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RESEARCH ARTICLE

How restoration engineering measures can enhance the ecological value of intertidal flats

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Restoration engineering measures, such as managed realignments or building groins, modify the environmental characteristics of coastal intertidal ecosystems. Creating physical modifications that are beneficial to an intertidal system's ecology necessitates an in-depth understanding of the relationships between the abiotic and biotic components of a given intertidal habitat. In this study, we evaluate how hydrodynamics and sediment characteristics drive the development of the benthic macrofauna community during the first 5 years following engineering measures to enhance benthic macrofauna diversity at three locations. The creation of low-energy habitats through groins (Knuitershoek and Baalhoek) and a managed realignment dike breach (Perkpolder) led to the accumulation of fine sediments in all three impact sites. Biomass of benthic macrofauna quickly increased between 2016 and 2020, with successional processes being more important in Perkpolder, where the habitat was started completely from scratch due to a managed realignment, than at Knuitershoek or Baalhoek, where habitat conditions were improved by adding groins. In addition, the density of benthos-eating birds, especially oystercatchers, increased at some of the modified sites. While a low-energy habitat may harbor more diverse assemblages of benthic macrofauna than a highly dynamic one, the extremely high silt content, which is typical for low-energy habitats, may slow benthic community development. The observed increase of biomass at our impact sites highlights the value of the interventions, while the delays in the response of the benthic macrofauna community emphasizes the need for extensive monitoring both in time and space and the identification of underlying abiotic–biotic mechanisms.

Key words: abiotic–biotic interactions, benthic macrofauna, birds, groins, hydrogeomorphology, low-energy, managed realignment, Scheldt estuary

Implications for Practice

- By creating low-energy habitat conditions and stimulating sediment import, engineering modifications in tidal flats such as groins and managed realignments can enhance habitat value for benthic macrofauna.
- The benefits of low-energy habitat for benthic macrofauna (i.e. greater sediment stability and food availability) can be reduced under exceptionally high silt content coupled with poor drainage.
- Benthic community composition can have a delayed response to engineering modifications to the habitat, necessitating extensive monitoring to properly characterize ecosystem response.

Introduction

Soft-sediment intertidal flats are some of the most productive systems globally and provide a vast array of ecosystem services (Barbier et al. 2011), many of which are driven by benthic macrofauna. These invertebrates, larger than 0.5 mm, provide food for birds and fish (Bocher et al. 2014) and are ecosystem engineers (Kristensen et al. 2012), driving both biogeomorphic (Cozzoli et al. 2021) and biogeochemical processes on tidal flats such as nutrient cycling (Aller & Aller 1998), organic matter decomposition (Levin et al. 2001), and pollutant removal (Mermillod-Blondin et al. 2004). Despite their importance, intertidal flats are highly degraded (Murray et al. 2019), prompting many restoration initiatives (Waltham et al. 2020). Restoration measures, such as managed realignments and building groins, can contribute to coastal protection as well as increasing the ecologically valuable habitat for infaunal species (French 2006; Elliott et al. 2007), including benthic macrofauna.

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In creating or enhancing intertidal areas, environmental characteristics of tidal flats (such as sediment accretion) are modified to trigger changes in the ecosystem's ecology and function (such as benthic macrofauna colonization) (Elliott et al. 2016). However, these projects do not always reach their ecological targets. For example, insufficient sediment accretion can severely delay the colonization of desired benthic macrofauna, which serve as food for birds (Garbutt et al. 2006), whereas rapid sediment accretion can harm benthic macrofauna by encouraging salt marsh colonization (Mazik et al. 2010). Therefore, creating beneficial physical modifications necessitates a good understanding of the relationships between the intertidal environment's abiotic and biotic components.

Understanding abiotic–biotic interactions is a longstanding goal of intertidal ecology (Pearson & Rosenberg 1978; Gray & Elliott 2009). Benthic macrofauna affect sediment characteristics such as erodibility, grain size, and permeability through their movements (Harris et al. 2016), but at the same time they have distinct environmental associations (Kraan et al. 2013) along environmental gradients (Ysebaert & Herman 2002). Key environmental variables for determining species assemblages are sediment grain size distribution, inundation time, and hydrodynamics (Ysebaert et al. 2002; Lange et al. 2020). The relationships between environmental drivers and benthic assemblages are well studied in equilibrium ecosystems (Ysebaert & Herman 2002; Holzhauer et al. 2022), but less so in intertidal systems undergoing physical modification due to restoration (Beauchard et al. 2013). Most intertidal restoration studies focus on benthic macrofauna colonization (Marquiegui & Aguirrezabalaga 2009; Mazik et al. 2010; Valdemarsen et al. 2018) and less on concurrent abiotic (e.g. hydrodynamics and sediment properties) and biotic (e.g. benthic macrofauna and birds) changes, which is the aim of this paper.

Since 2010, The Netherlands' province of Zeeland has implemented projects in the Western Scheldt to create intertidal estuarine habitat and develop benthic macrofauna, an important food source for foraging birds. In 2016, groins were modified or built at Knuitershoek and Baalhoek to reduce water flow and encourage sediment accretion (Fig. 1). In nearby Perkpolder, a dike was breached in 2015 to inundate old farmland and create a new tidal flat. These projects aimed to change the hydrogeomorphological conditions to enrich the benthic macrofauna community and overall biomass, thereby providing food to migratory birds. To assess the effectiveness of these measures and advise on future restoration designs, all study locations have been intensely monitored to track their physical and biological development.

In this paper, we evaluate how hydrodynamics and sediment characteristics drive the development of the benthic macrofauna community in our three case studies. We also briefly examine the bird density response to the interventions. All interventions were implemented near each other and at similar time, which allowed us to distinguish differences due to the interventions from natural spatiotemporal variability. We will (1) present key similarities and differences between the physical and biological trajectories of these sites, (2) identify the most important abiotic–biotic processes driving the emerging ecosystems of each location, and (3) summarize the general lessons learned from these large-scale interventions on the development of intertidal mudflat ecosystems.

Methods

Description of Study Locations

Knuitershoek and Baalhoek: Stimulating Sediment Accretion Through Groins. At both Knuitershoek and Baalhoek, several groins were either constructed or modified to create low-energy areas, facilitating the development of benthic macrofauna. In Knuitershoek (westernmost location; Fig. 1, top), a new Northern groin was constructed between April and October 2016, while two existing ones were raised. The Northern groin is elevated 3 m above mean sea level (i.e. above high water), and the two other groins are elevated half a meter above mean sea level, with the tips near the channel elevated 3 m above mean sea level. The tidal flat's elevation is, on average, 1 m below mean sea level. Similarly, at Baalhoek (easternmost location; Fig. 1, top), the Eastern groin was raised in 2016 to half a meter above mean sea level, and a new one was constructed at the western edge of the site, also to a height of half a meter (see Fig. 1, bottom). The tidal flat's elevation is, on average, 0.3 m below mean sea level. At both locations, sediment composition, bottom morphology, and benthic community composition were monitored through yearly sampling campaigns from 2016 through 2020.

Perkpolder: Creating New Tidal Areas Through Managed Realignment. Since June 2015, a dike-realignment pilot has been carried out at Perkpolder (the middle location among the three study sites; Fig. 1, top) to allow the former agricultural area to come under the influence of tidal inundation and sediment dynamics (i.e. low-energy tidal nature). As a result of the breach, the 75 ha tidal basin is flooded twice per day by the Western Scheldt. While the sedimentary and hydrodynamic changes varied across the basin, there was a net increase in sediment import of about 13–16 kT (5000–6000 m^3) over just a 5-month period of measurement. Additional estimates between 2016 and 2017 showed an influx of 16–48 kT per year (van de Lageweg et al. 2019). Annual monitoring from 2015 to 2020 tracked how benthic conditions changed over time.

