The effects of anthropogenic influence on soft sediment benthic macrofauna in the Dutch Wadden Sea and Oosterschelde (Eastern Scheldt).

By Robert Klerks, s1666347

Abstract

The Wadden Sea and the Eastern Scheldt are two unique Dutch National Parks placed under environmental monitoring by the Dutch Government. Historically both locations have proven to be of great economic value and over the years have been greatly impacted by anthropogenic use. More recent all large scale anthropogenic use (fishing, trawling) has been ceased while other impacts (power plant run-off, river run-off and dredging) are being closely monitored. Ecosystem succession (benthic filterfeeders → benthic depositfeeders) due to anthropogenic impacts are a large concern due to the effects on the trophic cascade. The decrease in primary production, biodiversity, abundance and even fish and bird presence have been reasons to limit human use of the areas. In order to establish methods of preservation and restoration of these historically important areas the causes and effects of the prolonged anthropogenic use needs to be studied. In order to formulate a plan that restores the areas previous wealth of biodiversity and abundance, starting with the group of ecosystem engineers known as infauna (soft sediment macrobenthic fauna), studies of all the interactions within this system should be combined for maximum effect.

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Introduction

The influence of human activity on the estuarine Dutch waters has been a point of interest for many years and even more studies. In 1986 UNESCO (United Nations Educational, Scientific and Cultural Organization) declared the Wadden Sea a “biosphere reserve” in order to reconcile the conservation of biodiversity with its sustainable use. Recently (summer of 2009) the Wadden Sea was placed on the World Heritage list by UNESCO. The Eastern Scheldt while not on the UNESCO World Heritage list is being recognized by the Dutch government in its uniqueness in biodiversity and economic importance that since 2002 it has been recognized as a National Park, strictly regulating human influence. Even though both locations are technically preserved areas there are still signs of current anthropogenic impacts and traces of currently ceased human activities. The goal of preservation has been to try and revert the biodiversity and biomass back to a more pristine/unimpacted system, even though for both systems it is complicated to determine what the unimpacted system actually looked like since the largest changes to the system occurred right as it was trawled/dredged for the very first time (Robinson 2008). Large scale physical anthropogenic and environmental disturbances have cascading effects throughout all resident communities even extending to nearby areas (Reise 1989, Piersma 2001).

The effects of human presence in the Wadden Sea and Eastern Scheldt areas have been well documented over the past decades but there is very little information available from before human interference. The decrease in primary production (Kraan 2007, Compton 2009), the decrease of biodiversity and abundance (Piersma 2001, Kraan 2007, Eriksson 2010, van Leeuwe 2010) and even the decrease of fish stock and bird presence (Piersma 2001, Kraan 2010, Compton 2013) however have been well documented over the past 50 years. Unfortunately one of the biggest challenges in coastal-zone management is catering to the different users without affecting the functioning of the marine ecosystems (Gonzalez 2010, Hiddink 2003)

While the Earth itself is influencing the intertidal ecosystems in many ways through storms, sea/earthquakes, the tides and the global environment it is of importance to separate the effects of anthropogenic use and the “random” occurrences that take place over time. While the effects of for instance storms on intertidal ecosystems are being studied (Harris 2011) it is important not to neglect the human impacts on these systems. In order to help re-establish and stabilize biodiversity identifying the key anthropogenic actors in these regions is important to help understand the impact of the effects these actors have on the water, the sediment and the water-sediment interactions first and worry about natural events later. There are many ways to quantify anthropogenic impact on an ecosystem but this essay will focus on the impact on the soft sediment macrobenthic fauna (infauna) of these regions. Misinterpretation of the effect of human exploitation decreases the ability to detect the multi-trophic consequences of the non-linear dynamics of biological feedback.

Soft sediment microbenthic fauna have been identified as central to the ecosystem functioning of these areas (Przeslawski 2009, Eriksson 2010, Compton 2013, Rossi 2013, Harris 2016) since they have the ability to influence nutrient cycling (Grant 1994, Volkenborn 2007, Przeslawski 2009, Braeckman 2014), bioturbation (Przeslawski 2009), the water-sediment interface (Przeslawski 2009), decomposition of organic matter (Orvain 2012, Compton 2013) and serve as food for higher trophic levels (Compton 2013). It is common to investigate functional groups of infauna rather than a per species investigation in order to be able to compare geographic locations to each other (Robinson 2008, Eriksson 2010, Orvain 2012, Whitton 2016). Therefore understanding of the anthropogenic impacts on benthic soft sediments systems is key in order to develop a plan to increase conservation and preservation methods.

Comparison of the effects of human impact on the benthic soft sediment systems of the Wadden Sea and the Eastern Scheldt could provide valuable general information on both the recent and the expected changes to these systems. The geographic locations are close enough together that they suffer from the same seasonal effects, with the only natural differences being the influx of fresh water (de Mesel 2009, Compton 2013), the input of salt water from the North Sea (de Mesel 2009, Compton 2013) and the tidal forces from the surrounding water (Piersma 2001, de Mesel 2009, Compton 2013). It is widely acknowledged that soft sediment macro fauna prefer a specific range of porosity of the sediment they reside in (Alexander 1993, Grant 1994, Orvain 2012), so much so that they to some degree can be characterized as sediment specialists or generalists (Alexander 1993). The Wadden Sea in particular could provide valuable information because of the West to East gradient that exist in both the exposure time (the Eastern part has longer dry periods than the Western part) and sediment particle composition (although these 2 physical attributes are linked) (Compton 2013) and has been slowly shifting from sandy/muddy areas to areas with finer silts (Volkenborn 2007).

