Positive Feedbacks in Seagrass Ecosystems: Implications for Success in Conservation and Restoration

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ABSTRACT

Seagrasses are threatened by human activity in many locations around the world. Their decline is often characterized by sudden ecosystem collapse from a vegetated to a bare state. In the 1930s, such a dramatic event happened in the Dutch Wadden Sea. Before the shift, large seagrass beds (*Zostera marina*) were present in this area. After the construction of a large dam and an incidence of the ''wasting disease'' in the early 1930s, these meadows became virtually extinct and never recovered despite restoration attempts. We investigated whether this shift could be explained as a critical transition between alternative stable states, and whether the lack of recovery could be due to the high resilience of the new turbid state. We analyzed the depth distribution of the historical meadows, a long-term dataset of key factors determining turbidity and a minimal model based on these data. Results demonstrate that recovery was impossible because turbidity related to suspended sediment was too high, probably because turbidity was no longer reduced by seagrass itself. Model simulations on the positive feedback suggest indeed the robust occurrence of alternative stable states and a high resilience of the current turbid state. As positive feedbacks are common in seagrasses, our findings may explain both the world-wide observed collapses and the low success rate of restoration attempts of seagrass habitats. Therefore, appreciation of ecosystem resilience may be crucial in seagrass ecosystem management.

Key words: positive feedback; restoration; alternative stable states; seagrass ecosystem; ecosystem engineer; turbidity; *Zostera marina*; Wadden Sea; wasting disease.

INTRODUCTION

Seagrasses are rhizomatous plants, forming extensive meadows in temperate to tropical coastal areas. Their ecosystems are among the most productive ecosystems on earth and serve as key-habitat in the

lifecycles of many marine animal species (Duarte 2002; Orth and others 2006). In the last decades, seagrasses have been increasingly threatened by human activities in many locations around the world. These disturbances recently resulted in a widespread loss of habitat, often characterized by sudden ecosystem collapse (Jackson and others 2001). Once seagrass beds are damaged, restoration costs are high and chances for success are remarkably low (that is, worldwide around 30% success) (Orth and others 2006).

Seagrasses are ecosystem engineers in the sense that they significantly modify the abiotic environment of their ecosystem. They lower nutrient levels in the water column (Moore 2004) and attenuate currents and waves (for example, Gambi and others 1990; Fonseca and Cahalan 1992; Granata and others 2001). Both mechanisms decrease turbidity through reduction of phytoplankton, epiphytes and suspended sediment (for example, Ward and others 1984; Twilley and others 1985; Granata and others 2001; Kemp and others 2005). As seagrass is often light limited, their growth is enhanced by the increased light availability. If this positive feedback is strong enough, theory suggests that it could lead to alternative stable states (Scheffer and others 2001; Scheffer and Carpenter 2003). This implies that through gradually changing conditions (for instance increasing turbidity), occasionally a critical threshold can be crossed, causing a collapse to an alternative stable state (Scheffer and others 2001). Such a shift can also be triggered by a sufficiently large perturbation of the ecosystem (for instance by a rampant disease). If the system is close to a critical threshold, resilience is low and only little disturbance is needed to trigger the shift. If subsequently the conditions (for example, turbidity) improve, they have to progress further than the point of collapse, before recovery may take place, a phenomenon called hysteresis (Scheffer and others 2001). It is even possible that the shift is irreversible, that is, that recovery is not possible by improving the conditions (for example, Carpenter and others 1999). Although these critical transitions are notoriously hard to predict, their implications for ecosystem management (that is, conservation and restoration) can be profound (Scheffer and others 2001; Scheffer and Carpenter 2003).

In the Dutch Wadden Sea such dramatic change took place in the 1930s (Den Hartog and Polderman 1975; Giesen and others 1990), when the large seagrass meadows of the species *Zostera marina* (commonly called eelgrass) in this area suddenly collapsed. After the construction of a large dam and a severe occurrence of the wasting disease, these meadows disappeared from the area and never returned despite positive evaluations of the general habitat suitability (Van Katwijk and others 2000) and several restoration attempts since 1950, using both plants and seeds (for example, Den Hartog and Polderman 1975; Van Katwijk and Hermus 2000).

Here, we determined whether the dramatic decline of the Wadden Sea eelgrass beds and their lack of recovery afterwards can be explained by a catastrophic shift between two alternative stable states. First we show that the turbidity is currently much higher than before the shift. Secondly, we analyzed the cause of the currently high turbidity. Based on these data, we constructed a minimal computer model describing a positive feedback between eelgrass, hydrography and light availability. We analyzed whether this model can have alternative stable states in realistic parameter ranges. We discuss the role of this feedback in the functioning and restoration of the ecosystem in light of possible alternative explanations like increased eutrophication and changed hydrodynamics.

STUDY SITE

The Wadden Sea is a largely micro-tidal system (amplitude 1.3–2.5 m) sheltered by barrier islands and characterized by shallow intertidal and subtidal mudflats and deeper tidal channels. Here, eelgrass was a widely distributed species at the beginning of the twentieth century. In the western part of the Dutch Wadden Sea, eelgrass beds originally covered an area of ±150 km^2 (both subtidal and intertidal) (Van Goor 1919). The dramatic collapse of the meadows at the beginning of the 1930s took place within a few years. Their massive die-off has typically been attributed to a combination of factors. In the first place, ''wasting disease'', which destroyed many eelgrass stands in the North Atlantic region, reached the Netherlands in that period (Den Hartog and Polderman 1975; Giesen and others 1990). Secondly, the 5-year construction (1927–1932) of a large dam (''Afsluitdijk'') also took place at the time, which led to increased turbidity during its construction (Den Hartog and Polderman 1975; Giesen and others 1990). Although populations in other areas recovered from the impact of the wasting disease at the end of the 1930s, the population in this part of the Wadden Sea disappeared nearly completely, leaving only a few sparse intertidal populations that eventually disappeared in the following decades (Den Hartog and Polderman 1975; Giesen and others 1990).