Impact and Adjacent Reference Sites. At Knuitershoek and Baalhoek, monitoring included both the impact sites and adjacent reference sites. Impact sites, located between the groins (Knuitershoek Center and Baalhoek Center), were expected to change rapidly due to the engineering measures. Adjacent reference sites, areas outside but next to the groins (Knuitershoek North, Knuitershoek South, Baalhoek East, and Baalhoek West) were expected to remain relatively unchanged. Monitoring both the impact and adjacent sites allowed us to compare the evolution of the impacted ecosystem between the groins with the less-impacted system adjacent to them. It is important to note that sediment accumulation and scouring occurred on both sides of the groins, affecting adjacent sites as well (see Fig. 1). We did not monitor adjacent sites in Perkpolder to use as a direct comparison, as the intervention affected the entire polder.

Data Collection

Benthic Macrofauna Sampling. All locations were sampled in September or October within a few days of one another using

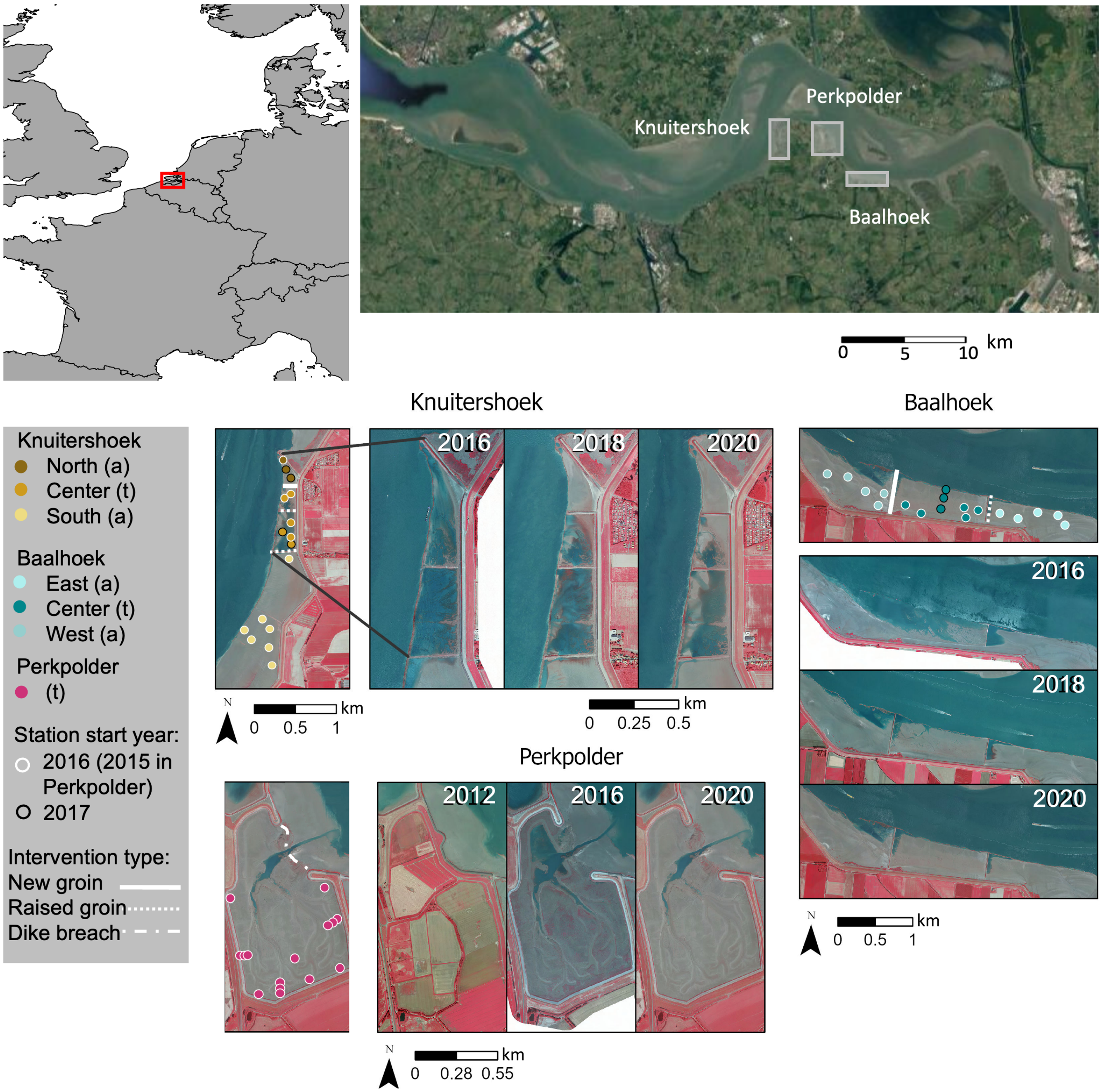

Figure 1. Top: Map of the Western Scheldt in the South of The Netherlands (*Source*: Google Maps) showing the location of our three case studies. Bottom: Aerial photographs (*Source*: Rijkswaterstaat) of Knuitershoek, Baalhoek, and Perkpolder showing the locations pre- and post-intervention. In the first photograph of each series, we show benthos and sediment sampling stations by site, and intervention type. The black circle around the station dot indicates that the station was added in 2017. In the legend, (t) and (a) indicate whether the corresponding site is an impact site (intended area of intervention impact) or an adjacent site (area next to the impact site). The northernmost groin at Knuitershoek is 3 m above mean sea level, while the other four groins at Knuitershoek and Baalhoek are elevated 0.5 m above mean sea level. Please note that we do not include the stations added in 2017 to Knuitershoek Center and Baalhoek Center in any analyses.

a 10 cm diameter × 50 cm long metal corer to collect macrofauna. At each sampling location, three replicates (down to 35 cm depth) were taken and pooled as one sample. The samples were sieved in the field through a 1 mm mesh sieve, preserved in a 4% buffered formaldehyde solution, and stained with Rose Bengal. The macrofauna were analyzed to the lowest taxonomic rank possible. Specimens were counted, then wet-weighed (blotted) to obtain biomass, which was later converted to ash free dry weight (AFDW) using species-specific conversion factors as described in Craeymeersch and Escaravage (2014). This allowed us to describe the community compositional patterns through species richness, abundance, and biomass.

Bird Counts. Since August 2017, birds have been counted and identified to species level monthly at the three locations during the outgoing tide. To limit disturbance, countings were carried out from a slowly moving car (less than 20 km/hour). Counts were performed for area blocks corresponding to the sites delineated in Figure 1, with the exception that the Knuitershoek impact site and the Baalhoek adjacent sites contained two bird counting blocks, and Perkpolder contained six. In our analyses, we used densities (counts/ha) of birds that mainly forage on benthos (waders, shelducks, and gulls) from October to February, which are the months that birds forage on benthic macrofauna as assessed from the autumn surveys.

Abiotic Measurements. In addition to the benthic macrofauna samples, the top 3 cm of the sediment were collected using a 2 cm-diameter cut-off syringe at the same locations as the benthic macrofauna. They were wet-weighed, freeze-dried, and the dry weight was recorded to calculate the sediment bulk density. Grain size composition was determined using a Malvern Mastersizer 2000 particle size analyzer (McCave et al. 1986) through laser diffraction, which quantifies five different sediment fractions: silt (≤63 μm), very fine sand (62.5–125 μm), fine sand (125–250 μm), medium sand (250–500 μm), and coarse sand (500–1000 μm). From these values, the median grain size (D50) was also calculated.

Tidal flat elevation was measured at each station using a Differential Global Positioning System (Topcon GR-3) with a 1 cm error margin. In addition, we used a penetrologger to measure the penetration resistance of the sediment up to 80 cm deep, and we measured the surface shear stress using a shear-vane. Five replicates were collected and averaged for both the penetration resistance and the surface shear stress. During analysis, penetration resistance measurements were truncated at 30 cm depth, as many profiles did not extend beyond this depth.

