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RESEARCH ARTICLE

Boosting efficiency of mussel spat collection for ecological sustainability: Identifying critical drivers and informing management

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Abstract

1. The long-term sustainability of natural and bottom-cultured mussel beds relies on the availability of spat (i.e. juvenile mussels). Traditional spat collection methods, which disrupt the donor population and its habitat, have prompted the adoption of suspended mussel spat collectors (SMCs) as an ecologically sustainable alternative. However, practical experience has demonstrated that SMC efficiency is subject to significant spatiotemporal variability, with the underlying biotic and abiotic drivers remaining unresolved.
2. Based on 11-year SMC practices in the Dutch Wadden Sea, we first validated, through field experiments, the inference that larval abundance and settlement rate in seawater are the primary determinants of SMC efficiency. Secondly, we screened the key factors driving variation in SMC efficiency using an integrated dataset that includes both management options (i.e. user-defined factors, like SMC types) and environmental conditions (i.e. site-specific factors, such as hydrodynamics). Lastly, we developed a predictive model to explore the sensitivity of SMC efficiency to these key factors.
3. The efficiency of SMCs was not affected by larval abundance and settlement rate, but rather regulated by management options and environmental conditions, with the key factors identified as SMC type, substrate size, mean wave height and starfish abundance.
4. Rope-based SMCs outperform net-based SMCs in terms of harvest efficiency. Both types of SMCs exhibit consistent sensitivity to environmental conditions, with harvest efficiency higher in areas with lower mean wave height and fewer starfish. Increasing substrate size (i.e. rope length and net area) in these areas has the potential to further improve SMC efficiency.
5. *Synthesis and applications*: Our study highlights the importance of environmental conditions over life cycle-related factors in regulating SMC efficiency. This offers optimistic prospects for investment in larger-scale deployment of SMCs

and maximizing efficiency through site suitability assessments beforehand. The predictive model we developed can provide information for this purpose. Furthermore, strategically adjusting management options would further optimize SMC efficiency, but it is necessary to balance the associated benefits and costs. Overall, our study underscores the predictability and controllability of SMC efficiency and informs management to maximize sustainable spat supply in both mussel culture and restoration.

KEYWORDS
aquaculture, ecological sustainability, feature selection, machine learning, mussels, spat collectors, Wadden Sea

1 | INTRODUCTION

Mussels (Bivalvia: Mytilidae) are a prominent feature in intertidal and subtidal habitats worldwide and play vital ecological roles in marine ecosystems (Schotanus et al., 2020; Troost et al., 2022). They exert top-down control on carbon-fixing phytoplankton populations and sequester carbon through shell production and sediment stabilization (Sea et al., 2022; Suplicy, 2018). Mussel beds provide intricate structures that accommodate diverse flora and fauna, and function as secondary habitats to enhance overall biodiversity (Beadman et al., 2004). As a biological barrier that regulates flow and reduces erosion, mussel beds are recognized as natural coastal defence structures for stabilizing coastlines (Schotanus et al., 2020). Alongside naturally settled beds, mussels are also cultured in 'artificial' beds, as seen in the bottom cultivation of mussels in Europe (Avdelas et al., 2021; Capelle et al., 2017). While providing a sustainable protein source with minimal environmental impact, mussel aquaculture also has positive contributions to the surrounding ecology in a manner that resembles wild mussel beds (see van der Schatte Olivier et al., 2020 for a review).

The life cycle of mussels begins with spawning, followed by the development of planktonic larvae, settling and metamorphosing into attached spat, and growth into adult mussels, which reproduce to start the cycle anew (South et al., 2022). During the cycle, the availability of settled spat is crucial for determining the abundance and resilience of wild mussel beds, as well as ensuring high yields in bottom-cultured mussel beds (Kamermans et al., 2002; Toone et al., 2022). Contrasting with the natural recruitment of wild mussel beds, traditional mussel bottom culture involves dredging spat from natural subtidal or intertidal beds and transferring them to suitable sites for on-growing (Smaal et al., 2021). However, uncontrolled spat collection can have detrimental and largely unquantified consequences on wild mussel populations and their habitat, driving the transition of the ecosystem into a declined state (Smaal et al., 2021; South et al., 2020). These concerns have prompted legislated restrictions on dredging spat from wild mussel beds in Europe (Avdelas et al., 2021). As an illustration, in the Dutch Wadden Sea, 50% of subtidal areas with wild mussel beds were protected from spat collection in 2022, with this proportion set to rise to 65% by 2026. These constraints ended the prospect of continuing bottom mussel culture using only dredging for spat provisioning, while also hinting at the vital necessity of finding sustainable alternatives to compensate for the resulting shortage of spat supplies (Jacobs et al., 2014; Kamermans & Capelle, 2019).

Suspended mussel spat collectors (SMCs) are artificial nursery structures (such as ropes or nets) suspended in seawater that attract and gather planktonic larvae, facilitating spat settling and growth (Jacobs et al., 2014; Kamermans et al., 2002). They effectively avoid damaging wild mussel beds and enable control of spat collection time and volume, making them an ecologically sustainable alternative (Filgueira et al., 2007; Kamermans & Capelle, 2019). The application of SMCs has been widely encouraged and implemented since the 21st century in Europe (Kamermans et al., 2002). For instance, the Netherlands has set a goal to fully replace wild spat dredging with SMCs by 2029. Despite their advantages, the harvest efficiency of SMCs is subject to significant variability due to multiple drivers that may interact over varying spatial and temporal scales (Jacobs et al., 2014). While some drivers, such as temperature, may typically impact SMC efficiency over larger spatiotemporal scales (Matoo et al., 2021), others can drive variation at smaller spatiotemporal scales, such as changes in wave height, current velocity and salinity in response to local oceanography and hydrodynamic regimes (Lin et al., 2016; Mascorda Cabre et al., 2021). Additionally, important drivers that may influence SMC efficiency include the abundance of mussel larvae in seawater and their settlement rate, as well as management options like the substrate type and size used in SMCs (Christensen et al., 2015; Filgueira et al., 2007; Fuentes-Santos & Labarta, 2015). The current ability to identify the dominant factors among them is highly limited by scarce evidence and hindered by the challenges associated with integrating data from multiple mussel farming companies and government agencies (South et al., 2022; Toone et al., 2022). Particularly, the absence of both quantitative and qualitative relationships between SMC efficiency and dominant factors presents a challenge in predicting and evaluating the effectiveness of SMCs at specific locations, as well as in informing management strategies aimed at fostering the development of sustainable mussel aquaculture (Kamermans & Capelle, 2019; Mascorda Cabre et al., 2021).

