

OIKOS

Research article

Structural complexity of hard substrates shapes shallow marine benthic communities

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Oikos

2025: e11080

doi: 10.1002/oik.11080

Subject Editor: Peter Todd

Editor-in-Chief:

Paulo R. Guimaraes

Accepted 23 March 2025



Structurally complex habitats offer niche diversity, with varying biotic and abiotic conditions, generally leading to higher biodiversity compared to simpler habitats. However, our understanding of the response of ecological communities to increased complexity and the underlying drivers remain ambiguous due to discrepancies in how complexity is measured across ecosystems, warranting further experimental testing. Here, we used 3D-printed reef structures to assess how structural complexity affects recruitment in a shallow coastal ecosystem in a highly standardised manner. We deployed fractal-like (self-similar) pyramid-shaped structures of three levels of standardized complexity on sandy intertidal and subtidal sandflats, keeping material, shape, and external dimensions consistent across levels. More complex structures had a higher surface area within the same total volume and more empty space. We examined the effects on taxonomic diversity, abundances, densities, and spatial patterning of five reef taxa: barnacles, mussels, tunicates, anemones, and algae. Increased complexity resulted in higher taxonomic richness in the intertidal zone but not in the subtidal. Taxonomic accumulation curves indicated increased within-sample heterogeneity and niche diversity in complex substrates. The effects of complexity on abundances (total n per structure) and densities (n per cm^2) varied by taxon and tidal zone, suggesting life-strategies shape these responses. Mussels benefited from increased structural complexity regardless of tidal elevation, which we hypothesise is due to reduced predation. Other taxa benefited from the increased surface area in more complex structures. Only barnacles, mainly found on the middle and outer parts of the structures, showed clear spatial patterning within structures, which could potentially be driven by a tradeoff between feeding efficiency and predation risk. Our findings demonstrate how standardised structural complexity shapes composition and diversity of epibenthic communities in coastal



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ecosystems. We argue that applying structural complexity in restoration efforts could enhance biodiversity in structurally complex ecosystems such as reefs, mangroves and streams.

Keywords: artificial substrates, coastal ecosystems, fractal-like substrates, reefs, taxonomic diversity, Wadden Sea

Introduction

Habitat complexity boosts biodiversity, because structurally complex habitats generally offer a variety of (micro-) niches that support more species and higher abundances than simple habitats (Pianka 2011). Furthermore, complex habitats can alter abiotic conditions locally to offer niches with varying temperature, irradiance, flow or available hiding space, which promotes the coexistence of species (Carvalho and Barros 2017). For example, the species diversity of dryland communities is structured by the spatially complex fractal geometry of their habitat and resources (Ritchie and Olff 2004). Larger-scale heterogeneity of habitat-elements within the landscape (habitat complexity), such as shellfish reefs, kelp forests, and tree epiphytes promote biodiversity globally (Thomsen et al. 2022). Complexity within the landscape has been studied in diverse ecosystems, mainly in aquatic systems, such as (coral) reefs, riverbeds or mangrove forests at different spatial scales (Kovalenko et al. 2012). On a finer scale, the physical arrangement of the (micro-)habitat structure (structural complexity) within for example freshwater macrophytes or coral reefs increases species richness (St. Pierre and Kovalenko 2014, Torres-Pulliza et al. 2020). Some authors argue the two spatial scales (habitat heterogeneity and structural complexity) should not be confused (Tokeshi and Arakaki 2012, Carvalho and Barros 2017), while others argue that both scales will influence communities when viewed at different spatial resolutions (Kovalenko et al. 2012, Loke and Chisholm 2022).

In coastal systems, the role of complexity on both habitat and finer structural scale has been studied and clear examples of complex habitats on multiple scales are reefs (Kovalenko et al. 2012). Reef ecosystems are biodiversity hotspots, because the structurally complex habitat acts as shelter, nursing ground and settling substrate for other species (Ponti et al. 2021). Reefs can be categorized as either geogenic or biogenic. Geogenic reefs, include rocky or artificial substrate covered with sessile benthic organisms, support high biodiversity, particularly in soft-sediment systems (Witte et al. 2024). Biogenic reefs are shaped by reef-building foundation species (habitat-forming species), such as corals, shellfish, or tube-dwelling worm species that create hard and structurally complex substrates (Ponti et al. 2021). The structural complexity of reefs interacts with and optimises local conditions by the reduction of hydrodynamics, desiccation of waves, reducing light availability, and offering shelter from predation (Carvalho and Barros 2017). Therefore, juvenile reef species are attracted to this complex structure and different species might be attracted to specific niches within the reef (Temmink et al. 2021). However, it remains ambiguous how structural complexity shapes reef communities.

Although structural complexity is widely acknowledged as an important factor that drives ecosystem functioning and diversity, there have been varying methods to quantify complexity and a standardised mechanistic approach is lagging (Kovalenko et al. 2012, Loke and Chisholm 2022). Geometric metrics that reflect the structure of objects in space or its 3D geometry, such as rugosity (R^* , the amount of surface area within a planar area) or fractal dimension (D , the complexity of scale-invariant spatial pattern or shape) are typically used to describe structural complexity (Loke and Chisholm 2022). While these geometric metrics capture aspects of a substrate's structural complexity, there is an almost infinite number of surface configurations possible for each possible value. Additionally, higher biodiversity or larger abundances observed on more complex substrates can, at least in part, be attributed to an increasing surface area or the substrate material (Matias et al. 2010, Witte et al. 2024). To circumvent these controversies and to thoroughly unravel the effect of structural complexity on coastal communities, a highly standardised approach is needed. Such an approach allows to compare the effect of structural complexity among different abiotic conditions on different taxa. Technological developments in 3D-printing have enabled affordable standardised design and printing of structures that allow to assess structural complexity independent of increase in surface area or material properties.

Here, we therefore tested the effect of structural complexity on the recruitment of reef communities in a coastal soft-sediment system using 3D-printed structures. We isolated effects of complexity from surface area or material properties by keeping the material, shape and total dimensions of the structures identical across varying complexities. We used a systematic approach with 3D-printed structures that were derived from Sierpiński fractal (repeated self-similar) pyramids with three different levels of structural complexity (Fig. 2A). To assess differences in response to structural complexity, we zoomed in on five abundant reef taxa with different life-strategies (barnacles, mussels, tunicates, anemones and algae). Furthermore, to test whether the effect of complexity varied among abiotic conditions, the structures were deployed in both the intertidal and subtidal zones for one growing season. We predict an increase of taxonomic richness and abundances of reef taxa with an increase of complexity. If these increases are driven solely by increased surface area, any observed effect of complexity will disappear when adjusting for available surface. In addition, we hypothesise that different taxa have distinct locations on the structures, influenced by gradients in environmental factors such as predation, light availability, desiccation, and hydrodynamics created by complexity.

Material and methods

Study area

The experiment was constructed in the Dutch Wadden Sea, a large intertidal soft sediment system that stretches from Den Helder in the Netherlands to Esbjerg in Denmark (Fig. 1A). The experiment was conducted on adjacent inter- (53°06'70"N, 04°54'42"E) and subtidal (53°06'58"N, 04°56'77"E) sites in the Western Dutch Wadden Sea (Fig. 1B). The intertidal zone had a depth of −65 cm (SD 3.5 cm) NAP (mean water level according to Amsterdam Ordnance Datum) and was exposed 18% of the time (Fig. 1C). The subtidal zone had a depth of −171 cm (SD 5.4 cm) NAP and was never exposed.