Flow Velocities From Modeling. Tidal flow velocities were computed for all benthic macrofauna and sediment sampling locations using a depth-averaged Delft3D Flexible Mesh numerical model covering the Western Scheldt from Vlissingen to the Belgian border (de Vet & Van der Werf 2022). The resolution of the computational mesh was 15 m in the project areas. The model was validated by flow velocity measurements and enforced with nested hydrodynamic boundary conditions. The bias and the root of the mean squared errors were less than 10 cm/second for most locations and less than 20 cm/second for all locations. Average peak velocities were calculated from a model simulation covering two spring-neap cycles.

Statistical Analysis

Station Inclusion. In Knuitershoek and Baalhoek, several sampling stations were added to treatment areas in 2017. Two stations were added to Knuitershoek Center (2017, $n = 5$), and three stations were added to Baalhoek Center (2017, $n = 8$). In addition, two stations were added to the adjacent area of Knuitershoek North (2017, $n = 3$). To ensure consistency and minimize variability across years, we restricted our analyses to stations that were sampled consistently over all years. Thus, we excluded the two additional stations from Knuitershoek Center (reduced $n = 3$) and the three stations from Baalhoek Center (reduced $n = 5$). The reduction in stations may have restricted the representation of the variability in macrofauna community and abiotic conditions within sites, especially the middle and seaward regions in Baalhoek Center and the seaward region in Knuitershoek Center.

We made an exception for Knuitershoek North due to limited stations, with only one sampled in 2016. We included the two stations added in 2017, resulting in three stations. Thus, temporal analyses for Knuitershoek North may misrepresent community variability for this site, as only one point was sampled in 2016. See Figure 1 for details on the station locations.

Abiotic Characteristics. We measured seven hydrogeomorphological characteristics to assess the development of the tidal flat over time: elevation (Normaal Amsterdams Peil [NAP], measured in reference to the mean water level for Amsterdam and is close to the mean sea level), bulk density (g/cm^3), shear stress (tkN/m^2), silt fraction (%), very fine sand fraction (%), penetration resistance (mPa), and peak current velocity (m/second). Due to a high correlation with silt fraction, D50 was not considered a parameter in our analyses.

We used linear regression to examine whether relationships between abiotic characteristics were location-specific or universal across all sites (Fig. 2). We used linear regressions over other nonparametric tests because we were interested in knowing the magnitude and direction of relationships between abiotic variables, as well as the magnitude and direction of year/location effects. In using linear regression, we may have missed relationships between abiotic characteristics that were not linear. We ensured assumptions of linear regression were met by using exploratory and diagnostic plots (i.e. plotting residuals against independent variables, qq-plots, histograms of the dependent variables, and residuals). We performed linear regressions between all possible pairs of the sediment characteristics, where we fit a first sediment characteristic (continuous) against a second sediment characteristic (continuous), location (three-level categorical: Baalhoek, Knuitershoek, or Perkpolder), and year (continuous). We tested for interactions between the independent variables, year, and location but did not include any in the final models, as the Akaike Information Criterion (AIC) showed these did not improve models. Results are summarized in Table S1. Analyses were performed using R v.4.2.0 (R Core Team 2022).

Benthic Macrofauna Total Biomass. We explored changes in total benthic macrofauna biomass over time, and whether trajectories differed between impact and reference sites. We evaluated year and site effects on total biomass using linear regressions. First, we summed the AFDW of all individuals in a sample to obtain the total biomass, excluding crab (*Hemigrapsus* sp.) and Pacific oyster (*Magallana gigas*), as these were too large to be reliably sampled with a 10 cm diameter corer.

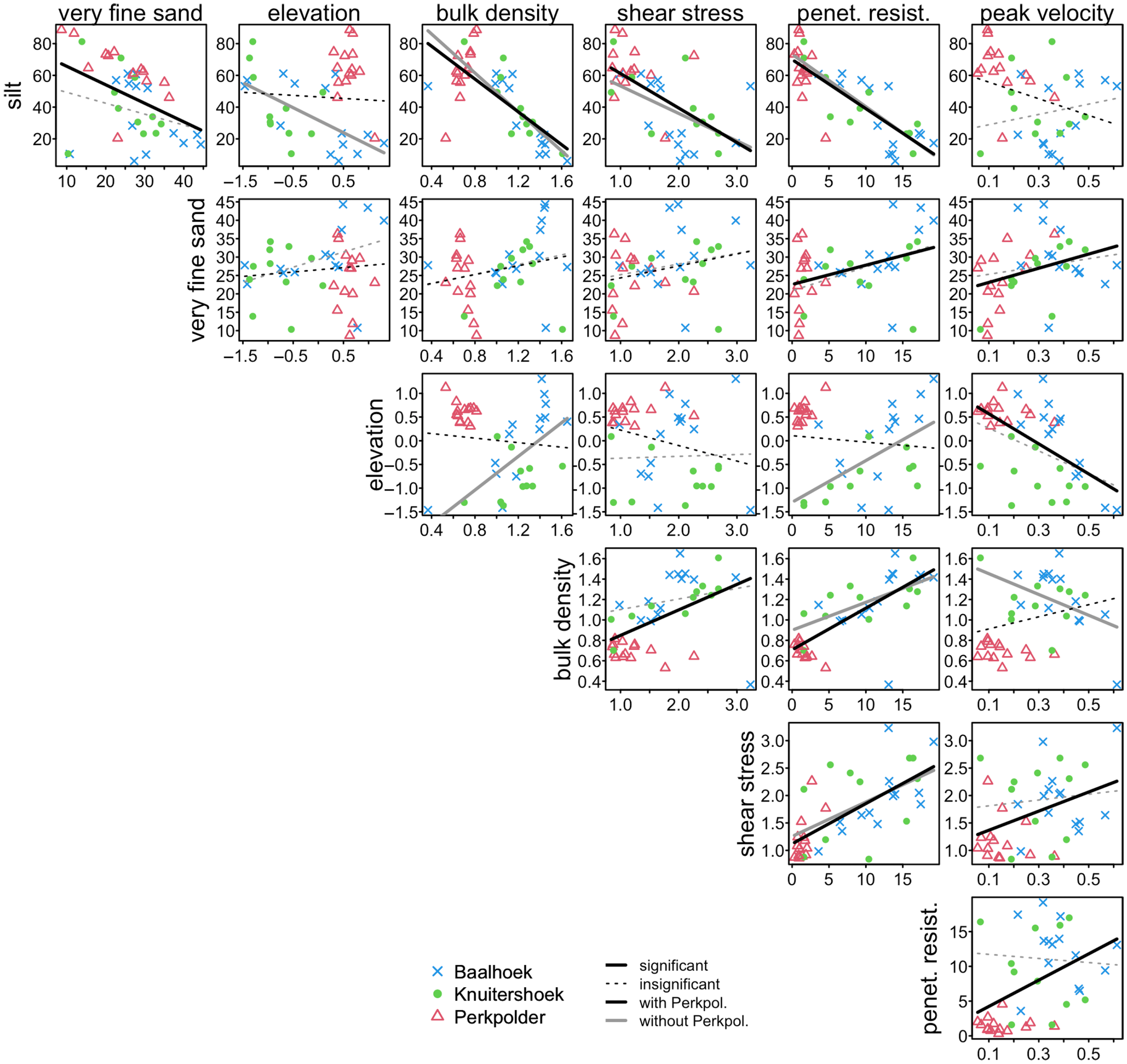

Figure 2. Correlations between abiotic variables in 2018 that were considered for inclusion in statistical models. The abiotic variables are elevation (NAP), bulk density (g/cm^3), shear stress (tkN/m^2), silt (%), very fine sand (%), penetration resistance (mPa), and peak velocity (m/second). The points represent all samples taken in 2018, from both impact and adjacent sites. Relationships for the full dataset are shown in black lines, relationships for the dataset that excludes Perkpolder are shown in gray.

Prior to analyses, we log-transformed total biomass so that it would be normally distributed.

