Received: 30 May 2022 | Revised: 7 March 2023 | Accepted: 20 March 2023
DOI: 10.1002/aqc.3945

RESEARCH ARTICLE

WILEY

Setting the stones to restore and monitor European flat oyster reefs in the German North Sea

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Funding information
Bundesamt für Naturschutz, Grant/Award Numbers: FKZ3516892001, FKZ3519892016, FKZ3520892013

Abstract

1. Ecological restoration includes specific technical phases over the course of an ecosystem recovery process. In the marine environment and for oyster reef restoration, the installation and implementation of pilot reefs close the gap between feasibility studies with small-scale experiments and designated upscaling for marine conservation measures.
2. Against this background, this study presents the design, planning and installation of the first pilot oyster reef in offshore sublittoral regions of the North Sea. The work was conducted as part of marine protected area management in the Natura 2000 site Borkum Reef Ground in the German Bight, in the area of historical offshore oyster grounds.
3. It includes logistical considerations, material selection, methodology for reef base construction and deployment of European flat oysters *Ostrea edulis* as spat-on-shell, young and adult single seed oysters, and spat-on-reef, as well as the development of an efficient monitoring approach for reef-associated biodiversity.
4. Native Oyster Restoration Alliance monitoring methodologies, such as underwater visual census and seabed images were selected, tested and successfully adapted for the pilot oyster reef and study site. The evaluation and optimization of offshore sublittoral oyster reef monitoring are presented here, and biodiversity metrics are put into perspective with data from recent and historical studies.
5. Results show a few mobile fauna species (e.g., fish and decapods) as first colonizers after reef construction. One year later, biodiversity increased due to a larger number of invertebrate and fish species. However, the pilot oyster reef community still represents an early recolonization stage, with lower biodiversity than historical records.
6. This study presents a proof of concept for the design, planning and construction of an offshore oyster reef and indicates stages in the recovery process. Strategies to optimize and to complement reef-monitoring in challenging environments are discussed, emphasizing additional molecular and functional analyses for future assessments.

KEYWORDS
biodiversity, German bight, monitoring methodology, offshore, *Ostrea edulis*, reef communities

1 | INTRODUCTION

Oyster beds and reefs were once common habitats in European bays and estuaries, tidal channels of the Wadden Sea, offshore areas of the German Bight and reaching into the English Channel (Figure 1; Olsen, 1883; Pogoda, 2019). The European flat oyster (*Ostrea edulis*) is an ecosystem engineer, building three-dimensional and complex biogenic reef habitats. These reefs are built through shell growth, by recruiting on conspecifics and accumulation of dead shells (Möbius, 1893). Like other benthic three-dimensional habitats, such as coral reefs (Roberts et al., 2002) or polar sponge assemblages (Gutt & Starmans, 1998), *O. edulis* reefs are recognized as biodiversity hotspots (e.g. Möbius, 1893; Pogoda et al., 2019; Pogoda et al., 2020a). Today, no such intact oyster habitats remain, as they were destroyed or depleted by intensive fishing pressure and other anthropogenic stressors. Currently, *O. edulis* populations are under threat throughout Europe and are considered as functionally extinct in the German North Sea (Pogoda, 2019).

Due to their ecological value, *Ostrea* reefs are now a focus of European conservation measures aimed at protecting and restoring biogenic reef structures (BfN, 2020). Over the last 2 decades, several oyster restoration projects have been set up across Europe. These are strongly supported by active networks, such as the Native Oyster Restoration Alliance (NORA) and Native Oyster Network and by international knowledge exchange (Pogoda et al., 2019; Pogoda et al., 2020a), mainly building on the rich experience of USA and Australian researchers (Gillies, Crawford & Hancock, 2017; Westby, Geselbracht & Pogoda, 2019; Fitzsimons et al., 2020). A number of European projects are now ready to move forward, progressing from feasibility studies and preliminary research on experimental scales to pilot reefs in the field, an extremely challenging endeavour when it comes to restoring the former offshore oyster grounds in Europe.

Belgium, the Netherlands and Germany are currently active in the historical offshore oyster grounds and have compiled valuable knowledge on site selection and habitat suitability (Kamermans et al., 2018; Bennema, Engelhard & Lindeboom, 2020; Pogoda et al., 2020c; Pogoda et al., 2023), oyster growth, condition and health in sublittoral environments (Merk, Colsoul & Pogoda, 2020; Sas et al., 2020), as well as on jurisdictions and logistical practice (Pogoda et al., 2020b). In Germany, the restoration of the European flat oyster and its biogenic reefs is implemented as a nature conservation measure for the Natura 2000 site Borkum Reef Ground (BRG; BfN, 2020), in the context of preservation and restoration of biodiversity, a key ecological function (Pogoda et al., 2020b; Pogoda,

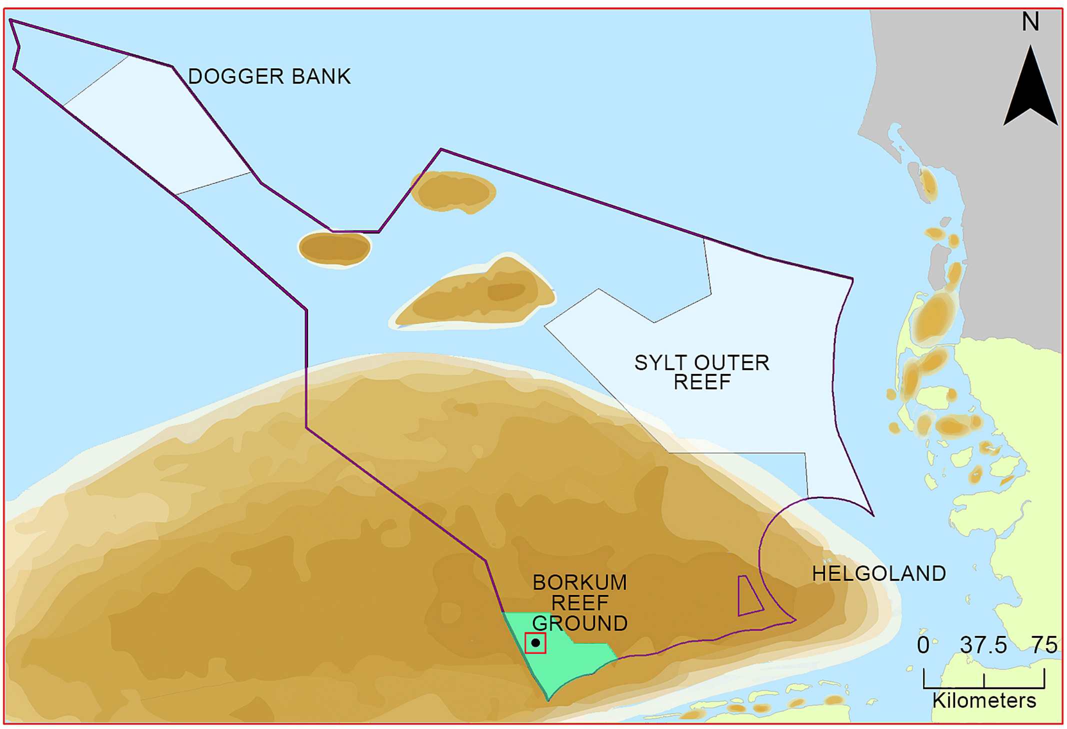

FIGURE 1 Map of the German Bight, including Germany's Exclusive Economic Zone in the North Sea and the marine protected areas Dogger Bank, Sylt Outer Reef and Borkum Reef Ground (BRG; green shade) with the study area (red polygon) where the pilot oyster reef (•) is located. Brown polygons represent the historical distribution of *Ostrea edulis* in the North Sea.

Peter & von Nordheim, 2021). Thus, German programmes focus on different aspects of *O. edulis* restoration, namely: (i) the supply of suitable seed oysters for supporting restoration efforts (project PROCEED); and (ii) the implementation and continuous monitoring of a pilot oyster reef in the German offshore site BRG (project RESTORE), where seed oysters are deployed to build the basis of a future oyster reef to increase and protect biodiversity.

Preliminary field studies confirmed the biological capacity of *O. edulis* to return to and thrive in the sublittoral of the German Bight (Merk, Colsoul & Pogoda, 2020). The next step in the restoration process is the creation of pilot oyster reefs. So far, pilot oyster reefs in substrate-limited sublittoral areas have only been achieved outside Europe (e.g. USA and Australia) by deploying a reef base composed of a stone layer and oyster shells in order to moderate potential negative effects of sediment dynamics and predation (e.g. Gillies, Crawford & Hancock, 2017; Fitzsimons et al., 2020). Furthermore, an elevated base has also been proven to improve oyster physiological performance by, for example, allowing for increased filtration rates, which, in turn, can increase their ability to meet energetic needs and oyster growth (Sawusdee et al., 2015). In the context of developing oyster restoration measures, this study presents the installation of the first offshore European flat oyster pilot reef in the historical oyster grounds of the Natura 2000 site Borkum Reef Ground (BRG) in the German Bight. Furthermore, this study provides information on the deployment strategy for the reef base, potential methods for deploying seed and adult oysters, as well as the development and testing of an offshore focused monitoring plan.

In this study, existing monitoring methods for *O. edulis* restoration were tailored to offshore environments, by implementing and evaluating the toolbox of the NORA monitoring working group, which provides a set of metrics and methodologies recommended for monitoring restoration efforts (zu Ermgassen et al., 2021). Among others, monitoring and restoration metrics relate to environmental factors (e.g. water temperature, salinity, chlorophyll *a* concentration), oyster performance (e.g. oyster density and cover, growth rate, condition, and disease prevalence) and biodiversity (epifaunal sessile invertebrates and macrophytes, small resident fish and mobile invertebrates, transient fish and crustaceans as population metrics). Biodiversity is a complex and flexible term with several definitions (e.g. Gray, 1997; Secretariat of the Convention on Biological Diversity, 2005; Sala & Knowlton, 2006). We are following the definition given by Sala & Knowlton (2006), which specifically relates to marine ecosystems and includes the following concepts for monitoring biodiversity and ecosystem functioning: (i) the number of species; (ii) the structural density of a community; (iii) the degree to which species differ; and (iv) the functional role of the species. This study focuses on the first two concepts, i.e. number of species and structural density of a community, and presents the first monitoring results. To define future restoration goals, these results were compared to data from recent benthic studies at BRG (Darr et al., 2015; Bildstein et al., 2018) and to historical data from former North Sea *O. edulis* reefs (Möbius, 1893; Hagmeier & Kändler, 1927; Caspers, 1950).

