



Original Article

Relationships between macrozoobenthos and habitat characteristics in an intensively used area of the Dutch coastal zone

Maarten F. de Jong^{1,2*}, Martin J. Baptist¹, Han J. Lindeboom^{1,2}, and Piet Hoekstra³

¹Department of Ecosystems, IMARES Wageningen UR, Institute for Marine Resources and Ecosystem Studies, PO Box 167, 1790 AD Den Burg, The Netherlands

²Department of Aquatic Ecology and Water Quality Management, Wageningen UR, PO Box 47, 6700 AA Wageningen, The Netherlands

³Institute for Marine and Atmospheric Research Utrecht, Faculty of Geosciences, Utrecht University, PO Box 80.115, 3508 TC Utrecht, The Netherlands

*Corresponding author: tel: +31 644 598 167; fax: +31 317 487 362; e-mail: maarten.dejong@wur.nl

de Jong, M. F., Baptist, M. J., Lindeboom, H. J., and Hoekstra, P. Relationships between macrozoobenthos and habitat characteristics in an intensively used area of the Dutch coastal zone. – ICES Journal of Marine Science, 72: 2409–2422.

Received 25 August 2014; revised 13 March 2015; accepted 19 March 2015; advance access publication 29 April 2015.

Distribution patterns and species composition of macrozoobenthos were studied in the Dutch coastal zone in front of the Port of Rotterdam. Relationships between macrozoobenthic assemblages and environmental variables were determined using non-metric dimensional scaling (nMDS) based on 470 boxcore, bottom sledge, and sediment samples collected in spring 2006 and 2008 in a 2500-km² research area. We investigated two types of benthic assemblages, infaunal assemblages sampled with a boxcorer and epifaunal assemblages sampled with a bottom sledge. Five main in- and epifaunal assemblages were distinguished using clustering techniques and nMDS ordinations. Macrozoobenthic species composition correlated with combinations of measured sediment variables and modelled hydrodynamic variables. Macrozoobenthic species richness and biomass were highest at 20 m deep areas with a grain size of 200 µm, elevated mud and sediment organic matter, and low mean bed shear stress. Considerable interannual differences in macrozoobenthic assemblage distribution were observed which resulted from more Echinoids, Phoronids, and jackknife clams. A distinct, highly productive and species-rich macrozoobenthic white furrow shell *Abra alba* assemblage coincided in a 8-m deepened shipping lane and near a disposal site for dredged fine sediment. This may be an indication that the benthic system can be changed by these human activities. Modelled bed shear stress is an important variable in addition to sediment variables in explaining distribution patterns in macrozoobenthos.

Keywords: bed shear stress, near-bed salinity, North Sea, sand extraction, sediment characteristics.

Introduction

The Dutch coastal zone in front of Port of Rotterdam (PoR) is marked by intensive human use, including activities such as fishery, shipping, wind farming, disposal of dredged sediment, as well as sand, gas, and oil extraction. These activities have different effects on the marine environment and some are likely to intensify (Jongbloed *et al.*, 2014).

Macrozoobenthos on the North Sea scale is correlated with environmental variables such as sediment mud content, water depth, water temperature, sediment median grain size, sediment chlorophyll *a* content, sediment organic carbon content, and latitude (Heip *et al.*, 1992; Künitzer *et al.*, 1992; Holtmann *et al.*, 1996; Degraer *et al.*, 1999; Van Hoey *et al.*, 2004, 2007; Degraer

et al., 2008; Verfaillie *et al.*, 2009). Near-bed salinity affected epifauna (EP) in the North Sea (Callaway *et al.*, 2002; Reiss *et al.*, 2010, 2011), whereas bed shear stress affected macrozoobenthos in Dutch intertidal areas (Herman *et al.*, 2001; Ysebaert *et al.*, 2003). Bed forms also influence small-scale macrozoobenthic distribution and composition (Baptist *et al.*, 2006; van Dijk *et al.*, 2012). Owing to climate and seasonal fluctuations, temporal variations in species composition commonly occur (Straile and Stenseth, 2007; Kröncke *et al.*, 2013). We studied distribution patterns, species composition, and temporal differences of in- and epifaunal assemblages in an intensively used Dutch coastal zone in front of PoR. Relationships between macrozoobenthos, measured environmental variables, and modelled hydrodynamic variables were determined

based on high-resolution data. This study can be used as a baseline for future comparisons and to help in the protection of marine biodiversity. Determined relationships between macrozoobenthos and environmental variables can be used for the prediction of ecological effects due to human activities.

We aim to answer the following questions:

- (i) Which environmental variables influence macrozoobenthos?
- (ii) Are there significant differences in macrozoobenthic assemblages in the intensively used area of the Dutch coastal zone?
- (iii) Are there temporal differences in the distribution of macrozoobenthic assemblages?

Material and methods

Research area

The research area stretches over 2500 km² in front of the PoR (Figure 1). The seabed consists of fine (125–250 μm) to medium (250–500 μm) sand deposited during the Holocene. The shallowest part is the shoreface (Figure 1, no. 1), an area with alongshore outer breaker bars and a maximum water depth of 10 m. The northern part of the research area is characterized by the presence of shoreface-connected ridges (Figure 1, no. 2) with crest orientations 20–35° clockwise with respect to the coast-parallel tide (van de Meene and van Rijn, 2000b). These ridges can be up to 30 km long, up to 2–4 km wide, between 2 and 6 m high, and are situated in water depths between 14 and 18 m (van de Meene and van Rijn, 2000a).

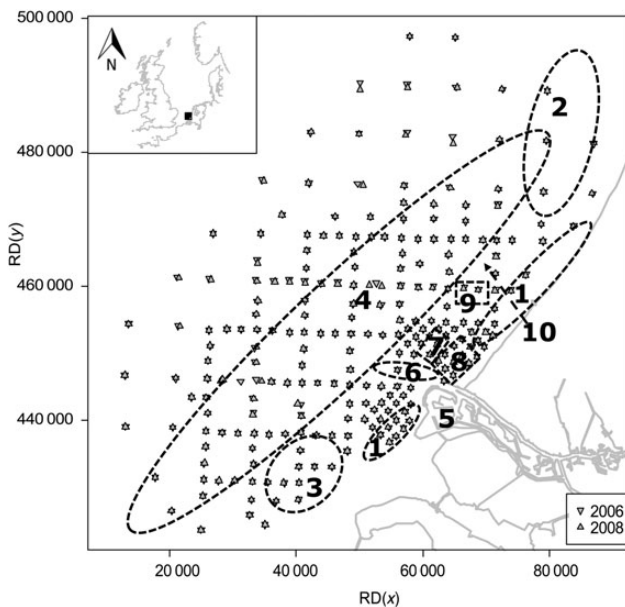


Figure 1. Two hundred and thirty-five sampling locations of the PoR baseline study in 2006 and 2008. Dashed ellipses show four distinct morphological units and three important user functions: (1) the shoreface, (2) shoreface-connected ridges, (3) Zeeland ridges, (4) sand waves, (5) the PoR without Maasvlakte 2, (6) Euromaasgeul shipping lane, (7) the lowered disposal site (Verdiepte Loswal) for fine sediment, (8) disposal site “North” (Loswal Noord) for coarser sediment, (9) disposal site “Northwest” (Loswal Noord West), and (10) sewage treatment effluent discharge (RWZI “Houtrust”). Coordinates are in Dutch National Grid.

The Voordelta region, the southern part of the research area, is characterized by Zeeland ridges (Figure 1, no. 3). Sand waves (Figure 1, no. 4) are found in deeper waters, with wavelengths of 100–800 m, amplitudes up to 5 m (Hulscher, 1996), and crests orientated perpendicular to the tidal current.

Human activities

A 57 km long and 8 m deepened shipping lane, the Euromaasgeul (de Ronde, 2008), was realized in the 1970s to guarantee access to the PoR (Figure 1, no. 6). Areas near the Euromaasgeul are used for anchoring of vessels. To guarantee accessibility, 2.6 million m³ of sediment was dredged out of the shipping lane and harbour from 2001 to 2005, and relocated to disposal sites “Northwest” (Figure 1, no. 9 and Supplementary Appendix VI, no. 9) and the lowered disposal site (Figure 1, no. 7 and Supplementary Appendix VI, no. 7). From 2007 to present, coarser sediment (~0.8 million m³) is relocated in the coastal foundation directly north of the shipping lane at the disposal site “North” (Figure 1, no. 8 and Supplementary Appendix VI, no. 8), whereas the finer sediment is relocated to the lowered disposal site. The disposal site “North” was earlier used from 1961 until June 1996. Fine particles are distributed to the near surrounding of disposal sites (Stronkhorst et al., 2003). In the Dutch coastal zone, 24 million m³ sand is extracted annually from local borrow pits outside the 20-m isobath. A sewage effluent discharge (RWZI “Houtrust”) is located 3.5 km northeast of disposal site “Northwest” (Figure 1, no. 10 and Supplementary Appendix VI, no. 11).

Fishing effort is not uniformly distributed in the study area. Higher intensities of beam trawling, seine fishing, and otter trawling are found in near shore waters. Outside the 12-mile zone, beam trawl fishery is uniformly distributed (WGSFD, 2014).

Macrozoobenthos sampling

We used data from the baseline study of the Environmental Impact Assessment (EIA) for the construction of Maasvlakte 2 of the PoR that were collected in spring 2006 and 2008. From this study, 470 boxcore, bottom sledge, and sediment samples collected at 235 sampling locations in a 2500-km² research area in front of PoR were selected (Figure 1). Sample stations were located in a grid. Two grid refinements were implemented in coastward direction, in order to sample more variation in biotic and abiotic variables resulting from the Rhine region of freshwater input (Rhine ROFI) and human activities.

Bottom sledge sampling locations matched boxcore sampling locations. Sampling was executed from 18 April to 22 June 2006 and 17 April to 17 June 2008. The ships’ GPS system logged position of the sampling locations. We used water depth data from the Netherlands Hydrographic Office (multibeam, 25 × 25 m resolution) with reference level lowest astronomical tide.

The boxcoring was used to sample macrobenthic infauna (IN), larger than 1 mm and mostly living in the seabed. The Monitor Taskforce of the Royal Netherlands Institute for Sea Research (NIOZ) executed the boxcore sampling. The boxcoring surface area was 0.0774 m², with a maximum penetration depth of 30 cm. Samples were wet-sieved using a 1-mm mesh sieve and the residue was stored in jars with a seawater solution of 6% buffered formaldehyde (Perdon and Kaag, 2006; Craeymeersch and Escaravage, 2010). Specimens were identified up to species level when possible. Infaunal ash-free dry weight biomass (g AFDW m⁻²) was analysed by loss on ignition, 2 days at 80°C followed by 2 h at 580°C. When sea urchins were smaller than 5 mm identification, up to species level was impossible and lumped as *Echinoidea* spp.