We used linear regression to test whether log biomass increased linearly over time by site. Because we were interested in evaluating the linear change of biomass within sites rather than between sites, we fitted separate linear models to each site with total log biomass as a function of sampling date (continuous) (see Fig. 3 for results and Table S2). We also examined how environmental characteristics explained total biomass variability using linear regressions, where total log biomass was modeled as a function of each environmental characteristic (continuous), year (continuous), and site (seven-level categorical). The results are summarized in Table S3 and Figure S2.

Multivariate Analysis. We explored the community structure of benthic macrofauna across the different physical environments in 2016, 2017, 2018, and 2020 through multivariate

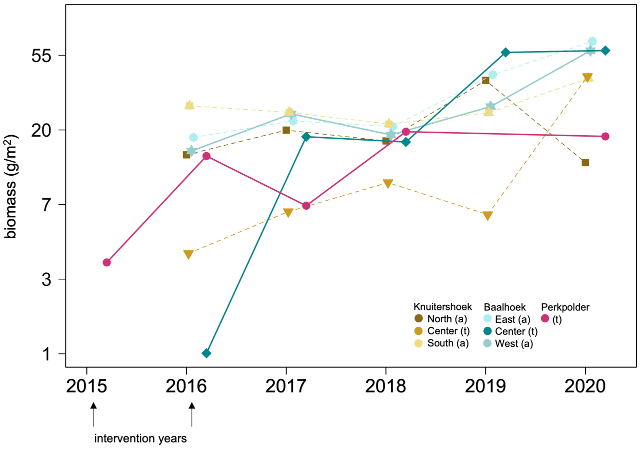

Figure 3. Mean biomass (g/m^2) at the Knuitershoek, Baalhoek, and Perkpolder sites from 2015 to 2020. At Perkpolder and Baalhoek (center and west), the biomass had a linear increase over time (unbroken line). At the other sites, biomass did not increase linearly over time. Please note that only one station was sampled in 2016 at Knuitershoek North and two were added in subsequent years.

methods. We restricted the dataset to those years to ensure a balanced analysis, as Perkpolder was not sampled in 2019. The 2016 results for Knuitershoek North are most likely misrepresenting community variability for this site, as only one point was sampled in 2016 and three points were sampled in subsequent years. Finally, to decrease redundancy in the environmental dataset, we removed "bulk density" as it had a correlation coefficient greater than 0.75 with silt. We used functions from the package "vegan" (Oksanen et al. 2019) to perform the multivariate analyses.

We first performed a redundancy analysis (RDA) to identify which physical characteristics best described abiotic variation. An RDA decomposes the total variance in environmental characteristics into its principal components. We retained the first two axes (75% of the variance explained). Prior to the RDA, we normalized the environmental data to avoid arbitrary units affecting the analysis. Results of the RDA highlight which abiotic variables contribute most to the variation in the dataset (see Fig. 4 top).

Next, we used a canonical correspondence analysis (CCA; Ter Braak & Verdonschot 1995) on community composition as a function of environmental characteristics (see Fig. 4 bottom) to examine which abiotic variables best correlated with biotic community structure. A CCA produces ordination axes that represent linear combinations of environmental variables that maximize the correlation with community data. Multivariate analyses of community composition used the Bray–Curtis dissimilarity index of log-transformed species biomass data via the "vegdist" function in the "vegan" package (Oksanen et al. 2019). A log-transformation stabilized the variance in the dataset and reduced the influence of highly abundant species. The statistical significance of the environmental variable constraints on the biomass data was tested with an analysis of variance-like permutation test (function anova.cca) with 999 permutations.

We explored community dissimilarities through a non-metric multidimensional scaling (nMDS) analysis (function metaMDS, package vegan; Oksanen et al. 2019; Fig. 5). An nMDS reduces the dimensionality of a dataset so that the distances between points in the nMDS plot approximate the dissimilarities between the corresponding communities. We used the Bray–Curtis dissimilarity index of log-transformed species biomass data for the analysis and checked the stress values for robustness.

Finally, we performed a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001; function adonis2, package vegan) to assess whether differences between the community composition were better explained by spatial (between site) or temporal (between year) partitioning. We tested a full model (community composition ~ site [seven-level categorical] × year [three-level categorical]); see Table S4a. Since we detected a significant interaction between site and year, we performed post hoc pairwise tests (pairwise PERMANOVA, function pairwise.perm.manova, package RVAideMemoire package; Hervé 2020) to identify significant year comparisons within sites (see Table S4b & S4c).

Bird Densities. We assessed changes in total bird density and oystercatcher (*Haematopus ostralegus*) counts between 2017 and 2020 using a negative binomial regression (function glm.nb, package MASS; Venables & Ripley 2002). We grouped the bird data by autumn/winter season rather than by year, so that the bird densities for 2017 include monthly counts from October 2017 to February 2018, and the 2020 densities include monthly counts from October 2020 to February 2021. A negative binomial regression was chosen due to overdispersion. A chi-square test showed that the negative binomial regression fit our data better than a Poisson regression. We evaluated model fit using a chi-square test and examined model residuals and qqplots. We modeled total bird density or oystercatcher density as a function of site (seven-level categorical) and year (two-level categorical), including an interaction between site and year. A significant interaction prompted a Tukey post hoc test using the function "ghlt" from the package "multcomp" (Hothorn et al. 2008). Because we did not have access to the full bird dataset (only Oystercatcher and total bird count numbers), we do not present a detailed analysis of the bird data, but rather discuss changes in benthos-eating bird assemblages in relation to the observed changes in their prey (see Fig. 6B).

Results

Low Current Velocity Led to an Import of Silty Sediment in Impact Sites

At Knuitershoek, reduced current velocities between the groins led to substantial accretion and bed-level change, whereas at Baalhoek and Perkpolder, the sediment accretion was less pronounced (Fig. S1). Peak current velocity decreased the most at the Knuitershoek impact site, from 0.51 m/second in 2016 to 0.34 m/second in 2020, while staying relatively high at the Baalhoek impact site (0.55 m/second). At the reference sites for both Knuitershoek and Baalhoek, peak current velocity was lower than in the impact sites in 2016 (0.35 m/second at Knuitershoek

