

BIVA-WATT: Roughness Effects of Oyster Reefs and Blue Mussel Beds in the Field, Hydraulic Model Experiments, and Numerical Simulations

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Summary

The bioinvasion of the non-native Pacific oyster (*Magallana gigas*) has transformed low-relief blue mussel (*Mytilus edulis*) beds in the German Wadden Sea into rigid, ultra-rough biogenic structures that strongly interact with waves, currents, and sediment dynamics. This work synthesizes results from the BMBF-funded KFKI research project BIVA-WATT, which investigates how biogenic structures formed by the non-native Pacific oyster and the native blue mussel modify the hydro- and morphodynamics of the German Wadden Sea. Field campaigns, hydraulic model experiments, and numerical modelling were combined to i) parameterize the topographical roughness and spatial configuration of mussel beds and oyster reefs, ii) quantify their influence on wave attenuation, flow resistance, and sediment accumulation, iii) resolve near-bed flow and force patterns around individual roughness elements, and iv) implement coupling strategies between ecological descriptions and process-based morphodynamic models.

High-resolution structure-from-motion photogrammetry, terrestrial laser scanning, and UAV mapping revealed distinct intra-reef structural classes and showed that mature oyster reefs form large, continuous, ultra-rough surfaces with vertical accretion and sediment accumulation rates that exceed local sea-level rise. Seasonal population data demonstrated



that vertical reef growth is tightly linked to temperature-driven shell production and recruitment. Volumetric analyses over a time span of two years indicated net gains in reef area and volume where suitable hard substrate is available, while lateral stability is controlled by local hydrodynamic exposure and episodic burial and re-exposure.

Scaled surrogate models of both biogenic structures were subjected to waves and currents in controlled flume experiments, demonstrating that oyster reefs dissipate roughly twice as much wave energy as mussel beds and that sharp-edged roughness elements are key drivers of turbulence production, bed shear stress, and frictional energy loss. High-fidelity LES simulations around a single oyster shell resolved vortex dynamics and force progression.

A data-based hindcast framework was developed to generate time-variant, 10 m grids from 1996 to 2020 and to transfer biologically derived roughness parameters into the MARINA model system. Together, these advances provide a basis for assessing the system-scale consequences of the ongoing shift from mussel beds to oyster reefs and for supporting informed coastal management under sea-level rise. In this way, the framework developed enables the development of scenarios of ecological change and their analysis in terms of their impact on the resilience of coastal areas and management strategies.

Keywords

Wadden Sea, tidal flats, biogenic structures, ecosystem engineering species, morphodynamics, hydraulic roughness, process-based modeling, sediment

Zusammenfassung

Die Bioinvasion der nicht-beimischen Pazifischen Auster (Magallana gigas) hat die Miesmuschelbänke (Mytilus edulis) im deutschen Wattenmeer in starre, ultra-raue biogene Strukturen umgewandelt, die in starkem Maße mit Wellen, Strömungen und Sedimentdynamiken interagieren. Diese Arbeit fasst die Ergebnisse des BMBF-geförderten KFKI-Forschungsprojekts BIVA-WATT zusammen, das untersucht, wie von der Pazifischen Auster und der Miesmuschel gebildete biogene Strukturen die Hydro- und Morphodynamik des deutschen Wattenmeeres beeinflussen. Feldkampagnen, hydraulische Modellversuche und numerische Modellierungen wurden kombiniert, um i) die topographische Rauheit und räumliche Konfiguration von Muschelbänken und Austernriffen zu parametrisieren, ii) ihren Einfluss auf Wellenabschwächung, Strömungswiderstand und Sedimentakkumulation zu quantifizieren, iii) Strömungs- und Kraftmuster im unmittelbaren sohnaben Bereich einzelner Rauheitsselemente aufzulösen und iv) Kopplungsstrategien zwischen ökologischen Beschreibungen und prozessbasierten morphodynamischen Modellen zu implementieren.

Hochauflösende Structure-from-Motion-Photogrammetrie, terrestrisches Laserscanning und UAV-Kartierungen offenbarten ausgeprägte intra-riff Strukturklassen und zeigten, dass ökologisch ausgereifte Austernriffe große, zusammenhängende, ultra-raue Oberflächen bilden, deren vertikales Wachstum und Sedimentakkumulationsraten den lokalen Meeresspiegelanstieg übertreffen. Saisonale Populationsdaten belegten, dass das vertikale Riffwachstum eng an temperaturgetriebene Schalenproduktion und die Ansiedlung juveniler Austern gekoppelt ist. Volumetrische Analysen über einen Zeitraum von zwei Jahren zeigten Nettozunwächse in Riffausdehnung und -volumen, sofern geeignete Hartsubstrate verfügbar sind, während die laterale Stabilität durch lokale hydrodynamische Exposition sowie episodische Überdeckung und Wiederfreilegung bestimmt wird.

In kleinskaligen Laborversuchen wurden 3D-gedruckte Ersatzmodelle beider biogenen Strukturen Wellen und Strömungen ausgesetzt. Dabei zeigte sich, dass Austernriffe etwa doppelt so viel Wellenenergie dissipieren wie Miesmuschelbänke und dass scharfkantige Rauheits Elemente entscheidende Treiber für Turbulenzerzeugung, Sohlschubspannung und Reibungsverluste sind. Hochaufgelöste LES-Simulationen um eine einzelne Auster erfassten Wirbeldynamiken und Kraftverläufe.

Ein datenbasiertes Hindcast-Framework wurde entwickelt, um zeitvariable 10-m-Raster von 1996 bis 2020 zu erzeugen und biologisch abgeleitete Rauheitsparameter in das MARINA-Modellsystem zu übertragen. Zusammengefasst schaffen diese Fortschritte eine Grundlage für die Bewertung der großräumigen Folgen des anhaltenden Übergangs von Muschelbeständen zu Austernriffen und für eine wissenschaftsbasierte Küstenbewirtschaftung unter Bedingungen des Meeresspiegelanstiegs. Auf diese Weise ermöglicht das entwickelte Rahmenkonzept die Entwicklung von Szenarien der ökologischen Veränderung und deren Analyse bezüglich ihrer Auswirkung auf die Resilienz der Küstengebiete und Management Strategien.

Schlagwörter

Wattenmeer, Gezeitenwatt, biogene Strukturen, ökosystemgestaltende Arten, Morphodynamik, hydraulische Rauheit, prozessbasierte Modellierung, Sediment

1 Introduction

Over the last 25 years, the non-native Pacific oyster *Magallana gigas* has become an established species in the German Wadden Sea, invading most of the previously predominant mussel beds formed by the blue mussel *Mytilus edulis* (Folmer et al. 2017, Reise 1998, Wehrmann et al. 2000). *M. gigas* populations expanded substantially, outcompeting the native *M. edulis* and assuming its function as the predominant ecosystem engineering species, resulting in an irreversible ecological shift in the Wadden Sea (Folmer et al. 2014, Nehls et al. 2011, Wehrmann 2006). In the process, blue mussel beds, which are low-relief biogenic structures with an internal flexible meshwork, have been almost completely transformed into rigid, ultra-rough reef structures (Brandt et al. 2008, Bungenstock et al. 2021, Markert et al. 2013). Due to the rigid framework, oyster reefs are more resistant to mechanical stresses induced by waves, tidal currents, or even ice drift, compared to *M. edulis* beds (Bungenstock et al. 2021, Donker et al. 2015) and are expected to persist, with long-term vertical accretion exceeding rates of local sea-level rise (SLR) (Troost 2010, Walles et al. 2015a). These established *M. gigas* reefs have altered the biological composition as well as local hydro- and morphodynamics in the Wadden Sea (Borsje et al. 2011, Bouma et al. 2014, van der Zee et al. 2012). The establishment of these extensive reef structures has been recognized to enhance wave attenuation (Borsje et al. 2011), increase sediment stabilization (Salvador de Paiva et al. 2018, Walles et al. 2015a), and alter sediment composition (Reddin et al. 2022). Thus, this transformation is expected to generate substantial, large-scale changes in the Wadden Sea's hydro- and morphodynamics, which have remained largely underexplored (Bouma et al. 2014). Such changes are likely to impact the Wadden Sea's ecological composition, the navigability of shipping lanes, and the long-term evolution of intertidal morphology and habitat diversity, particularly under climate change scenarios. Given its societal relevance, there is an urgent need to investigate the prevailing processes.

The work aims to elucidate, understand, and quantify the influence of biogenic structures formed by non-native oyster *M. gigas* and native blue mussel *M. edulis* on the Wadden

Sea ecosystem, both from biological and coastal engineering perspectives, thereby improving the understanding and quantification of their ecosystem effects. Specifically, the project pursued the following sub-objectives:

1. Parameterize topographical roughness and spatial distribution patterns of both biogenic structures, and apply advanced digital design and fabrication methods to reproduce the biogenic structures for hydraulic model experiments,
2. Quantify the effect of both biogenic structures on wave attenuation and flow resistance and determine the hydrodynamic roughness lengths, z_0 , and wave friction factors, f_w ,
3. Perform process-based high-fidelity numerical simulations of the near-bed ambient hydrodynamics around roughness elements at the mesohabitat scale,
4. Design and implement coupling strategies between hydro-morphodynamic models and descriptive ecological models, and
5. Quantify short-term lateral and vertical reef growth in relation to tidal level and seasonal population dynamics of the respective ecosystem engineers.

Methodologically, the research combined field studies, hydraulic model experiments, and conceptual work on integrating descriptive ecological models in hydro-morphodynamic models. The BIVA-WATT project consisted of four sub-projects:

- BIVA-WATT A: Quantification of the impact of biogenic structures formed by Pacific oysters (*Magallana gigas*) and the native blue mussel (*Mytilus edulis*) on waves (Leichtweiß-Institute for Hydraulic Engineering and Water Resources and Institute of Structural Design, Technische Universität Braunschweig)
- BIVA-WATT B: Quantification of the impact of biogenic structures formed by Pacific oysters (*Magallana gigas*) and the native blue mussel (*Mytilus edulis*) on currents (Leibniz University Hannover, Ludwig Franzius Institute of Hydraulic, Estuarine and Coastal Engineering)
- BIVA-WATT C: Monitoring the population structure and dynamics of the Pacific oyster (*Magallana gigas*) and the native blue mussel (*Mytilus edulis*) in their function as ecosystem engineering species in the Wadden Sea (Marine Research Department, Senckenberg am Meer)
- BIVA-WATT D: Concepts to couple hydro-morphodynamic simulation models with ecological model components – data-based and process-oriented approaches (smile consult GmbH)

This work summarizes key findings of the BIVA-WATT project and attempts to drive recommendations meeting the demands of stakeholders from the BIVA-WATT project, some of which have been published previously (Hitzegrad et al. 2022, Hitzegrad et al. 2024a, Hitzegrad et al. 2024b, Hitzegrad 2025, Hitzegrad et al. 2025b, Hoffmann et al. 2023, Hoffmann et al. 2025, Pfennings et al. 2024, Pfennings 2025). The study sites are described in Section 2. Section 3 summarizes the findings considering the spatial distribution patterns and topographical parameters of the biogenic structures formed by *M. gigas* and *M. edulis* based on field observations. Section 4 outlines the experimental and numerical studies performed to quantify the impact of the biogenic structures formed by *M. gigas* and *M. edulis* on wave attenuation and flow resistance. Section 5 outlines the concepts to couple hydro-morphodynamic simulation models with ecological model components. Section 6 provides a discussion on the findings and highlights future research directions. Section 7

presents key conclusions drawn from the research performed within the BIVA-WATT project. Further details can be found in the final report of the research project (Goseberg et al. 2023) and the respective publications outlined below.

2 Study sites

The research presented in this work focuses on three biogenic structures in the German Wadden Sea (Figure 1): the *M. gigas* reefs Kaiserbalje (KB) and Nordland (NOL), and the *M. edulis* bed Nordstrand (NOS). The sites were selected based on the availability of well-documented and previously monitored biogenic structures (Schmidt et al. 2008), enabling comparisons between established oyster reefs and a mussel bed that had not yet undergone reef transformation. All sites are situated in fine sand to silt environments (Benninghoff and Winter 2019) and experience similar hydrodynamic conditions characterized by semi-diurnal tidal forcing, moderate current velocities, and generally low wave exposure (Hagen et al. 2020). KB is located in the Lower Saxon Wadden Sea at the junction of the Jade and Weser estuaries (mean coordinates: 53.6470116° N, 008.2664760° E) and represents a mature, high-density oyster reef that developed from a former mussel bed following the establishment of Pacific oysters in 2004 (Schmidt et al. 2008). At the time of the study, the reef covered approximately 42,000 m² and consisted of a large continuous reef complex with predominantly muddy sediments in its central area. NOL, located south of the island of Juist (mean coordinates: 53.6424960° N, 006.9411970° E), hosts an older oyster reef where Pacific oysters were first recorded in 1998, allowing for a longer period of reef development and expansion (Wehrmann et al. 2000). NOS, situated in the northern Wadden Sea (mean coordinates: 54.4465005° N, 008.8728208° E), was included as a representative mussel bed to assess hydrodynamic and sedimentation dynamics prior to oyster reef formation.

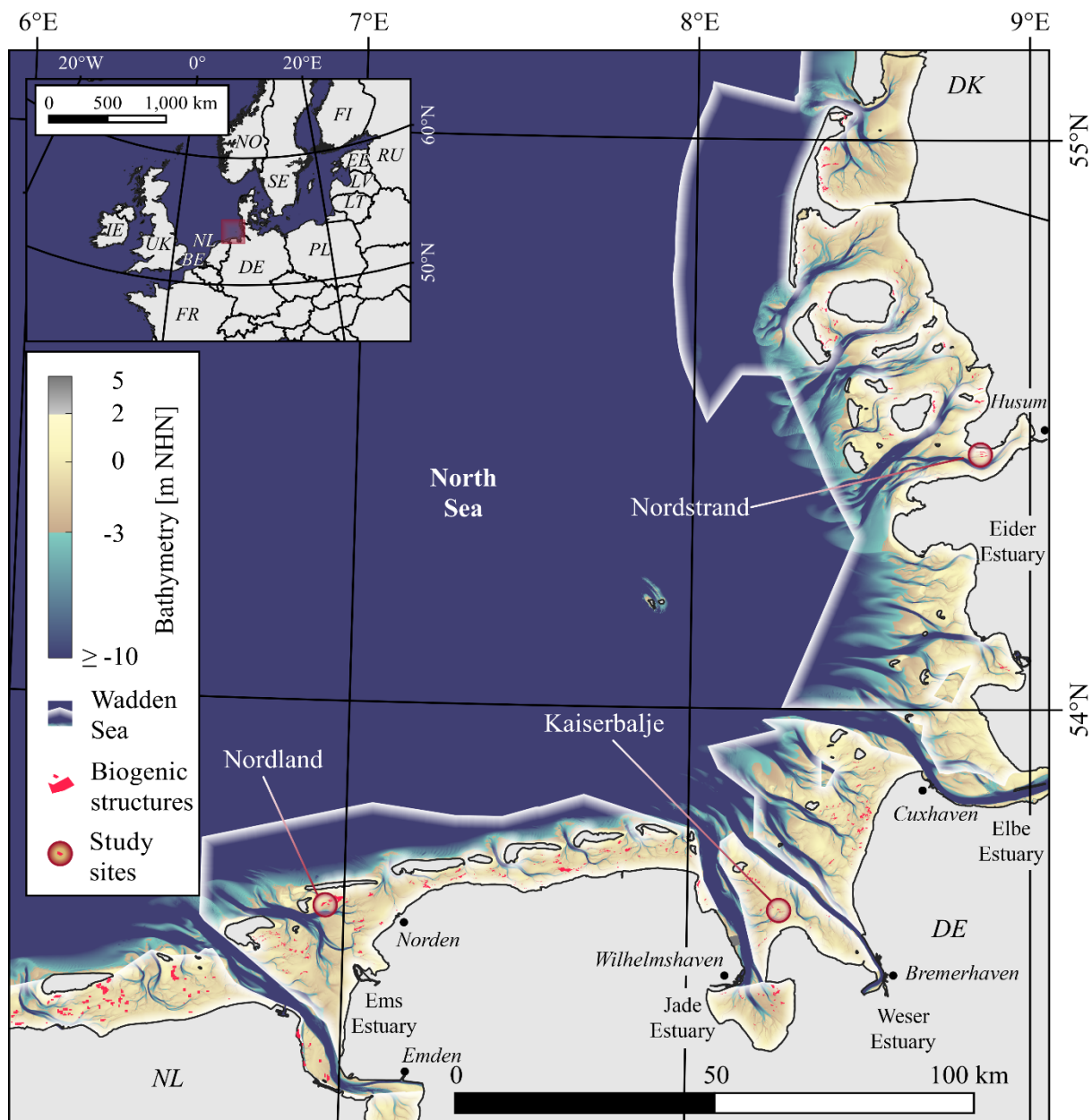


Figure 1: A bathymetric map of the German Bight (Milbradt and Pineda 2024), referenced to the standard elevation zero (NHN, vertical datum in Germany). The outlines of the World Heritage Site Wadden Sea are marked in white (UNESCO 2023), the biogenic structures are highlighted in pink (Schleswig Holstein Wadden Sea: Nationalparkverwaltung Schleswig-Holsteinisches Wattenmeer, 2018; Lower Saxon Wadden Sea: Nationalparkverwaltung Niedersächsisches Wattenmeer, 2021; Dutch Wadden Sea: Baptist et al., 2021), and the locations of the study sites, *Magallana gigas* reefs Kaiserbalje and Nordland and *Mytilus edulis* bed Nordstrand, are indicated by magenta circles. Projection: ETRS89/UTM Zone 32N. Taken from Hitzegrad (2025).

