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Macrozoobenthos as an indicator of habitat suitability for intertidal seagrass

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ABSTRACT

Seagrass meadows form the foundation of many coastal ecosystems, but are rapidly declining on a global scale. To conserve and restore these key-ecosystems, improved understanding of drivers behind seagrass presence and recovery is needed. Many animals are known to both facilitate and inhibit seagrasses, but biotic factors are still rarely used as indicators of seagrass presence. Hence, we investigate if macrozoobenthos could be used as an indicator for intertidal seagrass (*Zostera marina* and *Zostera noltii*) habitat suitability in the international Wadden Sea. Additionally, we explore if macrozoobenthos can explain the differing seagrass recovery rates that have been observed between the Northern (Denmark and Schleswig Holstein) and Southern (Lower Saxony and Netherlands) regions of the Wadden Sea. To achieve this, we performed a Wadden Sea-wide survey at 36 intertidal locations, across three countries, and investigated the importance of 21 abiotic and biotic variables in explaining the presence and absence of intertidal seagrasses. Seagrass presence or absence could be reliably predicted (prediction error: 16.7%) with a multivariate logistic regression with only four variables; chlorophyll *a*, bivalve, ragworm and mudsnail biomass. We also found higher chlorophyll concentrations and ragworm biomass in the South compared to the Northern Wadden Sea, suggesting that eutrophication and associated community shifts might still inhibit seagrass recovery in the South. Our findings highlight the potential of using macrozoobenthos as indicators for seagrass habitat suitability. In areas, like the Dutch Wadden Sea, where macrozoobenthic surveys are common and where benthic data is readily available, our findings can be used to improve the understanding of seagrass recovery dynamics and the selection of suitable seagrass restoration sites.

1. Introduction

Seagrasses form extensive meadows in coastal areas globally, where they act as ecosystem engineers that modify their environment by attenuating currents and waves, trapping suspended particles, and stabilizing the sediment (Hemminga & Duarte, 2000). Seagrass meadows are among the most productive ecosystems on earth and serve as a key-habitat in the life-cycles of many marine animal species (Heck et al., 2003; Bertelli & Unsworth, 2014). Moreover, due to their habitat-forming qualities, they also provide vital services to humanity, including coastal protection, carbon storage, nurseries for many commercially important fish, and water quality enhancement (Nordlund et al., 2016). At the same time, seagrass meadows are some of the most threatened ecosystems in the world. During the last century, ~29 % of the global seagrass area was lost (Orth et al., 2006; Waycott et al., 2009) and declines are still occurring although the rate of change has decreased since the 2000s (Dunic et al., 2021).

Eutrophication is one of the leading causes for seagrass decline

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worldwide (Waycott et al., 2009). Nutrient enrichment can hamper seagrasses through multiple pathways including light availability reduction and by triggering toxic events (Burkholder et al., 2007; Govers et al., 2014a). Major losses have also been caused by coastal development and destructive fishing practices which can inhibit seagrasses through direct habitat destruction, increased water turbidity, and enhanced sediment dynamics (both erosion and sediment accumulation) (Duarte, 2002). In the future, climate change is also predicted to contribute to further seagrass loss, through increased water temperatures and frequency of extreme climate events (Fraser et al., 2014; Short et al., 2016). Apart from these abiotic stressors, anthropogenic disruption of biotic interactions can also have detrimental effects on seagrass meadows. More specifically, interspecific facilitation, mutualistic interactions, bioturbation and herbivory have all been identified as important drivers controlling seagrass ecosystem functioning (e.g., Maxwell et al., 2016; van der Heide et al., 2012; Fonseca, 2011; Christianen et al., 2014), and the disturbance of these interactions can therefore have strong negative effects on seagrass stability. As a consequence, seagrass losses are often the result of interacting and cumulative abiotic and biotic stressors. For instance, the overexploitation of apex predators in combination with eutrophication has resulted in seagrass losses through trophic cascades (Hughes et al., 2013; Moksnes et al., 2008), and climate extremes have been shown to indirectly cause seagrass losses due to the breakdown of a crucial seagrass-bivalve mutualism (de Fouw et al., 2016).

In the Wadden Sea, seagrasses (*Zostera marina* and *Zostera noltii*) historically covered extensive areas, both in subtidal and intertidal areas. In the 1930s, most of the subtidal meadows vanished from the area due to a wasting disease, caused by the slime-mold *Labyrinthula zosterae* (Wohlenberg, 1935; den Hartog & Polderman, 1975). In the Dutch Wadden Sea, seagrasses were further harmed by the concurrent construction of the Closure Dam ("Afsluitdijk") that reduced light conditions and altered sediment dynamics (Giesen et al.,1990; van der Heide et al., 2007). Intertidal seagrass populations persisted for longer, but eventually nearly disappeared by the 1970–1980s (de Jonge et al., 1993), a trend that has typically been attributed to eutrophication effects (Philippart, 1995; van Katwijk et al., 1999). Lately, intertidal meadows in the northern Wadden Sea (Schleswig-Holstein & Denmark) have shown remarkable recovery highlighted by a 3 to 4x increase in areal extent from 1994 to 2006 (Reise & Kohlus, 2008; Dolch et al., 2013). However, similar recovery of intertidal seagrasses has not been observed in the southern parts of the Wadden Sea. Although seagrasses showed signs of recovery at the start of the 21st century in Lower Saxony, the meadows started to decline again after 2014, while recovery has remained absent in the Dutch Wadden Sea despite improved environmental conditions (Dolch et al., 2017). The exact reasons behind the large regional differences in recovery rates remain unclear (Dolch et al., 2017), but likely result from a combination of multiple stressors.