ANALYSIS OF FIELD DATA

Methods

We analyzed two datasets: (1) maps of eelgrass beds in 1930 and (2) a 26-year dataset on water quality from 1980 to 2005. We used these data to estimate the difference in turbidity before and after the 1930s collapse, and to determine the current cause of the high turbidity.

To compare the turbidity in the 1930s with the current situation, we reconstructed the vertical light attenuation based on the historical eelgrass distribution, as there are no historical turbidity data available. For this, we used the eelgrass lower depth limit, defined as the 5% percentile of the eelgrass depth distribution in the early 1930s (in meters below mean water level), calculated from the maps. We assumed that eelgrasses at this lower depth limit needed at least 5.9% of the light entering the water column. This value is rather low as populations in Dutch waters were adapted to relatively poor light conditions (Pellikaan 1980; Giesen and others 1990). Using these values, the vertical light attenuation could then be calculated using the Lambert–Beer equation.

To determine the historical depth distribution of eelgrass, we used digitized distribution (Reigersman 1939) and tidal (Klok and Schalkers 1980) maps from 1930. These data were combined with a high-resolution depth map (20×20 m grid-size) from this period (1926–1934), which was kindly provided by Rijkswaterstaat (Dutch National Institute for Coastal and Marine Management, RIKZ). We calculated the eelgrass depth distribution by spatially analyzing the acquired maps using GIS (Geographical Information System) at a resolution of 20×20 m.

Phytoplankton and suspended sediments are the primary factors controlling water column turbidity in estuaries (for example, Postma 1961; Colijn 1982; Giesen and others 1990; Kemp and others 2005). To determine the relative influence of these factors in the Wadden Sea, we related the vertical light attenuation coefficient to suspended matter and chlorophyll *a*, using linear and nonlinear regression. As a quality measure of our fits we used the *F*-test and R^2. Additionally, we determined the relative contribution of chlorophyll *a* to light attenuation, using its specific light attenuation coefficient (Gallegos 2001). For these analyses we used a 26-year dataset (1980–2005) from Rijkswaterstaat, which routinely sampled 13 locations scattered over the Wadden Sea area at least 4 times a year. We used year-averaged values in our calculations. Winter months were not excluded, as

both summer and winter turbidity levels are important for eelgrass survival (Van Goor 1919; Greve and Krause-Jensen 2005).

Internal sediment resuspension on the (shallow) mudflats and sediment transport between the channels and the mudflats are the two dominant processes with regard to turbidity caused by sediment dynamics in the Wadden Sea (Postma 1961; Janssen-Stelder 2000; Christiansen and others 2006). Therefore, we also related turbidity factors to the depth of the sampling sites. We expected the vertical light attenuation coefficient to increase with decreasing depth as resuspension of fine material increases under the growing influence of wind-driven currents and waves on the sediment bed (Postma 1961; Christiansen and others 2006; Condie and Sherwood 2006). We acquired the depths of the 13 locations from a high-resolution depth map (20×20 m grid-size) of corresponding period (1997–2002), provided by Rijkswaterstaat.

RESULTS

The eelgrass beds of the 1930s covered an area of 117 km^2 in the Wadden Sea and Zuiderzee combined. The total surface of the beds that was covered by our tidal and depth maps was 105 km^2 (Figure 1A). Ninety percent of all beds could be found at depths between 0.5 and 2.3 m below mean water level. Over 90% of the beds were located in the subtidal zone. The mean depth of the beds was 1.1 m below mean water level. The distribution was slightly left-skewed with a median depth of 1.0 m below mean water level (Figure 1B). We calculated that the vertical light attenuation coefficient was at maximum 1.2 m^{-1} inside the Wadden Sea eelgrass beds.

The vertical light attenuation coefficient showed good correlation with suspended matter and fit best using a linear equation (Table 1; Figure 2A). Further analysis revealed that both vertical light attenuation and suspended matter correlated well with depth. Both fit best to depth by a Monod equation (Table 1; Figure 2B, C). Chlorophyll *a* did not show a significant correlation with vertical light attenuation (Table 1; Figure 2D). Although correlation with depth was not very strong, it was significant (Table 1). Concentrations of chlorophyll *a* were generally slightly higher in shallow areas. Based on its specific light attenuation coefficient (Gallegos 2001), we calculated an average contribution of 9.7% by chlorophyll *a* to the total vertical light attenuation. This percentage was highest in the channels and lowest in the shallow areas.
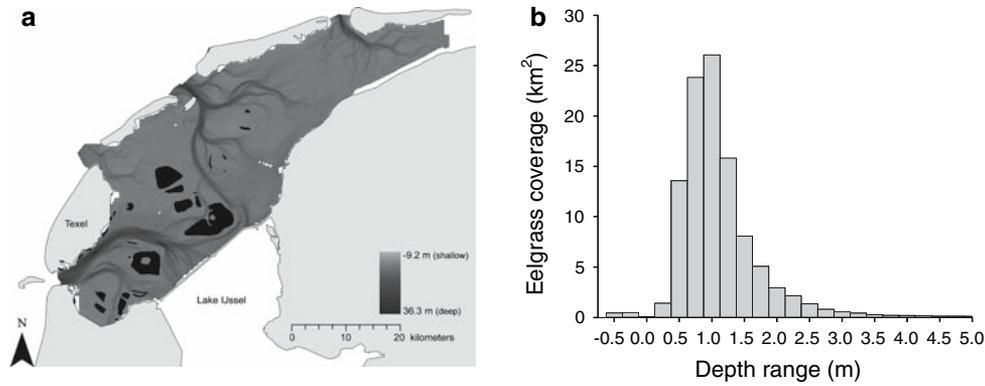
Figure 1. **A** Distribution of the examined historical eelgrass beds (*black areas*) on the 1930 depth map (m below mean water level). The indicated beds completely disappeared due the 1930s collapse. The topographical map is from the present situation, showing the position of the Afsluitdijk and Lake IJssel (the former Zuiderzee). **B** Eelgrass depth distribution below mean water level in the 1930s. The total covered area of the analyzed beds was 105 km^2, with a mean depth of 1.1 m. The distribution was slightly left-skewed with a median of 1.0 m.

