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Impact of mussel seed fishery on subtidal sediment and macrozoobenthos in the western Wadden Sea

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ABSTRACT

Mussel farming in the Netherlands is traditionally based on bottom culture. Mussel seed is collected in Autumn and Spring from natural stocks and translocated to on-bottom culture plots. Fishery starts in Autumn on beds which are most vulnerable for starfish predation or for being lost during winter storms. In Spring a second fishery takes place. We investigated the impact of seed fishery on sediment characteristics and the macrobenthic communities. A BACI designed experiment was run for 4 years in the subtidal western part of Wadden Sea. Sediment and benthos samples were taken directly before and after the seed fishery. Sampling was repeated for a longer period after fisheries. In this study the data before, directly after and 1–1.5 years after the fishery were analysed. The number of locations studied was less than initially planned. As a result the effect sizes that could be detected were larger than chosen at the start of the study. Yet, our study has shown a potential direct effect on sediment characteristics and the benthic communities. Although the effect was not significant, sediment became coarser and the percentage of clay lower in the fished areas compared to the control areas, and the effects were most pronounced after Spring fisheries. The effect on the number of species was significant, and although the interaction term with season was not significant, we did find a larger decrease in the Impact parts after Autumn fisheries, while after Spring fisheries there was a smaller increase. The short term effects on total density were most pronounced after Spring fisheries: a significant decline in total density in the Impact parts while density increased in the Control parts. Species composition was less similar between Impact and Control parts and was lower after fisheries, for both fishery seasons. After 1–1.5 years, the dissimilarity between the Impact and Control part gradually disappeared. Differences between Impact and Control parts in changes in median grain size and the number of species were no longer visible. For the Spring plots, however, also after 1.5 year, the percentage clay and the total densities were lower in the Impact parts then in the Control parts.

The observed differences are mainly caused by the changes in species associated to mussel beds, and as a consequence of the changes in mussel densities themselves. In conclusion, changes appears to follow the development of the mussel densities, including the effect of fishery on the mussel densities.

1. Introduction

On sedimentary coasts, mussel beds offer habitat for hard substrate epibenthic species, and shelter for many mobile epibenthic species because they form a three dimensional hard substrate structure. Mussels change the sediment characteristics, favouring endobenthic species with a high tolerance for organically enriched sediments. Thus, mussel beds do influence biodiversity by facilitation and inhibition of species and often this results in a higher species richness than the surrounding soft sediment habitat (see e.g. Buschbaum et al., 2009; Cole and McQuaid, 2010; Craeymeersch and Jansen, 2019; Tsuchiya, 2002; Ysebaert et al., 2009).

The mussel production in The Netherlands is traditionally carried out on bottom lease sites in the Wadden Sea and in the Oosterschelde estuary. Mussel spat is collected from natural stocks predominantly in the subtidal parts of the Dutch Wadden Sea and translocated to bottom culture plots within the same estuarine system (Baer et al., 2017; Smaal and Lucas, 2000; Smaal et al., 2021). Mussel seed is dredged in a fishery in Autumn and in Spring, in areas where fishing is permitted (Capelle, 2017). The fishery in Autumn is allowed on the newly formed spat beds

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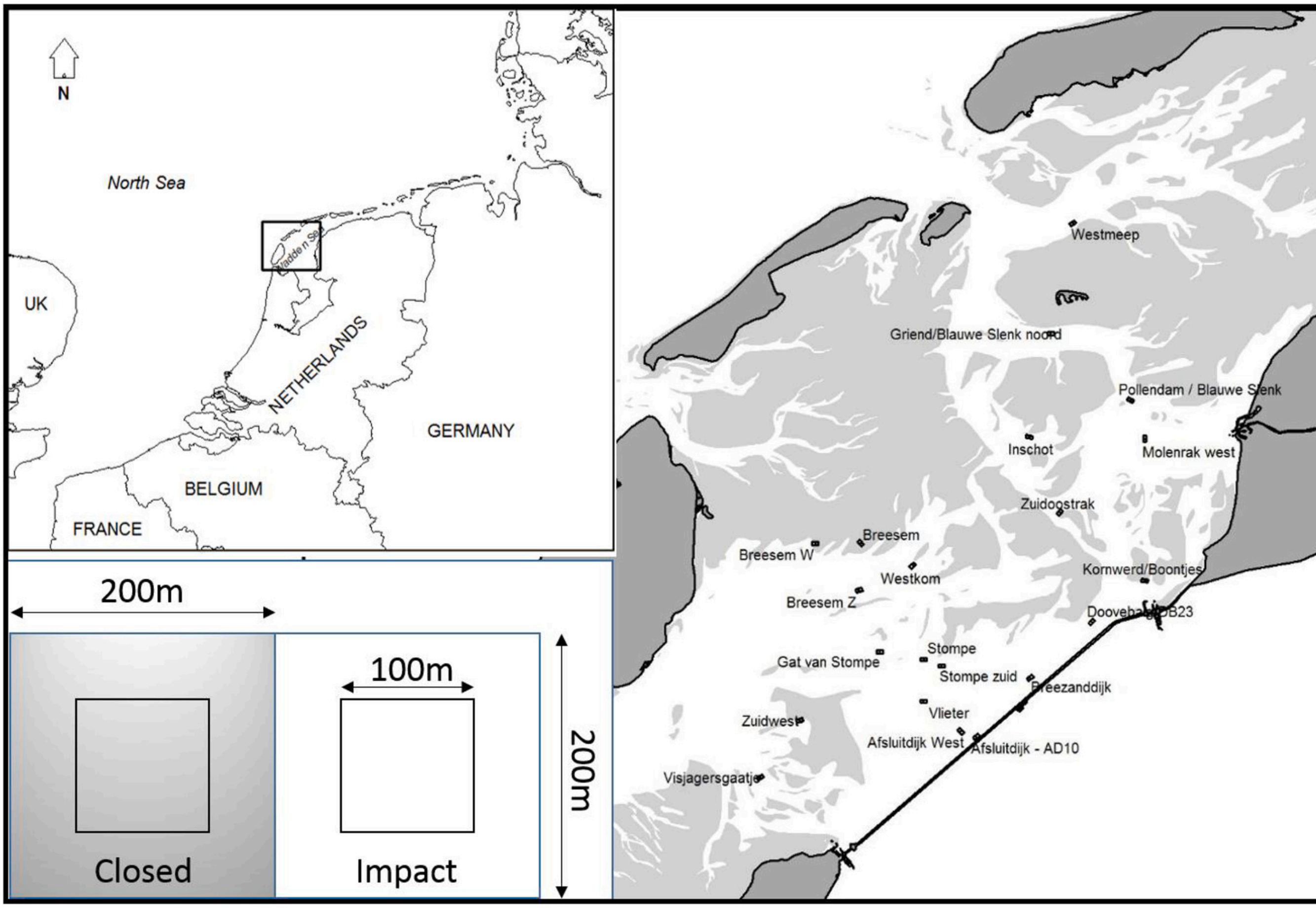

Fig. 1. Map of the western Dutch Wadden Sea with locations used in the study of this project. The setup at each location is shown on the bottom left side. The samples were taken in the 100*100 m center area of the 200*200 m control and impact subplots.

that have a greater chance of disappearing in winter, i.e. in areas that are – based on expert judgement - either more vulnerable for starfish predation or have a high risk of washing away during winter storms (Alterra, 2005; Smaal et al., 2021). In Spring, fishery is allowed on the remaining beds in more stable areas (LNV, 2004). If mussel stocks are still present in sufficient densities in the unstable areas after the winter, seed fisheries in Spring is also practiced in these areas.

Towed bottom-fishing gears are thought to constitute one of the largest global anthropogenic sources of disturbance to the seabed and its biota (Kaiser et al., 2006). The most severe impact is found in biogenic habitats in response to scallop-dredging. In sand habitats, the initial response was most severe with intertidal dredging. The impact of intertidal harvesting is recently confirmed by a new meta-analysis (Clarke et al., 2017). However, impacts are not only depending on the substrate (e.g. biogenic, muddy or sandy sediments) or gear (e.g. related to the disturbance depth) but also on the season of disturbance, the frequency of disturbance and the tidal range, and life history characteristics such as longevity and body size (Clarke et al., 2017; Ferns et al., 2000; Hall and Harding, 1997; Kaiser et al., 2006; Piersma et al., 2001; Tuck et al., 1998; Wijnhoven et al., 2011). This also holds for the recovery time.