3 Spatial Distribution Patterns and Geometric Parameters of Oyster Reefs and Blue Mussel Beds

To investigate the interactions between both biogenic structures and the ambient hydrodynamics, understanding the spatial distribution patterns and topographical roughness is essential. Based on *in-situ* observations, topographical data have been analyzed at three spatial

scales: mesohabitat scale (order of magnitude: 1 m²), intermediate scale (order of magnitude: 10,000 m²), and reef-wide scale (order of magnitude: 200,000 m²). Furthermore, the topographical data were linked to data of the seasonal population dynamics of the respective ecosystem engineers. The following sections summarize the key outcomes of the field observations.

3.1 Oyster Reef Surfaces: Intra-Reef Classification and Comprehensive Statistical Description

Hitzegrad et al. (2022) report on visual observations of *M. gigas* reef surfaces, proposing seven structural classes to account for the intra-reef complexity: Central Reef, Transitional Zone, Cluster I, Cluster II, Patch I, Patch II, and Garland. For each structural class, high-resolution digital elevation models (DEMs) were generated at the mesohabitat-scale (1 m²) using structure-from-motion photogrammetry with hand-held cameras (Figure 2). Measurements were conducted primarily at the KB reef and validated using additional samples collected at NOL. After applying a morphological filter to isolate the oyster-related roughness, the DEMs were analyzed using spatial statistics to derive probability density functions (PDF), vertical porosity distributions, abundances, orientations, and second-order structure functions (values listed in Table 1), all of which have been shown to influence hydraulic bed roughness (Chung et al. 2021).

Similar total roughness heights ($k_t = 103 \pm 15$ mm; arithmetic mean and standard deviations) and root-mean-square roughness heights ($k_{rms} = 23 \pm 5$ mm) were consistent across all structural classes, yet the shapes of the PDFs revealed differences. As abundance decreased, the PDFs became more positively skewed, with more outliers. Higher statistical moments reflected these differences in the PDFs' shapes, with skewness ranging from $Sk = 0.4$ to 2.1 and kurtosis between $Ku = 2.2$ and 11.5. The second-order structure functions revealed the oyster shells as significant roughness elements, except in the Cluster classes, where the clusters were identified as significant roughness elements.

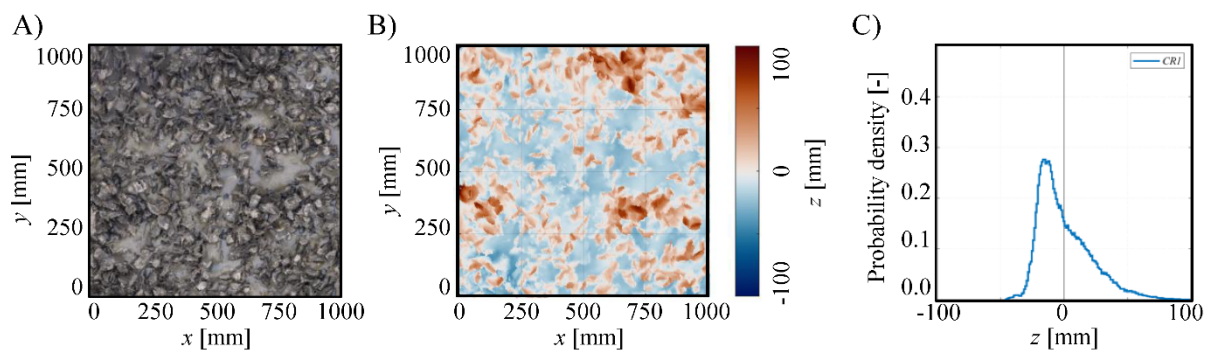


Figure 2: A) Orthophoto, B) Visualization of the digital elevation model (DEM), and C) Probability density function (PDF) of the surface level elevations, shown exemplarily for a sample of the structural class Central Reef (CR1), found in the oyster reef Kaiserbalje. Adapted from Hitzegrad et al. (2022).

Table 1: Statistical parameters (average arithmetic mean $\pm$ standard deviation) per proposed structural class (CR: Central Reef, TZ: Transitional Zone, CI: Cluster I, CII: Cluster II, PI: Patch I, PII: Patch II, and G: Garland), where k_t is the total roughness height, k_{rms} is the root-mean-square roughness height, Sk is the skewness, Ku is the kurtosis, Φ_{bulk} is the bulk porosity, A is the abundance, w_{mean} is the mean width of the oyster shells, and RE is the significant roughness element. Adapted from Hitzegrad et al. (2022).

Struc- tural class	Eleva- tion	k_t	k_{rms}	Sk	Ku	Φ_{bulk}	A	w_{mean}	RE
	[m ASL]	[mm]	[mm]	[-]	[-]	[-]	[inds./m ²]	[mm]	[-]
CR	-0.09 $\pm$ 0.03	104 $\pm$ 11	23 $\pm$ 3	0.9 $\pm$ 0.2	3.5 $\pm$ 0.5	0.66 $\pm$ 0.02	393 $\pm$ 50	39 $\pm$ 3	Shells
TZ	-0.20 $\pm$ 0.09	99 $\pm$ 5	23 $\pm$ 2	1.0 $\pm$ 0.2	3.7 $\pm$ 0.6	0.68 $\pm$ 0.03	466 $\pm$ 56	34 $\pm$ 1	Shells
CI	-1.07 $\pm$ 0.08	101 $\pm$ 8	20 $\pm$ 1	1.5 $\pm$ 0.6	7.0 $\pm$ 3.9	0.71 $\pm$ 0.05	256 $\pm$ 19	35 $\pm$ 1	Clus- ter
CII	-1.05 $\pm$ 0.10	100 $\pm$ 28	20 $\pm$ 8	1.7 $\pm$ 0.1	7.0 $\pm$ 2.3	0.70 $\pm$ 0.04	137 $\pm$ 6	36 $\pm$ 2	Clus- ter
PI	-0.46 $\pm$ 0.22	114 $\pm$ 5	28 $\pm$ 3	0.5 $\pm$ 0.2	2.6 $\pm$ 0.5	0.64 $\pm$ 0.04	408 $\pm$ 133	38 $\pm$ 6	Shells
PII	-0.22 $\pm$ 0.14	105 $\pm$ 18	25 $\pm$ 4	0.5 $\pm$ 0.1	2.8 $\pm$ 0.2	0.62 $\pm$ 0.05	279 $\pm$ 128	41 $\pm$ 9	Shells
G	-0.28 $\pm$ 0.13	103 $\pm$ 19	23 $\pm$ 5	1.4 $\pm$ 0.3	4.9 $\pm$ 1.5	0.74 $\pm$ 0.05	285 $\pm$ 89	38 $\pm$ 1	Shells

3.2 Linkage of Seasonal Population Dynamics and Vertical Oyster Reef Growth by TLS

High resolution terrestrial laser scanning (TLS) was applied in Pfennings et al. (2024) to representative oyster reef areas of approximately 80×80 m, at the oyster reef study sites KB and NOL reef (Figure 3), to determine seasonal vertical growth rates. Insights from *Crassostrea virginica* reefs along the US East Coast (Bost et al. 2021, Ridge et al. 2015, Rodriguez et al. 2014) suggest that intertidal oyster reefs can withstand current and projected rates of SLR through the continuous cementation of new oyster generations. This biogenic growth allows intertidal oyster reefs to maintain their vertical position within the tidal frame, with an optimal exposure window of 20 % to 40 % (50 % for reefs >50 years old after Bost et al. 2021) and an upper growth ceiling between 55 % and 70 %.

Results on vertical oyster reef growth (Figure 4) showed median vertical growth rates of 17.5 mm yr^{-1} (NOL) and 19.8 mm yr^{-1} (KB), exceeding current local rates of sea level rise of 2.5 and 3.7 mm yr^{-1} (Wahl et al. 2013). Growth saturation in the topmost reef areas, located at 47.8% MTR (mean tidal range) at KB and 48.4% MTR at NOL, indicates that the reefs are approaching an equilibrium in their vertical position.

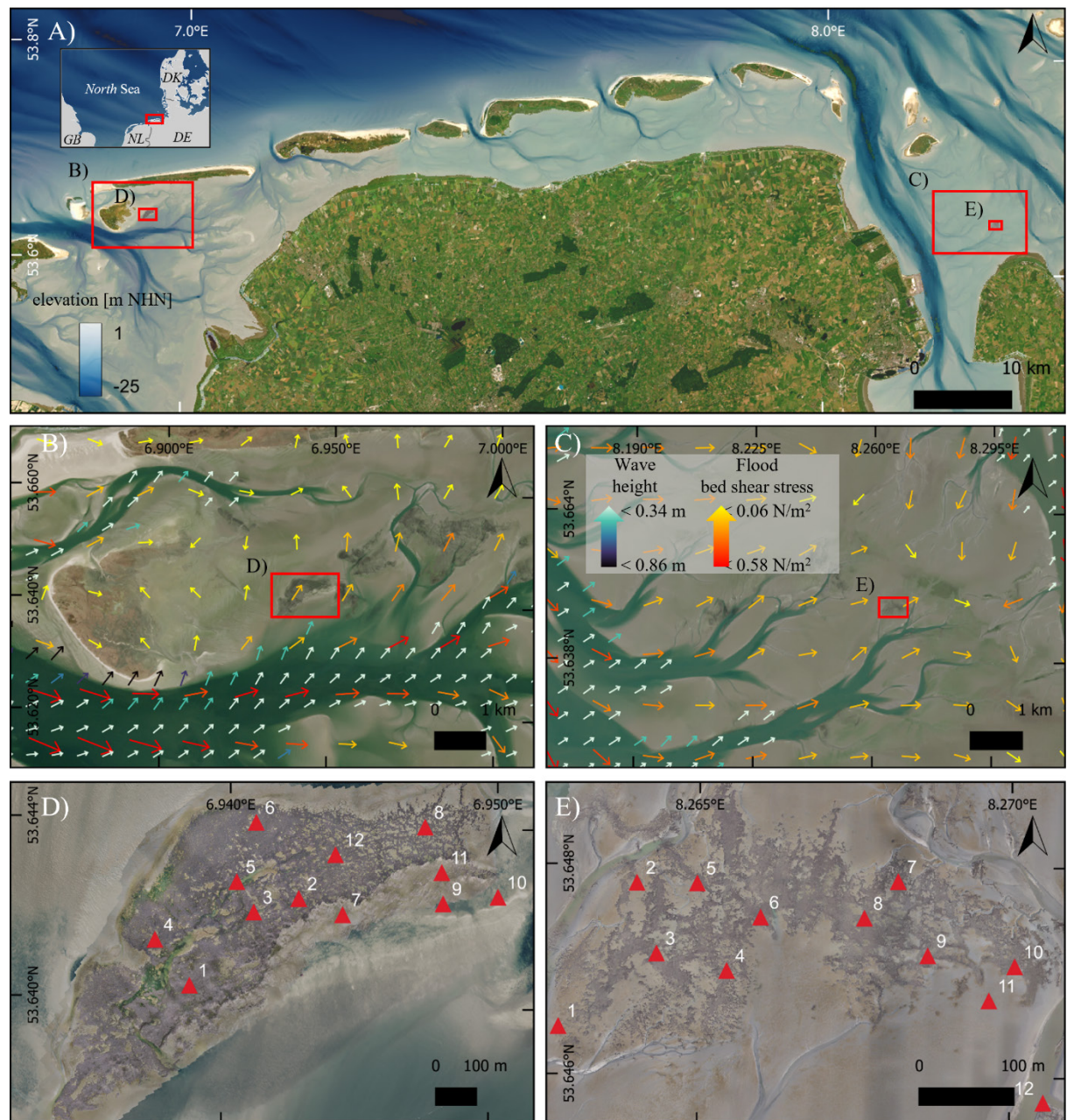


Figure 3: A) Overview map showing the location of the two oyster reef study sites Nordland and Kaiserbalje. Basemap composed of BING aerial imagery and elevation data from 2022 (Milbradt and Pineda 2024). B,C) Hydrodynamic context of the oyster reefs Nordland B) and Kaiserbalje C), displayed on Copernicus Sentinel-2A imagery from 06 April 2025. Blue arrows indicate wave direction and height based on 2022 model data (Lepper et al. 2025). Yellow-to-red arrows represent flood-phase bed shear stress direction and intensity based on model outputs for 2015 (Lepper et al. 2025). D,E) UAV-derived orthomosaics of the Nordland (D) and Kaiserbalje (E) reefs, red triangles: biological sampling sites surveyed from 2019 to 2022, dashed squares: terrestrial laser scanning area.

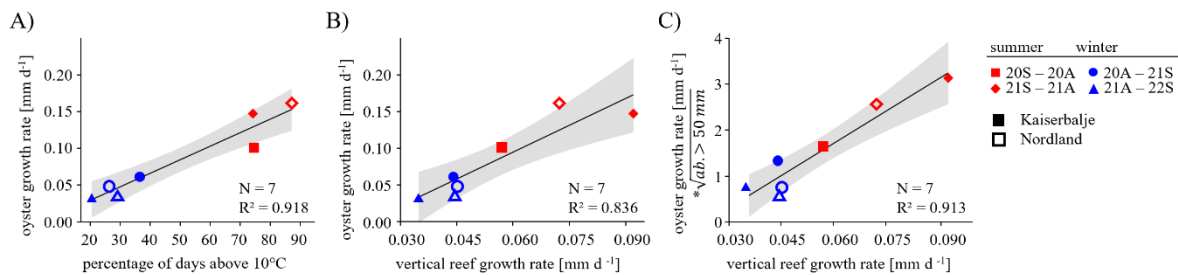


Figure 4: Correlation of biotic and abiotic factors in oyster and reef growth rates for seasonal intervals between spring (S) and autumn (A) surveys. A) Correlation of daily oyster growth rates with temperature (percentage of days above 10°C), based on the combined mean growth rate data from the 2018 and 2019 cohorts. B) Correlation between daily vertical reef growth rates and daily oyster growth rates from seasonal samplings. C) Correlation of daily vertical reef growth rate with the product of daily oyster growth rate and square root transformed abundance of oysters > 50 mm.

Highest vertical reef growth occurred at exposure times of 39.1 % MTR at KB and 36.1 % MTR at NOL, with corresponding annual growth rates of 32 mm yr⁻¹ and 29 mm yr⁻¹. Seasonal vertical reef growth differed between winter, with values of 0.03 to 0.05 mm d⁻¹, and summer, with values of 0.06 to 0.09 mm d⁻¹. In parallel to the TLS surveys, detailed population data of *M. gigas* were collected at 12 stations per reef. Length frequency distributions allowed cohort analysis to track seasonal oyster growth, which ranged from 0.03 to 0.06 mm d⁻¹ in winter and 0.10 to 0.16 mm d⁻¹ in summer.

