







RESEARCH ARTICLE

Enhancing ecological complexity in soft-bottom coastal ecosystems: the impact of introducing hard substrates

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Coastal ecosystems globally face pressures, with natural coastal habitats being replaced by engineered structures. While hard structures for navigation-purposes and coastal defense can negatively impact native communities, they can also be applied in ecological restoration as artificial reefs. This way substrates may facilitate establishment of biogenic (shellfish) reefs and provide habitat heterogeneity in soft-sediment ecosystems. In a 1.5-year experiment, we introduced six different types of natural or biodegradable hard substrates in a subtidal soft-sediment system. We compared the substrates with surrounding soft sediment and evaluated differences among substrate types using biodiversity indices, community composition analyses, and food web indicators. This offers a comprehensive understanding of how the introduced hard substrates affect ecosystem complexity. Overall ecological complexity indicators were higher in the second year of the experiment. We found a significant increase in species richness, community composition, and link density (number of feeding interactions per species) on hard substrates compared to the surrounding sediment. However, Shannon diversity index and food web connectance (measure of food web saturation) did not differ between substrates and the surrounding sediment. Although differences among types of hard substrates were small, certain species were uniquely associated with specific substrates with wood and granite performing best. While there was no establishment of epibenthic shellfish reefs within 1.5 years, we conclude that introducing hard substrates effectively enhances ecological complexity in soft-bottom coastal ecosystems within that timeframe. We recommend the use of substrates with a historical ecological relevance in the system for scaling up introduction of substrates for ecological restoration.

Key words: (artificial) reef, biodiversity, ecological restoration, food web, hard substrates, multivariate community analyses, soft-sediment systems

Implications for practice

- Introduced hard substrates in a soft-sediment system have higher species diversity, more trophic connections per species and a different ecological community composition than the surrounding sediment.
- The introduction of hard substrates at the small spatial scale of our experiment did not facilitate epibenthic shellfish reef formation in our subtidal study system.
- There were no functional differences, as measured by multivariate community analyses and food web connectivity and link density, among the introduced substrates.
- Considering the minor differences among the substrate types, choosing substrates with a historical or natural relevance to the system in which they are applied may be favorable for coastal restoration.

Introduction

Many coastal ecosystems worldwide are degrading, largely due to anthropogenic stressors (Lotze et al. 2006). Natural coastal habitats such as intertidal flats, seagrass beds, and natural rocky shores are gradually replaced by human-made structures for coastal defense (Reise 2005; Marzinelli et al. 2009). These anthropogenic hard substrates may replace natural substrates,

soft sediments, or biogenic reefs and can have adverse effects on the functional redundancy and biodiversity of coastal systems (Momota & Hosokawa 2021). On the other hand, hard substrates are deployed as artificial reefs in coastal systems worldwide for ecosystem restoration to counter decline in marine biodiversity (Vivier et al. 2021). Different types of hard substrates are applied to host or restore different communities (Bulleri & Chapman 2010; Wetzel et al. 2014). The installation of artificial reefs can, e.g. be used to enhance fish communities, coral reefs, kelp forests, or shellfish reefs (Seaman 2007).

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The hard substrates attract substrate-associated species, which could lead to cascading effects for other species groups (Krone et al. 2013). Especially in naturally more structurally homogenous areas, such as soft sediment systems, biogenic and geogenic reefs can provide spatial habitat heterogeneity (Munguia et al. 2011; van der Ouderaa et al. 2021). In soft-sediment environments, introduction of settlement substrate can, e.g. be applied to stimulate formation of native shellfish reefs (Berszoa Hernández et al. 2018; Goelz et al. 2020; Temmink et al. 2022). However, the physical properties of a substrate can structure the ecological community that settles on it (Sedano et al. 2020). Therefore, different types of substrate structures could have different restoration outcomes.

While comparing different types of structures is difficult, the most frequently used methods of comparing ecosystems and their communities are biodiversity measures such as species richness or biodiversity indices (Pereira et al. 2013). These methods mainly look at the number of unique species, but omit their interactions and functioning within the system, which limits their applicability in describing the ecological complexity of the system (McCann 2007; Rombouts et al. 2013). Multivariate community analyses can be used to detect the relative importance of environmental or spatial processes that influence the community composition (Gerwing & Hawkes 2021). These analyses allow comparison of communities of restored or introduced habitats to their surrounding ecosystems by analyzing the species composition (Hewitt et al. 2005). The analysis of trophic networks allows for better understanding of the condition of the food web in ecosystems. Recent studies have shown that using species composition and food web indicators can be effectively used to assess ecological complexity on artificial substrates and biogenic reefs (e.g. van der Zee et al. 2016; Christianen et al. 2017; Nauta et al. 2023). Additionally, the development of epibenthic communities was better expressed through network analyses than biodiversity metrics (Christianen et al. 2017). To understand ecological complexity and the functional effect of ecosystem restoration, it is vital to complement biodiversity indices with metrics of ecosystem functioning such as community composition and food web structure.

In the Wadden Sea UNESCO (United Nations Educational Scientific and Cultural Organization) World Heritage site, human interferences have resulted in considerable changes in the ecosystem and a shift from a rich heterogeneous system to a spatially more homogenous system (Eriksson et al. 2010). Although 44% of the Wadden Sea is classified as subtidal (permanently submerged) habitat, most experimental research has been carried out on the more accessible intertidal flats (Dekker & Drent 2013; Ricklefs et al. 2022). Studies from those intertidal areas have shown that the introduction of hard substrates can enhance epibenthic communities and promote species that are otherwise rare in the soft sediment dominated Wadden Sea (e.g. Wetzels et al. 2014). For example, intertidal hard substrates facilitate shellfish reef formation, which is limited by the availability of a settlement substrate (Smyth et al. 2016; Capelle et al. 2019; Nauta et al. 2023). Both biogenic reefs (such as formed by mussels, oysters, or Sabellaria) as well as geogenic reefs (reefs from non-living materials such as driftwood, glacial erratic stones, riverine pebbles, and dead shell material) were historically and still are to some extent present in the subtidal Wadden Sea (Ens et al. 2007;

Ricklefs et al. 2022). However, the largest share of natural hard substrates in the Wadden Sea has been removed or buried over time, which resulted in a declining availability of natural hard substrates (Franken et al. 2023). Therefore, a current focus in coastal restoration research in the Wadden Sea is how the introduction of hard substrates can be applied to enhance ecosystem functioning and restoration (Dickson et al. 2023). However, the effects of using different types of substrates on the community composition and food web structure and how these develop over time is poorly understood. Additionally, it is unclear if introduction of substrates in subtidal regions has the same desirable effect as in the intertidal areas.