Experimental setup

Reef structures were designed based on the shape of Sierpiński pyramids, consisting of a fixed set of fractal-like equilateral pyramid shapes, subdivided recursively into smaller

equilateral pyramids. Each more complex iteration was created by shrinking a pyramid to half of its original height, putting together six copies (5 upright, 1 upside-down) of this pyramid to recreate the original dimensions (Fig. 2A). The pyramid shape was chosen because it reduces drag and is easily scalable. By using a fractal-like shape, the overall shape and dimensions of the structure remained the same with different levels of complexity. We used the 1st, 3rd and 5th iteration of this Sierpiński-like pyramid in our experiment, which offered a range of complexity that has ecological relevance for reef ecosystems (Fig. 1D–2A). This resulted in three levels of complexity: a structure without crevices (low complexity), a structure with sub-pyramids and crevices at least 8.2 cm high (mid complexity), and a structure with sub-pyramids and crevices of at least 2 cm high (high complexity). The structures were 3D-printed with PLA (polylactic acid) at the Fieldwork Company in Groningen (the Netherlands) and were 46.5 by 46.5 cm at the base and 32.8 cm high. The surface area of each level of complexity was derived from 3D models (Table 1). We calculated the rugosity (R^*) by dividing the surface area of one side of a higher complexity

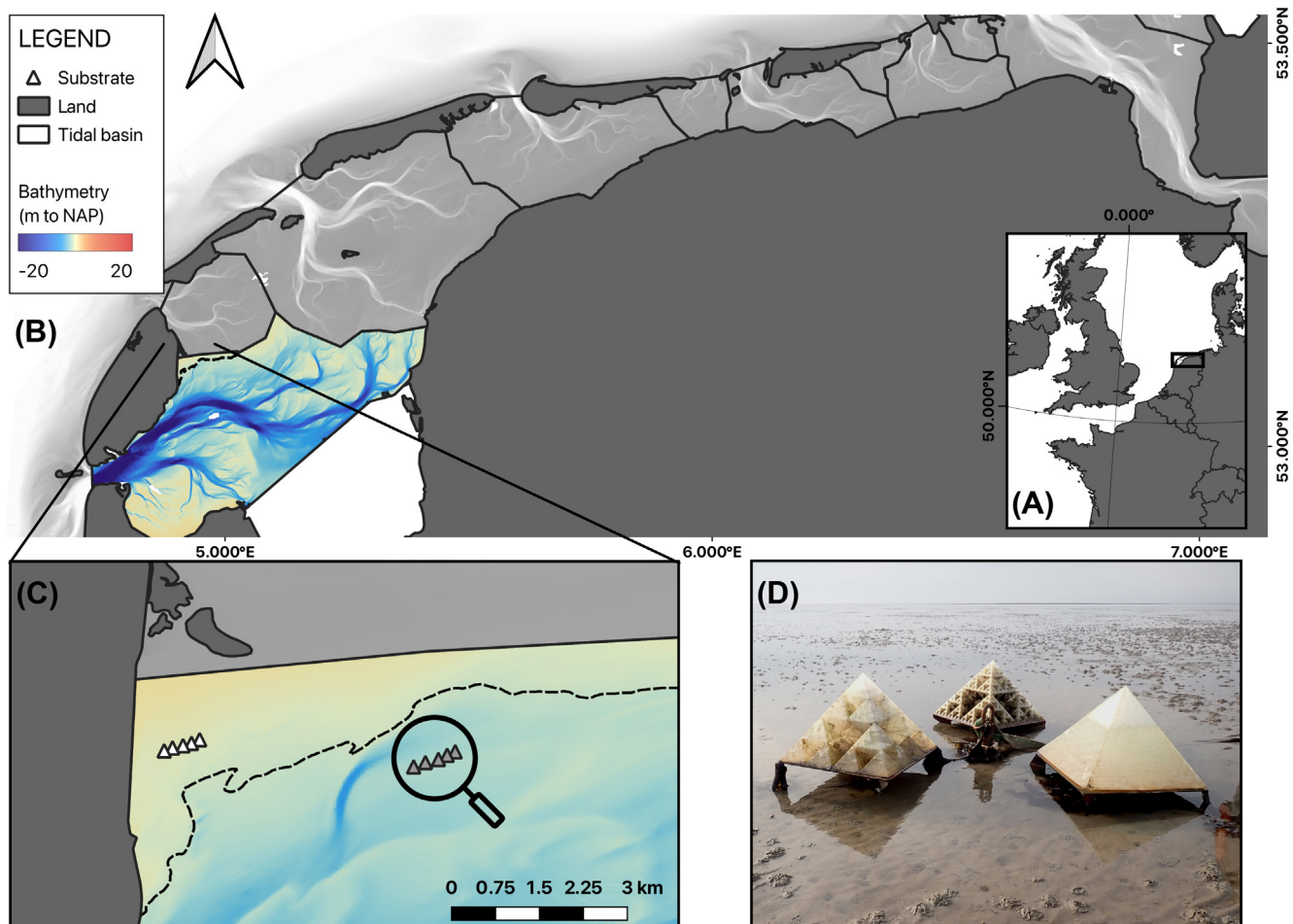


Figure 1. Experimental location in the Dutch Wadden Sea. (A) Europe and (B) the Dutch Wadden Sea. The bathymetry is colour-coded in the tidal basin where the experiment was conducted. (C) Location of the experiment in the sub (grey) and intertidal (white) below and above the dashed line respectively. (D) Experimental setup in the field with three structures on a steel frame.