Thus, we can expect effects of subtidal mussel seed fisheries. The decreasing mussel biomass will result in a decrease in densities of associated species and a decrease in species richness. Mussel beds accumulate fine sediments and organic material over time (Dankers et al., 2001; Ysebaert et al., 2009). Dredging will bring fine silt in suspension. Tidal currents, then, would move silt away from the fishing site and the original, often a more coarse sediment, is left behind (Hall et al., 1990; Piersma et al., 2001). It is likely that this change in sediment characteristics will also influence the species composition.

The present study investigates the impact of mussel seed fishery in the subtidal western part of the Wadden Sea. A BACI designed experiment was run for 4 years. We describe the effects on sediment characteristics and on the macrobenthic communities shortly after fisheries and 1–1.5 years later.

2. Material and methods

2.1. Study area

The Wadden Sea, stretching for over 500 km along the North Sea coast of Denmark, Germany and the Netherlands, is characterized by tidal flats and a barrier island system with extensive salt marshes. The rich and diverse habitats are important for many species of migratory birds. The Wadden Sea, therefore, now has the status of a protected area for >20 years in all three countries (CWSS, 2017). The ecological status of the Wadden Sea is being described and evaluated in Quality Status Reports (QSR). We refer to the latest online report (https://qsr.waddensea-worldheritage.org/) for a detailed description of the geomorphology, climate, habitats and communities, species, human activities, and pollution of the Wadden Sea. More detailed information on the macrobenthos in the subtidal of the western Wadden Sea in general and the species associated with mussels can be found in Dekker and Drent (2013) and Drent and Dekker (2013).

2.2. Experimental design

For this study a so-called split-plot design was implemented (Ens

Table 1
Number of locations where the macrobenthic infauna and sediment characteristics were studied, in total and for each season, on short-term and mid-term.

	Total	Season	
		Spring	Autumn
Infauna			
Short-term effects	21	6	15
Mid-term effects	12	5	7
Sediment			
Short-term effects	15	6	9
Mid-term effects	12	5	7

et al., 2007), i.e. a blocked experiment with hard-to change factors as whole plot factors (blocks) and easy-to-change factors in subplots (also called split plots) within these blocks (Mbegbu, 2012; Underwood, 1990). A total 40 of research sites was selected in areas with natural mussel seed beds that are relevant for the fisheries sector. Every area was 400 by 200 m, half of which was open for commercial fisheries (further referred as Impact part) and half of which was closed to fisheries (further referred as Control part), based on random selection. Fisheries was allowed around the control sites. Locations were sampled prior to fisheries, and one to several times thereafter.

The locations were not defined a-priori to avoid the high risk of no spat fall in certain areas during the study period. They also could not all be established at the same time because there needed to be enough new spat in each area, which depends on natural spat fall, and this varies from year to year. Therefore, selection was based on the regular seed surveys designed to identify new spat fall (Autumn) and to assess the mussel seed left over after the winter (Spring). On the basis of the seed surveys, the mussel farmers draw up a fishing plan and apply for fishing permits (Smaal et al., 2021). As such, the locations were situated in areas reflecting the real mussel seed fishery situation in the Netherlands.

To identify the impact of fisheries on mussels, all 40 locations were sampled with either a modified suction dredge or a benthic dredge (Smaal et al., 2021). The macrobenthic infauna (as sampled with box-corer; see next chapter) was studied in 21 of the 40 locations (in the period 2006–2010). Samples were taken at least 50 m from the border, within the central 100 by 100 m of each subplot (Fig. 1).

Some of the locations were sampled only once, others were sampled several times (Fig. 1 en 2). Six of them were situated on mussel beds with half grown mussels of year class 2005 (Afsluitdijk west, Breesem, Molenrak west, Stompe, Vlieter, ZuidWest). On these beds seed fishery has taken place in Autumn 2005 and Spring 2006.

At some locations new spat fall events occurred in the years following the time the locations were marked out. In some, therefore, commercial fisheries took place more than once: three were fished twice (Breesem, Zuidwest, Stompe) and one was fished five times (Visjagersgaatje). For these sites, we only included the initial sampling period, prior to new spatfall and subsequent fisheries. Hence, in this manuscript we focus on the impact of a single fishery event. In total, effects of Autumn fisheries was studied at 15 of the 21 stations, effects of Spring fisheries at 6 stations (Table 1).

The fishing activity was checked afterwards based on data on ship movements, registered by an on-board black box. The data showed that most Impact parts where intensively fished. The data also showed that the Control parts of three locations were fished during the study period. These locations (not included in Fig. 1 and Fig. 2) were excluded in the further analyses.

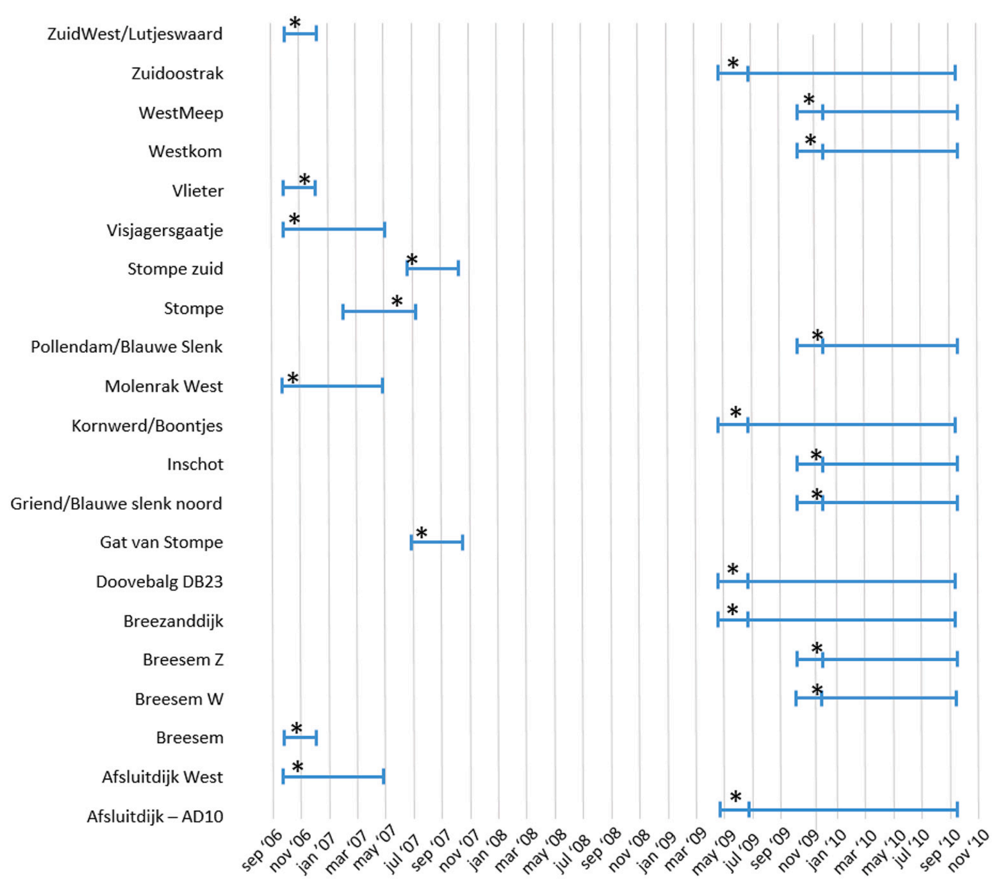

Fig. 2. Period of study (horizontal line) and time of sampling (vertical ticks) at the 21 locations studied. No sediment samples were taken at locations sampled in Autumn 2006. Asterisks indicate the moment of mussel seed fisheries. Due to failing spatfall no sampling was carried out in 2008.

2.3. Benthic sampling, laboratory analysis and data treatment

Most years, 12 samples were collected within the Control (closed for fisheries) and Impact (open for fisheries) parts of each location, except for 2007 when 20 cores were collected, resulting in a total of 1896 samples. All samples were taken within the central 1 ha of both the Impact and Control parts to avoid border effects.