In this study, our objective was to examine the variability of SMC efficiency under different habitat conditions and management options. Specifically, we dedicated to address the following key research questions (KRQ):

1. Is SMC efficiency consistent across time and space?
2. Does SMC efficiency rely on biotic drivers in response to mussel life cycle, such as larval abundance and spat settlement?
3. Are there critical drivers that would improve the predictability of SMC efficiency?
4. How does SMC efficiency change with potential management strategies targeting identified critical drivers?

Adopting the Dutch Wadden Sea as a model system, we first addressed KRQ_1 by investigating the deployment and harvesting of SMCs in this region over an 11-year period. Secondly, KRQ_2 was validated through a 4-year experiment at four representative sites. Thirdly, we utilized machine learning algorithms on an integrated 11-year dataset to identify dominant factors affecting SMC efficiency and develop a predictive model, addressing KRQ_3. Fourthly, KRQ_4 was addressed by conducting model experiments that evaluated the sensitivity of SMC efficiency to critical factors. Finally, we suggested management strategies targeting critical factors to mitigate the variability of SMC efficiency and discussed the ecological implications of SMC application.

2 | MATERIALS AND METHODS

2.1 | Describing the spatiotemporal dynamics of suspended mussel spat collector efficiency

The investigations into SMC efficiency were conducted in the Dutch Wadden Sea (Figure 1), where the blue mussel (*Mytilus edulis*) is widely distributed across wild intertidal and subtidal beds, as well as on subtidal bottom-culture lots (Capelle et al., 2017). Since 2006, SMCs have been introduced into this area and increased rapidly from 2009 onwards to compensate for the shortage of mussel spat supply caused by restrictions on harvesting spat from the wild beds. The SMCs practised in the Dutch Wadden Sea can be broadly distinguished into two categories: (1) *Rope-based collectors*, in which filamentous ropes are maintained in the water column using anchored floats like buoys or pipes horizontally connected between anchor piles; (2) *Net-based collectors*, where nets are suspended under buoys or tubes and secured in the seabed with anchor piles. By 2021, the SMC application area in the Dutch Wadden Sea has expanded to 216 hectares, with rope-based collectors under buoys and net-based collectors under tubes being the mainstream structures (see examples in Figure 1).

Typically, SMCs are installed between March and May, harvested in batches at different times and must be completely removed by November according to regulations. From 2006, the local management agency launched investigations targeting mussel farmers who deployed SMCs on government-leased lots. To keep their permit, farmers were obliged to complete separate questionnaires during the deployment and harvesting periods each year, reporting on (i) the location, date, type, size, etc. of deployed SMCs, and (ii) the location, date, batch, size, harvest, etc. of harvested SMCs. In this study, the SMC efficiency on a yearly basis (i.e. within a single installation period) in 63 plots across eight locations (Figure 1a) from 2011 to 2021 was calculated using collected information, expressed as biomass per unit of substrates (i.e. rope and net). Note that two types of SMCs were deployed in distinct plots without mixing, and not all locations installed both types of SMCs annually (see details in Figure 2). Harvesting for rope-based SMCs occurred at different sections of the rope, with each section being harvested once. The average efficiency of all harvested sections was utilized to indicate the harvest efficiency within the plot. In contrast, net-based SMCs were repeatedly harvested at different stages to minimize self-thinning effects. The sum of efficiencies from multiple harvests was used to indicate the harvest efficiency within the plot. To compare the efficiency across SMC types, a rope equivalent was introduced by dividing the annual average efficiency of net ($kg\,m^{-2}$) by that of rope ($kg\,m^{-1}$), which represents the metres of rope required to obtain a similar harvest per square metre of net. The rope equivalent from 2011 to 2021 was determined to be 12 m^{-1}, with which the SMC efficiency was uniformly translated into biomass per metre of rope/net ($kg\,m^{-1}$). The use of all involved data was authorized by the local management agency and farmers provided verbal consent.

2.2 | Verifying the effect of larvae abundance and settlement rate on SMC efficiency

To identify the effect of larval abundance and settlement rate on SMC efficiency, continuous monitoring was conducted at four locations (i.e. Bur, Gat, Zep and Mal; Figure 1a) in the Dutch Wadden Sea throughout the mussel reproduction season (March to June) from 2017 to 2020. At each location, surface water samples of 100 L were collected and sieved (55 μm) weekly. Three 2 mL subsamples from each sample were randomly taken to count the contained larvae. Data were averaged and converted to estimate larval abundance per 100 L of water. At the same location, a framed cotton net (0.15 m^2) with 0.4 cm meshes was suspended under a buoy 1 m below surface, which was replaced weekly. The settled mussel spat on retrieved nets were counted to estimate the weekly spat settlement rate. The weekly data were averaged to represent the mean larval abundance and settlement rate over the reproduction season for each site. The resulting data were further correlated with the SMC efficiency at the same year and statistically evaluated using two-way analysis of variance (ANOVA). All fieldworks were undertaken with the backing of the local management agency and do not require ethical approval or any specific permits.