While the monitoring methods proposed by NORA applied at the BRG pilot oyster reef are designed for biodiversity studies, they need to be adjusted to a specific study area. the main reason being the relationship that the number of species has with spatial and temporal scales (Arrhenius, 1921; Levin, 1992). However, there is a limit to the sampling effort researchers can do during offshore sampling campaigns. Hence, there is a need to optimize the sampling effort to balance resources spent for a given method and the representativeness it provides of the community structure. A way to achieve this optimization is the use of species accumulation curves, which grow exponentially with every increase in sampling effort until reaching an asymptote, after which any increase of sampling effort results in little further information gain (e.g. Arrhenius, 1921). An additional approach is the use of estimations of the potential maximum number of species for a given area (e.g. using Bayesian non-parametric methods), to further assess the current representativity of a given sampling method. As such, this study presents an optimized baseline methodology for conservation management, focusing on offshore restoration programmes in the German Bight.

2 | MATERIAL AND METHODS

2.1 | Study area and pilot reef set up

The site selection process was conducted by following the framework of marine protected area (MPA) management and nature conservation goals, as well as by considering defined criteria (Kamermans et al., 2018; Pogoda et al., 2020b; Hughes et al., this issue). The study area was defined in the north-western part of BRG, at 30 m water depth and on medium to coarse sand (Figure 1; details in Pogoda et al., 2020b). In collaboration with the German Federal Maritime and Hydrographic Agency (BSH) and the German Federal Waterways and Shipping Administration (WSV), a designated research area extending over ~55 km^2 was established as a no-enter-zone in 2020 to support and protect the European flat oyster reef restoration measure within the BRG MPA (Figure 1). For a detailed environmental description see Pogoda et al. (2020c).

The pilot oyster reef in BRG was set up in two steps during two cruises: the deployment of a reef base (boulders and shell material) and related underwater construction works were executed in July 2020 using an offshore multi-purpose vessel (MV Multrasalvor 4) and resulted in two reef areas with similar setups called East reef and West reef (Figures 2–4). Live oysters were deployed by scientific divers in September 2020 using a research vessel (RV Heincke, HE561; AWI, 2017). In total, the construction of the pilot reef required 16 days at sea. The base of the reefs consists of 80 tons of limestone boulders, covering an approximate area of 50 m^2 per reef area (Figure 4). This material was chosen, as limestone was once abundant in the German North Sea (Streif, 1990; Pogoda et al., 2020c), and can still be found along the few geogenic reefs remaining in the German Exclusive Economic Zone aggregated from

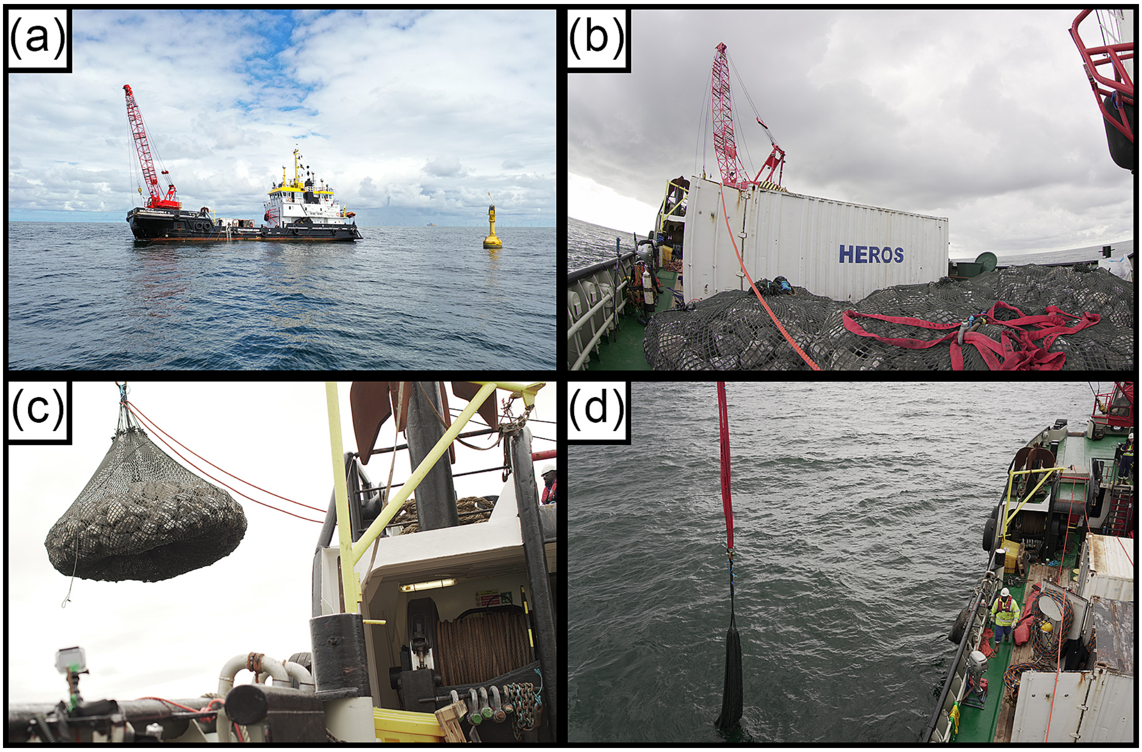

FIGURE 2 Reef base deployment operations on board MV Multrasalvor 4 (a), filter unit nets with stones before deployment (b), stone deployment (c) and retrieval of empty filter unit nets after the stones were released on the seabed (d).

frontal moraines (BfN., 2018; BfN, 2020). The boulders serve as an elevated and natural reef base for the deployed oysters and provide a degree of protection from mobile sand and wave action (Gillies, Crawford & Hancock, 2017). Limestone boulders were sourced from a Belgian quarry (Luths Baustoffe, Carrière des Limites) to minimize transportation distance and CO_2 footprint. They were packed into large nets known as filter units (Sumitomo), to allow for precise deployment from the ship. Filter units were deployed from the ship and emptied at the site in ~30 m water depth before being lifted back to the surface (Figure 2).

Additional to the reef base, 160 kg of *O. edulis* shells were deployed on top of the stone layer, providing potential settlement substrate for oyster larvae (Figure 4). These shells originated from France (La Bélon de Cancale) and were sorted and cleaned by hand and thoroughly disinfected using chlorine solution according to European biosecurity standards (zu Ermgassen et al., 2020). While the stones were deployed from the ship, the shells were filled in biodegradable jute bags (Figure 3) and placed randomly on the stone reef base by divers. Adjacent to each reef subunit, an ~50 m^2 reference area on the sandy sediment was covered with oyster shells in jute bags to assess the efficacy of a potential development of an oyster reef without a stone base.

Spat-on-shell, single seed juvenile oysters and adult oysters (Figure 3; Table 1) were deployed on the reefs in a second step, after the reef base was deployed. Seed oysters (spat-on-shell and single seeds) were purchased from France (Novostrea Bretagne) at a size of ~2.5–4 mm (certified disease-free) and transported to the Helgoland Oyster Hatchery and cultivated for approximately 2 months until deployment. Adult oysters were purchased as single seed oysters from France (Marinove) in 2017 at a size of ~2 mm (certified disease-free, GIP LABOCEA, Ploufragan) and raised in cages off Helgoland for 3 years in the preliminary phase of the RESTORE project to acclimatize these individuals to the environmental conditions of the German Bight at the relevant depths up to 30 m. These adult and mature individuals were deployed as potential broodstock for an initial larvae supply on the pilot oyster reef. All oysters were held in flow-through tanks until deployment at the reef.

Seed and adult oysters were deployed using several methods (e.g. mesh bags, nets, trays and baskets; Table 1; Figure 3). The biodegradable mesh cotton bags and jute nets used for single juvenile oyster deployment had a mesh size of ~4 mm, whereas those used for spat-on-shell deployment had a mesh size of ~30 mm. During the degradation process of the nets, the single individuals can grow normally, potentially forming oyster 'clumps'. Oyster baskets (SEAPA 15 L, 6 mm mesh size; Figure 3b) that exclude predators were deployed with spat-on-shell, single juvenile oysters and adult oysters at both reef areas, using lander systems (Figure 3; Merk, Colsoul & Pogoda, 2020). These were used as reference for growth without predation pressure, and to ensure survival of potential brood stock organisms. In addition, trays (Baggett et al., 2014) with single juvenile oysters in mesh bags and loose adult oysters were distributed out on the stone and sand fields to support holistic biodiversity monitoring (Figure 3). In total, 3,133 adult oysters, ~200,000 single seed oysters

