Spatial self-organized patterning in seagrasses along a depth gradient of an intertidal ecosystem

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Abstract. The spatial structure of seagrass landscapes is typically ascribed to the direct influence of physical factors such as hydrodynamics, light, and sediment transport. We studied regularly interspaced banded patterns, formed by elongated patches of seagrass, in a small-scale intertidal ecosystem. We investigated (1) whether the observed spatial patterns may arise from feedback interactions between seagrass and its abiotic environment and (2) whether changes in abiotic conditions may lead to predictable changes in these spatial patterns. Field measurements, experiments, and a spatially explicit computer model identified a "scale-dependent feedback" (a mechanism for spatial self-organization) as a possible cause for the banded patterns. Increased protection from uprooting by improved anchoring with increasing seagrass density caused a local positive feedback. Sediment erosion around seagrass shoots increased with distance through the seagrass bands, hence causing a long-range negative feedback. Measurements across the depth gradient of the intertidal, together with model simulations, demonstrated that seagrass cover and mean patch size were predictably influenced by additional external stress caused by light limitation and desiccation. Thus, our study provides direct empirical evidence for a consistent response of spatial self-organized patterns to changing abiotic conditions, suggesting a potential use for self-organized spatial patterns as stress indicators in ecosystems.

Key words: catastrophic shift; ecosystem monitoring; hydrodynamics; scale-dependent feedback; seagrass ecosystem; seagrass landscape; self-organization; spatial patterns; stress indicator.

Introduction

Seagrasses are rhizotomous marine angiosperms that cover about 0.1–0.2% of the global oceans. Their meadows are among the Earth's most productive ecosystems and serve as key habitat in the life cycles of many marine animal species (Orth et al. 2006). Seagrasses typically grow in littoral environments where they are exposed to multiple stressors. Depth zonation is mostly determined by light conditions at the lower depth limit, while tolerance to emersion often defines the upper depth limit (Philippart and Dijkema 1995, Leuschner et al. 1998). The spatial structure of the seagrass landscape within these boundaries is often mainly ascribed to the influence of physical factors such as wave action, currents, sediment transport, and light (Patriquin 1975, Robbins and Bell 1994, Marba and Duarte 1995, Bell et al. 1999, Fonseca et al. 2002). However, recent studies

have shown that seagrasses often improve their own growing conditions (van der Heide et al. 2007, 2008), for instance by attenuating currents and waves and reducing sediment resuspension (van der Heide et al. 2007). This suggests that the structure of seagrass landscapes may also arise from feedback interactions between seagrasses and their environment instead of straightforward physical forcing.