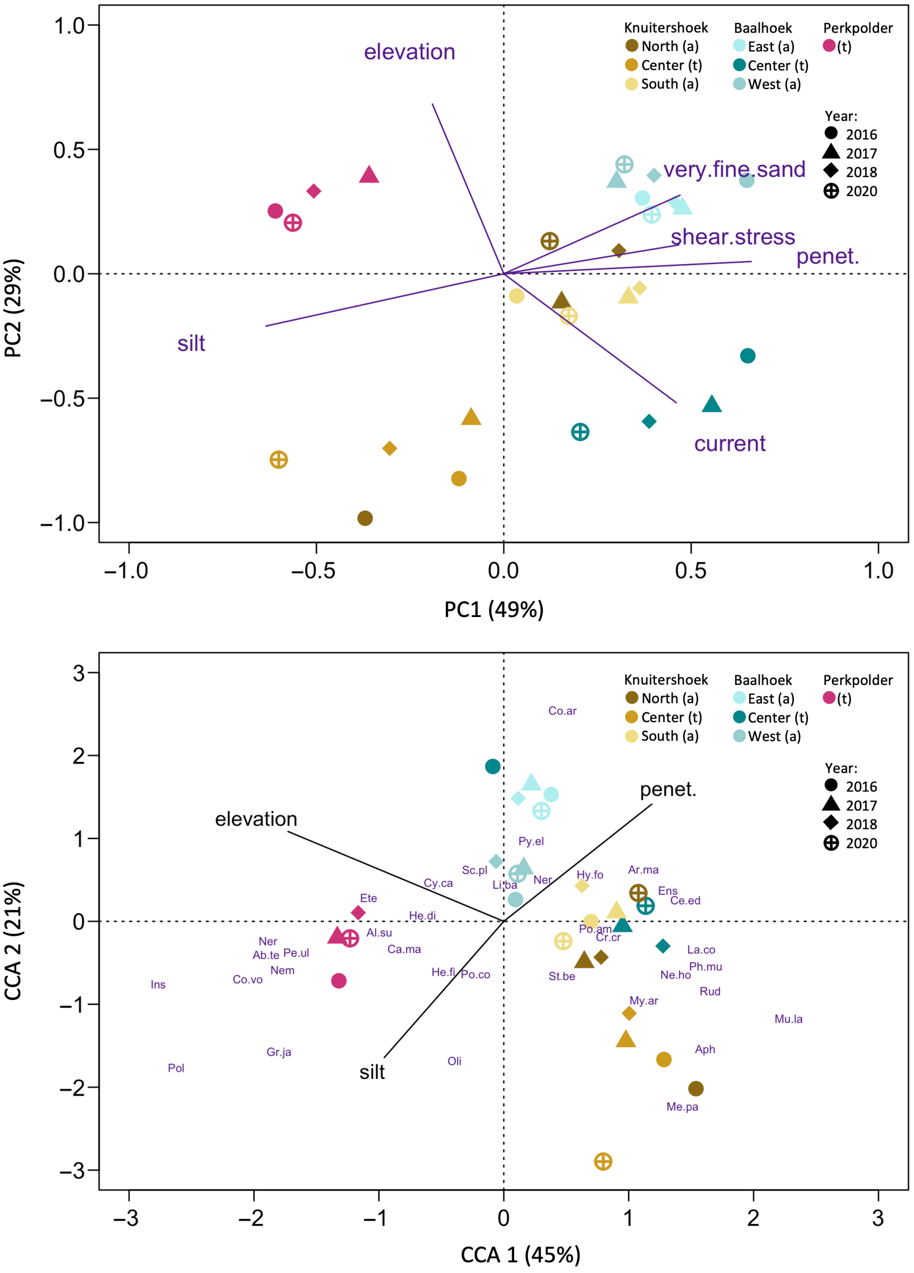

Figure 4. Top: Redundancy analysis (RDA) biplot illustrating the environmental dataset at the seven sites in Baalhoek, Knuitershoek, and Perkpolder in 2016, 2017, 2018, and 2020. The environmental dataset included: elevation (NAP), shear stress (tkN/m^2), silt (%), very fine sand (%), penetration resistance (mPa), and peak current velocity (m/second). Please note that only one station was sampled in 2016 at Knuitershoek North and two were added in subsequent years. The points represent centroids of sample groups partitioned by site and year (function "ordiellipse"), and the arrows represent the direction and strength of the environmental variables. The direction of the arrow represents the variable increase, and the length of the arrow represents the strength of the correlation between the environmental variable and the ordination axes. Bottom: Canonical correspondance analysis (CCA) biplot of the benthic macrofauna community in relation to environmental variables in 2016, 2017, 2018, and 2020. The points represent the group centroids for benthic communities partitioned by year and site (function "ordiellipse"). The plot was scaled so that both species and sites were scaled symmetrically. While the ordination includes the same six environmental covariates shown in the RDA plot, we only plot the three covariates that have statistical significance below less than 0.05 to reduce clutter. In addition, we plotted the 37 most influential taxa (i.e. taxa with the greatest absolute squared species scores). Ab.te, *Abra tenuis*; Al.su, *Alitta succinea*; Aph, Aphelochaeta; Ar.ma, *Arenicola marina*; Au.mo, *Austrominius modestus*; Ba.pi, *Bathyporeia pilosa*; Bra, Brachyura; Ca.ma, *Carcinus maenas*; Ce.ed., *Cerastoderma edule*; Chi, Chironomidae; Cir, Cirripedia; Co.ar, *Corophium arenarium*; Co.vo, *Corophium volutator*; Cr.cr, *Crangon crangon*; Cy.ca, *Cyathura carinata*; Ete, Eteone; Ens, Ensis; Gr.ja, *Grandidierella japonica*; He.di, *Hediste diversicolor*; He.fi, *Heteromastus filiformis*; Hy.fo, *Hypereteone foliosa*; Ins, Insecta; Li.ba, *Limecola balthica*; Me.pa, *Melita palmata*; Mu.la, *Mulinia lateralis*; My.ar, *Mya arenaria*; Nem, Nemertea; Ner, Nereidinae; Oli, Oligochaeta; Pe.ul, *Peringia ulvae*; Ph.mu, *Phyllodoce mucosa*; Po.am, *Potamocorbula amurensis*; Po.co, *Polydora cornuta*; Pol, Polychaeta; Py.el, *Pygospio elegans*; Rud, Ruditapes; Sc.pl., *Scrobicularia plana*; St. be, *Streblospio benedicti*.

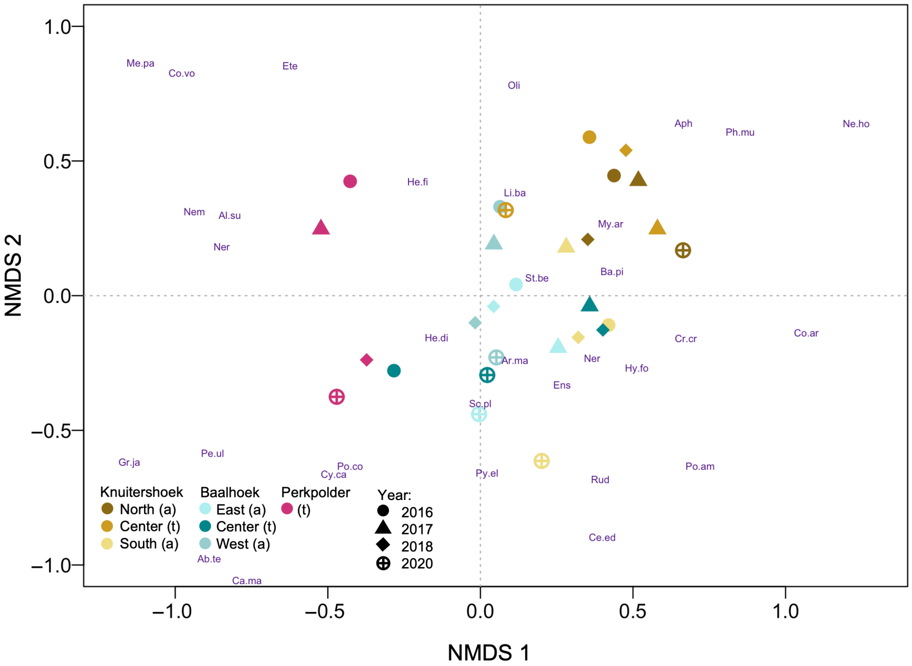

Figure 5. Non-metric multidimensional scaling (nMDS) plot of community composition for benthic community biomass at the seven sites from 2016, 2017, 2018, and 2020. The plot was generated using the Bray–Curtis dissimilarity, and we retained two dimensions (stress = 0.28). In the legend, (t) and (a) indicate whether the corresponding site is an impact site (intended area of intervention impact) or an adjacent site (area next to the impact site). To reduce clutter, we plotted only centroids for groups partitioned by year and site by using the ordiellipse function in the "vegan" package. Please note that only one station was sampled in 2016 at Knuitershoek North and two were added in subsequent years. In addition, we plotted the 37 most influential taxa (i.e. taxa with the greatest absolute squared species scores). Ab.te, *Abra tenuis*; Al.su, *Alitta succinea*; Aph, Aphelochaeta; Ar.ma, *Arenicola marina*; Ba.pi, *Bathyporeia pilosa*; Bra, Brachyura; Ca.ma, *Carcinus maenas*; Ce.ed., *Cerastoderma edule*; Chi, Chironomidae; Co.ar, *Corophium arenarium*; Co.vo, *Corophium volutator*; Cr.cr, *Crangon crangon*; Cy.ca, *Cyathura carinata*; Do.vi, *Donax vittatus*; Ens, Ensis; Ete, Eteone; Gl.tr, *Glycera tridactyla*; Gr.ja, *Grandidierella japonica*; He.di, *Hediste diversicolor*; He.fi, *Heteromastus filiformis*; Hy.fo, *Hypereteone foliosa*; Ins, Insecta; Li.ba, *Limecola balthica*; Mu.la, *Mulinia lateralis*; My.ar, *Mya arenaria*; Ne.ho, *Nephtys hombergii*; Nem, Nemertea; Ner, Nereidinae; Oli, Oligochaeta; Pe.ul, *Peringia ulvae*; Po.co, *Polydora cornuta*; Pol, Polychaeta; Po.am, *Potamocorbula amurensis*; Py.el, *Pygospio elegans*; Rud, Ruditapes; Sc.pl., *Scrobicularia plana*; St.be, *Streblospio benedicti*.

and 0.37 m/second at Baalhoek in 2016) and stayed relatively stable (0.36 m/second at Knuitershoek and 0.35 m/second at Baalhoek in 2020). The peak current velocity at Perkpolder was low after the dike breach (0.15 m/second) and has remained so, owing to its limited tidal prism (75 ha).

