Feedback between sediment and light for seagrass: Where is it important?

Matthew P. Adams,*[1] Renae K. Hovey,[2,3] Matthew R. Hipsey,[3,4] Louise C. Bruce,[4] Marco Ghisalberti,[5,6] Ryan J. Lowe,[3,4] Renee K. Gruber,[3,4] Leonardo Ruiz-Montoya,[2,3] Paul S. Maxwell,[1,7] David P. Callaghan,[8] Gary A. Kendrick,[2,3] Katherine R. O'Brien[1]

[1]School of Chemical Engineering, The University of Queensland, St Lucia, Queensland, Australia
[2]School of Plant Biology, The University of Western Australia, Crawley, Western Australia, Australia
[3]Oceans Institute, The University of Western Australia, Crawley, Western Australia, Australia
[4]School of Earth and Environment, The University of Western Australia, Crawley, Western Australia, Australia
[5]School of Civil, Environmental and Mining Engineering, The University of Western Australia, Crawley, Western Australia, Australia
[6]Department of Infrastructure Engineering, The University of Melbourne, Parkville, Victoria, Australia
[7]Healthy Waterways, Spring Hill, Queensland, Australia
[8]School of Civil Engineering, The University of Queensland, StLucia, Queensland, Australia

Abstract

A feedback between seagrass presence, suspended sediment and benthic light can induce bistability between two ecosystem states: one where the presence of seagrass reduces suspended sediment concentrations to increase benthic light availability thereby favoring growth, and another where seagrass absence increases turbidity thereby reducing growth. This literature review identifies (1) how the environmental and seagrass meadow characteristics influence the strength and direction (stabilizing or destabilizing) of the seagrass-sediment-light feedback, and (2) how this feedback has been incorporated in ecosystem models proposed to support environmental decision making. Large, dense seagrass meadows in shallow subtidal, non-eutrophic systems, growing in sediments of mixed grain size and subject to higher velocity flows, have the greatest potential to generate bistability via the seagrass-sediment-light feedback. Conversely, seagrass meadows of low density, area and height can enhance turbulent flows that interact with the seabed, causing water clarity to decline. Using a published field experiment as a case study, we show that the seagrass-sediment-light feedback can induce bistability only if the suspended sediment has sufficient light attenuation properties. The seagrass-sediment-light feedback has been considered in very few ecosystem models. These models have the potential to identify areas where bistability occurs, which is information that can assist in spatial prioritization of conservation and restoration efforts. In areas where seagrass is present and bistability is predicted, recovery may be difficult once this seagrass is lost. Conversely, bare areas where seagrass presence is predicted (without bistability) may be better targets for seagrass restoration than bare areas where bistability is predicted.

Seagrass meadows form the basis of many estuarine and coastal ecosystems (Barbier et al. 2011). Worldwide, these meadows have suffered ~30% areal losses due to human activities (Waycott et al. 2009), and 14% of seagrass species are at elevated risk of extinction (Short et al. 2011). Seagrasses provide numerous important ecosystem services, including nursery habitat for fish (Bertelli and Unsworth 2014), nutrient cycling (Human et al. 2015), and carbon storage (Fourqurean et al. 2012), all of which contribute to human well-being (Cullen-Unsworth et al. 2014). Thus, the loss of seagrass meadows needs to be addressed by immediate conservation (Orth et al. 2006) and restoration efforts worldwide (van Katwijk et al. 2009), to protect and recover the services that seagrass provide (McGlathery et al. 2012; Blandon and zu Ermgassen 2014; Marbà et al. 2015).

Seagrasses are often described as "ecosystem engineers," because their presence modifies the environment in several ways that also promote seagrass survival (Gutiérrez et al.

*Correspondence: m.adams5@uq.edu.au

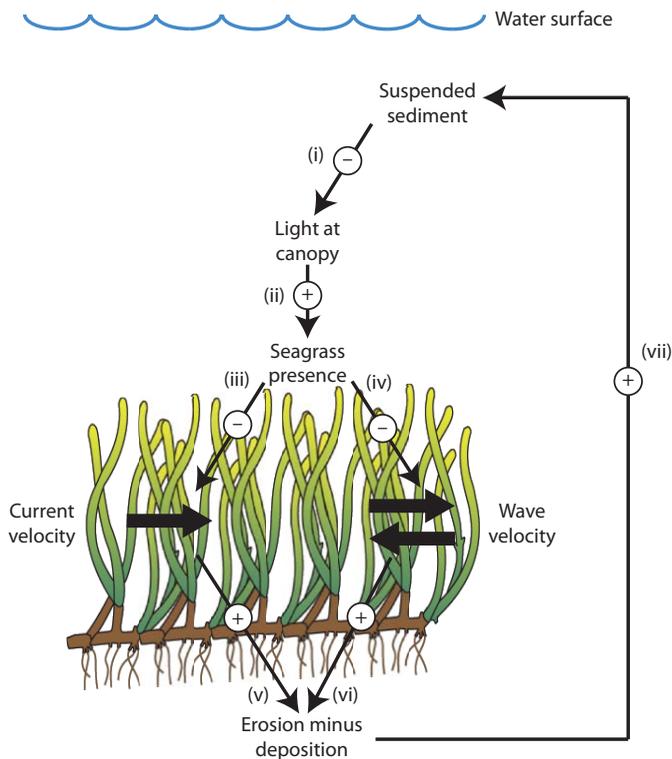Additional Supporting Information may be found in the online version of this article.

Fig. 1. Simplest conceptual model of the SSL feedback, consisting of seven linked processes. Positive and negative causal links are indicated with plus (+) and minus signs (−), respectively. For example, in process (i) an increase in suspended sediment will cause a decrease in light at the canopy (negative causal link); in process (ii) an increase in light at the canopy will cause an increase in seagrass presence (positive causal link) (adapted from van der Heide et al. 2007).

2011). Seagrasses remove nutrients from the water column (McGlathery et al. 2007); if seagrass is absent these nutrients would otherwise stimulate algal overgrowth (Burkholder et al. 2007). Seagrasses provide oxygen to the sediment through their below-ground tissues (Pedersen et al. 2004), which re-oxidises sediment sulphide that would otherwise invade seagrass tissues and act as a phytotoxin (Borum et al. 2005). Seagrasses can also modify sediment transport between the seabed and the water column to reduce water turbidity and increase the light available for seagrass growth (de Boer 2007); in this article we refer to this process as the seagrass-sediment-light (SSL) feedback.

When seagrass is lost, the simultaneous loss of ecosystem engineering benefits may hinder its recovery. For example, significant seagrass losses in the Dutch Wadden Sea (den Hartog and Polderman 1975) have not been reversed despite decades of research and management effort (van Katwijk et al. 2009). The turbidity of the water has increased (Giesen et al. 1990), and thus the SSL feedback is thought to be a major barrier to seagrass restoration in the Dutch Wadden Sea (van der Heide et al. 2007). Several modelling studies suggest that the SSL feedback can induce bistability (van der

Heide et al. 2007; Carr et al. 2010); i.e., a habitat which can support seagrass in either one of two alternative states—vegetated (low turbidity) or unvegetated (high turbidity)—and through this feedback there is resistance to change between the two states. There is also substantial evidence that a similar feedback between macrophyte abundance and turbidity contributes to alternative stable states in shallow lakes (Scheffer 1998).

In other seagrass ecosystems, however, the SSL feedback may not induce bistability. Seagrass was successfully restored with seeds in the coastal bays of the Virginia Coastal Reserve after 60 yr of local extinction (McGlathery et al. 2012). This successful restoration demonstrated that the increased turbidity following seagrass loss was not the primary reason for its inability to recover (Orth and McGlathery 2012).

Identification of locations where the SSL feedback may cause bistability is important for coastal management (Nyström et al. 2012), because at these locations seagrass may be resistant to loss when present, but difficult to recover once lost (van der Heide et al. 2007). First, monitoring data is required to identify the current health of a seagrass ecosystem (Dennison et al. 1993). Second, the extent to which feedback-induced bistability can be characterized depends on the available datasets and modelling tools (Maxwell et al. 2015). Efforts to conserve or restore seagrass will always be limited by available resources (cost, time, and personnel). In some cases, management decisions may rely on monitoring data only; in other cases, sophisticated modelling efforts may be available to aid in management decision making (Kelly et al. 2013).

The objective of this article is to provide a knowledge framework for how to identify the locations where the SSL feedback may cause bistability between seagrass presence and absence states. We first synthesized the experimental literature to identify the environmental and seagrass meadow characteristics which affect this feedback. As part of this synthesis, we quantitatively investigated the potential for bistability to arise from the SSL feedback using published field data. We then reviewed the consideration of SSL interactions in published mathematical models, especially focusing on two- and three-dimensional ecosystem model suites that are proposed to provide environmental decision support. Overall, this article acts as a guide for characterizing the bistability induced by the SSL feedback, which is an important step toward the consideration of this feedback in the management of seagrass ecosystems.

Overview of the seagrass-sediment-light feedback

The simplest conceptual form of the SSL feedback is given by the seven linked processes shown in Fig. 1. Suspended sediment present in the water column attenuates sunlight (Kirk 1985; Lawson 2004) and subsequently reduces the light available for seagrass (Fig. 1, process (i)). Light is a key
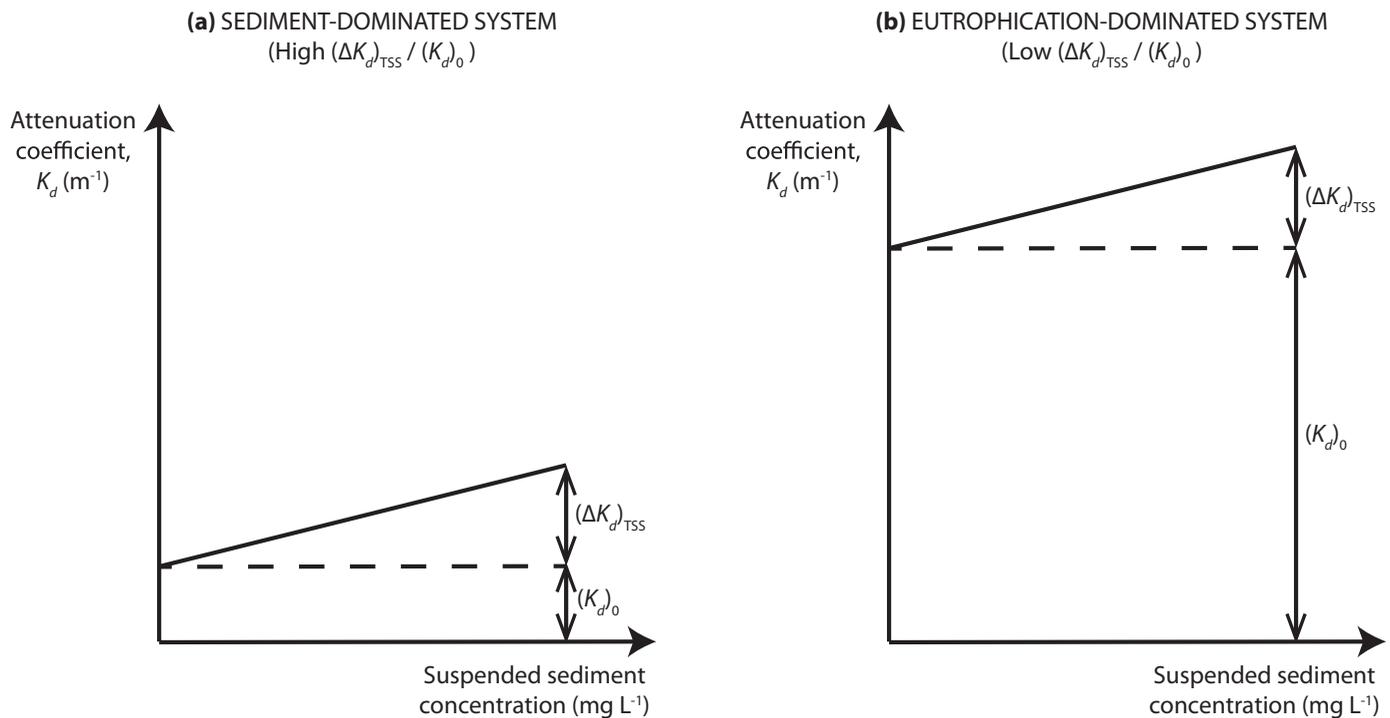
(a) SEDIMENT-DOMINATED SYSTEM
(High $(\Delta K_d)_{TSS} / (K_d)_0$)

(b) EUTROPHICATION-DOMINATED SYSTEM
(Low $(\Delta K_d)_{TSS} / (K_d)_0$)

Fig. 2. Impact of eutrophication on the SSL feedback. Suspended sediments increase the light attenuation coefficient by $(\Delta K_d)_{TSS}$, and this either (a) substantially affects total light attenuation when there are low concentrations of Chl *a* and CDOM present (represented by low $(K_d)_0$), or (b) negligibly affects total light attenuation due to the high concentrations of these other water constituents (high $(K_d)_0$).

requirement for seagrass growth (Dennison 1987; Duarte 1991) and hence seagrass can only be present when there is sufficient light reaching the canopy (process (ii)). Seagrass presence typically induces local reductions in both near-bed current velocities (process (iii)) and wave velocities (process (iv)) (Hansen and Reidenbach 2012). These hydrodynamic interactions are complex and can exert a major influence on the SSL feedback; we will later discuss these significant interactions in detail. The reduction of flow velocities changes the balance between sediment deposition and erosion at the seabed, tending to favor more depositional conditions (processes (v) and (vi)) (Gacia et al. 1999; Gacia and Duarte 2001), which in turn reduces suspended sediment concentrations (process (vii)) (Ward et al. 1984). These seven processes together can form a feedback loop in which the presence of seagrass has the potential to enhance its growth, by reducing suspended sediment and increasing light availability at the canopy (de Boer 2007).

