



## Water residence time controls the feedback between seagrass, sediment and light: Implications for restoration



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### ABSTRACT

Feedbacks between seagrass and the local environmental conditions may hinder attempts to restore seagrass by inducing alternative stable states. A one-dimensional physical-biological model was used to identify the conditions under which a feedback between seagrass, sediment and light can yield alternative stable states of seagrass presence and absence (bistability). Based on our model results, a prediction of whether a given seagrass meadow is large enough to promote seagrass growth can now be made. If the water residence time within the spatial area of the meadow is similar to or greater than the sediment settling time, which is calculated from the ratio of water depth to sediment vertical settling velocity, the meadow is large enough for the feedback to potentially reduce the local suspended sediment concentration. This has important implications for seagrass restoration: for a proposed restoration plot, if the water residence time is similar to or greater than the sediment settling time, the scale of restoration is large enough for the feedback between seagrass, sediment and light to locally improve water clarity. More generally, this calculation can be used to identify areas where this feedback is likely to generate bistability, and to estimate the minimum suitable meadow size in such locations.

### 1. Introduction

Environmental management increasingly aims to manage feedbacks (Nyström et al., 2012) and the resilience of ecosystems (Standish et al., 2014). Ignoring ecosystem feedbacks may lead to an incorrect valuation of the services that these ecosystems can provide (Costanza, 2015). When organisms in an ecosystem modify the local environment to increase their population or growth in a feedback loop, these feedbacks can lead to alternative stable states of the ecosystem, which are resilient to change and are separated by tipping points (Scheffer et al., 2012). A first step in environmental management of feedbacks and resilience is to identify which feedbacks substantially contribute to the ecosystem dynamics in the area being managed (Maxwell et al., 2017).

In seagrass ecosystems, a positive feedback between seagrass, sediment and light (SSL) has been proposed to produce alternative stable states (van der Heide et al., 2007) and potentially acts as a barrier to

seagrass restoration (van Katwijk et al., 2016). Briefly, the SSL feedback acts as follows. Suspended sediment in the water column attenuates sunlight (Kirk, 1985) and subsequently reduces the benthic light at the seagrass canopy. Benthic light is a major determinant of seagrass habitat suitability (Duarte, 1991). Seagrass can reduce near-bed water flow of both currents and waves due to the presence of the canopy (Hansen and Reidenbach, 2012), and this attenuation of near-bed flow reduces the shear stress at the seabed. Thus, the presence of seagrass can alter the balance between sediment deposition and erosion at the seabed towards more depositional conditions (Gacia and Duarte, 2001), which in turn reduces the suspended sediment concentration in the water column. Together, these processes can form a feedback loop in which the presence of seagrass enhances its growth, by reducing suspended sediment concentrations in the water column and thereby increasing benthic light availability (de Boer, 2007; van der Heide et al., 2007; Gurbisz et al., 2016).

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There is quantitative evidence that the SSL feedback has the potential to produce alternative stable states of seagrass presence and absence in the same location, which is an ecosystem characteristic called “bistability” (Adams et al., 2016a). Several theoretical models have also predicted that the SSL feedback can cause bistability (van der Heide et al., 2007; Carr et al., 2010; 2012a; 2012b; 2016). However, sediment trapping within seagrass meadows can sometimes be insignificant (Mellors et al., 2002) and thus this feedback will not always impact on ecosystem dynamics or cause bistability.

Water residence time within macrophyte beds is proposed to be an important control on community nutrient and carbon dynamics (Bartleson, 2004); however, the impact of water residence time on alternative stable states has not been previously investigated. Here we hypothesised that long residence time of water within the spatial area of a seagrass meadow is required for seagrass to sufficiently reduce local suspended sediment concentrations, and therefore long water residence time is required for the SSL feedback to significantly alter seagrass growth patterns. To test this hypothesis, we used a one-dimensional physical-biological model to investigate how the water residence time affects the impact of the SSL feedback on the local ecosystem dynamics, the potential for bistability, and ultimately the resilience of the seagrass provided by this feedback.

## 2. Methods

### 2.1. The seagrass-sediment-light feedback in two hydrodynamic extremes

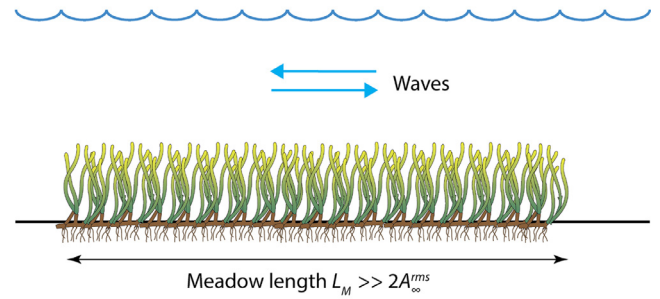
To test the hypothesis that long water residence time within a seagrass meadow is required for the SSL feedback to significantly alter seagrass growth patterns, we modelled two hydrodynamic extremes. The two hydrodynamic extremes we examine are pure waves and pure currents, both of which are far easier to investigate using models than mixed current-wave flows. More specifically, these two hydrodynamic extremes can be modelled using zero spatial dimensions or one horizontal dimension (length), respectively, if certain assumptions are satisfied. We next specify the assumptions and then describe the two hydrodynamic extremes.

We limited our considerations to seagrass meadows where the canopy height  $h$  is much smaller than the water depth  $H$ , i.e.,  $h \ll H$ . Many seagrasses can colonise depths that are far greater than their canopy height (Duarte, 1991), and thus the assumption  $h \ll H$  will be valid in a substantial number of seagrass ecosystems. (For completeness, in Section 4.6 we discuss how the model predictions are likely to differ in very shallow subtidal ecosystems where the seagrass depth constitutes a substantial portion of the overall water depth.) We also do not explicitly model the vertical distribution of either the seagrass canopy or the suspended sediment concentration since it can be shown (see Section 2.2.1 and Supplementary Material Section D.4, respectively) that these assumptions do not affect the validity of our results if  $h \ll H$  and the depth-averaged suspended sediment concentration above the canopy are known.

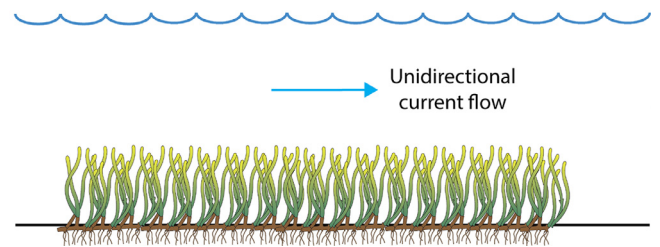
The two hydrodynamic extremes that we investigate represent the longest and shortest water residence times on the seagrass meadow, as follows:

1. *Seagrass subject to wave action with negligible net horizontal sediment transport (longest water residence time)*, as shown in Fig. 1a. In this wave-dominated flow environment, hereafter called oscillatory flow, suspended sediment within the meadow moves back and forth due to the waves, with potentially low exchange of sediment with surrounding bare areas. Therefore, the water residence time in these seagrass meadows is long. We assume that horizontal oscillatory flow due to waves is the main driver of the transport of suspended sediment, and that any wave-driven mean currents generated within canopies (Luhar et al., 2010; Abdolrahmanpour et al., 2017) and currents due to Stokes drift (Longuet-Higgins, 1953) can be neglected. Wave-driven

### a) Long water residence time



### b) Short water residence time



**Fig. 1.** (a) A seagrass meadow subjected to wave-driven oscillatory flow experiences the longest water residence time: the SSL feedback for this meadow is modelled using the equations in Table 1.  $L_M$  is the seagrass meadow length, and  $A_\infty^{rms}$  is the horizontal excursion length of the waves. (b) A seagrass meadow subjected to unidirectional flow experiences the shortest water residence time: the SSL feedback for this meadow is modelled using the equations in Table 2.

**Table 1**

Equations of the SSL feedback model, for a seagrass meadow in oscillatory flow conditions. The model variable  $\alpha_w$  is calculated from model variables  $A_\infty^{rms}$ ,  $L_s$ ,  $L_d$  and  $\lambda_p$  as described in Appendix A of Lowe et al. (2005). Parameter values for the model are shown in Table 3.

