Ecosystem Services of constructed oyster reefs

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Introduction

Ecosystem engineers are organisms that directly (or indirectly) modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials (Jones et al., 1994). Oysters are considered ecosystem engineers which can be potentially used to provide a natural solutions for coastal defence (Borsje et al., 2011). Oysters create, modify or maintain habitats and ecosystem processes through their activities as well as with the structures they create. They are capable of forming conspicuous habitats that influence tidal flow, wave action and sediment dynamics in the coastal ecosystem and, in doing so, reduce hydrodynamic stress and modify the patterns of local sediment transport, deposition, consolidation, and stabilization processes (Walles et al., 2014).

Bivalve reefs also provide habitat for numerous species of fish, crustaceans and other invertebrates and can contribute to food security and livelihoods for coastal people. A 'living shoreline' with artificial oyster reefs could be a self-sustained element for coastal protection and provision of ecosystem goods and services (Hossain et al., 2013).

Oyster reefs are valued for the many ecosystem services they generate, such us a potential stabilization of the shoreline (Meyer et al., 1997), improvement of the water quality (Newell et al. 2005) and influences many ecological processes such as maintenance of biodiversity, population and food web dynamics, and nutrient cycling (Ruesink et al., 2005). Oyster reefs facilitate settlements and shelter for living species in and around the oyster reefs. The ecological result is a greatly increased biodiversity in and around them (Troost, 2010). The vertical relief characterized by an oyster reef has a sufficient effect on the water flow, creating turbulence. This change in water flow generates a different kind of habitat than at a soft substrate area and will increase the species richness (Coen et al., 2007).

Oyster reefs can function as natural, living breakwaters (as opposed to human-designed), bulkheads, or jetties because they are structures that interact with tidal and wave energy just like engineered shoreline stabilization devices by baffling waves and increasing sedimentation rates (Meyer et al., 1997). The rate of vertical oyster reef growth on detached reefs is far greater than any predicted sealevel rise rate and therefore reefs could serve as natural protection against shoreline erosion, intertidal habitat loss, and property damage and loss along many estuarine shorelines (Walles et al., 2016). The current standard practice for inshore erosion protection is the use of engineered shoreline stabilization devices (Titus, 1998). Table 2.3 is a summary of the ecosystem services and processes which could be applied.

Table 2.3 - Ecosystem services provided by oyster reef habitat (Grabowski et al., 2012)

Ecosystem service	Ecosystem process	References	Bioeconomic model valuation metho			
Water quality improvement	Chlorophyll a removal	Newell et al. 2002, Grizzle et al. 2006	Replacement cost of using sewage treatment plant to remove nitrogen, nitrogen credit market			
	Reduce turbidity	Newell and Koch 2004				
	Denitrification	Piehler and Smyth 2011				
	Increase benthic algal or pseudofecal production	Newell et al. 2002	Not applicable			
	Bacterial biomass removal	Cressman et al. 2003	Not applicable			
Seashore stabilization	Shoreline stabilization	Meyer et al. 1997	Cost of a sill to stabilize salt marsh and seagrass habitat, value of protected habitats			
Carbon burial	Bury carbon dioxide	Not applicable	Traded carbon pollution credits			
Habitat provisioning for mobile fish and invertebrates	Increased fish production	Peterson et al. 2003	Commercial dockside landings value, recreational fisher willingness to pay for improved fishing			
Habitat for epibenthic fauna	Increased epibenthic faunal production and biodiversity	Wells 1961, Bahr and Lanier 1981, Lenihan et al. 2001	Already captured in fish values			
Diversification of the landscape	Synergies among habitats	Micheli and Peterson 1999, Grabowski et al. 2005	Not applicable			
Oyster production	Increased oyster production	Heral et al. 1990, Rothschild et al. 1994, Lenihan and Peterson 1998, 2004, Grabowski and Peterson 2007	Commercial oyster dockside value, recreational value-license program			

In locations where property owners would otherwise use these engineered devices, their cost can be used as a reasonable proxy for the economic value of oyster reef restoration. This assumes that reefs are perfect substitutes for human-made devices. Because oyster reefs can grow vertically faster than sea levels are expected to rise, it could be argued that they are more resilient to sea-level rise than a fixed engineered device, thus, they would have a higher value as a shoreline stabilizer. However, the relative risk of storm damage to engineered and oyster reef structures needs to be considered. Given that oyster reefs and unnatural engineered devices constitute similar physical structures, their value can be considered equivalent (Grabowski et al., 2012).

Nowadays oysters are increasingly being investigated for their eco-engineering propertied for potential application, as coastal protection. For this reason different approaches are used. There are two main methods which can be adopted, depending on the location of the reef in the intertidal area. Examples of these applications of these approaches for the shoreline restoration are briefly explained below (Figure 2.32). In The Sister Lake, Louisiana, USA, reefs of *Crassostrea virginica* were built as close as possible to the shoreline, demonstrating that, in low energy environments, this system provide a useful shoreline stabilization (Piazza et al., 2005). A similar example comes from the North Carolina (Harjer's Island, Swansboro and Snead's Ferry) where stabilization of sediments was achieved resulting from oyster cultch which are not located adjacent the marshes (Meyer et al., 1997). In Bangladesh, a research study was designed to explore the use of reef structure with oysters and other shellfish for enhancing coastal habitats in the near shore. In Viane and de Val in the Eastern Sheldt, the Netherlands, three artificial oyster reefs were constructed, and resulted in local protection of the tidal flat and shoreline against erosion (Walles, 2015).

