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# Mutual facilitation between foundation species *Mytilus edulis* and *Lanice conchilega* promotes habitat heterogeneity on tidal flats

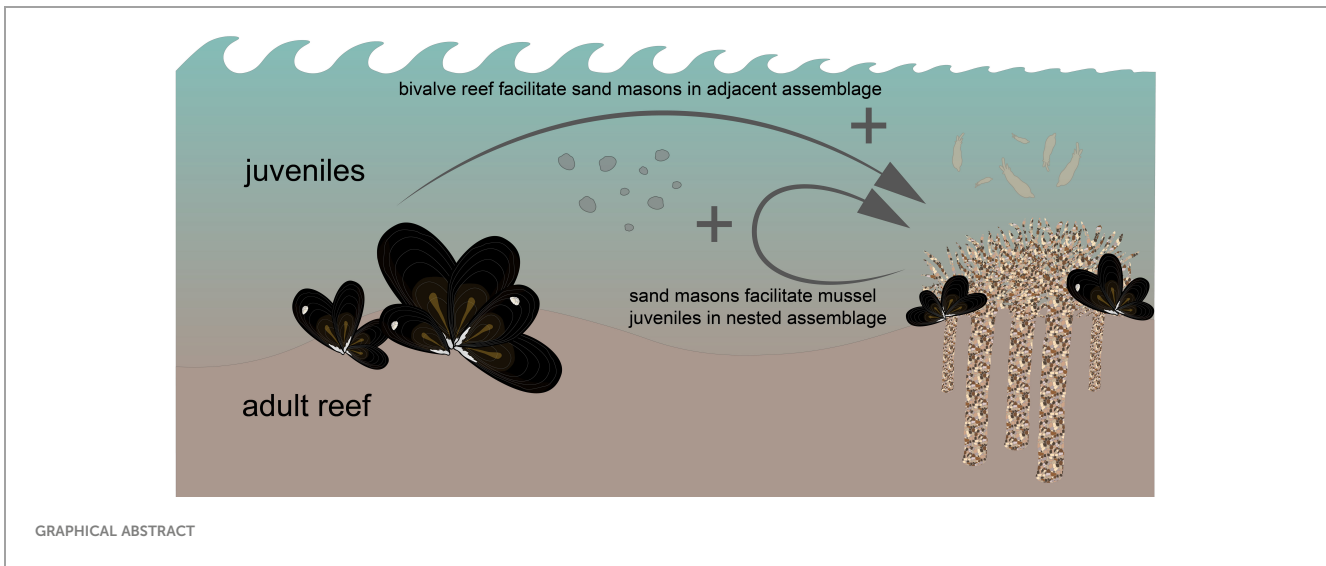
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Foundation species that modify their habitat can facilitate other species, including other foundation species. Most studies focus solely on a single foundation species, overlooking such facilitation cascades. In this study, we investigated the interactions between the two coastal foundation species *Mytilus edulis* (blue mussel) and *Lanice conchilega* (sand mason worm). We investigated whether these species engage in facilitative interactions or if their association simply reflects a shared ecological niche on the soft-sediment intertidal flats of the Dutch Wadden Sea. To do so, we performed species distribution modeling, manipulative field experiments, and field surveys. We found a positive association between both foundation species, with a 2.45 times higher occurrence of both species compared to a random distribution. In addition, these species partially occupied the same ecological niche. We demonstrated that *L. conchilega* provided settlement substrate for *M. edulis* spat, increasing densities by 400 times compared to bare plots. Furthermore, *M. edulis* reefs facilitated *L. conchilega* occurrence in the wake of the reef. Biogenic reef development revealed that this interspecific facilitation resulted in spatial habitat heterogeneity. Therefore, we conclude that interspecific facilitation can significantly enhance the occurrence of these two important intertidal foundation species. Acknowledgment of such complex facilitation interactions has an untapped potential for improving the success of restoration and conservation programs.

## KEYWORDS

facilitation, *Lanice conchilega*, *Mytilus edulis*, sand mason worm, mussel, foundation species, ecosystem engineers, tidal flats



## 1 Introduction

Positive interactions between species are important drivers for species distribution and survival in many ecosystems worldwide (Bertness and Callaway, 1994). Mutualisms, for example, refer to a relationship where both species involved obtain a benefit, often through a tightly evolved and obligate connection. Commensalisms, on the other hand, describe a scenario where one species benefits without affecting the other. One-way facilitation refers to a situation where one species creates favorable conditions for another species. Last, reciprocal facilitation is a type of relationship where both species promote conditions that are favorable for each other (Bronstein, 2009, 2015). Some of the numerous examples of positive interactions in the marine realm are between coral polyps and their symbiotic algae (mutualism), epizoic barnacles and their sea turtle hosts (commensalism), or mangroves providing nursery habitats for a diverse assemblage of fishes (facilitation) (Nagelkerken et al., 2000; Stachowicz, 2001; Zardus, 2021).

Foundation species, species that dominate in abundance and biomass within a system and modify the physical environment, are known for their role in facilitating the survival or growth of other species by creating new habitats (Dayton, 1972; Bruno et al., 2003). The biogenic structures of foundation species can change the physical environment by e.g., reducing physical stress and/or providing complex structure. Other organisms can find refuge from predation and competition within this structure (Dayton, 1972; Jones et al., 1994). Foundation species can support many ecosystem functions and services, such as providing benefits for biodiversity, coastal defense, carbon storage, fisheries, nutrient cycling, and primary and secondary production (Costanza et al., 1998; Temmerman et al., 2013; Alongi, 2018). Kelp, corals, and mangroves are examples of marine foundation species that provide these important ecosystem services by adding structural complexity to the ecosystem (Kovalenko et al., 2012).

The role of single-foundation species facilitating entire communities and food webs through habitat creation has been

extensively documented (Dayton, 1972; Bertness and Callaway, 1994). However, one foundation species can also facilitate another foundation species resulting in facilitation cascades (Altieri et al., 2007). Evidence is growing that ecosystems worldwide are structured by multiple foundation species that act within and among species and across different scales (Angelini et al., 2011; van de Koppel et al., 2015). Multiple foundation species can coexist in different assemblages: nested or adjacent (Angelini et al., 2011). In nested assemblages, the first foundation species inhabits a habitat and facilitates the colonization of a second foundation species by providing settlement substrate or shelter against biotic and abiotic stressors, such as cordgrass facilitating ribbed mussels (Altieri et al., 2007) or oysters attached to mangrove roots (Angelini and Silliman, 2014). In adjacent assemblages, foundation species change the environmental conditions to favorable conditions for others in an adjacent zone such as the interaction between corals, seagrasses, and mangroves (Gillis et al., 2017) or intertidal mussel beds facilitating nearby cockle beds (Donadi et al., 2013).

When facilitation is incorporated into the niche concept, it can expand the niche in a larger spatial range than predicted by the fundamental niche (Bruno et al., 2003; Chase and Leibold, 2011). For example, the realized niche of a species can be larger than the fundamental niche by increased resource availability, predation refuge, recruitment enhancement, and amelioration of physical stress (Bruno et al., 2003). These facilitative interactions can take place on both local and landscape scales (Bruno et al., 2003; Donadi et al., 2013; van de Koppel et al., 2015; Wang et al., 2022). Species rely more on positive interactions on the edges of their fundamental niche, where environmental factors determining species distribution are less optimal and more stressful for one or both species (Bruno et al., 2003). In these stressful environments, facilitation between species may be more important than competition because of stress amelioration, described as the stress-gradient hypothesis (Callaway, 2007).