Here, we studied the effects of introducing different types of hard substrate in the subtidal Wadden Sea on benthic communities. We conducted a 1.5-year experiment in which we placed six types of substrates in the subtidal Wadden Sea at 10 different locations (hereafter indicated as blocks). The substrates used were either materials that historically occurred in the Wadden Sea or materials that were specifically designed for ecological restoration. We aimed to compare the communities that settled on different types of substrates with the surrounding sediment and to assess the differences among substrates. This comparison was conducted using biodiversity indices, multivariate analyses, and trophic network analyses. We also assess if there are species that are specifically bound to one type of substrate. We evaluated how adding hard substrate in subtidal areas contributes to the formation of epibenthic shellfish reefs. With this study, we evaluate the effectiveness of introducing hard substrate in soft sediment systems for restoration purposes. We show how to apply multiple indicators for monitoring community development as well as ecological complexity using biodiversity, community composition, and food web analyses.

Methods

Study Area

The experiment was conducted in the Wadden Sea, a UNESCO World Heritage site that is the largest intertidal system in the world. The experiment was placed in the subtidal parts of the Dutch Wadden Sea. Within the subtidal, the locations were selected for bathymetric stability, measured by a maximum difference of 20 cm in bathymetry between 2003–2008 and 2009–2017 (De Kruif 2001). Additionally, the locations needed to be closed for shrimp fisheries to minimize disturbance and had an average depth of -2.24 NAP (mean water level according to Amsterdam Ordnance Datum) (standard deviation [SD] ± 0.70) to be accessible for research vessels. Based on these criteria, the experiment was placed in different gullies in two parts of the Wadden Sea: in the west in the Eierlandse Gat tidal basin and in the east in the Schild tidal basin (Fig. 1). Seven blocks were placed in the western part of the Dutch Wadden Sea, three blocks were placed in the east.

Substrates

To determine the effect of the introduction of different types of hard substrates, six types of hard substrates were used (Fig. 2). Four types of natural substrates that are, and historically have

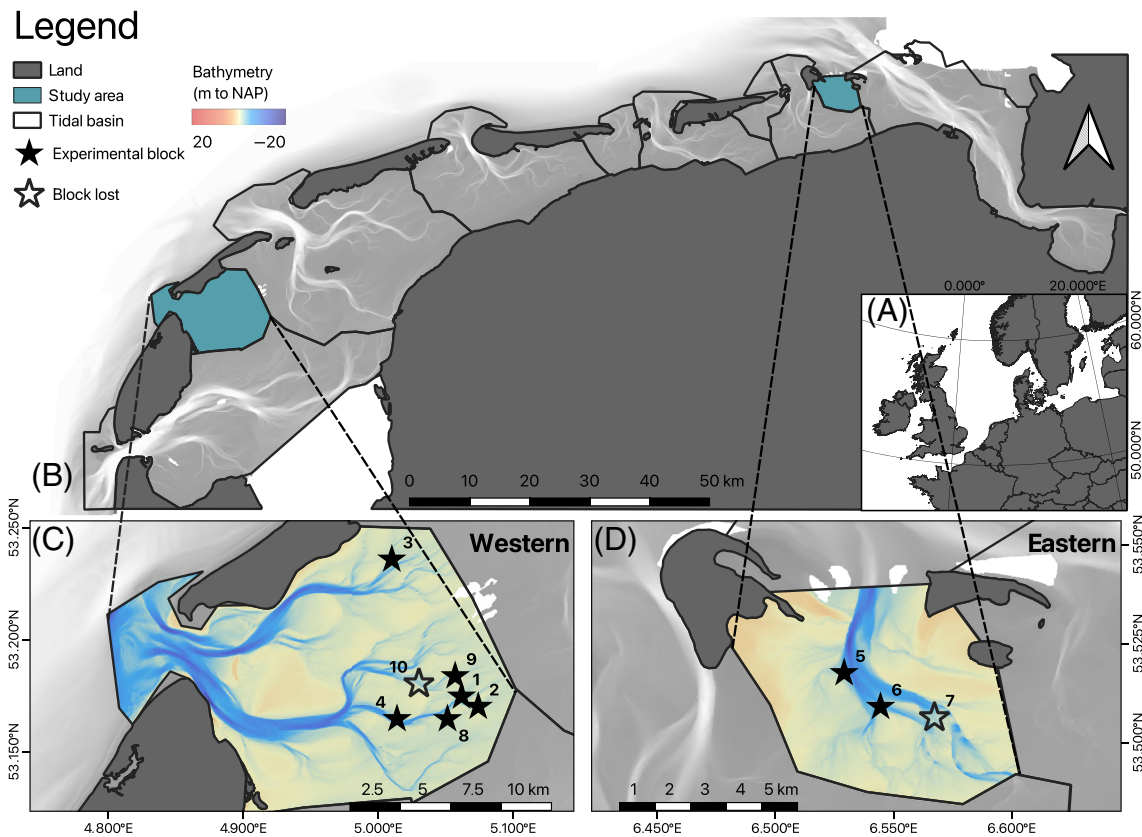


Figure 1. Map showing the study area. (A) a map of North-West Europe where the box indicates the Dutch Wadden Sea. (B) The Dutch Wadden Sea and its tidal basins. The Eierlandse Gat and Schild tidal basin are highlighted in blue. (C) A detail of the Eierlandse Gat tidal basin with the bathymetry. (D) A detail of the Schild tidal basin with the bathymetry. Bathymetry is shown relative to NAP (Amsterdam Ordnance Datum). Black lines indicate the edges of the tidal basins. Stars represent the locations of the blocks of the experiment where filled stars are the blocks that are included in the analyses and the open stars are the blocks that were completely buried under the sediment after only a few months (block 7 and block 10). At each block ($n = 10$), all six substrates have been deployed at the beginning of the experiment.

been, part of the Wadden Sea ecosystem were included in the experiment; bog wood (retrieved from the Wieden National Park) granite cobbles (diameter over 20 cm), pebbles (diameter up to 7.5 cm), and empty cockle shells. Historically, wood was transported to the Wadden Sea via the now closed off rivers and can also be found in the peat layers that lie underneath large parts of the Wadden Sea (Vos 2012; Wohl & Iskin 2021; Franken et al. 2023). Due to influences such as closing off rivers and upstream deforestation, the Dutch coastlines hardly have any driftwood nowadays. Large stones moved by glaciers, known as erratics, were likely exposed on the seafloor in areas where the current velocities were relatively high (Ens et al. 2007; Franken et al. 2023). Anecdotes suggest that many of these have either been fished up or buried by sediment over the last century (Franken et al. 2023). Pebbles and empty shells are frequently found hard substrates in the Wadden Sea (Franken et al. 2023). Additionally, two artificial substrates designed for epibenthic shellfish settlement (BESE [Biodegradable EcoSystem Engineering]-elements[®] and BESE-reef blocks) were tested. Reef-blocks were specifically designed to encourage oysters and have a concrete base with silex boulders covered with the calcareous BESE reef paste. BESE-elements

are mats of biodegradable structures interwoven with coconut fiber rope that were designed to stimulate settlement of mussels as they prefer to settle on fibrous surfaces (Van der Heide et al. 2014; Temmink et al. 2021).

