



Population dynamics of subtidal blue mussels *Mytilus edulis* and the impact of cultivation

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ABSTRACT: Fishery on subtidal mussel beds and subsequent relying on culture plots in the same system is a common practice in bottom mussel culture. We address factors that determine the population dynamics of subtidal blue mussels *Mytilus edulis* L. and to what extent total (natural plus cultured) subtidal mussel biomass in the system is affected by fishery practices. Mussel size and density of spatially segregated natural and cultured subtidal mussel populations in the western Wadden Sea were measured over time in 2 field studies. Spatial patterns in survival rates showed better spat survival in areas with lower salinity and lower density of sea stars *Asterias rubens*. This suggests that mussel survival is negatively related to sea star distribution which is to a large extent controlled by salinity. The *Asterias–Mytilus* relation in the Wadden Sea is an example of the concept that environmental stress determines the successes of the prey by affecting the prey–predator relationship. Natural beds that escape predation are found at lower salinities, and mussels on these beds showed low growth rates, also because of lower food quality in these areas. Mussel culture is strongly affecting the population dynamics of the subtidal mussel population, through relay of mussels from natural mussel beds to culture plots. This activity increases mussel growth and survival, because food quality on culture plots is high and predation is controlled. Despite harvesting, mussel biomass production on culture plots was higher than on natural mussel beds, enhancing total subtidal mussel stock.

KEY WORDS: Ecosystem goods and services · Salinity · *Asterias rubens* · Sea star · Aquaculture impact · Sampling · Bottom culture · Wadden Sea

INTRODUCTION

Bottom culture of mussels is an extensive large-scale form of aquaculture that is practiced in shallow subtidal and intertidal sand/mud flats in coastal areas (Gosling 2003). The overall impact of this type of culture is in general low compared to other more intensive forms of aquaculture (Davenport et al. 2009). However, the shallow sand/mudflats are habitats for ecologically important habitat-creating communities (e.g. mussels, sea grasses, oysters, *Sabellaria*) and vital foraging areas for birds and fishes

(Lenihan & Micheli 2001, Van de Kam et al. 2004). These ecological values may be impacted by culture activities, which include the translocation of juvenile mussels from natural beds (mussel seed) to culture plots.

Major concerns about the environmental impacts of mussel culture include the effects on predatory birds in subtidal areas, especially eider ducks, and to a lesser extent greater scaup (Smit et al. 1998, Piersma & Camphuysen 2001, Stillman et al. 2001, Laursen et al. 2009). Effects of mussel seed fishery on benthic biodiversity, habitat structure and natural

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mussel stocks are also debated (Dolmer et al. 1999, 2012, Herlyn & Millat 2000, Smith & Shackley 2004, Murray et al. 2007a). Mussel beds are considered among the most diverse temperate communities (Suchanek 1992). Effects of mussel dredging on soft sediment include the removal of larger substrates such as shell debris and gravel (Frandsen et al. 2015). Experiments in the Limfjord showed that abundance of several taxa (sponges, echinoderms, anthozoans, molluscs, crustaceans, ascidians) were still reduced 4 mo after dredging (Dolmer et al. 2001). Most of these species are associated with hard substrate, such as mussel shells, provided by the mussel bed. Apart from removing mussels with associated flora and fauna, impacts of dredging on biodiversity may be habitat specific, as such effects are less pronounced in more exposed and sandy environments (Kaiser et al. 2006).

Mussels are ecosystem engineers that provide important ecosystem functions, such as benthic–pelagic coupling, food and habitat for other species (Borthagaray & Carranza 2007, Gutiérrez et al. 2011). Most studies on mussel populations have been carried out on intertidal mussel beds, probably because they are more abundant and more accessible than subtidal mussel beds. Intertidal beds can persist on the same spots for decades, re-establishing periodically with new spatfall (McGrorty et al. 1990, Brinkman et al. 2002, Büttger et al. 2008, Commiato et al. 2014, Folmer et al. 2014). In contrast, subtidal beds and to some extent intertidal beds at exposed locations are often described as ephemeral as a result of sea star predation or dislodgement during storms (Nehls & Thiel 1993, Reusch & Chapman 1997, Beadman et al. 2003, Agüera 2015). Indeed, there are concerns on the impact of mussel culture on subtidal seed beds, specifically to what extent fishery prevents the development of viable subtidal mussel beds (Dankers & Zuidema 1995, Kaiser et al. 1998, Asmus & Asmus 2002, Lotze et al. 2005). Yet, factors determining the resilience of subtidal mussel beds are often unknown, and the effects of extensive aquaculture on the population dynamics of subtidal mussels are not clear (Commiato & Dankers 2001, Nehls et al. 2009).

In this study, we address which factors determine the population dynamics of subtidal blue mussel *Mytilus edulis* (hereafter simply ‘mussels’) and to what extent the total (natural plus cultured) subtidal mussel biomass in the system is affected by fishery practices, such as mussel seed dredging, relaying and subsequent harvesting. We compare mussel biomass development on both natural beds and culture plots within the western Wadden Sea, the largest

mussel bottom culture area in Western Europe. Culture takes place on 7700 ha of leased culture plots, of which 4000 ha are effectively used by about 60 mussel-producing companies. The Wadden Sea is also a globally important area for nature conservation. Mussel seed in the Wadden Sea is traditionally dredged from subtidal natural beds and translocated to culture plots within the same system. A substantial amount of mussel seed is also obtained from floating seed mussel collectors (SMCs).

Here, we tested whether mussel culture is an important factor in determining the population dynamics of the subtidal mussel population, because, due to management measures by the farmers, cultured mussels display higher growth and survival rates than mussels on natural subtidal beds that are subject to predation, physical factors such as waves and currents, and low site-specific recruitment. Mussel cohort dynamics on natural mussel beds and on culture plots were monitored over time. To test differences in growth and survival, mussel cohorts on natural mussel beds and culture plots were monitored for 6 and 4 yr, respectively; results were then integrated in a biomass production model, to compare mussel biomass development between natural and cultured mussel populations.

