

Bioengineering promotes habitat heterogeneity and biodiversity on mussel reefs

Isabelle B.C. van der Ouderaa^{a,c,*}, Jorn R. Claassen^a, Johan van de Koppel^b, Melanie J. Bishop^c, Britas Klemens Eriksson^a

^a Groningen Institute for Evolutionary Life-Sciences, GELIFES, University of Groningen, Nijenborgh 7, 9747, AG, Groningen, the Netherlands

^b Spatial Ecology department, Royal Netherlands Institute for Sea Research (NIOZ), P.O. box 140, 4400, AC, Yerseke, the Netherlands

^c Department of Biological Sciences, Macquarie University, North Ryde, 2109, NSW, Australia

ARTICLE INFO

Keywords:

Biodiversity
Niche
Habitat heterogeneity
Tidal pools
Shellfish reef
Self-organization

ABSTRACT

Loss of biodiversity is among the most pressing global problems. Yet, despite its pertinent nature, the biological processes involved in the maintenance of biodiversity are poorly understood. Habitat heterogeneity is widely regarded as a key factor underpinning the biodiversity of land- and sea-scapes. However, it remains unclear how species coexist in many of those ecosystems that lack conspicuous heterogeneity. We demonstrate how spatially self-organized mussel reefs create microhabitats/heterogeneity that facilitate diverse invertebrate communities. By comparing seawater filled pools with open inlets in a mussel reef, we found that natural reef pools, emerging due to the habitat engineering of the mussels, strongly increased variation in organic enrichment and promoted beta-diversity compared to the surrounding tidal flat. These findings significantly extend the scale of influence typically described for self-organized habitats and highlight the importance of bioengineering and its positive effects on habitat heterogeneity and community diversity.

1. Introduction

The decline in biodiversity is one of the most pressing global problems of current times, resulting in impoverished ecosystems and loss of ecosystem functioning (Oliver et al., 2015). Dramatic declines in for example coral species and associated coral reef fish (Bellwood et al., 2004; Pratchett et al., 2014) lead to declines in services that ecosystems can provide. Yet, despite the urgency of the problem, there is only a limited understanding of the processes and mechanisms that maintain the valuable biodiversity in many natural ecosystems.

Environmental and habitat heterogeneity are broadly regarded as key determinants of biodiversity (MacArthur and Wilson, 1967; Tewes et al., 2004). For example, in seaweed beds, introduced seaweed species add to the morphological complexity and increase habitat heterogeneity that positively affect biodiversity (Dijkstra et al., 2017). On rocky shores, topographic features such as rockpools that retain water at low tide, crevices that provide shaded and moist microhabitats increase niche space, and hence biodiversity, by creating habitat heterogeneity (Firth et al., 2013). However, many landscapes such as wetlands, tidal

flats and rocky shores support high biodiversity despite their lack of conspicuous habitat or environmental heterogeneity. Local disturbances in an otherwise homogeneous landscape can shape open patches of opportunity for other species (Levin and Paine, 1974) and can increase habitat heterogeneity by creating a mosaic of physically different microhabitats (Connell, 1978; Levin, 1976; Munguia et al., 2011).

Besides local disturbances, biological processes such as ecosystem engineering, facilitation and self-organization can also create environmental and habitat heterogeneity in coastal ecosystems, even in seemingly homogeneous environments (Jones et al., 1997, 1994; Van de Koppel et al., 2015; Wright et al., 2006). Ecosystem engineers can modify or create habitats through the indirect or direct control of (a) biotic materials, thereby controlling resource availability for other species (Jones et al., 1997). The importance of these processes on habitat heterogeneity is well established: shellfish reefs alter sediment deposition and hydrodynamic forces (Donadi et al., 2013), intertidal algae affect mud accumulation and alleviate temperature (Albrecht and Reise, 1994; Pocklington et al., 2019), kelp forests and seagrass patches alter light penetration and water flow (Gerard, 1984; Heiss et al., 2000).

* Corresponding author at: Groningen Institute for Evolutionary Life-Sciences, GELIFES, University of Groningen, Nijenborgh 7, 9747, AG, Groningen, the Netherlands.

E-mail address: i.b.c.van.der.ouderaa@rug.nl (I.B.C. van der Ouderaa).

<https://doi.org/10.1016/j.jembe.2021.151561>

Received 22 March 2020; Received in revised form 6 January 2021; Accepted 23 March 2021

Available online 31 March 2021

0022-0981/© 2021 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Through the alteration of environmental conditions, habitats provisioning multiple niches and resources are created in a system, and biodiversity can be enhanced via the partitioning of habitats among different species (e.g. [Gingold et al., 2010](#)).

On tidal flats of the Wadden Sea, blue mussel reefs (*Mytilus edulis* L.) form biogenic structures that are considered hotspots of biodiversity (e.g. [Christianen et al., 2017](#); [Engel et al., 2017](#); [Van der Zee et al., 2012](#)). Many species are facilitated by these mussel reefs, including the fucoid alga *Fucus vesiculosus* forma *mytili* (Nienburg), amphipods, periwinkles and crabs that find substrate to attach to and shelter from predators on the reefs ([Albrecht and Reise, 1994](#); [Andriana et al., 2020](#); [Saier, 2002](#)). These reefs are not homogeneously structured, but rather are strongly patterned by patches resulting from wave action and self-organization of the mussels ([Paine and Levin, 1981](#); [Van de Koppel et al., 2008](#)), resulting from short-range positive interactions between the mussels (e.g. byssal attachment of neighbouring mussels to one another to avoid dislodgement) and negative interactions (e.g. competition for food), thereby producing banded formations in which areas of high or low densities of mussels are interspersed with bare patches ([Van de Koppel et al., 2008](#)). Studies have already reported on the mosaic structure of bare patches on mussel reefs on rocky shores ([Hunt and Scheibling, 2001](#); [Paine and Levin, 1981](#)). By showing that large stretches of conspecific mussels – monotonous reefs – harbour a smaller diversity of species than stretches with patches, the importance of localized disturbances for the creation and colonization of microhabitats and associated biodiversity becomes clear.

In our study, the mosaic of habitats in the mussel reef includes pools that remain filled with water throughout the tidal cycles, as well as inlets that do not hold water but accumulate muddy sediment that falls dry during low tide. The water-filled pools deviate from the surrounding tidal flat in that benthic diatom presence and silt content appear much lower. In this they seem equivalent to the rockpools found on rocky shores. On rocky shores, the habitat heterogeneity provided by rockpools is recognized as promoting biodiversity ([Firth et al., 2014, 2013](#)). However, the value of pools and other microhabitats present in self-organized blue mussel reefs for associated biodiversity is yet unstudied.

