The Ecological Importance of Pools in the Mussel Bed

First master thesis
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Abstract
Blue mussels, *Mytilus edulis* L., in the Wadden Sea build intertidal beds on the mud flats. Mussel beds provide scale dependent ecosystem-engineering functions. For example, the settlement of cockles, *Cerastoderma edule* L., is facilitated up to a 100 m’s on the leeward side of the reefs. At the same time, the reefs facilitate the settlement of *Fucus vesiculosus* L. and other organisms on the bed itself. On the mussel bed, structural differences include pools, which are hollows in the mussel bed that retain water during low tide; and inlets, which are hollows that are for the most part surrounded by mussels but have an opening to the mudflats and do not retain water. In inlets, large heaps of mud and diatoms can be found. The consequences for biodiversity of the structural differences on mussel reefs remain largely unstudied. The aim of this research therefore is to analyse how the complexity created by mussels influences associated species. I studied the effects of structural differences on a mussel reef on abiotic factors, such as elevation, erosion and sediment transport, and how this in turn affected biotic factors, such as organic matter content and species composition. Pools, inlets and the mussel aggregations in between, differed from each other concerning both abiotic and biotic factors. Pools contain less organic matter and experience less erosion. Inlets have higher erosion rates, but also more organic matter content. This way, the different locations vary from stressful, but food-rich, to more calm spots, with also less food available. Different species of infauna prefer the different locations. So is *Scoloplos armiger* mostly found in the calm pools, filled with shell-debris, and *Macoma baltica* prefers the muddy heaps of diatoms in the inlets. My results suggest that the differences between pools, inlets and mussel bed, facilitate a complex community of different species and high biodiversity, by creating niches for many species.
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Introduction

The blue mussel, *Mytilus edulis* L., provides an important ecosystem function in the Wadden Sea. These bivalves are able to settle on loose substrate and aggregate, forming so-called mussel beds (Brinkman, Dankers, & van Stralen, 2002; Jacobs, Riegman, & van der Meer, 2016; Saier, 2002). The mussel beds provide hard substrates on the soft substrate. The elevation of the bed influences the force and patterns of the waves and tides. The elevated mussel bed forms a barrier that forces the flow of water to flow around or over the mussels. Wave stress is harsher on top of the bed, whereas it is reduced behind the mussel bed. These effects create new circumstances and habitats in relation to the environment. This is why the blue mussel in the Wadden Sea is an important ecosystem engineer and factor structuring the surroundings of the mussel bed (Donker, van der Vegt, & Hoekstra, 2013).

The ecosystem engineering function of the mussel bed influences a large scale of processes. On both the short and the long range it provides for and stimulates different habitat cascades (Thomsen et al., 2010). In such a cascade, the first settling species creates a habitat for a second species. This then in turn also provides habitats for other species. The mussels provide a hard substrate for different species, such as barnacles and *Fucus vesiculosus* L. to attach to. These in turn provide a food source and shelter for different species of benthic fauna (Buschbaum, 2001; Büttger et al., 2008; van der Zee et al., 2015). On the long range, the effects of the mussel bed on the force of the waves provide suitable habitats for infauna on the leeward, most often coastward, side. Cockles, *Cerastoderma edule* L., for example form endobenthic beds about a 100 metres from the mussel bed. They in turn stabilise the sediment and so provide habitat for other species of infauna. Cockles also are a food source for many bird species (Beukema & Cadée, 1996; van Gils, Spaans, Dekinga, & Piersma, 2006). Most of the above mentioned processes and species would not occur without the presence of a mussel bed. The mussel bed creates a more complex structure of habitats in the Wadden Sea and so provides in niches that can be used by a wide array of species.

On, or rather within, the mussel bed open pools exist that are devoid of mussels. Whether these patches form because of wave stress patterns or because of the self-organisation of *M. edulis*, is still open to speculation, but this goes beyond the span of this research. The pools are hollows in the mussel bed, completely surrounded by mussels. For this reason they retain water during low tide. The edges of the pools are generally covered by *F. vesiculosus*. The centres of the pools normally show no signs of vegetation or cover by *M. edulis* (pers. obs.). Some pools that are closer to the edge of the mussel bed have an open connection to the mudflats surrounding the bed. These inlets, as they will be referred to, do not retain water during low tide. Instead of a hollow in the mussel bed, inlets often contain a heap of mud in their centre, covered with diatoms (pers. obs.).

