



Modeling loss and recovery of *Zostera marina* beds in the Chesapeake Bay: The role of seedlings and seed-bank viability



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ABSTRACT

Loss and recovery processes following a documented large scale decline in *Zostera marina* beds in the York River, Virginia in 2005 were modeled by coupling production and sexual reproduction models. The reproduction model included formulations for reproductive shoot production, seed production, seed-bank density, seed viability, and seed germination. After the model was calibrated and validated using in situ water quality and plant performance measurements from two different sites, model scenarios were run for three years (1 year pre-decline, 2 years post-decline) to quantify the effects of (1) the presence or absence of sexual reproduction, (2) increases in water temperatures from ambient to ambient +5 °C in 1 °C increments, and (3) the potential interactive effects of light and temperature conditions on bed maintenance and re-establishment. Model projections of *Z. marina* production following the decline corresponded to in situ measurements of recovery only when sexual reproduction was added. However, a 1 °C increase in temperature resulted in a complete loss of biomass after two consecutive years of temperature stress following the depletion of the viable sediment seed bank. Interactions between light and temperature stress resulted in overall lower production and resilience to declines under lower light conditions due to corresponding decreases in photosynthetic rates and increases in respiration. Model results highlight (1) the need to incorporate sexual reproduction into *Z. marina* ecosystem models, (2) the projected sensitivity of established beds to consecutive years of stress, and (3) the negative effects of multiple stressors on *Z. marina* resilience and recovery.

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1. Introduction

Global declines in seagrass populations have been well documented (Orth et al., 2006; Waycott et al., 2009; Short et al., 2011). The increase in rate of loss of seagrasses has been attributed to coastal development (Short and Wyllie-Echeverria, 1996), eutrophication (Burkholder et al., 2007), and climate change (Short and Neckles, 1999). Within the mid-Atlantic region of the United States in the Chesapeake Bay large scale declines in *Zostera marina* populations have been attributed to chronic deterioration in water quality compounded by episodic stresses from short term events such as tropical storms or high water temperatures (Orth and Moore, 1983; Moore and Jarvis, 2008). Restoration attempts in the Chesapeake Bay have increased in response to continued declines; however, efforts

have proven to be primarily unsuccessful (Shafter and Bergstrom, 2008; Orth et al., 2010). In order to increase restoration efficiency, effectiveness, and success a better understanding of bed resilience to perturbations, as well as loss and recovery processes within established seagrass beds is required (Duarte, 2002; Orth et al., 2006).

Z. marina populations within the Chesapeake Bay are particularly at risk for temperature stress as they are located near the southern limit of the species distribution in the western Atlantic (Short and Moore, 2006). Temperature stress has been attributed to the development of annual *Z. marina* populations along the Pacific (Meling-López and Ibarra-Obando, 1999; Santamaría-Gallegos et al., 2000), where summer water temperatures can reach a maximum of 30–32 °C and result in a complete loss of above ground biomass. Average maximum summer water temperatures range from 28 to 30 °C in the Chesapeake Bay (Moore and Jarvis, 2008), which is warmer than temperatures recorded for populations in the Mediterranean (26.9 °C, Plus et al., 2010) and for *Z. marina* living near its southern limit in the eastern Atlantic in the Ria Formosa, Portugal (27 °C; Newton and Mudge, 2003; den Hartog, 1970). Evidence for the vulnerability of seagrass populations in this region to episodic stressors has been highlighted in the last

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decade following sudden large scale declines in 2005 (Moore and Jarvis, 2008) and in 2010 (Moore et al., 2013). In 2005, the *Z. marina* decline was related to a period of unusually high water temperatures (maximum 32 °C) in July and August 2005. The two month period of temperature stress in the summer of 2005 combined with chronically light stressed *Z. marina* populations (Moore, 2004) resulted in the loss of the majority of above ground biomass by October (Moore and Jarvis, 2008). The 2010 decline was also attributed to temperature and light impacts; however, the timing of the event was significantly different as the heat event was documented in June at the end of the maximum biomass period prior to stressful peak summer water temperatures (Moore et al., 2013).

Z. marina populations may continue to experience these types of large-scale event-driven declines, particularly in the Chesapeake Bay where between 1949 and 2002 Chesapeake Bay winter water temperatures increased 0.8–1.1 °C and are predicted to continue to increase by 2–5 °C over the next century (Preston, 2004; Najjar et al., 2010). In addition, climate change models predict that by the end of the 21st century a 10% increase in rainfall over the Chesapeake Bay watershed will subsequently increase river flow by 30%, thereby increasing the nutrient and sediment input into the bay (Najjar, 1999; Gibson and Najjar, 2000). As a result the amount of light available to *Z. marina* will likely decrease, further stressing *Z. marina* populations (Dennison et al., 1993). Quantifying possible interactions between environmental stressors on seagrass beds in the Chesapeake Bay is necessary to accurately predict persistence and resilience of these populations.

Ecological models are useful tools in quantitative analysis of complex ecosystems such as seagrass beds. Through models, the response of *Z. marina* to stressful environmental conditions such as low light, high nutrients, and high temperatures has been quantified under a variety of situations (Wetzel and Neckles, 1986; Bach, 1993; Aveytua-Alcázar et al., 2008). While these models provide insight into the singular and combined effects of environmental stressors on *Z. marina* production, the capacity to accurately model population responses to stressful conditions is limited by focusing solely on vegetative reproduction and ignoring sexual reproduction (van Lent, 1995). Exclusion of sexual reproduction in carbon based models has been accepted due to the dominance of vegetative reproduction in perennial *Z. marina* beds and the relatively low carbon value of seeds (Harwell, 2000). However, recent research has shown that sexual reproduction plays a significant role in *Z. marina* bed recovery from large scale declines (Plus et al., 2003; Greve et al., 2005); therefore a key component of the bed loss and recovery dynamic may be missing from *Z. marina* production models when sexual reproduction is excluded.