Here we investigate the effect of mussel reef topography on biodiversity. We posit that local habitat heterogeneity emerges in mussel

reefs in the form of a diverse topology of the landscape and a gradient in water retention. Consequently, we hypothesize that within the mussel reef, environmentally distinct microhabitats can be defined that support divergent communities of invertebrates. When compared to the adjacent tidal flat, we expect that mussel reefs will display greater environmental heterogeneity and hence greater beta-diversity. This study provides experimental assessments of variability in environmental conditions between microhabitats in the field; thereby describing the importance of microhabitats for biodiversity on tidal flats and extending the scale of spatial patterning beyond its classically considered microhabitat scale.

2. Materials and methods

2.1. Study site

This study was conducted on a tidal mussel reef on the mudflat south of Schiermonnikoog, an island in the eastern part of the Dutch Wadden Sea (53°28'3.54"N 6°13'30.68"E). The reef comprised a mixture of blue mussels, *Mytilus edulis*, and the invasive Pacific oysters, *Magallana gigas* (syn. *Crassostrea gigas*), and was representative of reef compositions which nowadays dominate the intertidal Wadden Sea ([Reise et al., 2017](#)). Two distinct soft sediment microhabitats were present on the mussel reef as a result of spatial self-organization by mussels and environmental factors such as wave action: inlets and pools ([Fig. 1](#)). Inlets were mud-filled features of the reef that were in open contact with the tidal flat and drained completely during low tide. They often had an elevated centre of heaped mud. Pools were hollows in the mussel reef ranging from 1 to 10 square meters. The pools retained water during low tide and were more or less devoid of mussels and generally had a sandy bottom.

2.2. Sampling design

To study the role of environmental conditions in different habitats and on associated infaunal communities, from March to September 2018 we sampled pairs of mussel reef microhabitats (inlets and pools) on the reef at four different sampling sites (blocks) and compared these with three different sampling sites on the surrounding tidal flat area.

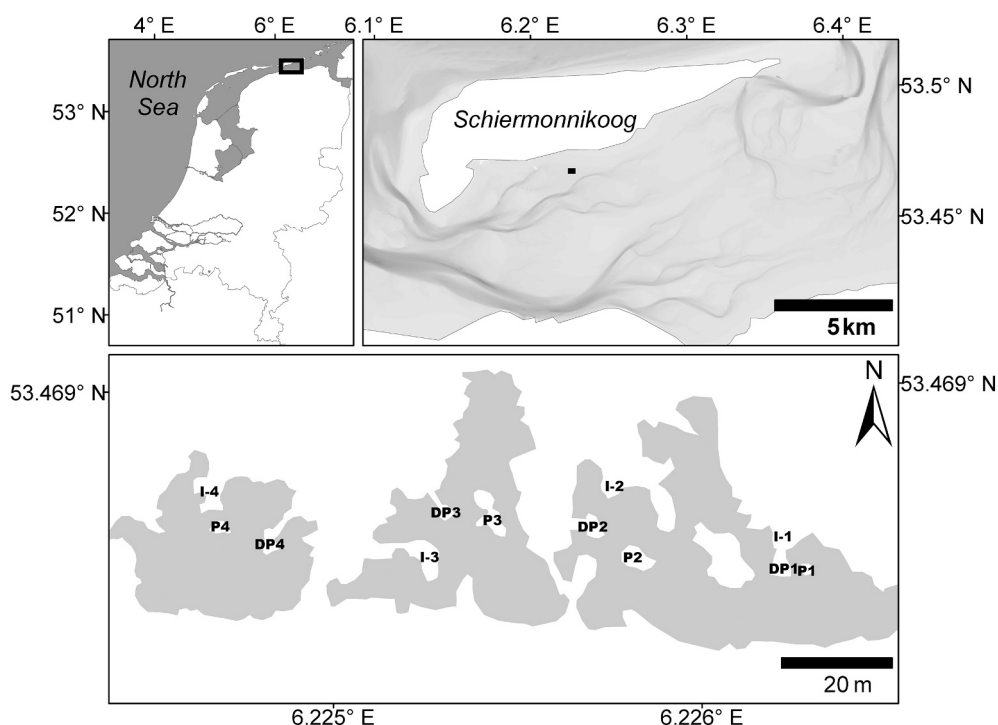


Fig. 1. Location of the sampling locations on the mussel reef, south of Schiermonnikoog, The Netherlands. Sampling locations on the reef include pools (P), formed through spatial self-organization by mussels and that retain water during low tide; drained pools (DP), created manually by allowing a natural occurring pool to drain during low tide; inlets (I), on the edge of the mussel reef and that drain during low tide. Numbers indicate the Block to which that sampling location belongs. Sampling locations on the tidal flat 50 m North, East and West of the mussel reef are not presented. Map data sources: ESRI Nederland Content and Rijkswaterstaat Nederland.

To be able to separate spatial effects due to the natural location of pools and inlets (i.e. further away from and on the edges of the reef, respectively) we also created a 'new' microhabitat in each block by draining pools. These drained pools were constructed by digging a single trench from a pool to the nearest side of the mussel reef (max. width 0.8 m and never wider than the pool itself), allowing it to drain completely during low tide. All mussels were removed from the trenches and trenches were dug no deeper than 5 cm below the lowest living mussel on the edge of the trench. To ensure mussels would not refill the trenches during the experiment, sides were secured with chicken fencing (1.2 × 1.2 cm plastic-coated metal mesh) and kept in place by pegs (24 cm, Stabilit), while not obstructing the mussel filter feeding capacities. The chicken fencing was left in place for the entire duration (6 months) of the experiment. Throughout the study, natural inlets and drained pools remained open and regularly drained of water at low tide.

Thus, each block on the reef consisted of three different microhabitats (sampling locations) with different water retention capacities, spaced ca. 3 m apart: 1) one natural occurring pool (mean length: width: depth = 4.9: 2.6: 0.12 m), 2) one inlet, located at the edge of the mussel reef (mean length: width = 7.6: 5.4 m) and 3), a drained pool (mean length: width: depth = 4.2: 2.4: 0.10 m), giving a total $n = 12$ (Fig. 1). Since these microhabitats are not present on the tidal area, three blocks were sampled on the tidal area, each containing four sample locations on the bare sediment (total $n = 12$), also spaced 3 m apart. Two blocks on the tidal flat were placed at the same tidal height 50 m to the East and West of the mussel reef, while the third block was placed 50 m to the North of the reef, coastward.

