THE MUD SHRIMP *COROPHIUM VOLUTATOR*:

A KEY SPECIES IN TIDAL FLAT SEDIMENTARY PROCESSES?

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DE SLIJKGARNAAL *COROPHIUM VOLUTATOR*:
EEN SLEUTELSOORT IN SEDIMENTPROCESSEN VAN SLIKKEN?

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CONTENTS

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SAMENVATTING

Estuariene slikplaten zijn intergetijdengebieden die ontstaan door sedimentafzetting in kustgebieden met beperkte dynamiek. Het zijn zeer productieve ecosystemen die gebruikt worden als rust- en foerageergebieden voor vogels, die dienst doen als kraamkamers voor platvissen en die een natuurlijke kustbescherming bieden tegen stormvloeden. Het sedimenttransport in deze estuariene getijdenplaten wordt gedomineerd door fysische processen (hoofdzakelijk getijdenstromingen en golven), die de omvang van het sedimenttransport bepalen. De voorbije decennia werd echter duidelijk dat ook kleinschalige biotische processen het sediment transport significant kunnen beïnvloeden en op die manier de morfologie van intertidale gebieden mee vorm kunnen geven. De invloed van biota op de topografie van landschappen is echter nog grotendeels onbekend. Daarom zijn sediment transport modellen nodig die de biotische effecten expliciet opnemen, om op die manier te bestuderen hoe deze kleinschalige biotische processen het intertidale landschap mee vorm kunnen geven. Voordat biologische effecten kunnen opgenomen worden in sediment transport modellen, moeten deze kleinschalige processen wel eerst bestudeerd worden. Het is geweten dat biota erosie zowel kunnen versterken als verzwakken, met respectievelijk destabilisatie of stabilisatie als gevolg. Biofilms van kiezelwieren bijvoorbeeld, scheiden een soort slijm af en vormen daardoor een beschermende laag die de stabiliteit van het sediment bevordert. Macrobenthos daarentegen, kan het sediment en zijn dynamiek op verschillende manieren beïnvloeden (bv. door bio-irrigatie, bioturbatie, mucussecretie, veranderen van de bodemruwheid,…). Doordat het macrobenthos verschillende levenswijzen kan aannemen, kan het het sediment zowel stabiliseren als destabiliseren. Daarom zijn gevalsstudies over benthos-sediment interacties nuttig en nodig om detail informatie te verstrekken over hoe macrobenthos de kleinschalige biotische processen kan beïnvloeden.

Corophium volutator (Pallas, 1766) (Crustacea, Amphipoda), ook gekend als de slijkgarnaal, leeft in U-vormige gangen en is een veel voorkomende soort in slikplaten langsheen de kust van de Noord-Atlantische Oceaan, zowel in Noord-Amerika als in Europa. De slijkgarnaal vertoont een breed gamma van gedragsactiviteiten afhankelijk

van de omstandigheden en bezit de mogelijkheid om zijn fysische omgeving te wijzigen. Daarnaast zijn er tegenstrijdige resultaten gekend over zijn effect op sediment stabiliteit. Samen met zijn dominant voorkomen, maakt dit alles *Corophium* een interessant modelorganisme voor de studie van biota-sedimentinteracties. De studie naar het gedrag van *Corophium* in slikplaten en naar zijn invloed op sedimenteigenschappen en sedimentdynamiek is daarom van groot belang en is het hoofddoel van deze doctoraatsstudie. Vermits bioturbatie één van de belangrijkste processen is waardoor organismen hun biofysische omgeving beïnvloeden, werden de bioturbatie door *Corophium* en de verschillende factoren die bioturbatie kunnen beïnvloeden in detail bestudeerd. Verder werd ook het gevolg van die bioturbatie op de erosiegevoeligheid van het sediment onderzocht.

In **hoofdstuk 2** werd een gedragsstudie uitgevoerd waarbij de verschillende bovengrondse en ondergrondse activiteiten die bijdragen tot de bioturbatie van *Corophium* tijdens de getijdencyclus in kaart werden gebracht. Hiervoor werd gebruikt gemaakt van een labo-opstelling met getijdensimulatie. Er werden negen activiteiten geobserveerd, waaronder één tot nog toe onbeschreven activiteit, namelijk het ‘flushen’ van de gang wat een belangrijk effect kan hebben op het bioturbatieproces. Globaal genomen was de activiteit aan het oppervlak laag (max. 3.7% van de tijd) en nam deze heel sterk af tot 0.1% na het blootstellen aan de lucht. Het ondergrondse gedrag werd gedomineerd door het ventileren van de gang gepaard gaand met filtervoeding (44% van de tijd) en door ondergrondse inactiviteit (51% van de tijd). Er werd een duidelijk cyclisch patroon gevonden gerelateerd aan de getijdenwerking: de activiteit piekt tijdens overspoeling, neemt daarna snel af tijdens de eerste uren na overspoeling en gedurende de laatste uren van blootstelling aan de lucht staat de activiteit op een laag pitje. Slechts één activiteit, namelijk het afschrapen van het sedimentoppervlak (= depositie voeding), gebeurt tijdens de volledige getijdencyclus (tijdsallocatie ± 1.5%). Uit deze studie leidden we af dat het bioturbatiepotentieel van een *Corophium* populatie het hoogst is tijdens overspoeling en dus bepaald kan worden door het aantal uren overspoeling. De bioturbatiesnelheid van een aan getijden onderworpen *Corophium* populatie was inderdaad laag, vergeleken met andere studies (**hoofdstuk 3**). Dit suggereerde dat de bioturbatiesnelheid beïnvloed wordt door de getijdenritmiek in het gedrag van *Corophium*. Hoofdstuk 3 had tot hoofddoel de densiteitsafhankelijkheid van bioturbatie, het belang van de biologische activiteit van *Corophium* en het differentiële effect op twee korrelgroottes te onderzoeken. De resultaten van de labostudie duidden aan dat de activiteiten van *Corophium* van het allergrootste belang zijn voor het herwerken van het sediment en dus de bioturbatiesnelheid beïnvloeden. De bioturbatiesnelheid was vijf maal hoger in aanwezigheid van *Corophium* activiteit vergeleken met wanneer enkel passief transport aanwezig is, dat veroorzaakt wordt door de statische structuur van *Corophium* gangen. Densiteit bleek een belangrijke factor, aangezien enkel hoge dichtheden van *Corophium* significant bijdroegen tot het deeltjestransport (1.1 cm^2/j), terwijl de rol van lage densiteiten in het herwerken van het sediment heel beperkt was (0.3 cm^2/j). De verschillende sedimentfracties werden op een gelijkaardige wijze bewerkt tijdens het deeltjestransport; er trad geen differentiatie op tussen de verschillende sedimentfracties. De impact van deze bioturbatie op de fysische sedimenteigenschappen werd onderzocht in **hoofdstuk 4** en tegelijkertijd werd de mogelijkheid onderzocht om deze impact vast te stellen via 'remote sensing'. Conventionele, destructieve technieken toonden een significante stijging van het watergehalte (2-3%) en een kleine, maar significante daling van de kleifractie (0.3%) aan in de aanwezigheid van hoge densiteiten *Corophium*. Via het meten van de spectrale reflectantie van het sediment oppervlak, kon de impact van *Corophium* op het watergehalte vastgesteld worden op een niet-destructieve manier, namelijk op basis van een verhoogde absorptie bij 1450 nm. De impact op het kleigehalte was te klein en kon daarom niet op deze manier vastgesteld worden. Deze studie toonde aan dat bioturbatie-activiteiten de spectrale reflectantie significant kunnen wijzigen en dat remote sensing in het laboratorium kan toegepast worden om de bioturbatie impact op sedimenteigenschappen te bepalen. Dit opent nieuwe mogelijkheden voor lange termijn experimenten omtrent de rol van bioturbatie in sedimentaire processen.

Het gevolg van bioturbatie door verschillende densiteiten van *Corophium* voor de erosiegevoeligheid van het sediment werd geëvalueerd in een stroomgoot, zoals beschreven in **hoofdstuk 5**. Erosiegevoeligheid werd uitgedrukt als erosiesnelheid gebaseerd op gesuspendeerd materiaal, kritische stroomsnelheid en kritische schuifspanning. Een significante stijging in erosiesnelheid met stijgende densiteit werd vastgesteld, waarbij de erosiesnelheid voor het sediment met een densiteit van 20,000 ind./m^2 vijf maal hoger was dan voor het sediment zonder *Corophium*. De kritische schuifspanning daarentegen bleek onafhankelijk van de densiteit, zeker voor densiteiten tot 15,000 ind./m^2. Voor een densiteit van 20,000 ind./m^2 werd een sterke daling van de kritische schuifspanning (-30%) gemeten. Vergelijking van de kritische stroomsnelheden gemeten in dit experiment met de hydrodynamisch gesimuleerde natuurlijke stroomsnelheden van de IJzermonding toonden aan dat het voorkomen van sedimenterosie bij natuurlijke stromingsomstandigheden onwaarschijnlijk is, tenzij bij stormweer. Deze veronderstelling werd ondersteund door de velddata verzameld in de IJzermonding gedurende drie opeenvolgende jaren (juli 2005-juni 2008), zoals voorgesteld in **hoofdstuk 6**. Deze veldstudie toonde aan dat sedimentstabiliteit varieerde op een korte (seizoenale) tijdsschaal en dat deze rechtstreeks beïnvloed werd door biota. De sedimentmorfologie daarentegen werd vooral beïnvloed door lange termijn (jaarlijkse) variabiliteit. De dynamische, korte termijn relaties tussen slibgehalte, watergehalte, fucoxanthine en macrobenthosdensiteit resulteren in een seizoenale cyclus van slibafzetting en erosie. Deze processen beïnvloeden de sedimentstabiliteit rechtstreeks. De aanwezigheid en densiteit van macrobenthos was de belangrijkste parameter voor de bepaling van sedimentstabiliteit. Op langere termijn werd een verschuiving waargenomen van een situatie met hoge fucoxanthine/chl*a* concentratie, hoog slibgehalte en geen tot lage densiteiten aan *Corophium,* naar een situatie met lage fucoxanthine/chl*a* en moddergehalte en hoge *Corophium* densiteiten. Dit leidde tot een overgang van netto accretie tot netto erosie. Nochtans bleken de meeste van deze variabelen slechte voorspellers voor lange termijn veranderingen in sedimenthoogte. Dit wijst erop dat externe fysische krachten, zoals golven en stormen, waarschijnlijk de belangrijkste factoren zijn die de sedimentdynamiek op lange termijn bepalen. Toch werd aangenomen dat de biota veranderingen in sedimenthoogte onrechtstreeks beïnvloeden doordat ze een rechtstreekse invloed uitoefenen op de sedimentstabiliteit op korte termijn en daardoor de erosiegevoeligheid van het sediment veranderen. De resultaten suggereren zelfs dat het macrobenthos, en dan vooral de slijkgarnaal *Corophium*, indirect de drijvende destabiliserende factor was in de staalnamepunten (hoog intertidaal) in de IJzermonding op de lange termijn.

Tenslotte werden in **hoofdstuk 7** de resultaten van deze thesis bediscussieerd en werden enkele mogelijke gevolgen voor de morfologie van slikken besproken. Verder werden ook nog enkele beschouwingen omtrent plaats-specifieke kenmerken (vb. de aard van het sediment, voedingswijze, overstromingstijd) gegeven. Zowel de experimentele data als de velddata van deze thesis bevestigden de significant negatieve impact van *Corophium* op slibgehalte, diatomeeën biofilm en sedimentstabiliteit. Dit alles wijst erop dat de sedimentologische toestand verschuift van een systeem gedomineerd door slib naar een systeem gedomineerd door slibbig zand in de aanwezigheid van *Corophium*. Densiteit bleek een belangrijke bepalende factor voor het plaatsvinden van de veranderingen in het slikkenecosysteem, want bij lage densiteiten was de impact klein. Daarom werd aangenomen dat, indien aanwezig in voldoende hoge densiteiten, *Corophium* een kritische drempel kan zijn die het slikkensysteem (of toch op zijn minst de lokale, door *Corophium* bewoonde plekjes in dit systeem) doet overhellen naar een stabiele toestand met een lager slibgehalte en lagere aantallen diatomeëen (*sensu* van de Koppel *et al.*, 2001) door de positieve diatomeëen-slib interactie te doorbreken. Op basis daarvan kan gesteld worden dat, indien *Corophium* inderdaad deze omstandigheden met laag slibgehalte, lage diatomeeëndensiteiten en verhoogde erosiviteit promoot, dit indirect een zeewaartse uitbreiding van het schor kan tegengaan. Op deze manier draagt de slijkgarnaal bij tot een geleidelijke overgang van het laag intertidaal naar de schorre. Dit zou de demping van de golfkracht ten goede kunnen komen en dit is op zich een belangrijke veronderstelling in het licht van ons veranderend klimaat. Verder werd ook gesteld dat *Corophium* mogelijks een belanrijke pionier soort zou kunnen zijn in het herstel van slikken waarbij ze de levensomstandigheden voor latere kolonisatoren verbeteren.

Tot slot, *Corophium volutator* is een belangrijke ecosysteemingenieur die zijn biofysische omgeving vorm geeft door veranderingen in sedimentsamenstelling, watergehalte, biofilmproductiviteit en sediment stabiliteit te veroorzaken. Daardoor verbetert hij zijn eigen leefomgeving bovenaan in de intergetijdenzone en beïnvloedt hij andere soorten. *Corophium* speelt daarnaast ook een belangrijke rol in het mengen van sediment, wat gevolgen heeft voor neerwaarts transport van organisch materiaal en dus de decompositie en mineralisatie processen bevordert. *Corophium* kan dan ook beschouwd worden als een essentiële schakel in het functioneren van het slikkenecosysteem. Dit alles impliceert ook dat het verdwijnen of de achteruitgang van *Corophium* grote gevolgen zou kunnen hebben voor de slikken, waar deze gravende vlokreeftjes welig tieren en tegelijkertijd hun abiotische en biotische omgeving vorm geven.

SUMMARY

Estuarine mudflats are sedimentary intertidal habitats created by sediment deposition in low energy coastal environments. They provide essential ecosystem services (e.g. natural coastal sea defense) and functions (e.g. high productivity, feeding and resting area for birds, nursery ground for flatfish). Sediment transport within estuarine intertidal mudflats is dominated by physical processes (mainly tidal currents and waves), which are relatively well studied, and which determine the magnitude of sediment transport. It became however, increasingly clear that small-scale biological processes can also exert significant influences on sediment transport, hence influencing the large-scale geomorphology of intertidal habitats. The influence of biota on topography and landscapes is, however, still largely unexplored. Sediment transport models that explicitly include biotic effects are needed to explore how intrinsically small-scale biotic processes can influence the form of entire landscapes. However, to include biotic effects into sediment transport models, these small-scale biotic processes need to be understood. Biota can either hamper or enhance erosion, resulting in respectively bed stabilisation or destabilisation. Diatom biofilms secrete mucus and form a protective shield, which enhances stability. Macrobenthos, on the other hand, can influence the sediment and its dynamics in several ways (bioirrigation, bioturbation, mucus secretion, the alteration of bottom roughness, …) and due to their highly diversified life styles, they can either stabilise or destabilise the sediment. Therefore, case studies on macrobenthos-sediment interactions are useful and necessary to provide in depth information on how macrobenthos may influence small-scale biotic processes.

Corophium volutator (Pallas, 1766) (Crustacea, Amphipoda), also known as the mud shrimp, lives in U-shaped burrows and is an abundant species in mudflats on both sides of the North Atlantic, along the coasts of North America and Europe. It exhibits a wide variety of context-based behaviours, it has the potential to modify the benthic physical environment and contrasting results on sediment stability have been observed. Hence, *Corophium* is an interesting exemplary species to study in detail organism-sediment interactions. The study of the behaviour of *Corophium* within intertidal mudflats and its

influence on sediment properties and sediment dynamics is therefore of great relevance and forms the main objective of this PhD thesis. Since bioturbation is one of the major processes through which organisms influence their biophysical environment, bioturbation by *Corophium volutator*, the different factors influencing its bioturbation and the resulting effects on sediment erodability were studied in depth.

In **Chapter 2**, a behavioural study was performed to discern the different surface and subsurface activities that contribute to the bioturbation by *Corophium* during the tidal cycle. The behaviour of *Corophium* was observed in the laboratory in a tide-simulated aquarium, and time allocation of the different activities was quantified. Nine different activities were observed, of which'flushing' of the burrow during submersion had not previously been described. This activity potentially has an important effect on the bioturbation process. Overall, the surface activity was low (max. 3.7%) and showed a steep decline after submersion to 0.1%. The subsurface activity was dominated by ventilating and feeding (time allocation of 44%) and by inactivity (time allocation of 51%). A clear tide-based cyclic pattern was found, with a boost of activity immediately after submersion, continuing during submersion, and shifting over a period with decreasing activity towards almost total inactivity at the end of emersion. Only scraping of the surface (i.e. deposit feeding) continued during the entire tidal cycle with a time allocation of ± 1.5%. From this study, we could deduce that the bioturbation potential of *Corophium* is highest during submersion and the first hours afterwards. Bioturbation rates of a tide-subjected *Corophium* population were indeed low compared to other studies (**Chapter 3**). This suggested an influence of the tidal rhythmicity in the behavioural activity of *Corophium* on the bioturbation rate. Additionally, the study described in chapter 3 aimed to investigate the density dependence of bioturbation, the importance of biological activity and its differential effect on two sediment size fractions. Results from a laboratory study indicated that the behavioural activities of *Corophium* are of the utmost importance in sediment reworking, since they contributed to a five-fold increase in bioturbation rate compared to the passive transport induced by the static structure of the burrows. Density proved to be an important parameter because only high densities played a prominent role in particle transport (1.1 cm^2/yr), while the role of low *Corophium* densities was limited (0.3 cm^2/yr). No evidence for differentiation in sediment size fractions was observed.

The impact of this bioturbation on physical sediment properties was investigated in **Chapter 4,** together with the ability to detect the bioturbation impact by using remote sensing. Results obtained with conventional destructive techniques showed a significant increase of water content (2-3%) and a significant, but small decrease of clay content (0.3%) in the presence of *Corophium*. Through measuring the spectral reflectance of the sediment surface, the impact of *Corophium* on water content was detected as an increase in absorption at 1450 nm. However, the animals impact on clay content was too small to be detected via spectral reflectance. This study demonstrated that spectral reflectance data are sensitive for bioturbation activities and that remote sensing can thus be applied in the laboratory to address the impact of bioturbation on sediment properties. This opens new perspectives for long term experiments concerning the role of bioturbation on sedimentary processes.

The consequence of bioturbation at different densities of *Corophium* on sediment bed erodability was evaluated in a flume study in **Chapter 5.** Sediment bed erodability was expressed in terms of suspension erosion rate, critical flow velocity and critical shear stress. A significant increase in suspension erosion rate with density was found, where sediment containing 20,000 mud shrimps per m^2 showed a five times higher erosion rate than sediment without *Corophium*. On the other hand, critical shear stress was found to be independent of *Corophium* density, at least for densities up to 15,000 ind./m^2. At 20,000 ind./m^2, a large decrease (-30%) in critical shear stress was measured. A comparison between critical flow velocities obtained in this experiment and hydrodynamically simulated flow velocities over the mudflat where *Corophium* was collected, indicated that bed erosion is unlikely to happen under natural flow conditions, but it might occur under storm conditions. This assumption was supported by field data collected in the IJzermonding tidal flat during three consecutive years (July 2005-June 2008), as described in **Chapter 6**. This field survey showed that sediment stability varied on a short (seasonal) timescale and was directly influenced by biota, while bed morphology was mainly influenced by long-term (interannual) variability. The short-term dynamic relationships between mud content, water content, fucoxanthin and macrobenthos density resulted in a seasonal mud deposition and erosion cycle, and directly influenced sediment stability. Macrobenthos proved to be the most important parameter determining sediment stability. On the longer term, a shift was observed from high fucoxanthin/chl*a* concentration, high mud content and zero to moderate densities of *Corophium* towards low fucoxanthin/chl*a* and mud content and high *Corophium* densities, which resulted in a transition from net accretion to net erosion. However, most variables proved to be poor predictors for these long-term bed level changes, indicating that external physical forces, such as waves and storminess, probably were the most important factors triggering longer-term sediment dynamics. Nevertheless, biota indirectly influenced bed level changes by mediating short-term changes in sediment stability, thereby influencing the erodability of the sediment. The macrobenthos, and especially the mud shrimp *Corophium*, was suggested as the (indirect) driving destabilising factor for the sampling plots in the IJzermonding when considering the long-term evolution.

Finally, **Chapter 7** contains the discussion on the thesis results and a description of implications for mudflat morphology. Furthermore, some considerations on site-specific features (e.g. nature of the sediment, feeding mode, inundation time) were discussed. Both the experimental and field data from this thesis confirmed the significant negative impact of the presence and activity of *Corophium* on mud content, diatom biofilm and sediment stability, which suggests that the sedimentary system shifts from a mud dominated system to a muddy sand system in the presence of *Corophium*. Since impacts at low densities were small, density appeared to be an important parameter triggering the changes in the tidal flat ecosystem. This lead to the suggestion that *Corophium* at sufficiently high densities might act as a critical threshold to direct the tidal flat system (or at least *Corophium* patches in this system) towards the stable state with low mud content and low diatom cover (*sensu* van de Koppel *et al.*, 2001) by disrupting the positive diatom-silt interactions. Based on the gathered information, it can be postulated that, by favouring this low mud, low diatom and more erosive conditions, *Corophium* can indirectly counteract seaward salt marsh expansion. As such, it contributes to a gradual transition between the low intertidal and the salt marsh. This might enhance dissipation of wave energy, which could be important in view of climate change. Furthermore, it was argued that *Corophium* could possibly be an important pioneer species in recovery of mudflats, as such improving the conditions for later colonisers.

In conclusion, *Corophium volutator* is an important ecosystem engineer that modifies its biophysical environment through changes in sediment composition, water content, biofilm productivity and sediment stability. Hereby, it improves its own survival in the high intertidal and affects other species. Furthermore, *Corophium* plays an important role in sediment mixing, which has implications for downward particle and organic matter transport, and thus for decomposition and mineralisation processes in the sediment. *Corophium* can thus be considered a vital link in the functioning of the tidal flat ecosystem. Hence, the disappearance or density declines of *Corophium* could have huge consequences for tidal flat ecosystems in which these burying amphipods thrive, and shape their abiotic and biotic environment.

CHAPTER 1

GENERAL INTRODUCTION

CHAPTER 1

GENERAL INTRODUCTION

1. RATIONALE

Mudflats provide essential ecosystem services and functions, and therefore contribute to human well-being and consequently, are of high ecological and economic value (Costanza *et al.*, 1997; Diaz *et al.*, 2006). They are highly productive ecosystems, that support a high biomass (McLusky and Elliot, 2004). Mudflats are very important habitats for birds and fish, providing feeding and resting areas for waders and waterfowl (Dyer *et al.*, 2000), and acting as nursery areas for flatfish and crustaceans (Dyer *et al.*, 2000; Beck *et al.*, 2001; McLusky and Elliot, 2004). Furthermore, they provide a natural coastal defense against storm surges (Cooper, 2005; Wolters, 2005). Nevertheless, estuarine mudflats are under increasing threat of climatic (e.g. sea level rise, increased wave action) and anthropogenic (e.g. habitat defragmentation, tourism, pollution, eutrophication,…) pressures (Worm *et al.*, 2006; Wolanski, 2007; Halpern *et al.*, 2008).

Estuarine mudflats are sedimentary intertidal habitats created by sediment deposition in low energy coastal environments. The sediments of mudflats consist of mixtures of sand and mud (van Ledden *et al.*, 2004; Winterwerp and van Kesteren, 2004). Mud is composed of clay and silt particles, which interact due to their electrically charged nature, resulting in the cohesiveness of the sediment (Paterson and Black, 1999). Cohesive sediments do not behave as separate entities like sand particles, but they form aggregates or flocs due to strong physico-chemical effects arising from surface ionic charges (Berlamont *et al.*, 1993). Sediment transport within estuarine intertidal mudflats is dominated by physical processes which are relatively well studied, and which are mainly driven by tidal currents during calm, depositional periods (Postma, 1961; Bell *et al.*, 1997; Ralston and Stacey, 2007) and by wind generated waves during stormy, erosional periods (de Jonge and van Beusekom, 1995; Bell *et al.*, 1997, Ralston and Stacey, 2007). These physical processes determine the magnitude of sediment transport to or from the mudflat (de Brouwer *et al.*, 2000). It became however, increasingly clear that small-scale biological processes can also exert significant influences on sediment transport (de Brouwer *et al.*, 2000; Widdows *et al.*, 2000a; Le Hir *et al.*, 2007; Montserrat *et al.*, 2008), hence influencing the large-scale geomorphology of intertidal habitats (Murray *et al.*, 2002). Biota can modify hydrodynamics, and in turn erosion and resuspension, by influencing microtopography via pellet production, track formation and different types of constructions such as mounds and pits (Herman *et al.*, 1999; Friedrichs *et al.*, 2000). Furthermore, biota can also actively resuspend sediment and increase turbidity of the water column (e.g. deposit feeding macrobenthos eject faeces or pseudofaeces in the water column), conversely biota can induce sediment deposition hereby decreasing turbidity (e.g. diatom films increase adhesion of sediments by mucus production or filter feeders capture food particles from the water column) (Graf and Rosenberg, 1997). The influence of biotic processes on topography is now an active field of investigation, and many studies stress the potential impact of small-scale interactions on the larger scale of landscapes (Dietrich and Perron, 2006). Yet, for most landscapes the importance of the biological imprint compared with the purely physical processes remains largely unknown (Meysman *et al.*, 2006). The particular role of burrowing organisms, but also other biotic influences remains difficult to quantify owing to the complexity of organism-sediment interactions at the microscale and the difficulty of extrapolating to a larger scale (Meysman *et al.*, 2006).

Macrobenthos (i.e. bottom fauna retained on a 0.5 or 1 mm mesh sized sieve) is an important and highly abundant group in estuarine ecosystems. Densities in the order of 10^4 ind./m^2 are typically found in estuaries (Heip *et al.*, 1995). Macrobenthic species change nutrient fluxes and improve thereby conditions for primary production (Emmerson *et al.*, 2001; Lohrer *et al.*, 2004), alter sediment transport processes considerably (Solan *et al.*, 2008), stimulate mineralisation (Mermillod-Blondin *et al.*, 2004), and are an essential component within the estuarine food web, consuming a significant part of the primary production by deposit and suspension feeding (Herman *et al.*, 2000; Van Oevelen *et al.*, 2006), and acting as a food source for epibenthic crustaceans, fish and birds (Daborn *et al.*, 1993; Hampel *et al.*, 2005). Macrobenthic bioturbation (i.e. sediment reworking by burrowing animals) and bio-irrigation (i.e. enhanced solute transport that results from bioturbation and burrow flushing) can thus strongly modify the benthic physical environment, i.e. ecosystem engineering (Jones *et al.*, 1994). Ecosystem engineering is now recognised as a critical process in most ecosystems (Wright and Jones, 2006), and it may strongly affect other organisms and ecosystem functioning (Lohrer *et al.* 2004; Meysman *et al.*, 2006). Ecosystem engineers tend to be most dominant in stressful habitats (e.g. tidal mudflats; Jones *et al.*, 1997). Typically, ecosystem engineers exert a strong influence on ecosystem properties, that exceeds what may be expected based on their abundance alone (Hooper *et al.*, 2005). Autogenic engineers change the environment via their own physical structures (Jones *et al.* 1994), for instance reef-building filter feeders affect local hydrodynamics and particle trapping by their epibenthic structure (Rabaut *et al.*, 2007; Montserrat *et al.*, 2008). Allogenic engineers, on the other hand, change the environment by transforming living or non-living material from one physical state to the other (Jones *et al.*, 1994), for instance bioturbation by the lugworm *Arenicola marina* and the cockle *Cerastoderma edule* changed sediment properties, sediment stability and resource flows (Volkenborn *et al.*, 2007; Montserrat *et al.*, 2009). However, the enormous diversity of macrobenthos, each with species-specific traits, ensures that the interpretation of ecosystem engineering effects is not straightforward, and even for single species opposite effects can exist (Le Hir *et al.*, 2007). Therefore, case studies on organism-sediment interactions are necessary to provide basic material that can be integrated in the broad ecosystem engineering concept (Wright and Jones, 2006). *Corophium volutator* is one of these macrobenthic species for which opposite phenomena are described. In addition, it is an abundant species in many mudflats along the North Atlantic, it exhibits a wide variety of context-based behaviours, and it has the potential to modify the benthic physical environment. Hence, *Corophium* is an interesting exemplary species to study in detail organism-sediment interactions. The study of the behaviour of *Corophium* within intertidal mudflats and its influence on sediment properties and sediment dynamics is therefore of great relevance and forms the basis of the case study in this PhD thesis.

2. THE MUD SHRIMP *COROPHIUM VOLUTATOR*

2.1. Biology and ecology

Corophium volutator (Pallas, 1766) (Crustacea, Amphipoda), also known as the mud shrimp (Fig. 1), is an abundant species present on both sides of the North Atlantic, along the coasts of North America and Europe, from Norway, to the Mediteranean and in the Baltic and the Black Sea (Lincoln, 1979). The wide distribution of *C. volutator* can be explained by its high tolerance to a wide variety of environmental conditions. It occurs over a wide range of inundation times from mean high water neap-tide level, even extending sometimes into the subtidal (Linke, 1939; Schmidt, 1951), in both mud and muddy-sand bottoms (Peer *et al.*, 1986) and at salinities ranging from 4 to 35 psu (McLusky, 1970). It generally occurs in the intertidal zone, where the upper limits are set by a minimal duration of immersion (+/- 10% of the time) (Beukema and Flach, 1995). The highest densities generally occur in the upper part of the tidal flat, as the lower distribution limits are determined by interspecific interactions, e.g. in the Wadden Sea bioturbation activities by the lugworm *Arenicola marina* or the cockle *Cerastoderma edule* negatively affected the occurrence of *Corophium* in the lower intertidal zone (Beukema and Flach, 1995). Patchy distribution in the field on scales of meters can also be related to biotic interactions e.g. competition between *Corophium* and other bioturbating tidal flat species (e.g. *Nereis diversicolor*, Olafsson and Persson, 1986; *Arenicola marina*, Flach, 1996; *Ilyanassa obsoleta*, Drolet *et al.*, 2009) or to differential emigration (Drolet and Barbeau, 2008). The distribution of *Corophium* in the field further shows a high degree of small-scale patchiness on the cm scale. This is caused by active aggregation or created and maintained by interactions between *Corophium* individuals, as juveniles establish near the maternal burrow in summer and these aggregations are maintained over winter (Lawrie *et al.*, 2000). There is no dispersive larval phase in the development. Development is direct in the brood pouch of the female (Fish and Mills, 1979). The life-cycle is based on one or two reproductive episodes per year, depending on the temperature (Wilson and Parker, 1996), and adults live for approximately one year (Fish and Mills, 1979). Post-settlement dispersal occurs by swimming (Hughes, 1988; Lawrie and Raffaelli, 1998b; Ford and Paterson, 2001). *Corophium* swims upward for periods of 5–10 s, often reaching the surface, before sinking to the sediment where burrowing behaviour begins (Meadows and Reid, 1966). This process may be repeated until a suitable site for colonisation is found.

Populations can easily reach densities of 10,000 ind./m^2 and locally, in summer months, densities can increase to 140,000 ind./m^2 (Gerdol and Hughes, 1994a). These high population densities make *Corophium* a major prey item for a number of migratory shorebirds on both sides of the Atlantic (Wilson and Parker, 1996 and references therein). For instance Semipalmated Sandpipers (*Calidris pusilla*) feed extensively on *Corophium* in the upper Bay of Fundy (Canada) during migration (Daborn *et al.*, 1993; Hamilton *et al.*, 2006), while Dunlins (*Calidris alpina*) are important predators of *Corophium* in the Wadden Sea (Damsgaard *et al.*, 2005). Furthermore, *Corophium* is also important in the diet of a number of fish like sea bass (*Dicentrarchus labrax*) and flounder (*Platichthys flesus*) (Hampel *et al.*, 2005) and invertebrates, mainly polychaetes such as *Hediste diversicolor* (Wilson and Parker, 1996).

Figure 1: Picture of *Corophium volutator*. Photographed by SEM, (www.mta.ca/dmf/coroph.jpg, J.M. Ehrman, Digital Microscopy Facility, Mount Allison University)

Corophium lives in U-shaped burrows (Meadows and Reid, 1966 and references therein), mainly in the upper 5 cm of the sediment (Flach, 1996). Burrow walls are strengthened with mucus secretions (Meadows *et al.*, 1990) and burrow openings can protrude 1 to 1.5 mm above the sediment surface, especially in fine mud (Meadows and Reid, 1966). When the openings protrude, mud is not drawn in with the respiratory current, which is created by the beating of the pleopods, and which also serves as a route for the expulsion of faeces and unwanted debris (Meadows and Reid, 1966). Møller and Riisgård (2006) and Riisgård and Schotge (2007) observed that *Corophium* can switch between two feeding modes. At low phytoplankton concentration (0.5 - 5 μg/l), surface deposit feeding is the main feeding mode, and then particles are predominantly gathered by scraping the sediment surface with its enlarged second antennae (Meadows and Reid, 1966). However, filter feeding can become the main feeding mode, when phytoplankton concentrations are sufficiently high. At that time, *C. volutator* extends its body along the burrow wall and pumps large amounts of water through a filter basket formed by the finely plumose setae of the second gnathopods (Miller, 1984; Møller and Riisgård, 2006, Riisgård and Schotge, 2007).

2.2. Biophysical interactions

Burrowing, feeding and ventilation, all contribute to the effect that *Corophium volutator* has on its biogeophysical environment. *Corophium* is considered an important contributor to the physical sediment structure, when present in high densities (Grant and Daborn, 1994). Density appeared also an important factor in the release of nutrients to the overlying water column due to bioturbation activities (Emmerson *et al.*, 2001). Moreover, Mermillod-Blondin *et al.* (2004) measured a significant effect of *Corophium* on chemical fluxes, microbial activity and sediment reworking, indicating that bioturbation and bioirrigation of *C. volutator* affect its surrounding habitat. However, its bioturbation effect on sediment properties and its effect on sediment stability, are contradictory (Le Hir *et al.*, 2007). For instance, both negative (Meadows and Tait, 1989), positive (Gerdol and Hughes, 1994a) and neutral effects (Grant and Daborn, 1994; Limia and Raffaelli, 1997; de Deckere *et al.*, 2000) on sediment water content have been observed. Similarly, no effect on sediment grain size distribution was observed by Limia and Raffaelli (1997) and de Deckere *et al.* (2003), while Mouritsen *et al.* (1998) observed a decrease in silt content due to the disappearance of *Corophium*. Furthermore, sediment stabilising effects (Mouritsen *et al.*, 1998; Meadows *et al.*, 1990) as well as destabilising effects (Grant and Daborn, 1994; Gerdol and Hughes, 1994a; de Deckere *et al.*, 2000) have been described. Table 1 gives an overview of the different studies measuring the effect of *Corophium* on sediment stability. This table summarises the main findings and shows that in these different studies both stabilising and destabilising effects were measured over a whole range of estuaries. By building its burrow, *Corophium* compacts the surrounding sediment and glues the sediment particles to the wall with a mucus secretion (Meadows *et al.*, 1990). This reduces the erodability of the sediment (Grant and Daborn, 1994) and may result in an elevation of the sea bed (Mouritsen *et al.*, 1998), and in an increased resistance to shear stress (Meadows and Tait, 1989). On the other hand, shear stress resistance may also decrease through indirect resuspension of sediment particles by grazing on the stabilising biofilm organisms (Gerdol and Hughes, 1994b; Grant and Daborn, 1994; Hagerthey *et al.*, 2002), and directly through resuspension of fine sediment due to feeding and burrowing (de Deckere *et al.*, 2000; Biles *et al.*, 2002).

Table 1: Summary of studies measuring the effects of *Corophium volutator* (*Cv*) on sediment stability. The sediment type is often briefly described and description of the hydrodynamics is mostly missing.

