

The macrozoobenthos in the subtidal of the western Dutch Wadden Sea in 2008 and a comparision with 1981-1982

Rob Dekker & Jan Drent

NIOZ Royal Netherlands Institute for Sea Research

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Contact information authors:

Royal Netherlands Institute for Sea Research

PO Box 59

1790 AB Den Burg, Texel

The Netherlands

Email: Rob.Dekker@nioz.nl

Jan.Drent@nioz.nl

Pictures on front and back cover are from Bert Brinkman.

Background, surface of a box core sample with mussel (*Mytilus edulis*) clump and associated fauna.

Pictures on back cover clockwise starting left. Box corer device. Core with *Asterias rubens* and empty shells of *Mytilus edulis. Enis directus* protruding from core sediment surface. Core surface with *Mytllus edulis* covered with *Balanus sp*., also empty shells of *Cerastoderma edule*, *Ensis directus* and *Mya arenaria* are visible*. Echinocardium cordatum* from a core washed over 1mm Ø mesh.

Contents

1 Abstract

A large part of the western Dutch Wadden Sea remains submerged during the entire tidal cycle or in other words is subtidal. Under the EU habitat directive 92/94/EEC the subtidal western Dutch Wadden Sea belongs to habitat type 1110_A, sandbanks which are slightly covered by sea water all the time. For conservation of this habitat type a first prerequisite is a good description of the natural values of the area. An important component in the subtidal ecosystem is the benthic invertebrate fauna. They are the largest herbivore link in the systems food web and in turn are an mojar food source for bird fish and other invertebrate species.

Mussels are an important species in the subtidal habitat. They can form dense mussel beds on the sediment surface. These are areas of high secondary production, but also sites where hard substrate species are able to find an attachment surface and other species may find a refuge within the matrix of the mussel bed. These biogenic structures or reefs can have marked higher species richness than the surrounding soft sediments. Recently a new biogenic reef creator has appeared in the western Dutch Wadden Sea, the pacific oyster, which may create additional hard substrate patches.

The subtidal of the western Dutch Wadden Sea has not been studied extensively, the last large survey dates from 1981-1982. Three transects have been monitored since 1989 and show strong trends in species composition suggesting that major changes have taken place in the area. In 2008 a new survey was carried out to update the information about the macrozoobenthos in the western Dutch Wadden Sea on a system wide scale. Based on the survey of 2008 we give a description of the macrozoobenthos in the subtidal western Dutch Wadden Sea with special emphasis on species richness and the role of the mussel. We also compare 2008 with 1981/82

In the survey covering 397 box core stations of 0.06 m^2 100 macrozoobenthos species were encountered during the survey of 2008. Compared too intertidal monitoring programs in the Dutch Wadden Sea that sampled larger areas the species richness was higher in subtidal than in the intertidal.

At the scale of a single box core species richness was strongly elevated at sites with mussels. A box core containing mussels had on average a species that was richness twice as high as boxes without mussel, 16 versus 8, count including mussels. This elevated number of species was caused by an increase in hard substrate and soft sediment species. The increase in soft sediment species was unexpected because literature suggested negative effects of mussel beds on the infauna. This may still be true but positive effects on species richness dominate.

Spatially mussel beds have distinct elevated species richness. There is a slight increase in species richness with decreasing distance towards mussel beds. This however only explained an increase in richness of less than two species instead of the seven observed without counting the mussels.

Sites with oysters are also more species rich than the surrounding bare sediments, but there is considerable overlap in the distribution of mussels and oysters. Species richness is higher and composition is different at stations with mussels and /or oysters.

Besides the species that are able to create biogenic structures also environmental gradients affect the species composition and richness. An important variable is salinity that could explain 7 % of the dissimilarity among the survey stations. The presence of mussels and or oysters could explain 2%.

Sites with mussels (and osyters) are twice as species rich as sites without mussel (and oysters), the difference is 8 versus 16 species in a box of 0.06 m2 including mussels (and oysters) in the species count.

There were 32 hard substrate species besides mussels and oysters. Of these species 11 were restricted to sites with mussels and or oysters (seven to sites with mussels). There were four hard substrate species that were only found outside sites with mussels and or oysters. Besides these four species there were seven more that were found more often outside mussel and/or oyster sites (33 stations). The majority of hard substrate species is not restricted to mussel and/or oyster sites.

Compared to 1981/82 the macrozoobenthos community composition was very different in 2008. Most striking was the change in contribution of invasive species to the total biomass. This was 2% in 1981/82 and 80 % in 2008. Mussels were the dominant species in terms of biomass in 1981/82. In 2008 the invasive bivalves *Mya arenaria* and *Ensis directus* contributed most to the total biomass. Also notable were the strong declines of the deposit feeders *Macoma balthica, Peringia ulvae* and *Heteromastus filiformis* and the very large contribution of the recent invasive deposit feeder *Marenzelleria viridis*. Despite the large changes in the species composition there was very little change in the distribution of biomass among the feeding groups, suspension feeders, deposit feeders, omnivores and carnivores. Also taxonomically the distribution of biomass among the Phyla represented by the macrozoobenthos remained remarkably stable.

The large changes in the macrozoobenthos of the subtidal are part of long term trends that were also observed in the monitoring series at three transects in the subtidal of the Western Dutch Wadden Sea.

2 INTRODUCTION

The Wadden Sea is the largest unbroken system of intertidal sand and mud flats in the world, where natural processes continue to function largely undisturbed (Reise et al. 2010). It is a biological highly productive coastal ecosystem behind barrier islands fringing a large part of the south eastern North Sea. Local primary production and import of organic material from the North Sea support large amounts of herbivorous benthic invertebrates, which in turn are an important food source for fish and migratory shorebirds. The area is appointed as a valuable area under the Ramsar Conventions, and also by EU as falling under Natura 2000 habitat- and bird directives. Since 2009 the German and Dutch Wadden Sea are listed as a UNESCO world heritage site.

A dominant feature of the Wadden Sea system are the tidal flats. In addition extensive areas remain continuously submerged. Such submerged or subtidal areas are especially important in the western Dutch Wadden Sea where the subtidal as a fraction of the total area is about 0.6, much larger than 0.4 in the eastern Dutch Wadden Sea (Elias et al. 2012). The subtidal of the Wadden Sea is not well studied compared to the intertidal areas (Wolff et al. 2010).

Available information suggest a rich benthic community and an important diversity enhancing role of biogenic structures, like oyster reefs and mussel beds, in the subtidal of the Wadden Sea. Historical accounts of the subtidal in the northern German Wadden Sea (Möbius 1877 & 1893, Hagmeier and Kändler 1927) describe a diverse epibenthos. This epibenthos was mainly associated with dense beds of subtidal eelgrass (*Zostera marina*) and mussels and reefs of oysters (*Ostrea edulis)* and *Sabellaria spinulosa* – a colonial and tube-building polychaete. These earliest investigations were repeated towards the end of the twentieth century by Buhs and Reise (1997) who found decreased epibenthic species richness and no sublitoral eelgrass beds, oyster- and *Sabellaria* reefs any more. A similar account can be made for biogenic structures in the western Dutch Wadden Sea. In the beginning of the twentieth century here also extensive eelgrass fields (Hartog and Polderman 1975) and mussel beds (Hoek 1911) were found. In that time also oysters occurred in the area but not as dense reefs (Hoek 1911). There is no evidence for *Sabellaria* reefs in the western Dutch Wadden Sea. More recent in a benthic survey of the subtidal western Dutch Wadden Sea during 1981 and 1982 (Dekker 1989), mussels were the only species left that create epibenthic biogenic structures. Compared to the intertidal in the western Dutch Wadden Sea the species richness of the macrozoobenthos in the subtidal was twice as high (Dekker 1989).
Mussels (*Mytilus edulis*) form beds on soft sediment surface. These beds are an important component in shallow marine ecosystems like the Wadden Sea. As mentioned above these beds are biogenic structures on the sediment surface offering hard substrate and refuge within the mussel matrix for species that are not able to live in the surrounding soft sediment habitat. In mussel beds species are different and diversity can be markedly higher than in the surrounding bare sediments (Dittmann 1990, Saier et al. 2002, Bushbaum et al. 2009, Norling & Kautsky 2008). Mussel beds also influence current velocities which results in increased sedimentation of fine sediment in the mussel bed (Ragnarsson & Raffaelli 1999, Kochmann et al. 2008). This increased deposition is further enhanced by the deposition of pseudo faeces and faeces by the mussels. Within a food web context mussel beds are sites of high secondary production fuelled by phytoplankton transported over the beds by tidal currents and filtered from the water column by the mussels (Asmus 1987). Mussels are an important food source for avian predators like oystercatchers (*Haematopus ostralegus*) herring

gulls (*Larus argentatus*) and eider ducks (*Somateria mollisima*). This last species and also *Goldeneys* (Bucephala clangulas) and greater scaups (*Aythya marila*) are diving ducks that feed on subtidal mussel beds in the western Dutch Wadden Sea (Ens et al. 2007).
In the western Dutch Wadden Sea mussels (Mytilus edulis) are cultured on designated culture plots (Fig. 1). These plots are normally stocked with young mussels less than 1 year old. These mussels are dredged from natural mussel spat beds in subtidal areas in the western Dutch Wadden Sea. In recent years seed mussels are also collected from mussel seed collectors. In essence mussel seed collectors are settlement surfaces suspended in the water column where mussel larvae will attach and develop into the sessile adult stage. These mussels can then be harvested and used to stock culture plots. Point of concern and reason for this study is whether mussel seed fisheries and mussel culture are affecting the natural values of the subtidal western Dutch Wadden Sea.
Under the EU habitat directive 92/94/EEC the subtidal western Dutch Wadden Sea belongs to habitat type 1110_A, sandbanks which are slightly covered by sea water all the time. In the Netherlands habitat type 1110 is categorized in two sub habitats distinguishing between tidal areas (subtype A) and the sand banks in the North Sea (sub type B). The Netherlands includes reefs which is habitat type 1170, within habitat type 1110 (Anonymous 2008). In the present-day subtidal western Dutch Wadden Sea the only reefs are biogenic structures of mussels (*Mytilus edulis*) and the invasive Pacific oyster (*Crassostrea gigas*).

The natural values of habitat type 1110-A are not well defined and are discussed in Ens et al. (2007), Herman et al. (2008) and Jak (2008). Besides that the recent status of the subtidal area is not known as the most recent survey was done in 1981/82 (Dekker 1989). To help solve these problems a new survey of the macrozoobenthos in the subtidal western Dutch Wadden Sea was done in the autumn of 2008. Based on this new survey a description is made of the abundance, biomass and species richness of the macrozoobenthos. Distributions of mussels and other species are mapped and related to environmental variables like salinity and depth. Specific questions are if the macrozoobenthos inside mussel culture plots differs from outside and how sites with mussels differ from sites without. In addition to this, results are compared with those from the 1981/82 survey.

3 METHODS

3.1 Description of the area

The area investigated comprises the subtidal part of the western Dutch Wadden Sea, westwards of the tidal watershed of the island of Terschelling, but excluding the relatively small part of this area nourished by the tidal inlet between the islands of Texel and Vlieland, i.e. Eyerlandse Gat (Fig. 1). The mean tidal range varies from around 1.4 m near Den Helder in the westernmost part, up to about 1.9 m near Terschelling. The area investigated falls apart in two tidal basins: the Marsdiep tidal basin, with a connection with the adjoining North Sea between the Dutch mainland and the island of Texel (Marsdiep), and the Vlie tidal basin with a connection with the North Sea between the islands of Vlieland and Terschelling. Both tidal basins are separated from the Eyerlandse gat tidal basin by relatively high tidal watersheds (Zimmerman, 1976), whereas the separation of Marsdiep and Vlie tidal basins is less clear, more diffuse and does not consist of high tidal flats. The Eierlandse Gat tidal inlet was excluded from the survey due to its relatively inaccessibility and the limited subtidal area.

The total surface of the western Dutch Wadden Sea west of the Terschelling watershed is $1.5*10^3$ km^2. The surface areas of the tidal basins Marsdiep and Vlie are about equal, both are $6.9*10^2$ km^2. The Eierlandse Gat is only $1.7*10^2$ km^2. The subtidal is the area where the seafloor is below lowest astronomical tide (LAT). The fraction of the area that is subtidal is 0.69 in the Marsdiep, 0.38 in the Vlie and only 0.21 in the Eierlandse Gat basin.

The seafloor in the subtidal parts of the western Dutch Wadden Sea mainly consists of sandy and silty sediments. The more seaward parts of the area generally have coarser sediments than the more inner parts, as a result of increasing current velocities towards the tidal inlets. Locally, the seafloor partly consists of eroded glacial deposits, characterized by the presence of gravel and stones on top of or in the sediment.

The salinity in the western Dutch Wadden Sea shows a decreasing gradient from the tidal inlets to the sluices in the Afsluitdijk discharging fresh water from IJsselmeer into the Wadden Sea, the residence time of the seawater within the area increases from the tidal inlet towards the innermost parts of the Wadden Sea (Zimmerman, 1976). The salinity in the Marsdiep tidal basin is lower than that in the Vlie basin, as the sluices in the Afsluitdijk discharge into the Marsdiep basin, and the seawater entering the Wadden Sea through the Marsdiep tidal inlet has a lower salinity because of fresh water originating from the river Rhine, than the seawater entering the Wadden Sea through the Vlie tidal inlet during flood (Zimmerman & Rommets, 1974). Additionally, due to a higher tidal amplitude in the Vlie tidal basin than in the Marsdiep tidal basin, and morphological differences between the two basins, a mean residual current exists from Vlie inlet towards the Marsdiep inlet (Ridderinkhof, 1988).

3.2 Selection of sampling points

During the survey carried out in 1981-1982 (Dekker, 1989) 459 stations have been sampled, most of them were arranged in transects transverse to depth gradients. The focus of the research in 1981-1982 was in the depth range between MLTL and MTL-5 m, with additional sampling points in deeper gullies. The 2008 survey was primarily meant as a resampling of the points of the 1981-1982 survey.

Additional interest in the associated fauna of the *Mytilus edulis* concentrations, both occurring naturally and in commercial culture plots, without extra funding to increase total sample number, led to the discard of 60 of the original sampling stations and a creation of 60 *Mytilus*-association dedicated stations (reported on in Drent and Dekker 2013). The choice which sampling points of the original 459 would be discarded was bases on the following criteria: 1- a 1981-1982 survey sampling point was changed from a subtidal into an intertidal point in 2008 (26 stations); 2- samples from points in 1981-1982 contained no macrozoobenthos at all (4 stations); 3- the remaining 30 stations to discard were selected based on their mutual distance. Of the 30 pairs of stations with the least mutual distance during the 1981-1982 survey 1 station of each pair was discarded in such a way, that the minimum distance between the remaining stations was largest. In the end, of the original 459 station, 397 stations were left for the present analysis and a comparison with previous data (Fig. 1, Appendix 1)

3.3 Sampling procedure

All stations were sampled in the period 6-24 October 2008. The autumn period was selected to maximize the comparability with the results of the survey in 1981-1982. During this earlier survey the majority of the samples (63%) was taken in the period September-December 1981, and 172 samples (37.5% of the total) in October 1981.

Sampling was carried out with the RV Navicula, a shallow draught (1.2 m) ship designed for work in the shallows of the Wadden Sea. Samples were taken with a 0.06 m^2 Reineck box corer, using NIOZ standard procedures for taking macrozoobenthos samples in the subtidal of the Wadden Sea. In short: sampling locations were found using GPS. Date, time, position and actual water depth were recorded. After taking the sample with the box corer, the water in the box on top of the sediment was siphoned away, and the sediment depth in the box was measured. Each sample should have at least penetrated to a depth of 15 cm. If after 3 repeated trials this depth was not achieved, the deepest of the 3 samples was selected as the best sample for the sampling point. In those cases where many visible small organisms (*Peringia ulvae*, juveniles of bivalve molluscs) were present at the sediment surface in the box core-sample, a subsample with a small corer, Ø 4.25 cm, was taken to a depth of 4 cm. All macrozoobenthos-samples were sieved on board over a Ø 1-mm round-hole sieve using running seawater, stored in jars with 6% buffered formaldehyde and stained with Rose Bengal.

From each station one sediment sample Ø 1.3 cm was taken from the box core to a depth of 8 cm. Sediment samples were stored in a freezer at -20 °C until laboratory processing.

3.4 Laboratory procedures

3.4.1 Macrozoobenthos

In the laboratory the preserved samples were rinsed during at least 15 minutes in a fume hood over a 500 µm mesh using tap water, to wash out the formaldehyde. After rinsing the samples were spread in white trays and all stained material was sorted out with the naked eye. The sorted material was stored in 4% formaldehyde until identification. All organisms were identified up to species level, except Nemerteans and Oligocheates, which were not further identified than to the phylum level and the acorn barnacles *Balanus crenatus* and *Amphibalanus improvisus*, which were not separated but are treated as *Balanus* spec. Additionally, bivalves were identified up to year class level. Of bivalves, crabs and shrimps maximum length (bivalves, shrimps) or carapace width (crabs) was measured. Of all organisms ash free dry mass (AFDM) was determined. For this purpose all animals were put in porcelain crucibles per species. Of bivalves only the soft parts were treated additionally per year class and length class. Their shells were dried and kept in store. The crucibles with their contents were dried in a ventilated stove for 3 days at 60 °C. After that period they were weighed on an analytical balance to the nearest 0.1 mg and subsequently ashed in an oven for 3 hours at a temperature of 560°C. After cooling to ambient temperature the crucibles were weighed again. The difference between both weights per crucible (ash free dry mass, AFDM) was used as a measure for biomass. Biomass was not determined for the hard substrate species *Alcyonidioides mytili*, *Clytia hemisphaerica*, *Conopeum reticulum*, *Electra pilosa*, *Hartlaubella gelatinosa*, *Obelia longissima* and *Smittoidea prolifica*.

3.4.2 Sediments

Grain size distribution of the sediments was determined from the mineral fraction of the sediment <2000μm. In the laboratory the samples were freeze dried, treated with HCL to remove shell particles and with H2O2 to remove particulate refractory organic matter (peat fragments etc.). The mineral fraction, after ultrasonic treatment, was analysed in a Coulter LS 230 particle counter. Procedures are described in Compton et al (2012). For the analyses the sediment parameters silt content, i.e. the mineral fraction of the total sediment fraction < 16 μm, and the median grain size of the sediment fraction < 2000μm, are used.

3.4.3 Other environmental parameters.

Depth in meters below NAP at each station was extracted from a GIS raster data set compiled from depth soundings made in the area in the period between 2003 and 2008 under responsibility of Rijkswaterstaat. Salinity information at the stations was approximated by averaging values extracted from two raster files describing salinity during a wet period in 1988 with high fresh water discharges and in a dry period in 1992 with very little fresh water inflow. These maps were made with a 2D water movement model for the coastal zone (Kuststrookmodel). For details and further references see Jager & Bartels (2002). Maximum current speed information was extracted from a raster data set accompanying Zwarts (2004).

3.5 Analyses

Although present in one or more samples, mysids (i.e. Mesopodopsis slabberi, Neomysis integer and Praunus flexuosus), belonging to the hyperbenthos instead of the macrobenthos (Mauchline, 1980), are omitted from the analyses. For most analyses of the macrozoobenthos and the relations with abiotic parameters, unless otherwise stated, numbers and biomass values per taxon or age-class we transformed to values per m². Analyses were carried out using R version 2.15.0 (2012-03-30). We used linear models with log transformed data to test for effects on numerical densities and biomass. In case of zeros 1 was added to the density data and minimum biomass value (0.002 gm^{-2}) to the biomass data. GLM (family='quasipoisson') models were used for tests on species richness data. Package beanplot was used to draw the beanplots (Kampstra, 2008). A bean consists of a one-dimensional scatter plot (white horizontal lines, which becomes longer with overlapping values), its distribution as a density shape and an average line (solid black line) for the distribution. Next to that, an overall average for the whole plot is drawn (stippled line over the entire width of the graph). Package Vega version 2.0-3 (Oksanen et al., 2012) was used for NMDS plots and the PERMANOVA analysis on similarity matrices.

3.6 Comparison surveys 1981/1982 and 2008 methodological differences

The survey of the subtidal macrozoobenthos in 1981/1982 was carried out, due to logistical and technical limitations on the research vessel, a Reineck box corer could not be used. Therefore, two alternative sampling gears were used: a modified Van Arkel flushing sampler (sampling surface 0.02 $m^{2,}$ 3 samples per station pooled together), and a 0.06 m^2 Van Veen grab. The flushing sampler could only be used on shallow stations, with a depth down to 5 m under low tide level. In sandy to silty sediments, it was able to penetrate to depths down to 40 cm (Dekker, 1989). A major disadvantage of this sampler was that it could insufficiently penetrate into sediments containing large dead shells, peat and tough clay layers, and mussel beds. The Van Veen grab could cover all sampling depths, but could only sample the top 8-10 cm of the sediment. Deep-living organisms were missed or only fragmentarily sampled by this gear. At each station, both sampling gears were used if possible was used. From the Van Veen grab at each station a sediment sample was taken. The samples collected with the flushing sampler were preserved in 10 % formalin, the Van Veen grab samples were deep frozen. At deeper stations, and stations were the flushing sampler did not obtain a proper sample, only the Van Veen grab sample was collected and preserved in formalin. This means, that at the stations only Van Veen grab samples were available, potentially an underestimate of the total macrozoobenthos was obtained, by missing the deeper living components.

During the 1981/1982 programme, the focus of the research was on molluscs and soft-sediment infauna, comparable to the faunal elements encountered and identified in the intertidal benthic sampling programma at Balgzand (Beukema *et al*., 1983). This means, that most sessile hard-substrate species (e.g. coelenterates, bryozoans, barnacles) were omitted or poorly quantified. For the comparison between both surveys these sessile hard-substrate species were excluded, as well as were the mysids.

4 RESULTS

4.1 Survey 2008

4.1.1 Environmental parameters

The locations of the sampling stations are shown in Fig. 1. The depth distribution of the stations along the depth gradient of the 397 stations sampled in 2008 was somewhat biased towards the shallower parts of the subtidal area (Fig. 2). This means, that the areas shallower than -5 m were overrepresented in the survey, whereas the deeper areas are underrepresented. The depth distribution of all mussel culture plots in relation to the total depth distribution of the research area showed roughly the same bias with the majority of beds between 0 and -5 NAP.

On average the sediment median grain size at the 397 stations was 206 µm. Minimum value was 17 and maximum 648 µm. At more than 95% of the stations the median grain size was between 75 and 375 µm. Sediment was fine outside the deep tidal gullies in the southern part of the Vlie tidal basin near the border with the Marsdiep basin (Fig. 3). The finest sediments were found near the Afsluitdijk. Sediments were coarsest along the main tidal channels in the Marsdiep basin. Stones of glacial origin were found in the western part of the Marsdiep tidal basin. Near the harbour of Harlingen in the Vlie basin several boxes contained bricks.

Modelled average salinity (Fig. 4)shows a clear gradient with saline water in the north west towards brakish water along the Afsluitdijk and Frisian coast on the south eastern side of the western Dutch Wadden Sea. Lowest modelled salinities are found near the sluices at Den Oever at the south western end of the Afsluitdijk.

Besides depth, median grain size and salinity also modelled maximum tidal current speeds are available at the stations. An overview is given in Fig. 5 with histograms and correlations among the environmental variables. The strongest correlation (r=0.66) is positive between log(depth) and maximum current speed, followed by the positive correlation between current speed and median grain size (r=0.38). Depth was log transformed because the skewed distribution and also because an expected nonlinear diminishing effect of wave action with increasing depth.

4.1.2.Macrozoobenthos

Species richness total density and total biomass

Two of the 397 station sampled contained no macrozoobenthos species. The total numerical density of the macrozoobenthos varied between 0 and $1.5*10^5$ individuals m^{-2} (Table 1). The distribution of densities was skewed towards 0 with a median of $7.2*10^2$ that strongly deviated from the average density of $2.6*10^3$ nm^{-2}. The geometric mean was $7.3*10^2$ nm^{-2}, very similar to the median.

Average total ash free dry mass of the macrozoobenthos of the subtidal western Dutch Wadden Sea was 55 gm^{-2} (Table 1). Like the total density the distribution of biomass was skewed towards 0 with a median biomass of only 6.7 gm^{-2} considerably lower than the arithmetic mean. The geometric mean was 6.5 gm^{-2}.

In the overall sample from the subtidal western Dutch Wadden Sea (total sampled surface 23.8 m2) 100 macrozoobenthos species/taxonomic units were found. Per station of 0.06 m^2 the number of species ranged between 0 and 34 species, the median was 8 and the mean 8.6 species (Table 1).

Community composition

The 100 species encountered during the 2008 survey are listed in Table 2 and appendix 2. Of these 16 species were invasive. Taxonomically Annelida were the largest phylum (Fig. 6) with 44 polychaete species and one taxonomic unit Oligochaetes. The second largest group are molluscs (20 species) which include bivalves and gastropods. The third phylum is the Athropods with 18 species, these all crustaceans. The remaining species are Cnidarians (5 species), Bryozoans (4 species), Echinoderms (4 species), Chordates (3 species) and one taxonomic unit of Nemertea. Occurrence of the phyla is proportional to number of species per phylum (Fig. 6). Molluscs contribute by far most to the total biomass of the macrozoobenthos, 85 % of the biomass is from this phylum (Fig. 6). Annelida were most abundant in the samples followed by Molluscs. The other phyla were relative to the number of species less abundant (Fig. 6).

Functionally the species were categorized according to substrate and feeding type. Substrate types were soft sediment, heterogeneous sediments and hard substrate. Hard substrate species were sub divided in mobile and sessile species. The largest group of species was of the soft sediment species, followed by the two hard substrate species groups (Fig. 7). Mobile and sessile hard substrate species groups were of about equal size. The smallest group of species were the species from heterogeneous sediments. Soft sediment species were encountered at almost every station (Fig. 7). Sessile and mobile hard substrate species were much less common and only found at about 30 and 10% of the sites respectively. Species of heterogeneous sediments were more common than mobile hard substrate species, and were found at about 20% of the stations. Total biomass and densities are dominated by soft sediment species.

Distinguished feeding types were deposit and suspension feeders and omnivores and carnivores. Most species were deposit feeders, followed by suspension feeders carnivores, the smallest group of species were omnivores (Fig. 8). At more than 95% of the stations deposit feeders were found. Suspension feeders were less common and only present at 66% of the stations. Carnivores inhabited more stations than the suspension feeders. The smallest species group of omnivores also occupied the smallest number of stations (Fig. 8). In terms of biomass suspension feeders dominate. Almost 90% of the biomass is suspension feeders (Fig. 8). Deposit feeders reach highest densities followed by suspension feeders, carnivores and omnivores. Omnivores occur in low densities, on average about 500 times lower than deposit feeders (Fig. 8).

In Fig. 9 the species and biomass distribution among functional groups of feeding and substrate type combinations are plotted as mosaic plots. Two largest groups of species are soft sediment carnivores and deposit feeders. The second largest group both in carnivores and deposit feeders are the mobile hard substrate species. Suspension feeding species are dominated by hard substrate species. The distribution of biomass among these functional groups is very different from species numbers (Fig.). By far most of the biomass is represented by only eight species of soft sediment suspension feeders, followed by sessile hard substrate suspension feeders. The group of mobile hard substrate carnivores and deposit feeders that together were 13 species represented less than 0.3% off the total biomass.

There were 16 invasive species. The largest group of invasive species were seven sessile hard substrate species. There were four soft sediment deposit feeders and two soft sediment suspension feeders. There was one mobile hard substrate carnivore, one soft sediment omnivore and one heterogeneous sediment suspension feeder. Invasive species contributed 79% to the total biomass. In Fig. 9 the contributions per functional category are indicated. The largest biomass category of soft sediment suspension feeders was for 95% made up by invasive species. Also the other categories with invaders had high biomass contributions of the invaders.

4.1.3 Effect of mussels and mussel culture plots

Of the 397 stations 53 (13%) stations fell inside mussel culture plots, 4 of these stations contained mussels. The other 344 stations were outside mussel culture plots, at 20 of these stations mussels were found. In total mussels occurred at 24 out of 397 stations (6%) in the subtidal of the western Dutch Wadden Sea. Of the total number of macrozoobenthos individuals collected in the survey 0.3% were mussels, while 35% of all individuals were found at stations with mussels (33% outside and 1.6% inside mussel culture plots). Mussel culture plots contained 11% of all individuals. At the system scale mussels contributed 17% to the biomass. Of the total biomass 23% was concentrated at sites with mussels (13% outside and 9% inside mussel culture plots). Mussel culture plots contained 18% of the total biomass.

At the ecosystem scale (all stations combined) 100 macrozoobenthos species were encountered. The number of species at stations with and without mussels and inside and outside mussel culture plots are listed in Table 3. There were 8 species (including mussel *M. edulis*) exclusively found at 24 stations with mussels, this were all hard substrate species. There were 27 species that only occurred at 373 stations without mussels. Of these 27 species 7 were hard substrate species. Three of these 7 hard substrate species were exclusively associated with oysters (*C. gigas*). Because number of stations depending on mussel presence and mussel culture plot are not equally distributed it is not easy to compare total species numbers depending on these factors. With species area relationships species numbers at the same number of stations can be compared (Fig. 10). There is a clear difference between the curves with and without mussels. Cumulative species number increases fasted with increasing station number in the subset of stations with mussels and slowest in the subset of stations without mussels. The difference in species accumulation curves between stations inside and outside was minor and did not diverge more than two standard deviations from the overall species accumulation curve.

At stations with mussels both densities and biomass of mussels were higher inside mussel culture plots (Fig. 11). Mean mussel densities were 70 and 600 nm^{-2} at stations occupied by mussels outside and inside mussel culture plots respectively. Medians were 50 and 608 nm^{-2}. Mean ash free biomass of mussels at stations occupied by mussels outside and inside mussel culture plots were 9.5 and 472 gm^{-2} respectively. Medians were 1.3 and 264 gm^{-2}. Mussel shell length distributions were different outside and inside mussel culture plots (Fig. 12). Small mussels dominated outside mussel culture plots. Inside mussel culture plots majority of the mussels were longer than 20 mm with large contributions of large mussels longer than 40 mm.

The total macrozoobenthos density excluding mussels at the stations with at least one mussel in the box core was significantly higher than at stations without mussels (LM with $\log_{10}$ transformed data +

1, $F_{1,393}$=28.1, p<0.001, Fig. 13). There was no significant effect of mussel culture plot or the interaction between mussel presence and mussel culture plot.

Total macrozoobenthos biomass excluding mussel biomass was significantly higher at stations with mussel than at stations without mussels (LM with log_{10} transformed data+0.002, $F_{1,393}$=16.3, p<0.001, Fig. 13). There was no significant effect of mussel culture plot on the biomass. There was also no effect of the interaction between mussel presence and mussel culture plot.

Number of species per box of 0.06 m2 is significantly higher at stations with mussels than without (GLM, $F_{1,395}$=48.9, p<0.001, Fig. 14). Mussel culture plot had no effect on the species richness. Stations without mussels had an average of 8 species per box, stations with mussel 16 species per box, excluding mussels from the species count (Fig. 14). Simpson diversity (Fig. 14) does not differ between stations without or with mussels, neither does mussel culture plot have an effect. Evenness is lower at the stations with mussels (LM arcsin transformed data, $F_{1,391}$=7.7, p<0.01). There was no effect of mussel culture plot on evenness.

Spatially species richness tended to increase with decreasing distance to the nearest station with mussels (Fig. 15). This increase in species number per box with decreasing distance towards a station with mussels leaving the observations with mussels at distance 0 out of the analysis was significant (GLM, $F_{1,371}$=17.6, p<0.001). The model estimate of the intercept is 9.5. This is considerably lower than the observed mean species number of 15.6 (median 15) in the boxes with mussels but without including mussels in the species counts. Distinguishing between hard substrate and soft sediment species which both increased significantly towards the mussel sites, the intercepts were 1.2 hard substrate species and 8.3 soft sediment species. Actual observed hard substrate species number at sites with mussel (but excluding mussels form the counts) was 4.8 (median 4.5), this is 3.6 more than the intercept value. Mean soft sediment species richness was 10.8 (median 11), 2.5 species higher than the intercept value.

Both increased numbers of hard substrate and soft sediment species cause the higher species numbers at stations with mussels compared to stations without mussels (Fig. 16). On average both substrate types contribute with 4 species to the increased species richness at stations with mussels. Both hard substrate (GLM, $F_{1,395}$=48.4, p<0.001) and soft substrate (GLM, $F_{1,395}$=18.5, p<0.001) species richness is significantly higher when mussels are present at the station. There also was a significant difference in hard substrate species number depending on mussel culture plot (GLM, $F_{1,394}$=7.3, p=<0.01). There were more hard substrate species inside mussel culture plots than outside on average 1.2 versus 0.7 without mussels and 8.5 versus 3.7 with mussels. There was no significant difference between soft sediment species number depending on mussel culture plot neither an effect of an interaction between plot and mussel.

Bray Curtis similarity in species composition among stations was calculated with abundance data excluding mussels and oysters. Instead presence absence of mussel and or oysters was used as factor in permanova model partitioning the variance of the similarity matrix among explanatory variables. Besides factor presence absence of mussels and oysters also factor mussel culture plot and environmental variables salinity, median grain size, depth, maximum current speeds and all possible two way interactions were used as explanatory variables. Model selection removing non-significant terms resulted in a final model excluding factor mussel culture plot and various two way interactions (Table 4). The final model explained 17% of the variance of the similarity among stations. Salinity had the largest effect explaining 7 % of the variance. Presence of mussels and or oysters was second explaining 2% followed by in decreasing order median grain size, depth, maximum current speed and the remaining two way interactions.

The similarity in species composition among stations was visualized in an NMDS plot (Fig. 17). Stations are arranged in a two dimensional space according to a Bray Curtis similarity matrix of square root transformed and Wisconsin standardized abundance data. Mussels and oysters were included in the similarity matrix. Species centroids are plotted to specify the differences in species composition among the stations. Also a GAM fitted surface of species richness is added to the ordination plot (fit explaining 58% of the deviance of the ordination). There is a clustering of stations with mussels and oysters corresponding with a clustering of hard substrate species centroids at maximum of the species richness surface. There is a separation between soft sediment species and hard substrate species centroids. Environmental variables are plotted as arrows in the direction of the strongest correlation with the projection of stations. The length of the arrows is proportional to the strength of the correlation. Salinity correlates best with this arrangement of stations (r^2=0.33). The other environmental variables median grain size (r^2=0.08), depth (r^2=0.05) and current speed (r^2=0.09) correlate in similar direction.

Hard substrate species mobile and sessile together made up 34% of the species pool and were strongly clustered (Fig. 18). Hard substrate species occurred at 138 stations out of 397. Biogenic hard substrate habitat creators mussels occurred at 24 stations and oysters occurred at 17 stations with 8 stations overlapping. In total there were 33 stations with either one or both of these species present. At 25 of these stations with hard substrate delivering species mussels (*M. edulis*)and/or oysters also other hard substrate species were found. There were 8 stations without additional hard substrate species, this were all stations that only contained mussels. Average hard substrate species richness at the 25 stations with mussels and/or oyster stations was 7 (without counting mussels and oysters). There were 105 stations with at least one hard substrate species but no mussels or oysters. At these stations average hard substrate species richness was only two , much lower than at the stations with mussels and/or oysters (Fig. 18).

Excluding mussels and oyster there were 32 hard substrate species identified. Four of these were only found at stations without mussels and/or oysters. This were *Lepidochitona cinerea, Monocorophium acherusicum*, *Pholoe minuta* and *Sthenelais boa*, all these species were only encountered once. There were 11 hard substrate species that only occurred together with mussels and or oysters. These were *Cheirocratus sundevalli*, *Didemnum vexillum*, *Eulalia viridis, Hartlaubella gelatinosa, Harmothoe imbricata, Hemigrapsus takanoi, Molgula socialis, Ophiothrix fragilis*, *Sabellaria spinulosa*, *Smittoidea prolifica* and *Styela clava*. Also these species were not common, *Styela clava* occurred most often, 4 times. Occurrence relative to the number of stations in each habitat was always higher in the mussel and/or oyster habitat, except for the four species only occurring without mussels and/or oysters (Fig. 19). Besides the four species that only occurred without mussels and/or oysters there were seven species more that occurred more often without mussels and/or oysters. Five of these species were also within the top six of most common species at mussel and/or oyster sites.

4.1.4 Spatial patterns and environmental gradients

Macrozoobenthos total densities are mapped in Fig. 20. Patterns are not strong but densities are larger along the inner southeastern shore and decline towards the tidal inlets. Numerical densities correlate negatively with depth, salinity and maximum current speed (Fig. 21). The correlation with salinity is the strongest.

The mapped total macrozoobenthos (Fig. 20)does not reveal strong spatial patterns. Biomass seems relatively large along the tidal divide between the Marsdiep and Vlie tidal basins. The central part of the Marsdiep tidal basin tends to have relatively low biomass values. At stations with mussels biomass values are relatively large. Total biomass correlates weakly negative with all four variables tested (Fig.22)

Species richness is largest at stations in the northern parts of both tidal basins (Fig. 20). The southern part of the Vlie tidal basin along the tidal divide with the Marsdiep basin is relatively species poor. Also the south western part of the Marsdiep tidal basin is not very species rich. Species richness is relatively large at stations with mussels. Species richness is plotted along gradients of median grain size, depth, salinity and maximum current speed in Fig. 23. At the level of single stations there is an increase in richness along a sediment gradient to a grain size around 200 µm, then richness declines with further increasing grain size. At the level of single stations species richness declines with depth along the entire gradient. Species richness at the scale of single stations along a salinity gradient does not show much of a trend. Species richness at the station scale declined at current speeds above 0.8 ms^{-1}. Stations along the environmental were also aggregated to cover an area of ~1m^2 (16 stations). At this larger scale species richness has pronounced optima along median grain size, depth and maximum current gradients. Species richness at the station scale also showed optima along the median grain size and maximum current speed gradients but not clearly along the depth gradient. Species richness depends most strongly on sampling scale along the salinity gradient. At the single box level no trend was obvious, aggregated samples of 16 boxes show a steep gradient of increasing species richness with increasing salinity. In addition also curves are shown in Fig. 23 that were corrected for environmental range width within aggregates. These curves are similar in shape compared to the uncorrected curves.

The mapped Simpsons biodiversity index does not reveal strong large scale patterns (Fig. 20)

4.2 Functional groups

Deposit feeder numerical densities are lowest along the large tidal channels towards the tidal inlets and increase further into the basin (Fig. 24). Abundance of deposit feeders correlated negatively with salinity depth and maximum current speed. Deposit feeder abundance and median grain size did not correlate significantly (Fig. 26). Biomass of deposit feeders shows a stronger spatial pattern than abundance but with the same declining trend towards the tidal inlets (Fig. 24). Biomass values were largest along the south eastern coast of the system. Several of these stations were sites were mussels occurred. Total deposit feeder biomass correlated negatively with salinity depth and maximum current speed and positively with median grain size Fig. 27)

There are no very obvious large scale patterns in the abundance of suspension feeders (Fig. 24). There are more stations without suspension feeders than deposit feeders. Suspension feeders seem to be more locally clustered than deposit feeders. Total numerical densities of suspension feeders were significantly positively related to depth (Fig. 26). There were no significant relationships with salinity, sediment median grain size and maximum current speed. Total suspension feeder biomass was high along the tidal divide between Vlie and Marsdiep tidal basins (Fig. 24). Also in the north of the Vlie basin large biomass concentrations were present. In the Marsdiep high biomass areas were more scattered with many stations with low values in between. There were two weak significant negative correlations with sediment median grain size and maximum current speeds (Fig. 27). Contrary to abundance there was no correlation with depth. Salinity was not correlated with total suspension feeder biomass.

Spatial pattern of omnivore abundance is scattered. Densities are much lower than those of deposit and suspension feeders. Many stations were not occupied by omnivores (Fig. 25). Omnivores only inhabit few stations. At these stations there were no significant relations found between omnivore abundance and environmental variables (Fig. 26). Omnivore biomass shows a spatial pattern similar to abundance (Fig. 25). There were no significant correlations between biomass at the occupied stations and environmental variables considered (Fig. 27).

