



Distinctly variable mudscapes: Distribution gradients of intertidal macrofauna across the Dutch Wadden Sea[☆]

Tanya J. Compton^{a,*}, Sander Holthuijsen^a, Anita Koolhaas^a, Anne Dekinga^a, Job ten Horn^a, Jeremy Smith^a, Ysbrand Galama^a, Maarten Brugge^a, Daphne van der Wal^b, Jaap van der Meer^a, Henk W. van der Veer^a, Theunis Piersma^{a,c}

^a Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB, Texel, Den Burg, The Netherlands

^b Department of Spatial Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 140, 4400 AC, Yerseke, The Netherlands

^c Animal Ecology Group, Centre for Ecological and Evolutionary Studies (CEES), University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands

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ABSTRACT

The Wadden Sea is a shallow coastal region, with a large area of sedimentary tidal flats that extends from The Netherlands to Denmark and has been declared a site of international importance in the Dutch and German parts (Ramsar status and UNESCO World Heritage Site). Benthic macrofauna are central to the ecosystem functioning of this area, as they recycle nutrients, decompose organic matter and are an important food source for many secondary consumers, like fish and waterbirds. Due to the environmental gradients characteristic of estuarine systems, it is expected that changes in assemblage composition will be observed across the physical and environmental gradients of the Wadden Sea. First, we explored the spatial variation in assemblage composition of benthic macrofauna across the intertidal part of the Dutch Wadden Sea using 3 years of biomass data. Then, we identified the relative importance of six environmental variables for explaining and predicting changes in assemblage composition across the intertidal areas of the Wadden Sea using generalised dissimilarity modelling (GDM). In accordance with the environmental gradients across this system, the biomass contributed by a few common species differed from west to east and were distinct in the Dollard. In the west, bivalves *Mya arenaria*, *Cerastoderma edule* and *Ensis directus* contributed a relatively large and equal share of the total biomass, whereas *C. edule* contributed the sole largest share of the total biomass towards the east. The polychaete *Alitta succinea* became a large share of the total biomass in the upper Ems and in the Dollard estuary, but contributed little elsewhere. Similar to the observed differences in species composition, the spatial patterns in assemblage composition, as predicted by the GDM models, identified the Dollard as distinct and that the prevalence of assemblage types in the west differed to the east. Median grain size, followed by microphytobenthic biomass, and exposure time were the most important variables describing differences in assemblage composition. That the Wadden Sea forms a heterogeneous landscape where assemblage composition varies across multiple gradients has repercussions for management and monitoring.

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1. Introduction

The Wadden Sea is a shallow coastal region, with a large area of sedimentary tidal flats, that stretches from The Netherlands to Denmark and is recognised as a wetland and heritage site of international importance in the Netherlands and Germany (Ramsar status, UNESCO World Heritage Site). Due to its geographic position, the ecosystem services provided to other ecosystems and human populations are wide-ranging. For

example, the Wadden Sea is a nursery area for commercial fish and shrimp and provides a staging area for waterbirds migrating along the East-Atlantic flyway (Boere and Piersma, 2012; van de Kam et al., 2004; Wolff, 1983; Zijlstra, 1972; Zwarts, 1996).

Benthic macrofauna are central to the maintenance of many ecosystem services in estuarine systems such as the Wadden Sea (Levin et al., 2001; Olf et al., 2009; Thrush et al., 2006). Defined as organisms greater than 1 mm in size, macrofauna recycle nutrients, decompose organic matter, regulate nutrient cycles and are an important food source to many species including humans. For example, species that shred organic material break-down and recycle this material, suspension feeders transport sediments across the sediment–water interface, bioturbators increase the turnover in nutrients and sediments, and biogenic builders generate structure and consolidate sediments (see review by Levin et al., 2001). Describing the assemblage composition of macrofauna across a

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* Corresponding author at: Royal Netherlands Institute for Sea Research, Department of Marine Ecology, P.O. Box 59, 1790AB, Den Burg, The Netherlands. Tel.: +31 222 369300; fax: +31 222 319674.

E-mail address: tanya.compton@nioz.nl (T.J. Compton).

system can thus be considered fundamental to understanding a system and can provide a basis for determining the influence of anthropogenic effects, e.g. eutrophication (Beukema and Cadée, 1997), species invasions (Lohrer et al., 2008), habitat alteration (Thrush et al., 2003a), gas extraction (Beukema, 2002), dredging for shellfish (Piersma et al., 2001) or combinations of these factors (Eriksson et al., 2010).

Previous syntheses examining macrofauna across the entire Dutch Wadden Sea identified that the system has a high standing stock of macrofauna with an annual average of $\sim 27 \text{ g/m}^2$ ash free dry mass (AFDM, Beukema, 1976). Only six out of more than 44 species made up 90% of the total standing stock in this system, i.e. *Mytilus edulis*, *Arenicola marina*, *Mya arenaria*, *Cerastoderma edule* and *Macoma balthica* (Beukema, 1976). Furthermore, areas of low salinity such as the Dollard were shown to be much poorer in terms of macrofaunal richness and biomass than other areas of the Wadden Sea (Wolff, 1983). Spatially extensive studies in the late 1970s and early 1980s provided knowledge on the distribution of common macrofaunal species across this system (Dankers and Beukema, 1981). However, we currently lack an understanding of how macrofaunal assemblages differ across environmental gradients of the Wadden Sea. A recent comparison of interspersed monitoring stations from the Dutch to the Danish Wadden Sea showed that assemblages differ between monitoring stations and along intertidal gradients, but other correlates of assemblage change were not examined (van der Graaf et al., 2009).

In the Dutch Wadden Sea, as in other estuarine systems (e.g. Thrush et al., 2003b; van der Meer, 1991; Ysebaert et al., 2002), it has been shown that macrofauna have distinct environmental associations (Beukema, 1976; Compton et al., 2009; Kraan et al., 2010). For example, Kraan et al. (2010) identified that *M. balthica* was more abundant in areas of relatively finer sediments and longer exposure times, whereas *C. edule* was more abundant in areas with relatively sandier sediments and shorter exposure times. Consequently, it is expected that differences in assemblage composition will be observed across the physical and environmental gradients of the Wadden Sea. On one hand, such compositional shifts could occur as one moves from west to east, with the exception of the Dollard, because the Wadden Sea system is known to have different physical properties in this direction, e.g. longer exposure times in the east compared to the west (Otto et al., 1990). On the other hand, composition might differ in a landward to seaward direction e.g. areas of low salinity close to the coast versus areas of high salinity near the island inlets. In addition, steep environmental gradients from the upper Ems to the Dollard are likely to affect species composition, as salinity decreases and suspended matter and total organic carbon increase towards the Dollard (Essink and Bos, 1985).

To examine the spatial patterns in compositional turnover, we here use 3 years of intertidal biomass data from a spatially comprehensive monitoring campaign (Bijleveld et al., 2012) and a generalised dissimilarity modelling approach (GDM) (Ferrier et al., 2007). GDM is a matrix regression approach that relates biological dissimilarities between pairs of sites to environmental or geographic distances (Ferrier et al., 2007; Legendre et al., 2005). GDM was selected as the approach for this analysis as it can deal with (1) the curvilinear relationship between observed compositional dissimilarity among sites and increasing ecological distance and (2) the variation in the rate of compositional turnover at different positions along environmental gradients in large data sets (Ferrier et al., 2007). Due to these properties, GDM can be used to predict assemblage composition across long environmental gradients in marine environments (e.g. Compton et al., 2013; Leaper et al., 2011). Using GDM, we thus aimed to identify the relative roles of six environmental variables in explaining and predicting compositional turnover, as quantified by among-site Bray–Curtis dissimilarities, across the Wadden Sea. In this study, six environmental variables were available for this analysis: median grain size, exposure time, salinity, microphytobenthic biomass, maximum tidal current speeds and orbital velocities. To identify whether other spatial processes could also explain variation in the model, we also examined the

model improvement when geographic distance was added as a variable to the model.

2. Materials and methods

2.1. Study site

The Wadden Sea is a long and narrow system that shares multiple connections with the North Sea via inlets between the barrier islands (Postma, 1982). The total area of the Wadden Sea is $\sim 8000 \text{ km}^2$ with approximately 50% of this area consisting of intertidal flats (de Jonge et al., 1993). Across the system, tidal ranges vary from 1.4 to 3.4 m (Postma, 1982). In the North Sea the tide propagates counter-clockwise around three amphidromical points, thus the tidal wave starts in the west and tidal amplitude increases as it progresses towards the Elbe (Otto et al., 1990).

Due to several inputs of fresh water (Fig. 1), the Wadden Sea can be described as an estuarine environment (cf. Nienhuis, 1992 in de Jonge et al., 1993). Freshwater discharges vary dramatically across the Wadden Sea due to precipitation, pumping for water regulation and the melting of snow in the Swiss Alps (de Jonge et al., 1993). Sedimentary particles are imported from the North Sea into the Wadden Sea through the tidal inlets. But the quantity of sediment loads can vary considerably (de Jonge et al., 1993) and are largely uncertain (T. Gerkema, pers. comm.). Estimates of the long-term suspended sediment flux in the Marsdiep inlet are 6–9 Mton/year based on long-term in-situ observations aboard the ferry crossing the mainland and the island of Texel (Nauw et al., in preparation).