Studies from a wide range of terrestrial and marine ecosystems have demonstrated that spatial patterns are often self-organized (Rietkerk and van de Koppel 2008). Spatial self-organization implies that patterns in ecosystems are not generated by any underlying abiotic heterogeneity, but arise from internal organization caused by feedback interactions between organisms and their environment (Pascual and Guichard 2005, van de Koppel et al. 2008). Self-organization may involve irregular patchiness, when localized positive feedback is the dominant force shaping the ecosystem (Kefi et al. 2007, Scanlon et al. 2007), but patches can also develop at regular distances from each other. In spatially explicit models, regular spatial patterns can be
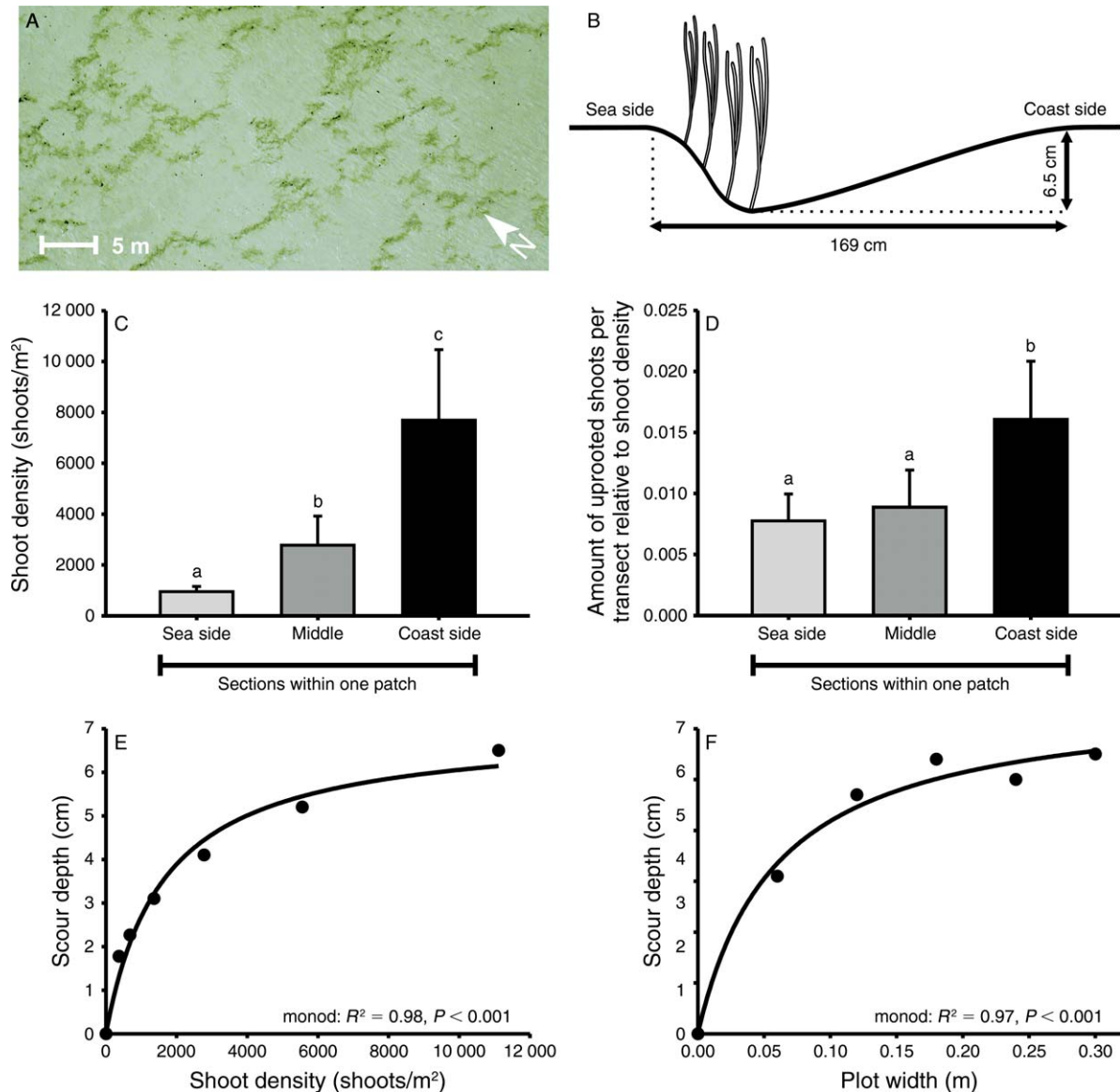
FIG. 1. Measured characteristics of the seagrass bands. (A) An aerial photograph of the seagrass patterns at low tide. (B) Schematic cross-section of an asymmetric depression characterizing the seagrass bands. The mean scour depth was 6.5 ± 0.4 cm (mean $\pm$ SD, $n = 6$), and the total length of the disturbance was 169 ± 28 cm ($n = 6$). (C) Significant change in shoot density of a seagrass band was found from the sea side to the coast side of the seagrass bands (ANOVA: $F_{2,10} = 24.1$, $P < 0.001$) and (D) in uprooting of shoots (ANOVA: $F_{2,6} = 11.1$, $P = 0.010$). (E) Maximum equilibrium scour depth at varying shoot densities (plot size 0.3×0.3 m) and (F) at different plot widths (shoot density = 5556 shoots/m²).

described mechanistically by an interaction between a local positive and a long-range negative feedback; a phenomenon called scale-dependent feedback (Rietkerk et al. 2004, Rietkerk and van de Koppel 2008). Because scale-dependent feedbacks seem a universal mechanism behind formation of regular patterns, several recent modeling studies suggest that these patterns may be used as stress indicator in ecosystems (Rietkerk et al. 2004, Rietkerk and van de Koppel 2008). At present, however, any empirical basis for a predictable and consistent

response of self-organized regular spatial patterns to changing abiotic conditions is lacking.

