

Microscale patchiness in microphytobenthos distributions: evidence for a critical state

Abstract

The two-dimensional microscale (for scales ranging from 5 cm to 1 m) distribution of microphytobenthic biomass is investigated from superficial sediment samples taken on two intertidal flats characterized by sharp differences in terms of hydrodynamic exposure, sediment nature and biotic properties. Microphytobenthos biomass exhibited a very intermittent behaviour at both study sites, with the occurrence of sharp local fluctuations. The exposed sandy and the muddy flats are nevertheless respectively dominated by high-density and low-density patches, leading to significantly positively and negatively skewed distributions. It is also shown that the patch patterns exhibit specific power-law behaviours, involving the appearance of a self-organized critical state. The implications of critical versus subcritical states in microphytobenthos distributions are theoretically investigated on the basis of very simple numerical models, and a mechanistic explanation for the emergence of criticality in microphytobenthic populations is introduced.

Introduction

A central issue in ecology is the spatio-temporal organization of community structure and dynamics (Wiens 1989; Levin *et al.* 1997). In particular, the goal of spatial ecology is to determine how space and spatial scales influence population and community dynamics (Tilman and Kareiva 1997). Theoretical studies have suggested that biotic properties of individuals and populations interact to produce spatio-temporal complexity in homogeneous environments (e.g. Deutschman *et al.* 1993; Bascompte and Solé 1995). Potentially, environmental complexity interacts with biotic processes and influences spatial patterns (Roughgarden 1974; Pascual and Caswell 1997). In addition, theoretical and empirical studies show that the analysis of large (i.e. regional) scale patterns must integrate processes occurring at the small (local) scales (Levin 1992). Biomass and species are thus rarely dispersed uniformly (e.g. Kolasa and Pickett 1991). Instead patchiness (also referred to as ‘spatial heterogeneity’; Seuront & Lagadeuc 2001) is the norm, and ecological field studies and environmental monitoring programs must be designed accordingly (Green 1979; Hurlbert 1984; Andrew and Mapstone 1987; Eberhardt and Thomas 1991).

In intertidal ecology, many studies focused on the interplay between abiotic processes and biotic community structure at different spatial scales (Archambault and Bourget 1996; Cusson and Bourget 1997; Guichard and Bourget 1998, 2001; Blanchard and Bourget 1999). More specifically, microphytobenthic communities are at the core of benthic primary production and the matter fluxes between benthic and pelagic domains. However, to our knowledge, only a few studies (e.g. Blanchard 1990; Pinckney and Sanduli 1990) have been devoted to investigate the distribution of microphytobenthos biomass on scales smaller than 1 m², i.e. usually the finest grain considered in landscape ecology (He *et al.* 1994) and intertidal ecology (MacIntyre *et al.* 1996; Blanchard and Bourget 1999). Alternatively, none have been confronted with the crucial question related to the phenomenology of the organization of microphytobenthic biomass at these scales where the most ecologically relevant processes of infection, nutrient uptake, cell division and behavior occur.

In this framework, the objective of the present work is (i) to demonstrate the heterogeneous nature of microphytobenthos biomass for scales smaller than 1 m², (ii) to quantify this heterogeneity in terms of critical behavior, (iii) to infer the nature of the observed behavior on the basis of a simple modeling approach, and (iv) to introduce a general phenomenological background likely to lead to critical dynamics in microphytobenthos communities.

Materials and methods

Sampling sites

The two study sites, located on the French coast of the Eastern English Channel, were chosen because of their intrinsic sharp differences in terms of hydrodynamic exposure, sediment nature and biotic properties. (Figure 1)

The first study site, an intertidal flat of sand in Wimereux (50°45'896 N, 1°36'364 E) is typical of the hydrodynamically sandy beach habitats that dominate the littoral zone along the French coast of the Eastern English Channel. Measurements were performed on a flat area located in the upper intertidal zone, without sharp topographical features such as ripple marks, high pinnacles or deep surge channels. The substrate was homogeneous medium size sand (200-250 μm, modal size), typical of the surrounding sandy habitat. Because of the substrate homogeneity and the weak biomass, productivity and production of both phyto- and zoobenthic organisms, the microphytobenthos biomass distribution is *a priori* expected to be rather homogeneous (Seuront and Spilmont 2002). In addition, due to the highly dynamic environment, microphytobenthos is expected to be resuspended and surface concentrations at low tide are low.

The second study site is located in the Bay of Somme, at Le Crotoy (50°13'524 N, 1°36'506 E) which is the second largest estuarine system, after the Seine estuary, and the largest sandy-muddy (72 km²) intertidal area on the French coasts of the Eastern English Channel. The sampling site was chosen in a topographically homogeneous

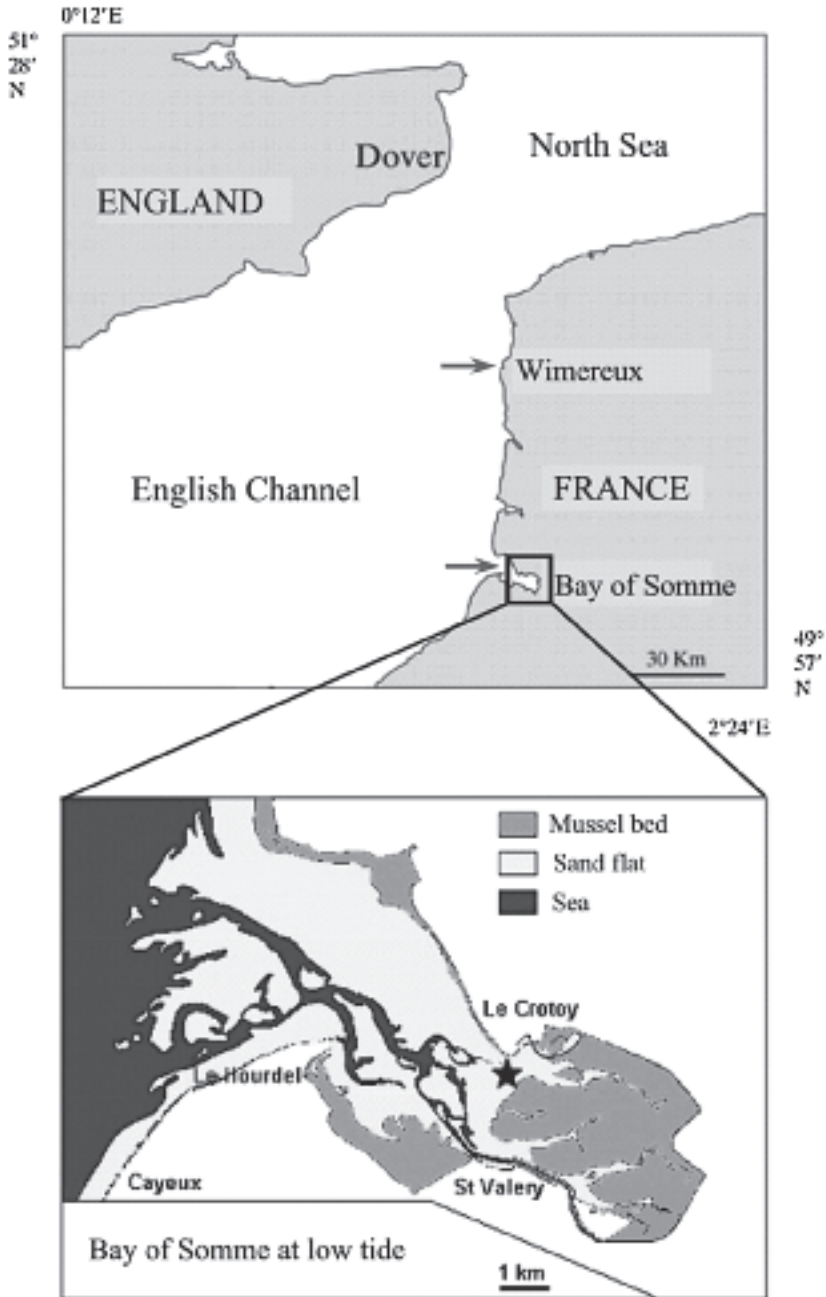


Figure 1. Location of the sampling stations in Wimereux and Le Crotoy on the east coast of the Eastern English Channel.

area, where the substrate grain size typically varied between 125 and 250 μm (modal size), and is characterized by higher phyto- and zoobenthos biomass and activity compared to the Wimereux site. Because of the weak hydrodynamic conditions, the microphytobenthos biomass is only weakly influenced by resuspension processes and surface concentrations at low tide are high.

