



# The longevity of subtidal mussel beds in the Dutch Wadden Sea

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## ABSTRACT

Soft-bottom beds of the blue mussel (*Mytilus edulis*) are of high ecological importance in intertidal and subtidal habitats. They create habitat, shelter and food for other organisms, and play a dominant role in energy flow and nutrient cycling. Intertidal beds are much better studied than subtidal beds. Though it is often assumed that subtidal mussel beds resemble their intertidal counterparts, major differences in factors driving recruitment, growth and survival can be expected. The aim of our study was to estimate survival chances of the mussel beds in the subtidal parts of the Dutch Wadden Sea in relation to environmental variables, and to compare the results with those obtained previously from the intertidal areas. We used data from a long-term annual survey, resulting in a survival analysis of 365 individual subtidal mussel beds. The average life span of subtidal mussel beds, once they have survived their first winter, was estimated at 2.3 years. This is lower than what was found in the intertidal (3.4 years) in a previous study. However, the survival of subtidal mussel beds in less-saline areas is comparable to survival of intertidal mussel beds, whereas survival of subtidal mussel beds in more-saline areas is significantly lower. The strong, significant effect of salinity is most likely an indication of an effect from starfish predation, since starfish (*Asterias rubens*) are virtually absent from the intertidal and their abundance is strongly reduced in the subtidal at lower salinities. Furthermore, the survival of individual beds is positively correlated with their size. This may be a direct effect of the bed size itself, or also an indirect effect of environmental factors that can affect the size of newly settled beds. A secondary aim was to compare two methods, based on different types of field data: 1) empirical point data and 2) estimated bed contours based on the point data and additional sources of information. Both methods give similar results. Advantages and disadvantages of both methods are discussed.

## 1. Introduction

Soft-bottom mussel beds (*Mytilus* sp.) fulfil a key function in intertidal and subtidal habitats (Commito and Dankers, 2001). By creating three-dimensional reef structures and through the production and retention of biodeposits, they provide habitat and shelter for many marine species (Buschbaum et al., 2009; Commito et al., 2008; Dittmann, 1987; Kochmann et al., 2008; Saier, 2002; Van der Zee et al., 2012). Mussels themselves are also important as a food source for several bird species (Blomert et al., 1996; Camphuysen, 2013; Cervencel et al., 2015; Dekinga and Piersma, 1993; Goss-Custard, 1996; Hilgerloh and Pfeifer, 2002). Moreover, through their suspension feeding activity, they can have a dominant role in energy flow and nutrient cycling in coastal marine ecosystems (Dame, 2012; Dame and Prins, 1998; Smaal and Prins, 1993).

The dynamics of mussel beds occurring on the intertidal mudflats of

the Wadden Sea are well studied. For example, Folmer et al. (2014) analysed the spatial distributions and growth patterns of intertidal mussel beds in the German and Dutch Wadden Sea. Spatial patterns in mussel beds and the mechanism and implications of self-organisation for survival and growth were studied by Van de Koppel et al. (Van de Koppel et al., 2012; Van de Koppel et al., 2005). The role of hydrodynamic processes in intertidal mussel bed stability was studied by Donker (2015), Donker et al. (2013) and Strasser et al. (2001). Multiple papers have been published about the role of predation by benthic and bird predators in structuring intertidal mussel communities (Nehls et al., 1997; Waser, 2018). More recently, Van der Meer et al. (2018) studied the recruitment and fate of 1436 individual mussel beds in the Dutch Wadden Sea and showed that large beds, beds in the lower intertidal and beds that experience a low orbital speed live longer. The longevity of individual beds is also increased when mussel beds are mixed with Pacific oysters (*Crassostrea gigas*).

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However, the subtidal soft-bottom mussel bed dynamics are less well studied (Knights, 2012; Ricklefs et al., 2020; Vorberg et al., 2017). Although subtidal beds are often assumed to resemble their intertidal counterparts, there are major differences in the factors that drive recruitment, growth and survival between both environments. An important difference is the presence of the common starfish (*Asterias rubens*), a voracious predator of mussels, known for its ability to exert a top-down control on its prey populations (Agüera García, 2015; Gaymer and Himmelman, 2002; Hancock, 1955; Paine, 1974). Starfish can reach very high densities on subtidal mussel beds, but hardly occur in the intertidal. Furthermore, hydrodynamic factors such as storminess (Nehls and Thiel, 1993), wave action (Kaiser et al., 1994) and ice scouring (Strasser et al., 2001) are likely to differ between the intertidal and subtidal areas. Furthermore, since 2004, mussel fisheries are only allowed in the subtidal (LNV, 2004).

