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Return of the native: Survival, growth and condition of European oysters reintroduced to German offshore waters

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Abstract

1. The European oyster (*Ostrea edulis*) is under significant threat across its natural distribution range and even functionally extinct in some regions, such as in the German North Sea. Due to its ecological significance in terms of biodiversity and other ecosystem services, the species, and the habitat it provides, are defined as highly endangered by the OSPAR Convention.
2. Restoration measures are gaining momentum in Europe and conclusive recommendations for large-scale biogenic reef restoration are relevant for example within the Marine Strategy Framework Directive and the Habitats Directive.
3. This study examined whether present-day environmental conditions of sublittoral offshore waters are ecologically suitable for the return of European oysters. Seed oysters (shell length ∼2 mm) were deployed in cages in offshore field experiments in 10–26 m water depth.
4. Survival, growth, and condition were investigated over the course of 2 years. Survival was high, even over winter. Growth was excellent, with oysters reaching a mean length of 55.0 ± 7.2 mm shell length and 19.2 ± 6.1 g wet weight after 2 years.
5. The formation of firmly aggregated oysters was observed and confirms *O. edulis* as a reef-building species.
6. The overall condition of oysters in the field was excellent, identified by high condition indices and early reproductive activity.
7. These findings are highly relevant for future restoration measures in the North Sea as they confirm that present-day environmental conditions and small, hatchery-produced seed oysters are suitable of supporting sustainable and successful restoration efforts even in sublittoral offshore waters.

KEYWORDS
benthos, ecological restoration, ecosystem services, invertebrates, ocean, reef, sublittoral

1 | INTRODUCTION

Worldwide, oyster reefs and beds are among the most endangered habitats, with over 85% already lost (Beck et al., 2009). Not only is this an issue for the oyster species under threat, but it has severe ecosystem consequences, as the three-dimensional, biogenic oyster reefs play a significant ecological role by providing crucial ecosystem functions. The structural features of oyster reefs serve as shelter, spawning ground, settlement substrate, and food source for many different species (Coen et al., 2007). Moreover, oysters remove large amounts of suspended material by filter-feeding and enhance bentho-pelagic coupling (Austen, 2011).

Due to their substantial ecological value, oyster reefs are listed among the most important marine key-habitats for ecological restoration (Sanjeeva Raj, 2008). Conservation and restoration efforts of oyster habitats have been undertaken around the world (Beck et al., 2011; Pogoda, 2019). Following the principles of ecological restoration, a full recovery of the ecosystem aims to create and enhance resilient, dynamic oyster reefs within their historical distribution (Gann et al., 2019).

In Europe, oyster restoration efforts are focusing on the native European oyster *Ostrea edulis*, historically highly abundant in the North-east Atlantic coastal and shelf seas as well as in parts of the Mediterranean and the Black Sea (Duchêne, Bernard, & Pouvreau, 2015; Fariñas-Franco et al., 2018; Kennedy & Roberts, 1999; Pogoda, 2019; Smaal, Kamermans, van der Have, Engelsma, & Sas, 2015; Todorova, Micu, & Klisurov, 2009). The main stressors have been anthropogenic changes of the habitat (such as pollution and eutrophication) and overexploitation (Lotze et al., 2005; Wolff, 2000). Since Roman times, *O. edulis* has always been part of the human diet and as such subject of intense fisheries (Günther, 1897). With the development of more efficient fishing techniques, fishery pressure on populations increased substantially and most stocks were overexploited. Oyster reefs also suffered from the removal of shell substrate by bottom trawling (Hagmeier & Kändler, 1927) thus denying larvae of suitable settlement substrates to maintain self-sustaining populations in these degraded habitats. Additionally, the common practice of oyster translocations to compensate for declining landings brought invasive diseases and resulted in mass mortalities caused by Bonamiosis and Marteiliosis (Berthe, Le Roux, Adlard, & Figueras, 2004; Bromley, McGonigle, Ashton, & Roberts, 2016; Culloty & Mulcahy, 2007). Data on historical distribution, stock size, composition, and reef structure, are available from fishery reports only (Thurstan, Hawkins, Raby, & Roberts, 2013). However, since fishery reports are not fully comprehensive and do not reflect an undisturbed condition of the ecosystem, the baseline for restoring oyster reefs is biased (Pogoda, 2019).

In German waters, the native oyster has been functionally extinct since the 1950s (OSPAR, 2009). Oyster beds were present in coastal areas, the tidal channels of the North and East Frisian Wadden Sea (Neudecker, 1990) as well as in offshore, subtidal areas around Helgoland (Caspers, 1950), and further offshore extending into the North Sea as large-scale oyster beds in 20–50 m water depth (Möbius, 1877) (Figure 1). Overexploitation began in coastal regions and expanded into deep water to the 21,000 km^2 offshore oyster ground and the Helgoland oyster bed (Neudecker, 1990). While coastal oyster beds and the Helgoland oyster bed were well-studied (Hagmeier & Kändler, 1927; Möbius, 1877), less is known about the offshore oyster ground. Based on landings, they were assumed to be at least 100–1,000 times bigger than coastal and Helgoland stocks, covering the sea floor and forming oyster clumps or ‘coarse oysters’ (Gercken & Schmidt, 2014). Furthermore the location and the development of the decline of the stocks in the Wadden Sea and around Helgoland imply that deeper oyster beds may have been an important factor in sustaining the coastal and Helgoland oyster beds by releasing significant amounts of larvae that recruited there (Berghahn & Ruth, 2005; Caspers, 1950). Historically, oyster reefs were the biggest biogenic structure on the otherwise unstructured sea floor of the North Sea, providing habitat for a rich species community and creating hotspots of biodiversity (Möbius, 1871; Pogoda, 2019).

