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TEMPERATURE EFFECTS ON MICROPHYTOBENTHIC PRODUCTIVITY IN TEMPERATE INTERTIDAL MUDFLAT

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DYNAMICS
MICROPHYTOBENTHOS
MUD SURFACE TEMPERATURE
PHOTOSYNTHETIC RESPONSE
TIME SCALES

DYNAMIQUE
ECHELLES DE TEMPS
MICROPHYTOBENTHOS
RÉPONSE PHOTOSYNTHÉTIQUE
TEMPÉRATURE DE SURFACE DE LA
VASE

ABSTRACT. – Based on field measurements and computer simulations, we describe the temporal (short- and long-term) and spatial dynamics of the mud surface temperature (MST) on temperate intertidal mudflats. We then document the photosynthetic responses of natural assemblages of epipellic microalgae to such variations by means of field observations and laboratory experiments. This synthetic work is an attempt to put into perspective our knowledge about the scales of variation of one major physical forcing (MST) and the relevant ecophysiological responses of microalgae.

RÉSUMÉ. – Effets de la température sur la productivité du microphytobenthos des vasières intertidales tempérées. Nous décrivons les dynamiques temporelle (à court et à long terme) et spatiale de la température de surface de la vase à partir de mesures de terrain et de simulations numériques. Nous présentons ensuite quelques réponses photosynthétiques des Algues épipéliques à ces variations sur la base d'observations *in situ* et d'expérimentations en laboratoire. Ce travail synthétique vise principalement à faire coïncider les échelles de variation d'un forçage physique (en l'occurrence, la température de surface de la vase) avec les réponses écophysologiques appropriées des microalgues.

INTRODUCTION

Estuaries are among the most productive ecosystems in the world due to the high primary productivity yield of their intertidal areas (Schelske & Odum 1962). When those flats are devoid of macrophytic vegetation, such as in the 'european type' estuary – according to McLusky's classification (1989) –, microphytobenthos may become the main primary producer (Admiraal 1984, Colijn & de Jonge 1984) and can contribute substantially to the total carbon budget of the whole estuary (de Jonge 1995, de Jonge & van Beusekom 1995, de Jonge & van Beusekom 1992). In that case, production is essentially realized by the community of motile epipellic microalgae (Pinckney & Zingmark 1991) – referred to as epipelon (Round 1971) – once they have migrated upwards in the photic zone of the mud. This vertical migration seems to be determined by an endogenous rhythm (Aleem 1950, Callame

& Debyser 1954, Hopkins 1963, Palmer & Round 1965, 1967, Round & Palmer 1966, Round 1979, Paterson 1986, Serôdio *et al.* 1997) : in outline, epipellic algae migrate upwards to the surface of the sediment at the beginning of diurnal emersion periods and migrate downwards in anticipation of submersion or night periods. Such a rhythm is controlled by the time difference between the tidal and diurnal cycles ; therefore, it completely determines the window within which epipellic algae can photosynthesize at the surface of the sediment, in the form of a very thin biofilm, as a function of the available incident irradiance.

Meanwhile, the mud surface temperature (MST) in temperate mudflats exhibits large (up to 10 °C) and rapid (at a rate of 2-3 °C h⁻¹) changes during diurnal emersion periods (Harrison 1985 ; Harrison & Phizacklea 1987). Those changes are due first to the variation in the supply of sunlight energy heating the mud – which is likewise entirely controlled by the phase difference between the tidal and diurnal cycles – and second

to the effect of local meteorological conditions and sedimentological properties. Although such MST variations are susceptible to force the photosynthetic capacity (photosynthetic rate at light saturation) of epipelagic algae at the surface of the sediment, the issue had been poorly documented (Colijn & van Buurt 1975, Henriksen *et al.* 1983).

Recently, we have addressed different aspects of this topic in a few articles which dealt with the effect of short-term (Blanchard *et al.* 1996, Blanchard & Guarini 1996) and long-term (Blanchard *et al.* 1997) temperature changes on the potential production of epipelagic algae, as well as with the dynamics of MST (Guarini *et al.* 1997). However, as each point has been analysed separately with very specific objectives, there is a comprehensive view missing. Therefore, we propose herein to synthesize into a single consistent frame all our data which come from the same site (Marennes-Oléron Bay, France), in order to assess critically the relevance of the methods and the main results. It is also our goal to emphasize the different aspects of the relationship between temperature and microphytobenthos photosynthesis which should be taken into account by ecologists if we are to understand the effect of temperature dynamics on that of microphytobenthos production.