To aid natural recovery, several seagrass restoration projects have been undertaken in the Dutch Wadden Sea since the 1980s (van Katwijk et al., 2009; Govers et al., 2022). These restoration efforts focused on intertidal areas, since the subtidal Wadden Sea has been considered unsuitable for seagrasses (Floor et al., 2018). However, despite numerous restoration trials, results have thus far mostly been meager (although see Govers et al., 2022) and no self-sufficient intertidal seagrass populations have been restored to date. Similar to global trends (Fraschetti, 2021), reliable identification of suitable restoration sites has proven one of the biggest hurdles hindering successful seagrass restoration in the Dutch Wadden Sea (van Katwijk et al., 2009; Govers et al., 2022). Several seagrass habitat suitability models have been developed for the area (de Jong et al., 2005; Folmer et al., 2016a; Folmer, 2019), but thus far the models have lacked the accuracy needed for field-application (Govers et al., 2022, MLE Gräfnings unpublished data). Determining habitat suitability can be very challenging, as an in-depth understanding of the environmental requirements of target species as well as high-quality spatial data of critical environmental variables is required. Previous research has almost exclusively focused on how abiotic factors (hydrodynamics, nutrient enrichment, sediment dynamics) affect seagrasses, while the potential impact of biotic factors remains largely unexplored. In the Dutch Wadden Sea, macrozoobenthos (defined as the invertebrates living in or on the sediment and retained on a 1 mm^2 sieve) could be a particularly important indicator for seagrass habitat suitability as 1) numerous macrozoobenthos-seagrass interactions have been documented (see Methods) and 2) detailed, multi-year large-scale spatial data are available for macrozoobenthos (SIBES; Bijleveld et al., 2012). Additionally, a shift from sediment stabilizing bivalve beds to high densities of sediment-destabilizing polychaetas has been observed in the intertidal Wadden Sea (Eriksson et al., 2010; Lotze, 2005; Philippart et al., 2007) and these benthic community shifts may have influenced seagrasses and their potential to recover. Yet, before macrozoobenthos can be properly used as an indicator, accurate information is needed about which (if any) species can predict seagrass habitat suitability, and how biotics in combination with abiotics influence seagrass dynamics on a Wadden Sea scale.

Here, we investigated which abiotic and biotic (macrozoobenthos) factors can reliably predict seagrass presence in the intertidal Wadden Sea. We hypothesized that the inclusion of macrozoobenthic data (together with traditionally used abiotic variables) would improve our ability to predict seagrass habitat suitability and offer novel indicators for seagrass presence. The discovery of new indicators might greatly enhance our ability to pinpoint suitable seagrass restoration sites in the intertidal Wadden Sea and thus pave the way for successful restoration projects. The secondary objective of this study is to provide insights as to why seagrass recovery has followed different trajectories in the Northern (Denmark and Schleswig-Holstein) and Southern (Lower Saxony and Netherlands) regions of the Wadden Sea. To achieve our goals (research flow visualized in Fig. S1), we performed a survey along the coast of the international Wadden Sea, during which we collected macrozoobenthos samples and measured abiotic variables commonly used for characterizing coastal habitats. By measuring local conditions over a large scale, we aimed to unravel small scale processes driving Wadden Sea scale seagrass dynamics.

2. Methods

2.1. Study site

The Wadden Sea is a shallow coastal sea that extends from the northwest coast of the Netherlands to the southwest coasts of Denmark. Approximately 50 % of the total area (~8000 km^2) of the Wadden Sea is made up by intertidal mudflats. The extensive intertidal mudflat-system provides a hotspot for migratory birds and marine biodiversity. For its globally unique geological and ecological values the Wadden Sea is listed by UNESCO as a "World Heritage"-site.

2.2. Data collection

All data were collected on the intertidal mudflats in the summer (July– August) of 2018. Sampling sites were semi-randomly selected (some of the sites were known to harbor seagrasses beforehand) and each site was sampled once during low tide. At each site, we recorded the presence or absence of both *Z. marina* and *Z. noltii* by walking three 30 m × 1 m belt transects. At sites where seagrass (*Z. marina* and/or *Z. noltii*) was present, we sampled both inside and outside (>20 m from the seagrass) the seagrass meadow. We sampled outside the meadows, so that seagrass sites could be compared with unvegetated sites (bare sites) without seagrasses affecting the measured variables. In total 36 sites (20 bare and 16 seagrass sites; *uneven design due to semi-random site selection*) were sampled across the whole Wadden Sea (Fig. 1). At each site, we sampled and pooled three replicates of sediment porewater (top 5 cm) and sediment (top 5 cm). Porewater was sampled using Rhizon

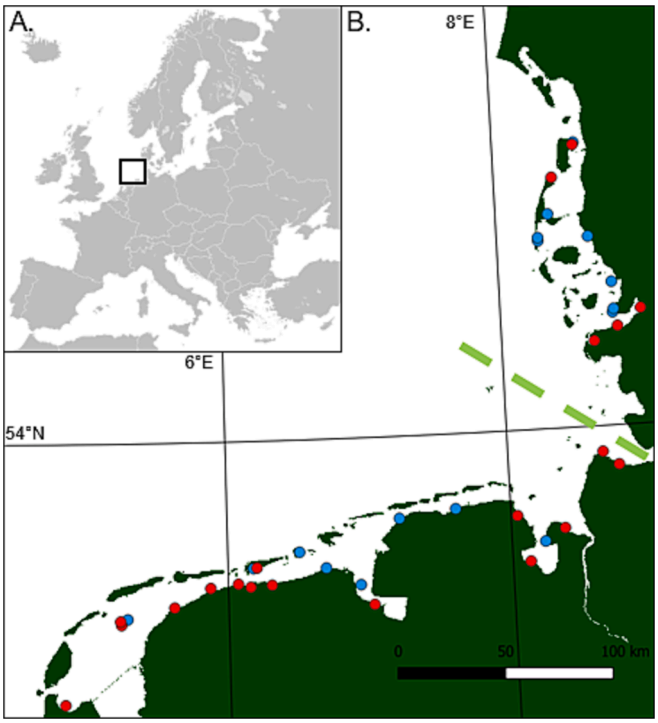

Fig. 1. (A.) Location of the Wadden Sea in North Western Europe, (B.) Locations of survey sites in the Wadden Sea. Red circles indicate bare sites without seagrass presence and blue circles sites with seagrass presence. The striped green line indicates the divide between what we consider South- and North Wadden Sea in this study. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

