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Self-organized criticality in intertidal microphytobenthos patch patterns

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Abstract

A 2D distribution of microphytobenthic biomass is determined from a superficial sediment sampling on an exposed sandy shore. The distribution undergoes a very structured pattern, displaying a few dense patches over a wide range of low density patches. We perform a statistical analysis of this 2D patterns using statistical tools developed in the field of fractal theory. It is shown that the patch pattern belongs to fractal and multifractal structures, and exhibits specific power-law in the probability space, involving the appearance of a self-organized critical state. To our knowledge, this is the first experimental study of self-organized criticality in benthic ecology. Some theoretical consequences are outlined, and their practical applications to improve our understanding of intertidal ecosystems structures and functions are discussed.

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Keywords: Intertidal ecology; Phytobenthos; Biomass; Patchiness; Scaling; Fractals; Self-organized criticality

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1. Introduction

Nature appears to be intermittent, i.e., it is characterized by large fluctuations interspersed among periods of relative stasis [1–3]. At the broadest evolutionary scales, adaptive radiations appear, in some cases, to occur in short bursts of evolutionary

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activity, a phenomenon know as punctuated equilibrium [4,5]. Extinction events observed in the fossil records may be episodic at all scales, with relatively long periods of stability alternating with short-lived extinction events [6]. Similarly, at the smallest ecological scales, biomass and species are rarely dispersed uniformly [7–11]. Instead, patchiness (also referred to as 'spatial heterogeneity' [12]) is the norm, and ecological field studies and environmental monitoring programs must be designed accordingly [13–17].

Because the issue of sampling (intermittent) patchily distributed populations cut across all habitat and taxa, a central issue in both terrestrial and marine ecology is thus to determine how space and spatial scales influence population and community dynamics [18–20]. Theoretical studies have suggested that internal (biotic) properties of individuals and populations interact to produce space–time complexity in homogeneous environments [21,22]. Potentially, environmental complexity interacts with biotic processes and influences spatial patterns [23,24]. Whatever that may be, we are confronted with a crucial question: is intermittency intrinsic to the organization of ecological communities and how to characterize patterns presenting structures at several, if not all, scales?

A attempt to explain the origin of intermittent fluctuations in nonequilibrium systems, and referred to as "self-organized criticality" (SOC), proposed that many complex systems naturally evolve to a critical state defined by the spontaneous emergence of fluctuations across a broad range of scales without any fine-tuning necessary from outside the system [25,26]. Because of their intrinsic scaling properties, self-organized structures can be described in terms of fractals objects. Following the pioneering studies of Mandelbrot [27], fractal objects have become a familiar class of structures in almost all areas of scientific knowledge. As previously discussed [28–31], different scales are necessarily related to different aspects of structure, and fractal methods can be applied in order to detect self-similar hierarchies in ecology. Such hierarchical scaling have been observed, for instance, in coral reefs [32], from patch perimeter measures in deciduous forests [33], vegetation patterns [34], landscapes [35,36], the structure of vertebrates [37,38] and invertebrates movement pathways [39–41] as well as the distribution of benthic [42,43] and planktonic organisms [10,11,44,45].

In benthic and more specifically intertidal ecology, many studies have been devoted to study the interplay between abiotic processes and biotic community structure at different spatial scales [46–51]. Only a few focused on the quantification of the scaling (fractal) properties of these communities [41,42], and none have been confronted with the crucial question related to the phenomenology of the organization of benthic communities, and especially microphytobenthic communities that are at the core of benthic primary production and the matter fluxes between benthic and pelagic domains.

In the following, we first propose a brief state of the art in studies related to self-organized criticality, in both physical and ecological fields, and detailed their link with fractal concepts (Section 2). We define intertidal environment and microphytobenthic organisms, and present our sampling and experimental procedures in Section 3. Section 4 presents our statistical analysis of microphytobenthos patches. Although our results have implications for the functioning of the whole intertidal ecosystem, we are more concerned with the kind of dynamical system that results from the process of biomass distribution. In particular, we show for the very first time that several patterns in microphytobenthos distribution support the theory of self-organized criticality [25,26]. We make three observations that show that the microphytobenthos patch pattern is consistent with self-organized criticality: (i) a power-law distribution of the number of microphytobenthos patches vs. patch spatial scale, (ii) a power-law distribution of patch frequency vs. patch concentration, and (iii) a discontinuity in the plot of patch frequency vs. microphytobenthos patch concentration suggesting a critical biomass. In Section 5 we discuss the consequences of our findings and we give some final comments and directions for future developments.

2. Self-organized criticality

2.1. Characterizing criticality

Recent studies on the behavior of nonlinear systems far from equilibrium with extended spatial and/or temporal degrees of freedom have shown that these systems often spontaneously evolve towards a critical state, referred to as a "self-organized critical state" [25,26,52] defined by the spontaneous emergence of intermittent fluctuations across a broad range of spatial and temporal scales without any "fine tuning" necessary from outside the system. The system is organized in a well-defined way that is characterized by the existence of order at all scales and where small perturbations evolve creating objects of all sizes, hence the concept of intermittency introduced above. This essential feature provides a physical explanation for some fractal objects and some natural power laws as the one observed for the so-called $1/f$ noise [25,52].

The most widespread example of self-organized criticality is a pile of sand to which grains are continually added [25,26]. Initially, when the pile is flat there is little interaction among the different regions of the pile and adding a single grain will only affect a few other grains nearby. The system is in a subcritical state. As the pile grows by adding grains of sand, avalanches of grains spill down the sides such that adding a single grain can initiate a cascade affecting many other grains. Eventually, the slope of the pile grows until the "angle of repose" is reached. The pile reaches a critical state and essentially does not get any steeper. Now, if grains are added avalanches occur with a wide range of sizes. The critical state is defined by a stationary statistical distribution of avalanches which propagate across all spatial and temporal scales (only limited by the finite size of the pile). Alternatively, the pile could be started in a supercritical state by forming a vertical cylinder of sand. A supercritical pile is highly unstable and is expected to collapse down to a critical state as grains are added. Thus, one can think of the critical state as an attractor for the dynamics of the pile.

2.2. Power laws and self-organized criticality

The dynamical and structural properties of self-organized criticality can be characterized through several scaling laws. In the specific case of the sand pile, the number of grains $N(d)$ falling a distance d at the same time step follows the power-law form

$N(d) \approx d^{-D}$ where D is a fractional quantity, the fractal dimension of the avalanches. More generally, for a critical system, the distribution of fluctuation sizes is described by a power-law that writes:

$$F(s) \approx s^{-D} , \tag{1}$$

where s is the size of an "avalanche" and $F(s)$ is the frequency of its occurrence. The negative exponent of the distribution leads to many small events or fluctuations punctuated by progressively rarer large events, hence the notion of intermittency introduced above. To estimate the fractal dimension D, the system in question is observed over a period of time and the frequency of events of size s is recorded. In the sandpile case, the events are avalanches of sand grains, and the size of an event is the number of grains in a particular avalanche. Frequency is estimated as the number of events of size s divided by the total number of events.

Self-organized criticality occurs in systems that build up stress and then release the stress in intermittent pulses. This can be generally described by a power-law that states that the probability of events with intensity I greater than a given threshold I_i follows:

$$\Pr(I > I_i) \approx I^{-\phi} , \tag{2}$$

where ϕ is the scaling exponent describing the distribution.