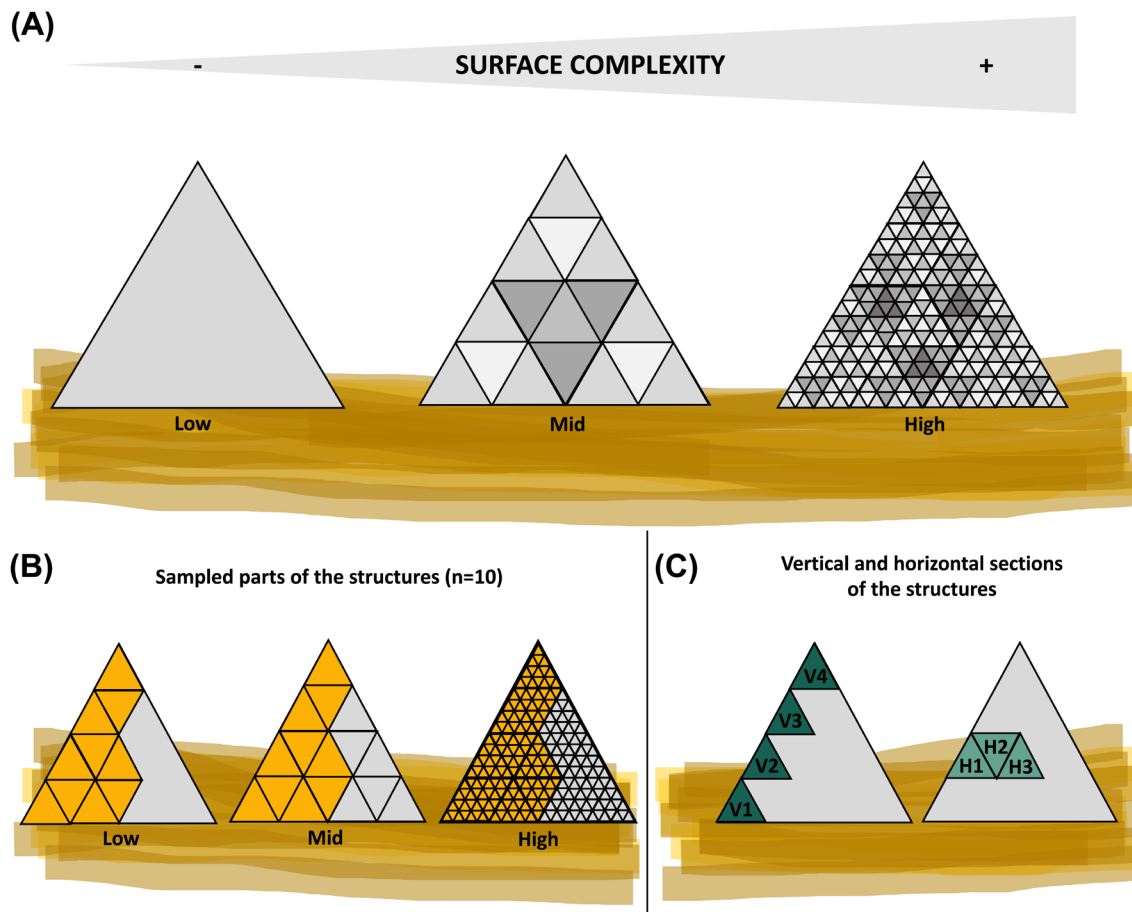


Figure 2. (A) Overview of the three complexity levels in 2D, one structure consisted of four sides as depicted here. (B) Sampling scheme where orange triangles indicate the ten samples taken per structure. (C) Samples included in the analyses to assess preferred locations on the structures. Small triangles indicate samples used to assess the vertical (dark green) and horizontal (light green) gradients.

structure by one side of the low complexity structure (planar surface, Table 1). As the structures are different iterations of a self-similar structure, the different levels of complexity have the same Hausdorff dimensions. We calculated the fractal (Hausdorff) dimension (D) for the structures following Mandelbrot and Wheeler (1983, Table 1):

$$D = \frac{\log(n)}{\log(r)}$$

Where n is the number of pyramids of the smallest size in the iteration that fit in the original ($n=36$ for mid complexity and $n=1296$ for high complexity) and r is the scale by which its size is reduced compared to the original size ($r=4$ for mid complexity and $r=16$ for high complexity).

Five experimental replicates were placed on the seafloor in both tidal zones (Fig. 1C). Each replicate consisted of a steel frame with one structure of each complexity level (three in total) with roughly 50 cm between the structures (Fig. 1D, 2). The distance between each replicate frame was on average 112.6 m (SD 25.1 m), wide enough for a ship could sail through to outplace, monitor, and collect the frames. The structures were deployed in May 2021, lifted from the seafloor monthly to monitor whether they were still intact, and collected at the end of one growing season in August 2021.

Laboratory work

After collection, 10 samples from one face of each structure were collected by cutting the structures into smaller pieces (Fig. 2B). The samples were fixed in a 6% buffered

Table 1. Structure properties of the three complexity levels.

Complexity	Dimensions (L × W × H in cm)	Surface area (cm ²)	Rugosity (R*)	Fractal (Hausdorff) dimension (D)
Low	46.5 × 46.5 × 33.2	4324.5	1	2.58
Mid	46.5 × 46.5 × 33.2	9730.13	2.25	2.58
High	46.5 × 46.5 × 33.2	21892.78	5.06	2.58

formaldehyde solution with $\sim 2 \text{ mg l}^{-1}$ Rose Bengal (CAS no. 632-68-8) to stain the proteins in living tissue. We assessed abundances of sessile (e.g. barnacles, mussels, anemones, solitary tunicates) and mobile (e.g. polychaetes, starfish, amphipods, crabs) benthic taxa in each sample (Supporting information for taxonomic groups). A subset of barnacles was assessed when the estimated abundance in a sample was higher than 100 individuals. The number of barnacles in the subset was divided by the assessed fraction of surface area of the sample to estimate of the total number of barnacles in the sample. Additionally, we evaluated the cover of colonial or encrusting taxa (e.g. algae, bryozoans, hydroid polyps). This was done by overlaying a raster with 16 triangles over the sample surface and counting the number of triangles in which the encrusting taxa occurred. The number of triangles with encrusting taxa present was then divided by 16 to obtain a fraction of coverage. The cutting process caused minor damage to the surface of some samples. Where required we estimated the fraction of damaged surface area of the samples the same way as the cover fraction of encrusting taxa was assessed. Observed sessile, mobile, and encrusting taxa in the sample were divided by this fraction to estimate the total abundances. Individuals that fell off the structure and remained in the sample container were also counted. The abundances of taxa in this residue were divided by the fraction of the sample that was assessed as part of the side of interest of the structure (0.25 for one side, 0.5 for two sides) and added to obtain the total abundances in the sample. Barnacles and encrusting taxa could not be included here as the reconstruction of their abundances post-detachment proved unfeasible. The abundances were rounded up to the nearest integer to facilitate statistical analyses.

Data analyses

The taxa count of all ten samples per structure were summed to assess recruitment preferences on the scale of the entire structure. We then evaluated differences between the three levels of complexity in the two tidal zones in terms of taxonomic richness and heterogeneity, abundance and densities of the four most frequently occurring taxa (barnacles, mussels, tunicates and anemones), and algae coverage. Next, we explored if different taxa preferred specific locations on the structures for species that occurred in at least 20% of the samples (barnacles, mussels and algae).

Taxonomic richness

We calculated the number of unique taxa on each structure. The taxonomic richness was then compared between tidal zones and among the three levels of complexity, including an interaction between the two, using a generalised linear mixed model (GLMM) with a Poisson distribution. Tidal zone and complexity were included as fixed factor, and we included the platform number as a random factor. We performed post hoc tests of estimated marginal means with false discovery rate in a planned paired comparison when predictors were significant. We only compared among different levels of complexity in the same tidal zone and between tidal zones for the same

level of complexity, omitting the post hoc pairs comparing different levels of complexity in different tidal zones. This planned paired comparison was performed for each model, resulting in a set of nine post hoc comparisons per model.

Taxonomic heterogeneity

Where abundances of species can be divided by the surface area for a more mechanistic understanding of the role of structural complexity, this is not possible with the presence-absence derived taxonomic richness. We therefore used taxa accumulation curves to test whether differences in observed species numbers between treatments were driven by heterogeneity created by the complexity of the structures. Accumulation curves were constructed using the sample-based rarefaction with the Mao Tau estimate (Colwell et al. 2012). All samples ($n=50$) of one complexity level in one tidal zone were pooled, resulting in one accumulation curve for each treatment. We fitted a Michaelis–Menten function to the accumulation curve using nonlinear (weighted) least-squares estimates (NLS). Michaelis–Menten curves are parameterised as:

$$S = \frac{S_m \times a}{K_m + a}$$

Where S is the number of taxa, S_m is the total number of taxa found in a treatment, a is the number of samples, and K_m is the number of samples needed to observe half the total number of taxa in a treatment. Therefore, samples with lower values of K_m accumulate taxa more rapidly and have a higher within-sample heterogeneity.

