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Transitioning from wild seed fishery to Seed Mussel Collectors (SMCs): Reviewing the efficiency of collectors for seed provisioning in mussel bottom culture

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ABSTRACT

The availability of mussel seed is a critical aspect in mussel farming. Since 2009, the Dutch mussel sector has been transitioning from wild seed fishery to suspended seed collectors (Seed Mussel Collectors, or SMCs). Collector systems using either ropes or nets as settlement substrate are placed in Oosterschelde Bay, the Wadden Sea, and the North Sea annually. We analyzed detailed harvest data from 2010 until 2022, to investigate the efficiency of different systems, identify differences between years and areas, and assess how production can be optimized. Additionally, numerical density, biomass, and shell lengths of mussels from 0.375 mm shell length were recorded on SMC ropes at one SMC location during a full growth season to evaluate biomass-density relations and assess the process of self-thinning on the ropes. Total harvest of SMC mussel seed increased over the period 2010–2022, from 8.0 $\times 10^6$ kg to 21.0 $\times 10^6$ kg fresh weight. Harvest per unit substrate was remarkably stable over the years across sites, with a lower mean in Oosterschelde Bay ($\sim$2.56 kg m^{-1}) than in the Wadden Sea ($\sim$3.28 kg m^{-1}). Ropes were found to provide a greater yield per unit area than nets, but nets are less labor-intensive to use. Occurrence of density-dependent growth on the ropes was indicated by the allometric relation between mussel biomass and mussel density. A positive relation between density and growth rate suggested that competition increased with growth rate. In the growth data covering a full SMC season, we first observed a rapid numerical increase as newly settled mussels continued to grow into the measured size range. This was followed by a period of rapid numerical reduction and increasing biomass, indicating self-thinning. Finally numerical reduction stabilized and biomass increase accelerated coupled with comparatively slower shell length increase. The self-thinning occurred between approximately 2.3 mm and 11.6 mm mean shell length. Our analysis of 12 years of production data shows that SMC seed is a robust and annually more reliable alternative to wild capture fishery as a seed provisioning resource for mussel culture. Production per unit substrate does not appear to be easily amenable to further improvement. Production per unit area showed no indication of overstocking on the scale of the SMC plots, suggesting that production gains could be made by increasing substrate density.

1. Introduction

1.1. Mussel culture and mussel seed provisioning

Mussel culture is an extensive aquaculture practice, relying on natural feed, and requiring mussel seed as an input resource (Smaal et al., 2019). This seed is usually collected from benthic wild mussel seed stocks or from suspended collectors (Kamermans and Capelle, 2019). The large year-to-year variability in recruitment success on wild mussel beds in the most important source area in the Netherlands, the Wadden Sea, is not explained well by any single factor (Van der Meer et al., 2018), and variation in seed availability contributes to the steady decline of EU mussel production (Avdelas et al., 2020; Smaal, 2002). Environmental factors that affect variation in seed recruitment include hydrodynamics (Fuentes-Santos and Labarta, 2015), predator population dynamics (Beukema, 1982), and food supply (Phillips, 2004).

Policy, regulations, and restrictions also affect availability of bivalve seed for aquaculture. Concerns about environmental effects of wild seed

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fishery have led to policy and regulations that set limits for wild seed harvesting in various areas (Kaiser et al., 1998; Nehls et al., 1997; Piñeiro-Corbeira et al., 2018). The same applies in the Dutch Wadden Sea, where mussel seed fished from wild seed beds has been re-laid on subtidal culture lease plots to grow to commercial size since the 19th century. Until harvest, mussels are generally relocated between one and three times between plots to increase growth rate, reduce density, or reduce losses due to dislodgement. Other active management includes removal of starfish (a major predator of mussels) and removal of silt from the plots after harvest (for details see Jansen et al., 2023). The average ratio between mussel biomass at any given point in the culture cycle, and seeded mussel biomass, is highly variable but on average sits between 1.3 and 2.8, depending on mussel size at seeding (Capelle et al., 2016). In the Dutch Wadden Sea, fishing for mussel seed has been strictly regulated since the 1990 s via exclusion from intertidal areas and via the application of food reserve floor levels for birds: shellfish population levels below which the fishery would be reduced or halted. This led to court battles between several environmental NGOs (ENGOs) and the mussel industry. In a 2008 court case brought by ENGOs, the Council of State ruled that mussel seed fishery licensing occurred unlawfully since it conflicted with the European Birds and Habitats Directives. The ruling threatened the existence of the Dutch mussel industry since it depended on mussel seed fishery in the Wadden Sea to obtain mussel seed as its input resource. To prevent further conflict, the Ministry of Agriculture, Nature, and Food Quality, four ENGOs, and the mussel producers' organization jointly set out, in a covenant, a "transition" process from wild seed fishery to alternative means of seed provision. The main points agreed in the covenant are that (i) ENGOs will cease legal challenges against fishery permits, and (ii) the Dutch Wadden Sea will gradually be closed to mussel seed fishery, under the condition that the mussel industry is given sufficient time to develop alternative means for resource provisioning (Van Hoof, 2012).

1.2. *Seed Mussel Collectors as an alternative seed source*

Experiments with seed mussel collectors (SMCs) as an alternative to wild seed started in the Netherlands at the beginning of the 21st century (Kamermans et al., 2002). The aim was to obtain a more reliable seed supply, since the availability of wild mussel seed fluctuated naturally. The covenant accelerated development from 2008, and the use of SMCs increased steadily until about 2015, after which total substrate deployed fluctuated around the same level.

As part of the covenant, the Wadden Sea is closed to wild seed fishery in a stepwise process, matching the pace of development of alternative seed supply. The aim of the covenant is to obtain 100% of the industry's mussel seed demand from SMCs, thus abolishing all seed fishery on wild mussel beds. To date, four steps have been fulfilled: (1) 14% of subtidal areas containing mussel seed beds were closed in 2010, corresponding to a seed supply of 5.5 $\times 10^6$ kg; (2) this area increased to 28% in 2014 with areas without current mussel beds but historically known to form mussel seed beds, corresponding to a cumulative 11 $\times 10^6$ kg of seed supply; (3) in 2021 a third step of 7.7% closure (total 35.7%, corresponding to a cumulative seed supply of 14 $\times 10^6$ kg. And a fourth step in 2022 to a total of 50% closure. Two more steps are foreseen: (1) 65% total closure by 2026, and 2) 100% by 2029, conditional on an assessment to be made in 2026 whether this will be feasible while maintaining a viable mussel industry.

Various studies have compared the performance characteristics of seed from collectors with seed from wild mussel beds. Mussels from suspended collectors have been shown to display more aggregation activity (Christensen et al., 2015). However, Kamermans et al. (2009) found no predation preference by crabs and starfish on mussels from various sources. Comparing performance of mussel seed from collector ropes and from intertidal rocky shores on raft culture in Spanish Rías, Fuentes et al. (1998) and Babarro et al. (2000) found no difference in terms of growth rate and mortality, and condition index, respectively. A monitoring program in the Netherlands found no major differences in overall performance between seed from SMCs and seed from fishery on wild mussel beds (in autumn and spring). The only differences could be related to mussel seed size (Capelle et al., 2016): a smaller seed size when seeding results in a higher overall yield. However, production of mussel seed via SMCs is much more labor-intensive than wild seed fishery, and the cost is estimated as five to six times higher (van Oostenbrugge et al., 2018). Consequently, there is a demand for significantly higher production efficiency of mussel seed harvested from SMCs.

1.3. *Aims of this paper*

Our aims are: 1) to evaluate the efficiency of the different SMC systems, 2) to identify potential differences between areas and any universal trends observed across SMC systems and areas, and 3) to assess whether production per unit of SMC system (e.g. m of culture rope), or per unit area (e.g. ha of SMC lease plot), can be optimized. The available data sets allowed to assess the influence on production of: deployment area, collector type, mussel seed density-biomass relations, SMC system density, and adverse events.

