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Analysis of the short-term dynamics of microphytobenthos biomass on intertidal mudflats

Abstract

The short-term dynamics of microphytobenthos on intertidal mudflats was studied over a 3-month period in late Winter-early Spring. Biomass changes during diurnal emersions and between diurnal emersions were assessed and statistically analysed. It turned out that most of the time there were an increase of biomass during diurnal emersions and a decrease of biomass during immersions and nocturnal emersions, but there was always a high variability in the magnitude of the biomass changes. As a whole, the increase of biomass during diurnal emersions and the decrease of biomass between diurnal emersions were significantly higher during Spring tides than during Neap tides, thus pointing out the importance of the coupling between biological and physical processes in the functioning of the primary production system. In addition, biomass-dependent processes were evidenced: there was an inverse relationship between the net biomass accumulation during diurnal emersion and the amount of biomass present at the beginning of the diurnal emersion. This relationship clearly shows that microphytobenthic biomass tends to converge towards an equilibrium point where production equals grazing. Therefore, both the characteristics of the semi-diurnal tidal cycle and the biomass-dependent processes explain a significant part of the observed variability of the short-term biomass changes. Based on these results, a conceptual model of the functioning of the primary poduction system is proposed which strongly indicates that the overall productivity of the system is related to the loss rates (grazing and resuspension).

Introduction

Intertidal mudflats are highly productive ecosystems associated to estuaries and semi-enclosed bays. In western Europe, these geomorphological structures are mostly devoid of macrophytes, but exhibit nevertheless a high primary productivity due to the presence of microphytobenthos. This benthic microalgal compartment is mainly composed of diatoms, closely attached to sand grains (epipsammon) or free and motile in fine muds (epipelon). When the mud is very fine, the dominance of these epipelic diatoms at the surface of mudflats gives rise to a particular and efficient system of primary production. Guarini *et al.* (2000a) have first provided a conceptual representation of this system and have derived from it a mathematical model of the short-term dynamics of the biomass (Guarini *et al.* 2000b; Guarini *et al.* this book).

Schematically, this conceptual model is shown in Figure 1; the production system can thus be described by three different states:

- The first state represents the diurnal emersion phase when the mudflat is exposed to the atmosphere and when sunlight reaches the sediment surface. This state can be characterized by a 2-compartment model: a bottom compartment which is the top 1 cm of the sediment, and a surface compartment which is the epipelic diatom biofilm occurring only during diurnal emersion after the upward migration of microalgae at the surface of the sediment. This biofilm structure has been fully described by Paterson (1989). Primary production only occurs during this phase and is entirely due to the biofilm; the effect of vertical migration on the constitution of the biofilm and on the dynamics of primary production has been clearly demonstrated by Pinckney and Zingmark (1991) and by Serôdio *et al.* (1997). Therefore, a significant increase of microalgal biomass can be expected over the course of emersion if the primary production rate overcomes the grazing rate by deposivores.
- The second state represents the nocturnal emersion phase when the mudflat is still exposed to the air, but there is no light. Microalgae are dispersed in the bottom compartment after downward migration and there is no biofilm at the surface of the sediment. There is no primary production but there might be grazing during this phase; as a result, microalgal biomass can be expected to decrease.
- The third state represents the immersion phase when the mudflat is covered with turbid water and light does not reach the sediment surface. There is no production, but there is grazing and also the possibility of resuspension of microalgae into the water column (see de Jonge and van Beusekom 1992; de Jonge and van Beusekom 1995, for the resuspension issue). Therefore, a decrease of microalgal biomass can be expected during this phase.