Micro-scale sampling

All measurements were performed at low tide, at the middle of the emersion period, on October 9 and 10, 2003 at Wimereux and Bay of Somme study sites, respectively. Samples were collected with a rigid 1m² aluminium quadrat constructed from 225, 1.9 cm² plastic cores resulting in an intersample distance of 6.67 cm. The cores were pushed into the sediment down to a depth of 1 cm, where the majority of the active cells are concentrated (Cadée and Hegeman 1974; Baillie 1987; Admiraal *et al.* 1988; Delgado 1989; de Jonge and Colijn 1994). This ensures that the observed spatial structure is not biased by any change in the spatial organisation of the microphytobenthos during the sampling process. Samples were then carefully removed, mixed to 5 ml of methanol and stored in a cool box, returned to the laboratory and stored in the dark at -20°C.

Chlorophyll content analysis

Standard lab techniques for chlorophyll *a* extraction from samples is time consuming and not easily compatible with large numbers of samples. A standard procedure (e.g. Brunet 1994; Seuront and Spilmont 2002) is to place a sediment section in 8 ml acetone and to extract pigments for 4 hours in the dark at 4°. After extraction, samples are centrifuged at 4000 rpm for 15 min. Chlorophyll *a* concentrations (, mg) in the supernatant are determined by spectrophotometry following the equation given by Lorenzen (1967). However, processing 225 sediment samples using this procedure would require more than 14 hours for two operators, we proposed hereafter an improved, faster method for extracting and measuring microphytobenthos biomass from sediment samples.

The proposed procedure consists of the addition 5 ml of methanol directly to the sampled sediment sections, and then assaying the extractant in a Turner 450 fluorometer previously calibrated with a pure Chlorophyll *a* solution (*Anacystis nidulans* extract, Sigma Chemicals) after an extraction time as short as 1 hour. Chlorophyll *a* concentrations in the sediment sections were then converted into Chl.*a* per surface unit (Chl.*a*, mg.m⁻²) taking into account the surface (1.9 cm²) of the sampling units. Using a set of homogeneous sediment sections we thus showed (i) that the chlorophyll extraction was complete after 1 hour, and remains stable in time (up to 10 days) when stored in the dark for temperature below 0°C, and (ii) that the chlorophyll concentrations were not significantly different from those estimated from the above standard procedure ($p > 0.01$). In addition, processing 225 samples now takes no more than 5 hours to a single operator.

Self-organized criticality

Defining criticality. The most widespread example of self-organized criticality (SOC) is a pile of sand to which grains are continually added (Figure 2; Bak *et al.* 1987, 1988). 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 (Figure 2). 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 (Figure 2). 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 (Figure 2). Thus, one can think of the critical state as an attractor for the dynamics of the pile.

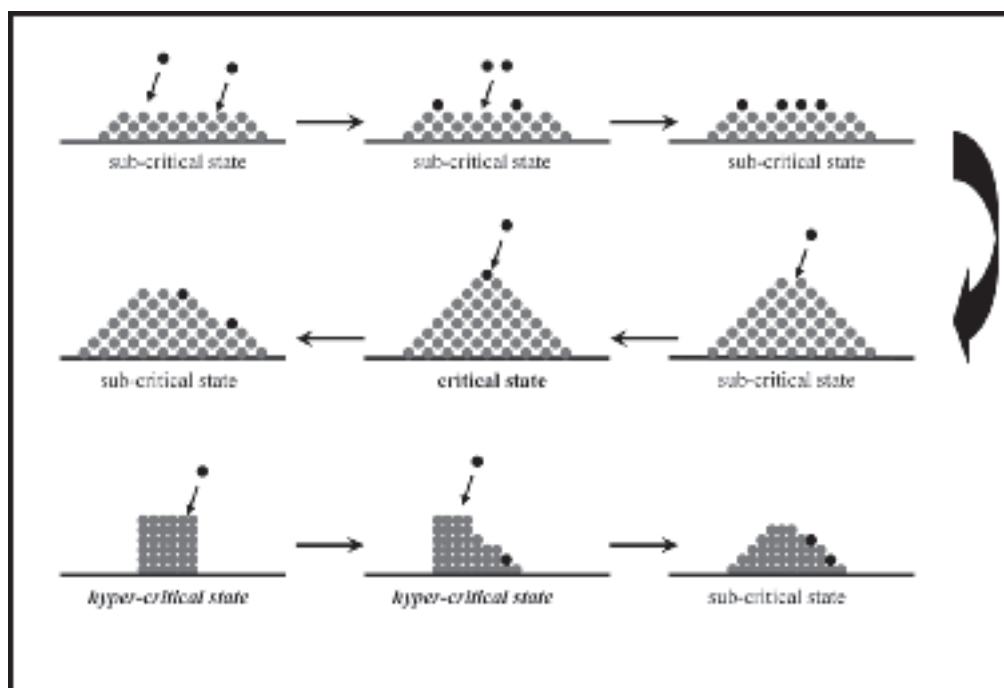


Figure 2. Schematic illustration of the dynamics of the sandpile as the most widespread example of self-organized criticality (SOC); see text for explanations.

Self-organized criticality signature. Because of the dynamical and structural properties of self-organized criticality it can be characterized through several scaling laws. In the case of the sand pile, the number of grains $n(l)$ falling a distance l at the same time step follows the power law form $n(l) \propto l^{-D}$, where D is the fractal dimension of the avalanches. More generally, for a critical system, the distribution of fluctuation sizes is describes as:

$$N(s) \propto s^{-D} \quad (1)$$

where s is the intensity of a given event (e.g. the size of an ‘avalanche’ in the sand pile example) and $N(s)$ the frequency of its occurrence. In practice, to estimate the fractal dimension D , the system under interest 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. A signature of self-organized criticality will be a straight line in a log-log plot of $N(s)$ vs. s . The slope of the straight line provides an estimate of the fractal dimension, D .

Self-organized criticality occurs in systems that build up stress and then release the stress in intermittent pulses. Indeed, the negative exponent in Eq. (1) leads to many small events (or fluctuations) punctuated by progressively rarer larger events. This intermittent behavior can thus be described by a power law stating that the probability of events with intensity X greater than a given threshold x as:

$$\Pr(X > x) \propto X^{-\phi} \quad (2)$$

where ϕ is the scaling exponent describing the distribution. As above, evidence for self-organized criticality will be given by the linear behavior of $\Pr(X > x)$ vs. X in a log-log plot, when X is a continuous or a discrete function (e.g. biomass and abundance measurements, respectively). However, because the computations of Eqs. (1) and (2) might not be as straightforward as it appears at first glance, we introduce in the next section a method that is strictly equivalent to Eq. (2) to identify self-organized criticality, but also and most importantly to differentiate random and non-random structures readily in any data sets.

