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Agent Based Modelling (ABM) of eelgrass (*Zostera marina*) seedbank dynamics in a shallow Danish estuary

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ABSTRACT

Odense Fjord (Denmark) has suffered from a drastic decline in eelgrass (*Zostera marina*) coverage during the last decades. In 1983 eelgrass still covered about 25% of the estuary, which in 2005 was reduced to less than 2%. The alarming decline in the past decades initiated preliminary restoration activities, where it was questioned whether the present low eelgrass biomass is able to produce a sustainable seed bank to support natural recovery. Field studies verified that the seed bank was hampered. Laboratory experiments were conducted to determine 1) seed dispersion along the sediment surface and in the water column; 2) settling rates of seeds and flowering shoots; 3) critical current speed for seed movement; 4) floating dynamic of flowering shoots and 5) seed dropping dynamics during transport of rafting shoots.

These parameters supported the development of an agent based model (ABM) predicting seed movements in estuaries. The model handled two ways of seed dispersal: 1) seeds dropped in eelgrass beds and transport by hydrodynamic forces along the seabed 2) seeds released by rafting shoots. This setup allowed assessment of both eelgrass seed loss and potential connectivity between beds. Seed losses were divided into direct losses, such as seeds lost on land due to desiccation or external boundary, and indirect losses affecting seedling establishment.

The model estimates that app. 92% of the seeds would be retained in the Odense fjord, while only 5.0% of the seeds ended up in areas supporting seedling establishment. Eelgrass seeds were also found in areas with insufficient light, high hydrodynamic pressure, excessive sediment reworking by lugworms or poor anchoring capacity. In addition, the model showed potential bed connectivity via rafting shoots, but also with individual seed movement along the bottom, when beds were not separated by deep areas, such as boating channels.

1. Introduction

Eelgrass, *Zostera marina*, is the most widespread seagrass species in the northern hemisphere (Moore and Short, 2006). Eelgrass beds provide a set of essential ecosystem functions and services such as increase of biodiversity (Boström and Bonsdorff, 2000; Duarte and Chiscano, 1999; Hemminga and Duarte, 2000; Moore and Short, 2006); nutrient cycling and therefore, contribute to improve the water quality by immobilising nutrients coming from land in the coastal zones (Flindt, 1994; Flindt et al., 1999; Hemminga and Duarte, 2000; Moore and Short, 2006; Ward et al., 1984); climate regulation through carbon sequestration and burial (Duffy, 2006; Fourqurean et al., 2012); erosion control, seabed stabilisation and coastal protection (Hansen and Reidenbach, 2012); and shelter for juvenile species (Hemminga and Duarte, 2000; Orth et al., 2006a; Terrados & Duarte, 2000). In 1900, a total area of approximately 6726 km^2 was covered by eelgrass in Danish coastal waters (Boström et al., 2003). Seagrass coverage has significantly decreased worldwide with global decline rates of 110 $km^2\ y^{-1}$ since 1980s (Waycott et al., 2009). Decline of eelgrass coverage was in the 1930s caused by the wasting disease (Short et al., 1987) and later by eutrophication (Lillebø et al., 2011; Waycott et al., 2009) leading to high blooms of phytoplankton and opportunistic macroalgae creating turbid waters (Canal-Vergés et al., 2014; Canal-Vergés et al.,

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2010; Flindt et al., 2007; Flindt et al., 1997; Salomonsen et al., 1997). In 1990s the eelgrass beds in Odense Fjord covered only 20–25% of the original eelgrass bed area in the 1900s (Boström et al., 2003). Due to the lack of eelgrass recovery, todays estuarine ecosystems are less stable. Nutrients, earlier immobilized by eelgrass uptake are today supporting macroalgae growth, that are hindering the natural recovery of eelgrass, where eelgrass seedlings are strongly impacted macroalgae movements due to generated ballistic impact (Flindt et al., 2016; Kuusemäe et al., 2016; Valdemarsen et al., 2010).

Nevertheless, successful large-scale recolonization strongly depends on the existence of a seed bank, as it is not feasible to recover large areas with clonal expansion (Boese et al., 2009; Olesen and Sand-Jensen, 1994). Restoration of eelgrass beds occurs by seed dispersal (Orth et al., 2006c) or transplantation of vegetative shoots (Van Katwijk et al., 2016). Vegetative growth is a slow process and not feasible for recolonization of extended areas of lost beds (Olesen, 1999). Thus, existence of a seed bank is crucial (Orth et al., 2006b) for seed germination and formation of new beds. The challenge is that eelgrass seed banks are transient (Harwell and Orth, 2002) with a fast turnover. In contradiction to most terrestrial species eelgrass seeds stay viable for only 11 months in laboratory conditions (Harrison, 1991; Moore et al., 1993). Field campaigns in Odense Fjord have not been able to locate seed banks near or within existing beds (Flindt et al., unpublished data). Rather, it is hypothesised that the seeds are dispersed to deeper areas or washed on land. In addition, the lack of seeds needed for natural recovery can be attributed the decline of pristine eelgrass beds, which act as donor and main seed production sites. Connectivity between sparsely located eelgrass beds may have been lost, hindering natural recovery, gene exchange and resilience to seascape changes (Kendrick et al., 2016). A high genetic diversity have also been shown to increase restoration success (Reynolds et al., 2013).

