SOFT-BOTTOM NEAR-SHORE ECOSYSTEMS

Seagrass–sediment interactions, positive feedbacks and critical thresholds for occurrence: a review

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Abstract This literature review summarizes the limiting factors for seagrass occurrence, and the effect positive feedbacks in seagrass systems have on these threshold levels. Minimum water depth is mainly determined by wave orbital velocity, tide and wave energy; and maximum depth by light availability. Besides these, other limiting factors occur, such as an upper current velocity threshold, above which seagrasses are eroded, or a lower water current velocity threshold below which carbon exchange is limiting. In some locations organic matter content, sulphide concentration or nutrient availability are limiting. N-limitation is mainly reported from temperate terrigenous sediments, and P-limitation from tropical carbonate sediments. However, limiting factors sometimes change over the year, switching from light limiting to N- or P-limiting, and show at times regional variation. The effect seagrasses have on current reduction, trapping sediment and decreasing resuspension can lead to several changes in both the sediment and the water column. In the sediment, an increase in nutrient availability has been reported, and increases in organic matter, sediment height increases, and burial of the seagrasses. In the water column the effect is a reduction of the turbidity through a decrease of the sediment load, decreasing the attenuation coefficient, thereby increasing light availability. Due to the large effect light availability has on seagrass occurrence, the effect of an improvement of the light conditions by a reduction of the turbidity by seagrasses is probably the most important positive feedback in seagrass systems. The latter effect should therefore be incorporated in models that try to understand or predict seagrass changes. Generalization are difficult due a lack of studies that try to find relationships between seagrass architecture and sediment trapping (studying both turbidity reduction and nutrient increase) on a global level under a variety of different conditions. Areas for research priorities are identified.

Keywords Water current velocity · Nutrient limitation · Sediment trapping · Resuspension · Turbidity · Light

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Introduction

The importance of seagrasses in the marine ecosystems has been documented in numerous studies in which seagrasses are noted as a nutrient

source, nursery area, and as a habitat for fishes, benthic organisms and marine mammals. However, seagrass habitats are highly dynamic, and a decrease in seagrass extent has been documented over the last centuries, mainly due to human disturbance (Cambridge et al., 1986; Short & Wyllie, 1996; Daby, 2003; Campbell & McKenzie, 2004; Cardoso et al., 2004; Hughes et al., 2004; Morris & Viknstein, 2004; Gonzalez et al., 2005; Polte et al., 2005; Waycott et al., 2005; Orth et al., 2006). An important phenomenon in seagrass meadows is that seagrasses are able to change their own environment, by sediment fixation, or by their capacity to enhance sediment and organic matter trapping (Moriarty & Boon, 1989). These processes are sometimes positive feedbacks (Herman et al., 2001; Rietkerk et al., 2004), and seagrasses could benefit from the changes they create, stimulating seagrass growth or decreasing the chance of mortality from erosion (Cardoso et al., 2004). The large, sometimes cascading effects generated by seagrasses have been the basis for some researchers to classify seagrasses as ecosystem engineers (Koch, 2001). Field studies normally emphasize only one or few mechanisms that are responsible for the effect seagrasses have at their specific study site. However, the effect seagrasses have on their direct environment can be the key in understanding seagrass distribution (Fonseca & Bell, 1998), and thereby the associated faunal community (Walters & Moriarty, 1993; Asmus & Asmus, 2000; de Boer, 2000; de Boer et al., 2001; de Boer & Prins, 2002a, b; Fisher & Sheaves, 2003; Healey & Hovel, 2004), or the nutrient coupling between mangroves, corals and seagrasses (Slim et al., 1996; Mumby et al., 2004).

A study is needed to describe the abiotic conditions of seagrasses under which positive feedbacks occur. Moreover, various authors hypothesize that the above positive feedback mechanisms operate (Moriarty & Boon, 1989; Koch, 1999; Fonseca et al., 2002), but hard evidence is often lacking. This review aims to fill this gap, as such contributing to a better understanding of seagrass dynamics, and constructing a knowledge-base that will be useful for modelling seagrass dynamics. Modelling will provide a tool for predicting the presence/absence or biomass of seagrass, and the resilience or recovery changes of seagrass systems. The objective of this review is to describe these positive feedbacks, to examine the effect they have on seagrass systems, and to investigate whether these feedbacks change the thresholds at which seagrasses are known to occur, such as the thresholds, or tolerance levels, related to water depth or water current velocity. In the first part of the paper the limiting factors and tolerance levels will be described: water depth, light availability, water currents, and nutrient availability. The second part of the paper examines the effect seagrasses have on sediment trapping, resuspension, and changes in the sediment, and in the water column, such as a reduction in turbidity.

Seagrass depth limits

What are the water depths at which seagrasses can be found, is there a maximum and minimum depth limiting seagrass occurrence? Koch (2001) reviewed the effect of waves and tides on the occurrence of seagrasses as related to the minimum depth where seagrasses can be found. Seagrass depth limits seem to be related to wave energy, as waves erode seagrass beds. Chambers (1987) reported a close correlation between the depth of surface wave mixing and the minimum depth of seagrass occurrence, suggesting that the minimum depth where seagrasses can occur is the wave mixing depth, calculated as:

$$Z_{\min} = L/2,$$

where L can be calculated from $L = (gT^2)/(2\pi)$, and g is the acceleration of gravity, i.e. 9.8 m/s, and

$$T = \left[\frac{0.46W}{g}\right]\left[\frac{gF}{W^2}\right]^{0.28}$$

where w is the wind velocity (m/s) and F the wind fetch.

The impact of waves also depends on the tidal amplitude. Consequently the upper water depth where seagrasses can occur is dictated by the wave energy and the maximum tidal amplitude.