Identifying self-organized criticality vs. randomness in ecological data. First, one must note that Eq. (2), also known as the Pareto’s law (Pareto 1896), can be equivalently rewritten in terms of the probability density function (PDF) as:

$$P[X = x] \propto x^{-\gamma} \quad (3)$$

where γ ($\gamma = \phi + 1$) is the slope of a log-log plot of $P[X > x]$ vs. x . Now following the Harvard linguistic professor G.K. Zipf (1902-1950), consider the Zipf’s law that states that the frequency f_r of the r^{th} largest occurrence of an event is inversely proportional to its rank r as (Zipf 1949):

$$f_r \propto r^{-\alpha} \quad (4)$$

where α is the slope of the log-log plot of f_r vs. r . Eq. (4) can be generally written as:

$$X_r \propto r^{-\alpha} \quad (5)$$

where X_r is the ‘weight’ of an occurrence of an event relative to its rank r . The concept of ‘weight’ is very general and refers without distinction to frequency, length, surface, volume, mass or concentration. Discrete processes such as linguistic or genetic structures would nevertheless still require frequency computations, and thus refer to Eq. (4). Alternatively, Eq. (5) can be thought of as a more practical alternative that can be directly applied to continuous processes such as microphytobenthos distributions. From Eq. (5), it can be directly seen that there are kr variables X_r (where k is a constant) greater than or equal to $r^{-\alpha}$. This leads to rewrite Eq. (2) as:

$$P[X > kr^{-\alpha}] \propto r \quad (6)$$

and

$$P[X > X_r] \propto X_r^{1/\alpha} \quad (7)$$

From Eqs. (3), (5) & (7), the relationship between the exponents α , ϕ and γ is expressed as:

$$\begin{cases} \alpha = \frac{1}{\phi} \\ \gamma = 1 + \frac{1}{\alpha} \end{cases} \quad (8)$$

As a consequence, the Zipf and Pareto distributions can be regarded as being strictly equivalent. More specifically, the x -axis of the Zipf distribution is conceptually identical to the y -axis of the Pareto distribution (Eqs. 6 & 7). As a consequence, the use of one or the other distribution is simply a matter of convenience, although we stress that Zipf’s law can be more easily and directly estimated than the Pareto’s one.

Because of the one-to-one correspondance between Zipf and Pareto distributions, for the sake of simplicity, in the next section we will only use the Zipf’s law, i.e. Eq. (5), to infer the presence of a self-organized critical state in microphytobenthos distributions. From the above statement, self-organized criticality will be identified by a linear behavior of X_r vs. r in a log-log plot. Alternatively, a random behavior stemming e.g. from a white noise or a Normal distributions will manifest itself as a continuous roll-off from a horizontal line (i.e. $\alpha \rightarrow 0$) to a vertical line (i.e. $\alpha \rightarrow \infty$). This is representative of the fact that no value is more likely to be more common than any other value.

To estimate the scaling exponents α , linear regression on the log-transformed data is preferred to nonlinear regression on the raw data because in the analysis of the log-transformed data the residual error will be distributed as a quadratic and thus

minimum error is guaranteed. This is not the case with nonlinear regression (Seuront and Spilmont 2002). Finally, because an objective criterion is needed for deciding upon the appropriate range of ranks to include in the regression, we used the ranks which maximized the coefficient of determination and minimized the total sum of the residuals in the regression (Seuront and Spilmont 2002).

Results

Descriptive statistics of microphytobenthos distributions

Microphytobenthos chlorophyll *a* biomass ranged from 10.1 and 29.0 mg m⁻², i.e. 21.78 ± 4.04 mg m⁻² (\bar{x} ±SD) in Wimereux and between 42.54 and 113.98 in Le Crotoy, 77.83 ± 10.17 mg m⁻² (\bar{x} ±SD). The biomass estimates in Le Crotoy were in the range of microphytobenthos biomass taken from biologically rich and active muddy flats, i.e. bounded between 50 and 200 mg m⁻² (Seuront and Spilmont 2002; Carrère *et al.* 2004). In contrast, the values observed on the sandy flat in Wimereux are (i) rather high for a hydrodynamically exposed sandy flat and (ii) significantly higher than microphytobenthos biomass estimated at the same location, one and two years earlier, i.e. 10.79 ± 4.15 mg m⁻² (25 September 2001, $p < 0.05$; Seuront and Spilmont 2002) and 2.75 ± 0.88 mg m⁻² (25 September 2000, $p < 0.01$; Seuront and Spilmont 2002). This may be a consequence of the relative intensity of the autumn phytoplankton blooms that occur in the coastal waters of the Eastern English Channel as well as the dominance of diatom species at that period of the year. Indeed, over the same period, phytoplankton chlorophyll *a* concentrations were estimated as 13.94 ± 2.52 µg l⁻¹ in 2003 (Seuront, unpubl. data), 10.72 ± 3.29 µg l⁻¹ in 2002 (Leterme and Seuront, unpubl. data) and 4.22 ± 1.12 µg l⁻¹ in 2001 (Seuront, unpubl. data) in the shallow water moving onto or off the investigated sandy flat. In addition, considering that diatoms dominate the autumn phytoplankton assemblages, it is reasonable to think that most of the chlorophyll *a* measured in the sediment comes from phytoplankton deposition on the sediment at low tide.

More specifically, microphytobenthos biomass exhibited a very intermittent behavior, with the occurrence of sharp local fluctuations clearly visible at both study sites (Figure 3). The nature of the distributions differed however, with dominance of ‘hotspots’ in Wimereux (Figure 3a) samples and ‘coldspots’ in the Le Crotoy samples (Figure 3b). Results of descriptive analysis, including skewness and kurtosis estimates, specify the previous observations by showing that the 225 microphytobenthos biomass estimated from Wimereux and Le Crotoy sampling are not normally distributed (Kolmogorov-Smirnov test, $p < 0.01$). Their frequency distribution rather exhibits positively and negatively skewed behaviors, reflecting a distribution characterized by a few low density patches over a wide range of high density patches in Wimereux ($g_1 = -0.73$) and a few dense patches and a wide range of low density patches in Le Crotoy ($g_1 = 0.48$). Finally, the positive kurtosis (i.e. $g_2 = 0.14$ in Wimereux and $g_2 = 1.39$ Le Crotoy) show a distribution that is peakier than expected in the case of normality, especially in the Bay of Somme. The comparisons of the