Finally, we stress here that to estimate the scaling exponents D (Eq. (1)) and ϕ (Eq. (2)), we preferred linear regression on the log-transformed data to nonlinear regression on the raw data because the residual error will be distributed as a quadratic and the minimum error is guaranteed. This is not the case with nonlinear regression. Finally, because an objective criterion is needed for deciding upon the appropriate range of scales to include in the regression, we used the scales and the intensities which maximized the coefficient of determination and minimized the total sum of the squared residuals for the regression [53].

2.3. Self-organized criticality in physical sciences

There are numerous studies devoted to the identification and the characterization of self-organized criticality in the physical sciences. A simple example is the stress that builds up the earth's crust and is released in earthquakes [54]. This is described by the well-known Gutenberg–Richter law of geophysics that states that the number of earthquakes N with energy E greater than a given threshold E_0 scales following Eq. (2) where the scaling exponent ϕ is estimated as $\phi = 1.91$ [55,56]. The earthquake intensity distribution is thus "scale free" with no typical size of the intensities. Volcanic activity, like that of earthquakes, is also intermittent, with events of all sizes. Using acoustic sensors placed at a distance from the volcano and another placed nearer to it, it has been shown that for both signals, the number of acoustic bursts follows Eq. (2). While one signal was weaker than the other, they exhibit similar linear behavior on logarithmic plots, with an exponent $\phi \approx 2.00$ [57]. Volcanic activity is thus also a self-organized critical phenomenon.

While the concept of sand pile initially emerged from a simple theoretical model [25,26], it has been recovered in a wide variety of materials piles, including granular pile [58], real sand pile [59] and rice pile [60]. The avalanche phenomena, related to self-organized criticality, observed in these laboratory studies have also found applications to explain landscape formation in nature (regarded as a granular pile subjected to erosion by water) [61,62], Himalayan avalanches [63], sediment deposition in the ocean (the sediment basically cascades along the continental slopes and forms layered structures at the bottom of the ocean) [64], the formation of river networks [65,66] and the dynamics of atmospheric flows [67].

Amazingly, self-organized criticality—as witnessed by Eqs. (1) and (2)—is not confined to the Earth, but can be found elsewhere in the universe. For instance, pulsar glitches follow the Gutenberg–Richter law, and have thus been referred to as "starquakes" [68] as well as X-ray intensity from solar flares [69].

2.4. Self-organized criticality in ecological sciences

Evidences for self-organized criticality in ecological sciences are still scarce, but nevertheless include a wide spectrum of ecological fields ranging from tree-fall gap formation in tropical rainforests [70] and bird population dynamics [71], to models of ecosystem [72] and evolution [73,74].

In particular, data sets related to the introduced Hawaiian avifauna support a scenario in which island communities build up to a critical number of species, above which avalanches of extinction occur [71]. The avalanches of extinction observed in the fossil record [6] may then be indicative of a self-organized critical state, as suggested from simple coevolutionary models [73,75,76]. In the case of coevolving species, one may note that exact analytical solutions have been given, demonstrating that extinction cascades following the distributions given in Eqs. (1) and (2) can emerge spontaneously in simple models of coevolution [76,77]. More generally, these results suggest that ecological communities are not characterized by a well defined equilibrium, but rather by a detailed balance which is minimally stable to perturbations such that the introduction of species can trigger extinction cascades.

Numerical perturbation experiments (i.e., an addition of individuals to a steady state) conducted in the framework of a very simple ecosystem model known as the "game of life" [72] led to power-laws resulting from the distributions of avalanches of size s, $F(s)$, i.e., $F(s) \approx s^{-D_1}$, and the distribution of the duration of perturbations $F(T)$, i.e., $F(t) \approx t^{-D_2}$, with $D_1 \approx 1.4$ and $D_2 \approx 1.6$, respectively. Despite its extreme simplicity, this model has subsequently been validated *via* Monte Carlo simulation studies [78], and extended to a wide variety of ecosystems situations [79,80]. Among them, a simple model of tree growth and competition for resources in a tropical rainforest led to scaling properties that cannot be distinguished from the one observed from a real forest. Eq. (1) has thus been verified over a wide range of scales and leads to fractal dimensions $D \approx 2.01$ and 2.06 for the real and modeled forests, respectively [81–83].

Finally, one may note that in coevolutionary models, as well as in the "game of life", the dynamics are generated by species interactions, or more generally perturbations, as opposed to transfers of momentum in physical systems.

3. Sampling microphytobenthos patches pattern

3.1. Intertidal environment and microphytobenthos

The intertidal environment is the part of the littoral zone that is directly influenced by an alternance of emersion/immersion phases related to the tidal cycle (Fig. 1). More specifically, the intertidal zone (B) is bounded between the supralittoral zone (A) and the infralittoral zone (B) that are never immersed nor emersed, respectively. The intertidal zone must nevertheless be regarded as a dynamic area, with boundaries that fluctuate in time. Its upper bound is found between the upper limits reached by the tidal flow at high tide in spring and neap tides. On the opposite, its lower bound oscillates between the lower limits reached by the tidal flow at low tide in spring and neap tides. Finally, note that a wide variety of sediment covers, ranging from rocky to sandy and muddy substrates, can be observed in the intertidal zone which can then allow the development of many kind of benthic ecosystems [84].

Microphytobenthos are photosynthetic cells living within the surface layers of coastal sediments. They provide as much as 50% of the carbon fixed in some coastal systems and have importance as a food resource [85] and as "ecosystem architects" altering the erosion potential of coastal sediments [86–88]. The majority of the cells belong to the Bacillariophyceae or diatoms, that can be found in the nearshore sediments, either attached to sand grains or rocks, or living on the mud [89–91]. Diatoms are usually robust with heavily silicified frustules (e.g. *Caloneis sp.*, *Diploneis sp.*; Fig. 2). Some of them are motile, they secrete mucus that allows them to glide freely on the sediment. In particular, vertical migration can be easily observed on both sandy and muddy flats

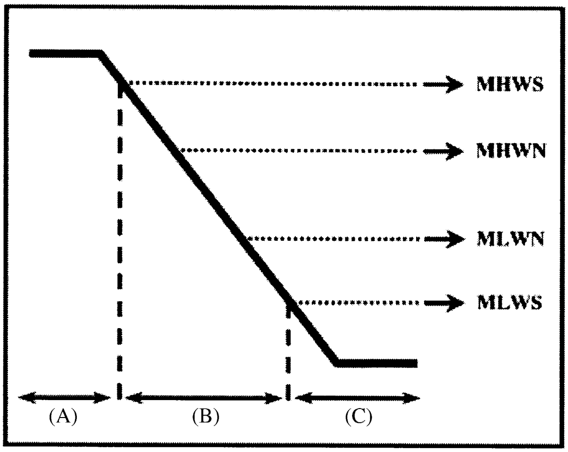


Fig. 1. Schematic zonation of a hydrodynamically exposed sandy flat in the Eastern English Channel. The intertidal zone (B) is bounded between supra-(A) and infralittoral (C) zones. The upper bound of the intertidal zone is bounded between the upper limits reached by the tidal flow at high tide in spring and neap tides, MHWS and MHWN, respectively. The lower bound is bounded between the lower limits reached by the tidal flow at low tide in spring and neap tides, MLWN and MLWS, respectively.