Samples were taken with a box-corer. From each box-core (0.06 m^2), two cylindrical subsamples were taken (diameter of each core: 10.3 cm; total area sampled: 0.01664 m^2). Both subsamples were simultaneously sieved over a 1 mm sieve and samples were fixed in 10% formalin.

In the laboratory the organisms were sorted, identified to species level if possible and counted. As the latter has been done by different laboratories, identifications were checked for differences as the laboratories used different identification keys – moreover, some keys were updated during the study period - or have different opinions on the taxonomy of some species, and not everyone differentiated all species (some laboratories identified taxa as e.g. sea anemones to the species level while others did not). Therefore, some species were lumped to genus or a higher taxonomic level. The original list of 243 taxa was, thereby, reduced to 185 taxa.

2.4. Sediment sampling and grain size analysis

Subsamples of the top 5 cm were taken for grain size analysis within each box-corer taken for benthos, with a 2 cm diameter tube, and stored in poly-ethylene bottles in a − 20 °C freezer. Shortly before further analysis, the subsamples were defrosted. No sediment samples were taken at the 6 locations sampled in Autumn 2006, reducing the number of locations to 15 instead of 21, of which 9 in Autumn and 6 in Spring (Table 1).

In the laboratory, sediment samples were sieved over a mesh size of 2 mm, and treated with HCl and H_2O_2 to remove shell particles and particulate refractory organic matter. The grain size distribution was then determined using a laser diffraction particle size analyser. More information and procedures are described in Compton et al. (2012) and Dekker and Drent (2013).

2.5. Data analyses

2.5.1. Sediment characteristics and univariate benthic indices

In studies on temporal changes of the benthic community, a great variety of benthic indices is used (see e.g. Quintino et al., 2006). In this study, two univariate indices were chosen: temporal changes in total density and in the number of species (S). Hiddink et al. (2020) showed that these are among the most suitable indicators of bottom trawling impacts. Other indices such as evenness and Shannon-Wiener only met few criteria. The calculations were done excluding mussels, to avoid bias in these parameters due to the treatment.

We choose median grain size as a measure for the overall sediment

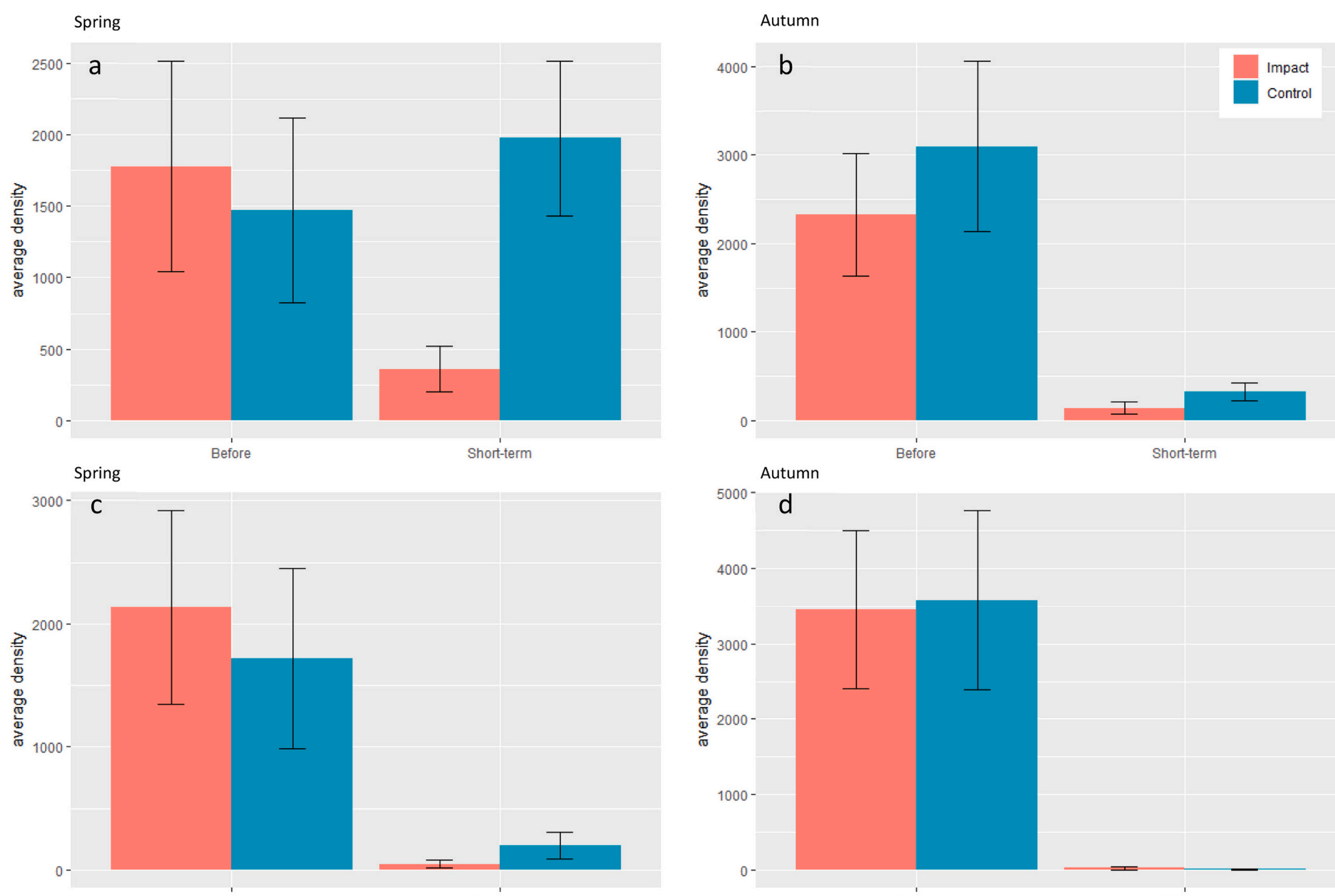

Fig. 3. Bar plots of the changes in mussel density in Impact and Closed parts shortly (Short-term) and 1–1.5 year after fisheries (Mid-term): average density per square meter and standard error of the mean. Distinction is made between fisheries in Spring and Autumn.

composition and volume percentage of grains smaller than 2 μm to reflect the clay fraction.

Temporal changes in these sediment and benthic characteristics were analysed using linear mixed effect models (Pinheiro, 2008), with the *lmer()* function in *lmerTest* package (Kuznetsova et al., 2017). This package provides *p*-values and degrees of freedom for all factors using a Satterthwaite approximation The full data model included two main effects and the interactions. Main effects were fishery season (spring or autumn) and treatment (Control or Impact). The focus of the current study is on the effects of fisheries, sampling location was modelled therefore as a random factor.

The estimation approach of the mixed model would have given the same results as a repeated measures Anova if the design had been balanced. As our setup is not (different number of locations in Spring and Autumn, see Table 1), the F-value for treatment differs from the one we would get with an Anova estimation approach. Linear mixed models accommodate for unbalanced designs (Laird and Ware, 1982; Lindstrom and Bates, 1990; Schielzeth and Nakagawa, 2013; Pinheiro and Bates, 2000).

The analyses were done for short-term effects of fisheries, i.e. shortly after mussel seed fisheries (6 times spring fishery, 15 times autumn fishery), and mid-term effects, i.e. a comparison of the situation before and 1 to 1.5 years after fisheries (5 times spring fishery, 7 times autumn fishery). Long-term effects (>2 years) were not analysed because of the low number of locations sampled with the box-corer for a longer period. The density and biomass of mussels, however, was followed up until no mussels were observed (Smaal et al., 2021).

Differences in changes among treatment and fishery season were visualized with box-and-whisker plots.

2.5.2. Benthic community comparisons

To test for differences between time (Before/After), fishing season (Spring or Autumn) and their interactions permutational multivariate analysis of variance was used (PERMANOVA; Anderson, 2001. The analyses were carried out on the basis of a Bray-Curtis dissimilarity index, quantifying the the distance between the species composition of Control and Impact parts of each location. As for the univariate indices, calculations were done on species density averages per treatment per location. Density data were fourth root transformed to reduce the influence of quantitatively dominant species.

