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Shellfish Reefs Increase Water Storage Capacity on Intertidal Flats Over Extensive Spatial Scales

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ABSTRACT

Ecosystem engineering species can affect their environment at multiple spatial scales, from the local scale up to a significant distance, by indirectly affecting the surrounding habitats. Structural changes in the landscape can have important consequences for ecosystem functioning, for example, by increasing retention of limiting resources in the system. Yet, it remains poorly understood how extensive the footprint of ecosystem engineers on the landscape is. Using remote sensing techniques, we reveal that depression storage capacity on intertidal flats is greatly enhanced by engineering by shellfish resulting in intertidal pools. Many organisms use such pools to bridge low water events. This storage capacity was significantly higher both locally within the shellfish reef, but also at extensive spatial scales up to 115 m beyond the physical reef borders. Therefore, the footprint of these ecosystem engineers on the landscape was more than 5 times larger than their actual coverage; the shellfish cover approximately 2% of the total intertidal zone, whereas they influence up to approximately 11% of the area by enhancing water storage capacity. We postulate that increased residence time of water due to higher water storage capacity within engineered landscapes is an important determinant of ecosystem functioning that may extend well beyond the case of shellfish reefs provided here.

Key words: ecosystem engineering; depression storage capacity; shellfish reef; mussel; oyster; intertidal pool; spatially extended effects; water retention.

INTRODUCTION

Since the introduction of the concept of ecosystem engineering by Jones and others (1994), the notion that certain species may drive ecosystem structuring and functioning through habitat modification has largely been accepted by the scientific community. Ecosystem engineering organisms are able to influence abiotic conditions and resource availability, thereby creating specific niches within the landscape that change community composition

(Bruno and others 2003; Crain and Bertness 2006) and boost biodiversity at larger spatial scales (Jones and others 1997; Wright and Jones 2004; Bouma and others 2009). These bioengineered systems are often characterized by feedbacks that increase stability (Gurney and Lawton 1996; Jones and others 1997; Hastings and others 2007) and resilience (Eriksson and others 2010). Although more recently it became evident that ecosystem engineering also affects ecosystem structure and functioning over long distances, well beyond the boundaries of the physical engineered structures (van de Koppel and others 2015), less is known about what determines the extent of ecosystem engineering.

A key feature of ecosystem engineering is that species can introduce or remove physical structure, altering the overall topography of the landscape (Wright and Jones 2004; Jones and others 2010). Habitat complexity, which is often used interchangeably with the notion of topographical complexity, is regularly used to explain dynamics in species distributions because it explains the amount of refuge space or food available through either increased niche space or increased surface area (Kovalenko and others 2012). Although structural complexity mainly increases niche space in benign systems, the interaction between biogenic structure and the abiotic environment results in additional effects that structure the landscape and boost heterogeneity. For example, structural changes due to ecosystem engineering can modify grain size distribution (Gutiérrez and others 2003; Bos and others 2007; Yang and others 2008; van Katwijk and others 2010; Meadows and others 2012), organic matter content (Jones and others 1994; van Katwijk and others 2010; van der Zee and others 2012) and moisture in sediments (Crain and Bertness 2006; Meadows and others 2012).

The interplay of the physical environment and added structure through ecosystem engineering is clearly exemplified by the beaver (*Castor* spp.), the archetypal example of an ecosystem engineer (Wright and others 2002, 2003). The beaver builds dams, which impound water upstream. The size of the water reservoir depends on the size of the dam, but also on the underlying landscape topography; in a steep canyon valley the reservoir can only extend to a moderate surface area before the dam overflows, but on flat wetlands the reservoir can be much larger (Johnston and Naiman 1987). The effects of these reservoirs on fish communities are generally beneficial because they provide extreme flow refuge, breeding sites and habitats (Kemp and others 2012). In addition, the retention in beaver ponds may improve water quality as particulate

matter can settle (Correll and others 2000). Yet, so far the beaver example is as idiosyncratic as it is iconic. Little is known about pond formation by other ecosystem engineering species, thereby limiting the generality of this example.

In this study, we investigated how bioengineering shellfish, in particular the blue mussel (*Mytilus edulis*) and the Pacific oyster (*Crassostrea gigas*), increase storage capacity (that is, depression storage capacity) within an estuarine landscape resulting in tidal pools. In a process referred to as self-organization, engineering by shellfish can lead to the formation of a regular or semi-regular mosaic of raised hummocks and depressions (van de Koppel and others 2005; Liu and others 2012). Raised hummocks are formed by trapping fine particulate sediment and organic matter locally causing variations in the elevation within reefs (ten Brinke and others 1995; Rodriguez and others 2014; Walles and others 2014). This increases the structural complexity of the landscape and increases water storage capacity (Gutiérrez and others 2011. Trapped water in depressions forms tidal pools which are typical features within shellfish reefs (see Figure 1). Increased storage capacity at spatially extended scales (surrounding the reefs) is likely the result of the influence shellfish reefs has on the hydrodynamic regime (waves and tidal flow) beyond the physical borders of the engineered structures (van Leeuwen and others 2010). This results in sedimentation of fine particulate matter around these reefs (van Leeuwen and others 2010; van der Zee and others 2012; Donadi and others 2013; Walles and others 2014). This, in turn, leads to the typical surface topography with high storage capacity associated with cohesive sediments, which may also trap water (Whitehouse and others 2000).

