

# CHAPTER 5

---

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

---

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 – experimental insights and field data.

*Biological Conservation.*



## 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/m<sup>2</sup> - Degraer *et al.*, 2003a; 343 ind/m<sup>2</sup> on a total of 983 ind/m<sup>2</sup> - Van Hoey *et al.*, 2004; mean modal density along a cross-shore transect of 505 ± 38 SE ind/m<sup>2</sup>, peaks up to 1880 ind/m<sup>2</sup> - 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  $14 \pm 2$  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/m<sup>2</sup>) 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  $\mu\text{m}$ , 125  $\mu\text{m}$ , 180  $\mu\text{m}$ , 250  $\mu\text{m}$ , 355  $\mu\text{m}$ , 500  $\mu\text{m}$  and 1000  $\mu\text{m}$ . 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 *Scolecopsis 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 ( $\mu\text{m}$ ), 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 (63-125 $\mu\text{m}$ ), 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).

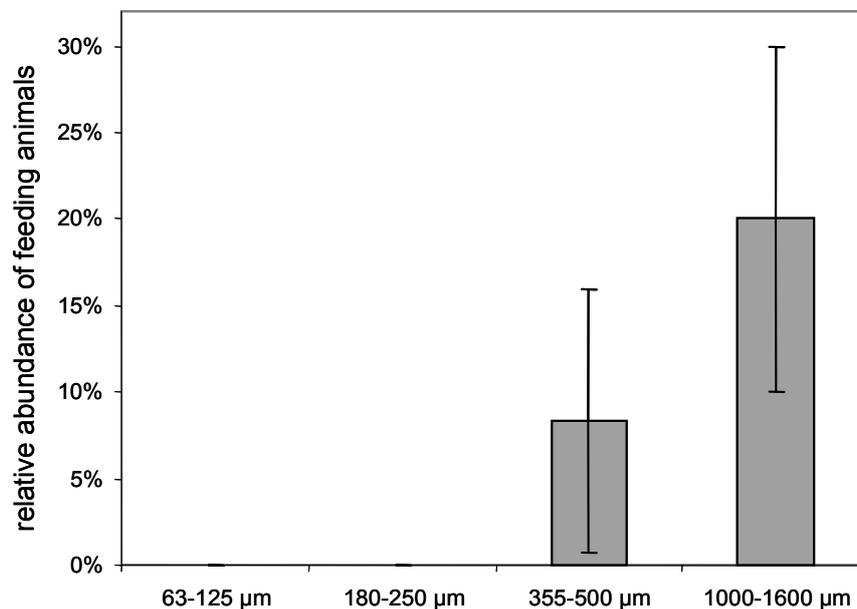


Figure 1. Feeding frequency of *Scolecipis squamata* in four different sediment types. Error bars are standard deviations.

#### 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 *Scolecipis squamata* in four sediment types, showed a trend for positive correlation between grain size and burrowing time (Ordered Heterogeneity test:  $r_{SPC} = 0.736$ ;  $p = 0.02$ ) (total mean:  $36.36 \pm 2.47$  SE seconds) (Fig. 2). Thus, coarser sand involved more difficult burrowing.

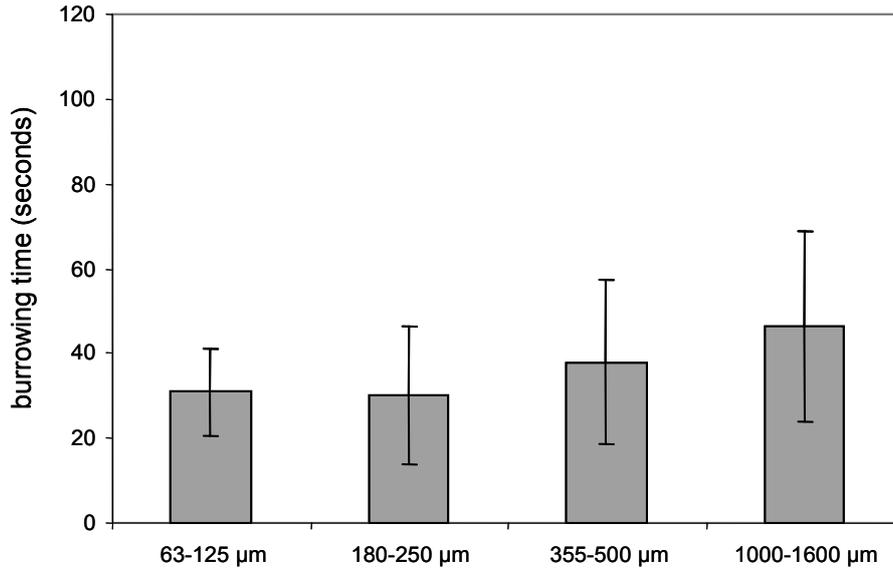


Figure 2. Burrowing time (in seconds) in four sediment types. Error bars are standard deviations.