Changes in species composition were visualized using Redundancy Analysis (RDA) and Principal Response Curves (PRC). RDA is the canonical form of principal components analysis (PCA) (Jongman et al., 1987; Legendre and Birks, 2012; ter Braak and Prentice, 1988), and we used *time* and *treatment* as well as the interaction term as explanatory variables. PRC are a special case of RDA (partial Redundancy Analysis) for multivariate responses in repeated observation design (a single factor for *treatment* and a single factor for *time* points in repeated observations). Instead of presenting data in diagrams that are often too cluttered to allow easy interpretation of the changes in treatment effects over time, the principal components of the treatment effects are plotted against time and expressed as deviations from the control treatment. Thus, PRC diagrams are much easier to interpret and visualize much clearer how treatment effects develop over a longer period than standard constrained ordination diagrams. The vertical axis of a PRC diagram contrasts each treatment with the control, expressed as a canonical regression coefficient. Associated with each PRC is a set of species weights, shown on the right side of the PRC diagram. Species' weights denote the relative contributions to the PRC, i.e. the strength of the response of each species. Thus, PRC allows a direct interpretation down to species level: species with high positive weights follow the same pattern as the PRC and are highly affected by the treatment, whereas taxa with negative values behave contrarily to the PRC (den Besten and van den Brink, 2005; van den Brink and Ter Braak, 1998; Van den Brink and Ter Braak, 1999).

As for the univariate indices, analyses were done on short-term and mid-term effects. Analyses were done with and without mussels. Results differed minimal (except for mussels obviously missing in the PRC graphs) and, therefore, results of analyses with mussels are presented. Moreover, PRC graphs are easier interpreted including mussels, as the influence of mussels and their associated species can be seen.

All calculations were performed using R (R Core Team, 2018) and the packages *RODBC* (Ripley and Lapsley, 2017), *lmerTest* (Kuznetsova et al., 2017) and *vegan* (Oksanen et al., 2019).

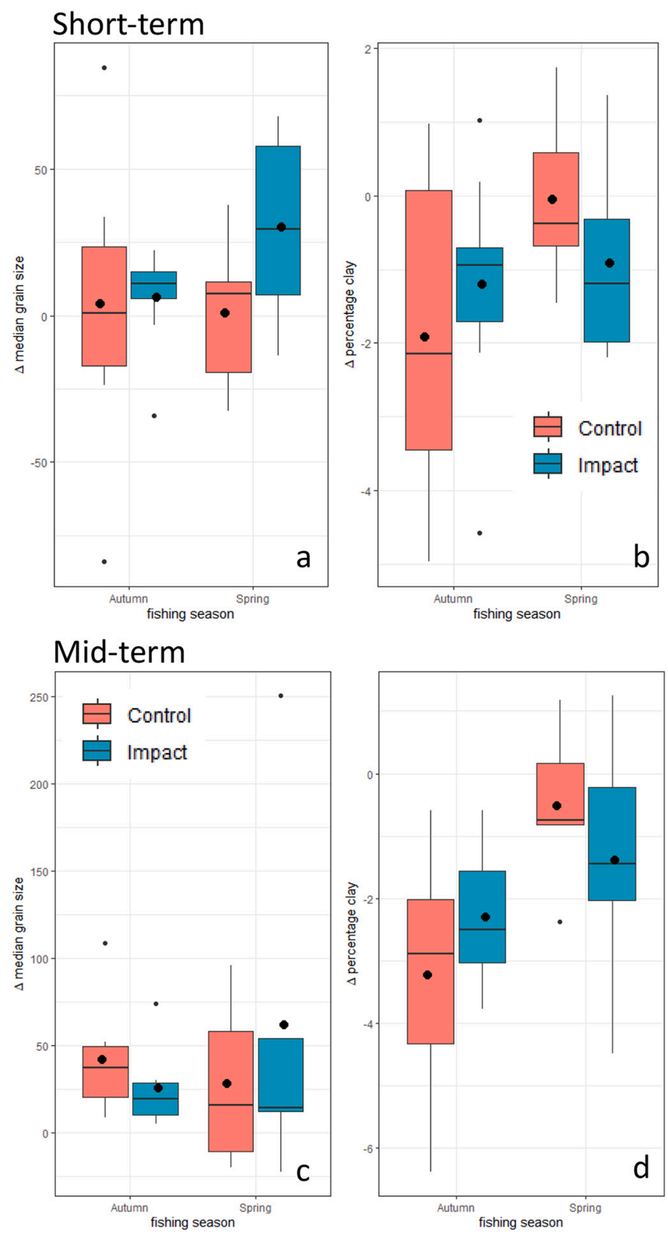

Fig. 4. Box plots of the changes in median grain size (left panels, a and c) and the percentage clay (right panels, b and d) in Impact and Closed parts shortly (Short-term) and 1–1.5 year after fisheries (Mid-term). Distinction is made between fisheries in Spring and Autumn. The lower and upper hinges of the box plot correspond to the first and third quartiles (the 25th and 75th percentiles). The upper whisker extends from the hinge to the largest value no further than 1.5 * IQR from the hinge (where IQR is the inter-quartile range, or distance between the first and third quartiles). The lower whisker extends from the hinge to the smallest value at most 1.5 * IQR of the hinge. Data beyond the end of the whiskers are called "outlying" points and are plotted individually as dots. Mean values are given as black dots.

Table 2
Results of mixed modelling for mid- and short-term effects on changes in median grain size and % clay (. $p < 0.10$ * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$). Degrees of freedom computed using Satterwaite's approximation (NumDF = numerator degrees of freedom; DenDF = denominator df).

Short-term effects						
Median grain size						
	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
Season	622.49	622.49	1	13	0.636	0.4395
Treatment	1753.66	1753.66	1	13	1.7917	0.2037
Season*treatment	1329.29	1329.29	1	13	1.3581	0.2648
Percentage clay						
	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
Season	7.0047	7.0047	1	13	2.5341	0.1354
Treatment	0.0376	0.0376	1	13	0.0136	0.909
Season*treatment	4.386	4.386	1	13	1.5867	0.2299
Mid-term effects						
Median grain size						
	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
Season	250.1	250.1	1	10	0.1459	0.7105
Treatment	433.3	433.3	1	10	0.2528	0.626
Season*treatment	3728	3728	1	10	2.1751	0.171
Percentage clay						
	Sum Sq	Mean S	q NumDF	DenD	F F value	Pr(>F)
Season	4.4315	4.4315	1	10	4.0375	0.07225
Treatment	0.0065	0.0065	1	10	0.0059	0.9402
Season*treatment	4.6953	4.6953	1	10	4.2779	0.06547

3. Results

3.1. Mussel density

At short-term we see a steep decline in mussel density after fishery in Spring (Fig. 3a). In Autumn, on the contrary, mussels disappear both from control and fished parts (Fig. 3b). At a longer term (1–1.5 year), we see no differences between treatments, both after Spring and Autumn fisheries (Fig. 3c and d).

3.2. Sediment characteristics

3.2.1. Short-term effects (before and direct after fishery)

The changes in median grain size as observed direct after the fishery appeared to be larger in the impact parts, especially after Spring fisheries (Fig. 4a). As the differences were positive, median grain size appeared to be higher after fishing than before. The differences were, however, not significant (Table 2).

For the Autumn fisheries, direct after the fishery, the percentage clay appeared to be in general lower than before. This was the case in the Impact as well as in the Control parts (differences are negative). After Spring fisheries, however, the decrease in percentage clay seems to be much higher in the Impact parts than in the Control parts where on average there is not much change (Fig. 4b). As for median grain size, these differences were also not significant (Table 2).

3.2.2. Mid-term effects (before and 1–1.5 years after fishery)

After 1–1.5 years in general the median grain size appeared to be higher than at the start of the experiment (differences mostly positive) (Fig. 4c). For the percentage clay, the pattern is more or less the same as seen at short-term, with a general lower percentage clay at mid-term (differences mostly negative), both in control and impact areas. And, again, after Spring fisheries we see a higher decrease in the Impact parts (Fig. 4d). At mid-term not a single factor was significant, although for percentage clay the interaction was nearly significant (Table 2).

3.3. Macrobenthos

3.3.1. Univariate indices

3.3.1.1. Short-term effects (before vs. short after the mussel seed fisheries). The change in the number of species direct after the fishery was different for the Autumn and Spring fishery (Fig. 5b). For the Autumn fishery, the Control as well as the Impact parts showed a decrease while for the Spring fishery the number of species in general increased. In Autumn the decrease appeared to be larger on the Impact parts than on the Control parts. For the Spring fishery, the increase on the Impact parts appeared to be smaller than on the Control parts, pointing towards a significant fishery effect. There was, however, no significant interaction for the number of species between time and fishing season indicating no significant difference (Table 3).