Tidal flats, soft-sediment ecosystems bordering land and sea and regulated by the rhythm of the tides, are examples of ecosystems that are organized by high physical (wave action) and

chemical (sulfides, anoxia, salinity) stresses (van Straaten, 1954; Gao, 2019). On tidal flats, emergent structures in the otherwise predominantly flat landscape contribute to the habitat complexity (Callaway, 2018; Nauta et al., 2023). Hence, organisms that form biogenic reefs, including oyster reefs, mussel beds, and reef-building polychaetes facilitate many other species by providing habitat complexity (De Smet et al., 2015; Christianen et al., 2017; van der Ouderaa et al., 2021). Under these challenging physical conditions, interspecific facilitation might be pivotal in community structure and ecosystem multifunctionality, such as regulating biological, geochemical, and physical processes of tidal flats (Angelini et al., 2011; Manning et al., 2018). For example, enhanced biodiversity and ecosystem multifunctionality, including decomposition, primary production, sediment accretion, and water infiltration rates, emerge exclusively where two or more foundation species overlap as seen with ribbed mussels aggregating around cordgrass stems (Angelini et al., 2015).

Two reef-building foundation species that can co-occur on tidal flats are the blue mussel, *Mytilus edulis*, and the sand mason worm, *Lanice conchilega* (Pallas 1766) (Hertweck, 1995). *M. edulis* is a foundation species that facilitates itself and other species in the surrounding tidal flat by decreasing near-bed hydrodynamic stress, increasing sediment stabilization, and increasing organic matter content through the production and deposition of pseudofeces (Graf and Rosenberg, 1997; Widdows et al., 1998; Gutiérrez et al., 2003; van der Zee et al., 2012). *L. conchilega* is a 10–20 cm long polychaete worm that builds tubes by cementing shell fragments and sand grains into a strong mucus layer. These tubes attenuate water flow velocity and change water flow direction, increasing sediment stabilization and sedimentation (Friedrichs et al., 2000; Borsje et al., 2014; Alves et al., 2017). Both foundation species facilitate a diverse assemblage of macroalgae, macrozoobenthos, fish, and birds (Albrecht and Reise, 1994; Van der Wal et al., 2014; De Smet et al., 2015; Christianen et al., 2017). Moreover, foundation species such as *M. edulis* and *L. conchilega* can contribute to the resilience of tidal flats as this process hinges on sediment budgets and accretion, especially in the face of rising sea levels (Huismans et al., 2022).

In this study, we investigated the interaction between *M. edulis* and *L. conchilega* and explored their general ecological niche on the tidal flats of the Dutch Wadden Sea. Specifically, we 1) examined species occurrence in a large-scale gridded sampling design (~4,500 samples per year) across the Dutch Wadden Sea, 2) explored the ecological niche of both species to examine their shared niche, 3) experimentally tested how *L. conchilega* tubes acted as settlement substrate for *M. edulis*, thereby facilitating nested assemblages, 4) observed whether *M. edulis* reefs enhanced the occurrence of *L. conchilega* in the adjacent hydrodynamic wake zone, 5) monitored the respective spatiotemporal biogenic reef development of both foundation species. In addition, we measured the effect of these two foundation species on the sediment properties to understand the mechanisms of facilitation. That is, we used sediment properties as proxies for hydrodynamic forces, where small grain sizes and high silt percentages are attributed to reduced hydrodynamic forces (Le Hir et al., 2000). We selected *M. edulis* and *L. conchilega* as study species because

both species provide observable emergent structures to the soft-sediment tidal flats (Widdows et al., 1998; Alves et al., 2017). Furthermore, *M. edulis* historically served as the primary reef-building species before the establishment of the Pacific oyster, *Magallana gigas* (Markert et al., 2010; Markert, 2020). Studying these interactions in contemporary times holds significance as pressures on tidal flats, including the Wadden Sea, increase due to climate change factors such as rising temperatures, sea level fluctuations, erosion, sedimentation, and intensified extreme weather events.

## 2 Methods

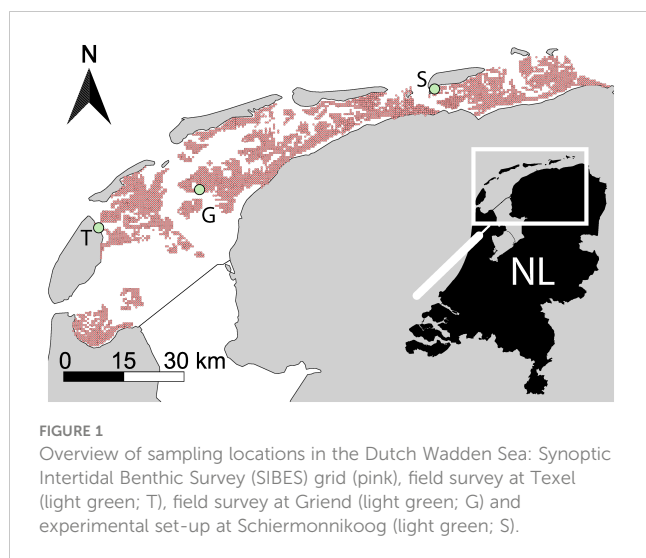
### 2.1 Field sites

The fieldwork was conducted in the Wadden Sea, the world's largest system of tidal flats, gullies, and barrier islands. Its total tidal areas cover nearly 10,000 square kilometers along the coast of the Netherlands, Germany, and Denmark (Reise, 2005) with around 1,000 km<sup>2</sup> of soft-sediment intertidal flats at mean low water and a total surface area of around 2,500 km<sup>2</sup> at mean high water in the Dutch part of the Wadden Sea (Elias et al., 2012). The Wadden Sea is classified as a UNESCO World Heritage site (Unesco, 2014) and is protected as a Natura 2000 area under the European Bird- and Habitat directives, because of its high productivity and supports large numbers of invertebrates, fish, and birds with many long-distance migrants (van de Kam et al., 2004; van der Veer et al., 2015). Around 1990, the Dutch Wadden Sea experienced a drastic loss of nearly all (~4000 ha) intertidal mussel beds, primarily attributed to overfishing, storms, and recruitment failures (Dankers et al., 2001; Christianen et al., 2017). In 1991, the first Pacific oyster that attaches to mussel beds was observed outside cultivation plots (Reise, 1998). Consequently, mussels located within the interspace of oyster reefs exhibited reduced growth rates and body conditions due to interspecific competition (Dankers et al., 2001; Folmer et al., 2017). Moreover, climate change has impacted the Dutch Wadden Sea, leading to a temperature increase of 2.3°C over the last ~120 years, a decline in wind speed averaging -2% per decade, an increase in heavy rainfall events subsequently influencing sediment transport, and occurrence of extreme droughts in the years 2018, 2019 and 2020 (Hoekstra and Philippart, 2022).

### 2.2 Ecological niche modeling

#### 2.2.1 Synoptic Intertidal Benthic Survey

We used the macrozoobenthos samples of the Synoptic Intertidal Benthic Survey (SIBES; (Bijleveld et al., 2012; Compton et al., 2013) to relate the abundance and biomass of *M. edulis* and *L. conchilega* to environmental predictors at the landscape scale. In the years 2008–2020, this large-scale gridded sampling design was sampled (~4,500 samples per year, in total 42,409 samples) with 500 m intervals and additional random points (Bijleveld et al., 2012) across all intertidal mudflats of the Dutch Wadden Sea (Figure 1).