At the beginning of the covenant, the SMCs were a new technique for the Dutch mussel sector, and development and scaling up were driven by trial and error. Therefore, we expected to find an increase over time in harvest per unit substrate (substrate production efficiency, kg m^{-1}), and in terms of harvest per unit area (plot production efficiency, kg ha^{-1}), since performance was expected to improve. Similarly, we expected to find a reduction of both types of production efficiency at high SMC densities per unit area (rope length or net surface ha^{-1}), as the boundaries of optimal production are explored. To test these hypotheses we investigated if production efficiency is affected by (a) growth rates of mussel seed on SMCs, (b) density of mussel seed on SMCs, and (c) density of SMCs per unit area.

2. Material and methods

2.1. *Dutch mussel industry and SMC deployment*

In 2018, the Dutch mussel industry consisted of 88 registered companies, 51 mussel fishing vessels, plus a smaller number of specialized vessels dedicated to rope culture, SMC operation, or facilitating commercial trade handling activities such as shuttling traded mussels between the auction and temporary holding plots (van Oostenbrugge et al., 2018). Annual mussel production from 2001 to 2021 ranged from 30 $\times 10^6$ kg to 68 $\times 10^6$ kg fresh weight, with an average of 46 $\times 10^6$ kg (https://agrimatie.nl/). Most mussels are grown on bottom lease plots, situated in the south-west of the country in the Oosterschelde Bay (2250 ha on 319 plots), and in the north in the Wadden Sea (6884 ha on 458 plots). A smaller surface area is licensed specifically for SMCs (Fig. 1), divided over three regions: the Wadden Sea (blocks of a total of 708 ha divided into 281 ha of licensed plots, of which 222 ha was used in 2022), the North Sea (a block of 65 ha divided into 27 ha of licensed plots, of which 15 ha was used in 2022), and Oosterschelde Bay (blocks of 316 ha divided into 116 ha of licensed plots, of which 40 ha was used in 2022).

2.2. *SMC systems*

The covenant incentivized mussel farmers to invest in SMCs from 2008 onwards. This led to a wide variety of systems and experiments (Poelman and Kamermans, 2010). A general distinction can be made between rope-based and net-based systems. Belt collector substrates, such as deployed in Taylor et al. (2019) were never tested. Rope systems use filamentous rope onto which mussels can attach, and can be categorized as (a) wound around rigid structures placed on the seabed, (b) suspended longlines continuously looped from a buoyed main line, (c) suspended horizontally between tubes (for shallow areas). Net-based systems can be categorized as nets suspended (a) under buoys or

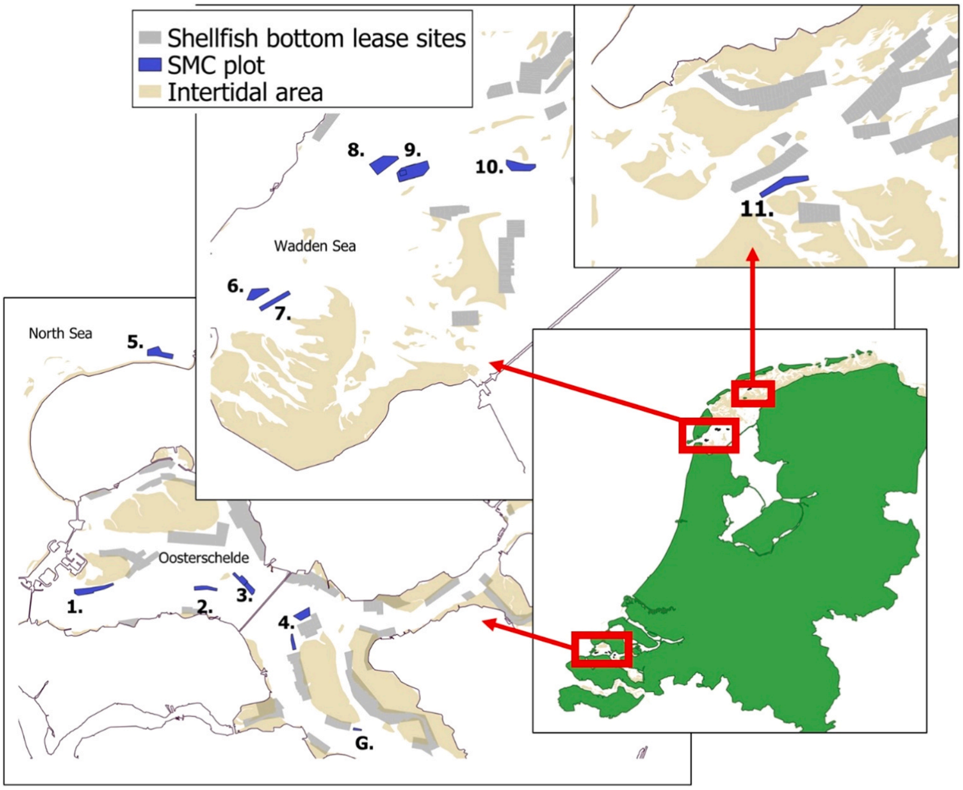

Fig. 1. SMC sites in use in the Netherlands (2022): 1 = Neeltje Jans (65 ha); 2 = Schaar van Colijnsplaat (28 ha); 3 = Vuilbaard (46 ha); 4 = Vondelingen Noord (40 ha); 5 = BH Gat (North Sea – 60 ha); 6 = Malzwin (55 ha); 7 = Zuidwal (50 ha); 8 = Burgzand (100 ha); 9 = Vogelzand (140 ha); 10 = Gat van Stompe (75 ha); 11 = Zuidmeep 80 ha. G = Galgeplaat: not in use in 2022 but source of self-thinning data in this study. Shellfish bottom lease plots are shown for reference.

tubes, and (b) under rafts. Examples are shown in Fig. 2. Systems are anchored with plough anchors, concrete blocks, anchor piles (ground anchors at sea floor level), or at the water surface on metal poles. From the wide array of experimental systems at the start of the transition, most disappeared over time due to impracticalities, or company take-overs. By 2022 two systems remained: (a) continuous longlines under a buoyed main line, and (b) suspended nets under tubes (110 m x 3–4 m). Until 2015, a proprietary system with nets suspended under rafts was implemented on a relatively large scale in Oosterschelde Bay by a single mussel farmer. These systems were characterized by a high density of substrate per farmed area. However, they yielded a lower harvest per square meter of substrate compared to other net-based systems (see paragraph 3.5).

Fig. 2. Examples of SMC systems: (a) lines wound around rigid structures placed on the seabed; (b) longlines suspended in continuous vertical loops under buoys; (c) lines suspended horizontally between tubes; (d) suspended nets under rafts; (e) suspended nets under buoys or tubes.

2.3. Data collection

2.3.1. SMC production monitoring

The data used to investigate production efficiencies including the effects of density-dependent growth, and differences between SMC systems and areas, were obtained from the production monitoring program. Mussel farmers using SMCs are required to report production statistics annually via two separate registration forms: (1) specification of SMC systems deployed, number of systems, amount of substrate, area, type of anchorage, and hours spent; and (2) SMC harvest (Wet Weight) for each day, with specification of date, number of systems harvested, first or consecutive harvest, hours spent, harvested volume (in the legacy unit “mussel ton” = 100 kg), size of the mussel seed (volumetric index ‘bustal’ = number of mussels that fit in a 880 ml tin can, converted to grams following Capelle et al. 2016), presence of starfish, destination (specific bottom or rope plot where the mussel seed will be brought to for growing out further), and any incidents or unusual observations. Mussel density (number) per unit substrate was calculated by dividing the biomass (g) per unit substrate (m or m^2) by the average mussel weight (g). The most recent results are reported by Capelle (2023).

We calculated the substrate production efficiency as kg harvest per m rope or per m^2 net. In order to compare efficiency between rope and net systems, a Rope Equivalent (REq) index was calculated by dividing the mean annual efficiency of nets (kg m^{-2}) by that of ropes (kg m^{-1}). This unit represents the length (m) of rope needed to obtain a similar harvest as 1 m^2 of net. Over the period 2010–2022, the REq was 12.0 m.