porewater samplers (Eijkelkamp, the Netherlands), while sediment samples were collected with a core sampler (3 cm diameter, 5 cm depth). The samples were stored under cooled conditions until analysis. Additionally, three macrozoobenthos cores (top 30 cm & 15.5 cm diameter) were sampled. The benthos samples were sieved (1 mm) and pooled, after which the samples were stored in 70 % ethanol until identification.

2.3. Model data

For each survey site, monthly average water clarity (diffuse attenuation coefficient, 2002–2009), sea water velocity at mean bottom depth (2000–2014), carbon phytoplankton biomass at sea surface (2000–2014), chlorophyll *a* concentration (2000–2014) and maximum monthly surface current velocity (2000–2014) were derived from BioORACLE (Tyberghein et al., 2012). All data layers from BioORACLE are available at the same spatial resolution (5 arcmin). Additionally, mean exposure time of tidal flat for each survey site was derived from data computed by Folmer et al. (2016a), (Folmer et al., 2016b). The GeoTIFF raster data set was downloaded from the Dryad Digital Repository 10.5061/dryad.q9c54.2 (Folmer et al., 2016b).

2.4. Sample analysis

Total sulfide concentration in the porewater was measured on the day of sampling in a mixture of 50 % sample and 50 % Sulfide anti-Oxidation Buffer (SAOB) (Lamers et al., 1998), using an ion-specific silver-sulfide electrode (Hanna Instruments). Salinity and pH were measured with a portable meter (Eutech pc 450) for both surface and porewater. In the lab, porewater ammonium, nitrate and orthophosphate concentrations were measured colorimetrically (Bran + Luebbe GmbH - AutoAnalyzer 3). Total inorganic carbon (TIC) in the pore water samples was measured with an infrared carbon analyzer (IRGA; ABB Analytical, Frankfurt, Germany). Sediment samples were freeze-dried, whereafter organic matter content was estimated as weight loss on ignition at 550 °C. Sediment particle size was determined by laser diffraction (Malvern Mastersizer 2000) on freeze-dried samples after sieving (1 mm mesh size). All individuals in the macrozoobenthos samples were counted and identified to the finest taxonomic level possible under a microscope (8–40 × magnification). Once counted and identified, the biomass of individuals of the same species in a sample was determined. Samples were first dried for 48 h at 60 °C in a ventilated stove, after which dry weight was measured. Following this, the samples were incinerated for 5 h at 560 °C and then weighed again to obtain the ash free dry mass (AFDM). The weights of the flesh and shells of bivalves were determined separately if possible. Only data on the flesh weight of bivalves was used for further analysis.

2.5. Macrozoobenthos

In this study, we chose to investigate only benthic organisms that are known to either facilitate or inhibit seagrasses. The polychaeta species, lugworm (*Arenicola marina*) and common ragworm (*Hediste diversicolor*) have been shown to negatively affect seagrasses through their bioturbation activities (Philippart, 1994; Suykerbuyk et al., 2016; Hughes et al., 2000). By bioturbating, these worms can dislocate adult seagrass plants, bury seeds, enhance local eutrophication and destabilize sediments (Govers et al., 2014b; Hughes et al., 2000). Ragworms have additionally been shown to prey on *Zostera marina* seeds (Kwaakernaak et al., 2023). Globally, bivalves are known to both facilitate and inhibit seagrasses (Gagnon et al., 2020; Fales et al., 2020). Facilitation mechanisms include decreasing water turbidity, increasing nutrient availability and stabilizing sediments, while bivalves can inhibit seagrasses e.g., through space competition (Gagnon et al., 2020 and references within). Bivalve-seagrass interactions are very context- and species dependent and as little is currently known about seagrass-bivalve interactions in the intertidal Wadden Sea, we included all bivalve species as a combined group in this study. Epiphyte grazers are commonly accepted as important organisms facilitating seagrass meadows. In the Wadden Sea, at least epifaunal gastropods are known to uptake this trophic role and have been shown to facilitate seagrasses (Philippart, 1995). In this study, only mudsnails (*Peringia ulvae*) were included in our analysis, because the species made up 99.7 % of all Gastropod AFDM.

2.6. Statistical analysis

To get an overview of the relations between all variables included in this study (Table S1), we first performed a standardized principal component analysis (PCA). The PCA only included data from bare sites and from outside the seagrass meadows on sites where seagrass was present. A multiple logistic regression (glm, stats), was performed to investigate how sites with and without seagrass presence differ in abiotic and biotic conditions. The model compared 20 bare-(sites without seagrass presence) and 16 seagrass sites (measurements from outside the actual seagrass meadows). Seagrass sites were represented by measurements from outside the seagrass meadows in order to exclude potential effects of the seagrasses on the measured variables. Before model optimization, we examined whether multicollinearity was present in the dataset and removed stepwise variables with high (>10) variance inflation factor (VIF) until no collinearity was observed between variables included in the model. The logistic regression model was optimized with backwards selection based on AIC (StepAIC). The optimized model was K-fold cross-validated with the 'cv.glm' function (package: boot; Canty and Ripley, 2021).

