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The impact of mussel seed fishery on the dynamics of wild subtidal mussel beds in the western Wadden Sea, The Netherlands

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ABSTRACT

For the cultivation of mussels, wild stocks of juveniles are harvested to collect mussel seed as starting material for the culture. These wild stocks are found in the sublittoral western Wadden Sea (NL). After summer spat fall, fisheries in Autumn on newly formed beds is carried out in areas that have the risk of washing away due to storms, or are vulnerable for starfish predation. These wild beds are considered as relatively unstable. On remaining more stable wild beds, seed fishery is carried out in next Spring. As the Wadden Sea is a nature conservation area, mussel seed fisheries is only allowed if no negative impacts on the nature management objectives can be expected. Seed fishery impacts were addressed in an extensive study including effects on sediment composition, macrobenthos and epifauna. In this paper we describe the effects of mussel seed fisheries on the development of the mussel stocks with and without fisheries in 39 pairwise studied impact and control plots.

Stocks on seed beds in areas of the sublittoral Western Wadden Sea that are known as unstable, show a large decline within one year after settlement, also when there is no seed fishery. Harvesting seed on more stable beds in Spring results in a statistical significant reduction in stock size, which lasts for a period of two years after the first fishery. For the longer term, there is a gradual decline of the mussel stocks on all studied plots. On three out of the 39 plots, mussel biomass showed a large increase, both on control and impact parts. Also these mussel beds declined and eventually disappeared. A difference in life expectancy of fished and unfished beds was not demonstrated.

It is concluded that sublittoral beds gradually disappear, also without fisheries. As a consequence, new recruitment is of critical importance for the long-term survival of sublittoral mussel beds. As we found no significant difference between recruitment on fished and control parts, there are no indications for negative impacts of seed fishery on new recruitment.

1. Introduction

Bivalve shellfish culture is an extensive type of aquaculture. There is no addition of feed or medicine, culture is carried out in the natural environment and in the traditional culture, the juveniles are collected from the environment. For mussel bottom culture, juveniles - called seed - are fished from wild beds and transplanted to culture sites. Seed fishery is done with mussel dredges that are towed across the bottom on wild mussel beds. The dredges are constructed in such a way that the mussels are caught in the dredge, while the underlying sediment remains intact. It can be questioned in how far this type of fisheries disturbs the bottom in such a way that it is detrimental to flora and fauna, to the development of the mussel beds and to the quality of the area for new recruitment (Dolmer et al., 2001; Dolmer, 2002; Ysebaert et al., 2009). Also, harvesting seed from wild beds may limit food availability in the area for higher trophic levels, such as foraging birds. According to Kaiser et al., 2006, towed bottom-fishing gears are thought to constitute one of the largest global anthropogenic sources of disturbance to the seabed and its biota (see also Hiddink et al., 2017). In a recent meta-analysis, Clarke et al., 2017, reviewed the effects of various types of intertidal invertebrate harvesting. Their study focused on benthic infauna fishery such as clams and cockles. Impact studies of mussel seed fishery in intertidal areas have shown effects of harvesting on the target species stock and subsequent limitation in food availability for foraging birds

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(Beukema, 1993; Nehls et al., 1997; Herlyn and Millat, 2000; Ens, 2006). Although some papers report about the impact of subtidal mussel fishery (Buhs and Reise, 1997; Dolmer et al., 1999; Saurel et al., 2004), to our knowledge no control – impact studies have been published about the effects of seed fisheries on subtidal wild mussel beds.

The Wadden Sea is a protected nature conservation area under the Natura 2000 regulations. Mussel seed fisheries is only allowed if no unacceptable negative impacts on the environment can be expected. Hence, knowledge is required about seed fishery impacts, in relation to the natural dynamics of wild subtidal seed beds. Therefore a study has been conducted in the western Wadden Sea (Smaal et al., 2013), addressing the effects on sediment composition, macrobenthos and epifauna (Craeymeersch et al., 2020), the role of starfish predation on seed bed dynamics (Auguëra, 2015), and the characteristics in terms of species composition and abundance of wild mussel beds, mussel culture plots, and other benthic habitats in the area (Waser et al., 2020).

In our study, we address the effects of mussel seed fishery on the mussel stock dynamics. The mussel seed fishery was carried out by the mussel farmers as part of their normal practice. This practice is based on successful recruitment of mussel seed, forming natural beds over summer. Recruitment is quantified by stock assessments (so called seed surveys) prior to fisheries. If the stock size allows profitable fisheries, a fishing plan and a request for a fishing permit, including an appropriate assessment in the framework of the nature conservation law, are drawn up. Fisheries is done in Autumn (September – October) and in next Spring (April - May). The Autumn fishery is carried out on newly formed beds in areas with a high risk of washing away due to storms, as well as in areas that are vulnerable for starfish predation. In the other areas with wild beds, seed fishery is carried out in the more stable beds in next Spring. 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. Fisheries on the wild beds can be repeated in the following fishery period i.e. Autumn and Spring, if sufficient (half-grown) mussels are still present. This practice of mussel seed fisheries has been debated and was subject to court cases after an appeal of Nature Conservation Organisations. In 2008 the State Court rejected the fishing permits that were issued by the government, because knowledge gaps did not allow the conclusion that mussel seed fishery had no significant impact on the maintenance goals of the Wadden Sea natural values. After a period of heated public debate an agreement was achieved between the government, nature conservation organisations and the producers organisation of the Dutch mussel culture (PRW, 2010). Parties agreed in a common approach to protect the natural values of the Wadden Sea by a stepwise reduction of bottom seed fisheries. Meanwhile alternative seed resources would be developed to maintain sufficient seed supply for an economically viable mussel bottom culture (Baer et al., 2017). As alternative source seed mussel collectors that are suspended in the water column, as introduced in 2006, appeared to be most promising (Kamermans et al., 2002).

In this paper we describe the effects of mussel seed fisheries on the dynamics of the subtidal mussel population. This is focused on the development of stock and recruitment in relation to fisheries. Following a beyond BACI design, mussel biomass and density were measured before and after fisheries in 40 fished and control plots. The fate of the stocks was monitored on the plots for a period of at maximum 8 years. We address the following research questions: (i) what is the short and long term impact of mussel seed fisheries on the development of the mussel stocks, and (ii) has fisheries an impact on future recruitment in the fished areas ?

