Advances in Water Resources 93 (2016) 315–325

Contents lists available at ScienceDirect

Advances in Water Resources

journal homepage: www.elsevier.com/locate/advwatres

Spatially explicit feedbacks between seagrass meadow structure, sediment and light: Habitat suitability for seagrass growth

Joel A. Carr[a,b,*], Paolo D'Odorico[a], Karen J. McGlathery[a], Patricia L. Wiberg[a]

[a] Department of Environmental Sciences, University of Virginia, 291 McCormick Rd, Clark Hall, Charlottesville, VA 22904, United States
[b] Patuxent Wildlife Research Center, U.S. Geological Survey, 12100 Beech Forest Road, Laurel, MD 20708, United States

ARTICLE INFO

Article history:
Available online 10 September 2015

Keywords:
Seagrass
Resilience
Shear partitioning
Bistable dynamics
Modeling
Sediment resuspension

ABSTRACT

In shallow coastal bays where nutrient loading and riverine inputs are low, turbidity, and the consequent light environment are controlled by resuspension of bed sediments due to wind-waves and tidal currents. High sediment resuspension and low light environments can limit benthic primary productivity; however, both currents and waves are affected by the presence of benthic plants such as seagrass. This feedback between the presence of benthic primary producers such as seagrass and the consequent light environment has been predicted to induce bistable dynamics locally. However, these vegetated areas influence a larger area than they footprint, including a barren adjacent downstream area which exhibits reduced shear stresses. Here we explore through modeling how the patchy structure of seagrass meadows on a landscape may affect sediment resuspension and the consequent light environment due to the presence of this sheltered region. Heterogeneous vegetation covers comprising a mosaic of randomly distributed patches were generated to investigate the effect of patch modified hydrodynamics. Actual cover of vegetation on the landscape was used to facilitate comparisons across landscape realizations. Hourly wave and current shear stresses on the landscape along with suspended sediment concentration and light attenuation characteristics were then calculated and spatially averaged to examine how actual cover and mean water depth affect the bulk sediment and light environment. The results indicate that an effective cover, which incorporates the sheltering area, has important controls on the distributions of shear stress, suspended sediment, light environment, and consequent seagrass habitat suitability. Interestingly, an optimal habitat occurs within a depth range where, if actual cover is reduced past some threshold, the bulk light environment would no longer favor seagrass growth.

Published by Elsevier Ltd.

1. Introduction

In shallow coastal bays that lack riverine discharge, sediment dynamics are dominated by internal resuspension due to wind-waves and tidal currents [1]. Primary production in coastal bays, typically dominated by benthic plants (seagrasses and algae) can be severely limited when sediment resuspension is high, resulting in low light environments [2]. This is more important for high light requirement species such as seagrass, which need roughly 20% of incident light at the seafloor for survival [2–6].

Both currents and waves are affected by the presence of benthic plants [7] and the magnitude and importance of resuspension may increase when rooted vegetation is absent due to the lack of the sediment stabilizing effects of the plants [8–10]. This reduction in sediment resuspension due to the presence of benthic primary producers results in a positive feedback between vegetation and sediment suspension/deposition and a more beneficial light environment for seagrass growth [7]. Positive feedbacks between the state of the system (e.g., seagrass cover) and limiting resources (e.g., light) can induce the emergence of alternate stable states in ecosystem dynamics [11]. In the case of seagrass ecosystems, these alternate states would be exhibited by either bare sediment beds with high suspended loads and poor light environments for seagrass growth, or seagrass meadows with relatively clear water and enough light penetration through the water column to sustain seagrass growth.

The emergence of alternate states in ecosystems is important as these systems tend to behave in nonlinear manners, with small changes in environmental conditions potentially causing rapid shifts between alternate states. Ecosystems with alternate state dynamics exhibit limited resilience [12,13]. Recovery from disturbances can only occur if the disturbance intensity (e.g., fraction of seagrass covered landscape disturbed) does not exceed some critical threshold. Beyond that threshold of disturbance intensity, the system would move into the attraction domain of the alternate stable state (a bare landscape). Moreover, once the external forcing causing the disturbance is eliminated, the system would then remain within the

* Corresponding author at: Patuxent Wildlife Research Center, U.S. Geological Survey, 12100 Beech Forest Road, Laurel, MD 20708, United States. Tel.: +1 3014975710.
E-mail address: jac6t@virginia.edu (J.A. Carr).

http://dx.doi.org/10.1016/j.advwatres.2015.09.001
0309-1708/Published by Elsevier Ltd.

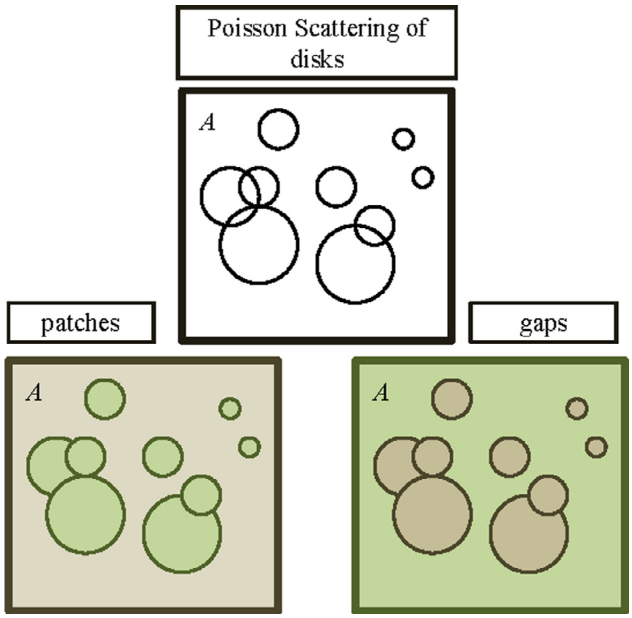

Fig. 1. Generation of landscape realizations from a spatial Poisson point process, scattering overlapping disks of radius r, sampled from an exponential distribution with mean of 1 m, on an area A, and then interpreting those disks as either patches on a bare seafloor or gaps in a continuous meadow landscape.

attractive domain of the alternate state and be unable to recover to its pre-disturbance state [14–16]. This alternate (bare) state possesses resilience as well, in that below some threshold level of disturbance (seeding, seagrass transplantation) the system will remain in the attractive domain of that state. As such, the emergence of bistable dynamics in seagrass ecosystems has significant implications for restoration, maintenance, and resilience of these ecosystems [17,18].