Carnivores are much more widely distributed than omnivores (Fig. 25). There is obvious spatial gradient of carnivore numerical densities except for several stations near the Afsluitdijk that are not inhabited by carnivores (Fig. 25). Carnivore numerical densities do correlated positively with salinity and median grain size (Fig. 26). There were no trends between carnivore abundance and environmental variables depth and maximum current speed. The spatial distribution of carnivore biomass shows a few sites with strongly deviating biomass values that were not obvious from the numerical densities (Fig. 25), several of these stations were occupied by mussels. Biomass is evenly distributed over the remaining stations. There were no significant correlations between carnivore biomass and the environmental variables salinity, sediment median grain size, depth and maximum current speed (Fig. 27).

4.2.1 Hard substrate species

Hard substrate species richness distribution in the subtidal western Dutch Wadden Sea is mapped in Fig. 28. Most species rich areas are the northern side of the Marsdiep tidal basin and the northern part of the Vlie tidal basin. In these areas stations with mussel and oysters harbour the largest amount of hard substrate species. Besides that in this area there are also several stations without mussels and or oysters that have intermediate hard substrate species richness. In the southern part of the Marsdiep tidal basin hard substrate species richness is lower. In this area were several stations with mussels as only hard substrate species. Mussels at these sites were mostly smaller than 25 mm.

Hard substrate species richness did not correlate well with any of the environmental variables, median grain size, depth, salinity and maximum current speed (Fig. 29). However the high hard substrate species richness at station with oysters was striking. Within the oyster stations there appears to be a positive trends of hard substrate species richness with salinity (Fig. 29).

4.2.2 Individual species

Species that ranked within the top 15 of highest numerical densities, biomass or number of occurrences are listed in table 5. This group of 26 species represents 98% of the total biomass and represents at 80% of the stations more than 80% of the total biomass.at these stations. The polychaets *Scoloplos armiger, Spio martinensis, Aphelochaeta marioni* and *Capitella capitata* were most common occurring at more than 50% of the stations. Most biomass was represented by the bivalves *Ensi directus, Mya arenaria, Mytilus edulis* and *Crassostrea gigas*. Three of these species are invaders, of which two recent ones; *E. directus* and *C. gigas* recent. Highest numerical densityies were reached by the invasive polychaete Marenzelleria viridis followed by the laver spire shell *Peringia ulvae* that only occurred at four stations and *A. marioni* that is among the most common species as well. Distribution maps of the numerical densities of these species are plotted in Figures 31 to 36. In appendix 3 environmental response curves of these species are presented.

Figure 30 shows maps of hard substrate species. The mussel *M. edulis* was found most often in the Marsdiep tidal basin. Densities were highest at mussel culture plots in the northern part of the Vlie tidal basin. The oyster, *C. gigas*, was found at 17 stations, most in the northern part of the Marsdiep tidal basin. At 6 stations, 1 or more large adult C. gigas were found. All these stations were restricted to the Marsdiep tidal basin. At the remaining stations with C. gigas there were only of few newly-settled recruits of year 2008. Barnacles (*Balanus sp.*) were mostly encountered in the northern part of the Marsdiep tidal basin. Overlap with mussels is not very large. Barnacle densities at stations with mussels on the mussel culture plots in the northern part of the Vlie basin are low compared to barnacle densities at stations with mussels in the Marsdiep tidal inlet. The distribution of the frilled anemone (*M. senile*) extended into the southern part of the Marsdiep tidal inlet with no strong overlap with mussels. At stations with mussels densities appear relatively high also at the mussel culture plots in the northern Vlie tidal basin. The encrusting Bryozaon, *C. reticulum* was the most widespread hard substrate species in the subtidal western Dutch Wadden Sea. The Australasian barnacle *E. modestus* was most abundant in the northern parts of the Marsdiep and Vlie tidal basins.

A species of heterogeneous sediments was *S. troglodytes* that had highest densities near the Marsdiep and Vlie tidal inlets (Fig. 31). Overall this species was not common. The invasive bivalve *Ensis directus* is widely distributed in most parts of the subtidal area (Fig. 31), except for stations near the Afsluitdijk. The sand gaper (*M. arenaria*) was most common and reached highest densities in the south east along the Afsluitdijk (Fig. 31). This pattern was even more pronounced in the invasive spionid (*M. viridis*) that also reached high densities along the south eastern side of the western Dutch Wadden Sea and was practically absent in the north western part of the area (Fig. 31). The sand mason worm (*L. conchilega*) had a much more North Sea ward distribution than the previous two species. Highest densities were found in the northern part of the Vlie tidal basin (Fig. 31). The shore crab (*C. maenas*) was wide spread but not very common in the subtidal of the western Dutch Wadden Sea (Fig. 31). Densities were highest at stations with mussels.

The king ragworm (*A. virens*) was widespread but not very coomon in the subtidal western Dutch Wadden sea (Fig. 32). The cockle (*C. edule*) occurred at a few sites in the south eastern part of the Marsdiep tidal basin. Highest densities were found at stations with mussels (Fig. 32). The laver spire shell (*P. ulvae*) was very abundant at three stations along the Afsluitdijk and occurred at a very near shore station on the border of the Marsdiep and Vlie tidal basin. The two stations with highest *P. ulvae* abundances were also occupied by mussels (Fig. 32). The bristleworm *Scoloplos armiger* was very common. It was only not found in deep tidal channels and at the most easterly stations against the Frisian coast (Fig. 32). The catworm, Nephtys hombergii, was commonly found except at stations close to the mainland coast and the Afsluitdijk (Fig.32). The small bristleworm *Apholechaeta marioni* was common and occurred at high densities. Densities and occurrences declined towards the tidal inlets (Fig. 32).

The small spionid *Spio martinensis*, was commonly found except at stations near the Afsluitdijk and the mainland coast (Fig. 33). Oligochaetes were among the most common species. It occupied landward stations and was less common towards the tidal inlets. Densities were relatively high at stations with mussels (Fig. 33). *Capitella capitata* was also one of the most common species. Highest abundances were found in the Marsdiep tidal basin (Fig. 33). The spionid *Pygospio elegans* had a distribution shifted towards the south eastern side of the area. It was only found at low densities towards the tidal inlets (Fig. 33). The capitellid *Heteromastus fililformis* was more concentrated towards the south eastern part of the area compared to the distribution of *C. capitata* (Fig. 33). The densities of *H. filiformis* at the stations with mussels were relatively high. The paddleworm, *Eteone longa*, was concentrated in the Marsdiep tidal basin with highest densities in the eastern part (Fig. 33).

The white catworm, *Nephtys cirrosa*, was distributed towards the northern parts of the Vlie and Marsdiep tidal basins (Fig. 34). It was absent along the Afsluitdijk and the mainland coast. The polychaete *Aricidea minuta* was almost entirely restricted to the central part of the Marsdiep tidal basin (Fig. 34).

4.3 Comparison between 2008 and 1981/82

4.3.1 Species

There were 88 species selected for the comparison between the two surveys. Of these species 69 occurred in 1981/82, in 2008 79 species out of 88 were found. Nine species were found in 1981/82 that were not encountered in 2008. These were *Aeolidia papillosa, Diastylis bradyi, Eteone flava, Lamprops fasciatus, Onchidoris bilamellata, Pholoe minuta, Pontocrates altamarinus, Scolelepis bonnieri, Scrobicularia plana*. These species were rare in 1981/82, the most common was *L. fasciatus*, that occurred at 10 stations out of 392. None of these species was invasive. Four are carnivores, five are deposit feeders.

There were 23 species in the 2008 dataset that were not found during the survey in 1981/82 (Table 6). Nine of these species were invasive. Two of them were very successful, *Marenzelleria viridis* found at 134 stations and *Ensis directus* found 105 stations in 2008. The invasive Pacific oyster *Crassostrea gigas* occupied 17 stations. There were 7 carnivores, 5 deposit feeders and 11 suspension feeders in this group.

Species occupancy showed large changes between both periods (Fig. 35).One of the most remarkable changes is the strong decrease of *Macoma balthica* the most common species in 1981/82. Also *Peringia ulvae* showed a very strong decline. Of the four invasive species already present all increased strongly in the number of occupied stations except *Petricolaria pholadiformis.* Also several new invasive species were very successful, *Marenzelleria viridis* occupied 34% of all stations, *Ensis directus* inhabited 27% of all stations.

4.3.2 Biomass

Average biomass of the surveys from 1981/82 and 2008 over 392 stations was remarkably similar in both periods it was 53.5 gm^{-2} AFDM (Fig. 36). Median biomass was 4.5 and 5.6 gm^{-2} in 1981/82 and 2008 respectively. Average biomass distribution among the different phyla the macrozoobenthos species belonged to was very similar between 1981/82 and 2008 (Fig.37). Mollusca were by far the most important group in terms of biomass. Total biomass of this group was 47 gm^{-2} in both periods. Annelids followed with about 5 gm-2 in each period and Athropoda were third with about 1 gm^{-2}.

Comparing the macrozoobenthos communities functionally categorized by feeding and substrate type showed some differences (Fig. 38). The share of deposit feeders declined while suspension feeders increased. Within the suspension feeders there was a strong shift in biomass from hard substrate to soft sediment species.

At the species level there were large changes in biomass between periods. Absolute biomass values are plotted for the 15 species contributing most to the total biomass (Fig. 39). These species are good for more than 98% of the total biomass. A dramatic shift in biomass dominance has taken place from mussel to the invasive species *Mya arenaria* and *Ensis directus*. *Peringia ulvae*, *Cerastoderma edule*, *Heteromastus filliformis*, *Macoma balthica* and *Petricolaria pholadiformis* showed large declines in biomass. After *E. directus* and *M. arenarial* two other invasive species *Crassostrea gigas* and *Marenzelleria viridis* contributed most to the total biomass. The contribution of invasive species to the total biomass was 2% in 1981/82 and 80% in 2008 (Fig. 40).

Relative changes in biomass of species that were present in both periods are plotted in Fig. 41. A majority of these species declined. The feeding types are evenly distributed among the declining and increasing species, except for the omnivores that all increased. Species that had largest relative declines were *Scolelepis foliosa*, *Travisia forbesii* and *Heteromastus filiformis*. Strongets increasing species were *Echinocardium cordatum*, *Ophiura ophiura*, *Angulus fabula* and *Mya arenaria*.

Overall the macrozoobenthos community in the western Dutch Wadden Sea showed a strong change in species composition. This is illustrated in a NMDS plot based on biomass data (Fig. 42). Stations are clearly separated by period in this ordination. The dominance of the different species in both periods is shown by the plotted species centroids. With a PERMANOVA the difference between the two periods was tested. Period significantly ($p<0.001$) explained 5% of the variance in the similarity matrix of all 392 station that were sampled both periods.

4.3.3 Individual species

Mussels

Mussels were more common in 1981/82 than in 2008, they were found at 68 stations out of 392 in 1981/82 and only at 24 out of 392 stations in 2008. Total biomass in 1981/82 was dominated by mussels, 63% of the macrozoobenthos biomass in the subtidal western Dutch Wadden Sea was of mussels. This was only 10% in 2008. In Table 5 a summary is given of the distribution of stations with mussels inside and outside culture plots together with mussel densities and biomasses. Density and biomass were higher inside than outside culture plots in both periods. In 1981/82 densities were higher than in 2008, both inside and outside culture plots. Mussel biomass within occupied mussel culture plots did not differ much between periods. In 1981/82 mussel biomass at occupied stations outside culture plots was about 5 times higher than in 2008 (Table 7).

The distribution of the mussels inside and outside mussel culture plots along salinity and a depth gradients are compared between the two periods in Fig. 43. In 1981/82 mussel culture plots were better stocked than in 2008. In 2008 mussels were found inside culture plots at the plots in the higher salinity ranges. Also only culture plots within a very narrow depth range between 2 and 5 m

NAP were used in 2008. In 1981/82, al large part of the mussel culture plots were used and masking any preference for certain areas for mussel culture. The distribution of mussels along the salinity gradients outside the mussel culture plots in 1981/82 showed an optimum around 15 PSU. In 2008 there was no clear optimum. In 1981/82 mussels outside the mussel culture plots were evenly distributed along the (log transformed) depth gradient. In 2008 most stations outside mussel culture plots were at a depth between 2 and 5 m NAP.

Mussel density and biomass distribution in the subtidal western Dutch Wadden Sea are mapped in Fig. 44. In 1981/82 mussels occur in highest densities and biomasses at the mussel culture plots but there are also several mussel beds outside the mussel culture plots with high biomass and numerical density values. In 2008 mussel occurrence is lower. Also biomass and density at the remaining mussel stations are lower than in 1981/82. In 2008 three out of four of the mussel culture plots with mussels were in the Vlie tidal basin.

Other species

Biomass of individual species mapped for 1981/82 and 2008 can be found in Figures 45-55. The mapped species were selected based on a ranking of the data according to total biomass, total density and occurrence. The top tens of each ranking were selected for the maps. Most spectacular were the establishment of the invasive *Ensis directus* (Fig. 45)and *Marenzelleria viridis* (Fig. 48) and the strong increase in *Mya arenaria* (Fig. 45). Strong declines were observed for *Peringia ulvae* (Fig. 46), *Heteromastus filiformis* (Fig. 47) and *Macoma balthica* (Fig. 49), all three deposit feeders. The small polychaete *Aphelochaeta marioni* increased (Fig. 52), while the samll polychaete *Magelona johnstoni* declined (Fig. 52). Another small polychaete *Spio martinensis* increased in biomass between 1981/82 and 2008 (Fig. 53). Spatial distributions did not change to the same extend as the changes in the biomass levels. Most notably were *Alitta virens* that became more wide spread and lower maximal biomass values in 2008 compared to 1981/82(Fig. 50). Another distributional change was seen in three spionids, *Pygospio elegans*, *Spio martinensis* and *Polydora coranuta* that had high biomasses concentrated around the eastern part of the tidal divide between the Marsdiep and Vlie tidal basins in 1981/82 (Figs. 53 and 55). In 2008 the biomass of these species was much more evenly distributed over the subtidal area of the western Dutch Wadden Sea.

5 DISCUSSION

5.1 Survey 2008

Total count of macrozoobenthos species was 100 in a sampled surface area of 27 m^2 in the subtidal of the western Dutch Wadden Sea. This is a high number comparing it to the intertidal of the Wadden Sea. At the Balgzand intertidal area in the south western part of the Marsdiep only 85 species were retrieved from samples collected each year in the end of summer during a ten year period on 12 transects and three permanent quadrates with a total sampled surface of 91 m^2. Transects were one km long and together with the quadrates covered the largest part of the tidal gradient (for details see e.g. Beukema and Dekker 2011). A sampling program SIBES covering the entire Dutch intertidal Wadden Sea with 4307 stations in 2008 together covering 75 m^2 found 86 species (Compton et al 2012).

Suspension feeders were by far the dominant group in biomass, almost 90% of the macrozoobenthos biomass was made up out of suspension feeders. However suspension feeders are only third in occupancy, deposit feeders and carnivores occupy more stations. Deposit feeders were the most abundant group of macrozoobenthos that occurred at almost everywhere but had only a small contribution to the total biomass. The distribution of biomass among deposit feeders and suspension feeders matches with the pattern in the Oosterschelde (Herman et al. 1999). Deposit feeders are omnipresent with low biomass while suspension feeders are concentrated at fewer sites with much higher biomasses.

When mussels are present, local species richness is double compared to bare sediment areas. The increase in species number is the case both for hard and, unexpectedly, also for soft sediment species. In general the idea that soft sediment species may be impaired by the presence of mussels (Commito 2008), therefore, is not supported by the data presented here as also observed by Commito et al. (2008).

Spatially sites with mussels are very distinct in their higher species richness. There is a small increase in species richness with decreasing distance towards a site with mussels. However this large scale pattern of species richness does not explain the species richness of the sites with mussels. This is no conclusive evidence but in line with the suggestion that mussels locally enhance species richness. It gives less support to the alternative idea that increased species richness associated with mussels is solely the consequence of mussel settlement in the most species rich sites. Even when only considering soft sediment species there is a strong jump between the spatial pattern of species richness towards sites with mussels and the richness of soft sediment species at the mussel site itself.

Environmental gradients are important in structuring the macrozoobenthos community (eg. Ysebaert et al. 2002, Thrush et al. 2003, Kraan et al 2010). Especially in estuarine systems salinity is an important determinant of species occurrences (Ysebaert et al. 2002) In the western Dutch Wadden Sea salinity was also the most important environmental factor determining differences in the community composition among stations (Figure. 17, Table. 4). Community composition also depends strongly on the presence of mussels and/or oysters. Intriguingly, no effect could be detected of whether the community was sampled on a mussel culture plot or not.

Species richness does increase with salinity (see Remane 1934) but this could only be detected when pooling box cores in this study. Apparently, there is no salinity effect on alpha diversity at the box core level, while there is a beta diversity effect (species turnover among samples) of salinity. This implies that sufficient effort to sample at a range of spatial scales is needed when attempting to measure diversity in this area. This agrees with scale dependence of species richness in the intertidal (Beukema and Dekker 2012).

About two third of the hard substrate species were often observed outside mussel and oyster beds. What they were attached to was not recorded during data collection, but this is likely to be dead shell material. This observation is interesting because it means that in the subtidal, much hard substrate fauna can also be found outside of the biogenic reefs. Nevertheless total hard substrate species richness at the system scale is larger at sites with mussels and oysters than at bare sediment sites.

5.2 Comparison between 2008 and 1981/82

Relatively large changes in community composition were observed going from 1981/82 to 2008, in terms of individual species. For example, among suspension feeders mussels have declined strongly, while invasive suspension species *E. directus* and *M. arenaria* have strongly established; similarly, among deposit feeders, *M. balthica*, *P.ulva* and *H. filiformis* have decreased, while the invasive deposit feeder *M. viridis* absent in 1981/82 had established as the most abundant deposit feeder with the highest biomass contribution of all deposit feeders in 2008.

In spite of the relatively large shifts in community composition in terms of individual species identities, there is no indication for change in the community composition in terms of feeding group biomass. Biomass of substrate types has changed, soft sediment species have increased while hard substrate sessile biomass declined, what is mainly caused by the decline in mussel biomass between 1981/82 and 2008.

Biomass has remained remarkably similar between 1981/82 and 2008. This was unexpected because biomass at three transects in the western Dutch Wadden Sea increased since 1989 and also the biomass of the intertidal macrozoobenthos at the Balgzand area increased between 1981/82 and 2008 (Van der Graaf et al. 2009). Why these biomass developments are dissimilar is unclear but fits the Wadden Sea wide picture that temporal biomass developments are far from uniform (Van der Graaf et al. 2009).

The present survey was carried out on a large spatial scale but compares only two points in time. A smaller survey consisting of three transects, in contrast, was done twice yearly from 1989 to the present; many of the changes detected here were also observed in that survey (Ens et al. 2007). This means that the changes documented here were not simply differences between particular years but, instead, developed over the course of decades.

5.3 Main Conclusions

- Macrozoobenthos is more species rich in the subtidal western Dutch Wadden Sea than in the intertidal Wadden Sea.

- Sites with mussels (and osyters) are twice as species rich as sites without mussel (and oysters), the difference is 8 versus 16 species in a box of 0.06 m^2 including mussels (and oysters) in the species count.
- Increased species richness at a site with mussels is very local, there are no large scale effects in the surrounding area.
- Both hard and soft substrate species richness are elevated in sites with mussels.
- Sites with mussels and oysters are rich in hard substrate species. Many hard substrate species also occur outside mussel sites.
- Beside presence of mussels and or oysters environmental gradients are important determinants of species richness and community compostion.
- The macrozoobenthos community species composition has changed a lot between 1981/82 and 2008. Mussels were much less abundant in 2008. The invasive *Mya arenaria* and *Ensis directus* were the dominant suspension feeders in 2008. Despite the large cahnges in the species composition there was very little change in the distribution of biomass among the feeding groups, suspension feeders, deposit feeders, omnivores and carnivores.
- Macrozoobenthos biomass was dominated by invasive species in 2008, 80% of the biomass was from invasive species. In 1981/82 only 2% of the biomass was of invasive species.

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Table 1. Summary statistics of total density, total biomass (in g afdm) and species richness (species per station of 0.06 m^2) of macrozoobenthos at 397 stations in the subtidal of the western Dutch Wadden Sea in 2008. Mean is the arithmetic mean, Geo Mean the geometric mean.

	Density nm^{-2}	Biomass gm^{-2}	Richness n box^{-1}
Min.	0	0	0
1st Qu.	266.7	1.25	5
Median	716.7	6.73	8
Mean	2621	54.82	8.6
3rd Qu.	2217	49.44	11
Max.	154000	1456	34
Geo mean	732	6.47	

Table 2. List of macrozoobenthos species with abbreviations found in 397 box cores (0.06 m^2)from the subtidal western Dutch Wadden Sea in autumn 2008. See appendix 2 for more details.

abbrev.	Scientific name	abbrev.	Scientific name
Abralb	*Abra alba*	Macbal	*Macoma balthica*
Alcmyt	*Alcyonidioides mytili*	Magjoh	*Magelona johnstoni*
Alisuc	*Alitta succinea*	Maldar	*Malmgreniella darbouxi*
Alivir	*Alitta virens*	Marvir	*Marenzelleria viridis*
Angfab	*Angulus fabula*	Melpal	*Melita palmata*
Angten	*Angulus tenuis*	Metsen	*Metridium senile*
Aphmar	*Aphelochaeta marioni*	Micmac	*Microprotopus maculatus*
Aremar	*Arenicola marina*	Micscz	*Microphthalmus sczelkowii*
Arimin	*Aricidea minuta*	Molsoc	*Molgula socialis*
Astrub	*Asterias rubens*	Monach	*Monocorophium acherusicum*
Balsp	*Balanus sp*	Monins	*Monocorophium insidiosum*
Barcan	*Barnea candida*	Myaare	*Mya arenaria*
Batele	*Bathyporeia elegans*	Myrpro	*Myrianida prolifera*
Batsar	*Bathyporeia sarsi*	Myspic	*Mysta picta*
Bodsco	*Bodotria scorpioides*	Mytedu	*Mytilus edulis*
Bylsar	*Bylgides sarsi*	Nemert	*Nemertea carnivore*
Capcap	*Capitella capitata*	Nepcae	*Nephtys caeca*
Carmae	*Carcinus maenas*	Nepcir	*Nephtys cirrosa*
Ceredu	*Cerastoderma edule*	Nephom	*Nephtys hombergii*
Chesun	*Cheirocratus sundevalli*	Neplon	*Nephtys longosetosa*
Clyhem	*Clytia hemisphaerica*	Obelon	*Obelia longissima*
Conret	*Conopeum reticulum*	Oligoc	*Oligochaeta deposit*
Corare	*Corophium arenarium*	Ophfra	*Ophiothrix fragilis*
Corvol	*Corophium volutator*	Ophoph	*Ophiura ophiura*
Cracra	*Crangon crangon*	Pagber	*Pagurus bernhardus*
Cragig	*Crassostrea gigas*	Parful	*Paraonis fulgens*
Crefor	*Crepidula fornicata*	Perulv	*Peringia ulvae*
Didvex	*Didemnum vexillum*	Petpho	*Petricolaria pholadiformis*
Donvit	*Donax vittatus*	Phomin	*Pholoe minuta*
Echcor	*Echinocardium cordatum*	Phymuc	*Phyllodoce mucosa*
Elepil	*Electra pilosa*	Polcil	*Polydora ciliata*
Elmmod	*Elminius modestus*	Polcor	*Polydora cornuta*
Ensdir	*Ensis directus*	Psepul	*Pseudopolydora pulchra*
Etelon	*Eteone longa*	Pygele	*Pygospio elegans*
Eulvir	*Eulalia viridis*	Retobt	*Retusa obtusa*
Eumsan	*Eumida sanguinea*	Sabspi	*Sabellaria spinulosa*
Eunlon	*Eunereis longissima*	Sagtro	*Sagartia troglodytes*
Gamloc	*Gammarus locusta*	Scoarm	*Scoloplos armiger*
Glyalb	*Glycera alba*	Scofol	*Scolelepis foliosa*
Glyuni	*Glycera unicornis*	Smipro	*Smittoidea prolifica*
Hargel	*Hartlaubella gelatinosa*	Spibom	*Spiophanes bombyx*
Harimb	*Harmothoe imbricata*	Spimar	*Spio martinensis*
Harimp	*Harmothoe impar*	Spisub	*Spisula subtruncata*
Heddiv	*Hediste diversicolor*	Sthboa	*Sthenelais boa*
Hemtak	*Hemigrapsus takanoi*	Strben	*Streblospio benedicti*
Hetfil	*Heteromastus filiformis*	Stycla	*Styela clava*
Kurbid	*Kurtiella bidentata*	Telfer	*Tellimya ferruginosa*
Lagkor	*Lagis koreni*	Trafor	*Travisia forbesii*
Lancon	*Lanice conchilega*	Uropos	*Urothoe poseidonis*
Lepcin	*Lepidochitona cinerea*	Vencor	*Venerupis corrugata*

Table 1. Overview of number of macrozoobenthos species in the subtidal of the western Dutch Wadden Sea in 2008, depending on presence of mussels and whether stations were inside or outside mussel culture plots. Species counts include mussels (*Mytilus edulis*). Between brackets are the number of stations in each category. Species counts include mussels.

	culture plots		
mussels	outside	inside	totals
present	65 (20)	41 (4)	73 (24)
absent	89 (324)	58 (49)	92 (373)
totals	96 (344)	69 (53)	100 (397)

Table 2. Permanova analysis of a similarity matrix based on macrozoobenthos density data from the subtidal western Dutch Wadden Sea. Mussel (*M. edulis*) and oyster (*C. gigas*) were not included calculating the matrix but instead presence of mussels or oysters was used as explanatory factor (muster). Non-significant terms were removed from the model, including factor mussel culture plot. The initial model contained single terms and only two way interactions.

Terms	Df	SumsOfSqs	MeanSqs	F.Model	R^2	Pr(>F)	
salinity	1	10.925	10.9254	31.812	0.0695	0.000999	***
grain size	1	2.427	2.4271	7.067	0.01544	0.000999	***
depth	1	2.106	2.1064	6.133	0.0134	0.000999	***
current	1	0.925	0.9253	2.694	0.00589	0.001998	**
muster	1	3.519	3.5188	10.246	0.02238	0.000999	***
sal:depth	1	1.402	1.4022	4.083	0.00892	0.000999	***
sal:grain	1	1.557	1.5568	4.533	0.0099	0.000999	***
sal:cur	1	0.651	0.6512	1.896	0.00414	0.022977	*
sal:muster	1	0.843	0.843	2.455	0.00536	0.003996	**
grain:depth	1	0.668	0.6679	1.945	0.00425	0.014985	*
grain:muster	1	0.597	0.5975	1.74	0.0038	0.025974	*
depth:cur	1	0.867	0.8675	2.526	0.00552	0.002997	**
depth:muster	1	0.556	0.5558	1.618	0.00354	0.030969	*
Residuals	379	130.162	0.3434		0.82797		
Total	392	157.207			1		

Table 3. Most important macrozoobenthic species found in the 397 stations in 2008 in the subtidal of the western Dutch Wadden Sea. Biomass and densities are the arithmetic means on the 397 stations. Included are the most dominant species in terms of biomass, densities and occurrence. NA means not analyzed.

code	species	occur.	biomass	density	inv.	feeding	substrate
Scoarm	*Scoloplos armiger*	0.6	0.32	53	no	depos.	soft
Spimar	*Spio martinensis*	0.58	0.04	153	no	depos.	soft
Aphmar	*Aphelochaeta marioni*	0.56	0.06	316	yes	depos.	soft
Capcap	*Capitella capitata*	0.54	0.02	63	no	depos.	soft
Oligoc	Oligochaeta	0.38	0.01	94	no	depos.	soft
Pygele	*Pygospio elegans*	0.37	0.01	48	no	depos.	soft
Nephom	*Nephtys hombergii*	0.35	0.17	9	no	carni.	soft
Marvir	*Marenzelleria viridis*	0.34	1.89	684	yes	depos.	soft
Hetfil	*Heteromastus filiformis*	0.33	0.08	23	no	depos.	soft
Ensdir	*Ensis directus*	0.27	21.09	60	yes	susp.	soft
Etelon	*Eteone longa*	0.24	0.01	9	no	carni.	soft
Conret	*Conopeum reticulum*	0.23	NA	63	no	susp.	hard, s
Myaare	*Mya arenaria*	0.23	16.89	196	yes	susp.	soft
Nepcir	*Nephtys cirrosa*	0.22	0.06	11	no	carni.	soft
Arimin	*Aricidea minuta*	0.17	0	15	no	depos.	soft
Alivir	*Alitta virens*	0.13	0.9	2	yes	omni.	soft
Metsen	*Metridium senile*	0.12	0.18	24	no	susp.	hard, s
Lancon	*Lanice conchilega*	0.12	1.48	38	no	susp.	soft
Balsp	*Balanus sp.*	0.1	0.62	79	no	susp.	hard, s
Elmmod	*Elminius modestus*	0.09	0.08	26	yes	susp.	hard, s
Carmae	*Carcinus maenas*	0.07	1.06	2	no	carni.	soft
Mytedu	*Mytilus edulis*	0.06	5.23	10	no	susp.	hard, s
Sagtro	*Sagartia troglodytes*	0.05	0.39	6	no	carni.	hetrog.
Cragig	*Crassostrea gigas*	0.04	2.35	5	yes	susp.	hard, s
Ceredu	*Cerastoderma edule*	0.04	0.44	11	no	susp.	soft
Perulv	*Peringia ulvae*	0.01	0.39	505	no	depos.	soft

Table 4. Species in dataset 2008 but not in dataset 1981/82. Occurences are the number of stations occupied out of 392.

Species	invasive	feeding	substrate	occurences
Barnea candida	no	deposit	heterogeneous	3
Bathyporeia elegans	no	deposit	soft	1
Bodotria scorpioides	no	deposit	soft	4
Crassostrea gigas	yes	suspension	hard sessile	17
Crepidula fornicata	yes	suspension	hard sessile	26
Didemnum vexillum	yes	suspension	hard sessile	2
Donax vittatus	no	suspension	soft	1
Ensis directus	yes	suspension	soft	105
Eumida sanguinea	no	carnivore	soft	5
Glycera alba	no	carnivore	soft	32
Glycera unicornis	no	carnivore	soft	14

Hemigrapsus takanoi	yes	carnivore	hard mobile	2
Lepidochitona cinerea	no	deposit	hard mobile	1
Marenzelleria viridis	yes	deposit	soft	134
Molgula socialis	yes	suspension	hard sessile	3
Myrianida prolifera	no	carnivore	hard mobile	21
Mysta picta	no	carnivore	soft	6
Ophiothrix fragilis	no	suspension	hard mobile	1
Pagurus bernhardus	no	carnivore	soft	4
Sabellaria spinulosa	yes	suspension	hard sessile	1
Styela clava	yes	suspension	hard sessile	4
Tellimya ferruginosa	no	suspension	soft	2
Venerupis corrugata	no	suspension	heterogeneous	2

Table 5. Overview per period, of stations distributed outside and inside culture plots, numbers of stations without or with mussels, average density and biomass of mussels at the stations containing mussels.

			mussels			
period	culture	stations	without	with	density	biomass
	plot	n	n	n	nm^{-2}	gm^{-2}
1981/82						
	outside	362	314	48	509	47
	inside	30	10	20	1151	552
2008						
	outside	339	319	20	70	9
	inside	53	49	4	600	472

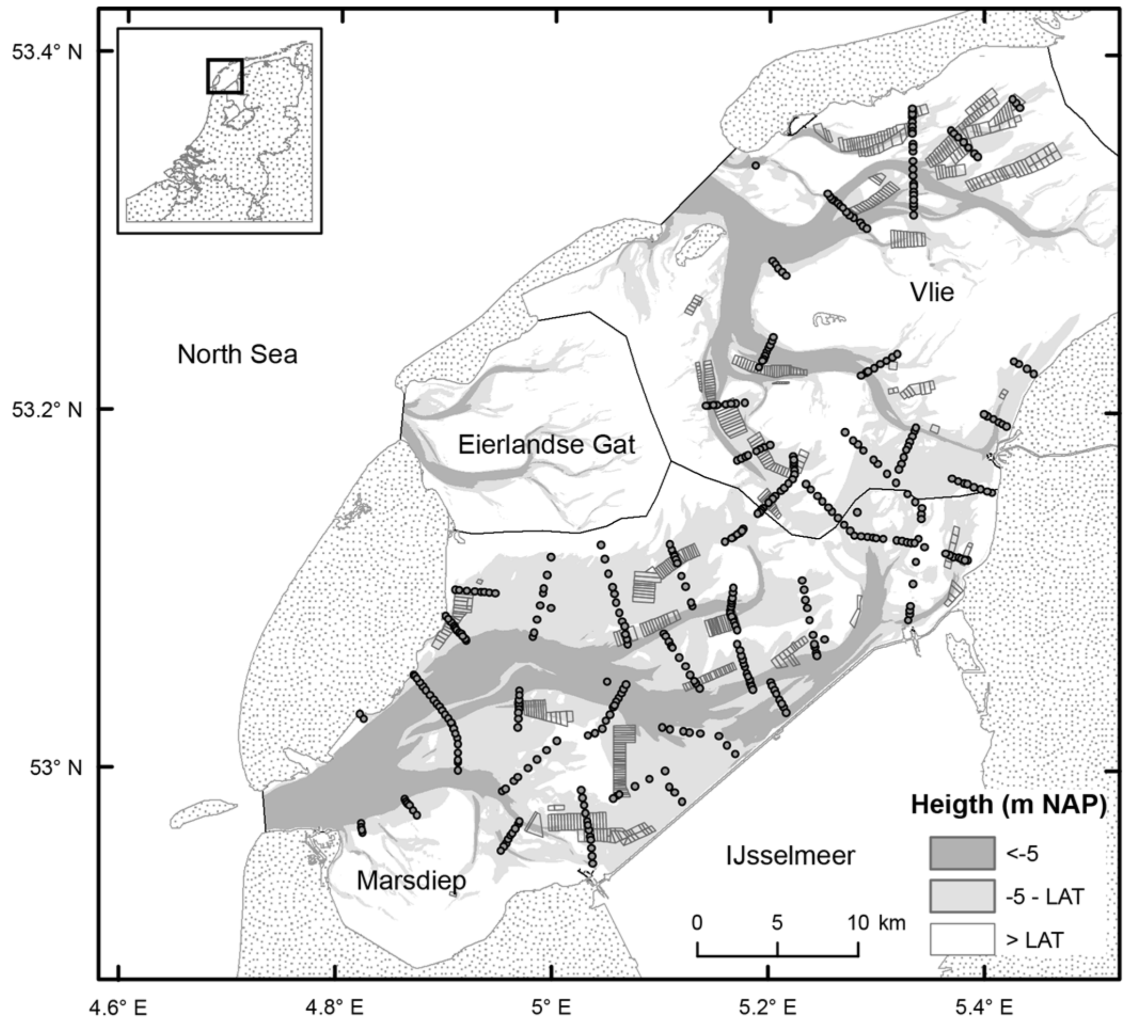

Figure 1. Western Dutch Wadden Sea with sampling stations (circles) of the macrozoobenthos survey in 2008, outlines of mussel culture plots and borders of the tidal basins (solid lines). Insert in the upper left shows the Netherlands. Shading representing height only applies to the Wadden Sea not to North Sea and IJsselmeer.

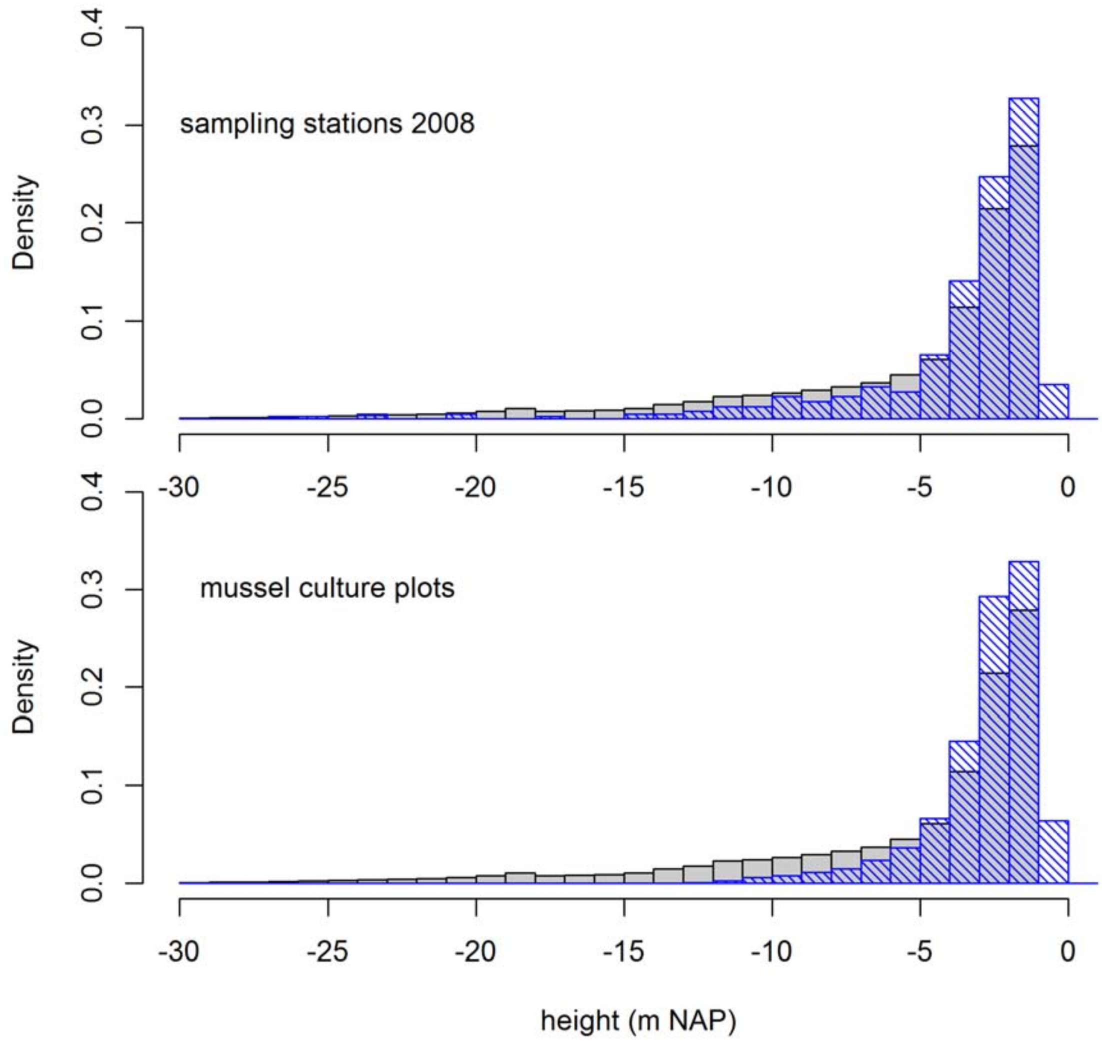

Figure 2. Histogram of height relative to NAP of the subtidal area of the Marsdiep and Vlie basins in western Dutch Wadden Sea with the depth distribution of sampling stations superimposed as hatched blue bars in the top panel and the depth distribution of mussel culture plots in the lower panel. The x axis is cut of at -30 m. Less than 0.5 % of the area is below -30 to a minimum of -49 m.

