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RESEARCH ARTICLE

Biodegradable artificial reefs enhance food web complexity and biodiversity in an intertidal soft-sediment ecosystem

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Abstract

1. Reef-forming species form integral aspects of coastal ecosystems, but are rapidly degrading world-wide. To mitigate these declines, nature managers increasingly rely on the restoration of habitat-structuring, reef-forming species by, for example, introducing artificial reefs that may directly function as complex reef habitat. Since the use of biodegradable structures to restore biogenic reefs is becoming a popular technique, its effectiveness as reef habitat must be assessed. Therefore, we examine the trophic complexity on experimental large-scale biodegradable artificial reefs using food web network analysis.
2. We placed biodegradable artificial reefs on soft-sediment intertidal flats in the Dutch Wadden Sea in a large-scale (~650 m) and 2.5-year-long experiment. We compared food web networks and biodiversity indicators between biodegradable reefs and bare controls and quantified species composition inside and near the artificial reef community to assess the expansion of the reef community.
3. During 2.5 years, we observed that artificial reefs changed food web networks compared to bare controls: in species richness (+76%), link density (the number of interactions per species; +15%) and the fraction of basal species (species of lowest trophic level; +40%), but lowered the connectance: the realized fraction

of all possible links between species (−33%). Their effects on food web networks increased over time with a higher species richness (+22%) and more complex food web (link density +13%) on the artificial reef 2.5 years after deployment compared to 1.5 years. However, the effects of the reefs did not extend beyond the reef structures; the species composition and biodiversity of macrozoobenthos near the reefs were comparable to the control.

4. *Synthesis and applications*. This study shows that biodegradable artificial reefs offer an effective tool for the restoration of food web complexity and biodiversity of intertidal soft-sediment systems. However, application needs to be carefully considered as the reef-building species did not expand beyond our structures, despite the ambitious spatial extent of this experiment. Therefore, we recommend restoration practitioners to design artificial reefs in such a way that they generate ecosystem connectivity (facilitation of higher trophic levels) and biogeomorphological effects on a landscape scale (reef expansion beyond the structures).

KEYWORDS

artificial reefs, biogenic reefs, coastal restoration, ecological networks, food web complexity, foundation species, mussel, self-facilitation

1 | INTRODUCTION

Biogenic reefs form biodiversity hotspots that facilitate trophic interactions in coastal ecosystems world-wide (Kent et al., 2017; Risk, 1972). Examples include reef-building corals, bivalve reefs and tube worm reefs that facilitate diverse communities with many trophic levels such as wading birds, fish and invertebrates (de Smet et al., 2013; Mcafee & Bishop, 2019; Risk, 1972). These reefs that are created by living organisms facilitate trophic interactions by providing habitat (substrate complexity and attachment surface) for lower trophic levels, and by increasing food sources for higher trophic levels (Brown et al., 1997). As such, these reef-building organisms can be considered foundation species since they significantly modify their environment and restructure the ecosystem (Angelini et al., 2011). However, biogenic reefs and its associated trophic complexity have strongly declined globally as a result of human activities such as harvesting, physical disturbance, coastal development and pollution (Beck et al., 2011; Cook et al., 2013; Zu Ermgassen et al., 2020). Hence, scientists, managers and conservationists are jointly aiming to compensate these losses by means of ecosystem restoration, conservation measures and by mitigating the effects of human activities on biogenic reefs (Zu Ermgassen et al., 2020).

Restoring reef functionality can be achieved by two approaches that are commonly applied simultaneously: (1) by initiating the growth of a biogenic reef through transplanting reef-building species (e.g. oysters, coral fragments; Schulte, 2012) and/or (2) by deploying spatially complex artificial reefs to bare coastal habitat (Jensen, 1997; OSPAR, 2013). Ideally, deployment of complex artificial reefs would result in the establishment of reef-building species that initiate self-facilitating mechanisms. These self-facilitating species often generate positive feedbacks that stimulate their own survival and growth (Schotanus et al., 2020). For example, mussel banks create greater resistance against hydrodynamic forces through grouping into large and dense aggregations (Schotanus et al., 2020; Temmink et al., 2021; Walles et al., 2016) and create favourable establishment conditions by providing a settlement substrate in the form of a mix of fibrous (i.e. byssus threads) and hard (i.e. shell) substrates (Schotanus et al., 2020). Promoting self-facilitation mechanisms has proven to be successful for the restoration of natural biogenic reefs (Schotanus et al., 2020; Walles et al., 2016) and mimicry with artificial reefs (Temmink et al., 2021).

Although the use of permanent artificial reefs to enhance trophic complexity is a millennia old concept (Reeder-Myers et al., 2022), novel restoration techniques to facilitate habitat building species have been emerging in recent years (de Santiago et al., 2019). However, these restoration techniques that use concrete or plastic come with the downside of high carbon emissions through manufacturing and transport or plastic pollution (Heery et al., 2017; Walters et al., 2022). Therefore, recent restoration projects advocate biodegradable, nature-based approaches that are more environmentally friendly than the artificial reef structures previously used. One of these technique novel techniques is the use of biodegradable structures that kick-start shellfish reef settlement (Gilby et al., 2021; Howie & Bishop, 2021; Temmink et al., 2021). In contrast, reef restoration approaches that use concrete or plastic also offer habitat to reef-building species, but remain in the environment for decades or longer (Howie & Bishop, 2021). Therefore, nature-based restoration techniques are temporary measures, as they temporarily help to overcome establishment thresholds, then biodegrade and leave no legacy of waste.

