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Burial of *Zostera marina* seeds in sediment inhabited by three polychaetes: Laboratory and field studies

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A B S T R A C T

The large number of seeds produced by eelgrass, *Zostera marina,* provides this plant with a potential to disperse widely and colonise new areas. After dispersal, seeds must be buried into sediment for assuring long-term survival, successful germination and safe seedling development. Seeds may be buried passively by sedimentation or actively through sediment reworking by benthic fauna. We evaluated the effect of three polychaetes on the burial rate and depth of eelgrass seeds. Burial was first measured in controlled laboratory experiments using different densities of *Nereis (Hediste) diversicolor* (400–3200 ind m^{-2}), *Arenicola marina* (20–80 ind m^{-2}), and the invasive *Marenzelleria viridis* (400–1600 ind m^{-2}). The obtained results were subsequently compared with burial rates of seed mimics in experimental field plots (1 m^2) dominated by the respective polychaetes. High recovery of seeds in the laboratory (97–100%) suggested that none of these polychaetes species feed on eelgrass seeds. *N. diversicolor* transported seeds rapidly (<1 day) into its burrow, where they remained buried at a median depth of 0.5 cm. *A. marina* and *M. viridis* buried seeds by depositing their faeces on top of the sediment. At their highest abundance, *A. marina* and *M. viridis* buried seeds to a median depth of 6.7 cm and 0.5 cm, respectively, after a month. The burial efficiency and depth of these species were, in contrast to *N. diversicolor*, dependent on animal abundance. Only 2% of seed mimics casted in the field plots were recovered, suggesting that physical dispersion by waves and currents was considerably important for horizontal distribution. However, polychaete affected significantly the vertical distribution of seeds. Overall the effects of these three polychaetes indicate that benthic macroinvertebrates may significantly impact eelgrass seed bank at the ecosystem scale. Some species have a positive effect by burying seeds to shallow depths and thereby reducing seed predation and facilitating seed germination, while other species bury seeds too deep for successful seed germination and seedling development.

1. Introduction

As most seagrass species, eelgrass (*Zostera marina*) uses both vegetative and sexual reproduction (Orth et al., 2006). The former strategy may be considered most reliable because new shoots can benefit from parent nutrient supply (Marba et al., 2002). However, vegetative reproduction only expands meadows locally and at a slow rate of <30 cm per year (Marba and Duarte, 1998; Olesen and Sand–Jensen, 1994). Seeds, on the other hand, are produced in large numbers (Orth et al., 2000) and can be dispersed from the parent plant over large distance by water currents, either along the sea floor (Orth et al., 1994) or by flotation (Churchill et al., 1985; Harwell and Orth, 2002). Seed dispersal represents therefore an important mechanism for the establishment of new eelgrass meadows at a large spatial scale. Eelgrass seeds deposited on the sediment surface are vulnerable if they are not rapidly buried into the sediment. They can be consumed by herbivores (Fishman and Orth, 1996; Wigand and Churchill, 1988) or dispersed to inappropriate sites (Chambers and Macmahon, 1994; Orth et al., 2006). Once eelgrass seeds are buried in anoxic sediment they will germinate after several months (Olesen, 1999; Orth et al., 2000; Greve et al., 2005) and form successfully juvenile plants the following spring if their cotyledon can reach the sediment surface (Churchill, 1983, 1992; Greve et al., 2005). Laboratory and field measurements indicate that the cotyledon of *Z marina* seeds can typically reach a maximum length of about 6 cm and seeds buried below this depth will be lost (Churchill, 1983; Greve et al., 2005; Delefosse et al., in preparation).

