The influence of mechanical habitat disturbance on the infauna of *Zostera marina* L. meadows

Marc Jürgen Silberberger

Master Thesis
Department of Biology
Program for Marine Biology

UNIVERSITETET I OSLO

1st June 2012

2012

The influence of mechanical habitat disturbance on the infauna of *Zostera marina* L. meadows

Marc Jürgen Silberberger

Cover photo by Jonas Thormar

http://www.duo.uio.no/

Print: Reprosentralen, Universitetet i Oslo

Abstract

Eelgrass (*Zostera marina*) meadows are a common feature in shallow waters along the Norwegian coast, where they provide a habitat for an infaunal community with a high biodiversity. A field experiment, comprised of two different disturbance events, was conducted to investigate the effects mechanical habitat disturbances have on the infauna of *Z. marina*.

The disturbances included the cutting of all the *Z. marina* leaves at the sediment surface and the removal of entire plants including the rhizomes. This experiment was conducted in three eelgrass meadows in the inner Oslofjord. The faunal composition of macrofauna and meiofauna in the sediment was analyzed after a recovery time of ten months to investigate the effects of the treatments.

The infaunal abundance of macrofauna and meiofauna varied between the three studied locations, with the fewest individuals at Sætrepollen, followed by Sandspollen and Hallangspollen with the highest infaunal abundance. The infauna of the cut treatments could not be separated from control samples by univariate or multivariate statistical analysis. The removed treatment resulted in a higher abundance of the gastropod *Peringia ulvae* and the bivalve *Mya arenaria* than in the control samples.

Each of the *Z. marina* meadows was characterized by a different abundance and composition of its infauna. *Z. marina* meadows in the removed patches did not regrow within ten months, what has the potential to change the functioning of the infaunal community. This should be considered for an appropriate management of *Zostera marina*.

Acknowledgements

First I want to thank my supervisors Stein Fredriksen and Jonas Thormar for the great support during the last two years. I could not have hoped for better supervisors during this thesis. Further I want to thank Hartvig Christie for the help with the sampling, Rita Amundsen for the help with the grain size analysis and Sissel Irene Brubak for the instructions on the use of the centrifuge. I also want to thank my lab partners for the discussions and the nice working atmosphere.

A special thank goes to Hans-Olav and Ulrike for proof reading of my thesis.

I want to thank my family for the support during all the years, especially my parents Petra and Jürgen, who support all the stupid ideas I have.

I want to thank Sabrina for the support during the last years and I want you to know that I wouldn't have been able to finish this without your support.

Further I want to thank everybody who I should thank, but forgot to name here.

Last, I want to thank Philipp for the support with YouTube playlists during the long days and nights in the lab.

Table of Contents

1 Introduction

1.1 Seagrasses

The 50-60 seagrass species which are known worldwide (Phillips & Menez 1988, Spalding et al. 2003, Orth et al. 2006) are the only flowering plants which evolved back into the oceans (Les et al. 1997) and have the ability to grow and reproduce completely submerged in full saline and brackish water (Hemminga & Duarte 2000, Spalding et al. 2003). In spite of the low number of species, seagrass ecosystems can be found at coasts from the tropics to the arctic regions of Alaska, southern Greenland or the White Sea and only the most polar waters have not been colonized (Phillips & Menez 1988, Green & Short 2003, Orth et al. 2006). Almost all seagrass species grow in areas sheltered from wave action, where they are anchored in soft sediments by a sub-surface root-rhizome system (Phillips & Menez 1988).

In terms of biomass, the sub-surface parts of the plants account for approximately 50% of the total biomass (Duarte & Chiscano 1999), even though this varies from species to species. Seagrasses are more dependent on a high light intensity than macroalgae (Duarte 1991, Dennison et al. 1993), since the respiratory needs of the root-rhizome system has to be covered by the photosynthesis of the leaves (Nielsen et al. 2002).

Seagrasses have an internal gas transport system (Hemminga & Duarte 2000), the lacunar system, which consists of gas filled channels that run from the leaves all the way down to the roots and serve the plant in two different ways (Roberts et al. 1984). Firstly the produced oxygen of the photosynthesis is transported into the roots, where it is used for respiration and to oxygenate the often anoxic sediment surrounding the roots (Sand-Jensen et al. 1982, Pedersen et al. 1998). Secondly, the gas in the leaves gives buoyancy which makes the leaves stand erected in the water (Phillips & Menez 1988).

1.1.1 The seagrass ecosystem

By means of their leaves, seagrass meadows provide a 3-dimensional structure that supports a high abundance of epiphytic and other benthic algae (Heijs 1984, 1985, Boström & Bonsdorff 2000, Fredriksen et al. 2005). The total primary production of the seagrass ecosystem, the sum of primary production of seagrasses and associated algae, is very high (Duarte &

Chiscano 1999). Seagrasses also support dense and diverse faunal assemblages (Heck Jr et al. 1989, Gray et al. 1996, Boström & Bonsdorff 1997, Connolly 1997, Baden et al. 2003, Fredriksen et al. 2005).

In addition to this, the leaves of seagrasses reduce water currents and thereby enhance the sedimentation of particles and associated nutrients in the seagrass meadow, while the root-rhizome system stabilizes the accumulated sediment and protects it against re-suspension (Scoffin 1970, Ward et al. 1984, Boström & Bonsdorff 2000).

An important part of the fauna in seagrass ecosystems is the infauna living in the sediment below, where the root-rhizome system creates a somewhat more structurally complex habitat compared to unvegetated sediments. Several studies have shown that seagrasses host a high infaunal abundance and diversity. In particular, a higher density of infauna can be found in vegetated sediments compared to close-by unvegetated sediments (Orth 1973, Stoner 1980, Ansari et al. 1991, Edgar et al. 1994, Boström & Bonsdorff 1997, Fredriksen et al. 2010). All these studies investigated macrofauna, not smaller than 250 µm. Some studies on meiofauna indicate that there might be a similar trend (Castel et al. 1989, Ansari & Parulekar 1994), but not all studies agree on this (Tietjen 1969, Fonseca et al. 2011).

1.1.2 The importance of seagrass ecosystems

Seagrass ecosystems provide a variety of services, which place them among the most valuable ecosystems of the world (Costanza et al. 1997). Seagrasses exhibit a net primary production which ranks among the highest of any ecosystem of the world (Duarte & Chiscano 1999). A large part of the produced organic carbon is entering the detrital pool and so the seagrasses play an important role in CO_2 sequestration (Duarte et al. 2004, Kennedy et al. 2010). Seagrass ecosystems are nursery habitats for many commercially used fish and shellfish species all over the world (Heck Jr & Orth 1980, Orth & Heck Jr 1980, Baden et al. 2003, Heck Jr et al. 2003). The accumulation of particles and associated nutrients is not only important for the seagrass ecosystem. The increased sedimentation is particularly important in tropical regions, where seagrasses enable the existence of adjacent coral reefs, which are dependent on clear water and low sedimentation rates.

1.2 *Zostera marina*

The eelgrass *Zostera marina* is a cosmopolitan species and can be found in North America, Asia and along the whole European coast, including the whole Norwegian coast (Phillips & Menez 1988, Green & Short 2003, Borum & Greve 2004). It is the most common seagrass in the northern hemisphere (Phillips & Menez 1988, Boström et al. 2003, Borum & Greve 2004), where it forms dense meadows on sand or mud in the littoral and sub-littoral zone down to a maximum depth of 10-15 m (Phillips & Menez 1988, Duarte 1991, Borum & Greve 2004, Bekkby et al. 2008). The observed growing depth is highly dependent on the water clarity and is often in accordance with the Secchi depth (Dennison 1987, Phillips & Menez 1988, Duarte 1991, Nielsen et al. 2002). *Z. marina* meadows can be found most frequently in sheltered areas with a gentle slope (Phillips & Menez 1988, Van Katwijk et al. 2000, Bekkby et al. 2008).

The wide distribution has to be at least partly attributed to the eurythermal and euryhaline nature of *Z. marina* (Phillips & Menez 1988). It grows in the high saline and warm Mediterranean Sea, the brackish Baltic Sea as well as in the White Sea, which is covered by ice for several months every year. Contributing to the wide distribution, the species *Z. marina* has the ability to follow annual as well as perennial life cycles (Hemminga & Duarte 2000).

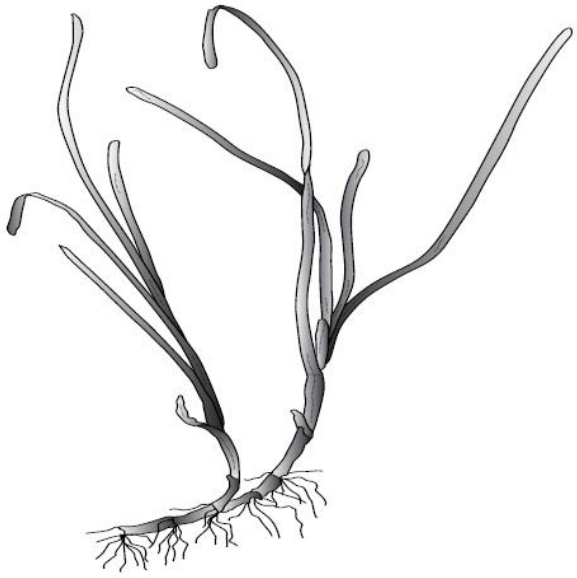

Figure 1 Drawing of a *Zostera marina* plant from Borum and Greve (2004)

The leaves of *Z. marina* (Figure 1) can become 150 cm long, but the regular growth height is 30-60 cm (Phillips & Menez 1988, Borum et al. 2004). The leaves are attached to a 2-6 mm thick horizontally growing rhizome, which bears fine roots (Phillips & Menez 1988, Borum et al. 2004). *Z. marina* is a species with a relatively high above ground to below ground biomass ratio (Duarte & Chiscano 1999).

1.2.1 Fauna of *Zostera marina* meadows

High faunal abundances and a high species richness of the faunal assemblage are typical for *Zostera* meadows.

In Skagerrak, many fish species are associated with *Z. marina* meadows. The meadows provide shelter as well as they serve as feeding area, spawning ground and nursery area (Pihl & Wennhage 2002, Wennhage & Pihl 2002, Heck Jr et al. 2003, Pihl et al. 2006). Aside from favoring the occurrence of fish, the *Z. marina* meadows in Skagerrak harbor a high number of invertebrates. The faunal biodiversity in the eelgrass canopy is thereby on the same level as in other macrophyte habitats (Fredriksen et al. 2005, Christie et al. 2009). In addition to this sessile and mobile fauna in the canopy, the eelgrass supports a high number of infaunal invertebrates, which is higher than in adjacent unvegetated sediments (Boström & Bonsdorff 1997, Fredriksen et al. 2010). This is in particular the case for macrofaunal infauna, but has not been described for meiofauna (Tietjen 1969).

Even though there is a high number of fish and invertebrates living closely associated with the eelgrass in Skagerrak, no fish species and hardly any invertebrates are known to graze directly on the fresh *Zostera* leaves in colder waters, making waterfowls the main group of grazers (Nienhuis & Van Ierland 1978, Nienhuis & Groenendijk 1986). Cebrián and Duarte (1998) specified the grazing in *Z. marina* to be less than 10% of the production, making the detrital pathway an important feature in the eelgrass based food web. A large fraction of the eelgrass production ends up in the sediment where it is eaten by infauna. This infauna serves as food for a variety of fish and invertebrates (Möller 1986, Beal 1994, Wennhage & Pihl 2002), making the infauna a key part of the eelgrass food web.

1.2.2 Threats to *Zostera marina*

Z. marina, like seagrasses in general, has been and is still facing threats of natural and anthropogenic origin (Short & Wyllie-Echeverria 1996). The wasting disease for example caused a large scale loss of *Z. marina* in the early 1930s (Milne & Milne 1951). Although this was the most severe threat to the complete global *Z. marina* population, it is by far not the only one. High sediment erosion from land or the appearance of algae, caused by eutrophication of the coastal zone, can negatively influence the light climate and thereby reduce the depth penetration of *Z. marina* or exclude it completely from an area (Short et al.

1995, Hauxwell et al. 2003). Chemical pollution has been shown to have severe negative effects on the eelgrass as well (Lyngby & Brix 1984).

In addition, there are several ways how *Z. marina* is disturbed mechanically. Grazing by waterfowls (Nienhuis & Van Ierland 1978, Nienhuis & Groenendijk 1986) and the influences of strong storms are some naturally occurring disturbances.

Fredriksen et al. (2004) described a destructive grazing of a complete *Z. marina* meadow at the Skagerrak coast through a mass occurrence of the gastropod *Rissoa membranacea*. Even though they were able to show that the gastropods were not grazing the eelgrass itself, the snails caused epidermal injuries with their radula, while grazing the epiphytes. This resulted in breakage and dislocation of the leaves (Fredriksen et al. 2004). The result of the described grazing event was a loss of virtually the complete above ground biomass of the *Z. marina* plants. A year later the eelgrass was regrown, but the shoot density was reduced.

Besides the obvious effect such a grazing has on the organisms living within the eelgrass canopy, Herkül and Kotta (2009) showed in a field experiment that canopy removal, without disturbance of the sediment, has a direct negative effect on infaunal abundance and diversity as well.

The naturally occurring mechanical disturbances of *Zostera* meadows are complemented by several disturbances through human activities. Dredging of seagrass meadows for boat traffic or the direct damage through the propeller or the anchor of boats are only some of them. The result of these activities is the removal of the eelgrass plants combined with a complete disturbance of the sediment.

1.3 Aims of this study

The objective of this study was to investigate if and how mechanical disturbance events affect the infauna of *Z. marina* meadows after a recovery period of 10 months.

The approach used was a field experiment with two different disturbance events. The cutting of the eelgrass at the sediment surface was meant to resemble the destructive grazing through a mass occurrence of *R. membranacea*, and the removal of the complete *Z. marina* plants was supposed to resemble a disturbance event through human activities, like anchoring of boats or

the dredging of the meadow. This experiment was conducted in three different *Z. marina* meadows in the inner Oslofjord.

The questions addressed in this thesis are the following:

1. Are the infaunal communities of the three studied meadows different from each other?
2. Is the infauna of eelgrass affected by the cutting of the leaves?
3. Is the infauna of eelgrass affected by the removal of the plants?
4. Are macrofauna and meiofauna affected in the same way by the treatments?

2 Material and Methods

The field experiment with the two disturbance events was conducted in three different *Z. marina* meadows. According to the EU water framework directive and the Norwegian implementation "Vanndirektivet", more or less all *Zostera* meadows in Norway are considered important. This includes all meadows studied during this project.

2.1 Study locations

All three study locations (Sandspollen, Sætrepollen and Hallangspollen) are located in the inner Oslofjord close to the city Drøbak (Figure 2). Each of the studied *Zostera* meadows lies within one of three landlocked bays, which are sheltered and have only narrow openings to the inner Oslofjord. All three bays lie north of the Drøbak Sound, where a 19.5 m shallow sill separates the inner from the outer Oslofjord (Gade 1968). The surface water of the inner fjord experiences a pronounced seasonality, with temperatures over 15°C in the summer and temperatures around 0°C and occasionally ice cover during the winter (Paasche & Ostergren 1980).

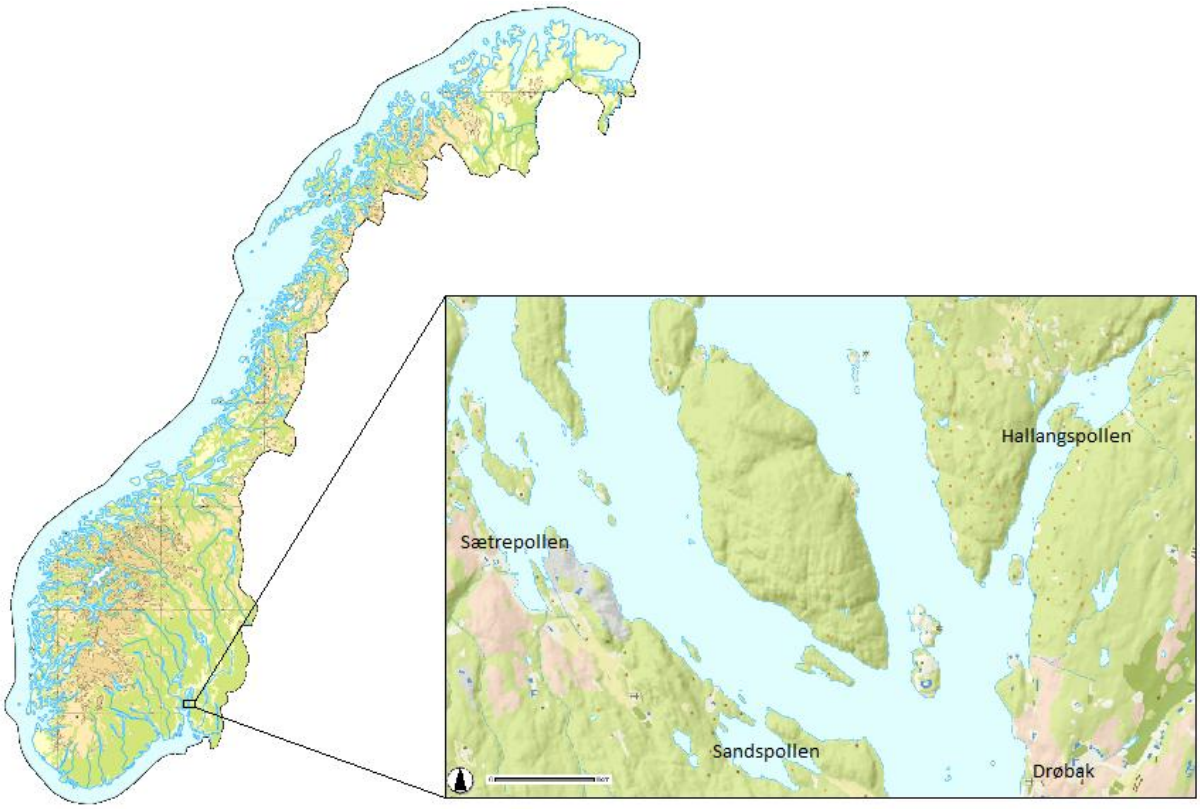

Figure 2 Map of Norway; detailed window showing the study locations and the city Drøbak, scale bar: 1 km

During the winter, the salinity reaches its maximum, with approximately 30‰, while it can be as low as 15‰ during the summer months (Gade 1968, Paasche & Ostergren 1980). The high winter salinity drops through the inflow of fresh water from the melting of ice and snow as well as through precipitation, during spring. During summer, the salinity is even lower (Gade 1968, Skadsheim 1983), although there is no big stream entering the inner Oslofjord. Skadsheim (1983) describes that brackish surface water from the outer Oslofjord penetrates into the inner fjord. This water from the Drammenselva and Glomma rivers might have a strong influence on the study locations, since they are all close to the Drøbak Sound, the only opening where the water can enter the inner fjord.

Because of the enclosed and shallow nature of the three study locations, the seasonality at the study locations might be even stronger than the variation described above.