The bottom sledge was used to sample macrobenthic IN and EP with a size range of 0.5–10 cm. Bottom sledge samples are hereafter called EP, although large IN are collected as well. The Institute for Marine Resources and Ecosystem Studies (IMARES Wageningen UR) executed the bottom sledge sampling. The sledge was equipped with a 5-mm mesh cage. On average, a surface area of 15 m² was sampled during each sledge haul of ~150 m length, 10 cm width, and a maximum penetration depth of 10 cm. Wet weight of EP was directly measured (g m⁻² WW). Jackknife clam *Ensis* spp. was not captured in whole, so biomass was determined by using regression equations based on previous IMARES field surveys (Craeymeersch and van der Land, 1998). Sea urchins (*Echinoidea* spp.) are too fragile and were completely damaged after a bottom sledge sampling procedure and therefore not countable.

Sediment sampling

Sediment samples from the upper 5 cm were collected from untreated boxcore samples and kept frozen until analysis. Sediment samples were freeze-dried, homogenized, and analysed with a Malvern Mastersizer 2000 particle size analyser. Percentile sediment grain size (D_{10} , D_{50} , and D_{90}) and sediment grain size distribution among the different classes: clay (<4 µm), silt (4–63 µm), mud (<63 µm), very fine sand (63–125 µm), fine sand (125–250 µm), medium sand (250–500 µm), and coarse sand (500–1600 µm) were measured as the percentage of total volume. Sediment grains larger than 1600 µm were not taken into account in this study. Sediment sorting (D_{90}/D_{10}) was calculated and sediment organic matter (SOM) was analysed by loss on ignition (LOI) and expressed as percentage of sediment mass; sediment samples were freeze-dried and placed for 2 h at 580°C.

The LOI method used to analyse infaunal ash-free dry weight biomass and SOM may be prone to overestimation due to the loss of carbon from the combustion of carbonate above temperatures of 550°C and from differences in dehydration rates of clays (Santisteban *et al.*, 2004). SOM values derived by LOI were compared with unbiased organic carbon values derived with a CHN analyser (CE Instruments NC2500). This comparison revealed a linear relationship in the range of 0–5% organic matter. Organic carbon values are six times lower than SOM values (Dorst, 2012).

Modelling of hydrodynamic variables

Hydrodynamic data were modelled for the year 2007 by using a hydrodynamic model for the Southern North Sea (Zuidelijke Noordzee: ZUNO) in the Delft3D FLOW simulation package. The year 2007 is commonly used in earlier reports (de Mesel *et al.*, 2011) and is considered as an average climatological year. The horizontal grid ranged from 6–20 by 5–30 km with finest resolution in the research area (6 × 5 km). Twelve vertical σ -layers were used with finer vertical resolution selected near the seabed and sea surface. From top to bottom, these layers, respectively, represent 4.0, 5.6, 7.8, 10.8, 10.9, 10.9, 10.9, 10.9, 10.8, 7.8, 5.6, and 4.0% of the water depth. Water flow is modelled using time-steps of 5 min and forced with open boundary conditions, meteorological and riverine discharge data for the modelled period (de Mesel *et al.*, 2011; Tonnon *et al.*, 2013). Yearly averaged (mean) and maximum values of bed shear stress (N m⁻²) and near-bed salinity (ppt) were calculated from the 2007 model run.

Statistical analysis

Infaunal and epifaunal species composition were analysed using hierarchical agglomerative clustering with the Bray–Curtis dissimilarity index based on fourth root-transformed abundance data and

average linkage (Legendre and Legendre, 1998) using the HCLUST function of package “vegan” (Oksanen, 2013). The number of significant macrozoobenthic species assemblages, with the assumption of no *a priori* groups, was assessed with the similarity profile routine SIMPROF of package “Clustsig” (Clarke *et al.*, 2008). Dufrene–Legendre indicator species analysis was applied using the *indval* function of package “labdsv” to determine indicator species of species assemblages based on the product of the relative frequency and relative average abundance (Dufrene and Legendre, 1997). Shapiro–Wilk test, Levene’s test, and diagnostic residuals plot were used to check for normality and homogeneity of abiotic variables. The non-parametric Kruskal–Wallis one-way multi-comparison tests (package “pgirmess”) were used to determine significant differences in biotic and environmental variables between assemblages. We used non-metric dimensional scaling (nMDS) of package “Vegan”. Bray–Curtis dissimilarities were used to calculate differences in species composition (Clarke and Ainsworth, 1993; Oksanen, 2013). The lowest-stress ordination was selected after repeating the nMDS routine with two-, three-, and four-dimensional settings with untransformed, square and fourth root-transformed data to reduce heteroscedasticity. Stress values below 0.2 are regarded as potentially useful, whereas values below 0.1 are regarded as good ordinations (Clarke and Warwick, 2001). Variables were fit to the nMDS ordination using the *envfit* function in package “vegan” (999 permutations) to find significant correlations. Assemblages in the nMDS ordination are positively correlated when they match with the superimposed correlation arrows of an environmental variable and are negatively correlated when they are in opposite direction. The arrow shows the direction of the increasing gradient of the environmental variable, and the length of the arrow is proportional to the correlation coefficient between the variable and the nMDS ordination. The *bioenv* function in “vegan” was used to determine the best subset of environmental variables, so that the Euclidean distances of scaled environmental variables have the maximum Spearman rank correlation with the macrozoobenthic community dissimilarities. When Spearman rank correlation coefficients between a set of environmental variables exceeded 0.9, one of the variables was dropped (Zuur *et al.*, 2007). Maps of biotic and abiotic variables were made using bicubic interpolation of package “akima”. For all analyses, we used R: A Language and Environment for Statistical Computing, version 3.0.1 (R Core Team, 2013).

Results

High macrozoobenthic biomass was found just outside the 20-m isobath (Figure 2). The highest biomass values were detected in 2006 near the Zeeland banks in the southern part of the research area (Figure 1, no. 3).

The largest D_{50} was found near the Zeeland ridges, whereas in front of PoR the smallest grain size and highest sediment mud content, SOM content, and very fine sand fraction were found (Figure 3). At disposal site “North”, the highest bed shear stress values were calculated due to decreased water depths and coarser sediment is found. Fine sediment rich in mud and SOM was found near the lowered disposal site and also 20 km north of PoR, which is the result of effluent discharge of a sewage treatment installation (RWZI “Houtrust”). Highest mean bed shear stress was calculated in the southern part of the research area and near-bed salinity decreased in coastward direction. Mean and maximum near-bed salinity and water depth were strongly correlated in 2006 and 2008 with a correlation coefficient of 0.8–0.9 (Supplementary Appendix I).

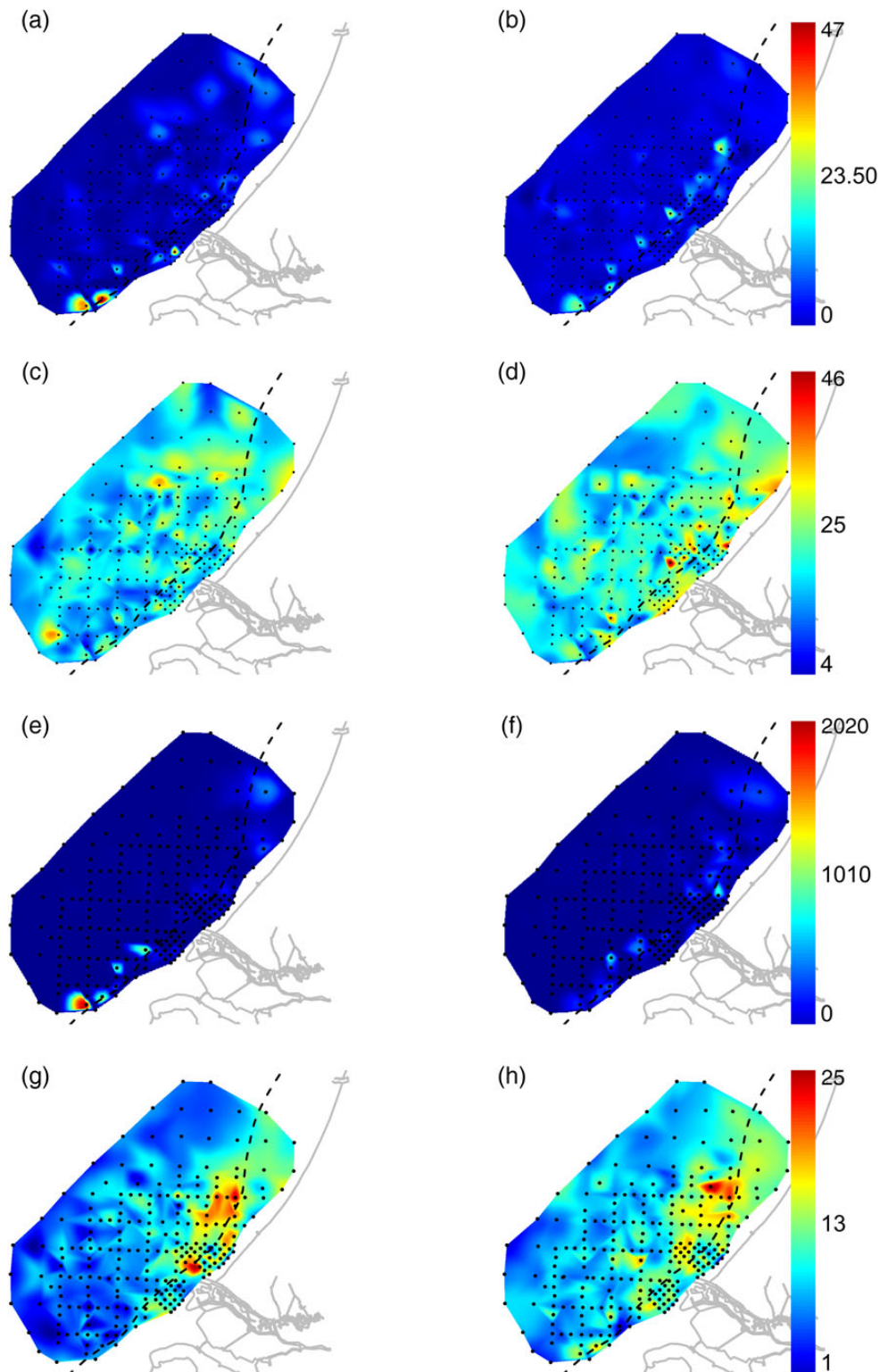


Figure 2. Measured biotic variables in 2006 and 2008, (a and b) infaunal ash-free dry weight (g AFDW m^{-2}), (c and d) infaunal species richness (number of species per sample), (e and f) epifaunal wet weight biomass (WW, g m^{-2}), and (g and h) epifaunal species richness. The 20-m isobath is depicted with the dashed line.