Table 1. Correlations of Fitted Equations and Parameter Values, Describing Relations between Light Attenuation (k) and Suspended Matter (SS), Light Attenuation and Depth (D), Suspended Matter and Depth, Light Attenuation and Chlorophyll a (ChP) and Chlorophyll a and Depth

	Equation type	R^2	F	P	Intercept	Slope	Maximum level	Half-saturation
k–SS	Linear	0.64	466.17	$<10^{-4}$	0.28 m^{-1}	36.1e−3 l mg^{-1}	–	–
k–D	Monod	0.79	1,053.06	$<10^{-4}$	–	–	18.58 m^{-1}	1.34 m
SS–D	Monod	0.60	464.00	$<10^{-4}$	–	–	192.28 mg l^{-1}	4.81 m
k–ChP	Linear	0.03	2.57	0.1101	2.96 m^{-1}	−34.3e−3 l µg^{-1} m^{-1}	–	–
ChP–D	Linear	0.05	13.18	0.0003	13.48 µg l^{-1}	−119e-3 µg m^{-1} l^{-1}	–	–

Plots are shown in Figure 2.

From the equations in Table 1 we calculate that the present average vertical light attenuation coefficient at the lower eelgrass depth limit (2.3 m) is 6.8 m^{-1}, indicating that turbidity increased nearly 6 times since the 1930s (that is, maximum estimated at 1.2 m^{-1}). This increase in turbidity since the 1930s cannot be explained by increased turbidity levels of the water entering the Wadden Sea. Water in channels with depths of over 30 m forms a good conservative proxy for the turbidity of water entering the Wadden Sea. The vertical light attenuation in these channels is currently as low as 0.8 m^{-1} or less. Even when we assume that the channels in the 1930s contained no suspended matter at all, calculations based on the background vertical light attenuation for seawater (0.3– 0.4 m^{-1}) (Colijn 1982; Gallegos 2001; this study, Table 1) clearly illustrate that turbidity in the channels increased much less compared to the shallow areas. Here, turbidity levels increased at maximum 2–3 times.

A SIMPLE MODEL

Description

Analysis of our field data shows that the influence of phytoplankton on turbidity in the Wadden Sea is negligible and that suspended sediment is the dominant factor determining suspended matter concentrations and light availability. The sediment concentration increases with decreasing depth as resuspension of sediment by a combination of waves and currents increases (Postma 1961; Christiansen and others 2006; Condie and Sherwood 2006). The excessive increase in turbidity in shallow areas compared to turbidity levels in the channels indicates that the extensive eelgrass meadows of the 1930s significantly reduced turbidity within the beds through sediment retention. We constructed a simple model to explore the positive feedback between eelgrass shoot density (Z) and sediment-related water clarity based on logistic growth:
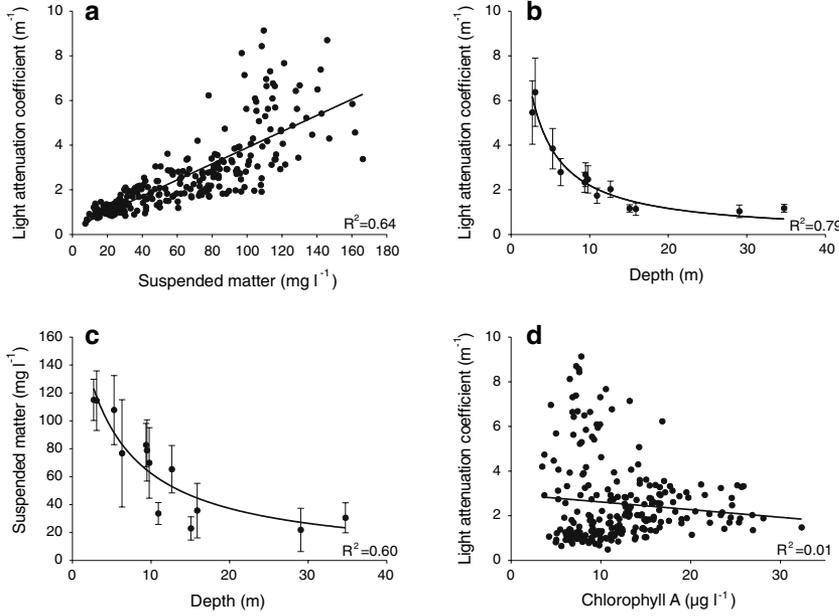
Figure 2. Relations between light attenuation (k), suspended matter (SS), chlorophyll a (ChP) and depth (D), based on data collected in 1980–2005. Light attenuation fits well to suspended matter (**A**) but not to chlorophyll a (**D**). Both light attenuation and suspended matter correlated well with depth (**B**, **C**, respectively). The *error bars* indicate standard deviations. Regression data are summarized in Table 1.