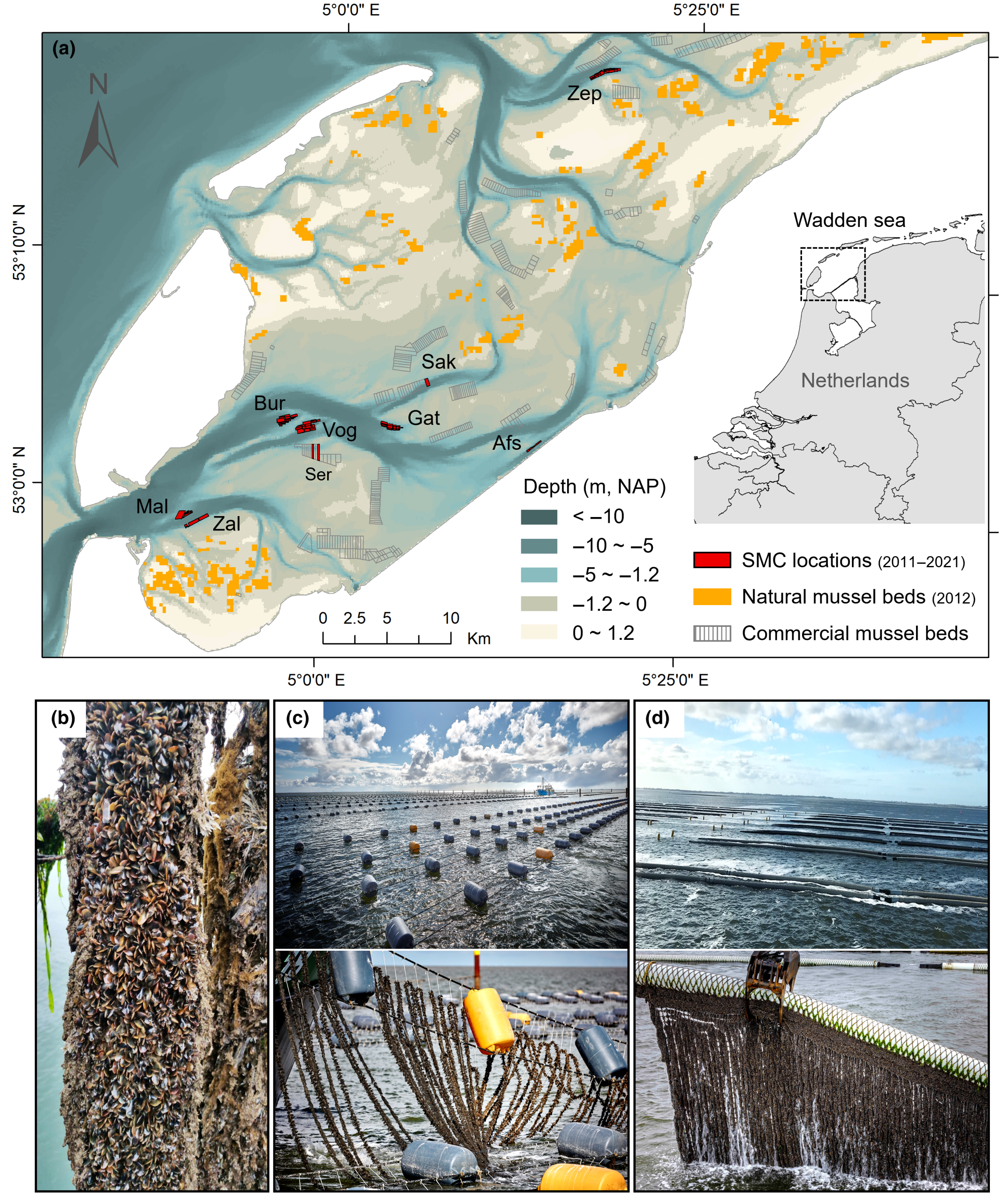

FIGURE 1 (a) Geographical distribution of the locations where suspended mussel spat collectors (SMCs) were deployed. See Table S1 for complete names and an overview of all locations. (b) Mussel spat attached to a rope. (c) Rope-based SMCs, where filamentous ropes are suspended in the water column by buoys to collect mussel spat. (d) Net-based SMCs, where nets suspended under tubes are utilized to collect mussel spat.

2.3 | Identifying factors dominating SMC efficiency

To screen for key factors driving the spatiotemporal variability of SMC efficiency, regression models containing 13 possible variables (see overview in Table S2) were fitted and variable selection was performed using the least absolute shrinkage and selection operator (LASSO), which is a regularization technique that shrinks the coefficients of less important variables to zero (Muthukrishnan & James, 2022). The variables with nonzero coefficient estimates in the final model were identified as the key factors that dominate SMC efficiency.

These 13 potential variables represent different management options and culture conditions associated with each SMC plot. Data regarding management options were obtained from the questionnaires, which included the type of involved SMCs (i.e. rope-based or net-based), substrate size (i.e. rope length or net area) and installation

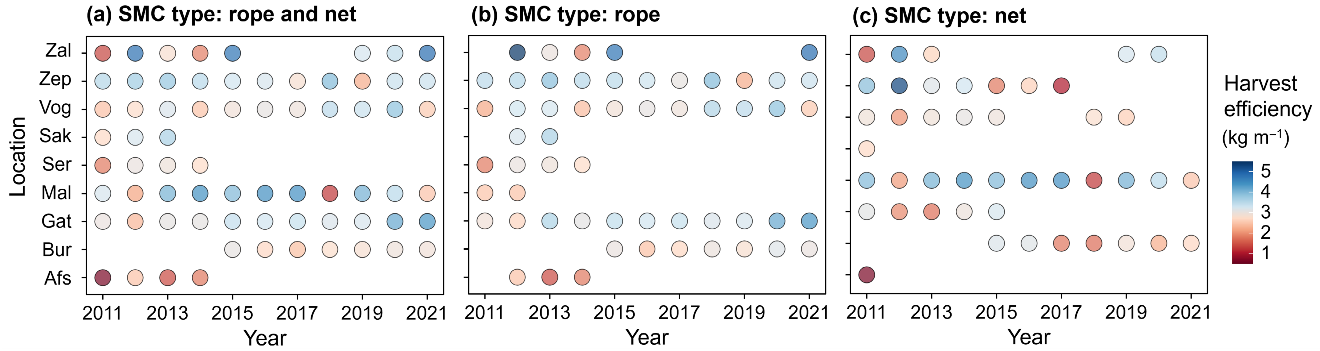

FIGURE 2 Spatiotemporal variability of suspended mussel spat collectors (SMCs) efficiency, which are visualized separately for (a) all types of SMCs, (b) rope-based SMCs and (c) net-based SMCs for each location per year. The SMC efficiency was calculated by averaging the data from all plots at each location and expressed as mussel spat biomass per metre of substrates (i.e. rope and net). No circle means that no SMCs were installed at that location that year. See Table S1 for complete names of all locations.

period. The installation period was determined by calculating the time between installation and each harvest. Additionally, the questionnaires investigated the presence of starfish, which may affect SMC efficiency by preying on spat (Capelle et al., 2017). Farmers assessed starfish abundance on six levels (none, rare, low, moderate, high and very high) based on visual assessments during harvesting. The SMC types and starfish abundance were encoded as one-hot numeric features (i.e. transforming categories as binary vectors) to make them suitable for LASSO regression.

