



Macrofauna associated with mussels, *Mytilus edulis* L., in the subtidal of the western Dutch Wadden Sea

Jan Drent & Rob Dekker



Macrofauna associated with mussels, *Mytilus edulis*, in the subtidal of the western Dutch Wadden Sea

Jan Drent & Rob Dekker

Royal Netherlands Institute for Sea Research



This study was part of a research project on sustainable shellfish culture (PRODUS). This project was implemented on behalf of the Ministry of Agriculture, Nature and Food Quality (LNV) and the shellfish sector. This assignment resulted from the new shellfish policy and the innovation agenda of the shellfish sector.

This work was conducted in a cooperation between:

I MARES Wageningen UR

(IMARES - Institute for Marine Resources & Ecosystem Studies)



Onderzoeksbureau MarinX, Elkerzee

Texel, April 2013

NIOZ-Report 2013-7

Royal Netherlands Institute for Sea Research

Contact information authors:

Royal Netherlands Institute for Sea Research
PO Box 59
1790 AB Den Burg, Texel
The Netherlands

Email: Jan.Drent@nioz.nl

Rob.Dekker@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*. *Ensis directus* protruding from core sediment surface. Core surface with *Mytilus 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

Abstract	4
Introduction	6
Methods	8
Results	10
Discussion	16
Acknowledgements	19
References	20
Tables	22
Figures	29

Appendices

- 1 Associated species list from literature sources
- 2 Species associated with mussels (*Mytilus edulis*), complete list, Table 3 extended
- 3 Species associated with oysters (*Crassostrea gigas*), complete list, Table 4 extended
- 4 Species associated with mussels (*Mytilus edulis*), complete list, Table 11 extended
- 5 Species list of mussel seed fisheries experiment

Abstract

Mussels (*Mytilus edulis*) form dense beds on the sea floor. In soft sediment systems like the Wadden Sea these biogenic structures offer an otherwise absent or scarce hard substrate settlement area for invertebrate fauna to attach to. Next to that the matrix of attached mussels may provide species a refuge from predation and physical stress. Another effect of mussel beds is an increased deposition of fine sedimentary and organic material on the sea bed because of the filtering and particle selection activities of the mussels and the reduction of current velocities by the structure of the bed. With these habitat modifying properties mussels can be regarded as physical ecosystem engineers. Sites with mussels are often more species rich than the surrounding area without mussels. This is also the case in the subtidal of the western Dutch Wadden Sea where samples of 0.06 m² with mussels were twice as rich in species as samples without mussels.

This report gives a description of the mussel associated macrozoobenthos in the subtidal of the western Dutch Wadden Sea. The following questions are addressed. What are the species that are associated with mussels? Is there a quantitative relationship between mussels and species richness? What is the effect of environmental variables, salinity, sediment grain size, depth (m NAP) and maximum current speed on the species associated with mussels? This question is treated on several levels, first on the level of the individual associated species by determining species response curves to the environmental gradients. Second at the level of one box core of 0.06 m², where the number of associated species is related to the environmental variables and finally at the level of aggregated samples along the gradients with number of associated species as response variable. A following question was if the mussel associated community differs between mussels inside and outside mussel culture plots? What is the effect of the age of a mussel bed on the associated species richness?

A dataset collected at 568 box core stations (183 with mussels) during a survey in 2008 and a comparison between mussels inside and outside mussel culture plots over the period 2008-2010, all in the subtidal western Dutch Wadden Sea was used to answer all of the above questions except the last one. Bed age effects were analysed using a boxcore dataset from a fisheries experiment where sites open and closed for fisheries were repeatedly sampled for up to several years.

There were 124 macrozoobenthos species identified in the survey and the comparison between mussels inside and outside mussel culture plots. Of these species 35 were significantly positively associated with mussels and 22 were significantly negatively associated with mussels. Of the associated species 8 occurred exclusively together with mussels. There were an additional 23 out of 42 "rare" species (species found in less than 7 box cores) that were only found with mussels. The positively associated and species exclusively found together with mussels were mainly hard substrate species (67%), both mobile and sessile. Deposit feeders were underrepresented in this group. These observations may suggest that the biogenic hard substrate structure of the mussel bed has a stronger effect on the associated species richness than the local organic enrichment of the sediment by the mussel bed.

Number of associated species in a box core containing mussels increases with the total biomass of these mussels.

The environmental variable that affects most associated species is salinity. Out of 33 associated species tested 19 respond to salinity, mostly positively. For each of the other three environmental variables depth, grain size and current speed 14 out of 33 species responded. Responses were mainly positive or showed optima.

Richness at the level of a box core not corrected for mussel biomass increases with salinity, depth and maximum current speed. Richness also increases with grain size, but this increase levels off above a median grain size of around 250 µm. However when mussel biomass is used as an explanatory variable only depth and median grain size explain a significant part of the variation in associated species number in a box core. Species numbers in aggregates of boxes within bins of equal parts of the environmental gradients show in general positive relationships with all four gradients studied. Most pronounced is the relationship with salinity. Crudely speaking at the system level mussel associated species richness is largest at highest salinities, maximum current speeds above 0.5 ms⁻², sites deeper than 5 m below NAP and a median grain size of around 200 µm.

Composition of the associated fauna community differs between mussels inside and outside mussel culture plots. The six species contributing most to this difference are *Alitta virens*, *Carcinus maenas* and *Conopeum reticulum* which were more abundant on culture plots and Oligochaeta, *Alitta succinea* and *Balanus crenatus*, which were more abundant outside culture plots. The difference between plots coincides with a difference in salinity, culture plot mussels are in more saline areas than mussels outside culture plots.

On the mussel beds followed through time associated species number was positively related with mussel cover. On top of that age had a positive effect on associated species number, however this effect was restricted to surviving beds that were followed for more than one year. At the level of individual taxonomic units half of the associated TU's responded positively to bed age, while only one had a negative response.

Mussels in the subtidal of the western Dutch Wadden Sea create biogenic structures with a large number of significantly positively associated species that is 28 % of the measured species pool in this habitat. The number of species that was exclusively found at stations with mussels was 31 (8 associated and 23 rare species) or 25 % of the species pool. This clearly shows the important role of mussels for species diversity in this habitat. However in the strict sense, because this is a descriptive study the causative role of the mussel enhancing species diversity is an assumption based on published experimental studies done outside the western Dutch Wadden Sea.

Introduction

The Wadden Sea is a coastal marine soft sediment system. In this system the mussel *Mytilus edulis* forms beds on the sediment surface, these are biogenic structures of mussels attached to each other with byssal threads. Especially in soft sediment systems mussel beds provide an otherwise scarce physical resource, which is a hard substrate suitable for attachment of epibionts, and within the mussel matrix a refuge from predation physical and physiological stress and also may affect transport of particles in the benthic environment (Gutiérrez et al. 2003). Considering these properties the mussel may be regarded a physical ecosystem engineer following the definition of Jones et al. (1997). This definition is: "Physical ecosystem engineers are organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials. Physical ecosystem engineering by organisms is the physical modification, maintenance, or creation of habitats. The ecological effects of engineering on other species occur because the physical state changes directly or indirectly control resources used by these other species."

It is a common observation that the species richness in mussel beds is higher than in the surrounding regions without mussels (Seed 1996, 2009, Dittmann 1990, Buschbaum et al. 2009, Norling & Kautsky 2008). Many of these species live attached to hard substrate surfaces like barnacles and Bryozoa, others find a refuge within the mussel matrix. The local changes in the environment in particular the presence of hard substrate caused by the presence of mussel beds have an effect on the biological community. Mussels increase habitat heterogeneity and can increase species richness at the system scale.

Mussels occur on tidal flats but also continuously submerged in the subtidal. These mussels have different associated species and the communities are more species rich than in the intertidal (Saier 2002) and have been called oasis of biodiversity (Saier et al. 2002). In the past in the Wadden Sea there were also beds with flat oyster with a typical associated community (Mobius 1877, Buhs & Reise 1997, Smyth and Roberts 2010). Nowadays these do not exist anymore and play no role in the biodiversity of the subtidal habitat of the Wadden Sea, making the role of subtidal mussels even more important.

This report is about the macrozoobenthos community associated with the mussel (*Mytilus edulis*). It is specifically aimed at describing the mussel associated macrozoobenthos species occurring in the subtidal of the western Dutch Wadden Sea. The western Dutch Wadden Sea is a part of the Wadden Sea where a relatively large part (50%) of the area is continuously submerged in contrast to tidal flat dominated tidal basins towards the east. In the western Dutch Wadden Sea subtidal mussels are of important ecological value for instance as food source for several species of diving ducks. Species richness of macrozoobenthos in this area at sites with mussels is higher than at sites without mussels. At the scale of one sample of 0.06 m² species richness is twice as high in samples containing mussels than in samples without (Dekker & Drent 2013). Besides an ecological value the mussels also have an economic value. Subtidal mussels are harvested for use as mussel seed that is used to stock mussel culture plots. Main question of the PRODUS project, of which this study is a part, is to what extent fisheries is impacting the ecological role of the mussel in this system.

The main aim of this report is to identify which species are associated with mussels and explore factors that affect richness of the associated macrozoobenthos species. These factors are properties

of the mussels and the abiotic environment. The mussel properties of interest are quantity (biomass per square meter or density in a bed) and age of the bed. Quantity because more mussels means more surface area for associated species to settle and age because with increasing amount of time chances for settlement of associated species increases.

First specific question addressed in this report is what are the mussel associated macrozoobenthos species? In general the answer is found by using published information on mussel associated species in the Wadden Sea area. In addition to that a more specific list of mussel associated species for the western Dutch Wadden Sea is made using data from a benthic survey done in 2008 (Dekker & Drent 2013) and a sampling program on mussels inside and outside mussel culture plots in the period 2008-2010 (Drent & Dekker 2013). Because the invasive Pacific oyster, also an epibenthic species like the mussel, associations with the oyster are also reported and compared to the mussel associations.

Second question is what is the quantitative relationship between mussels and associated species? More mussels can form a more complex matrix with a larger surface area which may increase associated species richness. On the other hand increasing biomass will also lead to increasing competition for limiting resources like food. This is explored at the level of one box core of 0.06 m² and at a larger scale of 12 cores within a mussel bed.

Third question is how local environmental conditions influence mussel associated species richness. A mussel bed may ameliorate physical conditions and in such way provide a niche for associated species (Dittmann 1990). However the local abiotic boundary conditions remain important. Seawater salinity is an important example and an already long recognized variable affecting species richness (Remane 1934). With the salinity range in the western Dutch Wadden Sea we expect a positive relationship between associated species richness and salinity. Salinity is relevant variable in the western Dutch Wadden Sea because of fresh water discharge from the IJsselmeer. The effect of salinity is especially important because mussel seed fisheries mainly take mussels from the more brackish areas and relay them on the mussel culture plots that are located in more saline areas. Beside salinity also the type of sediment can impact mussel associated species, where a study from the northern German Wadden Sea showed that mussels on fine sediments contained less attached species than mussels on coarse sediments (Westphalen 2006)

This naturally leads to the following question if the associated species community differs between mussels from inside or outside mussel culture plots? It may be expected that species composition is different because of the different environmental conditions where culture plots and natural beds occur and also because of effects handling by fisheries. This question is treated in more detail in Drent & Dekker (2013), but also some information is given here.

All processes need time. One process relevant in the context of associated species is colonisation of a mussel bed by associated species and a possible succession of the associated community through time. Previous studies have shown that mussel succession stage is an important determinant of faunal abundance, species richness and species assemblage (Koivisto et al. 2011), where richness increases with mussel bed age (Tsuchiya & Niihira 1986). The effects of bed mussel bed age on the associated species in the western Dutch Wadden Sea is investigated with data from a mussel fisheries experiment where beds open and closed for fisheries where repeatedly sampled over time, this sampling was continued up to several years (Craeymeersch et al 2013).

Methods

Literature data

Literature A literature search was done restricted to published accounts on associated species in the international Wadden Sea. All species reported were listed.

Field data

Macrozoobenthos abundance data from 568 stations in the subtidal western Dutch Wadden Sea were used for the analysis (Fig. 1). The data set was a combination of abundance data from 397 stations visited during a survey of the western Dutch Wadden Sea in 2008 (Dekker & Drent 2013), of 159 stations used for a comparison between natural mussel beds and mussel culture plots collected in 2008, 2009 and 2010 (Drent & Dekker 2013) and an additional 12 stations visited in 2008 for the mussel bed comparison, but not used in that comparison because no mussels were present. Sampling always took place in autumn with a box core of 0.06 m². For further details please see reference mentioned above.

Experimental plots on natural mussel beds

During 2008-2010 experimental plots were established on natural sublittoral mussel beds (Fig. 2). Each bed had two plots one open and one closed for fisheries. This setup was used to study the effects of mussel seed fishery on mussel seed beds. Results of this project were reported in Craeymeersch et al. 2013 and this report includes a description of the experimental setup and methods. Data from this project were used to test for mussel bed age effects on the macrozoobenthos associated with *M. edulis*. The original list of reported species was reduced from 185 to 108 by aggregating several species to higher taxonomic levels. A complete list of aggregations is included in appendix 5. The final dataset contained 1896 box cores with in total 108 taxonomic units collected from 21 mussel beds.

Environmental data

At each station a sediment sample (diameter 1.6 cm) was taken out of the box core of the top 8 cm from the surface downwards. This sample was taken out of the same box as the macrozoobenthos before washing it over the mesh. Sediment grain size distribution was analysed on a coulter laser diffraction analyser (Coulter LS 13 320) after freeze drying and HCl and H₂O₂ treatments to remove calcareous material and organic matter respectively.

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).

Analysis of species associations

Positive associations between species pairs were defined as those pairs that co-occur at sampling stations more often than expected by chance. The first assumption made was that the chance that species *a* will co-occur with species *b* depends on the number of occurrences of both species. The second assumption was that the chance of encountering a species at a certain station depends on the species richness at that station. There is a higher chance of finding a certain species at a species rich than at a species poor station. Based on these assumptions probability distributions were estimated for the number of co-occurrences given the occurrences of species *a* and *b* in the data. This was done by randomly drawing a number of stations equal to number of species *b* occurrences from the data set and then counting the number of *a* occurrences in the sample. The stations were sampled with a chance proportional to their species richness. This sampling was repeated 10 000 times. From the resulting distribution of random co-occurrences the 0.001, 0.01, 0.99, 0.999 quantiles were calculated. Any observation outside the 0.01 and 0.99 quantile values were regarded as significant negative or positive associations respectively. These one way significance levels of 0.01 were chosen instead of 0.05 to account at least partly for multiple testing. Probability distributions were estimated for *M. edulis* (183 occurrences) and *C. gigas* (43 occurrences) (Fig. 3). The strength of pair wise associations was quantified with the Ochiai index and the C-score.

The Ochiai index is $a/[(a+b)*(a+c)]^{0.5}$ where *a* is the number of cases with both species present, *b* and *c* the number of cases with single presence of either the one or the other respectively (Jackson et al. 1989).

The C-score (checkerboard score, Stone and Roberts 1990) is $(b*c)/((b+a)*(c+a))$. The Ochiai index gives more weight to absences and the C-score more weight to common occurrences.

Analyses of quantitative relationships were done with quasipoisson Generalized Linear Models. Species environment response curves were fitted with binomial GLM's. Permanova was used to analyse community composition data. Multivariate statistics were based on Bray Curtis similarity matrix of Wisconsin square root transformed abundance data.

Analyses were done with R version 2.15.0 (2012-03-30) (R Development Core Team 2012). 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 multivariate statistics.

Results

Associated species based on literature data

Six publications were found which reported lists of macrozoobenthos species associated with mussels (*M. Edulis*) in the Wadden Sea (Dittmann 1990, Buschbaum 2002, Saier 2002, Westphalen 2006, Büttger et al. 2008 and Markert et al. 2011). All studies except Markert et al. (2011) are from Sleswig Holstein in the northern German Wadden Sea. The investigations from Markert et al. (2011) were done near Juist in Lower Saxony. Three publications only reported species found in intertidal mussel beds (Dittmann 1990 and Büttger et al. 2008, Markert et al 2011). Buschbaum (2002) and Saier (2002) both include subtidal and intertidal observations. Westphalen (2006) is the only study focussing entirely on the species associated with subtidal mussels. None of the papers strictly defines which criteria were used to categorize the species as associated with mussels. For the combined list of these six studies it seems appropriate to define these species as been found together with *M. edulis*. In total these six studies reported 163 species or taxonomic units (see appendix 1 for the complete list). There were 81 species reported from the subtidal and 115 from the intertidal mussel beds. These species numbers are not corrected for sampling or searching effort and cannot be easily compared. In Table 2 species numbers are summarized per Phylum. Bryozoa and Cnidaria and of the last phylum especially the class of Hydrozoa are relatively well represented in the subtidal. There were also more species of Echinodermata reported from the subtidal. All other phyla had most representatives mentioned in the intertidal.

There were 59 matches between the literature list and the 124 species found in the combined macrozoobenthos dataset from the subtidal western Dutch Wadden Sea

Mussel associated species in the subtidal western Dutch Wadden Sea

The dataset of the survey from 2008 combined with data from a comparison between natural mussel beds and mussel culture plots covered 568 box core stations. Of these 427 were located outside mussel culture plots, 141 were inside mussel culture plots. At 99 stations outside mussel culture plots mussels were found in the box cores. Inside the mussel culture plots 84 boxes contained mussels. So in total there were 183 stations with mussels in the box cores. In total 124 macrozoobenthos species were found. Most species were encountered in cores that also contained mussels (Table 2, Fig. 4 for a species accumulation curve). This was most pronounced at stations with mussels inside mussel culture plots (Table 2). Just like stations with mussels stations with oysters are also much more species rich than stations without these epibenthic bivalves (Fig. 4). There is however a large degree of overlap between oysters and mussels, of the 43 stations with oysters 34 also contained mussels. This means that the species area relationship of the oyster samples mainly is a subset of the mussel relationship (Fig. 4). Species seem to accumulate faster in these samples containing oysters compared to the species accumulation curve of stations with mussels.

Associated species

There were 35 species that had a positive association with mussels, or in other words occurred more often together with mussels than expected in the case of randomly distributed species at the 0.01 level, one sided (Fig. 3, Table 3, see appendix 2 for a list including all species). There were 22 species negatively associated with mussels (Table 3). So in total 57 species, or 46 % of the total number of

species was not randomly distributed towards *M. edulis*. From the 35 positively associated species 8 were not in the list of associated species reported in literature. These species were *Hemigrapsus takanoi*, *Melita palmata*, *Molgula socialis*, *Monocorophium acherusicum*, *Mysta picta*, *Pedicellina cernua*, *Sagartia troglodytes* and *Streblospio benedicti*. Three of these species, *H. takanoi*, *M. socialis* and *S. benedicti* are invasive (Wolff 2005, Buschbaum 2012).

There were ten Natura 2000 typical species for habitat 1110 in the associated species list of the defined 11 species (Table 3) (profiedocument H1110 versie 18 dec 2008). The missing one is the mussel itself *Mytilus edulis*.

Associations were also tested for between oysters and each species of the species pool (Fig. 3, Table 4, complete list in appendix 3). Oysters were positively associated with 19 species and negatively associated with 12 species. Oyster has most of its associated species in common with mussel. There were 34 common occurrences. At 7 stations biomass of *C. gigas* was larger than that of *M. edulis*, so in most cases the mussel dominated. One of the species positively associated with oysters is mussels. Besides that there was only one species positively associated with oysters, *Elminius modestus*, which was not in the list of mussel associated species. All of the twelve species negatively associated with oysters were also negatively associated with mussels. Because of the strong interdependency between mussels and oysters only associations with mussels will be further analysed.

A large fraction of the total species pool consists of rare species (see appendix 2). There are 42 out of 124 species that occur in 1% or less of the stations. These species occur below the level required to be able to test for associations, the statistical power of the used test does not allow this. However more than half of this group, 23 species, were only found at stations with mussels. Because mussels maybe important for the existence of these species in the subtidal western Dutch Wadden Sea, these species are treated as a separate group in the following analysis.

Associated species differed from non-associated and negatively associated species in there feeding mode and the substrate they inhabit (Fig. 5). Compared to the non-associated species there were relatively more carnivores and suspension feeders among species positively associated with mussels. Among the rare species there were relatively many omnivores. Negative associated species were most often deposit feeders or carnivores and seldom suspension feeders. The majority of positively associated and rare species were hard substrate species or species from heterogeneous sediments. All negatively associated species were soft sediment species (Fig. 5).

Taxonomically the positive associated and rare species were richer and more evenly distributed among phyla (Fig. 6). The phyla Chordata, Cnidaria and Echinodermata lose importance moving from the rare and positive associated species to the non-associated species. Negative associated species represented only three phyla, Annelida, Arthropoda and Mollusca.

Besides mussels and oysters there were 22 stations with stones. Most were small stones with a diameter less than 5 cm, mainly from glacial origin. At a few sites also some anthropogenic hard substrate deposits (bricks) were encountered. This source of hard substrate other than the biogenic hard substrate did not attract more mussel associated species neither at stations without mussels nor at stations with mussels (Fig.7).

Effects of mussels and bed type on associated species

Mussels

As background information the distribution of mussels along four environmental gradients specifying between inside and outside mussel culture plots is plotted in Fig. 8. The distribution of mussels along a salinity gradient differs depending on bed type. Mussels on natural beds, outside mussel culture plots occur in less saline areas than mussels on culture plots (Fig. 8). Along the depth gradients mussel occurrence is highest around 5 m, especially because of the mussel culture plot mussels. Natural mussels are more evenly distributed below a depth of 2 m. Mussel occurrence declines with median grain size. Current velocity does not seem to have a large effect on the occurrence of mussels apart from the upper end of current speed gradient. Here occurrence on natural beds increases steeply. However there are only few observations made under these conditions (Fig. 8).

Mussel biomass at stations where mussels occur is positively correlated with salinity and depth (Fig. 9). Mussel biomass at stations with mussels present is unrelated to median grain size and maximum current speed (Fig. 9).

Quantitative relationships

Number of associated species per box core station is positively related to the biomass of *M. edulis* (Fig. 10, Table 5). There is a significant bed-type effect; natural beds have more associated species at the same mussel biomass than culture plots. There is no significant interaction between mussel biomass and bed-type. The effects of environmental conditions given the relationships between mussel biomass and bed type is visualised in fig. 11 In this figure the residuals of the glm model describing associated species numbers in Fig. 10 and Table 5 are plotted against salinity, median grain size, depth and maximum current speed. Residuals correlated most strongly and positively with median grain size and also correlated significantly positively with maximum current speed. Salinity and depth were unrelated with the residuals.

Including the four above mentioned environmental variables in a glm model and selecting the model with terms explaining a significant proportion of the deviance led to a model including median grain size and depth (Table 6). The interaction term between bed-type and mussel biomass was not significant and dropped from the model. Comparing the models without and with environmental variables residual deviance decreased from 384 (df=178) to 371 (df=177). Tables 5 & 6. In a similar procedure a GLM model was selected with next to mussel biomass only environmental explanatory variables. The resulting model (Table 7) contained median grain size and the interaction term depth : maximum current speed as significant contributing terms Residual deviance was 379 (df=176). Comparing these three model versions reveals that the models containing bed type explain a larger part of the variance using less degrees of freedom than the model without bed-type as explanatory factor. From these two models the difference in the residual deviance between the two best models with and without environmental variables is 13.3 at $df=1$, $p= 0.010$. Thus mussel associated species richness is best explained by both bed-type (more on natural beds) median grain size (positive effect) and depth (positive effect).

Bed-types do not only differ in the number of associated species but also in the associated species composition. A nonmetric multidimensional scaling plot of the mussel associated community shows a clear segregation between bed types (Fig. 12). Salinity is the environmental factor that correlates best with the ordination. Salinity and bed type are most important in explaining the variance of the similarity matrix (Table 8). Together these explanatory variables explain 8.3 %. However these variables are correlated and to a certain degree explain the same part of the variance. This can be quantified as a bed type effect alone accounting for 2.3 %, 1.9% exclusively to salinity and 4.1% to either salinity or bed-type. Other significant explanatory variables are grain size and depth, where depth is more important than grain size. A number of interactions terms explain a minor part of the variance. Finally 86% remains as residual variance. Maximum current speed was the only environmental term that did not contribute significantly to the permanova model.

A simper analysis showed the species with the largest contributions to the dissimilarity in associated species between mussel culture plots and natural mussel beds (Table 9). Contributions were rather evenly distributed among the species. This is probably the effect of using the same data transformation as for producing the MDS plot.

Environmental response of Individual associated species

Environmental response curves are plotted for all associated species in Figs 13 to 16. Two types of a logistic model were tested on the presence absence data, one with a single environmental term and the other also including a quadratic environmental term. Depending on the significance of the model terms a model was selected either describing a singular response along the gradient positive or negative or an optimum of occurrence within the gradient. In Table 10 results are presented. From all four environmental gradients most species, 19 out of 33, respond to salinity, responses are mostly positive (12) but there are also 5 negative responses and 2 optima. For depth there was 1 optimum and the remaining 13 species that responded to depth were all positively related. Grain size and current velocity had much more species showing an optimum distribution within the environmental range. Not any species responded negatively to these last two environmental factors.

The summed response curves of all associated species per environmental variable adequately describe the associated species richness relationships with environmental (Fig. 17). Associated species richness increases along gradients of salinity, depth and maximum current speed. Richness responds differently to sediment with an optimum at a median grain size of around 250 µm.

Richness at larger scale

Number of species within one sampling unit, alpha diversity, is not a good descriptor of the species pool at a larger scale, gamma diversity. At the largest scale available, of the entire dataset there were 51 associated and rare species solely occurring with mussels. How species richness is distributed along the environmental gradients at an intermediate scale of aggregation is shown in Fig. 18 . Environmental gradients were divided into ten bins with equal width. The total number of species was counted per bin. Because bins did not contain the same number of stations species counts were compared to a species accumulation curve with number of visited stations estimated with the total data set of 183 stations containing mussels. The differences between the species number found per bin and the expectation based on the species accumulation curve is plotted in Fig. 4. Residual number of species shows a clear increase with salinity. Maximum current speed and

medina grain size have a very similar looking pattern with lower number of species at the lower ends of the gradients (fine sediment and low currents) and further along the gradients no strong deviations from the expected number of species based on sample size. Generally residual species richness increases with depth but this pattern is not as strong as for salinity.

Experimental plots on natural mussel beds

Sequentially sampling through time took place on 21 mussel beds. This effort resulted in a dataset with information on 108 taxonomic units in 1896 (TU's) box cores. Of these boxes 692 contained at least 1 mussel (*M. edulis*). Associated species (TU's) were inferred from the presence absence data in boxes with and without mussels like described above. Following that method there were 21 TU's in the dataset significantly associated with mussels or more precisely co-occurring with mussels significantly (alpha 0.01 one sided) more often than expected from a random species distribution. There were 14 TU's negatively associated with mussels (Table 11).

Numbers of TU's in box cores aggregated per plot (12 boxes) were positively related with mussel cover (Fig. 19). Mussel cover was quantified as the number of boxes out of 12 that contained at least one mussel. This relationship is clearly different for associated and non-associated species, associated species are positively related, the non-associated species don't show any response to mussel cover (Fig. 19). This obviously is because this relationship is very similar to the selection procedure of associated species.

Bed age effects

In Fig. 20 information on bed age is added to relationship between number of associated species and mussel cover. The residuals of this relationship are plotted against bed age in Fig. 21 Every plot was sampled at least twice through time and in most cases more often. This makes it possible to follow the development of associated species number with increasing bed age. In Fig 21 this is done by plotting linear relationships between residual associated species number and the \log_{10} of bed age. In general these relationships are positive. With a one sample t-test it was tested if the slopes of these relationships were significantly larger than 0. This was done separately for plots open and closed for fisheries, because of the interdependence of paired plots. Analysis was restricted to beds that were followed for at least one year and that contained mussels in at least one out of twelve boxes at each sampling event. This procedure removes the most unstable and fastest degrading mussel beds from the analysis. Slopes of residual associated species richness were significantly greater than 0 in plots closed for fisheries (two sided $t = 3.702$, $df = 9$, $p\text{-value} = 0.005$) and also in plots open for fisheries ($t = 2.474$, $df = 6$, $p\text{-value} = 0.048$). For comparison the same test were also done including the shorter term observations with a maximum interval of less than one year. In both plots closed ($t = 1.218$, $df = 17$, $p\text{-value} = 0.240$) and open ($t = 0.6461$, $df = 10$, $p\text{-value} = 0.5327$) for mussel fisheries on average slopes were not different from zero. Increase of residual number of associated species with bed age was only observed in beds that were followed longer than a year.

Response of the individual associated species to bed age is plotted in Fig. 22. In contrast to the previous bed age effect analysis on plot level aggregates this analysis is done on presence absence information at the box level. All 618 boxes that contained at least one mussel were included in the analysis. Of the 21 associates TU's 11 occurred significantly (Logistic regression, Holm Bonferroni

adjusted p<0.05) more often with increasing bed age, or 12 without correcting for multiple testing. Only one TU, *Gammarus* occurred less with increasing bed age.

Discussion

Up to now mussel associated species in the subtidal Wadden Sea have received relatively little attention (Saier et al. 2002). The present study was intended to describe the associated species of the subtidal mussel beds in the western Dutch Wadden Sea. To explore environmental dependence of individual associated species, species richness and species composition of the associated community. Finally also to find out if aging of a mussel bed increases associated species richness.

