

Offshore oyster reef habitat restoration: Community structure after five years and implications for conservation management

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Abstract

Worldwide and across ecosystem types, national and international conservation and restoration efforts are increased to address and mitigate the challenges of the anthropocene. In marine environments, the restoration of oyster reef habitats has gained momentum since the end of the past century. But restoration trials of offshore oyster habitats, such as the historical offshore oyster grounds in the German Bight, are relatively new. Aiming at ecosystem functions such as habitat structure and biodiversity, we present the associated community and development of a restored European flat oyster reef in the nature conservation area Borkum Reef Ground, North Sea. Monitoring with seabed image transects along five years since reef construction showed a small-scale but steady development of an oyster population from year two onwards, while the local benthic community showed a strong development in terms of species richness and abundance. This early developed reef represents the first successes of initiating recovery by active restoration measures in marine offshore habitats in Europe. Our study highlights the potential of ecological restoration for MPA management to enhance the recovery of ecosystem functions, and its value for designated compensation measures for offshore interventions.

INTRODUCTION

Marine ecosystems suffer from severe and increasing anthropogenic pressure. To address consequences reflected in the triple planetary crisis and to mitigate specific negative effects, conservation and restoration gained momentum worldwide. Examples are the aims of the Strategic plan for Biodiversity 2011–2020 [1], the UN decade on ecosystem restoration 2021–2030 [2], the Global Biodiversity targets for 2030 and 2050 [3] and the EU Nature Restoration Regulation [4]. In monetary terms, the current loss of biodiversity represents a loss of 140 billion dollars per annum and could represent a loss of 14 trillion dollars per annum by 2050 [5]. These estimates further underline the economic importance of biodiversity and its importance as a key ecosystem function and basis for many ecosystem services.

Marine ecosystems such as reef habitats represent biodiversity hotspots and important service providers [6, 7]. Despite their importance, the combined effects of overfishing, habitat loss, and invasive diseases, have impacted some reef types decreasing their extension by up to 85% by the turn of the past century [8]. Coral, geogenic, and bivalve reef habitats are situated at the top of the 'loser's' list, the latter two being cataloged by the European Habitats Directive [9] as natural habitat types of interest whose conservation requires the designation of special areas of conservation. In this context, conservation implies both protection and restoration of these rich and ecologically important biodiversity habitats.

Restoration of reef habitats and its associated ecological functions and services [10] has been implemented for several decades [11], as restoration ensures recovering natural capital. Due to their historical ecological and economic importance, oyster reef restoration has increased since the late 1990s, especially in the US and Australia [11]. In Europe, restoration of destroyed or degraded European flat oyster (*Ostrea edulis*) habitats is a focus of biogenic reef recovery [12, 13, 14]. While most *O. edulis* habitat restoration activities are located in near-shore coastal environments, a handful target restoration of the once extensive so-called offshore oyster grounds (e.g. [15]).

Despite several *O. edulis* restoration programs having > 5 years of life and, correspondingly, > 5 years of monitoring data, the main focus seems to lay in the recovery of oyster populations. Against the background of restoration and biodiversity goals, monitoring and assessing the associated community in restored oyster reef habitats are of great importance [16]. This is especially true for projects aiming to restore the reef ecosystem in areas where fishery does/will not take place after restoration. Community level assessments allow to understand how succession during restoration occurs, how the species being restored interacts with potential competitors, predators, and facilitators [17], and how local biodiversity, natural capital and ecological services are being restored [18]. Furthermore, if restoration occurs within a conservation area such as nature conservation or marine protected areas, community level monitoring can provide insights into the complementary nature of restoration to guide their management [19, 20].

In this study we focus on community level assessments of offshore *O. edulis* reef habitat restoration in Borkum Reef Ground (BRG), a nature conservation area (NCA) in the German Bight, North Sea (Fig. 1). The studied reefs were constructed in 2020 and have been monitored since 2021 [15]. We aim to provide a description of the reef associated community and the succession occurring over 5 years recovery to evaluate benefits for NCA management [21] and significance as compensation measures in offshore regions [22].

RESULTS

In terms of biodiversity metrics, when pooling all monitoring years, 41 species were found to inhabit the reef, with 12 being present during all monitoring campaigns (Supplementary Table 1). Alpha species richness increased every year from zero in 2020 to four in 2021 to seven in 2025, whereas gamma species richness increased from zero in 2020 to 2021 (gamma S = 18) and to 2022 (gamma S = 27), remaining stable since then (Fig. 2). In terms of diversity H' , a sharp increase from 2021 ($H' = 1.05$) towards 2022 ($H' = 1.30$) could be observed. This was followed by a comparatively small drop of diversity H' in 2024 ($H' = 1.21$) and a recovery by 2025 ($H' = 1.34$; Fig. 2). Evenness showed a different pattern, with higher and comparable values for the monitoring campaigns of 2021 ($J' = 0.73$) and 2022 ($J' = 0.74$), and lower for 2024 ($J' = 0.68$) and 2025 ($J' = 0.68$; Fig. 2). In terms of abundance, the first two monitoring campaigns can be grouped together due to their low total abundance of < 10% (Fig. 2; Supplementary Table 1). In comparison, the abundance of 2024 (51.73%) and 2025 (48.54%) are approximately five times higher than that of 2022 (9.79%; Fig. 2; Supplementary Table 1).