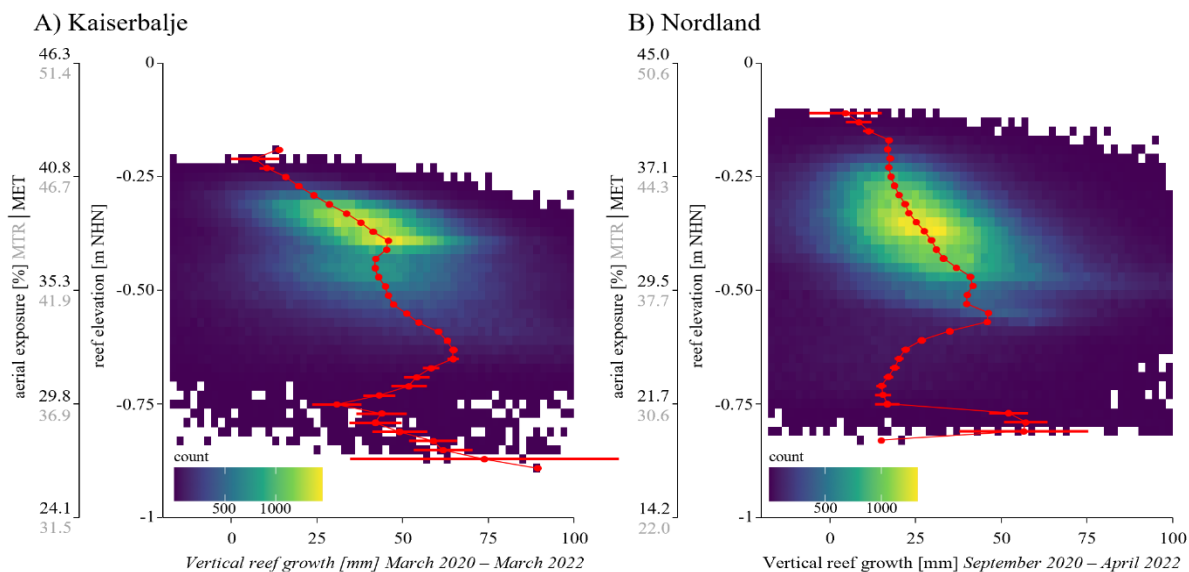


Figure 5: Analysis of oyster reef growth across elevation and aerial exposure gradients for A) Kaiserbalje and B) Nordland. The median vertical growth for 20 mm elevation bins is represented by red dots, with whiskers denoting the 95% confidence interval. The colour gradient illustrates the combined density for each 20 mm elevation bin and a 2 mm vertical reef growth bin. Aerial exposure time is given in percent in relation to data from nearby tide gauges and using mean low water to mean high water level (MTR).

By integrating local water temperature records, structural vertical reef growth was directly linked to seasonal, temperature driven shell growth patterns and local oyster abundance (Figure 5).

The results demonstrate that vertical reef growth is closely coupled to seasonal population dynamics of *M. gigas*. The correlation between structural reef growth and oyster growth confirms that vertical reef growth is a direct result of biological activity. Recruitment pulses, particularly those following warm summers, act as delayed amplifiers of vertical reef growth and can influence the vertical reef growth for several years. These findings provide a baseline explanation for how intertidal *M. gigas* reefs in the Wadden Sea grow vertically and potentially keep pace with local SLR.

3.3 Seasonal Volumetric Changes of Oyster Reefs by UAV Monitoring

Hoffmann et al. (2023) investigated the seasonal volumetric changes of an oyster reef in the German Wadden Sea, a dynamic and scarcely analyzed area in previous research (Bungenstock et al. 2021, Folmer et al. 2017). Consumer-grade unoccupied aerial vehicles (UAVs, DJI Phantom 4 Pro) were used to obtain high-resolution (20-megapixel) imagery. Structure-from-motion photogrammetry was applied to generate DEMs and orthomosaics with 5 cm/pixel. The DEMs were used to classify the coverage of a Pacific oyster reef using machine learning algorithms (Random Forest) and subsequently mapped and quantified within the orthomosaics. The primary objectives included identifying significant seasonal and spatial changes in reef dimensions and addressing the uncertainties linked to measurement and alignment errors of UAV monitoring.

The work was carried out at the oyster reef KB (Figure 6) and the analysis revealed that from March 2020 to March 2022, the oyster reef demonstrated variable growth and decline patterns across different regions (Figure 7). These changes may be the result of sediment accumulation, biodeposition (Mitchell 2006), sea bed subsidence (Behre 2003, Dijkema 1997) or reef consolidation (Ridge et al. 2017, Wehrmann 2009). However, the relative contribution of these geomorphological processes could not be separated during this study. Moreover, measurement inaccuracies due to GPS and photogrammetric errors necessitated careful consideration of uncertainties.

The study highlights the effectiveness of using a low-cost, consumer-grade UAV to obtain high-resolution imagery, which was accurately classified using the Random Forest algorithm to create precise oyster maps. This method facilitated successful change detection; however, uncertainties in measuring vertical growth posed challenges for quantifying small-scale changes. To address these challenges, an approach that incorporates error propagation throughout the processing stages was implemented, achieving a high confidence level (95 %) for the reported significant changes. Despite this, including confidence levels reduced the areas of minor growth changes, which may not fully represent the reef's evolution. Overall, the findings demonstrate that accounting for uncertainties provides reliable results and a baseline for detecting geomorphological changes with significance. Nevertheless, larger sections of the reef are excluded from analysis due to inherently high uncertainties. Despite these limitations in the data, an analysis that takes these uncertainties into account still allows for meaningful interpretations of reef dynamics and development trends.

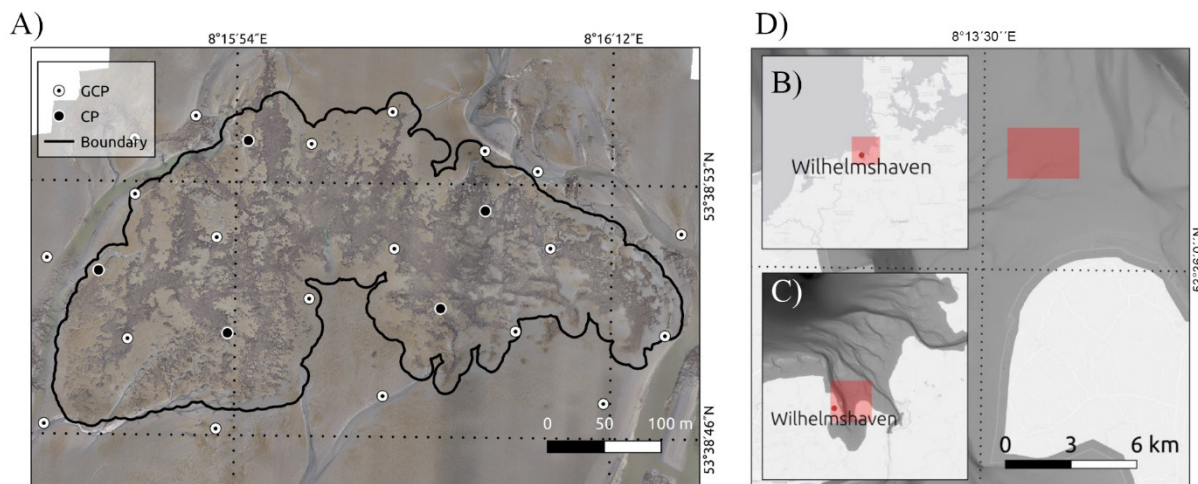


Figure 6: The left map A) shows an orthomosaic of the oyster reef at the Kaiserbalje with the distribution pattern of the ground control points (GCP) and check points (CP) for March 2022. The black contour line presents the rough reef boundary within the tidal creeks and a distance of 10 m to the oyster-identified area. Further, B) a map of the Northern European coast, C) the German Wadden Sea and D) the Jade Bight are presented with the bathymetry of the Wadden Sea (Sievers et al. 2020). Adapted from Hoffmann et al. (2023).

The results reveal a net gain in both the area and volume of the oyster reef, indicating its potential to continue expanding and keeping pace with the current local SLR. However, a further lateral expansion in all directions requires the presence of suitable hard substrates within the vertical growth zone for larval settlement. Although a precise growth ceiling for the reef top elevation of the Pacific oyster could not be established yet, a key question remains whether the reef might encounter a growth limitation as SLR persists. While extended periods of air exposure might have contributed to the observed reduction in area, no other stressors or seasonal effects impacting growth were identified.

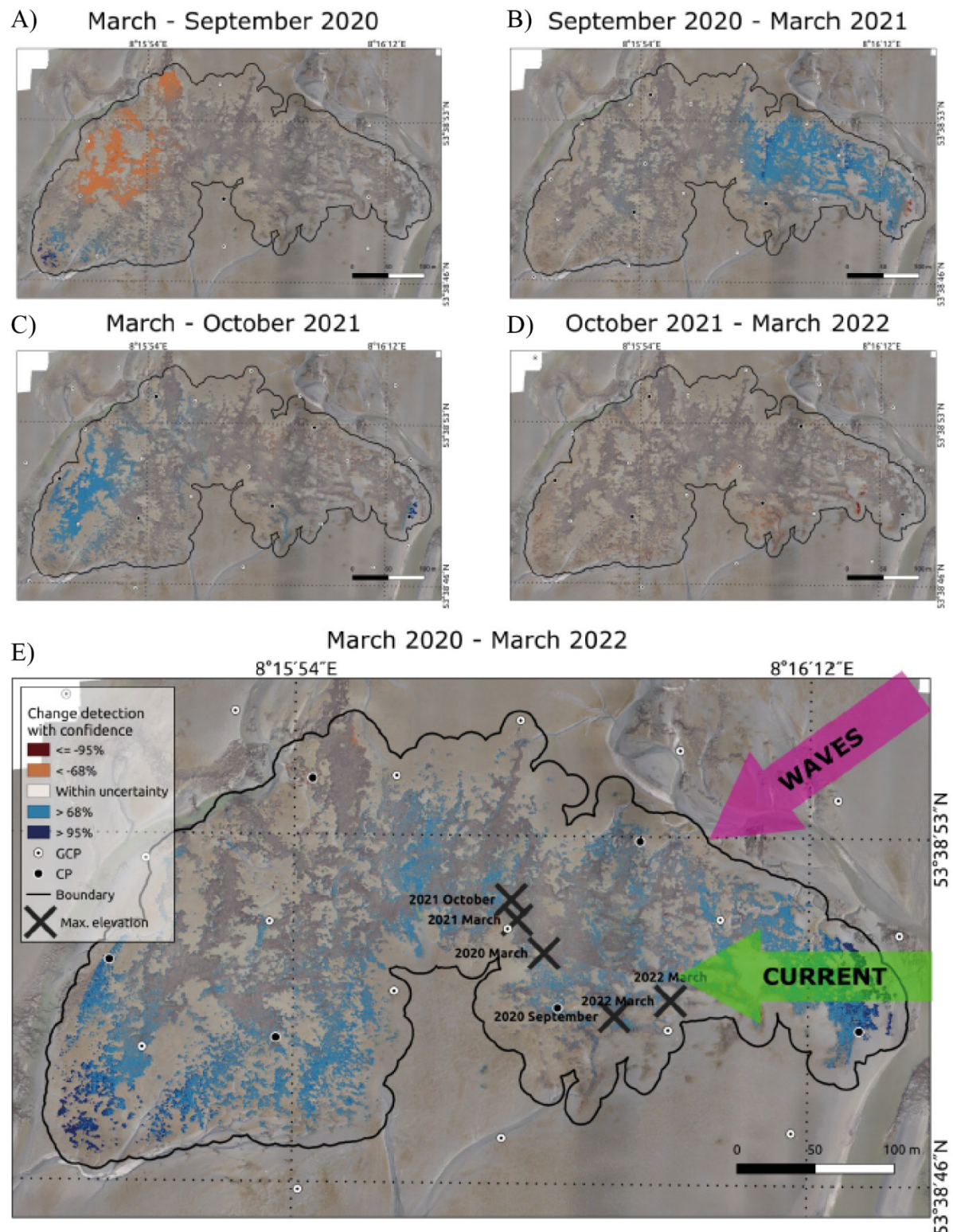


Figure 7: The subfigures A)–D) illustrate the seasonal and E) the total vertical changes of the reef between surveys, divided into loss (brown) and increase (blue). E) shows the topographical changes for the entire period from March 2020 to March 2022. The change detection with a confidence level of 68 % is presented with light blue and brown colour and the significant changes with a confidence of 95 % with a dark blue and brown colour. Within the range of the uncertainty, the elevation changes are kept transparent, i.e., changes with a confidence interval of 68 % and 95 % are included above the uncertainty. The green and magenta arrows present the main direction of the current and waves, and the surveys' maximum reef top elevations are marked with a black cross. Adapted from Hoffmann et al. (2023).

3.4 Sediment Accumulation by Coastal Biogenic Structures vs. Sea-Level Rise

The method developed by Hoffmann et al. (2023) was applied to other biogenic structures to (a) strengthen the robustness and reliability of results relating to volumetric growth and to (b) examine the geomorphological role of biogenic structures, focusing on the transformation of native blue mussel beds into Pacific oyster reefs and its implications for sediment accumulation in coastal ecosystems.

This transformation is expected to influence sedimentation patterns by altering intertidal flat roughness and morphology (Borsje et al. 2011, Hitzegrad et al. 2022, Reise et al. 2017), which is critical for predicting future coastal changes. The study investigates whether Pacific oysters enhance sediment accumulation more effectively than native mussels due to the increased roughness on the flats and contributes insights into potential resilience against accelerated SLR. In addition to the oyster reef KB studied by Hoffmann et al. (2023), the same method was applied to another oyster reef NOL and a blue mussel bed NOS with data obtained in 2020 and 2022.

Sediment dynamics displayed varied patterns across the sites. They were influenced by a combination of hydrodynamic forces and biogenic structures (Figure 8) which extended the influence on sediment dynamics beyond the circumference of the biogenic structures themselves. In addition, the oyster reefs in NOL and KB exhibited substantial increase in coverage while the blue mussel bed at NOS displayed a decline in mussel coverage over the study period and an overall lower mean elevation relative to the water level than the oyster reefs.

Sediment accumulation rates were quantified using the method of Hoffmann et al. (2023), offering a standardized measure of volumetric growth. This metric revealed that sediment accumulation exceeded erosion rates across nearly all areas of investigation. Moreover, they showed a relationship between sediment accumulation and elevation irrespective of the type of biogenic structure as structures at lower elevations generally experienced higher sediment accumulation rates (Figure 9).

Overall, the derived sediment accumulation rates up to $3.9 \text{ cm}^3/(\text{cm}^2\cdot\text{y})$ are higher than previously reported rates for intertidal flats (Benninghoff and Winter 2019) and exceed current rates of SLR in the Wadden Sea (Wahl et al. 2013).

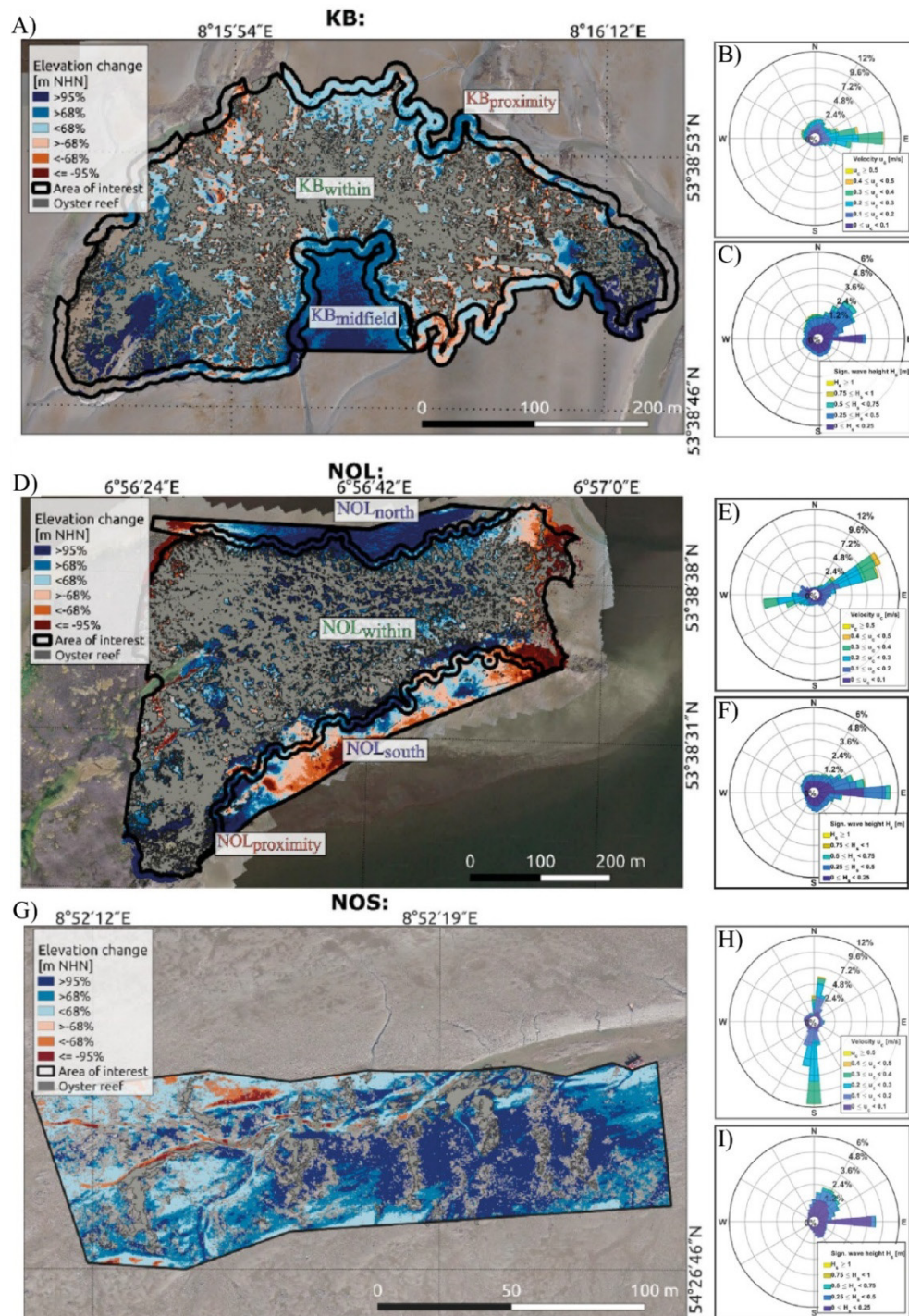


Figure 8: Total vertical changes in the sediment surfaces at the oyster reefs A) and D) and the blue mussel bed G) between 2020 and 2022, divided into erosion (red-hued shades) and accumulation (blue-hued shades). The change detection results with a confidence level of 68 % are presented in light blue and orange, and the changes with a confidence level of 95 % are shown in dark blue and red. All topographical changes that do not consider uncertainties, and hence no confidence level, are presented with either a pale red or blue colour. This study focuses on the results with a confidence level of 95 %. Location labels in panel a and b refer to sub-regions, for their detailed analysis see Hoffmann et al. (2025). Current and wave roses for each study site illustrate the direction, velocity magnitude, and frequency of currents B), E) and H) and the direction, significant wave height, and frequency of waves C), F) and I) during the period between 2005 and 2015 (Hagen et al. 2020). Digital elevation models of difference created with QGIS (version 3.16.16-Hannover, <https://qgis.org>). Projection: ETRS89/UTM zone 32 N. Illustrations of rose diagrams generated with MATLAB 2023a (<http://mathworks.com>). Figure taken from Hoffmann et al. (2025).