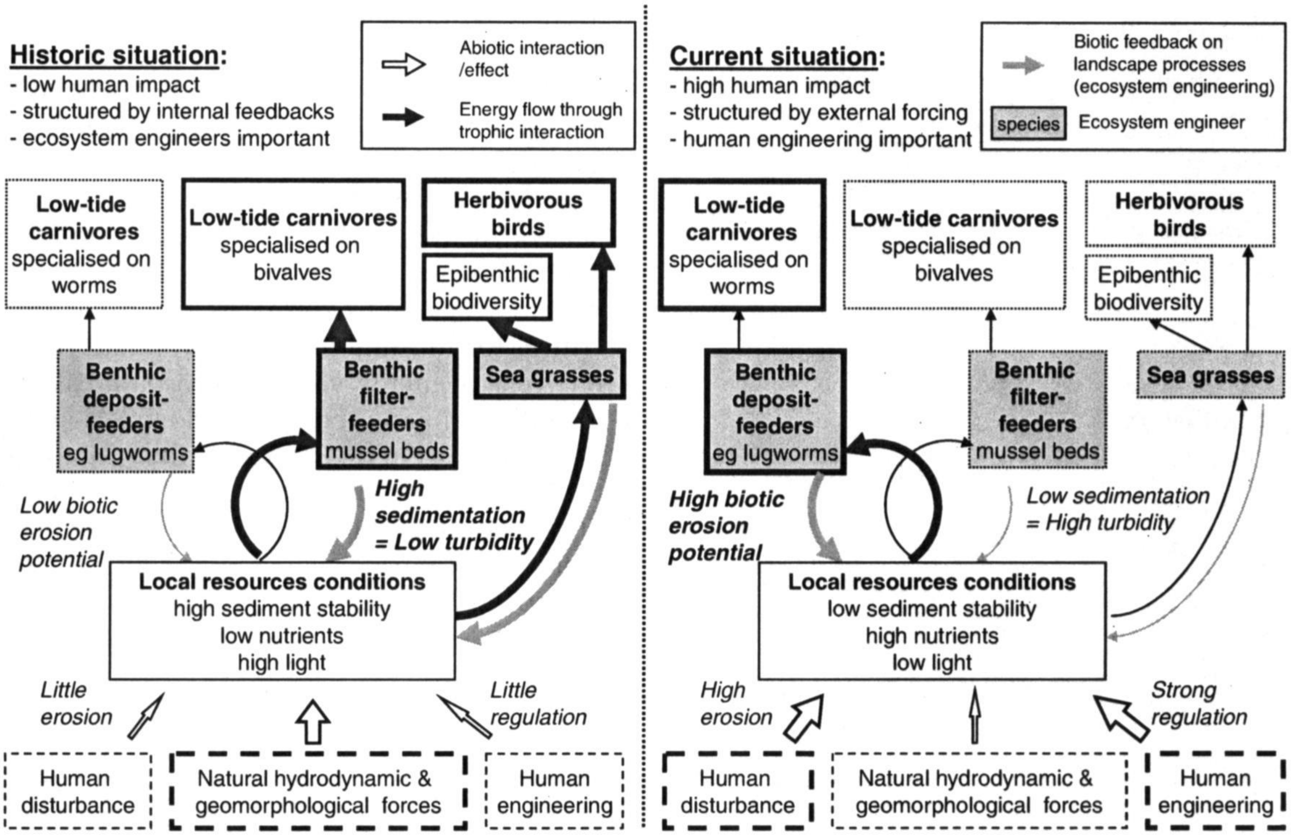


Figure 1. A comparison between the historic situation and the situation as established today. Note the strength of human impact compared to natural forces and the shift from filter feeders to deposit feeders. From Erikson et al. (2010).

Eriksson et al. (2010) compared the biological feedback loops of the pristine benthic soft sediment system with the more current situation (Figure 1). What we can extrapolate from this diagram is that human disturbance and engineering is capable of strongly influencing the nutrient availability and sediment stability. Clearly visible is the cascading effect through the trophic levels in this particular system. Both benthic deposit-feeding systems and benthic filter-feeder have their own particular biodiversity and abundance and therefore measures should be taken to support both systems in the Wadden Sea.

Understanding Interaction

As Figure 1. neatly points out the large role the benthic fauna have in this biological feedback loop. Understanding the effects of erosion on the flora (in this case seagrass) and the chemical contents (nutrition) of the water should provide extra information to aid in modeling the effects of the decrease in human disturbance. In the past years not only the diversity and the abundance of the infauna has been adapting to the large scale use, also the presence and distribution of seagrass has shifted in the Wadden Sea (Reise 1989, Folmer 2016) from a widespread presence of *Zostera marina* to the disappearance of *Z. marina* in the 1930's (Reise 1989) and the presence of *Z. noltii* during that period up to *Z. noltii* now being the dominant seagrass specie in the Dutch Wadden Sea, with a diminished presence of *Z. marina*. This has been coupled to the shift from the Wadden Sea being a sink for North Sea nutrients in the 1950's to the Wadden Sea becoming a major nutrient input die to the large riverine inputs today (Mclusky 1999). These seagrasses primarily occupy the slopes of the sand- and mudflats stabilizing the sediment and decreasing the influence of erosion due to wave action and tidal action (Reise 1989). Modelling based on the Northern part of the Wadden Sea (around Germany and Denmark) show that the Dutch Wadden Sea is in fact capable of re-establishing its seagrass abundance (Folmer 2016) (Figure 2). Investigation towards why this is not naturally occurring without external assistance like in the Northern Wadden Sea points toward the recent shift in infaunal abundance towards polychaetes and the effects of eutrophication (Folmer 2016). Eutrophication may negatively affect seagrass growth through a myriad of reasons the most important being the removal of nutrients necessary for growth, but also increased epiphyte and green macroalgal growth smothering the seagrass (Erftemeijer 2006, Folmer 2016). Finally the conditions in the Dutch Wadden Sea and the Eastern Scheldt are capable of sustaining *Zostera spp,* but the high input of nutrients and the decreased transparency of the water column (often linked to pollution) are plausible explanation as to why seagrass is having trouble re-establishing itself in these areas (Reise 1989).

