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# Spatio-temporal analysis of potential factors explaining fluctuations in population size of *Spisula subtruncata* in the Dutch North Sea

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Bivalves play a key role in coastal ecosystems by supporting food web, modifying habitats, and their economic value for fisheries. Many bivalve species are under pressure, showing large variations in population sizes and distributions, with climate change and human activities considered as important drivers. The Dutch North Sea hosts high densities of bivalve species, dominated by the cut trough shell *Spisula subtruncata*, with strong interannual variations and a patchy distribution. To explore the causes of this variation, data of an extensive long-term spatial benthic monitoring program (1995–2021) was analysed using a Bayesian spatio-temporal hurdle model. We considered indicators related to human activities, biological processes, climate change and habitat preference as explanatory variables for the observed long-term temporal and spatial variations. Results revealed that medium sediment grain size was key determinant of *S. subtruncata* occurrence and density. Increasing sea water temperatures during winter and the post-settlement phase positively affected annual population densities, while strong north-westerly winds led to lower densities. These climate change related factors had an overall positive effect on this species in the region. Human activities like shellfish dredging and sand nourishment had no measurable impact. However, shrimp and flatfish beam trawling overlapped with *S. subtruncata* occurrence and were negatively related to densities, suggesting higher beam trawling intensity in these areas may negatively impacts densities. Overall, the effects were stronger at medium to finer sediments where the highest densities occurred, indicating a strong habitat-dependent effect. Despite identifying multiple drivers, unexplained annual variation suggests other not included factors like predation pressure, also play a role. More

detailed studies on the combined effects of climate change-driven environmental stressors and human activities are needed to fully understand the population dynamics. This knowledge is essential for developing more adequate fisheries and coastal management strategies to sustain biodiversity.

#### KEYWORDS

anthropogenic impacts, bayesian statistics, climate change, Dutch North Sea, population dynamics, *Spisula subtruncata*

## Introduction

Many marine species exhibit large spatiotemporal variations in population sizes, distributions or other traits, driven by biological processes (e.g., predation, competition), local human activities (e.g., fisheries and coastal developments) and global climate change (oceanic warming and acidification, sea level rise and intensification of extreme weather events). Human-induced changes, including the global process of climate change and local activities, increasingly negatively affect marine ecosystems (Halpern et al., 2008; Waycott et al., 2009; Trégarot et al., 2024). Climate change effects often interact with local human related stressors that can be managed locally (Scheffer et al., 2015; Gissi et al., 2021). For example, reducing local fishing pressure can ensure that populations remain resilient to critical levels of climate change (e.g. Carpenter et al., 2017; Ramirez et al., 2021). The determination of boundaries, at which populations can withstand pressures due to climate change and ongoing intensification of local human activities, requires insights in which main factors are driving populations.

Bivalves, key benthic species in coastal ecosystems, are susceptible to effects of climate change and local human activities (Kroeker et al., 2010; Philippart et al., 2011; Gobler et al., 2014). They play important roles in ecosystems as food source and altering their physical environment (Norkko and Shumway, 2011; Sospedra et al., 2017; Ysebaert et al., 2019), facilitating themselves and many associated species (i.e. ecosystem engineers) (Bruno and Bertness, 2001; Rullens et al., 2019). Many bivalves are economically valuable for fisheries and often harvested in large amounts (Smaal et al., 2019). Without adequate local management measures, stocks are often at risk of overexploitation (Smaal et al., 2019; Huang et al., 2023). In addition, coastal development and pollution have resulted in decline of bivalve populations in the past (Lotze et al., 2006; Mackenzie, 2007). Besides local human activities, rising seawater temperature, linked to climate change, negatively affect recruitment and survival in many bivalve species (Sampaio et al., 2021; Kruff Welton et al., 2024). Despite considerable research, drivers of population dynamics particularly for sublittoral bivalve, remain unclear (but see: Weinberg, 2005; Narváez et al., 2015; Hofmann et al., 2018).

The cut trough shell *Spisula subtruncata* is a common bivalve in European sublittoral waters, from Norway, British Isles to northern Mediterranean (Hayward and Ryland, 2017). The species has an important role in the food web and is of economic value for fisheries, especially along the Dutch coast (Smaal and Lucas, 2000; Baptist and Leopold, 2009). Once dominant in Dutch coastal waters, its population collapsed after 2000, with a strong recovery in 2017 (Troost et al., 2023). Similar strong interannual variation has been observed for *Spisula* spp. in other regions (Fraschetti et al., 1997; Weissberger and Grassle, 2003; Degraer et al., 2007), likely driven by varying recruitment and mortality rates. The highest mortality occurs shortly after settlement, as in many bivalves (Gosselin and Qian, 1997), which is also the case for *S. subtruncata* (Ambrogi and Occhipinti Ambrogi, 1987; Degraer et al., 2007; Deval and Gokturk, 2008). In the Dutch North Sea, intensified human activities (such as coastal protection, harbour development, and shrimp fisheries) and climate change (Weijerman et al., 2005; Capuzzo et al., 2018; Herman et al., 2021; Wijsman et al., 2023) may drive the species' dynamics, but their precise role remains uncertain.

Seawater temperature increases in the North Sea, a well-documented effect of climate change (Dulvy et al., 2008; Høyer and Karagali, 2016), plays a key role in bivalve recruitment success in temperate waters (e.g. Dekker and Beukema, 1993; Philippart et al., 2003; Beukema et al., 2009). Spawning is triggered by a water temperature threshold in spring (Cardoso et al., 2007; Nicolle et al., 2013). Variations in seawater temperature may then cause temporal shifts with regard to optimal conditions for the larvae and juvenile bivalves, such as food availability and/or predation pressure (Beukema et al., 2002; Philippart et al., 2010; Poloczanska et al., 2016). While wind conditions can affect the dispersal off pelagic eggs and larvae (Thiébaud, 1996; Ellien et al., 2004), increase mortality due to displacement during storms and reduce food uptake and subsequently growth (Witbaard et al., 2005; Raven, 2022).

With respect to biotic factors, juvenile and adult *S. subtruncata* are food sources for shrimp, starfish, demersal fish and diving sea ducks, potentially affecting the local population size (Braber and de Groot, 1973; Pihl and Rosenberg, 1984; Camphuysen et al., 2002; Fox, 2003). Interspecific competition for space and food with other

bivalves may also influence the population dynamics of *S. subtruncata*. In the late 1970s, for example, the invasive razor clam *Ensis leei* established itself to become dominant across the northwest European coastline, after being presumably introduced as larvae from ballast water (Tulp et al., 2010). *S. subtruncata* may be affected locally by interspecific competition with *E. leei* and other co-occurring bivalve species with similar filter-feeding behaviour. Currently it is unclear whether these species interact by competing for space and food.

Shellfish dredge fisheries on *S. subtruncata* began in 1985 but were halted in 1999 after a strong decline in the local stocks (Craeymeersch et al., 2001). While shellfish dredging has been speculated to locally deplete *S. subtruncata* banks (Leopold, 1999; Camphuysen et al., 2002), its influence on the total Dutch population remains unclear. Beam trawl fisheries for shrimp and flatfish also physically impact the seabed (e.g. Eigaard et al., 2016; Hiddink et al., 2017; Tulp et al., 2020), affecting *S. subtruncata* densities (Bergman and van Santbrink, 2000).

Sand extraction and coastal nourishment, which increased in the past decade (Baptist and Leopold, 2009; van der Veer et al., 2015), can negatively affect the benthic biodiversity (Herman et al., 2021; Dauvin et al., 2022; Saengsupavanich et al., 2023). Some studies suggest benthic communities may take years to recover after nourishment (Wijsman et al., 2023), though others indicate a faster recovery (van Dalfsen and Essink, 1999). A large spatial link between sand nourishments and *S. subtruncata* could not be demonstrated (Baptist and Leopold, 2009).

To gain insight into the factors driving the dynamics of the *S. subtruncata* population in Dutch coastal waters we investigated i) the spatial patterns and temporal trends of *S. subtruncata* densities,

and ii) the potential contributions of biotic-, anthropogenic- and climate-related factors. Using data from an annual benthic survey along the entire Dutch North Sea coast, we present two analyses covering different periods: one excluding fisheries effort (1995–2021) and one including fisheries effort (2009–2020). We gathered all relevant available data on a high spatiotemporal resolution and a statistical model was used to assess the effects of climate conditions (temperature, wind), habitat (sediment and tidal current), and human disturbance (fishing intensities and sand nourishments). Additionally, we explored the relationship between predation (e.g., shrimp, fish and birds) and *S. subtruncata* densities in a descriptive manner, as information on these parameters was not available at the same spatial resolution. We discuss how our findings offer insights for improving adequate fisheries and coastal management strategies to sustain biodiversity.