When considering community composition and abundance, the fuzzy-k clustering separated each year as an individual group. A set of pairwise PERMANOVA tests showed all four groups to be significantly different from each other (all pairwise PERMANOVA p-values < 0.001; Table 1). The indicative species analysis defined the swimming crab *Liocarcinus* sp. to be indicative for 2021. For 2022, no exclusive indicator species was identified. A thecate hydrozoan (Leptothecata in Fig. 3), the plumose anemone *Metridium senile*, and hydrozoan OTU 2 were found to be indicative of 2024. For 2025, seven taxa were defined as indicative: the common starfish *Asterias rubens*, a tube forming amphipod (amphipod tubes in Fig. 3), the devil crab *Necora puber*, the European sea squirt *Ascidella aspera*, the butterflyfish *Pholis gunnellus*, the breadcrumb sponge *Halichondria panicea*, and the European flat oyster *Ostrea edulis*.

Table 1
Within- and between-group dissimilarities (bold), and operational taxonomic unit (OTU) contribution (%) resulting from the SIMPER analysis of between-monitoring year comparisons based on SBI abundance (%-cover). *Significantly different ($p < 0.001$) in a pairwise PERMANOVA.

2021	2021 (n = 41)	2022 (n = 55)	2024 (n = 136)	2025 (n = 50)
	65.14%			
2022	73.52%*	67.02%		
	<i>Cancer pagurus</i> (22.65%)			
	<i>Metridium senile</i> (15.75%)			
	<i>Tubularia</i> sp. (15.56%)			
	Sagartiidae (9.02%)			
	Leptothecata (8.25%)			
2024	91.02%*	83.71%*	49.29%	
	Leptothecata (36.65%)	Leptothecata (36.08%)		
	<i>Metridium senile</i> (18.67%)	<i>Metridium senile</i> (18.41%)		
	<i>Alcyonium digitatum</i> (17.27%)	<i>Alcyonium digitatum</i> (17.68%)		
2025	88.44%*	87.76%*	78.98%*	49.74%
	Amphipoda tubes (39.14%)	Amphipoda tubes (37.33%)	Amphipoda tubes (25.10%)	
	<i>Alcyonium digitatum</i> (16.35%)	<i>Alcyonium digitatum</i> (15.50%)	Leptothecata (24.62%)	
	<i>Cancer pagurus</i> (11.33%)	<i>Cancer pagurus</i> (10.80%)	<i>Metridium senile</i> (13.18%)	
	<i>Metridium senile</i> (10.27%)	<i>Metridium senile</i> (10.28%)	<i>Alcyonium digitatum</i> (10.77%)	

The non-metric multidimensional scaling (nMDS) graphically visualizes the differences between SBIs per year, with vectors representing taxa contributing most to between-year dissimilarities (except for *O. edulis*; Table 1) and their dominance (Fig. 3). While *O. edulis* could not be registered during 2021 (t1), its abundance increased since then, reaching a value of 0.10% by 2025 (Supplementary Table 1). This represents a comparatively low abundance but indicates population development over time. Between-year differences were high (> 70%) mainly driven by seven taxa (Table 1). From these, a thecate hydrozoan, the anemone *M. senile* and a sagartid anemone (Sagartiidae), the brown crab *Cancer pagurus* and the common starfish *A. rubens* were present in all four sampling campaigns, representing dominant groups or drivers of between-year differences (Table 1; Fig. 3). Tubularian hydrozoans settled on the reef in 2022, remaining an important component of the community in 2024; however, by 2025 their population and that of thecate hydrozoans were greatly diminished (Fig. 3). The habitat space of these hydrozoans appears to have been overtaken by a tube forming amphipod (Fig. 3). Two ecologically important additions to the pilot reefs occurring in 2022 were those of the soft coral *Alcyonium digitatum* and the breadcrumb sponge *H. panicea* (Fig. 3). Although only the former was an important driver of between-year differences, both species greatly contribute to the three-dimensional complexity of the oyster reefs. Overall, the results of our analyses point to four succession stages: a first and early stage in 2021 (t1) during which only a few pioneer and highly motile species were found; two intermediate stages in 2022 (t2) and 2024 (t4), during which community richness, diversity and abundance increased, including the first records of *O. edulis* and other typical reef taxa (e.g. *H. panicea*, *A. digitatum*); to a later stage in 2025, during which a significant turnover between hydrozoan and amphipod taxa occurred, as well as an increase of *O. edulis* and *A. digitatum* abundance.