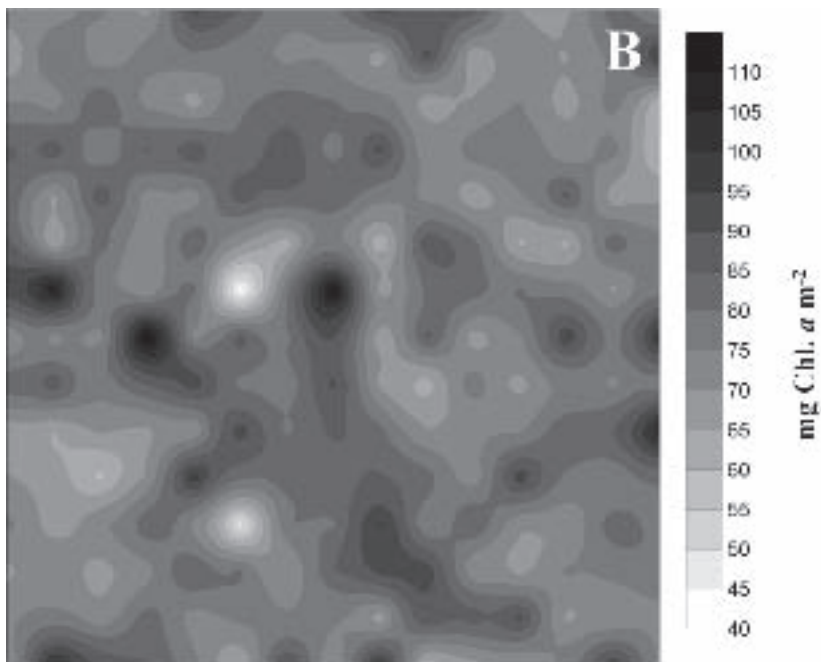
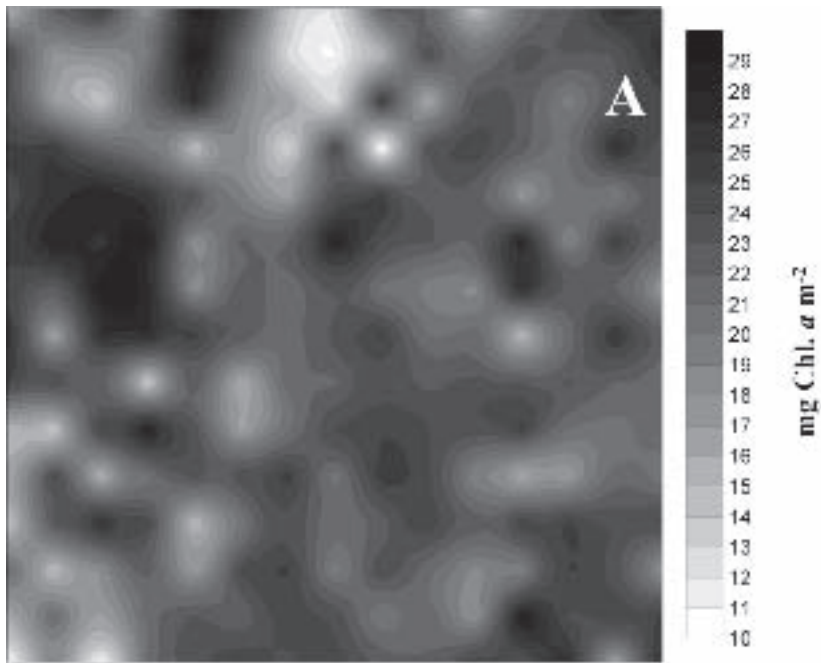


Figure 3. Two dimensional distributions of the microphytobenthos biomass (mg Chl. $a\ m^{-2}$) in Wimereux (A) and Le Crotoy (B).

observed distributions and simulated uniform distribution characterized by the same minimum and maximum values than the empirical data qualitatively confirms the non-random character of the microphytobenthos distribution in Wimereux (Figure 4) and Le Crotoy (Figure 5). In both cases, the differences between the field distributions (Figs. 4a & 5a) and uniform, homogeneous distributions, characterized by a regular alternance between high and low density areas (Figs. 4b & 5b) are clear.

Evidence for a self-organized critical state

The Zipf analysis of two-dimensional microphytobenthos patterns shows that microphytobenthos biomass was not randomly distributed (Figure 6). The Zipf plots show instead a very clear linear behavior with $\alpha = 0.071$ ($r^2 = 0.98$) for concentrations ranging from 24.15 to 28.18 mg m⁻² in Wimereux (Figure 6a) and with $\alpha = 0.079$ ($r^2 = 0.98$) for concentrations ranging from 82.60 to 113.98 mg m⁻² in Le Crotoy (Figure 6b). While the power law behavior expands to the maximum microphytobenthos concentration in Le Crotoy (Figure 6b), in Wimereux, the Zipf plot clearly diverges from a power law for concentrations higher than 28.18 mg m⁻² (Figure 6a). This indicates that the probability of the occurrence of high density patches is lower than expected in the case of a power law. On the other hand, for concentrations lower than 24.15 mg m⁻² in Wimereux and 82.60 mg m⁻² in Le Crotoy, the Zipf plots progressively roll-off towards the behavior expected in the case of randomness (Figure 6). Now, this indicates that the probability of the occurrence of low density patches that is lower than expected in the case of a power law. However, the continuous roll-off towards the lowest concentrations is clearly different in Wimereux (Figure 6a) and Le Crotoy (Figure 6b). This could be indicative of differential driving processes competing with the pure power law behavior observed for higher concentrations. In the next section, we present several potential functional hypotheses likely to reproduce the shapes of the Zipf plot observed in Wimereux and Le Crotoy that may help to corroborate the conjecture that the micro-scale microphytobenthos distribution is a living system with critical dynamics.

Discussion

Critical versus subcritical states in microphytobenthos distribution

The fact that microphytobenthos concentrations greater (or smaller) than a given threshold do not follow the same law as other events indicates that there is something unique about these events. In particular, the differences observed between microphytobenthos distributions in Wimereux (Figure 6a) and Le Crotoy (Figure 6b) could be related to differences in grazing pressure likely to occur in these two study sites.

Consider a pure power law relationship of the form:

$$C_r \propto r^{-\alpha} \tag{9}$$

where C_r is the microphytobenthos biomass and r its rank; see Eq. (5). Now consider a situation where the grazing pressure is assumed to be a random function of food