In this study, we investigated the mechanisms behind seagrass patterns and their response to changing abiotic stress on an intertidal depth gradient. In our study area, an intertidal beach at Saint Efflam Bay, France, elongated patches of the seagrass *Zostera noltii* form a regularly interspaced banded pattern (Fig. 1A) that has been present for at least a quarter of a century (T. van der Heide, *unpublished data*; see Plate 1). The seagrass

bands at this site are typically orientated perpendicular to the (north-south) current and wave direction. Because the seagrass patterns are situated on a depth gradient, they are subjected to small-scale gradients (<1 km) of multiple stressors caused by tide-induced differences in emersion time, exposure to hydrodynamics, and light availability. Therefore, the system provided a very suitable environment to empirically test (1) whether spatial patterns may arise from feedback interactions between seagrass and its abiotic environment (i.e., spatial self-organization) and (2) whether changing abiotic stress may lead to predictable and consistent changes in these spatial patterns. We first investigated the mechanisms causing seagrass patterning using a combination of field measurements and experiments. Next, we examined the effects of changing abiotic conditions (hydrodynamics, light, desiccation) on the pattern characteristics across the gradient. Based on results from this field study, we constructed a spatially explicit model to test whether the identified interactions and stressors could indeed explain the observed patterns and changes across the gradient.

SITE DESCRIPTION

Saint Efflam Bay covers an area of around 5 km^2 and is located in the north of Brittany (France), near the town of Lannion. The bay is enclosed by high rocky cliffs, except for the north side of the bay, the direction from where the water enters during flood tide. Incoming waves can move unobstructed and therefore travel far into the bay. Due to the relatively flat incline of the beach (<0.5%), waves keep on traveling over a distance of up to 500 m up to the shoreline after breaking (van Rijn 1990; see Plate 1). The breaking waves cause continuous resuspension of the upper sediment layer which is therefore sandy and homogeneous across the depth gradient (median grain size, 142 μm; organic matter content, 0.9%). The *Zostera noltii* patches are located at the west side of the bay and cover an area of about 0.5 km^2 (~0.7 × 0.7 km). In this system, seagrass follows a seasonal cycle with respect to growth and development. From October until March, patches lose all aboveground biomass and survive belowground on energy stored in the rhizomes. Shoots regrow in the following growth season (from April to September).

FIELD STUDY METHODS

Analysis of patterns and mechanisms.—We first tested whether patterning of the seagrass bands was regular. We mapped 15 quadrates (~15 × 15 m) located on a 700-m transect across the tidal gradient using RTK-GPS (real time kinematic global positioning system). Images obtained from these mappings were subsequently analyzed for pattern regularity by two-dimensional spectral analysis (Renshaw and Ford 1983, van de Koppel et al. 2005).

Next, we investigated the mechanism causing pattern formation. To detect any changes in the patterns over time, we tracked the spatial position and growth rate of six randomly selected seagrass bands over a two-year period using belowground stainless steel markers that could be located by GPS and a metal detector. We measured the change in shoot density and sediment height across six individual bands by analyzing these parameters in three equally large sections for each band (sea side, middle, and coast side). The relative number of uprooted shoots per section (standardized to shoot density) was determined on a much larger number of bands, by counting shoots with exposed rhizomes along four transects from the coast to the sea. Onsite hydrodynamics were measured in twofold using two simultaneously recording automated measuring frames. We measured wave height and current velocity for four tidal cycles (including spring and neap tide) across one month (Bouma et al. 2005a).

The effect of seagrass on sediment dynamics was first tested by removing all aboveground biomass from six randomly selected bands. Next, effects of density and width of the bands (north-south direction) were tested by setting up two experiments with 40 cm long seagrass mimics that were driven 15 cm into the sediment bed in varying configurations (Bouma et al. 2005b). To examine the influence of density, we planted 0.3 × 0.3 m plots with six different shoot densities (370 to 11 111 shoots/m^2). The effect of band width was tested by planting five plots with varying widths (0.05 × 0.3 to 0.3 × 0.3 m; shoot density, 5556 shoots/m^2). Changes in sediment height across the plots were recorded during six consecutive tidal cycles.