Effect	Reference	Location	Type of study	Sediment type	Main findings
Stabilising	Meadows and Tait, 1989	Firth of Clyde, Scotland	Lab experiments with different densities	muddy sand	Water content and permeability decreased, shear strength increased with *Cv* density
	Meadows *et al.*, 1990	Firth of Clyde, Scotland	Lab experiments	quartz sand and natural sediment (g.s.?)	1) mucus secretions bind quartz particles in mesh network; 2) *Cv* increased shear strength with 50% in natural sediment
	Grant and Daborn, 1994	Bay of Fundy, Canada, Starrs Point tidal flat	Flume experiment	silty-sand	juvenile *Cv* decrease erosion rate due to binding of sediment into burrows; adult *Cv* no effect on erosion rate and erosion threshold;
	Mouritsen *et al.*, 1998	Danish Wadden Sea, Høyer tidal flat, wave-exposed tidal flat	Field observation	median g.s. ± 100-110 µm, 10% mud, non-cohesive sediment	heterogeneous tidal flat with plateaus (+ *Cv*) and pools (- *Cv*), disappearance of *Cv* from the plateaus caused erosion, decrease in silt content and increase in median grain size, resulting in a homogeneous tidal flat
Destabilising	Gerdol and Hughes, 1994a	Southeastern England (Crouch and Blackwater)	In-situ experiment, insecticide to remove *Cv*	not mentioned	*Cv* reduced biofilm by grazing and increased water content => reduced shear strength. Sediment accreted on the sprayed patches (-*Cv*)
	Daborn *et al.*, 1993	Bay of Fundy, Canada, Starrs Point tidal flat	Field observation and in-situ experiment with formaldehyde spraying	silty-sand, < 20% clay	1) sprayed patches had higher chl*a* and critical shear stress because EPS secretion of diatoms increased cohesion, while *Cv* decreased cohesion by grazing; 2) predation by birds caused a decline of *Cv* of > 50% and a change in crawling behaviour, which increased diatom production and increased cohesive strength
	de Deckere *et al.*, 2000	Westerschelde, the Netherlands	Flume and aquaria experiments in lab with biofilm	median g.s. 120 µm	1) increase of suspended solids with *Cv* density, at low flow velocities (< 20 cm/s) active resuspension more important than physical; 2) no effect on porosity or EPS, negative correlation with chl*a*; 3) negative correlation between critical flow velocity and *Cv*
	de Deckere *et al.*, 2003	Westerschelde, the Netherlands	Flume experiment	40-45 µm in top half cm	Increase of erosion rate due to increase in bottom roughness and scour around burrows

The increased sediment suspension appeared to have a further negative effect on microphytobenthic biomass because of a reduction in photosynthesis due to attenuating light at the sediment surface caused by an increased turbidity (Dyson *et al.*, 2007). Furthermore, de Deckere *et al.* (2003) observed that the presence of protruding burrows increased the erosion rate by increasing the roughness of the sediment surface. These contrasting results could possibly be attributed to the complex and dynamic relationships between all these factors, masking the direct effect of *Corophium* on its physical environment, and resulting in erosion or accretion depending on the dominant relationships. Therefore, this thesis attempts to unravel the existing duality and to determine the importance of *Corophium* in tidal flat sediment dynamics. This was mainly done by examining the bioturbation process of *Corophium* and its effect on sediment properities in depth in mesocosm experiments. Mesocoms are controlled artificial systems, but they provide a mechanistic understanding of ecological processes, and they allow for the development of theories that are of fundamental importance to inform global ecological issues (Benton *et al.*, 2007). The main relationships studied in this thesis are indicated in figure 3 with dashed arrows.

3. STUDY AREA

All studies performed in this thesis took place in, or were exerted with sediment and animals collected from the IJzermonding Nature Reserve in Nieuwpoort, Belgium (51°08'N, 2°44'E) (Fig. 2). The IJzer is a river of 76 km long, originating in the North of France and flowing into the North Sea in the West of Belgium, in the proximity of the town of Nieuwpoort. The western bank of the IJzer river mouth was already consolidated since medieval times, and during the 20th century the western bank got completely urbanised by the development of the seaside resort Nieuwpoort-Bad (Deboeuf and Herrier, 2002). The eastern bank was still pristine and consisted of a sandy beach, mudflats, salt marshes and dunes. However, in the years 1950-1970, a military base was established on the eastern bank of the estuary leading to the construction of quay walls and docks, and the remaining salt marshes and dunes were covered up with 300,000 m^3 of dredge sludge, drastically reducing the intertidal surface area (Deboeuf and Herrier, 2002; Herrier *et al.*, 2005). In 1993, the military base was relocated and the area was declared a protected dune site by the Flemish Government.

Therefore, a nature restoration plan was established and in 1996, the 'Nature Restoration Plan for the IJzer river mouth' was finalised with the general aim to restore or create beach-dune-salt marsh ecotones (Herrier *et al.*, 2005; Hoffmann *et al.*, 2005). In order to reach this goal, several large buildings and roads were broken down, an entire dock was restructured and some 500,000 m^3 of dredge material was removed to restore or create intertidal and coastal dune habitats and their connecting ecotones. These activities took place between September 1999 and March 2004 (Herrier *et al.*, 2005; Hoffmann *et al.*, 2005). Today, the nature reserve consists of 130 ha of mudflat, salt marsh, sandy beach and coastal dune. Since the restoration works, the estuary-dune ecotone has been restored, showing continuous natural gradients of e.g. fresh-salt water, wet–dry areas, mud-sand habitats, however the estuary has not reached full recovery yet (Hoffmann *et al.*, 2005).

Figure 2: Aerial picture of the nature reserve Ijzermonding on the eastern bank of the Ijzer. Image acquired by the CASI Sensor (May 29, 2009), financed by the Federal Science Policy Office in the framework of the STEREO II program and by the Flemish Ministry of Mobility and Public Works, Coastal Division.

The average tide in the estuary is asymmetric with a mean flood duration of 5h34' and a mean ebb duration of 6h51'. Peaks in velocity during flood are about 0.9 m/s at spring tide and during neap tides velocities do not exceed 0.3 m/s, whereas peaks in ebb tides are about 0.6 m/s. This tidal asymmetry leads to enhancement in resuspension and sediment transport during the flood tide, so-called tidal pumping (Giardino *et al.*, 2009). Muddy suspended sediment constitutes the dominant source of sediment transport in the estuary (Giardino *et al.*, 2009). A morphodynamic model simulated a net overall deposition in the estuary after a spring-neap tidal cycle, which ranged between 0.1 and 0.5 cm on the tidal flat, while deposition in the navigation channel sometimes reached values up to 5-6 cm (Giardino *et al.*, 2009). The sediment over the entire area is characterised by a high variability in sediment distribution even on a small spatial scale. However, three characteristic sediment fractions are found: 1) a fine sand fraction with a median diameter of approximately 200 µm, 2) a clay fraction with a characteristic median diameter of 10 µm, and 3) a silt fraction with a median diameter of 60 µm (Hoffmann *et al.*, 2005).

Prominent macrobenthos species on the mudflat are the mud shrimp *Corophium volutator*, the oligochaetes *Tubifex costatus* and *Tubificoides benedeni*, the polychaetes *Hediste diversicolor*, *Eteone longa*, *Heteromastus filiformis* and *Pygospio elegans* and the bivalve *Macoma balthica* (Wittoeck *et al.*, 2004). In general, lowest densities are observed in the lower part (+1 m MLLWS), highest densities in the middle part (+2.5 m MLLWS), and intermediate densities in the upper part (+4.5 m MLLWS) of the intertidal mudflat. Furthermore, macrobenthos density and species richness are negatively correlated with median grain size, indicating the positive correlation between sediment silt content and macrobenthic fauna (Wittoeck *et al.*, 2004).

4. AIMS AND OUTLINE OF THE THESIS

4.1. Aims

The general objective of this thesis was to study the impact of the mud shrimp, *Corophium volutator*, on its biophysical environment by focusing on its influence on sediment properties and sediment dynamics. This will allow to get insight into small-scale biotic processes and how they might influence sediment dynamics on a larger scale. Since bioturbation is one of the major processes influencing the biophysical environment, bioturbation by *Corophium volutator*, the different factors influencing it and the resulting effects on sediment erodability were studied in depth (Fig. 3). The following research questions were assessed based on the ensuing underlying hypotheses:

- **What is the time allocation of *Corophium volutator* during the tidal cycle?**

Species do not just do one thing, they have different behaviours (locomotion, feeding, burrowing,…), all contributing to bioturbation to some extent. Furthermore, certain behaviours, or the behavioural activity in general, can be context-dependent, e.g. temperature-based (Ouellette et al, 2004), food supply-based (Nogaro *et al.*, 2006) or for intertidal animals it can also be tide-based (Rosa *et al.*, 2007). This knowledge of context-based behaviour can contribute to the interpretation of bioturbation. We hypothesised that *Corophium,* being an intertidal species, would show a tidal rhythmicity in its behavioural pattern. This was tested in the laboratory in a tide-simulated aquarium through observation of surface and subsurface activity.

- **How important is behavioural activity for the bioturbation process?**

Following the study on the behaviour of *Corophium*, quantification of this total tide-based activity was the logical next step. Since *Corophium* is a species living in U-shaped burrows, it was assumed that the physical presence of these burrow structures (without the animals) would also contribute to downward sediment transport (passive bioturbation), in addition to the active bioturbation caused by animal behaviour. To be able to distinguish between active (behaviour-driven) bioturbation and passive (physically-driven) bioturbation, a mesocosm experiment was constructed with 'only burrow' treatments and 'burrow + animal' treatments.

- **What is the importance of density on the bioturbation process?**

Bioturbation is not only influenced by context-based activity, but also population characteristics (e.g. species density, burrowing depth, …) are important in determining the intensity of bioturbation (Duport *et al.*, 2006; Braeckman *et al.*, 2010). Density-dependent effects of *Corophium* on bioturbation rate were not tested previously, and these would allow to estimate the relative importance of low and high *Corophium* densities, and hence the impact of density declines.

- **How does bioturbation by different densities of *Corophium* affect sediment properties?**

As previously mentioned, species bioturbating the sediment surface can strongly alter the benthic physical environment (Jones *et al.*, 1994). Therefore, we hypothesised that *Corophium*, through its bioturbation, can change sediment composition in the surface layers. Higher densities were expected to have a more pronounced impact than low densities. The change in sediment composition could be accompanied with a change in water content, but also the presence of burrows could change water content. These possible changes in the physical environment could cause changes in sediment erodability, which lead us to the next question.

- **What is the impact of *Corophium* on sediment erodability?**

Water content and grain size distribution are important factors influencing sediment erosion (Winterwerp and van Kesteren, 2004). By inducing changes in these factors, we hypothesised that bioturbation could indirectly influence erodability of the sediment. Furthermore, protruding burrows can influence the local hydrodynamics, either enhancing or hampering shear stress (Friederichs *et al.*, 2000), respectively increasing or decreasing the erodability. However, in the field, there are many other factors (e.g. biofilms, other species, currents, …) influencing the erosion and accretion of sediments, and different processes are dominant at different times. We therefore investigated long-term and short-term temporal sediment dynamics and the relative importance of *Corophium* in these processes.

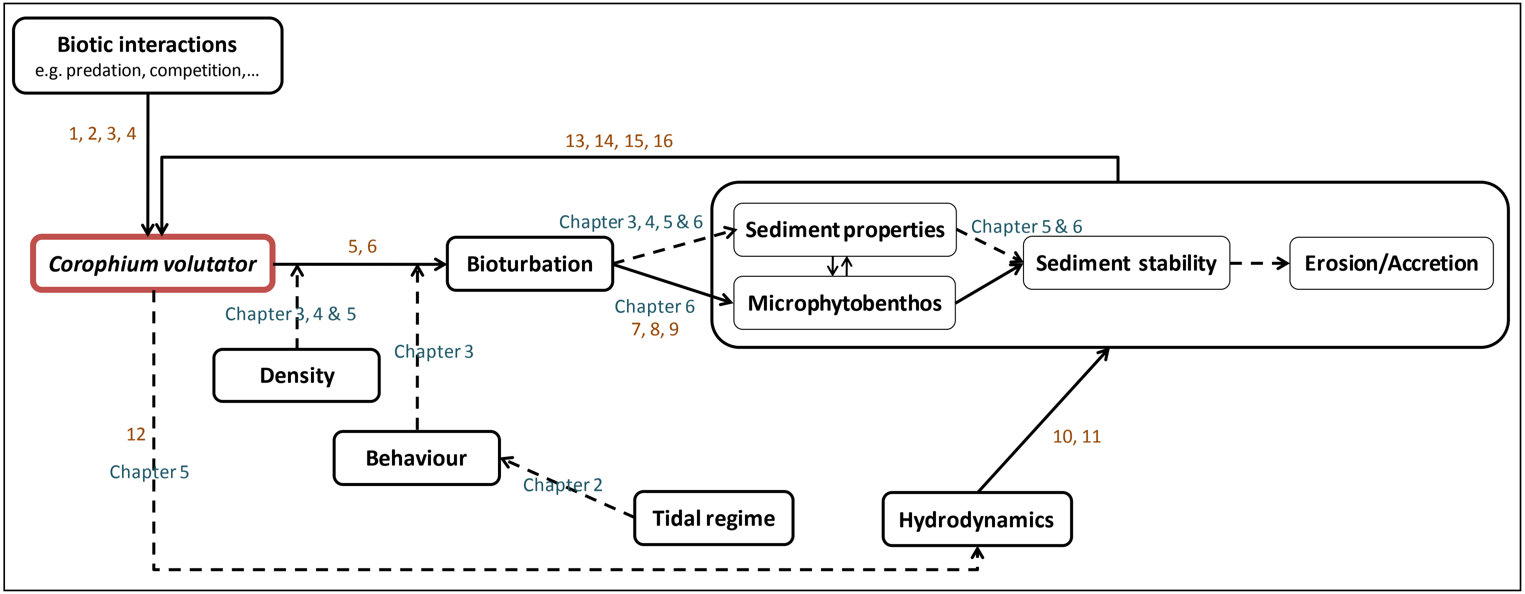

Figure 3: Schematic representation of the different factors that might influence the impact of *Corophium volutator* on sediment stability, and thus possibly erosion and/or accretion of the tidal flat. Dashed arrows indicate research questions investigated in detail during this study with, in blue, the chapters where the question was dealt with. Solid black arrows indicate relationships based on the literature with, in brown, some references where this relationship was investigated. 1: Beukema and Flach, 1995; 2: Wilson and Parker, 1996; 3: Hampel *et al.*, 2005; 4: Drolet *et al.*, 2009; 5: Emmerson *et al.*, 2001; 6: Mermillod-Blondin *et al.*, 2004; 7: Gerdol and Hughes, 1994b; 8: Hagerthey *et al.*, 2002; 9: Dyson *et al.*, 2007; 10: de Brouwer *et al.*, 2000; 11: Ralston and Stacey, 2007; 12: Friedrichs *et al.*, 2000; 13: Meadows, 1964; 14: Flach, 1996; 15: Huxham *et al.*, 2006; 16: Bulling *et al.*, 2008

4.2. Outline

Apart from the general introduction and the general discussion, this thesis is a compilation of research articles (published, currently under revision or submitted). For that reason, the outline and output of the chapters resembles almost exactly the published or submitted papers. Each chapter is therefore intended to be an autonomous part, which can be read separately from the other chapters. Inevitably, there is some overlap between the introductions and material and methods sections of the different chapters. Cited literature is compiled in a single list at the end of the thesis. The candidate is first author of all chapters, except chapter 5. For chapter 5, the candidate provided input for the experimental design, interpretation and processing of the results and the candidate wrote large parts of the text.

The impact on the biophysical environment by *Corophium volutator* is studied by focusing on the bioturbation process in Chapters 2, 3 and 4, while in later chapters the consequences for sediment erodability are studied, both in the laboratory (in cooperation with Hydraulics Laboratory, KULeuven; Chapter 5), and in the field (Chapter 6). In **Chapter 2,** the different surface and subsurface activities that contribute to the bioturbation by *C. volutator*, are investigated, and the time allocation of these activities during the tidal cycle is quantified. This chapter has been published as *De Backer A, Van Ael E, Vincx M and Degraer S (2010) Behaviour and time allocation of the mud shrimp, Corophium volutator, during the tidal cycle: a laboratory study. Helgoland Marine Research 64: 63-67.* **Chapter 3** quantifies the bioturbation rate in a mesocosm experiment where luminophores (fluorescent sand grains) were added to the sediment-water interface. Density-dependence of bioturbation is tested, as well as the selectivity of the bioturbation process on different sediment fractions. Furthermore, the importance of biological activity by *Corophium* against the physical presence of the burrow structures is studied. This chapter is submitted as *De Backer A, Van Coillie F, Montserrat F, Provoost P, Van Colen C, Vincx M and Degraer S. Bioturbation effects of Corophium volutator: importance of density and behavioural activity. Estuarine, Coastal and Shelf Sciences.* The impact of *Corophium* bioturbation on the physical sediment properties, water content and sediment composition is investigated in **Chapter 4**. Moreover, it is tested if remote sensing was a useful tool to detect the bioturbation impact. These results have been published as *De Backer A, Adam S, Monbaliu J, Toorman E, Vincx M and Degraer S (2009) Remote sensing of biologically reworked sediments: a laboratory experiment. Estuaries and Coasts 32(6):1121-1129*.

The consequences of the bioturbation effects on sediment erodability are examined in a flume experiment (**Chapter 5**). Critical current velocities, shear stresses and erosion rates are calculated for a density series of *Corophium*. The results of chapter 5 are being revised as *Adam S, De Backer A, Degraer S, Vincx M and Toorman E. Effect of Corophium volutator on the erodability of cohesive intertidal sediments. Ocean Dynamics Special Issue*.

In **Chapter 6**, mesocosm experiments are put aside and the research is taken to the field. The whole mudflat ecosystem with its short-term and longer-term sediment dynamics is considered and the relative importance of biophysical interactions on sediment dynamics is quantified. Moreover, *Corophium* was highly abundant in the sampling plots, which allowed to determine the role of *Corophium* on longer term sediment dynamics. This chapter has been accepted as *De Backer A, Van Colen C, Vincx M and Degraer S, The role of biophysical interactions within the IJzermonding tidal flat sediment dynamics. Continental Shelf Research*.

In the general discussion (**Chapter 7**), the ecosystem engineering effects of *Corophium volutator* are discussed based on the key issues derived from the different chapters, and possible implications for tidal flat morphology are suggested.

CHAPTER 2

BEHAVIOUR AND TIME ALLOCATION OF THE MUD SHRIMP, *COROPHIUM VOLUTATOR*, DURING THE TIDAL CYCLE: A LABORATORY STUDY

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Modified from:

De Backer A, Van Ael E, Vincx M and Degraer S (2010) Behaviour and time allocation of the mud shrimp, *Corophium volutator*, during the tidal cycle: a laboratory study. Helgoland Marine Research 64: 63-67, DOI 10.1007/s10152-009-0167-6 (Short communication)

CHAPTER 2

BEHAVIOUR AND TIME ALLOCATION OF THE MUD SHRIMP, *COROPHIUM VOLUTATOR*, DURING THE TIDAL CYCLE: A LABORATORY STUDY

ABSTRACT

Despite the numerous ecological and behavioural studies, relatively little is known about the behavioural dynamics of Corophium volutator during the tidal cycle. In the present study, the behaviour of C. volutator was observed in the laboratory in a tide-simulated aquarium, and time allocation of the different activities was quantified. Overall, the surface activity was low and showed a steep decline after submersion. A clear tide-based cyclic pattern was found, with a boost of activity immediately after first submersion, continuing during submersion, and shifting over a period with decreasing activity towards almost total inactivity at the end of emersion.

KEY WORDS: Amphipoda, *Corophium volutator*, behaviour, time allocation

1. INTRODUCTION

Corophium volutator (Crustacea, Amphipoda) is an abundant species in many mudflats worldwide. Population densities frequently reach >20,000 ind./m^2, and in summer months densities can locally exceed 100,000 ind./m^2 (Gerdol and Hughes, 1994a). The high population densities make this amphipod an important species in many mudflat ecosystems, where it is a significant prey for migratory shorebirds and juvenile flounders (Boates *et al.*, 1995). *Corophium volutator* lives in U-shaped burrows in the upper 5 cm of the sediment. It is known to switch between surface deposit feeding and filter feeding depending on the phytoplankton concentration in the water column (Riisgård and Schotge, 2007). However, relatively little is known about the behavioural dynamics of *C. volutator* throughout the tidal cycle. Therefore, this study aims to quantify the time allocation of the amphipod activities during a simulated tidal cycle.

2. MATERIAL AND METHODS

2.1. Experimental setup

To quantify the time allocation of the full spectrum of activities of C. *volutator*, it was necessary to perform both surface and subsurface observations. Since it was, however, impossible to make simultaneous observations of both the surface and subsurface activities of *C. volutator*, a surface and a subsurface survey were performed in parallel. The experimental setup comprised of a main aquarium (L:50 cm x W:10 cm x H:15 cm) used for surface and subsurface (animals against the glass wall) observations and a thin aquarium (L:30 cm x W:3 mm x H:15 cm) for subsurface observations. Both aquaria were placed in a temperature controlled room (15°C) with a 12:12h light:dark regime and submitted to a simulated tidal cycle of about 12h[1,2]. The experimental tidal regime was similar to the natural tidal conditions of the *C. volutator* habitat: 3h of submersion, followed by 9h of emersion.

The sediment and the animals were collected in January 2005 from a mudflat-saltmarsh area in Nieuwpoort (Belgium, 51°08'N, 2°44'E). After defaunation by freezing-thawing, the sediment was allowed to settle in the aquaria for 24h, before the amphipods were added. The test population reflected the natural composition, with a highly skewed sex ratio of one male to six females. In both aquaria, *C. volutator* was introduced at a density of 10,000 ind./m^2 (average field density = 10,762 ind./m^2 ± SE 406)[3]. Observations started three days after incubation of the animals. The test specimens were weekly fed *ad libitum* with benthic diatoms (*Navicula sp.*)[4].

2.2. Observations

Based on preliminary observations, nine behavioural activities were defined (Table 1). The tidal cycle was divided in 12 1-h observation periods (i.e. 3h of observation when submersed and 9h when emersed). Each observation period was replicated five times during the length of the experiment. Observations were done during a 3-week period with a maximum of five observation hours per day and a maximum of two successive observation hours to exclude biases due to fatigue of the observer. This implies that

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[1] The tidal cycle was initiated immediately after incubation of the test population.

[2] Seawater was filtered with a 45 μm sand filter, salinity = 32 psu

[3] Mortality during the experimental period did not exceed 3%.

[4] The diatoms were, together with the culture F2 medium, gently poured on the sediment surface during emersion. It was not a standardised amount, but just what was available after one week culturing.

some animals were possibly observed more than once on consecutive days, especially for subsurface observations where the number of observed animals was limited. Owing to practical constraints, observations were done during daylight.

Table 1: Description of the different activities observed under laboratory conditions. Mainly based on Meadows and Reid (1966)[5].

Activity	Description
Surface activity	
Surface inactivity	No visible forward/backward movement.
Surface crawling	The animal pushes itself forward with telson, uropods, second antennae, and pereopods.
Swimming	Mostly done vertical, and resulting from fast beating of the pleopods.
Scraping	Surface deposit feeding: second antennae are used to scrape surface sediment with microphytobenthos into the burrow.
Flushing (undescribed previously)	The pleopods create a faster water movement to get rid of excess sand grains and faeces from the burrow. Visible on the surface as a dust cloud.
Subsurface activity	
Subsurface inactivity	No visible motion, *Corophium* is completely in rest.
Ventilating and filter feeding	Beating pleopods create water current through the burrow (ventilation) and both gnathopods and mouthparts process the sand grains. Ventilation and feeding do not necessarily occur at the same time.
Subsurface walking	Walking up and down in the burrow.
Bulldozing	Pushing excess sand grains out of the burrow with the pleon.

During each observation period, approximately ten surface active or subsurface individuals were randomly selected for a detailed quantification of their surface or subsurface time allocation over a 5-min period. Their activities were recorded on a dictaphone. During a surface activity survey only surface activities (Table 1) were taken into account and vice versa for subsurface activity surveys. Because subsurface observations were complicated by logistic problems, more surface activity observations were made. The time expenditure for the different activities of each surveyed individual was converted to percentages (i.e. time allocation).

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[5] Short movies of certain behaviours can be found, when clicking on Video sequences or when using this URL: http://picasaweb.google.be/107878000542354590663/CorophiumBehaviour?authkey=Gv1sRgCJP6kuWq8Iu2bg&feat=directlink. Short explanations are provided under the video sequences.

2.3. Integrating surface and subsurface time allocation patterns

Each observation period started and ended with a surface scan to determine the relative abundance of surface active animals[6]. The average of both surface scan measurements allowed to quantify the average importance of surface activity relative to subsurface activity during a given observation period. These values were then used to rescale the observed time allocation of both the surface and subsurface surveys. If, for example, on average 6% of the individuals in the experimental setup were observed to be surface active 1h after flooding and only 4% 1h later, then the time allocation of all surface activities between 1h and 2h after flooding were rescaled to 5%, while the time allocation of all subsurface activities were rescaled to 95%.

2.4. Data analysis[7]

Count data from the surface scan were square-root transformed to achieve homogeneity of variance, and a t-test was performed to test for differences in surface active individuals between submersion and emersion.

All analyses were done using time allocation data. For each individual, the observed activities during the 5-min observation period were transformed to time allocation data, which implies a data dependency between activities within individuals, but not between individuals. The different time allocation data per individual can thus be used as true, independent replicates, observed over the course of the three-week experimental period, and allow the use of a one-way ANOVA. In most cases (except for subsurface inactivity), the data could not be corrected for heteroscedasticity. However, since ANOVA is considered robust to lack of homogeneity of variances when sample sizes are large, as is the case here, untransformed data were analysed (Underwood, 1997). Furthermore, the large sample size allows the statistics to follow a normal distribution (Central Limit Theorem) (Sokal and Rohlf, 1981). Tidal period (three periods demarcated by visual exploration of the data) was used as explanatory variable with the different observed activities as response variables. Significant differences for activities between tidal periods were based on $p < 0.05$. When significant, unequal N Tukey's HSD post-hoc testing was applied.

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[6] Relative abundance was calculated based on the total number of individuals added at the start of the experiment.

[7] This section is expanded compared to the published manuscript.

3. RESULTS

Surface counts of active individuals at the start of each observation period showed that surface activity rapidly decreased after emersion to 0.1% (± SD 0.1%) 3h after emersion. Even during submersion, the total proportion of surface active individuals was low, with maximum of 3.7% (Fig. 1). A significant difference in surface activity was found between submersion and emersion (t-test, t-value= 7.48, df=58, p<0.0001). Some activities were observed frequently but lasted shortly (e.g. scraping, subsurface walk), while others were long-lasting in comparison with the frequency of occurrence (e.g. subsurface inactivity) (Table 2). During the surveys for surface activity, the animals spent ≥ 80% of the time subsurface and especially during emersion often no animals were active on the surface. Over 90% of the subsurface time was spent with ventilating and filter feeding (44%) and being inactive (51%) (Table 2).

Table 2: Frequency of occurrence, total time allocation, and average duration of activities, separated for surface and subsurface observations.

	Activity	Freq. of occurrence (%) (ind. where behaviour observed)	Total time (%)	Average duration ± SD (s)
Surface survey (total n=443)	Invisible	62.5 (n=417)	86.9	276 ± 62
	Surface inactivity	6.4 (n=43)	3.9	119 ± 91
	Surface crawl	10.2 (n=68)	6.6	128 ± 81
	Swim	1.3 (n=9)	0.8	120 ± 141
	Scrape	16.0 (n=107)	1.3	16 ± 15
	Flush	3.4 (n=23)	0.6	22 ± 21
Subsurface survey (total n=152)	Subsurface inactivity	37.4 (n=108)	51.4	217 ± 105
	Ventilate and filter feed	33.6 (n=97)	43.8	206 ± 103
	Subsurface walk	27 (n=78)	4.4	26 ± 25
	Bulldoze	0.1 (n=6)	0.4	34 ± 22

Although variability among the observations of the different individuals was high, clear patterns could be distinguished. Visual exploration of time allocation data allowed to distinguish three periods in the tidal cycle: a period of submersion (0-3h after flooding), emersion A (3-6h after flooding) and emersion B (6-12h after flooding) (Fig. 1). This distinction was confirmed statistically by a one way ANOVA with 'tidal period' as independent variable and the activities as dependent variables[8]. All observed activities, except subsurface walking, differed significantly between the submersion period and

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[8] The full ANOVA table is given in Appendix 1.

both emersion periods. During submersion, the diversity of activities and the overall activity was highest, while consequently the subsurface inactivity was low (4-13%). Swimming, flushing and bulldozing only occurred during submersion (Fig. 1).

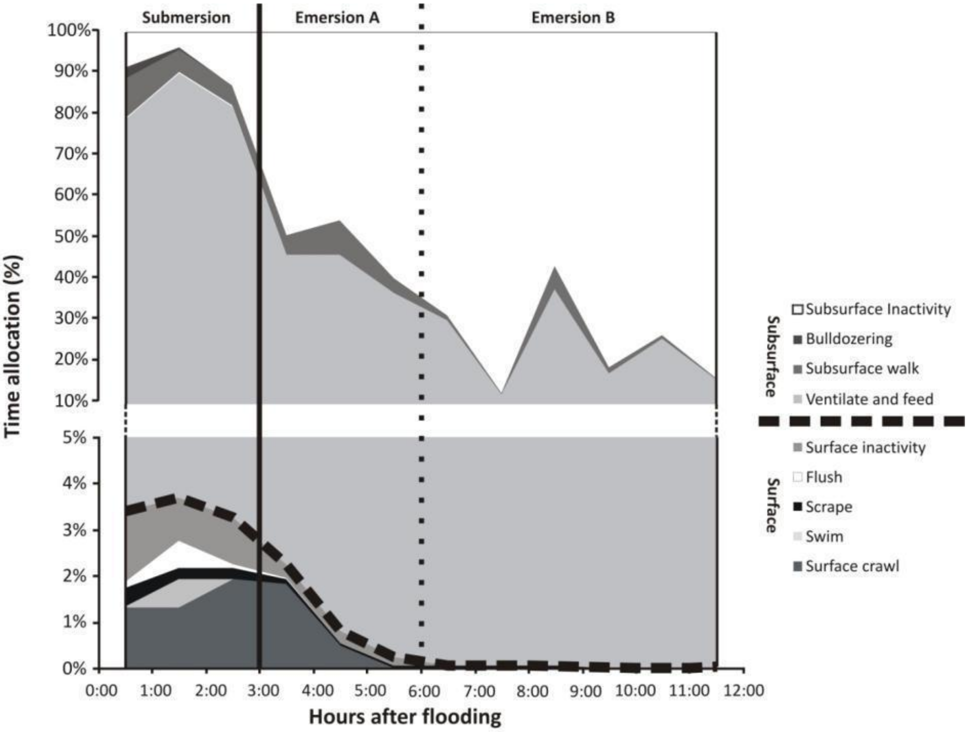

Figure 1[9]**: Behavioural pattern and time allocation of an average *C. volutator* throughout a simulated tidal cycle. The X-axis represents one tidal cycle starting with 3h of submersion followed by 9h of emersion. Time allocation for each activity of the different individuals is averaged per hour and is represented in a 2D surface area graph. The thick dotted line indicates the relative abundance of surface and subsurface active individuals during the tidal cycle (obtained from the surface scans). Beneath the dotted line, surface activities are represented, rescaled towards relative abundance of the surface active individuals. Above the dotted line, subsurface activities are represented, rescaled towards relative abundance of the subsurface active individuals.**

For the majority of activities during emersion (except scraping), significant differences were found between the first 3h of emersion (Emersion A) and the last hours of emersion (Emersion B). Emersion A can be seen as a transition period between submersion and emersion B, in which the activity level dropped and (subsurface)

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[9] Figure legend is expanded compared to the published manuscript.

inactivity showed a steep increase from 13 to 60%. During emersion B, (subsurface) inactivity showed a further increase towards 88%, and only three activities (i.e. scraping, ventilating and feeding and subsurface walking) remained (Fig. 1). Scraping was the only activity that continued at more or less the same frequency during the whole emersion period.

4. DISCUSSION

Surface activity showed a steep decline the first hours after emersion. During a field study, Lawrie and Raffaelli (1998) found similar results and explained this decline by the drying of the sediment. Another plausible explanation is the increasing risk of predation by shorebirds when the tide is receding (Boates *et al.*, 1995). However, the population used in this experiment is not heavily predated under natural conditions (Devos and De Groote, 2006), plus predation was absent in this experiment and *C. volutator* shows flexible surface crawling behaviour in relation to predation risk (Boates *et al.*, 1995). Hence, in this case, the drying of the sediment is the most likely reason for the observed decrease in surface activity[10]. Even during submersion, the number of surface active individuals was very low compared with the one in the sediment and was on average restricted to maximum 3.7% of the population. When animals were active on the surface, crawling was the dominant activity. Surface crawling can increase seasonally, since (large) males crawl around in search of a female (Meadows and Reid, 1966; Lawrie and Raffaelli, 1998). Since the experiment was done in January, no clear observations of reproductive behaviour were seen, but amphipods (both male and female) searching for another burrow during crawling were observed, as described in Meadows and Reid (1966). As reported in other studies, swimming frequency was low and variable patterns were observed in swimming activity, with peaks during periods of submersion (Lawrie and Raffaelli, 1998).

The behaviour of *Corophium* showed a cyclic pattern following the simulated tidal cycle with a boost of activity immediately after flooding, continuing during submersion, and shifting over a period with decreasing activity (emersion A) towards almost total inactivity at the end of emersion (emersion B). Although the length of the different

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[10] Resource depletion could possibly cause a decrease in surface activity but there was no indication in that direction. Microphytobenthos was refilled every week and could grow under the light regime provided. Furthermore, if resource depletion would have caused this decrease in activity, this should have been visible as well during submersion, while we observed clearly a decrease with the tidal rhythm.

activity periods may vary due to seasonal differences (e.g. temperature, light conditions or phytoplankton concentration) or due to different submersion/emersion times depending on the origin of the population, a similar cyclic pattern, in which these three different periods can be distinguished, is to be expected.

It is known that *C. volutator* can switch between feeding modes and that filter feeding is common when phytoplankton concentrations are above a certain trigger level (Riisgård and Schotge, 2007). However, the amount of time spent on different feeding modes is unknown and may greatly vary seasonally and geographically (Riisgård and Schotge, 2007), depending on the degree of down-mixing of phytoplankton, which is controlled by currents and wind mixing (Riisgård *et al.*, 2007). In the present study, the food offered consisted of benthic diatoms, and the used sea water was filtered, so phytoplankton concentrations were probably below the trigger level and surface deposit feeding was the main feeding mode. Nevertheless, filter feeding was observed as well, in co-occurrence with burrow ventilation, but since it was difficult to make a distinction between both with the naked eye, they were described as a single activity. However, because of the lack of phytoplankton, an underestimation of filter feeding during submersion is possible.

We observed that some individuals were deposit feeding at all stages of the tidal cycle, just as Gerdol and Hughes (1994b) concluded from chlorophyll *a* concentrations of the gut content. However, unlike them, we found a relation between stage of the tide and surface deposit feeding (= scraping), with a higher frequency of scraping during submersion.

To conclude, *C. volutator* showed a wide range of activities, which all contribute, to a greater or lesser extent, to bioturbation and bio-irrigation by this species. For these behavioural activities, a tidal pattern was observed with a relatively high rate of activity during submersion and a very high rate of inactivity during emersion.

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CHAPTER 3

BIOTURBATION OF *COROPHIUM VOLUTATOR*: IMPORTANCE OF DENSITY AND BEHAVIOURAL ACTIVITY

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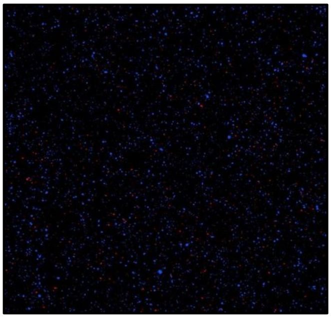
Magda Vincx and Steven Degraer





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CHAPTER 3

BIOTURBATION OF *COROPHIUM VOLUTATOR*: IMPORTANCE OF DENSITY AND BEHAVIOURAL ACTIVITY

ABSTRACT

Bioturbation is one of the major processes influencing ecosystem functioning. Population parameters such as species density, burrow density and species-specific life modes, determine the impact of bioturbation on the ecosystem. A laboratory experiment was developed, using microcosms mimicking a marine intertidal sediment-water interface which allowed for quantification of different population parameters. The vertical redistribution, bioturbation rate and maximum penetration depth of two sizes (41 and 129 µm) of luminophores were measured in five treatments (control, low density of burrows with and without Corophium (1,989 ind./m^2), and high density of burrows with and without Corophium (14,921 ind./m^2)) after 1, 7 and 14 days. Results indicate that the behavioural activities of Corophium are of the utmost importance in sediment reworking, since they contributed to a five-fold increase in bioturbation rate compared to the passive transport induced by the static structure of the burrows. Furthermore, density is an important parameter because only high densities play a prominent role in particle transport and hence in organic matter processing, while the role of low Corophium densities is limited in sediment reworking. No evidence for differentiation in sediment size fractions was observed. Finally, bioturbation rates in this study were low compared to other studies, and these results suggest an influence of the tidal rhythmicity in the behavioural activity of Corophium on the bioturbation rate.