2.1.1 Sandspollen

Sandspollen is located on the western side of the fjord. It is surrounded by forested hills and only a few houses or other permanent installations influence Sandspollen directly. During summer, Sandspollen is a recreational area for locals, who anchor with their boats in high numbers. Sandspollen has an area of approximately 365 000 m^2, a length of 1 200 m and a width of 500 m. It has four small bays, two each in the north-west and the south-east (Figure 3). The single opening to the North has a width of 100 m and is like Sandspollen itself 10 – 12 m deep. In the center of Sandspollen is a small elevation with only 4 m depth and it gets shallower to each of the bays as well. *Zostera marina* grows in 3 of the bays, according to 'Direktoratet for Naturforvaltning' (DN). The largest *Zostera* meadow is located in the northern one of the south-eastern bays. It covers an area of 31 000 m^2 in a depth range from 0.5 m to 5.5 m. The vegetation is very dense down to 3.5 m, from where it decreases with depth.

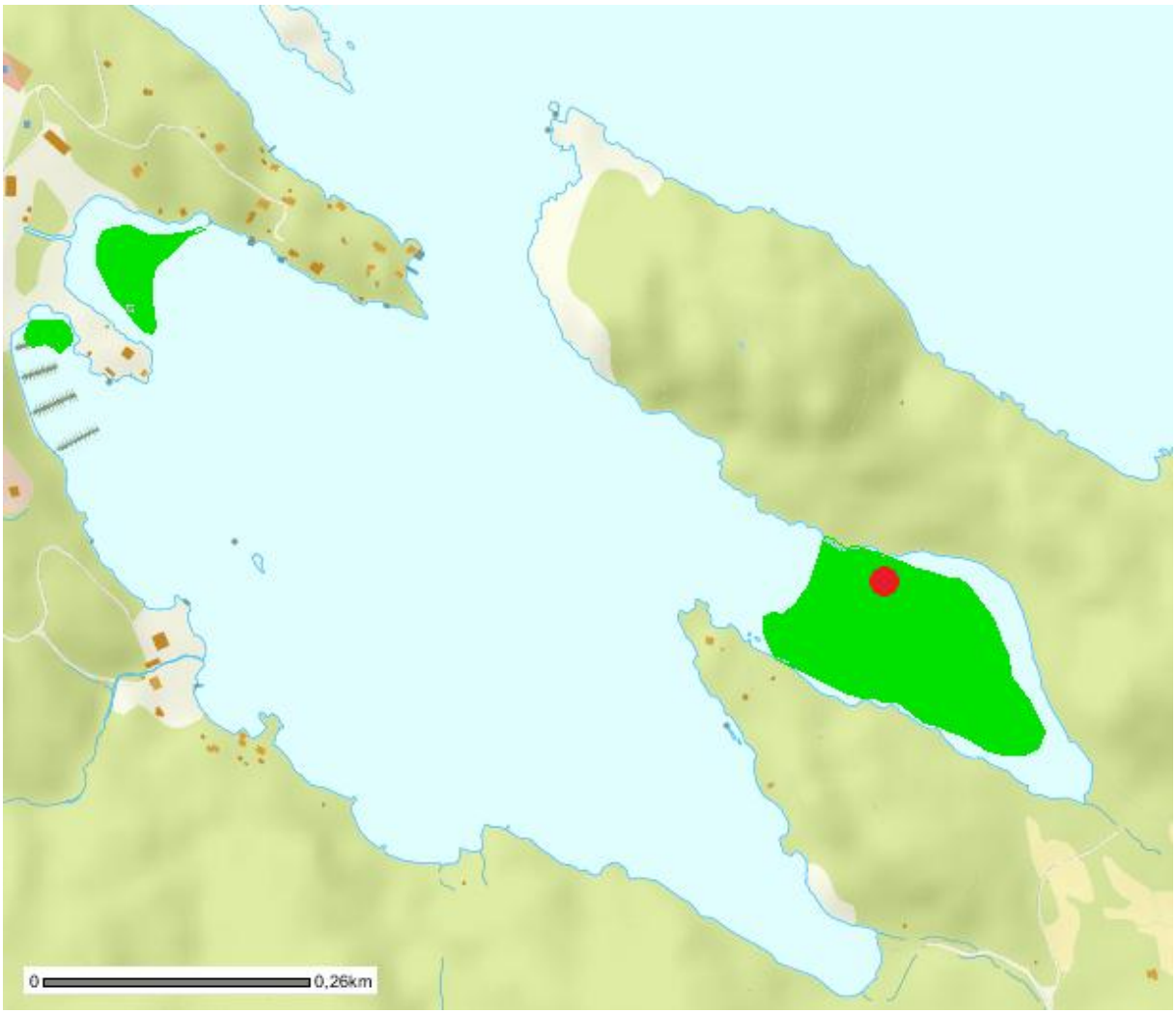

Figure 3 Detailed map of Sandspollen; *Zostera* beds in green, position of the experiment marked in red

2.1.2 Sætrepollen

Sætrepollen is located approximately three km north-west of Sandspollen. With an area of 600 000 m^2, Sætrepollen is the largest of the 3 studied bays. It has a length of 1 900 m, a width of 500 m and the largest part of Sætrepollen is 9 – 10 m deep. In contrast to the other two bays, Sætrepollen has two openings (Figure 4). The main opening to the east is 290 m wide and 16 m deep, while the smaller opening to the north is only 65 m wide and has a maximum depth of approximately 5 m. On the western shore of Sætrepollen lies Sætre, a city with approximately 3 000 inhabitants.

Sætrepollen has 2 shallow bays in the south, of which the larger one contains the studied *Zostera* bed. DN describes the eelgrass bed as a dense *Zostera* community covering an area of 46 000 m^2 in an extremely sheltered bay down to a depth of 3 m.

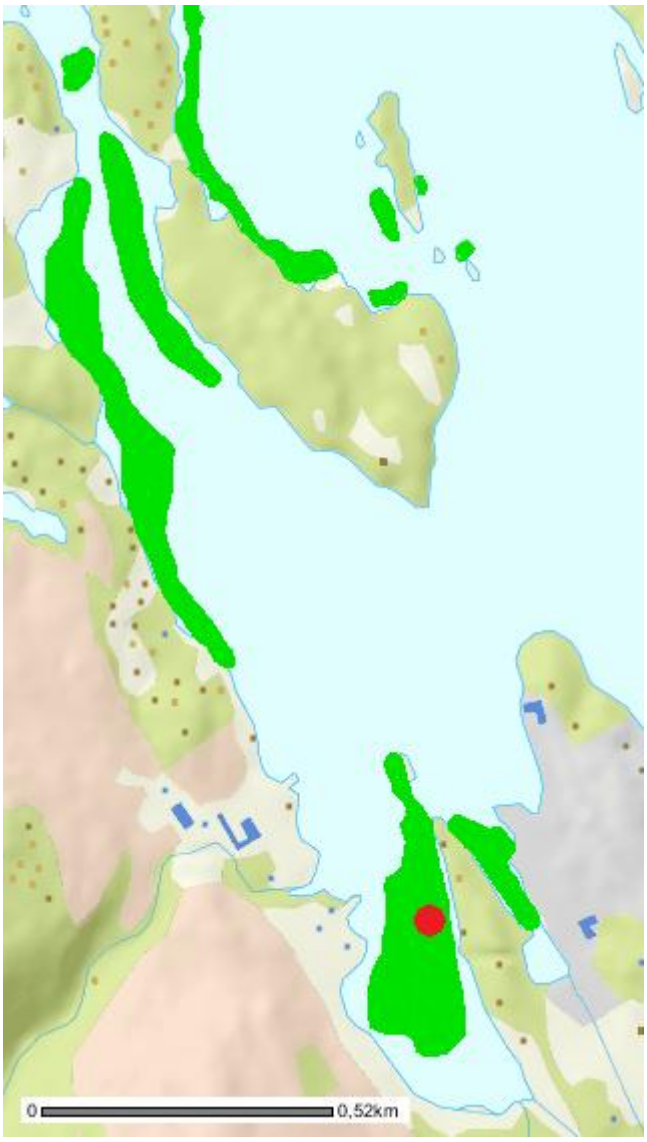

Figure 4 Detailed map of Sætrepollen; *Zostera* beds in green, position of the experiment marked in red

2.1.3 Hallangspollen

Hallangspollen has a total length of approximately 3 300 m, but it is divided by a peninsula into an inner and an outer part.

The opening between these two parts is only 100 m wide and 8 m deep. The inner Hallangspollen (Figure 5) has an area of 400 000 m^2, is 1 300 m long and the maximum width is 630 m. The width decreases to the north-east and reaches a minimum of 35 m at the site of the experiment. An 8 – 12 m deep channel runs through the opening of inner Hallangspollen and from there it turns south-east around a small island before it runs straight to the end of Hallangspollen, where the water gets shallow. The location of this deep channel is consistent with the *Zostera* free area in Figure 5.

The cumulative area of all *Zostera* meadows in the inner Hallangspollen is 85 000 m^2 and the meadow, which was chosen for the experiment accounts for 10 000 of them. In the end of Hallangspollen, close to the eelgrass bed, is an outlet from a small river. The freshwater from this river is expected to have a direct influence on the studied *Zostera* meadow. In addition to this, Hallangspollen is densely surrounded by cottages and recreational boat traffic appears all the way back to a slipway with some adjacent mooring locations in the small bay behind the studied *Zostera* meadow. Thereby it is exposed to a strong human influence.

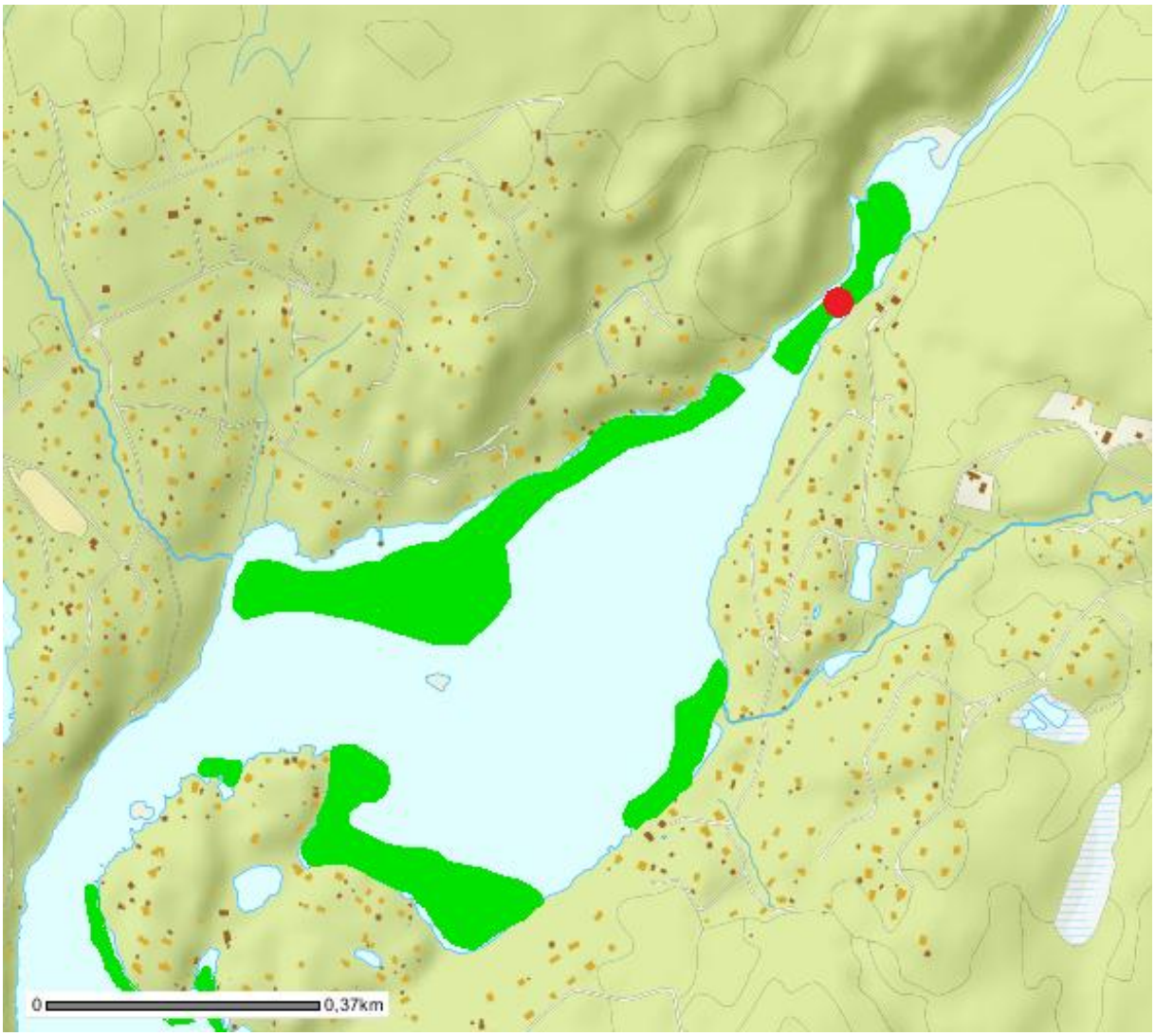

Figure 5 Detailed map of the inner Hallangspollen; *Zostera* beds in green, position of the experiment marked in red

2.2 Fieldwork

All fieldwork was conducted by SCUBA diving and the use of a boat owned by the marine biological station in Drøbak.

2.2.1 Pre-sampling

Before the experiment was set up on the 5th October 2010, a pre-sampling was conducted at the same day. 6 core samples were taken at random in each of the three meadows chosen for the experiment. The plastic corers used for the sampling have an inner core diameter of 5.1 cm.

To take a sample, one corer was carefully pushed and turned vertically into the sediment. The upper opening of the corer was then closed with a rubber cork and it was possible to pull the filled core out of the sediment, before the second opening was closed with another cork. The sample was handed to a person on the boat, where it was washed with seawater into a labeled 'Topit's Zip-Lock bag'. Only samples which contained at least the upper 10 cm of the sediment were accepted, and otherwise resampled. The samples were stored in a closed box on the boat during the sampling.

2.2.2 Setup of the experiment

The two different treatments of the experiment were set up in a distance of 4.5 m (Figure 6). This distance was chosen as a compromise of a short distance to ensure a similar environment and a large distance to avoid an influence on each other. The position of the experiment was always selected, so that a constant depth of approximately 2 m eliminated the factor depth for the analysis.

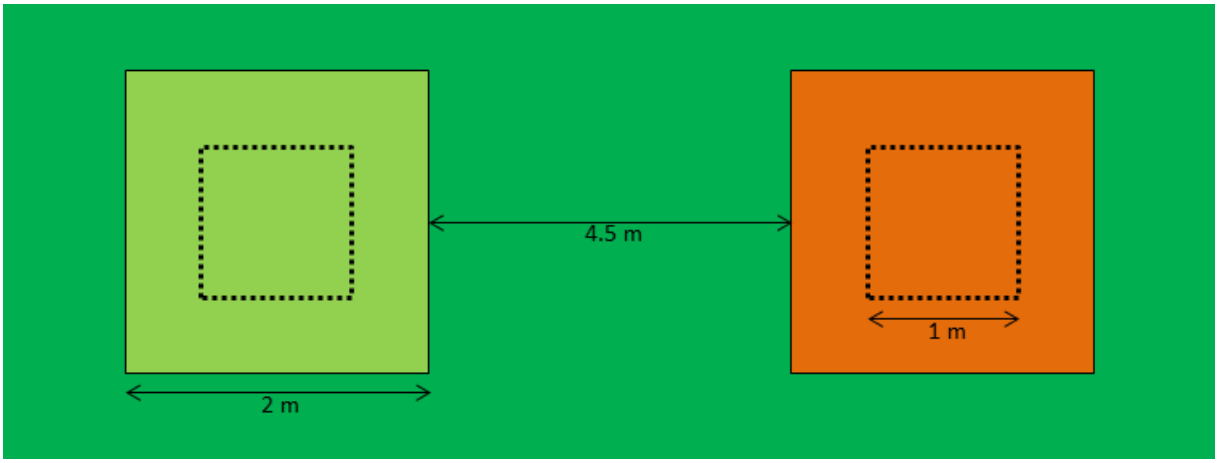

Figure 6 Experimental design; *Zostera* bed in dark green, cut treatment in light green, removed treatment in brown; dashed lines show the sampled area within the treatments.

For the cut treatment all eelgrass leaves of an area of 2x2 m, were cut at the sediment surface. The roots and rhizomes were not manipulated. Since the sediment was stirred up easily during the cutting, it was necessary to cut the same area again. This second cutting was conducted a month later. After the second cutting, the area was marked with a taped stick, to ensure the recovery during the following summer. Due to the fact that Sætrepollen was already covered by ice when the second cutting was conducted, it was not possible to cut and mark the area. As a consequence, the cut treatment at this location was lost.

The removed treatment consisted in the removal of the complete plants, including the whole root-rhizome system, from an area of 2x2 m. This treatment was directly marked for recovery and no further preparation was necessary.

2.2.3 Main sampling

The main sampling was conducted on the 27th July 2011 at Sandspollen and Sætrepollen, while Hallangspollen was sampled on the 28th of July 2011. The long recovery time was chosen because this study aimed to detect long term effects and not the direct effects of the disturbance as investigated in a cutting experiment by Herkül and Kotta (2009). Moreover, the removal of the complete plants was a particularly strong disturbance. Therefore, time was needed to give the *Zostera* meadow the opportunity to regrow and to give the infauna the opportunity to reestablish a stable community.

Three core samples with an inner core diameter of 5.1 cm for macrofauna and three smaller cores of 3.2 cm for meiofauna were taken from each treatment at every location. In addition, three core samples of each size were randomly taken in the *Zostera* meadow surrounding the prepared areas and used as control samples. Additional samples were taken for grain size analysis, as well as for a backup in case that more samples could be needed. The samples from the cut and the removed treatment were taken randomly in the central square meter of the prepared 2x2 m area (Figure 6). The decision to sample only the central square meter was made to avoid a possible edge effect that might have an influence on the fauna close to the edge of the treatment (Tanner 2005).

Besides taking the core samples, the diver also measured the canopy height and the shoot density of the different *Zostera* beds.

2.3 Laboratory work

In the end of every sampling day, all samples were transported to the facilities of the Biology department of the University of Oslo, where all laboratory work of this project has been conducted.

2.3.1 Pre-sampling

All samples were stored in a cooling room before they were washed with fresh water through a set of two sieves with diameters of 500 µm and 63 µm within two days after the sampling was conducted. The two retained fractions were transferred into labeled flasks, where they were preserved with 96% ethanol to ensure a high ethanol content after sieving with water. The fauna was stained with rose bengal.

Macrofauna

The fraction retained in the 500 µm sieve was scanned for fauna under a dissecting microscope and the animals were sorted into major taxonomic groups.

Later the fauna was identified to species or the lowest possible taxonomic level. All taxa in this thesis were named after the accepted names in the World Register of Marine Species (Appeltans et al. 2012).

Meiofauna

The term meiofauna has first been used by Mare (1942) and has since then been used to describe the size fraction of the fauna, which passes through a sieve used to collect macrofauna, but is retained in a sieve that is used to wash the silt fraction out of the sample (McIntyre 1969). Since the lower limit for macrofauna was set to 500 µm in this study, the meiofauna fraction was defined as the fauna smaller than this, but large enough to be collected in a 63 µm sieve.

Because of a large amount of detritus in the same size fraction, the meiofauna was separated from other particles by density gradient centrifugation with a colloidal silica polymer as the flotation medium (Levasil ®) and kaolin clay (Kaolin heavy, Powder 18616 – CAS Nr. 1332-58-7, Lot No. 33360. Riedl deHäen) to cover heavier particles (McIntyre & Warwick 1984).