$\frac{d(LAI)}{dt} = k_{LAI} \left[ \min \left\{ \bar{T}, \frac{I_k}{2} \right\} (1 - e^{-\beta LAI}) - I_{comp} \beta LAI \right]$	(1)
$\bar{T} = I_0 \exp(-K_d H)$	(2)
$K_d = (K_d)_{bg} + a_{TSS} [TSS]$	(3)
$[TSS] = \frac{M}{w_s} \max \left\{ \frac{\tau_b(U_{b,w})}{\tau_c} - 1, 0 \right\}$	(4)
$\tau_b = \frac{1}{2} \rho C_B U_{b,w}^2$	(5)
$C_B = \exp \left( -5.977 + 5.213 \left( \frac{U_{b,w} T}{2\pi k_{s,w}} \right)^{-0.194} \right)$	(6)
$U_{b,w} = \alpha_w (A_\infty^{rms}, L_s, L_d, \lambda_p) U_w$	(7)
$A_\infty^{rms} = U_w T / (2\pi)$	(8)
$L_s = 2h / C_f$	(9)
$L_d = 2h / (C_D LAI)$	(10)
$\lambda_p = 0$	(11)

currents generated within a submerged canopy negligibly affect the depth-averaged flow since  $h \ll H$ , and Stokes drift is a second order effect in wave amplitude (Santamaria et al., 2013).

To identify environments where alternative states of seagrass presence and absence may exist in oscillatory flow conditions, we introduce one further requirement, which is that the seagrass meadow size must be sufficiently large so that transport of suspended sediment between the meadow and surrounding bare areas can be neglected. This requirement is stated mathematically as  $L_M \gg 2A_\infty^{rms}$ : the seagrass meadow size, quantified by a characteristic meadow length scale  $L_M$ , is much larger than the distance that suspended sediment travels back and forth due to the waves, which is equal to double the horizontal orbital excursion length of the waves well above the seagrass canopy,  $2A_\infty^{rms}$ . This inequality ensures that sed-

**Table 2**

Equations of the SSL feedback model, for a seagrass meadow in unidirectional flow conditions. Parameter values for the model are shown in Table 3.

$$\frac{d(LAI)}{dt} = k_{LAI} \left[ \min \left\{ \bar{I}, \frac{I_k}{2} \right\} (1 - e^{-\beta LAI}) - I_{comp} \beta LAI \right] \quad (12)$$

$$\bar{I} = \frac{1}{L_M} \int_0^{L_M} I(x) dx \quad (13)$$

$$I(x) = I_0 \exp(-K_d(x)H) \quad (14)$$

$$K_d(x) = (K_d)_{bg} + a_{TSS}[TSS](x) \quad (15)$$

$$\frac{d[TSS](x)}{dx} = \frac{1}{HU_c(x)} \left( M \max \left\{ \frac{\tau_b(U_{b,c})}{\tau_c} - 1, 0 \right\} - w_s [TSS](x) \right) \quad (16)$$

$$[TSS](x=0) = \frac{M}{w_s} \max \left\{ \frac{\tau_b(U_c)}{\tau_c} - 1, 0 \right\} \quad (17)$$

$$\tau_b(x) = \rho g (U_{b,c}(x))^2 / C^2 \quad (18)$$

$$C = \frac{\sqrt{g}}{\kappa} \ln \left( \frac{12H}{k_{sc}} \right) \quad (19)$$

$$U_{b,c}(x) = \left[ U_{b,c,f}^2 + (U_c^2 - U_{b,c,f}^2) e^{-C_D LAI x / h} \right]^{1/2} \quad (20)$$

$$U_{b,c,f} = U_c \min \left\{ \left( \frac{C_f}{C_D LAI} \right)^{1/2}, 1 \right\} \quad (21)$$

iment transport between seagrass and bare areas, which may be a dominant process at meadow edges and has horizontal length scale of  $2A_\infty^{rms}$ , does not substantially alter the suspended sediment concentrations within most of the meadow area. The advantage of intro-

ducing the inequality  $L_M \gg 2A_\infty^{rms}$  for modelling the SSL feedback is that, for seagrass meadows present in oscillatory flow conditions, the depth-averaged suspended sediment concentration can be assumed to be horizontally homogeneous across the meadow.

2. *Seagrass subject to unidirectional flow, i.e., mean currents (shortest water residence time)*, as shown in Fig. 1b. In this unidirectional flow environment, waters above the seagrass canopy travel across the meadow at a velocity approximately equal to the depth-averaged velocity  $U_c$ , because the canopy height is small compared to the water depth. Since the water is travelling directly from one side of the meadow to the other side, the residence time of water  $T_{residence}$  on the seagrass meadow is the shortest possible residence time for this meadow size and current velocity. The water residence time is given by  $T_{residence} = L_M / U_c$ , the ratio of meadow length  $L_M$  to current velocity  $U_c$ .

2.2. Model equations

In this section, we summarise the models used to represent the SSL feedback in the two chosen hydrodynamic extremes. Model equations for the two extremes, oscillatory flow and unidirectional flow, are shown in Tables 1 and 2, respectively. All model variables and parameters are listed in Table 3, and justification for the values of all parameters is provided in Supplementary Material Section C. For model equations whose

**Table 3**

Variables and parameters used in the models. All parameters values are sourced from literature values, as described in Supplementary Material Section C. In this paper, <sup>a</sup>parameter  $k_{LAI}$  does not require specification, and <sup>b</sup>parameter  $L_M$  only requires specification for unidirectional flow. <sup>c</sup>Parameter  $\lambda_p$  is assumed to be much less than one, so is set to zero here.

Description	Symbol	Values		Unit
		Default	Tested range	
<i>Variables</i>				
Depth-averaged orbital excursion length without seagrass	$A_\infty^{rms}$			m
Sediment friction coefficient	$C_B$			–
Benthic light	$I$			mol m <sup>-2</sup> d <sup>-1</sup>
Benthic light spatially averaged over the seagrass meadow	$\bar{I}$			mol m <sup>-2</sup> d <sup>-1</sup>
Total light attenuation coefficient in the water column	$K_d$			m <sup>-1</sup>
Seagrass leaf area index	LAI			–
Canopy drag length scale	$L_d$			m
Canopy shear length scale	$L_s$			m
Total suspended sediment concentration in the water column	[TSS]			mg L <sup>-1</sup>
Horizontal distance from upstream edge of seagrass meadow	$x$			m
Near-bed unidirectional current velocity	$U_{b,c}$			m s <sup>-1</sup>
Near-bed unidirectional current velocity well within the meadow	$U_{b,c,f}$			m s <sup>-1</sup>
Near-bed orbital velocity	$U_{b,w}$			m s <sup>-1</sup>
Bed shear stress	$\tau_b$			N m <sup>-2</sup>
<i>Parameters</i>				
Specific attenuation coefficient for total suspended sediment	$\alpha_{TSS}$	0.026	0.013–0.101	m <sup>-1</sup> /(mg L <sup>-1</sup> )
Seagrass drag coefficient	$C_D$	0.7	0.2–0.7	–
Seagrass friction coefficient	$C_f$	0.05	0.04–0.08	–
Seagrass canopy height	$h$	0.3	–	m
Water depth	$H$	1.5	1.5–5	m
Surface light	$I_0$	41	17–41	mol m <sup>-2</sup> d <sup>-1</sup>
Minimum light requirements of seagrass	$I_{comp}$	4.5	2–10	mol m <sup>-2</sup> d <sup>-1</sup>
Saturation irradiance of seagrass	$I_k$	16	10–56	mol m <sup>-2</sup> d <sup>-1</sup>
Background attenuation coefficient in the water column	$(K_d)_{bg}$	0.35	0.18–0.72	m <sup>-1</sup>
Seagrass leaf area produced per light absorption <sup>a</sup>	$k_{LAI}$			m <sup>2</sup> mol <sup>-1</sup>
Nikuradse current-related roughness	$k_{sc}$	$62.5 \times 10^{-6}$	–	m
Nikuradse wave-related roughness	$k_{sw}$	$62.5 \times 10^{-6}$	$10^{-6}$ – $10^{-3}$	m
Seagrass meadow length <sup>b</sup>	$L_M$	100 or 1000	10–10,000	m
Erosion constant	$M$	0.01	0.001–1	g m <sup>-2</sup> s <sup>-1</sup>
Wave period	$T$	10	0–30	s
Depth-averaged unidirectional current velocity without seagrass	$U_c$	–	0.1–1	m s <sup>-1</sup>
Depth-averaged orbital velocity without seagrass	$U_w$	–	0.1–0.6	m s <sup>-1</sup>
Settling velocity of TSS particles	$w_s$	$10^{-3}$	$10^{-4}$ – $10^{-3}$	m s <sup>-1</sup>
Seagrass light absorption efficiency	$\beta$	0.3	0.3–0.7	–
von Kármán constant	$\kappa$	0.4	–	–
Volume fraction of canopy occupied by seagrass leaves <sup>c</sup>	$\lambda_p$	0	–	–
Density of water	$\rho$	1000	–	kg m <sup>-3</sup>
Critical shear stress for erosion	$\tau_c$	0.04	0.01–1	N m <sup>-2</sup>

explanations are not trivial, mathematical derivations are provided in Supplementary Material Sections B.1–B.9.