Sample sites were accessed by foot or boat and sampled with one (diameter 0.15 m, 0.0177 m<sup>2</sup>) or two cores (diameter 0.10 m, combined 0.0173 m<sup>2</sup>), respectively, to a depth of ~25 cm. At each sample site, densities and biomass of all macrozoobenthos and sediment characteristics were measured. All macrozoobenthos samples were sieved on a 1 mm round mesh and preserved in a 4% formaldehyde solution with rose Bengal dye (C.A.S. no. 632-68-8) for identification in the laboratory (Compton et al., 2013). All organisms were identified to the lowest taxonomic level possible. For this study, we only used the densities of *M. edulis* and *L. conchilega*. Sediment samples were collected and analyzed following the organic matter content, median grain size D50 (μm), and silt % <63 μm sampling procedures described in section 2.2.2.

### 2.2.2 Sediment properties sampling procedures

We collected the top-1 and top-5 cm of the sediment surface with a small core (Ø 3 cm, 50 ml syringe) to determine the sediment properties: organic matter content, median grain size D50 (μm), and silt % <63 μm. Following sampling, the sediment samples were kept frozen. For calculation of organic matter content, the sediment samples were dried for 24 hours at 60°C and incinerated for 4 hours at 550°C to determine Ash Free Dry Weight (AFDW) and calculate weight loss on ignition (LOI<sub>wt</sub>%). Sediment samples were freeze-dried for 48 hours at -56°C, sieved over 1-mm mesh, and analyzed with the Malvern Mastersizer 2000 (Malvern Instruments, Worcestershire, United Kingdom, serial number 34403/139, model APA 2000 with Hydro G 2000 introduction unit and Autosampler 2000) to determine median grain size and silt%.

### 2.2.3 Environmental predictors for niche modeling

To construct the ecological niche of *M. edulis* and *L. conchilega*, we used the environmental parameters tidal emergence time in percentage, flow rate in m/s, shear stress in Pascal, salinity in parts per trillion, orbital velocity in m/s, median grain size (D50) in μm, and silt percentage in percentage <64 μm. Tidal emergence time, flow rate, and shear stress were predicted by Van Weerdenburg and

Vroom (2021) according to the Dutch Wadden Sea Model (DWSM) in Delft3D-Flexible Mesh in the 2D version of the model with a horizontal resolution of 100x100 meter in the period between 23 June till 22 July 2017 (Van Weerdenburg and Vroom, 2021). This period represented the period from 2013 to 2017 because of similar average high-, and low-water levels (Van Weerdenburg and Vroom, 2021). Salinity was simulated by Van Weerdenburg and Vroom (2021) according to the 3D version of the DWSM with a horizontal resolution of 200x200 m for the year 2017. Orbital velocity was predicted by Van Weerdenburg and Vroom (2021) according to the SWAN-Kuststrook wave model with March 2020 as representative of the average annual wave conditions with a resolution of ~300 meters. Consequently, the root mean square of the amplitude of the predicted orbital movement within a certain time period was interpolated to a 100x100 meter grid (Van Weerdenburg and Vroom, 2021). In addition, sediment samples from the SIBES campaign were used and transformed into raster layers (grid cells 500x500m) for median grain size (D50), and silt percentage. If two samples were present within one grid cell (this was possible because of the random points), the mean of both samples was used. The DWSM may be too coarse to show the effects of biogenic reefs on the environment. On the other hand, sediment samples do reflect the effects of biogenic reefs on the surrounding tidal flat (lower grain size and higher silt percentage) (Widdows et al., 1998; Alves et al., 2017).

### 2.2.4 MaxEnt species distribution models

First, we studied the relation between *M. edulis* and *L. conchilega* occurrence in all sample locations of the SIBES data set by applying a Chi-square goodness of fit test ( $N=42409$ ) to test for independence i.e., co-occurrence by chance. Second, the realized niche concerning the environmental predictors of *M. edulis* and *L. conchilega* was determined by fitting MaxEnt species distribution models (Research Resource Identifiers, RRID: SCR\_021830). We used presence/background modeling; MaxEnt because it allows for complex, nonlinear responses between species presence and environmental parameters (Merow et al., 2013). To analyze the ecological niche of the species, we decided to use MaxEnt species distribution models (presence/background modeling) and not GLM (presence/absence modeling). The use of GLM is advised when absence data is available (Guillera-Arroita et al., 2014). However, the sampled surface of macrozoobenthos (0.0177 m<sup>2</sup>) was very small compared to the scale of the grid (500x500m). Foundation species might be absent in the sample but present in the nearby surroundings of the sampling point. Especially since our target species are both species that grow in patchy distributions with high variability from high densities to bare patches (Bertness and Grosholz, 1985; Callaway et al., 2010), sample points with absence data may be located in a suitable environment and not true absence samples (Degraer et al., 2008). Therefore, we choose to use presence/background modeling instead of presence/absence modeling. MaxEnt combined species presence data alongside randomly selected background locations, where species presence or absence could occur. The model then correlated this information with feature types: environmental parameters such as tidal

emergence time, flow rate, shear stress, salinity, orbital velocity, median grain size (D50), and silt percentage to compute a relative occurrence rate (ROR). Consequently, the probability of species presence was calculated by applying a logistic output to the ROR (Merow et al., 2013). Presence data was obtained from the SIBES data and summarized in a grid (grid cells 500x500m). Species were labeled as present when observed in more than 2 out of the 13 years within one grid cell. Background locations were randomly created with a minimum distance of 2.27 km to correct for spatial autocorrelation and with a total number of >5 times the species' presence sampling points within the intertidal area of the Dutch Wadden Sea (r-package: "sf"). The minimum distance between the background locations was calculated based on variograms (r-package: "gstats") to prevent spatial autocorrelation, the likelihood that two locations are similar because of the distance between them. Variograms were calculated and the correlation between the sample locations was plotted as a function of their distance from each other. Consequently, we could determine the minimum distance in which the two locations were not spatial auto-correlated. Last, we derived the MaxEnt predicted presence probability maps of both species and averaged these two maps per grid cell, providing a probability of the overlapping or shared ecological niche between *L. conchilega* and *M. edulis*.

### 2.3 *Mytilus edulis* establishment by *Lanice conchilega*: experimental tube removal

To test for the effect of *L. conchilega* tubes on mussel settlement, we performed a manipulative field experiment on an intertidal flat south of the island Schiermonnikoog (53°27'22.0"N, 6°9'30.2"E) from August 2020 until March 2022 (Figure 1 and Appendix S1A). This tidal flat was characterized by bare sandy sediment and a tidal emergence time of approximately 30% per day. *L. conchilega* was present in medium-dense aggregations (~800 individual m<sup>-2</sup>), and at ~200-meter distance patches of mussels and oysters were observed. Within the *L. conchilega* aggregations, we created a randomized block design with two treatments in 3x3 m plots: 'tubes present' and 'tubes removal' (n=6). The plots were orientated in blocks of two, with four meters in between the plots and eight meters in between each block. No manipulation of the treatment 'tubes present' was necessary since the tubes were naturally present. A sled with a blade was pulled over the sediment surface (top 1 cm) to remove all tubes and associated fauna for the 'tubes removal' treatment. To reduce the modification of the sediment properties, we installed a sieve (Ø 1 mm) behind the blade that redeposited the sediment after cutting the tubes. After tube removal, we suffocated all fauna by digging in agricultural plastic sheets made from low-density polyethylene. After six days, we removed the plastic and removed all dead organic tissue on the sediment surface. Since it was impossible to selectively remove *L. conchilega* only, we had to remove all benthic fauna to prevent immediate new tube build-up. Subsequently, we performed measurements in August, October, and December 2020, June and September 2021 and March 2022. During the sampling rounds, we

counted *L. conchilega* tubes with visible fringes and *M. edulis* abundance four times in the center of each plot with 20x20 cm frames. *M. edulis* was classified as a larva when its length measured less than one centimeter. We counted tubes with visible fringes because this indicates occupation by the worm itself (van Hoey et al., 2006). The fringes of the tubes are in general destroyed shortly after the worm abandons the tube or dies (van Hoey et al., 2006). In addition, we analyzed sediment properties according to the procedures described in section 2.2.2.