2. Material and methods

2.1. Characteristics of the study area

The Wadden Sea is a shallow estuarine area in the north of the Netherlands, extending to Germany and Denmark, the Dutch part covers about 2500 km2 (of a total area of 8000 km2), with half of the area consisting of tidal flats and a tidal range between 1.4 m and 3.4 m (see CWSS, 2017 for an extensive description of the area). The Wadden Sea borders with the North Sea divided by a range of small barrier islands and connected through tidal inlet channels. The bulk of the water flux is provided by ebb and flood tides through the narrow and deep inlet channels, from there the water is distributed into the Wadden Sea through an extensive system of branching gullies. Since 1932 the western Wadden Sea is separated from the former Zuiderzee, now the freshwater lake IJssel, by a dam of 32 km, the 'Afsluitdijk'. This dike has two sluices for freshwater discharge. Salinity shows a strong gradient from the tidal inlets (about 30 ppm) towards lake IJssel, (about 15 ppm). The western Wadden Sea is a dynamic area where constant changes occur in the morphology of channels, tidal flats and sediment composition. In the area there are wild intertidal and subtidal mussel beds. The subtidal beds extend to a depth of 15 m below low water. Since 2004, mussel seed fishery is only allowed on subtidal beds. (Ministerie van LNV, 2014). The area harbors the largest subtidal mussel bottom culture area in the world. The total surface of culture plots amounts 7671 ha, of which 3329 ha is suitable for mussel cultivation (Capelle, 2017).

2.2. Mussel seed surveys in the Wadden Sea

Traditional mussel culture in The Netherlands is practiced on subtidal bottom culture plots. They are located in the western Wadden Sea and in The Oosterschelde estuary (SW Netherlands). The quality of the plots for mussel production varies in space, the best sites are located near tidal inlets, with additional food supply from the North Sea. The culture cycle is 2 – 3 years and starts with juvenile mussels of which most are fished from wild subtidal beds in the western Wadden Sea. Recruitment usually occurs once a year in the period June – August. The collection of juvenile mussels is of critical importance for the bottom culture practice. Recruitment success is quite variable and can even fail in some years, resulting in temporary shortages of seed mussels (see review by Capelle, 2017). Since 1992, surveys are carried out to identify location and extension of seed beds and the amount of seed biomass suitable for harvesting. Samples are collected as described under sampling and data handling (see below). The sampling program follows a stratified design, with a standard grid of transects (van Stralen et al., 2019). In areas where higher concentrations of mussels are expected, based on previous experiences, the grid is more dense. The minimum fishable density is around 150 g. fresh weight m^{-2} (van Stralen et al., 2019). The time series indeed demonstrate large year to year variation in the abundance of juvenile mussels (Fig. 1). The mussel seed surveys are done twice a year, in September to identify the new spat fall and in March to assess the available seed left over after the winter period. Survey results are presented prior to fisheries in a report with detailed maps of the areas with mussel seed (see for example van Stralen et al., 2019). The maps have been integrated for the period 1992 – 2013, showing the frequency of mussel presence in different areas (Fig. 2).

2.3. Relative stability of sublittoral mussel seed beds

The results of the mussel seed surveys show distribution patterns over time in the sublittoral western Wadden Sea (Fig. 2). The life expectancy of newly settled mussel beds depends on a variety of factors such as vulnerability for storm damage and the level of starfish predation. The latter correlates with salinity levels, as starfish has ample tolerance for low salinity; this provides an opportunity for mussel beds to survive in areas under the influence of fresh water discharges (Smaal et al., 2014; Auguëra, 2015). In the surveys, special attention is given to starfish density as a factor that limits the chance of survival (van Stralen et al., 2019). Seed beds in areas with a low chance of survival are labelled as relatively unstable, while the other beds are identified as relatively stable (ALTERRA, 2005). Based on this knowledge, fishing

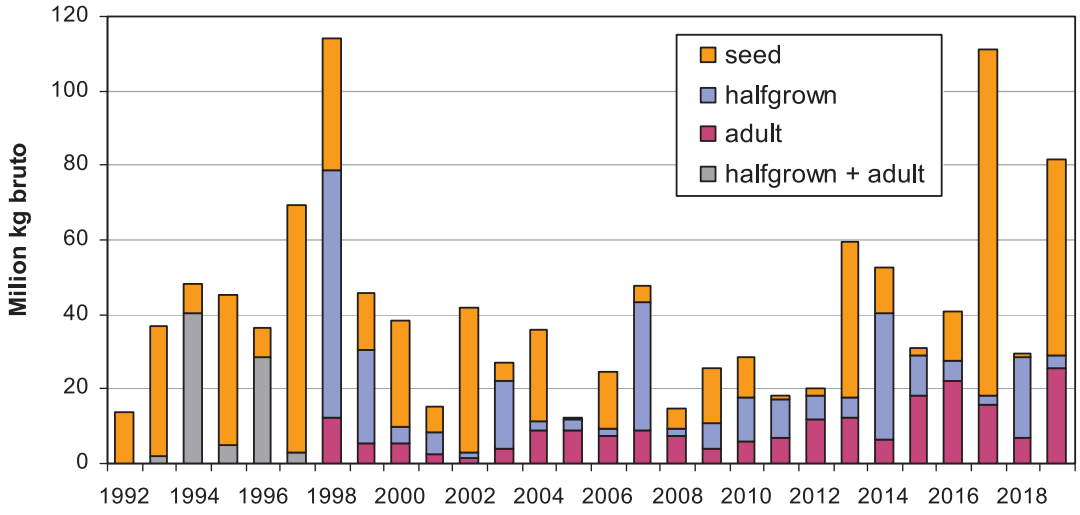

Fig 1. Composition and size of the mussel stocks on sublittoral wild mussel beds in the western Wadden Sea in Spring in the period 1992 – 2018, consisting of seed, half-grown and adult mussels. Prior to 1998, half-grown and adults were merged (van Stralen et al., 2019)

plans are drawn up by the mussel producers organisation for seed fishery in Autumn in areas with unstable beds. In Spring, in the fishing plans the more stable beds are open for fishery, as well as the beds from the Autumn fishery which are still present for profitable fisheries (i.e. > 150 g fresh weight per m^2). In the following years the beds can be included again in the fishing plans if they still have sufficient biomass for profitable fisheries.

2.4. Site selection

For this study a so-called split-plot design was implemented (Ens 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). Prior to the seed fishery impact study, a power analysis was carried out, showing that 40 plots would be sufficient for a detectable effect size of 10 % with an accuracy of 80 % (Ens et al., 2007). Yet, at the start of the study in Autumn 2006, the amount of newly formed seed beds was quite low. The Autumn as well as the following Spring 2007 fisheries was therefore focused on mussel beds with half-grown mussels that were established in 2005 (supplementary material Table A). It is noticed that on these beds seed fishery has taken place in Autumn 2005 and Spring 2006, before the study plots were selected. In our analysis in this paper these plots (9 plots in total) were not included in the BACI analysis. The data have been used for the time series.

