). Apart from beach cleaning (removal of strand line material), profiling of the dry beach, implant of brushwood hedges and trampling, beach nourishment strongly impacted Belgian beaches. Trying to draw a holistic ecosystem picture, this paper aims at presenting the biological values of Belgian sandy beaches based on literature. Thus, knowledge from quite different fields of research is compiled and put into an ecosystem perspective. The biodiversity of Belgian sandy beaches will be discussed within delimited zones along the cross-shore gradient. Anthropogenic pressures on this ecosystem will be discussed. Concerning the ecological impact of beach nourishment, the reader is referred to Speybroeck *et al.* (2006).

We apply a conventional zonation scheme: (1) supralittoral zone above the high water line but influenced by sea water): embryonic dunes, dry beach and strand line; (2) littoral zone (= intertidal zone): between high water and low water lines; (3) infralittoral zone, here only the foreshore zone, i.e. defined as the seaward continuation of the beach profile until a depth of 4 m below MLWS level. The biological aspects of these zones will be limited to five major ecosystem components: (1) microphytobenthos (consisting of photosynthetic micro-organisms; eukaryotic algae and cyanobacteria); (2) terrestrial arthropods (arthropods of the strand line, the dry beach and the embryonic dunes); (3) vascular plants; (4) zoobenthos (macrobenthos, meiobenthos, hyperbenthos and epibenthos) and (5) avifauna (birds). Biota of the beach ecosystem are strongly determined by its physical environment, thus hydrodynamics and sedimentology were also taken into account.

The physical environment

THE BELGIAN COAST

The Belgian coast is a 65 km, southwest to northeast directed, rectilinear sandy coastline which passes to the east, in the Netherlands, into the 5 km estuary of the Westerschelde river (Figure 1). Belgian beaches display a macrotidal, semi-diurnal tidal regime. The average amplitude at spring tide varies from about 5 m at the French border and descends until 4.3 m towards the east (Fremout, 2002). The climate of winds and waves is dominated by a southwest to northwest direction. The southwest/northeast directed flood current (> 1 m/s) is dominant, and gives rise to a residual drift towards the northeast. The dominant southwestern winds also induce a northeastern aeolian drift. Storm winds from the northwest until the north predominantly cause coastal erosion (Anonymous, 1993). Close to the shore, average significant wave heights of 0.5 to 1 metres occur with a period of 3.5 to 4.5 seconds (Anonymous, 1993).

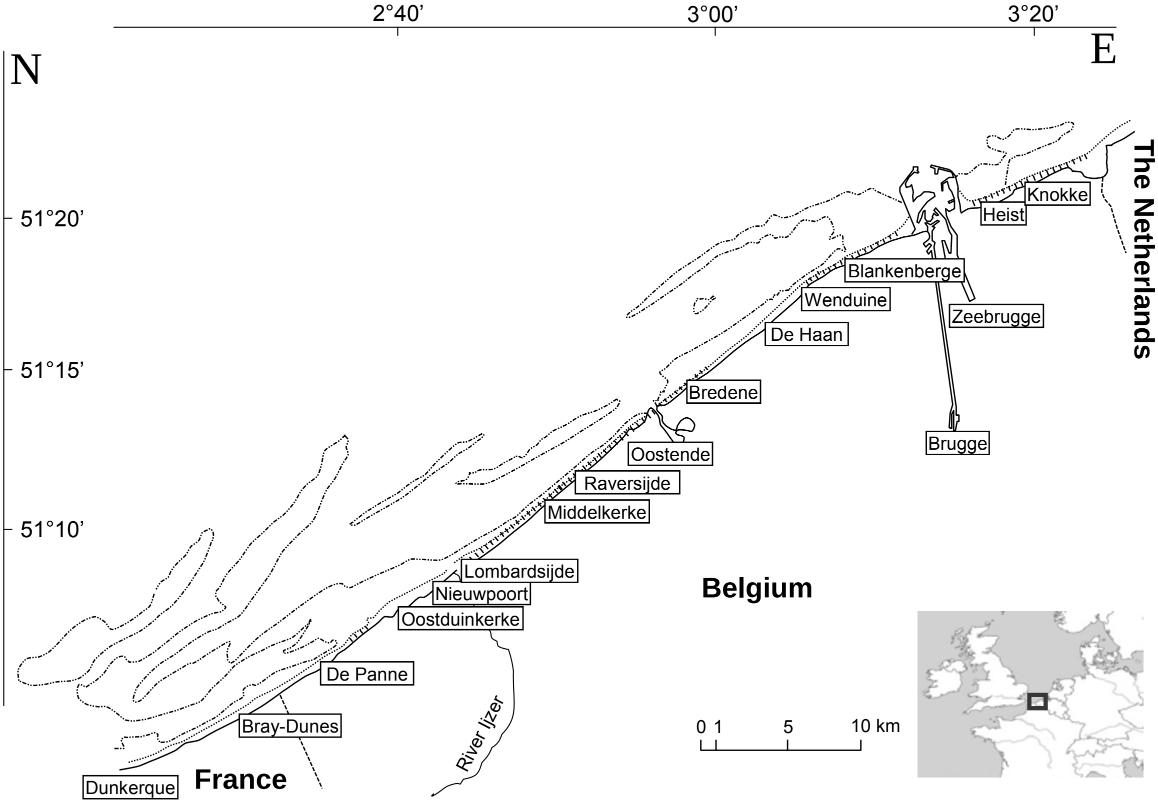


Figure 1. The Belgian coast with indication of municipalities.

The slope of the intertidal zone varies between 0.8 and 2.5 % (calculations based on digital field data of the VITO - Flemish Institute for Technological Research) and in general increases towards the east (Fig. 2). The width of the intertidal zone varies from 200 to 500 metres, and decreases towards the east. The broad, intertidal zone along the western coast has a slope between 1 and 1.3 % and is characterized by a typical morphology of runnels and ridges, breached by outlets, which carry off the water at the ebb tide. Beaches further to the east have a steeper slope (> 1.4 %) and their profile shows less relief. From Bredene to the east, the beach profile becomes more irregular. In the past, these beaches were subjected to the highest coastal erosion and they have been nourished frequently.

Sand on Belgian beaches has an average median grain size of 200-220 µm (cross-shore average of median grain size ranging from 160 µm to 380 µm – data from VITO 2001). The sediment becomes coarser from west to east. From the French-Belgian border to Raversijde this coarsening is rather uniform, while further east the trend is less straightforward: the highest oscillations are situated east of Heist, at least partially attributable to a long history of beach nourishment (De Moor, 2006). Cross-shore an overall, slight increase of about 70 µm in grain size can be observed in the direction of the hinterland. Belgian beach sand mainly consists of quartz (De Moor and Dedecker, 1981). The beach sediment includes a calcareous component due to the presence of shell hash, which locally may cause significantly elevated grain size values. In general the beach sediment does not contain significant levels of fines, apart from some local enrichment in runnels (Degraer *et al.*, 2003a).

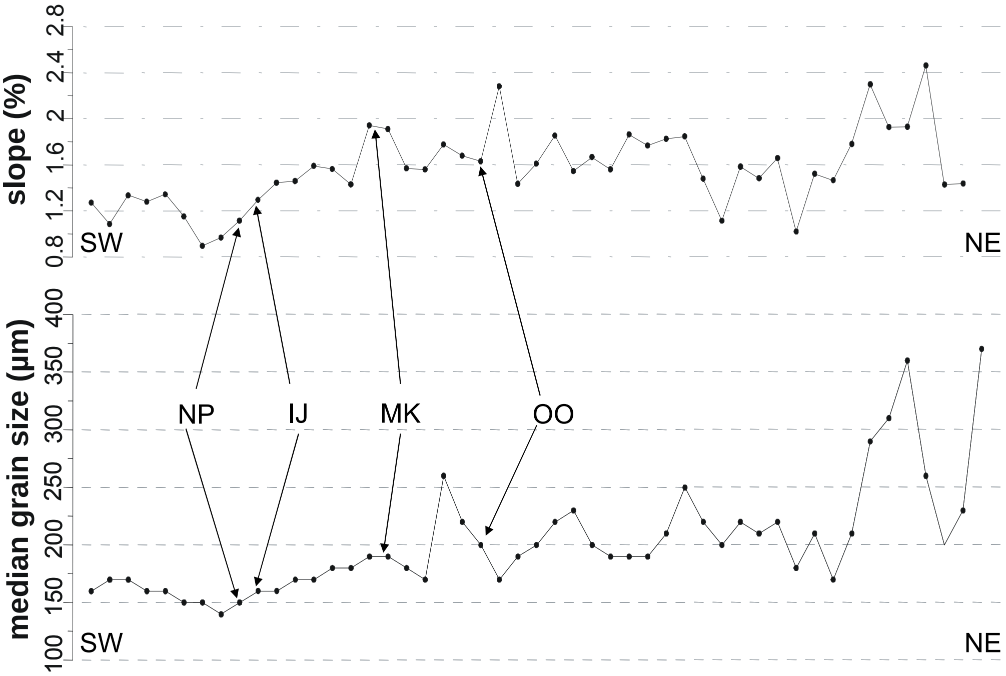


Figure 2. Intertidal slope and median grain size near low water line of Belgian beaches (from southwest to northeast = French to Dutch border) (Data source: VITO 2001). Western localities at the left, eastern ones at the right. Indicated are beaches sampled within this thesis (Chapters 3-4; NP = Nieuwpoort; IJ = Ijzermonding; MK = Middelkerke; OO = Oostende).

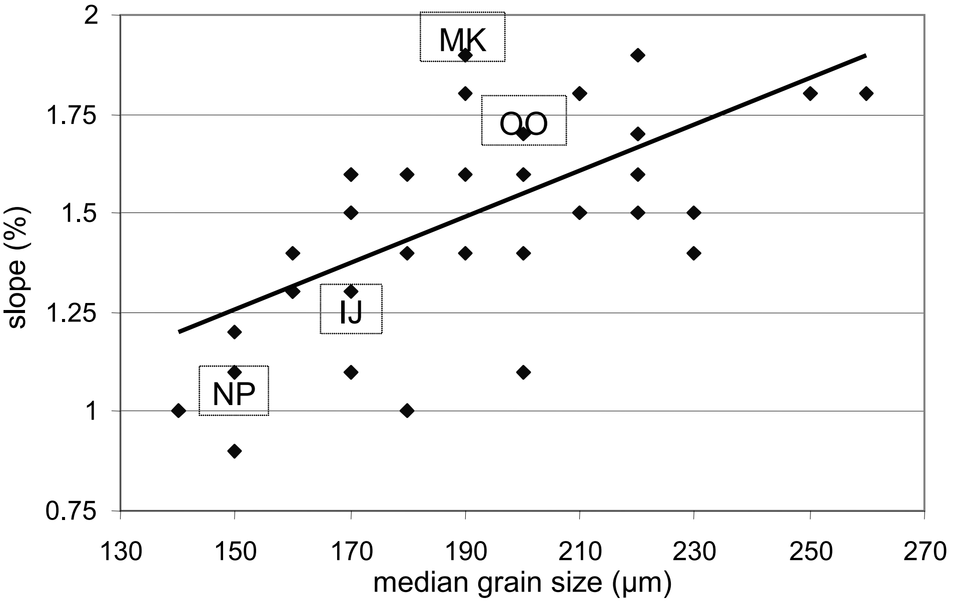


Figure 3. Slope (%) versus median grain size (µm) on Belgian beaches. Indicated are beaches sampled within this thesis (Chapters 3-4; NP = Nieuwpoort; IJ = Ijzermonding; MK = Middelkerke; OO = Oostende).

Based on sequential beach profiling, De Moor (1979, 1988, 1993, 2006) argued that a natural cycle explains the periodical behaviour of erosion and accretion on beaches. It remains however unresolved whether long term differences are due to slowly moving waves of sand (Verhagen, 1989) or to changes in wave energy.

Along the western coast, beaches are mostly stable and accreting. The beach sedimentology, further east until Oostende, does not evolve in accordance with any clear trend, while trends are variable east of Oostende. These beaches are subjected to severe human impact (management measures like nourishment, reprofiling, …). The foot of the coastal dunes is accreting along most of the Belgian coast, due to the consistent implant of brushwood hedges (De Wolf, 2002). De Wolf (2002) indicates that the beaches of Bredene to Wenduine, the beach immediately in the lee of the eastern harbour wall of Zeebrugge and the beaches in front of dykes with a rather pushed-forward position (Knokke), normally are erosive. Beaches further east (towards the Dutch border) are more or less stable, but at the mouth of the Zwin erosion occurs.

Based on tidal amplitude, modal breakers height, wave period and sediment characteristics, Belgian sandy beaches are classified as dissipative to ultradissipative beaches (according to Short, 1996, 1999), albeit with a slight decrease in their dissipative nature, from west to east (Fig. 4). This implies that processes related to the swash and surf zone will mainly dominate the morphodynamics of the upper intertidal zone with possible formation of a spring high tide ridge. The morphodynamical behaviour of the middle and lower intertidal zone is mainly related to the surf zone and dissipating waves. Swash processes can be locally significant and may cause formation of ridges. Tidal currents are of importance in the infralittoral zone. Morphodynamic classification allows correlations with ecosystem components (e.g. distribution of macrobenthic communities, Degraer *et al.*, 2003a).

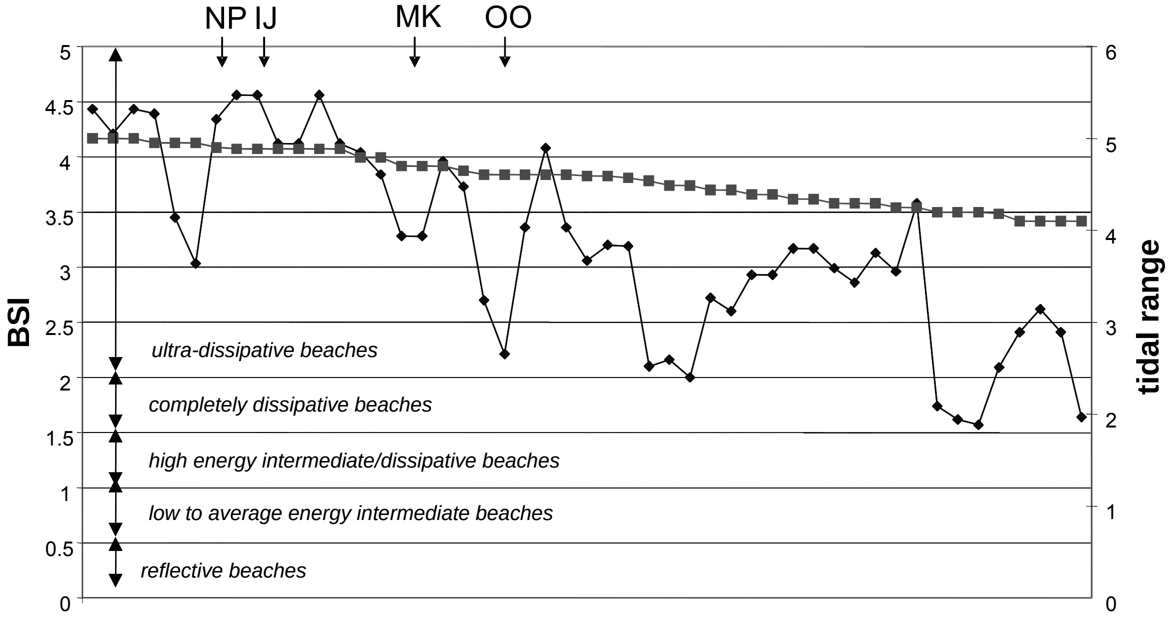


Figure 4. Morphodynamics (Beach state index (BSI) – McLachlan *et al.*, 1993) and mean amplitude of spring tidal range (m). Southwesternmost localities are at the left, northeasternmost ones at the right of the graph. Indicated are beaches sampled within this thesis (Chapters 3-4; NP = Nieuwpoort; IJ = Ijzermonding; MK = Middelkerke; OO = Oostende).

GENERAL FEATURES OF BEACHES SAMPLED WITHIN THIS THESIS RESEARCH (CHAPTERS 3 AND 4)

Based on previous knowledge, we selected 8 cross-shore transects for the investigation of population dynamics of macrobenthic key species (Fig. 5). The same samples were used for research on both *Scolelepis squamata* (Chapter 3) as the *Bathyporeia* species (Chapter 4). The transects were sampled monthly from October 2003 until October 2004, January 2004 excluded. Sampling started each time at high tide and continued until the low tide level was reached, taking a sample every half hour just above the upper swash limit. In order to minimise differences in tidal range among sampling months, sampling dates related to a fixed point in the lunar spring tide-neap tide cycle. Each sample involved a 0.1026 m² rectangle being dug out to a depth of 20 cm and sieved over a sieve with a 1 mm mesh width. An additional sample was taken for analysis of sedimentology. Elevation of sampling stations and the entire beach profile were measured using a leveller and corroborated afterwards with the output of the M2 tidal reduction model (Coastal Division of the Agency of Maritime and Coastal Services).

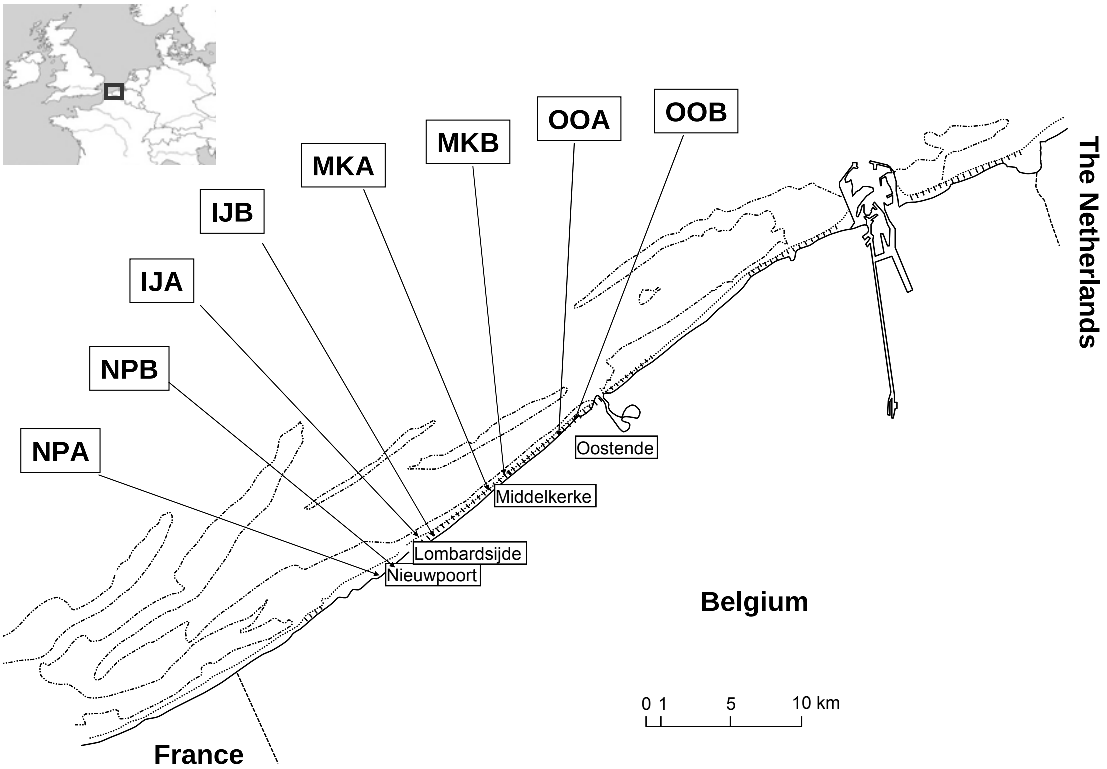
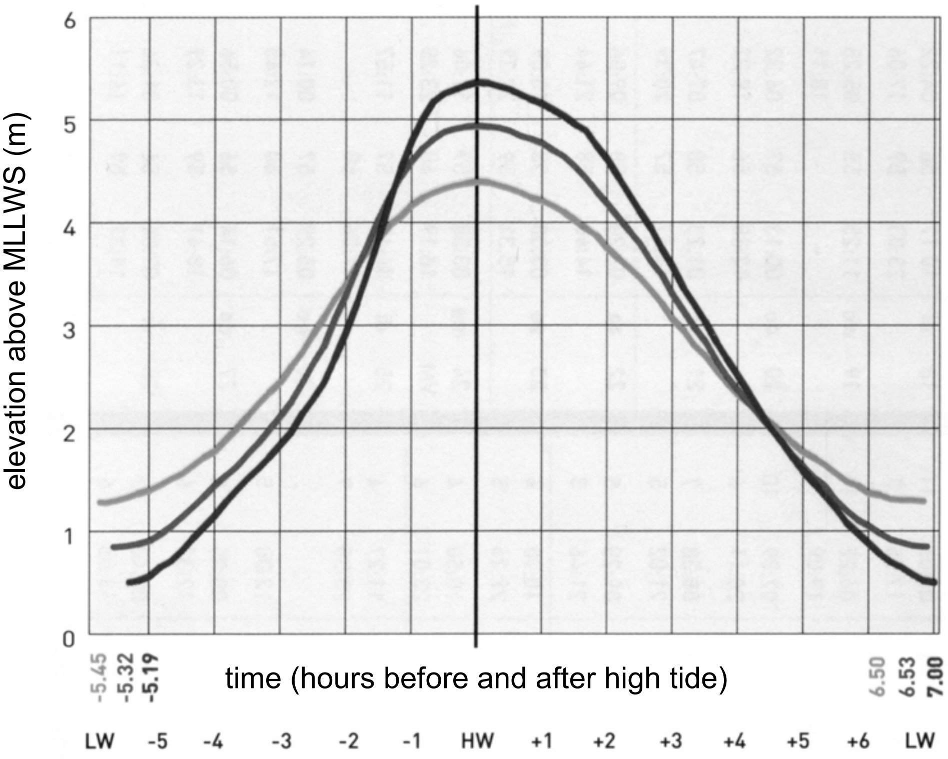


Figure 5. Location of sampled transects along the Belgian coast; NP = Nieuwpoort-Bad, IJZ = beach of Flemish nature reserve "Ijzermonding", MK = Middelkerke-Bad, OO = Oostende-Bad; capitals A and B are to identify each of the two transects within the same beach.

All sampled beaches are wide, macrotidal beaches with a sampled intertidal section ranging from about 170 to over 200 m in width and an average spring tide tidal range ranging more or less from 4.5 to 4.7 meter. Beach slope was weak (0.75-1.15°). Sediment analysis showed median grain size to range from 171 to 347 µm and the sediment to be well to moderately well sorted (SD of median grain size (µm) = 1.29-1.58). With a beach index (BI

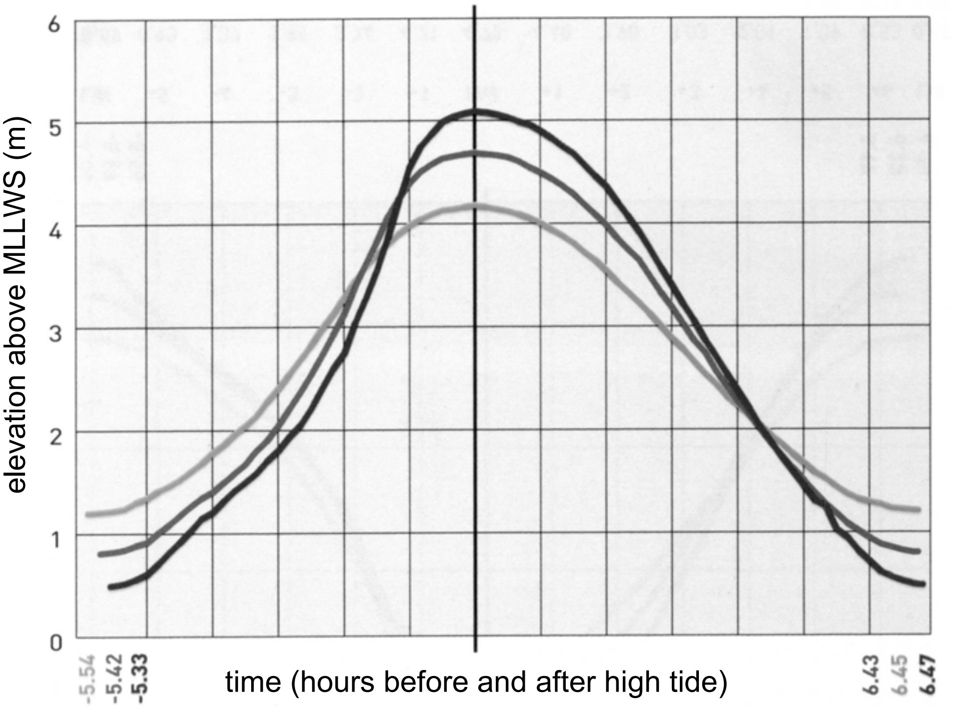
– McLachlan and Dorvlo, 2005) of 2.7 to 3.0, the morphodynamic type of all four beaches is clearly dissipative, in concordance to Degraer *et al.* (2003). Western transects have, however, higher beach index values (BI = 2.95 ± 0.03 SD) than eastern ones (BI = 2.75 ± 0.03 SD) (Mann-Whitney U Test: Z = 2.12; p = 0.03), suggesting eastern transects to be a little less dissipative.

In the next graphs, tidal curves and beach profiles are given for the most southwestern (Nieuwpoort) and most northeastern (Oostende) of the four sampled beaches (Figs. 6-9).



LW	-5	-4	-3	-2	-1	HW	+1	+2	+3	+4	+5	+6	LW	
0,49	0,55	1,14	1,83	2,92	4,78	**5,35**	5,14	4,60	3,56	2,50	1,57	0,87	**0,49**	mean spring tide
0,84	0,90	1,44	2,11	3,29	4,59	**4,93**	4,76	4,17	3,29	2,36	1,62	1,04	**0,84**	mean tide
1,28	1,39	1,77	2,44	3,39	4,16	4,39	4,20	3,74	3,05	2,32	1,76	1,36	1,28	mean neap tide

Figure 6. Tidal curves of Nieuwpoort beach (NP). Upper (darkest) line represents spring tidal curve, lower (palest) line represents neap tidal curve, mean tidal curve runs in between them.



LW	-5	-4	-3	-2	-1	HW	+1	+2	+3	+4	+5	+6	LW	
0,49	0,61	1,21	1,81	2,75	4,55	**5,09**	4,90	4,36	3,40	2,38	1,45	0,72	**0,49**	mean spring tide
0,81	0,92	1,41	2,05	3,13	4,40	4,69	4,50	3,99	3,19	2,27	1,51	0,95	0,81	mean tide
1,21	1,35	1,79	2,41	3,29	3,99	4,18	4,01	3,55	2,89	2,24	1,68	1,30	1,21	mean neap tide

Figure 7. Tidal curves of Oostende beach (OO). Upper (darkest) line represents spring tidal curve, lower (palest) line represents neap tidal curve, mean tidal curve runs in between them.

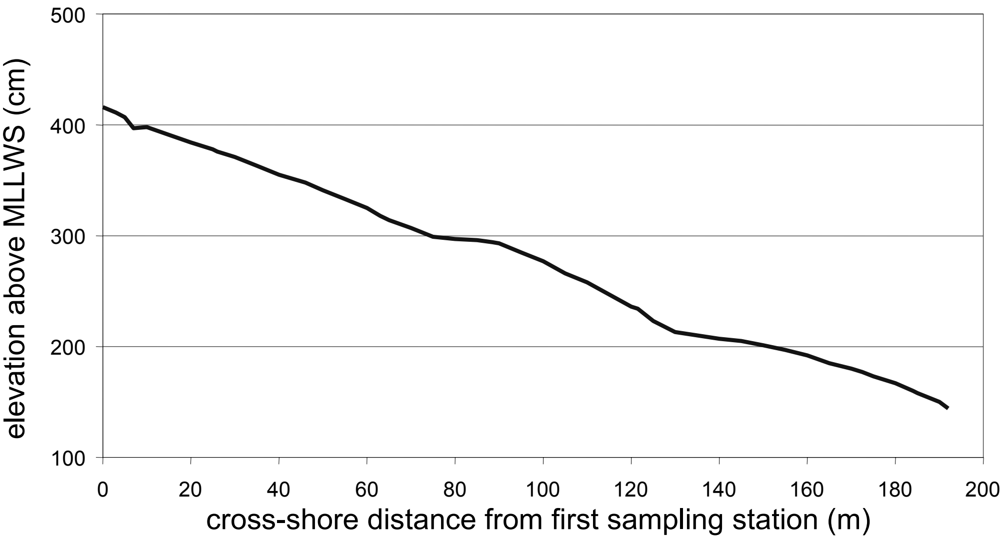


Figure 8. Sampled section of the intertidal beach profile of Nieuwpoort beach (NP) - October 2004.

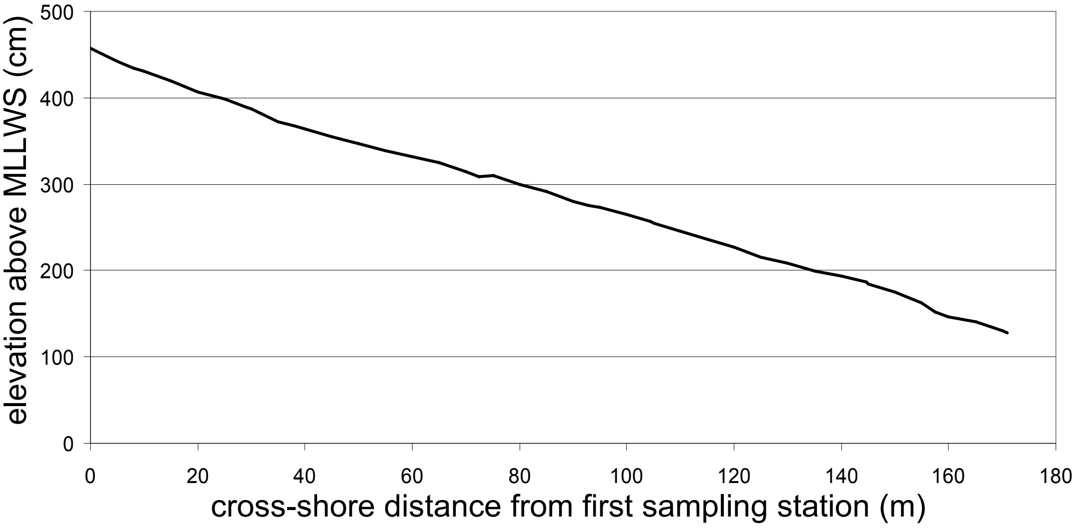


Figure 9. Sampled section of the intertidal beach profile of Oostende beach (OO) - October 2004.

Significant differences between transects were found in median grain size (Friedman Chi Square (N = 4, df = 6) = 22.39; $p < 0.01$). Western transects (IJA, IJB, NPA, NPB) exhibit lower median grain sizes, especially those from Nieuwpoort (NP; e.g. NPB: 192 ± 6 SD µm), whereas grain size on Middelkerke and Oostende beaches seems comparably larger (e.g. MKB: 268 ± 24 SD µm).

Minor quantities of fines (< 63 µm) were encountered in western transects (highest in NPB: 0.14 ± 1.00 SD % but at least 4x less in other western transects), but were usually completely absent from eastern transect sediment samples.

The biological environment

VASCULAR PLANTS

Vascular plants are limited to the Belgian supralittoral along the drift line, on dry beach and in embryonic dunes. Most species are short-lived and adapted to the dynamic nature of this biotope. In stable supralittoral areas perennial plant species can also settle (Provoost *et al*., 2004; Van Landuyt *et al*., 2004). Most species are dispersed by means of floating seeds that can resist seawater for a long time (i.e. thalassochory) and thus strand lines can easily be colonized (Rappé, 1996, 1997). The germinating plants benefit from the local nutrient enrichment and the temporary shelter of the strand line. A number of species naturally grows specifically in the supralittoral zone but their occurrence is not limited to natural locations; e.g. an important population of sea beet (*Beta vulgaris* ssp. *maritima*) is growing on the dyke, bordering the gully of the harbour of Nieuwpoort. All these taxa can be considered as tolerant to salty soils. Considering the ephemeral occurrence of many species, an accurate estimation of the population size would require surveys of several years.

The most common species along Belgian beaches is sea rocket (*Cakile maritima*), often accompanied by prickly saltwort (*Salsola kali* subsp. *kali*) and sea sandwort (*Honckenya peploides*). More rare are grassleaf orache (*Atriplex littoralis*) and sea beet (*Beta vulgaris* subsp. *maritima*) and only sporadically species such as frosted orache (*Atriplex laciniata*), yellow horned-poppy (*Glaucium flavum*) and Ray's knotgrass (*Polygonum oxyspermum* subsp. *raii*) can be found. The latter has a very limited distribution range in northwest Europe (Jalas and Suominen, 1979). Even though it has been mentioned for the first time only fairly recently (Rappé, 1984) Babington's orache (*Atriplex glabriuscula)* can regularly be observed on most of the Belgian beaches. Sea-kale (*Crambe maritima*) and rock samphire (*Crithmum maritimum*) are much rarer (Rappé and Goetghebeur, 1975; Rappé, 1989, 1996; Van Landuyt *et al.*, 2006). Sea couch (*Elymus farctus* subsp*. boreoatlanticus*), often within stands of *Cakile*, initiates the development of primary dunes. When the input of sand is sufficient, the embryonic dunes will grow and the soil salinity will gradually decrease to brackish or fresh. At this stage, marram (*Ammophila arenaria*) starts dominating and becomes the dune forming species. Locally, foredune species, such as sea holly (*Eryngium maritimum*), sea bindweed (*Calystegia soldanella*) and sea spurge (*Euphorbia paralias*), can be found in these embryonic dunes (Rappé *et al*., 1996; Provoost *et al*., 2004). On sheltered, gently sloping beaches, where silt accumulation takes place (so called 'green beach'), the flora is gradually enriched with salt marsh species e.g. annual sea-blite (*Suaeda maritima*), glasswort (*Salicornia* spp.) or sea-milkwort (*Glaux maritima*). Along the Belgian coast, this only occurs at the "Baai van Heist", which harbours the richest beach vegetation of Belgium (Devos *et al*., 1995; Cosyns *et al*., 1999; Van Landuyt *et al*., 2000). This seems to surprise, given the more erosive nature of beaches east of Zeebrugge, yet might be attributed to nature management of the specific site and special hydrodynamic conditions adjacent to harbour walls. All typical species of the supralittoral zone are classified on the Red List as rare to (highly) endangered (Van Landuyt *et al*., 2006). Apart from the impact of beach nourishment (burial and sediment budget disturbance), supralittoral vascular plants are affected by a number of human impacts. Recreation and mechanical beach cleaning can be considered as the most important threat to supralittoral vegetation and the development of embryonic dunes (Provoost *et al.*, 1996, 2004). Brushwood hedges, planted for coastal defence reasons, offer some shelter to these disturbances and are therefore a preferred habitat for species of the dry beach.

TERRESTRIAL ARTHROPODS

The arthropod fauna of strand line, dry beach and embryonic dunes contains a diverse range of species adapted to salty environments to a varying degree: (1) halobiontic species which can only live in salty environments, (2) halophilous species, living in both salty and fresh water environments, and (3) haloxene species which are rather incidental visitors. Many species depend on stranded material. The European arthropods living in and near this material have been studied rather intensively (Backlund, 1945; Ardö, 1957; Tsacas, 1959; Remmert, 1964; Egglishaw, 1959; Caussanel, 1970; Cheng, 1976; Dobson, 1976; Doyen, 1976; Moore and Legner, 1976; Louis, 1977; Bergerard, 1989). The wrack contains mainly kelps and brown algae, in which typical decomposers (mainly flies) and their predators and parasites are found. Common dune species (isopods, spiders and carabids) are often encountered in the wrack, especially if a natural connection between the dunes and the beach (still) exists (Maelfait, unpublished data). The sandhopper *Talitrus saltator* (Amphipoda, Talitridae) is a dominant species of the strand line (Lincoln, 1979) and plays an important role as primary comsumer of stranded dead plant and animal material (Robertson and Mann, 1980; Griffiths *et al.*, 1983; Stenton-Dozey and Griffiths, 1983; Adin and Riera, 2003). The species reaches high numbers on the beaches near the mouth of the river Ijzer and in the Flemish nature reserve “Baai van Heist” (Maelfait, unpublished data). During periods of spring tide, individuals migrate from the high water line to the frontal row of dunes, where consequently they can be found in high numbers (Maelfait, unpublished data). Predator mites (Gamasina), feeding on springtails (see below) and other invertebrates, play an important role in the ecosystem (Koehler *et al.*, 1995; Salmane, 2000). Certain species are restricted to the strand line (e.g. *Thinoseius* species; Egglishaw, 1959; Remmert, 1964), dry beach and/or embryonic dunes. Specialised species disappear if the beach dries up and the wrack quantity decreases. Detailed data on the distribution of predator mites along the Belgian coast are, however, unavailable. Beach-restricted spiders (Aranea) are absent on Belgian beaches. Sometimes Red List dune species can be found (Maelfait *et al.*, 1998). Furthermore, spiders can be found in the wrack due to anemohydrochory, i.e. winds bring them into coastal water and then they strand on the beach) (Palmen, 1944). The importance of this dispersal for the spider species remains unknown. On the dry beach, benthic springtails (Collembola) are known for their trophic relation with mycorrhiza (i.e. symbiosis of plants and fungi) of several plant species (e.g. creeping willow *Salix repens*) (Read, 1989). Because of the positive effect these mycorrhiza have on sediment stability, dispersal of mycorrhiza by springtails can affect sediment stability (Koehler *et al.*, 1995). Two species (*Folsomia sexoculata* and *Isotoma maritima*) only feed on rotting seaweeds (Janssens, 2002). However, due to their cryptic way of life, no further detailed ecological information is available on them. Fourteen beetle families (Coleoptera) have been recorded on Belgian beaches (Haghebaert, 1989). Most species rich families are Staphylinidae (thirty species) and Carabidae (twenty species) (Haghebaert, 1989). A total of 46 species were found on the strand line, of which 34 are true halobionts and 12 are halophilous or haloxene species. Most species were predators of e.g. sandhoppers (Bergerard, 1989), but grazers (e.g. *Bledius arenarius* and *B. subniger*) and parasites (e.g. *Aleochara* spp.) are also found. *Bledius* species play a key role in the strand line food web (Den Hollander and Van Etten, 1974; Steidle *et al.*, 1995). *Cafius xantholoma* is the most common rove beetle of Belgian beaches (Haghebaert, 1989). The predatory ground beetles and tiger beetles (Carabidae and Cicindelidae) are adapted to life on sandy and dynamic substrates (Turin, 2000) (i.e. psammophilous beetles with digging legs or long legs to counter overheating) and they are halobiontic or halophilous species. *Cicindela maritima* and *Bradycellus distinctus* are halophilous species that are mainly found on the dry beach and the foredunes (Turin, 2000). *Amara convexiuscula* and *Bembidion normannum* can be abundant underneath wrack (Turin, 2000). Desender (2004) provides an overview of the beach and dune carabid and cicindelid beetles of the Belgian coast. Very specific Diptera (flies and mosquitoes) are restricted to the supralittoral zone and they form the most abundant group of beach insects. Their larvae feed on the organic matter of the strand line (Ardö, 1957; Tsacas, 1959). After minor attention in the past (Meunier, 1898; Villeneuve, 1903; Bequaert, 1913; Bequaert and Goetghebuer, 1913; Goetghebuer, 1928, 1934, 1942), a thorough inventory of the Belgian dipteran fauna started around 1980 (Grootaert and Pollet, 1988; Grootaert, 1989; Grootaert and Pollet 1989). More ecologically oriented studies followed (Pollet and Grootaert, 1994, 1995, 1996). A summary can be found in Grootaert and Pollet (2004a). *Chersodromia* spp. (Hybotidae) are tiny flies whose larvae live in the burrows of sandhoppers (Tsacas, 1959). Prior to 1980, *Chersodromia hirta* was rather common but nowadays the species is threatened (Grootaert, unpublished data). *Aphrosylus* species (Dolichopodidae) are typically encountered on hard substrates, while foraging individuals can also be found on beaches. Kelp flies (Coelopidae), of which the larvae feed on seaweeds, almost exclusively occur on stranded brown algae (Egglishaw, 1959, 1961; Dobson, 1974). They may form an important food source for wading birds (Smit and Wolff, 1981). No typical fly species are found on the dry beach, even though species of the foredunes can be found there temporarily (Pollet, 2000; Pollet et al., 2004).

The arthropods of Belgian beaches are threatened by excessive recreation and systematic removal of wrack on most beaches, thus blocking the development of embryonic dunes. Examples are a negative correlation between trampling and the abundance of *Talitrus saltator* (Weslawski *et al.*, 2000) and rareness of kelp flies due to beach cleaning (Grootaert, unpublished data). The more dominant species (with exception of mites) are listed in table 1. This table is based on a sampling of ten beaches (Speybroeck *et al.*, 2005). Of the species caught as more than ten individuals, the total number caught and the number of beaches on which they were observed (frequency) are given. Besides the amphipod *Talitrus saltator*, a number of fly and beetle species are the most typical fauna elements.