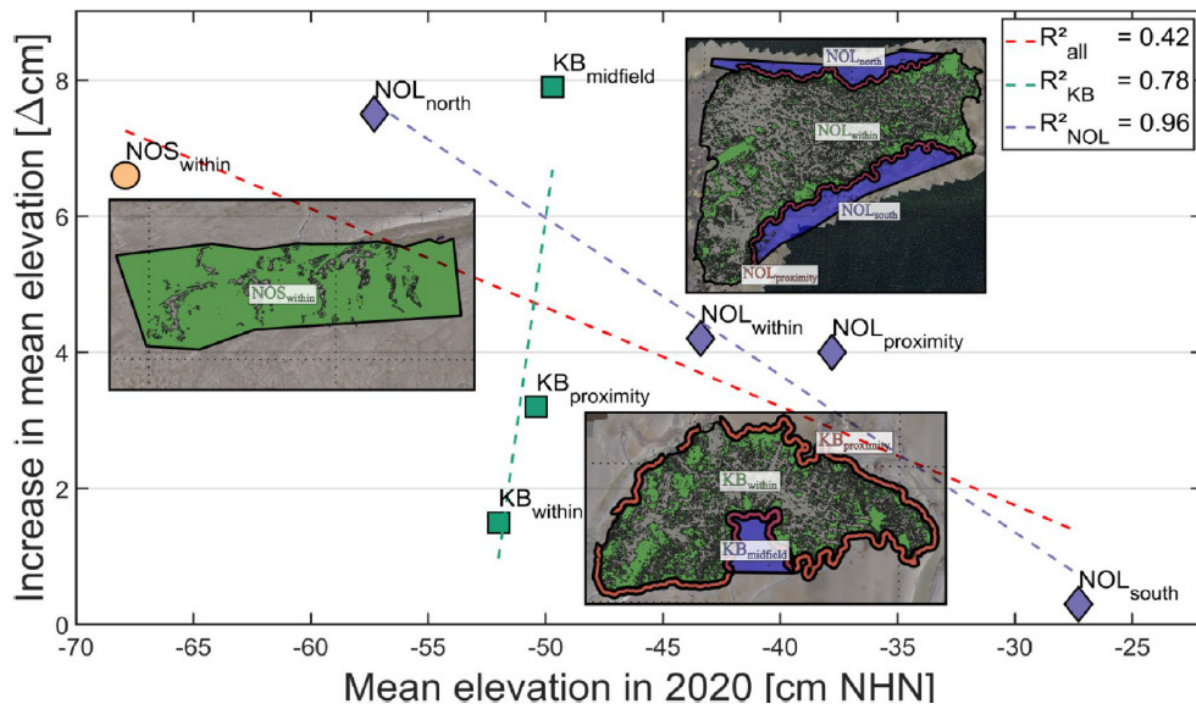


Figure 9: Correlation between the mean elevation (cm NHN) of all areas of interest in 2020 and the increase in the mean elevation of the sediment surface (Δcm) between 2020 and 2022. The dashed lines indicate the linear best fit for NOL (purple), KB (green), and all study sites (red) with a corresponding coefficient of determination. While NOS is located further north at a lower mean elevation, NOL and KB in the southern German Wadden Sea are on higher sediment surfaces. Illustrations generated with MATLAB 2023a (<http://mathworks.com>) and Inkscape 1.1 (<https://inkscape.org>). Figure taken from Hoffmann et al. (2025).

3.5 Spatial Characteristics and Lateral Stability of Non-Native Oyster Reefs

In Pfennings et al. (in prep.) spatial reef configuration and lateral reef dynamics were analysed using the UAV-derived and classified orthomosaics from Hoffmann et al. (2023) and (2025). The intra-reef classification developed by Hitzegrad et al. (2022) was applied across the full extent of both reefs, allowing the identification of reef wide structural patterns. Classified reef surfaces were converted into polygons and each polygon was assigned to one of five structural classes based on its perimeter: Clusters (<7 m), Patch I (7 to 20 m), Patch II (20 to 250 m), Transitional Zone (250 to 1500 m) and Central Reef (>1500 m). Connected Central Reef and Transitional Zone classes were further subdivided by internal reef coverage, with values above 66 % indicating Central Reef and lower values indicating Transitional Zone. Lateral reef dynamics were quantified through polygon intersections, differences between successive surveys and minimal distances between corresponding reef boundaries. Population data on *M. gigas* and *M. edulis* were integrated to estimate reef scale metrics of abundance and biomass.

The reef scale classification after Hitzegrad et al. (2022) (Table 2) showed that isolated structural classes at the Nordland reef, including Clusters, Patch I and Patch II structures, occurred mainly along the southeastern reef margin, while Central Reef and Transitional Zone classes formed a continuous biogenic surface of 237,378 m² (Figure 10). At KB, Cluster structures were concentrated along the southwestern margin and Patch I and

Patch II were distributed irregularly around the reef margin. Central Reef and Transitional Zone classes formed a continuous surface of 34,860 m² (Figure 11).

The analysis of lateral reef dynamics revealed progressive erosion at the wave and flood current exposed margin of NOL (Figure 12), resulting in retreat distances of 3.5 ± 3.0 m (Mean $\pm$ S.D.) over a two-year period. At KB, lateral change was governed by periodic sediment cover and subsequent re-exposure, which led to temporary reductions in visible reef extent before previously buried reef surfaces became exposed again (Figure 13 and Figure 14).

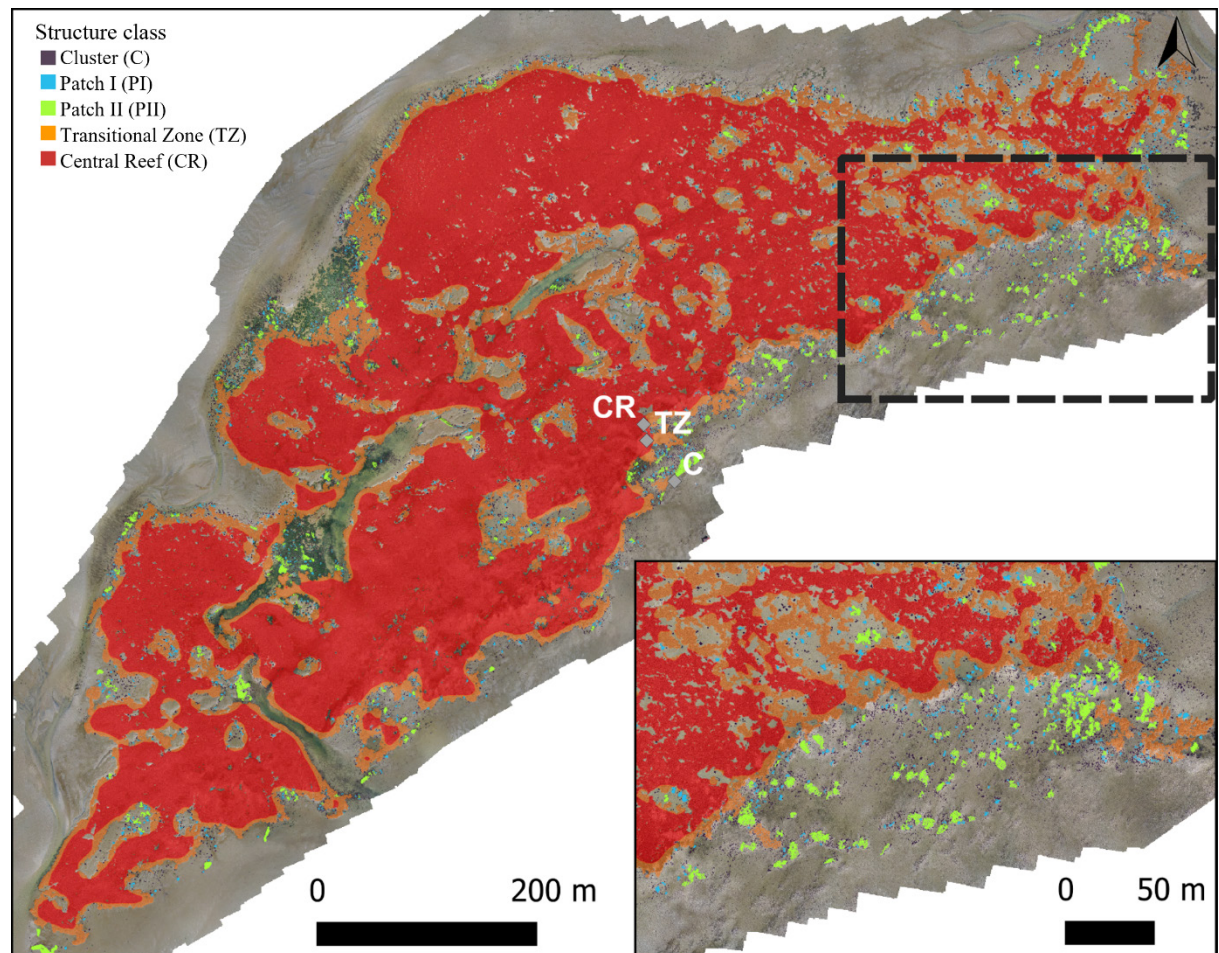


Figure 10: Intra-reef structural classification of the Nordland reef based on the UAV-derived ortho-mosaic from September 2021. The reef surface is subdivided into five structure classes following the framework of Hitzegrad et al. (2022).

The integration of population data on *M. gigas* and *M. edulis* allowed for reef scale estimates of abundance, live wet weight and dead shell weight, summarised in Table 3. Present day values support the interpretation of the KB and NOL reefs as mature reef systems approaching spatial saturation and align with the proposed carrying capacity of 30 to 50 kg m⁻² live wet weight for intertidal *M. gigas* reefs in the Wadden Sea (Nehls and Büttger 2007). The associated *M. edulis* population indicates a sustainable level of persistence and functional coexistence, although values remain below the moderate biomass range of natural blue mussel beds, classified as 3 to 6.2 kg m² (poor) and 6.2 to 9.4 kg m² (moderate) (Büttger et al. 2010).

The results show that integrating intra-reef structural classification by Hitzegrad et al. (2022), UAV based mapping by Hoffmann et al. (2023) and (2025) and population data provides a coherent framework for analysing spatial reef configuration and lateral dynamics of the Wadden Sea oyster reefs. While vertical reef growth is closely tied to oyster recruitment, individual growth and local exposure time, as shown by Pfennings et al. (2024), short term lateral dynamics are governed by highly local hydro-morphodynamic conditions. Key lateral drivers include erosion at exposed reef margins, episodic sediment burial in low energetic areas and subsequent re-exposure of reef surfaces.

Table 2: Proportional and absolute area of intra-reef structural classes after Hitzegrad et al. (2022) at the Kaiserbalje (March 2022) and Nordland (September 2021) reefs.

Reef	Coverage	Cluster (C)	Patch I (PI)	Patch II (PII)	Transitional Zone (TZ)	Central Reef (CR)
Kaiserbalje	%	1.5	2.5	5.9	43.3	46.7
	area [m ²]	622	1,006	2,396	17,431	18,821
Nordland	%	2.2	1.2	2.1	18.1	76.5
	area [m ²]	5,503	3,048	5,150	45,362	192,016

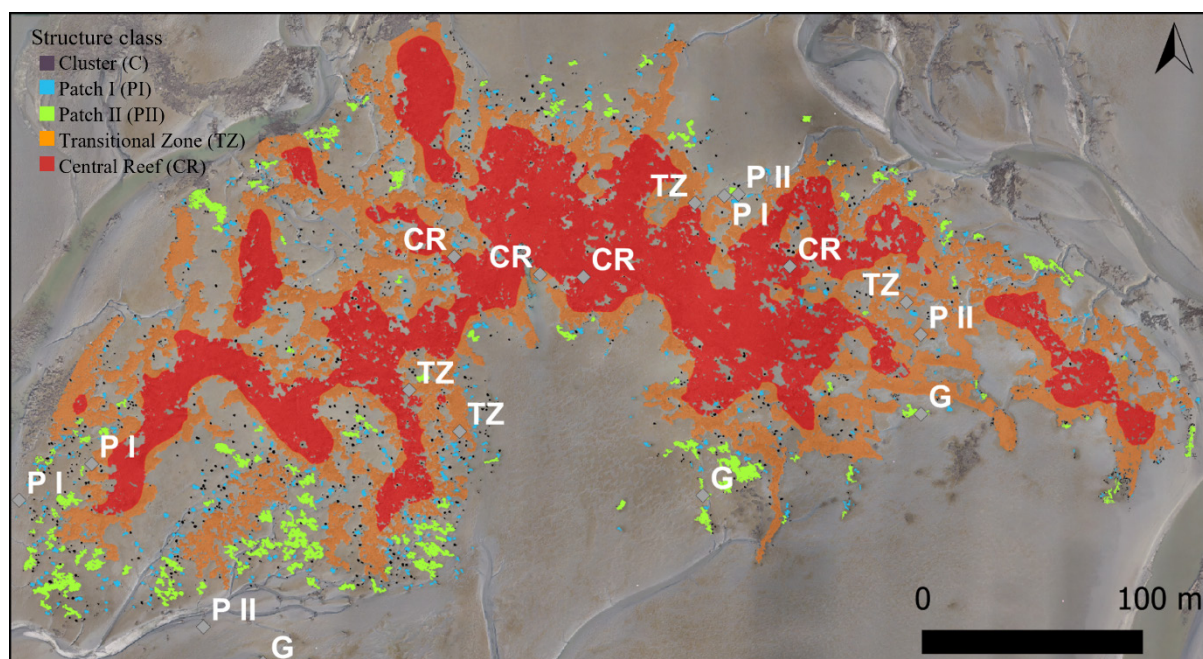


Figure 11: Intra-reef structural classification of the Kaiserbalje reef based on the UAV-derived orthomosaic from March 2022. The reef surface is subdivided into five structure classes following the framework of Hitzegrad et al. (2022). Previously identified Garland structures (G) are additionally indicated in the figure but not further listed.