From this theoretical analysis, it is clear that high-frequency variations are likely to be a prominent feature of intertidal microphytobenthic biomass and, as such, reflect the close coupling between biological and physical processes which might contribute to explain the high level of productivity of this epipelic diatom community. Unfortunately, only very few investigations have addressed so far this short time scale (Blanchard *et al.*, 1998; Blanchard *et al.*, 2001; Blanchard *et al.*, 2002), because most previous studies were interested in monthly and seasonal variations (see Underwood and Kromkamp 1999; McIntyre *et al.* 1996; Miller *et al.* 1996; Colijn and de Jonge 1984, for reviews). The available information is nevertheless sufficiently relevant to point out a series of oscillations of the biomass at short-term scale – consistent with the conceptual framework synthesized in Figure 1, due to increases during diurnal emersions and decreases during immersions. As these datasets only concerned particular situations, there is still a need to extend our knowledge to the

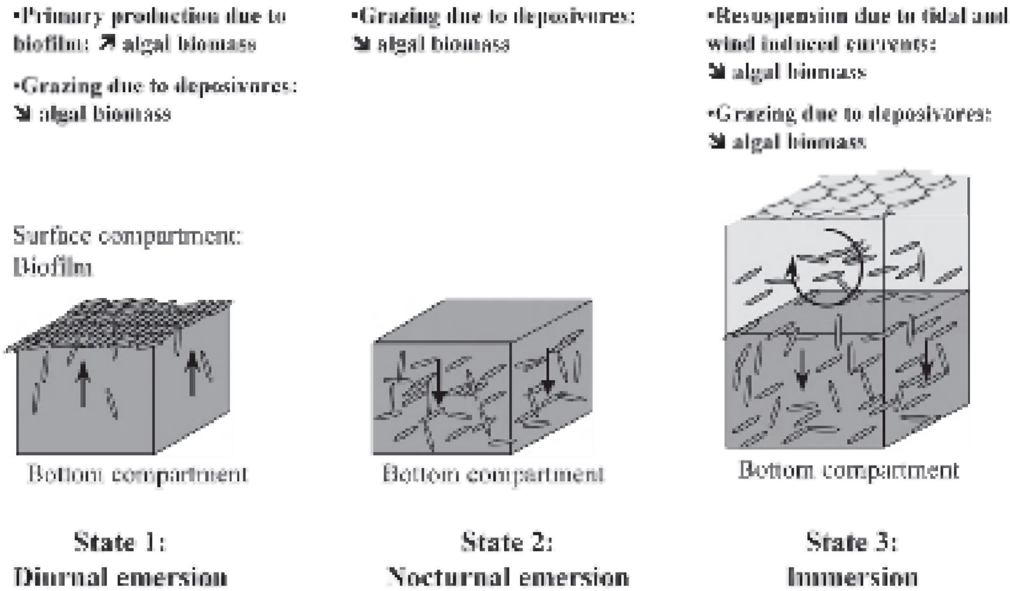


Figure 1. Simple schematic and conceptual representation of the primary production system on bare intertidal mudflats. Three states of the system can be distinguished: diurnal emersion, nocturnal emersion, immersion. For each state, the main processes responsible of the biomass changes are indicated: primary production, grazing, resuspension. Two compartments are taken into account: the surface compartment or biofilm when it is formed only during diurnal emersion; the bottom compartment which is the top 1 cm of the sediment.

full diversity of meteorological and tidal situations encountered on mudflats, and to fully characterize the emergent properties of this intertidal primary production system.

Therefore, this study aims at (i) describing and quantifying the high-frequency variability of intertidal microphytobenthos biomass over a period long enough to encompass different tidal and meteorological situations, (ii) identifying some of the underlying controlling factors, and (iii) bringing out some of the emergent properties of the system.

Material and methods

The study was undertaken in Aiguillon Bay which is located along the French Atlantic coast (47°00' N 1°05' W). It is dominated by bare intertidal mudflats composed of very fine muds. Sampling was carried out during three 16-day periods over 3 months in late Winter-early Spring: 17 February-4 March, 17 March-1 April, 14-29 April, respectively. Each period encompassed a Spring-Neap-Spring tidal cycle. For each of these 3 periods, biomass was measured at the beginning and at the end of every diurnal emersion periods and, for each sampling time (beginning or end of low tides), 6 replicate cores (10 cm inner diameter) were taken within 1 m^2. The same m^2 was sampled repeatedly for 4 days. Biomass was assessed as the mean chlorophyll *a* concentration in the top 1 cm of these 6 cores.