The precise geographical location and elevation of all sampling locations was recorded with a dGPS Trimble R8 TSC3. GPS coordinates were collected in the Dutch Rijksdriehoekcoördinaten system and were later converted to WGS84 coordinates. Elevation measurements were taken on the scale of the Amsterdam ordnance datum (NAP, similar to mean sea level) (Table S1).

2.3. Environmental variables

We collected data on the abiotic characteristics of each sampling location, including: erosive power, organic matter content and chlorophyll *a* concentrations. The erosive power of currents at the sampling locations was measured using cylindrical plaster dissolution poles (length: ± 6 cm, diameter: 2.5 cm) (Donadi et al., 2013; Engel et al., 2017). Laboratory experiments showed that plaster dissolution works as a measurement for water motion (Thompson and Glenn, 1994). However, abrasion of sediment suspended in the water column will affect plaster dissolution in the field, making it a general proxy of the water current's erosive power. The plaster poles ($n = 24$) were cast from model plaster (Knauf modelgips, Knauf B.V., Utrecht, The Netherlands) mixed with water in a 1:1 ratio, were air-dried for three weeks, pre-weighed (mean dry-weight (g) \pm SE = 45.85 \pm 0.40) and a single pole was placed vertically at the centre of each sampling locations, with its bottom touching the sediment, in Spring on 23 April and again in Autumn on 27 September 2018. Plaster poles were exposed to hydrodynamic conditions for two high tides in April and to one high tide in September, after which they were left to air-dry for three weeks and re-weighed.

Mussel reefs are strong producers of pseudo-faeces that accumulate in adjacent sediments, enriching the organic matter content on the tidal flat area and providing a food resource for different organisms (Commito et al., 2008; Donadi et al., 2014; Norling and Kautsky, 2008). In this study, sediment samples for organic matter content analysis were collected from each of the sampling locations on five occasions (19 March, 12 April, 25 April, 15 May, 27 September 2018) to track the change and development of the sediment accumulation in the different sampling locations over a longer time-period. We took two sediment cores (depths 0–1 and 0–5 cm) from each sampling location using a cut-off 50 mL disposable syringe (diameter: 2.6 cm). Upon collection, samples were immediately transferred to cool bags and transported to

the laboratory where they were frozen at -20°C until processing. Organic matter content was measured from oven-dried samples (48 h at 65°C) and calculated by Loss on Ignition (LOI: 4 h, 550°C). Chlorophyll *a* samples were collected from each of the sampling locations on three occasions (12 and 23 April, 15 May 2018), using the same cut syringes as for organic matter sampling, depressed to 1 cm depth. Upon collection, samples were immediately wrapped in aluminium foil and placed in cool bags for transport to the laboratory where they were freeze-dried. After freeze-drying, chlorophyll *a* was extracted from sediments using 90% acetone and concentrations measured spectrophotometrically using the method of Jeffrey and Humphrey (1975).

2.4. Infaunal community composition and diversity

Infauna samples were collected on 15 May 2018 at all sampling locations. Due to the destructive nature of benthic infaunal core sampling this was done once around the peak of infauna development. Infauna samples were collected with a core (diameter: 13.5 cm, depth: 10 cm), sieved over 1 mm mesh in the field, fixed in 70% ethanol and stained with Rose Bengal. In the lab, samples were poured over a sieve cascade down to 500 μm and enumerated to species, or where this was not possible, morphospecies, under a binocular microscope (40× magnification).

2.5. Data analyses

A covariance-based principal component analysis (PCA) was run in R (v3.5.1, vegan package) to ordinate and visualize infaunal community compositions and to identify species that contributed most to the spatial variation among habitats. Subsequently, possible relationships between the first two principal component axes and the different environmental variables (plaster erosion, organic matter content of the sediment between 0 and 1 and 0–5 cm depth, chlorophyll *a* and elevation) were explored with Pearson's correlations.

Differences in plaster erosion, organic matter content of the sediment between 0 and 1 and 0–5 cm depth, chlorophyll *a* and elevation between the different microhabitats were each analysed separately using linear mixed-effects models that included the fixed factor 'habitat' (four levels: inlet, drained pool, mussel pool and tidal flat) and the random factor 'block' (seven levels; four on the mussel reef and three surrounding the reef). Repeated measure ANOVAs showed that sampling date did not have any systematic effects (linear change over time) on the environmental variables (Erosion: $F_{1,3} = 5.35$, $p = 0.104$; Organic matter 1 cm: $F_{4,12} = 2.85$, $p = 0.072$; Organic matter 5 cm: $F_{4,12} = 0.22$, $p = 0.924$; Chlorophyll *a*: $F_{2,6} = 2.51$, $p = 0.161$). We therefore used averages across sampling dates in the models. All five models were fitted with REML (restricted maximum likelihood) estimation using the 'lme' function in the nlme package in R (v3.1–141). We also compared spatial turnover of both habitat characteristics and infaunal species composition on the mussel reef and the tidal flat. Spatial turnover of habitat characteristics was calculated as the Euclidean distances between the sampling locations in each block. Spatial turnover of species composition was calculated as Bray-Curtis dissimilarities between the sampling locations in each block. For each block we extracted the average Euclidean distance and Bryan Curtis dissimilarities of all possible pairwise comparisons of sample locations within the block. Spatial turnover was analysed using a linear model that included the fixed factor 'system' (two levels: mussel reef or tidal flat). Data were reciprocal root or log transformed where necessary to meet assumptions of normality and homoscedasticity. All post-hoc tests were analysed using the Tukey's HSD test (in R, v1.4–10, glht function, multcomp package). Statistical tests were considered significant at an alpha value of 0.05.

3. Results

3.1. Environmental variables

Clear differences were found in environmental conditions between the mussel reef microhabitats and the surrounding tidal flat. On the mussel reef hydrodynamic stress was generally lower than on the tidal flat, and the alternating pattern of pools, that retain water, and inlets that contain elevated diatom-covered hummocks produced high variation in organic enrichment and community composition across the mussel reef (Figs. 2 & 3). Erosion was lower in pools and inlets compared to the tidal flat (Table 1; Fig. 2), with pools having the lowest erosion of the four habitats sampled (mean % erosion \pm SE, pools: 11.75 ± 1.19 ; drained pools: 12.69 ± 0.46 ; inlets: 13.11 ± 1.48 ; tidal flat: 16.47 ± 0.55). Organic matter content did not differ significantly between the tidal flat and the different mussel reef habitats (Table 1; Fig. 2). However, differences were apparent among reef habitats: the organic matter content of shallow sediment (0–1 cm depth, OM1) was significantly less in the pools compared to the drained pools or inlets (Table 1; Fig. 2); and the organic matter content of deeper sediment (0–5 cm depth, OM5) was significantly higher in inlets than in pools and drained pools (Table 1; Fig. 2). Thus, drained pools had the same organic matter content as pools when looking at deeper sediment, but the same organic matter contents as natural occurring inlets when looking at shallower, newly deposited sediment; indicating that experimentally drained pools became increasingly similar to the natural inlets.