To quantitatively demonstrate that the SSL feedback loop can lead to bistability between seagrass presence and absence states, we later show, in the section "Case study: quantitative evidence that the SSL feedback has the potential to induce bistability," that seagrass can substantially increase the light available for its growth, using results from a field study of a seagrass meadow growing in a shallow coastal bay (Hansen and Reidenbach 2012) and some additional calculations. In

this example, we predict that bare seabed areas at the depth of the meadow (1.4–1.8 m) receive 4–8% surface light, which is below the typical minimum light requirements (MLR) for seagrass of 11% surface light (Duarte 1991), if the suspended sediment is characterized by a specific light attenuation coefficient of $a_{TSS} = 0.026$ m^{-1}/(mg L^{-1}) (Armengol et al. 2003). In contrast, for the same sediment type and depth range, seagrass areas are predicted to receive 12–20% surface light due to the improvement of water clarity that seagrass provides, clearly exceeding their MLR for growth. Thus the SSL feedback loop can lead to bistability between seagrass presence and absence states. However, if the suspended sediment has substantially lower or greater light attenuation properties (i.e., much smaller or larger value of a_{TSS}), we predict that the light conditions at the seabed are either sufficient or insufficient to support seagrass growth (respectively), regardless of the action of the SSL feedback. Hence, in the considered example (Hansen and Reidenbach 2012) the SSL feedback may be necessary for persistence of the seagrass meadow, but only if the local suspended sediment has particular light attenuation characteristics. This example demonstrates the major influence that local environmental conditions exert on whether the SSL feedback will be important in a given ecosystem or not.

The seven processes shown in Fig. 1, which form the SSL feedback loop, will be modified by the local ecosystem's

environmental characteristics (e.g., wave and current speed, sediment properties, seagrass morphology). In the following subsections, we account for this complexity by summarizing the current knowledge of the effects of environmental and meadow characteristics on the SSL feedback.

Suspended sediment reduces light availability

For subtidal seagrasses, light availability at the seagrass canopy I is reduced from the light at the water surface I_0. This reduction depends on the light attenuation coefficient K_d (m^{-1}) and depth of the water column H (m) according to Beer's law (Kirk 1985),

$$I = I_0 \exp(-K_d H). \tag{1}$$

Total attenuation K_d of light through the water column can be expressed as a summation of contributions from the different constituents present in the water column (Gallegos 1994). For example, if total suspended solids (TSS), chlorophyll a and colored dissolved organic matter (CDOM) are present, an empirical definition for K_d such as $K_d = (K_d)_{water} + a_{TSS}[TSS] + a_{Chl\ a}[Chl\ a] + a_{CDOM}[CDOM]$ is often assumed, where $(K_d)_{water}$ is the light attenuation due to water, a_{TSS}, $a_{Chl\ a}$, a_{CDOM} are specific attenuation coefficients and [TSS], [Chl a], [CDOM] are concentrations of TSS, Chl a and CDOM, respectively (Lawson et al. 2007). The light attenuation coefficient also varies with water depth; for example, resuspended sediment can produce near-bottom K_d values that are 1.6 to >30 times larger than values of K_d measured higher in the water column (Pedersen et al. 2012). However, for the SSL feedback, it is the changes in turbidity over the whole water column which are most relevant as it includes the entire path length of light from the water surface to the seagrass canopy.

Because the attenuation coefficient K_d depends on factors other than TSS concentration (e.g., Chl a and CDOM), the relative difference in light at the seagrass canopy due to variation of TSS depends also on the concentration of these other factors. We may distinguish, for example, between sediment-dominated and eutrophication-dominated systems. In a sediment-dominated system (Fig. 2a), the concentrations of Chl a and CDOM are low, so variations in TSS have a major impact on the attenuation coefficient and thus the light reaching the seagrass canopy. In an eutrophication-dominated system (Fig. 2b), high concentrations of Chl a or CDOM are the major contributors to light attenuation, and variation in TSS is unlikely to significantly alter K_d.

The SSL feedback may also be less important in intertidal zones, because the seagrasses present there are not always submerged. Erosion can be greater in intertidal zones due to the increased wave action present at shallow depths (de Boer 2007), but the seagrass colonization in these zones will likely depend on direct impacts from wave action (Vacchi et al. 2014) and desiccation (Shafer et al. 2007) rather than the SSL feedback.

Light promotes seagrass growth

The net carbon gain obtained from the balance of carbon fixed via photosynthesis and carbon lost due to respiration is the main rate-limiting step for plant growth (Fig. 1, process (ii)) (Ralph et al. 2007; Poorter et al. 2013). Seagrasses require photosynthetically active radiation (wavelength 400–700 nm) to fix inorganic carbon through photosynthesis (Dennison 1987; Borum et al. 2013). The photosynthesis rate of seagrass linearly increases with the availability of photosynthetically active radiation, until light conditions reach a "saturation" value at which the seagrass photosynthesis rate cannot further increase. The net rate of carbon fixation P (e.g., in units of g C g^{-1} d^{-1}) by seagrass is a balance of photosynthesis and respiration,

$$P = P_{max} \tanh\left(\frac{I}{I_k}\right) - R, \tag{2}$$

where P_{max} is the maximum photosynthesis fixation rate, which occurs at saturating light conditions, I_k is the irradiance at which onset of saturation occurs, and R is the respiration rate. The hyperbolic tangent function represents the saturation of the photosynthesis rate at high light levels, and can be replaced by any other appropriate empirical saturation function (Jassby and Platt 1976). The compensation irradiance I_c, which is the light value at which photosynthesis exactly balances respiration ($P = 0$ in Eq. 2), provides a coarse indication of the MLR of seagrass. Typically, the compensation irradiance is substantially less than the saturation irradiance, $I_c < I_k$ (Lee et al. 2007), and thus the light value I_c which roughly distinguishes between seagrass presence and absence occurs in the linear part of the photosynthesis-irradiance curve. Hence, it is the linear region of the photosynthesis-irradiance curve that is most relevant for investigating bistability arising from the SSL feedback. Parameters of Eq. 2 are species-dependent and are commonly reported in experimental studies (reviewed in Lee et al. 2007).

The rate of photosynthesis also depends on the proportion of exposed leaf area (Hedley and Enríquez 2010; Hedley et al. 2014) that varies between species (Lee Long et al. 1993) and with orientation of the leaves due to local hydrodynamics (McKone 2009). Photosynthesis and respiration rates can vary substantially within the same species (Olivé et al. 2013), through phenotypic plasticity (Maxwell et al. 2014) such as photoacclimation (Cayabyab and Enríquez 2007), epiphyte presence (Sand-Jensen 1977), and variations in external environmental factors such as temperature (Staehr and Borum 2011). Accounting for all drivers of plasticity in seagrass responses to light is beyond the scope of this review, but should be noted when discussing uncertainty in the SSL feedback.
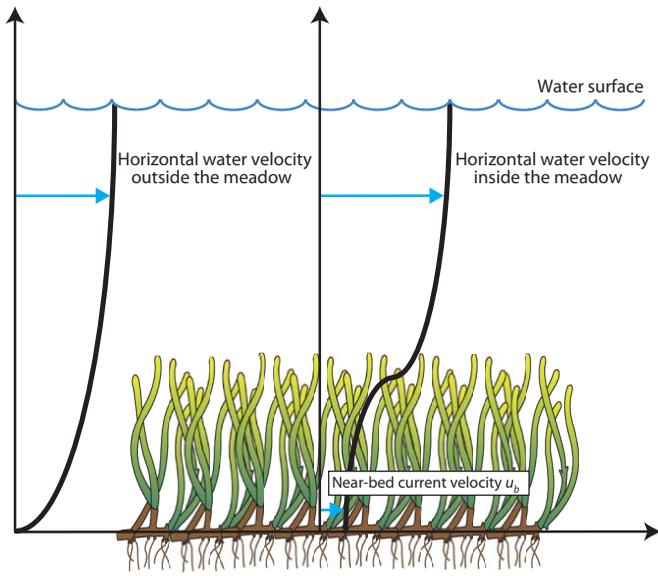
Fig. 3. Seagrass presence alters the current velocity profile from a logarithmic form outside/above the meadow to an exponential form inside the meadow.

Although many factors affect seagrass growth, the most important threshold for seagrass presence and absence is their MLR, which can be identified from the limits of seagrass depth range (Dennison et al. 1993). On average, seagrasses extend to depths receiving 11% surface light (Duarte 1991). However, light requirements vary between seagrass species (Collier et al. 2012), and globally seagrass MLR have been reported in the range of 4–36% of surface irradiance (Ralph et al. 2007).

Seagrass modifies the local hydrodynamics
Current-driven flow

Seagrasses reduce water velocities associated with unidirectional current-driven flows (Fig. 1, process (iii)) (Fonseca et al. 1982; Peterson et al. 2004; Fonseca and Koehl 2006). Within the seagrass canopy, the current velocity profile is modified from logarithmic to approximately exponential (Abdelrhman 2003; Nepf and Ghisalberti 2008) (Fig. 3). Complex models have predicted these flow interactions down to the scale of individual shoot segments (Abdelrhman 2007; Zeller et al. 2014).

While the presence of seagrass modifies the vertical structure of the current velocity profile as shown in Fig. 3, the current velocity inside the seagrass meadow depends on the horizontal distance from the meadow edge. The near-bed current velocity u_b decreases horizontally within the seagrass meadow, at approximately an exponential rate from its value $u_{b,0}$ at the upstream meadow edge,

$$u_b^2 = u_{b,f}^2 + \left(u_{b,0}^2 - u_{b,f}^2 \right) e^{-x/L_D}, \tag{3}$$

where x is the horizontal distance inside the meadow, L_D is the canopy drag length scale, and $u_{b,f}$ is the near-bed current
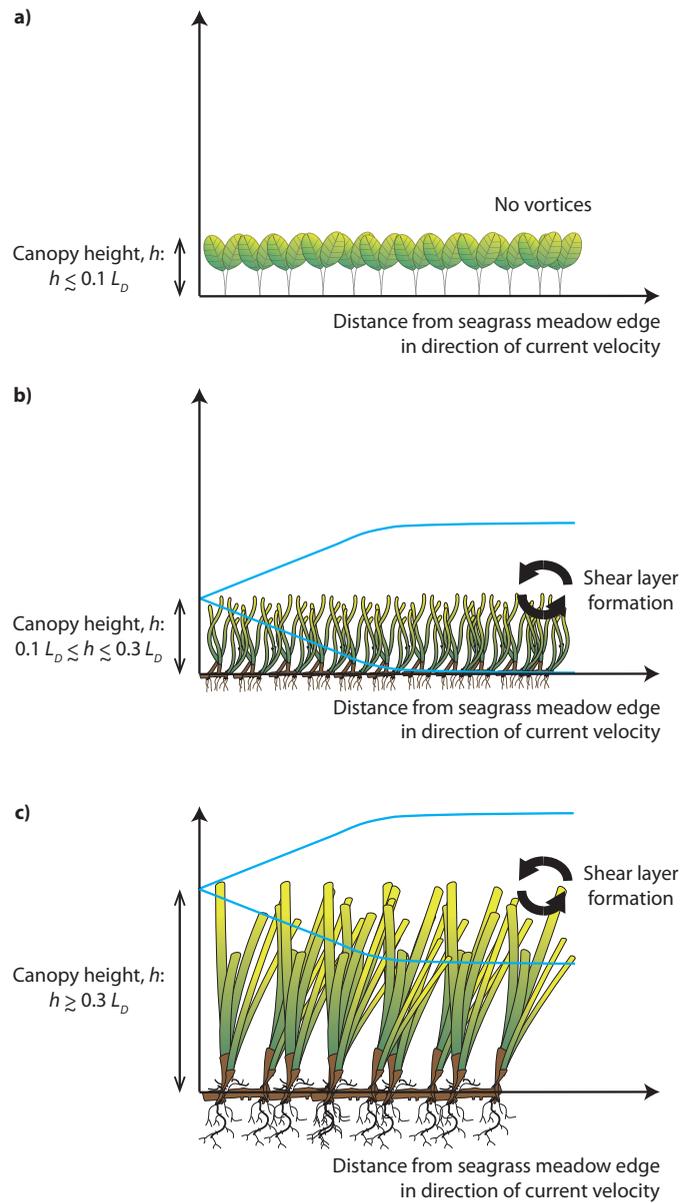