The 63 µm fraction from the pre-sampling was used to optimize a centrifugation program to retrieve the meiofauna from the sediment. The methods described by Vincx (1996) provided a basis for this centrifugation program.

For the centrifugation, the whole preserved sample was transferred to a 63 µm sieve and washed with tap water to remove the ethanol. The sample was then transferred with a spoon

into two centrifugation flasks with a volume of 250 ml each. The part of the sample retained in the sieve was flushed into the flasks with water.

In the next step, approximately three tea spoons of kaolin clay were mixed with water to produce a creamy, non-liquid, white pulp. Half of this pulp was added to each of the centrifugation flasks. Then at least 8 table spoons of levasil were added to each flask. By the use of levasil the weights of the flasks were balanced before the centrifugation was conducted.

Figure 7 Centrifugation flask after a centrifugation; sediment in the bottom, covered by the white kaolin clay and the liquid levasil on top. Detritus parts can be seen floating on the levasil

Several centrifugations were conducted with the sediment from the pre-sampling until the optimal setting was found, to reduce the amount of detritus as much as possible. The result was a running time of 30 min with 4 000 rpm.

The result of this centrifugation had two fractions. In the bottom a solid sediment fraction, covered by the kaolin clay. The other fraction, the liquid levasil phase, contained the fauna and some detritus that could not be removed with the centrifugation (Figure 7).

To collect the meiofauna, the liquid phase was decanted through a 63 µm sieve and washed with fresh water. The meiofauna was then preserved in ethanol and rose bengal was added to stain the fauna. Following every centrifugation, a subsample of the solid fraction was checked to ensure no fauna was retained.

The meiofauna of the pre-sampling was not analyzed in detail. Only a rough estimate of the abundance was made to decide what core diameter to use for the main sampling.

2.3.2 Main sampling

The samples from the main sampling were stored in a cooling room as soon as possible after the sampling and preserved in ethanol within two days. Due to time constraints, some macrofauna samples from Sandspollen and Sætrepollen were frozen in a -20°C freezer the day after they were sampled. For the use of the frozen samples, the sample bag was defrosted

in a water bath and then treated like the other samples. The results and the condition of the fauna did not give any indication that the freezing had an effect on the study.

Macrofauna

The macrofauna samples were washed with fresh water in a 500 µm sieve until the outflowing water was clear. The part of the sample retained in the sieve was then transferred into a flask, where it was preserved with ethanol (96%) until further processing took place.

During the next step all the animals were picked up under a dissecting microscope and sorted into taxonomic groups, before every individual was identified to species or to the lowest possible taxonomic level. To ensure a correct count, the number of heads was counted for animals with a good recognizable head, like annelids or arthropods. For the molluscs, which don't have such a head, the counting was based on shells containing an animal.

Meiofauna

The meiofauna samples were drained through a 63 µm sieve. From there, the sample was transferred with a spoon into a flask. The part of the sample which could not be collected with a spoon was washed with ethanol into the flask. The flask was then filled up with ethanol and mixed properly to guarantee that the whole sample was preserved until the centrifugation could be conducted as described in 2.3.1.

Since every part larger than 63 µm was used for the centrifugation, the resulting liquid phase was washed through a 500 µm sieve, before the meiofauna fraction was collected in a 63 µm sieve. The meiofauna fraction was preserved in ethanol and stained with rose bengal for further analysis (Figure 8). The 500 µm fraction was preserved in ethanol to check for possible retained meiofauna.

The individuals of the different major taxonomic groups were then counted under a dissecting microscope. For this purpose, the samples were transferred droplet wise into a small petri dish and water was added until the bottom of the petri dish was covered. Some soap water was also added to break the surface tension and bring all particles to sink. The animals were not collected, because even the smallest needles would have stirred up everything and a correct count would have been impossible (Figure 9). To make counting possible, a scissor was used to make parallel scratches in the petri dish.

Figure 8 Meiofauna samples before and after the centrifugation; left: in ethanol preserved sample before a centrifugation, middle: >500µm fraction in ethanol after the centrifugation, right: the meiofauna fraction in ethanol+rose bengal (just the thin layer on the bottom)

Grain size analysis

The grain sizes were analyzed for every treatment at every location. At Sandspollen and Sætrepollen, a complete frozen macrofauna sample was used for the analysis. Due to an error, all macrofauna samples from Hallangspollen were washed in a 500 µm sieve and preserved in ethanol. Because of this error, the only samples containing grain fractions worth analyzing were in the ethanol preserved meiofauna samples. For this reason the grain sizes from Hallangspollen were determined using a meiofauna sample, even though the grains smaller than 63 µm were missing. To check for the comparability of the results, the grain sizes for such meiofauna samples from the other locations were determined as well.

The samples were wet washed, with as little water as possible, through a set of sieves with mesh sizes of 2 000 µm, 1 000 µm, 500 µm, 250 µm, 125 µm and 63 µm. The grains collected in the sieves were washed with water into weighed and labeled plastic containers. The dry weight of the sediment was determined after it has been dried at 100°C for three days.

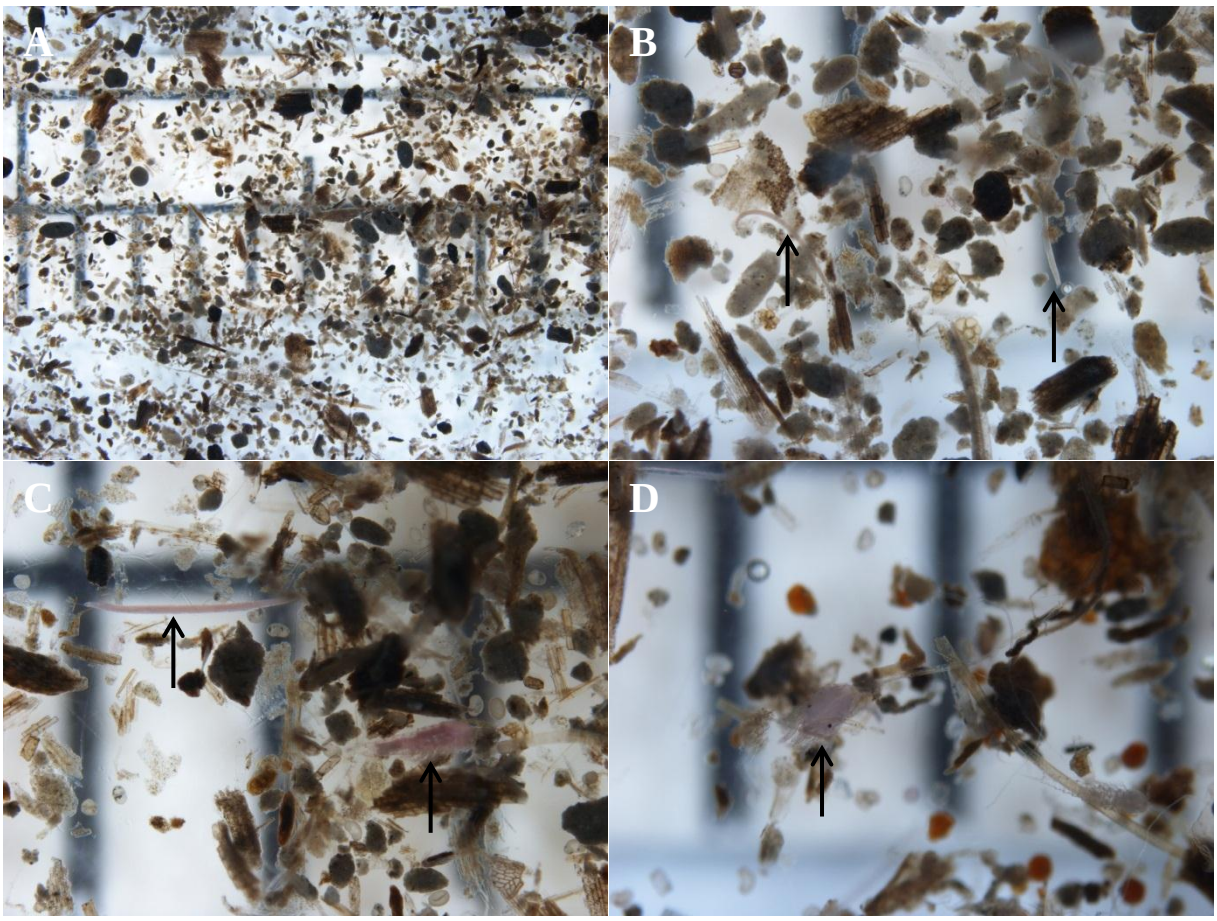

Figure 9 Counting of meiofaunal samples after the centrifugation; A: Overview over part of a control sample from Sandspollen, width of the photo 1 cm; B: detail from the same sample, black arrows point on two nematoda; C: detail from a removed sample from Sætrepollen, black arrows point to a nematoda and a harpacticoida; D: detail from a cut sample from Hallangspollen, black arrow points to an acarina; distance between 2 black lines in every photo 1 mm

The grains smaller than 63 µm were collected together with all the used water, after they passed the last sieve. Bottles were filled with this water and approximately a month was given for the particles to settle. After that the water was decanted carefully and the sediment was washed into weighed and labeled plastic containers. This sediment was dried at 100°C before the weight was determined. For the meiofauna samples this fraction has been lost when the samples were transferred into ethanol.

2.4 Numerical and statistical analysis

The grain size parameters for Sandspollen and Sætrepollen were determined according to the methods developed by Folk and Ward (1957) with the use of the GRADISTAT software (Blott & Pye 2001). This was not possible for the samples from Hallangspollen, because of the lost silt fraction.

The analysis of the fauna was done on species abundance data from the different replicates, given in the Appendices A, B and C. For the macrofauna 3 pairs of taxa, listed in the species lists, were grouped together. One reason for this was the fact that only the males of the amphipod family Aoridae and the genus *Ericthonius* can be identified to species level. The species *Microdeutopus gryllotalpa* was therefore added to the Aoridae, while *Ericthonius rubricornis* was added to *Ericthonius* sp. The other reason was that the species identified as Capitellidae were most probably *Capitella capitata*, but no certainty could be gained about this by the used methods. Therefore the identified *Capitella capitata* were counted as Capitellidae for the analysis as well. Each of these groups consists probably only of the one species that has been identified. Further the pure meiofaunal taxa (nematoda, harpacticoida, acarina) were excluded from the analysis of the macrofauna samples, since it was shown that their numbers could be reduced by more intense washing.

In the meiofauna, it was only possible to identify some polychaeta to a lower taxonomic level than the order. These different polychaete taxa were grouped together for the statistical analysis, since their identification was not possible with a satisfactory accuracy. The identification to a low taxonomic level was not possible for the other taxa in the meiofauna.

For estimations of the number of macrofaunal individuals m^{-2} presented in this thesis, the following formula was applied:

$$ind.m^{-2} = \frac{10\,000cm^2}{\pi r^2} \times \frac{total\ ind.}{no.cores}$$

And for the estimations of the number of meiofaunal individuals $10cm^{-2}$:

$$ind.10cm^{-2} = \frac{10cm^2}{\pi r^2} \times \frac{total\ ind.}{no.cores}$$

A triangular similarity matrix was created, using the Bray-Curtis similarities (Bray & Curtis 1957) of the square root transformed macrofauna data set. The square root transformation was applied to weaken the influence of the abundant species on the results. Based on this matrix a nMDS (Clarke 1993) plot was created and overlaid with the results of a Cluster analysis (Clarke 1993). To ensure that the nMDS plot used the best possible way to arrange the samples, the number of restarts was set to 100. A two-way crossed ANOSIM (Clarke 1993) with the factors ‘location’ and ‘treatment’ was conducted to identify similarities within and

between these groups. The number of maximum permutations was set to 9999 for the ANOSIM. Based on the result, a SIMPER analysis (Clarke 1993) was used to identify the taxa contributing most to the similarities and dissimilarities. The square root transformed data set was used for the SIMPER analysis as well. These analyses were all conducted with the PRIMER software, Version 6.1.13 (Clarke & Gorley 2006). In addition, the number of taxa, the number of individuals, the Shannon index (H') (Shannon 1948) and its evenness component (J') (Pielou 1977) were calculated for every sample using the same software.

The variance of these four univariate variables was analyzed with the IBM® SPSS® Statistics program version 19 for the different location and treatment groups. First, the distribution of each variable for each factor group was tested for its normal distribution by the use of a Shapiro-Wilk test (Shapiro & Wilk 1965). In case of a not normal distribution of a variable within one test group, the analysis of variance was conducted by the use of a non-parametric Kruskal-Wallis test (Kruskal & Wallis 1952). This was the case for the number of taxa and the number of individuals for the factor 'location', as well as for the number of individuals for the factor 'treatment'. When the test revealed a significant difference, a pairwise comparison was conducted with a Tamhane T2 test (Tamhane 1977). For the other cases with normal distributions, a Levene's test (Levene 1960) for the homogeneity of variance and a standard one-way ANOVA were conducted. The test used for the pairwise comparison of the groups which have been shown to be significantly different for a variable was chosen based on the results of the Levene's test. In case of homogeneity a Tukey test (Tukey 1949) was the test of choice, while in case of heterogeneity a Tamhane T2 was used. In addition to the before mentioned parameters, the abundance of every macrofaunal taxa, which was discovered at least 30 times, was analyzed with the same methods.

The statistical analyses applied to the meiofaunal data were essentially the same as for the macrofauna. Since the meiofauna analysis was based on major taxonomic groups, the Bray-Curtis similarity matrix was created based on fourth root transformed data. For the same reason the Shannon diversity and the evenness were not calculated and the univariate analysis took the number of taxa and the number of individuals into account. A Kruskal-Wallis test was conducted for the number of taxa in the samples for the factors, 'location' and 'treatment'. For the number of individuals per sample a standard one-way ANOVA was applied, followed by a Tukey test. In addition to this, the Nematode/Copepod ratio was

determined for every sample. This ratio was investigated with a standard one-way ANOVA and a post-hoc Tamhane T2.

To analyze the seasonal development of the macrofaunal community in the untreated *Zostera* beds, the data of the main sampling was combined with the data from the pre-sampling and data from another master thesis (Sømme 2012), which studied the same meadows at Sandspollen and Sætrepollen in May 2010 (see Appendix E). Since the core sizes and the number of cores varied for the different samplings, the estimated number of individuals m^{-2} and the total number of taxa were compared on a descriptive basis between the sites and the different times of the year.

The significance level for all tests and analyses was set to $p=0.05$.

3 Results

The raw data for faunal abundance and grain size analysis, which provide the basis for the results, are listed in the appendices A, B, C and D.

3.1 Non-faunal environment

An overview of the non-faunal parameters is given in Table 1.

In July 2011, when the main sampling was conducted, the cut treatment at every location was regrown and it was not possible to identify the cut treatment from the surrounding *Zostera* meadow without the help of the marker (Figure 10). The canopy height never differed between the cut area and the control. This also made it impossible to re-locate the cut treatment at Sætrepollen, which had no markers. The canopy at Sætrepollen was the highest with 120 cm, followed by Sandspollen (80 cm) and Hallangspollen (60 cm). In contrast, the removed areas were always free from *Z. marina*, with only some single shoots (Figure 10).

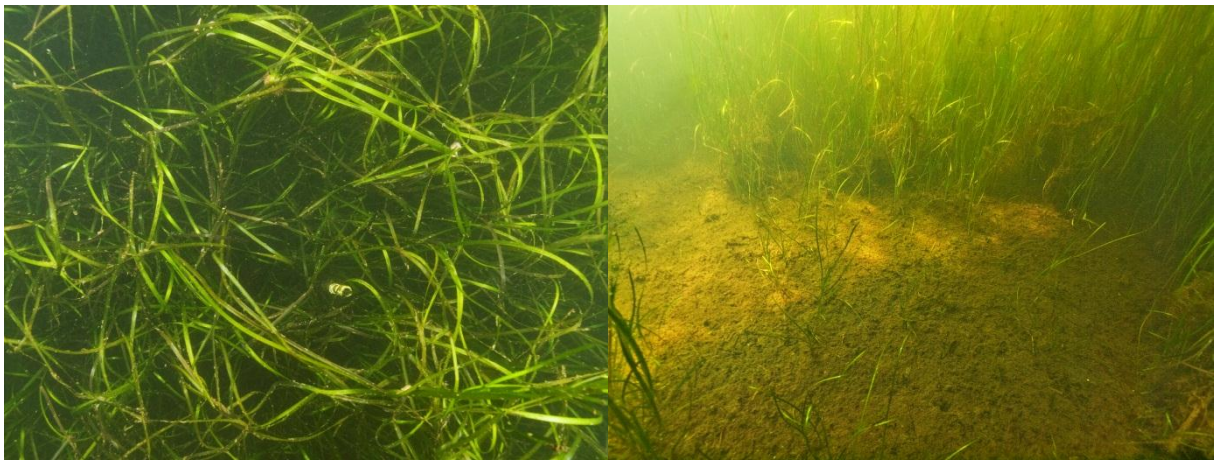

Figure 10 Left: the regrown *Zostera* meadow of the cut area at Sandspollen with a marker in the center; Right: the removed treatment at Sætrepollen; photos by Jonas Thormar

The *Zostera* meadows at Sandspollen and Sætrepollen have a similar shoot density of approximately 100 shoots m^{-2}, while the shoot density at Hallangspollen was considerably lower. The shoot density of the cut and control treatments in Sandspollen were identical, while the cut treatment in Hallangspollen was half of the control (16 vs. 31 shoots m^{-2}). Whether the lower value was an effect of the cutting or caused by selecting a plot which already had a lower shoot density is not known.

Table 1 Non-faunal parameters for the different locations and treatments; *Zostera marina* characteristics were complemented with information from Sømme (2012) for shoot density, where no measurement was conducted during this study: Shoot density in shoots m^{-2}, Canopy height in cm. Grain size parameters are presented after the Folk and Ward method (Folk & Ward 1957) for Sandspollen and Sætrepollen. Share of the different size fractions of the total dry weight is given for all 3 location, silt fraction missing for Hallangspollen.

		Sandspollen			Sætrepollen		Hallangspollen		
		control	cut	removed	control	removed	control	cut	removed
		Zostera marina characteristics							
Shoot density		113.6[a]	113.6[b]	0	93.6[a]	0	31	16	0
Canopy height		80	80	-	120	-	60	60	-
		Sediment characteristics							
Mean	(ϕ)	2.13	1.50	1.73	3.30	3.80	-	-	-
	(descriptive)	Fine Sand	Medium Sand	Medium Sand	Very Fine Sand	Very Fine Sand	-	-	-
Sorting	(ϕ)	1.85	1.70	1.87	2.15	2.50	-	-	-
	(descriptive)	Poorly Sorted	Poorly Sorted	Poorly Sorted	Very Poorly Sorted	Very Poorly Sorted	-	-	-
Skewness	(ϕ)	0.29	0.12	0.21	0.28	0.04	-	-	-
	(descriptive)	Fine Skewed	Fine Skewed	Fine Skewed	Fine Skewed	Symmetrical	-	-	-
Kurtosis	(ϕ)	1.08	1.23	1.21	1.23	0.98	-	-	-
	(descriptive)	Mesokurtic	Leptokurtic	Leptokurtic	Leptokurtic	Mesokurtic	-	-	-
>2000 µm (in %)		2.81	2.38	2.85	2.94	6.84	2.74	3.39	5.36
>1000 µm (in %)		8.68	16.77	14.93	3.54	2.50	1.93	1.97	1.71
>500 µm (in %)		16.99	25.09	25.36	8.56	5.09	2.78	3.24	4.29
>250 µm (in %)		28.51	25.94	22.75	20.33	17.82	11.39	41.57	42.30
>125 µm (in %)		17.16	14.56	15.82	23.37	16.03	47.94	22.79	15.08
<63 µm (in %)		12.50	6.46	8.84	14.64	13.18	33.23	27.05	31.25
>63 µm (in %)		13.34	8.81	9.46	26.63	38.53	-	-	-

[a] in May 2010 (Sømme 2012)

[b] no diverence between cut and control detected by the divers

Every sample of the pre-sampling as well as the samples of the main sampling had a sulfuric odor, which was particularly strong in the samples from Sætrepollen. The sediment from Sandspollen and Sætrepollen appeared to be very similar. Both were greyish brown and contained a large amount of detritus which seemed to originate from *Z. marina*. The grain size analysis characterized the sediments from the different treatments at Sandspollen as fine and medium sand, which is poorly sorted and the sediment from Sætrepollen as very fine sand and very poorly sorted. The overall difference between these two locations was that the sediments from Sætrepollen had a smaller grain size with a larger silt fraction and a stronger sulfuric odor than the Sandspollen sediments.