The calmer hydrodynamic conditions facilitated sediment accretion, and we observed bed-level changes at the benthic macrofauna sampling locations. Between 2017 and 2020, the impact sites' bed level (i.e. elevation) increased on average by 11 cm at Knuitershoek Center, 14 cm at Baalhoek Center, and 5 cm at Perkpolder. Additionally, we observed an increase in the sediment silt content: 29% at Knuitershoek Center, 49% at Baalhoek Center, and 16% at Perkpolder.

We found that sediment property relationships (silt content, bulk density, shear stress, and penetration resistance) were universal across all sampling locations, while the relationships between sediment properties and geomorphology (elevation and peak current velocity) were site-specific. The strongest universal linear correlation in geomorphological properties across sites (r^2 of 0.68, $p < 0.001$) was between sediment silt content and bulk density (Fig. 2). Similarly, silt content and penetration resistance also had a high correlation (r^2 of 0.61, $p < 0.001$). Siltier sediments were softer (lower bulk density and penetration resistance) than sandier sediments across all sites. However, the relationships between elevation and other geomorphological characteristics differed across locations. At both Knuitershoek and Baalhoek, higher elevation correlated with lower current velocities ($r^2 = 0.35$, $p < 0.001$), and stiffer, sandier sediment (elevation and bulk density $r^2 = 0.25$, $p < 0.001$, elevation and sediment silt content $r^2 = 0.24$, $p < 0.001$) (Fig. 2). In contrast, Perkpolder exhibited some high elevations paired with a high silt content of imported sediment. Sediment silt content and elevation were negatively correlated in Perkpolder ($r^2 = 0.35$, $p = 0.01$), but the intercept and coefficient were greater than at Knuitershoek and Baalhoek (Fig. 2). Unlike at Knuitershoek and Baalhoek, elevation at Perkpolder did not significantly correlate with average current velocity ($r^2 = 0.08$ and $p = 0.13$), largely due to its small, sheltered tidal basin with little alongshore flow.

Biomass Increased Over Time at Most Impact Sites, Following the Interventions

The biomass of benthic macrofauna significantly increased at the impact sites (Table S2; Figs. 3 & S3). The most dramatic increase in biomass occurred at the Baalhoek impact site (Fig. 3),

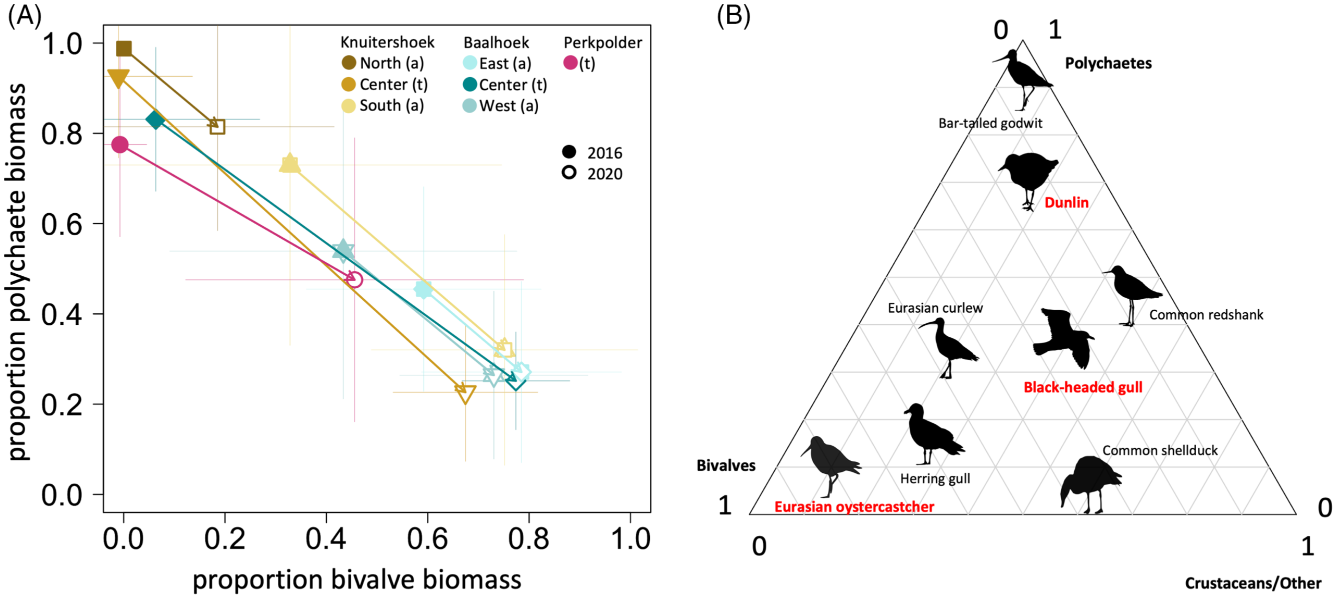

Figure 6. (A) Proportion of polychaetes to proportion of bivalves in the biomass (g/m^2) of impact and adjacent sites in 2016 and 2020. In the legend, (t) and (a) indicate whether the corresponding site is an impact site (intended area of intervention impact) or an adjacent site (area next to the impact site). Please note that only one station was sampled in 2016 at Knuitershoek North and two were added in subsequent years. (B) Triangle plot showing the proportion of bivalves, polychaetes, and crustaceans/other in the diets of the eight most common bird species at the sites. Birds close to the corners are specialized in one food category; birds close to the mid-sides target two food categories, and birds in the center of the triangle eat a mix of the three food categories. Birds with their names in red have increased in numbers at the impact sites from 2017 to 2020. Specifically, the number of oystercatchers increased in all impact sites (statistically significant increase at Baalhoek Center, this study), black-headed gulls in the Baalhoek impact site, and dunlins in Perkpolder (no statistical significance of increase; van der Werf et al. 2021). The bird diet information is from Leopold et al. (2004), and the bird silhouettes are from http://phylopic.org/.

largely due to an increase in bivalves. Indeed, the 2016 bivalve biomass in Baalhoek Center was 0.42 g/m^2 (32% of total biomass), and the 2020 bivalve biomass was 22.96 g/m^2 (85% of total biomass). The log biomass at both Perkpolder and the Baalhoek impact site had a significant linear increase over the project ($r^2 = 0.32$ and $p = <0.001$ for Perkpolder and $r^2 = 0.29$ and $p < 0.001$ for the Baalhoek impact site; Table S2) (Fig. 3). Conversely, biomass at the Knuitershoek impact site increased from 2016 to 2020, but in a nonlinear way (r^2 of 0.25, $p = 0.1$), with the largest increase in biomass occurring in the final year, from an average of 4.5 g/m^2 in 2019 to 18.5 g/m^2 in 2020 (Fig. 3). In 2016, all the impact sites had a lower average biomass than the adjacent sites' average biomass (Knuitershoek Center biomass = 3.8 g/m^2 vs. Knuitershoek South biomass = 30 g/m^2, Baalhoek Center biomass = 1.0 g/m^2 vs. Baalhoek East biomass = 18.1 g/m^2, and Baalhoek West biomass = 15.2 g/m^2). By 2020, the average biomass in the Baalhoek and Knuitershoek impact sites was similar to their respective adjacent sites (Knuitershoek Center biomass = 18.5 g/m^2 vs. Knuitershoek South biomass = 18.9 g/m^2, Baalhoek Center biomass = 56.4 g/m^2 vs. Baalhoek East biomass = 65.9 g/m^2, and Baalhoek West biomass = 58.1 g/m^2; Fig. 3).