Table 1. Terrestrial arthropods frequently found on 10 Belgian beaches (Speybroeck *et al.*, 2005). See text for details.

	family	species	number	frequency
Araneae	Erigonidae	*Erigone atra*	13	6
Araneae	Linyphiidae	*Tenuiphantes tenuis*	31	6
Araneae	Linyphiidae	*Stemonyphantes lineatus*	17	3
Araneae	Linyphiidae	*Bathyphantes gracilis*	15	4
Araneae	Linyphiidae	*Oedothorax fuscus*	11	6
Coleoptera	Anthicidae	*Anthicus bimaculatus*	48	8
Coleoptera	Carabidae	*Calathus mollis*	50	8
Coleoptera	Carabidae	*Dicheirotrichus gustavii*	40	1
Coleoptera	Carabidae	*Demetrias monostigma*	15	5
Coleoptera	Carabidae	*Harpalus tardus*	11	6
Coleoptera	Chrysomelidae	*Psylloides marcida*	59	7
Coleoptera	Chrysomelidae	*Aphtoma euphorbiae*	17	8
Coleoptera	Chrysomelidae	*Longitarsus anchusae*	13	7
Coleoptera	Curculionidae	*Philopedon plagiatus*	127	6
Coleoptera	Curculionidae	*Otiorrhynus atroapterus*	23	7
Coleoptera	Histeridae	*Hypocaccus metallicus*	10	6
Coleoptera	Histeridae	*Baeckmanniolus maritimus*	10	3
Coleoptera	Hydraenidae	*Helephorus guttulus*	26	7
Coleoptera	Hydrophilidae	*Cercyon littoralis*	14	5
Coleoptera	Scarabaeidae	*Aegialia arenaria*	175	7
Coleoptera	Staphylinidae	*Bledius (Cotysops) fergussoni*	47	1
Coleoptera	Staphylinidae	*Diglotta mersa*	45	4
Coleoptera	Staphylinidae	*Bledius (Cotysops) subniger*	42	4
Coleoptera	Staphylinidae	*Atheta (Mocyta) fungi*	37	8
Coleoptera	Staphylinidae	*Anotylus sculpturatus*	28	5
Coleoptera	Staphylinidae	*Anotylus (Oxytelops) tetracarinatus*	26	5
Coleoptera	Staphylinidae	*Drusilla canaliculata*	21	2
Coleoptera	Staphylinidae	*Anotylus (Styloxis) rugosus*	20	5
Coleoptera	Staphylinidae	*Coprophilus striatulus*	19	5
Coleoptera	Staphylinidae	*Xantholinus linearis*	15	4
Coleoptera	Staphylinidae	*Cafius xantholoma*	12	2
Coleoptera	Staphylinidae	*Aleochara (Coprochara) bipustulata*	11	3
Coleoptera	Staphylinidae	*Lestera sicula heeri*	10	2
Coleoptera	Tenebrionidae	*Phaleria cadaverina*	190	6
Collembola	Isotomuridae	*Isotoma caerulea*	40	2
Crustacea (Amphipoda)	Talitridae	*Talitrus saltator*	4581	10
Crustacea (Oniscoidea)	Porcellionidae	*Porcellio scaber*	115	8
Diptera	Anthomyiidae	*Fucellia maritima*	9710	10
Diptera	Anthomyiidae	*Fucellia tergina*	1028	10
Diptera	Canacidae	*Canace nasica*	14	4
Diptera	Dolichopodidae	*Aphrosylus celtiber*	31	4
Diptera	Dolichopodidae	*Sciapus maritimus*	22	3
Diptera	Empididae	*Hilara lundbecki*	16	3
Diptera	Ephydridae	*Scatella lutosa*	160	4
Diptera	Ephydridae	*Hydrellia obscura*	18	4
Diptera	Ephydridae	*Scatella tenuicosta*	13	4
Diptera	Ephydridae	*Hecamede albicans*	11	3
Diptera	Helcomyzidae	*Helcomyza ustulata*	392	9

Diptera	Helcomyzidae	*Heterochila buccata*	16	4
Diptera	Hybotidae	*Chersodromia incana*	245	4
Diptera	Hybotidae	*Chersodromia hirta*	177	5
Diptera	Hybotidae	*Tachydromia sabulosa*	26	3
Diptera	Hybotidae	*Platypalpus strigifrons*	23	8
Diptera	Sphaeroceridae	*Copromyza equina*	491	10
Diptera	Sphaeroceridae	*Thoracochaeta zosterae*	21	8
Diptera	Sphaeroceridae	*Opacifrons septentrionalis*	13	7
Diptera	Sphaeroceridae	*Spelobia (Spelobia) clunipes*	13	6
Diptera	Sphaeroceridae	*Leptocera (Leptocera) nigra*	12	5
Diptera	Sphaeroceridae	*Coproica vagans*	11	6
Diptera	Sphaeroceridae	*Opacifrons humida*	11	4
Diptera	Sphaeroceridae	*Borborillus nitidifrons*	10	5
Diptera	Tethinidae	*Tethina illota*	690	10
Diptera	Tethinidae	*Rhicnoessa grisea*	197	9
Diptera	Tethinidae	*Tethina albosetulosa*	136	9
Lepidoptera	Noctuidae	*Autographa gamma*	16	6

MICROPHYTOBENTHOS

For Belgian beaches, only preliminary data on microphytobenthos are available: in total about 120 species have been reported (Van der Ben, 1973; Blondeel, 1996). Microphytobenthos (eukaryote algae and Cyanobacteria) in intertidal sediments is usually dominated by diatoms but dense populations of Cyanobacteria, dinoflagellates, euglenoids, Crypto- and Chrysophyta may occur (MacIntyre *et al.* 1996, Barranguet *et al.* 1997, Noffke and Krumbein 1999). The microphytobenthos is the main primary producer in intertidal areas and contributes substantially to the biomass and primary production in the water column in shallow coastal areas and estuaries (de Jonge and van Beusekom 1995, MacIntyre et *al.* 1996). Sandy sediments are mostly dominated by attached life forms (epipsammon), while free-living forms (epipelon and tychoplankton) are dominant in sediments rich in fines. A strong relationship exists between sedimentological characteristics like stability, porosity, permeability, penetration of light and dissolved gasses and water content on one hand and the biological activity of the microphytobenthos in sediments on the other. Thus sediment type largely determines the distribution of the microphytobenthos (Sabbe, 1997; Paterson and Hagerthey, 2001).

Current knowledge on the diversity, structure and dynamics of sandy beach microphytobenthos is limited (Meadows and Anderson, 1968; Steele and Baird, 1968; Amspoker, 1977; Asmus and Bauerfeind, 1994; Fernandez-Leborans and Fernandez-Fernandez, 2002). Species richness in intertidal sediments may nevertheless be high: e.g. on tidal flats in the Westerschelde estuary about 200 benthic diatom species were encountered (Sabbe, 1997). While strong indications exist of microphytobenthos being an important food source for micro-, meio- and macrobenthos (e.g. Sundbäck and Persson, 1981; Middelburg *et al.,* 2000; Granéli and Turner, 2002; Moens *et al.,* 2002), until today little is known of the qualitative and quantitative role of the microphytobenthos in sandy beach food webs. Specialised surf zone diatoms are mainly known from the southern hemisphere (Campbell, 1996). The same species occur in Europe (and along the Belgian coast:

Blondeel, 1996), but nothing is known about their quantitative importance and their specific life history. Because of the high levels of turbidity in the infralittoral zone, little *in situ* primary production can be expected in sediments. Tychoplankton, plankton and resuspended microphytobenthos will play a major role here. At the moment, it remains unknown whether the foreshore contains specialised plankton communities (i.e. different from pelagic North Sea communities).

ZOOBENTHOS

Knowledge on intertidal meiofauna of Belgian beaches is limited (Gheskiere *et al*. 2002, 2004, 2006; Kotwicki *et al.*, 2005). At higher taxonomic level, in general 15 meiofauna taxa were recorded, Nematoda, Harpacticoida and Turbellaria being the dominant ones. On the beach of De Panne, average total meiofaunal densities increased from the upper littoral (56 ± 13 ind/10cm²) towards the lower littoral zone (3518 ± 540 ind/10cm²) (Gheskiere *et al.*, 2002). Nematode species richness increased from the upper littoral (8 ± 2 species) reaching a maximum around mid-tide level (34 ± 3 species). Three species associations were designated: dry beach (supralittoral, including typical marine, typical brackish as well as typical terrestrial free-living nematodes; *Rhabditis* sp. and *Axonolaimus helgolandicus*), upper intertidal (*Trissonchulus* sp., *Dichromadora hyalocheile* and *Theristus otoplanobius*) and lower intertidal (several species, among others *Odontophora phalarata, O. rectangula, Cyartonema elegans* and *Chaetonema riemanni*) (Gheskiere *et al.,* 2004).

Of the marine zoobenthos, the macrobenthos is best investigated. Like on most beaches worldwide (McLachlan and Jaramillo, 1995), polychaetes (bristle worms) and crustaceans dominate the Belgian sandy beach macrobenthos (Degraer *et al.*, 1999a; Degraer *et al.*, 2003a). Due to a relatively lower environmental stress on the ultradissipative beaches, the highest macrobenthic abundance and diversity are encountered on softly sloping, broad and fine grained beaches (Degraer *et al.*, 2003a).

More reflective beaches (east of Oostende) are clearly not as rich in species but they do harbour a number of rare species like the polychaetes *Hesionides arenaria* and *Ophelia rathkei* and the amphipod *Haustorius arenarius* (Degraer *et al.*, 2003a). Furthermore, a cross-shore gradient is distinguished with the upper littoral zone being inhabited by a species-poor, yet high density community. On Belgian beaches, this community is dominated by the polychaete *Scolelepis squamata*, the isopod *Eurydice pulchra* and two amphipods *Bathyporeia pilosa* and *B. sarsi* (Degraer *et al.*, 2003a; Van Hoey *et al.*, 2004). Remarkably, *Scolelepis squamata* occurs high up in the intertidal zone, like e.g. in Morocco (Bayed *et al.,* 2006) but not in the Netherlands (Janssen & Mulder, 2005). Lower in the littoral zone species richness is higher, but abundances are lower than in the upper intertidal community (Degraer *et al.*, 2003a). Typical species of the lower littoral zone are *Nephtys cirrosa, Donax vittatus* and several bristle worms like *Spio* spp. and *Spiophanes bombyx*. In the lower littoral, species are encountered which can withstand short exposure to the air, but they reach optimal conditions and thus higher numbers in the infralittoral (Degraer *et al.*, 1999a). The fact that cross-shore zonation can be observed more clearly on dissipative beaches (Jaramillo and McLachlan, 1993; McLachlan and Jaramillo, 1995), is confirmed. Zonation patterns of several species are subjected to seasonal oscillations: some species exhibit seasonal migrations, being located lower on the beach in winter (e.g. Degraer *et al.*, 1999a). Total biomass of Belgian sandy beach macrobenthos has been determined only once (ash free dry weight = AFDW) with values of 40 to 800 mg AFDW/m² (Elliott *et al.*, 1997). An initial increase below the high water mark was observed, followed by a decrease until below mid tide level and finally another yet slow increase towards the infralittoral zone.

Macrobenthic organisms represent a major food source for birds (see infra) and epibenthic fish (e.g. Plaice *Pleuronectes platessa*) and macro-crustaceans (e.g. Brown shrimp *Crangon crangon*) (Beyst *et al.*, 1999). A number of flatfish (e.g. Plaice *Pleuronectes platessa*) depend on intertidal infauna during their juvenile stages: the littoral zone acts as a nursery for these species. Juvenile flatfish migrate with the incoming tide towards the littoral zone, thus escaping predators from deeper zones and feeding there (Beyst *et al.*, 1999). This is also the case for hyperbenthic organisms like mysids (Mysida) (Beyst *et al.*, 2001a). For several fish species and species of the hyperbenthos, the intertidal surf zone also serves as a migration route between nursery grounds or between the nursery ground and the deeper marine environment (Beyst *et al.*, 2001a, 2001b). Both flat, ultradissipative beaches and intermediate beaches are inhabited by high numbers of flatfish, while the highest species richness seems to be reached on intermediate beaches (Beyst *et al.*, 2002a, 2002b). Lower species richness on the more reflective beaches along the eastern coast might be due to the influence of the nearby estuary of the Westerschelde. Several Belgian beaches, especially along the western coast, have runnels and ridges. The runnels stay submerged over a longer period of time and contain high levels of organic matter. They contain a benthic fauna which resembles infralittoral fauna (Boulez, 2002), e.g. high densities of *Spio* spp. Both in abundance and in diversity, the fauna exceeds that of neighbouring sand banks. Within beach benthos research, runnels were generally neglected.

From the Belgian foreshore, only data on macrobenthos are available. In contrast to the littoral zone, with only one typical macrobenthic community, several communities can be found on the foreshore. Four subtidal macrobenthic communities (*Abra alba – Mysella bidentata*, *Nephtys cirrosa* and *Ophelia limacina - Glycera lapidum* communities and *Macoma balthica* community (Degraer *et al*., 2003b; Van Hoey *et al*., 2004) are all found in specific sediments. These communities are, however, not homogeneously distributed on the Belgian foreshore. East of Oostende, the species poor, but highly abundant *M. balthica* community (87% of sample stations) dominates, while it more or less lacks west of Oostende (7% of sample stations) (Degraer *et al*., 2003b). Sample stations west of Oostende are rather evenly distributed over the three other subtidal communities. The species and abundance richest *A. alba – M. bidentata* community is dominant at the Western Coastal Banks. Within the latter community, many bivalves can be found (e.g. *A. alba*, *Spisula subtruncata* and *Tellina fabula*). In view of their role as food for species such as common scoter *Melanitta nigra* and Atlantic cod *Gadus morhua* (Degraer *et al*., 1999b) and the high species richness and abundance of macrofauna (Van Hoey *et al*., 2004), this community has been put forward as the ecologically most valuable community of the Belgian Continental Shelf (Degraer and Vincx, 2003).

Thus, more or less decreasing ecological macrobenthic value can be observed from west to east.

The dry beach and the strand line are most subjected to the influence of coastal tourism. Hence, the interstitial dry beach fauna of tourist beaches is characterised by only one or just a few extreme colonisers and taxonomically closely related species (Gheskiere *et al.*, 2005a, b). The benthic fauna in the littoral zone mainly suffers from coastal defence and tourism. On the Belgian foreshore, human activities are widely distributed (Maes *et al.*, 2000). Kerckhof and Houziaux (2003) offer an overview of the major threats the subtidal marine fauna of the Belgian Continental Shelf are facing, specifically for benthic fauna: (1) beam trawl fisheries, (2) dredging and dumping of dredged materials, (3) introduction of invasive species, (4) coastal defence, (5) eutrophication and (6) pollution. While not really as prominent in the nearshore shallow waters as less damaging types of fisheries, the impact of beam trawl fisheries on the benthic life is significant. Beam trawl (shrimp) fishery intensity is very high on the Belgian Continental Shelf and is treated as a real threat to sensitive benthic habitats and communities. Several reef building (and thus habitat structuring and biodiversity elevating) organisms, like oysters (oyster banks) and the sand mason worm *Lanice conchilega* ("*Lanice* reefs"), as well as larger, habitat structuring epibenthic species of the coastal zone, like sponges (Porifera), are under serious threat as a consequence of beam trawl fisheries. By creating new habitats (hard substrates) and altering the original habitats, coastal defence has had a drastic impact on the benthos of the Belgian foreshore. The impact on the original resident fauna is, however, poorly known. Finally, eutrophication and pollution (oil, solid waste, …) are also widely distributed problems on the Belgian Continental Shelf and they have an overall negative impact on the entire marine ecosystem.

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The supralittoral zone is important as a nesting area for birds. Mainly Kentish plover *Charadrius alexandrinus* and little tern *Sterna albifrons* can be expected to breed here. Both species are in the Red Data List as breeding birds threatened with extinction (Vermeersch *et al.*, 2004). During the twentieth century, most Belgian beaches became unsuitable for nesting of coastal birds because of anthropogenic pressure (mainly destruction of nesting habitat and disturbance) (Stienen and Van Waeyenberge, 2004). In 1954, 45 breeding pairs of Kentish plover where observed on Belgian beaches (Raes, 1989), while this species was almost absent from 1990 onwards. Only in 1994-1996 – in absence of high tourist pressure – a few pairs of Kentish plover nested on the Lombardsijde beach and at De Panne (Devos and Anselin, 1996; Anselin *et al.*, 1998). Also the Zwin nature reserve held some pairs (always < 4) during the 1990s. During the onset of the twenty-first century, breeding numbers in coastal environments dropped to less than 3 pairs (Vermeersch *et al.*, 2004; 2006). In the middle of the past century, several little terns were nesting on the beaches between Koksijde and Oostduinkerke (maximum of 30 pairs in 1951 and 1952, disappeared in 1962), at Lombarsijde (maximum of 11 pairs in 1959, disappeared in 1960) and at Knokke-Heist (maximum of 75 pairs in 1939, disappeared in 1957). In the Zwin nature reserve, numbers increased in the 1960s due to nature management (maximum of 15 pairs in 1962, disappeared in 1964). The last nesting in a natural habitat dates back to 1973 (Van Den Bossche *et al.*, 1995; Seys, 2001). However, with the development of the port of Zeebrugge in the 1980s vast areas of sandy, sparsely vegetated and relatively undisturbed land were created. These mimicked natural processes in coastal areas and attracted large numbers of coastal breeders (Stienen and Van Waeyenberge, 2002; 2004; Stienen *et al.*, 2005). The distribution of both

Kentish plover and little tern is now limited to the Zeebrugge port and the adjacent reserve “Baai van Heist” (Courtens and Stienen, 2004; Stienen *et al.*, 2005). In Zeebrugge-Heist, maximum numbers amounted to 108 and 425 pairs respectively for Kentish plover and little tern. A similar increase was noted in the port of Antwerp (max. 18 pairs; Vermeersch *et al.*, 2006). The supralittoral on Belgian beaches also functions as resting and foraging area, mainly in winter and during migration. At high tide, most gulls and waders use the supralittoral to rest or as a place to gather before moving to high water roosts (herring gull *Larus argentatus* and black-headed gull *L. ridibundus* but also common gull *L. canus* and lesser black-backed Gull *L. fuscus*). The most important high water roosts are located near larger tidal flats and on groynes. Tidal flats (reserves “IJzermonding”, “Baai van Heist” and until recently the port of Zeebrugge) are, apart from being used by gulls, also used by foraging wading birds (oystercatcher *Haematopus ostralegus* and dunlin *Calidris alpina*, smaller numbers of grey plover *Pluvialis squatarola*, ringed plover *Charadrius hiaticula* and common redshank *Tringa tetanus* - Speybroeck *et al.*, 2005). High tide roosts of turnstone *Arenaria interpres*, purple sandpiper *Calidris maritima* and sanderling *Calidris alba* are mainly on groynes along the midcoast (Engledow *et al.*, 2001; Becuwe *et al.*, 2006). Numbers of turnstone and purple sandpiper initially strongly increased after 1975 along with the increased use of hard substrates for coastal defence (Becuwe *et al.*, 2006). Turnstones feed in the supralittoral zone on strand line material (Smit and Wolff, 1981; Becuwe *et al.*, 2006).

In the intertidal area, standardized counts of wading birds at low tide were carried out within four recent studies (Engledow *et al.*, 2001; Stuer, 2002; De Groote, 2003; Speybroeck *et al.*, 2005). Many bird species feed on intertidal macrofauna. On Belgian sandy beaches, this applies primarily to gulls and wading birds, the latter being mainly oystercatcher, dunlin and sanderling (Engledow *et al.*, 2001; Stuer, 2002; Speybroeck *et al.*, 2005). During the winter of 2000-2001, approximately 1450 oystercatchers and up to 350 sanderlings were present along the Belgian coast (Engledow *et al.*, 2001). On average, more than 50% and 70%, respectively, were counted on the beach. During winter on sandy beaches, oystercatchers feed nearly exclusively on shellfish (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). They preferably feed on easily penetrable, wet substrates along the edges of gullies and along the low water line (Stuer, 2002). Sanderling feeds in the swash zone and are partly depending on the presence of the polychaete *Scolelepis squamata* as prey, but also 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). Among the gulls, common gull and black-headed gull frequently forage on worms and shrimps in the littoral zone, around the high tide mark and in puddles and pools of stagnant water; 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). Gulls also feed on stranded dead animals and on food left behind by man (Engledow *et al.*, 2001; Stuer, 2002). First in 1989 and 1990 and later from 1998 onwards, total counts of wintering gulls were executed (Spanoghe and Devos, 2002). The total number of gulls varied from about 7.000 to 32.000 individuals. A count executed in summer suggested that numbers are much lower then (about 6.000 individuals). Speybroeck *et al.* (2005) found peak numbers of gulls during autumn migration and a low during the breeding season. The herring gull is the most common species (40-70 %), black-headed gull is second (13-42%). The common gull, lesser black-backed gull and great black-backed gull mostly make up less than 10% of the total number of gulls (Spanoghe, 1999; Spanoghe and Devos, 2002). In the past decade, common tern *Sterna hirundo* and sandwich tern *Sterna sandvicensis* made use of both supralittoral and littoral zones in and around the harbours of Zeebrugge, Oostende and Nieuwpoort to roost but also to gather before and after the nesting season (Speybroeck *et al.*, 2005).

The shallow waters of the Belgian coast are of international importance for a number of seabirds (Seys, 2001; Van Waeyenberge *et al.*, 2001; Stienen *et al.*, 2002), of which most species can be called coast-dependent, at least in a specific season (common scoter *Melanitta nigra*, crested grebe *Podiceps cristatus*, little gull *Larus minutus* and terns (little tern, common tern and sandwich tern). Internationally of less importance but with a strong coastal connection are black-headed and common gulls. All these species are dependent on shallow waters and the associated food resources, which are within the first 10 kilometres from the shore. Only a minor portion of most species strongly depends on the actual foreshore zone. For the common scoter, the western coast is of primary importance, namely the areas “Trapegeer, Broersbank, Potje” and “Stroombank, Nieuwpoortbank, Oostendebank” often harbour high numbers in winter (especially February-March). While the former area was important during the 1980s, the importance of the latter increased from the 1990s onwards. Peak numbers occurred in 1994 (15475 in Belgian waters). Common scoters depend on the presence of small bivalves (*Spisula* spp., nowadays probably *Ensis* spp.) at shallow depths. They are extremely sensitive to disturbance (e.g. by shipping and air traffic) and oil pollution (Camphuysen, 1998). Shell fisheries (beam trawls) pose a threat to the species (Degraer *et al.*, 1999b). Crested grebes are winter visitors (mainly December-February) and they are tied to the coast (in general within 15 km offshore). Major areas are situated along the western coast (around “Westdiep”), further east (Middelkerkebank, Oostendebank, Wenduinebank) and on “Vlakte van de Raan” along the eastern coast. From 2000 onwards, numbers residing in Belgian coastal waters have increased, with peak numbers of 12700 individuals (corresponding to 2.6% of the biogeographical population) counted in January 2003. This species is strictly piscivorous. Grebes are not very sensitive to disturbance but due to their swimming lifestyle they are sensitive to oil pollution, although remarkably low numbers stranded along the Belgian coast during the Tricolor oil spill (Stienen *et al.*, 2004). Little gulls reach highest numbers during migration (March-April and September-October). Their distribution shows strong seasonal fluctuations. In autumn, they are most tied to the coast. Highest numbers are then along the eastern coast (especially Zeebrugge harbour) but elevated concentrations occur also around the harbours of Oostende and Nieuwpoort. At maximum, 3670 individuals were counted in Belgian waters (4.4% of biogeographical population), but Seys (2001) estimated that a much larger proportion of the biogeographical population (up to almost 100%) may use the Belgian coast as a migration corridor. Little gulls are not very sensitive to disturbance, but because they rest at sea during night they may be sensitive to oil pollution. The sandwich tern is both a summer visitor (nesting bird at Zeebrugge) and a passage migrant. The species is present in Belgian marine waters from April to November. The main feeding grounds of this species are scattered along the western coast (Westdiep, Smalbank), the central coast (Stroombank and western Wenduinebank) and the eastern coast at the “Vlakte van de Raan” and the “Scheur” (Seys, 2001; Del Villar d’Onofrio, 2005). Sandwich terns are visual predators, which feed on a limited number of fish species

(Stienen *et al.*, 2000). Thus, they are sensitive to water pollution with accumulating toxic substances and possibly also to elevated turbidity (Brenninkmeijer *et al.*, 2002). Breeding numbers peaked in 2005, when 4067 pairs (7.2% of the biogeographical population) nested in the port of Zeebrugge (Stienen *et al.*, 2004, Everaert and Stienen, in press). An estimated 67% of the biogeographical population uses the Belgian coastal waters as a migration corridor (Seys, 2001). The common tern is both a summer visitor (nesting at Zeebrugge) and a migrant, present from April until November. Highest numbers are reached at Zeebrugge port. Outside the port itself, mainly the coastal waters west of Zeebrugge the harbour (Wenduine bank and surroundings) and the southern part of "Vlakte van de Raan" are important foraging areas (Seys, 2001; Del Villar d'Onofrio, 2005; Courtens *et al.* 2006). In Zeebrugge port, breeding numbers peaked at 3052 pairs in 2003 (4.8 % of biogeographical population), but numbers of migrants passing along the Belgian coast may very well exceed 50%. Common terns are also sensitive to the presence of accumulating toxic substances and collisions with wind turbines (Becker *et al.*, 1998; Thyen *et al.*, 2000; Everaert and Stienen, in press). Unlike sandwich terns, they are often found foraging in turbid waters and are probably less sensitive to elevated water turbidity. For little tern mainly the Zeebrugge harbour and the surrounding area within a 2 km radius are of importance. Like the other two tern species, they are top predators that are sensitive to pollution of accumulating substances. A lower transparency of the seawater may have a negative effect on the feeding success of this visual hunter. All of the mentioned tern species are sensitive to changes in the abundance of their prey fish. This may lead to large fluctuations in breeding success and to changes in the size of their populations (Stienen, 2006). An overview of threats coastal nesting birds are facing in northwestern Europe, is given by Meininger and Graveland (2002). Important causes for loss of nesting grounds on beaches for terns and plovers in Belgium are disappearance of the grounds themselves, in part as a consequence of industrial development and the construction of bungalow parks (Arts *et al.*, 2000; Stienen *et al.*, 2005) and the loss of natural dynamics in these areas. Recreation also poses a serious threat on nesting areas, leading to decreased breeding success, lowered densities and shrinking global distribution (Pienkowski, 1993; Schulz and Stock, 1993). Seabird populations are often limited in size by the availability of their food (Birkhead and Furness, 1985; Croxall and Rothery, 1991). Changes in tern population have been linked to fluctuations in food resources, mainly fish of the families of Clupeidae and Ammodytidae (a.o. Monaghan *et al.*, 1989; Vader *et al.*, 1990; Brenninkmeijer and Stienen, 1994; Meininger *et al.*, 2000, Stienen, 2006). Thus, excessive fisheries of prey species can pose a serious threat (Furness and Tasker, 2000). Other threats are predation by mammals and gulls as well as competition for breeding space between gulls and terns (a.o. Thyen *et al.*, 1998; Quintana and Yoro, 1998; Meininger and Graveland, 2002; Becker and Ludwigs, 2004). Toxic components entering the food web and being accumulated in eggs may affect coastal breeding birds (Becker *et al.*, 1998; Thyen *et al.*, 2000).

Discussion

Figure 10 provides a schematic image of the spatial distribution and trophic role of some taxa.

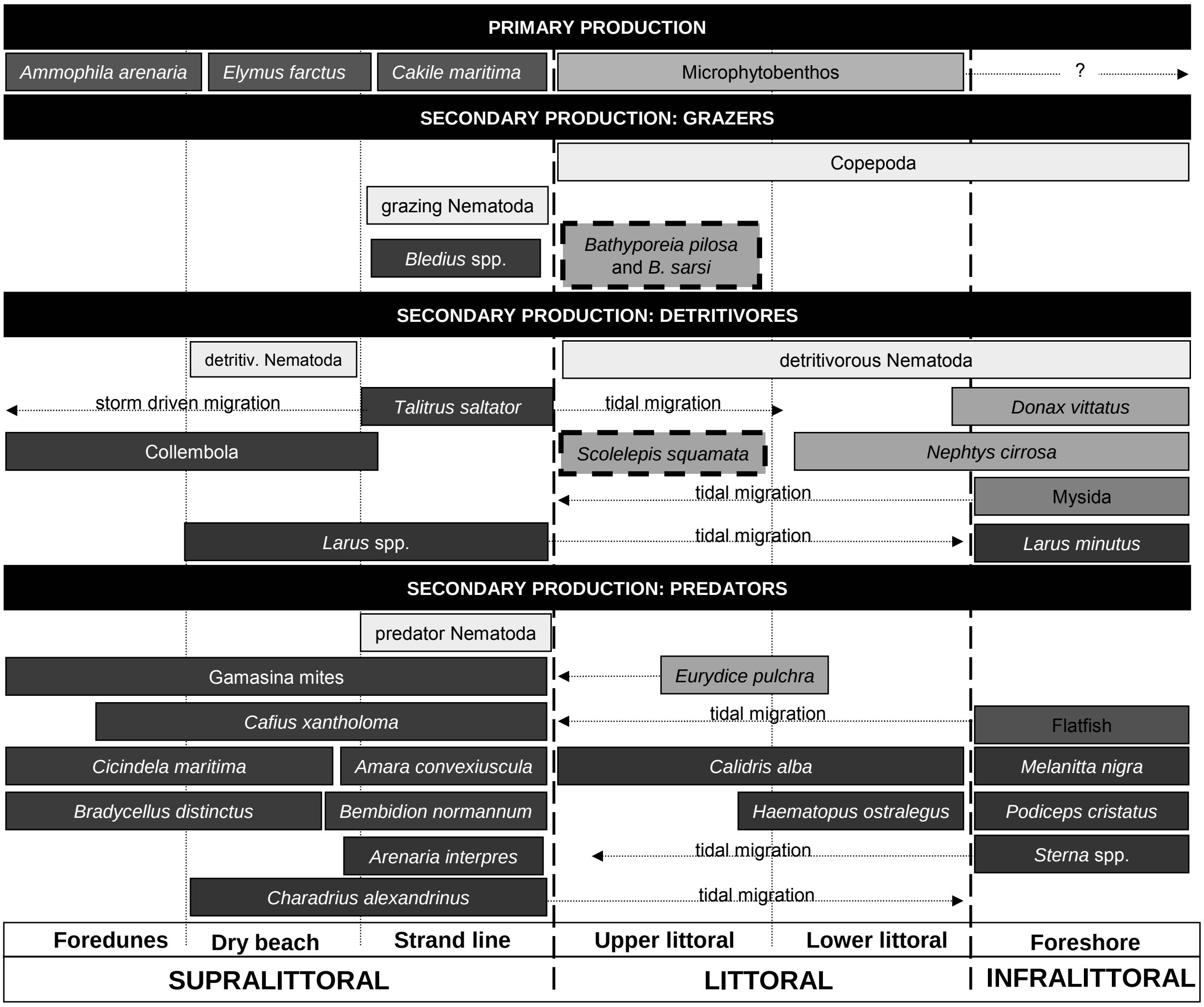

Figure 10. Productivity allocation on Belgian beaches represented by some abundant taxa. Data on Nematoda of the foredunes is lacking. The studied key species (Chapters 3-6) are indicated by boxes with bold, dashed borders.

The scheme demonstrates that the strand line present a rather sharp boundary between the marine and terrestrial environment, with little biological interaction across it. Stranded wrack presents an indispensable input of organic matter for typical species of fauna and flora, yet it is a more or less stand-alone system, with little connection to intertidal biota. Exceptions towards this boundary are the highly mobile avifauna and some venturing arthropods (at low tide). The boundary of the littoral and infralittoral parts is far less sharp, e.g. the gradual transition from lower intertidal macrobenthic community to foreshore communities and the tidal migration of flatfish.

In the supralittoral zone, vascular plants perform primary production, whereas microphytobenthos does so in the littoral zone and perhaps even further down. The importance of the latter for the zoobenthos is not known, although *Bathyporeia* species are said to feed on epipsammic diatoms. Detritivory is widespread: *Talitrus saltator* is a key decomposer of wrack in the supralittoral zone, and most macrobenthic fauna in the littoral zone are detritivorous as well. Very little is known about biological interactions on Belgian sandy beaches and this certainly offers perspective for future research.

While species richness and biodiversity may be lower on Belgian beaches than in some other ecosystems, each biological component plays a key role in the functioning of this highly productive ecosystem, specifically adapted to life in a dynamic physical environment. Sandy beaches can no longer be regarded as biological deserts. Therefore, management of beaches should involve more caution than is often the case. Even though a significant proportion of the beach inhabiting organisms is adapted to the naturally high environmental stress of tides, waves and winds, this adaptation has its limitations. Several aspects of recreation, beach management and commercial activities are the main threats that sandy beaches are facing along the Belgian coast.

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CHAPTER 2

Beach nourishment: An ecologically sound coastal defence alternative? A review.

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Abstract

1. Even though beach nourishment is generally considered as an environment friendly option for coastal protection and beach restoration, sizable impacts on several beach ecosystem components (microphytobenthos, vascular plants, terrestrial arthropods, marine zoobenthos and avifauna) are described in literature, as reviewed in this paper.

2. Negative, ecosystem-component specific effects of beach nourishment dominate on a short to medium term, with the size of the impact being determined by (1) activities during construction phase, (2) quality and (3) quantity of the nourishment sand, (4) timing, place and size of project, and (5) the nourishment technique and strategy applied. On a long term the speed and degree of ecological recovery largely depend on the physical characteristics of the beach habitat, mainly determined by (1) sediment quality and quantity, (2) the nourishment technique and strategy applied, (3) place and size of nourishment, and (4) the physical environment prior to nourishment.

3. The limited information available on indirect and cumulative ecological effects indicates that these effects cannot be neglected in an overall impact assessment. Hence, for ecologically good practice of beach nourishment it is advised (1) to choose nourishment sands with a sediment composition comparable to that of the natural sediment, (2) to avoid short term compaction by ploughing immediately after construction, (3) to execute the nourishment in a period of low beach use by birds and other mobile organisms, (4) to choose a number of smaller projects rather than a single large nourishment project and (5) to select the nourishment technique with respect to the local natural values.

4. In order to allow an objective, scientifically sound, ecological adjustment of future nourishments, research should aim at (1) taking into account the full sandy beach ecosystem, (2) avoiding strategic imperfections in experimental design and (3) elucidating the biological processes behind impact and recovery of all ecosystem components.

Keywords: sandy beaches, ecology, beach nourishment, beach replenishment, coastal erosion, coastal defence, ecological impact

Introduction

Beach nourishment is defined as '*the process of mechanically or hydraulically placing sand directly on an eroding shore to restore or form, and subsequently maintain, an adequate protective or desired recreational beach*' (Anonymous, 1984) or as '*deliberately placing an amount of sand on an eroding beach or creating a beach where no beach or only a narrow beach was present before*' (Anonymous, 1995). The process may, however, also include offshore deposition of material to build an artifical berm (e.g. Charlier and De Meyer, 1995).

The use of beach nourishment as a standard means of coastal protection is a rather recent phenomenon. In Europe and North America, the first large projects were executed only about 50 years ago (Anonymous, 1995). In Europe most projects were executed in Spain (over 600 between 1997 and 2002), the Netherlands (200), France (115), Italy (50), the UK and Denmark. Tens of millions of m^3 of sand have been deposited on the beaches, e.g. six million m^3 per year in the Netherlands since 1991. Hanson *et al.* (2002) and Hamm *et al.* (2002) offer overviews of the European beach nourishment history.

The coastal protection projects in the USA, carried out under the authority of the US Army Corps of Engineers, show a drop in the use of hard structures (breakwaters, dykes, groynes and harbour walls); around 1970 already 80% of all coastal protection measures were through beach nourishment and this percentage increased from 1970 onwards (Basco, 1999). Beach nourishment has been in use for a much longer time however, e.g. in California since 1919 (Clayton, 1991), on the US East Coast barrier islands since 1923 (Valverde *et al.,* 1999) and New England beach since 1935 (Haddad and Pilkey, 1998; Trembanis *et al.,* 1999). From 1970 to 1993, 49 large scale projects were executed. The total volume of deposited sand amounted to more than 145 million m^3, while in 1998, 31 further projects were under various degrees of construction (Basco, 1999). Besides these federally funded projects, many additional projects were conducted at the state or local level.

Awareness and attention towards problems of coastal erosion in general, and beach nourishment and physical and biological monitoring in particular, has increased over the last decades. As an alternative for "hard" coastal protection, both positive and negative aspects of beach nourishment are mentioned. Largely in contrast to nourishment, "hard" coastal protection may lead to increased erosion, often at downdrift locations rather than where the actual construction took place (through longshore transport of the sediment) (Peterson *et al.*, 2000a). An example of a higher risk of erosion is the disappearance of the dry beach section on many beaches along the eastern coast of Belgium after the construction of dykes at the foot of the coastal dunes about a century ago (Charlier and De Meyer, 1995, 2000). Beach nourishment gives rise to smaller changes in the dynamics of both sediment and water, thus a natural equilibrium is reached sooner, more easily and stays in effect for a longer time (Peterson *et al.*, 2000a). Negative aspects are the higher costs, as a consequence of the need of replenishment every few years, and the lower applicability on beaches with high wave energy (Esteves and Finkl, 1998). Some cost efficiency options are discussed by Raudkivi and Dette (2002).

Nowadays beach nourishment is widely considered as a better alternative than the construction of hard structures to protect a coast against detrimental erosive effects (e.g. Dankers *et al.*, 1983; Adriaanse and Coosen, 1991; Charlier *et al.*, 1998; Basco, 1999; Brown and McLachlan, 2002; Finkl, 2002; Greene, 2002; Hanson *et al.*, 2002; Hamm *et al.*, 2002).

Due to the highly dynamic nature of their environment (mainly determined by waves and tides but also winds), the benthic organisms inhabiting the littoral zone of sandy beaches are limited to species with a high tolerance towards several forms of environmental stress. Therefore, according to many authors, nourishment should cause only minor damage to the ecosystem (e.g. Löffler and Coosen, 1995; Anonymous, 2002b; Miller *et al.*, 2002). This high tolerance is, however, not unlimited (Jaramillo *et al.*, 1996; Moffett *et al.*, 1998). Even though beach nourishment is considered as the more ecologically sound option, this form of beach restoration also brings about sizable changes in the sandy beach ecosystem. In the short term, a large proportion of the resident flora and fauna is destroyed by the addition of a thick layer of nourishment sand. Changes in the beach habitat after nourishment, such as altered beach profile and sedimentology, will influence the rate of recovery of the ecosystem's natural equilibrium.

An impact of such magnitude can be expected to affect the entire beach ecosystem. Nevertheless, most research has been carried out on the intertidal benthic macrofauna (e.g. Rakocinski *et al.*, 1996; Peterson *et al.*, 2000a), while other ecosystem components remain mostly uninvestigated. Also, most studies are short term investigations of the benthic macrofauna. Little is known of long term effects, recovery after nourishment or the effects of repeated replenishment at the same site (cumulative effects).

Several strategies (classical or profile nourishment, foreshore nourishment and backshore nourishment) and techniques (rainbow spraying versus carrying the sediment to the beach as a mixture of water and sand under pressure via pipelines) of nourishment can be applied and their specific effect on the ecosystem will be discussed.

This paper aims at providing a complete ecosystem-encompassing perspective of the ecological effects of beach nourishment. Whereas the majority of past research focused on macrobenthic infauna, a more complete ecosystem approach offers much higher scientific value. Therefore, together with sedimentology and hydrodynamics, five major beach ecosystem components were taken into account in this review: microphytobenthos (benthic micro-algae), vascular plants, terrestrial arthropods, marine zoobenthos and avifauna (Figure 1). As referred to in this paper, microphytobenthos consists of benthic micro-algae inhabiting the top layer of the beach sediment. The vascular plants considered are those growing on the dry part of the beach including the dune foot, whilst terrestrial arthropods encompass insects and other arthropods inhabiting the strand line and the dry part of the beach, including the typical wrack fauna that depend for their survival on stranded seaweeds or other wrack dependent organisms. Marine zoobenthos comprises the marine benthic fauna, including those organisms living in the sediment (infauna) and larger than 1 mm. The avifauna consists of shorebirds and other birds depending on sandy beaches for nesting, foraging and/or resting.

The impact of nourishment is apparent at two different sites: the "borrow site" where the nourishment sediment comes from, together with adjacent indirectly impacted sites, and the "target site" or "nourishment site" (beach, foot of coastal dunes and/or foreshore), together with adjacent sites impacted indirectly through sediment transport (longshore transport but also aeolian transport). Within the scope of this paper only the nourishment site will be discussed and we refer to e.g. Hall (1994), Newell *et al.* (1998), Greene (2002) and Nelson (1993) for assessments of effects at the borrow site. In particular this paper offers an overview of the available knowledge on the ecological impact of beach nourishment on the beach ecosystem.

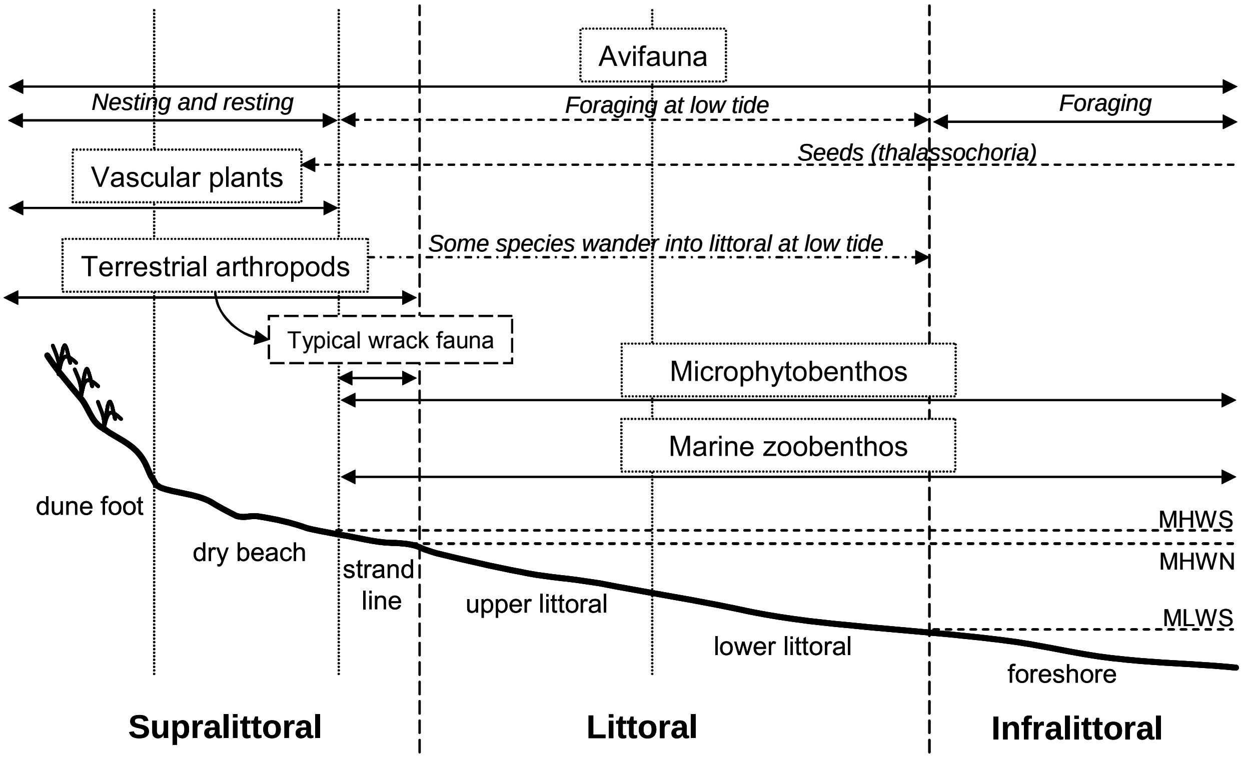

Figure 1. Scheme of the sandy beach ecosystem in the biological components considered in this paper. Supralittoral = here consists of strand line, dry beach and dune foot; littoral = intertidal zone; infralittoral= zone below MLWS; MHWS = mean high water level at spring tide; MHWN = mean high water level at neap tide; MLWS = mean low water level at spring tide. See text for further explanation.