DISCUSSION

The ongoing biodiversity crisis is forcing governments and scientists to increase the conservation and restoration of key habitats and species. In this study, we focused on reef habitat recovery of the European flat oyster *O. edulis* to increase biodiversity [12, 13, 14]. After five years, our data indicates that *O. edulis* as the target species and ecosystem engineer of reef creation is recruiting into the restored reef patches. A slowly developing natural population to support future reef growth and increasing habitat structure is an indicator for a positive recovery trend initiated by an active restoration measure. Based on studies done on larval dispersal [23], these recruits likely originated from the control population deployed with the reef or from smaller *O. edulis* populations located nearby within the BRG NCA [23]. Such a multi-year delay in the growth of the local *O. edulis* population has also been observed in restoration sites in the USA by Luckenbach et al. [17] and Shinn et al. [24]. The former registered the first oyster population growth after two years post-deployments; whereas the latter recorded a drastic oyster population loss within the first three years post-deployment, and a recovery after the fourth year. For the pilot oyster reef in BRG, a growing abundance of *O. edulis* suggests that a reef base constructed with limestones may offer some settlement substrate over the years, supporting the claims of Luckenbach et al. [17].

The observed population growth may also be delayed by predation. However, we found population growth occurs despite the presence of relevant predators of *O. edulis* such as *A. rubens*, *C. pagurus*, the European lobster *Homarus gammarus* [25]. This suggests that predation pressure on the European flat oyster is not larger than their population growth. Field observations of oyster restoration projects in the USA showed that oyster survival increases with a higher number of predator species, as this results in higher competition between predators or mutual predation [26]. Additionally, experiments show a similar pattern in which the presence of water-born cues of competitors might hamper predation over oysters as shown by Belgrad et al. [26] with decapod species in the USA and by Ellrich et al. [25] for brown crabs *C. pagurus* and European lobster *H. gammarus* in Europe. Additionally, *O. edulis* predators such as *C. pagurus* and *H. gammarus*, when given a choice, would predate over other easier to crush/catch taxa. Overall, literature and our results suggest that a more developed reef base is more attractive and 'safe' for *O. edulis* settlement than a less developed one, as more 'hiding places' can be found and a higher protection through interspecific predator regulation.

As an ecosystem engineer capable of building reefs, *O. edulis* was selected as a key species for restoration across Europe [13, 14]. The overarching objective, especially against the background of the Habitat Directive and Natura2000 network, is halting and reversing biodiversity loss and increasing habitat structure [9]. Following these requirements and regardless of the habitat type, restoration success is not reduced to growth or survival of the target species exclusively [10, 17, 27]. Assessing and evaluating the development of the associated species community is also of importance, for which our results show significant differences between all monitoring years, suggesting a clear succession over a five-year recovery phase. Similar to observations in shallow environments [17, 24, 28], the first species to settle on the pilot oyster reef were motile and pioneer species, such as *C. pagurus*, *M. senile* and *A. rubens*. While considered pioneer species, all three remained present in the newly created oyster reef habitat, increasing in abundance since 2020. Further pioneering and opportunistic species arriving and settling between 2022 and 2024 are a number of thecate hydrozoan species and a tubularian hydrozoan (*Tubularia* sp.). Both groups are usually representative for intermediate successional stages of hard substrate [29, 30, 31], and are usually outcompeted for space at later successional stages, e.g. by tube dwelling amphipods [32, 33]. Our results showed an abundance reduction for *Tubularia* sp. which coincides with an abundance increase of the soft coral *A. digitatum*; a similar observation made by Whomersley and Picken [34] and Stamp et al. [33]. Similarly, tube dwelling amphipods such as *Jassa* spp. construct their tubes on hydroids [32, 35], potentially overgrowing the hydroids and replacing them in the community. This could explain the absence of thecate hydrozoans in 2025, a group which could have been replaced by tube dwelling amphipods.

Assessing the degree of success of offshore restoration of *O. edulis* reef habitats requires the comparison of the observed ecosystem with either a reference ecosystem and/or ecological baseline [10, 27]. The latest descriptions of offshore *O. edulis* reefs (an optimal baseline and reference system) for the German Bight were done based on data collected in the late 19th / early 20th century [6, 36, 37]. But these historical habitats are challenging to be applied as reference ecosystems since they were already described as degraded in the 19th century [6], and are absent in the German Bight since several decades [38]. Additionally, the historical sampling was done by seafloor dredging, while today and especially in conservation areas, non-invasive and optical sampling technology is applied for biodiversity assessments. In search of alternatives, we identified and recommend geogenic (stone) reefs, a natural reef habitat present in BRG [39, 40], as a relevant and local unit for a potential reference model with regard to biodiversity and associated species of biogenic (oyster) reefs. In terms of abundance (as proportion of reef cover), the restored oyster reef habitat still shows a lower fauna cover than natural stone reefs in BRG. Michaelis et al. [39] described 41 reefs of similar stone sizes compared to the oyster reef base: Four showed a low abundance (< 50% cover), two showed a similar abundance (~ 50% cover), and 35 showed a higher abundance (> 55% cover) than that of the restored oyster reef in 2025. From these 35 geogenic reefs with high fauna abundance, 26 showed > 95% cover [39].