We investigated whether intertidal flats with shellfish reefs have a greater depression storage capacity, both within and around reef areas compared to non-engineered intertidal flats. First, we investigated local effects of shellfish on depression storage capacity and compared this to the reefs immediate surroundings by using high-resolution terrestrial laser scan data. Secondly, we used remotely sensed (airborne LiDAR for elevation measurement and space borne synthetic aperture radar for shellfish mapping specifically) data to compare storage capacity within reefs with that of the intertidal flat at increasing distances from the reefs to see to what spatially extended scales storage capacity is still significantly enhanced. Finally, to provide general understanding of how water storage capacity depends on landscape roughness, we ran simulations of different landscape structures to
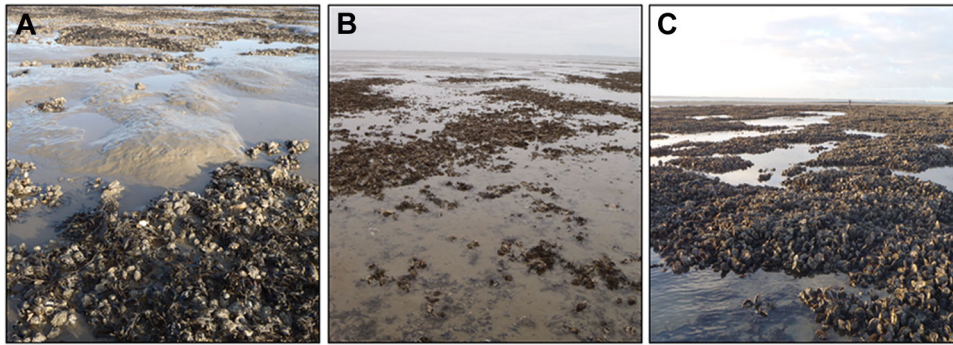
Figure 1. **A** Tidal pools between patches of mussels studied in this paper south of the island of Schiermonnikoog. **B** Tidal pools on and around an oyster reef south of the island of Schiermonnikoog. **C** Tidal pools observed in the Oyster reef at Neeltje Jans location. All of these pools have been verified to persist during low water events.

reveal how storage capacity depends on landscape structure and topography (more specifically the vertical and horizontal roughness elements, and slope).

METHODS

In this study, we estimate the depression storage capacity as a proxy for the potential for the amount of water that can be retained in a landscape, following the definition and methodology of Knecht and others (2012) and Schrenk and others (2014). We used standard GIS routines to fill depressions in elevation maps (more specifically MATLAB's imfill routine and ArcGIS 10.1's fill routine were used depending on the data type analyzed). The depression storage capacity map is calculated by subtracting the original elevation map from the filled elevation map. Statistical software R was used for statistics (R Development Core Team 2015).

It should be noted that in this study we use depression storage capacity to indicate the potential for tidal pool formation, yet depressions in an elevation map do not necessarily result in water accumulation. In reality, water may infiltrate or seep away in small-scale structures, too small to be captured by the resolution of the elevation map. However, field observations indicate that the majority of depressions on shellfish reefs and their surroundings do contain water throughout an entire low tide event. This is supported by the fact that low infiltration rates (in the order of 1–60 mm per day) caused by fine particulate matter and water saturated sediments are typical for the intertidal zone (for example, Harvey and others 1987; Nuttle and Harvey 1995; Hughes and others 1998). This was confirmed by water level measurements with pressure loggers placed in tidal pools within and

around an oyster reef, which revealed limited drainage during low tide (see Supplementary Material S1). In addition, reef structures slow down runoff and increase the residence time of water in the landscape. In the case of mussel and oyster reefs, this will likely result in hydrodynamically benign environments, which usually result in higher deposition or decreased erosion of fine particulate and organic matter (Rodriguez and others 2014). These associated differences in sediment characteristics will further emphasize the differentiation in water retention between shellfish influenced areas and bare intertidal flats, as the latter are usually sandier. Although such differences are not accounted for in the methodology used here, the concept of depression storage capacity is widely used in hydrological studies (for example, Mitchell and Jones 1978; Hansen and others 1999).

Study Sites

This study was carried out on two spatial scales. To study storage capacity at reef scale, three shellfish reefs, with their neighboring mudflats, were used to study the difference in ponding between reef surfaces and sandy surfaces. The small-scale sites included an oyster reef and a mussel reef on the tidal flats south of the island of Schiermonnikoog in the Dutch Wadden Sea. The Wadden Sea is a mesotidal eutrophic system, which was designated as an UNESCO world heritage site in 2009 because of diverse seascapes and the wildlife (particularly birds) that it supports. In addition, an oyster reef on the tidal flats bordering the island of Neeltje Jans was studied. Neeltje Jans is a mudflat in the Oosterschelde, a macrotidal sea arm located in the southwest delta region of the Netherlands. Pacific oysters were introduced for mariculture into this

Table 1. Locations, Areas, Tidal Characteristics and Average Sediment Fractions (Clay <2 μm, Silt 2–50 μm and Sand >50 μm) of the Reefs Studied

Basin	Location	Species	Coordinates	Mean elevation (m NAP) reef	Area inside reef (m²)	Area outside reef (m²)	Average tidal range (cm)[a]	Spring tidal range (cm)[a]	Inundation time reef structure	N soil sample	% Clay (±SD)	% silt (±SD)	% sand (±SD)	Median grain size, D50 (μm)
Wadden Sea	Schiermonnikoog	Mussel	53°28′42″N 6°13′29″E	−0.61	8782	17552	−124,104	−138,119	0.72	7	4.31 (0.80)	60.38 (12.94)	35.50 (13.63)	30.33 (28.46)
Wadden Sea	Schiermonnikoog	Oyster	53°28′16″N 6°12′42″E	−0.06	21537	13557	−124,104	−138,119	0.61	7	3.65 (0.56)	47.04 (9.11)	49.49 (9.58)	54.03 (23.93)
Oosterschelde Estuary	Neeltje Jans	Oyster	51°37′35″N 3°43′32″E	−0.48	9079	8570	−121,133	−123,152	0.63	6	3.28 (1.91)	40.63 (19.69)	56.11 (21.56)	139.69 (104.67)