Seagrasses are found in intertidal areas (especially *Zostera* spp., *Halophila* spp. *Phyllospadix* spp.), but are generally not fully exposed for prolonged periods, and disappear under excessive desiccation or freezing (Ramirez et al., 1998; Huong et al., 2003; Boese et al., 2005). So that Z_{min} becomes:

$$Z_{min} = \frac{A}{2} + \frac{gT^2/2\pi}{2}$$

Numerous publications have assessed the effect of light on seagrass distribution, and the largest depth Z_{max} where seagrasses occur (Duarte, 1991; Terrados & Ros, 1995; Abal & Dennison, 1996; Jagtap, 1996; Olesen, 1996; Moore et al., 1997; Nelson & Waaland, 1997; Terrados et al., 1997). Turbidity is an important factor decreasing irradiance, and thereby determining photosynthetic rates, plant survival and recruitment, and hence influencing seagrass occurrence (Duarte, 1991; Abal & Dennison, 1996; Jagtap, 1996; Olesen, 1996; Moore et al., 1997; Terrados et al., 1997). The lower distribution boundary depth Z_{max} is set by light availability, and is influenced to a large extent by the turbidity of the water, influencing K_d, the light attenuation in the water column:

$$Z_{max} = \frac{-\ln(I_z/I_o)}{K_d}$$

where I_z/I_0 is the species-specific percentage of light required (or the percentage of light at the maximum depth of the species).

From Z_{max} and Z_{min} the depth range at which the species may be found can be calculated, however the formula does not take into account the effect of wave energy reaching the seagrasses. Hence, with increasing wave energy Z_{min} will be larger, and Z_{max} unaffected (Koch, 2001).

Hence, the factors that limit seagrass maximum and minimum depth have been documented clearly. An overview of the above mentioned factors, such as wave energy and water column depth, together with their relative influence on seagrass occurrence is given in Table 1, and the main factors impact schematically depicted in Fig. 1.

Water current velocities

Erosion of bed material through shear stress or catastrophic events is an important phenomenon in seagrass meadows (Teeter et al., 2001). Seagrasses are absent under extreme water current levels, so there is an upper water velocity threshold above which seagrasses do not occur (Fonseca & Bell, 1998). The force acting on the seagrasses can be described as (Dawson & Robinson, 1984, cited in Madsen et al., 2001):

$$F = k * V^{l*bm}$$

where F is force in N, V is velocity in m/s, B is the seagrass biomass in kg Fresh Weight (FW) per plant, and k, l and m are season and species-specific coefficients.

The erosion impact depends on the bed material, with lower erosion values reported for beds with increased sand content (Aberle et al., 2004). Bulk density, and thereby the porosity of the sediment and the organic matter content, are important predictors for erosion rates, as cohesive sediments with increased clay content may reduce erosion. Salinity also influences erosion, with erosion rates up to five times lower in saltwater environments than in freshwater (Aberle et al., 2004). Especially in estuarine waters, with salinities <10‰, an increase in salinity increases the cohesive properties of sediments by influencing the inter-particle electrochemical bonds (Parchure & Mehta, 1985). A reduction in resuspension of bed material in seagrass meadows also contributes to an increase in sediment stability (Gacia & Duarte, 2001).

Fonseca & Bell (1998) showed that seagrass has a patchy distribution in North Carolina, and the patchy distribution was attributed to current speeds and the effect seagrasses have on sediment stabilization among other factors. Above 50% seagrass cover (i.e. the % seagrass cover within the meadow), currents speeds were typically <0.25 m/s, below the initial motion current speed of sand. Fonseca & Bell (1998) predicted to find a patchy distribution in high energy areas, whereas continuous seagrass meadows would be more typical for low energy areas. State transitions are quite rapid once the thresholds have been

Table 1 Overview of main factors influencing seagrass occurrence with a subjective estimate of their relative importance

Parameter	Importance	Spp	References
Seagrass minimum depth limits			
Maximum water column depth	+	y	Koch (2001), Chambers (1987)
Wave energy	+	y	Koch (2001), Madsen et al. (2001), Fonseca and Bell (1998)
Tidal range	+	n	Koch (2001)
Maximum temperature	–	y	Ramirez et al. (1998), Boese et al. (2005)
Wind force	+	n	Preen et al. (1995), Bell et al. (1999)
Wind velocity	+	n	Koch (2001)
Seagrass maximum depth limits			
Light attenuation	+	n	Duarte (1991)
Turbidity	+	n	Duarte (1991), Abbal & Dennison (1996)
Sediment reflectance	–	n	Zimmerman & Mobley (1997)
Tidal ranges	+	n	Koch (2001)
Self-shading	+	y	Fonseca et al. (1982), Ruiz & Romero (2001)
Hour of the day	+	n	Van Duin et al. (2001)
Season	+	n	Van Duin et al. (2001), Plus et al. (2003)
Waves (reflectance)	–	n	Van Duin et al. (2001)
Wave focussing	–	n	Van Duin et al. (2001)
Cloudiness	+	n	Van Duin et al. (2001)
Epiphyte biomass	+	y	Strand & Weisner (1996), Hays (2005)
Sediment burial	+	y	Preen et al. (1995), Vermaat et al. (1997)
Seagrass erosion mortality			
Grainsize	–	y	Teeter et al. (2001)
Wave energy	+	y	Koch (2001)
Water porosity	+	y	Aberle et al. (2004)
Salinity	–	n	Parchure & Mehta (1985), Aberle et al. (2004)
Seagrass aboveground biomass	+	y	Madsen et al. (2001)
Rhizome architecture	+	y	Marbà & Duarte (2001), Kendrick et al. (2005)
Above/belowground biomass ratio	+	y	Madsen et al. (2001)
Seagrass critical erosion force	+	y	Madsen et al. (2001)
Sediment plasticity	+	n	Aberle et al. (2004)
External factors:, e.g. diatom films, arenicola activity etc.	–	y	Herman et al. (2001), Cappuci et al. (2004), Louda et al. (2004)
Seagrass sediment trapping and resuspension reduction			
Water current velocity	+	n	Herman et al. (2001), van Duin et al. (2001)
Sediment composition (e.g. clay/silt fraction)	+	n	Teeter et al. (2001), Aberle et al. (2004)
Sediment cohesiveness	+	n	Aberle et al. (2004)
Seagrass vertical biomass profiles	+	y	Gacia et al. (1999a), Madsen et al. (2001)
Seagrass architecture (e.g. leaf shape, bending force)	+	y	van Keulen & Borowitzka (2002)
Seagrass bending flexibility	–	y	Madsen et al. (2001)
Water current attenuation	+	y	Fonseca & Kenworthy (1987)
Wave energy (& wind energy)	+	n	Madsen et al. (2001), Koch (2001)
Tidal energy	+	n	Koch & Beer (1996), Herman et al. (2001)
Turbulence	+	n	Wolanski (1992), Furukawa et al. (1997), Gacia & Duarte (2001), Louda et al. (2004)
Edge/meadow ratio	+	y	Fonseca et al. (1982)
Leaf/area index	+	y	Gacia et al. (1999a)
Sediment surface roughness	–	y	Madsen et al. (2001)
Sediment suitability			
Grain size	–	n	Erftemeijer & Middelburg (1993)
Nutrient composition (N, P)	+	y	Hughes et al. (2004)
Organic matter content	+	y	Koch (2001)
Sulphide concentration	+	n	Isaksen & Finster (1996), Koch (2001)