Experimental Setup

The substrates were contained in 1 m² steel cages, to facilitate lifting of the substrates from the seafloor onto the deck of a research vessel. The cages were open on the top, with a stainless-steel mesh on the lowest 10 cm of the sides to contain the substrates (Fig. 2). The cages filled with shell or pebbles had a synthetic cloth on the sides to reduce flow velocities and contain the substrates in the cage. The experiment was designed in 10 blocks with each six cages that were randomly assigned one of the six different types of substrates. A total of 60 cages were deployed in April–May 2020 and were left in the water until November 2021, about 1.5 years. The cages were visited approximately every 4 months to visually inspect if the substrates were still present.

The Wadden Sea is a dynamic system, which unfortunately meant that we lost 20 of the total of 60 cages with substrate over

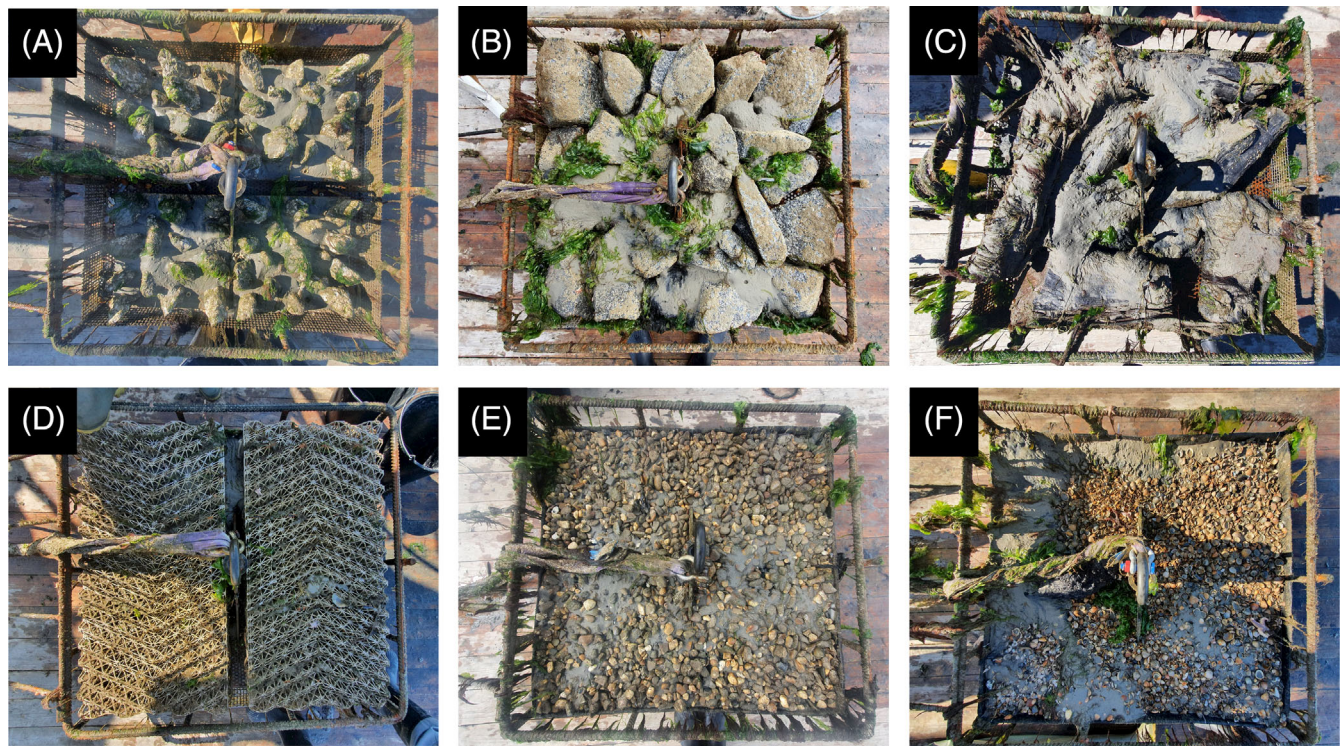


Figure 2. The different types of substrates used in the experiment in the cages at the first surveying in summer 2020. (A) Reef blocks, (B) granite, (C) wood, (D) BESE mats, (E) pebbles, and (F) shell.

the course of the experiment. All cages in block 7 and block 10 were completely buried half a year after placement and were therefore removed in autumn 2020. The cages with shells in block 1 and block 3 were almost completely flushed by autumn 2021, after which we refilled these cages and outplaced them again. The cage with pebbles in block 6 was lost in autumn 2020 and the cage with BESE in block 1 was lost in spring 2021. Additionally, the cages with shells from block 2, block 4, block 6, and block 8 were taken out in spring 2021 because all the shells had been washed away. The cage with shells in block 5 and the cage with granite in block 1 were lost in autumn 2021. Cages that were lost or taken out before the end of the experiment could not be sampled from that moment onwards and were therefore removed and excluded from any further analyses.