Abundances and algae cover

The abundances of the four most abundant epibenthic sessile taxa and the algae coverage were assessed in more detail and compared among the three levels of complexity in the two tidal zones. We constructed GLMMs that allowed for a potential interaction between the two predictors. Tidal zone and complexity level were included as fixed factor, while platform number was included as random factor. The model with the best fitting distribution was chosen with Akaike's information criterion (AIC). For barnacles we used a linear negative binomial distribution, for mussels and anemones we used a quadratic negative binomial distribution, for tunicates we used a quadratic negative binomial distribution with zero-inflation, and for algae cover we used a gaussian distribution. If model predictors were significant, we performed the same planned paired comparison as for taxonomic richness.

Densities

We calculated densities (n cm^{-2}) of the four most abundant taxa (barnacles, mussels, tunicates, and anemones) as the abundances divided by the available space in the samples in cm^2 . The surface area of the structures was calculated using the digital 3D models of structures (Table 1). We compared the densities among the three levels of complexity and between the two tidal zones. The same procedure was followed as for the analyses of abundances and algae cover. For these analyses

we omitted the residue in the sample container and fitted all models with a gaussian distribution.

Positions on structures

We assessed whether different taxa preferred specific positions on the structures. We assessed both a vertical (along the outer edge of the structure (V1–V4)) and a horizontal (from the middle section of the structure (H1–H3)) gradient over the structures (Fig. 2C). Only taxa that occurred in at least 20% of the samples along both gradients were included, as fewer observations were not sufficient to support the statistical models. The three remaining taxa (barnacles, mussels and algae) span different functional groups and traits, with potentially differing mechanisms underlying their preferences. We compared abundances or cover of these taxa among positions on the structure using GLMMs. We included a nested random factor of tidal zone, platform number, and level of complexity in the models. We chose the best-fitting model using AIC, resulting in a linear negative binomial distribution for barnacles and mussels, and a gaussian distribution for algae. The algae cover was logit transformed to improve the model fit. The abundances or cover of the different taxa on the different positions on the structures were compared in a post hoc test if there was a significant effect of position.

Programs and packages

Statistics were carried out in R ver. 4.3.1 and RStudio for Mac, figures were created with the 'ggplot2' package (Wickham et al. 2019, www.r-project.org). Accumulation curves were constructed with the 'vegan' package (Oksanen et al. 2022). Generalised linear models were generated using the 'glmmTMB' package (Brooks et al. 2017). Significance was determined with *Anova* from the 'car' package (Fox and Weisberg 2019). For significant predictors, post hoc testing of estimated marginal means (using the 'emmeans' package) with false discovery rate (FDR) adjustment was done to examine which

treatments differed significantly (Lenth 2023). Occasionally, the FDR-corrected post hoc yielded no significant contrasts, while model predictors were significant. To highlight these weaker differences, we then ran the more lenient Fisher's least significant difference (LSD).

Results

Taxonomic richness

The taxonomic richness increased with structural complexity in the intertidal, but not in the subtidal ($\chi^2 = 1.23$, $p < 0.01$, Fig. 3A). There was an interaction between complexity and tidal zone on richness ($\chi^2 = 8.97$, $p = 0.01$). In the intertidal, it was 2.3 times higher on the middle complexity than on the low complexity, and 3 times higher on the high complexity than on the low complexity structures. Taxonomic richness did not differ between the middle and high complexity structures in the intertidal. In the subtidal, richness did not differ among levels of complexity. Overall, the taxonomic richness was higher in the subtidal than in the intertidal ($\chi^2 = 5.71$, $p = 0.02$). On low complexity structures, it was 2.5 times higher in the subtidal than in the intertidal, while the difference was not significant for the other levels of complexity.

Taxonomic accumulation

The fitted Michaelis–Menten curves show that species accumulated slower on less complex structures and in the intertidal (Fig. 3B). Half-values of the maximum richness (K_m) were high for the low complexity structures in both tidal zones ($K_m = 4.98$ in the intertidal, and $K_m = 6.46$ in the subtidal) and the middle complexity structures in the intertidal ($K_m = 5.57$). Species accumulated rapidly in the complex treatments, especially in the subtidal. Lower values of K_m were observed for the

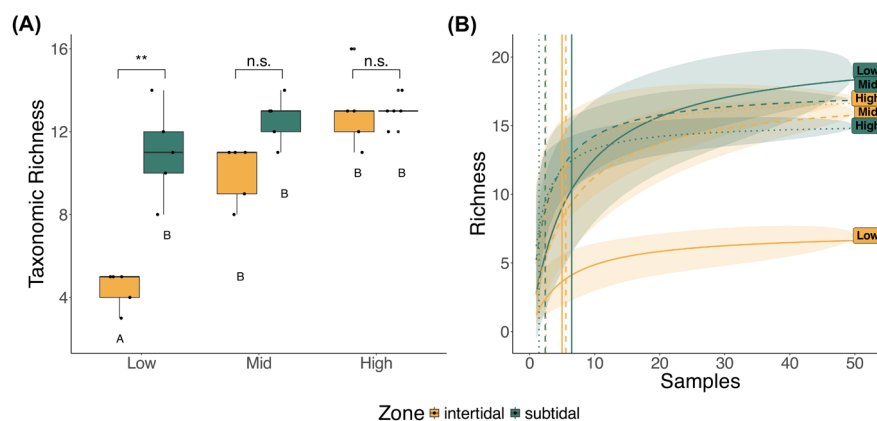


Figure 3. (A) The taxonomic richness for the three different levels of complexity in the two tidal zones. Jittered dots represent individual structures. The letters indicate statistical groups, where treatments that share a letter do not differ significantly. Square brackets above the boxes indicate significance of differences between tidal zones (** for $p < 0.01$, * for $p < 0.05$ and n.s. for $p > 0.05$). (B) Species accumulation curves for the different treatments. Solid lines are low complexity, dashed lines middle complexity and dotted lines high complexity treatments. The shaded area indicates the confidence intervals. Vertical lines are the number of samples where half the maximum richness is reached (K_m). In both panels orange indicates intertidal, and green subtidal treatments.

middle complexity in the subtidal ($K_m=2.39$) and the high complexity treatments in both tidal zones ($K_m=2.51$ in the intertidal and $K_m=1.44$ in the subtidal).

Abundances and algae cover

Abundances of the four most abundant epibenthic sessile taxa and the algae coverage were assessed in more detail. To explore how the three complexity levels affect abundances of

epibenthic sessile taxa and algae cover across different tidal zones, we compared the levels of complexity and tidal zones independently in our post hoc test. Barnacle abundances increased with increasing complexity ($\chi^2=21.19$, $p < 0.01$, Fig. 4A). The abundance of barnacles was 7 times higher in the intertidal than in the subtidal ($\chi^2=74.59$, $p < 0.01$). While barnacle abundances did not differ among complexity levels in the subtidal, they did in the intertidal. Here, barnacles were 2.8 times more abundant on high complexity than on low