MATERIALS AND METHODS

Study area

The Wadden Sea is a shallow intertidal area of about 6000 km², stretching over 3 countries, viz. The Netherlands, Germany and Denmark. It is separated from the North Sea by a range of barrier islands and from the mainland by dikes. The western part of the Wadden Sea (Fig. 1) is a very dynamic area, which receives a yearly average freshwater input of ca. 450 m³ s⁻¹ from Lake IJssel (Duran-Matute et al. 2014) and connects to the North Sea through 3 major inlets (Marsdiep, Eierlandse gat and Vlietstroom) in the north. The water volume exchange between the different tidal basins of the Wadden Sea is limited compared to the volume exchanged with the North Sea (Ridderinkhof et al. 1990). All mussel culture plots in the Dutch Wadden Sea are found in the western part (Fig. 1a). Fig. 1b (Alterra 2005) displays the areas in the same system where subtidal natural mussel beds were regularly observed from 1992 to 2005. Fishery on natural mussel beds is carried out in autumn and spring, and collects small (‘seed’) mussels to be relayed on the culture plots.

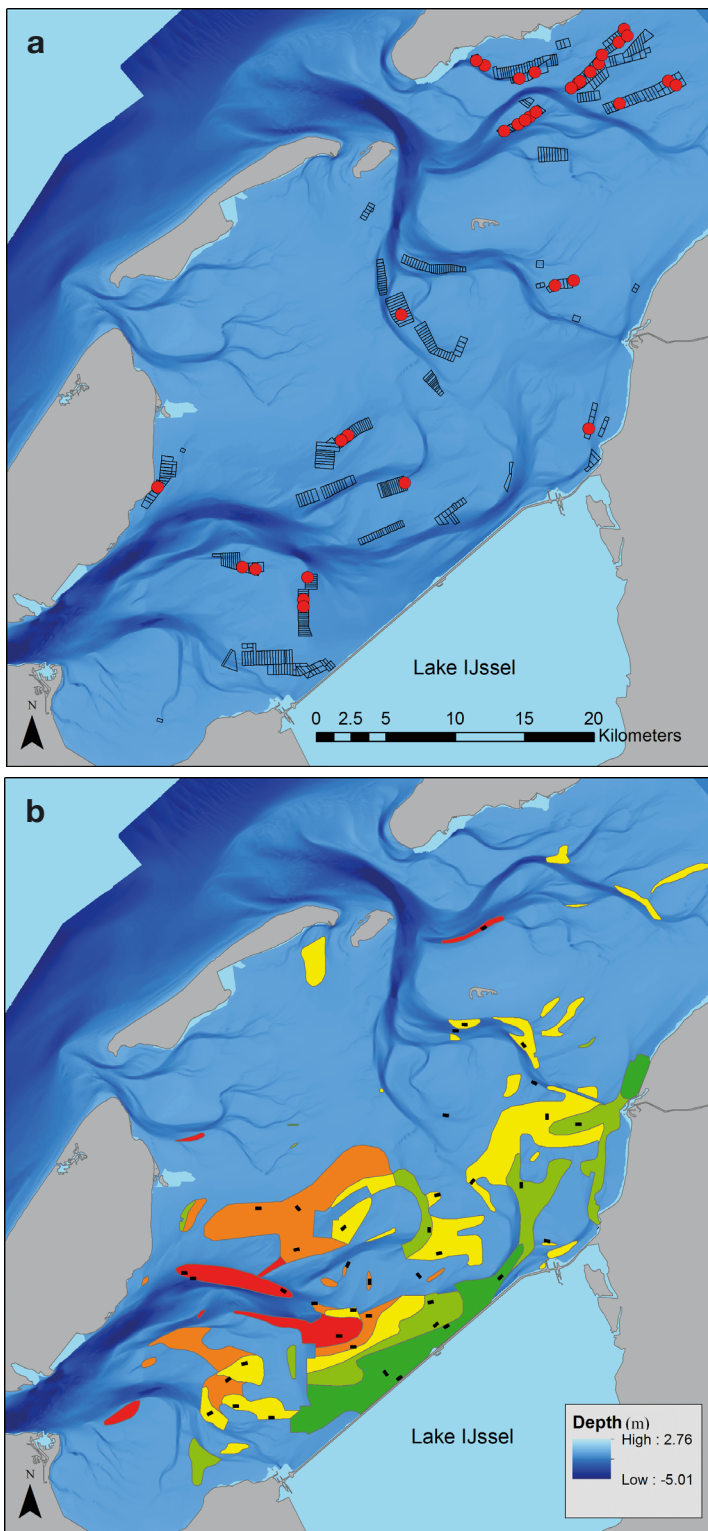


Fig. 1. Areas in the Wadden Sea (Netherlands) (a) with mussel *Mytilus edulis* culture plots (black polygons); red dots show sampling locations used in the analysis; and (b) where natural subtidal mussel beds are regularly formed, including 5 classes of relative stability (Alterra 2005), where red indicates relative stability and green indicates relative instability; black dots are experimental 8 ha plots. Depth is relative to mean water level

Culture plots are located in areas where natural seedbed formation seldom occurs, since farmers like to avoid spatfall on culture plots, because it causes an undesirable mixing of different size classes. As a result, culture plots are spatially separated from areas where the majority of natural mussel beds are found (Fig. 1). Natural mussel populations are found in areas with lower salinities (close to the Lake IJssel–Marsdiep area), whereas the majority of the culture plots are located in areas with higher salinities (close to the North Sea–Vlie area) (Drent & Dekker 2013). Suspended particulate matter (SPM) is also higher in the Marsdiep area compared with the Vlie area (on average respectively about 50 and 30 g m^{-3} , respectively; see Fig. 9 in De Jonge et al. 1996), because of discharges from Lake IJssel (De Jonge & De Jong 2002).

Sampling of natural subtidal mussel beds

Growth and specific loss rates of mussel populations on natural subtidal beds were determined from a sampling program designed to investigate the effects of mussel seed fishery on biodiversity and natural mussel stock (Van Stralen et al. 2013).

Natural mussel seed beds originate from natural spatfall and appear during summer. In autumn of every year from 2006 to 2009, all newly formed mussel seed beds were studied by the creation of experimental plots of 8 ha in the newly established mussel seed bed (Fig. 1b). The experimental plots were split in 2 (split-plot design), with one half (4 ha) closed and the other half open for mussel seed fishery. Within the 2 subplots (200 × 200 m, i.e. 4 ha each) inside the experimental plot, a buffer zone of 50 m was created at the edges, leaving an area of 100 × 100 m in the centre of the subplots. In total, 40 experimental plots were created this way. Sampling was carried out in the period 2006 to 2012 and continued beyond 2012 until the natural beds formed between 2006 and 2012 were all gone. In the present study, we only used data collected between 2006 and 2012. This set-up provided large-scale quantitative information on mussel growth and specific loss rates on plots closed for fishery, which can be seen as representa-

tive for all major natural seed beds formed in the western Wadden Sea between 2006 and 2012.