SMC systems are deployed from March until May, with most activity occurring in April. Regulations stipulate that SMCs be removed before November 1st. Harvest of seed takes place from late June until early October. Mussel farmers generally aim to harvest before large aggregations of mussels start to detach and fall off.

2.3.2. SMC growth data

The production data (paragraph 2.3.1) did not permit direct investigation of the effect of self-thinning (Fréchette et al., 2010) on the development of mussel seed density (# m^{-1}) and biomass (g AFDW m^{-1}). Instead, data originally presented by van Broekhoven et al. (2014) were re-evaluated for this purpose. This dataset comprised mussel seed numerical and biomass densities on collector rope sections on six sampling dates (27 June, 11 and 25 July, and 9, 14, and 22 August) spanning the 2012 growing season at Galgeplaat, an SMC location in Oosterschelde Bay (G in Fig. 1, currently inactive). The rope sections were placed on 4 May, and samples were taken starting from shortly after first observed settlement in large numbers, to the point of harvest which took place within days of last sample. The methods used are described by van Broekhoven et al. (2014).

2.4. Data analysis

Data exploration prior to the analysis was carried out following the protocol in Zuur et al. (2010), where appropriate. For each statistical model, histograms of residuals were produced to get an impression of normality. Residual diagnostic plots were used to obtain indications of heteroscedasticity and acf plots were used to detect autocorrelation for the models when appropriate.

2.5. SMC effort and mussel seed production over time

We analyzed trends in total harvest per year for each type of system (ropes or nets), with data available from 2011 to 2022, and for each area (Wadden Sea, North Sea, and Oosterschelde Bay), with data available from 2006 to 2022. Additionally, we examined seed collection effort, defined as the amount of substrate used in terms of length of rope (km) for rope substrate and length of Rope Equivalent (km) for net substrate, available from 2010 to 2022.

Given the nonlinear nature of both total harvest per year and effort over the study period, we employed generalized additive modeling (GAM) for analysis. GAMs were constructed in R using the ’mgcv’ package (Wood, 2011), and model diagnostics were conducted using the ’DHARMa’ package (Hartig, 2022).

All GAM models utilized cubic spline regression, with parameter estimation performed using Restricted Maximum Likelihood (REML). We modeled total harvest per year using an unpenalized smoother, while for harvest trends over time at different locations, efforts (km rope eq), and types of systems (ropes vs. nets), we employed a penalized smoother. To address heteroscedasticity in the relationship between effort and location, we applied a Tweedie distribution.

Model summaries, diagnostic plots, and partial effects for all GAM models are provided as supplementary material.

2.5.1. SMC mussel growth rates

Average annual growth rate (whole mussel wet weight [WW] per day [d]) on ropes was estimated for each of the last 12 years (2011–2022) by using the exponent of the slope from the log-log relation between size of the mussel at harvest and Julian day number (Figure S10). A distinction was made between the areas (Oosterschelde Bay and Wadden Sea), but not between locations within those areas. The North Sea SMC site was disregarded since it only represented an individual location.

2.5.2. Density-dependent growth

The relationship between the harvest per unit substrate (kg m^{-1}, with REq for nets) and the growth rate of mussels was analyzed using a multiple regression analysis. This analysis incorporated year and area (Wadden Sea or Oosterschelde Bay) as covariates to account for their potential effects. Furthermore, a parallel analysis was conducted using the average density of mussels per unit substrate as the explanatory variable, as mussel growth may exhibit density-dependent dynamics.

The occurrence of density-dependent growth on the ropes was evaluated by the relation between estimated mussel density per unit substrate at harvest (N, # m^{-1}) and harvested biomass per unit substrate (B, kg m^{-1}), where a curvilinear relation would suggest density-dependent growth (Fréchette et al., 2010). For July and August, the number of harvest observations was deemed sufficient (>50, VanVoorhis and Morgan, 2007) for this analysis. An F-test was employed to compare the suitability of a curvilinear model against a linear model using data pooled over the most recent years. Specifically, observations from the years 2016–2022 for the months of July and August were assessed separately for a log-log fit using an F-test.

2.5.3. Self-thinning

Specific investigation of self-thinning on ropes over the course of a growth season was based on growth data (density, # m^{-1}, and mean individual biomass, mg AFDW ind^{-1}) from one SMC location (paragraph 2.3.2). Hypothetical trajectories of density (# m^{-1}), mean individual biomass (mg AFDW m^{-1}), and biomass per unit culture rope (g AFDW m^{-1}), were calculated by means of fitted mathematical functions. Specifically, a cubic spline was fitted to the density data (calculated in R version 3.5.1 using function interpSpline in package spline), and a power function was fitted to the mean individual biomass data. Biomass per unit culture rope was calculated as the product of these two parameters.

2.5.4. Production efficiencies per SMC location and area

Differences in seed production efficiencies between SMC locations (see Fig. 1) and area (Wadden Sea, North Sea, and Oosterschelde Bay), were evaluated in terms of total harvest (kg) and harvest per unit substrate (kg m^{-1}, with REq for nets), using a two-way analysis of variance and a *post hoc* Tukey HSD test. Harvest per unit area (kg ha^{-1}) was log-transformed to normalize model residuals. Trends in harvest per unit substrate (kg m^{-1}, with REq for nets), substrate density (km ha^{-1}), and harvest per unit area (kg ha^{-1}) were analyzed per area with a linear model. Substrate density in the North Sea and Oosterschelde Bay, and harvest per unit area in Oosterschelde Bay, were log-transformed to normalize residuals. Also, differences in harvest per unit area between nets and ropes were tested with a linear model for the different areas.

The correlation between harvest per unit substrate (kg m^{-1} (REq)) and substrate density (km (REq) ha^{-1}) for the three production locations with the highest mean annual harvest over the period 2010–2022 (Vogelzand, Zuidmeep, and Gat van Stompe) was analyzed with a Kendall rank correlation procedure, after a Shapiro-Wilk test indicated a non-normal distribution of underlying variables.

3. Results

3.1. Deployment effort and mussel seed production over time

Seed collection effort, as defined by overall SMC placement (km of rope, or km REq for nets), exhibited a substantial increase from 2580 km in 2010–6565 km in 2022 (Fig. 3a), with a significant difference between the areas ($p<0.001$, Table S3). Most of the SMCs were deployed in the Wadden Sea, comprising 81% of the total in 2022. SMC usage in this area exhibited an upward trend until 2016, after which it plateaued (Table S3, Figure S5). In the North Sea, SMC use also demonstrated an overall positive trend over time ($p=0.01$, Table S3, Figure S5). There is also a significant change in production over time in Oosterschelde Bay ($p<0.001$, Table S3), but this trend is more complicated, with in increase up to 2013, followed by a decrease until 2018/2019 after which the trend increases again (Figure S5).

Total annual harvest of SMC mussel seed increased over the period 2006–2022, from 1.0 $\times 10^6$ kg in 2006–20.8 $\times 10^6$ kg in 2022 (Fig. 3b, $p<0.001$, Table S1). This contrasts with the harvest from mussel seed fisheries (Fig. 3c), which showed no clear trend since approximately 2006. SMC harvest differs between regions ($p<0.001$, Table S2): in the Wadden Sea ($p<0.001$, Table S2) and the North Sea ($p<0.001$, Table S2) it increased over this period (Figure S3). Harvest from Oosterschelde Bay also changes over time ($p<0.001$, Table S2), but in a similar pattern as for the amount of substrate: an increase up to 2012/2013, followed by a decrease up to 2018 and since then increasing (Figure S3).

Since 2011 data was available to distinguish between rope systems and net systems in the harvest reports (Fig. 3d). Harvest from rope systems displayed an increasing trend since 2011 ($p<0.001$, Table S4), whereas harvest from net systems showed no significant trend (Figure S7).