The tide values are with regard to NAP (Normaal Amsterdams Peil, which is the Dutch ordnance system and is approximately similar to mean sea level).
[a]Tidal conditions from (Rijkswaterstaat 2012). Schiermonnikoog tidal data were obtained at the Schiermonnikoog station, and Neeltje Jans tidal data were acquired at the Roompot binnen station.

estuary in 1964, after the collapse of the indigenous oyster species, and pacific oyster populations have gradually expanded throughout the system since the 1970s, building extensive reefs (Troost 2010). Sediment samples were taken in and around the reefs from the top 2 cm of the sediment bed, and particle size distributions were characterized using a Malvern 2600 particle sizer. See Table 1 for more general information about the shellfish reefs.

To study the effects of shellfish on storage capacity at basin scale, a part of the Wadden Sea south of the barrier island of Schiermonnikoog was investigated. In this part of the Wadden Sea both blue mussel beds, Pacific oyster beds and mixed beds are present (Figure 1).

Water Storage Capacity in and Around Individual Shellfish Reefs

Retrieval of Surface Topography Using Terrestrial Laser Scanning at the Reef Scale

During low tide (when the reefs were fully exposed) A RIEGL VZ-400 terrestrial laser scanner (TLS) was used to obtain laser scans from four sides of the selected reefs to avoid gaps in the data due to shadowing (accuracy of 5 mm). The scans were made on June 20, February 21 and March 22, 2012, for the mussel reef and oyster reef at Schiermonnikoog and the oyster reef at Neeltje Jans, respectively. The data were georeferenced using white reflectors, which were geolocated using a differential global positioning system (dGPS). Thereafter, the scans were merged and cleaned to provide coherent xyz-point-cloud data of each location using the software package RiScan Pro (v1.7.2). The scan of the oyster reef at Neeltje Jans, the oyster reef at Schiermonnikoog and the mussel reef at Schiermonnikoog contained 54, 46 and 42 million xyz-points, respectively. The point clouds were rasterized to grids with 0.25 m cell size by calculating mean height of the xyz-points within each cell using the R package "raster" (Hijmans 2015).

Because the terrestrial laser scanner used in this study operates in the near-infrared part of the spectrum, measuring the bathymetry underneath the water surface in tidal pools is problematic, due to high absorbance of water at these wavelengths and diffraction of the laser beam. In fact, 12.9, 41.8, and 18.3% of the grids of, respectively, the oyster reef at Neeltje Jans, the oyster reef and mussel reef at Schiermonnikoog, contains no data (Figure 2 second row). Because the storage capacity analysis requires a raster without missing cells, we filled
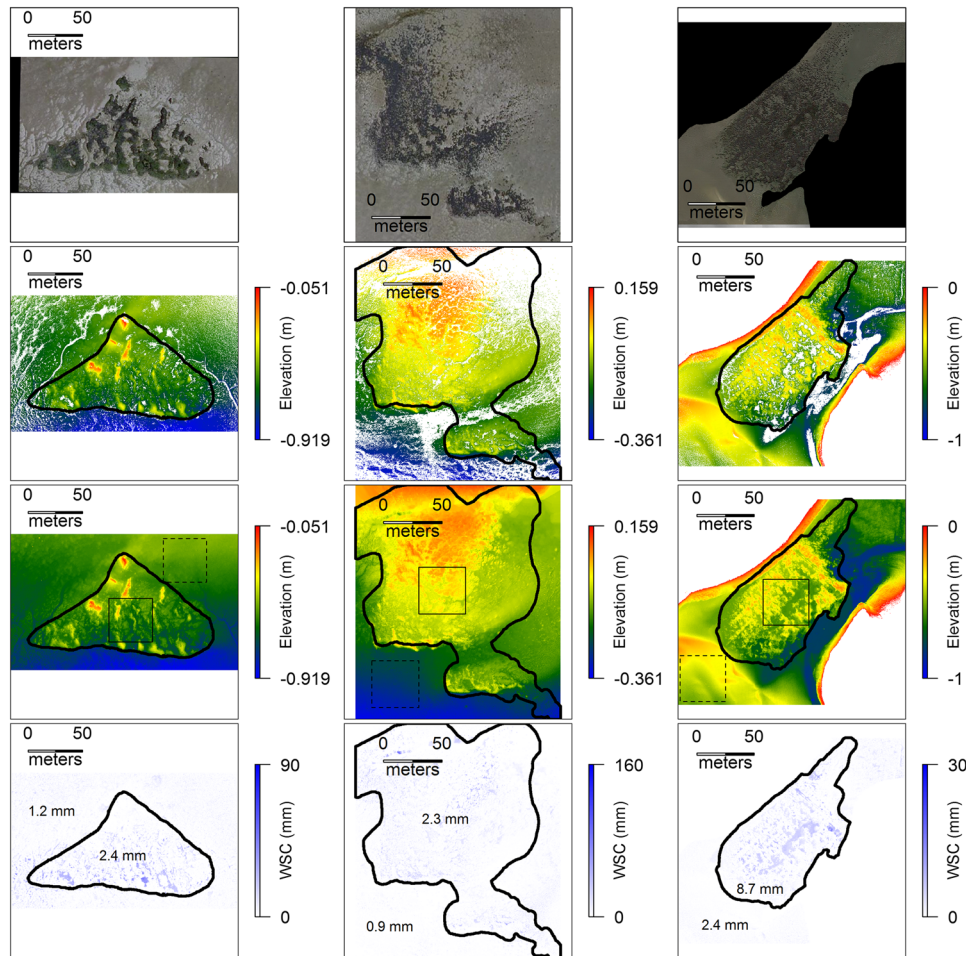
Figure 2. Elevation differences and water storage capacity across three shellfish reefs. Elevation maps before inverse distance weighting interpolation (*top row* pixels with no value are white), IDW interpolated elevation maps (*middle row*) and water storage capacity (WSC) maps (*lower row*, with average ponding per zone) of the mussel reef at Schiermonnikoog (*left column*), oyster reef at Schiermonnikoog (*middle column*) the oyster reef at Neeltje Jans (*right column*). The *black line* indicates the outline of the shellfish reef. The *squares* (in the *third row*) indicate the regions used for landscape characterization (see supplementary material).