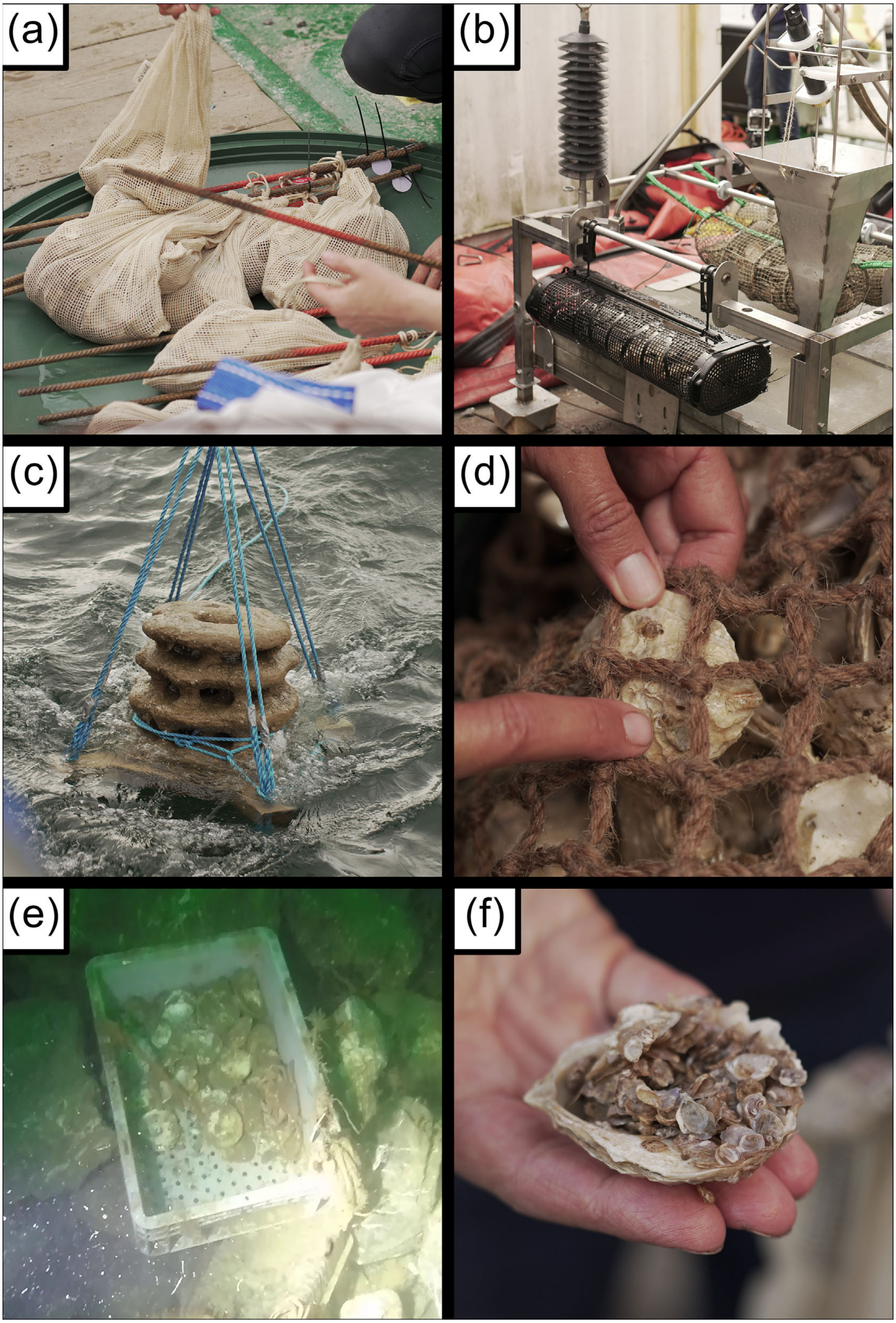

FIGURE 3 Deployment of different seed oyster stages and products (Table 1). (a) Cotton bags (single seed juveniles), (b) SEAPA baskets (broodstock oysters, spat-on-shell reference) and larval collectors, (c) sandstone reef (spat-on-reef), (d) jute nets (spat-on-shell), (e) trays (spat-on-shell, individual adult oysters), (f) single seed juveniles before deployment with cotton bags.

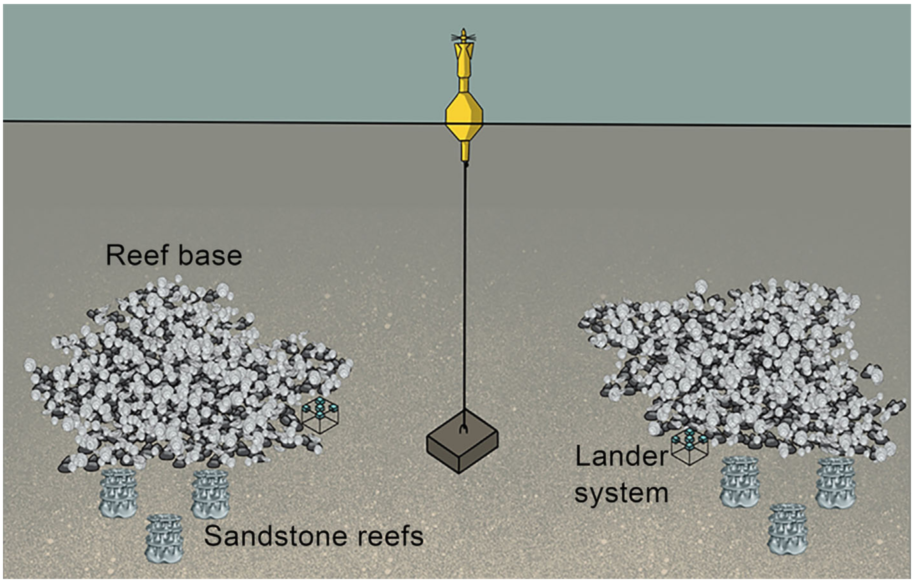

FIGURE 4 Technical scheme of the pilot oyster reef in Borkum Reef Ground, consisting of two reef areas with limestone reef base (boulders in dark grey), deployed oysters (spat-on-shell, single juvenile and adult seed oysters in light grey), as well as sandstone reefs and lander systems (including sensors for environmental parameters and broodstock oysters in SEAPA baskets). The marker buoy (yellow) was installed and is operated by the Federal Waterways and Shipping Administration (WSV). Please note: trays are not included here as their installation was not successfully completed and this sampling approach was not applied. Biodegradable bags are not included here as they degrade fast (8 weeks) and oysters lay loose on the reef base. Shell material and oysters deployed directly on the sandy seafloor are not included here: Due to sediment dynamics, this deployment trial was not successful.

TABLE 1 Overview of different oyster stages and deployment methods used at the pilot oyster reef at Borkum Reef Ground.

Deployment method	Oyster size/age class	Description
28× Cotton bags	4-mm single seed oysters	Young single seed oysters (500 g) were placed in biodegradable ~4-mm mesh bags, bags were cut open after random deployment at the reef base.
80× Cotton bags (Figure 3a)	4-mm single seed oysters, Spat-on-shell	A combination of young single seed oysters (200 g) and spat-on-shell (25 shells) were placed in biodegradable ~4-mm mesh bags, bags were cut open after random deployment at the reef base.
2× Oyster baskets (Figure 3b)	Adult oysters	Adult oysters were placed in SEAPA oyster baskets as a reference for oyster growth and fitness. Baskets allow for excluding predators and sediment dynamics.
2× Oyster baskets (Figure 3b)	Spat-on-shell	Spat-on-shell were placed in SEAPA oyster baskets as a reference for oyster growth and fitness. Baskets allow for excluding predators and sediment dynamics.
2× Sandstone reefs (Figure 3c)	Spat-on-reef	Spat settled on 3D-printed sandstone reefs in a hatchery set-up (Colsoul et al., 2020) were deployed on the sandy seafloor, offering protection from sediment dynamics.
12× Jute nets (Figure 3d)	Spat-on-shell	Biodegradable jute nets (~2.5 mm yarn thickness, 30-mm square mesh, 1 m × 0.5 m size) with spat-on-shell were randomly deployed on the reef base and sand field.
69× Trays (Figure 3e)	Adult oysters	Adult and young single seed oysters were placed onto plastic trays randomly distributed on the reef base and sandy. Trays were fixed to the seafloor by metal hooks to facilitate assessment of mesofauna.

(4 mm size), 2,000 shells with ~3,500,000 spat-on-shell in 20 × 1 m × 0.5 m jute bags and two spat-on-reef sandstone elements were deployed (Table 1, Figure 3).

To relate oyster growth with local environmental conditions, data loggers were deployed to measure temperature (Hobo Water-Temperature Pro v2 Logger), salinity (Sea-Bird SBE 16plus V2 CTD), oxygen saturation (Innovex oxygen and temperature Sensor) and chlorophyll *a* concentration (Sea-Bird ECO FLNTU Fluorometer). The data loggers were attached to the lander systems deployed at the West reef (Figure 3b).

2.2 | Biodiversity metrics and monitoring methodology

This study focuses on the assessment of changes in biodiversity over the first year of the pilot oyster reef and on the potential of applied monitoring methods. Oyster performance assessment, different deployment methods and environmental metrics are not part of this study, as for now data are not complete and still being processed. Biodiversity was assessed via biological community metrics (Gray, 1981) for which two imagery methods were selected:

(i) underwater visual census (UVC); and (ii) seabed image (SBI) transects. These quantitative methods are ideal for representing organisms > 1 cm size, which are here defined as megafauna following specialized literature on sampling methodologies (e.g. Grassle et al., 1975; Solan et al., 2003; Pineda-Metz & Gerdes, 2018). This definition of megafauna slightly differs from the one provided in the NORA monitoring handbook (zu Ermgassen et al., 2021) for fauna recorded using UVC. However, megafauna is the standard nomenclature used for benthic community surveys using imaging techniques (e.g. Solan et al., 2003; Eleftheriou & McIntyre, 2005; Clark, Consalvey & Rowden, 2016). Additional to the UVC and SBI transects, the associated fauna of broodstock oysters in the SEAPA baskets were recorded, as the baskets serve as habitat units (Preston et al., 2021). The associated fauna within the baskets provides a qualitative inventory of the species community complementing the UVC and SBI transects, by including smaller or cryptic species present in the reef, which can be missed by imagery surveys. In 2021, monitoring was greatly constrained due to weather conditions, resulting in less sampling effort than planned (see below).

The UVC transects were undertaken by divers along predefined tracks marked by a rope as a guide. Transects consisted of seven 1×1 m sampling units. To define these regions, divers used a 1-m measuring stick. At each sampling region, the diver spent approximately 1 minute counting and identifying, to the lowest taxonomic level possible, all visible organisms. This sampling approach follows the method used at another location of the German Bight by Wehkamp & Fischer (2013). Before the monitoring cruise, scientific divers tested the planned method, finding it to be efficient and applicable for other regions within the North Sea. Additionally, visible organisms were categorized as small (<10 cm), medium (10–20 cm) and large (>20 cm). All observations were communicated by the diver via intercom and were recorded by the scientific team on board the survey vessel. Due to limited underwater working time, UVC transects were only done at the West reef in 2021.

The SBI transects were done by divers along predefined tracks. The length of each transect varied based on the size of the reef. A Canon EOS M6 camera attached to a frame was used for taking the SBIs. The frame included a 0.5×0.5 m quadrant used for extrapolating counted individuals to 1 m^2, and a scale for animal size classification. SBIs were taken at approximately 0.5 m from each other. Two SBI transects were carried out at the East reef (42 SBIs), but due to limited underwater working time, only one SBI transect was done for the West reef (10 SBIs). Before any further analysis, poor quality SBIs (e.g., out of focus, too dark) were excluded. As SBIs of the surrounding sand bottom showed an absence of megafauna, these were also excluded from further analysis, due to constraints of the multivariate analyses. In total, 34 SBIs for the East reef (17 SBIs per transect) and 10 SBIs for the west reef were analysed in detail, and all individuals were counted and identified to the lowest taxonomic unit possible. Taxonomic identifications were based on Køie, Kristiansen & Weitemeyer (2001) and Hayward & Ryland (2007). Videos and abundances derived from the UVC transect, as well as all SBIs are available in the PANGAEA data repository (Pineda-Metz et al., 2022a; Pineda-Metz et al., 2022b).

To assess the progress of the restoration effort, results of September 2021 (t1, 1 year post-reef construction) were compared to observations from September 2020 (t0, reef construction), and data from benthic surveys of the area in 2012, 2015 and 2017 (Darr et al., 2015; Bildstein et al., 2018). To assess the degree of restoration of the oyster reef and its associated benthic community, historical reference values for biodiversity (van Loon et al., 2018; Heger et al., 2019) were also considered. These were estimated from historical biodiversity data of European flat oyster reefs from the German Bight (Möbius, 1893; Hagmeier & Kändler, 1927; Caspers, 1950). These datasets represent declining (Möbius, 1893), degraded or destroyed (Hagmeier & Kändler, 1927; Casper, 1950) *O. edulis* reefs, as well as geogenic reefs (stones and boulders assemblages on sandy seafloor; Darr et al., 2015; Bildstein et al., 2018). Since the reference datasets include both epi- and infaunal data collected with nets and grabs (Supporting information S1), only mega-epifauna (animals large enough to be visible in SBIs and UVC) were considered for this study. This allows for better comparability between the reference and the imagery data.