Sampling of experimental plots was done with a suction dredge or, when water depth exceeded 8 m, with a trawled dredge. Two transects of about 100 × 0.2 m (suction dredge) or about 100 × 0.1 m (trawled dredge) each were sampled per experimental subplot open for fishery, and similarly, 2 similar sized transects were sampled per closed subplot. Actual sampling track lengths were measured with a hand-held GPS for the suction dredge, while a rotating wheel with a magnetic counter was used for the trawled dredge. Experimental plots within new seed beds or on which a new seed bed was re-established during the course of the experiment were always sampled before and after fishery in autumn and spring. Experimental plots with mussels aged >1 yr were always sampled in spring. In the majority of cases, only 1 year-class remained per experimental plot. However, when new spatfall occurred on an existing plot, separate year-classes were considered in the analysis. An extensive schedule of sampling events per location can be found in the study of Van Stralen et al. (2013).

Average mussel density and biomass m⁻² were calculated by dividing the total number of mussels and total mussel wet weight by the sampled area. Year-classes of mussels used in the present study were followed by this method until April 2012.

We assumed that sampled plots are representative of the natural beds on which the plots were created. Hence, fishing activities around the area (4 ha) closed to fishery should not have a measurable effect on the experimental plots. This was tested by Van Stralen et al. (2013) by investigating gradients in mussel density on a 50 m buffer zone and on a 100 × 100 m inner plot. In that analysis, it was assumed that if fishing activities had any effect on mussels in experimental plots closed for fishery, it would have created gradients in mussel density from the edge to the middle of the plot. Results of the analysis showed no such patterns and suggest no effect of fishing activities in the area surrounding the plots closed for fishery.

Sampling of subtidal culture plots

Estimates of mussel growth and mortality rates from culture plots were obtained from a sampling program in which 66 mussel cohorts were followed over time on 42 different culture plots in the western Wadden Sea using a methodology published by Capelle et al. (2016). Mussels on the plots originated

from fishery on natural beds (n = 29) and from seed harvested from submerged mussel spat collectors (n = 22), or with seed relayed from other culture plots (n = 15).

Data analysis

Growth

A von Bertalanffy growth function (VBGF), with sinusoidal correction for seasonal temperature fluctuations (Somers 1988), was fitted to the length measurements (L , mm) from the culture plots and natural seed beds:

$$L_t = L_\infty \{1 - e^{-[K(t-t_0) + S(t)-S(t_0)]}\}, \quad (1)$$

$$\text{with } S(t) = \frac{CK}{2\pi} \sin[2\pi(t-t_s)/365]$$

where K is the growth coefficient (d⁻¹), L_∞ is the asymptotic length (mm), L_t is the length (mm) at age t (d), C is a dimensionless constant determining the magnitude of the oscillation, t_s defines the beginning of a sine wave (with a wave length of 1 yr), and t_0 is the theoretical age where L_t is 0 (Somers 1988). Fitting the model to the measured length data with Eq. (1) was achieved by a generalised nonlinear least-squares routine from the nlme library (Pinheiro et al. 2014) for the software R (R Core Team 2016), by which heterogeneous errors were accounted for and assumptions of the full model (fitted on data from natural beds and culture plots together) were met by the data.

Growth between mussels on natural beds and culture plots was compared following the likelihood methodology of Kimura (1980) and its implementation by Ogle (2015a), with the help of the FSA package for R (Ogle 2015b). In this method, a complex model with all parameters of the VBGF different for natural beds and culture plots are compared to simpler nested models, with 1 or more VBGF parameters in common. Models are compared with a likelihood ratio test, and this process stops when a more complex model is significantly different from every simpler nested model. The resulting best model was fitted to the data over a period of 2.5 yr, because mussels on culture plots were not followed for longer than 2.5 yr.

Mussel loss

Specific loss rates (r , d⁻¹) of the mussels on the natural mussel beds and culture plots were calculated by the change in mussel density (D , no. m⁻²) over

time (t , d) assuming an exponential population decline. Specific loss rates were calculated as the change in mussel density found between the first sampling (D_1) and subsequent second sampling (D_2), with t as the time interval in days.

$$r = -\frac{\ln(D_2) - \ln(D_1)}{t} \quad (2)$$

Densities of mussels older than 2.5 yr were excluded from the analysis, because mussels on culture plots were not followed for longer than 2.5 yr. Measurements were excluded from the analysis if both D_1 and $D_2 < 10$ ind. m^{-2} to prevent inflation of r . Average mussel length (\bar{L}) was calculated for each r as: $(L_2 - L_1)/2$, with L_1 and L_2 corresponding to D_1 and D_2 , respectively. Culture plots are located in areas with higher salinity, while natural mussel beds are found in areas where average salinity is lower with more fluctuations (Drent & Dekker 2013 and see Fig. 7.2 in Agüera et al. 2015). Annual average salinity values for each culture plot and for each experimental plot on the natural beds were calculated (data RIKZ; summarized in Fig. 2). Salinity in the Wadden Sea shows seasonal fluctuations, with the lowest values in winter and the highest in summer; van Aken (2008) reported that maximum and minimum values in the Marsdiep area (western part of the Wadden Sea) differed by ca. 2 ppt.

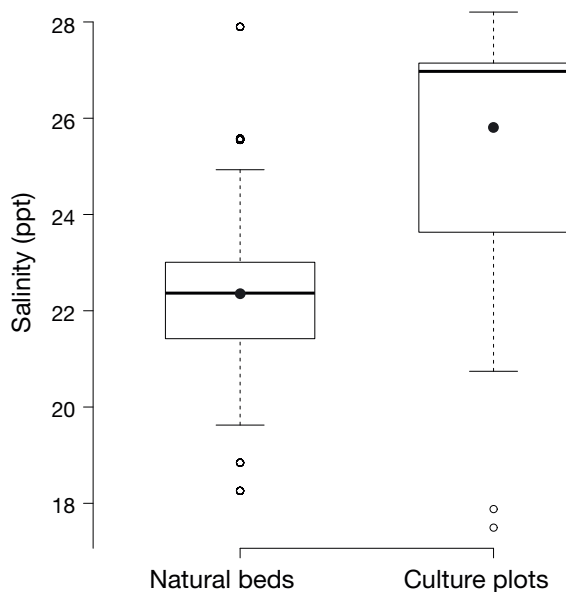


Fig. 2. Averaged yearly salinity values (boxplot with median, first and third quartile, 95 % confidence interval of median and outliers) for natural mussel *Mytilus edulis* beds and culture plots that were sampled in this study; filled dots represent mean values

Specific loss rates as a function of salinity and \bar{L} were investigated for natural mussel populations and for mussels on culture plots. We used a generalised least-squares model with the varIdent function in R allowing for different variances for each type (Pinheiro et al. 2014).