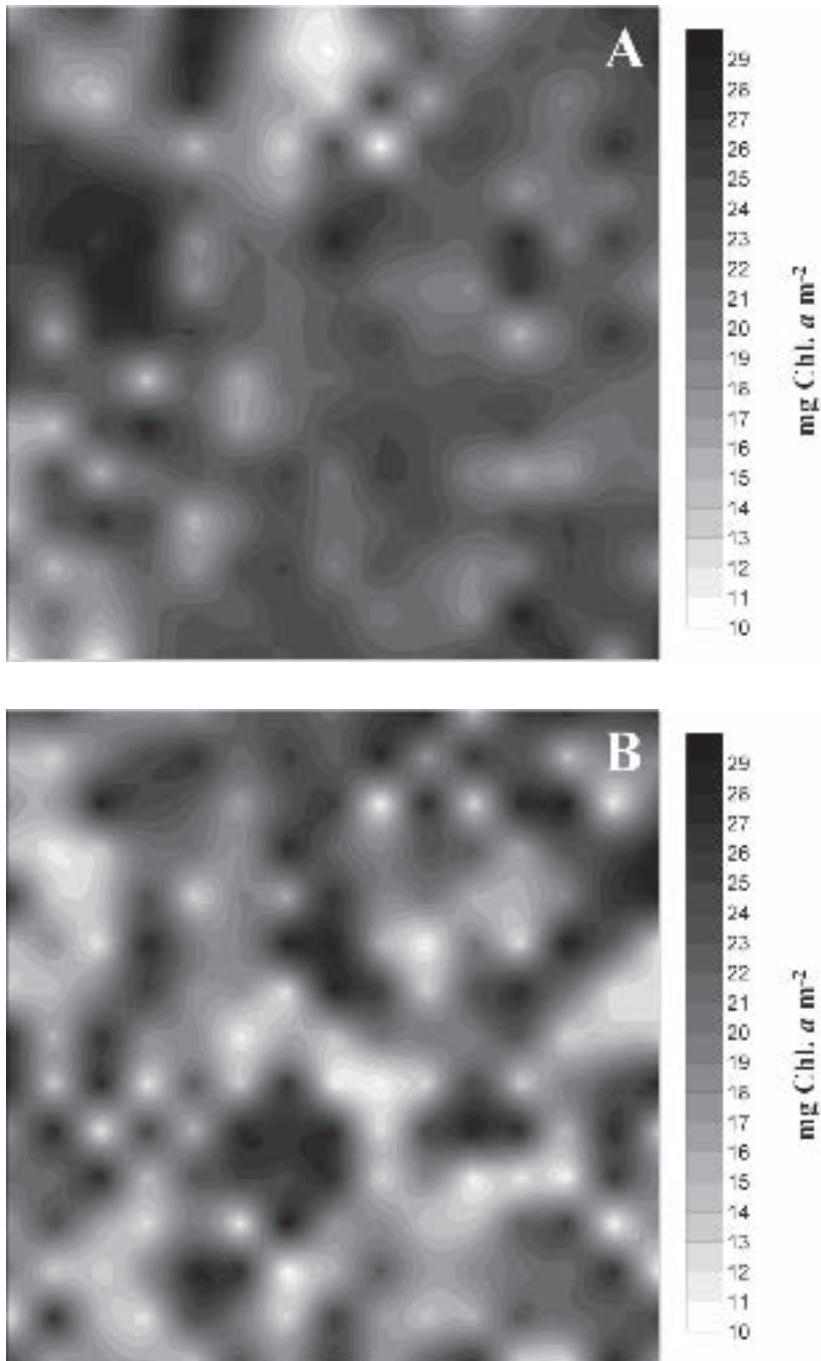


Figure 4. Comparison between the two-dimensional distribution of microphytobenthos biomass observed in Wimereux (A) and a simulated uniform distribution with the same minimum and maximum values (B).

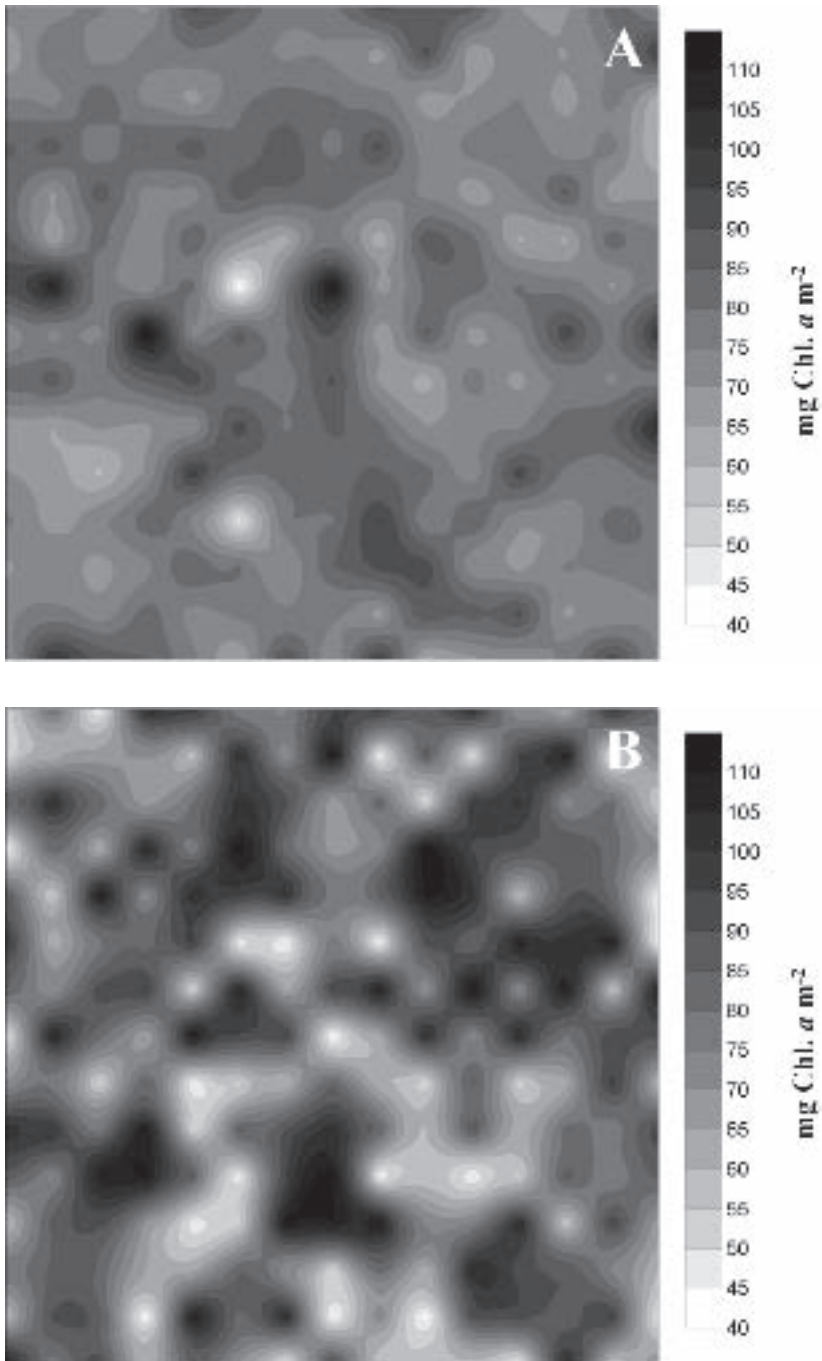


Figure 5. Comparison between the two-dimensional distribution of microphytobenthos biomass observed in Le Crotoy (A) and a simulated uniform distribution with the same minimum and maximum values (B).

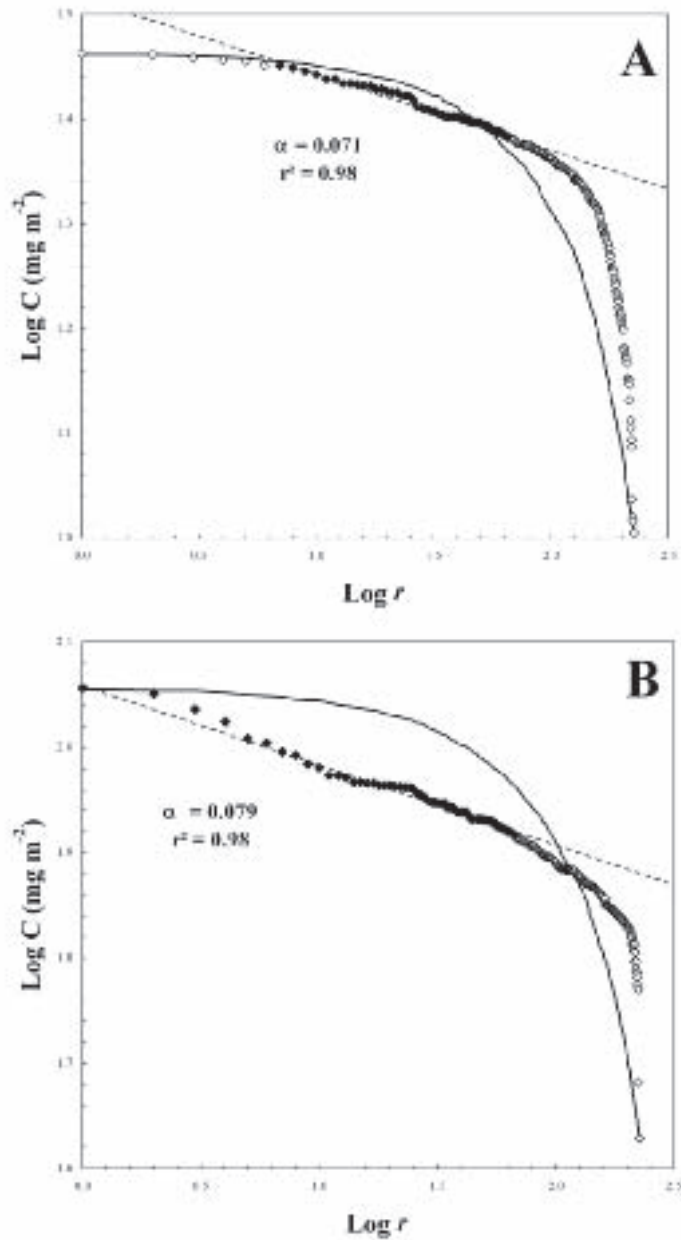


Figure 6. Zipf plots of the microphytobenthos biomass in Wimereux (A) and Le Crotoy (B). In both cases, the black diamonds correspond to the range of microphytobenthos concentrations exhibiting a power law behavior, i.e. a critical state, and used to estimate the exponent α as the slope of the linear fit maximizing the coefficient of determination and minimizing the total sum of the residuals in the regression (discontinuous lines). The continuous lines correspond to the Zipf plot obtained from 100 simulated uniform distributions with the same minimum and maximum values than the empirical ones.