### 2.2.1. Model of the SSL feedback in oscillatory flow conditions

For modelling the SSL feedback in oscillatory flow conditions, the one-dimensional model reduces to a zero-dimensional model (Table 1). This reduction occurs because the seagrass meadow is assumed to be sufficiently large ( $L_M \gg 2A_{\infty}^{rms}$ ) so that meadow edge effects can be neglected and thus the depth-averaged suspended sediment concentration is approximately horizontally homogeneous across the meadow.

Seagrass is modelled in terms of its leaf area index (LAI) using Eq. (1), which is derived in Supplementary Material Section B.1 and is a modified form of the daily-averaged light-limited seagrass growth equation reported by Baird et al. (2016). There are two main advantages of the model of Baird et al. (2016) over other aquatic plant models. Firstly, the carrying capacity for seagrass is not arbitrarily chosen, but rather is determined geometrically by self-shading limitation of the leaf surface area available to absorb photosynthetically active radiation. Secondly, the seagrass response to light is parameterised by the minimum light requirement of seagrass, which is measurable, commonly reported, and directly distinguishes between long-term predictions of seagrass presence and absence (Erftemeijer and Lewis, 2006).

Unlike the model of Baird et al. (2016), we write seagrass in units of LAI instead of biomass because we do not need to track the transfer of matter between seagrass and other parts of the ecosystem, and using units of LAI eliminates the need to specify an additional parameter (the ratio between leaf area and biomass). Overall, specification of the seagrass model for its usage here requires definition of only three parameters,  $I_k$ ,  $\beta$  and  $I_{comp}$ , all three of which are biologically meaningful and thus well-constrained (Adams et al., 2017). This model is therefore advantageous over other plant models that have a similar number of parameters, since these other models are typically written in terms of parameters whose values are not as easily constrained (e.g., growth rate, mortality rate and carrying capacity).

Benthic light availability for seagrass growth,  $I$ , which in oscillatory flow conditions is assumed here to be spatially homogeneous across the meadow,  $I(x) = \bar{I}$ , is obtained from the total light attenuation coefficient in the water column  $K_d$  via Beer's law (Eq. (2); Kirk (1985)). In this paper we assumed that benthic light is calculated at the seabed depth  $H$ . In practice, seagrass leaves protrude above the seabed to a maximum height  $h$ , and thus may experience slightly greater light conditions than predicted by Eq. (2). To account for this possibility, we performed additional model sensitivity tests which confirmed that our key results are unaffected by choosing the depth as  $H - h$  or  $H$  in Beer's law (results not shown). The total light attenuation coefficient is assumed to be proportional to the total suspended sediment concentration (Eq. (3); Gallegos and Moore (2000)).

The total suspended sediment concentration [TSS] is written in terms of the bed shear stress  $\tau_b$  via Eq. (4), and is derived in Supplementary Material Section B.2 from an advection–dispersion–reaction equation for sediment transport (Clarke and Elliott, 1998) by assuming that the local depth-averaged sediment concentration has reached a steady state and is approximately horizontally homogeneous. The bed shear stress is written in terms of the near-bed orbital velocity  $U_{b,w}$  using Eqs. (5) and (6); these equations are obtained from Kleinhans and Grasmeyer (2006) as described in Supplementary Material Section B.4.

Finally, near-bed orbital velocity under the seagrass canopy,  $U_{b,w}$ , is written in terms of the depth-averaged orbital velocity  $U_w$  using the model of oscillatory flow through submerged canopies introduced by Lowe et al. (2005). This flow model is written in the present paper with dependence on seagrass LAI, via Eqs. (7)–(11) that are derived from Lowe et al. (2005) in Supplementary Material Section B.7.

### 2.2.2. Model of the SSL feedback in unidirectional flow conditions

For unidirectional flow conditions, we use a one-dimensional model to represent the SSL feedback (Table 2), with horizontal dimension  $x$

representing the distance within the seagrass meadow from its upstream edge.

The biological model for seagrass in unidirectional flow conditions, Eq. (12), is identical to the seagrass model used for oscillatory flow conditions (Eq. (1)), and is thus also derived in Supplementary Material Section B.1 from the daily-averaged light-limited seagrass growth equation reported in Baird et al. (2016). We assume that the seagrass meadow growth depends on the mean benthic light  $\bar{I}$  received spatially over the whole meadow (Eq. (13)). Similarly to the model for oscillatory flow conditions, benthic light  $I(x)$  at any spatial point in the meadow depends on suspended sediment concentration [TSS]( $x$ ) via Beer's law (Eq. (14); Kirk (1985)) and the assumption of linear proportionality between total attenuation coefficient and [TSS] (Eq. (15); Gallegos and Moore (2000)).

The suspended sediment concentration [TSS]( $x$ ) is written in terms of bed shear stress  $\tau_b(x)$  via Eqs. (16) and (17). These formulae are derived in Supplementary Material Section B.3 from an advection–dispersion–reaction equation for sediment transport (Clarke and Elliott, 1998), under the assumptions of steady state conditions and negligible contribution of dispersion to the sediment dynamics (assumption justified in Supplementary Material Section B.3).

The dependence of bed shear stress  $\tau_b(x)$  on near-bed unidirectional current velocity,  $U_{b,c}(x)$  (Eqs. (18) and (19)), is written using a Chézy formulation and assumes that seagrass presence reduces bed shear stress proportionally to the square of the ratio of near-bed to depth-averaged current velocities,  $U_{b,c}/U_c$  (derived in Supplementary Material Section B.5). Thereafter, the near-bed unidirectional current velocity  $U_{b,c}(x)$  is written in terms of the distance  $x$  from the seagrass meadow's upstream edge and the near-bed current velocity well within the meadow  $U_{b,c,f}$  using Eq. (20). This equation was derived in Supporting Information Appendix A of Adams et al. (2016a) under the assumption that sediment bed drag within the seagrass meadow has negligible impact on near-bed current velocity, compared to the drag induced by the seagrass meadow. The near-bed current velocity well within the meadow,  $U_{b,c,f}$ , is written in terms of seagrass LAI via Eq. (21), which is derived in Supplementary Material Section B.8. To show that there is consistency between our SSL feedback models for unidirectional and oscillatory flow conditions, mathematical derivations which compare our model formulae between these two hydrodynamic conditions, are provided for bed shear stress in Supplementary Material Section B.6 and near-bed flow velocity in Supplementary Material Section B.9.

The models developed here, for both unidirectional and oscillatory flow conditions, are specifically designed to investigate our hypothesis regarding the potential for the SSL feedback to induce bistability and how it depends on water residence time. Hence the models we use are sufficiently complex to address this hypothesis, but still simple enough so that model predictions can be readily interpreted. Therefore, the models can only be used to identify generalities regarding the specific feedback and the specific hydrodynamic conditions examined, and they do not consider any other environmental factors that may limit seagrass viability. For example, we have assumed in the models that seagrass dynamics are not affected by other stressors such as extreme temperatures or nutrient loading. The models developed here are not therefore intended to be a standalone system for prediction of seagrass responses to suspended sediment concentration or a host of other environmental factors; models with this goal have been described elsewhere (e.g., Baird et al., 2016; Kuusemäe et al., 2016).

### 2.3. Modelling ecosystem stability and resilience

For the models described in Tables 1 and 2, the dependence of the seagrass growth rate  $dLAI/dt$  on leaf area index LAI was calculated, for several different parameters (default values and tested ranges shown in Table 3). For each plot of  $dLAI/dt$  versus LAI, we also calculated ball-in-cup diagrams using the mathematical procedure described in Supplementary Material Section D.1. In these ball-in-cup diagrams (Scheffer et al., 2001; 2015), the current state of the ecosystem is represented by

**Table 4**  
Resilience calculation of seagrass presence and absence states due to the SSL feedback, according to our mathematical definition of ecological resilience.