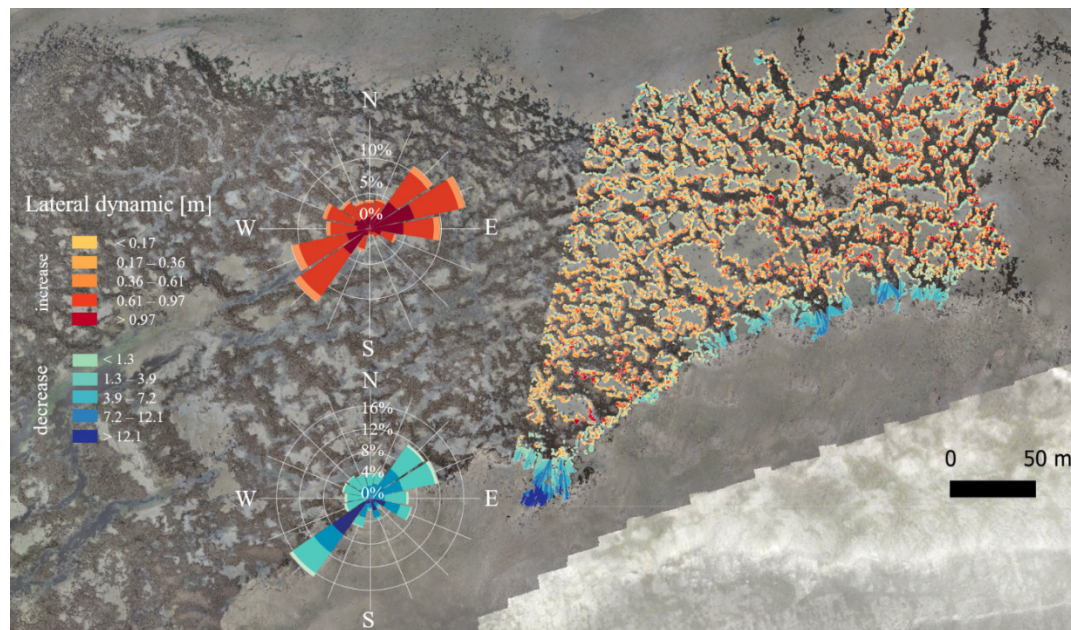


Figure 12: Distance-based analysis of lateral reef surface change at the subsection of the Nordland reef between July 2020 and April 2022. Each line represents the shortest distance between the corresponding reef outlines of both time points. The yellow-to-red gradient indicates lateral reef expansion and the blue gradient indicates contraction. The rose diagrams in the upper left show the dominant directions of surface increase (red) and decrease (blue).

Table 3: Mean and interpolated population parameters for *Magallana gigas* and *Mytilus edulis* at the Kaiserbalje (KB; March 2022) and Nordland (NOL; September 2021) reefs, including corresponding mean values for areas used for interpolation based on Inverse Distance Weighting (IDW). Live wet weight (LWW), abundance (ab.) and dead shell weight (DSW).

Reef	Parameter	Mean $\pm$ S.D.	On mean area	On area	IDW	IDW mean
KB			(38,801 m ²)	March 2022 (40,276 m ²)		
	<i>M. gigas</i> LWW	31.1 $\pm$ 3.5 [kg m ⁻²]	1,206.71 [t]	1,254.67 [t]	1,234.95 [t]	30.7 [kg m ⁻²]
	<i>M. gigas</i> ab. (>25 mm)	627 $\pm$ 43 [ind. m ⁻²]	24,328,227 [ind.]	25,257,527 [ind.]	23,481,594 [ind.]	583 [ind. m ⁻²]
	<i>M. gigas</i> DSW	19.5 $\pm$ 8.4 [kg m ⁻²]	756.62 [t]	787.13 [t]	860.42 [t]	21.4 [kg m ⁻²]
	<i>M. edulis</i> LWW	5.3 $\pm$ 0.670 [kg m ⁻²]	205.65 [t]	212.31 [t]	221.70 [t]	5.5 [kg m ⁻²]
NOL			(240,151 m ²)	September 2021 (247,956 m ²)		
	<i>M. gigas</i> LWW	19.0 $\pm$ 2.7 [kg m ⁻²]	4,562.87 [t]	4,772.27 [t]	6,268.96 [t]	25.0 [kg m ⁻²]
	<i>M. gigas</i> ab. (>25 mm)	338 $\pm$ 87 [ind. m ⁻²]	81,171,038 [ind.]	84,753,111 [ind.]	100,392,108 [ind.]	400 [ind. m ⁻²]
	<i>M. gigas</i> DSW	16.0 $\pm$ 5.9 [kg m ⁻²]	3,840.01 [t]	4,015.02 [t]	5,035.28 [t]	20.1 [kg m ⁻²]
	<i>M. edulis</i> LWW	3.5 $\pm$ 0.4 [kg m ⁻²]	840.53 [t]	888.30 [t]	1,004.05 [t]	4.0 [kg m ⁻²]

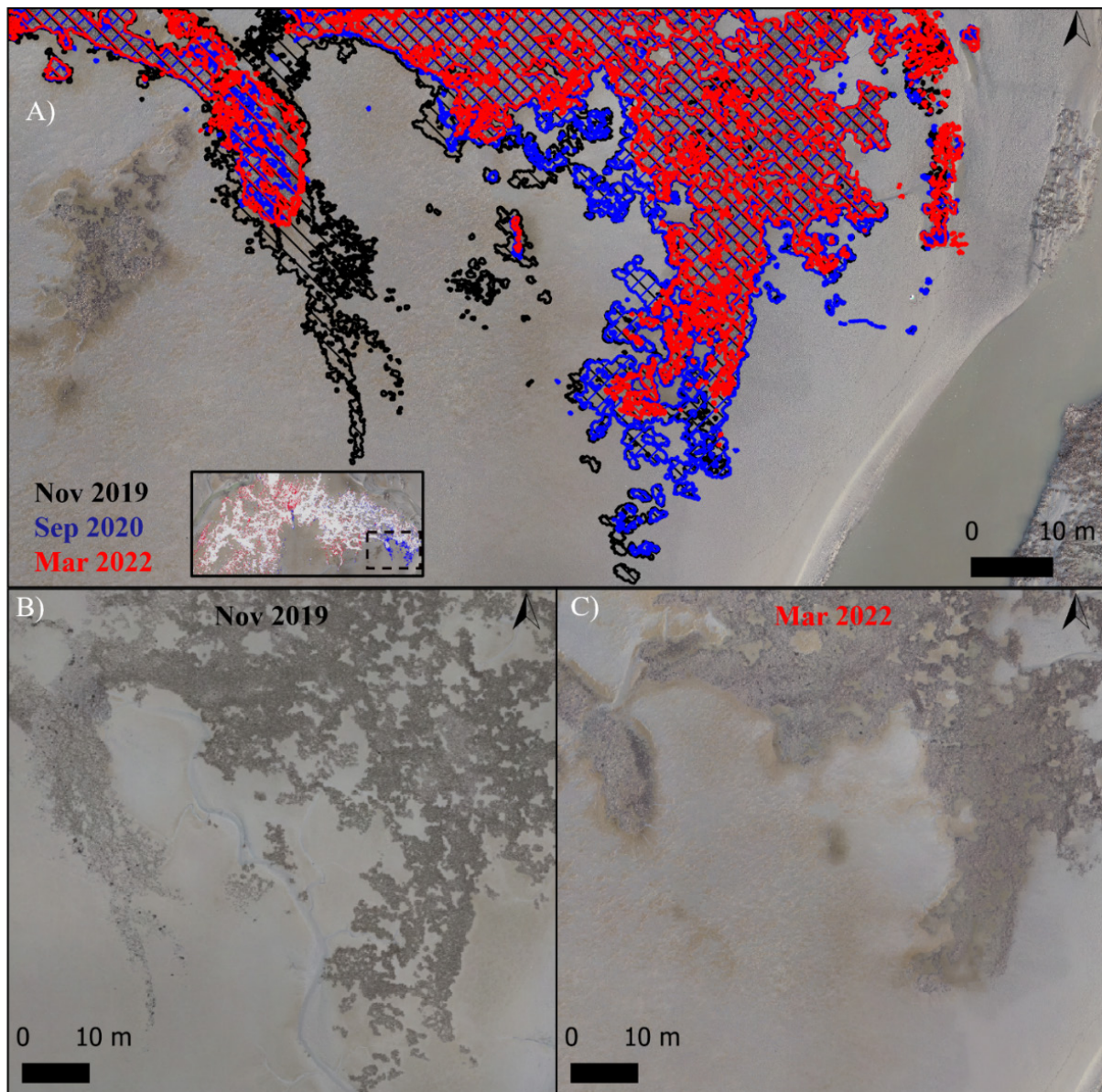


Figure 13: Temporal development at the southeastern margin of the Kaiserbalje reef based on UAV-derived orthomosaics from November 2019, September 2020, and March 2022. (a) Overlay of reef extents from the three time points. (b, c) Zoomed-in orthomosaic of the area in November 2019 (b) and March 2022 (c). The white arrow in (a) indicates the position and viewing direction of the photograph shown in Figure 13.

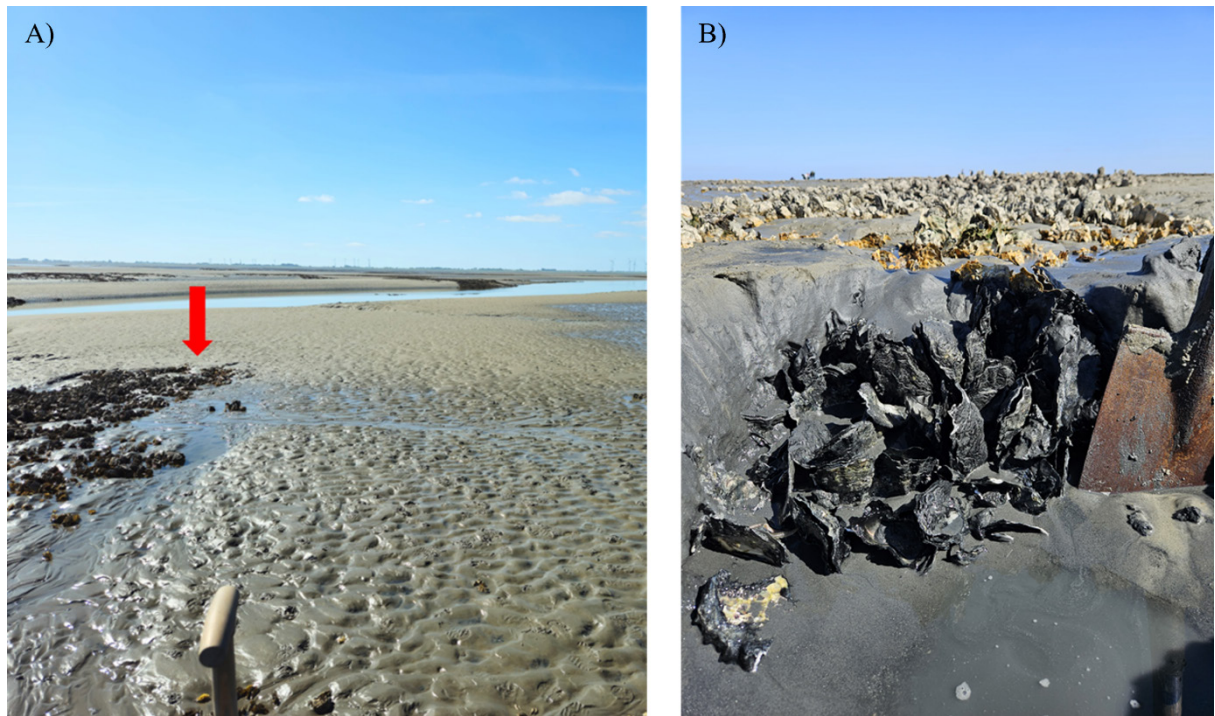


Figure 14: A) South-eastern margin of the Kaiserbalje reef showing sediment coverage by mobile sand layers. The brighter surface indicates recent sand deposition on top of the reef. B) Close up view of partial reef burial and re-exposure at the same margin. Dark oysters in life position are overlain by approximately 0.1 to 0.2 m of fine sediment, while yellowish shells above indicate recent oxidation and re-exposure. Images were taken in June 2025.

4 Quantification of the Impact of the Biogenic Structures on Wave Attenuation and Flow Resistance

The interactions between the biogenic structures and the ambient hydrodynamics were investigated in controlled hydrodynamic experiments using several experimental facilities (two-dimensional current and wave flumes as well as a three-dimensional wave-current basin). By doing so, wave-, current-, and wave-current-biogenic structure interactions have been investigated under controlled conditions. However, the physical dimensions of the experimental facilities required the use of scaled-down (1:3) surrogate models of the biogenic structures.

4.1 Oyster Reef and Blue Mussel Bed Surrogates: Digital Design and Fabrication Strategies

Approximating complex coastal surfaces for experimental modeling has long posed substantial challenges as conventional manufacturing methods rely on labor-intensive manual workflows that are time-consuming, prone to errors, and often yield oversimplifications that deviate substantially from *in situ* conditions (Aberle et al. 2021, Briggs 2013, Hughes 1993). Recent advances in digital manufacturing, including wider availability and the adaptation of fabrication technologies to larger-scale applications, enable efficient production of complex, three-dimensional surrogate models (Flack et al. 2020, Kloft et al. 2021, Stewart et al. 2019).

Hitzegrad et al. (2024a) investigated how complex topographies of coastal biogenic structures, i.e., *M. edulis* beds and *M. gigas* reefs, can be accurately replicated using advanced digital design and additive manufacturing strategies. Generic, scaled-down surrogate models of both biogenic structures were developed and produced in an iterative workflow (Figure 15). The workflow integrates parameterization, computer-aided design, and fabrication, accounting for i) topographical parameters, ii) the requirements of experimental setups, and iii) the possibilities and limitations of the fabrication method. Particle bed 3D printing with Selective Cement Activation was used as a novel fabrication method for experimental modelling, allowing the fabrication of complex geometries without increasing production time (Lowke et al. 2018).

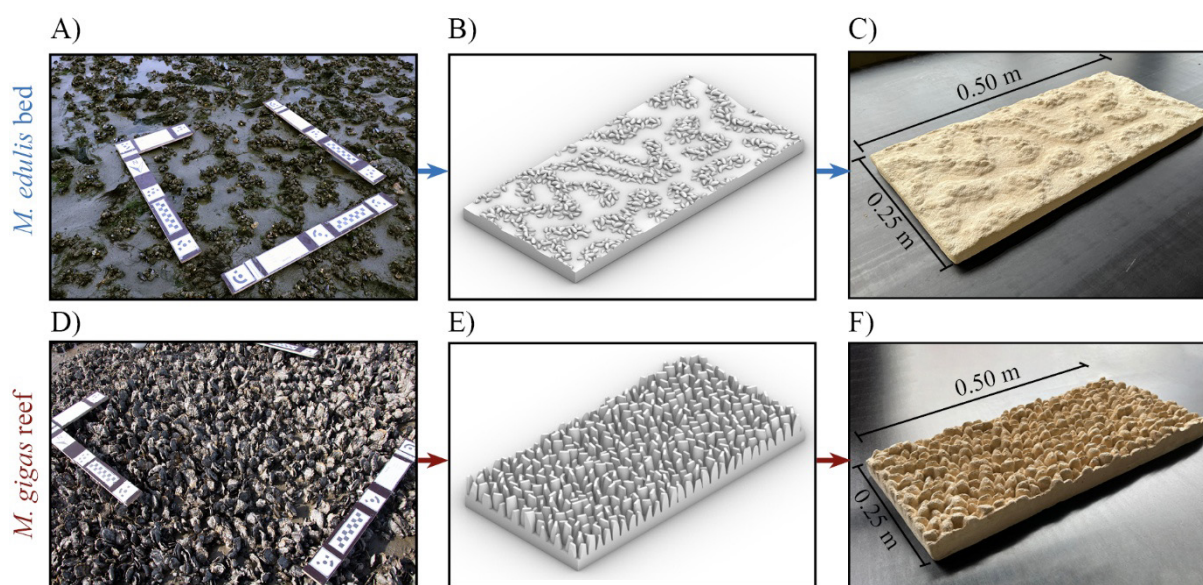


Figure 15: Visualization of the surrogate model design process, including photographs of A) a *Mytilus edulis* bed sample (sample MB2 in Hitzegrad et al. 2024a) and D) a *Magallana gigas* reef sample (sample CR3 in Hitzegrad et al. 2024a), visualizations of the digital models for the B) *Mytilus edulis* bed and E) *Magallana gigas* reef surrogate model tiles, and exemplary photographs of the fabricated C) *Mytilus edulis* and F) *Magallana gigas* surrogate model tiles. Adapted from Hitzegrad et al. (2024a) and Hitzegrad (2025).

A comparative analysis of topographical roughness parameters revealed apparent differences between natural *M. edulis* bed and *M. gigas* reef surfaces. In particular, the measured total roughness height of *M. edulis* beds ($k_t = 70 \pm 6$ mm) was lower than that of *M. gigas* reefs ($k_t = 101 \pm 10$ mm). Additional differences were observed in abundance, surface coverage, spatial arrangements, shell dimensions, probability density functions of the surface elevations, and porosity distributions.

Generic surrogate surfaces for both biogenic structures were digitally modeled through an underlying planar sediment layer, onto which modelled shells were placed according to characteristic spatial patterns. Shells were parameterized by length, width, horizontal orientation, and vertical inclination. For the blue mussel bed surrogate model, a generic pattern was developed that mimics the net-shaped arrangement of mussel agglomerations. In contrast, the oyster reef surrogate model featured densely packed oyster shells arranged in a honeycomb pattern. Following an iterative optimization of the digital models and fabrication process, 8 m² of surrogate surface were manufactured for each surrogate surface, subdivided into 64 uniform tiles. Quantitative comparison of the surface characteristics of

the fabricated surrogate surfaces with those of the natural biogenic structures revealed high accuracy in replicating the key topographical characteristics of the moderately complex *M. edulis* bed surrogate model. Challenges persisted in replicating the sharp ventral margins of natural oyster shells in the highly complex *M. gigas* reef surrogate model.