Chlorophyll *a* values and elevation levels did not differ significantly between any of the sampling locations (Table 1).

3.2. Infaunal community composition and diversity

The species composition of infauna correlated well with the differences in erosion and sediment characteristics. The first two principal components (PCs) of the principal component analysis accounted cumulatively for 77.6% of the variability in community composition (with 55.5% across PC1 and 22.1% across PC2; Fig. 3A), where PC1

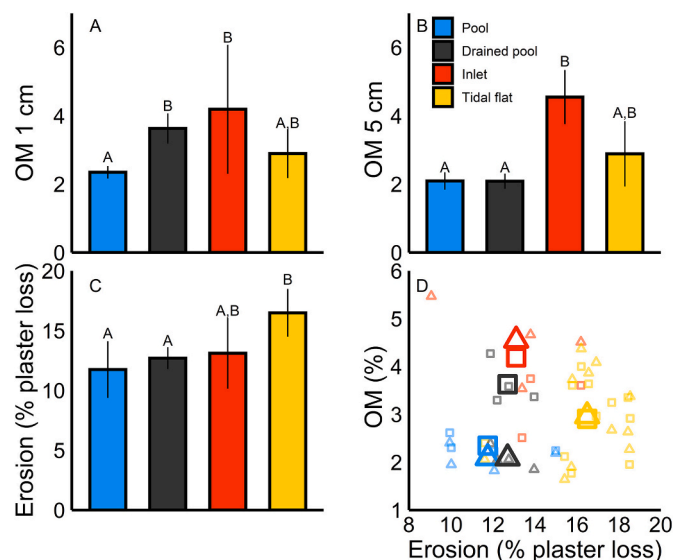


Fig. 2. Differences in mean \pm SD for organic matter (OM) contents in 0–1 cm depth (A), 0–5 cm depth (B) and erosion (C), measured as % dissolution of plaster, among the four different microhabitats. Letters represent significant differences. The combined plot (D) shows mean erosion values and organic matter content in shallow (0–1 cm depth; squares) and deep (0–5 cm depth; triangles) sediment per microhabitat, where each small shape represents a date-average per sampling location ($n = 5$ for OM) and big shapes represent the mean per sampling location ($n = 20$ for OM).

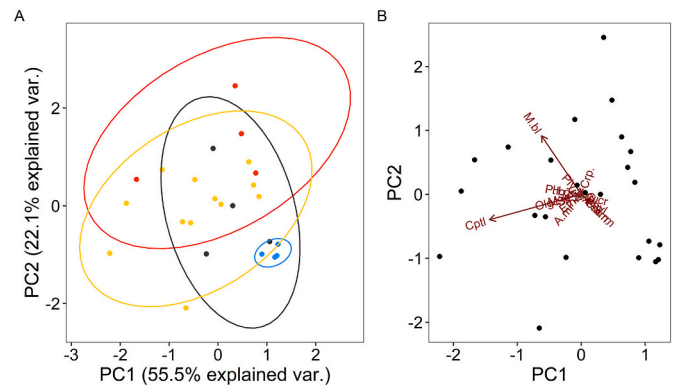


Fig. 3. Ordination (A) and biplot (B) of the infaunal community on the first two axes of the principal component analysis. Blue dots represent pools, red dots represent inlets, grey dots represent drained pools and yellow dots represent the tidal flat. Each dot represents a sampling location and ellipses are 95% confidence intervals, encircling the four different microhabitats. Species that most strongly contributed to the pattern in community composition were Capitellidae spp. (Cptl) and *Macoma balthica* (M.bl).

showed a positive relationship with elevation levels of the sampling locations (Pearson's correlation; $\rho = 0.52$, $p = 0.011$) and a negative relationship with erosion (Pearson's correlation; $\rho = -0.42$, $p = 0.046$; Fig. 4). PC2 did not relate significantly with any of the measured environmental variables (Table 2).

The two species that contributed most strongly to the pattern in community composition were Capitellidae spp. and *Macoma balthica* (Fig. 3B). Capitellidae spp., *Marenzelleria viridis*, *Pygospio elegans* and *Streblospio benedicti* were most abundant in the tidal flat, while the bivalve *M. balthica* was most abundant in the inlets. *Aphelochaeta marioni* and oligochaetes were most abundant in the drained pools, while *Phyllocoridae* spp., *Scoloplos armiger*, *Crangon crangon* and *Gammarus* sp. dominated in the pools. In total, we encountered 11 species of polychaetes, 1 species of bivalve, 3 species of arthropods, oligochaetes and entognatha (Table S2).

The mussel reef displayed a higher environmental and biological diversity compared to the tidal flat (Fig. 5). The variability in the environment measured as Euclidian distances, showed that sampling sites (blocks) on the reef in general were more heterogeneous in hydrodynamic conditions, sediment characteristics and production than the sampling locations on the tidal flat ($F_{1,5} = 9.9$, $p = 0.025$; Fig. 5A). The spatial beta-diversity of infauna species was also greater on the reef as indicated by the higher Bray-Curtis dissimilarities of species composition in the blocks on the mussel reef than on the tidal flat ($F_{1,5} = 42.9$, $p = 0.001$; Fig. 5B). Average species richness of the infauna was not higher in the blocks on the mussel reef compared to the surrounding tidal flat ($F_{1,5} = 0.6$, $p = 0.468$; Fig. 5C), but the higher dissimilarity in species composition on the reef was indicative of a greater number of unique species (17) compared to the tidal flat (13).

4. Discussion

The current rapid decline of global biodiversity (Blowes et al., 2019; Dornelas et al., 2014; Eriksson and Hillebrand, 2019) highlights the urgent need for a more complete understanding of the ecological processes that maintain and enrich the local diversity of species. The positive effect of habitat heterogeneity on biodiversity has been studied in various ecosystems, but it remains unclear how different species coexist in seemingly more homogeneous habitats. By studying the environmental and biological characteristics of microhabitats on a mussel reef, we show how the variability in the physical structure of self-organized mussel reefs plays a key role in the maintenance of biodiversity within habitats.