Species abundance data for September 2021 resulted in separate data matrices for UVC and for SBI transects. However, the reference datasets contained either abundance (ind m^{-2}) or presence/absence data. To homogenize datasets, all records were compiled in a single species/location table and standardized to presence/absence. The standardized data matrices were first used to calculate biodiversity metrics, namely species richness (S) and species diversity using Shannon–Wiener's index (H′; Shannon, 1948). These metrics provide information regarding number of species and the structural diversity of a community (Sala & Knowlton, 2006), and can be compared to evaluate the degree of development of the BRG pilot oyster reef, and the degree to which they resemble historical records of oyster reefs.

Based on the sampling effort invested in both imagery methods used in the pilot oyster reefs, species accumulation curves were plotted to determine an optimal number of UVC sampling regions and of SBIs. The optimal point is represented by reaching a balance between sampling effort and how well the method represents the species richness of the community, which is typically reached when approximately 75% of the species are recorded (e.g. Thompson & Withers, 2003; Ugland, Gray & Ellingsen, 2003; Pineda-Metz & Gerdes, 2018). To further optimize and assess the representativity of the methodology, the number of newly discovered species with increasing sampling effort was estimated (i.e. number of UVC sampling regions or SBIs). For this, a species sampling model (Bissiri, Ongaro & Walker, 2013) based on the Dirichlet process (Ferguson, 1973) was used. Based on the total abundance (i.e. abundance of all species found in a transect) and that of each species, the model estimates the maximum species richness of the sampled community. This calculation allows determination of: (i) how well the method represents the species richness of a community, reflected as the percentage of the species found in a given sample in relation to the calculated maximum; and (ii) the number of additional species that could potentially be found with any given higher sampling effort. For example, the species sampling model for an SBI or UVC transect with 13 species and a total benthic abundance (i.e., considering all species) of 45 ind. m^{-2} first develops a formula estimating the number of additional species to be found in the transect if 45 new SBIs/UVCs were taken (i.e. as many SBIs/UVCs as the total benthic abundance). This first formula can then be used to estimate the maximum number of species found in any SBI/UVC transect, assuming any number of SBIs or UVC sampling units done.

The UVC transect done during the monitoring of 2021 consisted of seven sampling units, and the total abundance was 6 ind. m^{-2}; whereas the SBI transects consisted of 10–17 SBIs, and the abundance ranged from 69–83 ind. m^{-2}. For the species sampling model based on UVC, the number of species was calculated for a 15-sampling-units-long UVC (i.e. approximately the sum of the total abundance and sampling units); whereas for the SBI, the model was used to estimate the number of species for 90 SBI-long transects (i.e. approximately the sum of the highest abundance and lowest number of SBIs taken). This number of UVC sampling units and SBIs was chosen to approach, as close as possible, the asymptote of the species accumulation curve (e.g. Zito & Rigon, 2022).

Data processing, statistical analyses and plots were done using the packages vegan (Oksanen et al., 2020), BNPvegan (Zito & Rigon, 2022), ggplot2 (Wickham, 2016) and extrafont (Chang, 2014) for RStudio (R Core Team, 2020).

3 | RESULTS

The tray set up (Figure 3e) was unsuccessful under offshore conditions as it was not possible to install trays securely on the reef base or sediment and allow for time-efficient sampling by divers at the same time. Thus, after the testing phase between July and September 2020 this sampling approach was ended. Due to rough weather conditions during the 2021 cruise, diving time was extremely limited and monitoring focused on quantitative results from SBI and UVC data, complemented by qualitative results of associated fauna from habitat units (oyster baskets instead of trays). In total, the imagery methodology recorded 25 megabenthic species (Table 2). From these, four were exclusively found in UVC, whereas 16 were exclusively found in the SBI transects (see Supporting information S1 for detailed species lists). The complementary analysis of associated fauna of oysters in the baskets recorded 21 additional species (Table 2).

Benthic surveys, conducted independent from this study before the BRG pilot oyster reef installation, investigated two habitat types, sandbank (sand and gravel fields) and geogenic reefs (boulder fields on sandy seafloor) using dredge and grab samples (Darr et al., 2015; Bildstein et al., 2018). This approach recorded six megafauna species associated with sand banks (five being fish species), whereas the community of the geogenic reefs comprised up to 20 megafauna species: four fish species, 15 invertebrate taxa, with sessile groups such as bryozoans, gorgonians and ascidians contributing the most species; the remaining species was the lancelet *Branchiostoma lanceolatus* (Figure 5; Supporting information S1). At t0, only mobile megafauna such as fish and decapods (especially *Cancer pagurus*) were observed to start colonizing the newly available rocky habitat provided by the reef base. No sessile organisms were present at the newly established reef base. One year later (t1), the reef showed an increase in the number of mobile species, especially decapods (Figure 5). In contrast to the benthic surveys of the geogenic reefs, only five sessile invertebrate species (four anthozoan and one sponge taxa) were recorded (Figure 5; Supporting Information S1).

Biodiversity data for historical European flat oyster reefs in the German Bight included data from three surveys done between 1869 (Möbius, 1893) and 1938 (Hagmeier & Kändler, 1927; Caspers, 1950). Results show a decline of biodiversity, with S ranging from 39–58 in the 19th century to 16–22 in the early-mid 20th century (Table 3; Figure 5). Surveys within BRG (Darr et al., 2015; Bildstein et al., 2018) previous to the deployment of the pilot oyster reef showed a similar S value to that of the early-mid 20th century (S = 20). When combining both imagery surveys (i.e. UVC and SBI combined), the S value for the pilot oyster reefs at t1 was also within the range described for the early-mid 20th century (S = 25, Table 3). Biodiversity based on H′ also decreased in a similar fashion, i.e. highest values were found in the 19th century decreasing by the 20th century, but remaining stable towards the 21st century (Table 3).

While there is stability in terms of megafauna S and H′ values from the early-mid 20th until the 21st century, species composition was different (Figure 5). Data for historical European flat oyster reefs showed the communities of the 19th and 20th centuries to be dominated by sessile organisms, especially hydrozoans and anthozoans, also with a higher S of motile groups such as decapods, polychaetes and fish (Table 3; Figure 5). The community of the BRG pilot oyster reefs during t1 had only five sessile taxa, four anthozoans (corals; S = 4, 16% of the pilot oyster reef's S) and one demosponge species (*Halichondria panacea*; 4% of the pilot oyster reef's S). This represents less richness of species and of major taxonomic groups compared to historical data (Hagmeier & Kändler, 1927; Caspers, 1950). Furthermore, motile groups such as decapods and fish showed a higher contribution to S at t1 than compared to historical descriptions. These motile taxa accounted for five and 14 species respectively, i.e., they represented ~76% of S of BRG pilot oyster reefs. Compositional differences can also be observed when comparing data from the pre-deployment surveys with t1 (Figure 5). For example, the benthic community described for geogenic reefs of the BRG MPA showed a larger contribution of sessile taxa to S, which was evenly distributed across higher taxonomic groups (e.g. order or class), i.e. several higher taxonomic groups were represented by at least one species (Figure 5).

UVC and SBI methodologies both show the effect of the pilot oyster reef on the benthic community, and how this community differs from reference data (Hagmeier & Kändler, 1927; Caspers, 1950; Darr et al., 2015; Bildstein et al., 2018). It is important to determine if the applied methodology is representative of the pilot oyster reef community. Based on the species accumulation curves, SBI

TABLE 2 Species list of associated reef megafauna found 1 year post pilot oyster reef construction, during the monitoring activities in September 2021. Twenty-five species were documented with underwater visual census (UVC) and seabed image (SBI) transects combined, whereas 26 species were found associated with oyster habitat units (baskets). Five species were documented by both assessments. Superscripts differentiate between species exclusively identified by either the UVC or SBI methodology.

Taxon	Species	Imagery methods (UVC & SBI transect)	Fauna associated with oyster baskets
Porifera	*Halichondria panicea*	+[s]	
	Leucosolenia sp.		+
	Sycon ciliatum		+
Alcyonacea	*Alcyonium digitatum*		+
Anthozoa	*Actinothoe* sp.	+[s]	+
	Metridium senile	+[s]	
	Metridium sp.		+
	Cylista undata		+
	Cerianthus sp.	+[s]	
	Unidentified Anthozoans	+	
Nemertea	*Siphonenteron bilineatum*		+
Bivalvia	*Heteranomia squamula*		+
	Mytilus edulis		+
Gastropoda	*Trivia* sp.		+
Polychaeta	*Hediste diversicolor*		+
	Nereis sp.		+
	Spirobranchus triqueter		+
	Spirorbis sp.		+
Cirripedia	*Balanus crenatus*		+
	Verruca stroemia		+
Decapoda	*Cancer pagurus*	+	+
	Carcinus maenas	+[u]	
	Homarus gammarus	+[s]	+
	Liocarcinus sp.	+	
	Necora puber	+[s]	
	Pilumnus hirtellus		+
	Pisidia longicornis		+
Echinoidea	*Psammechinus miliaris*		+
Asteroidea	*Asterias rubens*	+	+
Ophiuroidea	*Ophiothrix fragilis*		+
	Ophiura sp.		+
Fish	*Acantholabrus palloni*	+[s]	
	Callionymus cf. lyra	+[u]	
	Chelidonichthys lucerna	+[s]	
	Ctenolabrus rupestris	+	
	Zoarces cf. viviparus	+[u]	
	Myoxocephalus scorpius	+[s]	
	Pholis gunnellus	+[s]	+
	Pomatoschistus cf. Microps	+[s]	
	Pomatoschistus minutus	+[u]	
	Scophthalmus rhombus	+[s]	
	Scyliorhinus canicula		+
	Taurulus bubalis	+[s]	

(Continues)

TABLE 2 (Continued)

Taxon	Species	Imagery methods (UVC & SBI transect)	Fauna associated with oyster baskets
	Trachinus draco	$+^{s}$	
	Triglidae spp.	$+^{s}$	
	Labridae spp.	$+^{s}$	

