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# Site selection for biogenic reef restoration in offshore environments: The Natura 2000 area Borkum Reef Ground as a case study for native oyster restoration

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## Abstract

1. According to the EU Marine Strategy Framework Directive (2008/56/EC), marine protected areas (MPA) should contribute to a good environmental status of the Europeans seas. Measures maintaining or restoring a favourable conservation status of protected species and habitats are mandatory according to the EU Habitats Directive (92/43/EEC).
2. Identification of suitable sites for ecological restoration measures within MPAs is a crucial step towards successful conservation and sustainable MPA management. In terms of species restoration, it is important to restore the respective species with the best possible environment for growth, survival, fitness, and successful recruitment.
3. This study provides a comprehensive list of site-selection criteria for ecological species restoration. Three general categories were chosen: (1) ecological history: evidence for the historical distribution; (2) feasibility of restoration: regulating framework and logistics; and (3) environmental conditions: quality of abiotic and biotic factors. A total of 16 site-selection criteria were identified and applied to biogenic reef restoration, namely for reefs of the native European oyster *Ostrea edulis*, in the German Bight.
4. The Natura 2000 area Borkum Reef Ground was identified as a suitable site for oyster restoration. It is one of three MPAs in the German Exclusive Economic Zone of the North Sea, which have been declared as Nature Conservation Areas according to national legislation. The conservation objectives include maintenance or, if necessary, restoration of the habitat type 'reefs'. As a reef-building species, the European oyster *O. edulis* is of particular importance for this habitat type in terms of nature conservation.

5. The step by step approach for site selection presented here is applicable for biogenic reef restoration elsewhere. The selected Natura 2000 area showcases the potential role and future perspective of European MPAs with regards to active conservation measures.

**KEYWORDS**

invertebrates, marine protected area, reef, restoration, special area of conservation, subtidal

## 1 | INTRODUCTION

Ocean ecosystems are confronted with multiple human-induced stressors and have experienced countless negative shifts over the last two centuries. With industrialized ocean-use and extreme extravagance in terms of resource use and waste production, pressures are still increasing. Pollution, habitat degradation, species losses, and climate change demonstrate the magnitude of ecological problems and are well documented in coastal and shelf seas (BfN, 2017; Wiltshire, 2017). Indicators to assess the environmental status of European seas, including the North Sea, are being developed, e.g. in the context of the Oslo Paris Commission (OSPAR, 1992) and the EU Marine Strategy Framework Directive (MSFD) (European Parliament, 2008). In many cases, the application of these indicators has revealed a poor environmental status (BLANO, 2018; OSPAR, 2017b).

Against the background of biodiversity loss, marine protected areas (MPAs) have been designated worldwide. According to decisions by the United Nations (UN, 2002) and the Convention on Biological Diversity (CBD, 1992), a representative network of MPAs shall be established, which shall be effectively and adequately managed, ecologically representative and well connected (CBD, 2018). For the North and Baltic Seas, the OSPAR and Helsinki (HELCOM) Commissions have decided jointly to establish an ecologically coherent network of well-managed MPAs (HELCOM & OSPAR, 2003a, 2003b). Furthermore, the MSFD requires spatial protection measures contributing to coherent and representative MPA networks (Art. 13(4) MSFD). Such spatial protection measures according to the MSFD include protected areas designated within the framework of the EU Habitats Directive (European Parliament, 1992) or Birds Directive (European Parliament, 2009), which are part of the Natura 2000 network of protected areas. It is an ongoing effort to identify suitable areas and to develop effective management plans (CBD, 2018; OSPAR, 2017a).

Following the provisions on protected areas and spatial protection measures under EU law (Habitats Directive [HD], Birds Directive, MSFD) and agreements on MPAs under OSPAR and HELCOM, measures need to be implemented in protected areas to maintain or, if necessary, restore the favourable conservation status of the conservation features (i.e. the species and habitats protected at the respective site according to its conservation objectives). According to the MSFD, the MPAs will thus contribute to the achievement of good environmental status (GES) of European seas. The measures necessary for the achievement of these goals can be described in management plans (Art. 6(1) HD, § 32(5) Federal Nature Conservation Act), as particularly recommended by OSPAR for the North Sea (HELCOM & OSPAR, 2003b; OSPAR, 2010).

The Natura 2000 area Borkum Reef Ground (BRG) is one of three MPAs in the German Exclusive Economic Zone (EEZ) of the North Sea, which have been declared as nature conservation areas (NCAs) according to national legislation. The conservation objectives of this site are defined in the protected area ordinance establishing the NCA (NSGBRgV, 2017). These include the maintenance or, if necessary, restoration of a favourable conservation status of the habitat type 'reefs' (EU code 1170) and the conservation of its characteristic species by maintaining or restoring (1) the ecological quality of the habitat structures along with their extent, (2) the natural distribution, abundance and population dynamics of the characteristic species, as well as natural community structures, and (3) the role for the dispersal and resettlement of benthic fauna in surrounding areas. The habitat type 1170 'reefs' includes both geogenic and biogenic reefs (Boedeker, Krause, & von Nordheim, 2006; European Commission DG Environment, 2013).

Management plans comprising the necessary measures to achieve the conservation objectives (§ 7(3) NSGBRgV) are currently under consultation. A draft management plan includes measures for biogenic reef restoration, explicitly the "restoration of the European oyster to the necessary extent" (BUND, 2018). The European oyster is a reef-building species with extensive historical occurrence in the area (Gercken & Schmidt, 2014; Pogoda, 2019) and is thus considered to be a species of particular importance, in terms of nature conservation, for reefs in BRG (BfN, 2017). It is classified as an ecological key player in the North Sea ecosystem providing a variety of ecosystem functions and services (zu Ermgassen et al., 2016). The species was widely distributed throughout European sublittoral coasts and offshore in deeper waters. Before it was severely hit by overfishing (Beck et al., 2011; Caspers, 1950; Neudecker, 1990; Roberts, 2007; Thurstan, Hawkins, Raby, & Roberts, 2013; Yonge, 1960) it formed dense oyster beds on the so-called offshore oyster grounds (Figure 1). *Ostrea edulis* beds may differ from the massive oyster formations of the intertidal (*Crassostrea gigas*, *Crassostrea virginica*), but by providing a biogenic hard bottom habitat on different soft sediment types and by supporting a zonation of benthic communities with many associated species (Kamermans et al., 2018; Smyth & Roberts, 2010), including concretions and encrustations, they represent a sublittoral biogenic reef type (EUNIS 2019). Respective restoration measures will