This sampling design allows to calculate, on the same sampling unit, the biomass difference during diurnal emersions and between 2 successive diurnal emersions (i.e. 2 immersions and 1 nocturnal emersion). In parallel, relevant environmental parameters were recorded: irradiance and rainfall during diurnal emersions, wind speed during immersions, temperature.

In Aiguillon Bay, low tide occurs at midday during Spring tides, so that there is only one long diurnal emersion period in the middle of the day with a maximum sunlight input at the surface of the sediment; on the contrary, during Neap tides, high tide occurs at midday so that there are 2 short diurnal emersion periods, one early in the morning and the other one late in the afternoon, with a total amount of light reaching the sediment surface lower than during Spring tides.

Results and discussion

Only 2 other studies dealt with the short-term variations of microphytobenthos biomass on intertidal mudflats (Blanchard *et al.* 1998; Blanchard *et al.* 2002). They clearly pointed out that the dynamics was characterized by series of oscillations corresponding to increases of biomass during diurnal emersions and decreases of biomass during the other phases of the tidal cycle. This is also what we found in the present study (Figure 2). However, as in the previous studies, oscillations are not strictly regular; sometimes, there can be decreases of biomass during diurnal emersions and the magnitude of the biomass changes both during and between diurnal emersions is generally highly variable. It is therefore necessary to analyse thoroughly this variability and to find out which processes and factors may be responsible to be able to elaborate a consistent conceptual model of the functioning and dynamics of the primary production system of intertidal mudflats. The present investigation is the first one to provide such a detailed analysis.

Description and quantification of short-term biomass variations

The average Chl *a* concentration for the 3 periods was 135, 160 and 138 mg m^{-2}, respectively. The difference between the beginning and the end of every diurnal emersion for the 3 periods was calculated and reported in Figure 3A. This histogram thus shows the distribution of net biomass changes (n=48). When there was a net accumulation of biomass during emersion, primary production was higher than grazing; the biomass increase was most of the time between 0 and 30 mg m^{-2}, but it could be up to 60 mg m^{-2}. When there was a net loss of biomass, grazing was higher than production; the net loss was mostly up to 10 mg m^{-2}. The cumulative distribution shows that one third of the observations corresponds to a net loss of biomass while two thirds correspond to a net increase. So, during diurnal emersions of the whole