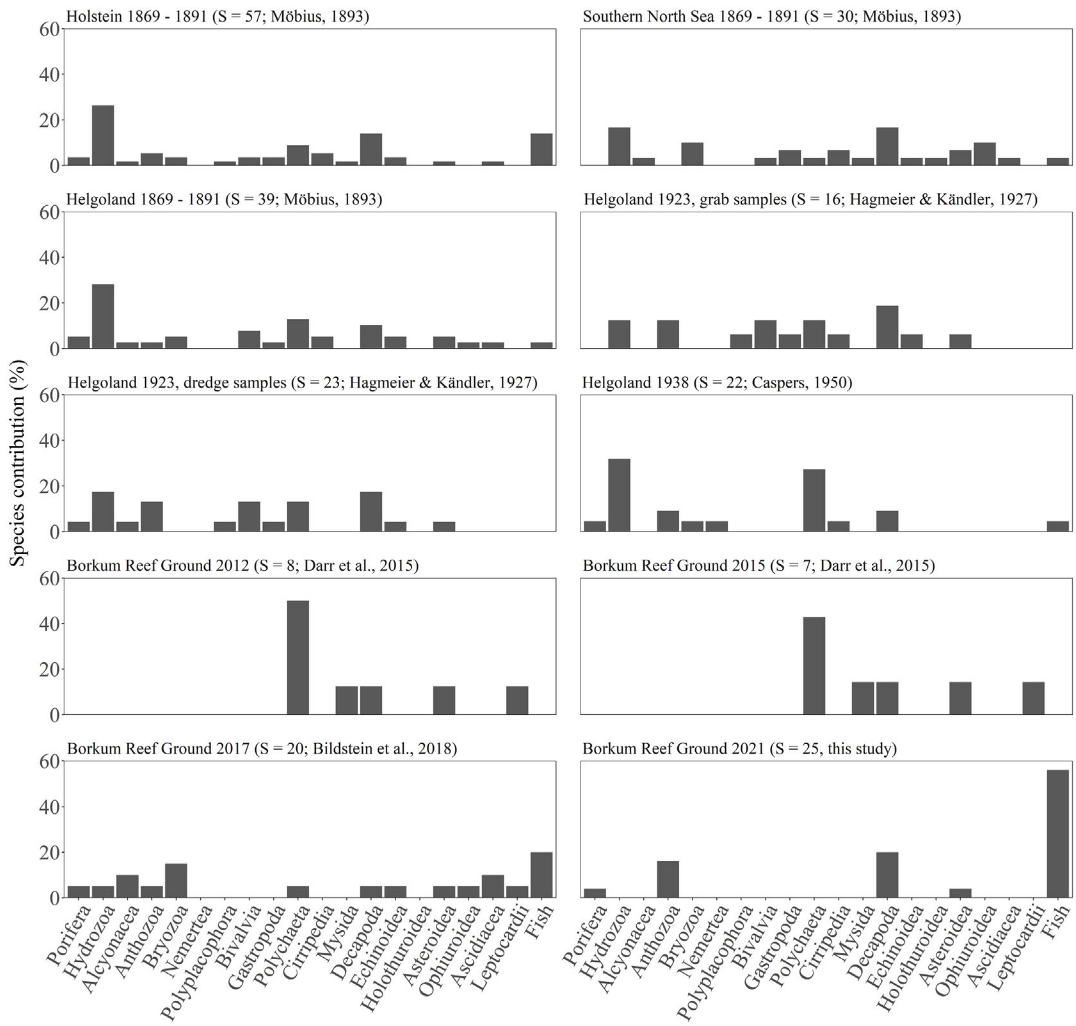

FIGURE 5 Species contribution of each major taxa to the species richness of offshore and deep sublittoral biogenic oyster reefs and biogeogenic reef habitats in the German Bight, North Sea.

transects included 75% of the species living on the reef after 4–10 SBIs were taken (Figure 6a). The species sampling model estimated all SBI transects to include at least 92% of the species which might be present at the reef. This was reflected by: (i) for most SBI transects, the species accumulation curve appears to reach the beginning of an asymptote, except for SBI transect 1 at East reef (Figure 6a); and (ii) the relatively low number of new species that could be found with a larger sampling effort (Figure 6b). If SBI transects were 90-SBIs long, the model estimated that only three to four new species would be recorded (Figure 6b) with a substantially higher sampling effort. For the UVC, the species accumulation curve reached an asymptote, and 75% of the species were found after four sampling units (Figure 6a). However, the species sampling model estimated that doubling the sampling effort would result in six new species, i.e. almost doubling the number of species recorded by UVC (Figure 6b). These findings will be considered for the development of future sampling procedures.

4 | DISCUSSION

Ecosystem degradation and biodiversity loss have resulted in an increased number of restoration programmes to re-establish

TABLE 3 Species richness, diversity and richest groups recorded in previous and historical studies at different regions of the German Bight in comparison to those recorded in the Borkum Reef Ground pilot oyster reef.

Source	Sampling Year	Region	Sampling method	Species Richness (S)	Diversity (H′)	Richest group(s)
Möbius (1893)	1869–1891	Helgoland	Dredge	39	3.66	Hydrozoans (S = 11)
		Holstein		57	4.04	Hydrozoans (S = 15)
		Southern North Sea		30	3.4	Hydrozoans (S = 5) Decapods (S = 5)
Hagmeier & Kändler (1927)	1923	Helgoland	Grab	16	2.77	Hydrozoans (S = 4) Decapods (S = 4)
Caspers (1950)	1938	Helgoland	Dredge	23	3.14	Decapods (S = 3)
			Grab	22	3.09	Hydrozoans (S = 7)
Darr et al. (2015)	2012	Borkum Reef Ground	Grab	8	2.08	Polychaetes (S = 4)
	2015			7	1.95	Polychaetes (S = 3)
Bildstein et al. (2018)	2017		Grab	20	3	Fish (S = 4)
This study	2021		Under Water Census	9	2.2	Fish (S = 4)
			Seabed Images	16	2.4	Fish (S = 11)

ecological characteristics of a given ecosystem (Benayas et al., 2009). In the North Sea, the restoration of the European flat oyster, *O. edulis*, is one of these programmes, involving several international working groups across European countries (Pogoda et al., 2019; Pogoda et al., 2020a).

The BRG pilot oyster reef was designed and implemented as a necessary step in the restoration process of offshore sublittoral regions of the southern North Sea, where the European flat oyster once covered wide areas, but is today functionally extinct. Any offshore work is conducted under challenging weather and hydrographic conditions (Gillies, Crawford & Hancock, 2017; Gilles et al., 2018; Fitzsimons et al., 2020). Underwater sampling and monitoring, such as UVC and SBI transects, as well as other methodologies proposed by NORA (zu Ermgassen et al., 2021) require relatively calm sea conditions for diving operations. Offshore work time is extremely limited due to high costs and weather restrictions, a fact that also applies to the operation of larger vessels for the deployment of boulders for a reef base or heavy gear (e.g. landers for environmental monitoring). Such considerations are important for the selection of adequate gear and structures which can be deployed at offshore sites, to avoid potential loss due to local hydrographic conditions or extreme weather events. As such, the construction and monitoring of offshore oyster reefs requires careful planning and a relatively large logistical effort (Gillies, Crawford & Hancock, 2017; Fitzsimons et al., 2020; Pogoda et al., 2020c). Furthermore, national and international regulations set strict standards regarding deployment procedures, materials to be used, protocols for diving operations, or allowed sampling gear and methodologies (Gillies, Crawford & Hancock, 2017; Fitzsimons et al., 2020; Pogoda et al., 2020b).

During design and installation of the pilot oyster reef, several methodologies were considered (see methods section) with the aim of optimizing restoration operations and facilitating not only a sustainable restoration process, but also monitoring effort and output. The deployment of the BRG pilot oyster reef proved the relevance of 3D structures through their positive effect on local benthic communities, as local diversity and abundance increased compared to the t0 observations. As shown for other restoration efforts (Gillies, Crawford & Hancock, 2017), the deployed pilot oyster reefs resulted in an increase of epifaunal abundance and species richness, especially of motile fauna and of early colonizers. Such observations are a typical effect of newly available hard, stable and structured substrate provided by oysters, used by benthic fauna as refuge, spawning, settling and feeding grounds (e.g. Coen & Luckenbach, 2000; Brown et al., 2014). In September 2020, after finalizing the pilot oyster reef construction, motile organisms (e.g. decapods such as *C. pagurus* and *Homarus gammarus*, fish species such as *Trisopterus luscus*) quickly colonized the reef base. One year later, in September 2021, an increase of motile fauna (e.g. starfish such as *Asterias rubens*, brittlestars such as *Ophiotrix fragilis*, additional decapod and fish species) and sessile organisms (e.g. sponges and anemones) were recorded, reflecting an early successional stage of a reef-associated community.

Ecological restoration is a process for which reference systems or reference models are required to estimate progress and status of restoration (van Loon et al., 2018; Gann et al., 2019; Heger et al., 2019). The nature of restoration studies is similar to that of successional studies. As such, while reference communities help to measure how close to the pre-disturbance stage a restored or recovered ecosystem or habitat is, it is important to define the successional stages the population and community undergo, and the time required between stages, as well as the time until partially or fully recovered ecosystem stages are reached. The studies of Möbius (1893), Hagmeier & Kändler (1927), and Caspers (1950) were