Macrofaunal Communities Were Best Distinguished by Elevation and Silt Content

Our RDA analysis showed that variables related to sediment composition and stiffness (silt content and penetration resistance) and elevation or immersion time were the most important physical characteristics for partitioning the variance in the abiotic dataset (Fig. 4 top). Penetration resistance, silt content, and very fine sand content contributed 28, 26, and 17% of the variance explained by the first RDA axis (49% of total variance explained). Elevation and peak current velocity contributed 53 and 32% of the variance explained by the second RDA axis (29% total variance explained). Elevation and penetration resistance/silt content were also the most important variables in driving community composition (Fig. 4 bottom). The permutation test for the CCA showed that elevation was the most important variable ($p = 0.001$), along with penetration resistance ($p = 0.02$) and silt content ($p = 0.01$), constraining the community composition variability.

Elevation had a similarly strong effect on total biomass as it did on community composition. Increased elevation ($p = 0.001$) and decreased peak current velocity ($p = 0.002$) led to an increase in total biomass (Table S3; Fig. S2). However, biomass at Perkpolder did not follow this pattern due to its semi-enclosed geography, as the elevation remained relatively high and peak current velocity was low during the period following the intervention.

Softer, siltier sediment led to greater biomass in low-energy sediments, however, this effect could diminish under extremely high silt conditions. Linear models showed that an increase in silt content ($p = 0.06$) and decrease in penetration resistance ($p = 0.06$) led to a marginally significant increase in total biomass, except in Perkpolder and Knuitershoek Center, the siltiest sites (Table S3; Fig. S2). Silt content increased in Knuitershoek Center from 63% in 2016 on average to 84% in 2020, and in

Perkpolder, from 58% in 2015 to 71% in 2020. Unlike at the other sites, the total biomass at Perkpolder and Knuitershoek Center stayed below 10 g/m^2 on average until 2020. Furthermore, Perkpolder and Knuitershoek Center had consistently lower proportions of bivalves in their biomass compared to the other sites (except Knuitershoek North). with bivalves comprising 53 and 57% of the biomass, respectively, whereas it was around 80% for other sites (Fig. 6A).

Biological Characteristics of Some Impact Sites Approach Adjacent Sites Faster Than Abiotic Characteristics

We observed greater temporal variability in the macrofaunal assemblages than in the abiotic characteristics. Indeed, the RDA plot of the environmental characteristics shows tight clustering of the site-year centroids by site (Fig. 4 top). In addition, the centroids for the adjacent sites clustered tightly together, while the centroids for the impact sites are more dispersed, which suggests that the impact sites had different and more varied abiotic characteristics than the adjacent sites. In particular, the environment of Knuitershoek Center and Baalhoek Center was not close to that of the adjacent sites, even in 2020.

Conversely, the nMDS plot of community composition showed less tight clustering of the site-year centroids by site (nMDS, Fig. 5), suggesting stronger temporal dynamics in biotic components than abiotic ones. Community trajectories are similar between year, especially for adjacent sites. Indeed, post hoc pairwise tests for the PERMANOVA, which assessed spatial (between site) or temporal (between year) variability in community composition, show that communities of the three adjacent sites were similar in all 3 years (significant differences only in the 2017 and 2020 South-West comparison, where $p = 0.018$ and $p = 0.008$; Table S4c). However, in 2016, impact site communities were distinct from each other and the adjacent site ($p < 0.1$ for all 2016 Knuitershoek Center and Baalhoek Center post hoc comparisons). While both Perkpolder and Knuitershoek Center remained distinct from all other sites in 2017, 2018, and 2020 (exception for Knuitershoek Center and Baalhoek East in 2018 and 2020, $p = 0.11$ and $p = 0.19$), Baalhoek Center's macrofaunal community became similar to the Baalhoek adjacent communities in 2017, and stayed similar in 2018 and 2020 ($p > 0.1$ for those post hoc comparisons, except Baalhoek Center-East in 2018 and Baalhoek Center-West in 2020 with $p = 0.07$ and 0.06, respectively), suggesting that the Baalhoek impact site community became more like surrounding communities post-intervention.

The Composition of Benthic Assemblages in Impact Sites Changed Post-Intervention

Colonization processes also influenced the benthic community trajectories. At Perkpolder, the newly created habitat experienced rapid succession (Figs. 5 & S4). Initially, smaller, shorter-lived species such as *Corophium volutator* dominated in the first year after the dike breach at Perkpolder (mean biomass 2.89 g/m^2), but these largely disappeared by 2018 (mean biomass 0.07 g/m^2); at which point, longer-lived bivalves such as *Scrobicularia plana* gained a foothold (mean 2018 and 2020 biomass of *S. plana* was 1.59 and 17.33 g/m^2; Fig. S4). In contrast, at Baalhoek and Knuitershoek, where existing biota was present at impact sites, the temporal community evolution was less strong than at Perkpolder (Fig. 5).

Overall, across all sites, the biomass of the assemblages shifted from polychaetes to bivalves over the monitored period (Fig. 6A). All the impact sites had communities initially dominated by polychaetes (or. *C. volutator* in Perkpolder), but the bivalves biomass shifted closer to those of the adjacent sites very quickly. By 2020, *S. plana* proportion of total biomass was greater than 50% for all sites except for Knuitershoek Center and Knuitershoek North, where *S. plana* was approximately 30% of the total biomass (Fig. S4). In the muddiest areas, Perkpolder and the Knuitershoek impact site, the shift from polychaetes to bivalves was slower compared to the Baalhoek and Knuitershoek South adjacent sites (Fig. 6A). In 2017, the first year where *S. plana* appeared, the mean biomass of *S. plana* in Knuitershoek South, Baalhoek East, and Baalhoek West was 14.45, 14.81, and 11.52 g/m^2, respectively, while in Knuitershoek Center and Baalhoek Center, *S. plana* mean biomass was 0.93 and 4.59 g/m^2, respectively, suggesting that abiotic conditions at adjacent sites were more amenable to *S. plana* than at the impact sites. The exception to this trend of polychaete to bivalve biomass shift was the sand-nourished adjacent site Knuitershoek North. Rather, the polychaetes *Heteromastus filiformis*, *Hediste diversicolor*, and *Arenicola marina* made the largest contributions to biomass in Knuitershoek North in 2020.

Benthos-Eating Birds May Have Responded to an Increase in Benthos Biomass

The changing composition and biomass of the benthic macrofauna community likely had an effect on the benthos-eating birds in the area (Fig. 6). The total number of benthos-eating-birds increased between 2017 and 2020 (negative binomial model year effect $p < 0.01$). The number of oystercatchers increased between 2017 and 2020, which seems to have been largely driven by increases in oystercatcher presence at the Baalhoek impact site, rising from 0.9 to 7.7 oystercatchers/ha (post hoc Tukey $p = 0.001$; Fig. S5). However, no statistically significant increase in total benthos-eating birds or oystercatchers was detected in Knuitershoek Center between 2017 and 2020, though the number of oystercatchers seemed to increase from 0.5 to 0.9 birds/ha. In Perkpolder, the number of benthos-eating birds increased between 2017 and 2020 from 1.6 to 2.4 birds/ha (post hoc Tukey $p = 0.01$), though the number of oystercatchers did not show a statistically significant increase.