KEY WORDS: behavioural activity, bioturbation, *Corophium volutator*, density, luminophores

1. INTRODUCTION

Bioturbation, i.e. sediment reworking and bioirrigation by benthic fauna is recognised as one of the major processes that influence the structure and function of aquatic sedimentary environments (Lohrer *et al.*, 2004; Meysman *et al.*, 2006). Sediment particle reworking results from various activities (i.e. burrowing, feeding and locomotion), and strongly affects the physical, chemical and biological characteristics of marine sediments (Rhoads, 1974; Aller, 1982; Hall, 1994; Rowden *et al.*, 1998; Solan *et al.*, 2008). Hence, macrobenthos-mediated effects on sediment processes are strongly influenced by species-specific life modes (Mermillod-Blondin *et al.*, 2005; Norling *et al.*, 2007). The intensity of sediment reworking can vary according to population characteristics such as species density, animal size, biovolume, burrowing depth, density of and spacing between animal burrows (e.g. Rhoads, 1974; Sandnes *et al.*, 2000; Duport *et al.*, 2006; Duport *et al.*, 2007; Gilbert *et al.*, 2007), and environmental factors such as temperature and the availability of food (Ouellette *et al.*, 2004; Lecroart *et al.*, 2005; Maire *et al.*, 2007; Nogaro *et al.*, 2008; Braeckman *et al.*, 2010).

Bioturbating benthic organisms have been classified in five types of functional groups according to their mode of particle mixing, and their main effects on sediment geochemistry and the benthic microbial community. Biodiffusers, upward conveyors, downward conveyors, regenerators and gallery-diffusers can be distinguished (François *et al.*, 2002; Gérino *et al.*, 2003). However, for a lot of bioturbators and bio-irrigators, no matter which functional group they belong to, population density is an important parameter determining the impact on ecosystem functioning, such as nutrient cycling and benthic mineralisation (Ieno *et al.*, 2006; Bulling *et al.*, 2008; Rossi *et al.*, 2008; Braeckman *et al.*, 2010). Furthermore, dominant species often contribute most to sediment reworking and ecological function (Mugnai *et al.*, 2003; Maire *et al.*, 2007), and the loss or density decline of dominant species might have serious repercussions for ecosystem functioning (Solan *et al.*, 2004a). *Corophium volutator* is an abundant species in intertidal ecosystems along the North-Atlantic, and population densities are frequently recorded at > 20,000 ind./m^2, while in summer, densities can locally increase to 100,000 – 140,000 ind./m^2 (Möller and Rosenberg, 1982; Jensen and Kristensen, 1990; Gerdol and Hughes, 1994b). Given the densities it can attain, its trophic position in the ecosystem (Murdoch *et al.*, 1986; Boates *et al.*, 1995), as well as the ecosystem engineering effect on the abiotic environment (Grant and Daborn, 1994), this amphipod can be considered a critical species in intertidal ecosystems. To our knowledge, there has been no attempt to assess the density effect of *C. volutator* on sediment reworking, and therefore, quantifying the density effect on sediment reworking is one of the objectives of the present study. In order to quantify sediment reworking, numerous tracer techniques have been developed over the last three decades (Maire *et al.*, 2008), and especially the luminophore technique (Mahaut and Graf, 1987) is frequently used in bioturbation studies. In most studies, one size class of luminophores is used to track vertical redistribution of sediment particles and/or to calculate bioturbation rate (Mermillod-Blondin *et al.*, 2004; Solan *et al.*, 2004b; Duport *et al.*, 2006; Gilbert *et al.*, 2007; Maire *et al.*, 2007). In this study, we used two different size classes of luminophores (median grain size 41 µm and 129 µm) to determine whether bioturbation by *Corophium* differentiates between the mud (< 63 µm) and the sand sediment fraction.

Bioturbation is regarded as a dynamic process caused by the behavioural activities of bioturbating species. However, burrowing species often construct an entire network of (semi)permanent burrows or tubes, which alter the 'static' sediment structure, and which could be equally important in (passive) downward sediment transport and particle burial (passive bioturbation). Therefore, we aimed at assessing the importance of the active contribution of species to bioturbation as compared with the potential passive bioturbation caused by changes in the physical sediment structure.

To achieve our different objectives, a microcosm experiment was set up in the laboratory with different density treatments, both 'passive' (burrows only) and active (burrows with animals), and with two size fractions of inert fluorescent sediment tracers (luminophores), to be able to assess density effects, to distinguish between passive and active bioturbation and to determine potential size differentiation of the bioturbation by *Corophium*.

2. MATERIAL AND METHODS

2.1 Collection of sediment and animals and experimental design

Sediment and *C. volutator* were collected in September 2006 in the Flemish nature reserve "IJzermonding", a mudflat-salt marsh area in Nieuwpoort (Belgium, 51°08'N, 2°44'E). The mudflat had a sediment consisting of muddy sand: 28% of mud (= silt + clay; <63 µm), 6% of very fine sand (63-125 µm), 50% of fine sand (125-250 µm) and 16% of medium sand (250-500 µm). The collected sediment was defaunated by three cycles 24h freezing-24h thawing. Freezing-thawing did not alter the sediment grain size characteristics (t-test, $p>0.05$). To reduce natural heterogeneity and to obtain equal starting conditions, the sediment was homogenised before use. Sediment microcosms were established by transferring the homogenised sediment into PVC cores (15 cm long and 8 cm internal diameter) to a depth of 10 cm. The PVC cores had four holes (8 mm Ø), covered with a 250 µm mesh, at the same level as the sediment surface (≈ 10 cm) to allow gentle inflow of seawater and to avoid escape of the test animals. Sixty cores were placed in a large aquarium in a temperature controlled climate room (16±1°C) with a

12:12h light:dark regime, and under a simulated tidal regime, resembling the natural tidal conditions of the collected *C. volutator* (i.e. 3h of submersion and 9h of emersion, salinity = 32 psu). The seawater was filtered with a 45 µm biological sand filter. *Corophium volutator* was added to the microcosms one day after sediment installation. Movement of test animals between microcosms was prevented by the edges of the tubes, which protruded 5 cm above the sediment surface.

Five treatments were performed (n = 4 replicates per treatment per time interval): (1) without *Corophium* and without burrows, i.e. control (C), (2) with 10 *Corophiums*, i.e. low density (LD; 1,989 ind./m^2), (3) burrows of 10 *Corophiums*, but without the animals (BLD), (4) with 75 *Corophiums*, i.e. high density (HD; 14,921 ind./m^2), and (5) burrows of 75 *Corophiums*, but without the animals (BHD). All treatments were randomised within the aquarium. No biofilm was present or no diatoms were added during the course of the experiment, but nevertheless the animals could be seen scraping, crawling or swimming.

To establish the treatments with burrows but without animals, *Corophium* was introduced as for the other treatments, but prior to the start of the experiment (after three days burrowing), these treatments were taken out of the aquarium and put carefully (without disturbing the sediment surface) in a 1% formaldehyde solution, chasing the animals out of their burrows immediately, but leaving the burrows intact. After all animals were removed with soft tweezers, the core was placed in seawater to dilute the formaldehyde. After ten minutes the cores were placed back in the aquarium. We should mention that in these formaldehyde treated cores, an increased oxygen penetration was observed after one day, most probably caused due to a change in bacterial community. However, this was restored quickly and oxygen penetration was relatively similar to the other treatments after seven days[11]. Furthermore, we are convinced that this had no effect on luminophore redistribution.

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[11] The vertical oxygen profiles, measured with Unisense oxygen microsensors (type ox25) in vertical increments of 100 µm, are added as supplementary material in Appendix 1.

2.2. Quantifying bioturbation

Bioturbation in the cores was quantified using the luminophore tracer technique (Mahaut and Graf, 1987). Two size types of luminophores were used (Environmental Tracing Systems, UK), corresponding to the two main sediment fractions: "UV Blue Mostyn" luminophores with 129 µm median grain size (i.e. fine sand, coarse tracer) and "Magenta" luminophores with 41 µm median grain size (i.e. mud, fine tracer). Two g of 129 µm and 1 g of 41 µm luminophores were added to 19 g of natural dried sediment and mixed homogeneously. Subsequently, seawater was gently added until a homogeneous mix was formed. The mix was poured in moulds of 8 cm diameter (= internal diameter of the experimental cores) and 4 mm deep and frozen at -20°C. On day 0 of the experiment, just after removal of *Corophium* from the 'only burrow' treatments and just before the start of submersion, the frozen luminophore slices were placed on the sediment surface of the experimental cores to equally distribute the luminophores over the sediment surface.

Sampling of the cores was done at three sampling occasions: one day, seven days and 14 days after the start of the experiment. At each sampling occasion, 20 cores (5 treatments x 4 replicates) were taken out of the aquarium and put immediately in the freezer (-20°C) to stop macrofaunal reworking. Frozen cores were subsequently sliced in layers of 2 mm down to 3 cm depth, then in 5 mm slices to 7 cm depth. However, the first two slices were combined, because the thickness of the initial luminophore slice was 4 mm. The sediment collected within each layer was homogenised thoroughly in a Petri dish, and pictures of a fixed surface area were taken under UV light under standardised conditions. Petri dish, camera and UV lamp (365 nm) were placed in a fixed setup. Pictures were taken with a digital mirror-reflex camera, Canon EOS 350D; aperture 1/8, shutter time 1s, ISO 400, manual focus and 46 mm focal length. Images were digitally processed in Matlab to count luminophore pixels. Using quadratic discriminant function analysis, pixels were classified into three classes (coarse tracer [129 µm; blue], fine tracer [41 µm; red] and background) based on their brightness value in the red, green and blue bands (Fig. 1). The use of the quadratic discrimant analysis prevented overlap between the three colour bands. Luminophore pixel counts of both size types were then converted to percentage of tracer in each sediment slice based on the total depth-integrated pixel counts for each size type. The image analysis revealed that no buried luminophores were present in the layers deeper than 3 cm (except for the artefactual one or two), for that reason, these data were not used for further analysis.

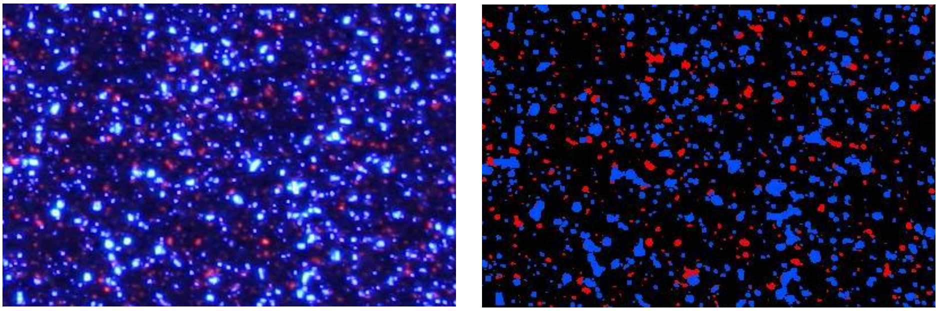

Figure 1: Example of a detailed area of an image before (left) and after (right) image analysis.

2.3. Bioturbation rate

Bioturbation rate was quantified by using a non-local model of bioturbation, the Continuous Time Random Walk model, based on Meysman *et al.* (2008). This model was preferred to the classical biodiffusion model, as the assumptions of the latter are usually not fulfilled in short-term bioturbation experiments (Meysman *et al.*, 2008). Particle displacement is assumed to be a Poisson process, as the probability distribution of the waiting time until the next displacement is an exponential distribution, with a Gaussian step-length distribution (see Maire *et al.*, 2007 for mathematical background on this model). Values for the two parameters σ (characteristic step-length) and τ (average waiting time) were determined by fitting the model to the respective log-transformed luminophore profiles using the R package FME (Soetaert and Petzoldt, 2009). Finally, a single quantity D_b^{NL}, representing the bioturbation rate, was calculated as follows:

$$D_b^{NL} = \sigma^2 / 2\tau$$

2.4. Data analysis

As it is of interest to determine differences in the shape or depth of tracer profiles between treatments, a split-plot ANOVA was performed. This allows for comparison of vertical tracer profiles between treatments (depth x treatment interaction) and between treatments over time (depth x treatment x time interaction). Tracer percentages were used as response variable, while time, treatment and tracer size were the ‘between effect' explanatory variables and depth the 'within effect' explanatory variable, since depth intervals of the luminophores within cores are not independent. To enable ANOVA analysis, core identity was introduced as a new parameter treated as a random factor, nested within the time x treatment x tracer size interaction. Significance of the between effects (time, treatment and tracer size) and their interactions were tested over the mean square between cores within treatment x time x tracer size. Significance of depth (within effect) and all interaction terms involving depth were tested over the error mean square (Quinn and Keough, 2002). To fulfill homogeneity of variances, tracer percentages were arcsine-square root transformed. Because the sphericity assumption was violated, adjusted F tests using the Greenhouse-Geisser correction were performed, resulting in more conservative p levels (Quinn and Keough, 2002).

Furthermore, differences in maximum penetration depth (MPD, depth integrating 99.5% of the tracer) and bioturbation rates between treatments, sampling times and tracer size were tested using a three-way ANOVA. Whenever the homogeneity assumption was not met (Bartlett's test), data (multiplied by a power of 10) were log transformed. Whenever appropriate, a Tukey's *post hoc* test was used to assess differences between treatments and experimental duration. When interactions, e.g. time x treatment, were significant for any of the above analyses, interpretation of the main effects was done by splitting the original data per treatment and/or sampling occasion to allow for interpretation of the main treatment or time effect (Quinn and Keough, 2002). All analyses were performed using Statistica 7.

3. RESULTS

3.1. Size selectivity

Corophium reworked the sediment particles irrespective of particle size (Fig. 2). No significant differences in vertical distribution or maximum penetration depth (MPD, depth integrating 99.5% of the tracer) were found between fine (41 µm) and coarse (129 µm) tracers for none of the treatments (Table 1 and 2; Fig. 2 and 3). Furthermore, bioturbation rates for both size fraction were not significantly different between similar treatments and sampling occasions (Table 3), with for instance for the high-density treatment (HD) after 14 days, a bioturbation rate of 0.0035±0.0007 cm^2/d for the fine tracer and 0.0029±0.0003 cm^2/d for the coarse tracer (Fig. 4).

Table 1: Time, treatment and tracer size differences for vertical tracer distribution patterns in five treatments at three sampling times (Split-plot ANOVA table). Adjusted p-levels were calculated for Depth effects based on the Greenhouse-Geisser correction. Tracer % was arcsine-square root transformed.

Model term	df	Tracer % MS	Tracer % F	p	Adjusted p level
Between effects					
Cte	1	28.11007	72351.01	**<0.001**	
Time	2	0.01123	28.91	**<0.001**	
Treatment	4	0.02222	57.20	**<0.001**	
Size	1	0.00027	0.68	0.411	
Time x Treatment	8	0.00196	5.05	**<0.001**	
Time x Size	2	0.00006	0.15	0.860	
Treatment x Size	4	0.00021	0.53	0.716	
Time x Treat x Size	8	0.00015	0.38	0.928	
Repl(Ti, Tr, Si)	90	0.00039	1.03	0.402	
Within effects					
Depth	13	221.2888	45217.67	**< 0.001**	**< 0.001**
Depth x Time	26	0.2282	23.31	**< 0.001**	**< 0.001**
Depth x Treatment	52	0.7645	39.06	**< 0.001**	**< 0.001**
Depth x Size	13	0.0033	0.68	0.781	0.479
Depth x Ti x Tr	104	0.1927	4.92	**< 0.001**	**0.013**
Depth x Ti x Si	26	0.0019	0.19	0.999	0.915
Depth x Tr x Si	52	0.0026	0.13	1,000	0.994
Depth x Ti x Tr x Si	104	0.0114	0.29	1,000	0.993
Depth x Repl(Ti, Tr, Si)	1170	0.4404	-	-	-

3.2. Effects of density and biological activity over time

Bioturbation effects changed significantly between the treatments over time (time x treatment x depth, p<0.001; Table 1). As time progressed, differences between treatments became more pronounced, and the percentage of luminophores worked down with time was higher for most treatments (Fig. 2)[12]. The empty burrows from the BLD and BHD treatments persisted during the experiment (personal observation during slicing), and they slightly influenced vertical tracer distribution in the sense that significant changes in tracer profile for both were observed over time, when analysing treatments separately (Fig. 2, Table 4). Also for the LD and HD treatments, luminophore depth profiles differed significantly between the sampling occasions (Table 4), only for the C treatment, no differences were found between the sampling occasions. For LD and BLD, the 1 day sampling occasion differed significantly from both the 7 days and 14 days sampling occasions, while for HD and BHD, the 14 days sampling differed significantly from the 1 day and 7 days sampling occasions (Tukey's *post hoc*, Table 4).

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[12] Analysed pictures of some depth slices from all treatments at day 14 are presented in Appendix 1.

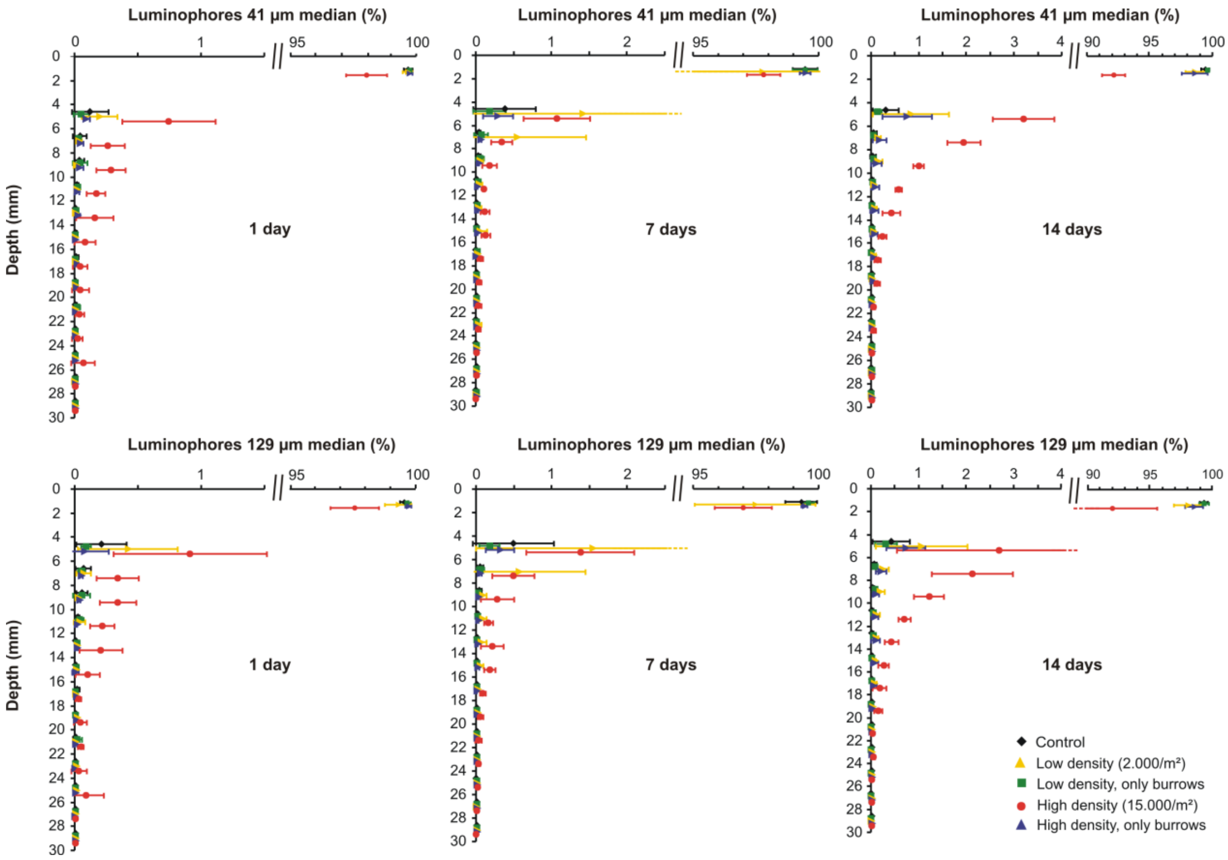

Figure 2: Depth profiles (mean±SD, n=4) from 41 µm (upper graphs) and 129 µm (lower graphs) luminophores for the different treatments at the three sampling occasions.No significant differences between luminophore sizes were observed.

Table 2: Three-way ANOVA table for the effect of time, treatment and tracer size on the Maximum Penetration Depth (MPD).

	df	MPD MS	MPD F	p
Cte	1	12040.03	864.8069	<0.001
Time	2	162.13	11.6457	**<0.001**
Treatment	4	419.87	30.1580	**<0.001**
Size	1	32.03	2.3009	0.133
Time x Treatment	8	32.97	2.3679	**0.023**
Time x Size	2	5.73	0.4118	0.664
Treatment x Size	4	9.20	0.6608	0.621
Ti x Tr x Si	8	6.40	0.4597	0.881
Error	90	13.92		

Table 3: Three-way ANOVA table for the effect of time, treatment and tracer size on the natural logarithmic transformed bioturbation rate (ln(BR)).

	df	Ln(BR) MS	Ln(BR) F	p
Cte	1	5708.18	6022.98	<0.001
Time	2	22.11	23.33	**<0.001**
Treatment	4	26.31	27.77	**<0.001**
Size	1	0.39	0.45	0.521
Time x Treatment	8	2.08	2.20	**0.036**
Time x Size	2	0.32	0.34	0.714
Treatment x Size	4	0.63	0.66	0.619
Ti x Tr x Si	8	0.25	0.26	0.976
Error	83	0.95		

On each sampling occasion, the depth profile of the HD treatment (14,921 ind./m^2) differed significantly from the C and LD treatments (Tukey's *post hoc*, $p<0.005$; Table 5), except on day 7 (HD not different from LD, $p=0.29$; Table 5). The LD treatment (1,989 ind./m^2) did not differ significantly from the C treatment in vertical distribution of the tracers on day 1 and day 7, but it differed significantly from the C treatment on day 14 ($p=0.015$, Tukey's *post hoc*; Table 5). Depth profiles from BLD and LD treatment were not significantly different from each other on the different sampling occasions (Tukey's *post hoc*, Table 5). However, for the BHD treatment significant differences were observed with the HD treatment at each sampling occasion (Tukey's *post hoc*, Table 5), with higher amounts of tracer transported downward for the HD treatment (Fig. 2).

Table 4: Tukey's *post hoc* results for differences in vertical tracer distribution per treatment between different sampling occasions. For the C treatment, no overall signicant effect of time was found, so no test was performed.

Treatment	Sampling occasion	Day 1	Day 7
BLD	Day 7	**0.002**	
	Day 14	**<0.001**	0.980
LD	Day 7	**0.039**	
	Day 14	**0.029**	0.994
BHD	Day 7	0.550	
	Day 14	**<0.001**	**<0.001**
HD	Day 7	0.998	
	Day 14	**<0.001**	**<0.001**

Table 5: Tukey's *post hoc* results for differences in vertical tracer distribution between the different treatments per sampling occasion.

Sampling occasion	Treatment	C	BLD	LD	BHD
Day 1	BLD	0.357			
	LD	0.811	0.948		
	BHD	0.965	0.770	0.993	
	HD	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Day 7	BLD	0.951			
	LD	0.117	0.454		
	BHD	0.999	0.980	0.168	
	BD	**<0.001**	**0.003**	0.290	**<0.001**
Day 14	BLD	0.929			
	LD	**0.015**	0.139		
	BHD	**0.013**	0.121	0.999	
	HD	**<0.001**	**<0.001**	**<0.001**	**<0.001**

Maximum penetration depth (MPD) was less subject to time (Fig. 3). MPD changed with time but this differed between treatments (time x treatment, p= 0.023; Table 4). MPD was only significantly different between sampling occasions for the LD and BHD treatment (Tukey's *post hoc*). MPD was deepest for the HD treatment with 18.5±2.7 mm (mean±SE) for the coarse (129 μm) tracer and 20±2.8 mm for the fine (41 μm) tracer after 14 days (Fig 3). We observed the same pattern in MPD as for the tracer profiles, where the HD treatment differed significantly from C and LD treatments on each sampling occasion, except not from the LD treatment on day 7 (p=0.31, Tukey's *post hoc*; Fig. 3). Furtermore, the HD treatment also differed significantly from the BHD treatment at each sampling occasion. The LD treatment (13±4 mm for fine and 11±1 mm for coarse) showed only significant differences in MPD with the C treatment (6±1 mm for both fraction sizes) on day 7, no significant differences with BLD treatment were observed (Tukey's *post hoc*; Fig. 3).

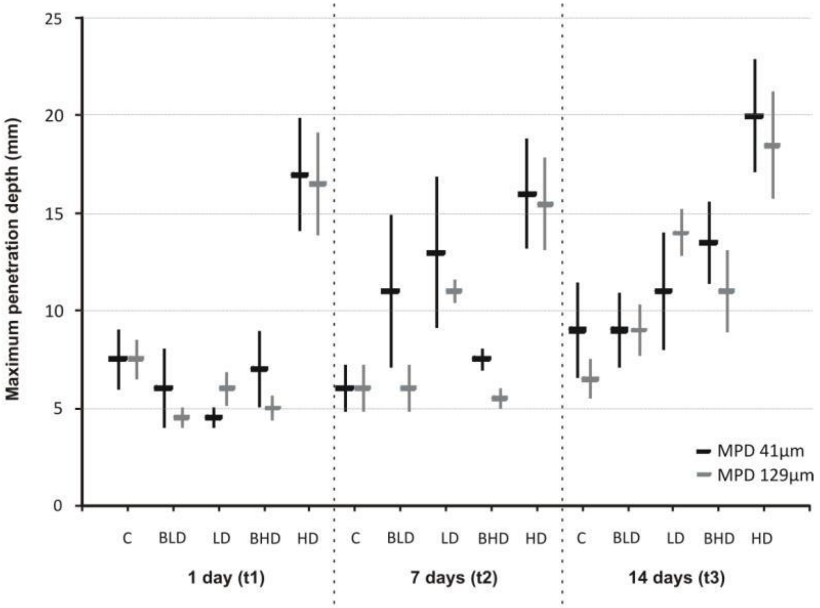

Figure 3: Maximum penetration depth (mean ± SE, n=4) for the different treatments (C = Control, BLD = Burrows Low Density, LD = Low Density, BHD = Burrows High Density, HD = High Density) from 41 µm (black) and 129 µm (grey) luminophores at the different sampling occasions. No significant difference between luminophore sizes were observed.

The bioturbation rate was significantly influenced by time (Table 3). For each treatment, except for the BLD treatment, the bioturbation rate at day 1 was significantly higher than the rates at day 7 and day 14 (Tukey's *post hoc*; Fig. 4). Bioturbation rate was usually one order of magnitude higher in the HD treatment compared to the other treatments. The HD treatment showed significantly higher values on days 1 and 14 (resp. 0.02 cm^2/d and 0.003 cm^2/d for the fine tracer) than the LD treatment (resp. 0.001 cm^2/d and 0.0007 cm^2/d) and it differed significantly from the C treatment and BHD treatment on all sampling occasions (Table 3, Fig. 4). Again, the BLD and LD treatment did not show any significant differences in bioturbation rate.

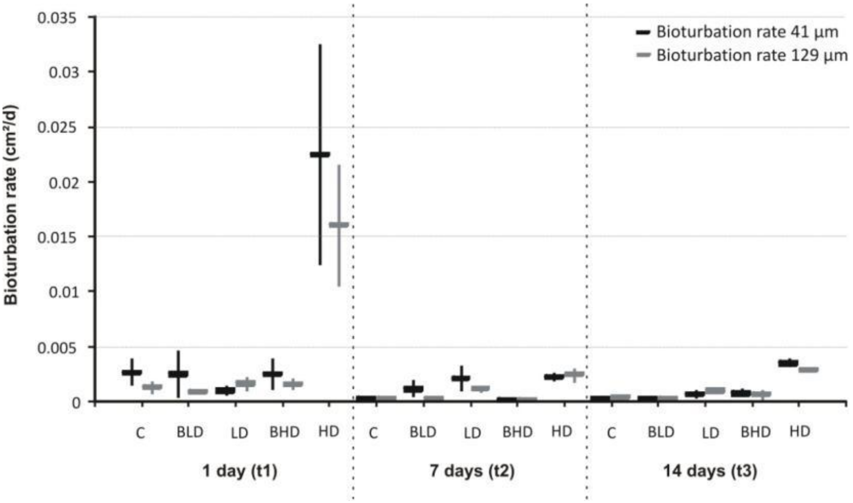

Figure 4: Bioturbation rate (mean ± SE, n= 4) for the different treatments (C = Control, BLD = Burrows Low Density, LD = Low Density, BHD = Burrows High Density, HD = High Density) from 41 µm (black) and 129 µm (grey) at the different sampling occasions. No significant differences between luminophore sizes were observed.

4. DISCUSSION

4.1. Size selectivity

No evidence for differentiation in sediment size fractions during sediment reworking by *Corophium* was observed, meaning that both the mud fraction and fine sediment fraction were transported at equal rates and in a similar way. In contrast with our results, high *Corophium* densities have been observed to stimulate loss of fine sediment (< 4 µm) from the surface layer in the laboratory (De Backer *et al.*, 2009= Chapter 4), and to induce a coarsening of the sediment in the field (Chapter 6). These contrasting results can probably be attributed to the fact that in the laboratory a loss of clay particles (particle diameter < 4 µm) was observed, while the fine tracer fraction used in this experiment had a median grain size of 41 µm. The difference with the field data can probably be explained by a large difference in external hydrodynamical forcing between laboratory and natural conditions. Furthermore, as *Corophium*, because of its bio-irrigating activities in a U-shaped burrow, was expected to induce non-local transport (i.e. transport of material from the surface directly to the deep part of the gallery) in addition to diffusive mixing, accumulations of (preferably coarse) particles were expected at the bottom of the burrow. Our vertical distribution profiles, however, showed no evidence of non-local transport, i.e. a peak of tracers at depth, which is consistent with the findings of Mermillod-Blondin *et al.* (2004). Mermillod-Blondin *et al.* (2004) attributed their results to an insufficient spatial resolution (slices of 5 mm), missing a possible luminophore peak at the bottom of the burrow. Our spatial resolution was higher (2 mm), but again no tracer peak at depth was observed. Possibly, *Corophium* removes the accumulation of sediment particles at the bottom of the burrow, whilst flushing during submersion (De Backer *et al.*, 2010). Further experiments on a very high spatial and temporal scale with the use of thin wall aquaria and time lapse camera could offer an outcome to actually see what is happening at the bottom of the burrow and to see if different sediment fractions are indeed transported in the same way (Solan *et al.*, 2004b).

4.2. Density effects and passive versus active bioturbation

Quantification of bioturbation by tracking the vertical distribution of luminophore tracers in different density treatments revealed that density is an important parameter determining sediment reworking by *Corophium*. High *Corophium* densities (± 15,000 ind./m^2) reworked a significantly higher amount of tracer at each sampling occasion, while low densities of *Corophium* (± 2,000 ind./m^2) had only a slight, and mostly insignificant, influence on sediment reworking. Furthermore, differences between control and density treatments became more pronounced with time. Bioturbation rate and maximum penetration depth as well were positively influenced by density. *Corophium volutator* is an important deposit feeder, at least in the absence of phytoplankton (Riisgård and Schotge, 2007), and while foraging as deposit feeder, *Corophium* partly leaves the burrow to scrape surface sediment in the burrow (Meadows and Reid, 1966; Riisgård and Schotge, 2007; De Backer *et al.* 2010). This feeding behaviour induces a displacement of surface particles down the burrow. If *Corophium* density increases, a larger surface area is occupied with burrows, and consequently the total scraping area, which surrounds the burrows, increases. Hence, a higher quantity of sediment tracers is buried at high densities. A similar particle displacement through feeding behaviour was described for *Hediste diversicolor* by Duport *et al.* (2006). It is, however, important to mention that no food was added to this experiment, so feeding activity might have been reduced and might have resulted in less intensive sediment reworking (cf. Nogaro *et al.*, 2008). This density-dependency of sediment reworking was also observed for other taxa and other functional traits, and our results add to the recognition that density is an important parameter in sediment mixing (Sun *et al.*, 1999; Sandnes *et al.*, 2000; Duport *et al.*, 2006; Braeckman *et al.*, 2010).

The limited importance of low densities of *Corophium* is supported by the close relation in both depth profile and bioturbation rate between the low density treatment and the treatment with only burrows at low densities, indicating that the influence of the behavioural activities at low densities of *Corophium* was of minor importance. There is a small environmental, abiotic driven flux of passive particle transport down into the empty burrows, which does not differ significantly from the net animal activity at low densities. However, for high densities, significant differences were found between the 'passive' burrow treatment and the 'active' treatment with animals. Furthermore, the bioturbation rate was one order of magnitude higher in the animal treatment compared to the 'burrow only' treatment, indicating that bioturbation is actively driven by the burrow-flushing and particle-burial activities of *Corophium*. The behavioural activities of *Corophium* an sich contribute to a downward sediment mixing of approximately 1 cm^2/y (for 15,000 ind./m^2), which is a five-fold increase compared to the passive transport induced by the static structure of burrows. These results indicate that in ecosystems where *C. volutator* is abundantly present, it may play a prominent role in downward particle transport and organic matter transformation, while a decline in *Corophium* densities due to natural or anthropogenic disturbances might have negative effects on downward transport of organic matter. Moreover, the density of *Corophium* also proved to be an important parameter in biogeochemical processes, where ventilation activity increased oxygen consumption, nitrification and denitrification, and the release of nutrients from the sediment (Pelegri *et al.*, 1994a; Pelegri and Blackburn, 1994b; Emmerson *et al.*, 2001; Mermillod-Blondin *et al.*, 2004) and furthermore, *Corophium* is known to stimulate microbial activity in the burrow (Mermillod-Blondin *et al.*, 2004).

These biogeochemical results, together with our quantification of sediment reworking imply that *Corophium*, at least at densities of 15,000 ind./m^2, is important in the functioning of intertidal mudflats. This density of 15,000 ind./m^2, and even much higher densities, are frequently observed in mudflats. For instance in the IJzermonding tidal flat, where the experimental animals were collected, average densities in summer easily reach 50,000 ind./m^2 with peaks towards 100,000 ind./m^2 (Chapter 6). Further evidence pointing at the importance of *Corophium* in ecosystem functioning of mudflats was provided by Gerdol and Hughes (1993), who concluded that *Corophium* (12,500 ind./m^2) prevented the establishment of *Salicornia europaea* partly by burial of seeds, but mostly by preventing the establishment of the seedlings, which inhibits the expansion of salt marsh vegetation.

4.3. Bioturbation rate

For each of the cores, the bioturbation rate measured after 24h was about one order of magnitude higher as compared to those measured on the later sampling occasions. These values are most probably not reliable because after one day only very small amounts of tracer particles have been reworked. At such short time scale, even minute percentages of tracer at depth (e.g. as a result of the slicing process) will result in an overestimation of the bioturbation rate by the model.

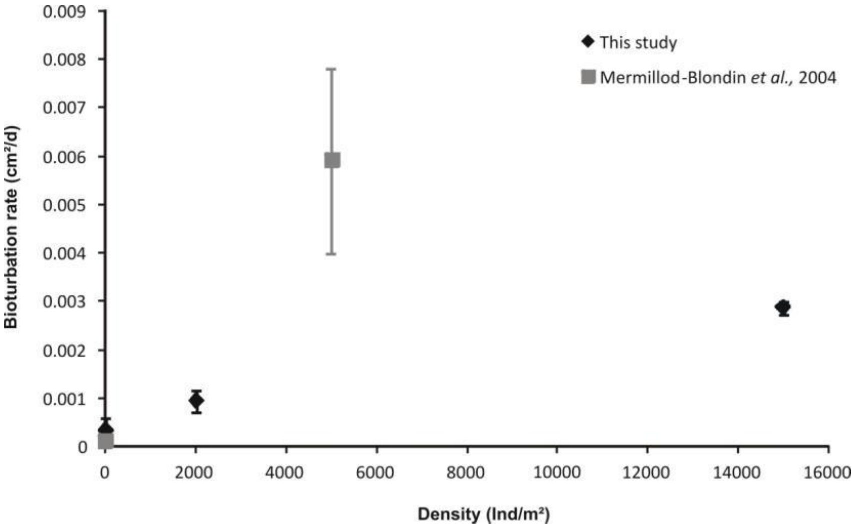

Figure 5: Comparison of bioturbation rates measured in Mermillod-Blondin *et al.* (2004) at densities of 0 and 5,000 ind./m^2 with rates measured in the current study at densities of 0, 2,000 and 15,000 ind./m^2.