3.2. SMC mussel growth rates

A positive and significant relationship was observed between the estimated growth rates of mussel seed on ropes from the Wadden Sea and from Oosterschelde Bay ($F_{(1,10)}=5.57$, $p=0.04$, $R^2=0.58$, Figure S9). This indicates that growth rates followed similar patterns in both regions.

3.3. Density-dependent growth

The Pearson correlation coefficient between the estimated growth rate, and the mussel density at harvest, was 0.40 (Fig. 4a). This relationship was statistically significant (t-test, $p<0.001$). In the analysis of the relationship between either growth rate or density, and harvest per unit substrate (Table S5 and Table S6), the model based on mussel density yielded the lowest Akaike Information Criterion (AIC) value and was consequently selected, while the other model (based on growth rate) was discarded. In the combined data of Oosterschelde Bay and Wadden Sea (the North Sea location was disregarded in the multiple

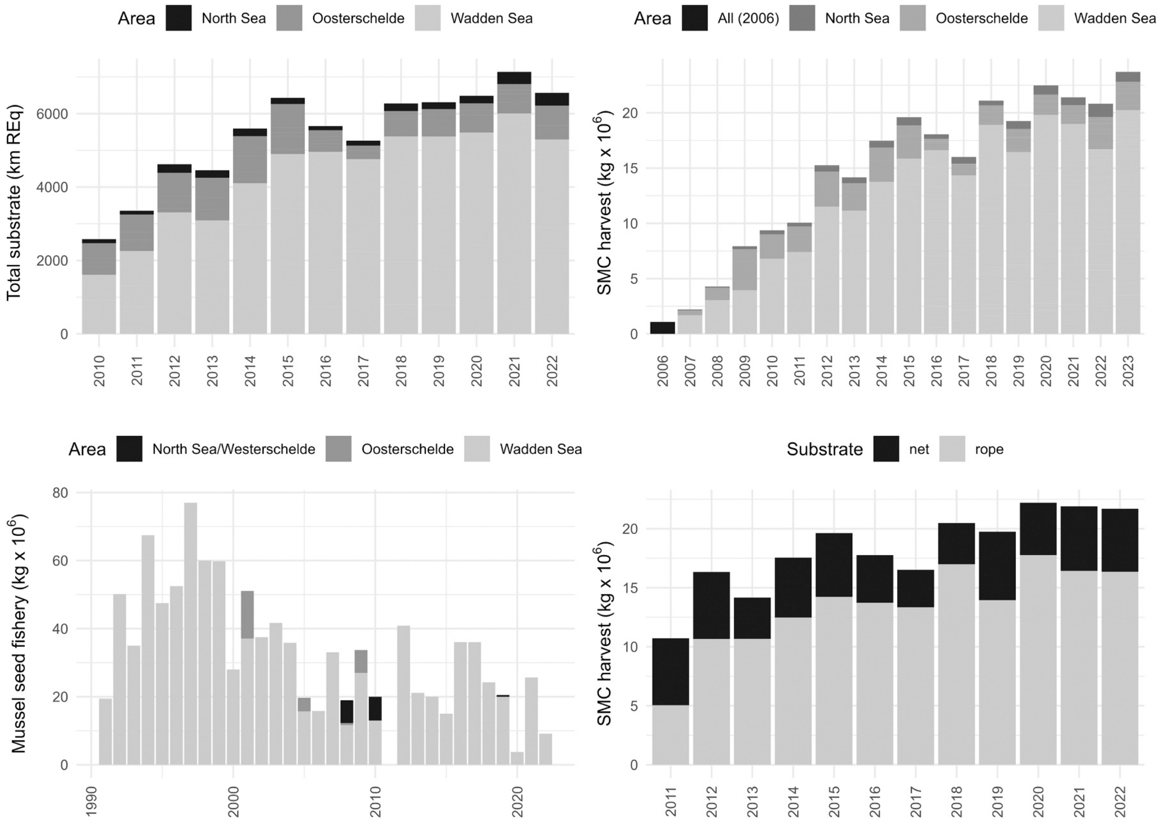

Fig. 3. (a) Annual amount of substrate deployed (REq in case of nets) in the three SMC areas in the Netherlands; (b) Annual SMC harvest in the same areas since 2006; (c) Annual seed production from seed fisheries in the Netherlands since 1991 in the same areas (Westerschelde included with North Sea); (d) Annual SMC harvest for net and rope systems; data available separately since 2011.

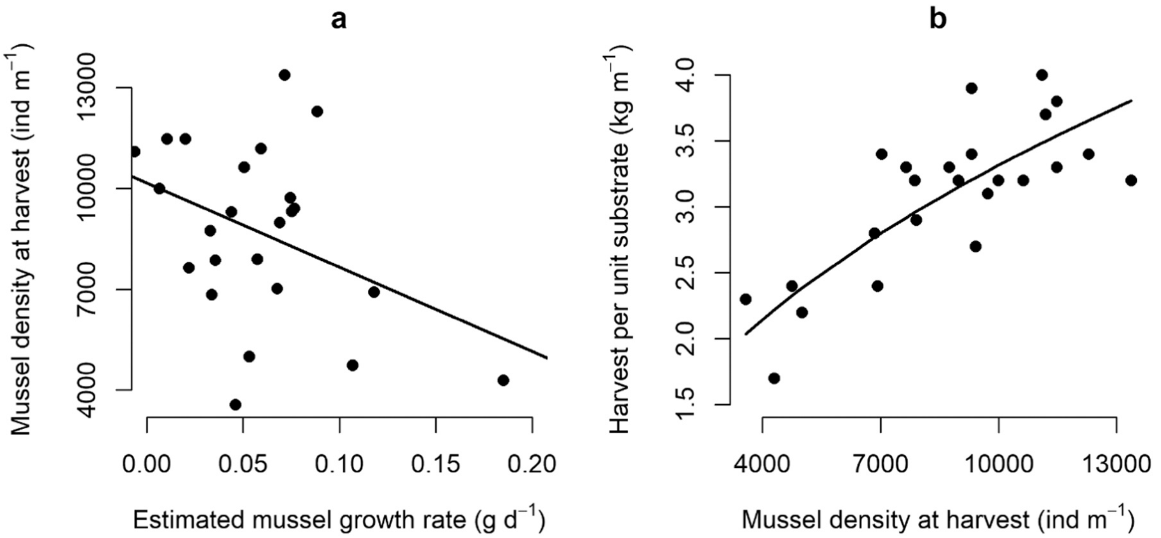

Fig. 4. (a) Linear relation between estimated mussel growth rate (g WW d^{-1}) and mussel density at harvest (# m^{-1}); (b) Logarithmic curvilinear relation between mussel density at harvest and harvest per unit substrate (kg m^{-1}). Data are only from ropes, not from nets. Each dot represents the mean of a year, Oosterschelde Bay and Wadden Sea areas combined, in the period 2011–2022. Lines indicate a significant relation.

regression since it was a single site, only consistently used by one farmer with net-based systems), the average harvest per unit substrate was found to be higher when the averaged mussel density was higher at harvest (F(1,22)=30, p<0.001, Fig. 4b, Table S6). There was no significant difference between the two areas. Moreover, a logarithmic curvilinear relationship between averaged harvest per unit substrate and averaged mussel density provided a significantly better fit (F-test, p<0.001) compared to a linear relationship.

The density-biomass relation was explored in more detail using the data for each reported harvest activity in the more recent period 2016–2022. A power relation between mussel density per unit substrate (N, # m^{-1}) and harvest per unit substrate (B, kg m^{-1}), provided a better fit (July $F_{(1460)}=134$ $p<0.001$, August: $F_{(1789)}=801$, $p<0.001$, Tables S7 and S8) for both months than a linear relation (Fig. 5): July ($F_{(1460)}=481.1$, $p<0.001$), August ($F_{(1789)}=1139$, $p<0.001$). The power function is remarkably similar between both months (July: $B=0.01*N^{0.61}$; August: $B=0.01*N^{0.62}$). This similarity suggests a comparable density dependence of growth on ropes between months, although size (median July = 0.27 g; August = 0.38 g) and density (median July = 12,174 seed m^{-1}; August = 8729 seed $^{-1}$) differed.