these gaps using inverse distance weighting interpolation to produce coherent elevation maps (Figure 2 third row). We expected that this interpolation would result in an underestimation of depression depth. Next, storage capacity was determined using MATLAB's imfill routine. In order to test whether our acquisition and rasterization procedure yields reasonable results, we compared the final raster to field measurements acquired using a dGPS for the Neeltje Jans site. A total of 117 wet points were compared revealing that there was a relatively good correspondence ($R^2 = 0.63$) between the dGPS and the rasterized and interpolated TLS data. Only 7 out of 117 interpolated points turned out to be slightly deeper than dGPS values and the average underestimation of depression values was about 11 cm. Although these measurements are just a snapshot and do not say anything about pool stability (and hence ecological function), measurements of water depth development in and around the oyster reef reveal that water is retained during an entire low tide event and water loss due to drainage is limited within pools (see Supplementary Material S1 for methods and results).

Comparing Water Storage Capacity Between Reef and Tidal Flat Area

To delineate reef area in the study site, aerial photographs (Figure 2 top row) were used to outline the convex hull of the shellfish reefs. Using these outlines, one part of the data was qualified as shellfish reef, while the other was qualified as bare mudflat without shellfish. MATLAB's imfill routine was used for estimating the storage capacity. The storage capacity within shellfish areas was compared with storage capacity outside of the reefs by calculating average storage capacity (in mm) (see Figure 2 bottom row).

Water Storage Capacity at Basin Scale

Retrieval of Surface Topography Using Airborne Laser Altimetry Data at the Basin Scale

To study how shellfish reefs influence water retention by influencing depression storage

capacity at extensive spatial scales (basin scale), we used high-resolution laser altimetry (LiDAR) data of the intertidal regions in the Wadden Sea. We acquired 5-m resolution LiDAR data (2009) of the mudflats south of Schiermonnikoog from Rijkswaterstaat (the Dutch agency for water management) for this purpose (see Figure 3). Gaps in the data on the intertidal flats due to the scanning method and the presence of water were filled using inverse distance weighting, while the subtidal region was excluded from the analysis. A 3*3 median filter was used to remove noise from the bathymetry data. Unrealistic ponding in small-scale channels was removed using a mask that was created in the regions where depressions were deeper than a standard deviation from the mean in a 7*7 moving window. Afterward, the fill algorithm of ArcMap 10.0 was used to fill all depressions and the original bathymetry map was subtracted from this data. The resulting map is the water storage capacity map, from which volumes and areas were determined for all intertidal pools. It should be noted that resolution differences between TLS and large-scale LiDAR affect the estimated amount of water retention in depressions, that is, overall retention is underestimated slightly with LiDAR, but the ratios of retention between the different classes are about the same (see Supplementary Material S2).

Shellfish Reef Delineation Using SAR Satellite Remote Sensing

Shellfish reefs were mapped using Synthetic Aperture Radar (SAR) satellite imagery. Dual polarized (HH and HV) C-band (5.3 GHz) images from Radarsat2 were downloaded through the Dutch Satellite Data Portal website (Netherlands Space Office). Image acquisition was at 5:53 AM on 5/23/2012, and the satellite was in descending orbit. Water level was 1.34 m below sea level and wind direction was 56° at 6.8 m/s. NEST 5.0.12 was used to (1) calibrate the image following product specifications to sigma naught, (2) filter noise using Lee's refined adaptive local filter, (3) perform ellipsoid correction (resampling using bilinear interpolation), and (4) convert pixel intensities to decibels. To map shellfish, we used a multivariate logistic regression method incorporating both cross- and co-polarized channels following (Nieuwhof and others 2015). SAR data resolution was approximately 12 m; but to match the LiDAR data, the resulting presence/absence map was interpolated to 5-m resolution using nearest neighbor interpolation and converted into polygons using the standard procedure available in ArcGIS 10.0.