The Dutch Wadden Sea forms more than a quarter of the international Wadden Sea; comprising ~ 2500 of its total extent of 8000 km^2 (Wolff, 2000). Main sources of freshwater include the Lauwersmeer, IJsselmeer and the River Ems (de Jonge et al., 1993). Anthropogenic developments have caused ongoing changes to the geomorphology of the Dutch part of the Wadden Sea. Until 1932 the western Wadden Sea was part of the larger Zuiderzee, a shallow, brackish inland sea. In 1932 the 'Afsluitdijk', the enclosure dyke between Cornwerd and Den Oever, split the Zuiderzee. Consequently, the brackish inland sea became the freshwater lake IJsselmeer. Some evidence suggests that the Afsluitdijk development reduced the surface areas of the Marsdiep and Vlie tidal basins and increased sedimentation in the areas of the Amsteldiep Balgzand, Malzwin and Wierbalg and along the Frisian coast (Elias and van der Spek, 2006; Elias et al., 2003). In addition to the Afsluitdijk, other rivers and estuaries, with a major one being Lauwersmeer, have also been dammed (the latter in 1969) and provided with sluices or pumping engines (Oost, 1995).

The boundaries defined by the tidal basins, 'watersheds' or 'tidal divides', are often used as the management unit across the Dutch Wadden Sea (e.g. Hoeksma et al., 2004). Tidal divides are identified as raised areas of tidal flat where the incoming water from two different inlets meet and where the flow velocities slow and sediments are allowed to settle (Fig. 1, e.g. Maas, 1997; Postma, 1982). In this paper, ten tidal basins are distinguished (Fig. 1) but we also refer to the 'western Wadden Sea' or the 'west' as the Marsdiep, Eierlandse Gat and Vlie Basins and the 'eastern Wadden Sea' or the 'east' as the remaining basins. The Dollard region has been divided into the upper Ems and Dollard.

2.2. Field sampling

The gridded sampling design (Synoptic Intertidal Benthic Survey, SIBES) encompasses the entire intertidal Dutch Wadden Sea (Fig. 1), with a combination of sample points taken at 500 m intervals and additional random sample points (Bijleveld et al., 2012). Compared with several other sampling designs this sampling approach was shown to be the most cost-effective (Bijleveld et al., 2012). From 2009 onwards, the Ems Dollard region, i.e. the upper Ems and the

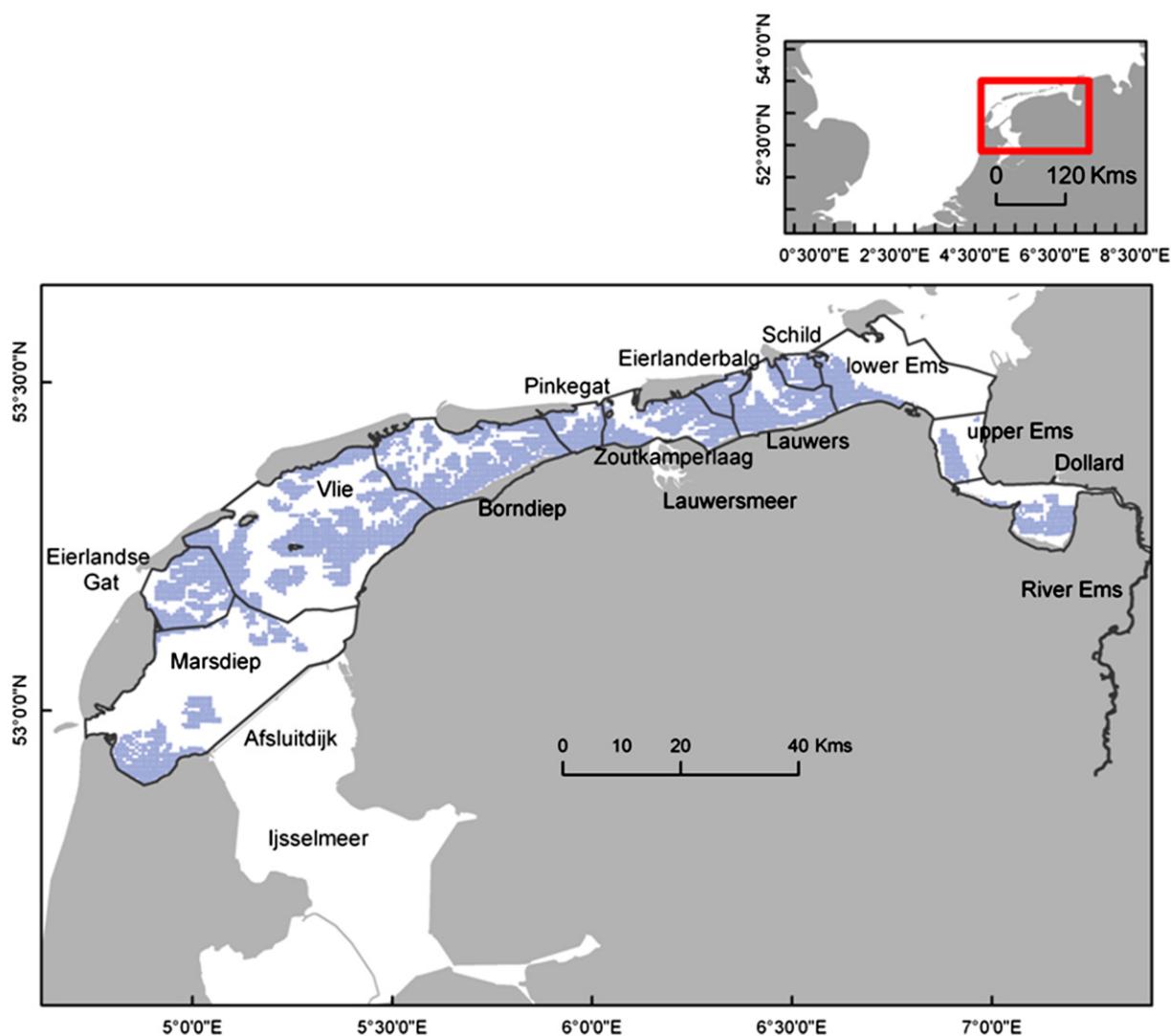


Fig. 1. Points sampled across the Dutch Wadden Sea during the SIBES monitoring programme. The inset shows the location of the Wadden Sea relative to the remainder of The Netherlands. The tidal basin names and boundaries are drawn in the main map. In 2008 the upper Ems and Dollard were not sampled.

Dollard, was incorporated into the SIBES monitoring (Fig. 1). This effort is complementary to the long-term monitoring of the macrofauna at the western end of our study area in the Balgzand (Beukema et al., 2002).

Sampling was completed in the summers from 2008 to 2010 (June to about October). The NIOZ research vessel, the *MS Navicula*, was used as a platform to access the sample areas across the Wadden Sea. During low-tide sample sites were accessed by foot. In areas where it was too deep or muddy to access by foot, small inflatable boats were used. Sampling locations, ~4800/year in total, were found with a hand-held GPS (WGS84 as map datum). At each site sampled by foot, a single core of 0.0177 m² was taken to a depth of ~25 cm. By boat, two cores were taken to a depth of ~25 cm (combined area of 0.0173 m²). The methods yield similar results (Kraan et al., 2007).

All macrofaunal samples were sieved on a 1 mm round mesh in the field. After sieving, bivalves were separated from the other macrofaunal species for later analysis in the laboratory. The bivalve samples were frozen, whereas the remaining macrofaunal species were preserved using a 4% formaldehyde solution. Sediment samples were taken using a centrifuge tube to a depth of 4 cm and then frozen at -20 °C. The sediment samples were taken at 500 m grid intervals in 2010 and at 1 km grid intervals in 2008. Sediment samples were unavailable for the 2009 data, so we have used the 2010 sediment data for the 2009 analysis.

2.3. Laboratory analysis

All molluscs were identified to species level. All other smaller organisms, predominantly crustaceans and polychaetes, were identified to the finest taxonomic level possible; hereafter named operational taxonomic units (OTUs). Small organisms were stained using rose Bengal dye (C.A.S. no. 632-68-8) for 24 h and then placed on a petridish for identification and counting under a binocular microscope (8–40× magnification). Identification of the macrofaunal species was completed according to Hartmann-Schröder (1996) and Hayward and Ryland (1995). Polychaetes and crustaceans were identified to either a genus or species level, whereas oligochaetes were identified to a class level. We currently recognize that there are cryptic species in the Wadden Sea. However, without further taxonomic and genetic analyses we cannot discriminate between these species (Luttikhuisen et al., 2011).

Once samples were counted and identified, the biomass of either individuals or multiple individuals of the same species (shells < 8 mm) was determined. The AFDM was determined by first drying the sample for 2 to 3 days at 60 °C in a ventilated stove, then taking a dry weight (dry mass). Following this, the sample was incinerated for 5 hours at 560 °C and then weighed again to obtain the ash free dry mass (AFDM). We chose to use biomass, rather than numerical densities, to

examine differences in assemblage composition because biomass estimates place less emphasis on the very small abundant species that would otherwise dominate the analysis. Prior to modelling the assemblage turnover with respect to environment, we first square-root transformed OTU biomass and excluded OTUs with fewer than three occurrences and sites where the total biomass was very low (less than 0.1 g/m^2). We also excluded the random sample points from the GDM analysis.