Direct after Autumn fisheries there was no change in total density (without mussels) (Fig. 5a). After Spring fisheries we noticed an increase in density in the Control parts while the density decreased in the Impact parts. That the change in total density is significantly related to the fishery season is also shown in Table 3.

The most important taxa responsible for the differences in changes in total density after Spring fishery are barnacles (Cirripedia), oligochaetes, and the polychaetes *Polydora cornuta* and *Alitta virens*. The first two show, as mussels, a decline in density in the Impact area (Fig. 6). The two others, on the contrary, show an increase in density in the Control area.

3.3.1.2. Mid-term effects (before vs. 1–1.5 year after the mussel seed fisheries). On the longer term (1–1.5 yr) the densities (without mussels) still show a larger decrease in the Impact parts than on the Control parts, especially after Spring fishery (Fig. 5c). As shown in the box plots, there is much variation between plots. For the changes in density the interaction between time and season was not significant (Table 3). Thus, effects lasting for 1–1.5 year on the total density of macrobenthos, excluding the mussels, could not be demonstrated.

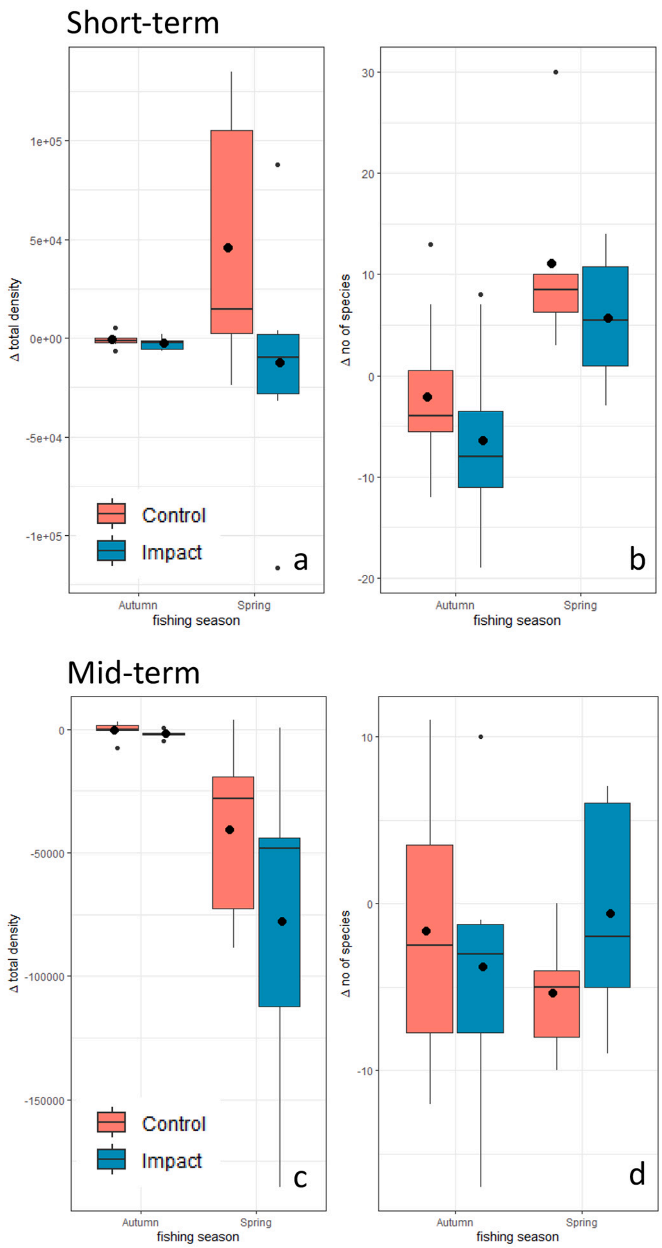

Fig. 5. Box plots of the changes in total density (left panels, a and c) and the number of species (right panels, b and d) in Impact and Closed parts shortly (Short-term) and 1–1.5 year after fisheries (Mid-term). Distinction is made between fisheries in Spring and Autumn. Mean values are given as black dots.

On most locations the number of species (Fig. 5d) at the mid-term was lower than at the start of the experiment (mostly negative differences). For the Spring fishery the decrease seemed to be smaller in the fished parts than in the control parts. Which is contrary to what was expected. However, none of the factors (treatment, season and interaction term) appeared to have a significant effect on the number of species (Table 3).

3.3.2. Benthic community comparisons

3.3.2.1. Short-term effects (before vs. short after the mussel seed fisheries). Community structure before and after fisheries was significantly different, as well as between seasons. There is a significant time:season interaction (Table 4). Fisheries (treatment) did not have a significant effect. Nevertheless, the RDA plots do show that the dissimilarity after fishing was larger than before (Fig. 7), The centroids of the samples taken in impact and control parts were, overall, further apart after fisheries than before, both after Spring and Autumn fisheries. And, consequently, the PRC curves too point to a larger difference in species composition between the Control and the Impact parts after fisheries than before (Fig. 8). This is, above all, due to differences in the densities of species such as *Mytilus edulis*, *Polydora cornuta* and Cirripedia indet. (after Spring fisheries). The absolute values of the weights of these species are the largest and, thus, they are the most important ones explaining the difference in species composition. Moreover, the values are negative. Negative species weights were much higher than positives ones. Thus, it was mainly the changes in density of these species that lead to a higher dissimilarity, *Mytilus edulis* had the lowest canonical coefficient, thus, had the most important contribution to the differences. The density of mussels decreased most in the Impact parts, as did the density of associated species such as *P. cornuta* and barnacles (Cirripedia).

3.3.2.2. Mid-term effects (before and 1–1.5 years after fishery). Mid-term comparison showed the same result as short-term differences in dissimilarity: a significant time:season interaction and no significant effect of fisheries. In contrast to the short-term results, the RDA diagrams showed less dissimilarity between the Control and Impact parts 1–1.5 year after fisheries (Fig. 9). PRC diagrams (not shown here) also showed less deviation at mid-term between Control and Impact.

4. Discussion

4.1. Spatial and temporal fluctuations

Benthic communities are well-known to show spatial differences. At larger scales this is generated by differences in physical processes, at smaller scales biologically generated patterns are important (Herman et al., 1996; Legendre et al., 1997; McArdle et al., 1997; Thrush et al., 1997). Mussel beds too show spatial patterns at different scales, including small-scale variation (Lawrie and McQuaid, 2001; van de Koppel et al., 2005). By calculating averages for the Control and Impact areas on forehand, our models dealt not with such small-scale spatial variation. We do, however, see considerable differences at the location scale: the PRC graphs show a differences in mussel densities and species composition between Control and Impact parts at the start of the study, indicating small-scale variation in species composition. There is also considerable spatial variation between locations, given the variation shown in the boxplots (Fig. 5) and the distance between locations in the ordination graphs (Fig. 7).

Macrobenthic communities are also characterized by large temporal fluctuations, resulting from differences in recruitment success, recruitment patterns and mortality rates (see e.g. Kröncke et al., 2011; Van Hoey et al., 2007). Opportunistic species, such as many members of the polychaete family Spionidae, with short reproductive and recruitment cycles, are periodically very abundant. Almost all areas of this study indeed show significant changes in species composition, irrespective of fishing activities. Some of these changes were large-scale and could be seen at many locations. For instance, high densities of the polychaete *Pygospio elegans*, are recorded in 2009 in most of the locations compared to earlier years.

Thus, to analyse the effect of mussel seed fisheries we have to deal with natural fluctuations in time that often are not parallel from place to place. To cope with these phenomena, a common strategy used to test for environmental impacts is a Before-After Control-Impact (BACI) design (Faith et al., 1991; Pitcher et al., 2009; Underwood, 1992). Non-parallelism (the time*treatment interaction) represents evidence of an environmental impact (Schwarz, 2013). In this study we followed such design.

Table 3
Results of mixed modelling for short- and mid-term effects on changes in total faunal densities and the number of species (.p < 0.10 * p < 0.05 ** p < 0.01 *** p < 0.001).