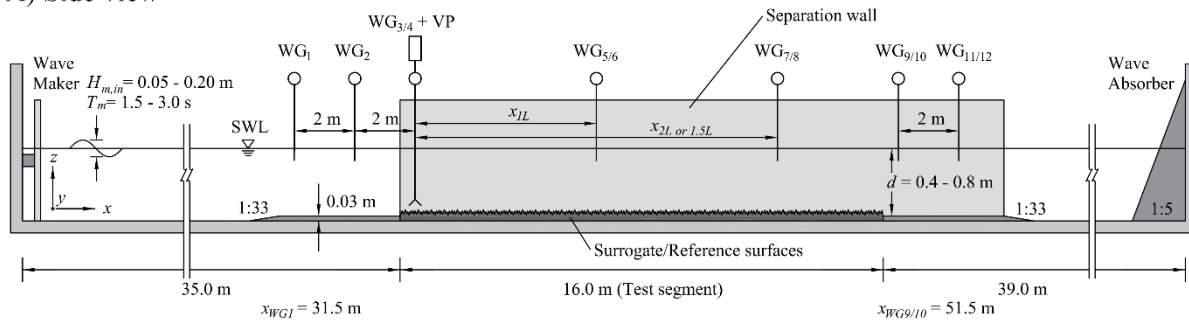
The results demonstrate that the workflow reliably produced surrogate surfaces that closely match the hydraulic-relevant features of complex coastal biogenic structures. Particle bed 3D printing with Selective Cement Activation proved to be a suitable method for manufacturing these complex geometries, enabling consistent production regardless of time and surface complexity. The fabricated surrogate models enabled systematic investigations of the influence of these biogenic structures on the ambient hydrodynamics.

4.2 Wave-Induced Hydrodynamics of Oyster Reefs

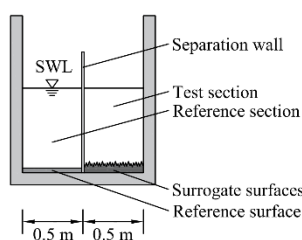
In the Wadden Sea, biogenic structures form low-crested, spatially extensive, and very to ultra-rough surfaces compared to the relatively smooth surrounding sand and mud flats (Bungenstock et al. 2021, Reise et al. 2017). Thus, wave energy dissipation due to bed friction is expected to substantially contribute to the overall wave attenuation (Donker et al. 2013). Hitzegrad et al. (2023, 2025b) subjected the surrogate models of *M. edulis* beds and *M. gigas* reefs (Hitzegrad et al. 2024a) to regular, non-breaking waves in reduced-scale 2D wave flume experiments to systematically investigate their influence on frictional wave energy dissipation (Figure 16). Water surface elevations and near-bed velocities were analyzed to determine estimates of the wave friction factor f_w , the hydraulic roughness lengths k_w , and the maximum wave-induced bed shear stress $\tau_{w,max}$. In controlled experiments, the surrogate models were subjected to regular, non-breaking waves with varying water depths $d = 0.4; 0.5; 0.6; 0.7; 0.8$ m, mean wave periods $T_m = 1.5; 2.0; 2.5; 3.0$ s, and incident mean wave heights $H_{m,in} = 0.05; 0.10; 0.15; 0.20$ m.

The analysis revealed that the *M. gigas* reef surrogate model dissipated approximately twice the frictional wave energy (wave friction factor $f_{w,OR} = 0.44 \pm 0.30$) as the *M. edulis* bed surrogate model ($f_{w,MB} = 0.21 \pm 0.18$) (Figure 17), in agreement with findings of preceding studies on frictional wave energy dissipation of biogenic structures in soft-bottom environments (Borsje et al. 2011, Donker et al. 2013) and substantially higher than typical ranges for sediment surfaces ($f_w = 0.01 - 0.10$; Kamphuis 1975).

A) Side view



B) Cross-section



C) Surrogate model tiles

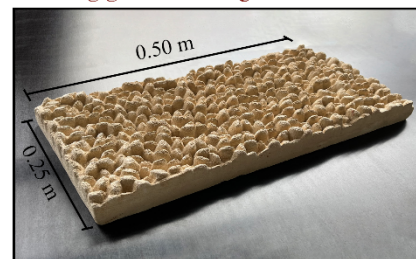
M. edulis bed surrogate model tile*M. gigas* reef surrogate model tile

Figure 16: A) Side view and B) cross-section schematics of the experimental setup in the wave flume (not to scale), where SWL denotes the still water level. The positions of the Vectrino Profiler (VP) and wave gauges (WG) are indicated. C) Tiles of the complex *M. edulis* bed and the *M. gigas* reef surrogate models are shown exemplarily. Adapted from Hitzegrad et al. (2025b).

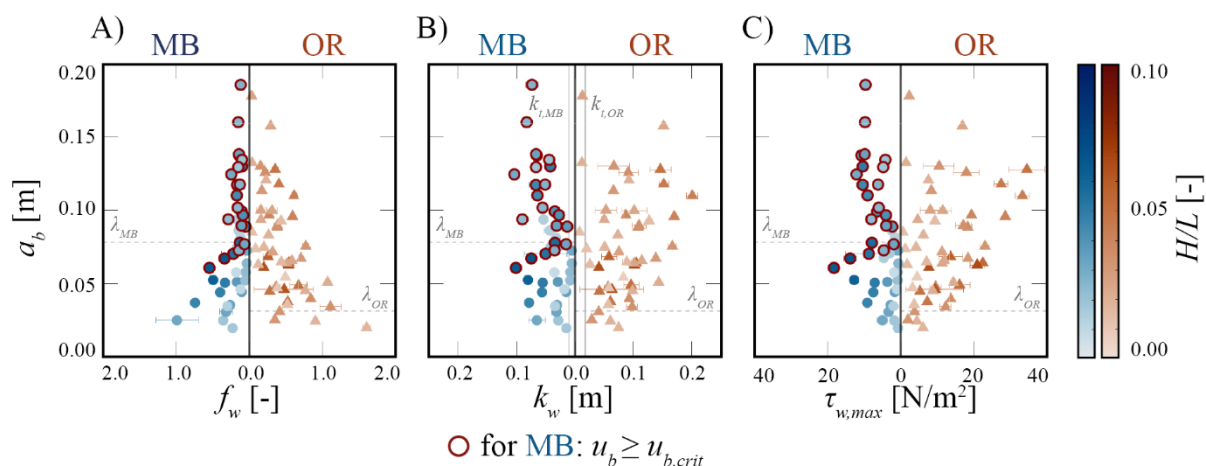


Figure 17: Averaged values and standard deviations of A) the wave friction factor, f_w , [-] B) the hydraulic roughness height, k_w , [m] and C) the maximum bed stress, $\tau_{w,max}$, [N/m²] as functions of the near-bed horizontal wave excursion amplitude, a_b , [m] on the y -axis and the wave steepness ratio, H/L , [-] light to dark colors (color scale: Cramer 2018). The results are sorted by surrogate model: blue mussel bed surrogate model (MB) center to left with blue markers and oyster reef surrogate model (OR) center to right with red markers. The vertical, solid gray lines mark the total roughness height, k_t , [m], of the respective surrogate model. The horizontal, dashed gray lines mark the characteristic roughness length scale, λ , [m] of the respective surrogate model. Red marker edges visualize the hydrodynamic cases for the MB that exceeded the threshold of dislodgement $u_b \geq u_{b,crit} = 0.23$ m/s (Smit et al. 2024). Adapted from Hitzegrad et al. (2025b).

Furthermore, the analysis revealed that distinct dissipation mechanisms prevail in both surrogate models, driven by differences in their respective significant roughness elements: Agglomerations for *M. edulis* beds and individual oyster shells for *M. gigas* reefs. Hereby, the wave-biogenic structure interactions are primarily governed by i) the total roughness height

k_r , ii) the shape of the significant roughness elements, and iii) the spacings λ between them, relative to the maximum near-bed excursion amplitude a_b . Under moderate hydrodynamic conditions ($\lambda/a_b < 1$), the *M. edulis* bed surrogate model induced wave attenuation predominantly due to form drag; however, flow separation substantially reduced its frictional resistance under intense wave action ($\lambda/a_b > 1$). The hydrodynamic conditions causing flow separation from the *M. edulis* bed surrogate model align with dislodgement thresholds of mussel individuals identified by Smit et al. (2024) and Zhao et al. (2025). In contrast, the *M. gigas* reef surrogate model maintained substantial wave energy dissipation across a broader range of hydrodynamic conditions due to their sharp-edged, rigid shells, making it more effective at attenuating wave energy.

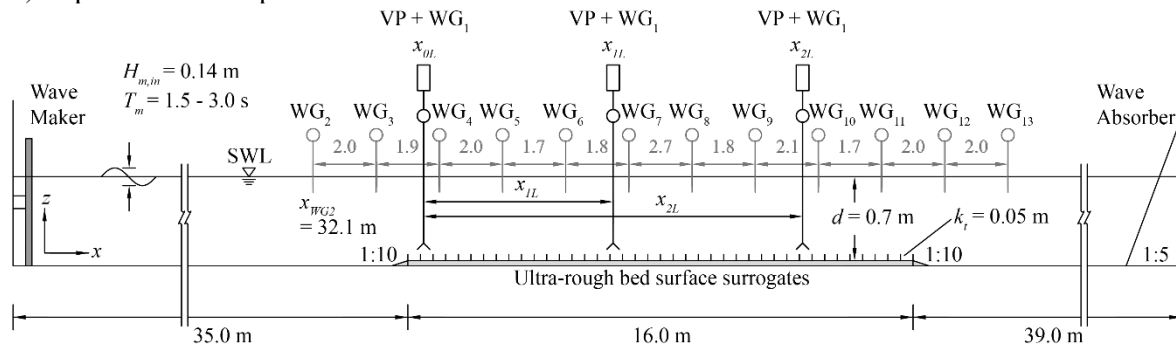
4.3 Understanding the Role of Sharp Edges in the Propagation of Surface Gravity Waves

The individual oyster shells with their sharp ventral margins have been identified as a key topographical characteristic that governs the hydraulic roughness of oyster reefs (Hitzegrad et al. 2022). Replicating these ventral margins in surrogate models proved technically challenging (Hitzegrad et al. 2024a), which may have led to underestimation of the frictional wave energy dissipation in the wave flume study by Hitzegrad et al. (2025b). To address this limitation, Hitzegrad et al. (2024b) report on a complementary wave flume study, investigating the role of the sharpness of roughness elements in wave attenuation in isolation.

Six abstract, rough surfaces were subjected to regular, non-breaking waves with systematically varying near-bed horizontal wave excursion amplitudes (Figure 18). The surfaces differed in the shape of the roughness elements (bluntly-shaped semicircle, sharp-edged Lamella, and a combination thereof Mix) and spacings between roughness elements ($\lambda = 0.10$ m and 0.20 m) with the same total roughness height ($k_r = 0.05$ m). In controlled experiments, the surfaces were subjected to regular, non-breaking waves with constant water depth of $d = 0.7$ m and varying mean wave periods $T_m = 1.5; 2.0; 2.5; 3.0$ s, and incident mean wave heights $H_{m,in} = 0.05; 0.10; 0.15; 0.20$ m.

Analysis of the water surface elevations and the near-bed velocities revealed that the surfaces with sharp-edged roughness elements dissipated substantially more wave energy than those with bluntly-shaped roughness elements. Turbulence production on the Lamella surfaces exceeded that of the bluntly-shaped surfaces by a factor of 2–27, whereas the Mix surfaces produced 1–18 times greater turbulence. Maximum bed shear stresses, hydraulic roughness lengths, and wave friction factors were 4–37, 10–140, and 6–45 times higher for sharp-edged compared to bluntly-shaped surfaces (Figure 19). Across all investigated surfaces, the most pronounced bed shear stresses were generated for moderate near-bed horizontal wave excursion and velocity amplitudes, suggesting a nonlinear threshold as the near-bed wave orbital horizontal velocity amplitude and relative roughness density increase. Comparing the bed shear stress estimates derived from an energy balance based on the water surface elevations with those derived from near-bed velocity profiles revealed that both shear stresses resulting from the turbulent fluctuations and dispersive stresses resulting from the work of the mean flow against the pressure drag of each roughness element contribute to the total bed shear stress of such ultra-rough surfaces.

A) Experimental Setup



B) Primitive Shapes

C) Ultra-Rough Bed Surface Configurations

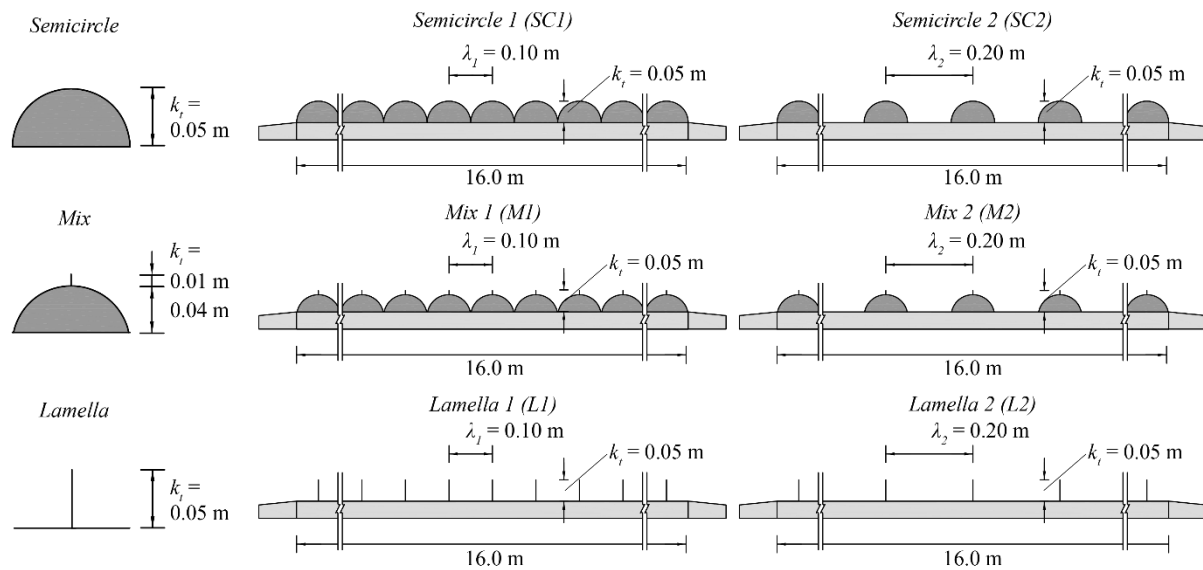


Figure 18: A) Schematic of the experimental setup in the wave flume (not to scale), where SWL is the still water level, and k_t is the total roughness height, $H_{m,in}$ is the mean incident wave height, and T_m is the mean wave period. The positions of the Vectrino Profiler (VP) and wave gauges (WG) are indicated. B) Side views of the abstract roughness element shapes. C) The six abstract surrogate models: Semicircle 1, Semicircle 2, Mix 1, Mix 2, Lamella 1, and Lamella 2. Adapted from Hitzegrad et al. (2024b).

These findings confirm that the sharpness of roughness elements of rough coastal surfaces is a key characteristic governing frictional energy dissipation and spacing between roughness elements further modulates this effect by influencing the roughness density and flow interaction. Consequently, the findings highlight the role of the sharp ventral margins characteristic of *M. gigas* reefs and spatial arrangement of *M. gigas* in governing the hydraulic roughness and wave attenuation capacity of oyster reefs, thereby complementing and extending the findings of Hitzegrad et al. (2025b).