To achieve our goal, we shall proceed into 2 steps. Firstly, we shall present recorded temporal series of mud temperature under different meteorological conditions to provide a schematic representation of mud temperature variations undergone by epipelagic diatoms and other benthic organisms. We shall further show model simulations of long-term time series and large-scale spatial series in MST. Secondly, we shall formalize and analyse the response of microphytobenthos photosynthetic capacity to short-term time scale temperature changes as a startpoint to test the effect of high frequency/high amplitude MST changes. In addition, we shall point out the response of microphytobenthos photosynthetic capacity to long-term time scale temperature changes which will give us the opportunity to discuss the problem of interaction between high- and low-frequency MST changes, that is the acclimation strategy to temperature changes.

CHARACTERIZING MST DYNAMICS : FROM MEASUREMENTS TO MODELLING

Analysis of the short-term time scale dynamics

Continuous *in situ* recordings are necessary to characterize the short-term dynamics of mud surface temperature. We thus provide (Fig. 1) a few examples of such recordings describing MST variations during a tidal cycle at 3 different periods

and under 3 different meteorological conditions. In all 3 cases, the short-term dynamics is characterized by a succession of daily oscillations resulting from the combination of both the tidal and diurnal cycles. The amplitude of each oscillation, however, is variable from one day to the next when the meteorological conditions are unstable (for instance, Fig. 1 upper and middle graphs). On the contrary, the oscillation characteristics exhibit a consistent scheme under stable anticyclonic meteorological conditions without cloudiness (Fig. 1 lower graph): the minimum and maximum temperatures together with the amplitude of temperature variation tend to increase from neap tides towards spring tides. It nevertheless turns out that these predictable temperature variations, indirectly induced by the tidal cycle, can be completely masked by the meteorological conditions (Fig. 1 upper graphs) which appear to be predominant in this respect.

Similar recordings of mud temperature at different depths in the mud (Fig. 2) show that the daily oscillations are still detectable at a depth of 5 cm but the amplitude is about twice as less as at the surface. At a depth of 15 cm, the oscillations are strongly deadened and they are no longer detectable at a depth of 30 cm. So, it is clear that the whole community of photosynthetically active microalgae, meiofauna, and macrofaunal organisms inhabiting the top 5 cm of the sediment undergo large and rapid temperature variations. Most of these organisms cannot avoid those variations by escaping deeper in the mud; they have to cope with those high frequency variations. It is further worth noting that there is a time lag of several hours between the peaks of highest temperatures at the surface and at a depth of 15 cm, due to temperature diffusion across the sediment (Fig. 2).

Assuming no meteorological interferences, such as in the situation depicted in figure 1C, we can further schematize the diel MST variations as a function of the tidal phasing. Let us take the example (Fig. 3) of a semi-diurnal tide when the tidal cycle is in opposition with the diurnal cycle during neap tides (slack high water coincides with midday) – correlatively, both cycles are in phase during spring tides.

In the former case (Fig. 3A), MST is in equilibrium with the water temperature during nocturnal high tide (phase 1), then MST decreases at the beginning of low tide until sunrise (phase 2). From sunrise onwards, MST rapidly increases (at a rate of about $2-3\text{ }^{\circ}\text{C h}^{-1}$) until the onset of submersion some time before noon (phase 3), which then corresponds to a drop in MST due to the rapid equilibrium with water temperature (phase 4). MST remains constant during the course of submersion; the water temperature during the day is higher than during the night because the water height at the point of temperature recording is small. The difference between the