Meteorological data for the Dutch Wadden Sea from 2011 to 2021, including hourly temperature and wind speed recorded by six weather stations (Figure S2), were provided by KNMI (Koninklijk Nederlands Meteorologisch Instituut). Voronoi polygons (i.e. shapes that divide a space based on proximity to points) were constructed to match weather stations with each SMC plot, and the maximum, minimum, average temperature and average wind speed during the installation period were calculated.

Model simulation data of seawater velocity and salinity in the Dutch Wadden Sea from 2011 to 2021 were extracted from the Copernicus Marine global reanalysis product (DOI: https://doi.org/10.48670/moi-00021) with a spatial resolution of approximately 8 km. Chlorophyll-a content in water columns, generated by time-series remote sensing analysis, was obtained from the COSYNA data portal with a spatial resolution of approximately 2.3 km. Grid sizes were not standardized across the different datasets to minimize potential errors. The same salinity, velocity or chlorophyll-a content data were used for multiple SMC plots within the same grid, while the average value of multiple grids was used to represent these parameters for SMC plots spanning multiple grids. Average salinity, velocity and chlorophyll-a content for each SMC plot during installation were calculated to match SMC efficiency data.

Tidal and wave data recorded from multiple tide gauge stations in the Dutch Wadden Sea (Figure S2) between 2011 and 2021 were provided by Rijkswaterstaat. These data were combined with wind speed dataset and digital elevation model to construct a one-dimensional wave statistical model that could extrapolate wave heights for the entire Wadden Sea. The extrapolation was performed based on the Young and Verhagen formula and linear wave theory, using calculated wind fetch and water depth. Calibration was based on existing data from wave buoys (see Appendix S1 for more details about the wave statistical model). Regional averages were computed to indicate the wave conditions of each SMC plot. The average and maximum wave heights during installation were calculated to match the SMC efficiency data.

Prior to variable selection, cleaning procedures were applied to all variables, including using the IQR (Inter Quartile Range) method to detect and remove outliers and using the near average value method to fill in missing values. Pairwise correlation analysis was conducted to identify potential associations between variables. Pairwise variables with strong correlation ($|\rho| > 0.5$) were fitted separately into generalized linear models and evaluated based on AIC (Akaike's information criterion). The variable corresponding to the model with higher AIC was excluded. To minimize the impact of variable scale on further variable selection with LASSO, all data were normalized using the MinMaxScaler method. Ten-fold cross-validation was adopted to determine the tuning parameter for regularization amount control, and 100 values along the path (min-lambda/max-lambda) were tested during the regularization process to find the optimal lambda value.

2.4 | Assessing key factor sensitivity to inform management

Random forest regression model (RFM) was developed to learn and predict the spatiotemporal variability of SMC efficiency. RFM is a low-variance bagging algorithm that builds decision trees using bootstrapped training samples and averages their output to prevent overfitting. The RFM was built using an integrated dataset of SMC efficiency and predictive variables spanning 2011 to 2020, with 80% and 20% of the dataset being used for training and validation, respectively. The dataset from 2021 was isolated for out-of-sample testing to evaluate the extrapolation performance of developed RFM on data that were not involved in the learning process. Five key hyperparameters were explored to obtain the relatively optimal model configuration, including estimator numbers, maximum tree depth, minimum sample splits, minimum leaf nodes and maximum feature numbers. This was achieved through two steps: (1) random search within an empirical range of hyperparameters; (2) grid search around the values from Step 1. To test whether LASSO-selected variables effectively characterize SMC efficiency, two RFMs were constructed using all 13 potential variables and four LASSO-selected variables (see Section 3.3 for the determination of these variables). Ten-fold cross-validation and the coefficient of determination (R^2) were used to evaluate the performance of developed RFMs. Fisher transformation was used to convert the R^2 values of the two models into z-scores and evaluate their difference statistically using *T*-test.

The final RFM was utilized to evaluate the sensitivity of SMC efficiency to its critical dominant variables (see Section 3.3 for the determination of these variables) by adjusting the values of individual or multiple variables while keeping the rest constant. The adjusted variables were within the range of maximum and minimum values recorded over a 10-year period (2011–2020), while constant variables were set to the representative value during the same period. Note that the efficiency sensitivity of the two types of SMCs was evaluated separately to compare their differences. All modelling and statistical analysis were performed using Python (v3.9.13) or R (v4.2.2).

3 | RESULTS

3.1 | Spatiotemporal variability of SMC efficiency

Significant variability in SMC efficiency was observed across different locations and years in the Dutch Wadden Sea ($p<0.05$; Table S3), with no clear trend towards increasing or decreasing efficiency (Figure 2a). These results suggest that management options and regional conditions may play a decisive role in SMC efficiency. When comparing different types of SMCs, the substrate used was found to have a significant impact on efficiency ($p<0.05$; Table S4). Rope-based SMCs demonstrated a superior average harvest efficiency of $3.20\pm0.97\,kg\,m^{-1}$, outperforming net-based SMCs which had an average harvest efficiency of $2.80\pm1.21\,kg\,m^{-1}$ (Figure 2b,c).

3.2 | Effects of larvae abundance and settlement rate on SMC efficiency

Contrary to our inference, the average abundance of larvae during the reproductive season was found to have no significant impact on SMC efficiency (df = 1, $F=0.65$, $p=0.44$; Figure 3a). Similarly, no relationship was detected between the average settlement rate of spat and SMC efficiency (df = 1, $F=0.01$, $p=0.94$; Figure 3b). This indicates that SMC efficiency in the Dutch Wadden Sea is not constrained by these two biotic factors.

3.3 | Critical factors dominating SMC efficiency

Among the 13 potential variables, average wind speed, minimum temperature and chlorophyll-a content showed significant correlation with average wave height, average temperature and salinity, respectively ($|\rho|>0.5$; Figure 4a). The former three variables were further excluded due to underperformance in the comparisons of generalized linear models based on AIC (Table S5). In the LASSO regression, four variables with non-zero coefficients were selected using the optimal lambda value, which included the SMC type, substrate size, mean wave height and starfish abundance (Figure 4b). These variables were considered critical factors governing SMC efficiency (see a summary in Figure S1).