Fig. 4. Relationship between vortex development and the ratio of canopy height to drag length scale h/L_D. The blue lines show how the shear layer, which contains the vortices, forms with increasing horizontal distance into the seagrass meadow. The seagrass canopy is either (a) too short to produce vortices, (b) of intermediate height and induces a shear layer which penetrates to the sediment bed, or (c) is sufficiently tall to induce a shear layer which is localized only to the canopy-water interface.

velocity well within the seagrass meadow (Supporting Information Appendix A). The drag length scale is defined by

$$L_D = (C_D a)^{-1} \tag{4}$$

where C_D is the drag coefficient of the seagrass meadow and a is the canopy frontal area per unit volume (in units of m^{-1}) (Nepf 2012). For seagrasses, L_D is typically $\mathcal{O}(0.1-1 \ m)$

(Luhar et al. 2008). For vertical seagrass blades, the normalized frontal area a is equivalent to the ratio of leaf area index (LAI) to canopy height h,

$$a = LAI/h. \tag{5}$$

LAI is equal to the area of one side of the leaf divided by the ground area, and is thus an indirect measure of shoot density and leaf size. Equations 3-5 therefore predict that greater shoot densities are characterized by smaller drag length scales and greater reductions in near-bed velocity with distance into the meadow. This prediction is supported by several field studies (e.g., Peterson et al. 2004; Widdows et al. 2008; Wilkie et al. 2012).

The presence of submerged seagrass induces the formation of a shear layer, characterized by the generation of coherent vortex structures that cause plant motion known as monami (Ackerman and Okubo 1993), at the top of the canopy (Fig. 4) (Gambi et al. 1990; Nepf and Vivoni 2000; Ghisalberti and Nepf 2002). These structures are responsible for the majority of scalar mixing into and out of the canopy and substantially elevated turbulent transport compared with the overlying water column (Luhar et al. 2008). The shear layer (and thus vortex size) grows with horizontal distance into the meadow up to a finite thickness (Ghisalberti and Nepf 2009).

Penetration of the shear layer to the bed depends on the ratio of canopy height h to drag length scale L_D (Nepf et al. 2007). Canopy drag is insufficient to form a canopy shear layer when $h/L_D \leq 0.1$ (Fig. 4a), resulting in a flow that resembles a rough-wall boundary layer. When this ratio increases above 0.1, a shear layer forms and penetrates fully to the seabed, potentially elevating the bed stress (Fig. 4b). When this ratio increases further ($h/L_D \gtrsim 0.3$), the shear layer does not penetrate to the seabed, decreasing the bed stress (Fig. 4c). Because the drag length scale L_D depends on the leaf friction and canopy density (Eq. 4), the form of the produced shear layer (Fig. 4a, b or c) depends on canopy height, shoot density and physical leaf properties. In other words, shear layer formation and penetration depends on the spatial and morphological characteristics of the seagrass meadow. We will see later that the turbulence induced by this shear layer has the potential to increase the suspended sediment concentration in the water column.

Wave-driven and combined current-wave flows

Seagrasses can dissipate wave energy through the drag forces they impart on the water column, which over broad scales can attenuate wave heights and associated wave-driven oscillatory flows (Fig. 1, process (iv)) (Fonseca and Cahalan 1992; Koch et al. 2006). This wave attenuation increases with plant stiffness and density (Bouma et al. 2005), with distance into the meadow (Bradley and Houser 2009), and with increasing amplitude and period of the waves (Luhar et al. 2010). On smaller scales, waves directly

drive oscillatory flows within seagrass canopies (Lowe et al. 2005). Waves can also generate coherent vortices at the canopy-water interface (Fig. 4) (Ghisalberti and Schlossser 2013) and considerably modify the near-bed turbulent flow structure (Pujol et al. 2013). Laboratory flume studies have recently investigated combined current-wave flows through aquatic canopies (Li and Yan 2007; Paul et al. 2012; Hu et al. 2014; Zeller et al. 2015). For simplicity in this article we consider the effects of seagrass presence on flow regimes that are predominantly either current- or wave-driven, and do not consider current-wave interactions.

Seagrass modifies sediment exchange at the seabed

Seagrasses are conventionally viewed as regions of enhanced net sediment deposition compared with surrounding areas, due to the drag they exert on the local flow and the corresponding reduction in bed shear stress (Fig. 1, processes (v) and (vi)) (Gacia et al. 1999; Gacia and Duarte 2001). However, in some cases enhancement of turbulence by seagrass can increase sediment resuspension (van der Heide et al. 2010; Lawson et al. 2012; Hansen and Reidenbach 2013).

The balance of deposition and erosion

The hydrodynamic force applied to bed sediments is quantified by the bed shear stress τ_b (in units of N m^{-2}). At low bed shear stress, there is no erosion, and the only sediment exchange between the water column and the seabed is due to passive deposition D. Once the bed shear stress τ_b exceeds a critical shear stress threshold τ_c, sediment is eroded at a rate E (in units of kg m^{-2} s^{-1}) so that the net sediment deposition is $D - E$. Although several formulations exist for erosion, many studies report a simple linear dependence on the bed shear stress (Sanford and Halka 1993; Sanford and Maa 2001),

$$E = \begin{cases} M\left(\dfrac{\tau_b}{\tau_c} - 1\right), & \tau_b \geq \tau_c, \\ 0, & \tau_b \leq \tau_c, \end{cases} \tag{6}$$

where M is an empirical constant.

Seagrass presence affects the erosion rate E (Koch 1999) by modification of both the actual shear stress τ_b (Hansen and Reidenbach 2012, 2013) and the critical shear stress threshold τ_c (Amos et al. 2004). Seagrass presence has been observed to reduce τ_b by factors of up to four (Hansen and Reidenbach 2012), and increase the critical threshold value τ_c by two-fold (Amos et al. 2004). While the decrease in τ_b within seagrass meadows can be attributed to the attenuation of currents and waves by seagrass leaves, the increase in τ_c is caused by the stabilizing effect of seagrass below-ground biomass (roots and rhizomes) on the bed sediment (Christianen et al. 2013). Of these two mechanisms, the most well-studied impact of seagrass on the balance of sediment deposition and erosion is via canopy reduction of local
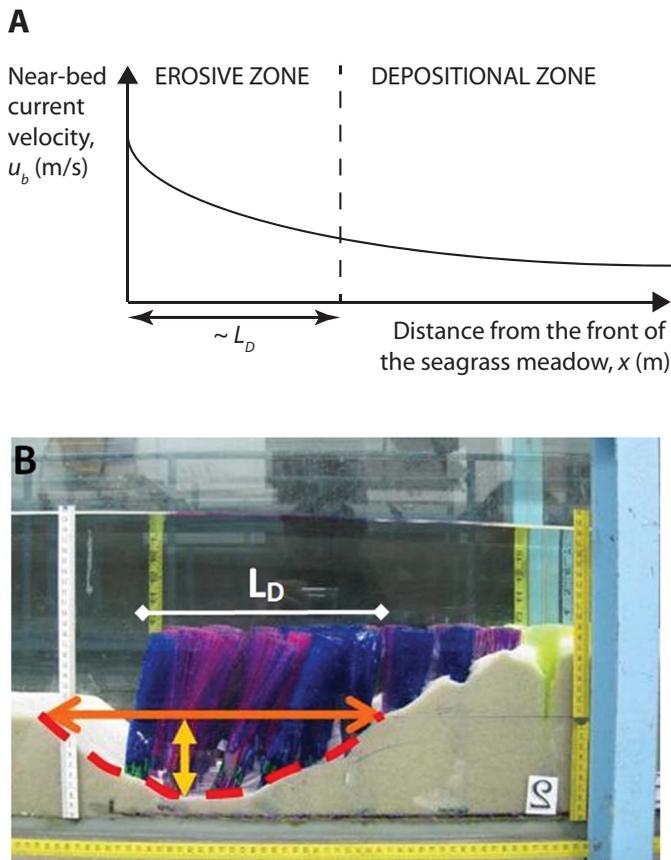
A

B

Fig. 5. (a) Reduction in near-bed velocity occurs over the drag length scale L_D, which defines the transition of the meadow from a net erosive zone to a net depositional zone. (b) A laboratory canopy showing the net erosive and depositional zones (modified from Chen et al. 2012); the orange arrow represents the initial sediment bed height.

hydrodynamic forces (Le Hir et al. 2007). In the following subsections, we discuss how the canopy-induced modification of the balance of sediment deposition and erosion is affected by the local meadow structure, sediment size distribution and flow conditions.

Impact of meadow height

The balance between sediment erosion and deposition is significantly affected by the height h of a seagrass meadow. If the shear layer that forms at the canopy-water interface penetrates fully to the seabed, bed shear stress is enhanced. This occurs when the ratio of meadow height to canopy drag length scale, h/L_D, is between 0.1 and 0.3 (Fig. 4b) (Nepf et al. 2007). Because the drag length scale L_D is inversely related to shoot density (Eqs. 4 and 5), seagrass meadows of low shoot density will increase the thickness of the shear layer and are more likely to enhance bed shear stress. Hence, a sufficiently large canopy height and shoot density ($h/L_D \gtrsim 0.3$, Fig. 4c) is required to ensure that the shear layer

does not reach the seabed, as this would increase τ_b and thus potentially increase sediment erosion.

Impact of meadow length

There has been some evidence that, below a minimum meadow size and/or shoot density, seagrass presence enhances erosion, thereby switching the SSL feedback from a stabilizing behavior (the modification of environmental conditions by seagrass presence that supports its growth) to a destabilizing behavior (the modification of environmental conditions by seagrass presence that hinders its growth) (Hansen and Reidenbach 2012; Lawson et al. 2012). The potential for destabilizing behavior to arise from the SSL feedback can be attributed to a difference in the horizontal length scales over which turbulence addition and the reduction in near-bed current velocities occur. At the edge of the meadow, turbulence is introduced almost immediately, at a length scale of the order of the spacing between seagrass shoots (Nepf 2012). This is a much smaller length scale than the canopy drag length scale L_D over which the near-bed current velocity is reduced (Eq. 3). Many seagrass meadows can therefore be separated into two zones, based on the distance x from the front of the meadow (Fig. 5): an erosive zone where the shoot-scale turbulence promotes erosion ($x \leq L_D$), and a depositional zone where the reduction in current velocities overcomes the shoot-scale turbulence to promote deposition ($x \gtrsim L_D$) (consistent with the observations of Bouma et al. 2007; Chen et al. 2012).

The distance from the front of the seagrass meadow to the zone where deposition is favored ($\sim L_D$) will decrease with increasing shoot density (see Eqs. 4 and 5). Hence, seagrass meadows of reduced length L and lower shoot density ($L/L_D \sim \mathcal{O}(1)$) are more likely to enhance erosion, while longer meadows with higher shoot density ($L/L_D >> \mathcal{O}(1)$) are more likely to be net depositional. This conceptual model is supported by laboratory studies that reported an increase in erosion associated with the presence of seagrass (Chen et al. 2012; Follett and Nepf 2012; Ortiz et al. 2013); in all of these studies, L/L_D was $\mathcal{O}(1)$. In the erosive zone, the volume of sediment eroded increases with flow velocity, plant size (Bouma et al. 2009) and shoot density (Lawson et al. 2012), all of which serve to increase the intensity of near-bed turbulence.