### 2.4 Facilitation of *Lanice conchilega* in the wake of bivalve reefs: field survey

To measure the facilitation of *L. conchilega* abundance in the adjacent habitat zones of mixed mussel/oyster reefs (*M. edulis* mixed with *Magallana gigas*), we conducted surveys along six transects with two distinct characteristics: covering a mussel/oyster reef and a bare control at the north-east of the island Texel (53°8'41.5"N, 4°54'18.7"E), in August 2019, March 2020 and August 2020 (Figure 1 and Appendix S1A). The control site was chosen to be as near to the reef as possible and selected based on a similar habitat type: elevation measured with Real Time Kinematics dGPS (Trimble R8, GNSS system; -36 - -40 cm N.A.P. at 50 m distance from the reef), distance to the gully (~50 m during low tide), sediment type (sandy without dead shells). Hence, the distance between the reef and control sites was ~1500 m at Texel. The distance between the transects within one treatment and sample points was 50 meters, measured from the center of the reef (0 m distance from the reef, Appendix S1B). The sampling station -50 was positioned 50 meters from the hydrodynamically exposed edge of the reef. The sampling stations 50, 100, 150, and 200 meters were located in the wake of the reef. The sample points were positioned perpendicular to the incoming tide (Appendix S1B). At each sampling point, we counted *L. conchilega* tubes with visible fringes four times in 20x20 cm frames and estimated mussel/oyster reef cover in 50x50 cm frames (Van Hoey et al., 2008). In addition, we analyzed sediment properties according to procedures described earlier in section 2.2.2 *Sediment properties sampling procedures* and measured elevation with RTK dGPS. Furthermore, we compared the stable mixed mussel/oyster reef at Texel with a young mussel bed at the south of the island Griend (53°14'20.6"N, 5°15'31.6"E). This mussel bed disappeared within one year after the start of the monitoring. The survey set-up replicated that of Texel, with the exception that at Griend the distance between the reef and nearby control was ~300 m. This adjustment aimed to maintain constant environmental parameters including elevation and sediment type.

### 2.5 Interspecific facilitation over time: field survey

To monitor the establishment of a mussel bed on *L. conchilega* aggregations on a temporal scale, we surveyed reef development south-east of the island Griend (53°14'34.6"N, 5°18'6.5"E; Figure 1

and Appendix S1C). In August 2019, we measured the contours of dense *L. conchilega* aggregations with handheld GPS (Garmin GPSMap 66 Series). In April 2021, this reef was displaced by a young mussel bed. We measured the contours of this reef with drone imagery (DJI Mavic Pro 2) and handheld GPS and determined contours in qGIS (3.6.3-Noosa). In addition, we surveyed transects ( $n=9$ ) that covered the young mussel bed and adjacent bare tidal flats in April and August 2021 (Appendix S1C). On these transects, we 1) counted *L. conchilega* tubes with intact fringes in 50x50 cm frames, and 2) measured elevation with RTK dGPS (Trimble R8, GNSS system) through sampling points (every 5 m).

## 2.6 Statistical analyses

We performed all statistical analyses in R (R Core Team, 2022). We validated model assumptions by 1) residuals versus fitted value plots to verify homogeneity of variances, 2) QQ-plots of the residuals to test for normality and 3) residuals versus each explanatory variable to check for independence. In addition, Shapiro-Wilks's test ( $p > 0.05$ ) and Bartlett's test ( $p > 0.05$ ) were used to test for normality and homogeneity of variance of the residuals, respectively.

For the removal experiment on Schiermonnikoog, *M. edulis* and *L. conchilega* tube counts were analyzed using generalized linear mixed models (GLMM) assuming a negative binomial, zero-inflated error distribution (absence was affected by the removal treatment; r-package: 'glmmTMB' (Brooks et al., 2017). The zero-inflation model (ZI) estimates the probability of an extra zero such that a positive estimate value indicates a higher chance of absence (e.g. ZI: tubes removal  $>0$  means more absence). This is the opposite of the negative binomial model (NB) where a positive contrast indicates a higher abundance (e.g., NB: tubes removal  $>0$  means higher abundances in this treatment) (Brooks et al., 2017). The sampling date and plot nested in blocks were included as random effects. For the transects on Texel, we summarized the counts of four pseudo-replicate *L. conchilega* tube counts per sampling station and analyzed these numbers by generalized linear models (GLM) with negative binomial distribution (glm.nb function from the R package MASS (Venables and Ripley, 2002). Tukey's post-hoc comparisons were used to test for significant differences ( $p < 0.05$ ) between treatments within distance from the reef (R package 'emmeans'; (Lenth, 2019). Sampling dates (August 2019, March 2020, and August 2020) were used as replicates since there was no variation in means among the sampling time points. To test for differences between the treatments within distance from the reef, sediment D50 and silt percentage were analyzed with GLM with a negative binomial distribution, organic matter content was log-transformed and analyzed with linear models, and Tukey's post-hoc comparisons were applied. To monitor biogenic reef development, we spatially visualized *L. conchilega* tube counts by ordinary kriging r-package: 'automap'; (Hiemstra, 2022). The function 'autoKrig' fits a variogram model to the given data set and returns the results of the interpolation: prediction, variance, and standard deviation. Consequently, the interpolated prediction was used to visualize *L. conchilega* tube counts.

## 3 Results

### 3.1 Relating the ecological niches of *Mytilus edulis* and *Lanice conchilega*

To investigate the interlinkage between *M. edulis* and *L. conchilega*, we examined the occurrence frequency of both species at individual sample locations within the SIBES dataset. We found that both foundation species were positively associated with each other because the observed value of sample locations with the presence of both *M. edulis* and *L. conchilega* was 2.45 times higher than the expected value ( $X^2(1, N=42409) = 831.45$ ,  $p < 0.001$ , Figure 2 and Appendix S2). In addition, MaxEnt species distribution modeling revealed that 125 km<sup>2</sup> and 81 km<sup>2</sup> of the total intertidal area of the Dutch Wadden Sea was highly suitable (occurrence probability of  $> 0.6$ ) for *M. edulis* and *L. conchilega*, respectively (Figure 3). Only 37 km<sup>2</sup> of the ecological niches between both foundation species overlapped (Figure 3), which means that they share 30% and 46% of their niche with the other foundation species for *M. edulis* and *L. conchilega* respectively. The highly suitable areas for *M. edulis* were positioned closer to the mainland (training data AUC = 0.705), while these areas for *L. conchilega* are found closer to the barrier islands and tidal inlets (training data AUC = 0.734) (Figure 3).