At Hallangspollen, the sediment was black and contained a lot of crushed shells. The amount of detritus found in the samples was lower than in samples from the other locations and the detritus seemed to originate from *Zostera* as well as from the terrestrial surroundings. As mentioned in 2.3.2, the silt fraction was missing in the samples used for the grain size analysis from Hallangspollen. Therefore, the grain sizes could not be investigated according to Folk and Ward (1957), but with regard to the known fractions and the impression gained during the work with the material, it is possible to assume that the mean grain size might be fine or medium sand and that the sorting of the sediment might be better than at the other two locations.

At the time the main sampling was conducted, the water at Hallangspollen was extremely rich of humic substances and the visibility was almost zero. In addition, every solid structure at Hallangspollen, even the *Zostera* shoots, was completely covered by juvenile individuals of *Mytilus*. If such a mass occurrence happens regularly, this might be the reason for the high amount of shells in the sediment.

3.2 Macrofauna

A total of 4 311 macrofaunal organisms were encountered and classified in the samples of this study. 271 of them were collected during the pre-sampling, while the remainder was found in the samples from July 2011. The individuals were assigned to 34 taxa which represent at least 31 species. The reason for the discrimination of 3 taxa has been described in 2.4. Of the 31 definite taxa, 9 have been present at both times of the year. 20 taxa were exclusively found in the main sampling, while 2 taxa were only found in samples from the pre-sampling.

All macrofauna belongs to 6 major groups: Insecta (1 taxon), Crustacea (6 taxa), Bivalvia (4 taxa), Gastropoda (7 taxa), Oligochaeta (2 taxa) and Polychaeta (11 taxa). Even though the polychaeta are the most diverse group, they are the least abundant (Figure 11, Figure 13). Due to the mass occurrence of *Mytilus* at Hallangspollen, the bivalvia are the most abundant group.

3.2.1 Pre-Sampling

With 215 individuals, the majority of the 271 individuals from the pre-sampling were found in the samples from Hallangspollen. The remainder of 56 individuals was divided almost equally between Sandspollen (30 ind.) and Sætrepollen (26 ind.).

At Hallangspollen, two species of the genus *Tubificoides* (oligochaeta) were responsible for more than 50% of the individuals (Figure 11). In addition to them only insects from the Chironomidae family occurred in larger numbers.

The Chironomidae were present in high numbers at the other locations as well, where they dominated the macrofauna due to a low number of other animals (Figure 11). The oligochaeta were dominating the *Zostera* meadow at Hallangspollen while only 3 individuals were found at Sætrepollen and none at Sandspollen.

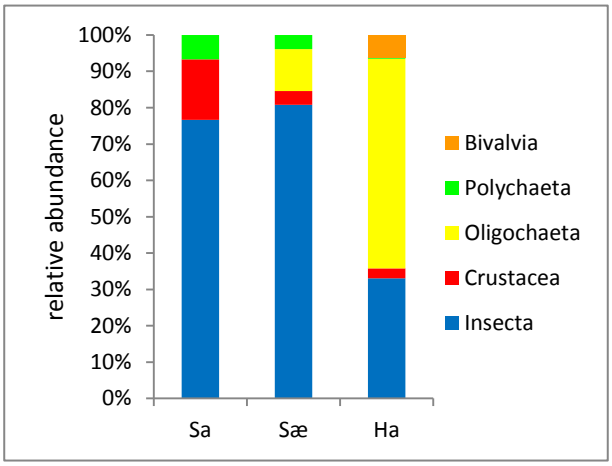

Figure 11 Relative abundance of the major macrofaunal taxa at the different locations during the pre-sampling; Abbreviations for the locations (Sa = Sandspollen, Sæ = Sætrepollen, Ha = Hallangspollen)

Even though the relative abundance of the insects was lower at Hallangspollen compared to the other two sites (Figure 11), the absolute number of individuals in the 6 samples was with 71 about 3 times as high as at Sandspollen (23 ind.) or Sætrepollen (21 ind.).

3.2.2 Main sampling

The analyses of the results from the main sampling were always based on two factors: location and treatment. Numbers for the different diversity parameters and indexes for the

macrofaunal communities are given in Table 3a. The variance of these four parameters between the two factor groups was tested and the results are given in Table 2.

Every single parameter has a p-value smaller than 0.05 for the location groups, but with regard to the treatments, only the Shannon diversity showed a significant different variance between the three groups.

Table 2 Macrofauna results of the analyses of variance; p-values for the different tested variables and factors are presented

	Location	Treatment
Number of taxa	$p < 0.01$	$p > 0.05$
Number of Individuals	$p < 0.01$	$p > 0.05$
Shannon index (H')	$p << 0.01$	$p < 0.05$
Evenness (J')	$p < 0.05$	$p > 0.05$

The following pairwise comparison revealed that the number of taxa that was found in each sample was significantly lower at Sætrepollen than it was at the other two locations. Sandspollen and Hallangspollen did not show such a significant difference. The total number of individuals found in the samples from Sandspollen was significantly higher than it was at Sætrepollen. Even though Hallangspollen has the highest mean number of individuals, it was not shown to be significantly different from the other two locations, due to the high variation between the samples. The Shannon index at Sandspollen significantly differs from the other two locations. The pairwise comparison of the evenness did not show a significant difference between two groups, although the preceding ANOVA had a p-value smaller than 0.05.

Table 3 Community parameters for a) macrofauna and b) meiofauna. Number of taxa, number of individuals, shannon index (H') and evenness (J') are presented for macrofauna. Number of taxa, number of individuals and the Nematoda/Harpacticoida ratio are presented for meiofauna. Numbers are means of the investigated samples ±SD of the sample

a) Macrofauna	Sandspollen			Sætrepollen		Hallangspollen	
	control	cut	removed	control	removed	control	cut	removed
Number of Taxa	11.67 ± 1.155	11.33 ± 2.517	8.67 ± 0.577	2.33 ± 0.577	6.00 ± 0.000	11.67 ± 2.887	10.33 ± 2.517	13.67 ± 3.055
Number of Individuals	109.00 ± 54.249	112.33 ± 45.742	136.67 ± 3.512	6.00 ± 5.196	66.00 ± 20.298	484.33 ± 562.216	85.67 ± 29.905	346.67 ± 178.590
Shannon index (H')	2.65 ± 0.063	2.60 ± 0.271	2.31 ± 0.206	0.96 ± 0.070	1.61 ± 0.313	1.17 ± 0.716	2.52 ± 0.236	1.92 ± 0.251
Evenness (J')	0.75 ± 0.040	0.75 ± 0.030	0.74 ± 0.048	0.83 ± 0.151	0.62 ± 0.121	0.34 ± 0.226	0.76 ± 0.117	0.51 ± 0.081

b) Meiofauna	Sandspollen			Sætrepollen		Hallangspollen	
	control	cut	removed	control	removed	control	cut	removed
Number of Taxa	7.00 ± 2.000	9.00 ± 1.000	8.00 ± 0.000	6.67 ± 1.528	8.33 ± 1.528	8.00 ± 0.000	8.33 ± 1.528	7.33 ± 1.155
Number of individuals	1790.33 ± 587.878	3465.67 ± 1267.768	2508.00 ± 840.500	1235.00 ± 733.464	1947.67 ± 278.173	3556.00 ± 1060.204	3049.33 ± 1012.467	2936.00 ± 463.706
Nematoda/Harpacticoida	34.42±18.728	20.48±10.099	26.26±15.233	7.81±2.208	5.75±1.642	78.46±16.264	43.25±13.461	53.82±23.658

The pairwise test for the treatment groups showed a significant difference between the Shannon index of the samples from the cut treatment and the other two groups. But since the cut treatment is missing at Sætrepollen, the location with the lowest Shannon indices, this result should be treated with care.

The Kruskal-Wallis tests conducted for the abundance of the single taxa (Table 4) showed a reaction to the treatment for only two taxa: *Peringia ulvae* and *Mya arenaria*. *P. ulvae* has a significant higher abundance in the removed treatment. For *M. arenaria* only the removed treatment and the control were significantly different from each other, with the higher abundance in the removed treatment. The significance of this result was relatively low, since the difference occurred only at Sandspollen and Sætrepollen, but not at Hallangspollen. The cut treatment is not different from any of the others for several reasons. Firstly the cut treatment at Sætrepollen is missing, secondly the cut area at Hallangspollen was, similar to the removed and the control, low in numbers and thirdly, the cut samples at Sandspollen have a high variation of *M. arenaria*.

Table 4 Macrofauna results of the analyses of variance; p-values for the different tested taxa and factors are presented

	location	treatment
Chironomidae spp.	$p > 0.05$	$p > 0.05$
Monocorophium insidiosum	$p << 0.01$	$p > 0.05$
Aoridae indet	$p << 0.01$	$p > 0.05$
Mytilus sp.	$p << 0.01$	$p > 0.05$
Mya arenaria	$p < 0.01$	$p < 0.05$
Peringia ulvae	$p > 0.05$	$p << 0.01$
Rissoa membranacea	$p > 0.05$	$p > 0.05$
Pusillina sarsii	$p < 0.05$	$p > 0.05$
Tubificoides benedii	$p << 0.01$	$p > 0.05$
Tubificoides pseudogaster	$p << 0.01$	$p > 0.05$
Arenicola marina	$p > 0.05$	$p > 0.05$
Capitellidae indet	$p < 0.01$	$p > 0.05$

One taxon that seems to be unaffected is the Chironomidae. With 509 individuals they were the second most abundant taxon and they did not show any difference with regard to location or treatment.

The results for the locations showed significant differences for many taxa (Table 4). The pairwise comparison always showed one location being different from one or both other locations. By combining the results for the different taxa, Sandspollen can be characterized by high numbers of *Monocorophium insidiosum*, Aoridae and *Mya arenaria*. Hallangspollen is characterized by *Tubificoides benedii, Tubificoides pseudogaster* and Capitellidae. The only taxon generally found in high numbers at Sætrepollen was the Chironomidae, which are abundant at the other locations as well. *Peringia ulvae* and *Mya arenaria* were the other two species found at Sætrepollen in numbers of more than single individuals, but they were found exclusively in the removed treatment.

Mytilus sp. of which the abundance at Sandspollen and Sætrepollen were shown to be significantly different has to be mentioned as well. It is present in relatively high numbers at Sandspollen and can be added to the list of typical species, but it has to be listed as the most characteristic taxa at Hallangspollen. This is not shown as a significant result by the univariate statistics, since the variation was extremely high (between 8 and 1066 individuals sample^{-1}) for *Mytilus* sp. at Hallangspollen. The individuals at Hallangspollen were in overall smaller than the individuals at Sandspollen. The largest individuals at Hallangspollen were of the same size as the Sandspollen individuals, which were juveniles as well.

The multivariate analysis of the dataset showed a similar result. The conducted ANOSIM gave a Global R of 0.795 with a significance level of 0.01% for the locations, while the Global R for the treatments was only 0.178 with a significance level of 7%. The pairwise test for the locations showed a significant difference for every pair, while the tests for treatments showed a significant difference only for the pairs including the removed treatment, but not for the combination of control and cut.

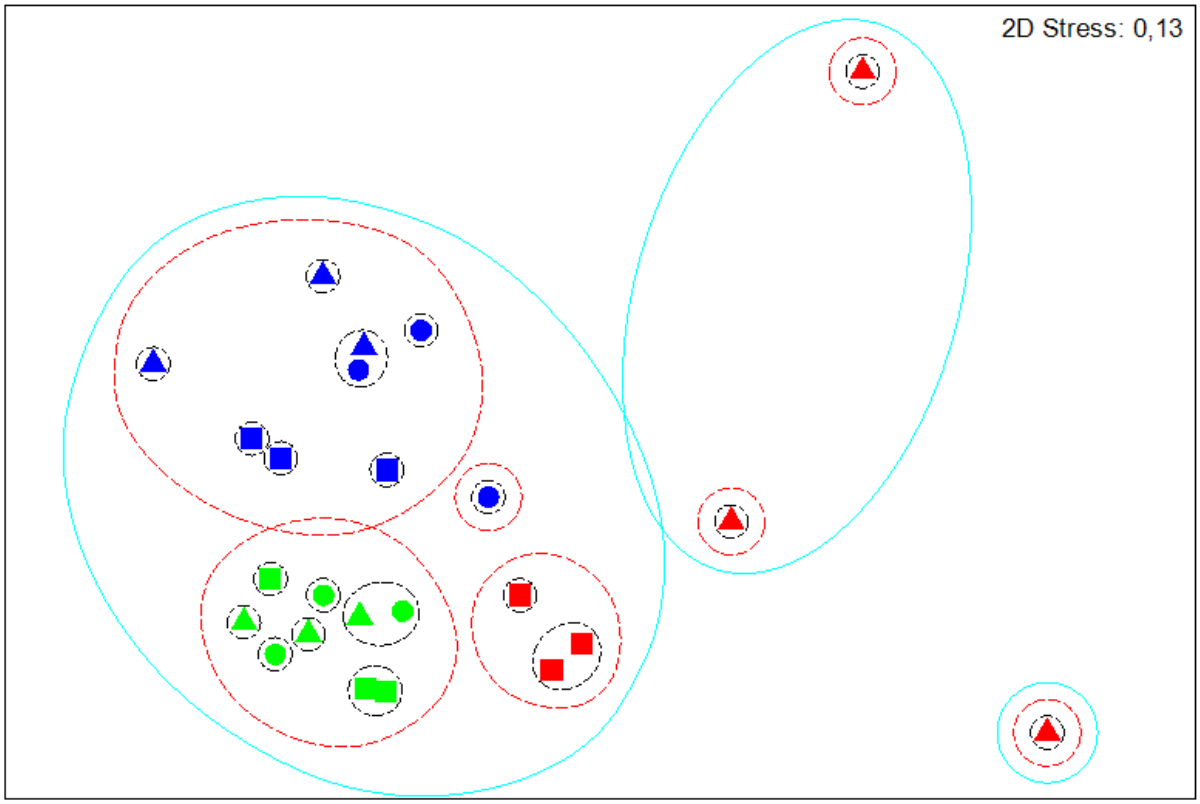

Figure 12 Two dimensional nMDS plot of macrofauna; based on Bray-Curtis similarities on square root transformed data; colours of the symbols represent the different locations (green = Sandspollen; red = Sætrepollen; blue = Hallangspollen) and the form represents the different treatments (triangle = control; circle = cut; square = removed; similarities are superimposed as blue (25%), red (50%) and black (75%) lines.

The nMDS plot given in Figure 12 shows the similarity and the relative position the single samples have to each other. It shows clearly that the samples from Sandspollen have the highest similarity, while the samples from Sætrepollen and especially the control samples are spread out over half of the plot. It should be noted that the Sætrepollen control samples are quite similar in being almost entirely free from macrofauna, with 12, 3 and 3 individuals. The samples from Hallangspollen are less similar than the Sandspollen samples, but they still form a clear group in the plot.

With regard to the treatments, no clear trend can be seen in the nMDS plot, with the exception that the groups of the Sætrepollen samples are separated in the plot.

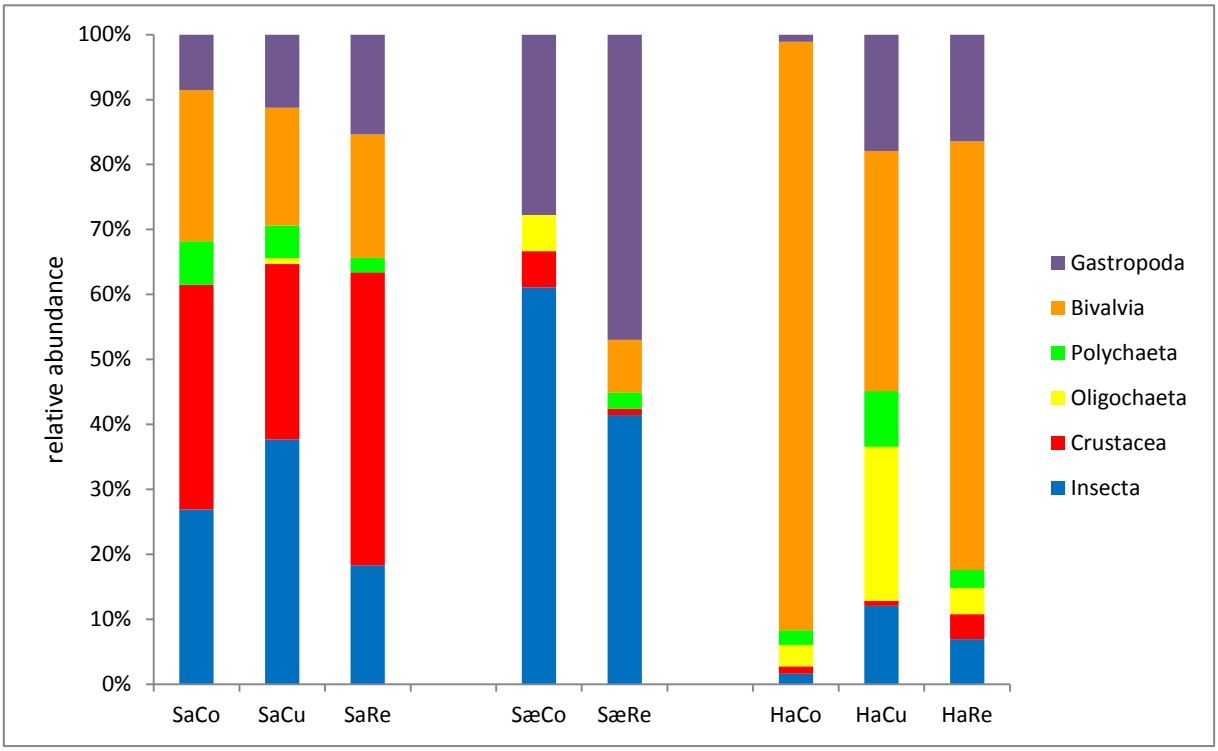

Figure 13 Relative abundance of the major macrofaunal taxa for the different treatments at all the locations during the main sampling. Abbreviations for the locations (Sa = Sandspollen; Sæ = Sætrepollen; Ha = Hallangspollen) and treatments (Co = control; Cu = cut; Re = removed)

The relative abundance of the major groups shown in Figure 13 indicates the same pattern. The color pattern seems to be typical for each site, with only small changes for the treatment groups.