2.4. Environmental variables

The six variables selected for the analysis in this study are well known to have functional linkages to benthic organisms in marine environments (see Appendix 1). Specifically, median grain size is likely to be important for macrofauna in that it is a measure of habitat association, e.g. some tube-building species need relatively coarse sediments to build their tubes (Dankers and Beukema, 1981), and is also correlated with physical variables like current speed, which is correlated with substrate stability (Bijleveld et al., 2012; Compton et al., 2012; Fegley, 1987). Microphytobenthic biomass could be important for macrofaunal assemblages as surface deposit feeders have shown to be associated with microphytobenthic biomass although suspension feeders have not (van der Wal et al., 2008). Exposure time is also likely to be an important variable, as it is correlated with the period of feeding time and thus may be a limiting factor for some suspension feeders like *C. edule*, *M. arenaria* and *M. edulis* (Smidt 1951 in Dankers and Beukema, 1981; Kamermans, 1993). Salinity is important, as only few species in the Wadden Sea are known for their ability to tolerate very low salinities ($<15\text{‰}$), e.g. *M. balthica* and *M. arenaria* (Beukema, 1979; Dankers and Beukema, 1981). Maximum tidal current speeds could be associated with the replenishment of phytoplankton food for suspension feeders or sediment erosion under very high velocities. Orbital velocities could be associated with sediment disturbance, and could thus affect water turbidity and food replenishment.

2.4.1. Sediment

Sediment samples were freeze-dried for up to 96 h and then homogenized with a mortar and pestle. Homogenized samples were weighed to within 0.5 to 5 g, depending on the observed estimated grain size and placed into 13 ml polypropylene auto-sampler tubes with degassed reversed osmosis water. Samples were then shaken vigorously with a vortex mixer for 30 s prior to determining the grain size using a particle size analyser. The particle size analyzer uses laser diffraction and Polarization Intensity Differential Scattering technology to estimate grain sizes (Coulter LS 13 320, optical module 'grey', grain sizes from 0.04 to 2000 μm in 126 size classes). All sediments were analysed according to the 'biological approach', i.e. the organic matter and calcium carbonate was not removed from the samples. Sediment samples were analysed for 2008 and 2010 and were interpolated across the Dutch Wadden Sea using an inverse distance weighting algorithm in ArcGIS 10.0.

2.4.2. Exposure time

The modelled estimates of the average fraction of exposure time for each sample year (2008, 2009 and 2010) were derived from measured water levels, from eight tidal poles around the Wadden Sea, and a bathymetric grid. Both the water levels and the bathymetric grid were implemented into a geometric triangular grid model, which interpolated exposure times across the Wadden Sea (Rappoldt and Ens, 2011). The water level data for this model was downloaded from the Rijkswaterstaat (www.waterbase.nl). The bathymetric layer is determined based on an interpolation using DIGIPOL and measured echosounder data (Perluka et al., 2006; Vaklodingen, 2009). The entire Dutch Wadden Sea is echosounded along transects of 200 m

apart over a five-year cycle, where each year a different part of the total grid is sounded (Perluka et al., 2006).

2.4.3. Microphytobenthic biomass

A common measure for photo-autotrophs is the Normalized Differential Vegetation Index, NDVI, computed from reflectance in the red (RR) and near-infrared (RNIR) part of the electro-magnetic spectrum, that is:

$$\text{NDVI} = (\text{RNIR} - \text{RR}) / (\text{RNIR} + \text{RR}).$$

As photo-autotrophs absorb most of the incoming light, notably in the red, NDVI gives higher values with increasing biomass or cover (Tucker, 1979). At low tide, and in the absence of macrophytes, NDVI is a good proxy for chlorophyll-a (Chl-a) of the sediment, indicating microphytobenthic biomass (mainly diatoms, van der Wal et al., 2008).

Here, the NDVI was derived from a time-series of daily composite Aqua MODIS satellite imagery from spring 2008, 2009 and 2010 (March, April and May), according to the methods in van der Wal et al. (2010). All images were obtained from the Land Processes Distributed Active Archive Center (LP DAAC, <http://www.lpdaac.usgs.gov>). The Aqua MODIS Surface Reflectance Daily L2G Global 250-m SIN grid product (MYD09GQ.005) contains surface reflectance RR (620–670 nm, central wavelength 645 nm) and RNIR (841–876 nm, central wavelength 859 nm). The associated MOD09GA quality assessment was used to retain highest quality reflectance data and to eliminate clouds and cloud shadow (van der Wal et al., 2010). NDVI was calculated provided $\text{RR} > 0\%$, $\text{RNIR} > 2\%$ and $\text{NDVI} > 0$ to avoid surface water, and averaged per pixel. Supratidal areas, intertidal seagrass and saltmarsh areas were excluded. No distinction could be made between benthic microalgae (diatoms) and benthic macroalgae (seaweeds) but by selecting spring images only, the presence of macroalgae was limited.

2.4.4. Salinity

Freshwater discharge into the Dutch Wadden Sea was estimated from data collected at fourteen freshwater discharge points in March 1988, a wet month (Jager and Bartelds, 2002). A more recent synthesis is currently not accessible. Based on this data and a 2-D model (Kuijper 1993 in Jager and Bartelds, 2002) salinity concentrations were interpolated across the Dutch Wadden Sea (Jager and Bartelds, 2002).

2.4.5. Maximum tidal current speed and bed orbital velocities

Maximum tidal current speed (ms^{-1}) was estimated based on dynamic model computations using the WADPLUS model (Rijkswaterstaat). The maximum tidal current speeds were computed given tides on 13–15 February 1989 when there was a NW storm ($500 \times 500 \text{ m}$ grid size, Brinkman et al., 2002). Maximum near-bottom orbital velocities (m s^{-1}) were computed with the HISWA model (Rijkswaterstaat) given the same climatic conditions and tides (Brinkman et al., 2002). The main shortcoming of these gridded layers is that they are calculated for these specific dates in 1989 and thus one climatic condition, but they are currently the only estimates readily available for the entire Wadden Sea.

As all gridded environmental data layers had different native gridded resolutions, and because our biological data was sampled at $500 \times 500 \text{ m}$ grid intervals, we opted for a $200 \times 200 \text{ m}$ gridded resolution of our environmental layers for our analysis. All layers were projected to the same grid size and spatial extent using the projection tool in ArcGIS 10. The biological data was matched to the environmental data using the extract function from the Raster package (Hijmans, 2011). Note that we matched the biological data of a particular year with respect to the median grain size, mean exposure time and spring NDVI estimates from the same year. The only exception was where the sediments from 2010 were matched with the biological data of 2009, based on our observations that the spatial variation in sediment

composition was similar between 2008 and 2010 (Compton et al., 2012). Although all six variables share similar characteristics in parts of their environmental space, they were uncorrelated with each other (Pearson correlation < 0.5).

2.5. Generalised dissimilarity analysis

To model among-site patterns of compositional differences (beta diversity) with respect to the six environmental variables, we used generalised dissimilarity modelling (GDM, Ferrier et al., 2002, 2007). The reason we chose GDM, is that other methods often used to relate assemblage responses to environment are restricted in that they are essentially linear models on Euclidean distances, e.g. canonical correlation analysis or redundancy analyses (Ferrier et al., 2007; Millar et al., 2005). But in many ecological problems, especially across long gradients, the relationship between the change in beta diversity and the change in environment will be non-linear (Ferrier et al., 2002, 2007; Millar et al., 2005), i.e. when many sites show large changes in beta diversity, indicating few or no shared species between sites, then the dissimilarity measure will take on an asymptotic value of close to 1, irrespective of environmental or ecological separation (Ferrier et al., 2007). This is a widely acknowledged problem and as such two similar approaches have also recently been presented to deal with these issues, i.e. non-linear canonical correlation analysis (Millar et al., 2005) and gradient forest analysis (Ellis et al., 2012).

In the case of GDM the two aforementioned problems are addressed by fitting a modified generalised linear model (Eq. (1), GLM, McCullagh and Nelder, 1989) where the asymptotic relationship between the predicted response and the environmental variables is accommodated via the specification of an appropriate link (Eq. (1)) and variance function (Ferrier et al., 2002, 2007).

$$\delta = 1 - e^{-\zeta} \quad (1)$$

where δ is the Bray–Curtis dissimilarities and ζ is the change in environment.

The link transformed Bray–Curtis dissimilarities can thus be modelled as a function of the change in environmental variables (Ferrier et al., 2007, Eq. (2)). To achieve the best fit of the link transformed Bray–Curtis dissimilarities within the modified GLM model, I-spline basis functions $f_p(x)$ (Winsberg and De Soete, 1997) are used to fit the change in the link transformed Bray–Curtis dissimilarities and the environmental variables between pairs of sites (Ferrier et al., 2002, 2007):

$$\zeta = \alpha + \sum \left| f_p(x_{pi}) - f_p(x_{pj}) \right| \quad (2)$$

where α is the intercept, p is the number of environmental variables, $f(x)$ are the I-spline transformed environmental variables and i and j are pairs of sites.

The intercept α is the estimated value of the link transformed Bray–Curtis dissimilarities where two sites have identical environmental characteristics (Overton et al., 2009). The response curves derived from the GDM model provide an indication of the total amount of variation explained by an environmental variable and also the rate of change of compositional turnover along a gradient, e.g. steep slopes indicate ranges of the predictors where there is a fast turnover, whereas flatter slopes indicate relatively homogenous assemblages (Ferrier et al., 2007). See Ferrier et al. (2007) for further details.

For each sample year separately (2008–2010), we used GDM models to explore the compositional turnover in the link transformed Bray–Curtis distances, as derived from the square-root transformed biomass data, as a function of the six environmental variables. Initially, all GDM models were run with all data that met the criteria mentioned above. Measures of GDM model performance were estimated for

these models, i.e. null deviance, unexplained deviance and percentage of deviance explained. Then to estimate confidence intervals around the response curves, we ran a bootstrapping procedure where random sites were subsampled from each year ($n = 2000$ rows with replacement) and then used to run GDM models ($n = 60$). Furthermore, to assess whether other spatial processes improved the explanatory power of the GDM model, i.e. spatial autocorrelation, we also added geographic distance between sites and assessed whether there was an improvement to model performance (Ferrier, 2002; Leaper et al., 2011).