### 3.1 *Lanice conchilega* provides settlement substrate for *Mytilus edulis*: nested assemblage

To investigate the role of *L. conchilega* tubes as settlement substrate for *M. edulis* spat within nested assemblages, we experimentally removed *L. conchilega* tubes and measured the

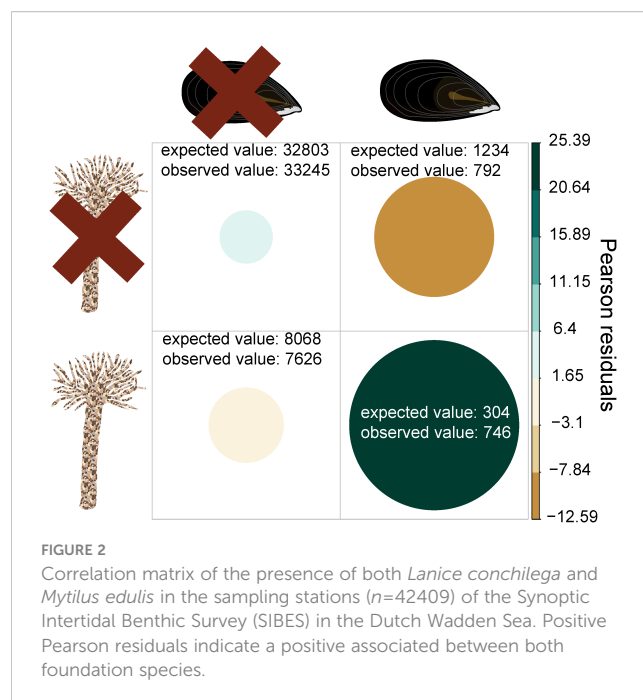
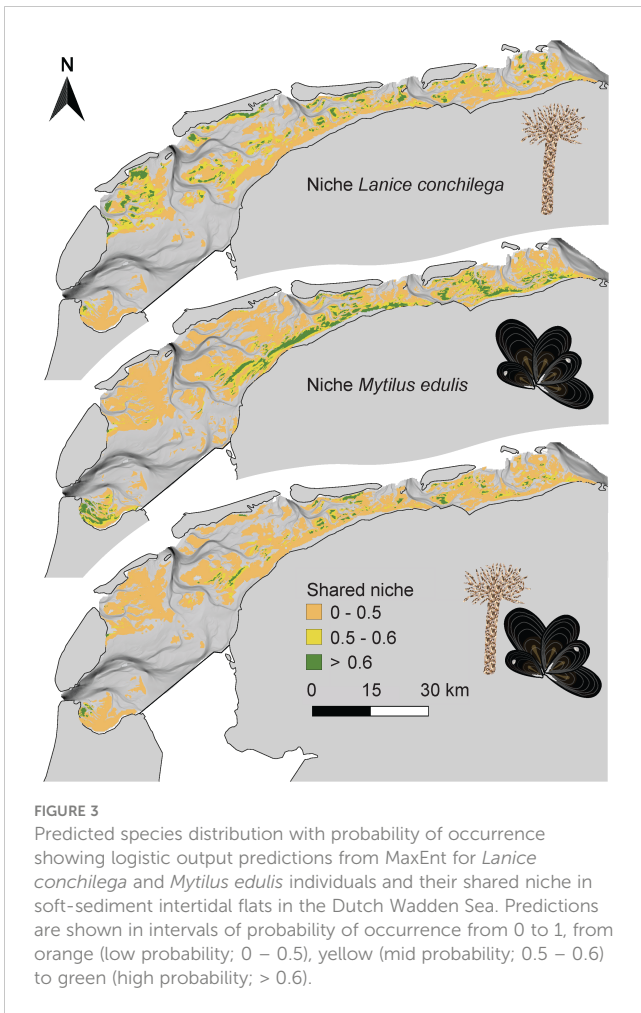


FIGURE 2  
Correlation matrix of the presence of both *Lanice conchilega* and *Mytilus edulis* in the sampling stations ( $n=42409$ ) of the Synoptic Intertidal Benthic Survey (SIBES) in the Dutch Wadden Sea. Positive Pearson residuals indicate a positive association between both foundation species.



**FIGURE 3**  
 Predicted species distribution with probability of occurrence showing logistic output predictions from MaxEnt for *Lanice conchilega* and *Mytilus edulis* individuals and their shared niche in soft-sediment intertidal flats in the Dutch Wadden Sea. Predictions are shown in intervals of probability of occurrence from 0 to 1, from orange (low probability; 0 – 0.5), yellow (mid probability; 0.5 – 0.6) to green (high probability; > 0.6).

effect on *M. edulis*. High *L. conchilega* tube densities of  $1542 \pm 160 \text{ m}^{-2}$  (mean $\pm$ SE) facilitated the settlement of *M. edulis* larvae (length: ~ 1 cm) (Figure 4A). *M. edulis* counts were 400 times higher in the ‘tubes present’ treatment compared to the ‘tubes removal’ treatment with  $177 \pm 36$  individual tube counts (mean $\pm$ SE) (Figure 4B and Table 1). This facilitation within nested assemblage was visible until the end of the experiment in April 2022, almost one year after the first *M. edulis* settlement. Sediment properties did not differ between treatments,

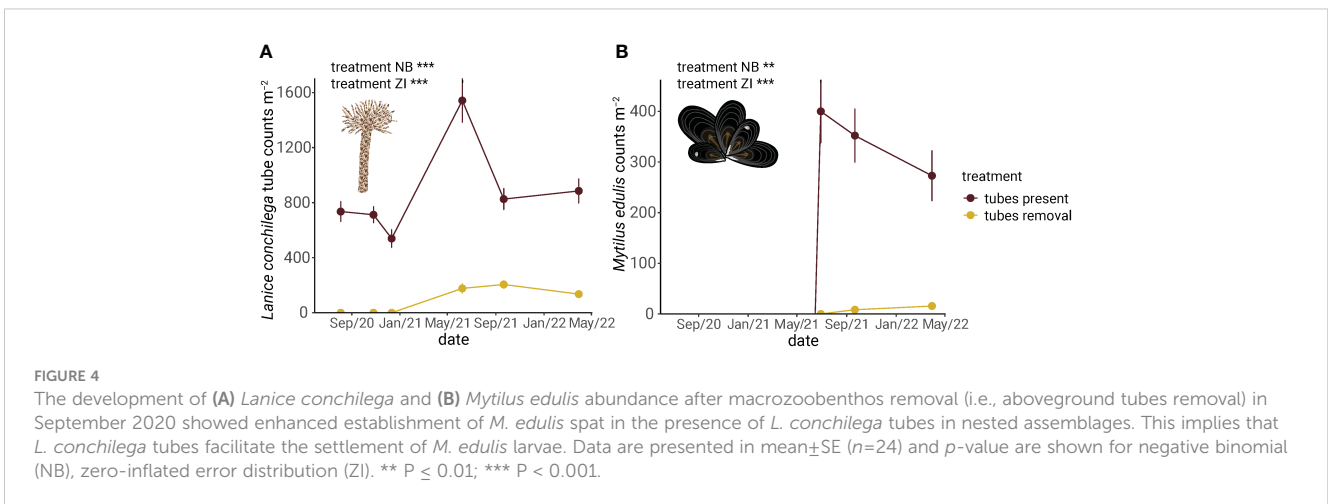
indicating that there was no significant attenuation of hydrodynamics by *L. conchilega* tubes (Appendix S3).