## Methods

### Benthic survey

Since 1995, an annual survey of shellfish stocks is carried out by Wageningen Marine Research, covering all Dutch North Sea coastal waters. The main aim of the survey is to monitor densities and biomass of exploited shellfish species for stock assessments. The number of benthic sampling stations differs between years due to logistic circumstances (756–1405 stations; min - max), spread out along transect perpendicular to the coast (Figure 1). Samples were taken either with a towed bottom cutting dredge or with a modified hydraulic dredge (see for details: Troost et al., 2023). Mesh size was

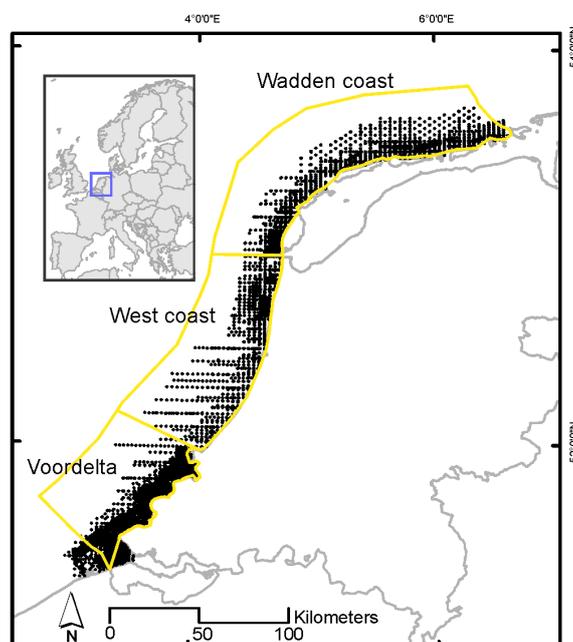


FIGURE 1

Study area with sampling grid with total sample stations (1995–2021) and coastal areas: Voordelta, West coast and Wadden coast.

5 millimetres and sampling depth 10 centimetres. Sampling distance was at most locations about 150 meters, width either 10 cm (towed dredge) or 20 cm (hydraulic dredge), covering 15 to 30m<sup>2</sup> respectively. Surveys were carried out from April to June except in 2020 when the sampling was delayed due to the COVID restrictions and was conducted between 25 May and 9 June (Troost et al., 2023). For our analyses, sampling stations were linked to a 5km hexagonal grid resolution (Supplementary Figure A1) which enables us to spatially link all explanatory variables, available on different scales, to the survey data.

Living bivalves were identified to species and representative subsamples were taken when the sample size was too large to process as a whole (see Troost et al., 2019). Species were grouped into length classes and weighted (fresh shell and flesh wet-weight to the nearest 0.1 gram). Broken shells were included when flesh and both sides of the hinge ligament was present, enabling species and length class determination. To test the potential effect of interspecific competition between *S. subtruncata* and other filter-feeding bivalve species, we included densities of *Ensis* spp., *Lutraria lutraria*, *Donax vitattus* and *Chamelea striatula* into the statistical analyses. Numbers of *Ensis* spp. and *L. lutraria* are underestimated in the survey as these species often burrow deeper than the sampling depth of 10 centimetres but relative comparison between years is possible as same methodology was used during the entire survey period (Troost et al., 2023).

## Spatiotemporal covariates

### Tidal current velocity and sediment median grain size

Tidal current velocity data were obtained from a hydrodynamical model with a resolution of 0.02° longitude and 0.05° latitude (~2.3×3.5 km) (van der Molen et al., 2016) (Supplementary Figure A2). For our analyses we used the annual total mean current velocity m s<sup>-1</sup> for each sampling point. Sediment median grain size (D50) was obtained from TNO Geological Survey of the Netherlands from Deltares OPeNDAP (<https://opendap.deltares.nl/thredds/catalog/opendap/tno/ncp/catalog.html>) (Supplementary Figure A2).

### Sea surface temperature and wind conditions

Sea surface temperature (SST) was used in our analyses, assuming that the coastal waters in our study area are permanently mixed and so that there are no differences in temperatures throughout the water column (van Leeuwen et al., 2015). Data on sea surface temperature (°C) was derived from daily values from 1995-2021 on a 0.05°×0.05° spatial resolution (~5.5×3.5 km) from European Space Agency (ESA) SST Climate Change Initiative (CCI) project downloaded from the Copernicus Climate Change Service (Merchant et al., 2019) and linked to the hexagon grid. Following Cardoso (2007), we assume that *S. subtruncata* started to spawn at the day of the year (DY) when water temperature reached 16°C. At this temperature, egg development time takes about 3 days from fertilization until

hatching, and the subsequent pelagic larval stage takes approximately 24 days, until settlement (Cardoso et al., 2007). Thus, we assume that the pelagic phase (from spawning to settlement) lasts 27 days. At *ad libitum* food availability, larval growth and survival correlates positively with seawater temperature (Verween et al., 2007; Enricuso et al., 2018). Therefore, we used the mean water temperature (daily values) between spawning and settlement as a proxy for the growth conditions during the pelagic phase (SST<sub>p</sub>, subscript refers to larval pelagic stage).

Brown shrimp *Crangon crangon* is a dominant benthic predator on bivalve recruits in marine systems (Hamerlynck et al., 1993; van der Veer et al., 1998) affecting post-settlement survival rates (Hiddink et al., 2002; Andresen and van der Meer, 2010). For *S. subtruncata*, it has been estimated that once settled, it takes 77 days to reach a length of 4 mm, the size at which *S. subtruncata* has outgrown shrimp predation (Cardoso et al., 2007; Campos and van der Veer, 2008) (see Supplementary Figure A3). Therefore, we used the mean water temperature of 77 days after the settlement as a proxy for post-settlement growth conditions (SST<sub>s</sub>, subscript refers to post-settlement).

We used mean sea surface temperature from November to February (SST<sub>w</sub>) as a proxy for winter temperatures as a factor potentially impacting adult mortality by low temperatures or starvation at high temperatures when metabolic rates increase but phytoplankton densities are low (Compton et al., 2007).

The index for local wind-driven wave stress was calculated as the total number of days with strong winds (> 10 m s<sup>-1</sup>) per year from the northwest (direction between 280° and 10°). In our study area, north-western winds have the longest fetch for waves to build up, creating the most turbulence in coastal waters (Witbaard et al., 2005). Wind data was derived from The Copernicus European Regional ReAnalysis (CERRA) datasets (Schimanke et al., 2021).

Bathymetry was downloaded from EMODnet bathymetry portal at a resolution of 0.05°×0.05° (<https://emodnet.ec.europa.eu/en/bathymetry>) and linked to the hexagon grid.

### Fishing intensity

Fishing intensity was based on Vessel Monitoring system (VMS) and fishery logbook data to produce spatial data layers on fishing intensity of different categories expressed in Swept Area Ratio (SAR) (see for methods: Eigaard et al., 2016; ICES, 2021). Data was available from 2009 until 2020 at a spatial resolution of 0.05°×0.05° and converted to hexagon resolution. For the intensity of fisheries on molluscs, fisheries data for *Ensis* spp. and *S. subtruncata* are combined, as there is no species-specific fishing effort data available. Beam trawling on shrimp and flatfish (mainly sole and plaice) and demersal otter trawl differ in sea bottom surface impact, varying from sliding over the bottom surface (shrimp trawl) to completely overturning the upper layer of the sediment (flatfish beam trawl) (Eigaard et al., 2016). Because we assume that different fishing gears have different impacts on the benthos including *S. subtruncata*, we differentiate between four gear groups, being mollusc dredge (SARdredge), shrimp beam trawl (SARshrimp), flatfish beam trawl (SARdmf) and otter trawl (SARotter).

## Sand nourishments

Data on coastal sand nourishments was supplied by ministerial institute Rijkswaterstaat ([Supplementary Figure A4](#)). Sand nourishment activities were conducted at the coastline and did not overlap with sampling points, however, sand from coastal nourishment is known to be redistributed along the coast and to deeper waters due to tidal currents and waves. Therefore, we calculated the distance from each benthos sampling point to the nearest active nourishment site (spatial polygon) on a yearly basis, and used this minimal distance as a covariate in the analyses to detect a possible effect. Sand extraction may also affect the benthos community, however, available data were insufficient to include in our statistical analyses.

## Temporal descriptive data

### Common scoter

Common scoter *Melanitta nigra* numbers were estimated from aerial midwinter surveys (since 1993) combined with ship based surveys and counts from the coast ([Sluijter et al., 2022](#)). Densities could not be converted to the hexagon grid spatial resolution due to the lack of resolution of the data at that scale. As there are large differences on larger spatial scale, we aggregated the data per coastal area ([Figure 1](#)).

### Demersal shrimp and flatfish

Indices for predation pressure by shrimp and flatfish was derived from the demersal fish survey (DFS). The DFS has been conducted annually since 1970 in September-October and covers the entire Dutch coastal waters, down to 25 meters depth ([Beek, 1997](#)). A 6m-wide beam bottom trawl was used at low speed (2-3 knots) with a fine mesh of 20 mm which selects brown shrimp > 20 mm. Species densities were calculated from total shrimp *C. crangon* and flatfish (*Pleuronectes platessa*, *Limanda limanda*, *Platichthys flesus* and *Solea solea*) per haul (see for details: [Tulp et al., 2012](#); [Aarts et al., 2019](#)). No correction for net selectivity was applied. Data on shrimp and flatfish densities were aggregated per coastal area and could not be converted to the hexagon grid spatial resolution due to the lack of small-scale resolution of the data.