3.4. Self-thinning

In the growth data covering a full SMC season at the Galgeplaat SMC (G in Fig. 1; Fig. 6), numerical mussel density first increased rapidly and subsequently rapidly reduced, together with an increase of mussel biomass, before finally levelling out together with an accelerating mussel biomass increase. Towards the end of the observation period (from day 97), mean shell length increased more slowly than mean individual biomass.

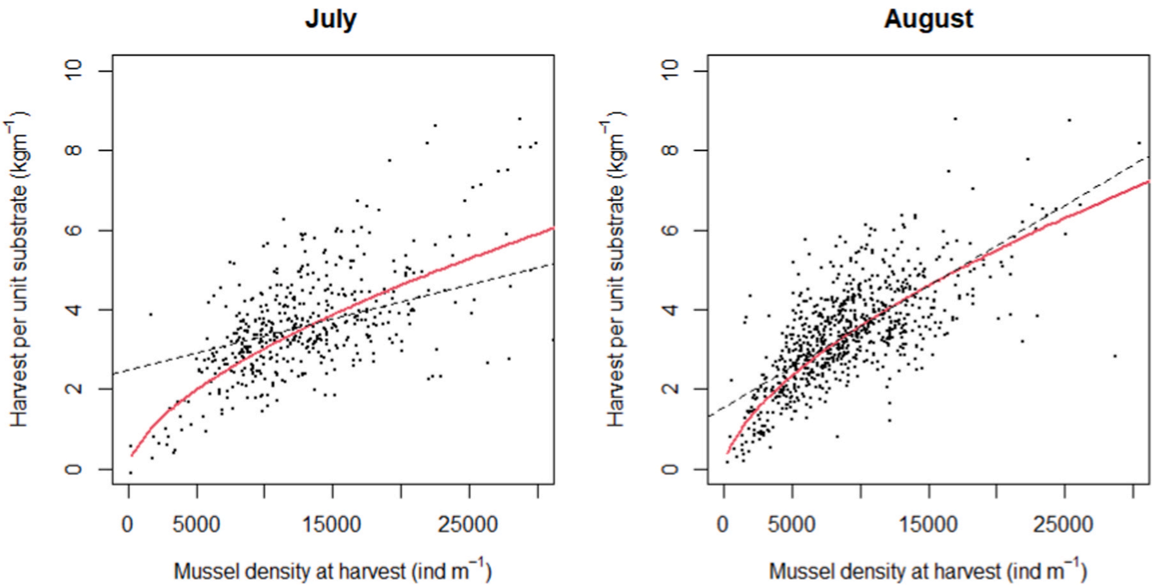

Fig. 5. Mussel harvest per unit rope substrate (kg m^{-1}) versus mussel density per unit rope substrate (# m^{-1}) for July and August over the years 2016 and 2022. Each dot represents a single harvest event. The red line shows a fitted logarithmic curvilinear relation, and the dotted line shows a fitted linear relation. For both months, the curvilinear relation provided a better fit.

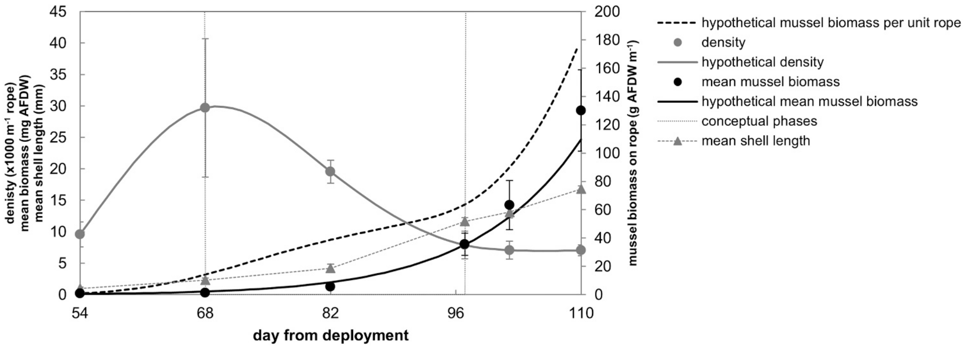

Fig. 6. Symbols represent mussel density, mean individual tissue mass, and shell length on the Galgeplaat SMC in Oosterschelde Bay during the 2012 season, from 27 June (day 54 from SMC deployment) to 22 August (day 110 from SMC deployment). The curves for density and mean mussel biomass were fitted to the data visualize the hypothetical trajectory over time as an approximation. The dashed line shows the product of these two parameters, indicating the hypothetical tissue biomass per unit rope. Mean shell length observations are connected by straight lines. Error bars indicate SD (n=5 ropes). The vertical dashed lines separate three apparent phases in the density of mussels on the ropes: i) increase, ii) decrease, iii) stabilization accompanied by accelerating biomass increase.

3.5. *Production efficiencies per SMC location and area*

Not all SMC locations (see Fig. 1) were used intensively. Mean annual production per location from 2015–2022 is summarized in Fig. 7a. Over this period, the majority of SMC seed (85% since 2015) was produced in the Wadden Sea. Overall, mean annual harvest (kg) and mean annual harvest per unit substrate (kg m^{-1} (REq), Fig. 7b) differed between locations ($F_{(8119)}=17$, $p<0.001$, Table S9 and $F_{(8119)}=2$, $p=0.03$, Table S10). Of note is the proprietary system with nets suspended under rafts was implemented on a relatively large scale in Oosterschelde Bay by a single mussel farmer who ceased operations after 2015. These systems were characterized by a high density of substrate per farmed area, but a lower harvest per square meter of substrate compared to other net-based systems. For instance, in Oosterschelde Bay in 2015, the substrate density for rafts with nets was 10,692 m^2 ha^{-1}, whereas other net-based systems had a substrate density of 1591 m^2 ha^{-1}. However, the harvest from the former was 13.9 kg m^{-2}, whereas the latter yielded 36.5 kg m^2.

There was a significant increase in substrate density in all three areas (km (REq) ha^{-1}) (Fig. 8, left panel set and Table S11). Between 2010 and 2022, an increase in efficiency in SMC harvest per unit substrate (kg m^{-1} (REq)) was only found in the Oosterschelde Bay area (Fig. 8, right panel set and Table S11). The mean harvest per unit substrate in Oosterschelde Bay was significantly lower ($p<0.001$) than in the Wadden Sea (Table 1). Harvest per unit substrate in the North Sea was also higher than in Oosterschelde Bay ($p=0.002$), while there was no significant difference between the Wadden Sea and the North Sea. This difference was caused by a lower density of mussels on ropes (# m^{-1}) in Oosterschelde Bay and not by size differences at harvest (Table 1).When considering all the data together, the harvest per unit area (Mg ha^{-1}) showed an overall increase over time ($F_{(12,56)}=3$, $p=0.006$, Table S11a). There were significant differences in the harvest per unit area between areas ($F_{(2,56)}=10$, $p<0.001$) and between substrate types ($F_{(1,56)}=16$, $p<0.001$). Furthermore, there were distinct differences in the trends between areas and substrate types, as indicated by the significant interaction between area and substrate type ($F_{(2,56)}=13$, $p<0.001$).

Specifically, the harvest per hectare in Oosterschelde Bay showed a substantial increase for ropes ($t_{(11)}=5.4$, $p<0.001$), while it did not change significantly for nets (Fig. 9). Conversely, in the North Sea ($t_{(11)=}5.4$, $p=0.006$) and Wadden Sea ($t_{(11)}=3.7$, $p=0.003$), there was an opposite trend, with nets showing an increase in harvest per hectare, while ropes did not exhibit a significant trend (Table S12). The relation between harvest per unit substrate (kg m^{-1}) and substrate density (km ha^{-1}) was tested for the top-three largest SMC locations with the highest mean annual harvest (all in the Wadden Sea and rope-based): Vogelzand (140 ha), Zuidmeep (80 ha) and Gat van Stompe (75 ha). No significant trend was found (Fig. 10).