Table 1

Univariate linear mixed-effects models results and associated post-hoc Tukey's HSD tests results of the effects of habitat treatments on environmental variables (OM1 = organic matter 1 cm depth, OM5 = organic matter 5 cm depth), where P = pool, DP = drained pool, I = inlet and T = tidal flat. **Bold:** significant ($p < 0.05$).

Linear mixed-effects models												
Env. variables	Habitat											
	df		F-value		p-value							
Erosion	3,14		4.44		0.022							
OM1	3,14		4.61		0.019							
OM5	3,14		30.85		<0.001							
Chlorophyll a	3,14		1.71		0.211							
Elevation	3,14		2.55		0.098							

Post-hoc Tukey's test												
	DP x P		DP x I		DP x T		P x I		P x T		T x I	
	z	p	z	p	z	p	z	p	z	p	z	p
Erosion	-0.759	0.873	0.328	0.988	2.801	0.026	1.087	0.697	3.504	0.002	2.497	0.060
OM1	-2.962	0.016	0.309	0.989	-1.538	0.414	3.271	0.006	1.068	0.708	-1.809	0.268
OM5	0.020	1.000	8.341	<0.001	1.400	0.480	8.321	<0.001	1.392	0.485	-2.332	0.083
Chlorophyll a	-1.704	0.321	-0.255	0.994	-1.731	0.308	1.449	0.469	-0.048	1.000	-1.479	0.450
Elevation	-1.394	0.485	-1.877	0.222	1.371	0.500	-0.482	0.961	2.029	0.165	2.257	0.099

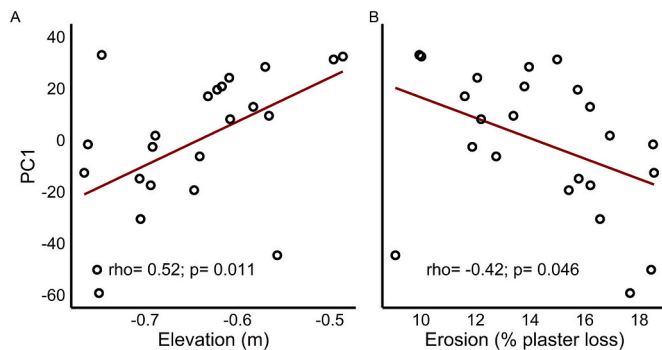


Fig. 4. Significant Pearson's correlations between the first principal component (PC1) of community composition and the elevation level of the sampling locations (A) and erosion values (B).

Table 2

Pearson's correlations between environmental variables and principal component (PC) axes 1 and 2 of the infaunal community. **Bold:** significant ($p < 0.05$).

Pearson's correlations				
Env. Variables	PC-axis 1		PC-axis 2	
	rho	p	rho	p
Erosion	-0.42	0.046	0.01	0.971
OM1	-0.24	0.452	-0.05	0.871
OM5	-0.48	0.113	0.36	0.231
Chlorophyll a	-0.09	0.78	-0.16	0.6
Elevation	0.52	0.011	0.04	0.849

Theoretical literature highlights that patterning in self-organized landscapes may increase biodiversity by creating variation in habitat conditions (Cornacchia et al., 2018; Nathan et al., 2013; Pringle et al., 2010). We found that different microhabitats, characterized by varying environmental conditions, develop during the growth of the mussel reef – in this case mussel pools that retain water during low tide and that are entirely unique in the tidal flat landscape and more akin to the habitats of rocky shores. Where on rocky shores, the surrounding rock protects the inhabitants of rockpools from the brunt of wave exposure, on mussel reefs it is the surrounding mussels that protect the pool environment (Hunt and Scheibling, 2001), creating a habitat with lower wave exposure and higher sediment stability than what is typical for tidal flat habitats. The pools and inlets of the mussel reef harbour distinct

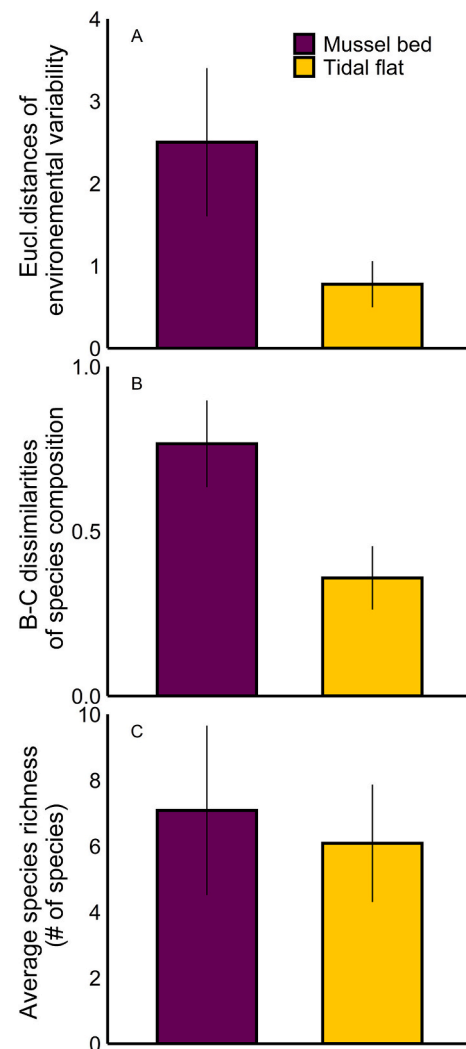


Fig. 5. Average variation (mean \pm SD) in environmental conditions (A), community composition (B), and species richness (C) within blocks on the mussel reef and on the tidal flat. Environmental differences are expressed as Euclidean distances and community differences as Bray-Curtis dissimilarities. Within blocks: $n = 3$ (mussel reef), $n = 4$ (tidal flat).

hydrodynamic conditions, sediment characteristics and infaunal communities, thereby diversifying the tidal landscape.

In our study, sediment conditions did not differ between the reef and tidal flat, but they differed among microhabitats on the reef itself. During the experiment, organic matter concentrations in the drained pools started to shift from that of pools to that of inlets and the tidal flat: the drained pools had low organic matter concentrations in the deeper sediment comparable to that of the pools; but in the shallow sediment layer, the drained pools had a higher organic matter concentration comparable to that of the inlets, hinting at a transformation. The low organic matter concentrations in pools at both depths is most likely due to the retained water in the pools in which organic matter such as extracellular polysaccharides will remain suspended. The relatively high organic matter contents at the locations that drain during low tide are presumably due to the presence of microphytobenthos. The extracellular polysaccharides they excrete create a layer of stabilizing biofilm in the drained pools, inlets and tidal flat during low tide (Eriksson et al., 2017; Jones et al., 1997; Stal, 2010) which keeps the organic matter from dissolving into the water column. The biofilm at the tidal flat erodes more easily during high tide, resulting in relatively lower organic matter contents (Van De Koppel et al., 2001; Van Straaten, 1961).