Impact of sediment size distribution

Seagrasses are traditionally viewed as environments where fine, poorly sorted, sediments are deposited, compared with adjacent unvegetated areas (Ward et al. 1984 and references within). As described above, this may only be true for seagrass meadows that have appropriate length, height and density to be net depositional. Recent evidence supports the more complex view that (1) seagrasses increase the relative bed concentration of fine sediments when they are net depositional environments (De Falco et al. 2000; Moore 2004; Bos et al. 2007), (2) seagrasses increase the relative bed

concentration of coarse sediments when they are net erosive environments (Fonseca and Koehl 2006), and (3) the change in sediment size distribution induced by seagrass presence also depends on whether the local sediments are predominantly sand (particle diameter > 62.5 μm) or mud (particle diameter < 62.5 μm) (van Katwijk et al. 2010).

As a first approximation, the dependence of critical shear stress τ_c on sediment size distribution can be inferred from Hjulström and Postma diagrams (Dade et al. 1992). These diagrams indicate that the erosion threshold is positively correlated with particle size for sandy sediments (>62.5 μm), but may become negatively correlated with particle size for clay (<2 μm) or muddy sediments (<62.5 μm) due to sediment cohesion (Roberts et al. 1998). The erodability of sediment may also depend on several other physical, geochemical and biological properties (Grabowski et al. 2011). We will later show, using a case study, that the light attenuation properties of the suspended sediment, which are size-dependent (Baker and Lavelle 1984), also play a critical role in determining whether the SSL feedback is important in a given ecosystem or not.

Impact of wave-driven flow

The mechanisms by which seagrass modifies net sediment deposition differ between current-driven and wave-driven flows (Koch and Gust 1999). Although wave-driven flows are reduced within seagrass canopies (Fonseca and Cahalan 1992; Manca et al. 2012), they may also induce a mean flow in the direction of wave propagation inside the meadow (Luhar et al. 2010). Despite the presence of these competing mechanisms, observations suggest that seagrasses overall reduce sediment resuspension in wave-driven flows, especially at higher shoot densities (Ros et al. 2014). While attenuation of both currents and waves by the presence of seagrass typically increases the net sediment deposition, this deposition is likely to be reduced in wave-driven flows compared with current-driven flows because mean currents are attenuated by seagrass canopies much more than oscillatory flows (Lowe et al. 2005), and the wave-driven movement of seagrass blades back and forth increases sediment movement between the seagrass canopy and the overlying water column (Koch and Gust 1999; Madsen et al. 2001).

Seagrass modifies the suspended sediment distribution

The vertical distribution of suspended sediment in the water column is modified by seagrass via (1) change in the balance of sediment deposition and erosion at the seabed (described above), (2) change in the flow structure which depends on the ratio of meadow height to drag length scale, h/L_D (Fig. 4), and (3) direct collision and deposition of sediment particles on seagrass leaves (Ackerman 2002; Agawin and Duarte 2002; Hendriks et al. 2008), although these leaf-deposited particles may be subsequently easily resuspended (Ganthy et al. 2015). Modification of flow structure induced by "tall" seagrass canopies ($h/L_D \gtrsim 0.3$, Fig. 4c) produces

three different layers of sediment transport (Carr et al. 2010): a layer near the seabed where sediment motion is reduced and deposition favored (relative to the overlying water column), a shear layer encompassing the canopy-water interface that rapidly exchanges sediment between the seagrass canopy and the overlying water column with a peak in sediment diffusivity at the canopy height h (Ghisalberti and Nepf 2005), and the overlying water column where the flow may be modified slightly by the seagrass present below (Fig. 3).

Overall, these changes in the suspended sediment distribution induced by the presence of seagrass modify the concentration of TSS above the seagrass canopy, thus completing the SSL feedback loop (Fig. 1, process (vii)). Reductions in TSS have been observed inside seagrass canopies compared with meadow edges and adjacent bare sediment (Ward et al. 1984; Granata et al. 2001; Gruber and Kemp 2010), with greater TSS reductions at higher seagrass biomass (Moore 2004). However, this relationship changes to result in increased TSS when the canopy frontal area of seagrass is sufficiently reduced (Hansen and Reidenbach 2013). Reduced turbidity with wide, dense and tall canopies, and elevated turbidity in smaller sparser meadows, has also been observed in other submerged aquatic plants (Gruber et al. 2011). These field results demonstrate the depositional and erosive zone concepts shown in Fig. 4, as the corresponding changes in frontal area alter the relative size of depositional and erosive zones L_D (see Eq. 4).

Case study: quantitative evidence that the SSL feedback has the potential to induce bistability

Here, we demonstrate quantitatively that differences in bed shear stress and therefore sediment resuspension between bare sediment and seagrass habitat can be sufficiently large to induce substantial differences in benthic light availability between areas where seagrass is present and absent. These calculations support the hypothesis that the SSL feedback loop has the potential to cause bistability in seagrass ecosystems.

To achieve this, we use the field experiment of Hansen and Reidenbach (2012) as a case study. A seagrass meadow (*Zostera marina*) present in a coastal bay of 1–2 m depth (South Bay, Virginia Coastal Reserve) was shown to attenuate near-bottom current velocities by 70–90% and high-frequency orbital velocities by 20%. This result agrees reasonably with model predictions of current attenuation and high-frequency wave attenuation by *Zostera marina* of 88–95% and 7–18%, respectively (Luhar et al. 2010). In the case study, the bed shear stress τ_b inside the seagrass meadow (0.03 ± 0.02 N m^{-2}) was substantially lower than in a nearby bare area (0.17 ± 0.08 N m^{-2}); this difference was attributed to the influence of seagrass presence on sediment stabilization (Hansen and Reidenbach 2012). For the majority of

Table 1. Predictions of benthic light availability at the seabed with or without seagrass presence, for suspended sediments possessing different light attenuation properties. Benthic light availability I/I_0 is calculated as a percentage of surface irradiance (% SI).

Properties of suspended sediment	a_{TSS} (m^{-1}/(mg L^{-1}))	Benthic light availability at 1.4–1.8 m depth	
		Seagrass is present ([TSS] = 31 mg L^{-1})	Seagrass is absent ([TSS] = 56 mg L^{-1})
Low light attenuation	0.013	26–35%	14–22%
Intermediate light attenuation	0.026	12–20%	4–8%
Greater light attenuation	0.094	0–1%	0%

the time of the field study (80% of 72 h), the reduced bed shear stress within the seagrass meadow fell below a conservative estimate of the critical shear stress necessary for sediment erosion, $\tau_c = 0.04$ N m^{-2} (Lawson et al. 2007).

Inside the seagrass meadow, the mean suspended sediment concentration (across three sites) was 31 mg L^{-1}, compared with 56 mg L^{-1} in the adjacent bare area. This difference can be attributed to the reduction in bed shear stress by seagrass presence, as follows. As a rough approximation, the depth-averaged suspended sediment concentration [TSS] (mg L^{-1}) may be related to bed shear stress via

$$[\text{TSS}] \approx \frac{M}{w_s} \max\left\{ \frac{\tau_b}{\tau_c} - 1, 0 \right\}, \qquad (7)$$

where M (g m^{-2} s^{-1}) is an empirical constant that represents the proportionality between the erosion rate and the exceedance of the bed shear stress τ_b (N m^{-2}) above the critical threshold for erosion τ_c (N m^{-2}), and w_s (m s^{-1}) is the sediment settling velocity. Equation 7 is derived by assuming that the local depth-averaged sediment concentration has reached a steady state and is approximately horizontally homogeneous, such that the local erosion E and deposition rates D are equal. The erosion rate E is assumed to follow Eq. 6, and the deposition rate is assumed to follow $D = w_s$ [TSS] (Chen et al. 2007). Subsequent rearrangement of the equation $E = D$ for [TSS] yields Eq. 7.

Note that Eq. 7 considers only suspended sediment that can be readily exchanged between the seabed and the water column. For example, this equation excludes background suspended sediment that settles too slowly to fall out of suspension during slack water (Sanford and Halka 1993). Here we will use Eq. 7 only to estimate the difference in [TSS] between the seagrass meadow area and the adjacent bare area, so the presence of background suspended sediment common to both areas is mathematically eliminated and does not affect our calculations that involve Eq. 7.

We assume that $\tau_c = 0.04$ N m^{-2} (Lawson et al. 2007), $M \sim \mathcal{O}(10^{-3} - 10^{-2})$ g m^{-2} s^{-1}, and $w_s \sim \mathcal{O}(10^{-3})$ m s^{-1}; both of the latter terms are calculated from Table 2 of Sanford and Halka (1993). As a caveat, we point out that quantities τ_c, M, and w_s may all vary from the above values by over an order of magnitude, depending on the sediment properties, and this will sub-

stantially affect the calculation of [TSS] and light levels (Odd 1988; Houwing 1999). Using these parameter values, Eq. 7 predicts that the [TSS] in the seagrass meadow ($\tau_b \approx 0.03$ N m^{-2}) is $\mathcal{O}(3-30)$ mg L^{-1} less than in the adjacent bare area ($\tau_b \approx 0.17$ N m^{-2}). This is consistent with the finding of Hansen and Reidenbach (2012) that the mean [TSS] within the seagrass meadow is 25 mg L^{-1} less than in the bare area.

At first order, the light attenuation coefficient K_d (m^{-1}) increases linearly with [TSS] concentration. Here, [TSS] was estimated following the formula of Gallegos and Moore (2000), approximated for an aquatic ecosystem in which the Chl a concentration is relatively low, 2 mg m^{-3} (Carr et al. 2010),

$$K_d \approx a_{TSS} [\text{TSS}] + 0.352, \qquad (8)$$

where a_{TSS}, the specific light attenuation coefficient for suspended solids, was estimated as 0.094 m^{-1}/(mg L^{-1}). However, in that study, the value of a_{TSS} varied between sites by nearly an order of magnitude (0.013–0.101 m^{-1}/(mg L^{-1})) (Gallegos and Moore 2000); this variation can be attributed to differences in sediment properties, including particle size (Baker and Lavelle 1984). We next show that, based on the value of a_{TSS}, for the seagrass meadow studied in Hansen and Reidenbach (2012), either (1) seagrass absence is predicted regardless of the feedback, (2) seagrass presence is predicted regardless of the feedback, or (3) bistability between seagrass presence and absence, induced by the SSL feedback, is predicted.

The fraction of surface light I/I_0 reaching the seabed can be calculated using Beer's law (Eq. 1). The seagrass meadow studied in Hansen and Reidenbach (2012) is located within a shallow coastal bay of 1–2 m depth, but the seagrass sites measured had mean depth ranging from 1.4 m to 1.8 m. To ensure our calculations represent the light conditions experienced by the majority of the seagrass meadow, we set $H = 1.4$ m and $H = 1.8$ m in Eq. 1 to obtain a range of mean benthic light conditions for the meadow. We also trial three different values of a_{TSS}: a lower value of 0.013 m^{-1}/(mg L^{-1}) [lowest value of a_{TSS} measured in Gallegos and Moore (2000)], an intermediate value of 0.026 m^{-1}/(mg L^{-1}) (e.g., Armengol et al. 2003), and an upper value of 0.094 m^{-1}/(mg L^{-1}) [final value of a_{TSS} reported in Gallegos and Moore (2000)]. The results of our calculations, obtained from Eqs. 1 and 8, are shown in Table 1.
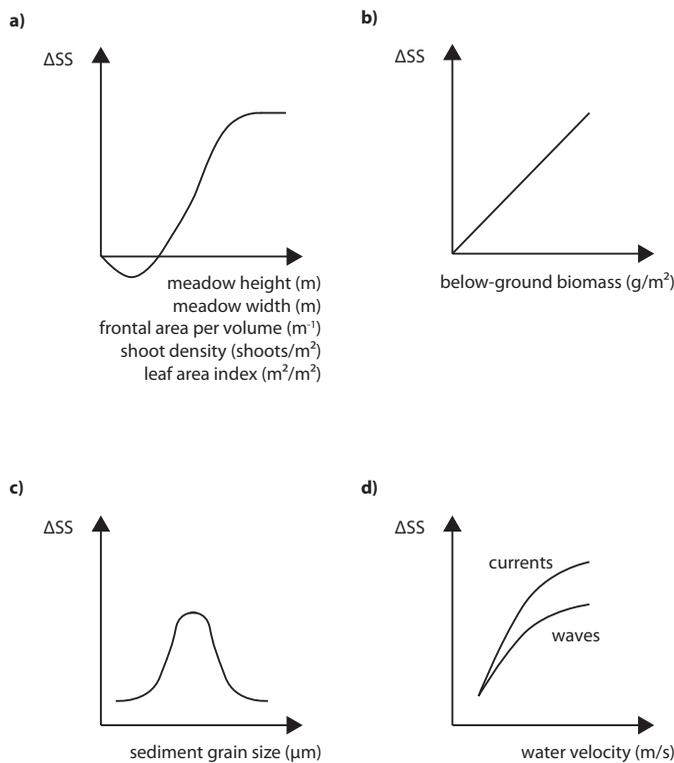
Fig. 6. Impact of environmental and seagrass meadow characteristics on the magnitude and direction of the SSL feedback, expressed as the difference between suspended sediment concentration between seagrass presence and absence states, ΔSS. Positive ΔSS represents decreased suspended sediment concentration due to seagrass presence, and negative ΔSS represents increased suspended sediment concentration due to seagrass presence.