## Spatiotemporal modelling

Data exploration showed that the abundance data of *S. subtruncata* was spatially clustered and contained a high proportion of zero observations, on average per year 35.4% (sd=10.7%). We assume all zeros are from structural source (true zeros). To analyse these zeros and accommodate for zero inflation within the data, we used a two-step modelling approach (hurdle model) ([Feng, 2021](#)). The hurdle model fits two distributions; a probability of occurrence assuming a binomial distribution or Bernoulli (presence and absence) and a Gamma distribution (because the values were on a continuous scale in numbers m<sup>-2</sup>) at locations where *S. subtruncata* was present. This approach allows to separate effects on the occurrence (presence/absence, binomial part) and on the actual densities once *S. subtruncata* is present

(gamma part). The combined distribution model is called a zero-altered Gamma (ZAG):

$$Spisula_{is} \sim ZAG(\mu_{is}, \pi_{is}, r)$$

$$E(Y_{is}) = \mu_{is} \text{ and } var(Y_{is}) = \mu_{is}^2 / r$$

$$Logit(\pi_{is}) = intercept + covariates_{is} + f(year_i)_{AR1} + u_i$$

$$Log(\mu_{is}) = intercept + covariates_{is} + f(year_i)_{AR1} + u_i$$

$$u_i \sim N(0, \Omega)$$

where  $Spisula_{is}$  ( $Y_{is}$ ) is the density of *S. subtruncata* (m<sup>-2</sup>) at location  $i$  in year  $s$ . Covariates described in the previous section are used in the model are either used in the year  $i$  or the year before  $i-1$  as some covariates have an effect on *S. subtruncata* during pre- and post-settlement phase the year before ([Table 1](#)). The ZAG distribution has three parameters:  $\pi$  is the Bernoulli part which denotes the probability of presence,  $\mu$  and  $r$  are parameters of the Gamma part resembling the mean and the shape of the distribution respectively. The estimated value is linked with a logit link for the binomial part and a log-link for the Gamma part. Both sides of the hurdle model use the same fixed and random effects. For the analysis prior information is incorporated in the model. For the intercept and fixed effect these are the default priors ( $N(0, 1000)$ ). All covariates are modelled linearly, but year trend with non-linear smoother to describe the temporal dependence. To account for temporal correlation between samples, the non-linear year smoother is modelled with an autoregressive process AR1 and incorporated a Penalized Complexity Prior scaled on the mean and SD $\times 3$  of the *S. subtruncata* density ([Wang et al., 2018](#)). To account for residual spatial correlation a first order intrinsic conditional autoregressive random effect (iCAR) is used to model the data ([Blangiardo and Cameletti, 2015](#); [Zuur et al., 2017](#)). On the spatial resolution of the hexagonal grid a spatial structured term  $u_i$  is added where (first order) spatial adjacency defines the variance-covariance structure. In this hierarchical structure, information from neighbouring areas is utilized, leading to a smoothing effect that reduces extreme values and produces more balanced predictions.

Models were compared according to the Watanabe-Akaike's Information Criterion ([Watanabe, 2010](#)), where the model with the lowest WAIC was considered as having the best support. Models of which WAIC differed less than 2  $\Delta$ WAIC from the best model are considered to be equally good ([Zuur et al., 2017](#)). Confidence intervals are reported as Bayesian Credibility Intervals (BCI) between 2.5–97.5%. When the BCI of an estimated coefficient does not contain zero we consider that an covariate has an effect on density or occurrence of *S. subtruncata*, and to be relevant of 'significance' in a Bayesian context ([McElreath, 2020](#)). Statistical modelling was performed in a Bayesian framework with INLA ([Rue et al., 2009](#); [Lindgren and Rue, 2015](#)) in R ([R Core Team version 4.1.1, 2021](#)).

Our sea surface temperature covariates exhibited interdependence and showed correlation. Therefore, to investigate the potential effect of

TABLE 1 Overview of the exploratory variables used in this study.

Covariable	Description (unit)	Spatial scale/resolution	Temporal resolution	Period in analyses (t=sampling year)
D50	Sediment median grain size ( $\mu\text{m}$ )	grid/0.05°	static	–
Tidalcur	Tidal current velocity ( $\text{m s}^{-1}$ )	grid/0.02°x0.05°	static	–
DY	Day of the year of onset of spawning SST > 16°C	grid/0.05°	annual/daily	t-1
SSTp	SST during pelagic phase (°C)	grid/0.05°	annual/daily	t-1
SSTs	SST during post-settlement (°C)	grid/0.05°	annual/daily	t-1
SSTw	SST during previous winter (°C)	grid/0.05°	annual/daily	Winter prior to t
DensC	Summed density of intraspecific competitive bivalves (ind. $\text{m}^2$ )	sample grid	annual	t-1
Winddays	North-West wind days > 10 $\text{m s}^{-1}$ (# days)	grid/0.05°	annual/daily	April-March in t-1
distNour	Minimum distance shoreface sand nourishment activity (meters)	Polygons	annual	t-1
SAR	Fishery intensity, swept area ratio (SAR: shrimp, dmf, otter and dredge)	grid/0.05°	annual	t-1

Median grain size and tidal current velocities were collinear, and therefore not used together in the same model (see text). Most time series span the period from 1995 to 2021, except for the time series on SAR (2009–2020).

sea surface temperature related to timing of spawning (DY), the pelagic phase (SSTp) and the post-settlement phase (SSTs) in relation to all other covariates, three models with other independent covariates were considered. VMS fishery intensity was only available for the period 2009–2020. To make optimal use of the available data, we analysed two different sets of the temperature-related models: one covering the entire data period excluding fisheries effort (1995–2021) and one shorter series including fisheries effort (2009–2020).

Tidal current velocity and median grain size showed high correlation, as they are both related to hydrodynamic processes (Supplementary Figure A5). Due to the collinearity and interdependence, it was not possible to include both covariates in the analyses. Median grain size is known to be an important variable for *S. subtruncata* occurrence and was therefore included in the analyses (Table 1). To show predicted relative effects of a covariate, we used the lower and the upper values for median grain size (150–250  $\mu\text{m}$ ) where the highest densities of *S. subtruncata* occur and all other covariates were standardized with a mean of zero in each covariate plot.

Temporal trends of all covariates were analysed with a linear regression in R (R Core Team version 4.1.1, 2021).

## Results

### *S. subtruncata* dynamics

The *S. subtruncata* population in the Dutch North Sea coastal zone showed strong interannual fluctuations, with different average densities but similar trends in the three coastal areas (Figure 2). High densities were observed from 1995 to 2000 in the West and

Wadden coast, and between 1995 to 1997 in the Voordelta, with a strong decrease to lower densities thereafter. In all coastal areas, densities remained low until 2015 and increased again from 2016. Densities stayed rather high in subsequent years, but showed a general decrease in the Wadden coast (Figure 2) after 2018. During the entire period, persistently high-density clusters of *S. subtruncata* occurred in the northern part of the Voordelta, the northern part of the West coast area and north of the Wadden islands Terschelling and Ameland (Figure 3).

## Spatial-temporal covariates

### Climate factors

The spawning threshold temperature of 16°C showed temporal and spatial variation, and was reached on average between 10 June (in 2017) and 22 July (in 1996) during the study period. The day at which the threshold was reached declined between 1995 and 2020 with 0.57-day  $\text{year}^{-1}$  ( $F_{1,25} = 8.97$ ,  $P < 0.01$ ; Figure 4A) and tended to be later in deeper- and more northern waters (Supplementary Figure A6). For the pelagic larvae phase (defined as 27 days after the spawning date) no clear significant trend in average sea surface temperature was detected ( $F_{1,25} = 0.38$ ,  $P = 0.54$ ; Figure 4B), but sea surface temperature during post-settlement phase (defined as 77 days after settlement, that starts 27 days after spawning) increased significantly, with 0.05°C  $\text{year}^{-1}$  ( $F_{1,25} = 6.21$ ,  $P < 0.05$ ; Figure 4C). Winter sea surface temperature also showed an increasing trend, with 0.04°C  $\text{year}^{-1}$  ( $F_{1,25} = 5.68$ ,  $P < 0.05$ ; Figure 4D). The annual number of days with strong (> 10  $\text{m s}^{-1}$ ) north-western winds increased over time, but this increase was just not significant ( $F_{1,25} = 3.42$ ,  $P = 0.08$ ; Figure 4E).

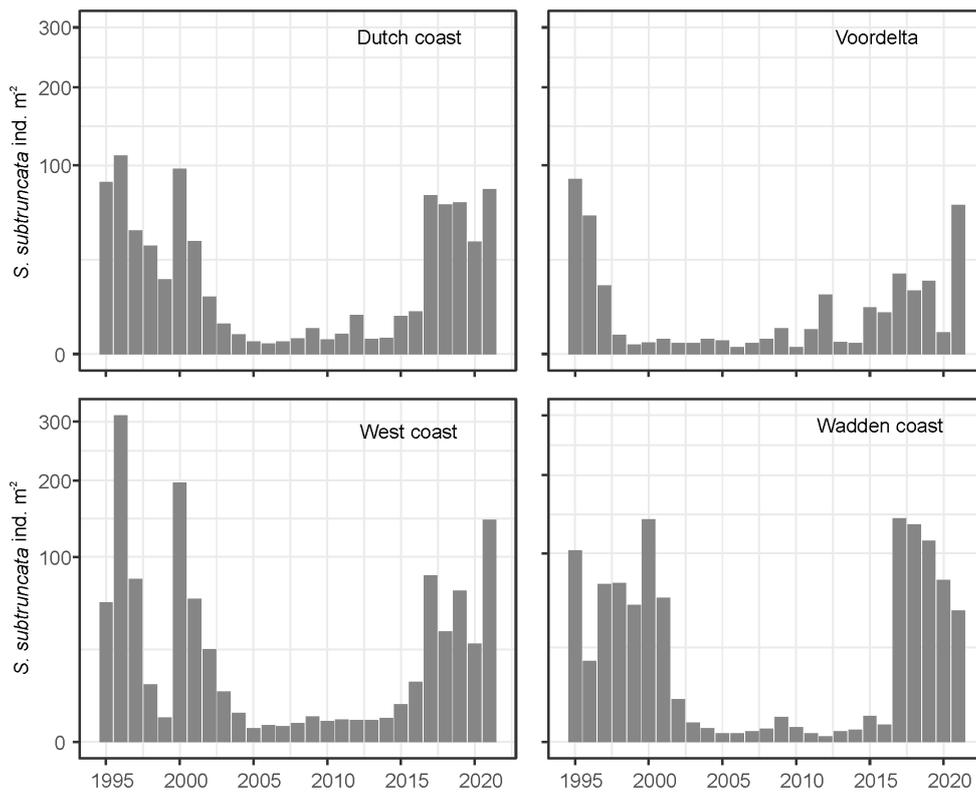


FIGURE 2 Total annual average *S. subtruncata* densities for the entire shallow Dutch North Sea coast (above left) and sub areas: Wadden coast, West coast and Voordelta.