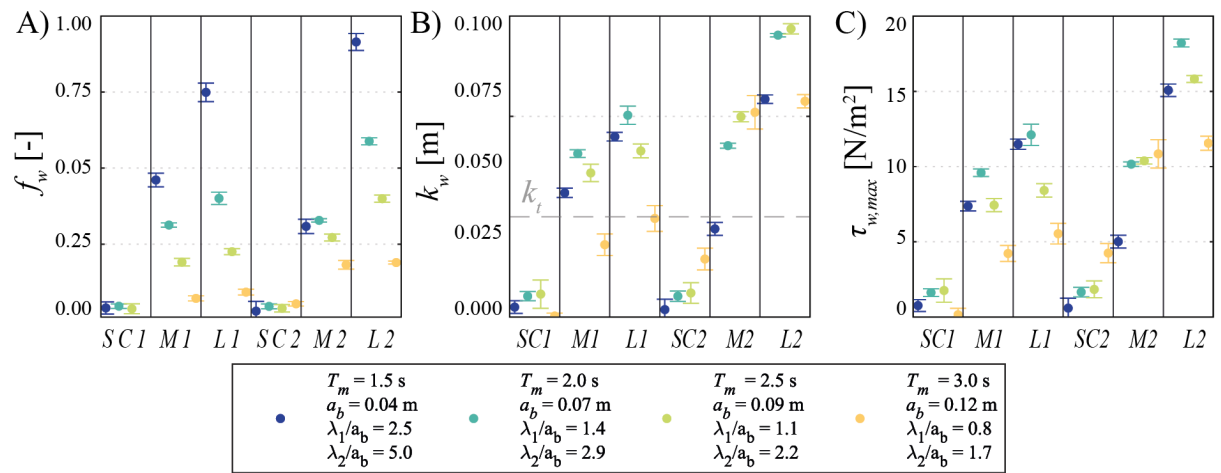


Figure 19: Averaged values and standard deviations of A) the wave friction factors f_w , B) the hydraulic roughness length k_w , and C) the bed shear stresses $\tau_{w,max}$ determined by applying the energy balance method. The results are sorted by bed surface configurations (SC1: semicircle 1, M1: Mix 1, L1: Lamella 1, SC2: Semicircle 2, M2: Mix 2, L2: Lamella 2) and hydrodynamic cases (mean wave period T_m and near-bed horizontal wave excursion amplitudes a_b). The parameter λ is the spacing between roughness elements. The dashed gray line in b) marks the total roughness height k_t of the roughness elements. Adapted from Hitzegrad et al. (2024b).

4.4 High-Fidelity Numerical Simulation of Oscillating Flows and Turbulence Structures past a Single Oyster Individual

The experimental studies by Hitzegrad et al. (2024b) and (2025b) provide in-depth datasets of wave-oyster reef interactions, which enable the calibration and validation of high-fidelity numerical simulations. Based on these findings, Hitzegrad et al. (2025c) report on a numerical study simulating wave-oyster reef interactions on a small scale, specifically an individual oyster shell at high fidelity to examine the wave-oyster interaction by analyzing the flow field, the turbulence production, and force progression.

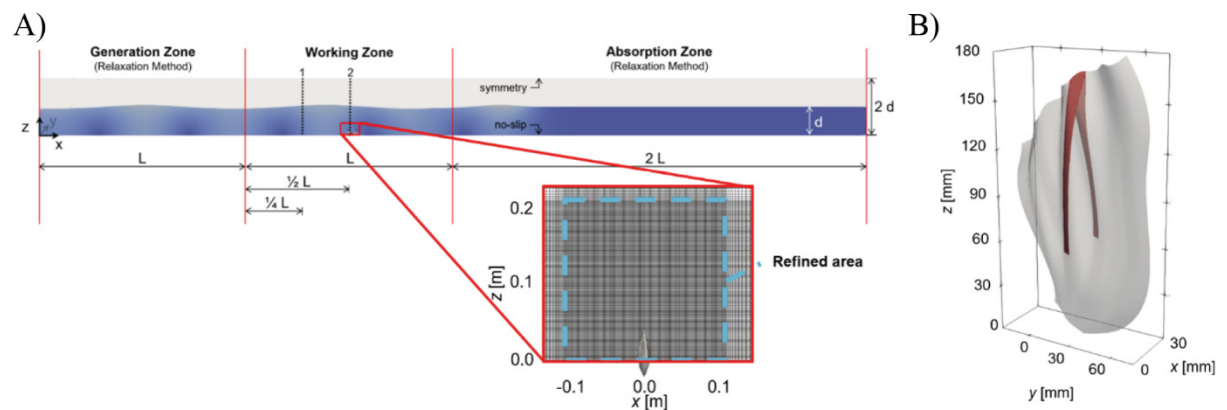


Figure 20: Visualizations of A) the numerical wave tank, including refined area surrounding the positions of the oyster shell (blue dashed box) and positions of the wave gauges and line probes (1 and 2) and B) the idealized oyster shell, where the red line marks the slice implemented in the numerical wave tank. L is the wave length and d is the water depth. Taken from Hitzegrad et al. (2025c).

A 2D numerical wave tank was implemented in REEF3D::CFD (Bihs et al. 2016) to solve the two-phase oscillatory flow field around an individual oyster (Figure 20). The model

employed high-order finite differences on rectilinear grids, the level set method for the free surface, and the immersed boundary method for the oyster shell. For Large-eddy simulation with a Smagorinsky subgrid-scale model was employed for the turbulence modeling (Cui et al. 2022, Prüter et al. 2025, Smagorinsky 1963). The oyster geometry was parameterized based on roughness parameters by Hitzegrad et al. (2022). A stretched Cartesian grid with a cell size of $dx = 1.25$ mm around the oyster shell was applied. To calibrate and validate the model, the vorticity field is compared to a reference case of a vertical plate subjected to oscillating flow (Lin and Huang 2012). Based on the validated model, a parametric study was conducted, including 36 hydrodynamic cases reflecting real conditions in the central Wadden Sea (Froude similitude with a length scale of 1:3) varying the water depth d , the wave period T_m , and wave height H_m ($d = 0.4; 0.6; 0.8$ m, $T_m = 1.5; 2.0; 2.5; 3.0$ s, and $H_{m,in} = 0.05; 0.10; 0.15$ m).

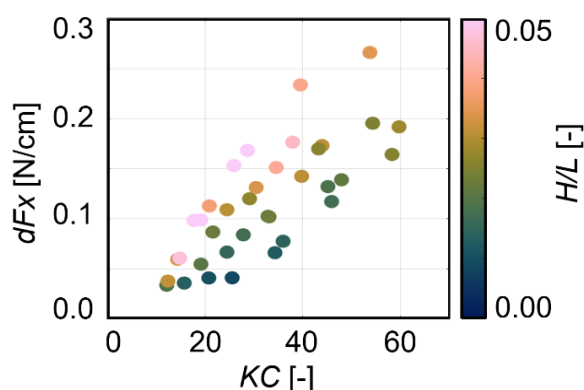


Figure 21: Phase-averaged maximum horizontal wave force amplitude dF_x as a function of the KC number and the wave steepness H/L . Taken from Hitzegrad et al. (2025c).

The vorticity fields revealed interacting vortices forming on both the lee and weather sides of the oyster shell due to flow separation at the shell margin. These vortices directly influenced the total force acting on the oyster shell (Figure 21), as the phase-averaged maximum horizontal wave force amplitude, dF_x , reflected the sum of drag and inertia forces. Hereby, dF_x reached values between 0.05 and 0.25 N/cm and exhibited dependencies on the Keulegan–Carpenter number, KC (defined as the ratio of the wave orbital excursion amplitude to the height of the oyster shell), and the wave steepness H/L .

This study provides new insights into the flow fields, turbulence structures, and wave-induced forces acting upon an individual oyster shell and establishes a basis for future experimental and numerical studies investigating the near-bed hydrodynamics of multiple interacting oysters.

4.5 Current-Induced Hydrodynamics of Biogenic Structures

As the biogenic structures are also exposed to substantial currents as a result of the tidal regime in the Wadden Sea, the current-biogenic structure interaction is also of high interest. Thus, comparable experiments to the ones outlined in Section 4.3 and Hitzegrad et al. (2024b) were conducted under unidirectional currents to i) investigate the influence of the sharpness of large roughness elements on flows, ii) determine velocity changes and turbulence in the near field and wake of the substitute models, and iii) parameterize roughness effects.

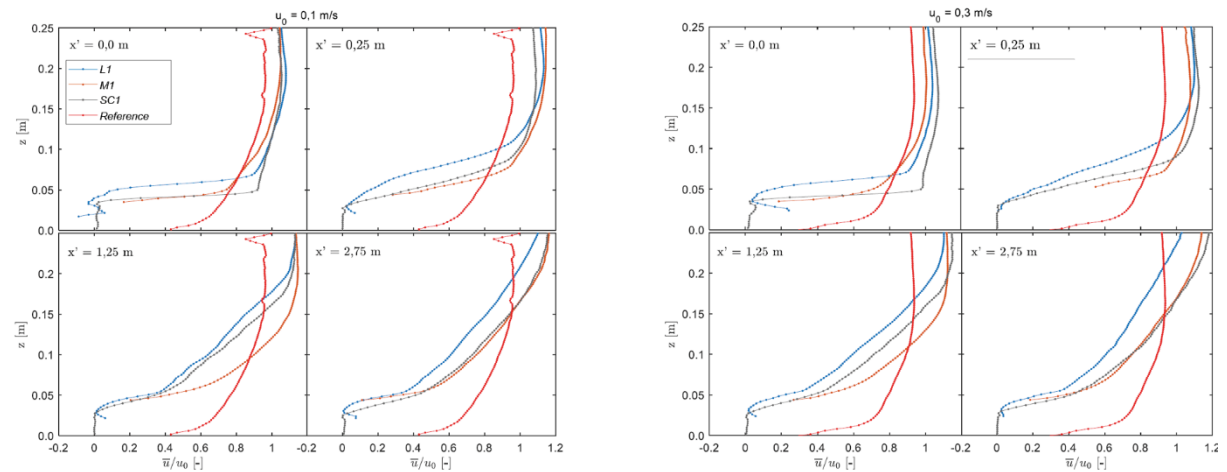


Figure 22: Normalized PIV flow profiles for the different surrogates and locations relative to the surface's leading edge ($x = 0.0$ m) for a mean streamwise velocity of 0.1 m/s (left) and 0.3 m/s (right), where *L1*: Lamella 1, *M1*: Mix 1, *SC1*: Semicircle 1, and Reference: Reference case without surrogates.

Experiments were carried out in the race-track flume at Ludwig Franzius Institute, Leibniz Universität Hannover where Acoustic Doppler Velocimetry (ADV) and Particle Image Velocimetry (PIV) were employed to capture flows in the near field of the biogenic structure surrogates. The length of the surrogates varied between 0.5 m and 4.0 m to capture effects of structure size while flow velocity varied between 0.1 m/s and 0.3 m/s, which represents scaled average conditions at the study sites (cp. Section 2). The results yielded a direct relationship between surrogate length and roughness influence due to the enhanced friction effect. Moreover, the largest velocity reduction was observed directly above the surrogates irrespective of their shape, while higher up in the water column the flow returned to an approximately logarithmic velocity profile (Figure 22). These findings demonstrate that rough structures, such as those present in reef configurations, can significantly impact flow velocity in their immediate vicinity.

The influence of the surrogates on the flow depended on the surrogate shape and was analogue to the results under waves (Section 4.3). The Lamella surfaces exerted the most significant influence on flow attenuation, whereas the bluntly-shaped semicircle surfaces had the least impact (Figure 22). The Mix surfaces exhibited values between the lamella profile and the bluntly-shaped profile, suggesting that the specific structure of the reef surface plays a crucial role in influencing flow conditions.

In line with the flow reduction, the examination of the turbulent kinetic energy (TKE) revealed the largest development directly above the model. Furthermore, the shape of the surrogate models influenced turbulence development with the lamellar surface leading to the highest increase in TKE. The same pattern was observed for the roughness coefficient and roughness length (Table 4).

In summary, the findings show that sharp-edged structures, such as vertically oriented oysters, can significantly impact hydrodynamics and turbulence. Furthermore, the results have illustrated that geometries influence the overlying flow layers differently, suggesting that the transformation of blue mussel beds to oyster reefs in the Wadden Sea will have an impact on the local flow regime. In this context, the present study suggests a resulting increase in surface roughness, which may increase wave dissipation and flow reduction.

However, further research is needed to investigate the specific mechanisms and the influence of various oyster reef structure types on flow dynamics and the resulting effects on the Wadden Sea in greater detail.

Table 4: Bottom shear stress τ_k , roughness coefficient c_w and roughness length z_0 at a model scale of 1:3 for the different surrogate types. Note that for τ_k two different velocities were applied.

	τ_k [N/m ²]		$c_{w,k}$ [-]	$z_{0,k}$ [cm]
u_0 [cm/s]	10	30		
Lamella	0.05 ± 0.01	0.48 ± 0.09	0.055 ± 0.021	0.17 ± 0.05
Blunt	0.04 ± 0.003	0.44 ± 0.05	0.018 ± 0.008	0.05 ± 0.03
Mix	0.06 ± 0.02	0.40 ± 0.32	0.026 ± 0.005	0.08 ± 0.002

5 Concepts for Coupling Hydrodynamic Simulation Models with Ecological Model Components - Data-Based and Process-Oriented Approaches

The field observations (Section 3) and experimental studies (Section 4) provide a detailed understanding of the topographical characteristics of blue mussel beds and oyster reefs and their influence on local hydrodynamics. To assess the effects of the observed ecosystem, shift from blue mussel beds to oyster reefs on the hydro- and morphodynamics on a regional scale of the entire Wadden Sea, this detailed, localized knowledge should be integrated into regional-scale numerical simulation models.

A major challenge for such an integration is the typically sparse and heterogeneous nature of ecological data, both spatially and temporally, across vast areas like the German Bight. To overcome this, a concept for a data-based, process-oriented hindcast model was developed to generate consistent, time-variant maps of key ecological parameters for both blue mussel beds and oyster reefs. This work extends the established Functional Bottom Model (Sievers et al. 2021), which already provides consolidated data on bathymetry and sedimentology.

The foundation of the model is a comprehensive collection of data from various sources, including long-term monitoring programs by national park authorities and high-resolution data from the BIVA-WATT field campaigns. To manage and unify this diverse dataset, a hierarchical database structure was implemented. This system processes the raw data (e.g., point samples of biomass and size distributions, monitoring polygons) into homogenized raster base data and, finally, into annual product raster maps (10 m resolution) that describe the properties of the mussel and oyster assemblages from 1996 to 2020.

Generating these comprehensive maps from sparse data required innovative interpolation techniques in both space and time.

- **Spatial Interpolation:** To translate discrete point measurements into spatially continuous information, a novel Co-Shepard interpolation method was developed. Inspired by geostatistical Co-Kriging, this approach categorizes variables based on their operational role within the interpolation framework rather than their biological derivation. In this context, the target parameters to be mapped – such as biomass and size-frequency histograms – are treated as primary variables. The local mussel settlement density, for which comprehensive spatial coverage is often available (e.g., from monitoring polygons), serves as a secondary variable. By using this

secondary variable to guide and 'normalize' the interpolation of the primary data, the method ensures that the resulting spatial distribution is physically constrained by the actual reef extent, leading to, a more physically plausible spatial distribution across the reef area.

- **Temporal Interpolation:** To model the development between observations, two different approaches were implemented and tested: a classic spatio-temporal interpolation and a dynamic growth model based on mathematical evolution equations with data assimilation. The latter simulates the change in biomass over time based on a simplified population dynamics equation, which considers growth, mortality, and larval dispersal. A key innovation here is the integration of time-variant "mussel potential maps" (Rubel et al. 2020). These maps function as spatially and temporally explicit habitat suitability index (ranging from 0 to 1), aggregating key abiotic factors – such as inundation duration, bottom shear stress, and sediment composition – to physically constrain the growth and mortality rates within the model. While both temporal modeling approaches showed promising yet locally varying results, a future combination of the two is deemed most effective for achieving robust, large-scale results.

Finally, the generated ecological data will be used for regional-scale hydro- and morphodynamic simulations. The annual grid product databases of ecological variables (e.g., biomass, density, and size distributions) serve as a basis for this. The methodology includes:

1. **Property-Conserving Data Transfer:** An algorithm was developed to transfer the information from the high-resolution (10 m) ecological raster maps onto the coarser, unstructured grids typically used in finite element models like the MARINA simulation system.
2. **Roughness Parameterization:** Based on literature and the project findings, relations were established to translate biological variables into hydraulic roughness parameters. For example, the absolute roughness height (R_z) can be approximated from the mussel size distributions.
3. **Model Implementation:** A prototype implementation to account for mussel roughness was implemented in the MARINA model system. At each node of the computational grid, an equivalent bed roughness is calculated using a morphing approach. This method weights the background roughness (from sediment and bedforms) and the specific mussel/oyster roughness based on the local settlement density variable derived from the hindcast model.

In summary, this work successfully drafted a comprehensive workflow from compiling and homogenizing heterogeneous field data to coupling descriptive ecological models with process-based hydrodynamic simulation systems. The developed databases, interpolation methods, and the prototype implementation in MARINA provide the necessary tools to parameterize the effect of large-scale biogenic structures in coastal models, enabling future studies to assess the Wadden Sea's morphodynamic response to the ongoing ecosystem shift.