There are roughly three clearly defined sediment types in the Wadden Sea and the Eastern Scheldt. There is the cohesive mud/silt sediment with a generally very fine grain size, generally poor in macrobenthic functional diversity (Rossi 2013, Dorgan 2015) and a strong inorganic matrix that is hard to penetrate for most infauna. Then there is the fine mud/sand sediment that is less cohesive than mud/silt and rich in functional macrobenthic diversity and can be considered to have an intermediate grain size (Rossi 2013, Dorgan 2015) and lastly there is the permeable sediment (sand) that is generally low in macrobenthic functional diversity with courser (larger) grain size, but the community composition is incomparable to the muddy sediment (Rossi 2013, Dorgan 2015). The difference between sand and a mud and sand combined sediment is that mud is more cohesive in nature due to the sediment being suspended in an organic matrix, while the larger grains (lower phi or ϕ) in sand need additional fluidization or rearrangement of the grains performed by the burrowers in order not to collapse on itself (Dorgan 2015). Each of these sediment types harbor different functional groups of infauna and are affected by erosion (human impact) in a distinct way. These sediments also generally dictate the vertical position of most infauna due to nutrient availability and oxygen dependence (Alexander 1993, Braeckman 2014) although vertical position of infauna is very species dependent. Of the three sediment types discussed here (silt, mud and sand) mud and sand are the preferred substrates since they can sustain the widest biodiversity. Experimental and modeling studies have shown that particle mixing (biological and through anthropogenic impact) exert strong control on permeability, stability, metabolic rates and composition (Rao 2014).

Human impact on the estuarine areas can be classified as two different types: (1) the biochemical impact, caused by influx of nutrients from river runoff (Emse and smaller rivers) and/or pollution from nearby power plants (*e.g.* the Eemshaven Power Plant) (Eriksson 2010), and (2) the mechanical impact, most notably erosion through the effects of shellfish dredging, bottom trawling, ship traffic and hydraulic engineering (*e.g.* Eastern Scheldt Storm Surge Barrier, diking and reclamation, the closing of the Zuiderzee and the gas extraction from under the Wadden Sea) (Eriksson 2010, Gonzales 2010). Whereas changes in the biochemistry of these large areas are not to be neglected this review will focus mainly on the mechanical effects of human impact and how the soft benthic macrofauna adapt/have adapted to the changes.

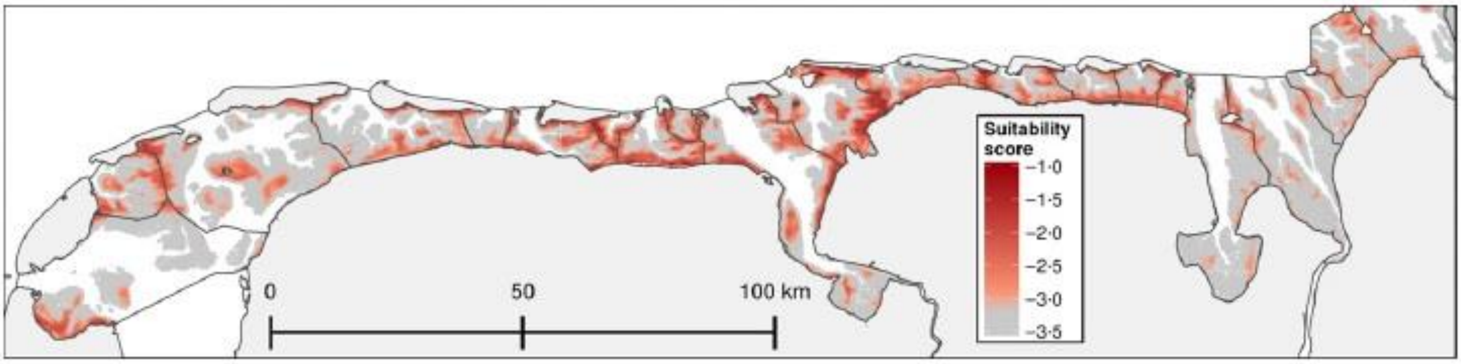


Figure 1. Predicted suitablity of intertidal seagrass in the Dutch Wadden Sea. Suitability score indicates if the area is expected to be suitable for the settlement of seagrass. (Adapted from Folmer 2016)

Anthropogenic Impacts

Natural events affect the intertidal systems in a similar way to anthropogenic use but the largest difference is that events like storms are in most cases sudden burst effects that do alter the system but usually stabilize shortly thereafter (Piersma 2001, Harris 2011), but there are more and more cases where human impacts mimic natural impacts and that are often long term due to continuing input and disturbance (Kranz 1974, Erftemeijer 2006, Harris 2011). For instance; trawling and dredging cause upwelling of sediment through mechanical interaction with the sediment where storms increase the power of the waves and the currents causing similar upwelling.