Furthermore, we used two-way ANOVAs (post hoc: Tukey's HSD) to investigate the effect of Wadden Sea region (Northern and Southern Wadden Sea) and site-type (bare site, outside meadow and inside meadow) on the four variables determined by the logistic regression; chlorophyll *a* concentrations and the AFDM of bivalves, ragworms and

mudsnails (Table 1). Measurements from inside the meadow were included in the analysis to investigate if and how seagrasses affected the variables of interest. However, only data from bare and outside meadow sites were included in the chlorophyll analysis, because the spatial resolution of the data is not accurate enough to compare sampling sites very close to each other (i.e., outside vs inside seagrass). Prior to analysis, data were tested for normality to meet the assumptions of parametric tests. Mudsnail data failed to adhere to normality and homogeneity of variance and was therefore analyzed with a non-parametric Kruskal–Wallis test and followed up with a Dunn's test. However, Dunn's test was not able to detect significant differences between treatments although the overarching model did and we therefore also ran the more liberal Fisher's Least Significant Difference (LSD; i.e., no correction of the significance level) to highlight weaker differences. As it is not possible to test interactions with non-parametric data, we analyzed all six combinations of Site-type*Wadden Sea region separately. All statistical analyses were performed in R version 4.0.3 (R Core Team 2020).

3. Results

The PCA revealed that many of the measured variables correlated with each other (Fig. 2) and proved the need to check for collinearity before proceeding with the logistic regression. The initial logistic regression model was run with 12 variables (Table S1), while the final optimized model consisted of only four variables (Table 1): Chlorophyll *a*, ragworm, bivalve, and mudsnail biomass (AFDM). Higher average chlorophyll concentrations decreased the odds (0.66) for seagrass presence (Fig. 3a). Similarly, common ragworm biomass strongly reduced the odds ratio (0.039) for each gram of AFDM (Fig. 3c). Bivalve biomass was the most significant parameter in the model, with higher biomasses increasing the odds for seagrass presence by 1.47 for each gram of AFDM (Fig. 3a). The common cockle (*Cerastoderma edule*) was the most abundant bivalve and made up 54 % of the total bivalve biomass (Fig. S2). Mudsnail AFDM, although not significant, improved the optimized model's performance. Higher mudsnail biomass improved the odds of seagrass presence (odds ratio: 1.4, Fig. 3d). The model's cross-validation estimate of the prediction error was low (16.7 %), indicating a relatively good ability of the model to predict sites with seagrass presence.

Secondly, we compared the abiotic and biotic differences between the Northern and Southern Wadden Sea based on these indicators. We found that chlorophyll *a* concentrations were 26 % higher in the Southern Wadden Sea (15.4 mg/m^3 ± 1.3 SEM) compared to the North (19.4 mg/m^3 ± 0.9 SEM; $F(1, 32) = 4.70$, $p = 0.038$), while no significant effect was found between the two Site-types (Bare vs Outside meadow; Table 2 & Fig. 4a). Ragworm biomass also differed significantly between the Wadden Sea regions ($F(1, 46) = 7.91$, $p < 0.001$; Table 2 & Fig. 4b), with ragworm biomass being on average over twice as high in the South compared to the Northern Wadden Sea (0.592 g/m^2 ± 0.1 SEM vs 0.209 g/m^2 ± 0.08 SEM). Bivalve AFDM significantly differed between site-types ($F(2, 46) = 7.12$, $p < 0.001$), with bare-sites having significantly smaller bivalve biomass than both outside ($p < 0.05$) and inside seagrass meadows ($p < 0.01$) (Fig. 4c). Bivalve biomass did not differ significantly between inside and outside seagrass meadows or the two Wadden Sea regions. Mudsnail AFDM differed significantly between the six groups (Kruskal-Wallis test; $\chi^2 = 11.7$, $p = 0.039$). However, the initial pairwise-comparison (Dunn's test) was not able to detect significant differences between the groups, but an LSD-based comparison revealed significant ($p < 0.05$) differences between bare sites in the Northern Wadden Sea and three other treatments (inside seagrass meadow Northern and Southern Wadden Sea, outside meadow Southern Wadden Sea; Fig. 4d).

Table 1
Logistic regression results for seagrass presence in the intertidal Wadden Sea. The analysis compares bare mudflats (0) with areas located outside seagrass meadows (1). The cross-validation prediction error of the model is 0.167. The star indicates significance of < 0.05 for *.

Parameter	Unit	Odds Ratio	Confidence Interval (95 %)	*p*
Intercept				0.035*
Chlorophyll *a*	mg/m^3	0.663	0.433–0.881	0.018*
Ragworm AFDM	g/m^2	0.039	0.001–0.543	0.045*
Bivalve AFDM	g/m^2	1.470	1.131–2.154	0.015*
Mudsnail AFDM	g/m^2	1.421	0.968–2.391	0.104

4. Discussion

To improve the conservation and restoration of seagrass meadows, we urgently need to advance our understanding of drivers and stressors that determine seagrass presence and natural recovery. Here, we show that presence or absence of intertidal seagrasses (*Z. marina* and *Z. noltii*) in the international Wadden Sea can, with good confidence, be predicted by long term chlorophyll concentrations (proxy for phytoplankton biomass) and three biotic variables: ragworm, bivalve and mudsnail biomass. Higher chlorophyll concentrations and ragworm biomass negatively affected the odds for seagrass presence, whereas higher bivalve and mudsnail biomass increased the odds for seagrass presence. Although there are many studies that have highlighted the importance of biotic interactions for seagrass ecosystem stability (Maxwell et al., 2016; Valdez et al., 2020), biotic factors have mostly been overlooked as potential indicators for seagrass habitat suitability (Bertelli et al., 2022). However, here we show that inclusion of animal data into habitat suitability studies can offer valuable information about seagrass habitat requirements and potentially explain large scale seagrass dynamics. Our findings can be used to increase the accuracy of suitable restoration site selection, thus improving one of the most important aspects found to enable successful seagrass restoration, both in the Wadden Sea and worldwide (Govers et al., 2022; Bayraktarov et al., 2016; Fraschetti, 2021).