Determination of the Spatial Extent of Increased Storage Capacity Around Shellfish Reefs

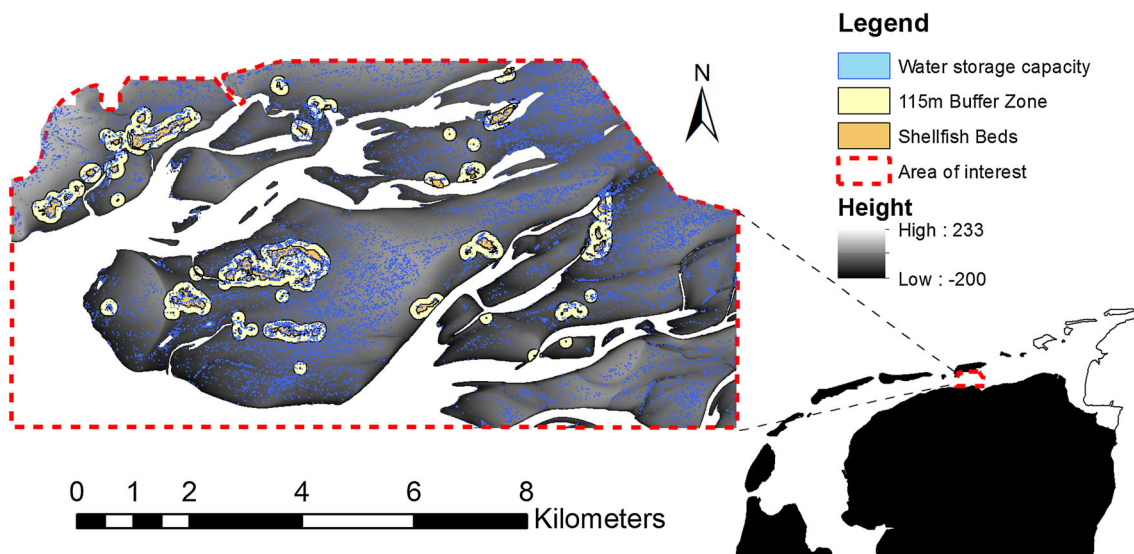A spatial analysis was performed to find how the storage capacity differed at increasing distances

Figure 3. Bathymetry map within the region of interest south of the island of Schiermonnikoog as detected by LiDAR (*dark-gray* values represent low elevations, whereas *light-gray* values represent higher elevations). SAR detected shellfish reefs are indicated in orange and the 115-m buffer zones in *green*. The water storage capacity is depicted in *blue*.

from the shellfish reefs. ArcGIS 10.0 (buffer tool) was used to find the storage capacity at the different distance intervals from the shellfish reefs using the ponding map. Storage capacity values of individual pixels were then binned (by calculating average storage capacity) to raster resolution (5 m) in the statistical software package R (the minimum amount of observation for a bin was 5280 pixels). A cumulative sum control chart (CUSUM) (Page 1954) was used to investigate at which distance the storage capacity was significantly different from background (mudflat) storage capacity. Background storage capacity was defined as the storage capacity between 900 and 1000 m from the reef. Based on the CUSUM analysis, the data were subsequently divided into three groups: (1) reef (0-m distance), (2) buffer (elevated storage capacity on the intertidal flat surrounding shellfish reefs) and (3) intertidal flat (distances at which storage capacity was not elevated). These groups were used to investigate differences in total storage capacity within these groups (average amount of mm per pixel). In addition, the area and volume of each pool (connected by pixels which together make up a depression) was determined to investigate differences in pool size distributions between the three different zones.

Effect of Surface Topography on Water Storage Capacity from Simulated Landscapes

Semivariogram statistics (*range, sill* and *nugget*) were used to describe the spatial correlation structures of intertidal landscapes (Legendre and Legendre 2012) using the gstat package in R (Pebesma 2004). The *range* parameter indicates the maximum lag distance over which there is still spatial correlation (Figure S3), whereas the *sill* parameter describes the maximum amount of vertical variation found in a surface (similar to the total variance, see Figure S3). Different *range* (1–10 m, with steps of a meter) and *sill* (1–10 mm, with steps of a millimeter) parameters were simulated with exponential correlation structures. To show that the used simulation settings are realistic, semivariogram statistics (*sill* and *range*) were determined for parts of the TLS data of the individual reefs and mudflats studied (see boxes in Figure 2 third row). For further details on the methods and results of this characterization, we refer the reader to the Supplementary Material S3. The simulated landscapes were 512*512 cells large (with 0.25 m cell sizes) and replicated 50 times. Finally, the simulations were also performed with a

5% slope (on intertidal flats that is about the maximum slope one would expect), to assess the impact of slope on the water storage capacity.

RESULTS

Water Storage Capacity in and Around Individual Shellfish Reefs

We found clear local effects of the presence of ecosystem engineering shellfish on water storage capacity in the three individual reefs (Figure 2). Visual inspection of the elevation maps reveals that complex surface structures occur within the boundaries of the shellfish reefs (see Figure 2, 2nd and 3rd row). These structures are characterized by spatially alternating hummocks and depressions, in which water can be trapped (see Figure 2 bottom row). Although there were large differences between the three study sites, there was a consistent difference between the two different substrate types (shellfish and bare mud). Storage capacity inside the reefs is consistently higher than outside the reef: at Schiermonnikoog 2.4 mm (that is, 2.4 L m^{-2}) in the mussel reef, and 2.3 mm in the oyster reef, and at Neeltje Jans 8.7 mm at the oyster reef, as opposed to 1.2, 0.8 and 2.4 mm outside the reefs, respectively.