Although technically not the same, the methods of dredging and trawling or “top layer displacement” affect the sediment and benthic communities in similar ways if, for the moment, we neglect the removal of biomass (vd Veer 1985). Be it the removal of the top layer of the sediment for the use building dikes or artificial elevation of the mudflats/beaches through suction dredging (Piersma 2001, Hiddink 2003) or the chain trawling and hook dredging on the mudflats or shipping gullies for fishing (e.g. shellfish or plaice) (Piersma 2001, de Mesel 2009), the sediment is welled up into the water column after destabilizing the top layer (Maurer 1982, Piersma 2001, de Mesel 2009, van Gils 2009, Eriksson 2010). This sediment settles down after dispersal through hydrodynamic forces (waves or currents) and the finer particles are easiest dispersed. This could potentially lead to an imbalance of present grain size distribution. When targeting a specific infaunal species (often bivalves) dredging can utilize hooks pushed into the sediment to lift up the bivalves from their specific depths and pushes them into the net that is above ground (Piersma 2001, Wijnhoven 2011). In a mud/silt or mud/sand (fine grained) sediment the tiny particles are welled up in the water column increasing turbidity and are exposed to the water current potentially causing direct displacement if currents are strong enough, but even without displacement the effects of the settling sediment are detectable. The removal of the top layer first exposes the deeper fraction of the sediment which is often more compact, less aerated and lower in nutrients (Reise 1989, Alexander 1993, Bilodeau 2004, Folmer 2016). Then the larger particles settle closer to where they were dispersed from, slowly increasing grain size in that location. This fraction of the sediment layer slowly becomes less ideal for the local infaunal individuals (vd Veer 1985, Alexander 1993) slowly prompting a shift in viable biodiversity. Even if the sediment is not displaced the infauna and flora could be effected through the covering by this settling sediment. Most organisms can adapt to a certain degree of this coverage, but only to a limited degree (Checa 1997). Reise et al. (1989) also discovered that re-suspended sediment could lead to hypoxia (oxygen deficiency) in the vicinity of mussel beds whereas strong tidal influences and their upwelling usually prevent hypoxia. The type of deposited material is also of influence of the effect of burial. In general, finer silts are more dangerous for the covered infauna than larger grains of sand because the finer silts can restrict the flow of water in the burrows (Checa 1997).

Wijnhoven et al. (2011) and Piersma et al. (2001) furthermore discovered that not only the ϕ of the sediment but also the nutrient availability within the sediment has an effect on the local ecosystem dependent on the functional groups present. Bilodeau (2004) investigated the possibilities of the displaced sediment (e.g. permeable sediment) settling in a location dominated by another sediment (mud) and was decidedly less optimistic, prompting the viability of infauna across different sediments and solidifying the thought that ϕ is indeed a dominant factor. The newly deposited sediments led to the elimination of well-established populations and even inhibiting recolonization of the target species. This change in sediment composition affects the viability of the range of infauna capable of surviving and establishing and possibly even affecting recruitment of infauna (vd Veer 1985, Piersma 2001, Bilodeau 2004, de Mesel 2009, van Gils 2009, Erikson 2010, Wijnhoven 2011). Managing marine protected areas is hindered through the discord between studies of the effect of trawling and suction dredging, although this is mainly due to the difference between the effect on the system and effects on target species (vd Veer 1985, Kondo 1987, Piersma 2001, Bilodeau 2004, Wijnhoven 2011, Compton 2013).

Nearby areas can be affected in more than just the advection of suspended material albeit on a smaller scale. The digging of shipping gullies is done by dredging the sand from the bottom of the gulley leaving a whole where the sediments used to be. This sand is used mostly for increasing the size of dunes, beaches and/or dikes (vd Veer 1985). Experiments done in the North Sea discovered that over time these holes fill up with sediment (mostly sand) from the surrounding structures. The created hole creates shear stress on the outside ridges of the hole increasing Bottom Shear Stress

(BSS) (le Hir 2007). Applying this knowledge to the gullies through the mudflats we can state that digging gullies for shipping while not directly affecting the mudflats does increase BSS on ridge stability and the infauna that is linked (*e.g.* oysters, mussels and cockles).
Although less obvious from the start this BSS can also be caused by anthropogenic influences from a completely different nature. The closing of the Zuiderzee (by means of the Afsluitdijk) closed off ±25% of what was then called the Wadden Sea (Bergman 1994). This reduction in surface area caused an increase in flow rate and even flow direction leading to a decrease of sediment deposition on the mudflats (van Leeuwe 2010). Nutrient and fresh water input was conversely affected due to the closing off of river flow (The Ijssel and the Eem) to the Wadden Sea. Although the closure occurred in the 1930's local hydrodynamics were still being affected up to 30 years later (Bergman 1994, Piersma 2001). Similarly, the placement of the storm surge barrier in the Eastern Scheldt experienced higher hydrodynamics in the Eastern Scheldt after building and decreasing the probability of cockle and mussel spat settlement and overall cockle and mussel stock in the area (vd Veer 1985, de Mesel 2009), but lower hydrodynamics in the rest of the Voordelta (Coosen 1994). This storm surge barrier was supposed to be permanently closed but local fisheries saw direct effect of the closure on the biomass stock and after ±10 years the barrier only closes when the water level rises above 3 meters above EVRS (European Vertical Reference System that is linked to the Dutch NAP or Normaal Amsterdams Peil) or in case of serious storms to prevent the Dutch southern provinces from flooding.