Recent studies have described that the use of ecosystem-level indicators (i.e. food web networks) is effective in monitoring trophic complexity on biogenic reefs (Borst et al., 2018; Christianen et al., 2016; Dunne et al., 2004; van der Zee et al., 2016). With simple food web metrics such as species richness (S), link density (L) and connectance (realized fraction of all possible links: L/S^2), important differences in food web complexity can be captured that would possibly not emerge from classic measures such as species richness, Shannon–Wiener diversity and Evenness (Christianen et al., 2016). For example, large, complex food webs are characterized by a high number of species and link densities (Williams & Martinez, 2000). In contrast, a lower connectance is found in larger food webs because of a higher species richness and consequently a lower probability of high saturation of all possible links (Borst et al., 2018; Dunne et al., 2004). Furthermore, trophic levels are indicated by the fraction of basal (species without prey in the food web (e.g. plants, algae)), intermediate and top species (species without consumer; Dunne et al., 2004; Williams & Martinez, 2000). As such, food web network analyses are needed to gain a better understanding of complex trophic interactions on biogenic reefs.

The use of biodegradable structures to restore biogenic reefs is becoming a popular technique and has proven to be successful in facilitating higher trophic levels (Gilby et al., 2021; Howie & Bishop, 2021; Walters et al., 2022). However so far, the effect of this biodegradable restoration technique on food webs and biodiversity is unknown. In addition, landscape-scale experimental testing of artificial reefs is poor and current studies of artificial reefs that investigate impacts on food webs focus on biodiversity and ignore impacts on the structure of the food web network. Therefore, we aimed to examine biodiversity and complexity of the food web network in biodegradable artificial reef structures that were geared towards the initiation of a self-facilitating shellfish reef in a soft-sediment intertidal ecosystem. To do so, we conducted a 2.5-year long large-scale restoration experiment (650 m) using bare controls and biodegradable artificial reefs, constructed on the intertidal flats of the Dutch Wadden Sea. The goal of our biodegradable reefs was to temporarily mimic key traits of adult mussel reefs *Mytilus edulis*, to kick-start the establishment of mussel recruits by providing attachment substrate, predation shelter and by reducing hydrodynamics (Temmink et al., 2022). The idea is that the structures, Biodegradable Ecosystem Engineering Elements (BESE-elements, BESE Ecosystem Restoration Products, Culemborg, The Netherlands), are designed to decompose once mussels mature so that the resulting reef can thus self-facilitate its own survival and support biodiversity and food web complexity (Temmink et al., 2021). Subsequently, we examined food web complexity between two different communities: artificial reef and bare controls.

We expected that our artificial reefs would increase food web complexity, through higher species richness (S), higher number of links between species (L) and lower link saturation (L/S^2) (Borst et al., 2018; Pimm, 1979). In addition, our artificial reefs would increase biodiversity, measured by species richness, Pielou's Evenness and Shannon–Wiener diversity. We expected that the reefs would increase food web complexity and biodiversity over time as the structures develop into fully functioning self-facilitating biogenic reef. Moreover, to specifically investigate whether our biogenic reefs were able to extend in space (near the reef structure) and how they would develop over time, we analysed the community composition of the macrozoobenthos. We examined differences in biodiversity indices and community composition between near- and inside reef and compared this with bare intertidal flat areas as controls. With this study, we not only present the hopeful tools to restore biogenic habitats through biodegradable artificial reefs, but also show how to assess the recovery of associated communities using the food web network and stable isotope analyses (Borst et al., 2018; Christianen et al., 2016).

2 | MATERIALS AND METHODS

2.1 | Field site

The experiment was carried out in the Wadden Sea, which stretches from the northern coast of the Netherlands up to Denmark. The Wadden Sea harbours the largest area of intertidal flats in the world and has been listed as UNESCO World Heritage Site since 2009. The experimental plots were located on an intertidal flat south of the island Griend in the Dutch Wadden Sea (53°14′24.97N, 5°14′53.56E, Figure 1a). Permission for field access was granted by the province of Friesland (registration number: 01262091, primary number: 01248425, by R.J. Deen). The intertidal flat was characterized by bare sandy sediment and a normal tidal range of ~190 cm (RWS, 2013). For more information on site selection and sediment characteristics, wind speed and directions, see Temmink et al. (2022) and Marin-Diaz et al. (2021). Appropriate ethics, permits and other approvals were obtained for the research included in this manuscript.

2.2 | Experimental set-up of artificial reefs

To determine the restoration success of artificial reefs, we placed the structures on the intertidal flat south of Griend in March 2017 (Figure 1a). The experiment was designed with 16 plots perpendicular to the nearest gully at a mean elevation of −0.32 ± 0.003 m NAP (Dutch ordinance level, close to the Dutch mean sea level) and a mean inundation frequency of 65%, that is, an average of 7.8 h submerged every 12 h (Marin-Diaz et al., 2021). The plots were randomly assigned and paired in blocks as (1) unmodified bare control (named control) or as (2) artificial reefs (named reef), with eight replicates each (Figure 1b,c). Each plot measured 20 × 10 m and the reef plots consisted of 10 bands of 5 m long and 16 cm high reef structures (Figure 1d). Each reef structure was made of five modules of eight8 layers of stacked biodegradable BESE-elements (BESE Ecosystem Restoration Products, Culemborg, The Netherlands; Temmink et al., 2022; see specifications in Appendix S1 in Supporting Information). Our experimental set-up is