The standard seed surveys were used to identify the occurrence of new mussel seed beds. Once these beds were detected, prior to fisheries, plots were selected for the impact study. This is illustrated in Table A in supplementary material, showing the stepwise extension of the number of plots. In the period 2007-2009, sufficient new seed beds were formed to include a total of 40 plots in the study (Fig. 3), of which 1 was skipped due to fishery in the control part. On 6 plots in the area, new seed beds were established and on one plot (VjG) a new seed bed was formed twice. In these cases the time series was reset. This is marked in Table A with blue lines. It implies that the study contains in total 46 time series. Plots that are first fished in Autumn are located in beds identified as unstable. The remaining plots were fished for the first time in Spring.

2.5. Location and size of the study plots

Within the seed beds, plots of 400*200m were chosen, of which half of it was open to mussel seed fishery (Impact) and the other half was closed to fisheries (Control). Impact and control parts were chosen at random (Fig. 3). Within the two 200 × 200 m (4 ha) parts inside the plot, a buffer zone of 50 m was created at the edges, leaving an area of 100 × 100 m in the centre of the control and impact parts. It is assumed that plots are representative for the natural beds on which the plots were created. Hence, fishery around the control part should not have a measurable effect on the inner 100x100 m part of the plots. This assumption was tested by investigating gradients in mussel density in the 50 m buffer zone in the unfished plots. In this analysis, it was assumed that if fishery had any effect on mussels in control parts, it would have created gradients in mussel density from the edge to the centre of the plot. Results of the analysis showed that no such patterns could be found; therefore, it was concluded that fishery in the area had no effect on the control parts (van Stralen et al., 2013).

2.6. Short and longer term effects

To identify the impact of fisheries on density and biomass of mussels, a before-after-control-impact approach with 37 replicates (46 minus 9 plots that originate from 2005) was followed (beyond BACI, Underwood, 1992). After establishing the short term effects, the plots were subject to annual monitoring in Spring of mussel density and biomass. For the period 2006 - 2012 the control and impact parts of the plots were sampled for at least 2 years and at maximum 6 years (Table A). Plots that still had mussel biomass at the end of the sampling period, this holds for the plots of Fig. 7, were monitored during the standard mussel seed surveys, until no mussels were observed.

2.7. Sampling and data handling

Sampling was done with commercial vessels for mechanical cockle fisheries (YE 42 and YE 172) with adapted fishing gear. Two devices were used. At depth <10 m the suction dredge was used.

The suction dredge is a modified cockle dredge of which the cutting blade opening is reduced to 20 cm wide. The gear was towed over a distance of about 100 m, of which the exact length of the sampled transect was measured by GPS. At a depth >10m a benthic dredge attached on a fishing line and was used. This dredge is an adapted version of the device as described by Bergman and van Santbrink, 1994, and has a volume of 600 L. This dredge has a cutting blade of 10 cm wide and was towed over about 100m of which the exact length of the sampled transect was measured by a wheel connected to a counter. In both dredges a mesh size of 5 mm was used.

On each plot 2*2 transects were sampled in an area of 100x100m in

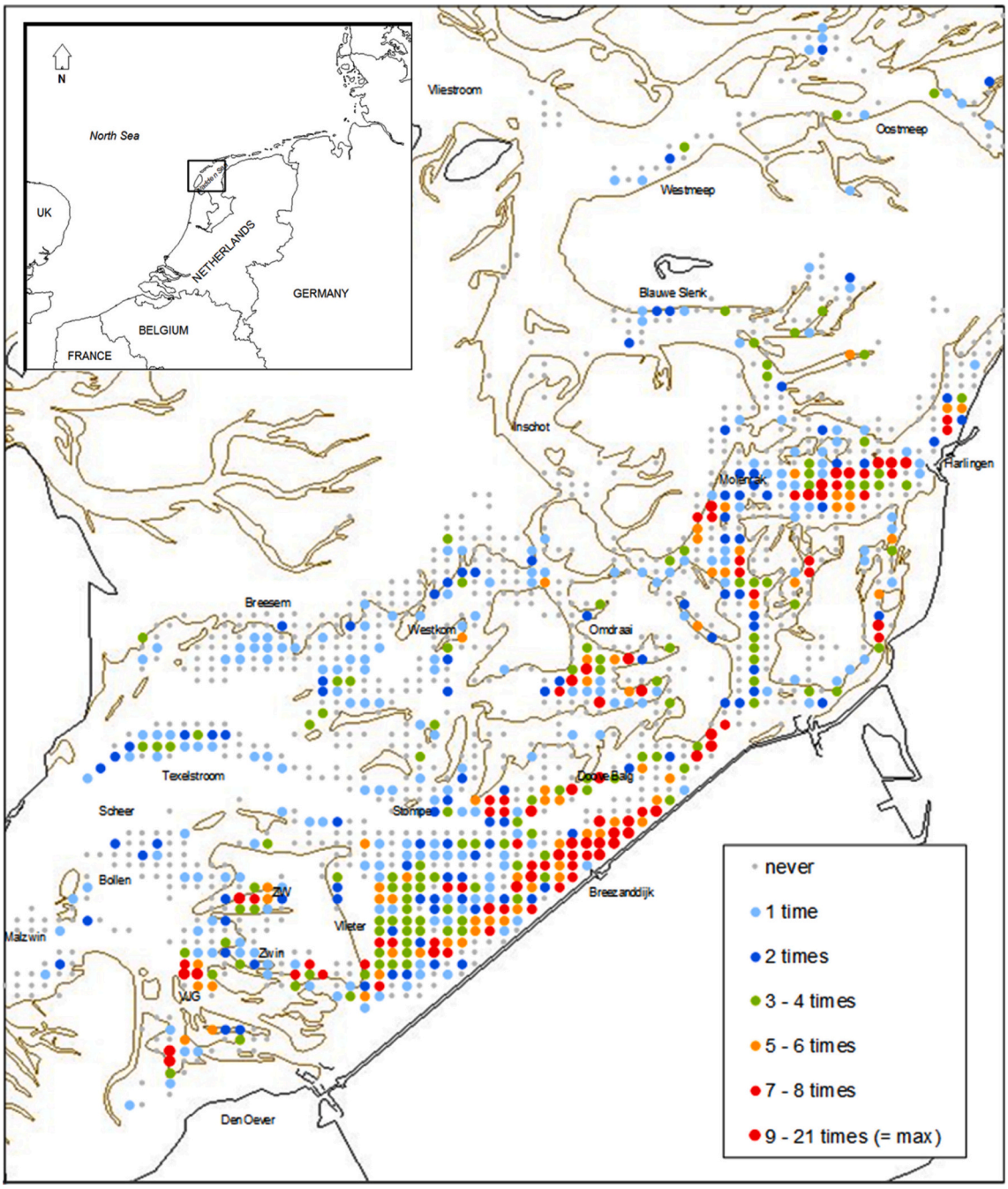

Fig 2. Frequency of mussel observations on wild beds in different areas of the Western Wadden Sea for the period 1992 – 2013 (Smaal et al., 2014).