4. Discussion

4.1. *Production of mussel seed with SMCs*

Analysis of 12 years of production data reveals that, from a biological perspective, seed collection is essentially self-regulating. Harvest per unit substrate did not show large inter-annual fluctuations between areas and between years (Fig. 8), especially when compared to natural recruitment into wild mussel seed beds, which is much more erratic (Van der Meer et al., 2018). Therefore, the increase in production over time and differences between areas can be explained by the increase in effort.

A variety of adverse events occurred over the years. The most prominent issues that have been reported that negatively affected yields and/or that required a large effort to mitigate, are summarized in Table 2. However, the only event that shows up as a lower value in overall production data was fouling by other organisms in Oosterschelde Bay in 2021 and 2022. Fouling on SMCs is often reported to be a problem, especially on nets in Oosterschelde Bay. Problematic fouling species are the ascidians *Ciona intestinalis*, *Molgula manhattensis* and *Styela clava* and the crustaceans *Monocorophium acherusicum* and *Jassa falcata*. This is considered to be the main reason why, at least for net-based systems, yields are generally lower in Oosterschelde Bay than in the Wadden Sea. The reason that nets are more prone to fouling is unclear, but, speculatively, might be related to nets creating more sheltered conditions than ropes. In 2021 and 2022, massive settlement of the bryozoan *Electra pilosa* on the substrate occurred at most locations. This has caused problems with harvesting and resulted in high tare (non-mussel material) percentages of the harvest. Rope substrate was especially affected, in Oosterschelde Bay and North Sea in 2021. This is reflected in a lower harvest per unit substrate and per unit area (for example, see Figs. 8 and 9). Apart from this recent problem, SMCs have generally proven to be a robust source of mussel seed.

The lack of a reliable seed provisioning source is referred to by studies from all parts of the world as a principal factor that limits mussel production (Avdelas et al., 2020; Fuentes and Molares, 1994; Jeffs et al., 1999; Kamermans and Capelle, 2019; Laxmilatha et al., 2011; Maguire et al., 2007). The nature of this problem is the dependency of extensive bivalve culture on natural processes, starting with recruitment for the provisioning of seed. In our study area, recruitment of mussel seed on natural mussel beds can show large annual variability (Beukema and Dekker, 2007; Dankers and Koelemaij, 1989; Van der Meer et al., 2018). However, the high annual variability in larval abundance and settlement does not appear to translate to recruitment success on SMCs and cannot be used to explain spatial variation (Zhao et al., *submitted*). On natural mussel beds, De Vooys (1999) was unable to find a relation between the adult mussel stock and the number of plantigrades, and between the number of plantigrades and recruitment. This suggests that mussel bed

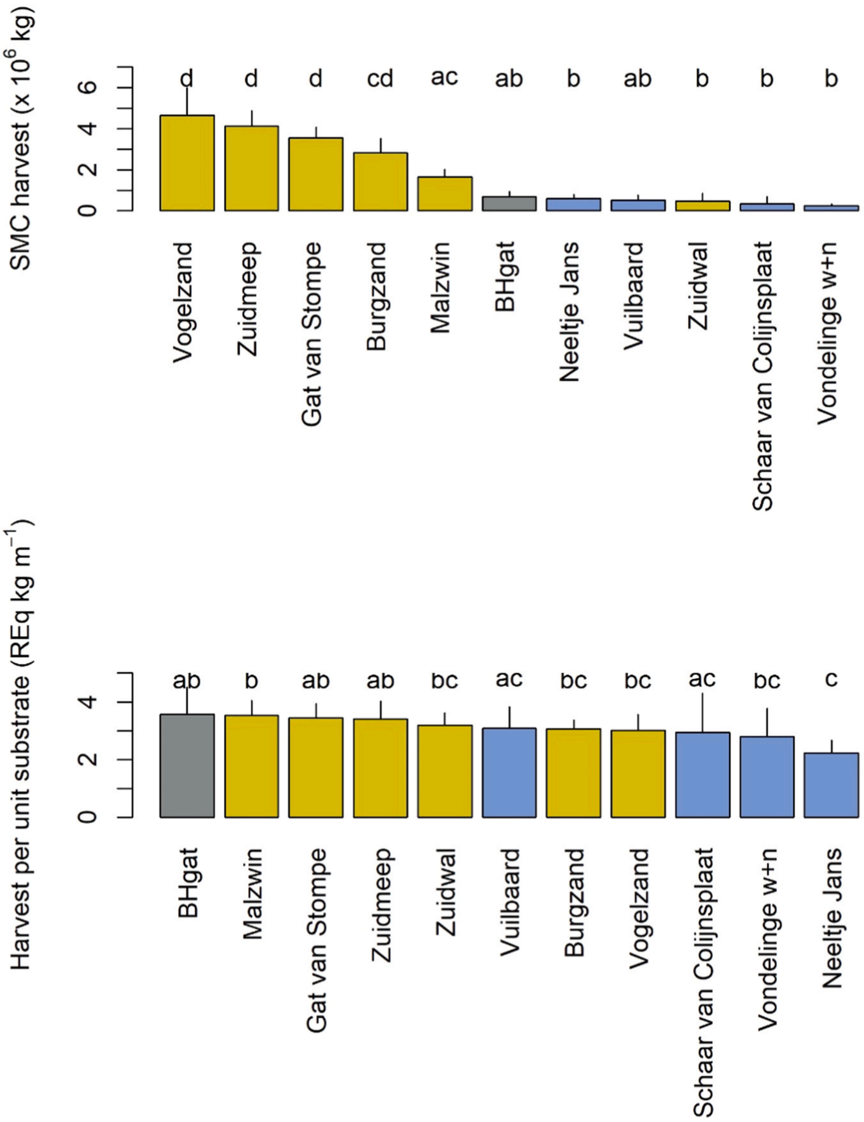

Fig. 7. (a) mean annual harvest per SMC location, and (b) mean annual harvest per unit substrate (kg m^{-1} (REq)), for the different SMC locations over the years 2015–2022 (error bars show standard deviation). Colors indicate SMC production area: yellow represents Wadden Sea, blue Oosterschelde Bay, and grey North Sea, letters indicate significance with an α-level of 0.05.

recruitment is limited by other factors, in which habitat availability and predator dynamics seem to be key processes (Van der Heide et al., 2014). These factors do not appear to play a role with SMCs. Here, artificial settling material is introduced every year and is therefore sufficiently available. Also, no observations were made of benthic or pelagic predators hampering mussel seed production. The heavy starfish predation in 2011 did not result in lower yields (Table 2). In other areas of the world, predation on suspended culture at this stage can be substantial, for example by fish (Peteiro et al., 2010; Šegvić-Bubić et al., 2011), or by waterfowl (Varennes et al., 2013). The overall absence of such major effects on SMCs appeared to result in a predictable harvest with low variation per unit of substrate (kg m^{-1} (REq)) and in a reliable seed supply.

4.2. Variation in harvest efficiency

Despite years of development in seed collection techniques, harvest per unit substrate (kg m^{-1} (REq)) did not increase significantly (Fig. 8) and no indicators were found in our analysis as to how this could be improved. Harvest per unit substrate fluctuated around 3 kg m^{-1} (REq) in all three areas; Oosterschelde Bay reached this level after cessation of the single dominant net-based production location that was producing lower levels of harvest per unit substrate until 2015, using a proprietary multi-net raft system (paragraph 2.2 and Fig. 2d). The lower harvest per unit substrate of the raft systems does show that not all tested substrates have achieved the same level of performance. The disappearance of this system also exemplifies that less productive and less practical SMC systems were phased out by trial and error, to the extent that, after 10 years, only two viable systems remain. At the North Sea production location, high harvest per unit substrate levels of approximately 4.5 kg m^{-1} (REq) were reached in 2015 and 2017, but the mechanism behind this is not clear.