Table 1 continued

Parameter	Importance	Spp	References
Salinity	–	y	van Katwijk et al. (1999)
Oxygen content	+	y	Isaksen & Finster (1996)

(+ = often cited as being important, or with high effect size; – = infrequently cited, or with low effect size), whether the factors are species-specific (y/n), and key references (for additional references consult the main text)
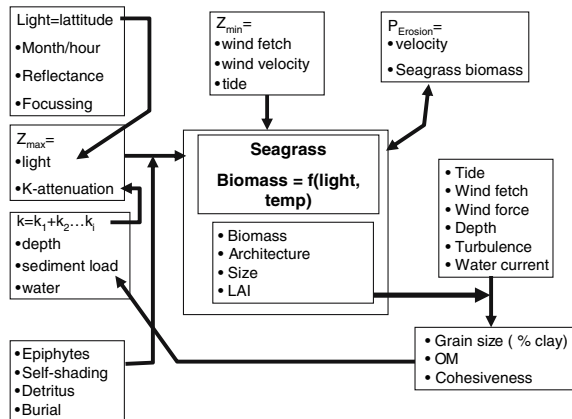
Fig. 1 Schematic representation of the main factors that determine seagrass occurrence, see text for explanation

reached. Thresholds do however seem to be species-specific, with different species exhibiting different patterning at similar current speeds or wave disturbance (Fonseca & Bell, 1998). The authors also described the formation of halo-like patterns in seagrass patches, and suggested that the pattern was caused by radial growth from plants that colonized the patches from the middle of the circle.

Sediment stabilization by seagrasses may enhance seagrass survival rates especially during periods of extreme conditions such as storms (Preen et al., 1995; Bell et al., 1999; Gacia & Duarte, 2001). However, few studies have been able to document the threshold above which meadows are eroded. Fonseca & Bell (1998) showed that belowground biomass increased with increasing wave disturbance, suggesting compensatory seagrass growth to adapt to unfavourable local conditions. One study indicated that *Zostera marina* beds can tolerate current velocities up to 120–150 cm/s (Fonseca et al., 1983). Koch (2001) reported minimum current velocities of

0.04–16 cm/s, and maximum velocities between 7 and 180 cm/s tolerated by seagrass, depending upon species, with intermediate velocities of 5–100 cm/s for optimal development. The latter values represent the upper water current velocity threshold for seagrasses, but there is also a lower water current velocity threshold. Low velocities could decrease photosynthetic rates through a reduction in the diffusion boundary layer limiting carbon availability (Fonseca & Kenworthy, 1987; Koch, 1994; Madsen et al., 2001), although carbon limitation mainly occurs at low blade friction velocities (<0.25 cm/s). These lower water velocities are probably only possible during slack tide. Hence, CO_2 exchange is improved and also nutrient limitation reduced at increasing current speed, with maximum values observed at 0.02–0.06 m/s (Madsen et al., 2001). At lower current speeds a thicker diffusion boundary layer will be built up. Higher mortalities have been observed due to carbon limitation if the diffusion boundary layer is larger than the critical diffusion boundary layer for each species (98–280 μm; Koch, 2001). Low densities of epiphytes may disrupt the diffusion boundary layer, stimulating carbon exchange, but generally epiphytes are regarded as having only negative effect on seagrasses (Koch, 2001).

Sediment stability can also be enhanced by numerous other factors, from diatom biofilms (Herman et al., 2001; Cappuci et al., 2004) to *Corophium* or *Arenicola* activity. Seagrasses might be able to enhance sediment stabilization indirectly, but according to Defew et al. (2002) it is unlikely that universal proxy parameters for sediment stability could be obtained. Louda et al. (2004) showed that seagrasses could be important catalysts in state transitions, by reducing wave energy levels, facilitating the development of hydrogels, built up from polysaccharides derived

from diatoms and cynobacteria, thereby enhancing sediment stabilization. Benthic microalgae increased sediment stabilization due to their production of extracellular polymeric substances (Austen et al., 1999). Another effect generated by lower water current levels, and impact of seagrass meadows is found in the increase of filamentous macroalgae in seagrass meadows (Piazi et al., 2002; Keuskamp, 2004), potentially leading to an even stronger negative effect on current speeds. Erosion is an important process, affecting seagrass occurrence. However, the species-specific thresholds, and the effect seagrasses have on sediment stabilization, thereby decreasing the erosion probability, are poorly documented.

Nutrient limitation

Some studies have addressed the role of seagrasses in increasing nutrient availability in seagrass meadows, thereby increasing seagrass growth. However, this effect can only be important if seagrasses are nutrient limited. There is a large ongoing debate (e.g. compare Koch, 2001; Hughes et al., 2004) about the relative importance of nutrient limitation versus light limitation.

N-limitation in seagrass has been reported in various studies (Boon, 1986; Kenworthy & Fonseca, 1992; McGlathery et al., 1992; Lee & Dunton, 2000), similar to P-limitation (Short et al., 1985, 1990; Fourqurean et al., 1992; Erftemeijer & Middelburg, 1993; Perez et al., 1994; Fourqurean & Cai, 2001; Gras et al., 2003). An important distinction between N- and P-limitation occurs in relation to sediment type, with typical N-limitation of seagrasses in temperate areas on terrigenous or sandy sediments, and P-limitation in tropical environments on carbonate sediments (Short, 1987; Touchette & Burkholder, 2000). However, some studies have reported N-limitation in carbonate sediments (Udy et al., 1999). Terrigeneous run-off is larger in coastal systems than in off-shore oligotrophic reefs systems, so that the location of the seagrasses, i.e. the distance to the nutrient source, is also important (Carruthers et al., 2002; Fourqurean & Zieman, 2002). Nutrient availability is also determined partly by sediment types, as porewater nutrient

concentrations depend on grain size and sediment origin (Fourqurean et al., 1992; Holmer et al., 2001). Coarse-grained carbonate sediments have larger phosphate availability due to the sediments' limited adsorption capacity, compared to fine-grained sediments (Erftemeijer & Middelburg, 1993). However, carbonate sediments are generally low in organic matter content (Erftemeijer, 1994).