However, when we compare our bioturbation rates measured at the later sampling occasions with other studies, lower values were observed. Mermillod-Blondin *et al.* (2004) for instance, measured a diffusion rate of 0.006 cm^2/d for *Corophium* at a density of 5,000 ind./m^2 after 20 days, while in this study for both densities much lower values were observed, although control values in both studies are similar (Fig. 5). Other studies on intertidal animals, but using fully submersed experimental mesocosms, showed values ranging from 0.003 to 0.009 cm^2/d (François *et al.*, 2002; Duport *et al.*, 2006).

We hypothesise that this difference in bioturbation rates could be caused by the imposed tidal regime (3h submersion versus 9h emersion) in this study. A previous study (De Backer *et al.*, 2010) showed that *Corophium* is completely inactive for on average 70% of the time during emersion, meaning that sediment reworking is mainly restricted to submersion. Furthermore, comparison with the study of Mermillod-Blondin *et al.* (2004), which was done under similar temperature conditions (14°C versus 16±1°C in this experiment) and also without the addition of food, but with 100% submersion, indicates that shifts in activity periods caused by the tidal regime, may be responsible for the different values in bioturbation rates, with a possible overestimation of bioturbation rates in the absence of a tidal regime. To our knowledge, no supporting literature exists linking tidal rhythmicity in behaviour to bioturbation rates. Therefore, it would be very interesting to test this hypothesis under experimental conditions with different tidal regimes. However, studies on seasonal variation in bioturbation rates measured lower sediment reworking rates in winter due to reduced feeding, burrowing and/or ventilation activities (Maire *et al.*, 2007; Braeckman *et al.*, 2010). Similarly, reduced bioturbation activity was also measured for *Hediste* due to decreased feeding behaviour without a food supply (Nogaro *et al.*, 2008). Hence, the observed decrease in activity of *Corophium* during emersion (De Backer *et al.*, 2010) could similarly result in lower reworking rates.

5. CONCLUSION

The population density of *C. volutator* is a key parameter determining the impact of its bioturbation. Only when abundantly present in the mudflat ecosystem, *Corophium* will play an important role in reworking of the sediment surface. Density declines of *Corophium*, be it natural or anthropogenic, can thus have negative effects on downward particle and organic matter transport. We found, however, no evidence for size selectivity during bioturbation of *Corophium*. Furthermore, our results indicated that the bioturbation measured at high densities was actively driven by the burrow-flushing and particle-burial activities of *Corophium*, which contributed to a five-fold increase in sediment transport compared to the small abiotic driven flux of passive particle transport induced by the static burrow structures. Consequently, this suggests that all factors causing a decrease in behavioural activity (e.g. tidal regime, temperature, food supply,), cause a decrease in bioturbation activity.

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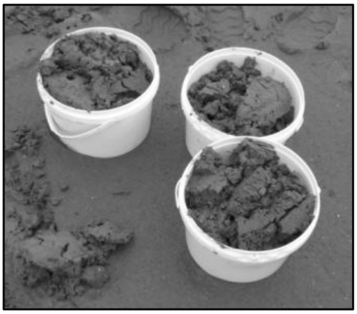
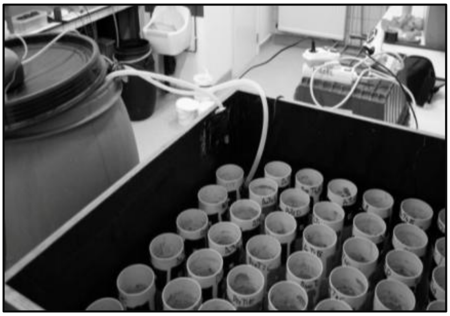
CHAPTER 4

REMOTE SENSING OF BIOLOGICALLY REWORKED SEDIMENTS: A LABORATORY EXPERIMENT

Annelies De Backer, Stefanie Adam, Jaak Monbaliu, Erik Toorman, Magda Vincx, Steven Degraer





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CHAPTER 4

REMOTE SENSING OF BIOLOGICALLY REWORKED SEDIMENTS: A LABORATORY EXPERIMENT

ABSTRACT

The present study aims to test the application of remote sensing to address the impact of bioturbation on physical sediment properties. Therefore, a laboratory experiment was developed, using microcosms mimicking a marine intertidal water-sediment interface to test the influence of Corophium volutator densities on sediment properties. Three main variables (water content, clay content and mean grain size) were measured in three treatments (no Corophium, 5,000 Corophium/m^2 and 20,000 Corophium/m^2) after 16 days of bioturbation. Results obtained with conventional – destructive – techniques showed a significant increase of water content and a significant, but small decrease of clay content in the presence of Corophium. The remote sensing technique detected the impact of Corophium on water content as an increase in absorption at 1,450 nm, but was not able to detect the animal impact on clay content. This study demonstrates that remote sensing data could be significantly modified by bioturbation activities and that remote sensing can be applied in the laboratory to address the impact of bioturbation on sediment properties. This possibly opens new perspectives for long term experiments concerning the role of bioturbation on sedimentary processes.

KEY WORDS: clay content, *Corophium volutator,* grain size, hyperspectral measurements, remote sensing, water content

1. INTRODUCTION

Dependent on the surface materials, various fractions of electromagnetic radiation incident on the surface are reflected, absorbed and/or emitted (Lillesand and Kiefer, 2000). Some materials, such as the pigment chlorophyll *a*, water and clay absorb light at specific wavelengths due to molecular vibration and rotation, while other materials, such as vegetation, scatter near-infrared light due to the internal structure of plant leaves (Lillesand and Kiefer, 2000). Remote sensing devices capture the reflected radiation which can be used to identify and quantify surface materials. With the development of high spectral resolution laboratory, field and airborne sensors, the reflected signal can be used to predict surface properties qualitatively (Thomson *et al.*, 1998; Adam *et al.*, 2006; Deronde *et al.*, 2006) and, to some extent, quantitatively (Rainey *et al.*, 2003; Carrère *et al.*, 2003). Remote sensing has the great advantage that it is a nondestructive method and less time consuming than conventional sampling.

In laboratory conditions, hyperspectral signals have been used to quantify mud (Kooistra *et al.*, 2003; Lagacherie *et al.*, 2008; Adam, 2009), organic matter (Ben-dor *et al.*, 2002; Kooistra *et al.*, 2003), chlorophyll *a* (Méléder *et al.*, 2003; Combe *et al.*, 2005) and moisture content (Ben-dor *et al.*, 2002; Adam, 2009) in sediments. In the field, good results have been obtained to estimate chlorophyll *a* content (Méléder *et al.*, 2003; Carrère, 2004; Combe *et al.*, 2005; Murphy *et al.*, 2005; Adam, 2009) and moderate results to quantify mud (Kooistra *et al.*, 2003; Rainey *et al.*, 2003; Lagacherie *et al.*, 2008) and moisture (Ben-dor *et al.*, 2002; Adam, 2009) content.

Few studies used remote sensing data to predict distribution of macrobenthos on an intertidal flat (Yates *et al.*, 2003; van der Wal *et al.*, 2008). However, the effect of bioturbation on the remotely sensed signal, and hence, the potential of remote sensing to detect bioturbation, have not been investigated. Nevertheless, bioturbation is recognised as one of the major processes that influence the structure and function of sediment environments (Lohrer *et al.*, 2004; Meysman *et al.*, 2006). Sediment reworking results from various activities, and strongly affects the physical, chemical and biological characteristics of marine sediments (Rhoads, 1974; Aller, 1982; Hall, 1994; Jones *et al.*, 1994; Rowden *et al.*, 1998). As such, bioturbation could potentially influence remote sensing analyses through changing sediment properties.

The mud shrimp, *Corophium volutator* (Crustacea, Amphipoda) is an abundant deposit and/or filter feeding species in intertidal mudflats, where it lives in U shaped burrows in the upper 5 cm of the sediment (Meadows and Reid, 1966). Population densities frequently reach > 20,000 ind./m^2 and in summer months densities can locally increase up to 100,000 – 140,000 ind./m^2 (Gerdol and Hughes, 1994b). The high population densities make *C. volutator* a critical species in many mudflat ecosystems, where it is a significant prey of migratory shore birds and juvenile flounder (Murdoch *et al.*, 1986; Boates *et al.*, 1995). Through its activities, *Corophium* alters sediment properties by changing porosity, water content, grain size distribution and the chemistry of the sediment (Jones and Jago, 1993; Gerdol and Hughes, 1994a; Pelegri and Blackburn, 1994b; Limia and Raffaelli, 1997; Mermillod-Blondin *et al.*, 2004). However, contradicting results are often found and still no consensus on the real effect of *Corophium* on the physical characteristics of the sediment is reached.

The objectives of the present study were twofold:

1) to examine the physical impact of bioturbation by *C. volutator* on water content and grain size of the sediment with conventional, destructive techniques using microcosms in laboratory conditions, i.e. without any confounding factors such as the presence of microphytobenthos and differences in sediment characteristics,

2) to investigate whether physical changes caused by bioturbation of a macrobenthic species influence the hyperspectral signal

2. MATERIAL AND METHODS

2.1. Experimental setup

Sediment and *C. volutator* were collected in October 2007 in the Flemish nature reserve "IJzermonding", a mudflat-saltmarsh area in Nieuwpoort (Belgium, 51°08'N, 2°44'E). The sediment was defaunated by three cycles of 24h freezing-24h thawing. Grain size analysis (Malvern Mastersizer 2000 laser diffraction) showed that freezing-thawing did not alter median grain size (t-test, $p=0.48$). To reduce natural heterogeneity and to obtain equal starting conditions, the sediment was homogenised by thorough mixing before use. Sediment microcosms were established by transferring the homogenised sediment into PVC cores (15 cm deep and 8 cm internal diameter) to a depth of 10 cm. Fifteen cores were placed in an aquarium (0.8 x 0.8 m) in a temperature controlled climate room (16±1°C) with a 12:12h light:dark regime, and subjected to a simulated tidal regime, resembling the natural tidal conditions (i.e. 3h of submersion and 9h of emersion, salinity= 32 psu). Three days after microcosm preparation, *C. volutator* was added to the PVC cores in different densities. Three treatments were set up (five replicates per treatment): (1) no *Corophium* i.e. control (C), (2) 25 *Corophium*, i.e. low density (5,000 ind./m^2; LD), and (3) 100 *Corophium*, i.e. high density (20,000 ind./m^2; HD). All treatments were placed randomly in the aquarium during 16 days[13]. On day 16, hyperspectral measurements of the sediment surface were performed 3h after emersion. Immediately thereafter, the surface sediment was frozen with liquid nitrogen (± 1 cm deep), based on the contact coring technique pioneered by Wiltshire *et al.*

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[13] Mortality was very low, on average 1% ± SD 1.2%.

(1997). This technique allows for undisturbed surface samples and avoids changes in water content by draining of the pore water. Afterwards the upper 0.5 cm of the core was used to determine water content and grain size in the surface layer.

2.2. Hyperspectral and physical measurements

Spectral reflectance measurements Hyperspectral measurements were acquired with the Analytical Spectral Device (ASD) spectrometer (FieldSpec® Pro FR, Analytical Spectral Devices Inc., Boulder, Colorado, USA), recording the reflectance from 350 till 2,500 nm, i.e. in the visible (VIS), near-infrared (NIR) and shortwave-infrared (SWIR) region of the spectrum. The spectral resolution is 3 nm for the 350-1,000 nm region and 10 nm for the 1,000-2,500 nm region. Spectral reflectance measurements were acquired at 50 cm height, nadir looking with a field of view of 1°, so that a small area of 0.6 cm^2 was sampled. The reflectance was measured at four positions in each microcosm on the sediment surface to include spatial heterogeneity. Black cloths, which absorb more than 95% of the light, were hung around the experimental setup and put on the table to avoid diffuse light entering the sensor. The light source was a tungsten halogen 50-W OSRAM lamp and calibration was performed every 10 min using a Spectralon® panel (0.30 x 0.30 m Labsphere, North Sutton, USA), which has a quasi-Lambertian reflectance higher than 98 % over a range from 400 to 1,500 nm and higher than 93 % from 1,500 to 2,500 nm. Hence, the Spectralon® panel is characterised by a reflectance factor for each wavelength. The relative reflectance from the sediment (radiant exitance from the sediment/radiant exitance from the Spectralon® panel) was multiplied by the Spectralon® reflectance factors to obtain absolute reflectance. In laboratory conditions, the instrument and the light source are stable enough for calibration to be performed with a 10 min time interval, since 10 min after the calibration, the reflectance of the Spectralon® panel was almost equal to 100%, except for small deviations situated at the extreme upper and lower ends of the spectrum.

In order to avoid measurements with an incorrect position of the sample under the ASD, causing reflectance from the PVC cores, a quality procedure based on the overall brightness of the spectrum was performed. One spectrum of the high density treatment had to be removed, because the difference in the visible light between this spectrum and the mean of the other high-density spectra was very large (more than five times the standard deviation of the correctly measured high-density spectra).

Water content Frozen sediment from 0 to 0.5 cm depth is weighed after removal of the animals to determine wet weight, subsequently freeze-dried for 12h, and weighed again. Water content[14] was calculated as follows:

$$Water\ content\ (\%) = \frac{Wet\ sample\ weight\ (g) - Dry\ sample\ weight\ (g)}{Wet\ sample\ weight\ (g)} * 100$$

Grain size Grain size analysis was carried out on the freeze-dried samples (8 cm Ø) after determination of the water content. Grain size distribution (according to the Wentworth scale)[15] and mean grain size (µm) were determined using a Malvern Mastersizer 2000 laser diffraction, capable of detecting the 0.02 µm to 2 mm grain size range.

2.3. Absorption features

Absorption can be quantified by 1) the ratio between minimal reflectance in the absorption feature and reflectance outside the absorption feature: R_b/R_c (R_b is reflectance at maximum absorption, R_c is reflectance out of absorption feature), 2) the scaled band depth after continuum removal, and 3) the scaled band area of the absorption feature after continuum removal (Fig. 1). Continuum removal is a normalisation technique in order to compare absorption features from a common baseline. This continuum consists of straight-line segments that connect local spectra maxima. It is then removed by dividing it into the actual spectrum (Clark and Roush, 1984). The continuum is calculated preferably between the local maxima of the absorption feature of interest. If there is no local maximum, the shoulder of the dip or a pre-defined wavelength is considered for continuum removal.

Specifically, we used the absorption dips at 1,450 nm and 2,206 nm as assessors for respectively water and clay content. A laboratory spectrum for dry fine sand with clay shows absorption features of clay at around 1,420 nm, 1,950 nm and 2,206 nm (Fig. 2; Adam *et al.*, 2008), where the latter is caused by Al-OH bonds in the clay mineral (Yang *et al.*, 2000). Absorption at around 1,420 nm and 1,950 nm is also due to clay molecular water absorbing light (Hunt, 1977; Yang *et al.*, 2000). Therefore, the best assessor for clay content is the absorption dip at 2,206 nm.

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[14] We measured bulk water content in the top 0.5 cm layer.

[15] The clay fraction was defined as all particles < 4 µm.

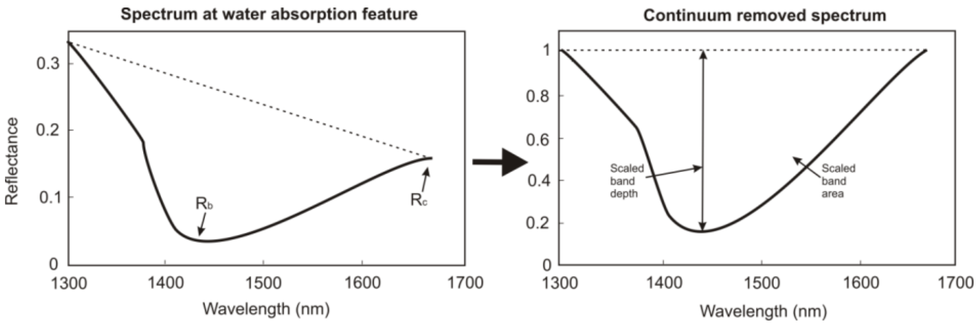

Figure 1: Measures that quantify absorption features. R_b is the reflectance at maximum absorption, R_c is the reflectance out of absorption feature. Example for the water absorption feature at 1450 nm.

The spectrum of moist fine sand shows water absorption features at 970 nm, 1,190 nm, 1,450 nm and 1,950 nm (Fig. 2; Adam *et al.*, 2008). The first two disappear when the sediment is drier, and the latter becomes saturated at relatively low moisture contents (measurements by S. Adam). Furthermore, the best prediction potential of relative moisture content in laboratory conditions was obtained using the scaled band area of the water absorption feature at 1,450 nm (measurements by S. Adam). For these reasons, the absorption at 1,450 nm was considered in the further analysis.

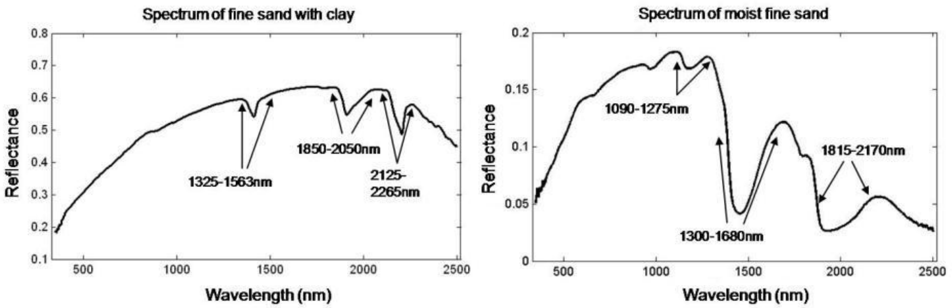

Figure 2: Spectrum of dry fine sand with clay (66% by weight) (left) and of moist fine sand (RMC=27%) (right) (from Adam *et al.*, 2008)

2.4. Data analysis

Differences in density treatments were tested using one-way ANOVA. Percentage data (clay, water content) were arcsine-square root transformed, reflectance (x10) and mean grain size data were log transformed to meet assumptions of normality (Shapiro Wilks' test) and homogeneity of variances (Cochran and Bartlett tests). Whenever appropriate, a Tukey's Post Hoc test was used to assess differences between treatments.

Furthermore, to investigate relationships between density, physical characteristics and spectral measurements, Spearman rank or Pearson correlations were performed.

3. RESULTS

3.1. Physical characteristics

The high-density treatment (HD) had a significantly ($p<0.01$, Tukey's Post Hoc) lower percentage clay (mean±SD, 3.3±0.1%) in the upper layer than the low-density (LD; 3.6±0.2%) and the control treatment (C; 3.6±0.06%) (Fig. 3a). Furthermore, we found a negative correlation between density and clay percentage (Spearman r= -0.70, p= 0.0037). Although, mean grain size of HD (179±3 μm) was larger compared to C and LD (LD = 177±3 μm, C = 176±2 μm; Fig. 3b), no significant differences in mean grain sizes were found.

Table 1: One-way ANOVA table to determine significant differences for the different physical characteristics (clay percentage, mean grain size and water content) between the different treatments. Clay percentage and water content were arcsine-square root transformed, median grain size was log-transformed. Significant p-levels are highlighted.

	df	Clay % MS	Clay % F	p	Mean MS	Mean F	p	Water % MS	Water % MS	p
Treat	2	0.0001	8.9	**0.004**	0.00005	1	0.4	0.002	37.4	**<0.001**
Error	12	0.00002			0.00004			0.00005		

Water content increased significantly when *Corophium* was present, both for LD (19±0.7%) and HD (20±0.6%), compared to C (17±0.4%; Fig. 3c, Table 1). No difference however, was found between LD and HD (Tukey's Post Hoc, $p>0.05$). Water content correlated positively with density (Spearman r = 0.74, p= 0.0017).

3.2. Hyperspectral measurements

The reflectance in the visible region of the spectrum differed significantly between the density treatments, as shown in Table 2 for the reflectance at 545 nm and 630 nm and in Fig. 4. The continuum removed spectra at the absorption dip of water at 1,450 nm (Fig. 5) show that the dips are maximum for the treatments with *Corophium* and minimum for C. As expected, the scaled band area of the water absorption feature at 1,450 nm was positively correlated with water content (Pearson's r= 0.8, p= 0.0006). Differences between the three treatments (Table 2) were significant for the scaled band area at

1,450 nm, where C differed significantly from LD and HD (Tukey's Post Hoc, resp. p= 0.0003 and p= 0.005; Fig. 6).

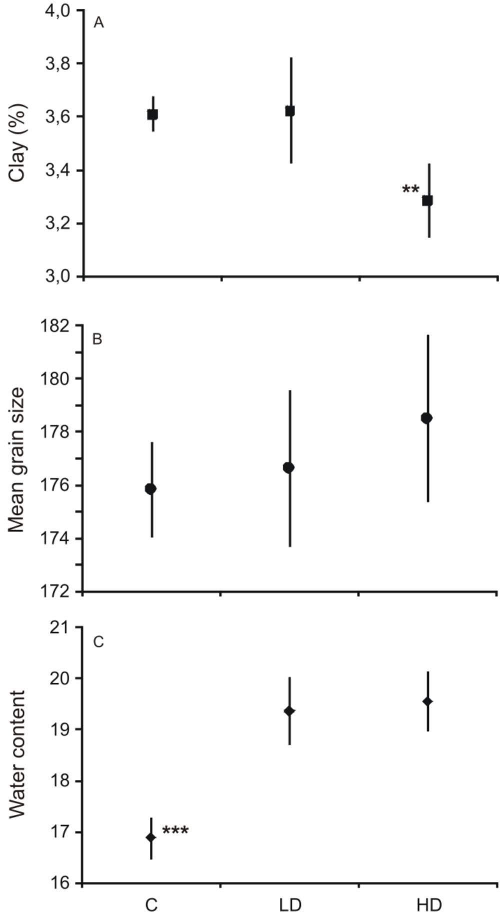

Figure 3: (A) Average percentage of clay (B) average mean grain size and (C) average water content (in %) for the different treatments (n= 5 ± S.D.) (C = Control, LD = Low Density, HD = High Density), * * and * indicate significance levels of Tukey's Post Hoc**

Table 2: One-way ANOVA table to determine significant differences for the hyperspectral measurements (reflectance at 545 nm, reflectance at 630 nm and scaled band area 1,450 nm) between the different treatments. All variables were log (x10) transformed. Significant p-levels are highlighted.

	df	Refl 545 MS	Refl 545 F	p	Refl 630 MS	Refl 630 F	p	Area 1450 MS	Area 1450 F	p
Treat	2	0.01	15.9	**<0.001**	0.01	16.8	**<0.001**	0.02	21	**<0.001**
Error	11	0.0009			0.0007			0.0008		

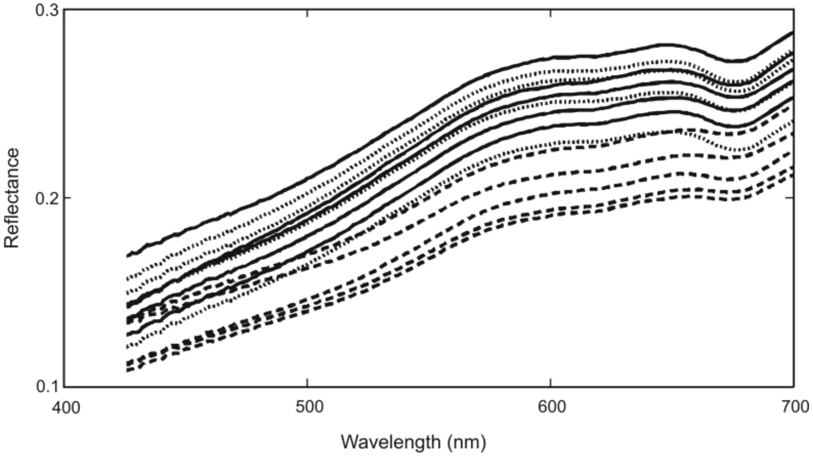

Figure 4: Detail of the reflectance spectra in the visible region of the light (545 nm and 630 nm) from all five replicates of the three different treatments. Control :dashed lines, low density: solid lines and high density: dotted lines.

For the clay absorption feature at 2,206 nm, scaled band area was zero for all treatments. The absence of a clay absorption feature was due to the absorption by water and the high signal noise in this region of the spectrum.

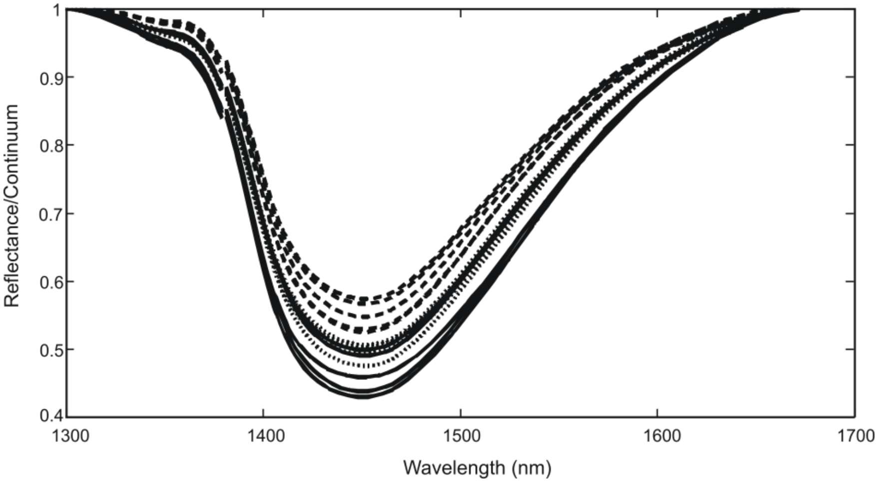

Figure 5: Continuum removed reflectance spectra at the water absorption feature at 1450 nm for all five replicates from the different density treatments. Control: dashed lines, low density: solid lines and high density: dotted lines.

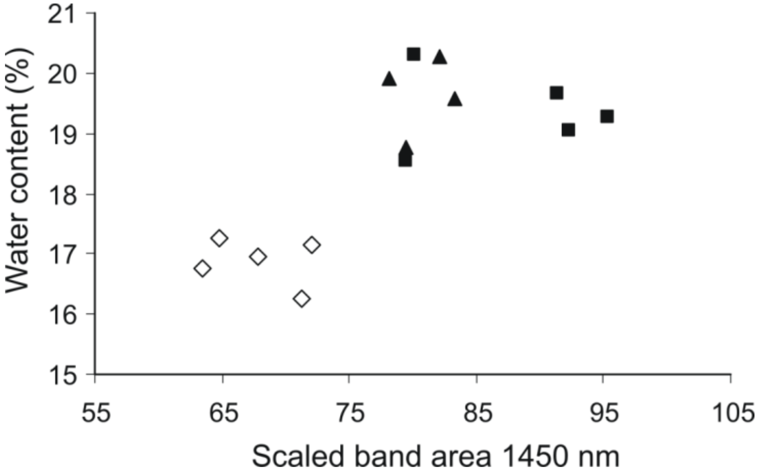

Figure 6: Scatterplot of scaled band area 1,450 nm versus water content (in %) for the different treatments (□ = Control, ■ = Low Density, ▲ = High Density)

4. DISCUSSION

4.1 Physical impact of *Corophium volutator*

Our experiment showed that whenever *Corophium* was present, both in low and high density, changes in water content of the surface sediment were visible, i.e. water content of the top half cm increased. No difference was detected between the two density treatments, but the difference between control sediment and sediment with *Corophium* was significant. Gerdol and Hughes (1994a) found results consistent with our study, while other studies found opposite results (Meadows and Tait, 1989) or no influence of *Corophium* on water content (Grant and Daborn, 1994; Limia and Raffaelli, 1997; de Deckere *et al.*, 2000). In our study, however, no biofilm was present (unlike in the above mentioned studies), to be able to focus on the effect caused solely by *C. volutator.* Thus, in our experiment, complexity was reduced by excluding confounding factors such as the presence of a biofilm, since it has been proven more than once that the presence of a biofilm increases water content of the sediment surface (Defew *et al.*, 2003; Orvain *et al.*, 2003). The presence of a biofilm might explain why in some studies no difference was found between a control with biofilm and treatments with *Corophium*. In a control treatment, the biofilm retains water, which increases water content. On the other hand, in the *Corophium* treatment, the biofilm is grazed upon by *Corophium* (Gerdol and Hughes, 1994b), so it does not retain water, but then again *Corophium* influences the water content due to bioturbation. This indicates that the impact of the presence of a biofilm and the presence of *Corophium* on the water content counterbalance each other and no significant effects are found. On the other hand, the absence of a biofilm could possibly affect bioturbation rates, since food is absent. As is generally the case for infauna (Rhoads, 1974), the presence of *C. volutator* led probably to an increase in pore space. In addition, the saturation on emersion increased, caused by retention of water due to the secretion of burrow linings (Meadows *et al.*, 1990; Gerdol and Hughes, 1994a), and this caused an increase in water content in the sole presence of *Corophium*. It should be considered however, that the drainage in the laboratory was different from natural conditions, since groundwater level was not able to drain as in natural conditions, and there was also no drying due to sun or wind. Nevertheless, conditions were constant and standard for all treatments, so we can expect that observations made were consistent, but the water content for this top layer was higher than in natural conditions, both for control and density treatments.

Another physical change visible in the top half centimeter due to bioturbation of *C. volutator* was the increase in mean grain size at high density. This increase was mainly caused by the significant loss of the clay fraction in the top layer. *Corophium volutator* is known to actively resuspend particles during feeding and burrowing (de Deckere *et al.*, 2000), and moreover, *Corophium* was observed to flush its burrows immediately after submersion (De Backer *et al.*, 2010). Both activities probably contribute to the loss of the finest particles, since these smallest, and thus lightest, particles resuspend easier and get washed away with the tides, while the heavier and biggest particles remain on the sediment surface. Only at high density, the decrease in clay percentage was significant indicating that only at high densities *Corophium* considerably contributes to the sediment grain size distribution. This result is consistent with a previous study that quantified bioturbation effects of *Corophium* using luminophores (De Backer *et al.*, unpublished data= Chapter 3). In that study, density of *Corophium* was found an important factor affecting the magnitude of bioturbation, and mainly high densities of *C. volutator* significantly contributed to sediment mixing (De Backer *et al.*, unpublished data).

4.2 Physical changes influencing remote sensing

Results showed that the changes in water content due to bioturbation of *C. volutator* affected the spectral reflectance. The higher percentage of water content in the treatments with *Corophium*, increased the reflectance of the visible light (545 and 630 nm). At low sediment moisture conditions, the sediment becomes darker (decrease in reflectance) with increasing sediment moisture, but this relation is reversed at a certain water content which is dependent on the soil hydrodynamic properties (Weidong *et al.*, 2002). This means that, for the high water contents of our sediment samples, the reflectance increases for higher water content and the change in reflectance is the highest in the visible light for sediment with high water content (Weidong *et al.*, 2002). This increase in reflectance can be explained by a water film covering all the sediment particles and changing the scattering processes (Neema *et al.*, 1987). The difference in water content between control and density treatments was also noted in an increase in light absorption at around 1,450 nm by water. The light absorption was quantified by the scaled band area of the water absorption feature, which is a better measure than the scaled band depth to quantify water content, because at these high water contents, the absorption dip not only becomes deeper, but also wider (Adam *et al.*, 2008). No differences in water absorption between density treatments were measured, which was consistent with the analysed water contents.

The small, but significant decrease in clay content on the sediment surface for the high density treatment did not influence the hyperspectral measurements. The clay absorption dip at 2,206 nm has been used in laboratory conditions in dry soils to assess differences in clay content (Lagacherie *et al.*, 2008; Adam, 2009) with a root mean square error of prediction between 3.5 and 5.8 weight % (Lagacherie *et al.*, 2008) and between 1.3 and 1.4 weight % (Adam, 2009). Since the differences in clay content for the control, low-density and high-density treatments were smaller than these error values, the clay absorption dip was not successful to detect changes in clay content between the treatments. Furthermore, the absorption dip was not visible in the spectra, since clay absorption degrades with increasing moisture content due to water absorbing light in this region of the spectrum (Adam *et al.*, 2008; Adam, 2009). In general, quantification of clay content in moist sediments using hyperspectral remote sensing is very difficult (Rainey *et al.*, 2003; van der Wal and Herman, 2007; Adam, 2009).

4.3 Some considerations and conclusions

Our laboratory results showed that the bioturbation activity of a species can influence the hyperspectral signal. *Corophium volutator* was used to test this objective, and we observed an increase in water content in the presence of *Corophium*. This increase could be measured hyperspectrally, through an increased reflectance in the visible light and an increase of scaled band area of the water absorption feature at 1.450 nm. With conventional destructive sampling, no difference was found between the low-density and high-density treatment, and this was consistently measured hyperspectrally. However, generalisation to other macrobenthic species should be done with care, because each species alters physical, chemical and biological characteristics of marine sediments in a different way (Rhoads, 1974; Aller, 1982; Meadows and Meadows, 1991; Hall, 1994; Rowden *et al.*, 1998). These macrobenthos-mediated effects on sediment processes are strongly influenced by species-specific life modes (Mermillod-Blondin *et al.*, 2005). Nevertheless, the application of remote sensing in the laboratory seems promising to address the impact of bioturbation in terms of water content. For *Corophium*, there was no difference in water content between different densities, but the hyperspectral results indicate that, if for other species differences in water content would exist and also be large enough and consistent, hyperspectral laboratory measurements should be able to detect them.

A decrease in clay content was measured at high densities of *Corophium*, probably due to resuspension and wash out of this finest fraction by bioturbation. This decrease was too small to be detectable by remote sensing. Airborne spectral measurements have been used to determine in situ sediment properties in an undisturbed manner (Ben-dor *et al.*, 2002; Carrère *et al.*, 2003; Deronde *et al.*, 2006; Lagacherie *et al.*, 2008). But even though hyperspectral airborne sensors, such as HyMap, contain the spectral detail necessary to quantify water absorption, it is not possible to extrapolate the obtained results from this study to field conditions, because we used a simplified ecosystem in which only one mechanism was studied. Yet in natural intertidal sediments, these comparatively simple relationships disappear, being replaced with complex interactions between the biological and physical components which create considerable temporal and spatial variability, resulting in apparently site-specific responses in the properties of sediment (Riethmüller *et al.*, 1998; Defew *et al.*, 2002; Chapman and Tolhurst, 2004). Nevertheless, this study showed that bioturbation can significantly influence remote sensing analyses. Thus, remote sensing for the assessment of environmental variables needs to take into account the potential impact of bioturbation activities, because they significantly affect reflectance properties.

Furthermore, this study proved the usefulness of the application of remote sensing to study biologically induced changes in sediment properties in a nondestructive manner. Future laboratory experiments studying animal-sediment relationships can gain advantage in using hyperspectral measurements. Changes in physical surface properties can be measured without disturbing the sediment surface and it is possible to follow up biologically reworked sediments in time. This can, especially, open new perspectives for long term experiments concerning the role of bioturbation on sedimentary processes.