3.4 | Response of SMC efficiency to critical factors

Both the RFM developed using all potential variables and the one using selected variables can effectively reproduce the variability in SMC efficiency, with predicted results exhibiting R^2 values of 0.84 and 0.81, respectively (Figure 5a,b; Table S6). T-test showed no significant difference in their performance ($p>0.05$). When the sub-dataset from 2021 was used for independent testing, the RFM using selected variables ($R^2=0.85$) demonstrated a comparable performance to the one incorporating all variables ($R^2=0.86$) and was chosen as the final model (Figure 5c,d). The results validate the effectiveness of the

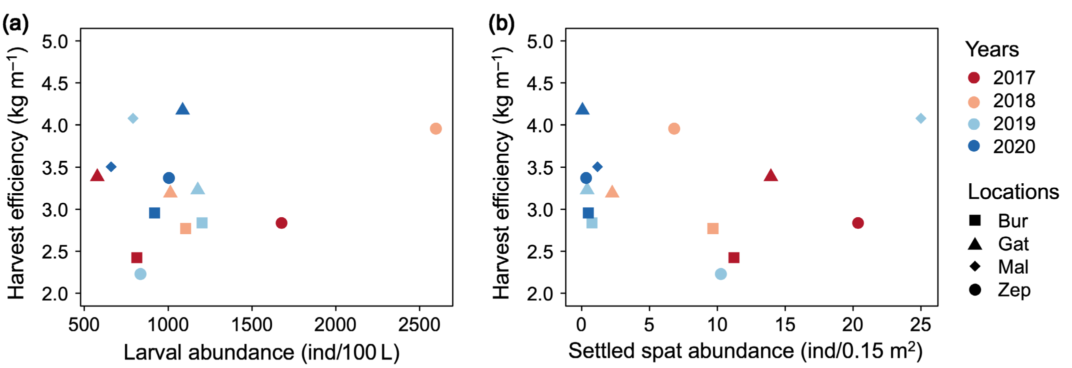

FIGURE 3 Harvest efficiency of suspended mussel spat collectors (SMCs) in relation to larval abundance (a) and spat settlement (b) over four locations from 2017 to 2020. The harvest efficiency was averaged per year at each location, while larval abundance and spat settlement were expressed as the average number of larvae per 100 L of seawater and the average number of spat settled on framed nets ($0.15\,m^2$), respectively, during the mussel reproduction season at each location per year. See Table S1 for complete names of all locations.

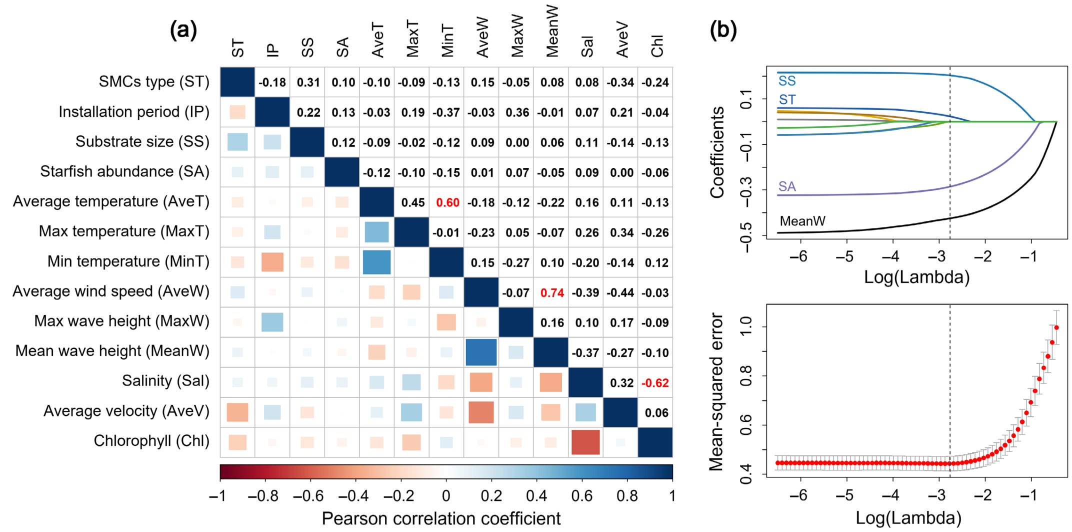

FIGURE 4 Selection of variables dominating MSC efficiency. (a) Results of Pearson correlation tests for the 13 potential variables. (b) Bottom panel: selection of tuning parameter (Lambda) in the LASSO model through 10-fold cross-validation based on minimum criteria, with the optimal Log(Lambda) is indicated by a vertical black dashed line. Top panel: four variables with non-zero coefficients were selected at the optimal Log(Lambda) and considered critical factors governing SMC efficiency. The four variables are labelled using the colours that correspond to their respective lines.

LASSO-selected variables in determining SMC efficiency and demonstrate the extrapolation capability of the developed RFM. The final model revealed the relative importance of selected variables in determining SMC efficiency (Figure 5e), suggesting that environmental conditions were relatively more important than management options, with the average wave height emerging as the most crucial factor.

When using the final model to predict the harvest efficiency of SMCs under specific scenarios with varying critical factors, the dissimilarities between SMC types were effectively reproduced. Specifically, rope-based SMCs outperformed net-based SMCs in terms of harvest efficiency within the same scenario (Figure 6). Nevertheless, both types of SMCs showed consistency in their sensitivity to critical factors. Higher harvest efficiency consistently occurred in areas with lower mean wave height, and augmenting the size of SMCs magnified their harvesting efficiency under particular wave conditions (Figure 6). Additionally, the harvest efficiency of SMCs, regardless of their type, dwindled with an increase in starfish abundance owing to heightened predation pressure (Figure 6).