In order to be able to study the potential effect feedbacks have on seagrass performance, it is important to distinguish the seagrass species in terms of nutrient limitation. Duarte (1995) described the effect of a gradient of nutrient addition to seagrass sediments, and expected a shift from slow-growing seagrasses and large macro-algae, to fast-growing macro-algae, ultimately leading to a phytoplankton dominated state, with these three states reflecting a change from nutrient to light limitation (see also Harlin & Thorne, 1981; Davis & Fourqurean, 2001; Plus et al., 2003). Seagrasses have low nutrient requirements and are able to recycle nutrients efficiently, so that they are strong competitors under low nutrient levels (Koch, 2001; Armitage et al., 2005). Seagrass species react differently to different nutrient levels so that changes in community composition are expected when the nutrient pool changes (Duarte 1992; Agawin et al., 1996; Udy & Dennison, 1997; Ferdie & Fourqurean, 2004).

Seagrasses are however often limited by different factors according to the seasons, such as light limitation in winter, and N-limitation in summer or during the peak growing season (Short et al., 1993; Herzka & Dunton 1998; McMahon & Walker 1998; Campbell 2001; Plus et al. 2003). Similarly, spatial variation exists in different limiting factors at different locations (Terrados et al., 1999; Ferdie & Fourqurean 2004). In fact, some systems show both N- and P-limitation depending on the local conditions (Fourqurean & Zieman, 2002; Alcoverro et al. 1997). The various seagrass life stages may exhibit different tolerance to nutrient levels (Kenworthy & Fonseca, 1992).

Effective nutrient resorption from senescing leaves becomes important when nutrients are limited (Hemminga et al., 1999). If the sediment nutrient pool is limited, water nutrient flow

becomes more important (Sfriso & Marcomini, 1999), emphasizing the role leaves have in nutrient intake (Stapel et al., 1996). Lepoint et al. (2002) calculated that leaf and root contribute respectively 40% and 60% to the annual N-uptake for *Posidonia oceanica* in the Mediterranean. In fact, standing stock nutrient pools are a poor indicator of nutrient limitation, and understanding the dynamics of nutrient pools, sinks and flows is important to untangle the role specific nutrients have in limiting seagrass growth (McGlathery et al., 2001). The importance of nitrogen fixation and denitrification in seagrass beds needs to be understood (Rysgaard et al., 1996; Welsh et al., 2000) in order to be able to estimate the impact of an increased nutrient availability on the nitrogen budget in seagrass systems.

Eutrophication is also important, as it stimulates macroalgae and phytoplankton growth, increases the concentration of solids, and triggers anoxic effects, resulting in reduced light availability and the loss of seagrass cover (Valiela et al., 1990; Powell et al., 1991; Abal & Dennison, 1996; Livingston et al., 1998; Lee et al., 2004). The global decrease in seagrass cover has been attributed to eutrophication increasing epiphyte biomass (Hughes et al., 2004). Direct toxic effects of eutrophication, such as ammonia toxicity or excessive nitrate concentrations, have also been reported (Touchette & Burkholder, 2000; Peralta et al., 2003). Salinity and eutrophication interact, and can explain decrease in *Zostera* beds in the northern hemisphere (van Katwijk et al., 1999).

Some authors do however emphasize light as the main limiting factor for seagrass occurrence or seagrass growth (Duarte, 1991; Terrados & Ros, 1995; Hillman et al., 1995; Abal & Dennison, 1996; Jagtap, 1996; Olesen, 1996; Moore et al., 1997; Nelson & Waaland, 1997; Terrados et al., 1997). Various studies were unable to find any effect of nutrient availability on seagrass performance or occurrence, both in correlative studies or experiments (Erftemeijer et al., 1994; Vermaat & Verhagen, 1996; Ceccherelli & Cinelli, 1999; Rose & Dawes, 1999; Worm & Reusch 2000; Holmer et al., 2001), so that it is still difficult to generalize about the light versus nutrient limitation effects. In comparison to the limiting factors described above, factors such as salinity or temperature (Perez & Romero, 1992; Hillman et al., 1995) have a smaller impact on seagrass performance or on seagrass distribution.

Sediment trapping

One of the most frequently quoted impacts of seagrasses on their environment is their capacity to trap sediments. The ability of seagrass to influence sediment settling is related to water velocity and sediment particle size. Absolute current velocities over time determine the fraction of the sediment that will be deposited, depending on the differential settling velocity of the different particles in relation to the upward force. The fall velocity is proportional to the diameter squared of the different particles and densities differences (Stoke's Law; van Duin et al., 2001). Sand particles settle at speeds <0.20 m/s, whereas coarse sand gravel settles at higher current speeds (<1 m/s). The clay fraction has the smallest grain size, but because of its cohesiveness, requires larger current speeds to erode. Deposition of finer particles is therefore strongly influenced by tidal current and tracks the tidal cycles (Herman et al., 2001). The silt and clay fraction will only settle under very low current levels, and is increased in areas that cope with high siltation levels (Cappuci et al., 2004).