Patterns of assemblage turnover in geographic space were estimated by predicting the GDM fitted I-spline response across the gridded environmental variables. Predictions were estimated from the GDM models where all available data were used. To visualise the patterns in assemblage turnover, we used a Principal Component Analysis (PCA, covariance matrix) to simplify the six transformed environmental variables into three factors, which were assigned a red–blue–green (RGB) colour scheme (Ferrier et al., 2007; Pitcher et al., 2012). The three factors were then plotted in PCA space to provide an overview of the associations between the variables. The most influential environmental variables from the GDM analysis were then plotted as vectors onto this projected PCA space, analogous to a conventional biplot. The RGB colour palette was then mapped into geographic space, providing a representation of the predicted patterns in beta diversity. Note that our analysis represents assemblage turnover at the same scale as the gridded environmental covariates (200×200 m grid-scale) and thus do not capture turnover at smaller scales.

To implement GDM, we used software available from <www.biomaps.net.au/gdm> (ver. 1.1) in R 2.12 (R Development Core Team, 2011). GDM is currently available only for Bray–Curtis dissimilarities, and the code needs to be modified in R before running count data (G. Manion, pers. comm.). The gridded layers were produced by the raster package (Hijmans, 2011) in R and mapped in ArcGIS 10.

3. Results

3.1. Environmental variables

The Marsdiep had the smallest proportion of intertidal area (8% of area as intertidal), whereas the Schild and Eilanderbalg tidal basins had the largest proportion of intertidal area (>58%, Table 1). The mean highest exposure times (ET) were observed at the sample sites in the tidal basins of the Zoutkamperlaag, Eilanderbalg, Lauwers and Schild (mean ET = > 0.3, Table 1 & Fig. 2). The sampled mean sediments showed that the Eierlandse Gat in the west had the coarsest sediments (MGS 2008 and 2010: 192 and 187 μm) and the Dollard in the east had the finest sediments (MGS: 84 μm). The tidal basin with the greatest range in sediment grain sizes between 2008 and 2010 was the Vlie (range 259–309 μm , Table 1 & Fig. 2). Mean estimates of microphytobenthic biomass (NDVI) were highest in the upper Ems and Dollard. Although there was variability in microphytobenthic biomass between tidal basins over time, the basins where microphytobenthic biomass was generally low were the Eierlandse Gat and the Vlie, both in the west (mean NDVI: 0.06–0.09). Lowest salinities were observed in the Dollard (mean 10‰), followed by the Vlie and Borndiep basins (both mean 17‰). Orbital velocities were highest in the lower Ems (orbgolf 0.4 ms^{-1}), whereas maximum tidal current speeds were highest in the Eierlandse gat (maxcurr 0.6 ms^{-1}) and lowest in the Dollard (maxcurr 0.45 ms^{-1}).

3.2. Macrofauna

In total 112 operational taxonomic units (OTUs) were sampled, of which 22 OTUs occurred fewer than 5 times in the 3 years of sampling. Within a single sample point there were on average ~6 OTUs. Three of the 112 OTUs had a wide prevalence and occurred at more

Table 1

A description of the twelve tidal basins across the Dutch Wadden Sea, names ordered from west to east. The total area (Ha), the approximate area of intertidal flats (>0.2 ET, Ha), the proportion of each area that constitutes intertidal (%), the mean and range (maximum minus minimum values, in brackets) of exposure time (ET), median grain size (MGS, μm), vegetation index (NDVI), salinity, maximum current velocity (maxcurr, ms^{-1}) and orbital velocity (orbgolf, ms^{-1}) in each tidal basin.

Tidal basin	Total	Intertidal	%	ET			MGS			NDVI			Salinity	maxcurr	orbgolf
				2008	2009	2010	2008	2009	2010	2008	2009	2010			
Marsdiep	67,736	5610	8	0.16 (0.84)	0.17 (0.87)	0.17 (0.87)	165 (234)	163 (226)	163 (226)	0.09 (0.20)	0.10 (0.24)	0.10 (0.19)	18 (20)	0.54 (0.74)	0.28 (0.44)
Eierlandse Gat	15,806	6732	43	0.24 (0.91)	0.25 (0.94)	0.26 (0.93)	192 (164)	187 (216)	187 (216)	0.06 (0.13)	0.07 (0.15)	0.07 (0.18)	23 (8)	0.60 (0.90)	0.26 (0.47)
Vlie	68,937	14,640	21	0.20 (1.00)	0.20 (1.00)	0.21 (1.00)	165 (259)	159 (309)	159 (309)	0.08 (0.22)	0.08 (0.19)	0.09 (0.21)	17 (21)	0.56 (1.00)	0.28 (0.58)
Borndiep	333,279	127,748	38	0.22 (1.00)	0.22 (1.00)	0.23 (1.00)	136 (193)	135 (212)	135 (212)	0.09 (0.32)	0.10 (0.31)	0.12 (0.27)	17 (25)	0.56 (0.97)	0.26 (0.49)
Pinkgat	6156	2698	44	0.21 (1.00)	0.22 (1.00)	0.22 (1.00)	152 (171)	150 (164)	150 (164)	0.08 (0.20)	0.08 (0.22)	0.11 (0.24)	20 (13)	0.56 (0.96)	0.27 (0.55)
Zoutkamperlaag	16,015	7809	49	0.30 (1.00)	0.31 (1.00)	0.32 (1.00)	140 (140)	136 (154)	136 (154)	0.09 (0.19)	0.10 (0.25)	0.11 (0.23)	24 (15)	0.54 (0.78)	0.29 (0.60)
Ellanderbaag	3685	2162	59	0.30 (0.99)	0.31 (1.00)	0.31 (1.00)	139 (152)	141 (169)	141 (169)	0.09 (0.16)	0.10 (0.20)	0.11 (0.18)	25 (9)	0.52 (0.63)	0.24 (0.63)
Lauwers	14,206	7588	53	0.30 (0.98)	0.31 (0.99)	0.32 (0.99)	140 (167)	138 (172)	138 (172)	0.10 (0.25)	0.10 (0.19)	0.09 (0.20)	25 (11)	0.50 (0.65)	0.30 (0.50)
Schild	3588	2081	58	0.32 (1.00)	0.33 (1.00)	0.33 (1.00)	169 (64)	159 (147)	159 (147)	0.10 (0.26)	0.10 (0.11)	0.08 (0.20)	28 (5)	0.50 (0.72)	0.31 (0.40)
lower Ems	31,350	6573	21	0.22 (0.98)	0.23 (0.99)	0.24 (0.99)	141 (116)	139 (144)	139 (144)	0.09 (0.19)	0.10 (0.19)	0.09 (0.16)	28 (8)	0.58 (0.97)	0.40 (0.88)
upper Ems	9080	2673	29	0.17 (0.52)	0.18 (0.54)	0.19 (0.54)		110 (151)	110 (151)	0.16 (0.22)	0.12 (0.18)	0.14 (0.28)	21 (10)	0.56 (0.60)	0.25 (0.44)
Dollard	16,672	8083	48	0.38 (1.00)	0.40 (1.00)	0.40 (1.00)		84 (187)	84 (187)	0.21 (0.28)	0.16 (0.21)	0.15 (0.27)	10 (13)	0.45 (0.60)	0.29 (0.55)

than 35% of the sampled points, i.e. *Scoloplos armiger*, *Pygospio elegans* and *Aphelocheata marioni* (Table 2).

The mean benthic biomass across the sampled points was 24 g AFDM m^{-2} (median 6.1, $n = 3467$) in 2008, 26 g AFDM m^{-2} (median 6.4, $n = 4179$) in 2009 and 25 g AFDM m^{-2} (median 6.7, $n = 4035$) in 2010. Macrofaunal biomass was relatively low (<18 g AFDM m^{-2}) where the Marsdiep and Vlie tidal basins meet, in the northern part of the Vlie and Borndiep tidal basins and in the Dollard (cf. Figs. 1, 3). Furthermore, from west to east across the tidal basins, there was a trend for mean biomass to be highest in the basins of the eastern Wadden Sea (>25 g m^{-2}), lower in the western Wadden Sea (<25 g AFDM m^{-2}) and lowest in the upper Ems and the Dollard (<5 g AFDM m^{-2} , Fig. 4). Mean biomass also appeared to be consistently lowest across all basins in 2008, except the Schild basin (Fig. 4). The OTUs with the highest mean biomass across the sampled points for all sample years included: *C. edule* (4–7 g AFDM m^{-2}), *M. arenaria* (2–3 g AFDM m^{-2}), and *A. marina* (1–3 g AFDM m^{-2} , Table 3 & Fig. 5).

3.3. Species contributions

The relative contribution of individual macrofauna at sites changed from west to east across the Wadden Sea (Fig. 6). Specifically, for each tidal basin and for the three sampling years, the common cockle *C. edule* contributed proportionally the largest share of the benthic biomass in the eastern part, from the Borndiep to the lower Ems. By contrast, the soft-shell *M. arenaria*, the common cockle *C. edule* and the razor clam *E. directus* contributed a relatively large and equal share of the biomass in the western part of the system, from the Marsdiep to the Borndiep (Fig. 6). The lugworm *A. marina* was also an important share of the biomass, but this species did not vary greatly in its contributed share of biomass across the tidal basins. The upper Ems and the Dollard shared species with the remainder of the system but the relative contribution of these species differed. Notably, the relative contribution of the pile-worm *Alitta succinea* was highest in the upper Ems and Dollard. In addition, species like the soft-shell *M. arenaria* and the Baltic tellin *M. balthica* also contributed a relatively large share of the biomass in the upper Ems and Dollard (Fig. 6).