In terms of species, a comparable fauna survey on geogenic reefs extending to the south and beyond the BRG NCA defined 25 faunal species that can be either considered ecosystem engineers (16 species) or reef dwellers (9 species) [40]. Associated to the restored oyster reef, we observed five ecosystem engineer matches: the breadcrumb sponge *H. panicea*, the tubularian hydrozoan *Tubularia* sp., the soft coral *A. digitatum* and plumose anemone *M. senile*; and one thecate hydrozoan of the order Leptothecata (the report differentiated five species of this order); as well as seven reef-dwelling matches: sagartiid anemones, the brown crab *C. pagurus*, the European lobster *H. gammarus*, the devil crab *N. puber*, the common starfish *A. rubens*, the starfish *Astropecten irregularis*, and the European sea squirt *A. aspera*. Overall, the local benthic abundance and species composition associated with the restored oyster reef are still developing and do not reach natural levels observed in the geogenic reefs. Furthermore, oyster abundances rather represent an early stage of restoration (*sensu* Pouvreau et al. [41]). Such observations of restoration being still in an early state of recovery after 5 years is not unknown for oyster restoration, and point to the need for long-term (up to 25 years) planning and implementation of restoration interventions [11, 17, 18]. However, our results indicate a successful initiation of recovery: The restored oyster reef maintains some characteristics of the surrounding natural habitats, and the local oyster population is slowly increasing in abundance.

In the context of the Native Oyster Restoration Alliance (NORA), a European network developed to support *O. edulis* restoration [13, 14], our results have broader applications. They directly address two relevant questions of importance for the practice of restoration of *O. edulis* [42]: 1) Can the success of restoration efforts be increased by using species distribution modelling to identify suitable oyster habitats/areas for restoration?, and; 2) How can remote (e.g. ROVs, AUVs) monitoring methods be adapted to provide an accurate and cost-effective measure of the density and size distribution of *O. edulis* and their associated communities? For question 1), we prove that initiating oyster reef habitat restoration in areas identified as suitable for *O. edulis* supports reef recovery, even when the initial mortality on site is high e.g. under high predation pressure. The pilot oyster reefs were constructed in an area identified as suitable for *O. edulis* development [43, 44] but mortality after deployment was considerable [15]. After this high initial mortality, *O. edulis* abundance increased from 2022 onwards, despite high abundances of brown crabs *C. pagurus*, a known oyster predator [25]. For question 2), the first adjustment of the method was proposed by Pineda-Metz et al. [15], which ensures a time-efficient yet ecologically representative analysis of the restored oyster reef's community, including presence and density of *O. edulis* individuals. We then used the same approach for adjusting the number of SBIs needed for 2025 (see methods section). Based on our experience, we propose that bi-yearly adjustments of SBI numbers to be analyzed per reef or reef unit, ensures the optimization of monitoring effort with stable quality. Worth noticing is that, while our results are focused on *O. edulis* reef habitat restoration, they can be transferred and applied for other sessile and hard substrate associated monitoring approaches.

Active restoration is a complementary tool to or an integral part of NCA and MPA management, potentiating positive effects for biodiversity, habitat structure and associated ecological services [20]. Our results show how the habitat creation associated to *O. edulis* restoration improves local biodiversity, supporting the settlement of red listed sessile species such as *H. panicea*, *M. senile* (both threaten to an unknown extent) and *A. digitatum* (a vulnerable species), as well as those of endangered species such as *H. gammarus* [45]. The restored oyster reef habitat also provides a refuge for economically important species such as *C. pagurus*, inhabiting the reef from the first days post-construction, and pouting *Trisopterus luscus* (SPM personal observation). Biogenic and geogenic reef habitat restoration are management measures of high and of moderate priority in the management plans for the BRG and Sylt Outer Reef/Eastern German Bay, respectively [21]. The implementation and related monitoring of such measures, their associated communities, their development and their wider ecological effects facilitate conservation planning, to ensure strategic decisions and to optimize the return on investment in terms of ecosystem services [20, 21].