Ecological effects of beach nourishment

The ecological effects of nourishment can be divided into three main groups: (1) effects related directly to aspects of the nourishment project – the construction, (2) effects related to quality characteristics of the nourishment sediment and (3) effects related to quantity characteristics of the nourishment sediment (Figure 2). Aspects of all three groups affect the biota through impacts on their habitat. The size of the effects is also influenced by (1) place, time and size of the nourishment project and (2) the chosen nourishment technique and strategy. Indirect and cumulative effects are discussed separately.

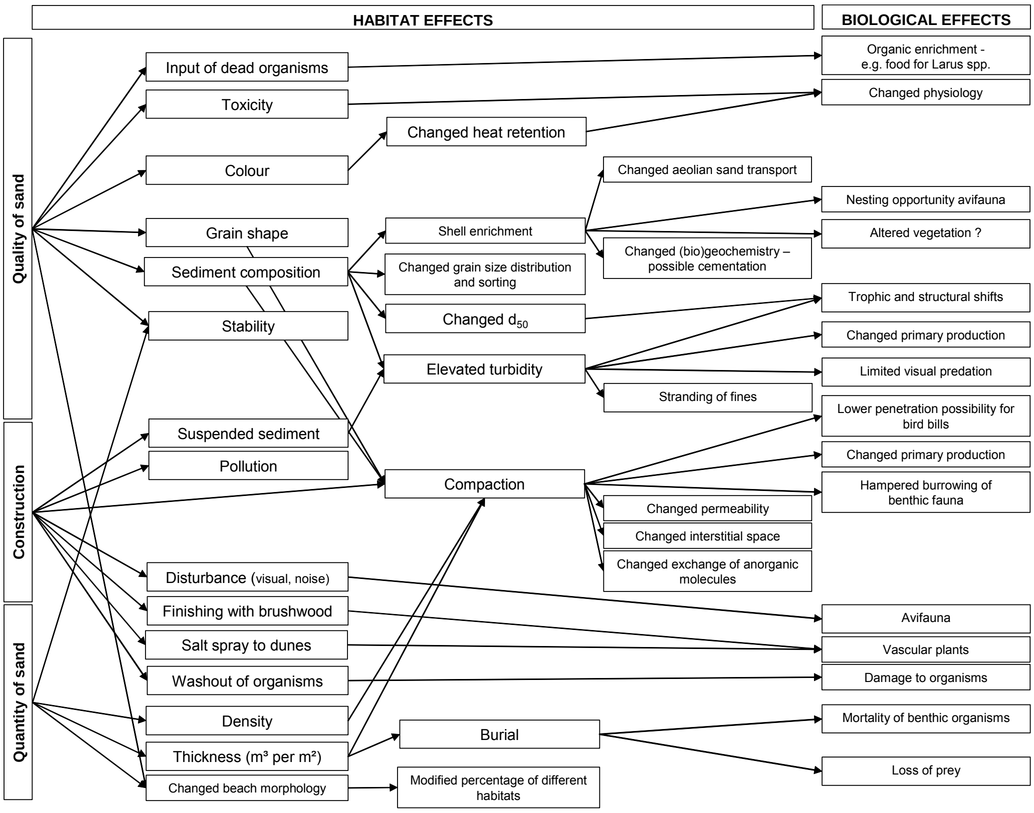

Figure 2. Integrated network of the ecological effects of beach nourishment. The scheme is a tentative summary resulting from the compiled literature data and consultation of all authors, each of them expert in a specific ecosystem component. Effects at the borrow site are not considered.

DIFFERENTIAL ECOLOGICAL EFFECTS OF BEACH NOURISHMENT RELATED ASPECTS

Activities during construction

During the construction phase of the beach nourishment, disturbance of the fauna can occur, which can be both visual and auditive, e.g. shorebirds abandoning their nests because of the disturbance (Peterson and Manning, 2001). Temporary noise overload during construction (associated with the use of pumps, bulldozers, outlet pipes, …) (Anonymous, 2002b) may cause disturbance to foraging birds. The use of bulldozers may destroy the primary dune vegetation and increases the degree of compaction of the beach sediment with many smaller vehicles causing more damage than fewer but larger ones (Anonymous, 1989). This can affect vascular plants (and associated terrestrial arthropods) living on the dry parts of the beach. Furthermore, some pollution may occur due to exhaust gases, fuel leaks etc.

Although no data are available on the subject, it seems likely that the microphytobenthos and the marine zoobenthos are only affected to a minor degree by the activities of the construction phase of the nourishment project per se; nevertheless, it is possible these benthic organisms are affected through a high compaction brought about by bulldozers and other equipment installed on the beach.

Quality characteristics of the nourishment sediment

Beach nourishment is characterized by a number of aspects related to the quality of the fill sediment: (1) sediment composition (proportion of shells or other coarse matter, proportion of fines, grain size distribution), (2) beach morphology and beach profile, (3) presence of toxic substances and/or dead organisms and (4) sediment colour.

SEDIMENT COMPOSITION

Shells and other coarse matter

If the fill sediment contains a high proportion of shells, shell fragments may become dissolved. Subsequently, sometimes a solid floor of shells is formed through cementation. Cementation is a process of lithification, in which chemical precipitates (in the form of new crystals) form in the pores of a sediment or rock, binding the grains together. Thus, a solid shell layer is formed and this causes a drop in the natural aeolian (van der Wal, 1998) and hydrodynamic sand transport. A shell lag layer may also be left by winnowing out of sand by the wind without subsequent cementation. This layer too, can reduce Aeolian sand transport. Sand dispersion by winds is an important factor for the development of dunes and vegetation on beaches (McLachlan, 1991). Frequent input of wind dispersed sand is essential for the viability of European beachgrass or 'marram' (*Ammophila arenaria*) (van der Putten and Peters, 1997) because it inhibits growth of fungi and nematodes damaging their roots.

Coarse materials in fill sediments also affect invertebrates. Den Hollander and Van Etten (1974) showed that beetles of the genus *Bledius* do not live in sand too rich in shells due to their digging behaviour. Peterson *et al.* (2000a) noted a slower recovery of a *Donax* (intertidal clam) population after nourishment with sediment containing a high percentage of shell fragments.

On the other hand a certain percentage of shells can create favourable nesting conditions on the dry beach for some birds like Kentish plover (*Charadrius alexandrinus*) (Melvin *et al.*, 1991). During nature restoration projects in the Dutch Delta area, the natural succession of vegetation seemed to be slowed down considerably when the nourished surface contained a lot of stones or pebbles and thus this surface remained suitable as a nesting habitat for shorebirds for a longer time (Stienen and Schekkerman, 2000).

No specific results are available on how high concentrations of coarse material may affect microphytobenthos.

Given the apparent contrasting impact of coarse material on some nesting birds on one hand and most other ecosystem components on the other, the use of a fill containing high concentrations of shells or other coarse material should be evaluated regarding the actual or desired natural values of a certain beach. Aeolian sand transport may possibly often even be greater after nourishment but all depends on the characteristics of the chosen fill sediment.

Fines

Fines are fine materials like mud (mineral clay and silt) and particulate organic matter. High proportions of these can cause a temporary increase in turbidity of both interstitial water and adjoining water masses. However, this increase disappears quite rapidly due to wave action (Van Dolah *et al.*, 1992). Fine particles, which can contain a considerable amount of organic matter and contaminants, are rapidly moved further offshore (Naqvi and Pullen, 1982). Thus, elevated turbidity is mostly not regarded as an ecological problem in the nearshore zone of high energy beaches. Furthermore, the foreshore biological communities possess a natural resilience towards shifts in turbidity, being a natural phenomenon (Van Dolah *et al.*, 1994; Anonymous, 2001, 2002b) and turbidity levels caused naturally during storms most likely exceed those arising from nourishment.

Prolonged nourishment and/or erosion of the fill sediment can, however, indirectly influence turbidity-sensitive plants and animals. As it may offer protection against visual predators in an environment with little natural refuge, elevated turbidity might temporarily be advantageous for surf zone fish (Beyst *et al.,* 2002a), but an eventual oxygen deficit will consequently affect breathing and embryonic development (Goldberg, 1989; Anonymous, 1995). Turbid waters can also limit the penetration of light through the water (decreasing phytoplankton and benthic algal productivity), lower underwater visibility for visual predators such as fish, crabs and birds, and can hamper the feeding and breathing of polychaetes and bivalves (e.g. *Donax* species) (Essink, 1999).

Intertidal amphipods *Bathyporeia pilosa* and *B. sarsi*, both common species of north-west European sandy beaches, in lab experiments were shown to have a clear preference for low levels of fines (ca. 1 %) (Rivas Higuera, 2003). For *B. pilosa* this was also shown in field data (mud content < 2%; Khayrallah and Jones, 1980b). High level of fines in the fill sediments can result in a slow recovery of macrobenthic organisms (Saloman and Naughton, 1984; Gorzelany and Nelson, 1987; Rakocinski *et al.*, 1996), due to limited juvenile survival (as demonstrated for *Donax, Scolelepis squamata*; Reilly and Bellis, 1983). Aggregations of fines, such as clay balls, in the fill sediment can cause a long lasting input of fines and thus can elevate turbidity long after the actual nourishment event (e.g. seven years - Hume and Pullen, 1988; Goldberg, 1989).

Silt accumulation may positively stimulate microphytobenthos growth, probably because of higher nutrient concentrations (van de Koppel *et al.* 2001), but deposition of thicker layers of fines will, at least temporarily, have a negative effect on microphytobenthos populations.

Grain size distribution

Grain size, beach profile, beach morphology and the morphodynamic type of the beach are related parameters. Grain size distribution strongly influences the structure and functioning of the ecosystem (e.g. benthic community structure) (McLachlan, 1983; Degraer *et al*., 2003a; Rodil and Lastra, 2004) and therefore it is an important aspect in the evaluation and prediction of the ecological effects of beach nourishment. For reasons of stability after nourishment (and less frequent need for replenishment) and to minimize the amount of sand needed, nourishment is mainly conducted using sands with a median grain size higher than that of the original sands (Dean, 1987; Raudkivi and Dette, 2002). The role of changes in grain size is often not investigated independently from the importance of beach morphology and thus the hydrodynamics at hand, determining this morphology. McLachlan (1996) studied a beach on which grain size was artificially increased while tidal range, wave energy and turbidity remained constant. As a consequence, the beach's morphodynamic state evolved from dissipative to intermediate. Changes in grain size and slope could both separately be correlated with a decreasing species richness and macrobenthic abundance. Thus, in this study grain size and beach morphology were assessed independently. Eventually, the local *Donax* species disappeared. Other research also related changes in median grain size with a decreased abundance of benthic macrofauna and a structural shift in the benthic communities (e.g. Rakocinski *et al*., 1996; Peterson *et al*., 2000a; Peterson and Manning, 2001). The common north-west European sandy beach amphipod *Bathyporeia pilosa* prefers sediments with a median grain size of 150-220 µm (Khayrallah and Jones, 1980b); a range which is well below conventionally used median grain sizes of fill sediment.

Through changes in grain size and grain shape, nourishment can cause changes in sediment density and set off an augmented compaction of the sediment (Anonymous, 1989). Effects of compaction are manifested through changes in the interstitial space, the capillarity, the water retention, the permeability and the exchange of gases and nutrients (Anonymous, 1989). The penetration of bills of wading birds, and vertical locomotion of the infauna are inhibited when grain size and composition of the fill sediment differ too much from the original beach sediment resulting in increased compaction (Maurer *et al*., 1978). Heavily compacted beaches consequently typically have a lower abundance of burrowing organisms (Lindquist and Manning, 2001). Burrowing of female sea turtles can also be hampered by compaction and the significance of sediment characteristics to the use of nourished beaches for turtle nesting, egg viability, and hatchling success has been documented (Nelson and Dickerson, 1988; Crain *et al.,* 1995; Steinitz *et al.,* 1998; Rumbold *et al*., 2001).

Sediment grain size has a profound effect on microphytobenthos community structure (e.g. Sabbe and Vyverman 1991, Paterson and Hagerthey 2001); this, however, is mainly caused by the hydrodynamical forces regulating the distribution of sediment types and simultaneously also micro-algal functional groups. There is as yet no information of the effects of sediment grain size per se on the taxonomic and functional structure of microphytobenthic communities.

No results are available on how the grain size distribution can be related directly or indirectly to the populations of vascular plants and terrestrial arthropods, though for the latter the work of Den Hollander and Van Etten (1974) suggested grain size preferences of the burrowing beetles of the genus *Bledius*.

BEACH MORPHOLOGY

The morphology of beaches and their morphodynamic characteristics are known to largely determine the benthic community structure (Degraer *et al.*, 2003a; Rodil and Lastra, 2004).

Changes in the beach profile (linked to the grain size distribution of the nourishment sands) can lead to changes in the hydrodynamics of the intertidal zone; an increase of the slope angle will increase wave energy on the beach (Kaufman and Pilkey, 1983), creating a hydrodynamically more stressful environment, leading to a reduction in diversity and abundance of the infauna (McLachlan, 1983). Significant changes of the profile can give rise to a change in the morphodynamic state, causing a slow recovery and maybe even a permanent shift in the ecological community structure.

Some researchers have suggested that changes in geomorphology and sediment characteristics even have a larger impact on the recovery rates of invertebrate populations than the direct effects of burial or mortality (Greene, 2002) and this in turn can indirectly affect the populations of foraging birds. For the other ecosystem components considered (vascular plants, microphytobenthos and terrestrial arthropods) no data are available. Altered beach morphology (but also compaction) may affect sea turtle nesting.

PRESENCE OF TOXIC SUBSTANCES AND/OR DEAD ORGANISMS

Sometimes the supplied sediment contains dead organisms, originating from the extraction site resulting in a temporal increase in organic matter and providing food for various birds including gulls and waders. This (temporary) organic enrichment could also have an effect on the entire beach ecosystem but no data are available on the subject.

The absence of toxic substances (heavy metals, PACs, PCBs, …) is of importance for all ecosystem components and thus it is often mentioned as an important quality criterion (Anonymous, 1989, 2002a; Adriaanse and Coosen, 1991).

SEDIMENT COLOUR

Colour, density and grain shape can change the heat retention capacity of the sand and thus alter the temperature of the beach sand (Anonymous, 1989). The ecological consequences of such alterations in the beach habitat are unknown. Changes in sediment temperature could influence respiration rates and reproductive success of benthic organisms.

Quantity characteristics of the nourishment sediment

Thickness of the applied sand determines the degree of burial of the organisms leading to high or even total mortality of buried benthic organisms and to potential loss of prey for predators feeding on these organisms (Dankers *et al.*, 1983; Adriaanse and Coosen, 1991; Anonymous, 1995; Löffler and Coosen, 1995; Charlier *et al.*, 1998; Peterson *et al.*, 2000b). The lethal thickness of a layer of deposited sand goes up to a maximum of 90 cm at the most for some polychaetes (Löffler and Coosen, 1995; Essink, 1999). In most cases of traditional nourishment the deposited sand layer is about 1 to 2.5 m and remains for a long period of time (pers. comm. Coastal Waterways Division), thus resulting in total mortality of benthic macrofauna. Normally, macrofauna originating from the borrow site also dies off completely, thus no input of offshore organisms to the beach occurs (Menn *et al.*, 2003). No information on mortality of other ecosystem components is available, yet with the exception of birds it can be supposed that all other components will be affected similarly.

The consequences of deep burial have to be taken into account at the species level. Species-specific life-history traits will influence rate of recovery. While the originally resident organisms will die off, the newly nourished beach will be re-colonized after nourishment. This recolonisation mainly occurs through settlement of pelagic juvenile life stages of marine benthic organisms. Several species, however, do not have a pelagic stage and their populations recover at a much slower rate after nourishment (e.g. *Bathyporeia* and *Haustorius*, Saloman and Naughton, 1984; crustaceans in general, van Dalfsen and Essink, 2001).

Very little information exists on the effects of burial on microphytobenthos. Wulff *et al.* (1997) documented the response of a sand-dwelling microbenthic community to burial by a 2.5 mm thick layer of mud. After a week active upward migration of the microalgae (mainly diatoms) had resulted in the restoration of photoautotrophic activity in the surface layers. Saburova and Polikarpov (2003) buried a natural sandy sediment microphytobenthos community under a 4 cm layer of sterile sand. After 24 hours the first cells reached the surface, but after five days about 20 % was still present in the original layers. The experiments in both papers were conducted on intact cores placed in plastic tubes, so it is not possible to determine to what degree horizontal movement of the microphytobenthos might influence recolonisation of 'new' sediments. In both experiments, however, the thickness of the experimental covering layer is much less than those applied in nourishment. Given the fact that even a layer of 4 cm significantly hinders restoration of microphytobenthic activity, it is to be expected that beach nourishment will result in a very low survival and hence upward migration of the in situ microphytobenthos. Recolonization will probably mainly be the result of new colonization via the water column or adjacent unburied sediments, or via deep reworking of the nourishment layers.

The impact of beach nourishment on the foraging behaviour of wading birds is also poorly investigated, but there are indications that such impacts do occur. The die off of the polychaete *Scolelepis squamata* after nourishment on the Dutch island of Texel resulted in a measurable drop in the number of foraging sanderling *Calidris alba* and catching success also decreased on the nourished beach (Dankers *et al.*, 1983). *Scolelepis squamata* is known as a primary food item of sanderling along the North Sea coast (Glutz von Blotzheim *et al.*, 1984).

FACTORS DETERMINING SCALE OF IMPACT

Timing, place and size of beach nourishment

Disturbance during the construction phase can cause nesting birds to leave their nests permanently or can cause them to stop foraging on nearby beaches, thus winter is proposed as the best season for undertaking nourishment (Melvin *et al.*, 1991; Peterson and Manning, 2001). High numbers of birds are often present in winter on many beaches and they will surely be affected by nourishment events, yet the nesting period remains the most vulnerable phase in the birds' annual cycle. Timing of nourishment should be considered in relation to the importance of the specific beach for nesting birds on one hand and resting and foraging birds on the other. Winter is, however, also the best season for a low impact on epibenthic organisms, as they are found in the shallow infralittoral zone and not on the beach itself during winter (Grober, 1992). Also for the larger benthic infauna this timing is preferable. If timing is chosen well, a swift recovery can be observed (e.g. Saloman and Naughton, 1984).

Conclusively, the preferred time of nourishment entirely depends on the nature and location of the beach and the species inhabiting or exploiting it.

Nourishment strategies and techniques

NOURISHMENT STRATEGIES

Three common nourishment strategies exist: classic or profile nourishment, foreshore nourishment and backshore nourishment. Classic, profile nourishment involves the deposition of the sediment across the entire intertidal zone. With foreshore nourishment and backshore nourishment the sand is deposited on a narrower zone of the beach and gradually it is redistributed 'naturally' by wave action and winds (respectively on the foreshore and on the dry part of the beach). Whereas profile nourishment is expected to impact mainly the benthic fauna and flora of the littoral zone and through those also foraging birds, the foreshore and backshore nourishment would be expected to affect mainly the biota residing in the zones where the sediment is deposited (infralittoral benthos and foraging birds for foreshore nourishment and terrestrial arthropods, vascular plants and nesting birds for backshore nourishment).

In reality, the difference between the effects of different strategies is somewhat more complex. Classic nourishment ensures that the maximum width of the beach is maintained and the material is sorted by wave action, lowering compaction (Anonymous, 1989). With this strategy the installed profile should be rather stable. Little should change given the reigning hydrodynamics and aeolian forces and only a minority of the sediment will be redistributed in an offshore direction (Anonymous, 2002c).

Foreshore nourishment is being used in many countries and it minimizes the size of the directly impacted surface area (Charlier *et al.*, 1998). The foreshore is nourished by dumping the fill sediment directly from the ship. While the intertidal organisms are only gradually covered with sand and should be able to survive, the overall damaging impact of this strategy could be higher (Thompson, 1973; Oliver and Slattery, 1976): in wintertime some seasonally migrating benthic beach animals like bivalves (e.g. *Donax*) and crabs often live on the foreshore and thus they will be covered with sand by foreshore nourishment if executed in winter (Grober, 1992). Furthermore, resident foreshore species may be adversely affected. In the context of Belgian beaches, foreshore nourishment may seem a desirable strategy to apply. Backshore and profile nourishment will affect the unique macrobenthic *Scolelepis squamata-Eurydice pulchra* community more intensively. Foreshore nourishment will –evidently- affect foreshore fauna most drastically. Yet, while the *Scolelepis squamata-Eurydice pulchra* community is restricted to the intertidal beach, the foreshore is mainly inhabited by the *Nephtys cirrosa* community (Van Hoey *et al.,* 2005). The latter is very widespread throughout the subtidal areas of the Belgian Continental Shelf. Therefore, recovery will most likely be easier than for the spatially much more restricted *Scolelepis squamata-Eurydice pulchra* community. Furthermore, also other ecosystem components will probably be less affected (terrestrial arthropods, vascular plants, ...).

With backshore nourishment the sediment becomes gradually distributed towards the sea over the entire profile until a dynamic equilibrium is reached. Although this is said to result in minimal physical and ecological damage, in contrast to foreshore nourishment it gives rise to a narrower dry section of the beach (Anonymous, 2002c) which may be unfavourable for possible nesting birds. Van Dolah *et al.* (1992) advise to deposit the sand high on the beach, far above the average sea level. This should result in a gradual sand distribution (Niemeyer *et al.*, 1996) and lower mortality of the burrowed animals. Effects of backshore nourishment on organisms of the dry beach including vascular plants, terrestrial arthropods and nesting birds have, however, been neglected in nearly all studies.

Dankers *et al.* (1983) investigated two nourishment projects in the Netherlands: on the isle of Texel, sand was spread across the entire beach (i.e. classic, profile nourishment), while on the isle of Ameland the sand was deposited at the base of the coastal dunes as a bank of sand (backshore nourishment). Recovery of the macrobenthos on Ameland occurred faster (hardly any impact) than on Texel (not until after 20 months).

Piling sand on the dry beach ('bulldozing') may lead to an elevated slope of the beach, causing higher wave energy on the beach (Kaufman and Pilkey, 1983) and thus creating a more stressful environment, decreasing diversity and abundance of infaunal assemblages (McLachlan, 1983).

It is, however, likely that this is only a temporary effect, as wave energy is expected to rapidly restore the beach profile. Mechanically distributing sand across the beach is said to pose a superfluous -but also unknown- pressure on the ecosystem because the sand can be distributed naturally across the beach by waves and winds (Basco, 1999).

NOURISHMENT TECHNIQUES

Rainbow spraying increases the chance for an elevated flux of salt towards the coastal dunes, significantly exceeding natural spray and causing the dunes to become salty and damaging the vegetation (Adriaanse and Coosen, 1991; van der Wal *et al.,* 1995 – see also below).

Density and compaction strongly increase if the sand is pumped as a mixture of sediment and water ('slurry') (Anonymous, 1989). Compaction may be three or four times higher than on the original beach and might even increase after the construction phase (Ryder, 1991). Elevated compaction might hamper burrowing of benthic organisms.

Supplying the nourishment sand by means of pipelines is the most commonly used method. If the supply is deposited from the backshore side of the beach towards the foreshore, the coarse material will settle near the backshore deposit bank and the fine material will be deposited downhill together with the slurry (Kana and Mohan, 1998). This kind of nourishment concentrates the coarsest fraction where it is needed most and improves the lifespan of the (backshore) sand bank but the downhill movement of the fines into the swash zone can cause elevated turbidity of the coastal waters, resulting in ecological effects associated with elevated levels of fines. With foreshore nourishment, turbidity might increase too. Through suspension of the sediment, this may also cause washout of the biota.

INDIRECT AND CUMULATIVE EFFECTS

Indirect and cumulative ecological effects of beach nourishment are hardly known (Nordstrom, 2000; Greene, 2002). These effects were not incorporated in Figure 1. but will be mentioned briefly here.

Nearby beaches (including their coastal dunes, foreshore and groynes) but also adjacent wetlands might be influenced by nourishment through the *longshore transport* (by water) (e.g. Thomalla and Vincent, 2003) and aeolian transport of sand. As species associations of deeper, subtidal underwater zones are less capable of surviving nourishment and as they recover slower, seawards transported sand should be avoided (Rakocinski *et al.*, 1996). It can however be expected that foreshore areas and their inhabiting organisms, are used to routinely inundation with sand layers during storms. Furthermore, avoiding offshore movement of sand is difficult in practice, as storms naturally move sand seaward.

An input of sediment into the system will diminish deficits in the sediment budget, in and upstream of the nourishment site. Beach nourishment affects the sediment budget (Eitner and Ragutzki, 1994), but has no effect on tides, waves, currents or changes in storm frequency if the applied volume of sand is kept at a minimum and no hard structures are built in combination with nourishment (Anonymous, 2002b). Background erosion remains constant and the sand volume lost in storms will not alter; beach nourishment does, however, slow down the landward progression of background erosion and offers storm protection to the hinterland. Finally, it should be noted that the shape of the sand grains affects compaction (Anonymous, 1989) but not sediment transport (van der Wal, 1998). Indirect effects such as elevated pressure on the ecosystem caused by augmented tourist activities after enlarging the dry beach should not be ignored.

Greene (2002) stressed the possibility of cumulative effects, both (1) temporal as a consequence of the replenishment frequency and (2) spatial as a consequence of the overall impact of several nourishment projects in the same region and (3) synergisms between temporal and spatial aspects.

Currently, little is known of the physical and ecological effects of long lasting and repeated nourishment. An example is the grain size becoming coarser over the years because of repeated nourishment with coarse sands. Repeated nourishment can furthermore initiate (1) higher compaction of the beach sediment, (2) long term elevated turbidity and (3) permanently altered sediment composition and beach morphology (Anonymous, 1989).

The combined effects of simultaneous nourishment projects along an entire coastline should be considered (Anonymous, 1999). Several short projects are preferred over long lasting ones, especially in areas where short term morphological changes are unpredictable (Hillen and Roelse, 1995).

Conclusions

Focusing on the ecological damage beach nourishment may cause, we have reviewed the impact nourishment can have on a natural beach. Thus, we have pointed out that nourishment is not an entirely ecologically sound coastal defence alternative. We should, however, stress that in practice, coastal defence alternatives to nourishment will generally be far more damaging to shoreline ecology (e.g. Dankers *et al.*, 1983; Adriaanse and Coosen, 1991; Brown and McLachlan, 2002; Greene, 2002) and it seems likely that nourishment is the most ecologically sound coastal defence alternative available. In addition, a beach requiring nourishment is often in an already unnatural condition beforehand, making it somewhat dangerous to assess the differential impact of nourishment. Local natural values may have been already lowered prior to nourishment due to a number of reasons including recreation, pollution and earlier coastal defence history (including previous nourishment) at a certain beach. In some cases, nourishment may even create suitable habitats for rare or threatened organisms like Piping plovers (*Charadrius melodus*) (Nordstrom *et al.*, 2000) and sea turtles (Witham, 1990; Lebuff and Haverfield, 1992; Crain *et al.*, 1995).

Yet, even while nourishment may be more benign than other types of coastal protection, an impact of such magnitude brings sizable changes about in the beach ecosystem. From this review, some guidelines for future nourishment are gathered and/or deduced and some considerations for future research on the ecological impact of beach nourishment are provided.

GUIDELINES FOR AN ECOLOGICALLY GOOD PRACTICE OF BEACH NOURISHMENT

Based on the review of known impacts of beach nourishment on elements of the beach ecosystem, some guidelines for executing nourishment with minimal detrimental effects on the sandy beach ecosystem, are summarised below.

- Sediment

Sediment characteristics play a very important role in the impact of beach nourishment on the ecosystem sediment composition and beach morphology.

The importance of grain size distribution of the nourishment sand for ecological recovery could be questioned, as it can be expected that the grain size distribution will be restored very rapidly by natural conditions like currents and storms. A gradual shift towards a morphological equilibrium (depending on the current hydrodynamic conditions) can be expected but it is crucial to understand that ecological recovery can only be expected after this equilibrium is established. Thus, to limit the ecological impact, nourishment sands with a comparable sediment composition to that of the natural sediment should be used, to allow swift recovery of the benthic fauna (Parr *et al.*, 1978; Nelson, 1993; Löffler and Coosen, 1995; Peterson *et al.,* 2000a). The ecological arguments for retaining the original grain size are further supported by geomorphologists to avoid a sharp transition from dissipative to reflective beaches (Anfuso *et al.*, 2001).

Compaction may be three or four times higher than on the original beach and increases sometimes (Ryder, 1991). This can be solved by ploughing or ‘tilling’ the beach (Dean, 2002) but it is mainly a short term problem, as wave action will soften the beach, especially during storms.

While the impact of sediment colour is largely unknown it seems precautionary to use sands with the same colour as the original sediment. Finally, toxic substances should be absent (Anonymous, 1989; Adriaanse and Coosen, 1991; Anonymous, 2002a).

- Timing

When aiming at a minimal ecological impact, nourishment should be completed within a single winter, starting after October and ending around March, regardless of the applied strategy (Anonymous, 1989). This timing is optimal for nesting birds in the northern hemisphere (Anonymous, 1999).

As a number of organisms spend the winter months in the shallow infralittoral zone, it is possible that the reduced impact due to this timing becomes undone with foreshore nourishment. It should be noted that this guideline relates only to mesothermic zones of the northern hemisphere. As a rule, nourishment should be executed during periods of low beach use by birds and other migrating or mobile organisms and the preferred season is entirely site-specific, depending on an area’s location and natural heritage interests.

- Size

Generally, a number of smaller projects (< 800 m length of shore) is preferred over a single large nourishment project (Adriaanse and Coosen, 1991; Löffler and Coosen, 1995; Peterson *et al.,* 2000b). The short distance between nourished and unnourished beach strips allows swift recolonisation, depending on species-specific dispersal capacities. This may very well be the case for infauna but seems to be doubtful for birds.

- Nourishment strategy

No clear choice can be made among the three mentioned nourishment strategies (classic or profile nourishment, foreshore nourishment and backshore nourishment). It seems advisable to decide on this point in respect to the local natural values of the beach ecosystem at the nourishment site. Each strategy has its major impact on a different part of the beach. Choices will have to be made in view of the vulnerability of the organisms residing in each zone of the beach.

SHORTCOMINGS OF FORMER RESEARCH AND OPTIONS FOR FUTURE RESEARCH

Notwithstanding the fair amount of literature on the ecological effects of beach nourishment, it still remains impossible to objectively assess the ecological effects of future nourishment projects and thus to formulate a scientifically sound, ecological adjustment of these projects.

Most studies only take into account one ecosystem component, failing to address the overall ecological effects thus making it very difficult to form a general picture of the effects on the whole ecosystem necessary in order to effectively ecologically adjust future nourishment projects. Since in many cases the available information on the ecosystem of a certain beach is only fragmentarily available, it is advisable to enlarge and integrate this body of information prior to the impact assessment. Knowledge on local conditions of the beach ecosystem (e.g. breeding bird colonies or fish nursery grounds) might help to prioritize among the information needed.

Secondly, because of pragmatic restrictions inherent to field experiments, such as the investigation of the ecological effects of beach nourishment, imperfections in the design of the research strategy often diminish the scientific value and thus convictive power of the investigations (e.g. Stauble and Nelson, 1985; Adriaanse and Coosen, 1991; Nelson, 1993; Elzinga *et al.*, 2001; Peterson and Manning, 2001; Finkl, 2002). Imperfections often encountered include the lack of (1) sampling prior to nourishment (e.g. Parr *et al.*, 1978; McLachlan, 1996; Rakocinski *et al.*, 1996), (2) control sites or badly chosen control sites (e.g. Reilly and Bellis, 1983; McLachlan, 1996), (3) replication of impact and/or control site (e.g. Rakocinski *et al.*, 1996), (4) detailed sampling through time (e.g. Rakocinski *et al.*, 1996), (5) interspersion (i.e. spatial alternation) of impact and control sites (e.g. Dankers *et al.*, 1983), (6) long-term monitoring, failing to monitor full ecological recovery (e.g. Rakocinski *et al.*, 1996) and (7) monitoring the physico-chemical environment along with the biological characteristics (e.g. Reilly and Bellis, 1983). Only by avoiding the above mentioned strategic imperfections will a solid basis for future adjustments of nourishment projects be set.

Finally, all studies describe the effects rather than investigating the biological processes responsible for these effects. Only by investigating underlying processes such as those related to impact size and rate of recovery, the effects of future projects can be predicted and thus objective ecological adjustments in nourishment practice suggested. The biological processes, relevant for nourishment effects, comprise (1) the process of disturbance and survival during nourishment (short term) and (2) the process of recolonisation after nourishment (medium to long term) (van Dalfsen and Essink, 2001). Disturbance and survival are mainly determined by species specific tolerances, while recolonisation is determined by (1) species specific dispersal and migration capacities and (2) species specific habitat demands and tolerances, including physical and biological elements. If scientific attention can be paid to these processes, this will finally allow scientists to objectively execute an ecosystem directed evaluation and adjustment of future nourishments.

In conclusion to our review, we acknowledge the need for coastal protection. Yet, while coastal protection is necessary for a number of socio-economic reasons related to e.g. tourism, housing and urban development, we feel that the ecological impact of any form of coastal protection needs careful consideration. Protection of often highly productive beach habitats is crucial to safeguard natural resources. Therefore, fine-tuning of nourishment practice for the sake of ecological damage control deserves attention. Even rethinking the design of nourishment projects in order to combine coastal protection with enhancing biota has been suggested (Nordstrom, 2005).

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CHAPTER 3

Understanding the life of a sandy beach polychaete of functional importance - *Scolelepis squamata*

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This research has partially been conducted within the framework of a master thesis (Alsteens, 2005).

Abstract

The cosmopolitan sandy beach polychaete *Scolelepis squamata* constitutes an important food resource for juvenile flatfish and wading birds in the northeastern Atlantic, thus playing an important role in sandy beach ecosystem functioning. However, its population dynamics and life history in this part of the world have gone widely uninvestigated. Eight beach transects on Belgian sandy beaches were monthly sampled from October 2003 until October 2004, in order to investigate seasonal trends in the species' abundance, biomass, secondary production, and patterns in reproduction and zonation.

Average density, modal density and modal biomass (ash free dry weight)(mean average density = 169 ± 9 SE ind/m²; mean modal density = 505 ± 38 SE ind/m²; mean modal biomass = 0.25 ± 0.02 SE g/m²) did not exhibit major seasonal changes, whereas average biomass (0.081 ± 0.005 SE g/m²) and individuals and biomass per strip transect (IST = 16286 ± 1330 SE ind/m; BMST = 7.8 + 0.7 SE g/m) did, peaking in May 2004. Production was calculated at 1.9 g/(m²*y) (size frequency method = SFM) and 0.88 g/(m²*y) (mass specific growth rate method = MSGR) and mean annual biomass was 0.797 g/m²; resulting in a P/B ratio of 2.40 / y (SFM) and 1.11 / y (MSGR), which is intermediate to moderately low compared to other polychaete species. Fertile individuals were found from February until August and a single recruitment period was observed from July until September. An average sex ratio of 1.41 ± 0.08 SE was calculated, with a female predominance. Highest densities (> 200 ind/m²) were mostly found above 3 m above MLLWS and at a median grain size from 190 to 320 µm. Average modal or peak density along each transect was situated from 3.95 m up to 4.40 m above MLLWS, in contrast to some other studies where the species was restricted to mid-tidal levels. Significant differences in elevation of peak density were found between non-fertile (411 ± 4 SE cm above MLLWS) and fertile (402 ± 5 SE cm above MLLWS) animals, but none between fertile males and females. The portion of the tidal range that was occupied by the species in the vertical dimension, just failed to differ significantly between non-fertile and fertile individuals, while fertile males (48.2 ± 5.6 SE cm) occupied a significantly wider range than fertile females (36.8 ± 4.7 SE cm), corresponding with a horizontal range difference of 6-9 m cross-shore. The observed zonation pattern, together with a trend in the difference of peak abundance elevation between males and females, are hypothesised to be a result of a strategy of fertile animals to ensure co-occurrence in a narrower zone during reproduction. Observed differences between Brazilian, Moroccan and Belgian populations (e.g. density, biomass, productivity, P/B, life span, body width, period of presence of fertile individuals and recruitment) do not seem to concur with differences in morphodynamics and might be attributed to latitude-associated gradients like climate. Furthermore, the fact that *Scolelepis squamata*, as defined today, might be a superspecies, cannot be ruled out.

Keywords: *Scolelepis squamata*; population dynamics; ecological zonation; beaches; biological production; polychaetes; NE Atlantic; North Sea; Belgium.

Introduction

Scolelepis squamata is a cosmopolitan bristle worm, forming a significant part of abundance and biomass of the macrobenthic fauna from sandy beaches of the North and South Atlantic, North Pacific, Indian Ocean, and the Mediterranean (Souza and Borzone, 2000) and encompassing a latitudinal range from 58°N to 35°S (Bayed *et al.*, 2006). It is known to be abundant on many Atlantic beaches (Eleftheriou and McIntyre, 1976; Withers, 1977; McDermott, 1987; Souza and Gianuca, 1995; Elliott *et al.*, 1997; Degraer *et al.*, 2003a). At the Belgian part of the North Sea, it is largely restricted to the upper intertidal zone, around and somewhat above 4m above the mean lower low water spring level (MLLWS) (Elliott *et al.*, 1997; Degraer *et al.*, 2003a; Van Hoey *et al.*, 2004) but elsewhere, including in the neighbouring Netherlands, it has been reported from mid-tidal levels (Knott *et al.*, 1983; Souza and Borzone, 2000; Janssen and Mulder, 2005) and subtidal sediments as well (Knott *et al.*, 1983; Hartmann-Schröder, 1996; Souza and Borzone, 2000; Janssen and Mulder, 2005).

The species lives in fine, medium or coarse sand in temporary vertical tubes, built up by sand and mucus and it is said to dig occasionally onto a depth of 40 cm below the sediment surface (Hartmann-Schröder, 1996; Van Hoey *et al.,* 2004). In contrast to other spionid polychaetes, this species lacks a sulcus with ciliary food transport (Dauer, 1983). Its sticky palps collect a wide range of suspended food (organic matter, planktonic animals, fragments of algae, …), which is brought to the mouth by complete contraction of these (Dauer, 1983; Pardo and Amaral, 2004). This is clearly an adaptation to the dynamic intertidal environment: wave action would wash food particles from the usual spionid palps before they can reach the mouth.

In Belgium, *Scolelepis squamata* is a species indicative for the upper intertidal *Eurydice pulchra-Scolelepis squamata* community, of which it comprises a large part in abundance and biomass (500 ind/m² - Degraer *et al.*, 2003a; 343 ind/m² on a total of 983 ind/m² - Van Hoey *et al.,* 2004). Similar communities have been found in the upper intertidal parts of many beaches all over the world (McLachlan and Jaramillo, 1995). In northwestern Europe, the species also plays an important functional role, being an important food item for wading birds, especially Sanderling (*Calidris alba*) (Glutz Von Blotzheim *et al.*, 1984), and juvenile flatfish, mainly Plaice (*Pleuronectes platessa*) (Beyst *et al.*, 1999; 2002a), but also e.g. the syntopic occurring isopod *Eurydice pulchra* (Hayward and Ryland, 1995) and the predacious polychaete *Eteone longa* (Hartmann-Schröder, 1996; Michaelis and Vennemann, 2005).

Early studies from the northeastern Atlantic, focusing mainly on reproductive biology and larval development, established *Scolelepis squamata* to be gonochoric, its reproduction and spawning spread over a long period consisting of pelagic fertilisation. The species is a 'broadcast spawner', in contrast to several other spionids exhibiting brooding (e.g. Gudmundsson, 1985). Broadcast spawning can be interpreted as an evolutionary valuable feature for an intertidal species, allowing hydrodynamically facilitated dispersal. Its development involves planktotrophic larvae being found from June to October, possibly even until January (Hannerz, 1956; Joyner, 1962; also adopted by Giangrande, 1997; Blake and Arnofsky, 1999). One study from Barbados surprised by showing that the species' reproduction involves spermatophores (Richards, 1970), which are likely to be washed off of the female body of intertidal polychaetes by waves and tidal currents. However, it has strongly been questioned that this relates to the species *Scolelepis squamata* (Blake and Arnofsky, 1999) and therefore we will not consider the results of Richards (1970). An unpublished study from the northern Netherlands was one of the first to assess benthic biomass, seasonal variation and secondary production of the species and suggested a two year life cycle with a single recruitment every year, resulting from the reproduction of the two year old (and afterwards dying) animals (Mooij, 1982). More recently, two studies on the population dynamics of the species were published from other parts of the Atlantic (Brazil – Souza and Borzone, 2000; Morocco - Bayed *et al.*, 2006). The results show some remarkable differences, stressing the need for additional research in other parts of the world. Therefore, population dynamics, local life history and zonation patterns of *Scolelepis squamata* were investigated.