The OSPAR Convention lists *O. edulis* as a threatened species and habitat, worthy of protection and conservation. The EU Habitats Directive and the Marine Strategy Framework Directive put particular emphasis on the protection and conservation of biogenic reefs, e.g. oyster reefs. For successful restoration, the suitability of the biotic and abiotic environment needs to be tested at adequate scales (Seddon, Armstrong, & Maloney, 2007). Best practice excludes the translocation of oysters from foreign water bodies to avoid introducing invasive species and diseases, and further depletion of wild populations (Bromley et al., 2016; Jeffs, Hancock, zu Ermgassen, & Pogoda, 2019; Pogoda et al., 2019). European restoration efforts are mainly addressing coastal oyster beds (Ashton & Brown, 2009; Harding, Nelson, & Glover, 2016; Smaal et al., 2015). Studies on reintroducing *O. edulis* to the deeper offshore regions of the North Sea have not been conducted so far. Those areas differ significantly in their environmental parameters from areas within the coastal influence (Frohse et al., 2016). Offshore areas are more stable concerning salinity and temperature and are less influenced by nutrient transportation from the adjacent land (Rees, Eggleton, & Rachor, 2007). Most recent trials on the performance of *O. edulis* in the German North Sea were carried out in hanging cultures close to the surface and indicated offshore sites as suitable for *O. edulis* (Pogoda, Buck, & Hagen, 2011). The aim of this paper is to confirm that sublittoral environmental conditions in the German North Sea are suitable for the reintroduction of the native European oyster, by investigating the offshore performance of oysters in seabed cages. Novel field experiments were conducted in sublittoral waters to test survival, growth, and condition of juvenile oysters and to provide relevant information for the practical implementation of future restoration efforts.

2 | MATERIAL AND METHODS

In this study, 3-month-old European oysters were exposed to *in-situ* conditions in areas where the species is classified as functionally