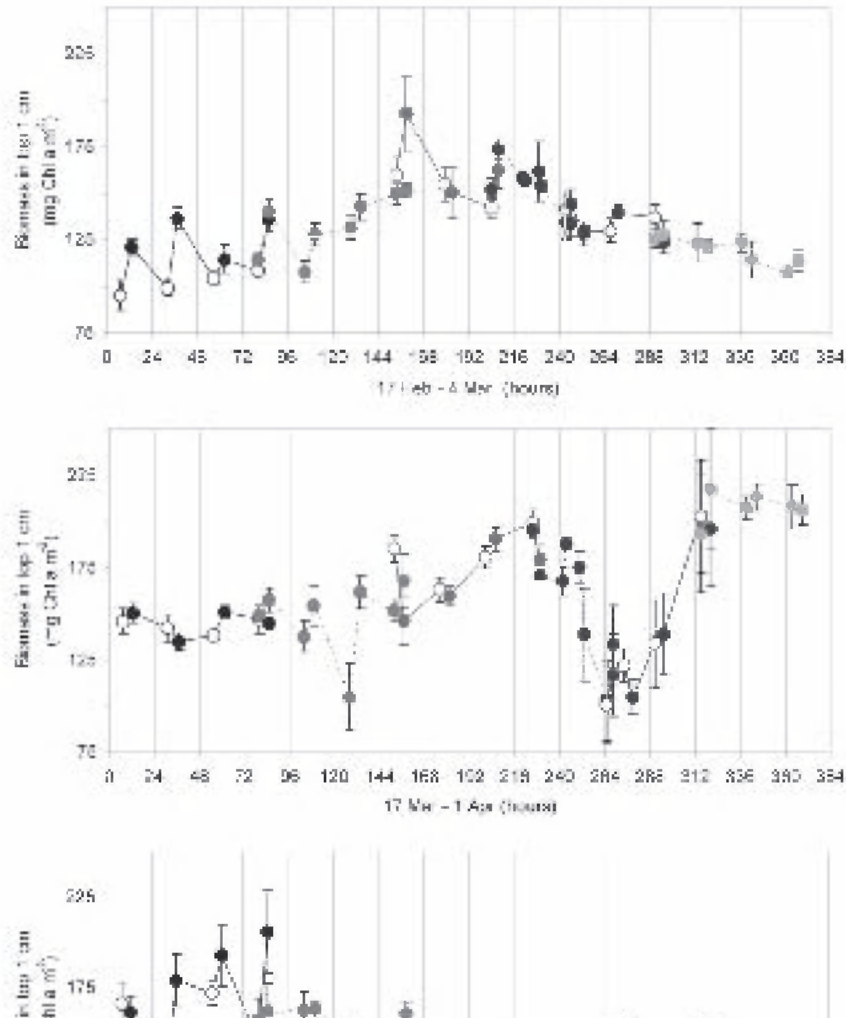


Figure 2. Short-term kinetics of intertidal microphytobenthic biomass (mg Chl *a* m^{-2} in the top 1 cm). Biomass was measured at the beginning and at the end of every diurnal emersions during three 16-day periods: 17 February-4 March, 17 March-1 April, 14-29 April (the X-axis is given in hours, the origin being the first sample taken). Empty circles represent biomass at the beginning of diurnal emersions; full circles represent biomass at the end of diurnal emersions. Solid and dotted lines connect samples taken within the same m^2.

3-month period, biomass increases were more frequent than biomass decreases, but the biomass loss or accumulation was always subject to a great deal of variability.

Likewise, the difference in biomass between successive diurnal emersions (during the 2 immersions and the nocturnal emersion separating 2 diurnal emersions) was calculated and reported in Figure 3B (n=48). The histogram shows that the change can be negative due to grazing and resuspension into the water column, or positive presumably due to sediment advection from other neighboring areas since there was no primary production. Two thirds of the available observations showed a loss of biomass and one third showed an increase. The decrease can be up to about 50 mg m^{-2}. So, most of the time there was a decrease of biomass between diurnal emersions.