Spatial variation in specific loss rates were visualised by plotting r in graduated symbols on a map of the area for culture plots and natural beds, respectively. Spatial variation in salinity is indicated in the same map with contour lines.

Biomass

Biomass (B , $kg\ m^{-2}$) on culture plots and natural mussel beds was simulated over time, using the output of Eqs. (1) and (2) as:

$$B_t = W_t \times D_t \quad (3)$$

with W_t (g) obtained by converting mussel length as output of Eq. (1) to mussel wet weight according to $W_t = 1.43 \times 10^{-4} \times L_t^{2.89}$ (Capelle et al. 2016). D_t was obtained from change in mussel density over time:

$$D_t = D_0 \times e^{-rt} \quad (4)$$

with r as either r_{culture} or r_{natural} as a constant, or as function of length and salinity when regression analysis indicated a significant relation. Additionally, the loss is corrected for density-dependent seeding loss estimated by: $D_{t1} = e^{[0.52 \cdot \ln(D_{\text{seed}}) + 2.62]}$ (Capelle et al. 2016), where D_{t1} is mussel density on the culture plot after seeding, and D_{seed} is seeding density. Total mussel loss on culture plots is the combination of r_{culture} and density-dependent loss directly after seeding.

RESULTS

Data are summarized in Fig. 3, with the biomass distribution ($kg\ m^{-2}$) of mussels at the subsequent sampling times on natural mussel beds and on culture plots.

Mussel growth

The likelihood ratio test between VBGF with separate versus common parameters for mussel growth provides evidence that VBGF parameters differ between mussels on natural beds and mussels on culture plots. The most parsimonious model had sepa-

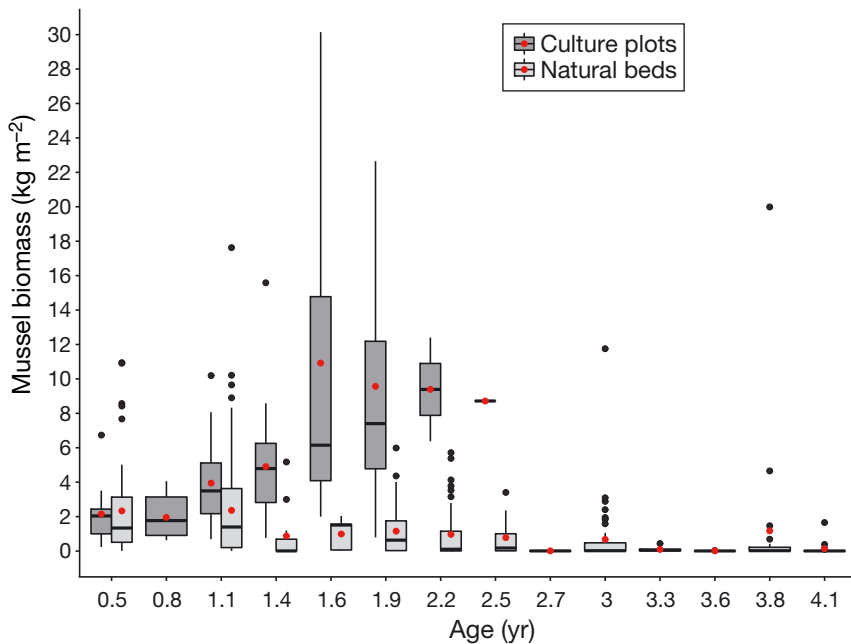


Fig. 3. Accumulated mussel biomass found on culture plots and on natural mussel *Mytilus edulis* beds in the Wadden Sea for different mussel ages; reference date of age 0 is 17 April. Red dots represent mean values. Other boxplot details as in Fig. 2

rate VBGF parameters L_{∞} and C between groups (Table 1). The difference between this 'best model' and the model with all VBGF parameters in common ($\chi^2 = 108.69$, $p < 0.001$) confirms that differences between groups exist and that the difference is only evident for the L_{∞} and C parameters in Eq. (1).

Growth fitted with 2 VBGFs for natural mussel beds and culture plots, with parameter estimates from Table 1, is displayed in Fig. 4. Cultured mussels reached a higher asymptotic length and a faster growth than mussels on natural beds. The length difference between the 2 groups was on the order of 20 to 25 %.

Table 1. Estimated parameters of the von Bertalanffy growth function (VBGF) for culture plots and natural mussel *Mytilus edulis* beds. L_{∞} : asymptotic length (mm), K : growth coefficient (d^{-1}), t_0 : theoretical age at which length is 0, C : constant determining the magnitude of the oscillation, t_s : beginning of a sine wave

VBGF Parameter	Culture plots		Natural mussel beds	
	Estimate	SE	Estimate	SE
L_{∞}	69.86	2.28	60.20	1.59
K	0.82	0.072	0.82	0.072
t_0	0.13	0.029	0.13	0.029
C	0.95	0.11	0.68	0.096
t_s	0.19	0.018	0.19	0.018

Mussel loss rate

Mean \pm SD specific loss rate for natural beds (r_{natural}) was $1.05 \times 10^{-2} \pm 1.40 \times 10^{-2}$. However, for the natural mussel population, loss rate was significantly related to shell length and salinity (Fig. 5), with a negative linear relation between specific loss rate and shell length: $r_{\text{natural}} = -2.65 \pm 10^{-4} \times \bar{L} + 1.95 \times 10^{-2}$ (with SE slope = 9.05×10^{-5} , SE intercept = 3.63×10^{-3} , $p = 0.004$, $R^2 = 0.05$) and a positive linear relation with annual averaged salinity according to: $r_{\text{natural}} = (2.96 \times 10^{-3}) \times \text{salinity} - (5.57 \times 10^{-2})$ (with SE slope = 6.77×10^{-4} , SE intercept = 1.49×10^{-2} , $p < 0.001$, $R^2 = 0.11$).

No such relation was found for mussels on culture plots. The mean \pm SD specific loss rate for the culture plots (r_{culture}) was $2.71 \times 10^{-3} \pm 5.01 \times 10^{-3}$.

