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Short communication

Vulnerability to eutrophication of a semi-annual life history: A lesson learnt from an extinct eelgrass (*Zostera marina*) population

Marieke M. van Katwijk [a,*], Arthur R. Bos [a,b], Peer Kennis [a], Rob de Vries [a]

[a] *Department of Environmental Science, Radboud University Nijmegen, PO Box 9010, 6500 GL Nijmegen, The Netherlands*
[b] *Davao del Norte State College, New Visayas, 8105 Panabo City, Philippines*

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ABSTRACT

A semi-annual eelgrass (*Zostera marina* L.) population became extinct in 2004. It had flourished for many decades at Terschelling in the western Wadden Sea, one of the most eutrophied locations where seagrass growth has been recorded. Semi-annual populations survive the winter season by seed (annual), and by incidental plant survival (semi-annual). We compared seed bank dynamics and fate of plants between this impacted site and a reference site in the winter of 1990–1991. Seed bank density at Terschelling was extremely low (5–35 seeds m^{-2}) in comparison to the reference site (>60 seeds m^{-2}) and also in comparison to seed bank densities of (semi-)annual eelgrass populations in other parts of the world. Plant survival during winter was nil. Nevertheless, the population more than doubled its area in 1991, implying maximum germination and seedling survival rates. However, from 1992 onwards the decline set in and continued – while the nutrient levels decreased. To establish the cause of the low seed bank density, we conducted a transplantation experiment in 2004 to study the relationship between seed production and macro-algal cover. The transplantation experiment showed a negative relationship between the survival of seed producing shoots and suffocation by macro-algae, which is associated with light limitation and unfavourable biogeochemical conditions. The plants died before they had started to produce seeds. Thus, it is likely that macro-algal cover was responsible for the low seed bank density found in Terschelling in 1990–1991. Both the recorded low seed bank density and absence of incidental plant survival during winter were related to eutrophication. These parameters must have been a severe bottleneck in the life history of the extinct population at the impacted site, particularly as *Z. marina* seed banks are transient. Therefore we deduce that this population had survived at the edge of collapse, and became extinct after a small, haphazard environmental change. We argue that its resilience during these years must have been due to (i) maximum germination and seedling survival rates and (ii) spatial spreading of risks: parts of the population may have survived at locally macro-algae-free spots from where the area could be recolonised. As a consequence, the timing of the collapse was unpredictable and did not synchronise with the eutrophication process. The lesson learnt for conservation is to recognise that eutrophication may be a cause for seagrass population collapse and its eventual extinction, even years after nutrient levels stabilised, or even decreased.

1. Introduction

Seagrass beds inhabit coastal zones throughout the world and many populations have declined due to eutrophication (e.g. Duarte, 1995; Hauxwell et al., 2001; Valiela and Cole, 2002; Orth et al., 2006a; Burkholder et al., 2007; Fox et al., 2008). In the western Wadden Sea, nutrient loads had increased approximately five to six times by the mid-1980s compared to the relatively pristine situation prior to the 1930s (van Beusekom, 2005). Valiela and Cole (2002) showed that the western Wadden Sea had one of the highest nutrient loads ever recorded for natural seagrass populations. In the late 1980s, nutrient loads stabilised and slightly decreased in the 1990s and 2000s (van Beusekom, 2005; van Beusekom et al., 2008). Notwithstanding the high nutrient loads in the 1970s and 1980s, a semi-annual eelgrass (*Zostera marina* L.) population flourished for decades in Terschelling in the western Wadden Sea (Polderman and den Hartog, 1975; van Katwijk et al., 1998, 2000, Fig. 1), but became extinct in 2004 (Fig. 2). During the 1990s, this seagrass population was frequently observed to have seed-bearing shoots that died prematurely due to algal overgrowth and shading in late summer, mainly by epiphytic diatom blooms and macro-algae (van Katwijk et al., 1997, 1998). At a transplantation site at a similar type of location in the Wadden

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* Corresponding author. Tel.: +31 243652478; fax: +31 243653030.
E-mail addresses: m.vankatwijk@science.ru.nl (M.M. van Katwijk), arthurrbos@yahoo.com (A.R. Bos), p.kennis@groenewoud.nl (P. Kennis), Robaj.devries@inter.nl.net (R. de Vries).

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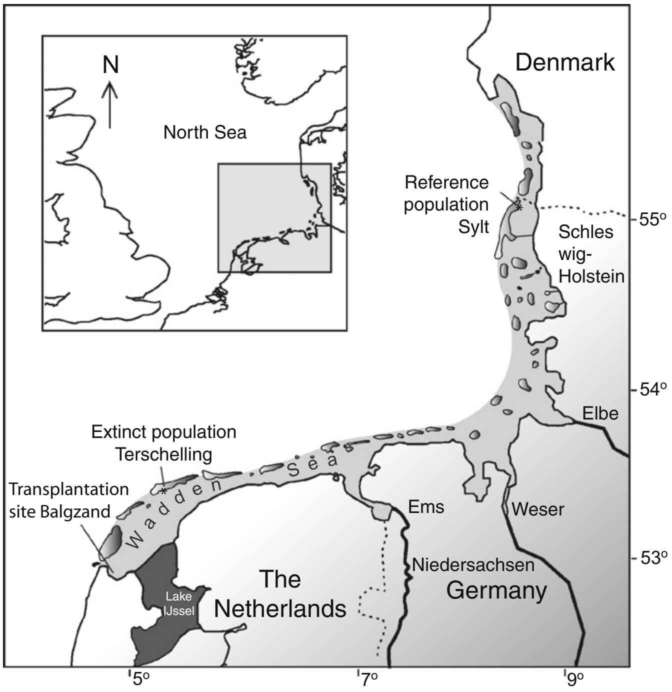

Fig. 1. Map of the Wadden Sea, showing the research locations (∗).