availability. Considering the diversity of microphytobenthos grazers observed in Le Crotoy (McLusky *et al.* 1996), their differential grazing rates and abilities, as well as their differential spatial distribution, the grazing pressure on microphytobenthos biomass is likely to be of a purely stochastic nature. Eq. (9) can then be rewritten as:

$$C_{1r} = C_r - \varepsilon C_r \quad (10)$$

where ε is a random noise process, i.e. $\varepsilon \in [0,1]$. For increasing amount of noise, the characteristic ‘noise roll-off’ occurring for low rank values is more violent and mimics the behavior observed in Wimereux and Le Crotoy (Figure 7). In addition, one must note here that the fluctuations generated by the noise contamination around a power law behavior are fully compatible with the irregularities observed over the scaling ranges identified in Wimereux and Le Crotoy Zipf plots (See Figure 6). The smoother roll-off observed in Wimereux (Figure 6a) when compared to Le Crotoy (Figure 6b) thus suggests a lower grazing impact in Wimereux where the meiobenthic biomass is negligible (Seuront and Spilmont 2002).

The previous approach, however, did not take into account the potential behavioral adaptation of grazers to varying food concentrations (Johnson *et al.* 1997). If one considers that remote sensing abilities can lead to aggregation of grazers and/or preferential grazing in areas of high microphytobenthos concentrations as investigated both empirically and numerically (e.g. Decho and Fleeger 1988; Montagna *et al.* 1995; Johnson *et al.* 1998), Eq. (9) can be modified as:

$$C_{2r} = C_r - 10^{(C_r/k)} \quad (11)$$

where k is a constant and the ingestion function $I(C_r) = 10^{(C_r/k)}$ represents an increased predation impact on higher phytoplankton concentrations. The advantage of the function $I(C_r)$ is that it can be regarded as a representation of the aggregation of grazers with constant ingestion rates and/or evenly distributed grazers with increasing ingestion rates in high density microphytobenthos patches. Decreasing values of the constant k increases the grazing impact on high density patches. The grazed microphytobenthos population then diverges from a power law form for high values of C_{2r} , but asymptotically converges to the original power law for the smallest values of C_{2r} , i.e. $C_{2r} \propto r^\alpha$ for $r \rightarrow r_{\min}$ (Figure 8). The divergence from a power law observed in Wimereux (Figure 6b) could thus be explained by the low microphytobenthos biomass. Indeed, according to the optimal foraging theory (Pyke 1984) grazers living in food depleted and/or heterogeneous environments develop strategies to exploit high density patches and then to optimize the energy required to capture a given amount of food. Grazers living in a low microphytobenthos concentration environment (i.e. Wimereux) are thus more likely to graze preferentially on high density patches than grazers living in a high microphytobenthos concentration environment (i.e. Le Crotoy). As a consequence, the microphytobenthos communities investigated here can be regarded as being in a critical state when they follow a power law relationship (Figure 6). Alternatively, below and above a critical biomass in Wimereux and below a critical biomass Le Crotoy they are in a subcritical state.

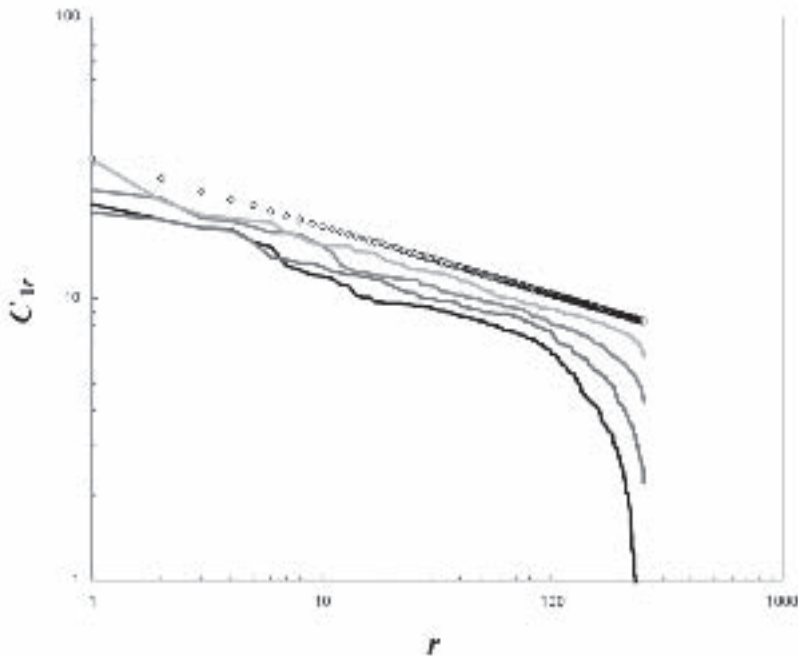


Figure 7. Log-log plot signature of the Zipf behavior expected in case of a power law C_r (open diamonds) competing with a random mortality component ($C_{1r} = C_r - \epsilon C_r$), where $\epsilon = 0.05, 0.25, 0.50$ and 0.75 (from top to bottom).

Toward a mechanistic explanation of SOC in microphytobenthos communities

The decrease in the number of patches above a critical biomass observed in Figure 6 suggests that the development of patches is 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 the addition of sand grains which raises the height of the pile. The structure of the pile thus emerges from the interaction of these forces. While we previously mainly addressed the constraints likely to lead to a divergence from self-organized criticality in microphytobenthos distribution, it is crucial to understand that it is actually the constraints, and their potential effects, acting on the structure and dynamics of a microphytobenthos assemblage that are responsible for the emergence of a critical behavior. The microscale distribution of microphytobenthos biomass is thus a function of exogenous (e.g. tides, hydrodynamism, sediment microtopography, porosity and cohesivity, competition for nutrient and light, predation) and endogenous processes (e.g. nutrient uptake, growth, migration, death) that can act to increase and/or decrease microphytobenthos biomass. A crucial issue is that most of these constraints do not act uniformly over the whole spatial domain. For instance, biomass gains related to cell division necessarily occur in the vicinity of a microphytobenthos individual. Alternatively, biomass losses related to cell death and grazing can occur anywhere and are