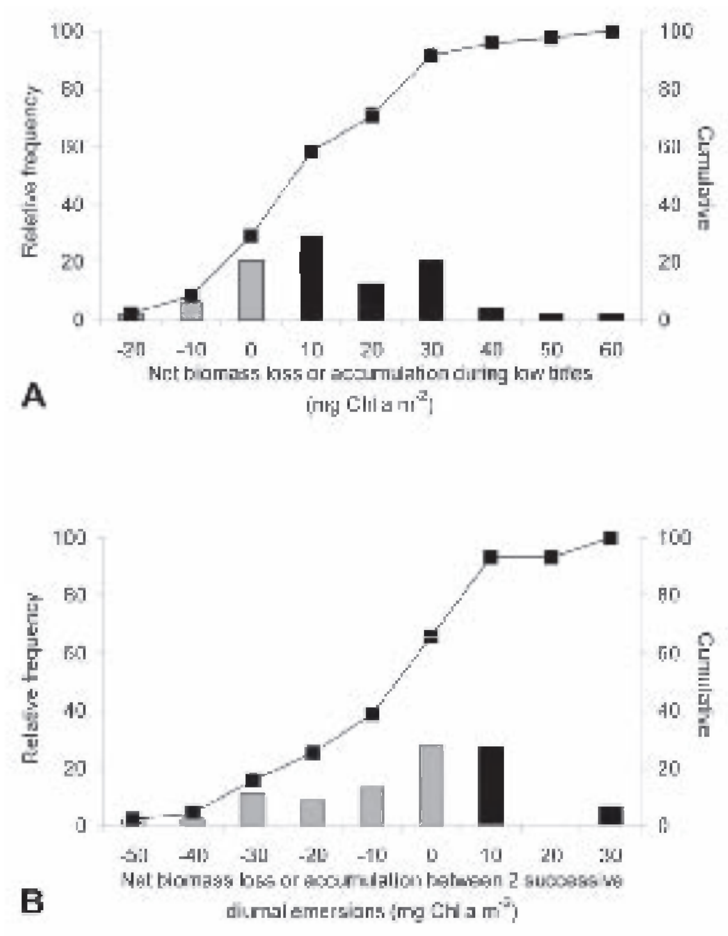


Figure 3. Variability of biomass changes. A. Frequency distribution of the biomass change (mg Chl *a* m^{-2}) during diurnal emersions over the 3-month period (n=48). B. Frequency distribution of the biomass changes (mg Chl *a* m^{-2}) between successive diurnal emersions over the 3-month period (n=48). The right-hand Y-axis gives the cumulative distribution.

Identification of the controlling factors

None of the physical parameters monitored during the sampling period, taken individually, can explain the observed variability of the biomass change during or between diurnal emersions. However, there appears to be an effect of the characteristics of the semi-diurnal tidal cycle – which reflects a combination of all these factors – on the amount of net biomass accumulated or lost during and between diurnal emersions, respectively.

When plotting the biomass changes as a function of the tidal range, it turns out that both the gain of biomass during emersions and the loss of biomass between emersions increase during Spring tides (Figure 4A). Calculations further show (Figure 5) that the average gain of biomass during emersions for large tidal coefficients (>75; 13.0±3.5 mg m^{-2}) was significantly higher (one side t-test, $P=0.03$) than for small tidal coefficients (<75; 4.6±2.6 mg m^{-2}), and that the average loss of biomass between emersions was significantly higher (one-side t-test, $P=0.01$) for large tidal coefficients (>75; 13.5±3.1 mg m^{-2}) than for small tidal coefficients (<75; 0.7±4.7 mg m^{-2}).

This may be explained by the fact that during Spring tides diurnal emersions are much longer and occur in the middle of the day, thus receiving a higher input of sunlight at the surface of the mud and increasing the probability of higher rates of primary production by the microphytobenthic biofilm; meanwhile, tidal currents are also higher during immersions, thus increasing the probability of biomass resuspension. As a result, over the course of the 14-day lunar cycle, the difference of the biomass level between emersions and immersions is expected to be higher during Spring tides.

As those biomass changes (during and between diurnal emersions) are functionally related through the tidal cycle, this means that the accumulation of biomass during diurnal emersions was directly proportional to the immediate previous loss during immersions (Figure 4B; $P<0.001$). This clearly points out the close coupling between biological (primary production) and physical (resuspension) processes.

Besides, apart the direct effects of physical factors, it has also been shown that the dynamics of microphytobenthos in intertidal mudflats can be controlled by biomass-dependent processes (Blanchard *et al.* 2001). This was clearly evidenced in the February and March datasets (Figure 6). When the biomass change during diurnal emersions is plotted against the level of biomass at the beginning of those emersions, we can observe an inverse relationship ($P<0.05$): the higher the biomass already present, the lower the net accumulation during emersion; there can even be a loss of biomass due to grazing when conditions for primary production are poor. In each case, biomass converges towards an equilibrium value where production is equal to grazing, and which was different from one season to the other (ca. 150 and 185 mg Chl *a* m^{-2} in February and March, respectively). This biomass-dependent process is therefore susceptible to explain a significant part of the observed variability in the level of biomass change during diurnal emersions (Figure 3).