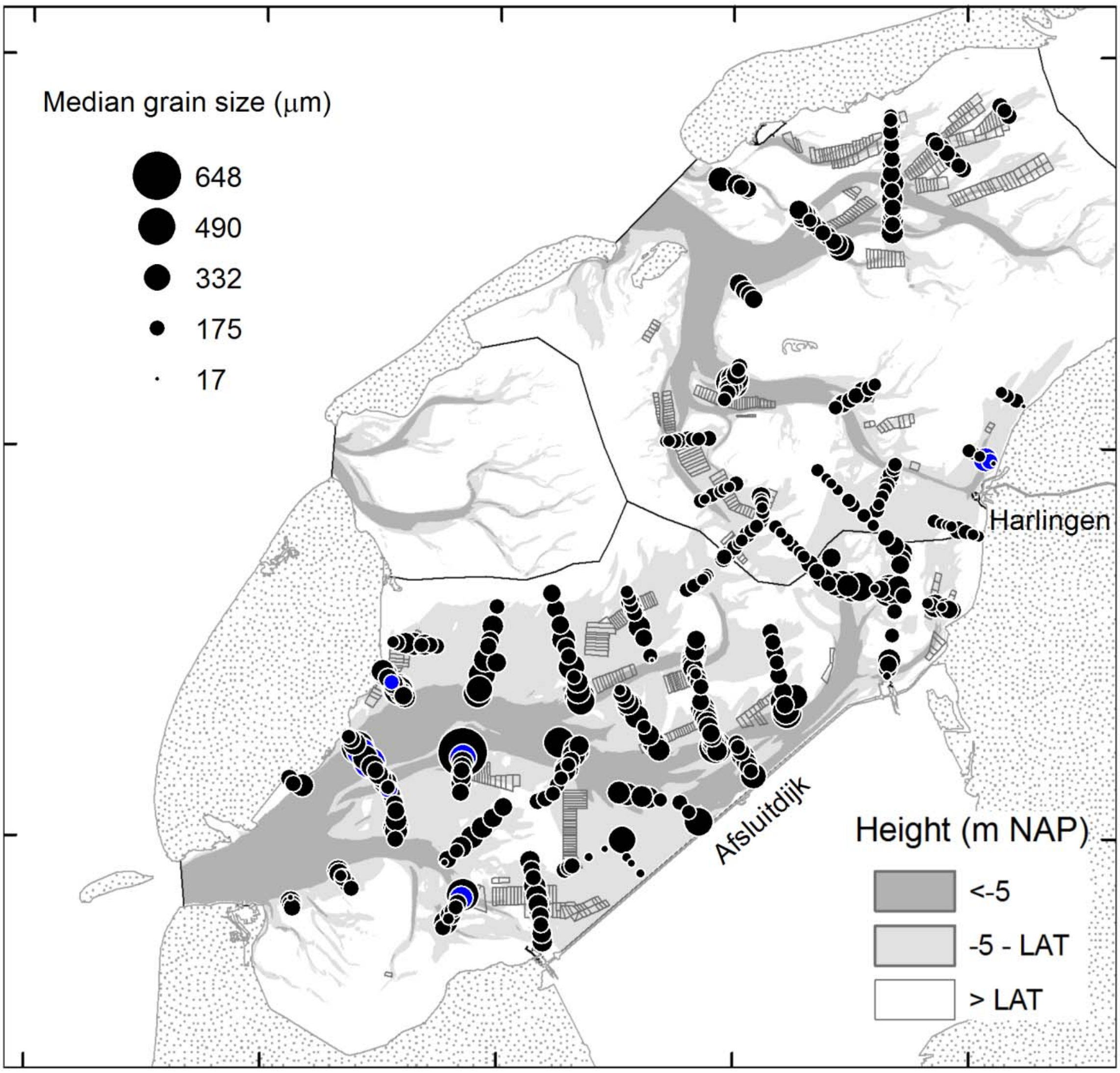

Figure 3. Median grain size of the top 8 cm of the sediment at the sampling stations in autumn 2008. Stations with stones > 2 cm are in shown blue.

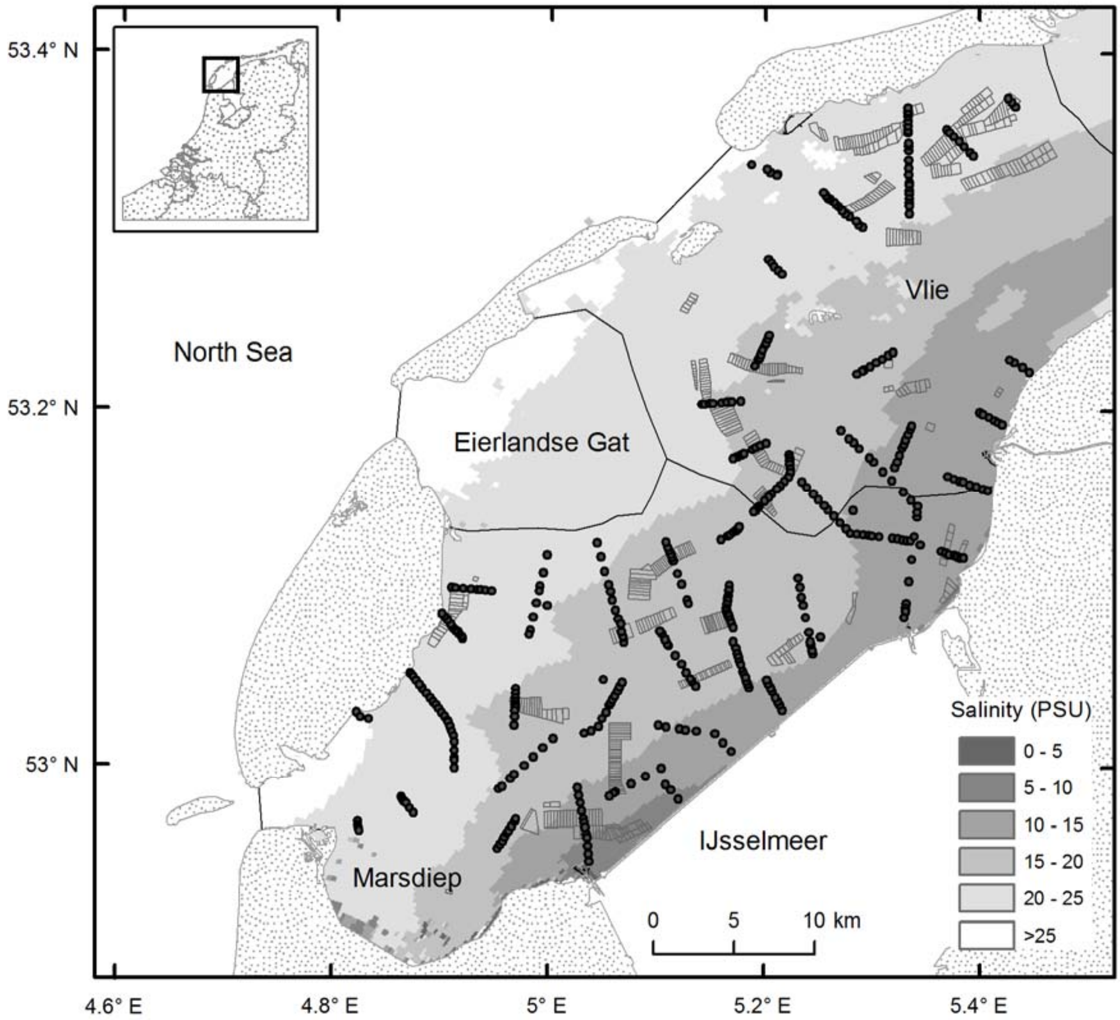

Figure 4. Map of the average of modelled sea water salinity in a dry period with little fresh water discharge and a wet period with a large water discharge from the IJsselmeer. Sampling stations and mussel culture plots are also shown.

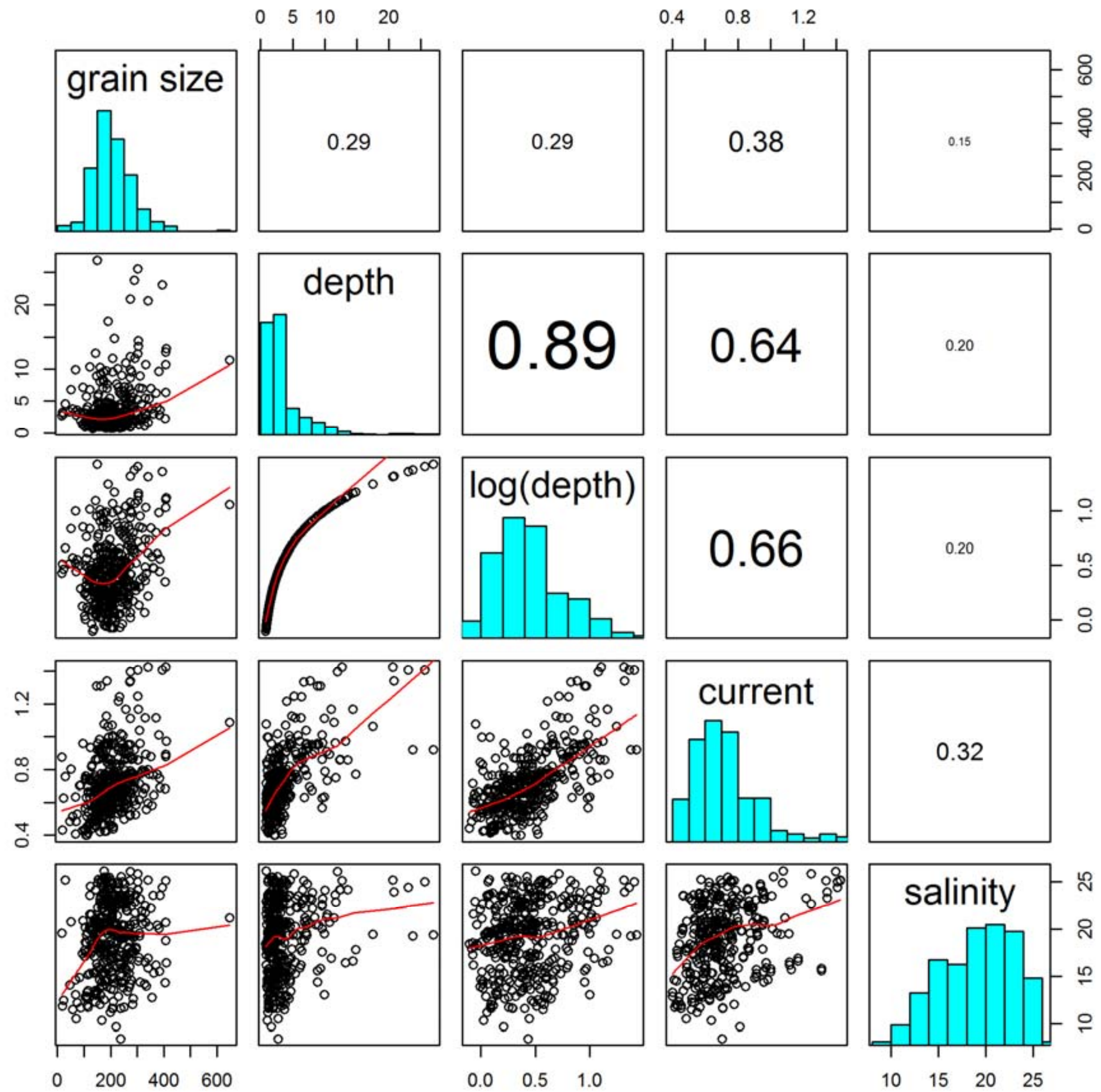

Figure 5. Pair plot of environmental variables at the sampling stations in the western Dutch Wadden Sea. Pearson correlation coefficients between the variables are given above the diagonal. Below the diagonal the variables are plotted against each other together with a lowess smoother. Grain size is measured the depth is extracted from a sounding map. Maximum current speed (current) and salinity are both model predictions. Depth is included untransformed as well as the $\log_{10}$ transformed.

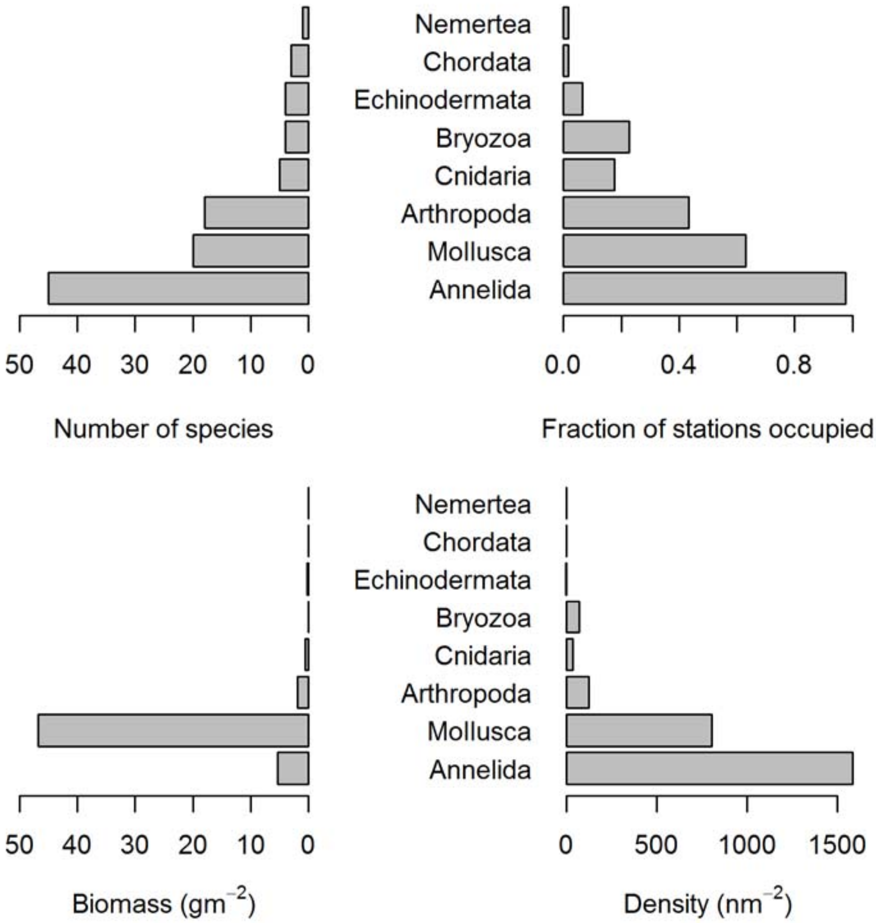

Figure 6. Taxonomic summary at the phylum level of macrozoobenthos species found in the subtidal western Dutch Wadden Sea during a survey in 2008. Upper left shows the number of species distributed among the phyla. Upper right shows the fraction of stations occupied by members of each phylum. Lower left shows the contribution of each phylum to the overall ash free dry mass of the macrozoobenthos. Lower right panel represents average numerical densities per phylum.

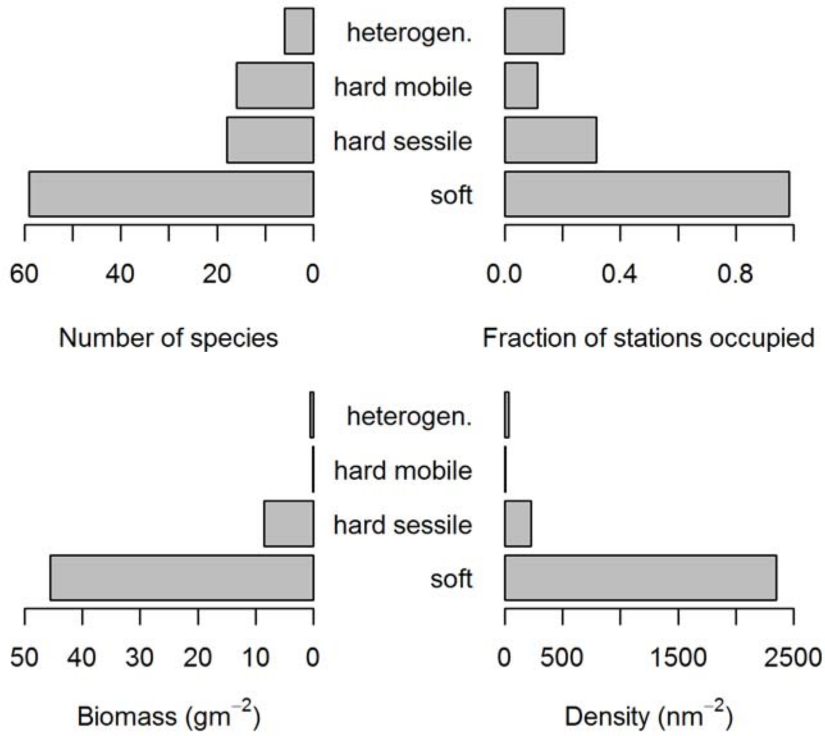

Figure 7. Macrozoobenthos species of the western Dutch Wadden Sea found in the survey of 2008 categorized according to substrate type. Hard substrate species are sub divided into mobile and sessile. Upper left shows the number of species per substrate type. Upper right is the fraction of stations occupied by members of the substrate groups. Lower left shows the biomass distribution among and lower right the numerical densities per substrate group.

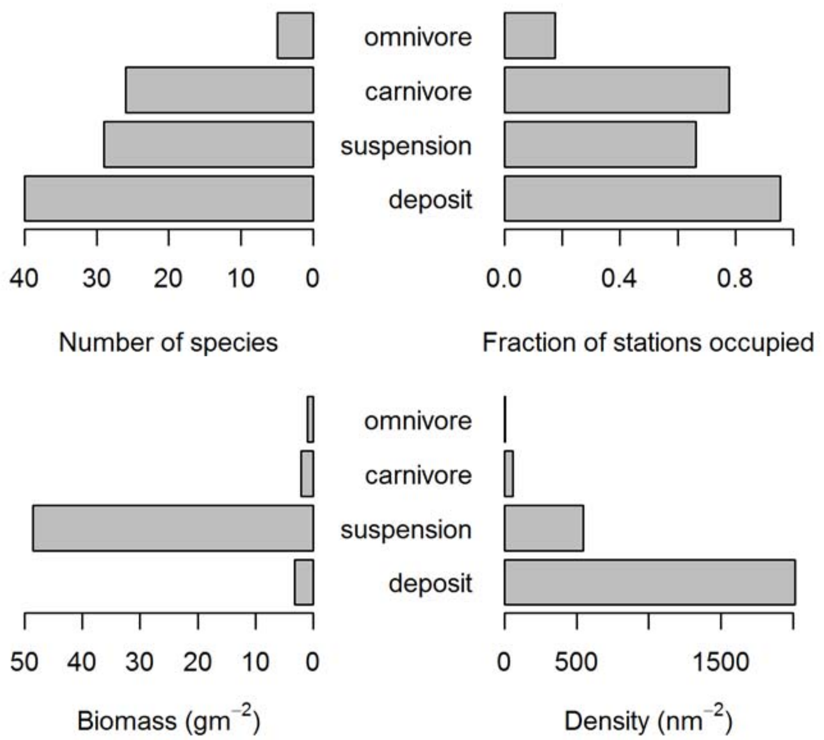

Figure 8. Macrozoobenthos of the subtidal western Dutch Wadden Sea found during a survey in 2008, categorized according to feeding type. In the upper left number of species in per feeding type are shown.

The upper right panel gives the fraction of stations occupied by representatives of each feeding type. Lower left is the distribution of total biomass over the feeding types. Lower right shows the average numerical densities per feeding type.

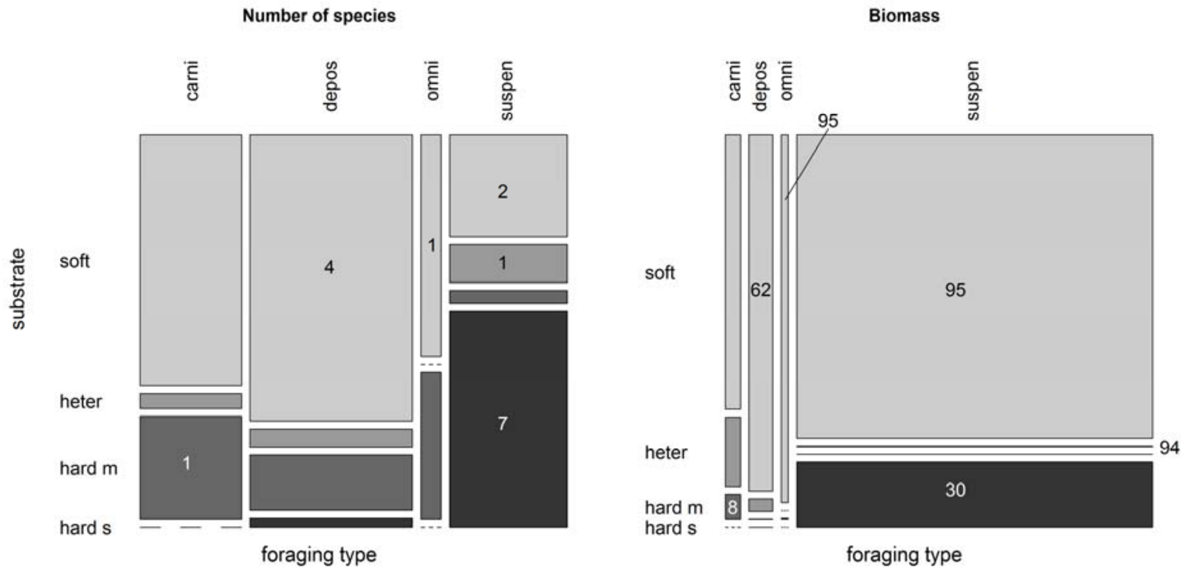

Figure 9. Mosaic plot of species numbers (left) and biomass (right) of macrozoobenthos, from the subtidal western Dutch Wadden Sea in 2008, distributed among substrate and feeding types. Numbers in the left panel are the number of invasive species in each category. Numbers in the right panel are invasive species biomass as percentages of the biomass in each category.

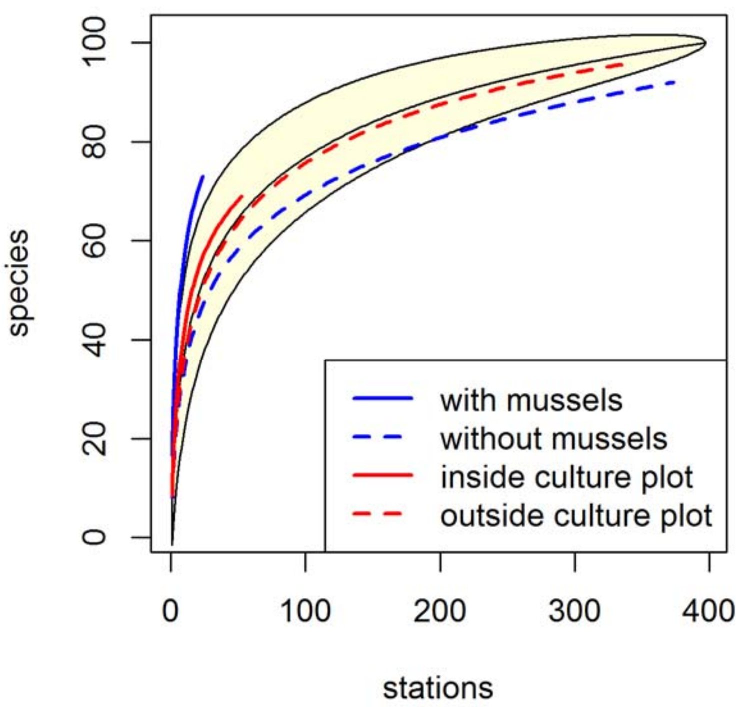

Figure 10. Macrozoobenthos species accumulation curves with increasing number of stations. The black curve with yellow polygon (twice the standard error of the estimate) is based on the entire dataset of 397 stations (0.06 m^2 each). In addition curves were estimated from subsets of the data. Subsets were based on mussel presence absence and position of the station inside or outside the mussel culture plot.

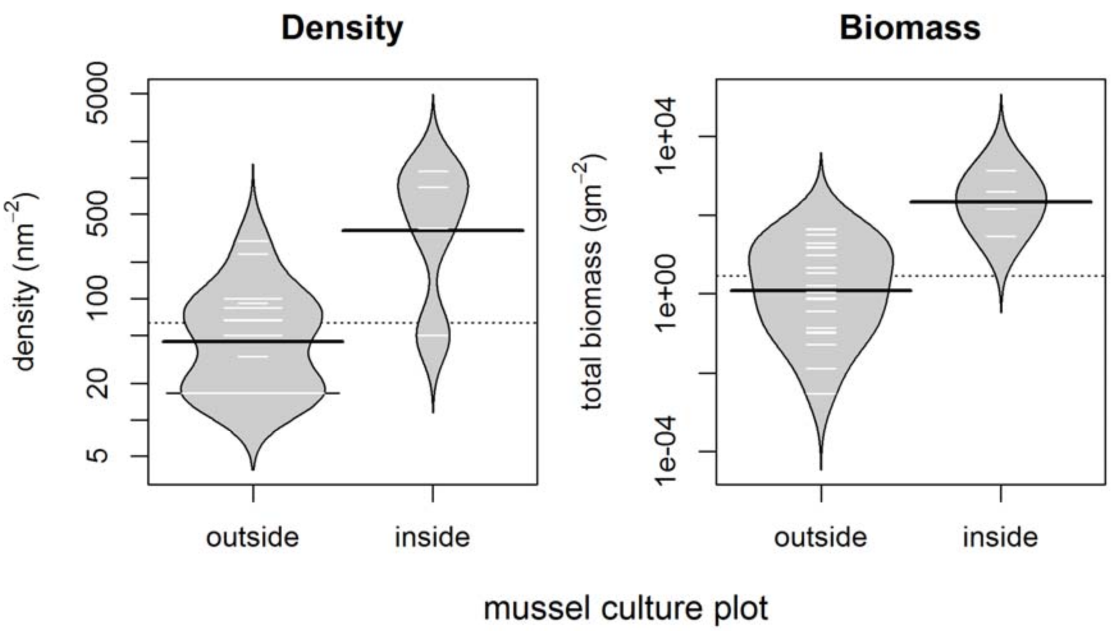

Figure 11. Numerical density (left panel) and biomass (right panel) of mussels (*Mytilus edulis*) at mussel occupied stations outside (n=20) and inside (n=4) mussel culture plots.

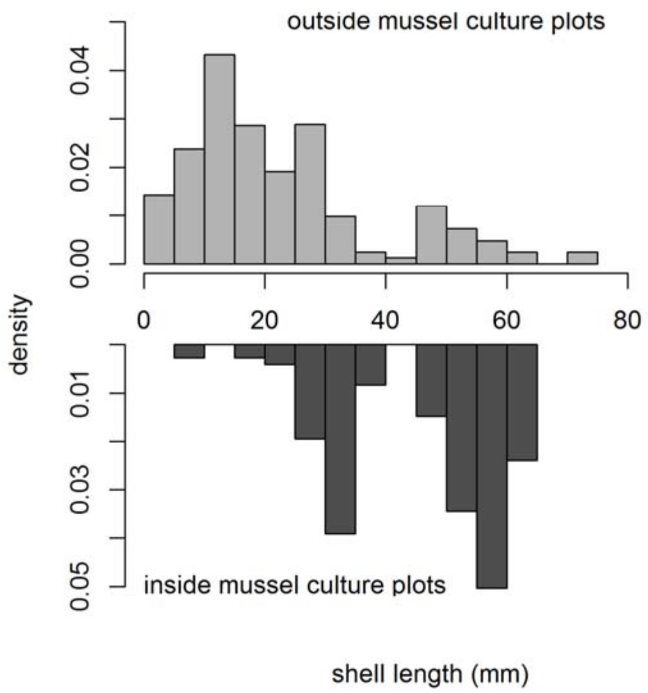

Figure 12. Length distributions of mussels outside (upper panel) and inside (lower panel) mussel culture plots. Y-axis is the probability density.

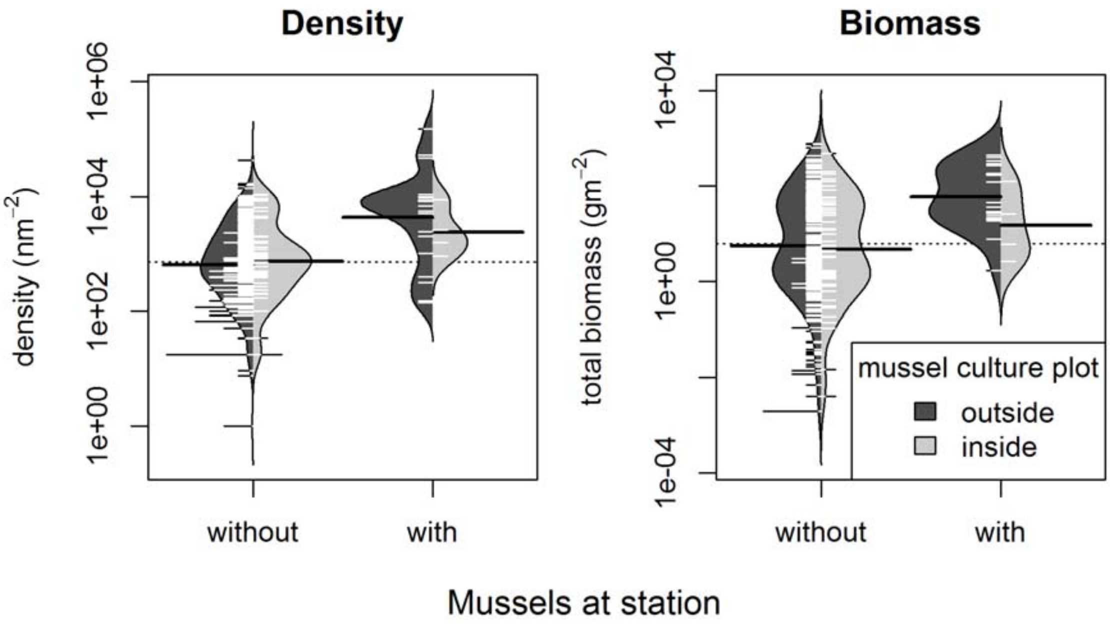

Figure 13. Total numerical density and biomass excluding mussels at stations without and with mussels either outside or inside mussel culture plots.

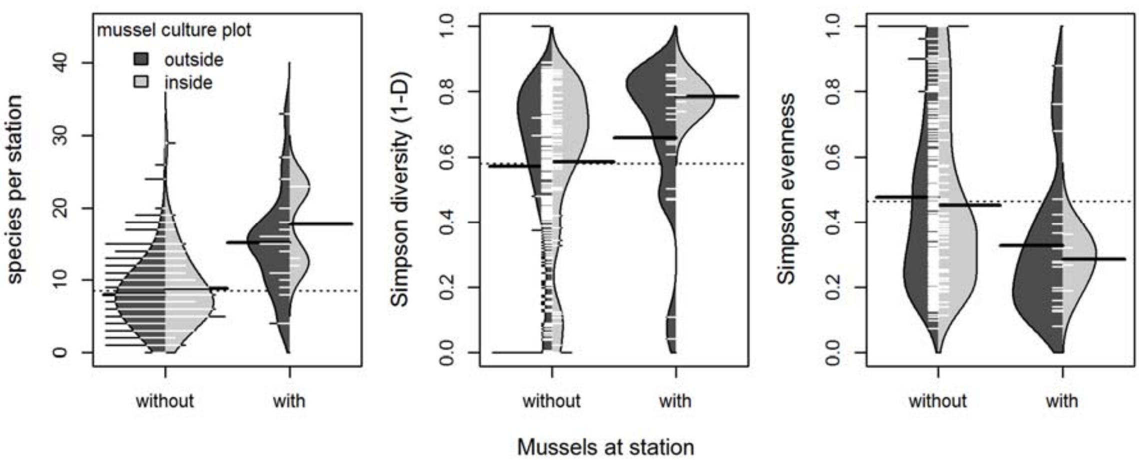

Figure 14. Macrozoobenthos species richness, Simpson diversity and evenness at stations without and with mussels and outside or inside mussel culture plots. Mussels are not included in the species counts and diversity and evenness calculations. Stations had a surface area of 0.06 m^2.

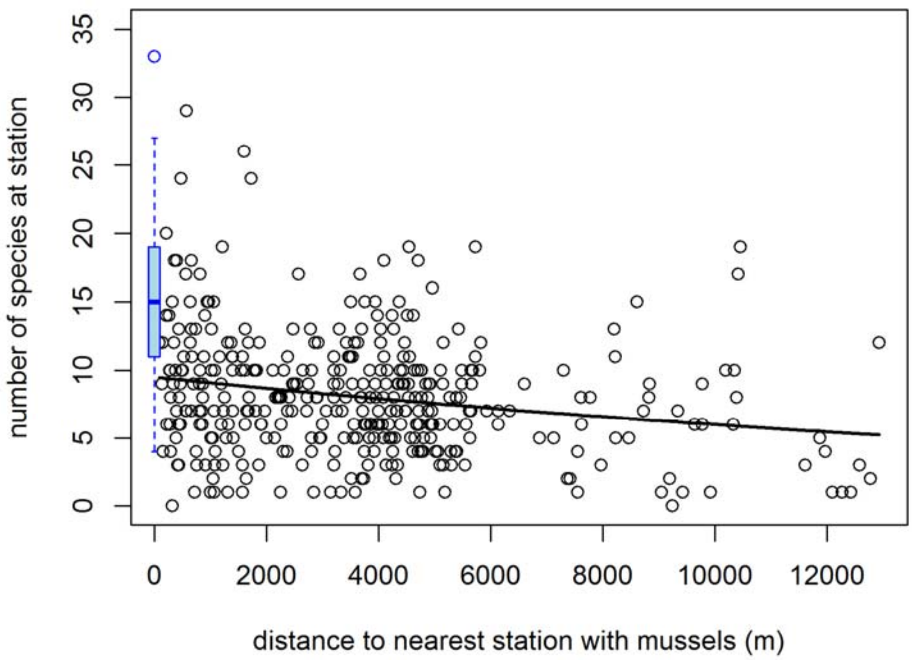

Figure 15. Number of macrozoobenthos species collected with one box core of 0.06 m2 related to the distance to the nearest station with mussels. The number of species in the boxes with mussels (at distance = 0) are summarized with box and whiskers (in blue). The plotted relationship is the result of GLM analysis excluding distance = 0.

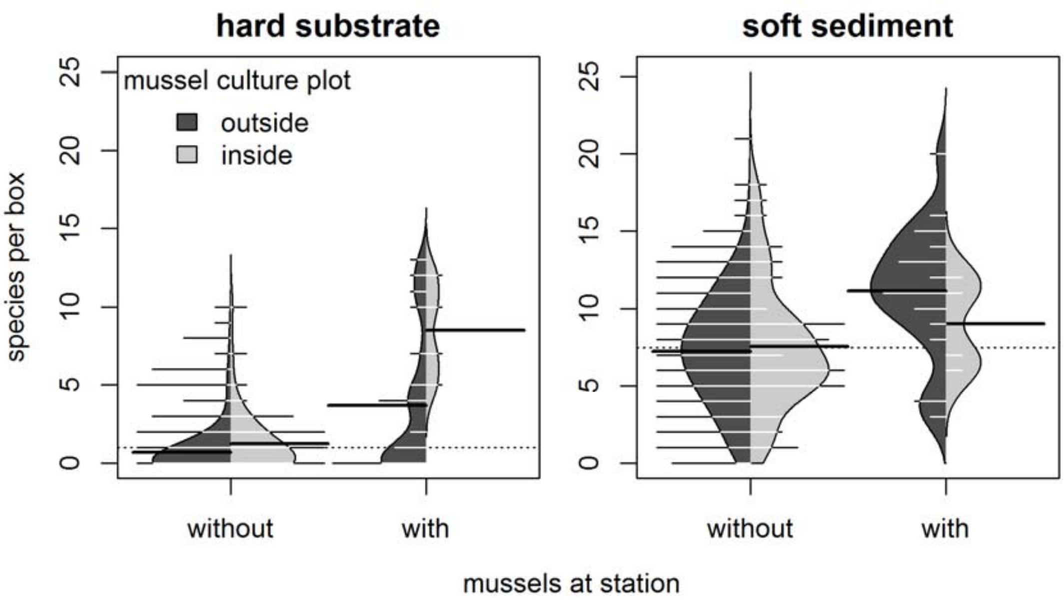

Figure 16. Species richness of hard substrate (left panel) and soft sediment species (right panel) at stations without and with mussels outside and inside mussel culture plots in subtidal of the western Dutch Wadden Sea. Mussels (*M. edulis*) are not included in the species counts.

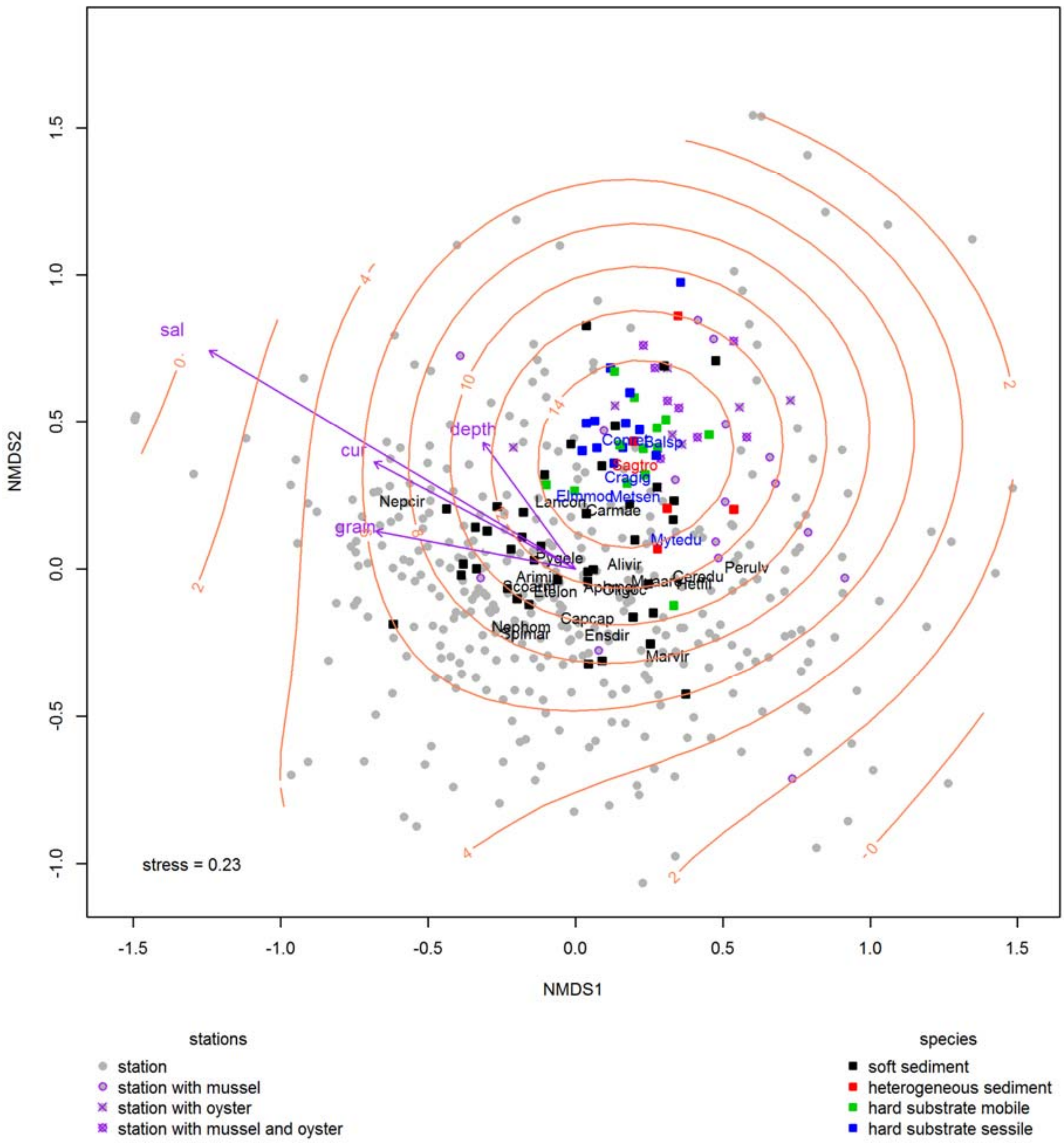

Figure 17. Nonmetric multidimensional scaling plot of stations sampled in the subtidal of the western Dutch Wadden Sea. Based on a Bray Curtis similarity matrix from square root transformed and Wisconsin double standardized numerical density data. Stations are categorized based on presence of mussels and oysters. Centroids of major species are indicated with codes, other species centroids are indicated with squares. The colour code applies to both species codes and symbols. Arrows show angle and direction of the strongest correlation between stations and environmental variable. Isolines are from a species richness surface fitted to the ordination diagram.