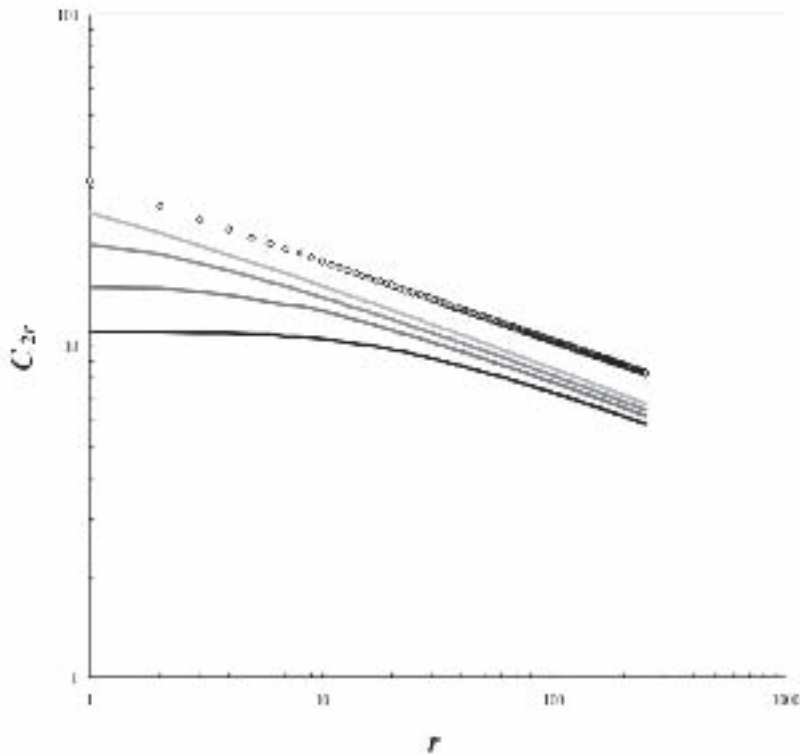


Figure 8. Log-log plot signature of the Zipf behavior expected in case of a power law C_r (open diamonds) competing with a preferential grazing component for high phytoplankton concentrations ($C_{2r} = C_r - 10^{(C_r/k)}$). The grazed microphytobenthos population diverges from a power law form for high concentrations, but asymptotically converges to the original power law for the smallest values. The extent of the observed divergence is controlled by increasing grazing pressure k (from top to bottom).

dependent on both the spatial distribution and foraging abilities of predators, respectively. Growth and death are dependent on nutrient and light availability that, in turn, is a function of the burying depth of microphytobenthos cells, the density, cohesivity and the spatial distribution of the sediment and the duration of the emersion. The microphytobenthos population may also be disturbed by turbulence and shear stress generated by tidal currents or wind-waves leading to the resuspension of microphytobenthos in the water column. One must also note that some constraints do not act uniformly in time. For instance, resuspension processes occur during the whole immersion period and lead to microphytobenthos biomass losses. Conversely, the resettling of cells occurs at the beginning of the emersion and can be regarded as a crucial event in the observed patch pattern. These constraints, acting to increase and/or decrease microphytobenthos biomass differentially in time and/or in space, result in a dynamic balance, or critical state, as in the sand pile model. Although we have shown on the basis

of simple hypotheses related to predator-prey relationships how a disturbance can create a divergence from criticality it still remains unclear how a critical behavior can emerge. A simple mechanism is nevertheless suggested in the next section.

Interspecific competition is likely to be a driving force in structuring microphytobenthos community (e.g. Egge and Aksnes 1992; Sommer 1996; Stal 2001). The most relevant dynamics would then be observed in the niche space occupied by different species (MacArthur 1960; Hutchinson 1961; Odum 1971). Competitive pressure should be high in regions of niche space where species are densely packed, as would happen when a number of phytoplankton species share the same food source (Siegel 1998; Huisman and Weissing 2000). As in the steep region of the sandpile, avalanches are more probable, species occupying dense regions of niche space could be subject to higher extinction probabilities, thus reducing the 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. The system is in a critical state. In contrast, species occupying sparse regions of the niche space (i.e. areas depleted in microphytobenthos cells) are subject to weaker competition pressure and extinction probabilities. The system is in a more stable, or subcritical, state.

Conclusions

We have shown that microphytobenthos biomass sampled at scales ranging from 6.67 cm to 1 m in two structurally different intertidal ecosystems was far from homogeneous, but instead was strongly structured and exhibited some fingerprints for self-organized criticality. While the emergence of a self-organized critical state can be generally thought as being the result of conflicting constraints acting on microphytobenthos community, it is still difficult to identify precisely the processes responsible for the observed patterns. We have nevertheless proposed simple mechanisms likely (i) to generate a critical state and (ii) to induce a divergence from a critical state.

Finally, we stress that the above demonstrated structure in microphytobenthos distribution may have salient consequences on microphytobenthos biomass and production estimates. As illustrated from a recent literature survey (Seuront and Spilmont 2002) the variability observed from a localized high frequency microscale sampling strategy can be of the same order of magnitude as the seasonal and annual variability observed in the sediment in a wide variety of intertidal environments. This suggests that the sampling error might account for much of the variation in biomass at the seasonal and annual scales, especially when the microphytobenthos is sampled with relatively few cores as is usually the case, e.g. 6 in Sagan and Thouseau (1998), and 5 in Barranguet and Kromkamp (2000). In such a framework it is indeed doubtful that a small number of samples can be representative of a microphytobenthos population. While to our knowledge no alternative solution exists to unbiased regular biomass estimates, we believe that a proper parameterization of microphytobenthos microscale variability, as illustrated here in the framework of self-organized criticality, could form the basis of routine procedures devoted to infer variability from a limited number of samples.

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References

- ADMIRAAL W., M.A. ARKEL, J.W. VAN BARETTA, F. COLIJN, W. EBENHÖH, V.N. DE JONGE, A. DE KOP, P. RUARDIJ, and H.G.J. SCHRÖDER. 1988. The construction of benthic submodel. In: Baretta J., and P. Ruardij (eds.), Tidal flat estuaries. Simulation and analysis of the Ems estuary. Ecological Studies 71. Springer-Verlag, Heidelberg, 105-152.
- ANDREW, N.L., and B.D. MAPSTONE. 1987. Sampling and the description of spatial pattern in marine ecology. *Oceanogr. Mar. Biol. Ann. Rev.* **25**: 39-90.
- ARCHAMBAULT, P., and E. BOURGET. 1996. Scales of coastal heterogeneity and benthic intertidal species richness, diversity and abundance. *Mar. Ecol. Prog. Ser.* **136**: 111-121.
- BAILLIE, P.W. 1987. Diatom size distribution and community stratification in estuarine intertidal sediments. *Estuar. Coast. Shelf Sci.* **25**: 193-209.
- BAK, P., C. TANG, and K. WIESENFIELD. 1987. Self-organized criticality: an explanation of $1/f$ noise. *Phys. Rev. Lett.* **59**: 381-384.
- BAK, P., C. TANG, and K. WIESENFIELD. 1988. Selforganized criticality. *Phys. Rev. A* **38**: 364-374.
- BARRANGUET, C., and J. KROMKAMP. 2000. Estimating primary production rates from photosynthetic electron transport in estuarine microphytobenthos. *Mar. Ecol. Prog. Ser.* **204**: 39-54.
- BASCOMPTE, J., and R.V. SOLÉ. 1995. Rethinking complexity: modelling spatiotemporal dynamics in ecology. *Trends Ecol. Evol.* **10**: 361-366.
- BLANCHARD, D., and E. BOURGET. 1999. Scales of coastal heterogeneity: influence on intertidal community structure. *Mar. Ecol. Prog. Ser.* **179**: 163-173.
- BLANCHARD, G.F. 1990. Overlapping microscale dispersion patterns of meiofauna and microphytobenthos. *Mar. Ecol. Prog. Ser.* **68**: 101-111.
- BRUNET, C. 1994. Analyse des pigments photosynthétiques par HPLC: communautés phytoplanctoniques et productivité primaire en Manche orientale. Ph.D. Thesis. Université Pierre & Marie Curie, Paris.
- CADÉE, G.C., and J. HEGEMAN. 1974. Primary production of the benthic microflora living on tidal flats in the Dutch Wadden Sea. *Neth. J. Sea Res.* **8**: 260-291.
- CARRÈRE, V., N. SPILMONT, and D. DAVOULT. 2004. Comparison of simple techniques for estimating Chlorophyll a concentration in the intertidal zone using high spectral resolution field spectrometer data, in press.
- CUSSON, M., and E. BOURGET. 1997. Influence of topographic heterogeneity and spatial scales on the structure of the neighbouring intertidal endobenthic macrofaunal community. *Mar. Ecol. Prog. Ser.* **150**: 181-193.
- DECHO, A.W., and J.W. FLEEGER. 1988. Microscale dispersion of meiobenthic copepods in response to food-resource patchiness. *J. Exp. Mar. Biol. Ecol.* **118**: 229-244.
- DE JONGE, V.N., and F. COLIJN. 1994. Dynamics of microphytobenthos biomass in the Ems estuary. *Mar. Ecol. Prog. Ser.* **104**: 185-196.
- DELGADO, M. 1989. Abundance and distribution of microphytobenthos in the bays of Ebro Delta (Spain). *Estuar. Coast. Shelf Sci.* **29**: 183-194.
- DEUTSCHMANN, D.H., G.A. BRADSHAW, W.M. CHILDRESS, K. DALY, D. GRUNBAUM, M. PASCUAL, N.H. SCHUMAKER, and J. WU. 1993. Mechanisms of patch formation. In: Levin, S., T. Powell, and J. Steele (eds.), Patch Dynamics, Springer, Berlin, 184-209.
- EBERHARDT, L.L., and J.M. THOMAS. 1991. Designing environmental field studies. *Ecol. Monogr.* **61**: 53-73.
- EGGE, J.K., and D.L. AKSNES. 1992. Silicate as regulating nutrient in phytoplankton competition. *Mar. Ecol. Prog. Ser.* **83**: 281-289.