Except for a research that shows that intertidal eelgrass, *Zostera marina*, can profit from the pools (Bos & Van Katwijk, 2007), they remain rather unstudied. In a first, visual comparison, pools and inlets seem to be unique spots in their surroundings. For that reason the question arose if these spots could add something to the Wadden Sea mussel bed ecosystem. Could they in fact be an additional niche, yet unexplored. This idea is based on studies done in intertidal rock pools, showing that a more complex habitat provides for more niches (Beaugrand & Helaouët, 2008; Coffin, Drolet, Hamilton, & Barbeau, 2008; Faria & Almada, 2006; Marshall, Semmens, & Cook, 2004). The presence of the pools suggests a more complex habitat than the until now studied mudflats and mussel beds. In this research we will test if the pools are indeed different from the surrounding habitat-types. Comparing them with inlets and the mussel bed, we expect that these different structures will add multiple niches to the ecosystem.
Material & Methods

Location & field trips

The mussel bed chosen for this research is located south of the island of Schiermonnikoog in the Dutch Wadden Sea, at approximately 53.467709 °N, 6.224157 °E. It is an intertidal mussel bed, approximately 1km of the coast of the island and reachable by foot during low tide. This normally gives an operating window from 2 hours before until 2 hours after the lowest water level.

The mussel bed is ±150m long (east to west) and 40m across. The bed is mostly formed of blue mussels, *Mytilus edulis*, and Pacific oysters, *Magallana gigas*. In most places, the bed is covered by *Fucus vesiculosus*. It is elevated in comparison to the surrounding mudflats. Hollows in the bed form pools, which retain water, or inlets, which are in open connection with the mudflat and do not retain water.

The experiment started on the 19th of March 2018 and ran for 4 weeks until the 16th of May. I monitored the progress of abiotic and biotic variables once every month (Appendix 1).

Experimental setup

We established 4 blocks on the mussel bed. Approximately 50 steps east-, north- and westward of the mussel bed 12 control plots were placed on the mudflats in groups of 4, blocks 5, 6 & 7. For a schematic overview, see Figure 1.

All pools and inlets were measured for length, the longest diameter, width, halfway the length, and depth, in the middle. Coordinates and elevation were noted down of every plot.

Mussel bed plots (MB)

Every block contained 1 plot entirely covered by mussels, of ±1m². These plots function as a control for the properties of the mussel bed.

Control pools (CP)

Pools on the mussel bed are patches devoid of mussels. They are hollows in the bed and therefore retain water during low tide. For this reason, the pools seem unique spots of stagnant water on both the mussel bed and mudflat. The control pools in every block were left unmanipulated. For this research we did not look into which processes influence the formation of the pools.

Control inlets (CS)

Inlets are situated on the edges of the mussel bed. On 2 or 3 sides, they are surrounded by mussels, the remaining sides are in open connection with the mudflat. Sometimes they retain some water on the sides, but are mostly intertidal and drain during low tide. Heaps of mud and diatoms are formed in the middle.

Manipulated pools (MP)

These pools were located near the edge of the mussel bed. A trench was dug from the pool to the side of the mussel bed, ±1m wide or as wide as the pool itself. This way, the pools were drained from water during low tide and so acquired the...
characteristics of inlets. Along the sides of the trenches, the mussels and oysters of the bed were covered with chicken wire. This to prevent them from rearranging and closing the trench, but still allow them to filter feed. The dug-away mussels were placed on the mussel bed, outside the blocks. Except for block 1, manipulated pools did not drain into pre-existing inlets used in the research. The manipulated pools were used to check if the differences we found between natural pools and inlets, were indeed the result of inlets being open to the mudflats and their draining during low tide.

**Sandy control plots (SC)**

Blocks 5, 6 & 7 consisted of four plots, lined up from east to west. We used these plots to compare the mussel bed to its surroundings. Each block on the mussel bed consisted of 4 plots, 1 of every type. The blocks were placed in such a way that the plots they contained were under roughly the same conditions, due to their proximity to each other. By assigning the different blocks, we could test for differences between different parts of the mussel bed. For example, if the difference between blocks were to be significant, the east of the bed could not be compared to the west.