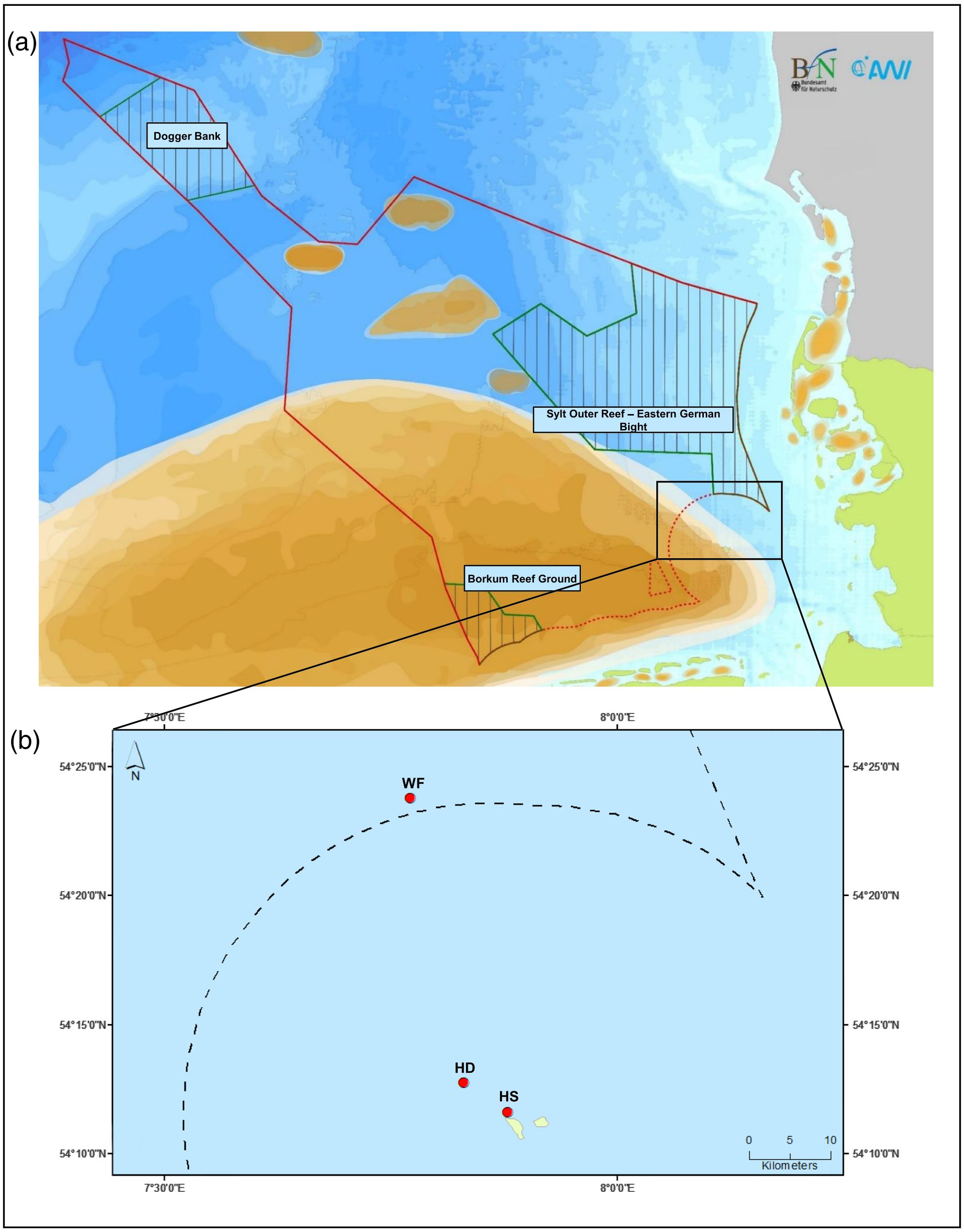

FIGURE 1 (a) Historical distribution of native European oysters in the German Bight and marine protected areas under Natura 2000 and national legislation (AWI/BfN). (b) Island of Helgoland and offshore study sites in the German Bight: Windfarm (WF), Helgoland deep (HD), and Helgoland shallow (HS), dashed line: German Economic Exclusive Zone

extinct, to investigate the restoration potential by assessing survival, growth, and condition over 2 years. For logistical reasons, oysters were deployed in cages, and factors such as predation and sediment dynamics were not investigated.

2.1 | Study area

The field experiments were conducted at three offshore study sites in the German North Sea (Figure 1), located within the range of historical oyster beds, 25 NM off the German Coast.

The first study site was located at 54°23.8′N 007°46.3′E in the security zone of an offshore wind farm (*WF*, Meerwind Süd|Ost, WindMW GmbH) at 25 m water depth (all depth data at mean high water). The second and third study sites were located at 54°12.8′N 007°49.8′E at 26 m water depth (*HD)* and 54°11.6′N 007°52.8′E near Helgoland at 10 m water depth (*HS*); both sites within the marine protected area (MPA) 'Helgoländer Felssockel'. In comparison to the offshore study sites *WF* and *HD*, *HS* was classified as semi-offshore due to its proximity to the island Helgoland and its shallower water depth (Table 1). The sediment type of the sea bottom was sand and occasionally stones at all study sites. Details on the selected offshore study sites are provided in Table 1.

2.2 | Origin of test animals

Seed oysters of 2-mm shell length were obtained from a hatchery, hatched and reared in sterilized sea water (Marinove, France). Additionally, a health certificate was issued by GIP LABOCEA (Ploufragan, France). Seed oysters were purchased once and cultivated on Helgoland for later use in a controlled continuous flow-through system with filtered North Sea water (18 μm, unsterilized, at 14°C), with minimum food (*Rhodomonas salina*) to avoid significant growth in the lab.

2.3 | Experimental design and sampling

Metal cage constructions were moored at the sea floor, connected to marker buoys. The solid cage set up allowed the attachment of lightweight oyster baskets (6 mm mesh size, 15-L baskets, 600 × 140 × 260 mm, SEAPA). Cages were hanging ~0.5 m above the sea floor and excluding potential predators. Deployment, recovery, redeployment, and maintenance was conducted by scientific divers.

Seed oysters were deployed at site *WF* in May 2017 (*Group 1*) and August 2017 (*Group 2*). *Group 3* was deployed in October 2017 at site *HS*. Due to logistical reasons, *Group 1 and 2* were moved to site *HD* in April 2018. *Group 4* was deployed at site *HD* in April 2018. Each group started with 6,000 seed oysters, sorted into 10 mesh bags (mesh size <2 mm) within two oyster baskets (200,000 individuals/m^3). In the course of the experiment, bigger oysters (>10 mm) were taken out of the mesh bags and kept loosely in the oyster baskets. The number of oyster baskets for each group was increased according to the growth of the oysters.

Measurement and collection of subsamples from each group were carried out at least once in spring, summer, and autumn of 2017 and 2018 and in spring 2019. Recovered oyster baskets were transferred to the research vessels. Handling time was kept to a minimum and collected oysters were kept in flow-through systems using natural sea water. Subsamples ($N \geq 20$) for analysis on weight and condition index (CI) were kept in the lab; remaining oysters were re-deployed to the respective study sites after growth measurements were taken.

2.4 | Analysis of growth, CI, mortality, and reproduction activity

Growth was examined as an increase in shell length (SL, umbo hinge to longest edge) and dry mass meat (DM) between sampling events. SL was measured to the closest 0.1 mm. For each group and sampling, $N \geq 200$ oysters were measured. Daily growth was calculated by dividing the increase in shell length between sample dates by the days passed between samplings. For subsamples ($N \geq 20$), total wet weight, to the closest 0.1 mg, was determined individually, before dissection and storage at −80°C. During dissection, oysters were visually inspected for signs of reproduction, which were recorded and documented. Samples were then dry frozen (24 h, Alpha 1–4 LSC, Christ). DM and dry mass shell (DMS) were measured to the closest 0.1 μg (MSA2.7S-000-DM Cubis Ultra Micro Balance, Sartorius) for the individual CI calculation (Davenport & Chen, 1987; Walne & Mann, 1975). Oysters were deployed as single seeds and during the course of the experiment inspected for the formation of permanently aggregated oyster clusters of two or more oysters caused by