The faunal composition was investigated with the SIMPER function of PRIMER for the factor 'location' and the average similarity within each site and the taxa contributing most to this similarity are given in Table 5.

Table 5 Average similarity of the macrofauna within every site and the list of taxa contributing most to this similarity. Cut of percentage was set to 70%; numbers based on square root transformed data

a) Sandspollen Average similarity: 66.44					
	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Monocorophium insidiosum	5.60	15.62	2.30	23.51	23.51
Chironomidae indet	5.49	15.31	5.26	23.04	46.56
Mytilus sp.	3.81	8.96	2.35	13.48	60.03
Mya arenaria	2.33	7.37	3.07	11.09	71.12

b) Sætrepollen Average similarity: 46.81					
	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Peringia ulvae	3.14	19.23	1.27	41.07	41.07
Chironomidae indet	3.27	18.67	1.24	39.89	80.96

c) Hallangspollen Average similarity: 58.35					
	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Mytilus sp.	12.59	21.53	3.14	36.90	36.90
Chironomidae indet	3.59	9.34	3.13	16.00	52.90
Tubificoides benedii	2.96	6.97	1.68	11.95	64.85
Peringia ulvae	3.40	5.81	1.49	9.95	74.80

The one thing all the locations have in common is that the insect larvae from the Chironomidae family are the second most important taxa to characterize the location.

The most typical species for Sandspollen is the amphipod *Monocorophium insidiosum*. The bivalves *Mytilus* sp. and *Mya arenaria* follow on the places 3 and 4. The mass occurrence of *Mytilus* sp. at Hallangspollen, described in 3.1, can be seen in the sediment samples as well, where it accounted for more than one third of the similarity. At Sætrepollen the gastropod *Peringia ulvae* was the only macrofaunal species which had a considerable contribution to the similarity beside the Chironomidae. This picture, drawn by the SIMPER analysis, is similar to the result of the analysis of the single taxa described before.

The average dissimilarity between pairs of locations and the most contributing taxa to this dissimilarity are given in Table 6. Since the most typical species at the different locations are different, it is not surprising that these taxa have the largest contribution to the dissimilarity between the different locations.

Table 6 Average dissimilarity between the locations and the list of taxa contributing most to this dissimilarity of the macrofauna; a pairwise comparison between the locations was conducted; the cut of percentage was set to 70%; numbers based on square root transformed data

a) Sandspollen & Sætrepollen Average dissimilarity: 67.96						
	Sa: Av.Abund	Sæ: Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Monocorophium insidiosum	5.60	0.33	13.81	2.88	20.32	20.32
Mytilus sp.	3.81	0.24	9.98	1.75	14.69	35.01
Chironomidae indet	5.49	3.27	7.77	1.33	11.44	46.45
Aoridae indet	2.64	0.00	7.48	3.58	11.01	57.46
Pusillina sarsii	1.47	0.00	4.38	1.32	6.45	63.90
Peringia ulvae	2.29	3.14	4.03	1.22	5.93	69.83
Mya arenaria	2.33	1.03	3.65	1.86	5.38	75.20

b) Sandspollen & Hallangspollen Average dissimilarity: 58.77						
	Sa: Av.Abund	Ha: Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Mytilus sp.	3.81	12.59	12.14	1.27	20.66	20.66
Monocorophium insidiosum	5.60	0.93	7.43	2.35	12.64	33.30
Tubificoides benedii	0.11	2.96	4.51	2.19	7.67	40.97
Chironomidae indet	5.49	3.59	3.63	1.30	6.17	47.14
Tubificoides pseudogaster	0.16	2.31	3.46	1.74	5.88	53.02
Peringia ulvae	2.29	3.40	3.17	1.23	5.39	58.41
Aoridae sp.	2.64	1.13	2.83	1.61	4.81	63.22
Mya arenaria	2.33	0.69	2.70	1.99	4.60	67.81
Capitellidae indet	0.00	1.64	2.51	1.34	4.26	72.08

c) Sætrepollen & Hallangspollen Average dissimilarity: 72.25						
	Sæ: Av.Abund	Ha: Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Mytilus sp.	0.24	12.59	31.16	2.65	43.13	43.13
Tubificoides benedii	0.00	2.96	6.16	1.87	8.52	51.65
Tubificoides pseudogaster	0.17	2.31	4.33	2.12	6.00	57.65
Chironomidae indet	3.27	3.59	3.22	1.00	4.45	62.10
Peringia ulvae	3.14	3.40	3.09	1.29	4.28	66.38
Scoloplos (Scoloplos) armiger	0.00	1.00	2.85	0.77	3.94	70.32
Aoridae indet	0.00	1.13	2.67	1.24	3.69	74.01

As shown before, no significant overall difference could be identified between the treatments. Nonetheless, the SIMPER function was applied to the dataset for this factor. The result as well supported the difference of *Peringia ulvae* in the removed treatment, but unlike the univariate analysis, it did not identify the difference in the abundance of *Mya arenaria*.

3.3 Meiofauna

The meiofauna in all samples was completely dominated by nematodes (Figure 14). They accounted between 82 and 98 % of all the individuals in every single sample group. Beside the nematoda, the harpacticoida, acarina and ostracoda are typical meiofaunal metazoans found in the *Zostera* sediments (Figure 9). These four typical meiofaunal taxa account for over 96% of the individuals found in every location and treatment. In addition, some chironomidae, oligochaeta, polychaeta, gastropoda, bivalvia, and amphipoda were present in the meiofauna samples. Among these six taxa, the polychaete family Syllidae was the only group which was not identified regularly in the macrofauna samples. The rest of the counted individuals were most probably juveniles of the species listed in the macrofauna results. Beside the Syllidae, two other polychaete species were encountered in higher numbers. These were *Fabriciola baltica* in samples from Sandspollen and Sætrepollen and *Arenicola marina* in samples from Sandspollen.

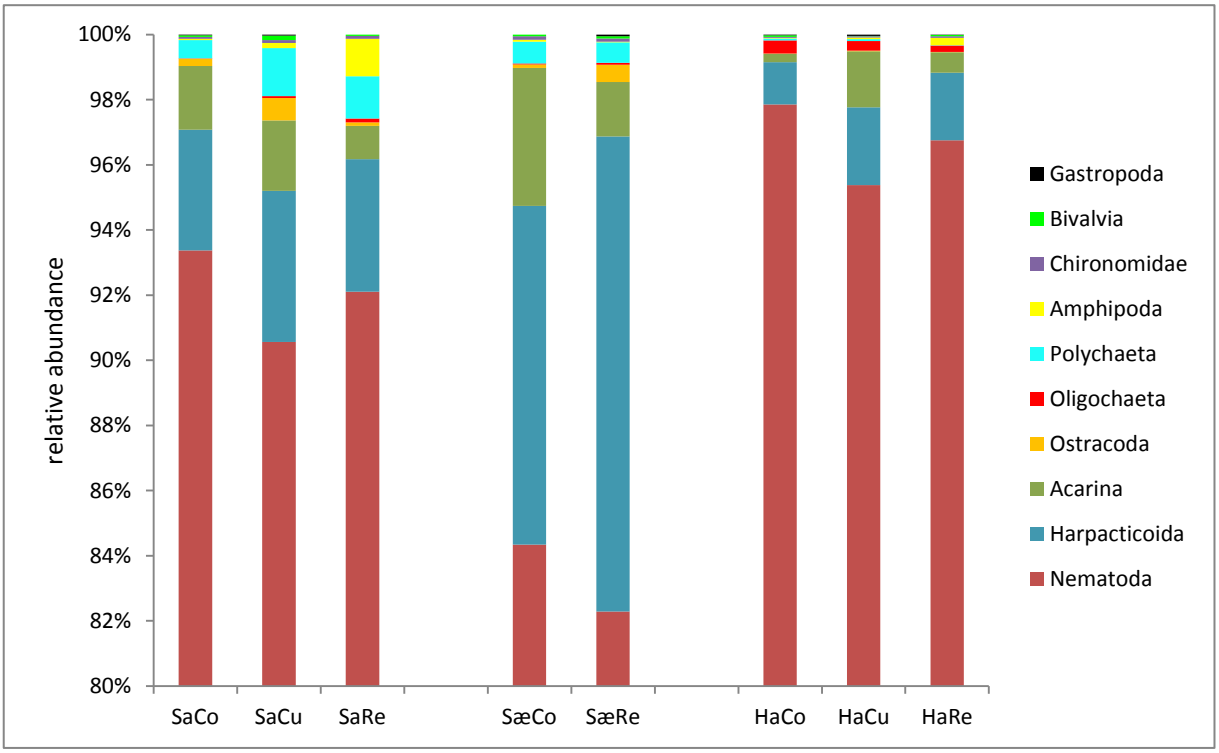

Figure 14 Relative abundance of the meiofaunal taxa; scale on the y-axis starts at 80%; Abbreviations for the locations (Sa = Sandspollen; Sæ = Sætrepollen; Ha = Hallangspollen) and treatments (Co = control; Cu = cut; Re = removed)

3.3.1 Locations and treatments

As for the macrofauna, the variables presented in Table 3b were investigated for differences of the variances and the results of this analysis are given in Table 7. A significant difference

between groups was only detected for the number of individuals per core and for the Nematoda/Copepoda ratio at the different locations. A Tukey test revealed a significant difference for the number of individuals between the samples from Sætrepollen and Hallangspollen, with a p-value for this couple of 0.008. The mean number of individuals found in the Hallangspollen samples was approximately twice as high as in samples from Sætrepollen. The Tamhane T2 test for the pairwise comparison of the Nematoda/Copepoda ratio revealed a significant difference for every pair of locations. Hallangspollen had the highest ratio, followed by Sandspollen and Sætrepollen.

Table 7 Meiofauna results for the analysis of variance; the p-values for the tested variables and factors are presented

	Location	Treatment
Number of taxa	$p > 0.05$	$p > 0.05$
Number of Individuals	$p < 0.01$	$p > 0.05$
Nematoda/Copepoda	$p << 0.01$	$p > 0.05$

The estimated number of individuals $10cm^{-2}$ varies between 1 536 and 4 422 for the different factor groups. The numbers of the three treatments at Hallangspollen are more at the upper end of this range and the numbers from Sætrepollen at the lower end.

The multivariate analysis of the meiofauna data set revealed a high overall similarity of all meiofauna samples, but one control sample from Sætrepollen differed from the rest of the samples (Figure 15). Due to the fact that the number of individuals in this sample was lower than in the other samples, this sample was excluded from the following analysis.

A two-way crossed ANOSIM for the factors location and treatment showed that there was a difference between the locations (Global R=0.594; significance level=0.04%) but not between the treatments (Global R=0.056; significance level=30.6%). The pairwise test for the locations clearly showed that Sandspollen and Sætrepollen were not significantly dissimilar, while Hallangspollen differed from the other two locations. The same grouping is shown in the result of the cluster analysis (Figure 15), where the Hallangspollen group separates from the group with the other two locations at a similarity of 78%.

Because of these results, a SIMPER analysis was run on the same fourth root transformed data set. The factor for the SIMPER analysis was ‘location’, but Sandspollen and Sætrepollen were treated as a single location, due to the results of the cluster analysis and the ANOSIM. The taxa contributing most to the similarity within the groups are presented in Table 8. The three most abundant taxa (nematoda, harpacticoida and acarina) were the same for the two location groups and they accounted for at least 70% of the similarity of each group. The taxa

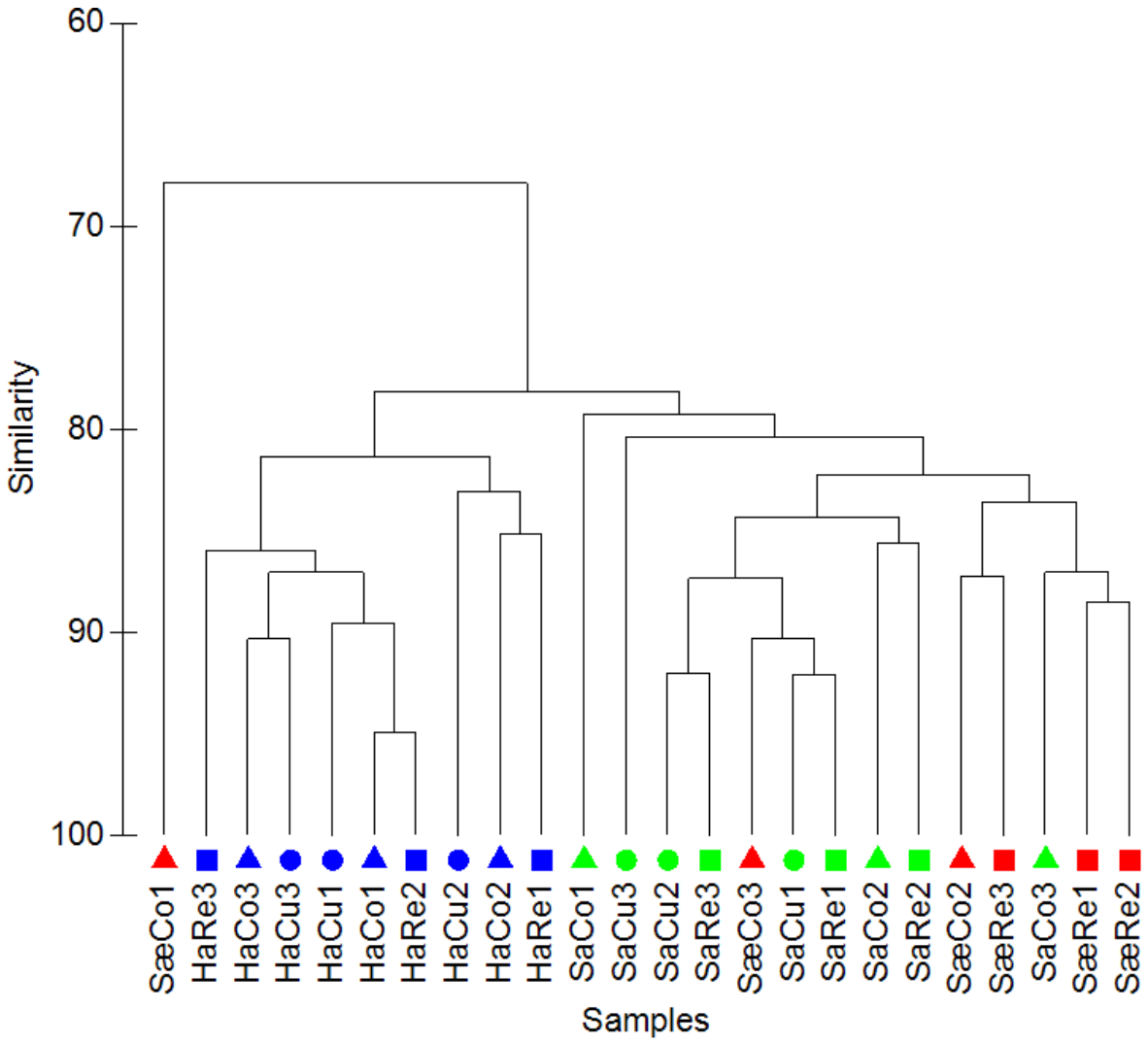

Figure 15 Similarity Cluster for meiofauna; based on group average of Bray-Curtis similarities of fourth root transformed data; Abbreviations for locations and treatments, sample numbers were given to identify the different replicate samples and have no further meaning; colours of the symbols represent the diffent locations (green = Sandspollen; red = Sætrepollen; blue = Hallangspollen) and the form represents the different treatments (triangle = control; circle = cut; square = removed)

on position 4 of these lists are the first that differ, with polychaeta in the Sandspollen & Sætrepollen group and oligochaeta in the Hallangspollen group.

The taxa contributing to the low average dissimilarity of only 21.97 are not listed here, since each of the 10 taxa used for the analysis had a contribution of 5-15 % and no single taxa seems to be more important than the others.

Table 8 Average similarity of the meiofaunal composition within the two groups and the list of taxa contributing most to it; only the 4 most contributing taxa are presented; numbers based on fourth root transformed data

a) Sandspollen & Sætrepollen Average similarity: 83.17					
	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Nematoda indet	6.65	32.24	10.84	38.76	38.76
Harpacticoida indet	3.41	15.73	6.27	18.92	57.68
Acarina indet	2.44	10.49	4.03	12.61	70.29
Polychaeta indet	2.07	9.16	7.19	11.01	81.30

b) Hallangspollen Average similarity: 83.65					
	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Nematoda indet	7.41	39.44	13.59	47.15	47.15
Harpacticoida indet	2.73	14.03	16.02	16.77	63.92
Acarina indet	1.96	8.48	4.85	10.14	74.06
Oligochaeta indet	1.66	8.06	18.18	9.64	83.70

4 Discussion

The results of this study have shown that the location is the factor determining the infaunal composition of macro- as well as meiofauna. The treatments conducted during the experiment had an influence on two macrofaunal species.

4.1 Infauna of *Zostera marina*

The estimated number of macrofauna m^{-2} from the control samples at the three study locations has a wide range. With only 2 937 individuals m^{-2}, Sætrepollen is below the normal densities reported for infauna of *Z. marina* (Orth 1973, Boström & Bonsdorff 1997, Fredriksen et al. 2010). Only Orth (1973) investigated a single meadow where the faunal density (2 348 ind. m^{-2}) was as low as the density at Sætrepollen, but since he used a 1 mm sieve to isolate the fauna, the densities of his study have to be treated as underestimations when comparing them to the present study. The density of 53 358 ind. m^{-2} at Sandspollen is at the upper end of the range of 19 098 – 53 645 ind. m^{-2} reported by Fredriksen et al. (2010) or the 24 994 – 52 682 ind. m^{-2} in Boström and Bonsdorff (1997). With regard to this numbers it has to be taken into consideration that Fredriksen et al. (2010) used a 250 µm sieve for the collection of the fauna. The density of 237 090 ind. m^{-2} at Hallangspollen in the present study is far above all the reported numbers from Scandinavia. This high density at Hallangspollen was caused by the mass occurrence of juvenile *Mytilus*. In a study of similar mass occurrences in *Z. marina* meadows at the American Atlantic coast, Bologna et al. (2005) found *Mytilus edulis* densities of 175 000 ind. m^{-2}, what is similar to the densities at Hallangspollen.

The average number of taxa that has been found in every core sample at Sandspollen (11.7 taxa $core^{-1}$) and Hallangspollen (11.7 taxa $core^{-1}$) is within the range of 6 – 14 taxa $core^{-1}$ found by Fredriksen et al. (2010) and higher than the 5.9 – 8.8 taxa $core^{-1}$ from the Baltic sea (Boström & Bonsdorff 1997). The inner core diameters used in these studies were 5 cm (Fredriksen et al. 2010) and 4.7 cm (Boström & Bonsdorff 1997). Although the cores are not exactly the size of the cores used in the present study (5.1 cm), it seems reasonable to compare the values with each other. The 2.3 taxa $core^{-1}$ found in the control samples from Sætrepollen are much lower than the results of any other study.