The compilation of literature data on associated species resulted in a very extensive list of species. The list is however not very specific because in none of the studies associated species were strictly defined and maybe best described as found occurring together with mussels. The higher number of species reported in the intertidal mussel beds compared to the subtidal beds contrary to Saier (2002) is likely a sampling effect of more effort spent on intertidal beds. Bryozoa and Hydrozoa are the only two species groups standing out as more diverse in the subtidal beds compared to intertidal beds. Interestingly in intertidal oyster beds there are more species Bryozoa and Hydrozoa than in intertidal mussel beds (Markert et al. 2010). Maybe these oyster beds contain a larger range of conditions like pools at low tide than mussel beds such that these normally subtidal species may survive.

Mussels and oysters were found at the most species rich sites in the subtidal of the western Dutch Wadden Sea. Stations with oysters are mainly a species rich subset of mussel stations. Areas with epibenthic bivalves mussels and oysters are richer than bare sediment.

Most species that were identified as significantly associated with mussels based on the subtidal data from the western Dutch Wadden Sea matched with the literature based species list, apart from a few species from which three were invasive species. About a quarter of the species pool in the western Dutch Wadden Sea was significantly associated with mussels. The next question then of course is if there is any mechanism underlying this connection between mussels and associated species. In this we consider several possible links, direct trophic relationship between mussel and its predators, organic enrichment by biodeposition of organic material, substrate for attachment and space within the matrix (Norling & Kautsky 2007). Five of the 35 species are either predators or parasites of the mussel. Two are main predators of the mussel, the shore crab *Carinus maenas* and the common starfish *Asterias rubens*. There were two parasitic or commensal species that live enclosed in the bivalve shell, the pea crab *Pinnotheres pisum* and the intestinal parasite *Mytilicola orientalis*. One species the shell boring polychaete *Polydora ciliata* lives in a tube in the living mussel shell. Besides *P. ciliata* there are 13 more polychaetes associated, the majority of these are carnivores preying on small invertebrates like polychaetes and amphipods or scavenging omnivores feeding on damaged mussels and barnacles. Two are deposit feeding spionids who may profit from local organic enrichment by the mussel bed (Kihslinger & Woodin 2000). Finally Lanice conchilega is a species where a positive feedback from the mussel bed may not be so obvious but in contrast could facilitate *M. edulis* settlement with its tubes protruding from the sediment surface (Pulfrich 1996). Then there is a large group of 12 sessile hard substrate species that live attached to the hard substrate offered by the mussels. The barnacle *Balanus crenatus* is an important example further these species belong to the phyla Bryozoa, Cnidaria, Chordata and Entoprocta. This are all suspension feeders that collect phytoplankton but also zooplankton (carnivores) with diverse foraging mechanisms. Finally there are still three Athropoda two of which are deposit feeders and

the invasive carnivore *Hemigrapsus takanoi*. These species probably find a refuge within the mussel bed matrix, and the deposit feeders may benefit from the organic enrichment of the sediment by the mussels. The majority of the associated species are hard substrate species either mobile or sessile, most of these are suspension feeders or carnivores. A minority of the associated species directly preys or parasitizes on mussels. There are very few soft sediment deposit feeding species that might profit from organic enrichment of the sediment by the mussels. So in line with earlier experimental approaches to separate the structural and functional effect of mussel beds on species richness (Ragnarsson and Raffaelli 1999, Norling and Kautsky 2007) we could conclude that physical structure provided by the mussel bed seems most important in causative explanation for the large species richness associated with mussels .

However it must be mentioned that another hard substrate type, stones did not attract many mussel associated species. This could be an effect of environmental conditions, stones will be exposed at dynamic sites with strong currents, which may not be suitable for many of the associated species.

Associated species number at the level of one box core sample is positively related to mussel biomass, environmental factors sediment grain size and depth. Associated species richness also depends on mussel bed type. Corrected for mussel biomass natural mussel beds are more species rich at the box core level than mussel culture plots.

The associated community of mussel beds and mussel culture plots differs. The most important effect explaining community variation is mussel bed-type, however the amount of explained variance by this factor is less than 3%.

At the level of individual species salinity was the environmental factor that affected most species, while salinity had no effect on species richness at the box level with mussel biomass as covariate. More than half of the associated species shows a response to salinity. For most species salinity had a positive effect on presence. Less species were affected by depth, except one the response was always positive. Species distributions along median grain size and current velocity gradients were more often modelled as optima.

The individual species response curves to environmental gradients nicely add up to the richness of associated species along the gradients (Fig. 17). In general associated species richness increases along all the gradients considered. Also salinity has a positive effect while salinity did not significantly contribute to the model explaining associated species richness with mussel biomass and environmental variables. The problem is that mussel biomass and associated species richness show the same positive trends along the salinity gradient (Fig. 9 and Fig. 17) and because of this confounding in this dataset their effects cannot be separated.

The general positive effect of sediment grain size or in other words the negative effect of fine sediment on the associated species richness is interesting when realizing that mussel beds may accumulate fine sediment by reduction of flow and active deposition of fine material that mussels have filtered from the water column. This functional sediment accumulating property of the mussel bed has negative effects on both endofauna (Beadman et al. 2004) and epifauna (Westphalen 2006).

Richness at larger scales

Species richness is a scale dependent metric see Fig. 4. Species richness at the level of one box core may not say much about the richness in the entire system the Gamma diversity. It may neither be a good representation of the richness effects along gradients. This very much depends on the Beta diversity, the dissimilarity between individual samples. With a higher dissimilarity between samples total species numbers increase faster by adding up samples than when individual samples are very similar. By aggregating samples within bins of equal portions of the gradient an illustration is made of the associated species richness at a higher level of aggregation. Richness at this higher aggregated level shows a clear positive relationship with salinity. In other words beta diversity increases with salinity. Beta diversity is also positively related with the other three environmental variables. Crudely speaking at the system level mussel associated species richness is largest at highest salinities, maximum current speeds above 0.5 ms^{-2} , sites deeper than 5 m below NAP and a median grain size of around 200 μm .

Bed age

An independent dataset from a fishery experiment that followed natural mussel bed development in the western Dutch Wadden Sea (Craeymeersch et al. 2013) was used to analyse the temporal development of associated species as function of bed age. Because for this dataset the species were not identified to the same taxonomic detail associated species were defined separately for this dataset. There was a reasonable resemblance between the two tables of positively associated species. Phyla specifically not recorded in the fishery experiment dataset were Bryozoa, Cnidaria and Chordata. The connectedness between mussels and the associated species is confirmed by a positive relationship between mussel cover and associated species number. On top of this relationship the age of the mussel bed has a positive effect on the number of associated species.

Of the 21 positively associated species 12 occurred significantly more often with increasing bed age. Only one taxonomic group occurrence was negatively related to bed age, that of Gammarus. This is a mobile species group that may be one of the first colonizing mussel beds (Tsuchiya & Niihira 1986).

Limitations of the study

This is a descriptive study where the causative role of mussel enhancing biodiversity is not formally tested. It is assumed based on earlier studies (e.g. Ragnarsson & Raffaelli 1999 and Norling & Kautsky 2007) that mussels drive the increase in species richness compared to the surrounding area instead of the scenario that mussels preferably settle and develop at sites that already were species rich beforehand.

Conclusions

Stations with mussels are important sites for species richness of the Wadden Sea. Out of 124 species 58 were positively associated with mussels (35) or were rare and occurred exclusively with mussels (23).

Species richness were positively related with mussel biomass and mussel cover. These quantitative measures could be interpreted as proxies for habitat heterogeneity of the mussel patch. Age of the bed had a small added effect for beds that were followed and survived for at least one year.

Salinity, depth (m NAP), sediment grain size and current speed affect the distribution of the individual associated species. Salinity affects most species. At the scale of the number of species in a box of 0.06 m² corrected for mussel biomass only sediment coarseness and depth affected species numbers both positively. Species richness in aggregated samples within bins of equal environmental width showed that in general species richness is positively related to all environmental variables tested.

Besides the positive effect of the physical structure of the mussel bed there may be a negative effect of fine sediment accumulation by the mussel bed on the richness of mussel associated species.

The mussel is an important ecosystem engineer in the Wadden Sea while its effects depend particularly on salinity. With increasing salinity species richness increases.

Acknowledgements

We thank our PRODUS colleges for sharing data with us. Ideas and suggestions of Jeroen Jansen, Aad Smaal, Johan Craeymeersch and Marnix van Stralen were helpful during the project. Jaap van der Meer commented on an earlier draft. Bert Brinkman is thanked for letting us use his pictures for the cover.

References

- Beadman, H. A., M. J. Kaiser, et al. (2004). Changes in species richness with stocking density of marine bivalves. *Journal of Applied Ecology* 41: 464-475.
- Buschbaum, C. 2002. Recruitment patterns and biotic interactions of barnacles (Cirripedia) on mussel beds (*Mytilus edulis* L.) in the Wadden Sea. *Ber. Polarforsch. Meeresforsch.* 408: 1-143
- Buschbaum, C., S. Dittmann, et al. (2009). "Mytilid mussels: global habitat engineers in coastal sediments." *Helgoland Marine Research* 63: 47-58.
- Bush, F. and K. Reise (1997) Epibenthic fauna dredged from tidal channels in the Wadden Sea of Schleswig-Holstein: spatial patterns and a long-term decline. *Helgolander Meeresuntersuchungen* 51: 343-359
- Büttger, H., Asmus, H., Asmus, R., Buschbaum, C., Dittmann, S., Nehls, G. 2008. Community dynamics of intertidal soft-bottom mussel beds over two decades. *Helgol Mar Res* 62: 23–36
- Dekker, R. and J. Drent (2013) The macrozoobenthos in the subtidal parts in the western Dutch Wadden Sea. Survey 2008 and a comparison with the survey in 1981-1982. PRODUS/NIOZ Report 2013-5
- Dittmann, S. 1990 Mussel beds - amensalism or amelioration for intertidal fauna? *Helgoländer Meeresunters.* 44: 335-352
- Drent, J and R. Dekker (2013) How different are sublittoral *Mytilus edulis* L. communities of natural mussel beds and mussel culture plots in the western Dutch Wadden Sea? PRODUS/NIOZ Report 2013-6
- Gutiérrez, J. L., C. G. Jones, et al. (2003). Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos* 101: 79-90.
- Jager, Z & Bartels, W (2002) Optimale zoetwateraanvoer naar de Waddenzee. Werkdokument RIKZ/AB/2002.604x. 41 pp
- Jones, C. G., J. H. Lawton, et al. (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78: 1946-1957
- Kampstra, P. (2008) Beanplot: A Boxplot Alternative for Visual Comparison of Distributions. *Journal of Statistical Software, Code Snippets*, 28(1), 1-9. URL <http://www.jstatsoft.org/v28/c01/>
- Kihslinger, R. L. and S. A. Woodin (2000). Food patches and a surface deposit feeding spionid polychaete. *Marine Ecology-Progress Series* 201: 233-239.
- Koivisto, M., M. Westerbom, et al. (2011). Succession-driven facilitation of macrofaunal communities in sublittoral blue mussel habitats. *Marine Biology* 158: 945–954
- Norling, P. and N. Kautsky (2007) Structural and functional effects of *Mytilus edulis* on diversity of associated species and ecosystem functioning. *Marine Ecology-Progress Series* 351: 163-175.

Norling, P. and N. Kautsky (2008) Patches of the mussel *Mytilus* sp. are islands of high biodiversity in subtidal sediment habitats in the Baltic Sea. *AQUATIC BIOLOGY* 4: 75-87.

Markert, A., Wehrmann, A., Kröncke, I. 2010 Recently established *Crassostrea*-reefs versus native *Mytilus*-beds: differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German Bight). *Biol Invasions* 12: 15–32

Möbius, K., 1877. Die Auster und die Austernwirthschaft. Wiegandt, Hempel & Parey, Berlin, 126 pp

Oksanen, J., F.G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R. B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens and H. Wagner (2012). *vegan*: Community Ecology Package. R package version 2.0-3. <http://CRAN.R-project.org/package=vegan>

Pulfrich, A. 1996 Attachment and settlement of post-larval mussels (*Mytilus edulis* L.) in the Schleswig-Holstein Wadden Sea. *Journal of Sea Research* 36: 239-250

R Development Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>

Ragnarsson, S. Á. and D. Raffaelli (1999). "Effects of the mussel *Mytilus edulis* L. on the invertebrate fauna of sediments." *Journal of Experimental Marine Biology and Ecology* 241: 31-43.

Remane, A. (1934). Die Brackwasserfauna. Verzeichnis der Veröffentlichungen Goldsteins, 36: 34–74

Saier, B. 2002. Subtidal and intertidal mussel beds (*Mytilus edulis* L.) in the Wadden Sea: diversity differences of associated epifauna. *Helgol Mar Res* 56: 44–50

Saier, B., C. Buschbaum, et al. (2002) Subtidal mussel beds in the Wadden Sea: threatened oases of biodiversity. *Wadden Sea Newsletter* 2002-1: 12-14.

Seed, R. (1996). Patterns of biodiversity in the macro-invertebrate fauna associated with mussel patches on rocky shores. *Journal of the Marine Biological Association of the United Kingdom* 76: 201-210.

Smyth, D. and D. Roberts (2010). The European oyster (*Ostrea edulis*) and its epibiotic succession. *Hydrobiologia* 655: 25–36.

Stone, L. and A. Roberts (1990). The checkerboard score and species distributions. *Oecologia* 85: 74-79.

Tsuchiya, M. and M. Niihira (1986). Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of *Mytilus* age structure on the species composition of the associated fauna and community organization *Marine Ecology Progress Series* 31: 171-178.

Westphalen, A. 2006. Assoziierte Lebensgemeinschaften von natürlichen Muschelbänken und Muschelkulturflächen im Wattenmeer. Diplomarbeit, Institut für Zoologie, Anthropologie und Entwicklungsbiologie an der Biologischen Fakultät der Georg-August-Universität zu Göttingen. 86 pp

Zwarts, L. (2004). Bodemgesteldheid en mechanische kokkelvisserij in de Waddenzee. Rapport RIZA/2004.028. 129 pp

Table 1. Summary of species associated with *Mytilus* and *Crassostrea*, showing number of species/taxonomic units per Phylum found in intertidal and subtidal mussel beds and totals over both habitats. For some phyla classes are specified as well. This list is based on Dittmann 1990, Buschbaum 2002, Saier 2002, Westphalen 2006, Büttger et al. 2008 and Markert et al. 2011. This list is not corrected for searching or sampling effort which is likely to differ between habitats.

Phylum	Class	subtidal	intertidal	total
Annelida		19	54	60
	Clitellata		4	4
	Polychaeta	19	50	56
Arthropoda		16	19	26
	Collembola		1	1
	Malacostraca	8	10	13
	Maxillopoda	4	5	6
	Pycnogonida	4	3	6
Bryozoa		9	1	9
Chordata		4	4	8
Ciliophora		2		2
Cnidaria		15	5	17
	Anthozoa	2	2	3
	Hydrozoa	13	3	14
Echinodermata		3	1	3
Echiura			1	1
Entoprocta		1		1
Mollusca		10	22	28
	Bivalvia	1	12	12
	Gastropoda	8	8	14
	Polyplacophora	1	2	2
Nemertea			7	7
Porifera		2	1	2
Grand Total		81	115	164

Table 2. Summary of number of species found at 568 stations in the subtidal of the western Dutch Wadden Sea, depending on the location of the station relative to mussel culture plots and whether mussels were found at the station. Number of stations is shown between brackets.

Mussels at station	mussel culture plots		
	outside	Inside	totals
With	90 (99)	103 (84)	111 (183)
Without	89 (328)	63 (57)	92 (385)
Totals	109 (427)	109 (141)	124 (568)

Table 3. Species positively and negatively associated with *Mytilus edulis* in the subtidal western Dutch Wadden Sea. Associations are defined as co-occurring more often or less often than expected from a random species distribution. Table is based on 568 box core stations with 183 occurrences of *M. edulis*. See table 3 for table explanatory footnotes. Specode with * are typical species for habitat h1110

specode	occ	comm	Ochiai	C.score	sign	AphiaID	species	Phylum	Class	inv.	substrate	feeding
Alisuc	189	152	0.817	0.033	+++	234850	<i>Alitta succinea</i>	Annelida	Polychaeta	no	hetrog.	depos
Carmae*	143	126	0.779	0.037	+++	107381	<i>Carcinus maenas</i>	Arthropoda	Malacostraca	no	soft	carni
Conret	237	156	0.749	0.05	+++	111351	<i>Conopeum reticulum</i>	Bryozoa	Gymnolaemata	no	hard, s	suspe
Alcmyt	127	114	0.748	0.039	+++	468026	<i>Alcyonidiooides mytili</i>	Bryozoa	Gymnolaemata	no	hard, s	suspe
Balsp*	154	124	0.739	0.063	+++	106215	<i>Balanus sp.</i>	Arthropoda	Maxillopoda	no	hard, s	suspe
Metsen*	171	130	0.735	0.069	+++	100982	<i>Metridium senile</i>	Cnidaria	Anthozoa	no	hard, s	suspe
Oligoc	289	149	0.648	0.09	+++	2036	<i>Oligochaeta</i>	Annelida	Clitellata	no	soft	depos
Polcor	152	108	0.648	0.119	+++	131143	<i>Polydora cornuta</i>	Annelida	Polychaeta	no	hetrog.	suspe
Crefor	104	88	0.638	0.08	+++	138963	<i>Crepidula fornicata</i>	Mollusca	Gastropoda	yes	hard, s	suspe
Harimp	74	73	0.627	0.008	+++	130770	<i>Harmothoe impar</i>	Annelida	Polychaeta	no	hard, m	carni
Alivir*	148	100	0.608	0.147	+++	234851	<i>Alitta virens</i>	Annelida	Polychaeta	yes	soft	omni
Strben	152	101	0.606	0.15	+++	131191	<i>Streblospio benedicti</i>	Annelida	Polychaeta	yes	soft	depos
Astrub*	62	61	0.573	0.011	+++	123776	<i>Asterias rubens</i>	Echinodermata	Astroidea	no	hard, m	carni
Harimb	45	45	0.496	0	+++	130769	<i>Harmothoe imbricata</i>	Annelida	Polychaeta	no	hard, m	carni
Lancon	117	72	0.492	0.233	+++	131495	<i>Lanice conchilega</i>	Annelida	Polychaeta	no	soft	suspe
Sagtro*	70	55	0.486	0.15	+++	100994	<i>Sagartia troglodytes</i>	Cnidaria	Anthozoa	no	hetrog.	carni
Obelon	38	33	0.396	0.108	+++	117389	<i>Obelia longissima</i>	Cnidaria	Hydrozoa	no	hard, s	suspe
Molsoc	30	29	0.391	0.028	+++	103804	<i>Molgula socialis</i>	Chordata	Asciidiacea	yes	hard, s	suspe
Craig	43	34	0.383	0.17	+++	140656	<i>Crassostrea gigas</i>	Mollusca	Bivalvia	yes	hard, s	suspe
Eumsan	36	31	0.382	0.115	+++	130644	<i>Eumida sanguinea</i>	Annelida	Polychaeta	no	soft	carni
Hemtak	25	25	0.37	0	+++	389288	<i>Hemigrapsus takanoi</i>	Arthropoda	Malacostraca	yes	hard, m	carni
Melpal	32	28	0.366	0.106	+++	102843	<i>Melita palmata</i>	Arthropoda	Malacostraca	no	hard, m	depos
Polcil	39	30	0.355	0.193	+++	131141	<i>Polydora ciliata</i>	Annelida	Polychaeta	no	hard, s	depos
Myspic	26	23	0.333	0.101	+++	147026	<i>Mysta picta</i>	Annelida	Polychaeta	no	soft	carni
Monach	19	18	0.305	0.047	+++	225814	<i>Monocorophium acherusicum</i>	Arthropoda	Malacostraca	no	hard, m	depos
Eulvir	17	17	0.305	0	+++	130639	<i>Eulalia viridis</i>	Annelida	Polychaeta	no	hard, m	carni
Clyhem	62	41	0.385	0.263	++	117368	<i>Clytia hemisphaerica</i>	Cnidaria	Hydrozoa	no	hard, s	suspe
Phymuc	21	17	0.274	0.173	++	334512	<i>Phyllocoete mucosa</i>	Annelida	Polychaeta	no	soft	carni
Petpho	17	15	0.269	0.108	++	156961	<i>Petricolaria pholadiformis</i>	Mollusca	Bivalvia	yes	hetrog.	suspe
Phomin	15	14	0.267	0.062	++	130603	<i>Pholoe minuta</i>	Annelida	Polychaeta	no	hard, m	carni
Pedcer	8	8	0.209	0	++	111806	<i>Pedicellina cernua</i>	Entoprocta	NA	no	hard, s	suspe
Pinpis	8	8	0.209	0	++	107473	<i>Pinnotheres pisum</i>	Arthropoda	Malacostraca	no	undef.	paras
Lepsqu	7	7	0.196	0	++	130801	<i>Lepidonotus squamatus</i>	Annelida	Polychaeta	no	hard, m	carni
Mytori	7	7	0.196	0	++	128901	<i>Mytilicola orientalis</i>	Arthropoda	Maxillopoda	yes	undef.	paras
Stycla	7	7	0.196	0	++	103929	<i>Styela clava</i>	Chordata	Asciidiacea	yes	hard, s	suspe
Macbal*	81	30	0.246	0.526	--	141579	<i>Macoma balthica</i>	Mollusca	Bivalvia	no	soft	depos
Nepcae	68	24	0.215	0.562	--	130355	<i>Nephtys caeca</i>	Annelida	Polychaeta	no	soft	carni
Angfab	17	3	0.054	0.81	--	152829	<i>Angulus fabula</i>	Mollusca	Bivalvia	no	soft	depos
Ensdir	163	58	0.336	0.44	--	140732	<i>Ensis directus</i>	Mollusca	Bivalvia	yes	soft	suspe
Myaare*	137	50	0.316	0.462	--	140430	<i>Mya arenaria</i>	Mollusca	Bivalvia	yes	soft	suspe
Scoarm	302	71	0.302	0.468	--	334772	<i>Scoloplos armiger</i>	Annelida	Polychaeta	no	soft	depos
Marvir	184	55	0.3	0.49	--	131135	<i>Marenzelleria viridis</i>	Annelida	Polychaeta	yes	soft	depos
Pygele	202	55	0.286	0.509	--	131170	<i>Pygospio elegans</i>	Annelida	Polychaeta	no	soft	depos
Nephom*	168	38	0.217	0.613	--	130359	<i>Nephtys hombergii</i>	Annelida	Polychaeta	no	soft	carni
Cracra	69	20	0.178	0.633	--	107552	<i>Crangon crangon</i>	Arthropoda	Malacostraca	no	soft	carni
Etelon	112	24	0.168	0.683	--	130616	<i>Eteone longa</i>	Annelida	Polychaeta	no	soft	carni
Spibom	58	13	0.126	0.721	--	131187	<i>Spiophanes bombyx</i>	Annelida	Polychaeta	no	soft	depos
Spimar*	255	23	0.106	0.795	--	131185	<i>Spio martinensis</i>	Annelida	Polychaeta	no	soft	depos
Neplon	23	4	0.062	0.808	--	130364	<i>Nephtys longosetosa</i>	Annelida	Polychaeta	no	soft	carni
Arimin	70	6	0.053	0.884	--	130564	<i>Aricidea minuta</i>	Annelida	Polychaeta	no	soft	depos
Uropos	26	2	0.029	0.913	--	103235	<i>Urothoe poseidonis</i>	Arthropoda	Malacostraca	no	soft	depos
Nepcir	94	3	0.023	0.952	--	130357	<i>Nephtys cirrosa</i>	Annelida	Polychaeta	no	soft	carni
Batsar	42	2	0.023	0.942	--	103073	<i>Bathyporeia sarsi</i>	Arthropoda	Malacostraca	no	soft	depos
Magjoh	43	2	0.023	0.943	--	130269	<i>Magelona johnstoni</i>	Annelida	Polychaeta	no	soft	depos
Angten	51	2	0.021	0.95	--	146492	<i>Angulus tenuis</i>	Mollusca	Bivalvia	no	soft	depos
Glyuni	14	0	0	1	--	130131	<i>Glycera unicornis</i>	Annelida	Polychaeta	no	soft	carni
Retobt	12	0	0	1	--	141134	<i>Retusa obtusa</i>	Mollusca	Gastropoda	no	soft	carni

Table 4 Species positively and negatively associated with *Crassostrea gigas* in the subtidal western Dutch Wadden Sea. Associations are defined as co-occurring more often or less often than expected from a random species distribution. Table is based on 568 box core stations with 43 occurrences of *C.gigas*.

species	occ	comm	Ochiai	C.score	sign	AphiaID	Species	Phylum	Class	inv.	substrate	feeding
Crefor	104	35	0.523	0.123	+++	138963	<i>Crepidula fornicata</i>	Mollusca	Gastropoda	yes	hard s.	susp.
Balsp	154	40	0.492	0.052	+++	106215	<i>Balanus crenatus</i>	Arthropoda	Maxillopoda	no	hard s.	susp.
Elmod	65	24	0.454	0.279	+++	106209	<i>Elminius modestus</i>	Arthropoda	Maxillopoda	yes	hard s.	susp.
Alisuc	189	40	0.444	0.055	+++	234850	<i>Alitta succinea</i>	Annelida	Polychaeta	no	heter.	depos.
Polcor	152	35	0.433	0.143	+++	131143	<i>Polydora cornuta</i>	Annelida	Polychaeta	no	heter.	susp.
Metsen	171	37	0.431	0.109	+++	100982	<i>Metridium senile</i>	Cnidaria	Anthozoa	no	hard s.	susp.
Polcil	39	17	0.415	0.341	+++	131141	<i>Polydora ciliata</i>	Annelida	Polychaeta	no	hard s.	depos.
Strben	152	33	0.408	0.182	+++	131191	<i>Streblospio benedicti</i>	Annelida	Polychaeta	yes	soft.	depos.
Conret	237	40	0.396	0.058	+++	111351	<i>Conopeum reticulum</i>	Bryozoa	Gymnolaemata	no	hard s.	susp.
Mytedu	183	34	0.383	0.17	+++	140480	<i>Mytilus edulis</i>	Mollusca	Bivalvia	no	hard s.	susp.
Carmae	143	30	0.383	0.239	+++	107381	<i>Carcinus maenas</i>	Arthropoda	Malacostraca	no	soft.	carni.
Clyhem	62	19	0.368	0.387	+++	117368	<i>Clytia hemisphaerica</i>	Cnidaria	Hydrozoa	no	hard s.	susp.
Myspic	26	12	0.359	0.388	+++	147026	<i>Mysta picta</i>	Annelida	Polychaeta	no	soft.	carni.
Stycla	7	6	0.346	0.123	+++	103929	<i>Styela clava</i>	Chordata	Asciidiacea	yes	hard s.	susp.
Alcmyt	127	26	0.352	0.314	++	468026	<i>Alcyonidiooides mytili</i>	Bryozoa	Gymnolaemata	no	hard s.	susp.
Harimp	74	17	0.301	0.466	++	130770	<i>Harmothoe impar</i>	Annelida	Polychaeta	no	hard m.	carni.
Molsoc	30	10	0.278	0.512	++	103804	<i>Molgula socialis</i>	Chordata	Asciidiacea	yes	hard s.	susp.
Hemtak	25	9	0.274	0.506	++	389288	<i>Hemigrapsus takanoi</i>	Arthropoda	Malacostraca	yes	hard m.	carni.
Lepsqu	7	4	0.231	0.389	++	130801	<i>Lepidonotus squamatus</i>	Annelida	Polychaeta	no	hard m.	carni.
Marvir	184	15	0.169	0.598	--	131135	<i>Marenzelleria viridis</i>	Annelida	Polychaeta	yes	soft.	depos.
Nephom	168	12	0.141	0.669	--	130359	<i>Nephtys hombergii</i>	Annelida	Polychaeta	no	soft.	carni.
Etelon	112	7	0.101	0.785	--	130616	<i>Eteone longa</i>	Annelida	Polychaeta	no	soft.	carni.
Magjoh	43	0	0	1	--	130269	<i>Magelona johnstoni</i>	Annelida	Polychaeta	no	soft.	depos.
Scoarm	302	23	0.202	0.43	--	334772	<i>Scoloplos armiger</i>	Annelida	Polychaeta	no	soft.	depos.
Pygele	202	13	0.139	0.653	--	131170	<i>Pygospio elegans</i>	Annelida	Polychaeta	no	soft.	depos.
Myaare	137	8	0.104	0.766	--	140430	<i>Mya arenaria</i>	Mollusca	Bivalvia	yes	soft.	susp.
Spimar	255	8	0.076	0.788	--	131185	<i>Spio martinensis</i>	Annelida	Polychaeta	no	soft.	depos.
Arimin	70	2	0.036	0.926	--	130564	<i>Aricidea minuta</i>	Annelida	Polychaeta	no	soft.	depos.
Macbal	81	2	0.034	0.93	--	141579	<i>Macoma balthica</i>	Mollusca	Bivalvia	no	soft.	depos.
Nepcir	94	2	0.031	0.933	--	130357	<i>Nephtys cirrosa</i>	Annelida	Polychaeta	no	soft.	carni.
Angten	51	0	0	1	--	146492	<i>Angulus tenuis</i>	Mollusca	Bivalvia	no	soft.	depos.