Clustering and species composition of IN samples

Based on a 70% Bray–Curtis dissimilarity threshold, 18 infaunal species assemblages were distinguished. In total, 450 sampling

locations were grouped into five main assemblages (Supplementary Appendix II). The remaining smaller assemblages are indicated with an *R* in Figure 4. According to the simprof analysis, all 18 infaunal assemblages were significantly different.

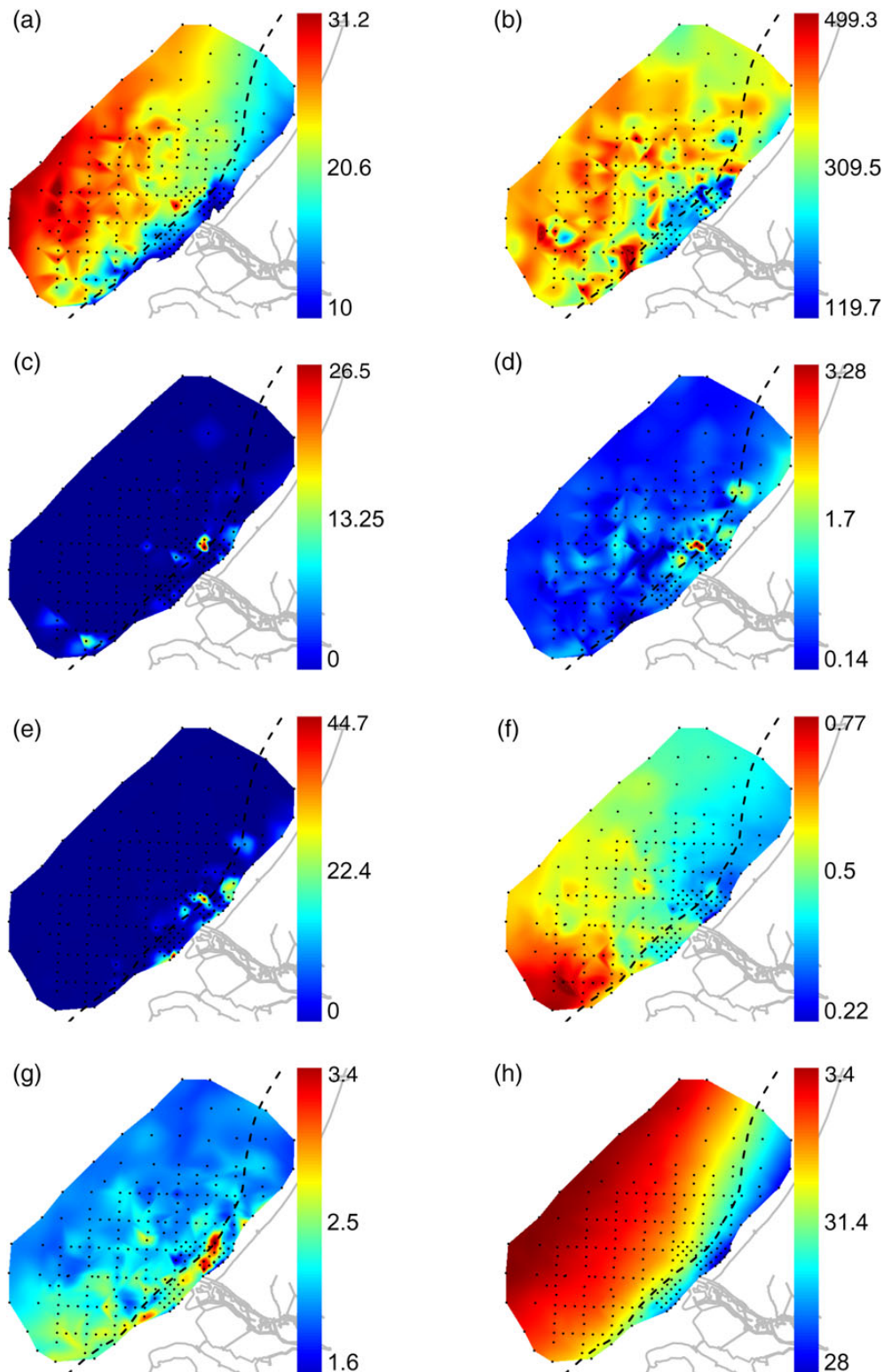


Figure 3. Measured abiotic variables in 2008 (a) water depth (m), (b) median grain size D50 (μm), (c) mud content(%), (d) SOM (%), (e) very fine sand (%), (f) mean bed shear stress (N m^{-2}), (g) maximum bed shear stress (N m^{-2}) and (h) mean bed salinity (ppt) with the 20-m isobath depicted with the dashed line. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

Infaunal assemblage 1 (IN1) was dominated by subsurface deposit-feeding sea urchins *Echinoidea* spp. and suspension-feeding sand mason worm *Lanice conchilega*. In 2006 and 2008, respectively, 47 and 72 sampling locations belonged to this assemblage. The

average biomass of assemblage IN1 was $5.6 \text{ g AFDW m}^{-2}$ with 24.5 species per boxcore (Supplementary Appendix II). Assemblages IN1 occurs also near the sewage effluent discharge location (Supplementary Appendix VI, no. 11). Assemblage IN2 was

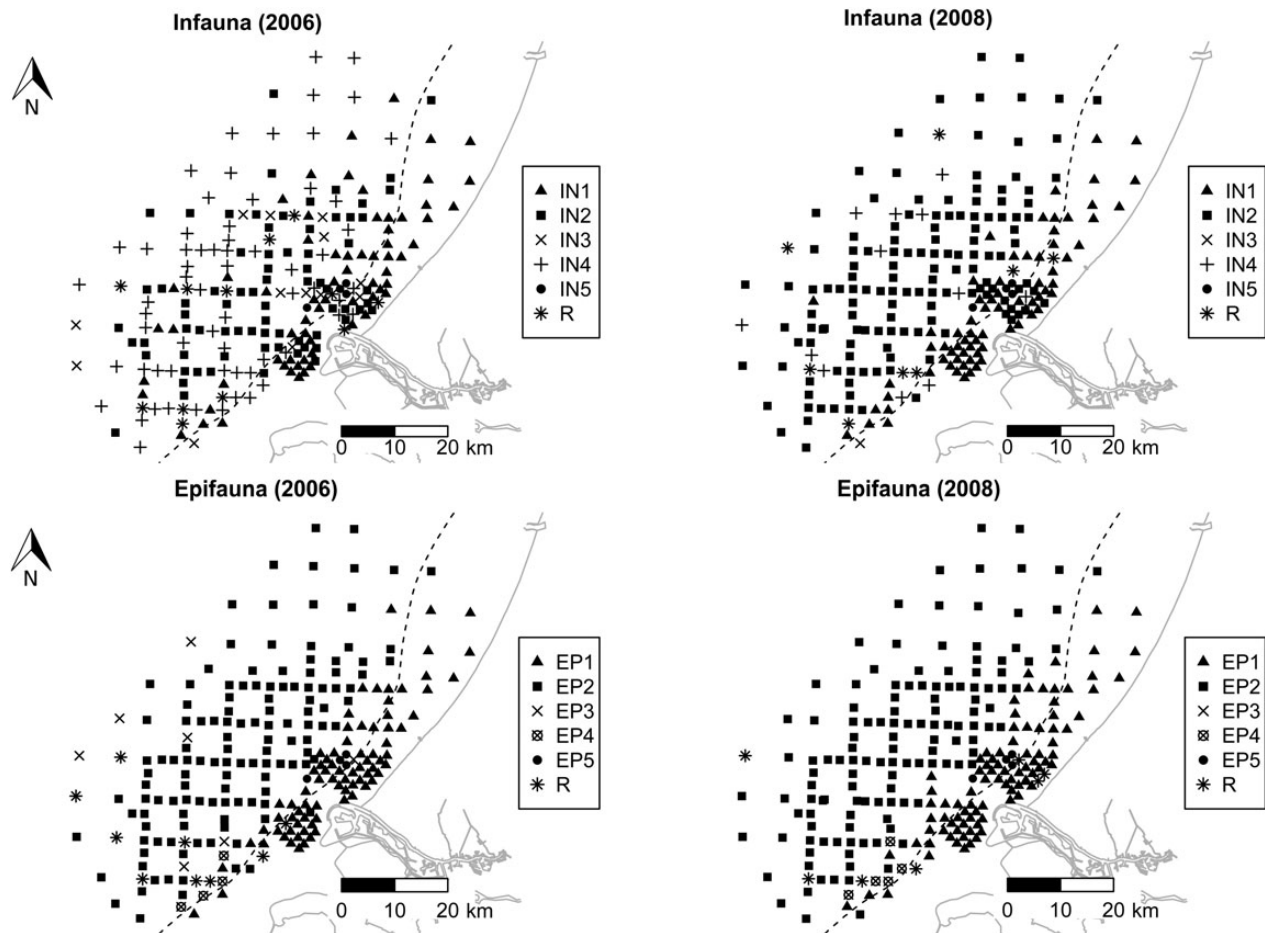


Figure 4. Upper panels: distribution of the main infaunal assemblages in spring 2006 and 2008 (IN1: *Echinoidea* spp. – *L. conchilega*; IN2: *Echinoidea* spp. – *Phoronida* spp.; IN3: *N. cirrosa* – *S. bombyx*; IN4: *Spio* spp. – *N. cirrosa*; assemblage IN5: *O. fusiformis* – *A. alba* – *L. conchilega*, and R: remaining locations). Lower panels: distribution of the main epifaunal assemblages (assemblage EP1: *Ensis* spp. – *O. albida* – *S. subtruncata*; assemblage EP2: *Ensis* spp. – *O. albida*; assemblage EP3: *O. albida*; assemblage EP4: *Ensis* spp. – *O. albida*; assemblage EP5: *A. alba* – *Actinaria* spp.; and R: remaining locations). Dufrière – Legendre indicator species are indicated in bold.

dominated by sea urchins *Echinoidea* spp. and suspension-feeding horseshoe worms *Phoronida* spp., and occurred 94 times in 2006 and 139 times in 2008 (1.6 g AFDW m⁻², 19.0 species per boxcore). The most abundant species of assemblage IN3 were the scavenging polychaete *Nephtys cirrosa* and the deposit-feeding polychaete *Spiophanes bombyx* (0.1 g AFDW m⁻², 11.7 species per sample). Assemblage IN3 occurred 13 times in 2006 and 1 time in 2008. Assemblage IN4, which showed a high species composition similarity with assemblage IN3, was dominated by the deposit-feeding polychaete *Spio* spp. and *N. cirrosa* (0.4 g AFDW m⁻², 14.5 species per boxcore) and occurred 64 times in 2006 and 12 times in 2008. IN2, IN3, and IN4 were found near and in the area of disposal site “North”, which received coarser sediment, loads. IN4 assemblage was also found near the lowered disposal site which may be induced by recent fine sediment disposal and successive recolonization. Assemblage IN5 was dominated by the deposit-feeding polychaete *Owenia fusiformis*, the deposit-feeding white furrow shell *Abra alba*, and the sand mason worm. *Owenia fusiformis* and white furrow shell are the only Dufrière – Legendre indicator species of the infaunal assemblages. Assemblage IN5 is exceptional because of the highest biomass and species richness (8.1 g AFDW m⁻², 26.4 species per boxcore). The assemblages were detected four times both in 2006

and in 2008 at identical locations near the lowered disposal site and in the deepened shipping lane Euromaasgeul (Supplementary Appendix III; mud content: 15.5%, SOM: 2.1%, and D_{50} : 157.1 μm). The specific part of the shipping lane was not recently dredged and no maintenance dredging has taken place before sampling.