With the aim of stocking bottom culture plots in the Dutch Wadden Sea and Oosterschelde Bay, mussel spat is dredged from natural stocks predominantly in the western Dutch Wadden Sea (Baer et al., 2017). Mussel spat may be dredged twice a year, in the autumn and spring (Capelle, 2017). The fishery in autumn is allowed on newly-formed spat beds that are relatively unstable and have a greater risk of disappearing in the following winter. In contrast, spring fisheries are allowed on all beds in areas open for seed fishery (Smaal et al., 2021; Van Stralen, 2014).

In 2014, large subtidal areas in the Dutch Wadden Sea were closed to mussel fisheries, to facilitate the undisturbed development of subtidal mussel beds (Van Stralen, 2014). A large-scale study on the effects of the mussel fishery on subtidal mussel beds and associated benthic fauna showed that the biomass of mussels in a bed is strongly reduced by the activity. The remaining biomass of mussels is generally sufficient for

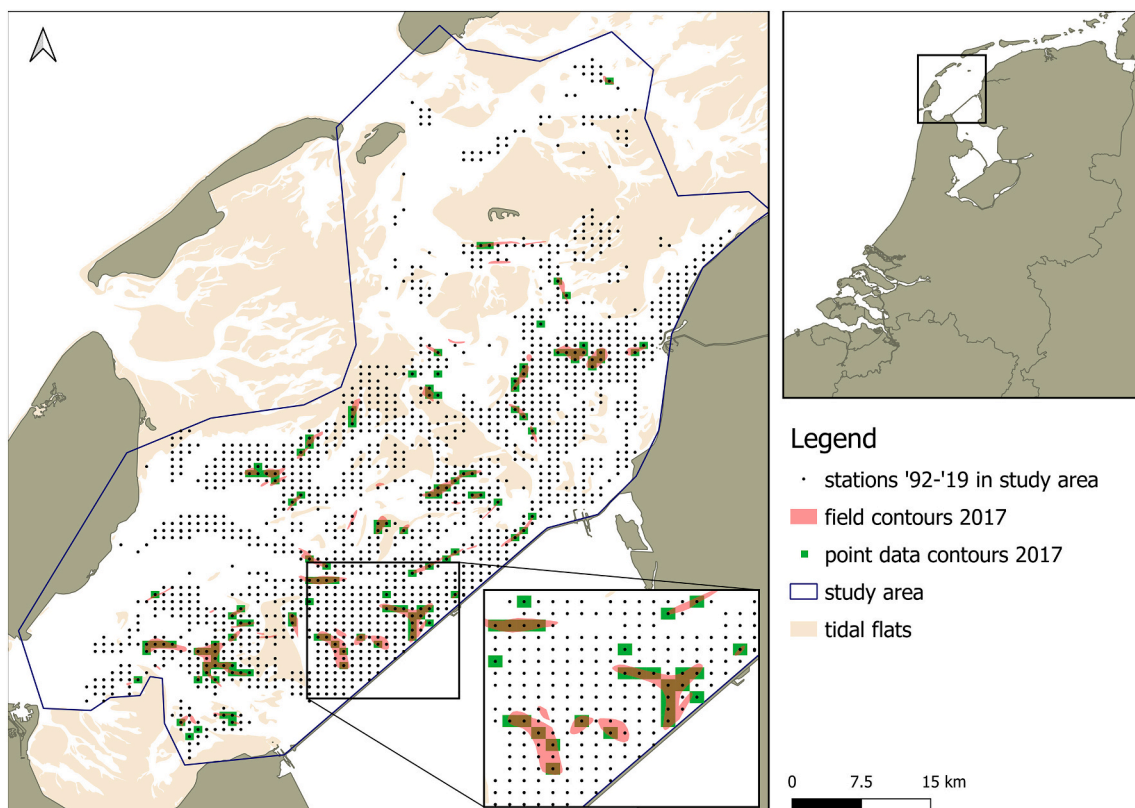
development into mature beds, as long as the environmental conditions are favourable. Further survival and development of these beds is determined by natural factors, mainly storms and predation by starfish (Smaal et al., 2021). None of the beds studied, comprising both fished and unfished beds, survived for longer than seven years.

Since 1992, the annual stock assessments of wild mussels in subtidal parts of the Dutch Wadden Sea are carried out for seed-fishery management. Here, we analyse this 28-year data set to estimate the chances of survival for sublittoral mussel beds in relation to the age of the bed and to relevant environmental variables. Results are compared to those from a similar analysis on intertidal beds (Van der Meer et al., 2018). We compare two methods based on different types of field data: 1) empirical point data and 2) estimated bed contours based on the point data and additional sources of information.