Occs. Occurrences

Comm common occurrences

Sign sign of the association, +++ and --- are significant at the 0.001 level (onesided) ++ and -- significant at the 0.01 level

Subs.	substrate type,	soft	soft sediment
	hetr.		Heterogeneous sediments
	hard m		hard substrate mobile
	hard s		hard substrate sessile
feeding	feeding mode	suspe	suspension
		depos	deposit
		omniv	omnivore
		carni	carnivore

Table 5. Coefficients and analysis of deviance table of a GLM model describing the number of mussel associated species at a station with explanatory variables factor bed-type with two levels, natural bed and culture plot and mussel biomass.

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	2.076	0.083	25.031	<0.001	***
log10(Mytbm)	0.251	0.05	5.035	<0.001	***
bed-type _{culture}	-0.546	0.192	-2.844	0.005	**
log10(Mytbm):bed-type _{cultur}	0.145	0.084	1.718	0.087	.

(Dispersion parameter for quasipoisson family taken to be 2.027644)

Analysis of deviance:

	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)
NULL			181	514.71	
log10(Mytbm)	1	101.729	180	412.99	<0.001 ***
bed-type	1	22.605	179	390.38	0.001 ***
log10(Mytbm):bed-type	1	6.035	178	384.35	0.084 .

Table 6. Coefficients and analysis of deviance table of a generalized linear model describing the number of associated species at a station including factor bed-type with two levels, natural mussel bed and mussel culture plot. Mytbm is Mytilus edulis biomass.

Coefficients :

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	1.738	0.116	15.014	<0.001	***
log10(Mytbm)	0.285	0.041	6.948	<0.001	***
bed-type _{culture}	-0.227	0.075	-3.019	0.003	**
grain size	0.001	0	1.501	0.135	
depth	0.277	0.138	2.007	0.046	*

(Dispersion parameter for quasipoisson family taken to be 1.998535)

Analysis of deviance:

	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)
NULL			181	514.71	
log10(Mytbm)	1	101.729	180	412.99	<0.001 ***
bed-type	1	22.605	179	390.38	<0.001 ***
grain size	1	11.317	178	379.06	0.017 *
depth	1	8.033	177	371.03	0.045 *

Table 7 . Coefficients and analysis of deviance table of a generalized linear model describing the number of associated species at a station including factor bed-type with two levels, natural mussel bed and mussel culture plot. Mytbtm is *Mytilus edulis* biomass.

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	2.458	0.366	6.722	<0.001	***
log10(Mytbtm)	0.238	0.037	6.431	<0.001	***
grain size	0.001	0	2.352	0.02	*
depth	-0.649	0.481	-1.35	0.179	
current	-1.218	0.57	-2.139	0.034	*
depth : current	1.328	0.636	2.089	0.038	*

(Dispersion parameter for quasipoisson family taken to be 2.05214)

Anlysis of deviance table

	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)	
NULL			181	514.71		
log10(Mytbtm)	1	101.729	180	412.99	<0.001	***
grain size	1	18.37	179	394.62	0.003	**
depth	1	5.428	178	389.19	0.104	
current	1	0.802	177	388.39	0.532	
depth : current	1	8.785	176	379.6	0.039	*

Table 8. Permanova results of similarity in mussel assocaited species between stations in the subtidal western Dutch Wadden Sea.

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)	
bed-type	1	3.826	3.826	12.816	0.064	0.001	***
salinity	1	1.135	1.135	3.801	0.019	0.001	***
grain size	1	0.777	0.777	2.603	0.013	0.004	**
depth	1	0.908	0.908	3.043	0.015	0.001	***
bed-type : salinity	1	0.589	0.589	1.972	0.01	0.031	*
bed-type : depth	1	0.579	0.579	1.941	0.01	0.03	*
grain size : depth	1	0.571	0.571	1.914	0.01	0.035	*
Residuals	173	51.641	0.299		0.86		
Total	180	60.026			1		

Table 9. Mussel associated species with largest contribution to the difference in mussel associated community between natural mussel beds and mussel culture plots in the subtidal western Dutch Wadden Sea. This analysis is done on a wisconsin square root transformed abundance matrix (same transformation as used for the NMDS. Substrates are: 1)soft sediment, 2)heterogeneous sediment, 3) hard substrate mobile and 4) hard substrate sessile. The column Abundance mentions the bed type where the average abundance is highest. Cumsum is the cummulative fraction of the difference accounted for.

shortname	Genus	Species	substrate	abundance	cumsum
Alivir	<i>Alitta</i>	<i>virens</i>	1	culture	0.08
Carmae	<i>Carcinus</i>	<i>maenas</i>	1	culture	0.16
Oligoc	<NA>	<NA>	1	natural	0.22
Alisuc	<i>Alitta</i>	<i>succinea</i>	2	natural	0.28
Conret	<i>Conopeum</i>	<i>reticulum</i>	4	culture	0.33
Balcre	<i>Balanus</i>	<i>crenatus</i>	4	natural	0.38
Strben	<i>Streblospio</i>	<i>benedicti</i>	1	natural	0.43
Polcor	<i>Polydora</i>	<i>cornuta</i>	2	natural	0.47
Harimp	<i>Harmothoe</i>	<i>impar</i>	3	culture	0.52
Metsen	<i>Metridium</i>	<i>senile</i>	4	natural	0.56
Lancon	<i>Lanice</i>	<i>conchilega</i>	1	culture	0.6
Alcmyt	<i>Alcyonioides</i>	<i>mytili</i>	4	culture	0.63
Clyhem	<i>Clytia</i>	<i>hemisphaerica</i>	4	natural	0.66
Crefor	<i>Crepidula</i>	<i>fornicata</i>	3	natural	0.69
Astrub	<i>Asterias</i>	<i>rubens</i>	3	culture	0.72
Harimb	<i>Harmothoe</i>	<i>imbricata</i>	3	culture	0.75
Melpal	<i>Melita</i>	<i>palmata</i>	3	culture	0.78
Sagtro	<i>Sagartia</i>	<i>troglodytes</i>	2	culture	0.8
Hemtak	<i>Hemigrapsus</i>	<i>takanoi</i>	3	culture	0.82
Obelon	<i>Obelia</i>	<i>longissima</i>	4	culture	0.85

Table 10. Summary of reponses of 33 individual mussel associated species to four environmental gradients.

	no response	optimum	negative	positive
salinity	14	2	5	12
depth	19	1	0	13
grain size	19	9	0	5
current	19	7	0	7

Table 11. Associated taxonomic units positive as well as negative in the mussel seed fisheries experimental plots.

species	occ	comm	Ochiai	C.score	sign	species	phylum	class
Nereid	1343	616	1.243	-1.281	+++	Alitta succinea	Annelida	Polychaeta
Polyno	358	312	1.219	-0.091	+++	Harmothoe	Annelida	Polychaeta
Cirrip	545	379	1.2	-0.326	+++	Cirripedia	Arthropoda	Maxillopoda
Polydo	917	463	1.13	-0.758	+++	Polydora	Annelida	Polychaeta
Gammar	314	268	1.118	-0.068	+++	Gammarus	Arthropoda	Malacostraca
Anthoz	740	394	1.071	-0.539	+++	Anthozoa	Cnidaria	Anthozoa
Carmae	425	298	1.069	-0.188	+++	Carcinus maenas	Arthropoda	Malacostraca
Lancon	430	256	0.913	-0.161	+++	Lanice conchilega	Annelida	Polychaeta
Astrub	156	126	0.746	0.06	+++	Asterias rubens	Echinodermata	Asteroidea
Crefor	161	104	0.606	0.153	+++	Crepidula fornicata	Mollusca	Gastropoda
Decapo	110	83	0.585	0.134	+++	Decapoda	Arthropoda	Malacostraca
Eumida	145	94	0.577	0.171	+++	Eumida	Annelida	Polychaeta
Meliti	103	72	0.524	0.183	+++	Melita	Arthropoda	Malacostraca
Micropr	82	61	0.498	0.171	+++	Microprotopus	Arthropoda	Malacostraca
Polych	64	43	0.397	0.251	+++	Polychaeta	Annelida	Polychaeta
Nemato	35	29	0.362	0.144	+++	Nematoda	Nematoda	
Procer	25	23	0.34	0.07	+++	Proceraea	Annelida	Polychaeta
Isopod	23	22	0.339	0.038	+++	Isopoda	Arthropoda	Malacostraca
Hemigr	23	21	0.324	0.077	+++	Hemigrapsus	Arthropoda	Malacostraca
Pontop	32	23	0.301	0.246	++	Bathyporeia	Arthropoda	Malacostraca
Mytili	15	15	0.286	0	+++	Mytilicola	Arthropoda	Maxillopoda
Cirrat	1439	557	1.085	-1.253	---	Tharyx	Annelida	Polychaeta
Hetfil	1163	473	1.025	-0.94	--	Heteromastus filiformis	Annelida	Polychaeta
Capcap	1066	428	0.969	-0.801	---	Capitella capitata	Annelida	Polychaeta
Pygele	707	268	0.745	-0.288	---	Pygospio elegans	Annelida	Polychaeta
Ensdir	366	126	0.487	0.204	---	Ensis directus	Mollusca	Bivalvia
Scoarm	591	152	0.462	0.126	---	Scoloplos armiger	Annelida	Polychaeta
Eteone	251	96	0.448	0.294	--	Eteone	Annelida	Polychaeta
Marvir	404	117	0.43	0.256	---	Marenzelleria	Annelida	Polychaeta
Microph	183	59	0.322	0.459	---	Microphthalmus	Annelida	Polychaeta
Nephty	189	42	0.226	0.599	---	Nephtys	Annelida	Polychaeta
Spio	211	43	0.219	0.609	---	Spio	Annelida	Polychaeta
Aricid	88	23	0.181	0.646	---	Aricidea	Annelida	Polychaeta
Ophiur	61	19	0.18	0.617	--	Ophiura	Echinodermata	Ophiuroidea
Strweb	15	0	0	1	---	Streptosyllis websteri	Annelida	Polychaeta

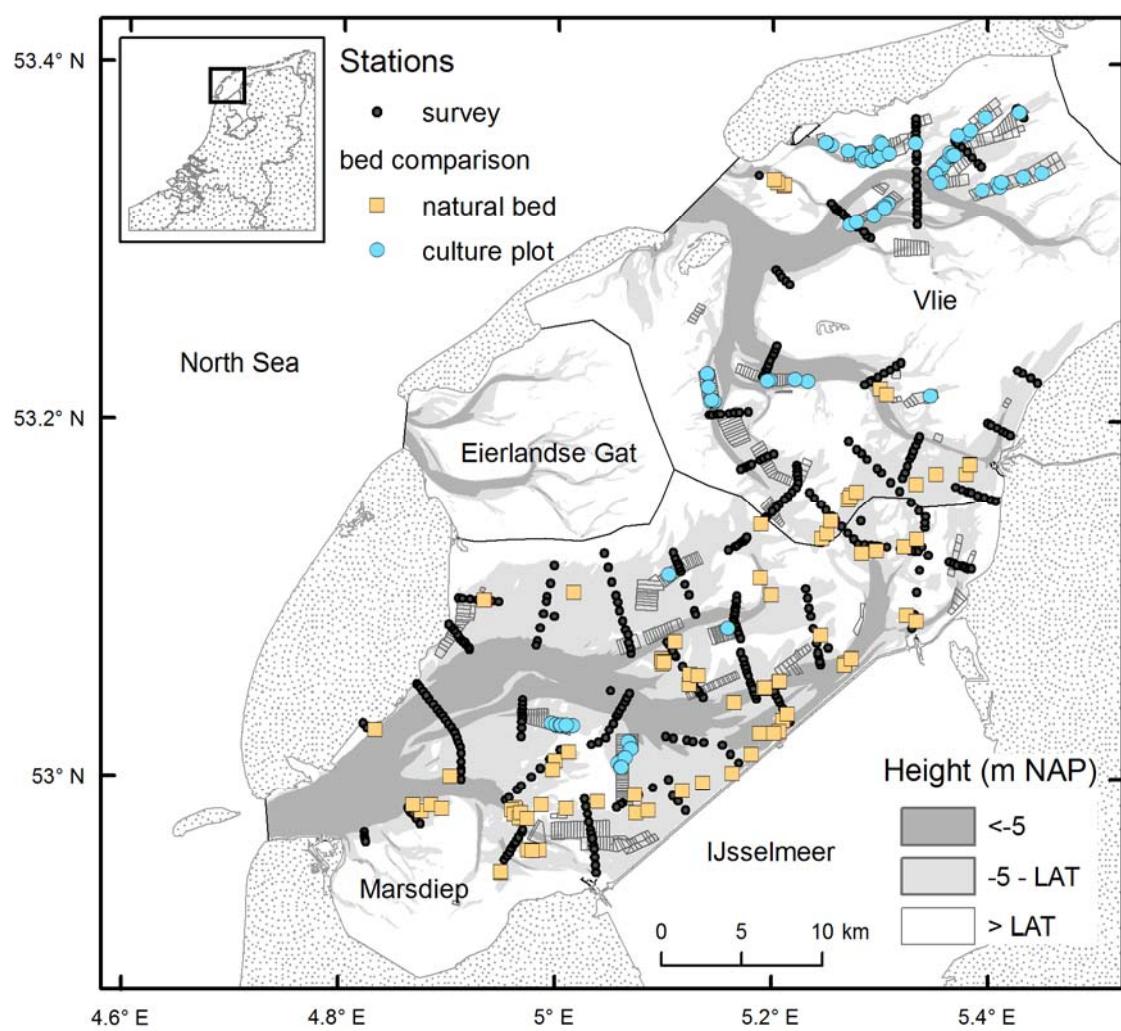


Figure 1. Map of the western Dutch Wadden Sea showing sampling stations of a benthic survey in 2008 and from a study comparing natural mussel beds and mussel culture plots.

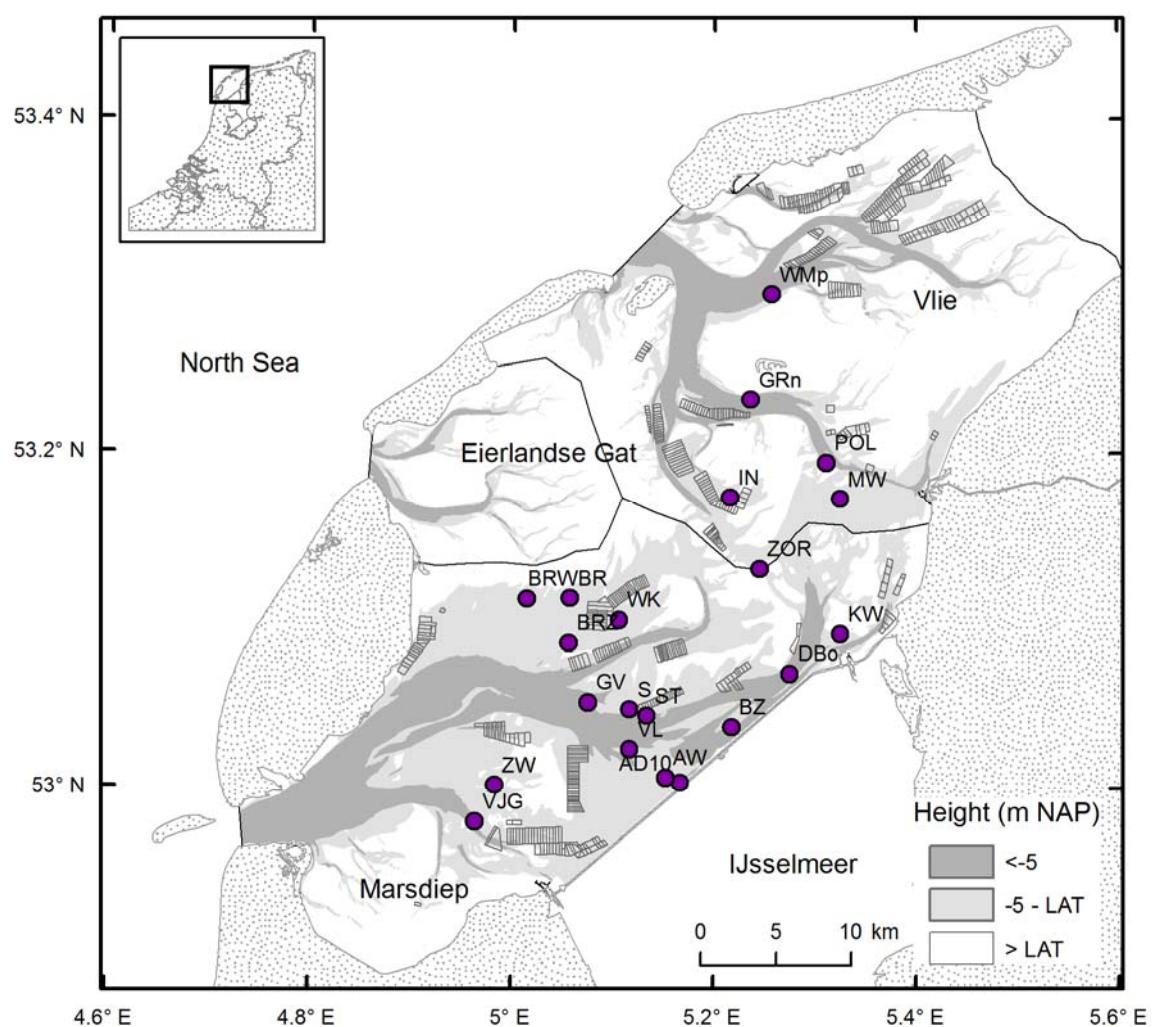


Figure 2. Map of the western Dutch Wadden Sea with locations of the subtidal natural mussel beds where experimental plots were established. Each bed had two plots one open for mussel seed fisheries and one closed fro fisheries. More details are reported in Craeymeersch et al. (2013).

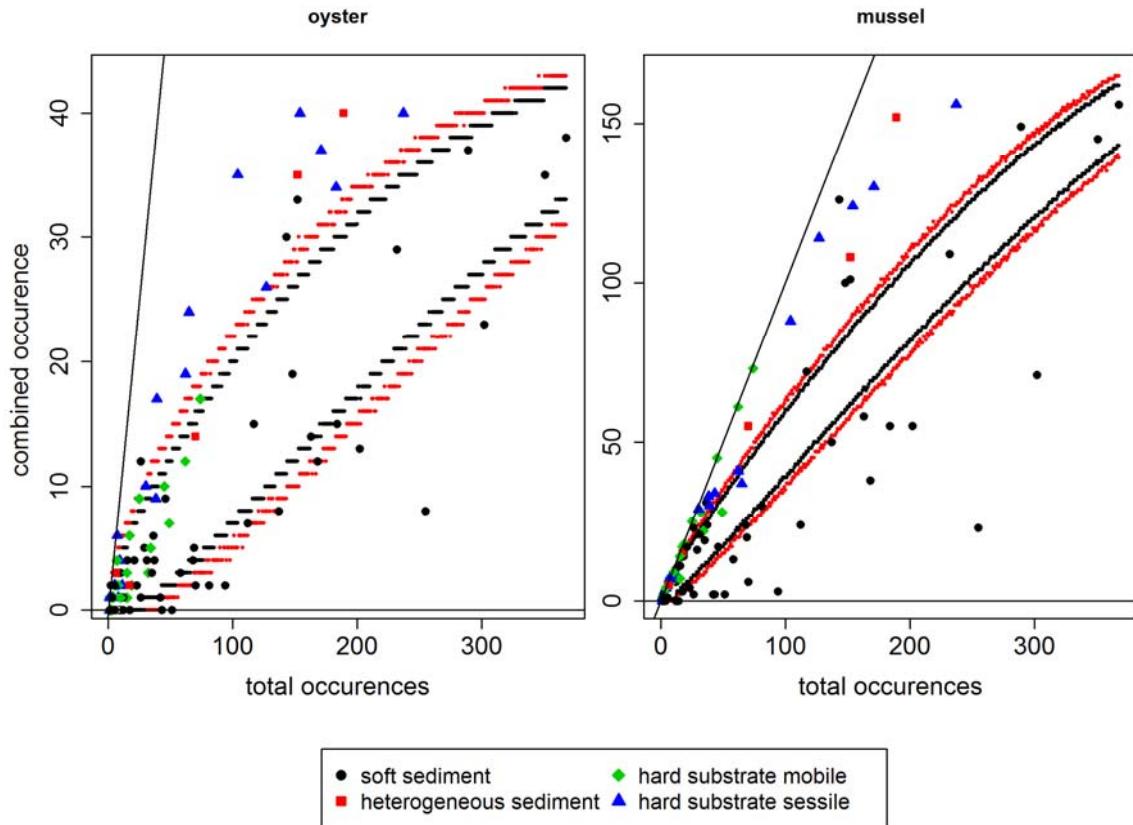


Figure 3. Combined occurrence (co-occurrence) of species with the focal species oyster (43 occurrences, left panel) or mussel (183 occurrences right panel) plotted against total occurrence of the non focal species. The 0.001 and 0.999 quantiles of the probability distribution of random species occurrences are shown as stippled red lines. The black stippled lines are the 0.01 and 0.99 quantiles. Values between the two black stippled lines are of species with no significant association with the focal species. Strait solid black lines enclose the area of possible observations. Symbols indicate species from different substrates.

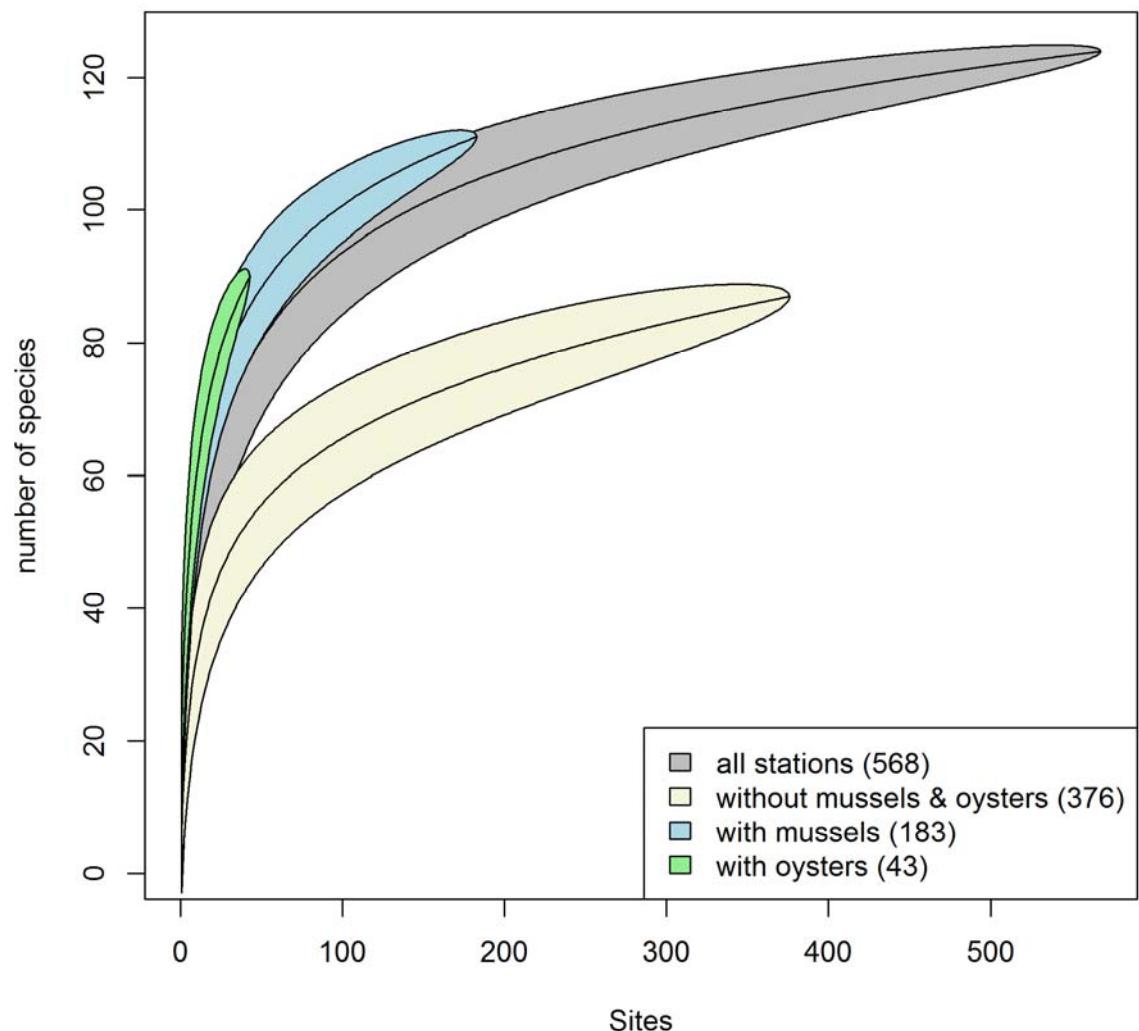


Figure 4. Relationship between the cumulative number of species found depending on the number of stations sampled in the subtidal of the western Dutch Wadden Sea. Besides the total dataset with 568 sites subsets of the dataset with stations containing mussels or oysters were used to estimate species area curves. The number of stations per category are given between brackets in the legend.

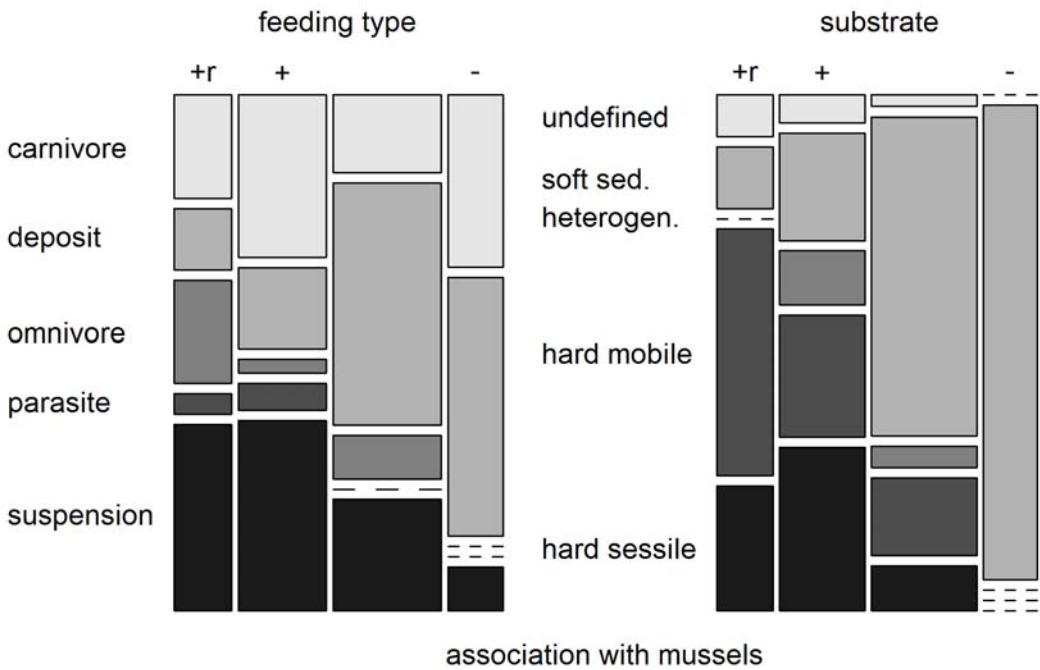


Figure 5. Mosaicplots of feeding types (left panel) and substrate (right panel) distributed over rare species only occurring together with mussels (+r), positively associated (+), unrelated (), or negatively associated (-) species with mussels.

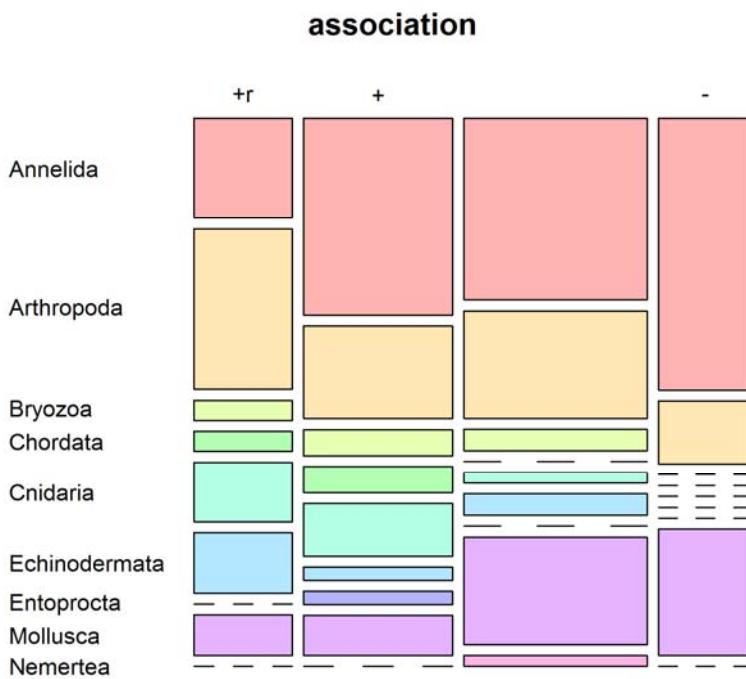


Figure 6. Mosaic plot of species counts categorized by phylum and the type of association with mussels in the western Dutch Wadden Sea. Associations are: +r) rare species only occurring together with mussels, +) species positively associated with mussels,)non-associated species, -) species negatively associated with mussels.