The increased heterogeneity on the mussel reef was also reflected in beta-diversity. The pools on the reef are similar to pools on rocky shores. Rockpools are well-studied small-scale habitats that harbour increased biodiversity compared to their surroundings (Firth et al., 2014, 2013; Pinn et al., 2005), can serve as nurseries (Delany et al., 1998) and add feeding and refuge spaces (Moran, 1985; Noël et al., 2009). We found a higher beta-diversity of infauna on the mussel reef than on the surrounding tidal flat. Pools and inlets showed the biggest difference in species composition, whereas drained pools are in a transitional state from pools to inlets and the community compositions found at these locations reflect this transition (Fig. 3). This transformation can be argued to represent a developmental stage, where organic matter contents and community composition are at an intermediate stage between that of pools and inlets. The development of pool to inlet adds to the microhabitat diversity on the mussel reef and increases its number of available niches, consequently supporting a higher infauna community diversity than the more homogeneous tidal flat.

The importance of habitat heterogeneity for diversity in community compositions is well-documented in a range of marine systems: on tidal beaches, an exposure gradient creates different microhabitats that harbour distinct nematode communities (Gingold et al., 2010); on coral reefs, where coral species function as microhabitats, different fish communities are supported by different coral species (Messmer et al., 2011); within seagrass meadows, macrofaunal communities are affected by the distribution of shoots of seagrass and bare patches (Lewis and Stoner, 1983). In the pools in our mussel reef, characterized by bigger grain size and higher sediment stability, the polychaete species *S. armiger* was most abundant due to its preference for coarser sediments (Kraan et al., 2010; Zühlke and Reise, 1994). The low erosive conditions and the water retained in the pools during low tide most likely explain the higher numbers of *Crangon crangon* and *Gammarus* sp. found in the pools (Reise, 1983). Unlike pools, inlets and the tidal flat are characterized by high erosion rates and high organic matter contents in 0–5 cm depth. Especially organisms that thrive in organic matter enriched habitats, such as the silt-loving bivalve *M. balthica* and polychaetes Capitellidae spp. and *P. elegans* were dominant at these locations. Both polychaetes are opportunists that feed on organically enriched sediments, with Capitellidae spp. being particularly insensitive to the higher erosion on the tidal flat (Dittmann, 1990; Kotta et al., 2001; Raffaelli et al., 1991; Tsutsumi, 1987). *Aphelocheata marioni* and oligochaetes were most abundant in the drained pools. The high abundance of oligochaetes may be due to their preference for finer sediments mixed with a relatively high amount of sand, in combination with low erosion (Ysebaert and Herman, 2002; Zühlke and Reise, 1994).

In this study we only quantified infauna once. By sampling in May we

intended to capture the highest variety of settled species present at our sampling locations. Later in Summer, sampled species and their biomass would probably have been higher due to growth and (second) recruitment periods of certain polychaete species. However, due to time restrictions and the destructive nature of infauna sampling, we did not sample a second time.

Furthermore, inclusion of epifauna would most likely have strengthened the claim of importance of microhabitats in the tidal landscape. Pools were observed harbouring different algal species (e.g. *Ulva lactuca*, *Fucus vesiculosus* f. *mytili*, *Gracilaria* sp.), snails (e.g. *Littorina littorea*), crabs and gobies (I. van der Ouderaa personal observations). The differences in community composition between the microhabitats in this study demonstrate the importance of variability in environmental conditions for biodiversity in seemingly homogeneous landscapes.

5. Conclusions

Our work provides empirical evidence that microhabitats on mussel reefs, characterized by different environmental conditions, support distinct infaunal communities and are indispensable for the maintenance of biodiversity in otherwise seemingly homogeneous habitats. By structuring the mussel reef topology via the process of spatial self-organization, different microhabitats are created by the organisms themselves, resulting in new niche space for other species. Therefore, homogenization of land- and sea-scapes through anthropogenic interference can indirectly result in the loss of biodiversity.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Acknowledgments

We thank Vereniging Natuurmonumenten and the Province of Friesland for their permission to execute our field work on the tidal flat area of Schiermonnikoog. A special thanks goes to the 2018 Marine Research master students Danielle Megan Crowley and Sorsha Passmore for helping us setting up the field experiment in typical Dutch winter conditions. This research was funded by the Adaptive Life Scholarship from GELIFES, University of Groningen.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2021.151561>.

References

- Albrecht, A., Reise, K., 1994. Effects of *Fucus vesiculosus* covering intertidal mussel beds in the Wadden Sea. *Helgoländer Meeresun.* 48, 243–256. <https://doi.org/10.1007/BF02367039>.
- Andriana, R., van der Ouderaa, I., Eriksson, B.K., 2020. A Pacific oyster invasion transforms shellfish reef structure by changing the development of associated seaweeds. *Estuar. Coast. Shelf Sci.* 235, 106564. <https://doi.org/10.1016/j.ecss.2019.106564>.
- Bellwood, D.R., Hughes, T.P., Folke, C., Nyström, M., 2004. Confronting the coral reef crisis. *Nature* 429, 827–833. <https://doi.org/10.1038/nature02691>.
- Blowes, S.A., Supp, S.R., Antão, L.H., Bates, A., Bruelheide, H., Chase, J.M., Moyes, F., Magurran, A., McGill, B., Myers-Smith, I.H., Winter, M., Bjorkman, A.D., Bowler, D. E., Byrnes, J.E.K., Gonzalez, A., Hines, J., Isbell, F., Jones, H.P., Navarro, L.M., Thompson, P.L., Vellend, M., Walldock, C., Dornelas, M., 2019. The geography of biodiversity change in marine and terrestrial assemblages. *Science* 366, 339–345. <https://doi.org/10.1126/science.aaw1620>.
- Christianen, M.J.A., van der Heide, T., Holthuijsen, S.J., van der Reijden, K.J., Borst, A.C. W., Olff, H., 2017. Biodiversity and food web indicators of community recovery in