TABLE 1 Nomenclature and description of offshore study sites in the German North Sea

Study site	Code	Depth at MHW [m]	Experiment time	Coordinates	Status	Sediment type of sea bottom	Currents [m/s]	Oxygen concentration [mg/L]
Wind farm	*WF*	25	05/2017–04/2018	54°23.8′N 007°46.3′E	Offshore	Sand	0.28–0.29	7.24–10.88
Helgoland deep	*HD*	26	04/2018–05/2019	54°12.8′N 007°49.8′E	Offshore	Sand, stones	0.20–0.22	7.47–10.80
Helgoland shallow	*HS*	10	10/2017–05/2019	54°11.6′N 007°52.8′E	Semi-Offshore	Sand	0.21–0.31	7.36–10.75

Abbreviation: MHW, mean high water.

individual shell growth. Survival was estimated by counting alive oysters in mesh bags and oyster baskets. If counting of total animals per oyster basket was not possible (due to high numbers of individuals and time limitation between diving intervals), subsamples or oysters in randomly selected meshes were counted (*N* ≥ 600).

3 | RESULTS

3.1 | Environmental conditions

Environmental parameters of the offshore study sites were taken from the Operational Circulation Model of Federal Maritime and Hydrographic Agency (BSH, BSHcmod) (Dick, Kleine, Müller-Navarra, Klein, & Komo, 2001) at maximum water depth (Figure 2). Temperature and oxygen concentrations were similar between sites and years. Growing season is related to water temperatures above 7°C (Ashton & Brown, 2009). In 2017 and 2018, it ranged from May to December and in 2019 from April until the end of the experiment. Chlorophyll-*a* concentrations were similar at all sites, peaking in August 2017 and 2018 and March 2018 and 2019. However, in August 2018, the peak was significantly lower than in the previous year (Figure 2). Salinity was stable and always ≥30. In 2018, variation was slightly higher and salinity ranged between 31.9 and 34.6. Mean current velocity ranged between 0.20 and 0.31 m/s (Table 1).

3.2 | Survival

Survival was assessed by counting live oysters in mesh bags and oyster baskets. Seasonal survival in relation to previous season is shown in Figure 3. In all groups, the highest mortality was observed in the first season after deployment. Maximum initial mortality occurred in *Group 1* (89.98%), but decreased to 0.00% over the course of the experiment, despite a winter mortality of 10.05%. Cumulative mortality added up to 90% in *Group 1*. *Group 2* showed an initial mortality of 41.28%, and no winter mortality (0.00%). Cumulative combination of initial and winter mortality added up to 71.67% in *Group 3*. *Group 4* showed an initial mortality of 51.93% and the lowest total mortality of 52.00% at the end of the experiment (Figure 3). No winter mortality occurred in 2019.

3.3 | Growth

Oysters were deployed with a SL of ∼2 mm (sorted in size class T2) and DM of 0.12 ± 0.36 mg in October 2017 (*Group 1*), August 2017 (*Group 2*), October 2017 (*Group 3*), and May 2018 (*Group 4*).

All four groups showed an increase in SL over time (Figure 3), directly proportional to the cultivation time in the field. At the end of the field experiment, mean SL and mean total animal wet weight, respectively, were 55.0 ± 7.2 mm and 19.2 ± 6.1 g for *Group 1*; 39.6 ± 10.5 mm and 5.8 ± 3.9 g for *Group 2*; 34.9 ± 5.3 mm and 3.9 ± 1.6 g for *Group 3*; and 13.7 ± 6.1 mm and 1.1 ± 0.6 g for *Group 4*. All groups represent a mix of faster, average, and slower growing animals resulting in considerable variations of SL, wet weight, and growth rates. Highest differences in SL of ±50.27 mm appeared in September 2018 in *Group 2*. In 2017, daily shell growth reached a maximum in September followed by a considerable decrease over winter. In July 2018, *Group 1* and *Group 2* showed a second, but smaller peak in daily shell growth. *Group 3* and *Group 4* showed maximum daily shell growth in August 2018, again followed by a decrease over winter.

For the first 2 months after deployment, DM of *Groups 1* and *2* was below 20 mg and DM of *Groups 3* and *4* below 1 mg but increased steadily (Figure 3). At the end of the experiment, maximum DM was 344.87 ± 130.96 mg (*Group 1*), 108.74 ± 31.22 mg (*Group 2*), 68.44 ± 28.27 mg (*Group 3*), and 17.10 ± 8.33 mg (*Group 4*). Daily DM growth of *Group 1* showed seasonal variation: a peak in autumn 2017, a minimum in spring 2018, followed by a second maximum in summer 2018, and a second minimum in autumn 2018. A similar, but less prominent development was observed for *Groups 2*, *3*, *Group 4*.