Gradient analysis.—After determining the general mechanism of pattern formation, we examined how the seagrass bands changed across the depth gradient due to changes in abiotic stress. We calculated seagrass cover and mean patch size for each of the 15 quadrates, by analyzing the RTK-GPS data in a GIS (geographical information system). Additionally, we determined the change in wavelength of the patterns by spectral analysis (Renshaw and Ford 1983, van de Koppel et al. 2005).

Next, we performed experiments and measurements to unravel the influence of different stressors on seagrass cover and patch size across the gradient. The effects of varying exposure to hydrodynamics was tested experimentally with seagrass mimics, by planting 14 plots (0.3 × 0.3 m) across the 700-m gradient (shoot density, 5556 shoots/m^2). The influence of sediment resuspension on light conditions during submersion was examined by measuring light availability in duplicate, using two simultaneously recording automated measuring frames. We measured four tidal cycles (including spring and neap tide) across one month (Bouma et al. 2005a). Average emersion periods were determined from RTK-GPS data together with calculations on the mean tidal cycle in the bay.

Finally, we investigated the influence of desiccation stress on seagrass patterning across the gradient. We determined photosynthetic yield by pulse amplitude-

PLATE 1. A typical seagrass band growing in a depression at Saint Efflam Bay, Brittany, France. The environment is characterized by strong hydrodynamics: because of the flat slope of the beach, waves keep on traveling for several hundreds of meters after breaking. Photo credit: T. van der Heide.

modulated (PAM) fluorometry as an indication of the vitality of photosystem II (PSII) (Rohacek and Bartak 1999), because damage to the plants photosynthetic capacity is one of the first signs of dehydration in *Z. noltii* (Leuschner et al. 1998). Measurements were performed on dark-adapted shoots (one hour of adaptation) from the optimum and the upper and lower depth limit. Because spatial variation was high, we used 60 randomly selected replicates for each location.

Statistical analyses.—Prior to analysis, data of each tested variable was tested for normality and equality of variance, and following tests were selected accordingly. Yearly change in the spatial position of seagrass bands and change in shoot density within bands were tested with repeated measures ANOVA with Bonferroni comparisons. Counts of uprooted shoots were tested using ANOVA combined with Tukey's hsd as post hoc test. Kruskal-Wallis and Mann-Whitney *U* post hoc tests with Bonferroni significance correction were used on PAM results. Change in seagrass cover and patch size across the gradient and all experiments with mimics were analyzed by linear and nonlinear regression. Tested functions were: linear, exponential and monod. We adopted the equation that fitted best to each relation. R^2 and the *F* test (with associated *P* value) were used as quality measure for each fit.

FIELD STUDY RESULTS

Analysis of patterns and mechanisms.—Spectral analysis of images obtained with RTK-GPS revealed clear regularity in the patterns, suggesting a mechanism for spatial self-organization. Individual bands were characterized by asymmetric depressions (Fig. 1B) with a maximum depth of 6.5 ± 0.4 cm (mean $\pm$ SD, $n = 6$) at

the coast-side edge of the seagrass bands. The maximum depth of the depressions equaled mean seagrass rooting depth, suggesting that shoots eroded at the coast side. This was further supported by shoot density measurements together with counts of uprooted shoots, showing that numbers of exposed rhizomes were significantly higher on the coast side, compared to the middle and sea side sections (Fig. 1C, D). Measurements on the spatial position of the seagrass bands confirmed that they mainly eroded at the coast side while expanding on the sea side, resulting in an average net seaward migration of 17 ± 10 cm/yr ($n = 6$) that was significant for each year (ANOVA: $F_{1,5} = 17.5$, $P = 0.009$).