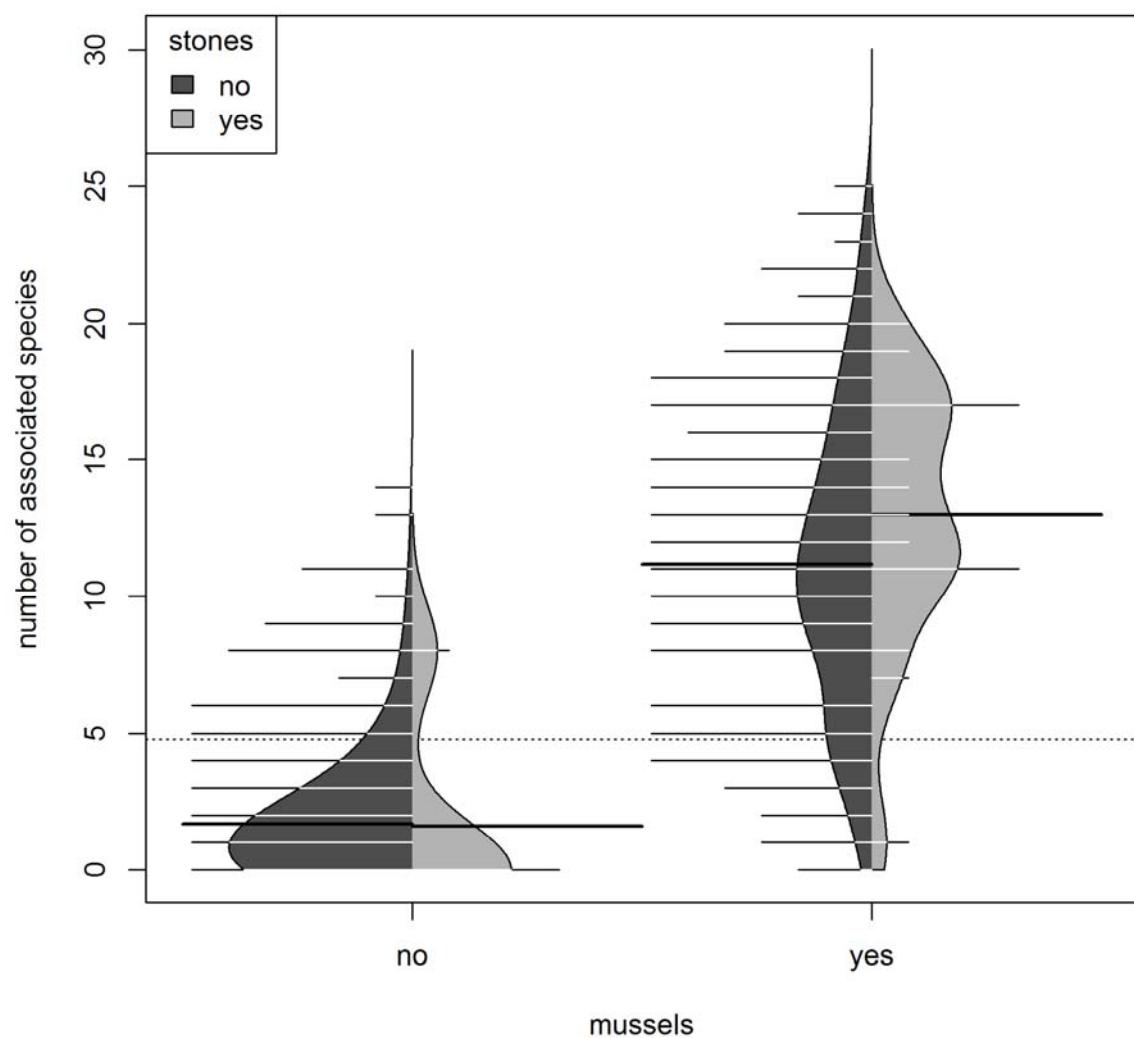


Figure 7. Effect of stones and mussels on the number of associated species in a box core.

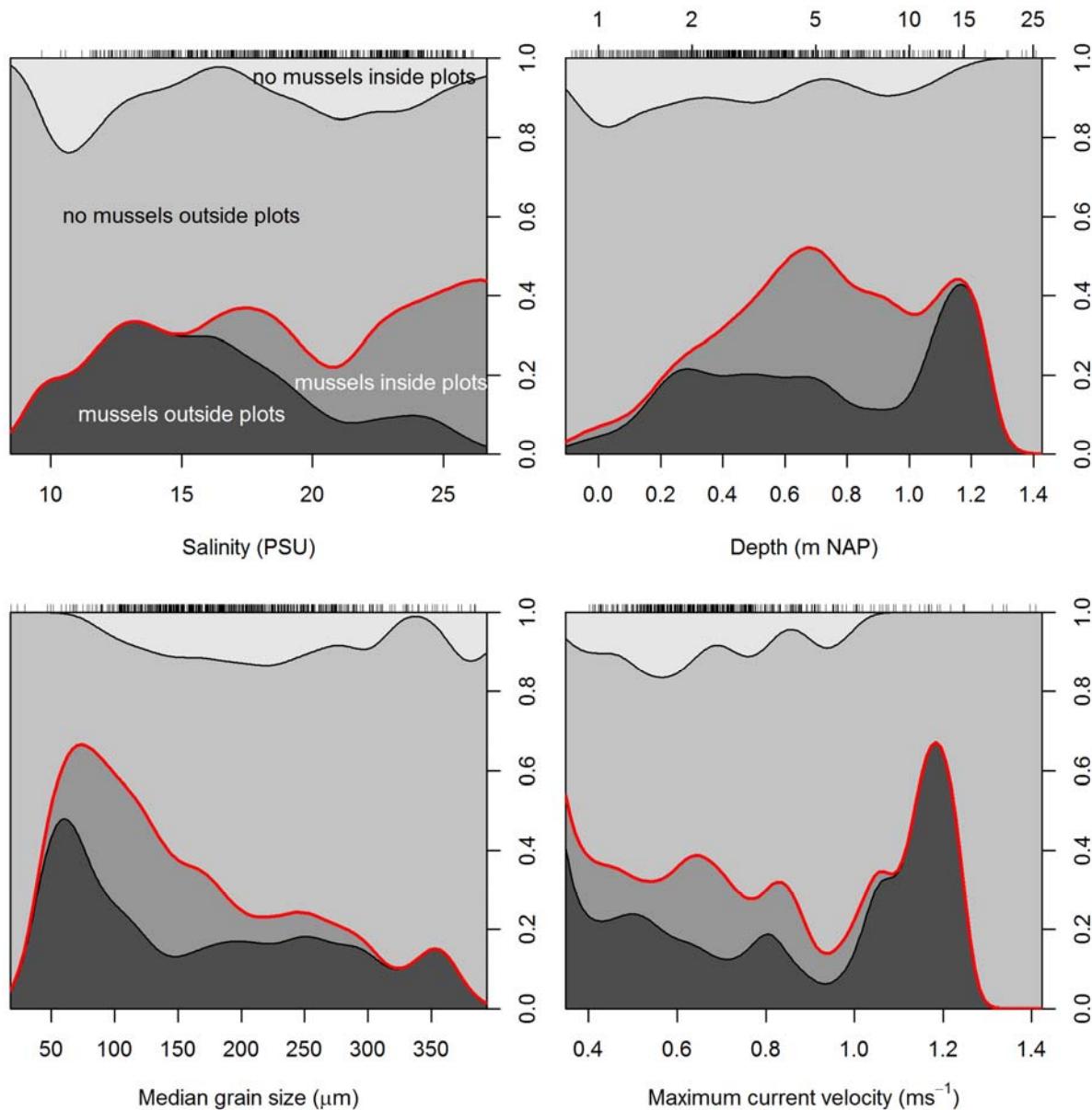


Figure 8. Conditional density plots with the distribution of 568 box core stations distributed along four environmental gradients in the subtidal of the western Dutch Wadden Sea. Stations are categorized by location either inside or outside mussel culture plots and depending on the presence of mussels in the box core. The red line is to emphasize the overall mussel occurrence in the dataset. Along the upper margins a rug is plotted with the distribution of the samples along the gradients. The dataset is a combination of a subtidal survey in 2008 and a comparison between mussel culture plots and natural mussel beds done during 2008, 2009 and 2010.

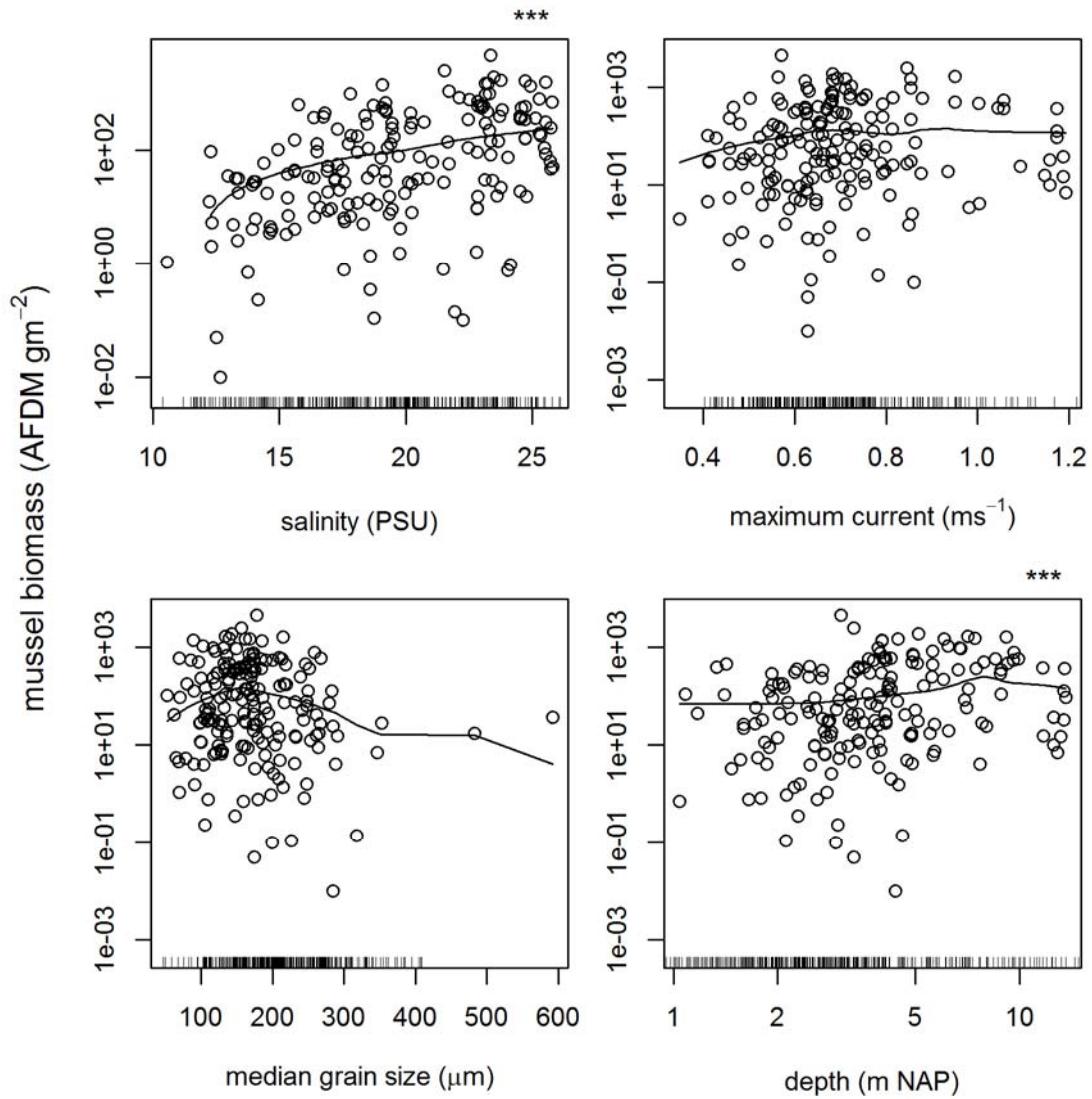


Figure 9. Biomass of *Mytilus edulis* along four environmental gradients in the Western Dutch Wadden Sea. Lowes lines are fitted only to the observations with mussels. Stations without mussels are shown as a rug along the lower margins of the panels. Significant Pearson correlations between mussel biomass and environmental variables are indicated with * ($p<0.001$).**

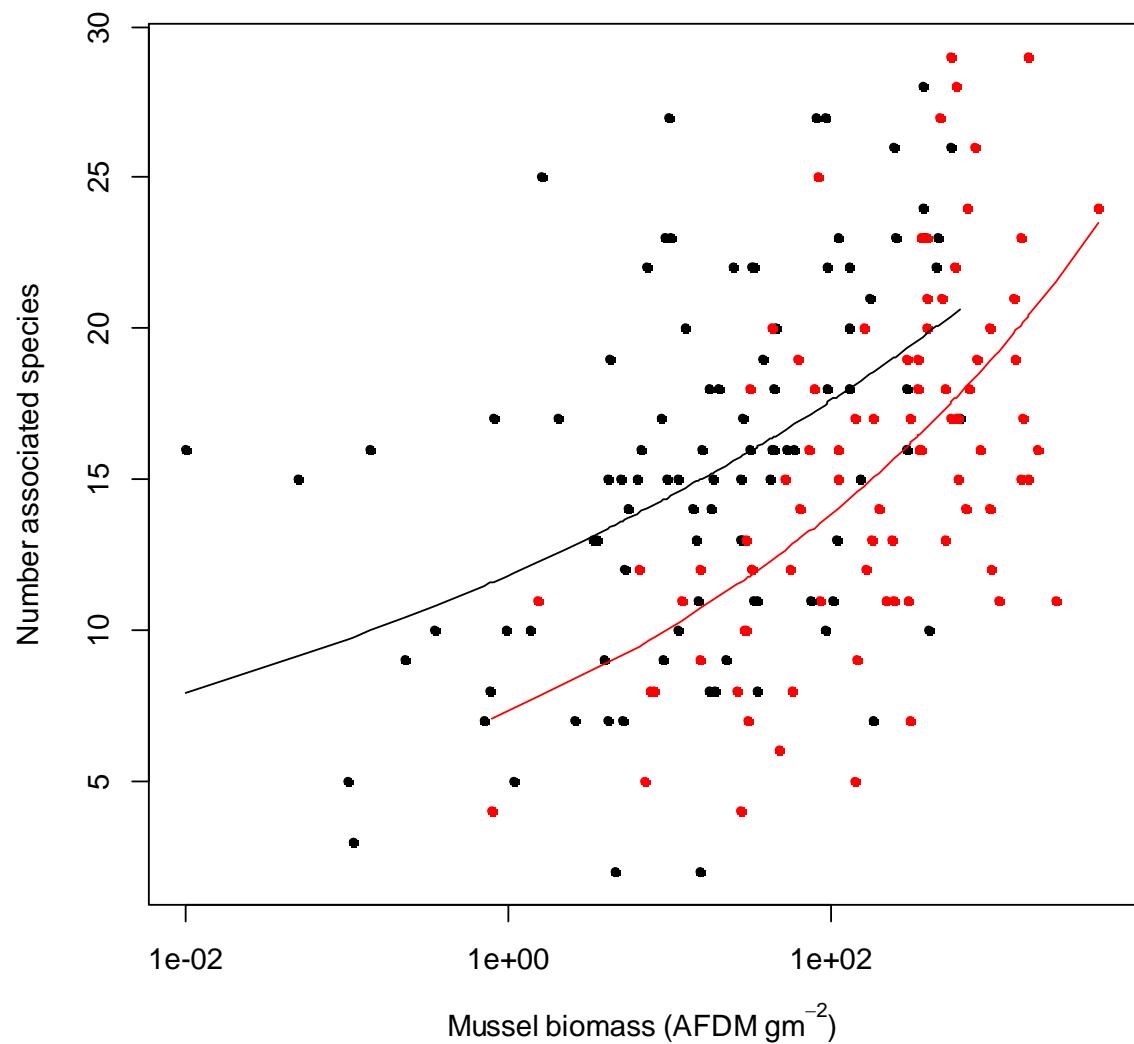


Figure 10. Number of mussel associated species depending on mussel biomass in natural beds and on mussel culture plots. Lines are the predictions of a GLM model describing associated species as a function of mussel biomass bed-type and the interaction biomass:bed-type.

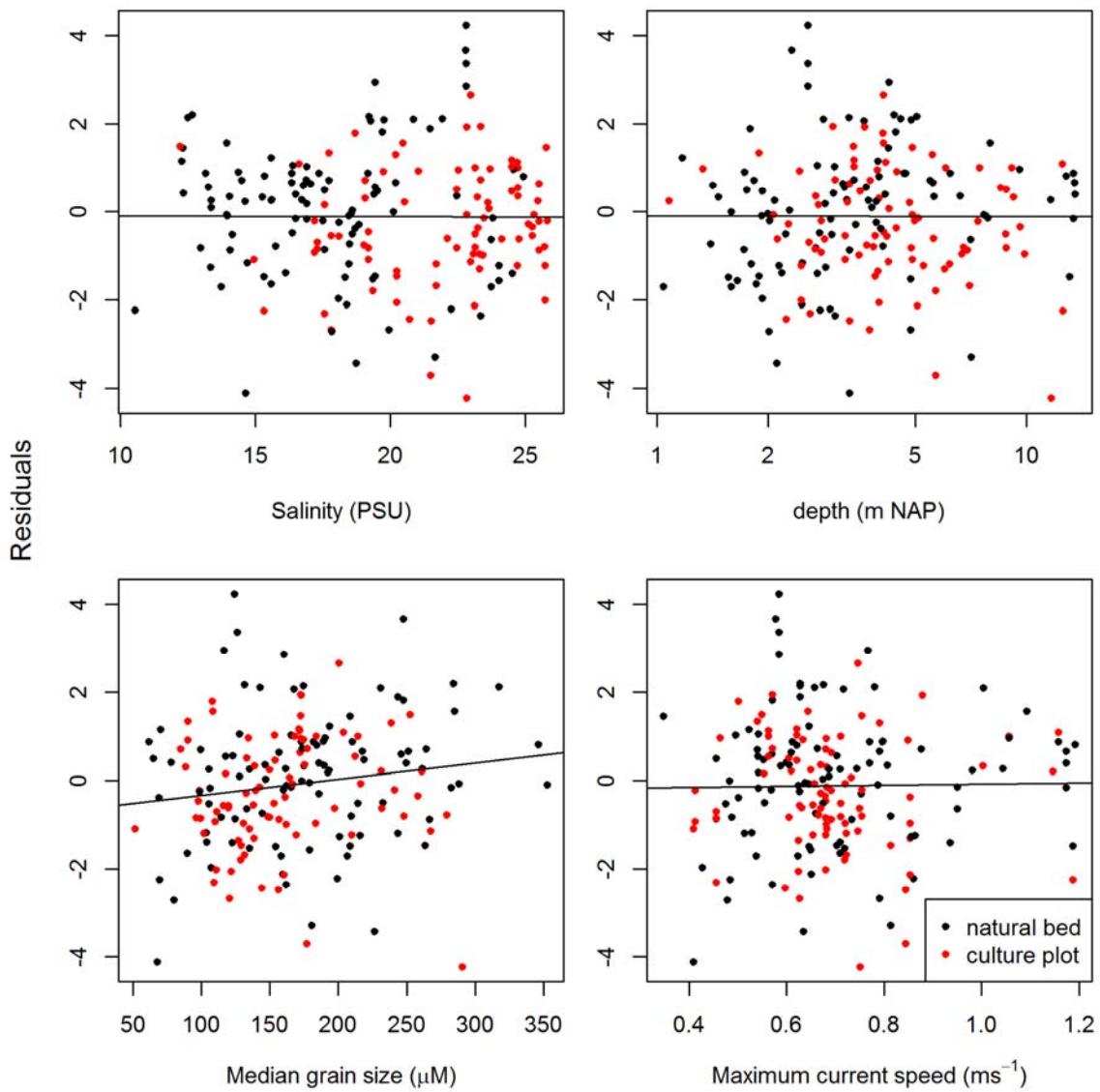


Figure 11. Residuals of a GLM model explaining number of mussel associated species with mussel biomass, bed type and the interaction between the two, plotted against environmental variables. Residuals are significantly related with depth and median grain size. Salinity and maximum current speed are both not related to the residuals.

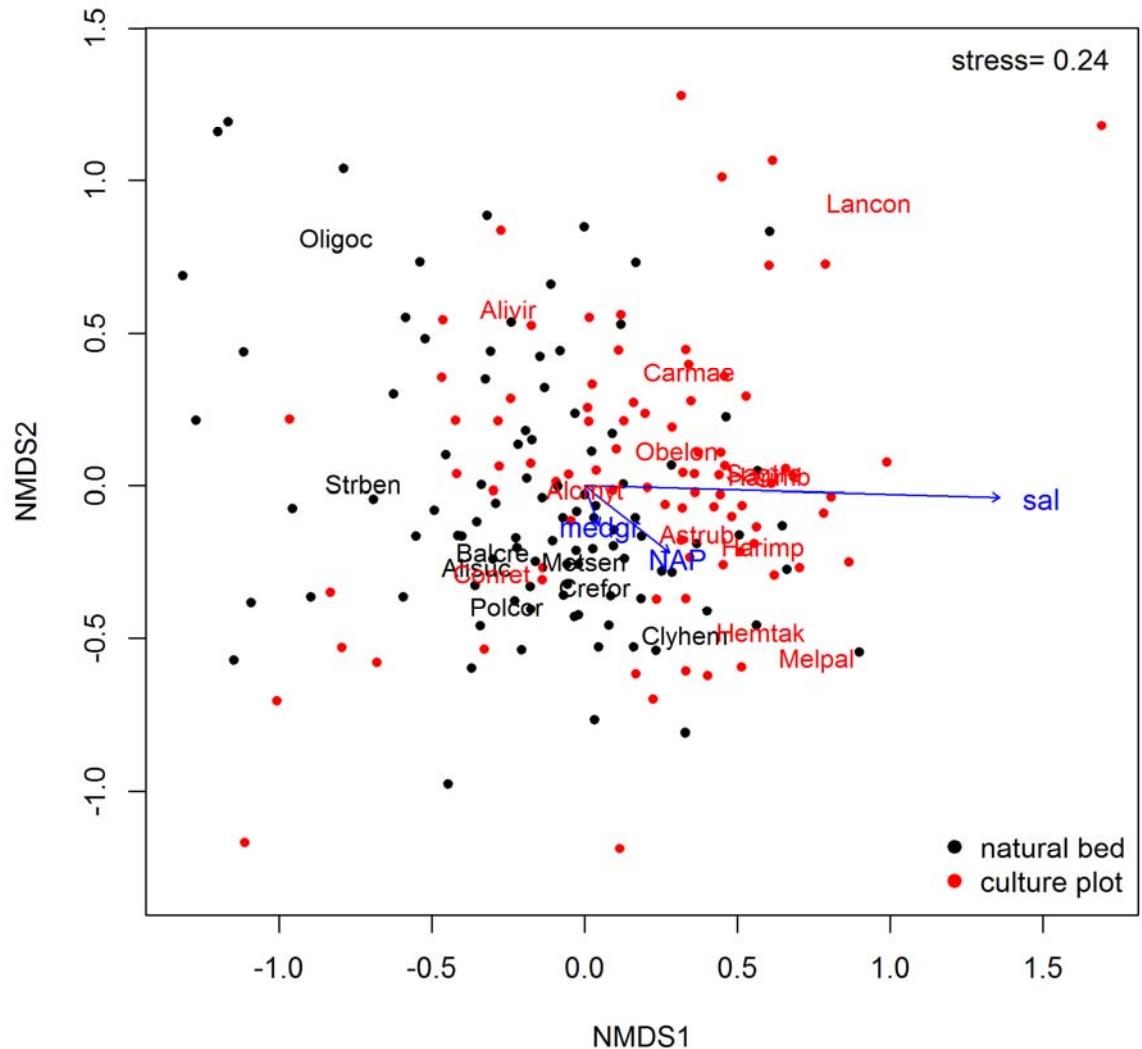


Figure 12. Nonmetric Multidimensional Scaling plot of the community associated with *Mytilus edulis* in the subtidal of the western Dutch Wadden Sea. Colours of abbreviated species names correspond to the habitat where they are most abundant. Only the twenty species contributing most to the differences between natural beds and culture plots are shown.

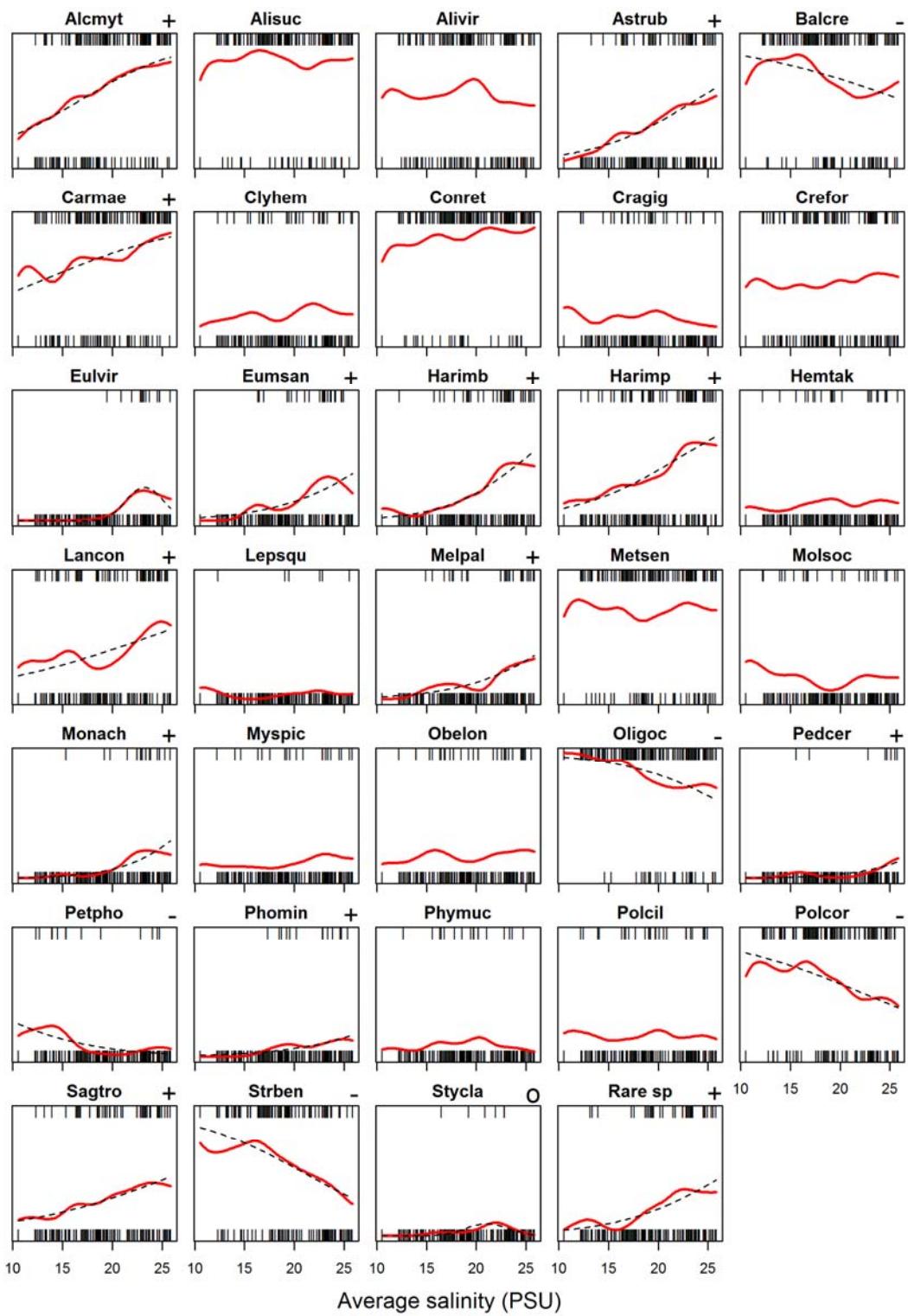


Figure 13. Conditional density curves for presence absence of mussel associated macrozoobenthos depending on salinity. Presences are plotted as a rug along the upper margins, absences along the lower margins of the panels. Salinity effects on presence of the associated species were tested with two logistic 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”.