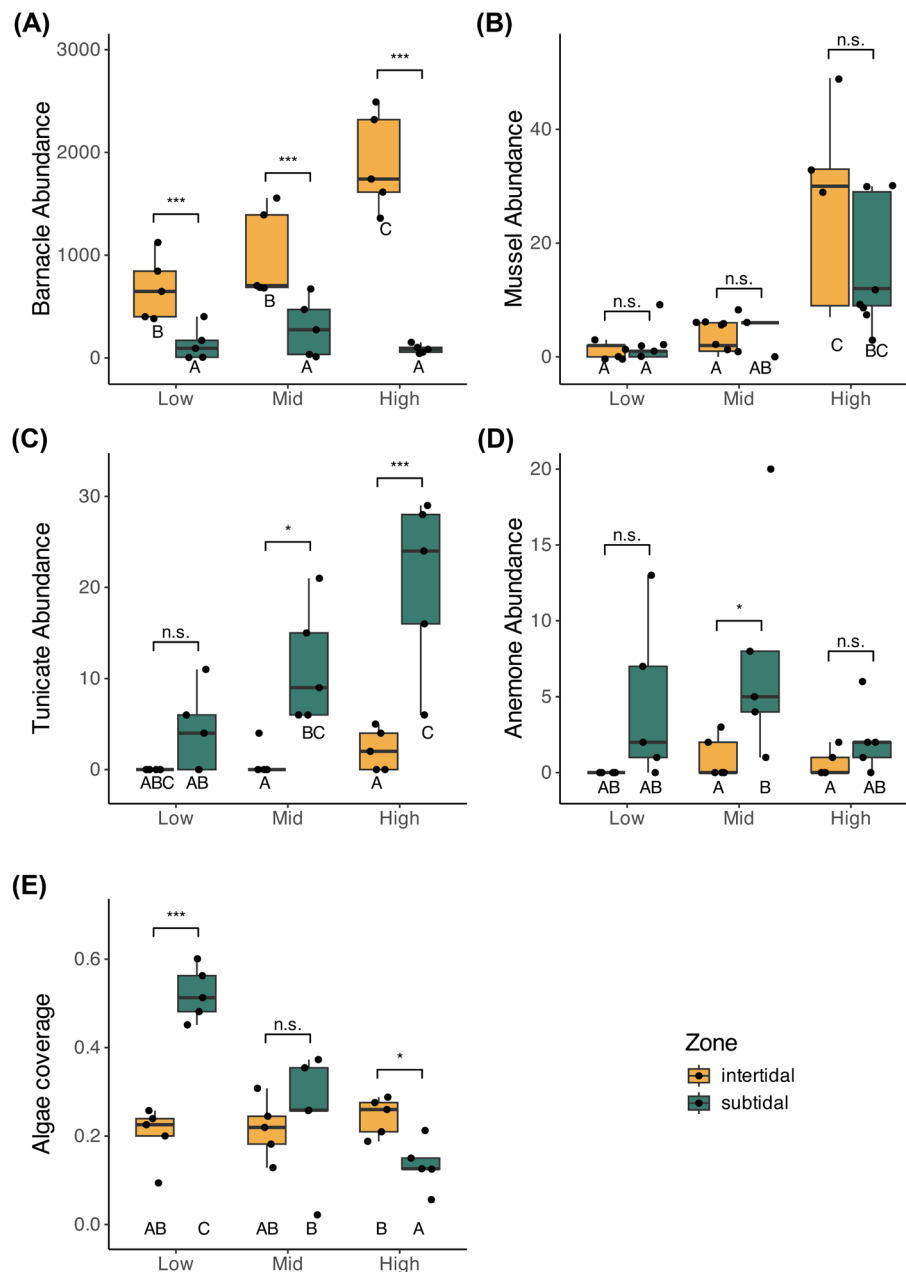


Figure 4. Abundances or coverage of different taxa for the complexity levels in the two tidal zones. (A) Barnacles, (B) mussels, (C) tunicates, (D) anemones, (E) algae cover in fractions ranging from 0 to 1. Orange boxes represent intertidal, and green boxes represent subtidal treatments. Jittered dots represent individual structures. The letters indicate statistical groups, where treatments that share a letter do not differ significantly. Square brackets above the boxes indicate the significance of differences between tidal zones (***) for $p < 0.001$, ** for $p < 0.01$, * for $p < 0.05$, and n.s. for $p > 0.05$.

complexity structures, and 1.9 times more than on the middle complexity. However, the interaction between complexity and tidal zone was not significant ($\chi^2=4.15$, $p=0.13$).

Mussel abundances increased with complexity levels ($\chi^2=42.84$, $p < 0.01$, Fig. 4B), but there was no difference between tidal zones ($\chi^2=0.10$, $p=0.75$). Mussels were 7.6 and 18.3 times more abundant on high complexity than on the low complexity in the subtidal and intertidal respectively. Mussel abundances were 8.5 times higher on the high complexity than on the middle complexity in the intertidal, and 3.1 times higher in the subtidal. There was no interaction between the effects of structural complexity and tidal zone on mussel abundances ($\chi^2=2.39$, $p=0.30$).

Tunicate abundances increased with increasing levels of complexity in the subtidal ($\chi^2=9.93$, $p=0.02$, Fig. 4C). Here, tunicates were 4.9 times more abundant on the high than on the low complexity. Although higher than the low complexity, and lower than the high complexity, tunicate abundances on the middle complexity did not differ from the other levels of complexity. While there was no interaction between tidal zone and complexity, tunicate abundances did not differ among complexity levels in the intertidal where they did in the subtidal ($\chi^2=0.14$, $p=0.93$). Tunicates were 14.3 and 9.4 times more abundant in the subtidal than in the intertidal for the middle and high complexity respectively ($\chi^2=21.24$, $p < 0.01$).

Anemone abundances did not differ among the different levels of complexity ($\chi^2=3.96$, $p=0.27$ Fig. 4D). Anemones were generally more abundant in the subtidal than in the intertidal ($\chi^2=10.08$, $p < 0.01$). The difference between tidal zones was only significant for the middle complexity, where abundances were 7.6 times higher in the subtidal than in the intertidal. There was no interaction between the effect of tidal zone and complexity on anemone abundances ($\chi^2=0.42$, $p=0.81$).

Algae cover decreased with increasing complexity in the subtidal zone ($\chi^2=32.85$, $p < 0.01$, Fig. 4E). Here, coverage was 2.1 times higher on low complexity than on the middle complexity, and 1.9 times higher on the middle complexity than on high complexity. Algae coverage did not differ with complexity in the intertidal, indicating an interaction between tidal zone and complexity ($\chi^2=48.23$, $p < 0.01$). Coverage differed between tidal zones for the low and high complexity structures ($\chi^2=10.15$, $p < 0.01$). On low complexity structures, the algae coverage was 2.6 times higher in the subtidal than in the intertidal. On high complexity structures however, the algae coverage was 1.8 times higher in the intertidal than in the subtidal.

Densities

As many studies indicate that an increase in surface area might drive increased recruitment on complex structures, we also assessed the effect of complexity on densities (individuals per cm^2) of the four most common taxa. To explore how the three complexity levels affect densities of these common taxa across different tidal zones, we compared the levels of

complexity and tidal zones independently in our post hoc test. We found no difference in barnacle densities among the three levels of complexity ($\chi^2=4.52$, $p=0.10$). Barnacle densities in the intertidal were 5, 3.4 and 21.8 times higher than in the subtidal for the low, middle, and high complexity respectively ($\chi^2=74.79$, $p < 0.01$, Fig. 5A). There was no interaction between complexity and tidal zone for barnacle densities ($\chi^2=0.51$, $p=0.77$).

Mussel densities increased with increasing levels of complexity ($\chi^2=14.15$, $p < 0.01$, Fig. 5B). There was no difference in mussel densities between the tidal zones and no interaction between complexity and tidal zone ($\chi^2=0.06$, $p=0.81$; $\chi^2=1.3$, $p=0.52$). In the intertidal, mussel densities were 5.1 and 4.2 times higher on the most complex structures than on the middle and low complexity respectively.