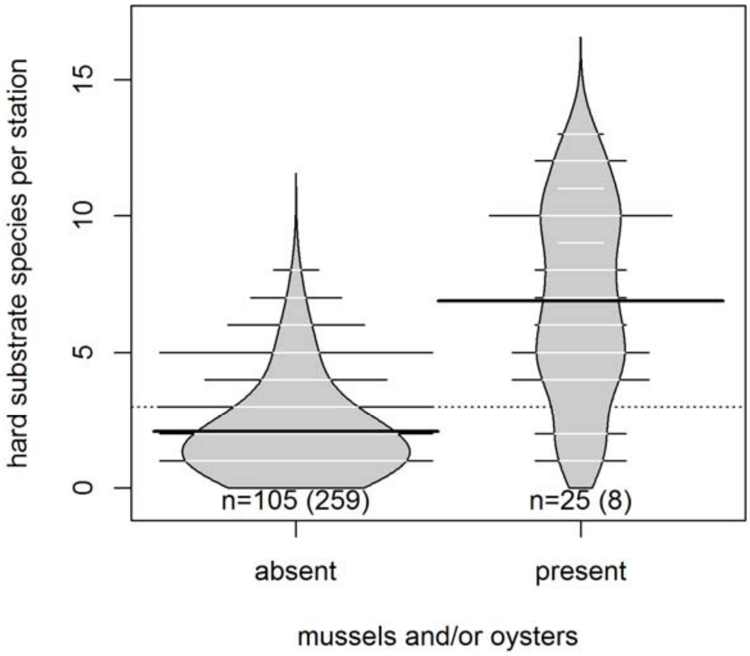

Figure 18. Hard substrate species richness at stations with at least 1 hard substrate species present other than mussel or oyster depending on the absence or presence of mussels (*M. edulis*)and/or oysters (*C. gigas*). Species richness does not include mussels and oysters. Number of stations included in each category is indicated along the x-axis. Between brackets is the number of stations that contained no hard substrate species other than mussels or oysters and that were not included in the graph.

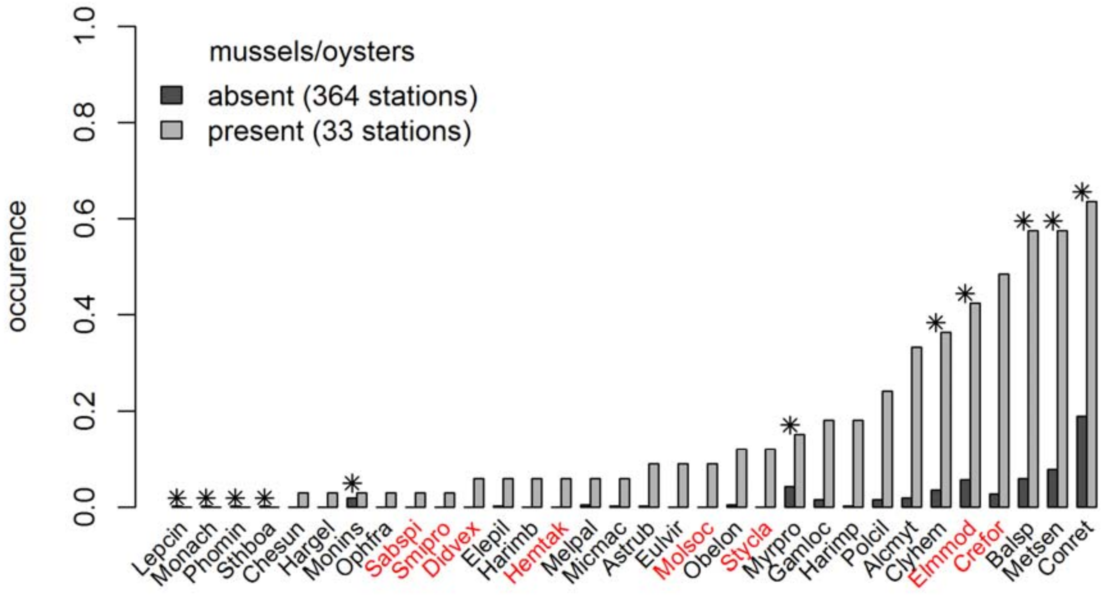

Figure 19. Occurrence (fraction of stations occupied within habitat) of hard substrate species at stations without and with mussels and/or oysters. Species that occurred more often at stations without mussels

and/or oysters are marked with *. Number of stations are included in the legend. Invasive hard substrate species abbreviations are printed in red.

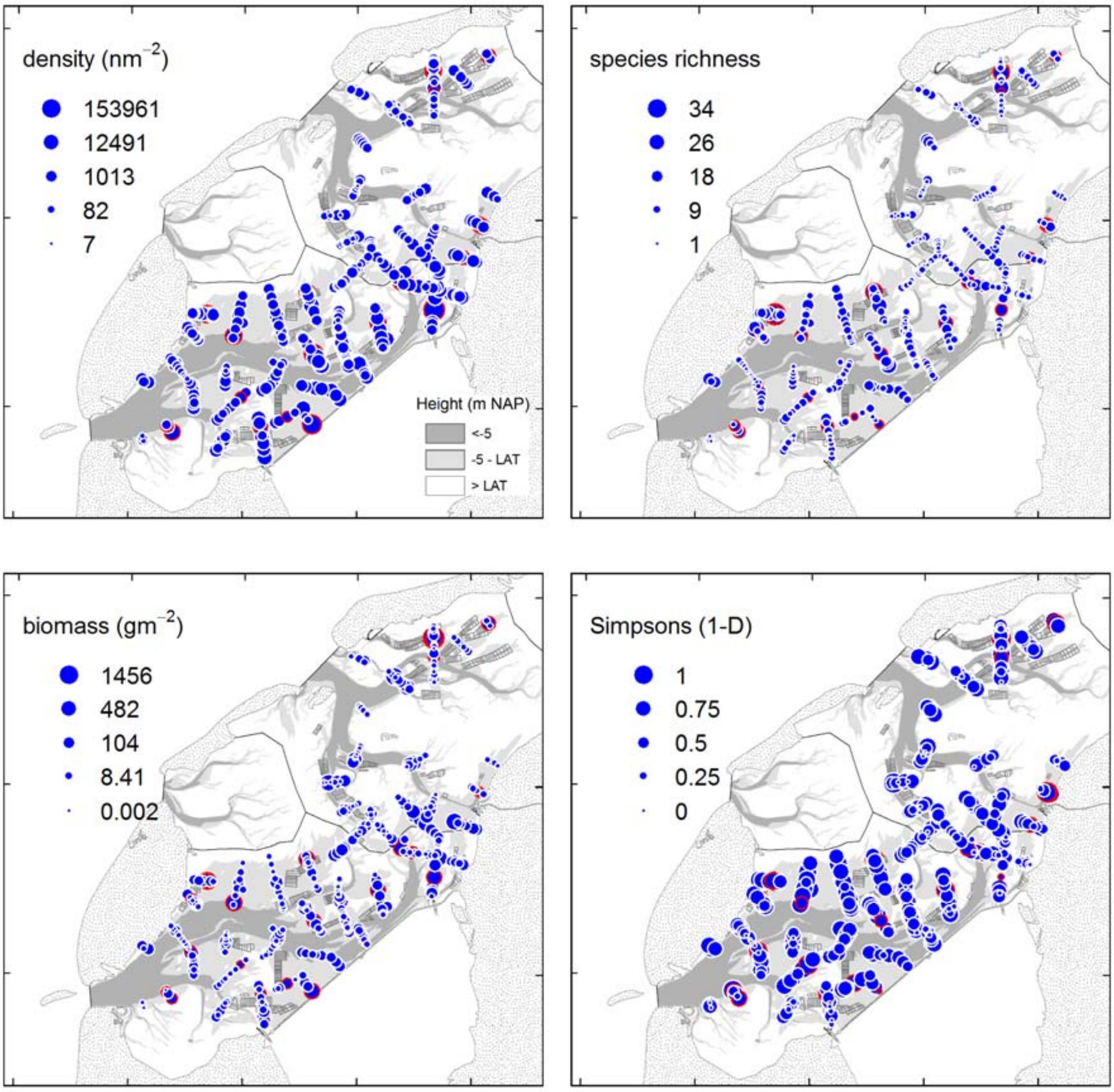

Figure 20. Macrozoobenthos total densities, biomass, species richness, and Simpsons (1-D) biodiversity index in the subtidal western Dutch Wadden sea in autumn 2008. Stations with mussels are either indicated with a red dot or a symbol with a red border.

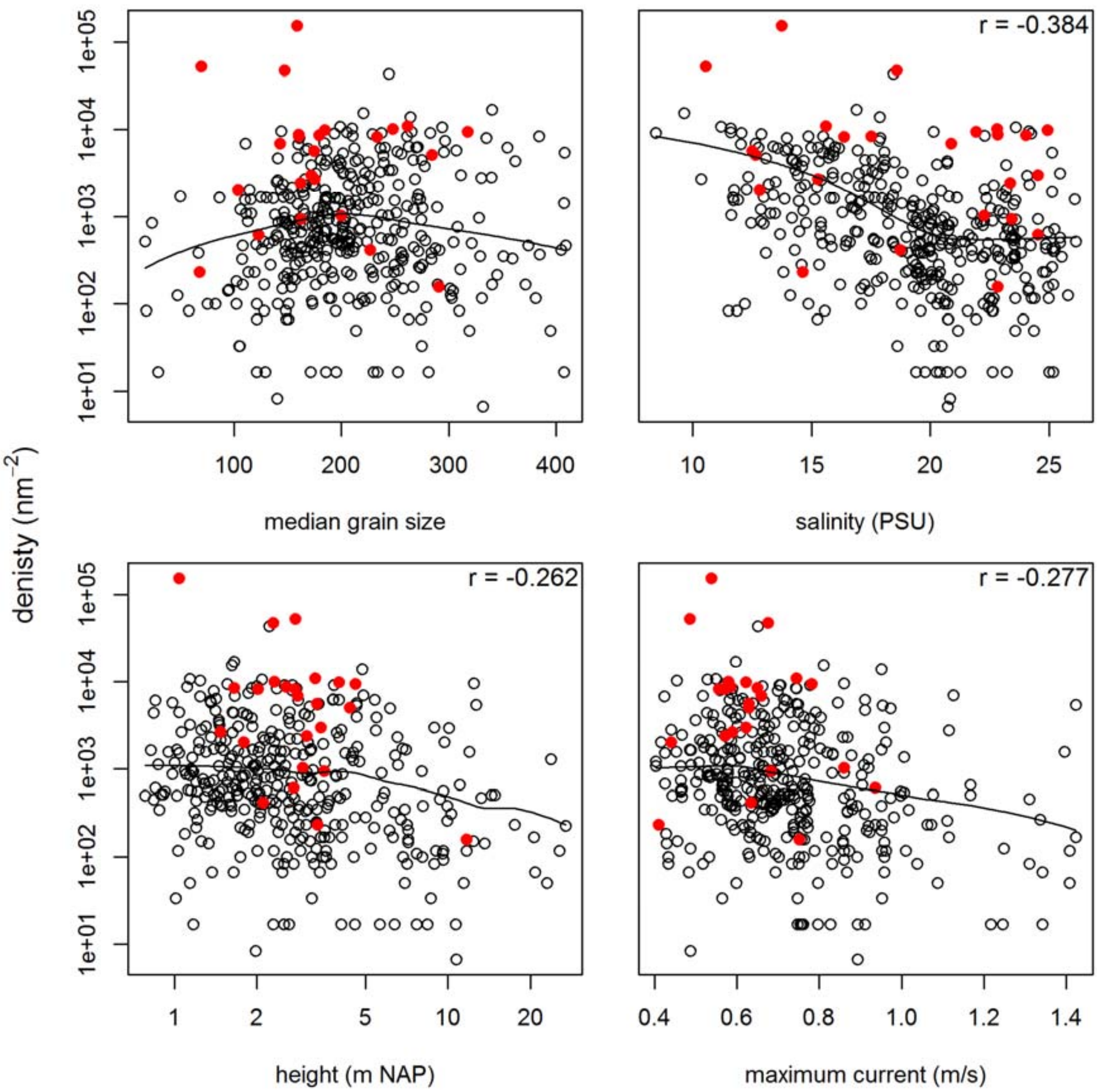

Figure 21. Macrozoobenthos total density along four environmental gradients. Values of stations with mussels are shown in red. Lines are lowess smoothers. Correlation coefficients of significant Pearson correlations (p<0.05) are printed along the top margin of the panels.

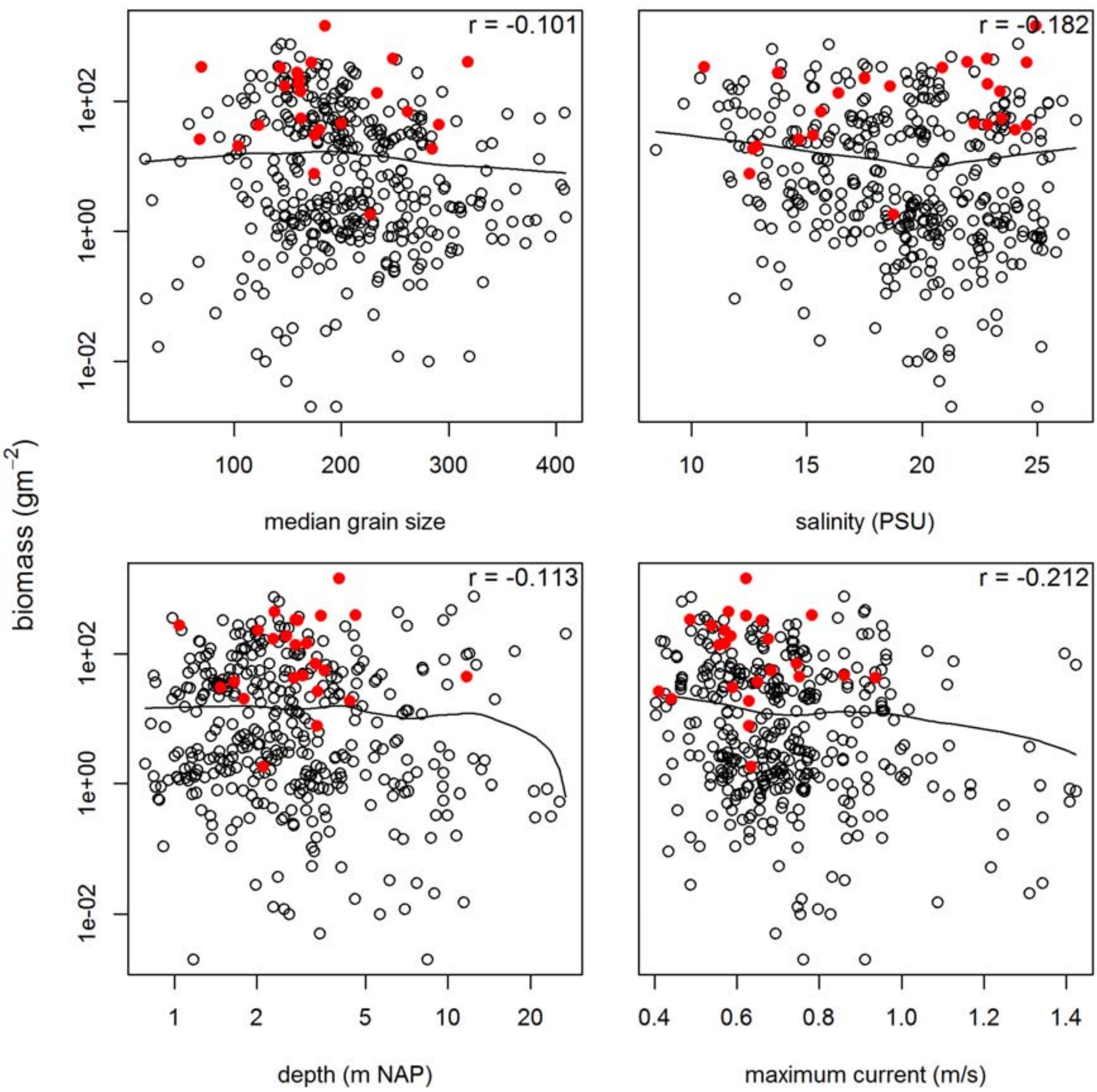

Figure 22. Total macrozoobenthos biomass (ash free dry mass) along gradients of median grain size, salinity, depth and maximum current speed. Lines are lowess smoothers. Correlation coefficients of significant Pearson correlations (p<0.05) are printed in the top of the panels. Stations with mussels are plotted in red.

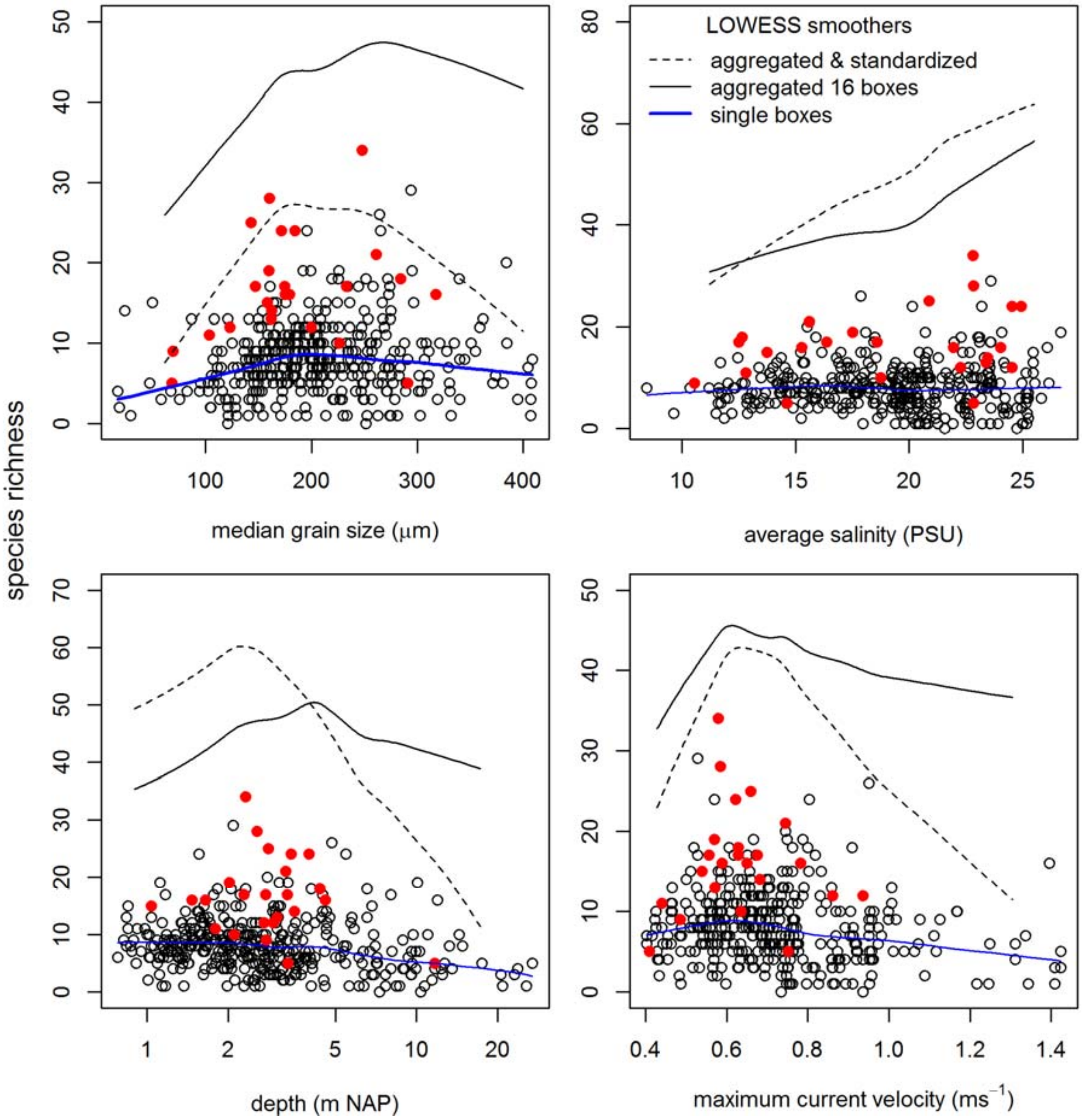

Figure 23. Species richness along four environmental gradients. Stations with mussels are shown in red. Mussels are included in the species counts. Lines are lowess smoothers. Smoothers were either based on species counts from individual boxes (0.06m^2, blue lines) or aggregates of 16 neighbouring boxes (0.96 m^2, black lines) along the gradient. Dashed lines are the aggregated species numbers standardized for the gradient range within the aggregate. Standardized aggregated species numbers are relative and only show the shape of the species richness response along the gradient, not absolute species numbers.

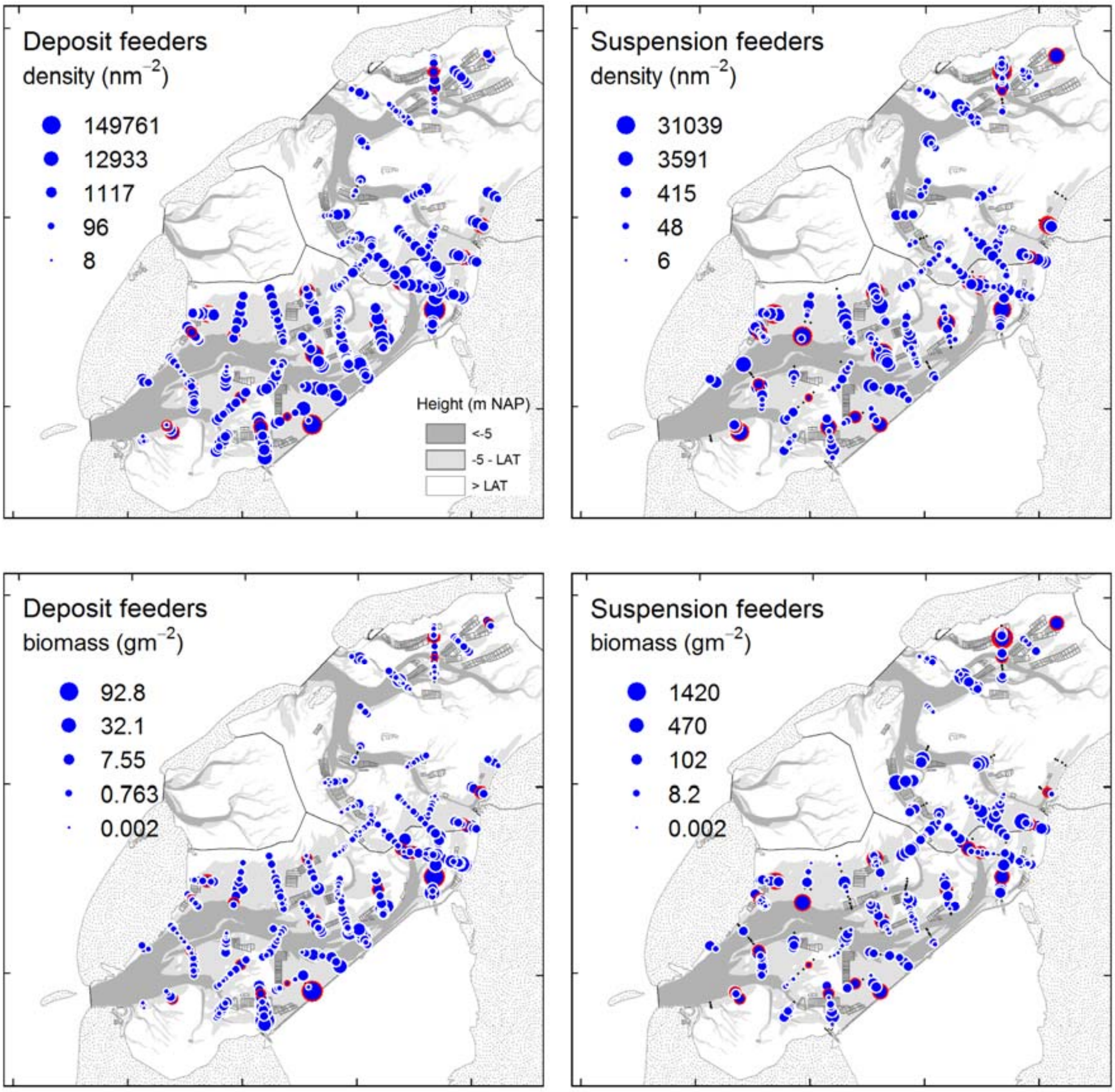

Figure 24. Maps of total density (top row) and total biomass (bottom row) of deposit (left column) and suspension feeding (right column) macrozoobenthos in the western Dutch Wadden Sea. Stations with mussels have symbols with red borders.

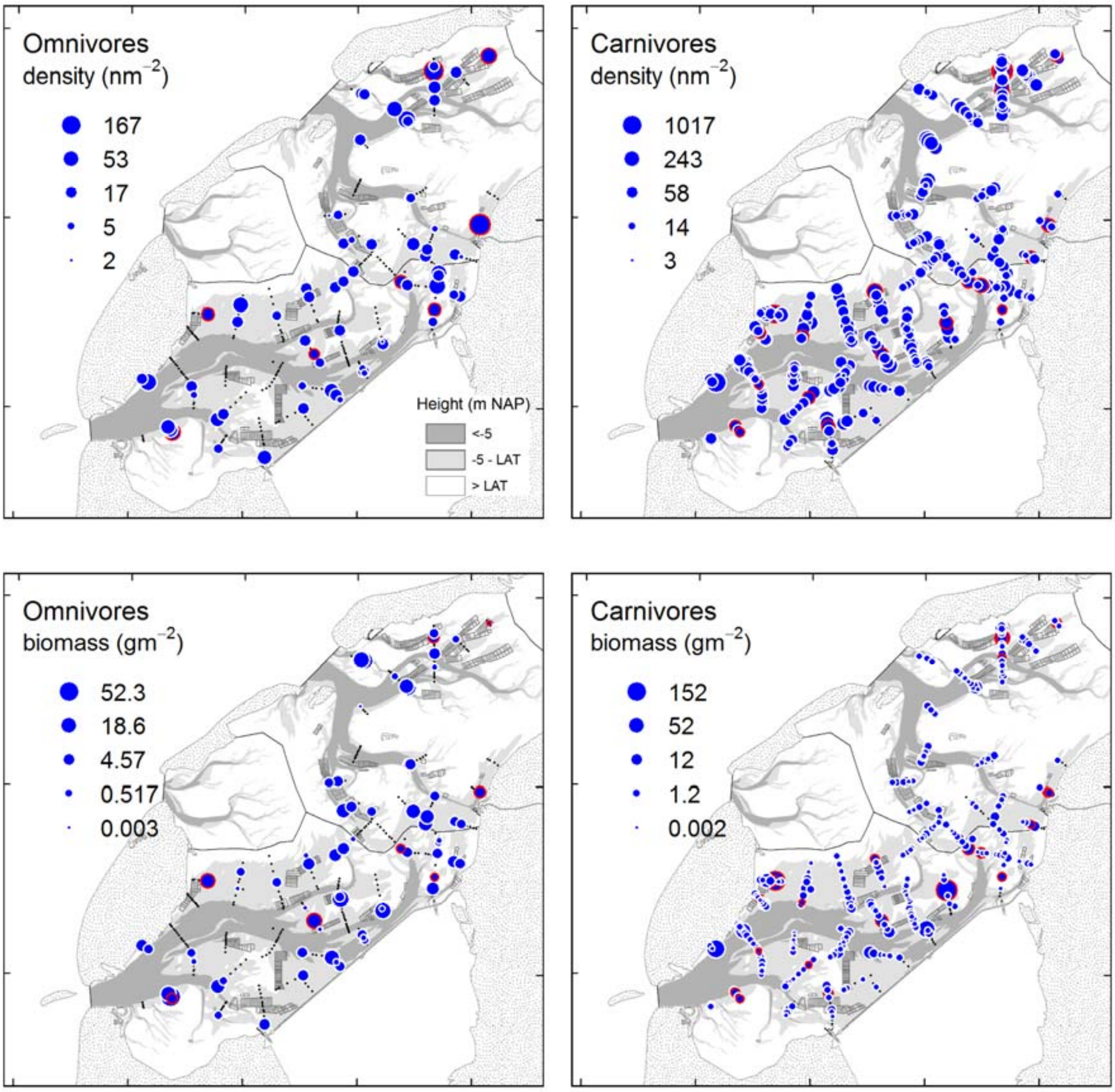

Figure 25. Maps of total density and total biomass of omivorous and carnivorous macrozoobenthos in the western Dutch Wadden Sea. Stations with mussels have symbols with red borders.

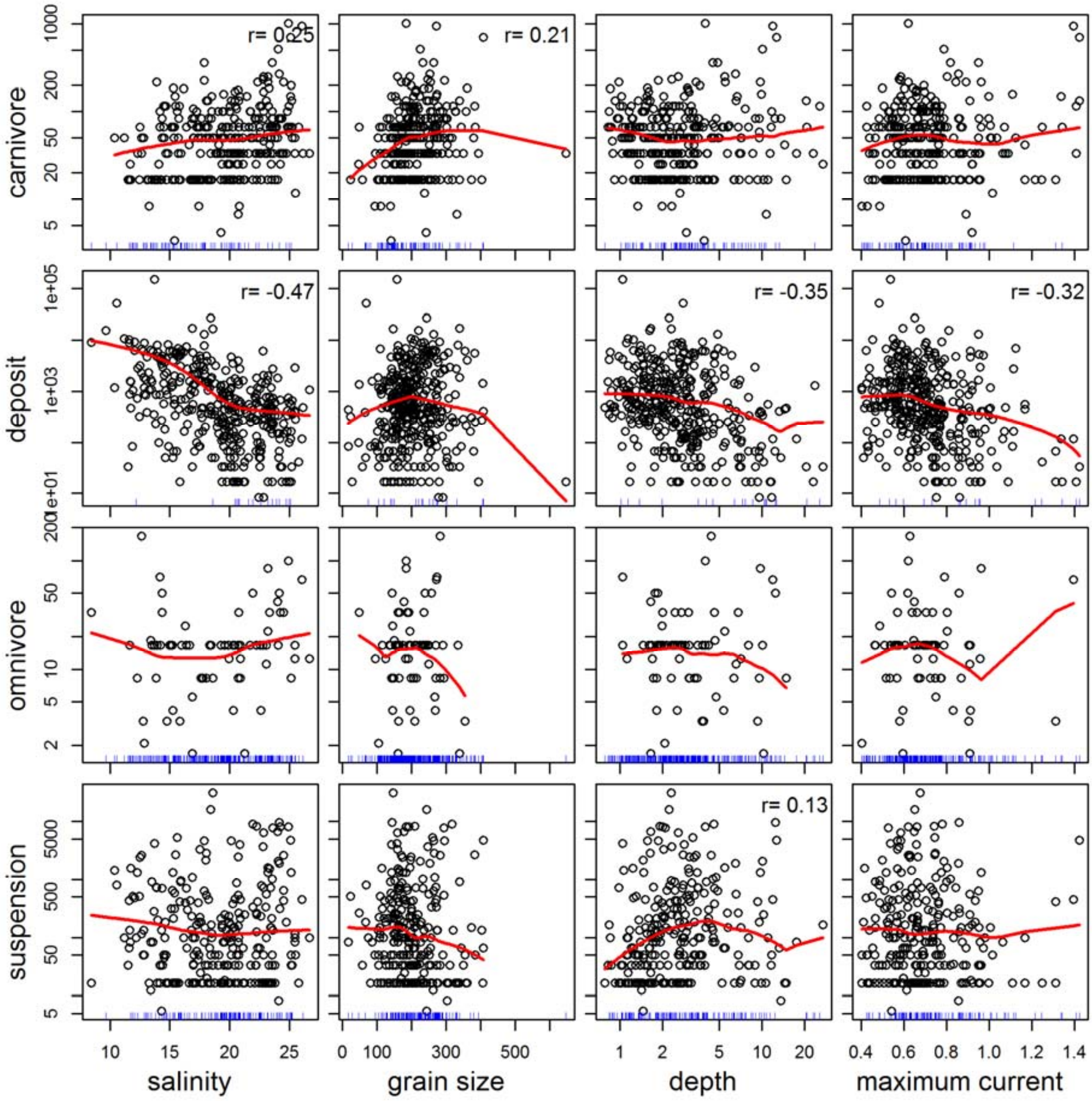

Figure 26. Relationships between numerical densities of four macrozoobenthos foraging-types and four environmental gradients in the subtidal western Dutch Wadden Sea. Red lines are lowess smoothers. Correlation coefficients of significant Pearson correlations (p<0.05) are plotted in the panels. Zeros are plotted as a blue rug along the x- axis. Zeros were not included in the correlation analysis and lowess estimation.

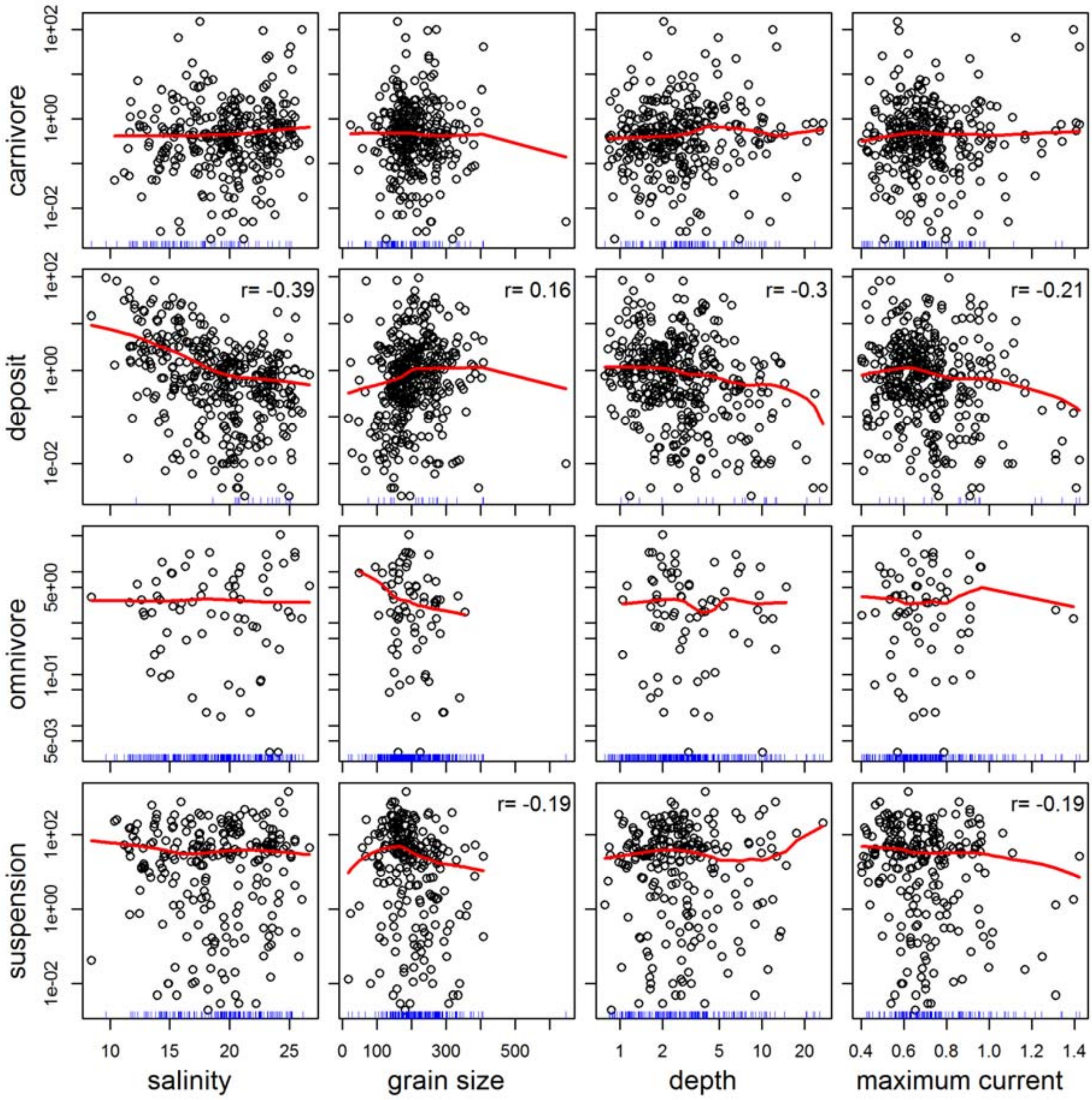

Figure 27. Total biomass (AFDM gm^{-2}) of for macrozoobenthos feeding types along four environmental gradients in the subtidal of the western Dutch Wadden Sea. Red lines are lowess smoothers. Correlation coefficients of significant Pearson correlations (p<0.05) are plotted in the top of the panels. Zeros are plotted as rug along the x axis. Zeros were excluded from the correlation analysis and smoother estimation

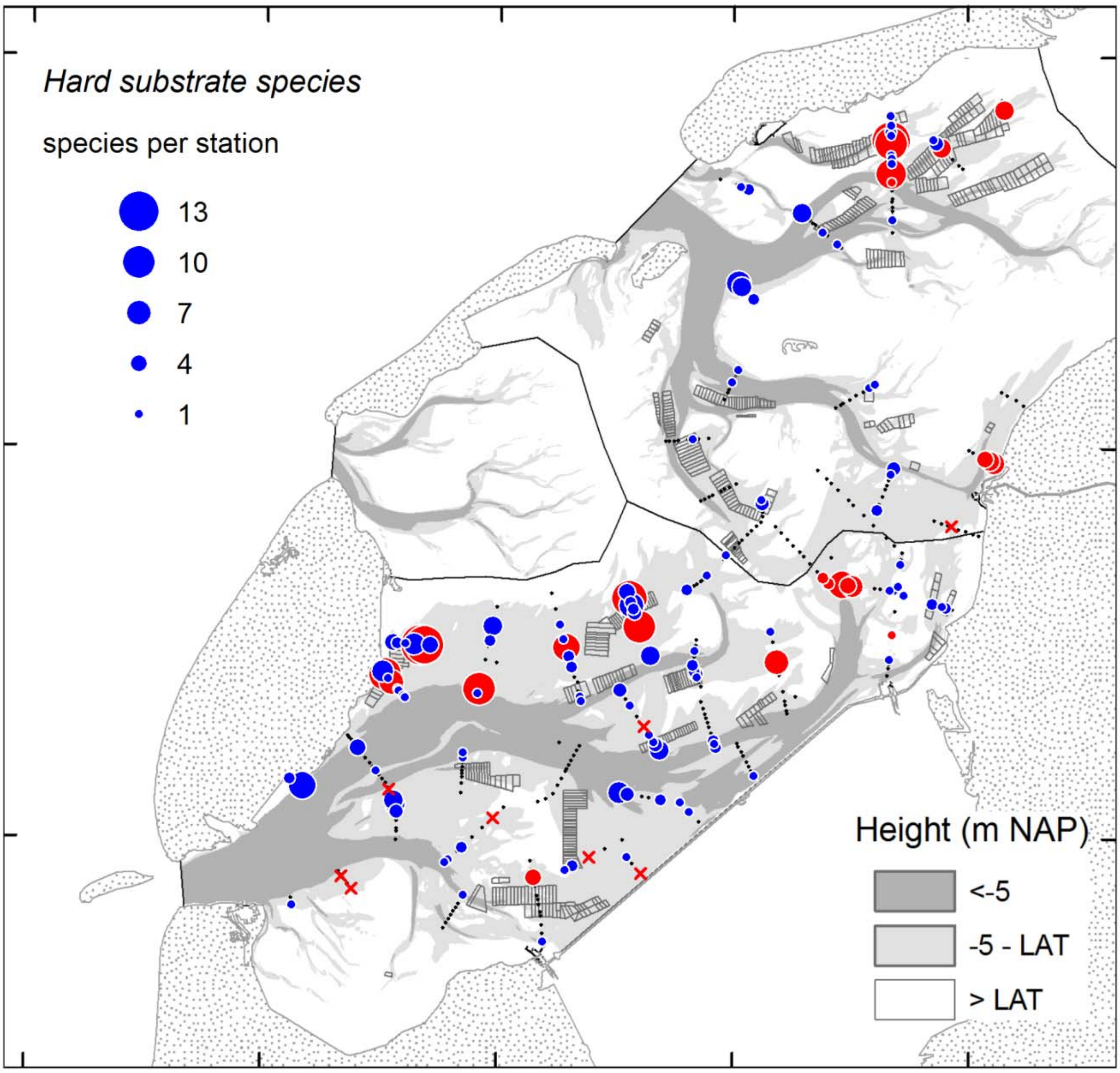

Figure 28. Hard substrate species richness at subtidal box core stations (0.06 m^{-2} each) in the western Dutch Wadden Sea. Species numbers do not include mussels (*M. edulis*) and oysters (*C. gigas*). Stations with these species are shown in red. Stations where only mussels or oysters were present but no other hards substrate species are indicated by red a red 'x'.