4 | DISCUSSION

4.1 | Potential of SMCs as an alternative for dredging wild mussel spat

A significant limitation of the global mussel industry is the lack of reliable sources for resource provisioning (Avdelas et al., 2021). This issue fundamentally arises from the broad dependence of mussel cultivation on natural processes, beginning with spat recruitment (South et al., 2022). In the Netherlands, dredging 65×10^6 kg of spat is necessary to sustain an annual yield of 100×10^6 kg of mussels (Kamermans et al., 2009). These spats were sourced from wild mussel beds before the implementation of SMCs (Smaal et al., 2021). It is a fact that achieving the spat dredging target was not always possible, partly because of the high mortality rates from predation on larvae and spat during the natural recruitment in wild mussel beds (Kamermans et al., 2009). Additionally, wild mussel beds are typically characterized by a short lifespan (ca. 2–3 years) with significant fluctuations in both their area and biomass between years (Troost et al., 2022). In contrast, SMCs offer stable substrates and improved conditions for free-swimming larvae and settled spat (Jacobs et al., 2014). SMCs also help reduce predation pressure from adult starfish and crabs by being suspended above the seafloor (Kamermans et al., 2002). Based on our collected data, the harvested biomass of mussel spat from SMCs in the Dutch Wadden Sea has increased from 6×10^6 kg in 2011 to 16×10^6 kg in 2021, with an anticipated further rise due to the expansion of installation areas. Undoubtedly, this helps address the scarcity of mussel spat resources. Existing studies have confirmed that there are no notable disparities in the overall performance (including growth, survival rates and predation preferences) between spat from SMCs and those from wild mussel beds (Capelle et al., 2016; Kamermans et al., 2009). Spat from SMCs even exhibit enhanced aggregation after bottom redeployment (Christensen et al., 2015).

Nevertheless, our 11-year investigation revealed significant spatio-temporal variability in the harvesting efficiency of SMCs. Surprisingly, this variability is not primarily driven by larval abundance and settlement rates, but rather by regional wave regimes. Once waves propagate, they generate heightened turbulence and vertical circulation along the sides of the SMC structures (i.e. spaced ropes or nets), accelerating the currents beneath them (Suplicy, 2018; Tseung et al., 2016).

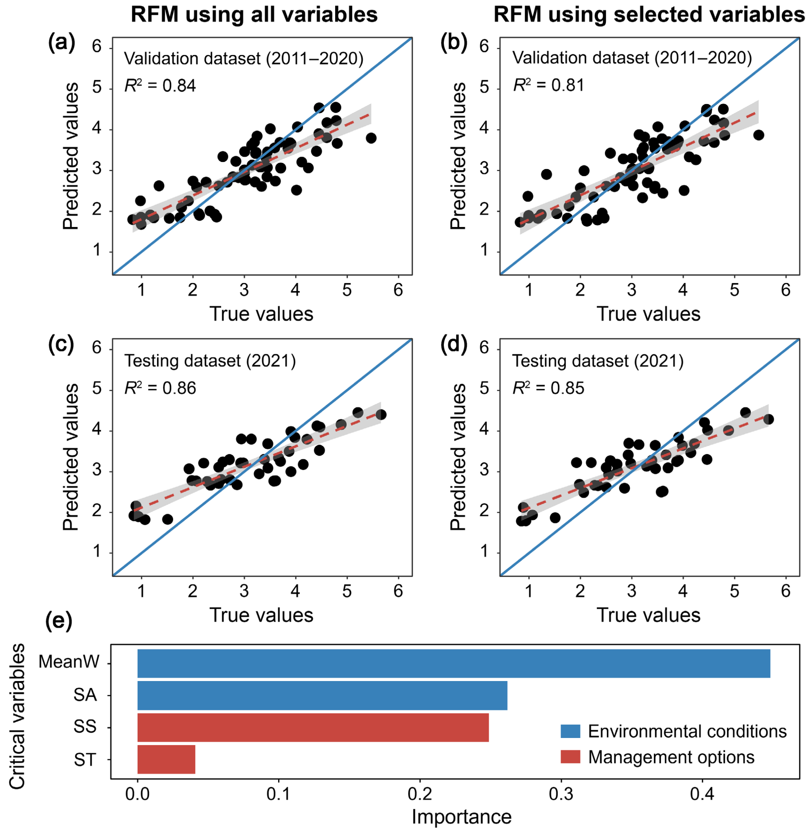

FIGURE 5 Performance of random forest models (RFM) constructed using all possible variables (a) and LASSO-selected variables (b), respectively, based on the evaluation using the validation dataset spanning 2011 to 2020. The blue solid line represents the 1:1 reference line between the actual values and the model predictions, while the red dashed line is the linear regression line between the two, with the grey background representing the 95% confidence interval. (c, d) Extrapolation performance of both RFM assessed using out-sample testing dataset from 2021. The testing dataset was not involved in the development process of both RFM. (e) Relative importance of critical variables (MeanW, mean wave height; SA, starfish abundance; SS, substrate size; ST, SMC type) in determining SMC efficiency, revealed by the RFM constructed using LASSO-selected variables. These critical variables can be categorized into environmental conditions (blue bars) and management options (red bars).

This, in turn, may lead to the detachment of mussel spat, particularly those situated in the peripheral areas of the SMCs. Additionally, the increased stress caused by stronger waves would force mussel spat to allocate more energy to develop robust byssal threads for stability and thus decrease growth (Roberts et al., 2021; Schotanus et al., 2019). These potential mechanisms collectively result in lower harvest efficiency of SMCs under strong waves. Our finding underscores the importance of assessing local wave regimes before installing SMCs, as wave-sheltered locations having the potential to maximize SMC harvest efficiency. Notably, SMCs as suspended structures can provide substrates for organisms other than mussel larvae, including free-swimming starfish larvae. As starfish larvae grow, they may prey on mussel spat on SMCs. Small starfish have been documented to consume around 0.3 spat per day, while large starfish can consume up to 1.7 spat per day (Kamermans et al., 2009). Strategic management should be implemented to mitigate the impact of starfish on SMCs harvest efficiency. One possible approach is to adapt the 'starfish mopping' commonly used in mussel bottom culture (Calderwood et al., 2016), although method improvements may be required for its application on SMCs.