Material and methods

SAMPLING

Eight cross-shore transects were sampled on the Belgian shore from October 2003 until October 2004, January 2004 excluded. Sampling started each time at high tide and continued until low tide was reached, taking a sample every half hour just above the swash zone. Sampling dates related to a fixed point in the lunar spring tide-neap tide cycle. While sampling at spring tide would have been optimal, this would have involved monthly night time sampling. Due to this practical limitation, we scheduled sampling just in between spring and neap tides. Each sample consisted of a 0.1026 m² rectangle, being dug out to a depth of 20 cm and sieved over a sieve with a 1 mm mesh width. An additional, adjacent sample was taken for analysis of granulometry, of which those from October 2003 and February, June and October 2004 were processed and used in analysis. Elevation of sampling stations and the entire beach profile were measured using a leveller and corroborated afterwards with results of the M2 tidal reduction model (Coastal Waterways Division of the Flemish Community).

LAB PROCEDURES

To obtain a length-biomass regression, allowing calculation of biomass from measurement data, one hundred undamaged specimens of all sizes were randomly collected from March and September samples. Four parts of the animal's body were measured: (1) width of prostomium, (2) length of prostomium, (3) width of third setiger, and (4) width of tenth setiger. All 100 specimens were dried (4h at 110°C) and dry weight was established. Subsequent combustion (2h at 550°C) delivered the specimen's ash weight and subtraction of both weights delivered ash-free dry weight (AFDW). After square root transformation of AFDW, linear regression analyses between the individual biomass and all four body measurements were executed. Comparison of level of significance (p) and explicatory power (R^2) between the five obtained equations, urged selection of width of the 3rd setiger (S3) as the best length proxy ((1) prostomial width: $R^2 = 0.74$; $p = 0.01$; (2) prostomial length: $R^2 = 0.61$ $p = 0.02$; (3) S3; $R^2 = 0.91$; $p < 0.01$; (4) S10: $R^2 = 0.88$; $p = 0.01$), and a mathematical relationship between S3 and AFDW was established (sqrt(AFDW) = 2.84 * (width S3) – 0.92; intercept: –0.92 ± SE 0.072; slope: 2.84 ± SE 0.096; $R^2 = 0.91$; F = 870.37; $p < 0.01$; SE of predicted y-values = 0.23).

Subsequently, S3 was measured on all collected specimens (11958 ind.), allowing calculation of the individual biomass (AFDW). Individuals were counted and attributed to four groups: fertile (ovigerous) females, fertile males, non-fertile animals, and a group of damaged specimens for which reproductive status and sex could not be determined.

DATA ANALYSIS

Counts were used for abundance-related analysis. Biomass calculation allowed calculation of secondary production, using two methods (cf. Souza and Borzone, 2000): size frequency method (SFM: Hynes and Coleman, 1968) and mass specific growth rate method (MSGR: Crisp, 1984). Growth (von Bertalanffy growth function – parameters estimated by (1) preliminary estimation of L_{inf} with Powel-Wetherall plot (Wetherall, 1986) and (2) using the obtained value as seeding value for growth curve fitting), mortality (instantaneous mortality rate Z, calculated assuming a single negative exponential model and applying a size-converted catch curve with the ELEFAN II routine (Pauly, 1990; Gayanilo *et al.*, 1996)) and a cohort analysis using the entire sampled population (decomposition of size-frequency distributions into Gaussian components with Bhattacharya's method (Bhattacharya, 1967) and NORMSEP (Hasselblad, 1966; Tomlinson, 1971)) were conducted with FiSat II software (Gayanilo *et al.*, 1996), using ELEFAN routines (Pauly and David, 1981; Pauly, 1986). The growth function was determined by its parameters, being L_{inf} = maximum asymptotic width of third setiger; K = growth curve parameter; C = parameter reflecting the strength of the seasonal growth oscillation; WP = wintering point = moment of minimal growth; R_n = index for the goodness of fit provided by the ELEFAN I routine. If similar units and definitions are used, growth performance parameters have been shown to be remarkable constant between different populations of the same species (Munro and Pauly, 1983). For the first time to our knowledge, values for marine invertebrates are presented; both the weight-related phi (ø) and size-related phi prime (ø').

Due to its more descriptive rather than predictive capacity (Short, 1999), the beach index (BI) was preferred over the more conventional omega and RTR parameters for characterisation of morphodynamics (BI = log (((-log2(median grain size in µm) + 1) * tidal range) / slope) (McLachlan and Dorvlo, 2005).

Given the spatially (intra-transect comparisons - zonation) and temporally (monthly sampling at the same transect locations) dependent nature of the data, statistical tests were chosen accordingly.

Results

PHYSICAL ENVIRONMENT

All sampled beaches were wide, macrotidal beaches with an average spring tide tidal range ranging more or less from 4.5 to 4.7m. Beach slope was weak (0.75-1.15°) though regular, while along some transects, the small-scale relief displayed a seasonal change in morphology concerning the presence of beach runnels. Sediment analysis showed the median grain size to range from 171 to 347 µm (including lower intertidal stations were the species was absent) and the sediment to be well to moderately well sorted (SD µm = 1.29-1.58). Values for BI of 2.7 to 3.0 indicate the highly dissipative morphodynamic nature of all sampled transects, as has been shown to be the case for many Belgian beaches (Degraer *et al.*, 2003a).

LIFE CYCLE, DEMOGRAPHY, REPRODUCTION AND RECRUITMENT

No difference between the overall pattern and patterns per transects or per beach was observed. Four cohorts could be observed (Fig. 1; Tab. 1). The oldest one (C1) was only observed in samples of the first sampling month (October 2003). Most likely, specimens belonging to this cohort died subsequently. Two other cohorts were present throughout the entire sampling period (larger, older C2 and younger, smaller C3). The decrease in S3 from October to November 2003 might be attributed to early winter conditions and associated loss of body weight. Unfortunately, the applied methods did not allow separation of these two cohorts from December 2003 until July 2004. Erratic positive and negative growth, as observed for the combined group of both cohorts, is most likely to be attributed to shifts in the relative abundance measures of both cohorts. Comparison of their numbers just before (November 2003: C2 = 89%; C3 = 11%; (n_{C2} = 1174; n_{C3} = 151)) and after (August 2004: C2 = 1%; C3 = 70%; (n_{C2} = 7 and n_{C3} = 433)) the period during which they cannot be told apart, suggests a gradual decrease of dominance of the older C2, whereas the opposite can be observed for the younger C3. Though it may appear strange for C2 to reappear after colliding with C3, the low number of animals in C2 after the merged period indicates that only a couple of larger animals are still found, while the main part of this cohort has died after reproducing. Settlement of recruits could be observed first in July 2004, and subsequent increase of average S3 relates to growth of this C4 cohort.

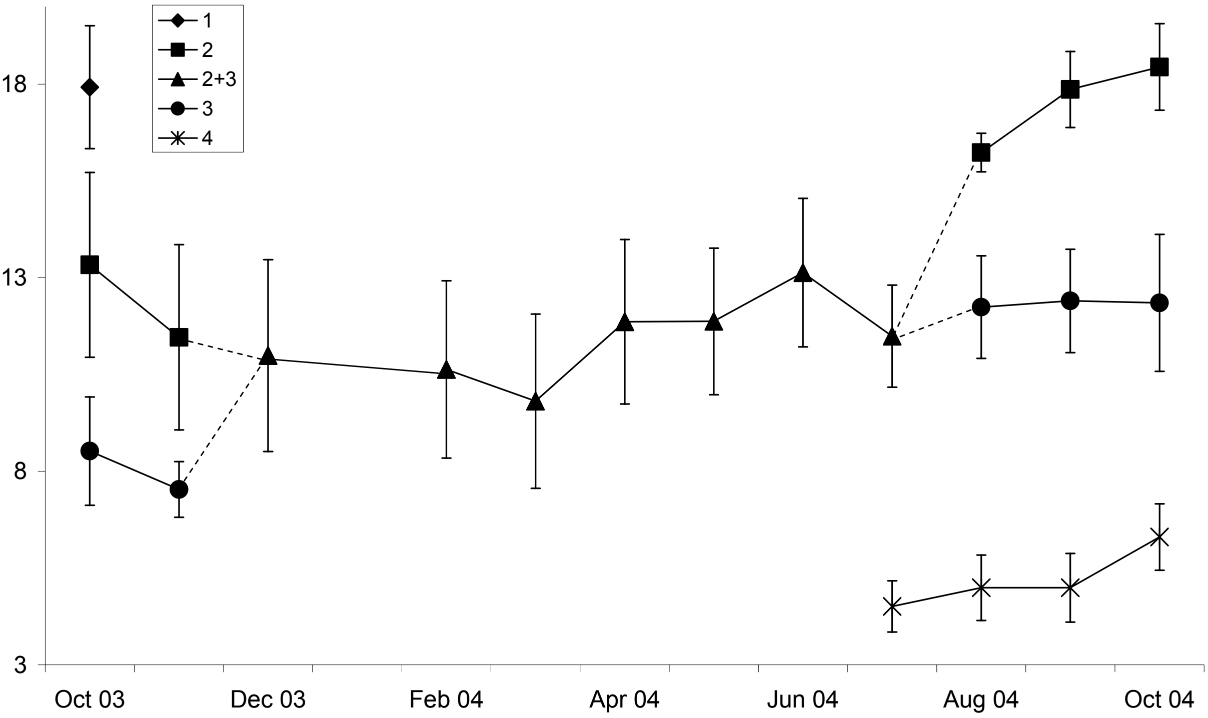

Figure 1. Variation of S3 width of each cohort over time, as differentiated by Bhattacharya's method and consolidated by NORMSEP; dotted lines indicate fusion (November 2003 to December 2003) and split (July 2004 to August 2004) of cohorts 2 and 3. Based on combined data from all sampled locations.

Table 1. Total number (n), relative number (n %; percentage of total), average S3 width (avg; tenths of mm) and standard deviation to that width (stdev; tenths of mm), as obtained from the cohort analysis; C1 = cohort 1 = oldest cohort, C2 = cohort 2, C3 = cohort 3; C4 = cohort 4 = youngest cohort, C2+C3 relates to animals that cannot be attributed to a single cohort but belong to either C2 or C3; see also Fig. 1. Based on combined data from all sampled locations.

n	Oct 03	Nov 03	Dec 03	Feb 04	Mar 04	Apr 04	May 04	Jun 04	Jul 04	Aug 04	Sep 04	Oct 04
C1	27	0	0	0	0	0	0	0	0	0	0	0
C2	580	1174	0	0	0	0	0	0	0	7	3	3
C2+C3	0	0	1198	1111	773	1154	1381	805	701	0	0	0
C3	229	151	0	0	0	0	0	0	0	433	178	452
C4	0	0	0	0	0	0	0	0	126	183	185	253
n %	Oct 03	Nov 03	Dec 03	Feb 04	Mar 04	Apr 04	May 04	Jun 04	Jul 04	Aug 04	Sep 04	Oct 04
C1	3.2	0	0	0	0	0	0	0	0	0	0	0
C2	69.4	88.6	0	0	0	0	0	0	0	1.1	0.8	0.42
C2+C3	0	0	100	100	100	100	100	100	84.8	0	0	0
C3	27.4	11.4	0	0	0	0	0	0	0	69.5	48.6	63.8
C4	0	0	0	0	0	0	0	0	15.2	29.4	50.6	35.7

avg	Oct	Nov	Dec	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
	03	03	03	04	04	04	04	04	04	04	04	04
C1	17.9											
C2	13.3	11.5								16.2	17.9	18.4
C2+C3			11.0	10.6	9.8	11.9	11.9	13.1	11.5			
C3	8.5	7.5								12.2	12.4	12.4
C4									4.5	5.0	5.0	6.3

stdev	Oct	Nov	Dec	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
	03	03	03	04	04	04	04	04	04	04	04	04
C1	1.6											
C2	2.4	2.4								0.5	1.0	1.1
C2+C3			2.5	2.3	2.2	2.1	1.9	1.9	1.3			
C3	1.4	0.7								1.3	1.3	1.8
C4									0.7	0.8	0.9	0.9

Highest numbers of fertile adults were present from the end of April until early June (Fig. 2). By September, fertile adults had disappeared from the data (Fig. 2) and only very low numbers of the reproducing C2 cohort were left (Tab. 1). The start of appearance of fertile adults was situated in the period of merged C2 + C3 cohorts (Tab. 1, Figs. 1 and 2). On average, more females than males could be found in a single sample (sample averaged sex-ratio = 1.41 females / male). Some samples contained up to seven times more females than males.

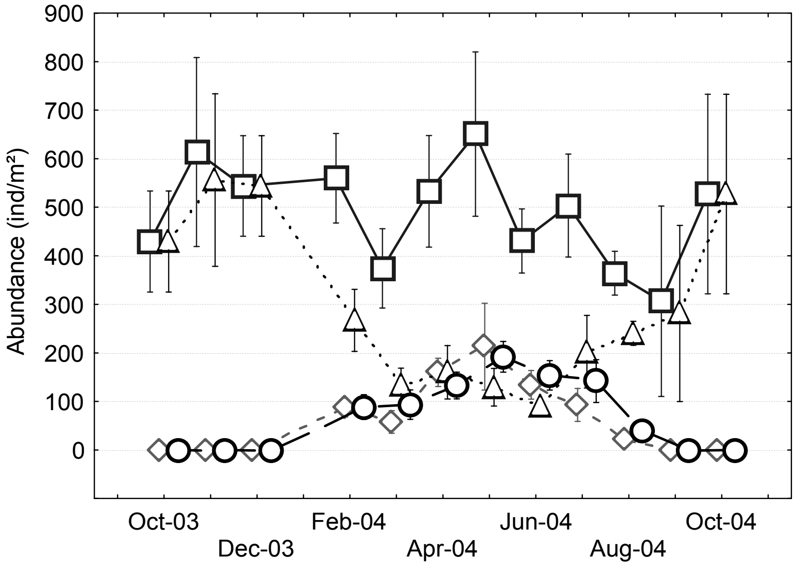

Figure 2. Variation of total and partial abundance (ind/m²) over time; squares & solid line = total abundance – triangles & dotted line = non-fertile animals abundance – diamonds & short-dashed line = fertile male abundance – circles & long-dashed line = fertile female abundance; error bars are standard errors.

ABUNDANCE AND BIOMASS PATTERNS

Mean average density was 169 ± 9 SE ind/m². Due to the species being restricted to an upper intertidal zone, this figure comprises many samples of lower elevations where the species is absent. Therefore, also the mean maximum (or modal) density along each transect is given: 505 ± 38 SE ind/m²; one sample represented a maximal abundance value of 1880 ind/m². A different way to express abundance is as individuals per strip transect or running (long-shore) meter: $IST_r = (w_r / n_r) * \Sigma q_i$ [ind / m], which is the sum of all ind/m² (q_i) from all n samples of transect r, multiplied by the horizontal width of the species distribution (w) on the beach (Defeo and Rueda, 2002). Average IST_r was 16286 ± 1330 SE ind/m and displayed significant seasonal variation (Friedman Chi Square (N = 8, df = 10) = 22.6 p = 0.013) with lower values being apparent from June until October (Fig. 3).

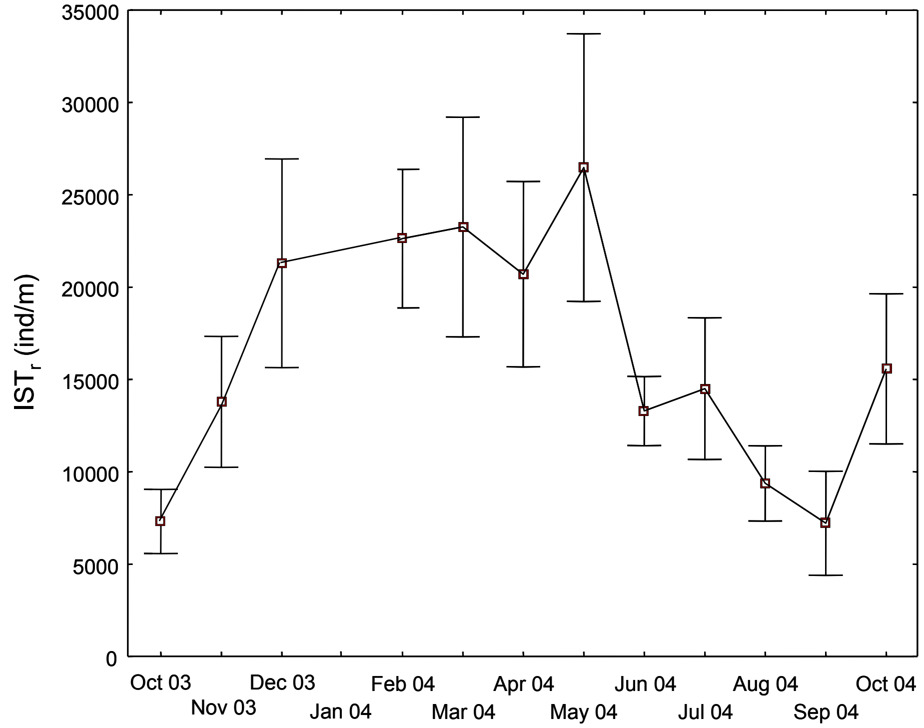

Figure 3. Variation of individuals per strip transect (ind/m) over time; error bars are standard errors.

Mean average biomass was 0.081 ± 0.005 SE g AFDW/m²; mean maximum biomass along each transect was 0.25 ± 0.02 SE g AFDW/m². Like with IST, a biomass-related BMST was calculated. On average, this was 7.8 ± 0.7 SE g AFDW/m. BMST also displayed significant temporal variation (Friedman Chi Square (N = 8, df = 10) = 26.98 p = 0.0026), peaking simultaneously with the above estimated period of reproduction.

GROWTH AND MORTALITY

A von Bertalanffy growth curve was fit to the S3 width – frequency distributions (Fig. 4): L_{inf} = 2.489 mm; K = 0.51 / year; C = WP = 0.00; R_n = 0.343. Growth performance indices were also calculated: weight-related phi (ø)= 0.166; size-related phi prime (ø') = 2.5. Instantaneous mortality rate Z was 4.08 / year.

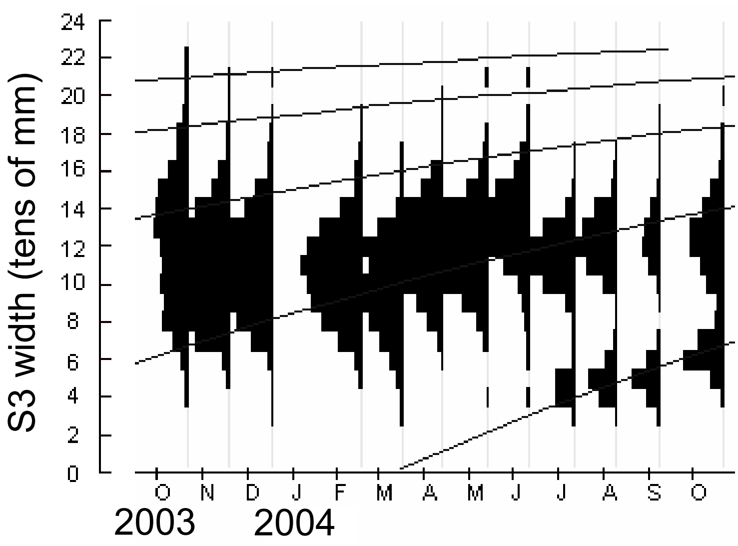

Figure 4. Available length-frequency distributions (histograms) with fitted von Bertalanffy growth curves (curved lines).

MEAN ANNUAL BIOMASS, SECONDARY PRODUCTION AND P/B RATIO

Mean annual biomass was 0.797 g AFDW/m². As with Souza and Borzone (2000), values for the secondary production and P/B ratio as obtained with the SFM were higher than those estimated with the MSGR method. Annual production was 1.9 (SFM) and 0.88 (MSGR) g/(m²*year). Deduced P/B ratio's were 2.40 (SFM) and 1.11 (MSGR) / year.

ZONATION

Densities of more than 500 ind/m² occurred in sand with median grain size ranging from 210 µm to 320 µm (Fig. 5a). Maximum density of *Scolelepis squamata* along each transect was usually encountered between 3.95 and 4.40 m above MLLWS (Fig. 5b). No significant seasonal variation in the elevation of the maximum density was detected (Friedman Chi Square (N = 7, df = 9) = 11.23178; p = 0.26).

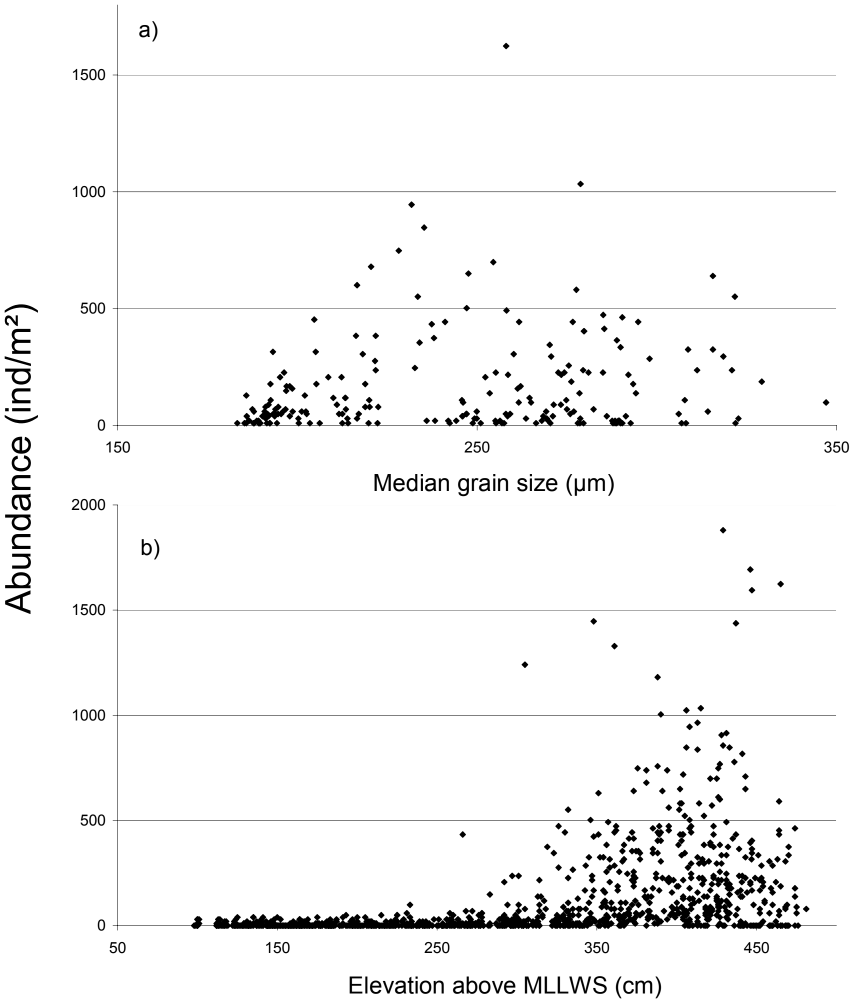

Figure 5. Abundance (ind/m²) as a function of (a) median grain size (n = 214) and (b) height above MLLWS (n = 1229). Median grain size data from four sampling months (October 2003 and February, June and October 2004); sediment data from other months unavailable.

Maximum density of non-fertile animals (i.e. mainly younger, pre-fertile animals) was located significantly higher on the beach than that of fertile animals (Wilcoxon Matched Pairs Test: p = 0.026), with peak abundances of non-fertile animals located at 411.15 ± 4.19 SE cm above MLLWS and those of fertile animals at 401.71 ± 4.95 SE cm above MLLWS. No significant year-round difference was found between males and females (Wilcoxon Matched Pairs Test: p = 0.59). Yet, looking at the different months, the difference in elevation between peak densities of both sexes seemed to display a trend (Fig. 6), by which this difference is minimal at the (deduced) time of reproduction.

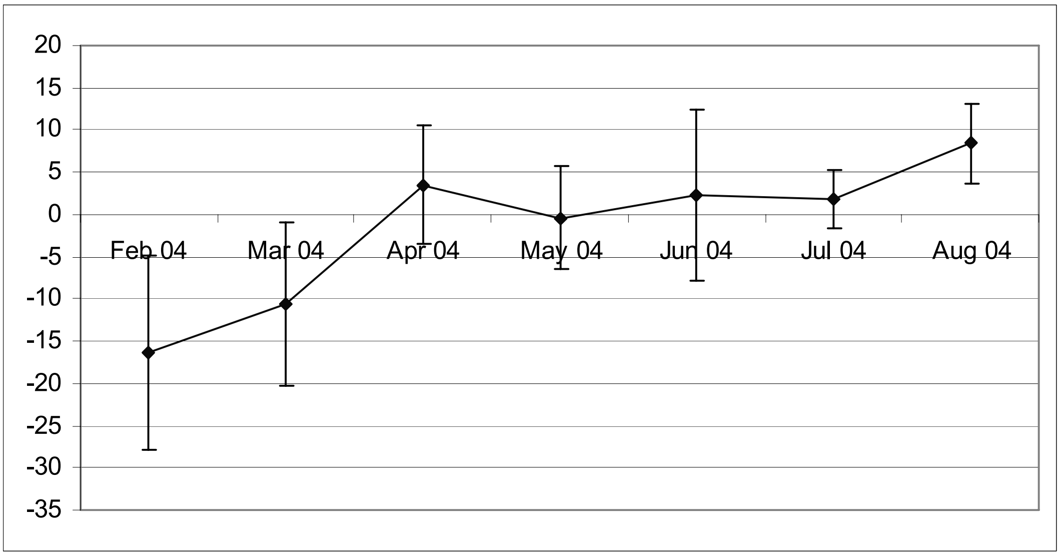

Figure 6. Average difference between fertile males and females regarding the elevation of their maximum abundance (in cm; male peak abundance minus female peak abundance) displayed over time; error bars are standard errors.

In contrast to earlier studies, the occupied width of the vertical intertidal range was investigated. This zone width is defined as the difference in elevation between both the lowest and highest sample containing at least five specimens (~ 50 ind/m²) and was 68.0 ± 4.1 SE cm on average. Males (48.2 ± 5.6 SE cm) occupied a significantly wider range than females (36.8 ± 4.7 SE cm) (Wilcoxon Matched Pairs Test: $p = 0.02$). In view of the beach slope, this seemingly small difference corresponds to a horizontal range difference of 6-9 m cross-shore. Fertile animals seemed to tend to occupy a wider range than non-fertile animals, being significant at the 10% level (Wilcoxon Matched Pairs Test: $p = 0.08$).

Discussion

LIFE CYCLE, DEMOGRAPHY, REPRODUCTION AND RECRUITMENT

Compared to spionid family averages, as calculated by McHugh and Fong (2002), Belgian *Scolelepis squamata* especially differs regarding its elevated age at first (and single) reproduction (Tab. 2). Also egg size (as determined by Joyner, 1962) and life span attain higher values, whereas body size is identical to McHugh and Fong's calculated family average, even though it has been mentioned that the species may reach 80-138mm elsewhere (Hartmann-Schröder, 1996).

Table 2. Comparison of Belgian *Scolelepis squamata* to family averages, as calculated by McHugh and Fong (2002). Spionidae error values are standard deviations; n = number of species.

	Spionidae	***Scolelepis squamata***
Age at first reproduction (years)	0.5 ± 0.4 (n = 12)	1.8
Life span (years)	1.8 ± 0.7 (n = 11)	2.2
Body size (mm)	40 ± 22 (n = 8)	40
Fecundity (# eggs/embryos)	3676 ± 9597 (n = 20)	?
Egg size (diameter in µm)	145 ± 60 (n = 29)	192-280µm x 106-142µm (from UK: Joyner, 1962)

The discontinuous presence of fertile adults (February to August) suggests discontinuous reproduction, coinciding with discontinuous recruitment. Bayed *et al.* (2006) also found discontinuous reproduction, albeit fertile animals were found over a longer period (ten months instead of seven) and four different peaks of recruitment (instead of one), whereas Souza and Borzone (2000) found continuous reproduction (with two recruitment peaks) to be highly probable. Taking into account a duration of larval development of about 1 to 2 months (Hannerz, 1956; Joyner, 1962), the (maximum) reproductive effort can be estimated to run from the end of April until early June. This coincides with the highest observed relative abundance of fertile adults.

The observed predominance of females is in contrast to the findings of Bayed *et al.* (2006) but not exceptional among polychaetes (e.g. Fidalgo e Costa, 2003).

ABUNDANCE AND BIOMASS

Significant seasonal variation in IST, with lower values from June until October, suggests that the number of recruits settling in that period, is too low to compensate for the mortality among the C1 cohort, which most likely gave birth to these recruits. Whether this is a recurrent phenomenon on Belgian beaches has to be addressed with a multi-annual study, allowing assessment of interannual variation. However, we cannot rule out that this observed pattern is generated by the choice of sieving mesh width. Possibly, a bottle-neck effect for recruit abundance is at hand during the period that they are too small to be retained by a 1mm mesh width sieve. On the other hand, demonstration of different zonation of adults and non-fertile animals (as discussed below), was possible, despite potential loss of the smallest individuals.

Concerning biomass, the only previously available assessment from Belgian beaches concerns a beach at De Panne, with total macrobenthic biomass ranging from 0.040 to 0.800 g AFDW/m² (Elliott *et al.*, 1997). Thus, with considerable reservation, we might estimate *Scolelepis squamata* to be able to build up one third of total biomass.

Despite the results from this study and earlier work, it is still not possible to identify *Scolelepis squamata*'s population size controlling factors and the role of stochasticity at different geographical scales remains poorly understood.

GROWTH AND MORTALITY

Remarkably, growth does not seem to be seasonally oscillating, whereas the cohort analysis suggested a decrease of S3 and biomass from October 2003 to November 2003. The goodness of fit value is slightly higher than those of Souza and Borzone (2000) (0.28 and 0.29). Unfortunately, no previously obtained growth performance indices of the species or related animals are available. We advocate the use of these more species-specific parameters in growth studies, in order to allow better a comparison across different studies.
The observed mortality value (Z = 4.08 / year) is of the same order of magnitude as those obtained by Souza and Borzone (2000) (Z = 2.52 / year and 5.52 / year).

MEAN ANNUAL BIOMASS, SECONDARY PRODUCTION AND P/B RATIO

The observed P/B ratio of 1.76 / year (average of SFM and MSGR) and by previous research (2.1-2.5 /year in Mooij, 1982; 2.7 /year in Souza and Borzone, 2000; 2.03 / year in Bayed *et al.,* 2006), is intermediate to moderately low in comparison with other polychaetes and other spionids (e.g. Heip and Herman, 1979; Méndez *et al.*, 1997; Abrantes *et al.*, 1999; Thompson and Schaffner, 2001; García-Arberas and Rallo, 2002, 2004; Kevrekidis, 2005; see also compilation of 16 spionid species in Souza and Borzone (2000)) (Tab. 3).

Table 3. Some examples of the P/B ratio of polychaete species.

Family	**Species**	**P/B ratio (/ year)**	**Location - Author**
Spionidae	*Scolelepis squamata*	1.76 (average)	Belgium - this study
Spionidae	*Scolelepis squamata*	2.03	Morocco - Bayed *et al.* (2006)
Spionidae	*Scolelepis squamata*	2.7 (average)	Brazil - Souza & Borzone (2000)
Spionidae	*Streblospio benedicti*	4.46	Spain - García-Arberas & Rallo (2004)
Spionidae	*Streblospio shrubsolii*	2.14 and 2.23	Greece - Kevrekidis (2005)
Spionidae	16 species, compiled by Souza & Borzone (2000)	1-12.9	various - Souza & Borzone (2000)
Nereididae	*Nereis (Hediste) diversicolor*	2.5	Belgium - Heip & Herman (1979)
Nereididae	*Nereis (Hediste) diversicolor*	1.97	Spain - García-Arberas & Rallo (2002)
Nereididae	*Nereis (Hediste) diversicolor*	4.4-7.9	Portugal - Abrantes *et al.* (1999)
Capitellidae	*Capitella capitata*	23.7 and 36.7	Spain - Méndez *et al.* (1997)
Chaetopteridae	*Chaetopterus* cf. *variopedatus*	1.0-3.5	USA - Thompson & Schaffner (2001)

Given the harsh nature of the sandy beach environment, a higher secondary production and turnover as well as a shorter life span, would be expected. Although not visibly substantiated by data (i.e. comparable median grain size, slope and morphodynamics), it is possible that Belgian beaches provide a more benign habitat than e.g. the Brazilian ones (Souza and Borzone, 2000), the latter inducing higher secondary production and shorter life span (P/B ratio, as average of SFM and MSGR output, 2.7) and life span of about 6 months, in contrast to 1.76 and 1.8 here). It is noted that the use of different biomass assessment techniques may hamper objective comparability of results (4 hours at 110°C and 2 hours at 550°C (AFDW) in this study; 24 hours at 80°C in Bayed *et al.* (2006) (DW); 6 hours at 500°C in Souza and Borzone (2000)).

Furthermore, it is noted that given the total macrobenthic biomass values of 2.3 g AFDW for Dutch beaches (Janssen and Mulder, 2005), the high MAB and P values of Mooij (1982) (Tab. 4) are most likely due to a calculation error.

ZONATION

Peak abundance elevation seems to concur with Moroccan observations (Bayed *et al*., 2006) but not to Brazilian (Souza and Borzone, 2000) nor Dutch (Mooij, 1982) results. Sedimentology, slope and morphodynamics of Belgian, Dutch and Brazilian beaches seem comparable, in contrast to those of the Moroccan beach. Opposite to the results of Souza and Borzone (2000) at a local scale, no clear explanation for global differences seems to reside within these abiotic factors. Due to the relatively low number of sampled transects, local variability of abundance of *Scolelepis squamata* on Belgian beaches can for now not be attributed to grain size diameter nor to clear morphodynamic differences.

In contrast to observations made on some other macrobenthic animals, like the syntopic occurring amphipod *Bathyporeia pilosa* (Persson, 1982; as *Bathyporeia* sp. in Degraer *et al.*, 1999a), no seasonal cross-shore migration could be demonstrated and presumed limited adult mobility (Joyner, 1962), is thereby partially confirmed.

The established segregation of younger specimens and adults, with the latter situated lower on the beach than the former, has already been observed for other macrobenthic species (McLachlan and Jaramillo, 1995; Gaspar *et al.,* 2002) and, although it was also proven for *Scolelepis squamata* by Mooij (1982), it seems -to our knowledge- to have gone unpublished so far for polychaetes (Defeo and McLachlan, 2005). This segregation might be explained by smaller specimens being poorer intraspecific competitors than adults (de Alava and Defeo, 1991), but also easier water maintenance of a smaller animal body and preference for lower levels of predation found at higher elevation might explain the observed zonation of smaller individuals. Water maintenance is likely to be more restrictive for soft-bodied polychaetes than e.g. for more robustly built crustaceans. The main predators of *Scolelepis squamata* are birds (especially Sanderling) and submerged predators (e.g. epibenthic fish and larger crustaceans but also other infauna species, especially *Eurydice pulchra*). Whereas the former are visual predators, likely to detect larger specimens more easily, submerged predators will have more difficulty reaching more shallow zones. The observed segregation goes accompanied by a at the 10% level significant difference in vertical tidal range zone width, with adults occupying a somewhat wider zone, suggesting that intraspecific competition for space might indeed be at work here. Additionally, the omnivorous nature of the adult animals might hamper settlement through cannibalism on their recruits. Intraspecific segregation in *Arenicola marina* has been attributed to a negative response of settling juveniles towards the presence of adults (Hardege *et al.,* 1998; Reise *et al.*, 2001). However, sandy beaches, in contrast to more stable muddy environments such as tidal flats, exhibit far less biological interactions and are essentially physically driven ecosystems (Defeo and McLachlan, 2005).

The observed trend in difference of elevation of peak abundance might indicate cross-shore aggregation of males and females during reproduction, in order to minimise distances to be travelled by their spawn prior to successful fertilisation. Aggregation should, however, be tested both in the cross-shore and long-shore direction involving sampling at an adequate scale, smaller than the scale at which we sampled.

In contrast to most studies on intertidal fauna, width of the vertical intertidal range was considered and showed significant differences between males and females, with males being distributed wider in the cross-shore direction than fertile females. Therefore, it seems valuable to us to include zone width in sandy beach fauna research.

Lab experiments have shown *Scolelepis squamata* to be tolerant towards sediments with a wide range of median grain sizes (Speybroeck *et al.*, in prep.). Thus, the role of sediment as a population structuring element seems limited. The detected pattern of abundance as a function of median grain size has to be regarded as largely depending on the “by coincidence” available range of grain sizes at a given site and elevation.

TOWARDS GLOBAL PATTERNS OF INTRASPECIFIC VARIATION IN LIFE HISTORY CHARACTERISTICS

It has been suggested that global differences in secondary production might be attributed to sediment stability during recruitment, environmental stress and differences in successful recruitment (Souza and Borzone, 2000; Bayed *et al.*, 2006), while the global variation in reproductive patterns and zonation cannot (or, at least, not for now) readily be linked to abiotic factors (slope, median grain size, morphodynamics, ...). It is not possible to fit the available data to general trends of latitudinal variation in population features, as presented by Defeo and McLachlan (2005) and all available studies are too short termed to allow assessment of the importance of episodic environmental events. A clinal gradient induced by climatology might be at work, yet with only a handful of studies available, a worldwide pattern cannot be drawn, thus, this hypothesis cannot be tested. Disregarding possible taxonomical imperfection, northwestern European populations of *Scolelepis squamata*, like those from this study and those studied by Mooij (1982), are leaning more towards K-strategy than the apparently more short-lived, multivoltine populations from Morocco and especially Brazil. An accordingly anticipated, lower P/B ratio is, however, not immediately apparent; the Brazilian ratio is higher, while the Moroccan one is not. As mentioned, comparability of these values might be hampered by differences in applied methodology. Whereas observed differences in abundance and biomass, secondary production, P/B ratio, life span, reproductive patterns and zonation might be attributed to both intraspecific plasticity of life history characteristics and a differential response to morphodynamical variation of the studied beaches, one might ponder upon the limits of intraspecific variation. A remarkable fact is the observed variation in body size between the available studies. Recalculation and comparison of the applied body length proxy measures shows animals from Belgian beaches to be of comparable size as those from the Wadden Sea (Mooij, 1982). In contrast, animals from southern Brazil seem to be only half as broad (setiger width) as Belgian one, whereas Moroccan ones would have a prostomium length twice that of the Belgian populations. Without being able to draw any certain conclusions, these differences should at least raise some suspicion. Confusion on whether the same species is being dealt with has already arisen (Richards, 1970; see Blake and Arnofsky, 1999), in part being evoked by propagation of the older name *Nerine cirratulus* (e.g. Bhaud, 1986). Therefore, taxonomical research seems desirable, in order to assess whether *Scolelepis squamata* as defined today might be a superspecies, as already hinted by Pardo and Amaral (2004).

Table 4. Comparison of results on the population dynamics, life history and zonation patterns of *Scolelepis squamata.*

	This study	**Bayed *et al.* (2006)**	**Souza & Borzone (2000)**	**Mooij (1982)**
MATERIAL & METHODS				
Country	Belgium	Morocco	Brazil	the Netherlands
Sieve mesh width (mm)	1	1	0.5	0.5 / 1
Size proxy; alternatives?	S3 width; yes	l of prostomium; yes	S5 width; no (?)	S10 width; no (?)
Biomass quantifier	AFDW	DW	AFDW	AFDW
Sampling period (years)	1	2.25	1	1
Sampling frequency	monthly	monthly	monthly	6 / year
LIFE CYCLE & POPULATION CHARACTERISTICS				
Reproduction	discontinuous	discontinuous	continuous	discontinuous
Presence fertile animals	Feb-Aug	Jan-Feb to Nov-Dec	all year; 2 peaks	?
Life span (months)	24-26	12 (summer recruits)	6 and 9	23
Sex ratio	1.41 ♀♀ / ♂♂	more ♂♂	?	?
ABUNDANCE & BIOMASS				
Mean abundance (ind/m²)	169	130-2800	?	?
Mean modal abundance (ind/m²)	505	1310-1348	20	?; 4800 ad. and 17000 juv. peaks
Mean biomass (g/m²)	0.081	?	?	?
Mean modal biomass (g/m²)	0.25	?	?	?
Mean IST_r (ind/m)	16286	?	peaks of 92 and 319	?
Mean $BMST_r$ (g/m)	7.8	?	?	?
GROWTH & MORTALITY				
Growth - VBGF parameters	L_{inf} = 24.89; K = 0.51; C = WP = 0	?	L_{inf} = 0.7mm; K = 3; C = 0.92; WP = 0.70 and 0.25	?
Mortality (/year)	4.08	?	2.5 and 5.5	?
MEAN ANNUAL BIOMASS, PRODUCTION & P/B ratio				
Mean annual biomass (g/m²)	0.80	5.57	0.21	22.8 (? – see text)
*P (g/(m²*year)*	1.4	11.28	0.57	56.2 (? – see text)
P/B ratio (/year)	1.76	2.03	2.7	2.5 (? – see text)
ZONATION				
Elevation of modal density	3.95-4.40 m above MLLWS	retention zone	mid-tidal	mid-tidal
Height segregation	juv higher than ad	?	?	juv higher than ad
Width of vertical range (cm)	68	?	?	?

Conclusions

Clearly differing to the discussed extent from studies from other parts of the world, Belgian *Scolelepis squamata* are semelparous with a long life span of about 24 months. A single recruitment per year (from July continuing at least until October) is produced by each cohort after about 2 years of growth (although occasional spawning of larger one year-old specimens cannot be ruled out) and followed by death, making the species monotelic. Absence of a winter stop in growth can be regarded as a somewhat surprising result. Differences between different studies might be related to taxonomical imperfections and some molecular assessment seems desirable. The -to our knowledge- first evidence of sandy beach polychaete intraspecific cross-shore size segregation provides a novel result for sandy beach ecology research.