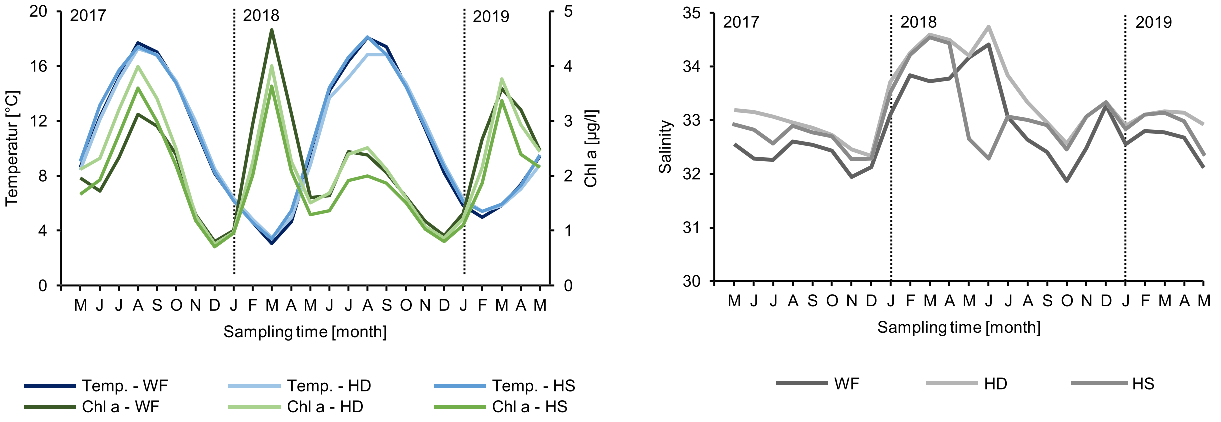

FIGURE 2 Temperature, chlorophyll-*a* (Chl-a), and salinity at offshore study sites wind farm (WF), Helgoland deep (HD), and Helgoland shallow (HS) in the German North Sea. All environmental parameters were modelled to the corresponding experiment depth and years using the Operational Circulation Model of BSH (Dick et al., 2001)