For perennial *Z. marina* populations, seeds in the sediment seed-bank provide a measure of resilience to large scale loss (Leck et al., 1989; Combroux et al., 2001). Recolonization of *Z. marina* beds following sudden large scale declines through seed germination and seedling establishment have been documented throughout the species range (Plus et al., 2003; Greve et al., 2005; Lee et al., 2007; Jarvis and Moore, 2010). However, for the seed-bank to provide any function, seed viability must be maintained (Leck et al., 1989). Successful germination of viable seeds is dependent upon environmental cues and the surrounding sediment microenvironment (Hootsmans et al., 1987; Moore et al., 1993; Probert and Brenchly, 1999). Therefore, ecological models need to consider seed production, seed-bank density, seed viability, and germination to accurately incorporate sexual reproduction into seagrass production models.

The objective of this study was to evaluate the role of sexual and asexual reproduction in providing resilience to and recovery from disturbance in perennial *Z. marina* beds in the lower Chesapeake Bay. A sexual reproduction sub-model was developed and coupled to a *Z. marina* production model building upon established

Table 1

Governing equations for (1) epiphyte biomass (C_{epi} ; $g C m^{-2}$); (2) *Z. marina* vegetative shoot biomass (C_{zms} ; $g C m^{-2}$); (3) *Z. marina* vegetative root/rhizome biomass (C_{zmr} ; $g C m^{-2}$); (4) *Z. marina* seed-bank density (Zm_{seeds} ; seeds m^{-2}); and (5) *Z. marina* seedling density (Zm_{sd} ; seedlings m^{-2}). Terms include P = production; M = mortality; G = grazing; R = respiration; T_d = translocation down; T_{czms} = transfer of seedling biomass to vegetative shoot biomass; T_{czmsr} = transfer of seedling root/rhizome biomass to vegetative root/rhizome biomass; $Seeds_{germ}$ = germinated seeds; $Seeds_{prod}$ = total seeds produced; $Seeds_{via}$ = viable seeds; PR_{seeds} = seed predation; Zm_{sd} = germinated seedling density.

Differential equations

$$C_{epi} = C_{epi}(t - dt) + (P_{epi} - M_{epi} - G_{epi} - R_{epi}) \times dt \quad (1)$$

$$C_{zms} = C_{zms}(t - dt) + (P_{zms} + T_{czms} - M_{zms} - R_{zms} - T_d) \times dt \quad (2)$$

$$C_{zmr} = C_{zmr}(t - dt) + (T_d + T_{czmsr} - M_{zmr} - R_{zmr}) \times dt \quad (3)$$

$$Zm_{seeds} = Zm_{seeds}(t - dt) + (Seeds_{prod} - M_{seeds} - PR_{seeds}) \times Seeds_{via} \times dt \quad (4)$$

$$Zm_{sd} = Zm_{sd}(t - dt) + (Seeds_{germ} - M_{zmsd}) \times dt \quad (5)$$

models of submerged aquatic vegetation in the Chesapeake Bay (Madden and Kemp, 1996; Buzzelli et al., 1999; Cerco and Moore, 2001). Model simulations were then used to quantify the effects of (1) the presence or absence of sexual reproduction, (2) projected increases in water temperature from ambient to ambient +5 °C, and (3) the potential interactive effects of light and temperature on bed maintenance and re-establishment following a large scale decline. Specifically we quantified percent change between ambient (base model conditions) and model scenarios in *Z. marina* above and below ground biomass, total seed production, seed-bank density, and seed germination.

2. Methods

2.1. Model description

An established perennial *Z. marina* bed in the lower York River, Virginia USA (Fig. 1) was chosen as a basis for the production and sexual reproduction sub-models due to the documented large-scale die-off of eelgrass around the lower Chesapeake Bay in the fall of 2005 in response to elevated water temperatures (Moore and Jarvis, 2008). The base *Z. marina* productivity model was modified from the models of Madden and Kemp (1996), Buzzelli et al. (1999), and Cerco and Moore (2001) (Fig. 2). The sexual reproduction sub-model was developed based on monthly observations of *Z. marina* beds in the York River as well as field and laboratory experiments conducted either in this region or using seeds collected from populations from the local area (Jarvis, 2009; Jarvis and Moore, 2010; Jarvis et al., 2012).

2.2. Model formulation

2.2.1. Production model

Governing equations for *Z. marina* vegetative and seedling shoot biomass were balanced between gains through photosynthesis and losses due to mortality, respiration and translocation to roots and rhizomes (Table 1). Epiphytes were balanced similarly with the added loss of grazing but no loss due to translocation. Production terms for both epiphytes and *Z. marina* shoots were computed as the product of a temperature dependent maximum rate (P_{max}) and a limiting factor in which either nutrients (dissolved inorganic nitrogen, DIN, or dissolved inorganic phosphorous, DIP) or light (PAR) was limiting (Madden and Kemp, 1996; Cerco and Moore, 2001). Maximum epiphyte production rates were taken from Buzzelli et al. (1999) and production rates for *Z. marina* were determined from Evans et al. (1986). In both cases maximum production is related to ambient (T_w) and optimum water temperatures (T_{opt} ; Table 2).

Z. marina shoot and epiphyte production (P_{zms} and P_{epi} , respectively) were limited by available light and nutrient concentrations.

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