4.1. Lasting impact of eutrophication on seagrass presence

Eutrophication is often regarded as the largest single cause of seagrass declines worldwide (Burkholder et al., 2007; Waycott et al., 2009). In the Wadden Sea, eutrophication has undoubtedly negatively affected seagrasses, with intertidal populations suffering most heavily during the 1970s and 1980s (Philippart, 1995; van Katwijk et al., 1999). Since the 1980s, nutrient inputs and phytoplankton biomass (measured as chlorophyll *a*) have decreased in the entire Wadden Sea, now reaching much lower levels compared to historic highs (van Beusekom et al., 2019). Nevertheless, our analyses link recent (2000–2014) average chlorophyll concentrations directly to seagrass presence in the Wadden Sea. We found that bare sites had, on average, 23 % higher chlorophyll concentrations than seagrass sites in the Wadden Sea. This finding suggests that eutrophication is variable in the Wadden Sea and may still present an important hurdle for seagrass recovery. Although light limitation due to eutrophication is not expected to be a serious problem for intertidal seagrass (van Katwijk et al., 1998; van Katwijk & Hermus, 2000), other eutrophication-related mechanisms, such as increased epiphyte/macroalgae loads or ammonium toxicity might still pose threats (Burkholder et al., 2007; van Katwijk et al., 1997). In addition to immediate negative effects of eutrophication, sediments may also trap and slowly release nutrients on longer time scales, causing a potential lag-effect (Beck et al., 2008; Røy et al., 2008). However, the Wadden Seas regionally different eutrophication situations suggest chlorophyll concentrations may still simply be too high for seagrass recovery, particularly in the Southern parts where nutrient level exceed those observed in the North where seagrass has recovered (van Beusekom et al., 2019).

Eutrophication has also been identified as one of the main causes for benthic community shifts in the Wadden Sea (e.g., Eriksson et al., 2010; Lotze, 2005), which may indirectly have negatively affected intertidal

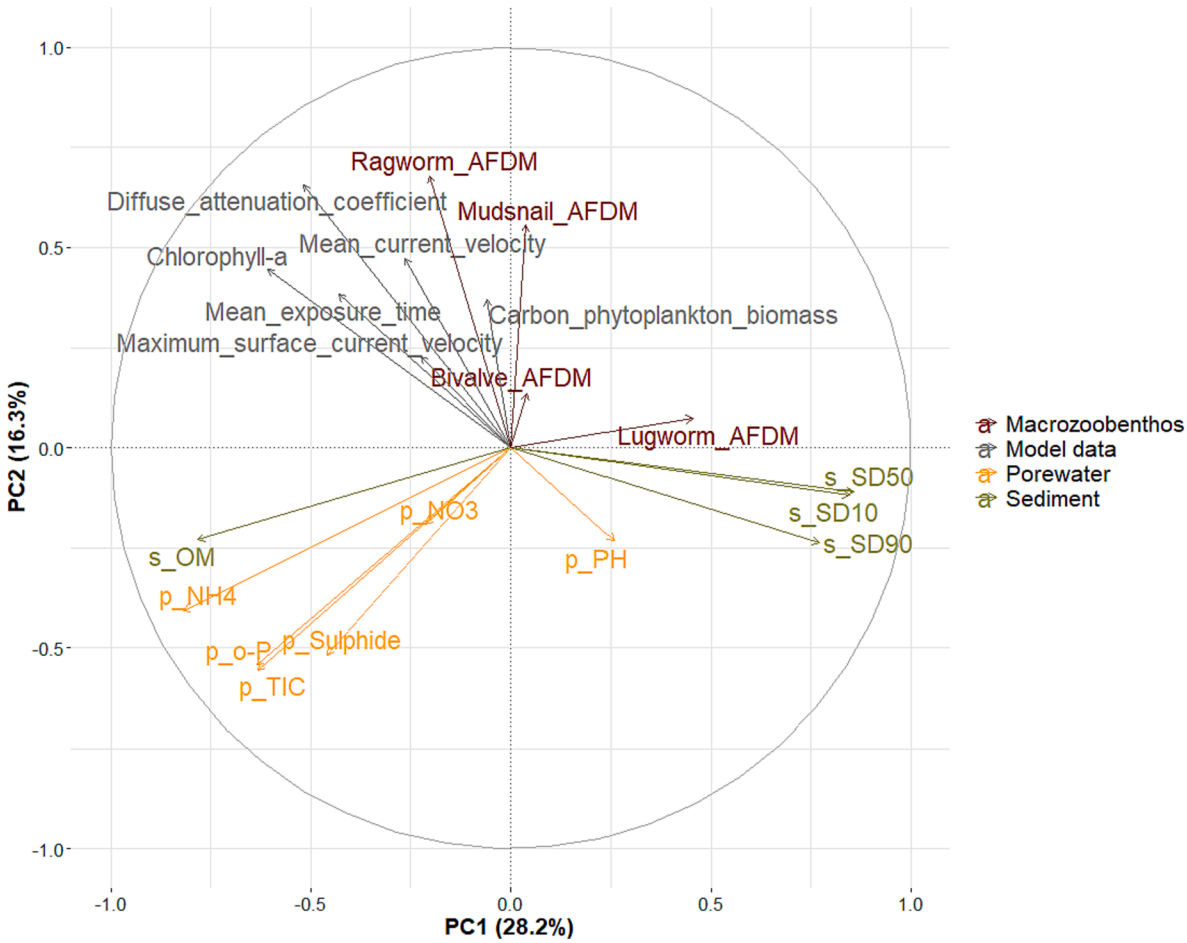

Fig. 2. Results of the PCA showing the relations between all variables examined in this study.