Tunicate densities did not differ among levels of complexity ($\chi^2=0.75$, $p=0.69$, Fig. 5C). Tunicates were not present on the low complexity structures in the intertidal, whereas we did observe tunicates on the low complexity structures in the subtidal. Tunicate densities were 11.5 and 17.3 times higher in the subtidal than in the intertidal for the middle and high complexity structures respectively ($\chi^2=22.17$, $p < 0.01$).

While anemone densities decreased with increasing complexity, this was not significant ($\chi^2=4.17$, $p=0.12$, Fig. 5D). There was no interaction between complexity and tidal zone ($\chi^2=3.65$, $p=0.16$). Although anemone densities were higher in the subtidal than in the intertidal ($\chi^2=8.99$, $p < 0.01$), individual contrasts were not significant. Post hoc testing with the more lenient LSD correction showed that anemone densities on the low complexity structures were higher in the subtidal than in the intertidal. Anemones were not present on the low complexity structures in the intertidal, whereas anemone densities were highest on the low complexity structures in the subtidal. Although the anemone densities on the middle complexity structures were higher in the subtidal than the intertidal, this difference was near significant ($p=0.06$).

Position on structures

Settlement of organisms may depend on the small-scale gradients created by complexity. Therefore, we analysed the most abundant taxa (barnacles, mussels and algae) along a vertical and horizontal gradient (Fig. 2C). Barnacles were 4.2 times more abundant on the middle sections (V2 and V3) than on the top and bottom sections (V4 and V1) of the structure on all complexity levels in the intertidal ($\chi^2=41.83$, $p < 0.01$, Fig. 6A). This pattern was more pronounced with increasing complexity and was absent in the subtidal. Barnacles preferred the outside (H1) or middle (H2) sections of the structures ($\chi^2=46.68$, $p < 0.01$, Fig. 7A). This was strongest on the most complex structures in the intertidal, where barnacles were 2.7 and 5.4 times more abundant on the outside (H1) and middle (H2) than on the inside (H3). A preference was absent from the low complexity structures. Mussels had no preference for any vertical section of the structures ($\chi^2=2.38$, $p=0.50$, Fig. 6B). Although mussels seemed to be more abundant on the inside than on the outside parts

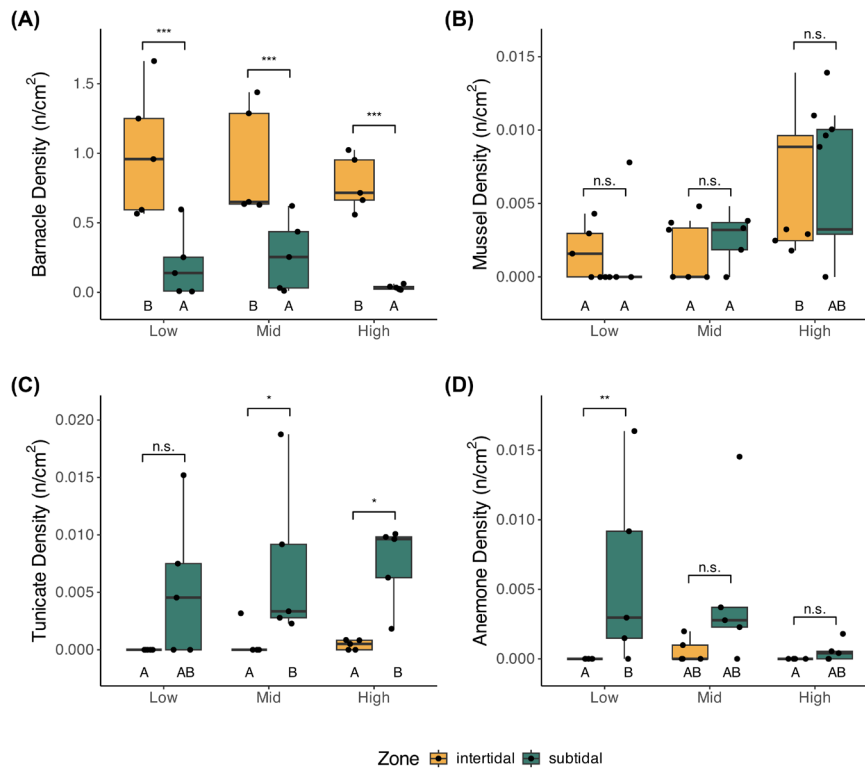


Figure 5. Densities of different taxa for the complexity levels in the two tidal zones. (A) Barnacles, (B) mussels, (C) tunicates, (D) anemones. Orange boxes represent intertidal, and green boxes represent subtidal treatments. Jittered dots represent individual structures. The letters indicate statistical groups, where treatments that share a letter do not differ significantly. Square brackets above the boxes indicate the significance of differences between tidal zones (*** for $p < 0.001$, ** for $p < 0.01$, * for $p < 0.05$, and n.s. for $p > 0.05$).

of the structures, this preference was just short of significant ($\chi^2 = 5.40$, $p = 0.07$, Fig. 7B). Again, this pattern was not visible on the low complexity structures. Algae had no preferred vertical ($\chi^2 = 7.52$, $p = 0.06$) or horizontal ($\chi^2 = 1.16$, $p = 0.56$) section of the structures (Fig. 6C–7C).

Discussion

In this study, we show that taxonomic richness and overall abundances increase with increasing complexity with 3D-printed fractal-like pyramids as standardized proxies of increasing marine reef complexity. We found stark contrasts in effect of structural complexity between two tidal zones, indicating that diverse biotic or abiotic conditions affect response to structural complexity. Moreover, we found that the preferred level of complexity and the spatial position on the structures differed among taxa. While barnacles, tunicates and algae primarily benefitted from the increased surface area of higher structural complexity, mussel densities increased with complexity regardless of the surface area. When correcting for available settlement space, anemones were least found on the structures with high complexity. We found that higher complexity increases the within-sample heterogeneity and resulted in a faster accumulation of species. These results suggest that there could be an interaction between the mechanisms shaping the observed relation with structural

complexity and the physical environment that differs among functional groups.

Structural complexity creates niches

Lower numbers of samples were needed to obtain half the total number of taxa (K_m) in the taxonomic accumulation curves for the more complex substrates, suggesting an increase in within-sample heterogeneity and niche diversity. Structural complexity can interact with resource availability, inter- and intraspecific interactions such as competition and predation, and abiotic stressors, such as hydrodynamics and desiccation, to create a variety of niches (Carvalho and Barros 2017). The role of structural complexity in shaping communities has been shown in different ecosystems ranging from coastal and aquatic systems (Kovalenko et al. 2012) to spider community in tree trunks (Villanueva-Bonilla et al. 2021) or invertebrates in epiphytes (Borst et al. 2019). We observed that different taxa, with inherently different life-strategies and vulnerabilities to various drivers, used the array of niches created by structural complexity differently. This supports the hypothesis that the role of structural complexity differs with life-strategies of taxa. For example, mussel abundances in our experiment were highest on the most complex structures in both tidal zones. In various terrestrial and aquatic systems, the presence of structural elements in the landscape changes predator behaviour (Heck and Crowder 1991,