In contrast to the number of taxa in each core sample, the total number of taxa recorded in the control samples from Sandspollen and Hallangspollen was, with 17 and 19 respectively, similar to the 11 – 22 taxa reported by Boström and Bonsdorff (1997) and lower than the 21 – 38 taxa in Fredriksen et al. (2010). With only 5 taxa recorded in the control samples, Sætrepollen had fewer taxa than any other meadow in the mentioned studies. Although the number of taxa was lower in the present study than the numbers presented by Fredriksen et al. (2010), it can be expected that the meadows at Sandspollen and Hallangspollen are providing a habitat for a similar number of infaunal species. As mentioned before, Fredriksen et al. (2010) used a smaller mesh size. In addition, they have taken 8 – 12 replicate samples in every meadow, compared to 3 control samples in this study. Therefore, their sampling of rare species can be assumed to be more effective. This assumption is further supported by the fact that the total number of taxa (over all treatments) found at Sandspollen (22 taxa) and Hallangspollen (24 taxa) is within the same range reported by Fredriksen et al. (2010). In this context, only Sætrepollen (12 taxa) seems to differ from other meadows in Norway, but this number is based on fewer samples, since the cut treatment has been lost.

The Shannon index and evenness at Sandspollen (H'=2.65; J'=0.75) are virtually the same as the highest values reported by Fredriksen et al. (2010)(H'=2.71; J'=0.75), while the Shannon indices of the other two locations (0.96 at Sætrepollen; 1.17 at Hallangspollen) are in the range of the lowest values reported in the same study (H'=1.19). At Hallangspollen, this correlates with the low evenness (J'=0.34) and at Sætrepollen with the low faunal abundance of only 6 individuals sample^{-1}. The Shannon indices in the Baltic meadows investigated by Boström and Bonsdorff (1997) were less variable than in the meadows at the Norwegian coast in this study and in Fredriksen et al. (2010). The Baltic values were comparable to the Sandspollen samples, some values being exactly the same while others were a little below.

Compared to the macrofauna, the variation of the total meiofauna abundance was relative low in the *Zostera* meadows. Sætrepollen (1 536 ind. 10cm^{-2}), Sandspollen (2 226 ind. 10cm^{-2}) as well as Hallangspollen (4 422 ind. 10cm^{-2}) are all within the same range as the numbers reported by Tietjen (1969) for meiofauna of *Zostera marina* sediments in two estuaries at the American Atlantic coast. The meiofaunal abundance in samples from *Zostera muelleri* in New Zealand (2 519 – 4 979 ind. 10cm^{-2}) reported by Leduc and Probert (2011) is similar to the numbers of this study as well. Only Fonseca et al. (2011) reported a wider range for infaunal abundances for *Zostera capricorni* meadows in eastern Australia (1 100 – 8 446 ind.

10cm^{-2}). With regard to these studies, which have been conducted in different parts of the world and in the sediments of different *Zostera* species, one may assume that meiofaunal abundance in *Z. marina* varies in general less than the abundance of macrofauna.

All over the world nematodes are the dominating meiofaunal taxa in *Zostera* sediments, complemented by some copepods and a small number of individuals from other taxa, which are different in all the studies (Tietjen 1969, Fonseca et al. 2011, Leduc & Probert 2011). Leduc and Probert (2011) detected that the abundance of copepods is low when the seagrass meadow has a high shoot density. This stands in contrast to the present study, where the only samples with a similar low copepod number were the samples from Hallangspollen, the location with the lowest shoot density.

4.1.1 Seasonal change

Due to the pre-sampling and the fact that the *Zostera* meadows at Sandspollen and Sætrepollen have been sampled by Sømme (2012) in May 2010, it is possible to get a brief insight in the seasonal development of the macrofauna communities.

Sømme (2012) took 5 core samples with a diameter of 10 cm. The total number of taxa found in these samples was compared with the total number of the 3 control samples from the main sampling and the 6 samples from the pre-sampling of the present study (Figure 16a). Even though the sampling intensity was by far the lowest in summer, a clear peak in the number of taxa can be seen at Sandspollen. In spring and autumn, less than half as many taxa were found than in summer, with slightly more taxa in spring than in

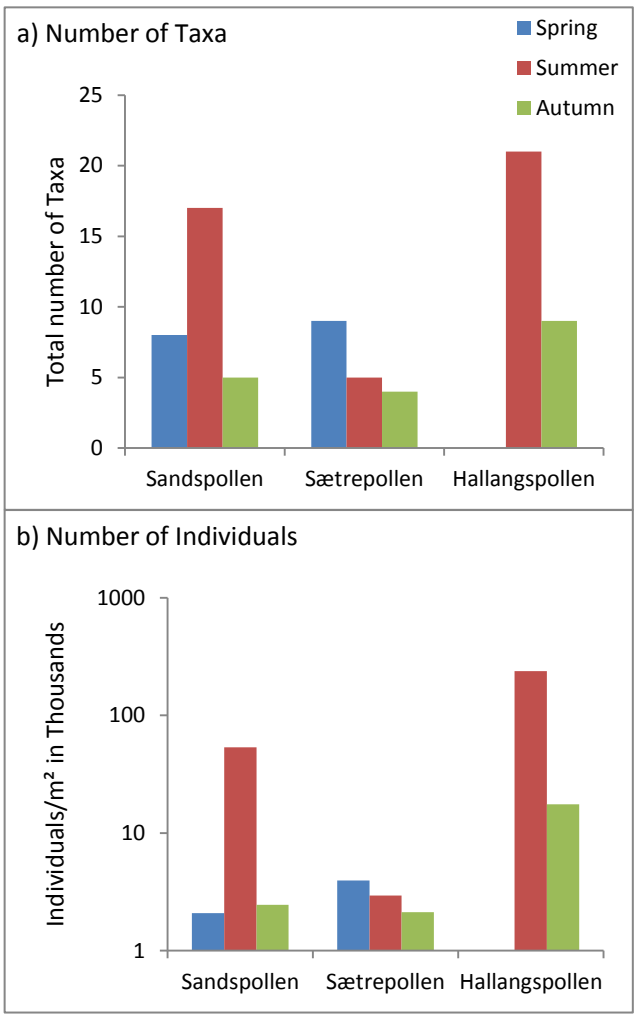

Figure 16 Macrofauna: Development of a) the total number of taxa and b) the estimated number of individuals/m^2 over the season; Blue = Spring; Red = Summer; Green = Autumn; total number of individuals on a log scale

autumn. The samples from Hallangspollen suggest a similar peak in the summer, but since the number of taxa during the spring is unknown, this cannot be said with certainty. The observed trend at Sætrepollen looks quite different, with the most taxa recorded during spring and less taxa during summer and autumn.

The estimated number of individuals (Figure 16b) shows basically the same trend as the number of taxa. So it is possible to say that for the used data a high number of taxa was present, when the density of animals was high. This does not mean that the Shannon index follows the same trend, since some samples were dominated by one or two species. Especially the samples at Hallangspollen were extremely dominated by *Mytilus* sp. during summer.

The Chironomidae was the only taxon present at every location at every time of the year and this not only with single individuals. The few taxa which were not found during summer were always found in low numbers in spring or autumn. The lack of these taxa in the summer might be a result of the low sampling intensity at that time.

With regard to this seasonal development, it has to be kept in mind that the summer samples are from 2011, while the spring and autumn samples are from 2010. Therefore the order of the sampling was spring, autumn, summer and the difference observed for the summer samples might be a difference between the two years and not the seasons.

The seasonality of the infauna of seagrasses has not been studied extensively and only few studies examined the faunal development for a whole year. Two such studies were conducted in seagrass meadows in Florida (Stoner 1980, Sheridan & Livingston 1983). Both of them recorded a seasonal change of infaunal abundance with highest numbers in winter and spring. Stoner (1980) found peak abundances in November and in April/May. This trend is different from the summer peak identified during this study. This difference is most probably reflecting the different geographical location and the associated climate of Norway and Florida.

Orth (1973) sampled the same eelgrass meadows twice during 1970, in March and July. He found higher species numbers in March than in July, for most *Zostera* meadows in Chesapeake Bay. In Norwegian waters Fredriksen et al. (2010) sampled infauna from four meadows at two different times of the year. They sampled two meadows in August and the other two in November, but did not detect a major influence of the sampling time on the infauna.

In contrast, the results in the present study suggest a peak abundance and species richness in summer for two of the three locations, a trend that has not been reported in any of the other studies. In a study of a *Zostera marina* meadow at the Swedish west coast, Möller (1986) describes that most species peaked for only a short period immediately after recruitment. Therefore, it seems realistic that the summer samples at Sandspollen and Hallangspollen were taken during such a peak.

If there is no seasonal change at Sætrepollen or if the seasonal change is just different from the other two locations and the summer peak was missed by the sampling, cannot be answered with the results of this study. One argument for a different pattern of seasonality is the fact that the ice cover appeared earlier at Sætrepollen than at Sandspollen and Hallangspollen (see 2.2.2), but this is purely speculative.

4.2 Treatments

The influence the two treatments had on the infaunal communities seemed to be relatively small in overall. For the macrofauna only the removed treatment at Sætrepollen was clearly separated in the nMDS plot from the control (Figure 12), while for meiofauna no separation could be made at all.

The results of this study have shown no indication that the cutting of the eelgrass could have an effect on the infauna. Since no sampling was conducted during the recovery time of ten months, this study gives no insight if there was a change in the species composition, before the eelgrass was regrown. The results of Herkül and Kotta (2009) from a similar cutting experiment in the Baltic Sea showed a significant reduction of the faunal diversity and abundance after two months without the leaves. At this point no statement can be made, if the infaunal community in the cut treatment of this study has reestablished with the regrowing *Zostera* meadow or if it hasn't changed in the beginning.

In contrast to the cut treatment, the removed treatment showed an effect on the abundance of *Peringia ulvae* and *Mya arenaria*.

4.2.1 *Peringia ulvae*

The mudsnail *Peringia ulvae* is the only species that showed a clear response to the treatments at every location. The univariate analysis showed a significant higher number of snails in the removed treatment, compared to the other two groups.

This difference in the abundance might be related to a somehow different accumulation of drift algae in the removed treatment, than in the control and the cut areas. *Peringia ulvae* was shown to occur in high numbers on mudflats which are covered by algal mats (Soulsby et al. 1982). Hull (1987) described that high numbers of *P. ulvae* have been transported inevitably with *Ulva* spp. for a field experiment and Norkko et al. (2000) demonstrated the ability of *P. ulvae* to take advantage and live on algal mats. This suggests drift algae not only as food, but also as a probable origin of *P. ulvae*. In addition to this, it seems to be unlikely that such drift algae can easily leave the removed patch again, since once they are in there they are surrounded by a 'cage' of *Zostera marina* shoots and no stronger currents can be expected to occur within the patch.

Since no epifauna sampling was conducted in the control and cut treatment, it is not known if *P. ulvae* have been abundant as epifauna on the *Zostera* plants. Species of the herbivorous Hydrobiidae are common on eelgrass (Boström & Bonsdorff 1997), where they can feed on epiphytic algae and trapped drift algae that are abundant in high numbers in eelgrass meadows (Boström & Bonsdorff 2000, Fredriksen et al. 2005).

It is not unlikely that *P. ulvae* is transported with drift algae and accumulates with them in the eelgrass meadow as well as on the removed treatment. Therefore it would be premature to state that removal of eelgrass results in an increased abundance of *P. ulvae*, but the results show that the sediment in the removed treatments are at least more directly influenced by the snails.

4.2.2 *Mya arenaria*

The soft-shell clam *Mya arenaria* was the second species that showed a response to the removed treatment of the experiment. The overall numbers of *M. arenaria* were low and the discovered individuals were so small, that the mortality rate can be expected to be high (Brousseau 1978). Nonetheless, the clams were more abundant in the removed area than in the control at Sandspollen and Sætrepollen.

Beal (1994) has shown a negative influence of *Z. marina* on the survival and growth of juvenile *Mya arenaria*. He explained the lower survival rate by a higher predation pressure through the higher abundance of *Carcinus maenas* within the eelgrass. This could be a possible explanation for the discovered difference of the abundance in the removed treatment at Sandspollen and Sætrepollen. The low overall abundance at Hallangspollen, even though it could be caused by a high abundance of predators, is more probably the result of oxygen depletion and high amounts of hydrogen sulfide (see 4.3.3) (Rosenberg et al. 1991).

Möller (1986) found high abundances of juvenile *Mya arenaria* in unvegetated sediments after an unusual cold winter. He explains the higher settlement rate with the high amount of unoccupied sediment and a late arrival of epibenthic predators, both due to the cold winter. Further he describes that a high abundance of *Mya arenaria* in warm years correlated with a low abundance of epibenthic mobile predators (*Crangon crangon* and *Carcinus maenas*).

4.2.3 *Arenicola marina*

It has been reported that *Zostera noltii* as well as *Z. marina* are restricted in their growth in areas with high numbers of the lugworm *Arenicola marina* (Philippart 1994, Valdemarsen et al. 2011). Valdemarsen et al. (2011) came to the result that even low numbers of adult *A. marina* (5-10 ind. m^{-2}) are capable of reworking the sediment strong enough to prevent *Z. marina* from reestablishing in areas where it has grown before and was lost because of eutrophication. Here it has to be mentioned that it is doubtful that the used corers were large enough and that the sampling depth of 10 cm was sufficient to sample adult individuals of *A. marina*. Nonetheless is it unlikely that a large number of adult lugworms were present during the sampling, since the worms produce obvious mounds on the sediment surface. No mounds were observed by the divers or on photos taken by the divers.

Even though no adult specimens were present in the removed treatments at the time the sampling was conducted, a high number of juvenile *A. marina* were found in some samples, especially in the meiofauna samples from Sandspollen.

With regard to the conducted experiment it is of great interest, if the juvenile *A. marina* are able to settle in sufficient high numbers in the removed treatment before the eelgrass can regrow. In that case it might be possible that the eelgrass cannot reestablish there. Even though the removed patches are really small and should not be compared directly to the

eutrophication affected area described by Valdemarsen et al. (2011), an establishment of lugworms in the removed areas is something that should be considered possible.

If such an establishment of lugworms occurs, this could cause a complete change of the functioning of the infaunal community, aside from the exclusion of *Zostera*. A change in the functional groups (Volkenborn & Reise 2007), as well as a negative influence on the recruitment of other species and the emigration of mobile species (Flach 1992) have been attributed to the activities of *A. marina*.

4.2.4 Macrofauna and meiofauna

This study has shown only two species that were directly affected by the removed treatment. Even though both of these species were recorded in the macrofauna samples, this study gives no indication to believe that macrofauna and meiofauna were affected differently by the treatments, since the overall numbers of both, macrofauna and meiofauna were not affected by any of the treatments.

It should be remarked that the possibility exists that the meiofaunal species composition has changed because of the treatments, but since the meiofauna was not identified to a low taxonomic level, this study cannot give an insight here.

4.3 Location

The results of this study have shown that every investigated *Z. marina* meadow provides a habitat for a specific infaunal community. Some of the taxa characterizing the different locations were unique at one location, while others occurred at two or at all three locations.

4.3.1 The Chironomidae

Insect larvae of the Chironomidae were the only taxon found in relative high numbers at all locations and treatments.

They are a common group, which is often found in *Z. marina* (Boström & Bonsdorff 1997, Fredriksen et al. 2005). These studies reported the insects more commonly as epifauna, but they have been found in infaunal samples as well (Boström & Bonsdorff 1997, Sømme 2012).

4.3.2 The Amphipoda at Sandspollen

Three amphipod taxa were present in samples from Sandspollen: *Monocorophium insidiosum*, Aoridae and *Ericthonius* sp.

M. insidiosum were the most abundant, but the Aoridae were abundant in considerably high numbers as well. *M. insidiosum* is a tube-dwelling amphipod that is capable of living at a wide range of salinities and is not specialized on a specific sediment grain size (Prato & Biandolino 2006). *Microdeutopus gryllotalpa*, the species all the male Aoridae belonged to, are typically found in areas with high detritus accumulation, such as *Zostera* meadows (Myers 1969). Several species of the genus *Ericthonius* are common amphipods along the Scandinavian Coasts (Myers & McGrath 1984).

Monocorophium insidiosum, Microdeutopus gryllotalpa as well as *Ericthonius differmis* are common amphipod species associated with *Zostera marina* meadows at the west coast of Sweden (Jephson et al. 2008). Although the only *Ericthonius* individual identified to species level in this study was from a different species, this shows that potential species compositions in the inner Oslofjord doesn't differ from species compositions in the other parts of Skagerrak. Möller (1986) identified *Microdeutopus gryllotalpa* and *Ericthonius* spp. as dominating species in an eelgrass meadow at the Swedish west coast as well.

4.3.3 Oxygen depletion at Hallangspollen

The oligochaetes *Tubificoides benedii* and *T. pseudogaster* as well as the polychaetes *Capitella capitata* and *Scoloplos armiger* have been found in relative high numbers in the samples from Hallangspollen, while they were virtually absent from the other locations. Thiermann et al. (1996) points out that *Tubificoides benedii, T. pseudogaster* and *Capitella capitata* are capable of handling temporary hypoxia and high levels of hydrogen sulfide, which are normally toxic to other species. They also reported high numbers of *Scoloplos armiger* at the same sampling locations during some part of the season.

This species composition and the sulfuric odor of the sediment are strong indicators that the infauna at Hallangspollen might experience times of oxygen depletion and high hydrogen sulfide levels.

4.3.4 *Mytilus* sp. at Sandspollen and Hallangspollen

Mytilus sp. has been found at Hallangspollen and Sandspollen, but the numbers of mussels and their sizes differed between the two locations.

The development of *Mytilus edulis*, as described by Bayne (1964), includes a planktonic phase, which is followed by a primary and at least one secondary settlement. The primary settlement occurs normally outside of adult mussel beds and *Z. marina* blades are not unusual to function as a primary settlement site for *M. edulis* (Newell et al. 1991). They found single blades with up to 3 000 individuals, what characterizes the situation at Hallangspollen as not being unusual. When the mussels grow, they get detached and often reattach or aggregate and drift around before they finally settle. Therefore a large number of *Mytilus* can be expected to be found in the sediment, like it was the case at Hallangspollen. Similar high numbers of *M. edulis* were also reported by Bologna et al. (2005) from core samples taken during such mass occurrence events.

The numbers of *Mytilus* in the samples from Sandspollen were too low to be the result of such a larval settlement event. During the sampling it was observed that other nearby areas in the Oslofjord were covered by juvenile *Mytilus* as well. Aggregates of mussels, released from such an area close to Sandspollen, might have drifted to the eelgrass meadow. In comparison to bare sediment, eelgrass meadows have a general positive influence on the recruitment of *Mytilus edulis* (Reusch 1998). Reusch and Chapman (1995) showed that drifting aggregates of juvenile *Mytilus* tend to accumulate in eelgrass meadows and that the eelgrass protects established mussel beds from getting dislocated during intermediate storms. The fact that the individuals found in the samples from Sandspollen were larger than the individuals from Hallangspollen further supports this theory.

Another interesting feature of the mass occurrence at Hallangspollen is its possible role as driver of the benthic-pelagic coupling (Bologna et al. 2005). The mussels feed on phytoplankton and are a potential large food source for benthic predators and decomposers. Bologna et al. (2005) reported a water clearing rate of the juvenile mussels that might even be able to prevent the appearance of brown tides. Such a huge amount of animals produces a lot of feces, which are directly deposited on the sediment below. Thereby the mussels are responsible for the organic enrichment of the sediment (Matisson & Lindén 1983). This might have contributed to the situation described in 4.3.3.

4.3.5 The low number of macrofauna at Sætrepollen

The low number of macrofauna at Sætrepollen is quite surprising, since the *Zostera* bed looked healthy above the surface.