Sampling

The cages were surveyed in autumn 2020 (4 months later) and 2021 (1.5 years later) to assess the ecological communities. Before samples were taken, an estimate of the percentage sediment coverage of the cage surface was made. Then, the number of individuals of mobile species larger than 5 cm were identified and counted. Any fish or large invertebrates were released back into the water directly after identification. These individuals were classified as “mobile species.” Samples of the rest of the benthic community were taken subsequently, these are classified as “non-mobile benthos.” To sample the non-mobile benthos, a quarter of the substrate (approximately 0.125 m²) was taken out

of the cage and transferred to a sieve with a 1 mm mesh size, scraped clean, and all benthic life was collected. For sampling the BESE, two cores of 0.018 m² were taken directly next to each other and sieved over a 1 mm mesh sieve. Any sediment in the sampled section was sieved out over the 1 mm sieve. Adjacent sides of the cage were sampled in autumn 2020 and 2021, to account for possible succession of the ecological community in the consecutive sample years. Two box core samples were taken from the middle of each block as soft-sediment control with a total combined surface area of 0.12 m². These samples were also sieved over a 1 mm sieve, separating the sediment and fauna. The macrozoobenthos collected from each sample was fixed in a 6% buffered formaldehyde solution with approximately 2 mg/L Rose Bengal (CAS no. 632-68-8) to stain the proteins in living tissue. Macrozoobenthos was then identified to the lowest possible taxonomic level in the laboratory at NIOZ (Royal Netherlands Institute for Sea Research) on Texel. Densities of marine life were expressed as individuals per square meter to allow for comparisons between the different substrates and control treatments.

Data Analyses

The analyses of different substrates and years were done in several steps. First, differences in sedimentation rate were compared among the six substrate types and between sample years. Then, we compared the benthic communities between years. Next, the benthic communities on the introduced hard substrates were compared to the surrounding soft sediment. In this comparison, the

mobile species were excluded as the chances of catching mobile species with a box core are limited and therefore the numbers of mobile species would be underestimated on the soft sediment. Lastly, we compared differences among the hard substrate types. We assessed if specific species (both non-mobile and mobile benthic species including fish) were especially linked to one of the substrate types. Here, we only included species that were found in at least three samples. We then calculated the fraction of occurrence of the species on the different types of substrates. The 15 species with the strongest link to one specific substrate type will be discussed in more detail. We also assessed densities of reef-building epibenthic shellfish as well as mobile species and fishes on the different types of substrate. Then, we compared benthic communities among the different substrates, where we included mobile benthic species as well as non-mobile benthic species. The benthic communities were compared using three different metrics: biodiversity indices, community composition, and food web metrics.

Biodiversity Indices. To evaluate the benthic biodiversity on the introduced hard substrates and the surrounding sediment, we calculated the species richness and Shannon–Wiener diversity index for all samples. These were compared between the introduced substrates and the surrounding sediment, as well as among the six different types of hard substrates for the two sampling years.

Community Composition Analyses. The species compositions on the different substrates and the controls in the different sampling years were compared using redundancy analyses (RDA) that was restricted by the substrate type and block on Hellinger-transformed species density data. The significance of the model was tested using ANOVA (Analyses of Variance)-like permutation tests. The difference among the six different substrate types was tested using a pairwise permutational multivariate analysis of variance based on distance matrices (adonis by Pedro Martinez Arbizu).

Food Web Metrics. To compare the trophic networks on the different substrates, trophic interactions were derived by performing a literature study. We constructed the interaction matrix that contains all trophic interactions between the over 170 species that were found across all samples. This interaction matrix was subsetted to create a food web for each sample. Macroalgae, zooplankton, phytoplankton sediment particulate organic matter and water column particulate organic matter were added to every sub-interaction matrix to form the basis of the food web. A food web was then created from each adjacency matrix. Two metrics of the food web were compared between the different sample years and among the six types of substrates.

The link density is the average number of links per species (Borst et al. 2018), was calculated as:

$$\text{Link density} = \frac{\text{Total links}}{\text{Number of species}}$$

in which total links are the number of trophic interactions between the species in the community, derived from the

interaction matrix, and number of species the total number of species in the sample.

Connectance is a measure of the saturation of the food web (Dunne et al. 2004), which is calculated as:

$$\text{Connectance} = \frac{\text{Total links}}{\text{Number of species}^2}$$

in which total links are the number of trophic interactions between the species in the community, derived from the interaction matrix, and number of species² the total number of possible interactions in the community.

Statistic Modeling

Statistics were carried out in R4.0.4 & RStudio for Mac, figures were created using ggplot2 and the tidyverse (Wickham et al. 2019; R Core Team 2021). Shannon–Wiener diversity indices were calculated using the vegan package (Oksanen et al. 2022). The adjacency matrices for the food webs were constructed using the igraph package (Csárdi et al. 2024). For plotting purposes, the trophic levels of species were calculated using the NetIndices package (Kones et al. 2009). Sediment coverage, species richness, numbers of mobile species, and fishes were compared among substrates and between sample years using generalized-linear mixed-effect models with a Poisson distribution with the lme4 package (Bates et al. 2015). Shannon–Wiener diversity indices, densities of epibenthic shellfish, link-density, and connectance were compared among substrates and between sample years using linear mixed-effect models with the lme4 package (Bates et al. 2015). The epibenthic shellfish densities were square-root transformed to improve the model fit. The link-density was log-transformed to improve the model fit. Experimental blocks were included as random factor in the models. To determine the significance of the model predictors, “Anova” from the car package was used (Fox & Weisberg 2019). If predictors were significant, post hoc testing of estimated marginal means with false discovery rate (FDR) adjustment was done using the emmeans package to examine which substrates differ significantly (Lenth 2023). In some cases, the FDR-corrected post hoc testing yielded no significant contrasts while model predictors were significant. To highlight such weaker differences, we ran the more lenient Fisher’s Least Significant Difference (LSD) in these cases. The significance of the effect of block (location) on the results is evaluated by comparing Akaike’s Information Criterion (AIC) of models with and without random factor block. This difference is reported as $\Delta\text{AIC}_{\text{block}}$, where a $\Delta\text{AIC}_{\text{block}}$ less than -2 indicates a substantially better model fit and an effect of location. However, we found that even when $\Delta\text{AIC}_{\text{block}}$ greater than -2 , the overall results with or without random factor remained the same. We therefore included the random factor block for every test.

Results

Sedimentation of the Hard Substrates

Average sedimentation differed among blocks, ranging between 28.75 and 81.17% of the cage surface covered in sand.

Sedimentation within blocks also differed greatly, some cages had low sand coverage (<5%) while others in the same block were almost completely covered (>95%). Surface sedimentation was significantly lower on BESE than on all other substrates (-38.38% , $\chi^2 = 181.9$, $p < 0.01$, $\Delta\text{AIC}_{\text{block}} = -528.5$). However, in many blocks, the internal structure of the BESE filled up with sediment, which was not captured with the surface sedimentation cover. Granite, pebbles, and shell had significantly less surface sedimentation than reef-blocks and wood (-23.7% , $\chi^2 = 181.9$, $p < 0.01$). Sedimentation was significantly higher in 2021 than in 2020 ($+25.27\%$, $\chi^2 = 28.44$, $p < 0.01$, $\Delta\text{AIC}_{\text{block}} = -501.9$).