Short-term effects							
Total density (without mussels)							
	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
Season	5.65E+08	5.65E+08	1	19	1.4094	0.249788	
Treatment	7.74E+09	7.74E+09	1	19	19.305	0.000312	***
Season*treatment	6.89E+09	6.89E+09	1	19	17.1781	0.000551	***
Number of species							
	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
Season	509.5	509.5	1	19	16.1038	0.000744	***
Treatment	197.49	197.49	1	19	6.2419	0.021815	*
Season*treatment	2.44	2.44	1	19	0.0771	0.784319	
Mid-term effects							
Total density (without mussels)							
	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
Season	3.03E+09	3.03E+09	1	10	7.1887	0.02516	*
Treatment	2.03E+09	2.03E+09	1	10	4.8243	0.05566	.
Season*treatment	1.72E+09	1.72E+09	1	10	4.0834	0.07403	.
Number of species							
	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
Season	0.081	0.081	1	10	0.0037	0.9528	
Treatment	9.456	9.456	1	10	0.4302	0.5283	
Season*treatment	66.183	66.183	1	10	3.0111	0.1167	

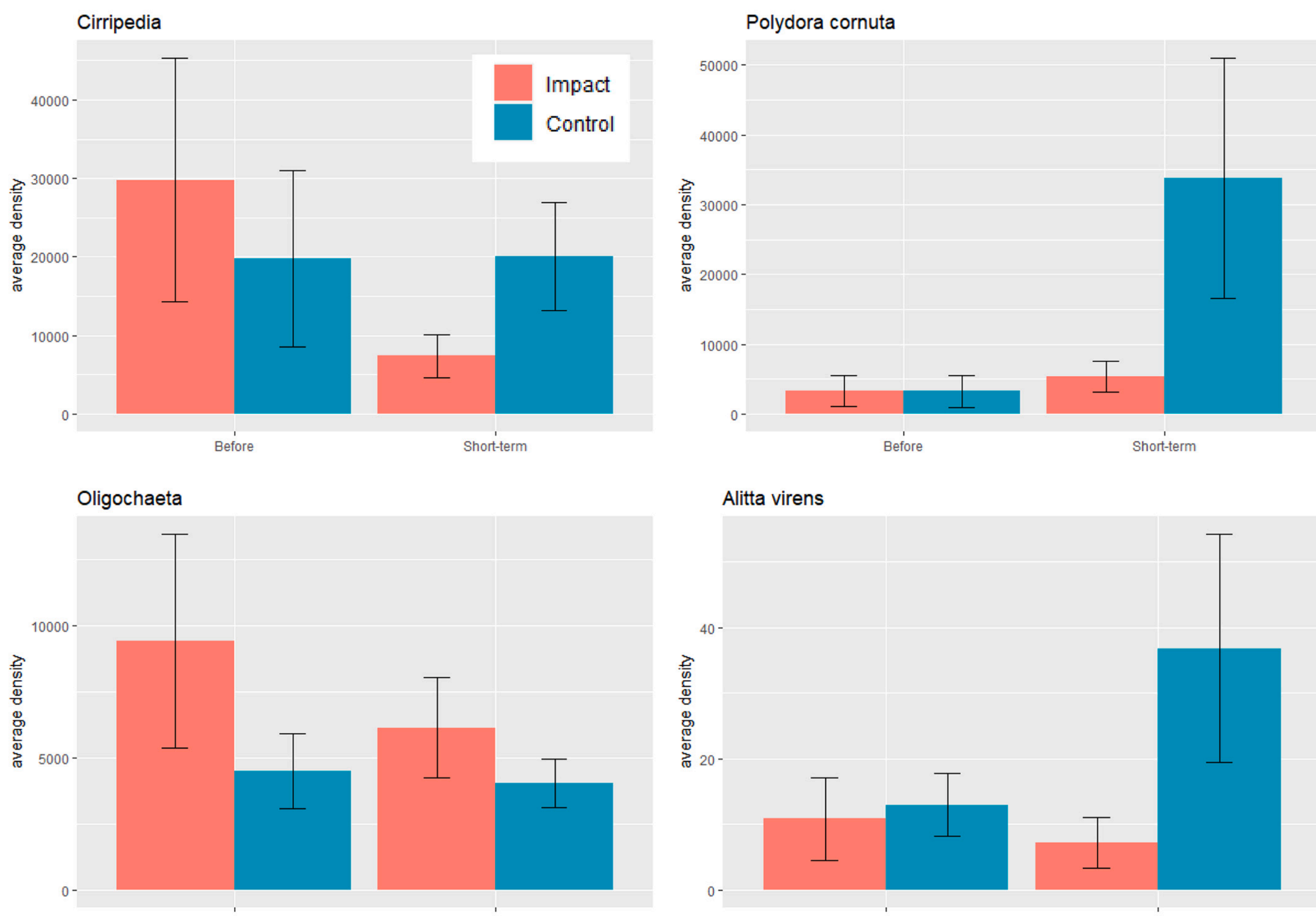

Fig. 6. Bar plots of the changes in the density of taxa responsible for the differences in changes in total density after Spring fisheries in Impact and Closed parts shortly after fisheries: average density per square meter and standard error of the mean. Distinction is made between fisheries in Spring and Autumn.

Table 4
PERMANOVA results for changes in dissimilarities between Impact and Control parts, after fisheries in Spring and Autumn (.p < 0.10 * p < 0.05 ** p < 0.01 *** p < 0.001).

Short-term effects						
	Df	SumOfSqs	R2	F	Pr (>F)	
Treatment	1	0.0961	0.00827	0.7783	0.658	
Time	1	0.2942	0.02531	2.3818	0.01	**
Season	1	1.3923	0.11979	11.2716	0.001	***
Treatment:time	1	0.0667	0.00573	0.5396	0.932	
Treatment:season	1	0.0603	0.00519	0.4886	0.958	
Time:season	1	0.2895	0.02491	2.3441	0.009	**
Treatment:time: season	1	0.0357	0.00307	0.2893	0.997	
Residual	76	9.3876	0.80771			
Total	83	11.6225	1			
Mid-term effects						
	Df	SumOfSqs	R2	F	Pr (>F)	
Treatment	1	0.0468	0.00822	0.4536	0.956	
Time	1	0.7077	0.12428	6.861	0.001	***
Season	1	0.8152	0.14316	7.9029	0.001	***
Treatment:tijdstip	1	0.0098	0.00173	0.0953	1	
Treatment:season	1	0.0448	0.00787	0.4347	0.96	
Time:season	1	0.296	0.05198	2.8693	0.004	**
Treatment:time: season	1	0.0606	0.01064	0.5873	0.868	
Residual	36	3.7134	0.65213			
Total	43	5.6943	1			

4.2. Short term effects

The present study showed that directly after mussel seed fisheries in Spring, changes in the total density of all species besides mussels were significantly different in the Control parts than in the Impact parts: an increase in Control, a decrease in Impact parts. For fisheries in Autumn, no significant differences were found. This was also the case for the mussel densities: no significant difference between control and impact parts in Autumn in contrast to Spring fishery effects. This is in agreement with results based on dredge samples (Smaal et al., 2021). Lower benthos density in the fished parts as we observed in Spring is in accordance with Dolmer et al. (2001) who found 40 days after dredging in Spring lower density in the trawled area.

The modelling did not point to a significant impact of fishery, neither on sediment characteristics nor on the number of species. We did see, however, some indications for an impact. Median grain size values appeared higher after fishing than before. And, in Spring fisheries the decrease in percentage clay seemed to be much higher in the Impact parts than in the Control parts. These differences were statistically not significant, but are in agreement with our expectations. Mussel beds accumulate fine sediments and organic material over time (Dankers et al., 2001; Ysebaert et al., 2009). After fisheries silt is moved away from the fishing sites and a coarser sediment is left behind (Hall et al., 1990; Piersma et al., 2001). In addition, where mussel beds remained, i.e. the Control parts, silt accumulation will further continue. In accordance with the fate of the mussels in Autumn, we did see a decrease in clay percentage after Autumn fisheries on control as well as on impact parts.