Seagrasses reduce the water flow above the sediment, enhancing sedimentation (Fonseca & Kenworthy, 1987). Sediment trapping has been reported for various seagrass species and numerous locations (see overview in Koch, 2001 and Madsen et al., 2001; Gacia et al., 2003), although some studies, mainly concentrating on relatively small species such as *Halodule* spp. and *Halophila* spp. found no significant difference between vegetated and unvegetated sites in terms of sediment structure or nutrient status (Mellors et al., 2002). Sediment trapping has also been recorded for kelp forests (Eckman et al., 1989), bryozoan meadows (McKinney & Jaklin, 2001) and other macrophyte vegetations (Vermaat et al., 2000; Madsen et al., 2001). Rhizome architecture is highly variable among seagrass species (Marbà & Duarte, 2001; Kendrick et al., 2005; Sintes et al., 2005), and has probably an

important impact on current reduction. Water velocity profiles normally show log–profile relationships, and are reduced with a factor 2–10 in seagrass beds compared to above the canopy (Gambi et al., 1990; Koch, 2001). This reduction in water velocity depends on the architecture and biomass of the seagrass meadows. For instance, in meadows where sheaths hold the leaves above the surface, the water velocity near the bottom were three times stronger than the ones passing through the seagrass leaf strata (Koch, 1999). Hence, the water velocity profile is strongly influenced by the vertical seagrass biomass distribution. Seagrasses with branched erect stems with terminal leave clusters, such as *Amphibolis*, are characterized by high water velocities just beneath the leaf canopy (van Keulen & Borowitzka, 2002). When seagrasses cover the entire water column (e.g. during neap tide), current velocities are efficiently reduced and suspended sediments can settle; in areas where the water depth is larger than the meadow height, both resuspension and deposition occurs simultaneously (Koch, 1999, 2001). Shoot bending is a mechanism to reduce current velocity (up to 50% reduction in current velocity; Madsen et al., 2001), but it also increases self-shading and thereby reduces the photosynthetic capacity. The effect of current reduction on sedimentation also depends on the local hydrodynamic climate, as unidirectional flows (tides) lead to lower mixing between water above and within the meadows, whereas waves increase water exchange between the two layers (Koch & Gust, 1999).

There is not only a vertical gradient in the impact of seagrasses on water velocity but also a horizontal component. Current velocity intrusion into the meadows proceed by a factor 1.25 into the meadow per cm/s current velocity, before diminution, or by a factor 2.1 before maximum current reduction (Fonseca et al., 1982), indicating that the meadow edge is the most dynamic zone of seagrass habitats.

Fonseca & Kenworthy (1987) reported that canopy height decreases linearly with increasing current speed. However, there is no general relationship between the water current reduction, wave attenuation and seagrass biomass profiles, complicating the possibility of including

the latter relationship in mathematical models (Madsen et al., 2001). Sedimentation is stratified horizontally and vertically, and depends on currents, waves, wind energy transfer (Lund et al., 1993) and seagrass biomass profiles. The effect of the seagrass biomass and architecture on current reduction and associated increase in sedimentation has been investigated in few studies. Water current velocity reduction is positively correlated with the height of the plants, and the surface area of the plants is significantly correlated with the amount of trapped particles (Gacia et al., 1999a). Gacia et al. (1999a) showed that the downward sediment flux increased from 5 to 11 g DW/m^2/d under an increase of the Leaf Area Index from 1 to 5 m^2 leaves/m^2. Gacia et al. (2003) documented daily deposition rates between 19 and 681 g DW/m^2/d, with the majority < 200 g DW/m^2/d, and organic matter (OM) content <8%. The latter study also made a summary of the sedimentation values reported in other studies showing average values 2.3–67.4 g DW/m^2/d.

Organic matter is also trapped in seagrass meadows, however this is not always advantageous. Koch (2001) showed that sediment with >5% OM had a negative effect on marine macrophyte development. There is a negative effect of current speeds on nutrient availability and organic matter content (Chambers et al., 1991), which might influence seagrass biomass either linearly (nutrients) or unimodally (organic matter). Hence, resuspension may be an important process, preventing OM from building up above critical levels. Water currents are thus able to constrain seagrass growth through their effect on sediment composition. The silt concentration in the water column also has other effects; seagrass species composition and leaf biomass values change under an increasing silt fraction in the sediment, with relatively low species richness (from five to one species) and reduced leaf biomass (from 150 to <50 g DW/m^2) with increasing silt and clay content of the sediment from about 3–45% (Terrados et al., 1998).

Besides small organic matter particles, also larger biogenic material can be trapped in seagrass beds. *Posidonia oceanica* beds accumulate

roots, rhizomes and shoots over thousands of years, with an average of 0.175 cm/yr, equivalent to 58 g C/m^2/yr, 0.59 g N/m^2/yr, and 0.03 g P/m^2/yr (Mateo et al., 1997). Other studies reported accretion rates of 0.34–1.50 cm/yr (references cited in Mateo et al., 1997).

Sedimentation of organic sediments is determined by the differential settling velocity of the particles. Organic matter is a food resource for a wide variety of benthic species and can be used as a nutrient pool by the seagrasses. Besides a direct impact on the nutrient and OM pools, the OM content can also influence colonization of animals, for example corophiid amphipods (Ford et al., 2001), or other benthic species (Fisher & Sheaves, 2003). There is an interaction between hydrodynamics and sediment composition in determining colonization rate and size distribution of amphipods. High organic matter contents (>1%), decreased oxygen levels and increased sulphur levels had a negative effect on amphipod colonization rate. Isaksen & Finster (1996) also reported the positive effect of degradation of leaf fragments in the sediment on pH, redox potential and sulphate reduction. This could potentially lead to the build-up of toxic sulphide concentrations from sulphate reducing bacteria in anoxic sediment above seagrass tolerance levels. Sulphate reduction rates were about twice as high in the root zone (0–4 cm) of by *Zostera noltii* vegetated sediments than in unvegetated sediments, but no significant difference could be found below the root zone (Isaksen & Finster, 1996). An increase in the clay and silt fraction in the sediment through sediment trapping leads to a reduction in pore water exchange with the water column, contributing as such to anoxic conditions. Koch (2001) reported that seagrasses normally occur at sediment sulphide concentration <1–2 mM. Clay and silt fraction in seagrass meadows vary widely between 0.4% and 72%, with highest values reported from lower salinity environments. In higher salinity environments coarser sediments are needed to reduce sulphide concentration can be reduced through increased porewater advection rates (Koch, 2001). OM content >5% generally cause nutrient limitation due to the high organic deposits, or increase sulphide concentrations to toxic levels (Koch, 2001). The negative effect of sulphide concentrations on seagrass production seems clear, but no hard thresholds are available to characterize habitat suitability (Koch, 2001).