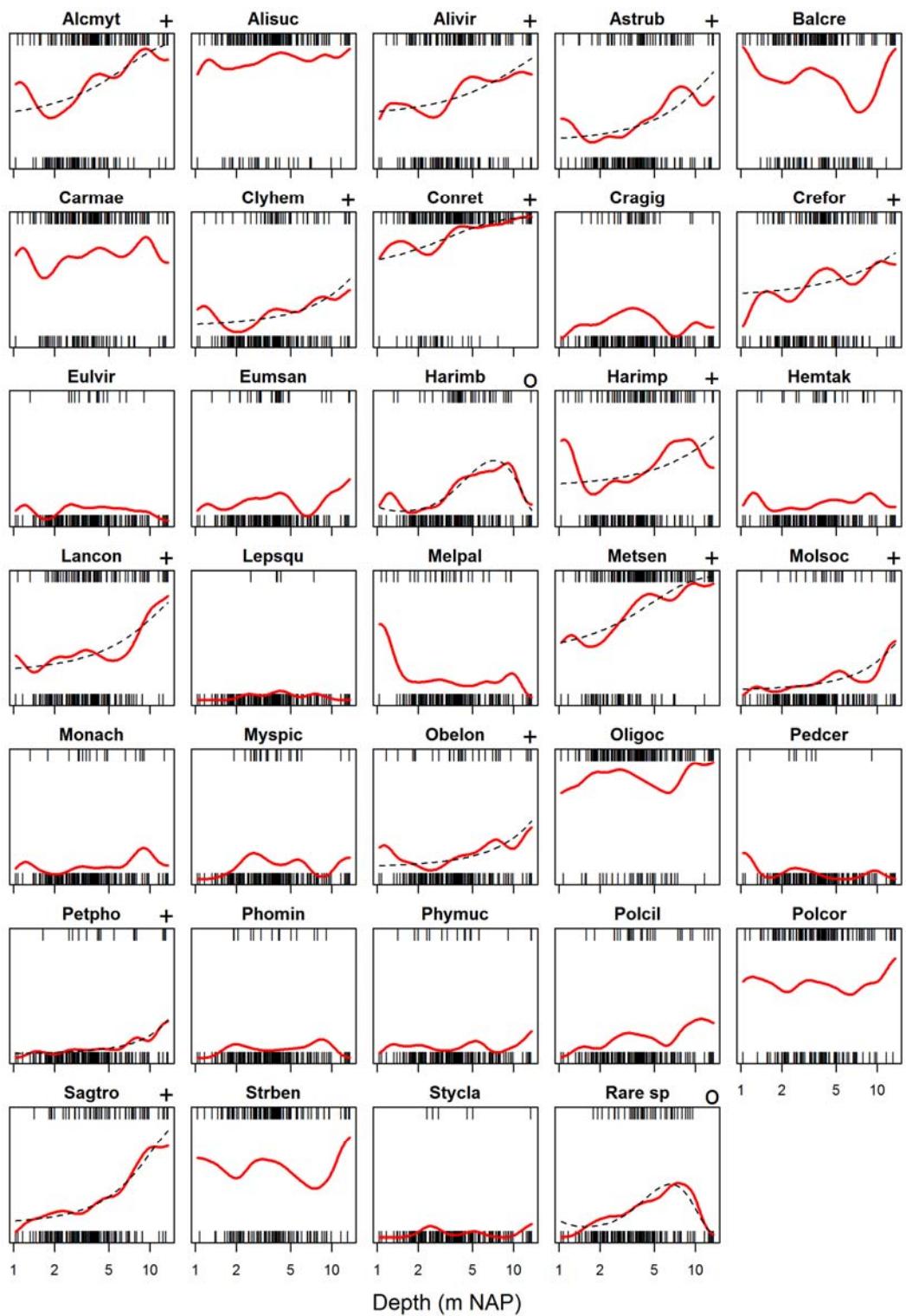


Figure 14. Conditional density curves for presence absence of mussel associated macrozoobenthos depending on depth in meters relative to Dutch ordinance level NAP. See Fig. for more details.

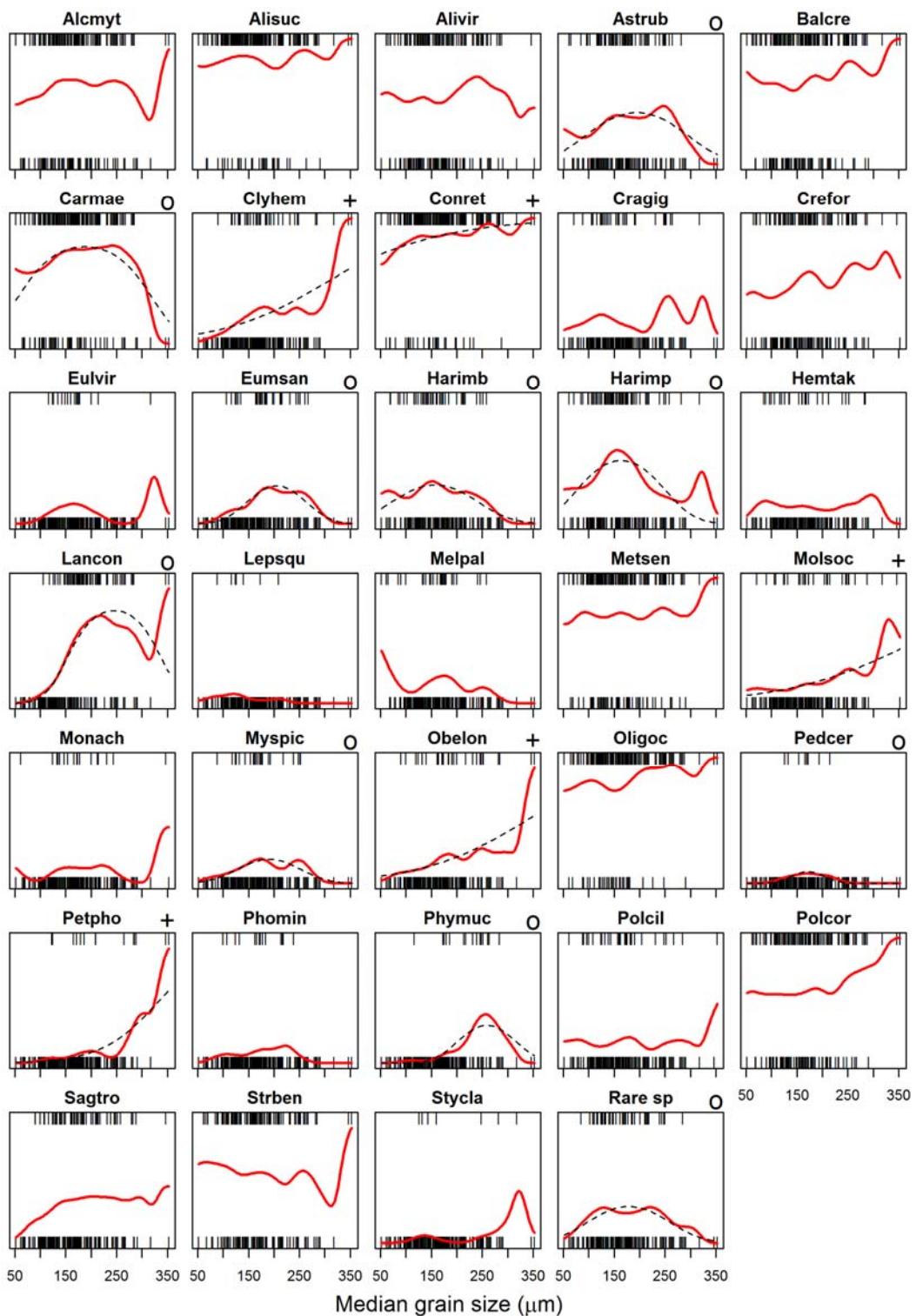


Figure 15. Conditional density curves for presence absence of mussel associated macrozoobenthos depending on median grain size. See Fig. for more details

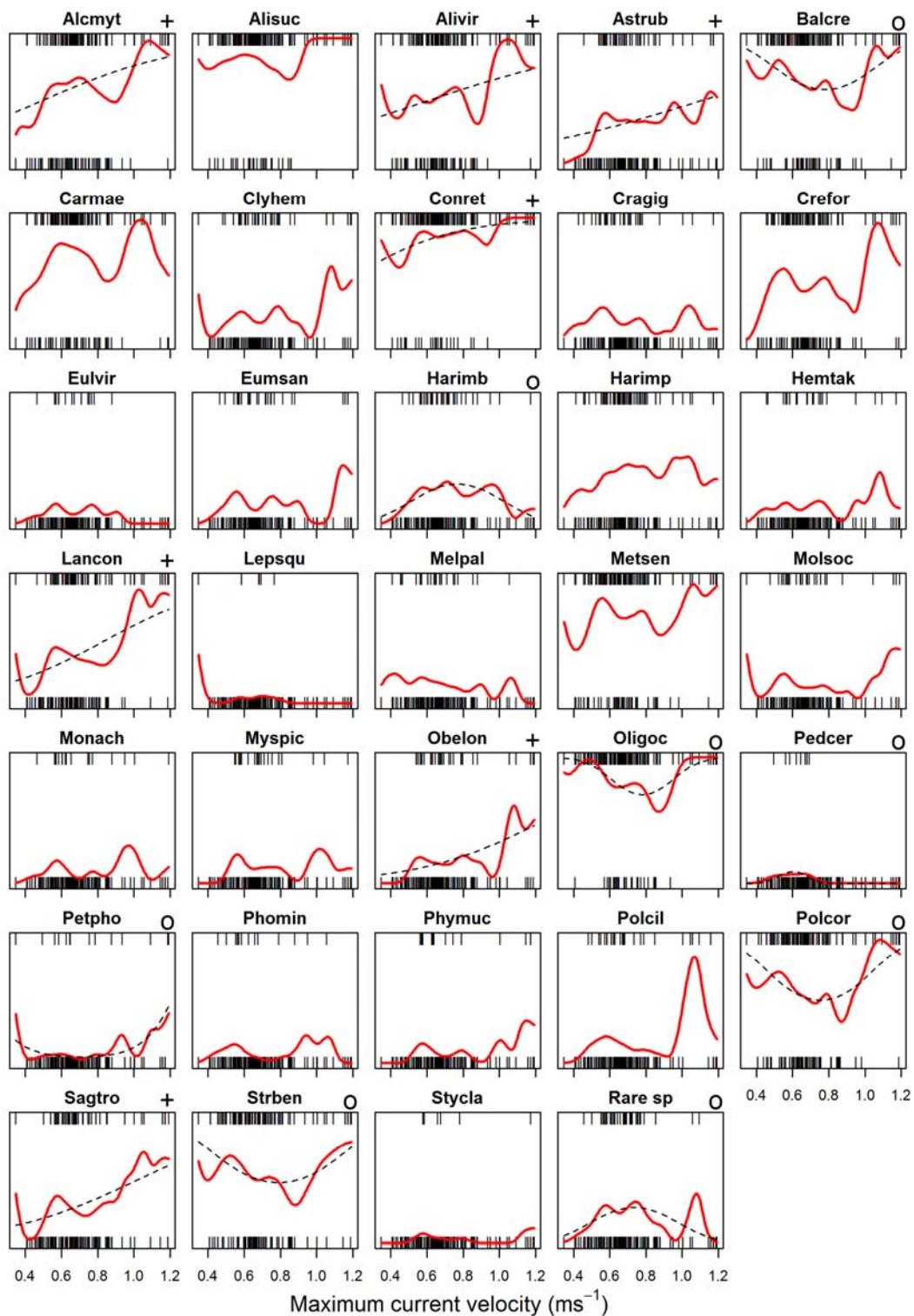


Figure 16. Conditional density curves for presence absence of mussel associated macrozoobenthos depending on maximum current velocity. See Fig. for more details

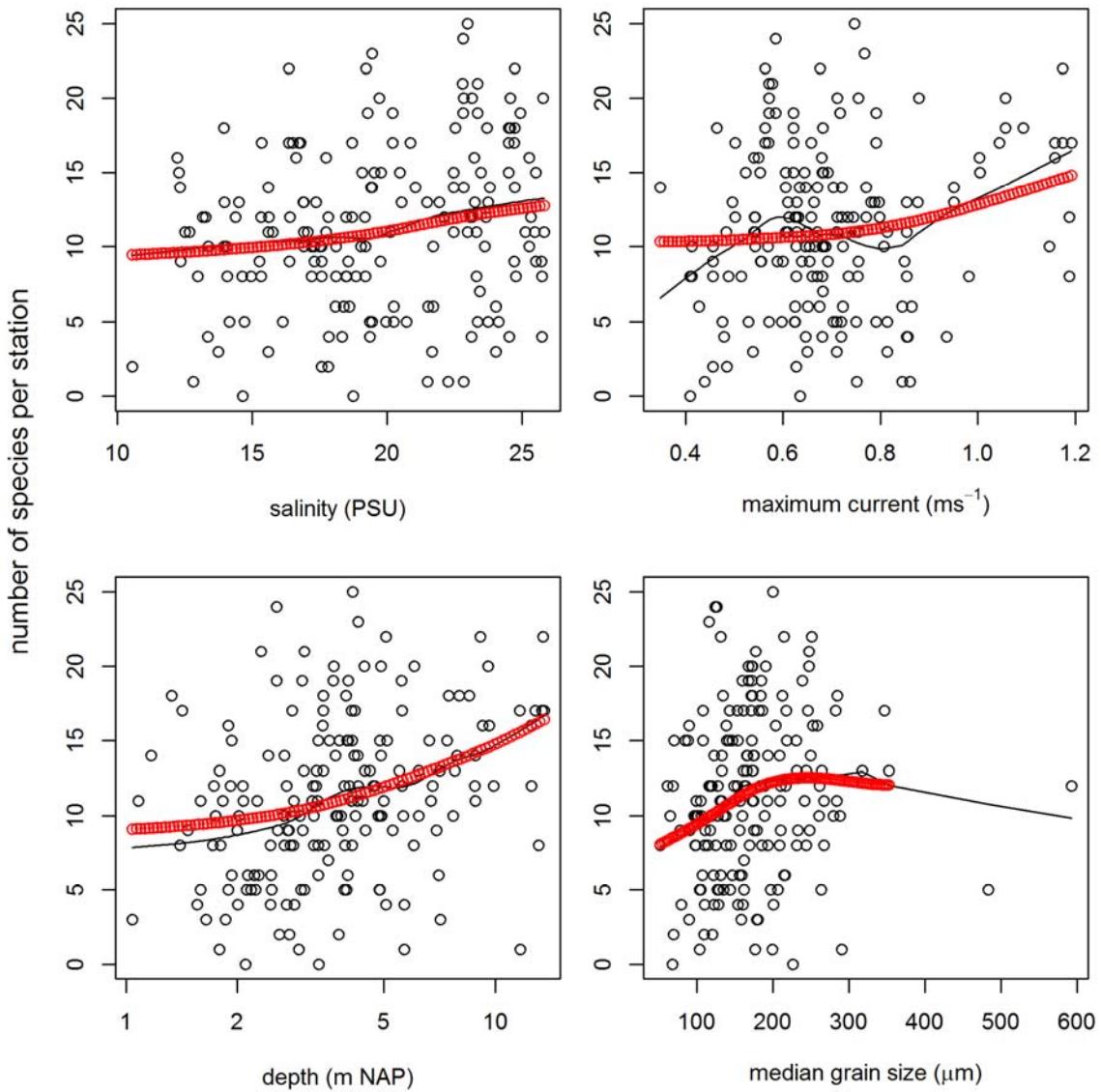


Figure 17. Number of mussel associated species depending on environmental gradients. Black lines are lowess fits. The red lines are the summed environmental response curves of the individual associated species.

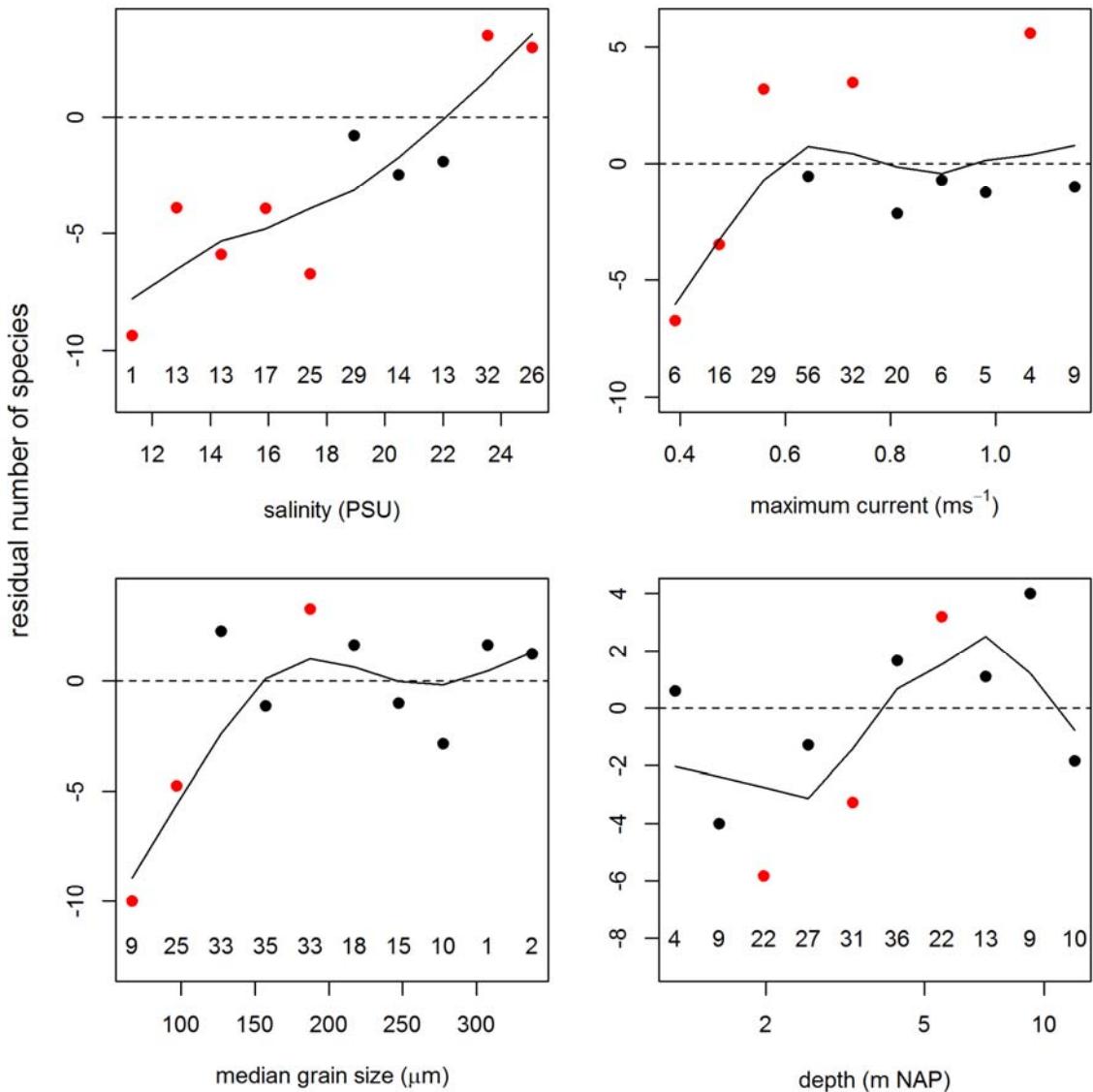


Figure 18. Residual number of species associated with mussels in sample aggregates along four environmental gradients. The box core data were divided in 10 equal fractions along the environmental gradient. Number of cores per bin are printed along the x axis. Number of species in each bin were compared to the expected number of species from a species area curve estimated with all the 183 stations containing mussels. Residuals larger than one standard error are printed in red. A lowess line is fitted to the data.

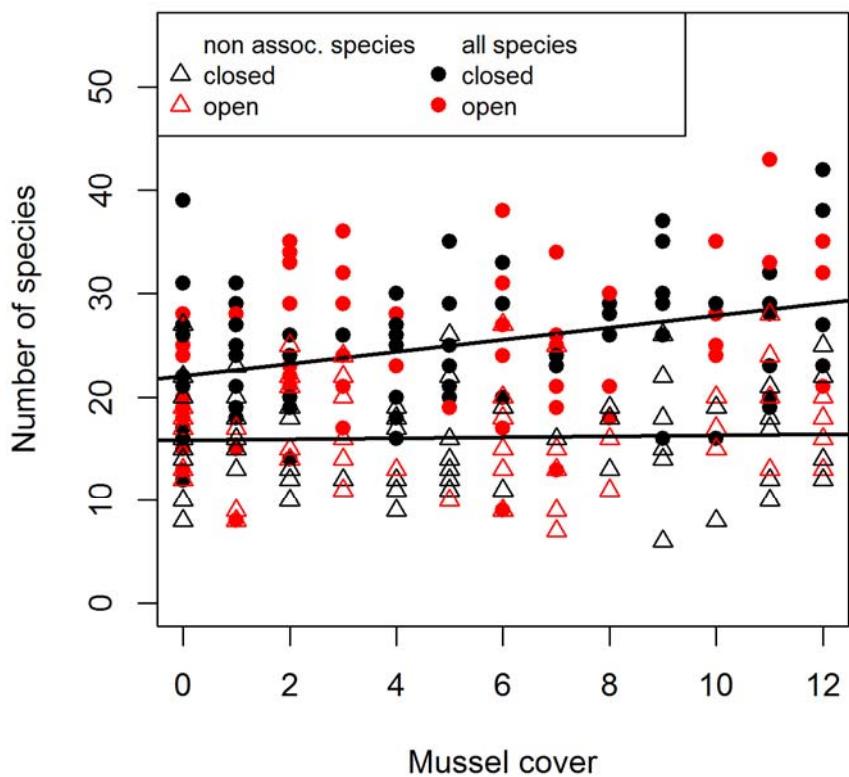


Figure 19. Number of species (totals in 12 box cores) plotted as a function of mussel cover (number of boxes out of 12 containing at least one mussel). Species are specified as non-associated (difference between non-associated and all species) or associated with mussels (*M. edulis*)

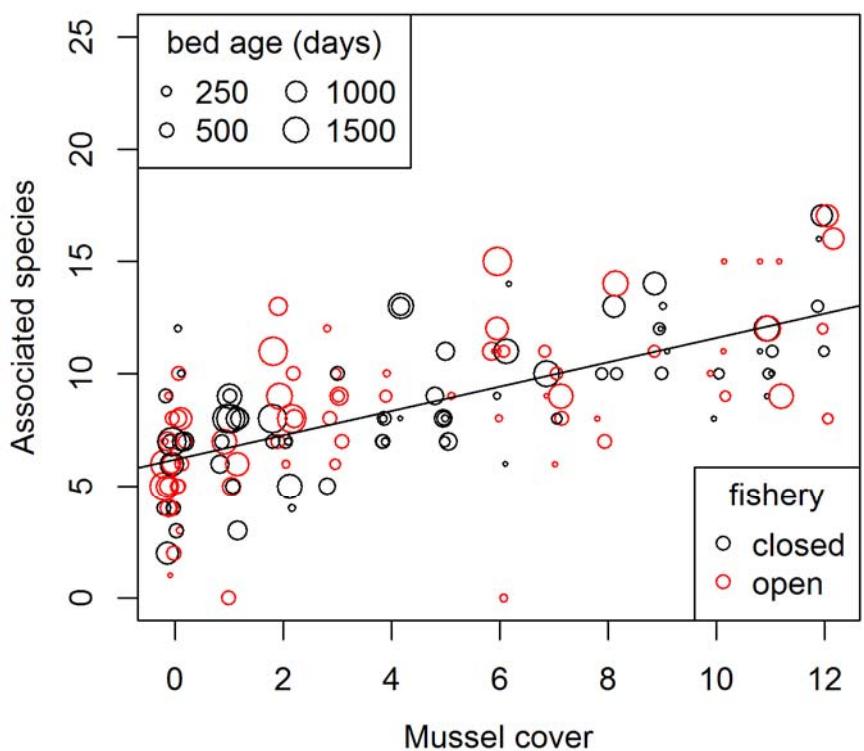


Figure 20. Number of species associated with mussels (*M. edulis*) (totals from 12 box cores) related to mussel cover (number of boxes out of 12 containing at least one mussel) with dot size representing the bed age. To show overlapping values slight random jitter is added to the x values. Box cores were taken sequentially through time at 21 subtidal mussel beds in the western Dutch Wadden Sea. At each bed 12 boxes were collected from a plot closed and a plot open for mussel seed fisheries.

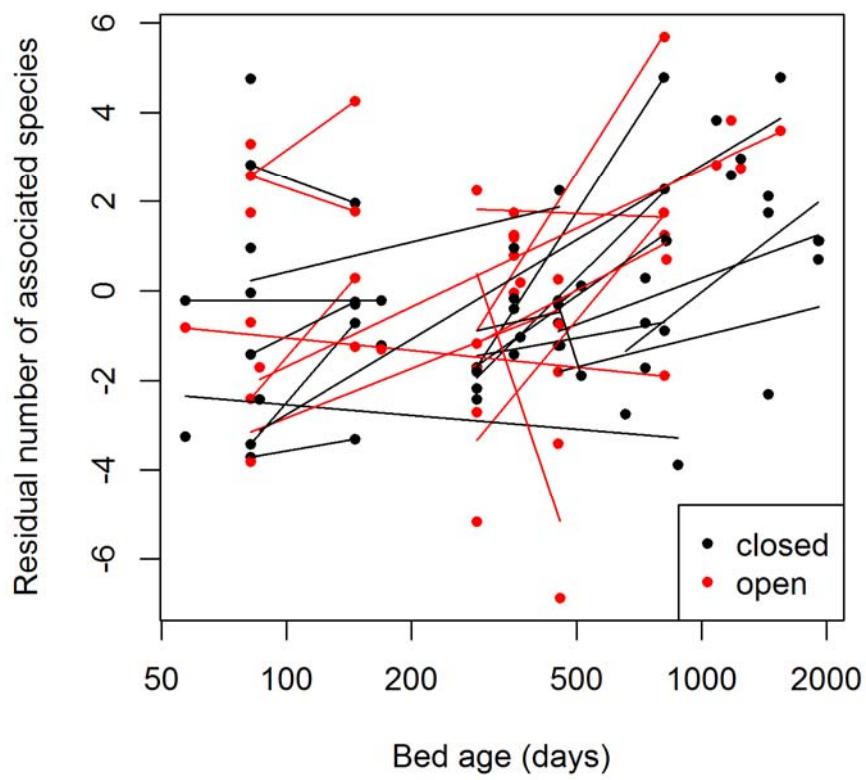


Figure 21. Residuals from a GLM model describing number of associated species with mussel cover plotted against mussel bed age. Regression lines describe residual associated species number as a linear function of mussel bed age for each plot as long as it still contained mussels in at least one box core out of 12. Plots were either closed or open for mussel seed fishery.

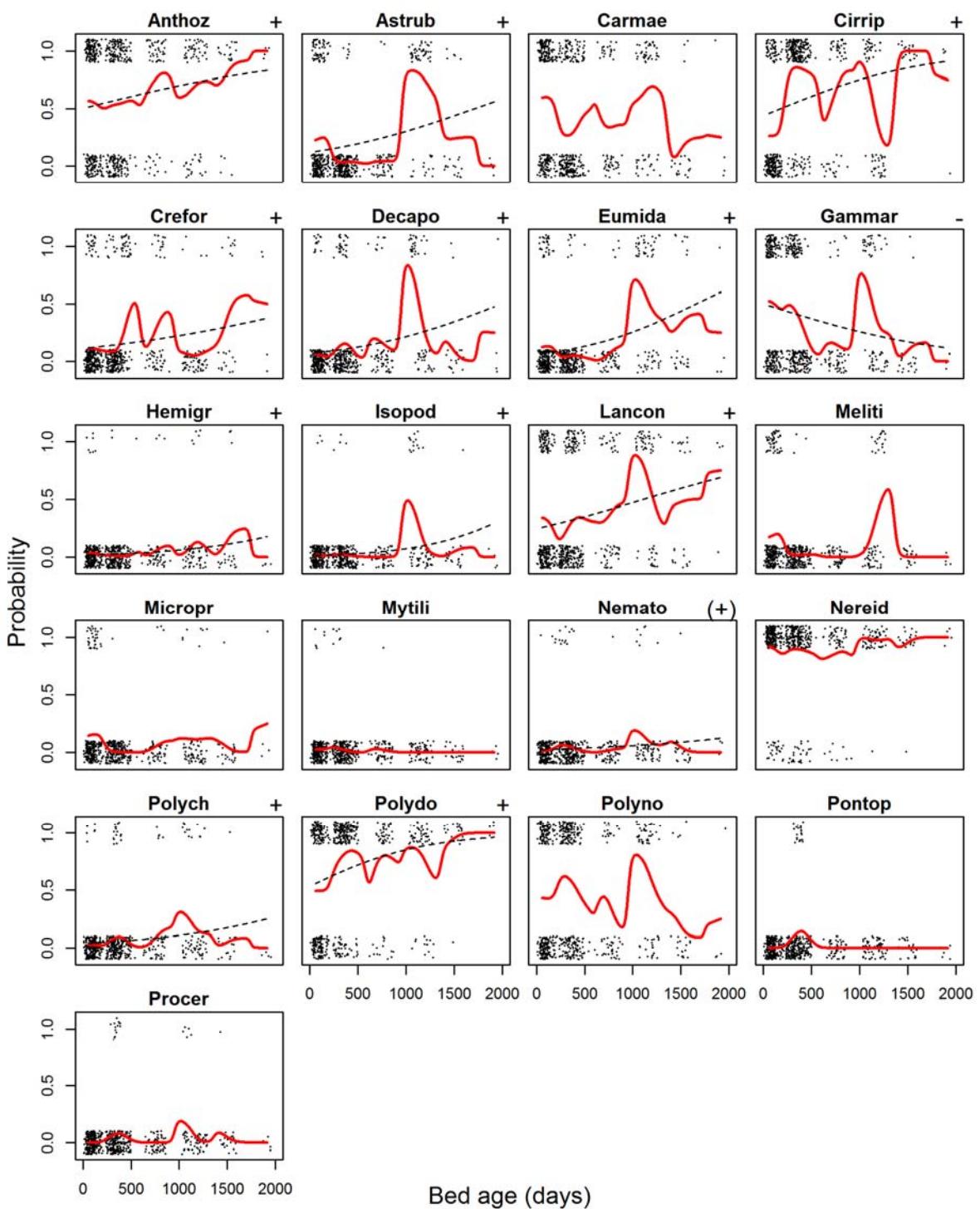


Figure 22. Occurrence of macrozoobenthos associated with mussels (*M. edulis*) depending on the age of the mussel bed. Presences and absences of the species per box ($n=618$) are plotted with slight random jitter. Red curves are the conditional distributions of species presences depending on bed age. Logistic probability curves (black dashed lines) are shown when in a logistical model bed age was significantly explaining part of the presence absence data. Sign of significant models is plotted next to the species names. P values were adjusted for multiple testing with a Holm modified Bonferroni correction. When the original p values were significant but the corrected not the sign is given between brackets. See table x for an explanation of the name abbreviations.