The difference between the two approaches is determined by the proximity of the oyster reef to the shoreline (Figure 2.32). The image on the left shows an eco-engineering structure placed at a certain distance from the shoreline, instead, the one on the right is located at the edge of marsh vegetation. Both of them perform as breakwaters to prevent shoreline erosion, but the first one also promotes the shoreline growth (Walles, 2015). In the first case, mangrove and vegetation can grow behind the reef. This vegetation can break the waves before they reach the land. At the same time, it forms a natural habitat for fish, crabs and recreates a new ecosystem. The second one is a more natural

protection instead that artificial, and protects the land from the waves recreating the habitat around it.

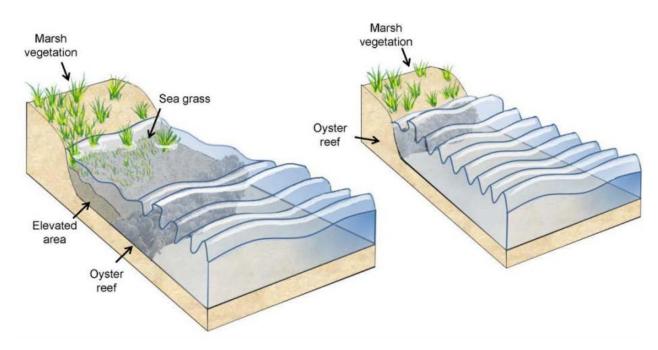


Figure 2.32 - Different approach of placing oyster reefs (Walles, 2015)

As part of the CoE Oesterdam sand nourishment project, four artificial oyster reefs were placed in strategic locations around the sand nourishment. These oyster reefs were intended to reduce the hydraulic energy of the water and reduce the erosion of the sand nourishment as well as provide habitat for various other species (Borsje et al., 2011). In this way the oyster reefs would potentially prolong the existence of the sand nourishment and thereby delay the necessary maintenance of the dyke while increasing biodiversity. Furthermore, if the artificial oyster reefs were to develop into living oyster reefs through larval oyster settlement and growth, these reefs would be adaptable to changing environmental situations.

This study investigated the conditions that influence the effectivity of the constructed oyster reefs at the Oesterdam. Several aspects were considered as a measure of effectivity; the ability to stabilise the surrounding sediment and therefore protect the sand nourishment; the biodiversity that developed on the reef and the type of species that occupied this newly added habitat; and the likelihood of enough oyster larvae settling and developing on the reefs as a measure of reef longevity and adaptability.

Methods

The Eastern Scheldt

The research was conducted near the Oesterdam at the Eastern-most part of the Eastern Scheldt, one of the delta waters in the South-East of the Netherlands (Figure 1). The Eastern Scheldt was originally an estuary, but since the mouth of the estuary was partially closed off from the North Sea by a storm

surge barrier (completed in 1986), which can be closed in times of dangerously high water levels and surges, it is now considered a tidal bay (Troost, 2009). The storm surge barrier has resulted in reduced tidal amplitude and current velocities by 30 % in the system and consequently a sand deficit in the Eastern Scheldt. This sand deficit leads to the erosion of 11 000 ha of intertidal sand flats by 2 cm per year, gradually reducing the intertidal area of the Eastern Scheldt (de Winder et al., 2014). This erosion has threatened the dyke reinforcements at the Oesterdam, with the impact of wave action and tidal currents, enough to necessitate preventative measures to delay the inevitable and expensive dyke reconstruction. A sand nourishment was therefore constructed at the Oesterdam to reduce the erosion around the dyke and restore the soft bottom intertidal area which provides a habitat for various benthic invertebrate species and is therefore used as a feeding ground for migrating birds (de Winder et al., 2014).



Figure 1. Location of the Oesterdam (indicated by the yellow ring) in the Eastern Scheldt of the Dutch delta in the SW Netherlands.

Ovster reefs

Four oyster reefs were constructed on the sand nourishment to stabilise the sediment and prevent erosion of the sediment, thereby extending its durability. Four of these oyster reefs were built on the sand nourishment, two (Reefs A and B) on the north facing side and two (Reefs C and D) on the east facing side of the sand nourishment (Figure 2). The oyster reefs were constructed from loose oyster (*Crassostrea gigas*) shells caged by wire mesh and measured between 90-250 m in length and 7,5-8 m wide. The reefs were designed with the intention of sufficient oyster spat settling on the loose shells so that the reef would develop into a living oyster reef able to adapt to changing environmental conditions. Since construction, each reef has provided slightly different relative conditions for the resident organisms. The main physical differences between the reefs was the relative level of sedimentation (high or low) and the quality of the construction (intact or damaged) (see Table 1).



Figure 2. The sand nourishment at the Oesterdam and placement of the constructed oyster reefs (Photo by Edwin Paree, Rijkswaterstaat).

Table 1. Relative conditions on each of the constructed reefs.

Reef	Size	Relative Condition			
		Construction quality	Sedimentation		
Α	250x7,5x0.25	Intact	Low		
В	90x8x0.25	Intact	High		
С	100x7,5x0.25	Damaged	Low		
D	94x8x0.25	Intact	Low		

Monthly Monitoring

From July 2015 to June 2016 (but excluding August 2015) the type and abundance of organisms present on all four reefs were monitored. Because the wire mesh with which the oyster reef was constructed restricted access to the interior of the reefs, it was not possible to count and identify all organisms within the quadrats. Therefore abundances were estimated using an abundance code (Table 2).