the centre of the control and the impact parts. Samples were sorted out on-board. For the mussels, subsamples were taken and the amount of small (seed), medium and large mussels was registered. For other macrobenthos species present and for sediment separate samples were taken (see Craeymeersch et al., 2020). Mussel data are expressed as numbers and live fresh weight per m^2.

Before – after sampling was done a few weeks prior to fisheries and shortly after fisheries had taken place, both for Autumn and Spring fisheries. For the time series, sampling was done annually in Spring as long as there were mussels present on at least one of the plots.

2.8. Fishing effort

The fished plots were opened for fishery as part of the regular mussel seed fisheries in the subsequent years and as described in the fishing plans. The fishery campaign takes about 4 weeks and is organised by the Producers Organisation. Mussel farmers have individual seed quota and the progress in fishery is weekly evaluated to adjust the fishing plan if necessary. During the fishing campaign the fishery takes place in intervals of a few days per week in order to achieve recovery and aggregation of the not yet fished mussels in the time in between.

During the fishery campaign, it was not allowed to fish or sail in the closed plots. This was verified by analysing the black box data of the vessels, registering location and sailing speed of the vessel every 6 seconds (Fig. 4). However, in 3 plots fisheries has been practiced on the control site. One of these plots was relocated (TX-o2), for one plot only (undisturbed) short term effects could be analysed (DB), and one plot (BS-w) was excluded from the analysis, so the study was done on 39 plots.

The black box data were also used to quantify the fishing effort per

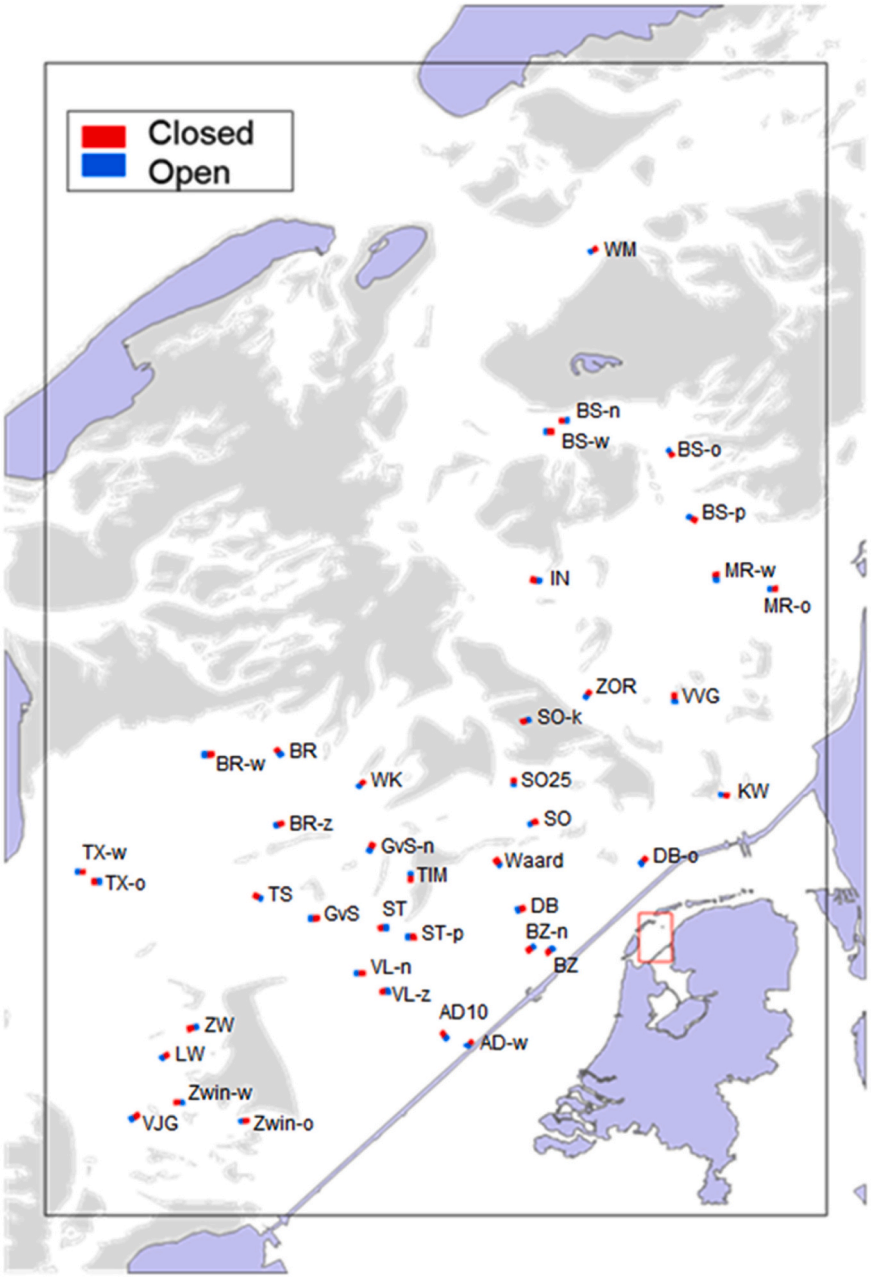

Fig. 3. Control (red) and Impact (blue) parts of the 8 ha plots on subtidal mussel beds in the western Wadden Sea. In total 40 plots have been monitored for at least 2 years and at maximum 6 years. Plot names correspond with the plots mentioned in Figs 5 and 7 (see also supplementary Table A).(For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

plot, expressed as hours fishing in the different areas. Given an average fishing speed of 4.6 km.h^{-1} and the use of 4 dredges of 1.9 m width, and assuming that effective fishing occurs 66 % of the time as dredges have to be hauled to be emptied, each black box registration covers 39 m^2 plot area. The total surface per impact part of the plot that was hit by the dredge was extrapolated by taking correction for overlap of fishing tracks into account and assuming that the fishery within the plot was randomly distributed. This gives the surface hit at least once by a dredge, as a function of fishing time.