In all six bands where aboveground biomass was removed, depressions disappeared within two tidal cycles. Next, experiments with seagrass mimics revealed that the asymmetric depressions indeed developed as a result of seagrass presence, by erosion of sediment around seagrass shoots (Fig. 1E, F). Equilibrium depth of the depression was always reached within five tidal cycles (2.5 days). The maximum erosion depth (scour depth), at the coast-side edge of the plots, was dependent on both shoot density and the width of individual bands. This indicated that erosion was caused by interactions between hydrodynamics and seagrass itself. Hydrodynamics measurements demonstrated that tidal currents were relatively slow (maximum measured water speed 0.2 m/s) and that breaking waves with an average significant wave height of 0.5 m form the main hydrodynamic force in the system.

Gradient analysis.—The relative amount of surface covered by seagrass bands varied along the depth gradient. GIS analysis of the 15 quadrates along the 700-m transect showed that seagrass coverage increased
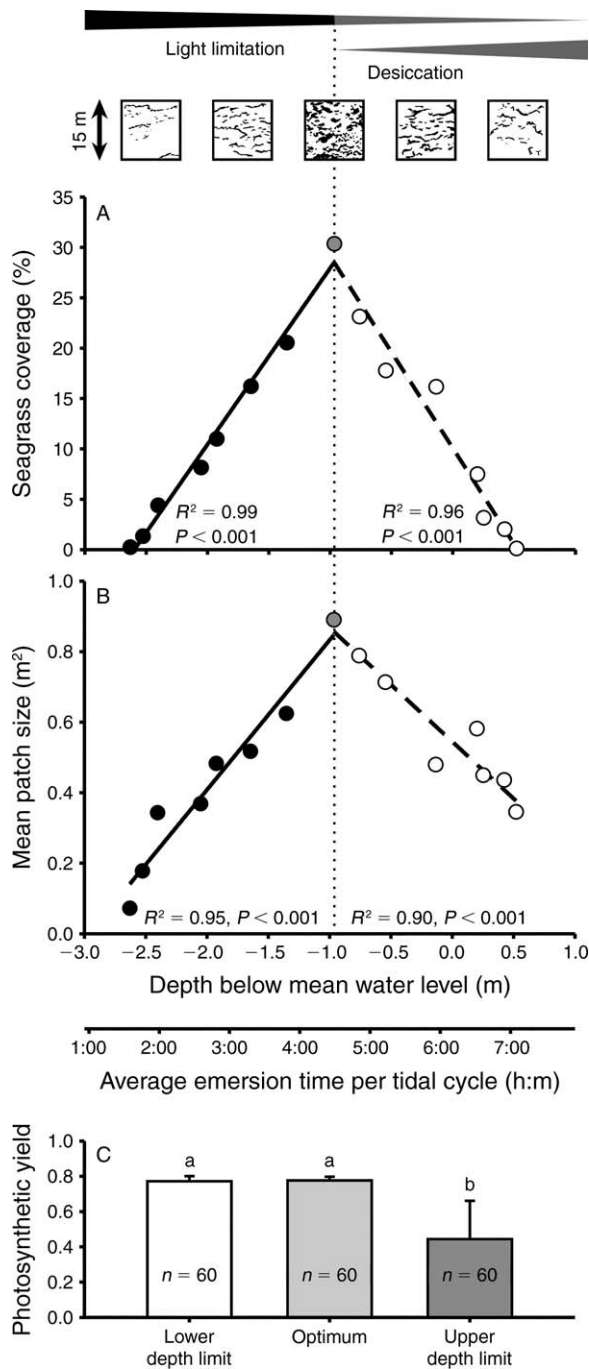
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FIG. 2. Measured characteristics of seagrass patterning across the depth gradient. Boxes above panel (A) depict actual measurements on the presence of seagrass bands (dark areas) on the beach (white area) for five of the 15 quadrates. (A) Seagrass cover and (B) mean patch size show optima at around 1 m below the mean water level or an emersion (light) period of 4.5 hours. Both cover and mean patch size decrease linearly in the direction of the upper and lower depth limits. (C) Measurements by pulse amplitude-modulated (PAM) fluorometry reveal that desiccation is a significant stressor in the upper (shallow) part of the gradient (Kruskal-Wallis: $\chi^2 = 116.7$, df $= 2$, $P < 0.001$). The lower part of the gradient is light limited as the optimal emersion period for *Zostera noltii* is between 5 and 8 hours.

linearly from the upper depth limit to a maximum of around 30%, after which coverage declined again in a linear fashion toward the lower depth limit (Fig. 2A). Moreover, mean patch size showed the same trend along the gradient (Fig. 2B) and wavelength of the patterns changed from 2 m near the maximum to about 5 m near the outer limits.