$$\frac{dZ}{dt} = r\,fI(I)Z - \frac{r-m}{K}Z^2 - mZ. \qquad (1)$$

In this model, the maximum gross growth rate r is light limited [$fI(I)$]. We assumed a constant mortality rate m due to senescence. Intraspecific competition causes the population to grow to the carrying capacity K. For light limitation $fI(I)$ we used the P-I (Photosynthetic Irradiation) curve for eelgrass (Zimmerman and others 1995):

$$fI = 1 - e^{(-I/I_k)} \qquad (2)$$

where I_k is the irradiance saturation constant. We assume that light intensity (I) at the bottom (D) determines the eelgrass growth rate (Verhagen and Nienhuis 1983). This value is calculated from the vertical light attenuation coefficient (k) and incoming irradiation (I_0) using the Lambert–Beer equation. The light attenuation coefficient is linearly dependent on the amount of suspended sediment SS in the water column (Table 1; Figure 2A). In our model, the suspended sediment concentration depends on the shear stress on the sediment bed. The suspended sediment concentration is constant (SS_b) below the critical bed shear stress boundary τ_0. Above the threshold, the amount of eroded sediment per m^2 that is suspended in the water column, relates to bed shear stress in a linear fashion (Houwing 1999). The total suspended sediment concentration can be obtained by dividing this relation with depth and adding the outcome to the background level:

$$SS = SS_b + \frac{p\tau - q}{D} \quad \text{if } \tau > \tau_0 \qquad (3)$$

with p, q and τ_0 as constants depending on the sediment type. We used general formulations to describe the combined effect of currents and waves on the bed shear stress and assumed a collinear flow of waves and currents. Total bed shear stress (τ) is defined as the sum of the shear stress caused by currents (τ_c) and waves (τ_w) (for example, Davies and Lawrence 1994; Janssen-Stelder 2000):

$$\tau = \tau_c + \tau_w. \qquad (4)$$

The bed shear stress caused by currents is described as (for example, Van Rijn 1990; Kleinhans and Grasmeijer 2006):

$$\tau_c = \rho g \frac{U_c^2}{C^2}. \qquad (5)$$

Here ρ is the fluid density, g is the gravitational acceleration, U_c is the depth averaged current velocity and C is the Chézy grain roughness (for example, Van Rijn 1990; Kleinhans and Grasmeijer 2006):

$$C = 18\log_{10}\frac{12D}{k_{sc}} \qquad (6)$$

where k_{sc} is the grain roughness constant for currents. We used the 90% cumulative grain size distribution (d_{90}), recommended for a flat bed (Van Rijn 1990).

The wave related bed shear stress is calculated as (for example, Van Rijn 1990; Davies and Lawrence 1994; Kleinhans and Grasmeijer 2006):

$$\tau_{\mathrm{w}} = \frac{1}{2}\rho f_{\mathrm{w}} U_{\mathrm{w}}^2 \qquad (7)$$

where U_{w} is the orbital velocity amplitude. The friction coefficient f_{w} is described as (for example, Van Rijn 1990; Kleinhans and Grasmeijer 2006):

$$f_{\mathrm{w}} = \exp\left[-6 + 5.2\left(\frac{(U_{\mathrm{w}}T)/2\pi}{k_{\mathrm{sw}}}\right)^{-0.19}\right] \qquad (8)$$

with T as the wave period and k_{sw} is the grain roughness for waves ($2.5\ d_{50}$). Finally, current and orbital velocity depend on the eelgrass shoot density. Based on multiple sources, it can be concluded that shoot density related attenuation per meter in the canopy, of both currents (Gambi and others 1990; Worcester 1995; Peterson and others 2004) and waves (Bouma and others 2005), can be readily described by Monod equations (Figure 3):

$$U = U_{\max}\frac{h_z}{h_z + Z} \qquad (9)$$

where U is the actual current (U_{c}) or orbital (U_{w}) velocity, $U_{\max}$ is the maximum (free-stream) current (U_{cmax}) or orbital (U_{wmax}) velocity and h_z is the eelgrass half-constant for either currents (h_{cz}) or waves (h_{wz}). In our model we consider conditions 1 m from the edge of the bed. We assume that any excess sediment particles entering our eelgrass bed will settle in the outline of the bed as observed in the historical meadows (Oudemans 1870), and that shoots in this area are supported through clonal translocation of resources (Marbà and others 2006). Parameter settings, variables and units from our model analyses are presented in Table 2.