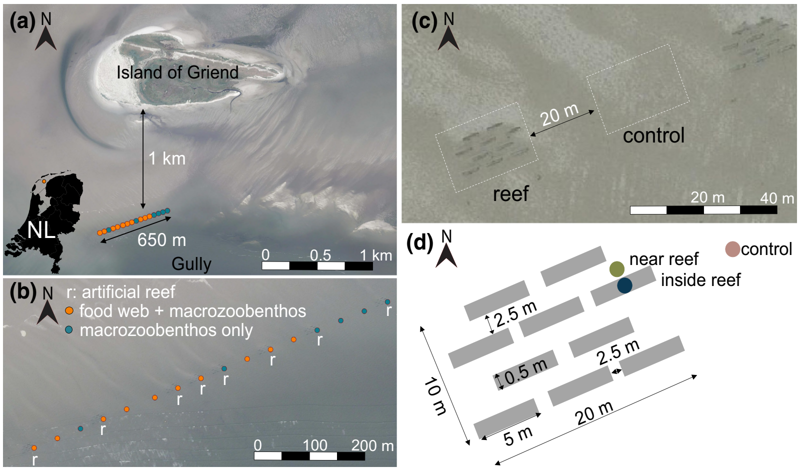

FIGURE 1 Overview of experimental set-up: (a) the location of the experiment on the tidal flats, near the gully south of the island of Griend in the Dutch Wadden Sea 53°14′2′.97 N 5°14′53.56E), colours indicate plots with selection for food web analyses (orange) and macrozoobenthos (all colours), aerial image the Netherlands 2018, orthomosaic, ground resolution: 25 cm, 0% cloud cover, (b) layout of all experimental plots on the intertidal flat treatments (reef = r, bare control = no label) in randomized block design, (c) experimental plots (reef and bare control) used for food web analyses and (d) the set-up of one artificial reef plot made of biodegradable BESE-elements with macrozoobenthic core sampling points (bare control, inside reef and near reef) given in circles.

missing a natural mussel bed as reference site since food web analyses on mussel reefs was already performed by Christianen et al. (2016). We will elaborate on this comparison in the discussion.

2.3 | Sampling procedures for food web networks and biodiversity

To measure the differences between two communities, we sampled multiple trophic levels of the food web. We collected primary producers, species attached to the reef structure, macrozoobenthos, mobile crustaceans and fish species per plot and treatment ($n = 5$), similar to Christianen et al. (2016). We only sampled five of the eight plots per treatment due to logistic constraints (Figure 1b). The plots were chosen randomly and sampled in pairs (reef vs. control, Figure 1b). All groups (carbon sources, molluscs, annelids, crustaceans, other invertebrates, jellyfish and fish) were collected at the end of the growing seasons, 1.5 (August 2018) and 2.5 years (August 2019) after deployment (March 2017) according to the following procedures.

Macroalgae and other species attached to the reef structure were sampled by hand. Benthic diatoms were collected from the sediment by sampling the upper 1 cm of the sediment surface layer with a ∅ 3 cm, 50 ml syringe. After migration through a mesh (100 μm) into combusted sand, diatoms were collected in filtered seawater and filtered over a Whatman GF/F glass fibre filter (Eaton & Moss, 1966).

The macrozoobenthos in the controls were sampled with a PVC corer of ∅ 15 cm to a depth of 25 cm after which each sample was sieved over a 1 mm round mesh (Compton et al., 2013). The macrozoobenthos inside the reef structure (Figure 1d) was sampled with a custom-made metal soil sampler of ∅ 15 cm to a depth of ~25 cm to clean-slice through the structures (Temmink et al., 2022). All plots ($n = 5$) were randomly subsampled, twice per treatment. After sample collection, all macrozoobenthos were fixated in 10% formaldehyde and identified at the species level. After identification, the species were dried for 24 h at 60°C and incinerated for 4 h at 550°C in ovens to determine the dry weight free of ash (AFDW).

We quantified mobile crustaceans and fish species using two methods (see Appendix S1). First, we deployed fykes (net size: ~9 × 0.6 m [length × height], mesh size: 25 mm) that were emptied twice a day with receding tide for each plot. Two fykes were placed simultaneously in a control and reef plot of one block perpendicular to the incoming tide. Species wet weight (WW) was determined following length–weight ratios; see Appendix S1 for formulas and regression coefficients used for transformation (Robinson et al., 2010; Tien et al., 2004). Subsequently, we transformed these WW into AFDW according the WW/AFDW ratios in Horn and de la Vega (2016) and Ricciardi and Bourget (1998). Second, we used a custom-made technique to limit escape rates of small mobile crustaceans (e.g. shrimps) before sampling. With this technique, we placed an aluminium box with an open top and bottom (size: 0.4 × 0.4 × 0.25 m [length × width × height], surface area: 0.16 m^2) to the end of a telescopic stick (~3 m long) haphazardly on the tidal flat. After box deployment, we scraped the inside box top ~5 cm sediment layer with a net (width: 0.4 m, mesh size: 1 mm), which was then sieved over a 1 mm mesh. Species collection, fixation, identification and calculation of biomass followed the same protocol as macrozoobenthos. Furthermore, we counted the abundance of birds (see Appendix S1) to cover all trophic levels of the food web. However, we decided to exclude these data from the food web analyses because the birds were only counted on two occasions (i.e. limited to two replicates).