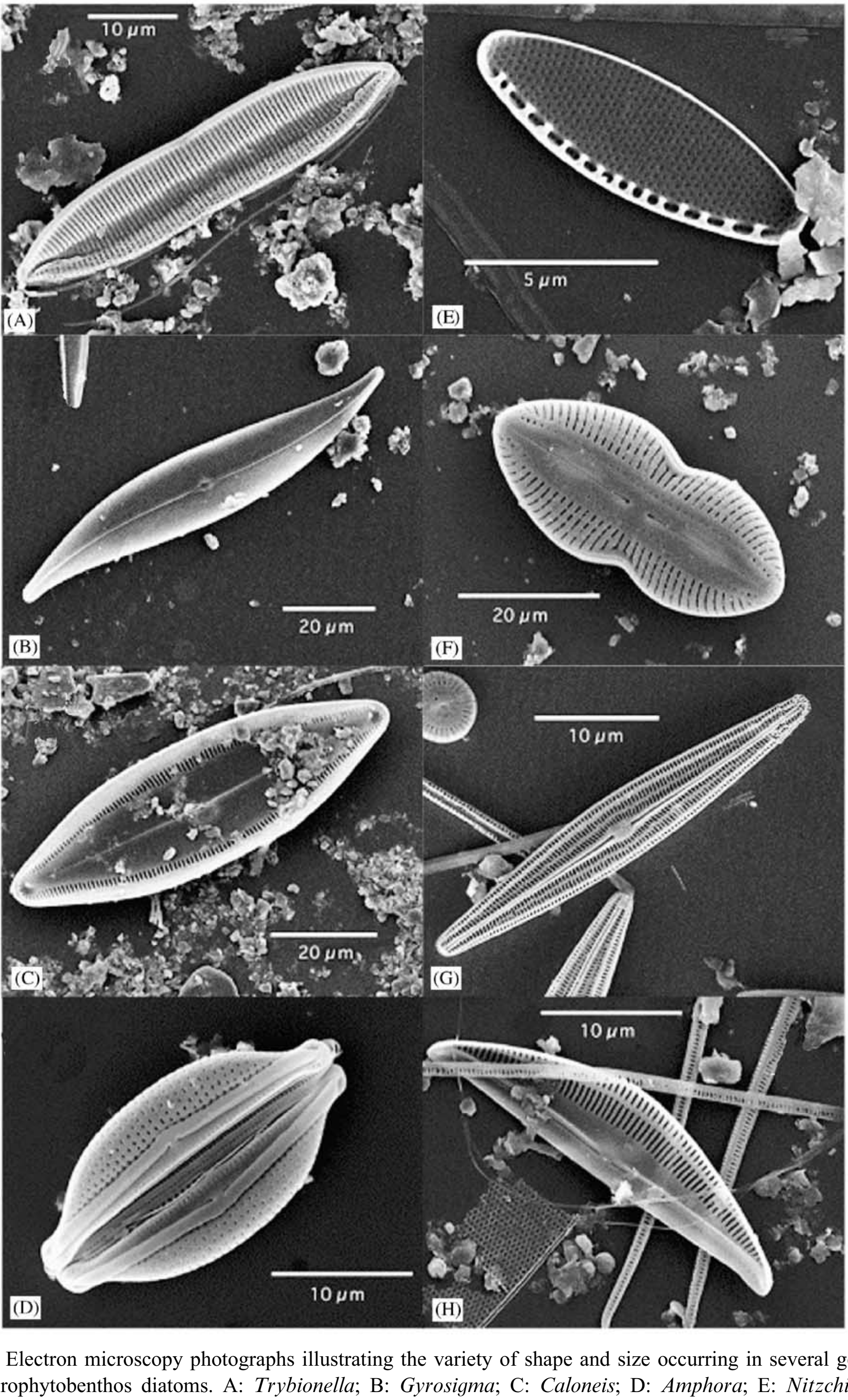


Fig. 2. Electron microscopy photographs illustrating the variety of shape and size occurring in several genera of microphytobenthos diatoms. A: *Trybionella*; B: *Gyrosigma*; C: *Caloneis*; D: *Amphora*; E: *Nitzchia*; F: *Diploneis*; G: *Brachysira*; H: *Amphora*.

and exhibits diel rhythms. Microphytobenthos cells then move upwards to the surface when the sediment is exposed at low tide and migrate downwards before it is flooded [92]. One must nevertheless note here that these migrations occur at low tide, but only when low tides occur during the day [93]. Recent results have revealed that the high diversity and rapid turnover of microphytobenthos populations make them ideal as model system for the study of ecological theory (such as diversity vs. productivity issues) and aspects of ecosystem change (e.g. global warming) [94].

3.2. Study site, living material collection and conservation

The study site chose, an intertidal flat of sand in Wimereux (France) was typical of the hydrodynamically exposed sandy beach habitats that dominate the littoral zone along the French coast of the Eastern English Channel. We chose an area in the upper intertidal zone without elevational gradient and without sharp topographical features as ripple marks, high pinnacles or deep surge channels. The specific study plot ($50^{\circ}45'896$ N, $1^{\circ}36'364$ E) was selected because it is characterized by homogeneous medium size sand (200–250 μm, modal size), weak biomass, productivity and production of both phyto- and zoobenthic organisms [95], then an a priori homogeneous distribution of microphytobenthos biomass, and was typical of the surrounding sandy habitat. Air temperature at the site range from about 1°C–10°C in the winter to highs of about 10–25°C in the summer [96]. Water temperature vary from 5°C to approximately 18°C depending on the season. Salinity is usually about 31‰ but can also vary with the season, being lower in late winter and early spring and higher in late summer and fall [96].

For estimated microphytobenthos patch pattern, we focused on scales smaller than 1 m^2, that is usually the finest grain considered in both landscape ecology [97] and intertidal benthic ecology [50,98]. A rigid 1 m^2 aluminum quadrat of the design shown in Fig. 3 was used, and 225 equidistant samples were collected every 6.67 cm using 1.9 cm^2 plastic cores. The cores were pushed into the sediment down to a depth of 1 cm, where most of the active cells are concentrated [99–103], carefully removed and then stored in a cool box, brought back to the laboratory and stored in the dark at -20°C.

3.3. Measurements of microphytobenthos biomass

Chlorophyll *a* is usually used as an index for primary producers biomass [98, 104–106]. In the laboratory, sections of sediment were placed in 8 ml acetone and pigments were extracted for 4 h in the dark at 4° [107]. After extraction, samples were centrifuged at 4000 rpm for 15 min. Chlorophyll *a* concentrations (Chl.*a*, mg) in the supernatant were determined by spectrophotometry following the equation given by

$$\begin{aligned}\text{Chl.}a = V[(11.64(\text{OD}_{663} - \text{OD}_{750}) - 2.16(\text{OD}_{645} - \text{OD}_{750})\\ + 0.1(\text{OD}_{630} - \text{OD}_{750})] ,\end{aligned} \tag{3}$$

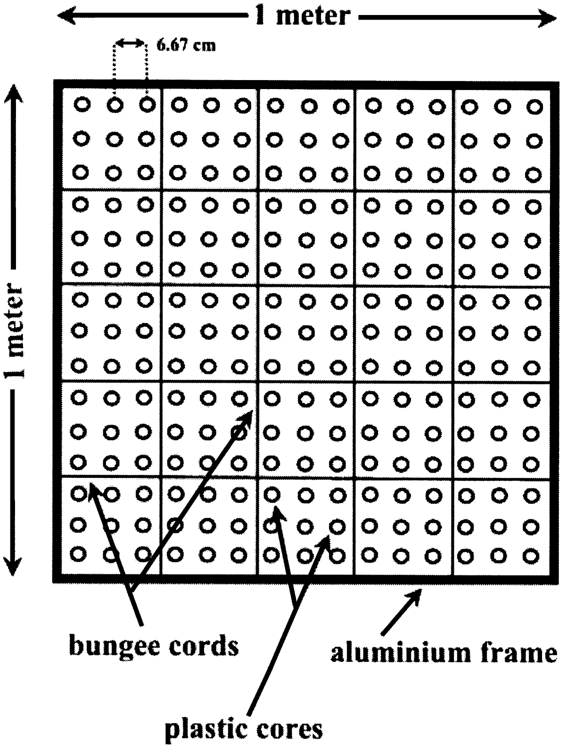


Fig. 3. Quadrat design for microphytobenthos biomass estimation. The resolution and the extent are 1 m and 6.67 cm, respectively.