seagrasses. Specifically, polychaetas have been hypothesized to benefit from eutrophication (Lotze, 2005). Although their ratio in benthic communities increased in the whole Wadden Sea during the last decades, their dominance is extra pronounced in the Southern parts (Drent et al., 2017). We found the polychaeta common ragworm (*H. diversicolor*) to negatively affect seagrass presence odds, suggesting that benthic community shifts may in part explain why seagrasses fail to recover in the South. After the eutrophication peaks, macrozoobenthic communities in the Wadden Sea have stabilized (in numbers, biomass and species composition; Drent et al., 2017), hinting at a new community state (Eriksson et al., 2010) detrimental to seagrasses. However, further research is needed to better understand if and how benthic communities affect seagrass recovery.

4.2. Animals as indicators for seagrass presence

Animals have been reported to facilitate seagrasses through mutualistic interactions and trophic cascades (van der Heide et al., 2012; Zhang et al., 2021; Hughes et al., 2013), and inhibit them via bioturbation, uprooting and grazing (e.g., Philippart, 1994; Malyshev & Quijón, 2011; Christianen et al., 2014). Here, we provide evidence that macrozoobenthos can function as an indicator for intertidal seagrass presence, as all three groups identified by our predictive model are known to facilitate or inhibit seagrasses. Ragworms, that reduced seagrass presence odds, can inhibit seagrasses by decreasing sediment stability through bioturbation and by eating seeds/seedlings ragworms could limit seagrass recovery and establishment (Hughes et al., 2000; Kwaakernaak et al., 2023). Grazing mudsnails may benefit seagrasses in nutrient-loaded regions by reducing epiphyte loads. Lastly, although several studies globally have shown beneficial (e.g., enhanced water clarity and increased nutrient availability) and negative impacts (e.g., bioturbation) of bivalve presence, it is still unclear how bivalves, and especially individual species, affect seagrasses in the Wadden Sea. Potentially, intertidal seagrasses can benefit from enhanced water clarity and sediment stabilization provided by the common cockle (*Cerastoderma edule*) (Carss et al., 2020 and references within). Further research is needed to unravel if, when, and which animal-seagrass interactions (especially for bivalve species) can alter seagrass dynamics on a large scale in the intertidal Wadden Sea.

While our study focuses on macrozoobenthos as a potential predictor of seagrass, it does not elaborate if animal-seagrass interactions drive seagrass habitat suitability, or if animals function as indicators due to similar/dissimilar habitat requirements. For instance, high local bivalve biomass might signify undisturbed areas (e.g., less dredging/fishing) or areas with increased sediment stability while high mudsnail biomass might indicate areas with low hydrodynamics (Schanz et al., 2002), which most likely would benefit seagrasses. *In situ* manipulations are needed to determine the extent animal presence has on environmental conditions and habitat suitability. Furthermore, we did not observe a positive effect of seagrasses on the benthic species of interest (Fig. 4), which suggests that the plants and animals have similar habitat requirements, or that seagrass is facilitated/inhibited by the animals, but not vice-versa. Studies have also previously shown that macrozoobenthos has distinct environmental associations in the Dutch Wadden Sea (Compton et al., 2009) and other estuarine systems (e.g., Thrush et al., 2003; Ysebaert and Herman, 2002). Thus, macrozoobenthos data/biotic factors can potentially be used to characterize suitable abiotic conditions for seagrasses and pinpoint suitable restoration sites. This