After species tissue collection, we measured $\delta^{13}C$ and $\delta^{15}N$ isotope signals in the laboratory. To test that the $\delta^{13}C$ and $\delta^{15}N$ isotope signals in our experiment were comparable to the isotope database by Christianen et al. (2016), we collected >3 replicates of the most abundant species in our experiment. Whenever possible, we used muscle tissue of fish, crustaceans and bivalves, and soft tissue of other invertebrates and macroalgae. For species too small (~2 cm) to separate calcified body parts from muscle and/or soft tissue, we used the entire organism. All tissue was rinsed with demineralized water, dried for 48 h at 60°C, ground with Mixer Mill (MM400) including small balls until homogenized. If the tissue contained calcified body parts (i.e. *Gammarus* sp. and *Urothoe Poseidonis*), we decalcified the tissue with 3 M HCL (drop-by-drop technique, Jacob et al., 2005). The subsamples were weighed in preburned tin cups and analysed for δ^{13}C and δ^{15}N isotope composition with Isotope Ratio Mass Spectrometry (Delta V Advantage IRMS, Thermo Fischer Scientific). The target weights of the subsamples differed per tissue (in mg): diatoms 5, detritus 4, POM 1.5, zooplankton 1.5, sediment 50–60, macroalgae 0.5, plant tissue 0.8, animal tissue 0.3–0.4.

2.4 | Sampling procedures of the macrozoobenthos community

In addition to food web analyses, we analysed biodiversity and species composition of macrozoobenthos within one community (inside and near the artificial reef) and compared this with the bare control. To do so, we used the same samples that were used for food web analyses inside the reef and the control, but in all plots (n = 8, Figure 1b). For the near reef, we sampled additional cores adjacent to the reef structures (Figure 1d). All plots (n = 8) were subsampled twice per plot. We ensured that the location of the cores in all plots was spatially similar by taking the distance (7–10 m) from the start of the plot. The macrozoobenthos near the reef (Figure 1d) and control were sampled with a PVC corer of ⌀ 15 cm to a depth of ~25 cm. The macrozoobenthos inside the reef structure (Figure 1d) were sampled with a custom-made metal soil sampler of ⌀ 15 cm to a depth of ~25 cm to clean-slice through the structures (Temmink et al., 2022). After sample collection, all macrozoobenthos were fixed in 10% formaldehyde and identified at the species level. After identification, the species were dried for 24 h at 60°C and incinerated for 4 h at 550°C in ovens to determine ash free dry weight (AFDW).

2.5 | Statistical analyses

We performed all statistical analyses in R (R Core Team, 2022, versions 4.0.3 and 3.6.3): a language for statistical computing and graphics, using open-source R studio (version 1.2.1335). We validated all model assumptions by plotting (1) residuals versus fitted values to verify homogeneity, (2) Q–Q plots of the residuals to test for normality and (3) residuals versus each explanatory variable to check for independence. Additionally, the Shapiro–Wilks test ($p > 0.05$) and the Bartlett test ($p > 0.05$) were used to test for normality and homogeneity of variance respectively.

2.5.1 | Analyses of food web networks and biodiversity

After sample collection, we analysed the structure of the food web based on δ^{13}C and δ^{15}N isotope values and stable isotope mixing models, 'simmr' (Parnell, 2021) per plot (n = 5). First, we used a constructed maximized interaction matrix with all possible trophic links between consumers and their food resources ('prey') by Christianen et al. (2016) and adjusted this matrix for the species found in our study. Trophic relations were determined on the basis of scientific literature, databases and expert knowledge (World Register of Marine Species, WoRMS Editorial Board, 2022). Second, we used stable isotope mixing models, 'simmr' (Parnell, 2021) to produce δ^{13}C and δ^{15}N bi-plots and to infer dietary proportions of consumers from stable isotope values. In this process, food resources were combined based on their taxonomic relatedness (e.g. species of the same family) and isotopic value within the SIMMR package to reduce the total number of food resources per consumer to a maximum of 10. After combining and reducing resources, we removed resources (combinations) that contributed <5% to the consumer's diet. Finally, we use the interaction matrix obtained to calculate basic food web properties according to Borst et al. (2018) and node-weighted food web metrics according to Kortsch et al. (2021) (see Appendix S1). The node sizes were calculated according to the formula with a minimum node size of 1:

$$\text{node size} = (\text{biomass} / \max(\text{biomass})) * 25 + \text{minimum node size}.$$

Third, we calculated the diversity indices Shannon–Wiener and Pielou's Evenness (Oksanen, 2019) and sample-size-based rarefaction and extrapolation (a correction for higher species richness in larger samples) on the reefs compared to bare control (R-package INEXT, Chao et al., 2014; Hsieh et al., 2016).

The food web parameters obtained per plot were used to test for significant differences between the artificial reef and control communities using linear mixed-effects models (LMMs) with 'block' as a random factor. When the data did not meet the assumptions for the linear regression model, the data were transformed (basal species and Shannon–Wiener with squared root and log transformation respectively, see Appendix S2). If the data did not fit a linear regression after transformation (species number, see Appendix S2), we used generalized linear mixed models (GLMMs) with Poisson distribution and checked for overdispersion. Since the GLMM showed singularity for species richness, we simplified the model by removing 'block' as a random effect. Differences were considered significant with a p-value < 0.05. All transformations and model fits are described in Appendix S2.