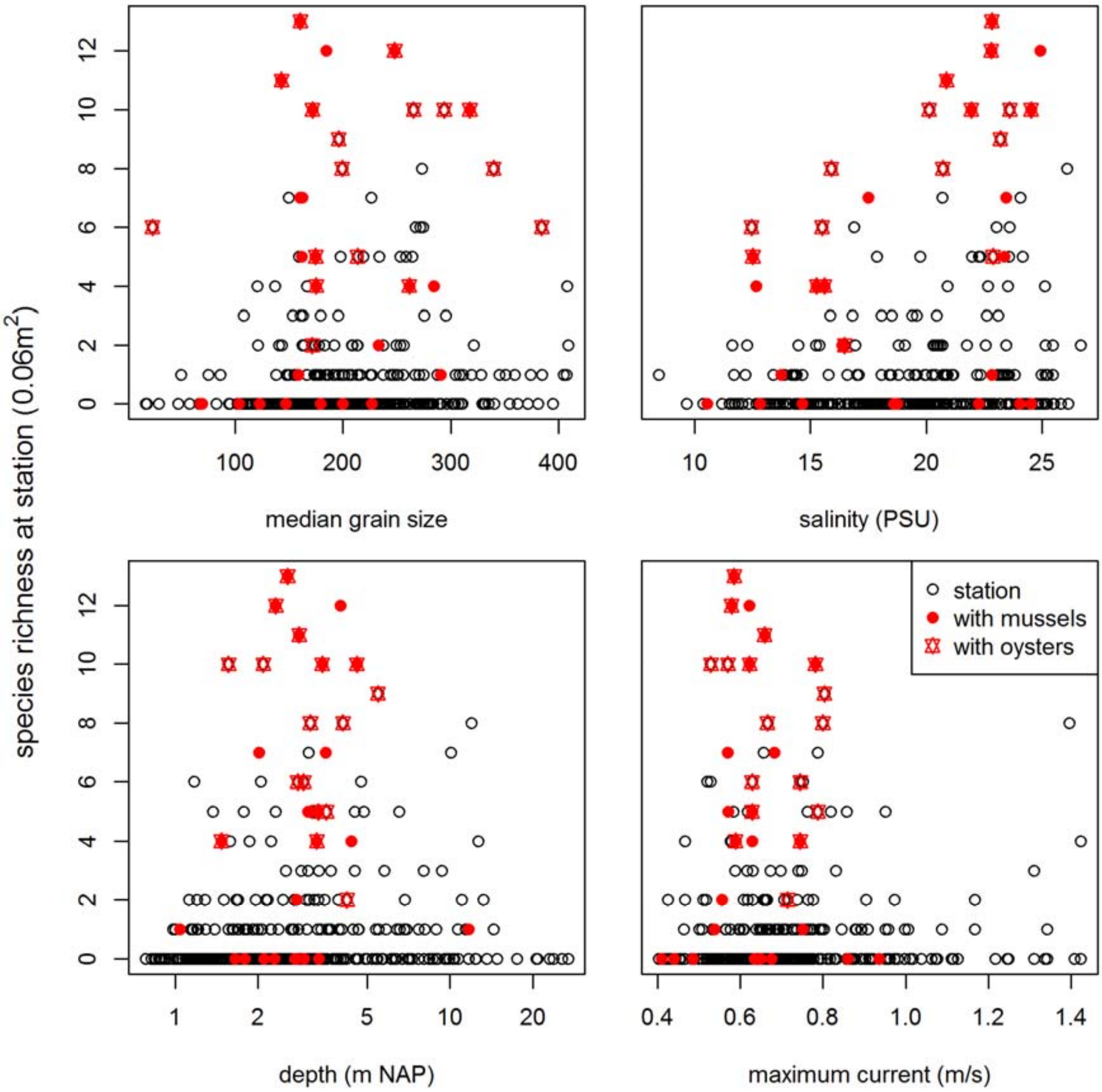

Figure 29. Hard substrate species richness along median grain size, depth, salinity and maximum current velocity gradients in the subtidal of the western Dutch Wadden Sea. Species counts do not include mussels and oysters. Presence of mussels and oysters at a station is indicated.

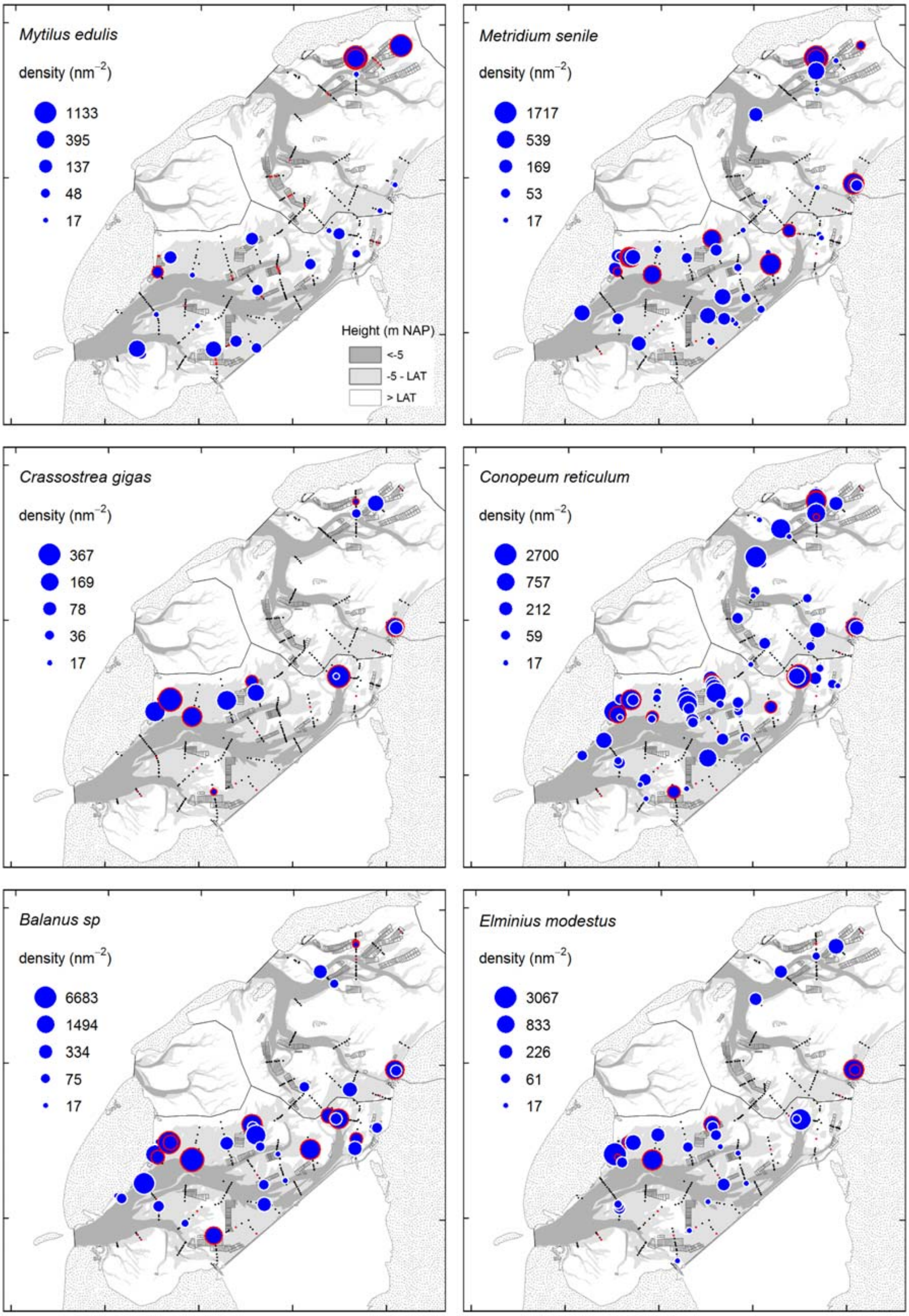

Figure 30. Hard substrate macrozoobenthos numerical densities in the western Dutch Wadden Sea in 2008. In the top left map of *Mytilus edulis* red dots or symbols with red circles indicate mussel culture plots. In the other panels stations with mussels are shown with red dots or symbols with red borders.

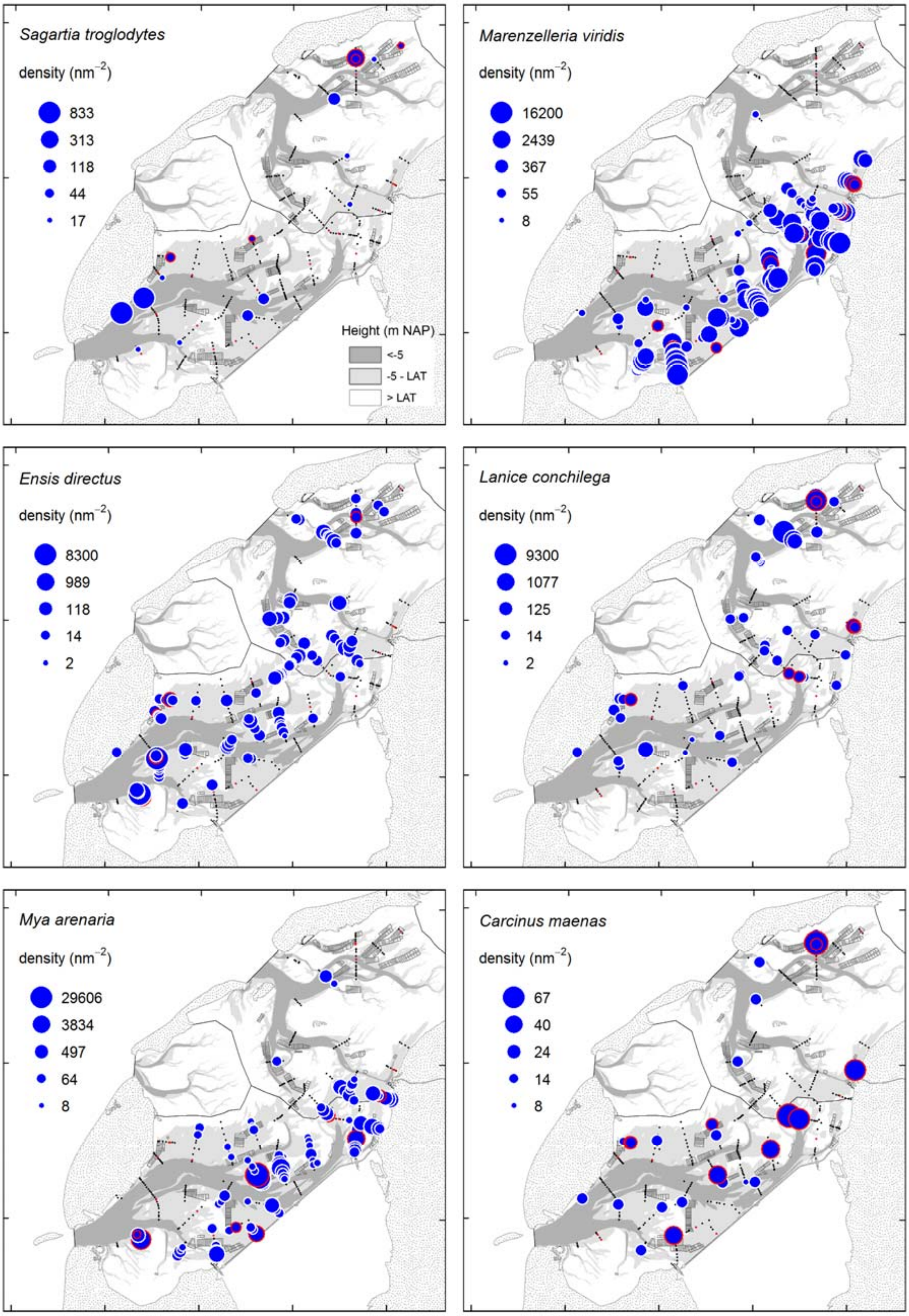

Figure 31. Maps with numerical densities of *Sagartia troglodites* a species of heterogeneous sediments and five soft sediment species in the western Dutch Wadden Sea. Stations with mussels are indicated by a red dot or a symbol with a red border.

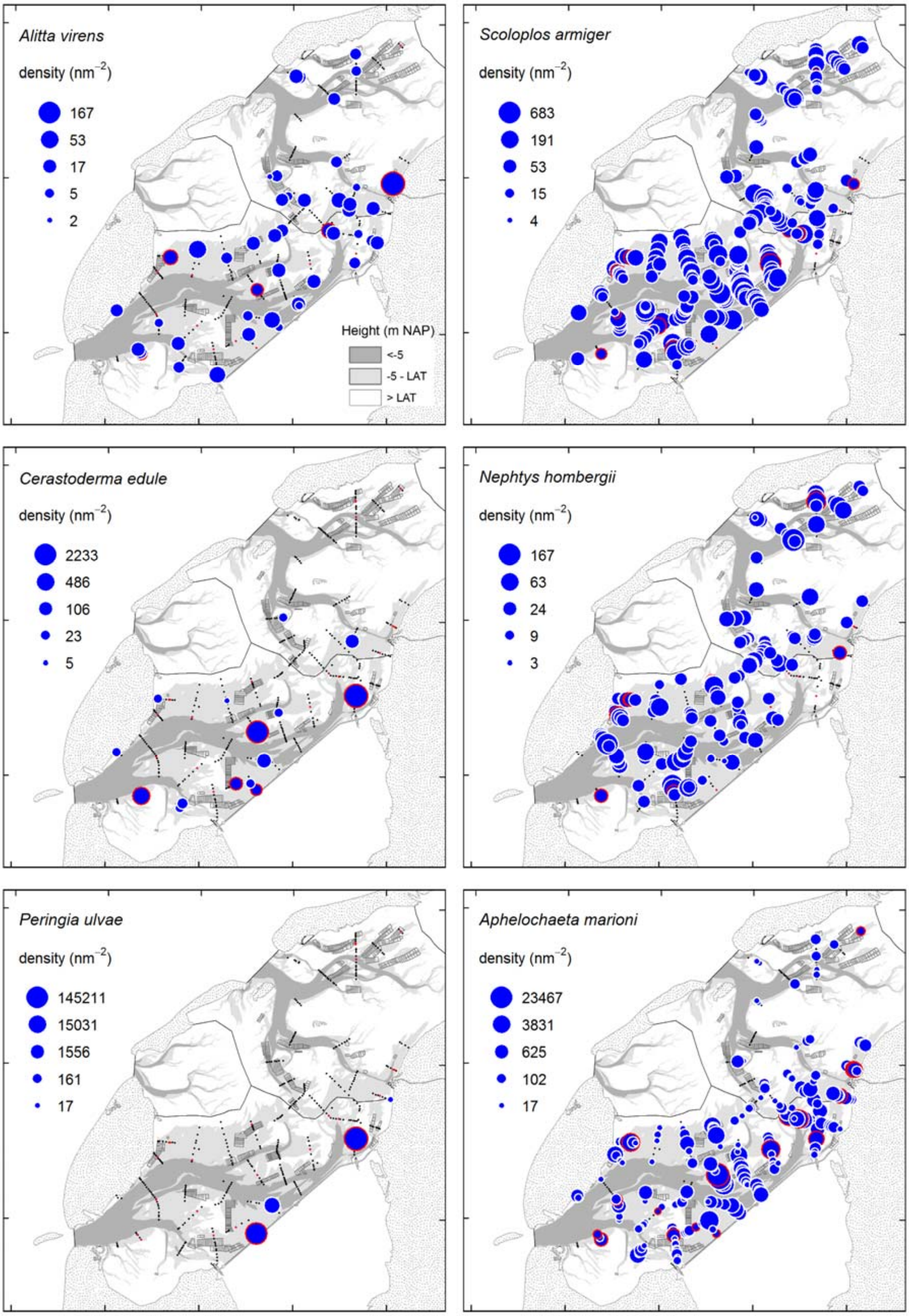

Figure 32. Maps of numerical densities of six macrozoobenthos species in the western Dutch Wadden Sea. Species names are mentioned in the panels. Red dots and symbols with red borders indicate stations with mussels.

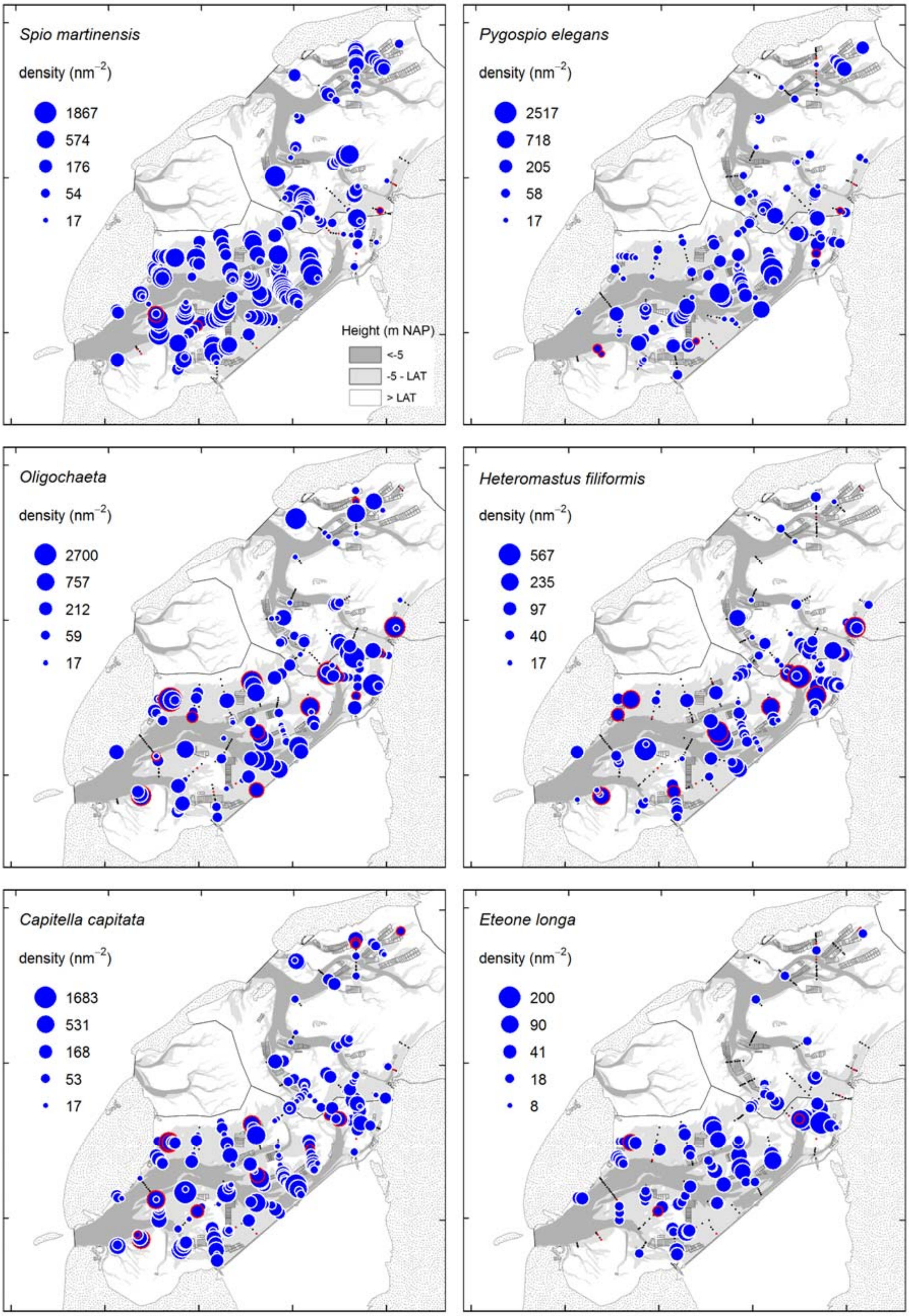

Figure 33. Maps of numerical densities of six macrozoobenthos species in the western Dutch Wadden Sea. Species names are mentioned in the panels. Red dots and symbols with red borders indicate stations with mussels.

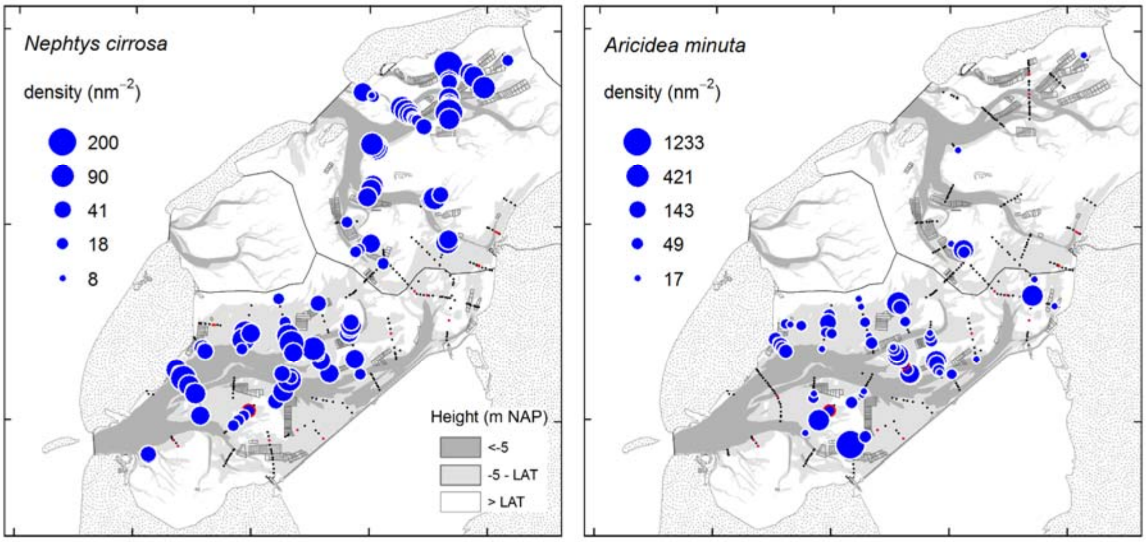

Figure 34. Numerical densities of *Nephtys cirrosa* and *Aricidea minuta* in the subtidal of the western Dutch Wadden Sea in 2008. Symbols with red borders indicate that mussels are present at the station.

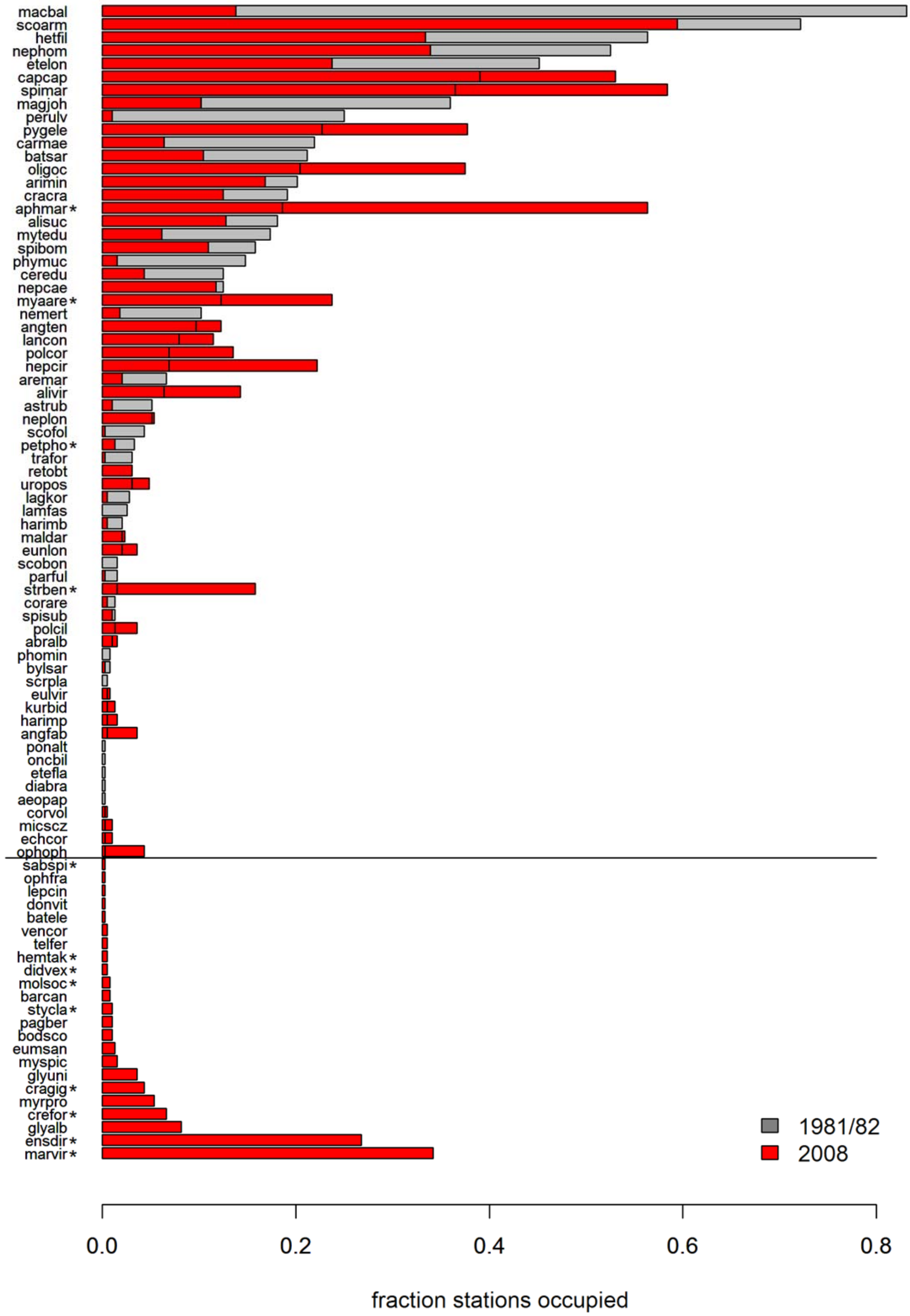

Figure 35. Occupancy of species as fraction of the stations occupied by a species. Species are arranged in decreasing order of occupancy in 1981/82. Species below the horizontal line were not encountered in the 1981/82 survey and arranged in increasing order of occupancy in 2008. Invasive species are marked by a *.

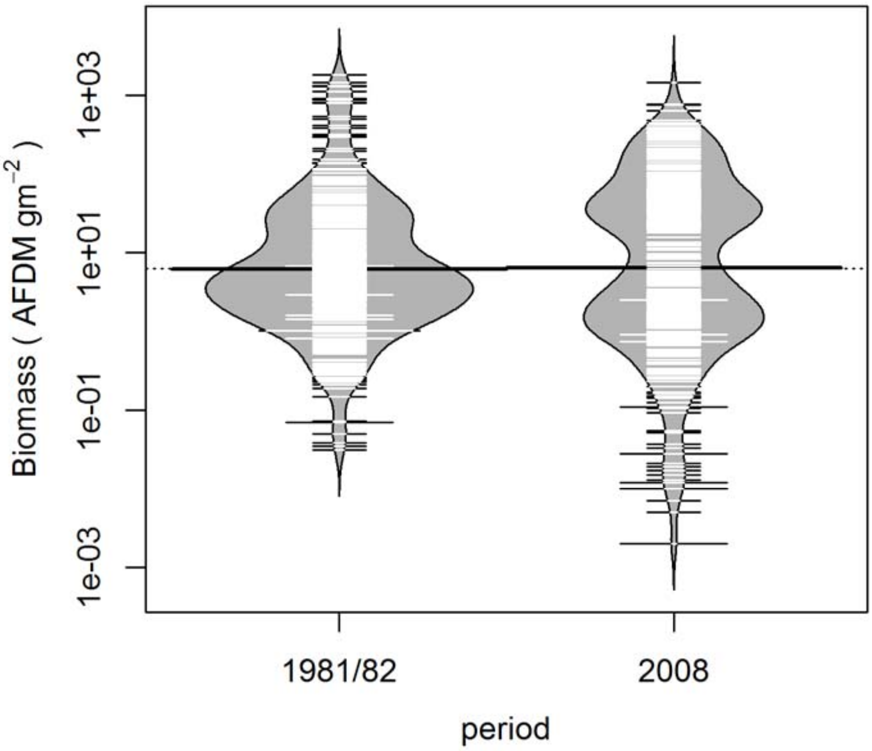

Figure 36. Total macrozoobenthos biomass in 1981/82 and 2008 in the subtidal of the western Dutch Wadden Sea.

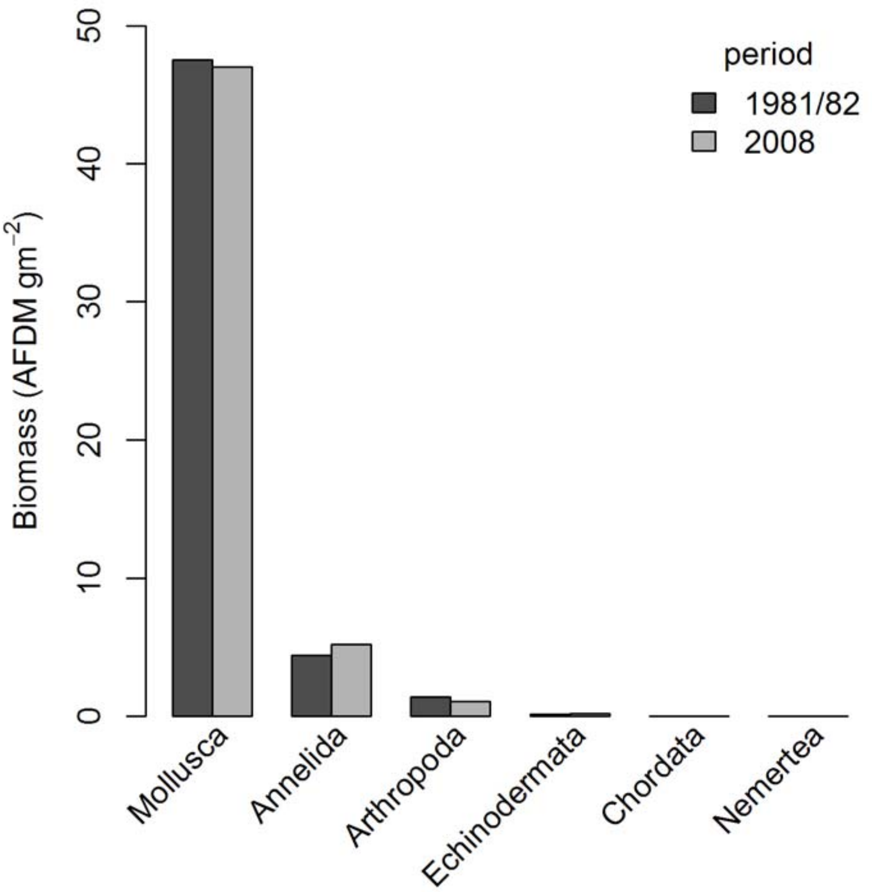

Figure 37. Total macrozoobenthos biomass in the subtidal western Dutch Wadden Sea specified per phylum and compared between periods.

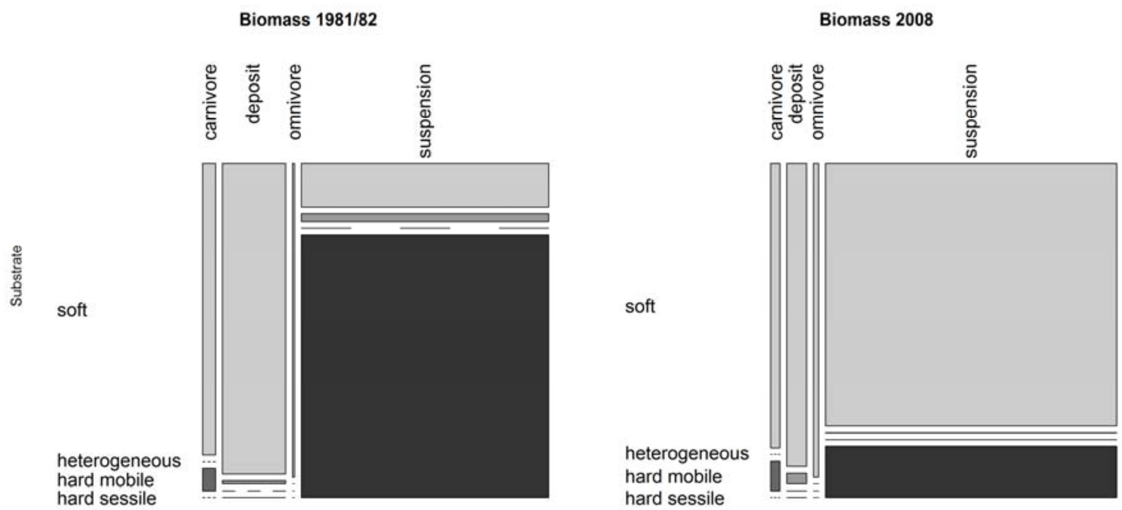

Figure 38. Mosaicplots of macrozoobenthos biomass distributed among feeding types and substrate use in 1981/82 and 2008 in the subtidal western Dutch Wadden Sea

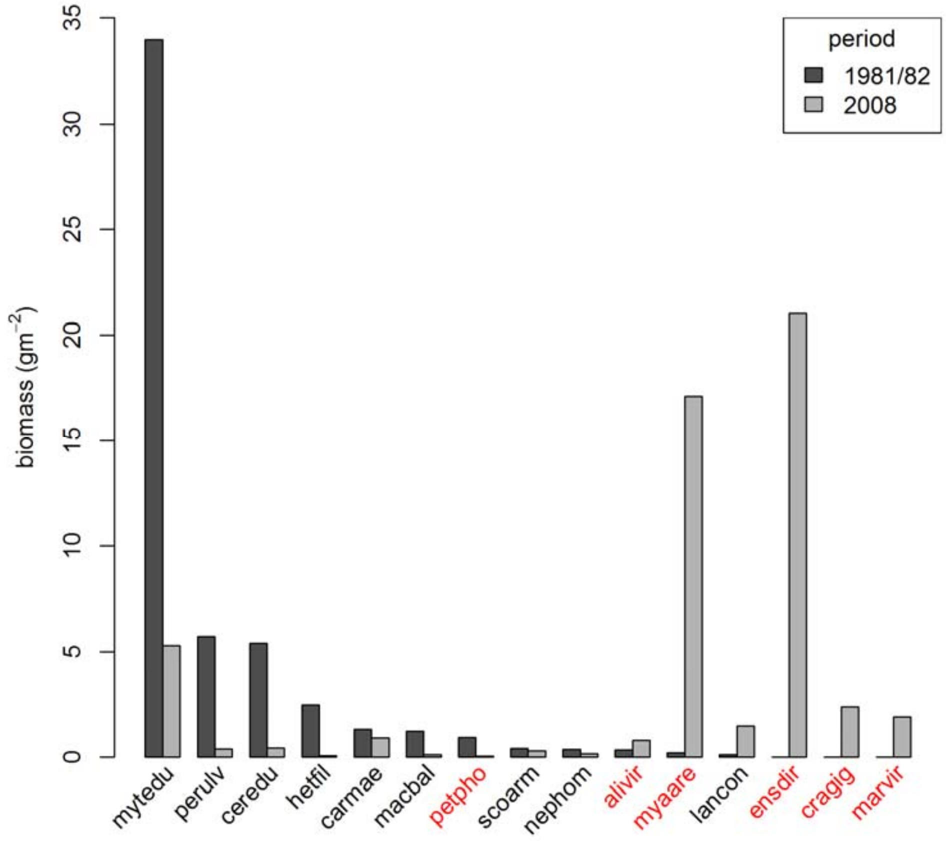

Figure 39. Biomass of species that contribute most to the total biomass in the subtidal western Dutch Wadden Sea, compared between 1981/82 and 2008. Invasive species abbreviations are printed in red. Species are ordered by decreasing biomass in 1981/82. The last three species along the x-axis, ensdir, cragig and marvir are recent invaders that were not present in 1981/82.

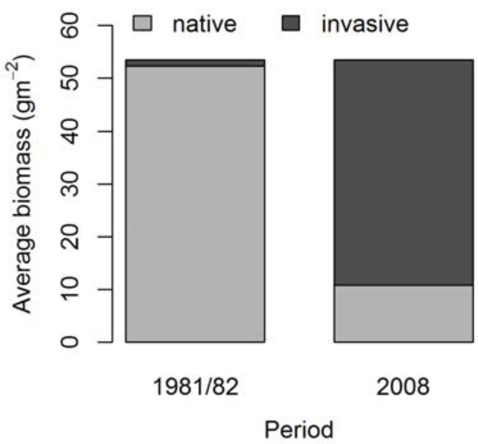

Figure 40. Total macrozoobenthos biomass in 1981/82 and 2008 divided in the shares of native and invasive species.

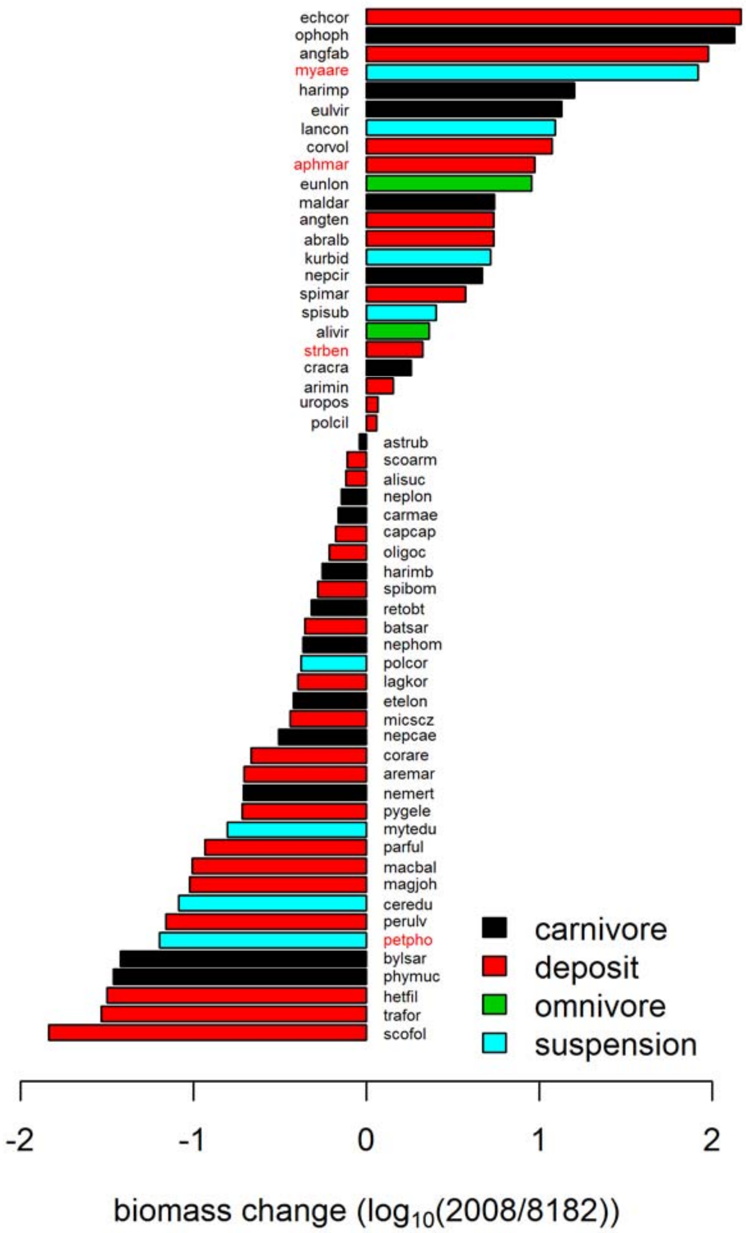

Figure 41. Biomass changes as the log_{10} of the ratio 2008:1981/82 of species that were present in both periods. Species abbreviations of invasive species are red.