How do the anthropogenic impacts affect the benthic macrofauna?

The soft sediment benthic macrofauna play a large role in the internal feedback loops of the intertidal ecosystem. Across the world there are many different intertidal zones and their biodiversity is vastly different. Therefore a species by species comparison is unfortunately hard to extrapolate, the difference in species composition between the Dutch Wadden Sea and for instance the Japanese intertidal coast renders a direct comparison futile (Kondo 1987, de Mesel 2009, Eriksson 2010, Kraan 2010). Therefore it is more informative to look at ecosystem function and in particular functional groups (Harris 2011, Braeckman 2014, Harris 2016). The functional groups of infauna have been identified as key in (de)stabilizing the sediment and facilitation of exchange of nutrients across the sediment-water interface (Przeslawski 2009). Removal and/or disturbance of these functional groups can have implications that affect ecosystem stability and sediment stability. To determine viability and stability of these benthic ecosystems investigating the reactions of the functional groups to anthropogenic impacts could provide valuable insight. Anthropogenic effects discussed in this paper will be reaction to burial (Maurer 1982, Maurer 1986) due to sediment deposition, increase in turbidity (Reise 1989, Eriksson 2010), removal of the top layer of sediment (Alexander 1993, Compton 2009, Compton 2013), relocation (Coffen 1999) and the shift in sediment composition (the and/mud/silt ratio)(Alexander 1993, le Hir 2007, Orvain 2012, Dorgan 2015).
In particular bivalves, gastropods and polychaetes in these sediments have ecosystem engineering properties stabilizing the sediment (suspension feeders), de-stabilizing the sediment (bioturbators) or stabilizing the sediment by building structures in the top layer (biogenic builders) (Alexander 1993, le Hir 2007, Orvain 2012, Compton 2013). Each of these groups reside in different areas of the intertidal mudflats and are therefore not affected in the same way. In general the bivalves reside in the upper layers of the sediment (for most species the exact locations are dependent on

size)(Alexander 1993) or on the edge of the mudflats (e.g. mussels and oysters)(Eriksson 2010), the gastropods reside on the sediment (at maximum in first 5 cm)(Orvain 2012) and the polychaetes usually can be found deeper than the bivalves with a maximum of up to 1 meter (rare)(Volkenborn 2007).

Historically the Wadden Sea and Eastern Scheldt were grounds for fisheries with economic importance. Biodiversity and biomass have been in decline (Piersma 2001, de Mesel 2009, Kraan 2010, Compton 2013) and one of the reasons UNESCO made the Wadden Sea a World Heritage location is to try and bring back the historical state of the Wadden Sea with as little of anthropogenic influence as possible. Therefore not only establishing what functional groups these ecosystems are supporting but also trying to identify what the reason are behind the changes and if it is possible to re-establish the historic state of the area. For this study I have identified the 7 most important macrobenthic ecosystem engineers and the most economically viable species to investigate adaptability and theorize future prospects.

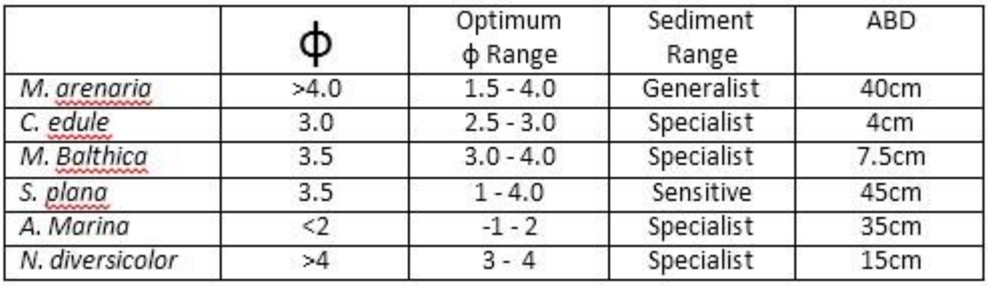
The benthic macrofauna species investigated are devided into three groups: the bivalves (*Mya arenaria*, *Limecola balthica*, *Cerastoderma edule* and *Scrobicularia plana)*, the polychaetes (*Nereis diversicolor* (also known as *Hediste diversicolor*) and *Arenicola marina)* and the gastropods (*Peringia ulvae* (also known as *Hydrobia ulvae*)).

Bivalves

When bivalves occur in high densities they can have specific soft sediment stabilizing effects like the bivalve-reefs formed by *M. edulis* to the bank-forming *C. edule* (Eriksson 2010, Compton 2013). Stabilization only occurs when the bivalves are actually in the sediment prompting the importance of burrowing depth and burrowing rate of the bivalves. Both burrowing rate and optimal burrowing depth are largely influenced by the same factors: water temperature, grain size and shell size (Pfitzenmeyer 1967). As a general rule Kondo et al. (1987) stated that active burrowers (high burrowing rate) are found within the top 15cm of the sediment and the deep burrowers are found at around 30cm or even deeper. Kondo et al. (1987) also stated that burial depth is dependent on interspecific shell size, grain size and maybe even more variables. Later research confirmed this adding water temperature to the important variables linked to (re-)burrowing and linking syphon length to shell size (Pfitzenmeyer 1967, Kondo 1987, Alexander 1993, Leitao 2011). Burrowing rate is generally the same across bivalves but range between 45 mins to 48 hours (within species) and depend mostly on their size and age (Alexander 1993). Unfortunately bivalve stock is rapidly declining in the Wadden Sea due to overfishing and the continual shift in sediment type from mudflats (used to be > 50%, currently 7%) to a finer silted sediment (Volkenborn 2007).