As discussed earlier, MLR for seagrass are on average 11% of the surface irradiance (Duarte 1991). From Table 1, if $a_{TSS} = 0.013$ m^{-1}/(mg L^{-1}) (low light attenuation by suspended sediment), there is sufficient light available for seagrass survival regardless of the SSL feedback. On the other hand, if $a_{TSS} = 0.094$ m^{-1}/(mg L^{-1}) (greater light attenuation by suspended sediment), seagrass cannot grow because there is insufficient light at the seabed. Finally, for an intermediate value of $a_{TSS} = 0.026$ m^{-1}/(mg L^{-1}), seagrass can sufficiently improve water clarity to exceed its MLR for survival, whereas seagrass absence may lead to a turbid environment in which the light levels at the seabed are too low to support seagrass growth. This latter result indicates the possibility of bistability between seagrass presence and absence states at depths of 1.4–1.8 m (Table 1), which is consistent with the depth range for bistability of 1.6–1.8 m predicted by a more detailed seagrass growth model parameterized for the same seagrass species and coastal system (*Zostera marina* growing in the Virginia Coastal Reserve) (Carr et al. 2012a).

Since there is a persistent seagrass meadow in the coastal bay examined by Hansen and Reidenbach (2012), of the three possibilities explored above, it is likely that a_{TSS} is

sufficiently low so that either (1) seagrass presence occurs without bistability, or (2) this system expresses bistability between seagrass presence and absence states. Our calculations show that bistability between seagrass presence and absence states, induced by the SSL feedback, is possible, but is highly dependent on the light attenuation properties of the sediment.

Synthesis

From the laboratory experiments and field observations outlined in the previous sections, we have summarized the impact of local environmental and seagrass meadow characteristics on the ability of the SSL feedback to modify suspended sediment concentration. The magnitude and direction of this feedback can be defined by the difference in suspended sediment concentration between seagrass presence and absence states, which we write as ΔSS. When ΔSS is large and positive, seagrass presence substantially reduces the TSS concentration that further promotes seagrass growth (stabilizing feedback). When ΔSS is negative, seagrass presence increases the TSS concentration that potentially reduces seagrass growth (destabilizing feedback).

The impacts of local environmental and seagrass meadow characteristics on the ability of the SSL feedback to induce bistability (i.e., act as a stabilizing feedback) are summarized in Table 2. This table can be used as an initial checklist to identify the ecosystems where the SSL feedback may need to be considered in environmental management. For the environmental and meadow characteristics where further information is available, their impact on ΔSS is shown in Fig. 6.

A synthesis of the relationships proposed in Table 2 and Fig. 6 is as follows:

i. *Meadow depth*: The SSL feedback will be most important in shallow subtidal areas. Intertidal seagrasses at low tides are exposed to air, during which time the processes shown in Fig. 1 do not occur. For deep subtidal seagrasses, the influence of seagrass on the vertical distribution of suspended sediment will be reduced. This effect was observed by Ward et al. (1984), who found that subtidal seagrass was less effective at reducing the local TSS levels compared with the surrounding unvegetated area during a wind-induced resuspension event at high tide ($H - h > 60$ cm) than during a similar event at low tide ($H \approx h$). The SSL feedback may or may not induce bistability in shallow subtidal areas, as several other factors need to be present as well (see (ii) to (v) below). For example, if sediment is not easily resuspended or has low light attenuation characteristics (iv), the reduction in light by seagrass presence will be small and hence may not be sufficient to induce bistability. However, shallow subtidal areas provide the best conditions for seagrass to reduce the vertical distribution of suspended sediment, and this conclusion is also supported by modelling efforts

Table 2. Impact of environmental and seagrass meadow characteristics on the ability of the SSL feedback to induce bistability between seagrass presence and absence states (i.e., act as a stabilizing feedback), and the implications for seagrass conservation and restoration.

	Potential for seagrass-sediment-light (SSL) feedback to induce bistability	
	Lower potential	Higher potential
Environmental and seagrass meadow characteristics:		
(i) Meadow depth	Intertidal or deep subtidal	Shallow subtidal
(ii) Eutrophication	High	Low
(iii) Meadow size/density	Sparse/small	Dense/large
(iv) Sediment size	Narrow range of sizes	Broad range of sizes
(v) Water velocity	Low	High
Impact on environmental management:		
Seagrass conservation	SSL feedback unlikely to make seagrass decline difficult to reverse	Seagrass decline may be difficult to reverse
Seagrass recolonization or restoration	May occur naturally	Difficult once seagrass is lost

which predict that the range of wave velocities, over which the SSL feedback induces bistability, is largest in shallow areas and decreases with increasing depth [Fig. 5c of van der Heide et al. (2007)].

ii. *Eutrophication*: The SSL feedback will have greater influence on seagrass presence/absence in non-eutrophic systems, because the modification of light availability at the seagrass canopy due to changes in suspended sediment concentration will only be substantial if TSS is the dominant contributor to light attenuation through the water column (Fig. 2a). While the presence of substances other than suspended sediment in the water column, such as CDOM and Chl *a*, may reduce the light reaching the seagrass to a critical regime close to their MLR, the presence of these substances also dampens the improvement in water clarity that seagrass presence provides over bare areas.

iii. *Meadow size/density*: Meadows of greater size (height and length) and density have the potential to more significantly reduce turbidity and hence increase the light available to seagrass, due to their greater impact on the local hydrodynamics. However, seagrass meadows of low height, low length, and/or low frontal area per unit volume may actually enhance turbidity due to the penetration of the shear layer to the seabed (Fig. 4b), larger areal fraction of the meadow occupied by the erosive zone (Fig. 5), and larger absolute size of the erosive zone (indicated by L_D in Eqs. 3 and 4), respectively. This transition between enhancement of turbidity at low meadow size/density, and reduction of turbidity at high meadow size/density, is illustrated in Fig. 6a. The impact of meadow size/density on light availability is also partially attributed to the stabilization of bed sediments by belowground biomass (Fig. 6b), although the importance of this mechanism has been somewhat overlooked in the literature (Christianen et al. 2013).

iv. *Sediment size*: Seagrass presence will only influence the resuspension of particles within a particular size range (Fig. 6c). Sediment particles that are outside this size range will either be resuspended or remain in the seabed regardless of whether seagrass is present or absent, because seagrass presence does not alter τ_b and/or τ_c sufficiently to alter these particles' erodability. Additionally, as seen in the case study, the specific light attenuation coefficient of suspended sediment will also determine whether the SSL feedback is substantial.

v. *Water velocity*: The near-bed current velocity u_b within the seagrass meadow is reduced from its value upstream of the meadow $u_{b,0}$. Absolute attenuation $u_{b,0} - u_b$ of the current velocity, due to seagrass presence, increases with the magnitude of the upstream current $u_{b,0}$ (Eq. 3); this indicates that seagrass has a greater impact on local hydrodynamics (and hence suspended sediment concentrations) under high flow conditions. However, an effect not shown in Eq. 3 is that the relative attenuation $(u_{b,0} - u_b)/u_{b,0}$ of the current velocity due to seagrass presence, decreases with increasing velocity (Fig. 6d) because the bending angle of seagrass blades (relative to the horizontal) decreases with increasing current velocity (Fonseca et al. 1982; Abdelrhman 2007). The bending of seagrass leaves then decreases the frontal area so that the canopy is less effective at flow attenuation (Eqs. 3–5). This reduction in relative attenuation with increasing velocity is expected to occur in both current- (Gambi et al. 1990; Lacy and Wyllie-Echeverria 2011) and wave-dominated flows (Bradley and Houser 2009). Most of the field studies that directly show the impact of seagrass presence on TSS concentrations are in wave-dominated systems (Ward et al. 1984; Moore 2004; Hansen and Reidenbach 2013). Although sediment resuspension may be more greatly reduced in current-dominated environments than in

Table 3. Two- and three-dimensional ecosystem model suites that have included mechanisms for the impact of suspended sediment on seagrass presence, the impact of seagrass presence on sediment dynamics, or both.

	Is the SSL feedback included in the model?	
Ecosystem model suite	Suspended sediment affects seagrass	Seagrass affects suspended sediment
Chesapeake Bay Environmental Modelling Package (Cerco and Moore 2001; Cerco et al. 2013)	✓	✓
Model for Applications at Regional Scale (Kombiadou et al. 2014)	✓	✓
Coupled finite element and fuzzy rule-based model (Milbradt and Schonert 2008)	✓	✓
CSIRO Environmental Modelling Suite (Baird et al. 2014, 2016)	✓	
Environmental Fluid Dynamics Code (Estes et al. 2015)	✓	
Regional Ocean Modeling System (del Barrio et al. 2014)	✓	
Delft3D (Dijkstra 2012)		✓

wave-dominated environments (Fig. 6d) (Koch and Gust 1999; Madsen et al. 2001), this difference is difficult to quantify and hence we do not distinguish between wave- and current-dominated regimes in Table 2.

Modelling the seagrass-sediment-light feedback

Mathematical models are an important tool to support environmental decision-making, especially in ecosystems whose degradation and recovery trajectories may diverge due to the presence of feedback processes (Suding et al. 2004). Here, we review the significant progress in modelling of the SSL feedback that has occurred mostly over the past decade (de Boer 2007).

Statistical models

Feedbacks in seagrass ecosystems have been investigated statistically using Bayesian networks and structural equation models. A Bayesian network was used to identify the regions in Moreton Bay, Australia that potentially express bistability in seagrass presence/absence due to environmental feedbacks (Maxwell et al. 2015). The results of this model found that sediment resuspension increased with water movement, and reduced with increasing seagrass biomass. A structural equation model was applied to 83 sites across Western Europe, and its results supported the presence of a stabilizing feedback between high light availability and high seagrass density (van der Heide et al. 2011).

Deterministic models

When the mechanistic relationships between important environmental variables are sufficiently well known, these relationships can be combined into a deterministic model that predicts the steady state or temporal changes in the state of an ecosystem (Scheffer 2009). Even if these deterministic models do not explicitly include horizontal landscape variation, they can still provide crucial insights into ecosystem dynamics (Scheffer et al. 2001; Mumby et al.

2007). For example, the first non-spatial deterministic model of the SSL feedback demonstrated that bistability arising from this feedback is possible for a wide range of environmental conditions (van der Heide et al. 2007). A more comprehensive deterministic model (Carr et al. 2010) has since been used to predict the depths at which the SSL feedback induces bistability (Carr et al. 2012a) and the response of seagrass at these depths to temperature disturbance events associated with climate change (Carr et al. 2012b). Most recently, a deterministic model that includes spatial variation in seagrass meadow structure (and is not location-specific) has shown how seagrass patches may influence the suspended sediment and light conditions in the larger landscape (Carr et al. 2015).

Two- and three-dimensional ecosystem-scale models

Two- and three-dimensional ecosystem model suites have included mechanisms for the impact of suspended sediment on seagrass presence, the impact of seagrass presence on suspended sediment, and both (Table 3). Ecosystem models require formulations for both of these mechanisms to complete the SSL feedback loop and assess the spatially explicit impact of this feedback on the wider aquatic ecosystem dynamics.

The SSL feedback has been parameterized in the Chesapeake Bay Environmental Modelling Package (CBEMP) (Cerco and Cole 1993) in two ways. First, seagrass presence induces a reduction in fixed solids concentration via settling at a rate proportional to seagrass biomass, and this increases the light available at the canopy because light attenuation depends on the fixed solids concentration according to Beer's law (Eq. 1) (Cerco and Moore 2001). Second, bed shear stress declines exponentially with seagrass biomass, which in turn affects the erosion rate via the standard linear formulation (Eq. 6) (Cerco et al. 2013).

The SSL feedback has been considered more comprehensively in a modification (Kombiadou et al. 2014) of the Model for Applications at Regional Scale (MARS) (Lazure and

Dumas 2008). In the model of Kombiadou et al. (2014), seagrass presence directly modifies water momentum, turbulent kinetic energy production and dissipation, vertical water velocity profile, sediment settling rate and sediment erosion rate; and light availability at the seagrass canopy is modified by the suspended sediment concentration due to Beer's law.