### Trend in other filter feeding bivalves

The total density of suspension-feeding bivalve species increased during the study period with a yearly increase of 0.85 ind. m<sup>-2</sup> to on average of 22.2 ind. m<sup>-2</sup> ( $F_{1,25} = 21.22, P < 0.001$ , Figure 5A). This trend was mainly due to the exponential increase of the invasive *E. leei* since 2000, with average densities reaching up to 100 m<sup>-2</sup> in the Wadden coast area. Densities of *E. leei* fluctuated

strongly between years for all coastal areas, but in general showed a decreasing trend after 2016 (Supplementary Figure A7).

### Human activities

Fishing intensities (SAR) differed over time and between coastal areas between 2009 and 2020. Mollusc dredge fishery intensity differs between years ( $F_{1,27} = 19.66, P < 0.001$ ) and coastal areas ( $F_{2,27}$

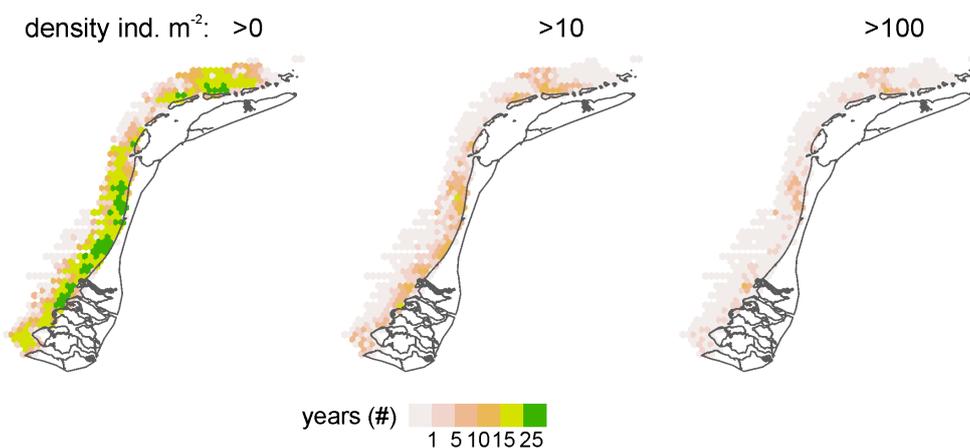


FIGURE 3 Spatial plots of the number of years when *S. subtruncata* densities reached >0, >10 or >100 individuals m<sup>2</sup> per hexagon. Zero observations in grey.

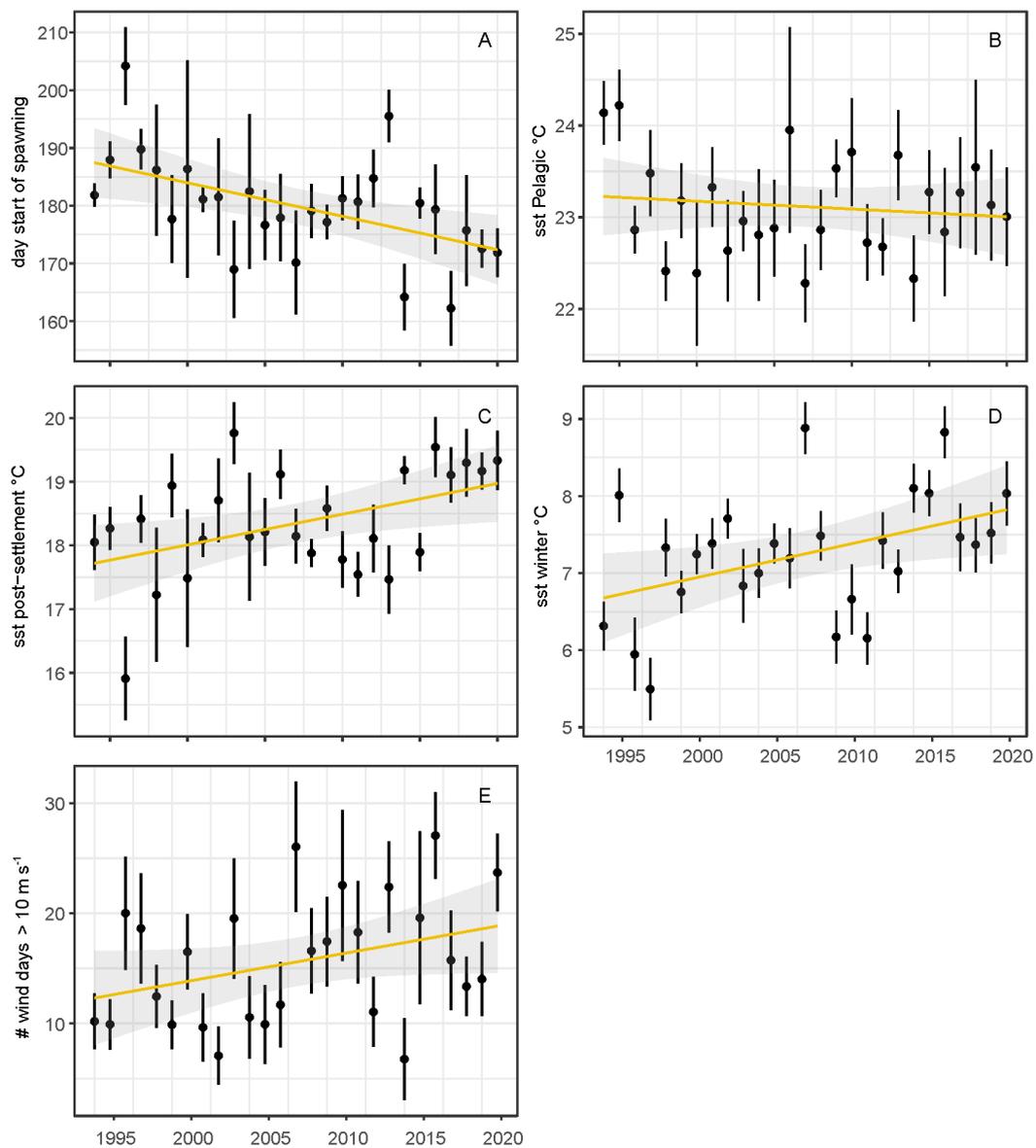


FIGURE 4

Average day of the year when the threshold for spawning was reached (16°C) (A) and average sea surface water temperature during pelagic phase (day: 0–27) (B), post settlement phase (day: 28–77) (C), sea surface water temperature in winter (D) and wind days with strong North-West winds > 10 m s<sup>-1</sup> (E). Error bars represent standard errors.

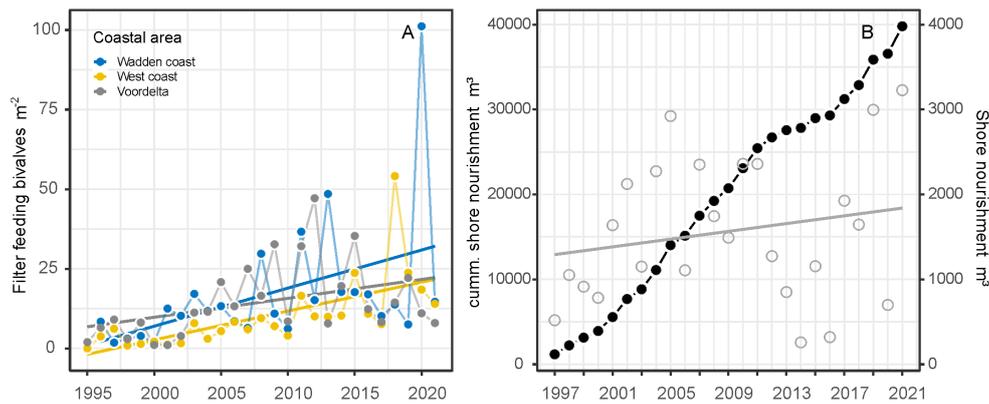
= 34.28,  $P < 0.001$ ). Trends were different between coastal areas ( $F_{2,27} = 18.74$ ,  $P < 0.001$ ), increased in the Voordelta and were stable in the West and Wadden coast (Figure 6A). Sole and place beam trawl fishing intensity declined over the years ( $F_{1,30} = 30.18$ ,  $P < 0.001$ ) between areas ( $F_{2,30} = 74.74$ ,  $P < 0.001$ ), were highest in the West coast, low and stable in the Voordelta over the years and very low in the Wadden coast ( $F_{2,30} = 17.04$ ,  $P < 0.001$ ) (Figure 6B). Shrimp beam trawl intensity had the highest intensity of all fisheries, however no showed significant trend over the years ( $F_{1,32} = 0.32$ ,  $P < 0.57$ ) but differed between coastal areas ( $F_{2,32} = 43.16$ ,  $P < 0.001$ ). The fishing intensity was generally highest in the Wadden coast and was quite low in the West coast (Figure 6C). Total otter trawl fishing intensity declined over the years ( $F_{2,30} = 23.78$ ,  $P < 0.001$ ) and

differed between coastal areas ( $F_{2,30} = 8.45$ ,  $P < 0.01$ ). Otter trawl fishing intensity was relatively high in the Wadden coast but strongly decreased after 2010 and fishing intensity was relatively low in the West coast and Voordelta (Figure 6D). Shore nourishment increased over the years along the entire Dutch coastline ( $F_{1,26} = 7.76$ ,  $P < 0.01$ ), especially since 2000 (Figure 5B).