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CHAPTER 4

In situ study of the autecology of two closely related, co-occurring sandy beach amphipods

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Abstract

Population dynamics and zonation of the amphipods *Bathyporeia pilosa* and *B. sarsi*, co-occurring on some Belgian beaches, were studied through monthly sampling of eight cross-shore transects (October 2003-October 2004). Their biomass and production were assessed for the first time. Abundance and biomass of *B. pilosa* were ten times higher along western ultra-dissipative transects than along slightly more reflective, eastern transects. For *B. sarsi*, (less prominent) differences between the two westernmost transects (2-5x higher) and all others were observed, whereas P/B ratio was comparable for all. *Bathyporeia pilosa* could reach two times higher abundance and biomass and higher levels of production (max. *B. sarsi* = 7580 mg*m^{-2}*y^{-1}; max. *B. pilosa* = 16040 mg*m^{-2}*y^{-1}), while nearly absent along eastern transects. Continuous reproduction and recruitment with three relative peaks of the latter (February, July, October) were observed. Fecundity showed parallel temporal variation for both species, peaking in February and September-October. Interestingly, the July relative recruitment peak could not be explained by relative abundance of gravid females or fecundity, but is probably caused by adult mortality. Both species displayed comparable gonad production (*B. pilosa*: P_g = 0.73 mg/ind*year; *B. sarsi:* P_g = 0.71 mg/ind*year), but *B. pilosa* produced fewer yet larger embryos. Peak abundances were found at 436 ± 25 SD cm (*B. pilosa*) and 357 ± 40 SD cm (*B. sarsi*) above MLLWS, corresponding to a 40-62 m cross-shore distance between the peaks of both species. The occupied cross-shore range was larger for *B. sarsi* than for *B. pilosa* (35-54 m), for females than for males (15-23 m), and for adults than for juveniles of *B. pilosa* (5-8 m). Both species displayed many comparable life history features. Differences in abundance and biomass may be related to beach morphodynamics and zonation.

Keywords: sandy beaches, population dynamics, amphipods, zonation

Introduction

Bathyporeia pilosa and *B. sarsi* are common amphipod species of beaches of the eastern Atlantic, from Norway to France (Gulf of Biscay), with *B. sarsi* stretching even a little further south (until southern Portugal) (Marques and Bellan-Santini, 1991). *Bathyporeia pilosa* is found in the upper parts of the intertidal zone of sheltered beaches, between MHWS and mid-tide level (Fish and Preece, 1970a); in the retention zone and the upper parts of the resurgence zone, but not in the saturation zone (Salvat, 1962, 1964). It is absent from strongly exposed beaches (Vader, 1965), yet also encountered in subtidal areas, namely in estuarine and brackish conditions (Lindström, 1855; Dahl, 1944; Vader, 1966; Persson, 1982; Köhn and Gosselck, 1989). Slight morphological differences have been observed between intertidal and subtidal populations (d'Udekem d'Acoz, 2004), which may provoke doubt on the conspecifity of those populations. Along an open coastline, *Bathyporeia sarsi* is a strictly intertidal species (Toulmond, 1964; Vader, 1965), where it can be found between MHWN and MLWS (Toulmond, 1964). In some estuaries, however, the species has been found to live below the low water line (Vader, 1965, 1966; Degraer *et al.*, 2002). On Belgian beaches, *B. pilosa* is a species of 'drying sands' (around MHWN), while B. sarsi is said to occur somewhat below it (Degraer et al., 2003). Both species can be highly abundant; in Belgium they can frequently be found together on the same beaches, reaching abundances of up to 10.000 ind/m² (Degraer *et al.*, 2003). These high numbers of amphipods are of high functional importance as food source for wading birds (mainly Sanderling (*Calidris alba*)) and surf zone fish (Lasiak, 1983; Nicolaisen and Kanneworff, 1983; Gibson and Robb, 1996) like juvenile plaice (*Pleuronectes platessa*) (Beyst *et al.*, 2002a) and sand-eel species like *Ammodytes tobianus* (Persson, 1982). Both *Bathyporeia* species are said to feed solely on epipsammic food items and their mouthparts are considered to be specialised for that purpose (Nicolaisen and Kanneworff, 1969). Diatoms (and more specifically species of the genus *Coconeis*) comprise an important part of their diet (Nicolaisen and Kanneworff, 1969; Sundbäck and Persson, 1981).

While *Bathyporeia pilosa* is rather well studied (Vader, 1965, 1966; Nicolaisen and Kanneworff 1969, 1983; Fish and Preece, 1970a, 1970b; Preece, 1970, 1971a, 1971b; Fish, 1975; Khayrallah and Jones, 1980a, 1980b; Sundbäck and Persson, 1981; Persson, 1982; Mettam, 1989; Köhn and Sammour, 1990), far less is known on the ecology of *B. sarsi* (Vader, 1965, 1966; Nicolaisen and Kanneworff 1969, 1983; Bamber, 1993). Several studies have focused on both *B. pilosa* and a third species, *B. pelagica* (Fish and Preece, 1970a, 1970b; Preece, 1971a; Fish, 1975). To a certain degree, *Bathyporeia sarsi* might be regarded as intermediate between *B. pilosa* and *B. pelagica* concerning a number of ecological traits e.g. cross-shore distribution and substrate preferences (Vader, 1965, 1966). Only occasionally, their syntopic occurrence on beaches has been investigated (Vader, 1965, 1966; Nicolaisen and Kanneworff, 1969, 1983). Thus, a combined ecological study of *B. pilosa* and *B. sarsi* was conducted to investigate their life history, population dynamics and zonation patterns and to try to unravel elements of their interspecific ecological segregation in co-occurrence. The first published assessment of biomass and secondary production of these sandy beach key species is presented. Tests were conducted to identify significant spatial and temporal patterns within both species and to compare between them. Based on literature data, we *a priori* hypothesise *B. pilosa* to be the more stress tolerant species, due to life higher up on the beach. We expect interspecific differences in population dynamics characteristics to be related to these different environmental conditions.

Methods

SAMPLING

Along the Belgian shore, eight cross-shore transects were sampled monthly from October 2003 until October 2004, January 2004 excluded (Fig. 1). Sampling started each time at high tide and continued until the low tide level was reached, taking a sample every half hour just above the upper swash limit. In order to minimise differences in tidal range among sampling months, sampling dates related to a fixed point in the lunar spring tide-neap tide cycle. Each sample involved a 0.1026 m² rectangle being dug out to a depth of 20 cm and sieved over a sieve with a 1 mm mesh width. An additional sample was taken for analysis of sedimentology. Elevation of sampling stations and the entire beach profile were measured using a leveller and corroborated afterwards with the output of the M2 tidal reduction model (Coastal Division of the Agency of Maritime and Coastal Services).

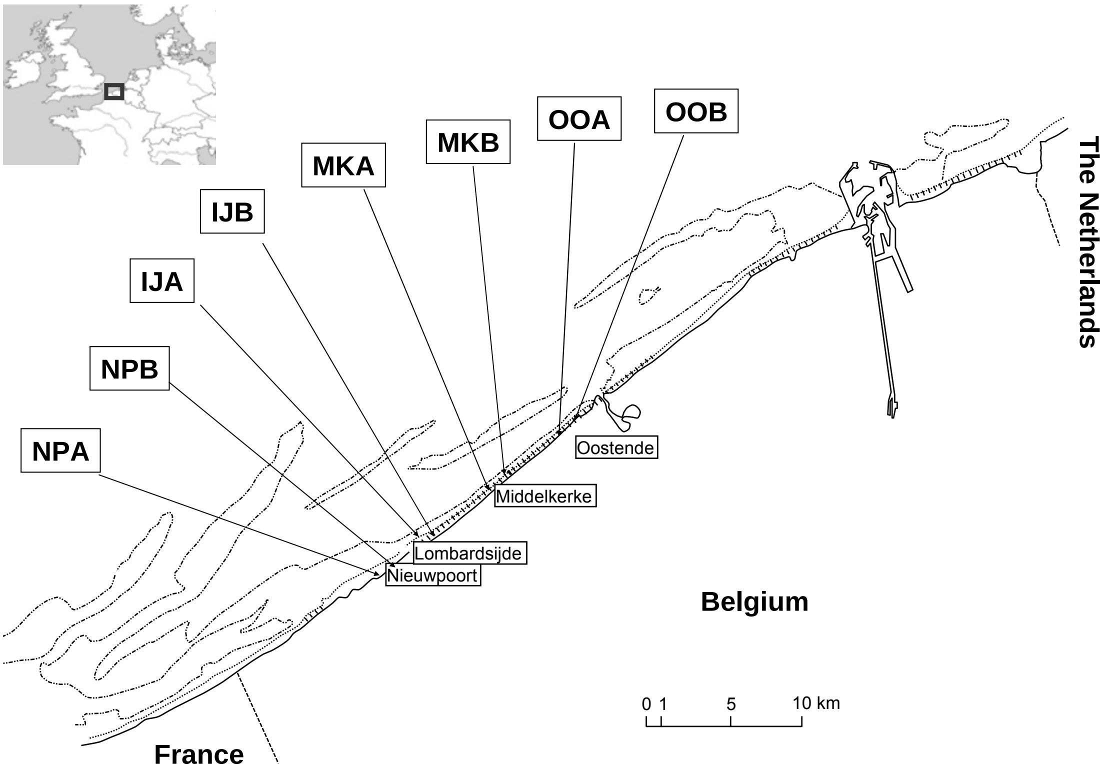

Figure 1. Location of sampled transects along the Belgian coast; NP = Nieuwpoort-Bad, IJZ = beach of Flemish nature reserve "Ijzermonding", MK = Middelkerke-Bad, OO = Oostende-Bad; capitals A and B are to identify each of two transects within the same beach.

On two occasions, a part of the data was intentionally omitted from analysis. First, after the Oostende nourishment of June 2004, involving nourishment of the previously selected OOB transect, samples from the affected transect were not taken into consideration anymore. Furthermore, due to an unanticipated low elevation of high tide and high elevation of low tide, sampling in September 2004 covered a clearly smaller tidal range than during the other sampling months. This resulted in incomplete sampling of the populations of *B. pilosa*, and therefore this month was left out from further analysis of the data for that species.

LABORATORY PROCEDURES

Species identification was achieved with the key by d'Udekem d'Acoz (2004). To obtain a length-biomass regression, allowing calculation of biomass from measurement data, 100 undamaged specimens of both species and all sizes were randomly collected from March (50 ind.) and September (50 ind.) samples. Total body length was measured as in Persson (1982): from the basal segment of the first antenna or antennule (= pseudorostrum) to the end of the telson. Fish and Preece (1970a) and Mettam (1989) chose to measure body length until the spine of the fourth pleon segment. We believe measurement of the entire body to be preferable, even though this might somewhat limit comparability between studies. One hundred specimens of each species were dried (4h at 110°C) and dry weight was established. Subsequent combustion (2h at 550°C) delivered the specimens' ash weight and subtraction of both weights delivered ash-free dry weight (AFDW). After log transformation of the biomass data and having ensured that assumptions were met, linear regression analyses were executed. Thus, with the obtained equations (*B. pilosa*: $R^2 = 0.863$; $p < 0.01$; df = (1. 86); *B. sarsi*: $R^2 = 0.885$; $p < 0.01$; df (1. 97)) and measurement of body length of all collected specimens (10.588 individuals of *B. pilosa* and 3.275 of *B. sarsi*), AFDW was calculated. Three percent of the collected specimens (495 individuals) were damaged to a degree that they could not be identified up to species level. These specimens were omitted from the data.

Individuals were counted and identified as males, females and juveniles according to Watkin (1938). Stations delivering zero values (lower intertidal area) have been omitted to obtain values of abundance and biomass, relating to the occupied long-shore strip of the beach only. Embryos, if present within the female's marsupium or brood pouch, were counted to assess fecundity.

For *Bathyporeia pilosa*, zonation was studied based on the western transects (IJA, IJB, NPA and NPB) only because their numbers at the eastern transects (MKA, MKB, OOA en OOB) are very low.

DATA ANALYSIS

Count data were used for abundance-related analysis. Biomass calculation allowed calculation of secondary production, using the size frequency method (SFM: Hynes and Coleman, 1968): $E_{j\text{-}j+1} = (M_j + M_{j+1})^{0.5} * (N_j - N_{j+1})$; with M_j and M_{j+1} being mean biomass for respectively size class j and j+1 and N_j and N_{j+1} being the mean number of individuals in respectively class j and j+1. Elimination of the average cohort (as all cohorts are spread over the applied size classes and maximum life span is not taken into account yet) is given by: $E_{ac} = \Sigma (E_{j-j+1})$; with j = (1, 2, 3,...m). Production equals elimination of the entire population, taking life span (A_{max}) and number of size classes (m) into account: $E = E_{ac} * m/A_{max}$. Female gonad production, relating to gonadal products released between times t and t+1 was calculated with the formula for direct measurement: $P_{g.ind.t=>t-1} = \Sigma N_{egg} * M_{egg}$ (egg mass* ind^{-1} *time^{-1}). Cohort analysis (decomposition of size-frequency distributions into Gaussian components with Bhattacharya's method (Bhattacharya, 1967) and NORMSEP (Hasselblad, 1966; Tomlinson, 1971)) was conducted with FiSat II software (Gayanilo *et al.*, 1996). Due to the confusing output of the cohort analysis, no von Bertalanffy growth function was fit, nor was the instantaneous mortality rate calculated, but this had no further bearing on other estimates of population characteristics, except for a more indirect determination of the adult life span.

Due to its more descriptive rather than predictive capacity (Short, 1999), the beach index (BI) (McLachlan and Dorvlo, 2005) was preferred over the more conventional Dean's parameter and relative tidal range parameters for characterisation of morphodynamics: $BI = \log ((-\log_2 (\text{median grain size in µm}) + 1) * \text{tidal range}) / \text{slope}$. Given the spatial (intra-transect comparisons - zonation) and temporal (monthly sampling at the same exact transect locations) dependent nature of the data, statistical tests were chosen accordingly.

Results

Due to the strong interconnectivity of marine habitats, we consider the entire Belgian coastline to harbour a single population of both species. Therefore, transects can be regarded as samples of one population. This was confirmed by the fact that only differences in abundance, biomass, production and zonation, related to small-scale variation of the physical environment rather than to the geographical position of the transects, were observed; no spatial variation was observed in most of the population characteristics. In our analyses, no beach effect was evident (among-transect variation comparable to or even less than among-beach variation), thus transects could be used as independent replicates. Given the dependent nature of the data and the type of statistical tests used, spatial comparison (between transects) was, however, possible using sampling months as repeated observations on the same items.

PHYSICAL ENVIRONMENT

All sampled beaches are wide, macrotidal beaches with a sampled intertidal section ranging from about 170 to over 200 m in width and an average spring tide tidal range ranging more or less from 4.5 to 4.7 meter. Beach slope was weak (0.75-1.15°). Sediment analysis showed median grain size to range from 171 to 347 µm and the sediment to be well to moderately well sorted (SD of median grain size (µm) = 1.29-1.58). With a beach index (BI) of 2.7 to 3.0, the morphodynamic type of all four beaches is clearly dissipative, in concordance to Degraer *et al.* (2003). Western transects have, however, higher beach index values (BI = 2.95 ± 0.03 SD) than eastern ones (BI = 2.75 ± 0.03 SD) (Mann-Whitney U Test: $Z = 2.12$; $p = 0.03$), suggesting eastern transects to be a little less dissipative. Significant differences between transects were found in median grain size (Friedman Chi Square (N = 4, df = 6) = 22.39; $p < 0.01$). Western transects (IJA, IJB, NPA, NPB) exhibit lower median grain sizes, especially those from Nieuwpoort (NP; e.g. NPB: 192 ± 6 SD µm), whereas grain size on Middelkerke and Oostende beaches seems comparably larger (e.g. MKB: 268 ± 24 SD µm).

Minor quantities of fines (< 63 µm) were encountered in western transects (highest in NPB: 0.14 ± 1.00 SD % but at least 4x less in other western transects), but were usually completely absent from eastern transect sediment samples.

ABUNDANCE AND BIOMASS

While sampled transects were initially selected as morphodynamically similar, data analysis revealed some clear spatial variation regarding the abundance and biomass of the present *Bathyporeia* populations. Concerning *B. pilosa,* a sharp distinction can be made between western and eastern transects, with significantly higher abundance (Friedman Chi Square (N = 11, df = 6) = 51.74 $p < 0.01$) (Fig. 2) and biomass (Friedman Chi Square (N = 11, df = 6) = 41.63 $p < 0.01$)) on western ones. Whereas western abundance averages are all above 150 ind/m^2, eastern ones are lower than 10 ind/m^2. Biomass supports the same distinction, with biomass ranging from 3 ± 5 SD mg/m^2 for MKA to 714 ± 476 SD mg/m^2 for IJA.

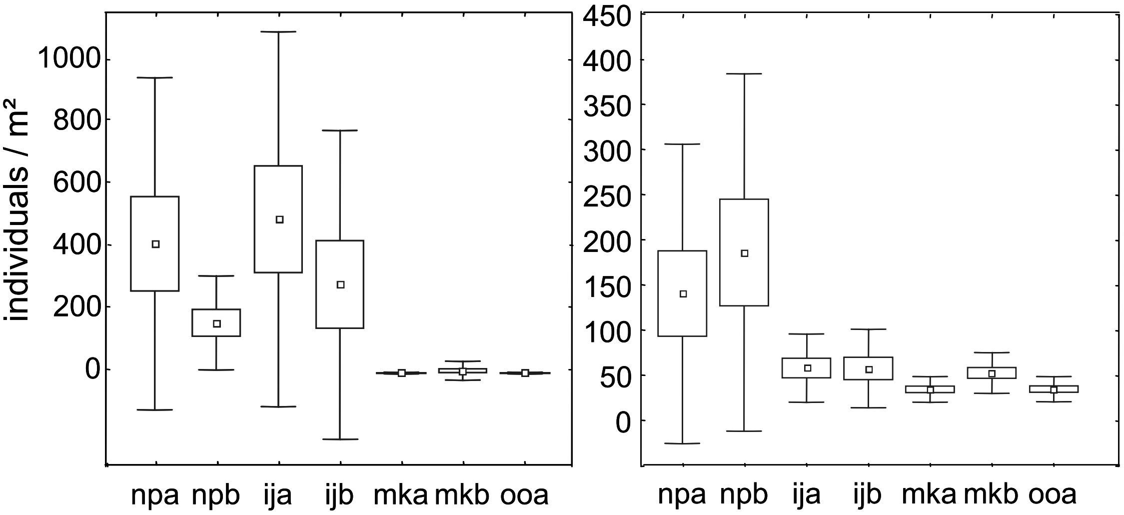

Figure 2. Spatial variation of abundance of *Bathyporeia pilosa* (left) and *B. sarsi* (right) (ind/m^2). Box: SE; whisker: SD. Transects ordered from west (left) to east (right) in both graphs.

Also *B. sarsi* shows significant differences between transects regarding both abundance (Friedman Chi Square (N = 9, df = 6) = 35.48; $p < 0.01$) and biomass (Friedman Chi Square (N = 9, df = 6) = 25.19; $p < 0.01$), however, grouping those differently. In this species, only the Nieuwpoort transects have higher densities (averages of more than 125 ind/m^2), while all other beaches maintain moderate densities of the species (averaging at 40 ind/m^2). The difference between transects is clearly not as strong as with *B. pilosa* and all transects seem to maintain viable populations of *B. sarsi*. From a -rather trivial- comparison between the densities of both species, we can conclude that *B. pilosa* is significantly more abundant on the IJA, IJB and NPA (Wilcoxon Matched Pairs Test: respectively $Z = 2.82$ and $p < 0.01$; $Z = 2.43$ and $p = 0.02$; $Z = 2.51$; $p = 0.01$) transects, while *B. sarsi* is significantly more abundant than *B. pilosa* on MKA, MKB and OOA (Wilcoxon Matched Pairs Test: respectively $Z = 3.06$ and $p < 0.01$; $Z = 2.12$ and $p = 0.03$; $Z = 3.06$ and $p < 0.01$). Finally, both occur in comparable numbers on the NPB transect (Wilcoxon Matched Pairs Test: $Z = 0.40$ and $p < 0.69$).

Maximum observed densities were 8209 ind/m^2 for *B. pilosa* (NPA in July 2004) and 2205 ind/m^2 for *B. sarsi* (NPB in May 2004).

While no significant temporal variation was observed for *B. pilosa* (abundance: Friedman Chi Square ($N = 3$, $df = 10$) = 10.18 $p = 0.42$; biomass: Friedman Chi Square ($N = 3$, $df = 10$) = 8.08 $p = 0.21$), both numbers and biomass of *B. sarsi* peaked in spring and were lowest in autumn and winter (abundance: Friedman Chi Square ($N = 4$, $df = 11$) = 21.80 $p = 0.03$; biomass: Friedman Chi Square ($N = 4$, $df = 11$) = 11.87 $p < 0.01$).

Conclusively, significant differences in size between both species were found (Wilcoxon Matched Pairs Test: $Z = 2.90$ and $p < 0.01$), with *B. sarsi* (6.10 ± 0.68 SD mm) being about 10% larger than *B. pilosa* (5.45 ± 0.73 mm).

LIFE CYCLE, DEMOGRAPHY, REPRODUCTION AND RECRUITMENT

Cohort analysis for both species delivered confusing results, making it impossible to track down any age group through time and suggesting continuous reproduction. Therefore, we also prefer to refrain from any, undoubtedly confusing, graphic representation. A nine months maximal adult life span for both species could be deduced from partially traceable cohorts. Arrival of new, small *B. pilosa* individuals (i.e. recruitment) was e.g. observed in October, with an average length of 3.11 mm in 2003 and 3.86 in 2004. Another peak in recruitment was observed in February, with individuals of 4.08 mm of average length. Tracing individual cohort life history from month to month proved to be very difficult, if not pointless. This is due to continuous reproduction and recruitment and merging and re-splitting of groups of recruits of the same age. The February 2003 recruitment cohort can be traced somewhat more clearly than that of October 2003, growing from February until September-October, albeit with exception of collision in April 2004. Besides the juvenile cohort in February, a second cohort is present of 5.98 mm in average size. This cohort consists most likely of recruits of October 2003. They will give raise to peak recruitment in October 2004, after which most of them die.

In *B. sarsi*, as in *B. pilosa*, a new cohort appears in October (average size: 4.22 mm in 2003; 4.52 mm in 2004). Also another recruitment peak can be observed in February (average size: 4.39 mm).

Again, drawing temporal growth patterns for single cohorts was hardly possible. The cohort of October (2003) recruits collided with a group of larger and older individuals in December. Again, like with *B. pilosa*, the February recruits are a little easier to follow during the consecutive months, however, being inseparable from another cohort in June and August.

The number of gravid, egg-bearing females displayed two peaks for both species. A spring peak in April and an autumn one (September-October), separated by low values in winter (December) and summer (July) were observed (Fig. 3 - above). In *B. pilosa*, the spring adult cohort responsible for reproductive peak activity contained individuals of 5.98 mm on average; those of October 2004 were of 5.05 mm on average, while in October 2003 two non-juvenile cohorts seemed to be present (5.88 mm and 4.26 mm on average). A comparable pattern is observed for *B. sarsi*: from February onwards the number of gravid females grew, peaking in May, dropping to a July low and peaking again in autumn (October). Relative abundance apparently can differ strongly between years: 55% in October 2003 and only 29% in October 2004 for *B. sarsi* and 29% versus 11% in the same respective years for *B. pilosa* (Fig. 3 - above).

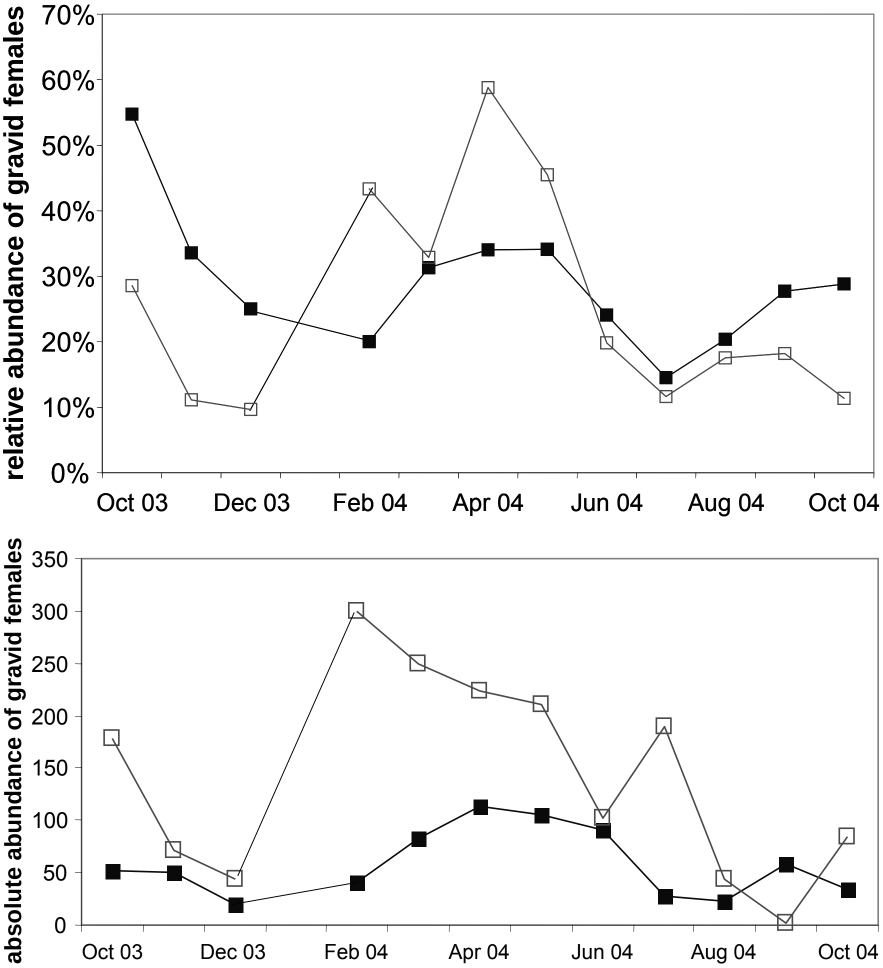

Figure 3. Temporal variation of relative (above) and absolute (below) number gravid females (percentage of gravid females on total of females); solid squares: *B. sarsi*; open squares: *B. pilosa.* Error bars omitted for graphic representation.

Fecundity patterns were clearer (Fig. 4). *Bathyporeia sarsi* females carried about 1.75 times as much eggs as *B. pilosa* (Wilcoxon Matched Pairs Test: $Z = 5.07$; $p < 0.01$), whereas the weight of an individual *B. pilosa* egg was about 1.8 times the weight of one belonging to *B. sarsi*. Thus, total carried egg mass was comparable for both species and this is confirmed by their gonad production values (*B. pilosa*: P_g = 0.73 mg/ind*year; *B. sarsi:* P_g = 0.71 mg/ind*year). Fecundity peaked for both species in February 2004 and was lowest in August 2004, the latter low coinciding with rather low numbers of gravid females for both species. Both species showed a -rather trivial albeit weak- correlation between female size and egg load (Spearman Rank Order Correlation: *B. pilosa*: SR = 0.35; p < 0.01; *B. sarsi*: SR = 0.33; p < 0.01).

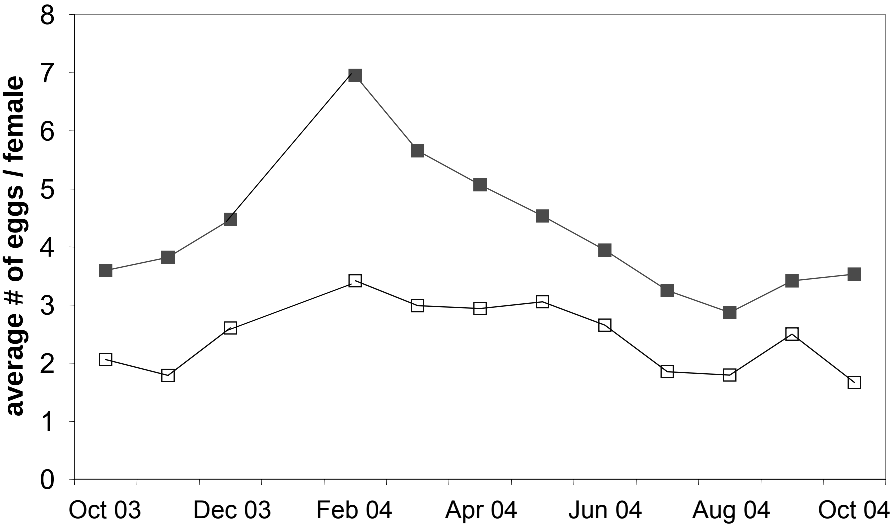

Figure 4. Temporal variation of fecundity (average number of eggs per female); solid squares: *B. sarsi*; open squares: *B. pilosa*. Error bars omitted for graphic representation.

Juvenile abundance, expected to result from the combined variation in both number of gravid females and fecundity, shows a February-March, a July and an October peak for both species (Fig. 5). Peaks are more pronounced in *B. pilosa*, indicating somewhat less continuous recruitment patterns.

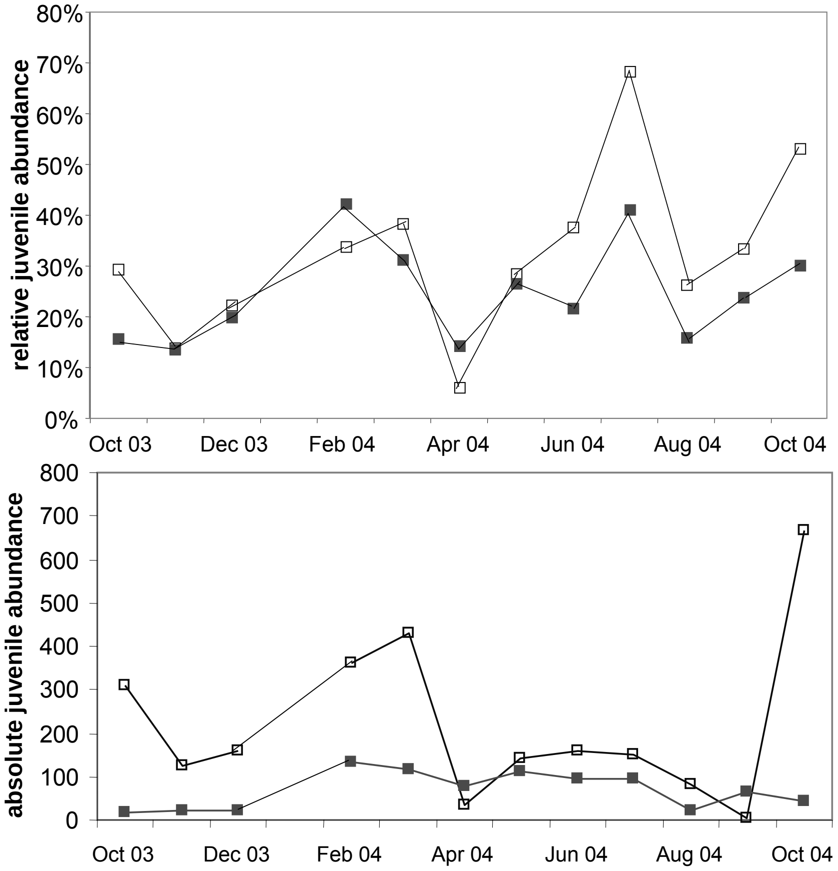

Figure 5. Temporal variation of relative (above) and absolute (below – total number) juvenile abundance; solid squares: *B. sarsi*; open squares: *B. pilosa.* Error bars omitted for graphic representation.

The sex ratio displayed a largely similar trend for both species, both showing about twice as much females as males from December 2003 until May 2004 (Fig. 6). From June 2004 onwards, a clear increase in female predominance is observed, up to ratios of 6 females per male. The only difference between both species is found at the start of the sampling period (October-November 2003), with *B. sarsi* displaying a ratio similar to that of summer months (up to 6x more females), while *B. pilosa* already had the typical winter-spring ratio (about 2x more females).

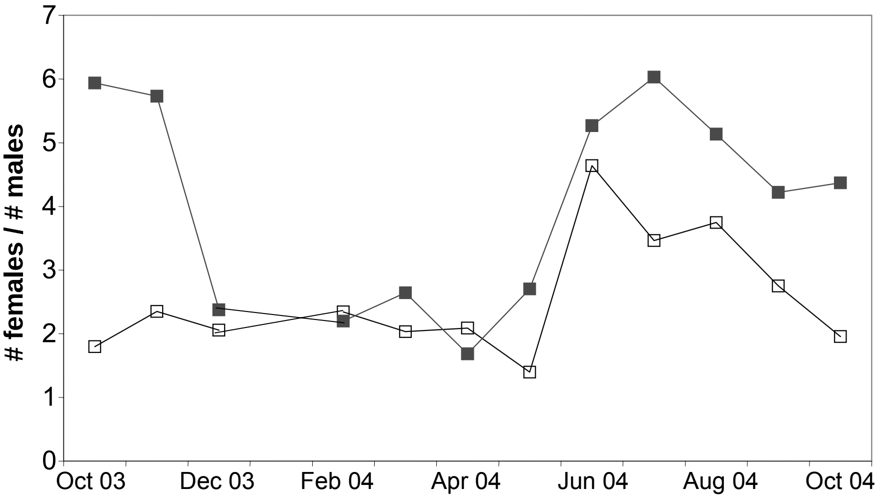

Figure 6. Sex ratio (# females / # males) over time; solid squares: *B. sarsi*; open squares: *B. pilosa.* Error bars omitted for graphic representation.

In conclusion, both species display continuous reproduction and recruitment, with two absolute peaks of the latter being visible in October and February. The third peak in July is most probably more relative (see Discussion).

MEAN ANNUAL BIOMASS, SECONDARY PRODUCTION AND P/B RATIO

For *B. pilosa*, mean annual biomass (MAB), secondary production and P/B ratio all reached clearly higher values along the western transects (Tab. 1).

Table 1. Mean annual biomass (MAB; mg AFDW/m²), secondary production (P - Size Frequency Method; mg * m^{-2} * y^{-1})) and P/B-ratio (P/B; y^{-1}); NP = Nieuwpoort; IJ = Ijzermonding; MK = Middelkerke; OO = Oostende

	NP			**IJ**			**MK**			**OO**		
	MAB	**P**	**P/B**	**MAB**	**P**	**P/B**	**MAB**	**P**	**P/B**	**MAB**	**P**	**P/B**
B. pilosa	2035	16040	7.88	1458	10165	6.97	9.13	28	3.08	3	1.84	0.59
B. sarsi	1005	7580	7.54	209	1245	5.95	496	3279	6.62	187	1260	6.74

P/B ratios varied more than tenfold with regard to sampling location. Also in *B. sarsi*, large differences in the MAB values can be recognised, yet somatic production seemed to vary to the same degree, resulting in rather comparable P/B ratio values for all beaches. Nevertheless, P/B ratios show high relative productivity of the Nieuwpoort transects for both *Bathyporeia* species.

CROSS-SHORE ZONATION

Figure 7 offers a schematic overview of the cross-shore distribution of the investigated species, introducing investigated variables.

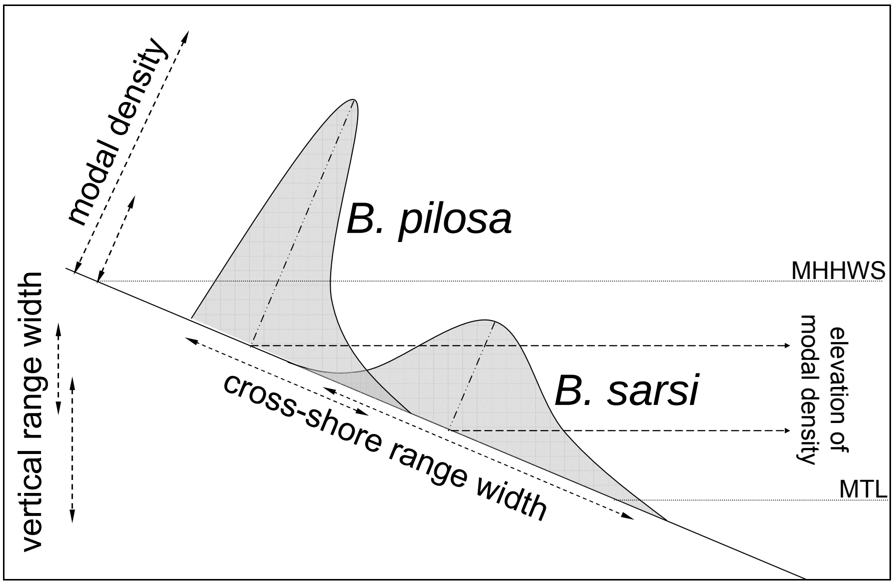

Figure 7. Schematic overview of cross-shore distribution of *Bathyporeia pilosa* and *B. sarsi* across the intertidal gradient. MHHWS = level of mean highest high water at spring tide; MTL = mid-tidal level.

First, elevation of the maximum density sample of each transect at each sampling month is considered. Secondly, we will address the width of the occupied vertical range.

Peak abundances of *B. pilosa* were found at 436 ± 25 SD cm above MLLWS, while those of *B. sarsi* were found at 357 ± 40 SD cm above MLLWS. *Bathyporeia pilosa* was found significantly higher on the beach than *B. sarsi* (Wilcoxon Matched Pairs Test: Z = 4.11, $p < 0.01$). This vertical difference of about 80 cm corresponds (depending on beach slope) to a 40 to 62 m cross-shore distance.

Significant differences in elevation of peak abundance were found as well between the four transects under consideration for *B. pilosa* (Friedman Chi Square (N = 10, df = 3) = 14.39; $p < 0.01$) (Fig. 8 - left).

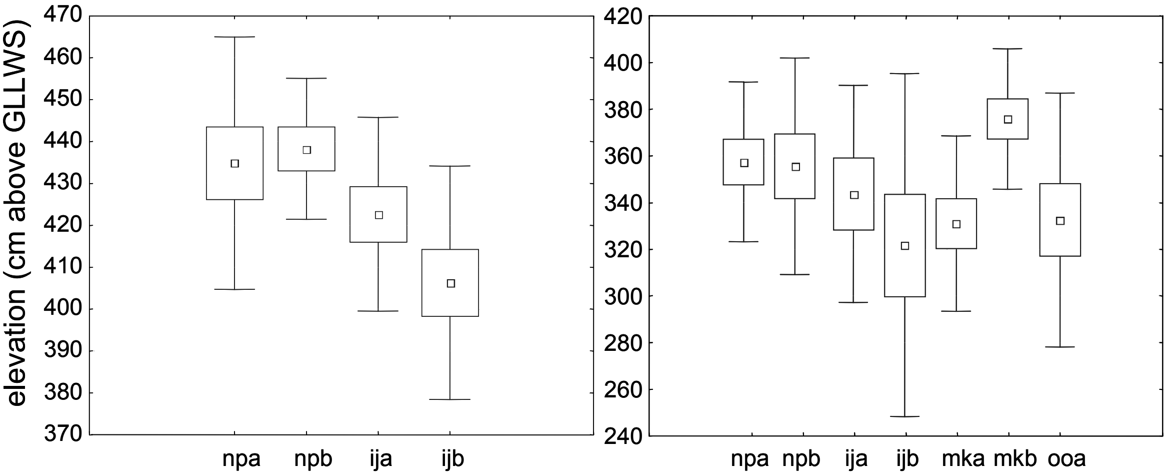

Figure 8. Spatial variation of elevation of peak abundance of *Bathyporeia pilosa* (left) and *B. sarsi* (right)(in cm). Box: SE; whisker: SD. Transects ordered from west (left) to east (right) in both graphs.

For *B. sarsi*, differences were significant at the 10% level (Friedman Chi Square (N = 8, df = 6) = 11.78; p = 0.07) (Fig. 8 - right), with, like in *B. pilosa*, a tendency of peak abundances being found higher up on the beach of Nieuwpoort than on that of the Ijzermonding and a remarkable 40 cm difference between both transects at Middelkerke.

Considering only western transects (npa, npb, ija and ijb), no significant variation over time was observed (Friedman Chi Square (N = 3, df = 10) = 14.01; p = 0.17) for *B. pilosa*. Yet, peak density elevation was highest from May to July and lowest from October to February. For *B. sarsi* there was significant variation over time (Friedman Chi Square (N = 4, df = 11) = 24.31; p = 0.01), with peak abundances being found higher up on the beach in summer, but interannual variation seems to be high too (comparing October 2003 and October 2004).

No differences in modal height were detected between juveniles and adults (Wilcoxon Matched Pairs Test: *B. pilosa*: Z = 1.069, p = 0.29; *B. sarsi* Z = 0.1825, p = 0.86) nor between females vs. males (Wilcoxon Matched Pairs Test: *B. pilosa*: Z = 0.700, p = 0.48; *B. sarsi* Z = 0.1778, p = 0.86) for either species, thus no evidence for intraspecific cross-shore segregation was found.

Comparing both species (while considering western transects only), it is clear that *B. sarsi* occupies a wider vertical range or zone than *B. pilosa* (Wilcoxon Matched Pairs Test: Z = 3.38, p < 0.001). This difference is of about 70 cm in vertical distance, corresponding with 35-54 m cross-shore.