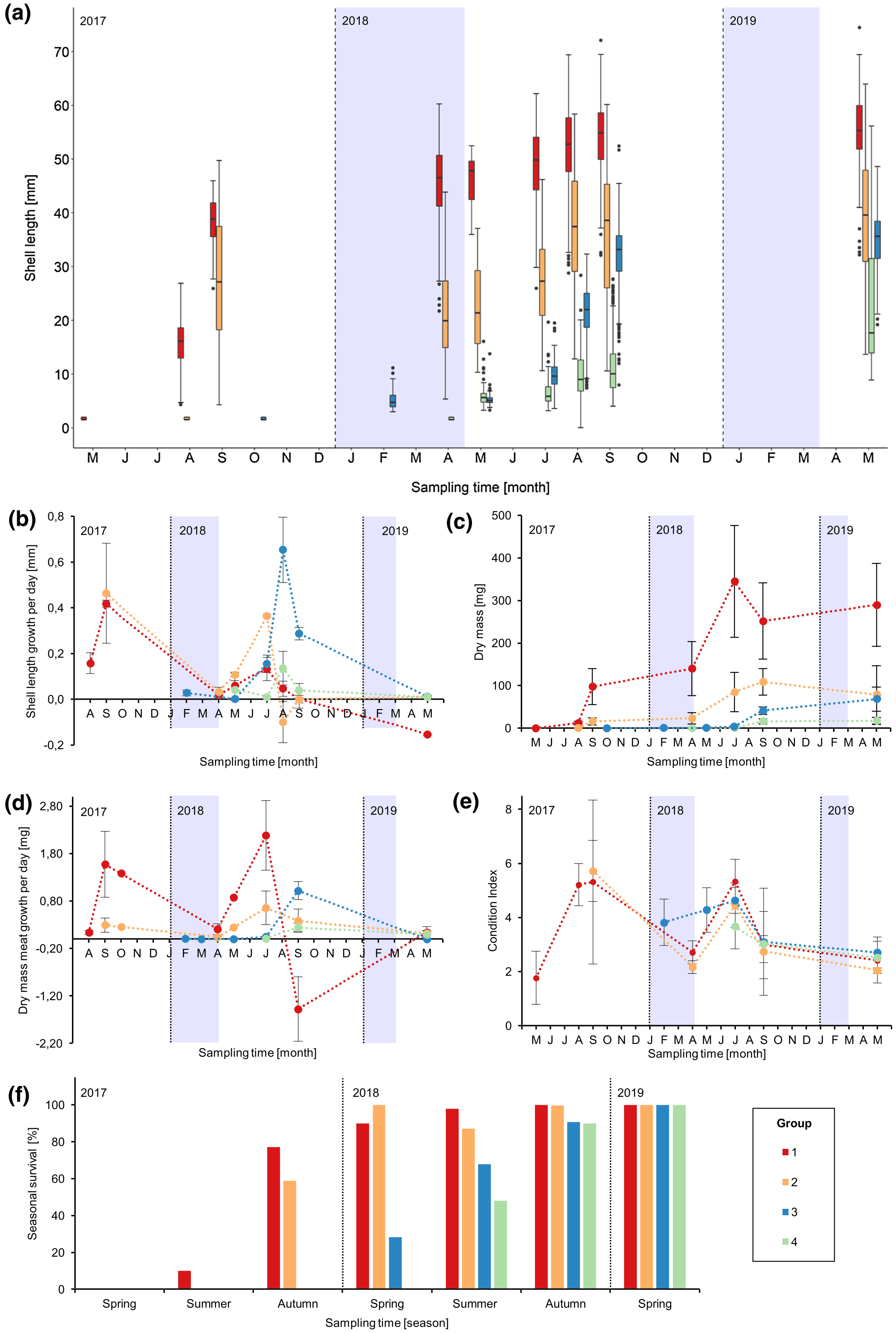

FIGURE 3 Growth, condition, and survival of oysters in offshore experiments. Indicated in grey is the period of water temperatures below 7°C, where no or reduced growth is expected, dotted lines for visualization purposes only. (a) Shell length at sampling time is presented as boxplots with the upper and lower limits of the box being the third and first quartile, including the median line and whiskers that represent 1.5 times the interquartile range, outliner are indicated as dots. (b) Shell length increase per day, (c) dry mass meat, and (d) dry mass meat increase per day are presented as average and standard deviation. (e) Condition index over experimental time for all four groups is presented as average and standard deviation. *N* = 6,000 seed oysters (mean shell length 2 mm) were deployed at offshore study sites in the German Bight in May 2017 (Group 1), August 2017 (Group 2), October 2017 (Group 3), and May 2018 (Group 4). Samples sizes were *N* ≥ 200 individuals for shell length and *N* ≥ 20 individuals for dry mass measurements and calculation of condition index. (f) Percentage of survival between samplings

All groups showed the formation of firmly aggregated oyster clusters (Table 2). We define these oyster clusters as clumps of two or more oysters, permanently merged together by their own shell growth, achieved after their deployment as single seeds. *Groups 1* and *2* both formed 26 oyster clusters. *Groups 3* and *4* formed four and 37 oyster clusters, respectively. Predominantly, the clusters included two individuals (2.34 ± 0.92 Ind.) and, a maximum of eight live individuals was documented. Formation of new clusters was an ongoing process throughout the field study and occurred in both mesh bags and oyster baskets.

3.4 | Condition

At the beginning of the experiment, in May 2017, CI of seed oysters was 1.77 ± 0.98. CI of *Group 1* oysters increased in summer 2017 (5.22 ± 0.78) and autumn 2017 (5.32 ± 2.96). After winter, CI was low in spring 2018 (2.71 ± 0.44), but increased to a second maximum in summer 2018 (5.33 ± 0.82), before decreasing to 2.99 ± 1.24 in autumn 2018. *Groups 2*, *3*, and *4* showed similar CI patterns (Figure 3e).

Reproductive activity was detected in several oysters of *Groups 1*, *2*, and *3* in summer and autumn 2018 (Figure 4). In summer 2018, 7.32% of *Group 1* and 2.38% of *Group 2* showed evidence of reproductive activity and reproduction: *O. edulis* larvae of different developmental stages, from early embryogenesis of gastrula to early veliger were present in the mantle cavity of different sampled oysters. In autumn 2018, the percentage of reproducing oysters had reached 12.00 and 6.00% in *Group 2* and *Group 3*, respectively. Size of reproducing oysters ranged from 29.88–52.39 mm SL.

4 | DISCUSSION

The native European oyster has vanished from the once abundant and extensive offshore oyster grounds in the North Sea. The decline and loss happened several decades ago, and besides fisheries reports and data, there is no further and specific information on the ecological baseline regarding the extent, density, and ecological role this species played in the surrounding offshore ecosystem.

This study is the first to investigate the potential for the return of *O. edulis* to offshore areas via active reintroduction and restoration measures. For logistical reasons, oysters were deployed in cages and factors such as predation and sediment dynamics were not investigated (Ashton & Brown, 2009; Pogoda et al., 2020; Yonge, 1960). Following best-practice standards to prevent the translocation of invasive species, diseases, and parasites, and the further depletion of natural stocks, only small-sized and certified disease-free, hatchery-produced seed oysters were deployed at experimental scales (Pogoda et al., 2019). Growth, condition, and survival of reintroduced oysters in cages indicate that present-day conditions and the use of small seed oysters allow for sustainable and successful restoration. As the experimental set-up (baskets) excluded predators, the impact of predators and respective effects on overall survival needs to be addressed in further studies.

Results of this study show survival rates similar to coastal stocks and commercial aquaculture (Guesdon, Mazurie, & Lassale, 1989; Walne & Mann, 1975). Previous field studies reported higher survival rates but only for significantly larger individuals of *O. edulis* (Pogoda et al., 2011; Utting, 1988; Valero, 2006). In this study, young seed oysters showed the lowest survival rates within the season of deployment (initial survival). Adapting logistics and oyster handling by

TABLE 2 Formation of oyster clusters in all four experimental groups

Group	Study site	Oyster clusters	Max. ind./cluster	*SL* of cluster oysters [mm]	Oyster clusters (5 of 8 ind. visible)
1	*WF/HD*	26	3	10.19–67.30	
2	*WF/HD*	26	8	7.95–54.11	
3	*HS*	4	2	6.82–19.24	
4	*HD*	37	4	17.05–49.78	

Note: Clumps of oysters, permanently merged together by shell growth, were considered as oyster clusters. Numbers of living oysters per clusterranged from two to eight individuals. Digital coloration of cluster-forming individuals.
Abbreviation: SL, shell length.