Resilience of which stable state?	Predicted model behaviour		
	Presence	Bistability	Absence
Seagrass presence	100%	$\left(\frac{\text{LAI}_{\text{presence}} - \text{LAI}_{\text{critical}}}{\text{LAI}_{\text{presence}}}\right) \times 100\%$	0%
Seagrass absence	0%	$\frac{\text{LAI}_{\text{critical}}}{\text{LAI}_{\text{presence}}} \times 100\%$	100%

a ball, and a landscape surface consisting of hills and valleys (defined mathematically by a conceptual variable called the “potential energy”) guides the current ecosystem state (ball) towards a stable equilibrium (valley). The obtained plots of  $d\text{LAI}/dt$  versus LAI, and associated ball-in-cup diagrams, were used to identify how the SSL feedback affected the presence or absence of seagrass, for a range of environmental and seagrass characteristics.

### 2.3.1. Three stability regimes

Due to the SSL feedback, there are three different ecosystem behaviours, called here “stability regimes”, that the seagrass ecosystem can express (van der Heide et al., 2007): (1) seagrass is present, (2) seagrass can be present or absent, because the SSL feedback causes alternative stable states that are resistant to change, or (3) seagrass is absent. In this paper we denote these three stability regimes as presence, bistability and absence, respectively. When seagrass can be present, there is a value of leaf area index at which seagrass growth will exactly balance its mortality; we define this steady state leaf area index as  $\text{LAI}_{\text{presence}}$ . For the stability regime of bistability, there is a value of leaf area index above which seagrass will survive and below which seagrass will decline; we define this threshold leaf area index as  $\text{LAI}_{\text{critical}}$ . The three stability regimes were identified from plots of  $d\text{LAI}/dt$  versus LAI calculated from the model equations in Tables 1 and 2, as well as from corresponding ball-in-cup diagrams calculated using equation (D.4) from Supplementary Material Section D.1. We thereafter distinguished between these three stability regimes using mathematical conditions that define the boundaries between these regimes, as described in Supplementary Material Section D.2.

### 2.3.2. Calculation of ecological resilience due to the feedback

Several metrics of resilience have been developed and applied in ecology (Meyer, 2016). We employ a mathematical definition of resilience which can be used for an ecosystem expressing (at most) two stable states: “The ecological resilience of a stable ecosystem state is defined as the ratio of (1) the difference between the population or density of the stable state and the threshold value of population or density that separates the basins of attractions of the two stable states, to (2) the difference in population or density between the two stable states, expressed as a percentage”. This mathematical definition, which has its basis in the conceptual definition of ecological resilience provided by Gunderson (2000), yields a value of ecological resilience that always falls between 0 and 100%: the higher the percentage, the more resilient the stable state is. The resilience of both stable states must add up to 100%.

In seagrass ecosystems affected by the SSL feedback, the two stable states are seagrass presence and absence, and the ecological resilience of each of these states can be calculated from Table 4. Whilst the definition of ecological resilience typically presumes the existence of alternative stable states (Gunderson, 2000), we extended our mathematical definition of resilience to areas where either only seagrass presence or seagrass absence is predicted by assuming that the basin of attraction for the stable state that does not exist has no resilience. Thus, ecological resilience can be calculated for any of the three stability regimes of seagrass ecosystems, with the caveat here that we are only considering the resilience associated with the SSL feedback.

Our mathematical definition of ecological resilience for the seagrass presence state has an additional useful physical interpretation: it is the minimum percentage of the seagrass LAI that must be lost, due to a disturbance, to cause catastrophic decline of the seagrass ecosystem. It was convenient therefore in our analysis to present results only for ecological resilience of the seagrass presence state. As part of our analysis, we plotted the environmental conditions that corresponded to an ecological resilience of 50%. Under these environmental conditions, our model predicts that a loss of more than half of the seagrass LAI is required to cause catastrophic decline of the seagrass ecosystem.

## 3. Results

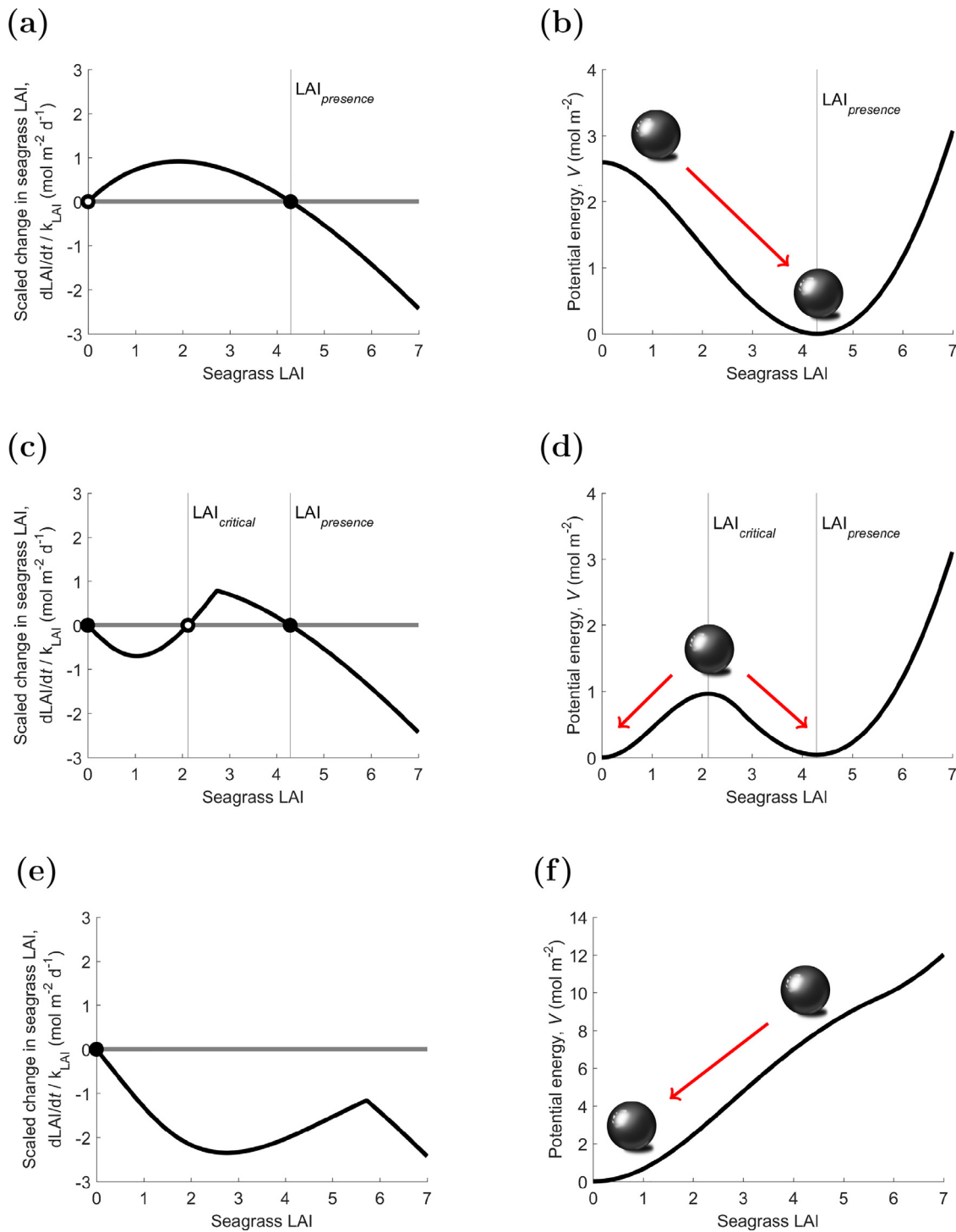
### 3.1. Model predictions of the three stability regimes

Our model predicts all three potential stability regimes of the seagrass ecosystem due to the SSL feedback - presence, bistability and absence - depending on the hydrodynamic conditions and the values of parameters that define the environmental and seagrass meadow characteristics of the system. Examples of the three stability regimes expressed by our model are shown in Fig. 2, both as plots of the change in seagrass leaf area index over time,  $d\text{LAI}/dt$ , and as ball-in-cup diagrams. For illustrative purposes, results are shown for oscillatory flow conditions; the difference between results for unidirectional and oscillatory flow conditions is discussed later in Section 3.2.

For seagrass growing in oscillatory flow conditions (model shown in Table 1), when using default values of our model parameters (see Table 3), presence is predicted for a depth-averaged orbital velocity  $U_w$  of  $0.1 \text{ m s}^{-1}$ . As shown both by plotting  $d\text{LAI}/dt$  versus LAI and the associated ball-in-cup diagram (Figs. 2a and b), a stable equilibrium only exists at an LAI value of  $\approx 4.3$ . This leaf area index value is reasonable, since seagrass LAI values of up to  $\approx 5$  have been observed in the field (e.g., Gacia et al., 1999; Hedley et al., 2014). At this low value of orbital velocity, there is insufficient sediment resuspended when seagrass is absent to prevent any potential seagrass growth, so this area is completely suitable for seagrass habitat.