With regard to the results of Sømme (2012), pollution seems unlikely to be the reason for the low abundance. He found no single pollutant that was higher at Sætrepollen than at Sandspollen. Further he reported less oxygenated, but not hypoxic sediment at Sætrepollen, compared to the meadow at Sandspollen. Therefore hypoxia is unlikely to be the cause for the absence of infauna. In case of hypoxia one would normally expect to find some individuals of the species discussed in 4.3.3.

Another possible explanation for the absence of infauna could be a high predation pressure in the eelgrass. If the abundance of mobile epibenthic predators was extremely large, they might prey on the relative immobile infauna. Nonetheless these mobile predators are normally hiding in the seagrass, but preying in adjacent non-vegetated areas (Summerson & Peterson 1984).

At this point it has to be stated that the low number of infauna at Sætrepollen cannot be explained with the known facts.

4.3.6 Nematode/copepod ratio

Meiofauna has been suggested as a tool in pollution monitoring. The proposal of Raffaelli and Mason (1981), to use a high nematode/copepod ratio as indicator in pollution monitoring, is maybe the most used approach. The idea is based on the assumption that nematoda are less vulnerable to organic enrichment than copepoda and therefore a high ratio could be used as an indicator for organic enrichment. The use of this ratio has been discussed quite intense, with some studies giving clear evidence that the ratio cannot be used as a general indicator for organic enrichment (Gee et al. 1985), since the ratio declined with organic enrichment in an experiment. Others found an equally negative effect of organic enrichment on both taxa (Sandulli & De Nicola Giudici 1989) and Shiells and Anderson (1985) proposed the use of only the interstitial copepod species for the ratio. New approaches are however still made to make use of this ratio (Rubal et al. 2009), despite the controversy.

The results from this study show a clear location specific nematode/copepod ratio. The fact that Hallangspollen has the highest ratio would suggest a higher organic enrichment at this location. This would be in accordance with the results discussed before, but the fact that Hallangspollen has the highest total abundance of meiofauna stands in contrast to the reported negative influence on all groups (Sandulli & De Nicola Giudici 1989).

4.4 Study evaluation

All numbers in the results of this study, except for the macrofauna at Sætrepollen, were directly comparable to numbers reported in the literature. Therefore it can be assumed that the methods used for the sampling and the isolation of the fauna, meet the scientific standards of other published studies.

Since this study was investigating the macrofauna as well as the meiofauna, it has to be questioned if the separation at 500 µm was the correct choice. With regard to the results, 500 µm was the right choice for this study, but it has to be highly recommended to use a 250 µm sieve for studies that focus only on macrofauna. Without the meiofauna results, the high abundance of juvenile *Arenicola marina* at Sandspollen would not have been discovered. The chances are expected to be high to collect a large fraction of these *A. marina* with a 250 µm sieve as well.

The low number of replicate core samples is one weakness of the present study. Due to the lack of time, the number of samples from every treatment at every location was restricted to 3. Such a low replicate number results in a low statistical power. Especially for the meiofauna it would have been easy to increase the statistical power by taking more samples of a smaller size. With regard to the high numbers of meiofauna in the samples, a reduction of the sample size by 50% can be expected to deliver the same results. This reduction would have made it possible to raise the sample number to 6 without increasing the work load.

In addition to the low replicate samples, the fact that the cut treatment at Sætrepollen was lost due to the earlier ice cover was weakening the results with regard to the influence of the cutting.

The meiofauna of this study was only identified to the major taxonomic groups. Sub-sampling of a defined number of individuals in these groups is a possible way to get an insight in the

actual species composition what is desirable since it might reveal a functional difference between the meiofaunal communities.

Certainly the non-faunal parameters are a part of this study where room is left for improvement. More stringency with the measuring of shoot density and canopy height as well as an improvement of the grain size analysis could help to give further explanations for the observed faunal composition. A higher number of replicate core samples should be taken for the grain size analysis, since results based on a single core sample assume homogeneity of the sediment. There is furthermore the possibility that a single large stone, a shell or something similar is sampled by chance. This would then have a large influence on results based on a single core.

In addition to the single sample design for the grain size analysis in this study, the samples from Hallangspollen were lost due to a wrong preservation of the samples.

At this point it has to be mentioned that this study focused only on the faunal abundance and completely ignored the biomass of this fauna. Additional biomass measurements would give additional information about the role of the recorded individuals. Not only is the survival rate of larger specimens often higher than for juveniles and small species, but also the influence a large specimen can have on the rest of the community is normally higher.

5 Conclusion and further perspective

The results of this study have shown that the infaunal composition, macro- and meiofauna, of the different *Zostera marina* meadows in the inner Oslofjord were very different. The number of individuals, the number of taxa as well as the taxa composition changed from meadow to meadow.

Ten months after the eelgrass leaves had been cut, the leaves were regrown and no difference between the infauna in the cut area and the control was detected. Therefore this study finds no negative effect of such a cutting or grazing event after the long recovery period. Nonetheless, it should be kept in mind that it is not known how long it took for the infauna to reestablish. The cutting in this study consisted of only two events, cutting and re-cutting. If repeated cutting or grazing occurs over a longer time, more severe changes in the eelgrass structure can be expected, since the regrowth of the eelgrass is dependent on energy stored in the rhizome.

When the complete *Z. marina* plant has been removed, a patch with bare sediment was present in the eelgrass meadow ten months later. These patches are a habitat for a higher number of *Peringia ulvae* and *Mya arenaria* than the surrounding meadow. The present study has further pointed out the possibility of an establishment of juvenile *Arenicola marina* in the removed patches. Therefore, it would be of great interest to investigate the further development of such a removed patch – both the faunal succession and the potential for regrowth. With or without the establishment of *A. marina* it is unsure how long it takes before the eelgrass can reestablish in the removed area. Knowledge of this length is essential for an appropriate management of eelgrass meadows.

Furthermore, I see the need for an investigation of the seasonal changes of the infauna of *Z. marina* meadows in Norway. An understanding of the seasonal changes can help to optimize the study design of other field studies and it might help to gain a better understanding of the role *Z. marina* ecosystems have along the Norwegian coasts.

References

Ansari ZA, Parulekar AH (1994) Meiobenthos in the sediments of seagrass meadows of Lakshadweep atolls, Arabian Sea. Vie et Milieu 44:185-190

Ansari ZA, Rivonker CU, Ramani P, Parulekar AH (1991) Seagrass habitat complexity and macroinvertebrate abundance in Lakshadweep coral reef lagoons, Arabian Sea. Coral Reefs 10:127-131

Appeltans W, Bouchet P, Boxshall GA, De Broyer C, de Voogd NJ, Gordon DP, Hoeksema BW, Horton T, Kennedy M, Mees J, Poore GCB, Read G, Stöhr S, Walter TC, Costello MJ (2012) World register of marine species. Accessed 2012-05-16. http://www.marinespecies.org

Baden S, Gullström M, Lundén B, Pihl L, Rosenberg R (2003) Vanishing seagrass (*Zostera marina*, L.) in Swedish coastal waters. AMBIO: A Journal of the Human Environment 32:374-377

Bayne BL (1964) Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). The Journal of Animal Ecology 33:513-523

Beal BF (1994) Effects of seagrass (*Zostera marina*) cover on growth and survival of softshell clams (*Mya arenaria*). Journal of Shellfish Research 13:311-312

Bekkby T, Rinde E, Erikstad L, Bakkestuen V, Longva O, Christensen O, Isæus M, Isachsen PE (2008) Spatial probability modelling of eelgrass (*Zostera marina*) distribution on the west coast of Norway. ICES Journal of Marine Science 65:1093-1101

Blott SJ, Pye K (2001) Gradistat: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surface Processes and Landforms 26:1237-1248

Bologna PAX, Fetzer ML, McDonnell S, Moody EM (2005) Assessing the potential benthic–pelagic coupling in episodic blue mussel (*Mytilus edulis*) settlement events within eelgrass (*Zostera marina*) communities. Journal of Experimental Marine Biology and Ecology 316:117-131

Borum J, Duarte CM, Krause-Jensen D, Greve TM (2004) European seagrasses: an introduction to monitoring and management. The M&MS project, online

Borum J, Greve TM (2004) The four European seagrass species. In: Borum J, Duarte CM, Krause-Jensen D, Greve T (eds) European seagrasses: an introduction to monitoring and management. The M&MS project, online. p 1-7

Boström C, Baden SP, Krause-Jensen D (2003) The seagrasses of Scandinavia and the Baltic Sea. In: Green EP, Short FT (eds) World atlas of seagrasses. University of California Press, Berkeley, USA. p 27-37

Boström C, Bonsdorff E (1997) Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in the northern Baltic Sea. Journal of Sea Research 37:153-166

Boström C, Bonsdorff E (2000) Zoobenthic community establishment and habitat complexity - the importance of seagrass shoot-density, morphology and physical disturbance for faunal recruitment. Marine Ecology Progress Series 205:123-138

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325-349

Brousseau DJ (1978) Population dynamics of the soft-shell clam *Mya arenaria*. Marine Biology 50:63-71

Castel J, Labourg PJ, Escaravage V, Auby I, Garcia ME (1989) Influence of seagrass beds and oyster parks on the abundance and biomass patterns of meio-and macrobenthos in tidal flats. Estuarine, Coastal and Shelf Science 28:71-85

Cebrián J, Duarte CM (1998) Patterns in leaf herbivory on seagrasses. Aquatic Botany 60:67-82

Christie H, Norderhaug KM, Fredriksen S (2009) Macrophytes as habitat for fauna. Marine Ecology Progress Series 396:221-233

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117-143

Clarke KR, Gorley RN (2006) Primer v6: user manual/tutorial. Primer-E, Plymouth

Connolly RM (1997) Differences in composition of small, motile invertebrate assemblages from seagrass and unvegetated habitats in a southern Australian estuary. Hydrobiologia 346:137-148

Costanza R, d'Arge R, De Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P, van den Belt M (1997) The value of the world's ecosystem services and natural capital. Nature 387:253-260

Dennison WC (1987) Effects of light on seagrass photosynthesis, growth and depth distribution. Aquatic Botany 27:15-26

Dennison WC, Orth RJ, Moore KA, Stevenson JC, Carter V, Kollar S, Bergstrom PW, Batiuk RA (1993) Assessing water quality with submersed aquatic vegetation. BioScience 43:86-94

Duarte CM (1991) Seagrass depth limits. Aquatic Botany 40:363-377

Duarte CM, Chiscano CL (1999) Seagrass biomass and production: a reassessment. Aquatic Botany 65:159-174

Duarte CM, Middelburg JJ, Caraco N (2004) Major role of marine vegetation on the oceanic carbon cycle. Biogeosciences Discussions 1:659-679

Edgar GJ, Shaw C, Watson GF, Hammond LS (1994) Comparisons of species richness, size-structure and production of benthos in vegetated and unvegetated habitats in Western Port, Victoria. Journal of Experimental Marine Biology and Ecology 176:201-226

Flach EC (1992) Disturbance of benthic infauna by sediment-reworking activities of the lugworm *Arenicola marina*. Netherlands Journal of Sea Research 30:81-89

Folk RL, Ward WC (1957) Brazos River bar: a study in the significance of grain size parameters. Journal of Sedimentary Research 27:3-26

Fonseca G, Hutchings P, Gallucci F (2011) Meiobenthic communities of seagrass beds (*Zostera capricorni*) and unvegetated sediments along the coast of New South Wales, Australia. Estuarine, Coastal and Shelf Science 91:69-77

Fredriksen S, Christie H, Boström C (2004) Deterioration of eelgrass (*Zostera marina* L.) through destructive grazing by the gastropod *Rissoa membranacea* (J. Adams). Sarsia 89:218-222

Fredriksen S, Christie H, Sæthre BA (2005) Species richness in macroalgae and macrofauna assemblages on *Fucus serratus* L. (Phaeophyceae) and *Zostera marina* L. (Angiospermae) in Skagerrak, Norway. Marine Biology Research 1:2-19

Fredriksen S, De Backer A, Boström C, Christie H (2010) Infauna from *Zostera marina* L. meadows in Norway. Differences in vegetated and unvegetated areas. Marine Biology Research 6:189-200

Gade HG (1968) Horizontal and vertical exchanges and diffusion in the water masses of the Oslo Fjord. Helgoland Marine Research 17:462-475

Gee JM, Warwick RM, Schaanning M, Berge JA, Ambrose Jr WG (1985) Effects of organic enrichment on meiofaunal abundance and community structure in sublittoral soft sediments. Journal of Experimental Marine Biology and Ecology 91:247-262

Gray CA, McElligott DJ, Chick RC (1996) Intra- and inter-estuary differences in assemblages of fishes associated with shallow seagrass and bare sand. Marine and Freshwater Research 47:723-735

Green EP, Short FT (eds) (2003) World atlas of seagrasses. University of California Press, Berkeley, USA

Hauxwell J, Cebrián J, Valiela I (2003) Eelgrass *Zostera marina* loss in temperate estuaries: relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. Marine Ecology Progress Series 247:59-73

Heck Jr KL, Able KW, Fahay MP, Roman CT (1989) Fishes and decapod crustaceans of Cape Cod eelgrass meadows: species composition, seasonal abundance patterns and comparison with unvegetated substrates. Estuaries and Coasts 12:59-65

Heck Jr KL, Hays G, Orth RJ (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. Marine Ecology Progress Series 253:123-136

Heck Jr KL, Orth RJ (1980) Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay—decapod Crustacea. Estuaries and Coasts 3:289-295

Heijs FML (1984) Annual biomass and production of epiphytes in three monospecific seagrass communities of *Thalassia hemprichii* (Ehrenb.) Aschers. Aquatic Botany 20:195-218

Heijs FML (1985) Some structural and functional aspects of the epiphytic component of four seagrass species (Cymodoceoideae) from Papua New Guinea. Aquatic Botany 23:225-247

Hemminga MA, Duarte CM (2000) Seagrass ecology. Cambridge University Press, Cambridge

Herkül K, Kotta J (2009) Effects of eelgrass (*Zostera marina*) canopy removal and sediment addition on sediment characteristics and benthic communities in the Northern Baltic Sea. Marine Ecology 30:74-82

Hull SC (1987) Macroalgal mats and species abundance: a field experiment. Estuarine, Coastal and Shelf Science 25:519-532

Jephson T, Nyström P, Moksnes P-O, Baden SP (2008) Trophic interactions in *Zostera marina* beds along the Swedish coast. Marine Ecology Progress Series 369:63-76

Kennedy H, Beggins J, Duarte CM, Fourqurean JW, Holmer M, Marbà N, Middelburg JJ (2010) Seagrass sediments as a global carbon sink: isotopic constraints. Global Biogeochemical Cycles 24:1-8

Kruskal WH, Wallis WA (1952) Use of ranks in one-criterion variance analysis. Journal of the American statistical Association 47:583-621

Leduc D, Probert PK (2011) Small-scale effect of intertidal seagrass (*Zostera muelleri*) on meiofaunal abundance, biomass, and nematode community structure. Journal of the Marine Biological Association of the United Kingdom 91:579-591

Les DH, Cleland MA, Waycott M (1997) Phylogenetic studies in Alismatidae, II: evolution of marine angiosperms (seagrasses) and hydrophily. Systematic Botany 22:443-463

Levene H (1960) Robust tests for equality of variances. In: Olkin I, Ghurye S, Hoeffding W, Madow W, Mann H (eds) Contributions to probability and statistics: essays in honor of harald hotelling. Stanford University Press, Stanford. p 278-292

Lyngby JE, Brix H (1984) The uptake of heavy metals in eelgrass *Zostera marina* and their effect on growth. Ecological Bulletins 36:81-89

Mare MF (1942) A study of a marine benthic community with special reference to the micro-organisms. Journal of the Marine Biological Association of the United Kingdom 25:517-554

Matisson J, Lindén O (1983) Benthic macrofauna succession under mussels, *Mytilus edulis* L. (Bivalvia), cultured on hanging long-lines. Sarsia 68:97-102

McIntyre AD (1969) Ecology of marine meiobenthos. Biological Reviews 44:245-288
McIntyre AD, Warwick RM (1984) Meiofauna techniques. In: Holme N, McIntyre A (eds) Methods for the study of marine benthos. Blackwell Scientific Publications, Oxford. p 217-244
Milne LJ, Milne MJ (1951) The eelgrass catastrophe. Scientific American 184:52-55
Möller P (1986) Physical factors and biological interactions regulating infauna in shallow boreal areas. Marine Ecology Progress Series 30:33-47
Myers AA (1969) A revision of the amphipod genus *Microdeutopus* Costa (Gammaridea: Aoridae). Bulletin of the British Museum (Natural History) 17:91-148
Myers AA, McGrath D (1984) A revision of the north-east Atlantic species of *Ericthonius* (Crustacea: Amphipoda). Journal of the Marine Biological Association of the United Kingdom 64:379-400
Newell CR, Hidu H, McAlice BJ, Podniesinski G, Short F, Kindblom L (1991) Recruitment and commercial seed procurement of the blue mussel *Mytilus edulis* in Maine. Journal of the World Aquaculture Society 22:134-152
Nielsen SL, Sand-Jensen K, Borum J, Geertz-Hansen O (2002) Depth colonization of eelgrass (*Zostera marina*) and macroalgae as determined by water transparency in Danish coastal waters. Estuaries and Coasts 25:1025-1032
Nienhuis PH, Groenendijk AM (1986) Consumption of eelgrass (*Zostera marina*) by birds and invertebrates: an annual budget. Marine Ecology Progress Series 29:29-35
Nienhuis PH, Van Ierland ET (1978) Consumption of eelgrass, *Zostera marina*, by birds and invertebrates during the growing season in Lake Grevelingen (SW Netherlands). Netherlands Journal of Sea Research 12:180-194
Norkko J, Bonsdorff E, Norkko A (2000) Drifting algal mats as an alternative habitat for benthic invertebrates: Species specific responses to a transient resource. Journal of Experimental Marine Biology and Ecology 248:79-104
Orth RJ (1973) Benthic infauna of eelgrass, *Zostera marina*, beds. Chesapeake Science 14:258-269
Orth RJ, Carruthers TJB, Dennison WC, Duarte CM, Fourqurean JW, Heck Jr KL, Hughes AR, Kendrick GA, Kenworthy WJ, Olyarnik S, Short FT, Waycott M, Williams SL (2006) A global crisis for seagrass ecosystems. BioScience 56:987-996
Orth RJ, Heck Jr KL (1980) Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay—fishes. Estuaries and Coasts 3:278-288
Paasche E, Ostergren I (1980) The annual cycle of plankton diatom growth and silica production in the inner Oslofjord. Limnology and Oceanography 25:481-494
Pedersen O, Borum J, Duarte CM, Fortes MD (1998) Oxygen dynamics in the rhizosphere of *Cymodocea rotundata*. Marine Ecology Progress Series 169:283-288
Philippart CJM (1994) Interactions between *Arenicola marina* and *Zostera noltii* on a tidal flat in the Wadden Sea. Marine Ecology Progress Series 111:251-257
Phillips RC, Menez EG (1988) Seagrasses. Smithsonian Contributions to the Marine Sciences 34:1-104
Pielou EC (1977) Mathematical ecology. Wiley, New York
Pihl L, Baden S, Kautsky N, Rönnbäck P, Söderqvist T, Troell M, Wennhage H (2006) Shift in fish assemblage structure due to loss of seagrass *Zostera marina* habitats in Sweden. Estuarine, Coastal and Shelf Science 67:123-132
Pihl L, Wennhage H (2002) Structure and diversity of fish assemblages on rocky and soft bottom shores on the Swedish west coast. Journal of Fish Biology 61:148-166
Prato E, Biandolino F (2006) *Monocorophium insidiosum* (Crustacea, Amphipoda) as a candidate species in sediment toxicity testing. Bulletin of Environmental Contamination and Toxicology 77:1-8