In terms of production per unit area (kg ha^{-1}), no indications of overstocking were found as this would have led to reduction at higher substrate densities (km (REq) ha^{-1}), which was not observed (Fig. 10). No data are available to determine whether variation within the SMC systems occurs, such as reduced efficiency in the center of SMC clusters resulting from seston depletion (Cranford et al., 2008, 2014; Strohmeier et al., 2005). However, seston depletion is associated with low current speeds, where rope or net systems further reduce the current. Contrary to suspended mussel culture, which is usually found in sheltered areas to avoid mussel fall-offs (Aure et al., 2007; Drapeau et al., 2006), seed

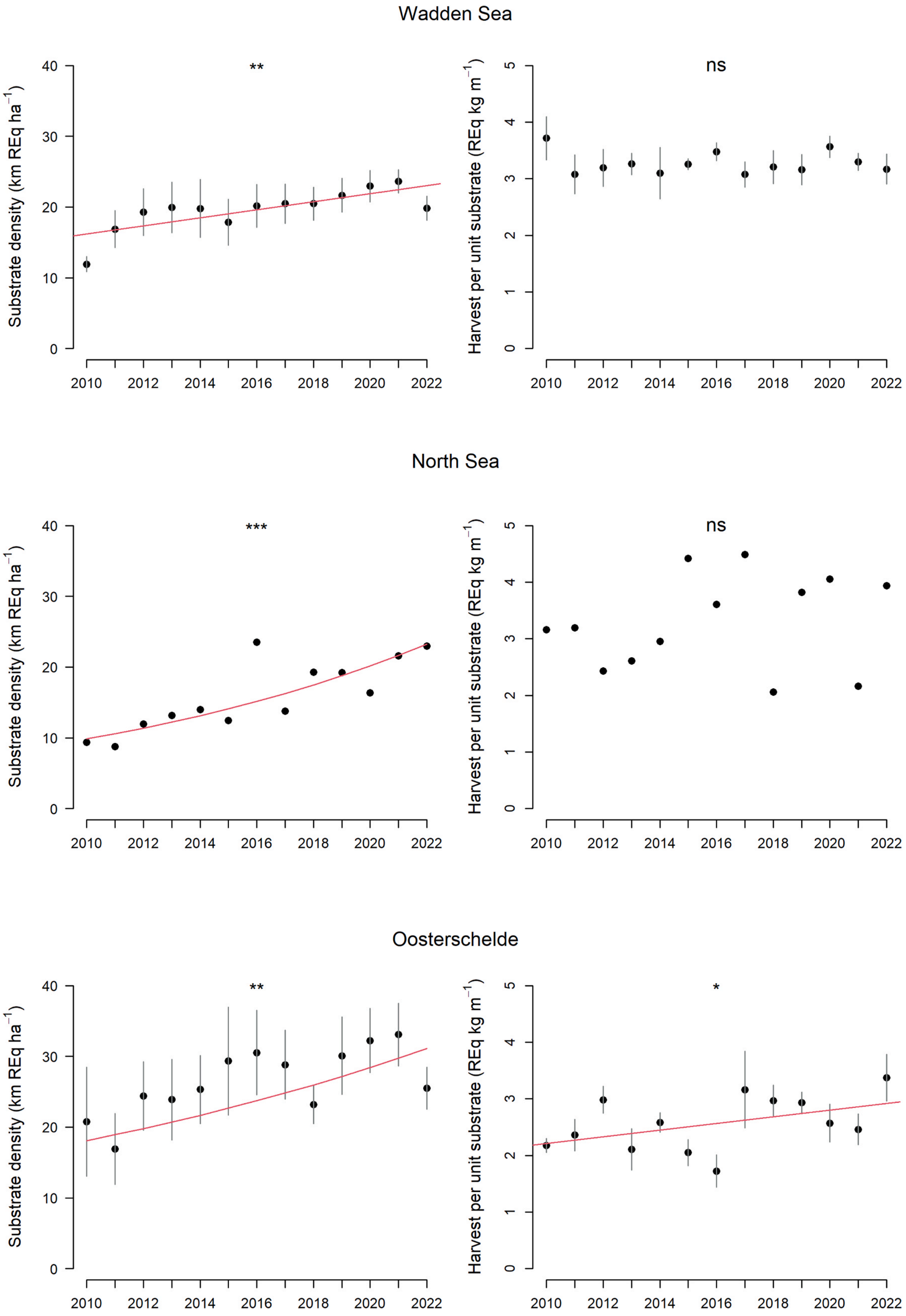

Fig. 8. Left panels: annual mean substrate density (km (REq) ha^{-1}). Right panels: annual mean SMC harvest per unit substrate (kg m^{-1} (REq)). Error bars show standard error; trend: ^{ns} not significant, * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

Table 1

Harvest per unit substrate per area, with mussel density and mean mussel biomass.

Area	Harvest biomass (kg m^{-1} (REq) substrate ± s.e.m.)	Mussel density on substrate(# m^{-1} (REq))	Mean mussel biomass (g)
Oosterschelde Bay	2.57 ± 0.10	7967	0.46
Wadden Sea	3.27 ± 0.07	9646	0.37
North Sea	3.30 ± 0.22	9556	0.46

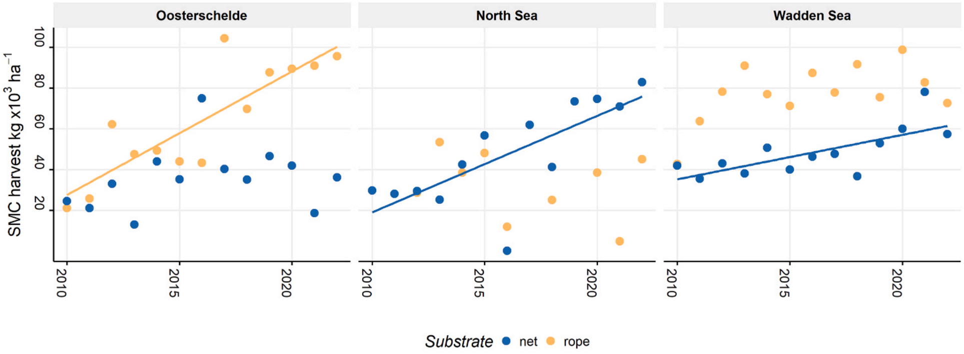

Fig. 9. Mean harvest of SMC seed per unit area from rope and net-based systems in the three production areas. Lines indicate significant trends.

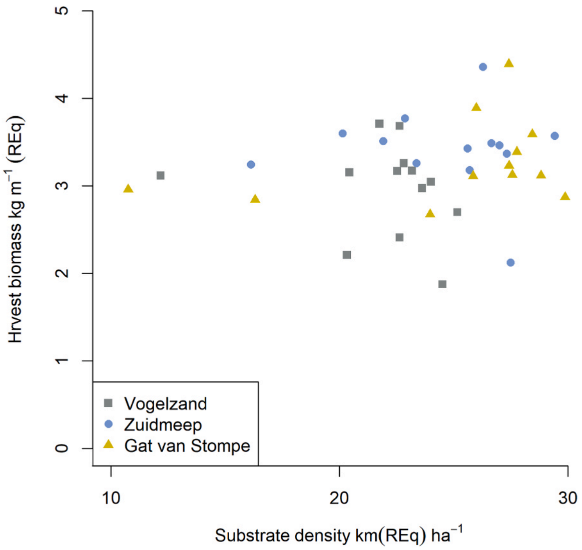

Fig. 10. Relation between harvest per unit substrate (kg m^{-1} (REq)) and substrate density (km ha^{-1}) for the three SMC areas with the highest mean annual harvest over the period 2010–2022. No significant trend was found.

collection for mussel bottom culture using SMCs occurs at exposed sites (maps in Capelle, 2023) where current velocities are relatively high and can reach 1 m s^{-1} (Nienhuis and Smaal, 1994; Jiang et al., 2019).