Eelgrass seeds are dispersed by several documented methods. Firstly, seeds are negatively buoyant, with settling rates of 1.4–8.6 cm s^{-1} (Delefosse et al., 2016; Infantes et al., 2016). As a result, several authors concluded that dispersal distances were short (Berkovic et al., 2014; Orth et al., 2006b; Orth et al., 1994). Jahnke et al. (2016) modelled dispersal capacity for *Z. marina* with distances from cm to m. In reality this might not be the case, as recent studies have shown that eelgrass seeds can be dispersed along the bottom by rolling around (Flindt et al., unpublished data, Koch et al., 2010). They are even capable of overcoming small seabed structures, such as sand ripples (Flindt et al., unpublished data). Secondly, long distance seed dispersal has been shown by detached flowering shoots and fragments by rafting or as bedload transport (Erftemeijer et al., 2008, Flindt et al., 1997; Hosokawa et al., 2015; Källström et al., 2008). Flowering shoots are buoyant and float from 2 weeks to several months depending on the condition of the flowering shoot at the time of detachment (Harwell & Orth, 2002; Källström et al., 2008).

Taking into account the various methods of seed transport (Erftemeijer et al., 2008; Hosokawa et al., 2015; Koch et al., 2010; Källström et al., 2008; Orth et al., 2006b), they all contribute to seed losses from the production sites. Seeds can be transported: 1) to land where they dry out and the germination capacity is lost (Pan et al., 2012); 2) to deeper areas in the fjord/estuary where seedling growth is impossible due to insufficient light intensities; 3) to areas with high densities of lugworms that rework the sediment, burry the seeds and uproot the seedlings (Valdemarsen et al., 2011); 4) to areas with a high organic content that reduces the sediment anchoring capacity of seedlings; 5) to areas with high sediment mobility (Valdemarsen et al., 2010). In many Danish estuaries, eelgrass seedlings are yearly supporting attempts to recover lost areas. However, in majority of the locations the low densities of emerging seedlings are lost within a few months (Valdemarsen et al., 2010). Combining the results with field surveys documenting very high seed losses from donor sites and seed broadcasting experiments (Lange, 2010, unpublished), suggests that loss rates of produced seeds may be an important explanation for the low success rates for natural recovery in Danish estuaries.

Therefore, the aim of this work was to develop a dynamic model to assess eelgrass seed production, dispersion and distribution, as well as eelgrass bed connectivity, using Agent Based Modelling (ABM) techniques. Keeping mass conservation of seeds in the model, it may provide explanation for the lacking natural recovery in Danish estuaries as well as predictions of optimal sites for eelgrass conservation actions. For the model calibration and validation a field campaign and flume experiments were performed to quantify the flowering shoot densities, seed densities, seed losses and seed mobility. Understanding seed production and losses may support the identification of threshold quantities for seeds needed for natural recovery. Furthermore, modelling a complex ecological function as seed dispersal will aid in revealing knowledge gaps. Understanding seed dispersal and seed banks in Odense Fjord will also support future restoration efforts (Orth et al., 2006b). Currently, several transplanting methods are being tested to increase the large-scale transplantation success. The existence of a viable seed bank may play a part in site selection for eelgrass conservation or restoration in order to increase its success. The model will also be able to predict restoration sites where seeds would stay in their "biosphere" and hereby support the natural recovery process.

2. Materials and methods

2.1. Study site

Odense Fjord is a shallow estuary divided into inner and outer part with a mean depth of 0.9 m and 2.7 m, respectively (Fyns-Amt., 2006). It is located on the northern part of Funen, Denmark (Fig. 1). The fjord has a total area of 62 km^2 and is connected to the open sea through a narrow opening. The tidal amplitude fluctuates between 0.3–0.5 m (Riisgård et al., 2008; Valdemarsen et al., 2010). The fjord is influenced by freshwater input from Odense River at the Southern part of the fjord together with several smaller rivers and streams along the coastline. The mixing zone of salt and freshwater generates salinity gradient throughout the fjord, hence the salinity ranges from 5 to 17 in the inner part and 15–25 at the outer part of the fjord (Valdemarsen et al., 2010).

Odense Fjord, with a catchment area of 1046 km^2, is heavily influenced by nutrient inputs. Prior to 1990 the annual external loading exceeded 2500 t total N y^{-1} and 300 t total P y^{-1}. Due to national environmental regulations the nutrient loading has decreased to current levels of about 1700 t N y^{-1} and 64 t P y^{-1} (Windolf et al., 2013). As a result of long term nutrient inputs, wave protected and deeper areas in the fjord have acted as sinks for suspended organic matter and associated nutrients, contributing to the internal nutrient loading (Valdemarsen et al., 2014). Eelgrass meadows cover about 2% of the fjord, extending out to a maximal depth of 2.6 m (Naturstyrelsen, 2011).

2.1.1. Field campaign

Field campaigns to Dalby Bay (Fig. 5) were established to quantify the flowering shoot densities, seed densities and seed loss rates. Weekly measurements of flowering shoot densities were performed using a metal frame (0.5 × 0.5 m) that was thrown randomly and the flowering shoots within the frame were counted (n = 5). Flowering shoots were also collected and taken to the laboratory to estimate the seasonality of seed numbers in reproductive shoots. Experimental areas were designated specifically for both reproductive shoot counts and for collection of reproductive shoots to avoid interference between the measurements. Seed release from repro-