For IN in general, the best noticeable difference between the 2006 and 2008 samples was the increase in occurrence of IN2 assemblages (94 times in 2006 and 139 times in 2008) due to higher abundance of *Echinoidea* spp., *Phoronida* spp., and *L. conchilega*. These assemblages replaced the low-biomass and species-poor IN3 and IN4 assemblages inhabiting the deeper part of the study area (Figures 4 and 5).

Biomass of assemblages IN1 and IN5 is significantly higher than that of assemblages IN2, IN3, and IN4 for both years (Kruskal–Wallis: $p < 0.05$). Biomass of assemblage IN2 is significantly higher than that of assemblages IN3 and IN4. Assemblage IN5 has the highest species richness followed by assemblage IN1 (24.5 species per boxcore), which is significantly higher than those richness of assemblages IN2, IN3, and IN4. Species composition, biomass, and species richness are summarized in Supplementary Appendix II, accompanying data on sediment variables are summarized in Supplementary Appendix III.

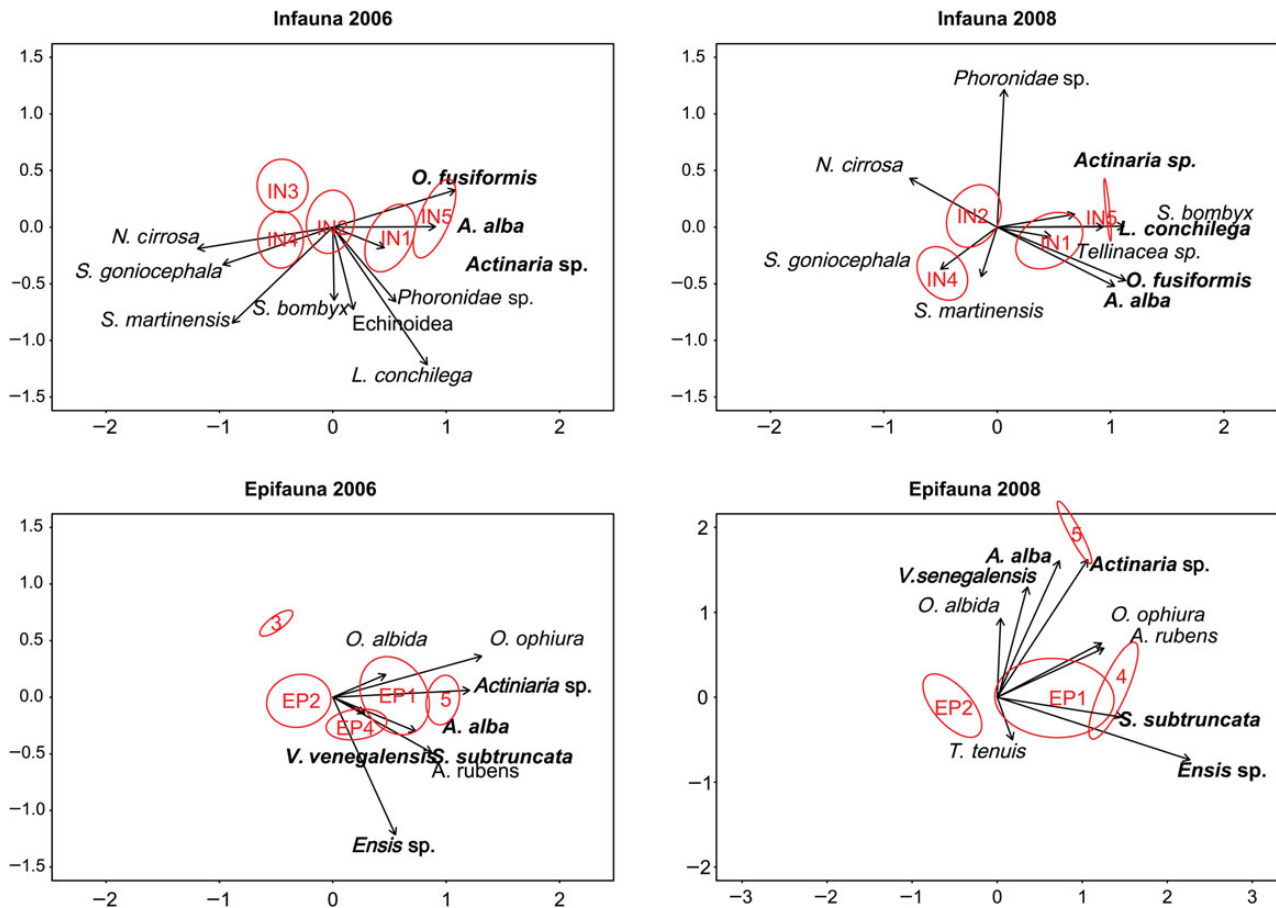


Figure 5. nMDS ordination with correlation of most abundant species and Dufrene–Legendre indicator species (in bold) of determined assemblages depicted with centroids in red. Upper panels: distribution of the main infaunal assemblages (IN1: *Echinoidea* spp.–*L. conchilega*; IN2: *Echinoidea* spp.–*Phoronida* spp.; IN3: *N. cirrosa*–*S. bombyx*; IN4: *Spio* spp.–*N. cirrosa*; IN5: *O. fusiformis*–*A. alba*–*L. conchilega*). Lower panels: distribution of the main epifaunal assemblages (EP1: *Ensis* spp.–*O. albida*–*S. subtruncata*; EP2: *Ensis* spp.–*O. albida*; EP3: *O. albida*; EP4: *Ensis* spp.–*O. albida*; EP5: *A. alba*–*Actinaria* spp.). Only centroids of assemblages are used to maintain readability and in some cases assemblage names are shortened; individual sample points are depicted in Figure 6. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.

Clustering and species composition of epifaunal samples

Ten species assemblages of EP (bottom sledge samples) were distinguished based on a threshold of 60% Bray–Curtis dissimilarity. According to the simprof analysis, all assemblages were significantly different. In total, 455 epifaunal samples were grouped into five main assemblages. Epifaunal assemblage 1 (EP1) was characterized by the filter-feeding Dufrene–Legendre indicator species cut trough shell *Spisula subtruncata*, *Ensis* spp. (filter-feeding bivalve), and the scavenging serpent’s table brittlestar *Ophiura albida* (Supplementary Appendix II). In 2006, 81 and in 2008, 91 samples belonged to assemblage EP1 with an average wet weight biomass of 95.4 g m⁻² and 13.1 species per sample. *Ensis* spp. and the brittlestar were also the two most dominant species of assemblages EP2 and EP4. Assemblage EP2 had an average biomass of 15.8 g WW m⁻² and 8.3 species per haul. Assemblage EP3 was unique by the low biomass and species richness (1.3 g WW m⁻², 3 species per haul). *Ophiura albida* was the most abundant species of EP. In 2006 and 2008, respectively, four and five samples from the troughs of the Zeeland ridges (Figure 1, no. 3) were grouped in assemblage EP4. This assemblage was unique by the high biomass, low species richness, and high *Ensis* spp. abundance (670.9 g WW m⁻², 6.4 species per haul, 85.8 ind. haul⁻¹). *Ensis* spp. was also indicated as a Dufrene–Legendre indicator

species for this assemblage. Assemblage EP5 contained Dufrene–Legendre indicator species *A. alba*, the sea anemone (*Actinaria* spp.), the serpent’s table brittlestar, the pullet carpet shell (*Venerupis senegalensis*), and the suspension-feeding blunt gaper (*Mya truncata*). Assemblage EP5 had the second highest biomass and species richness (139.1 g WW m⁻², 11.9 species per haul). Assemblage EP5 was detected four times both in 2006 and in 2008 near the lowered disposal site for dredged sediment and in the deepened shipping lane Euromaasgeul. For EP, the most noticeable difference between the 2006 and 2008 was the spatial replacement of low-biomass and species-poor assemblage EP3 by assemblage EP2 (Figures 4 and 5). Biomass of epifaunal assemblages EP1, EP4, and EP5 is significantly higher than that of assemblages EP2 and EP3 (Kruskal–Wallis: $p < 0.05$). Species richness of assemblages EP1 and EP5 are significantly higher than those of assemblages EP2, EP3, and EP4 (Kruskal–Wallis: $p < 0.05$).

Variables explaining macrozoobenthos distribution

The defined macrozoobenthic assemblages grouped together in the nMDS ordination (Figures 5 and 6). For IN, ordination stress with four dimensions was ~0.16 in both years and for EP, ~0.12 in 2006 and 0.09 in 2008 (Table 1).