Differences Between Sample Years

In total, 171 non-mobile benthic species and 22 mobile species were found over the duration of the experiment. We found a significant increase in the number of species in our samples between 2020 and 2021 ($+24.0\%$, $\chi^2 = 19.85$, $p < 0.01$). This was the case for all substrates except for shells, where a small decrease was observed (Fig. 3). There was a significantly lower number of mobile species present on the substrates in 2021 than 2020 (-24.4% , $\chi^2 = 5.39$, $p = 0.02$; Fig. S3). Only on wood and granite, more or an equal number of mobile species was found in the second year. There was no significant difference in the number of fish species between the two sample years ($\chi^2 = 3.61$, $p = 0.06$), but there were higher fish densities in 2021 than in 2020 ($+52.6\%$, $\chi^2 = 12.80$, $p < 0.01$; Fig. S3). The community composition differed significantly between the sample years ($F_{[1,86]} = 7.68$, $p < 0.01$; Fig. 3). While there was no difference in link-density between the two sample years ($\chi^2 = 3.14$, $p = 0.07$), the connectance was significantly lower in 2021 than in 2020 on all substrates except for shells (-8.7% , $\chi^2 = 7.19$, $p < 0.01$; Fig. 3).

Substrates Compared to Control

Even though many cages were sanded in, the species richness of non-mobile benthic species was significantly higher on granite, shell, and wood than in the surrounding sediment ($+39.6\%$, $\chi^2 = 40.87$, $p < 0.01$, $\Delta\text{AIC}_{\text{block}} = -58.00$; Fig. 3). The Shannon diversity index did not significantly differ between substrates and control ($\chi^2 = 5.92$, $p = 0.43$, $\Delta\text{AIC}_{\text{block}} = 7.03$; Fig. 3). The non-mobile benthic community composition differed significantly between all six introduced substrate types and the control samples ($F_{[6,86]} = 2.51$, $p < 0.01$; Fig. 3). The fixed terms year, block, and substrate are significant and together explain a substantial amount of variance (31.8% of variation explained by the constrained axes).

There was a significant effect of substrate on link-density of non-mobile benthic species ($\chi^2 = 13.85$, $p = 0.03$, $\Delta\text{AIC}_{\text{block}} = 20.31$; Fig. 3). However, individual contrasts were not significant (p values 0.12) due to the FDR correction. With the more liberal LSD-comparison, granite, wood, and shell have a significantly higher link density than the surrounding sediment ($+25.75$, p values ranging from 0.01 to 0.03). Notable is that the median link density is lower on BESE than in the surrounding

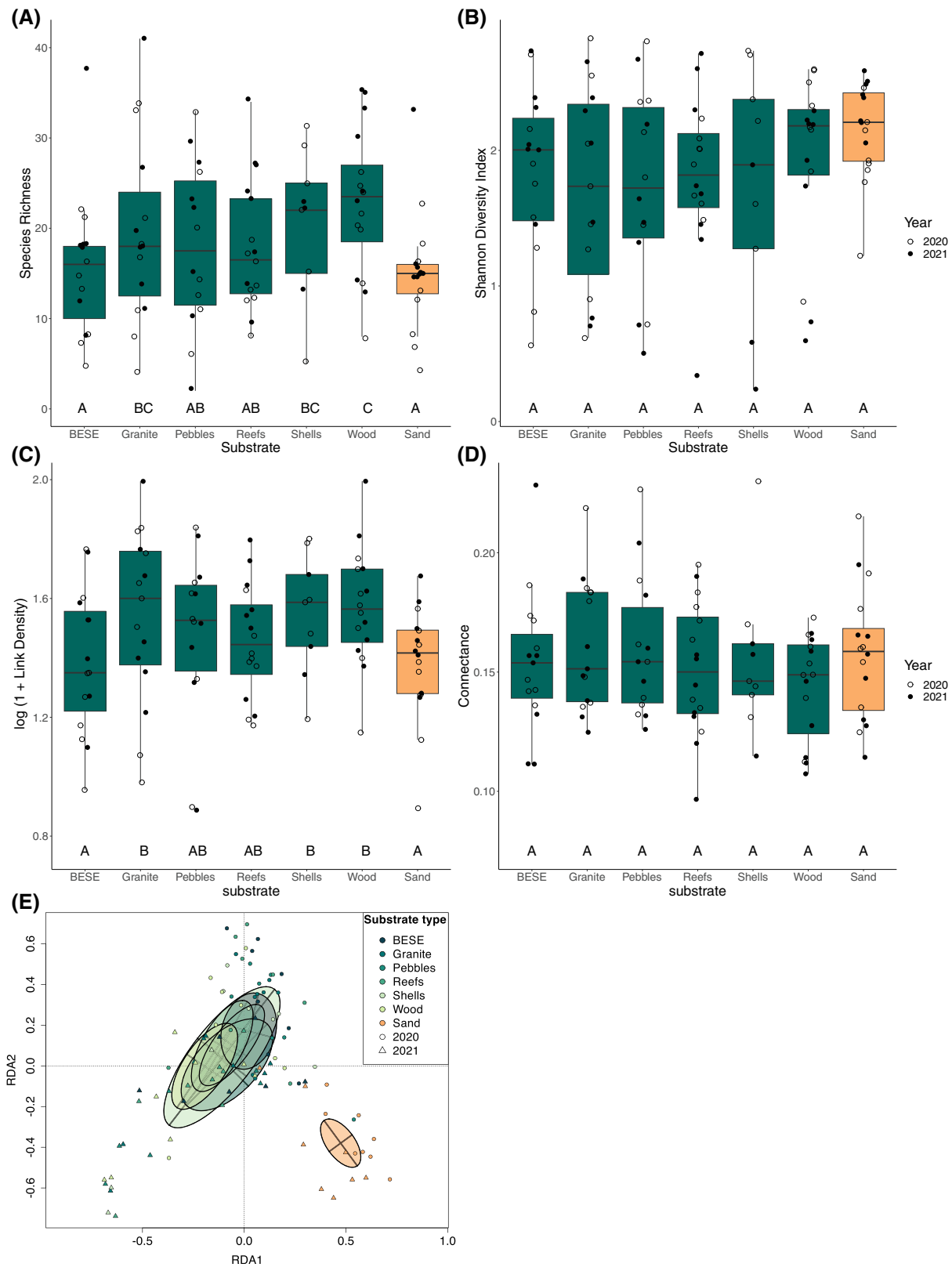
sediment (-8.5% ; Fig. 3). There was no significant difference in connectance of non-mobile benthic species between the introduced substrates and the control sediment samples ($\chi^2 = 4.82$, $p = 0.57$, $\Delta\text{AIC}_{\text{block}} = 65.75$; Fig. 3). Figure 4 shows an example of the difference between a food web on a hard substrate (wood) and the surrounding soft sediment in the same block and sample year. This is an example of how the food web complexity was enhanced on the introduced substrates as compared to the surrounding sediment.