While a number of authors have investigated the dependence of hydrodynamic conditions on shoot density within homogenous seagrass meadows [17–23], only few studies [24–26] have addressed these interactions on a larger scale within a mosaic of seagrass patches and bare sediment. Some authors have linked disturbances and environmental conditions to meadow patchiness and general meadow landscape patterns [27–33], however, the consequential effect of meadow patch density on sediment resuspension and the resultant light environment as it pertains to seagrass persistence, growth and the emergence of alternate state dynamics has been neglected. Here, we use a simplified representation of seagrass modified hydrodynamics to explore how the patchy structure of seagrass meadows on a landscape may affect sediment resuspension, the consequent light environment, and the emergence of landscape scale alternate state dynamics under tidal and wind-wave forcing.

2. Methods

2.1. Modeling approach

We generated heterogeneous vegetation covers comprising a mosaic of circular patches randomly distributed according to a two-dimensional Poisson process, with rate λ (i.e., number of patches per unit area). Thus, in an area A the centers of λA disks were randomly placed (Fig. 1). The radius of each circular region was sampled from an exponential distribution with a mean of 1 m, similar to results from Oleson and Sand-Jensen [34]. Overlaps between circular regions were allowed, creating larger meadows. Two approaches were used to generate heterogeneous 250 m by 250 m seagrass landscapes. First, circular patches were randomly placed on a bare landscape; each circular patch was assumed to be a seagrass meadow represented as a collection of homogenous spaced cylinders with a "shoot density" of 500 shoots/m^2 ("patch scattering scenario"). Second, starting from a landscape assumed to be a continuous homogenous meadow with a shoot density of 500 shoots/m^2, circular gaps were randomly generated; each gap was considered as a disturbance that completely removed all seagrass from the circular region ("gap scattering scenario"). In order to facilitate comparisons across each landscape realization, $R(\lambda)$, with differing patch and gap sizes, the actual cover, $a_{cover}(\lambda)$, of seagrass on the landscape was calculated as the fraction of the surface covered by seagrass. Each landscape realization allowed for calculation of hourly combined wave-current shear stresses across the landscape. These shear stresses were then used to estimate hourly values of suspended sediment concentrations and light conditions at the top of the canopy or the seafloor if the landscape is completely bare.

Thus for a single landscape realization, $R(\lambda)$, with corresponding actual cover, $a_{cover}(\lambda)$ and mean water depth, H (m); hourly time series of winds (m/s), photosynthetically active radiation, PAR (μmol/m^2/s), tides (m) and currents (m/s), and water temperature(°C) for the year 2002 (subset of drivers shown in Fig. 2), were used to construct cumulative distribution functions (cdf's) of 1) shear stress on the surface (Pa), 2) suspended sediment concentration SSC (mg/l), and 3) the irradiance in PAR (μmol/m^2/s) reaching the top of the canopy. For each average patch density λ, two realizations were generated and their respective cdf's averaged. Subsequent modification of λ (i.e., number of patches (or gaps) per unit area), and H, for multiple $R(\lambda)$, allowed for exploration of how landscape structure (expressed as a function of λ) and water depth affect the average cdf's of surface shear stresses and the consequent sediment and light environment. The model was run for the year 2002, with an hourly time step for mean water depths ranging from 1 to 4 m MSL, actual landscape cover from 0 to 1, with two realizations for each λ, for both patch and gap scattering perspectives. Each 250 m by 250 m landscape realization was gridded in 0.5 m increments with shear stress, sediment, and light calculated for all 250,000 grid points with a periodic boundary condition. In this manner each 250 m by 250 m landscape realization represents an infinite landscape. Thus, due to the total number of realizations, a quasi-analytical approach was used to estimate the vegetation-modified hydrodynamics, shear stress, sediment and light environment at each grid point allowing for realistic computational times.

2.2. Habitat suitability

Zostera marina is a species requiring a high level of light, roughly 20% of the water surface irradiance for survival [2]. When the light environment is described in terms daily hours of light saturated conditions [4,5] which are temperature dependent [35], roughly 3–5 h [36] are required. In this study, we define habitat suitability in terms of water depths and actual landscape covers, where the spatiotemporal average daily hours of saturation, $\overline{H_{sat}}$ exceeds 3–5 h. It is important to note that measurements of the hours of saturated conditions required is quite variable [6,37]. Photosynthetic saturation was calculated directly following Zharova et al. [38]

$$I_K = I_{K20}\theta_K^{T-20} \tag{1}$$

where I_{K20} is the saturation irradiance value at 20 °C set to 25.5 mol/m^2 per day [39] and θ_K is a shape value which controls the impact of temperature on saturation and is set to 1.04 [40]. Light reaching the canopy is then calculated as a function of water column light attenuation given hourly records of photosynthetically active radiation (PAR) at the water surface, I_0 (μmol m^2/s). Using the Lambert-Beer law, and a light attenuation coefficient, K_d (m^{-1}) we calculate PAR reaching the seagrass canopy, I_{canopy} (μmol/m^2/s), under hourly