Appendix 1

Associated species list from literature sources

List of invertebrate species associated with mussels (*Mytilus edulis*) and pacific oyster (*Crassostrea gigas*) in the international Wadden Sea. This list is based on six reports five from the northern German Wadden Sea in Schleswig-Holstein (1, 2, 3, 5 and 6) and one (4) from the southern Wadden sea in Lower Saxony. The criterion to include a species was solely based on the mentioning as such by the used reports. The sources were: 1) Buschbaum 2002, 2) Büttger et al. 2008, 3) Dittmann 1990, 4) Markert et al 2010, 5) Saier 2002 and 6) Westphalen 2006. The species were found at intertidal or subtidal shellfish beds or in both habitats. Phylum and class are mentioned in the shaded rows before and after the slash respectively. The species names are checked against the World Register of Marine Species (WoRMS) species list and the WoRMS AphiaID number is included in the table.

AphiaID	Scientific name	Habitat	source
Annelida/Clitellata			
2036	<i>Oligochaeta</i>	int	2,4
137485	<i>Paranais litoralis</i>	int	3
137571	<i>Tubificoides benedii</i>	int	3,4
137582	<i>Tubificoides pseudogaster</i>	int	3
Annelida/Polychaeta			
883	<i>Polychaeta</i>	int	4
129868	<i>Arenicola marina</i>	int	2,3
129876	<i>Capitella capitata</i>	int	2,3,4
129884	<i>Heteromastus filiformis</i>	int	2,3,4
130500	<i>Ophelina acuminata</i>	int	2
334772	<i>Scoloplos (Scoloplos) armiger</i>	int	2,3,4
130164	<i>Kefersteinia cirrata</i>	int	2,3
130168	<i>Microphthalmus aberrans</i>	int	3
130174	<i>Microphthalmus sczelkowii</i>	int	4
956	<i>Nephtyidae</i>	int	2
130359	<i>Nephtys hombergii</i>	int	4
22496	<i>Nereididae</i>	int	2
129379	<i>Nereis</i>	sub	6
130375	<i>Eunereis longissima</i>	sub	6
152302	<i>Hediste diversicolor</i>	both	3,4,5,6
234850	<i>Alitta succinea</i>	both	3,5
234851	<i>Alitta virens</i>	sub	5
130599	<i>Pholoe baltica</i>	int	2
130603	<i>Pholoe minuta</i>	int	3
130613	<i>Eteone flava</i>	int	2
130616	<i>Eteone longa</i>	int	2,3
130624	<i>Eulalia bilineata</i>	sub	6
130639	<i>Eulalia viridis</i>	both	2,3,5,6
130644	<i>Eumida sanguinea</i>	int	2,3
129455	<i>Phyllodoce</i>	both	2,6

AphiaID	Scientific name	Habitat	source
334512	<i>Phyllodoce mucosa</i>	both	3,4,5
939	<i>Polynoidae</i>	int	2
130735	<i>Bylgides sarsi</i>	int	2
130749	<i>Gattyana cirrhosa</i>	both	2,6
130769	<i>Harmothoe imbricata</i>	both	2,3,5,6
130770	<i>Harmothoe impar</i>	both	2,3,5,6
130801	<i>Lepidonotus squamatus</i>	both	2,3,5,6
129659	<i>Myrianida</i>	both	3,6
131362	<i>Proceraea cornuta</i>	int	2
130926	<i>Manayunkia aestuarina</i>	int	2
555935	<i>Spirobranchus triqueter</i>	sub	1
129642	<i>Spirorbis</i>	sub	1
889	<i>Spionida</i>	int	4
129614	<i>Malacoceros</i>	int	2
131131	<i>Malacoceros fuliginosus</i>	int	3
333954	<i>Malacoceros tetracerus</i>	int	3
129619	<i>Polydora</i>	int	2
131121	<i>Dipolydora quadrilobata</i>	int	3
131141	<i>Polydora ciliata</i>	both	1,3,4,5,6
131143	<i>Polydora cornuta</i>	int	3
131170	<i>Pygospio elegans</i>	int	2,3,4
131183	<i>Spio filicornis</i>	int	2
131187	<i>Spiophanes bombyx</i>	int	2
131188	<i>Spiophanes kroyeri</i>	int	2
129775	<i>Ampharete acutifrons</i>	int	2
129778	<i>Ampharete finmarchica</i>	int	3
919	<i>Cirratulidae</i>	int	2
129938	<i>Aphelochaeta marioni</i>	int	4
155177	<i>Tharyx marioni</i>	int	3
152367	<i>Lagis koreni</i>	int	2
131495	<i>Lanice conchilega</i>	both	1,2,4,6
131504	<i>Neoamphitrite figulus</i>	both	3,5,6
Arthropoda/Collembola			
118139	<i>Anurida maritima</i>	int	4
Arthropoda/Malacostraca			
148603	<i>Monocorophium sextonae</i>	sub	1
102283	<i>Gammarus marinus</i>	int	2
101537	<i>Gammarus</i>	sub	6
102281	<i>Gammarus locusta</i>	both	2,3,5
102285	<i>Gammarus oceanicus</i>	int	2
102431	<i>Jassa falcata</i>	sub	1
107552	<i>Crangon crangon</i>	int	3
107232	<i>Pagurus bernhardus</i>	both	2,3,5
107381	<i>Carcinus maenas</i>	both	2,3,4,5,6
119039	<i>Idotea balthica</i>	both	2,6

AphiaID	Scientific name	Habitat	source
119042	<i>Idotea chelipes</i>	int	3
264171	<i>Jaera (Jaera) albifrons</i>	both	2,3,4,5
118917	<i>Limnoria lignorum</i>	int	1
Arthropoda/Maxillopoda			
106210	<i>Semibalanus balanoides</i>	both	1,3,4
712167	<i>Austrominius modestus</i>	both	1,4,6
106122	<i>Balanus</i>	int	2
106213	<i>Balanus balanus</i>	sub	1
106215	<i>Balanus crenatus</i>	both	1,3,4,6
Arthropoda/Pycnogonida			
134643	<i>Callipallene brevirostris</i>	sub	6
134591	<i>Nymphon</i>	int	2
134688	<i>Nymphon grossipes</i>	int	3
150520	<i>Nymphon brevirostre</i>	sub	6
134723	<i>Anoplodactylus petiolatus</i>	sub	6
239867	<i>Pycnogonum litorale</i>	both	2,6
Bryozoa/Gymnolaemata			
111351	<i>Conopeum reticulum</i>	both	1,4,6
111352	<i>Conopeum seurati</i>	sub	6
111355	<i>Electra pilosa</i>	sub	1,6
111367	<i>Flustra foliacea</i>	sub	1
468026	<i>Alcyonidioides mytili</i>	sub	1,6
111023	<i>Bowerbankia</i>	sub	6
111665	<i>Bowerbankia gracilis</i>	sub	1,6
111667	<i>Bowerbankia imbricata</i>	sub	1
Bryozoa/Stenolaemata			
111696	<i>Crisia eburnea</i>	sub	1
Chordata/Asciidae			
1839	<i>Ascidiae</i>	int	2
103656	<i>Aplidium nordmanni</i>	int	1
103484	<i>Ascidia</i>	int	1
103732	<i>Ciona intestinalis</i>	sub	1
103509	<i>Molgula</i>	int	1
103788	<i>Molgula manhattensis</i>	sub	6
103862	<i>Botryllus schlosseri</i>	sub	1
103929	<i>Styela clava</i>	sub	1
Ciliophora/Heterotrichaea			
111849	<i>Eufolliculina</i>	sub	1
Ciliophora/Oligohymenophorea			
163573	<i>Vorticella</i>	sub	1
Cnidaria/Anthozoa			
1360	<i>Actiniaria</i>	int	2
100982	<i>Metridium senile</i>	both	1,3,5,6
101002	<i>Sagartiogeton undatus</i>	sub	1,5,6
Cnidaria/Hydrozoa			

AphiaID	Scientific name	Habitat	source
117471	<i>Coryne pusilla</i>	sub	1
117491	<i>Sarsia tubulosa</i>	sub	1,6
117644	<i>Hydractinia echinata</i>	sub	1,6
151761	<i>Hydractinia borealis</i>	sub	6
117258	<i>Tubularia</i>	both	4,6
157933	<i>Ectopleura larynx</i>	sub	1,6
117368	<i>Clytia hemisphaerica</i>	sub	6
117382	<i>Laomedea flexuosa</i>	int	4
117034	<i>Obelia</i>	both	1,4,6
117386	<i>Obelia dichotoma</i>	sub	1
117388	<i>Obelia geniculata</i>	sub	1
117389	<i>Obelia longissima</i>	sub	1,6
117890	<i>Hydrallmania falcata</i>	sub	1
117913	<i>Sertularia cupressina</i>	sub	1
Echinodermata/Asteroidea			
123776	<i>Asterias rubens</i>	both	2,3,5,6
Echinodermata/Echinoidea			
124319	<i>Psammechinus miliaris</i>	sub	5,6
Echinodermata/Ophiuroidea			
124929	<i>Ophiura ophiura</i>	sub	6
Echiura/Echiuroidea			
110377	<i>Echiurus echiurus</i>	int	3
Entoprocta/			
111796	<i>Pedicellina</i>	sub	6
Mollusca/Bivalvia			
138333	<i>Ensis</i>	int	2
140430	<i>Mya arenaria</i>	int	2,3
140480	<i>Mytilus edulis</i>	int	2,3
140656	<i>Crassostrea gigas</i>	both	1,2
138998	<i>Cerastoderma edule</i>	int	2,3,4
345281	<i>Kurtiella bidentata</i>	int	2
141424	<i>Scrobicularia plana</i>	int	4
235	Tellinidae	int	2
146492	<i>Angulus tenuis</i>	int	2
141579	<i>Macoma balthica</i>	int	2,3,4
156961	<i>Petricolaria pholadiformis</i>	int	2
181364	<i>Venerupis corrugata</i>	int	4
Mollusca/Gastropoda			
137616	<i>Acmaea</i>	int	2
140685	<i>Patella vulgata</i>	int	2
138963	<i>Crepidula fornicata</i>	both	1,2,5,6
151628	<i>Peringia ulvae</i>	int	2,3
140261	<i>Littorina fabalis</i>	int	2
140262	<i>Littorina littorea</i>	both	2,3,4,5
140263	<i>Littorina obtusata</i>	int	2,3

AphiaID	Scientific name	Habitat	source
140264	<i>Littorina saxatilis</i>	int	2
138878	<i>Buccinum undatum</i>	sub	5
138709	<i>Aeolidia papillosa</i>	sub	5,6
139765	<i>Eubranchus exiguus</i>	sub	6
140629	<i>Adalaria proxima</i>	sub	6
150457	<i>Onchidoris bilamellata</i>	sub	5
141641	<i>Tergipes tergipes</i>	sub	6
Mollusca/Polyplacophora			
138089	<i>Lepidochitona</i>	int	2
140143	<i>Lepidochitona (Lepidochitona) cinerea</i>	both	1,4,5
Nemertea/			
152391	Nemertea	int	2
Nemertea/Anopla			
122536	<i>Lineus ruber</i>	int	4
122543	<i>Lineus viridis</i>	int	3
Nemertea/Enopla			
122666	<i>Amphiporus lactifloreus</i>	int	3
122389	<i>Malacobdella</i>	int	4
122419	<i>Tetrastemma</i>	int	4
Nemertea/Palaeonemertea			
122596	<i>Cephalothrix linearis</i>	int	3
Porifera/Calcarea			
132216	<i>Leucosolenia botryoides</i>	sub	1
Porifera/Demospongiae			
165853	<i>Halichondria (Halichondria) panicea</i>	both	1,3

References

- Buschbaum, C. 2002. Siedlungsmuster und Wechselbeziehungen von Seepocken (Cirripedia) auf Muschelbänke (*Mytilus edulis* L.) im Wattenmeer. Berichte zur Polarforschung 408:1-143.
- Büttger, H., H. Asmus, R. Asmus, C. Buschbaum, S. Dittmann, and G. Nehls. 2008. Community dynamics of intertidal soft-bottom mussel beds over two decades. Helgoland Marine Research 62:23-36.
- Dittmann, S. 1990. Mussel beds - amensalism or amelioration for intertidal fauna? Helgolander Meeresuntersuchungen 44:335-352.
- Markert, A., A. Wehrmann, and I. Kröncke. 2010. Recently established *Crassostrea*-reefs versus native *Mytilus*-beds: differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German Bight). Biological Invasions 12:15-32.
- Saier, B. 2002. Subtidal and intertidal mussel beds (*Mytilus edulis* L.) in the Wadden Sea: diversity differences of associated epifauna. Helgoland Marine Research 56:44-50.

Westphalen, A. 2006. Assoziierte Lebensgemeinschaften von natürlichen Muschelbänken und Muschelkulturflächen im Wattenmeer. Institut für Zoologie, Anthropologie und Entwicklungsbiologie an der Biologischen Fakultät der Georg-August-Universität, Göttingen.

Appendix 2

Species associated with mussels (*Mytilus edulis*), complete list, Table 3 extended

specode	occ	comm	Ochiai	C.score	sign	AphialID	species	Phylum	Class	inv.	substrate	feeding
Alisuc	189	152	0.817	0.033	+++	234850	<i>Alitta succinea</i>	Annelida	Polychaeta	no	hetrog.	depos
Carmae*	143	126	0.779	0.037	+++	107381	<i>Carcinus maenas</i>	Arthropoda	Malacostraca	no	soft	carni
Conret	237	156	0.749	0.05	+++	111351	<i>Conopeum reticulum</i>	Bryozoa	Gymnolaemata	no	hard, s	suspe
Alcmyt	127	114	0.748	0.039	+++	468026	<i>Alcyonidiooides mytili</i>	Bryozoa	Gymnolaemata	no	hard, s	suspe
Balcre*	154	124	0.739	0.063	+++	106215	<i>Balanus crenatus</i>	Arthropoda	Maxillopoda	no	hard, s	suspe
Metsen*	171	130	0.735	0.069	+++	100982	<i>Metridium senile</i>	Cnidaria	Anthozoa	no	hard, s	suspe
Oligoc	289	149	0.648	0.09	+++	2036	Oligochaeta	Annelida	Clitellata	no	soft	depos
Polcor	152	108	0.648	0.119	+++	131143	<i>Polydora cornuta</i>	Annelida	Polychaeta	no	hetrog.	suspe
Crefor	104	88	0.638	0.08	+++	138963	<i>Crepidula fornicate</i>	Mollusca	Gastropoda	yes	hard, s	suspe
Harimp	74	73	0.627	0.008	+++	130770	<i>Harmothoe impar</i>	Annelida	Polychaeta	no	hard, m	carni
Alivir*	148	100	0.608	0.147	+++	234851	<i>Alitta virens</i>	Annelida	Polychaeta	yes	soft	omni
Strben	152	101	0.606	0.15	+++	131191	<i>Streblospio benedicti</i>	Annelida	Polychaeta	yes	soft	depos
Astrub*	62	61	0.573	0.011	+++	123776	<i>Asterias rubens</i>	Echinodermata	Asteroidea	no	hard, m	carni
Harimb	45	45	0.496	0	+++	130769	<i>Harmothoe imbricata</i>	Annelida	Polychaeta	no	hard, m	carni
Lancon	117	72	0.492	0.233	+++	131495	<i>Lanice conchilega</i>	Annelida	Polychaeta	no	soft	suspe
Sagtro*	70	55	0.486	0.15	+++	100994	<i>Sagartia troglodytes</i>	Cnidaria	Anthozoa	no	hetrog.	carni
Obelon	38	33	0.396	0.108	+++	117389	<i>Obelia longissima</i>	Cnidaria	Hydrozoa	no	hard, s	suspe
Molsoc	30	29	0.391	0.028	+++	103804	<i>Molgula socialis</i>	Chordata	Asciidae	yes	hard, s	suspe
Cragig	43	34	0.383	0.17	+++	140656	<i>Crassostrea gigas</i>	Mollusca	Bivalvia	yes	hard, s	suspe
Eumsan	36	31	0.382	0.115	+++	130644	<i>Eumida sanguinea</i>	Annelida	Polychaeta	no	soft	carni
Hemtak	25	25	0.37	0	+++	389288	<i>Hemigrapsus takanoi</i>	Arthropoda	Malacostraca	yes	hard, m	carni
Melpal	32	28	0.366	0.106	+++	102843	<i>Melita palmata</i>	Arthropoda	Malacostraca	no	hard, m	depos
Polcil	39	30	0.355	0.193	+++	131141	<i>Polydora ciliata</i>	Annelida	Polychaeta	no	hard, s	depos
Myspic	26	23	0.333	0.101	+++	147026	<i>Mysta picta</i>	Annelida	Polychaeta	no	soft	carni
Monach	19	18	0.305	0.047	+++	225814	<i>Monocorophium acherusicum</i>	Arthropoda	Malacostraca	no	hard, m	depos
Eulvir	17	17	0.305	0	+++	130639	<i>Eulalia viridis</i>	Annelida	Polychaeta	no	hard, m	carni
Clyhem	62	41	0.385	0.263	++	117368	<i>Clytia hemisphaerica</i>	Cnidaria	Hydrozoa	no	hard, s	suspe
Phymuc	21	17	0.274	0.173	++	334512	<i>Phyllodoce mucosa</i>	Annelida	Polychaeta	no	soft	carni
Petpho	17	15	0.269	0.108	++	156961	<i>Petricolaria pholadiformis</i>	Mollusca	Bivalvia	yes	hetrog.	suspe
Phomin	15	14	0.267	0.062	++	130603	<i>Pholoe minuta</i>	Annelida	Polychaeta	no	hard, m	carni
Pedcer	8	8	0.209	0	++	111806	<i>Pedicellina cernua</i>	Entoprocta	NA	no	hard, s	suspe
Pinpis	8	8	0.209	0	++	107473	<i>Pinnotheres pisum</i>	Arthropoda	Malacostraca	no	undef.	paras

specode	occ	comm	Ochiai	C.score	sign	AphialD	species	Phylum	Class	inv.	substrate	feeding
Lepsqu	7	7	0.196	0	++	130801	<i>Lepidonotus squamatus</i>	Annelida	Polychaeta	no	hard, m	carni
Mytori	7	7	0.196	0	++	128901	<i>Mytilicola orientalis</i>	Arthropoda	Maxillopoda	yes	undef.	paras
Stycla	7	7	0.196	0	++	103929	<i>Styela clava</i>	Chordata	Asciidae	yes	hard, s	suspe
Bodsc0	18	14	0.244	0.205	+	110445	<i>Bodotria scorpioides</i>	Arthropoda	Malacostraca	no	soft	depos
Perulv	12	10	0.213	0.158	+	151628	<i>Peringia ulvae</i>	Mollusca	Gastropoda	no	soft	depos
Sthboa	10	9	0.21	0.095	+	131074	<i>Sthenelais boa</i>	Annelida	Polychaeta	no	hard, m	omni
Caplin	6	6	0.181	0	+	101839	<i>Caprella linearis</i>	Arthropoda	Malacostraca	no	hard, m	omni
Heddiv	9	1	0.025	0.884	-	152302	<i>Hediste diversicolor</i>	Annelida	Polychaeta	no	soft	omni
Macbal*	81	30	0.246	0.526	--	141579	<i>Macoma balthica</i>	Mollusca	Bivalvia	no	soft	depos
Nepcae	68	24	0.215	0.562	--	130355	<i>Nephtys caeca</i>	Annelida	Polychaeta	no	soft	carni
Angfab	17	3	0.054	0.81	--	152829	<i>Angulus fabula</i>	Mollusca	Bivalvia	no	soft	depos
Ensdir	163	58	0.336	0.44	--	140732	<i>Ensis directus</i>	Mollusca	Bivalvia	yes	soft	suspe
Myaare*	137	50	0.316	0.462	--	140430	<i>Mya arenaria</i>	Mollusca	Bivalvia	yes	soft	suspe
Scoarm	302	71	0.302	0.468	--	334772	<i>Scoloplos armiger</i>	Annelida	Polychaeta	no	soft	depos
Marvir	184	55	0.3	0.49	--	131135	<i>Marenzelleria viridis</i>	Annelida	Polychaeta	yes	soft	depos
Pygele	202	55	0.286	0.509	--	131170	<i>Pygospio elegans</i>	Annelida	Polychaeta	no	soft	depos
Nephom*	168	38	0.217	0.613	--	130359	<i>Nephtys hombergii</i>	Annelida	Polychaeta	no	soft	carni
Cracra	69	20	0.178	0.633	--	107552	<i>Crangon crangon</i>	Arthropoda	Malacostraca	no	soft	carni
Etelon	112	24	0.168	0.683	--	130616	<i>Eteone longa</i>	Annelida	Polychaeta	no	soft	carni
Spibom	58	13	0.126	0.721	--	131187	<i>Spiophanes bombyx</i>	Annelida	Polychaeta	no	soft	depos
Spimar*	255	23	0.106	0.795	--	131185	<i>Spio martinensis</i>	Annelida	Polychaeta	no	soft	depos
Neplon	23	4	0.062	0.808	--	130364	<i>Nephtys longosetosa</i>	Annelida	Polychaeta	no	soft	carni
Arimin	70	6	0.053	0.884	--	130564	<i>Aricidea minuta</i>	Annelida	Polychaeta	no	soft	depos
Uropos	26	2	0.029	0.913	--	103235	<i>Urothoe poseidonis</i>	Arthropoda	Malacostraca	no	soft	depos
Nepcir	94	3	0.023	0.952	--	130357	<i>Nephtys cirrosa</i>	Annelida	Polychaeta	no	soft	carni
Batsar	42	2	0.023	0.942	--	103073	<i>Bathyporeia sarsi</i>	Arthropoda	Malacostraca	no	soft	depos
Magjoh	43	2	0.023	0.943	--	130269	<i>Magelona johnstoni</i>	Annelida	Polychaeta	no	soft	depos
Angten	51	2	0.021	0.95	--	146492	<i>Angulus tenuis</i>	Mollusca	Bivalvia	no	soft	depos
Glyuni	14	0	0	1	--	130131	<i>Glycera unicornis</i>	Annelida	Polychaeta	no	soft	carni
Retobt	12	0	0	1	--	141134	<i>Retusa obtusa</i>	Mollusca	Gastropoda	no	soft	carni
Aphmar	368	156	0.601	0.085		129938	<i>Aphelochaeta marioni</i>	Annelida	Polychaeta	yes	soft	depos
Capcap	351	145	0.572	0.122		129876	<i>Capitella capitata</i>	Annelida	Polychaeta	no	soft	depos

specode	occs	comm	Ochiai	C.score	sign	AphialD	species	Phylum	Class	inv.	substrate	feeding
Hetfil	232	109	0.529	0.214		129884	<i>Heteromastus filiformis</i>	Annelida	Polychaeta	no	soft	depos
Elmodim	65	37	0.339	0.344		106209	<i>Elminius modestus</i>	Arthropoda	Maxillopoda	yes	hard, s	suspe
Myrpro	49	28	0.296	0.363		238200	<i>Myrianida prolifera</i>	Annelida	Polychaeta	no	hard, m	carni
Eunlon	37	24	0.292	0.305		130375	<i>Eunereis longissima</i>	Annelida	Polychaeta	no	soft	omni
Gamloc	34	22	0.279	0.311		102281	<i>Gammarus locusta</i>	Arthropoda	Malacostraca	no	hard, m	depos
Maldar	31	21	0.279	0.286		130812	<i>Malmgreniella darbouxi</i>	Annelida	Polychaeta	no	soft	carni
Ophoph	35	19	0.237	0.41		124929	<i>Ophiura ophiura</i>	Echinodermata	Ophiuroidea	no	soft	carni
Ceredu	29	16	0.22	0.409		138998	<i>Cerastoderma edule</i>	Mollusca	Bivalvia	no	soft	suspe
Abraalb	15	11	0.21	0.251		141433	<i>Abra alba</i>	Mollusca	Bivalvia	no	soft	depos
Hargel	11	9	0.201	0.173		117378	<i>Hartlaubella gelatinosa</i>	Cnidaria	Hydrozoa	no	hard, s	suspe
Gyalb	46	17	0.185	0.572		130116	<i>Glycera alba</i>	Annelida	Polychaeta	no	soft	carni
Elepil	9	7	0.172	0.214		111355	<i>Electra pilosa</i>	Bryozoa	Gymnolaemata	no	hard, s	suspe
Obedic	5	5	0.165	0		117386	<i>Obelia dichotoma</i>	Cnidaria	Hydrozoa	no	hard, s	suspe
Kurbid	10	7	0.164	0.289		345281	<i>Kurtiella bidentata</i>	Mollusca	Bivalvia	no	soft	suspe
Micscz	10	7	0.164	0.289		130174	<i>Microphthalmus sczelkowii</i>	Annelida	Polychaeta	no	soft	depos
Micmac	8	6	0.157	0.242		102380	<i>Microprotopus maculatus</i>	Arthropoda	Malacostraca	no	hard, m	omni
Lagkor	6	5	0.151	0.162		152367	<i>Lagis koreni</i>	Annelida	Polychaeta	no	soft	depos
Vencor	6	5	0.151	0.162		181364	<i>Venerupis corrugata</i>	Mollusca	Bivalvia	no	hetrog.	suspe
Campsp	4	4	0.148	0		117029	<i>Campanularia</i>	Cnidaria	Hydrozoa	no	hard, s	suspe
Farrep	4	4	0.148	0		111652	<i>Farrella repens</i>	Bryozoa	Gymnolaemata	no	hard, s	suspe
Mytint	4	4	0.148	0		128900	<i>Mytilicola intestinalis</i>	Arthropoda	Maxillopoda	yes	undef.	paras
Pislone	4	4	0.148	0		107188	<i>Pisidia longicornis</i>	Arthropoda	Malacostraca	no	hard, m	omni
Monins	15	7	0.134	0.513		148592	<i>Monocorophium insidiosum</i>	Arthropoda	Malacostraca	no	hard, m	depos
Ablobt	3	3	0.128	0		102788	<i>Abludomelita obtusata</i>	Arthropoda	Malacostraca	no	hard, m	depos
Aeopap	3	3	0.128	0		138709	<i>Aeolidia papillosa</i>	Mollusca	Gastropoda	no	hard, m	carni
Ampsqua	3	3	0.128	0		125064	<i>Amphipholis squamata</i>	Echinodermata	Ophiuroidea	no	hard, m	suspe
Aremar	12	6	0.128	0.484		129868	<i>Arenicola marina</i>	Annelida	Polychaeta	no	soft	depos
Canpag	2	2	0.105	0		107276	<i>Cancer pagurus</i>	Arthropoda	Malacostraca	no	hard, m	omni
Didvex	2	2	0.105	0		250126	<i>Didemnum vexillum</i>	Chordata	Ascidiae	yes	hard, s	suspe
Ophfra	2	2	0.105	0		125131	<i>Ophiothrix fragilis</i>	Echinodermata	Ophiuroidea	no	hard, m	suspe
Phymac	2	2	0.105	0		334510	<i>Phyllodoce maculata</i>	Annelida	Polychaeta	no	soft	carni
Aonoxy	1	1	0.074	0		131106	<i>Aonides oxycephala</i>	Annelida	Polychaeta	no	soft	depos

specode	occ	comm	Ochiai	C.score	sign	AphialID	species	Phylum	Class	inv.	substrate	feeding
Eteosp	1	1	0.074	0		129443	<i>Eteone</i> sp	Annelida	Polychaeta	no	undef.	carni
Euacra	1	1	0.074	0		156083	<i>Eualus cranchii</i>	Arthropoda	Malacostraca	no	hard, m	omni
Hydech	1	1	0.074	0		117644	<i>Hydractinia echinata</i>	Cnidaria	Hydrozoa	no	hard, s	suspe
Macstu	1	1	0.074	0		140299	<i>Mactra stultorum</i>	Mollusca	Bivalvia	no	soft	suspe
Palele	1	1	0.074	0		107614	<i>Palaemon elegans</i>	Arthropoda	Malacostraca	no	hard, m	omni
Phorei	1	1	0.074	0		102387	<i>Photis reinhardi</i>	Arthropoda	Malacostraca	no	hard, m	depos
Prohal	1	1	0.074	0		131367	<i>Procerastea halleziana</i>	Annelida	Polychaeta	no	hard, m	carni
Psamil	1	1	0.074	0		124319	<i>Psammechinus miliaris</i>	Echinodermata	Echinoidea	no	hard, m	carni
Sabspi	1	1	0.074	0		130867	<i>Sabellaria spinulosa</i>	Annelida	Polychaeta	yes	hard, s	suspe
Chesun	2	1	0.052	0.497		102798	<i>Cheirocratus sundevallii</i>	Arthropoda	Malacostraca	no	hard, m	depos
Lepcin	2	1	0.052	0.497		140143	<i>Lepidochitona cinerea</i>	Mollusca	Polyplacophora	no	hard, m	depos
Trafor	2	1	0.052	0.497		130512	<i>Travisia forbesii</i>	Annelida	Polychaeta	no	soft	depos
Nemert	9	2	0.049	0.769		152391	<i>Nemertea</i>	Nemertea	NA	no	undef.	carni
Echcor	5	1	0.033	0.796		124392	<i>Echinocardium cordatum</i>	Echinodermata	Echinoidea	no	soft	depos
Pagber	5	1	0.033	0.796		107232	<i>Pagurus bernhardus</i>	Arthropoda	Malacostraca	no	soft	carni
Spisub	5	1	0.033	0.796		140302	<i>Spisula subtruncata</i>	Mollusca	Bivalvia	no	soft	suspe
Barcan	3	0	0	1		140767	<i>Barnea candida</i>	Mollusca	Bivalvia	no	hetrog.	depos
Batele	1	0	0	1		103058	<i>Bathyporeia elegans</i>	Arthropoda	Malacostraca	no	soft	depos
Bylsar	1	0	0	1		130735	<i>Bylgides sarsi</i>	Annelida	Polychaeta	no	soft	carni
Corare	2	0	0	1		102087	<i>Corophium arenarium</i>	Arthropoda	Malacostraca	no	soft	depos
Corvol	2	0	0	1		102101	<i>Corophium volutator</i>	Arthropoda	Malacostraca	no	soft	depos
Donvit	1	0	0	1		139604	<i>Donax vittatus</i>	Mollusca	Bivalvia	no	soft	suspe
Parful	1	0	0	1		146932	<i>Paraonis fulgens</i>	Annelida	Polychaeta	no	soft	depos
Psepul	1	0	0	1		131169	<i>Pseudopolydora pulchra</i>	Annelida	Polychaeta	no	soft	depos
Scofol	1	0	0	1		334741	<i>Scolelepis foliosa</i>	Annelida	Polychaeta	no	soft	depos
Smipro	1	0	0	1		396735	<i>Smittoidea prolifica</i>	Bryozoa	Gymnolaemata	yes	hard, s	suspe
Telfer	3	0	0	1		146952	<i>Tellimya ferruginosa</i>	Mollusca	Bivalvia	no	soft	suspe