## Temporal descriptive data

### Predation

Annual average shrimp densities and trends differed between coastal areas. In the Voordelta, shrimp densities increased over the



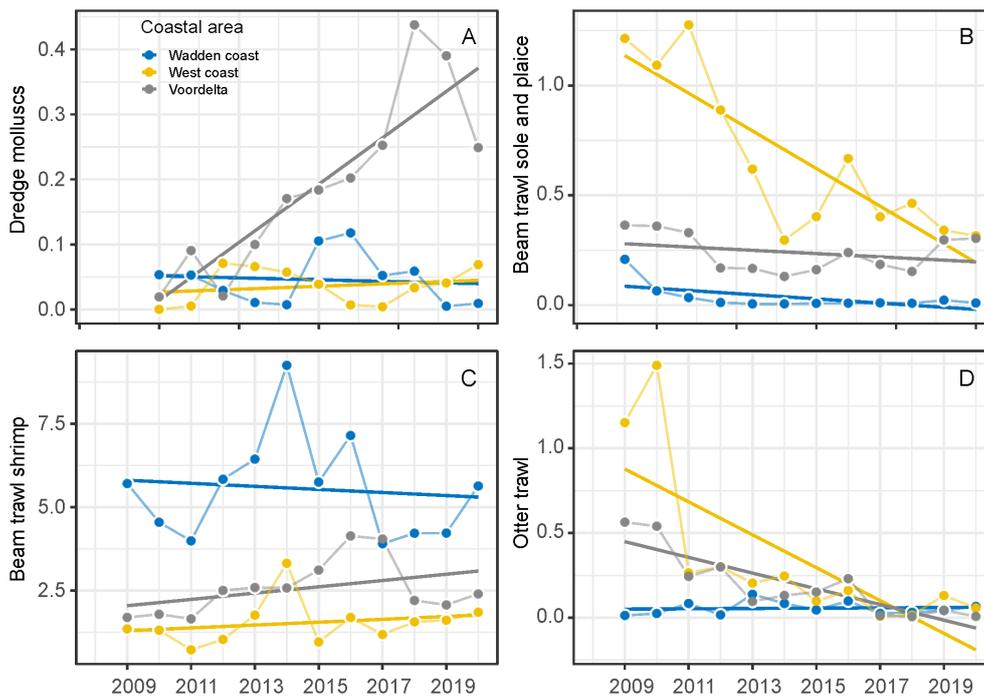
**FIGURE 5** Trends of average densities of the sum of filter feeding bivalves (*Ensis* spp., *Lutraria lutraria*, *Donax vitattus* and *Chamelea striatula*) (A) and cumulative sand nourishment over the years (black dots) and yearly total shore nourishment volumes (grey circles) (B).

years, while in the West coast and Wadden coast area they decreased (Figure 7A). Similar to shrimp, total flatfish numbers slightly increased in the Voordelta and decreased in the West and the Wadden coast (Figure 7B). The flatfish species plaice and dab were the numerically dominant species in the survey (Supplementary Figure A8). Common scoters are commonly found in all coastal areas but highest numbers were found in the eastern Wadden coast (Figure 7C). Incidentally, high numbers were also found in the other coastal areas.

## Spatial-temporal statistical ZAG model

### Model selection and performance

To investigate the effect of sea surface temperature from the moment of spawning three models (with respective temperature-effects at the moment of spawning, the pelagic phase and the post-settlement phase) were considered for both sets of time series (Table 2). Based on the WAIC values model 1 and 2 were assumed similarly supporting the data for both time series, as they did



**FIGURE 6** Fisheries intensity in the coastal areas expressed in Swept Area Ratio (SAR) in the coastal areas from 2009-2020. Dredge mollusc (*S. subtruncata* and *E. leeii*) (A), beam shrimp trawl (B), beam sole and plaice trawl (C) and otter trawl fisheries (D).

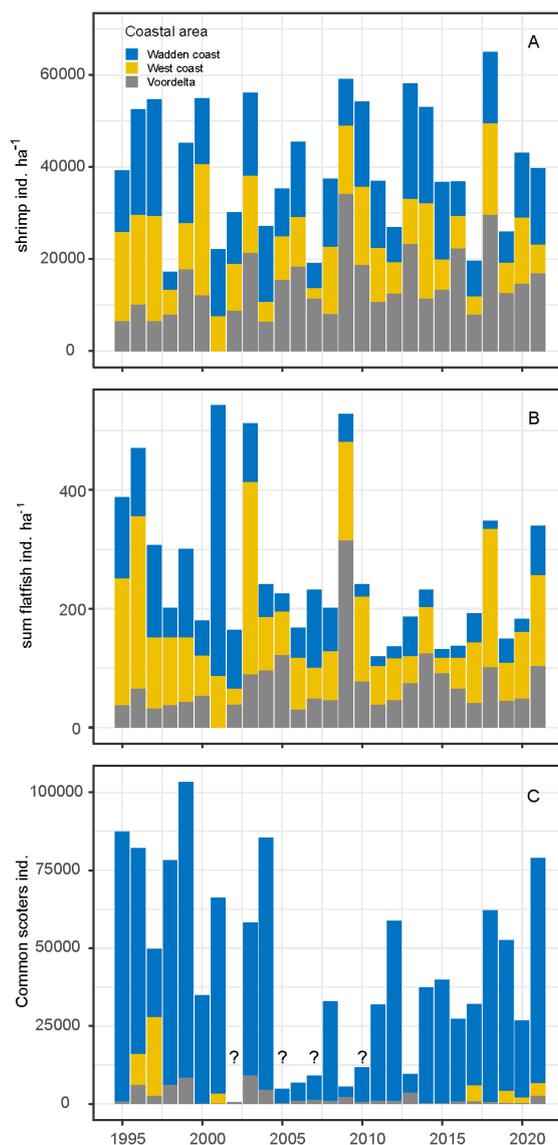


FIGURE 7

Trends of average densities of shrimp (A) and total number of flatfish species (B) and common scoter, uncomplete surveys are indicated with question mark (source: Sluijter et al., 2022) (C).

not differ more than 2  $\Delta$ WAIC (Table 2). Based on model performance we conclude that model 2 had a satisfactory fit and correctly estimates occurrence and densities of *S. subtruncata* (Supplementary Material B). In addition, we considered this model biologically the most relevant and interpretable, because it includes average sea surface temperature in the post settlement phase (SSTs) instead the start of spawning date (DY). The post settlement phase is a critical period during which biological processes likely influence mortality and survival of *S. subtruncata* recruits, providing interpretability and stronger basis for causal understanding.

### Covariates effects (1995-2021), excluding fisheries

Model 2 shows that median grain size (D50) had the largest effect on densities and occurrence (Figure 8). The highest densities of *S.*

*subtruncata* were at median grain sizes of 160-280  $\mu$ m (Figure 9A). We used this range to standardise the effects of all other contributing covariates, as it indicates the preferred habitat for *S. subtruncata* based on median grain size (Figure 9A, between the blue and yellow lines). Median grain size showed a negative association (when all other variables were standardised) with occurrence and density, indicating higher abundances of *S. subtruncata* at intermediate fine compared to coarse sediments (Figure 9B). Sea surface temperature during the post settlement phase (SSTs) showed a positive association with densities (Figures 8, 9C). This effect became stronger with decreasing median grain size (Figure 9C). Likewise, increasing water temperature during winter had a positive effect on *S. subtruncata* densities (Figure 8) which also became stronger with decreasing median grain size (Figure 9D). The number of NW-wind days above 10  $m s^{-1}$  (winddays) showed a negative effect on *S. subtruncata* densities and

TABLE 2 Models ranked according Watanabe-Akaike information criterion (WAIC), with the  $\Delta$ WAIC of the best (equally good) models printed in bold.

model	WAIC	$\Delta$ WAIC
<b>Time series: 1995-2021 (excluding fishing efforts)</b>		
1. D50+DY+SSTw+densC+winddays+distNour+f(year <sub>i</sub> )	78991.36	<b>0.00</b>
2. D50+SSTs+SSTw+densC+winddays+distNour+f(year <sub>i</sub> )	78991.63	<b>0.27</b>
3. D50+SSTp+SSTw+densC+winddays+distNour+f(year <sub>i</sub> )	78997.70	6.34
<b>Time series: 2009-2020 (including fishing efforts)</b>		
1. D50+DY+SSTw+densC+winddays+disSupp+SARshrimp+SARdmf+SARotter+SARdredge+f(year <sub>i</sub> )	34485.82	<b>0.00</b>
2. D50+SSTs+SSTw+densC+winddays+disSupp+SARshrimp+SARdmf+SARotter+SARdredge+f(year <sub>i</sub> )	34486.16	<b>0.34</b>
3. D50+SSTp+SSTw+densC+winddays+distNour+SARshrimp+SARdmf+SARotter+SARdredge+f(year <sub>i</sub> )	34493.49	7.67

Models include fixed factors: median sediment grain size (D50), day of the year start of spawning (DY), sea surface temperature pelagic phase (SSTp), SST settlement phase (SSTs), SST winter (SSTw), density competing bivalves (densC), number of days NW-wind > 10 m s<sup>-1</sup> (winddays), distance to sand nourishment (distNour) and Swept Area Ratio for fishing intensity (SARshrimp, SARdmf, SARotter and SARdredge) and smoother year (f(year<sub>i</sub>)). Distinctive covariables in bold.

no effect on occurrence as the 95% confidence intervals overlap with zero (Figure 8). A negative association was found between densities and NW-wind days at high grain size, but a positive association at low grain size (Figure 9E). The cumulative density of filtering bivalves (densC) showed a positive effect on *S. subtruncata* densities but no effect on occurrence, as the 95% confidence intervals overlapped with zero (Figure 8). This positive effect with other filter-feeding bivalve species and *S. subtruncata* densities became stronger with increasing median grain size (Figure 9F). Shoreface sand nourishment (DistNour) did not contribute importantly to the models, as the 95% confidence intervals overlapped with zero (Figure 8).