Resuspension of deposited material

Sedimentation in seagrass beds is not only the result of the reduced water current velocities and subsequent sediment deposition, but also a decrease in resuspension of deposited sediments (Terrados & Duarte, 2000). Bed material is normally eroded when critical friction velocity (U_{*crit}) is exceeded by the shear stress τ, where $U_*^2 = \tau/\rho$ (ρ is the water density; Madsen et al., 2001). The suspended particle concentration normally increases exponentially until U_{*crit} has been reached. However, this depends on the local surface roughness, something which has not been studied in seagrass meadows. Another factor is whether wave energy reaches the sediment surface. Hence, resuspension is a frequent phenomenon in shallow water where the water column depth is <1/3 of the wavelength (Carper & Bachman, 1984). Local turbulence is another key factor in resuspension of bed material (Wolanski, 1992; Furukawa et al., 1997). The effect of seagrasses on turbulence has been described as increasing, decreasing, or unaltering turbulence levels by various studies (see review in Madsen et al., 2001), complicating the matter further. One of the problems in our understanding is that the smaller particles (silt and clay) and OM tend to form cohesive sediments, aggregates with special properties, and that the resuspension and settling of these sediments is poorly understood (Furukawa et al., 1997; Teeter et al., 2001). Terrados & Duarte (2000) used dried leaf fragments in their experiment and found daily particle loss rates of 38–98% in seagrass beds compared to 63–99% outside these beds. Near-bottom turbulence stress decreased with a factor 2.5–3 in seagrass meadows, restricting resuspension to the top 1 mm, instead of the top 3 mm in unvegetated sediments (Gacia & Duarte, 2001; Louda et al., 2004). The resuspension rate depends on the local hydrological climate, and is typically lower in sediments that are covered by bending seagrasses in areas

dominated by unidirectional, skimming flows (e.g. tide dominated), and higher in wave-dominated areas where friction velocities can be as high as in unvegetated areas (Koch & Gust, 1999). The effect seagrasses have on water velocity and especially on water currents just above the surface also depends on the vertical biomass stratification and architecture of the species, differing for round or flat-bladed species (Fonseca & Fisher, 1986), and meadow or canopy forming species (Best et al., 2001).

Gacia & Duarte (2001) reported that the effect *Posidonia* meadows had on sedimentation was mainly through a reduction in resuspension, than from an increase of captured material from the water column. Resuspension accounted for 85–95% of the total deposited material in other studies (Gacia & Duarte, 2001; Louda et al., 2004). Dauby et al. (1995) estimated that 70% of deposited sediment ($1.3 kg/m^2/yr$) consisted of resuspended material, and emphasized that the resuspended material consisted mainly of seagrass-derived detritus, while during phytoplankton blooms planktonic material was deposited. Resuspension is increased during gales and is a major factor in determining water column nutrient availability (Cowan et al., 1996). Unvegetated areas and vegetated areas show strong differences in water column phosphorus concentration, with wind speeds having a positive effect on water nutrient concentration, and stable P-concentrations in areas covered by freshwater macrophytes (Madsen et al., 2001), as the meadows prevent the captured nutrients from escaping. Resuspension is an important source of nutrients, as nutrient release from resuspension can provide the majority of nutrients required by phytoplankton (Cowan et al., 1996; Asmus & Asmus, 2000). Eckman et al. (1989) showed similar processes in kelp environments. The similar trends indicate that the higher sedimentation rates in kelp forests are not the result of an increased primary deposition, but are created by the inhibition of transport of suspended particles, longer residence times, and higher redeposition chances. Hence, the decrease in resuspension in seagrass meadows is an important factor changing the local environment, increasing OM content and nutrient availability.

Sediment changes

What are the consequences of increased sedimentation in seagrass meadows? Water depths of seagrass meadows tend to decrease over time due to net sedimentation, and seagrass meadows are therefore slightly raised above the surrounding unvegetated sediments. Hence, sedimentation typically leads to larger exposure times during low tide in intertidal areas (Madsen et al., 2001). However, a decrease in depth increases the shear stress, thereby increasing erosion rates. So a new balance between sediment erosion and deposition fixes the depth of the seagrass meadows, together with other local factors (Koch, 1999). As seagrass meadows accumulate sediments and increase in height, water flow is directed towards the lower lying areas and velocities increase as these channels become narrower; so erosion occurs in the smaller channels and sedimentation within the meadows (Madsen et al., 2001). Under extreme conditions, meadows accumulate sediments until they emerge and become islands (Hine et al., 1987). Subaqueous dunes covered by seagrasses can migrate over long distance, due to the combined effect of erosion and sedimentation (Marbà et al., 1994; Marbà & Duarte, 1995; Vermaat et al., 1997; Koch, 1999). Sediments in areas with dune transgressions and where seagrasses were present but disappeared are therefore similar in grain size distribution (Hine et al., 1987).

There are several adaptations seagrasses have to assist survival following burial. Vermaat et al. (1997) expected that seagrasses can cope with sediment deposition of 2-13 cm/yr through their vertical stem or rhizome growth (see also Marbà et al., 1994; Sheridan et al., 1998). Horizontal rhizome growth is another method to survive burial. Large variations in horizontal elongation are reported for different species. Elongation rate depends on their location within the patch (inside/edge), with values ranging from 1 cm/yr to 1,000 cm/yr (Vermaat et al., 1997). Branching and distances between internodes also increased under increased burial (Marbà et al., 1994; Duarte et al., 1997). Besides the impact of burial, stem or rhizome growth is also seasonal, temperature-dependent, and species-specific (Duarte, 1989,

1996; Vermaat et al., 1993, 1995; Marbà et al., 1996; Vermaat & Verhagen, 1996). There is a hump-shaped relationship between seagrass growth and burial depth, with highest reaction at burial depth of about 5 cm (Marbà & Duarte, 1994). Negative effects of storm events on seagrass meadows have been reported; massive seagrass die-off have been recorded after storm events that increased sediment loads far above average levels or uprooting the plants (Preen et al., 1995; Koch, 1999). Cyclones might resuspend so much sediments that seagrass meadows become buried, seed germination is reduced, and light penetration is below the minimum requirements resulting in meadows die-off (Preen et al., 1995). Resuspension can also be caused by human activities, such as eutrophication, trawling, or dredging (Short & Burdick, 1996; Short & Wyllie, 1996). At high sedimentation levels a negative effect on seagrass production is generally a consequence.