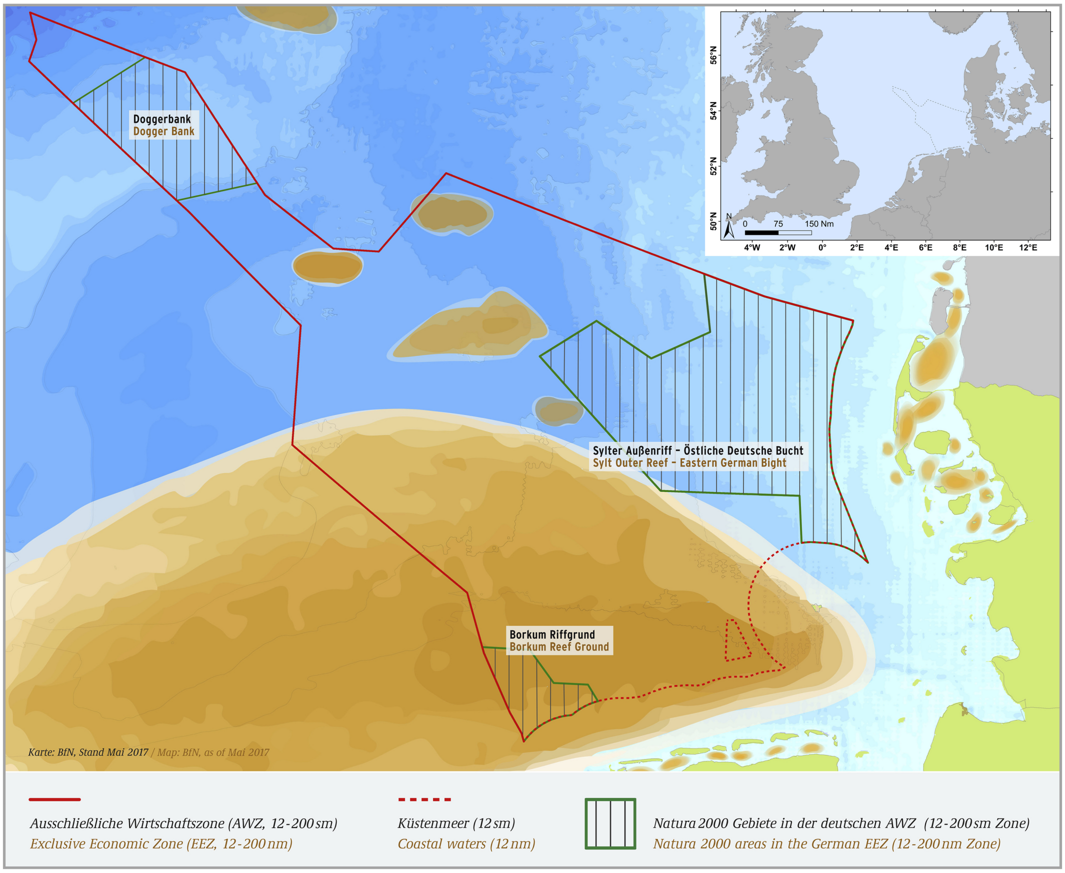


**FIGURE 1** Map of the German Bight, showing the German Exclusive Economic Zone (EEZ), the Natura 2000 areas of the EEZ and the historical distribution of *Ostrea edulis* (orange) based on historical fishing records and publications between 1883 and 1968, see Gercken and Schmidt (2014)

increase biodiversity and will contribute to improve the degree of conservation at the site (BfN, 2017).

Progressing from the identification and establishment of MPAs to implemented and effective conservation measures is a challenging and crucial step towards effective conservation and (sustainable) MPA management (according to the ecosystem approach, Art 1(3) MSFD). The identification of suitable sites for specific measures within the MPAs is of fundamental importance. In terms of species restoration, it will provide the respective species with the best possible environment for growth, survival, and successful recruitment.

This study describes the identification of suitable sites for biogenic reef restoration, namely reefs of the native European oyster *O. edulis*, in the German Bight. We considered historical distribution, abiotic and biotic factors, marine spatial planning, and logistical challenges for successful native oyster restoration against the background of marine nature conservation measures. This study provides a comprehensive list of site-selection criteria, especially for sublittoral oyster reef restoration, and analyses the Natura 2000 area BRG as a site-selection case study. As a result, this study offers a systematic site-selection approach for further application in ecological restoration and highlights the potential role of MPAs. If successful, restored native oyster beds will become self-seeding in the long term, and may even generate further oyster beds, facilitating a revival of this species in other suitable North Sea ecoregions.

## 2 | MATERIAL & METHODS

Site selection starts with the definition of appropriate site-selection criteria. It depends on the individual requirements of the target species and for ecological restoration, its ultimate goal is to identify sites where restoration measures are most likely to succeed (Ashton & Brown, 2009; Elsäßer, Fariñas-Franco, Wilson, Kregting, & Roberts, 2013; McDonald, Gann, Jonson, & Dixon, 2016; Westby, Geselbracht, & Pogoda, 2019). For restoration and reinstallation measures, three general site-selection categories are of relevance (Ashton & Brown, 2009; Gillies, Creighton, & McLeod, 2015; Laing, Walker, & Areal, 2005; McDonald et al., 2016; Shelmerdine & Leslie, 2009; Smaal, Kamermans, van der Have, Engelsma, & Sas, 2015) and have been addressed in this study.

1. Ecological history: evidence for the historical distribution
2. Feasibility of restoration: regulating framework and logistics
3. Environmental conditions: quality of abiotic and biotic factors

## 2.1 | Ecological history

Data on the historical distribution of *O. edulis* in the German North Sea was obtained from an in-depth study of literature and historical fisheries records provided by the feasibility study (Gercken & Schmidt, 2014). Twelve references were considered to support the historical distribution of the European oyster, five of which were used to produce the geographical maps. These maps document the former oyster grounds in the German North Sea and serve as templates for this study. Further entries for *O. edulis* are documented in Olsen's (1883) Piscatorial Atlas of the North Sea. Fishermen's accounts indicated abundant oyster beds within the BRG. This oyster ground was only discovered in the mid-19th century and was overfished shortly after, so that no accurate distribution data other than the Piscatorial Atlas and notes of the area in several fishery reports are available (Gercken & Schmidt, 2014).

Additionally, a literature search was conducted in February 2019 to gain possible up-to-date information on the historical distribution of *O. edulis* published after 2014. The keywords *Ostrea edulis*, European flat oyster, native oyster, (historical) distribution, and (German) North Sea were used in the bibliographic search engines Web of Science and Google Scholar. However, no recent literature was found to be incorporated into the existing distribution maps.

→ Preselection: Selecting a location within the historically documented distribution of the native oyster corresponds to the procedure for reintroduction measures defined by the International Union for Conservation of Nature and by the Standards of the Society for Ecological Restoration as the intended release of an organism in its original range from which it has disappeared (Gann et al., 2019; IUCN/SSC, 2013; McDonald et al., 2016).

## 2.2 | Feasibility of restoration

Successful restoration requires absence of impacts from contra-indicated uses. Furthermore, a number of logistical criteria influence the implementation of an active restoration measure, by either enabling or facilitating, or by preventing, impeding, or complicating the practical restoration work (McDonald et al., 2016). Different user groups with claims and contra-indicative activities will incapacitate certain areas for biogenic reef restoration. Accordingly, those user groups and their spatial demand were identified via marine spatial planning tools of the Federal Maritime and Hydrographic Agency (BSH) using CONTIS maps and GeoSeaPortal, as well as a literature search. In the light of these uses, existing regulation frameworks were included in relevant site-selection criteria, considering marine spatial planning and the protection status of MPAs, in particular in terms of existing and planned measures, addressing relevant contra-indicated uses. While water depth is not an issue for the oyster within its natural distribution, it is of logistical significance as a site selection criterion. Pilot restoration projects of smaller scale with high monitoring demands will be implemented and surveyed by diving operations. As underwater working time is limited by water depth, it is advisable to select sites of moderate depths (≤30 m), although European oysters have historically occurred in water depths of up to 50 m or more (Pogoda, 2019).

→ Preselection: The Natura 2000 site BRG is located well within the historical distribution of the target species and, as an MPA, provides certain legal pre-conditions to reduce impacts from uses, such as fishery exclusion zones. Accordingly, it is identified as a suitable target site for ecological restoration of the native European oyster.

## 2.3 | Data on environmental conditions

Following the preselection, data on abiotic and biotic factors were collected and analysed for the Natura 2000 site BRG.

### 2.3.1 | Full coverage data

Data on water depth, temperature, salinity, current velocity, and chlorophyll concentration were extracted from the BSH circulation model for the German Bight (BSHcmod), provided by the BSH (Dick, Kleine, Müller-Navarra, Klein, & Komo, 2001). Data on substrate quality were collected via assessment of sediment distribution and of habitat types. The sediment distribution map was created on the basis of hydroacoustic surveys. Full coverage sidescan sonar surveys were carried out between August 2012 and June 2014 using the research vessels RV Senckenberg and RV Heincke (AWI, 2017) (Table 1). The Benthos SIS-1624 sidescan sonar (Teledyne Benthos Inc.) was operated with a simultaneously emitted high-frequency chirp signal of 370–390 kHz and a low-frequency chirp signal of 110–130 kHz. The low-frequency beam size was 0.5° (horizontal) and 55° (vertical), whereas the high-frequency beam size was 0.5° (horizontal) and 35° (vertical). High-frequency data were used for seafloor classification. A range of 150 m was selected. Sidescan sonar data were collected with a line-spacing of 250 m at a vessel speed of 5 knots and a tow depth of ca. 10–15 m below the sea surface. Vessels were positioned by D-GPS, whereas tow-fish positions were defined by means of layback corrections. Areas of special interest (e.g. stony deposits) were re-surveyed using a smaller range of 75 m at a vessel speed of 5 knots and a line spacing of 125 m. The along-track resolution of these data was 0.25 m. The hydroacoustic data were ground-truthed during the surveys in the form of sediment samples using a Shipek grab and underwater-video transects using a Kongsberg Simrad OE 1366 camera system. Grain size analyses of the grab samples were carried out by sieving (>2 mm), the settling-tube technique (2 mm–0.063 mm), and Micromeritics SediGraph III (<0.063 mm). For data acquisition and post processing, the software package Sonarwiz™ Vers. 6.05 (Chesapeake Technology) was used. The processing steps included bottom tracking, slant range correction, layback correction, and empirical gain normalization. The pixel resolution of the resulting mosaics was 1 m for the whole BRG area and 0.25 m for areas characterized by stony deposits. The sidescan sonar backscatter data were displayed as a grey scale comprising 256 values, where 0 is assigned to black,