Comparison Among Substrates

Some non-mobile benthic species were found mainly on one specific type of substrate or exclusively in control samples (Table 1). The razor clam (*Ensis leei*), sand digger shrimps (*Bathyporeia elegans* and *B. sarsi*), the bulldozer amphipod (*Urothoe poseidonis*), shovelhead worms of the genus *Magelona*, spionid worms (*Spio martinensis*), and the white cat-worm (*Nephtys cirrosa*) were almost uniquely found in sand. The naval shipworm (*Teredo navalis*) was found exclusively burrowed in wood. The major share of barnacles was found on granite cobbles, while most of the observations of the modest barnacle (*Austrominius modestus*) were on pebbles. Most flat worms (*Platyhelminthes*), gammarids of the genus *Gammarus* and spider crabs (*Macropodia* sp.) were found on granite. More than three quarters of the mud snails (*Peringia ulvae*) were found on the reef-blocks. We only found one oyster (*Magallana gigas*) in one granite sample. Mussel (*Mytilus edulis*) densities on the introduced substrates were generally low and varied much among samples (mean 33.43 individuals/m², SD 55.43 individuals/m²; Fig. S2). Wood had significantly higher mussel densities (mean 80.81 individuals/m², SD 89.39 individuals/m²) than all other substrates except for shells ($+144.4\%$, $\chi^2 = 31.91$, $p < 0.01$, $\Delta\text{AIC}_{\text{block}} = -14.03$).

There was a significant difference in the number of mobile species on the six different types of substrate ($\chi^2 = 22.31$, $p < 0.01$, $\Delta\text{AIC}_{\text{block}} = -7.46$; Fig. S3). Shells had a significantly lower number of mobile species than BESE, granite, reef-blocks, and wood (-50.1%) and pebbles had a significantly lower number of mobile species than granite and wood (-43.6%). There was a significant effect of substrate type on the fish species richness ($\chi^2 = 11.53$, $p = 0.04$, $\Delta\text{AIC}_{\text{block}} = 0.70$; Fig. S3). BESE, granite, and wood had the highest fish diversity and shells the lowest (-73.0%). However, individual contrasts were insignificant (p values ranging from 0.06 to 0.08) due to the FDR correction. With the more liberal LSD-comparison, these differences were significant (p values ranging from ≤ 0.02). The different substrate types attracted significantly different fish densities ($\chi^2 = 75.45$, $p < 0.01$, $\Delta\text{AIC}_{\text{block}} = -143.72$; Fig. S3). Fish densities were significantly higher on BESE, granite, and wood than on reefs, shells, and pebbles ($+382.9\%$). The fish densities on reef-blocks were also significantly higher than on shells and pebbles ($+133\%$).

To compare among the six different types of substrate, we included mobile species as well as the non-mobile benthic species (Fig. S1). Species richness was significantly higher on granite, shells, and wood than on BESE, and species richness on wood was significantly higher than on pebbles and reefs



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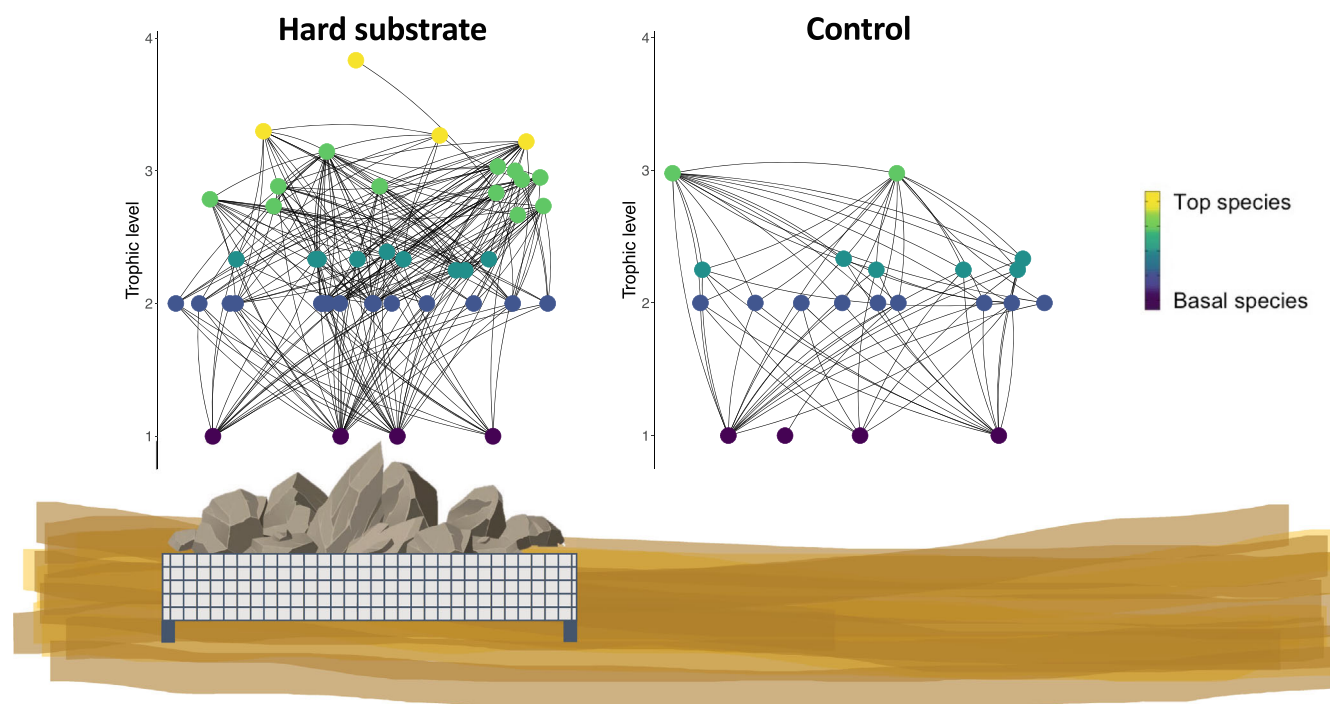


Figure 4. Example of two food webs, hard substrate on the left (wood block 3 in 2021) and control on the right (sand block 3 in 2021). The food webs are structured vertically by trophic level with the lowest levels at the bottom. Colors indicate the trophic level of the nodes (species).