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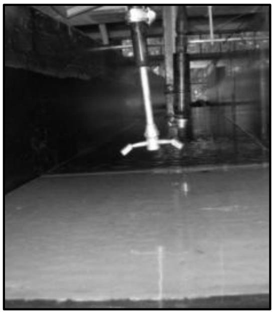
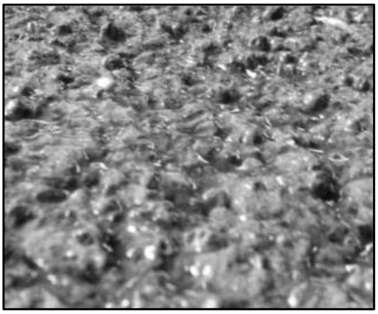
CHAPTER 5

EFFECT OF *COROPHIUM VOLUTATOR* ON THE ERODABILITY OF COHESIVE INTERTIDAL SEDIMENTS

Stefanie Adam, Annelies De Backer, Steven Degraer, Magda Vincx and Erik Toorman

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CHAPTER 5

EFFECT OF *COROPHIUM VOLUTATOR* ON ERODABILITY OF COHESIVE INTERTIDAL SEDIMENTS

ABSTRACT

Despite the importance of mudflats as natural sea defenses and wildlife habitats, the effects of various biota on cohesive sediment erosion are poorly understood. In this study, the influence of Corophium volutator on sediment bed erodability, expressed in terms of suspension erosion rate, critical flow velocity and critical shear stress for erosion, was investigated in a laboratory flume on cohesive sediment from a mudflat without and with different densities (4,000 – 20,000 ind./m^2) of Corophium volutator. Suspension erosion rate at the onset of erosion was determined with an Optical Backscatter Sensor, and critical shear stress for erosion was derived from turbulence measurements using an Acoustic Doppler Velocimeter. A significant exponential increase in suspension erosion rate with density was found, where sediment with 20,000 ind./m^2 showed a five times higher erosion rate than sediment without Corophium. On the other hand, critical shear stress was found to be independent of Corophium density, at least for densities up to 15,000 ind./m^2. At 20,000 ind./m^2, a large decrease (-30%) in critical shear stress was measured. Comparison between critical flow velocities obtained in this experiment and hydrodynamically simulated flow velocities over the mudflats where Corophium was collected indicates that bed erosion is unlikely to happen under natural flow conditions, but it might occur under storm conditions.

KEY WORDS: bioturbation, *Corophium volutator*, erosion rate, flume experiment, intertidal sediments

1. INTRODUCTION

The influence of biota on topography and landscapes is still largely unexplored (Gabet *et al.*, 2003; Dietrich and Perron, 2006). Erosion laws that explicitly include biotic effects are needed to explore how intrinsically small-scale biotic processes can influence the form of entire landscapes. To include biotic effects into erosion laws, these small-scale biotic processes need to be understood (Borcard *et al.*, 2004; Dietrich and Perron, 2006), e.g. explaining the self-organisation processes which are often seen in ecosystems requires knowledge on the small-scale biotic processes (van de Koppel *et al.*, 2005; van der Wal *et al.*, 2008b), and models including spatially explicit bio-physical interactions and scale-dependent processes (Borcard *et al.*, 2004).

The erodability of cohesive intertidal sediments is influenced by physicochemical sediment factors and biological factors (Berlamont *et al.*, 1993; de Brouwer *et al.*, 2000; Paterson *et al.*, 2000; Andersen, 2001; Amos *et al.*, 2004). Important physicochemical factors, which influence the erosion, but also the transport, deposition and consolidation of the surface sediment, are the water content, bulk density, grain size distribution and the mineralogy of the sediment particles (Dyer, 1986; Mitchener and Torfs, 1996; Winterwerp and van Kesteren, 2004; Yang, 2003). Physicochemical factors of cohesive sediments have been correlated with surface sediment stability for some time (Hayter and Mehta, 1986; Black, 1997; Dade *et al.*, 1992; Mitchener and Torfs, 1996; Winterwerp and van Kesteren, 2004), whilst it is only recently that biota have been included in the prediction of surface sediment stability (Paterson *et al.*, 2000; Paarlberg *et al.*, 2005). The biotic components can either hamper or enhance erosion, meaning that the consequences for sediment transport are either stabilisation or destabilisation (Willows *et al.*, 1998; Grant and Daborn, 1994; de Brouwer *et al.*, 2000; Widdows and Brinsley, 2002). Microphytobenthos has a stabilising effect through secreting extracellular polymeric substances (EPS), which stick sand grains together and form a protective biofilm (Yallop *et al.*, 1994; de Brouwer *et al.*, 2005; Le Hir *et al.*, 2007). Macrobenthos (bottom living animals > 1 mm) may influence the sediment and its dynamics in several ways: (1) by increasing the bottom roughness and/or making it more heterogeneous, (2) by inducing particulate fluxes, and (3) by changing the sediment erodability through bioturbation or stabilising processes (Le Hir *et al.*, 2007). The influence of macrobenthos on sediment behaviour is complex due to the diversity of the macrobenthos with different life modes for different species, and the fact that even for a single species, opposite effects can exist (Jumars and Nowell, 1984a).

For the mud shrimp, *Corophium volutator* (Crustacea, Amphipoda), some controversy exists about the (de)stabilising effect, since contradictory results have been reported (Grant and Daborn, 1994; de Deckere *et al.*, 2003), depending upon the age of the animals, density of the burrows and the sediment grain size (Le Hir *et al.*, 2007). *Corophium* is an abundant deposit and/or filter feeding species in intertidal mudflats. Population densities frequently reach > 20,000 ind./m^2, and in summer months densities can locally exceed 100,000 ind./m^2 (Gerdol and Hughes, 1994a). The high population densities make this amphipod an important species in many mudflat ecosystems, where it is a significant prey for migratory shorebirds and juvenile flounders (Boates *et al.*, 1995; Murdoch *et al.*, 1986). It lives in U shaped burrows in the upper 5 cm of the sediment (Meadows and Reid, 1966), and the burrow walls are strengthened with a mucus secretion (Meadows *et al.*, 1990). This reduces the erodability of the sediment (Grant and Daborn, 1994; Meadows and Tait, 1989), and may result in an elevation of the seabed (Mouritsen *et al.*, 1998). On the other hand, the U shaped tubes can protrude 1 to 1.5 mm above the sediment surface, and thereby increase sediment roughness (Meadows and Reid, 1966), which increases erosion rate (de Deckere *et al.*, 2003). Eckman and Nowell (1984) suggested that the protruding burrows enhance the microturbulence, resulting in scour around the burrow causing destabilisation. However, high densities of protruding structures can also hamper local hydrodynamics, and protect the sediment from erosion by increasing the height of the benthic boundary layer or even by replacing it to a higher position in the water column (cf. skimming flow by Friedrichs *et al.*, 2000). Furthermore, sediment erodability was observed to increase indirectly by grazing on the biofilm (Gerdol and Hughes, 1994a; Grant and Daborn, 1994; Hagerthey *et al.*, 2002), and directly through an increase in erosion rate caused by resuspension of fine sediment due to feeding and burrowing (de Deckere *et al.*, 2000). In addition, the resuspension of fine sediment can reduce biofilm biomass by inhibiting photosynthesis due to an increased turbidity (Dyson *et al.*, 2007).

Due to bioturbation of the top few centimeters, a mucus- and biodeposit-rich surface layer (often called the "fluffy" layer) is formed. Resuspension of these flocs and recently deposited material, not incorporated into the bed, occurs at low flow velocities and is termed type Ia erosion (Amos *et al.*, 1992; Orvain *et al.*, 2006; Widdows *et al.*, 2009). Widdows *et al.* (2009) found small influences of biota densities on the onset of type 1a erosion, and considered these critical velocities as not of great environmental significance. Erosion of the actual bed layer occurs at higher shear stresses, when large layers of sediment are eroded and mobilised. Bed erosion can be time dependent, i.e. exponential decrease of sediment release with time at constant flows (type Ib), or constant with time with a continuous release of sediment to the water column (type II) (Amos *et al.* 1992).

In this study, the main objective was to investigate the influence of *Corophium volutator* density on major bed erosion. For that reason, a flume experiment was set-up in which only one parameter i.e. density, varied between the treatments. We chose not to include a diatom biofilm, since this could be a confounding factor interfering with the interpretation of the density-erodability relationship, considering that biofilm biomass would probably be affected differently over time between the different density treatments.

2. Material and methods

2.1. Erosion flume and its instruments

The flume in the Hydraulic Laboratory of the K.U.Leuven is a straight flume of about 9 m long, 40 cm wide and 40 cm deep with a closed recirculating water system (Fig. 1). The water used in the flume is fresh water (0 psu), because of environmental constraints when discharging the water after the experiments in the Dijle river. The first 4 m of the flume is the inflow region with a rigid, wooden false bottom of 8 cm high to provide a fully developed turbulent flow in the test section. The test section is 2.9 m long but had to be shortened with a wooden false bottom to 40 cm for this experiment, because with the large section of 1.16 m^2, it was logistically impossible to collect enough animals to reach appropriate densities. The test section has glass walls on one side facilitating visual inspection of the sediment bed and the erosion processes. Downstream of the test section, a sediment trap was constructed with a length of 0.6 m to measure the bed load. The last part of the flume is the outflow section of 1.5 m long which prevents the flow from being disturbed by the sediment trap. A tail gate at the end of the flume can be used to regulate water levels, which varied between 14.3 and 20.5 cm.

The discharge through the flume was measured continuously with a calibrated Kent-Veriflux electromagnetic flow-meter (EMF). Velocities and turbulence were measured in three dimensions and at high frequencies (25 Hz) with a 16 MHz microADV (Acoustic Doppler Velocimeter) from Sontek. This instrument measures velocities in a cylinder of water with a diameter of 4.5 mm and a height of 5.6 mm at 5 cm from the instrument's transmitter and receivers. The turbidity was measured every second with an Optical Backscatter Sensor (OBS) at a distance of 3.5 cm from the bottom. The instrument was calibrated to relate the amount of scattering to the suspended sediment concentration (SSC).

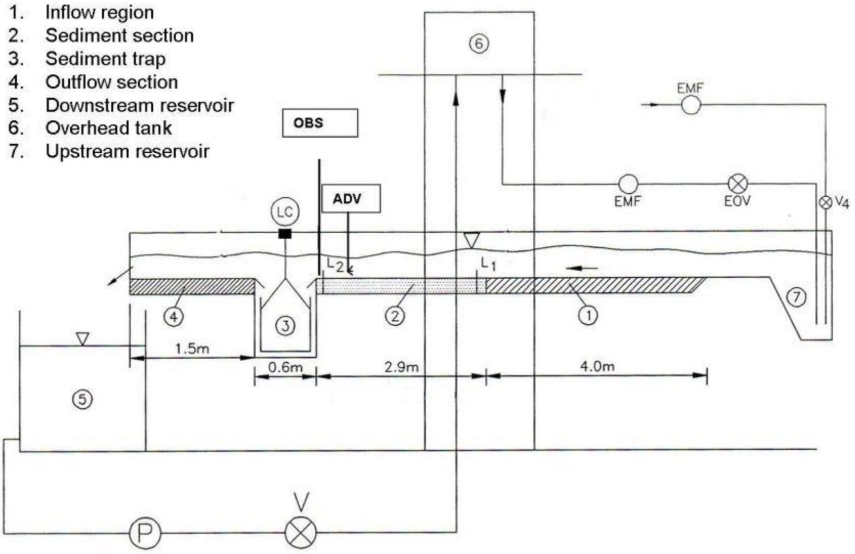

Figure 1: Side view of the rectangular flume.

2.2. *Corophium volutator* and sediment

Sediment and *C. volutator* were collected in June 2008 in the Flemish nature reserve "IJzermonding", a mudflat-saltmarsh area in Nieuwpoort (Belgium, 51°08'N, 2°44'E). The sediment was defaunated by three cycles of 24h freezing – 24h thawing. Grain size analysis (Malvern Mastersizer 2000 laser diffraction) showed that freezing-thawing did not alter median grain size (t-test, p=0.48). To reduce natural heterogeneity and to obtain equal starting conditions, the sediment was homogenised by thorough mixing and saturation with seawater before use. The sediment had an average median grain size of 140.6±SD 2 µm, and the following distribution over the different fractions: 7.6% was smaller than 4 µm, 25.1% between 4-38 µm and 4% between 38-63 µm, 9% between 63-125 µm, 33.8% between 125-250 µm, 20.3% between 250-500 µm and 0.04% between 500-800 µm. Eight sediment mesocosms were established by transferring the homogenised sediment into wooden boxes with the size of the test section (L:40 cm x W:40 cm x H:8 cm). Each box was filled completely with sediment, and gently submersed (without disturbing the sediment surface) in separate plastic aquaria for three days to allow the sediment to consolidate. All aquaria were placed in a temperature controlled climate room (16 ± 1° C) with a 12:12h light:dark regime.

After consolidation of the sediment, *C. volutator* was added to the sediment mesocosms in different densities. A density series of 0 (2x); 4,000; 6,000; 8,000; 10,000; 15,000 and 20,000 ind./m^2 was set up, leading to eight erosion experiments in total (2 references and 6 with *Corophium*). The density treatments were not replicated due to logistic and time constraints. The length and the sex of the experimental *Corophium* population was determined for 100 individuals: 69% females (9.2±0.3 mm), 16% males (9.4±0.3 mm) and 15% juveniles (1.6±0.01 mm). After the addition of *Corophium*, the aquaria were subjected to a simulated tidal regime, resembling the natural tidal conditions (i.e. 3h submersion and 9h emersion). Mortality in the mesocosm was very low and never exceeded 1.25%. After 6 days of biological activity, the mesocosms were put one by one, and ad random in the test section of the erosion flume before the start of the erosion experiment.

2.3. Erosion experiment

Sediment erodability is expressed in terms of critical shear stress for erosion, representing the interaction between the flowing water and the sediment bed at the onset of erosion, and the erosion rate, a measure of the amount of material eroded during time (Graf, 1971). During the erosion experiments, the average flow velocity, calculated as:

$$\overline{U} = \frac{Q}{WH}$$

with Q is the discharge, W is the width of the flume and H is the water level. Discharge in the flume was stepwise increased until erosion occurred, while flow parameters and suspended sediment concentration were measured. Stepwise increase in flow velocity was not constant between treatments, as a manual discharge regulator was used with which it was impossible to obtain constant discharge intervals.

2.4. Shear stress determination

Bed shear stress (for short ‘shear stress’ in this paper) was estimated from turbulence measured by an ADV (Song and Chiew, 2001; Biron *et al.*, 2004; Pope *et al.*, 2006; Andersen *et al.*, 2007). These single point measurements of turbulence should be acquired at the elevation of maximum Reynolds stresses. Based on low-Reynolds boundary layer theory and data, the peak stress can be estimated to occur at ±3% of the water depth (± 0.6 cm for a water level of 18 cm). However, it is practically not possible to position the ADV at such a distance of the sediment surface, because 1) the sampling volume of the ADV has a vertical dimension of 0.56 cm, 2) the sediment surface is not completely smooth, and 3) due to erosion the distance to the bed surface will change, hereby possibly positioning the sampling volume within the sediment. Therefore, the ADV sampling volume was placed at a distance of 1.5 cm from the sediment bed, which is equal to 7 to 10% of the water levels. In an experimental study in a similar laboratory flume, Biron *et al.* (2004) suggested undertaking single-point measurements at 10% of the water level, corresponding to the experimentally determined peak value height in profiles of Reynolds and TKE shear stress. The velocities should be measured for three minutes at 25 Hz to acquire enough samples for these methods based on second order statistics (Adam, 2009).

Shear stress was derived from the turbulent kinetic energy (TKE) as:

$$\tau_{TKE} = C_1\left[0.5\rho\left(\langle u'^2\rangle + \langle v'^2\rangle + \langle w'^2\rangle\right)\right]$$

where u', v' and w' are the velocity fluctuations in the stream wise, lateral and vertical directions respectively, < > denotes an average and C_1 is an empirically derived coefficient and equal to 0.19 (Huntley, 1988; Soulsby, 1983).

The critical flow velocity and shear stress were assumed to correspond to the flow velocity or local bed shear stress at the onset of a continuous increase in suspended sediment concentration measured by the OBS.

2.5. Erosion rate determination

The erosion flux is defined as the mass of sediment eroded per unit of time and per unit of area (kg/m^2s). It consists of bed load and suspended sediment.

The bed load could not be determined, because the load cell of the sediment trap was not sensitive enough for the small weights of the trapped sediment.

The rate of suspension is defined as the mass of sediment suspended per unit of time and per unit of area (kg/m^2s):

$$E_s = \frac{dC}{dt}H$$

where C is the depth-averaged suspended sediment concentration (SSC) and H is the average water depth. In practice, the change in SSC (= dC) was calculated as the difference between the averaged SSC (average of all OBS loggings at a discharge step) at discharge step *i+1* and the averaged SSC at discharge step *i*, where erosion starts at step *i*. In this formula, it was assumed that the water column was well mixed so that the suspended sediment concentration measured by the OBS at one water depth i.e. 3.5 cm, could be used as estimator of *C*. A SSC profile would increase the accuracy of E_s estimates considerably, but this was not available. Therefore, estimates of E_s should be considered qualitatively.

2.6. Statistical analyses

Simple linear models (lm) were applied in the statistical environment R (www.r-project.org) to test for relations between density and average critical flow velocity, critical shear stress and suspension erosion rate. The assumptions of linearity, homoscedasticity and independence of the errors were verified graphically. Normality of the residuals was confirmed numerically with a Shapiro Wilks test. Suspension erosion rate was square root transformed to meet the assumptions. Although, Cook's distance revealed that the density treatment of 20,000 ind./m^2 was an influential data point for erosion rate, it was biologically relevant and important to keep this treatment in the analyses. For critical shear stress, the normality and linearity assumptions were violated, no data transformation was appropriate, but addition of a quadratic term allowed to meet the assumptions. To test if density affected the relationship between suspended sediment concentration and average flow velocity after the onset of erosion, analysis of covariance was conducted to compare slopes of the regressions. Therefore, SSC values were dimished with SSC at the start of erosion to allow for comparison between the different treatments. To meet the assumption of linearity, average flow velocity was squared.

3. Results

3.1. Visual observations

At the highest density of *Corophium volutator* (20,000 ind./m^2), burrows were evenly distributed and covered the entire sediment surface (Fig. 1e), while for the lower densities, patchiness in burrow densities was observed (Fig. 1c). The sediment surface with *Corophium* burrows was heterogeneous, and with a more muddy and humid appearance compared to control treatments (Fig. 1). The turbidity of the water in the aquaria with *Corophium* increased at each flooding event. Even though the water velocity was almost 0, material was resuspended due to active resuspension of the animals flushing their burrows to remove accumulated faeces and excess sand grains (De Backer *et al.*, 2010). At the onset of the erosion experiments, active resuspension was observed as plumes of sediment flushed out the burrows. At higher velocities ($\bar{U}$=0.2-0.25 m/s), the sediment between the burrows eroded, leaving a smooth surface with protruding burrows. After further increase of the current velocity ($\bar{U}$) up to 0.35-0.5 m/s dependent on the treatment, a ridge appeared around the burrows, which eroded further till grooves were formed (Fig. 1d and f). This indicated the start of continuous erosion. For all *Corophium* treatments, local erosion around the burrows was observed, also for the low density treatmens (Fig. 1d).

3.2. Erodability measurements

Figures 3a and b show the critical average flow velocity and critical shear stress in relation to *Corophium* density. No significant regressions were found between critical average flow velocity or critical shear stress and density (Table 1), indicating that (lower) densities of *C. volutator* did not influence critical flow velocity or critical shear stress compared to the control sediment. However, for the density treatment of 20,000 ind./m^2, a large decrease in critical average flow velocity and critical shear stress was measured, on average respectively -25% and -30% compared to the sediment with no or less *Corophium* (Fig. 3).

For the initial suspension erosion rate (Fig. 3c), a significant (p=0.035) linear increase was found with density (Table 1). The significant relationship was influenced by the highest density of 20,000 ind./m^2, where the erosion rate of 0.0022 g/m^{2}s was five times higher than for the sediment without *Corophium* at the onset of erosion (Fig. 3c).

Table 1: Results of simple linear (polynomial) regression models to test for significance of *Corophium* density on critical average flow velocity (U_{crit}), critical shear stress (τ_{crit}) and suspension erosion rate. Significant p-levels are bold.

Variable	Predictor	Coefficient (SE)	p-value	Regression	
				p-value	R² adj
τ_{crit}	Intercept	0.16 (0.014)	0.0007	0.19	0.28
	Density	$4.7*10^{-6}$ ($3.4*10^{-6}$)	0.24		
	Density²	$-3.1*10^{-10}$ ($1.7*10^{-6}$)	0.13		
U_{crit}	Intercept	47.1 (2.7)	<0.0001	0.13	0.23
	Density	$-4.6*10^{-4}$ ($2.6*10^{-4}$)	0.13		
Erosion rate (sqrt)	Intercept	$2.1*10^{-2}$ ($3.4*10^{-3}$)	<0.0001	**0.035**	0.48
	Density	$9.1*10^{-7}$ ($3.3*10^{-7}$)	**0.035**		

Figure 2: Pictures showing different density treatments before and after erosion. A: Control before erosion, B: Detail of control after erosion with visible erosion of thin sediment flakes, C: 4,000 ind./m² before erosion, D: Detail of 4,000 ind./m² after erosion with local erosion around the burrows, E: 20,000 ind./m² before erosion and F: Detail of 20,000 ind./m² after erosion with protruding burrows and visibly erododed sediment between the burrows.

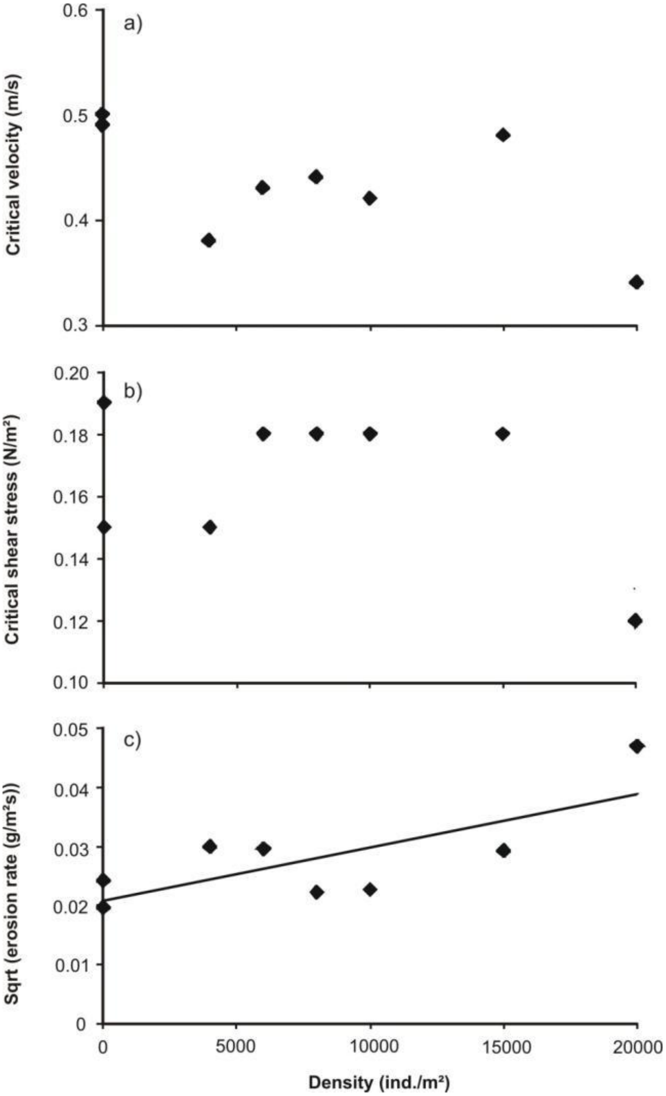

Figure 3: Critical average flow velocity (a), critical shear stress (τ_{crit}) (b) and square root transformed erosion suspension rate (c) for different densities of *Corophium volutator.*

The relationships between delta SSC (SSC dimished with SSC at the start of erosion) and the squared average flow velocity at the different *C. volutator* densities are illustrated in Figure 4. Slopes are significantly different between treatments (ANCOVA, $F_{7,\ 31} = 9.6$, $p<0.0005$), and although not consistent, the general trend is that the suspended sediment concentration increases faster with average flow velocity for higher densities of *Corophium volutator*, once erosion has started. This indicates that a higher degree of bioturbation due to higher densities, increases the amount of sediment that is eroded. Especially for the treatment of 20,000 ind./m^2, larger amounts of sediment were eroded at lower flow velocities compared to the lower densities and the references (Fig. 4).

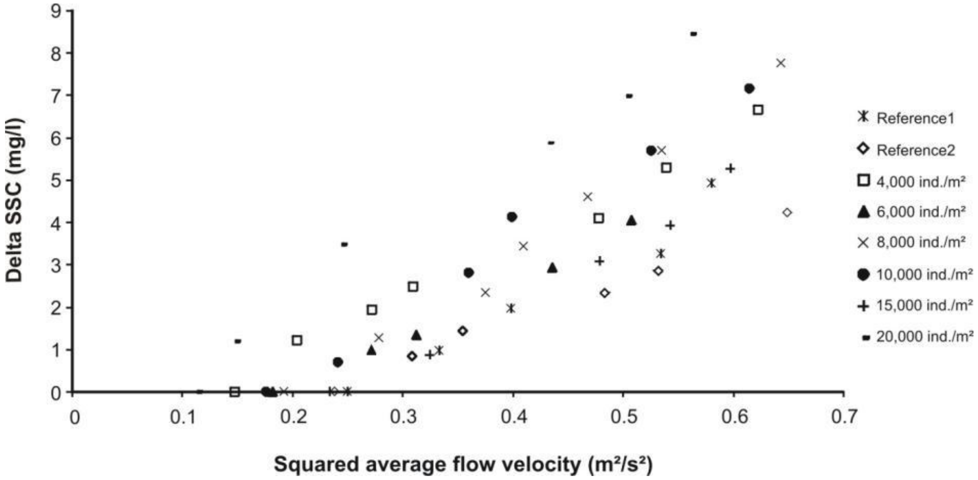

Figure 4: Relationship between suspended sediment increase (SSC, mg/l) and squared average flow velocity for varying densities of *Corophium volutator* after the onset of erosion.

4. Discussion

4.1. Considerations on flume experiments

Although it is the shear stress that controls the incipient motion of particles in flowing water (Léonard and Richard, 2004), the use of critical average flow velocity (Widdows *et al.*, 2000b; Ciutat *et al.*, 2007) can be justified, because in similar flow conditions in the same erosion flume, there exists a relation between average flow velocity and bed shear stress of the form $\tau_b = \mathrm{A}\overline{U}^2$, where A is a characteristic of the flume (Toorman and Luyckx, 1997). Until now, there exists no standardised experimental set-up or method to determine shear stress. Therefore, it is difficult to compare absolute values of shear stress between different studies, since differences in the experimental set-up and the determination of shear stress will give different absolute values (Tolhurst *et al.*, 2000; Adam, 2009). In our flume, turbulence measurements were preferred to bottom shear stress derived from the logarithmic profile, since the flume was too short to develop a logarithmic profile (Adam, 2009). Moreover, turbulence was easier and quicker measurable than a velocity profile. Reynolds stresses were neither measured, because these are highly sensitive to tilt and secondary currents (Adam, 2009; Kim *et al.*, 2000; Nezu and Nakagawa, 1993), which cannot be avoided in a narrow flume. Turbulence measurements at a certain depth rely on the assumption that the sampling volume of the ADV is located at the peak stress elevation, which was taken as 7-10% from the water depth. From Direct Numerical Simulation (DNS) data, it is known that the shear stress is not constant over the transition layer near the bottom, and that the peak stress elevation is very close to the bottom (~3% of the water depth for the present flume). However, as explained above, it was practically impossible to take measurements at this peak stress distance. Nevertheless, Adam (2009) concluded that turbulence measurements were reproducible and easiest to perform. Since the sediment bed is homogeneous and air bubbles are avoided by thorough mixing, the point ADV measurements can be assumed to be valid for the whole sediment bed.

4.2. Impact of *Corophium volutator* on erodability

Corophium has several mechanisms to influence sediment erodability. It is essentially a deposit feeder, and deposit feeders have the tendency to physically eject sediment into the overlying water column (Graf and Rosenberg, 1997). *Corophium* was previously observed to flush its burrows during submersion (De Backer *et al.*, 2010), and the same observation was made in this study. de Deckere *et al.* (2000) concluded that this active resuspension significantly affected the suspended sediment concentration (SSC) in the water column at low flow velocities (<0.2 m/s), and that the SSC increased with increasing density. Deposit feeders are also known to disrupt the cohesive sediment structure making the surface sediment more susceptible to erosion (Graf and Rosenberg, 1997). Disruption of the surface sediment structure by *Corophium* is mainly due to feeding (scraping) and crawling on the sediment surface, which loosens sediment particles, so they can be more easily eroded. In the presence of a biofilm, feeding might as well indirectly influence sediment stability by decreasing the sediment stability due to reduction of the stabilising diatoms (Daborn *et al.*, 1993; Gerdol and Hughes, 1994a; Chapter 6). However, no biofilm was added in this flume experiment to stabilise the sediment, since this could impede the interpretation of the density-erodability relationship. Hence, feeding activity was most probably reduced, which might result in lower bioturbation activity (Nogaro *et al.*, 2008). Furthermore, *Corophium* activities increase the surface water content (Gerdol and Hughes, 1994a; De Backer *et al.*, 2009), which is positively related to erosion rate (Fukuda and Lick, 1980; Aberle *et al.*, 2004). The burrows built by *Corophium* might also influence sediment erodability, since they increase bottom roughness on the one hand, and strengthen the sediment with mucus secretions on the other hand. The activities of *Corophium* mainly impact the surface layer, and as such they mainly influence fluff layer erosion, characterised by (passive) floc resuspension at low stresses (Type 1a erosion; Amos *et al.*, 1992). In this experiment, fluff layer erosion was not directly measured, since that occurs at low current velocities of ± 9 cm/s and 11-12 cm/s (de Deckere *et al.*, 2003; Widdows *et al.*, 2009), and our erosion experiments started at 11 cm/s. Therefore, we measured bed erosion in relation to different densities of *Corophium*. We are aware that replication of our density treatments would have been much more powerful, but due to time and logistic constraints, replication was not possible. Therefore, the results should be treated with caution and ideally, similar experiments should be repeated with replicated treatments. Nevertheless, we observed that the effect of *Corophium* was predominantly an increase in suspension erosion rate with increasing density, and not a change in erosion threshold (τ_{crit}). A similar relationship between erosion rate and density was observed for other deposit feeders such as *Macoma balthica* (Willows *et al.*, 1998), *Nereis diversicolor* (Fernandes *et al.*, 2007; Widdows *et al.*, 2009) and *Hydrobia ulvae* (Andersen *et al.*, 2002; Orvain *et al.*, 2006). de Deckere *et al.* (2003) had results consistent with ours for *Corophium*, although the density range was much smaller. The increase in erosion rate was mainly caused by an increase of bottom roughness due to the burrow structures of *Corophium*, but active resuspension due to flushing and passive resuspension due to disruption of the sediment structure probably also contributed slightly to the increase in suspended sediment. Initial erosion of the sediment between the burrows was most probably due to a combination of a local increase in shear stress between the burrows and the sediment being more susceptible to erosion because of *Corophium* bioturbation. This led to a surface with protruding burrows, which resisted erosion due to the strengthening with mucus (Meadows *et al.*, 1990). These protruding burrows caused a further local increase in shear stress (Eckmann and Nowell, 1984), and this resulted in scour around the burrows and increased suspended sediment concentration.

No relationship was found between critical shear stress and *Corophium* density. Several authors found a similar independence of τ_{crit} for macrobenthos density of different species (*Cerastodema edule* by Ciutat *et al.*, 2007; *Hydrobia ulvae* by Andersen *et al.*, 2002 and Orvain *et al.*, 2006; *Macoma balthica* by Willows *et al.*, 1998 and *Nereis diversicolor* by Widdows *et al.*, 2009). However, for a density of 20,000 ind./m^2, a large decrease in critical shear stress was observed, which could be explained by the increase in bottom roughness with increasing densities. At this density, the entire sediment surface was covered with burrows, which resulted in a surface covered with small elevations and pits (Fig. 1e), and this influences the bottom current. In contrast, at the lower densities, burrows were more aggregated in patches (often at the edges of the mesocosm) (Fig. 1c), and in between the sediment surface was smooth, resembling the control sediments. These aggregations of *Corophium* individuals are the result of natural behaviour because high density patches on the cm-scale are also observed in the field, especially in winter when densities are lower. This patchiness is caused by intraspecific interactions among *Corophium* individuals or possibly through active aggregation (Lawrie *et al.*, 2000). Our results for independence of τ_{crit} at densities lower than 15,000 ind./m^2 are consistent with de Deckere *et al.* (2003) and Grant and Daborn (1994) for *C. volutator.* However, to our knowledge no other flume studies measuring critical shear stresses were performed with densities higher than our density of 20,000 ind./m^2. So, it would be interesting to see if shear stress further decreases when density is further increased or if it increases. When the density of burrows is high enough, theoretically at 47,000 ind./m^2 according to Nowell and Church (1979), a skimming flow may develop. A 'skimming flow' occurs when the spacing between the roughness elements is equal to or less than the element height (Vogel, 1994), and it leads to a shift of the stress peak above the tube tips resulting in sediment stabilisation and sediment deposition (Friedrichs *et al.*, 2000), which might also decrease suspension erosion rate.

Whether erosion of the intertidal sediments inhabited by *Corophium volutator* will occur in the field, not only depends on sediment stability, but also on the hydraulic stresses present on the tidal flat. A hydrodynamic model for the IJzermonding (Giardino *et al.*, 2009) shows that maximum average flow velocities over the intertidal flats with *Corophium* are around 0.1-0.25 m/s (equivalent to a bed shear stress of 0.024 - 0.15 N/m^2) dependent on the location on the mudflat. This means that, according to our results (see Figure 2a), bed erosion will rarely occur under normal weather conditions, since erosion started only at 0.34-0.5 m/s (0.12 – 0.18 N/m^2) in our experiments. However, hydraulic stresses can be higher under storm conditions or on *Corophium* inhabited mudflats with a different morphology. For instance on the Heringplaat in the Dollard Estuary, a maximum flood current was measured of 0.4 m/s equivalent to a maximum shear stress of 0.3 N/m^2 (de Deckere, 2003), which could cause enhanced erosion in the presence of *Corophium* in the field. On the other hand, a study in the Westerschelde, showed that *Corophium* predominantly occurred at low current velocities upto 0.25 m/s (Ysebaert *et al.*, 2002b). The preference for low current velocities could, hence, be a matter of ensuring its own habitat because bed layer erosion could favour other competing species because sediment properties change. SSC was not measured at low flow velocities in this study but active resuspension by *Corophium,* especially at high densities, and fluff layer erosion may significantly contribute to resuspension of sediment in the water column (de Deckere *et al.*, 2000).

Although this paper is limited to a laboratory experiment to assess the influence of *Corophium* on sediment erodability, we believe that this kind of experiments are needed to include the complex effect of biota in sediment transport models. Firstly, the results of such flume experiments should be used to calibrate a model explaining the rate of erosion. E.g. Willows *et al.* (1998) modeled the increase in resuspension due to the bivalve, *Macoma balthica*, with 9 parameters, including the excess flow velocity above a critical flow velocity. Secondly, the model should be checked for its application in natural situations by performing field experiments with realistic flow conditions. A third step could be the inclusion of the model in sediment transport models which have enough spatial detail to include *Corophium* inhabited areas. Since our experiments show that *Corophium* enhances sediment erodability only if highly abundant, the decrease in critical shear stress for erosion and the increase in rate of suspension should only be included in simulations covering late spring and summer time when the *Corophium* densities are highest (Chapter 6). However, currently, sediment transport models are not accurate enough and can not run simulations with the high detail needed to include biotic effects.

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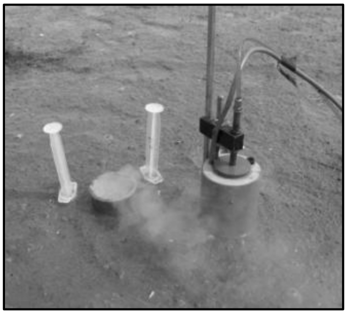
CHAPTER 6

THE ROLE OF BIOPHYSICAL INTERACTIONS WITHIN THE IJZERMONDING TIDAL FLAT SEDIMENT DYNAMICS

Annelies De Backer, Carl Van Colen, Magda Vincx, Steven Degraer





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CHAPTER 6

THE ROLE OF BIOPHYSICAL INTERACTIONS WITHIN THE IJZERMONDING TIDAL FLAT SEDIMENT DYNAMICS

ABSTRACT

This paper focuses on the importance of biophysical interactions on short-term and long-term sediment dynamics. Therefore, various biological (macrobenthos, photopigments, colloidal EPS) and physical parameters (grain size, water content, sediment stability, bed level) were determined (bi)monthly in nine sampling plots on the IJzermonding tidal flat (Belgium, 51° 08'N, 2°44'E) during three consecutive years (July 2005-June 2008). Results showed that sediment stability varied on a short timescale and was directly influenced by biota, while bed level varied mainly on the long-term due to interannual variability. The short-term dynamic relationships between mud content, water content, fucoxanthin and macrobenthos density resulted in a seasonal mud deposition and erosion cycle, and directly influenced sediment stability. Moreover, macrobenthos was proven to be the most important parameter determining sediment stability. On the long-term, a shift was observed from high fucoxanthin/chla concentration, high mud content and zero to moderate densities of Corophium volutator towards low fucoxanthin/chla and mud content and high Corophium densities, which resulted in a transition from net accretion to net erosion. However, most measured variables proved to be poor predictors for these long-term bed level changes, indicating that external physical forces, such as waves and storminess, probably were the most important factors triggering long-term sediment dynamics. Nevertheless, biota indirectly influenced bed level changes by mediating short-term changes in sediment stability, thereby influencing the erodability of the sediment. The macrobenthos, and especially the mud shrimp Corophium, was suggested as the (indirect) driving destabilising factor for the sampling plots in the IIzermonding when considering the long-term evolution.