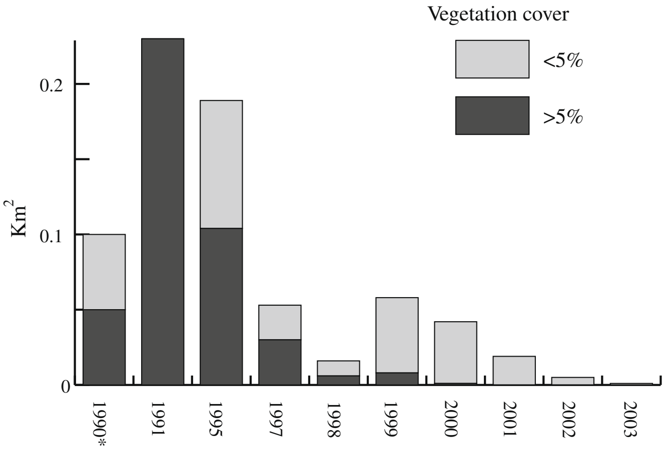

Fig. 2. Population dynamics (area and plant cover) of the semi-annual *Zostera marina* population at Terschelling, western Wadden Sea 1990*: Surveyed by the authors, 1991–2003. Monitoring data of the Ministry of transport, public works and water management, www.zeegras.nl.

Sea, a negative relationship between algal overgrowth and recruitment in the subsequent year had been observed (van Katwijk et al., 2009).

The seagrass *Z. marina* usually employs a perennial life history (Olesen, 1999). However, numerous examples of (semi-) annual populations are known from many parts of North-west Europe, the northern part of the Atlantic coasts of the United States and Canada and from Pacific coasts of the United States and Japan (e.g. Keddy and Patriquin, 1978; van Lent and Verschuure, 1994; van Katwijk et al., 1998; Morita et al., 2007). In these *Z. marina* populations, seed production is generally higher. Reviewing literature on a large number of eelgrass beds worldwide, Olesen (1999) found an average of 24,000 seeds m^{-2} produced in (semi-)annual populations, whereas significantly less (6200 seeds m^{-2}) in perennial populations.

Seagrass seed losses may occur due to burial, seed predation, rotting and autonomous death (Churchill, 1983; Harrison, 1993; van Lent and Verschuure, 1994; Greve et al., 2005; Orth et al., 2006b). Seed banks of *Z. marina* are transient and seeds seldom survive longer than one year (Orth et al., 2000). Germination percentages and seedling survival rates are highly variable at a spatio-temporal scale (e.g. Keddy and Patriquin, 1978; Churchill 1983; van Katwijk and Wijgergangs, 2004; Orth et al., 2006b; van Katwijk et al., 2009). For a population that relies on recruitment from seed, its traits are vital for survival. In strictly annual populations, all seedlings evolve into seed-bearing shoots (e.g. Keddy and Patriquin, 1978; Keddy, 1987). However, in semi-annual populations, a small percentage of vegetative shoots (plants) survive winter and produce new shoots in spring (van Lent and Verschuure, 1994; van Katwijk et al., 1998). Incidental rhizome survival (including the meristems) during winters also provides an additional chance for survival of semi-annual populations. Incidental rhizome survival however is restricted to coarse sediments (van Katwijk et al., 1998), whereas in hypoxic sediments, eelgrass rhizomes do not sprout (Greve et al., 2005).

We hypothesised that (i) the transient seed bank density of the Terschelling population was lowered by eutrophication as a consequence of reduced seed production due to algal cover in summer, and (ii) vegetative plant or rhizome survival was reduced in comparison to less eutrophied locations with low algal cover in late summer. If verified, this would imply that eutrophication reduces the recruitment potential of *Zostera marina* populations, thus indirectly contributing to a reduced resilience. As a result, smaller external (environmental) or internal (population dynamics) fluctuations may lead a population toward collapse. The timing of the collapse may remain unpredictable and may not be attributed to a direct and instantaneous cause.

2. Materials and methods

2.1. Study area

The Wadden Sea is one of the world's largest international marine wetland reserves (approx. 6000 km^2), bordering the coasts of The Netherlands, Germany and Denmark (Fig. 1). In the Wadden Sea, two species of seagrass occur, *Zostera marina* and *Z. noltii*, both in the mid-intertidal zone. Tides are semi-diurnal, with a tidal amplitude of ca. 1.80 m. Eutrophication levels at the western parts of the Wadden Sea are 1.5–3 times higher in comparison to the north-eastern parts (van Beusekom, 2005; van Beusekom et al., 2005). Additionally, nutrient loads vary at a local scale. At sheltered locations macro-algae accumulate during summer, by indrifting algae as well as by local settlement and proliferation of these algae. Epiphytes develop abundantly on the seagrass leaves. Also, fine particles such as clay or organic matter, often rich in nutrients, settle out. Remineralisation, following algal mortality at the end of summer, provides an additional nutrient source in comparison to less-sheltered sites, where algae do not to accumulate and settlement of fine particles is reduced (e.g. van Beusekom and de Jonge, 2002). This process has been referred to as 'internal nutrient loading' (Duarte, 1995; Burkholder et al., 2007).

2.2. Overwintering dynamics and seed bank density (1990–1991)

Differences in nutrient loads within the Wadden Sea, as well as observations of premature end-of-season die-off in a seagrass bed with high loads (Terschelling, western Wadden Sea, Fig. 1; van Katwijk et al., 1998), lead us to study the overwintering features of this particular seagrass population and comparing it to a less nutrient-loaded location in the northern Wadden Sea (Sylt). The