## 2. Methods

### 2.1. Study area

Our study area is within the subtidal zone of the western Dutch Wadden Sea (Fig. 1). The Wadden Sea is the world's largest non-tropical barrier-island tidal system (Wolff, 1983). It is found between the North Sea and mainland of the Netherlands, Germany and Denmark. The seafloor consists mainly of soft sediments (Vorberg et al., 2017), ranging from coarse-grained sands close to the inlets and in the tidal gullies to fine mud in the shallow areas close to the mainland and tidal watersheds (Philippart and Epping, 2010). There is a wide range in the salinity due to freshwater discharge from several rivers (e.g. Ems and Elbe) and through Lake IJsselmeer. For a more detailed description of biotic and abiotic properties of the Wadden Sea, see (Philippart and Epping, 2010).



**Fig. 1.** Map showing the study area with all individual stations that were sampled in the period from 1992 to 2019. As an example, both field contours and contours based on the point data are shown for the year 2017, including a close-up. Depicted field contours (pink) are mussel bed contours estimated from the survey results of spring 2017 and autumn 2016 and other sources of information through expert judgement. Depicted point data contours (green) are mussel bed contours estimated directly from the results per individual sampling station in the 2017 spring survey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Intertidal mussel beds are well-documented and occur throughout the entire Wadden Sea (Folmer et al., 2014). In contrast, subtidal mussel beds are less well-documented because of the relative difficulty in gathering data for these permanently-submerged structures in the highly turbid and dynamic system of the Wadden Sea (see also Ricklefs et al., 2020). Subtidal mussel beds are known to occur in the North Frisian Wadden Sea in Germany (Ricklefs et al., 2020; Vorberg et al., 2017) and in the western Dutch Wadden Sea (Smaal et al., 2021; Vorberg et al., 2017). In the Wadden Sea of Lower Saxony in Germany, most subtidal beds appear to consist of intertidal mussel beds continuing into the shallow subtidal (Vorberg et al., 2017). The same is also the case for the eastern Dutch Wadden Sea, where subtidal mussel seed beds are found incidentally by shrimp fishermen and fisheries inspectors, and have always disappeared before attempts could be made to localize and demarcate them.

## 2.2. Field data

Since 1992, surveys are carried out annually to assess the total stock of blue mussels in the subtidal of the western Dutch Wadden Sea, and the amount of juvenile mussel ("seed") biomass that is suitable for harvesting. In spring, the total stock of mussels is assessed by sampling according to a stratified sampling grid in the period from March–April. A fixed grid of approximately  $500 \times 500$  m is used as a basis. In areas where mussel occurrence is expected, all of the grid stations are sampled. In areas with a moderate expectancy or confirmed low densities, the sampling effort is reduced to a lower density (2–3 times lower). Outside these areas, the sampling effort is reduced further (5–7 times lower). Annually, an average of 539 stations (range: 347–824) are sampled. Because a fixed grid is used, the positions of sampling stations within mussel beds generally remain unchanged between the years.

The expected occurrence of mussel beds is based on a combination of ad hoc knowledge, historical data and expert judgement. Each autumn, newly formed mussel beds are located in the period August–September, aided by information from fishermen, fisheries inspectors, satellite images (for the shallower parts) and historical occurrences. Mussel bed presence is established through sampling with a mussel dredge (a device used for mussel fisheries). The contours of the newly-formed beds are roughly estimated based on multiple dredge tracks and expert judgement. In addition, the presence or absence of older beds is usually also determined.

Sampling in spring is done using two devices. Stations at water depths below 10 m are sampled with a commercial suction dredge that was modified specifically for the sampling of mussels and other macrobenthic fauna. At water depths over 10 m, a specially-constructed towed dredge is used. Both devices consist of a cage (5 mm mesh) that is towed along the seafloor, with a knife that cuts to a depth of 7 cm into the sediment. The suction dredge has a 10-cm wide opening and is towed along the sea floor with the suction tube. The sample is flushed directly onto the deck through the ship's suction and flushing system. The towed dredge has a 20-cm wide opening and is towed along the sea floor using a steel cable. The sample is collected in the cage and emptied on deck after hauling the device. The total area sampled is dependent on the towing distance, which is measured using either a counting wheel (towed dredge) or by demarcating the beginning and end of the track in MaxSea marine navigation software using a DGPS (suction dredge). The towing distance is approximately 150 m, resulting in a sampled surface area of about 15–30 m<sup>2</sup>. Dredge tracks pass the intended position of the sampling station within a distance of 25 m. On deck, mussels (and other species) are sorted, counted and weighed (wet weight including the shell).