3.4. Generalised dissimilarity analysis

The GDM models explaining the compositional turnover between sites using the six environmental variables had relatively low deviances explained (4% in 2008, 6% in 2009 and 9% in 2010, Table 4). Furthermore, the improvement in the deviance explained was marginal when geographic distance between sites was added as a predictor variable (~1% improvement, Table 4). Median grain size played the largest role in explaining the compositional turnover in all three GDM models (maximum height of the fitted response curves, Table 4, Fig. 6), followed by exposure time (ET) in 2008 and microphytobenthic biomass (NDVI) in 2009 and 2010. The other variables played a smaller role, but had a similar ranked importance across all three models i.e. salinity (salwet), maximum current speed (maxcurr) and orbital velocity (orbgolf, Table 4, Fig. 7). Orbital velocity did not contribute to the explanatory power of the 2010 model and was thus excluded in this case.

The heights of the I-spline fitted response curves were also similar between years, except for median grain size. Rates of compositional change along a gradient, represented by the slopes of the I-spline fitted response curves, were relatively similar between years, except for 2010 where the response to microphytobenthic biomass differed (Fig. 6). In the case of median grain size (mgs), rates of compositional change were continuous along the entire gradient, with the greatest rates of change from ~0 to 200 μm . In the case of exposure time, assemblage composition change was greatest at the low fractions of

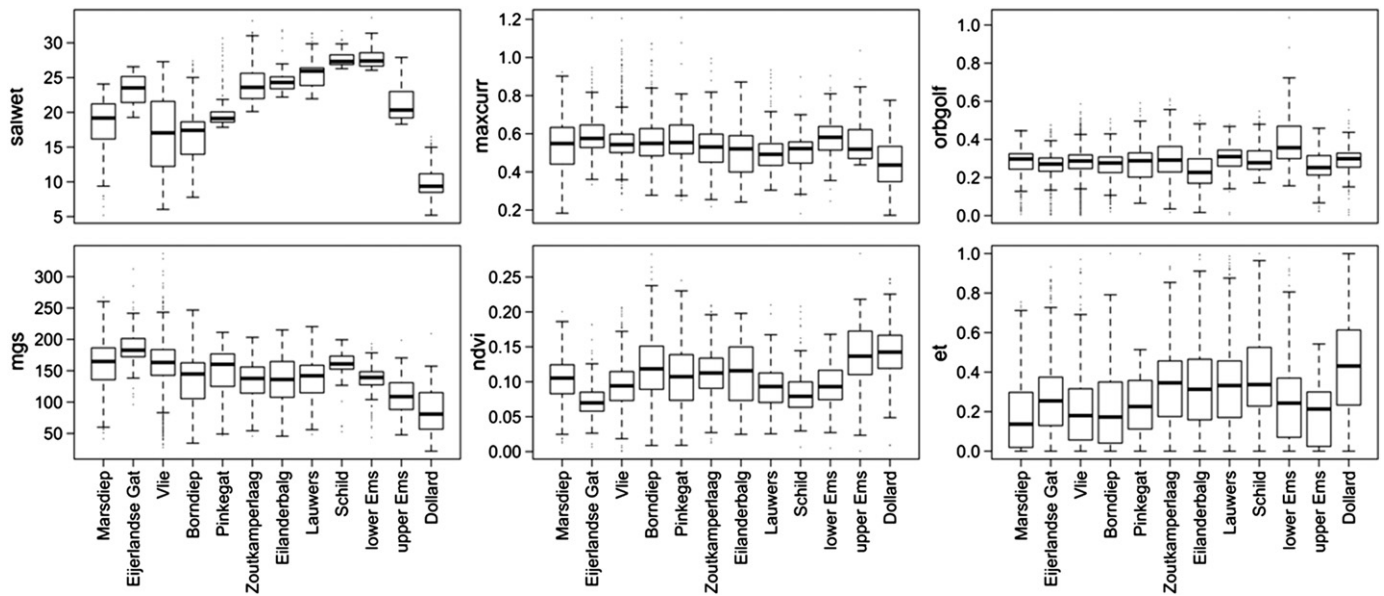


Fig. 2. The variation in the six environmental variables across each of the watersheds shown using boxplots. Boxplots represent the median value (solid middle line) and the upper and lower quartile (upper and lower hinges of the box), and the whiskers represent the range of values around the box. The environmental variables are described in Table 1.

exposure time (~ 0 – 0.2 ET) and became relatively homogenous towards high exposures (~ 0.2 – 1.0 ET). Rates of assemblage change were also fast from ~ 0 to 0.2 microphytobenthic biomass (NDVI) and ~ 0 – 17% salinity (salwet). Assemblages also showed the greatest turnover at high orbital velocities ($> 0.6 \text{ m s}^{-1}$) and low current speeds ($< 0.6 \text{ m s}^{-1}$).

Similar to the observed patterns, the spatial predictions representing assemblage change across the Wadden Sea (Fig. 8) showed similar gradients in assemblage composition across the system in all three years. Specifically, in the western part of the system, assemblages on the tidal flats near to the Texel and Vlieland inlets were associated with coarse grain sizes, shorter exposure times, relatively faster current speeds, larger orbital velocities and higher salinities on the edges of the flats. Assemblages on the high intertidal areas of Balgzand were associated with fine grain sizes, high microphytobenthic biomass and low salinities, whereas towards the Marsdiep assemblages were associated with short exposure times, coarser grain sizes and high salinities. Along the Frisian coastline, opposite to Terschelling, assemblages were strongly associated with longer exposure times, high microphytobenthic biomass, low salinities, slow current speeds, and fine grain sizes. In the narrowing part of the Wadden Sea, from Ameland to Schiermonnikoog and the upper Ems, assemblages were associated

with longer exposure times and finer sediments, or with short exposure times on the edges of the tidal flats near the gullies. In the area of the Dollard, assemblages were identified as being associated with relatively high exposure times, fine sediments, high microphytobenthos, and low salinities.

4. Discussion

In accordance with the multiple environmental gradients observed across the Wadden Sea, we showed that assemblages were distinct in the Dollard Region and that there was a different prevalence of assemblage types from the west to east across the system. First, species-level patterns showed that in the west, *M. arenaria*, *C. edule* and *E. directus* contributed the largest share of the total biomass. Whereas, *C. edule* contributed the sole largest share of the total biomass in the east. These changes in relative biomass contributions likely reflect the tolerance of *M. arenaria* to low salinities and the high density of the razor clam *E. directus* in the transition zone between the subtidal and intertidal in the western Wadden Sea (Dekker and Beukema, 2012). A possible reason for the biomass dominance of *C. edule* in the eastern Wadden Sea is an increase in intertidal flats with suitable habitat (Kamermans, 1993) or higher microphytobenthos in

Table 2

The ten most prevalent species in the Wadden Sea in 2008, 2009 and 2010. The number of positive observations (nr) recorded across the sampling grid in each year and also the relative percentages observed (%) are given.

2008			2009			2010		
spp.	Nr	% sites	spp.	Nr obs	% sites	spp.	Nr obs	% sites
<i>Scoloplos armiger</i>	1881	44	<i>Pygospio elegans</i>	2905	68	<i>Pygospio elegans</i>	2743	64
<i>Pygospio elegans</i>	1499	35	<i>Scoloplos armiger</i>	2637	62	<i>Scoloplos armiger</i>	2575	60
<i>Aphelocheata marioni</i>	1359	32	<i>Aphelocheata marioni</i>	2159	51	<i>Marenzelleria viridis</i>	2258	53
<i>Hediste diversicolor</i>	1066	25	<i>Eteone longa</i>	1818	43	<i>Aphelocheata marioni</i>	2117	50
<i>Macoma balthica</i>	1063	25	<i>Capitella capitata</i>	1643	39	<i>Capitella capitata</i>	2028	48
<i>Capitella capitata</i>	1024	24	<i>Macoma balthica</i>	1340	31	<i>Eteone longa</i>	1836	43
<i>Lanice conchilega</i>	1009	24	<i>Oligochaeta</i> sp.	1303	31	<i>Macoma balthica</i>	1710	40
<i>Oligochaeta</i> sp.	841	20	<i>Hediste diversicolor</i>	1282	30	<i>Arenicola marina</i>	1518	36
<i>Cerastoderma edule</i>	821	19	<i>Arenicola marina</i>	1241	29	<i>Oligochaeta</i> sp.	1418	33
<i>Urothoe poseidonis</i>	799	19	<i>Urothoe poseidonis</i>	1157	27	<i>Hediste diversicolor</i>	1417	33
TOTAL nr sites	4257		TOTAL nr sites	4673		TOTAL nr sites	4473	