Where V is the extraction volume (1) and OD_λ is the optical density of the supernatant at wavelength λ (nm) [108]. Chlorophyll a concentrations estimated in the supernatant have subsequently been expressed in terms of chlorophyll a per surface unit ($\mu\mathrm{g\,m^{-2}}$) taking into account the 1.9 cm^2 surface of the sampling unit.

4. Microphytobenthos patches and self-organized criticality

4.1. Statistical analysis of microphytoplankton patches

Microphytobenthos biomass exhibits a very intermittent behavior, where sharp fluctuations occurring locally are clearly visible (Fig. 4). Results of descriptive analysis, including skewness and kurtosis estimates, show that the 225 microphytobenthos biomass estimates are obviously not normally distributed (Kolmogorov–Smirnov test, $p < 0.01$). Their frequency distribution rather exhibits a positively skewed behavior ($G_1 = 0.60$), reflecting a distribution characterized by a few dense patches and a wide range of low density patches. Finally, the positive kurtosis shows a distribution that is peakier than expected in the case of normality ($G_2 = 1.83$).

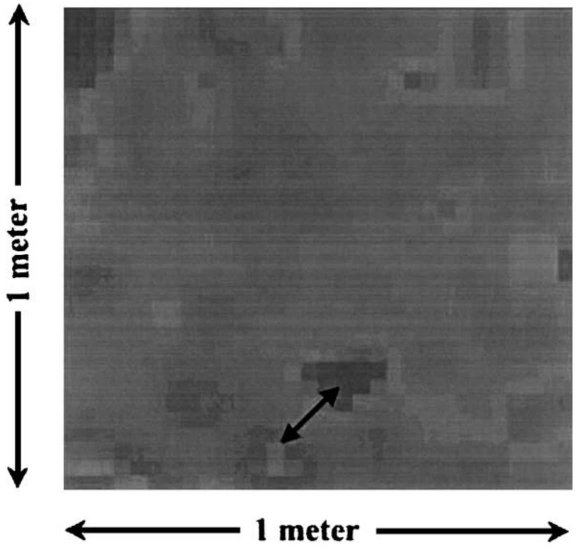


Fig. 4. Two-dimensional distribution of microphytobenthos chlorophyll *a* content in our 100 × 100 cm sampling area. The greener the contour area the higher the chlorophyll concentration. The maximum gradient (double arrow) is a 12 times change over 13.34 cm, i.e. two times the resolution of our sampling.

More specifically, microphytobenthos biomass is bounded between 1.90 and 27.15 mg m^{-2}, i.e., 10.79 ± 4.15 mg m^{-2} ($\bar{x} \pm \mathrm{SD}$). These biomass estimates are low when compared to the biomass estimates of microphytobenthos taken from biologically rich and active muddy flats (i.e., bounded between 45 and 110 mg m^{-2}) [95]. However, chlorophyll *a* concentrations estimated here on a sandy flat are significantly higher (Wilcoxon–Mann–Whitney U-test, $p < 0.01$) than microphytobenthos biomass estimated at the same spot 1 year earlier, 25 September 2000 (2.75 ± 0.88 mg m^{-2}, $\bar{x} \pm \mathrm{SD}$). This can be thought as a consequence of the autumn bloom (i.e., a period of growth of phytoplankton populations) that occurred in th coastal waters of the Eastern English Channel. Indeed, over the same period, chlorophyll *a* concentrations were estimated as 10.72 ± 3.29 μg l^{-1} ($\bar{x} \pm \mathrm{SD}$) in the shallow water moving onto or off of the investigated sandy flat and 8.33 ± 3.52 μg l^{-1} ($\bar{x} \pm \mathrm{SD}$) in the adjacent coastal water masses (Leterme and Seuront, unpublished data).

4.2. Self-organized criticality fingerprints in microphytobenthos patch pattern

A precise knowledge of the distribution of organisms is of fundamental importance in understanding the relationships between organisms and the subsequent fluxes of matter [109]. Generally speaking, the distribution of resources is a prime interest for higher trophic consumers, as recently numerically investigated in marine systems [110,111]. Benthic organisms especially represent the link between benthic and pelagic ecosystems and then play a fundamental role in marine ecosystem functioning [112]. More specifically, food availability changes depending on the dimension [11]. Low fractal

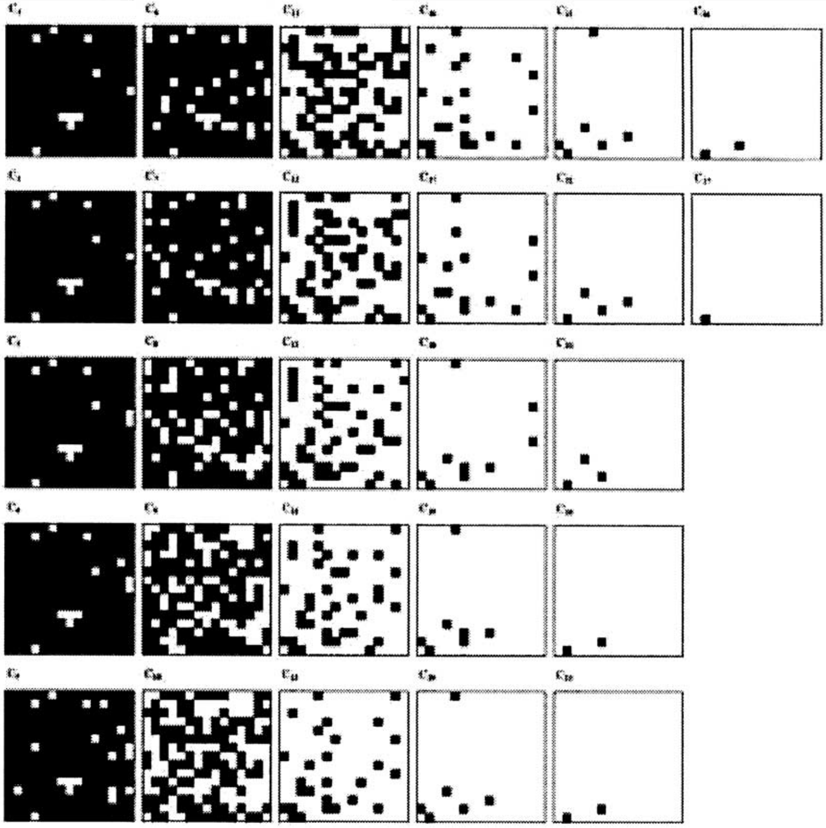


Fig. 5. Two-dimensional distributions of microphytobenthos chlorophyll *a* content, where patch concentration C has been discretized using critical patch concentration C_i such as $C > C_i$ with C_i ranging from 1.9 to 26.6 mg Chl.*a* m^{-2} (with 0.95 mg m^{-2} increments). Black areas indicate locations where $C > C_i$.

dimension means a smooth and predictable distribution of particles gathered in small numbers of patches. High dimensions means rough, fragmented, space-filling and less predictable distribution. Therefore, when a predator can remotely detect its surroundings, prey distributions with low dimension should be more efficient. In contrast, when a predator has no detection ability, prey distributions with high dimension should be relatively better, because available food quantity (or encounter rate) becomes proportional to the searched volume as fractal dimension increases [11]. These statements even become more crucial when considering the widespread behavioral adaptation of consumers to food concentration [110,113,114]. As a consequence, the quantification of the spatial distribution of microphytobenthos patches at different concentration is critical to our understanding of intertidal communities structures and functions.