Experiments with 14 plots of seagrass mimics planted across the gradient showed that the equilibrium scour depth of the depressions was not influenced by the location of the plots (linear fit: $R^2 = 0.03$; $P = 0.591$). Hence, differences in hydrodynamic exposure were not responsible for the observed gradient in seagrass coverage. PAM measurements revealed that shoot fitness was reduced by 43% from the optimum to the upper depth limit, but that desiccation was no significant factor on the lower part of the depth gradient (Fig. 2C). This indicated that desiccation is the most important stressor shaping the pattern gradient between the upper depth limit and the optimum.

Finally, turbidity measurements of the water column showed that light availability at the bottom ranged from 5% in the first and last 15 minutes of submersion to less than 1% halfway through the submersion period. As even 5% of light is not nearly enough for seagrass photosynthesis to even reach its light-compensation point (Philippart 1995, Vermaat and Verhagen 1996), seagrass can only grow during emersion. Average emersion periods at the upper depth limit, optimum, and lower depth limit were about 7, 4.5, and 1.5 hours, respectively (Fig. 2A, B). Because the optimal emersion period of *Z. noltii* usually varies between 5 and 8 hours (Philippart and Dijkema 1995), light limitation seems to be the driving force behind the gradient in seagrass cover and mean patch size between the optimum and lower depth limit.

MODEL

Model description.—Results from our field study suggest that the banded patterns arise due to scale-dependent feedbacks between hydrodynamics and seagrass growth. The seagrass roots and rhizomes cause a local positive feedback. A high root density improves sediment stability and anchoring capacity of the plants, thereby locally preventing uprooting of seagrass shoots (Peralta et al. 2005). Contrastingly, aboveground parts cause a negative feedback on a longer range. The interaction of the shoots with the hydrodynamics causes a disruption of sediment dynamics (i.e., scouring). This disruption intensifies with distance through each seagrass band (van Rijn 1990, Nepf 1999), resulting in increased erosion of both sediment and seagrass shoots toward the coast-side edge of a band. Apart from stress caused by this scale-dependent feedback, field results also illustrate that additional stress caused by desiccation and light limitation causes consistent change in seagrass cover and mean patch size.

To test whether observed seagrass patterns and changes in patterns can indeed be caused by the
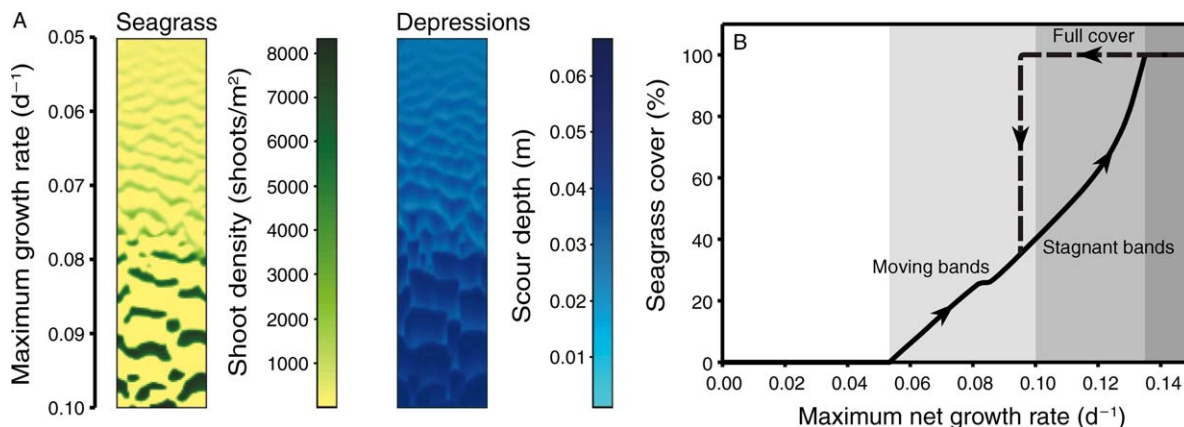
Fig. 3. Effect of the maximum net growth rate on seagrass cover in the model. (A) Modeling results after two years of simulation on a 200×50 grid with a gradually declining growth rate from the bottom to the top. The size of one grid cell compares to about 5×5 cm in the field. (B) Bifurcation diagram describing the effect of the maximum net growth rate on seagrass cover. Note that the maximum net growth in the field was ± 0.1 d^{-1}.