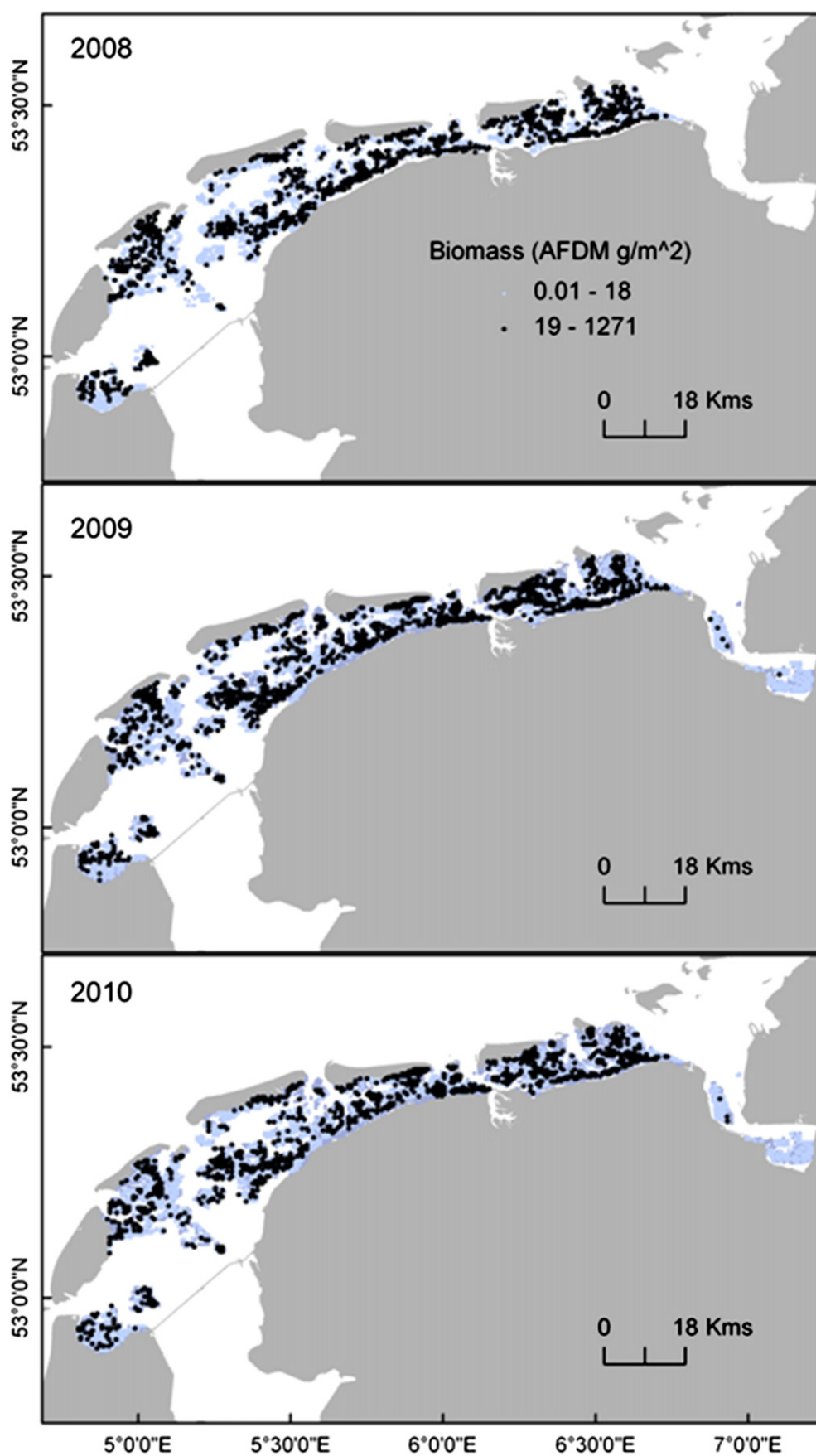


Fig. 3. The spatial distribution of benthic biomass (g/m²) across the Dutch Wadden Sea in 2008, 2009 and 2010. Darker symbols indicate areas where the benthic biomass was greater than 18 g/m² and lighter symbols indicate where the benthic biomass was less than 18 g/m².

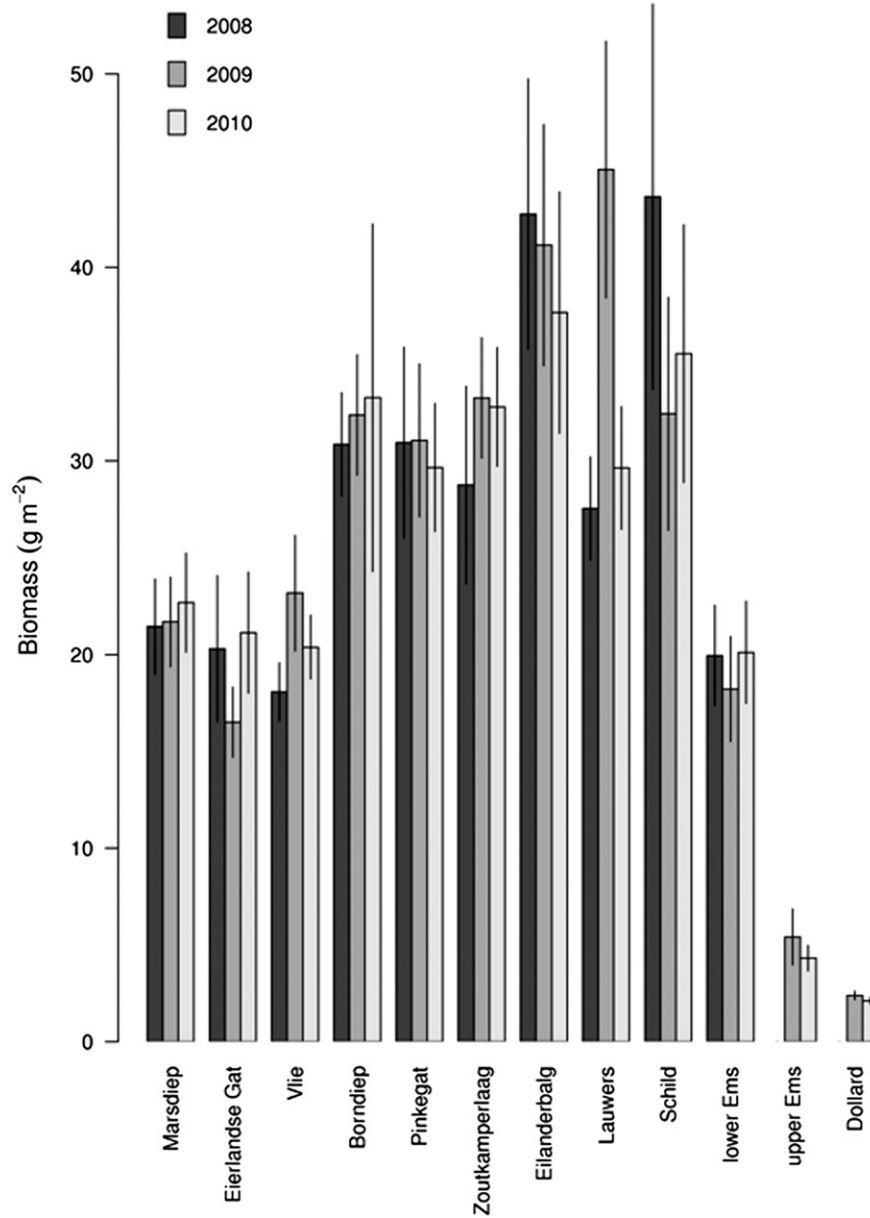


Fig. 4. Average benthic biomass (g m^{-2}) at each of the tidal basins from west to east across the Dutch Wadden Sea for each sample year. Standard error bars are shown.

Table 3

The average biomass (mean AFDM g m^{-2}) of 19 species that together constituted 95–97% of the total biomass across the sampling sites in the three sampling years. The percentage contribution of each species to the total biomass for all three years combined is shown (%).

Species	Biomass (AFDM g m^{-2})			
	2008	2009	2010	%
<i>Cerastoderma edule</i>	5.9637	7.0751	4.8013	27
<i>Mya arenaria</i>	2.3298	2.9774	3.4134	13
<i>Arenicola marina</i>	1.3729	2.2353	3.2166	10
<i>Ensis directus</i>	1.4562	2.6145	1.4310	8
<i>Lanice conchilega</i>	2.5950	1.3476	0.4710	7
<i>Macoma balthica</i>	0.5865	1.0015	2.2282	6
<i>Mytilus edulis</i>	0.8445	1.6354	1.2413	6
<i>Hediste diversicolor</i>	0.9111	0.8463	0.8370	4
<i>Crassostrea gigas</i>	0.9207	0.7402	0.8102	4
<i>Scoloplos armiger</i>	0.3201	0.5140	0.8396	3
<i>Carcinus maenas</i>	0.4889	0.3660	0.1464	2
<i>Scrobicularia plana</i>	0.2406	0.2635	0.4771	2
<i>Marenzelleria viridis</i>	0.1813	0.2056	0.4040	1
<i>Alitta virens</i>	0.2577	0.1544	0.2919	1
<i>Nephtys hombergii</i>	0.2346	0.1772	0.0856	1
<i>Alitta succinea</i>	0.1208	0.1488	0.1743	1

this area (see Supplementary material of this manuscript and van der Wal et al., 2010). In the upper Ems and Dollard, the pile worm *A. succinea* became a large part of total biomass. *A. succinea* is known for its ability to tolerate low salinities (Glasby and Timm, 2008) and its ability to thrive in areas with very fine sediments (R. Dekker, pers. comm.). *A. marina*, known as the largest and quantitatively most important bioturbating deposit feeder in the Wadden Sea (Cadée, 1976), was also an important part of the biomass that contributed a relatively equal proportion of biomass across all watersheds, except for the Dollard where the proportion was smaller. In addition, we also showed that total biomass increased from west to east across the system and that this trend appeared largely consistent across the three sample years.