At a higher value of orbital velocity,  $U_w = 0.35 \text{ m s}^{-1}$ , bistability is predicted because two stable equilibria exist, at LAI values of zero and  $\approx 4.3$  (Figs. 2c and d). When seagrass is absent at this orbital velocity, sediment resuspension is sufficient to reduce benthic light availability below the minimum light requirements of seagrass, and therefore hinder seagrass colonisation. However, when seagrass of  $\text{LAI} \geq 2.1$  is present at this orbital velocity, sediment resuspension is sufficiently dampened so that the benthic light availability is above the minimum light requirements of seagrass, and therefore seagrass can persist. Thus, while this area can support seagrass presence, loss of seagrass would be difficult to reverse.

At an even higher orbital velocity,  $U_w = 0.6 \text{ m s}^{-1}$ , absence is predicted because one stable equilibrium exists only at  $\text{LAI} = 0$  (Fig. 2e and 2f). At this orbital velocity, sediment resuspension will reduce benthic light availability below the minimum light requirements of seagrass, regardless of whether seagrass is present or not, so this area is completely unsuitable for seagrass habitat.

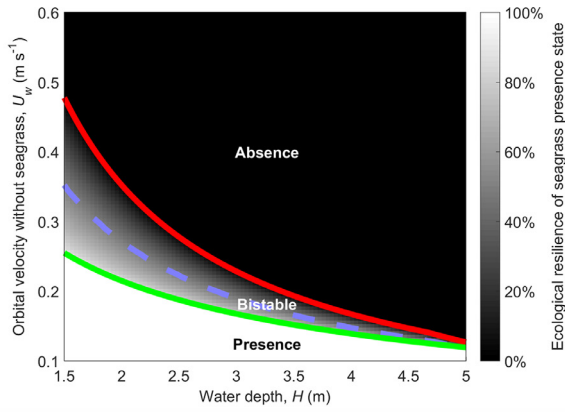


**Fig. 2.** Predictions of the SSL feedback model for oscillatory flow conditions (Table 1), by specifying  $U_w = 0.1 \text{ m s}^{-1}$  (a,b),  $U_w = 0.35 \text{ m s}^{-1}$  (c,d) or  $U_w = 0.6 \text{ m s}^{-1}$  (e,f), and using default values for all other parameters (Table 3). The three velocities  $U_w = 0.1, 0.35$  and  $0.6 \text{ m s}^{-1}$  were chosen for plotting here to demonstrate that our model can predict the three stability regimes of presence, bistability and absence. For plots of the scaled change in seagrass leaf area index over time (a,c,e), closed circles represent stable equilibria and open circles represent unstable equilibria. Sharp changes at  $\text{LAI} \approx 2.7$  in (c) and  $\text{LAI} \approx 5.7$  in (e) indicate saturating benthic irradiance for seagrass growth,  $\bar{I} = I_k/2$ . Ball-in-cup diagrams (b,d,f) are calculated using equation (D.4) from Supplementary Material Section D.1.

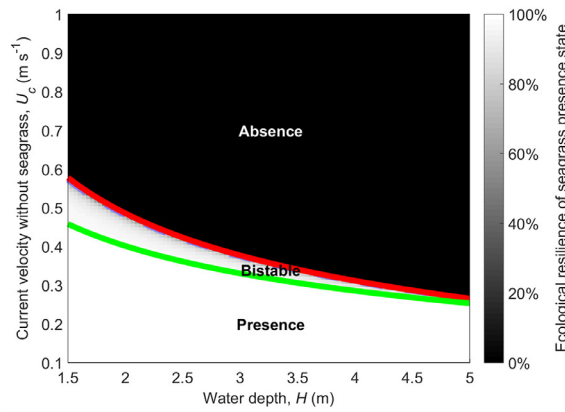
In summary, with increasing water velocity, our model predicts that the stability regime of a seagrass ecosystem changes from presence to bistability to absence. For oscillatory flow, the dependence of stability regime on several other environmental and meadow characteristics is also shown in Supplementary Material Fig. E.1–E.13.

### 3.2. Long water residence time is required for the SSL feedback to cause bistability

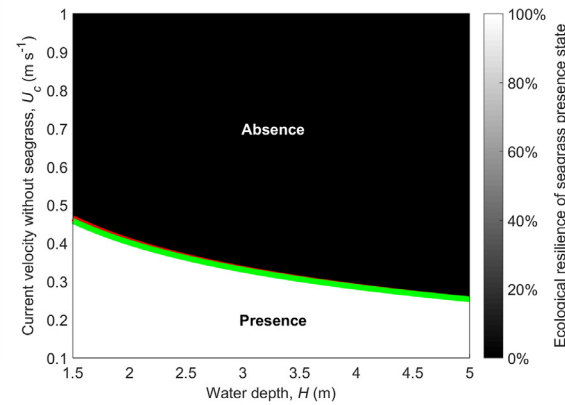
Whilst bistability is predicted for a range of environmental conditions for oscillatory flow (Fig. 3a), bistability is only predicted for unidirectional flow when the meadow length is sufficiently long (Fig. 3b



(a) Resilience of seagrass in oscillatory flow conditions, for a sufficiently large seagrass meadow.

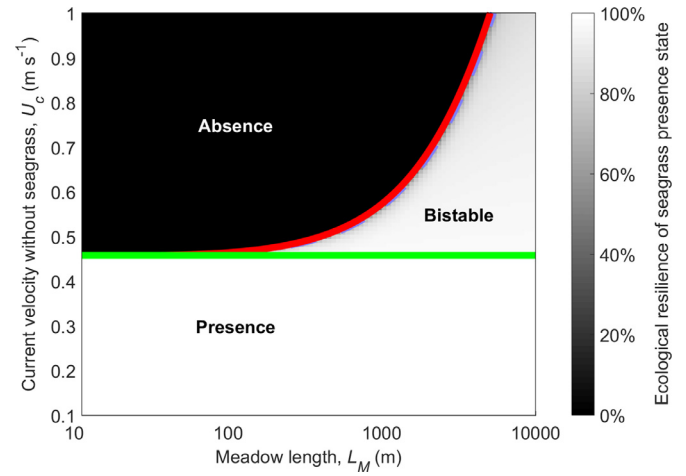


(b) Resilience of seagrass in unidirectional flow conditions, for a meadow of length 1000 m.



(c) Resilience of seagrass in unidirectional flow conditions, for a meadow of length 100 m.

**Fig. 3.** Ecological resilience of a seagrass meadow subject to (a) oscillatory flow conditions, (b) unidirectional flow conditions with longer meadow length, and (c) unidirectional flow conditions with shorter meadow length, versus flow velocity ( $U_w$  or  $U_c$ ) and water depth ( $H$ ). Parameter values are specified in Table 3. The green line is the boundary between presence and bistability, and the red line is the boundary between absence and bistability. The blue dashed line represents equal resilience of both the presence and absence states (50% resilience of each state): below this line, seagrass is predicted to recover from a disturbance that removes less than half of its leaf area index. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 4.** Ecological resilience of a seagrass meadow subject to unidirectional flow conditions, versus flow velocity ( $U_c$ ) and meadow length ( $L_M$ ). All other parameters are set to their default values specified in Table 3.

and 3c). In fact, the range of environmental conditions for which bistability is possible in unidirectional flow, increases with meadow length (Fig. 4).

The reason why bistability is not observed in unidirectional flow for the smaller seagrass meadow length is that the water does not spend sufficient time within the meadow for the suspended sediment concentration to be substantially reduced by the seagrass, as follows. Seagrass reduces the near-bed current velocity rapidly so that the bed shear stress reduces below the critical shear stress for erosion within metres of the meadow edge (Fig. 5a). However, this decrease in near-bed current velocity occurs over a much shorter spatial scale than the resulting decrease in suspended sediment concentration and increase in benthic light availability (Fig. 5b).