Raffaelli DG, Mason CF (1981) Pollution monitoring with meiofauna, using the ratio of nematodes to copepods. Marine Pollution Bulletin 12:158-163
Reusch TBH (1998) Differing effects of eelgrass *Zostera marina* on recruitment and growth of associated blue mussels *Mytilus edulis*. Marine Ecology Progress Series 167:149-153
Reusch TBH, Chapman ARO (1995) Storm effects on eelgrass (*Zostera marina* L.) and blue mussel (*Mytilus edulis* L.) beds. Journal of Experimental Marine Biology and Ecology 192:257-271
Roberts DG, McComb AJ, Kuo J (1984) The structure and continuity of the lacunar system of the seagrass *Halophila ovalis* (R. Br.) Hook F. (Hydrocharitaceae). Aquatic Botany 18:377-388
Rosenberg R, Hellman B, Johansson B (1991) Hypoxic tolerance of marine benthic fauna. Marine Ecology Progress Series 79:127-131
Rubal M, Veiga P, Besteiro C (2009) Nematode/copepod index: importance of sedimentary parameters, sampling methodology and baseline values. Thalassas 25:9-18
Sand-Jensen K, Prahl C, Stokholm H (1982) Oxygen release from roots of submerged aquatic macrophytes. Oikos 38:349-354
Sandulli R, De Nicola Giudici M (1989) Effects of organic enrichment on meiofauna: a laboratory study. Marine Pollution Bulletin 20:223-227
Scoffin TP (1970) The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. Journal of Sedimentary Petrology 40:249-273
Shannon CE (1948) A mathematical theory of communications. The Bell System Technical Journal 27:379-423, 623-656
Shapiro SS, Wilk MB (1965) An analysis of variance test for normality (complete samples). Biometrika 52:591-611
Sheridan PF, Livingston RJ (1983) Abundance and seasonality of infauna and epifauna inhabiting a *Halodule wrightii* meadow in Apalachicola Bay, Florida. Estuaries and Coasts 6:407-419
Shiells GM, Anderson KJ (1985) Pollution monitoring using the nematode/copepod ratio: a practical application. Marine Pollution Bulletin 16:62-68
Short FT, Burdick DM, Kaldy III JE (1995) Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. Limnology and Oceanography 40:740-749
Short FT, Wyllie-Echeverria S (1996) Natural and human-induced disturbance of seagrasses. Environmental Conservation 23:17-27
Skadsheim A (1983) The ecology of intertidal amphipods in the Oslofjord. Distribution and responses to physical factors. Crustaceana 44:225-244
Sømme HOO (2012) The effect of marinas on infaunal communities in *Zostera marina* meadows and unvegetated sediments. Master of Science Thesis, University of Oslo, Oslo
Soulsby PG, Lowthion D, Houston M (1982) Effects of macroalgal mats on the ecology of intertidal mudflats. Marine Pollution Bulletin 13:162-166
Spalding M, Taylor M, Ravilious C, Short F, Green E (2003) Global overview: the distribution and status of seagrasses. In: Green EP, Short FT (eds) World Atlas of Seagrasses. University of California Press, Berkeley. p 5-26
Stoner AW (1980) The role of seagrass biomass in the organization of benthic macrofaunal assemblages. Bulletin of Marine Science 30:537-551
Summerson HC, Peterson CH (1984) Role of predation in organizing benthic communities of a temperate-zone seagrass bed. Marine Ecology Progress Series 15:63-77
Tamhane AC (1977) Multiple comparisons in model-I one-way ANOVA with unequal variances. Communications in Statistics - Theory and Methods 6:15-32

Tanner JE (2005) Edge effects on fauna in fragmented seagrass meadows. Austral Ecology 30:210-218

Thiermann F, Niemeyer A-S, Giere O (1996) Variations in the sulfide regime and the distribution of macrofauna in an intertidal flat in the North Sea. Helgoland Marine Research 50:87-104

Tietjen JH (1969) The ecology of shallow water meiofauna in two New England estuaries. Oecologia 2:251-291

Tukey JW (1949) Comparing individual means in the analysis of variance. Biometrics 5:99-114

Valdemarsen T, Wendelboe K, Egelund JT, Kristensen E, Flindt MR (2011) Burial of seeds and seedlings by the lugworm *Arenicola marina* hampers eelgrass (*Zostera marina*) recovery. Journal of Experimental Marine Biology and Ecology 410:45-52

Van Katwijk MM, Hermus DCR, de Jong DJ, Asmus RM, De Jonge VN (2000) Habitat suitability of the Wadden Sea for restoration of *Zostera marina* beds. Helgoland Marine Research 54:117-128

Vincx M (1996) Meiofauna in marine and freshwater sediments. In: Hall GS (ed) Methods for the examination of organismal diversity in soils and sediments. Cabi Publishing, Wallingford. p 187-195

Volkenborn N, Reise K (2007) Effects of *Arenicola marina* on polychaete functional diversity revealed by large-scale experimental lugworm exclusion. Journal of Sea Research 57:78-88

Ward LG, Kemp WM, Boynton WR (1984) The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. Marine Geology 59:85-103

Wennhage H, Pihl L (2002) Fish feeding guilds in shallow rocky and soft bottom areas on the Swedish west coast. Journal of Fish Biology 61:207-228

Appendices

Appendix A – Meiofauna July 2011

Meiofauna – Compiled List of species/taxa recorded in samples taken on the 27th/28th July 2011. Numbers are the number of individuals registered in the different core samples from the different locations and treatments.

	Sandspollen									Sætrepollen						Hallangspollen								
	Control			Cut			Removed			Control			Removed			Control			Cut			Removed		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Phylum Nematoda																								
Nematoda indet	2100	1063	1852	2229	2732	4455	2542	1425	2963	327	1347	1451	1941	1336	1531	2864	4665	2910	2861	2013	3851	3007	2353	3162
Phylum Arthropoda																								
Class INSECTA																								
Chironomidae indet	2	1	0	1	2	6	3	4	0	0	1	3	3	2	1	1	1	1	2	0	1	0	3	1
Class ARACHNIDA																								
Acarina indet	23	14	68	25	85	115	8	10	59	3	63	91	5	18	75	5	9	14	2	21	134	3	14	38
Class OSTRACODA																								
Ostracoda indet	0	2	10	7	23	41	4	1	3	3	0	1	5	11	15	0	1	0	1	1	0	1	0	0
Class MAXILLOPODA																								
Harpacticoida indet	61	20	118	140	203	139	58	85	163	54	190	141	254	275	323	43	65	30	49	52	118	38	47	98
Class MALACOSTRACA																								
Amphipoda indet	0	2	0	4	9	3	5	53	28	0	0	2	0	1	0	1	0	1	2	0	3	0	1	19
Phylum Mollusca																								
Class BIVALVIA																								
Bivalvia indet	0	1	2	4	2	9	1	0	2	0	1	1	1	3	0	5	1	0	1	0	0	1	1	2
Class GASTROPODA																								
Gastropoda indet	0	0	1	0	0	3	0	0	0	0	0	0	1	2	0	0	0	2	2	1	1	0	0	1
Phylum Annelida																								
Class CLITELLATA																								
Oligochaeta indet	0	1	0	0	1	5	0	5	4	0	1	0	0	1	2	4	35	4	6	14	7	3	5	9
Class POLYCHAETA																								
Polychaeta indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Syllidae indet	4	10	3	3	15	16	6	8	20	1	0	0	2	5	8	0	0	1	0	0	0	0	0	0
Maldanidae indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Fabriciola baltica Friedrich, 1939	2	1	3	6	10	51	2	1	12	2	5	17	2	5	14	0	0	0	1	0	0	0	0	0
Arenicola marina Linnaeus, 1758	3	1	3	7	10	35	39	6	3	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0
Capitellidae indet	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	2	1	0	1	0	0	0	0

Appendix B – Macrofauna July 2011

Macrofauna – Compiled List of species/taxa recorded in samples taken on the 27th/28th July 2011. Numbers are the number of individuals registered in the different core samples from the different locations and treatments. Taxa marked with [a] were excluded from the macrofaunal analysis, since they are retained meiofauna and could be reduced through more intense washing in samples marked with [b]

	Sandspollen									Sætrepollen						Hallangspollen								
	Control			Cut			Removed			Control			Removed			Control			Cut			Removed		
	1	2	3[b]	1	2[b]	3[b]	1	2	3[b]	1	2[b]	3[b]	1	2[b]	3[b]	1	2	3[b]	1	2	3[b]	1	2	3[b]
Phylum Arthropoda																								
Class INSECTA																								
Chironomidae spp.	33	19	36	37	16	74	38	11	26	9	2	0	14	47	21	6	13	4	8	12	11	25	20	27
Class OSTRACODA																								
Heterocythereis albomaculata Baird, 1838	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Class MALACOSTRACA																								
Order Isopoda																								
Idotea chelipes Pallas, 1766	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Order Amphipoda																								
Monocorophium insidiosum Crawford, 1937	56	2	30	20	21	33	50	39	62	1	0	0	1	0	0	3	0	0	0	1	0	9	7	0
Aoridae indet	5	5	9	7	2	7	2	11	15	0	0	0	0	0	0	4	1	0	0	0	1	5	11	0
Microdeutopus gryllotalpa Costa, 1853	0	0	0	0	0	0	1	2	3	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0
Ericthonius sp.	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	4	0
Ericthonius rubricornis Stimpson, 1853	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Phylum Mollusca																								
Class BIVALVIA																								
Mytilus sp.	36	11	19	8	10	25	1	47	3	0	0	0	2	0	0	1066	63	184	23	62	8	381	187	109
Mya arenaria Linnaeus, 1758	3	3	2	3	5	10	9	9	9	0	0	0	6	3	4	2	0	0	1	0	0	2	1	2
Macoma balthica Linnaeus, 1758	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1
Parvicardium exiguum Gmelin, 1791	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	1	0
Class GASTROPODA																								
Nassarius nitidus Jeffreys, 1867	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Peringia ulvae Pennant, 1777	1	0	9	2	17	0	29	2	18	2	0	1	19	31	42	1	1	7	2	1	16	86	13	44
Rissoa membranacea J. Adams, 1800	3	1	5	1	2	5	0	0	0	0	0	2	0	0	1	0	0	1	0	1	10	1	0	2
Pusillina sarsii Lovén, 1846	0	6	1	0	1	8	2	10	2	0	0	0	0	0	0	4	0	0	0	8	7	0	4	17
Retusa truncatula Bruguière, 1792	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Bittium reticulatum da Costa, 1778	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Littorina littorea Linnaeus, 1758	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Phylum Annelida																								
Class CLITELLATA																								
Tubificoides benedii Udekem, 1855	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	12	11	8	18	18	2	14	4	2
Tubificoides pseudogaster Dahl, 1960	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	10	6	1	18	5	0	11	9	2
Class POLYCHAETA																								
Harmothoe spp.	3	0	2	1	1	0	0	4	1	0	0	0	0	0	0	2	1	0	0	0	0	0	1	0
Fabriciola baltica Friedrich, 1939	5	1	0	5	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nereididae indet	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scoloplos (Scoloplos) armiger Müller, 1776	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1	11	0	1	2	0	0	0
Arenicola marina Linnaeus, 1758	9	1	0	7	0	1	1	0	0	0	0	0	0	0	0	4	0	0	0	0	0	3	6	0
Capitella capitata Fabricius, 1780	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	6	5	0	7	6	1
Capitella minima Langerhans, 1881	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Capitellidae indet	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	3	1	0	1	0	3
Eteone longa Fabricius, 1780	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	5	2	0	1	1	0	1	0
Hediste diversicolor Müller, 1776	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Nereimyra punctata Müller, 1788	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
[a]Acarina indet	1	3	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
[a]Harpacticoida indet	1	1	0	3	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
[a]Nematoda indet	208	131	24	241	41	56	100	116	16	37	0	1	26	8	3	185	402	38	208	275	9	193	189	5

Appendix C – Macrofauna October 2010

Macrofauna – Compiled List of species/taxa recorded in samples taken on the 5th October 2010. Numbers are the number of individuals registered in the different core samples from the different locations.

	Sandspollen						Sætrepollen						Hallangspollen					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Phylum Arthropoda																		
Class INSECTA																		
Chironomidae indet	2	2	0	0	10	9	5	9	3	2	2	0	20	7	22	12	10	0
Class MALACOSTRACA																		
Order Amphipoda																		
Monocorophium insidiosum Crawford, 1937	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Aoridae indet	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0
Ericthonius sp.	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Ericthonius rubricornis Stimpson, 1853	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinogammarus stoerensis Reid, 1938	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Phylum Mollusca																		
Class BIVALVIA																		
Mytilus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	4	4	0	5	0
Phylum Annelida																		
Class CLITELLATA																		
Tubificoides benedii Udekem, 1855	0	0	0	0	0	0	0	3	0	0	0	0	2	16	5	11	8	0
Tubificoides pseudogaster Dahl, 1960	0	0	0	0	0	0	0	0	0	0	0	0	2	41	28	3	8	0
Class POLYCHAETA																		
Fabriciola baltica Friedrich, 1939	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Eteone longa Fabricius, 1780	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Platynereis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Appendix D – Grain size

Results of the grain size analysis. Numbers for the different size fractions are given in gram dry weight for a) samples from macrofauna cores stored in a freezer and b) samples from meiofauna cores stored in ethanol

a) Macrofauna core

	Sandspollen			Sætrepollen		Hallangspollen		
	control	cut	removed	control	removed	control	cut	removed
>2000µm	1.41	0.87	1.38	2.28	5.94	-	-	-
>1000µm	4.36	6.13	7.23	2.74	2.17	-	-	-
>500µm	8.53	9.17	12.28	6.63	4.42	-	-	-
>250µm	14.32	9.48	11.02	15.75	15.46	-	-	-
>125µm	8.62	5.32	7.66	18.11	13.91	-	-	-
>63µm	6.28	2.36	4.28	11.34	11.44	-	-	-
<63µm	6.70	3.22	4.58	20.63	33.44	-	-	-

b) Meiofauna core

	Sandspollen			Sætrepollen		Hallangspollen		
	control	cut	removed	control	removed	control	cut	removed
>2000µm	0.60	0.22	0.41	0.28	1.46	1.18	1.53	2.76
>1000µm	0.28	0.13	0.30	0.26	0.57	0.83	0.89	0.88
>500µm	1.31	0.60	1.24	1.79	1.87	1.20	1.46	2.21
>250µm	3.86	5.97	7.56	5.49	9.53	4.91	18.75	21.77
>125µm	4.83	3.15	5.08	7.54	7.27	20.66	10.28	7.76
>63µm	3.62	1.99	2.76	5.48	4.03	14.32	12.20	16.08

Appendix E – Macrofauna May 2010 (Sømme 2012)

Macrofauna – Compiled List of species/taxa recorded by Sømme (2012) in samples from 2012. Numbers are the number of individuals registered in the different core samples from the different locations.

	Sandspollen					Sætrepollen				
	1	2	3	4	5	1	2	3	4	5
Phylum Arthropoda										
Class INSECTA										
Chironomidae indet	12	13	21	11	16	7	22	24	15	31
Class MALACOSTRACA										
Order Amphipoda										
Aoridae indet	0	0	1	0	0	0	0	0	0	0
Microdeutopus gryllotalpa Costa, 1853	0	0	0	0	0	0	1	0	0	0
Phylum Mollusca										
Class BIVALVIA										
Macoma sp.	1	0	0	0	0	0	0	0	0	0
Class GASTROPODA										
Nassarius reticulatus Linnaeus, 1758	0	0	0	1	0	0	0	0	1	0
Rissoa membranacea J. Adams, 1800	1	0	0	0	0	0	0	0	0	0
Rissoa parva da Costa, 1778	0	0	2	0	1	0	0	0	0	0
Phylum Annelida										
Class CLITELLATA										
Tubificoides benedii Udekem, 1855	0	0	1	0	0	0	19	9	13	7
Tubificoides pseudogaster Dahl, 1960	0	0	0	0	0	0	0	1	1	0
Oligochaeta indet	0	0	0	0	0	0	0	0	1	0
Class POLYCHAETA										
Harmothoe sp.	0	0	0	0	0	0	0	0	0	1
Arenicola marina Linnaeus, 1758	0	1	0	0	0	0	0	0	0	1
Eteone longa Fabricius, 1780	0	0	0	0	0	0	0	0	1	0

Appendix F – Identification literature

Bondesen P (1975) Danske havsnegle, Vol 1. Naturhistorisk Museum, Århus

Bousfield EL, Hoover PM (1997) The amphipod superfamily Corophioidea on the Pacific coast of North America. Part V. Family Corophiidae: Corophiinae, new subfamily. Systematics and distributional ecology. Amphipacifica: Journal of Systematic Biology 2:67-139

Brinkhurst RO (1982) British and other marine and estuarine oligochaetes: keys and notes for the identification of species, Vol 21. Published for the Linnean Society of London and the Estuarine and Brackish-Water Sciences Association by Academic Press, London

Crawford GI (1937) A review of the amphipod genus *Corophium*, with notes on the British species. Journal of the Marine Biological Association of the United Kingdom (New Series) 21:589-630

de Kluijver MJ, Ingalsuo SS. Macrobenthos of the North Sea - Crustacea. Accessed 2012. http://species-identification.org/species.php?species_group=Crustacea&menuentry=inleiding

de Kluijver MJ, Ingalsuo SS, de Bruyne RH. Mollusca of the North Sea. Accessed 2012. http://species-identification.org/species.php?species_group=Mollusca&menuentry=inleiding

de Kluijver MJ, Ingalsuo SS, van Nieuwenhuijzen AJL, Veldhuijzen van Zanten HH. Macrobenthos of the North Sea - Polychaeta. Accessed 2012. http://species-identification.org/species.php?species_group=Macrobenthos_polychaeta&menuentry=inleiding

Hayward PJ, Ryland JS (1995) Handbook of the marine fauna of North-West Europe. Oxford University Press, Oxford

Kirkegaard JB (1992) Havbørsteorme, 1, Errantia, Vol 83. G.E.C. Gads Forlag, København

Kirkegaard JB (1996) Havbørsteorme, 2, Sedentaria, Vol 86. G.E.C. Gads Forlag, København

Myers AA (1969) A revision of the amphipod genus *Microdeutopus* Costa (Gammaridea: Aoridae). Bulletin of the British Museum (Natural History) 17:91-148

Myers AA, McGrath D (1984) A revision of the north-east Atlantic species of *Ericthonius* (Crustacea: Amphipoda). Journal of the Marine Biological Association of the United Kingdom 64:379-400

Pleijel F (1993) Polychaeta Phyllodocidae. Scandinavian University Press, Oslo

Ponder WF (1984) A review of the genera of the Rissoidae (Mollusca: Mesogastropoda: Rissoacea). Records of the Australian Museum Supplement 4:1-221

Sneli J-A (1975) Mollusca prosobranchia: forgjellesnegler: nordiske marine arter. Universitetsforlaget, Trondheim

Tebble N (1976) British bivalve seashells: a handbook for identification. Royal Scottish Museum, Edinburgh

Warén A (1996) Ecology and systematics of the north European species of *Rissoa* and *Pusillina* (Prosobranchia: Rissoidae). Journal of the Marine Biological Association of the United Kingdom 76:1013-1059