**Abiotic factors**

**Elevation**
The elevation of the plots was measured in metres below NAP (Normaal Amsterdamse Peil / Amsterdam Ordnance Datum), using a height measurer (brand: Trimble, R8 TSC3).

**Erosion**
We placed poles made of plaster (brand: ‘Knauf’, 1 part water: 1 part plaster, dried to constant weight, height: 5cm, Ø: 3cm) in all plots, ±10cm north of the pole indicating the plot. We did this to measure the differences in wave-stress between the plots. The poles were weighed before placement. They remained in the plots for 2 consecutive tidal cycles. After retrieving them, the sediment was carefully cleaned of and the poles were set to dry for 2 weeks. After that period, they were weighed again. The percentage of weight lost over the 2 tides measures abrasion at the sediment surface and that we used as a proxy for hydrodynamic stress.

**Sediment transport**

Bottles (sediment traps, height: 9cm, width: 6cm, volume: 250mL) were placed in all plots, except for the mussel bed plots (MB), to look at sediment transportation. We dug the traps into the sediment so the brim aligned with the sediment and filled with water, ±10cm eastward of the pole indicating the plot. They remained for 2 consecutive tides. After retrieving them, they were left standing for 2 weeks, to let the sediment settle. I measured the height of the settled sediment on 4 sides of the bottle and the average of those 4 sides was used to calculate the volume of the trapped sediment.

**Biotic factors**

**Organic matter content**
We collected organic matter samples to analyse the amount of (pseudo-)faeces and other organic compounds in the plots, to determine food availability for infauna and detritivores. The samples were taken during every field trip on every plot, except for the mussel bed plots (MB). It was not possible to place the cores in the sediment between the mussels. We took cores of 1cm and 5cm depth using syringes (Ø=2.5cm). The pointed end of the syringes had been sawed off and the different depths were indicated. These cores were stored separately in Ziploc bags in a freezer at −18°C before analysis in the lab. In the lab, the samples were placed in pre-weighed ceramic cups. All of the 1cm-samples was used, for the 5cm-samples a similar amount. The cups were placed in an oven (65°C) for 48 hours and left in a desiccator overnight. After the dry weight was measured, the samples were put in a burning-oven (550 °C) for 4 hours and again left in a desiccator overnight. After this their burned weight was measured and the organic matter content calculated as the percentage of weight lost during the burning process.

**Mussel condition**
We collected mussels from all plots, except for the ‘sandy control’ plots (SC), to calculate the Condition Index (CI), to analyse the differences that different locations make for the mussels. On the
first and third field trip, we collected 20 mussels per plot. In the pools and inlets, the mussels were collected along the edges. In the pools, they were collected from underwater, the same height was used in the inlets. The mussels were stored in the freezer before they could be analysed. The CI was established according to the following formula (Petersen et al., 2004; Riisgård, 2001; Stier, Drent, & Thieltges, 2015):

\[ \text{CI} = \frac{\text{DW}}{L^3} \]

where CI is the condition index, DW is the dry weight (in mg) and L is the shell length (in cm). We scraped all mussel flesh out of their respective shells to calculate DW. The flesh was put in pre-weighed tin foil cups and placed in an oven (65 °C) for 72 hours. The dry-weight was measured after this. We measured the longest length of every shell for L. We also measured width, halfway the length-measurement.

Infauna
We took infauna cores from all plots, except for the full mussel bed plots (MB). The crude core (Ø=13.5cm) was stuck in the sediment up until 10cm deep. We washed away the sediment over a sieve with a 1mm mesh. We stored the remaining infauna and shell debris (almost all plots in the mussel bed contained this debris) in labelled bottles. Since this procedure leaves a gap in the plot, we only did this at the end of the research. Back in the field station lab, we replaced the water in the bottles with ethanol and added Bengal Rose® to colour all organic material.

In the lab, we poured the samples over a sieving cascade (4.00mm till 500µm in 7 steps) and distributed each one of them over size-specific petridishes. Using a binocular microscope, we separated the infauna from the debris and determined it to the lowest level possible. That is, mostly until genus- and family-level, sometimes till species-level (in case of bivalves). Others were not determined further than the phylum (e.g. Nematoda). The different types found were counted and stored.