## 2.3. Definition of individual mussel beds

The definition of an intertidal mussel bed, as agreed upon by Danish, German and Dutch researchers (CWSS, 2002) and also referred to by Van

der Meer et al. (2018) is not applicable to subtidal beds, since the contours and contents of the beds are estimated in a different way. Since 2009, mussel bed contours are estimated based on the individual sampling stations in the spring survey. A sampling station is considered as part of a mussel bed if the biomass is higher than 150 g m<sup>-2</sup>. Based on the results from both the spring and previous autumn surveys, as well as spatial information on fishing effort (black box data), and taking the local bathymetry and historical occurrences into account, the bed contours are estimated through expert judgement. All estimated bed contours are drawn by placing waypoints in MaxSea and converting them to a shapefile using GPS Utility. GIS software (QGIS) is then used to connect the waypoints into polygons. This method is both less reliable and accurate than the intertidal method. Because it is highly dependent on expert judgement, this method is also less reproducible. In addition, contour estimates are lacking for the previous 17 years (1992–2008). Therefore, we used an additional, alternative approach, in which we estimated bed contours for the entire time series (1992–2019, 28 years) purely based on the spring survey data per sampling station. Out of the data points located on the fixed grid of approximately  $500 \times 500$  m (0.50 min longitude x 0.25 min latitude, WGS84) (Fig. 1), all sampling stations with a mussel biomass less than 150 g fresh weight (including the shell) per m<sup>2</sup> were eliminated. All remaining sampling stations, regardless of the original stratification, were assumed to correspond to a mussel bed with a surface area of 256,700 m<sup>2</sup>, which was drawn as a square with the sampling station in the centre (see example in Fig. 1). All adjoining squares and squares connected diagonally were considered to belong to the same mussel bed.

Further analysis followed the same methodology as was used by Van der Meer et al. (2018). Spatially-overlapping patches in consecutive recordings were considered observations from the same bed. This means that beds can neither be split nor merged.

## 2.4. Survival analysis

Mussels in the Dutch Wadden Sea spawn around late spring / early summer. After a pelagic phase of several weeks, larval settlement takes place (Maas Geesteranus, 1942). We consider this to be the moment of 'birth' of an individual mussel bed. These newly-formed 'seed' beds become visible to the human eye around late summer. When they first appear in the spring survey ('recruitment'), they are almost a year old and have survived their first winter. Beds are assumed to disappear (or 'die') shortly after their last appearance in the spring survey. We followed the methodology of Van der Meer et al. (2018) and assumed that the lifetime of a bed equals the number of years it occurred in the survey. As shown in that same study, this assumption could not be made for beds that were still present in the last year of the study. For such beds, we only know their minimum lifetime and not their moment of death.

We performed the same survival analysis as Van der Meer et al. (2018) using Cox's proportional hazard model (Klein and Moeschberger, 2003). As was also the case in that study, we excluded beds that were already present in the first year of our study, since their year of birth is unknown. Our model contained the following quantitative and time-independent covariates: longitude, log bed size, orbital speed, salinity and water depth of the midpoint of each bed. Like in Van der Meer et al. (2018), we assumed that these covariates did not change during the study period. For orbital speed, salinity and water depth, there was only a single measurement available. However, these variables are not expected to change much over time. For longitude and bed size, annual measurements were available, but these also hardly changed over time. Therefore, we used the initial value in the analysis, following the methodology from Van der Meer et al. (2018). To allow for an easier interpretation and comparison of the estimated regression parameters, all quantitative covariates were standardised (with a mean of zero and a standard deviation of one).

We used the same data on water depth and wave orbital speed as were also used by Van der Meer et al. (2018). Depth data were derived

from a bathymetric grid at a resolution of 20 by 20 m throughout the Dutch Wadden Sea. This bathymetry was largely based on LIDAR soundings performed by Rijkswaterstaat in the period 2006–2012. For more details, see [Elias and Wang \(2013\)](#). Wave orbital speed was modelled using SWAN, a two-dimensional horizontal wave model ([Booij et al., 1999](#)) based on the bathymetric grid. For more details, see [Van der Meer et al. \(2018\)](#) and [Donker \(2015\)](#). Salinity data were obtained from the General Estuarine Transport Model (GETM, [Burchard and Bolding, 2002](#)) on a  $200 \times 200$  m grid by [Folmer et al. \(2016\)](#). For further details, see [Folmer et al. \(2016\)](#). Salinity values in the study area ranged from 12 to 31 ppt, with salinities of up to 20 ppt only occurring close (<4 km) to the sluices of Den Oever.