Seed burial is driven by an array of abiotic and biotic factors. Current and wave driven resuspension and sedimentation may bury seeds slowly in coastal areas (Berner, 1980). However, these physical processes are irregular and unreliable as they also can resuspend sediment and seeds. Benthic macroinvertebrate fauna, on the other hand, may through their ecosystem-engineering reworking action (Jones et al., 1994; Kristensen et al., 2012) affect seed bank dynamics of seagrasses at a much shorter time-scale (Luckenbach and Orth, 1999; Inglis, 2000; Dumbauld and Wyllie-Echeverria, 2003; Valdemarsen et al., 2011). Experiments have shown that seeds of other angiosperms are buried efficiently by benthic species such as the polychaete *Nereis (Hediste) diversicolor*

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and tubificid oligochaetes (Grace, 1984; Hughes et al., 2000). No studies have to our knowledge reported the efficiency of benthic macroinvertebrates on eelgrass seed burial. Seed/animal interactions are likely to be species-specific and related to seed and animal size, seed nutritional value as well as animal feeding habit and bioturbation (Forey et al., 2011).

In this study, we investigate the effect of three common polychaete species on the burial of eelgrass seeds. We have chosen species with different life habits (*i.e.* size, feeding mode and burrowing activity). The gallery diffusor *N. diversicolor* lives in ramified burrows rarely reaching deeper than 15 cm with multiple connections to the surface of the sediment (Davey, 1994). It either feeds by scavenging the sediment surface or filter feed, but it does not mix the sediment strongly (Duport et al., 2006). The upward conveyor *Arenicola marina* is a large polychaete (up to 15 g; Valdemarsen et al., 2011) that lives head down in L- or J-shaped burrows. It feeds on sediment at a depth of 20–40 cm and deposits faecal pellets at the surface of the sediment (Cadée, 1976). The feeding/burrowing activities of *A. marina* populations may mix sediment to a depth of 40 cm per year (Kristensen et al., 2012). The gallery diffusor *Marenzelleria viridis* lives in burrows that typically reach more than 30 cm into the sediment (Atkins et al., 1987). It is a deposit feeder that collects sediment and detritus with its palps and deposits faecal pellets at the sediment surface (Dauer et al., 1981).

Our motivation for investigating the effect of these three polychaete species on burial of eelgrass seeds is driven by the fact that *A. marina* and *N. diversicolor* are the prevailing benthic macroinvertebrates in European coastal waters (Cadée, 1976; Scaps, 2002) where eelgrass is threatened. Furthermore, the invasive polychaete *M. viridis* has become a significant component of the benthic macrofauna in the same regions with potential repercussions on the population dynamics of *A. marina* and *N. diversicolor* (Delefosse et al., in press). Finally, field observations have revealed that these three species occurs close to eelgrass meadows (Valdemarsen et al., 2010; Delefosse et al., in preparation), where most seeds necessary for eelgrass recovery are deposited (Orth et al., 1994; Ruckelshaus, 1996).

The aim of this study is therefore to determine eelgrass seed burial efficiency in sediments inhabited by populations of *N. diversicolor*, *A. marina* and *M. viridis*. We apply a combined laboratory and field approach where the burial rate of seeds and seed mimics by the three species is measured under controlled laboratory conditions and verified at a relevant field site. The significance of the results on seed survival and seedling success is evaluated at a larger scale using the shallow Danish estuary, Odense Fjord, as case study.

2. Materials and methods

2.1. Study site

Sampling and field work were conducted from August 2010 to May 2011 in Bregnør Bay located on the South East coast of Odense Fjord (55.48° N; 10.61° E) on the island of Fyn, Denmark (Fig. 1). The dominating burrowing polychaetes at this location are separated spatially with high abundance of *N. diversicolor* in a near-coastal zone and a high-density of *A. marina* zone in the mid-bay area (Papaspyrou et al., 2007). In recent years, a third zone characterised by a growing population of the invasive polychaete *M. viridis* has become distinct in the outer bay and partly overlapping with the *A. marina* zone. The water depth is <1.2 m, but the *N. diversicolor* and *A. marina* zones are sporadically exposed to air during low tides and strong easterly winds. Otherwise, the environmental conditions in the three zones are similar. The sediment consists of low organic (<1%) sand. The Bay was sparsely vegetated with scattered occurrence of seagrasses *Ruppia maritima* and *Z. marina*, but located near (500 m) a 10-hectare coherent *Z. marina* meadow.