We, therefore, also expected an indirect effect on the species composition besides the effect of the removal of mussels. After Autumn fisheries Impact parts showed a substantial decrease in the number of species, but the Control parts showed about the same decrease. This is not surprising. Mussel beds fished in Autumn are considered unstable, due to high risk of starfish predation and/or losses during storm events (Alterra, 2005). A larger decrease in the number of species in the Impact parts compared to the Control parts was only observed in a few plots. These were the plots where the mussel density also showed a larger decrease. Consequently the larger decrease in species diversity can be attributed to the larger decrease of mussels.

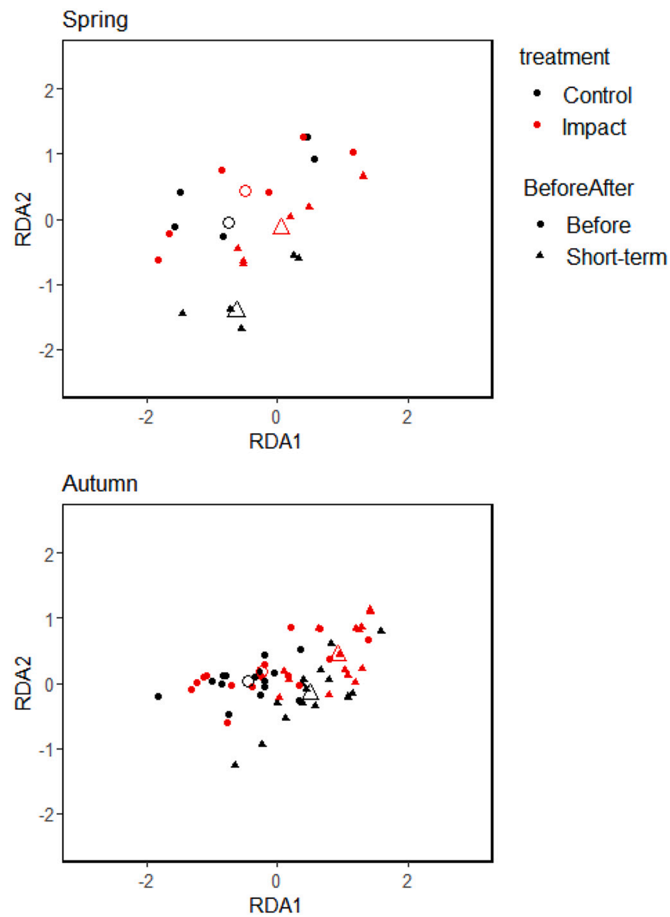

Fig. 7. Short-term effects on species composition. RDA plots showing the ordination of the locations in relation to treatment (Control, Impact) and time (Before, Short-term). For clarity, locations fished in Spring and Autumn are shown in separate diagrams. Centroids of the four groups are shown as larger symbols.

However, after Spring fisheries, we did find differences in community characteristics. Species such as barnacles logically decrease in density as they are attached to mussels. But also other taxa, such as oligochaetes, show lower densities. On the other hand, we also noticed an increase in density of some species (e.g. *P. cornuta*, *A. virens*). These changes resulted in a larger difference in species composition between Control and Impact parts after fisheries than before, although not significantly. The spionid *P. cornuta* showed the most spectacular increase in density. *P. cornuta* is an alien, opportunistic species with a short life cycle. It inhabits mud tubes constructed in the bottom sediment, and female worms produce egg capsules in these mud tubes (Takata et al., 2011). Mussel fishery likely results in a decrease in mud content, destroying the habitat of this species. Indeed, *P. cornuta* considered to be associated with mussels. This is also the case for the other taxa mentioned above (Dolmer et al., 2001; Drent and Dekker, 2013; Markert et al., 2010; Ysebaert et al., 2009; Ricklefs et al., 2020). Thus, the changes could for the largest part be attributed to fisheries, either directly due to lower densities of mussels or indirectly due to changed sediment characteristics.

Directly after the fishery, the changes in the number of species were different between the Impact and Control parts. The number of species is generally higher in Autumn than in Spring (Reiss and Kröncke, 2005; Ysebaert et al., 2003). Thus, we do expect an increase in diversity in the months May–June, an increase we indeed saw in the period between

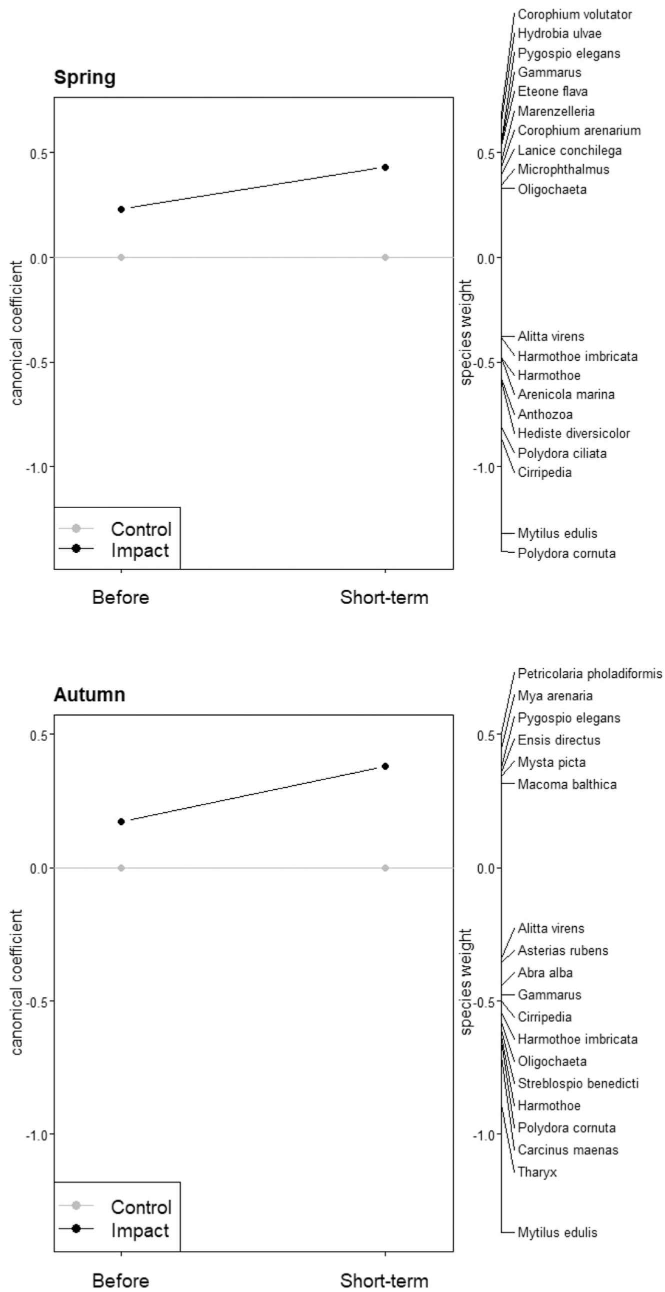

Fig. 8. Short-term effects. Diagram for the first component of the PRC of differences in species composition of the benthic fauna between the control and impact parts of all locations. Separate analyses were done for locations fished in Spring (above) or Autumn (below). The species weights in the right part of the diagram represent the affinity of species with the response shown in the diagram. Only species with an absolute weight larger than 0.3 are shown.

sampling before and soon after fisheries in Spring. However, the increase was smaller in the Impact parts compared to the Control parts. In Autumn, we found a larger decrease in the Impact parts. Again, the observed changes are mainly caused by species associated to mussel beds and consequently related to the changes in mussel densities themselves. So, in general, the decline in mussel densities in the fished and unfished parts was about the same and statistically not different (Smaal et al., 2021). In those plots where the decline was larger in the Impact parts, this went along with a larger decline in diversity.