A potentially important aspect of increase of sedimentation and OM levels is the effect on the nutrient pools in seagrass meadows. Nutrient availability in sediments can be limited for seagrass development; roots might not be able to supply enough nutrients to the plants so that the nutrient uptake capacity of leaves becomes more important (Agawin et al., 1996; Stapel et al., 1996, 1997; Gras et al., 2003; Hughes et al., 2004). It is possible that the seagrass beds are mostly closed systems, and that the trapped leaf fragments and other nutrient sources within the meadows fulfil a key role in the nutrient balance of seagrasses (Morell & Corredo, 1993; McGlathery et al., 1994; Stapel et al., 1997). Detritus is important in terms of carbon, nitrogen and phosphorus, but the importance of detritus in terms of N-source is probably the most important (Pedersen et al., 1997). Nutrient reclamation increases during nutrient stress (Alcoverro et al., 1997). Particulate detritus and dissolved compounds in the interstitial water accounted for 92-99% and 0.4-0.9% respectively of the total amount of nitrogen in the bed in subtropical Australian study (Boon, 1986). However, detritus can function both as a nutrient sink, as well as a nutrient source, depending on the productivity of the system (Perez et al., 2001). Nutrient trapping

by seagrasses in combination with the effect of rhizophytic algae improve the sediments in such a way that nutrients accumulate, facilitating seagrass colonization (Williams, 1990). However, few studies have investigated the effect sediment trapping has on nutrient limitation. Sediment trapping is expected to be more important in offshore systems and in oligothrophic reef systems, with lower turbidity and higher irradiance in deeper waters, where carbonate sediments are nutrient poor. In subtidal or tidal systems, closer to shores or in estuaries (where most of the fieldwork to date has been conducted, and where the majority of the seagrass beds are located) other limiting factors, such as light are likely to be more important.

Another rare positive effect of sediment trapping is an increased germination rate, as documented in Zostera marina (Moore et al., 1993). An interaction between water temperature and oxygen content are the main factors controlling germination (Hootsmans et al., 1987). Seeds buried 15–25 mm below the surface had a significantly higher germination rate (63%) than seeds buried at 5 mm. Postponed germination could be an adaptation to allow for bioturbation, stimulating burial deeper in the sediment to permit the development of an effective root-anchoring system, enhancing seedling establishment (Moore et al., 1993). This effect has however only been documented for Zostera, and no direct positive effect of increased sedimentation on germination has been recorded in other seagrass meadows.

A decrease in water velocity does not only change sedimentation and resuspension rates, altering indirectly the sediment composition, but also decreases self-shading, resulting in lower drag, so that photosynthesis is increased (Fonseca et al., 1982; Perez & Romero, 1992; Vermaat & Verhagen, 1996; Ruiz & Romero, 2001).

Sediment trapping and a decrease in resuspension operate in almost all seagrass beds, leading to changes in the sediment. Besides the effect of burial, increases in OM content or available nutrients are the most important factors. However, little is known about the relative importance of the latter feedback on seagrass performance.

Water column changes

Seagrasses depend on available penetrating light for photosynthesis. Irradiance normally decreases exponentially with increasing depth, and the suspended sediment concentration has a direct linear effect on light attenuation (van Duin et al., 2001). The relation between irradiance and depth is given by the Lambert–Beers Law:

$$E(\lambda, 0) = E(\lambda, 0)e^{-kd(\lambda)z}$$

where $E(\lambda,0)$ is the irradiance at wavelength λ at the water surface, K_d the vertical attenuation coefficient, and z is the depth.

Turbidity decreases the amount of light available for photosynthesis. Light attenuation is wavelength specific, and often described by a linear trend that sums the downward attenuation coefficients of water, gilvin (plant degradation products), solids and phytoplankton (van Duin et al., 2001). The average attenuation coefficient K_d for lakes in the Netherlands varied between 1 and 5. Turbidity is an important factor decreasing irradiance and Z_{max}, and thereby determining photosynthetic rates, plant survival and recruitment, and consequently seagrass occurrence (Duarte, 1991; Terrados & Ros, 1995; Abal & Dennison, 1996; Jagtap, 1996; Olesen, 1996; Moore et al., 1997; Nelson & Waaland, 1997; Terrados et al., 1997; Ruiz & Romero, 2003). Tidal ranges are important in influencing turbidity and thereby light availability (Koch & Beer, 1996). Light availability is not only influenced by depth, or turbidity, but also by seagrass shoot density and the reflectance of the sediment, which is higher for sand than for muddy sediments (Zimmerman & Mobley, 1997)

Seagrasses increase sedimentation rates and reduce resuspension rates; hence, the occurrence of seagrasses reduces the water sediment load, and thereby reduces turbidity, promoting further seagrass growth (Madsen et al., 2001). Total suspended material varied between 18 mg/l near seagrass beds to 150 mg/l in unvegetated areas in Laguna Madre, Texas (Brown & Kraus, 1997 cited in Teeter et al., 2001). Light extinction depends on suspended sediment concentrations, particle state and flocculation, adsorption and

water chemistry (van Duin et al., 2001). Teeter et al. (2001) assumed that seagrasses can still occur when 20% of the light reaches the meadows, and that the water column extinction coefficient can, even at low levels of resuspension, limit the depth range of seagrasses. In fact Kemp et al. (2004) were able to model seagrass occurrence in Chesapeake Bay with a high predictive power ($R^2 = 75\%$) with light availability as the driving factor, and tidal ranges, light attenuation and epiphyte influence as covariates.

There is an annual time window during which non-structural carbohydrates can be built up, following seasonal trends in light availability and turbidity (Auby & Labourg, 1996; Burke et al., 1996; Zimmerman & Alberte, 1996). During suboptimal conditions, biomass decreases (Burke et al., 1996). The effect turbidity has is related to the capacity of seagrasses to overcome periods of reduced light availability, and is therefore strongly coupled to season (Alcoverro et al., 1995; Nelson & Waaland, 1997; Madsen et al., 2001).