Females of both species occupy a significantly wider zone than males (*B. pilosa*: Wilcoxon Matched Pairs test: Z = 2.52, p = 0.01; *B. sarsi*: Wilcoxon Matched Pairs Test: Z = 2.37, p = 0.02), and, strikingly, the female range is an equal 30 cm wider in vertical distance (15-23 m cross-shore) in both species. Adults of *B. pilosa*, occupied a somewhat wider zone than juveniles (Wilcoxon Matched Pairs test: Z = 2.02, p = 0.04) with a difference of 10 cm in vertical distance (5-8 m cross-shore). For *B. sarsi*, this was only significant at the 10% level (Wilcoxon Matched Pairs Test: Z = 1.85, p = 0.06), corresponding to about 20 cm vertical range difference (10-16 m cross-shore). Comparing all transects for *B. sarsi*, vertical range width appeared to be significantly higher on western transects (Friedman Chi Square (N = 12, df = 6) = 30.02; p < 0.01) (Fig. 9 – left) and the widest range is occupied in April, while autumn and winter values are lower (Friedman Chi Square (N = 7, df = 11) = 20.06; p = 0.04) (Fig. 9 – right). For *B. pilosa*, it is most likely that the fact that only the western transects were available as replicates, disallowed observation of such differences (spatial: Friedman Chi Square (N = 11, df = 3) = 2.74, p = 0.43; temporal: Friedman Chi Square (N = 4, df = 10) = 4.76; p = 0.91).

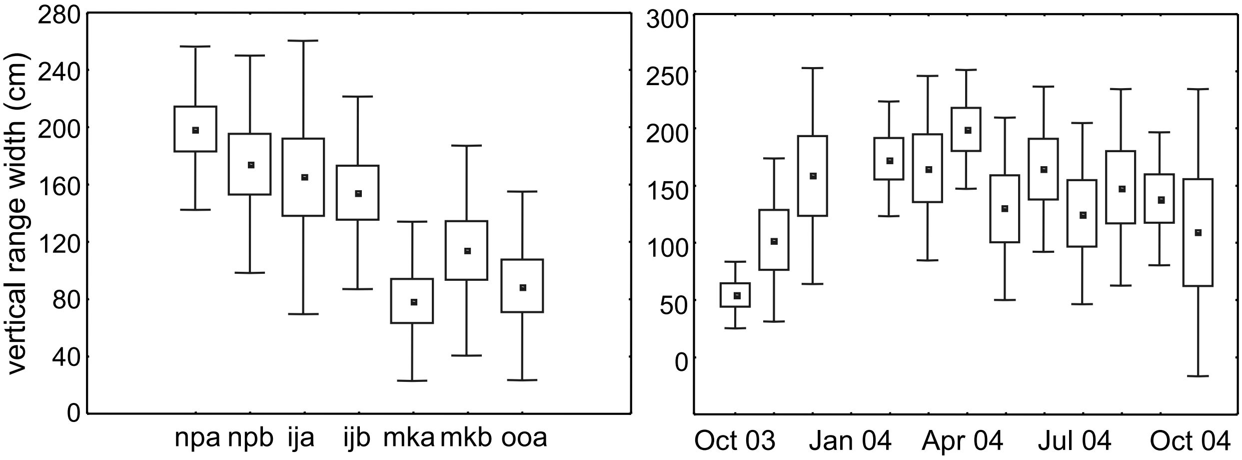

Figure 9. Spatial (left - transects ordered from west (left) to east (right)) and temporal variation (right) of width of vertical range *Bathyporeia sarsi* (cm). Box: SE; whisker: SD

MEDIAN GRAIN SIZE RELATED TO PEAK ABUNDANCE

Median grain size at stations of peak abundance along each transect were considered. Attempting reliable comparison of species, once more only western transects are considered. *Bathyporeia pilosa* just failed to show significant differences between those transects (Friedman Chi Square (N = 3, df = 3) = 7.40, p = 0.06), whereas significant differences for *B. sarsi* were found within those same transects (Friedman Chi Square (N = 3, df = 3) = 8.20, p = 0.04). No significant temporal fluctuation was observed for either species (all p > 0.05).

Discussion

ABUNDANCE AND BIOMASS

At transects where both species co-occurred in reasonable numbers (i.e. where also *B. pilosa* lives), densities of *B. sarsi* are clearly lower than those of *B. pilosa*. Burrowed in the sand at low tide, *B. pilosa* seems to display a patchy distribution (Khayrallah and Jones, 1980b; Persson, 1982; Nicolaisen and Kanneworff, 1983). Comparison of observed densities with those found by other authors (Vader, 1965, 1966; Salvat, 1967; Persson, 1982; Bamber, 1993), suggests that observed differences might be attributed to differences in habitat conditions, related to mainly tidal range, sediment characteristics and slope. In general, these findings have to be considered taking into account their temporal (only one year studied) and spatial (only 7 usable transects) constraints.

The presence of strong spatial abundance differences in *B. pilosa* and their absence in *B. sarsi*, might be attributed to small-scale differences in morphodynamics. The sampled eastern transects are somewhat less dissipative than the western ones (Degraer *et al*., 2003a), as corroborated by a steeper slope, coarser sediment. This might concur with well established links between species richness and morphodynamics (e.g. Defeo and McLachlan, 2005) but no such assessment is available from our data. Nicolaisen and Kanneworff (1969) stated that *B. sarsi* dominates on exposed shores, and *B. pilosa* on sheltered localities. In this study, *Bathyporeia sarsi* was found in comparable numbers along the different transects. Both species seem to reach their highest numbers on both transects at Nieuwpoort. The other transects, namely those at the Ijzermonding beach, might be less favourable, due to a somewhat steeper slope, coarser sediment and stronger changes in the beach profile throughout the year. *Bathyporeia sarsi* seems to be able to cope with the somewhat more reflective conditions at the eastern transects, in contrast to *B. pilosa*. Vader (1965) stated that *B. sarsi* prefers, or maybe better tolerates, somewhat coarser sands than *B. pilosa,* but both have been found in both finer and coarser sands. *Bathyporeia pilosa* has been described as preferring fine sands containing some fines (Vader, 1965, 1966). Concentrations of fines were clearly lower along eastern transects (always practically zero). Conditions might also differ on a small scale for both species, as they live at different heights on the beach.

In both species, biomass trends coincide with those in abundance, with a similar distinction between western and eastern transects. Yet, total biomass of *B. pilosa* at transect MKB is comparable with that at transect IJB, whereas MKB abundance was clearly lower than that of IJB. No significant differences between sampling months were observed, while November and December show somewhat higher values, implying higher food availability for predators in that period. These higher values might be due to the presence of a higher number of cohorts present: juveniles from the autumn recruitment peak, adults born in spring and survivors of the reproducing population of spring, with especially the two latter groups producing high biomass values. Given this interpretation, a similar pattern could be expected just before summer in May and June. Compared to July, this is indeed the case. In this month, biomass drops due to mortality of larger animals, i.e. parent animals of the earliest recruitment peak.

Remarkable in comparing both species is the contrast in abundance versus biomass patterns. At all western transects, *B. pilosa* abundance ranges from comparable to ten times larger than that of *B. sarsi*, whereas *B. sarsi* biomass has a relative importance that runs from five to ten times higher. Thus, predators of *Bathyporeia* are offered a choice between more abundant, smaller prey and somewhat larger, yet scarcer food items. Higher individual biomass of *B. sarsi* seems only related to their larger adult size, as biomass increment with growth seems comparable for both species and in fact even a little higher in *B. pilosa*.

No significant temporal variation in abundance was observed for *B. pilosa*, while it was present in *B. sarsi.* Significant higher densities of *B. sarsi*, as observed in spring and early summer, might be artefacts attributable to random aggregations, and sample size might have to be reconsidered in that respect. Yet, comparable variations in density have been observed for *B. pilosa* in the past (Persson, 1982; Nicolaisen and Kanneworff, 1983).

Fincham (1971) related low numbers in autumn and winter to mortality. Maranhão *et al*. (2001), investigating *Echinogammarus marinus*, showed water temperature and salinity to influence seasonal changes in abundance, with higher temperatures and salinity levels relating to lower densities. High temperatures might enhance desiccation of the animals during emersion periods, causing lower numbers in summer. However, in this Portuguese study winter temperatures may present less stress than they do in Belgium. High densities earlier in the year are attributable to a peak of successful reproduction in spring and rising temperatures after spring, creating favourable conditions for development and reproduction.

LIFE CYCLE, DEMOGRAPHY, REPRODUCTION AND RECRUITMENT

Confusing output of the cohort analysis made it hard to unravel *Bathyporeia* life history; cohorts are often inseparable due to continuous reproduction. This is not new to the research on these species (Fish and Preece, 1970a). Nevertheless, two relative peaks of reproduction, as indicated by the relative abundance of gravid females and to a large degree corroborated by trends in fecundity and juvenile abundance, were visible in this study. Peaks in the number of gravid females (April and September-October) are pretty much in concordance with earlier findings (Salvat, 1967; Fish and Preece, 1970a) and can be summarised as a (broader) spring peak and an autumn peak. Timing of these peaks may differ slightly between locations and probably among years. This may be due to small differences in microclimate and food availability. Lower reproductive activity in winter and summer is probably an indirect effect of elevated female mortality after reproduction, as hinted by drops in female abundance (see gravid females' abundance and sex ratio data). In contrast to Fish (1975), only a single peak of male abundance (in October for *B. pilosa*; in April in *B. sarsi*) was apparent, coinciding with the peak in gravid females' abundance, rather than preceding it. It is likely that our sampling frequency was too low to observe this precedence pattern.

Mettam (1989) also found sex ratio to be shifted towards female predominance, but observed a nearly equilibrium during the major reproduction peak. This is not the case in our Belgian populations, where male relative abundance peaks in May, being still 50% less than female abundance. From June until the end of summer, five to six times more females are observed. Mettam (1989) suggested this might be due to slower growth and shorter life span in males and difficulties in sexing juveniles. Watkin (1939) attributed these differences to sampling method, giving contrasting results between towing and digging results. Digging samples out, like we did, should however reflect the true population best.

As sex ratio, also fecundity (number of embryos per female) showed a highly comparable trend in both species, peaking in February and again -but less sharp- in autumn (September in *B. pilosa*; October in *B. sarsi*). The lower fecundity of *B. pilosa* shows less clear peaking, with a rather continuous period of higher fecundity from February to May and an additional peak in September. Peaking fecundity in spring was also found by Fish (1975), with lower values afterwards due to adult mortality. Maranhão *et al.* (2001) related lower fecundity to lower temperature and salinity drops due to rainfall. Lower fecundity in those conditions in the year should favour individual development. This could also be the case for Belgian *B. pilosa* in autumn and early winter, yet peak fecundity was observed as soon as February. This might be due to the mild winter of 2003-2004. The observed correlation between fecundity and female body size has been found for several amphipods before (Fish, 1975).

Differences in fecundity between *B. pilosa* and *B. sarsi* reveal a different reproduction strategy (cf. Maranhão *et al.*, 2001). *Bathyporeia pilosa* has fewer embryos of larger size and containing more yolk, giving each single embryo a higher chance of survival, as a response to its more stressful environment in the highest parts of the intertidal zone. The upper parts of the intertidal zone exhibit strong fluctuations in temperature, salinity and sediment water content. Gonad production showed energy costs for both strategies to be of the same magnitude.

Continuous recruitment occurs but is low in between recruitment peaks. Fish (1975) mentions hatchlings size of about 1.5 mm. Next to differences in measuring methodology, applied mesh width did not allow retention of animals of this size. This is likely to result in loss of data in cohort analysis and the study of age/size-based cross-shore segregation. Furthermore, monthly sampling might cause new recruitment to be observed not until after already over three weeks of growth. Yet, throughout all our data we never encountered such small animals, the smallest individual being 1.977 mm. Three peaks in recruitment, as apparent by the appearance of new cohorts in the cohort analysis and peaks in juvenile abundance, were observed (February-March, July and October). Remarkable is that the peaks of juvenile abundance only in part seem to coincide with those in abundance of gravid females: the July peak in juvenile abundance does not coincide with a peak in neither gravid female abundance nor fecundity. Yet, sex ratio does and perhaps higher proportional numbers of females in June-July may have compensated for lower fecundity and the lower abundance of gravid females. However, adult mortality, as observed by a drop in biomass in July samples, seems most likely to explain an artificial relative peak in juvenile abundance, and the shift in sex-ratio may be due to a (relatively) higher male mortality. A spring plus autumn recruitment peak scenario seems most likely and is confirmed by the fecundity data, absolute numbers of juveniles per month and the output of the cohort analysis, showing new cohorts appearing in February and October. Thus, a bivoltine life cycle was observed, with a broad spring peak of reproductive activity and recruitment and a second, concerning fecundity much smaller one in autumn, which may slightly vary in magnitude and timing from one location to another.

Some interesting temporal spring-autumn and year-year differences require further discussion. In *B. pilosa*, spring females are larger than autumn ones, formerly explained as a consequence of a longer period of growth (Fish and Preece, 1970a). Yet, individuals hatched in February have six to seven months to grow before they reproduce, as have the wintering ones, born in autumn. The spring reproduction peak is, however, rather wide and lasts in fact until May, giving late hatchlings little time to grow during summer and perhaps, thus, resulting in lower average adult size.

Juveniles from February are larger than those from October. Due to the lack of January data, no precise assessment of the time of hatching could be made and this could not be tested properly.

Gravid females of *B. pilosa* were much less abundant in October 2004 than in October 2003, while the opposite was observed for juveniles. Peak recruitment might have occurred just before the 2004 sampling, with hatchlings having already left the marsupial pouch to a higher degree, resulting in fewer gravid females and more juveniles in the samples. A higher sampling frequency may be useful in this respect. Higher average size of October 2004 juveniles compared to the ones from October 2003 has to be attributed to the power of the cohort analysis. In 2004, two small cohorts, as they were found in 2003, could not be separated, resulting in one cohort of intermediate average body size and larger than the smallest cohort from 2003. Thus, interannual variation in juvenile abundance seems to allow important differences in the result of the cohort analysis.

GROWTH AND MORTALITY

A growth function could not be defined, as the output of the cohort analysis provided confusing results.

The magnitude of adult cohort growth, observed in part from one month to the next, suggests quasi-linear growth in the investigated populations of *Bathyporeia pilosa*. In juvenile cohorts of the same species, continuous reproduction and recruitment, together with considerable juvenile mortality, seem to induce strong monthly oscillations in average cohort body length, disallowing assessment of growth for these younger animals. No evidence of the presence of a growth stop can be found. Growth assessment was, due to an even more erratic pattern in the cohort analysis, even harder in *Bathyporeia sarsi*, yet, again a linear growth pattern seemed present. There seems to be no indication of difference in growth rate between the species, as suggested by comparable slopes of the calculated regression equations (*B. pilosa*: 0.2687; *B. sarsi*: 0.2616). Yet, given their comparable life span and, as *B. sarsi* reaches larger adult size than *B. pilosa* and the former has smaller eggs with less yolk, to be expected to result in smaller hatchlings, *B. sarsi* might be thought to grow faster. This might be also facilitated by more benign conditions governing the habitat somewhat lower down on the beach, i.e. where *B. sarsi* reaches highest numbers. The available data, however, shows *B. sarsi* juveniles of February and October to be 1 mm larger on average than those of *B. pilosa.* This confusing phenomenon has to be considered in view of the snapshot nature of monthly sampling and it is possible that more frequent sampling, combined with sieving over a finer mesh, could corroborate our hypothesis of higher growth rate in *B. sarsi.*

Also mortality could not be quantified, as small month-to-month variations need not be due to mortality, but can be caused by incidental aggregations of individuals (Defeo and McLachlan, 2005). Disappearance of entire adult cohorts might, however, indicate mortality more truly. This seems to occur from June to July, when the disappearance of adults causes biomass to drop. The described bivoltine life cycle of the species, with 2 generations per year (as also found by Salvat, 1967; Fish and Preece, 1970a), explains two peaks in adult mortality, as observed in disappearance of adult cohorts in February and July. *Bathyporeia pilosa* is a highly tolerant species, resistant to different forms of environmental stress (Mettam, 1989), while *B. sarsi*'s stress tolerance can be assumed lower (Vader, 1965). Nicolaisen and Kanneworff (1983) mentioned a discrete episode of high mortality in a population from Denmark during the reproductive season, from May to September, most likely occurring in both juveniles and adults. Winter mortality until March and summer mortality at least seem to confirm the existence of two generations.

SECONDARY PRODUCTION

Considering P/B ratios per beach, *Bathyporeia pilosa* showed clear differences between beaches, with eastern beaches delivering ratios half those of western ones (see Tab. 1). To assess the value of the studied beaches for higher trophic levels, total macrobenthic biomass should be considered, besides other factors, e.g. levels of disturbance for wading birds as potential predators. In any case, the eastern beaches showed both low abundance and low P/B ratios for this species. Higher P/B ratios as found on the western beaches are comparable to those found by Maranhão *et al.* (2001) for *Echinogammarus marinus,* (from 4.14 to 6.56). In contrast, P/B ratios of *B.sarsi* were highly similar for all beaches. Thus, intertidal *B. pilosa* can, if present, provide a highly abundant food source for any predator able to manage itself in the upper parts of the intertidal zone. In second place, also *B. sarsi* is a fairly abundant food source, but it is more widespread across the shore and occupies a part of the intertidal zone that might be easier to reach for submerged predators. *Bathyporeia* P/B ratios are in general much higher than those of the syntopic polychaete *Scolelepis squamata* (reaching 2.40 / year) (Speybroeck *et al.,* 2007).

HABITAT (1) – CROSS-SHORE ZONATION

Bathyporeia pilosa was always found higher up on the beach than *B. sarsi*, in confirmation of earlier work (e.g. Salvat, 1962, 1964; Degraer *et al.*, 2003a). Peak abundances of *B. pilosa* occurred always above 4 m above MLLWS, while modal density of *Bathyporeia sarsi* was found between 3 and 4 m above MLLWS. Our results demonstrate differences in the optimal elevation for both species, without strict separation of both: low numbers of both species can frequently be found together in a single sample, resulting in a bimodal combined *Bathyporeia* distribution. No intraspecific segregation based on sex or age was observed for either species, and neither did Nicolaisen and Kanneworff (1983).

Differences in the elevation of the modal density (along each transect) of *B. pilosa* were observed between the western transects. It is unclear whether the higher variability in beach morphology at the Ijzermonding beach might cause changes in microhabitat conditions, influencing the presence of *B. pilosa* and *B. sarsi*, as suggested for the former by Khayrallah and Jones (1980b).

Judging from the temporal variability in zonation pattern and elevation of modal density, no significant seasonal migration was observed for *B. pilosa*, while contrasting results have been obtained in the past (Salvat, 1967; Fish and Preece, 1970a; Persson, 1982). Most likely, habitat type can explain this, with Fish and Preece (1970a) investigating an estuarine population, while Persson (1982) worked at the Baltic Sea. Temperature, light intensity and length of day might trigger seasonal migration, somewhat complicating comparison between studies. Our intertidal sandy beach population seems to show a (poorly significant) more onshore presence from the end of summer until November, observed in the elevation of the modal density. Fish and Preece (1970a) found the same from April to October, but with animals being situated higher up on the beach in winter. Though generally confusing, differences in climate and hydrology might explain this. Stress by desiccation (mainly in summer) might be less immanent on Belgian beaches, whereas freezing in winter might urge animals to migrate to areas of longer submersion, buffered in temperature and less subjected to storms and heavy rainfall. Further, on beaches where runnels are present, highest numbers of *B. pilosa* but also *B. sarsi* have been observed within these runnels, retaining water throughout the tidal cycle (pers. obs.). This might possibly cause both seawards and landwards, or better 'runnelwards', migration in autumn.

On the other hand, *Bathyporeia sarsi* displayed a clear seawards shift of animals from January to March, comparable to findings of Nicolaisen and Kanneworff (1983) in the Baltic Sea and to what Persson (1982) described for *B. pilosa*. Again, animals were found higher up in summer.

The lack of intraspecific segregation of both species is in contrast to the size-segregation observed in the syntopic polychaete *Scolelepis squamata* (Speybroeck *et al.,* 2007).

HABITAT (2) – WIDTH OF THE OCCUPIED VERTICAL RANGE

Bathyporeia sarsi occupies a wider vertical, thus also cross-shore, range on the beach than *B. pilosa*. Due to lack of knowledge of the former species, explaining this is hard. Small spatial differences can be observed for *B. pilosa* between transects from Nieuwpoort and Ijzermonding. In *Bathyporeia sarsi*, more erratic, hard to explain variation through space and time could be observed and variation seemed to be due primarily to local fluctuations. Range width might be related to abundance, thus explaining a narrower range of *B. pilosa* at the Ijzermonding beach. Differences between eastern and western transects in *B. sarsi* might be due to established differences in median grain size and beach slope, causing harsher conditions on eastern transects and resulting in lower abundance and smaller vertical range width. No temporal variation was found, yet, in October 2004, the *B. pilosa* occupied zone is wider than that in October 2003, perhaps due to annual variation in temperature, wave energy, food supply and/or patchiness.

Interestingly, females occupied a wider range than males in both species, concurring Preece's (1970, 1971a) experimental results for *B. pilosa*, demonstrating higher stress tolerance of females towards extremes in temperature and salinity, even though Preece's results might have been hampered by shorter male life span. No experimental data on intraspecific variation of stress are available for *B. sarsi.* Furthermore, range width was higher in adults (being mainly females, as established earlier) than in juveniles. Combining sex and age analysis was not possible due to too small numbers remaining within each category.

Finally, it is striking that the species inhabiting the widest range (*B. sarsi*) shows the fewest evidence for intraspecific segregation within its occupied zone.

HABITAT (3) – MEDIAN GRAIN SIZE AT PEAK ABUNDANCE

Apparent differences between the two species in median grain size at stations of peak abundance were observed, as well as significant spatial differences in median grain size. All these cannot be considered independently from the differences in elevation of these abundances peaks. On one hand, a species living lower in the intertidal zone will of course live in a somewhat, finer sediment. On the other hand, both species occur lower on Ijzermonding transects than in Nieuwpoort transects. It is possible that they can live higher up in Nieuwpoort because of the finer sediment. Thus, intertidal zonation is related to both substrate characteristics and elevation.

Observed non-significant seasonal changes in grain size preference are most likely an indirect effect of seasonal migration, caused by climate and hydrology. Thus, elevation and median grain size are, once more, strongly related. To allow drawing relations between abundance and grain size, sampling of much more transects at specific elevations seems necessary. This fell, however, out of the scope of this study and an experimental approach, dealing with grain size preference of both species has been pursued (Speybroeck *et al.*, submitted). Available sands on the investigated beaches were largely situated well within mentioned ranges of tolerance for both species, although Vader (1965) stated *B. sarsi* to prefer somewhat coarser sands than *B. pilosa* and to be more tolerant regarding grain size. Still, differences in exposition as mentioned by Nicolaisen and Kanneworff (1969) seem more explanatory than strict grain size responses.

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CHAPTER 5

The ecological impact of beach nourishment and the restrained habitat of a key species – experimental insights and field data

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Abstract

Nowadays, beach nourishment is widely considered as a better alternative than the construction of hard structures to protect a coast against detrimental erosive effects, both from an ecological as from an engineering perspective. Most 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 ruling biological processes during and after nourishment. To allow recolonisation after nourishment, habitat demands will have to match the characteristics of the nourished beach. The benthic habitat of the intertidal key polychaete *Scolelepis squamata* was investigated through lab experiments and field data analysis, aiming at guidelines for impact mitigation of beach nourishment. Survival, feeding frequency, burrowing time and grain size selection were investigated to assess tolerance and preference for sediment types varying in median grain size. Remarkable preference for very coarse sands contrasted with longer burrowing time. Feeding frequency was higher in coarser sands. Survival was total in all but very fine sands, where total mortality was observed. Data from five beaches were used to model *Scolelepis* abundance based on three environmental variables (elevation, median grain size and slope). Slope did not contribute significantly to any model. The selected model used median grain size, elevation and a second degree term of the latter. The degree of overdispersion remained large across models. Experimentally observed grain size preference seems to conflict with in situ distribution. High levels of overdispersion in our field data analysis suggest other additional factors (additional physical variables, interspecific and intraspecific interactions) determine *Scolelepis* abundance and post-nourishment recovery. For swift recolonisation of nourished beaches, we advocate nourishment to be executed in winter by means of foreshore nourishment in sections with alternation of nourished and unnourished stretches of beach. Concerning the fill quality, very fine sands and high concentrations of fines should be avoided, while also very coarse sands may hamper *Scolelepis squamata* populations. Factors explaining cross-shore and long-shore distribution of the species are still poorly known, as apparent from our field data analysis.

Keywords: beach replenishment, sandy beaches, median grain size, *Scolelepis squamata*, polychaete

Introduction

Beach nourishment acts as an episodic, dramatic impact on the sandy beach ecosystem, consisting of a broad range of impact aspects (Speybroeck *et al.*, 2006; Chapter 2 in this thesis). As common nourishment practice does not allow any survival of macrobenthic infauna, 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-dependent characteristics, albeit local geography and hydrodynamics of the area surrounding the nourished beach will play an important role. Large man-made structures like harbour walls may hamper long-shore drift of pelagic larvae. The benthic species which possess pelagic larvae can be assumed to be swifter colonisers than those lacking a pelagic life cycle phase e.g. marsupial breeders like peracarid crustaceans. The second aspect comes into play once the impacted beach has been reached. The animals will have to be able to settle, burrow and survive on the nourished beach. All this will depend on their specific tolerances and preferences, in relation to the encountered fill sediment.

In this paper, we focused on the second aspect, investigating the benthic habitat of a single key species, the polychaete *Scolelepis squamata*. This species possesses pelagic larvae and thus is expected to be among the more swift colonisers, in relation to dispersal (Günther, 1992). The species is a cosmopolitan bristle worm, constituting a significant part of abundance and biomass of the macrobenthic fauna from sandy beaches of the North and South Atlantic, North Pacific, Indian Ocean, and the Mediterranean Sea (Souza and Borzone, 2000; Bayed *et al.*, 2006; Speybroeck *et al.,* 2007). Within the Belgian part of the North Sea, the species is restricted to upper intertidal areas, around and somewhat above 4m above the mean low water level (MLLWS) (Elliott *et al.*, 1997; Degraer *et al.*, 2003a; Van Hoey *et al.*, 2004; Speybroeck *et al.,* 2007), while elsewhere, including in the neighbouring Netherlands, it has been reported from mid-tidal levels (Knott *et al.*, 1983; Souza and Borzone, 2000; Janssen and Mulder, 2005) and subtidal sediments as well (Knott *et al.*, 1983; Hartmann-Schröder, 1996; Souza and Borzone, 2000). The species lives in fine, medium or coarse sands in temporary vertical tubes, built up by sand and mucus and it is said to dig occasionally onto depths of 40 cm below the sediment surface (Hartmann-Schröder, 1996; Van Hoey *et al.,* 2004). In Belgium, *Scolelepis squamata* is a species indicative for the upper intertidal *Scolelepis squamata-Eurydice pulchra* community, of which it comprises a large part in both abundance and biomass (500 ind/m² - Degraer *et al.*, 2003a; 343 ind/m² on a total of 983 ind/m² - Van Hoey *et al.,* 2004; mean modal density along a cross-shore transect of 505 ± 38 SE ind/m², peaks up to 1880 ind/m² - Speybroeck *et al.,* 2007). Similar communities were found in the upper intertidal parts of many beaches all over the world (McLachlan and Jaramillo, 1995). The species also has an important functional role, being an important food item for wading birds, especially Sanderling (*Calidris alba*) (Glutz Von Blotzheim *et al.*, 1984), and juvenile flatfish, mainly Plaice (*Pleuronectes platessa*) (Beyst *et al.*, 1999), but also e.g. the syntopically occurring isopod *Eurydice pulchra* (Hayward and Ryland, 1995) and the predacious polychaete *Eteone longa* (Hartmann-Schröder, 1996; Michaelis and Vennemann, 2005).

The aim of this study was to investigate the habitat demands of *Scolelepis squamata* in relation to potential population recovery subsequent to beach nourishment. To achieve this goal, we conducted experiments focused on the following hypotheses: (1) survival and feeding frequency are highest and burrowing time shortest in sediments resembling in situ, natural sands at best; (2) sediment preference, observed as grain size selection, is towards the sediment best resembling in situ sands. Because the outcome of the experiments suggested an unanticipated preference for sands that are much coarser than *in situ* inhabited sediments, we tried to determine whether other factors might explain *in situ* patterns in the distribution and abundance of the species. Thus, we investigated the importance of a number of environmental factors through analysis of available field data from the Belgian coast by Degraer *et al.* (2003a): (1) elevation (and correlated submergence period), (2) median grain size and (3) beach slope. Besides these environmental variables, sandy beach ecology theory also emphasises the importance of wave energy and tidal range (McLachlan and Brown, 2006). Yet, these are known to be highly comparable across all Belgian beaches (Degraer *et al.,* 2003a), thus unsatisfactory to explain between-beach differences in our Belgian case-study area.

Material and methods

EXPERIMENTAL DATA

Collection and stocking of experimentally used specimens and general remarks

Live individuals were collected at the beach of Raversijde, Belgium (N 51°12' E 02°51'). This is an ultradissipative beach which has been known to have high numbers of the species (Degraer *et al.,* 2003). As these animals are rather fragile, they were picked out by hand and only undamaged, equally sized adult specimens (6-8 cm) were gathered. Preliminary observations in the lab, showed that all undamaged specimens can survive for several weeks in sterile sediments, submerged in seawater and without added oxygen supply. After 24h, specimens still showing no signs of damage, were released randomly into the different experimental setups, as described below. All experiments were conducted at an air temperature of 14 ± 2 SD °C and in the dark. Experimental sediments (thus animals) remained submerged with seawater throughout the experiments, ruling out desiccation.

Survival and feeding frequency related to median grain size

Twenty individuals (corresponding to 1768 ind/m²) were released into the water column above four sediment types, differing in grain size distribution (63-125µm (median: 124µm); 180-250µm; (median: 242µm); 355-500µm (median: 478µm); 1000-1600µm (median: 1338µm)). For preparation of the sediment types, sand was collected at the Belgian beaches of Raversijde and Vosseslag. After removal of organic matter, the sand was sieved over a sequence of seven sieves with mesh width of 63 µm, 125 µm, 180 µm, 250 µm, 355 µm, 500 µm and 1000 µm. As the *in situ* collected beach sand contained too low levels of the finest and coarsest extremes of the desired grain size gradient, additional sand sediments were obtained from industrial suppliers.

Three replicates of each sediment type were provided in plastic containers with a depth of 10cm and a cross-section of 12cm. Each container was filled with 6cm of sand and 4cm of non-aerated sea water on top. Thus, in total 240 worms were distributed over a 3 by 4 setup.

We interpreted the number of feeding animals as an indication of the overall well-being of the species in a given artificially provided habitat. After seven days, the number of actively feeding animals, observed by tentacles reaching into the water column, was counted. Subsequently, the experiment was terminated and the number of surviving specimens was counted and used as another indication of grain size tolerance.

Relative data on survival in different sediment types were analysed by fitting a generalised linear mixed model (GLMM), using a binomial distribution and *logit* link function. Feeding frequency data were analysed by means of generalised linear model (GLM), also using a binomial distribution and *logit* link function.

Burrowing time related to median grain size

Individual specimens were randomly released across the same four sediment types (see above). Burrowing time was measured, starting from the start of burrowing until the moment of complete submergence into the sediment. Start of burrowing was observed by rapid lateral undulation of the foreparts of the specimen's body. Only adult animals of comparable body size (6-8cm) were used and for each sediment type, the experiment was repeated with 15 different individuals. All animals were eventually completely burrowed.

Burrowing time data were analysed with an ordered heterogeneity test, incorporating both heterogeneity among groups, i.c. the four sediment types (cf. analysis of variance) and the order of the groups (cf. rank order correlation) (Rice and Gaines 1994).

Sediment preference – grain size selection

Twenty individuals were released into three replicate Petri dishes (cross-section = 14cm; h = 2.3cm). Each dish was subdivided into four quarters of their surface and each quarter was covered with a 1.3cm layer of one of the four sediment types mentioned above. The remaining centimetre was filled with seawater. While *Scolelepis squamata* is known to burrow much deeper than 1.3cm, this shallow sediment layer depth was chosen deliberately, in order to force the animals to undertake horizontal movement, thus sediment selection. This is desirable in view of the limited (natural) horizontal movement displayed by the species (Michaelis and Vennemann, 2005). Animals were released one by one, with each next specimen in a different quarter and resulting in an equal amount of specimens (= 5) in each quarter. The experiment was terminated after 24 hours and the number of individuals per sediment type was counted.

Grain size selection data were analysed by means of log-linear analysis of frequency tables through a GLM, using a Poisson distribution and logarithmic link function. Replicate effect was included as a random effect and tested as well.

FIELD DATA

Data from five ultra-dissipative beaches, as obtained by Degraer *et al.* (2003a), was used: De Panne, Heist, Sint-Laureins, Raversijde and Fonteintjes (Blankenberge). We chose these beaches because of their comparable morphodynamics, allowing understanding of cross-shore, rather than long-shore variability. *Scolelepis* density was regarded as the dependent variable, whereas median grain size (µm), intertidal elevation (cm above MLLWS) and local slope (degrees) were considered as potential predictor variables.

An ordination analysis (principal component analysis - PCA) was conducted and a partial correlation matrix was calculated to assess the degree of relatedness among the three environmental predictor variables (median grain size, elevation and slope) within all beaches simultaneously. Subsequently, different GLMMs were fit to the data, trying to optimally describe *Scolelepis* density, based the three available physical variables. A Poisson distribution was applied to the count-type density data and a logarithmic link function was used. Bell-shaped optimum response links between density on one hand and both elevation and median grain size on the other hand were incorporated in the linear equation as square or second degree terms (elevation*elevation, median grain size*median grain size). Random factors were beach location (to account for variation among beaches) and transect (2 transects per beach, nested per beach, to account for within-beach variation). The degree of overdispersion (as quantifier for the ratio of observed and model-predicted noise in the data) and graphic exploration were used to compare statistically significant models.

Results

EXPERIMENTAL DATA

Survival and feeding frequency related to median grain size

Survival data showed an extremely strong contrast between one sediment type and the three others. After one week, survival was total (100%) in all sediments and all replicates, except in the very fine sands sediment type (63-125µm), where no survival at all (0%) was observed. Consequently, obvious highly significant differences in tolerance were observed ($F = 561.24$; $df = 3$; $p < 0.0001$; no replicate effect).

Significant differences were observed (Chi-square = 28.31; df = 3; $p < 0.0001$; no replicate effect) in the number of feeding individuals as well, showing more intense feeding activity in coarser sediment and no feeding activity in finer sands (Fig. 1).

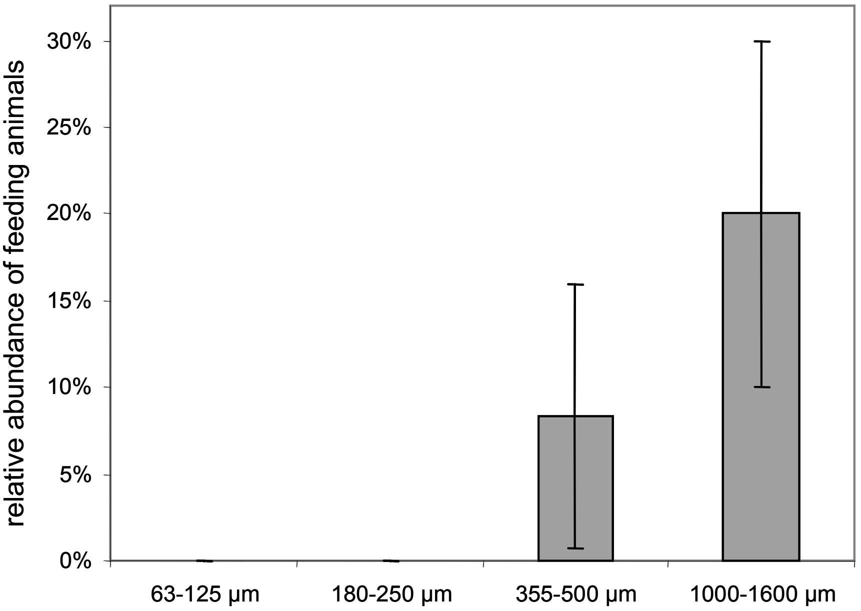

Figure 1. Feeding frequency of *Scolelepis squamata* in four different sediment types. Error bars are standard deviations.

Burrowing time related to median grain size

Most individuals started digging immediately (within 30 seconds), regardless of the sediment type and in the same way as observed upon releasing them in the other experiments. Some first swam around for a few minutes. The latter behaviour was mainly observed in coarser sediments, and animals could be observed touching the sediment with their palps. Two burrow techniques were observed: (1) swiftly and freely and (2) slowly with tube. When using the first technique, the animal tried to enter the sediment as quick as possible. In the second technique, the animal exhibited the same short-wave lateral undulating motion as in the first technique. Yet, instead of submerging immediately, the body does not enter the sediment and stays on top of the substrate, while sand grains are being transported over the animal's body in a caudal direction. Hence, a tube enveloping the entire animal is produced. Subsequently, this initial tube is abandoned and the animal finally but slowly penetrates the substrate. Both techniques were observed in all four sediment types. To compare burrow rates, only animals using the first technique were taken into account. Animals using the second technique were too few (< 5%) to allow separate analysis of them.

Burrowing time of *Scolelepis squamata* in four sediment types, showed a trend for positive correlation between grain size and burrowing time (Ordered Heterogeneity test: $r_S P_C = 0.736$; $p = 0.02$) (total mean: 36.36 ± 2.47 SE seconds) (Fig. 2). Thus, coarser sand involved more difficult burrowing.

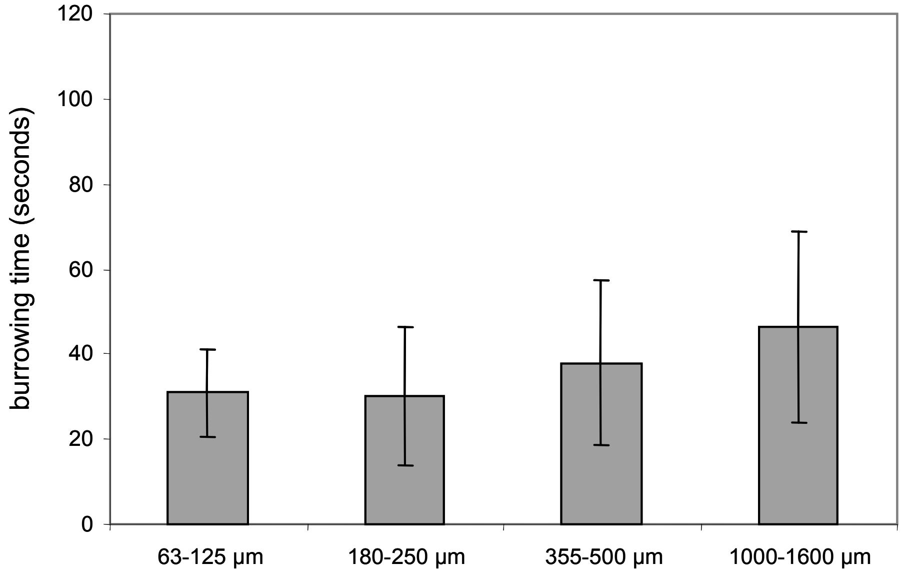

Figure 2. Burrowing time (in seconds) in four sediment types. Error bars are standard deviations.

Experimental sediment preference – grain size selection

The animals significantly selected the coarsest sediment type (1000-1600µm) more often (Log-Linear Analysis: Chi-Square = 40.88; df = 3; p < 0.0001; no replicate effect) (Fig. 3). All other sediment types were selected unfrequently.

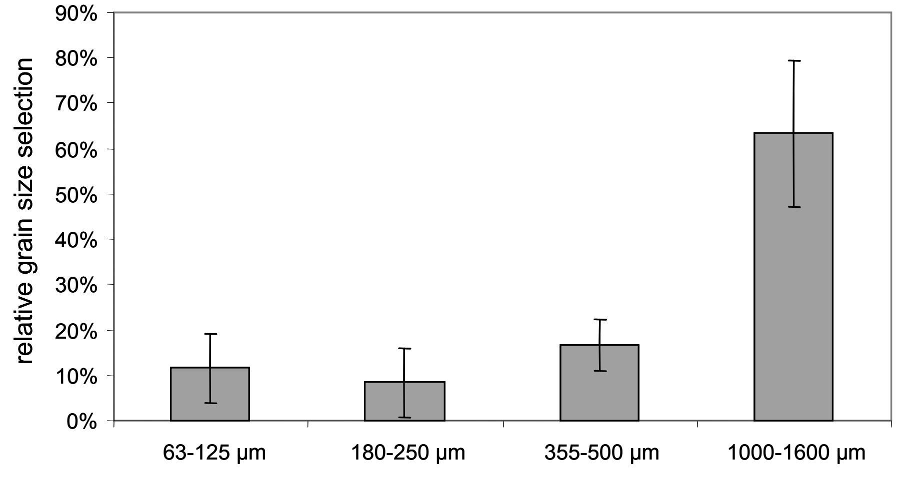

Figure 3. Grain size selection of four sediment types. Error bars are standard deviations.

FIELD DATA

Individual responses

As initial exploration of the field data, we graphically investigated the one-on-one responses of density and each of the three predictor variables (Figs. 4-6 – six high density outlier stations removed for scaling purposes).

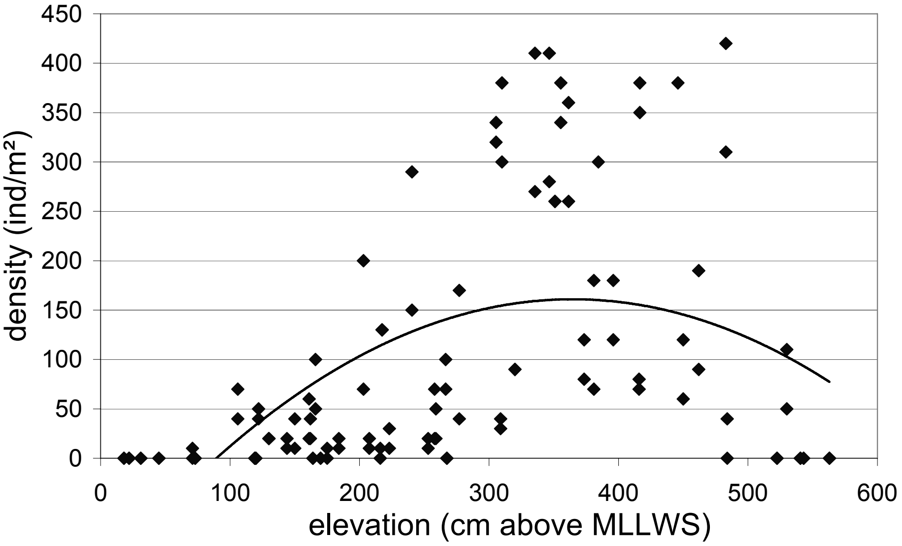

Figure 4. Density of *Scolelepis squamata* as a function of elevation.