**TABLE 1** Research cruises in Borkum Reef Ground for underwater video recording, dredge and grab sampling, sidescan sonar, and multibeam data collection

| Year | Cruise name | Ship name | Number of transects | Source |
|---|---|---|---|---|
| 2002 | NAN BRGSK SK | Dr. Nansen | 18 | BfN |
| 2012 | P495 1212 | Damkerort | 10 | BioConsult |
| 2012 | Senckenberg 34/2012 | Senckenberg | 20 | SaM |
| 2012 | HE389 | Heincke | 5 | SaM |
| 2012 | Senckenberg 45/2012 | Senckenberg | 20 | SaM |
| 2012 | HE385 | Heincke | 8 | AWI |
| 2013 | Senckenberg 05/2013 | Senckenberg | 24 | SaM |
| 2013 | Senckenberg 36/2013 | Senckenberg | 27 | SaM |
| 2013 | Senckenberg 40/2013 | Senckenberg | 14 | SaM |
| 2013 | Senckenberg 45/2013 | Senckenberg | 7 | SaM |
| 2014 | Senckenberg 02/2014 | Senckenberg | 7 | SaM |
| 2014 | Senckenberg 05/2014 | Senckenberg | 8 | SaM |
| 2014 | Senckenberg 22/2014 | Senckenberg | 23 | SaM |
| 2015 | GR03 | Grinna | 6 | AWI |
| 2015 | UT03 | Uthörn | 1 | AWI |
| 2017 | P617 MZB 0617 BRG | Damkerort | 19 | BioConsult |
| 2019 | HE529 | Heincke | 3 | AWI |

Abbreviations: AWI, Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research; BfN, Federal Agency for Nature Conservation; BioConsult, BioConsult Schuchardt & Scholle; SaM, Senckenberg Research Institute.

corresponding to strong backscattering, and 255 to white, corresponding to low backscattering. The interpretation of the backscatter mosaics generally followed the 'Guideline for Seafloor Mapping in German Waters' (BSH, 2016).

Full coverage data on soft bottom types were made available by the Federal Agency for Nature Conservation (BfN). Biotopes are here defined as potential occurrences of defined soft bottom communities commonly known in the German EEZ of the North Sea. Communities were identified by aggregating species specific abundance data using fuzzy clustering methods. The site-specific data on the derived communities were intersected with full coverage data on bathymetry, slope, sediment types, grain size fractions, and other sedimentological variables. Random forests (Breiman, 2001) were then applied to model the occurrence of both communities within the entire BRG.

Selected sites were bathymetrically and optically re-surveyed in April 2019 with RV Heincke. Bathymetric data were acquired with a hull-mounted multibeam echosounder (MBES) Kongsberg EM710 (Kongsberg, Norway) operating with frequencies between 70 and 100 kHz. The length of the individual transect lines was 1–1.5 nm and the distance between the transect lines was set to 120 m. The vessel speed was 5 knots. Raw data were post processed with regard to the cleaning of outliers using Hypack2019. The data were further corrected for tidal effects using gauge data from the research platform FINO1 (position: N 54°00′53.5″ and E 6°35′15.5″). The resulting resolution of the map was 1 m. Optical data were obtained using an underwater camera system consisting of a HD-camera (CT3009, C-Tecnics, Aberdeen, UK) and a GoPro camera (HERO 3+ black edition, GoPro, Inc., San Mateo, CA, USA). The camera system was deployed from the ship while drifting (maximum speed 1 knot) over the study sites.

### 2.3.2 | Benthic biological measurement data

Benthic biological data from video, dredge, and van Veen grab observations were collected and analysed. A total of 60 digital underwater videos of the seafloor served as the primary data source for the present study. Video files and protocols were provided by the BfN, the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Section Functional Ecology, and BioConsult Schuchardt & Scholle GbR. All underwater videos were recorded for the purpose of monitoring substrate quality, reefs, and associated organisms during research cruises in 2002, 2012, 2015, and 2017 (Table 1). Video length varied between 5 and 60 minutes. Meta information about the video recordings, such as geographical coordinates and local water depth as recorded by a GPS and ship lead was also analysed.

The videos were recorded in assigned areas to host biotopes protected under §30 of the Federal Environmental Law – 'reefs' (also protected under the HD) and 'species rich gravel, coarse sand. and shell gravel areas' (Figure 3b) – and at stations assisting in the national biotope mapping, coordinated by the Federal Agency for Nature Conservation (Pesch et al., 2016). Towed underwater video systems of Mariscope Meerestechnik or similar systems were used, consisting of a steel camera carriage, a digital underwater video camera with integrated laser pointers and two spotlights for illumination, a cable drum with trailing cable including power and data connection, and a control unit with computer and monitor. The camera was equipped with four front-laser pointers for size estimation, arranged around the camera lens and connected to the control unit via the trailing cable. When recording, the ship typically sailed at 0.5–1.0 knots above ground or drifted on the prevailing current. The camera sled was lowered to the seabed and dragged along by a cable near the seabed. Current ship position (GPS coordinates) and water depth (per ship lead) were recorded for georeferencing. Potential predators were documented via UW-video (Figure 6).

Further data on epibenthic organisms were available from 10 trawl transects performed in 2012 as part of national monitoring and mapping activities. Epibenthos was sampled with a 2-m beam trawl (codend 1-cm mesh size) towed for 5–10 minutes at 1–3 knots. The epibenthos was sorted and species identified. The individual number and the fresh weight of each species was documented and standardized to 1 $m^2$ before analysis.

Data on the benthic infauna were available for a total of 152 benthos stations sampled in 2012 and 2017. Van Veen grab samples (area: 0.1 $m^2$, weight: 90 kg) were taken for infauna assessment. Samples were sieved (mesh size: 1,000 μm), and stored in buffered 4% formalin-seawater solution for further processing. In the laboratory all organisms of the benthic macro-infauna were extracted and determined to the lowest taxonomic level possible. All infauna species were recorded with regard to abundance (Ind/$m^2$) and biomass (fresh weight (FW) g/$m^2$). To describe the benthic infauna of potential oyster restoration sites, data on species abundances and presence were selected from grab stations within a 2-km radius. Correspondingly, species information on seven grab stations were available for site BRG-KGS-V2, three for site BRG-KGS-V-3, three for site BRG-KGS-V4–2, and two for site BRG-SF-V2 (Figures 2 and 3).

Furthermore, a thorough literature search was conducted in March 2019 to gain information on the biological requirements of the target species, on site-selection criteria for ecological restoration in general and more specifically, for oyster restoration. The keywords oyster, restoration, site selection, ecological restoration, and *Ostrea edulis* were used in various combinations in the bibliographic search engines Web of Science and Google Scholar. The resulting literature was further considered for the identification of valid site-selection criteria.

## 3 | RESULTS

A comprehensive list of relevant site-selection criteria for ecological restoration of the native European oyster in the German Bight is presented in Table 2. This takes into account the regulating framework for MPAs and for conservation measures, marine spatial planning in the EEZ, and the results of the literature search and data collection. In the next step, oyster-restoration sites were then identified upon the evaluation of all criteria.

### 3.1 | Ecological history

In the German Bight, the historical distribution of *O. edulis* is documented for tidal channels of the North and East Frisian Wadden Sea, for the Helgoland Oyster Bed, and also for the North Sea Oyster Ground in deeper offshore waters (Figure 1) (Berghahn & Ruth, 2005; Gercken & Schmidt, 2014; Pogoda, 2019).

→ Site selection: The Natura 2000 area BRG is located within the historical offshore oyster grounds and meets the criterion: former presence of *O. edulis* and *O. edulis* beds for ecological restoration.

### 3.2 | Feasibility of restoration

The North Sea is intensively used by a variety of different user groups, e.g. fishing, shipping, wind energy production, oil and gas exploration and exploitation, and sand and gravel extraction, and is accordingly a highly stressed area (BfN, 2017; BLANO, 2018; OSPAR, 2017b; Pogoda, 2019). In contrast, reintroduction sites should be free from any contraindicated uses, such as fishing, sand and gravel extraction, oil and gas exploitation, and underwater cables (existing or planned). For pilot restoration projects with high monitoring demands, it is advisable to select sites outside shipping lanes with high traffic density. Minimized utilization pressure in the selected area will facilitate the logistical implementation and will increase the long-term success of the reintroduction measure(s).