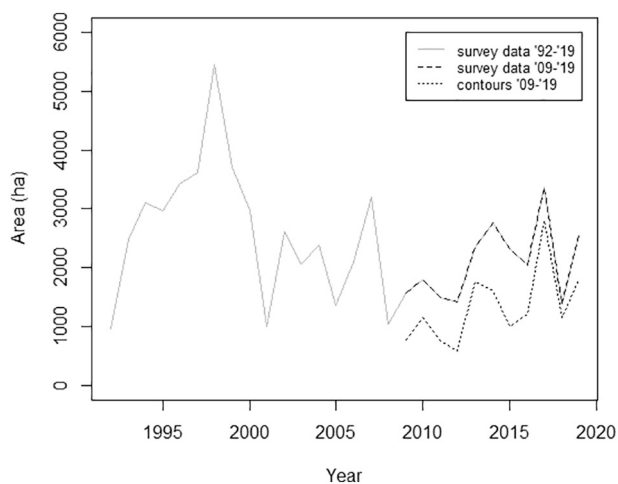
## 2.5. Software

We performed all analyses using the program R (R Core Team 2016). For spatial analysis, we used the packages ‘sp’, ‘maptools’, ‘rgeos’, ‘rgdal’, ‘raster’ and ‘spdep’. For survival analysis, we used the package ‘survival’. Scripts are available from the corresponding author.

## 3. Results

Both the contour data and point data showed a similar development, with a slightly higher surface area estimate for the point data in the period 2009–2019 ([Fig. 2](#)). From the point data in the period 1992–2019, a total of 365 beds were identified. The fate of all these beds in terms of their year of birth and year of death is summarised in [Table 1](#). Of all 365 beds, a total of 223 beds (61%) are on the main diagonal, which means that they disappeared after approximately one year. Another 67 beds (18%) disappeared one year later. The average life span was 2.3 years. Thus, the majority of the beds disappeared quickly after their ‘birth’. The estimated survival curve indeed shows that the probability of being alive drops down quickly in the first few years after ‘birth’ ([Fig. 3](#)). However, after an age of about 4 years, the survival function decreases slowly, which implies that the chance of disappearing (the hazard rate) becomes low. Survival curves are similar for both the point data and contour data, as can be seen in [Fig. 4](#) where the survival curves are plotted for both datasets for the period 2009–2019.

The standardised covariates of bed size and salinity showed a significant effect on the chance of disappearing ([Table 2](#)). For beds that are one standard deviation larger than the mean bed size, the chance of disappearing is 22% lower than the average chance of disappearing. For beds one standard deviation higher in salinity, the chance of disappearing is 39% higher than the average. The other covariates showed relatively weak effects that were statistically insignificant. [Fig. 5](#) shows



**Fig. 2.** Development of the surface area of new beds in spring according to the datasets used.

the large difference in survival of beds at higher and lower salinities. No beds occurred at salinities below 20 ppt. At salinities below the median (20–26 ppt), 54% of the beds survive their first year, and the chance of surviving in the first four years is 20%. At salinities above the median (26–31 ppt), 37% of the beds survive their first year, while the chance of surviving within the first four years is 4%. Particularly in the first two years, a large difference in the rate of loss is observed.

After deleting the nonsignificant variables (longitude, water depth and orbital speed), the proportional hazard assumption was tested for each covariate of the fitted Cox model by correlating the scaled Schoenfeld residuals with time (following [Van der Meer et al. \(2018\)](#)). The test for independence between time and residuals yielded an insignificant result for all model variables. A similar result was obtained for the global test for the complete model ( $X^2 = 1.73$ ,  $p = 0.42$ ).

## 4. Discussion

Both methods (point data vs. contours) have their advantages and disadvantages. Although the field contours represent the best information available on mussel bed distribution in the spring, they are arguably too dependent on the expertise of only one person (MRS who has set up the surveys in 1992 and has been leading them ever since) and are therefore lacking in reproducibility. The point data approach lacks additional information and refinement through expert judgement, but can be considered more reproducible and significantly less dependent on one person's expert judgement. Nevertheless, one of the main advantages of the point data method comes from the longer time series available; 28 years instead of 11 years. Despite the differences stated above, the estimated survival curves for the period 2009–2019 were highly similar. For both methods, the Cox proportional hazard model revealed significant effects of both bed size and salinity on the chance of disappearing. Therefore, we conclude that both methods are equally suitable for the performed analyses, albeit with preference for the point data approach because of the longer time series.

We compared our results to the study on dynamics of intertidal mussel beds by [Van der Meer et al. \(2018\)](#), which was also performed in the Dutch Wadden Sea. It should be noted that survey methods differ significantly between the intertidal and subtidal areas. Intertidal mussel beds emerge during low tide, when they can be easily mapped by walking around them with a hand-held GPS. Subtidal mussel beds in the Wadden Sea are always submerged in water with a generally high turbidity. Contours therefore need to be estimated based on multiple sampling points. Apart from a lower contour precision, subtidal beds may be missed more frequently than in the intertidal. This should not affect the analysis if beds are missed from the start. Once beds have been detected, however, they will be followed until their (near) disappearance.