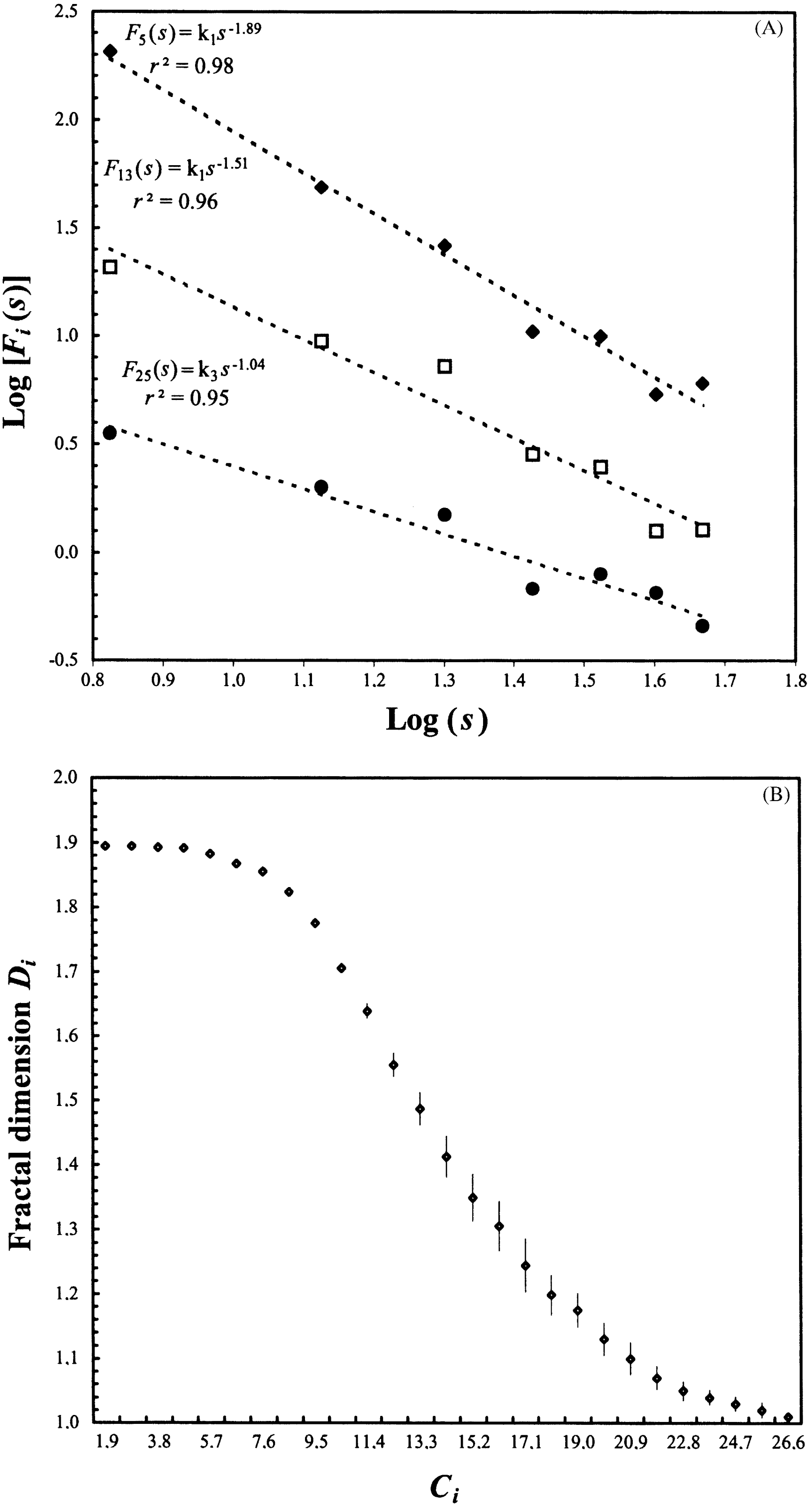
Fig. 5 shows the distribution of microphytobenthos patches, where patch concentration C has been discretized using critical patch concentration C_i such as $C > C_i$ with C_i ranging from 1.9 to 26.6 mg Chl.*a* m^{-2} (with 0.95 mg m^{-2} increments). In each of the 22 patch patterns investigated, patches such as $C > C_i$ are shown as black dots. We subsequently quantified the distribution of these categorized patches rewriting Eq. (1) as

$$F_i(s) \approx s^{-D_1} , \tag{4}$$

where $F_i(s)$ is the frequency of occurrence of patches of concentration C_i, and D_i is the related fractal dimension. To estimate the fractal dimensions D_i of the patch patterns the pictures have been transformed into a binary matrix. A value 1 has been assigned to black sites, and 0 to white ones. The occupied boxes having sizes between 1×2 (or 2×1) and 7×7, in plot units. The system has been covered by rectangular and square boxes in both directions, and all integer box sizes s have been used. The whole plot has size 15×15 in plot units, and each pixel represents a surface of 6.67×6.67 cm in the field. Fig. 6 shows the results. The power-laws relating the frequency of occurrence of patches of concentration C_i and the box size s (Eq. (4)) are clearly linear over the whole range of available scales, with coefficient of determination r^2 ranging from 0.93 to 0.99 (Fig. 6A). The existence of self-similar (i.e., scaling) behavior here is suggestive of self-organization near a phase transition, where large-scale correlations can emerge. In a equilibrium state, correlations are limited to local scales [115]. Phytobenthos patches, which at first appears featureless, are actually remarkably correlated, whatever their concentrations. However, the fractal dimensions D_i (Fig. 6B) lead to specify these results. Low density patches (i.e., $C \leqslant 6.65$ mg Chl.a m^{-2}) are characterized by high fractal dimensions, $D_i = 1.89 \pm 0.01$. Such high dimensions (the maximum values that D_i can reach is $D_i = 2.00$) characterizes very complex processes where short-range, local variability is highly developed and tends to obfuscate long-range trends; the variable is more evenly or regularly distributed (i.e., less structured) in space. In other words, this indicates that the variation within a sampling unit is equal to the variation among sampling units [53]. On the opposite, fractal dimensions related to high density patches (i.e., $C \geqslant 22.80$ mg Chl.a m^{-2}) are very low $D_i = 1.03 \pm 0.02$, cannot be statistically distinguished ($p < 0.05$) from the lowest D_i value (i.e., $D_i = 1$). This indicates that the variability of the variable is dominated by long-range effects, and remains the so-called aggregated clumped point pattern (Li, 2000). Finally, patches corresponding to intermediate chlorophyll a concentrations ($7.60 \leqslant C \leqslant 21.85$ mg Chl.a m^{-2}) are characterized by decreasing fractal dimensions D_i from $D_i = 1.85$ to 1.07. Following the behavioral statement introduced above, and the demonstrated sensorial abilities of intertidal organisms [116,117], in the specific case studied here, microphytobenthos grazers will derive maximum benefit from high concentration patches. An approximate randomization procedure [118] has been used to test the null hypothesis that the number of patches was not related to their size. The probability that the observed correlation between patch number and patch intensity was

→

Fig. 6. Box-counting carried over the sets of Fig 5. Fractal dimensions D_i are estimated from the best linear fit of the log–log plot of the frequency of occurrence of patches of concentration $C_i, F_i(s)$, vs. the size of the boxes s. Results shown here correspond to three critical patch concentrations C_i, $C > 5.7$, $C > 13.3$ and $C > 24.7$ mg Chl.a m^{-2} (A). The nonlinear distribution of the fractal dimensions D_i (B), plotted against critical concentrations C_i, indicate the multifractal character of microphytobenthos patchiness.