One novel approach that has been used to consider the SSL feedback is the coupling of a partial differential equation model for the hydrodynamics and morphodynamics to a fuzzy logic model for the ecological processes (Milbradt and Schonert 2008). The model includes a negative, fuzzy, effect of turbidity on seagrass density, and conversely a deterministic friction force acting on water movement that depends on seagrass density and blade bending angle. This coupling of different modelling techniques reflects the greater uncertainty that is present in ecological processes compared with physical processes (Evans et al. 2013).

Grid sizes of ecosystem model suites are typically much larger than the length scale over which erosive zones form due to seagrass presence ($\mathcal{O}(0.1-1$ m), Luhar et al. 2008). For example, the grid sizes of the models described above that include the SSL feedback were: variable and equal to the horizontal distance between the shore and 2 m water depth (Cerco and Moore 2001), not reported (Milbradt and Schonert 2008), or constant, $\mathcal{O}(100-1000$ m) (Cerco et al. 2013; Kombiadou et al. 2014). Therefore within each grid cell, the bathymetry can vary significantly from shallow intertidal or subtidal zones to deeper waters where either the SSL feedback is no longer relevant or seagrass colonization is not possible due to low light availability (Duarte 1991).

Ecosystem models that incorporate the SSL feedback can be used to identify if this feedback has the capacity to generate alternative states in a given location, which is potentially valuable information for environmental managers (Thrush et al. 2009). Currently, these ecosystem models can approximate the stabilizing effect of a large seagrass meadow on local sediments, but are unable to predict the formation of erosive zones. Predictions of localized seagrass biomass and sediment dynamics at length scales of $\mathcal{O}(\leq 100$ m) using these model suites would require specification of sub-grid scale models of seagrass-sediment interactions (Cerco and Moore 2001). These smaller length scales must be considered if accurate predictions of the spatial patterning of seagrass distributions are sought (Kendrick et al. 2008). However, parameterization of the SSL feedback at these smaller scales requires a greater fundamental understanding of the relevant processes (Cerco et al. 2013) matched with fine-scale data that captures the local heterogeneity and dynamic conditions of seagrass-sediment interactions; this data is unlikely to be available.

Conclusions

For environmental management, an initial evaluation of the importance of the seagrass-sediment-light (SSL) feedback can be made by comparing the characteristics of the ecosystem being studied to Table 2. This table can help managers to identify (1) healthy seagrass ecosystems which seem to be resistant to environmental stressors but may also be difficult to recover when lost, and (2) whether the recovery of degraded seagrass ecosystems may be impeded by the SSL feedback. Mathematical models provide powerful tools that can investigate the strength of feedbacks in seagrass ecosystems, but the implementation of the SSL feedback in ecosystem model suites is not yet widespread. Future research focused on identification of the quantitative relationships that control the SSL feedback will improve both our understanding of this coupled physical-ecological process, and the predictive power of mathematical models used to support decision-making for seagrass ecosystems.

References

Abdelrhman, M. A. 2003. Effect of eelgrass *Zostera marina* canopies on flow and transport. Mar. Ecol. Prog. Ser. **248**: 67–83. doi:10.3354/meps248067

Abdelrhman, M. A. 2007. Modeling coupling between eelgrass *Zostera marina* and water flow. Mar. Ecol. Prog. Ser. **338**: 81–96. doi:10.3354/meps338081

Ackerman, J. D. 2002. Diffusivity in a marine macrophyte canopy: Implications for submarine pollination and dispersal. Am. J. Bot. **89**: 1119–1127. doi:10.3732/ajb.89.7.1119

Ackerman, J. D., and A. Okubo. 1993. Reduced mixing in a marine macrophyte canopy. Funct. Ecol. **7**: 305–309. doi:10.2307/2390209

Agawin, N. S. R., and C. M. Duarte. 2002. Evidence of direct particle trapping by a tropical seagrass meadow. Estuaries **25**: 1205–1209. doi:10.1007/BF02692217

Amos, C. L., and others. 2004. The stability of tidal flats in Venice Lagoon—the results of in-situ measurements using two benthic, annular flumes. J. Mar. Syst. **51**: 211–241. doi:10.1016/j.jmarsys.2004.05.013

Armengol, J., and others. 2003. Sau reservoir's light climate: Relationships between Secchi depth and light extinction coefficient. Limnetica **22**: 195–210.

Baird, M. E., and others. 2014. CSIRO Environmental Modelling Suite: Scientific Description of the Optical, Carbon Chemistry and Biogeochemical Models Parameterised for the Great Barrier Reef. Commonwealth Scientific and Industrial Research Organisation Marine and Atmospheric Research, Hobart, Australia. Available from http://www.emg.cmar.csiro.au/www/en/emg/software/EMS/biogeochemisty.html

Baird, M. E., and others. 2016. A biophysical representation of seagrass growth for application in a complex shallow-water biogeochemical model. Ecol. Model. **325**: 13–27. doi:10.1016/j.ecolmodel.2015.12.011

Baker, E. T., and J. W. Lavelle. 1984. The effect of particle size on the light attenuation coefficient of natural

suspensions. J. Geophys. Res. **89**: 8197–8203. doi:10.1029/JC089iC05p08197

Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier, and B. R. Silliman. 2011. The value of estuarine and coastal ecosystem services. Ecol. Monogr. **81**: 169–193. doi:10.1890/10-1510.1

Bertelli, C. M., and R. K. F. Unsworth. 2014. Protecting the hand that feeds us: Seagrass (*Zostera marina*) serves as commercial juvenile fish habitat. Mar. Pollut. Bull. **83**: 425–429. doi:10.1016/j.marpolbul.2013.08.011

Blandon, A., and P. S. E. zu Ermgassen. 2014. Quantitative estimate of commercial fish enhancement by seagrass habitat in southern Australia. Estuar. Coast. Shelf Sci. **141**: 1–8. doi:10.1016/j.ecss.2014.01.009

Borum, J., O. Pedersen, T. M. Greve, T. A. Frankovich, J. C. Zieman, J. W. Fourqurean, and C. J. Madden. 2005. The potential role of plant oxygen and sulphide dynamics in die-off events of the tropical seagrass, *Thalassia testudinum*. J. Ecol. **93**: 148–158. doi:10.1111/j.1365-2745.2004.00943.x

Borum, J., R. K. Gruber, and W. M. Kemp. 2013. Seagrass and related submersed vascular plants, p. 111–127. *In* J. W. Day, B. C. Crump, W. M. Kemp and A. Yáñez-Arancibia [eds.], Estuarine ecology, 2nd ed. Wiley.

Bos, A. R., T. J. Bouma, G. L. J. de Kort, and M. M. van Katwijk. 2007. Ecosystem engineering by annual intertidal seagrass beds: Sediment accretion and modification. Estuar. Coast. Shelf Sci. **74**: 344–348. doi:10.1016/j.ecss.2007.04.006

Bouma, T. J., M. B. de Vries, E. Low, G. Peralta, I. C. Tánczos, J. van de Koppel, and P. M. J. Herman. 2005. Trade-offs related to ecosystem engineering: A case study on stiffness of emerging macrophytes. Ecology **86**: 2187–2199. doi:10.1890/04-1588

Bouma, T. J., L. A. van Duren, S. Temmerman, T. Claverie, A. Blanco-Garcia, T. Ysebaert, and P. M. J. Herman. 2007. Spatial flow and sedimentation patterns within patches of epibenthic structures: Combining field, flume and modelling experiments. Cont. Shelf Res. **27**: 1020–1045. doi:10.1016/j.csr.2005.12.019

Bouma, T. J., and others. 2009. Effects of shoot stiffness, shoot size and current velocity on scouring sediment from around seedlings and propagules. Mar. Ecol. Prog. Ser. **388**: 293–297. doi:10.3354/meps08130

Bradley, K., and C. Houser. 2009. Relative velocity of seagrass blades: Implications for wave attenuation in low-energy environments. J. Geophys. Res. **114**: F01004. doi:10.1029/2007JF000951

Burkholder, J. M., D. A. Tomasko, and B. W. Touchette. 2007. Seagrasses and eutrophication. J. Exp. Mar. Biol. Ecol. **350**: 46–72. doi:10.1016/j.jembe.2007.06.024

Carr, J., P. D'Odorico, K. McGlathery, and P. Wiberg. 2010. Stability and bistability of seagrass ecosystems in shallow coastal lagoons: Role of feedbacks with sediment resus-

pension and light attenuation. J. Geophys. Res. **115**: G03011. doi:10.1029/2009jg001103

Carr, J. A., P. D'Odorico, K. J. McGlathery, and P. L. Wiberg. 2012a. Stability and resilience of seagrass meadows to seasonal and interannual dynamics and environmental stress. J. Geophys. Res. **117**: G01007. doi:10.1029/2011jg001744

Carr, J. A., P. D'Odorico, K. J. McGlathery, and P. L. Wiberg. 2012b. Modeling the effects of climate change on eelgrass stability and resilience: Future scenarios and leading indicators of collapse. Mar. Ecol. Prog. Ser. **448**: 289–301. doi:10.3354/meps09556

Carr, J. A., P. D'Odorico, K. J. McGlathery, and P. L. Wiberg. 2015. Spatially explicit feedbacks between seagrass meadow structure, sediment and light: Habitat suitability for seagrass growth. Adv. Water Resour. doi:10.1016/j.advwatres.2015.09.001

Cayabyab, N. M., and S. Enríquez. 2007. Leaf photoacclimatory responses of the tropical seagrass *Thalassia testudinum* under mesocosm conditions: A mechanistic scaling-up study. New Phytol. **176**: 108–123. doi:10.1111/j.1469-8137.2007.02147.x

Cerco, C. F., and T. Cole. 1993. Three-dimensional eutrophication model of Chesapeake Bay. J. Environ. Eng. **119**: 1006–1025. doi:10.1061/(ASCE)0733-9372(1993)119:6(1006)

Cerco, C. F., and K. Moore. 2001. System-wide submerged aquatic vegetation model for Chesapeake Bay. Estuaries **24**: 522–534. doi:10.2307/1353254

Cerco, C. F., S.-C. Kim, and M. R. Noel. 2013. Management modeling of suspended solids in the Chesapeake Bay, USA. Estuar. Coast. Shelf Sci. **116**: 87–98. doi:10.1016/j.ecss.2012.07.009

Chen, S.-N., L. P. Sanford, E. W. Koch, F. Shi, and E. W. North. 2007. A nearshore model to investigate the effects of seagrass bed geometry on wave attenuation and suspended sediment transport. Estuaries Coast. **30**: 296–310. doi:10.1007/BF02700172

Chen, S.-C., H.-C. Chan, and Y.-H. Li. 2012. Observations on flow and scour around submerged flexible vegetation. Adv. Water Resour. **43**: 28–37. doi:10.1016/j.advwatres.2012.03.017

Christianen, M. J. A., J. van Belzen, P. M. J. Herman, M. M. van Katwijk, L. P. M. Lamers, P. J. M. van Leent, and T. J. Bouma. 2013. Low-canopy seagrass beds still provide important coastal protection services. PLoS One **8**: e62413. doi:10.1371/journal.pone.0062413

Collier, C. J., M. Waycott, and A. G. Ospina. 2012. Responses of four Indo-West Pacific seagrass species to shading. Mar. Pollut. Bull. **65**: 342–354. doi:10.1016/j.marpolbul.2011.06.017

Cullen-Unsworth, L. C., L. M. Nordlund, J. Paddock, S. Baker, L. J. McKenzie, and R. J. F. Unsworth. 2014. Seagrass meadows globally as a coupled social-ecological system: Implications for human wellbeing. Mar. Pollut. Bull. **83**: 387–397. doi:10.1016/j.marpolbul.2013.06.001

Dade, W. B., A. R. M. Nowell, and P. A. Jumars. 1992. Predicting erosion resistance of muds. Mar. Geol. **105**: 285–297. doi:10.1016/0025-3227(92)90194-M

de Boer, W. F. 2007. Seagrass-sediment interactions, positive feedbacks and critical thresholds for occurrence: A review. Hydrobiologia **591**: 5–24. doi:10.1007/s10750-007-0780-9

De Falco, G., S. Ferrari, G. Cancemi, and M. Baroli. 2000. Relationship between sediment distribution and *Posidonia oceanica* seagrass. Geo Mar. Lett. **20**: 50–57. doi:10.1007/s003670000030

del Barrio, P., N. K. Ganju, A. L. Aretxabaleta, M. Hayn, A. García, and R. W. Howard. 2014. Modeling future scenarios of light attenuation and potential seagrass success in a eutrophic estuary. Estuar. Coast. Shelf Sci. **149**: 13–23. doi:10.1016/j.ecss.2014.07.005

den Hartog, C., and P. J. G. Polderman. 1975. Changes in the seagrass populations of the Dutch Waddenzee. Aquat. Bot. **1**: 141–147. doi:10.1016/0304-3770(75)90019-4

Dennison, W. C. 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. Aquat. Bot. **27**: 15–26. doi:10.1016/0304-3770(87)90083-0

Dennison, W. C., and others. 1993. Assessing water quality with submersed aquatic vegetation. BioScience **43**: 86–94. doi:10.2307/1311969

Dijkstra, J. T. 2012. Macrophytes in estuarine gradients: Flow through flexible vegetation. Ph.D. thesis. Delft Univ. of Technology.