#### 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.

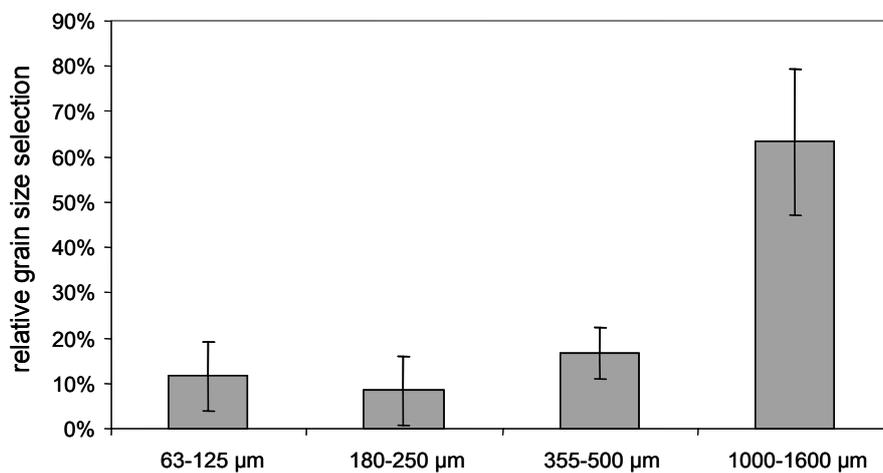


Figure 3. Grain size selection of four sediment types. Error bars are standard deviations.

## 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).

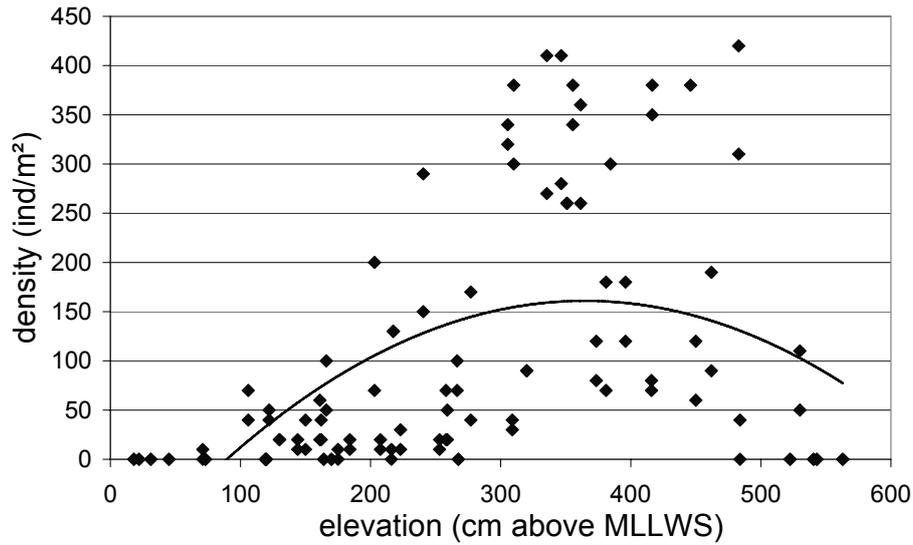


Figure 4. Density of *Scololepis squamata* as a function of elevation.