(+32.0 and 27.1%, respectively, $\chi^2 = 26.91$, $p > 0.01$, $\Delta\text{AIC}_{\text{block}} = -55.41$; Fig. S1). There were no differences in Shannon diversity index ($\chi^2 = 1.45$, $p = 0.92$, $\Delta\text{AIC}_{\text{block}} = 2.25$) and community composition ($F_{[5,71]} = 1.14$, $p = 0.20$, 32.3% of variation explained by constrained axes) among the different substrates (Fig. S1). Link density ($\chi^2 = 5.26$, $p = 0.39$, $\Delta\text{AIC}_{\text{block}} = 17.75$) and connectance ($\chi^2 = 6.65$, $p = 0.25$, $\Delta\text{AIC}_{\text{block}} = 58.49$; Fig. S1) did not differ significantly among the different substrate types.

Discussion

To counter the decline in marine biodiversity, the introduction of hard substrates as artificial reefs is applied in coastal systems worldwide to enhance different ecosystems such as fish communities, corals, and oyster reefs (Baine 2001; Goelz et al. 2020; Vivier et al. 2021). In this study, we tested the effectiveness of six types of hard substrate in enriching the subtidal areas of the Wadden Sea. We found that the introduction of hard substrates increased species richness, altered the composition of benthic

species community, and enhanced the benthic food web complexity compared to the surrounding soft sediment. Interestingly, there were only minor differences among the substrate types. Our results suggest that adding hard substrates to a subtidal soft-sediment system can be a valuable tool for recovering habitat heterogeneity and enhancing ecosystem functioning, but that the type of substrate used is less important.

We found minor differences among the six different substrates in our experiment. Certain taxa were specifically associated with one type of substrate, although the community composition did not differ significantly between substrates. Barnacles, e.g. preferred stony substrates whereas the naval shipworm was exclusively found in wood. Sessile species preferentially settle on certain substrate materials, therefore characteristics of different substrate types could shape the species community (Ushiyama et al. 2016). There are many suggested explanations for species-specific substrate preferences such as surface properties, substrate complexity, chemical cues, and microbial film development (Rodríguez et al. 1993; Jenkins & Marshall 2009). Wood, granite, and shells had a higher species richness than BESE, which was

(Figure legend continued from previous page.)

Figure 3. Comparison of the non-mobile benthic communities on different types of substrate and the controls for the two sample years. (A) Species richness. (B) Shannon diversity index. (C) Log-transformed link density. (D) Connectance of the food web. Jittered dots represent individual samples. Open dots represent samples taken in 2020, filled dots are samples taken in 2021. Green boxes are the introduced substrates, the orange boxes are the control samples from the soft sediment surrounding. The letters indicate statistical groups where substrates that share a letter do not differ significantly, for panels (A), (B), and (D) with a FDR correction, for panel (C) with an LSD correction. (E) RDA plot showing the community composition on the different types of substrates and the control with shaded 95% CI hulls. The scattered datapoints each represent one sample. Dots are samples taken in 2020, triangles are samples taken in. The colors indicate the types of substrates, where green shades are the introduced hard substrates and orange is the sediment control.

Table 1. Species with Latin and common names that are dominantly found on one type of substrate. The column “mobile” indicates if the species is found in the benthic non-mobile sample or in the mobile species survey. “No. of cages” indicates the number of cages in which the species is found. Total abundance shows how many individuals of the species are found and the respective fractions show in which proportions the species are found on different substrates. NA (Not Applicable) Orange highlighted cells indicate the substrate on which the highest fraction of a species is found.

Species name	Common name	Mobile species	No. of cages	Total abundance	BESE fraction	Granite fraction	Pebble fraction	Reefs fraction	Shells fraction	Wood fraction	Sand fraction
<i>Teredo navalis</i>	Naval shipworm	No	5	2306	NA	NA	NA	NA	NA	1.00	NA
<i>Bathyporeia elegans</i>	Sand digger shrimp	No	3	84	NA	NA	NA	NA	NA	NA	1.00
<i>B. sarsi</i>	Sand digger shrimp	No	3	118	NA	NA	NA	NA	NA	NA	1.00
<i>Ensis leei</i>	Atlantic razor clam	No	4	108	NA	NA	NA	NA	NA	NA	1.00
<i>Urothoe poseidonis</i>	Bulldozer amphipod	No	12	1537	0.01	NA	NA	NA	0.01	0.02	0.96
<i>Austrominius modestus</i>	Modest barnacle	No	8	2686	NA	0.06	0.89	0.01	0.01	0.01	0.02
<i>Platyhelminthes</i>	Flatworms	No	4	410	NA	0.86	NA	NA	0.12	0.02	NA
<i>Magelona</i>	Shovelhead worms	No	3	118	0.14	NA	NA	NA	NA	NA	0.86
<i>Spio martinensis</i>	Spionid worm	No	15	689	0.05	0.02	NA	0.03	0.05	NA	0.85
<i>Sessila</i>	Barnacles	No	12	13,506	NA	0.85	0.05	0.02	0.00	0.06	0.02
<i>Nephtys cirrosa</i>	White catworm	No	9	336	NA	NA	0.05	0.05	0.05	NA	0.85
<i>Magelona johnstoni</i>	Shovel head worm	No	6	169	NA	NA	NA	0.10	0.10	NA	0.80
<i>Peringia ulvae</i>	Mud snail	No	4	235	NA	0.07	0.15	0.78	NA	NA	NA
<i>Gammarus</i>	Gammarid amphipods	No	4	202	NA	0.75	NA	0.17	NA	NA	0.08
<i>Macropodia</i> sp.	Spider crabs	Yes	18	72	0.03	0.74	0.05	0.14	0.01	0.03	NA

designed for ecosystem restoration. Wood has been used as a reef material in freshwater and marine systems, initially mainly to attract fish (Prince et al. 1977; Ito 2011). Shell material has been widely applied in restoration projects, targeting mainly oysters and mussels (Berssoza Hernández et al. 2018; Benjamin et al. 2022). Granite has been suggested as a suitable material to enhance coastal engineering structures passively as it can facilitate bivalves and gastropods (MacArthur et al. 2019; ter Hofstede et al. 2024). High species richness on shells was caused by a large diversity of non-mobile benthic species, indicated by the low mobile species richness. However, this result might be biased because only three shell-cages remained, in those areas that were suitable for the shell substrate with potentially a higher-than-average species richness. Interestingly, wood attracted most shellfish in our experiment rather than the BESE products, which have been designed and applied for this purpose (Nitsch et al. 2021; Temmink et al. 2021; Nauta et al. 2023). However, due to high complexity and available interstitial space, BESE as well as granite and wood and reefs attracted high numbers of mobile species and fish (Gilby et al. 2021). These differences among substrates could lead to a difference in community and food web structure on longer timescales than the 1.5-year timespan of this study.