KEY WORDS: Belgium, biophysical interactions, *Corophium volutator*, mudflat, short-term and long-term variability, sediment dynamics, sediment stability

1. INTRODUCTION

Estuarine mudflats are sedimentary intertidal habitats created by sediment deposition in low energy coastal environments. They are areas of both ecological and economic importance and are increasingly threatened by climatic and anthropogenic pressures (Dyer *et al.*, 2000; Worm *et al.*, 2006). Therefore, it is important to understand and predict the morphodynamics of these estuarine environments, and thus knowledge on tidal flat erosion and deposition processes is indispensable. The physical processes that dominate sediment transport have been relatively well studied, and they determine the magnitude of sediment transport to or from a mudflat. These physical processes are mainly driven by tidal currents (Postma, 1961; Bell *et al.*, 1997) and wind generated waves (de Jonge and van Beusekom, 1995; Bell *et al.*, 1997; Ralston and Stacey, 2007). However, it has become increasingly clear that biotic components of the ecosystem can exert significant influences on the erosion and deposition processes in sediments (Woodin and Jackson, 1979; de Brouwer *et al.*, 2000; Montserrat *et al.*, 2008). The biotic components can either hamper or enhance erosion, resulting in bed stabilisation or destabilisation respectively (Orvain and Sauriau, 2002). Microphytobenthos has a stabilising effect due to the secretion of extracellular polymeric substances (EPS), glueing sand grains together and forming a protective biofilm (Yallop *et al.*, 1994; De Brouwer *et al.*, 2005; Le Hir *et al.*, 2007). Macrofauna may influence the sediment and its dynamics in several ways, for instance by (1) increasing the bottom roughness and/or the heterogeneity, (2) inducing particulate fluxes, and (3) changing the sediment erodability through bioturbation processes (Le Hir *et al.*, 2007). The influence of macrobenthos on sediment behaviour is complex due to the highly diversified life styles, and the fact that even for a single species, opposite effects can exist (Jumars and Nowell, 1984). For instance, some controversy exists about *Corophium volutator*, for which both stabilising (Meadows and Tait, 1989; Mouritsen *et al.*, 1998) and destabilising (Gerdol and Hughes, 1994; de Deckere *et al.*, 2003) effects have been described depending upon the age of the animals, the density of the burrows and the sediment grain size (Le Hir *et al.*, 2007). The overall importance of the role of *Corophium* in the long term sediment dynamics of an intertidal flat, however, remains unclear.

Morphological changes of intertidal areas are the net result of competing accretionary and erosionary processes, with different processes dominant at different times. Long-term changes are the balance of larger changes occurring over shorter time-scales (Wood and Widdows, 2002). The biotic components in estuarine systems are often seasonally and annually influenced, so it is important to include this temporal variability in measurement programs to understand the sediment dynamics (Defew *et al.*, 2002). Borsje *et al.* (2008) demonstrated that excluding the temporal variability from their model of sediment transport generated a less accurate model, because the influence of the biota was no longer visible. So far, most field studies lasted for one year or less, as such including seasonal variability, but disregarding interannual variability to investigate sediment dynamics and the role of biophysical interactions. We investigated longer term variability on a spatially limited scale, in order to enable the assessment of the main biophysical factors determining long term sediment dynamics.

The objectives of the study were:

1) to analyse the long-term (interannual), short-term (seasonal) and small-scale spatial dynamics between biota, physical sediment properties and sediment dynamics
2) to quantify the relative importance of the different biophysical variables on long-term erosion and deposition and on sediment stability
3) to determine the importance of *Corophium volutator* density in relation to long-term sediment dynamics

2. MATERIAL AND METHODS

2.1. Study site and sampling design

The study was conducted in the Flemish nature reserve ‘IJzermonding’, a mudflat-salt marsh area along the eastern shore of the river IJzer in Nieuwpoort (Belgium, 51° 08’N, 2°44’E) with a tidal range of approximately 4.5 m (Fig. 1). Between 1999 and 2003, nature restoration works were conducted in the northern part of the area and until today, this part of the area is still recovering from the restoration works (Herrier *et al.*, 2005). Because one of our objectives was to determine the importance of *Corophium volutator* in sediment dynamics, our study took place in the undisturbed SE part of the mudflat. More precisely in the upper part of the middle flat (+3.72 m - +4.13 m TAW (Tweede Algemene Waterpassing)), where *Corophium volutator* is the dominant deposit feeding organism with densities as high as 120,000 ind/m^2 in summer.

Nine rectangular sampling plots (0.7 m x 1 m) were installed over a horizontal distance of 110 m at the study site, so all plots had a similar inundation time (3-4 hours)(Fig. 1). Each sampling plot constituted of a rectangle of 0.7 m^2 and with at each side in the middle a metal pole (separated by 1m) used for bed level measurements. These poles had a total length of 1 m 50 cm, of which 1 m 20 cm was pushed in the sediment to avoid movement of the poles; the remaining 30 cm rose above the surface.

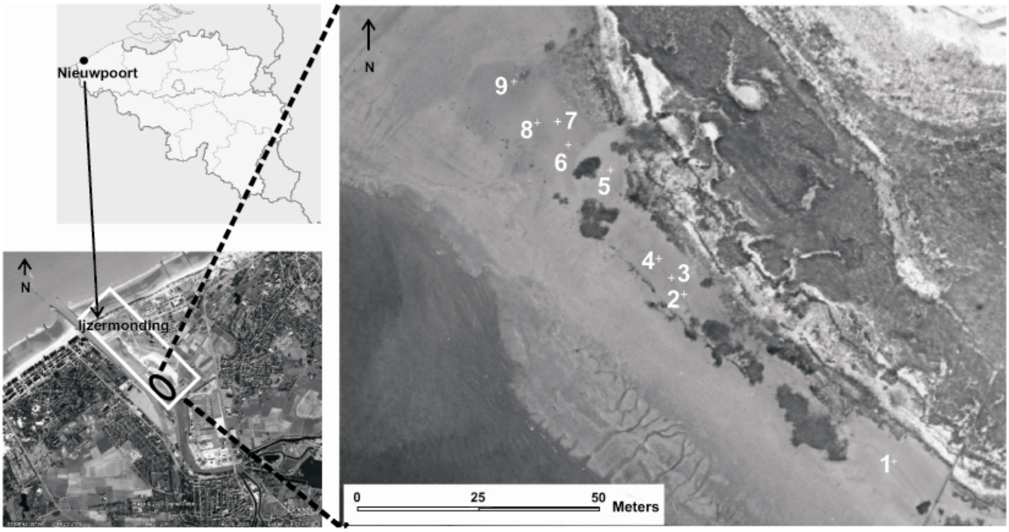

Figure 1: Location of the intertidal mudflat area 'IJzermonding' (Nieuwpoort, Belgium) and the sampling plots within the study area.

Sampling was carried out monthly from July 2005 to December 2006 (except July 2006) and bimonthly from January 2007 to June 2008. In order to minimise edge effects, the outer rim of the plot, next to the poles (0.1 m wide), was not sampled, while the middle section of the plot between the poles (0.3 m wide) was not sampled to avoid disturbance of the bed level. The remaining area at both sides of the poles was divided into 15 subquadrats (0.1 m x 0.1 m) (Fig. 2). On each sampling day, 2 replicate subquadrats (randomly chosen *a priori*), one at each side of the poles, were sampled. When all subquadrats were sampled once (i.e. after 15 months), random selection of subquadrats started again, making sure that there was at least 5 months between sampling of the same subquadrat. At all sampling times, bed level measurements were made in the undisturbed middle section, and sediment was sampled in the subquadrats for analysis of grain size, chlorophyll a (chl*a*), water content and macrobenthos. From November 2005 onwards, fucoxanthin was determined as well. Sediment strength and colloidal EPS (extracellular polymeric substances) were measured from March 2007 onwards. After collecting the samples, the holes were refilled with similar sediment from just outside the plot to avoid changes in current patterns, which might affect erosion processes or bed level.

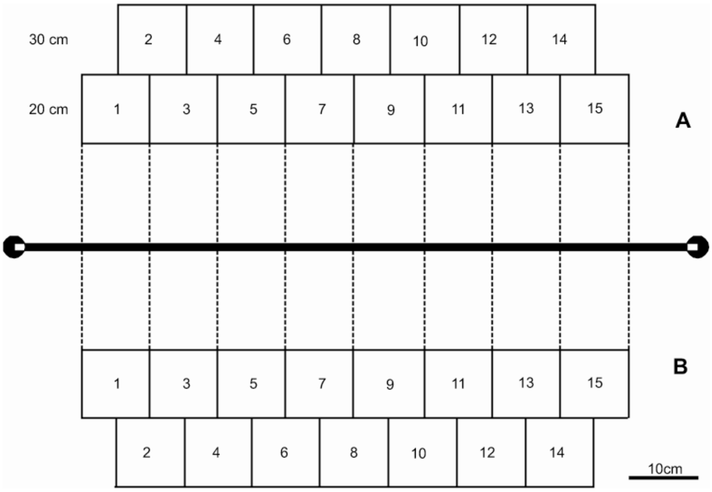

Figure 2: Overview of one sampling plot with indication of the poles (black circles) and horizontal bar (thick black solid line) used for bed level measurements. The area between the poles and 15 cm at both sides of the horizontal bar (length of the dotted lines) was not sampled to avoid disturbance of the sediment surface. The numbered squares indicate the different subquadrats (10 x 10 cm), in which the different variables were sampled. At each sampling occasion, two randomly selected subquadrats were sampled, one at the A side and one at the B side to incorporate possible small-scale variation.

2.2. Sampling and laboratory analyses

***Chla, fucoxanthin and colloidal EPS**:* Chl*a* and fucoxanthin are both photopigments present in diatom cells, and were measured because they provide a good proxy for diatom biomass. cEPS consists mainly of polysaccharides, excreted by diatoms and involved in vertical migration (Underwood and Smith, 1998). Since, cEPS is known to play an important role in sediment stabilisation (e.g. Underwood and Paterson, 1993; Le Hir *et al.*, 2007), it was important to measure the cEPS concentration in conjunction with the erosion threshold. Sediment material for quantification of photopigments (chl*a* and fucoxanthin) and colloidal EPS (cEPS) was collected using contact cores (Ø 43 mm), enabling the collection of ± 2 mm thick frozen discs of sediment (Wiltshire *et al.*, 1997), which were wrapped immediately in aluminium foil and stored in liquid nitrogen. On return to the laboratory, all samples were stored in the dark at -80°C until analysis. Prior to analysis, the frozen discs were lyophilised in the dark. Chl*a* and fucoxanthin concentration were determined by HPLC analysis from the supernatant, extracted from a subsample of the freeze-dried sediment by adding 10 ml 90% acetone – 10% milliQ water solution (Wright and Jeffrey, 1997). Colloidal EPS was quantified by spectrophotometer using the phenol-sulfuric acid assay (Dubois *et al.*, 1956) and calibrated standards of D-glucose dissolved in MQ water. Carbohydrates were extracted from 1 g of freeze-dried sediment with 5 ml of MQ water for 1h at 30°C followed by centrifugation for 15 min at 1500 rpm.

***Grain size and water content**:* Samples were taken from the upper 6 cm of the sediment with 10 ml syringes (Ø 13mm), stored in an icebox and sliced at 1 cm depth upon return in the laboratory. Awaiting analysis, samples for water content were stored in the freezer (-20°C), whereas samples for grain size were left to dry at the air until analysis. For water content, sediment was weighed wet, lyophilised and weighed dry to yield water mass percentage or absolute water content (Flemming and Delafontaine, 2000). Water content was calculated as the difference of wet and dry sample weights divided by the wet sample weights.

Grain size distribution was determined using a Malvern Mastersizer 2000 laser diffraction, capable of analysing the 0.02 μm to 2 mm grain size range. The mud/sand boundary was determined at 63 μm, with the mud fraction defined as < 63 μm. Since it are the surface sediment properties that influence the biofilm, erosion threshold and bed level, only the results of the top 1 cm slice were used in the statistical analyses and throughout the entire paper.

***Macrobenthos**:* The macrobenthos was sampled to a depth of 10 – 15 cm with a 10.2 cm^2 core. Macrobenthos samples were taken on the same spot as the contact core to reduce disturbance of the plot as much as possible. When animals were retained in the contact core, these were removed and added to the macrobenthos sample. Samples were fixed with a buffered 4% formalin solution and taken to the lab in closed containers. The samples were sieved over a 0.5 mm mesh sieve and preserved using a neutralised 4% formalin solution with 0.01% Rose Bengal until processing. All macrobenthos was sorted under a stereomicroscope, counted and identified to species level, except for tubificid oligochaetes and insect larvae.

Bed level and sediment strength measurements: For bed level measurements, a horizontal bar of 1 m was placed on top of the two poles. The bar had five holes, separated from each other by 15 cm starting 20 cm from the edge of the bar. Bed level changes were measured in the undisturbed middle section of the plot at these holes as the distance between the bar and the sediment surface (accuracy of ± 1mm). The results from July 2005 were used as reference point. The sediment strength or erosion threshold was quantified as a measure of erodability of the sediment under a certain bottom shear stress using a cohesive strength meter (CSM) (Tolhurst *et al.*, 1999; Defew *et al.*, 2002). The CSM fires a jet of water to the sediment surface, disrupting the sediment matrix at the sediment-water interface. A series of tests with increasing pressure of the water jet is performed, according to the 'Mud 3' program of the CSM Mk 4 (Sediment Services, UK). The point of incipient erosion was determined as the pressure at which the light transmission in the measuring cell decreased below 90%.

2.3. Statistical analyses

Multivariate analysis: To be able to visualise the temporal evolution in the different sampling plots, the plots were grouped based on the normalised environmental variables measured during the first sampling occasion (July 2005). Therefore, a group averaging cluster analysis was performed based on Euclidean distance similarity followed by a similarity profile test (SIMPROF) using the software package Primer v6 (Clarke and Gorley, 2006). The defined groups were used for further visual representation.

ANOVA of univariate data: To conduct ANOVA, the categorical predictor 'season' was introduced with 'winter' representing sampling occasions from December to February, 'spring' representing sampling occasions from March to May, 'summer' representing sampling occasions from June to August, and 'autumn' representing sampling occasions from September to November. Main effects ANOVA was carried out in Statistica 7 to test whether the variation in *Corophium volutator, Hediste diverisolor*, total abundance of other macrobenthos (i.e. total abundance – abundance of *Corophium* and *Hediste*) and environmental variables depended on the categorical predictors year, season and sampling plot, and the interaction term year x season. Sampling plot was identified as a random effect in the analysis. To warrant homogeneity of variance, some variables were transformed i.e. ln(x+1) for colloidal EPS and erosion threshold.

Regression analysis: Two generalised linear models (GLMs) based on maximum likelihood estimation were applied in the statistical environment R (www.r-project.org) to test the response of bed level variation and sediment stability to the environmental variables and the faunal densities. Before running the model, collinearity among variables was examined using Spearman rank correlation coefficients. If a linear dependency between variables was identified ($r>0.8$) only one of the variables was retained in the model. The models were based on stepwise elimination/addition (both forward and backward) of predictors. The minimal adequate model (MAM) was reached based on the lowest Akaike's Information Criterion[16] (AIC, Sakamoto *et al.*, 1986; Crawley, 2005;). We used a gaussian distribution with an identity link[17]. In addition, $D^2_{adjusted}$ was calculated for each model as an estimate of deviance reduction, adjusted for the available degrees of freedom, analogous to R^2_{adj} in least-squares regression (Guisan and Zimmerman, 2000). Furthermore, in order to partition the effects of all significant predictors, the relative importance for each predictor was calculated using the R package relaimpo (Grömping, 2006). From this package, the metric 'lmg' was used, which is based on sequential D^2's by using simple unweighted averages (Grömping, 2006). This metric allowed the calculation of the amount of variance explained from the total variance of the model by each significant predictor in the model.

To test for the variables contributing to bed level changes, the bed level variation between two successive sampling occasions was combined with the averages of the variables measured during these two sampling occasions. Bed level variation was expressed as a polynomial function (linear predictor) of the mud content (median grain size was omitted from the model because of collinearity), chl*a* concentration, water content, *Corophium volutator* density, *Hediste diversicolor* density and other macrobenthos density. Mud and water content were arcsine-square root transformed; all other variables were natural-log transformed to obtain normal distribution of the residuals. Only cases with information on all variables were used in the modeling. Assumptions were verified graphically (residual errors vs fitted values, scale-location plot, Cook's distance), and normality of the residuals was confirmed numerically with a Shapiro-Wilks test. Six cases appeared to be extreme outliers (Cook's distance) and these were omitted from the analysis (n=434).

Log transformed sediment stability was regressed as a polynomial function (linear predictor) of mud content (median grain size was omitted from the model because of collinearity), water content, fucoxanthin concentration (chl*a* omitted because of collinearity), cEPS concentration, *Corophium* density, *Hediste* density and other macrobenthos density. Only cases with information on all variables were used in the

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[16] AIC compares the trade-off between goodness-of-fit of the models and parsimony of the models, smaller values of AIC indicate a better model. The model with the lowest AIC is the best model, aka the MAM.

[17] Since the response variables, bed level variation and sediment stability, are continuous variables that are normally distributed, we used the Gaussian distribution for which the identity link is most commonly used.

modeling (n=138). Assumptions here were also verified graphically, and normality of the residuals was confirmed numerically with a Shapiro-Wilks test.

3. RESULTS

Based on the SIMPROF analysis of the environmental data of the first sampling occasion (July 2005), two groups of sampling plots could be defined: plots 1 to 5 ('southern' plots) and plots 6 to 9 ('northern' plots) (for SIMPROF results see Appendix 1). We use these two groups throughout the paper for better visualisation.

3.1. Spatio-temporal dynamics of environmental variables

Spatial variation between plots was significant for all environmental variables measured, except for cEPS (ANOVA, $F_{8,\,126}$=1.3, p=0.25; Table 1; Figs. 3 and 4). For mud content and median grain size (not visualised), spatial variation between plots was high and ANOVA showed highly significant differences between most plots (resp. $F_{8,\,441}$=41.8 and $F_{8,\,441}$=57.3, p>0.0001; Table 1). Differences between plots for water content were significant but small, and less outspoken as for grain size (ANOVA, $F_{8,\,441}$=4.7, $p < 0.0001$). The photopigments, chl*a* and fucoxanthin, both differed significantly between plots (resp. ANOVA, $F_{8,441}$=3.6 and p=0.0005, $F_{8,\,373}$=2.9 and p=0.004), however, Tukey's HSD tests revealed that overall significance was mainly based on significant differences between plot 9 and plots 6 and 7 for chl*a*, and between plot 9 and plots 4, 5, 6 and 7 for fucoxanthin. Despite these spatial differences, an overall long-term (interannual) pattern could be observed, which showed for mud content and median grain size a coarsening of the sediment over the years, especially in the muddier sampling plots 1, 2, 3, 4 and 5 (Fig. 3a). This went with a decrease in water content towards 2007, slightly increasing again in 2008, resulting in significant differences between years for water content (ANOVA, $F_{3,\,441}$=24.4, $p< 0.0001$; Table 1; Fig. 3c and 4c). Furthermore, a pronounced interannual variation was present for chl*a* (Table 1), with higher concentrations in 2005 and 2006 as compared to 2007 (Tukey's HSD, resp. p=0.001 and 0.048; Fig. 3e and 4e). These higher values were especially measured in the muddier plots 1, 2, 3 and 4 and in plot 9, probably caused by the temporal appearance of algal mats. Similarly, a decrease of fucoxanthin in 2006-2007 was observed (8.5±0.2 µg/g) and the highest values were measured in 2005-2006 (17±1 µg/g).

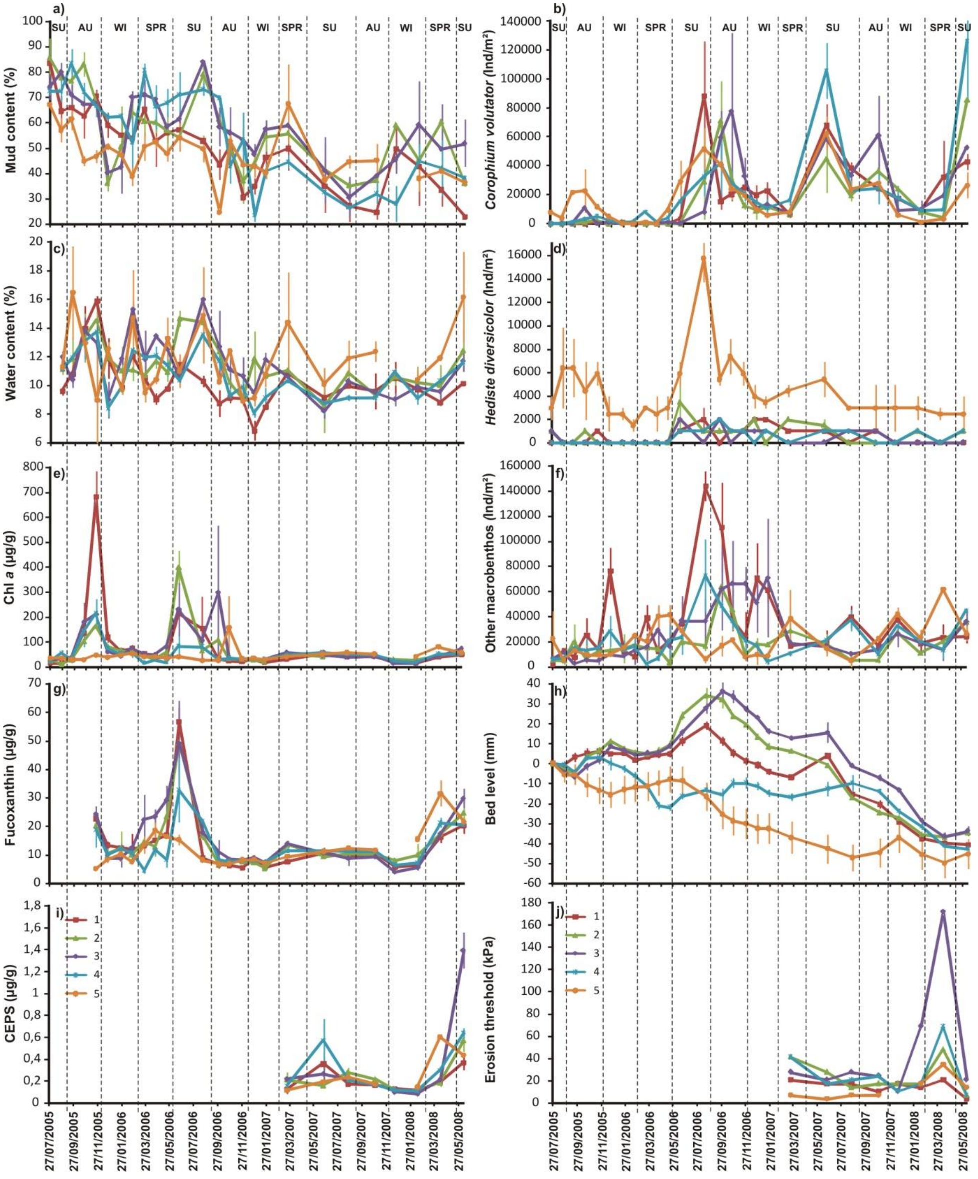

Figure 3: Temporal distribution of mean ± SE from a) mud content (%), b) Corophium density (ind./m²), c) water content (%), d) Hediste density (ind./m²), e) chla (µg/g), f) other macrobenthos density (ind./m²), g) fucoxanthin (µg/g), h) bed level (mm), i) colloidal EPS (µg/g) and j) erosion threshold (kPa), for plots 1 to 5 with indication of the seasons. Note the scale differences for mud content, chl*a*, bed level, cEPS and erosion threshold in comparison with Fig. 4.

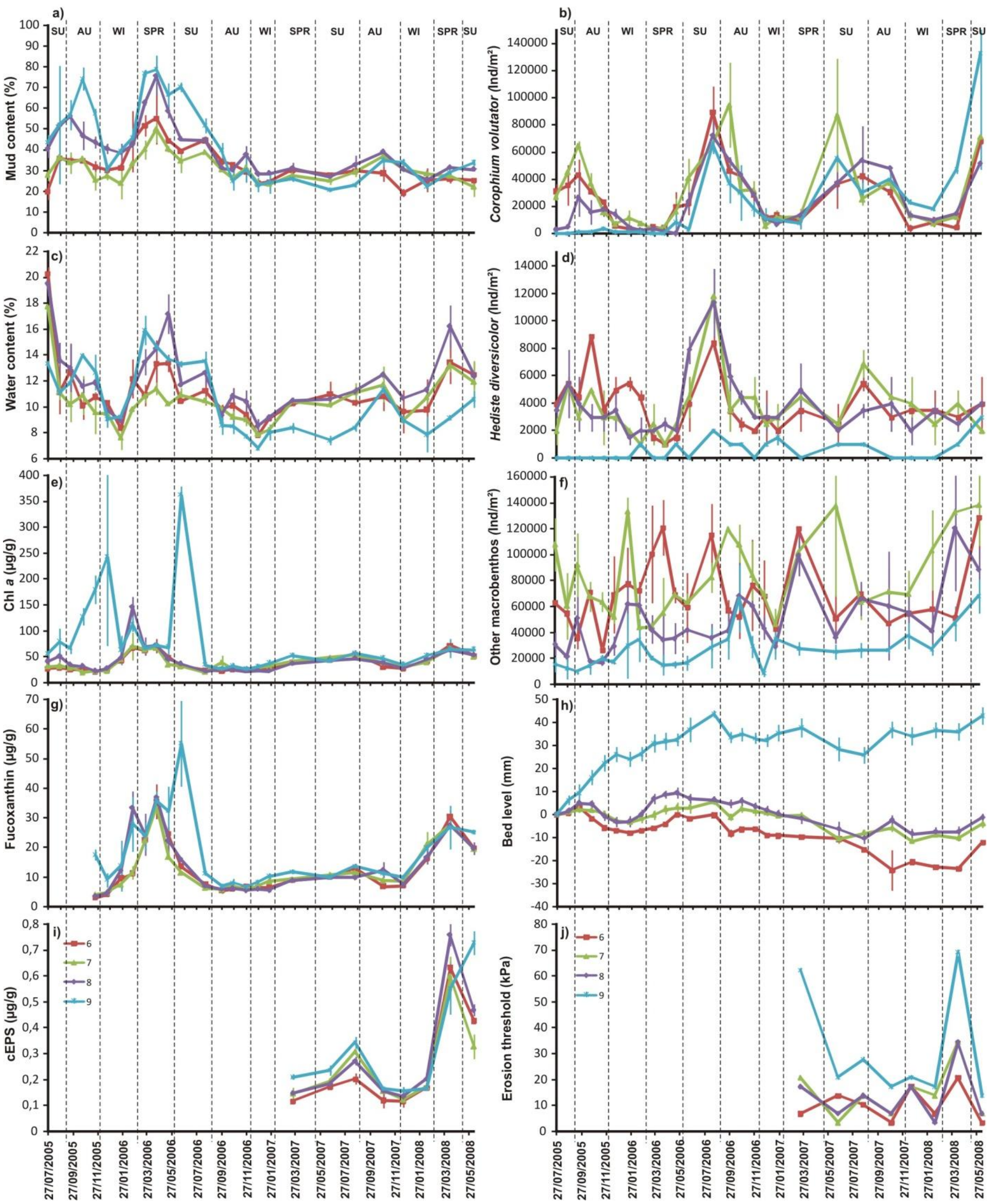

Figure 4: Temporal distribution of mean ± SE from a) mud content (%), b) *Corophium* density (ind./m^2), c) water content (%), d) *Hediste* density (ind./m^2), e) chl*a* (µg/g), f) other macrobenthos density (ind./m^2), g) fucoxanthin (µg/g), h) bed level (mm), i) colloidal EPS (µg/g) and j) erosion threshold (kPa), for plots 6 to 9 with indication of the seasons. Note the scale differences for mud content, chl*a*, bed level, cEPS and erosion threshold in comparison with Fig. 3.

Although, cEPS was only determined from 2007 onwards, concentrations were higher in samples from 2008 as compared to those of 2007, related to the low chl*a* and fucoxanthin concentrations in 2007 (Fig. 3i and 4i).

Furthermore, for most variables, except for chl*a*, short-term seasonal responses were discerned within these long-term trends in the different sampling plots (Table 1). These seasonal responses could differ between years, since 'Year x Season' interactions were significant (Table 1). Mud content was significantly lower in winter compared to the other seasons (Tukey's HSD). However, in summer 2007 and 2008, mud content decreased compared to the previous spring and following autumn and winter (Fig. 3a). Water content followed this seasonal pattern with the lowest values in winter (10±1 SE %), and the highest values in summer (13±1 SE %) (Fig. 3c and 4c). For fucoxanthin, the highest values were observed in spring or summer, decreasing towards autumn and winter. In 2006, values were highest in summer for sampling plots 1 to 4 and 9, while for the other sampling plots, the measured concentrations were highest in spring. In the other sampling years, fucoxanthin concentration was highest in spring for all sampling plots (Fig. 3g and 4g). Also for cEPS, a clear seasonal pattern was observed (ANOVA, $F_{3,\ 126}=33.1$, $p<0.0001$) with higher spring and summer concentrations than in autumn and winter (Fig. 3i and 4i).

3.2. Spatio-temporal sediment dynamics

Bed level and erosion threshold varied considerable between most sampling plots (ANOVA, resp. $F_{8,\ 441}=32.5$ and $p<0.0001$, $F_{8,\ 55}=7.2$ and $p<0.0001$; Table 1; Fig. 3h & j and 4h & j). For bed level measurements, no significant seasonal trend was detected. However, a highly significant interannual trend was observed (ANOVA, $F_{3,\ 441}=47.9$, $p<0.0001$) with erosion starting from summer/autumn 2006 onwards (Table 1; Fig. 3h and 4h). This trend was most outspoken in plots 1, 2 and 3.

The opposite was observed for erosion threshold, with no differences measured between the two sampling years, while seasonality significantly influenced erosion threshold (ANOVA, $F_{3,\ 55}=20.8$, $p<0.0001$; Table 1). In spring, sediment stability was highest and erosion thresholds reached a maximum (Tukey's HSD, $p<0.001$; Fig. 3j and 4j).

Table 1: Summary of the ANOVA results for the environmental variables and the faunal densities for spatial and temporal factors. Time: sampling period when variables were measured. Variable: different variables analysed and when appropriate transformations are mentioned between parantheses. Sign: significance level; ns = not significant, * = p<0.05, ** = p≤0.01, *** = p≤0.001, ! = p≤0.0001.

Time	Variable	Source of variation	SS	df	MS	F	p	Sign.
July 2005 - June 2008	**Mud (<63 µm)**	Intercept	672241	1	672241	5679.427	< 0.0001	
		Plot	39621.8	8	4952.7	41.843	**< 0.0001**	!
		Year	21138.8	3	7046.3	59.530	**< 0.0001**	!
		Season	5406.8	3	1802.3	15.226	**< 0.0001**	!
		Year x Season	9629.2	7	1375.6	11.622	**< 0.0001**	!
		Error	52198.6	441	118.4			
July 2005 - June 2008	**Median grain size**	Intercept	4093707	1	4093707	2834.016	< 0.0001	
		Plot	661645	8	82706	57.256	**< 0.0001**	!
		Year	187240	3	62413	43.208	**< 0.0001**	!
		Season	55917	3	18639	12.904	**< 0.0001**	!
		Year x Season	101600	7	14514	10. 048	**< 0.0001**	!
		Error	637020	441	1444			
July 2005 - June 2008	**Water content**	Intercept	45192.10	1	45192.10	7847.927	< 0.0001	!
		Plot	214.48	8	26.81	4.656	**< 0.0001**	!
		Year	421.84	3	140.61	24.418	**< 0.0001**	!
		Season	450.88	3	150.29	26.100	**< 0.0001**	!
		Year x Season	343.28	7	49.04	8.516	**< 0.0001**	!
		Error	2539.49	441	5.76			
July 2005 - June 2008	**Surface chl*a***	Intercept	1100530	1	1100530	247.0921	< 0.0001	
		Plot	127909	8	15989	3.5898	**0.0005**	***
		Year	50861	3	16954	3.8064	**0.0103**	*
		Season	13876	3	4625	1.0385	0.3752	ns
		Year x Season	182280	7	26040	5.8465	**< 0.0001**	!
		Error	1964182	441	4454			
Nov. 2005 - June 2008	**Surface fucoxanthin**	Intercept	56329.40	1	56329.40	428.2267	< 0.0001	
		Plot	1316.36	8	164.55	2.8611	**0.0042**	**
		Year	3464.38	3	1154.79	20.0797	**< 0.0001**	!
		Season	4712.73	3	1570.91	27.3151	**< 0.0001**	!
		Year x Season	2539.99	6	423.33	7.3609	**< 0.0001**	!
		Error	21451.44	373	57.51			
Mar. 2007- June 2008	**Colloidal EPS** (ln x + 1)	Intercept	6.523759	1	6.523759	8.800588	< 0.0001	
		Plot	0.096212	8	0.012027	1.3027	0.2480	ns
		Year	0.655978	1	0.655978	71.0556	**< 0.0001**	!
		Season	0.917651	3	0.305884	33.1334	**< 0.0001**	!
		Year x Season	0.256007	2	0.128003	13.8654	**< 0.0001**	!
		Error	1.163218	126	0.009232			
July 2005 - June 2008	***Corophium* density**	Intercept	167745.4	1	167745.4	428.1518	< 0.0001	
		Plot	9880.1	8	1235.0	3.1522	**0.0018**	**
		Year	43546.0	3	14515.3	37.0488	**< 0.0001**	!
		Season	93097.8	3	31032.6	79.2073	**< 0.0001**	!
		Year x Season	20727.2	7	2961.0	7.5577	**< 0.0001**	!
		Error	172779.2	441	391.8			

Table 1 continued

Time	Variable	Source of variation	SS	df	MS	F	p	Sign.
July 2005 - June 2008	***Hediste* density**	Intercept	1166.747	1	1166.747	434.7989	< 0.0001	
		Plot	1440.890	8	180.111	67.1201	**< 0.0001**	!
		Year	36.858	3	12.286	4.5785	**0.0036**	**
		Season	70.010	3	23.337	8.6966	**< 0.0001**	!
		Year x Season	181.116	7	25.874	9.6421	**< 0.0001**	!
		Error	1183.388	441	2.683			
July 2005 - June 2008	**Other macrofauna density**	Intercept	593407.5	1	593407.5	906.4623	< 0.0001	
		Plot	238876.0	8	29859.5	45.6120	**< 0.0001**	!
		Year	17888.7	3	5962.9	9.1086	**< 0.0001**	!
		Season	3830.4	3	1276.8	1.9504	0.1207	ns
		Year x Season	22987.5	7	3283.9	5.0164	**< 0.0001**	**!**
		Error	288696.8	441	654.6			
July 2005 - June 2008	**Bed level**	Intercept	16542179	1	16542179	313914.9	< 0.0001	
		Plot	28425	8	3553	32.5	**< 0.0001**	!
		Year	15697	3	5232	47.9	**< 0.0001**	!
		Season	164	3	55	0.5	0.6828	ns
		Year x Season	1281	7	183	1.7	0.1167	ns
		Error	23069	211	109			
Mar. 2007- June 2008	**Erosion threshold** (ln x +1)	Intercept	92.65472	1	92.65472	843.4292	< 0.0001	
		Plot	6.29733	8	0.7871	7.1655	**< 0.0001**	!
		Year	0.12101	1	0.12101	1.1016	0.2985	ns
		Season	6.87209	3	2.29070	21.2235	**< 0.0001**	!
		Year x Season	2.04509	2	1.02254	9.3081	**0.0003**	***
		Error	6.04201	55	0.10985			

3.3. Spatio-temporal dynamics of macrobenthos

The macrobenthos was split in three ‘groups’ which could possibly contribute to changes in bed level or erosion threshold: 1) *Corophium volutator*, a dominant species constituted 33% of all fauna identified, 2) *Hediste diversicolor* (3% of all fauna), a large species known to influence sediment stability (Fernandes *et al.*, 2006; Widdows *et al.*, 2009), and 3) other macrobenthos. The dominant species in the ‘other macrobenthos group’ were *Manayunkia aestuarina* (48% of all other fauna), Oligochaeta species (37% of all other fauna) and *Hydrobia ulvae* (13% of all fauna). Furthermore, low to very low densities of insect larvae, *Macoma balthica*, *Pygospio elegans*, Nemertea and *Eteone longa* were present.