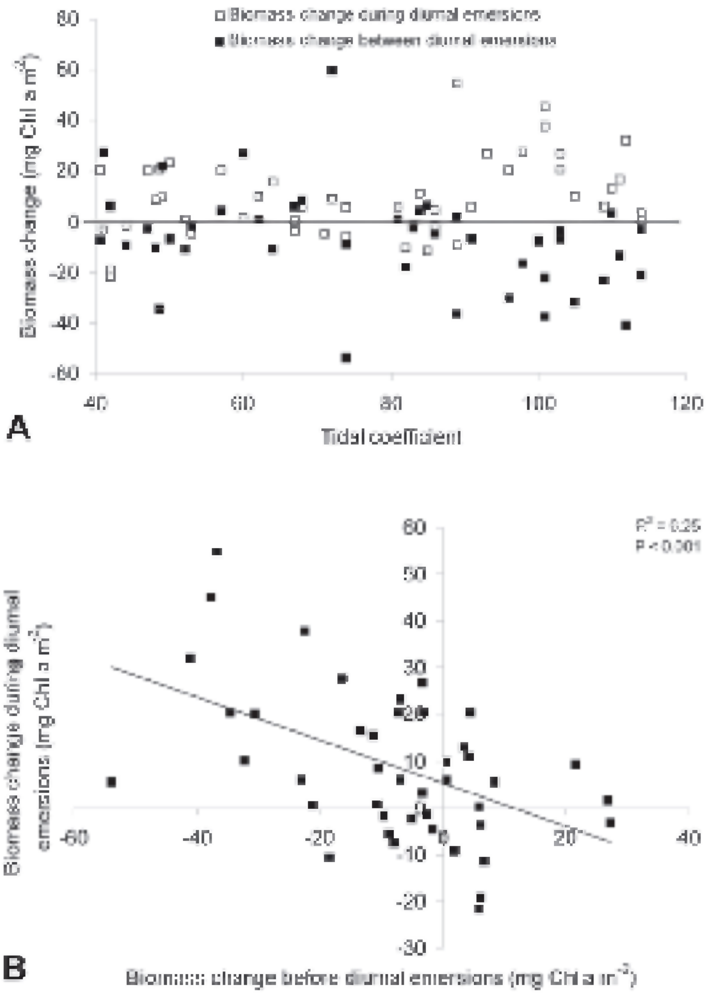


Figure 4. Effect of the semi-diurnal tidal characteristics. A. Biomass changes (mg Chl *a* m^{-2}) during diurnal emersions (empty squares) and between successive diurnal emersions (full squares) over the whole sampling period as a function of the tidal coefficient (index of tidal range: small coefficients for Neap tides and large coefficients for Spring tides). B. Inverse linear relationship ($P<0.001$; $R^2=0.25$) between the change of biomass during diurnal emersions and the change of biomass during the preceeding immersions and nocturnal emersions (mg Chl *a* m^{-2}).

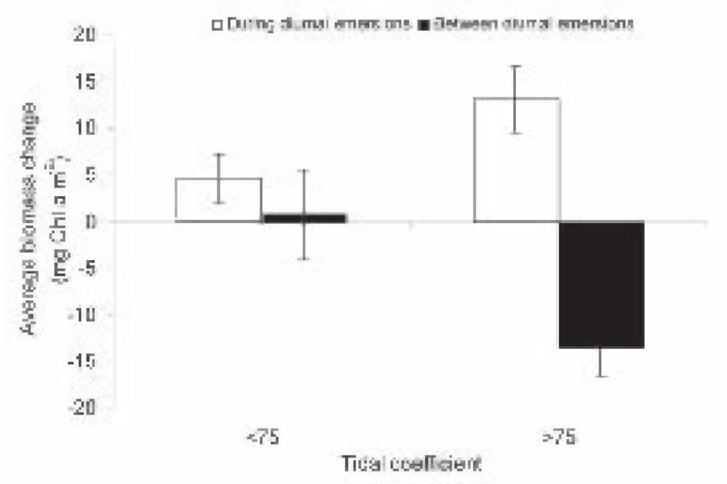


Figure 5. Difference between Neap and Spring tides. Average biomass change (mg Chl *a* m^{-2}) (±SD) during (empty bars) and between (full bars) diurnal emersions for tidal coefficients smaller (including Neap tides) and larger (including Spring tides) than 75, respectively.