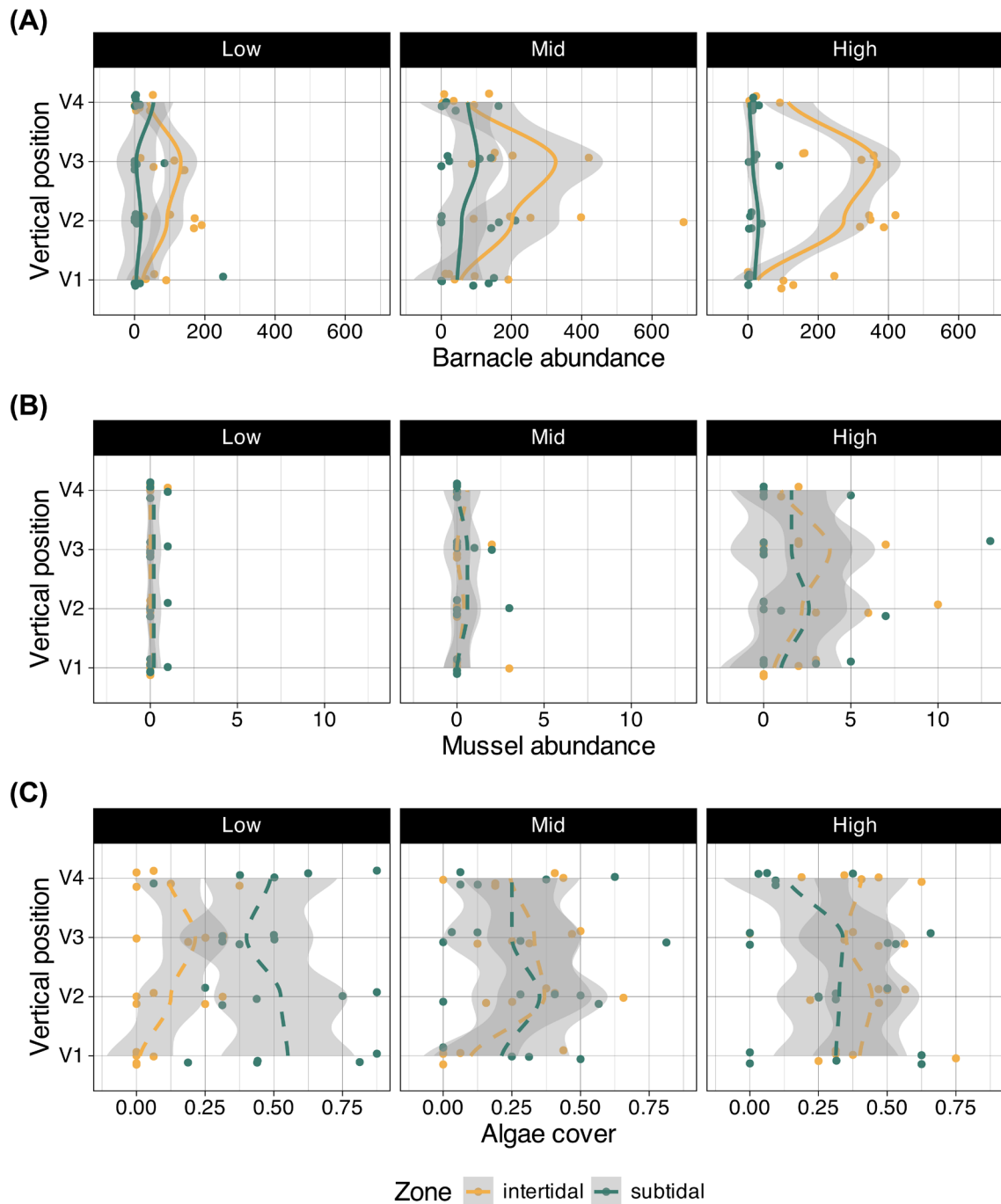


Figure 6. Preferred vertical positions on the structures for (A) barnacles, (B) mussels, (C) algae cover in fractions ranging from 0 to 1. The y-axes indicate the vertical positions (the bottom is V1, the top is V4) on the structures as illustrated in Fig. 2C. Lines are fitted local polynomial regressions with their 95% confidence intervals indicated in grey. Solid lines indicate a significant preference for vertical location on the structures, dashed lines indicate no such relation. Individual dots represent individual samples. Orange represents intertidal structures and green represents subtidal structures.

Langellotto and Denno 2004). Indeed, predation is also a limiting factor for mussel recruitment (Van der Heide et al. 2014, Cockrell et al. 2015) and settlement on more complex structures can relieve this predation pressure by reducing predator access (Bolton et al. 2018). Anemones, as the only predatory taxon, were abundant on the intermediate

complexity, which we hypothesise could be driven by competition or a combination of shelter and availability of their amphipod prey (Shick 2012). Algae cover decreased with an increase of complexity in the turbid subtidal treatments. This might be due to reduced light availability as structural complexity increases. More complex structures block light from