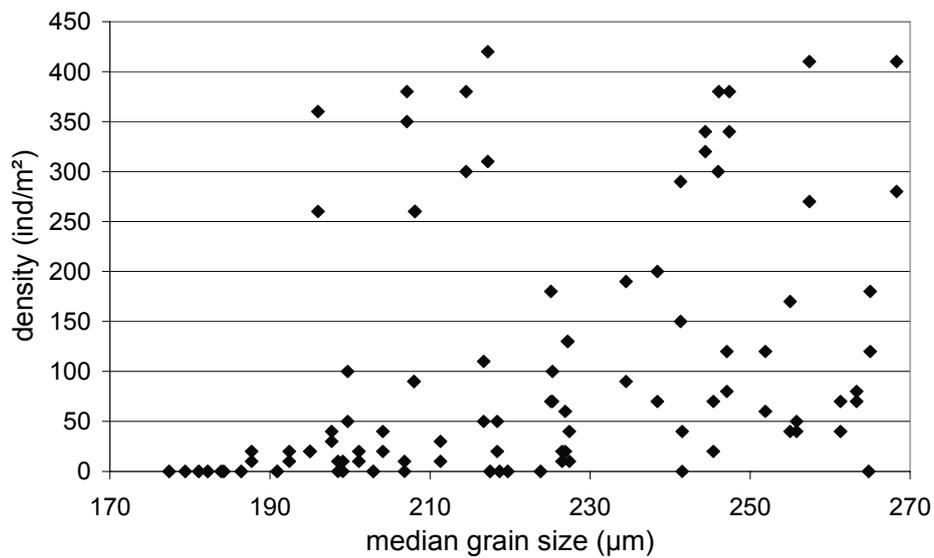


Figure 5. Density of *Scololepis squamata* as a function of median grain size.

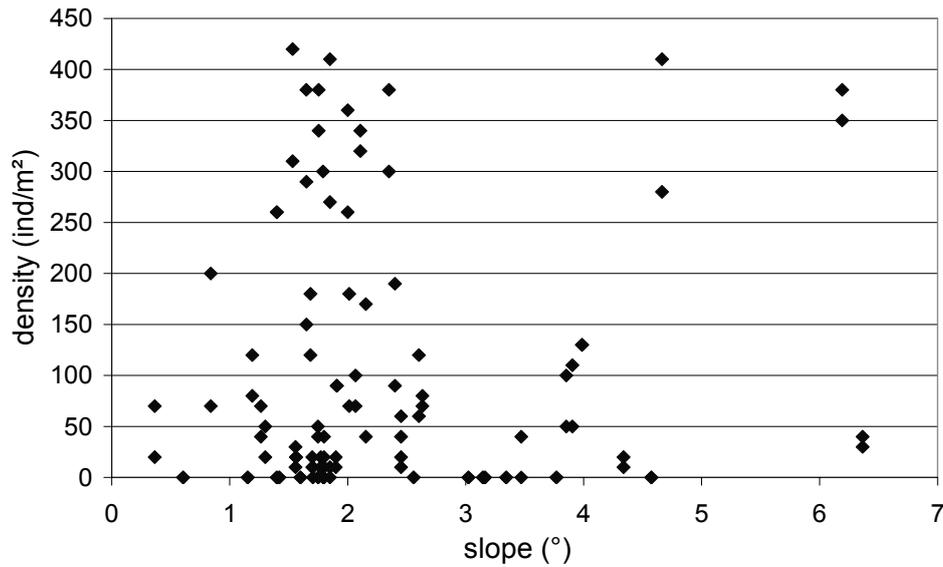


Figure 6. Density of *Scolelepis squamata* as a function of slope.

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.

	<b>PC1</b>	<b>PC2</b>	<b>PC3</b>
<b>elevation</b>	0.68	-0.11	-0.73
<b>median grain size</b>	0.63	-0.41	0.65
<b>slope</b>	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 led 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/m<sup>2</sup>; 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).