Statistical methods
I performed all statistical analyses in R v 3.5.1 (R Core Team, 2018). I could not normalise the data, even after trying several transformations. However, I judged the deviances from normality minimal enough to have the parametric tests yield adequate results.

I analysed all different sampled variables differently. I did this for the all plots on the mussel bed, i.e. blocks 1, 2, 3 & 4. The remaining blocks, outside the mussel bed, I pooled to serve as comparison, but did not include them in the statistical model.

Erosion, sediment transport & plot-elevation
Erosion, sediment transport & plot-elevation were analysed for differences between plot-types using an Analysis of Variance (ANOVA). The blocks were assigned randomly and were therefore included as a random effect. The significance of this random effect was tested with a random effect ANOVA (RANOVA). Both the plot-types and blocks were the two factors included in the primary model. The model was stepwise reduced to the Minimal Adequate Model (MAM). The factors were tested stepwise for their influence on the results. When a factor was not of significant influence, it was removed from the model. The factors that remained were compared pairwise with a Tukey HSD post-hoc analysis.

Organic matter content
Organic matter content till 1cm and till 5cm were analysed separately for differences between plot-types, blocks and sample dates. Blocks were again included as a random effect and analysed with a RANOVA. Since the samples were taken from the same plots on four different dates, the samples were handled as repeated measurements in the ANOVA. The primary model contained plot-types, blocks and sample dates as factors. This model was reduced to the MAM. The remaining factors were analysed with a Tukey HSD post-hoc analysis.

Mussel Condition Index
Mussel Condition Indices were analysed for differences between plot-types, blocks and the two sample dates. Blocks were included as a random effect and analysed
with a RANOVA. When the two sampling dates proved to be significantly different, these two were further analysed separately from each other using an ANOVA. The model was reduced to the MAM. The remaining predictor variables were analysed with a Tukey HSD post-hoc analysis. Infauna counts

First, I analysed the abundances per species-group for differences between plot-types and blocks using an ANOVA. Blocks were included as a random effect and analysed with a RANOVA. The model was reduced to the MAM and then analysed with a Tukey HSD post-hoc analysis. This process was repeated on the genus-level for the polychaetes. This was the only phylum that contained usable genera, i.e. genera that were found in sufficient amounts to be tested. Other phyla and groups could either not be further determined, or contained not enough genera to test.

After that, the overall species composition was analysed for differences between plot-types using a Permutation ANOVA (PERMANOVA). This was done on species-group-level and genus-level. A multiple comparison post-hoc test was done using a Pairwise Adonis Test.

Results

In all analyses the influence of the blocks, included as a random factor and tested

![Image](https://example.com/image1.png)

**Figure 2** The elevation of the different plot-types in metres below NAP (Normaal Amsterdams Peil or Amsterdam Ordnance Datum) (df=3, F=12.908, *p<0.001)

with a RANOVA, proved to be not significant (p>0.05) and could be taken out of the primary models. I.e. the different locations, east to west, on the mussel bed did not influence the differences between the samples taken at each plot. Because of this result, it was possible to pool the same plot-types from the different blocks.

**Abiotic factors**

The mussel bed plots (MB) were about 2 dm higher than the other types of plots (df=3, F=12.908, p<0.001; Fig. 2). There were no significant differences in

![Image](https://example.com/image2.png)

**Figure 3** The erosion measured for the different plot-types, expressed in % of weight loss of the plaster poles

![Image](https://example.com/image3.png)

**Figure 4** The amount of sediment trapped in sediment traps for the different plot-types (df=2, F=26.352, *p<0.001)
erosion between plot-types were not significant (df=3, \( F=1.4185 \), \( p=0.286 \); Fig. 3). The volume of sediment trapped in the natural inlets was significantly less than in the other plot-types (df=2, \( F=26.352 \), \( p<0.001 \)).