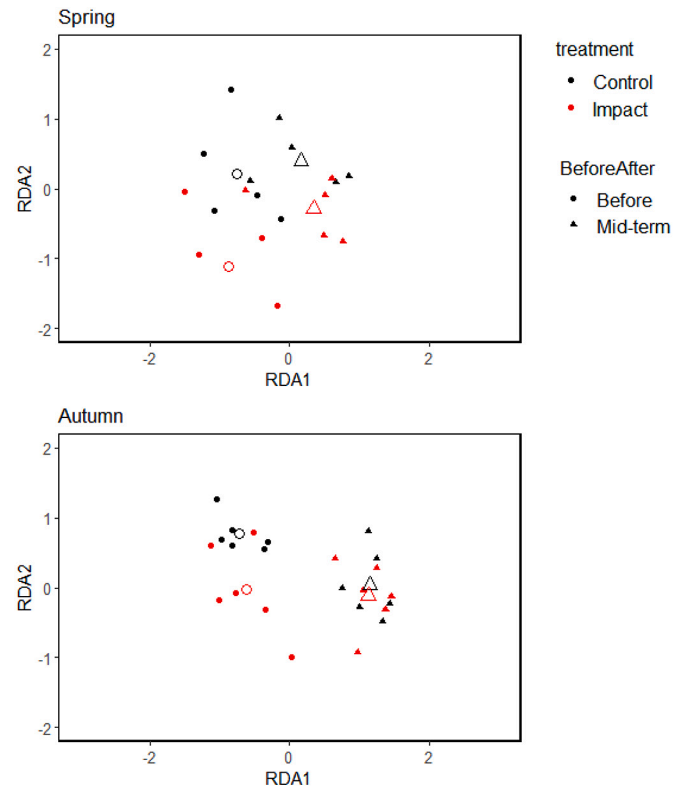

Fig. 9. Mid-term effects on species composition. RDA plots showing the ordination of the locations in relation to treatment (Control, Impact) and time (Before, Mid-term). For clarity, locations fished in Spring and Autumn are shown in separate diagrams. Centroids of the four groups are shown as larger symbols.

4.3. Effects after 1–1.5 years

In Spring, the effect of fishing is visible on the mussel stock dynamics both directly after fishery as well as in the subsequent two years, in contrast to Autumn fisheries where mussel stocks decline faster, independent of the treatment (Smaal et al., 2021). This is reflected in the sediment and biotic characteristics, although the changes are not statistically different. After fisheries, the decrease of the clay percentage is higher in the areas fished in Spring compared to Control parts, as recorded shortly after fisheries. And, especially in Spring, the results indicate a non significant but larger decrease in density in the Impact parts. On the other hand, differences in changes in median grain size were no longer observed. Sediment was coarser in both control and impact areas. There is neither any indication anymore on differences in the changes in number of species or similarity in species composition. Negative effects at mid-term might not have been seen because of recolonization by mobile species. Locations were situated within larger dredged areas, hence any recolonization of the Impact parts should have come from the Control parts. The distance between the exact sampling points and the border of the Impact part was between 50 and 75 m. As discussed for a BACI study on cockle fisheries (Wijnhoven et al., 2011), recolonization of non-target species within the Impact areas from the surrounding dredged area as well as from the Closed areas was very unlikely given the small area not fished compared to the total area dredged. Moreover, negative effects in the short term observed in our study were mainly found for species associated with mussels, mainly sessile organism such as barnacles (Cirripedia) and the tube-building polychaete *Polydora cornuta*. We therefore conclude that after 1–1.5 years we did not find negative impacts of fisheries anymore on the various parameters addressed in this study.

4.4. Long-term effects of mussel seed fisheries

Longevity of subtidal mussel beds depends on natural factors such as eutrophication, severe winters, failing recruitment, storm damage and predation (Reise and Buschbaum, 2017; Smaal et al., 2021). It has further been suggested that fishery might have resulted in a decline of the longevity of subtidal mussel beds, and in a loss of biodiversity (Buhs and Reise, 1997; Reise and Buschbaum, 2017). These authors recommended to carry out control-impact studies to mark out effects of fisheries and other factors. In this study mussel seed fishery impacts have explicitly been addressed in comparison with natural loss, and it has been demonstrated that the development of subtidal mussel beds in the western Wadden Sea had a limited time-span, also in the absence of fishery (Smaal et al., 2021).

Mussel seed fishery does not result in the total removal of mussels in the fished beds. On average Autumn fishery results in a 75% decrease in mussel biomass, Spring fishery on average in a 77% decrease (Smaal et al., 2021). Seed fishery seems not to influence the life expectancy of the beds; it is noticed that the observed maximum longevity of sublittoral beds was not >7 years, also in the absence of fishery (Smaal et al., 2021). These decreased densities are still high enough to allow mussel beds to develop to adult beds. On the mussel bed with a longevity of 7 years (Gat van Stompe) the highest biomass was finally found on the Impact part (Smaal et al., 2021). Mostly life span of subtidal mussels is much shorter, on average 2.3 years once they survived the first winter (Troost et al., 2022).

It is likely that associated species abundances will decrease with decreasing mussel biomass, which is happening when beds gradually disappear due to natural factors. Also small patches of mussels have a large influence on the associated fauna, and the number of species present (Norling and Kautsky, 2008). However, external factors such as storms and predation by starfish can result in a complete removal of mussel beds and, consequently, the associated fauna. At one of the locations in our study (Afsluitdijk West) there were still mussels 3 years after spat fall. Associated species such as *Alitta succinea* and *Polydora cornuta* were most abundant in the Control part. PRC analyses of all locations separately (Craeymeersch et al., 2013) showed that at all but 3 stations the percentage variance explained by time was larger than that explained by treatment regime. This is in agreement with Hoffmann and Dolmer (2000). Their investigations showed no long-term effects of mussel dredging on the distribution of fish and epibenthic invertebrates, and the closed area appeared to have no significant influence on the epibenthic fauna, again suggesting that other factors than mussel dredging determine the observed spatial and temporal variability of the ecosystem.

Our study took place in the western Wadden Sea, an area characterized by strong natural dynamics. In such areas, trawl and natural disturbance affect benthic communities in similar ways (van Denderen et al., 2015) and, consequently, the adverse effects of fisheries may be limited (Rijnsdorp et al., 2018) and difficult to assess. Moreover, sediment and macrobenthos was studied in less locations than initially planned. A maximum of 21 locations were sampled for macrofauna, 14 locations for sediment composition, divided over Spring and Autumn fisheries. Therefore, the detectable effect sizes are larger than chosen at the start of the study (power of 80% and significance level of 0.05 for a detectable effect size of 10%). In a large-scale survey in the western Wadden Sea in 1981, the number of species was found to range between 0 and 20, with a standard deviation of 4. The number of locations required to detect a difference of 10% in the number of species, given α set to 0.05 and β set to 0.20, was estimated as 32. Given the lower number of sampling stations, the effect size below which we cannot precisely distinguish the effect from zero is larger than 2. In fact, with 21 locations (short-term) the detectable effect size increases to 2.5, with 12 locations (mid-term) to 3.3 (16.5% of the range). Moreover, when divided over season, the minimum number of locations sampled was 5 (Spring, Autumn fisheries), which means an effect size of 25%. Moreover, the variation among location is relatively large too (Fig. 5), resulting in large confidence intervals. Thus, finding no significant results on the mid-term might be due to both a large detectable effect size and large confidence intervals. This most likely also holds for other indices, leading to not significant effects or to marginal effects, i.e. with *p*-values between 0.05 and 0.10 (e.g. mid-term effects on total density).

In conclusion, this study has shown a potential direct effect on sediment characteristics and the benthic communities. Although the effect was not significant, sediment became coarser and the percentage of clay lower in the fished areas compared to the control areas, and the effects were most pronounced after Spring fisheries in the more stable mussel beds. The effect of fisheries on the number of species was significant, and although the interaction term was not significant, we did find a larger decrease in the Impact parts after Autumn fisheries, while after Spring fisheries there was a smaller increase. The short term effects on total density were most pronounced after Spring fisheries: a decline in total density in the Impact parts while density increased in the Control parts. The similarity in species composition between Impact and Control parts was lower after fisheries, for both fishery seasons, and could be attributed to lower densities of mussels and associated species. On the longer term, after 1–1.5 years, the dissimilarity between the Impact and Control part gradually disappeared. Differences between Impact and Control parts in changes in median grain size and the number of species were no longer visible. For the Spring plots, however, also after 1.5 year, the percentage clay and the total densities were lower in the Impact parts as in the Control parts, where also the mussel densities were still relatively high.

As this study shows, fishing leads to a reduction in the mussel biomass in the shorter term. In the somewhat longer term (> 1.5 years) this effect disappear as a result of the natural conditions on each site (risk of storm damage, predation, recruitment success) that determine the further development of the mussel densities. Changes in sediment and benthic community characteristics follow the developments of the mussel densities.

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

Data will be made available on request.

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