With our study, we provide a first and timely proof of concept for offshore *O. edulis* reef habitat restoration in the North Sea. The valuable and promising fact, that recovery of (at least parts of) the once massive - both in geographical extension and in ecological impact - offshore oyster grounds is possible, is also of importance for the designation of compensation measures. Countries like Germany have adopted such measures for environmentally relevant seabed interventions such as offshore construction, to compensate for negative effects on seafloor integrity and related habitat loss [25]. Following up on previous findings [13, 14, 15, 25, 43, 44], the results of this study strengthen and increase the knowledge basis for the further development and future implementation of large-scale biogenic reef habitat measures [46]. Considering the standards and principles for restoration, further developing a comprehensive and reliable reference model and integrating this data into a recovery wheel is a logical next step to further strengthen decision-making for efficient and robust conservation management [41].

MATERIAL AND METHODS

Data for this study was collected during annual monitoring campaigns at the pilot oyster reefs in Borkum Reefground (BRG) (Fig. 1).

The pilot oyster reefs consist of a reef base of natural stones to mitigate sanding up of oysters in areas where no biogenic structure on the seabed remains. The reef was constructed in 2020 (t0) and consists of two reef patches (East reef and West reef) [15]. Monitoring campaigns were conducted yearly from 2021 (t1) to 2025 (t5; see Data Availability for details). Due to logistical constraints, no monitoring was done in 2023 (t3). To assess the associated fauna, photo transects producing seabed images (SBIs) were realized over the reef patches. To allow for statistical comparisons, both reef units have been analyzed separately. The 2021 monitoring campaign served as a proof of concept and to identify and define the required sampling effort for 2022, whereas the 2024 campaign was used to optimize the sampling effort for 2025. As the stone layer of the pilot oyster reef represents a newly available substrate free of attached fauna, we assume faunal abundance to be zero for the year of deployment, 2020.

In 2021 and 2022, SBIs were taken by scientific divers with a Canon EOS M6 camera attached to a 0.5 x 0.5 m quadrant frame. In 2024 and 2025, divers were substituted by the A.IKANBILIS™ hovering autonomous underwater vehicle (HAUV) of BeeX (<https://beex.sg/a-ikanbilis/>), which flew over the reefs along predefined transects at a depth of 0.5 m above seabed and at a speed of 1 m s⁻¹. From the dive videos of the HAUV, SBIs were extracted every 0.5 seconds for 2024, and every 1 second for 2025 to avoid overlap between SBIs. For 2021, two transects with at least 15 SBIs were planned per reef. Two transects were done at the East reef (42 SBIs in total). Due to bad weather conditions, only one transect was done at the West reef (10 SBIs). After removing poor quality SBIs (i.e., those out of focus or too dark), a total of 31 SBIs for the East reef and 10 SBIs for the West reef were analyzed in detail. For 2022, a total of 33 SBIs from the East reef and 22 SBIs from the West reef were taken. For 2024, 161 SBIs were taken at the East reef and 170 at the West reef. For 2024, SBIs with the best quality were selected if SBIs showed overlaps. After removing all poor quality SBIs, 55 and 81 usable SBIs remained for the East and West reefs, respectively. To reduce the effort spent on analyzing SBIs while ensuring the number of SBIs still properly represent the reef species richness, SBIs taken in 2024 were used to calculate the minimum number of SBIs needed to find at least 75% of the operational taxonomic units present at the pilot oyster reef. Based on this optimization, we reduced the number of analyzed SBIs for 2025 to 25 images per reef.

Invertebrate and fish species found in all SBIs were identified to the lowest taxonomic unit possible based on the classification guides of Køie, Kristiansen & Weitemeyer [47] and Hayward & Ryland [48], and by consulting experts. In case an organism could not be identified to genus or species level, they were further identified based on morphology as operational taxonomic units (OTU). For all taxa, and to facilitate inclusion and consideration of colonial organisms into the analysis, abundance was recorded as percentage coverage per area per taxa.

Abundance data (as percentage cover) for all SBI transects of each reef patch and year was $\log(x + 1)$ transformed and used to construct a similarity matrix based on Bray-Curtis similarity [49]. This similarity matrix was used to conduct a series of pairwise PERMANOVAs [50] to test for differences between reef subunits for each monitoring year. Please note, as results showed no significant differences between reef patches, the following statistical analyses were done only considering sampling years, i.e. data of both reef patches was pooled for each year.

Untransformed abundance data (in percentage cover) from all SBIs were used to calculate standard biodiversity metrics, namely alpha and gamma species richness as number of species (S), Shannon's diversity index (H') [51] and Pielou's evenness (J') [52] for each sampling year. These biodiversity metrics allow for a basic description of the composition and structure of the restored oyster reef habitat.

In a next step, abundance data was $\log(x + 1)$ transformed and used in a fuzzy k-means clustering [53]. Prior to calculating the fuzzy k-means clustering, the fuzzy silhouette index was calculated [54] considering different numbers of clusters (2 to 4) and matrices in all species were considered. This *a priori* approach showed the best clustering to happen when considering a 4-cluster solution, thus, fuzzy k-means clustering was done using this setup. The matrix used for clustering stations was used to calculate a between-monitoring-year Bray-Curtis [49] similarity matrix. This matrix was used in a PERMANOVA [50] to test for differences between all sampling station, and a SIMPER test [55] was used to calculate within- and between-group dissimilarities, as well as to differentiate the taxa contributing to between-group dissimilarities. Additionally, an indicative species analysis [56] was also computed to define which taxa act as indicator for each station cluster. To visualize the similarity between years and taxa driving this, a non-parametric multidimensional scaling was used (nMDS).