Against the background of logistical feasibility and long-term success, a catalogue of existing relevant uses was compiled for the Natura 2000 area BRG. It includes fishing pressure, sand and gravel extraction, submarine cables, and other contraindicated uses, e.g. oil and gas extraction, shipping lanes, and priority areas for shipping (Table 2). Data on the existing relevant uses are summarized in Figure 2. At present, bottom trawling is permitted throughout the German EEZ, including the Natura 2000 areas. In a flatfish conservation area, established in 1989 and covering most of the BRG area, beam-trawl fisheries are regulated to some degree, but not totally excluded. Recently, Germany together with other European fishing nations has recommended fisheries regulation to the European Commission according to Art. 11 of the European Common Fisheries Policy (European Parliament, 2013). These Joint Recommendations intend exclusion of all mobile bottom-contacting fishing-gear in parts of the Natura 2000 areas: BRG, Sylt Outer Reef, and Doggerbank (BMU, 2019). This would substantially reduce impacts from fisheries on the seafloor. Shipping lanes dominate the southern part of BRG. Underwater cables cross BRG to connect the offshore wind farms in the north and are monitored on a regular basis. For some existing cables and all planned and/or currently approved cables, after-use reconstruction is a statutory condition (BSH, 2017a). Licences for sand and gravel extraction are currently not contracted in BRG.

*Ostrea edulis* occurs at depths of up to 50 m. Depth is, however, considered as a logistical site-selection criterion, since scientific diving operations are an important monitoring tool particularly for pilot restoration sites, but also for assessment of the effectiveness of restoration measures in MPA management. Water depths in BRG range from 18 to 33 m.

→ Site selection: BRG is a marine Natura 2000 area, an OSPAR MPA, and an NCA according to national legislation. It is subject to general legal protection according to European law (particularly HD) and respective national legislation, including requirements for impact assessment. A management plan for the site has not been established yet, but is under consultation. The BRG area meets the criterion: MPA with a certain degree of protection.

→ Site selection: Exclusion of mobile bottom-contacting fishing gear is planned for a large part of BRG. The respective exclusion zone will meet the criterion: absence of mobile bottom-contacting fishing-gear.

→ Site selection: Large areas of BRG are free of cables (Figure 2a) and meet the criterion: absence of underwater cables.

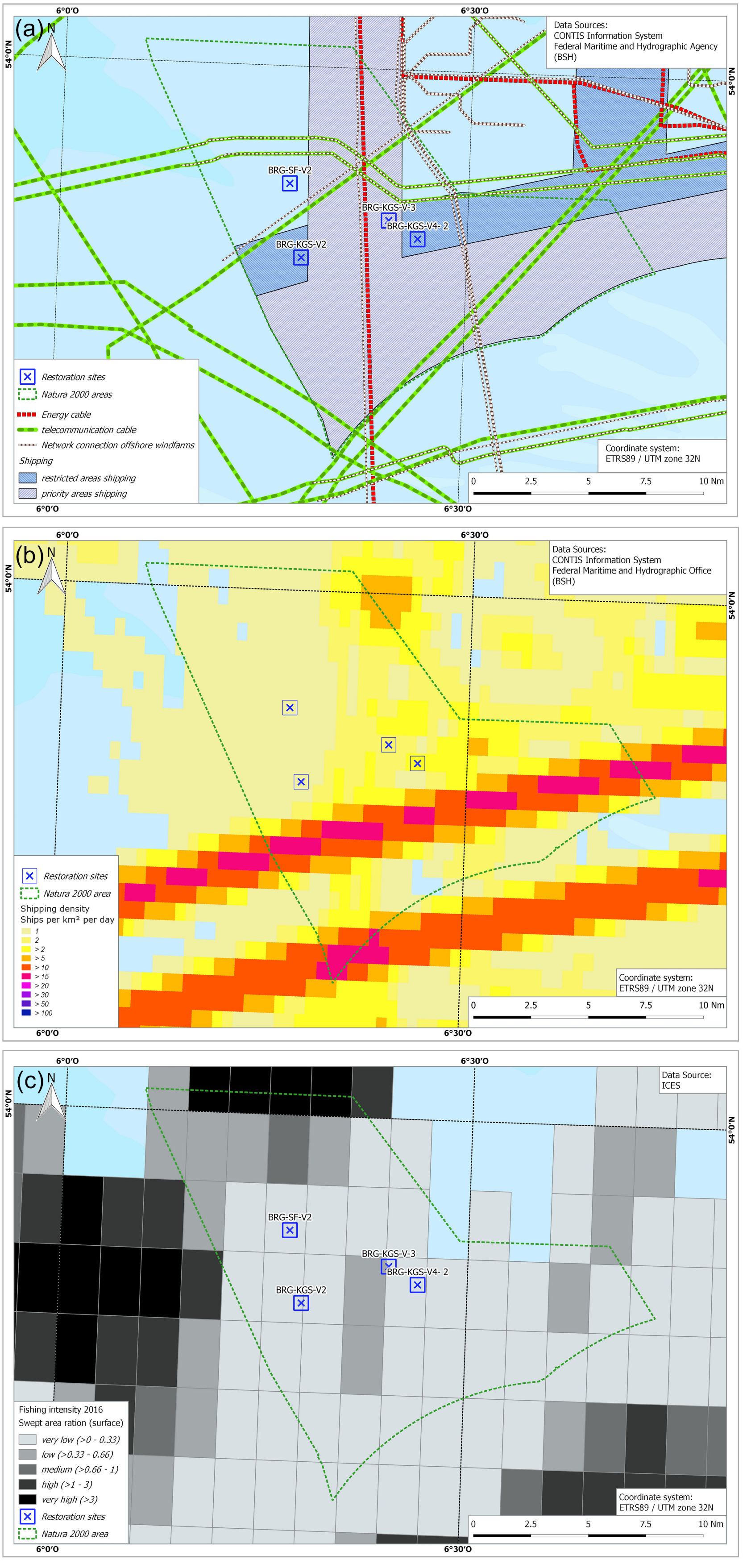


**FIGURE 2** Anthropogenic stressors in the Natura 2000 area Borkum Reef Ground and location of selected restoration sites. (a) Energy cables (red), telecommunication cables (green), network connections for offshore windfarms (red dots), priority areas for shipping (blue and light blue) (CONTIS Information System, Federal Maritime and Hydrographic Agency [BSH]). (b) Shipping intensity in 2017 (CONTIS Information System). (c) Fishing intensity of bottom contacting fishing gear in 2016: beam trawl, dredge, otter trawl, seines (ICES, 2016)