Sensitivity Analysis

We chose default parameter settings to mimic average Wadden Sea conditions, based on literature and our field data analysis (Table 2). In a sensitivity analysis we analyzed the robustness of the results by varying settings of key parameters in the model. In this analysis, critical thresholds were determined by the following numerical procedure: a key parameter value was increased in small steps. After each step, the model was run to stabilize to its equilibrium point. For every step, the equilibrium biomass was plotted to find a discontinuity (critical threshold, also called a bifurcation point). Subsequently, this analysis was also performed in a backward manner (that is, a decrease in small steps)
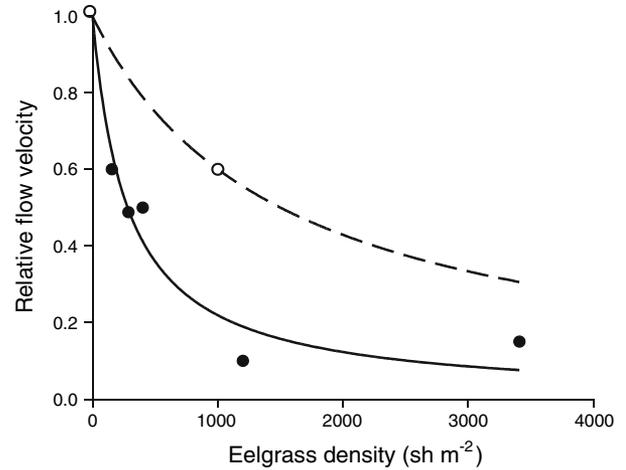
Figure 3. The relative remaining flow velocity (that is, U_{wmax} and $U_{\mathrm{cmax}} = 1$ in the absence of vegetation) as a function of eelgrass density, one meter into the bed. The relation between U_{cmax} and eelgrass shoot density (*closed dots*) is based on multiple sources (Gambi and others 1990; Worcester 1995; Peterson and others 2004). h_{cz} has a value of 281 sh m^{-2}. $R^2 = 0.96$; $F = 87.80$; $P = 7e{-}4$. The relation between U_{wmax} and eelgrass density (*open dots*) was derived from data of Fonseca and Cahalan (1992). Results from Bouma and others (2005) revealed that wave attenuation at different shoot densities can be described by a Monod equation. h_{wz} has a value of 1,500 sh m^{-2}.

the find the other critical (return) threshold. By combining these analyses we constructed two-dimensional bifurcation plots of various parameters.

Results

The model has two stable equilibria at the default parameter settings (Figure 4A). The population will crash if shoot densities are below the unstable equilibrium, which is between both stable equilibria at a density of 988 sh m^{-2}. Above this threshold, the population will stabilize to the carrying capacity (3,370 sh m^{-2}).

Alternative equilibria can be found over a wide range of current and orbital velocities. Hysteresis occurs from 0.06 to 0.39 m s^{-1} for orbital velocity (Figure 4B) and from 0 to 3.72 m s^{-1} for current velocity (Figure 4C). In these ranges both eelgrass dominance and a bare state are stable. An eelgrass population with high shoot density reduces currents and waves (and thereby turbidity) enough to sustain itself. The population collapses when a disturbance, for instance disease, pushes the shoot density below the critical threshold (Figure 4B, C; dashed lines). Past the bifurcation points ($U_{\mathrm{wmax}} = 0.39$ m s^{-1} and $U_{\mathrm{cmax}} = 3.72$ m s^{-1}) the population cannot reduce

Table 2. Variables and Parameters used in the Model

	Values		Unit	Description	Sources
	Default	Tested range			
Variables					
Z			sh m^{-2}	Eelgrass density	
I			μmol m^{-2} s^{-1}	Light availability in PAR	
SS			g m^{-3}	Suspended sediment concentration	
U_c			m s^{-1}	Current velocity	
U_w			m s^{-1}	Orbital velocity	
k			m^{-1}	Light attenuation coefficient	
τ			Pa (N m^{-2})	Total bed shear stress	
τ_c			Pa (N m^{-2})	Bed shear stress by currents	
τ_w			Pa (N m^{-2})	Bed shear stress by waves	
C			m$^{1/2}$ s^{-1}	Chézy grain roughness	
f_w				Friction coefficient	
Parameters					
r	0.08		day^{-1}	Maximum growth rate	1[a]
m	0.013		day^{-1}	Mortality rate	1[a]
K	3,500		sh m^{-2}	Carrying capacity	1[a], 2[a]
I_k	31.63		μmol m^{-2} s^{-1}	Saturation irradiance in PAR	1[a]
I_0	372.61		μmol m^{-2} s^{-1}	Year-averaged irradiation at the surface in PAR	3[a]
D	1.0	0.5–3.0	m	Depth below the mean water level	[c]
a	0.28		m^{-1}	Background light attenuation coefficient	[c]
b	36.1e-3		m^2 g^{-1}	Constant in suspended matter–light attenuation equation	[c]
SS_b	26.2	0–120	g m^{-3}	Minimum SS. The default value is based on levels in the historical eelgrass beds	[c]
P	14,133		g N^{-1}	Sediment erosion constant (Eq. 3)	4[a,c]
Q	2,120		g m^{-2}	Sediment erosion constant (Eq. 3)	4[a,c]
τ_0	0.15	0.01–1	Pa (N m^{-2})	Critical bed shear stress boundary	4[a]
ρ	1,000		kg m^{-3}	Fluid density	
g	9.81		m s^{-2}	Gravitational acceleration	
d_{90}	110e-6		m	90% percentile cumulative grain size distribution	4[a]
d_{50}	80e-6		m	50% percentile cumulative grain size distribution	4[a]
T	1.2		s	Wave period	5[a]
U_{cmax}	0.3	0–5	m s^{-1}	Maximum (free-stream) flow velocity	6[a]
U_{wmax}	0.2	0–1	m s^{-1}	Maximum orbital velocity amplitude	5[a], 6[a]
h_{cz}	281		sh m^{-2}	Eelgrass density where U_{cmax} is reduced by 50%	7[b,c]
h_{wz}	1,500		sh m^{-2}	Eelgrass density where U_{wmax} is reduced by 50%	8[b,c]