All statistical analyses and plots were done using the vegan [57], fclust [58], indicpecies [56], and ggplot2 [59] packages for R [60].

Declarations

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ADDITIONAL INFORMATION

The authors declare no competing interests.

DATA AVAILABILITY

All seabed images taken during the monitoring campaigns from 2021 to 2025 are published or have been submitted for publication in the PANGAEA Data repository: For 2021 at <https://doi.org/PANGAEA.941836>; for 2022 at <https://doi.org/10.1594/PANGAEA.963246>. Data can be submitted under request to S.E.A.P.M. to santiago.pineda.metz@awi.de.

AUTHOR CONTRIBUTION

S.E.A.P.M. wrote the original draft, curated the data, collected data on field, conducted the statistical analyzes, and developed the figures and tables, B.P. and H.L. contributed with development of the original research idea. All authors reviewed the manuscript.

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Figures

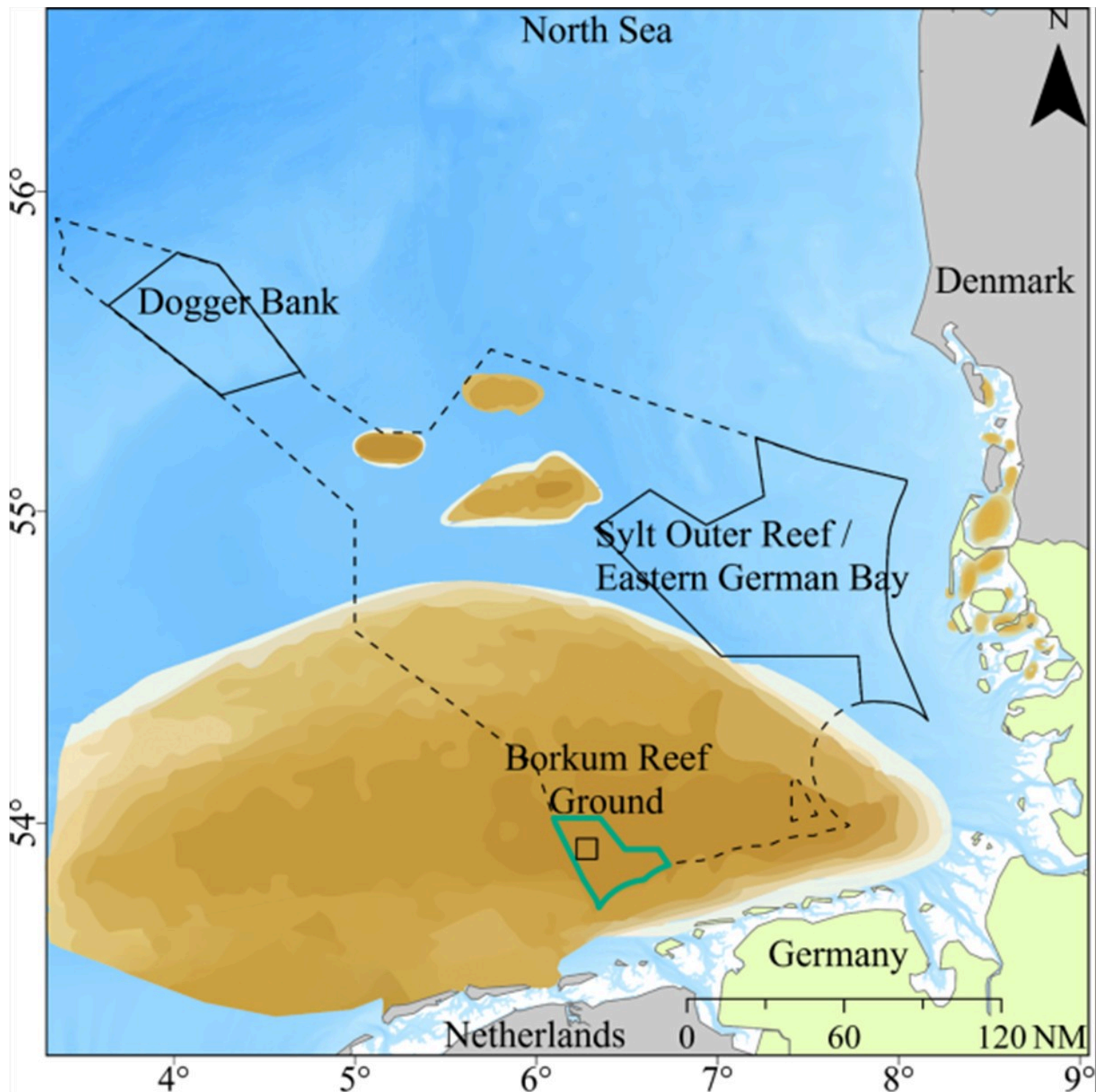


Figure 1

Map of the German Bight with Germany's Exclusive Economic Zone (black), and the Nature Conservation Area (NCA) Borkum Reef Ground (green) with restored pilot oyster reefs (black point) monitored for this study and other NCAs (black full lines) within Germany's EEZ (black dashed line). Orange areas indicate the massive historical distribution of *O. edulis* in the German Bight. Modified from Pineda-Metz et al. [15].

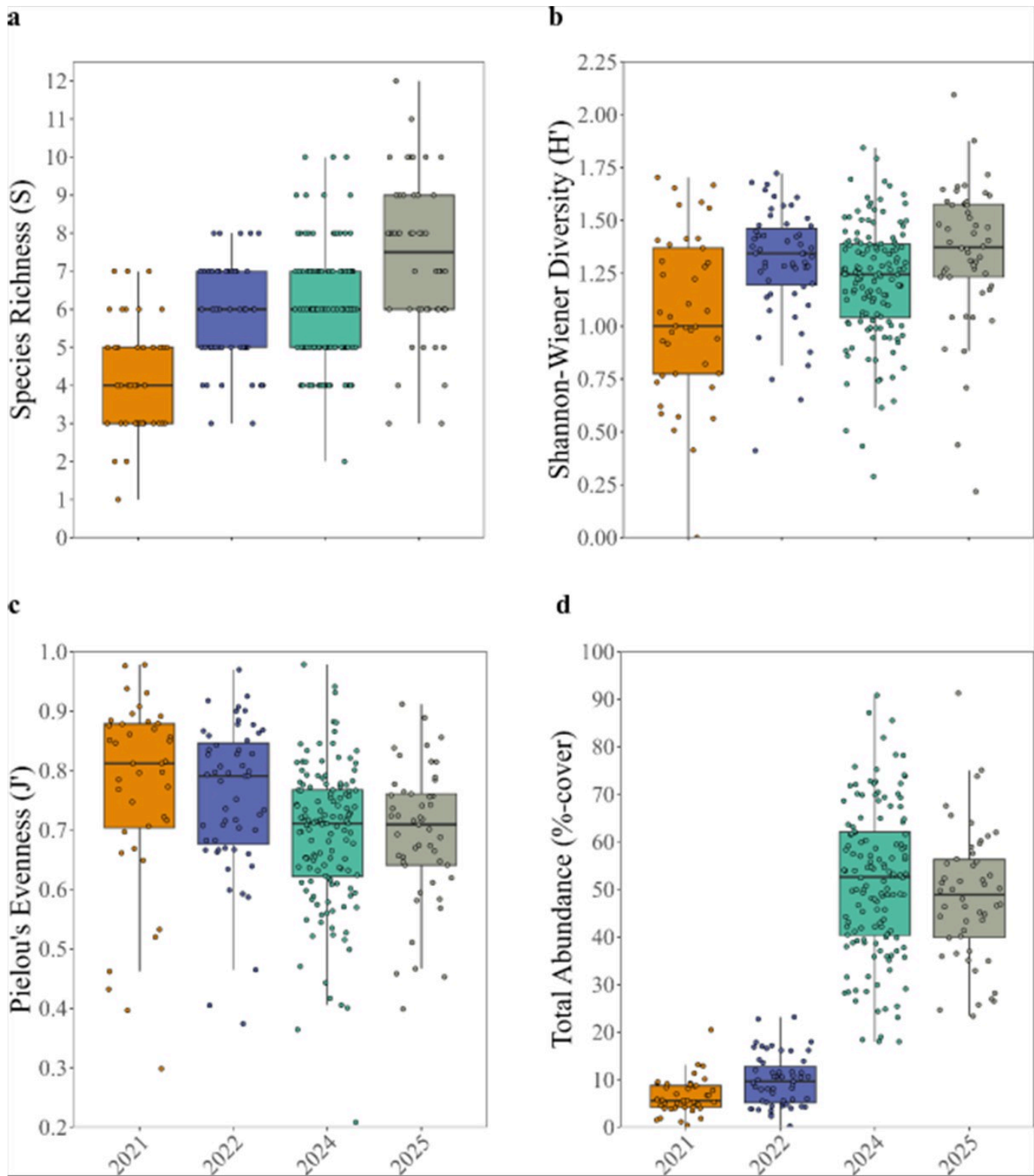


Figure 2

Biodiversity metrics plots: Boxplots showing a) species richness (S), b) Shannon-Wiener's diversity index (H'), c) Pielou's evenness index (J') and d) total abundance (%-cover) calculated for each year (color) and each SBI for 2021 (n = 41), 2022 (n = 55), 2024 (n = 136) and 2025 (n = 50).