Bivalves are the infauna most targeted species when using trawling and dredging due to their economic value, but occur across a variable depth (figure 2 and 3) making fishing difficult. Therefore many of the methods of trawling/dredging are adapted and try to cause as little impact to non-targeted species as possible, for instance by shortening the hooks to decrease depth of disturbance or the place the hooks farther apart in order to only catch the mature population of a particular size (Coffen 1999). However as most bivalves in the Wadden Sea and Eastern Scheldt are sessile burrowing bivalves they are unable to actively avoid the dredges. Researchers experimented with bivalves to test if uprooting, re-localization, increased dry periods or stress/damage had any effect on burrowing depth and burrowing rate and unless there was actual inhibition through damage both burrowing rate and burrowing depth appear not to be effected (Pfitzenmeyer 1967). Increasing burrowing depth in response to dredging/trawling is not an effective solution most bivalves have access to. Gradually some bivalves have been adapting to a wider range of sediments, like *C. edule* and *L. balthica*, at least in the Wadden Sea (Eriksson 2010) to increase their chances of survival but not all bivalves are adapting, case in point; *S. plana* (Alexander 1993, Kraan 2010, Compton 2013) and simply burrowing deeper would cut of access to food and oxygen.

The dependence of contact with the water interface for breathing and feeding and the relative increase in size needed to bridge the distance is simply not viable in the short term. Some studies (van Gils 2009, Kraan 2010) even showed in *L. balthica* that long term limited food availability (organic matter on the sediment surface) decreased anti-predator behavior and influenced perception of future reproductive value, leading to shallow burrowing even when predation risk increases as a result. The bivalves *M. arenaria* and *S. plana* do not have this particular issue since they developed ways to burrow deeper and still make direct contact with the water. The syphon off *M. arenaria* does not make contact with the sediment surface, it has a burrow that facilitates filter feeding (microscopic plankton and organic detritus) (Pfitzenmeyer 1967, Alexander 1993, Wijnhoven 2011) while *S. plana* employs long thin syphons that do make contact with the sediment surface and are able to regenerate (van Gils 2009), making non-targeted dredging less of a danger (Figure 3). Besides burrowing depth and burrowing rate, food availability and sediment type are also important factors. The 4 most common bivalves can be subdivided into the groups of sediment specialist (*C. edule and L. Balthica*), sediment sensitive (*S. plana*) and sediment generalist (*M. arenaria*)(Reading 1978, Alexander 1993)(Table 1). The sediment type has a large influence on oxygen availability, food availability and bivalve recruitment (Compton 2009, van Gils 2009, Eriksson 2010). Destabilizing the sediment through dredging or advection of suspended material causes *S. plana, L. balthica* and *C. edule* difficulties in spat fall and food availability (Jensen 1992, Coffen 1999, Piersma 2001, Eriksson 2010) due to lack of finer silts and finer organic material. Especially the benthos generated fluffy layer that *S. plana* and *L. balthica* are dependent on for food availability is effected by the resuspension and deposition of sediment (Orvain 2012). Sediment deposition can also promote a shift in sediment type with the added effect of possibly promoting hypoxia (Reise 1989, Bonsdorff 1999, Volkenborn 2007, Donadi 2013, Braeckman 2014). Sudden burial under up to 10cm due to sediment displacement is stated as a general upper limit of what most bivalves can survive (Kranz 1974, Checa 1997) due to their general ability to vertically migrate both ways. The effects of sudden burial is also influenced by the type of sediment that is deposited, made apparent in the case of *M. arenaria* where Checa et al. (1997) stated that they can only migrate upwards if the porosity of the deposited sediment is high enough because they need access to water for their peristaltic propulsion.



	ϕ	Optimum ϕ Range	Sediment Range	ABD
M. arenaria	>4.0	1.5 - 4.0	Generalist	40cm
C. edule	3.0	2.5 - 3.0	Specialist	4cm
M. Balthica	3.5	3.0 - 4.0	Specialist	7.5cm
S. plana	3.5	1 - 4.0	Sensitive	45cm
A. Marina	<2	-1 - 2	Specialist	35cm
N. diversicolor	>4	3 - 4	Specialist	15cm

Table 1. A side by side comparison between the 6 burrowing species. Column 1 is optimal φ for burrowing. Lower φ is more course grain size (sand) and higher φ is smaller grain size (with silt starting at φ of 4). ABD is Average Burrowing Depth.

