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Burial of seeds and seedlings by the lugworm *Arenicola marina* hampers eelgrass (*Zostera marina*) recovery

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ABSTRACT

Eelgrass (*Zostera marina*) used to dominate the vegetation in Odense Fjord, Denmark, and covered >17 km^2 of the shallow fjord in 1983. Decades of excessive nutrient loading has lead to decreased eelgrass distribution, and only ~2 km^2 is covered at present. The state of low eelgrass coverage has not changed despite significant improvements of water quality in the past >10 years, and lugworms, *Arenicola marina*, have colonized the former eelgrass areas (1–8 ind. m^{-2}). It was hypothesized that the lack of eelgrass recovery was due to *A. marina*, which was investigated by a combined field and laboratory approach. At a study site where eelgrass used to dominate, a seasonal study of lugworm population dynamics and sediment reworking activity was performed. Additionally, density dependent burial of eelgrass seeds and seedlings due to sediment reworking by *A. marina* was investigated in mesocosm experiments. Our results indicate that *A. marina* may negatively impact eelgrass recovery, since sediment reworking lead to rapid burial of eelgrass seeds and seedlings; within 1–2 months, 95% of seeds and 75% of seedlings were buried below critical depth. Considerations based on empirical modeling suggest that negative impact occur even at low *A. marina* density (5–10 ind. m^{-2}). Therefore the spread of *A. marina* into former eelgrass areas is critical, since eelgrass recovery may be severely impaired, even when water quality favors eelgrass recolonization.

1. Introduction

The lugworm, *Arenicola marina* L., is a common polychaete along European Atlantic coasts where it inhabits intertidal and subtidal sandy sediments at typical densities of 3–80 individuals m^{-2} (Cadée, 1976; Jones and Jago, 1993; Volkenborn and Reise, 2006). *A. marina* is an upward conveyor that feeds head-down at depth in the sediment and it has an impressive capacity for particle reworking. For example, Cadée (1976) estimated that *A. marina* is capable of mixing the upper 6–33 cm of the sediment per year in the Dutch Wadden Sea, and similar estimates (1–18 cm y^{-1}) are reported from many other areas (*e.g.* Retraubun et al., 1996a; Riisgard and Banta, 1998; Valdemarsen et al., 2010b).

Arenicola marina is considered an important "ecosystem engineer", since its intense particle mixing and associated physicochemical changes affect the biological properties of sediments. Since particles larger than 1–2 mm are not ingested by *A. marina* (Jones and Jago, 1993), the intensely mixed sediment inhabited by *A. marina* is often characterized by a zone of homogeneous sand overlying a zone of coarser particles such as gravel and shells (Andresen and Kristensen, 2002). As a consequence of the constant disturbance of surface sediment, *A. marina* modifies the composition and abundance of other infauna by excluding for instance tube building polychaetes and crustaceans (Flach, 1992; Volkenborn and Reise, 2006, 2007). Additionally, *A. marina* interacts with the distribution of rooted marine macrophytes. In areas where lugworms are present near beds of seagrasses (*Zostera noltii* and *Z. marina*) or cordgrass (*Spartina anglica*), almost no transition zone is observed between areas with vegetation and bare *A. marina* inhabited sediment. Such a distribution pattern may only occur if roots and rhizomes prevent the settling of *A. marina* or if sediment reworking by *A. marina* prevents growth of vegetative shoots and seedlings (Philippart, 1994; Valdemarsen et al., 2010b; van Wesenbeeck et al., 2007). Competition between rooted macrophytes and *A. marina* was also indicated by the spread of seagrasses into large scale lugworm exclusion plots in the German Wadden Sea (N. Volkenborn, personal comm.).

Does *Arenicola marina* also affect the recovery of eelgrass following its eutrophication driven decline along European and North American coasts during the 20th century? Excessive nutrient loading led to poor growth conditions for eelgrass, by lowering light availability and by stimulating hypoxic events and poor sediment conditions (Greve et al., 2005; Hauxwell et al., 2001; Mascaro et al., 2009; Valdemarsen et al., 2010a). This situation has been somewhat reversed during the last decades, due to restrictions on nutrient loading (Petersen et al., 2009). The enhanced environmental quality, evidenced by for instance reduced levels of phytoplankton and improved sediment conditions, was expected also to facilitate eelgrass recovery. However, this appears not to be the case or only occurs slowly in

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many areas, which indicates that other parameters than environmental quality, for instance disturbance by benthic invertebrates, are critical during seagrass recovery (Dumbauld and Wyllie-Echeverria, 2003; Valdemarsen et al., 2010b).

We speculate that *Arenicola marina* enter/invade former eelgrass areas and effectively prevent eelgrass recovery. *A. marina* has a high dispersive potential with 50–400 juveniles m^{-2} during settling events and is therefore an effective colonizer of areas formerly vegetated by eelgrass (Flach and Beukema, 1994, Reise et al., 2001). This has been observed in Odense Fjord, Denmark, where 13 km^2 that was covered by eelgrass in 1983 is now bare sediment inhabited by 1–8 *A. marina* m^{-2} (Fig. 1; E. Kristensen, Unpublished results). Moreover *A. marina* density is up to 80 m^{-2} in other areas of Odense Fjord, where eelgrass dominated in the beginning of the 20th century (Ostenfeldt, 1908).