2.5.2 | Analysis of macrozoobenthos

To examine the differences in species composition of the macrozoobenthic community inside and near the artificial reefs compared to bare control, we performed community analysis, calculated species biomass per taxon group and calculated biodiversity indices. First, community analysis was performed with the VEGAN package (Oksanen, 2019) using nonmetric multidimensional scaling (NMDS; Kruskal & Wish, 1978) on Bray–Curtis dissimilarity indices (Clarke & Green, 1988). To correct for disproportional effects of rare species, we selected only the species with abundance >1. Differences of community compositions on the reef structures were tested using permutation analysis of variance (PERMANOVA) with 'block' as random effect. Since the plots were paired by treatment within 'block', this random effect corrected for the two subsamples per plot and spatial differences. Second, species biomass was calculated per taxon group and analysed with LMM with 'block' as random effect and GLM (per taxon group; no random effect because of singularity) to test for differences in biomass between inside reef, near reef and control and years. Third, we calculated diversity indices Shannon–Wiener and Pielou's Evenness (Oksanen, 2019) based on abundance data. After validating model assumptions as described above, LMMs were used with 'block' as random effect to test for differences in biodiversity indices between inside reef, near reef and control and years. Furthermore, Tukey's post-hoc comparisons were used to test for significant differences ($p < 0.05$) between treatments and years (R-package EMMEANS, Lenth, 2019).

3 | RESULTS

3.1 | Observational biological trends

In 2018 (1.5 years after reef deployment), artificial reefs facilitated species richness of fish (+30%), crustaceans (+57%), annelids (+22%) and molluscs (+15%) compared to the control. In the same year, the abundance was higher on reefs for fish (+70%), crustaceans (+2650%), annelids (+373%) and molluscs (+6728%). One year later (in 2019, 2.5 years after initiation), species richness decreased between reef and control for fish (−11%). In contrast, differences in species richness of crustaceans (+72%), annelids (+104%) and molluscs (+70%) became more evident. With the exception of molluscs (+18,182%), differences in abundance between the treatments reduced over the year, but were still higher on the artificial reef compared to control for fish (+18%), crustaceans (+959%) and annelids (+156%). In addition, the reefs provided substrate for six macroalgal species that were not found in the control (more information in Appendices S3 and S7). Furthermore, the study of Marin-Diaz et al. (2021) described, for the exact same experiment, that the reefs attenuated ~30% of the wave height and affected the sediment surface by max. 11 cm of accretion behind the reef structures and max. 10 cm of scouring around the structures. Nevertheless, these effects did not reach beyond 10 m from the reefs and sediment properties were not affected (Marin-Diaz et al., 2021). Moreover, only 24 ± 4% (mean ± SE) of the biodegradable reef structure was intact after 2.5 year (Temmink et al., 2022). As a consequence, we observed that the abundance of species decreased for all groups except molluscs along with the degradation of the structure.

3.2 | Food web networks and biodiversity: Treatment effects relative to bare control

The deployment of artificial reefs resulted in a more complex food web network on the reefs than in the bare control plots (Figure 2), with more pronounced effects observed 2.5 years after deployment in August 2019 (Figure 3). Within our artificial reefs, we found a higher species richness compared to the bare control (+54% and +76% in 2018 and 2019 respectively, Figure 3a, GLMM with Poisson distribution, $p < 0.001$), a higher link density (+2% and +15% in 2018 and 2019 respectively, Figure 3b, ANOVA, $F_{2,12} = 10.14$, $p < 0.01$), and lower connectance (i.e. lower saturation of all possible links, −35% and −33% in 2018 and 2019 respectively, Figure 3c, ANOVA, $F_{1,12} = 203.98$, $p < 0.0001$). Furthermore, the distribution of trophic

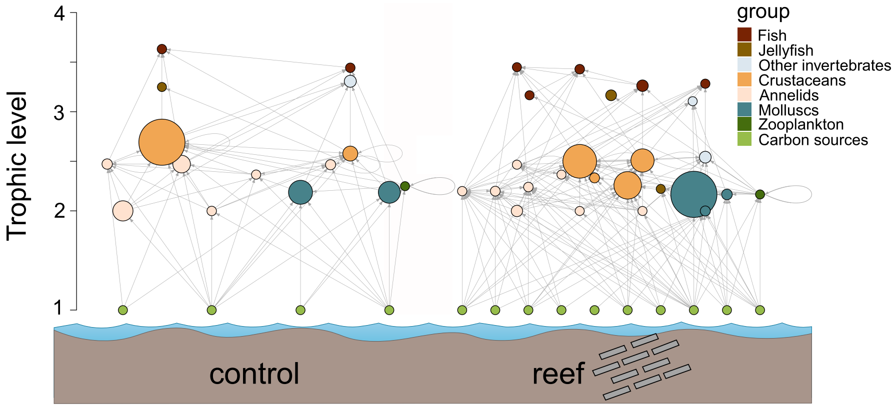

FIGURE 2 Stable isotope-based food web network reconstruction of artificial reefs compared to the bare control bare tidal flats (in groups: carbon sources, zooplankton, molluscs, annelids, crustaceans, other invertebrates, jellyfish and fish). The node-weighted food web networks of one median plot per treatment are presented. Node size indicates the relative species biomass in AFDW g m^{-2}: Node size = (biomass/max(biomass))*25 + minimum node size. Note that the food web on artificial reefs has a higher species richness (# nodes), link density (lines per node; L/S), but not a higher trophic level of top predators (see Appendix S2 for means and statistics).

levels changed over time on artificial reefs compared to bare controls due to a +65% (2018) and +40% (2019) higher fraction of basal species (i.e. species with the lowest trophic level, Figure 3d, ANOVA, $F_{1,13} = 114.47$, $p < 0.001$). Moreover, sample-size-based rarefaction and extrapolation (a correction for higher species richness in larger samples) additionally proved a higher species richness (+64% and +82% in 2018 and 2019 respectively, see Appendix S4) on the reefs compared to bare control. Responses to the presence of artificial reefs on various other food web parameters, species biomass and abundance can be found in Appendices S2 and S3.