### 3.2 Facilitation of *Lanice conchilega* in the wake of bivalve reefs: adjacent assemblage

To explore the facilitation of *L. conchilega* by mixed mussel/oyster reefs (*M. edulis* mixed with *M. gigas*), we surveyed *L. conchilega* tube densities and reef cover. No tubes  $0 \pm 0$  (mean $\pm$ SE) were counted at sampling stations -50 m and 0 m mussel bed. The highest tube densities of  $1606 \pm 122 \text{ m}^{-2}$  (mean $\pm$ SE) were found at 50 meters in the wake of the reef, and the lowest tube densities of  $128 \pm 38 \text{ m}^{-2}$  (mean $\pm$ SE) were found at 200 m in the wake of the reef. The tube counts were on average 24 and 22 times higher at 50 ( $\beta = 3.17$ , SE  $\pm 0.66$ ,  $p < 0.001$ ) and 150 m distances ( $\beta = 3.08$ , SE  $\pm 0.67$ ,  $p < 0.001$ ), respectively, in the wake of the reef compared to the nearby control (Figure 5 and Table 1). The mussel/oyster reef area extent covered the sampling stations -50 and 0 m with an average reef cover of 45% at sampling station -50 and 75% at sampling station 0 (Figure 5A). At 50 meters in the wake of the reef, sediment silt percentage was higher (+17% silt), median grain size was lower (D50:  $-32 \mu\text{m}$ ) and organic matter content was higher (+1% LOI) compared to the nearby control (Figure 5B and Appendix S4). The sediment surface around the reef center was elevated by ~ 0.35 meters (0 meters; Figure 5C). To compare these counts with a young mussel bed located south of the island Griend that disappeared within one year after the start of the monitoring, we observed the highest *L. conchilega* tube densities  $3956 \pm 631 \text{ m}^{-2}$  at 50 meters in the wake of the reef compared to the control with  $171 \pm 106$  tubes  $\text{m}^{-2}$ . One year later, however, this mussel bed had disappeared, and *L. conchilega* tube densities were reduced to almost zero counts (Appendices S1, S5).

### 3.3 Interspecific facilitation creates dynamic habitat heterogeneity

To study the interlinkage between *M. edulis* and *L. conchilega*, we monitored biogenic reef development (Figure 6). In 2019, the



**FIGURE 4**  
 The development of (A) *Lanice conchilega* and (B) *Mytilus edulis* abundance after macrozoobenthos removal (i.e., aboveground tubes removal) in September 2020 showed enhanced establishment of *M. edulis* spat in the presence of *L. conchilega* tubes in nested assemblages. This implies that *L. conchilega* tubes facilitate the settlement of *M. edulis* larvae. Data are presented in mean $\pm$ SE ( $n=24$ ) and  $p$ -value are shown for negative binomial (NB), zero-inflated error distribution (ZI). \*\*  $P \leq 0.01$ ; \*\*\*  $P < 0.001$ .

TABLE 1 Statistical outcome of a) *Lanice conchilega* tube counts in removal experiment indicating a lower abundance (negative binomial part of the model < 0) and higher absence (zero-inflated part of the model > 0) of *L. conchilega* in the tubes removal treatment, b) the effect of tube removal on *Mytilus edulis* larvae settlement in nested assemblages indicating a lower abundance and higher absence of *M. edulis* in tubes removal, c) higher *L. conchilega* tube counts around mussel beds (50 and 150 m) in adjacent assemblages compared to nearby control.

a)	parameter	estimate	SE	95% CI		p-value
<i>Lanice conchilega</i> tube counts	<b>negative binomial part</b>					
	intercept	6.71	0.13	6.45	6.97	
	tubes removal	-1.52	0.16	-1.82	-1.22	<0.001
	<b>zero inflated part</b>					
	intercept	-4.96	1.01	-6.94	-2.99	
	tubes removal	5.08	1.02	3.08	7.08	<0.001
b)	parameter	estimate	SE	95% CI		p-value
<i>Mytilus edulis</i> counts	<b>negative binomial part</b>					
	intercept	5.75	0.21	5.34	6.16	
	tubes removal	-1.49	0.47	-2.40	-0.57	<0.01
	<b>zero inflated part</b>					
	intercept	-2.78	0.54	-3.83	-1.73	
	tubes removal	4.17	0.63	2.92	5.41	<0.001
c)	parameter	estimate	SE	95% CI		p-value
<i>Lanice conchilega</i> reef vs. control	-50	-23.51	3142.21	-10300	10200	1
	0	-22.46	3142.21	-10300	10200	1
	50	3.17	0.66	1.01	5.33	<0.001
	100	1.76	0.66	-0.40	3.92	0.2429
	150	3.08	0.67	0.89	5.26	<0.001
	200	1.53	0.66	-0.64	3.69	0.4748

monitored reef consisted of almost exclusively *L. conchilega* tubes with  $2201 \pm 121$  individual tubes  $m^{-2}$  (mean  $\pm$  SE,  $n=20$ ) and covered a surface area of  $383,507 m^2$  (Figure 6). In 2021, the reef was instead dominantly shaped by *M. edulis*, and *L. conchilega* tubes were mostly present in the adjacent habitat zone (50 – 150 m). The total surface of the biogenic reef dominated by *M. edulis* was  $33,047 m^2$  and the highest *L. conchilega* tube densities (660 individual tubes  $m^{-2}$ ) were found within 50 m in the wake of the reef in 2021. Hence, biogenic reef development of *M. edulis* and *L. conchilega* indicated spatiotemporal dynamic habitat heterogeneity that consequently is important to promote biodiversity (van der Ouderaa et al., 2021).

## 4 Discussion

In this study, we defined the positive association of two coastal foundation species, *Mytilus edulis* and *Lanice conchilega*, from an ecological, experimental, and statistical perspective. These two reef-building species co-occurred in the same environment and partially occupied the same ecological niche (30-46%). In nested assemblages, *L. conchilega* tubes provided settlement substrate for *M. edulis* spat. On the other hand, mussel and mixed mussel/oyster reefs facilitated *L. conchilega* settlement in their wake (~50-150 m),

sheltered from hydrodynamic forces. The interaction between these species may result in spatial and temporal habitat heterogeneity with fluctuating dominance of *M. edulis* and *L. conchilega* in which both foundation species facilitate their own survival indirectly: 1) *L. conchilega* tubes provide settlement substrate for *M. edulis* spat, 2) development of *M. edulis* beds drives to the exclusion of *L. conchilega*, 3) *M. edulis* beds facilitate *L. conchilega* in their wake, and this, as well as the eventual loss of the reef after a storm, followed by *L. conchilega* re-colonization, can initiate the cycle once again. Hence, we conclude that interspecific facilitation mechanisms may enhance the occurrence of both foundation species. While not being strictly necessary for the occurrence of either species, these species may and possibly expand each other's niche on the tidal flats of the Wadden Sea. Therefore, these interactions among foundation species contribute to the species distribution of tidal flat communities and organize landscape-scale species patterns.