For each reef three cross sections were marked; one at each end and one in the middle of the reef, spanning the width of the reef. Each cross section was further divided down the centre line of the reef so that there was a 'seaward' and 'landward' side. Six quadrats were then haphazardly placed within each cross section, three in the seaward, and three in the landward side to maintain a representative cover of the reef. In total 18 quadrats were placed on each reef during each monitoring period (Figure 3).

Within each quadrat the species of organisms and whether each was native or exotic was recorded. A visual estimate of the number of organisms was also recorded using an abundance code of a, b, c, d, or e (Table 2) for fauna and % coverage for algae (attached to the shells and not the wire mesh). As a representative species within each quadrat, the actual abundance of observed periwinkles (Littorinidae) was recorded instead of being estimated. While adult oysters were not counted (they were considered part of the substrate rather than the epifauna), oyster spat was recorded during the monitoring. The average density or % coverage per m² between all quadrats was calculated and compared over time. Furthermore,

Table 2. Abundance codes used for the visual estimate of species abundances on the reefs

Abundance code	Estimated abundance (individuals)	
Α	1-10	
В	10-20	
С	20-30	
D	30-40	
E	40+	

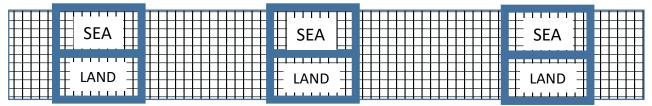


Figure 3. Schematic diagram of the sampling locations on each reef. Three 3 m cross sections of the reef were divided into the land- and seaward side of the reef. Organisms were recorded from within three quadrats in each section outlined in blue.

Reef Core samples

Between September 2016 and October 2016 reef core samples were taken in the four reefs. In each reef 15 samples, 5 in front, 5 in the middle and 5 in the back were taken as it is presented on figure 4. To collect the reef cores PVC pipes with 12.5 cm of diameter and 15 cm in length were pressed thru the reef matrix and its interior was collected after. The sample was separated in shells and sand and after drying its composition was determined. The organic content and the amount of sediment with a diameter lower than 0,062 mm were also determined.

Front (sea Side)

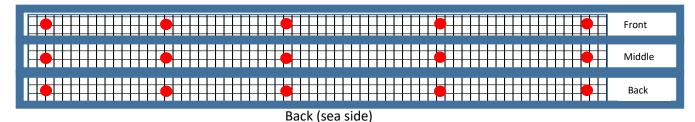


Figure 4 . Schematic diagram of the Reef core sampling locations on each reef. The reef was divided in 3 zones(outlined in blue) front middle and back. In each zone 5 reef core samples were taken(red dots).

Oyster recruitment

Along with the monthly monitoring where the presence of oyster spat was also recorded, settlement plates were used to evaluate the recruitment of new oysters on the artificial oyster reefs. For each area considered on figure 4 ate least fifteen settlement plates were installed. The settlement plates consist of sanded pvc plates of 14 cm by 14 cm which were analysed two time per year. One time after the settlement period and another just after winter. In this way besides settlement winter mortality was also determined. The measurements were performed between 2013 and 2016.

Results

There was no significant difference in species richness between the reefs. On all reefs the species richness and abundance also showed similar seasonal changes throughout the monitoring period (Figure 5).

Relative abundance (Evenness) was significantly lower on Reef B compared with the other reefs

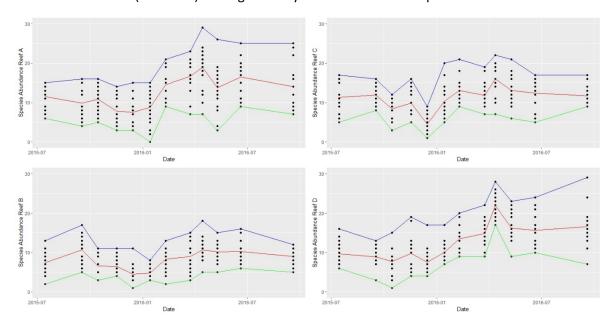


Figure 5. Species abundance (fauna and algae combined) over time with maximum (blue), average (red) and minimum (green) values.

There was a statistically significant difference in evenness of fauna between Reefs as determined by one-way ANOVA ($F_{3,68}$ = 231.7 p < 0.01). A Tukey's HSD post hoc test revealed that evenness on Reef C (0.34 ± 0.05) was significantly lower than Reef A (0.63 ± -0.29, p = 0.02), Reef B (0.67 ± 0.33, p < 0.01) and Reef D (0.6 ± 0.26, p < 0.01). Evenness on Reef B was also significantly higher than Reef A (0.63 ± 0.04, p = 0.019) and Reef D (0.60 ± 0.07, p < 0.01). Evenness on Reef A was, however, not significantly different to Reef D (0.60 ± 0.03, p = 0.19) (Figure 6).

The differences in evenness can be explained when considering the ten most common fauna species found. Excluding *C. gigas* the most common species on all reefs were Littorinidae and *Mytilus edulis* (Figure 7). On Reef C Littorinidae was particularly dominant (comprising 77%) compared with the other reefs (Reef A: 25%, Reef B: 36%, Reef D: 24%), and was therefore responsible for the low evenness score and the lower proportion of other species.