The effects of mean shell length (\bar{L}) and salinity on specific loss rate for the natural mussel population were further investigated using a combined model, according to: $r_{\text{natural}} = a + b \times \bar{L} + c \times \text{salinity} + d \times \bar{L} \times \text{salinity}$, with estimated coefficients (SE) $a = -0.16$ (4.70×10^{-2}), $b = 2.80 \times 10^{-3}$ (1.18×10^{-3}), $c = 8.23 \times 10^{-3}$ (2.10×10^{-3}), $d = -1.37 \times 10^{-4}$ (5.26×10^{-5}). The significance of the model parameters was tested with an analysis of variance (ANOVA), the results of which are summarized in Table 2. Shell length (\bar{L}) and salinity were very weakly correlated ($r = -0.05$).

Specific loss rate from plots on natural mussel beds (Fig. 5) shows a general pattern that is very similar to the map of annual mean salinity (Duran-Matute et al. 2014), while for culture plots, no obvious spatial relation appeared (Fig. 6). Salinity contours on the map confirm that no viable natural mussel populations were found in high-salinity zones, or in the extreme low-salinity zones (<17.5 ppt), while the majority of the cultured population was found within the higher-salinity zones (Fig. 2).

Table 2. Statistical result of ANOVA performed to examine relation between specific loss rates on natural mussel *Mytilus edulis* beds with mean shell length (\bar{L}) and salinity (S) and their interaction; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Variable	df	MS	F	p
\bar{L}	1	1.56×10^{-3}	10.09	0.002**
S	1	3.36×10^{-3}	21.72	<0.001***
$\bar{L} \times S$	1	1.06×10^{-3}	6.83	0.01*
Residuals	152	1.55×10^{-4}		

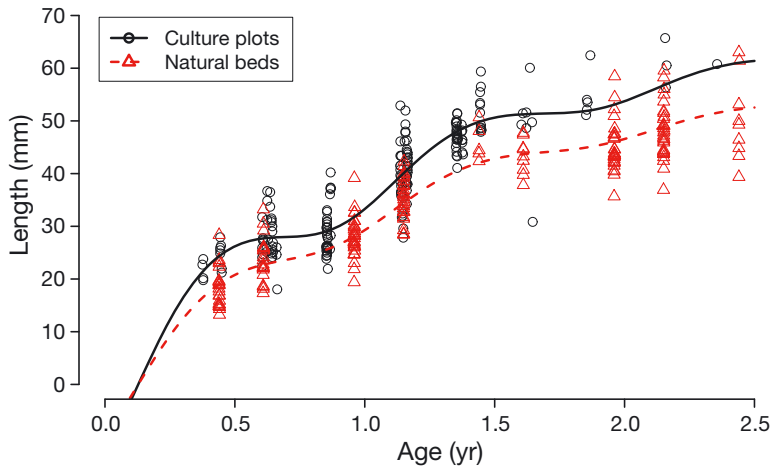


Fig. 4. Mean individual mussel *Mytilus edulis* shell length from culture plot sampling (2009–2012) and natural mussel bed sampling (2006–2012); data are fitted with a von Bertalanffy growth equation with sinusoidal correction for seasonal oscillations

Biomass simulation

A biomass simulation with 1 kg m^{-2} of mussel seed on culture plots over time was performed based on VBGF growth parameters found for culture plots (Fig. 7) and with a constant specific loss rate of $2.71 \times 10^{-3} \text{ d}^{-1}$ (Fig. 7). Seeding mortality results, on average, in a loss of 28% of the mussel seed. This causes the initial biomass on culture plots to be lower than on natural beds.

A biomass simulation of 1 kg m^{-2} of mussel seed on a natural mussel bed over time was performed with specific loss rate related to salinity and to shell length and with shell length estimated from the VBGF with parameters for the natural mussel population (Table 1). In Fig. 7, an average biomass simulation is plotted with r_{natural} estimated by using the average salinity of all sampled plots on natural mussel beds (22.35 ppt). The average biomass on natural mussel beds shows a continuous decrease, whereas an overall increase of biomass is predicted for culture plots; this is also evident from observations (Fig. 3). Both curves intersect about 90 d after 'seeding' (at a mussel age of 240 d), around the end of the year, when mussels are still in their 0 year-class.

In the following spring season, the increase in growth rates on culture plots, and especially the lower mortality on these plots compared to natural beds, cause a divergence of the curves. The dotted lines in Fig. 7 represent biomass simulation for natural beds with relatively low salinity (mean – SD = 20.7) and relatively high salinity (mean + SD = 24.0). At low salinity, mussel biomass development is similar to development on culture plots, but with a decreasing trend. At high salinity, loss processes dominate, and biomass shows a fast exponential

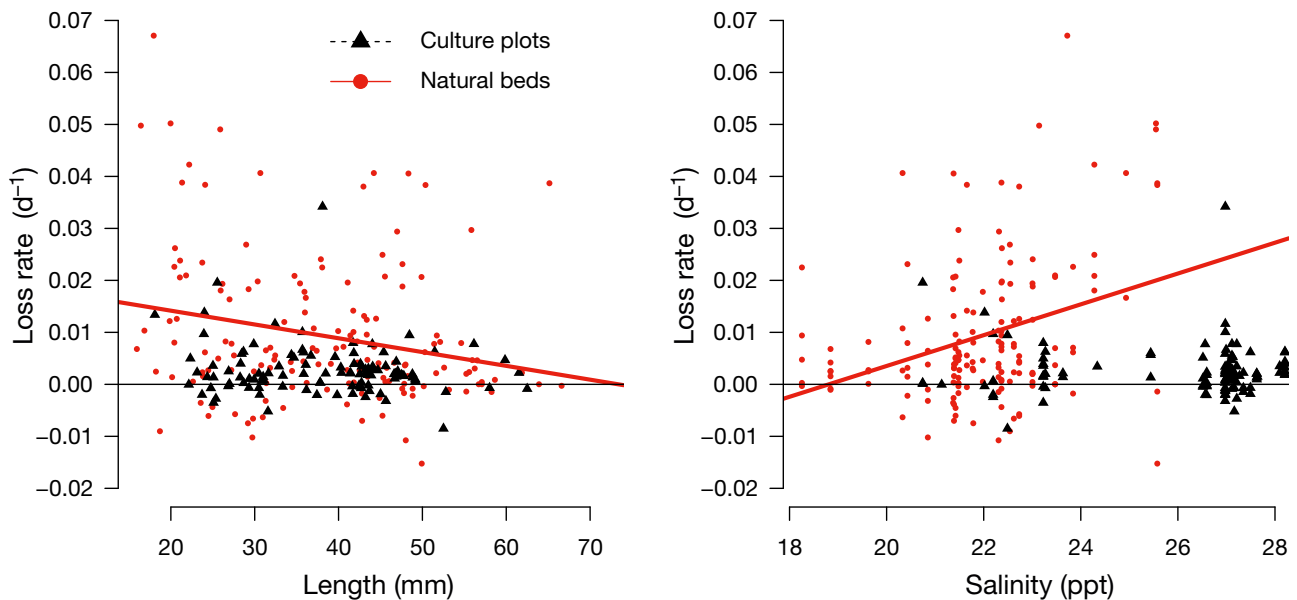


Fig. 5. Relations between specific loss rate and: (a) mean shell length of mussels *Mytilus edulis* in the corresponding time interval and (b) annual averaged salinity of the sampling location. Both relations are significant for natural mussel beds (red lines), but not for culture plots