By the end of the second year of our experiment, the communities on the introduced hard substrates were still developing. This was indicated by an increase in benthic species richness and link density, decreasing connectivity, as well as increasing fish densities on the hard substrates between the two sample years. Hard substrate communities have been shown to develop up to decades after introduction of hard substrates. For example: shellfish reefs on hard substrates in Virginia were still developing after a decade, whereas epibenthic communities on artificial reefs in the Mediterranean have been shown to change up to 5 or even 20 years (Relini et al. 1994; Nicoletti et al. 2007; Smith et al. 2022). In line with our observations, other studies following the effects of

artificial reefs on fish communities show steady increases in abundance over time (e.g. Bombace et al. 1994). Especially reefs with a complex structure can attract high fish abundances and diversity (Charbonnel et al. 2002; Gratwicke & Speight 2005). We also observed higher fish densities on substrates with more hiding spaces (wood, granite, and BESE), while pebbles and shells were unattractive for mobile species.

In the intertidal Wadden Sea, that fall dry during low tide, the absence of hard substrate is a limiting factor for formation of shellfish reefs (Nauta et al. 2023). Therefore, (re-)introducing hard substrate is a successful method of facilitating shellfish reefs (Commito et al. 2014; Goelz et al. 2020). However, the introduction of hard substrates in this subtidal experiment did not attract high settlement of reef-building shellfish. In the mussel fisheries sector, densities of 150 g of mussels/m² are typically considered a subtidal reef (Smaal et al. 2013). Reef densities over 100 g of mussels/m² could be considered a functional mussel reef, because they collect significantly more mussel spat than lower densities (Smaal et al. 2013). Although we did not weigh the mussels in our experiment, the mussels found were small. Therefore, densities were far below either definition of a reef. This implies that introduction of substrates alone on the spatial and temporal scale of our experiment is not sufficient to start a shellfish reef in the subtidal areas of the Wadden Sea. de Paoli et al. (2015) suggest hydrodynamic conditions caused a lack of persisting mussel reefs in their experiment. In our case, high sedimentation could have decreased the available settlement substrate for epibenthic shellfish. A larger setup with more elevation than the one we used could be more suitable for the dynamic conditions in the Wadden Sea. However, our substrates also attracted large numbers of species that predate on shellfish such as crabs and starfish. These predators could have hampered reef formation, as predation limited dispersal and settlement of epibenthic shellfish into subtidal areas in other study systems (Rilov & Schiel 2006; Johnson & Smee 2014).

There was a large variation among blocks, for which we compensated in our statistical models. However, this highlights the importance of the local environment as well as the scale of the setup when introducing hard substrates. Sedimentation was higher in the second year of our experiment, and our experimental setup would possibly have been buried on longer timescales. The loss of 30% of our experimental units over 1.5 years emphasizes the importance of well-informed site selection. Although bathymetric stability was a criterion in our selection procedure, 2 out of 10 blocks were clearly too dynamic. Recent advancements on sediment stability estimates, such as the Terrain Ruggedness Index (Meijer et al. 2022), could improve results in the future. To ensure availability of the hard substrates, height above the sediment as well as structural complexity of the substrate are important to consider (Wilhelmsson et al. 2006; Dickson et al. 2023).

We evaluated ecological complexity by comparing taxonomic diversity, community composition, and food web indicators. Incorporating these metrics in the monitoring of ecosystem restoration, helps to anticipate the impact on both biodiversity and functioning of the ecosystem (Pereira et al. 2013; Dajka et al. 2022). Assessing functionality such as species composition or food webs will give more insight in the ecosystem resilience than metrics like species richness (Bowker et al. 2021; Nauta et al. 2023). Similar to our results, introduction of substrates in the intertidal Wadden Sea enhanced the community composition as well as food web complexity to levels comparable to natural shellfish reefs (van der Zee et al. 2015; Christianen et al. 2017; Nauta et al. 2023). Other studies found differing community composition among substrates, dependent on the availability of interstitial space (Callaway 2018). While we found differences in ecological complexity between the introduced substrates and the surroundings, we did not find functional differences among the six substrate types. This indicates that although hard substrate introduction increases the ecological complexity, there might be no functional difference among different substrate types in our soft sediment study system.

Hard substrate availability, rather than substrate type, seems crucial for benthic communities, alternative considerations might become more important. Cost, or practical concerns should be considered for restoration efforts. Because it is stable, easy to build with and relatively cheap, and efficient when applied with a high surface roughness, concrete is a frequently used substrate (Vivier et al. 2021). However, concrete has a relatively high environmental impact, which has led to the development of more sustainable concrete mixtures (e.g. Perkol-Finkel et al. 2018; Kong et al. 2022). Elsewhere, biodegradable materials have been applied in coastal restoration to overcome settlement thresholds, where the reef community will take over when the structure degrades (Nitsch et al. 2021; Nauta et al. 2023). Using these structures to mimic emergent traits of communities can be a successful way to enhance restoration success (Temminck et al. 2020, 2021). However, natural substrates might be the best option as they have been shown to promote the settlement of native species, whereas artificial substrates host more alien epibenthic species (Tyrrell & Byers 2007; Buschbaum et al. 2012). In our study, wood seemed to be a favorable substrate and it is perhaps best-suited for ecosystem

restoration because of its historical relevance in soft-sediment coastal systems. In fact, Dickson et al. (2023) show that reefs built out of trees enhance benthic as well as fish communities, thereby enhancing ecosystem heterogeneity. This way, innovative use of innocuous natural materials could be a valuable ecosystem restoration tool that enhances benthic and mobile communities that depend on hard substrates.

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Supporting Information

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

Figure S1. Comparison of all non-mobile and mobile benthic species combined on the different types of substrate for the two sample years.

Figure S2. The mussel densities (square-root transformed) on the different types of substrates for the two sample years.

Figure S3. Comparison of mobile species and fish on the different types of substrate for the two sample years.

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