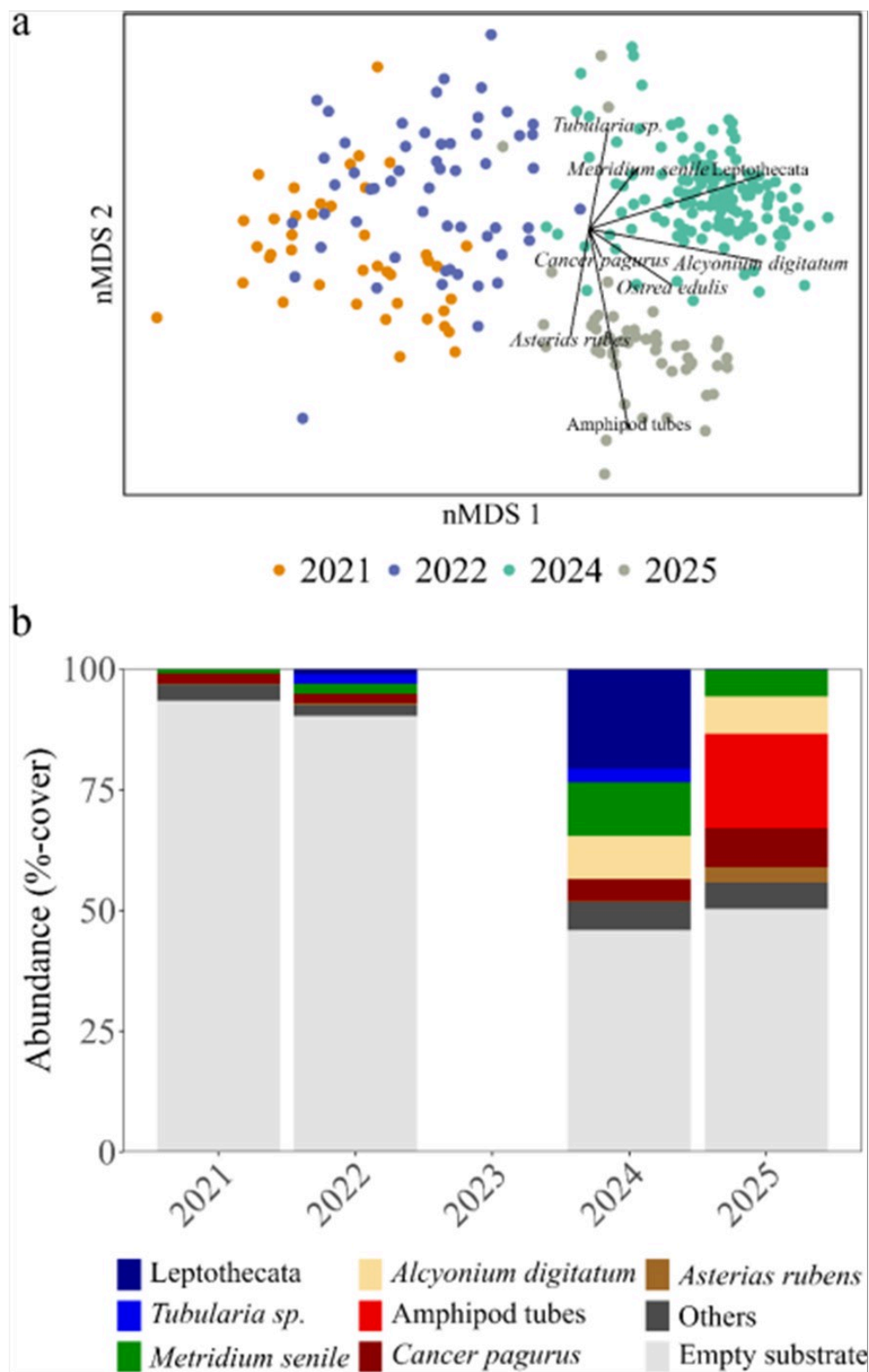


Figure 3

Two-dimensional non-metric multidimensional scaling (nMDS) and Mean abundance values (%-cover) per year: a) nMDS plot visualizing the among-SBI resemblance pattern of the reef associated fauna identified in SBIs. The pattern is based on between-SBI Bray-Curtis similarities calculated from abundance data. Grouping obtained from fuzzy-k means is shown by colors. b: Mean abundance values (%-cover) of dominant taxa identified in SBIs for the years 2021 (n = 41), 2022 (n = 55), 2024 (n = 136) and 2025 (n = 50). The category others represent all operational taxonomic units (OTUs) with an abundance of <1%. Data used for making the plot can be found in Supplementary Table 1.

Supplementary Files

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