2.9. Data analysis

The statistical analysis was performed in accordance with a (beyond) BACI design in which each plot is considered as an independent observation. For all plots, the ratio of mussel biomass data Before and After fisheries (X_{BI}/X_{AI}) of the Impact part was divided by the X_{BC}/X_{AC} ratio of the Control part. The resulting outcome was log transformed. The non-parametric Wilcoxon signed-rank test was used, as the test statistic had a very skewed distribution due to many close to zero values resulting from the almost absence of mussels in the course of time on many plots (Sokal and Rohlf, 1981).

Tests were performed for the Autumn and the Spring plots separately. For the subsequent time series data (T2...T6), the initial mussel biomass data before fisheries were used as T0 values.

The comparison of densities in newly formed seed beds after fisheries, in control and impact parts, was also tested with the Wilcoxon signed rank test.

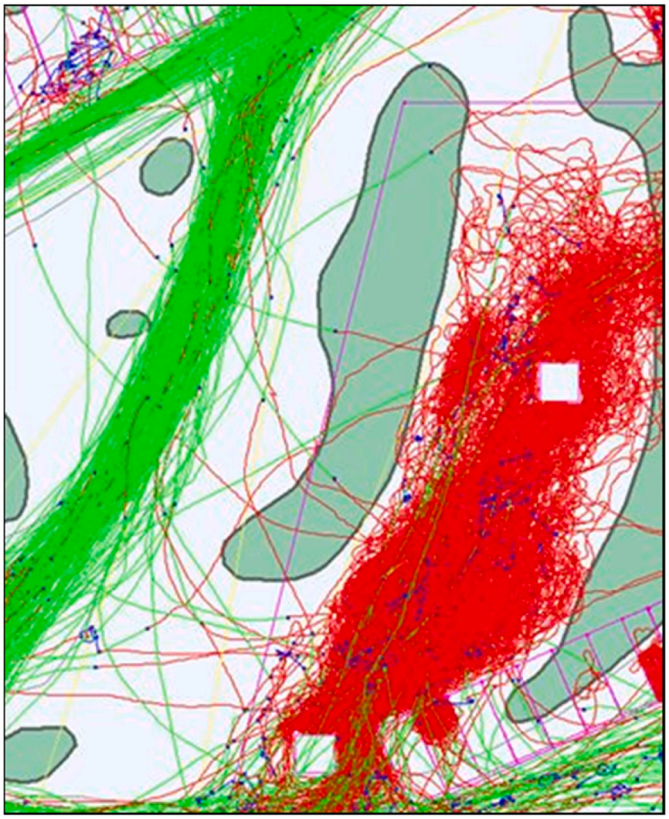

Fig. 4. Fishing (red) and sailing (green) activity of mussel vessels in the western Wadden Sea according to the black box data. The white squares are the control parts of the monitoring plots on a mussel seed bed.(For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Fishing effort

Fishing effort in the impact parts of the plots has been registered by the black box on board of the vessels. This is relevant in order to quantify the treatment and to establish if fishery has been carried out as usual in mussel seed fishery. As shown in Fig. 5, in most plots fishing has touched the whole surface of the impact parts. Fished surface was 90-100 % on 27 plots, 7 plots had between 50 and 100 % fished surface and another 6 plots showed lower fishing activity 10 – 40%). The latter indicates relatively low initial mussel densities, preventing a longer lasting profitable fishery. Fig. 5 illustrates intensive fishery on the majority of the plots.

3.2. Autumn fishery effects

Autumn fishery took place on 21 locations; 4 locations were set in Autumn 2006, starting with half grown mussels and therefore not included in the BACI analysis. Five of the locations had new spat fall during the study. In total 22 Before-After-Control-Impact observations were done of seed mussel fishery in Autumn. As shown in Table 1, biomass decreased on average by 73 % in the period September – November on the Impact as well on the Control parts. There was no statistical difference between the treatments.

3.3. Spring fishery effects

Spring fishery on stable sites took place on 19 locations; 1 of the plots was skipped due to fishing in the control part. On 5 locations fishery in Spring 2007 was on beds that had been fished before and these were excluded from the BACI analysis. On 2 of the locations new spat fall took place in the course of the study, so in total there are 15 BACI observations (Table 1). In Spring, biomass increased in the control part (132%) while it decreased by 77 % in the fished part (Table 1). This difference is statistically significant and can be ascribed to fishery.

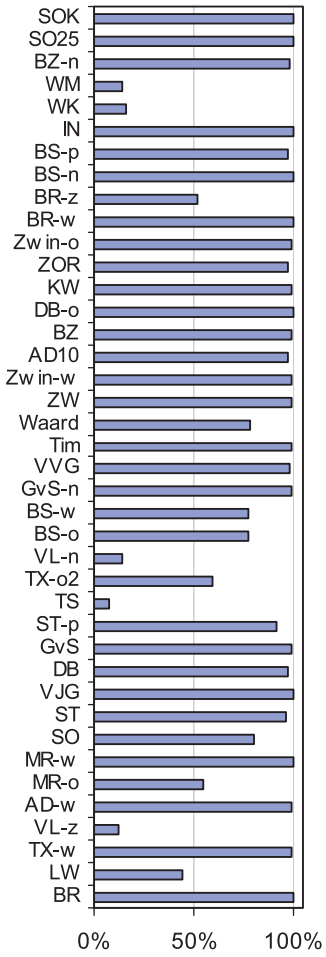

Fig. 5. Fishing efforts as % age of total plot surface that was effectively fished, i.e. touched at least once by the dredge. Data based on black box registrations during seed fishing. Locations of the plots are given in Fig. 2.

In Spring, fishery was repeated on Autumn plots. Biomass before fishery on these plots was on average 0.68 kg.m^{-2} and 0.38 kg.m^{-2} on control and impact parts respectively. After fishery, biomass had increased in the control parts (to 0.98 kg.m^{-2}) while in the impact parts biomass hardly showed net change (0.35 kg.m^{-2}, Table 1). A separate BACI test showed that the effect of this treatment was not significant ($p=0.2094$)

3.4. Long term effects

In the years after the first fishery, mussel densities and biomass were monitored in Spring each year (Table 1). Fig. 6 shows a decrease in density over time on the plots. The biomass also shows a decreasing trend, although sometimes there is an increase due to growth.