3.3 | Composition of the macrozoobenthos community: Treatment effects on inside and near reef communities relative to bare control

The artificial reefs did not change the macrozoobenthos community in the space outside the reef: the reefs altered the macrozoobenthic species composition inside the reef structure (Figure 4a, PERMANOVA based on Bray–Curtis dissimilarities, $df_{total} = 93$, $p < 0.001$), but the species composition near the reef was comparable to the bare control in both years (Figure 4a). Specifically, biomass inside the reef was higher for the mollusc *M. edulis*, crustaceans: *Carcinus maenas*, *Hemigrapsus* spp. and annelid (Family: Nereididae) species such as *Hediste diversicolor*, *Alitta virens* and *Alitta succinea* (see Appendices S3–S7, statistical model output in Appendix S6). In addition, mollusc biomass, dominantly *M. edulis*, increased 3x over time (2018–2019, Figure 4b). Consequently, we found a higher (+41% and +44%) Pielou's evenness biodiversity index in the bare control and near the reef, respectively, compared to inside the reef 2.5 years after deployment (August 2019, Figure 4c, $df = 73$, $p < 0.0001$). This lower evenness is likely a result of the high biomass of *M. edulis* on reef structures compared to other species.

4 | DISCUSSION

Restoration is implemented globally as a tool to reverse the ongoing declines in biogenic reefs that provide a foundation for marine biodiversity. We tested here the potential of a novel restoration approach for biogenic reefs: the deployment of biodegradable artificial reefs that initiate settlement of reef-building species and subsequently enhance food web complexity. Our data reveal that these biodegradable artificial reefs enhanced food web complexity and increased biodiversity compared to bare controls 2.5 years after deployment. Although reefs promoted the establishment of reef-building species (*M. edulis*), such effects only occurred within the reef structure and did not reach beyond the artificial structures. In general, this study provides a proof of concept that biodegradable artificial reefs can be a valuable tool to restore the complexity of the food web in biogenic reefs in intertidal soft-sediment systems.

4.1 | Complexity of the food web on artificial reefs compared to natural biogenic reefs

In August 2018, only 1.5 years after deployment, the complexity of the food web in our biodegradable artificial reefs had

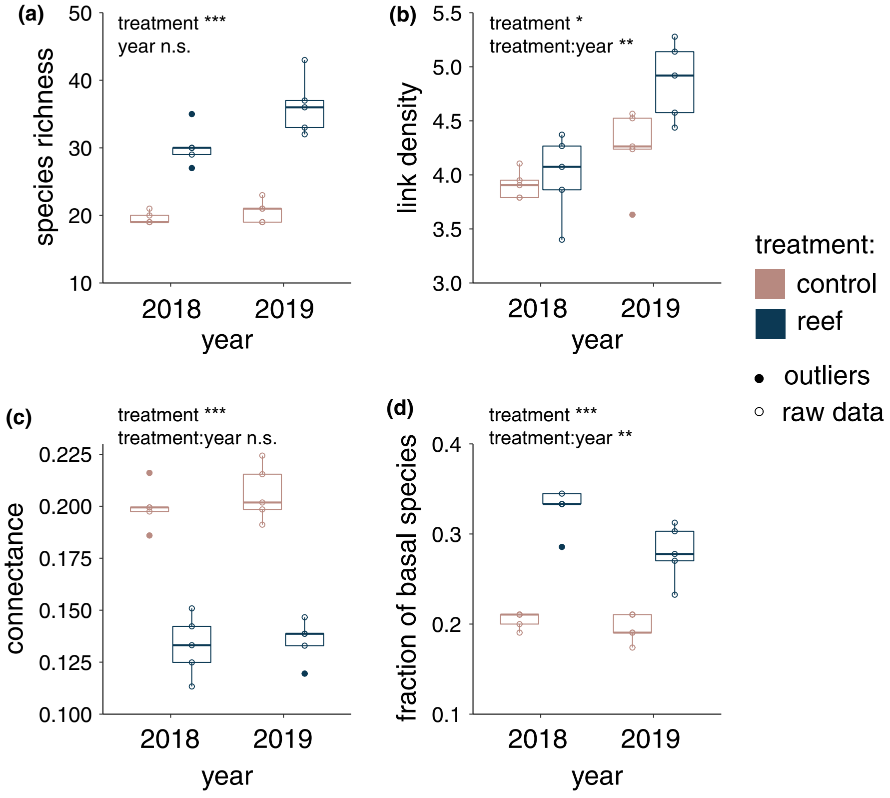

FIGURE 3 The presence of artificial reefs consistently increased food web complexity compared to the bare control community measured by food web indices: (a) species richness, (b) link density, (c) connectance (i.e. saturation of all possible links) and (d) fraction of basal species (i.e. species without resources). Data are shown as raw data points (open circles) and boxplots with median, first and third percentile, minimum (10th percentile) and maximum (90th percentile) and outliers (filled circles; $n = 5$) with linear mixed-effects models and ANOVA, except for species richness we used generalized linear model with Poisson distribution and removal of block as random effect to prevent singularity (see Appendix S2 for more food web indices).