### Covariates effects (2009-2020), including fisheries

To investigate the effect of fishery intensity in combination with other covariates we used model 2, which was the most parsimonious model based on WAIC and included average sea surface temperature during the post settlement phase (SSTs) (Table 2). The fisheries covariates showed different effects in both parts of the model (Figure 10). Beam shrimp fishing intensity showed a positive association with occurrence of *S. subtruncata* but a negative with densities (Figure 10). This indicates that shrimp fisheries are associated with the species' occurrence, but at locations where *S. subtruncata* is present, there is a negative association that became stronger with lower median grain size (Figure 11A). The effect of beam trawl fishing intensity on sole and plaice showed a similar association on occurrence and densities (Figure 10), with a negative association on *S. subtruncata* densities that was stronger at lower

median grain size (Figure 11B). Otter trawling did not show a relevant association on occurrence as the 95% confidence interval overlapped with zero, implying no strong overlap between otter trawl fishing intensity and the presence of *S. subtruncata* (Figure 10). However, a weak positive effect of otter trawl fishing intensity on *S. subtruncata* densities was found (Figures 10, 11C). Mollusc dredge fisheries showed a positive association with the occurrence of *S. subtruncata* but no effect on densities (Figures 10, 11D). Most other (non-fishery) covariates within this model (DistNour, DensComp, SSTs and SSTw) showed similar results to the first model analyses on the longer time series (Figure 10). Only the number of NW-wind days above 10 m s<sup>-1</sup> showed a positive association with *S. subtruncata* occurrence and no association with densities (Figure 10).

### Year effect

Although several covariates were considered important in our models, the relative effect of the smoother year was high and captured the temporal trend of *S. subtruncata* densities to a large extent (Supplementary Material B). This was less apparent for the binomial part of the models. Year has no direct biological meaning as such. Therefore, there is some unexplained annual variation in densities and other factors which could not be captured by our model covariates should be considered.

## Discussion

Our study suggests that both local human activities and climate conditions are important factors influencing the *S. subtruncata* population dynamics in the Dutch North Sea. Water temperature in winter and after settlement, were positively linked to *S. subtruncata* occurrence and densities, while strong north-westerly winds (>10 m s<sup>-1</sup>) had a negative effect. Overall, recent climate conditions seem to have benefited the population. Shellfish dredging and sand nourishment showed no apparent effect in recent years. However, our analyses shows that shrimp and flatfish beam trawling were positively associated with *S. subtruncata* occurrence but negatively with densities, suggesting higher trawling intensity where the species is found, which then negatively affects densities. An unexplained year effect, indicates additional unknown factors may also affect recruitment and survival. While our observational, correlative analysis is no proof of causality, it sheds light on factors potentially driving the population. Further discussion of our model results, the year effect and, possible mechanisms is provided below.

### Sediment grain size

Our analyses shows that medium sediment grain size (D50) is an important determinant explaining occurrence and the density of *Spisula subtruncata*, with highest densities found at medium fine sediments (160-280  $\mu$ m), aligning with earlier studies (Degraer

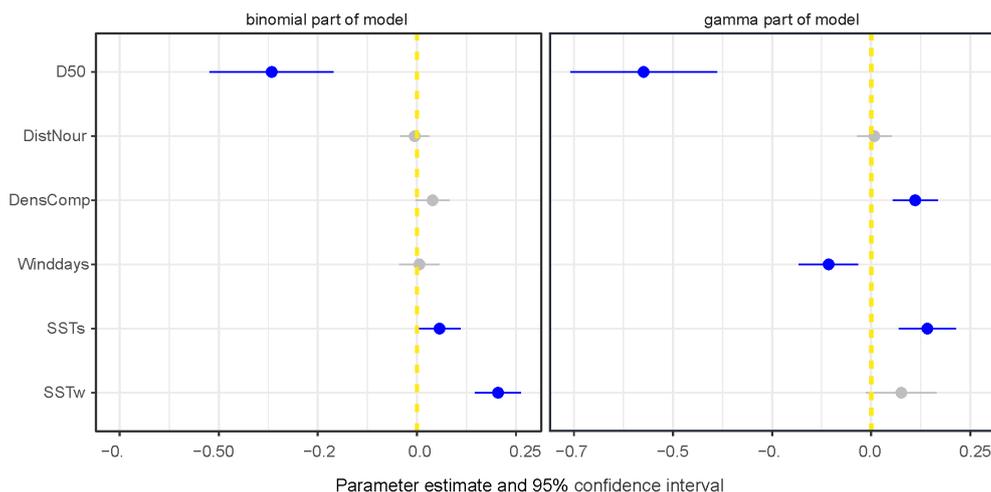


FIGURE 8

Estimated weights of the covariate effects indicated with posterior means with 95% confidence interval (CI) plotted for most parsimonious model excluding fisheries (for the dataset 1995–2021) for binomial and gamma part (best model in Table 2), blue points and lines show effects differing from zero with 95% CI. Median sediment grain size (D50), SST settlement phase (SSTs), SST winter (SSTw), density competing bivalves (DensComp), number of days NW wind > 10 m s<sup>-1</sup> (winddays), distance to sand nourishment (DistNour).

et al., 2006, 2007). Sediment grain size, shaped by tidal current velocities and wave action, is commonly linked to the distribution of macro zoobenthos (Ellis et al., 2017; Bosco Gusmao et al., 2022). Our study indicates that habitat, as indicated by grain size, is a good proxy for habitat preference for *S. subtruncata*, with stronger effect of stressors at lower sediment grain size. Similar sediment-related effects on benthic communities have been observed in the North Sea (van Denderen et al., 2014; Rijnsdorp et al., 2018; van der Reijden et al., 2018).

Changes in sediment texture can affect *S. subtruncata* densities, with beach and foreshore sand nourishment altering sediment texture and impacting benthic communities (Herman et al., 2021; Dauvin et al., 2022; Saengsupavanich et al., 2023; Wijsman et al., 2023). While our analysis treated median grain size as an annual static variable, potential changes from nourishment were not fully accounted for. Although no direct effect of sand nourishment was detected (cf., Baptist and Leopold, 2009), we may be unable to assess its potential impact as it is currently unknown how to examine nourishment effects on the spatiotemporal scale of our study. In addition, the lack of detailed sand extraction data hindered a comprehensive assessment of its impact on *S. subtruncata* population.

## Winter temperatures

We found a positive association between winter temperatures and the occurrence and densities of *S. subtruncata*. Warmer winters may reduce mortality by increasing mobility, allowing *S. subtruncata* to bury themselves faster in the sediment to escape from storms and predation. Moreover, the absence of prolonged sub-zero water temperatures may avert direct mass mortality of

shellfish as has been observed during severe winters (Armonies et al., 2001; Baptist and Leopold, 2009). Thus, increasing winter temperatures may lead to higher adult survival of *S. subtruncata*.

## Spring and summer temperatures

The positive association between water temperature during the post-settlement phase (77 days after settlement) is likely related to increased survival of recruits. Warmer seawater increases growth rates of *S. subtruncata*, helping juveniles to outgrow predators like brown shrimp (van der Veer et al., 1998; Hiddink et al., 2002; Andresen and van der Meer, 2010), which feed on recruits up to 4 mm in size (Cardoso et al., 2007; Campos and van der Veer, 2008). Faster growth shortens the duration of the shrimp predation window, enhancing survival (Hiddink et al., 2002; Andresen and van der Meer, 2010). While shrimp reproduction and shoreward migration are also temperature-dependent (Boddeke, 1976; Beukema, 1992; Penning et al., 2021), rising North Sea temperatures could create a mismatch between shrimp and prey, potentially benefiting *S. subtruncata*. However, warming may also shift predator communities, with increasing cold water species in the coastal zone, negatively affecting bivalves. For example, flatfish such as sole and plaice, appear to be moving from the Wadden Sea to the cooler coastal zone in the North Sea (van der Veer et al., 2022).

The positive association between post-settlement water temperature and *S. subtruncata* densities may also be related to food availability. Phytoplankton blooms play a crucial role for benthic fauna, driving rapid growth and changes in benthic communities (Zhang et al., 2015). There are indications that changes in North Sea phytoplankton have occurred in the recent and more distant past.