- intertidal shellfish reefs. *Biol. Conserv.* 213, 317–324. <https://doi.org/10.1016/j.biocon.2016.09.028>.
- Comitato, J.A., Como, S., Grupe, B.M., Dow, W.E., 2008. Species diversity in the soft-bottom intertidal zone: biogenic structure, sediment and macrofauna across mussel bed spatial scales. *J. Exp. Mar. Biol. Ecol.* 366, 70–81.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
- Cornacchia, L., van de Koppel, J., van der Wal, D., Wharton, G., Puijalon, S., Bouma, T.J., 2018. Landscapes of facilitation: how self-organized patchiness of aquatic macrophytes promotes diversity in streams. *Ecology* 99, 832–847. <https://doi.org/10.1002/ecy.2177>.
- Delany, J., Myers, A.A., McGrath, D., 1998. Recruitment, immigration and population structure of two coexisting limpet species in mid-shore tidepools, on the west coast of Ireland. *J. Exp. Mar. Biol. Ecol.* 221, 221–230. [https://doi.org/10.1016/S0022-0981\(97\)00129-9](https://doi.org/10.1016/S0022-0981(97)00129-9).
- Dijkstra, J.A., Harris, L.G., Mello, K., Litterer, A., Wells, C., Ware, C., 2017. Invasive seaweeds transform habitat structure and increase biodiversity of associated species. *J. Ecol.* 105, 1668–1678. <https://doi.org/10.1111/1365-2745.12775>.
- Dittmann, S., 1990. Mussel beds - amensalism or amelioration for intertidal fauna? *Helgoländer Meeresun.* 44, 335–352. <https://doi.org/10.1007/BF02365471>.
- Donadi, S., Van Der Heide, T., Van Der Zee, E.M., Eklöf, J.S., Van De Koppel, J., Weerman, E.J., Piersma, T., Olff, H., Eriksson, B.K., 2013. Cross-habitat interactions among bivalve species control community structure on intertidal flats. *Ecology* 94, 489–498. <https://doi.org/10.1890/10.1890.10.0048.1>.
- Donadi, S., van der Zee, E.M., van der Heide, T., Weerman, E.J., Piersma, T., van de Koppel, J., Olff, H., Bartelds, M., van Gerwen, I., Eriksson, B.K., 2014. The bivalve loop: intra-specific facilitation in burrowing cockles through habitat modification. *J. Exp. Mar. Biol. Ecol.* 461, 44–52. <https://doi.org/10.1016/j.jembe.2014.07.019>.
- Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., Magurran, A.E., 2014. Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344, 296–299. <https://doi.org/10.1126/science.1248484>.
- Engel, F.G., Alegria, J., Andriana, R., Donadi, S., Gusmao, J.B., van Leeuwe, M.A., Matthiessen, B., Eriksson, B.K., 2017. Mussel beds are biological power stations on intertidal flats. *Estuar. Coast. Shelf Sci.* 191, 21–27. <https://doi.org/10.1016/j.ecss.2017.04.003>.
- Eriksson, B.K., Hillebrand, H., 2019. Rapid reorganization of global biodiversity. *Science* 366, 308–309. <https://doi.org/10.1126/science.aaz4520>.
- Eriksson, B.K., Westra, J., Van Gerwen, I., Weerman, E., Zee, E., Vander, Heide, T., Vander, Koppel, J., Vande, Olff, H., Piersma, T., Donadi, S., 2017. Facilitation by ecosystem engineers enhances nutrient effects in an intertidal system. *Ecosphere* 8, 1–12. <https://doi.org/10.1002/ecs2.2051>.
- Firth, L.B., Thompson, R.C., White, F.J., Schofield, M., Skov, M.W., Hoggart, S.P.G., Jackson, J., Knights, A.M., Hawkins, S.J., 2013. The importance of water-retaining features for biodiversity on artificial intertidal coastal defence structures. *Divers. Distrib.* 19, 1275–1283. <https://doi.org/10.1111/ddi.12079>.
- Firth, L.B., Schofield, M., White, F.J., Skov, M.W., Hawkins, S.J., 2014. Biodiversity in intertidal rock pools: informing engineering criteria for artificial habitat enhancement in the built environment. *Mar. Environ. Res.* 102, 122–130. <https://doi.org/10.1016/j.marenvres.2014.03.016>.
- Gerard, V.A., 1984. The light environment in a giant kelp forest: influence of *Macrocystis pyrifera* on spatial and temporal variability. *Mar. Biol.* 84, 189–195. <https://doi.org/10.1007/BF00393004>.
- Gingold, R., Mundo-Ocampo, M., Holovachov, O., Rocha-Olivares, A., 2010. The role of habitat heterogeneity in structuring the community of intertidal free-living marine nematodes. *Mar. Biol.* 157, 1741–1753. <https://doi.org/10.1007/s00227-010-1447-z>.
- Heiss, W.M., Smith, A.M., Probert, P.K., 2000. Influence of the small intertidal seagrass *Zostera novaezelandica* on linear water flow and sediment texture. *New Zeal. J. Mar. Freshwat. Res.* 34, 689–694. <https://doi.org/10.1080/00288330.2000.9516970>.
- Hunt, H.L., Scheibling, R.E., 2001. Predicting wave dislodgment of mussels: variation in attachment strength with body size, habitat, and season. *Mar. Ecol. Prog. Ser.* 213, 157–164.
- Jeffrey, S.W., Humphrey, G.F., 1975. New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. *Biochem. Physiol. Pflanz.* 167, 191–194. [https://doi.org/10.1016/S0015-3796\(17\)30778-3](https://doi.org/10.1016/S0015-3796(17)30778-3).
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78, 1946–1957.
- Kotta, J., Orav, H., Sandberg-Kilpi, E., 2001. Ecological consequence of the introduction of the polychaete *Marenzelleria cf. viridis* into a shallow-water biotope of the northern Baltic Sea. *J. Sea Res.* 46, 273–280. [https://doi.org/10.1016/S1385-1101\(01\)00088-0](https://doi.org/10.1016/S1385-1101(01)00088-0).
- Kraan, C., Aarts, G., Van Der Meer, J., Piersma, T., 2010. The role of environmental variables in structuring landscape-scale species distributions in seafloor habitats. *Source Ecol. Ecol.* 91, 1583–1590.
- Levin, S.A., 1976. Population dynamic models in heterogeneous environments. *Annu. Rev. Ecol. Syst.* 7, 287–310.
- Levin, S.A., Paine, R.T., 1974. Disturbance, patch formation, and community structure. *Proc. Natl. Acad. Sci. U. S. A.* 71, 2744–2747. <https://doi.org/10.1073/pnas.71.7.2744>.