mechanisms suggested from our field study, we constructed a minimal, spatially explicit model. The model describes changes in shoot density (dZ_{ij}/dt) and scour depth (dD_{ij}/dt) on a 200×50 grid by two differential equations:

$$\frac{dZ_{ij}}{dt} = r\left(1 - \frac{Z_{ij}}{K}\right)Z - m f_1(D_{ij})\frac{h_1}{h_1 + Z_{ij}}Z_{ij} + d_z \Delta Z_{ij} \quad (1)$$

$$\frac{dD_{ij}}{dt} = e\frac{f_2(Z_{ij})}{f_2(Z_{ij}) + h_2} - sD_{ij}. \quad (2)$$

Here, Z_{ij} and D_{ij} are the seagrass shoot density (shoots/m^2) and the scour depth of grid cell i, j, respectively. The maximum net logistic growth rate is described by r (d^{-1}), m is the maximum mortality rate due to uprooting of shoots (d^{-1}), e is the maximum scouring rate (m/d), and s is the depth dependent sedimentation rate (d^{-1}). K is the carrying capacity (shoots/m^2), h_2 is the half rate constant for the enhancing effect of seagrass on e (shoots/m^2), and d_z describes the lateral dispersal of Z_{ij} from and to neighboring grid cells. The short-range positive effect of seagrass on their own growth is described in a Monod equation with half saturation h_1 that locally causes a lower loss rate. The function $f_1(D_{ij})$ describes the effect of scour depth on seagrass mortality m:

$$f_1(D_{ij}) = \frac{D_{ij} - D_T}{D_{max} - D_T} \qquad \text{if } D_{ij} > D_T. \quad (3)$$

With D_{max} as the maximum scour depth (m) and D_T as the minimum seagrass rooting depth (m) after which $f_1(D_{ij})$ increases in a linear fashion. Finally, $f_2(Z_{ij})$ describes the longer range effect of seagrass on the scouring rate e. Field measurements on the depth profiles of the bands revealed that the effect of seagrass decreased exponentially with distance n. The cumulative eroding effect of all seaward seagrass can thus be described as

$$f_2(Z_{ij}) = \int_{n=x}^{n=x+\infty} e^{-dn} Z_n \, dn$$

which was approximated in our model in a discrete way:

$$f_2(Z_{ij}) = \sum_{n=0}^{N} (1 - d/L)^n Z_{x+n}. \quad (4)$$

Here, L is the grid size, which was normalized to 1 m, d (m^{-1}) describes how the eroding effect of seagrass decays toward the coast side with increasing distance. We obtained parameter values from our field experiments and observations. The values used in the model analysis were: $K = 12\,000$, $m = 0.6$, $D_{max} = 0.07$, $D_T = 0.03$, $h_1 = 554$, $d_z = 0.1\,r$, $h_2 = 2959$, $s = 2$, $e = D_{max}$, $s = 0.14$, and $d = 0.1$.

Effects of the light availability and desiccation gradients were analyzed in the model by using a gradual stepwise increase of r. After each small increase of the net maximum growth rate r, the model was allowed to stabilize again. Next, the same analysis was also performed in a backward manner, i.e., a stepwise decrease of r toward zero. For this bifurcation analysis, we used a range of 0–0.15 d^{-1}. Note that the maximum net growth rate in the field was 0.1 d^{-1}. For the calculation of seagrass cover, we defined an area as vegetated if the density exceeded 1000 shoots/m^2, which was approximately the minimum shoot density in the field (Fig. 1B).