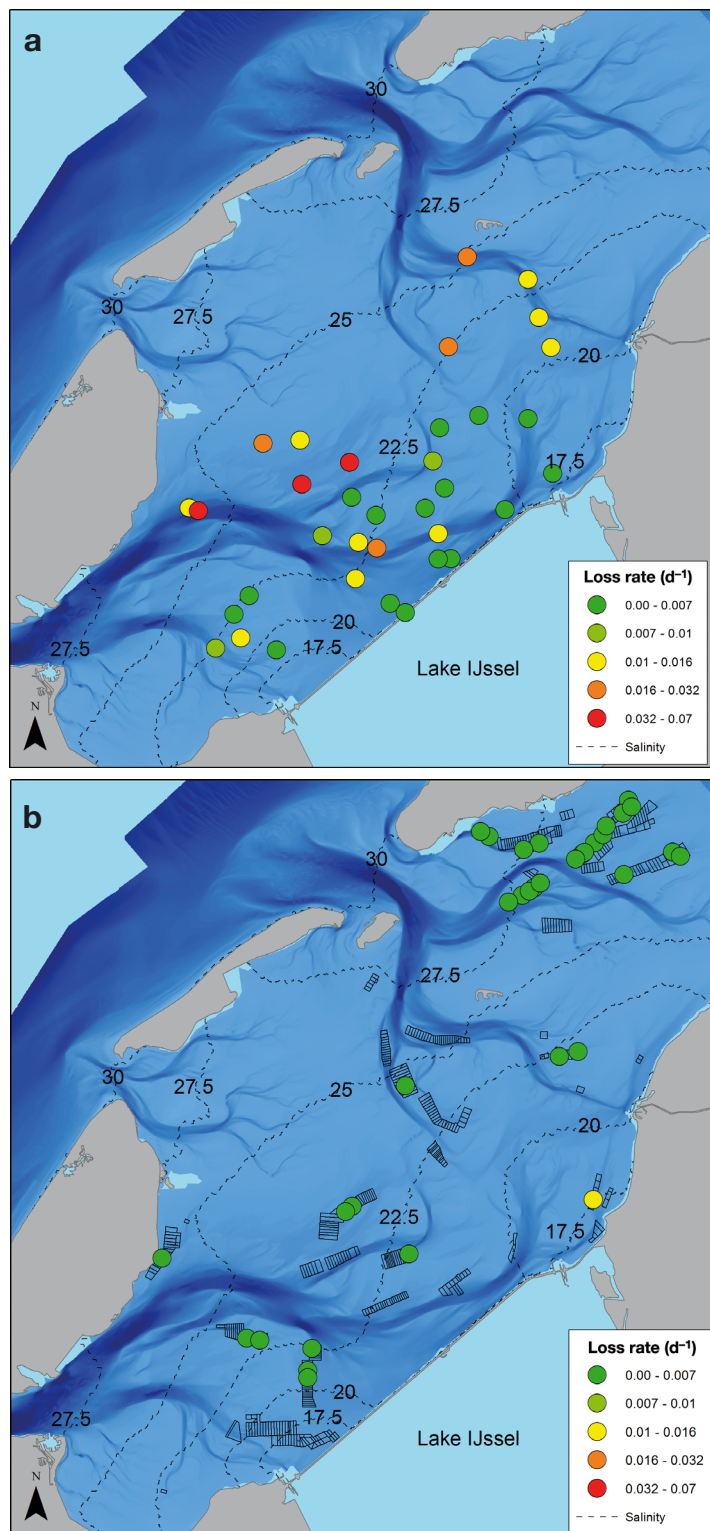


Fig. 6. (a) Spatial patterns in mussel *Mytilus edulis* loss (d^{-1}) per natural mussel bed, showing only sampling stations that were used in the analysis. (b) Average specific loss rates per culture plot (only plots that were used in the analysis). Annual averaged salinity (ppt) is indicated with contour lines

decline. These results demonstrate the high sensitivity of mussel biomass development to salinity, caused by the relation between loss rate and salinity.

DISCUSSION

The sampling program on culture plots was dependent on cooperation with the mussel farmers and followed their activities. On natural mussel beds, monitoring was set up to test fishery effects, and sampling was limited to natural beds in the areas where they were established. Because of these limitations, an experimental approach was not feasible. For example, it would have been interesting to experimentally manipulate mussels in the natural populations (relay seed, control for predation), in order to determine the pure effects of location, salinity and predation control in natural and culture plots. However, this manipulation was not feasible. Nonetheless, the combined sampling programs made it possible to collect a considerable amount of unique data on subtidal mussel populations from natural beds and from culture plots. Both populations were compared, and our results give insight in the survival, growth and impact of cultivation on the dynamics of subtidal mussel populations.