### Biotic factors

The sampling date had a significant effect on the shallow organic matter content (OM) samples (i.e. the 1cm samples, (df=3, \( X^2=16.439 \), \( p<0.001 \))). The first date, before the start of the manipulation experiment, is significantly different from the other dates. This pattern also came up when I analysed the differences between plot-types. On March 19th CSs had significantly higher OM than both CPs and MPs (df=3, \( X^2=16.439 \), \( p<0.001 \)). On April 12th & 23rd and May 15th, the CPs had a significantly lower OM compared to both the CSs and MPs (df=2, \( X^2=14.152 \), \( p<0.001 \), see Fig.5). The deeper OM samples (i.e. the 5cm samples) did not differ between sampling dates (df=3, \( X^2=1.3256 \), \( p=0.72 \)). Here the CSs consistently had a significantly higher OM compared the CPs and MPs (df=2, \( X^2=64.411 \), \( p<0.001 \)).

The mussel condition index was higher in May compared to March (df=1, \( F=7.844 \), \( p=0.005 \); Fig. 6). I therefore analysed the dates separately. However, there were no significant differences found between plot-types any of the months.

I firstly analysed the infauna counts on the species-group-level. To get a more complete view of the differences between plot-types, I then did an analysis on the genus-level. For the groups, I found a trend towards differences in the over-all species-composition between plot-types (PERMANOVA: \( F=1.6649 \), \( p=0.083 \)). Analysing the species groups separately showed that this depended on that there were significantly more amphipods in the natural pools (CP) (df=2, \( F=13.8 \), \( p<0.001 \)), and significantly more bivalves in the inlets (CS) (df=2, \( F=10.356 \), \( p=0.002 \)), compared to other plot types. Only amongst the polychaetes I found enough genera that were found in sufficient amounts to analyse. *Scoloplos*
armiger was mainly found in CP plots and not at all in CS plots, but the differences were not significant (df=1, F=3.4225, p=0.124).

The PERMANOVA on the genus-level showed a significant difference between CP and CS plots in species composition (df=2, F=2.6385, p=0.005, see Fig. 8).

**Discussion**

Previous research has shown that the influence of mussel beds are far-reaching and creates greatly varying conditions on seemingly homogeneous mudflats (Beukema & Cadée, 1996; Brinkman et al., 2002; Donadi et al., 2013; Engel et al., 2017; Saier, 2002; van der Zee et al., 2012, 2015; Wa Kangeri et al., 2014). This research confirms/adds that the mussel bed itself is very a heterogeneous habitat. First of all, the mussel bed itself is higher than its surroundings. The pools and inlets are also consistently lower than the bed, but mostly higher than the surrounding mudflats. This higher elevation, together with the solid structure of the mussel bed, influences conditions on the different locations. Wave stress for example, measured using the erosion plaster poles, is higher on the unprotected areas, i.e. on top of the mussel bed and the surrounding mudflats. The pools and inlets are shielded from the water flow by the mussel bed and therefore show less erosion. The higher erosion in the manipulated pools and inlets, compared to the natural pools, can be explained by water flowing in and out with the tides. The water in the mussel pools remains stagnant during low tide.
The sediment transport results, however, show a contradicting pattern. While I expected more transport with more erosion and influence from the tides, the inlets show less transport of sediment. This contradiction can be the result of the heaps of diatoms in the natural inlets. The diatoms create a biofilm that allows them to stick to their spot when a strong current washes over them (Daniel, Chamberlain, & Jones, 1987). This biofilm also traps the sediment and prevents large amounts of sediment transport.

The organic matter content (OM) is also higher in the natural inlets. This could be because of all the diatoms and support the theory about the biofilm trapping the sediment, but a chlorophyll-α analysis has to be run to confirm that properly. The higher OM would also suggest there is more food available for organisms in the natural inlets. The natural pools contain less organic matter.

At the end of the research period, the top-layer of the manipulated pools had started to resemble the OM content in the inlets, whereas the lower layer still resembled the OM content in the natural pools. It appears that a diatom heap has started to form in the manipulated pools, profiting from the new periods without water, during low tide. The research did not take long enough for the lower layers in the sediment to also show this change.

For the mussels themselves their location on the mussel bed does not seem to influence their condition. They were of better condition later in the season, when food was again available in larger quantities.

However, that location on the mussel bed does not influence the condition of the mussels, does not mean other processes of the mussels are not influenced. Juvenile mussels could for example profit from the ameliorated currents in pools just after settlement. To fully understand the influence of the different locations on the bed on the mussels, further specified research into mussel life-history traits on these locations is needed.