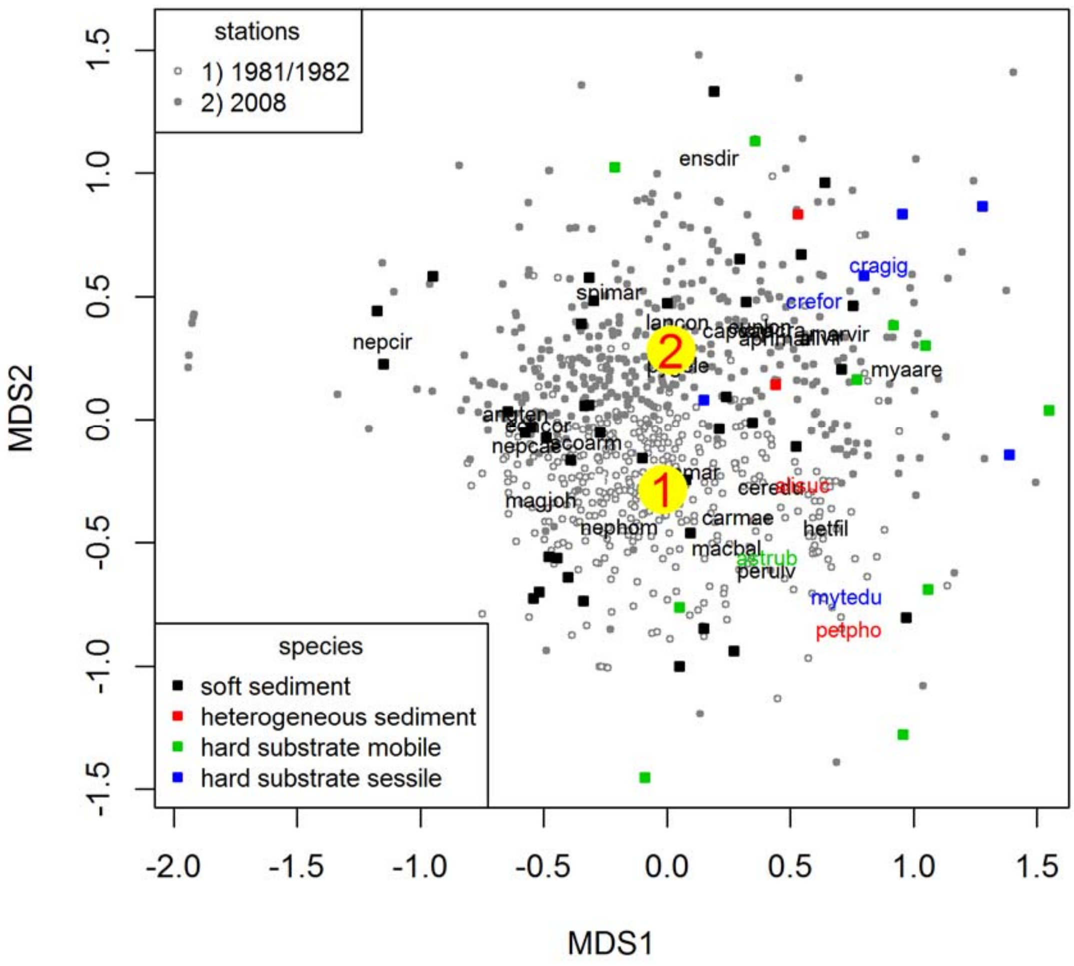

Figure 42. NMDS plot of stations in the surveys of 1981/82 and 2008 based on a Bray Curtis similarity matrix of square root transformed biomass data of macrozoobenthos species from the subtidal western Dutch Wadden Sea. Centroids of stations samples in period 1981/82 (1) and 2008 (2) are plotted on a yellow background. Species centroids are plotted with expanded coordinates. Only species names of the most important species are plotted, other species centroids are plotted as squares. Colour codes for substrate type are the same for names and symbols.

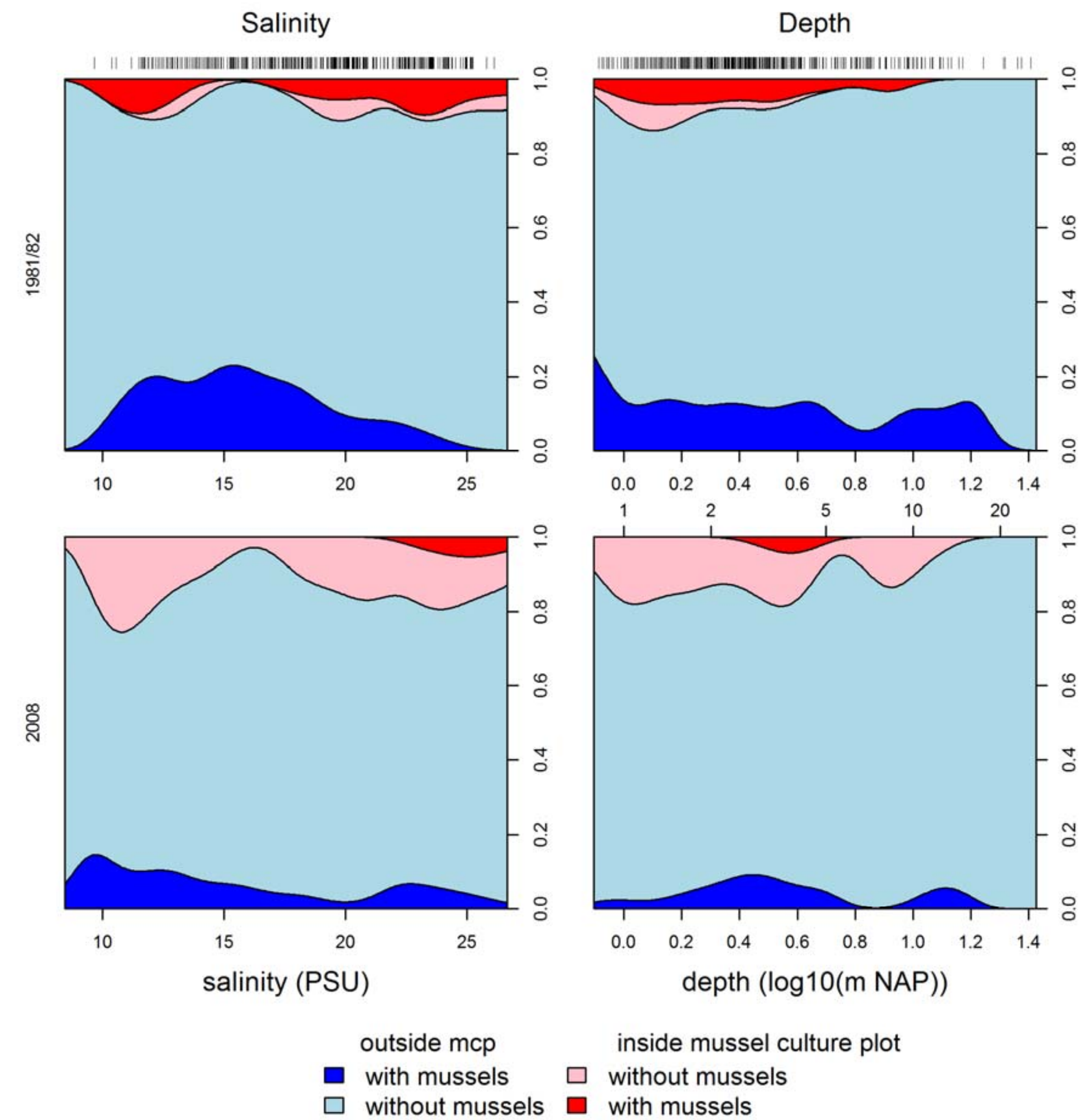

Figure 43. Conditional density displays of mussels (*M. edulis*) along a salinity and a depth gradient in the subtidal western Dutch Wadden Sea in 1981/82 and 2008

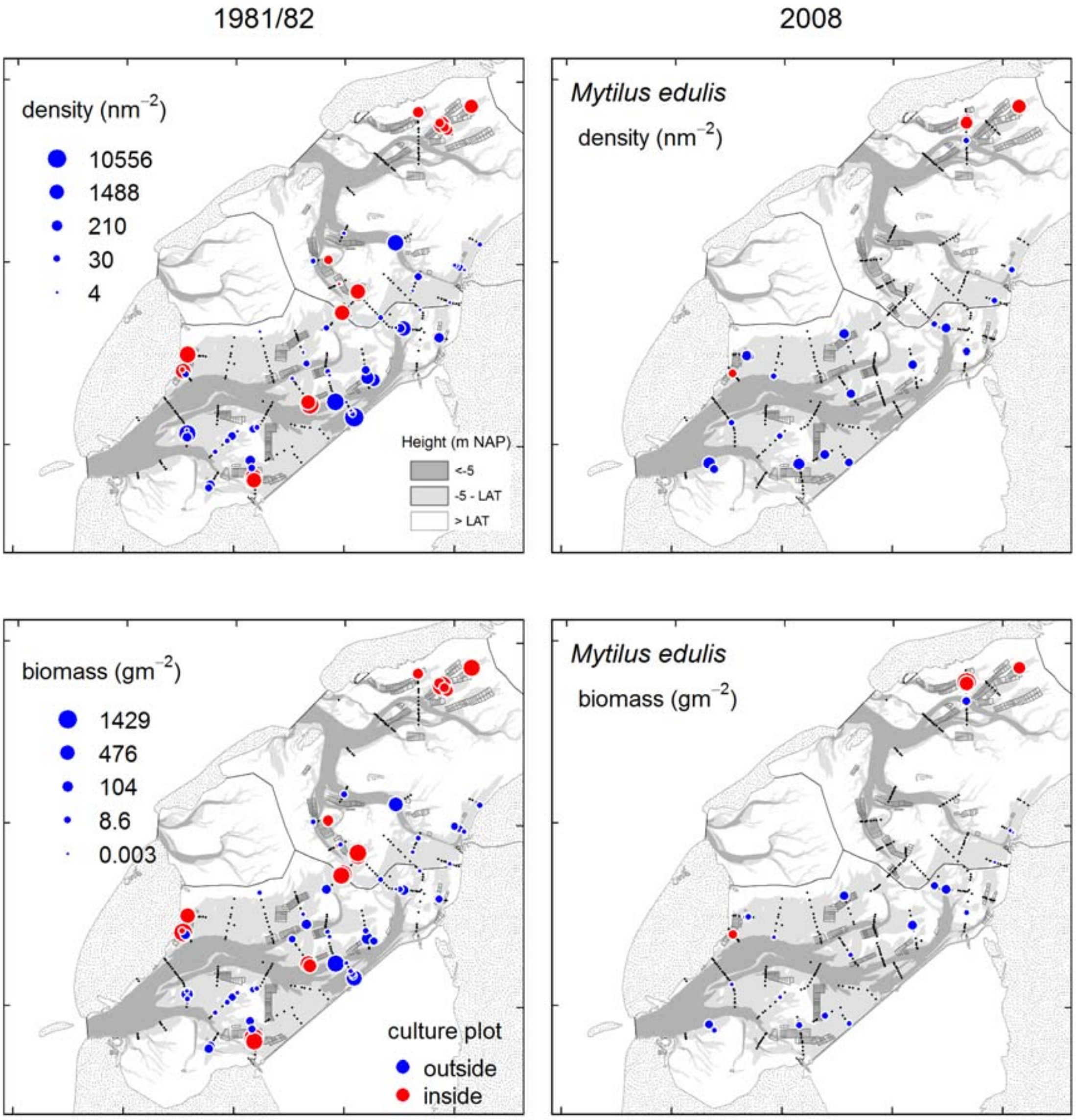

Figure 44. Map of mussel (*Mytilus edulis*) density (top row) and biomass (bottom row) in 1981/82 (left column) and 2008 (right column). Red symbols are for mussels on mussel culture plots.

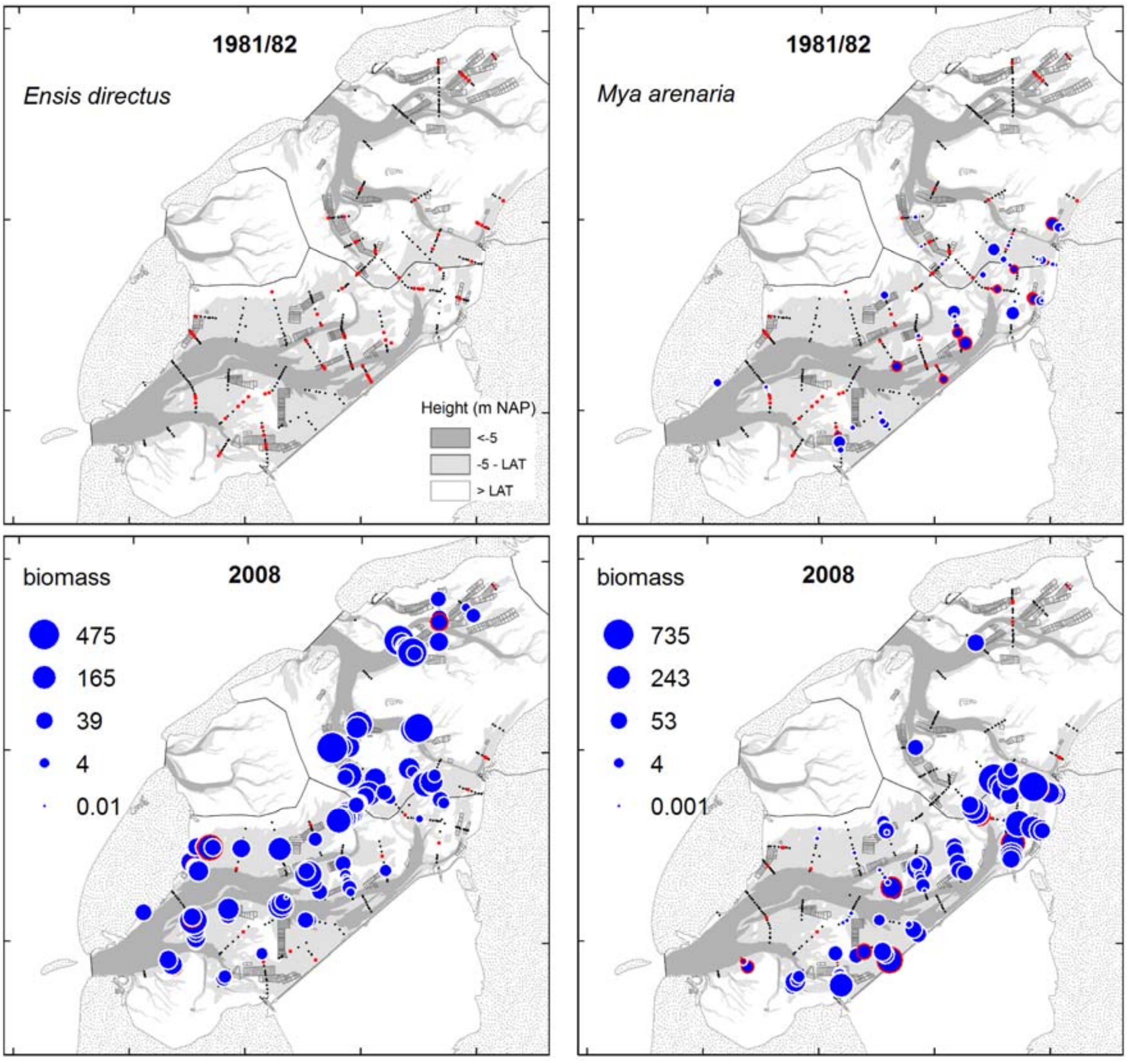

Figure 45. Biomass (AFDM gm^{-2}) of recent invader *Ensis directus* and the long-time established invasive *Mya arenaria* in 1981/82 and 2008 in the western Dutch Wadden Sea. Stations with mussels are indicated by a red dot or symbols with a red border.

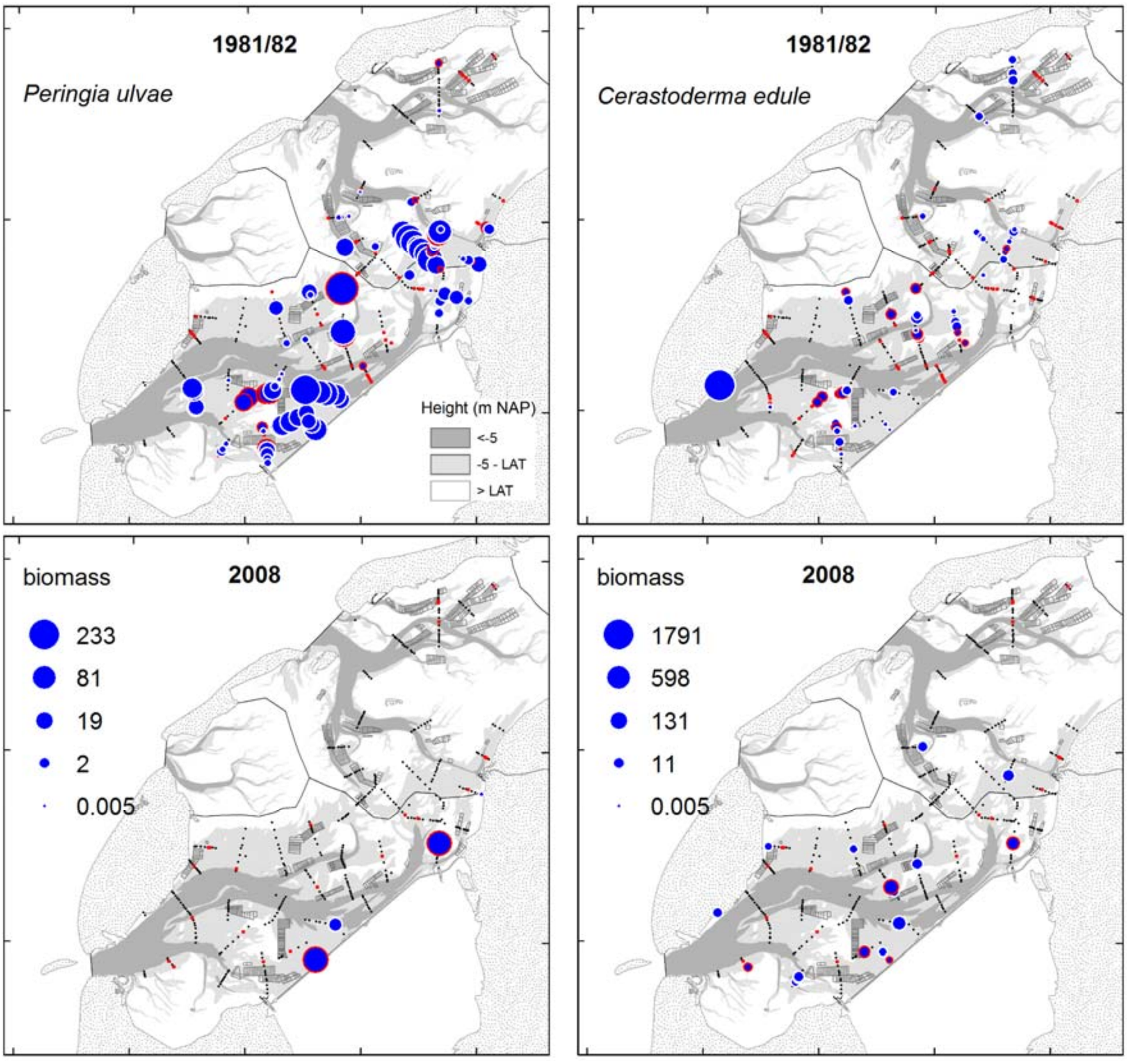

Figure 46. Biomass (AFDM gm^{-2}) of *Peringia ulvae* and *Cerastoderma edule* in 1981/82 and 2008 in the western Dutch Wadden Sea. Stations with mussels are indicated by a red dot or a symbol with a red border.

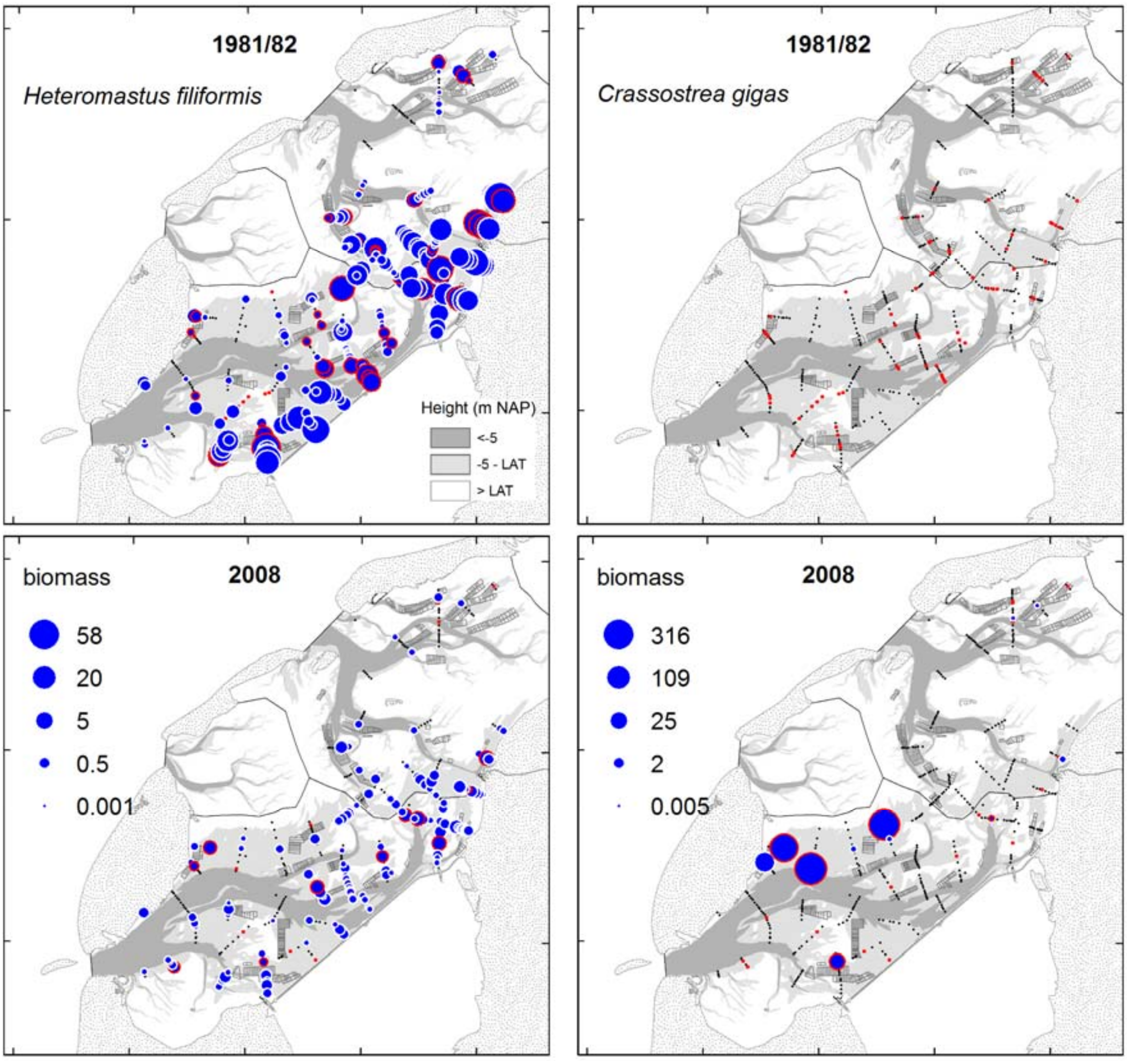

Figure 47. Biomass (AFDM gm^{-2}) of deposit feeder *Heteromastus filiformis* and recent invasive suspension feeding *Crassostrea gigas* in 1981/82 and 2008 in the western Dutch Wadden Sea. Stations with mussels are indicated by a red dot or a symbol with a red border.

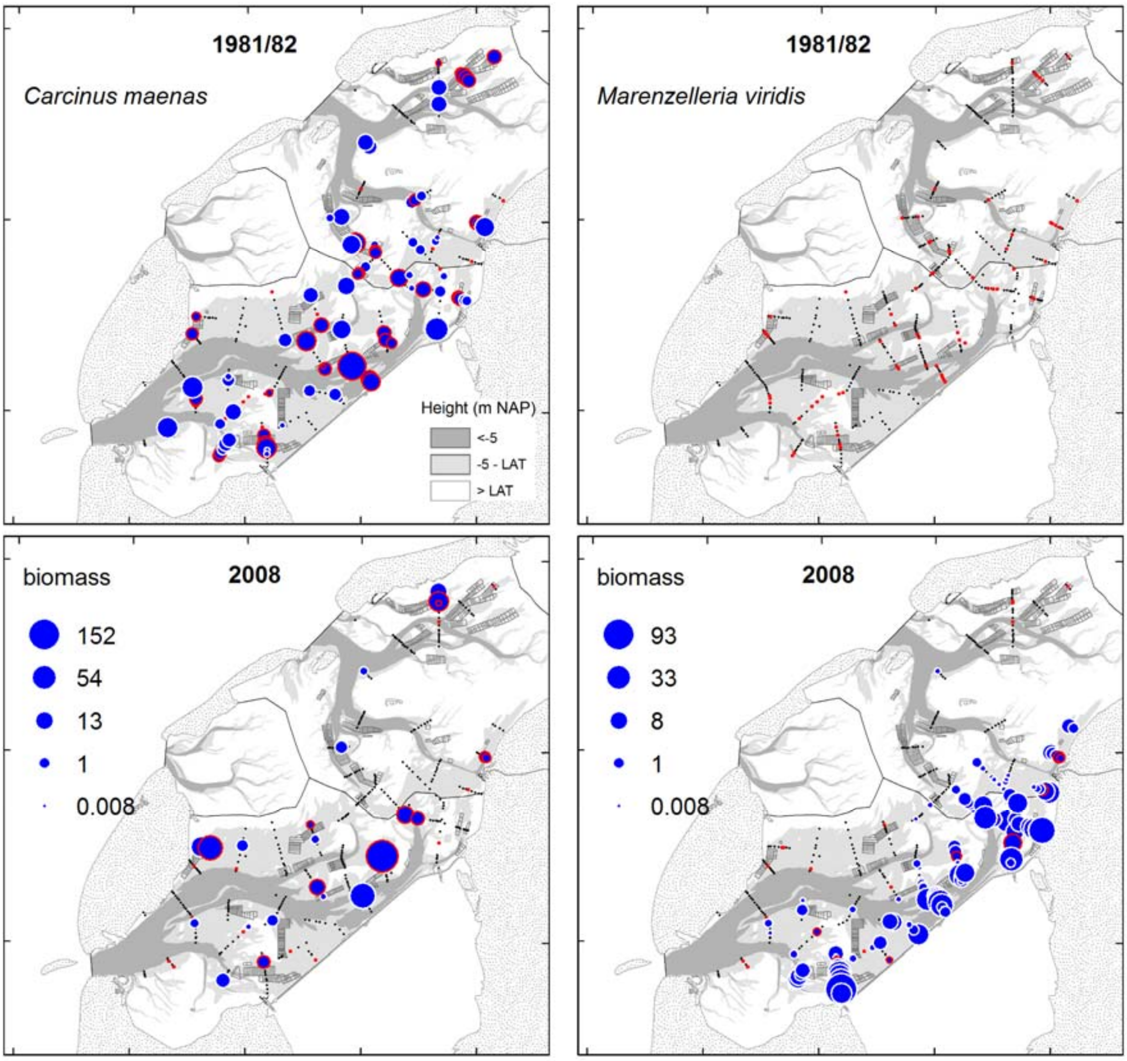

Figure 48. Biomass (AFDM gm^{-2}) of carnivorous *Carcinus maenas* and invasive deposit feeder *Marenzelleria viridis* in 1981/82 and 2008 in the western Dutch Wadden Sea. Stations with mussels are indicated by a red dot or symbols with a red border.

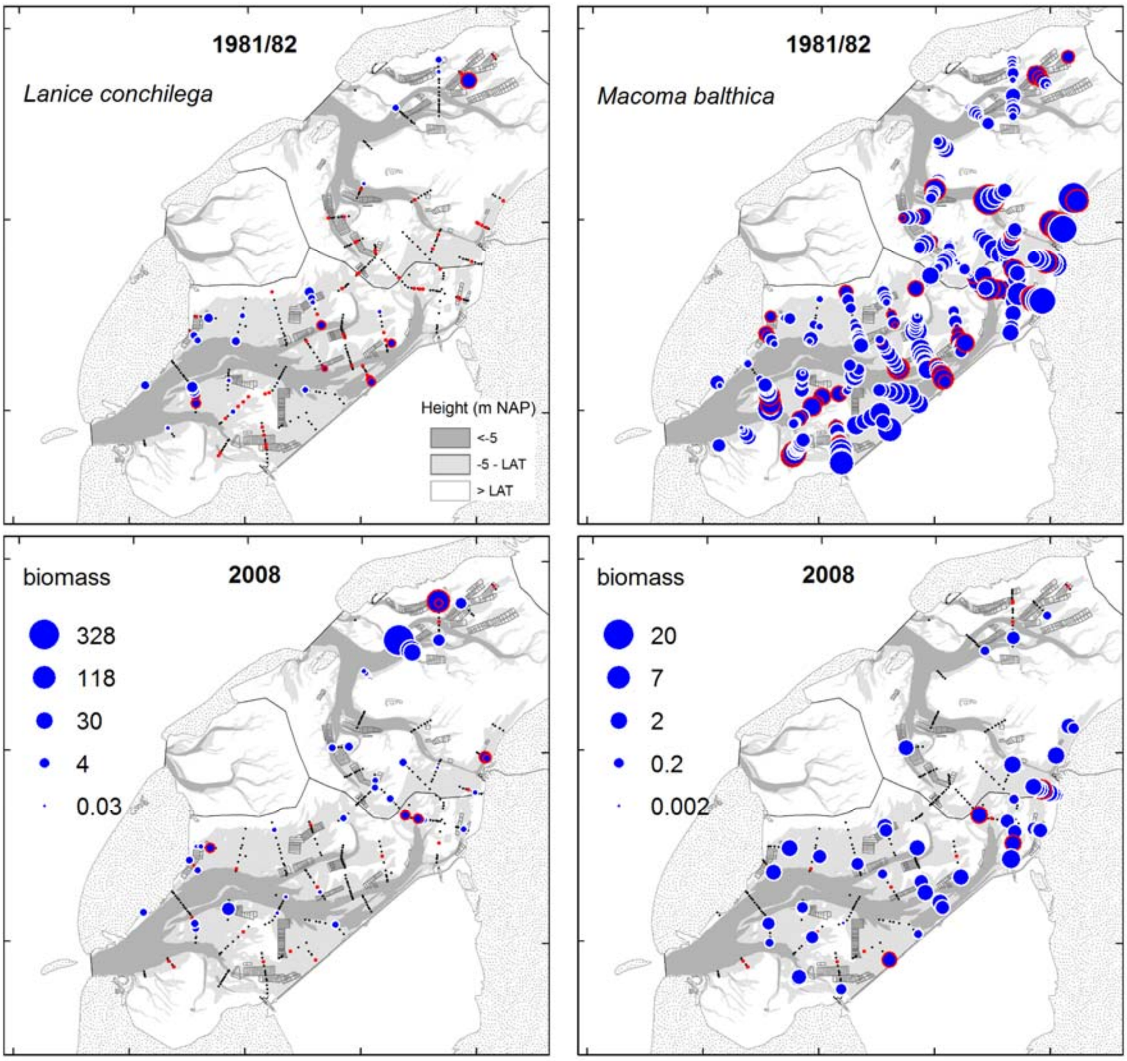

Figure 49. Biomass (AFDM gm^{-2}) suspension feeding *Lanice conchilega* and deposit feeder *Macoma balthica* in 1981/82 and 2008 in the western Dutch Wadden Sea. Stations with mussels are indicated by a red dot or a symbol with a red border.

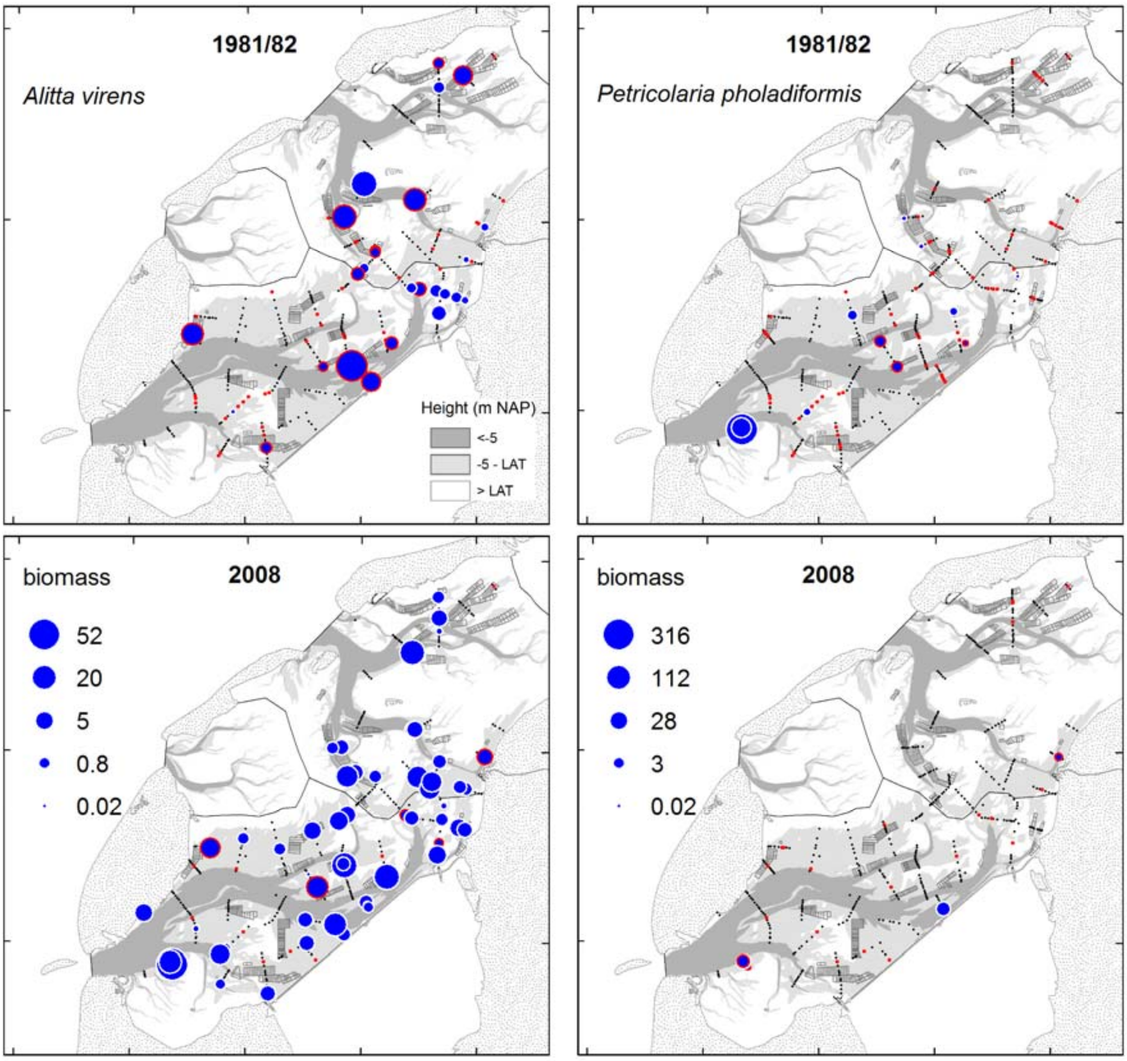

Figure 50. Biomass (AFDM gm^{-2}) of long established invasive omnivorous *Alitta virens* and invasive suspension feeding *Petricolaria pholadiformis* in 1981/82 and 2008 in the western Dutch Wadden Sea. Stations with mussels are indicated by a red dot or symbols with a red border.

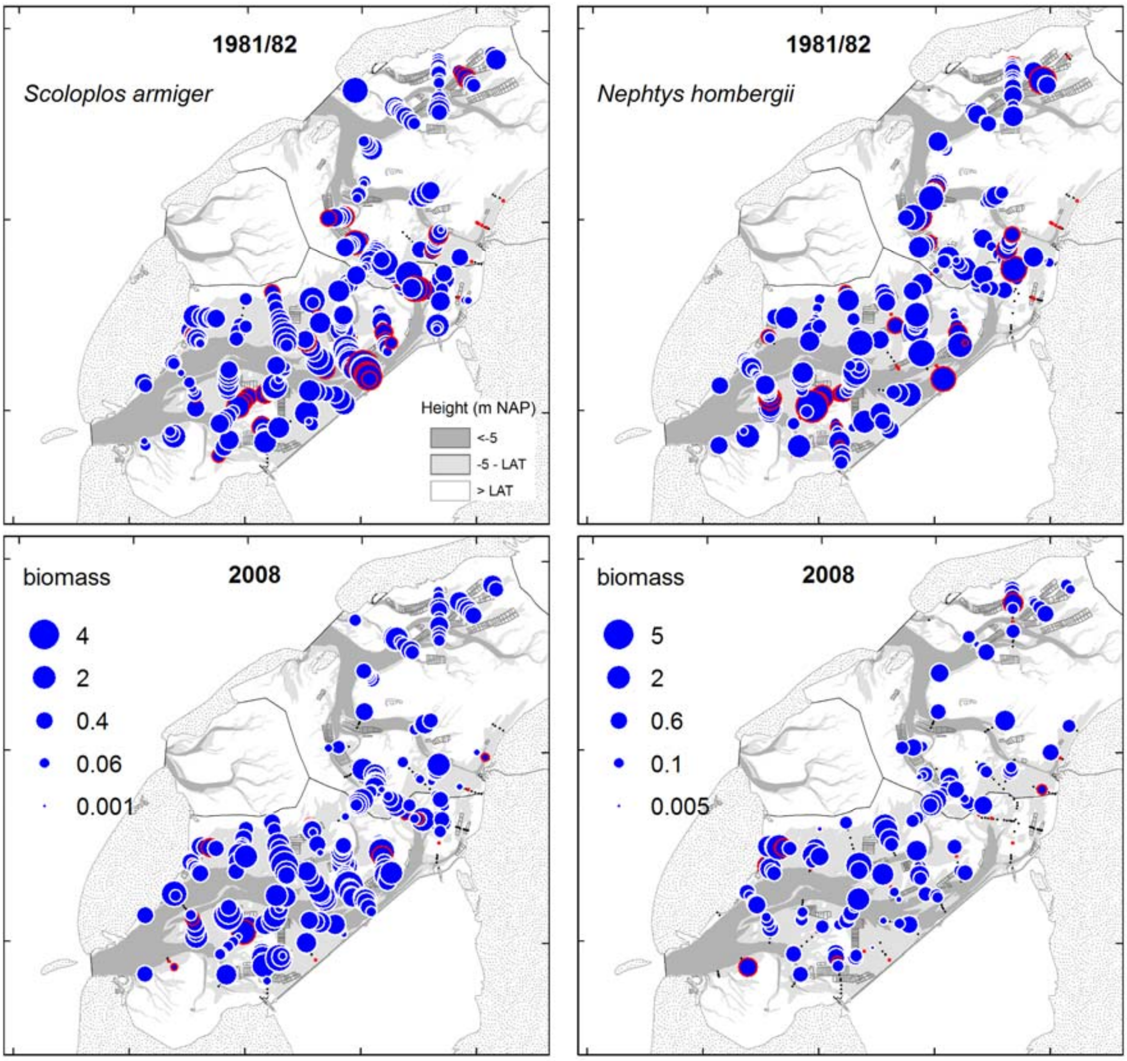

Figure 51. Biomass (AFDM gm^{-2}) of deposit feeder *Scoloplos armiger* and carnivorous *Nephtys hombergii* in 1981/82 and 2008 in the western Dutch Wadden Sea. Stations with mussels are indicated by a red dot or a symbol with a red border.