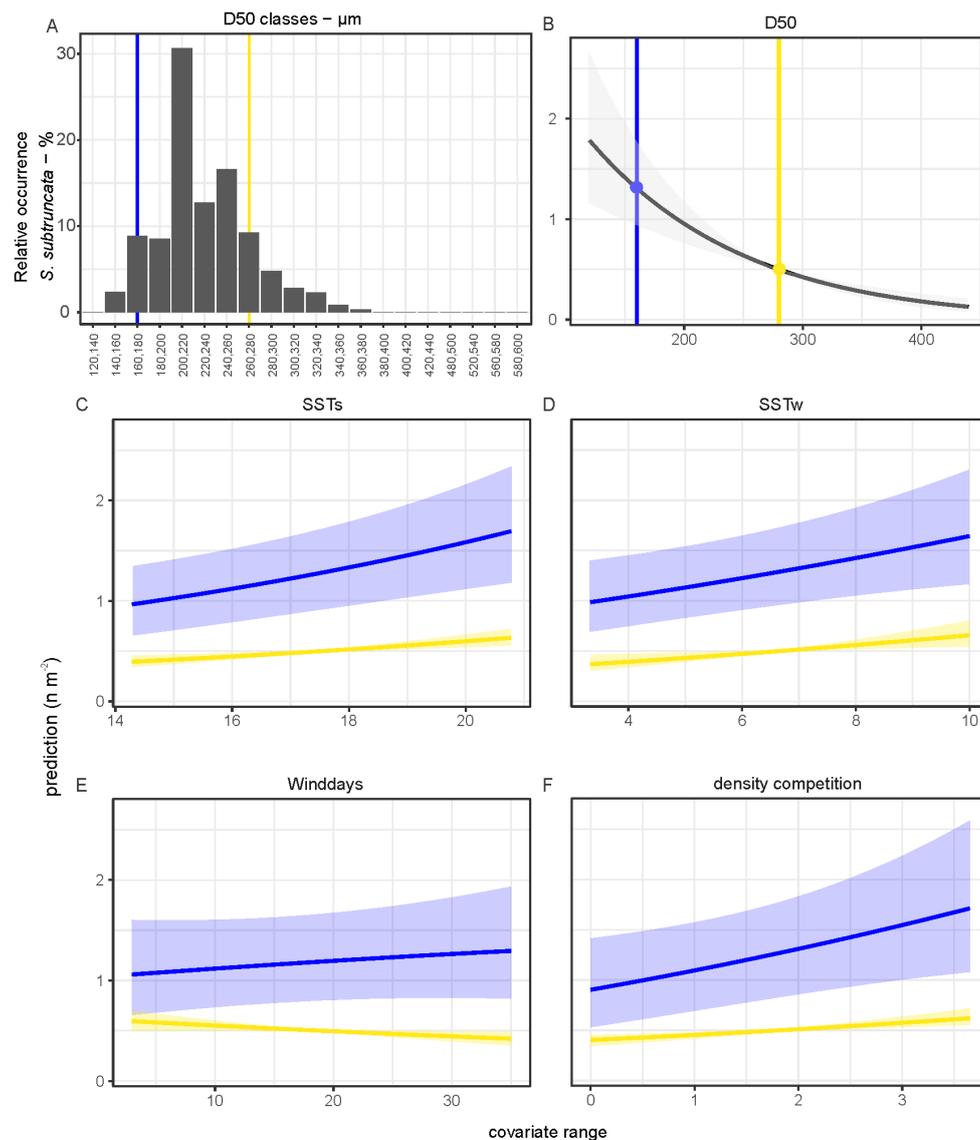


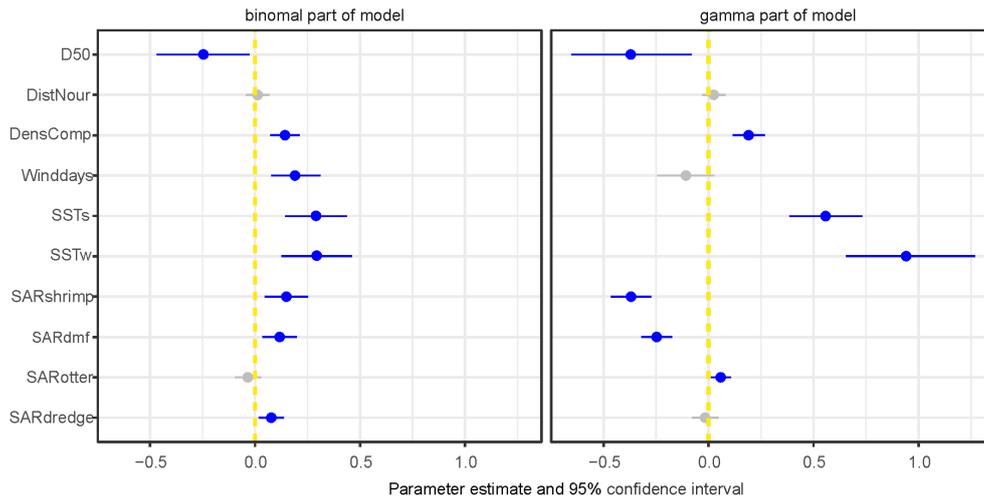
FIGURE 9

Frequency plot of sediment grain size where *S. subtruncata* occurred (A). Predicted contribution of covariates from the hurdle model (B–F) Prediction per measured range of covariates with minimum (blue) and the maximum (yellow, for values see B) of the optimal range of occurrence of *S. subtruncata* for median grain size while all other covariates standardized with a mean of zero. Shaded areas represent 95% confidence interval around the prediction.

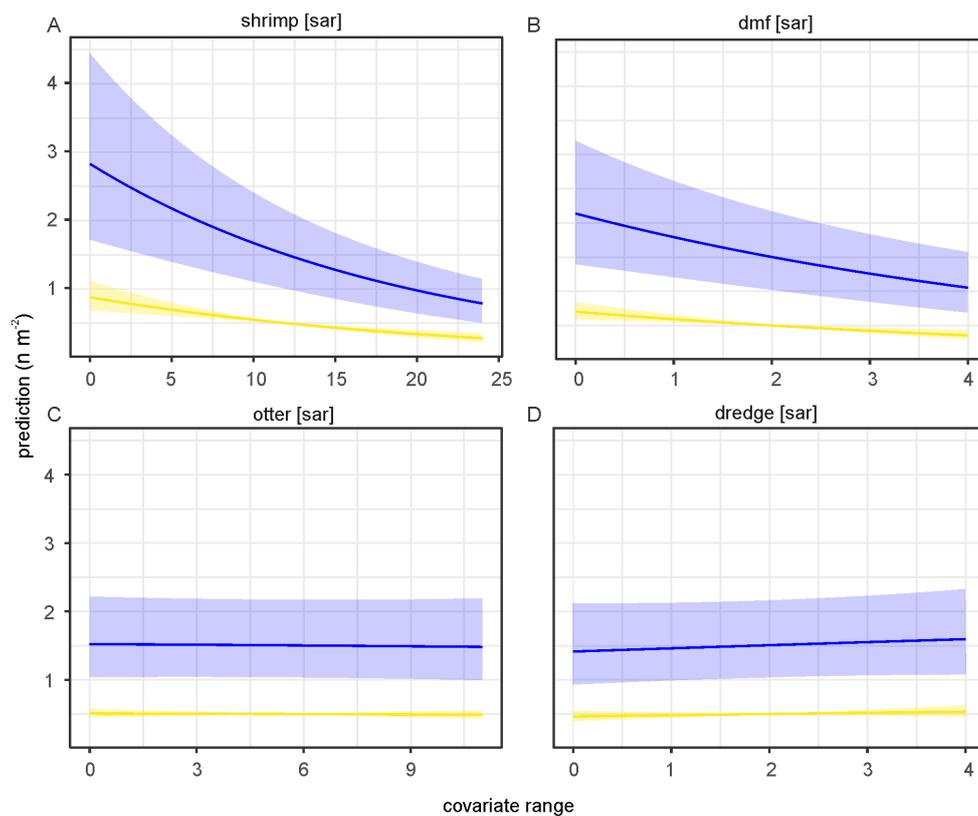
Over the last century, for example, it is estimated that a reduced water transparency resulted in a delay of the spring bloom by 3 weeks (Opdal et al., 2019). Between 1988 and 2016, however, phytoplankton biomass declined and the timing of the spring bloom advanced (Desmit et al., 2020). While, shifts in phytoplankton species composition that have occurred (Baretta-Bekker et al., 2009), may have affected growth and survival of juvenile bivalves in Dutch North Sea coastal waters. Currently, the net consequences of altering phytoplankton bloom as a food source for benthic animals in the North Sea are difficult to evaluate due to the multifaceted changes in phytoplankton and unknown food preferences of the bivalves.

## Strong north-western winds

Strong north-westerly winds affected *S. subtruncata* densities negatively. Strong winds cause resuspension of fine sediments which might reduce filtering efficiency of feeding bivalves, hampering their growth (Witbaard et al., 2005). Additionally, the disturbance of waves can disturb the buried *S. subtruncata* and release them from the seafloor. As *S. subtruncata* live at the sediment surface, they are also vulnerable to strong under water currents which can transport them to the beach or other unfavourable habitat. Mass mortality events due to strandings are



**FIGURE 10**  
 Estimated weights of the covariate effects indicated with posterior means with 95% confidence interval (CI) plotted for most parsimonious model including fisheries (for the dataset 2009-2020) for binomial and gamma part (best model in Table 2), blue points and lines show effects differing from zero with 95% CI. Median sediment grain size (D50), SST settlement phase (SSTs), SST winter (SSTw), density competing bivalves (DensComp), number of days wind > 10 m<sup>-s</sup> (Winddays), distance to sand nourishment (DistNour) and Swept area ratio for fishing intensity (SARshrimp, SARdmf, SARotter and SARdredge).



**FIGURE 11**  
 Predicted contribution of covariates the hurdle model. (A–D) Prediction per measured range of covariates with minimum (blue) and the maximum (yellow, for values see Figure 9B) of the optimal range of occurrence of *S. subtruncata* for median grain size while all other covariates standardized with a mean of zero. Shaded areas represent 95% confidence interval around the prediction.

known to happen after strong north-westerly winds followed by wind from the land creating a reversed current at the bottom (Raven, 2022).