Emergent properties of the intertidal primary production system

When looking at the whole data series and taking into account the effect of the semi-diurnal tidal characteristics as well as the occurrence of biomass-dependent processes, general properties of the primary production system on intertidal mudflats emerge.

It is obvious that microphytobenthos biomass converges towards an equilibrium point (Figure 6) with a slope which sets the maximum limit of net production (Figure 7A; theoretically, this slope depends on the value of the equilibrium point and the growth rate of microphytobenthos). At the equilibrium point, production is equal to grazing. The same property had also been evidenced by Blanchard *et al.* (2001) on another mudflat.

The implication of such a property is that there must be a loss of biomass – due to grazing and resuspension – between 2 successive diurnal emersions to pull the biomass away from the equilibrium value, so that production is allowed and can be realized during the next diurnal emersion if the weather conditions are appropriate. This brings the biomass back to its equilibrium point. Therefore, it turns out that the primary productivity of the system is highly dependent on the loss processes, and is fundamentally determined by a close coupling between the physical and biological processes.

This is illustrated by the fact that the gains or losses of biomass on the mudflat are significantly higher during Spring tides than during Neap tides (Figure 4 and 5). Schematically (Figure 7B), the coupling between high primary production and high resuspension rate (as during Spring tides) promotes a productive system since the

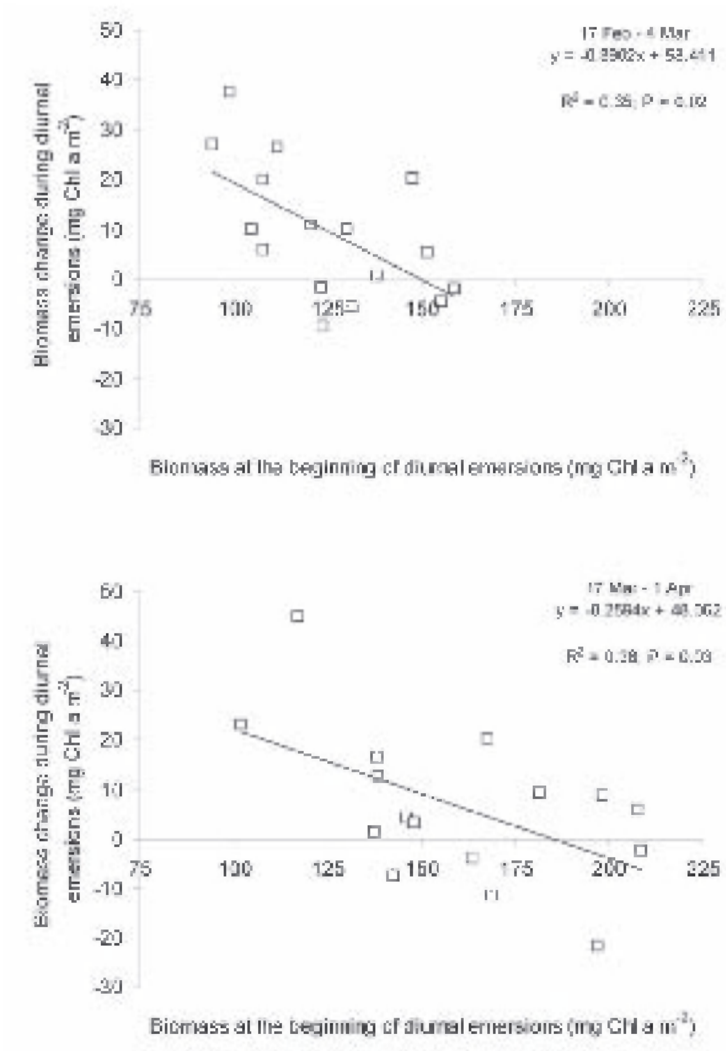
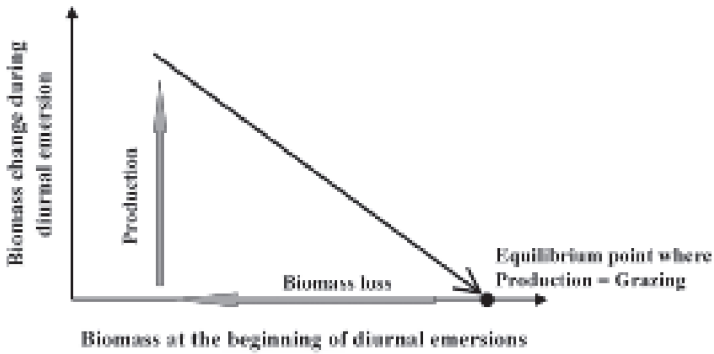