Discussion

The groins and managed realignment successfully enhanced the habitat value for the benthic macrofauna community. Lowering the hydrodynamics at impact sites stimulated sediment import, and, as a result, we observed an increase in the benthic macrofauna biomass at the impact sites post-implementation. Additionally, densities of benthos-eating birds, particularly oystercatchers, increased at some impact sites. However, we also found slower development of benthic macrofauna biomass under extremely high silt content (>70%) conditions. While improving the habitat is important to attract benthic macrofauna, biotic processes such as colonization and succession are also important for determining the evolution of benthic macrofauna assemblages. Because of this, delays may occur in how the benthic macrofauna community responds to changes in their habitat.

The Pros and Cons of Low-Energy Areas for Stimulating Benthic Macrofauna

One of the core goals of the restoration initiatives was to create low-energy (peak current velocity <0.6 m/second) intertidal flats, based on the principle that low-energy areas are more species rich than highly dynamic areas (Van Colen et al. 2010*a*; van der Wal et al. 2017), though not always (Dutertre et al. 2013). Indeed, fewer species can maintain a foothold under highly dynamic conditions (Warwick & Uncles 1980; Van Colen et al. 2010*a*). Furthermore, coarse sediments in highly dynamic areas are unstable for large burrowers and offer little food to deposit feeders (Donadi et al. 2015), and high hydrodynamic stress can reduce recruitment by resuspending sediment and larvae (Bouma et al. 2001). However, the key difference between low-energy and highly dynamic areas may have more to do with the types of assemblages that these habitats can support than the species richness. Low-energy areas favor burrowing deposit feeders, whereas highly dynamic areas favor omnivorous crawling or swimming species (van der Wal et al. 2017). Low-energy environments may also bring challenges, such as bottom-waters becoming susceptible to oxygen depletion because of reduced mixing (Dutertre et al. 2013), which could be exacerbated due to rising temperatures. Finally, spatial heterogeneity enhances species richness (Ellingsen et al. 2007), so focusing solely on creating low-energy habitat may reduce macro-scale diversity in both the environmental and biological components of the ecosystem.

In the impact sites of our three cases, the low hydrodynamics led to the accumulation of fine-grained sediment with a high silt content, especially at Perkpolder and Knuitershoek Center. High silt content means a food-rich environment for deposit feeders and greater bed-level stability than coarse sand (Ysebaert & Herman 2002). Yet, rapid accumulation of extremely silty sediments (Lohrer et al. 2006) coupled with poor drainage (Dale et al. 2019), can hinder animal functioning. Though low bulk densities can facilitate animal movement (Wiesebron et al. 2021), animals may expend more energy to maintain their position in highly silty sediment or unclog their feeding apparatus of mud particles (Lohrer et al. 2006; Mestdagh et al. 2018). The rapid silt accumulation may have slowed benthic community development at Perkpolder and Knuitershoek Center, where biomass built up more slowly than other impact sites. Therefore, while silt content benefits benthic macrofauna, especially deposit-feeding burrowers, extremely high silt content may hinder overall benthic macrofauna community development, which should be considered when designing low-energy areas for restoration purposes.

Bottom-Up Effects on Birds

As benthic macrofauna are the prey of many other intertidal fauna, their biomass increase should attract predators such as birds. Indeed, we observed more benthos-eating birds, in particular oystercatchers, at the impact sites over the project years. We also observed an area-wide shift in benthic macrofauna biomass from polychaetes to bivalves, dominated by *Scrobicularia plana*, with the biggest shifts occurring at impact sites. Oystercatchers prefer to eat bivalves, and *S. plana* is one of the oystercatcher's most profitable prey (Zwarts et al. 1996). Thus, it is possible that oystercatchers specifically responded to this prey source. However, links between bird assemblages and the availability of their preferred prey are frequently weak (Horn et al. 2020). Instead, bird distribution patterns are more strongly related to abiotic factors such as the tidal cycle (Dias et al. 2006), distance to roost (Rogers et al. 2006), and anthropogenic disturbance (Velando & Munilla 2011). Thus, it remains unclear how much the observed changes in bird use of the impact sites are linked to benthic prey availability. To explain bird observation, we should also consider the geomorphological changes as important factors.

Contextualizing Intervention Success: a Perspective Over Time and Space

The interventions succeeded in achieving the management goal of increasing benthic macrofauna biomass at the impact sites. This was the result of careful design, but such interventions are sometimes unsuccessful. In fact, at Knuitershoek, several groins and channel edge fixation works were already present, but the groins were not sufficiently high to stimulate sedimentation and hindered drainage instead, resulting in low sediment bulk densities. Conversely, in another project, rapid sediment accumulation caused an intended intertidal flat to become a marsh within 10 years (Mazik et al. 2010). The challenge is that a single intervention can have opposing ecomorphological consequences at different locations due to different hydrodynamics and sediment supply (de Vet et al. 2020). Thus, effective interventions require appropriate forethought and hydromorphodynamic modeling of the impact of various designs.

Though both kinds of interventions (groins and managed realignment) engendered an increase in benthic macrofauna biomass, their long-term consequences differ, especially when they are implemented en masse and under the threat of sea-level rise. The estuaries where these tidal flat interventions are implemented typically face ongoing human disturbance, such as dredging to keep shipping channels open. Managed realignments could help counteract intertidal steepening under sea-level rise by widening the area, thus increasing the accommodation space for intertidal flats (Leuven et al. 2019). Groins, however, restrict channels and might steepen the intertidal. For example, in the Yangtze delta, groins resulted in sediment accretion and current dampening between the groins, but eroded and deepened the channel (Luan et al. 2018). Steeper tidal flats have a negative, long-term effect on benthic macrofauna by restricting their habitat (Cozzoli et al. 2017). Thus, groins' local effect in increasing benthic macrofauna biomass at the local scale should be weighed against their impact on the estuarine system as a whole, since the long-term and large-scale morphological changes may have negative ecological effects that surpass the current short-term and localized benefits.

Engineering modifications of the tidal flats at Knuitershoek, Baalhoek, and Perkpolder led to the creation of habitat with low hydrodynamics, the accumulation of fine, silty sediment, and an increase in benthic macrofauna biomass. However, abiotic conditions and biotic responses at these sites are still in flux. While improving habitat is of crucial importance to attract benthic macrofauna, biotic processes such as colonization and recruitment success also determine the evolution of macrobenthic assemblages (Zajac et al. 1998), especially in the early years post-intervention. Thus, there may be a delay in the benthic community response to changing abiotic characteristics (or even a delayed environmental response to intervention; see de Vet et al. 2020). Indeed, slow recovery rates of benthic communities have been often observed post-disturbance (Lohrer et al. 2010; de Juan et al. 2014) and recovering benthic communities can diverge from that of the surrounding area and/or even their pre-disturbance state (Van Colen et al. 2010*b*). Diverging benthic macrofauna community responses necessitate a well-planned intertidal flat alterations, preferably informed by local studies on abiotic–biotic coupling. Continuous monitoring is essential to track the initial impact of the intervention and the long-term development of the benthic macrofauna community post-intervention.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Coefficients, p values, and r^2 values for models of linear relationships between pairs of environmental variables.
Table S2. Total log biomass as a function of year.
Table S3. p Values for linear models of total log biomass as a function of environmental variables, sites, and year.
Table S4. Variability in community composition partitioned by spatial (between site) and temporal (between year) components.
Figure S1. The evolution of the sediment properties at sites in Knuitershoek, Baalhoek, and Perkpolder.
Figure S2. Relationship between biomass (g AFDW) and suite of environmental parameters.
Figure S3. Boxplot of total log biomass partitioned by site and year.
Figure S4. The fifteen most massive species at sites in Knuitershoek (north, center, and south), Baalhoek (west, center, and east), and Perkpolder.
Figure S5. Time series showing oystercatcher densities (top) and the total benthos-eating bird densities (bottom) from 2017 to 2020.

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