The seed bank is critical for the reproductive cycle of seagrasses since it represents the recolonization potential (Jarvis and Moore, 2010; Orth et al., 2006) and eelgrass recovery after large scale disturbance may occur exclusively from seeds (Greve et al., 2005; Lee et al., 2007; Plus et al., 2003). Eelgrass seeds are, however, sensitive to burial, since the ability of seeds to germinate and develop into self-sustaining plants depends on the sediment depth where they are positioned (Greve et al., 2005; Probert and Brenchley, 1999). If seeds of *Zostera marina* are buried below 5–6 cm depth due to for instance sediment reworking by *Arenicola marina*, the germination process will fail because the limited energy storage in seeds does not allow the hypocotyls to reach the sediment surface (Greve et al., 2005; Harrison, 1993). Similarly, *A. marina* may lead to burial of eelgrass seedlings (Philippart, 1994; Valdemarsen et al., 2010b).

In this study we evaluate the impact of lugworms (*Arenicola marina*) on eelgrass (*Zostera marina*) reestablishment by a combined field and laboratory approach. The *A. marina* population dynamics and seasonal sediment reworking activity were quantified at a study site in the northern part of Odense Fjord, where eelgrass is diminishing despite favorable light conditions and water quality. Additionally, *A. marina* burial of eelgrass seeds and seedlings was investigated in laboratory mesocosm experiments at a fixed worm density (60 m^{-2}). The results obtained from field and laboratory experiments were combined to evaluate the importance of *A. marina* for the reestablishment of eelgrass at the study site. Furthermore, a simple empirical model for the assessment of *A. marina* impact during eelgrass reestablishment was developed with worm size and density as input variables.

2. Materials and methods

2.1. Study site

The population characteristics and activity of *Arenicola marina* was followed during 2009–2010 at Enebærodde in the outer part of Odense Fjord, Denmark (consult Valdemarsen et al., 2010b for location of study site). The area was extensively covered with eelgrass in the past and in 1983 it consisted of a 7–8 km^2 continuous eelgrass meadow that covered ~50% of the outer Odense Fjord (Fyns Amt, 2006). Eelgrass coverage has since then declined dramatically in Odense Fjord (Fyns Amt, 2006; Greve et al., 2005) and was at the study site in 2009 reduced to a 400 m wide zone that extended ~100 m from the shore to 1–1.5 m water depth. The remaining eelgrass vegetation in the area was patchy and covered only half of the surface, and small to intermediate eelgrass patches (1–100 m^2) were fractionated with areas of bare sediment. The infauna on bare sediment was dominated by the polychaetes *A. marina* (3–5 m^{-2}) and *Marenzelleria viridis* (Quintana et al., 2011; Valdemarsen et al., 2010b).

2.2. Population characteristics and activity of Arenicola marina

The dynamics, size and distribution of the *Arenicola marina* population and its *in situ* reworking activity at the study site were evaluated by combining various approaches. A laboratory experiment was first conducted to obtain the relationship between *A. marina* size and feces diameter. This relationship was later used to estimate the size distribution of the *A. marina* population based on underwater photographs of fecal casts taken during a 13 months survey. These photographs were also used to monitor the seasonal variation of *A. marina* density. Finally, the seasonality of *in situ* sediment reworking activity was monitored during the same period to obtain an estimate of the sediment mixed by *A. marina* at the study site.

2.2.1. Relationship between Arenicola marina size and feces diameter

A. marina (n = 31) with different sizes were collected and acclimatized for ~4 days at 15 °C in buckets with sediment. The worms were then carefully retrieved from the sediment and kept in aerated seawater for 24 h to ensure that they had voided their guts. Subsequently, they were gently dried with a paper tissue and weighed to determine wet weights. The worms were hereafter placed individually in 25 cm in diameter (i.d.) plastic buckets containing 20 cm sediment and ~2 cm overlying seawater. After 10–12 h, the newly produced fecal casts were photographed together with a known scale. Photographs were registered as non-earth projections in GIS software (MapInfo) and the average diameter of feces was determined with 0.1 mm precision. The data were used to generate a relationship between *A. marina* weight and feces diameter, which formed the basis for evaluating the size distribution of *A. marina* population at the study site. The size distribution was based on photographs of fecal casts taken during the 13 months survey of *in situ* reworking activity (n = 142).

2.2.2. Arenicola marina density

The density of active *Arenicola marina* on bare sediment in the vicinity of eelgrass vegetation (<5 m distance) was determined on several occasions during 2009–2010 by photographing and counting the

Fig. 1. Left; in Odense Fjord, Denmark, the lugworm, *Arenicola marina*, has invaded former eelgrass areas. Middle; eelgrass seedlings, which are critical for eelgrass recovery, are found in the same areas as *A. marina*. Right; when considering the size of fecal casts and feeding funnels negative impact of *A. marina* during eelgrass recovery seem likely.