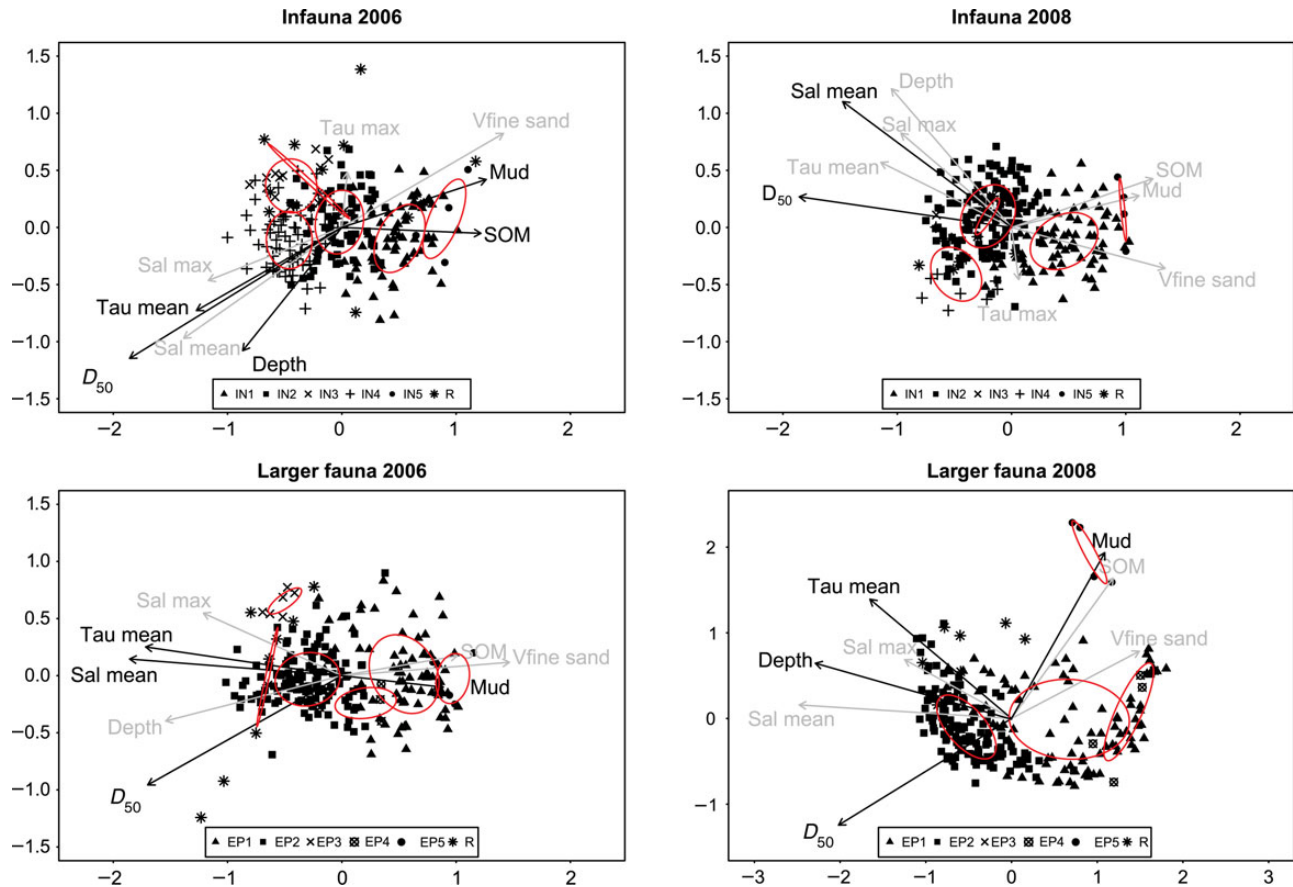


Figure 6. nMDS ordination with the first two axis and correlation of all significant environmental variables superimposed in grey (D_{50} : median grain size; Sal mean: mean near-bed salinity; Sal max: maximum near-bed salinity; Tau mean: mean bed shear stress; Tau max: maximum bed shear stress; Vfine sand: fraction very fine sand; Mud: fraction mud; SOM: fraction sediment organic matter). Upper panels: sample locations and centroids of the main infaunal assemblages (IN1: *Echinoidea* spp. – *L. conchilega*; IN2: *Echinoidea* spp. – *Phoronida* spp.; IN3: *N. cirrosa* – *S. bombyx*; IN4: *Spio* spp. – *N. cirrosa*; IN5: *O. fusiformis* – *A. alba* – *L. conchilega*, and R: remaining locations). Lower panels: sample locations and centroids of the main epifaunal (EP1: *Ensis* spp. – *O. albida* – *S. subtruncata*; EP2: *Ensis* spp. – *O. albida*; EP3: *O. albida*; EP4: *Ensis* spp. – *O. albida*; EP5: *A. alba* – *Actinaria* spp., and R: remaining locations). Correlation arrows in bold are the variables selected with the bioenv function. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.

For the distribution of IN in 2006, depth, grain size, SOM, mean bed shear stress, and mud was selected with the bioenv function with a combined Spearman's rank correlation of 0.37 (Table 2 and Figure 6). In 2008, grain size and mean near-bed salinity were selected with a combined Spearman's rank correlation of 0.50. Infaunal assemblage IN1 (*Echinoidea* spp. – *L. conchilega*) was positively correlated with shallow water depth, low near-bed salinity, and higher levels of mud, SOM, and very fine sand. Assemblage IN2 (*Echinoidea* spp. – *Phoronida* spp.) showed a correlation with intermediate near-bed salinity, depth, and D_{50} (Table 1 and Figure 6). Assemblage IN3 (*N. cirrosa* – *S. bombyx*) correlated in areas without mud. Assemblage IN4 (*Spio* spp. – *N. cirrosa*) was more abundant in 2006 than in 2008 and generally correlated with highest values of D_{50} , bed shear stress, and near-bed salinity. Assemblage IN5 (*O. fusiformis* – *A. alba*) was found in the deepened shipping lane Euromasgeul and lowered disposal site, and correlated with the highest percentages of mud, SOM and very fine sand, smallest D_{50} , largest water depth, and lowest bed shear stress.

Percentages mud, SOM, and very fine sand are the highest for assemblages IN1 and IN5 and are significantly higher compared with other assemblages (Kruskal–Wallis: $p < 0.05$). D_{50} of

assemblage IN5 is significantly lower than for assemblages IN2, IN3, and IN4 (Kruskal–Wallis: $p < 0.05$). Mean bed shear stress is lower for assemblages IN1 and IN5, respectively, 0.43 and 0.37 N m^{-2} , than for assemblages IN2 and IN4, both above 0.5 N m^{-2} (Kruskal–Wallis: $p < 0.05$). Values of environmental variables of infaunal assemblages are given in Supplementary Appendix IV.

In 2006, the distribution of EP was correlated with grain size, mean near-bed salinity, mean bed shear stress, and the fraction of mud and very fine sand (Figure 6). In 2008, EP were correlated with depth, grain size, mean bed shear stress, and mud. The combined Spearman's rank correlation was, respectively, 0.42 and 0.52 (Table 3).

For EP, assemblage EP1 (*Ensis* spp. – *Ophiura* spp. – *S. subtruncata*) was positively correlated with higher percentages mud, SOM, and very fine sand, and negatively correlated with near-bed salinity, bed shear stress, and water depth (Figure 6). Assemblage EP2 (*Ensis* spp. – *O. albida*) showed a negative correlation with mud, SOM, and very fine sand, and a positive correlation with near-bed salinity, bed shear stress, and depth. Assemblage EP3 (*O. albida*) occurred in areas characterized by an absence of mud

and very fine sand and high bed shear stress. Assemblage EP4 (*Ensis* spp.) was found at the Zeeland ridges in shallow waters with coarse sediments (360.7 μm) and was further characterized, for shallow waters, by very high mean shear stress values. Assemblage EP5 (*A. alba*–*Actinaria* spp.–*O. albida*–*V. senegalensis*) responded in a similar way as infaunal assemblage IN5 and was again found in the deepened shipping lane and lowered disposal site. Percentages mud, SOM, and very fine sand were highest for assemblage EP5, significantly higher than the values of the other assemblages except for assemblage EP1 (Kruskal–Wallis: $p < 0.05$). Mean bed shear stress is significantly lower for assemblages EP1 and EP5 (0.42 and 0.37 N m^{-2} , respectively), compared with the other assemblages ($>0.50 \text{ N m}^{-2}$). Values of environmental variables of epifaunal assemblages are given in Supplementary Appendix V; a graphical summary of the characteristics of the assemblages and relationships with abiotic and hydrodynamic variables is presented in Figure 7.

Discussion

The distribution of IN in 2006 correlated with depth, grain size, SOM, mean bed shear stress, and mud was selected. In 2008, grain size and mean near-bed salinity were selected. The highest species richness was found for assemblage IN5 (*O. fusiformis*–*A. alba*) in

areas with 15.4% mud and 2.1% SOM. At these sampling locations, an increase from 21.5 species per sample in 2006 to 31.2 species per sample in 2008 was observed. On the Belgian continental shelf (BCS), Van Hoey *et al.* (2004) found that species richness was positively related to sediment mud content and sediment median grain size, and negatively related to distance to the coast. Samples with high mud values ($>20\%$) showed reduced species richness (15–30 instead of 30–50 species). SOM was not measured in their study. Species richness in the German bight was found to be negatively correlated with sediment mud content, total organic carbon (TOC), and fishing effort on the short term (Reiss *et al.*, 2009). On the NCS, species richness was found to be negatively correlated with trawling intensity, sediment grain size, and primary productivity, and positively correlated with biomass (van Denderen *et al.*, 2014).

The risk of reduced species richness from total organic carbon loading is relatively low at TOC values below 10 mg g^{-1} , high at values over 35 mg g^{-1} , and intermediate at in between values. Our results showed lower species richness at SOM values exceeding 3% (30 mg g^{-1} ; Hyland *et al.*, 2005). We observed highest infaunal biomass in the shipping lane and near the lowered disposal site with sediment with 15.4% mud content. We noted an increase in biomass for infaunal assemblage IN5 from 6.4 g AFDW m^{-2} in 2006 to 9.9 g AFDW m^{-2} in 2008. Heip and Craeymeersch (1995) found that infaunal biomass increased consistently in finer sediments and sediments with higher chlorophyll *a* content. Reiss *et al.* (2010) found that infaunal biomass in part of the German Bight was positively related to sediment mud content and SOM, and negatively related to fishing effort. In their study, the highest infaunal biomass (20 g AFDW m^{-2}) was detected at a location with the highest mud content (24%). Total infaunal biomass and *A. alba* biomass were found to be positively correlated with SOM (Thiebaut *et al.*, 1997). In the southwestern Baltic Sea, large variation in biomass was found for white furrow shell *A. alba*, one of the dominant species of this assemblage (Rainer, 1985). The higher biomass and species

Table 1. Stress values of two-, three-, or four-dimensional nMDS ordinations.

Variable	Two-dimensional	Three-dimensional	Four-dimensional
Infauna 2006	0.25	0.20	0.16
Infauna 2008	0.25	0.19	0.16
Epifauna 2006	0.21	0.15	0.12
epifauna 2008	0.20	0.13	0.11

Table 2. Multiple regressions of environmental variables and infaunal nMDS scores for four-dimensional ordination, r^2 is the squared Spearman’s rank correlation coefficient, r^2 combined is the squared Spearman’s rank correlation coefficient of the best subset, and $\text{Pr}(> r)$ is the p -value.