4.2 | Rope-based SMCs vs net-based SMCs

SMCs typically can be categorized as either rope-based or net-based. Despite their widespread use in many regions (Filgueira et al., 2007; Kamermans et al., 2002), this study is the first to quantify the harvest efficiency differences between these two types. Our findings reveal that rope-based SMCs outperform net-based SMCs in terms of harvest efficiency. This disparity may arise from dissimilarities in shape, layout, and response to hydrodynamic regimes and nutrient transport between the two types (Mascorda Cabre et al., 2021; South et al., 2022). The dispersed arrangement and flexible properties of rope-based SMCs allow them to effectively absorb and transfer wave energy by moving and bending. This characteristic contributes to comparatively higher harvest efficiency by reducing the growth inhibition and fall-off of attached spat caused by wave-induced disturbances (Lin et al., 2016; Mascorda Cabre et al., 2021). In contrast, net-based SMCs function as suspended physical barriers due to their larger surface area and smaller mesh size, resulting in greater surface friction and total drag (Plew et al., 2006; Stevens & Petersen, 2011). This

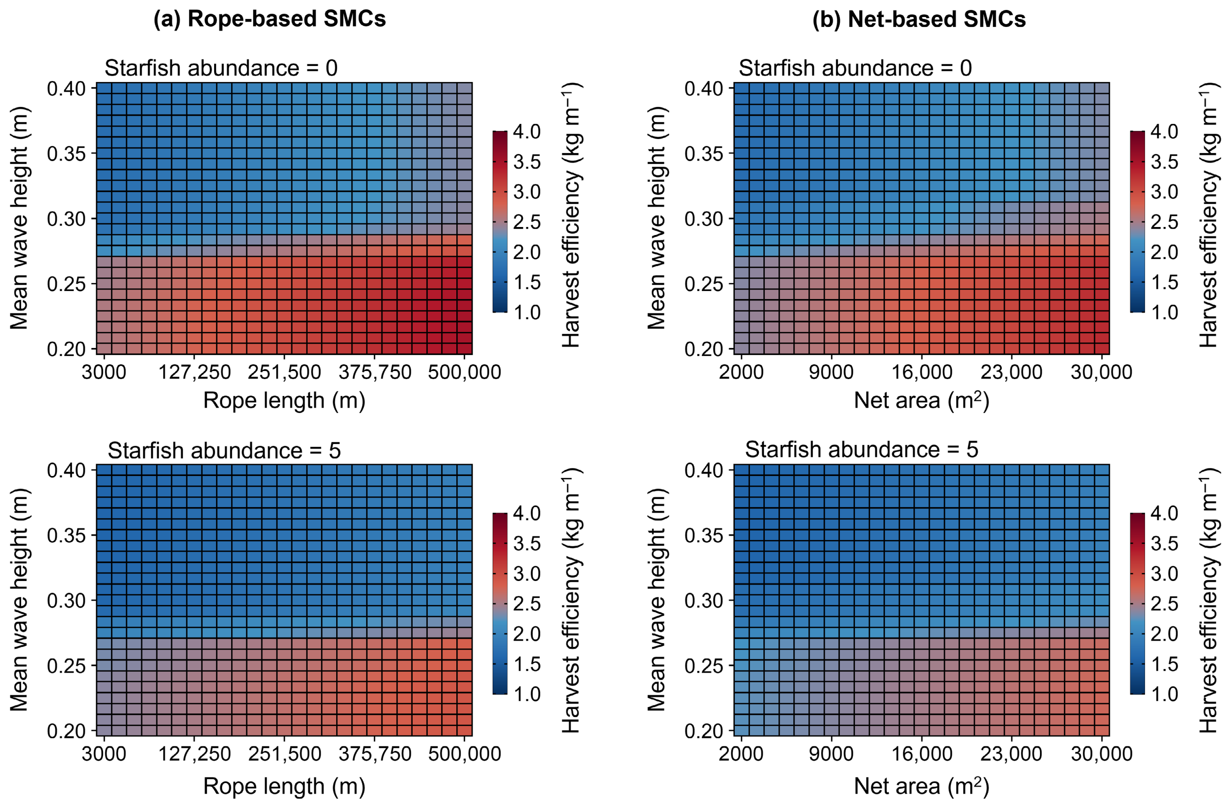

FIGURE 6 Response of the harvest efficiency of rope-based (a) and net-based (b) suspended mussel spat collectors (SMCs) to varying key factors, namely SMC type, starfish abundance, mean wave height and substrate size (rope length and net area), predicted by the constructed random forest model. Two contrasting levels of starfish abundance were examined and utilized as grouping factors: 0 denoted the absence of starfish, while 5 indicated a substantial presence of starfish. See the delineation of starfish abundance levels in Section 2.3. Note that: to make the two types of SMCs directly comparable, their harvest efficiency was uniformly converted into biomass per metre of substrate ($kg\,m^{-1}$; see details in Section 2.1).

means that their performance in attenuating waves is inadequate, making them more vulnerable to wave actions. Additionally, the barrier effect may affect material transport and residence time (Lacoste et al., 2018; Plew et al., 2006), thereby limiting nutrient and biodeposition flux into and out of net-based SMC structures. These factors collectively contribute to stronger growth inhibition and a higher likelihood of spat detachment, ultimately leading to relatively lower harvesting efficiency. To quantitatively understand the difference between both types of SMCs, it is imperative to conduct in situ measurements on key processes. This may entail deploying paired instruments such as wave loggers and nutrient sensors within their installation areas.

Despite the fact that rope-based SMCs exhibited higher harvest efficiency compared with net-based SMCs, it does not necessarily mean that large-scale installation of rope-based SMCs is the optimal choice. In practical applications, we advocate for a comprehensive evaluation from multiple dimensions to select the most suitable type of SMCs and its installation scale, including (1) *Installation cost*. Rope-based SMCs typically require a large amount of ropes, necessitating larger horizontal spans and higher costs (including additional support structures like buoys). Conversely, installing net-based SMCs is relatively simple and requires smaller spatial spans, making it relatively cheaper; (2) *Location conditions*: Our findings indicate that in wave-sheltered areas, moderate-sized SMCs can achieve relatively higher harvest efficiency. Conversely, in wave-exposed areas, maximizing the substrate size can compensate for the decrease in harvesting efficiency caused by wave actions, which in turn may offset the increase in installation costs; (3) *Ecological impacts*. Despite the ecological sustainability of SMCs, their widespread installation may cause certain impacts on the local community (see Section 4.3).

