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Spatial organisation and biomass development after relaying of mussel seed

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ABSTRACT

It is not known whether and by what factors spatial heterogeneity in mussels (*Mytilus edulis* L.) affects mussel production in human-created mussel beds. In a field experiment, the same number of mussels was relayed on four different areas within plots of the same size, resulting in four treatments with different mussel densities. Density, individual weight and spatial structure of mussels were followed per treatment. The uniformly placed mussels on different areas redistributed into new patches, but mussels did not spread out over a larger area. Initial mussel density affected redistribution and mussel survival. At high densities mussels redistributed into a uniform matrix or in a few larger patches, that showed larger losses than at low densities, where mussels redistributed into a high number of patches. Growth rate and condition index of the mussels did not differ between treatments and no relation was found between treatment and number of foraging shore crabs, which was the major predator of mussels in this experiment. We hypothesise that the relation between initial mussel density and mussel loss after relaying is associated with redistribution, with less competition for space when mussels are positioned at the edge of a mussel patch. The very high mussel losses that we observed in the experiment within four weeks after relaying were the major factor in biomass development. Mussel bed formation concerns mussel growers and managers involved in natural mussel bed restoration. Initial mussel survival determines the success of these activities. The present study shows the effects of mussel relaying on spatial redistribution for the first time under field conditions, and underlines the importance of edge effects in understanding mussel loss in redistribution. Mussel survival after relaying will be higher when the mussels are distributed homogeneously and in relatively low density.

1. Introduction

Mussel beds on soft bottom substrate show a hierarchal spatial structure (Commito et al., 2006; Snover and Commito, 1998). On a large scale, in natural mussel beds that can stretch out over several square kilometres, mussels are found in banded or fractal structures (Crawford et al., 2006; Van de Koppel et al., 2005). Within a bed, mussels are found uniformly in net-like structures or scattered in loose patches (Commito and Rusignuolo, 2000; Svane and Ompi, 1993).

At the scale of cm to dm, De Jager et al. (2011) found that individual mussels actively search for substrate to attach to. On soft bottoms, substrate consists mainly of conspecifics and therefore they aggregate into clumps (aggregation of a few mussels) or strings that make patches. According to Van de Koppel et al. (2012), processes that occur on an individual scale define small-scale organisation into structures like clumps and patches, while physical forcing on landscape scale defines large-scale organisation into spatially-organised mussel beds.

Mussel growth, condition and reproductive output decrease, going from edge to centre at the scale of mussel beds (Knights, 2012), patches (Newell, 1990; Svane and Ompi, 1993) and clumps (Okamura, 1986). Okamura (1986) showed furthermore that growth, reproductive output and condition, when averaged over a clump, decrease with clump size. This shows that the spatial aggregation of mussels increases competition for food at an individual level on all scales. On group level, however, food availability can be improved by increasing near bed turbulence (Liu et al., 2012; Newell and Shumway, 1993; Van de Koppel et al., 2005).

Spatial structure affects mussel loss, and relations between spatial structure and predation are particularly well documented. The aggregation of mussels decreases predation rates (Dolmer, 1998;

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Frandsen and Dolmer, 2002), which are higher in solitary mussels than in aggregated individuals and higher in mussels located at the edges of patches than in those in the centres (Brown et al., 2011; Burch and Seed, 2000). In the absence of predators, patches become larger (Okamura, 1986; Reusch and Chapman, 1997). This suggests that at lower food levels, food availability affects success at the edges of a patch more than predation does, whereas at high food levels, food availability is also high for mussels within the patch that are less affected by predation. Consistent with general theories on trade-offs between food availability and mortality in group aggregations, the optimal situation for an individual is to be at the edges of an aggregation when food levels are intermediate (Morrell and Romey, 2008).

The profitability of positioning at the edge of a patch can change over an individual's lifetime, because, for example, predation decreases with size, meaning that mussels at the edge can outgrow crab predation sooner, with crabs being major predators on intertidal mussel beds (Bertness and Grosholz, 1985; Murray et al., 2007; Okamura, 1986; Smallegange and Van Der Meer, 2003). However, fast-growing mussels will be quicker to reach the prey size preferred by shellfish-eating birds like oystercatchers in the intertidal and eider ducks in the sub-tidal area (Ens et al., 1996; Hamilton et al., 1999).

Besides the effects of individual positioning on growth and mortality, the size of patches and amount of coverage affects dislodgement risk by waves and currents. Mussels attach to the substrate and to each other with their byssus threads. In an aggregation, mussels profit from having neighbours to attach to and this provides a refuge against hydrodynamic forces (Aveni-Deforge, 2007; Denny, 1987). Positioning within a patch can therefore be understood as a trade-off between food limitation and predation/bed stability in relation to hydrodynamic forces.

Humans create mussel beds in mussel bed restoration and in on-bottom mussel culture. Restoration can occur when mussel beds are endangered or contaminated. For example in the Wadden Sea the area of mature natural mussel beds has declined over the last 3 decades (Nehls et al., 2009), opportunities to restore mussels beds are studied (Donker et al., 2013) and in Alaska mussel beds were restored after oil spillage (Carls et al., 2004).

In on-bottom mussel culture, mussel seed dredged from natural seed beds or collected from spat mussel collectors, is positioned at intertidal or sub-tidal lease sites, where they are harvested when they reach commercial size (Dijkema, 1997; Dolmer et al., 2012; Smaal, 2002). Commercial beds are laid at high tide by mussel vessels which flush the seed (juvenile mussels) through shafts below water level (seeding). While seeding, the vessel moves in circular patterns. As a result mussels are distributed on multiple plots in concentric patterns. Seeding of high biomasses (up to 150 metric tonnes) is done as fast as possible around slack tide, to prevent mussels flushing out from the lease site by tidal currents. This results in highly concentrated mussel formations (Fig. 1), that might be multi-layered within seeding tracks, especially where seeding tracks overlap. The spatial structure that forms by redistribution might affect production through individual position effects and dislodgment risk (Newell, 1990; Okamura, 1986; Reusch and Chapman, 1997; Widdows et al., 2002).

When the density of mussels increases, the amount of mussels will be sufficient to form a uniform matrix. When the density of mussels is lower we can expect a threshold to be reached, after which there will not be enough mussels to form a uniform matrix, and instead they will redistribute into smaller patches. Therefore, we hypothesise that mussels in high densities will show low levels of redistribution in different patches, whereas those in lower densities will redistribute into a number of small patches. This can affect production because of a higher perimeter-to-area ratio in smaller patches. Based on the effects reviewed here, a higher perimeter will increase predation risk but also food availability, while a larger patch size will decrease vulnerability to dislodgement by hydrodynamic forces (Reusch and Chapman, 1995; Widdows et al., 2002) but increase density-dependent loss (Newell, 1990).

To investigate the occurrence and relative importance of these processes for production in the period after relaying, we studied the redistribution of mussels at several experimental plots with different mussel densities, and measured growth and survival over a three month period. Results can be applied in situations where mussels are repositioned especially for seeding optimisation in on-bottom mussel culture, and in improving mussel bed restoration success.

2. Material and methods

2.1. Location

We executed a field experiment on an intertidal lease site from 16 August 2011 to 2 November 2011. This site is located in a sheltered area of the Oosterschelde estuary in the Netherlands (Fig. 2). The entire site spans a total area of 112,500 m^2, 35.6% (40,000 m^2) of which was laid with mussel seed by a mussel grower on 11 August 2011. The mussel seed used originated from spat mussel collectors (SMC, Fig. 2) and

Fig. 1. Mussels laid at an intertidal lease site at the Oosterschelde estuary.