Water Storage Capacity at Basin Scale

The combination of airborne laser altimetry (LiDAR) and satellite SAR data of the Wadden Sea area, allowed us to analyze 5,508 ha of intertidal flat, of which 105 ha was occupied by shellfish (approximately 2%). The storage capacity analysis revealed a total of 14,097 depressions that are potentially tidal pools, of which 488 were located in shellfish occupied areas. We found that oyster and mussel reefs increased storage capacity in the area directly surrounding the reef up to 115 m from the reef edge, that is, the storage capacity at distances between 0 and 115 m from the reef is significantly different from the background retention (see Figure 4). Within this zone of 115 m, there is a steady decrease in storage capacity with increasing distance from the shellfish reefs. Water storage capacity was largest within the shellfish reefs (at 0 m distance). Note that the CUSUM analysis also reveals a small but significant peak at around 300 m, probably associated with periodic topographic features intrinsic to mudflat morphology. The periodic pattern was not caused by a lack of observations (the minimum amount of observations in a distance class was 5280).
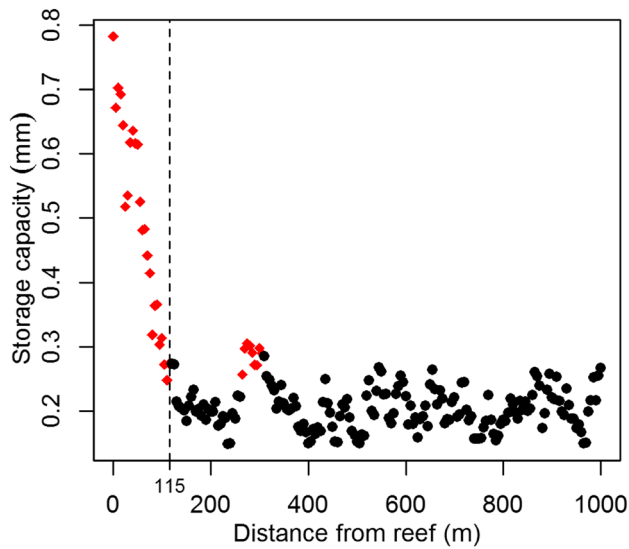
Figure 4. Average storage capacity values for different distances from the reef edges. 0 m indicates ponding within the reef. The values are binned to 5-m classes. The *red triangles* indicate significant changes from background ponding (last 20 points in this graph). The *dotted line* indicates the 115-m zone used in the buffer analysis.
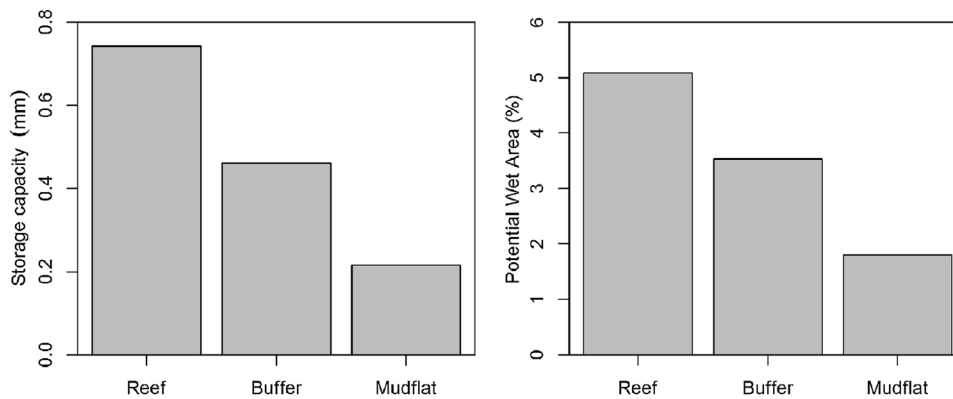

Figure 5. *Left* Differences in water storage capacity in mm between the Reef, Buffer (115-m zone) and Mudflat zone calculated from the LiDAR data. *Right* Differences in percentage of potential wet area between the Reef, Buffer and Mudflat zone.

The buffer zone that we have identified significantly extends the zone of influence of the shellfish reefs (see Figure 3). Within this buffer zone around the shellfish reefs, which is 495 ha large, 1472 tidal pools are located. Although the effects on water storage capacity in terms of total pool volume and surface area is strongest locally within the reefs, at extensive spatial scale up to 115-m storage capacity is still elevated compared to surrounding unaffected intertidal flats (Figure 5). Moreover, despite the fact that shellfish reefs only occupy a little less than 2% of the total area, up to 11% of the intertidal zone is influenced by shellfish by changing surface topography and influencing water retention by modifying the depression storage capacity (Figure 3). This implies that the footprint of the shellfish reefs is increased by more than 5 times, because of this long-range influence of the reefs on their surrounding habitat. In addition, while the highest storage capacity values are found within the reefs, the largest pools, both in terms of area and volume, are on average found in the buffer

zone, followed by the reef pools and the smallest on uninfluenced mudflat (see Figure 6).

Effect of Surface Topography on Water Storage Capacity from Simulated Landscapes

Water storage capacity was found to depend on landscape characteristics (vertical and horizontal complexity, and slope). Using a geostatistical analysis on the TLS data, the vertical surface complexity could be expressed by the *sill* and the horizontal surface complexity by the *range* of a semivariogram (S3). Indeed, the shellfish reefs scanned using the TLS have a high vertical complexity and short range, as compared to the surrounding mudflat (see Table S3).