Values for I_k and I_0 were converted into μmol m^{-2} s^{-1} PAR (photosynthetically active radiation) using standard conversion factors (Ross and Sulev 2000)
[a]*Indicates either a direct value from the source or a value obtained via straightforward calculations*
[b]*Is a value derived from the source*
[c]*This study, (1) Verhagen and Nienhuis 1983, (2) Van Lent and Verschuure 1994, (3) Royal Dutch Meteorological Institute 2006, (4) Houwing 1999, (5) Christiansen and others 2006, (6) Janssen-Stelder 2000, (7) Gambi and others 1990; Worcester 1995; Peterson and others 2004, (8) Fonseca and Cahalan 1992; Bouma and others 2005.*

hydrodynamics enough to keep turbidity low. From these thresholds on, the only stable state is the bare state. When the population has collapsed, recovery can only take place when the orbital velocity is reduced below 0.06 m s^{-1}. Interestingly, the current velocity graph shows a non-reversible alternative equilibrium, that is, it is impossible to recover the vegetated state by reducing the current velocity alone. This is because the default orbital velocity (0.2 m s^{-1}) is high enough to prevent recovery, even when current velocity is zero.

Simulations of the interactive effect of current and orbital velocity reveal that orbital velocity needs to be below average Wadden Sea conditions to facilitate eelgrass colonization (Figure 5A). Current velocity should remain below 0.37 m s^{-1} and should even be lower if orbital velocity is above zero. Alternative equilibria can be found over a wide range of current and orbital velocities.

We analyzed the influence of minimum levels of suspended sediment by varying the background sediment concentration constant SS_b between 0
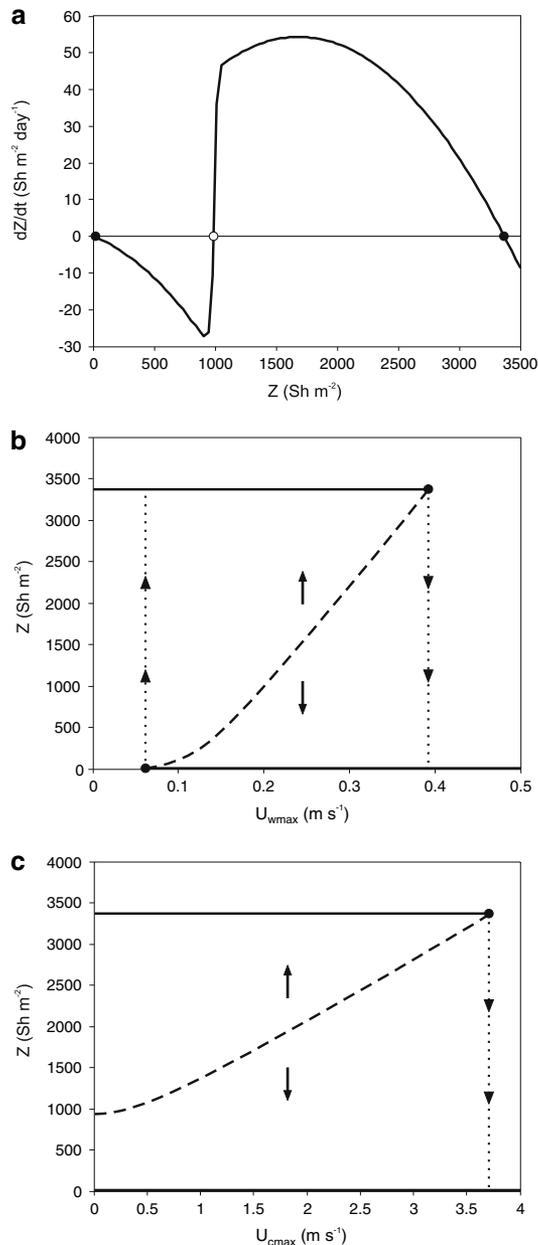
Figure 4. **A** The change in shoot density per day (dZ/dt) for different shoot densities (Z) at default parameter settings. The *dots* indicate equilibrium points; the *open dot* represents an unstable equilibrium. **B**, **C** Show the stable states for different maximum orbital (U_{wmax}) and current (U_{cmax}) velocities, respectively. *Dots* indicate bifurcation points; *arrows* indicate the direction of change. The *dashed* equilibria are unstable. Note that the bifurcation point of 3.72 m s^{-1} for current velocity is unrealistically high for the Wadden Sea as currents reach velocities of at maximum 2 m s^{-1} in this system (Rijkswaterstaat).

and 120 g m^{-3} at different values for orbital velocity (Figure 5B). If sediment concentrations are

low, an established eelgrass bed tolerates high orbital velocities. The critical orbital velocity for vegetation decreases as sediment concentrations increase. If background levels of suspended sediment increase above 108 g m^{-3}, seagrass cannot reduce light availability enough for a sustainable population.

The effect of water depth is very similar to the effect of background suspended sediment concentrations as light availability is determined by a combination of both factors. In the analysis, depth was varied between 0.5 and 3 m below mean water level. At shallow depths hysteresis occurs between 0.12 and 0.40 m s^{-1} for U_{wmax} (Figure 5C). For U_{cmax} these values are 0.35 and 4.47 m s^{-1} (not shown). At greater depths, the potential for alternative equilibria significantly decreases.