6 Discussion

6.1 Impact of Results

The field observations presented in Section 3 provide new insights into the spatial distribution patterns and topographical characteristics of the biogenic structures formed by *M. gigas* and *M. edulis*. Hitzegrad et al. (2022) showed that by applying the structural classification and their distinct topographical parameters, the oyster reef surfaces found in the central Wadden Sea can be described appropriately, accounting for their complexity. The intra-reef structural classification introduced by Hitzegrad et al. (2022) aligns with the growth stages described by Markert (2020). Differences in reported abundance can be attributed explained to by the use of different methods compared to biological sampling (Markert 2020, Reise et al. 2017). The classification enables a more accurate determination of the topographical roughness, as a foundation to determine assess hydrodynamic bed roughness effects, as well as the population dynamics. Furthermore, Hitzegrad et al. (2022) and (2024a) provide previously unavailable statistical parameters for both Pacific oyster reefs and blue mussel beds, which can be related to topographical descriptions in former studies (Hitzegrad 2025). Considering blue mussel beds, Wehrmann (1999) estimated spacings between agglomerations to range from 0.15 – 0.30 m and Peine et al. (2005) reported agglomerations heights of up to 0.1 m, similar to the findings of Hitzegrad et al. (2024a). Additionally, a methodology was developed that utilizes structure-from-motion photogrammetry to derive detailed, high-resolution digital elevation models under adverse conditions in the central Wadden Sea. The methodology can be applied to other reefs or comparable biogenic structures to compare the effects of hydrodynamic roughness, e.g., a constructed oyster reef in an estuary in New South Wales, Australia, (Barclay et al. 2025) and natural and constructed oyster reefs along the Jiangsu coast, China (Zhuang et al. 2024).

The findings of Hoffmann et al. (2023) provide insights into volumetric changes of oyster reefs and underscore the importance of conducting long-term studies to deepen the understanding of oyster reef growth dynamics and limitations. The developed method based on UAV data enables studies of bio-geomorphological changes at low cost. Furthermore, Hoffmann et al. (2025) illustrated that despite the potential for species transformation, biogenic structures are anticipated to sustain vertical growth, outpacing current SLR and helping stabilize intertidal flats in the Wadden Sea. The observations underscore the complex interplay between biotic factors and sediment dynamics and highlight the relevance of biogenic structures in stabilizing the Wadden Sea, also in light of SLR.

The findings of Pfennings et al. (2024) provide the first quantitative assessment of vertical oyster reef growth in the Wadden Sea based on terrestrial laser scanning. Vertical reef growth exceeds current local rates of SLR. These results align with observations from *C. virginica* reefs along the US east coast and allow a direct comparison of the future vertical growth capacity of the Wadden Sea reefs (Bost et al. 2021, Ridge et al. 2015). Since vertical reef growth depends on oyster recruitment and individual shell growth, population dynamics form the primary control on vertical reef development. Earlier studies addressed this link only indirectly, either by relating spatial abundance to the position of the optimal growth zone (Ridge et al. 2015) or by inferring growth patterns primarily from biological parameters (Walles et al. 2015a, Walles et al. 2016). Pfennings et al. (2024) integrate spatially resolved terrestrial laser scanning with detailed population data and showed that vertical reef growth is not only exposure dependent, but strongly shaped by seasonal fluctuations

in oyster abundance and growth conditions. Temperature driven growth cycles and recruitment events determine the magnitude of vertical reef growth. These findings underscore that vertical reef growth is fundamentally linked to oyster shell production, which peaks during warm summer periods, and that fluctuations in spawning events create temporal lags that highlight the sensitivity of vertical reef growth to seasonal and interannual biological variability.

In Pfenning et al. (in prep.) complementary analyses of spatial reef configuration and lateral reef dynamics were conducted using UAV derived orthomosaics from Hoffmann et al. (2023) and (2025). By applying the intra- reef classification developed by Hitzegrad et al. (2022) across the full extents of the KB and NOL reefs, the study provides the first reef scale structural classification and quantitative assessment of *M. gigas* reef morphology in the Wadden Sea. A key finding is the presence of large, continuous reef surfaces. These represent a characteristic and regionally unique feature of the Wadden Sea oyster reefs and are attributed to the legacy pattern of previously extensive blue mussel beds. Such continuous reef surfaces likely enhance both internal heterogeneity and their influence on the surrounding hydro-morphodynamic regime (Hitzegrad et al. 2025b, Hoffmann et al. 2025). Larger reef bodies exert a stronger effect on local flow fields, promoting wave attenuation and reducing current energy in leeward zones (Wu et al. 2024). They differ markedly from native large scale intertidal oyster reef systems composed of small patch- and string reefs. Such configurations generate distinct wake structures and sedimentation patterns around individual units (Luo et al. 2022, Zhuang et al. 2025). In contrast, a continuous surface such as the NOL reef likely reduces flow velocity and wave energy more gradually, creating a more coherent hydrodynamic footprint (Hitzegrad et al. 2024b). In addition to the findings on vertical reef growth capacity by Pfenning et al. (2024), several key processes can be identified that will control future lateral reef development. Lateral stability depends on highly local drivers, as erosion at exposed margins, episodic sediment burial in low energetic areas and subsequent re-exposure collectively shape the reefs spatial footprint.

The experimental studies outlined in Section 4 provide new insights into the interactions of biogenic structures with the ambient hydrodynamics. The findings of Hitzegrad et al. (2024b) and Hitzegrad et al. (2025b) revealed substantially stronger wave attenuation of oyster reef compared to blue mussel bed surrogates, in line with findings by Borsje et al. (2011). Furthermore, the estimates for wave friction factors for blue mussel beds by Hitzegrad et al. (2025b) ($f_w = 0.21 \pm 0.18$) compare to those reported by Donker et al. (2013) for a juvenile blue mussel bed ($f_w = 0.11 - 0.22$). Lee et al. (2025) estimate average roughness heights for oyster reefs $k_w = 272 - 351$ mm increasing proportionally with the abundance for the structural classes provided by Hitzegrad et al. (2022). Differences to estimates by Hitzegrad et al. (2025b) may be explained by limitations in replicating the sharp shell margins of natural oyster shells in the surrogate models (Hitzegrad et al. 2024a).

The observation of flow resistance caused by the abstract surrogates (Section 4.5) are comparable to those of natural oyster reef surfaces with similar hydraulic roughness length, as reported by Whitman and Reidenbach (2012), Styles (2015) or Lee et al. (2025).

6.2 Perspectives on Oyster Reef Development in the Wadden Sea

By synthesizing the studies of Pfennings et al. (2024) and (in prep.) three conceptual future reef development scenarios emerge from the combined assessment of vertical and lateral reef dynamics (Figure 23).

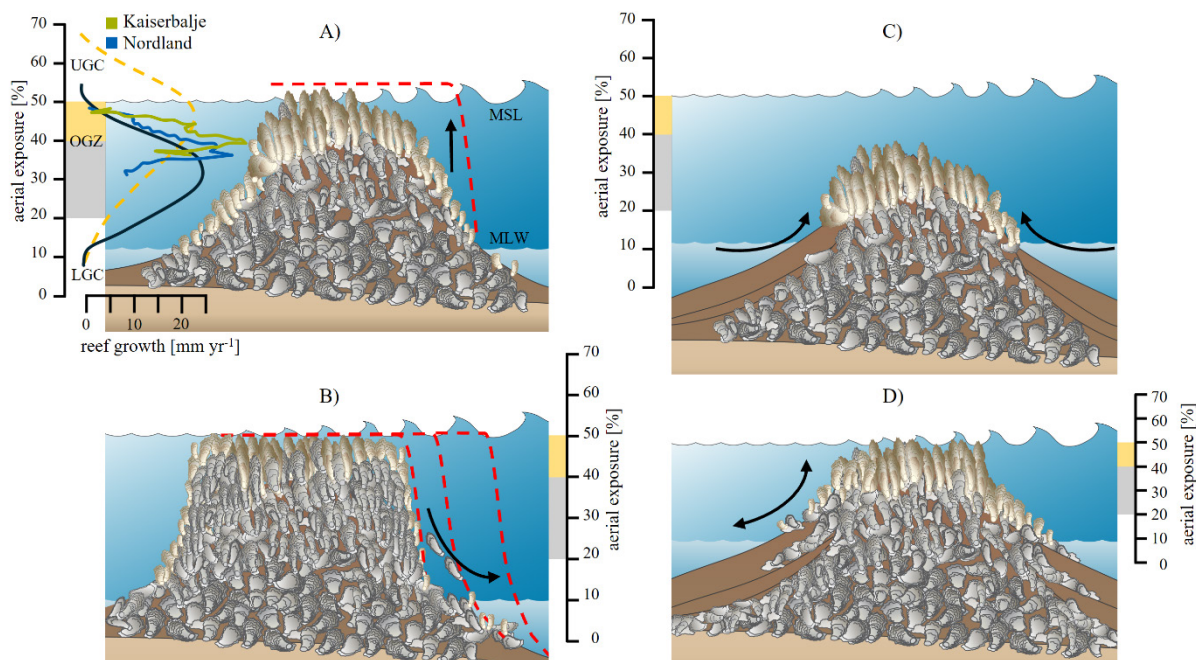


Figure 23: Conceptual scenarios of oyster reef development under varying sea-level rise and sedimentary regimes. A) Vertical reef growth in relation to tidal exposure. The red dashed line indicates the potential reef aggradation space. The Optimal Growth Zone (OGZ), Lower Growth Ceiling (LGC) and Upper Growth Ceiling (UGC) from Ridge et al. (2015; black) and Bost et al. (2021; yellow) are shown alongside OGZ data from the Kaiserbalje and Nordland reefs derived in Section 3. B) Saturation plateau scenario; C) Burial and contraction scenario; D) Facies inter-fingering scenario.

Plateau scenario

This scenario applies when SLR remains below the vertical growth capacity of the reefs. Reef surfaces approach their upper growth ceiling and vertical growth stagnates near mean sea level (Pfennings et al. 2024, Ridge et al. 2015, Ridge et al. 2017). Reef morphology becomes increasingly stable in the central zones, while lateral progradation continues at the margins. Biological productivity gradually declines as exposure conditions move beyond the optimal range for growth, reducing long term population resilience.

Contraction and decline scenario

This scenario occurs when SLR exceeds the capacity of the reefs to maintain vertical growth. Reef surfaces fall below the optimal growth zone and lower reef areas become progressively buried. Marginal areas contract and the overall spatial footprint decreases. Under moderate environmental conditions, this scenario is favored when biological productivity is reduced by stressors such as disease, heatwaves or hypoxia.

Facies interfingering scenario

This scenario reflects alternating phases of accretion, burial and re-expansion driven by non-linear sea level trends and sediment redistribution. The reef crest remains comparatively stable, while the margins respond dynamically to changing hydro-morphodynamic forcing (erosion and burial). Periods of high biological productivity promote reef building, whereas phases of low productivity favor erosion and burial. The resulting morphology is characterized by spatially interbedded reef and sediment facies.

6.3 Perspectives and Future Research Priorities

Despite the advances considering spatial distributions patterns as well as parametrization of geometric and hydrodynamic roughness of both biogenic structures achieved through the project BIVA-WATT, substantial knowledge gaps remain regarding the quantification of oyster reef influences on surrounding tidal flats.

Worldwide, oyster reefs are actively employed in coastal protection (Morris et al. 2018, Narayan et al. 2016, Wu et al. 2024, Xu et al. 2024). However, research has primarily focused on their wave-breaking effect, while energy dissipation due to increased bottom friction is frequently neglected. The findings of the project BIVA-WATT demonstrated that this mechanism is a key process in wave attenuation over ultra-rough surfaces such as oyster reefs. The studies outlined in Section 4 indicate strong local hydrodynamic impacts of oyster reefs but were unable to fully capture their structural complexity. Hence, further research should be initiated that helps elucidate the spatial and temporal effects of extensive ultra-rough reef areas on shallow coastal regions.

Future research should focus on optimizing the representation of natural biogenic structures in experimental modeling to enable in-depth analysis of the ambient hydrodynamics around these biogenic structures (Hitzegrad 2025). Improved representations could be achieved by refining the fabrication of surrogate models, e.g., by adjustments in mixture proportions or enhancements of printing strategies (Herding and Lowke 2024), or by applying alternative fabrication methods to include the response of biogenic structures to hydrodynamic forces, e.g., resin 3D printing (Keimer et al. 2024). Alternatively, experimental investigations could employ live mussel and oyster individuals, which would require research facilities to replicate realistic hydrodynamic conditions at prototype scale and controlled environmental conditions replicating natural conditions in the Wadden Sea (e.g., temperature, salinity, sediments, and food provision), e.g., the Saltwater-Wave-Current Flume at the Leichtweiß-Institute (Krautwald et al. 2024).

Process-oriented studies on the dissipation of wave and tidal current energy in relation to sediment redistribution caused by erosion and accumulation within and around oyster reefs are still lacking. In particular, the role of oyster and blue mussel filtration in sediment dynamics and their impact on local hydro-morphodynamic processes has not yet been sufficiently investigated. Research is missing on the effects of filtered organic particles and sediments that are deposited as biodeposits within the reefs and may influence sediment accumulation and reef functionality in the long term (Bungenstock et al. 2021). Both aspects are essential for realistic numerical modeling and predictive assessments.

Another aspect is the lack of projections of future spread of the Pacific oyster under climate change scenarios. Previous projections have primarily addressed the global expansion of recruitment areas (King et al. 2021), but little attention has been given to the spatial

development within a recruitment area, e.g., the Wadden Sea, nor its implications for morphodynamics and sediment dynamics (Hitzegrad et al. 2025a, Hitzegrad 2025). The spatial development of reefs and their interactions with biological and morphodynamic processes have been investigated by Hoffmann et al. (2023), Pfennings et al. (2024), and Hoffmann et al. (2025) at small spatial and temporal scales in the immediate vicinity of reefs. They observed positive growth rates, suggesting that oyster reefs may be resilient to SLR. Walles et al. (2015b) and Salvador de Paiva et al. (2018) documented a sediment-stabilizing effect of these reefs, showing a correlation between reef size and the extent of the morphologically influenced area. Future projections of Pacific oyster spread within recruitment areas would likely require coupling climate change scenarios with large-scale hydro-morphodynamic models that explicitly represent the biological processes and spatial dynamics governing reef recruitment, growth, lateral expansion, and persistence.

A further major research focus concerns the quantification of potential habitats for blue mussels and Pacific oysters (Gade et al. 2015, Nieuwhof et al. 2015, Westinga et al. 2021). Novel habitat suitability models have been developed by Key et al. (2021) and Flores et al. (2022). To assess mussel habitat suitability in the Wadden Sea, Brinkman (2021) applied a statistical data analysis approach (Zero-Inflated Negative Binomial Model). However, critical factors such as water turbidity, temperature, and terrain characteristics were not considered. Hereby, new datasets, e.g., remote sensing satellite data from Sentinel, PRISMA, PlanetScope, or Landsat, could fundamentally improve future model development by incorporating these parameters. Furthermore, habitat suitability models could be enhanced by integrating predictive simulations under future climate scenarios, employing machine learning approaches, and linking them with static or Maximum Entropy models.

Consequently, further research is required to improve understanding and quantification of key influencing factors and their interactions under current environmental conditions as well as under projected climate change scenarios, while the findings from the BIVA-WAT'T project provide a robust foundation for such efforts.

7 Conclusions

This work aimed to examine the influence of biogenic structures formed by invasive Pacific oysters and native blue mussels from both biological and coastal engineering perspectives, thereby improving the understanding and quantification of their ecosystem effects. In summary, the following conclusions are drawn:

- Field observations revealed distinct structural classes and population dynamics of oyster reef and mussel bed surfaces, enabling the parametrization of their topographical roughness surfaces.
- Based on experimental studies of wave, current, and combined wave-current interactions with biogenic structures, estimates of the roughness length, z_0 , and the wave friction factor, f_w , can be determined for a wide range of realistic hydrodynamic boundary conditions in the Wadden Sea.
- A high-fidelity numerical model of a single oyster individual revealed insights into the flow fields and turbulence structures in the near-field and the wave-induced forces acting on individual oyster shells.
- The successful implementation of coupling strategies within the MARINA model system demonstrates a viable framework for integrating biologically derived, time-

variant roughness parameters into large-scale hydro-morphodynamic simulations. This integration bridges the gap between descriptive ecological data and process-based modeling, providing an essential tool for assessing the system-scale morphodynamic response of the Wadden Sea to the ongoing ecosystem shift from mussel beds to oyster reefs

The findings will equip coastal engineers, spatial planners, and regulatory agencies with actionable parameters and workflows to better assess and ultimately manage the impacts of these two bivalve species on the Wadden Sea environment. Hence, the findings can inform and improve future coastal planning, as they enable a more informed assessment of the impact of the Pacific oysters' bioinvasion on the ecologically and economically vital Wadden Sea and by guiding the development of effective management strategies.

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