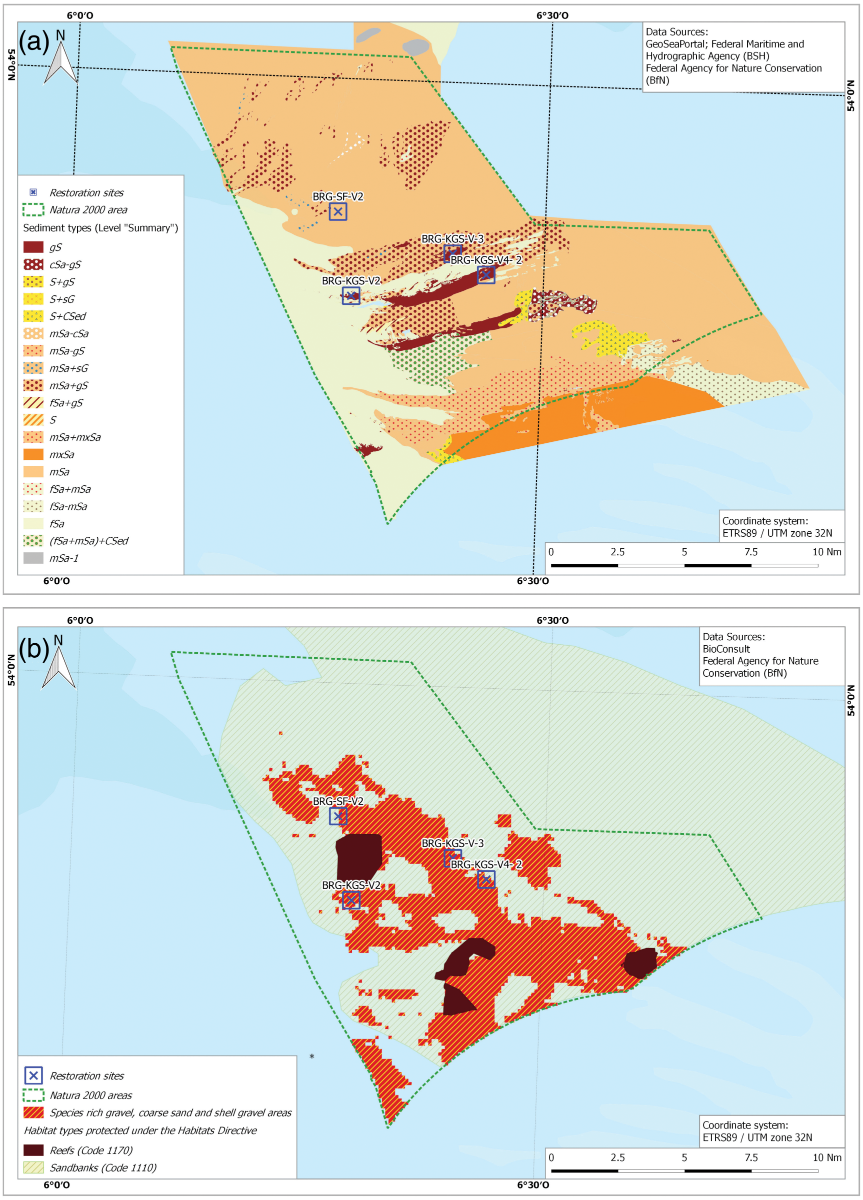


**FIGURE 3** Sediment conditions (a) and habitat structures (b) in the Natura 2000 area Borkum Reef Ground; sediment types (a) refer to a classification system of the Guideline for Seafloor Mapping in German Marine Waters (BSH, 2016): gS (gravelly sand), cSa (coarse sands), S (sand), CSed (coarse sediments), mSa (medium Sand), sG (sandy Gravel), fSa (fine sand), mxSa (Mixed Sand), −1 (not defined); - means that it is not possible to differentiate further between the sediment types in the backscatter mosaic, + means that the area shows a small-scale, heterogeneous texture with respect to the named sediment types (BSH, 2016)

→ Site selection: BRG meets the criterion: absence of sand and gravel extraction (Figure 2a).

→ Site selection: Shipping lanes and priority areas interfere with intensive monitoring demands of pilot studies. Hence, these areas will not be considered for a pilot reef site, but may be appropriate for large-scale biogenic reef restoration as soon as practical implementation has been successfully tested and established.

→ Site selection: Water depths within BRG range between 18 and 33 m and meet the criterion: depth allowing scientific diving operations for the monitoring of pilot reefs.

## 3.3 | Environmental conditions

Environmental data in the Natura 2000 site BRG are shown in Table 3. Water temperature controls the life cycle of oysters. In spring, food intake and growth of *O. edulis* start at temperatures above 7°C (Ashton & Brown, 2009; Kamermans et al., 2018), which applies for ca. 8 months/year (Table 3), with maximum growth rates between 16 and 18°C (Laing et al., 2005). Temperature and salinity are always within the tolerance range defined *O. edulis*. In water depths ≤20 m, the required temperature for reproduction (onset of spawning at approx. 15°C, see (Colsoul et al., n.d.; Gercken & Schmidt, 2014) is reached earlier in the year compared to water depths ≥20 m. Hydrodynamic processes influence larval transport, food availability and food intake. Excessively high current velocities result in mechanical stress such that oysters invest more energy in shell growth to protect themselves or are no longer able to filter food out of the water column. Previous studies have shown that the filtration rate of oysters rises to a maximum with increasing current velocity (Ashton & Brown, 2009; Walne, 1979) but results in low growth rates at a daily maximum tidal current of 0.45 m/s

**TABLE 2** Relevant site-selection criteria for the ecological restoration of biogenic reefs, namely of the native European oyster in the North Sea

| Site-selection category | Site-selection criteria |
|---|---|
| 1. Ecological history | 1. Former presence of *Ostrea edulis* and *O. edulis* beds |
| 2. Feasibility of restoration | 2. Marine protected area (NCA, Natura 2000) |
| | 3. Absence of bottom-contacting fishery |
| | 4. Absence of sand and gravel extraction |
| | 5. Absence of submarine cable areas |
| | 6. Absence of other contraindicated uses |
| | 7. Depth |
| 3. Environmental conditions (abiotic) | 8. Temperature |
| | 9. Salinity |
| | 10. Current velocity |
| | 11. Oxygen concentration |
| | 12. Substrate quality (sediment type/dynamics) |
| 3. Environmental conditions (biotic) | 13. Food availability (chlorophyll concentration) |
| | 14. Predation |
| | 15. Competition |
| | 16. Disease |

*Note:* Criteria are assigned to three categories: 1) Ecological history, 2) Feasibility of restoration, 3) Environmental conditions.
Abbreviation: NCA, nature conservation area.

(Pogoda, Buck, & Hagen, 2011). Extremely low currents allow elevated siltation rates, which limit filtration efficiency of food particles. Current velocities of 0.05–0.1 m/s are necessary to avoid sedimentation and sediment accumulation (Ashton & Brown, 2009). Current velocity in BRG ranges between 0.27–0.31 m/s, high enough to avoid sedimentation and low enough to ensure good food availability. Currents in the German Bight predominate in easterly and northerly directions (BSH, 2017b). Substrate quality is defined by sediment composition and sediment dynamics. Nineteen different sediment types were identified for BRG (Figure 3a). European oysters settle on various soil substrates, such as stones, gravel, and coarse or medium sand (Figure 6) (Airoldi & Beck, 2007; Colsoul et al., 2020; Laing et al., 2005). Sediment dynamics includes the formation of sand waves and ripples resulting from bed shear stress. Influenced by currents and waves, sand waves can move over the seabed of the German Bight, eventually covering benthic sessile organisms (Kamermans et al., 2018). In deeper waters, waves tend not to reach down to the seabed and therefore their influence decreases with depth. Modelled data of the southern North Sea calculate maximum bed shear stress in BRG of 0.4 N/m$^2$, which is within the tolerance range of <0.6 N/m$^2$ for oyster restoration (Kamermans et al., 2018). Water turbidity at the site also depends on the grain size of the predominant sediments and influences oyster growth and health (Soletchnik, Ropert, Mazurié, Gildas Fleury, & Le Coz, 2007).

→ Site selection: Abiotic environmental conditions in the Natura 2000 area BRG are within the ecological tolerance range of *O. edulis* and meet the criteria: temperature, salinity, oxygen concentration, and current velocity.

→ Site selection: Maximum bed shear stress in BRG is 0.4 N/m$^2$ and areas with larger grain sizes (medium sand, coarse sand, gravelly sand, sandy gravel, gravel, and shell gravel areas) within BRG are identified as suitable for the construction of a pilot reef and for the implementation of large-scale biogenic reef restoration and meet the criterion: substrate quality.

Chlorophyll concentration indicates the food availability, relevant for metabolic rates and growth performance of oysters. Optimum chlorophyll concentration for *O. edulis* is 2–3 μg/L (Rogan &

**TABLE 3** Environmental parameters at Borkum Reef Ground (average values per month in 25 m depth) extracted from the BSH circulation model for the German Bight (BSHcmod), provided by the German Federal Maritime and Hydrographic Agency (BSH) (Dick et al., 2001)

| Month | Temperature [°C] | Salinity [g/L] | Oxygen concentration [mg/L] | Current velocity [m/s] | Chlorophyll concentration [μg/L] |
|---|---|---|---|---|---|
| Sep 2017 | 17.63 | 33.54 | 7.38 | 0.31 | 3.06 |
| Oct 2017 | 15.38 | 34.11 | 7.99 | 0.31 | 1.57 |
| Nov 2017 | 12.14 | 34.34 | 8.59 | 0.31 | 1.11 |
| Dec 2017 | 8.59 | 34.66 | 9.39 | 0.32 | 0.94 |
| Jan 2018 | 6.49 | 34.29 | 9.88 | 0.32 | 1.17 |
| Feb 2018 | 5.19 | 33.14 | 10.18 | 0.31 | 2.69 |
| Mar 2018 | 3.15 | 32.74 | 10.80 | 0.32 | 3.92 |
| Apr 2018 | 4.91 | 32.30 | 10.29 | 0.31 | 1.73 |
| May 2018 | 8.92 | 32.68 | 9.16 | 0.27 | 1.55 |
| Jun 2018 | 13.07 | 33.72 | 8.28 | 0.24 | 1.57 |
| Jul 2018 | 14.81 | 33.56 | 7.65 | 0.31 | 2.36 |
| Aug 2018 | 16.75 | 33.07 | 7.23 | 0.31 | 3.13 |
| Sep 2018 | 17.36 | 33.44 | 7.53 | 0.31 | 2.38 |