For subtidal mussel beds, we calculated an average life span of 2.3 years after survival of the first winter, approximately 9 months after initial settlement. This is lower than the 3.4 years calculated for intertidal mussel beds in [Van der Meer et al. \(2018\)](#). The average life span of beds that have survived their first winter, from initial settlement in summer until “death” is 3.1 years in the subtidal and 4.2 years in the intertidal. The average life span of all newly settled mussel beds is expected to be significantly lower, because many beds do not survive the first months, as has also been shown by [Steenbergen et al. \(2006\)](#) for the intertidal and [Smaal et al. \(2021\)](#) for the subtidal zone. The driving factors in the intertidal environments are exposure time and mixing with Pacific oysters ([Van der Meer et al., 2018](#)), which fits with observations showing that the survival of intertidal mussels beds is highly limited by wave action during storms and ice scouring during severe winters ([Donker, 2015](#); [Donker et al., 2015](#); [Kaiser et al., 1994](#); [Nehls and Thiel, 1993](#); [Strasser et al., 2001](#)). Subtidal mussel beds are much less exposed to wave action and ice scouring, which fits with the insignificant and weak effects of orbital speed and water depth that we observed. The large and highly-significant negative effect of salinity is likely a

**Table 1**  
Year of 'Birth' Versus Year of 'Death' for the point data (1992–2019).

Year of 'birth'	Year of 'death'																												
	'92	'93	'94	'95	'96	'97	'98	'99	'00	'01	'02	'03	'04	'05	'06	'07	'08	'09	'10	'11	'12	'13	'14	'15	'16	'17	'18	'19	
1992	6	2	1	0	1	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	
1993		5	6	2	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
1994			8	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
1995				12	6	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
1996					10	0	1	2	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
1997						10	7	6	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
1998							11	5	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
1999								9	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
2000									11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
2001										3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
2002											15	7	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	
2003												3	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
2004													10	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
2005														4	1	2	1	0	0	0	0	0	0	0	0	0	0	0	
2006															5	4	1	0	0	0	1	0	0	0	0	0	0	0	
2007																9	4	1	0	2	0	0	0	0	0	0	0	0	
2008																	4	1	0	0	0	0	0	0	0	0	0	0	
2009																		8	2	2	0	0	0	2	0	1	0	1	
2010																			8	3	0	0	0	0	0	0	0	1	
2011																				4	0	1	0	0	0	0	0	1	
2012																					3	0	2	0	0	0	0	0	
2013																						8	1	2	0	2	0	0	
2014																							7	4	0	1	2	1	
2015																								4	2	0	1	2	
2016																									3	1	0	2	
2017																											12	4	4
2018																												4	3
2019																													27

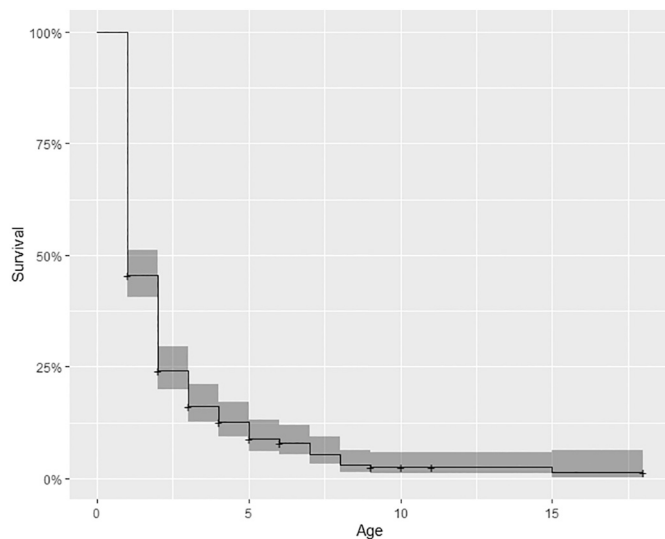


Fig. 3. Survival curve for subtidal mussel beds (point data 1992–2019).

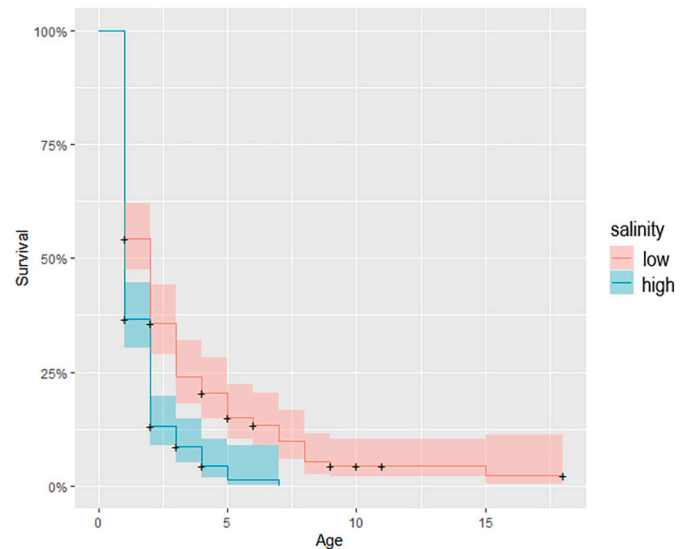


Fig. 5. Survival curves for beds at high (26–31 ppt) and low (20–26 ppt) salinity.