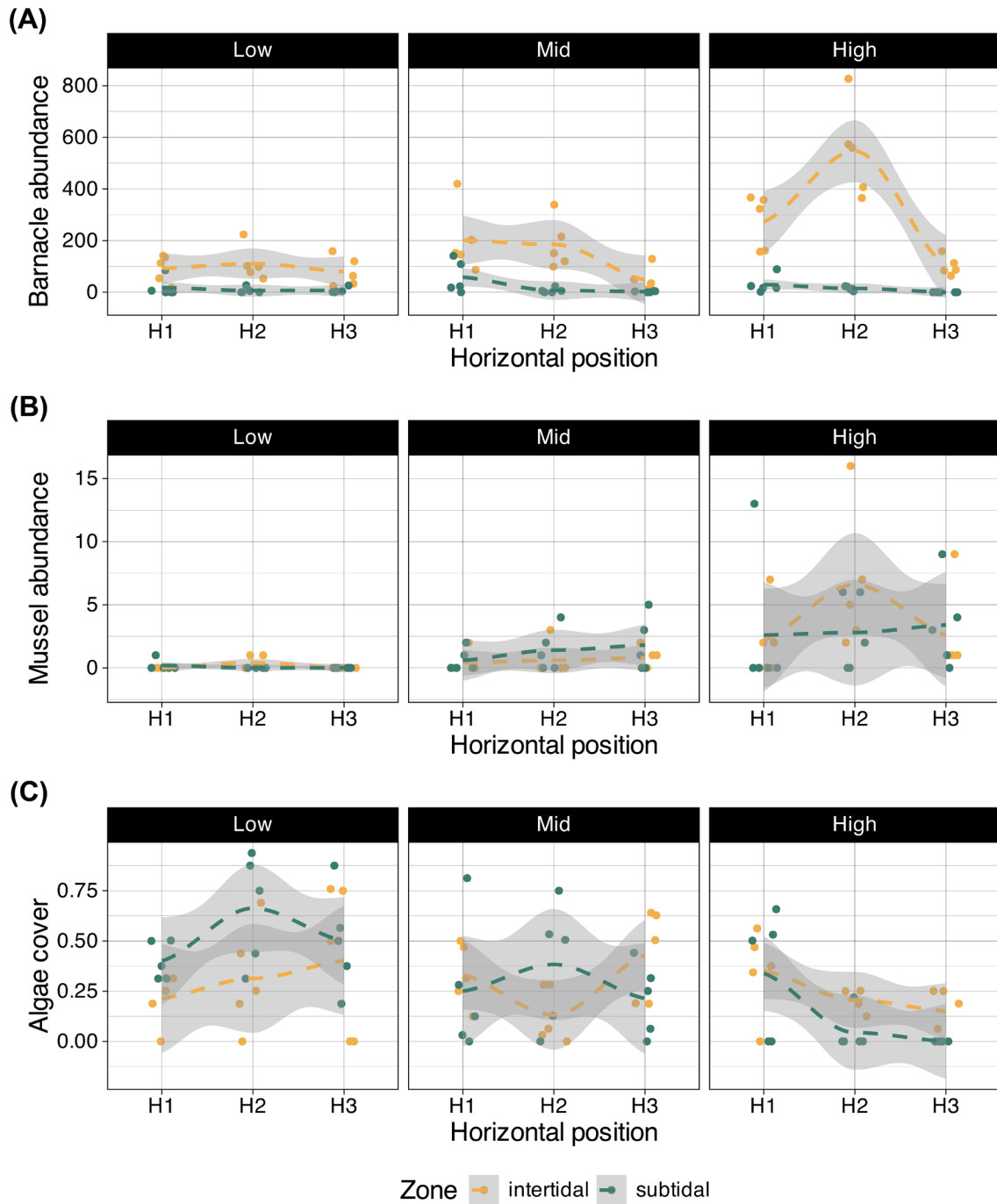


Figure 7. The preferred horizontal positions on the structures for (a) barnacles, (b) mussels and (c) algae. The x-axes indicate the horizontal positions (the outside of the structure is H1, the middle is H3) on the structures as illustrated in Fig. 2. Lines are fitted local polynomial regressions with their 95% confidence intervals indicated in grey. Solid lines indicate a significant preference for horizontal location on the structures, dashed lines indicate no such relation. Individual dots represent individual samples. Orange represents intertidal structures and green represents subtidal structures.

reaching inward-facing surfaces which could limit photosynthesis and consequently restricts algae growth (Schorie et al. 1997, Strain et al. 2020). Our results indicate that within an ecosystem, life-strategy might shape the response to increased structural complexity. We argue that this is a viable topic for future studies to better understand the role of structural complexity in shaping (coastal) communities.

Increasing surface area has species-specific effects

Compensating for the available settlement surface resulted in differing results among taxonomic groups, the response of barnacle, tunicate and anemone densities to complexity differed from mussels. This contrasts the paradigm that increasing surface area is the main driver for any effects of structural

complexity on coastal benthic communities (Matias et al. 2010). After compensating for available surface area, densities of barnacles, tunicates and anemones did not change with complexity. Increasing complexity is correlated with an increase of available settlement space. If competition for space is the limiting mechanism, settlement densities should not be influenced by increasing complexity (Kovalenko et al. 2012). Barnacles, tunicates and anemones may be limited by inter- and intraspecific competition for space (Otsuka and Dauer 1982, Hui and Moyse 1987, Shick 2012), which we hypothesise might explain their response to complexity in our experiment. For mussels however, the structural complexity itself rather than the resulting increased surface area dictated the preference for more complex structures. This agrees with findings by Loke and Todd (2016), who found that structural complexity itself, in combination with structure type, alters community composition by resource partitioning.

Tidal zones and complexity control species diversity

Whereas the overall species diversity in the subtidal zone of the Wadden Sea is higher (Dekker and Drent 2013), we only observed an increase in taxonomic richness with increasing complexity in the intertidal zone. This contrasts Loke and Todd (2016), who only found increasing diversity with complexity on lower (inter)tidal elevations. They attribute this to limited moisture retention and conclude that recruitment was limited by physical stress. We propose that in our experiment, the niche of some predominantly subtidal species was extended into the intertidal on the most complex structures, because structural complexity alters the local abiotics. The added complexity provided shelter from drought and temperature stress in the intertidal zone, which is not relevant in the subtidal (Navarro-Barranco et al. 2022). However, a comparable taxonomic richness does not imply uniform communities, as complexity can impact community composition regardless of the biodiversity (Chee et al. 2021). Though abundances of tunicates and anemones did not differ among intertidal treatments, they were not found on the low complexity structures at all in this zone. Contrarily, the positive effect of complexity for barnacles might have been disguised by increased predation pressure in the subtidal zone (Buschbaum 2002). This aligns with the results from Strain et al. (2021), who conclude that although structural complexity of coastal structures can create variation in stressors, local unfavourable abiotic conditions may outweigh the benefits of added complexity.

Gradients within structures

Even though complexity could interfere with stressors such as desiccation, hydrodynamic action, or sedimentation, only barnacles had a preferred position on the structures. Structural complexity creates microhabitat variability in various terrestrial and aquatic environments, which can structure communities horizontally and vertically. For example, vertical structure increases shelter and reduces intraguild predation in

in spider communities on macrophytes (Cunha et al. 2012). Likewise, vertical gradients alter resource availability and predator visibility which dictates fish communities in coral reefs (Helder et al. 2022). The preferred middle vertical position of intertidal barnacles was unaffected by complexity. The abiotic conditions could be too unfavourable at the bottom and the top to be mediated by the structural complexity, with high sedimentation and current velocities respectively. Barnacle's preference for horizontal positions was mediated by niche creation through structural complexity. They had no preference on the least complex structure, where there was patterning on structures with increased complexity. We hypothesise that this preference for the central horizontal positions could be shaped by a tradeoff between feeding and predation risk (Johnston et al. 2012).

Implications for practice

There has been increasing interest in the use of structural complexity for ecosystem restoration or improving ecological value of infrastructure (O'Shaughnessy et al. 2019, Yanovski and Abelson 2019). Especially in degraded or homogenised areas, adding structural complexity might improve recovery of target species and increase biodiversity (Yanovski and Abelson 2019). Future studies using standardised structural complexity, potentially using 3D-printing, could elucidate the role of complexity across ecosystems and the interaction with abiotic or biotic (e.g. predation or competition) stressors. We found that the effect of structural complexity varies among taxonomic groups and between tidal zones. Additional experimental studies could assess if the mechanisms we hypothesise indeed determine the different reactions to structural complexity. Especially mussels, a foundation species that forms structurally complex and biodiverse reefs in both the subtidal and intertidal of coastal systems (Saier 2002), benefit from structural complexity regardless of their tidal elevation. This knowledge can be leveraged by for example the mimicry of complexity observed in natural reefs to facilitate settlement and the positive feedback that this foundation species would normally provide (Temminck et al. 2021). While this principle is already applied in ecosystem restoration research in forests, lakes and in coastal zones (Eckert et al. 2021, Meerhoff and de los Angeles González-Sagrario 2022, Nauta et al. 2023), more insight in the mechanisms that underlie the species responses to complexity may further improve the success of restoration projects. As such, tailored knowledge about the effects of structural complexity in different structurally complex ecosystems, such as marine coastal systems to freshwater systems and forests, can therefore help to conserve or restore these ecosystems.

Acknowledgements – We would like to thank skippers J. Visser of the HA2 Pescador and W. J. Boon of RV Stern for helping us with the structure placement and collection. We thank M. Sikkema, J. ten Horn and L. Kleine Schaars for assistance in the field and in the lab. **Funding** – This study is part of project “Waddentools: habitat heterogeneity” (also known as “Waddenmozaïek”), a

collaboration between the University of Groningen, the NIOZ Royal Netherlands Institute for Sea Research and Natuurmonumenten. The project is registered under reference number WF2018-187059, and funded by the Waddenfonds, the Directorate General for Public Works and Water Management (Rijkswaterstaat) and the provinces of Noord-Holland, Fryslân and Groningen.

Permits – Permission to execute the experiment here was granted by the Province of Fryslân and Rijkswaterstaat (Nature Conservancy Act: WNb01597179, Dutch Water Act: RWSZ2021-00008229).

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Data availability statement

Data are available from: <https://doi.org/10.25850/nioz/7b.b.rh> (Witte et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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