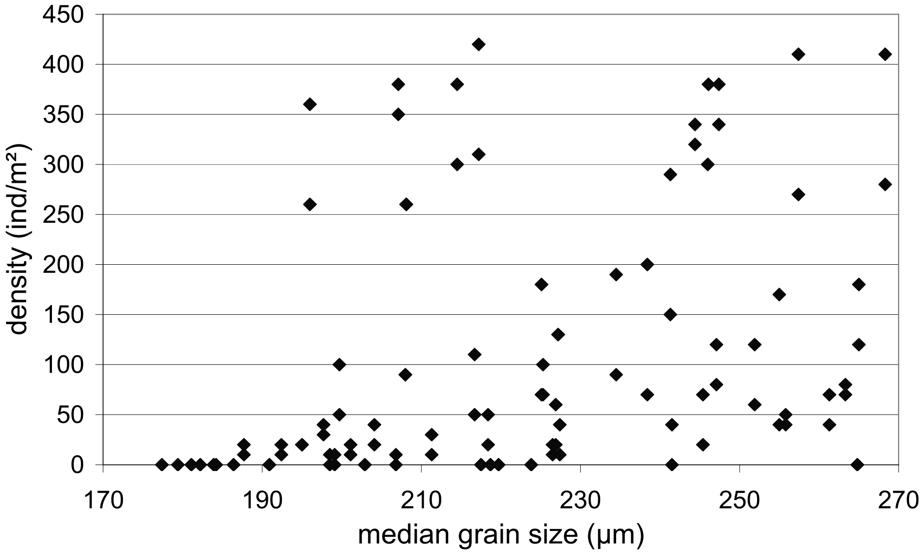

Figure 5. Density of *Scolelepis squamata* as a function of median grain size.

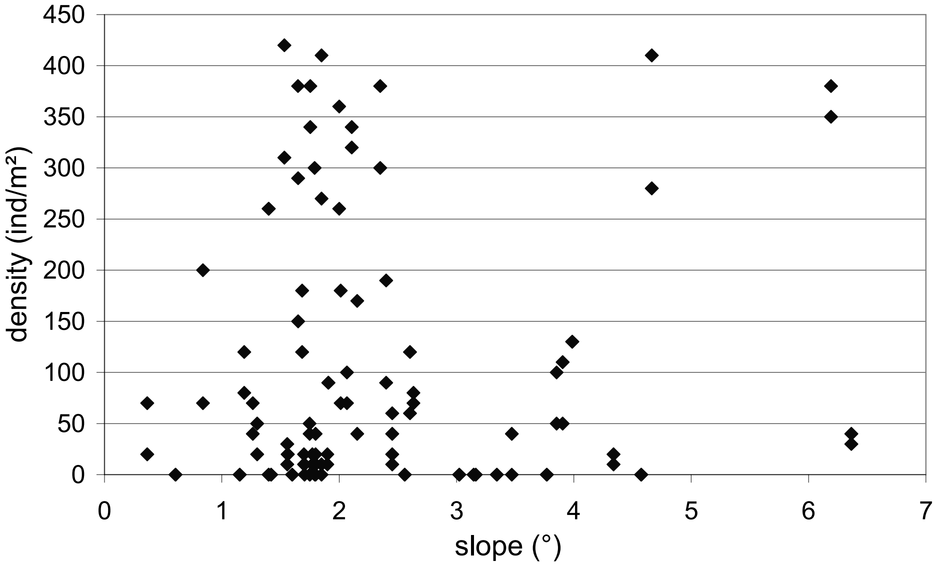

Figure 6. Density of *Scolelepis squamata* as a function of slope.

The bell-shaped trend of relatedness between density and intertidal elevation rightfully advocates inclusion of a second degree elevation term into the model (Fig. 4), but higher degree terms were included into tested models for all three variables. Median grain size and slope did not display obvious x-y connections with density: very fine sands were inhabited by low numbers of *Scolelepis squamata* (Fig. 5); high numbers of the species may occur across the range of observed intertidal slope values, yet steep slopes are rare within the dataset (Fig. 6).

Relatedness of environmental variables

Both elevation and median grain size seem to be equally linked to the first ordination axis, while slope is only strongly related to the second axis (Table 1).

Table 1. Eigenvector values for first (PC1), second (PC2) and third (PC3) ordination axis of the PCA.

	PC1	PC2	PC3
elevation	0.68	-0.11	-0.73
median grain size	0.63	-0.41	0.65
slope	0.38	0.90	0.22

The partial correlation matrix is concordant with this pattern: elevation and median grain size are correlated to each other, whereas slope is far less related to either of them (Table 2).

Table 2. Partial correlation matrix of the three considered physical predictor variables.

	elevation	median grain size	slope
elevation	1.00	0.72	0.35
median grain size	0.72	1.00	0.14
slope	0.35	0.14	1.00

Modelling density

No model that included slope as predictor variable was significant (all slope effects: $p > 0.10$). Therefore, subsequently only elevation and median grain size were used to build models. The elevation-median grain size interaction (all $p > 0.10$) and median-median square (all $p > 0.20$) term never provided significant contribution to any model as well. This lead to a best fitting significant model including median grain size ($p < 0.0001$), elevation ($p < 0.0001$) and a second degree term for elevation ($p < 0.0001$) as fixed factors. Other higher degree terms, which may be expected from the graphs (Figures 4-6) were never significant (all $p > 0.20$).

In general, overdispersion values were very high in all models fitted (generalised Chi-square / DF); a large amount of residual variability in the data could not be explained by the predictor variables. Overdispersion of the best explanatory model (including elevation, median grain size and elevation*elevation as fixed factors) was 19.3, meaning 19.3 times more variance in the data than expected by the model. Removal of six high abundance stations (>1000 ind/m²; see six solid circles most at the right in – Fig. 7) allowed improvement of the model, reducing overdispersion to 6.77 and approaching observed values much more closely (Fig. 7).

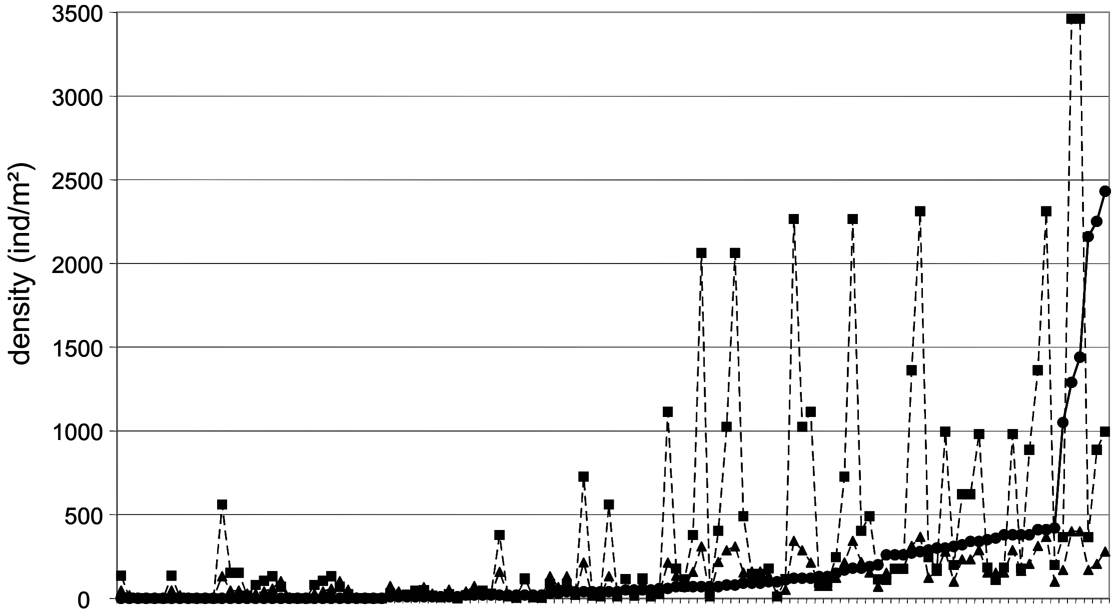

Figure 7. Comparison of observed (solid line and circles) and predicted abundance (models including elevation, median grain size and a square term for elevation - dashed lines). Squares relate to the model for all stations, triangles relate to model for all stations except six stations with abundance > 1000 ind/m². X-axis represent a simple sorting gradient from lowest observed abundance at the left to highest observed abundance at the right.

This means that extreme, high values of density cannot be predicted by the included physical variables and that these high abundances can occur at stations with a combination of environmental variable values that is not unique to high abundance stations only. However, even after (subjective) removal of these high abundance stations, overdispersion still indicates a large degree of unexplained variability, as illustrated in Fig. 8.

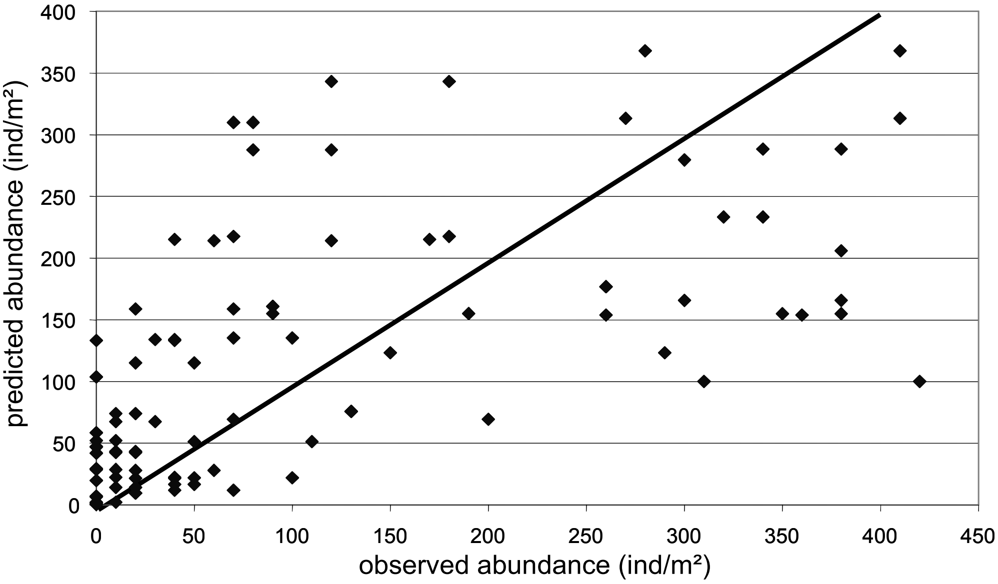

Figure 8. Predicted versus observed abundance values. A model with high predictive power would show data points running closely along the bisecting line.

Discussion

Judging from experimental results and field data, *Scolelepis squamata* seems to be a robust species, tolerant towards a wide array of environmental variability. Survival data, as observed in the tolerance experiment, suggests a wide range of grain size tolerance, except for the finest grain size. Hampered breathing and gill obstruction may be causing the mortality observed in very fine sands. Most likely, this is even more so the case in even finer sediments (<63µm). Increasing the running time of the experiment might help to elucidate finer scale differences among the three remaining sediment types. Now, all three show complete survival. These are, however, also addressed by means of the sediment preference experiment. From our burrowing time assessment, *Scolelepis squamata* seems to be an apt burrower in sediments over a wide range of grain sizes. Nevertheless, a positive relation between burrowing time and sediment grain size is observed.

The experimentally observed sediment preference for very coarse sands seems to contradict field data from the same part of the world (Degraer *et al.*, 2003a): on coarse-grained low tide bar/rip beaches of Belgium, cross-shore zonation of the species seems to be restricted. The upper parts of the intertidal zone, characterised by the coarsest sediment, are not inhabited by *Scolelepis squamata*, even though this sediment is still far less coarse than the one preferred in our experiment. On this type of beaches, the species occurs lower in the intertidal zone and in lower abundance than on ultra-dissipative beaches. On ultra-dissipative beaches, grain sizes are considerably smaller, *Scolelepis squamata* densities higher and the species seems to occupy a wider, more optimal range. Our results suggest that other factors than grain size will have to inhibit colonisation and persistence in the coarser sands of the upper parts of low tide bar/rip beaches. The significant preference for coarse sediments in the selection experiment is surprising, evoking the question wether this significance is indeed only to be attributed to grain size. Due to the lack of organic matter, no small-scale within-replica variation in oxygen content is to be expected. Furthermore, the species is said to mainly breath oxygen from the water column (Dauer, 1983). It seems to us that -strangely enough- the observed preference has to be attributed to grain size, as other factors where constant for all treatments.

Our results on both grain size tolerance and preference, confronted with *in situ* observed long-shore variation in zonation as a function of median grain size from field data, surprisingly suggest grain size as such, if not lower than 150µm, to be of limited damaging effect. The *in situ* observed relation between abundance and grain size is likely to be an indirect effect of e.g. intertidal elevation, slope, ..., associated with the wave- and tide-induced connection between median grain size and elevation (cf. high values in partial correlation matrix). Yet, despite strong correlation between intertidal elevation and median grain size, models showed that both variables account -in part- for *Scolelepis* density. Whereas models demonstrated the importance of elevation and median grain size and an apparent lack of importance of beach slope for our dataset, other non-included factors have to be at work, observed by very large overdispersion values. Other factors may involve additional physical variables, while interspecific and intraspecific interactions may not be ruled out. Concerning the latter, cross-shore segregation of adults and juveniles (Speybroeck *et al.,* 2007) and its role in explaining overall zonation patterns has not yet been assessed.

We believe patchiness takes part in the explanation of *in situ* distribution of *Scolelepis squamata* and may complicate any straightforward modelling of abundance as a function of a set of environmental (abiotic and biotic) variables. Personal observations showed specimens of *Scolelepis squamata* to occur somewhat aggregated, without apparent changes in beach morphology or sedimentology, within longshore stretches of a few metres. While the species is a ‘broadcast spawner’ (see Chapter 3), and fertilisation occurs in the water column, co-occurrence may enhance the chances of succesfull mating, as suggested by Speybroeck *et al.,* (2007). Recruits appear to settle at the same elevation as their parents (or even higher – Speybroeck *et al.,* 2007), with settled recruits are hardly found below mid-tide level. Chemical orientation clues, settlement behaviour or larval body design are among the possible explanations for this rigorous zonation pattern.

To further reduce levels of overdispersion and to model *Scolelepis* abundance more precisely, sampling over a wider range of variability in our three environmental variables as well as additional ones, seems desirable. This stresses the necessity of collecting data over a wider morphodynamical and geographical range. As additional variables, tidal waves and currents may be useful to measure among others, as well as predation levels and food availability (suspended organic matter content). To account for patchiness, however, small-scale, longshore sampling seems necessary in order to unravel patch sizes, patch spacing, etc.

Conclusions – guidelines for beach nourishment

Our experiments suggest a strong tolerance towards coarse sands, as observed in our survival and feeding data. However, sand is not everything – coarsening of the sediment goes hand in hand with comprehensive changes in beach morphology and morphodynamics, which are likely to affect *Scolelepis squamata* abundance. Fill characteristics will also determine the profile equilibrium, beneficial for macrobenthic community development. The shape of this dynamic equilibrium as well as the time it will take to be reached, will depend on the link between slope and grain size. While in an experimental setup very coarse sand might be preferred due to large interstitial spaces and more favourable respiratory conditions (Dauer, 1983), associated slope and wave energy at beaches with such coarse sands might be too harsh for the species, rather than the sediment itself. However, our knowledge on both physical and biological factors explaining the cross-shore and long-shore distribution of the species is still too limited, as apparent from our analysis of field data.

While only very fine sands would appear to be a bad choice for the selected fill sediment for nourishment, sands containing fines should be avoided as well, while the presence of very coarse elements (e.g. shell hash) has not been assessed here.

Data from a population study (Speybroeck *et al.*, 2007) suggest preferable nourishment timing in winter, thus damaging reproduction and recruitment in indirectly impacted, neighbouring source populations to a minimal degree. Technically, foreshore nourishment will be less damaging than nourishment across the entire intertidal profile, as the fill sediment will cover only gradually the area occupied by *Scolelepis squamata*, thus allowing partial or total survival. To allow swift colonisation, nourishment in sections with alternation of nourished and unnourished stretches of beach, is suggested.

Post-nourishment recolonisation will most likely occur through the most dispersive, pelagic larval life cycle stage of the species. The settling recruits may display different sediment preferences and tolerances than the adult specimens. Juvenile settlement experiments (tolerances and preferences) would add valuable information to our results.

Acknowledgements

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CHAPTER 6

Competition and sediment-related responses explaining segregated zonation of two closely related, co-occurring key species on sandy beaches?

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This research has partially been conducted within the framework of a master thesis (Pede, 2006).

Abstract

To address their role in promoting and/or maintaining observed cross-shore segregation of the co-occurring amphipods *Bathyporeia pilosa* and *B. sarsi*, sediment preferences and tolerances were investigated through lab experiments. Preferences were investigated in both allotopic and syntopic conditions, in order to investigate possible avoidance (as a proxy for interspecific competition). Selection of grain size showed no significant differences between the species, nor did the presence of the other species affect the selection. Both species avoided the finest (63-125 µm) and coarsest (>500 µm) grain sizes. Potential niche width with regard to grain size, as established from our experiments, was larger than the occupied width, as observed from field data. Selection of level of fines did not show any difference between species or condition (allo- vs. syntopy) either, while the highest abundance of *B. pilosa* occurred in 5% fines, whereas that of *B. sarsi* occurred in the absence of fines. Mortality of animals forced to survive in a single given sediment, was significantly higher in *B. sarsi* and both species had low mortality levels at a grain size best resembling natural beach sediment (255-350 µm). Thus, whereas preferences of both species are largely comparable, tolerances are not. Conclusively, no clear evidence for interspecific competition could be found, disallowing full explanation of observed segregation. Other possibly determining (abiotic and biotic) factors should be investigated to understand cross-shore segregation, as observed in these closely related yet coexisting species of sandy beach macrofauna.

Keywords: sandy beaches, interspecific competition, zonation patterns, Amphipoda, sediment preference, sediment tolerance

Introduction

Cross-shore zonation patterns displayed by species and communities of sandy beach macrobenthic animals have been related to sediment characteristics, beach morphodynamics, slope, wave energy, tidal range and related habitat parameters (e.g. McLachlan and Jaramillo, 1995; McLachlan *et al.,* 1996; Degraer *et al.,* 2003a; Veloso *et al.,* 2003; Ramalho Fernandes and Soares-Gomes, 2006). Biological interactions, and especially competition, are largely believed to be of minor structuring importance in the physically determined sandy beach ecosystem, thus they are supposed to have little bearing on zonation as well (McLachlan, 1983, 1996, 2001; Jaramillo and McLachlan, 1993). This is in contrast to rocky shores and mudflats, where more benign benthic habitats are available and competition can play an important part in structuring communities and influencing zonation patterns (e.g. Underwood and Denley, 1984; Reise, 1985; Wilson, 1991; Williams *et al.,* 2004). Among others, environmental stress has been suggested to limit competition, thus facilitating syntopic coexistence of species (e.g. Wiens, 1977). It is has been postulated that more dissipative beaches might allow more competition than reflective ones (Defeo and McLachlan, 2005). Very few studies have tried to elucidate the role of biological interactions in sandy beaches (Croker and Hatfield, 1980; Defeo *et al.,* 1997; Dugan *et al.,* 2004) and to our knowledge only one has focused on congeneric intertidal species (Defeo *et al.,* 1997), providing a niche segregation perspective at the lowest possible taxonomic level together with the opportunity to compare between the experimentally established potential niche and the realised niche documented by field data. As the role of substrate characteristics is obvious for burrowing infauna, we choose to focus on this aspect of the benthic habitat and its association with the ecological niche of the benthic fauna. Swift burrowing and efficient breathing seem to be the most important demands (McLachlan and Brown, 2006), limiting the survival of the species in a given sediment. Although it has been argued that experiments to elucidate the role of competition by means of sediment response (preferences and tolerances), follow a too indirect approach (Dugan *et al.*, 2004), previous research has shown it to have merit (Defeo *et al.,* 1997).

We used two co-occurring and closely related sandy beach amphipods from dissipative Belgian beaches to understand observed patterns of cross-shore zonation and segregation, focusing on possible interspecific avoidance (as a proxy for competition, which might cause avoidance) between both species and the role of the sandy substrate in order to unravel differences in aspects of their ecological niche (as defined by Hutchinson, 1957).

Bathyporeia pilosa and *B. sarsi* are widespread and abundant amphipod species of sandy beaches of the NE Atlantic (d'Udekem d'Acoz, 2004). On these beaches, *Bathyporeia pilosa* is found in the upper parts of the intertidal zone of sheltered beaches, between MHWS and mid-tide level (Fish and Preece, 1970a), while *B. sarsi* can be found between MHWN and MLWS (Toulmond, 1964; Nicolaisen and Kanneworff, 1983). The striking cross-shore spatial segregation and possible avoidance in co-occurrence of these closely related and morphologically highly similar species has not been explained. Besides the obvious difference in the submersion period of each species' specific zone, interspecific competition - possibly achieving and/or maintaining space partitioning - and a species-specific response to differences in the sandy beach sediment might be important. Moreover, *Bathyporeia* species are believed to feed on epipsammic microphytobenthos (Sundbäck and Persson, 1981), thus potentially intensifying their dependency on certain sediment characteristics that allow the development of a sufficient food source. This latter type of sediment dependency has not been of importance in previous studies, mainly dedicated to suspension or filter feeders (Croker and Hatfield, 1980; Dugan *et al.,* 2004) or carnivorous scavengers (Defeo *et al.,* 1997).

We will test three hypotheses: (1) differences in sediment preferences (regarding grain size and level of fines) between the two species (a) exist and (b) can be related to *in situ* sediment; (2) one or both species avoid presence of the other species, observed as altered sediment preference in syntopy in one or both species; (3) differences in sediment tolerance, with the most tolerant species being able to inhabit harsher conditions, exist. Testing was done in order to compare (1) sediment preferences (grain size and level of fines) and tolerances (grain size) between both species and (2) sediment preferences in allotopy versus in syntopy for each species.

Material and methods

Animals were collected along the Belgian coast at De Panne and Raversijde beaches. Collection was carried out in two opportunistic ways in order to catch enough live specimens: long-shore towing with a hand net (1mm mesh width), at relevant time with regard to high tide and digging out of the beach sediment with subsequent sieving out of the animals (sieve mesh also 1mm). Best net catch success was achieved outside winter months, during receding tide and at spring tide, as corroborated by earlier research (Watkin, 1939; Preece, 1971b). *Bathyporeia pilosa* was usually most successfully collected at about 1h30 after high tide, whereas *B. sarsi* was most easily encountered at about 2h30 after high tide. Swift identification of live specimens could be achieved by the colour of the caeca of the hepatopancreas, being green in *B. sarsi* and brown in *B. pilosa* (Nicolaisen and Kanneworff, 1983). At the end of the experiments, animals were also identified based on external morphology – no identification errors on the basis of the hepatopancreal caeca were determined. Stock supplies of living animals received air supply, but no extra food, besides that present in the provided beach sediment (a couple of centimetres thick), was provided. Stocks were left overnight to allow acclimatisation of the animals.

All experiments were conducted from October 2005 until April 2006 at an air temperature of 14 ± 2 SD °C and in the dark, as light is believed to decrease swimming activity (Watkin, 1939), thus hamper swift sediment type selection. This inhibition has been attributed to avoidance of predation (Fincham, 1970). Sediments (thus animals) remained submerged throughout the experiments, ruling out desiccation.

Sediment preference and tolerance were investigated for both species in both allotopic and syntopic conditions.

SEDIMENT PREFERENCE

Sediment preference was assessed for both (1) sand grain size and (2) percentage of fines in both allotopic and syntopic conditions. For both experiments, seven different sediment types were prepared to be selected from: (1) seven types of sediment differing in median grain size and (2) seven types of sediment with differing levels of fines. For preparation of the first set of seven sediment types, sand was collected at the Belgian beaches of Raversijde and Vosseslag. Organic matter was removed and the sand was subsequently sieved over a sequence of seven sieves with mesh width of 63 µm, 125 µm, 180 µm, 250 µm, 355 µm, 500 µm and 1000 µm. As the *in situ* collected beach sand contained too low levels of the finest and coarsest extremes of the grain size gradient, additional sand sediments were obtained from industrial suppliers.

Table 1. Sediment types of grain size preference experiment.

sieving class limits (µm)	**median grain size (µm)**
63-125	124
125-180	154
180-250	242
250-355	342
355-500	478
500-1000	733
1000-2000	1338

For preparation of the second set of sediment types, sand (median: 221 µm) was collected *in situ* from the Raversijde beach, were high numbers of both *Bathyporeia* species can be encountered. This sand was decanted for removal of organic matter. Fines were mixed in different concentrations in the shape of a ceramic clay powder with median grain size of 5.8 µm, and seven sediment types were obtained (0%, 1%, 3%, 5%, 10%, 25%, 50% of sediment volume being fines).

Both preference experiments (grain size and level of fines) were conducted in round-shaped aquaria (diameter: 50 cm), divided into seven pie sections by seven inox partitions, each section containing a different sediment type. Sediment depth was 4 cm, as was the seawater depth on top of the sediment. Aquarium experiments were started at the time of low tide, after removal of the partitions, and animals were released *ad random* into the aquarium. Both experiments were replicated five times, with each replicate involving three aquarium setups: one for each species, containing 100 specimens of either species (allotopy setups), a third containing 50 individuals of both species, i.e. again 100 animals in total (syntopy setup), resulting in a density of 509 ind/m² for each aquarium. After 24 hours, corresponding to two swimming cycles (Watkin, 1939), the experiment was terminated and animals were extracted from each pie section, identified (using the keys of d'Udekem d'Acoz, 2004) and counted. Sediment preference in allotopic conditions was analysed by log-linear analysis of frequency tables, treating abundance as dependent variable and sediment type and replicates as independent variables. Comparisons between species and between conditions (allotopic vs. syntopic) were achieved through two-way ANOVA analyses, including assumption testing and arcsin data transformation.

SEDIMENT TOLERANCE

Compulsory survival and subsequent mortality were used to assess sediment tolerance in allotopic conditions. Three out of the seven grain size sediment types mentioned beforehand were used: both extremes (63-125 µm and 1000-2000 µm) and the *in situ* sediment resembling sediment (250-355 µm). Petri-dishes (depth: 2.3 cm; diameter: 14 cm) were used, filled half with sediment and half with seawater. Twenty specimens (1299 ind m^{-2}) were released in each dish and survivors were counted after one week. The few individuals that died during the experiment were often found on top of the sediment but also burrowed. For each species, three replicate experiments were executed. Sediment effect for each separate species was analysed by one-way ANOVA, whereas two-way ANOVA was used for between-species comparison (independent variables: species and sediment type).

Results

SEDIMENT PREFERENCE

Grain size

While no significant differences in allotopic grain size preference were found between the two species (ANOVA: df = 6; F = 1.43; p = 0.22), each species showed significant sediment type preference (log-linear analysis: *B. pilosa*: df = 6; chi-sqr= 331.73; p < 0.001; *B. sarsi*: df = 6; chi-sqr= 371.78; p < 0.001). Both sediment type extremes were avoided and a broad optimum, rather than clear preference for a single type was observed for either species surpassing the range of *in situ* sediments (Fig. 1).

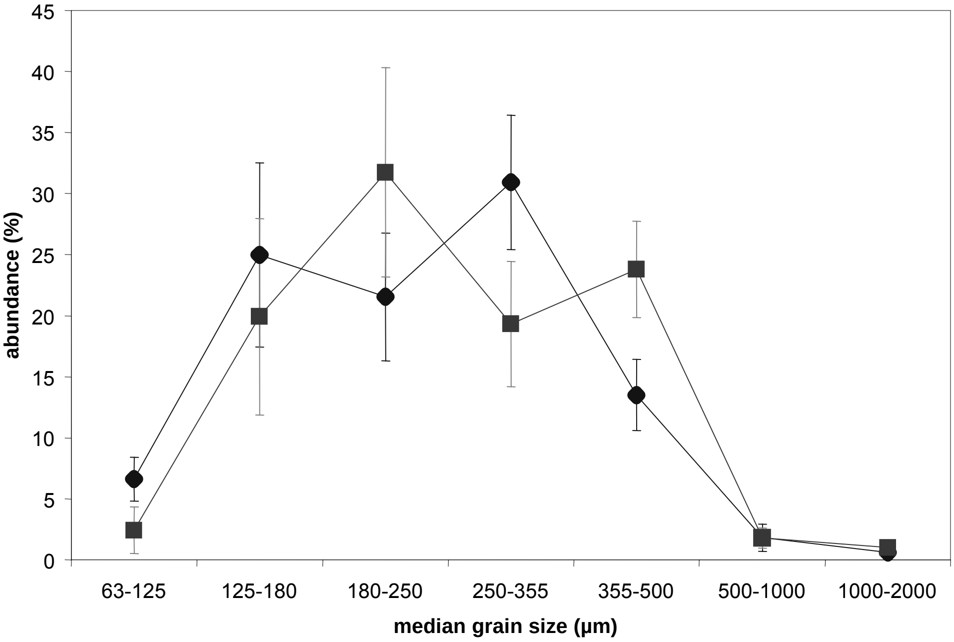

Figure 1. *Bathyporeia sarsi* and *B. pilosa.* Grain size selection in allotopic conditions ; squares = *B. sarsi;* circles = *B. pilosa* ; error bars are standard errors.

Presence of the other species had no significant effect on the grain size selection of both species (two-way ANOVA: *B. pilosa*: df = 1; F = 0.00; p = 0.99; *B. sarsi*: df = 1; F = 0.00; p = 0.97) (Fig. 2).

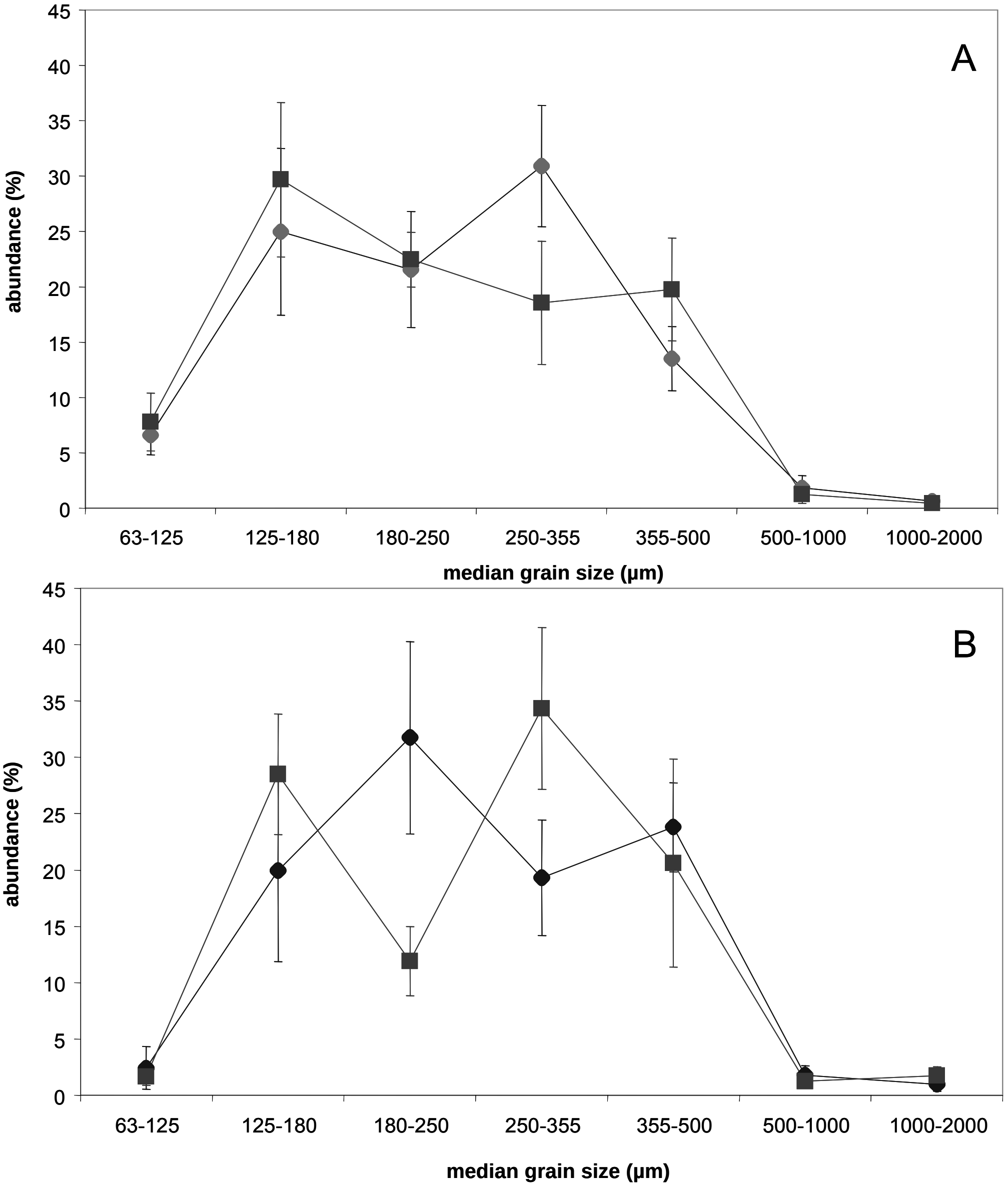

Figure 2. *Bathyporeia sarsi* and *B. pilosa.* Grain size selection of *B. pilosa* (A) and *B. sarsi* (B) in allotopic (circles) and syntopic (squares) conditions; error bars are standard errors.

Fines

While no significant differences in allotopic grain size preference were found between the two species (ANOVA: df = 6; F = 1.17; p = 0.35), each species showed a significant sediment type preference (log-linear analysis: *B. pilosa*: df = 6; chi-sqr= 186.73; p < 0.001; *B. sarsi*: df = 6; chi-sqr= 173.72; p < 0.001) (Fig. 3). Both species did strongly avoid the highest fines levels (25% and 50 %), with highest abundance of *B. pilosa* encountered in the 5% mixture and highest abundance of *B. sarsi* in the absence of fines.

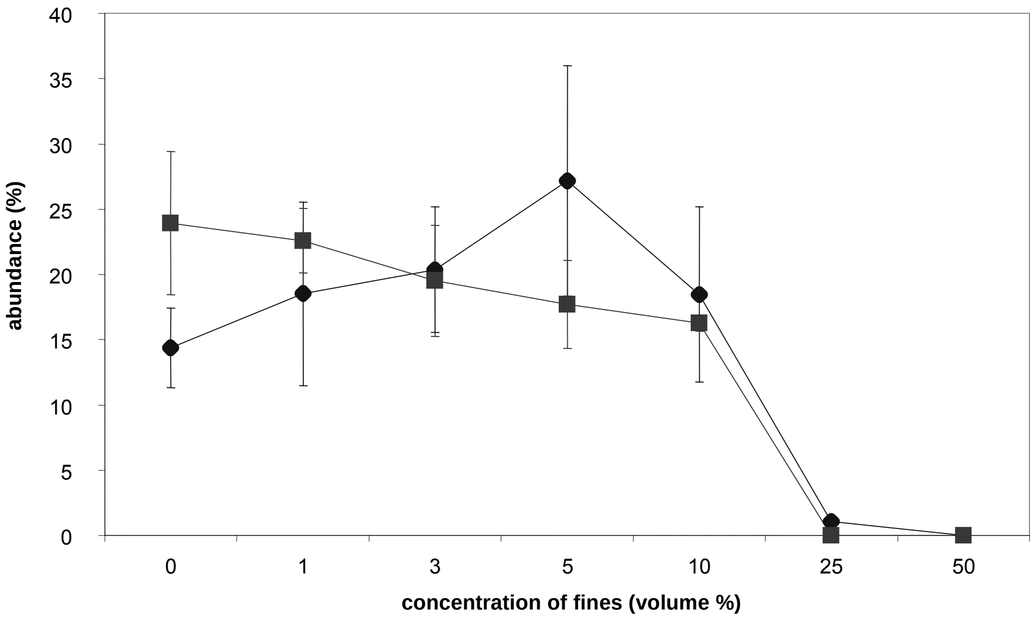

Figure 3. *Bathyporeia sarsi* and *B. pilosa.* Fines concentration selection in allotopic conditions ; squares = *B. sarsi;* circles = *B. pilosa* ; error bars are standard errors.

Presence of the other species had no significant effect on the selection of level of fines of either species (ANOVA: *B. pilosa*: *df* = 1; F = 0.04; p = 0.99; *B. sarsi*: *df* = 1; F = 0.00; p = 0.97) (Fig. 4).

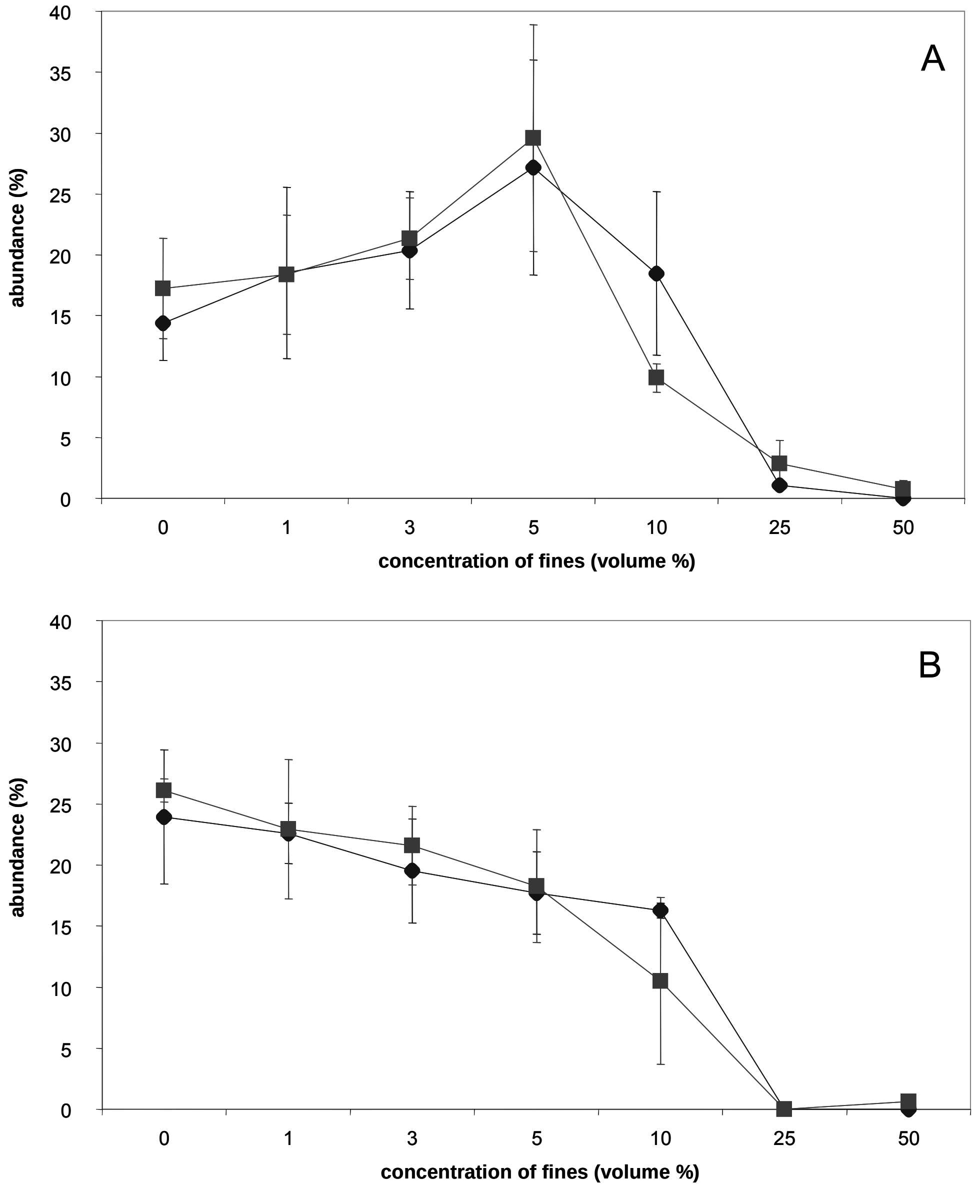

Figure 4. *Bathyporeia sarsi* and *B. pilosa.* Fines concentration selection of *B. pilosa* (A) and *B. sarsi* (B) in allotopic (circles) and syntopic (squares) conditions; error bars are standard errors.

SEDIMENT TOLERANCE

Mortality after one week was significantly higher for *B. sarsi* than for *B. pilosa* (ANOVA: df = 1; F = 10.34; p = 0.007) and a significant effect of grain size was observed (ANOVA: df = 2; F = 19.56; p < 0.001), which is species-dependent (interaction effect of ANOVA: df = 2; F = 4.03; p = 0.046) (Fig. 5).

Both species display highest mortality in the 63-125 µm sediment and comparable, low mortality in the 250-355 µm sediment.