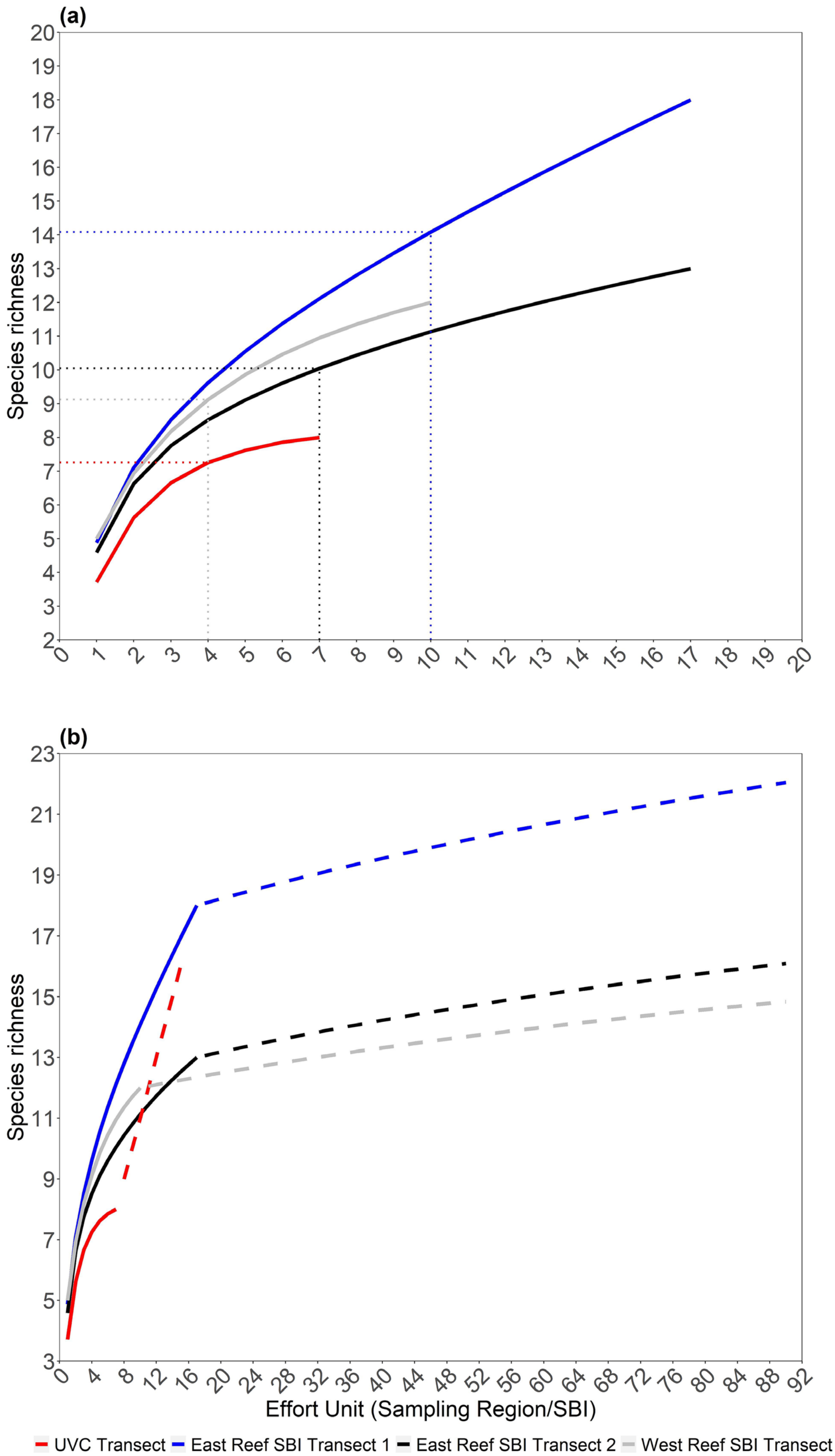

FIGURE 6 Species accumulation curve for all imagery transects done during the September 2021 monitoring campaign to the Borkum Reef Ground oyster pilot reefs. (a) Observed species richness and dotted lines show at which effort unit (underwater visual census (UVC) sampling region or seabed image (SBI)) the 75% of the species in a transect are found. (b) Observed (solid line) and expected (dashed lines) species richness by unit effort.

considered as reference states to be reached during the restoration process of European flat oyster restoration (Gann et al., 2019). While these studies do not represent a pre-disturbance stage as they represent reefs that were already declining (Möbius, 1893) or collapsed (Hagmeier & Kändler, 1927), they provide a reference for successional stages and a provisional baseline to compare restoration efforts against. Taking this into account, the BRG pilot oyster reef can be considered to represent an early stage of succession, where only motile and pioneer groups dominate. This phase is still relatively far from the successional stages reflected by declining (Möbius, 1893), collapsed and depleted historical reefs (Hagmeier & Kändler, 1927; Caspers, 1950). Typical sessile groups, such as hydrozoans were not documented at the pilot oyster reef after the first year. The ichthyofaunal diversity appears to have recovered or benefitted by the introduction of the reef, as 14 fish species were found, i.e., six more than described by Möbius (1893). However, this could be also an artefact of methodological approaches, as grabs tend to underrepresent highly motile groups, such as fish, in comparison to imagery surveys (Solan et al., 2003). Additionally, as the study of Möbius (1893) nor the current data sets for the pilot oyster reefs at BRG include information on size and age of the fish populations, it is difficult to draw further conclusions. Other successional studies on the North Sea's hard substrate show that communities dominated by sessile organisms can take at least 3–6 years to develop and provide a reef effect, by providing a complex three-dimensional configuration (Taormina et al., 2020). Regular monitoring will show if an increase of sessile organisms and further increases in biodiversity will be facilitated and sustained by the pilot oyster reef, and will inform about the time span of the recovery process.

Monitoring needs to comprehensively represent the structure and characteristics of any associated reef-community and, thus, the species which comprise these communities. Selecting and optimizing methodologies is of great importance to balance the quality and quantity of the obtained data with the sampling effort. The use of imaging techniques has consistently increased over the last decades for monitoring temporal and spatial changes of benthic communities (e.g. Gutt et al., 2013; Michaelis et al., 2019; Pineda-Metz, Gerdes & Richter, 2020), and has been recommended as an appropriate monitoring tool for biodiversity metrics and conservation efforts (Cummings et al., 2021; zu Ermgassen et al., 2021). The imagery transects (Pineda-Metz et al., 2022b) will also provide data on universal metrics such as oyster habitat area, shell cover and oyster density, as well as oyster size frequency (zu Ermgassen et al., 2021). These tools are ideal to investigate benthic communities, their structure and the services they provide, over both small and large areas in a non-destructive way (Solan et al., 2003; Eleftheriou & McIntyre, 2005; Clark, Consalvey & Rowden, 2016). To optimize the sampling, the number of images or videos to be taken (or area to be sampled) needs to be adjusted, so that the sampling method adequately represents the community's structure, without involving any unnecessary high sampling effort and, consequently, high time consumption and cost. Here, the SBI transects comprehensively represent the community present at the pilot oyster reef and, currently, little optimization of the strategy is required. The UVC is complementary to the SBI transect as it better represents large and mobile species such as decapods and fish (Pineda-Metz et al., unpublished data), albeit underrepresenting the species richness of the pilot oyster reef. As such, UVC methodology may require an increased sampling effort for the following monitoring phases. Sampling units would be slightly increased, and an additional UVC transect would be conducted per reef area to improve monitoring efficiency. Consequently, this would increase diving times and efforts, with the respective risks and challenges. Remote observation vehicles (e.g. autonomous underwater vehicles) or other imagery systems (e.g. drop or towed camera systems; e.g. Grange & Smith, 2013; Barnes & Sands, 2017; Purser et al., 2019) have been also tested at the pilot oyster reef. However, deployment of these gears can be greatly hampered by sediment resuspension (Solan et al., 2003), or they are inadequate for relatively small areas such as the two ~50-m^2 areas of the pilot oyster reef. This is mainly due to most camera systems being conceived to sample over several km^2, rather than a few m^2 (Eleftheriou & McIntyre, 2005; Clark, Consalvey & Rowden, 2016). The designated up-scaling of oyster restoration in the near future, might prove the application of automated imagery key for monitoring, e.g. to minimize diving operations, and allow for assessments of larger and deeper restoration sites.

The restoration of biogenic reefs such as European flat oyster habitats is a designated conservation management measure under the European Habitats Directive (Directive 92/43/EEC; European Parliament, 2012) and contributes to the EU Marine Strategy Framework Directive (Directive 2008/56EC; BLANO, 2016). Furthermore, it is relevant under respective national conservation laws, or as a mitigation measure to compensate for destructive interventions in marine ecosystems, such as construction of offshore wind farms and laying of offshore cables (Pogoda et al., 2020b; Pogoda et al., this issue). Thus, the development, application and continued improvement of non-destructive (non-invasive), and at the same time scientifically robust and efficient monitoring methods is of great importance (Pineda-Metz, Merk & Pogoda, 2023). This study strengthens the understanding that there is not one ideal biodiversity monitoring method, but that a combination of sampling techniques will achieve the most complete species inventories. Additional non-invasive and potentially adequate methods for biodiversity monitoring are environmental DNA assessments. These molecular approaches allow for collection of DNA fragments from environmental samples (e.g. seawater or sediment), which can be used for identification of cryptic or migrating reef-associated species that are usually missed by classical monitoring approaches such as grab sampling or imagery methods (Beng & Corlett, 2020). Such environmental DNA methods are currently being developed and adapted for oyster reef monitoring and will be integrated into the assessments (Pogoda & Laakmann, personal communication). Future assessments of the species community composition and structure can be complemented by including biological trait analyses (BTA; Bremner, Rogers & Frid, 2006). BTAs focus on modalities and traits of a community, providing insights on its functional structure and functional diversity, indicating performance and community resilience to disturbance (Beauchard et al., 2017). Applying BTAs to the pilot oyster reef community will contribute to a holistic observation of the recovery of ecosystem services and functions at and by the oyster reef.

The results of this study describe, to the best of the authors knowledge, the design, planning and construction of the first pilot oyster reef in sublittoral offshore waters of the German Bight. This first proof of concept is an important step for scaling up restoration operations in marine conservation and management in challenging environments, such as the North Sea. It provides valuable knowledge for projects in similar settings, e.g. for offshore oyster restoration in the Netherlands and in Belgium (Pogoda et al., 2020c). Furthermore, a monitoring concept was tailored to the offshore study site, which proved efficient for quantitative and qualitative approaches. While some methodological improvements and fine tuning will facilitate and improve future work, basic aspects have been addressed successfully by defining reference communities based on historical records, providing key information (e.g. species lists, richness and diversity) and relevant steps to consider for offshore oyster reef deployment and monitoring (e.g. reef base construction, substrates, oyster deployment, logistical considerations, monitoring performance).

In Germany, oyster restoration will be implemented across suitable areas in the Natura 2000 site BRG (Pogoda et al., this issue) as a conservation management measure with high priority (BfN, 2020), as well as a mitigation measure for environmentally relevant interventions such as offshore construction to compensate for negatively affected seafloor areas (BfN & BMU, 2021). The presented knowledge provides the basis for the development of such compensation measures to be applied by governmental bodies and respective stakeholders, such as the offshore wind sector (BfN, 2019). Against this background, the planning and implementation of large-scale reefs is a relevant next step. The results of this study in combination with respective habitat suitability analysis (Pogoda et al., this issue) provide the necessary information to move forward and to realize upscaling operations. Following the strategies that have proven successful in the USA and in Australia, a reef established over a 2-ha area is recommended here, before scaling up to 10 ha (e.g. Gilles et al., 2018). These restoration steps of European flat oyster reef ecosystems are setting the scene for the recovery of a structured biogenic habitat and hotspots of biodiversity, improving the conservation status of MPAs and aiming at a good environmental status of the European seas (European Parliament, 1992; BLANO, 2016).

AUTHOR CONTRIBUTIONS

Santiago E. A. Pineda-Metz: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing—original draft; writing—review and editing. **Bérenger Colsoul:** Conceptualization; investigation; methodology; writing—original draft; writing—review and editing. **Miriam Niewöhner:** Data curation; formal analysis; writing—review and editing. **Tanja Hausen:** Funding acquisition; investigation; methodology; project administration; writing—original draft; writing—review and editing. **Corina Peter:** Conceptualization; investigation; methodology; project administration; writing—original draft; writing—review and editing. **Bernadette Pogoda:** Conceptualization; funding acquisition; investigation; methodology; project administration; supervision; writing—original draft; writing—review and editing.