Mytilus edulis was also particularly common on all reefs (Reef A: 46%, Reef B: 35%, Reef C: 15%, Reef D: 50%). The anemone *Actinia equina* was observed in noticeably higher proportions on Reef B (5.2%) compared with the other reefs (Reef A: 13%, Reef C: 0.8%, Reef D: 4%). *Hemigrapsus takanoi* was found in similar proportions on Reef A (7%), Reef B (5%) and Reef D (8%), but on Reef C the dominance of Littorinidae resulted in the proportion of *H. takanoi* being somewhat lower (2%).

The exotic oyster drill, *Ocinibrellus inornatus* was only present in the top ten most common species on Reef A (4%) and Reef B (0.3%). The cockle *Cerastoma edule* was only present in the top ten most common species on Reef B (1%).

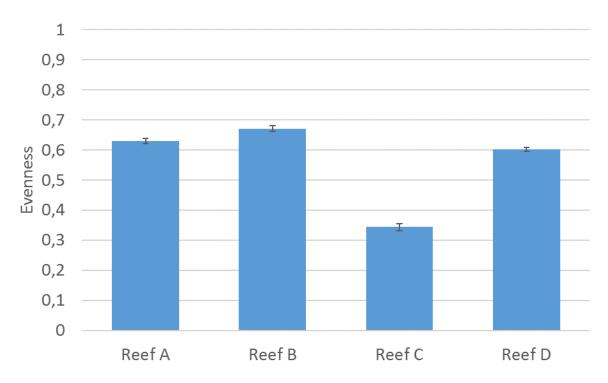


Figure 6. Evenness (fauna) combined over time on each reef

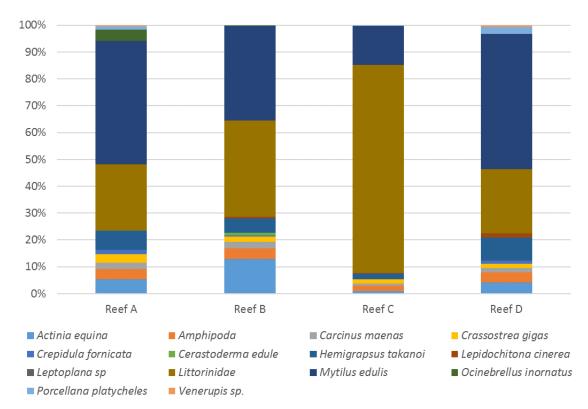


Figure 7. Composition and relative abundance of the ten most common fauna species on each reef combined over time.

There was a statistically significant difference in evenness between Reefs as determined by one-way ANOVA ($F_{3,68} = 3,26 p = 0.03$). However a Tukey's HSD post hoc test revealed no significant differences in evenness in pairwise comparisons (p > 0.05 in all cases) (Figure 8).

This lack of difference in evenness between the reefs was apparent when considering the ten most common algae species (Figure 9). All reefs comprised predominantly of *Ulva lactuca*, *U. intestinalis*, *Fucus vesiculosus* and *Callithamnion roseum*. *Polysiphonia lanosa* found in larger proportions on Reef A (25%) and Reef B (17%) compared with Reefs C and D (both 2%). *Blidingia minima* was found in much higher proportions on Reef B (30%) compared with the other Reefs (Reef A: 2%, Reefs C and D: 2%).

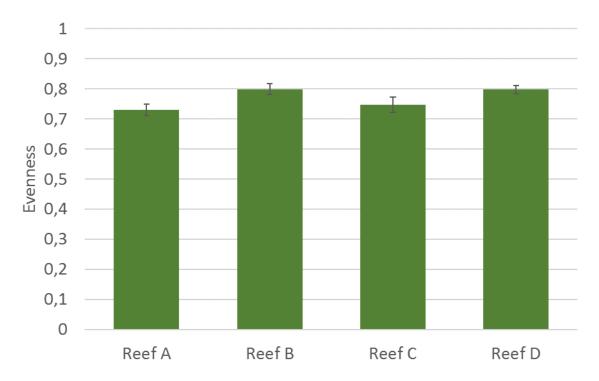


Figure 8. Evenness (Algae, Didemnum sp. and colonial bryozoans) combined over time on each reef

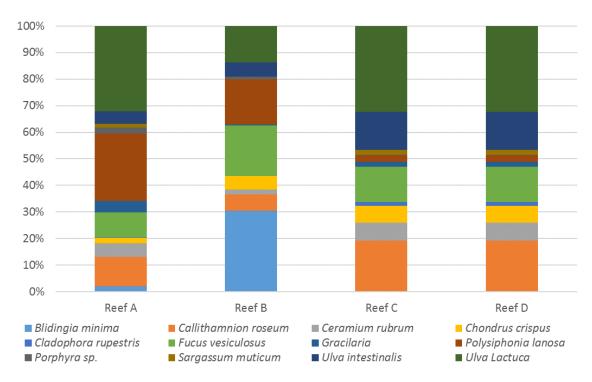


Figure 9. Composition and relative abundance of the ten most common algae species on each reef combined over time.

Estimated abundance of fauna on the reefs generally increased over the two or three years of monitoring on Reefs A, C and D, but showed little change on Reef B. In all three years, and on all four reefs Littorinidae and *M. edulis* were the dominant species, but on Reef A Littorinidae was by far the most abundant.