The simulations reveal that the combined effect of vertical (as measured by the *sill*) and horizontal (*range*) complexity regulates the water storage capacity on simulated landscapes with different roughness characteristics (Figure 7). Storage
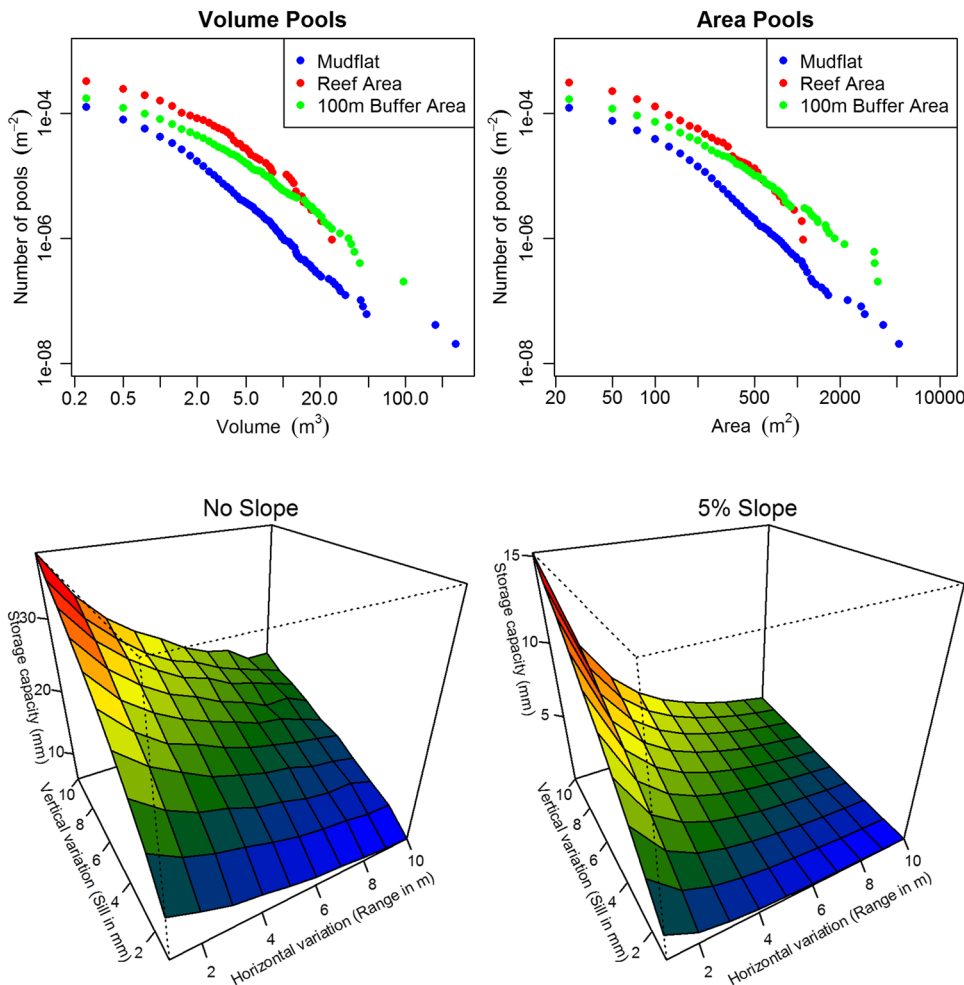
Figure 6. Water storage capacity in the three different classes (mudflat, reef area and 115 m Buffer Area) results in pools with different sizes in terms of volume and area. The log–log plot reveals that the buffer zone has the largest pools and the mudflat the smallest both in terms of area and volume.

Figure 7. Mean predicted water storage capacity based on landscapes without a slope effect and one with a 5% slope. Different *range* and *sill* parameters (each combination is replicated 50 times) indicate a positive effect of *sill* and a negative effect of *range* on water storage capacity.

capacity is positively influenced by the vertical component of the surface, whereas the horizontal component has a negative impact on the capacity to retain water. The 5% slope as opposed to a flat surface decreases water storage capacity overall and mainly affects landscapes with high *range* values (highly autocorrelated landscapes). This likely explains the apparent discrepancies between the empirically obtained storage capacity (with slope of intertidal flat) and those in the simulated landscape with similar landscape characteristics (without slopes). It also highlights that flat surfaces are influenced most by induced surface complexity with regard to capacity for water storage.

DISCUSSION

Ecosystem engineering has been recognized as an important structuring mechanism in ecological systems, affecting its functioning and stability both at local and extensive spatial scales (Jones and others 1994, 1997; Hastings and others 2007). The

driving mechanisms have been mostly attributed to resource mediation (Lawton 1994; Wright and Jones 2006) and stress amelioration (Stachowicz 2001; Bruno and others 2003). Here, we show for intertidal ecosystems how ecosystem engineering, that is, the addition of biogenic structure to the landscape, affects the capacity to retain water (and thereby possibly other vital resources) through the formation of tidal pools, thereby alleviating desiccation stress for many marine organisms. Within shellfish reefs, mussels and oyster reefs create vertical surface complexity through the formation of hummocks and hollows (Gutiérrez and others 2003; van de Koppel and others 2005; Liu and others 2012; Rodriguez and others 2014), which has been suggested to be the result of spatial self-organization processes (van de Koppel and others 2005, Liu and others 2012). Locally, these hollows form tidal pools retaining significant amounts of water. Most strikingly, the effects were found to extend well beyond the physical borders of the shellfish reefs with significantly higher storage

capacity values up to 115 m away from shellfish reefs. The size of these ponds close to the beds was found to be larger, as opposed to the ponds in and further away from the bed. This implies that, in the study area considered, the footprint of shellfish determined by increased storage capacity on the intertidal flats is more than 5 times their actual coverage, affecting up to about 11% of the intertidal area. Hence, ecosystem engineering shellfish can modify the functioning of the ecosystems to significant parts of the entire estuary due to local and spatially extended modifications of the surface structure.