Variable	NMDS1	NMDS2	NMDS3	NMDS4	r^2	$\text{Pr}(> r)$	r^2 combined
2006							
Depth	−0.44	−0.52	0.40	0.62	0.37	***	0.37
D_{50}	−0.82	−0.49	−0.01	0.31	0.59	***	
SOM	0.99	−0.03	−0.11	0.09	0.18	***	
Mean near-bed salinity	−0.69	−0.47	0.40	0.38	0.41	***	
Maximum near-bed salinity	−0.74	−0.29	0.54	0.27	0.23	***	
Mean bed shear stress	−0.85	−0.49	0.05	0.20	0.26	***	
Maximum bed shear stress	0.07	0.71	−0.38	−0.59	0.05	*	
Mud	0.91	0.32	−0.21	0.18	0.22	***	
Very fine sand	0.76	0.43	−0.36	−0.32	0.36	***	
2008							
Depth	−0.56	0.67	−0.18	−0.43	0.54	***	0.50
D_{50}	−0.84	0.11	−0.21	−0.48	0.68	***	
SOM	0.9	0.31	0.29	−0.04	0.33	***	
Mean near-bed salinity	−0.75	0.55	−0.26	−0.26	0.63	***	
Maximum near-bed salinity	−0.70	0.60	−0.28	−0.24	0.32	***	
Mean bed shear stress	−0.84	0.42	−0.19	−0.29	0.32	***	
Maximum bed shear stress	0.07	−0.63	0.52	0.58	0.09	***	
Mud	0.86	0.21	0.41	−0.24	0.27	***	
Very fine sand	0.90	−0.24	0.36	0.06	0.38	***	

Significance codes: (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Variables in bold are the subset variables selected with the bioenv function.

Table 3. Multiple regression of environmental variables and NMDS scores for EP, r^2 is the squared Spearman's rank correlation coefficient, and p -values are based on 999 permutations.

Variable	NMDS1	NMDS2	NMDS3	NMDS4	r^2	Pr(> r)	r^2 combined
2006							
Depth	-0.61	-0.15	0.76	0.19	0.50	***	0.42
D_{50}	-0.87	-0.50	-0.01	-0.05	0.51	***	
SOM	0.63	0.13	0.55	0.53	0.20	***	
Mean near-bed salinity	-0.77	0.06	0.63	0.04	0.56	***	
Maximum near-bed salinity	-0.70	0.32	0.59	-0.24	0.29	***	
Mean bed shear stress	-0.87	0.15	0.45	0.14	0.44	***	
Maximum bed shear stress	0.15	0.63	-0.60	-0.46	0.05	*	
Mud	0.72	-0.01	0.44	0.55	0.18	***	
Very fine sand	0.84	0.07	-0.22	0.50	0.33	***	
2008							
Depth	-0.72	0.54	-0.02	-0.43	0.63	***	0.52
D_{50}	-0.80	0.17	0.37	0.45	0.57	***	
SOM	0.49	0.28	-0.07	-0.82	0.37	***	
Mean near-bed salinity	-0.89	0.41	-0.10	-0.17	0.70	***	
Maximum near-bed salinity	-0.84	0.49	-0.21	-0.13	0.33	***	
Mean bed shear stress	-0.93	-0.36	0.07	0.04	0.39	***	
Maximum bed shear stress	0.25	-0.69	-0.49	0.47	0.18	***	
Mud	0.40	0.30	0.09	-0.87	0.31	***	
Very fine sand	0.57	-0.17	0.18	-0.78	0.39	***	

The best subset is determined with the bioenv function; in case of collinearity between environmental variables, one was dropped. Significance codes: (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Variables in bold are the subset variables selected with the bioenv function.

richness around the 20-m isobath may also be induced by sand extraction and sediment disposal sites. Although studies on the DCS showed that macrozoobenthos returned within 2–4 years to pre-dredged conditions (van Dalfsen et al., 2000; van Dalfsen and Essink, 2001), in the figures of Supplementary Appendices I and II, deviations are visible around the 20-m isobath which overlap with shallow borrow pits, fine sediment disposal site “Northwest”, and sediment disposal site “North”.

Environmental variables and EP

In 2006, the distribution of EP correlated with grain size, mean near-bed salinity, mean bed shear stress, and the fraction of mud and very fine sand. In 2008, EP correlated with depth, grain size, mean bed shear stress, and mud. Reiss et al. (2010) found relationships with hydrodynamic variables such as water temperature, near-bed salinity, and wave stress.

Epibenthic biomass was high along the continental coast, and a limited number of free-living species was responsible for this pattern. In shallow parts of the North Sea along the continental coast, the starfish *Asterias rubens* and the brittlestars *O. albida* and *O. ophiura* were abundant (Callaway et al., 2002). A similar trend was found in our study with high biomass values along the coast with also brittlestars being abundant. Jackknife clam (*Ensis* spp.) was the most abundant species, which was also found by Tulp et al. (2010).

Number of significant different assemblages

We found significant differences in species composition. Five infaunal and epifaunal assemblages were distinguished using clustering techniques and confirmed by the nMDS ordinations. A variety of macrozoobenthic assemblages was earlier distinguished within the Southern Bight in the North Sea and the English Channel (Govaere et al., 1980; Duineveld et al., 1991; Künitzer et al., 1992; Holtmann et al., 1996; Degraer et al., 1999; Ghertsoos et al., 2000; Desroy et al., 2003; Kröncke et al., 2011).

On the BCS, which is most comparable to our research area, four main infaunal assemblages were distinguished in the most recent study: (i) a muddy fine sand *A. alba*–*Mysella bidentata* assemblage characterized by high abundance and species richness; (ii) a *N. cirrosa* assemblage that occurred in well-sorted sandy sediments and is characterized by low densities and species richness; (iii) an assemblage with very low densities and species richness typified by the *Ophelia limacinae*–*Glyceria lapidum* community, which is found in coarse sandy sediments (Van Hoey et al., 2004). The fourth macrobenthic assemblage is typical for the upper intertidal zone of sandy beaches and beyond the scope of our study.

We distinguished a comparable “muddy fine sand” assemblage consisting of *O. fusiformis*, *A. alba*, and *Kurtiella bidentata* near the lowered disposal site and in the Euromaaasgeul shipping lane with a similar macrobenthic abundance and species richness (8250 ind. m^{-2} , 31.2 species m^{-2}); the median grain size was smaller, and sediment mud content and SOM content were higher. Dumping of dredged fine harbour sediment took place a few hundred metres south, and maintenance dredging did not occur in that specific area of the shipping lane. A similarity between impacts of sand extraction and sediment disposal was also found on the BCS (De Backer et al., 2014).

Biomass values of comparable *A. alba* assemblages in the Eastern English Channel–southern North Sea in water depths <15 m were 8.1 g AFDW m^{-2} (Desroy et al., 2003). In the Bay of Seine, biomass was around 25 g AFDW m^{-2} mainly due to polychaetes and echinoderms (Thiebaut et al., 1997) and in Gravelin biomass exceeded values of 100 g AFDW m^{-2} (Ghertsoos et al., 2000).

We also distinguished a similar *N. cirrosa* assemblage with comparable densities and species richness. This assemblage was also found in earlier research on the DCS (Duineveld et al., 1991; Künitzer et al., 1992; Holtmann et al., 1996). Kröncke et al. (2011) found differences in an *N. cirrosa* assemblage between 1986 and 2000 (assemblages F2 and L2) in the eastern North Sea and in the

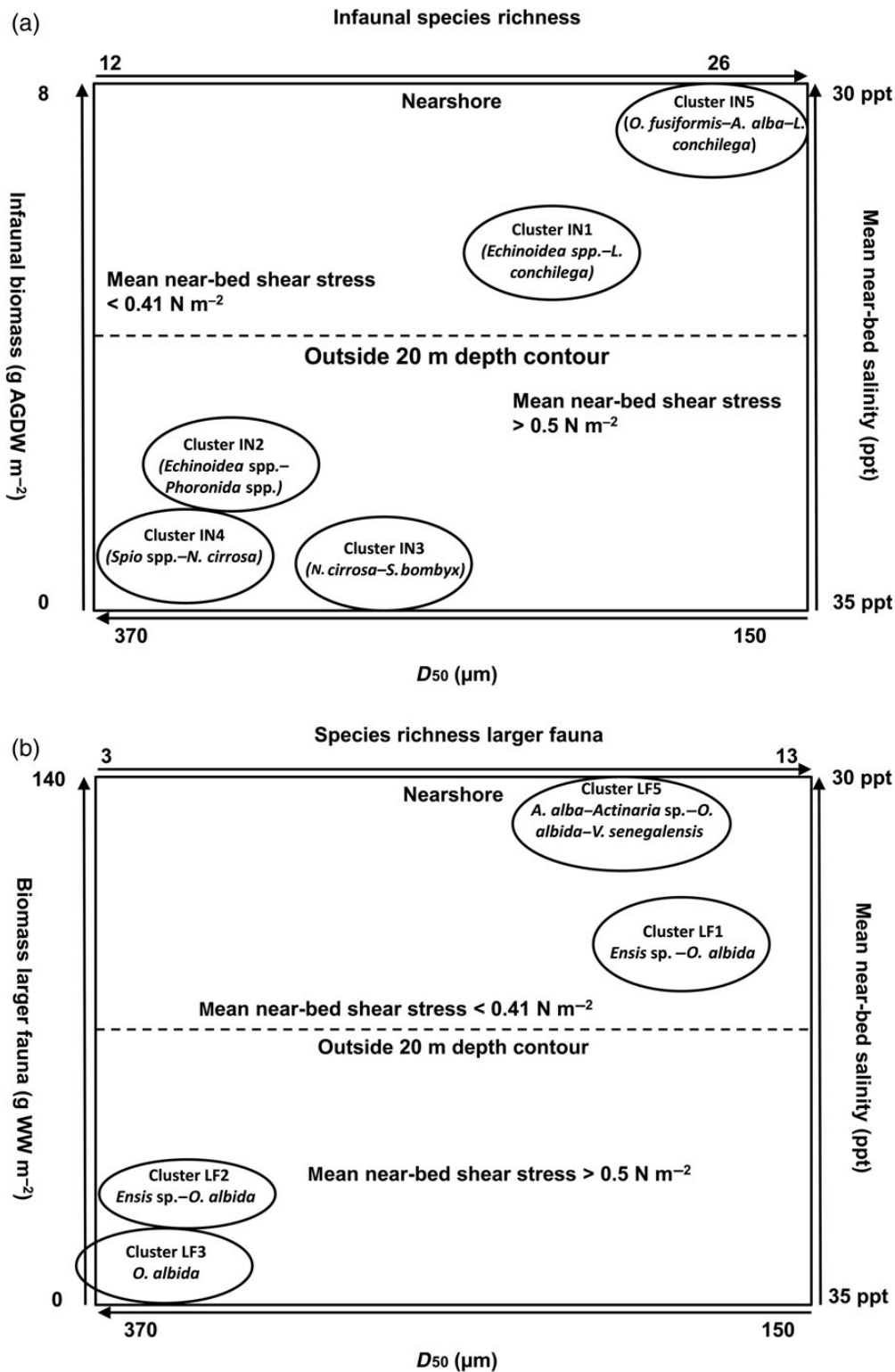


Figure 7. Summary of (a) infaunal and (b) epifaunal assemblages with biotic variables in relation to grain size and mean near-bed salinity and bed shear stress variables. In (b), assemblage EP4 is not depicted in the graph due to its extreme combination of abiotic and biotic variables (high mean bed shear stress: 0.6 N m⁻²; mean near-bed salinity: 32.7 ppt; grain size: 360 μm; biomass: 670.9 g WW m⁻², and 6.4 species per haul).

central Southern Bight to be induced by an increase in the abundance of Phoronids, the polychaetes *S. bombyx*, *L. conchilega*, *Magelona* spp., and the amphipod *Urothoe poseidonis*, whereas the abundance of the amphipod *Bathyporeia* spp. and the polychaete

Ophelia borealis decreased in 2000. Assemblages IN1 and IN2 did not match with a defined assemblage from the literature, but shows some similarity with the *Lanice* assemblage determined by Degraer et al. (1999).