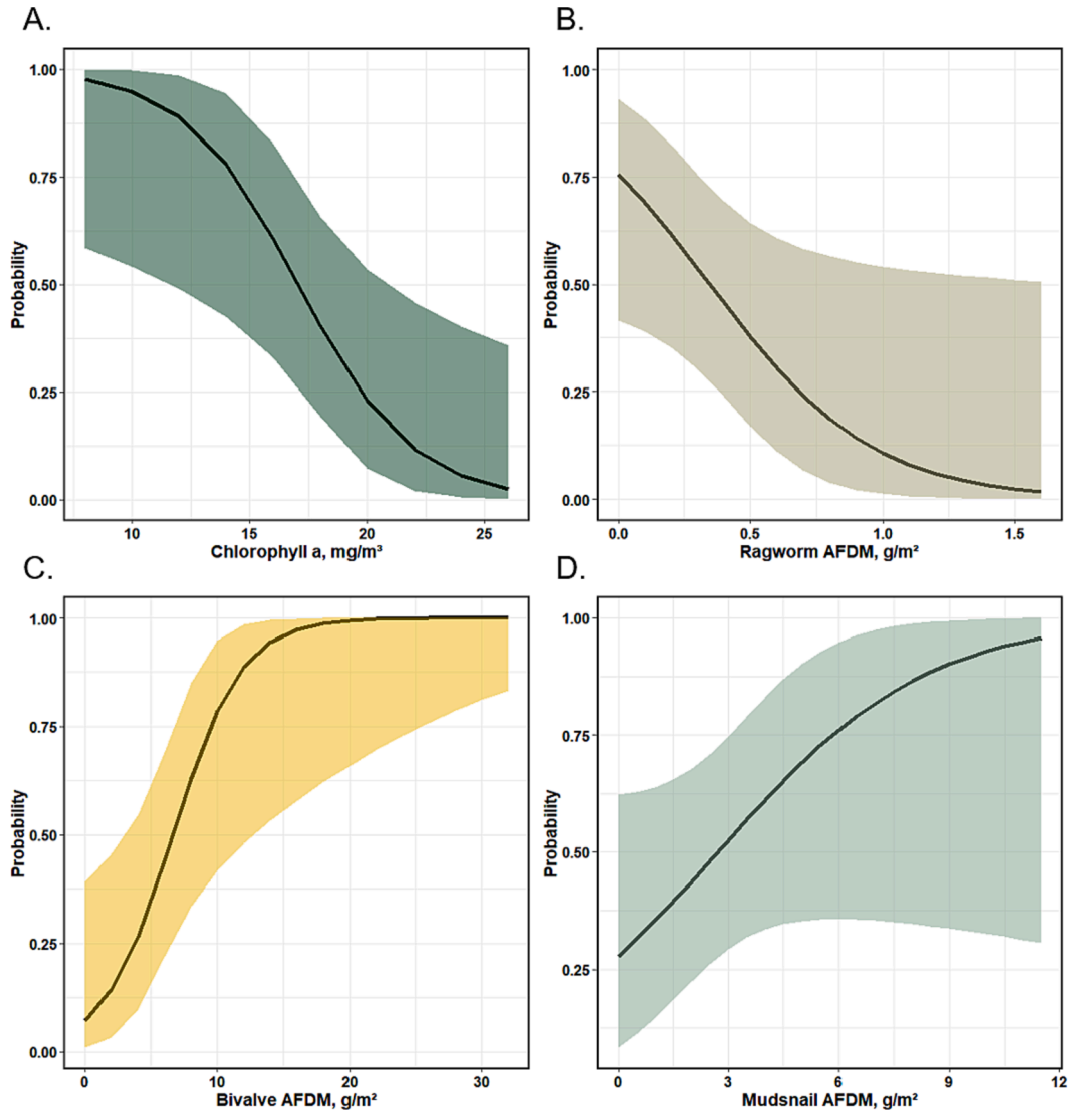

Fig. 3. Regression curves (95 % confidence intervals) for the four variables included in the optimized logistic regression; (A) Chlorophyll *a* (B) Ragworm (*H. diversicolor*) AFDM. (C) Bivalve AFDM (D) Mudsnail (*P. ulvae*) AFDM. 1 = Seagrass site and 0 = Bare site.

Table 2
Results of Two-Way ANOVA models testing Chlorophyll *a*, Bivalve AFDM and ragworm AFDM as a function of Site-type (Bare mudflat, outside seagrass meadow and inside seagrass meadow) and Region (Northern and Southern Wadden Sea). 'Inside seagrass meadow' was not included as a Site-type in the Chlorophyll *a* model. The data of Bivalve AFDM and ragworm AFDM were square root transformed. The stars indicate significance of < 0.001 for ***, <0.01 for**, <0.05 for *.

	Chlorophyll *a*			Ragworm AFDM			Bivalve AFDM		
	SumSQ (*df*)	*F*	*p*	SumSQ (*df*)	*F*	*p*	SumSQ (*df*)	*F*	*p*
Site-type (A)	65.17 (2)	3.80	0.062	0.64 (2)	2.05	0.140	1.37 (2)	7.12	0.002**
Region (B)	80.7 (1)	4.70	0.038*	1.23 (1)	7.91	0.007**	0.08 (1)	0.80	0.377
A × B	0.36 (2)	0.02	0.896	0.58 (2)	1.87	0.167	0.09 (2)	0.47	0.630
Residuals	549.4 (32)			7.17 (46)			4.43 (46)		

would prove especially useful in areas like the Dutch Wadden Sea, where accurate and extensive biotic datasets are already present (SIBES, Bijleveld et al., 2012), thus not requiring high additional investments/sampling campaigns to determine suitable seagrass sites.

4.3. Potential of combining abiotic and biotic variables in habitat suitability models

Surprisingly, no measured abiotic variables functioned as indicators of seagrass presence in this study. For example, sediment sulphide is known to be harmful for seagrasses (e.g., Carlson et al., 1994; Marba et al., 2006) and we therefore expected that high sulphide concentrations would negatively correlate with seagrasses. With that being said, it is important to note that our results do not imply that intertidal seagrasses in the Wadden Sea are only dependent on the predictor variables included in the optimized model. Our results merely show that the variables together are good indicators for intertidal seagrass presence. For instance, the distribution range of intertidal seagrasses is clearly dependent on several abiotic factors, including mudflat elevation and emergence times (desiccation stress, Boese et al., 2005), hydrodynamic