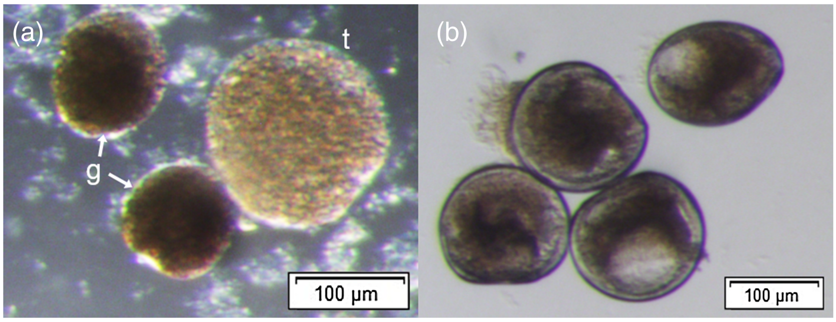

FIGURE 4 First indications of reproduction activity in 1-year-old *Ostrea edulis*, growing at offshore study sites: (a) early stage of embryogenesis: gastrula (g) and trochophore (t) stage, (b) early veliger

optimizing transportation (constant water supply and shorter transport periods), improved initial survival, and mortality steadily decreased towards zero in the course of the experiment. Temperature acclimatization prior to deployment of seed oysters will potentially increase the initial survival even further (Buxton, Newell, & Field, 1981). Mortality of deployed seed oysters was low in winter, indicating that a natural drop in temperature occurring over winter was not the main driving factor for historical extinction of oysters in the sublittoral offshore regions (Gercken & Schmidt, 2014; Wehrmann et al., 2000). In addition, no increase in mortality was observed after maturation, indicating a good health status of the studied oysters. However, monitoring of relevant diseases, such as Bonamiosis needs to be implemented in any future restoration and reintroduction efforts to inform about health status and natural disease dynamics (Baggett et al., 2014).

Interestingly, the small size of deployed seed oysters did not negatively affect total survival as initially suspected. This is an important and meaningful outcome, as for cost–benefit and biosecurity reasons, ecological oyster restoration will explicitly depend on the feasibility of using small seed animals in the long term. In many regions, so-called recruitment-limited areas, natural spawning is insufficient for establishing a self-sustaining oyster reef (Westby, Geselbracht, & Pogoda, 2019). Oyster populations need to be reinforced or reintroduced using animals from sustainable allochthone sources, such as seed oysters produced in hatcheries and ponds, or from wild spat collection (Colsoul et al., *submitted*). The production of certified disease-free *O. edulis* seeds is a current bottleneck of large-scale sustainable restoration and is therefore addressed in several reintroduction programmes (Pogoda et al., 2019). Production time, costs, and biosecurity risks can be significantly reduced by using smaller seed oysters.

Furthermore, seed oysters in this study showed excellent growth and good condition during the course of the experiment. Shellfish growth depends on various factors such as temperature, food availability and quality, and origin of broodstock (da Silva, Fuentes, & Villalba, 2005; Utting, 1988). Accordingly, growth analyses reflect the general suitability of current environmental conditions (Brumbaugh, Beck, Coen, Craig, & Hicks, 2006) and provide essential information for the reintroduction of an extinct species for which only limited knowledge of the historical habitat and the ecological baselines exist (Pogoda, 2019). Introduced oysters of this study showed a steady and considerable increase in shell length and dry mass. Daily growth showed seasonal variation: high growth rates were observed in summer 2017, related to elevated chlorophyll-*a* concentrations and maximum temperature. A less prominent chlorophyll-*a* peak led to lower daily growth rates in summer 2018, which resulted in a lower CI (ratio of dry mass to shell mass). CI values followed a distinct seasonal pattern and underline the hypothesis that *O. edulis* invests in shell growth in early life (Pogoda et al., 2011). Moderate growth rates of *Group 3* and *Group 4* animals can also be related to less optimal cultivation conditions regarding food composition and quality, prior to the deployment. Several studies addressing growth and condition of European oysters, mainly in aquaculture contexts and in coastal regions, have been conducted so far (da Silva et al., 2005; Ivanov, 1966; Valero, 2006). First offshore trials on the performance of *O. edulis* in the German North Sea were conducted with submerged oyster lanterns (Pogoda et al., 2011; Pogoda, Buck, Saborowski, & Hagen, 2013) where increase in shell length was similar to the data presented in this study. However, seed oysters studied by Pogoda et al. (2011) were significantly larger when deployed and food availability, according to chlorophyll-*a* concentrations, was significantly higher. We postulate that detritus might function as a relevant additional food source for oysters at deeper sites, balancing out effects of seasonal variation of phytoplankton concentrations (Mackinson & Daskalov, 2007). However, oysters were kept in cages, elevated from the sea floor, hence any potential negative impacts of predation pressure and sediment interaction were excluded (Sawusdee, Jensen, Collins, & Hauton, 2015).