- GREEN, R.H. 1979. Design and statistical methods for environmental biologists. Wiley, New York.
- GUICHARD, F., and E. BOURGET. 1998. Topographic heterogeneity, hydrodynamics, and benthic community structure: a scale-dependent cascade. *Mar. Ecol. Prog. Ser.* **171**: 59-70.
- GUICHARD, F., and E. BOURGET. 2001. Scaling the influence of topographic heterogeneity on intertidal benthic communities: alternate trajectories mediated by hydrodynamics and shading. *Mar. Ecol. Prog. Ser.* **217**: 27-41.
- HE, F., P. LEGENDRE, and C. BELLEHUMEUR. 1994. Diversity pattern and spatial scale: a study of a tropical rain forest in Malaysia. *Environ. Ecol. Stat.* **1**: 265-286.
- HUISMAN, J., and F.J. WEISSING. 2000. Biodiversity of plankton by species oscillations and chaos. *Nature* **402**: 407-410.
- HURLBERT, S.T. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54**: 187-211.
- HUTCHINSON, G.E. 1961. The paradox of the plankton. *Am. Nat.* **95**: 137-145.
- JOHNSON, M.P., M.T. BURROWS, R.G. HARTNOLL, and S.J. HAWKINS. 1997. Spatial structure on moderately exposed rocky shores: patch scales, and the interactions between limpets and algae. *Mar. Ecol. Prog. Ser.* **160**: 209-215.
- JOHNSON, M.P., M.T. BURROWS, and S.J. HAWKINS. 1998. Individual based simulations of the direct and indirect effects of limpets on a rocky shore *Fucus* mosaic. *Mar. Ecol. Prog. Ser.* **169**: 179-188.
- KOLASA, J., and S.T.A. PICKETT. 1991. Ecological heterogeneity. Springer-Verlag, New-York.
- LEVIN, S.A. 1992. The problem of patterns and scale in ecology. *Ecology* **73**: 1943-1967.
- LEVIN, S.A., B. GRENFELL, A. HASTINGS, and A.S. PERELSON. 1997. Mathematical and computational challenges in population biology and ecosystems science. *Science* **275**: 334-343.
- LORENZEN, C.J. 1967. Determination of chlorophyll and phaeopigments: spectrometric equations. *Limnol. Oceanogr.* **12**: 343-346.
- MACARTHUR, R.H. 1960. On the relative abundance of species. *Am. Nat.* **94**: 25-36.
- MACINTYRE, H.L., R.J. GEIDER, and D.C. MILLER. 1996. Microphytobenthos: the important role of the 'secret garden' of unvegetated, shallow-water marine habitats. I. Distribution, abundance and primary production. *Estuaries* **19**: 186-201.
- McLUSKY, D.S., N. BRICHE, M. DESPREZ, S. DUHAMEL, H. RYBARCZYK, and B. ELKAÏM. 1996. The benthic production of the Baie of Somme, France. *Biol. Ecol. Shallow Coast. Wat.* **28**: 225-231.
- MONTAGNA, P.A., G.F. BLANCHARD, and A. DINET. 1995. Effect of production and biomass of intertidal microphytobenthos on meiofaunal grazing rates. *J. Exp. Mar. Biol. Ecol.* **185**: 149-165.
- ODUM, E.P. 1971. Fundamentals in ecology. Saunders, Philadelphia.
- PARETO, V. (1896) Oeuvres complètes. Droz, Geneva.
- PASCUAL, M., and H. CASWELL. 1997. Environmental heterogeneity and biological pattern in a chaotic predator-prey system. *J. Theor. Biol.* **185**: 1-13.
- PINCKNEY, J., and R. SANDULLI. 1990. Spatial autocorrelation analysis of meiofaunal and microalgal populations on an intertidal sandflat: scale linkage between consumers and resources. *Est. Coast. Shelf Sci.* **30**: 341-353.
- PYKE, J.H. 1984. Optimal foraging theory: a critical review. *Ann. Rev. Ecol. Syst.* **15**: 523-575.
- ROUGHGARDEN, J. 1974. Population dynamics in a spatially varying environment: how population size tracks spatial variation in carrying capacity. *Am. Nat.* **108**: 649-664.
- SAGAN, G., and G. THOUZEAU. 1998. Variabilité spatio-temporelle de la biomasse microphytobenthique en rade de Brest et en manche occidentale. *Oceanol. Acta* **21**: 677-693.
- SEURONT, L., and Y. LAGADEUC. 2001. Towards a terminological consensus in ecology: variability, inhomogeneity and heterogeneity. *J. Biol. Syst.* **9**: 81-87.
- SEURONT, L., and N. SPILMONT. 2002. Self-organized criticality in intertidal microphytobenthos patch patterns. *Physica A* **313**: 513-539.
- SIEGEL, D.A. 1998. Resource competition in a discrete environment: why are plankton distribution paradoxical? *Limnol. Oceanogr.* **43**: 1133-1146.
- SOMMER, U. 1996. Nutrient competition experiments with periphyton from the Baltic Sea. *Mar. Ecol. Prog. Ser.* **140**: 161-167.
- STAL, L.J. 1996. Coastal microbial mats: the physiology of a small-scale ecosystem. *South African J. Bot.* **67**: 399-410.
- TILMAN, D., and P. KAREIVA. 1997. Spatial ecology: the role of space in population dynamics and interspecific interactions. Monographs in Population Biology, Vol. 30, Princeton University Press, Princeton.
- WIENS, J. 1989. Spatial scaling in ecology. *Funct. Ecol.* **3**: 385-387.
- ZIPF, G.K. (1949) Human behavior and the principle of least effort. Hafner, New York.