(A)
$F_5(s) = k_1 s^{-1.89}$
$r^2 = 0.98$
$F_{13}(s) = k_1 s^{-1.51}$
$r^2 = 0.96$
$F_{25}(s) = k_3 s^{-1.04}$
$r^2 = 0.95$
Log [$F_i(s)$]
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
0.8
0.9
1.0
1.1
1.2
1.3
1.4
1.5
1.6
1.7
1.8
Log (s)
(B)
Fractal dimension D_i
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
1.9
3.8
5.7
7.6
9.5
11.4
13.3
15.2
17.1
19.0
20.9
22.8
24.7
26.6
C_i

due to chance was $p = 0.0024$ (of 10 000 randomizations, 24 resulted in a correlation greater than or equal to the observed correlation).

One must note here that the distribution of the fractal dimensions D_i (Eq. (3); Fig. 6B) is reminiscent of the spectrum of the correlation dimensions $D(q)$ [119]. Even if we agree that the nonlinear behavior shown in Fig. 6B is indicative of multifractality in our data [10,30], we did not use the standard multifractal framework for both computational and conceptual reasons. Let us recall that in the specific framework of correlation dimensions $D(q)$, the fractal dimension D introduced in Eq. (1) must be rewritten as

$$D = D(0) = \lim_{s \to 0} \left(\frac{\log[F(s)]}{\log(s)} \right) . \tag{5}$$

More generally, the dimensions $D(q)$ are written as

$$D(q) = \lim_{s \to 0} \left(\frac{1}{q-1} \frac{\log[X(q)]}{\log(s)} \right) , \tag{6}$$

where $X(q) = \sum_{i=1}^{N(l)} p_i^q$. The statistical order of moments q are defined as $-\infty < q < +\infty$, and the probability of every ith box p_i can be arbitrarily defined over the set, with the only requirement being the normalization: $\sum_{i=1}^{N(l)} p_i = 1$. From Eqs. (5) and (6) it is easily seen that estimates of D and $D(q)$ require estimates of their asymptotic behaviors when $s \to 0$. However, these behavior cannot be statistically investigated nor tested in the present work because of the small range of scales, and then the weak number of data points, available in Fig. 6A. This is the reason why we generalize Eq. (1) and propose Eq. (4). Moreover, we claim here that the framework related to the multifractal framework, especially the statistical order of moments q and the exponent of singularity α used in the x-axis of the spectrum of the correlation dimensions $D(q)$ and the spectrum of singularities $f(\alpha)$ [120,121] are far from intuitively comprehensive for ecologists. This last statement represents a major limitation to the spreading of scientific knowledge between fields as different as nonlinear dynamics and benthic ecology, and then an intrinsic limitation to the progress of the actual scientific thought process [122]. On the opposite, the proposed multifractal spectrum of the dimensions D_i can be directly interpreted in terms of ecological processes because fractal dimensions are directly plotted against biomass which is the most fundamental measure in ecology. Finally, we claim that the validity of our analyses is fully ensured by the highly significant ($p < 0.01$) linear behaviors shown from Eq. (4) for all the values of patch concentrations investigated.

In this final section, we present additional results that help to corroborate the conjecture that microphytobenthos patches are actually a living microscale system with critical dynamics. Fig. 7 shows the log–log plot of the probability of microphytobenthos patches with a concentration in chlorophyll a C greater than a given threshold C_i ranging from 1.9 to 26.6 mg Chl.a m^{-2} (with 0.95 mg m^{-2} increments). On the basis of the objective criteria introduced in Section 2, we found a clear scaling behavior for patch concentration C such as $C \geqslant 11.40$ mg Chl.a m^{-2} with the scaling exponent $\phi = 5.31$, i.e., $\Pr(C > C_i) \approx C^{-5.31}$ ($r^2 = 0.99$). Using an approximate randomization test, the probability that the observed power-law relationship between the number of

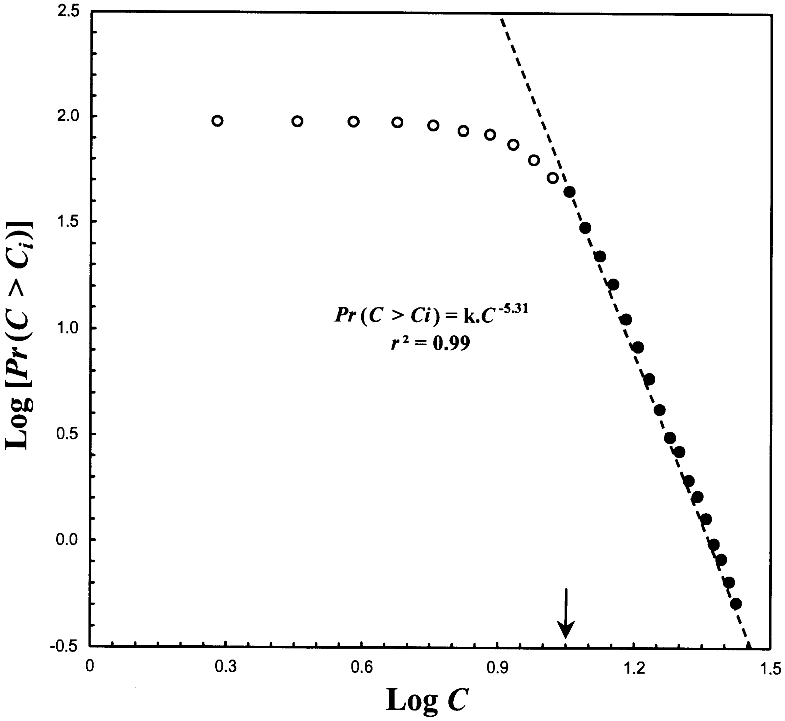


Fig. 7. Log–log plot of the probability of microphytobenthos patches with a concentration in chlorophyll a, C, greater than a given threshold C_0 ranging from 1.9 to 26.6 mg Chl.*a* m^{-2} (with 0.95 mg m^{-2} increments). The linear behavior observed above a critical biomass $C \geqslant 11.40$ mg Chl.*a* m^{-2} (arrow) is a fingerprint for self-organized criticality.

patches and their intensity was due to chance was $p = 0.001$, i.e., over 10000 randomizations, 10 resulted in a correlation greater than or equal to the observed correlation. The fact that events greater than 11.40 mg Chl.*a* m^{-2} do not follow the same law than smaller events indicates that there is something special about these events. In particular, the smooth transition from low to high concentration patches observed in Fig. 7 indicates a scenario in which microphytobenthos community build up to a critical biomass, above which "avalanches" of patches occur. In other words, the microphytobenthos community investigated here can be regarded as being in a subcritical state for low concentration patches. On the opposite, patches of higher concentration (i.e., $C \geqslant 11.40$ mg Chl.*a* m^{-2}) characterized by a power-law behavior are in a critical state, resulting in a dynamic balance as the sand pile.