ACKNOWLEDGEMENTS

We thank the German Federal Agency for Nature Conservation (BfN) for funding and supporting this study in close cooperation. We thank involved authorities, such as the German Federal Maritime and Shipping Agency (BSH) and the Waterways and Shipping Administration (WSV, GDWS) for their administrative and practical support to implement marine conservation measures. We thank our colleagues of the Helgoland Oyster Hatchery, and especially the following colleagues for their help throughout this study: Dr. Aldi Nel, Clemens Kozian-Fleck and Lennard Klingforth. We thank captain and crew of RV Heincke, Mya II, Uthörn and of MV Multrasalvor 4 and the Centre for Scientific Diving at AWI, namely Prof. Dr. Philipp Fischer, Dr. Markus Brand, Lisa Spotowitz, Christopher Groß and Marco Warmuth for their constant and valuable support to implement and investigate the fieldwork and especially the following colleagues for their help throughout this study: Verena Merk, Anna-Lena Böger, Lena Blum and Anna Feuring. This research is part of the testing and development project RESTORE (2016-2025), funded by the German Federal Agency for Nature Conservation, grant numbers FKZ 3516892001, FKZ 3519892016, FKZ 3520892013. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no potential conflict of interest.

DATA AVAILABILITY STATEMENT

Benthic megafauna presence/absence data considered for this publication are provided as Supporting information 1. Seabed images and data pertaining the underwater visual census of the monitoring program in September 2021 can be accessed in the PANGAEA data repository (Pineda-Metz et al., 2022a,b). Data can also be provided upon request to the corresponding author.

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REFERENCES

Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung (AWI). (2017). Research vessel HEINCKE operated by the Alfred-Wegener-institute. *Journal of Large-Scale Research Facilities*, 3, A120. https://doi.org/10.17815/jlsrf-3-164

Arrhenius, O. (1921). Species and area. *Journal of Ecology*, 9(1), 95–99. https://doi.org/10.2307/2255763

Baggett, L., Posers, S., Brumbaugh, R., Coen, L., DeAngelis, B. & Greene, J. (2014). *Oyster habitat restoration monitoring and assessment handbook*. Arlington: The Nature Conservancy.

Barnes, D.K.A. & Sands, C.J. (2017). Functional diversity is key to Southern Ocean carbon pathways. *PLoS ONE*, 12(6), e0179735. https://doi.org/10.1371/journal.pone.0179735

Beauchard, O., Veríssimo, H., Queirós, A.M. & Herman, P.M.J. (2017). The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. *Ecological Indicators*, 76, 81–96. https://doi.org/10.1016/j.ecolind.2017.01.011

Benayas, J.M.R., Newton, A.C., Diaz, A. & McBullock, J.M. (2009). Enhancement of biodiversity and ecosystem services by ecological restoration: a metadata analysis. *Science*, 325(5944), 1121–1124. https://doi.org/10.1126/science.1172460

Beng, K.C. & Corlett, R.T. (2020). Applications of environmental DNA (eDNA) in ecology and conservation: opportunities, challenges and prospects. *Biodiversity and Conservation*, 29, 2089–2121. https://doi.org/10.1007/s10531-020-01980-0

Bennema, F.P., Engelhard, G.H. & Lindeboom, H. (2020). *Ostrea edulis* beds in the Central North Sea: delineation, ecology, and restoration. *ICES Journal of Marine Science*, 77(7–8), 2694–2705. https://doi.org/10.1093/icesjms/fsaa134

BfN. (2018). BfN-Kartieranleitung für "Riffe" in der deutschen ausschließlichen Wirtschaftzone (AWZ). https://www.bfn.de/sites/default/files/BfN/meeresundkuestenschutz/Dokumente/BfN-Kartieranleitungen/bfn-kartieranleitung-riffe-in-der-deutschen-awz.pdf [Accessed 6th May 2022].

BfN. (2019). *Mögliche Maßnahmen für eine Realkompensation von Eingriffen (Ausgleichs- und Ersatzmaßnahmen) in der deutschen AWZ von Nord- und Ostsee*. Available from: web01.bfn.cu.ennit.de/fileadmin/BfN/awz/Dokumente/Uebersicht_Kompensationsmassnahmen.pdf [Accessed 30th May 2022].

BfN. (2020). *Managementplan für das Naturschutzgebiet "Borkum Riffgrund" (MPBRg)*. Bundesamt für Naturschutz. Report (BAnz AT): Az. MAR-34324-04.

BfN & BMU. (2021). *Handreichung zum Vollzug der Bundeskompensations-verordnung, November 2021*. https://www.bfn.de/sites/default/files/2021-11/Handreichung%20zur%20BKompV.pdf [Accessed 19th May 2022].

Bildstein, T., Schuchardt, B., Kramer, M., Bleich, S., Schückel, S., Huber, A. et al. (2018). *Die Meeresschutzgebiete in der deutschen ausschließlichen Wirtschaftszone der Nordsee*. Bonn: Bundesamt für Naturschutz. https://doi.org/10.19217/skr477

Bissiri, P.G., Ongaro, A. & Walker, S.G. (2013). Species sampling models: consistency for the number of species. *Biometrika*, 100(3), 771–777. https://doi.org/10.1093/biomet/ast006

BLANO. (2016). *MSRL-Maßnahmenprogramm zum Meeresschutz der deutschen Nord- und Ostsee: Bericht gemäß § 45h Absatz 1 des Wasserhaushaltsgesetzes*. https://www.meeresschutz.info/berichte-art13.html [Accessed 8th July 2021].

Bremner, J., Rogers, S.I. & Frid, C.L.J. (2006). Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecological Indicators*, 6(3), 609–622. https://doi.org/10.1016/j.ecolind.2005.08.026

Brown, L.A., Furlong, J.N., Brown, K.M. & La Peyre, M.K. (2014). Oyster reef restoration in the northern Gulf of Mexico: effect of artificial substrate and age on nekton and benthic macroinvertebrate assemblage use. *Restoration Ecology*, 22(2), 214–222. https://doi.org/10.1111/rec.12071

Caspers, H. (1950). Die Lebensgemeinschaft der Helgoländer Austernbank. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, 3, 119–169.

Chang, W. (2014). *extrafont: tools for using fonts*. R Package Version 0.17. https://CRAN.R-project.org/package=extrafont

Clark, M.R., Consalvey, M. & Rowden, A.A. (2016). *Biological sampling in the deep sea*. New Jersey: Wiley-Blackwell.

Coen, L.D. & Luckenbach, M.W. (2000). Developing success criteria and goals for evaluating oyster restoration: ecological function or resource exploitation? *Ecological Engineering*, 15(3–4), 323–343. https://doi.org/10.1016/S0925-8574(00)00084-7

Cummings, V.J., Bowden, D.A., Pinkerton, M.H., Halliday, N.J. & Hewitt, J.E. (2021). Ross Sea benthic ecosystems: macro- and mega-faunal community patterns from a muilti-environment survey. *Frontiers in Marine Science*, 8, 629787. https://doi.org/10.3389/fmars.2021.629787

Darr, A., Zettler, A., Zettler, M.L., Ebbe, B. & Gutow, L. (2015). Monitoringbericht. In: *Zustand benthischer Arten und biotope in der deutschen Ausschließlichen Wirtschaftszone von Nord und Ostsee. Untersuchungsjahr 2015*. Bonn: Bundesamt für Naturschutz.

Eleftheriou, A. & McIntyre, A.D. (2005). *Methods for the study of marine benthos*. Oxford: Blackwell Publishing Company.

European Parliament. (1992). Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. 43 (47–50).

Ferguson, T.S. (1973). A bayesian analysis of some nonparametric problems. *Annals of Statistics*, 1(2), 209–230. https://doi.org/10.1214/aos/1176342360

Fitzsimons, J.A., Branigan, S., Gilles, C.L., Brumbaugh, R.D., Cheng, J., DeAngelis, B.M. et al. (2020). Restoring shellfish reefs: global guidelines for practitioners and scientists. *Conservation Science and Practice*, 2(6), e198. https://doi.org/10.1111/csp2.198

Gann, D.G., McDonald, T., Walder, B., Aronson, J., Nelson, C.R., Jonson, J. et al. (2019). *International principles and standards for the practice of ecological restoration*. Washington: Society for Ecological Restoration.

Gilles, C.L., McLeod, I.M., Alleway, H.K., Cook, P., Crawford, C., Creighton, C. et al. (2018). Australian shellfish ecosystems: past distribution, current status and future direction. *PLoS ONE*, 13(2), e0190914. https://doi.org/10.1371/journal.pone.0190914

Gillies, C.L., Crawford, C. & Hancock, B. (2017). Restoring Angasi oyster reefs: what is the endpoint ecosystem we are aiming for and how do we get there? *Ecological Management & Restoration*, 18(3), 214–222. https://doi.org/10.1111/emr.12278

Grange, L.J. & Smith, C.R. (2013). Megafaunal communities in rapidly warming fjords along the West Antarctic peninsula: hotspots of abundance and beta diversity. *PLoS ONE*, 8(11), e77917. https://doi.org/10.1397/journal.pone.0077917

Grassle, J.F., Sanders, H.L., Hessler, R.R., Rowe, G.T. & McLellan, G.T. (1975). Pattern and zonation: a study of the bathyal megafauna using the research submersible *Alvin*. *Deep Sea Research and Oceanographic Abstracts*, 22(7), 457–462. https://doi.org/10.1016/0011-7471(75)90020-0

Gray, J.S. (1981). *The ecology of marine sediments*. Cambridge: Cambridge University Press.

Gray, J.S. (1997). Marine biodiversity: patterns, threats and conservation needs. *Biodiversity and Conservation*, 6, 153–175. https://doi.org/10.1023/A:1018335901847

Gutt, J., Cape, M., Dimmler, W., Fillinger, L., Isla, E., Lieb, V. et al. (2013). Shifts in Antarctic megabenthic structure after ice-shelf disintegration in the Larsen area east of the Antarctic peninsula. *Polar Biology*, 36, 895–906. https://doi.org/10.1007/s00300-013-1315-7

Gutt, J. & Starmans, A. (1998). Structure and biodiversity of megabenthos in the Weddell and Lazarev seas (Antarctica): ecological role of physical parameters and biological interactions. *Polar Biology*, 20, 229–247. https://doi.org/10.1007/s003000050300

Hagmeier, A. & Kändler, R. (1927). Neue Untersuchungen im nordfriesischen Wattenmeer und auf den fiskalischen Austernbänken. *Wissenschaftliche Meeresuntersuchungen (Helgoland)*, 16, 1–90.

Hayward, P.J. & Ryland, J.S. (2007). *Handbook of the marine fauna of North-West Europe*. Oxford: Oxford University Press.