Cross, 1996). In BRG, these conditions allow optimum growth rates for around 5 months/year (Table 3). Another important factor for oyster survival is the oxygen saturation of the surrounding sea water. Hypoxia thresholds for short-term survival are 3.5 mg/L (Smaal, Kamermans, Kleissen, van Duren, & van der Have, 2017; Vaquer-Sunyer & Duarte, 2008). BRG is located within a well-mixed area of the North Sea with no documented oxygen concentrations <6 mg $O_2$/L (Topcu & Brockmann, 2015; van Leeuwen, Tett, Mills, & van der Molen, 2015). As data of 2017/2018 constantly exceed 7 mg $O_2$/L, there is no risk of oxygen depletion in BRG (Table 3). Oyster predators are starfish, e.g. *Asteria rubens*, *Astropecten irregularis*; crabs, e.g. *Cancer pagurus*, *Homarus gammarus*; and oyster drilling snails, e.g. *Urosalpinx cinerea* (invasive). Oyster stages with a shell diameter of up to 3 cm are particularly vulnerable to predation pressure due to their relatively soft shell (Yonge, 1960). Figure 4 shows the composition of potential predators in the investigated areas of BRG. Competition for food or settlement substrate will be of importance for the successful and sustainable recruitment of *O. edulis* at restoration sites. Available hard substrate, namely the stone fields in BRG, are completely covered by sessile invertebrates. Dominating groups of sessile (filter-feeding) epifauna are: Porifera (e.g. *Halichondria (halichondria) panicea*), Cnidaria (e.g. *Alcyonium digitatum*, *Metridium senile* (syn. *Metridium dianthus*), *Sagartia elegans*), and Bryozoa (e.g. *Flustra foliacea*) (Fritsch, 2017; Michaelis et al., 2019). Pathogens can infect oysters at any stage of the life cycle. To date, no pathogens, such as *Bonamia ostreae* and *Marteilia refringens* have been documented in BRG (Merk, Colsoul, & Pogoda, n.d.; TSIS, 2019). Macroparasitic species e.g. *Mytilicola intestinalis* are of minor relevance at offshore sites, due to their parasite–host life cycle, which often depends on coastal hosts (e.g. seabirds) (Pogoda, Jungblut, Buck, & Hagen, 2012).

Within the national biotope mapping project two corresponding soft bottom communities could be identified in the Natura 2000 area by aggregating species-specific abundance data using fuzzy clustering methods (Figure 5): *Tellina fabula*, mostly found in areas with fine sands and *Goniadella–Spisula*, mostly found in areas with coarse sands and gravel as a typical characteristic of the biotope type 'species rich gravel, coarse sand, and shell gravel areas', which is associated with *Goniadiella bobretzkii*, *Spisula subtruncata*, *S. elliptica*, *Aonides paucibranchiata*, *Branchiostoma lanceolatum*, and *Ophelia limacina* (Rachor & Nehmer, 2003; Salzwedel, Rachor, & Gerdes, 1985). The modelling showed good results with average misclassification rates of 15.5% (BioConsult, in preparation) and illustrate the benthic ecological conditions for potential restoration sites.

→ Site selection: Biotic environmental factors in the Natura 2000 site BRG reflect the conditions of the natural distribution of *O. edulis* and meet the criterion: food availability. Predation, competition, and disease need to be investigated in the pilot phase.

→ Site selection: The soft bottom community *Goniadella–Spisula* is associated with areas with coarse sands and gravel and indicates that the criterion substrate quality is fulfilled.

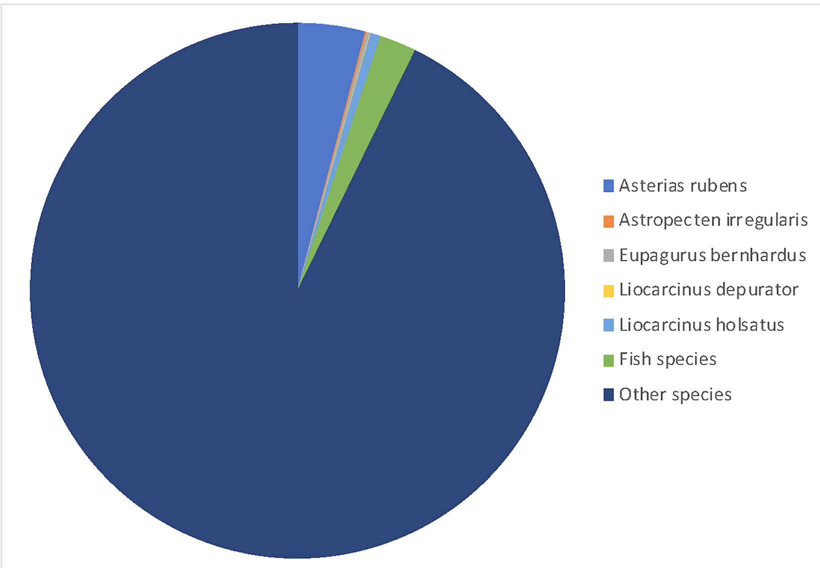


**FIGURE 4** Composition of macrofauna at potential restoration sites in the Natura 2000 area Borkum Reef Ground (BRG). Proportions of potential predators, summarized for 10 stations within BRG. Fish species as potential larvae predators: *Agonus cataphractus*, *Arnoglossus latern*, *Buglossidium luteum*, *Callionymus lyra*, *Callionymus reticulatus*, *Ciliata mustela*, *Clupea harengus*, *Gadus morhua*, *Gasterosteus aculeatus*, *Hyperoplus immaculatus*, *Limanda limanda*, *Liparis liparis*, *Merlangius merlangus*, *Mullus surmuletus*, *Myoxocephalus scorpius*, *Osmerus eperlanus*, *Pholis gunellus*, *Pleuronectes platessa*, *Pomatoschistus minutus*, *P. pictus*, *Scyliorhinus canicula*, *Sprattus sprattus*, *Syngnathus rostellatus*, *Trachurus trachurus*, *Trisopterus luscus*. Other species: *Alcyonidium* sp., *Alloteuthis subulate*, *Aora typica*, *Bougainvillia* sp., *Chamelea gallina*, *Clytia hemisphaerica*, *Conopeum reticulum*, *Corophium acherusicum*, *Crangon allmanni*, *C. crangon*, *Echinocardium cordatum*, *Electra pilosa*, *Flustra foliacea*, *Hydractinia echinate*, *Macropodia rostrata*, *Mactra corallina*, *Melita obtusata*, *Membranipora membranacea*, *Obelia dichotoma*, *Obelia geniculate*, *Ophiura albida*, *Ophiura ophiura*, *Pandalina brevirostris*, *Pariambus typicus*, *Phaxas pellucidus*, *Philocheras trispinosus*, *Phyllodoce* sp., *Processa parva*, *Sepiola atlantica*, *Sertularia cupressina*. Abundance of all species <1 Ind./$m^2$

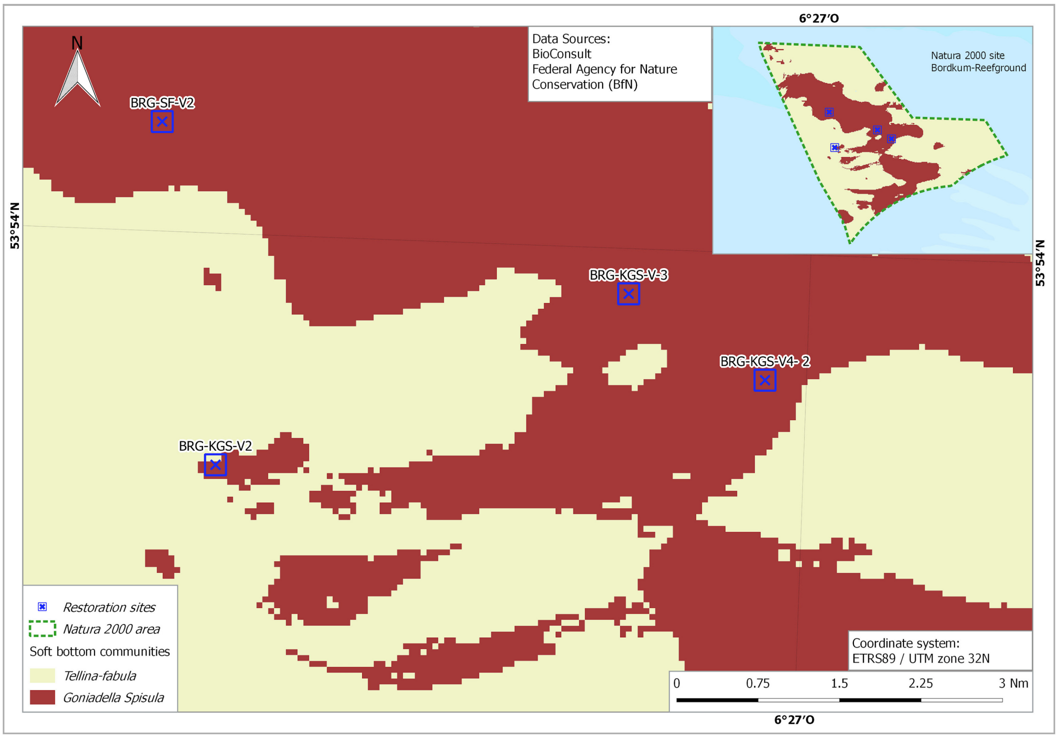


**FIGURE 5** Soft bottom communities (*Tellina fabula* and *Goniadella–Spisula*) and location of selected restoration sites within the Natura 2000 area Borkum Reef Ground in the German Exclusive Economic Zone