Intertidal rock pools play a major role in determining ecosystem structure and functioning (Firth and others 2014 and references therein), but much less is known about the importance and dynamics of soft-bottom pools and their relation to ecosystem engineering bivalves. Intertidal pools provide an extension of the vertical distribution of many species into areas which normally would be unsuitable for them because of desiccation stress (Metaxas and Scheibling 1993; Firth and others 2013); they provide refuges from predators to a wide variety of intertidal organisms (White and others 2014); they form a temporary shelter for migratory fish during low water, thereby effectively linking marine systems to freshwater systems upstream (Davis and others 2014); they are used by many fish species as nurseries (Chargulaf and others 2011). Different pool characteristics suit different species (White and others 2014), for example, larger pools tend to be more stable in temperature, pH and nutrient levels and are thus more valuable to the widest range of species (White and others 2014). Furthermore, the mosaic of different substrate types created by shellfish at larger spatial scales promotes heterogeneity and provides a habitat for a wide range of species (Eklöf and others 2014). The associated higher biodiversity can be expected to increase ecosystem stability (Tilman and others 1996). Moreover, retention of resources in pools may contribute to increased system resilience through indirect mechanisms involving trophic interactions (Sanders and others 2014). Likewise, the presence of pools associated with shellfish reefs allows species more sensitive to emersion (for example, due to desiccation stress) to persist within intertidal communities, both locally within the reefs and at larger spatial scale beyond their physical borders (that is, buffer zone), resulting in more diverse intertidal flats. This implies that biodiversity may be boosted by increasing landscape heterogeneity. This might hold especially for the buffer zone, since the pool volumes are

larger, and thus probably more stable, beyond the borders of the reef.

The ability to create pools is not unique to shellfish reefs. In terrestrial systems, many mammals, such as elephants, rhinos, buffalos and warthogs, engage in wallowing, that is, they cover themselves in mud to protect themselves from the sun, parasites and it helps to disinfect wounds (Vanschoenwinkel and others 2011). The resulting wallows trap rain water, resulting in ephemeral ponds that sometimes retain water for weeks due to compaction of soil (Polley and Collins 1984). Buffalo wallows have an important role in the dynamics and functioning of grassland vegetation (Polley and Collins 1984). Likewise, wallows created by alligators provide environments beneficial to a wide range of organisms (Campbell and Mazzotti 2004). Ponds in elephant footsteps harbor many aquatic insects (Remmers and others 2016), and finally, peccary wallows have more value for anurans and biodiversity than naturally formed ponds (Beck and others 2010). These examples underline the generality and importance of pond formation by ecosystem engineering species.

The effect of physical structure on ponding is largely dependent on the large-scale landscape structure. The simulations in this paper provide support for the idea that the effectiveness of structures to retain water depends for an important part on the height of the hummocks (*sill*), the horizontal scaling parameter (*range*) and the slope of the surface. The relation between retention and hummock height is positive, while the relation between retention and the *range* parameter as well as the overall tidal flat slope is negative. Reef depth along with the tidal range are important in determining how much vertical variation can be added to the landscape locally because these factors together determine a growth ceiling for reefs (Rodriguez and others 2014; Walles and others 2015). It can be expected that ponding effects are larger in lower locations in the intertidal with large tidal amplitudes, because the potential for vertical accretion of shellfish reefs is largest in these locations. The tidal cycle is probably less important since the sediments remain saturated with moisture and infiltration is low ensuring the persistence of pools during low tide events. In general, the contribution of ecosystem engineering is likely more relevant on landscapes which naturally exhibit low surface complexity, whereas the contribution is less significant on rough surfaces (like for instance shellfish on rocky shores). Yet, a thorough exploration of the interaction between landscape topography and added surface complexity due to

ecosystem engineering is missing in the scientific literature.

Here we approximated the capacity for water retention of a landscape in a very generic way, that is, water is potentially trapped in depressions creating tidal pools during low water, which remains stagnant thereafter. Water flows are not measured or modeled in detail. To more fully comprehend water retention around biogenic structures, we should also distinguish increased residence time of water due to hydrodynamic obstruction, which results in decreased flow rates. The occurrence of engineered structure has important implications for regional hydrodynamics caused by tidal flow (van Leeuwen and others 2010). Biogenic material, such as shellfish reefs, may slow down flows due to friction, or reroute water entirely due to full obstruction which has consequences for residence time of water in the landscape (Lenihan 1999). The spatial arrangement of geomorphological features on a mudflat such as sandbars, gullies and mud deposits may very well depend on the spatial distribution of biogenic structures such as reefs created by shellfish (van Leeuwen and others 2010) and vice versa since they are coupled by the prevailing hydrodynamics. Yet, our simple approach is a good first approximation to get general insights into how ecosystem engineering can affect ecosystem functioning by modifying water retention.

In our study, we used near-infrared TLS and airborne LiDAR to assess depression storage capacity. Our assessments of the capacity for water storage were conservative, as these systems could not measure topography under water. LiDAR systems that use green light are better able to penetrate water and can be used to measure topography under water (for example, Hannam and Moskal 2015). Further research that assesses actual stagnant water ponding could incorporate LiDAR techniques combined with VNIR (visible and near-infrared) or TIR (thermal infrared) photography from unmanned aerial vehicles to delineate ponds over the tidal cycle.

Our findings highlight that modification of the physical landscape by ecosystem engineering, causing increased water storage capacity, can be significant and should be considered in future research to unravel the implications for ecosystem structure and functioning, as well as biogeomorphological processes. In intertidal systems, this extended engineering might be beneficial to adjacent ecosystem engineering species resulting in facilitating cascades (Gillis and others 2014). Such facilitation interactions are especially beneficial for improving the resilience of ecosystem-based coastal defense practices (Temmerman and others 2013). The importance of spatially extended water impoundment for biodiversity, as well as local and cross-system resilience, should be the focus of future research.

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