Appendix 3

Species associated with oysters (*Crassostrea gigas*), complete list, Table 4 extended

Appendix 3

Species associated with *Crassostrea gigas*, based on a dataset of 568 box core stations in the subtidal western Dutch Wadden SeaThe dataset contained 43 stations with *C. gigas*.

spnum	species	occ	comm	Ochiai	C.score	sign	sig.lev	AphiaID	Phylum	Class	Genus	Species	invasive	feeding	substrate
135	Crefor	104	35	0.52338	0.123435	+	***	138963	Mollusca	Gastropod:Crepidula	fornicata	yes	suspension	4	
81	Balcre	154	40	0.491547	0.051646	+	***	106215	Arthropod:Maxillipod	Balanus	crenatus	no	suspension	4	
68	Elmmod	65	24	0.453963	0.278712	+	***	106209	Arthropod:Maxillipod	Elminius	modestus	yes	suspension	4	
12	Alisuc	189	40	0.443706	0.055002	+	***	234850	Annelida	Polychaeta Alitta	succinea	no	deposit	2	
24	Polcor	152	35	0.432924	0.143207	+	***	131143	Annelida	Polychaeta Polydora	cornuta	no	suspension	2	
101	Metsen	171	37	0.431489	0.109343	+	***	100982	Cnidaria	Anthozoa Metridium	senile	no	suspension	4	
147	Polcil	39	17	0.415128	0.341085	+	***	131141	Annelida	Polychaeta Polydora	ciliata	no	deposit	4	
130	Strben	152	33	0.408186	0.182069	+	***	131191	Annelida	Polychaeta Streblospicus	benedicti	yes	deposit	1	
105	Conret	237	40	0.396234	0.057992	+	***	111351	Bryozoa	Gymnolaera Conopeum	reticulum	no	suspension	4	
50	Mytedu	183	34	0.383283	0.170416	+	***	140480	Mollusca	Bivalvia Mytilus	edulis	no	suspension	4	
80	Carmae	143	30	0.382577	0.238901	+	***	107381	Arthropod:Malacostraca	Carcinus	maenas	no	carnivore	1	
133	Clyhem	62	19	0.367979	0.387097	+	***	117368	Cnidaria	Hydrozoa Clytia	hemisphaera	no	suspension	4	
19	Myspic	26	12	0.358889	0.388193	+	***	147026	Annelida	Polychaeta Mycta	picta	no	carnivore	1	
104	Alcmyt	127	26	0.351834	0.314411	+	**	468026	Bryozoa	Gymnolaera Alcyonidio	mytili	no	suspension	4	
168	Stycla	7	6	0.345834	0.122924	+	***	103929	Chordata	Ascidiae Styela	clava	yes	suspension	4	
3	Harimp	74	17	0.301369	0.465745	+	**	130770	Annelida	Polychaeta Harmothoe	impar	no	carnivore	3	
106	Molsoc	30	10	0.278423	0.511628	+	**	103804	Chordata	Ascidiae Molgula	socialis	yes	suspension	4	
95	Hemtak	25	9	0.274497	0.506047	+	**	389288	Arthropod:Malacostraca	Hemigrapsus	takanoui	yes	carnivore	3	
34	Lepsqu	7	4	0.230556	0.388704	+	**	130801	Annelida	Polychaeta Lepidonotus	squamatus	no	carnivore	3	
144	Eulvir	17	6	0.221918	0.556772	+	*	130639	Annelida	Polychaeta Eulalia	viridis	no	carnivore	3	
44	Phymac	2	2	0.215666	0	+	*	334510	Annelida	Polychaeta Phyllodoce	maculata	no	carnivore	1	
108	Elepl	9	4	0.203331	0.503876	+	*	111355	Bryozoa	Gymnolaera Electra	pilosa	no	suspension	4	
20	Scoarm	302	23	0.201832	0.429694	-	***	334772	Annelida	Polychaeta Scoloplos	armiger	no	deposit	1	
29	Marvir	184	15	0.168635	0.598079	-	**	131135	Annelida	Polychaeta Marenzelle	viridis	yes	deposit	1	
62	Ensdir	163	14	0.167225	0.616493	-	*	140732	Mollusca	Bivalvia Ensis	directus	yes	suspension	1	
16	Nephom	168	12	0.141186	0.669435	-	**	130359	Annelida	Polychaeta Nephtys	hombergii	no	carnivore	1	
26	Pygele	202	13	0.139487	0.652775	-	***	131170	Annelida	Polychaeta Pygospio	elegans	no	deposit	1	
63	Myaare	137	8	0.104231	0.766423	-	***	140430	Mollusca	Bivalvia Mya	arenaria	yes	suspension	1	
7	Etelon	112	7	0.100868	0.784884	-	**	130616	Annelida	Polychaeta Eteone	longa	no	carnivore	1	
23	Spimar	255	8	0.076399	0.788418	-	***	131185	Annelida	Polychaeta Spio	martensi	no	deposit	1	
17	Nepcae	68	4	0.073973	0.853625	-	*	130355	Annelida	Polychaeta Nephtys	caeca	no	carnivore	1	
21	Arimin	70	2	0.036454	0.926246	-	***	130564	Annelida	Polychaeta Aricidea	minuta	no	deposit	1	
59	Macbal	81	2	0.033889	0.929945	-	***	141579	Mollusca	Bivalvia Macoma	balthica	no	deposit	1	
141	Nepcir	94	2	0.031458	0.932201	-	***	130357	Annelida	Polychaeta Nephtys	cirrosa	no	carnivore	1	
71	Batsar	42	1	0.023531	0.953488	-	*	103073	Arthropod:Malacostraca	Bathyporei	sarsi	no	deposit	1	
33	Magjoh	43	0	0	0	1	-	130269	Annelida	Polychaeta Magelona	johnstoni	no	deposit	1	
60	Angten	51	0	0	0	1	-	146492	Mollusca	Bivalvia Angulus	tenuis	no	deposit	1	
120	Oligoc	289	37	0.331909	0.121671			2036	Annelida	Clitellata NA	NA	no	deposit	1	
35	Aphmar	368	38	0.302082	0.104272			129938	Annelida	Polychaeta Aphelochaetes	marioni	yes	deposit	1	
37	Hetfil	232	29	0.290349	0.284884			129884	Annelida	Polychaeta Heteromasis	filiformis	no	deposit	1	
36	Capcap	351	35	0.284892	0.167495			129876	Annelida	Polychaeta Capitella	capitata	no	deposit	1	
103	Sagtro	70	14	0.255179	0.539535			100994	Cnidaria	Anthozoa Sagartia	troglodytes	no	carnivore	2	
13	Alivir	148	19	0.238171	0.486486			234851	Annelida	Polychaeta Alitta	virens	yes	omnivore	1	
125	Astrub	62	12	0.232408	0.581395			123776	Echinoderr	Asteroidea Asterias	rubens	no	carnivore	3	
2	Harimb	45	10	0.227331	0.596899			130769	Annelida	Polychaeta Harmothoe	imbricata	no	carnivore	3	
107	Obelon	38	9	0.222647	0.603427			117389	Cnidaria	Hydrozoa Obelia	longissima	no	suspension	4	
42	Lancon	117	15	0.211477	0.56768			131495	Annelida	Polychaeta Lanice	conchilega	no	suspension	1	
32	Glyalb	46	9	0.202362	0.635996			130116	Annelida	Polychaeta Glycera	alba	no	carnivore	1	
139	Vencor	6	3	0.186772	0.465116			181364	Mollusca	Bivalvia Venerupis	corrugata	no	suspension	2	
187	Mytori	7	3	0.172917	0.531561			128901	Arthropod:Maxillipod	Mytilicolana	orientalis	yes	parasite	0	
57	Abralb	15	4	0.1575	0.665116			141433	Mollusca	Bivalvia Abra	alba	no	deposit	1	
9	Eumsan	36	6	0.152499	0.717054			130644	Annelida	Polychaeta Eumida	sanguinea	no	carnivore	1	
30	Myrpro	49	7	0.152499	0.717608			238200	Annelida	Polychaeta Myrianda	prolifera	no	carnivore	3	
207	Prohal	1	1	0.152499	0			131367	Annelida	Polychaeta Proceraste	halieziana	no	carnivore	3	
118	Sabspi	1	1	0.152499	0			130867	Annelida	Polychaeta Sabellaria	spinulosa	yes	suspension	4	
152	Smipro	1	1	0.152499	0			396735	Bryozoa	Gymnolaera Smittoidea	prolifica	yes	suspension	4	
22	Micscz	10	3	0.144673	0.651163			130174	Annelida	Polychaeta Microphthys	sczelkowii	no	deposit	1	
52	Ceredu	29	5	0.141591	0.731355			138998	Mollusca	Bivalvia Cerastoderma	edule	no	suspension	1	
205	Obedic	5	2	0.136399	0.572093			117386	Cnidaria	Hydrozoa Obelia	dichotoma	no	suspension	4	
76	Pagber	5	2	0.136399	0.572093			107232	Arthropod:Malacostraca	Pagurus	bernhardi	no	carnivore	1	
10	Phymuc	21	4	0.133112	0.734219			334512	Annelida	Polychaeta Phyllodoce	mucosa	no	carnivore	1	
70	Gamloc	34	5	0.130766	0.753762			102281	Arthropod:Malacostraca	Gammastrus	locusta	no	deposit	3	
78	Caplin	6	2	0.124515	0.636569			101839	Arthropod:Malacostraca	Caprella	linearis	no	omnivore	3	
6	Phomin	15	3	0.118125	0.744186			130603	Annelida	Polychaeta Pholoe	minuta	no	carnivore	3	
4	Maldar	31	4	0.109558	0.789947			130812	Annelida	Polychaeta Malmgrenia	darbouxi	no	carnivore	1	
155	Chesun	2	1	0.107833	0.488372			102798	Arthropod:Malacostraca	Cheirocrates	sundevallii	no	deposit	3	
153	Didvex	2	1	0.107833	0.488372			250126	Chordata	Ascidiae Dideumnum	vexillum	yes	suspension	4	
122	Micmac	8	2	0.107833	0.715116			102380	Arthropod:Malacostraca	Microprotoc	maculatus	no	omnivore	3	
14	Eunlon	37	4	0.100282	0.808925			130375	Annelida	Polychaeta Eunereis	longissima	no	omnivore	1	
138	Hargel	11	2	0.09196	0.780127			117378	Cnidaria	Hydrozoa Hartlaubellia	gelatinosa	no	suspension	4	
79	Cracra	69	5	0.091793	0.819683			107552	Arthropod:Malacostraca	Crangon	crangon	no	carnivore	1	
113	Telfer	3	1	0.088045	0.651163			146952	Mollusca	Bivalvia Tellimya	ferruginea	no	suspension	1	
69	Melpal	32	3	0.080875	0.843023			102843	Arthropod:Malacostraca	Melita	palmata	no	deposit	3	
126	Ophoph	35	3	0.077331	0.850498			124929	Echinoderr	Ophiuroidea	ophiura	no	carnivore	1	
160	Campsp	4	1	0.076249	0.732558			117029	Cnidaria	Hydrozoa Campanula	NA	no	suspension	4	
109	Farrep	4	1	0.076249	0.732558			111652	Bryozoa	Gymnolaera Farrella	repens	no	suspension	4	
166	Mytint	4	1	0.076249	0.732558			128900	Arthropod:Maxillipod	Mytilicolana	intestinalis	yes	parasite	0	
121	Pislion	4	1	0.076249	0.732558			107188	Arthropod:Malacostraca	Pisidia	longicornis	no	omnivore	3	

spnum	species	occ	comm	Ochiai	C.score	sign	sig.lev	AphiaID	Phylum	Class	Genus	Species	invasive	feeding	substrate
53	Petpho	17		2	0.073973	0.841313		156961	Mollusca	Bivalvia	Petricolaria	pholadifor	yes	suspension	2
91	Bodso	18		2	0.071889	0.847545		110445	Arthropod:	Malacostra	Bodotria	scorpioides	no	deposit	1
96	Monach	19		2	0.069971	0.853121		225814	Arthropod:	Malacostra	Monocorona	acherusicu	no	deposit	3
18	Neplon	23		2	0.063596	0.870576		130364	Annelida	Polychaeta	Nephthys	longosetos	no	carnivore	1
27	Spibom	58		3	0.060072	0.882117		131187	Annelida	Polychaeta	Spiophane	bombyx	no	deposit	1
117	Pedcer	8		1	0.053916	0.854651		111806	Entoprocta	NA	Pedicellina	cernua	no	suspension	4
180	Pinpis	8		1	0.053916	0.854651		107473	Arthropod:	Malacostra	Pinnothere	pisum	no	parasite	0
43	Sthboa	10		1	0.048224	0.87907		131074	Annelida	Polychaeta	Sthenelais	boa	no	omnivore	3
39	Aremar	12		1	0.044023	0.895349		129868	Annelida	Polychaeta	Arenicola	marina	no	deposit	1
45	Perulv	12		1	0.044023	0.895349		151628	Mollusca	Gastropod:	Peringia	ulvae	no	deposit	1
31	Glyuni	14		1	0.040757	0.906977		130131	Annelida	Polychaeta	Glycera	unicornis	no	carnivore	1
123	Monins	15		1	0.039375	0.911628		148592	Arthropod:	Malacostra	Monocorona	insidiosum	no	deposit	3
77	Uropos	26		1	0.029907	0.939177		103235	Arthropod:	Malacostra	Urothoe	poseidonis	no	deposit	1
157	Ablobt	3		0	0	1		102788	Arthropod:	Malacostra	Abludomel	obtusata	no	deposit	3
150	Aeopap	3		0	0	1		138709	Mollusca	Gastropod:	Aeolidia	papillosa	no	carnivore	3
204	Ampsqu	3		0	0	1		125064	Echinoderr	Ophiuroidea	Amphipholis	squamata	no	suspension	3
61	Angfab	17		0	0	1		152829	Mollusca	Bivalvia	Angulus	fabula	no	deposit	1
116	Aonoxy	1		0	0	1		131106	Annelida	Polychaeta	Aonides	oxycephala	no	deposit	1
114	Barcan	3		0	0	1		140767	Mollusca	Bivalvia	Barnea	candida	no	deposit	2
112	Batele	1		0	0	1		103058	Arthropod:	Malacostra	Bathyporei	elegans	no	deposit	1
5	Bylsar	1		0	0	1		130735	Annelida	Polychaeta	Bylgides	sarsi	no	carnivore	1
131	Canpag	2		0	0	1		107276	Arthropod:	Malacostra	Cancer	pagurus	no	omnivore	3
74	Corare	2		0	0	1		102087	Arthropod:	Malacostra	Corophium	arenarium	no	deposit	1
73	Corvol	2		0	0	1		102101	Arthropod:	Malacostra	Corophium	volutator	no	deposit	1
55	Donvit	1		0	0	1		139604	Mollusca	Bivalvia	Donax	vittatus	no	suspension	1
128	Echcor	5		0	0	1		124392	Echinoderr	Echinoidea	Echinocardis	cordatum	no	deposit	1
8	Eteosp	1		0	0	1		129443	Annelida	Polychaeta	Eteone	NA	no	carnivore	0
129	Euacra	1		0	0	1		156083	Arthropod:	Malacostra	Eualus	cranchii	no	omnivore	3
11	Heddiv	9		0	0	1		152302	Annelida	Polychaeta	Hediste	diversicolor	no	omnivore	1
115	Hydech	1		0	0	1		117644	Cnidaria	Hydrozoa	Hydractinia	echinata	no	suspension	4
51	Kurbid	10		0	0	1		345281	Mollusca	Bivalvia	Kurtiella	bidentata	no	suspension	1
41	Lagkor	6		0	0	1		152367	Annelida	Polychaeta	Lagis	koreni	no	deposit	1
64	Lepcin	2		0	0	1		140143	Mollusca	Polyplacop	Lepidochitona	cinerea	no	deposit	3
188	Macstu	1		0	0	1		140299	Mollusca	Bivalvia	Mactra	stultorum	no	suspension	1
1	Nemert	9		0	0	1		152391	Nemertea	NA	NA	NA	no	carnivore	0
124	Ophfra	2		0	0	1		125131	Echinoderr	Ophiuroidea	Ophiothrix	fragilis	no	suspension	3
83	Palele	1		0	0	1		107614	Arthropod:	Malacostra	Palaemon	elegans	no	omnivore	3
146	Parful	1		0	0	1		146932	Annelida	Polychaeta	Paraonis	fulgens	no	deposit	1
206	Phorei	1		0	0	1		102387	Arthropod:	Malacostra	Photis	reinhardti	no	deposit	3
127	Psamil	1		0	0	1		124319	Echinoderr	Echinoidea	Psammechis	miliaris	no	carnivore	3
38	Psepul	1		0	0	1		131169	Annelida	Polychaeta	Pseudopoly	pulchra	no	deposit	1
48	Retobt	12		0	0	1		141134	Mollusca	Gastropod:	Retusa	obtusa	no	carnivore	1
28	Scofol	1		0	0	1		334741	Annelida	Polychaeta	Scolelepis	foliosa	no	deposit	1
54	Spisub	5		0	0	1		140302	Mollusca	Bivalvia	Spisula	subtruncata	no	suspension	1
140	Trafor	2		0	0	1		130512	Annelida	Polychaeta	Travisia	forbesii	no	deposit	1

Appendix 4

Species associated with mussels (*Mytilus edulis*), complete list, Table 11 extended

Appendix 4

Species associated with *Mytilus edulis* in the western Dutch Wadden Sea

Samples were collected on natural mussel beds in plots open and closed for fisheries

Number of samples was 1896 occurrences of *M. edulis* 692

species	occ	comm	Ochiai	C.score	sign	sig.lev	Phylum	Class	Order	Family	Genus	Species
2 Nereid	1343	616	1.242559	-1.28084	+	***	Annelida	Polychaeta	Phyllodocidae	Nereididae	Alitta	succinea
65 Polyno	358	312	1.218955	-0.09058	+	***	Annelida	Polychaeta	Phyllodocidae	Polynoidae	Harmothoe	NA
32 Cirrip	545	379	1.200094	-0.32622	+	***	Arthropod:	Maxillopoidea	NA	NA	NA	NA
150 Polydo	917	463	1.13024	-0.75752	+	***	Annelida	Polychaeta	Spionida	Spionidae	Polydora	NA
58 Gammar	314	268	1.118007	-0.06804	+	***	Arthropod:	Malacostraca	Amphipod:	Gammaridae	NA	NA
7 Anthoz	740	394	1.070668	-0.53911	+	***	Cnidaria	Anthozoa	NA	NA	NA	NA
28 Carmae	425	298	1.068553	-0.18779	+	***	Arthropod:	Malacostraca	Decapoda	Portunidae	Carcinus	maenas
79 Lancon	430	256	0.912599	-0.16142	+	***	Annelida	Polychaeta	Terebellida	Terebellidae	Lanice	conchilega
14 Astrub	156	126	0.745732	0.059899	+	***	Echinoderr	Asterioidea	Forcipulatii	Asteriidae	Asterias	rubens
41 Crefor	161	104	0.605891	0.152836	+	***	Mollusca	Gastropod:	Littorinimorpha	Calyptaeic	Crepidula	fornicata
22 Decapo	110	83	0.585	0.134128	+	***	Arthropod:	Malacostraca	Decapoda	NA	NA	NA
54 Eumida	145	94	0.577056	0.171057	+	***	Annelida	Polychaeta	Phyllodocidae	Phyllodocidae	Eumida	NA
92 Meliti	103	72	0.524431	0.182556	+	***	Arthropod:	Malacostraca	Amphipod:	Melitidae	Melita	NA
96 Microp	82	61	0.497963	0.170732	+	***	Arthropod:	Malacostraca	Amphipod:	Microprotoc	Microprotoc	NA
85 Macbal	113	64	0.445057	0.281977	+	*	Mollusca	Bivalvia	Veneroida	Tellinidae	Macoma	balthica
149 Polych	64	43	0.397331	0.251025	+	***	Annelida	Polychaeta	NA	NA	NA	NA
113 Nemato	35	29	0.362358	0.144262	+	***	Nematoda	NA	NA	NA	NA	NA
155 Procer	25	23	0.340042	0.069945	+	***	Annelida	Polychaeta	Phyllodocidae	Syllidae	Proceraea	NA
74 Isopod	23	22	0.339104	0.038251	+	***	Arthropod:	Malacostraca	Isopoda	NA	NA	NA
69 Hemigr	23	21	0.32369	0.076978	+	***	Arthropod:	Malacostraca	Decapoda	Varunidae	Hemigraps	NA
15 Pontop	32	23	0.300557	0.245902	+	**	Arthropod:	Malacostraca	Amphipod:	Pontoporei	Bathyporei	NA
109 Mytili	15	15	0.286299	0	+	***	Arthropod:	Maxillopoidea	Poecilostomatiformes	Mytilicolidae	Mytilicola	NA
52 Eulali	9	8	0.197126	0.106254	+	*	Annelida	Polychaeta	Phyllodocidae	Phyllodocidae	Eulalia	NA
40 Cragig	8	7	0.182948	0.120219	+	*	Mollusca	Bivalvia	Ostreoida	Ostreidae	Crassostrea	gigas
179 Syllid	6	6	0.181071	0	+	*	Annelida	Polychaeta	Phyllodocidae	Syllidae	NA	NA
127 Pycnog	5	5	0.165295	0	+	*	Arthropod:	Pycnogonida	Pantopoda	Nymphoniidae	Nymphon	gracile
183 Cirrat	1439	557	1.085424	-1.25265	-	***	Annelida	Polychaeta	Terebellida	Cirratulida	Tharyx	NA
72 Hetfil	1163	473	1.025288	-0.94019	-	**	Annelida	Polychaeta	NA	Capitellida	Heteromorpha	filiformis
26 Capcap	1066	428	0.969035	-0.80127	-	***	Annelida	Polychaeta	NA	Capitellida	Capitella	capitata
159 Pygele	707	268	0.745074	-0.28841	-	***	Annelida	Polychaeta	Spionida	Spionidae	Pygospio	elegans
48 Ensdir	366	126	0.48686	0.204246	-	***	Mollusca	Bivalvia	Euheterodontida	Pharidae	Ensis	directus
163 Scoarm	591	152	0.462194	0.125831	-	***	Annelida	Polychaeta	NA	Orbiniidae	Scoloplos	armiger
49 Eteone	251	96	0.447929	0.29358	-	**	Annelida	Polychaeta	Phyllodocidae	Phyllodocidae	Eteone	NA
89 Marvir	404	117	0.430298	0.256208	-	***	Annelida	Polychaeta	Spionida	Spionidae	Marenzelleria	NA
95 Microph	183	59	0.322404	0.459136	-	***	Annelida	Polychaeta	Phyllodocidae	Hesionidae	Microphthys	NA
117 Nephty	189	42	0.225836	0.599271	-	***	Annelida	Polychaeta	Phyllodocidae	Nephtyidae	Nephtys	NA
166 Spio	211	43	0.218827	0.609121	-	***	Annelida	Polychaeta	Spionida	Spionidae	Spiophanes	NA
10 Aricid	88	23	0.181243	0.645802	-	***	Annelida	Polychaeta	NA	Paraonidae	Aricidea	NA
132 Ophiur	61	19	0.17983	0.617038	-	**	Echinoderr	Ophiuroidea	Ophiurida	Ophiuridae	Ophiura	NA
37 Crango	32	9	0.117609	0.683402	-	*	Arthropod:	Malacostraca	Decapoda	Crangonidae	Crangon	NA
178 Strweb	15	0	0	1	-	***	Annelida	Polychaeta	Phyllodocidae	Syllidae	Streptosyllis	websteri
128 Oligoc	1499	618	1.179946	-1.39705			Annelida	Clitellata	NA	NA	NA	NA
177 Strben	840	369	0.941155	-0.56991			Annelida	Polychaeta	Spionida	Spionidae	Streblospio	benedicti
102 Myaare	422	197	0.708899	-0.04079			Mollusca	Bivalvia	Myoida	Myidae	Mya	NA
146 Phyllo	217	113	0.567052	0.183325			Annelida	Polychaeta	Phyllodocidae	Phyllodocidae	Phyllodocidae	NA
139 Petpho	155	80	0.475005	0.272343			Mollusca	Bivalvia	Veneroida	Veneridae	Petricolaria	pholadiformis
8 Coroph	134	72	0.459785	0.280646			Arthropod:	Malacostraca	Amphipod:	Corophiidae	Apocorophiidae	lacustre
20 Cumace	132	65	0.418216	0.327289			Arthropod:	Malacostraca	Cumacea	Bodotriidae	NA	NA
13 Ascidi	82	47	0.383677	0.317206			Chordata	Ascidiae	NA	NA	NA	NA
29 Ceredu	105	47	0.339061	0.410513			Mollusca	Bivalvia	Veneroida	Cardiidae	Cerastoderma	edule
73 Perulv	103	41	0.298634	0.46708			Mollusca	Gastropod:	Littorinimorpha	Hydrobiidae	Hydrobia	ulvae
23 Bryozo	49	26	0.274568	0.402699			Bryozoa	NA	NA	NA	NA	NA
104 Myrian	79	33	0.274457	0.477277			Annelida	Polychaeta	Phyllodocidae	Syllidae	Myriida	NA
1 Abralb	24	15	0.226339	0.344262			Mollusca	Bivalvia	Veneroida	Semelidae	Abra	alba
99 Mollus	24	14	0.21125	0.384791			Mollusca	NA	NA	NA	NA	NA
143 Phomin	13	9	0.184521	0.29256			Annelida	Polychaeta	Phyllodocidae	Pholoidae	Pholoe	minuta
77 Kurbid	24	12	0.181071	0.467213			Mollusca	Bivalvia	Veneroida	Montacutidae	Kurtiella	bidentata
78 Pectin	17	10	0.179287	0.389264			Annelida	Polychaeta	Terebellida	Pectinariidae	Lagis	koreni
19 Bivalv	45	15	0.165295	0.612022			Mollusca	Bivalvia	NA	NA	NA	NA
27 Caprel	8	6	0.156813	0.241803			Arthropod:	Malacostraca	Amphipod:	Caprellidae	NA	NA
62 Glycer	38	13	0.155893	0.611159			Annelida	Polychaeta	Phyllodocidae	Glyceridae	Glycera	NA
108 Myspic	13	7	0.143516	0.443884			Annelida	Polychaeta	Phyllodocidae	Phyllodocidae	Mysta	picta
5 Amphip	7	5	0.1397	0.277908			Arthropod:	Malacostraca	Amphipod:	NA	NA	NA
9 Aremar	14	7	0.138296	0.480874			Annelida	Polychaeta	NA	Arenicolidae	Arenicola	marina
174 Sthene	11	6	0.13373	0.439642			Annelida	Polychaeta	Phyllodocidae	Sigalionida	Sthenelais	NA
147 Pimpis	3	3	0.128037	0			Arthropod:	Malacostraca	Decapoda	Pinnotheridae	Pinnotheres	pisum
24 Campan	11	5	0.111442	0.530551			Cnidaria	Hydrozoa	Leptothecidae	Campanulidae	NA	NA