In particular, we stress that the decrease in the number of patches above a critical biomass observed in Fig. 7 suggests that the development of the patches are structured by conflicting constraints. In the case of the sandpile model, the constraints are gravity which acts to lower the height of the pile and addition of sand grains which raises the height of the pile. The structure of the pile emerges from the interaction of these forces. It is a salient issue to realize that, although gravity acts uniformly on all grains in the pile, the probability of an avalanche is not spatially uniform across the pile. Some areas of the pile will have steeper slopes and thus, a higher probability of sliding. Each avalanche changes the spatial pattern of slopes and thereby affects the size of subsequent avalanches, which in turn determine the structure of the pile yet again. It is this pattern of long-range correlations among avalanches that is the key to understanding self-organized criticality. We will outline hereafter the constraints, and there potential effects, that act on the structure and dynamics of a microphytobenthic assemblage. In the case of microphytobenthos biomass, the microscale distribution of patches is the result of both endogenous (e.g. microphytobenthos growth, migration and death) and exogenous processes (e.g. tides, hydrodynamism, sediment quality, interspecific and intraspecific competition for nutrient, grazing) that can act to decrease and/or increase the microphytobenthos biomass. As illustrated in the sandpile model, these constraints do not act uniformly over the whole spatial domain. For instance, biomass losses related to grazing are dependent on both the spatial distribution and foraging abilities of predators [116,117]. Growth and death are dependent on nutrient and light availability that is also a function of the burying depth of microphytobenthos cells, the density and the spatial distribution of the sediment and the duration of the emersion. The microphytobenthic community at the sediment surface may be disturbed by turbulence and shear stress generated by tidal currents or wind-waves and lead to microphytobenthos cells load in the water column [98]. The degree of disturbance depends on the interplay of a number of factors including sediment type, stability of the sediment surface, mean water depth, tidal height, magnitude of tidal currents, wave height, and macrofaunal abundance and activity. In particular, resuspension processes occur during immersion and lead to biomass losses for the microphytobenthic system. On the opposite, resettling of cells occurring at the beginning of emersion can be regarded as playing a major role in the observed patch pattern. It has thus been shown that the distribution of biotic particles (i.e. phytoplankton cells and resuspended microphytobenthos cells) are very patchy in turbulent coastal waters as shown in Fig. 8 [10,44,45,123]. The patch pattern identified from analysis of the chlorophyll *a* content in the first centimeter of sediment may then be a indirect consequence of the patchiness of chlorophyll *a* suspended in the water column; see the similarity between Figs. 4 and 8.

These constraints, acting quite obviously to increase and/or decrease microphytobenthos biomass, result in a dynamic balance as in the sand pile model. However, the cause of patchiness, and in particular the self-organized criticality observed in patch pattern are less clear. Let us illustrate here a potential mechanism for patch formation, with specific reference to the critical biomass observed in the microphytobenthos patch pattern. A candidate mechanism for patchiness is competition among species. If competition is a driving force in structuring microphytobenthos community, then the important dynamics would be observed in the niche space occupied by different species [124–126]. Competitive pressure would be expected to be high in regions of niche space where species are densely packed, as would happen, for instance, when a number of phytoplankton species share the same food resource [127,128]. It is possible that, like steep region of the sandpile, species occupying dense regions of niche space (i.e., $C > 11.40$) are subject to higher extinction probabilities, and then reduce the

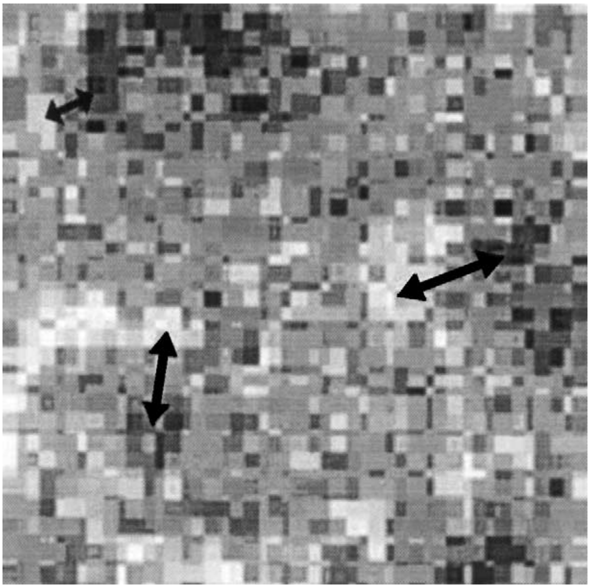


Fig. 8. A two-dimensional simulation of phytoplankton distribution following the parameterization and the simulation methods described in Ref. [11]. The redder the contour area the higher the phytoplankton concentration. Note the similarity between this pattern and the microphytobenthos patchiness shown in Fig. 4, especially the sharp gradients (double arrows) occurring between high- and low-density areas.

probability of high density patches. The loss of species would change the distribution of species in niche space and, in turn, change the probability of extinction and patches, much like the dynamics of the sand pile model. The system is in a critical state. In contrast, species occupying sparse regions of the niche space (i.e., $C \leqslant 11.40$) are subject to weaker competition pressure and extinction probabilities. The system is then in a more stable, or subcritical state, and do not exhibit any fingerprints of self-organized criticality.

5. Discussion and concluding remarks

Let us summarize here the main results of this paper, and briefly discuss their potential implications. We have presented for the very first time empirical evidence for a strong patchiness in microphytobenthos biomass from a microscale two-dimensional sampling. It has been shown that the microphytobenthos patch pattern exhibits some fingerprints for self-organized criticality, i.e., scaling properties of patch intensity vs. spatial scales and patch probability vs. patch intensity. In particular, the results presented here have several potential implications on our understanding of structures and functions in intertidal benthic ecosystems. For instance, does the observed self-organized criticality in microphytobenthos patch patterns have any consequences on microphytobenthos biomass, or on the subsequent primary production estimates?

In order to address these questions more thoroughly, we conducted a survey of all papers reporting microphytobenthos biomass and/or production estimates that appeared from 1968 and 2000. We then gathered the minimum and maximum chlorophyll contents and production rates observed in the sediment from a wide variety of intertidal environments for time scales ranging from 0.5 to 57 months. These chlorophyll contents have subsequently been normalized by the thickness of the sediment samples. Table 1 shows the ratios r_b and r_{prod} of normalized minimum and maximum values of chlorophyll contents and production rates, respectively. Comparisons of the data gathered from our literature survey with our results lead to three major conclusions.

First, comparisons between the chlorophyll contents estimated in the present study from sediment samples of 1 cm thickness and the normalized chlorophyll contents from our literature survey (data not shown) indicate the low density of microphytobenthos biomass estimated from our 225 samples. Indeed, 80% and 83% of the minimum and maximum normalized chlorophyll contents taken from the literature survey are larger than the minimum and maximum values estimated in the present work. Sandy intertidal environments are generally not considered as highly concentrated in microphytobenthos nor very productive, and the absolute measures of biomass per surface unit reported here (bounded between 1.9 and 27.15 mg Chl m^{-2}) are indeed not very dense. These results, together with the strong photosynthetic active radiation (PAR) and the saturating productive properties of microphytobenthic organisms observed during the sampling experiment (spilmont, Davoult, and Migné, unpublished data) [129], nevertheless suggest that microphytobenthos cells accumulated in the first centimeter of sediment are highly productive.