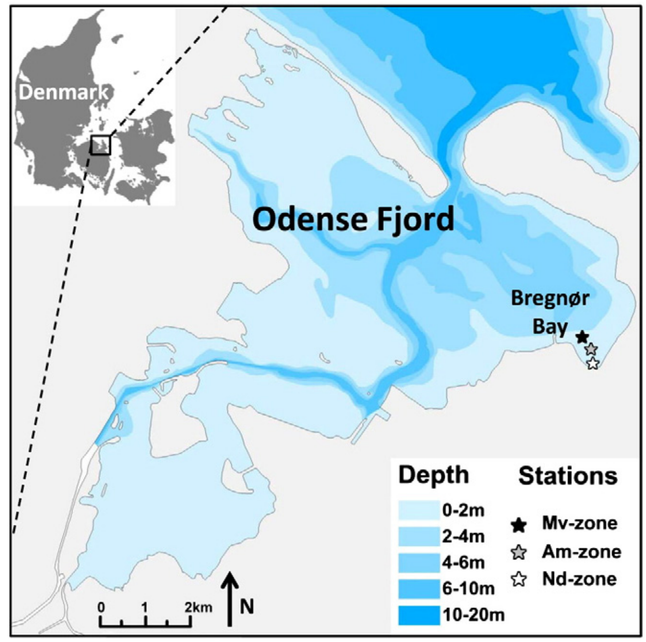

Fig. 1. Map showing the study sites in Odense Fjord (Denmark).

2.2. Laboratory experiment

2.2.1. Sampling and initial preparation

The density effect of the three polychaetes, *N. diversicolor, A. marina* and *M. viridis* on the burial of eelgrass seeds was tested in the laboratory. Worms were collected in Bregnør Bay by digging and sieving sediment through a 1 mm mesh. Only intact animals were retrieved and kept in seawater until further use. The sediment that passed through the sieve was saved in buckets for later use in the laboratory. Seawater with salinity of 20 was collected from a marine field station few kilometres from the sampling site.

Seed bearing shoots of *Z. marina* were taken from the meadow adjacent to Bregnør Bay in July 2010. The shoots were kept in aerated seawater until seeds matured and detached up to 2 months after collection. The collected seeds were frozen until further use. Preliminary tests have shown that freezing has no consequence for seed integrity but eliminated storage problems (*e.g.*, fungal infection) and prevented germination once thawed and introduced in the sediment.

Seed mimics were produced from 1.33 mm (SD: 0.07, n = 60) in diameter nylon cords that were cut into 3.14 mm (SD: 0.15, n = 60) long pieces weighing 4.98 mg (SD: 0.23, n = 60), matching the size of natural seeds (Wyllie-Echeverria et al., 2003; Delefosse et al., in preparation). We found that nylon is the most appropriate material to fabricate seed mimics because it has high specific density (nylon: 1.14 g cm^{-3}) that makes seed mimics sink as seeds in seawater (Orth et al., 1994). Nylon cords can be cut easily into the desired length and can as well be used in a wide range of colours that makes them easier than seeds to sort out from the confounding background colour of the sediment (Fig. 2). The possibility of large scale production also provided the required amount of seed mimics for field experiments (Orth et al., 1994).

The reliability of seed mimics as a tracer for determining the burial of seeds in the sediment was tested by simultaneous introduction of equal proportions of seeds and seed mimics at the surface of the sediment in all laboratory treatments. The total number introduced matched the average natural eelgrass seed abundance of about 10,000 seeds m^{-2} in Danish eelgrass meadows (Olesen, 1999).

2.2.2. Experimental units

Two different experimental units were used: core tubes with an internal diameter (i.d.) of 8 cm and length of 30 cm filled with sediment