Corophium densities were spatially influenced (ANOVA, $F_{8,\ 441}$=3.2, p=0.0018; Table 1). Especially in the first sampling year, differences between plots were considerable, since *Corophium* was (almost) absent from plots 1, 2, 3, 4 and 9 in 2005-2006 (Fig. 3b and 4b). *Corophium* first appeared in these plots in summer 2006, indicating that *Corophium* was expanding its coverage, resulting in an increase of density over the years. Consequently, significant annual differences were observed (ANOVA, $F_{3,441}$=37, p<0.0001; Table 1). Highly significant differences were also found between the different stations for *Hediste* densities (ANOVA, $F_{8,\ 441}$=67.1, p<0.0001; Table 1). Sampling plots 1 to 4 and 9 differed significantly in *Hediste* density from plots 5 to 8 (Tukey's HSD, all p<0.0001) with lower densities in plots 1 to 4 and 9, ranging from 189±SE 66 to 416±SE 133 ind./m^2, while densities ranged from 3,420±SE 356 to 4,421±SE 455 ind./m^2 in plots 5 to 8 (Fig. 3d and 4d). Interannual variation was significant, though limited (ANOVA, $F_{3,\ 441}$=12.3, p=0.0036). Spatial variation was as well significant for 'other macrobenthos' densities (ANOVA, $F_{8,\ 441}$=45.6, p<0.0001), and plots 6, 7 and 8 differed highly significant from plots 1 to 5 and from plot 9 (Tukey's HSD, all p<0.0001; Table 1; Fig. 3f and 4f). In sampling plots 6, 7 and 8, very high densities of *Manayunkia* (on avg. 30,414±SE 3,713 to 62,196±SE 4,686 ind./m^2) were found, while in plots 1 to 4 and 9, Oligochaeta was the dominant taxon (on avg. 15,301±SE 9,952 to 27,963±SE 11,207 ind./m^2). Densities fluctuated interannually (ANOVA, $F_{3,\ 441}$=9.1, p<0.0001), with sampling year 2005 differing significantly from the other years (Tukey's HSD). On the shorter (seasonal) term, however, no significant seasonal variation was observed for 'other macrobenthos' densities. *Corophium* densities, on the other hand, were strongly influenced by seasonality (ANOVA, $F_{3,441}$=79.2, p<0.0001; Table 1). Densities peaked in summer (36,296±SE 3,269 ind./m^2), slightly decreased towards autumn (26,713±SE 2,139 ind./m^2) and were low in winter and spring (resp. 7,661±SE 645 ind./m^2 and 6,997±SE 1103 ind./m^2) (Fig. 3b and 4b). *Hediste* densities fluctuated also seasonally, especially in the plots with high densities of *Hediste.* Highest densities were observed in summer, decreasing towards autumn, while lowest densities were recorded in winter and spring (Fig. 3d and 4d).

3.4. Biotic – abiotic relationships

Many of the measured variables showed similar or opposite patterns on the interannual and/or seasonal scale, as demonstrated above. This was reflected in the spearman rank correlations with many significant lower or higher degree correlations between the different variables (Table 2). On the long term, an overall trend was observed with a coarsening of the sediment, a decrease in water content, chl*a* and fucoxanthin concentration, an increase in *Corophium* density and erosion of most plots. This was supported by the fact that mud content was negatively correlated with median grain size and *Corophium* density, whereas positive correlations between mud content and chl*a*, fucoxanthin, water content, bed level variation and erosion threshold existed (Table 2). *Corophium* density was negatively correlated with most environmental variables, except with median grain size and cEPS. Furthermore, chl*a* was strong positively correlated with fucoxanthin (r_S=-0.81, df=394) and cEPS (r_S=0.86, df=141), and between fucoxanthin and cEPS was also a strong positive correlation (r_S=0.77, df=141) (Table 2). Erosion threshold was not correlated with any of the biofilm pigments or cEPS. The significant correlations for erosion threshold were negative, and weak, with the macrobenthos densities, median grain size and water content, and positive, but weak, with mud content (Table 2). Bed level variation was highly significant positive correlated with the biofilm pigments (chl*a* and fucoxanthin) and cEPS. Other, weaker, positive correlations existed with mud content and water content, and negative correlations existed with median grain size and *Corophium* density (Table 2).

Since interactions between variables were complex, and not always straightly linear, we regressed bed level variation and erosion level to find the set of variables which best explained sediment dynamics. For bed level variation, the MAM (minimal adequate model) explained 30% of the variability in bed level changes and all predictors, except water content, were retained in the model (Table 3). The three most important predictors in this model were ln(chl*a*) (positive influence), explaining 11% of the variance, ln(chl*a*)^2, explaining 10% and ln(*Corophium*) (negative influence), explaining 2.5% (Table 3). Erosion threshold (log transformed to obtain normal distribution of the residuals) was regressed against mud content, water content, fucoxanthin concentration, cEPS concentration, *Corophium* density, *Hediste* density and other macrobenthos densities. The MAM explained 42% of the variability in erosion threshold. The predictors, fucoxanthin and other macrobenthos, were rejected from the model (Table 3). The best predictor was *Corophium* density (negative influence) contributing to 12% of the explained variance, followed by *Hediste* density (negative influence), which explained 9%, and cEPS (positive influence) which explained 5% (Table 3).

Table 2: Spearman rank correlation coefficients between the different environmental variables and macrobenthos densities. Significant values are bold. Significance levels: ns = not significant, * = $p<0.05$, ** = $p\leq0.01$, *** = $p\leq0.001$, ! = $p\leq0.0001$.

	Mud % (n = 463)	Median (n=463)	Water % (n=463)	Chl*a* (n=463)	Fucoxanthin (n= 393)	cEPS (n=140)	*Corophium* (n = 463)	*Hediste* (n = 463)	Other (n = 463)	Erosion (n=140)
Median	**- 0.97** $^{!}$									
Water %	**0.49** $^{!}$	**- 0.44** $^{!}$								
Chl*a*	**0.2** $^{!}$	**- 0.23** $^{!}$	**0.30** $^{!}$							
Fucoxanthin	**0.27** $^{!}$	**- 0.31** $^{!}$	**0.42** $^{!}$	**0.81** $^{!}$						
cEPS	**-0.21** $^{!}$	0.11 ^{ns}	**0.22** *	**0.86** $^{!}$	**0.77** $^{!}$					
Corophium	**- 0.5** $^{!}$	**0.49** $^{!}$	**- 0.24** $^{!}$	**- 0.25** $^{!}$	**- 0.26** $^{!}$	**0.44** $^{!}$				
Hediste	**- 0.34** $^{!}$	**0.41** $^{!}$	0.03 ^{ns}	**- 0.22** $^{!}$	**- 0.17** ***	0.03 ^{ns}	**0.35** $^{!}$			
Other macrofauna	**- 0.44** $^{!}$	**0.49** $^{!}$	**- 0.11** *	-0.08 ^{ns}	-0.05 ^{ns}	**0.18** *	**0.43** $^{!}$	**0.42** $^{!}$		
Erosion threshold	**0.19** *	**-0.22** **	**-0.29** **	0.07 ^{ns}	0.08 ^{ns}	0.06 ^{ns}	**-0.32** ***	**-0.39** $^{!}$	**-0.28** $^{!}$	
Bed level variation	**0.15** ***	**-0.15** ***	**0.25** $^{!}$	**0.46** $^{!}$	**0.51** $^{!}$	**0.5** $^{!}$	**-0.24** $^{!}$	-0.04 ^{ns}	0.06 ^{ns}	-0.03 ^{ns}

Table 3: Parameter estimates and their SE for all predictor variables retained in the generalised linear models with resp. bed level variation and erosion threshold as dependent variables. For each predictor in the model relative importance was determined.

Dependent variable	Explained deviance and AIC	Predictors retained in model	Estimate	SE	t	p	Relative importance
Bed level variation	**AIC: 2442.2**	Intercept	-1.296	7.6361	-0.17	0.87	
	D^2=0.31	Ln Chl*a*	11.3659	2.9898	3.802	0.00017	11.23 %
	D^{2}adj= 0.30	Ln (Chl*a*)^2	-0.9445	0.3537	-2.67	0.0079	9.93 %
		Ln (*Corophium*)	-1.5740	0.5682	-2.77	0.0058	2.48 %
		Ln (*Corophium*)^2	0.2348	0.1273	1.844	0.066	1.51 %
		Ln (*Hediste*)	3.5017	1.0151	3.449	0.00062	1.43 %
		Ln(Other)	0.6049	0.3152	1.919	0.056	1.40 %
		Asin (Mud)^2	18.5253	7.1791	2.58	0.01	1.22 %
		Asin(Mud)	-27.8318	11.223	-2.48	0.014	1.09 %
		Ln (*Hediste*)^2	-1.3594	0.4899	-2.775	0.0058	1.01 %
Log(ET)	**AIC: -97.405**	Intercept	1.36	0.28	4.91	2.66e-06	
	D^2=0.45	*Corophium*	-0.0058	0.001	-5.79	4.96e-08	11.93 %
	D^{2}adj=0.42	*Hediste*	-0.026	-0.0077	-3.41	0.00088	9.02 %
		cEPS	0.89	0.195	4.57	1.14e-05	5.36 %
		Water content	-0.13	0.046	-2.91	0.0042	4.54 %
		Mud	0.0038	0.0013	2.94	0.0039	4.34 %
		Corophium^2	1.80e-05	5.90e-06	3.045	0.0028	4.12 %
		Water content^2	0.0039	0.0019	2.108	0.037	3.15 %
		cEPS^2	-0.44	0.15	-2.97	0.0035	2.48 %

In Fig. 5 and 6, the modelled versus observed values for resp. bed level changes and erosion threshold in the different sampling plots are shown. When bigger bed level changes occurred, modelled values strongly deviated from this pattern (Fig. 5). The modelled values for erosion threshold were in better agreement with the observed values, especially in sampling plots 1, 4, 5 and 7 (Fig. 6).

4. DISCUSSION

The results of this study, in which multiple biotic and abiotic variables were measured in conjunction with bed level and sediment stability, highlight the complexity of the factors controlling erosion and deposition processes of intertidal sediments. First of all, although the sampling plots were situated on the same shore height and the distance over which the plots were spread was only ±110 m, spatial variation was high for most variables. This is consistent with the fact that estuarine mudflats are intrinsically variable and that small-scale patchiness (cm to m scale) is common in muddy sediments (Kendall and Widdicombe, 1999; Ysebaert and Herman, 2002). Furthermore, many dynamic relationships were observed between the different abiotic and biotic variables, and all these variables have been reported as influencing the erosion and deposition process in a direct or indirect way (De Brouwer *et al.*, 2000; Widdows *et al.*, 2000a; Le Hir *et al.*, 2007; Montserrat *et al.*, 2008). Nevertheless, both on the short-term and on the long-term, distinct patterns could be observed.

4.1. Short-term sediment dynamics

A seasonal cycle of mud deposition was observed within all plots with low mud content in winter and deposition of fine sediments towards spring/summer. Similar seasonal cycles of mud content were reported several times for other intertidal flats (De Brouwer *et al.*, 2000; Herman *et al.*, 2001; Widdows *et al.*, 2004; Borsje *et al.*, 2008). This deposition of mud is temporary, since it disappears in winter, probably due to storms and higher wave energy (Herman *et al.*, 2001). Diatom biomass, measured as fucoxanthin concentration, increased in spring and attracted fine sediment. Diatoms produce secretions of extracellular polymeric substances (EPS) during their daily migrations in the surficial sediments of mudflats (Decho, 1990; Underwood and Smith, 1998).

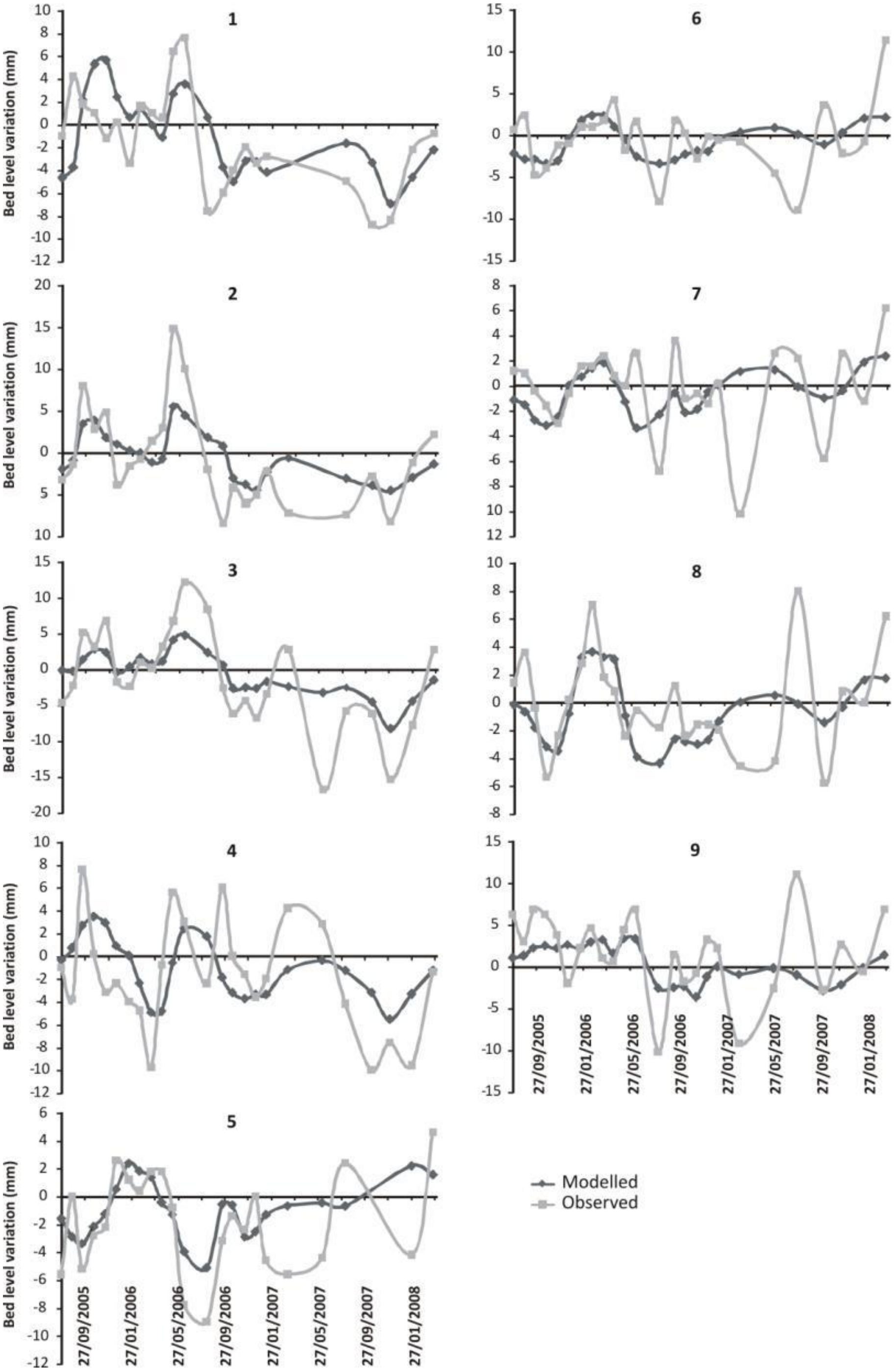

Figure 5: Modelled versus observed bed level changes over the three sampling years.

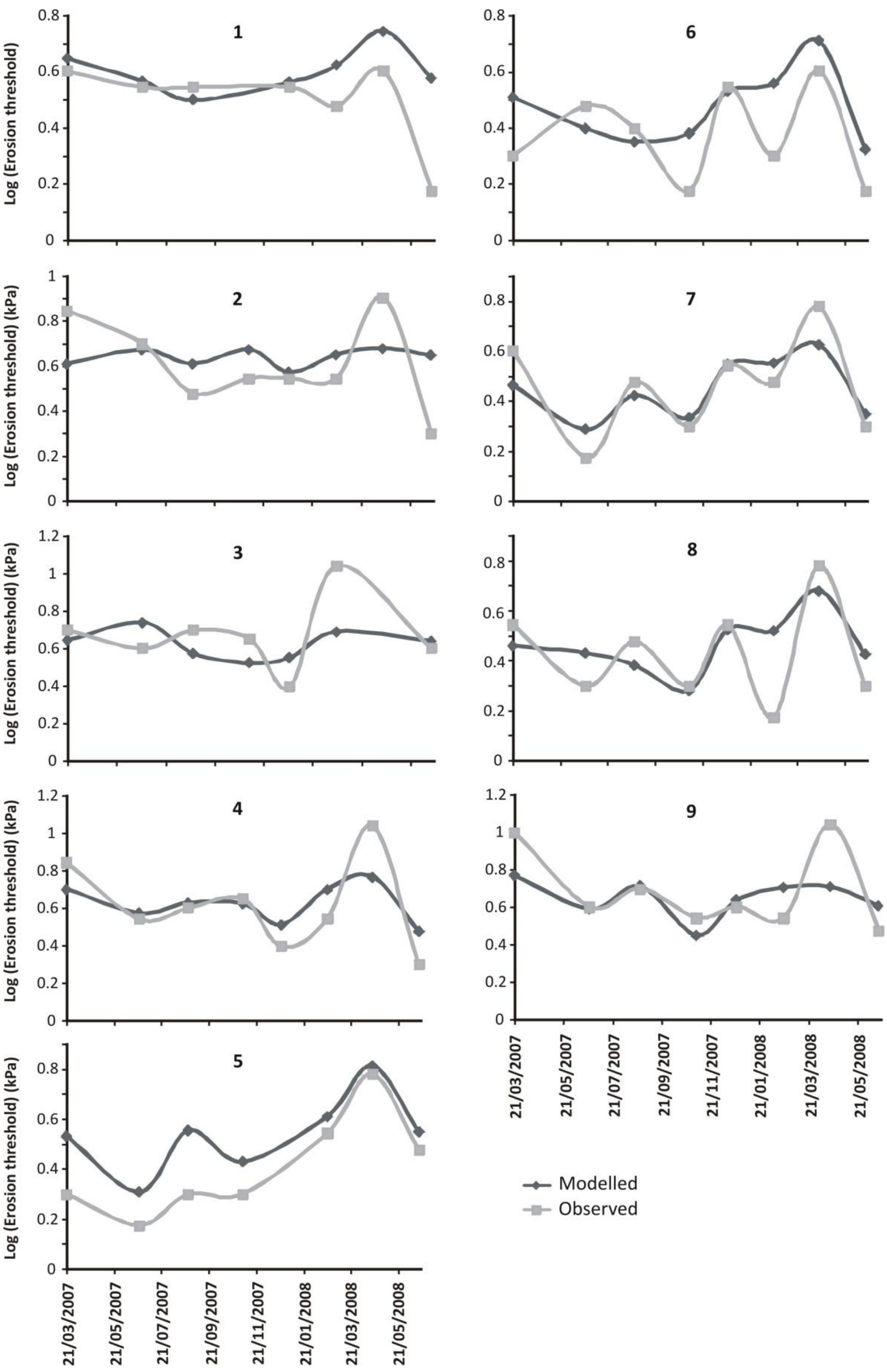

Figure 6: Modelled versus observed values for Log(erosion threshold) from March 2007 onwards.

These EPS secretions are known to play an important role in the binding of fine sediment particles, and they increase sediment stability (Underwood and Paterson, 1993; Yallop *et al.*, 1994; de Brouwer *et al.*, 2005; Le Hir *et al.*, 2007). We found indeed a strong positive correlation between the diatom pigments chl*a* and fucoxanthin and colloidal EPS (cEPS) concentrations. Furthermore, a weak, though significant positive correlation was found between both photopigments and mud content. However, cEPS correlated negatively with mud content. In summer, mud content decreased again, together with fucoxanthin and chl*a*, and macrobenthos densities simultaneously increased. The regulative power of macrobenthos on diatom densities has been reported in a number of studies (Widdows *et al.*, 2000a, 2000b; Andersen, 2001; Hagerthey *et al.*, 2002; Orvain *et al.*, 2004). In our plots, *Corophium* densities showed an outspoken seasonal pattern, with a steep increase from late spring to summer. *Corophium* grazes on diatoms and thereby disrupts the biofilm, leading to increased erosion (Gerdol and Hughes, 1994b; Defew *et al.*, 2002; de Deckere *et al.*, 2002), and an indirect decrease in mud content. Furthermore, *Corophium* is also known to flush its burrows, which leads to active resuspension (de Deckere *et al.*, 2000; De Backer *et al.*, 2010), and a 'fluff' layer which is easily eroded leading to a direct decrease of the clay fraction (De Backer *et al.*, 2009). Moreover, active resuspension increases turbidity, which can inhibit biofilm productivity through attenuation of the light (Dyson *et al.*, 2007). Additionally, in summer 2005 and 2006, when *Corophium* was still absent from plots 1, 2, 3, 4 and 9, we observed a further increase in fucoxanthin (and to a smaller extent in chl*a*) towards summer, and also mud content increased or remained *status quo*. Another variable covarying in this seasonal mud cycle was water content. Water content depends to a large extent on mud content; the higher the mud content, the higher the water content (Flemming and Delafontaine, 2000). However, biofilms affect the water content as well, since they retain water and thus increase water content (Defew *et al.*, 2003; Orvain *et al.*, 2003). This is consistent with our finding of positive correlations between water content, chl*a*, fucoxanthin and cEPS. Since water content measurements were sampled during low water, the values were probably also influenced by exposure duration and the prevailing wind, temperature and sunshine conditions during exposure.

Although, the observed mud deposition and erosion was temporal, it may be a significant factor in the mud balance of an estuary by bringing fine sediment in suspension (Herman *et al.*, 2001). This is important for redistribution of sediment within the intertidal zone, and biota significantly contribute to this sediment transport on short (monthly) timescales (Wood and Widdows, 2002). Our study agrees upon the fact that biota are very important in short-term sediment dynamics. Sediment stability (measured as critical erosion threshold with a CSM) was used as a measure for susceptibility to erosion, and the variation in sediment stability could be explained for 45% with the measured variables; significant explanatory variables were *Corophium* density (+ polynomial factor), *Hediste* density, cEPS (+ polynomial), water content (+ polynomial) and mud content. 33% of this explained variation was accounted for by biota (macrobenthos and microphytobenthos), with *Corophium* density (12 + 4%) and *Hediste* density (9%) as most important destabilising predictors, followed by cEPS (5 + 2.5%, stabilising). This suggests that biological activity is a more important factor determining critical erosion threshold than the physical sediment properties, and that biological variables and their seasonal dynamic relationships directly influence short-term sediment dynamics. Widdows *et al.* (2000a) did not find any significant influence of the physical sediment variables (porosity, grain size), whereas influence of the biological variables (chl*a*, colloidal carbohydrates and *Macoma* density) was highly significant. As already mentioned before, the role of biofilms in stabilisation is widely agreed upon in the literature, and more especially the role of secreted carbohydrates is considered very important in biogenic stabilisation (Paterson, 1989; Yallop *et al.*, 1994; Lucas *et al.*, 2003; de Brouwer *et al.*, 2005; Le Hir *et al.*, 2007). Furthermore, macrobenthos is also generally recognised to influence sediment stability (Gerdol and Hughes, 1994a; Orvain *et al.*, 2004; Ciutat *et al.*, 2007; Montserrat *et al.*, 2008; Widdows *et al.*, 2000b, 2009), but it is extremely difficult to reach a conclusion on the effects on sediment stability, since so many different species with different geomechanical traits exist, and even for a single species opposing results are found (Jumars and Nowell, 1984; Le Hir *et al.*, 2007). For instance, *Corophium* has been described as stabilising (Meadows and Tait, 1989; Mouritsen, 1998) as well as destabilising (Gerdol and Hughes, 1994a; de Deckere *et al.*, 2003) depending upon the age of the animals, the density of the burrows and the sediment grain size (Le Hir *et al.*, 2007). Similarly, *Hediste* displays a whole array of locomotion and feeding modes, thereby processing the sediment in different ways and exerting various influences, both stabilising and destabilising (Banta *et al.*, 1999; Palomo and Iribarne, 2000; Fernandes *et al.*, 2006). Although plenty of field studies described the effects of biological parameters and physical sediment parameters on sediment stability, most of these studies were observational or quantified simple linear regressions of either biofilm characteristics related to sediment stability or macrobenthos densities related to sediment stability. Few field studies used multiple regressions combining both macrobenthos and biofilm parameters in trying to explain the observed variance in sediment stability (e.g. Defew *et al.*, 2002; Montserrat *et al.*, 2008), but none of these determined the relative importance of the different parameters. Recently, some models were developed in which the effects of biological activity on sediment transport including seasonal dynamics were tested, and they all agreed upon the importance of macrobenthos on sediment transport (Wood and Widdows, 2002; Paarlberg *et al.*, 2005; Le Hir *et al.*, 2007; Borsje *et al.*, 2008). In addition, our study shows that macrobenthos can even be the most important biological parameter in determining sediment stability: *Corophium* and *Hediste* density together contributed to more than half of the variance explained by the model (25% of 45%). Nevertheless, extrapolation to other mudflats should be done with great care, since factors influencing stability are site-specific (Defew *et al.*, 2002). Our results on sediment stability indicate that part of this site-specificity may be explained by macrobenthic patchiness and the way that dominant species influence their biotic and abiotic environment.

4.2. Long-term sediment dynamics

Bed level variation was much less affected by these short-term seasonal cycles of mud content, water content, photopigments and macrobenthos. Linear correlations between bed level variation and most of the measured variables were weak or not significant, except with the biofilm variables (chl*a,* fucoxanthin and cEPS) correlations were stronger. Moreover, multiple regression of bed level against chl*a*, mud content, water content, *Corophium* density, *Hediste* density and other macrobenthos density explained 30% of the variation in bed level changes that appeared during the three sampling years, which is noticeably less than for erosion threshold. Chl*a* was the best explanatory variable, contributing to 21% (11 + 10%) of the explained variance, but nevertheless total explained variance is low. This indicates that on longer time scales, the morphology of the sediment bed in mudflats is probably largely shaped by physical forces such as tidal currents and wind generated waves. This is consistent with Wood and Widdows (2002), who simulated sediment transport over an intertidal transect, comparing biological and physical influences, and they concluded that the fundamental forcing was the tidal current, which provides energy to cause intertidal transport. Additionally, the smaller degree of explained variation for bed level changes could result from the fact that the measurements of the variables at the actual day of sampling are actually a snapshot. These snapshots do not take into account the day by day variation between two field visits, while bed level variation integrates all changes that occurred since the last measurements. Especially biofilms may change with days, and even within hours, depending on the temperature, sunshine or tidal cycle (Guarini *et al.*, 2000) and for that reason day by day variability in e.g. biofilm productivity, may as well contribute to the lower explained variation in bed level.

Wood and Widdows (2002) also concluded that biota have a significant effect on sediment redistribution within the intertidal zone, which is important for the morphological evolution of intertidal areas. Our observations indeed suggest an important influence of biota, and especially of *Corophium*, on bed level changes, despite the low degree of explained variance for the regression. In agreement with the findings of Widdows *et al.* (2000b) for *Macoma balthica* and microphytobenthos on the upper shore of the Skeffling mudflat, we observed a temporal shift from net accretion (July 2005 – August 2006) to net erosion (September 2006 – June 2008), which coincided with a shift in key biota known to influence the sediment erosion. After August 2006, the balance changed from a situation with (almost) no or moderate *Corophium* densities, high photopigment concentrations and high mud content to a situation where *Corophium* densities were high and fucoxanthin, chl*a* and mud content were low. The shift in bed level was most outspoken in the plots 1, 2 and 3 where a temporal shift occurred from no *Corophium* to high densities of *Corophium*. Of course, *Corophium* was not the only species present, *Hediste* and some other macrobenthos species occurred as well in higher densities, which presumably contributed also to the disruption of the biofilm. Furthermore, *Hediste* is known to make a significant contribution to erosion and transport of fine intertidal sediment (Widdows *et al.*, 2009). Hence, macrobenthos, and especially *Corophium*, is considered the driving destabilising factor in our sampling plots, and, at least indirectly, a critical trigger in the mud deposition and erosion cycle on the long-term timescale. A recent flume study investigating the influence of *Corophium* on erodability of cohesive sediments, concluded that *Corophium* at densities of 20,000 ind./m^2 significantly influenced sediment stability, measured as an increase in suspension erosion rate (Chapter 5). However, bed erosion proved unlikely to occur under normal flow conditions in the IJzermonding, because calm flow conditions (0.2 m/s, equivalent to a shear stress of ≈ 0.096 N/m^2) are lower than the measured critical shear stresses (0.12 – 0.18 N/m^2) in the flume. Nevertheless, bed erosion could perfectly occur under storm conditions, when current and wave energy could cause shear stress to be much higher (Chapter 5). This additionally supports the assumption that physical forces are of main importance to shape the bed morphology.

Despite this clear observational evidence, the explained variance for the regression of bed level variation is quite low. This supports the complex relationship between all interdependent factors governing bed level variation (chl*a*, *Corophium* density, *Hediste* density, other macrobenthos density and mud content), that were retained in the model and the external factors (e.g. local hydrodynamics, temperature, sunshine, …) interacting with them. To gain further insight into the driving environmental variables shaping bed morphology, future research should further disentangle the relationships between all those interdependent factors. Wood and Widdows (2002) argued that bed morphology is the net result of different processes dominant at different times, and that changes over long timescales are the balance of larger changes occurring over shorter timescales. In addition, our data suggest that external physical forces directly influence bed morphology, while the biotic and abiotic variables indirectly influence erosion and deposition processes by changing sediment stability, and thereby making the sediment to a greater or lesser extent susceptible to erosion or accretion. Therefore, it is important to include data on external physical forces in future regression models on bed morphology of tidal mudflats.

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CHAPTER 7

GENERAL DISCUSSION:

IMPLICATIONS FOR TIDAL FLAT MORPHOLOGY

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The overall aim of this PhD study was to assess the impact of the mud shrimp, Corophium volutator, on its biophysical environment. Therefore, the previous chapters of this thesis presented and discussed results from several micro- and mesocosm experiments as well as from a field survey, dealing with different aspects of the bioturbation process (Chapters 2, 3 and 4), and the consequences of bioturbation on the erodability of the sediment (Chapters 5 and 6). In this last chapter, I integrate this newly gathered knowledge into a discussion on the ecosystem engineering effects of Corophium volutator. At the same time, I put forward some hypotheses on the implications for the tidal flat morphology. It is important to bear in mind that these are hypotheses, and as such need further scientific verification. Consequently, these hypotheses should be considered topics for further research.

1. Ecosystem engineering by *Corophium volutator*

van de Koppel *et al.* (2001) suggested the existence of alternate stable states in tidal flats with low bottom shear stress. At one end of the equilibrium, there is a highly productive state with a high amount of primary producers, characterised by high diatom biomass, high silt content and low levels of erosion. The state at the other end of the equilibrium has a low primary productivity and is highly erodable. Hence, both diatom cover and silt content are low, but secondary production by macrobenthos can be high. The high silt-high diatom state is maintained by a positive feedback governing the diatom-silt interactions (van de Koppel *et al.*, 2001). Actual shifting from one state to the other in the system is expected when the positive feedback is broken by crossing critical thresholds (Bouma *et al.*, 2009a). For instance, a seagrass vegetated stable state can collapse when turbidity of the water increases above a certain threshold turbidity, because the growth is inhibited by limited light availability (Van der Heide *et al.*, 2007), or a certain threshold density of shoots is needed for the formation and persistence of *Spartina* tussocks, because as such they are able to modify the environment to their own advantage (Bouma *et al.*, 2009b). If the system is close to a critical threshold, resilience is low and only little disturbance is needed to trigger the shift (Van der Heide *et al.*, 2007). However, it is possible that a system never reaches the stable state due to continuous perturbation by, for instance, the weather (van de Koppel *et al.*, 2001).

We found evidence that the presence of *Corophium* in a tidal mudflat induces changes in sediment characteristics, which suggest that the sedimentary system shifts from a mud dominated system to a muddy sand system. Although, *Corophium* at densities of 15,000 ind./m^2 significantly reworked the sediment, no evidence was found for differentiation between sediment fractions in downward transport (Chapter 3). Both the fine fraction and the coarser fraction were transported at similar rates, and with a similar vertical depth profile. Nevertheless, results from the microcosm experiment in Chapter 4 and from the field study (Chapter 6) both showed evidence for a coarsening of the surface sediment layer in the presence of *Corophium*. These results strongly indicate that disruption of the sediment surface during scraping and active resuspension by *Corophium* through flushing of the burrows (Chapter 2), causes a segregation in sediment fractions at the sediment surface. The finest particles are washed away with the overlying water (measured in Chapter 5 as a significant increase in suspended sediment concentration in presence of *Corophium*). These particles might be captured from the water column by diatom mats (de Brouwer *et al.*, 2000), dense aggregations of tube worms (Montserrat *et al.*, 2008) or by vegetation (Bouma *et al.*, 2005), while the coarser particles settle relatively fast. This mechanism causes a decrease in mud or clay concentration at the sediment surface (Chapter 4; Chapter 6). Similar mechanisms were attributed to the lugworm *Arenicola marina* in the German Wadden Sea, which was suggested to prevent the succession from sand towards mudflats (Volkenborn *et al.*, 2007), and to the cockle *Cerastoderma edule*, which caused a selective removal of fine material from the surface sediment (Montserrat *et al.*, 2009). Moreover, *Corophium* grazes on the biofilm, and thereby reduces the diatom cover (Gerdol and Hughes, 1994b; Chapter 6). Hence, less fine sediment particles are accumulated by the diatom film and resistance against erosion decreases (de Brouwer *et al.*, 2000; Yallop *et al.*, 2004). Additionaly, in the Bay of Fundy (Canada) and in intertidal mudflats in southeastern England, an increase in sediment stability was observed after removal of *Corophium*, due to bird predation and spraying with insecticide, respectively. This increase in sediment stability was as well attributed to an increase in diatom productivity without grazing pressure of *Corophium* (Daborn *et al.*, 1993; Gerdol and Hughes, 1994b).

Therefore, the presence of *Corophium* at sufficiently high densities might act as a critical threshold to direct the tidal flat system towards the stable state with lower mud content and lower diatom cover by disrupting the positive diatom-silt interactions. Averaging of the environmental variables measured during the field study over density classes of *Corophium*, support the suggested hypothesis (Fig. 1). Loss of fine sediment particles is supported by the exponential decrease and increase of respectively mud content and median grain size with increasing densities of *Corophium* (Fig. 1 a & c). The sudden collapse of fucoxanthin concentration at densities higher than 5,000 ind./m^2, indicate the possible disruption of the positive diatom-silt interaction due to a lower diatom biomass caused by grazing (Fig. 1d). This all contributes to a less stable system, which is more susceptible to erosion (Fig. 1e & f), and which supports the low silt-low diatom state defined by van de Koppel *et al.* (2001). However, tidal flats are in general characterised by small-scale patchiness (cm to m scale) (Kendall and Widdicombe, 1999; Ysebaert and Herman, 2002). Moreover, the distribution of *Corophium* in the field shows a high degree of small-scale patchiness (Lawrie *et al.*, 2000) and the bioturbation effects of the patchy distributed *Corophium* might thus create a patchwork of areas with lower mud content and lower diatom cover alternated with areas with higher mud content and higher diatom cover, just as observed in mudflats. In general, biofilm-grazer interactions are often important in determining the spatial heterogeneity (Hillebrand, 2008). Thereby, biofilms drive some central ecosystem functions such as primary production and nutrient cycling in mudflats (Decho, 2000), whereof other species depend. In that respect, the diatoms can be regarded as key stone species in the tidal flat, while *Corophium* is an important ecosystem engineer affecting the diatoms (seasonally) by grazing, physical disturbance and changes in nutrient cycling (this study and e.g. Daborn *et al.*, 1993; Gerdol and Hughes, 1994a; Biles *et al.*, 2002; Dyson *et al.*, 2007).