On the Autumn plots there is no clear difference between treatments; mussels tend to disappear evenly from control and fished parts of the plots. Also the Spring plots showed a gradual decline of the mussel stocks, but less steep than for the Autumn plots. In the Spring plots the effect of harvesting mussels through fishing is significant both directly after fishery as well as in the subsequent two years (Table 1).

The box and whisker plots in Fig. 6 demonstrate the large variation

Table 1
Fishery impacts according to the BACI approach: average biomass in kg.m^{-2} in control and impact parts before and after fishery. Autumn plots are located in beds that were identified as relatively unstable and first fished in Autumn. Spring plots are located in beds that were identified as relatively stable, these beds were first fished in Spring (see supplementary Table A). After fishery the plots were sampled each year in Spring. Number of plots decreases over time as plots in beds that disappeared are excluded from the tests. Data were tested with the Wilcoxon signed-rank test with the initial values before the fisheries as T0. The BACI tests show a significant effect of Spring fishery, directly after fishery, after one year and after two years, respectively. *=p<.05, **=p<.01. n.d. = not determined due to very low densities

Sampling scheme	Mussel age		Biomass kg.m^{-2}		n	p-value
Autumn plots			Control	Impact		
Autumn fishery	Before	0 yr (seed)	2.97	2.05	22	
	After	0 yr (seed)	0.80	0.55	22	
Spring		0 yr (seed)	0.98	0.35	22	0.0869
Spring		1 yr (half grown)	0.38	0.16	22	0.8785
Spring		2 yr	0.16	0.14	21	0.7671
Spring		3 yr	0.33	0.12	12	0.6858
Spring		4 yr	0.00	0.00	5	n.d.
Spring		5 yr	0.00	0.00	0	n.d.
Spring plots						
Spring fishery	Before	0 yr (seed)	3.00	2.80	15	
	After	0 yr (seed)	3.96	0.63	15	**0.0012****
Spring		1 yr (half grown)	1.36	0.66	15	**0.0157***
Spring		2 yr	1.01	0.23	15	**0.0076****
Spring		3 yr	1.31	0.27	11	0.3105
Spring		4 yr	0.19	0.12	4	0.3173
Spring		5 yr	0.00	0.00	1	n.d.

between plots, for the Autumn as well for the Spring plots. On 3 out of the 39 plots high biomass values were recorded for a longer period (Fig. 7). Control parts showed highest values, but also on the impact parts biomass was relatively high, in comparison with the average values of the other plots (Fig. 7, grey lines). Maximum longevity of a mussel bed was 7 years, as observed on the impact part of this plot (GvS-n).

3.5. Impact on recruitment

Recruitment of mussels after fishing is expressed as the number of newly settled mussel seed in the fished and the unfished parts of the plots, based on samples in the time series, or prior to fisheries in case new seed beds were found on plots that were already part of the time series. The latter occurred in six cases. In other cases mussel seed was normally found in low densities. In Fig. 8 all mussel seed data found in the impact parts are plotted against the densities in the control parts. There was no statistical difference in new settlement on the control and impact parts.

4. Discussion

The effectively fished surface area is determined on the basis of black box data. Fished surface varied between 10 and 100 %, with most plots fished for nearly 100 %. In mussel fishery, the area is fished more than once, as gear efficiency is limited because loose mussels easily escape from the dredges. The fishery is often done with intervals on a certain location, as after fishery mussels aggregate and can be fished again later during the campaign. If mussel densities become relatively low, fishermen tend to move to other sites. Because the fishery on the plots of this study was done as part of the regular seed fishery activity, the before-after-control-impact comparison delivers data that can be considered representative for the effects of the regular intensity of seed fishery on wild subtidal mussel seed beds.

The results show a difference in the fate of the mussels in Autumn and in Spring. On the plots that were fished in Autumn, the fished parts showed a substantial decrease in stock, but also on the control parts, mussel stock declined substantially. The decline in stock under both treatments was about the same (73%) and statistically not significantly different. The seed beds open to fisheries in Autumn were on forehand identified as unstable, due to the high risk of starfish predation and/or losses during storm events (ALTERRA, 2005). That is why these beds were included in the fishing plans for the Autumn fishery. Our results show for the Autumn plots that also without fishery a large part of the seed stock is lost. This is observed in the sampling directly after fisheries, so the main losses occurred in Autumn, rather than in Winter. The subsequent time series showed a further decline in mussel stocks with no significant differences between control and impact parts of the plots that were first fished in Autumn.

This is in contrast to the seed beds that were fished for the first time in Spring. In Spring, harvesting seed mussels results in a considerable decrease in stock size. In the control parts of the Spring plots, the stock increased in the period from pre- to post fishery surveys to 132% while on the fished parts the stock was reduced to 23% of the initial stock. So, the short term effect of seed fishery in Spring results in a stock with a significant lower size in comparison with the control parts. A significant difference in mussel biomass between control and impact parts on the Spring plots was maintained for two years after fishery. After this period, the mussel stock further declined with no difference between impact and control parts.

In contrast to the loss of biomass in Autumn, in Spring, biomass increased on the control parts, apparently due to net growth of the mussels. This change in biomass was also observed on the Autumn plots in Spring: an increase in biomass on the control parts and a (limited) decrease in the impact parts. Yet, in this case the effect of the treatment was not significant. It demonstrates also that factors that determine mussel bed dynamics, are quite different in Spring compared to Autumn.

On three out of 39 sites (GvS-n, ZW and Zwin-o, Fig. 7), mussel biomass showed a large increase over time, with after 3 – 5 years the highest biomass on control parts. After 5 years the beds ZW and Zwin-o disappeared. On the remaining bed (GvS-n) after 6 – 7 years the highest biomass was found on the impact parts, in the end also this bed disappeared. Compared to the other studied plots, the biomass values in the fished and unfished parts were in general higher than elsewhere, pointing to a site rather than a fishery effect. In statistical sense these plots are outliers, but for the impact study it is relevant as it raises the question what typical conditions on these sites may explain the good growth and survival. Absence of starfish predation is excluded, as starfish density was not different from other plots (van Stralen et al., 2013). Data about other environmental factors at the scale of these plots would be required for a further analysis, and these are not available in sufficient detail. Also, this analysis is beyond the scope of this study.