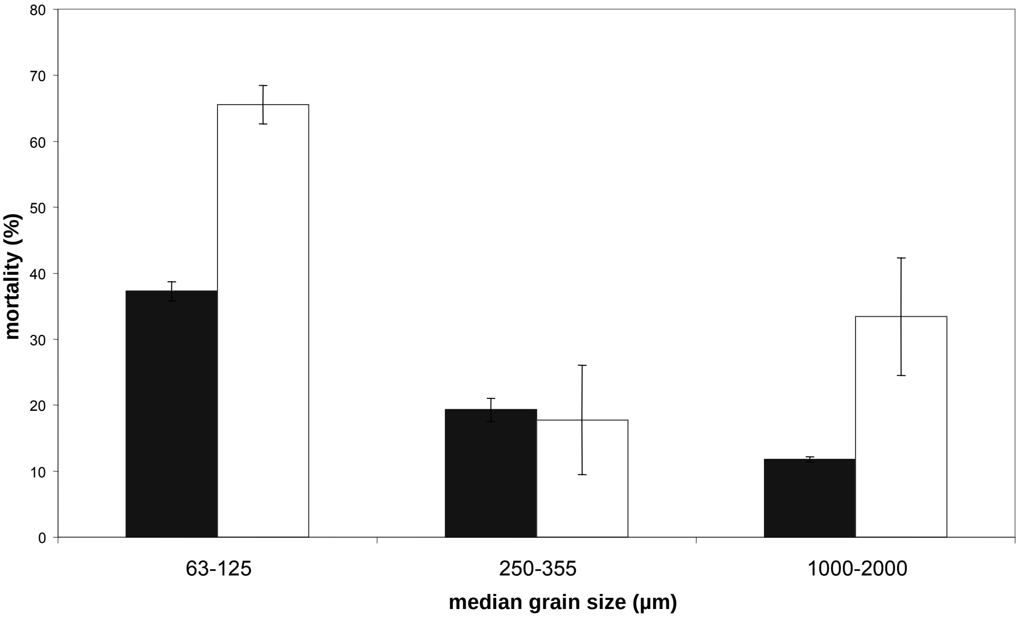

Figure 5. *Bathyporeia sarsi* and *B. pilosa.* Mortality as an inverse indicator for grain size tolerance of *B. pilosa* (solid bars) and *B. sarsi* (open bars); error bars are standard errors.

Discussion

The hypotheses, put forward in the introduction of this paper, suppose the observed cross-shore segregation of the investigated species to be the combined result of *B. sarsi* being a stronger competitor, displacing *B. pilosa* from lower intertidal elevations on one hand, and *B. pilosa* avoiding the proximity of *B. sarsi* but being more tolerant to environmental stress like more extreme grain sizes and a shorter period of submersion (and related desiccation, possible salinity drops and temperature shocks) on the other. From our research, results are available conflicting to our hypotheses, while others seem to confirm them.

BOTH SPECIES EXHIBIT THE SAME SEDIMENT PREFERENCES

The observed grain size selection of both species relates rather well to *in situ* sediment. Avoidance of finest grain sizes (63-125 µm) and higher levels of fines (>25%) by both species can be related to breathing (Nicolaisen and Kanneworff, 1969) through likely gill obstruction. Sediments of coarser grain sizes exhibit larger interstitial areas and better oxygen penetration. Too coarse sediments (>500 µm), however, hamper digging (Nicolaisen and Kanneworff, 1969). The role of permeability and oxygenation has been stressed before (Khayrallah and Jones, 1980b).

Field data document *B. pilosa* to reside in fine and medium sands (Vader, 1965: 70% sediment <210 µm; Khayrallah en Jones, 1980b: 125-250 µm; Persson, 1982: 125-250 µm; Nicolaisen and Kanneworff, 1983: 150-

220 µm). Specimens of *Bathyporeia pilosa* used in our experiments were taken from *in situ* sediments with a median grain size of 180-217 µm (Elliott *et al.*, 1997). Our experimentally established preferences are broader than what field data might suggest, indicating the difference between the potential and realised niche of the study subjects. Consequently, with regard to grain size, both species should be able to inhabit the entire intertidal zone. In the field, however, interspecific segregation is observed. This has been related to very high numbers reached by *B. pilosa* making it impossible for *B. sarsi* to colonise the upper intertidal zone (Vader, 1965), presenting to our opinion a somewhat partial view. If indeed, *B. pilosa* would dominate possible competition between both species, at least an explanation for the lower limit of the intertidal distribution of this species seems desirable. Furthermore, *B. sarsi* is not found to inhabit these upper intertidal parts on beaches where *B. pilosa* is absent. Non-significant between-species differences showing highest abundance of *B. pilosa* at 5% of fines, in contrast to 0% in *B. sarsi*, are corroborated in part by earlier field findings (Vader, 1965: maximum 5-10% of fines).

Dealing with our first hypothesis, no significant between-species differences in preference could be observed, thus disallowing further explanation of the observed cross-shore segregation by means of grain size preference.

OCCUPIED GRAIN SIZE RANGE IS NOT INFLUENCED BY AVOIDANCE

Concerning our second hypothesis, the presence of the other species did not cause any significant change in sediment selection (both in grain size and level of fines experiments). Thus, no avoidance was observed and no proof for possible interspecific competition provided. This is in contrast to comparable results obtained from Uruguay by Defeo *et al.* (1997) with two also closely related and cross-shore segregated species of intertidal sandy beach isopods (*Excirolana braziliensis* and *E. armata*). In the latter study, preference and tolerance experiments were also conducted in allotopy and syntopy, however, only two sediment types (fine and coarse sand) were used. Both this and the observed *Bathyporeia* zonation patterns suggest space partitioning to reduce competition, as already suggested by other authors (Croker, 1967; Croker and Hatfield, 1980; Dugan *et al.,* 2004). Yet still, evidence for competition is lacking from our data. Other habitat parameters besides grain size and level of fines, and other mechanisms than interspecific competition are likely to be of importance to explain the observed cross-shore segregation. The density of animals released within the experiment and the scale size of the experimental setup are also of importance, as a higher density within the setup is likely to enhance the possibility of identifiable interspecific competition (Defeo *et al.,* 1997). As a side note, it seems to us that density and scale size would be yet more important or even problematic when dealing with predacious species, exhibiting a large degree of cannibalism, like *Excirolana* isopod species or their NE Atlantic counterparts of the genus *Eurydice.*

BATHYPOREIA PILOSA IS MORE TOLERANT TOWARDS GRAIN SIZE EXTREMES THAN *B. SARSI*

With regard to our third and final hypothesis, preference for intermediate grain size was evident in both species. More importantly, *B. pilosa* appeared to be more tolerant to grain size extremes than *B. sarsi*, thus corroborating this aspect of our hypothesis. While tolerance comparisons between both species were unavailable up to now, we can safely state that *B. pilosa* has a high stress tolerance. This has already been demonstrated in contrast to another species, *B. pelagica* (Preece, 1970, 1971a). One could argue that the observed lower tolerance of *B. sarsi* might not as such be related to grain size rather than to the overall lab environment conditions. This is, however, contradicted by the observed comparable mortality of both species at the intermediate sediment type, thus the observed difference can rightfully be attributed to the investigated variable, i.c. grain size. When confronting results of grain size preference and tolerance experiments, we can conclude that both species avoid coarse sediments if possible, while only *B. sarsi* seems to be clearly negatively affected by too coarse sediments. Both species avoid finer sediments, while, if unavoidable, again *B. sarsi* is the most sensitive species. This sensitivity seems, however, in contrast to the practical absence of *B. pilosa* from a number of Belgian beaches where only *B. sarsi* can be found (Speybroeck *et al.,* submitted, c).

CONCLUSIONS

Addressing the title question of this paper, our research has shown signicifant differences in tolerance between both study species, while sediment preferences were comparable and avoidance (as a proxy for interspecific competition) was not visible from our data. Both species seem to exhibit a moderately wide preference for fine to medium sands, largely concurring with field data and this preference seems to be unable to explain for observed cross-shore segregation. Explaining zonation patterns or their maintenance as related to avoidance and/or competition remains equally unascertained. Both species are known to occur at lower densities when co-occurring at a microscale (Speybroeck *et al.*, in prep.) but no competition-related explanation can be provided as for now. Our tolerance data, however, seem to suggest likely physiological limitations of *B. sarsi* for survival in the upper beach zone commonly occupied by *B. pilosa*. Yet, why the occurrence of *B. pilosa* does rarely extend onto the zone occupied by *B. sarsi* remains to be resolved, as do the factors which preclude both species from occupying the lower parts of the intertidal zone. We believe that these species provide an ideal test case for the ecological theory of sandy beaches concerning biological interactions and factors determining zonation at the species level. This paper has initiated the enhancement of our understanding in these elements but additional research is advocated. Therefore, a comprehensive more in-depth assessment of this two-species system (as other macrofaunal species are supposed to account only marginally for *Bathyporeia* zonation), involving both experimental work and field studies seems desirable, taking the scale- and density-dependent nature of biological interactions into account. Long-term field studies should address the temporal variability of the observed segregation, in a circumtidal, but more importantly, seasonal perspective, while experimental work might include a wider range of quantifiers of possible competition (e.g. survival, reproduction, burrow rate, …).

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CHAPTER 7

Towards a methodological framework for the prediction and mitigation of the ecological impact of beach nourishment – a case study on intertidal benthic macrofauna

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Abstract

Beach nourishment is a widely applied means for coastal protection in Europe and North America. Nowadays, beach nourishment is widely considered as a better alternative than the construction of hard structures to protect a coast against detrimental erosive effects, both from an ecological as from an engineering perspective. Even though beach nourishment is considered as the more ecologically sound option, this form of beach restoration also brings about sizable changes in the sandy beach ecosystem. Most studies conducted on the ecological impact of beach nourishment are short-term, *post hoc* monitoring investigations of the benthic macrofauna. Little is known of long-term effects, recovery after nourishment, effects of repeated replenishment at the same site (cumulative effects) or what processes are of ecological importance during and after nourishment, to understand recovery. Therefore, little or no effort has been made to facilitate recovery by investigating the ecosystem prior to nourishment and drawing guidelines for impact mitigation.

A methodological scheme is developed for pre-impact assessment of the ecological impact of beach nourishment. First, data needs on the physical and biological environment are specified. Secondly, methodological aspects of data collection are presented and a distinction is made between indispensable and less essential types of data. Cost-benefit considerations are made and options to cut costs are raised. Thirdly and finally, we applied the scheme to a case study on the intertidal macrobenthic fauna of Belgian beaches. We selected three key species (*Scolelepis squamata*, *Bathyporeia pilosa* and *B. sarsi*) and conducted field research on their population on Belgian beaches, as well as experiments on their habitat charactertistics. The results from this research allowed drawing guidelines for ecological impact reduction of beach nourishment. For the focal species, nourishment would preferably be executed by foreshore nourishment in winter (December-January). Desirable characteristics of the fill sediment are a good match with the natural sediment and especially low levels of fines. The applied methodology is proposed for use on other species, other ecosystem components and even other impact studies.

Keywords: beach nourishment, ecological impact, macrobenthos, sandy beaches, *a priori* assessment, pre-impact research, methodology

Introduction

Over the last decades, beach nourishment has become widely applied as a means for coastal protection in Europe and North America and the use of hard structures (breakwaters, dykes, groynes and harbour walls) has dropped proportionally (Anonymous, 1995; Basco, 1999; Hanson *et al.*, 2002; Hamm *et al.*, 2002). Awareness and attention towards problems of coastal erosion in general, and beach nourishment and its physical and biological monitoring in particular, have increased over the last decades. As an alternative for "hard" coastal protection, both positive and negative aspects of beach nourishment have been mentioned (Speybroeck *et al.,* 2006). Largely in contrast to nourishment, "hard" coastal protection may lead to increased erosion, often at down-drift locations rather than where the actual construction took place (through long-shore transport of the sediment) (Peterson *et al.*, 2000). One of many examples of a higher risk of erosion was the disappearance of the dry beach section along parts of the eastern coast of Belgium after the construction of dykes at the foot of the coastal dunes about a century ago (Charlier and De Meyer, 1995, 2000). Beach nourishment gives rise to smaller changes in the dynamics of both sediment and water, thus a natural equilibrium is reached sooner, more easily and stays in effect for a longer time (Peterson *et al.*, 2000). Negative aspects are the higher costs, as a consequence of the need of replenishment every few years, and the lower applicability on beaches with high wave energy (Esteves and Finkl, 1998). Some cost efficiency options have been discussed by Raudkivi and Dette (2002).

Nowadays, beach nourishment is widely considered as a better alternative than the construction of hard structures to protect a coast against detrimental erosive effects, both from an ecological as from an engineering perspective (e.g. Dankers *et al.*, 1983; Adriaanse and Coosen, 1991; Charlier *et al.*, 1998; Basco, 1999; Brown and McLachlan, 2002; Finkl, 2002; Greene, 2002; Hanson *et al.*, 2002; Hamm *et al.*, 2002; Speybroeck *et al.,* 2006). Due to the highly dynamic nature of their environment (mainly determined by waves and tides but also winds), the benthic fauna inhabiting the littoral zone of sandy beaches is limited to species with a high tolerance towards environmental stress. Therefore, according to many authors, nourishment should cause only minor, short-termed damage to the ecosystem (e.g. Löffler and Coosen, 1995; Anonymous, 2002; Miller *et al.*, 2002). The high ecological tolerance is, however, not unlimited (Jaramillo *et al.*, 1996; Moffett *et al.*, 1998). Even though beach nourishment is considered as the more ecologically sound option, this form of beach restoration also brings about sizable changes in the sandy beach ecosystem. In the short term, a large proportion of the resident flora and fauna is destroyed by the addition of a thick layer of nourishment sand. Changes in the beach habitat after nourishment, such as altered beach profile and sedimentology, will influence the rate of recovery of the ecosystem's natural equilibrium. Several strategies (classical or profile nourishment, foreshore nourishment and backshore nourishment) and techniques (rainbow spraying versus carrying the sediment to the beach as a mixture of water and sand under pressure via pipelines) of nourishment can be applied and each has a specific effect on the ecosystem (Speybroeck *et al.*, 2006).

Most studies conducted on the ecological impact of beach nourishment are short-term, *post hoc* monitoring investigations of the benthic macrofauna (Speybroeck *et al.*, 2006). Little is known of long-term effects, recovery after nourishment, effects of repeated replenishment at the same site (cumulative effects) or what processes are of ecological importance during and after nourishment, to understand recovery. Therefore, little or no effort has been made to facilitate recovery by investigating the ecosystem prior to nourishment and using this baseline data to draw guidelines for impact mitigation. The biological processes, relevant for nourishment effects, comprise (1) the process of disturbance and survival during nourishment (short term) and (2) the process of recolonisation after nourishment (medium to long term) (van Dalfsen and Essink, 2001). Disturbance and survival are mainly determined by species specific tolerances, while recolonisation is determined by (1) species-dependent dispersal and migration capacities and (2) species-dependent habitat demands and tolerances, including physical and biological elements.

In this paper, we aim at building an *a priori* assessment scheme of scheduled nourishment projects, involving attempted impact prediction and highlighting options for impact reduction. First, data requirements for comprehensive assessment were identified. Secondly, we elaborated on how to fulfill these requirements and prioritise among them, based on both scientific need (benefit) and financial restraints (cost). Figure 1 gives a schematic overview of the applied scheme.

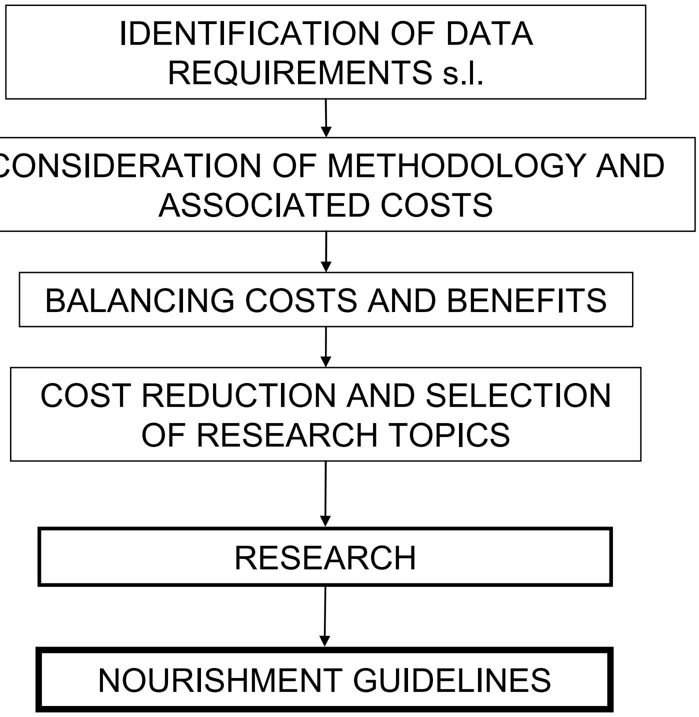

Figure 1. Schematic overview of methodological steps as in this paper.

Data requirements, methodology and cost-benefit considerations

For an ideal, fully comprehensive, *a priori* study on a specific nourishment project, intending impact mitigation and facilitation of recovery, a wide array of data types is needed, as identified by Speybroeck *et al.* (2006) and summarised in Table 1. Relevant data on both the physical and biological environment relate to features of the pre-nourishment beach, the nourishment project itself, and prediction of post-nourishment recovery.

Table 1. Data requirements for *a priori* assessment of ecological impact of beach nourishment (after Speybroeck *et al.*, 2006). Data types apply especially to the focal benthic fauna.

	DATA TYPE
PHYSICAL ENVIRONMENT	pre-nourishment features
	beach slope and morphology
	substrate features (sedimentology)
	nourishment features and predicted post-nourishment features
	(1) construction:
	timing, place, size and strategy
	(2) fill quality:
	changed substrate features (sedimentology; toxicity)
	(3) fill quantity:
	fill thickness
	changed beach slope and morphology
	physical recovery
	recovery rate
	characterisation of physically recovered beach (new equilibrium)
BIOLOGICAL ENVIRONMENT	pre-nourishment features
	community-level information
	species richness, total abundance and biomass
	population-level information
	temporal changes in abundance and biomass
	reproduction and recruitment patterns a.o. life history traits
	prediction of post-nourishment survival
	burrowing experiments
	prediction of post-nourishment recolonisation and recovery rate
	dispersal assessment
	habitat characteristics assessment

Subsequently, we discuss how to meet up to the data requirements, as specified in the previous section. We discuss both practical and financial aspects. In the third and final paragraph, we order the data requirements based on their scientific importance and financial implications. It is, however, important to consider that financial and practical restraints will differ widely between countries, sites and projects.

Physical data collection

Obtaining data on the pre-nourishment physical conditions is rather straight-forward and inexpensive in general. Measurement of beach slope and morphology are fairly easy, even when more advanced geomorphological surveying equipment is lacking. Analysis of sediment features is only slightly more time consuming and can be achieved by sieving (slower, so more expensive in manpower, but cheaper in the investment of equipment) or laser diffraction (faster, but more expensive in equipment). Adding enhanced long-shore resolution to this type of data will enhance effort and costs, but still this is not problematic.

Concerning the actual nourishment, further data types should be equally easy to obtain. If a nourishment project is scheduled, chief engineers should be able to supply specifics on the intended timing, place, size (long-shore dimensions) and strategy (cross-shore dimensions). Like pre-nourishment sedimentology, also fill sediment characteristics can be established with equal ease. Examining toxicity levels of the fill sediment (heavy metals, PCBs, PAHs, …) may concern more expensive methods of analysis but are crucial for both ecological impact mitigation and public health, as it is obligatory in many countries (e.g. Greene, 2002). Sediment suspension shortly after nourishment may be hard to predict but will be related to the characteristics of the fill sediment and local hydrodynamics. Besides sedimentology data of the borrow site, also the distance to be travelled between borrow and impact site and associated transportation costs should be considered.

Predicting (1) recovery rate and (2) characteristics of the newly established equilibrium, involves predictive modelling (generally provided by engineers involved in the nourishment project), incorporating known relations between beach morphology and hydrodynamics. The former relates to optimal timing of nourishment in view of reproduction of the intertidal benthos, whereas the latter determines the potential standing stock. Labour costs related to this modelling may be high, due to the need for educated experts.

Biological data collection – intertidal macrobenthos

Collecting data on the organisms of the sandy beach ecosystem involves much more effort and costs than the physical characterisation. Community-level information might be gathered by a one time sampling campaign across the intertidal gradient, preferably just after the major reproductive activities of the species present at the specific beach (Nelson, 1993), but repeated sampling will importantly enhance the information level. A stratified random sampling scheme is suitable to draw a across-beach perspective (cross- and long-shore) and samples should be replicated within each stratum. Strata can be delimited *a priori* (e.g. three equally sized zones – upper, mid and lower shore), involving some degree of subjectivity. For macrotidal, dissipative beaches, we advocate a time-driven pseudo-stratification, by sampling stations just above the water level at a fixed time interval (e.g. thirty minutes). Sampling starts at the time of high tide and ends at low tide. Sampling is preferably done at the day of spring tide, enabling maximum intertidal width sampling. In our opinion, time is the biologically most relevant station delimiter, as it relates to the duration of periods of submergence and emergence. Sampling just above the swash zone allows collection of both swash-active animals (e.g. peracarid crustaceans) and deeper burrowers (e.g. polychaetes). On beaches with known presence of swash-riding fauna, moving significantly up and down with the tide, a different sampling strategy may be necessary (Jones *et al.*, 1998). Regardless of using either cylindrical cores or rectangular frames to border the sample, its surface should by somewhat around 0.1 m², in order to allow representative sampling. Total sampled surface should be at least 3 m² for a minimally reliable species richness estimation (McLachlan & Brown, 2006), whereas even 5 m² does not sample all species (Schoeman *et al.*, 2003). Also, when using time as a stratifier, we need replication at each station e.g. three samples. These replicate samples can be spaced in relation to the impact site size and research goals: closely spaced samples (e.g. 1 m apart) may be more suitable for species-directed studies, while long-shore separation of replicates along the entire impact site may be more suitable when aiming at characterisation of the entire site.

For species-dependent population studies, the same sampling strategy and technique may be used, but more frequent sampling is required. Reproductive periods of the species are especially useful to delimit in terms of timing the nourishment impact. These can only be identified by means of a time series. Whereas a year-round interval sampling may give rough indication of reproduction period, annual variability of the timing of reproduction can only be addressed by a multi-annual study. As interval, monthly sampling seems advisable: less frequent sampling will cause large insecurity about reproduction and recruitment patterns; highly frequent sampling may offer higher resolution of observation surpassing interannual variation. Besides reproduction and recruitment, also seasonal changes in abundance and biomass, important in relation to trophic ecosystem links, and other features (growth and mortality, production, …) may be worth studying.

Having addressed pre-nourishment data collection and having drawn a comprehensive pre-impact image, we now need to consider anticipated changes due to the specific nourishment project. Therefore, we need (1) a prediction of the physical environment (recovery rate and equilibrium characterisation – see above) and –what we will address next- (2) established links between nourishment features and the sandy beach species from experimental research. Survival after nourishment can be investigated by means of “burial and burrowing” experiments, literally mimicking the deposition of the fill sediment over a range of different layer widths. Recolonisation after nourishment depends on macrobenthic dispersal and species-dependent habitat demands. Experimental assessment of dispersal in the field may well be the most difficult aspect to achieve, especially when dealing with animals that are too small to attach physical tags to their body. This is corroborated by the limited amount of literature on this subject (Dugan & McLachlan, 1999) and confirmed by our own failed attempts, as mentioned in this thesis’ outline. Lab experiments, however diminishing extrapolation power, could be designed to get a rough idea of the species’ mobility, possibly including imitation of hydrodynamic forces as monitored *in situ*. As data on the matter is usually lacking, experiments of habitat characteristics offer interesting options for assessment of recovery. Three major quantifiers can be used in lab experiments to document benthic habitat suitability: burrow rate, mortality (or survival) and selection. In the two former cases, we offer separate sediment types to different individuals (or a number of individuals) of the species. The speed at which they dig themselves in (relative to body size) as well as the level of mortality (or survival) after a certain amount of time, provide indications for the sediment tolerance limits of the species. When considering selection, animals are allowed to actively choose between different sediment types. Confronting both tolerance-directed and preference-directed results offers valuable insights on sediment responses. A range of different sediment types seems most valuable to investigate, mainly when varying in median grain size and level of fines, because these are the sediment characteristics most likely to vary between potential borrow sites. Furthermore, other environmental changes, if anticipated given a specific nourishment project, may also be worth looking in to (slope, hydrodynamics, …). Experiments may be useful for both adult individuals and the specific recruitment life cycle stage (e.g. pelagic larval phase), as they might differ concerning habitat demands. If sufficient field data is available, encompassing a significantly wide array of sandy beaches, differing in e.g. grain size, level of fines, …,

these should be confronted with aforementioned experimental results to try to unravel the importance of experimentally not assessed variables like e.g. hydrodynamics, emergence period, … .
Combining data on anticipated physical changes and habitat responses of the macrobenthic species, should allow predictive judgement on ecological recovery rate.

Prioritisation among data requirements - options for economising

As mentioned above, gathering biological data is expected to demand much more effort and resources than gathering information on the physical environment and its anticipated changes. Minimising total costs of the research project can be achieved at two different levels: (1) removal of data types and/or (2) economising within single data types. In view of the former level, it seems appropriate to distinguish between more and less essential data types. The latter level implicates that within some data types there is room for economising as well, albeit every cutback will involve loss of predictive power. Thus, resources and requirements will have to be balanced as costs and benefits (Tab. 2). All physical data are indispensable and most of them are inexpensive, thus inclusion seems mandatory for any study. Furthermore, these data are often readily available from the engineers in charge of the nourishment project. Only predictive modelling of the expected rate at which an equilibrium will be reached and what this equilibrium will look like, seems harder to accomplish. Basic data on species composition, total species number, abundance and biomass are mandatory. Habitat response experiments involve more effort and time, but often the necessary equipment does not need to be expensive and they offer crucial output. Sampling of time series to study reproduction and recruitment patterns is crucial for ecological adjustment of the timing of nourishment and prediction of recovery, even though it involves intensive sampling. Seasonal and interannual changes in abundance and biomass may be less primordial but no extra sampling effort is needed, if other temporal aspects (e.g. reproduction) are studied. Assessment of species-dependent, adult and (if applicable) larval dispersal is useful for the estimation of the population’s recovery rate. Extrapolation is, however, difficult and field studies with smaller animals, hard to tag and pursuit, are likely to fail. Burrowing experiments can suggest to break up the construction phase over smaller fill packets and a longer period of time but can be pointless for upper intertidal marine animals (see below – application example).
In this paper, we have restricted ourselves to pre-impact assessment and mitigation of ecological damage. However, time constraints may often govern prioritisation among data requirements and cutbacks. Nourishment projects may be planned and executed without the possibility for long advanced planning and research, often disallowing *a priori* monitoring and detailed investigation of key species. Nevertheless, sampling adjacent, unimpacted beaches and comparing them with samples from the impacted beach, may be one way to assess the impact. If time before impact is limited, the minimal requirement would be at least a single baseline sampling campaign of the pre-impact beach. Combined with data on the fill sediment and available knowledge, some mitigative adjustments of the way the nourishment project is executed could be proposed. From the ecological and research viewpoint, this does, however, represent a suboptimal situation.

Table 2. Data scoring for *a priori* assessment of ecological impact of beach nourishment. Scientific relevance (necessity) and resource and effort demands (costs) scored from + (low necessity, costs) to ++++ (high necessity, costs). “but ?” refers to problems to fulfill the need for data.

	DATA TYPE	NECESSITY	COSTS
PHYSICAL ENVIRONMENT	pre-nourishment features		
	beach slope and morphology	++++	+
	substrate features	++++	++
	nourishment features and predicted post-nourishment features		
	(1) construction	++++	+
	(2) fill quality	++++	+
	(3) fill quantity	++++	+
	physical recovery		
	recovery rate	++++	++++ but ?
	characterisation of recovered beach	++++	++++ but ?
BIOLOGICAL ENVIRONMENT	pre-nourishment features		
	community-level information	++++	++
	population-level information		
	temporal changes in abundance and biomass	++	++++
	reproduction and recruitment patterns a.o. life history traits	++++	++++
	prediction of post-nourishment survival	++(++)	++
	prediction of post-nourishment recolonisation and recovery rate		
	dispersal assessment	++	++++ but ?
	habitat characteristics assessment	++++	++

To conclude this section, we discuss options for minimising costs at the level of some specific data types. At any sampling survey, sampling effort and laboratory-processing efforts can be reduced by lowering the number of samples taken. In order to obtain a full picture of the present fauna, cross-shore distribution seems to be more valuable than long-shore distribution, as the variability observed along the former is expected to be largest. Based on this notion, the sampling strategy has to be balanced concerning how many strata will be sampled (cross-shore variability) and how many replicates will be collected (long-shore variability). Another option to reduce the effort to process samples and to execute experiments, is to identify and select a limited number of key species. This, however, requires baseline information, which, if not available beforehand, has to be collected first. Key species can be selected among others based on their (1) relative abundance, (2) established trophic role and (3) dependency on sandy beaches or uniqueness for the sandy beach ecosystem (observed by their absence from neighbouring ecosystems like dune areas and the shallow intertidal).

An example from intertidal macrobenthos

In this section, we applied the abovementioned guidelines to a pre-nourishment study on beaches of the southern North Sea (Belgium, NE Atlantic, Europe).

Physical sampling and research are relatively simple and straightforward. We will focus on the biological part of the research. First, we focused on three key species: the spionid polychaet *Scolelepis squamata* and the closely related amphipods *Bathyporeia pilosa* and *B.sarsi*. Selecting these species enabled an important reduction of cost and effort (Fig. 2).

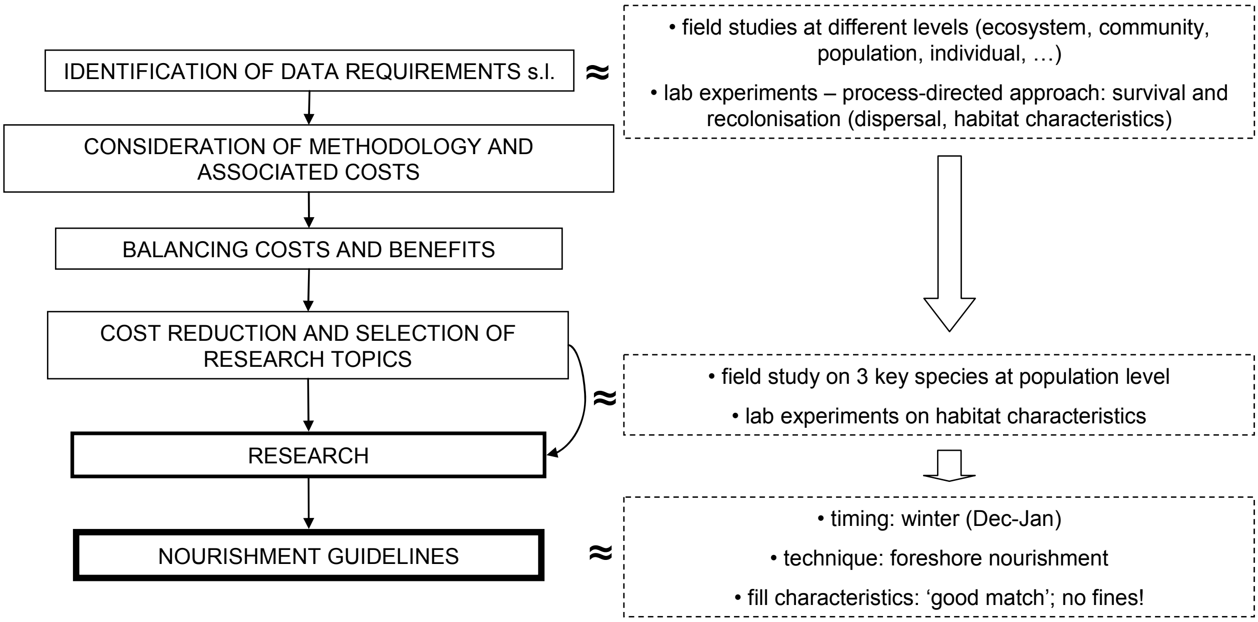

Figure 2. Schematic overview of the application of the proposed methodology.

We selected these focal species, keeping our three criteria in mind: (1) relative abundance: all three species are known major contributors to biomass and abundance and part of the species-poor but highly dense *Scolelepis squamata-Eurydice pulchra* community (Elliott *et al.,* 1997; Degraer *et al.*, 1999, 2003; Van Hoey *et al.*, 2004), (2) trophic role: they are known to be of high importance for juvenile flatfish like Plaice (*Pleuronectes platessa*) and wading birds like Sanderling (*Calidris alba*) (Glutz von Blotzheim *et al.*, 1984; Beyst *et al.*, 1999) and (3) with the Belgian part of the North Sea, they are indicative of upper intertidal areas, solely being found there. What species did we consequently not select? Lower parts of the Belgian intertidal zone are inhabited by an impoverished form of the *Nepthys cirrosa*-community, a community which reaches its optimum in the shallow intertidal and is extremely widespread in the Belgian part of the North Sea (Van Hoey *et al.*, 2004). Thus, species within this community are not particularly abundant on beaches. Furthermore, at population level they depend on beaches to a far lesser extent than our selected key species.

For pre-nourishment assessment of population features of our key species, we used 8 cross-shore transects as replicates, taking samples as described at half hour-intervals. We did this for 12 monthly sampling campaigns. Thus, a total number of 8 (cross-shore transect replicates) x 13 (stations per replicate at half hour-intervals) x 12 (sampling months) = 1248 was collected, equalling over 128 m^2 of sampled surface in total. If a single impact site is to be considered, closely spacing replicates may be advisable. Belgian *Scolelepis squamata* were found high up in the intertidal area (peak abundances at 3.95-4.40 m above MLLWS, i.e. at or just below MHWN) and proved to be semelparous, reproducing after little less than two years of growth and producing a single peak in the settlement of recruits starting from July (Speybroeck *et al.*, 2007). Both investigated *Bathyporeia* species were also found high in the intertidal zone (peak abundances of *B. pilosa* at 4.10-4.60 m above MLLWS; *B. sarsi* at 3.20-4.00 m above MLLWS) and, while both species display continuous reproduction and recruitment, absolute peaks were found in February and September-October (Speybroeck *et al.*, submitted, c).

Besides field study results, we also conducted a number of experiments. In our case, we chose not to spend time and money on nourishment survival experiments. The investigated species all live high up in the intertidal zone. After nourishment, the high water line and the zone occupied by each species will have moved offshore for 100-200 m. Therefore, any surviving individual will find itself on the newly created dry beach zone. As the species dealt with are clearly not adapted to terrestrial live, survival is impossible. This means that even if the species would be able to burrow upwards through the fill sediment, mortality would be close to 100%. Thus, we chose not to do this kind of experiments.

Field experiments were conducted in an attempt to quantify dispersal of *Bathyporeia* spp. by means of capture-mark-recapture experiments. However, no recapture was accomplished. No attempt was made to quantify dispersal of *Scolelepis squamata*. In this latter species, however, we know dispersal capacities to be considerably higher than that of marsupial breeders like the mentioned peracarids, due to the presence of pelagic larval life cycle stage (Günther, 1992).

Recolonisation rate also depends on habitat demands of the species as well. We investigated habitat demands by means of (1) tolerance and (2) preference experiments (Speybroeck *et al.*, submitted, a, b). Tolerance was investigated by means of survival in sediment types differing in grain size (from 63-125µm to 1000-1600µm) and level of fines (from 0% to 50%), as well as burrowing time for *Scolelepis squamata*. Preference was investigated by means of selection between sediment types differing in grain size and level of fines (varying over the same ranges). Sediment type extremes were chosen in order to surpass *in situ* values, aiming at a unimodal Gaussian response with lows at both extremes of the curve. Results for *Scolelepis squamata* revealed strong selection for very coarse sands (1000-1600 µm) and very low tolerance for very fine sands (63-125 µm), though extrapolation problems were noted (Speybroeck *et al.,* submitted, a). Both *Bathyporeia* species avoided both finest and coarsest sands (preference range: 125-500 µm) and higher levels of fines (> 10%) (Speybroeck *et al.,* submitted, a).

From both these main groups of results (field research and lab experiments), a number of nourishment-related conclusions can be drawn.

Field data suggest that nourishment should preferable be executed in winter (December-March) for *Scolelepis squamata*, with foreshore nourishment (perhaps including a grind berm) seeming to be the least harmful nourishment strategy for this species (see Chapter 2). This seems to comply with the results obtained for *Bathyporeia* spp., yet when trying to minimise the impact on these species the preferential time frame for nourishment would be slightly narrower (December-January). Our experiments provided valuable guidelines concerning desirable characteristics of the fill sediment. A good match with the natural beach sand is expected to be highly beneficial. This is in concordance with earlier results from impact monitoring (Saloman and Naughton, 1984; Gorzelany and Nelson, 1987; Nelson, 1993; Rakocinski *et al.*, 1996). In our case, especially very fine sands and even finer material (high levels of fines) would most likely prove to be detrimental. Extrapolation of experimental results were, however, not always easy and experimental results can be contradictive, stressing the need for more fundamental research in order to understand the importance of environmental variable to explain macrobenthic abundance (Speybroeck *et al.,* submitted, a).

To conclude our test case, we tried to establish (1) what information we would have gained if we would have collected more data (more data types or more effort per data type) and (2) what information we would have lost if we would have collected less data (less data types or less effort per data type). Considering our results in view of the first point, we feel that with our field studies, fortnightly sampling might have added a valuable higher level of temporal resolution. Even more so, we lack assessment of interannual variability of the observed populations and community characteristics. Therefore, we strongly advise in favour of multi-annual studies. With regard to the experimental research, the need for dispersal quantification remains present and, while rather difficult, offers a challenging field for future research. Furthermore, mimicking more population-structuring environmental characteristics (besides grain size and level of fines) in lab conditions and investigating species-dependent preferences and tolerances in the field, seem two highly advisable pathways in order to facilitate extrapolation of experimental results to field conditions. If we regard the second point, and attempt to consider what type of data might have been less than essential (thus optional for cost reduction), we may wonder whether in the case of nourishment at a specific site pre-impact sampling along e.g. three transects instead of eight may be equally adequate. A rough cost estimate, considering the regular Dutch price of nourishment of 5 euro/m³, amounts up to 4 million euro in total, including half of the costs for nourishment of the entire Belgian coastline and the other for the proposed ecological research (Janssen, pers. comm.). More specific data for the Belgian case could, unfortunately, not be obtained. These costs would have to be balanced against the benefits of the project. Though hard to express in numbers, the benefits of the proposed research will contribute to a.o. maintenance of the standing stock of animals feeding on sandy beach organisms, including commercially important species like brown shrimp and plaice. Furthermore, we advocate preservation of beaches as a unique transitional ecosystem between the terrestrial and marine environments, and refrain from attributing monetary value to the intrinsic value of sandy beaches. Efforts to attribute value and to define the goods and services of the marine environment have been made recently (Weslawski *et al.*, 2006; Beaumont *et al.,* 2007; Pendleton *et al.,* 2007). Nevertheless, especially beaches and their spatial and biological resources seem to deserve further attention concerning societal demands and the balancing of economy and environment, which falls, however, out of the scope of this paper. Without intending to elaborate on this, we feel that especially the uniqueness and functional role of sandy beaches are of importance, rather than traditionally as valuable experienced characteristics as species richness.

As a final note, we want to stress that the obtained guidelines for the practice of beach nourishment and the reduction of its impact only apply to the investigated species. Even though they represent a pivotal role in the sandy beach ecosystem, they cannot represent the entire sandy beach ecosystem. Therefore, research on other groups and species of sandy beach flora and fauna are highly needed. While we used intertidal macrobenthos as an example, we feel confident that application of our general methodology to the entire sandy beach ecosystem, including further, if not all, ecosystem components, should be easy to achieve.

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APPENDIX

Publication list Jeroen Speybroeck (as on 10/V/2007)

A1 Publications

Speybroeck J, Bonte D, Courtens W, Gheskiere T, Grootaert P, Maelfait J-P, Mathys M, Provoost S, Sabbe K, Stienen EWM, Van Lancker V, Vincx M, Degraer S (2006) Beach nourishment: an ecologically sound coastal defence alternative? A review. *Aquatic Conservation: Marine and Freshwater Ecosystems* 16(4): 419-435.

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Speybroeck J, Bonte D, Courtens W, Gheskiere T, Grootaert P, Maelfait J-P, Provoost S, Sabbe K, Stienen EWM, Van Lancker V, Van Landuyt W, Vincx M, Degraer S (in press) The Belgian sandy beach ecosystem – a review. *Marine Ecology: An Evolutionary Perspective*.

Speybroeck J, Hendrickx F, Vincx M, Degraer S (submitted) The ecological impact of beach nourishment and the restrained habitat of a key species – experiments insights and field data. *Biological Conservation.*

Speybroeck J, Pede A, Rivas Higuera H, Van Tomme J, Vincx M, Degraer S (submitted) Competition and sediment-related responses explaining segregated zonation of two closely related, co-occurring key species on sandy beaches? *Journal of Experimental Marine Biology and Ecology*.

Speybroeck J, Van Tomme J, Vincx M, Degraer S (submitted) *In situ* study of the autecology of two closely related, co-occurring sandy beach amphipods. *Helgoland Marine Research*.

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Speybroeck, J, Vandewalle S, Vincx M, Degraer S (in prep.) How may beach nourishment affect the intertidal isopod *Eurydice pulchra*?

Speybroeck J, Vincx M, Degraer S (**in prep.**) Towards a methodological framework for the prediction and mitigation of the ecological impact of beach nourishment – a case study on intertidal benthic macrofauna.

C1 Publications

Speybroeck J, Bonte D, Courtens W, Gheskiere T, Grootaert P, Maelfait J-P, Mathys M, Provoost S, Sabbe K, Stienen E, Van de Walle M, Van Lancker V, Van Landuyt W, Vercruysse E, Vincx M, Degraer S (2005) How may beach nourishment affect the sandy beach ecosystem? The case of Belgian beaches. In: J-L Herrier, J Mees, A Salman, J Seys, H Van Nieuwenhuyse, I Dobbelaere (eds) *Proceedings 'Dunes and Estuaries 2005' – International Conference on Nature Restoration. Practices in European Coastal Habitats, Koksijde, Belgium, 19-23 September 2005.* VLIZ Special Publication 19(xiv): 557-568.

Scientific reports

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