Factors that determine mussel survival on natural mussel beds and culture plots

There are no indications that the lack of recruitment in the high-salinity zone where the culture plots are located is caused by a lack of larvae in the water or by a lack of natural spatfall. Harvest from mussel seed collectors at various locations shows that spatfall does occur on a yearly basis outside the seed bed establishment areas. Also, the availability of substratum is not a limiting factor (Brinkman et al. 2002). Extensive research mostly on intertidal mussel populations showed that the survival of soft-bottom mussel beds in their early phase depends on the magnitude of physical disturbance and predation pressure (Seed & Suchanek 1992, Nehls & Thiel 1993, Hilgerloh et al. 1997, Reusch & Chapman 1997, Herlyn & Millat

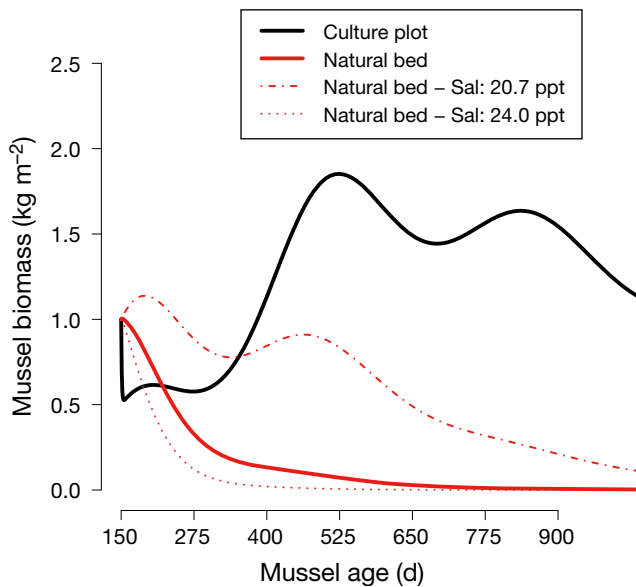


Fig. 7. Simulation of mussel *Mytilus edulis* biomass, with average loss and growth values calculated from sampling on natural mussel beds and culture plots, including seeding (handling) loss on culture plots; same state variables are used for natural mussel beds and culture plots, dotted lines represent biomass simulations for natural beds with the lower value (mean – SD: 20.7 ppt) and the upper value (mean + SD: 24.0 ppt) of the salinity distribution from all natural beds (mean: 22.4 ppt)

2000, Brinkman et al. 2002, Beukema & Dekker 2007, Van der Heide et al. 2014).

In general, the areas where the culture plots are located are subject to stronger current and wave action than the areas where most of the natural mussel beds are found, as dominant winds come from the SW in the Wadden Sea, and the best performing natural beds are found in areas protected from long-fetch waves such as areas at the downstream end of the tidal channel system (Fig. 1). The higher survival rate on the culture plots cannot be attributed to higher physical disturbance on natural mussel beds. Furthermore, in the present study, mussel survival was monitored when seed beds were already established. Mussel seed on these beds have reached a size refuge against predation by fish and shrimps, which are major predators on newly settled mussel spat (Dare 1976, Beukema et al. 1998). Also, the impact of crab predation reduces with mussel size (McGrorty et al. 1993, Murray et al. 2007b). However, predation by the sea star *Asterias rubens* is a very likely cause for the spatial pattern in survival success in the natural beds (Fig. 6). Notably, a reduction in salinity results in a reduction of sea star feeding activity, and can even diminish the effects of sea

stars completely (Agüera et al. 2015). Sea stars can wipe out entire mussel beds in a short period of time (Kristensen & Lassen 1997, Agüera 2015), but are less tolerant to changes in or low values of salinity than mussels are (Binyon 1976, Shumway 1977, Saranchova & Flyachinskaya 2001). Monitoring data, published by Ens et al. (2007) and summarized in Fig. 7.2 and 7.3 in Agüera (2015), showed that the frequency of sea stars in a sample (y) increased with salinity (x) according to the power function: $y = 0.00016x^{1.34}$. Abundance of sea stars in the study area is lower in winter, which is attributed to the lower salinity in winter (Agüera 2015). High temporal fluctuations in salinity occur in regions where water from Lake IJssel enters the Wadden Sea (Duran-Matute et al. 2014). Areas with high temporal fluctuations in salinity are the areas where we find natural mussel beds (Fig. 6). Farther away from these fluctuations, at higher salinities, natural subtidal mussel beds were absent or only survived for a short period (Van Stralen et al. 2013). Hence, better survival of mussels on natural beds in the vicinity of freshwater inputs may be explained by the lower sea star predation pressure in these areas.

Culture plots are located in areas with substantially higher salinities (Figs. 5b & 6), but are less affected by sea star predation, because sea stars are actively removed by the mussel farmers (Barkhouse et al. 2007). This is also observed in other culture areas. Sea stars are found in large numbers on mussel beds in areas where mussel bottom culture or mussel fishery is practiced: in Wales (Gallagher et al. 2008), the German Wadden Sea (Saier 2001) and Denmark (Kristensen & Lassen 1997). In these areas, sea star control is common practice.

For large mussels (around 6 cm shell length), survival is similar in natural subtidal beds and culture plots (Fig. 5a). The positive relation between mussel length and survival in natural mussel populations can be the result of a reduction in sea star predation pressure when mussels are larger (Sommer et al. 1999). Survival of a natural bed would require the bed to pass through the bottleneck of intense predation during several years, which, despite its location in low-salinity zones, has a low probability (see generally higher loss rate of natural beds in Fig. 5, but note that some natural beds do have low loss rates). It can be hypothesized that size-dependence could lead to persistence of the natural beds once a threshold of size-dependent predation is passed. Interestingly, the relation between mussel length and survival was not found on culture plots, which is consistent with the hypothesis that the presence of

sea stars promotes a length-dependent increase in survival. Similar effects were suggested for the relation between the starfish *Pisaster ochraceus* and the mussel *Mytilus californianus*, where the coexistence of predator and prey was only possible when *M. californianus* reached a size refuge against *P. ochraceus* predation (Paine 1976b). The *Pisaster–Mytilus* relation (in Washington State, USA), is similar to the *Asterias–Mytilus* relation (NW Europe), to the extent that it involves subtidal populations, with dynamics that are determined by predation and physical disturbance. Furthermore, *A. rubens* seems to have the same keystone predatory function on *M. edulis* as *P. ochraceus* has on *M. californianus* (Paine 1976a, Agüera 2015). The mechanism was worked out by Menge & Sutherland (1987), assuming that environmental stress has a higher impact on mobile consumers than on sessile organisms. Their theory predicts that in high-stress environments (e.g. at low salinities) consumers and sessile organisms are absent or not active. In more moderate environments, sessile organisms are less affected by environmental stress than consumers, resulting in the establishment of sessile populations. In benign environments, sessile organisms can only thrive when they pass through an intense predation bottleneck. This theory is consistent with the *Asterias–Mytilus* relation in the Wadden Sea, where mussel populations can most likely only persist in benign environments if they pass the predation bottleneck through mediation of the mussel farmer. Furthermore, Fig. 6 shows that viable mussel populations were also absent in the very low-salinity regions (<17.5 ppt). Yet, the outcome of the long-term monitoring on the plots closed to fishery is that all mussels disappeared in a period of 7 yr (Van Stralen et al. 2015). Therefore, the question remains to what extent longer-term survival of a natural mussel population in the subtidal zone of the western Wadden Sea is probable. In the period when natural beds were monitored, large-scale recruitment regularly resulted in new mussel seed beds (Van Stralen et al. 2015). When frequent recruitment on older mussel beds does not take place, the longevity of a cohort is limited, in our study to about 7 yr. Hence, the long-term survival of subtidal natural mussel populations appears to be recruitment driven.