## Fishery impact

Our analyses showed a positive association between beam trawling for shrimp and flatfish and the presence of *S. subtruncata*, indicating that areas where the species is abundantly present, were more frequently fished. This aligns with observations that areas rich in bivalves attract shrimp and flatfish, and thus fisheries (van der Reijden et al., 2018; Hintzen et al., 2020). We also found a negative association between intensity of beam trawling for shrimp and flatfish and *S. subtruncata* density. While flatfish trawling, which penetrates the seabed, is known to increase bivalve mortality and affecting benthic communities (Tillin et al., 2006; Eigaard et al., 2016; Hiddink et al., 2017; Rijnsdorp et al., 2018), shrimp trawling, which lightly disturbs the seabed, is more frequent in the study area (Figure 6). However, studies on the impact of shrimp trawling on the benthic community in coastal waters are very limited (Tulp et al., 2020; Sala et al., 2023; van der Meer et al., 2024). The limited studies on the effects of shrimp beam trawling suggest it may shift benthic communities in the Wadden Sea (Tulp et al., 2020). This shift as observed in dredge sampling was mainly due to an increase in *E. leei* densities, likely able to relocate and quickly colonise disturbed shrimp trawl areas (Tulp et al., 2020), though a follow-up study based on box-core sampling within the same study did not find support for this hypothesis (van der Meer et al., 2024). A similar observation was found in an experimental study in the Wadden Sea, where *E. leei* preferred the manipulated unstable sediments (van der Heide et al., 2014).

The impact of bottom trawling on the benthic community varies between habitats. In highly dynamic habitats, with larger median grain size, benthic communities are less affected by trawling (van Denderen et al., 2014; Rijnsdorp et al., 2018; van der Reijden et al., 2018). Our study also found a stronger negative association between *S. subtruncata* and flatfish and shrimp trawl fisheries in areas with lower median grain size (Figures 11A, B), suggesting potential trawling effects are habitat dependent. In fine-medium sediment grain size, the bottom trawl gear may impact the seabed more strongly as it penetrates deeper into the seafloor, potentially increasing shellfish mortality and disrupting larval settlement. To disentangle the causal relationships and potential mechanisms, empirical research on the effects of beam trawl, especially shrimp fisheries, is needed, considering sediment characteristics.

Intensive fisheries on *S. subtruncata* can have strong effects on local abundances (Leopold, 1999; Smaal et al., 2001; Camphuysen et al., 2002), however, within our study, we did not find a relation between bivalve dredging and *S. subtruncata* densities. The absence of an effect may be because our analyses, covering fisheries data from 2009–2020, only includes two years of bivalve fisheries (2019–2020). In addition, the harvested quantities of adult *S. subtruncata* in these years were low, at  $5.0 \times 10^6$  kg in 2019 and  $6.5 \times 10^6$  kg in 2020, representing 0.3% and 0.6% of the estimated standing adult stocks respectively (Perdon et al., 2019; Troost et al., 2023). In

earlier years (1995–1999), fishing pressure was much higher (1% to 22% of the total estimated standing adult stock) which might have contributed to the population decline at the end of the 1990s (estimated harvest data supplied by A. Seinen, Meromar; Troost et al., 2023).

## Window of opportunity

The relative effect of the smoother year in our models was high and captured the temporal trend to a large extent. This means that the unexplained annual variation in densities is likely related to yearly recruitment fluctuations (Fogarty et al., 1991) which were not captured by our model covariates. Therefore, additional factors during pre- and post-settlement are likely responsible for the observed variation. Recruitment success of shellfish is highly dependent on factors that must be optimal during a critical ‘window of opportunity’ (Balke et al., 2011; Capelle et al., 2019). Here, we discuss factors not included in our model analyses that are potentially related to recruitment success.

Larval settlement largely depends on the wind conditions for survival, dispersal and local settlement conditions. Wind-induced mixing of the water column can affect the vertical distribution of phytoplankton, influencing food availability for fish and invertebrate larvae and in turn their survival (Corten and van de Kamp, 1996; Turley and Rykaczewski, 2019). Wind direction and force during the pelagic larval phase determine the dispersal and location of shellfish larvae settlement (Belgrano et al., 1995; Armonies et al., 2001). The optimum conditions for *S. subtruncata* during the pelagic and settlement phases are unknown, however the pelagic phase for *S. subtruncata* larvae is relatively long, making them vulnerable to predation and environmental fluctuations, leading to high recruitment variability (Fogarty et al., 1991; Cardoso et al., 2007).

## Predation

We used shrimp densities in the North Sea (Tulp et al., 2012) (Figure 7A) and energy requirements of shrimp (Jung et al., 2017) to estimate shrimp predation pressure (Supplementary Figure A3). Based on average estimated shrimp densities of  $1.35 \text{ m}^{-2}$  ( $13,500 \text{ shrimp ha}^{-1}$ ), with a maximum observed of  $22 \text{ m}^{-2}$  ( $220,000 \text{ ha}^{-1}$ ) (Tulp et al., 2012) (Supplementary Figure A3), we estimate that brown shrimps reduce *S. subtruncata* densities by 1,800 to 30,000 recruits  $\text{m}^{-2}$  over a 77 day predation window respectively. The net effect depends on the starting settlement density of *S. subtruncata* recruits. For example, a recruit density of  $15,000 \text{ m}^{-2}$  may lead to a local reduction ranging from 10% to a potential complete depletion of recruit density. However, based on the maximum observed *S. subtruncata* recruit densities of  $150,000 \text{ m}^{-2}$  (Degraer et al., 2007), we estimate a local potential predation mortality by brown shrimp ranging from 1% to 20%. The trends in our descriptive data on shrimp predation did not provide a clear indication that they can explain the unexplained year effect. However, there is a large uncertainty on shrimp densities and are likely underestimated

(Aarts et al., 2019; Supplementary Material A3). For other bivalve species it was shown that a predation pressure of this order of magnitude can drive population dynamics (Hiddink et al., 2002; Andresen and van der Meer, 2010; Weerman et al., 2014).

Flatfish also prey on bivalves, especially for dab and plaice it can be an important prey (Braber and de Groot, 1973; Rijnsdorp and Vingerhoed, 2001; Tulp et al., 2010). Stomach content analyses showed that *S. subtruncata* can be the dominant prey for plaice (Rijnsdorp and Vingerhoed, 2001). The same uncertainties as for brown shrimp apply for the estimation for flatfish densities. Moreover, larger flatfish (> 150 mm) are underrepresented in the DFS survey (Aarts et al., 2019) because the gear is not suited for larger, faster swimming fish, and diets are poorly known. Therefore, reliable estimates of flatfish predation pressure cannot be made.

Diving ducks, particularly common scoters, feed on adult *S. subtruncata* during winter in Dutch coastal waters (Camphuysen et al., 2002; Fox, 2003). Common scoters can potentially consume 4% to 20% of the local adult *S. subtruncata* (van de Wolfshaar et al., 2023). Since the ducks prefer larger specimens and are mainly present in winter, we can assume that scoter predation pressure on recruits during autumn is relatively low.

## Implications for research and management

Our results showed that *S. subtruncata* was spatially aggregated on a large scale, occurring in high densities in distinct areas year after year. This spatial aggregation offers opportunities for conservation management. While European Union directives (e.g. Species and Habitats Directive 92/43/EEC and Birds Directive 79/409/EEC) permit anthropogenic activities within protected areas in the Dutch North Sea, provided that they do not significantly impact designated species and habitats. However, currently shrimp trawl fisheries, mollusc dredge fisheries and sand nourishment are occurring within protected areas (Natura 2000) and in areas with high densities of *S. subtruncata* (Hintzen, 2021; van de Wolfshaar et al., 2023), raising concerns about their potential impacts. Apart from the uncertainty about the impacts of shellfish dredging, shrimp trawl fisheries, there are uncertainties about the effects of sand extraction and nourishments. Due to the limitations of available data and methodological challenges for sand extraction and nourishments, we were unable to investigate potential impact over large spatiotemporal scales. The potential for climate effects to interact with local anthropogenic activities may complicate management, as they may amplify, neutralize or counteract each other's impact on the benthic community (Wakelin et al., 2015). The net outcome of such interactions is currently unknown and may contribute to the strong temporal variations of the unexplained year effect.

The effects of potential drivers in our study appear to be context-dependent, with sediment grain size serving as a proxy for habitat. This implies that a nuanced understanding of habitat dependency at finer spatial scales could be critical. Additionally, further insights into what determines the critical window of opportunity driving *S. subtruncata* population dynamics are

needed. Questions remain about how climate change and intensifying local human activities may significantly affect the *S. subtruncata* population. Addressing these uncertainties would benefit from focused empirical research, particularly observational and experimental studies during the early recruitment phases. This more in-depth empirical research on (a)biotic and anthropogenic effects, and their cumulative impacts is essential to develop adequate fisheries and coastal management strategies, to sustain biodiversity.

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

## Author contributions

JdF: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Supervision, Validation, Visualization, Writing – original draft. PvH: Conceptualization, Data curation, Formal analysis, Methodology, Software, Visualization, Writing – review & editing. JC: Data curation, Investigation, Methodology, Writing – review & editing. ML: Data curation, Investigation, Methodology, Writing – review & editing. JP: Data curation, Investigation, Writing – review & editing. KT: Data curation, Investigation, Methodology, Project administration, Writing – review & editing. IT: Data curation, Investigation, Methodology, Writing – review & editing. JvZ: Data curation, Investigation, Writing – review & editing. CP: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2024.1476223/full#supplementary-material>

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