## 4 | DISCUSSION

Biogenic reefs are three-dimensional structures, produced by the reef building capacity of specific marine organisms, which are referred to as ecosystem engineers or habitat-forming species. Such reefs are of particular ecological importance as they provide significant habitats for associated species or life stages and effectively enable a broad set of ecosystem services and interactions (Balzer, Boedeker, & Hauke, 2002; OSPAR, 2008; Rabaut, Vincx, & Degraer, 2009). Highly relevant examples are coral reefs in the tropics and shellfish reefs in temperate regions. In the North Sea, tube worms (e.g. *Sabellaria spinulosa*, *S. alveolata*, *Lanice conchilega*), mussels (e.g. *Mytilus edulis*, *Modiolus modiolus*) and oysters (e.g. *Ostrea edulis*) are typical reef-building species, which in many regions are either under threat, declining or functionally extinct (Dubois, Commito, Olivier, & Retière, 2006; Fürhaupter, Bildstein, Darr, & Boedeker, 2017; Holt, Rees, Hawkins, & Seed, 1998; Kent, Last, Harries, & Sanderson, 2017). The European oyster *O. edulis* once formed extensive beds and reefs along the North Sea coast and in offshore regions of moderate depth, but over 90% of former oyster reefs have been lost (Pogoda, 2019).

The maintenance or, if necessary, restoration to favourable conservation status of the habitat type 'reefs' (EU code 1170), including the conservation of its characteristic species, is mandatory according to the EU HD, and is therefore an objective of MPAs hosting this habitat type and designated as Natura 2000 areas under the HD. Accordingly, respective conservation objectives for reefs have been defined for European MPAs in different countries, e.g. for NCAs in Germany (which are Special Areas of Conservation according to the HD), for Special Areas of Conservation in the UK and The Netherlands.

Ecological restoration projects aim at the recovery of the rich species-community of native oyster beds with all its ecosystem functions and services to fulfil the conservation requirements of Natura 2000 areas. The selection of suitable sites is of fundamental importance, as it influences the survival, growth, fitness, reproduction, and recruitment of the species and will determine the success of the whole restoration project (Baine, 2001; Kerckhof, Coolen, Rumes, & Degraer, 2018; Laing et al., 2005; Pollack, Cleveland, Palmer, Reisinger, & Montagna, 2012).

Site-selection criteria were identified for three categories: ecological history (natural distribution range and historical distribution of the target species), feasibility of restoration (regulating framework and logistical considerations for the practical implementation), and environmental conditions (suitability of abiotic and biotic factors for the target species; Table 2). Considering these three categories, a step-by-step approach is recommended for successful site selection. Step 1: ecological restoration aims at the return of species and habitats. It is the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (Gann et al., 2019). This implies that the former existence of the species and habitat in the area should be considered first (McDonald et al., 2016; SER, 2004). Step 2: ecological restoration has a certain area demand, potentially free of other contra-indicated uses (Figure 2). These regulating and logistical criteria should be the next consideration, before collating the inventory of environmental data. Step 3: the ecosystem baseline inventory identifies current ecosystems and their condition, including current abiotic and biotic conditions with respect to the ecological range of the target species and any native and non-native species evidently persisting on the site, which may interact (McDonald et al., 2016). The suggested hierarchy is well-fitting for the German North Sea. In general, this approach will be transferable to other regions and species, by carefully revising the site-selection criteria, as this list may not be exhaustive, and by adapting the hierarchy to address the specific local requirements.

Within the three categories, a total of 16 site-selection criteria were identified and applied (Table 2, Figures 1–6). Site-selection criterion 1, former presence of *O. edulis*, resulted in the general suitability of the former offshore oyster grounds, reaching from the central German Bight far west and northwest to the Dogger Bank (Figure 1). This extensive area may play a significant role for ecological restoration of *O. edulis* as it may have served as a highly productive broodstock population for the German Bight and the Wadden Sea populations.

The application of site-selection criteria 2–7 (feasibility of restoration), resulted in large areas of BRG that come into consideration for biogenic reef restoration, namely of the native oyster *O. edulis*. Priority shipping areas and water depths ≥30 m were defined as not appropriate for the installation of pilot reefs, due to the need for frequent survey intervals at the pilot stage. But in general, offshore shipping areas and water depths ≤30 m do not seem object to future large-scale restoration measures.

The application of site-selection criteria 8–11 (abiotic factors temperature, salinity, current velocity, oxygen concentration) demonstrated the general suitability of BRG in terms of the ecological tolerance range of *O. edulis*. Criterion 12 (abiotic factor substrate quality) is, however, more difficult to apply. Considering the continuous fishing activity over the last decades, the seabed in the area can be defined as highly modified. The natural and preferred settlement substrate, conspecific shells, no longer exists in BRG and data on the general performance and larval recruitment of *O. edulis* on different soft bottom substrates is scarce. Fine sediments of smaller grain sizes (≤ fine sand) were classified as not suitable, due to low current velocities and high concentrations of suspended particles in the water column, which increase pseudo-faeces production and energy demand in filter-feeding oysters. Existing literature identified coarse sediments, firm sands, and gravel as advantageous for settlement (Colsoul et al., 2020; Kamermans et al., 2018; Sawusdee, Jensen, Collins, & Hauton, 2015). These larger grain sizes are often associated with the soft bottom community *Goniadella–Spisula*. Accordingly, selected sites are located in areas of medium sand and gravelly sand (Figure 3a) within species-rich gravel, coarse sand, and shell gravel areas (Figure 3a) and within the *Goniadella–Spisula* distribution (Figure 5). We postulate that, historically, the epibenthic species community of *O. edulis* beds and reefs was eventually associated with the endobenthic species community *Goniadella–Spisula*, which may therefore indicate appropriate restoration sites for the European oyster today. Restoration pilot studies should investigate if *Goniadella–Spisula* can be defined and applied as a relevant indicator for site selection. For this, the full coverage biotope map presented in this paper should be used as one of the main input variables. The map was produced from quality-assured sampling data on the benthic infauna intersected with full coverage and high-resolution data on potential influence factors as, e.g. the sedimentological map presented in Figure 3a.

Recruitment success will not only depend on substrate quality and on-site environmental factors: larval import from and connectivity between sites is a crucial factor for the long-term success of restoration and recovery (McDonald et al., 2016; Puckett et al., 2018). Current speed and direction are important for the spread and successful colonization of the larvae. These factors determine the potential connectivity of restoration sites, e.g. by offering settlement substrate at appropriate locations and at appropriate times. Recent studies, modelling *O. edulis* larvae as passive particles, show the dispersal of larvae, originating from the closest Dutch restoration area, into the BRG area (Kamermans et al., 2018; Smaal et al., 2017). Hence, broodstock of Dutch restoration projects could act as a potential larval source for future oyster populations in the German North Sea. However, larvae of *O. edulis* do show an active settlement behaviour (Rodriguez-Perez et al., 2019) and the development and application of a model for more detailed predictions on larval drift and successful