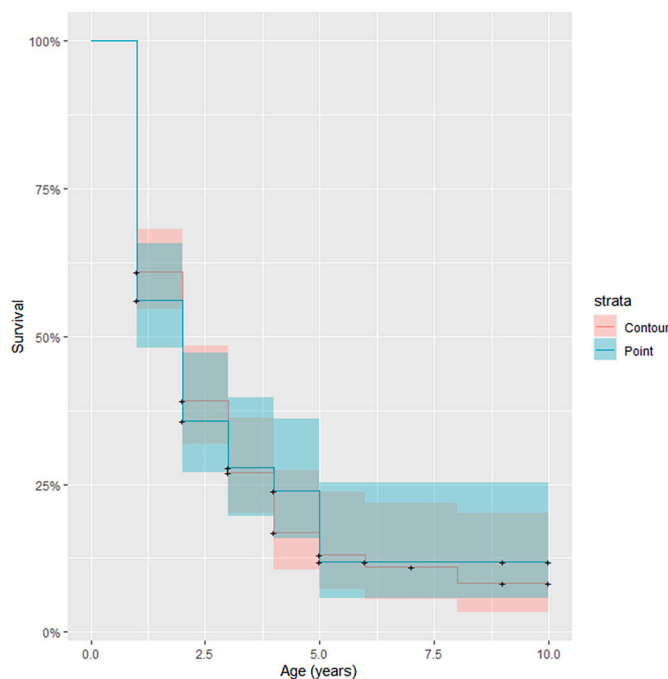


Fig. 4. Survival curves for beds based on the contour data (red) and point data (blue) in the period 2009–2019. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 2**  
Results of Cox's proportional hazard model for the point data (1992–2019).

Variable	<i>b</i>	exp( <i>b</i> )	se( <i>b</i> )	<i>z</i>	<i>P</i>	Likelihood ratio test (df = 5)
Longitude	−0.0546	0.9469	0.0699	−0.78	0.440	
Bed size	−0.2453	0.7825	0.0602	−4.07	<0.001	
Water						
depth	0.2045	1.2269	0.1307	1.56	0.120	
Orbital						
speed	−0.0531	0.9483	0.1309	−0.41	0.690	
Salinity	0.3263	1.3859	0.0680	4.80	<0.001	
Overall model					<0.001	48.58

reflection of the effect of predation by starfish, since both the distribution and feeding activity of starfish are limited at low salinity levels (Agüera García, 2015; Capelle et al., 2017). As Smaal et al. (2021) already summarised for the subtidal of the western Dutch Wadden Sea, starfish densities correlate with salinity levels (Agüera García, 2015). High starfish densities severely limit the survival of subtidal mussel beds (Agüera García, 2015) and mussel bed survival is higher in areas under the influence of fresh water discharges (Smaal et al., 2014). Because starfish represent such a considerable threat to mussel bed survival, the recent annual survey reports are paying special attention to starfish densities (Van Stralen and Troost, 2021; Van Stralen and Van den Ende, 2020). Although there are potentially other environmental factors that were not included in our analysis that nevertheless may correlate with salinity and/or freshwater discharge, such as food availability and quality for bivalve filter-feeders, we do not expect a detectable effect from these on our results and conclusions.

A comparison between survival curves (Table 3) shows that the survival of subtidal mussel beds is clearly lower than the survival of intertidal mussel beds, with a loss of 90% after 5 years in the subtidal and after 8–9 years in the intertidal. However, we see a striking similarity in survival curves of intertidal mussel beds and subtidal mussel beds at lower (below median) salinity levels. By excluding the beds at higher (above median) salinity levels, of which 90% have disappeared after 3 years, the period of 90% loss is extended to 7 years. As Smaal et al. (2021) argued, soft-bottom mussel beds are ephemeral structures that are highly dependent on new spat for prolonged survival. Our results suggest that this necessary new spat fall is often decimated by starfish predation in the subtidal zone, but to a lesser extent in areas with lower salinity levels.

The survival of larger beds was significantly higher, as was also found by Van der Meer et al. (2018). Although previous studies presented some possible explanations, the exact mechanisms require further study (Denny, 1995; Donker et al., 2013). It has been shown that mussels living at the edge of the beds form a stronger attachment to the substrate than mussels in the centre of a bed (Kangeri et al., 2016; Witman and Suchanek, 1984). Since the circumference (the edge) relative to the surface area of a bed is reduced with bed size, the higher survival of larger beds may be caused by relatively lower rates of erosion due to hydrodynamic forces on the entire bed (Denny, 1995; Donker et al., 2013). The higher number of individuals in larger beds may also offer safety in numbers against predation (Bertram, 1978; Pulliam and Caraco, 1984) although the density within a mussel bed seems to be

**Table 3**

Survival of subtidal mussel beds compared to survival of intertidal mussel and oyster/mixed beds from Van der Meer et al. (2018).