The loss of mussels over time on most of the plots supports the concept of ephemeral mussel beds (Seed, 1976; Seed and Suchanek, 1992; Saurel et al., 2004; Maguire et al., 2007). Subtidal beds tend to fade away and new beds are formed in years with a good spat fall. Longevity appears to be due to natural factors like predation and storm damage. It is debated whether long-term bottom fishery, including mussel seed fishery, has resulted in a decline in subtidal wild mussel stocks and a loss in benthic biodiversity. Buhs and Reise, 1997 report a decline of benthic species numbers in the German Wadden Sea of 50 % over 100 years, and suggest that this may be attributed to fishery disturbance. Yet, other factors, like pollution, may have played a role as well. They recommend to carry out control-impact studies - as done in this study -, to sort out the impact of mechanical disturbance from other factors.

It can be questioned indeed whether other anthropogenic factors, such as shrimp fishery, play a role in the loss of sublittoral beds. Although in our study, the control parts were closed to mussel fishery, this was not the case for shrimp fisheries. In the Wadden Sea area,

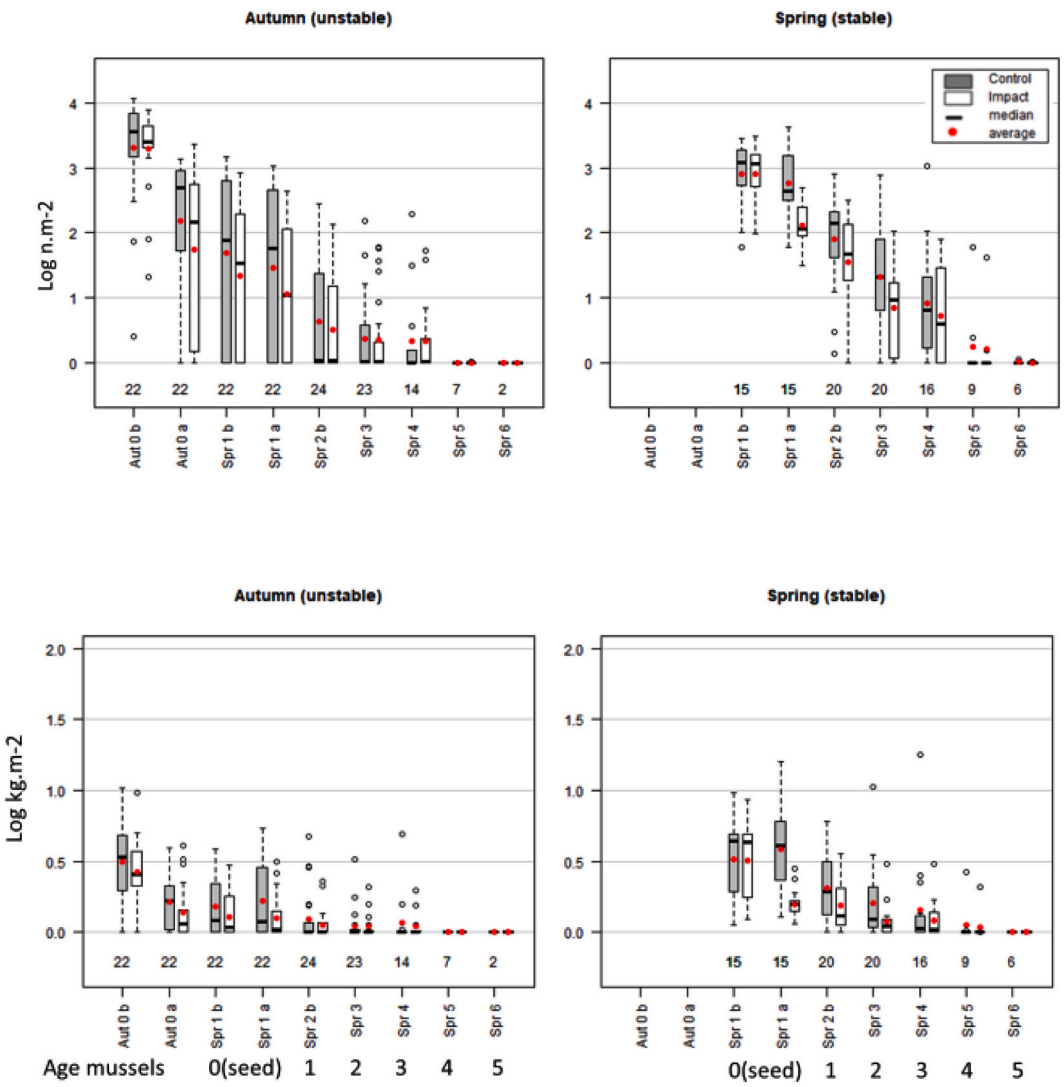

Fig. 6. Box and whisker graphs of the development of mussel density in log n.m^{-2} and biomass in log kg.m^{-2} on control and impact parts of the monitoring plots for a period of maximum 6 years after first fishery, for the plots in unstable areas (Autumn plots) and in more stable areas (Spring plots). Bars are the 50% quartiles, based on 50 % of the observations, the dotted lines are 1.5* the 50 % quartiles, other data (open circles) are outside this range. Horizontal bars are median values and red dots mean values. X-axis: Aut = Autumn, Spr = Spring, nr = year nr, b= before fishing, a = after fishing. Under the bars the number of observations is presented. In Spring 2 the data from the plots in Autumn 2006 and Spring 2007, which started with half grown mussel, are included. The number of observed plots subsequently decreases as not all plots had a complete time series. The age of the mussels i.e. the year classes are shown along the X-axis.

fishery on shrimp (*Crangon crangon*) is the major bottom fisheries that may have an impact on subtidal mussel beds. However, shrimp fishermen avoid mussel beds, as it is detrimental for their fisheries technique, given the risk of damaging their nets when they get filled with mussels. So shrimp fishery is unlikely to have occurred on the study plots and an analysis of the Vessel Monitoring System data gave no indications as well.

Reise and Buschbaum, 2017, made a reconstruction of historic subtidal mussel stocks in the German Wadden Sea. Although factors like eutrophication, severe winters, failing recruitment and invasive oysters are addressed, they specifically address the possible impact of subtidal mussel seed fishery as a cause of a decline in stock size and longevity of subtidal mussels, and a loss of biodiversity. In our study, we followed the fate of mussels on control and impact parts for a period of 9 years and found a limited longevity of subtidal mussel beds, also on the control plots. So we explicitly addressed mussel seed fishery impacts in comparison with natural loss factors, and demonstrated that the development of subtidal mussel beds in the western Wadden Sea had a limited time-span, also in the absence of fishery.