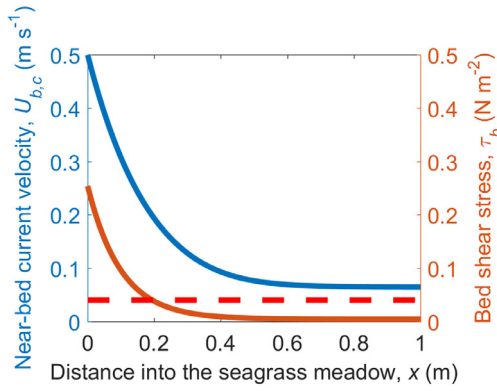
To investigate this further, we estimated how long the water needs to be present within a seagrass meadow for the suspended sediment concentration to substantially change from its concentration outside the meadow. Under both unidirectional and oscillatory flow conditions, the change in the depth-averaged total suspended sediment concentration with time  $[TSS](t)$  due to presence of seagrass can be approximated as (Supplementary Material Section B.10)

$$[TSS](t) \approx [TSS]_f + ([TSS]_0 - [TSS]_f) \exp\left(-\frac{w_s}{H}t\right), \quad (22)$$

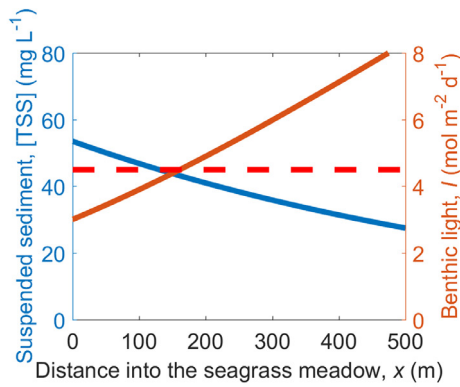
where  $[TSS]_0$  is the total suspended sediment concentration outside the seagrass meadow,  $[TSS]_f$  is the minimum value of total suspended sediment that is possible within the meadow,  $w_s$  is the particle vertical settling velocity ( $\text{m s}^{-1}$ ) and  $H$  is the water depth (m). Eq. (22) does not depend on the seagrass canopy height  $h$  since we have assumed that the canopy height is much smaller than the water depth,  $h \ll H$ .

The exponent of Eq. (22) can be expressed in terms of the approximate settling time of the sediment particles  $T_{settle}$  (s), via  $T_{settle} = H/w_s$ . This equation, together with Eq. (22), demonstrates that a substantial change in  $[TSS]$  due to seagrass presence requires that the water containing the suspended sediment stays within the seagrass meadow for timescales  $T_{residence}$  of similar order of magnitude to  $T_{settle}$ , i.e.,  $\mathcal{O}(T_{settle})$ , or longer. For example, when  $t = T_{settle}$  in Eq. (22), the suspended sediment concentration has changed by  $\sim 63\%$  from its initial value  $[TSS]_0$  towards its minimum value  $[TSS]_f$ . Hence,  $T_{settle} = H/w_s$  provides an order-of-magnitude estimate for the length of time that water needs to spend on the seagrass meadow for the SSL feedback to substantially reduce the suspended sediment concentration there.

To explicitly demonstrate that long water residence time,  $T_{residence} \gtrsim T_{settle}$ , is required for the SSL feedback to produce bista-



(a) Near-bed current velocity and bed shear stress versus distance into the seagrass meadow.



(b) TSS concentration and benthic light versus distance into the seagrass meadow.

**Fig. 5.** In unidirectional flow conditions, bistability was only predicted for long meadows ( $L_M \gtrsim \mathcal{O}(100\text{m})$ ), because suspended sediment concentration changes over a much larger spatial scale than near-bed current velocity within the seagrass meadow. (a) Spatial profile of near-bed current velocity  $U_{b,c}$  (blue line) and bed shear stress  $\tau_b$  (red line) over 1 m into the seagrass meadow. Bed shear falls below the critical shear stress for erosion  $\tau_c$  (red dashed line) in less than 1 m. (b) Spatial profile of total suspended sediment concentration [TSS] and benthic light  $I$  over 500 m into the seagrass meadow. Benthic light exceeds minimum light requirements  $I_{comp}$  (red dashed line) after more than 150 m. In both plots,  $LAI = 4.3$  and  $U_c = 0.5 \text{ m s}^{-1}$ ; all other parameter values are specified in Table 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

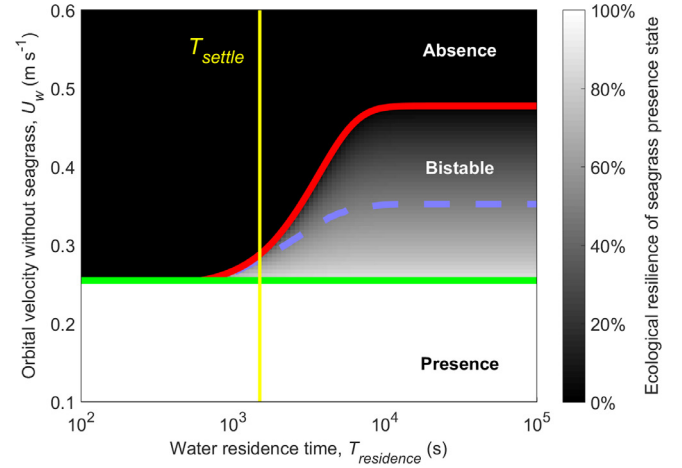
bility, we next modified the models for oscillatory flow conditions (Table 1) and unidirectional flow conditions (Table 2) to include  $T_{residence}$  as an input parameter. For the oscillatory flow model, this was accomplished by replacing Eq. (4) with the following three equations,

$$[TSS] = [TSS]_f + ([TSS]_0 - [TSS]_f) \exp\left(-\frac{w_s}{H} T_{residence}\right), \quad (23)$$

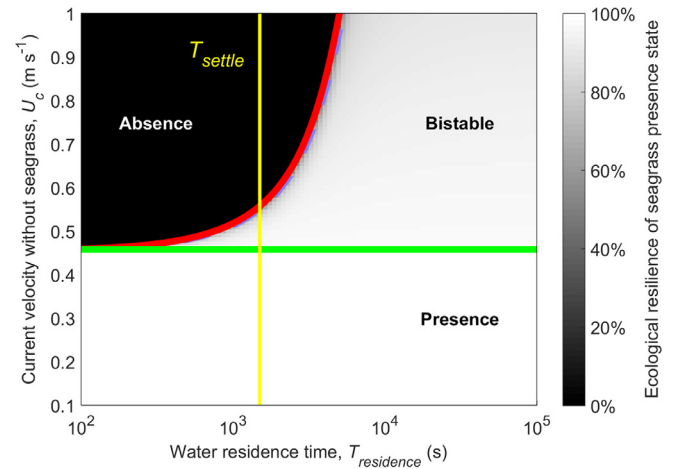
$$[TSS]_f = \frac{M}{w_s} \max\left\{\frac{\tau_b(U_{b,w})}{\tau_c} - 1, 0\right\}, \quad (24)$$

$$[TSS]_0 = \frac{M}{w_s} \max\left\{\frac{\tau_b(U_{w,c})}{\tau_c} - 1, 0\right\}. \quad (25)$$

For the unidirectional flow model,  $T_{residence}$  was included as an input parameter by making the value of meadow length  $L_M$  depend on  $T_{residence}$



(a) Resilience of seagrass in oscillatory flow conditions, versus water residence time.



(b) Resilience of seagrass in unidirectional flow conditions, versus water residence time.

**Fig. 6.** Ecological resilience of a seagrass meadow subject to (a) oscillatory flow conditions and (b) unidirectional flow conditions, versus flow velocity ( $U_w$  or  $U_c$ ) and water residence time ( $T_{residence}$ ). Panel (a) is calculated using the model described in Table 1 but with Eq. (4) replaced by Eqs. (23)–(25). Panel (b) is calculated using the model described in Table 2 and the extra Eq. (26). The yellow line shows the sediment settling time  $T_{settle}$ . All parameters are set to their default values specified in Table 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

via

$$L_M = U_c \times T_{residence}. \quad (26)$$

For the default parameters of our model, the sediment settling time is 1500 s. This timescale represents muddy sediments ( $w_s = 10^{-3} \text{ m s}^{-1}$ ) settling in a water column of 1.5 m depth. We therefore plotted ecological resilience of a seagrass meadow versus water residence times ranging from  $10^2$  to  $10^5$  s, in Fig. 6. This figure clearly demonstrates that bistability caused by the SSL feedback only occurs if  $T_{residence} \gtrsim T_{settle}$ , regardless of whether the local hydrodynamic conditions are wave- or current-dominated. Since this conclusion is predicted by our models to be true for both pure wave and pure current flows, it seems highly plausible that SSL feedback-induced bistability requires  $T_{residence} \gtrsim T_{settle}$  also



in the mixed flows of currents and waves that seagrasses are likely to experience in the field.