### 4.1 Species distribution

Our results showed a positive association between the occurrence of *M. edulis* and *L. conchilega*. In addition, *M. edulis*



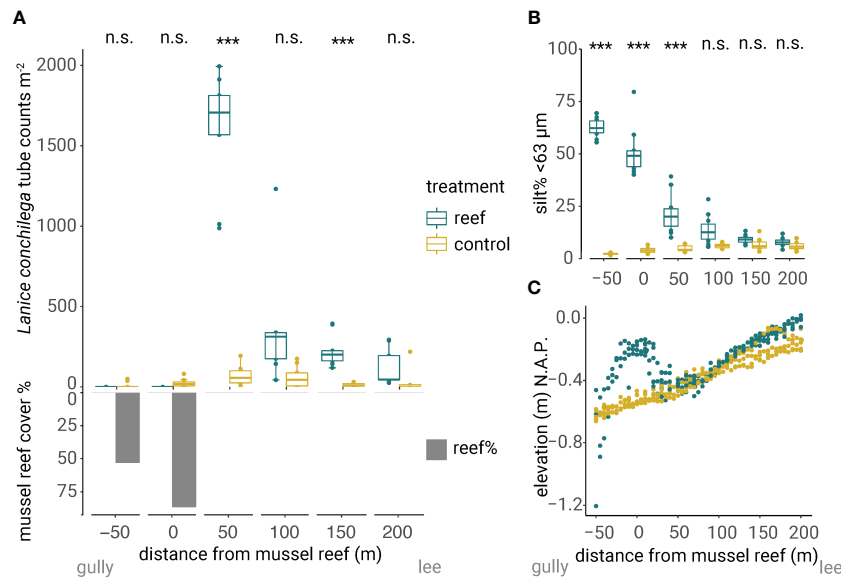


FIGURE 5

Field surveys indicate (A) interspecific facilitation in adjacent assemblages of *Lanice conchilega* densities at 50 and 150 meters in the wake of the mussel bed. The mussel bed affected environmental conditions by (B) higher sediment silt percentage at -50:50 meters distance from the reef and (C) elevation of the sediment surface around the reef center (0 meters). Significance levels show the difference between the mussel bed and nearby control. n.s.  $P > 0.05$ ; \*\*\*  $P < 0.001$ .

and *L. conchilega* share 30% and 46% of their ecological niche, respectively. These combined results suggest that interspecific facilitation may contribute to the enlargement of the ecological niche into the realized (and observed) ecological niche. Enlargement of the niche by facilitation has been described previously for mussel beds that stabilize the substratum and increase salt marsh production via the deposition of nutrients into the sediment (Bertness and Leonard, 1997; Stachowicz, 2001). Analyses of the large SIBES dataset (sampling stations:  $n=42409$ ) establish a robust basis for the assumption that *M. edulis* and *L. conchilega* are positively correlated, potentially enhancing each other's fundamental niche. For example, interspecific facilitation can ameliorate the environmental stressors that otherwise would limit species occurrences, such as providing settlement substrate or reducing hydrodynamic forces (Callaway, 2003; Walles et al., 2015).

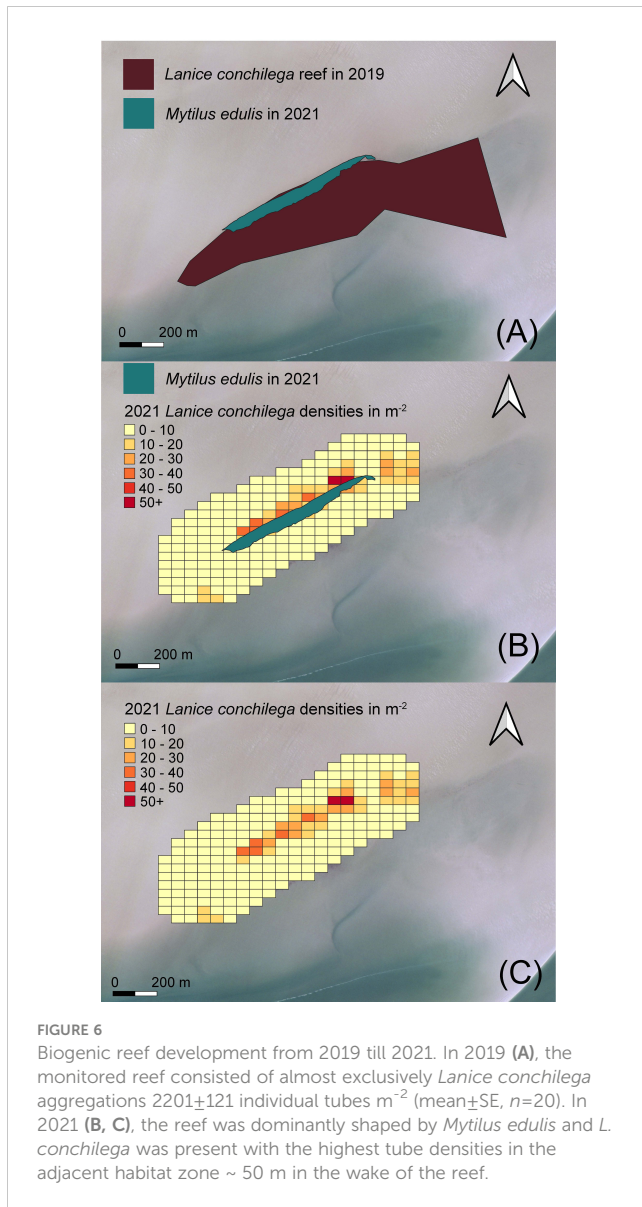
#### 4.1 Facilitation in nested assemblage

Previous studies found that *M. edulis* settlement prefers structured habitat surfaces over bare substrata (Dean, 1981; Bourget et al., 1994) and that the structure of imitation tubes can provide settlement substrate for *M. edulis* larvae (Callaway, 2003). However, imitation tubes differed from natural tubes of *L. conchilega* because they were more rigid, more solid, not hollow, more persistent over time, and had no tentacle fringes (Callaway, 2003). This raised the question of whether natural *L. conchilega* tubes can also facilitate *M. edulis* larvae settlement. In this study, we showed that *L. conchilega* can indeed provide a suitable settlement substrate for *M.*

*edulis* spat in natural conditions. The mechanisms behind this facilitation may be explained by two factors: the structure of the tubes reduces the hydrodynamic forces (Borsje et al., 2014) and/or the tubes provide a complex attachment substrate (Callaway, 2003). *M. edulis* larvae may use different factors to find a suitable substratum for settlement, e.g., physical [flow conditions, light, or gravity; (Bayne, 1964; Pernet et al., 2003)] or chemical [metabolites of algae or invertebrates; (Dobretsov, 1999)] cues. Our findings suggest that *L. conchilega* tubes provided settlement substrate for *M. edulis* spat, as we did not find indications of altered hydrodynamics based on sediment properties in the tubes removal plots compared to the tubes present plots (Le Hir et al., 2000). However, an additional effect of chemical metabolites produced by *L. conchilega* attracting *M. edulis* cannot be excluded since we have not been able to measure such cues.

#### 4.2 Facilitation in adjacent assemblage

By attenuating hydrodynamic forces from waves and currents, bivalve reefs typically have a much larger-scale impact on their surrounding physical landscape than the area they actually cover (Walles et al., 2015). This may facilitate other species such as seagrasses, salt marsh plants, and cockles in adjacent assemblages i.e., long-distance, cross-habitat facilitation (Wall et al., 2008; Donadi et al., 2013; van de Koppel et al., 2015; Walles et al., 2015). These reefs create habitat for other species by e.g., trapping water and increasing tidal emergence time (Nieuwhof et al., 2018; van der Ouderaa et al., 2021) or wave attenuation (Cheong et al., 2013). Walles et al. (2015) found that the spatial extent of habitat



modification by bivalve reefs is of the same order of magnitude as the reef area (length, width, height). In our study area, the sediment surface of the bivalve reef was around 100 meters wide and on average 0.35 meters higher than the surrounding tidal flat. A similar elevation of the bare tidal flat to the height of the reef was reached at around 110 – 140 meters in the wake of the reef. Hence, the modified area leeward of the reef was expected to be around 100 – 140 meters. In addition, we found that the bivalve reefs increased silt percentage and reduced median grain size up to 50 meters in their wake. Both measurements are indicators of reduced hydrodynamic forces (Le Hir et al., 2000). However, mixed mussel/oyster reefs facilitated *L. conchilega* occurrence at 50 and 150 meters in their wake, but not at 100 meters. This might be because of the high patchy distribution of *L. conchilega* (Callaway et al., 2010). In general, our results imply that bivalve reefs create suitable habitats for *L. conchilega* in adjacent assemblage by mitigating hydrodynamic forces.