The spatial patterns in biomass observed during our study were similar to those observed by Beukema (1976). Specifically, that standing stock of biomass increased from west to east, and that the Vlie basin had the lowest biomass. Interestingly, these patterns are matched closely by the microphytobenthic biomass, i.e. lowest values in the Vlie basin and highest values in the eastern Wadden Sea (van der Wal et al., 2010). Another similarity between our studies is that

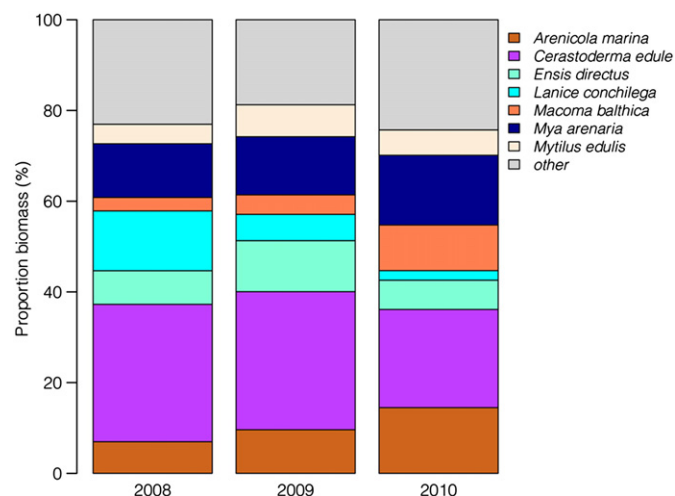


Fig. 5. The proportion (%) of the total biomass (A) constituted by nine common OTUs relative to the remaining OTUs (others), grouped together, for each of the sampling years. Common species were selected from Table 3.

we both found that few species comprised the majority of the biomass and that the identities of these species were largely the same, although the rank importance differed. In the case of Beukema (1976) the six most important species were, in ranked order: *M. edulis*, *A. marina*, *M. arenaria*, *C. edule*, *M. balthica* and *Hediste diversicolor*. In our study, these were, in ranked order: *C. edule*, *M. arenaria*, *A. marina*, *E. directus*, *Lanice conchilega*, *M. balthica* and *M. edulis*. Finally, the average biomass per sample point observed in

the three years of sampling was similar to those observed by Beukema (1976). However, the absolute values should be interpreted with caution as Beukema's estimates were based on an annual average, whereas our data is based on a summer average, a time of the year that biomass values are at their highest (Beukema, 1974, 1982).

Spatial patterns in assemblage composition as predicted by the GDM modelling approach, followed the observed species-level results, but provided a more detailed view of how assemblages differed with respect to the environmental variables and across geographic space. Although model performance was lower relative to other studies that have examined assemblage composition with respect to environment using similar approaches (Compton et al., 2013; Leaper et al., 2011; Pitcher et al., 2012), it is notable that this is probably an indication of different sampling intensities between studies (van der Meer, 1991). But other reasons for the low explanatory power of our models could be the quality of the predictor variables, the inability of GDM to model interactions between the variables or the role of other factors like historical events, connectivity, recruitment variability and species interactions (predation, competition and facilitation; e.g. Piersma, 1987; Piersma et al., 1993; van der Zee et al., 2012), which are not taken into account using approaches like GDM (Pitcher et al., 2012). Specifically, our current measures of salinity, orbital velocity and maximum current speeds might lower the GDM performance as they are derived from model simulations of specific climatic events in a single year in the 1980s. Furthermore, although geographic distance did not improve the performance of our models, suggesting that we did not miss variables, other environmental variables that might provide other insights into the turnover in assemblage composition would have included phytoplankton biomass or the spatial distribution of minimum winter temperatures prior to

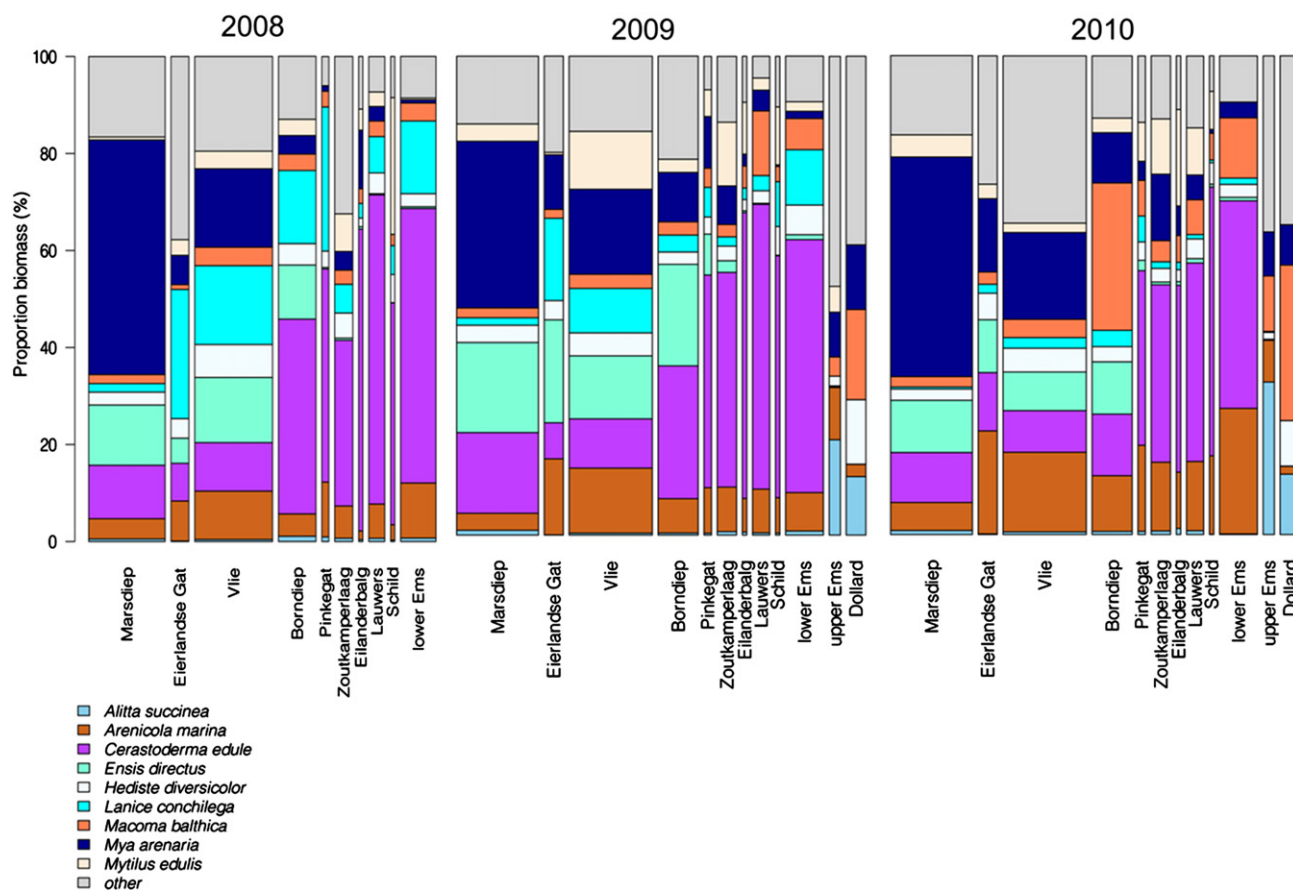


Fig. 6. The proportion (%) of biomass contributed by common OTUs across the tidal basins of the Dutch Wadden Sea. The proportions of the less common OTUs were summed to give a combined percentage (other). The width of the bars is proportional to the total area of each tidal basin.

Table 4

Model performance of the GDM models for 2008, 2009 and 2010 using the six predictor variables alone (Env) and the six predictor variables and geographic distance (Env + xy). The measures of performance include the null deviance (Null), the unexplained deviance (Dev) and the percentage explained deviance (% Expl). The number of sites (nsites) and species modelled are provided (nsp). The contribution of each variable to explaining the change in assemblage composition is provided and variables with the most influence are shown in bold. Variables used for the model are explained in the results.

yr	nsites	nsp	Env			Geo			Variable contributions					
			Null	Dev	%	Null	Dev	%	orbgolf	salwet	mgs	ndvi	et	maxcurr
2008	2339	66	889093	855877	4	889093	848815	5	0.46	0.22	0.80	1.00	0.64	0.60
2009	2692	79	1116520	1050137	6	1116520	1041383	7	0.58	0.41	1.50	0.90	0.61	0.45
2010	2600	71	1059632	960816.8	9	1059632	951526.8	10	0.00	0.48	2.23	1.17	0.77	0.58

sampling. For example, a number of species are known to decline in biomass after severe winters: *L. conchilega*, *C. edule*, *A. succinea* and *Nephtys hombergii* (Beukema et al., 1993) and indeed we observed that *L. conchilega* declined in biomass after a cold-spell in a previous winter.

Across all three years, the variable most important for explaining the spatial variation in the composition of macrofaunal assemblages was median grain size, followed by microphytobenthic biomass and exposure time. Salinity during a wet period, maximum current speeds and orbital velocities all played smaller roles. These results accord with other studies that identified similar variables as important for explaining the distribution of macrofaunal species (e.g. Beukema, 1976; Kraan et al., 2010; van der Meer, 1991; van der Wal et al., 2008; Ysebaert et al., 2002) and benthic assemblages (van der Meer, 1999; Ysebaert et al., 2003). But note that like other species or community modelling approaches, these relationships are correlative and thus inform us as to possible drivers of composition change but do not necessarily imply a causal link (Pitcher et al., 2012). The similarity in the slopes and heights of the response curves between years suggests that compositional changes are determined largely by the order of species along an environmental gradient rather than non-environmentally driven temporal changes in the biota due to other drivers of biological variability (also discussed by van der

Meer, 1999). A comparison with the raw data also showed that the relative contribution of the species across the systems appeared to be relatively constant, e.g. more *C. edule* in the east compared to the west, although the total biomass of the individual species varied between years. This matches with other community analyses that have shown that although abundances can fluctuate dramatically between years, assemblage composition is relatively constant between years (van der Meer, 1999; Ysebaert and Herman, 2002). Although the response curves for most of the environmental variables were largely similar between years, there were two exceptions: median grain size and microphytobenthic biomass. These differences could indicate a change in species composition or a change in biomass, but these aspects cannot be separated because Bray–Curtis similarities are an index. Interestingly, these were two variables that were measured around the period of sampling.