We found five epifaunal assemblages, whereas Callaway *et al.* (2002) found three epifaunal assemblages in the southern North Sea using a 2-m beam trawl at depths <50 m (Callaway *et al.*, 2002). No similarities in the assemblage are found due to differences in spatial scales and differences in mesh size of the studies. The most similar assemblage consisted of *Crangon crangon*, *Crangon allmanni*, and *Philocheirus trispinosus*. In shallow parts of the North Sea along the continental coast, the starfish *A. rubens* and the brittlestars *O. albida* and *O. ophiura* were abundant (Callaway *et al.*, 2002). Epifaunal biomass (wet weight) ranged between 500–1000 near shore and between 1000–8840 at the Zeeland banks, whereas species richness ranged between 6 and 19. In the troughs of the Zeeland banks, aggregations of *Ensis* spp. were found.

Interannual differences in assemblage distribution and the NAO winter index

Differences in macrozoobenthic assemblage distributions were found. In 2008, a more infaunal samples were grouped as assemblages IN1 and IN2 due to higher abundance of subsurface deposit-feeding sea urchins *Echinoidea* spp., horseshoe worms *Phoronida* spp., and suspension-feeding sand mason worms *L. conchilega*. These assemblages replaced the low-biomass and species-poor assemblages IN3 and IN4 inhabiting deeper water. The higher abundances may be the result of successful recruitment during two successive mild winters after the strong winter of 2006. The Northern Atlantic Oscillation (NAO) winter index was -1.1 , 2.9 , and 2.1 in 2006, 2007, and 2008, respectively (Hurrell, 2012).

Several species such as *L. conchilega*, *A. alba*, *Bathyporeia* spp., *U. poseidonis*, and *S. bombyx* increased in abundance and distribution between 1986 and 2000, which was associated with an increase in sea surface temperature, primary production or food supply, and positive NAO winter index values (Kröncke *et al.*, 2011). Beukema (1985) reported mass mortality of *Echinocardium cordatum* in the Dutch coastal zone during the severe winter of 1979 (NAO winter index = -1.43). Kirby *et al.* (2007) found evidence that the elevated North Sea temperature after 1987 (NAO winter index = -0.77) favoured the reproduction and survival of *E. cordatum*.

Regarding EP, we found an increase in *Ensis* spp. abundance in 2008 (e.g. for epifaunal assemblage EP1, 8.4 ind. m^{-2} in 2006 to 22.6 ind. m^{-2} in 2008). This was also observed by Tulp *et al.* (2010), who noted an increase in Dutch coastal waters (10 ind. m^{-2} in 2006 to 18 ind. m^{-2} in 2007 and 2008). Low winter temperatures have been shown to negatively affect recruitment success in *Ensis directus* (Tulp *et al.*, 2010; Dannheim and Rumohr, 2012). Epibenthos showed strong seasonal fluctuations due to the severe winters of 1996 (NAO winter index = -1.43), resulting in strong differences in the abundance of the serpent's table brittlestar *O. albida* and the common starfish *A. rubens* and showing a gradual decrease in abundance in the following decade (Neumann *et al.*, 2009). We found the highest abundance of *O. albida* in 2006 (e.g. epifaunal assemblage EP4, $14.15 \text{ ind. m}^{-2}$ in 2006 to 1.15 ind. m^{-2} in 2008).

Relevance for management

For human activities, effects on assemblages, biomass, and species richness of macrozoobenthos can be predicted with the detected relationships with environmental and hydrodynamical variables. The information on the distribution patterns and species composition of macrozoobenthic assemblages can function as a baseline for future comparisons and help in the conservation of marine biodiversity. Autonomous temporal variation in species composition has to be taken into account in the assessment of impact of future

human activities. This study can be of value for EIAs and in the assessment of Marine Framework strategy Directive's (MFSD) Good Environmental Status (GES) descriptors biodiversity, seabed integrity, hydrographical conditions, and foodwebs.

The occurrence of the *A. alba* assemblages near the lowered disposal site for dredged fine sediment and in the deepened shipping lane may be an indication that the benthic system can be changed by human activities. Median grain size is considerably smaller; sediment mud and SOM content are higher. Macrozoobenthic species composition is significantly different compared with the surrounding assemblages. Smaller shifts in species composition, species richness, and biomass may be induced by activities such as shallow (-2 m) sand extraction, disposal of coarse dredged sediment, sewage treatment effluent discharges, and sand nourishments.

Relevance for monitoring activities

Macrozoobenthos was analysed with a boxcorer and bottom sledge. The advantage of a boxcorer is the combination of IN and sediment sampling. Collecting information about the occurrence of *Ensis* spp. is only possible with the bottom sledge due to their fast escape behaviour. On the other hand, the fragile *E. cordatum* is severely damaged in the epifaunal sampling procedure with the bottom sledge and gets undistinguishable. Biomass estimates from the bottom sledge can therefore be severely underestimated. To maintain a full coverage of data, a combination of boxcore and bottom sledge data is recommended.

Conclusion

Maximum macrozoobenthic species richness and biomass were observed at locations with a water depth of 20 m, a median grain size of $200 \mu\text{m}$, elevated mud and SOM content, and low mean bed shear stress. Five in- and epifaunal assemblages were distinguished, and correlations were found with measured sediment variables and modelled hydrodynamic variables. Interannual differences in macrozoobenthic assemblage distribution were found resulting from more Echinoids, Phoronids, and jackknife clams in 2008.

A distinct, highly productive and species-rich macrozoobenthic deposit-feeding white furrow shell *A. alba* assemblage coincided near a disposal site for dredged fine sediment and in a 8-m deepened shipping lane which may be an indication that the benthic system can be changed by these activities. Smaller shifts in infaunal species composition may also be linked to shallow sand extraction, disposal of coarse sediment, and to the discharge of sewage effluent. Modelled bed shear stress is an important variable in addition to sediment variables in explaining distribution patterns in macrozoobenthos.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

Acknowledgements

We thank the Port of Rotterdam (PoR) for providing the baseline data and Pieter Koen Tonnon, Geert Keetels, and Bas Borsje for the hydrodynamical modelling. Furthermore, we thank the anonymous reviewers for their useful comments. This study is part of the public-private innovation programme "Building with Nature" (BwN). This programme received funding from several sources, including the Subsidieregeling Innovatieketen Water (SIW, Staatscourant nos 953 and 17009), sponsored by the Dutch Ministry

of Transport, Public Works and Water Management and partner contributions of the participants to the Foundation EcoShape. The programme received co-funding from the European Fund for Regional Development EFRO and the Municipality of Dordrecht.