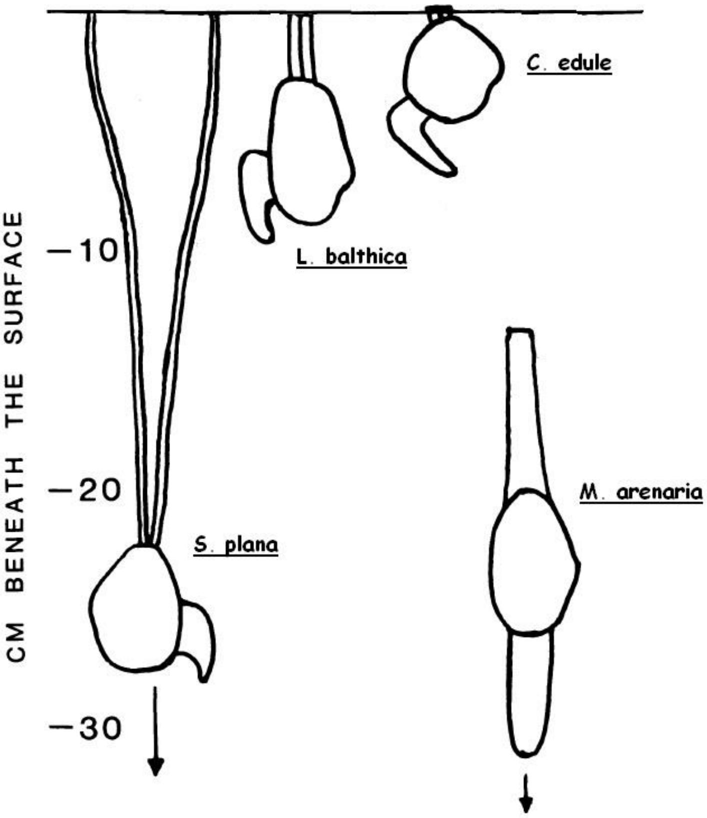


Figure 2. Distribution of the 4 bivalves discussed in this paper. The arrow depicts that it commonly burrows deeper than 30cm. Adapted and modified from Alexander et al. (1993).

Polychaetes

The more mobile infauna that actually have appendages are the polychaetes. The polychaetes with the highest biomass in the Wadden Sea and Eastern Scheldt region are *N. diversicolor* and *A. marina* both bioturbators and benthic feeders (detritivores)(Maurer 1982, Volkenborn 2007, Rossi 2013, Rao 2014) where they construct burrows in the “J”/”U” and “J” shape respectively. These burrow walls are compressed by the polychaetes in order to reduce possibility of collapse (Volkenborn 2007). These polychaetes have little economic value (except for bait used in fishing) but are suspected to be the force stopping the sandy parts of the Wadden Sea becoming mudflats (Volkenborn 2007). Since *A. marina* and *N. diversicolor* reside deeper within the sediment dredging and trawling are dissimilarly affected from bivalves. Destroying the burrows off *N. diversicolor* causes them to relocate and wander the sediment surface suffering increased risk of predation (Maurer 1982) whereas *A. marina* just rebuilds/reconstructs its burrow. Although fairly sensitive to the sediment type they burrow into due to food availability, experiments where soil was deposited on top of them pointed out that even in unfavorable sediment both *N. diversicolor* and *A. marina* were able to dig their way to the surface (Volkenborn 2007, Rossi 2013). Usually not directly affected by anthropogenic impact it is their bioturbating and bioirrigating ecosystem engineering capabilities that exponentially increase the effects of erosion on the sediment surface. Their fecal strings (excretion outside the burrow) accumulate on the sediment surface and when density is high enough (>50 individuals per m2) they can even affect surface elevation (Whitton 2016). Their fecal strings are high in organic nutrients, but are (unlike the benthos generated fluff layer) quick to suspend into the water column (Volkenborn 2007, Whitton 2016) after a strong wave or other mechanical stress.

Gastropods

Unlike most bivalves and polychaetes discussed in this paper gastropods are mostly epifaunal (on the sediment) suspension feeders with appropriate reactions. Burial under deposited sediment is a potent problem and generally 1cm overburden too much to escape (Maurer 1986). The effect of increased turbidity is not particularly well known but since their primary role is formation of the BGFL (Benthos-Generated Fluff Layer (Orvain 2012)) and facilitating sediment-water interactions (Orvain 2012) we can expect the increase in nutrient availability to have a positive effect on gastropod viability, but the mechanics behind this upwelling (the actual trawling and dredging) damages the gastropods (Orvain 2012, Compton 2013). Since gastropods are considered sediment specialists removal of the top layer decreases their overall viability (Rossi 2013). In a similar way gastropods are affected by relocation, there should be little effect if the sediment is similar, however due to the lack of general burrowing capacity, exposure to predators due to ebb and flow could be taken into account.

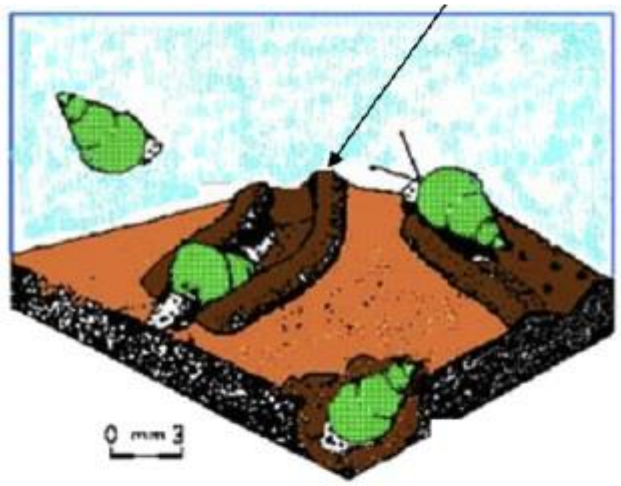


Figure 3. The ridges (shears) the gastropod H. ulvae creates when crawling across the sediment surface. Although small (1-3mm) these shears are affected by increased hydrodynamical pressure. Adapted from Orvain et al. (2012).