Shell growth of oysters in the present study resulted in the formation of firmly aggregated oyster clusters, by two or more oysters, providing a complex three-dimensional structure. The ability and capacity of *O. edulis* to form reefs and the process itself is not fully understood yet. There are no existing data on how the structure of a pristine *O. edulis* habitat looks; existing historical data on reefs mainly refer to harvesting numbers and include only rare notes on ‘coarse oysters’ and ‘clumps of oysters’ (Möbius, 1877). However, there is no knowledge on how the undisturbed sublittoral oyster habitat looked like since the area had already encountered a constantly high fishing pressure for several decades (Gercken & Schmidt, 2014; Thurstan et al., 2013). Accordingly, historical density, structure, and succession of this important North Sea habitat are unknown. The oyster clusters or aggregations *O. edulis* formed by shells growing together in the present study correspond to the historically described ‘coarse oysters’ (Möbius, 1877). The number of clusters increased over time, regardless of them being cultivated in mesh bags in the first months or later laying in oyster baskets. It was observed that many more oysters formed clumps, held together by epifauna, such as *Lanice conchilega* or *Spirobranchus triqueter*. Substantial dead reef structures of *O. edulis*, found in the Black Sea, showed the presence of *Sabellaria taurica* that could have had the same function (Todorova et al., 2009). The documented clusters indicate an initial nucleus for reef formation. Less movement of the animals may end up in the formation of even bigger clusters and reefs. The formation of the clusters in this study was documented in cages and needs to be verified on the sea bed, inducing oyster movements due to sediment dynamics or the effects of mobile macrofauna. But, the formation of any three-dimensional structure will increase the complexity of the habitat and ecosystem functions (Pogoda, 2019).

During the experiment, oysters reproduced 9–14 months after deployment. Reproduction of *O. edulis* is strongly influenced by environmental parameters, such as temperature, food availability, and composition (Berntsson, Jonsson, Wängberg, & Carlsson, 1997). European oysters have been recorded to spawn from their first year and eventually multiple times per year (Cole, 1941; Walne & Mann, 1975). Timing and number of spawning events correlate with latitude and regionally specific environmental factors (Cole, 1941;

Korringa, 1941; Walne & Mann, 1975). Past observations showed that for North Sea conditions, the first spawning event usually takes place in the second or third year (Cole, 1941). However, exceptional spawning events of 1-year-old oysters have been recorded (Cole, 1941), whereas reproductive cycles of more than once per year were rarely recorded (Orton, 1924). *O. edulis* is a protandrous alternating hermaphrodite maturing as male, followed by a female phase. In this study, larvae were found in the mantle cavity of female oysters. In an area where *O. edulis* is functionally extinct fertilization by wild oysters can be excluded. Hence, deployed oysters have matured as males and changed sex to females already within their first year after deployment. This early reproductive activity confirms the good condition of young *O. edulis* in the offshore sublittoral environment over the course of 2 years.

The results of this study are of major importance for future restoration approaches, they confirm that the abiotic environment still supports a functional extinct species, reintroduced one century after its loss. They indicate the potential of young seed oysters for oyster restoration in sublittoral environments and accordingly, apply to other offshore areas where sublittoral *O. edulis* reefs were historically present, such as in the Netherlands, in Belgium, or the English Channel (Gercken & Schmidt, 2014; Kerckhof, Coolen, Rumes, & Degraer, 2018). Detailed modelling of larval drift and hydrodynamics can now help to identify potential larval sources and sinks to reveal connectivity of restoration sites and to inform restoration management in offshore environments. However, the effects of specific substrate types and sediment dynamics, and of prey–predator relationships, which were not included in the present study, are of relevance for the long-term recovery of biogenic oyster reefs and need to be investigated thoroughly.

Furthermore, marine spatial planning, and the potential role of MPAs and fishery exclusion zones will influence the success of ecological oyster restoration (Pogoda et al., 2020). For the Natura 2000 area Borkum Reef ground (Figure 1), located within the historical oyster grounds, Germany is in the process of excluding bottom-contact fisheries under the Common Fishery Policy and the designated MPA's management plan includes large-scale restoration measures for the native European oyster and its associated species community and valuable ecosystem services (BMU, 2019; CBD, 2018; European Parliament, 2013).

From this study, we conclude that present-day environmental conditions in sublittoral offshore waters of the German Bight, allow for the successful reintroduction and sustainable restoration of the European oyster. The deployed and investigated oysters showed (1) high survival, (2) excellent growth and condition, (3) the formation of firmly aggregated oyster clusters, and (4) unexpectedly early reproductive activity within the first year. We further conclude that large-scale restoration measures can be implemented with hatchery-produced seed oysters.

These findings are timely and of high importance as they address current biosecurity risks and limitations of seed oyster availability, as formulated in the Berlin Oyster Recommendation (Pogoda et al., 2019). Furthermore, these findings are not limited to the German North Sea but also applicable to other sublittoral restoration measures of *O. edulis*.

Excellent growth rates can be related to optimal food conditions. If phytoplankton alone provides these optimal conditions, or if detritus may also play a – so far – underestimated role needs further investigation. If oysters in greater water depth benefit from detritus as an additional and reliable food source, similar results can be expected in other sublittoral or offshore areas. The early reproductive activity in the offshore sublittoral may also point to optimal food conditions and to detritus as an additional food source. This provides an important first indication regarding the scale of historical larval productivity of the offshore oyster grounds in the German Bight and is highly promising for achieving self-sustaining populations in the future, but should be confirmed by detailed modelling.

To address these open questions, we recommend: (1) measuring detritus concentration at restoration sites and specific food composition of restored oysters; (2) modelling of *O. edulis* larval drift in the German Bight considering different larval sources; and (3) the installation of a pilot oyster-reef in the field to provide relevant information on prey–predator relationships and the potential effects of sediment properties.

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