References

- Baptist, M. J., Van Dalfsen, J. A., Weber, A., Passchier, S., and Van Heteren, S. 2006. The distribution of macrozoobenthos in the southern North Sea in relation to meso-scale bedforms. *Estuarine Coastal and Shelf Science*, 68: 538–546.
- Beukema, J. J. 1985. Growth and dynamics in populations of *Echinocardium cordatum* living in the North Sea off the Dutch North coast. *Netherlands Journal of Sea Research*, 19: 129–134.
- Callaway, R., Alsvag, J., de Boois, I., Cotter, J., Ford, A., Hinz, H., Jennings, S., *et al.* 2002. Diversity and community structure of epibenthic invertebrates and fish in the North Sea. *ICES Journal of Marine Science*, 59: 1199–1214.
- Clarke, K. R., and Ainsworth, M. 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series*, 92: 205–219.
- Clarke, K. R., Somerfield, P. J., and Gorley, R. N. 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology*, 366: 56–69.
- Clarke, K. R., and Warwick, R. M. 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 2nd edn. PRIMER-E, Plymouth.
- Craeymeersch, J. A., and Escaravage, V. 2010. Effecten Zandwinning Aanleg Maasvlakte 2: Vaarrapport Nulmeting Rekolonisatie Benthos 2008. IMARES Wageningen UR, Institute for Marine Resources & Ecosystem Studies, Yerseke.
- Craeymeersch, J. A., and van der Land, M. A. 1998. De schelpdierbestanden in de Voordelta 1993–1997. C056/98, RIVO-DLO.
- Dannheim, J., and Rumohr, H. 2012. The fate of an immigrant: *Ensis directus* in the eastern German Bight. *Helgoland Marine Research*, 66: 307–317.
- De Backer, A., Van Hoey, G., Coates, D., Vanaverbeke, J., and Hostens, K. 2014. Similar diversity-disturbance responses to different physical impacts: three cases of small-scale biodiversity increase in the Belgian part of the North Sea. *Marine Pollution Bulletin*, 84: 251–262.
- de Mesel, I., Craeymeersch, J. A., Schellekens, T., van Zweedden, C., Wijsman, J., Leopold, M., Dijkman, E., *et al.* 2011. Kansenkaarten voor schelpdieren op basis van abiotiek en hun relatie tot het voorkomen van zwarte zee-eenden. C042/11, IMARES Wageningen UR, Institute for Marine Resources & Ecosystem Studies, Yerseke.
- de Ronde, J. G. 2008. Toekomstige langjarige suppletiebehoefte. Deltares, Delft.
- Degraer, S., Verfaillie, E., Willems, W., Adriaens, E., Vincx, M., and Van Lancker, V. 2008. Habitat suitability modelling as a mapping tool for macrobenthic communities: an example from the Belgian part of the North Sea. *Continental Shelf Research*, 28: 369–379.
- Degraer, S., Vincx, M., Meire, P., and Offringa, H. 1999. The macrozoobenthos of an important wintering area of the common scoter (*Melanitta nigra*). *Journal of the Marine Biological Association of the UK*, 79: 243–251.
- Desroy, N., Warembourg, C., Dewarumez, J. M., and Dauvin, J. C. 2003. Macrobenthic resources of the shallow soft-bottom sediments in the eastern English Channel and southern North Sea. *ICES Journal of Marine Science*, 60: 120–131.
- Dorst, L. 2012. Bepaling van het Particulate Organic Carbon (POC) gehalte in sediment. NIOO-CEME, Yerseke.
- Dufrene, M., and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67: 345–366.
- Duineveld, G. C. A., Kunitzer, A., Niermann, U., De Wilde, P. A. W. J., and Gray, J. S. 1991. The macrobenthos of the north sea. *Netherlands Journal of Sea Research*, 28: 53–65.
- Ghertsov, K., Luczak, C., Dewarumez, J. M., and Dauvin, J. C. 2000. Influence of spatial scales of observation on temporal change in diversity and trophic structure of fine-sand communities from the English Channel and the southern North Sea. *ICES Journal of Marine Science*, 57: 1481–1487.
- Govaere, J. C. R., Vandamme, D., Heip, C., and Deconinck, L. A. P. 1980. Benthic communities in the Southern Bight of the North-Sea and their ecological monitoring. *Helgolander Meeresuntersuchungen*, 33: 507–521.
- Heip, C., Basford, D., Craeymeersch, J. A., Dewarumez, J. M., Dorjes, J., de Wilde, P., Duineveld, G., *et al.* 1992. Trends in biomass, density and diversity of North Sea macrofauna. *ICES Journal of Marine Science*, 49: 13–22.
- Heip, C., and Craeymeersch, J. A. 1995. Benthic community structures in the North Sea. *Helgolander Meeresuntersuchungen*, 49: 313–328.
- Herman, P. M. J., Middelburg, J. J., and Heip, C. H. R. 2001. Benthic community structure and sediment processes on an intertidal flat: results from the ECOFLAT project. *Continental Shelf Research*, 21: 2055–2071.
- Holtmann, S. E., Groenewold, A., Schrader, K. H. M., Asjes, J., Craeymeersch, J. A., Duineveld, G. C. A., Van Bostelen, A. J., *et al.* 1996. Atlas of the Zoobenthos of the Dutch Continental Shelf. Rijswijk. Ministry of Transport, Public Works and Water Management, North Sea Directorate.
- Hulscher, S. J. M. H. 1996. Tidal-induced large-scale regular bed form patterns in a three-dimensional shallow water model. *Journal of Geophysical Research*, 101: 20727–20744.
- Hurrell, J. 2012. The Climate Data Guide: Hurrell North Atlantic Oscillation (NAO) Index (Station-Based). <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based> (last accessed 20 December 2012).
- Hyland, J., Balthis, L., Karakassis, I., Magni, P., Petrov, A., Shine, J., Vestergaard, O., *et al.* 2005. Organic carbon content of sediments as an indicator of stress in the marine benthos. *Marine Ecology and Progress Series*, 295: 91–103.
- Jongbloed, R. H., van der Wal, J. T., and Lindeboom, H. J. 2014. Identifying space for offshore wind energy in the North Sea. Consequences of scenario calculations for interactions with other marine uses. *Energy Policy*, 68: 320–333.
- Kirby, R. R., Beaugrand, G., Lindley, J. A., Richardson, A. J., Edwards, M., and Reid, P. C. 2007. Climate effects and benthic-pelagic coupling in the North Sea. *Marine Ecology Progress Series*, 330: 31–38.
- Kröncke, I., Reiss, H., and Dippner, J. W. 2013. Effects of cold winters and regime shifts on macrofauna communities in shallow coastal regions. *Estuarine, Coastal and Shelf Science*, 119: 79–90.
- Kröncke, I., Reiss, H., Eggleton, J. D., Aldridge, J., Bergman, M. J. N., Cochrane, S., Craeymeersch, J. A., *et al.* 2011. Changes in North Sea macrofauna communities and species distribution between 1986 and 2000. *Estuarine, Coastal and Shelf Science*, 94: 1–15.
- Kunitzer, A., Basford, D., Craeymeersch, J. A., Dewarumez, J. M., Dorjes, J., Duineveld, G. C. A., Eleftheriou, A., *et al.* 1992. The benthic infauna of the North Sea: species distribution and assemblages. *ICES Journal of Marine Science*, 49: 127–143.
- Legendre, P., and Legendre, L. 1998. *Numerical Ecology*. Elsevier, Amsterdam.
- Neumann, H., Reiss, H., Rakers, S., Ehrich, S., and Kroncke, I. 2009. Temporal variability in southern North Sea epifauna communities after the cold winter of 1995/1996. *ICES Journal of Marine Science*, 66: 2233–2243.
- Oksanen, J. 2013. *Multivariate Analysis of Ecological Communities in R: Vegan Tutorial*. <http://cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf> (last accessed 8 February 2013).

- Perdon, K. J., and Kaag, N. H. B. M. 2006. Vaarrapport Maasvlakte 2 (nulmeting zandwinning). IMARES Wageningen UR, Institute for Marine Resources & Ecosystem Studies, Yerseke.
- Rainer, S. F. 1985. Population dynamics and production of the bivalve *Abra alba* and implications for fisheries production. *Journal of Marine Biology*, 85: 253–262.
- R Core Team. 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reiss, H., Cunze, S., König, K., Neumann, H., and Kröncke, I. 2011. Species distribution modelling of marine benthos: a North Sea case study. *Marine Ecology Progress Series*, 442: 71–88.
- Reiss, H., Degraer, S., Duineveld, G. C. A., Kroncke, I., Aldridge, J., Craeymeersch, J. A., Eggleton, J. D., et al. 2010. Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. *ICES Journal of Marine Science*, 67: 278–293.
- Reiss, H., Greenstreet, S. P. R., Sieben, K., Ehrich, S., Piet, G. J., Quirijns, F., Robinson, L., et al. 2009. Effects of fishing disturbance on benthic communities and secondary production within an intensively fished area. *Marine Ecology Progress Series*, 394: 201–213.
- Santisteban, J. I., Mediavilla, R., Lopez-Pamo, E., Dabrio, C. J., Zapata, M. B. R., Garcia, M. J. G., Castano, S., et al. 2004. Loss on ignition: a qualitative or quantitative method for organic matter and carbonate mineral content in sediments? *Journal of Paleolimnology*, 32: 287–299.
- Straile, D., and Stenseth, N. C. 2007. The North Atlantic Oscillation and ecology: links between historical time-series, and lessons regarding future climate warming. *Climate Research*, 34: 259–262.
- Stronkhorst, J., Ariese, F., van Hattum, B., Postma, J. F., de Kluijver, M., Den Besten, P. J., Bergman, M. J. N., et al. 2003. Environmental impact and recovery at two dumping sites for dredged material in the North Sea. *Environmental Pollution*, 124: 17–31.
- Thiebaut, E., Cabioch, L., Dauvin, J. C., Retiere, C., and Gentil, F. 1997. Spatiotemporal persistence of the *Abra alba*–*Pectinaria koreni* muddy-fine sand community of the eastern Bay of Seine. *Journal of the Marine Biological Association of the UK*, 77: 1165–1185.
- Tonnon, P. K., Borsje, B., and De Jong, M. 2013. BwN HK2.4 Eco-morphological Design of Landscaped Mining Pits. Deltares, Delft.
- Tulp, I., Craeymeersch, J., Leopold, M., van Damme, C., Fey, F., and Verdaat, H. 2010. The role of the invasive bivalve *Ensis directus* as food source for fish and birds in the Dutch coastal zone. *Estuarine Coastal and Shelf Science*, 90: 116–128.
- van Dalssen, J. A., and Essink, K. 2001. Benthic community response to sand dredging and shoreface nourishment in Dutch coastal waters. *Senckenbergiana Maritima*, 31: 329–332.
- van Dalssen, J. A., Essink, K., Madsen, H. T., Birklund, J., Romero, J., and Manzanera, M. 2000. Differential response of macrozoobenthos to marine sand extraction in the North Sea and the Western Mediterranean. *ICES Journal of Marine Science*, 57: 1439–1445.
- van de Meene, J. W. H., and van Rijn, L. C. 2000a. The shoreface-connected ridges along the central Dutch coast—part 1: field observations. *Continental Shelf Research*, 20: 2295–2323.
- van de Meene, J. W. H., and van Rijn, L. C. 2000b. The shoreface-connected ridges along the central Dutch coast—part 2: morphological modelling. *Continental Shelf Research*, 20: 2325–2345.
- van Denderen, P. D., Hintzen, N. T., Rijnsdorp, A. D., Ruardij, P., and van Kooten, T. 2014. Habitat-specific effects of fishing disturbance on Benthic species richness in marine soft sediments. *Ecosystems*, 17: 1216–1226.
- van Dijk, T. A. G. P., van Dalssen, J. A., Van Lancker, V., van Overmeeren, R. A., van Heteren, S., Doornenbal, P. J., Peter, T. H., et al. 2012. Benthic habitat variations over tidal ridges, North Sea, the Netherlands. *In* Seafloor Geomorphology as Benthic Habitat, pp. 241–249. Elsevier, London.
- Van Hoey, G., Degraer, S., and Vincx, M. 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. *Estuarine Coastal and Shelf Science*, 59: 599–613.
- Van Hoey, G., Vincx, M., and Degraer, S. 2007. Temporal variability in the *Abra alba* community determined by global and local events. *Journal of Sea Research*, 58: 144–155.
- Verfaillie, E., Du Four, I., Van Meirvenne, M., and Van Lancker, V. 2009. Geostatistical modeling of sedimentological parameters using multi-scale terrain variables: application along the Belgian Part of the North Sea. *International Journal of Coal Geology*, 23: 135–150.
- WGSFD, I. 2014. OSPAR Request on Mapping of Bottom Fishing Intensity Using VMS Data. ICES, Copenhagen.
- Ysebaert, T., Herman, P. M. J., Meire, P., Craeymeersch, J., Verbeek, H., and Heip, C. H. R. 2003. Large-scale spatial patterns in estuaries: estuarine macrobenthic communities in the Schelde estuary, NW Europe. *Estuarine Coastal Shelf Science*, 57: 335–355.
- Zuur, A. F., Ieno, E. N., and Smith, G. M. 2007. *Analysing Ecological Data*. Springer-Verlag, New York.

Handling editor: Rochelle Seitz