The predicted spatial patterns in assemblage composition identified that assemblages high on the tidal flats near to the inlets were associated with coarser sediments and low microphytobenthic biomass. Some macrofauna known to occur in exposed areas with coarse grain sizes include *Bathyporeia* sp., *Scolecopsis squamata* and *Tellina tenuis* (Dankers and Beukema, 1981). By contrast, assemblages on the tidal flats along the Frisian coast were predicted to be associated with finer sediments and high microphytobenthic biomass. In the Balgzand

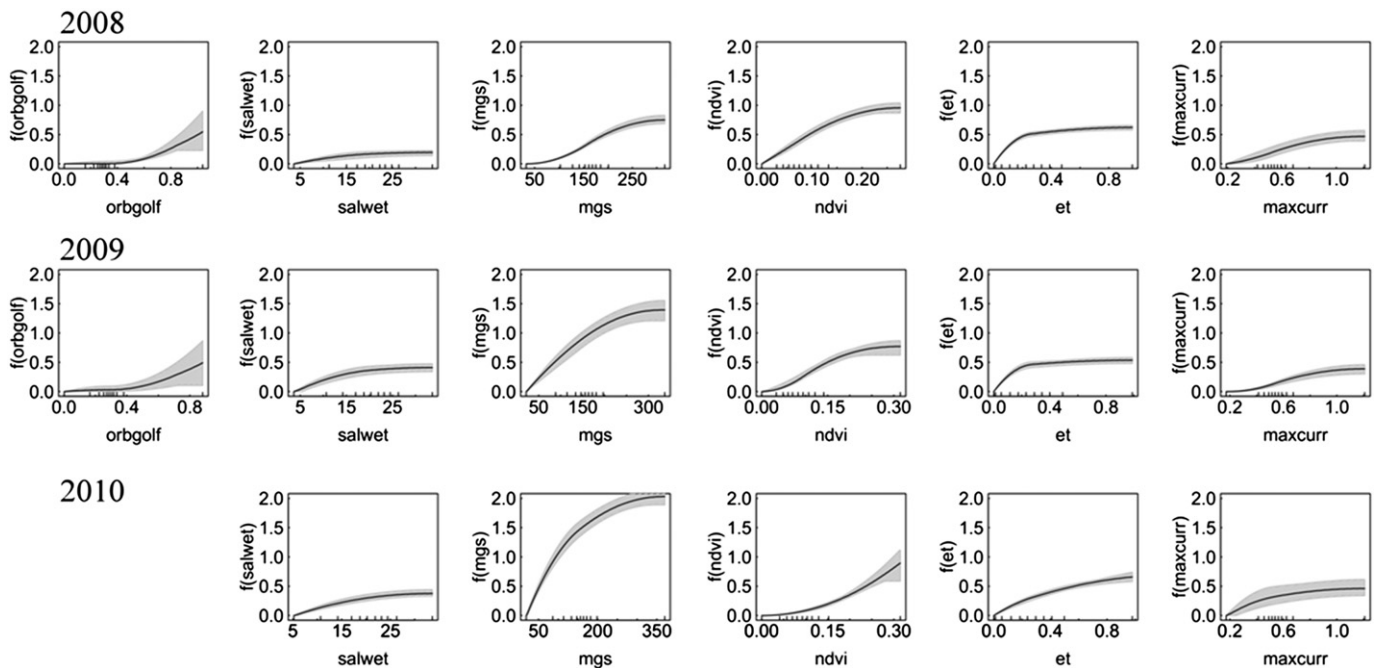


Fig. 7. The GDM I-spline basis and their bootstrapped confidence intervals representing the turnover in compositional change with respect to the environmental variables in each sample year (2008, 2009, and 2010). The y-axes represent the transformed Bray–Curtis dissimilarities in the units of the additive exponential link function (see Eq. (1)). The maximum height of the transformed Bray–Curtis dissimilarities represents the contribution of a variable to explaining compositional turnover, and the non-linearity in the response of to each of the environmental variables indicates where along a gradient the compositional turnover is steepest. The rug on the bottom of the plot indicates the distribution of the raw data.

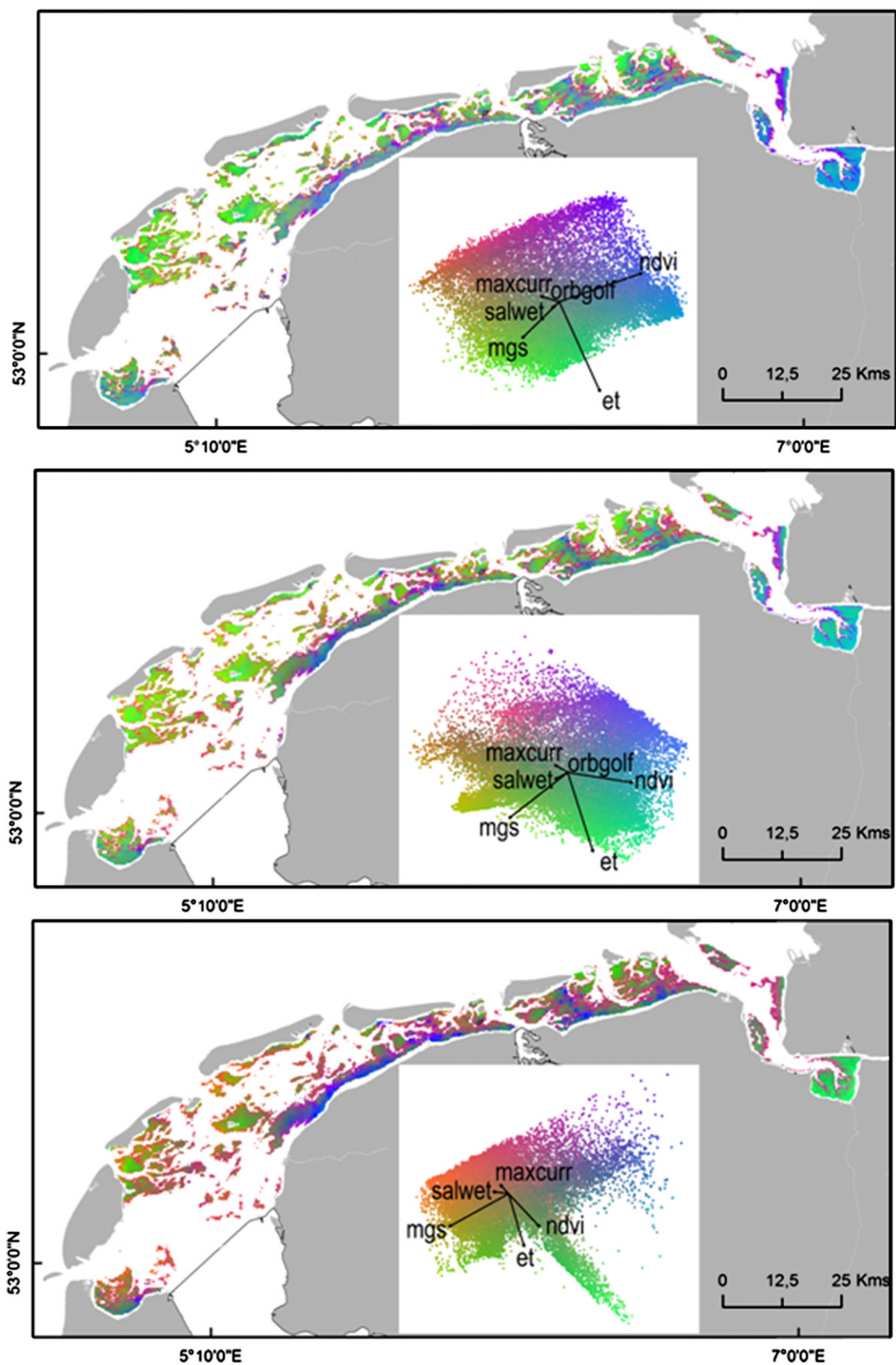


Fig. 8. The maps represent the spatial pattern in assemblage composition as predicted by the GDM models. The colours represent gradients in assemblage turnover as derived from the GDM model and the environmental gradients across the Wadden Sea. The vector plots indicate the contribution of the environmental variables to the predicted patterns of assemblage turnover. Although sampling was not conducted in the German part of the Ems, predictions have been extrapolated into this region based on the GDM model and the gridded environmental layers (see Appendix 1).

area three assemblage types were predicted: high, middle and relatively low intertidal. These results concur with a recent study that showed assemblage composition changed along the tidal gradient in the Balgzand (van der Graaf et al., 2009). On the high intertidal *M. balthica* and *Nephtys diversicolor* were shown to dominate the assemblage, in the middle *M. arenaria* dominated, and in the low intertidal *E. directus* was the species with the most biomass (van der Graaf et al., 2009).

5. Conclusions

We have presented the first exploration of benthic assemblage patterns across the intertidal part of the Dutch Wadden Sea using three years of spatially extensive data. Between years patterns were consistent and showed that assemblages in the Dollard differed to other areas, but also that there was a different prevalence of assemblage types from west to east. The variables most associated with the turnover in benthic assemblages were median grain size, microphytobenthic biomass and exposure time. Our results show that the biological and environmental complexity of the Wadden Sea necessitates a comprehensive monitoring of assemblage composition to manage biodiversity in this ecologically important mudflat system in fully informed ways.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.seares.2013.02.002>.

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