Heger, T., Bernard-Verdier, M., Gessler, A., Greenwood, A.D., Grossart, H.-P., Hilker, M. et al. (2019). Towards an integrative, eco-evolutionary understanding of ecological novelty: studying and communicating interlinked effects of global change. *Bioscience*, 69(11), 888–899. https://doi.org/10.1093/biosci/biz095

Kamermans, P., Walles, B., Kraan, M., van Duren, L., Kleissen, F., van der Have, T. et al. (2018). Offshore wind farms as potential locations for flat oyster (*Ostrea edulis*) restoration in the Dutch North Sea. *Sustainability*, 10(11), 3942. https://doi.org/10.3390/su10113942

Køie, M., Kristiansen, A. & Weitemeyer, S. (2001). *Der große Kosmos-Strandführer: Tiere und Pflanzen in Nord-und Ostsee*. Stuttgart: Franckh-Kosmos.

Levin, S.A. (1992). The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology*, 73(6), 1943–1967. https://doi.org/10.2307/1941447

Merk, V., Colsoul, B. & Pogoda, B. (2020). Return of the native: survival, growth and condition of European oysters reintroduced to German offshore waters. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30(11), 2180–2190. https://doi.org/10.1002/aqc.3426

Michaelis, R., Hass, H.C., Mielck, F., Papenmeier, S., Sander, L., Gutow, L. et al. (2019). Epibenthic assemblages of hard-substrate habitats in the German bight (South-Eastern North Sea) described using drift videos. *Continental Shelf Research*, 175, 30–41. https://doi.org/10.1016/j.csr.2019.01.011

Möbius, K. (1893). *Über die Thiere der Schleswig-holsteinischen Austernbänke, ihre physikalischen und biologischen Lebensverhältnisse*. Berlin: Deutsche Akademie der Wissenschaften.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. et al. (2020). Vegan: community ecology package. *R Package Version*, 2, 5–7. https://CRAN.R-project.org/package=vegan

Olsen, T.O. (1883). *The piscatorial atlas of the North Sea, English Channel, and St. George's channels: illustrating the fishing ports, boats, gear, species of fish (how, where, and when caught), and other information concerning fish and fisheries*. London: Taylor and Francis.

Pineda-Metz, S.E.A., Brand, M., Böger, A.-L., Blum, L & Pogoda, B. (2022a). Underwater visual census at pilot oyster reefs in the Brokum reef ground marine protected area during September 2021. *PANGAEA*, https://doi.org/10.1594/PANGAEA.946722

Pineda-Metz, S.E.A., Brand, M., Merk, V., Feuring, A. & Pogoda, B. (2022b). Seabed images taken at the pilot oyster reefs in the Borkum reef ground marine protected area during September 2021. *Pangaea*. https://doi.org/10.1594/PANGAEA.941836

Pineda-Metz, S.E.A. & Gerdes, D. (2018). Seabed images versus corer sampling: a comparison of two quantitative approaches for the analysis of marine benthic communities in the southern Weddell Sea (Southern Ocean). *Polar Biology*, 41, 515–526. https://doi.org/10.1007/s00300-017-2211-3

Pineda-Metz, S.E.A., Gerdes, D. & Richter, C. (2020). Benthic fauna declined on a whitening Antarctic continental shelf. *Nature Comunications*, 11, 2226. https://doi.org/10.1038/s41467-020-16093-z

Pineda-Metz, S.E.A., Merk, V. & Pogoda, B. (2023). A machine learning model and biometric transformations to facilitate European oyster monitoring. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 2023, 1–13. https://doi.org/10.1002/aqc.3912

Pogoda, B. (2019). Current status of European oyster decline and restoration in Germany. *Humanities*, 8(1), 1–12. https://doi.org/10.3390/h8010009

Pogoda, B., Boudry, P., Bromley, C., Cameron, T.C., Colsoul, B., Donnan, D. et al. (2020a). NORA moving forward: developing an oyster restoration network in Europe to support the Berlin oyster recommendation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30(11), 2031–2037. https://doi.org/10.1002/aqc.3447

Pogoda, B., Brown, J., Hancock, B., Preston, J., Pouvreau, S., Kamernas, P. et al. (2019). The native oyster restoration Alliance (NORA) and the Berlin oyster recommendation: bringing back a key ecosystem engineer by developing and supporting best practice in Europe. *Aquatic Living Resources*, 32, 13. https://doi.org/10.1051/alr/2019012

Pogoda, B., Colsoul, B., Hausen, T., Merk, V. & Peter, C. (2020b). *Wiederstellung der Bestände der Europäischen Auster (*Ostrea edulis*) in der deutschen Nordsee (RESTORE Voruntersuchung)*. Bonn: Bundesamt für Naturschutz. https://doi.org/10.19217/skr582

Pogoda, B., Hausen, T., Rothe, M., Bakker, F., Hauser, S., Colsoul, B. et al. (2023). Come, tell me how you live: Habitat suitability analysis for Ostrea edulis restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems*. Portico. https://doi.org/10.1002/aqc.3928

Pogoda, B., Merk, V., Colsoul, B., Hausen, T., Peter, C., Pesch, R. et al. (2020c). Site selection for biogenic reef restoration in offshore environments: The Natura 2000 area Borkum reef ground as a case study for native oyster restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30(11), 2163–2179. https://doi.org/10.1002/aqc.3405

Pogoda, B., Peter, C. & von Nordheim, H. (2021). Wiederansiedlung und ökologische Bedeutung der Europäische Auster in der deutschen Nordsee. *Natur Und Landschaft*, 96(2), 83–88. https://doi.org/10.17433/2.2021.50153881.83-88

Preston, J., Sanderson, W., Pogoda, B., Baxter, J.M., Cameron, T.C., Davies, I.M. et al. (2021). Restoration goal-based monitoring metrics. In: zu Ermgassen, P.S.E., Bos, O., Debney, A., Gamble, C., Glover, A., Pogoda, B. et al. (Eds.) *European native oyster habitat restoration monitoring handbook*. London: The Zoological Society of London, pp. 33–53.

Purser, A., Marcon, Y., Drutter, S., Hoge, U., Sablotny, B., Hehemann, L. et al. (2019). Ocean floor observation and bathymetry system (OFOBS): a new towed camera/sonar system for deep-sea habitat surveys. *IEEE Journal of Oceanic Engineering*, 44(1), 87–99. https://doi.org/10.1109/JOE.2018.2794095

R Core Team. (2020). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Roberts, C.M., McClean, C.J., Veron, J.E., Hawkins, J.P., Allen, G.R., McAllister, D.E. et al. (2002). Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science*, 295(5558), 1280–1284. https://doi.org/10.1126/science.1067728

Sala, E. & Knowlton, N. (2006). Global marine biodiversity trends. *Annual Reviews of Environment and Resources*, 31, 93–122. https://doi.org/10.1146/annurev.energy.31.020105.100235

Sas, H., Deden, B., zu Ermgassen, P.S.E., Pogoda, B., Preston, J. et al. (2020). Bonamia infection in native oysters (*Ostrea edulis*) in relation to European restoration projects. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30(11), 2150–2162. https://doi.org/10.1002/aqc.3430

Sawusdee, A., Jensen, A.C., Collins, K.J. & Hauton, C. (2015). Improvements in the physiological performance of European flat oysters *Ostrea edulis* (Linnaeus, 1758) cultured on elevated reef structures: implications for oyster restoration. *Aquaculture*, 444, 41–48. https://doi.org/10.1016/j.aquaculture.2015.03.022

Secretariat of the Convention on Biological Diversity. (2005). *Handbook of the convention on biological diversity including its Cartagena protocol on biosafety*. Montreal: Secretariat of the Convention on Biological Diversity.

Shannon, C.E. (1948). A mathematical theory of communication. *Bell System Technical Journal*, 27, 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

Solan, M., Germano, J.D., Rhoads, D.C., Smith, C., Michaud, E., Parry, D. et al. (2003). Towards a greater understanding of pattern, scale and process in marine benthic systems: a picture is worth a thousand worms. *Journal of Experimental Marine Biology and Ecology*, 285-286, 313–338. https://doi.org/10.1016/S0022-0981(02)00535-X

Streif, H. (1990). *Das Ostfriesische Küstengebiet-Nordsee, Inseln, Watten und Marschen*. Berlin & Stuttgart: Gebrüder Borntraeger.

Taormina, B., Percheron, A., Marzloff, M.P., Caisey, X., Quillien, N., Lejart, M. et al. (2020). Succession in epibenthic communities on artificial reefs associated with marine renewable energy facilities within a tide-swept environment. *ICES Journal of Marine Science*, 77(7–8), 2656–2668. https://doi.org/10.1093/icesjms/fsaa129

Thompson, G.G. & Withers, P.C. (2003). Effects of species richness and relative abundance on the shape of the species accumulation curve. *Austral Ecology*, 28(4), 355–360. https://doi.org/10.1046/j.1442-9993.2003.01294.x

Ugland, K.I., Gray, J.S. & Ellingsen, K.E. (2003). The species-accumulation curve and estimation of species richness. *Journal of Animal Ecology*, 72 (5), 888–897. https://doi.org/10.1046/j.1365-2656.2003.00748.x van Loon, W.M.G.M., Walvoort, D.J.J., van Hoey, G., Vina-Herbon, C., Blandon, A., Pesch, R. et al. (2018). A regional benthic fauna assessment method for the southern North Sea using Margalef diversity and reference value modeling. *Ecological Indicators*, 89, 667–679. https://doi.org/10.1016/j.ecolind.2017.09.029

Wehkamp, S. & Fischer, P. (2013). The impact of coastal defence structures (tetrapods) on decapod crustaceans in the southern North Sea. *Marine Environmental Research*, 92, 52–60. https://doi.org/10.1016/j.marenvres.2013.08.011

Westby, S., Geselbracht, L. & Pogoda, B. (2019). Shellfish reef restoration in practice. In: Fitzsimons, J., Branigan, S., Brumbaugh, R.D., McDonald, T. & zu Ermgassen, P.S.E. (Eds.) *Restoration guidelines for shellfish reefs*. Arlington VA, USA: The Nature Conservancy, pp. 36–48.

Wickham, H. (2016). *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag.

Zito, A. & Rigon, T. (2022). *BNPvegan: Bayesian nonparametric methods for ecology*. R Package Version 0.1.0. https://github.com/alessandrozito/BNPvegan

zu Ermgassen, P.S.E., Bos, O., Debney, A., Gamble, C., Glover, A., Pogoda, B. et al. (2021). *European native oyster habitat restoration monitoring handbook*. London: The Zoological Society of London.

zu Ermgassen, P.S.E., Gamble, C., Debney, A., Colsoul, B., Fabra, M., Sanderson, W.G. et al. (2020). *European guidelines on biosecurity in native oyster restoration*. London: The Zoological Society of London.

SUPPORTING INFORMATION

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How to cite this article: Pineda-Metz, S.E.A., Colsoul, B., Niewöhner, M., Hausen, T., Peter, C. & Pogoda, B. (2023). Setting the stones to restore and monitor European flat oyster reefs in the German North Sea. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 33(7), 661–677. https://doi.org/10.1002/aqc.3945