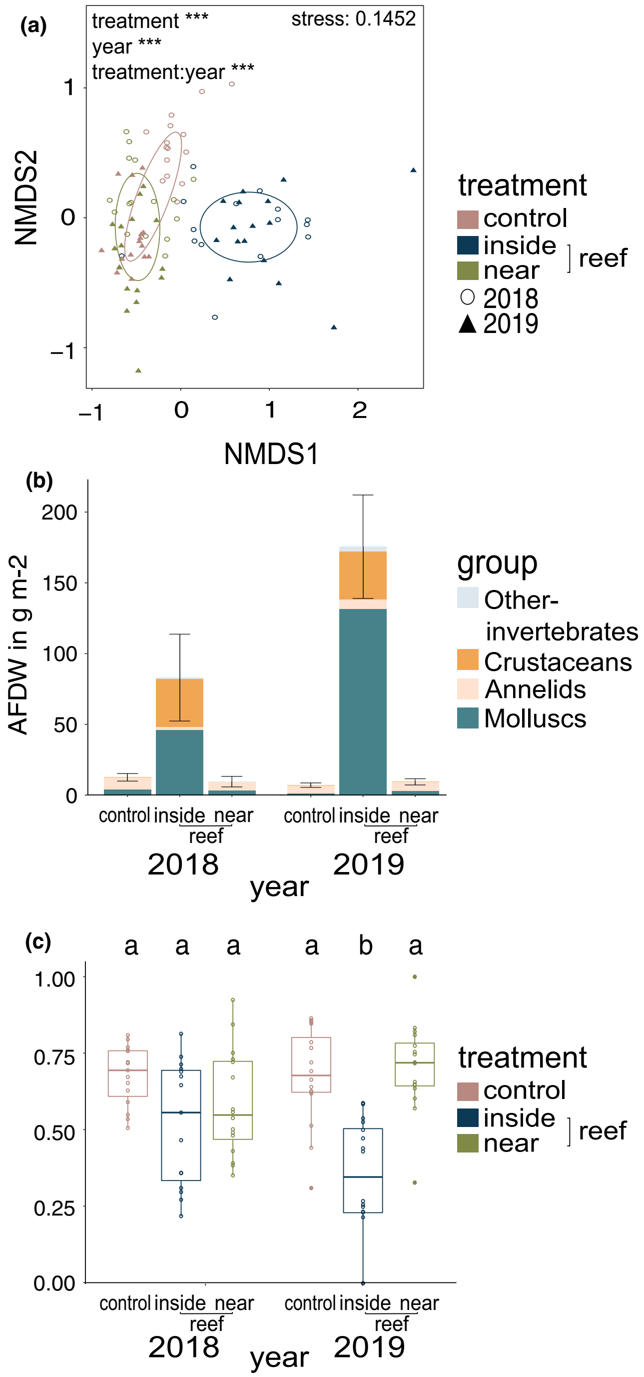

FIGURE 4 Community composition changed only inside the artificial reef, and not near the reef compared the bare control on macrozoobenthic community (crustaceans, annelids and molluscs): (a) nonmetric multidimensional scaling (nMDS) on Bray–Curtis dissimilarity indices with pairwise PERMANOVA and reliable ordination (stress value <0.2; *n* = 8, two subsamples per plot), (b) biomass in ash free dry weight per group in mean ± SE (*n* = 8), SEs are for total biomass and (c) biodiversity index Pielou's evenness in raw data points (open circles) and boxplots with median, first and third percentile, minimum (10th percentile) and maximum (90th percentile) and outliers (filled circles) with linear mixed-effects model and Tukey's post-hoc (see Appendix S5 and S6 for means and statistical output).

already changed considerably towards that of a natural mussel bed (Christianen et al., 2016). Christianen et al. (2016) found that blue mussel beds, in the Wadden Sea (same study system and methodology as our research), altered food web complexity: species richness (+42%), link density (+5%) and connectance (−28%), compared to the food webs on bare intertidal flats. These results are in line with the complexity of the food web in artificial reefs in this study: species richness (+54%), link density (+4%) and connectance (−32%). However, Christianen et al. (2016) found no effect of shellfish reefs on the fraction of basal species (+0%), but instead observed a higher fraction of top species (+62%). In contrast, our artificial reefs did change the distribution of trophic levels to bias a higher fraction of basal species (+42% and +29% in 2018 and 2019 respectively) while lowering the fraction of top species (−6% and −17% in 2018 and 2019 respectively) compared to bare flats. However, the underlying mechanism of how foundation species facilitate other species may differ between habitat types and ecosystems (Mcafee & Bishop, 2019). In general, provision of settlement substrate and a three-dimensional structure facilitates many species, such as reef-building species (Bertness & Callaway, 1994; Jones et al., 1994), and exactly these characteristics were mimicked by our artificial reefs (Temmink et al., 2021, 2022). In addition, natural reef habitats facilitate other species by creating a heterogeneous landscape (Liu et al., 2014). Due to the structural integrity, the artificial reefs in this study did not create a heterogeneous landscape, as our reefs did not affect sediment properties and pool formation (Marin-Diaz et al., 2021; Temmink et al., 2022). Furthermore, our data revealed that the reefs facilitated basal species (i.e. lower trophic level), while natural reefs normally facilitate top-level species in the food web (Christianen et al., 2016). Yet, it is expected that the facilitation of restored biogenic reefs at higher trophic levels may take up to a decade to fully establish (Zu Ermgassen et al., 2016). As such, the addition of substrate rather than landscape modification is the main driver for the improvement of the complexity and biodiversity of the food web on our artificial reefs, while natural biogenic reefs modify their environment and associated species by creating a heterogeneous facilitation landscape (Liu et al., 2014).