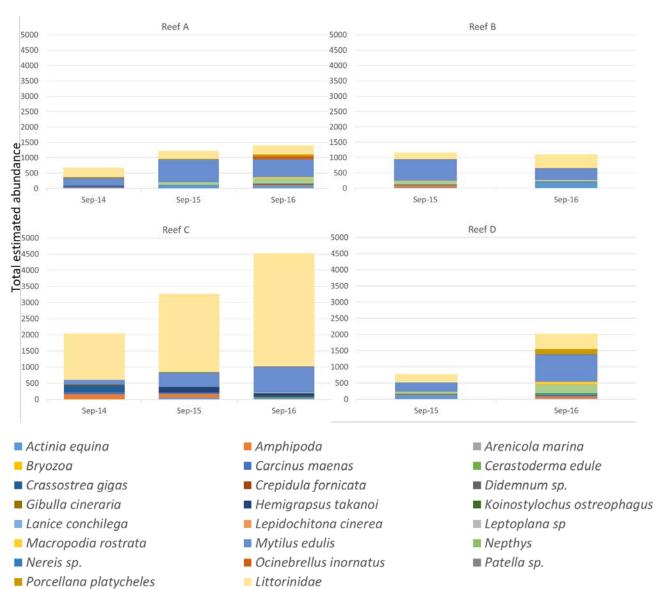


Figure 10. Composition and relative estimated abundance of fauna species on each reef in September of 2014, 2015 and 2016.

Estimated coverage of algae varied between reefs. Reef C show considerably lower algae coverage compared with the other reefs. *Ulva lactuca* dominated Reefs A and C in September 2014, while there were no obvious dominant species in September 2015. In September 2016 *Polysiphonia lanosa* dominant on Reefs A, B and D, while *Fucus vesiculosus* was dominant on Reef C (Figure 11).

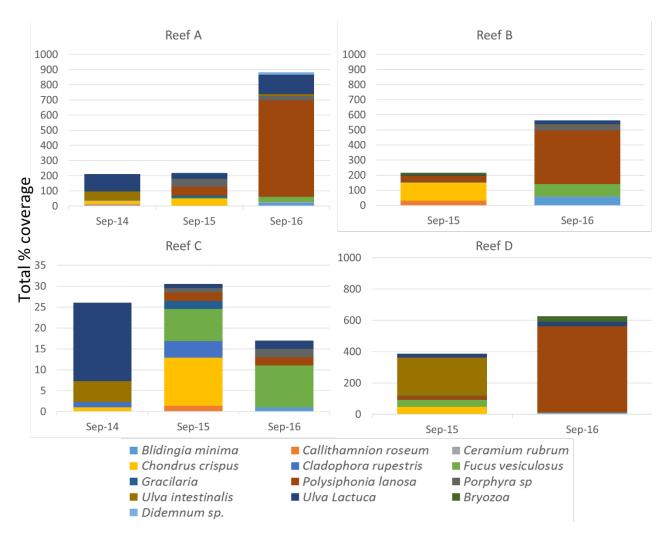


Figure 11. Composition and relative estimated percent coverage of algae species on each reef in September of 2014, 2015 and 2016. Note the different scale in the y-axis for Reef C.

The species richness was comprised of between 20 and 30% exotic species on all four reefs. Eleven of the 44 species on Reef A, eight of the 37 species on Reef and 10 of the 29 species on both Reefs C and D were exotic (Figure 12).

The composition of exotic species was also comparable between all four reefs. Excluding *C. gigas*, two exotic mollusc species (*Crepidula fornicata* and *Ocinibrellus inornatus*), one crab (*Hemigrapsus takanoi*) two algae species (*Gracilaria* sp. and Sargassum muticum), and two tunicates (*Ciona intestinalis* and *Didemnum* sp.) were found on all four reefs. The tunicates, *Botrylloides violaceus* and *Styela clava*, were found on all reefs except reef B. The flatworm, *Koinostylochus ostreophagusm*, was found on only one occasion and only on reef A (Figure 13).

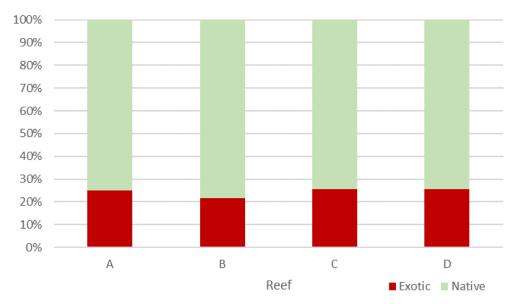


Figure 12. Percentage of native and exotic species found on each reef.

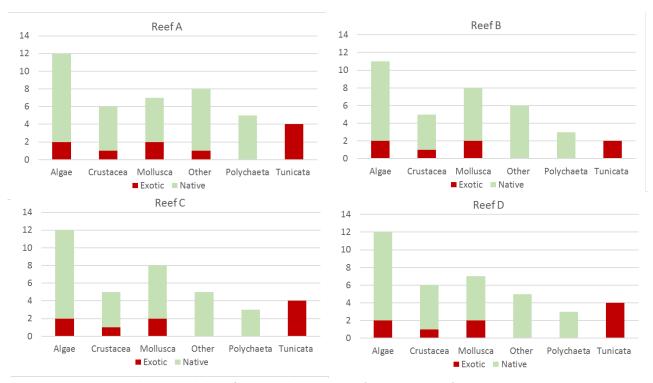


Figure 13. Species richness per phylum of native and exotic species found on each reef.