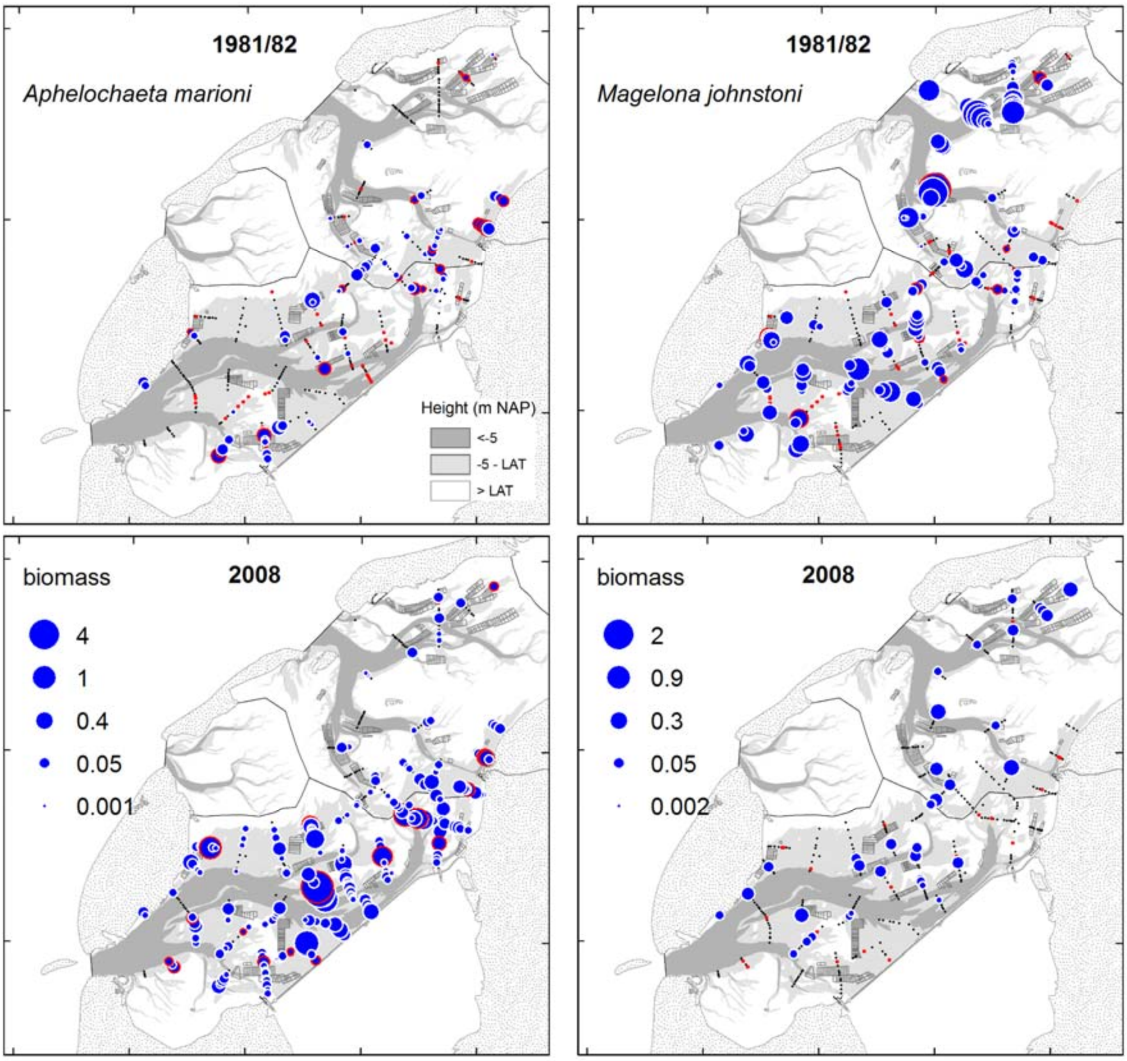

Figure 52. Biomass (AFDM gm^{-2}) of invasive deposit feeder *Aphelochaeta marioni* and deposit feeder *Magelona johnstoni* in 1981/82 and 2008 in the western Dutch Wadden Sea. Stations with mussels are indicated by a red dot or a red circle.

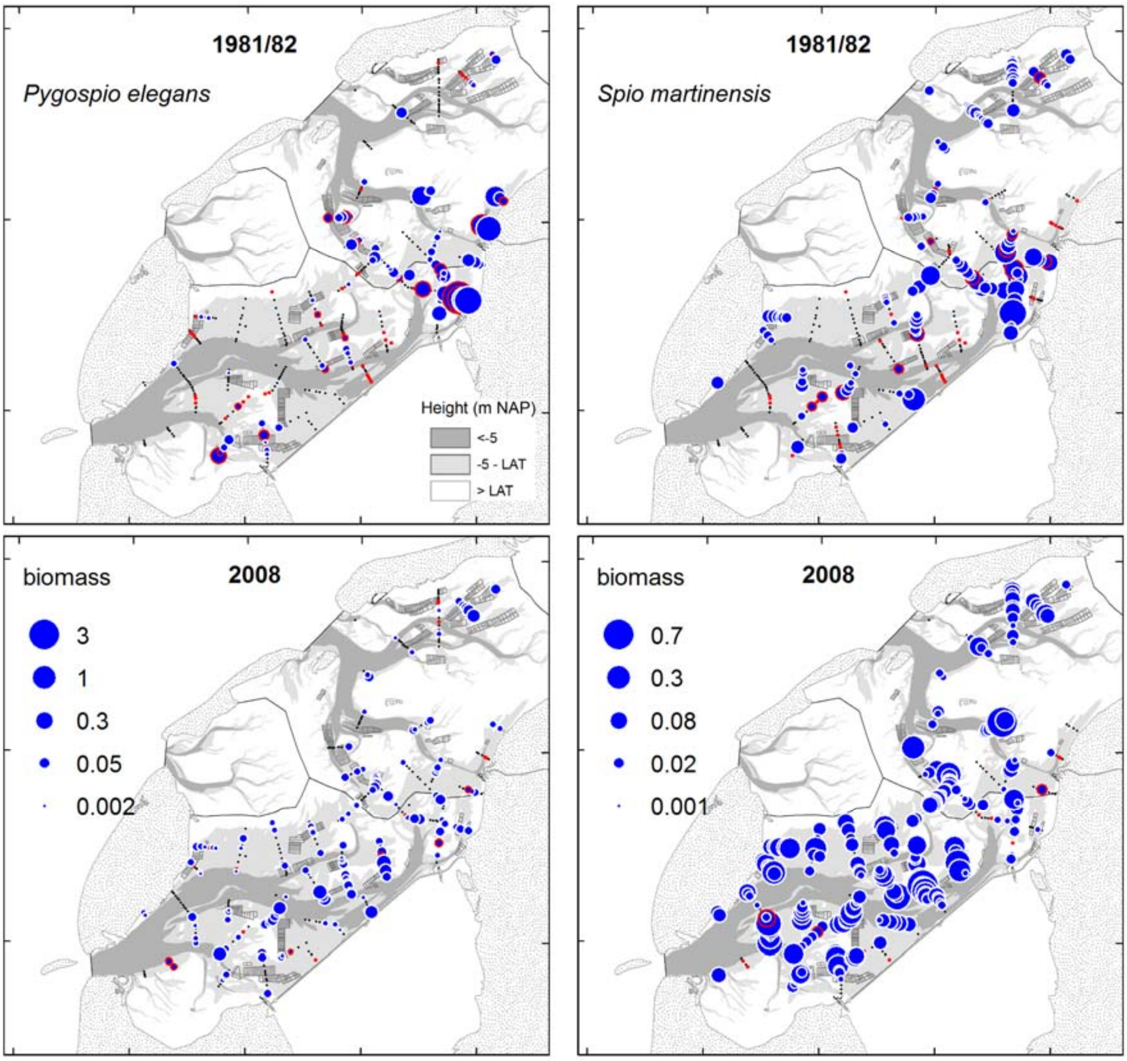

Figure 53. Biomass (AFDM gm^{-2}) of two deposit feeders *Pygospi elegans* and *Spio martinensis* in 1981/82 and 2008 in the western Dutch Wadden Sea. Stations with mussels are indicated by a red dot or a symbol with a red border.

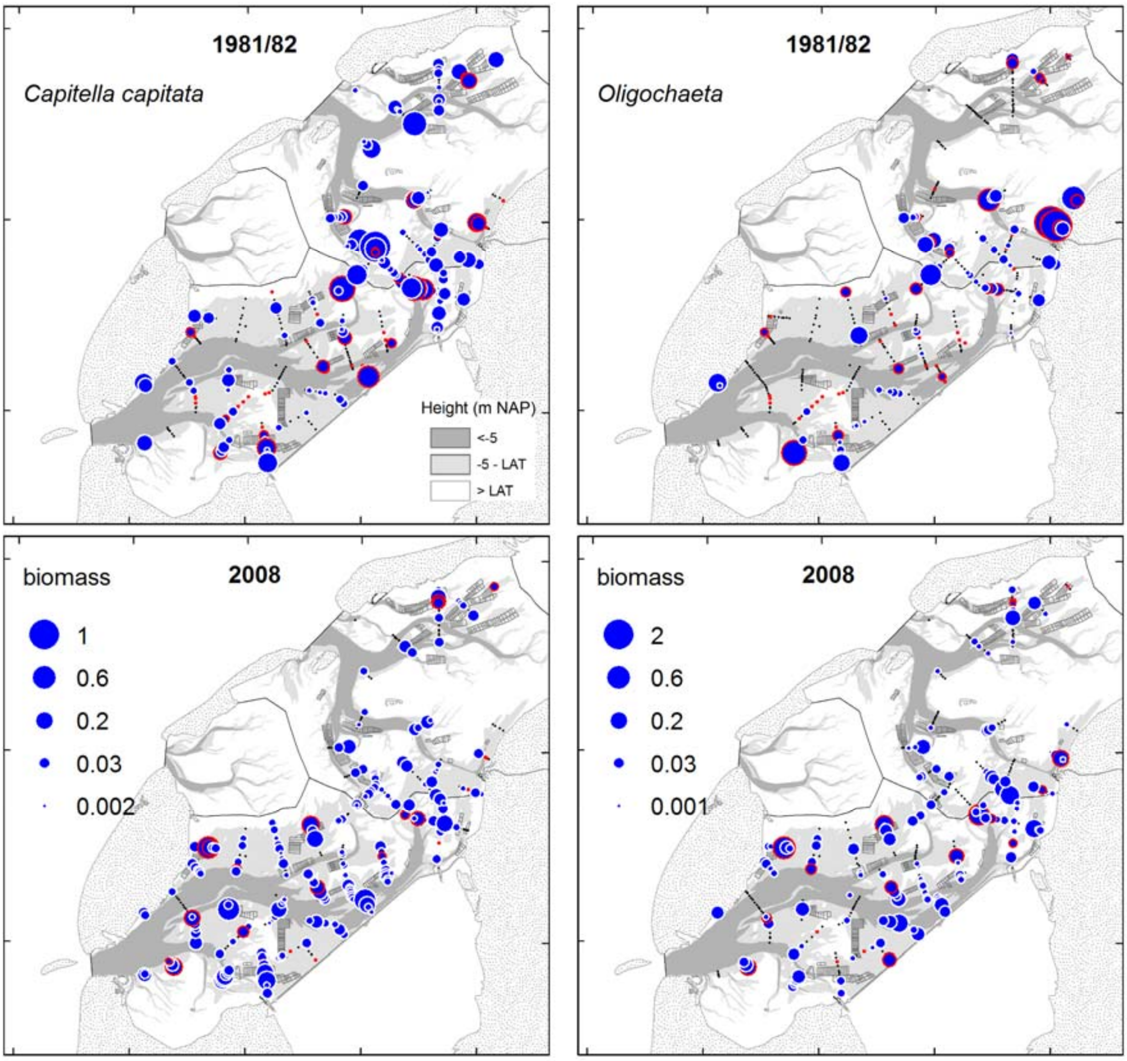

Figure 54. Biomass (AFDM gm^{-2}) of deposit feeder *Capitella capitata* and deposit feeding Oligochaeta in 1981/82 and 2008 in the western Dutch Wadden Sea. Stations with mussels are indicated by a red dot or a red circle.

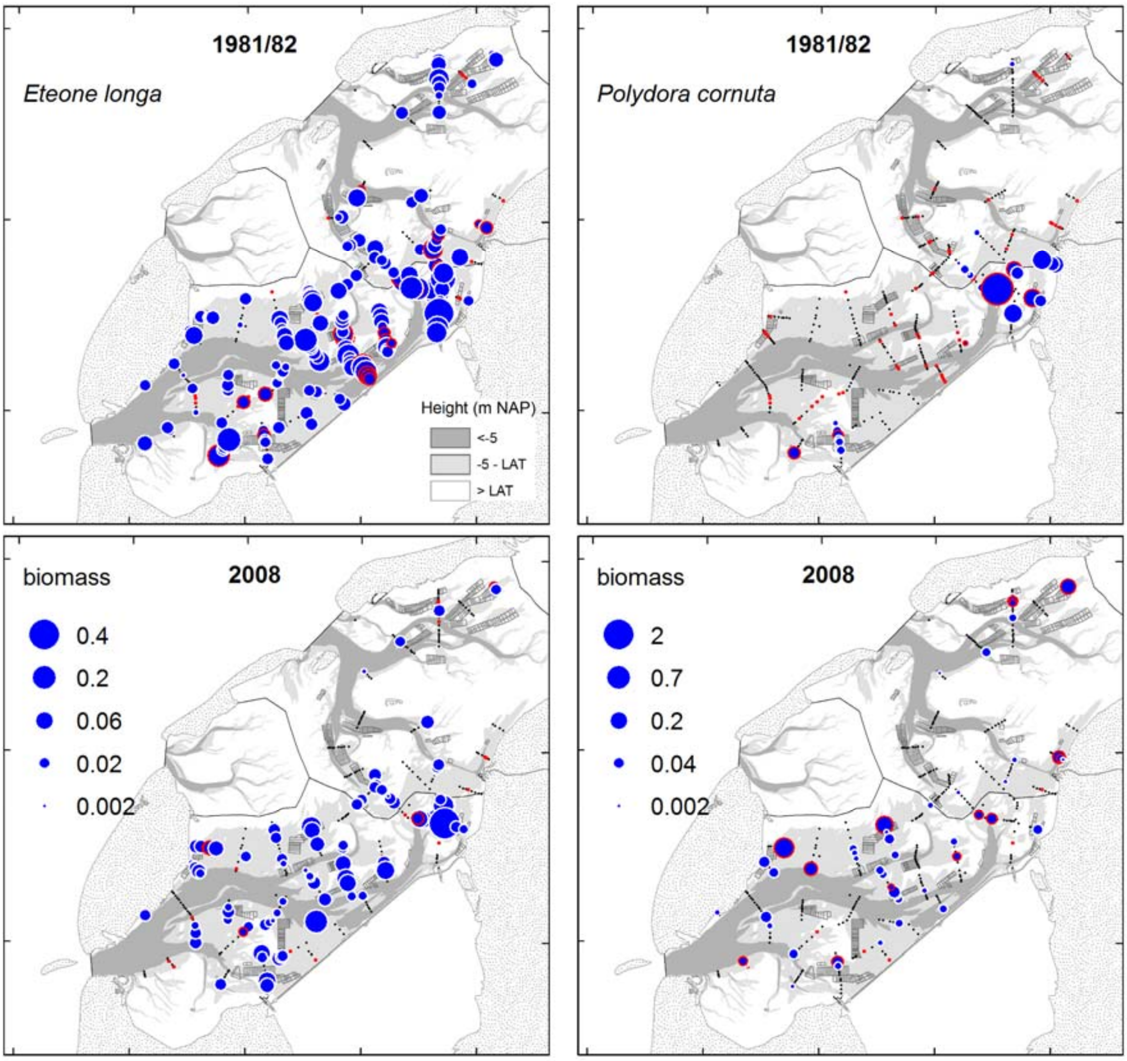

Figure 55. Biomass (AFDM gm^{-2}) of carnivore *Eteone longa* and suspension feeder *Polydora cornuta* in 1981/82 and 2008 in the western Dutch Wadden Sea. Stations with mussels are indicated by a red dot or a symbol with a red border.

Appendix 1

Station list

Environmental information about box core stations of the 2008 subtidal macrozoobenthos survey in the western Dutch Wadden Sea.

Positions are in the Dutch RD coordinate system. Positions inside and outside mussel culture plots are based field observations of marker stakes of the culture plots. Sediment median grain size (µm) and sediment fraction <16 µm were measured from a sediment sample (Ø 1.5 cm depth 8 cm) taken out of the box core. Stones larger than 2 cm as observed after washing the sample over a 1 mm^2 mesh. Tidal basin, M is Marsdiep and V is Vlie. Depth in meters relative to NAP (Dutch ordinance level). Maximum current speed extracted from a GIS raster supplied with Zwarts (2004). Average salinity values were extracted from two raster files describing salinity during a wet period in 1988 with high fresh water discharges and in a dry period in 1992 with very little fresh water inflow. These maps were made with a 2D water movement model for the coastal zone (Kuststrookmodel). For details and further references see Jager & Bartels (2002).

station	X-position RD	Y-position RD	mussel culture plot	sediment median grain size	sediment percentage < 16 µm	stones > 2 cm	tidal basin	depth (m NAP)	maximum current speed (ms2)	average salinity (PSU)
2	117203	553047	0	195.2	2.49	0	M	1.17	0.76	25.0
3	117163	553211	0	226.1	1.43	0	M	1.78	0.76	25.0
4	117135	553365	0	247	1.33	0	M	2.65	0.76	25.0
6	117096	553629	0	29	40.1	0	M	4.56	0.76	25.2
8	120571	554134	0	179.1	2.96	0	M	1.65	0.65	24.0
9	120363	554413	0	193.3	5.97	0	M	2	0.66	24.2
10	120102	554745	0	188.3	3.81	0	M	2.44	0.73	24.5
11	120000	554857	0	122.9	20.9	0	M	2.72	0.94	24.5
12	119906	554979	0	228.6	2.09	0	M	4.11	0.94	24.7
13	119840	555133	0	251.4	2.3	0	M	7.28	0.94	24.7
14	117041	560411	0	191.8	2.16	0	M	1.12	NA	26.7
15	117257	560093	0	175.1	2.44	0	M	0.89	1.08	26.1
20	125794	551893	0	173.5	6.33	0	M	2.11	0.87	17.9
22	125967	552177	0	283.6	5.74	0	M	6.34	0.87	17.7
23	126120	552395	0	107.2	16.7	0	M	2.06	0.76	17.5
24	126261	552628	0	236.1	2.29	0	M	1.14	0.67	17.6
25	126394	552848	0	180.9	2.63	0	M	1.64	0.70	17.6
26	126528	553034	0	160.9	3.37	0	M	1.39	0.70	17.9
27	126674	553277	0	201.7	2.21	0	M	1.46	0.77	18.8
28	126866	553593	0	271.6	4.4	1	M	3.19	0.88	18.8
29	126954	553739	0	407.3	1	0	M	6.39	0.88	18.8
30	123119	556924	0	186.5	2.64	0	M	7.01	0.95	23.2
32	123138	557415	0	274.4	1.39	0	M	2.64	0.77	23.2
33	123144	557560	0	310.7	1.1	0	M	2.35	0.77	23.2

station	X-position RD	Y-position RD	mussel culture plot	sediment median grain size	sediment percentage < 16 µm	stones > 2 cm	tidal basin	depth (m NAP)	maximum current speed (ms2)	average salinity (PSU)
34	123140	558013	0	255.1	1.43	0	M	2.31	0.87	23.0
35	123138	558541	0	195.4	2.82	0	M	2.53	0.83	22.6
36	123076	558909	0	197.8	3.64	0	M	3.13	0.76	22.3
37	122975	559178	0	219	1.99	1	M	2.32	0.76	22.3
38	122849	559516	0	210.4	2.49	0	M	1.91	0.74	22.3
39	122737	559792	0	199.6	3.08	1	M	2.94	0.86	22.3
40	122703	559880	0	152.5	9.97	0	M	5.71	0.86	22.3
41	120387	562872	0	162.5	2.14	0	M	1.97	0.70	24.9
42	120459	562775	0	152.5	2.91	0	M	3.37	0.70	24.9
43	120583	562635	0	205	0	0	M	3.86	1.07	24.9
44	120759	562381	0	272.3	1.21	0	M	6.71	1.34	25.1
45	120950	562141	0	407.7	2.52	0	M	12.69	1.42	25.1
46	121140	561902	0	340	0	1	M	20.6	1.42	25.2
47	121375	561588	0	302.8	0	0	M	25.57	1.41	25.0
48	121627	561294	0	394.6	0	1	M	23.04	1.41	24.4
49	121806	561069	0	274.2	0	0	M	20.81	1.34	23.9
50	121973	560857	0	185.7	12.7	0	M	7.67	1.34	23.2
51	122153	560610	0	229.8	0	0	M	4.06	1.22	23.2
52	122344	560400	0	233.6	3.15	0	M	6.38	1.25	22.6
53	122529	560158	0	278.7	0	0	M	9.59	0.86	22.4
54	130768	555693	0	236.1	1.54	0	M	0.85	0.60	16.2
55	130877	555209	0	193.7	1.89	0	M	1.51	0.59	15.8
56	130967	554744	0	175	3.53	0	M	1.47	0.59	15.3
57	131056	554263	1	261.2	1.24	0	M	2.36	0.59	14.9
58	131172	553719	1	248.6	1.36	0	M	2.47	0.61	13.8
59	131218	553488	1	262.6	1.43	0	M	1.42	0.61	13.4
60	131272	553197	1	229	1.85	0	M	1.11	0.57	12.9
61	131357	552779	1	249.6	0	0	M	1.8	0.57	11.7
62	131379	552560	1	198.8	1.89	0	M	1.14	0.55	11.2
63	131430	552054	0	166	3.14	0	M	1.06	0.64	10.4
64	131462	551574	0	220.3	1.66	0	M	1.62	0.81	9.7
65	131482	551093	0	237	2.26	0	M	2.7	0.70	8.4
66	129268	558762	0	211.6	1.83	0	M	0.84	0.72	18.5
67	128646	558160	0	226.5	1.5	0	M	2.11	0.63	18.7
68	128052	557593	0	256.8	0	0	M	1.18	0.66	19.3
69	127463	557050	0	267.5	0	0	M	2.28	0.71	20.0
70	126849	556486	0	249.5	1.36	0	M	2.71	0.66	20.4
71	126596	556246	0	153.2	23.5	0	M	2.87	0.66	20.7
72	126089	555776	0	195.8	4.26	0	M	3.94	0.73	20.8
74	125891	555600	0	49.7	16.8	0	M	6.82	0.80	20.8
75	126834	559591	0	200.6	2.27	0	M	1.57	0.73	20.1
76	126865	560122	0	232.9	1.91	0	M	1.59	0.64	20.0
77	126889	560500	0	203.4	1.87	0	M	2.02	0.68	20.0
79	126901	560691	0	229.4	1.54	0	M	2.03	0.68	20.1
80	126907	560851	0	184.2	3.83	0	M	4.62	0.76	20.3
81	126914	561077	1	215.8	2.57	0	M	3.49	0.76	20.3
83	126933	561315	0	252.4	0	0	M	2.51	0.80	20.4
84	126950	561585	0	318.9	2.89	1	M	6.95	0.80	21.2

station	X-position RD	Y-position RD	mussel culture plot	sediment median grain size	sediment percentage < 16 µm	stones > 2 cm	tidal basin	depth (m NAP)	maximum current speed (ms2)	average salinity (PSU)
85	126965	561875	0	647.7	0.59	0	M	11.42	1.09	21.2
87	122371	566518	0	274.2	2.77	0	M	1.17	0.53	23.6
88	122523	566319	1	293.7	1.34	0	M	2.09	0.53	23.6
89	122706	566109	1	216.1	1.64	0	M	2.67	0.66	23.5
90	122892	565881	1	162.2	3.18	1	M	3.53	0.68	23.4
91	122983	565776	0	234.6	1.36	0	M	1.61	0.68	23.4
92	123068	565667	0	236.5	1.31	0	M	1.99	0.69	23.6
93	123224	565497	0	384.7	0.95	0	M	3.61	0.69	23.6
94	123314	565393	0	359.1	0.83	0	M	3.01	0.77	23.6
95	123426	565267	0	257.1	1.26	0	M	3.32	0.77	23.6
96	123556	565107	0	208.2	1.87	0	M	4.44	1.01	23.5
97	123651	564999	0	246.9	0	0	M	5.85	1.01	23.5
98	122968	568151	1	120.8	5.5	0	M	1.58	0.47	23.5
100	123202	568133	1	174.4	2.49	0	M	1.5	0.47	23.5
101	123684	568098	1	249.9	1.28	0	M	1.56	0.50	23.3
102	124183	568052	0	271.8	2.83	0	M	2.05	0.52	23.0
105	124585	568009	0	160.3	4.19	0	M	2.56	0.58	22.8
106	124768	568003	0	247.8	2.29	0	M	2.32	0.58	22.8
107	125095	567980	0	166.7	3.52	0	M	2.23	0.58	22.7
108	125440	567940	0	178.1	2.49	0	M	2.19	0.56	22.6
109	128927	570179	0	167.3	2.96	0	M	1.35	0.54	22.2
110	128676	569086	0	258.1	1.65	0	M	1.77	0.62	22.0
111	128492	568244	0	208.2	1.78	0	M	2.17	0.66	21.8
112	128418	567919	0	187.8	2.19	0	M	2.54	0.66	21.8
113	128249	567155	0	291	1	0	M	2.02	0.69	21.7
114	128051	566296	0	329.3	0.83	0	M	3.07	0.69	21.8
115	127881	565505	0	317.5	0.96	0	M	4.58	0.78	21.9
116	127806	565228	0	350.8	0.93	0	M	6.93	0.88	22.2
117	128897	567001	0	223.6	0	0	M	2.02	0.73	21.4
118	131211	559065	0	185.8	1.91	0	M	0.95	0.66	18.2
119	131665	559250	0	182.5	1.88	0	M	0.87	0.65	18.2
120	132095	559517	0	158.9	2.93	0	M	1.63	0.70	18.2
121	132354	559994	0	164.7	2.65	0	M	1.47	0.63	18.4
122	132572	560394	0	153.7	2.67	0	M	1.54	0.59	18.5
123	132797	560810	0	243.5	2.78	0	M	2.94	0.92	19.3
124	132873	560948	0	288.9	2.22	0	M	23.75	0.92	19.3
125	132995	561173	0	149.6	7.24	0	M	26.89	0.92	19.4
126	133132	561427	0	190.7	3.91	0	M	17.49	1.06	19.4
127	133288	561715	0	273.4	0	0	M	9.94	1.11	19.5
128	133434	561983	0	309.3	1.13	0	M	7.08	1.04	19.6
129	133585	562262	0	229.2	1.55	0	M	7.13	0.92	19.6
130	132434	562431	0	380.9	2.04	0	M	9.6	1.01	20.1
132	132777	555177	0	186.8	2	0	M	1	0.51	14.7
133	133039	555320	1	184.7	1.96	0	M	1.04	0.42	14.5
134	133193	555409	1	177.4	2.09	0	M	1.28	0.42	14.5
135	134147	555911	0	67.9	24.7	0	M	3.33	0.41	14.6
136	135041	556383	0	47.2	29	0	M	3.3	0.49	14.1
137	136024	556897	0	334.9	3.16	0	M	2.69	0.56	14.0

station	X-position RD	Y-position RD	mussel culture plot	sediment median grain size	sediment percentage < 16 µm	stones > 2 cm	tidal basin	depth (m NAP)	maximum current speed (ms2)	average salinity (PSU)
138	137095	554971	0	69.4	12.1	0	M	2.77	0.48	10.6
139	136598	555543	0	58	20.6	0	M	3.73	0.52	11.5
140	136291	555901	0	75.2	15.7	0	M	3.57	0.53	12.2
141	140386	557932	0	354.6	1.59	0	M	3.78	0.58	12.8
142	139867	558472	0	150.1	9.19	0	M	4.65	0.65	13.4
143	139339	559017	0	166.3	3.78	0	M	4.62	0.64	14.4
144	138209	559181	0	140.8	5.76	0	M	3.91	0.61	15.4
145	137534	559293	0	255.7	0	0	M	3.11	0.71	15.8
146	137151	559361	0	252.2	1.44	0	M	3.36	0.74	15.9
147	136336	559489	0	275.2	1.65	0	M	4.49	0.70	16.8
148	135847	559584	0	267.4	1.36	0	M	4.75	0.75	16.9
149	138155	562007	0	264.4	2.09	0	M	4.86	0.95	17.9
150	137928	562327	1	295.1	0	0	M	3.33	0.75	18.1
151	137840	562451	1	266.6	1	0	M	1.63	0.75	18.1
152	137575	562874	0	244.2	1.87	0	M	2.22	0.65	18.4
153	137283	563359	0	147	5.13	0	M	2.29	0.68	18.6
154	136880	563930	0	283.8	0.96	0	M	1.49	0.68	19.1
155	136500	564521	0	308	1.04	0	M	2	0.71	19.3
156	136396	564666	0	260.9	1.26	0	M	2.24	0.71	19.2
157	136236	564918	0	212.9	2.65	0	M	4.2	0.65	19.3
159	136026	565240	0	206.8	0	0	M	1.43	0.65	19.4
160	135906	565416	0	108	9.4	0	M	5.76	0.74	19.4
161	132016	570962	0	205.2	1.5	0	M	0.85	0.62	21.6
162	132241	570054	0	205.9	1.55	0	M	1.39	0.70	21.3
163	132496	569146	0	204.8	6.06	0	M	1.61	0.60	21.1
164	132718	568320	0	287.6	1.2	0	M	2.07	0.61	20.9
165	132847	567871	0	199	2.45	0	M	3.1	0.67	20.7
166	132987	567369	0	172.7	1.63	0	M	3.2	0.66	20.6
167	133159	566735	0	321	0.83	0	M	2.47	0.66	20.5
168	133325	566155	0	155.2	2.58	0	M	3.12	0.64	20.5
169	133496	565892	0	243.6	0	0	M	0.92	0.64	20.5
170	133543	565353	1	289.3	1.34	0	M	4.09	0.72	20.5
171	133643	565047	1	373.9	0.95	0	M	4.03	0.77	20.4
173	133702	564780	0	344.8	0.93	0	M	5.36	0.77	20.3
174	136320	571004	0	136.7	15.1	0	M	1.86	0.58	20.9
175	136450	570643	0	143	8.26	0	M	2.82	0.66	20.9
176	136524	570438	1	213.1	1.77	0	M	3	0.66	20.7
177	136600	570233	1	149.7	6.46	0	M	3.06	0.66	20.7
178	136670	570033	1	213.6	1.61	0	M	3.07	0.66	20.4
179	136753	569814	1	179	4.3	0	M	3.04	0.62	20.4
180	137033	569012	0	265.3	1.67	0	M	1.56	0.57	20.1
181	137283	568379	0	200.6	1.74	0	M	2.25	0.53	20.0
182	137627	567376	0	159	11.8	0	M	1.37	0.58	19.7
183	137726	567117	0	17.1	48.5	0	M	2.69	0.87	19.6
185	140518	565634	0	175.8	2.98	0	M	1.5	0.53	18.2
186	140403	565921	1	193.4	1.59	0	M	1.6	0.61	18.3
187	140299	566139	1	225.2	1.83	0	M	1.83	0.61	18.5
189	140227	566353	1	107.8	8.31	0	M	3.68	0.63	18.5

station	X-position RD	Y-position RD	mussel culture plot	sediment median grain size	sediment percentage < 16 µm	stones > 2 cm	tidal basin	depth (m NAP)	maximum current speed (ms2)	average salinity (PSU)
190	140143	566499	1	121.3	10.3	0	M	6.83	0.63	18.8
191	140083	566679	1	241.8	1.14	0	M	1.88	0.63	19.0
192	140061	566844	0	252.9	0	0	M	3.31	0.76	19.1
193	140095	567072	0	266.6	0	0	M	7.16	0.76	19.3
194	140130	567329	0	281	0	0	M	5.62	0.75	19.4
195	140153	567471	0	275.3	0	0	M	5	0.75	19.4
196	140182	567653	0	226.6	1.34	0	M	3.3	0.75	19.5
197	140242	567969	0	255.9	1.24	0	M	1.47	0.59	19.5
198	140267	568293	0	216.9	0	0	M	1.16	0.61	19.6
199	140524	564766	0	197.7	1.94	0	M	1.45	0.50	18.0
200	140649	564356	0	296.3	0.96	0	M	1.86	0.59	17.9
201	140748	564057	0	277.8	1.03	0	M	2.05	0.66	17.6
202	140822	563835	0	268.6	1.16	0	M	2.26	0.66	17.4
203	140909	563556	0	247.2	1.41	0	M	2.63	0.69	17.3
204	140989	563324	0	234.3	1.48	0	M	2.63	0.69	17.2
205	141113	562956	0	206	1.88	0	M	2.76	0.83	17.1
206	141179	562757	0	224.5	1.6	0	M	2.95	0.83	17.0
208	141246	562556	0	256.5	2.25	0	M	11.02	1.17	16.9
209	141314	562340	0	304.1	1.19	0	M	14.41	1.17	16.6
210	141379	562149	0	408.6	0.74	0	M	13.22	0.97	16.5
211	141454	561948	0	238.6	1.36	0	M	6.12	0.97	15.9
212	142572	562372	0	184	2	0	M	4.9	1.13	15.7
214	142656	562192	0	159	2.82	0	M	2.35	0.91	15.7
215	142832	561890	0	201.3	2.29	0	M	4.62	0.95	15.5
216	142947	561672	0	269.4	2.21	0	M	5.38	0.91	15.3
217	143119	561315	0	240.5	1.41	0	M	4	0.91	15.0
218	143246	561069	0	210.5	3.78	0	M	3.87	0.90	14.8
219	143376	560820	0	157	4.84	0	M	4.56	0.98	14.6
220	143533	560513	0	311	3.56	0	M	8.91	0.96	14.4
222	144519	568733	0	179.3	9.03	0	M	1.69	0.69	18.4
223	144638	568162	0	171.7	2.16	0	M	1.91	0.60	18.1
224	144749	567539	0	201.2	2.14	0	M	1.3	0.56	17.8
225	144857	566988	0	160	3.52	0	M	2.02	0.57	17.5
226	145001	566264	0	197.7	1.45	0	M	0.84	0.53	17.3
229	145220	565346	0	208.1	0	0	M	1.71	0.68	17.0
230	145302	564784	0	340	1.05	0	M	1.65	0.60	16.9
231	145339	564558	0	198.7	2.95	0	M	2.44	0.70	16.7
232	145405	564232	0	330.4	2.31	0	M	5.44	1.12	16.5
233	145433	564072	0	371.1	1	0	M	6.27	1.12	16.2
234	145917	565049	0	306.7	1.09	0	M	1.36	0.62	17.0
235	140880	571940	0	147.4	3.61	0	M	2.06	0.66	20.0
236	140776	571839	0	125.9	4.76	0	M	2.61	0.66	20.0
237	140653	571718	0	119	5.09	0	M	2.84	0.74	20.0
239	140524	571605	0	149.5	2.49	0	M	2.39	0.74	20.0
241	140291	571446	0	163.8	2.67	0	M	1.74	0.74	20.1
242	140154	571365	0	148.9	6.09	0	M	1.8	0.73	20.1
244	139734	571132	0	162.4	2.81	0	M	1.67	0.90	20.3
246	140975	579780	0	172.9	4.08	0	V	1.76	0.56	20.8

station	X-position RD	Y-position RD	mussel culture plot	sediment median grain size	sediment percentage < 16 µm	stones > 2 cm	tidal basin	depth (m NAP)	maximum current speed (ms2)	average salinity (PSU)
247	140412	579744	0	140.2	4.47	0	V	1.98	0.49	20.8
248	140095	579713	1	148.3	5.79	0	V	1.81	0.54	20.9
249	139785	579690	1	185.1	0	0	V	1.02	0.54	21.1
251	139247	579646	1	171.3	2.44	0	V	8.41	0.91	21.3
252	139037	579622	1	161.1	3.77	0	V	10.25	0.91	21.3
253	138734	579605	0	120.8	8.27	0	V	10.36	0.73	21.6
254	138550	579594	0	127.8	4.52	0	V	2.51	0.73	21.6
255	142543	577180	0	164.5	2.02	0	V	1.85	0.59	20.2
256	142179	576991	1	105.1	13.4	0	V	3.18	0.75	20.2
257	141886	576876	1	121.3	5.83	0	V	2.29	0.75	20.3
258	141694	576766	1	146.5	2.52	0	V	1.81	0.59	20.3
259	141201	576522	0	150.7	3.01	0	V	1.64	0.96	20.7
260	141013	576435	0	150.8	3.98	0	V	4.52	0.96	20.7
261	140765	576313	0	95.3	13.2	0	V	7.14	0.96	20.9
262	140516	576193	0	156.9	2.32	0	V	2.77	0.92	21.2
264	143973	576456	0	220.1	1.81	0	V	1.63	0.56	19.7
265	143997	576251	0	155.2	5.19	0	V	2.37	0.56	19.6
266	144014	576039	0	153.4	9.96	0	V	2.87	0.59	19.6
267	144034	575833	0	113.4	3.74	0	V	3.03	0.59	19.6
268	144051	575571	1	145.1	2.39	0	V	1.1	0.58	19.4
269	144065	575316	1	146.9	2.31	0	V	1.09	0.58	19.4
270	143950	574999	0	147.4	2.74	0	V	1.14	0.53	19.5
271	143707	574765	0	145	2.61	0	V	1.25	0.45	19.5
272	143420	574501	0	148	3.32	0	V	1.29	0.56	19.5
273	143208	574291	0	182.2	2.07	0	V	1.86	0.63	19.8
276	142871	573961	0	127.9	2.85	0	V	2.94	0.82	19.8
277	142714	573812	0	129	5.85	0	V	2.62	0.83	19.8
278	142453	573561	0	177.6	1.75	0	V	1.15	0.58	19.7
279	142118	573214	0	177.8	1.7	0	V	1.32	0.46	19.9
280	141985	573105	0	201.4	1.43	0	M	1.39	0.46	19.9
281	141893	572997	0	166.1	3.5	0	M	1.45	0.46	19.9
282	141801	572913	0	193.8	1.54	0	M	1.46	0.46	20.1
283	147807	571498	0	171.3	6.53	0	M	4.21	0.71	16.5
284	147504	571823	0	232.8	4.38	0	M	2.76	0.56	16.4
285	147183	572166	0	183.5	5.03	0	M	2.43	0.55	16.7
286	146765	572630	0	201.6	2.71	0	V	1.98	0.57	16.9
287	146410	573019	0	124.8	3.45	0	V	3.16	0.58	17.4
288	146165	573274	0	130.3	3.22	0	V	1.23	0.48	17.7
289	145797	573650	0	136.4	2.49	0	V	0.82	0.48	18.0
290	145476	573988	0	127.4	2.51	0	V	0.91	0.51	18.4
291	145109	574394	0	104.6	5.53	0	V	1.01	0.56	18.6
292	144790	574724	0	140.5	2.26	0	V	1.12	0.56	19.0
293	147968	572969	0	222.1	2.45	0	M	2.84	0.60	15.9
294	151559	571066	0	327.8	1.16	0	M	1.16	0.68	14.2
295	151315	571082	0	404.5	0.86	0	M	2.23	0.68	14.3
296	151081	571127	0	277.1	1.11	0	M	2.61	0.78	14.6
298	150750	571171	0	206.4	3.08	0	M	4	0.78	14.7
299	150446	571213	0	82.4	19.9	0	M	3.17	0.70	14.9