Age (years)	Subtidal mussel beds 1992–2019 (this study)									Intertidal beds 1999–2013 (Van der Meer et al., 2018)					
	All beds			Lower salinity			Higher salinity			Mussel beds			Oyster and mixed		
	Survival	95% c.i.		Survival	95% c.i.		Survival	95% c.i.		Survival	95% c.i.		Survival	95% c.i.	
	(%)	Lower	Upper	(%)	Lower	Upper	(%)	Lower	Upper	(%)	Lower	Upper	(%)	Lower	Upper
0	100.0	NA	NA	100.0	NA	NA	100.0	NA	NA	100.0	NA	NA	100.0	NA	NA
1	45.6	40.6	51.1	54.3	47.4	62.2	36.8	30.3	44.7	45.3	42.5	48.3	81.7	76.0	87.7
2	24.2	19.8	29.4	35.7	28.9	44.1	13.1	8.8	19.6	30.6	27.9	33.5	71.0	64.4	78.3
3	16.2	12.5	21.0	24.1	18.0	32.1	8.8	5.2	14.7	22.3	19.9	25.0	60.3	53.2	68.3
4	12.7	9.3	19.2	20.4	14.8	28.2	4.4	1.8	10.4	18.2	15.9	20.8	55.6	48.4	63.8
5	8.9	6.0	13.0	15.1	10.2	22.4	1.5	0.2	9.0	15.0	12.9	17.6	50.3	43.2	58.7
6	7.9	5.2	12.0	13.4	8.8	20.5	NA	NA	NA	13.3	11.3	15.8	47.3	40.2	55.6
7	5.5	3.2	9.3	9.9	5.8	16.6	0.0	NA	NA	11.7	9.7	14.1	46.6	39.6	55.0
8	3.0	1.4	6.3	5.4	2.5	11.4	NA	NA	NA	10.6	8.6	13.0	46.0	38.9	54.4
9	2.5	1.1	5.7	4.5	1.9	10.3	NA	NA	NA	9.6	7.7	12.1	44.8	37.8	53.1

more effective than bed size. The higher survival of larger beds may also be merely due to larger beds taking more years to disappear completely, assuming that erosion rates would be independent of the bed size. Apart from these potential explanations, there may also be an indirect effect of yet undetermined environmental factors that facilitated the formation of larger beds in the first place.

Unlike Van der Meer et al. (2018), we did not make a distinction between mussel beds and Pacific oyster beds (plus mixed beds) (see also Table 3) because only a few mussel beds in the subtidal contain high densities of Pacific oysters. We are confident that a comparison between our results and those of Van der Meer et al. (2018) for pure mussel beds is justified, although we cannot entirely exclude the possibility that the survival of pure mussel beds in the subtidal would be slightly lower when excluding the few beds with oyster densities above a certain threshold value.

Apart from environmental driving factors, there are also large differences in fishery activities to consider, which have not been included in our study. Shrimp fisheries are limited to the subtidal, and their effects on the survival of mussel beds have not been studied. Removal of mussel beds by shrimp fisheries, however, is unlikely because mussels are unwanted bycatch and may even clog the nets, causing damage or potentially even capsizing the vessel. To help avoid the beds, geographical bed positions are shared with the shrimp fishermen. Damage on newly settled and yet uncharted beds may occur, but this will mainly be limited to the first few months after settlement, a period that is not included in our study. Whereas hardly any mussel fisheries have taken place on the intertidal flats since 1993, the subtidal part of the western Dutch Wadden Sea is an important source of juvenile mussels for the Dutch mussel culture (Capelle et al., 2017; Smaal et al., 2021). Mussel fisheries take place almost every year in both spring and autumn. Although the density of mussels is significantly reduced by fishing, the fished beds can still develop into adult beds if environmental conditions are favourable, as shown by Smaal et al. (2021). In this study, mussel biomass and associated benthic fauna were monitored on 40 pairs of experimental plots, with each pair consisting of a fished and unfished plot. After the mussel fishing had taken place, a significant reduction in the biomass of mussels and associated species was initially found in the fished plots. However, after 1.5 years, no significant differences between fished and unfished plots could be observed. Our results, which point to a strong effect of a salinity-related factor (most likely starfish predation), are in agreement with the results of Smaal et al. (2021), which showed that the development of subtidal mussel beds in the Dutch Wadden Sea is predominantly governed by natural processes.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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