Oyster spat was found on all four reefs during the warmer months, with the majority being recorded in Spring (March – May). While variation was high, it appears that Reef B showed the lowest, while Reef C showed the highest number of oyster spat per m².

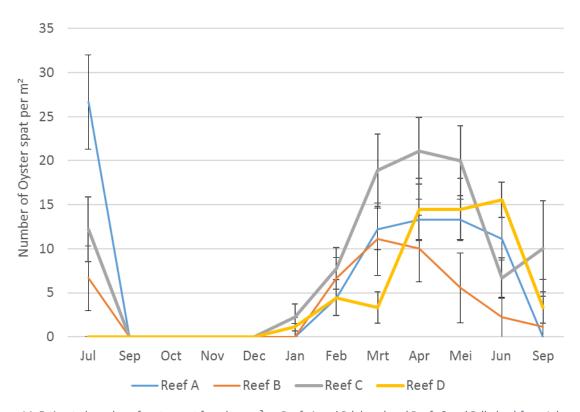


Figure 14. Estimated number of oyster spat found per m^2 on Reefs A and B (above) and Reefs C and D (below) from July 2015 – September 2016.

The organic content in all reefs is similar with the average varying between 2.2 and 2.9% and there is no statistical difference between the results of each reef. within each reef the variability between samples is very high which explains the high values for the standard deviation.

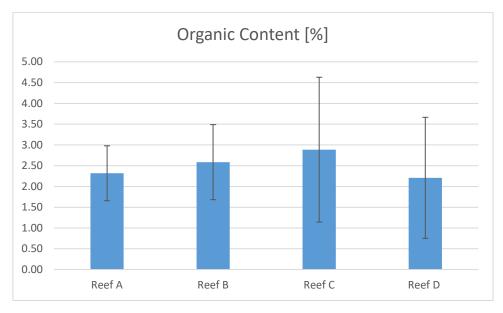


Figure 15 organic content(%) and standard deviation values for each reef

The agregate content (sand) within the reef is higher on reef A and B wich are located on the nothern part of the nourishment but not statistical difference is observed between reefs or between reef A and B and C and D.

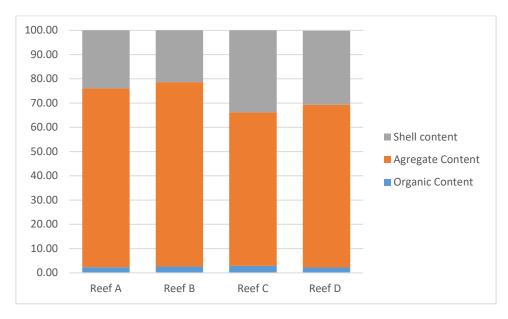


Figure 16 Percentage of shells, agregate and organic content per reef

The settlement observed on the settlement disks shows that reef A and D had a higher average settlement values on the first years but in 2016 reef B and C had registered the highest values. In all reefs some settlement disks didn't register any settlement and the highest settlement was higher than 1200 new oyster per m² observed on reef C in 2016.

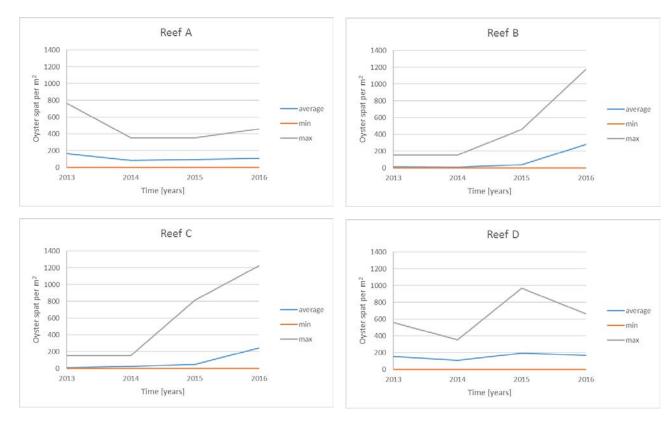


Figure 17 Settlement of new oysters per year, including maximum numbers, average and minimum number of new oysters settled per m^2

Discussion

The number and type of epifaunal species varied little between the four oyster reefs. Typical hard substrate species, common in the Eastern Scheldt such as the periwinkle (*Littorinidae*), mussels (*Mytilus edulis*), and various crabs (*Carcinus maenas, Hemigrapsus takanoi* and *Porcellana platychelles*) were found on all reefs throughout the year. Similarly, the number and type of algal species were also similar between reefs. The proportion of exotic species was also comparable between reefs. The local environments on each reef differ so negligibly that they all fall within the range of suitable habitat for the species present.

Furthermore, the relative abundance of each faunal species was also comparable between reefs. In general the majority of the fauna observed on the reefs were mussels and periwinkles. However it is notable that while on Reefs A, B and D both species showed similar relative abundance, Reef C was dominated by periwinkles. Whether this dominance of periwinkles on Reef C can be attributed to any of the specific properties of the reef is unclear, but this dominance of periwinkles was consistent throughout the sampling period, which suggests there was an environmental influence. As Reef D shared more or less the same orientation and inundation time as Reef C, but did not show such an obvious periwinkle dominance, these factors are unlikely to result in the observed differences. The most obvious difference between Reefs C and all other reefs was the intactness of the reef itself. It is possible that the loose packing of the oyster shells within Reef C was more favorable to periwinkles due to a lack of competitors who were less tolerant of the scouring experienced on the reef when the

shells moved with the wave action. Alternatively, the difference in dominance of periwinkles on Reef C may be due to the lower success of mussels on the Reef. Mussels require a stable substrate on which to attach. As Reef C did not provide as stable a substrate compared with the other reefs, it may have resulted in lower success of mussels and therefore proportionally more periwinkles.