station	X-position RD	Y-position RD	mussel culture plot	sediment median grain size	sediment percentage < 16 µm	stones > 2 cm	tidal basin	depth (m NAP)	maximum current speed (ms2)	average salinity (PSU)
301	149604	571295	0	361.9	1.34	0	M	2.99	0.64	15.3
302	149163	571335	0	384.1	1.25	0	M	2.79	0.74	15.5
303	148950	571372	0	261.3	1.49	0	M	3.27	0.74	15.6
304	148593	571413	0	339.5	1.44	0	M	4.07	0.80	15.9
305	148207	571451	0	271.1	2.4	0	M	3.8	0.71	16.0
306	151959	572855	0	239.6	1.63	0	M	1.84	0.54	14.4
307	151932	572545	0	215.5	2.26	0	M	2.63	0.73	14.2
308	151784	571293	0	274.5	1.16	0	M	1.04	0.79	14.2
309	151613	569889	0	168.8	3.52	0	M	1.35	0.66	14.0
310	151430	568526	0	158.5	5.64	0	M	1.04	0.54	13.7
311	151264	567131	0	270.5	2	0	M	1.71	0.72	13.9
313	151239	566858	0	200.7	12.8	0	M	3.49	0.73	13.7
314	151210	566637	0	211.7	2.3	0	M	2.83	0.72	13.6
315	151160	566238	0	67	23.5	0	M	9.95	0.63	13.1
316	152127	570800	0	185.9	1.78	0	M	0.98	0.84	13.9
319	153461	570383	0	110.6	5.22	0	M	1.66	0.52	12.6
320	153723	570306	1	143.4	7.3	0	M	3.07	0.52	12.3
321	153919	570209	0	282.4	1.68	0	M	3.82	0.78	12.1
323	154308	570140	0	86.4	23.8	0	M	1.93	0.71	11.7
324	154476	570074	1	237.2	1.64	0	M	1.96	0.71	11.6
325	154664	570008	1	205.3	1.8	0	M	2.53	0.71	11.6
326	154858	569982	0	210	2.46	0	M	1.24	0.45	11.6
327	147214	577954	0	132	2.53	0	V	0.78	0.44	18.4
328	147705	577455	0	102.3	5.22	0	V	1.09	0.43	17.7
329	147983	577201	0	94.1	4.64	0	V	1.33	0.43	17.4
330	148373	576810	0	102.2	4.25	0	V	1.74	0.43	17.1
331	148977	576248	0	146.4	5.82	0	V	1.98	0.49	16.3
332	149226	575953	0	152.3	4.19	0	V	2.3	0.49	15.9
333	149819	575373	0	141.2	5.11	0	V	2.4	0.51	15.4
334	150390	574810	0	115.5	8.07	0	V	2.52	0.54	15.1
335	151113	574105	0	186.2	3.75	0	M	1.77	0.59	14.7
336	151570	573635	0	226	1.34	0	M	1.47	0.53	14.5
337	152001	573210	0	243.9	0	0	M	1.45	0.54	14.3
338	142756	583850	0	185.4	0	0	V	1.34	0.60	20.8
339	142665	583649	0	148.7	13.7	0	V	3.4	0.69	20.8
340	142547	583393	0	221.6	1.82	0	V	7.66	0.69	20.6
341	142442	583170	0	331.8	1.21	0	V	10.7	0.89	20.7
342	142342	582958	0	407.1	0.68	0	V	10.69	0.89	20.7
343	142222	582707	0	274.9	0	0	V	8.64	0.95	20.5
344	142132	582522	0	241.8	1.48	0	V	9.02	0.95	20.4
345	142059	582373	0	171.8	4.09	0	V	7.08	0.95	20.4
346	141864	581979	1	140.7	6.99	0	V	2.57	0.75	20.6
350	148217	581489	0	154.3	3.85	0	V	6.11	0.86	18.0
351	148523	581671	0	214.7	2.34	0	V	14.82	0.77	17.8
352	148655	581751	0	207.6	2.42	0	V	9.59	0.57	17.6
353	149023	581961	0	177.7	2.27	0	V	2.84	0.52	17.5
354	149398	582202	0	176	2.12	0	V	3.42	0.65	17.2
355	149795	582406	0	257.2	1.23	0	V	3.13	0.67	17.1

station	X-position RD	Y-position RD	mussel culture plot	sediment median grain size	sediment percentage < 16 µm	stones > 2 cm	tidal basin	depth (m NAP)	maximum current speed (ms2)	average salinity (PSU)
356	150142	582613	0	175.1	2.43	0	V	2.81	0.67	17.0
357	150475	582829	0	138	4.43	0	V	1.68	0.66	17.1
358	150559	575664	0	164	6.44	0	V	2.14	0.51	15.2
359	150691	575970	0	120.9	8.9	0	V	2.48	0.48	15.3
360	150881	576423	0	133.9	3.47	0	V	2.05	0.64	15.3
361	151047	576844	0	139.8	3.13	0	V	1.62	0.76	15.4
362	151159	577086	0	177.8	1.8	0	V	1.27	0.76	15.4
363	151241	577350	0	206.9	1.4	0	V	1.02	1.00	15.5
364	151380	577675	0	192.3	2.15	0	V	1.21	1.00	15.8
365	151531	578052	0	162.8	1.65	0	V	9.32	1.31	15.8
366	151620	578248	0	147.9	8.18	0	V	8.9	1.31	15.6
367	156389	574184	0	114.5	3.78	0	M	1.23	0.42	11.7
368	156069	574272	0	110.1	7.44	0	M	1.3	0.45	11.9
369	155639	574437	0	159.6	6.03	0	V	1.24	0.42	12.0
370	155229	574528	0	209.7	1.53	0	V	1.25	0.44	12.3
371	154824	574722	0	103.7	5.55	0	V	1.79	0.44	12.8
372	154603	574786	0	105.7	4.58	0	V	2.07	0.40	12.9
373	154274	574892	0	111	10.8	0	V	2.32	0.40	13.3
374	153859	575048	0	139.7	9.41	0	V	2.41	0.47	13.5
378	155839	579062	0	140.6	4.08	0	V	1.41	0.58	13.1
379	156054	578945	0	146.1	3.42	0	V	1.39	0.58	13.0
380	156433	578746	0	112.7	11.6	0	V	4.11	0.69	12.9
381	156775	578549	0	284.2	7.11	1	V	4.38	0.63	12.7
382	157008	578456	0	174.5	15.3	1	V	3.31	0.63	12.5
383	157236	578312	0	23.4	43.7	0	V	2.93	0.63	12.4
386	157708	582363	0	116	9.44	0	V	1.94	0.66	13.5
387	158006	582179	0	145.2	4.2	0	V	1.36	0.68	13.2
388	158522	581926	0	161.2	2.86	0	V	3.9	0.69	13.0
389	158945	581606	0	18.4	47.3	0	V	3.23	0.43	11.9
390	143540	587681	0	208.8	1.71	0	V	1.2	0.62	22.6
391	143313	587936	0	210.8	1.59	0	V	1.59	0.70	22.9
392	143075	588178	0	217.5	1.57	0	V	3.16	0.72	23.2
393	142880	588406	0	233.8	1.77	0	V	4.49	0.82	23.6
394	142708	588592	0	226	2.03	0	V	10.06	0.79	24.1
403	141666	594528	0	301.4	0	0	V	5.22	1.25	25.8
405	146116	592780	0	226.8	0	0	V	2.88	0.66	24.4
406	146299	592610	0	253.3	1.24	0	V	6.54	0.86	24.2
407	146401	592488	0	301.2	1.01	0	V	12.36	0.86	24.1
408	146525	592386	0	303.5	0.95	0	V	13.58	0.86	24.1
409	146755	592186	0	143.8	4.48	0	V	12.45	0.86	24.2
411	146930	592037	0	190.1	1.76	0	V	3.58	0.86	24.3
412	147089	591923	0	200.9	1.88	0	V	2.74	0.86	24.2
413	147296	591688	1	192.2	1.92	0	V	3.55	0.95	24.0
414	147479	591483	1	174.2	2	0	V	8.1	0.95	23.8
415	147755	591319	0	206.6	0	0	V	11.66	0.96	23.6
416	148146	590979	0	184.5	2.58	0	V	9.71	0.96	23.2
417	148329	590798	0	251.2	2.03	0	V	6.56	0.91	23.1
419	148543	590625	0	330.8	0.85	0	V	2.3	0.79	22.5

station	X-position RD	Y-position RD	mussel culture plot	sediment median grain size	sediment percentage < 16 µm	stones > 2 cm	tidal basin	depth (m NAP)	maximum current speed (ms2)	average salinity (PSU)
420	151378	598104	1	154.7	2.66	0	V	1.2	0.58	25.2
421	151378	597899	1	153.7	2.63	0	V	1.2	0.58	25.2
422	151389	597753	0	166.6	2.2	0	V	2.12	0.58	25.2
423	151393	597566	0	199.1	0	0	V	3.64	0.69	25.2
424	151389	597234	0	164	2.96	0	V	3.49	0.78	25.1
425	151401	596992	0	177.5	2.41	0	V	3.68	0.78	25.1
426	151402	596705	1	184.6	5.29	0	V	4	0.62	24.9
427	151404	596548	1	171.6	2.64	0	V	3.42	0.62	24.5
428	151421	595885	0	183.8	1.68	0	V	1.29	0.57	23.8
429	151422	595696	0	173.3	1.99	0	V	1.91	0.60	23.8
430	151425	595405	0	213.6	0	0	V	1.14	0.60	23.6
432	151417	594820	0	195.8	3.25	0	V	5.46	0.80	23.2
434	151442	594338	0	290.7	1.14	0	V	11.71	0.75	22.8
435	151444	593900	0	172.3	3.66	0	V	9.55	0.63	22.6
436	151456	593418	0	249	1.22	0	V	2.73	0.75	22.6
437	151448	593253	0	249.9	0	0	V	3.52	0.75	22.6
438	151473	592928	0	188.4	1.57	0	V	2.01	0.87	22.5
439	151461	592697	0	194.3	1.65	0	V	2.38	0.83	22.6
440	151478	592426	0	219.1	0	0	V	1.03	0.83	22.7
441	151472	592169	0	255.7	1.41	0	V	5.5	0.89	22.3
442	151461	591963	0	172.8	4.15	0	V	8.04	0.89	22.2
443	151460	591488	0	262.5	2.04	0	V	1.37	0.87	21.9
444	153816	596736	0	190.8	1.78	0	V	1.15	0.67	23.4
446	153982	596532	1	160.6	5.4	0	V	8.02	0.67	23.1
448	154256	596285	1	213.4	2.02	0	V	3.55	0.79	22.9
449	154566	595997	1	186.6	1.78	0	V	2.35	0.75	22.7
450	154911	595656	1	199.7	0	0	V	1.43	0.58	22.4
451	155269	595286	0	166.6	2.52	0	V	2.14	0.57	22.2
452	155472	595095	0	203.1	0	0	V	0.98	0.55	22.1
453	157632	598706	1	185	1.68	0	V	1.21	0.56	23.6
454	157861	598448	1	161.9	6.78	0	V	3.04	0.57	23.4
455	158097	598124	0	184.8	1.62	0	V	0.88	0.60	22.9
520	143226	593855	0	195.1	2.41	0	V	1.7	0.74	25.5
521	143244	593951	0	183	2.22	0	V	1.69	0.74	25.5
522	142828	594079	0	175.9	3.43	0	V	1.92	0.74	25.5
523	142604	594246	0	238.7	0	0	V	2.64	1.02	25.5
524	117774	559996	0	273	8.24	0	M	11.95	1.40	26.1

References

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Appendix 2

Subtidal macrozoobenthos species information 2008

Table with all macrozoobenthos species encountered in the subtidal western Dutch Wadden Sea during a survey in autumn 2008. In total 397 stations were sampled with a 0.06 m^2 box core. Occurrence is the presence as fraction of 397 stations. Biomass is the average ash free dry mass in gm^{-2} and density is numerical density is in nm^{-2}. Four feeding types were distinguished; deposit feeders (depso.), suspension feeders (susp.), omnivores (omni.) and carnivores (carni.). Substrate types were; soft sediment (soft), heterogeneous sediment (heter.), and hard substrate. Hard substrate species were categorized as mobile and sessile, hard m. and hard s. respectively. Substrate type was not always defined (undef.). Species were defined invasive (inv.) based on Wolff (2005) and Buschbaum et al. (2012). Nomenclature follows the World Register of Marine Species, accessible through www.marinespecies.org. Names in the sub headers are Phylum and Class.

shortname		feeding	subst.	inv.	occur.	biomass	density
Annelida / Clitellata							
Oligoc	Oligochaeta	depos.	soft	no	0.378	1.35E-02	9.36E+01
Annelida / Polychaeta							
Scoarm	*Scoloplos armiger*	depos.	soft	no	0.597	3.16E-01	5.29E+01
Capcap	*Capitella capitata*	depos.	soft	no	0.537	1.77E-02	6.27E+01
Hetfil	*Heteromastus filiformis*	depos.	soft	no	0.33	7.68E-02	2.31E+01
Arimin	*Aricidea minuta*	depos.	soft	no	0.166	2.40E-03	1.46E+01
Aremar	*Arenicola marina*	depos.	soft	no	0.02	3.33E-02	4.00E-01
Parful	*Paraonis fulgens*	depos.	soft	no	0.003	0.00E+00	4.20E-02
Trafor	*Travisia forbesii*	depos.	soft	no	0.003	2.00E-04	4.20E-02
Nephom	*Nephtys hombergii*	carni.	soft	no	0.345	1.66E-01	9.28E+00
Etelon	*Eteone longa*	carni.	soft	no	0.237	7.20E-03	8.65E+00
Nepcir	*Nephtys cirrosa*	carni.	soft	no	0.224	5.73E-02	1.09E+01
Alivir	*Alitta virens*	omniv.	soft	yes	0.131	9.01E-01	2.05E+00
Alisuc	*Alitta succinea*	depos.	heter.	no	0.128	7.75E-02	1.45E+01
Nepcae	*Nephtys caeca*	carni.	soft	no	0.116	3.91E-02	3.36E+00
Glyalb	*Glycera alba*	carni.	soft	no	0.083	9.10E-03	2.06E+00
Myrpro	*Myrianida prolifera*	carni.	hard m.	no	0.053	4.00E-04	2.85E+00
Neplon	*Nephtys longosetosa*	carni.	soft	no	0.053	1.16E-02	2.20E+00
Eunlon	*Eunereis longissima*	omniv.	soft	no	0.035	4.20E-02	1.07E+00
Glyuni	*Glycera unicornis*	carni.	soft	no	0.035	3.10E-03	5.06E-01
Maldar	*Malmgreniella darbouxi*	carni.	soft	no	0.025	1.50E-03	1.03E+00
Heddiv	*Hediste diversicolor*	omniv.	soft	no	0.02	8.10E-03	5.08E-01
Harimp	*Harmothoe impar*	carni.	hard m.	no	0.018	1.20E-03	6.30E-01
Myspic	*Mysta picta*	carni.	soft	no	0.015	3.00E-04	3.78E-01
Phymuc	*Phyllodoce mucosa*	carni.	soft	no	0.015	3.00E-04	2.52E-01
Eumsan	*Eumida sanguinea*	carni.	soft	no	0.013	4.00E-04	7.14E-01
Micscz	*Microphthalmus sczelkowii*	depos.	soft	no	0.01	0.00E+00	2.52E-01
Eulvir	*Eulalia viridis*	carni.	hard m.	no	0.008	2.00E-04	2.10E-01
Harimb	*Harmothoe imbricata*	carni.	hard m.	no	0.005	3.80E-03	4.62E-01

shortname		feeding	subst.	inv.	occur.	biomass	density
Bylsar	*Bylgides sarsi*	carni.	soft	no	0.003	1.00E-04	4.20E-02
Phomin	*Pholoe minuta*	carni.	hard m.	no	0.003	0.00E+00	4.20E-02
Sthboa	*Sthenelais boa*	omniv.	hard m.	no	0.003	3.10E-03	1.68E-01
Sabspi	*Sabellaria spinulosa*	susp.	hard s.	yes	0.003	1.00E-04	4.20E-02
Spimar	*Spio martinensis*	depos.	soft	no	0.584	3.64E-02	1.53E+02
Pygele	*Pygospio elegans*	depos.	soft	no	0.373	7.50E-03	4.79E+01
Marvir	*Marenzelleria viridis*	depos.	soft	yes	0.34	1.89E+00	6.84E+02
Strben	*Streblospio benedicti*	depos.	soft	yes	0.159	2.10E-03	1.34E+01
Polcor	*Polydora cornuta*	susp.	heter.	no	0.139	3.50E-03	1.34E+01
Spibom	*Spiophanes bombyx*	depos.	soft	no	0.116	6.00E-03	2.77E+00
Magjoh	*Magelona johnstoni*	depos.	soft	no	0.103	5.70E-03	3.80E+00
Polcil	*Polydora ciliata*	depos.	hard s.	no	0.035	5.00E-04	2.69E+00
Psepul	*Pseudopolydora pulchra*	depos.	soft	no	0.003	1.00E-04	4.20E-02
Scofol	*Scolelepis foliosa*	depos.	soft	no	0.003	4.00E-04	2.10E-02
Aphmar	*Aphelochaeta marioni*	depos.	soft	yes	0.562	6.11E-02	3.16E+02
Lancon	*Lanice conchilega*	susp.	soft	no	0.118	1.48E+00	3.76E+01
Lagkor	*Lagis koreni*	depos.	soft	no	0.005	1.00E-03	1.26E-01
Arthropoda / Malacostraca							
Batsar	*Bathyporeia sarsi*	depos.	soft	no	0.103	3.50E-03	4.62E+00
Uropos	*Urothoe poseidonis*	depos.	soft	no	0.058	2.40E-03	3.74E+00
Gamloc	*Gammarus locusta*	depos.	hard m.	no	0.03	2.00E-03	1.22E+00
Monins	*Monocorophium insidiosum*	depos.	hard m.	no	0.02	1.00E-04	4.62E-01
Melpal	*Melita palmata*	depos.	hard m.	no	0.01	3.00E-04	1.05E+00
Micmac	*Microprotopus maculatus*	omniv.	hard m.	no	0.008	0.00E+00	1.68E-01
Corare	*Corophium arenarium*	depos.	soft	no	0.005	1.00E-04	2.10E-01
Corvol	*Corophium volutator*	depos.	soft	no	0.005	7.00E-04	3.11E+00
Batele	*Bathyporeia elegans*	depos.	soft	no	0.003	0.00E+00	1.26E-01
Chesun	*Cheirocratus sundevalli*	depos.	hard m.	no	0.003	1.00E-04	3.36E-01
Monach	*Monocorophium acherusicum*	depos.	hard m.	no	0.003	0.00E+00	4.20E-02
Bodsco	*Bodotria scorpioides*	depos.	soft	no	0.01	1.00E-04	1.68E-01
Cracra	*Crangon crangon*	carni.	soft	no	0.123	1.42E-01	2.20E+00
Carmae	*Carcinus maenas*	carni.	soft	no	0.068	1.06E+00	1.64E+00
Pagber	*Pagurus bernhardus*	carni.	soft	no	0.01	1.04E-02	1.68E-01
Hemtak	*Hemigrapsus takanoi*	carni.	hard m.	yes	0.005	1.07E-02	1.26E-01
Arthropoda / Maxillopoda							
Balsp[1]	*Balanus sp.*	susp.	hard s.	no	0.103	6.16E-01	7.86E+01
Elmmod	*Elminius modestus*	susp.	hard s.	yes	0.088	7.95E-02	2.60E+01
Bryozoa / Gymnolaemata							
Conret	*Conopeum reticulum*	susp.	hard s.	no	0.227	0.00E+00	6.28E+01
Elepil	*Electra pilosa*	susp.	hard s.	no	0.008	0.00E+00	5.04E-01
Smipro[2]	*Smittoidea prolifica*	susp.	hard s.	yes	0.003	0.00E+00	8.40E-02
Alcmyt	*Alcyonidioides mytili*	susp.	hard s.	no	0.045	0.00E+00	8.82E+00
Chordata / Ascidiacea							
Didvex	*Didemnum vexillum*	susp.	hard s.	yes	0.005	6.50E-03	8.40E-02
Stycla	*Styela clava*	susp.	hard s.	yes	0.01	2.83E-02	3.78E-01

shortname		feeding	subst.	inv.	occur.	biomass	density
Molsoc	*Molgula socialis*	susp.	hard s.	yes	0.008	1.60E-03	1.26E-01
Cnidaria / Anthozoa							
Metsen	*Metridium senile*	susp.	hard s.	no	0.121	1.81E-01	2.35E+01
Sagtro	*Sagartia troglodytes*	carni.	heter.	no	0.048	3.88E-01	5.58E+00
Cnidaria / Hydrozoa							
Clyhem	*Clytia hemisphaerica*	susp.	hard s.	no	0.063	0.00E+00	3.90E+00
Obelon	*Obelia longissima*	susp.	hard s.	no	0.015	0.00E+00	9.24E-01
Hargel	*Hartlaubella gelatinosa*	susp.	hard s.	no	0.003	0.00E+00	4.20E-02
Echinodermata / Asteroidea							
Astrub	*Asterias rubens*	carni.	hard m.	no	0.01	1.25E-01	5.46E-01
Echinodermata / Echinoidea							
Echcor	*Echinocardium cordatum*	depos.	soft	no	0.013	8.90E-02	3.15E-01
Echinodermata / Ophiuroidea							
Ophoph	*Ophiura ophiura*	carni.	soft	no	0.043	2.37E-02	9.24E-01
Ophfra	*Ophiothrix fragilis*	susp.	hard m.	no	0.003	0.00E+00	4.20E-02
Mollusca / Bivalvia							
Ensdir	*Ensis directus*	susp.	soft	yes	0.27	2.11E+01	5.99E+01
Myaare	*Mya arenaria*	susp.	soft	yes	0.234	1.69E+01	1.96E+02
Barcan	*Barnea candida*	depos.	heter.	no	0.008	3.23E-02	3.78E-01
Mytedu	*Mytilus edulis*	susp.	hard s.	no	0.06	5.23E+00	9.55E+00
Cragig	*Crassostrea gigas*	susp.	hard s.	yes	0.043	2.35E+00	5.42E+00
Macbal	*Macoma balthica*	depos.	soft	no	0.136	1.20E-01	4.30E+00
Angten	*Angulus tenuis*	depos.	soft	no	0.121	4.13E-02	3.13E+00
Ceredu	*Cerastoderma edule*	susp.	soft	no	0.043	4.38E-01	1.13E+01
Angfab	*Angulus fabula*	depos.	soft	no	0.038	1.27E-02	7.98E-01
Abralb	*Abra alba*	depos.	soft	no	0.015	2.90E-03	6.30E-01
Kurbid	*Kurtiella bidentata*	susp.	soft	no	0.015	5.00E-04	2.94E-01
Petpho	*Petricolaria pholadiformis*	susp.	heter.	yes	0.013	5.88E-02	3.78E-01
Spisub	*Spisula subtruncata*	susp.	soft	no	0.01	3.00E-04	1.68E-01
Telfer	*Tellimya ferruginosa*	susp.	soft	no	0.008	7.00E-04	2.10E-01
Vencor	*Venerupis corrugata*	susp.	heter.	no	0.005	5.00E-04	8.40E-02
Donvit	*Donax vittatus*	susp.	soft	no	0.003	0.00E+00	4.20E-02
Mollusca / Gastropoda							
Retobt	*Retusa obtusa*	carni.	soft	no	0.03	3.00E-04	8.40E-01
Crefor	*Crepidula fornicata*	susp.	hard s.	yes	0.065	1.01E-01	6.59E+00
Perulv	*Peringia ulvae*	depos.	soft	no	0.01	3.91E-01	5.05E+02
Mollusca / Polyplacophora							
Lepcin	*Lepidochitona cinerea*	depos.	hard m.	no	0.003	0.00E+00	4.20E-02
Nemertea							
Nemert	Nemertea	carni.	undef.	no	0.018	1.60E-03	2.94E-01

1 Balsp is a combination of *Balanus crenatus* and *Amphibalanus improvisus*

2 *Smittoidea prolifica* is invasive following De Blauwe (2009)

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Appendix 3

Species response curves along environmental gradients

Of the 23 most important species in 2008 (see Table 5 main report) species response curves along four environmental gradients were plotted as conditional density displays and fitted with logistic first and second order regression models. Species abbreviations are explained in Table 1 of the main report.

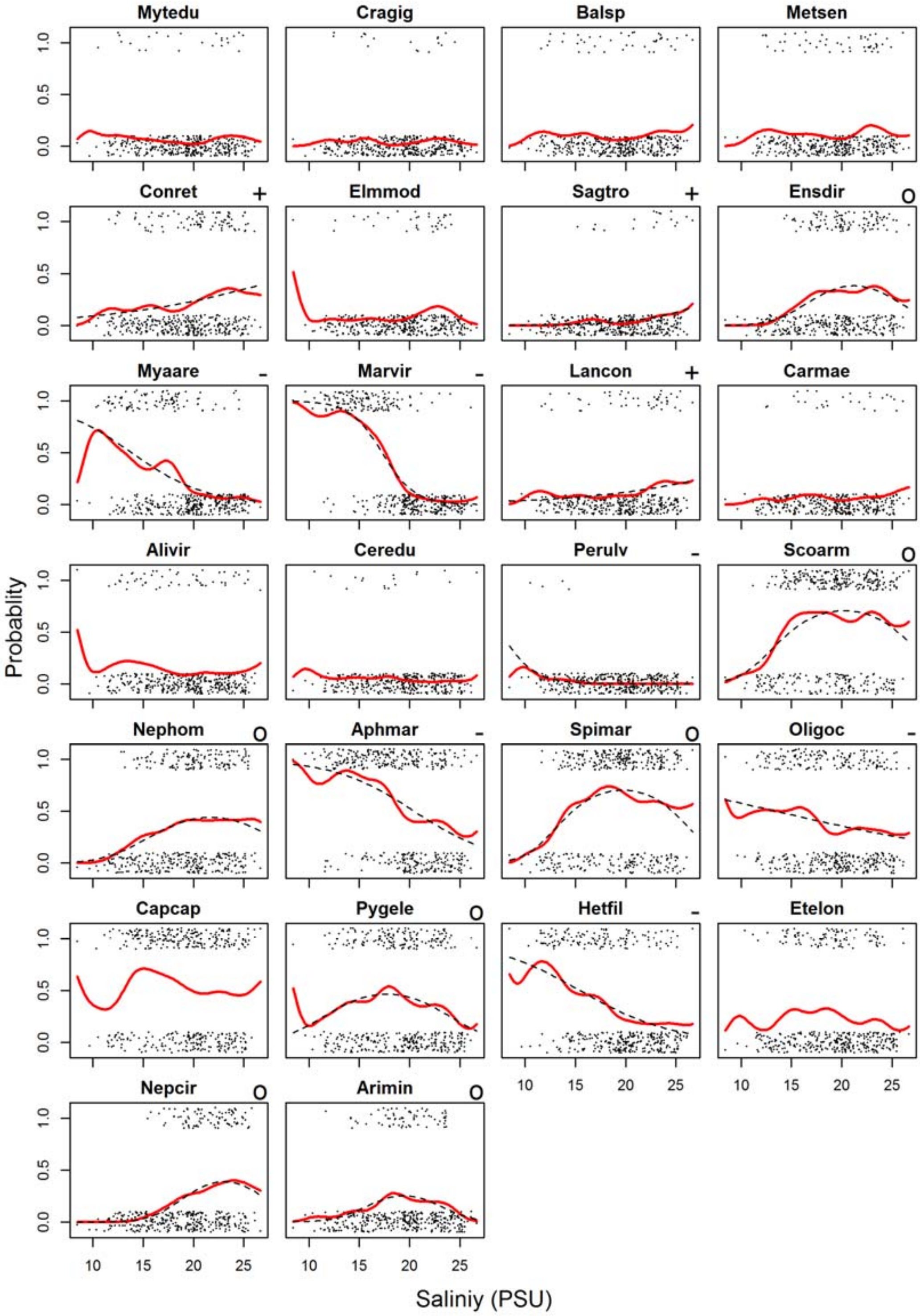

Figure A3.1 Conditional density curves for presence absence of the most important macrozoobenthos species in 2008 depending on salinity. Presences are plotted jittered dots along the upper margins, absences along the lower margins of the panels. Salinity effects on presence of the species were tested with two logistic models, a single term model and a model with an additional quadratic term. Logistic curves are plotted in the figures of the species that had a presence absence distribution significantly related to salinity. The sign of the relationship is plotted next to the species abbreviation, in case of a single term model. Species that were best described by a significant quadratic model are assumed to have an optimum distribution and are marked with "o".

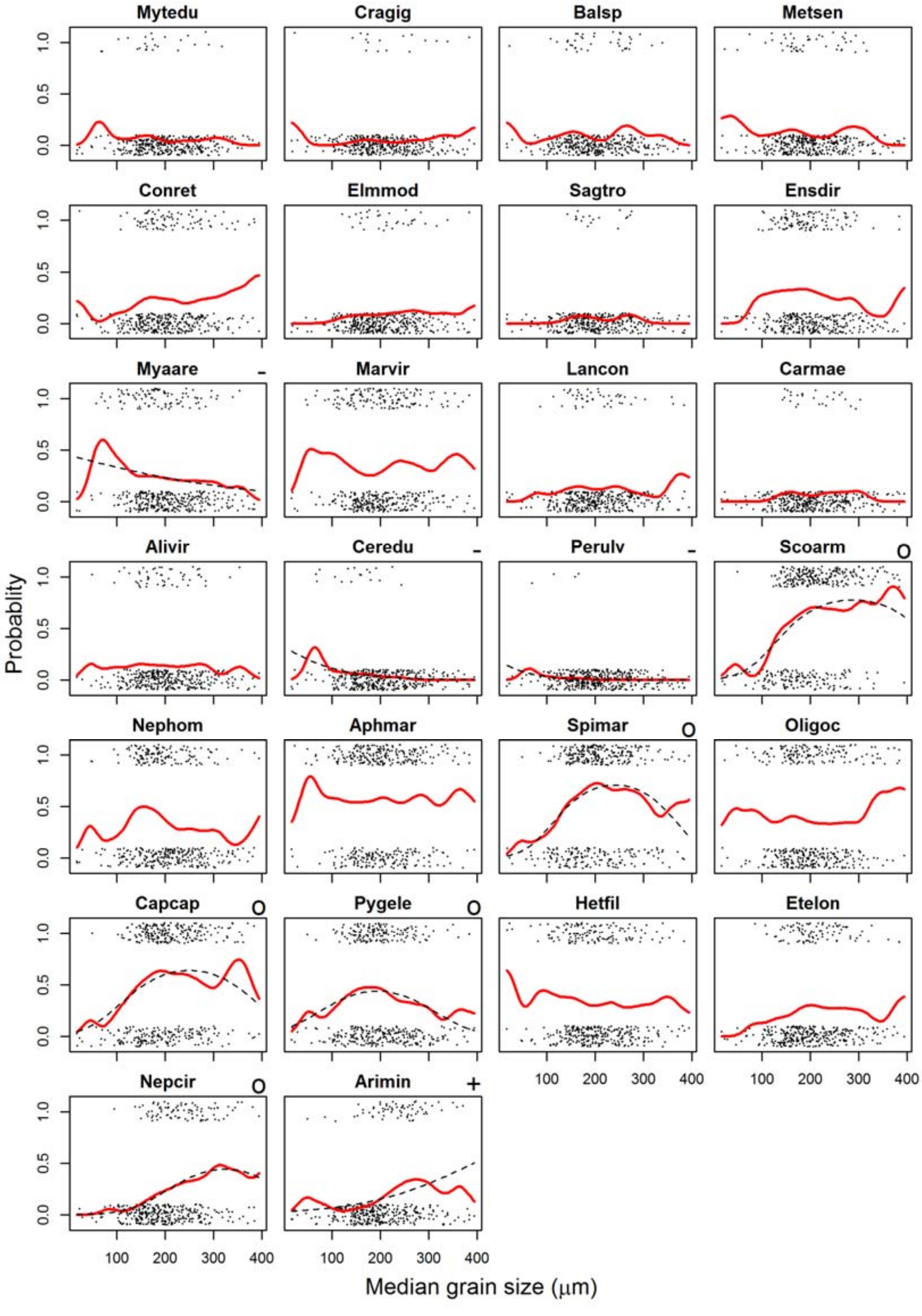

Figure A3.2. **Conditional density curves for presence absence of the most important macrozoobenthos species in 2008 depending on sediment median grain size. Presences are plotted jittered dots along the upper margins, absences along the lower margins of the panels. Median grain size effects on presence of the species were tested with two logistic models, a single term model and a model with an additional quadratic term. Logistic curves are plotted in the figures of the species that had a presence absence distribution significantly related to median grain size. The sign of the relationship is plotted next to the species abbreviation, in case of a single term model. Species that were best described by a significant quadratic model are assumed to have an optimum distribution and are marked with "o".**

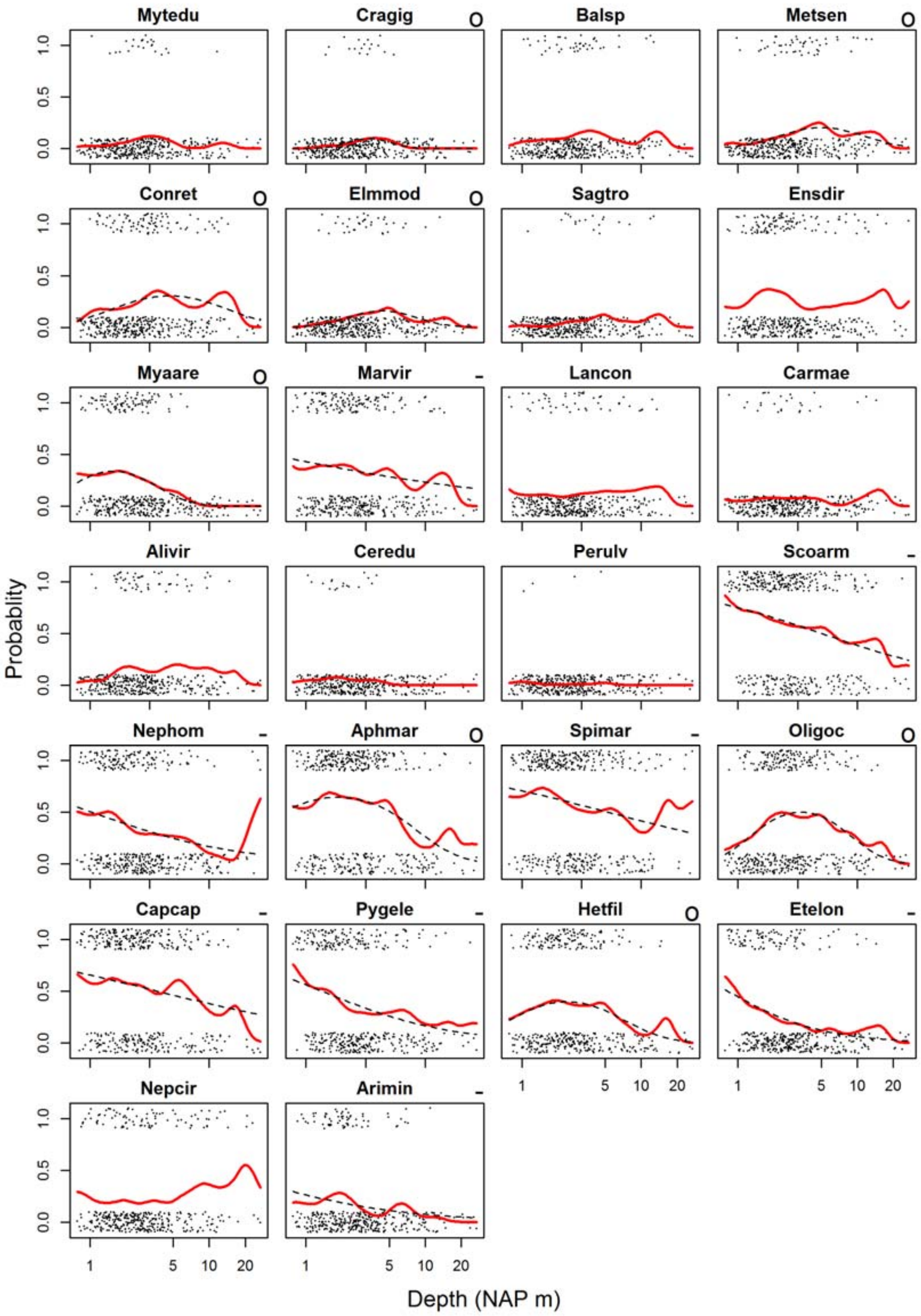

Figure A3.3. Conditional density curves for presence absence of the most important macrozoobenthos species in 2008 depending on depth. Presences are plotted jittered dots along the upper margins, absences along the lower margins of the panels. Depth effects on presence of the species were tested with two logistic models, a single term model and a model with an additional quadratic term. Logistic curves are plotted in the figures of the species that had a presence absence distribution significantly related to depth. The sign of the relationship is plotted next to the species abbreviation, in case of a single term model. Species that were best described by a significant quadratic model are assumed to have an optimum distribution and are marked with "o".

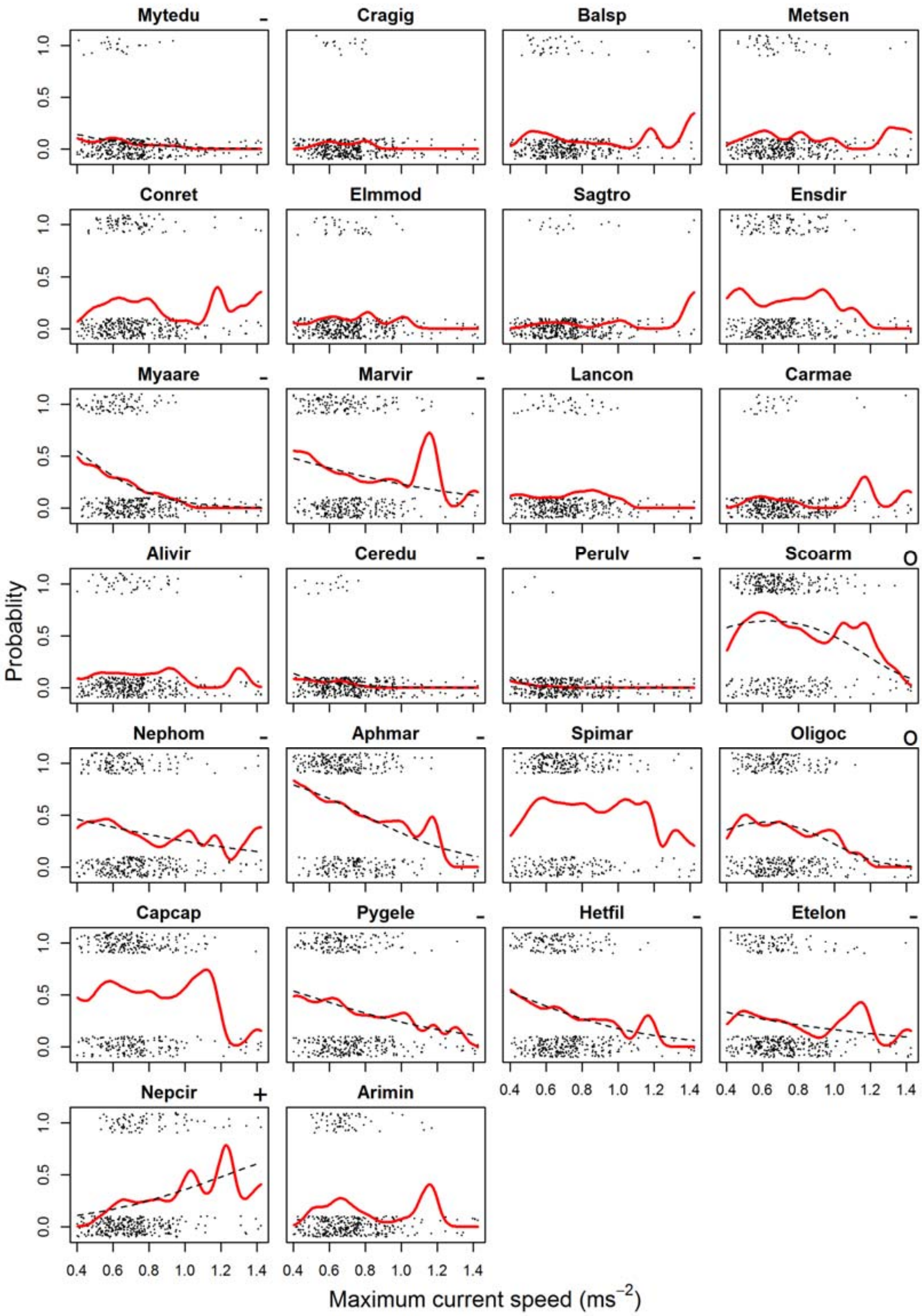

Figure A3.4. Conditional density curves for presence absence of the most important macrozoobenthos species in 2008 depending on maximum current speed. Presences are plotted jittered dots along the upper margins, absences along the lower margins of the panels. Current speed effects on presence of the species were tested with two logistic models, a single term model and a model with an additional quadratic term. Logistic curves are plotted in the figures of the species that had a presence absence distribution significantly related to maximum current speed. The sign of the relationship is plotted next to the species abbreviation, in case of a single term model. Species that were best described by a significant quadratic model are assumed to have an optimum distribution and are marked with "o".

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NIOZ Texel
Landsdiep 4
1797 SZ 't Horntje, Texel

Postbus 59
1790 AB Den Burg, Texel
Nederland
Telefoon: +31(0)222 - 369300
Fax: +31(0)222 - 319674

NIOZ Yerseke
Korringaweg 7
4401 NT Yerseke

Postbus 140
4400 AC Yerseke
Nederland
Telefoon: +31(0)113 - 577417
Fax: +31(0)113 - 573616

www.nioz.nl

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