species	occ	comm	Ochiai	C.score	sign	sig.lev	Phylum	Class	Order	Family	Genus	Species
171 Spibom	17	6	0.107572	0.625844			Annelida	Polychaeta	Spionida	Spionidae	Spiophane	: bombyx
4 Amphil	2	2	0.104542	0			Arthropod:	Malacostra	Amphipod:	Amphiloch	Amphiloch	NA
30 Chaeto	2	2	0.104542	0			Chaetogna	NA	NA	NA	NA	NA
47 Dulich	2	2	0.104542	0			Arthropod:	Malacostra	Amphipod:	Dulichiidae	Dulichia	NA
134 Pagber	2	2	0.104542	0			Arthropod:	Malacostra	Decapoda	Paguridae	Pagurus	bernhardus
140 Petric	2	2	0.104542	0			Mollusca	Bivalvia	Veneroida	Veneridae	NA	NA
126 Nudibr	5	3	0.099177	0.393443			Mollusca	Gastropod:	Nudibranc	NA	NA	NA
61 Mysida	10	4	0.093505	0.586885			Arthropod:	Malacostra	Mysida	Mysidae	Gastrosacc	spinifer
182 Angten	6	3	0.090536	0.491803			Mollusca	Bivalvia	Veneroida	Tellinidae	Angulus	tenuis
161 Sagitt	3	2	0.085358	0.32969			Chaetogna	Sagittoidea	Aphragmo	Sagittidae	Sagitta	NA
25 Canpag	1	1	0.073922	0			Arthropod:	Malacostra	Decapoda	Cancridae	Cancer	pagurus
36 Coslong	1	1	0.073922	0			Annelida	Polychaeta	NA	Cossuridae	Cossura	longocirrat
46 Dipcoe	1	1	0.073922	0			Annelida	Polychaeta	Spionida	Spionidae	Dipolydora	coeca
83 Litlit	1	1	0.073922	0			Mollusca	Gastropod:	Littorinidae	Littorina	littorea	
114 Nemert	9	3	0.073922	0.655738			Nemertea	NA	NA	NA	NA	NA
116 Neofig	1	1	0.073922	0			Annelida	Polychaeta	Terebellida	Terebellida	Neoamphit	figulus
125 Notlat	1	1	0.073922	0			Annelida	Polychaeta	NA	Capitellida	Notomast	latericeus
144 Photid	1	1	0.073922	0			Arthropod:	Malacostra	Amphipod:	Photidae	Photis	reinhardi
162 Scobon	1	1	0.073922	0			Annelida	Polychaeta	Spionida	Spionidae	Scolelepis	bonnieri
172 Spiell	1	1	0.073922	0			Mollusca	Bivalvia	Veneroida	Mactridae	Spisula	elliptica
76 Ischyr	2	1	0.052271	0.497268			Arthropod:	Malacostra	Amphipod:	Ischyroceri	Jassa	falcata
80 Lepcin	2	1	0.052271	0.497268			Mollusca	Polyplacop	Chitonida	Lepidochit	Lepidochit	cinerea
148 Pislom	2	1	0.052271	0.497268			Arthropod:	Malacostra	Decapoda	Porcellanid	Pisidia	longicornis
129 Opheli	10	2	0.046752	0.791257			Annelida	Polychaeta	NA	Opheliidae	Ophelia	NA
170 Spioni	10	2	0.046752	0.791257			Annelida	Polychaeta	Spionida	Spionidae	NA	NA
60 Gastro	3	1	0.042679	0.663024			Mollusca	Gastropod:	NA	NA	NA	NA
86 Magelo	12	2	0.042679	0.824226			Annelida	Polychaeta	Spionida	Magelonid	Magelona	NA
142 Phoino	3	1	0.042679	0.663024			Annelida	Polychaeta	Phyllodoc	Pholoidae	Pholoe	inornata
42 Crusta	4	1	0.036961	0.745902			Arthropod:	NA	NA	NA	NA	NA
181 Angfab	2	0	0	1			Mollusca	Bivalvia	Veneroida	Tellinidae	Angulus	fabula
71 Hesaug	2	0	0	1			Annelida	Polychaeta	Phyllodoc	Hesionura	augeneri	
81 Lepsqu	1	0	0	1			Mollusca	Bivalvia	Veneroida	Lasaeidae	Lepton	squamosur
82 Liocar	1	0	0	1			Arthropod:	Malacostra	Decapoda	Polybiidae	Liocarcinus	NA
84 Lutlut	1	0	0	1			Mollusca	Bivalvia	Veneroida	Mactridae	Lutraria	lutraria
87 Malaco	1	0	0	1			Annelida	Polychaeta	Spionida	Spionidae	Malacocer	NA
135 Parful	3	0	0	1			Annelida	Polychaeta	NA	Paraonidae	Paraonis	fulgens
160 Retobt	2	0	0	1			Mollusca	Gastropod:	Cephalaspi	Retusidae	Retusa	obtusa
164 Sigali	1	0	0	1			Annelida	Polychaeta	Phyllodoc	Sigalionida	Sigalion	NA
173 Spisub	1	0	0	1			Mollusca	Bivalvia	Veneroida	Mactridae	Spisula	subtruncat
176 Stomat	1	0	0	1			Arthropod:	Malacostra	Stomatop	NA	NA	NA

Appendix 5

Species list of mussel seed fisheries experiment

namecode	AphiaID	Kingdom	Phylum	Class	Order	Family	benthos	scname
Abralb	141433	Animalia	Mollusca	Bivalvia	Veneroida	Semelidae	1	<i>Abra alba</i>
Nereid	234850	Animalia	Annelida	Polychaeta	Phyllodocida	Nereididae	1	<i>Alitta succinea</i>
Nereid	234851	Animalia	Annelida	Polychaeta	Phyllodocida	Nereididae	1	<i>Alitta virens</i>
Amphil	101450	Animalia	Arthropoda	Malacostraca	Amphipoda	Amphilochidae	1	<i>Amphilochus</i>
Amphip	1135	Animalia	Arthropoda	Malacostraca	Amphipoda	NA	1	<i>Amphipoda</i>
Amphip	123613	Animalia	Echinodermata	Ophiuroidea	Ophiurida	Amphiuridae	1	<i>Amphiura</i>
Anthoz	1292	Animalia	Cnidaria	Anthozoa	NA	NA	1	<i>Anthozoa</i>
Coroph	148594	Animalia	Arthropoda	Malacostraca	Amphipoda	Corophiidae	1	<i>Apocorophium lacustre</i>
Aremar	129868	Animalia	Annelida	Polychaeta	NA	Arenicolidae	1	<i>Arenicola marina</i>
Aricid	129430	Animalia	Annelida	Polychaeta	NA	Paraonidae	1	<i>Aricidea</i>
Aricid	130564	Animalia	Annelida	Polychaeta	NA	Paraonidae	1	<i>Aricidea minuta</i>
Aricid	130572	Animalia	Annelida	Polychaeta	NA	Paraonidae	1	<i>Aricidea suecica</i>
Ascidi	1839	Animalia	Chordata	Asciidiacea	NA	NA	1	<i>Asciidiacea</i>
Astrub	123776	Animalia	Echinodermata	Asteroidea	Forcipulatida	Asteriidae	1	<i>Asterias rubens</i>
Pontop	101742	Animalia	Arthropoda	Malacostraca	Amphipoda	Pontoporeiidae	1	<i>Bathyporeia</i>
Pontop	103058	Animalia	Arthropoda	Malacostraca	Amphipoda	Pontoporeiidae	1	<i>Bathyporeia elegans</i>
Pontop	103066	Animalia	Arthropoda	Malacostraca	Amphipoda	Pontoporeiidae	1	<i>Bathyporeia pelagica</i>
Pontop	103073	Animalia	Arthropoda	Malacostraca	Amphipoda	Pontoporeiidae	1	<i>Bathyporeia sarsi</i>
Bivalv	105	Animalia	Mollusca	Bivalvia	NA	NA	1	<i>Bivalvia</i>
Cumace	110378	Animalia	Arthropoda	Malacostraca	Cumacea	Bodotriidae	1	<i>Bodotriidae</i>
Ascidi	103862	Animalia	Chordata	Asciidiacea	Stolidobranchia	Styelidae	1	<i>Botryllus schlosseri</i>
Decapo	106673	Animalia	Arthropoda	Malacostraca	Decapoda	NA	1	<i>Brachyura</i>
Bryozo	146142	Animalia	Bryozoa	NA	NA	NA	1	<i>Bryozoa</i>
Campan	1607	Animalia	Cnidaria	Hydrozoa	Leptothecata	Campanulinidae	1	<i>Campanulinidae</i>
Canpag	107276	Animalia	Arthropoda	Malacostraca	Decapoda	Cancridae	1	<i>Cancer pagurus</i>
Capcap	129876	Animalia	Annelida	Polychaeta	NA	Capitellidae	1	<i>Capitella capitata</i>
Caprel	101361	Animalia	Arthropoda	Malacostraca	Amphipoda	Caprellidae	1	<i>Caprellidae</i>
Carmae	107381	Animalia	Arthropoda	Malacostraca	Decapoda	Portunidae	1	<i>Carcinus maenas</i>
Ceredu	138998	Animalia	Mollusca	Bivalvia	Veneroida	Cardiidae	1	<i>Cerastoderma edule</i>
Chaeto	2081	Animalia	Chaetognatha	NA	NA	NA	1	<i>Chaetognatha</i>
Coroph	148582	Animalia	Arthropoda	Malacostraca	Amphipoda	Corophiidae	1	<i>Chelicorophium curvispinum</i>
Cirrip	1082	Animalia	Arthropoda	Maxillopoda	NA	NA	1	<i>Cirripedia</i>
Coroph	101489	Animalia	Arthropoda	Malacostraca	Amphipoda	Corophiidae	1	<i>Corophium</i>

namecode	AphiaID	Kingdom	Phylum	Class	Order	Family	benthos	scname
Coroph	102087	Animalia	Arthropoda	Malacostraca	Amphipoda	Corophiidae	1	<i>Corophium arenarium</i>
Coroph	102101	Animalia	Arthropoda	Malacostraca	Amphipoda	Corophiidae	1	<i>Corophium volutator</i>
Coslong	129984	Animalia	Annelida	Polychaeta	NA	Cossuridae	1	<i>Cossura longocirrata</i>
Crango	107007	Animalia	Arthropoda	Malacostraca	Decapoda	Crangonidae	1	<i>Crangon</i>
Crango	107552	Animalia	Arthropoda	Malacostraca	Decapoda	Crangonidae	1	<i>Crangon crangon</i>
Coroph	237004	Animalia	Arthropoda	Malacostraca	Amphipoda	Corophiidae	1	<i>Crassicorophium bonellii</i>
Cragig	140656	Animalia	Mollusca	Bivalvia	Ostreoida	Ostreidae	1	<i>Crassostrea gigas</i>
Crefor	138963	Animalia	Mollusca	Gastropoda	Littorinimorpha	Calyptraeidae	1	<i>Crepidula fornicate</i>
Crusta	1066	Animalia	Arthropoda	NA	NA	NA	1	<i>Crustacea</i>
Cumace	1137	Animalia	Arthropoda	Malacostraca	Cumacea	NA	1	<i>Cumacea</i>
Cumace	110465	Animalia	Arthropoda	Malacostraca	Cumacea	Bodotriidae	1	<i>Cumopsis goodsir</i>
Decapo	1130	Animalia	Arthropoda	Malacostraca	Decapoda	NA	1	<i>Decapoda</i>
Dipcoe	131117	Animalia	Annelida	Polychaeta	Spionida	Spionidae	1	<i>Dipolydora coeca</i>
Dulich	101734	Animalia	Arthropoda	Malacostraca	Amphipoda	Dulichiidae	1	<i>Dulichia</i>
Ensdir	140732	Animalia	Mollusca	Bivalvia	Euheterodonta	Pharidae	1	<i>Ensis directus</i>
Eteone	129443	Animalia	Annelida	Polychaeta	Phyllodocida	Phyllodocidae	1	<i>Eteone</i>
Eteone	130613	Animalia	Annelida	Polychaeta	Phyllodocida	Phyllodocidae	1	<i>Eteone flava</i>
Eteone	130616	Animalia	Annelida	Polychaeta	Phyllodocida	Phyllodocidae	1	<i>Eteone longa</i>
Eulali	129445	Animalia	Annelida	Polychaeta	Phyllodocida	Phyllodocidae	1	<i>Eulalia</i>
Eulali	130639	Animalia	Annelida	Polychaeta	Phyllodocida	Phyllodocidae	1	<i>Eulalia viridis</i>
Eumida	129446	Animalia	Annelida	Polychaeta	Phyllodocida	Phyllodocidae	1	<i>Eumida</i>
Eumida	130641	Animalia	Annelida	Polychaeta	Phyllodocida	Phyllodocidae	1	<i>Eumida bahusiensis</i>
Eumida	130644	Animalia	Annelida	Polychaeta	Phyllodocida	Phyllodocidae	1	<i>Eumida sanguinea</i>
Nereid	130375	Animalia	Annelida	Polychaeta	Phyllodocida	Nereididae	1	<i>Eunereis longissima</i>
Gamma	101383	Animalia	Arthropoda	Malacostraca	Amphipoda	Gammaridae	1	<i>Gammaridae</i>
Gamma	101537	Animalia	Arthropoda	Malacostraca	Amphipoda	Gammaridae	1	<i>Gammarus</i>
Gastro	101	Animalia	Mollusca	Gastropoda	NA	NA	1	<i>Gastropoda</i>
Mysida	120020	Animalia	Arthropoda	Malacostraca	Mysida	Mysidae	0	<i>Gastrosaccus spinifer</i>
Glycer	129296	Animalia	Annelida	Polychaeta	Phyllodocida	Glyceridae	1	<i>Glycera</i>
Glycer	130116	Animalia	Annelida	Polychaeta	Phyllodocida	Glyceridae	1	<i>Glycera alba</i>
Glycer	130131	Animalia	Annelida	Polychaeta	Phyllodocida	Glyceridae	1	<i>Glycera unicornis</i>
Polyno	129491	Animalia	Annelida	Polychaeta	Phyllodocida	Polynoidae	1	<i>Harmothoe</i>
Polyno	130769	Animalia	Annelida	Polychaeta	Phyllodocida	Polynoidae	1	<i>Harmothoe imbricata</i>

namecode	AphiaID	Kingdom	Phylum	Class	Order	Family	benthos	scname
Polyno	130770	Animalia	Annelida	Polychaeta	Phyllodocida	Polynoidae	1	Harmothoe impar
Nereid	152302	Animalia	Annelida	Polychaeta	Phyllodocida	Nereididae	1	Hediste diversicolor
Hemigr	106964	Animalia	Arthropoda	Malacostraca	Decapoda	Varunidae	1	Hemigrapsus
Hemigr	389288	Animalia	Arthropoda	Malacostraca	Decapoda	Varunidae	1	Hemigrapsus takanoi
Hesaug	130646	Animalia	Annelida	Polychaeta	Phyllodocida	Phyllodocidae	1	Hesionura augeneri
Hetfil	129884	Animalia	Annelida	Polychaeta	NA	Capitellidae	1	Heteromastus filiformis
Perulv	151628	Animalia	Mollusca	Gastropoda	Littorinimorpha	Hydrobiidae	1	Peringia ulvae
Isopod	1131	Animalia	Arthropoda	Malacostraca	Isopoda	NA	1	Isopoda
Isopod	264171	Animalia	Arthropoda	Malacostraca	Isopoda	Janiridae	1	Jaera (Jaera) albifrons
Ischyry	102431	Animalia	Arthropoda	Malacostraca	Amphipoda	Ischyroceridae	1	Jassa falcata
Kurbid	345281	Animalia	Mollusca	Bivalvia	Veneroida	Montacutidae	1	Kurtiella bidentata
Pectin	152367	Animalia	Annelida	Polychaeta	Terebellida	Pectinariidae	1	Lagis koreni
Lancon	131495	Animalia	Annelida	Polychaeta	Terebellida	Terebellidae	1	Lanice conchilega
Lepcin	140143	Animalia	Mollusca	Polyplacophora	Chitonida	Lepidochitonidae	1	Lepidochitona (Lepidochitona) cinerea
Lepsqu	140218	Animalia	Mollusca	Bivalvia	Veneroida	Lasaeidae	1	Lepton squamosum
Liocar	106925	Animalia	Arthropoda	Malacostraca	Decapoda	Polybiidae	1	Liocarcinus
Litlit	140262	Animalia	Mollusca	Gastropoda	Littorinimorpha	Littorinidae	1	Littorina littorea
Lutlut	140295	Animalia	Mollusca	Bivalvia	Veneroida	Mactridae	1	Lutraria lutaria
Macbal	141579	Animalia	Mollusca	Bivalvia	Veneroida	Tellinidae	1	Macoma balthica
Magelo	129341	Animalia	Annelida	Polychaeta	Spionida	Magelonidae	1	Magelona
Malaco	129614	Animalia	Annelida	Polychaeta	Spionida	Spionidae	1	Malacoceros
Polyno	129499	Animalia	Annelida	Polychaeta	Phyllodocida	Polynoidae	1	Malmgreniella
Marvir	129615	Animalia	Annelida	Polychaeta	Spionida	Spionidae	1	Marenzelleria
Marvir	131135	Animalia	Annelida	Polychaeta	Spionida	Spionidae	1	Marenzelleria viridis
Coroph	423507	Animalia	Arthropoda	Malacostraca	Amphipoda	Corophiidae	1	Medicorophium affine
Meliti	101679	Animalia	Arthropoda	Malacostraca	Amphipoda	Melitidae	1	Melita
Mysida	120072	Animalia	Arthropoda	Malacostraca	Mysida	Mysidae	0	Mesopodopsis slabberi
Anthoz	100982	Animalia	Cnidaria	Anthozoa	Actiniaria	Metridiidae	1	Metridium senile
Microph	129313	Animalia	Annelida	Polychaeta	Phyllodocida	Hesionidae	1	Microphthalmus
Micropr	101561	Animalia	Arthropoda	Malacostraca	Amphipoda	Microprotopidae	1	Microprotopus
Micropr	102379	Animalia	Arthropoda	Malacostraca	Amphipoda	Microprotopidae	1	Microprotopus longimanus
Micropr	102380	Animalia	Arthropoda	Malacostraca	Amphipoda	Microprotopidae	1	Microprotopus maculatus
Mollus	51	Animalia	Mollusca	NA	NA	NA	1	Mollusca

namecode	AphiaID	Kingdom	Phylum	Class	Order	Family	benthos	scname
Coroph	225814	Animalia	Arthropoda	Malacostraca	Amphipoda	Corophiidae	1	<i>Monocorophium acherusicum</i>
Coroph	148592	Animalia	Arthropoda	Malacostraca	Amphipoda	Corophiidae	1	<i>Monocorophium insidiosum</i>
Myaare	138211	Animalia	Mollusca	Bivalvia	Myoida	Myidae	1	Mya
Myaare	140430	Animalia	Mollusca	Bivalvia	Myoida	Myidae	1	<i>Mya arenaria</i>
Myrian	129659	Animalia	Annelida	Polychaeta	Phyllodocida	Syllidae	1	<i>Myrianida</i>
Myrian	238198	Animalia	Annelida	Polychaeta	Phyllodocida	Syllidae	1	<i>Myrianida langerhansi</i>
Myrian	238200	Animalia	Annelida	Polychaeta	Phyllodocida	Syllidae	1	<i>Myrianida prolifera</i>
Mysida	149668	Animalia	Arthropoda	Malacostraca	Mysida	NA	0	<i>Mysida</i>
Myspic	147026	Animalia	Annelida	Polychaeta	Phyllodocida	Phyllodocidae	1	<i>Mysta picta</i>
Mytili	128677	Animalia	Arthropoda	Maxillopoda	Poecilostomatoidea	Mytilicolidae	1	<i>Mytilicola</i>
Mytili	128900	Animalia	Arthropoda	Maxillopoda	Poecilostomatoidea	Mytilicolidae	1	<i>Mytilicola intestinalis</i>
Mytedu	211	Animalia	Mollusca	Bivalvia	Mytiloida	Mytilidae	1	<i>Mytilidae</i>
Mytedu	140480	Animalia	Mollusca	Bivalvia	Mytiloida	Mytilidae	1	<i>Mytilus edulis</i>
Nemato	799	Animalia	Nematoda	NA	NA	NA	1	<i>Nematoda</i>
Nemert	152391	Animalia	Nemertea	NA	NA	NA	1	<i>Nemertea</i>
Neoamp	129702	Animalia	Annelida	Polychaeta	Terebellida	Terebellidae	1	<i>Neoamphitrite</i>
Neofig	131504	Animalia	Annelida	Polychaeta	Terebellida	Terebellidae	1	<i>Neoamphitrite figulus</i>
Nephty	129370	Animalia	Annelida	Polychaeta	Phyllodocida	Nephtyidae	1	<i>Nephtys</i>
Nephty	130353	Animalia	Annelida	Polychaeta	Phyllodocida	Nephtyidae	1	<i>Nephtys assimilis</i>
Nephty	130355	Animalia	Annelida	Polychaeta	Phyllodocida	Nephtyidae	1	<i>Nephtys caeca</i>
Nephty	130357	Animalia	Annelida	Polychaeta	Phyllodocida	Nephtyidae	1	<i>Nephtys cirrosa</i>
Nephty	130359	Animalia	Annelida	Polychaeta	Phyllodocida	Nephtyidae	1	<i>Nephtys hombergii</i>
Nephty	130364	Animalia	Annelida	Polychaeta	Phyllodocida	Nephtyidae	1	<i>Nephtys longosetosa</i>
Nereid	129379	Animalia	Annelida	Polychaeta	Phyllodocida	Nereididae	1	<i>Nereis</i>
Nereid	130404	Animalia	Annelida	Polychaeta	Phyllodocida	Nereididae	1	<i>Nereis pelagica</i>
Notlat	129898	Animalia	Annelida	Polychaeta	NA	Capitellidae	1	<i>Notomastus latericeus</i>
Nudibr	1762	Animalia	Mollusca	Gastropoda	Nudibranchia	NA	1	<i>Nudibranchia</i>
Pycnog	134687	Animalia	Arthropoda	Pycnogonida	Pantopoda	Nymphonidae	1	<i>Nymphon gracile</i>
Oligoc	2036	Animalia	Annelida	Clitellata	NA	NA	1	<i>Oligochaeta</i>
Opheli	129413	Animalia	Annelida	Polychaeta	NA	Opheliidae	1	<i>Ophelia</i>
Opheli	130494	Animalia	Annelida	Polychaeta	NA	Opheliidae	1	<i>Ophelia limacina</i>
Opheli	130496	Animalia	Annelida	Polychaeta	NA	Opheliidae	1	<i>Ophelia rathkei</i>
Ophiur	123574	Animalia	Echinodermata	Ophiuroidea	Ophiurida	Ophiuridae	1	<i>Ophiura</i>

namecode	AphiaID	Kingdom	Phylum	Class	Order	Family	benthos	scname
Ophiur	124929	Animalia	Echinodermata	Ophiuroidea	Ophiurida	Ophiuridae	1	Ophiura ophiura
Pagber	107232	Animalia	Arthropoda	Malacostraca	Decapoda	Paguridae	1	Pagurus bernhardus
Parful	146932	Animalia	Annelida	Polychaeta	NA	Paraonidae	1	Paraonis fulgens
Caprel	101857	Animalia	Arthropoda	Malacostraca	Amphipoda	Caprellidae	1	Pariambus typicus
Pectin	129437	Animalia	Annelida	Polychaeta	Terebellida	Pectinariidae	1	Pectinaria
Pectin	130590	Animalia	Annelida	Polychaeta	Terebellida	Pectinariidae	1	Pectinaria (Amphictene) auricoma
Petpho	156961	Animalia	Mollusca	Bivalvia	Veneroida	Veneridae	1	Petricolaria pholadiformis
Petric	246	Animalia	Mollusca	Bivalvia	Veneroida	Veneridae	1	Petricolinae
Pholoe	129439	Animalia	Annelida	Polychaeta	Phyllodocida	Pholoidae	1	Pholoe
Phoino	130601	Animalia	Annelida	Polychaeta	Phyllodocida	Pholoidae	1	Pholoe inornata
Phomin	130603	Animalia	Annelida	Polychaeta	Phyllodocida	Pholoidae	1	Pholoe minuta
Photid	102387	Animalia	Arthropoda	Malacostraca	Amphipoda	Photidae	1	Photis reinhardi
Caprel	101864	Animalia	Arthropoda	Malacostraca	Amphipoda	Caprellidae	1	Phtisica marina
Phyllo	129455	Animalia	Annelida	Polychaeta	Phyllodocida	Phyllodocidae	1	Phyllodoce
Pinpis	107473	Animalia	Arthropoda	Malacostraca	Decapoda	Pinnotheridae	1	Pinnotheres pisum
Pislom	107188	Animalia	Arthropoda	Malacostraca	Decapoda	Porcellanidae	1	Pisidia longicornis
Polych	883	Animalia	Annelida	Polychaeta	NA	NA	1	Polychaeta
Polydo	129619	Animalia	Annelida	Polychaeta	Spionida	Spionidae	1	Polydora
Polydo	131141	Animalia	Annelida	Polychaeta	Spionida	Spionidae	1	Polydora ciliata
Polydo	131143	Animalia	Annelida	Polychaeta	Spionida	Spionidae	1	Polydora cornuta
Polyno	939	Animalia	Annelida	Polychaeta	Phyllodocida	Polynoidae	1	Polynoidae
Lepcin	55	Animalia	Mollusca	Polyplocophora	NA	NA	1	Polyplacophora
Procer	129671	Animalia	Annelida	Polychaeta	Phyllodocida	Syllidae	1	Proceraea
Procer	131362	Animalia	Annelida	Polychaeta	Phyllodocida	Syllidae	1	Proceraea cornuta
Cumace	110628	Animalia	Arthropoda	Malacostraca	Cumacea	Pseudocumatidae	1	Pseudocuma (Pseudocuma) simile
Pycnog	1302	Animalia	Arthropoda	Pycnogonida	NA	NA	1	Pycnogonida
Pygele	131170	Animalia	Annelida	Polychaeta	Spionida	Spionidae	1	Pygospio elegans
Retobt	141134	Animalia	Mollusca	Gastropoda	Cephalaspidea	Retusidae	1	Retusa obtusa
Sagitt	105410	Animalia	Chaetognatha	Sagittoidea	Aphragmophora	Sagittidae	1	Sagitta
Scobon	131171	Animalia	Annelida	Polychaeta	Spionida	Spionidae	1	Scolelepis bonnierii
Scoarm	334772	Animalia	Annelida	Polychaeta	NA	Orbiniidae	1	Scoloplos (Scoloplos) armiger
Sigali	129594	Animalia	Annelida	Polychaeta	Phyllodocida	Sigalionidae	1	Sigalion
Sphbal	131089	Animalia	Annelida	Polychaeta	Phyllodocida	Sphaerodoridae	1	Sphaerodoropsis baltica

namecode	AphiaID	Kingdom	Phylum	Class	Order	Family	benthos	scname
Spio	129625	Animalia	Annelida	Polychaeta	Spionida	Spionidae	1	Spio
Spio	131183	Animalia	Annelida	Polychaeta	Spionida	Spionidae	1	<i>Spio filicornis</i>
Spio	131184	Animalia	Annelida	Polychaeta	Spionida	Spionidae	1	<i>Spio gonicephala</i>
Spio	131185	Animalia	Annelida	Polychaeta	Spionida	Spionidae	1	<i>Spio martinensis</i>
Spioni	913	Animalia	Annelida	Polychaeta	Spionida	Spionidae	1	Spionidae
Spibom	131187	Animalia	Annelida	Polychaeta	Spionida	Spionidae	1	<i>Spiophanes bombyx</i>
Spiell	140300	Animalia	Mollusca	Bivalvia	Veneroida	Mactridae	1	<i>Spisula elliptica</i>
Spisub	140302	Animalia	Mollusca	Bivalvia	Veneroida	Mactridae	1	<i>Spisula subtruncata</i>
Sthene	129595	Animalia	Annelida	Polychaeta	Phyllodocida	Sigalionidae	1	<i>Sthenelais</i>
Sthene	131074	Animalia	Annelida	Polychaeta	Phyllodocida	Sigalionidae	1	<i>Sthenelais boa</i>
Stomat	14355	Animalia	Arthropoda	Malacostraca	Stomatopoda	NA	1	Stomatopoda
Strben	131191	Animalia	Annelida	Polychaeta	Spionida	Spionidae	1	<i>Streblospio benedicti</i>
Strweb	131402	Animalia	Annelida	Polychaeta	Phyllodocida	Syllidae	1	<i>Streptosyllis websteri</i>
Syllid	948	Animalia	Annelida	Polychaeta	Phyllodocida	Syllidae	1	Syllidae
Syllid	129680	Animalia	Annelida	Polychaeta	Phyllodocida	Syllidae	1	Syllis
Angfab	152829	Animalia	Mollusca	Bivalvia	Veneroida	Tellinidae	1	<i>Angulus fabula</i>
Angten	146492	Animalia	Mollusca	Bivalvia	Veneroida	Tellinidae	1	<i>Angulus tenuis</i>
Cirrat	129249	Animalia	Annelida	Polychaeta	Terebellida	Cirratulidae	1	Tharyx
Tubula	1603	Animalia	Cnidaria	Hydrozoa	Anthoathecata	Tubulariidae	1	Tubulariidae
Vencor	181364	Animalia	Mollusca	Bivalvia	Veneroida	Veneridae	1	<i>Venerupis corrugata</i>

NIOZ Royal Netherlands Institute for Sea Research is an Institute of the Netherlands Organization for Scientific Research (NWO).

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

NIOZ Rapport 2013-7

The mission of NIOZ is to gain and communicate scientific knowledge on seas and oceans for a better understanding and sustainability of our planet, to manage the national facilities for sea research and to support research and education in the Netherlands and in Europe.