Duarte, C. M. 1991. Seagrass depth limits. Aquat. Bot. **40**: 363–377. doi:10.1016/0304-3770(91)90081-F

Estes, M. G., and others. 2015. A modeling system to assess land cover land use change effects on SAV habitat in the Mobile Bay estuary. J. Am. Water Resour. Assoc. **51**: 513–536. doi:10.1111/jawr.12263

Evans, M. R., and others. 2013. Predictive systems ecology. Proc. R. Soc. B **280**: 20131472. doi:10.1098/rspb.2013.1452

Follett, E. M., and H. M. Nepf. 2012. Sediment patterns near a model patch of reedy emergent vegetation. Geomorphology **179**: 141–151. doi:10.1016/j.geomorph.2012.08.006

Fonseca, M. S., J. S. Fisher, J. C. Zieman, and G. W. Thayer. 1982. Influence of the seagrass, *Zostera marina* L., on current flow. Estuar. Coast. Shelf Sci. **15**: 351–364. doi:10.1016/0272-7714(82)90046-4

Fonseca, M. S., and J. A. Cahalan. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. Estuar. Coast. Shelf Sci. **35**: 565–576. doi:10.1016/S0272-7714(05)80039-3

Fonseca, M. S., and M. A. R. Koehl. 2006. Flow in seagrass canopies: The influence of patch width. Estuar. Coast. Shelf Sci. **67**: 1–9. doi:10.1016/j.ecss.2005.09.018

Fourqurean, J. W., and others. 2012. Seagrass ecosystems as a globally significant carbon stock. Nat. Geosci. **5**: 505–509. doi:10.1038/ngeo1477

Gacia, E., T. C. Granata, and C. M. Duarte. 1999. An approach to measurement of particle flux and sediment retention within seagrass (*Posidonia oceanica*) meadows. Aquat. Bot. **65**: 255–268. doi:10.1016/S0304-3770(99)00044-3

Gacia, E., and C. M. Duarte. 2001 Sediment retention by a Mediterranean *Posidonia oceanica* meadow: The balance between deposition and resuspension. Estuar. Coast. Shelf Sci. **52**: 505–514. doi:10.1006/ecss.2000.0753

Gallegos, C. L. 1994. Refining habitat requirements of submersed aquatic vegetation: Role of optical models. Estuaries **17**: 187–199. doi:10.2307/1352568

Gallegos, C., and K. A. Moore. 2000. Factors contributing to water-column light attenuation, p. 16–27. *In* R. A. Batiuk and others [eds.], Chesapeake Bay submerged aquatic vegetation water quality and habitat-based requirements and restoration targets: A second technical synthesis. U.S. Environmental Protection Agency, Chesapeake Bay Program, Annapolis, Maryland.

Gambi, M. C., A. R. M. Nowell, and P. A. Jumars. 1990. Flume observations on flow dynamics in *Zostera marina* (eelgrass) beds. Mar. Ecol. Prog. Ser. **61**: 159–169. doi:10.3354/meps061159

Ganthy, F., L. Soissons, P.-G. Sauriau, R. Verney, and A. Sottolichio. 2015. Effects of short flexible seagrass *Zostera noltei* on flow, erosion and deposition processes determined using flume experiments. Sedimentology **62**: 997–1023. doi:10.1111/sed.12170

Ghisalberti, M., and H. M. Nepf. 2002. Mixing layers and coherent structures in vegetated aquatic flows. J. Geophys. Res. **107**: 3. doi:10.1029/2001JC000871

Ghisalberti, M., and H. Nepf. 2005. Mass transport in vegetated shear flows. Environ. Fluid Mech. **5**: 527–551. doi:10.1007/s10652-005-0419-1

Ghisalberti, M., and H. Nepf. 2009. Shallow flows over a permeable medium: The hydrodynamics of submerged aquatic canopies. Transport Porous Med. **78**: 309–326. doi:10.1007/s11242-008-9305-x

Ghisalberti, M., and T. Schlosser. 2013. Vortex generation in oscillatory canopy flow. J. Geophys. Res. Oceans **118**: 1534–1542. doi:10.1002/jgrc.20073

Giesen, W.B.J.T., M. M. van Katwijk, and C. den Hartog. 1990. Eelgrass condition and turbidity in the Dutch Wadden Sea. Aquat. Bot. **37**: 71–85. doi:10.1016/0304-3770(90)90065-S

Grabowski, R. C., I. G. Droppo, and G. Wharton. 2011. Erodibility of cohesive sediment: The importance of sediment properties. Earth Sci. Rev. **105**: 101–120. doi:10.1016/j.earscirev.2011.01.008

Granata, T. C., T. Serra, J. Colomer, X. Casamitjana, C. M. Duarte, and E. Gacia. 2001. Flow and particle distributions in a nearshore seagrass meadow before and after a storm. Mar. Ecol. Prog. Ser. **218**: 95–106. doi:10.3354/meps218095

Gruber, R. K., and W. M. Kemp. 2010. Feedback effects in a coastal canopy-forming submersed plant bed. Limnol. Oceanogr. **55**: 2285–2298. doi:10.4319/lo.2010.55.6.2285

Gruber, R. K., D. C. Hinkle, and W. M. Kemp. 2011. Spatial patterns in water quality associated with submersed plant beds. Estuaries Coast. **34**: 961–972. doi:10.1007/s12237-010-9368-0

Gutiérrez, J. L., and others. 2011. Physical ecosystem engineers and the functioning of estuaries and coasts, p. 53–81. *In* E. Wolanski and D. McLusky [eds.], Treatise on estuarine and coastal science. Academic Press.

Hansen, J. C. R., and M. A. Reidenbach. 2012. Wave and tidally driven flows in eelgrass beds and their effect on sediment suspension. Mar. Ecol. Prog. Ser. **448**: 271–287. doi:10.3354/meps09225

Hansen, J. C. R., and M. A. Reidenbach. 2013. Seasonal growth and senescence of a *Zostera marina* seagrass meadow alters wave-dominated flow and sediment suspension within a coastal bay. Estuaries Coast. **36**: 1099–1114. doi:10.1007/s12237-013-9620-5

Hedley, J., and S. Enríquez. 2010. Optical properties of canopies of the tropical seagrass *Thalassia testudinum* estimated by a three-dimensional radiative transfer model. Limnol. Oceanogr. **55**: 1537–1550. doi:10.4319/lo.2010.55.4.1537

Hedley, J. D., K. McMahon, and P. Fearns. 2014. Seagrass canopy photosynthetic response is a function of canopy density and light environment: A model for *Amphibolis griffithii*. PLoS One **9**: e111454. doi:10.1371/journal.pone.0111454

Hendriks, I. E., T. Sintes, T. J. Bouma, and C. M. Duarte. 2008. Experimental assessment and modelling evaluation of the effects of the seagrass *Posidonia oceanica* on flow and particle trapping. Mar. Ecol. Prog. Ser. **356**: 163–173. doi:10.3354/meps07316

Houwing, E.-J. 1999. Determination of the critical erosion threshold of cohesive sediments on intertidal mudflats along the Dutch Wadden Sea coast. Estuar. Coast. Shelf Sci. **49**: 545–555. doi:10.1006/ecss.1999.0518

Hu, Z., T. Suzuki, T. Zitman, W. Uittewaal, and M. Stive. 2014. Laboratory study on wave dissipation by vegetation in combined current-wave flow. Coast. Eng. **88**: 131–142. doi:10.1016/j.coastaleng.2014.02.009

Human, L. R. D., G. C. Snow, J. B. Adams, G. C. Bate, and S.-C. Yang. 2015. The role of submerged macrophytes and macroalgae in nutrient cycling: A budget approach. Estuar. Coast. Shelf Sci. **154**: 169–178. doi:10.1016/j.ecss.2015.01.001

Jassby, A. D., and T. Platt. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. **21**: 540–547. doi:10.4319/lo.1976.21.4.0540

Kelly (Letcher), R. A., and others. 2013. Selecting among five common modelling approaches for integrated environmental assessment and management. Environ. Modell. Softw. **47**: 159–181. doi:10.1016/j.envsoft.2013.05.005

Kendrick, G. A., K. W. Holmes, and K. P. van Niel. 2008. Multi-scale spatial patterns of three seagrass species with different growth dynamics. Ecography **31**: 191–200. doi:10.1111/j.0906-7590.2008.5252.x

Kirk, J. T. O. 1985. Effects of suspensoids (turbidity) on penetration of solar radiation in aquatic ecosystems. Hydrobiologia **125**: 195–208. doi:10.1007/BF00045935

Koch, E. W. 1999. Sediment resuspension in a shallow *Thalassia testudinum* banks ex König bed. Aquat. Bot. **65**: 269–280. doi:10.1016/s0304-3770(99)00045-5

Koch, E. W., and G. Gust. 1999. Water flow in tide- and wave-dominated beds of the seagrass *Thalassia testudinum*. Mar. Ecol. Prog. Ser. **184**: 63–72. doi:10.3354/meps184063

Koch, E. W., L. P. Sandford, S. N. Chen, D. J. Shafer, and J. M. Smith. 2006. Waves in seagrass systems: Review and technical recommendations. US Army Corps of Engineers, Washington DC.

Kombiadou, K., F. Ganthy, R. Verney, M. Plus, and A. Sottolichio. 2014. Modelling the effects of *Zostera noltei* meadows on sediment dynamics: Application to the Arcachon lagoon. Ocean Dyn. **64**: 1499–1516. doi:10.1007/s10236-014-0754-1

Lacy, J. R., and S. Wyllie-Echeverria. 2011. The influence of current speed and vegetation density on flow structure in two macrotidal eelgrass canopies. Limnol. Oceanogr. Fluids Environ. **1**: 38–55. doi:10.1215/21573698-1152489

Lawson, S. E. 2004. Sediment suspension as a control on light availability in a coastal lagoon. Masters thesis. Univ. of Virginia.

Lawson, S. E., P. L. Wiberg, K. J. McGlathery, and D. C. Fugate. 2007. Wind-driven sediment suspension controls light availability in a shallow coastal lagoon. Estuaries Coast. **30**: 102–112. doi:10.1007/BF02782971

Lawson, S. E., K. J. McGlathery, and P. L. Wiberg. 2012. Enhancement of sediment suspension and nutrient flux by benthic macrophytes at low biomass. Mar. Ecol. Prog. Ser. **448**: 259–270. doi:10.3354/meps09579

Lazure, P., and F. Dumas. 2008. An external-internal model coupling for a 3D hydrodynamical model for applications at regional scale (MARS). Adv. Water Resour. **31**: 233–250. doi:10.1016/j.advwatres.2007.06.010

Le Hir, P., Y. Monbet, and F. Orvain. 2007. Sediment erodability in sediment transport modelling: Can we account for biota effects? Cont. Shelf Res. **27**: 1116–1142. doi:10.1016/j.csr.2005.11.016

Lee, K.-S., S. R. Park, and Y. K. Kim. 2007. Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses: A review. J. Exp. Mar. Biol. Ecol. **350**: 144–175. doi:10.1016/j.jembe.2007.06.016

Lee Long, W. J., J. E. Mellors, and R. G. Coles. 1993. Seagrasses between Cape York and Hervey Bay, Queensland,

Australia. Aust. J. Mar. Freshw. Res. **44**: 19–31. doi: 10.1071/MF9930019

Li, C. W., and K. Yan. 2007. Numerical investigation of wave-current-vegetation interaction. J. Hydraul. Eng. **133**: 794–803. doi:10.1061/(ASCE)0733-9429(2007)133:7(794)

Lowe, R. J., J. R. Koseff, and S. G. Monismith. 2005. Oscillatory flow through submerged canopies: 1. Velocity structure. J. Geophys. Res. **110**: C10016. doi:10.1029/2004JC002788

Luhar, M., J. Rominger, and H. Nepf. 2008. Interaction between flow, transport and vegetation spatial structure. Environ. Fluid Mech. **8**: 423–439. doi:10.1007/s10652-008-9080-9