#### 4. Discussion

##### 4.1. Water residence time can identify ecosystems where the SSL feedback may be important

The main outcome of this study is a method to estimate whether the seagrass meadow size is sufficiently large for the positive feedback between seagrass, sediment and light to substantially promote seagrass growth. The spatial scale of seagrass planting is recognised as the most important requirement for successful seagrass restoration worldwide (van Katwijk et al., 2016). To identify whether the seagrass planting area is sufficiently large for the SSL feedback to promote successful seagrass restoration in any ecosystem, the water residence time  $T_{residence}$  must be similar to or greater than the sediment settling time  $T_{settle}$ , which can be calculated from

$$T_{settle} = H/w_s, \quad (27)$$

where  $H$  is the water depth (m) and  $w_s$  is the sediment vertical settling velocity ( $\text{m s}^{-1}$ ). For an area proposed for restoration,  $H$  can be easily obtained from the local bathymetry, whereas  $w_s$  will depend on the local sediment characteristics, including particle size which can be calculated from Stokes' law (Adams et al., 2016b). The estimate of  $w_s$  that is of best use here is an effective settling speed that encompasses the mixing effects of turbulence, and also accounts for the potentially broad particle size distribution expected in the field. However, given these caveats, we point out that a precise calculation of  $w_s$  is not necessarily required. An order of magnitude estimate of sediment settling time, calculated from  $w_s$  and  $H$ , is sufficient for comparison to the water residence time to identify if the SSL feedback could locally induce bistability.

If the water residence time  $T_{residence}$  on the proposed seagrass restoration area exceeds  $T_{settle}$ , this restoration area is large enough for the SSL feedback to potentially promote local seagrass growth. Conversely, if  $T_{residence} \ll T_{settle}$ , then the SSL feedback can be disregarded in this area. Eq. (27) is equally applicable in both wave-dominated and current-dominated aquatic environments (see Supplementary Material Section B.10), and so we argue that this equation is likely to be applicable in any hydrodynamic environment (e.g., environments with simultaneous currents and waves).

Long water residence time is typically associated with negative impacts on seagrass due to reduced flushing and therefore declines in water quality (Defne and Ganju, 2015). In areas where water residence time is long, eutrophication as well as the potential resulting phytoplankton blooms (Basterretxea et al., 2007) can reduce benthic light available for seagrass growth (Valiela et al., 1997; Orfila et al., 2005). Conversely, the potentially positive impact of water residence time on seagrass health and resilience, via the modification of the local suspended sediment concentration, has thus far received little research attention (Wiberg et al., 2015). Our study suggests that water residence time can modify the benthic light available for seagrass growth via regulation of the feedback between seagrass and suspended sediment.

For a specific area proposed for seagrass restoration, the water residence time  $T_{residence}$  can be estimated by either (1) using back-of-the-envelope calculations, if the hydrodynamic conditions are relatively predictable and not too complex, or (2) using hydrodynamic simulations. Back-of-the-envelope calculations can, for example, be performed for seagrass growing in areas with predictable tidal cycles, since the root-mean-squared (RMS) water speed on these meadows could be used as a coarse approximation of  $U_c$  to estimate  $T_{residence} \approx L_M/U_c$  where  $L_M$  is the spatial extent (in units of distance) of the seagrass meadow parallel to the direction of tidal flows. Whilst using the RMS water speed in tidal flow conditions to estimate water residence time is a rather coarse approximation, it may be sufficient since we are mostly interested in obtaining an order of magnitude estimate for  $T_{residence}$  to decide whether

there is any possibility that the SSL feedback may induce bistability in the seagrass ecosystem of interest.

On the other hand, hydrodynamic simulations can more accurately predict  $T_{residence}$ , without explicitly requiring an ecological process model to be run simultaneously. This is convenient because large-scale ecosystem model suites are often structurally designed so that the hydrodynamic model runs separately and prior to the ecological model, which means that it is difficult to explicitly simulate ecological feedbacks on the local hydrodynamics in these model suites (Adams et al., 2016a). For ecosystem model suites that allow feedbacks of ecological processes back onto the hydrodynamics (e.g., Hipsey et al., 2016; Beudin et al., 2017), calculation of the sediment settling time can first be used together with the hydrodynamic simulation to identify areas where the local water residence time is sufficient for the SSL feedback to promote seagrass growth. Then, for areas where the feedback may be important based on water residence time, the hydrodynamics and ecology processes of the ecosystem model suite could be run simultaneously to make quantitative and location-specific predictions of the impact of the SSL feedback on seagrass growth.

In some cases, hydrodynamic flows are diverted horizontally around seagrass meadows (Fonseca and Koehl, 2006; Vandenbruwaene et al., 2011), particularly if seagrass presence has altered the local bed elevation (e.g., van der Heide et al., 2010). More generally, the presence of aquatic vegetation may substantially alter the water residence time in shallow coastal areas (Nepf et al., 2007). In our model, the modification of water residence time due to seagrass presence could be ignored because we assumed that the seagrass canopy height is much smaller than the water depth,  $h \ll H$ . In ecosystems where aquatic vegetation fills much of the water column, the water residence time in the meadow can be estimated from additional hydrodynamic simulations, by assuming that a drag force is imposed on the local water flow in areas where macrophytes are present (e.g., Vilas et al., 2017; Woodward et al., 2017). These additional hydrodynamic simulations also do not require explicit modelling of ecological processes.

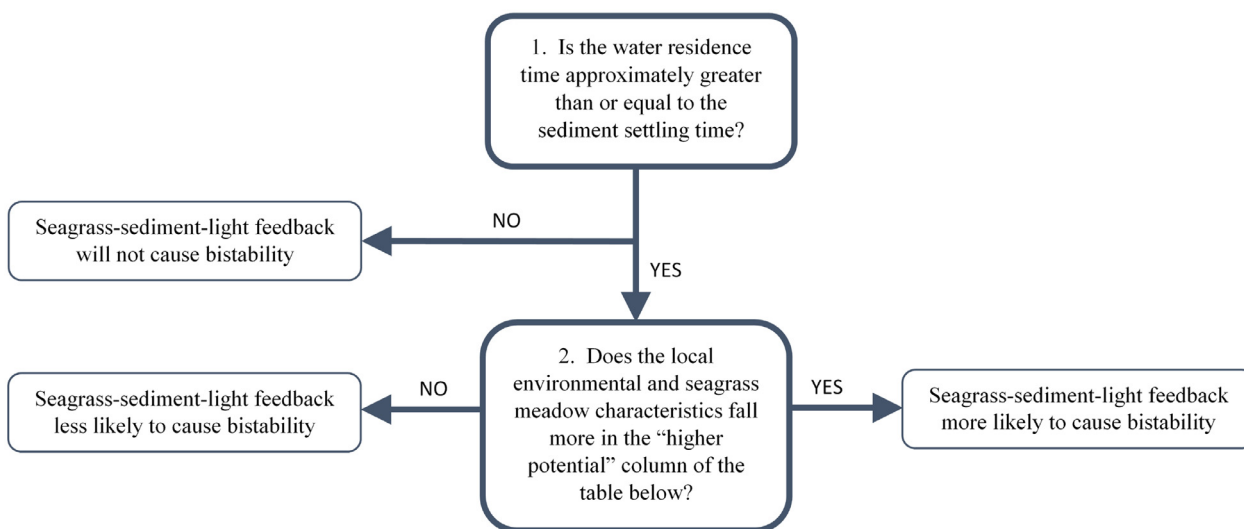
##### 4.2. Water residence time is not the only control of the SSL feedback

Whilst the comparison of water residence time  $T_{residence}$  to the sediment settling time  $T_{settle}$  can identify if the water is spending sufficient time in the seagrass meadow to increase water clarity via sediment settling, this comparison does not identify whether or not the potential reduction in suspended sediment concentration by seagrass affects its presence or absence. For seagrass to survive in a bistable environment, it is additionally required that (1) the benthic light availability outside the meadow must be unsuitable for seagrass habitat and (2) the benthic light availability well within the meadow must be suitable for seagrass habitat: these two requirements affect the terms  $[TSS]_0$  and  $[TSS]_f$  in Eq. (22) but they do not alter the sediment settling time or water residence time. Long water residence time is therefore a necessary, but not sufficient, condition for the SSL feedback to cause bistability. Thus, calculation of water residence time is best used in tandem with an assessment of the local ecosystem characteristics as shown in Fig. 7, to identify if the suspended sediment reduction provided by the SSL feedback could be significant in the area proposed for seagrass restoration. Fig. 7 highlights that the SSL feedback can only promote seagrass growth in ecosystems with sufficiently long water residence time and high plant density.