At the substrate level, a lower seed density (# m^{-1} (REq)) resulted in a lower harvest in Oosterschelde Bay than in the Wadden Sea and the North Sea (Table 1). This was not due to differences in growth rate, since this was not found to differ between Oosterschelde Bay and Waddenzee. Between years, harvest per unit substrate was remarkably stable. Considering that larval supply and settlement were not limiting (Zhao et al., *submitted*), this stability suggests environmental factors as driving forces of the lower numerical density and thus lower harvest per unit substrate in Oosterschelde Bay. However, it is not clear which environmental factors are responsible. Oosterschelde Bay is a semi-closed off basin, in contrast to the North Sea and Wadden Sea. The Wadden Sea is an open and much more dynamic environment than Oosterschelde Bay, with greater current velocities, greater food concentrations, but lower food quality (Capelle et al., 2021), and the North Sea SMC location is even more physically exposed than the Wadden Sea. In the North Sea we found higher densities of mussels, with similar sizes as in Oosterschelde Bay or the Wadden Sea. Food availability is higher in the North Sea than in Oosterschelde Bay (Smaal and Van Stralen, 1990) and probably also in the Wadden Sea, which suggests that not only space, but also food availability, modulates density on the SMCs.

4.3. Density-dependent growth

The allometric relation between mussel biomass and mussel density (# m^{-1} (REq), Fig. 5) corresponds with the occurrence of density-dependent growth on the ropes, which is expected, because the availability of substrate is limited (Fréchette et al., 1992; Guiñez, 2005). Growth rate was inversely related to density per unit substrate, and

Table 2

Most prominent major reported issues that negatively affected SMC production (only *Electra pilosa* fouling) and/or required a large effort to mitigate.

Year	Location	Cause
2011	Oosterschelde Bay and Wadden Sea	Massive starfish (*Asterias rubens*) settlement on SMCs. A significant manual cleaning effort was made but the mussels outgrew the starfish and untreated ropes ultimately produced equal amounts of seed.
2015	Wadden Sea	Summer storm in June damaged and entangled systems. No clear yield reduction followed.
2016	Oosterschelde Bay	Mass mortality event resulted in loss of most mussel seed in parts of the Bay, but overall Oosterschelde Bay production was not clearly affected.
2018	Wadden Sea	Unusual levels of fall-offs from net substrate caused by silt accumulation between mussels and substrate reduced yield. This did not clearly affect production.
2021-2022	All locationsWadden Sea	Heavy fouling with *Electra pilosa* causing problems with harvesting, resulting in reduced harvest per unit substrate and per unit area.

density per unit substrate was positively related to harvest per unit substrate (Fig. 4), suggesting that competition for space and / or for food at the substrate level increases with growth rate.

4.4. Self-thinning

We complemented the 2010–2022 SMC seed production data set with observations at the Galgeplaat SMC location (Fig. 6), where we observed mussel growth on culture ropes throughout a full mussel seed growing season. In the available literature, the development of densities, numbers, and biomass are not well described in the early stages of growth. For example, although Lachance-Bernard et al. (2010) argued that smaller mussels should be included in the study of self-thinning processes on mussel longlines because this captures more of the high mortality rates in early life, the authors still implemented a 5 mm shell length cutoff to accommodate methodological constraints in quantifying small specimens. In contrast, we were able to study the process from a much smaller lower shell length limit of 0.375 mm. Based on the trajectory of mussel density on the ropes we distinguish three apparent developmental phases (indicated by vertical lines in Fig. 6): a first phase in which density increased, a second phase in which density decreased, and a third phase in which density stabilized, accompanied by an accelerating biomass increase and a comparatively slower shell length growth. Numerical reduction, and thus self-thinning, dominated in the second phase. This phase corresponded to a mean shell length of around 2.3 mm (day 68 from SMC deployment, 11 July) to 11.6 mm (day 97, 9 August) (Van Broekhoven et al., 2014). Our data do not permit to distinguish between possible mechanisms of self-thinning. South et al. (2020), investigated *Perna canaliculus* seeded on ropes from a shell length of around 2 mm, a similar size as the start of the second phase in our data. These authors reported a combination of mortality, secondary settlement, and a proportion with an unknown fate. In both studies, the majority of mussels in this small size range were lost: 76% in our study and up to 85% in South et al., (2020). The general sequence observed on ropes can be expected to also take place on nets since these consist of ropes. We do not expect the lack of perpendicular filaments on nets, which are typically abundant on SMC ropes, to result in fundamentally different dynamics. A possible difference might occur if ropes and nets would be left in the water for extended periods of time, and fall-off of aggregations formed by mussels and associated species and organic material starts to occur. On nets, mats can form along a two-dimensional plane which does not exist on ropes. However, harvest of SMCs is typically aimed to take place before substantial fall-offs occur. The self-thinning phase in our study occurred prior to the phase in which most of the biomass was generated. This latter phase presumably contributed most to the observed density-dependent growth (paragraph 4.3). In other words, the outcome of apparent competition for space and / or for food shifted from high mussel seed losses to growth reduction during the course of the second half of the growth season.

4.5. Improving commercial production

Van Oostenbrugge et al. (2018) estimated that the production cost of SMC mussel seed is five to six times greater than seed from wild capture fishery. Furthermore, SMCs also require substantially more labor, which has forced a greater degree of cooperation between companies (van Oostenbrugge et al., 2018). Overall, the ongoing transition from wild capture fishery to SMCs has resulted in higher cost for seed provisioning, which has created a need for cost reduction to maintain a profitable operation.

Since SMC production per unit substrate (kg m^{-1} (REq)) does not appear to be amenable to improvement, and because production per unit area (kg ha^{-1}) did not show signs of overstocking, the logical avenue to increase production would be to increase substrate density per unit area to optimize the use of available space.

Other efficiencies could be sought in reducing processing effort via technical innovations. The main distinction between prevailing SMC implementations is between ropes and nets. Ropes provide a denser substrate than nets and result in greater yield per unit area. However, nets are less labor-intensive to use. Nets are bound up on the floaters when not in use, and when anchored at the start of the SMC season, the nets are simply rolled down. Ropes, on the other hand, are presently manually bound to a main line which is attached to floaters. Pilots using robotics technology have taken place. These pilots consisted of a platform that could move over an SMC system and that automatically installed and harvested the ropes (Brouwer et al., 2015a, 2015b). However, thus far this system has not been successful in marine conditions, due to biofouling problems.

Furthermore, to optimize the contribution of SMCs as a seed provisioning service for mussel culture, research should be directed to reducing the large post-seeding mortalities of collector seed, thought to relate to seeding practices, in order to make more efficient use of the resource (Capelle et al., 2016; Van den Bogaart et al., 2023).

5. Conclusion

Twelve years of production data show that SMCs can be a robust alternative seed provisioning resource for mussel culture compared to wild capture fishery: SMCs are more reliable yearly, and SMC seed quality is comparable to wild-caught seed. Substrate production efficiency (kg m^{-1} (REq)) fluctuated around a similar level between areas, and therefore did not appear to be amenable to further improvement. Plot production efficiency showed no signs of approaching a maximum, which suggests that going forward, production gains could potentially be made by increasing substrate density (kg ha^{-1}) above current levels. In addition, given the greater overall costs associated with SMCs compared to seed fishery, operating cost efficiencies and post-seeding mortality reduction are priority areas for further research.

CRediT authorship contribution statement

Karin Troost: Writing – review & editing, Conceptualization. **Jacob Capelle:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis. **Wouter van Broekhoven:** Writing – review & editing, Investigation, Formal analysis, Visualization. **Marnix van Stralen:** Writing – review & editing, Methodology, Conceptualization.

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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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aquaeng.2024.102414.

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