The only gastropod that has a presence in the Wadden Sea and Eastern Scheldt is *Hydrobia ulvae* (Piersma 2001, de Mesel 2009, Eriksson 2010, Compton 2013). This small snail with its spiral tipped shell aides the erodibility of the surface layer by excreting the BGFL and shearing the sediment (Figure 4). As epifauna *H. ulvae* suffers from all human interaction in the Wadden Sea and the Eastern Scheldt, but the ecosystem interactions facilitated by *H. ulvae* should not be neglected (Orvain 2012). *H. ulvae* shines a BGFL engineer when biodiversity is high but impact on the local ecosystem is often underestimated because its impact on sediment transport is not yet fully understood (Orvain 2012).

Conclusion

What most studies conclude is that the interaction between and within the trophic levels (Figure 1) is especially important (Kranz 1974, Alexander 1993, Piersma 2001, Volkenborn 2007, de Mesel 2009, Eriksson 2010, Kraan 2010, Orvain 2012, Compton 2013) for understanding restoration of the Wadden Sea sand- and mudflat ecosystem. Analysis of the Dutch Wadden Sea shows that muddy sediments and permeable sediments are poor in macrobenthic diversity in comparison to finer sandy sediments but fulfil completely different roles on a biogeochemical level (Grant 1994, Braeckman 2014). Bioturbation potential can be linked to macrobenthic functional biodiversity (high macrobenthic functional diversity leads to more stability) in certain sediments due to the availability of the biogeochemical nutrients to the phytoplankton present in the system. Controlling the biogeochemical cycling through bioturbation within the system in theory suggests control of the availability of biochemical elements, maybe even restricting for instance eutrophication or at least the suffocating effects it has by keeping the sediment oxygenated (Volkenborn 2007, Braeckman 2014). The processes bioturbation and irrigation, performed by the benthic infauna, have been proven to influence coupled nitrification-denitrification, benthic carbon mineralization, oxygenation and organic matter cycling (Volkenborn 2007, Braeckman 2014) and are of vital importance to the microorganisms in the area.

The ability to support more than one stable benthic community is what characterizes the Dutch Wadden Sea (Volkenborn 2007). As stated previously *A. marina* dominated mudflats are becoming more common in the Dutch Wadden Sea and as Table 1 shows this could lead to local incompatibility with some of the bivalves that reside in the Dutch waters. *A. marina* being as useful as they are in controlling the ammonium, phosphate and silicate concentrations in the upper layer of the sediment (Volkenborn 2007) and their ecosystem engineering capabilities (Orvain 2012), they are oftentimes in direct competition with the settlement of bivalves. Direct competition for food availability and conversion of the sediment structure (Volkenborn 2007) and elevation (Orvain 2012) potentially negatively affect spat fall for bivalves (Whitton 2016). One of the factors controlling the spread and density of *A. marina* is the presence of seagrass (Folmer 2016). Seagrass has a higher chance to take root in areas not ideal for *A. marina* and converts the sediment around it decreasing its viability but this is a 2-way interaction. As an added bonus seagrass settlement promotes surface layer stability and even aids in certain bivalve spat fall (Boström 2000).

Like *A. marina*, the bivalves *M. balthica* and *S. plana* aid in producing the BGFL through the production of pseudo-faeces at the surface (also modifying the surface sediment layer) (Orvain 2012) stabilizing it but also affecting the bed level profile.

Most of the studies discussed in this essay suggest that the Dutch Wadden Sea and the Eastern Scheldt are prone to a phenomenon called hysteresis, also known as alternative stable states (Eriksson 2010, Kraan 2010, Compton 2013). Under the influence of variable anthropogenic effects the systems went from a macrobenthic functionally diverse state that supported a wide range of trophic levels (dominated by filter feeders) to a state that mostly supported less trophic levels (dominated by deposit feeders) highly influenced by and adapted to human input (Eriksson 2010). Evidence of both states supports the theory that both are stable and because of the way the areas are designed both are not mutually exclusive. History even supports a theory of a single stable state since this is the case in Kondo (1987) his study, although the environmental differences between the study site in Japan and the Dutch regions are not as easy to compare 1-on-1.

External (human) influence has had a tremendous impact on these systems and even though some of the infauna is able to adapt to the “new” environment it will not be fast enough to stabilize in a sustainable way. Reducing the high impact humans have had on this system is showing promising results. Although in the Wadden Sea we can see a divide between the Eastern and Western parts when looking at sediment structure and benthic biodiversity, there is too little historic evidence from before anthropogenic impact to determine if this has always been the case.

Future prospects

The effects of changing sediments on biodiversity and functional biodiversity are well studied across a large section of the worlds intertidal areas. Research has been making progress in understanding the effects of specific marcofauna on the intertidal flats through exclusion experiments and experimental lab studies. What in my opinion is lacking is the understanding on how exactly the ecosystem engineers cope with the settlement of unfavorable sediment. It has been investigated that the bioturbators change the sediment matrix to a certain degree with excretions and… Valuable information could be exactly how much silt can be processed and “neutralized” by a defined density of *Arenicola marina* (or any other combination of organisms) in order to determine the flexibility of the system. Also more attention should go towards the interaction studies (although that makes for a very complicated study).

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