The effect of different degrees of cohesiveness of the sediment was simulated by varying the critical shear stress boundary (τ_0). τ_0 was tested in the range of 0.01–1 Pa, which can be regarded as values common for different types of sediment (Houwing 1999). Results show that at low values for τ_0, establishment of an eelgrass bed is much more difficult than at high values (Figure 5D). The hysteresis range increases when τ_0 values increase.

The most important thing to note from the bifurcation analysis is that the occurrence of alternative stable states is very robust. They occur over a wide range of maximum current and orbital velocities, even when crucial environmental parameter settings are changed.

Discussion

Marine ecosystems were among the first ecosystems to illustrate the potential importance of alternative equilibria. Evidence has been presented from coral reefs, soft sediments and rocky substrates from both the subtidal and intertidal (Knowlton 2004). Remarkably, detailed studies on the subject in seagrass ecosystems are lacking, although there are many studies pointing at a potential positive feedback in seagrasses. From tropical to temperate species, positive effects on water quality (Moore 2004), hydrodynamics (for example, Gambi and others 1990; Fonseca and Cahalan 1992; Granata and others 2001; Bos and Van Katwijk 2007) and substrate (Ward and others 1984; Gacia and Duarte 2001; Kemp and others 2005) have been demonstrated. Our study suggests that this positive feedback is most likely strong enough to lead to alternative equilibria in many seagrass ecosystems. This result has important implications for the management and restoration of
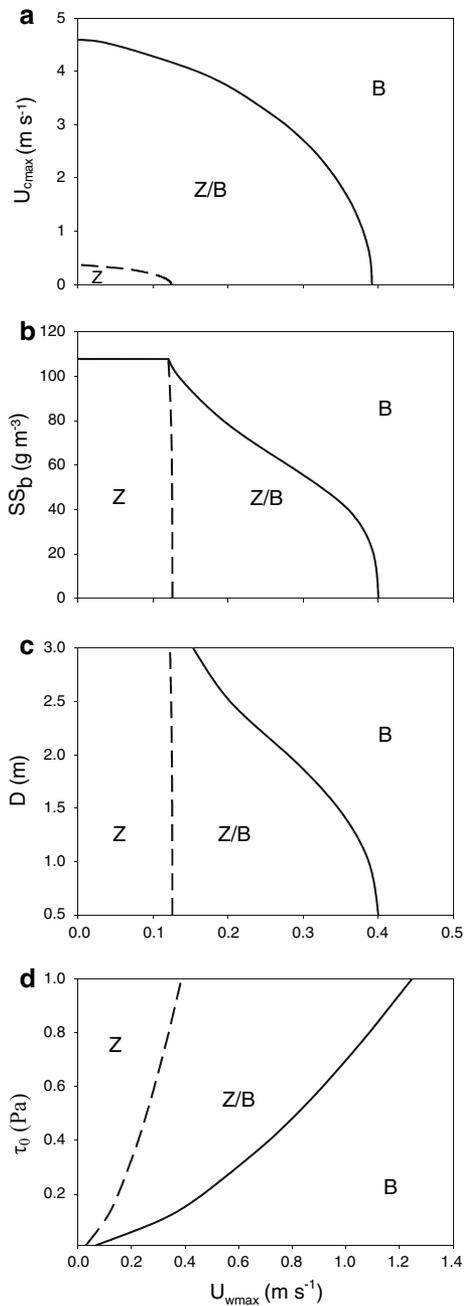
Figure 5. Bifurcation analysis on the maximum orbital velocity (U_{wmax}) for varying current velocity (U_{cmax}), depth (D), background levels of suspended sediment (SS_b) and the critical bed shear stress boundary (τ_c). *B* indicates a bare state; *Z/B* indicates the area where alternative stable states occur. *Left* of the *dashed lines* (indicated with *Z*), eelgrass presence is the only stable state. To get a clear view of the model behavior, we set current velocity to zero when analyzing the effects on orbital velocity and vice versa. Note that at a set wave height, the near-bed orbital velocity decreases with depth. This effect is ignored in **B**, as we were solely interested in examining the sensitivity of the model to varying depths.

seagrass communities in general. As shown in this study on the Wadden Sea, it might help to explain dramatic shifts such as the 1930s decline of eelgrass in the Dutch Wadden Sea and lack of recovery despite intense restoration efforts.

Our study suggests that the Wadden Sea eelgrass beds could not recover due to threshold behavior, caused by positive feedback mechanisms in the system. In the absence of eelgrass, current and wave velocities were no longer reduced and suspended sediment concentrations and related turbidity levels became too high to sustain eelgrass growth. However, an alternative explanation could be that the conditions in general have changed in such a way that eelgrass cannot grow. Indeed, the lack of recovery since the 1930s has been typically attributed to increased turbidity levels (Giesen and others 1990). Even for the intertidal beds, light conditions proved to be too poor. The eelgrass lower depth limit for obtaining sufficient light shifted up high into the intertidal zone, beyond the upper depth limit marked by the intertidal beds. Thus, required emersion periods became too long for eelgrass to survive, as desiccation becomes a limiting factor for eelgrass at these shallow depths (Giesen and others 1990). The poor light conditions were allegedly caused by eutrophication related high phytoplankton levels and dredging and sediment extracting activities (Giesen and others 1990). Additionally, enhanced deposition of fine material from the river Rhine (De Jonge and De Jong 2002) and erosion caused by increased tidal currents due to the Afsluitdijk construction, may also have led to an increase in turbidity in the western part of the Wadden Sea (Den Hartog and Polderman 1975; Giesen and others 1990). Our analyses suggest that phytoplankton had no significant part in the failure of eelgrass to recover, as turbidity is only weakly related to phytoplankton. We show that the main factor determining turbidity in shallow areas is suspended sediment, a factor that is closely related to depth. This can be explained by an increasing shear stress on the sediment bed with decreasing depth, caused by the combined effects of wind-driven currents and waves (Postma 1961; Houwing 1999; Christiansen and others 2006; Condie and Sherwood 2006). The effect of enhanced deposition from the river Rhine seems moderate at a large scale. Data used in our analyses include locations from both the western and the eastern part of the Wadden Sea, and are not restricted to the western part that is more influenced by the river. The relations we derived seem to apply to the Dutch Wadden Sea as a whole,