Given the limited longevity of subtidal mussel beds, long term development of mussel beds depends on new recruitment of viable spat, forming new beds. This also holds for intertidal mussel beds; the importance of recruitment for intertidal mussel bed subsistence is clearly demonstrated by van der Meer et al., 2019; see also Steenbergen et al., 2006. Recruitment shows large variability both in time and place. During our study, only on 6 out of 40 plots new recruitment was recorded. Recruitment success of bivalves in the Wadden Sea has been extensively studied (Beukema and Dekker, 2007, 2014) and is annually registered in the monitoring program (van Stralen et al., 2019). For mussels, it was suggested that recruitment failure can be linked to subsequent predation by shrimps, crabs and starfish (Beukema and Dekker, 2005). After cold winters, there might be a mismatch between predators and prey, as the predators return later from deeper waters than after a mild winter, hence mussel spat has better survival. Moreover, low temperatures seem to synchronize spawning and stimulate massive spat fall, that is less vulnerable for predation due to dominance in numbers. Under these conditions, large scale recruitment has been observed (Beukema and Dekker, 2014; Beukema et al., 2015). Other

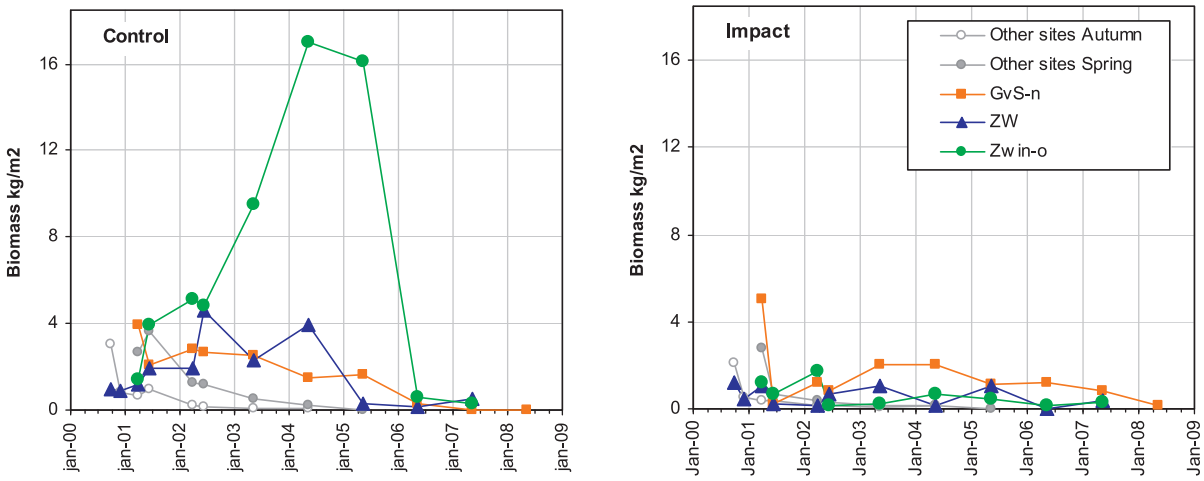

Fig. 7. Biomass of mussels in kg.m^{-2} on control (left) and impact (right) parts of three outlier plots with high maximum values in comparison with average values of the other plots (in grey). Time series of this monitoring program, expressed in years since spat fall, lasted for nine years.

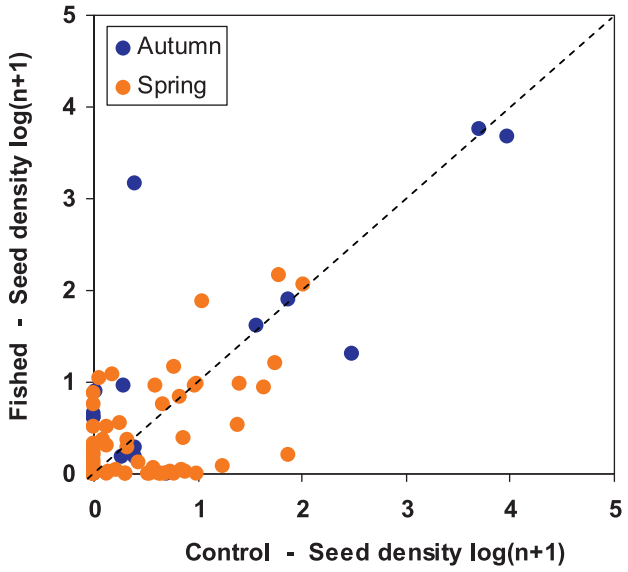

Fig. 8. Newly settled mussel seed densities (log (n+1).m^{-2}) after fishery on Autumn and Spring plots, in control and impact parts. Differences in densities between the impact and control parts were not found (Ts = 0.37, ns with α = 0.05, N = 180).

factors, such as substrate quality may also play a role in recruitment success. Craeymeersch et al. (2020) studies the impact of seed fishery on substrate composition. They show that median grain size and clay content was slightly different between control and impact parts, with less clay and a larger grain size after fishery. The difference, however, was not significant. As settlement of mussel spat requires coarse rather than fine sediment, these results do not point to negative impacts of fishery on substrate quality for recruitment. As we have shown, a comparison of recruitment on control and impact parts after fishery showed no difference in seed densities. Hence, we found no indications of impacts of mussel seed fisheries on subsequent new recruitment.

The harvested seed is transplanted to culture plots in the western Wadden Sea, and in limited amounts to the Oosterschelde. Capelle et al., 2017, demonstrate that mussels transplanted to culture plots show significant better growth and survival than on wild beds. Despite the fact that the mussels on the culture plots in the Wadden Sea are harvested in the end, the net effect was estimated to be a 15 % stock increase compared with no culture activities (Capelle et al., 2017).

In conclusion, stocks on seed beds in areas of the sublittoral Western Wadden Sea that are known as unstable, show a large decline within one year after settlement, also when there is no seed fishery. In areas with a better survival of seed beds in winter, the first fishery is done in Spring. This fishery results in a significant decrease in biomass in comparison to the control parts. The difference remains significant for a period of two years after fishery. The long term development shows a gradual decline of the mussel stocks, and on all plots the mussel beds disappeared in the end. The maximum lifetime recorded was 7 years. A difference in life expectancy of beds in relation to fishery was not demonstrated. So, sublittoral beds gradually disappear, also without fisheries. As a consequence, new recruitment is of critical importance for the long-term survival of sublittoral mussel beds. As we found no significant difference between recruitment on fished and control parts, there are no indications for negative impacts of seed fishery on new recruitment.

Declaration of Competing Interest

None.

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Appendix A. The following are the supplementary data related to this article

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2020.101978.

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