No obvious dominance was observed in the algae species in general, but there was some differences between years in both coverage and species present. Reef C had considerably total lower algae coverage compared with the other reefs. On Reefs A, B and D the total amount of algae coverage had also increased in September 2016 compared with previous year(s), while on Reef C the coverage had decreased. Furthermore on Reefs A, B and C, *Polysiphonia lanosa* made up the majority of the algae coverage in 2016, while *Fucus vesiculosus* made up the majority of the algae coverage. Again the likely explanation of these results is the lower intactness of Reef C compared with the other, more intact reefs. The movement and scouring effect of the shells in the loosely packed reef is likely detrimental to the establishment and survival of algae species.

The number of settled oyster spat was also comparable between reefs during the monthly monitoring. On all four reefs there was a peak in observed oyster spat in the Spring. When analysing the settlement disks some differences can be observed. Reef A and D registered much higher settlement than reef B and C in 2013, 2014 and 2015. The average values for these two reefs remained more or less constant during the whole monitoring period. On the contrary reef B and C registered a very high oyster settlement in 2016. Therefore settlement is confirmed in all reefs which suggest that eventually these constructed structures will have a more natural appearance and that the new settlement will eventually substitute the role of the wire mesh.

From the reef core samples it is possible to observe that all the reefs have a similar composition. The two reefs located on the North (reef A and B) have slightly lower organic content and shell content meaning that the reef structure is more saturated with sand than the two reefs on the east side(reef C and D). This fact can be probably linked to the function of the structures as they are located on the northern part of the nourishment and their function is to block the sediment movement, from south to north, keeping the sand in the tidal flat area.

Conclusion

The differences between reefs in terms of species composition appears to be negligible as the reefs all provide comparable habitats for the same type of species. Regarding the oyster settlement similar conclusion was observed as even though there are some differences all reefs are suitable habitats for oyster settlement and therefore they will likely turn into a more natural appearance structure in the future.

Despite some differences in organic content and sand content all the reefs have a similar structure with no significant differences in organic content, sand content and shell content. The fact that Reef C was more loosely packed compared with the other reefs may have resulted in the considerable dominance of periwinkles, the noticeably lower algae coverage, and dominance of the algae cover being *F. vesiculosus* rather than *P. lanosa*.

Bibliography

- Borsje, B.W., van Wesenbeeck, B.K., Dekker, F., Paalvast, P., Bouma, T.J., van Katwijk, M.M., de Vries, M.B., 2011. How ecological engineering can serve in coastal protection. Ecol. Eng. 37, 113–122. doi:10.1016/j.ecoleng.2010.11.027
- Coen, L.D., Brumbaugh, R.D., Bushek, D., Grizzle, R., Luckenbach, M.W., Posey, M.H., Powers, S.P., Tolley, S.G., 2007. Ecosystem services related to oyster restoration. Mar. Ecol. Prog. Ser. 341, 303–307.
- de Winder, B., van Zanten, E., van den Boom, B., van Herk, J., van der Linden, G., 2014. Zandhonger Oosterschelde aangepakt met "Building with Nature" [WWW Document]. URL https://www.h2owaternetwerk.nl/vakartikelen/353-zandhonger-oosterschelde-aangepaktmet-building-with-nature (accessed 8.29.17).
- Grabowski, J.H., Brumbaugh, R.D., Conrad, R.F., Keeler, A.G., Opaluch, J.J., Peterson, C.H., Piehler, M.F., Powers, S.P., Smyth, A.R., 2012. Economic Valuation of Ecosystem Services Provided by Oyster Reefs. BioScience 62, 900–909. doi:10.1525/bio.2012.62.10.10
- Hossain, M.S., Rothuis, A., Chowdhury, S.R., Smaal, A., Ysebaert, T., Sharifuzzaman, S.M., van Sluis, C., Hellegers, P., van Duijn, A., Dankers, P., others, 2013. Oyster aquaculture for coastal defense with food production in Bangladesh. Aquac. Asia 18, 15–24.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as Ecosystem Engineers. Oikos 69, 373. doi:10.2307/3545850
- Meyer, D.L., Townsend, E.C., Thayer, G.W., 1997. Stabilization and erosion control value of oyster cultch for intertidal marsh. Restor. Ecol. 5, 93–99.
- Piazza, B.P., Banks, P.D., La Peyre, M.K., 2005. The potential for created oyster shell reefs as a sustainable shoreline protection strategy in Louisiana. Restor. Ecol. 13, 499–506.
- Ruesink, J.L., Lenihan, H.S., Trimble, A.C., Heiman, K.W., Micheli, F., Byers, J.E., Kay, M.C., 2005. Introduction of Non-Native Oysters: Ecosystem Effects and Restoration Implications. Annu. Rev. Ecol. Evol. Syst. 36, 643–689. doi:10.1146/annurev.ecolsys.36.102003.152638
- Titus, J.G., 1998. Rising seas, coastal erosion, and the takings clause: how to save wetlands and beaches without hurting property owners. Md Rev 57, 1279.
- Troost, K., 2010. Causes and effects of a highly successful marine invasion: Case-study of the introduced Pacific oyster Crassostrea gigas in continental NW European estuaries. J. Sea Res. 64, 145–165. doi:10.1016/j.seares.2010.02.004
- Troost, K., 2009. Pacific oysters in Dutch estuaries: causes of success and consequences for native bivalves. s.n.]; University Library Groningen] [Host, S.I.; Groningen.
- Walles, B., 2015. The role of ecosystem engineers in the ecomorphological development of intertidal habitats. Wageningen University, Wageningen.
- Walles, B., Salvador de Paiva, J., van Prooijen, B.C., Ysebaert, T., Smaal, A.C., 2014. The Ecosystem Engineer Crassostrea gigas Affects Tidal Flat Morphology Beyond the Boundary of Their Reef Structures. Estuaries Coasts 38, 941–950. doi:10.1007/s12237-014-9860-z
- Walles, B., Troost, K., van den Ende, D., Nieuwhof, S., Smaal, A.C., Ysebaert, T., 2016. From artificial structures to self-sustaining oyster reefs. J. Sea Res. 108, 1–9. doi:10.1016/j.seares.2015.11.007