Model results.—Model simulations demonstrated that scale-dependent feedback between hydrodynamics and seagrass could indeed explain the observed banded patterns (Fig. 3A). At realistic growth rates, patterns are typically migrating toward the sea as observed in the field. Our model confirms that self-organization is a potential mechanism behind the observed spatial patterns.

Bifurcation analysis of growth rate r reveals that the model predicts alternative stable states (bistability) between a homogeneous seagrass cover and a patterned state of regularly spaced stagnant bands at high growth rates (i.e., low stress levels; Fig. 3B). Bistability in the model disappears when stress levels are increased and the maximum net growth rate resembles those measured in the field (maximum $\pm$ 0.1 d^{-1}): only a state of migrating banded patterns remains stable. As stress levels are increased even further, the model predicts an almost linear decrease of seagrass cover as observed in the field.

DISCUSSION

In this study, we report on self-organized, regular, spatial patterns in a small-scale, intertidal, seagrass ecosystem. Even though our ecosystem is possibly unique in the sense of the specific interactions causing pattern formation, the underlying principle of scale-dependent feedback has been reported for a wide range of ecosystems (Rietkerk et al. 2004, Rietkerk and van de Koppel 2008), including (semi-)arid systems, peatlands and forests, but also in marine systems like mussel beds and diatom mats (Rietkerk and van de Koppel 2008). Although patterning has previously been described for seagrasses (Patriquin 1975, Marba and Duarte 1995, Fonseca et al. 2002), direct physical forcing rather than interactions between seagrass and hydrodynamics were proposed as an explanation for these phenomena. This implies that straightforward translation of the driving mechanism in our system to other seagrass ecosystems is difficult, because factors other than scale-dependent feedback may also cause patterning in seagrasses. Moreover, it illustrates that understanding the underlying driving mechanisms is critical when using regular patterns as a stress indicator for ecosystems.

Although recent modeling studies suggest that characteristics of self-organized spatial patterns might be indicative for increased stress and degradation (Rietkerk et al. 2004, Rietkerk and van de Koppel 2008), experimental evidence has so far remained scarce. In this study, we provide clear empirical evidence that regular spatial patterns can be indicative for increased stress and degradation. Our results demonstrate that properties of self-organized patterns respond predictably to changes in external stressors (light limitation and desiccation in this instance). Changes in properties of regular patterns like decreasing cover and patch size may therefore be regarded as signs of increasing overall stress in ecosystems, caused by for instance eutrophication, climate change or overexploitation.

At present, ecological monitoring studies largely rely on abundances and range shifts of species or functional groups (Barbier et al. 2006). Self-organized spatial patterns can make a valuable contribution to monitoring, since they can yield important information on changes in main stressors in ecosystems. Moreover, once presence of spatial self-organized patterns has been determined, monitoring of spatial patterns may reduce costs and efforts because spatial data are relatively easy to obtain by for instance aerial photography or satellite imagery. Such a perspective is promising for many ecosystems, including seagrasses. In the last decades, seagrass ecosystems have been increasingly disturbed by human activities (e.g., eutrophication, siltation, dredging), resulting in dramatic and large-scale losses worldwide that were in many cases unexpected (Orth et al. 2006, van der Heide et al. 2007). As a result, monitoring and conservation efforts have recently greatly increased (Orth et al. 2006).

In contrast with results typically obtained from most terrestrial ecosystem models (Rietkerk et al. 2004), we found no indication in either the field data or our model suggesting a potential for catastrophic shift from a vegetated to a bare state. Instead, our model predicts bistability at high growth rates between a patterned and a fully covered state. Our results differ from analyses of terrestrial ecosystems because in contrast to these models, our model has no threshold mechanism for colonization like, for instance, a limiting resource (e.g., water, nutrients). Instead, feedback control is driven by adverse conditions (i.e., erosion) that are generated by interactions between hydrodynamics and the seagrass itself. Still, despite obvious differences with respect to predicted ecosystem dynamics, all existing models predict a consistent effect of abiotic stresses on spatial patterns, suggesting that self-organized spatial patterns may be used as stress indicator for ecosystems.

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