Luhar, M., S. Coutu, E. Infantes, S. Fox, and H. Nepf. 2010. Wave-induced velocities inside a model seagrass bed. J. Geophys. Res. **115**: C12005. doi:10.1029/2010JC006345

Madsen, J. D., P. A. Chambers, W. F. James, E. W. Koch, and D. F. Westlake. 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. Hydrobiologia **444**: 71–84. doi:10.1023/A:1017520800568

Manca, E., I. Cáceres, J. M. Alsina, V. Stratigaki, I. Townend, and C. L. Amos. 2012. Wave energy and wave-induced flow reduction by full-scale model *Posidonia oceanica* seagrass. Cont. Shelf Res. **50–51**: 100–116. doi:10.1016/j.csr.2012.10.008

Marbà, N., and others. 2015. Impact of seagrass loss and subsequent revegetation on carbon sequestration and stocks. J. Ecol. **103**: 296–302. doi:10.1111/1365-2745.12370

Maxwell, P. S., K. A. Pitt, D. D. Burfeind, A. D. Olds, R. C. Babcock, and R. M. Connolly. 2014. Phenotypic plasticity promotes persistence following severe events: Physiological and morphological responses of seagrass to flooding. J. Ecol. **102**: 54–64. doi:10.1111/1365-2745.12167

Maxwell, P. S., K. A. Pitt, A. D. Olds, D. Rissik, and R. M. Connolly. 2015. Identifying habitats at risk: Simple models can reveal complex ecosystem dynamics. Ecol. Appl. **25**: 573–587. doi:10.1890/14-0395.1

McGlathery, K. J., K. Sundbäck, and I. C. Anderson. 2007. Eutrophication in shallow coastal bays and lagoons: The role of plants in the coastal filter. Mar. Ecol. Prog. Ser. **348**: 1–18. doi:10.3354/meps07132

McGlathery, K. J., L. K. Reynolds, L. W. Cole, R. K. Orth, S. R. Marion, and A. Schwarzschild. 2012. Recovery trajectories during state change from bare sediment to eelgrass dominance. Mar. Ecol. Prog. Ser. **448**: 209–221. doi: 10.3354/meps09574

McKone, K. L. 2009. Light available to the seagrass *Zostera marina* when exposed to currents and waves. Masters thesis. Univ. of Maryland.

Milbradt, P., and T. Schonert. 2008. A holistic approach and object-oriented framework for eco-hydraulic simulation in coastal engineering. J. Hydroinf. **10**: 201–214. doi: 10.2166/hydro.2008.029

Moore, K. A. 2004. Influence of seagrasses on water quality in shallow regions of the lower Chesapeake Bay. J. Coastal Res. **45**: 162–178. doi:10.2112/SI45-162.1

Mumby, P. J., A. Hastings, and H. J. Edwards. 2007. Thresholds and the resilience of Caribbean coral reefs. Nature **450**: 98–101. doi:10.1038/nature06252

Nepf, H. M. 2012. Flow and transport in regions with aquatic vegetation. Annu. Rev. Fluid Mech. **44**: 123–142. doi: 10.1146/annurev-fluid-120710-101048

Nepf, H. M., and E. R. Vivoni. 2000. Flow structure in depth-limited, vegetated flow. J. Geophys. Res. **105**: 28547–28557. doi:10.1029/2000JC900145

Nepf, H., M. Ghisalberti, B. White, and E. Murphy. 2007. Retention time and dispersion associated with submerged aquatic canopies. Water Resour. Res. **43**: W04422. doi:10.1029/2006WR005362

Nepf, H., and M. Ghisalberti. 2008. Flow and transport in channels with submerged vegetation. Acta Geophys. **56**: 753–777. doi:10.2478/s11600-008-0017-y

Nyström, N., and others. 2012. Confronting feedbacks of degraded marine ecosystems. Ecosystems **15**: 695–710. doi:10.1007/s10021-012-9530-6

Odd, N. V. M. 1988. Mathematical modelling of mud transport in estuaries, p. 503–531. *In* J. Dronkers and W. van Leussen [eds.], Physical processes in estuaries. Springer-Verlag.

Olivé, I., J. J. Vergara, and J. L. Pérez-Lloréns. 2013. Photosynthetic and morphological photoacclimation of the seagrass *Cymodocea nodosa* to season, depth and leaf position. Mar. Biol. **160**: 285–297. doi:10.1007/s00227-012-2087-2

Orth, R. J., and others. 2006. A global crisis for seagrass ecosystems. BioScience **56**: 987–996. doi:10.1641/0006-3568(2006)56[987:agcfse]2.0.co;2

Orth, R. J., and K. J. McGlathery. 2012. Eelgrass recovery in the coastal bays of the Virginia Coast Reserve, USA. Mar. Ecol. Prog. Ser. **448**: 173–176. doi:10.3354/meps09596

Ortiz, A. C., A. Ashton, and H. Nepf. 2013. Mean and turbulent velocity fields near rigid and flexible plants and the implications for deposition. J. Geophys. Res. Earth Surf. **118**: 2585–2599. doi:10.1002/2013JF002858

Paul, M., T. J. Bouma, and C. L. Amos. 2012. Wave attenuation by submerged vegetation: Combining the effect of organism traits and tidal current. Mar. Ecol. Prog. Ser. **444**: 31–41. doi:10.3354/meps09489

Pedersen, O., T. Binzer, and J. Borum. 2004. Sulphide intrusion in eelgrass (*Zostera marina* L.). Plant Cell Environ. **27**: 595–602. doi:10.1111/j.1365-3040.2004.01173.x

Pedersen, T. M., C. L. Gallegos, and S. L. Nielsen. 2012. Influence of near-bottom re-suspended sediment on benthic light availability. Estuar. Coast. Shelf Sci. **106**: 93–101. doi:10.1016/j.ecss.2012.04.027

Peterson, C. H., R. A. Luettich, F. Micheli, and G. A. Skilleter. 2004. Attenuation of water flow inside seagrass

canopies of differing structure. Mar. Ecol. Prog. Ser. **268**: 81–92. doi:10.3354/meps268081

Poorter, H., N. P. R. Anten, and L. F. M. Marcelis. 2013. Physiological mechanisms in plant growth models: Do we need a supra-cellular systems biology approach? Plant Cell Environ. **36**: 1673–1690. doi:10.1111/pce.12123

Pujol, D., X. Casamitjana, T. Serra, and J. Colomer. 2013. Canopy-scale turbulence under oscillatory flow. Cont. Shelf Res. **66**: 9–18. doi:10.1016/j.csr.2013.06.012

Ralph, P. J., M. J. Durako, S. Enríquez, C. J. Collier, and M. A. Doblin. 2007. Impact of light limitation on seagrasses. J. Exp. Mar. Biol. Ecol. **350**: 178–193. doi:10.1016/j.jembe.2007.06.017

Roberts, J. S., R. Jepsen, D. Gotthard, and W. Lick. 1998. Effects of particle size and bulk density on erosion of quartz particles. J. Hydraul. Eng. **124**: 1261–1267. doi:10.1061/(ASCE)0733-9429(1998)124:12(1261)

Ros, À., J. Colomer, T. Serra, D. Pujol, M. Soler, and X. Casamitjana. 2014. Experimental observations on sediment resuspension within submerged model canopies under oscillatory flow. Cont. Shelf Res. **91**: 220–231. doi:10.1016/j.csr.2014.10.004

Sand-Jensen, K. A. J. 1977. Effect of epiphytes on eelgrass photosynthesis. Aquat. Bot. **3**: 55–63. doi:10.1016/0304-3770(77)90004-3

Sanford, L. P., and J. P. Halka. 1993. Assessing the paradigm of mutually exclusive erosion and deposition of mud, with examples from upper Chesapeake Bay. Mar. Geol. **114**: 37–57. doi:10.1016/0025-3227(93)90038-W

Sanford, L. P., and J.P.-Y. Maa. 2001. A unified erosion formulation for fine sediments. Mar. Geol. **179**: 9–23. doi:10.1016/S0025-3227(01)00201-8

Scheffer, M. 1998. Ecology of shallow lakes. Chapman and Hall.

Scheffer, M. 2009. Critical transitions in nature and society. Princeton Univ. Press.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature **413**: 591–596. doi:10.1038/35098000

Shafer, D. J., T. D. Sherman, and S. Wyllie-Echeverria. 2007. Do desiccation tolerances control the vertical distribution of intertidal seagrasses?. Aquat. Bot. **87**: 161–166. doi:10.1016/j.aquabot.2007.04.003

Short, F. T., and others. 2011. Extinction risk assessment of the world's seagrass species. Biol. Conserv. **144**: 1961–1971. doi:10.1016/j.biocon.2011.04.010

Staehr, P. A., and J. Borum. 2011. Seasonal acclimation in metabolism reduces light requirements of eelgrass (*Zostera marina*). J. Exp. Mar. Biol. Ecol. **407**: 139–146. doi:10.1016/j.jembe.2011.05.031

Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. Trends Ecol. Evol. **19**: 46–53. doi:10.1016/j.tree.2003.10.005

Thrush, S. F., and others. 2009. Forecasting the limits of resilience: Integrating empirical research with theory. Proc. R. Soc. B **276**: 3209–3217. doi:10.1098/rspb.2009.0661

Vacchi, M., M. Montefalcone, C. F. Sciaffino, V. Parravicini, C. N. Bianchi, C. Morri, and M. Ferrari. 2014. Towards a predictive model to assess the natural position of the *Posidonia oceanica* seagrass meadows upper limit. Mar. Pollut. Bull. **83**: 458–466. doi:10.1016/j.marpolbul.2013.09.038

van der Heide, T., E. H. van Nes, G. W. Geerling, A. J. P. Smolders, T. J. Bouma, and M. M. van Katwijk. 2007. Positive feedbacks in seagrass ecosystems: Implications for success in conservation and restoration. Ecosystems **10**: 1311–1322. doi:10.1007/s10021-007-9099-7

van der Heide, T., and others. 2010. Spatial self-organized patterning in seagrasses along a depth gradient of an intertidal ecosystem. Ecology **91**: 362–369. doi:10.1890/08-1567.1

van der Heide, T., E. H. van Nes, M. M. van Katwijk, H. Olff, and A. J. P. Smolders. 2011. Positive feedbacks in seagrass ecosystems—evidence from large-scale empirical data. PLoS One **6**: e16504. doi:10.1371/journal.pone.0016504

van Katwijk, M. M., A. R. Bos, V. N. de Jonge, L.S.A.M. Hanssen, D. C. R. Hermus, and D. J. de Jong. 2009. Guidelines for seagrass restoration: Importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. Mar. Pollut. Bull. **58**: 179–188. doi:10.1016/j.marpolbul.2008.09.028

van Katwijk, M. M., A. R. Bos, D. C. R. Hermus, and W. Suykerbuyk. 2010. Sediment modification by seagrass beds: Muddification and sandification induced by plant cover and environmental conditions. Estuar. Coast. Shelf Sci. **89**: 175–181. doi:10.1016/j.ecss.2010.06.008

Ward, L. G., W. M. Kemp, and W. R. Boynton. 1984. The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. Mar. Geol. **59**: 85–103. doi:10.1016/0025-3227(84)90089-6

Waycott, M., and others. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. USA **106**: 12377–12381. doi:10.1073/pnas.0905620106

Widdows, J., N. D. Pope, M. D. Brinsley, H. Asmus, and R. M. Asmus. 2008. Effects of seagrass beds (*Zostera noltii* and *Z. marina*) on near-bed hydrodynamics and sediment resuspension. Mar. Ecol. Prog. Ser. **358**: 125–136. doi:10.3354/meps07338

Wilkie, L., M. T. O'Hare, I. Davidson, B. Dudley, and D. M. Paterson. 2012. Particle trapping and retention by *Zostera noltii*: A flume and field study. Aquat. Bot. **102**: 15–22. doi:10.1016/j.aquabot.2012.04.004

Zeller, R. B., J. S. Weitzman, M. E. Abbett, F. J. Zarama, O. B. Fringer, and J. R. Koseff. 2014. Improved parameterization of seagrass blade dynamics and wave attenuation based on numerical and laboratory experiments. Limnol. Oceanogr. **59**: 251–266. doi:10.4319/lo.2014.59.1.0251

Zeller, R. B., F. J. Zarama, J. S. Weitzman, and J. R. Koseff. 2015. A simple and practical model for combined wave-current canopy flows. J. Fluid Mech. **767**: 842–880. doi: 10.1017/jfm.2015.59

Conflict of Interest
None declared.