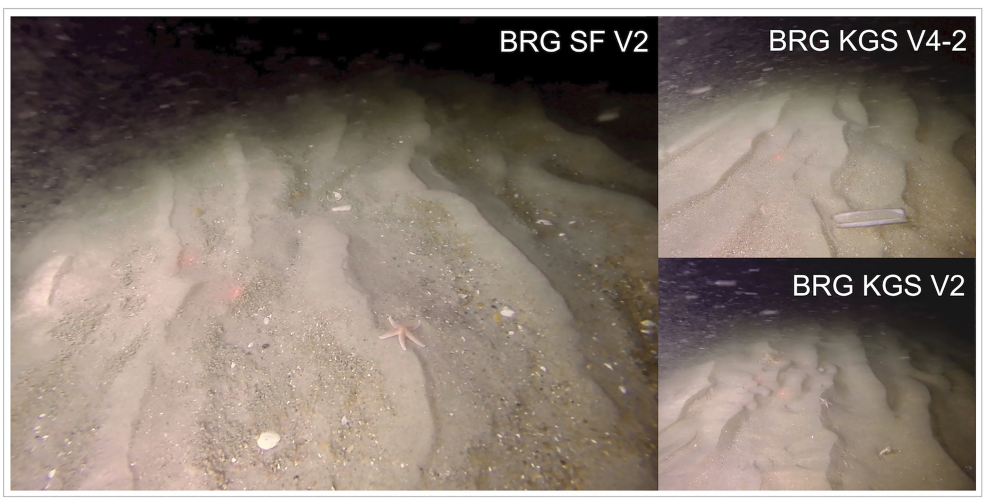


**FIGURE 6** Substrate of seabed at the selected restoration site within the Natura 2000 area Borkum Reef Ground in the German Exclusive Economic Zone, assessed in April 2019 (Heincke HE529) (BRG SF V2 = Borkum Reef Ground Sand Field V2)

recruitment for the German Bight is a relevant next step for selecting further restoration sites. Ecological connectivity with the surrounding environment will optimize colonization and gene flow potential between restoration sites (McDonald et al., 2016).

The application of site-selection criterion 13 (biotic factor food availability), resulted in the general suitability of BRG with rich food conditions for oyster growth and reproduction (Martin, Littaye-Mariette, Langlade, & Allenou, 1997; Rogan & Cross, 1996). The application of site-selection criterion 14 (biotic factor predation) was clearly limited as oysters are absent so far. However, common predators on bivalve shellfish reefs, such as the starfish *A. rubens* and *A. irregularis*, were present (Castilla, 1972; Spencer, 2008). The establishment of a new habitat will attract a number of associated species, including predators, such as *C. pagurus*, *H. gammarus*, and *Hyas araneus* (Mascaró & Seed, 2001; Shelmerdine & Leslie, 2009). Furthermore, predation on oyster larvae will affect successful recruitment. As the biogenic hard substrate provided by the oysters offers an extensive habitat, predation on oyster larvae by associated sessile filter-feeding epifauna or associated fish species must be considered as a factor (Auby & Maurer, 2004; Tamburri & Zimmer-Faust, 1996). The role of potential higher order predators e.g. of diving seabirds at water depths >20 m is unclear so far (Spencer, 2008). Predator–prey interactions should be assessed carefully once oysters are being restored at a selected site. These data, e.g. in a pilot reef phase, will allow guidance to define numbers and size classes of seed oysters for successful reef establishment. Likewise, site-selection criterion 15 (biotic factor competition) needs to be assessed during a pilot reef phase. Competition for food and settlement surface is expected from filter-feeding epifauna and sessile reef-associated organisms. Food availability is high and not considered a limiting factor, but settlement substrate should be closely investigated for successful recruitment. In substrate-limited areas, competition is a relevant factor and can be outbalanced by orienting substrate deployment to reproduction cycles of *O. edulis* (Westby et al., 2019). The application of site-selection criterion 16 (biotic factor disease) resulted in the general suitability of BRG. Critical diseases caused by the protozoans *B. ostrea* and *M. refringens* have not been detected in the German Bight so far (Merk et al., n.d.). But, having caused massive die-outs in *O. edulis* populations in the past (Culloty & Mulcahy, 2007; Heral, 1990), infection status and potential ecological impact of these diseases should be closely investigated once oysters are being restored at a selected site. Recent recommendations provide further guidance regarding the restoration of *O. edulis* in disease-free areas (Colsoul et al., n.d.; Jeffs, Hancock, zu Ermgassen, & Pogoda, 2019; Pogoda et al., 2019; Sas et al., 2019).

### 4.1 | Implications for marine conservation and ecological restoration

The application of the identified criteria provided a number of suitable sites for biogenic reef restoration within the Natura 2000 area BRG. As site selection was identified as one of four critical bottlenecks by the Native Oyster Restoration Alliance (NORA) when founded in Berlin 2017, a working group was established to address country and region-specific needs and to facilitate the identification of appropriate sites in terms of practical feasibility (Pogoda, Brown, Hancock, & von Nordheim, 2017; Pogoda et al., 2019). Within the 23 coastal member states, 3,150 marine Natura 2000 areas, covering 551,898 km$^2$ (8.5% of the total European Union marine area) have been designated so far (European Commission of Environment, 2019). Correlating the natural and historical distribution range of the European oyster, several Natura 2000 areas can be considered for restoration of biogenic oyster reefs and associated conservation measures. In general, and with reference to criteria 2–7, MPAs are considered as potentially adequate sites for species restoration. This requires, however, that they are well-managed to reduce or avoid impacts from contraindicated uses. MPAs can be considered particularly adequate for species restoration if the conservation objectives explicitly include conservation or restoration of the species in question – not only as part of the community associated with habitat types, which are protected under the HD, but also as conservation features 'as such', e.g. because of their ecological values or threat status. MPAs can thus contribute substantially to conservation or restoration of threatened and/or declining species, as suggested by OSPAR for various species including the European oyster (OSPAR, 2013). At the same time, restoration projects can assist in achieving, or are necessary to achieve the conservation objectives of MPAs. Furthermore, species restoration can be an important step towards achievement of GES according to the MSFD. Accordingly, Germany has defined "restoration of populations of regionally extinct species, e.g. European oysters" as an objective to be achieved under the MSFD (BLANO, 2012), but no according measures have been described or implemented so far (BLANO, 2016).

In conclusion, European oyster restoration in BRG will not only contribute to meeting the conservation objectives of the Natura 2000 area and to achieving the aims of the HD, a favourable conservation status of reefs in the biogeographic region. It will also contribute to meeting the national environmental objectives defined under the MSFD, and thus to achievement of GES as the overall aim. The same may apply for native oyster restoration in other European countries.

## 5 | CONCLUSIONS & RECOMMENDATIONS

1. In this study, categories and criteria were attributed to a specific hierarchy, well-fitting for the German North Sea. In general, this approach will be transferable to other regions and species, by carefully revising and adapting the site-selection criteria and the hierarchy to meet the specific requirements.
2. In summary, the collected site-selection data are reflecting an enormously shifted baseline, since the original habitat of sublittoral oyster reefs was lost a long time ago (Pogoda, 2019). In consequence, pilot studies will verify the true qualification of the selected criteria and the selected sites for biogenic reef restoration before scaling up. To extract entire areas best suited for the restoration of the native oyster, GIS-based multicriteria decision analysis

(Eastman, 1999; Pollack et al., 2012) allows to calculate suitability maps by defining constraints and by including different potential influencing factors in terms of a weighted average approach.

3. Implementation plans for restoration and upscaling need to integrate species-specific traits with site-specific dynamics and consider transdisciplinary restocking approaches.
4. The following criteria should be assessed carefully once oysters are being restored at a selected site: predator–prey interactions; the role of competition for food and space (settlement substrate); and the role and succession of macroparasites and diseases, as the application of these criteria is limited during the site-selection process.
6. We postulate that, historically, the epibenthic species community of *O. edulis* beds and reefs was associated with the endobenthic species community *Goniadella–Spisula*, which may therefore indicate appropriate restoration sites for the European oyster today. Restoration pilots should seek to verify if *Goniadella––Spisula* can be defined and applied as a relevant indicator for site selection.
7. Besides reefs, sandbanks, and species-rich gravel, coarse sand, and shell gravel areas are protected habitat types within the BRG. Negative impacts of oyster restoration on these habitat types are not expected for BRG, but a specific monitoring to assess potential (positive or negative) effects during the pilot phase is recommended. In general, site selection within MPAs must target to avoid conflicts of conservation aims.
8. Besides implementation of measures at selected sites, MPA management also requires an assessment of management effectiveness to enable adaptive management. In this context, the success of oyster restoration in terms of reef structures and species inventory needs to be assessed. Furthermore, the necessary extent of restoration to achieve, along with other measures, the conservation objectives of the respective MPA needs to be defined.
9. Site selection for ecological restoration measures needs to address the connectivity of restored populations and of MPAs respectively to achieve the recovery of self-sustaining populations and intact habitats.

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