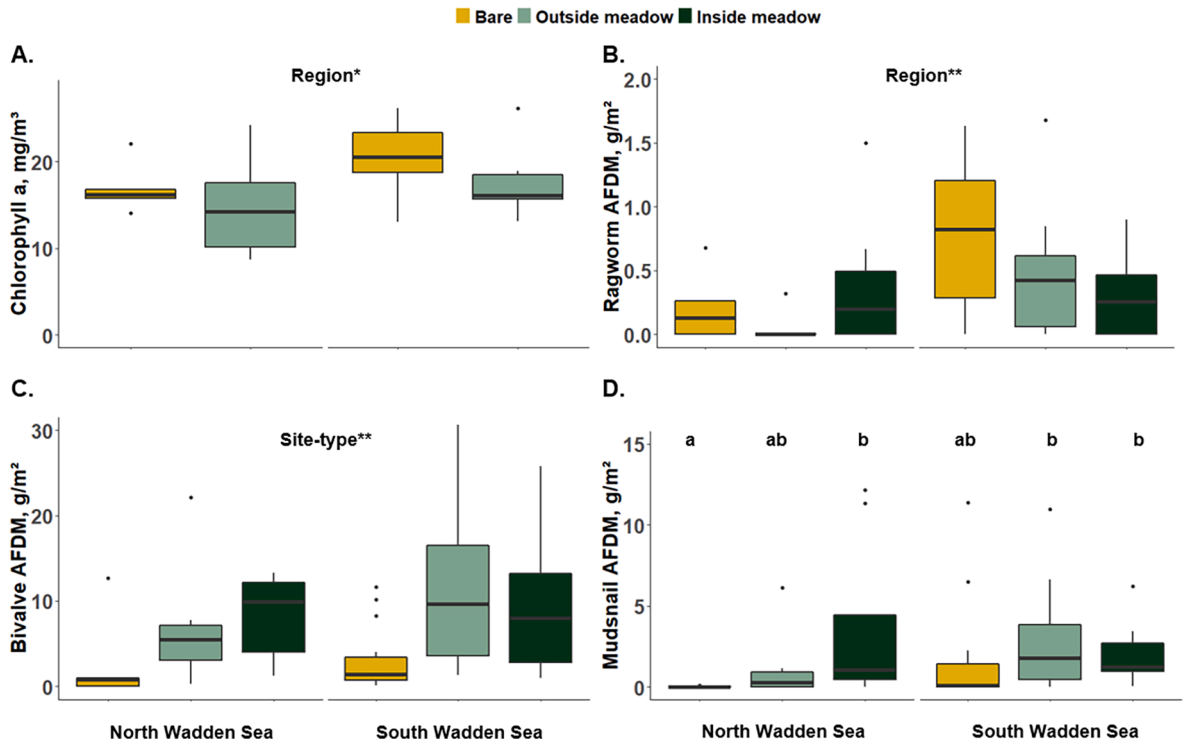

Fig. 4. Differences between site-types and Wadden Sea regions visualized for (A) Chlorophyll *a*, (B) Ragworm (*H. diversicolor*) AFDM, (C) Bivalve AFDM, and (D) Mudsnail (*P. ulvae*) AFDM. Boxplots show median (line in box), upper and lower quartile (box), 1.5 × interquartile range (vertical line) and outliers (circle). Significant variables and significance levels provided. The stars indicate significance of < 0.01 for ** and < 0.05 for *.

stress (Fonseca and Bell, 1998), local nutrient levels (van Katwijk et al., 2010; Dolch et al., 2013) and sediment dynamics (Suykerbuyk et al., 2016). For many of the above-mentioned abiotic factors, data collection on large spatial scales is difficult and expensive, which means that projects often need to rely on modeled data. While modeling is a great way to generate data for complex systems like the intertidal Wadden Sea (e.g., Gräwe, 2016; Baptist et al., 2019), modeled data can generally not match the fine scale spatial resolution of data collected in the field. As modeled abiotic data is well suited for large scale habitat classification (Baptist et al., 2019), while biotic data can potentially offer more accurate information about local (fine scale) processes/conditions, we suggest that future habitat suitability models should combine both abiotic and biotic indicators to reach maximum predictive power and accuracy. An additional benefit of biotic (macrozoobenthic) data is that it holds a temporal dimension, as community compositions at least to some degree depend on historical environmental conditions. In contrast, one-time measurements of traditional abiotic factors usually only offer snapshots of the conditions at the point of measurement and might thus offer less detailed information on small spatial scales.

4.4. Implications for seagrass restoration

Seagrass restoration is challenging in practice (van Katwijk et al., 2016). In addition to suitable restoration sites, practitioners are in need of effective restoration methods and strategies. Seagrass restoration strategies often focus on reducing physical stressors (Bastyan & Cambridge, 2008), while biotic factors are seldom taken into account in restoration projects (Zhang et al., 2018). For instance, abiotic conditions can be ameliorated with establishment structures (Temmink et al., 2020) or by targeting density-dependent feedbacks that ameliorate abiotic conditions (Valdez et al., 2020 and references within). Recently, harnessing biotic interactions in coastal restoration designs has gained attention (Renzi et al., 2019; Valdez et al., 2020). The potential of such strategies has been shown in practice for seagrasses (e.g., Zhang et al., 2021; Meysick et al., 2020), with the incorporation of positive interspecies interactions (facilitation or mutualism) showing promise. Limiting negative biotic factors has also been targeted in seagrass restoration pilots with success, e.g., the suppression of negative bioturbation of lugworms has been targeted in several restoration studies (e.g., Suykerbuyk et al., 2012; Costa et al., 2022). Our results suggest that, next to using biotic variables in predictive habitat suitability models for site selection, incorporation of biotic factors into restoration designs could be an important next step in the Wadden Sea. For instance, avoiding areas with high densities of lugworms or ragworms, while co-transplanting epiphyte grazing mudsnails could increase restoration yields. Moreover, once the positive relationship between bivalves and seagrasses are further elucidated, seagrasses and bivalves can perhaps also be co-restored (as suggested by: Maxwell et al., 2016; Valdez et al., 2020; Gagnon et al., 2020). However, before co-restoration is performed on large scales the animal-seagrass interactions and their co-restoration potential should be investigated with small scale experiments *in situ*.

5. Conclusions

Correctly pinpointing suitable seagrass restoration sites is challenging and one of the largest hurdles hindering successful seagrass restoration efforts worldwide. Our results show that biotic factors (macrozoobenthos in our case) can offer vital information about seagrass habitat suitability and thus potentially aid in the characterization of suitable restoration sites. Previously, biotic factors have been systematically overlooked in seagrass habitat modeling (Bertelli et al., 2022) and we hope that our results will encourage practitioners to incorporate animals better in their habitat suitability models, improving their models and consequent restoration outcomes.

Declaration of Competing Interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Our data has been stored in a data repository (Dataverse.nl) and can be accessed through: https://doi.org/10.34894/ULQALK.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.109948.

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