Epiphyte biomass is another important factor (Strand & Weisner-Stefan, 1996; Hays, 2005) potentially limiting seagrass biomass. Best et al. (2001) assumed that light attenuation due to epiphytes is a hyperbolic function approaching 0.75 of maximum attenuation at maximum epiphyte biomass. Epiphyte biomass is negatively related to wave exposure, illustrated by the sometimes positive relationship between wave exposure and macrophytes biomass (Pinckney & Micheli, 1998; Gacia et al., 1999b; Hays, 2005). Moreover, epiphytes are sometimes controlled by grazers (invertebrates or fishes) and increase under eutrophication, so that different trophic levels and nutrient input become important variables in the system, indirectly determining seagrass growth (Gacia et al., 1999b; Hays, 2005). Moore et al. (1996) reported an effect of epiphytes on seagrass biomass, but not on mortality, indicating the necessity to separate these effects when studying seagrasses.

Although a direct consequence of increased sedimentation is an improvement in light availability, negative effects have also been reported, such as burial of photosynthetic tissue (Duarte et al., 1997; Manzanera et al., 1998; Brun et al.,

2005). To my knowledge no study has measured the effect of increased sediment load in the water column within seagrass meadows on the seagrass photosynthetic rate.

Modelling

Most of the processes and mechanisms mentioned above are important for our understanding with regard to the changes in seagrass occurrence. These can be used in modelling studies to predict changes in occurrence or performance under changing conditions, e.g. under eutrophication. Modelling sediment transport has been carried out in various studies. It is difficult to include wind, tide, seasonal effects or wave energy in a three dimensional dynamic model that includes the different sediment sources together with the positive feedbacks in seagrass meadows (Fonseca et al., 2002; Cappuci et al., 2004; Widdows et al., 2004). A good overview of the modelling possibilities is given by Teeter et al. (2001) who modelled the effect of aquatic vegetation on the hydrodynamics of the area, and the consequences for sediment transport. Van Duin et al. (2001) modelled light availability in relation to sedimentation and resuspension, and Beste et al. (2001) the relationship between macrophyte growth and light. Valiela et al. (2004) modelled nitrogen pools in seagrass meadows in relation to nitrogen inputs (such as nitrogen fixation, external inputs, atmospheric deposition), and losses (burial and denitrification). The above approaches illustrate the multidisciplinary character needed for modelling studies, but also the knowledge gaps. A challenge would be to integrate the different models in a spatially explicit 3D environment, combining the effect of water currents and turbulence on the differential sediment loads in the water column, and the effects seagrasses have on the sedimentation rates of the different sediment fractions and OM content.

From here to there, challenges for the future

Seagrasses occur in areas where the biotic and abiotic conditions are within the specific tolerance levels. Important factors are the minimum and maximum water depths at which seagrasses can be found, determined by wave orbital velocity, tide, and light. Other factors such as maximum and minimum current velocity pose other thresholds. Besides these factors others might be locally important that could limit seagrass occurrence, such as nutrient availability (mainly N or P), toxic sulphide conditions, eutrophication, temperature, oxygen, or organic matter content (unimodal relationship). However, the latter factors are likely to be globally less important.

Understanding the role seagrasses have on their own system is fundamental in order to predict or understand their distribution. Light availability is a key factor in their distribution, sometimes explaining about 75% of the variation in seagrass distribution. Light availability is influenced to a large extent by attenuation, and therefore by the sediment concentration in the water column. The impact of seagrasses on sedimentation, trapping sediments from the water column and decreasing resuspension rates, is therefore the most important positive feedback within seagrass systems, as it increases light availability, stimulating primary productivity and increasing the maximum depth seagrasses can occur (Fig. 1). A second factor that also increases light availability is a reduction of self-shading due to decreased water currents inside seagrass meadows. Seagrass models should incorporate these positive feedbacks, especially the effect seagrasses have on light availability, in their algorithms, in order to be able to improve prediction about seagrass occurrence.

Besides these latter positive feedbacks others have been reported, such as sediment stabilization, increased germination rates, or an increase in nutrient or organic matter availability. All these factors seem to be less important than factors directly improving light conditions. It is possible that these factors are limiting in certain locations, as occurs in terrestrial systems, where grass productivity is in some locations limited by nutrient availability (e.g. moist savannas), in others by water availability (desert). Similarly, light limitation in seagrasses might occur in winter, and N-limitation in summer, as also occurs in terrestrial vegetation. It is difficult to compare

the effect seagrasses have on turbidity reduction compared to the increase in nutrient availability, because, to my knowledge, no study has attempted to quantify these different effects in seagrass meadows. Moreover, few studies have investigated the effect seagrasses have on light or nutrients availability at multiple scales over a wide variety of local conditions, incorporating different seagrass species differing in their impact or reaction (Table 1). As such, generalizations are difficult to make.

In order to improve our understanding of seagrass biomass dynamics and occurrence, there is an urgent need for data on the following aspects:

- the impact of seagrasses on turbulence, and the effect turbulence has on resuspension rates; and modelling turbulence effect on resuspension of bed material (including cohesive sediments) under the influence of seagrasses

- the effect of species-specific seagrass biomass stratification and architecture on current reduction and sedimentation rates; synthesize field findings to general patterns

- the effect of seagrass sediment trapping on sediment composition, and especially the effect of the sediment composition via increasing sulphide concentrations on seagrass performance

- the impact of waves (under influence of wind and tides) on the effect seagrasses have on sedimentation and resuspension

- although light availability is often regarded as the major limiting factor of seagrasses, an overview is needed that describes the effect of other limiting factors (e.g. nutrient limitation, sulphide concentrations) in relation to seagrass occurrence.

Most of the papers reported important effects seagrasses have, modifying their direct environment in terms of light availability or sediment composition. Indeed, it is generally accepted that this should have a positive effect on seagrass growth, or extent of the seagrass meadows. However, few publications have been able to quantify the effects of positive feedbacks on seagrass performance. The hypothesis that positive feedbacks are essential for the survival or growth of seagrasses has not been tested yet. Will seagrass primary production decrease, erosion of seagrasses increase, or the extent of seagrass meadows reduce when positive feedbacks are not present? In order to be able to predict or model the performance of seagrasses under changing conditions these questions should be answered. Hence, there remains an important challenge for ecologists investigating the importance of positive feedbacks in seagrass systems, necessitating an experimental approach. We know they are there, but how important are they for the performance or resilience of the seagrass systems?

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