On culture plots, other loss factors may be more dominant than sea star predation, such as loss associated with relaying or density-dependent losses (Gascoigne et al. 2005, Capelle et al. 2016). The loss rate of mussels surviving the initial seeding is uncorrelated with length or salinity, and is notably less variable than loss rate in natural beds (Fig. 5). This

constancy may be the result of measures by mussel farmers (e.g. adjusting seeding density, mud removal), and reflect the quality-based selection of the culture plots.

Effects of relay on mussel growth

Fig. 4 and underlying data indicate that growth rates of natural mussels, even when they persist for longer periods, are lower than on culture plots. This is ascribed to lower salinity and a higher turbidity near Lake IJssel (Piersma & Camphuysen 2001, De Jonge & De Jong 2002, Drent & Dekker 2013, Duran-Matute et al. 2014), which can both individually or jointly reduce growth. Mussels remain smaller and display low growth rates in areas where salinity is low or strongly fluctuating (Bøhle 1972, Almada-Villela 1984, Gruffydd et al. 1984, Westerboom et al. 2002, Riisgård et al. 2012, 2013). However, Maar et al. (2015) observed significant reductions in growth only at salinity values <15 ppt. This value is well below the average values found at the mussel bed locations (Fig. 2); we therefore expect that differences in growth are more related to spatial differences in food quality. Spatial variability in chlorophyll *a* in the Marsdiep basin is not very well described, but appears to be limited, based on long-term monitoring data of Rijkswaterstaat. It is expected that variability in food quality mainly depends on the spatial variability in SPM, as the ratio of chlorophyll *a* to SPM is a well-documented measure of food quality. Hawkins et al. (1996) found that mussels are able to cope with high silt concentrations and can adapt to short-term changes in silt-related food quality, by altering their feeding behaviour (Bayne 1998, Hawkins et al. 1998). This adaptability was demonstrated for a range of SPM levels (10–90 mg l⁻¹) that is very similar to the natural range reported for the Marsdiep area in the Wadden Sea (De Jonge et al. 1996). Although mussel populations can persist under these conditions, inorganic matter reduces food quality and thus mussel growth rates in shellfish production (Newell et al. 1998, Scholten & Smaal 1999). Furthermore, high SPM levels can reduce primary production in estuaries by limiting light penetration through the water column (Wilson 2002).

Impact of cultivation

Traditional culture relies on the relay of mussel seed from natural mussel beds to culture plots. Our

results point out that culture potentially leads to an increase in mussel biomass within the Wadden Sea. Mussels from culture plots are harvested after they reach market size, or even before when transplanted to culture plots outside the Wadden Sea, notably the Eastern Scheldt, resulting in a short turnover time of mussel biomass. Nonetheless, it was estimated over the period 2004 to 2012 that mussel culture for this period resulted on average in 1.27 times more mussels than there would be in the absence of culture, in a study based on a budget calculation approach using mussel stock estimations, seed fishery statistics, harvest and transplantation data (Wijsman et al. 2014). An increase in mussel biomass may reduce the carrying capacity of the system for other shellfish, such as cockles, an important food source for birds. Model calculations by Kamermans et al. (2014) predicted that when mussel numbers increase because of an increase in mussel seed collectors, some negative effects on shellfish biomass can be expected for confined areas in the western Wadden Sea, although due to spatial differences in the distribution of shellfish stocks, such effects are less probable for areas where culture plots are located.

Bivalve aquaculture provides ecosystem goods and services (Smaal et al. 2001a, Newell 2004, Saurel et al. 2014, Ferreira & Bricker 2016), including a reduction in eutrophication, increase in water column visibility and provision of habitat and food for higher trophic levels (Suchanek 1992, Inglis & Gust 2003, Newell & Koch 2004, Rönnbäck et al. 2007, Diana 2009). A healthy mussel population, by means of extensive mussel culture, supports more subtidal biodiversity, and provides a food source for birds (Buschbaum et al. 2009, Ysebaert et al. 2009). In fact, species richness on subtidal culture plots in the western Wadden Sea was not lower than on natural mussel beds (Drent & Dekker 2013), but those authors noted that species richness generally increased with salinity, so that the effect could partly be caused by the higher salinity at the location of the culture plots, compared to the natural beds. Furthermore, cultured mussels are a suitable food source for birds not only because of the size of the stock, but also because better growth conditions on culture plots will result in mussels with more meat (Capelle et al. 2016). Consistently, bird counts confirm that culture plots are vital foraging grounds for eider ducks (Smaal et al. 2010, Cervencí et al. 2015). Eider ducks prefer medium and large sized mussels above other food sources and are therefore also an important predator on culture plots; annual mussel consumption from culture plots between 2008

and 2011 was estimated to range between 4.5 and 8.2 million kg fresh weight of mussels (Cervencí et al. 2015).

CONCLUSIONS

Survival of mussels on natural beds in the Wadden Sea was lower than on culture plots except for larger mussel sizes, which had probably reached a size refuge for predation. Survival of natural mussel populations decreased with salinity. Natural mussel populations in this region are limited to areas with low and strongly fluctuating salinities. This pattern is consistent with the explanation that the natural subtidal mussel population is controlled by sea star predation. Sea stars are keystone predators on subtidal mussels in the Wadden Sea, but have a lower tolerance for low or strongly fluctuating salinities than mussels. The vast majority of culture plots are situated in areas with a relative high salinity and food quality, beneficial to both sea stars and mussels, which explains why natural mussel beds seldom establish in that area. However, the cultured mussel population can pass through the predation bottleneck by mediation of the mussel farmers who actively remove sea stars from the culture plots. On culture plots, mussel growth was higher and growing conditions were more favourable than on natural beds where mussels must cope with lower food quality. Mussel culture affects the population dynamics of the subtidal mussels in the system by relaying mussels from natural beds to culture plots. This activity results in a higher mussel biomass production on culture plots than on natural beds; it also enhances the total subtidal mussel stock within the system, favouring ecosystem services such as the provision of subtidal biodiversity and a high-quality food source for birds.

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