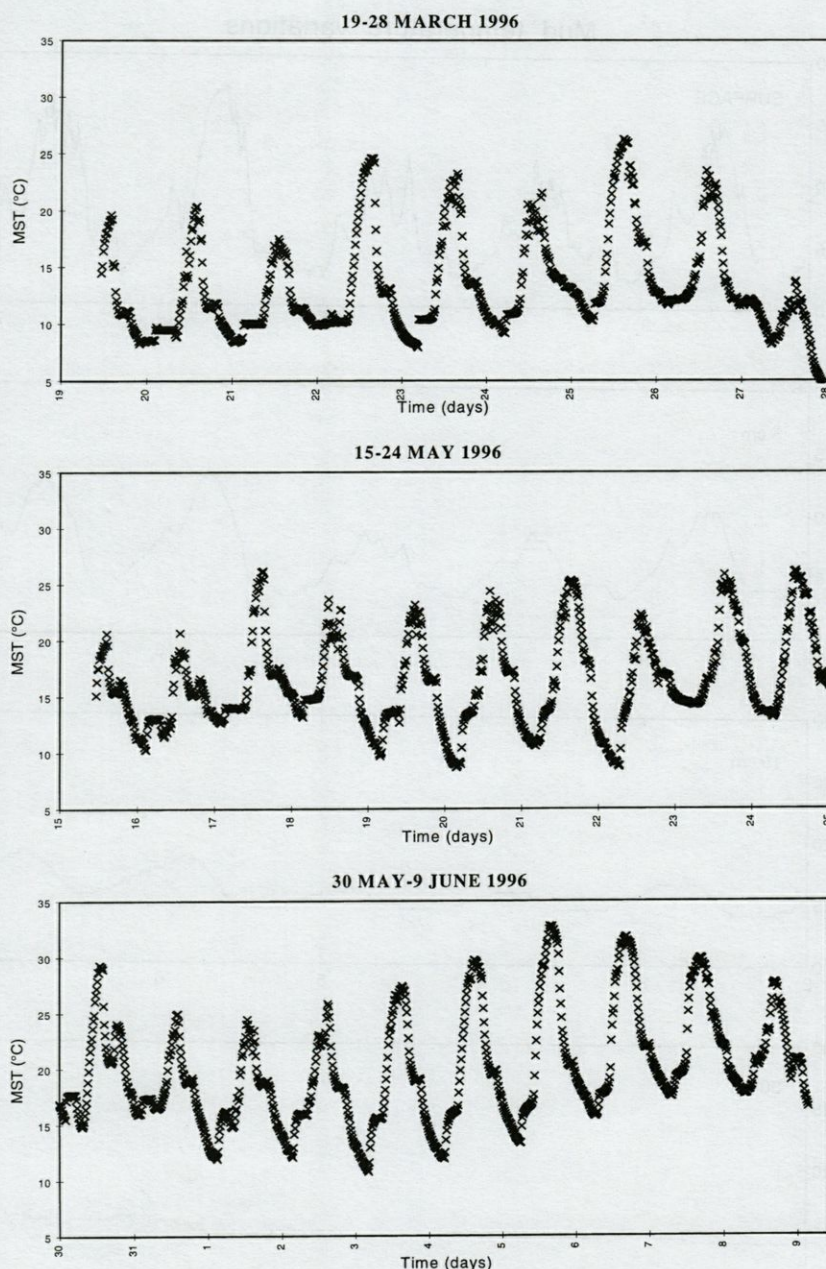


Fig. 1. – MST time series in March (upper graph), May (middle graph) and June (lower graph) from an intertidal mudflat close to La Rochelle on the French Atlantic coast (modified from Guarini *et al.* 1997).

water temperature during the day and during the night is large when the water height is small, and it is small when the water height is large. MST starts again to increase when late afternoon emersion occurs because sunlight is still strong enough (phase 5). At sunset, MST goes on decreasing (because of heat loss) until it reaches a minimum when high tide comes back (phase 6). After a rapid equilibrium with water temperature, MST is back to phase 1.

In the case where slack low tide coincides with midday (Fig. 3B), MST is in equilibrium with water temperature during the early morning high

tide (phase 1); water temperature tends to increase after sunrise – due to the supply of sunlight energy – because the water height is small in the highest part of the mudflat. During the diurnal emersion period (phase 2), MST increases steadily and rapidly (at a rate of about $2-3\text{ }^{\circ}\text{C h}^{-1}$) until noon, and starts to decrease in early afternoon. At the beginning of the afternoon high tide, MST quickly reaches an equilibrium with water temperature (phase 3). Finally, compared to water temperature, MST decreases during the nocturnal emersion period (phase 4) before getting back to phase 1.