4.3 | Ecological implications of SMC application

It is essential to recognize that SMCs, as externally introduced artificial structures, undoubtedly have broader-scale ecological implications on, for example, the seabed, water column and other biota (Keeley et al., 2009). This could involve negative outcomes, such as altered benthic habitats due to biodeposition and phytoplankton blooms induced by the release of dissolved nitrogen (more extensive list see Mascorda Cabre et al., 2021). Conversely, it might also entail positive impacts, such as enhancing water quality and serving as substrates, shelters or food sources for other species (see van der Schatte Olivier et al., 2020 for a review). The magnitude of these effects tends to be context-dependent, with some negative effects potentially offset by positive effects (Keeley et al., 2009). For instance, while the benthic community beneath SMCs may undergo changes, improvements in water quality and the provision of fouling habitat might bolster local biodiversity and productivity (Mascorda Cabre et al., 2021). Moreover, the negative effects would diminish rapidly with distance (Keeley et al., 2009). Therefore, context-specific management strategies for SMCs are crucial to counterbalance their impacts. A promising approach involves meticulously selecting installation sites for SMCs: *Firstly*, SMC sites should not overlap with ecologically important or sensitive habitats to avoid potential changes in system composition. *Secondly*, SMC sites should be configured with moderate to fast flow velocity to aid biodeposition dispersion at the local scale, while compensating for detachment and growth inhibition caused by strong waves through adjusting SMC types or size. *Lastly*, SMCs should obviously never be installed beyond the dispersal range of wild mussel larvae to ensure settlement.

The rational utilization of SMCs implies reducing damage to wild mussel beds while sustaining aquaculture (Jacobs et al., 2014). Importantly, SMCs offer promising prospects for restoring degraded mussel beds located in intertidal, subtidal and offshore areas (Schotanus et al., 2020; van den Bogaart et al., 2023). Traditional spat dredging not only harvests broodstock, but also disrupts substrates (e.g. shells) crucial for larval settlement (Smaal et al., 2021), hindering the natural recovery of mussel populations in some regions. In such context, SMCs can act as a constantly available settlement substrate for free-swimming larvae, while the build-up of shed mussels and/or shells below may create windows of opportunity for the spontaneous rebuilding of mussel beds (Capelle et al., 2019; Kamermans et al., 2002). An illustration arises from the offshore biodiversity restoration project in England, where the installation of SMCs led to the formation of new mussel beds on the seafloor within 2 years (Bridger et al., 2022). Moreover, the implementation of SMCs enhanced water quality while providing shelter and feeding grounds, consequently boosting the diversity and biomass of surrounding marine life even before the formation of mussel beds below (Bridger et al., 2022). For intertidal and subtidal areas, challenges to mussel bed restoration also involve the impact of stronger hydrodynamics (Capelle et al., 2019). This is particularly evident in Europe, where mussel beds thrive on soft sediments, relying on spatial self-organizing patterns formed by mussel aggregations for stability (de Paoli et al., 2017). Therefore, successful restoration typically requires the translocation of substantial mussel juveniles or adults to overcome density thresholds, thereby triggering positive feedback mechanisms that promote the establishment of resilient mussel beds (Schotanus et al., 2020; van den Bogaart et al., 2023). SMCs have been effectively employed for this purpose, with an increasing number of cases demonstrating their effectiveness in aiding mussel bed restoration (Schotanus et al., 2020; van den Bogaart et al., 2023). This is evident not just because SMCs can supply abundant mussel spat, but also because SMCs-collected spat exhibit greater plasticity than adults in harsh environments (Schotanus et al., 2019), and they demonstrate stronger aggregation ability compared with wild spat (Christensen et al., 2015).

5 | CONCLUSIONS

This study identified the key factors dominating SMC efficiency, enhancing the predictability of SMCs in practical applications and informing strategic management to maximize efficiency. While our study focused on the Dutch Wadden Sea, the findings and management advice apply equally to SMCs use in other mussel aquaculture regions and are relevant for similar practices, such as longline mussel farming or SMCs-based ecological restoration. *Firstly*, proper site selection is fundamental for maximizing SMC efficiency while minimizing negative effects on habitats. This primarily entails evaluating the hydrodynamic regimes, the presence of starfish and the ecological significance of the target sites. *Secondly*, by strategically adjusting the types and substrate size of SMCs while carefully weighing the benefits against the costs, SMC efficiency could be further optimized. *Lastly*, machine learning models using realistically obtainable datasets can effectively predict SMC efficiency, helping practitioners evaluate context-dependent variability in targeted regions. Follow-up research should consider more variables that potentially affect mussel growth and behaviour, as well as long-term in situ multi-parameter monitoring, to improve the precision of predicting SMC efficiency and boost mussel spat collection efficiency for ecological sustainability.

AUTHOR CONTRIBUTIONS

Zhiyuan Zhao, Jacob J. Capelle and Tjeerd J. Bouma conceived the ideas and designed methodology. Jacob J. Capelle collected the data. Zhiyuan Zhao analysed the data. Zhiyuan Zhao, Jacob J. Capelle, Jaco C. de Smit, Theo Gerkema, Johan van de Koppel, Lin Yuan and Tjeerd J. Bouma led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available via the 4TU. Research data Repository https://doi.org/10.4121/9b381ed1-de8d-4e44-bf52-c4e8bd8669e7 (Zhao et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Overview of the locations where suspended mussel spat collectors (SMCs) were deployed.

Table S2. Overview of the 13 variables that may affect SMCs efficiency.

Table S3. Two-way ANOVA results on the differences in SMCs efficiency between locations and years.

Table S4. One-way ANOVA results on the differences in SMCs efficiency between types (i.e. rope-based SMCs vs. net-based SMCs).

Table S5. Results of candidate generalized linear models filtering the autocorrelated variables.

Table S6. Structure and performance of the random forest model developed for predicting SMCs harvest efficiency.

Figure S1. Spatiotemporal variability of LASSO-selected variables dominating SMCs efficiency, including (a) mean wave height, (b) starfish abundance, substrate type, and substrate size.

Figure S2. Geographical distribution of the used tide gauges, wave buoys, and weather stations.

Figure S3. Performance of the developed wave model.

Appendix S1. Set-up of the wave statistical model.

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