##### 4.3. The spatial scale required for successful seagrass restoration?

The present work highlights one mechanism by which spatial scale can influence the success of seagrass restoration. From a global analysis of seagrass restoration, van Katwijk et al. (2016) found that net positive growth rate of seagrass transplants was more likely for plots with greater than 1000–10,000 shoots. Assuming a seagrass planting density of 100 shoots per  $\text{m}^2$  (e.g., Reynolds et al., 2012), this corresponds to

## Will the seagrass-sediment-light feedback induce bistability?



Potential for seagrass-sediment-light (SSL) feedback to induce bistability		
	Lower potential	Higher potential
<b>Environmental and seagrass meadow characteristics:</b>		
(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

Fig. 7. A flowchart to identify if the SSL feedback may induce bistability. In the flowchart, Question 1 is the contribution of the present study. Question 2 and the associated table is modified from Adams et al. (2016a). Comparison between model predictions from this study and the review of Adams et al. (2016a) is also provided in Supplementary Material Section A.

a planting area of 10–100 m<sup>2</sup>. While a direct comparison of water residence time with seagrass planting area requires a site-specific hydrodynamic simulation, a back-of-the-envelope calculation for a meadow length  $L_M$  of 10 m, sediment settling velocity  $w_s$  of  $10^{-3}$  m s<sup>-1</sup> (e.g., mud), and water depth  $H$  of 1.5 m, gives that the net velocity of water transported into and out of the meadow must be similar to or less than  $L_M/(H/w_s) \approx 0.7$  cm s<sup>-1</sup> for the SSL feedback to generate bistability, which seems unfeasibly small.

Hence, the SSL feedback is unlikely to be the only mechanism contributing to the threshold planting density for successful seagrass restoration identified by van Katwijk et al. (2016). This is an important point to note, since overcoming feedbacks is a proposed justification for large planting densities in seagrass restoration efforts (van Katwijk et al., 2016). Ecosystems where the SSL feedback hinders seagrass colonisation may therefore require an unfeasibly large transplantation area for seagrass restoration. Conversely, bare areas where the benthic light is already sufficient for seagrass presence are better targets for seagrass restoration than bare turbid areas where the SSL feedback has the potential to inhibit recolonisation (Adams et al., 2016a). More generally, when choosing a site for seagrass restoration (Short et al., 2002), water residence time may be worth assessing to identify whether the SSL feedback may be contributing to seagrass ecosystem dynamics or not (Fig. 7).

#### 4.4. Quantifying ecological resilience

Ecological resilience was the key model output that we used to assess the relative importance of the SSL feedback in a variety of environmental conditions (Figs. 3,4,6 and Supplementary Material Figures E.1–E.13), and thus our work contributes to recent research efforts to quantify and assess resilience of environmental systems (Angeler and Allen, 2016; Quinlan et al., 2016). Our mathematical definition of ecological resilience (defined in Section 2.3.2) is analogous, though not identical, to the definition introduced by Beisner et al. (2003), who used a deterministic lake model to investigate alternative stable states of areal chlorophyll concentrations in a temperate lake produced by a positive feedback between phosphorus recycling and anoxia in the sediment. Our metric of ecological resilience is also similar to the “latitude” aspect of resilience proposed by Walker et al. (2004) and mathematically defined by Mitra et al. (2015). For a recent mathematical review of resilience metrics, the reader is directed to Meyer (2016). We caution here that our mathematical model can only be used to predict resilience associated with the SSL feedback, and does not predict the total resilience of the seagrass ecosystem.

#### 4.5. Bistability in unidirectional flow conditions is unlikely due to physiological limitations of seagrass

Bistability in unidirectional flow conditions may not be possible, because the large seagrass meadow size required will not be sustainable due to physiological limitations, as follows. Fig. 3 suggests that bistability may only occur in meadow lengths  $L_M \gtrsim \mathcal{O}(100 \text{ m})$  subject to unidirectional flow. In this case, (1) some “upstream” portion of the seagrass meadow will be present in turbid conditions that are unsustainable for seagrass, (2) some “downstream” portion of the seagrass meadow will be growing in higher benthic light conditions that are required for seagrass, because the SSL feedback has sufficiently clarified the water column there, and (3) resources from the downstream portion of the seagrass meadow must be translocated horizontally between physiologically-connected below-ground seagrass ramets to support survival of the upstream portion of the seagrass meadow. Survival of this seagrass meadow therefore depends critically on the ability of below-ground seagrass ramets to transport resources for distances of  $\sim \mathcal{O}(100 \text{ m})$ .

Whilst estimates of the distances that below-ground seagrass ramets can transport resources are relatively scarce in the literature (Schwarzschild and Ziemann, 2008; Terrados et al., 1997), they have been reported up to 80 cm (Marbà et al., 2002). Although these distance values are typically based on short-term experiments so may underestimate the maximum horizontal translocation distance that is possible in seagrasses, it seems unlikely that below-ground seagrass ramets can translocate resources for distances that are more than two orders of magnitude larger than the longest distances thus far reported. Therefore, even though canopies in unidirectional flow can reduce suspended sediment concentrations, our results suggest that the SSL feedback is unlikely to generate bistability in unidirectional flow conditions.

#### 4.6. Future work

While spatial extension of the SSL feedback has been previously modelled with periodic boundaries to represent a closed system such as a sheltered bay (Carr et al., 2016), our model is the first to consider this feedback also in open systems such as rivers and coastally exposed zones. Coastal zones represent an important seagrass habitat (Coles et al., 2015) for which knowledge of the most important feedbacks is currently lacking. Other advantages of our model include: (1) seagrass growth does not require definition of a fixed carrying capacity, but rather this capacity depends physically on the maximum light absorbable by self-shaded seagrass leaves (Baird et al., 2016), and (2) wave attenuation by seagrass is calculated from canopy geometry and associated forces (Lowe et al., 2005).

There are several mechanisms that were not considered in our SSL feedback model. For example, for oscillatory flow conditions our model neglected the possibility of sediment transport into/out of the meadow due to wave-driven currents, which are generated by the meadow itself (Luhar et al., 2010). These mean currents can have a local magnitude of up to 75% of the wave orbital velocities above the canopy (Abdolahpour et al., 2017), although when distributed over the water column their depth-averaged magnitude would be much lower. Conversely, our model considered only seagrass canopies that have much smaller height than the water column depth. For seagrass with canopies that occupy a large proportion of the water column, there is greater attenuation of flow due to seagrass, which increases water residence time: both of these processes yield a greater likelihood of bistability from the SSL feedback. However, for these seagrass canopies, the vertical distance between the water surface and the top of the seagrass canopy may be small so that seagrass growth is not light-limited. Hence, if our model is applied to areas where the seagrass canopy occupies a large proportion of the water column, it may overestimate or underestimate the range of

environments that support bistable states of seagrass presence/absence induced by the SSL feedback.

Our model only considered the interaction between seagrass, suspended sediment and benthic light availability, and thus ignored several other coastal controls of seagrass distribution, including temperature (Collier et al., 2017), nutrients (Lee et al., 2007), grazing (Hughes et al., 2013), and competition with other biota (Greve and Binzer, 2004). For example, phytoplankton is a major control on benthic light availability, and eutrophication-induced algal growth can, in some ecosystems, provide a greater limitation to seagrass recovery than increased sediment resuspension (Gruber and Kemp, 2010; Gruber et al., 2011). Numerous other feedbacks can occur in seagrass ecosystems (Maxwell et al., 2017), and the prediction of resilience conferred by these other feedbacks would require a more complex model that specifically includes them. Finally, environmental fluctuations have the potential to cause regime shifts in ecosystems expressing bistability (Guttal and Jayaprakash, 2007). Potential future research directions therefore include: (1) modelling of multiple interacting feedbacks in seagrass ecosystems (Maxwell et al., 2017), (2) extensions of our model to consider seagrass canopy heights that are substantial compared to the water depth, and (3) investigating the contribution of stochastic environmental fluctuations to regime shifts between alternative stable states (Gurbisz and Kemp, 2014) of seagrass presence and absence.

## 5. Conclusion

A comparison of water residence time and sediment settling time can be used to identify the potential for bistability between seagrass presence and absence states caused by the SSL feedback, and to estimate the minimum meadow size required to overcome this feedback. This information fills an important gap for managing seagrass habitat and planning seagrass restoration projects. In some cases, the minimum planting area and shoot density required to overcome the SSL feedback may be unfeasibly large. Thus, the minimum planting area required for successful seagrass restoration may depend on the dominant feedbacks at the site.

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## Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi: [10.1016/j.advwatres.2018.04.004](https://doi.org/10.1016/j.advwatres.2018.04.004).

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