Appendix 1. Characteristics of species observed on the reefs

Phylum	Species	Habitat requirment	Feeding type	Motility	Status	Reef A	Reef B	Reef C	Reef D
Crustacea	Amphipoda	generalist	scavenger	motile	Native	х	х	х	х
	Carcinus maenas	generalist	scavenger/predator	motile	Native	х	х	х	х
	Hemigrapsus takanoi	generalist	scavenger/predator	motile	Exotic	х	х	х	х
	Isopoda	generalist	scavenger	motile	Native	х	х		х
	Macropodia rostrata	generalist	scavenger/predator	motile	Native	х		х	х
	Porcellana platycheles	hard	filter	motile	Native	х	х	х	х
Mollusca	Cerastoderma edule	soft	filter	somewhat motile	Native	х	х	х	х
	Crassostrea gigas	hard	filter	not motile	Exotic	х	х	х	х
	Crepidula fornicata	hard	predator	somewhat motile	Exotic	х	х	х	х
	Gibulla cineraria	generalist	grazer/detritovore	somewhat motile	Native			х	
	Lepidochitona cinerea	hard	grazer	somewhat motile	Native	х	х	х	х
	Littorinidae	hard	grazer	somewhat motile	Native	х	х	х	х
	Mya arenaria	soft	filter	somewhat motile	Native		х		
	Mytilus edulis	generalist	filter	somewhat motile	Native	х	х	х	х
	Ocinibrelus inornatus	hard	predator	motile	Exotic	х	х	х	х
	Patella sp.	hard	grazer	barely motile	Native	х	х	х	х
	Venerupi s sp.	soft	filter	somewhat motile	Native	х	х	х	х
Other	Actinia equina	hard	sessile predator	somewhat motile	Native	х	х	х	х
	Bryozoa	hard	filter	not motile	Native	х	х	х	х
	Ctenophora	water	predator	motile	Native	х			
	Koinostylochus ostreophagus	hard	grazer	somewhat motile	Exotic	х			
	Leptoplana sp	hard	grazer	somewhat motile	Native	х	x	х	х
	Lipura maritima	hard	scavenger	motile	Native	х	х		
	Nudibranchia	hard	grazer/detritovore	motile	Native				х
	Phyllodoce maculata	soft	detritvore	motile	Native	х	х	х	х
	Pleurobrachia pileus	water	predator	motile	Native	х			
	Red mite	hard	scavenger	motile	Native		х	х	
Polychaeta	Arenicola marina	soft	detritvore	motile	Native	х	х	х	х
rolycliaeta	Glycera sp.	soft	detritvore		Native	х			
	Lanice conchilega	soft	detritvore	somewhat motile	Native	х			
	Nepthys sp.	soft	detritvore	somewhat motile	Native	х	х	х	х
	Nereis sp.	soft	detritvore	somewhat motile	Native	х	х	х	х
Tunicata	Botrylloides violaceus	hard	filter	not motile	Exotic	х		х	х
	Ciona intestinalis	hard	filter	not motile	Exotic	х	х	х	х
	Didemnum sp.	hard	filter	not motile	Exotic	х	х	х	х
	Styela clava	hard	filter	not motile	Exotic	х		х	х
Algae	Blidingia minima	Green algae			Native	х	х	х	х
	Callithamnion roseum	Red algae			Native	х	х	х	х
	Ceramium rubrum	Red algae				х	х	х	х
	Chondrus crispus	Red algae				х	х	х	х
	Cladophora rupestris	Green algae				x		x	X
	Fucus vesiculosus	Brown algae			Native Native	X	Х	Х	X
	Gracilaria sp.	Red algae			Exotic	x	Х	Х	X
	Polysiphonia lanosa	Red algae			Native	x	х	Х	X
	Porphyra sp.	Red algae			Native	x	х	Х	X
	Sargassum muticum	Brown algae			Exotic	x	х	Х	Х
	Ulva intestinalis	Green algae			Native	X	X	X	X
	Ulva Lactuca	Green algae			Native	X	X	X	X