4.2 | Assessing food web structure to determine restoration success

The goal of artificial reefs as a restoration tool is to not only restore the biogenic reef itself, but also the associated community in all its complexity. The use of food web networks provides a better understanding of this complexity by understanding the distribution of trophic levels, compared to classic biodiversity indices (Christianen et al., 2016). For instance, Christianen et al. (2016) found that differences in ecosystem complexity between mussel beds and intertidal flats emerged by including food web indicators. This effect did not appear from classic biodiversity indices such as Shannon–Wiener diversity and evenness. Contrastingly, we found effects of artificial reefs on the associated community in both biodiversity indices and food web properties, indicating that these indices may not be mutually exclusive. However, the complexity of the food web provides more information on the distribution of trophic levels and reveals that our artificial reefs support the lowest trophic levels (i.e. basal species), while bivalve reefs also support higher trophic levels (i.e. predators; Christianen et al., 2016). While we found more nuanced effects of artificial reefs on food web structure, species richness and food web complexity indices (link density and connectance) were enhanced in a direction comparable to ecosystems dominated by natural foundation species (i.e. Seagrass meadows, Cordgrass, Watermilfoil, Water starwort, Spanish moss, Marram grass; Borst et al., 2018). So, in comparison to foundation species dominated food webs (Borst et al., 2018), the use of our biodegradable artificial reefs turned out to be a successful approach to restore trophic complexity.

4.3 | Management implications of artificial reefs as a restoration tool in soft-sediment systems

The biodegradable artificial reefs in this study provided a proof of concept for their potential as a tool to promote the recovery of biodiversity and food web complexity in soft-sediment intertidal flats through biogenic reef restoration. Because of their light-weight and ease of installation, these biodegradable structures can be deployed incrementally, over time to build up larger restored areas. Consequently, small-scale successes can be built into large-scale successes overtime, and importantly, the ease of installation means community or small conservation groups can restore large areas without heavy machinery—solutions that are needed for sustainable restoration. However, the applicability of biodegradable reefs for restoration purposes will rely on both environmental and logistic parameters (Walters et al., 2022). Ideally, biodegradable artificial reefs are designed to decompose once biogenic reef builders mature, and the resulting reef can thus self-facilitate its own survival. However, despite the ambitious spatial extent of this restoration project (plot size 20×0 m, spread over ~650 m), no mussels that settled on the structures dispersed beyond the reef structures, probably due to the lack of settlement substrate on the surrounding sandy substrate. In addition, the loss of artificial reef material, albeit biodegradable, can be an unwanted side effect for environmental pollution reasons and the loss of species attached to the structure. So, whereas the biodegradable units used in this study (structural integrity and height) are not suited for high hydrodynamic energy environments (Temmink et al., 2022), future designs could incorporate more robust features (e.g. thicker and stronger structures) designed to withstand wave energy, as such environments are often the focus of restoration of eco-engineers for coastal protection. Furthermore, coastal restoration success via mimicry of self-facilitating biogenic reefs is context dependent (van der Heide et al., 2021) and careful site selection is essential since habitat modification of these reefs rely on environmental parameters (Salvador de Paiva et al., 2018). Moreover, natural biogenic reefs facilitate ecosystem connectivity or biogeomorphological feedbacks, such as diversification of the landscape, stabilization of adjacent habitats and coastal defence (van de Koppel et al., 2015). However, these effects were not found in our artificial reefs on a landscape scale (Marin-Diaz et al., 2021). So, more small-scale research and trials on the environmental context dependency are needed before application in large-scale projects.

5 | CONCLUSIONS

Our biodegradable artificial reefs provided a proof of concept for the recovery of the complexity and biodiversity associated with the biogenic reef food web. Hence, we recommend restoration practitioners to use this approach to generate higher biodiversity and food web complexity (indicators: species richness, link density and connectance). It is, however, essential that the application of biodegradable reefs for biodiversity and food web enhancement is used in an appropriate way that implements suitable site selection (i.e. low hydrodynamics) and structural integrity of the reefs with consequently reduced loss of structure and expanding, self-facilitating biogenic reefs. In fact, future artificial reefs should be designed in such a way that they also generate ecosystem connectivity (e.g. by providing habitat for mobile species) and biogeomorphological effects on a landscape scale: structures should target landscape heterogeneity and ensure availability of settling substrate in reef surroundings rather than just providing settlement substrate only for the reef itself (Gillis et al., 2014; van de Koppel et al., 2015). However, further work and application is required to achieve the goal of generating biogenic reefs and ecosystem connectivity from artificial structures.

AUTHOR CONTRIBUTIONS

Janne Nauta analysed the data and led the writing of the manuscript. Marjolijn J. A. Christianen, Ralph J. M. Temmink, Gregory S. Fivash, Karin Didderen, Valérie C. Reijers, Wouter Lengkeek, Leon P. M. Lamers, Tjisse van der Heide, Tjeerd J. Bouma, Han Olff, Laura L. Govers, Daphne van der Wal, Beatriz Marin-Diaz, Emma Penning, Annieke C. W. Borst, Jannes H. T. Heusinkveld, Maarten Zwarts, Peter M. J. M. Cruijsen and Nadia Hijner collected the data and conceived and designed the research. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the DataverseNL Repository https://doi.org/10.34894/0PG4CQ (Nauta et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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