Bivalves and oligochaetes seem to prefer the more muddy sediment of the inlets, polychaetes are found more in the shell debris of pools. On both the species-group and genus-levels of the analysis, the manipulated pools appear to be in a transition stage from pool to inlet, just like with the OM analysis.

The analyses on the genus-level show the same pattern as those on the species-group-level. The bivalves we found most were Macoma baltica. This therefore is the most common species in the inlets. The polychaetes in the pools are best represented by Scoloplos armiger, which is found less in the manipulated pools and not at all in the natural inlets. Cirratulidae and Polydora show the same preference for pools. Capitellidae, on the other hand, are polychaetes that are found mostly around the mussel bed and in the inlets.

I have found many differences between plot-types, as well as indications for different processes like the formation of diatom heaps. The structural differences between these locations, create separate habitats, with unique combinations of biotic and abiotic factors. This research shows pools to be locations with ameliorated stress conditions, i.e. erosion, and less food abundance, i.e. organic matter. Inlets on the other hand receive more stress from the water current, but more stable and muddier sediment, with higher OM content. Many other combinations can be found on and around the mussel bed.

The niche-concept explains that slight differences in the environment can stimulate different species (Groom, Meffe, & Carroll, 2006; Krebs, 2014). This would suggest that the different locations on the mussel bed are different niches for different species. This can also be seen in the preference of species as S. armiger for pools and how M. baltica is most common in the muddy inlets.

The questions that now remain are which factors create niches for which species. For example; does S. armiger prefer pools because of the type of sediment, the ameliorated currents or something else that was not analysed in this research? Also important to know is how the pools are formed. Is it a result of wave stress or some kind of disturbance that moves the mussels away from that particular spot?
And if a new pool of inlet is formed, how does that influence the composition of the infauna? A large proportion of the infauna counted in manipulated pools consists of nematodes. This could be a sampling error, or nematodes are the first to flourish after a disturbance and what was analysed here, was a succession stage. All in all, the mussel bed is a very divers system, that adds even more diversity to the Wadden Sea ecosystem. Its influence is both far- and short-ranging. The mussel bed shows how the influence of an ecosystem engineer shapes its environment, both direct and indirect.
References


## Appendix

### Appendix 1 Overview of all fieldtrips

<table>
<thead>
<tr>
<th>Date</th>
<th>Conditions</th>
<th>Samples taken</th>
</tr>
</thead>
</table>
| **March 19 & 20** | 19<sup>th</sup>: Low tide: 18:00  
Temperature: 2 °C  
Wind: 4 bft east  
Sunny  
20<sup>th</sup>: Low tide: 06:26  
Temperature: 3 °C  
Wind: 4 bft east  
Clear sky | 19<sup>th</sup>: Descriptive measurements, plots assigned, organic matter (1+5cm), mussel collection  
20<sup>th</sup>: Setup manipulation experiment |
| **April 12**   | Low tide: 14:50  
Temperature: 12 °C  
Wind: 6 bft east  
Cloudy | Organic matter, Chl a |
| **April 23 & 24** | 23<sup>rd</sup>: Low tide: 11:36  
Temperature: 14 °C  
Wind: 4 bft west  
Partly cloudy  
24<sup>th</sup>: Low tide: 11:45  
Temperature: 12 °C  
Wind: 7 bft west  
Cloudy | 23<sup>rd</sup>: Organic matter (1+5cm), Chl a, plaster pole placement, sediment trap placement  
24<sup>th</sup>: Plaster poles and sediment traps collection |
| **May 15 & 16** | 15<sup>th</sup>: Low tide: 17:30  
Temperature: 22 °C  
Wind: 3 bft north  
Sunny  
16<sup>th</sup>, 1<sup>st</sup> tide: Low tide: 5:30  
Temperature: 10-13 °C  
Wind: 4 bft north  
Partly cloudy  
16<sup>th</sup>, 2<sup>nd</sup> tide: Low tide: 18:10  
Temperature: 11 °C  
Wind: 6 bft north  
Cloudy | 15<sup>th</sup>: Organic matter (1+5cm), Chl a and mussel samples  
16<sup>th</sup>, 1<sup>st</sup> tide: Infauna cores from blocks 1, 2, 3 & 5  
16<sup>th</sup>, 2<sup>nd</sup> tide: Infauna cores from blocks 4, 6 & 7 |