irrespective of local differences in sediment composition. Finally, increased tidal currents are unlikely to have caused substantial additional sediment erosion. Even at present conditions, tidal current velocities alone are not nearly strong enough to initiate sediment erosion. Instead, erosion in the Wadden Sea is primarily controlled by weather conditions (for example, wind-driven currents and waves) (Janssen-Stelder 2000; Christiansen and others 2006).

Our model cannot determine what triggered the disappearance of the eelgrass beds in the 1930s. We can only show that there is probably a critical density of eelgrass below, which the population collapses. In the 1930s, there were two external impacts that may have pushed the eelgrass population below this critical density: the wasting disease and the increased concentrations of suspended sediment caused by the Afsluitdijk construction (Giesen and others 1990).

As our results suggest that eelgrass recovery at default model settings is very difficult, it raises the question of how eelgrass colonized the Wadden Sea in the first place. First of all, it is obvious that the conditions in the Wadden Sea are not homogeneous, whereas our predictions were made with average conditions. This means that colonization may still be possible in optimal areas (for example, sheltered areas with firm sediment and low concentrations of suspended solids). Secondly, it should be noted that in the past, eelgrass could develop in much calmer hydrodynamic conditions in this region. Around 7,000 years ago, sheltered tidal basins developed behind an extensive barrier coast when the rate of the sea level rise in that era decreased (Van der Molen and Van Dijck 2000). It seems likely that initial colonization had already taken place millennia ago in these ancient lagoons (Olsen and others 2004).

Although our analysis suggests that alternative stable states occur over a wide range of parameter settings, some processes are represented in a very simple way in our model. The most significant simplification is that we disregarded a possible turbidity gradient from the edge to the center of the bed. Turbidity of the water entering the bed may be higher due to sediment resuspension in adjacent barren areas. Water clarity towards the center will increase as suspended particles settle due to reduced hydrodynamics. By considering conditions near the edge of the bed we underestimated the general clearing effect of large eelgrass beds. These effects may be described by a spatially explicit model. However, at present the spatial processes involved are poorly understood. Calculations on

particle settling velocities and traveling distance into the bed are extremely complex, depending on particle size and shape (Le Roux 2005), particle flocculation (for example, Pejrup and Edelvang 1996; Edelvang and Austen 1997), water turbulence (Ward and others 1984; Granata and others 2001), flow velocity (for example, Ward and others 1984; Gambi and others 1990; Fonseca and Cahalan 1992; Granata and others 2001) and direct trapping of particles by seagrass canopies (Agawin and Duarte 2002).

In recent decades, restoration and protection of seagrasses have gained a strong foothold in the ecosystem management of marine ecosystems worldwide (Orth and others 2006) as well as in the Wadden Sea (for example, Van Katwijk and Hermus 2000; Van Katwijk and others 2000). A better understanding of feedbacks and threshold behavior in seagrasses is important as the lack of recognition may in part explain the seemingly high resilience, related sudden collapses (Jackson and others 2001) and the high number of failed restoration attempts that are observed worldwide (Orth and others 2006). Currently, numerous restoration projects, using a wide variety of transplantation techniques, are being planned mostly at small scales (<1 ha) (Orth and others 2006). Our results suggest that it is in fact this small scale that may be responsible for the low overall success rate, as small populations cannot modify their environment sufficiently to cross-critical thresholds. As our model is not spatially explicit, we can only speculate on the minimum viable population size for either transplantation or conservation efforts in seagrass ecosystems. Much will depend on the maximum expansion rate of the meadow under consideration and the spatial exchange rates of both recourses and stressors (Van Nes and Scheffer 2005). With respect to the Wadden Sea situation, we estimate that future transplantations should be at least on the order of several hectares as turbidity in adjacent bare areas will be high and rhizotomous expansion rates near de edges will be relatively slow. Currently, such large-scale transplantations are most likely not feasible. Therefore, restoration may only be possible if the water layer in a considered area is temporally cleared using devices such as enclosures or artificial seagrass to obtain a sufficiently large eelgrass meadow that can sustain itself.

In other ecosystems, the success rate of restoration is often related to the scale of management measures. In for instance shallow lake management, where the relevance of alternative stable states has been recognized for over a decade (Scheffer and others 1993), a shift to clear water

can only be achieved by large-scale manipulation, targeting the trophic structure of the ecosystem as a whole (Meijer and others 1999). In this perspective, some important implications for the management of ecosystems emerge from these studies. (1) The possibility of positive feedback mechanisms in a target area should be studied to improve chances for conservation or restoration efforts. (2) Where there is an important feedback, the transplanted population size (and density) should be adjusted according to the ecosystem resilience to invoke a shift, whereas in conservation the focus should be on preventing the system from exceeding the critical threshold in the first place.

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