Second, semi-annual and annual variability in sediment chlorophyll *a* contents reported in Table 1 and evaluated as r_b, $r_b \in [2.10\text{–}300.00]$, are relatively weak when compared to the variability estimated from our single, localized sampling where $r_b = 14.29$. Indeed, 49% of the r_b values taken from our literature survey are smaller than the r_b estimated from our sampling. These data suggest that the error in sampling might account for much of the variation in chlorophyll reported in the seasonal and annual studies summarized in Table 1, particularly when the microphytobenthos has been sampled with relatively few and small cores as it is usually the case [130]. It is then doubtful that a (small) finite number of samples (e.g. 5 and 6, as in Refs. [130,131], respectively) can be representative of a microphytobenthos population. Alternatively, an appropriate parameterization of microphytobenthos patchiness, as illustrated here by self-organized criticality fingerprints can provide an efficient framework to infer patch pattern from a limited number of samples.

Let us finally note that the previously demonstrated patchiness may also have salient implications on microphytobenthos primary production. Basically stating that primary production is a linear function of chlorophyll content [132], it can be thought that the observed variability in microphytobenthos biomass (i.e. r_b, see above) will be directly reflected in primary production estimates, leading to a ratio $r_{prod} = 14.29$ between minimum and maximum production. This values is greater than 32% of the r_{prod} values gathered in Table 2, and that characterize semi-annual and annual variability in primary production by microphytobenthos. The impact of microphytobenthos patchiness on primary production estimates can even be sharpened considering the combination of

Table 1
Temporal variability in sediment chlorophyll content, ordered by thickness of sediment sample and experiment duration, and expressed as the ratio r_b between maximum and minimum chlorophyll contents, a wide variety of intertidal environments

Location	Thickness (nm)	Biomass, r_ϕ	Duration (months)	Source
German Wadden Sea, Germany	1	300.00	3	[139]
Danish Wadden Sea, Denmark		45.00	4	[139]
Westershelde estuary, The Netherlands		60.00	12	[138]
Westershelde estuary, The Netherlands		90.00	12	[138]
San Antonio Bay, Texas, USA	2	15.00	9	[141]
North Inlet Estuary, South Carolina, USA		3.67	12	[140]
Bay of Brest, France	3	11.3	10	[131]
Ems Estuary, The Netherlands	5	7.67	6	[146]
San Antonio Bay, Texas, USA		18.00	9	[141]
Graveline Bay, Mississippi, USA		11.29	11	[150]
Mugu Lagoon, California, USA		9.76	14	[144]
Dour duff Estuary, France		6.19	17	[143]
Dona Paula Bay, India		15.00	17	[151]
North Inlet Estuary, South Carolina, USA		5.50	19	[149]
Morbihan Bay, Karguelen Island, France		28.03	24	[152]
Ems Estuary, The Netherlands		112.00	26	[147]
Laholm Bay, Sweden		11.25	33	[145]
Ems Estuary, The Netherlands		42.00	35	[148]
Baie de Morlaix, France		21.52	39	[142]
Marennes-Oléron Bay, France	10	4.00	0.5	[168]
Marennes-Oléron Bay, France		2.53	0.5	[168]
Chukchi Sea, Alaska USA		3.20	7	[153]
San Antonio Bay, Texas, USA		18.67	9	[141]
Potter Pond Lagoon, Rhodes Island, USA		46.00	12	[159]
Delaware Estuary, Delaware, USA		2.10	12	[161]
Netrats Bay, Oregon, USA		31.50	12	[155]
Firth of Lorne, Scotland, UK		23.00	12	[165]
Long Island Sound, New York, USA		112.50	13	[160]
Dutch Wadden Sea, The Netherlands		22.91	14	[166]
Ria de Arosa, Spain		3.43	14	[157]
Ria de Arosa, Spain		3.50	14	[157]
Boston Harbor, Massachusetts, USA		6.60	14	[158]
Chesapeake Bay, Virginia, USA		13.00	15	[162]
Peel-Harvey Estuary, Australia		18.67	16	[163]
La Jolla, California, USA		4.20	20	[167]
Bay of Piran, Slovenia		2.78	21	[164]
Dutch Wadden Sea, The Netherlands		4.36	23	[99]
Golfe de Fos, France		75.00	28	[156]
Lake Gravelingen, The Netherlands		20.50	47	[154]
Dutch Wadden Sea, The Netherlands		14.00	57	[99]
Ems Estuary, The Netherlands	20	49.00	10	[90]
Bussards Bay, Massachussets, USA		4.25	11	[170]
Vostok Bay, Russia		3.91	13	[169]
Loch Ewe, Scotland, UK		192.00	22	[171]
Western English Channel, France	100	3.31	2	[131]
Eastern English Channel, France	10	14.29	0.001	Present study

Table 2
Temporal variability in gross primary production by microphytobenthos in sediment, ordered by experiment duration and expressed as the ratio r_{prod} between maximum and minimum production rates in a wide variety of intertidal environments

Location	Production, r_{prod}	Duration (months)	Source
Marennes-Oléron Bay, France	17.50	0.5	[168]
Smalandshavet, Denmark	110.00	6	[178]
Oresund, Denmark	36.67	7	[177]
Chukchi Sea, Alaska, USA	11.40	7	[153]
San Antonio Bay, Texas, USA	11.00	8	[141]
San Antonio Bay, Texas, USA	86.00	8	[141]
Graveline Bay, Mississippi, USA	11.20	11	[150]
Westershelde estuary, The Netherlands	150.00	12	[130]
Netarts Bay, Oregon, USA	17.60	12	[155]
Ythan Estuary, Scotland, UK	11.50	12	[172]
Ythan Estuary, Scotland, UK	25.11	12	[172]
River Lynther, England, UK	23.00	12	[173]
Block Island Sound, Rhodes Island, USA	164.00	12	[175]
Bolsa Bay, California, USA	8.33	12	[176]
Duplin River Marsh, Georgia	578.00	12	[180]
Tijuana Estuary, California, USA	51.57	13	[179]
Mugu Lagoon, California, USA	4.50	14	[144]
Dutch Wadden Sea, The Netherlands	18.40	14	[166]
Ria de Arosa, Spain	14.67	14	[157]
Chesapeake Bay, Virginia, USA	34.00	15	[162]
Long Island Sound, Connecticut, USA	8.25	18	[100]
Bay of Piran, Slovenia	23.00	19	[164]
North Inlet Estuary, South Carolina, USA	9.47	19	[149]
La Jolla, California, USA	365.00	23	[167]
Sippewissett Marsh, Massachussets, USA	17.00	26	[174]
Ems Estuary, The Netherlands	11.50	26	[147]
Ems Estuary, The Netherlands	2.28	26	[147]
Golfe de Fos, France	21.00	28	[156]
Laholm Bay, Sweden	57.80	31	[145]
Lake Gremvelingen, The Netherlands	58.00	47	[154]
Dutch Wadden Sea, The Netherlands	74.67	57	[99]

microscale vertical distribution of microphytobenthos biomass [133,134], the effect of sediment properties on light penetration (and then availability to primary producers) in the sediment [130,135,136] and the physiological properties of microphytobenthos cells [130] that can be species specific [137]. This question will be studied more thoroughly elsewhere, but already represents a promising area of future research in marine sciences.

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