### 4.3 Interplay between foundation species creates dynamic habitat heterogeneity

We observed that *L. conchilega* tubes facilitated *M. edulis* settlement and consequently reef establishment south-east of the island Griend. In addition, we observed that the *M. edulis* reef facilitated *L. conchilega* densities in the wake of the reef, which is hydrodynamically less exposed. This suggests that interspecific facilitation may promote the co-occurrence of both species by creating temporal shifts between both species. Our findings find support in the observations made by (Hertweck, 1995), who found *M. edulis* spatfall attached to *L. conchilega* tubes in dense aggregations on the tidal flats south of the island Spiekeroog, German Wadden Sea. In addition, *L. conchilega* is frequently found surrounding mussel beds (Hertweck, 1995; Bungenstock et al., 2021). Although the interplay between both species appears evident, these cause-effect relationships must be interpreted with caution since they rely on observational data (Hertweck, 1995; Bungenstock et al., 2021). Moreover, additional research approaches, such as experiments and species distribution modeling, further support the interdependency of the two species. This extensive effort was essential for testing the interdependency across various local contexts, long-term temporal scales, and large spatial scales, ensuring objectivity in statistical analyses. Yet, the question remains which environmental factors promote the dominance of a certain foundation species? For example, it is known that cold winters limit the growth of *L. conchilega* populations (Strasser and Pieloth, 2001). On the other hand, *L. conchilega* tubes are more resistant to storms or winter ice because they are anchored deeper ( $\sim 30$  cm) into the sediment than *M. edulis* beds (Alves et al., 2017). Furthermore, *M. edulis* beds are attached to the sediment surface and winter ice can dislodge the mussels from the substratum (Bertness and Grosholz, 1985; Bungenstock et al., 2021). Therefore, this study emphasizes the importance of supporting optimal growth strategies for biogenic reef development by biological interactions.

### 4.4 Long-term reef development

Long-term reef development of *M. edulis* and *L. conchilega* on tidal flats is a dynamic process shaped by complex interactions between environmental factors and biological interactions. *M. edulis* spat aggregate densely on substrates, such as rocks, and shells (Wehrmann, 2003). Over time, the accumulation of mussel beds alters sedimentation patterns, stabilizes substrates, and enhances the survival of the reef (Widdows et al., 1998). In this study, we described that *L. conchilega* tubes function as settlement substrates for *M. edulis* larvae. Eventually, the *M. edulis* spat may develop into the physical habitat structure of a *M. edulis* bed, as evidenced by Callaway (2003) findings from a six-year-long experiment. The settlement of *L. conchilega* larvae relies on the hydrodynamic conditions and the substrate to settle on (D'Hurlaborde et al., 2022). Whether *L. conchilega* aggregations will develop into a biogenic reef, depends on their resistance to

disturbance, recovery potential, and their large-scale persistence (Rabaut et al., 2009; Callaway et al., 2010). We described that *M. edulis* beds create favorable conditions for *L. conchilega* reef development in their wake. Although we were unable to assess this long-distance facilitation over an extended duration, similar long-distance facilitation of the edible cockle *Cerastoderma edule* by *M. edulis* beds was reported in 2009 and 2011 (Donadi et al., 2013). Hence, the influence of interspecific facilitation seems to contribute to the long-term development of biogenic reefs.

## 4.5 Consequences for nature management

The existence of biogenic reefs such as *M. edulis* and *L. conchilega* relies on the establishment and survival of the reefs. This existence can be enhanced by the optimization of the environmental variables as settlement substrate and/or reduced hydrodynamics. For instance, the protection of areas with relatively stable *L. conchilega* aggregations can improve reef settlement of *M. edulis*. Re-establishment of mussel beds after storm events may be encouraged when *L. conchilega* aggregations are present. For active restoration, it might be necessary to temporarily mimic the physical structure of biogenic reefs with artificial structures to improve the local environmental conditions for reef establishment (Temmink et al., 2022; Nauta et al., 2023). However, sufficient structure and size of the biogenic reef is needed to achieve the restoration of landscape-scale connectivity (Gillis et al., 2017). Biogenic reef structure and size of *L. conchilega* aggregations can be classified by using a ‘reefiness’ score with highest ‘reefiness’ scores for densities of  $>1,500$  individual  $m^{-2}$ , a total area extent of  $>100,000$   $m^2$ , and a relative height of  $>9$  cm (Hendrick and Foster-Smith, 2006; Rabaut et al., 2009). Based on this ‘reefiness’ classification, the *L. conchilega* aggregation in this study can be classified as high-scoring biogenic reefs. Restoring landscape-scale connectivity means that the one biogenic reef-building species needs to be restored to a sufficient physical scale to generate positive effects on the other (foundation) species. The methodology applied in this study, incorporating field surveys, experiments, and species distribution models, could serve as a recipe for further understanding and co-restoration of interspecific dependency in the Dutch Wadden Sea. Moreover, biogenic reefs including *M. edulis* and *L. conchilega* provide numerous ecosystem services such as enhanced biodiversity and fisheries, sediment stabilization, and reduced hydrodynamics (Rabaut et al., 2007, 2010; De Smet et al., 2015; Alves et al., 2017; zu Ermgassen et al., 2020). Therefore, we suggest that possibilities for co-restoring foundation species with other foundation species need to be further explored.

## 5 Conclusions

Our findings emphasize the significance of interspecific facilitation between foundation species. Hence, enhancing restoration and conservation initiatives centered around these

foundation species can be achieved by integrating interspecific facilitation processes. We suggest that it is valuable to look beyond the target species itself and focus on co-restoring foundation species and landscape-scale ecosystem connectivity. Given the increasing pressures from climate change, especially on tidal flats where species are constantly subjected to environmental stressors, species strongly rely on each other for establishment and survival. Foundation species living in these dynamic and harsh circumstances can benefit from interspecific facilitation interactions, with associated advantages for higher biodiversity (De Smet et al., 2015; Christianen et al., 2017). Therefore, interspecific facilitation on landscape scales requires more attention in nature conservation and restoration programs.

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## Author contributions

JN: Conceptualization, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft. KM: Investigation, Methodology, Validation, Writing – review & editing. LD: Investigation, Methodology, Writing – review & editing. VR: Conceptualization, Investigation, Methodology, Supervision, Writing – review & editing. TB: Conceptualization, Supervision, Writing – review & editing. DW: Conceptualization, Supervision, Writing – review & editing. HO: Conceptualization, Supervision, Writing – review & editing. SH: Investigation, Writing – review & editing. AB: Writing – review & editing. HV: Writing – review & editing. OF: Writing – review & editing. LG: Supervision, Writing – review & editing.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2024.1354009/full#supplementary-material>

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