Figure 6. Biomass-dependent process. Relationship between the biomass change during diurnal emersions (mg Chl *a* m^{-2}) and the biomass level at the beginning of diurnal emersions (mg Chl *a* m^{-2}), for the February and March 16-day periods. Both inverse linear relations are statistically significant ($P<0.05$), and the coefficient of determination is indicated in each case.



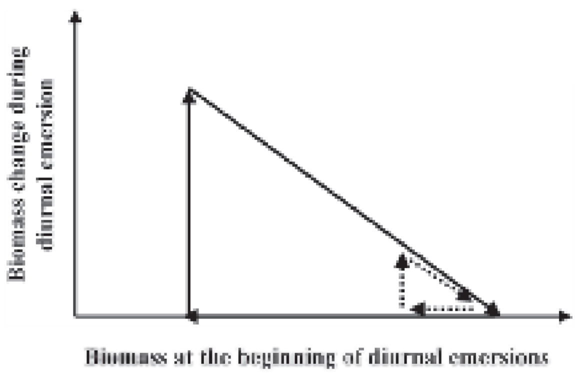


Figure 7. Schematic and conceptual representation of the dynamics of intertidal microphytobenthos primary production, through the coupling of physical and biological processes. A. Net biomass accumulation decreases as the quantity of biomass increases, thus indicating a convergence towards an equilibrium point where production is equal to grazing. There must be a loss of biomass (through grazing and resuspension) to pull it away from its equilibrium point and to allow it to grow again (through primary production). B. Two exemples to illustrate the dynamics of the primary production system (see text for explanations): (i) when there are good conditions for primary production and low resuspension (dashed arrows), the overall productivity is low because biomass remains in the vincinity of its equilibrium point; (ii) when there are good conditions for primary production and high resuspension (solid arrows), the overall productivity is higher because biomass is pulled away from its equilibrium point (loss processes enhance production).

biomass is pulled far away from its equilibrium point and is then brought back quickly (solid arrows). On the opposite, in situations with lower loss rates (even with good irradiance conditions), for instance during Neap tides, the overall productivity of the system is strongly reduced because biomass remains in the vicinity of its equilibrium point (dashed arrows). Intermediate situations can also be considered, for instance when poor conditions for primary production are associated with high loss rates: there would be a rapid and important decrease of the biomass in a few days. The biomass can come back to its initial level also within a few days when meteorological conditions improve.

Conclusion

The main outcome of the present study is that it confirms the existence of an equilibrium point towards which microphytobenthic biomass tends to converge. This is a key point in the understanding of the dynamics of the biomass since it brings a new insight in the interpretation of the short-term variability and proves to be of great ecological value. Indeed, taking into account this equilibrium point together with the coupling between physical and biological processes (succession of production and resuspension phases through the tidal cycle) leads to the elaboration of a conceptual scheme which strongly suggests the importance of loss processes on the system overall productivity. However, in the present state of our knowledge, we cannot separate grazing from resuspension, and we need to know how much of the production goes to grazing and how much to resuspension; the fate of the high microphytobenthic production is therefore a very important line of research for which we still have too little information. Finally, and more generally, the analysis of the biomass dynamics emphasizes the difficulty of upscaling isolated single measurements, because of the strong variability of the biomass at hourly and daily scales.

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