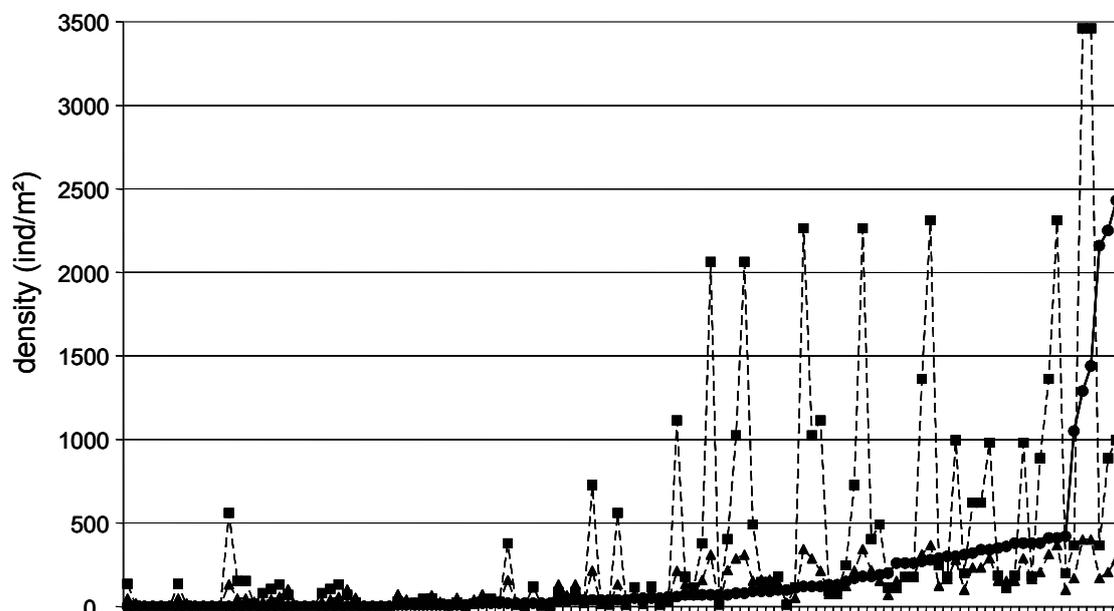


Figure 7. Comparison of observed (solid line and circles) and predicted abundance (models including elevation, median grain size and a square term for elevation - dashed lines). Squares relate to the model for all stations, triangles relate to model for all stations except six stations with abundance  $> 1000$  ind/m<sup>2</sup>. 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.

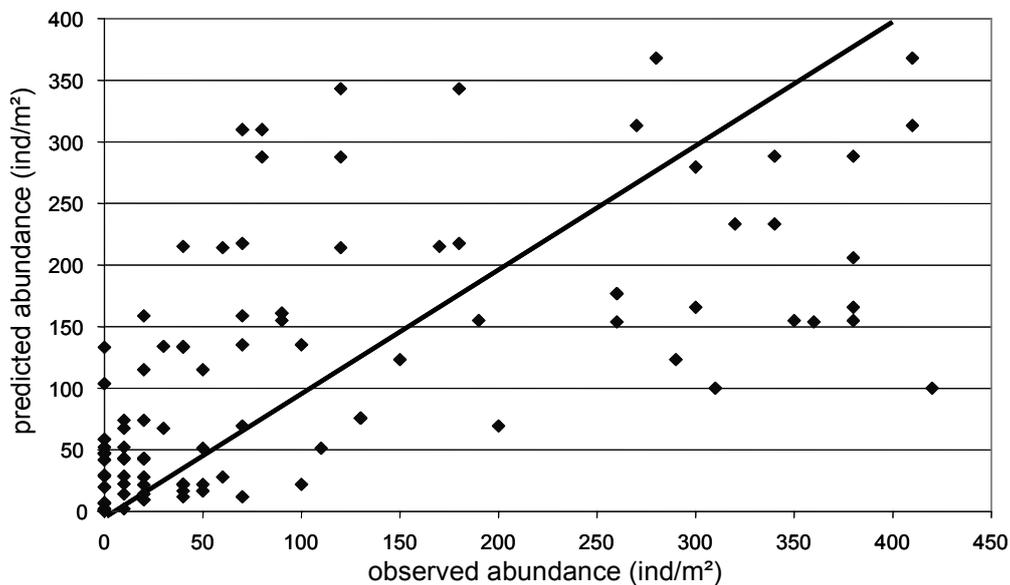


Figure 8. Predicted versus observed abundance values. A model with high predictive power would show data points running closely along the bisecting line.

## 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 (<63 $\mu$ m). 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 whether 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 breathe 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 were 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 150 $\mu$ m, 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 successful 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

---

This research was funded by the Flemish Coastal Waterways Division (formerly AWZ-WWK, now called Agency for Maritime Services and Coast – Department Coast (Agentschap voor Maritieme Dienstverlening en Kust (MD&K) – Afdeling Kust)), contract number 204.295, and Ghent University (BOF-GOA 2005 (01GZ0705)). Bart Beuselinck is thanked for help in the field.