Density of *Corophium* appears to be an important threshold triggering the changes in the tidal flat ecosystem, since impacts at low densities proved to be small (Chapters 3, 4, 5; Fig. 1). In Chapter 3, no significant effect of sediment reworking was detected at densities of 2,000 ind./m^2, and in Chapter 4, only at the high density of 20,000 ind./m^2, a significant decrease of the clay fraction was found. Furthermore, in chapter 5, erodability became only clearly apparent at 20,000 ind./m^2, while at lower densities the effects of *Corophium* on critical shear stress and critical erosion velocity were negligible. Nevertheless, organisms with low impact at the individual level can have huge ecological effects, providing they occur at sufficiently high densities over large areas and for a sufficiently long period of time (Lawton, 1994). Figure 1 indicates that a density of *Corophium* of approximately 15,000-20,000 ind./m^2 is necessary, to establish clear and persistent ecological effects on the biophysical environment. Further increase in density appears not to stimulate further changes in the investigated biophysical parameters, but the established environmental settings are maintained.

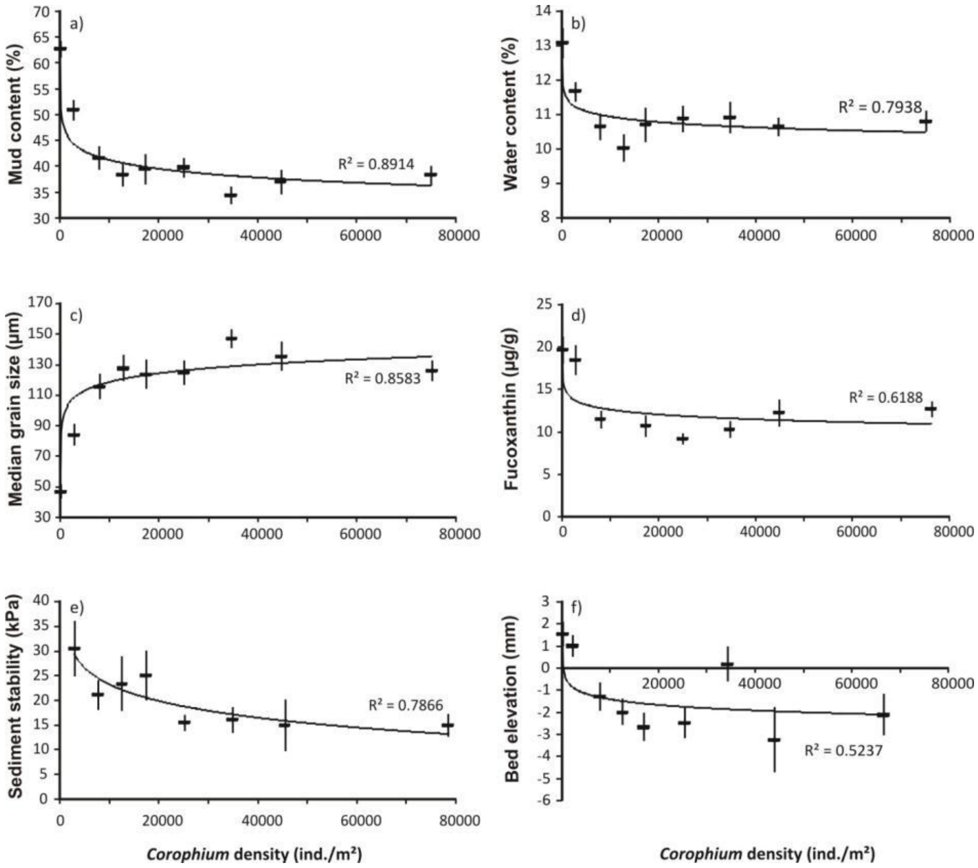

Figure 1 a - f: Relationships between density classes of *Corophium volutator* and biophysical parameters of the sediment, (a) mud content, (b) water content, (c) median grain size, (d) fucoxanthin concentration, (e) sediment stability and (f) erosion/accretion measured as bed level changes between successive surveys. Data points indicate averages±SE of the available data per density class collected during the field survey presented in Chapter 6.

2. *Corophium volutator* and habitat succession

Corophium is often dominant at the interface between the intertidal flat and the salt marsh (Beukema and Flach, 1995). The low salt marsh zone, also called pioneer zone, where primary colonisers such as *Salicornia* spp. and *Spartina* spp germinate (Long and Mason, 1983), might therefore be most susceptible to the ecosystem engineering effects of *Corophium*. Direct inhibition of the salt marsh pioneer *Salicornia europaea* was observed by Gerdol and Hughes (1993), who concluded that disturbance of the surface sediment by bioturbation of *Corophium* buries the seeds, which inhibits germination, and prevents the *Salicornia* seedlings to achieve root anchorage. In addition, indirect inhibition through habitat modification by bioturbating invertebrates can also prevent the development of suitable pioneer conditions (high silt content, accretion of sediment by benthic diatoms, higher critical erosion threshold) for salt marsh development (Hughes, 2001; van Wesenbeeck *et al.*, 2007). For instance, *Arenicola marina* was observed to negatively interact with the settlement of *Spartina anglica* through modifying the habitat by a decrease in silt content, bulk density and sediment stability, and through continuous stirring which resulted in burial of the seeds (Van Wesenbeeck *et al.*, 2007). Similarly, the sand prawn *Callianassa kraussi* excluded the eelgrass *Zostera capensis* in a South-African coastal lagoon due to high sediment transport, increased surface burial and greater penetrability (Siebert and Branch, 2006). If, as suggested above, *Corophium* promotes low mud, low diatom and more erosive conditions, this is an additional argument to postulate that salt marsh expansion is indirectly counteracted by the presence of *Corophium*, and as such *Corophium* protects its own habitat by inhibiting salt marsh development. On the other hand, it may seem contradicting that *Corophium* activity results in erosion, because a coarser sediment with a lower mud content improves the habitat conditions for competing species, e.g. *Cerastoderma edule* or *Arenicola marina*. Both species are known to have their natural abundance peak in fine to medium sands, with an optimum between 100 and 150 µm for *Cerastoderma* and around 155 µm for *Arenicola* (Ysebaert *et al.*, 2002b). Moreover, bioturbation effects by these two species are known to negatively affect *Corophium* by interference competition (Jensen, 1985; Beukema and Flach, 1996), and as such they might displace *Corophium volutator*. However, turbulence is normally low in the upper part of the mudflats where *Corophium* occurs, and sedimentation of fine particles will probably continuously take place in these areas. Consequently, by its eroding activity in the high intertidal, *Corophium* counteracts the sedimentation to provide for its own survival against establishment of salt marsh plants, but due to this continuous sedimentation and the more stressful environment in the high intertidal where *Corophium* lives, species like *Cerastoderma* and *Arenicola* have difficulties to survive in this upper tidal flat area. Nevertheless, on the lower parts of the tidal flat, where sedimentation and environmental stress is lower, *Corophium* is mostly outcompeted by larger bioturbating species, and in Köningshafen Sylt (Wadden Sea), *Corophium* disappeared even in the upper tidal area because sand accretion due to sea level rise at the salt marsh edge, facilitated *Arenicola* and inhibited *Corophium* (Reise *et al.*, 2008). However, in absence of these competing species on the tidal flat and in presence of suitable sediments, the spatial range of *Corophium* might even extend towards the lower tidal areas, although in lower densities, as is the case in the IJzermonding tidal flat (Wittoeck *et al.*, 2004).

Furthermore, the high intertidal area on tidal flats is by many intertidal benthic species used as nursery area, e.g. by *Macoma balthica* (Hiddink and Wolff, 2002 and references therein). Destabilisation of the sediment, inhibition of microphytobenthos development and changes in sediment chemistry are known to indirectly affect juvenile recruitment (Woodin *et al.*, 1995; Woodin and Marinelli, 2002; Van Colen *et al.*, 2009). Therefore, I assume that physical ecosystem engineering by *Corophium* in the upper tidal flat, together with the changes *Corophium* causes in sediment chemistry (Pelegri *et al.*, 1994a; Emmerson *et al.*, 2001; Biles *et al.*, 2002; Bulling *et al.*, 2008), might affect or even inhibit juvenile recruitment. In each case, negative effects on *Hediste diversicolor* recruitment by *Corophium* bioturbation, have been suggested by Olafsson and Persson (1986). To my knowledge, no other studies have been performed to study the effects of *Corophium* bioturbation on juvenile recruitment, but this could be an interesting angle for further research.

Given its ecosystem engineering, the different biotic interactions and its trophic position in the food web, *Corophium* can be considered a vital link in the functioning of the tidal flat ecosystem. For that reason, it is an important species in the conservation of these ecological and economical important habitats. *Corophium* is especially important in the functioning and preservation of the high intertidal area, because there it attains high densities and it is often the species dominating sediment processes in this area of the mudflat. Assuming *Corophium* preserves the mudflat by counteracting the seaward salt marsh expansion, it contributes to a gradual transition between the low intertidal flat and the salt marsh. This might be important in dissipating wave energy, and thus reduce the risk of salt marsh erosion or flooding low-lying land, especially in view of the possible increase in storm surges due to climate change. Moreover, anthropogenic disturbances such as for instance dredging or dredge disposal (e.g. Newell *et al.*, 1998), hypoxia (Van Colen *et al.*, 2008) caused by eutrofication or global warming or toxic chemicals (Lenihan *et al.*, 2003) can cause mass mortality in tidal flats, where the defaunated areas can cover several km^2 (Diaz and Rosenberg, 1995). Once, the disturbance disappears, macrobenthic recovery may occur and *Corophium* might play an important role in recovery. In a defaunation experiment on the Swedish west coast, *Corophium* was a pioneer species in recolonisation, showing an opportunistic response (overshoot in abundance in defaunted plot compared to control) after 30 days (Norkko *et al.*, 2006a). Since *Corophium* is a mobile species and capable of active habitat selection (Hughes, 1988; Lawrie and Rafaelli, 1998), it reacted on the absence of large bioturbators (*Arenicola* in this case) and on the ample supply of food, a microphytobenthic mat growing on the defaunated plots (Norkko *et al.*, 2006a). This example shows that *Corophium* is capable of playing an important role in recovery of disturbed tidal flats ecosystems by improving the environmental conditions for later colonisers.

3. Considerations on site-specific features: feeding mode, sediment properties and inundation time with perspectives for future research

The field data from this PhD study are derived from the upper shore of a sheltered, tidal, muddy flat with cohesive sediments (avg. mud content = 46 ± SD 16%, avg. clay content = 10% ± SD 5% and avg. median grain size = 103 ± SD 58 μm) and with benthic diatoms as an important source of primary production. This is often the environment where *Corophium volutator* thrives, and where I hypothesise that in such an environment *Corophium* destabilises its physical environment by decreasing the mud content and the diatom biofilm.

It has, however, been proven that conditional outcomes depending upon environmental constraints can cause inconsistent patterns (Norkko *et al.*, 2006b; Rossi *et al.*, 2008).

Therefore, site-specific environmental features such as sediment properties, inundation time, flow velocities, phytoplankton concentration and the feeding mode depending thereupon, … could show a different picture of the effects due to *Corophium* bioturbation (Fig. 2). For instance, on a wave-exposed flat in the Danish Wadden Sea with non-cohesive sediments (mud content ≈ 10%) , *Corophium* was observed to accumulate sediment, resulting in sediment elevations raising circa 5 cm above the surrounding sediment (see also Table 1 in Chapter 1; Mouritsen et al, 1998). Densities of > 100,000 ind./m^2 were recorded in these sediment bed elevations. The different sediment composition of this tidal flat might be at the origin of these contrasting observations. The natural sediment (cohesive versus non-cohesive) will probably play a very important role in determining the physical effect of *Corophium* on its environment (Fig. 2). Cohesive sediments form a coherent mass because of electrochemical interactions between the sediment particles (a clay content of 5-10% is needed), while non-cohesive sediments have a granular structure and the individual sediment particles do not stick together (Van Ledden *et al.*, 2004). When *Corophium* burrows in non-cohesive sediments, the mucus secretions, used to build its burrow are probably much more effective in providing a glue between the grains (cf. Meadows *et al.*, 1990) compared to in cohesive sediments. In that respect, *Corophium* adds cohesion to non-cohesive sediments and that can enhance sediment stability as observed by Meadows *et al.* (1990) (Table 1 in Chapter 1; Fig. 2). Therefore, it would be very interesting to further examine the ecosystem engineering effects of *Corophium volutator* in a non-cohesive tidal flat system. In addition, a shift in feeding mode might further enhance the opposite effects, because a different feeding mode might result in a different modification of the sediment characteristics (Fig. 2). Recently, it was shown that filter feeding by *Corophium* is more important than hitherto believed, at least in Danish fjord systems (Möller and Riisgård, 2006; Riisgård and Schotge, 2007). *Corophium* can switch between filter feeding and deposit feeding, with the phytoplankton concentration of the water acting as a triggering factor: above a threshold of 0.5-5 µg chl*a*/l, *Corophium* was observed to predominantly filter feed (Möller and Riisgård, 2006; Riisgård and Schotge, 2007). The link between flow velocity and filter feeding by *Corophium* was not investigated in these studies, but for other animals that are known to switch feeding mode, an increase in flow velocity triggered filter feeding as well (e.g. spionid polychaetes Miller *et al.*, 1992; *Macoma balthica* Peterson and Skilleter, 1994; *Pygospio* *elegans* Herman *et al.* 2000). Filter feeders can accelerate the settling of organic particles considerably by their activities (Miller *et al.*, 1992; Malmqvist *et al.*, 2001), since they meet their nutritional demands by extracting suspended particles (e.g. phytoplankton) from ventilation currents (Riisgård and Larsen, 1995), thus enhancing the deposition at the sediment surface directly in the form of biodeposited faecal pellets (Graf and Rosenberg, 1997; Norkko *et al.*, 2006b). When in the Danish Wadden Sea, as observed in Danish fjord systems, the dominant feeding mode of *Corophium* in these more sandy systems would have been filter feeding, the effects on sediment dynamics could be totally different: biodeposition could take over, and fine sediment particles could get captured and deposited on the surface (Graf and Rosenberg, 1997). Furthermore, if *Corophium* filter feeds, the burrows probably have chimney-like extensions of 1 to 1,5 mm above the surface (Meadows and Reid, 1966; cf. filter feeding by *Hediste diversicolor,* Christensen *et al.*, 2000). At high densities of *Corophium*, these protruding 'chimneys' increase the roughness density (i.e. the ratio of planar area of the roughness elements to total bed area) and attenuate flow velocity, favouring biodeposition (Friedrichs *et al.*, 2000). This phenomenon of altered hydrodynamics by animal tubes with deposition of fine sediment was also described for the polychaetes *Lanice conchilega* (Rabaut *et al.*, 2007) and *Pygospio elegans* (Montserrat *et al.*, 2008), which both are known to stabilise the sediment surface resulting in elevations above the sediment surface. Moreover, biodeposition of silt or clay particles in a non-cohesive tidal flat could again result in a shift towards cohesive sediment in the *Corophium* patches, further increasing stability, and causing the sediment bed elevations observed by Mouritsen *et al.* (1998). Of course, this is an assumption, and hence the consequence of switching feeding modes needs more attention. It would be very interesting to set-up an experiment where the influence of feeding mode on sediment characteristics and sediment stability could be further investigated. Additional support for the assumption that feeding mode could be an important feature influencing sediment stability, is offered by *Hediste diversicolor*. *Hediste* is also known to switch feeding modes (Vedel, 1998; Riisgard *et al.*, 1996) and also for this species both stabilising and destabilising effects have been observed (Widdows *et al.*, 2009 and references therein).

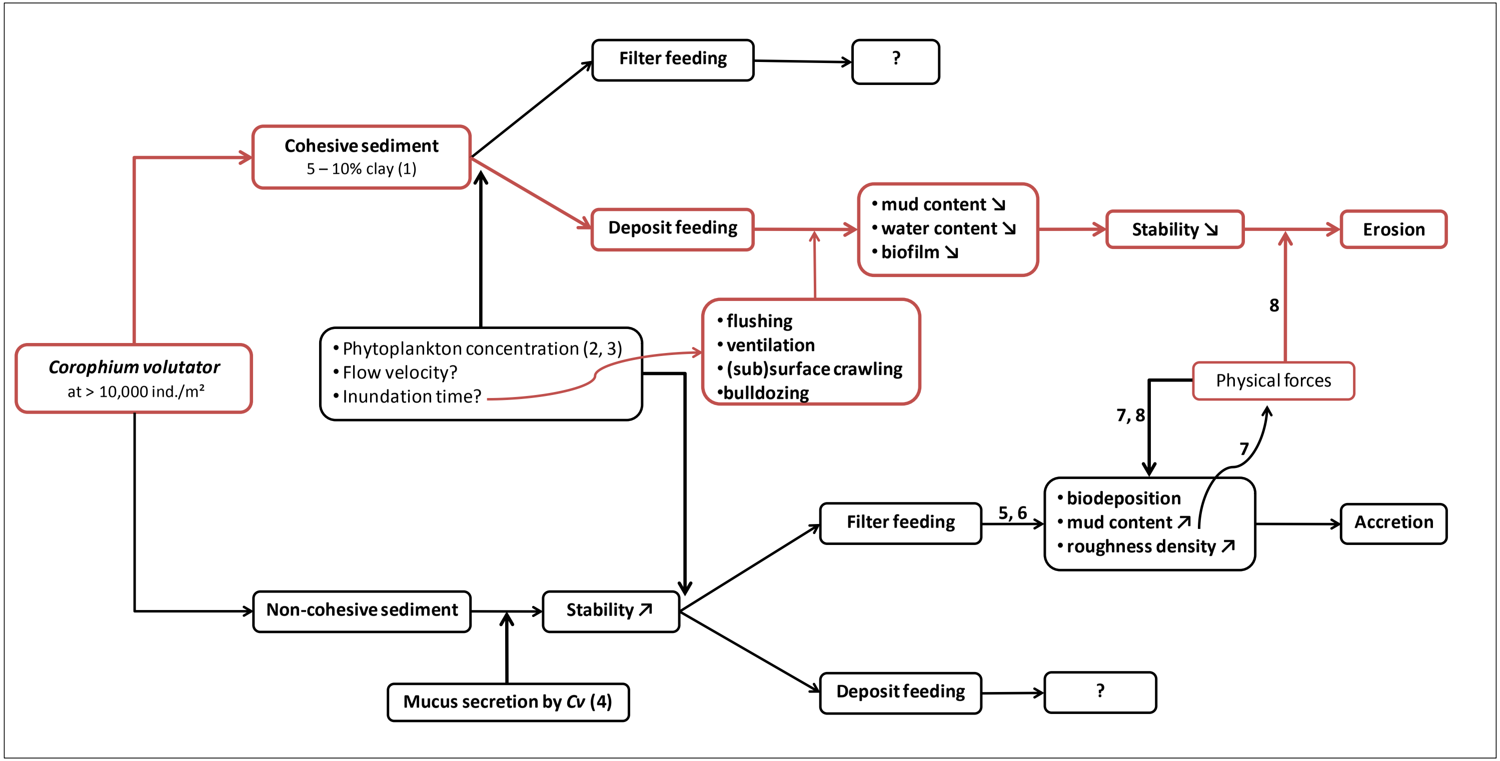

Figure 2: Schematic representation of how site-specific features might create contrasting results on sediment stability. The nature of the sediment (cohesive versus non-cohesive) and feeding mode are probably the most important factors determining the eventual effect on sediment stability and the resulting erosion/accretion of the sediment surface. Evidence for relationships between red boxes was collected during this PhD study. Other relationships are assumptions discussed in paragraph 3 of this chapter. Numbers refer to the following literature references: (1) Van Ledden *et al.*, 2004; (2) Möller and Riisgard, 2006; (3) Riisgard and Schotge, 2007; (4) Meadows *et al.* 1990; (5) Malmqvist *et al.*, 2001; (6) Graf and Rosenberg, 1997; (7) Friedrichs *et al.*, 2000; (8) Ralston and Stacey, 2007

Another feature, that could possibly cause site-specific differences is the inundation time. In this study, inundation time was 3h in all experiments, which was based on the period of inundation in the field. On other tidal flats inundation can be up to 9h or even more, and might result in more distinct changes. Activity proved to be very low during emersion, only scraping the sediment surface (≈ deposit feeding) continued during the entire tidal cycle (Chapter 2). This could have had its impact on the sediment reworking activities of *Corophium*, which were much lower compared to other studies (Chapter 3). Nevertheless, already in this study with short inundation time, ecosystem engineering effects of *Corophium* are considerable (first paragraph). However, further research on this subject is needed, and an experimental set-up as in Chapter 3 with different tidal regimes as treatment could be a first step to elucidate the influence of the tidal regime on sediment reworking.

4. Conclusion

The general objective of this thesis was to study the impact of the mud shrimp *Corophium volutator* on its biophysical environment. Both the experimental and field data from this thesis confirm that *Corophium volutator* is an important ecosystem engineer that modifies its biophysical environment through changes in sediment composition, water content, biofilm productivity and sediment stability. Hereby, it improves its own survival in the high intertidal and affects other species. Furthermore, *Corophium* plays an important role in sediment mixing, which has implications for downward particle and organic matter transport, and thus for decomposition and mineralisation processes in the sediment. For all the observed impacts, density proved to be an important parameter: significant changes were only observed from 5,000-10,000 ind./m^2 onwards. Therefore, disappearance or density declines of *Corophium* could have huge consequences for the tidal flat ecosystems, where these burying amphipods thrive, and shape their abiotic and biotic environment.

Finally, the answer to the title question "The mud shrimp *Corophium volutator*: a key species in tidal flat sedimentary processes?" is clearly *'YES'*, on the condition that the species is abundantly present in the tidal flat in question.

APPENDIX 1

SUPPLEMENTARY MATERIAL

APPENDIX 1

SUPPLEMENTARY MATERIAL

SUPPLEMENTARTY MATERIAL TO CHAPTER 2

Table 1: Summary of the one-way ANOVA results for the different surface and subsurface activities with 'tidal period' as categorical predictor.

Variable	Source of variation	SS	df	MS	F	p
Surface crawl	Intercept	28115	1	28115	92	< 0.0001
	Tidal period	18514.4	2	9257.2	30.3	**< 0.0001**
	Error	134419.3	440	305.5		
Swim	Intercept	463.6	1	463.6	6.6	0.01
	Tidal period	851.2	2	425.6	6.1	**0.0025**
	Error	30839.8	440	70.1		
Scrape	Intercept	969.2	1	969.2	96.2	< 0.0001
	Tidal period	612.4	2	306.2	30.4	**< 0.0001**
	Error	4434.5	440	10.1		
Flush	Intercept	623.4	1	623.4	9.8	0.0019
	Tidal period	1144.5	2	572.2	9.0	**0.00015**
	Error	28055.6	440	63.8		
Surface inactivity	Intercept	2842647	1	2842647	4288.9	< 0.0001
	Tidal period	93259	2	46630	70.3	**< 0.0001**
	Error	291628	440	663		
Ventilate and feed	Intercept	327171	1	327171	269.6	< 0.0001
	Tidal period	97041.1	2	48520.5	40	**< 0.0001**
	Error	180815.5	440	1213.5		
Subsurface walk	Intercept	3677.4	1	3677.4	78.8	< 0.0001
	Tidal period	1099.8	2	549.9	11.8	**< 0.0001**
	Error	6956.7	440	46.7		
Bulldozing	Intercept	35.6	1	35.6	6	0.016
	Tidal period	72.5	2	36.2	6.1	**0.0029**
	Error	887.4	440	5.9		
Subsurface inactivity (asin(sqrt))	Intercept	70.3	1	70.3	266.9	< 0.0001
	Tidal period	26.2	2	13.1	49.8	**< 0.0001**
	Error	39.2	440	0.3		

APPENDIX 1

SUPPLEMENTARTY MATERIAL TO CHAPTER 3

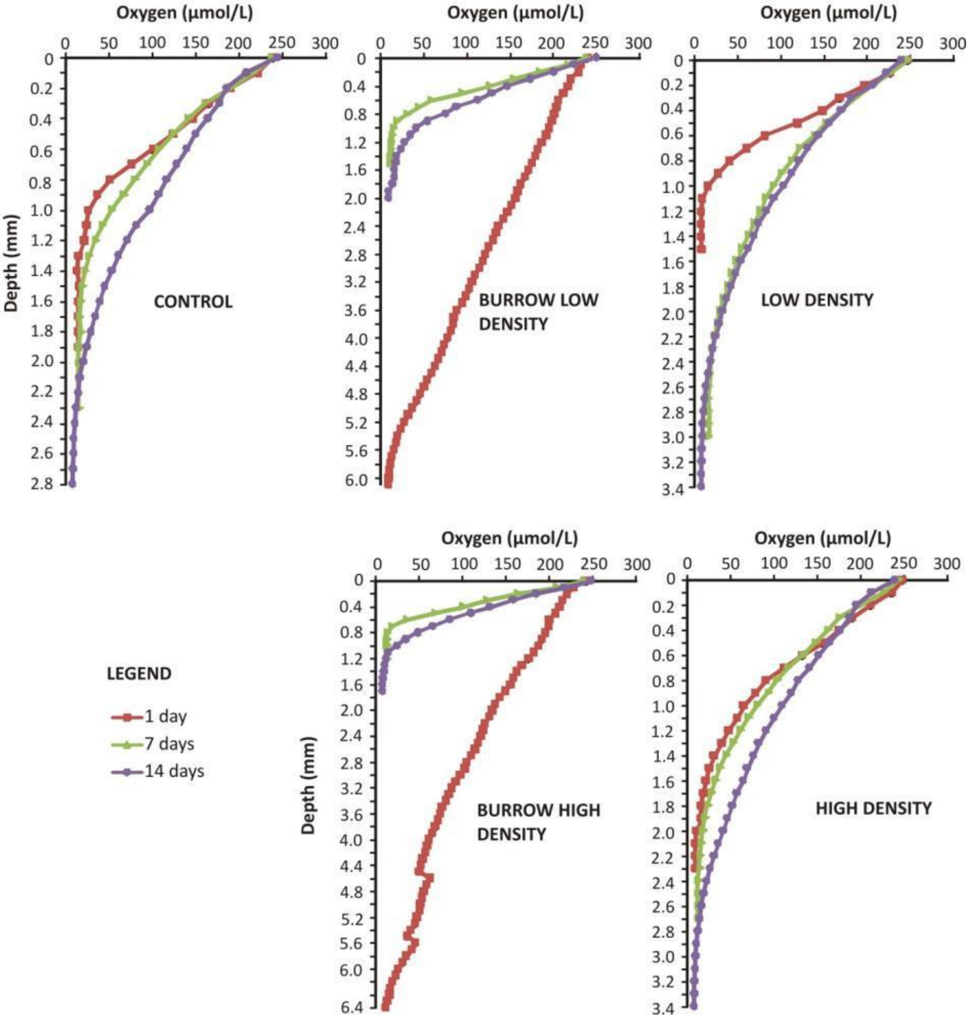

Figure 1: Oxygen profiles for the five different bioturbation treatments on the three sampling occasions. Oxygen was measured with Unisense oxygen microsensors (type ox25) with vertical increments of 100 µm.

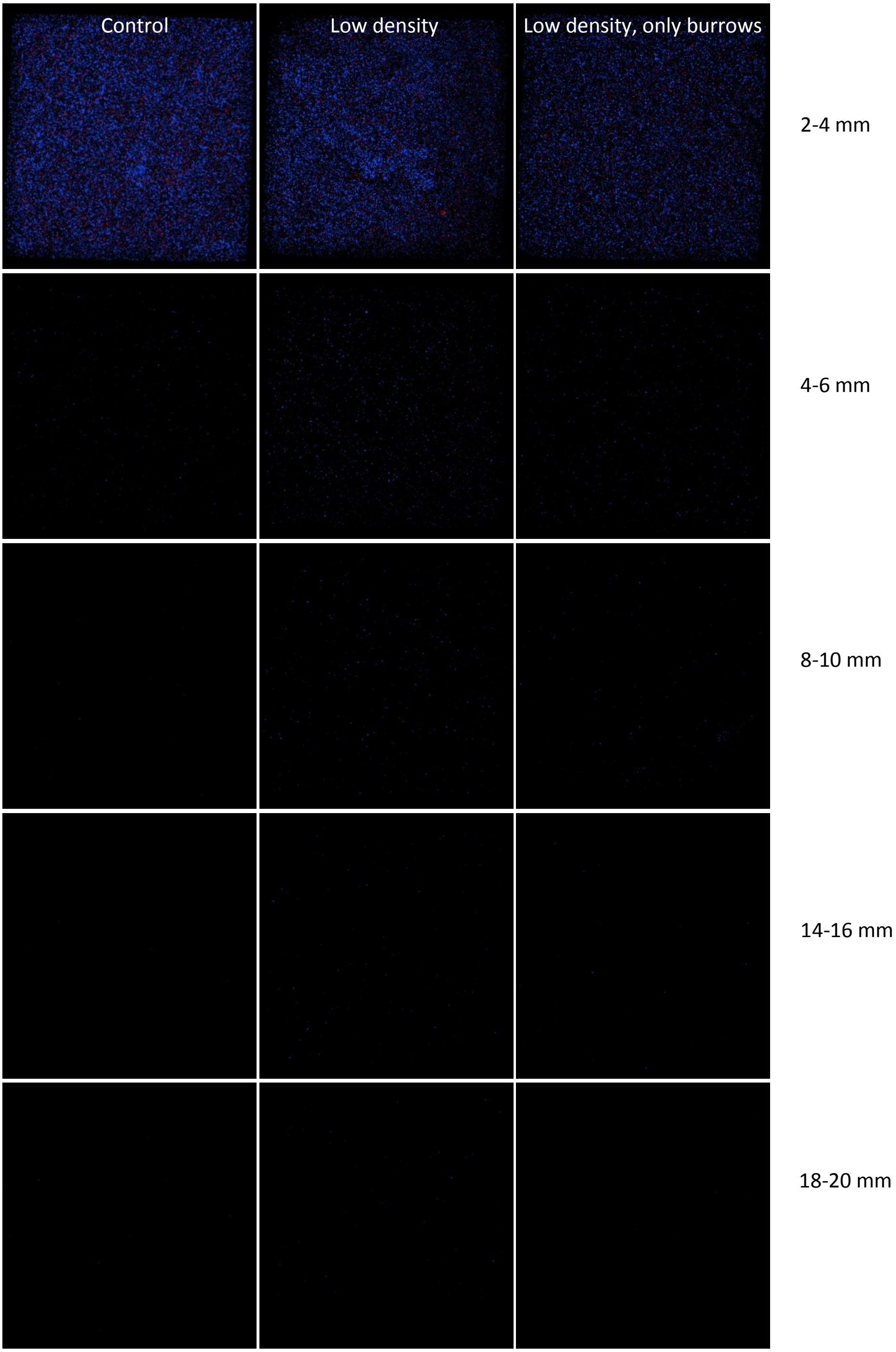

Figure 2: Overview of the vertical distribution of luminophores for the different treatments at day 14 on the basis of analysed images from five different depth layers (continued on next page).

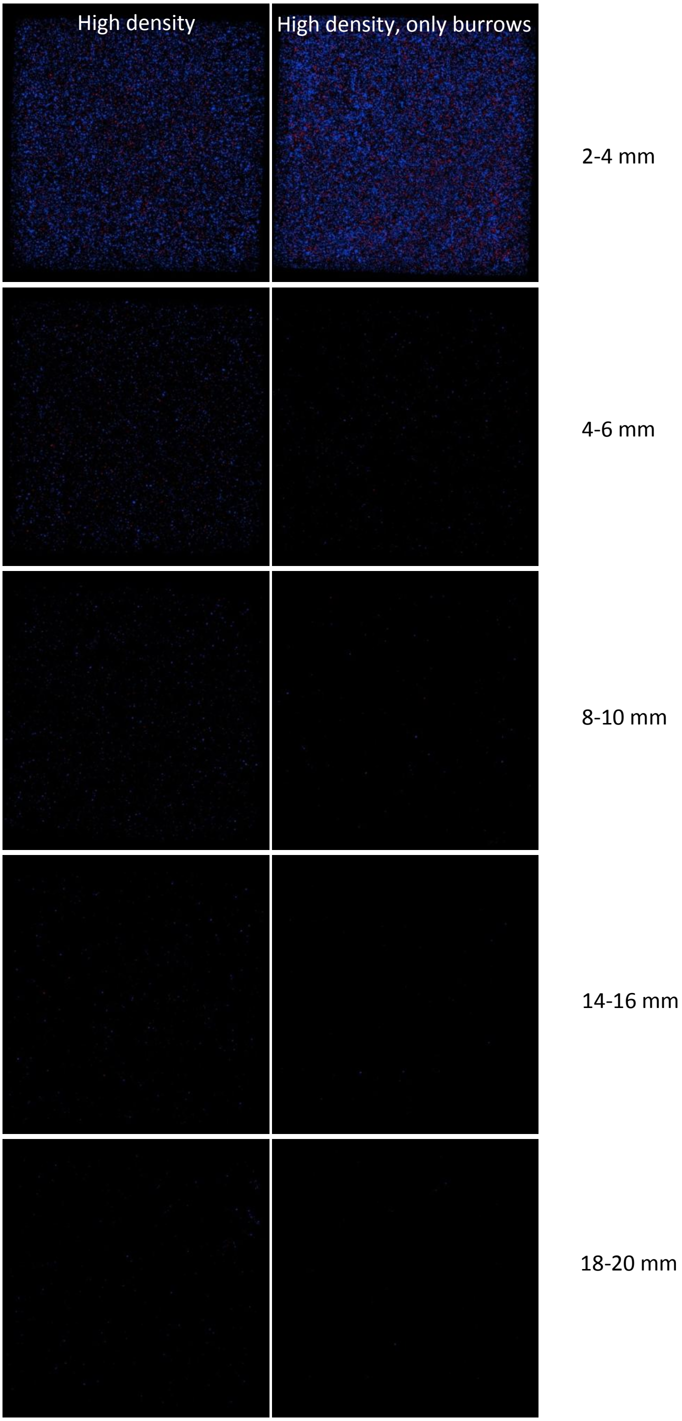

Figure 2 continued

SUPPLEMENTARTY MATERIAL TO CHAPTER 6

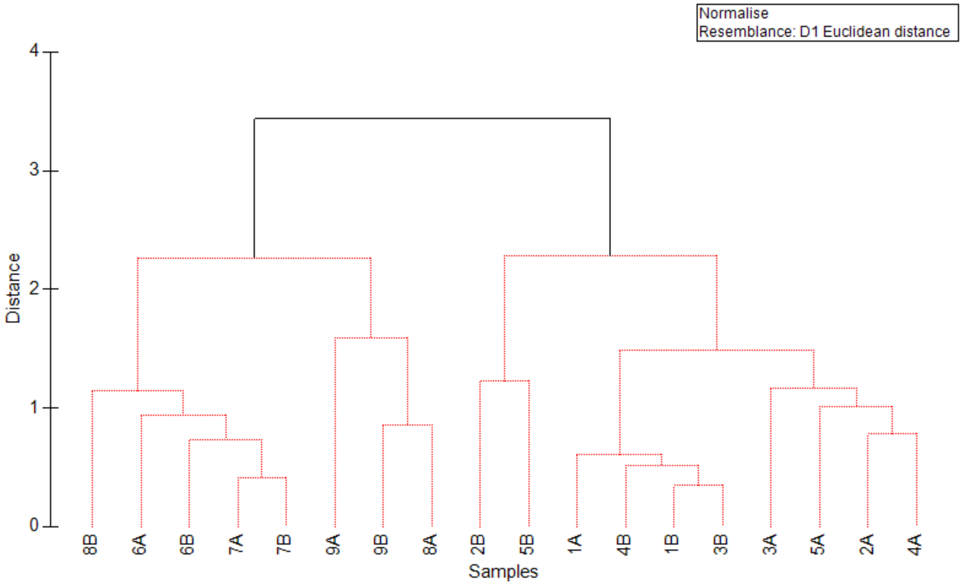

Figure 3: SIMPROF dendrogram based on measured environmental variables (mud content, chl*a*, water content and median grain size) from the first sampling occasion.

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