- Lewis, F.G., Stoner, A.W., 1983. Distribution of macrofauna within seagrass beds: an explanation for patterns of abundance. *Bull. Mar. Sci.* 33, 296–304.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, New Jersey, USA.
- Messmer, V., Jones, G.P., Munday, P.L., Holbrook, S.J., Schmitt, R.J., Brooks, A.J., 2011. Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology* 92, 2285–2298. <https://doi.org/10.1890/11-0037.1>.
- Moran, M.J., 1985. The timing and significance of sheltering and foraging behaviour of the predatory intertidal gastropod *Morula marginalba* Blainville (Muricidae). *J. Exp. Biol. Ecol.* 93, 103–114.
- Munguia, P., Osman, R.W., Hamilton, J., Whitlatch, R., Zajac, R., 2011. Changes in habitat heterogeneity alter marine sessile benthic communities. *Ecol. Appl.* 21, 925–935. <https://doi.org/10.1890/09-2398.1>.
- Nathan, J., Meron, E., von Hardenberg, J., 2013. Spatial instabilities untie the exclusion-principle constraint on species coexistence. *J. Theor. Biol.* 335, 198–204. <https://doi.org/10.1016/j.jtbi.2013.06.026>.
- Noël, L.M.L.J., Hawkins, S.J., Jenkins, S.R., Thompson, R.C., 2009. Grazing dynamics in intertidal rockpools: connectivity of microhabitats. *J. Exp. Mar. Biol. Ecol.* 370, 9–17. <https://doi.org/10.1016/j.jembe.2008.11.005>.
- Norling, P., Kautsky, N., 2008. Patches of the mussel *Mytilus* sp. are islands of biodiversity in subtidal sediment habitats in the Baltic Sea. *Aquat. Biol.* 4, 75–87.
- Oliver, T.H., Isaac, N.J.B., August, T.A., Woodcock, B.A., Roy, D.B., Bullock, J.M., 2015. Declining resilience of ecosystem functions under biodiversity loss. *Nat. Commun.* 6. <https://doi.org/10.1038/ncomms10122>.
- Paine, R.T., Levin, S.A., 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.* 51, 145–178.
- Pinn, E.H., Mitchell, K., Corkill, J., 2005. The assemblages of groynes in relation to substratum age, aspect and microhabitat. *Estuar. Coast. Shelf Sci.* 62, 271–282. <https://doi.org/10.1016/j.ecss.2004.09.002>.
- Pocklington, J.B., Keough, M.J., O'Hara, T.D., Bellgrove, A., 2019. The influence of canopy cover on the ecological function of a key autogenic ecosystem engineer. *Diversity* 11. <https://doi.org/10.3390/D11050079>.
- Pratchett, M.S., Hoey, A.S., Wilson, S.K., 2014. Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. *Curr. Opin. Environ. Sustain.* 7, 37–43. <https://doi.org/10.1016/j.cosust.2013.11.022>.
- Pringle, R.M., Doak, D.F., Brody, A.K., Jocqué, R., Palmer, T.M., 2010. Spatial pattern enhances ecosystem functioning in an African savanna. *PLoS Biol.* 8, 1000377. <https://doi.org/10.1371/journal.pbio.1000377>.
- Raffaelli, D., Limia, J., Pont, S., Hull, S., 1991. Interactions between the amphipod *Corophium volutator* and macroalgal mats on estuarine mudflats. *J. Mar. Biol. Assoc. UK* 71, 899–908. <https://doi.org/10.1017/S0025315400053558>.
- Reise, K., 1983. *Tidal Flat Ecology: An Experimental Approach to Species Interactions*. Springer-Verlag, Berlin Heidelberg, New York, Tokyo.
- Reise, K., Buschbaum, C., Buttger, H., Wegner, M.K., 2017. Invading oysters and native mussels: from hostile takeover to compatible bedfellows. *Ecosphere* 8, 1–14. <https://doi.org/10.1002/ecs2.1949>.
- Saier, B., 2002. Subtidal and intertidal mussel beds (*Mytilus edulis* L.) in the Wadden Sea: diversity differences of associated epifauna. *Helgol. Mar. Res.* <https://doi.org/10.1007/s10152-001-0097-4>.
- Stal, L.J., 2010. Microphytobenthos as a biogeomorphological force in intertidal sediment stabilization. *Ecol. Eng.* 36, 236–245. <https://doi.org/10.1016/j.ecoleng.2008.12.032>.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J. Biogeogr.* 31, 79–92.
- Thompson, T.L., Glenn, E.P., 1994. Plaster standards to measure water motion. *Limnol. Oceanogr.* 39, 1768–1779.
- Tsutsumi, H., 1987. Population dynamics of *Capitella capitata* (Polychaeta; Capitellidae) in an organically polluted cove. *Mar. Ecol. Prog. Ser.* 36, 139–149.
- Van De Koppel, J., Herman, P.M.J., Thoolen, P., Heip, C.H.R., 2001. Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. *Ecology* 82, 3449–3461.
- Van de Koppel, J., Gascoigne, J., Theriault, G., Rietkerk, M., Mooij, W.M., Herman, P.M.J., 2008. Experimental evidence for spatial self-organization and its emergent effects in mussel bed ecosystems. *Sci. Report.* 322. <https://doi.org/10.1126/science.1163952>.
- Van de Koppel, J., Van der Heide, T., Altieri, A.H., Eriksson, B.K., Bouma, T.J., Olff, H., Silliman, B.R., 2015. Long-distance interactions regulate the structure and resilience of coastal ecosystems. *Annu. Rev. Mar. Sci.* 7, 139–158. <https://doi.org/10.1146/annurev-marine-010814-015805>.
- Van der Zee, E.M., Van der Heide, T., Donadi, S., Eklöf, J.S., Eriksson, B.K., Olff, H., van der Veer, H.W., Piersma, T., 2012. Spatially extended habitat modification by intertidal reef-building bivalves has implications for consumer-resource interactions. *Ecosystems* 15, 664–673. <https://doi.org/10.1007/s10021-012-9538-y>.
- Van Straaten, L.M.J., 1961. Sedimentation in tidal flat areas. *J. Alberta Soc. Petrol. Geol.* 9, 1961–1968.
- Wright, J.P., Jones, C.G., Boeken, B., Shachak, M., 2006. Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. *J. Ecol.* 94, 815–824. <https://doi.org/10.1111/j.1365-2745.2006.01132.x>.
- Ysebaert, T., Herman, P.M.J., 2002. Spatial and temporal variation in benthic macrofauna and relationships with environmental variables in an estuarine, intertidal soft-sediment environment. *Mar. Ecol. Prog. Ser.* 244, 105–124. <https://doi.org/10.3354/meps244105>.
- Zühlke, R., Reise, K., 1994. Response of macrofauna to drifting tidal sediments. *Helgoländer Meeresun.* 48, 277–289. <https://doi.org/10.1007/BF02367041>.