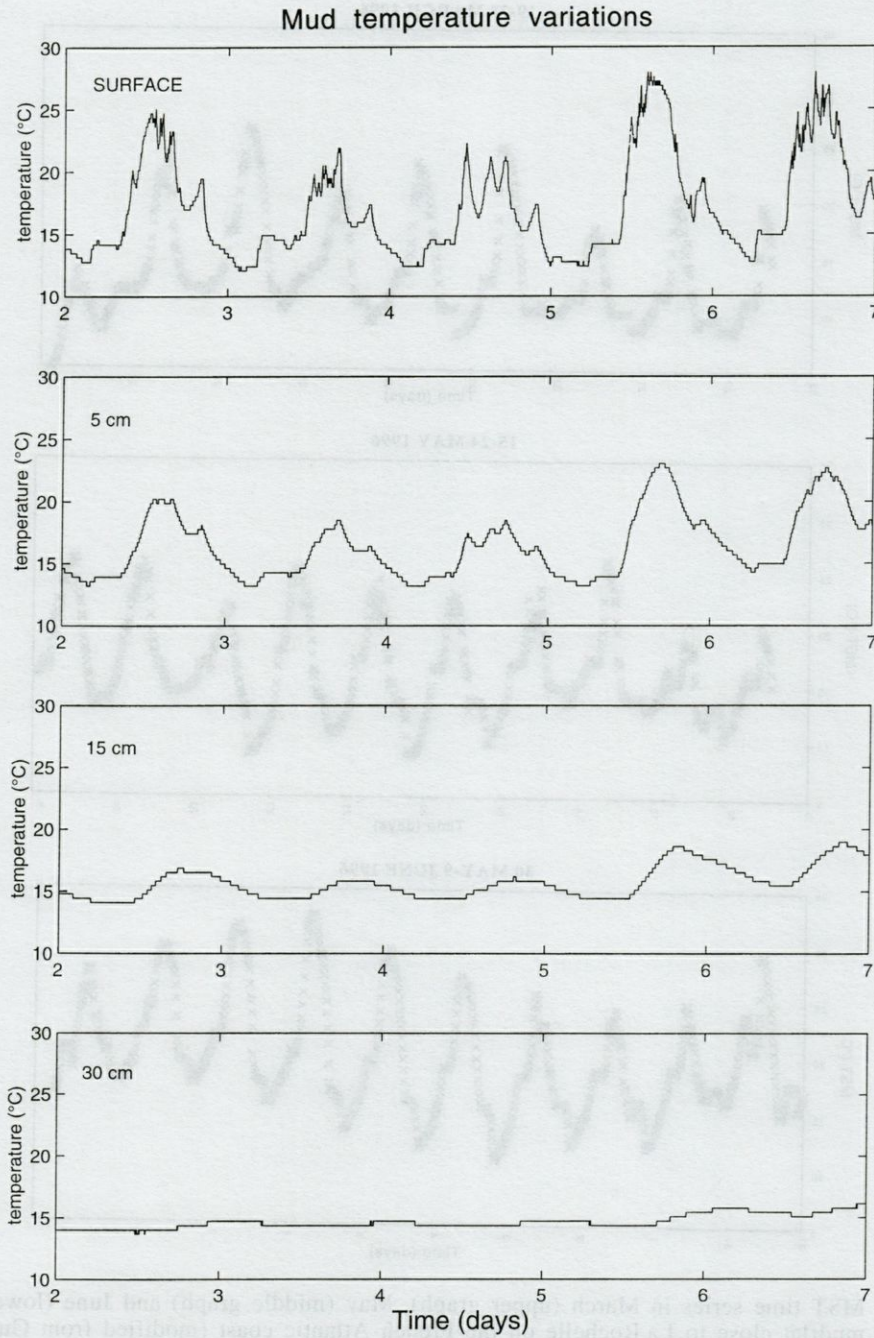


Fig. 2. – MST time series as a function of depth in July from an intertidal mudflat in the Humber estuary, U.K.

Therefore, according to the tidal phasing, these successions of phases are typical of MST dynamics, and should be taken into account when studying metabolic responses of intertidal organisms inhabiting mudflats.

Modelling MST dynamics

In consideration of the ecological implications of MST dynamics, its prediction in space and time is thus of prime importance. However, as MST

measurement at any time and at any point on a mudflat is practically impossible, it is necessary to have recourse to modelling. Therefore, we have modelled MST dynamics of intertidal mudflats (Guarini *et al.* 1997).

Basically, the temporal evolution of MST, $T_M(z_0,t)$, is governed by the first law of thermodynamics with isobaric transformation :

$$\rho_M C_{PM} \frac{\partial T_M(z_0,t)}{\partial t} = R_S + R_{Atm} - R_M - S_{Mud \rightarrow Air} - V_M$$

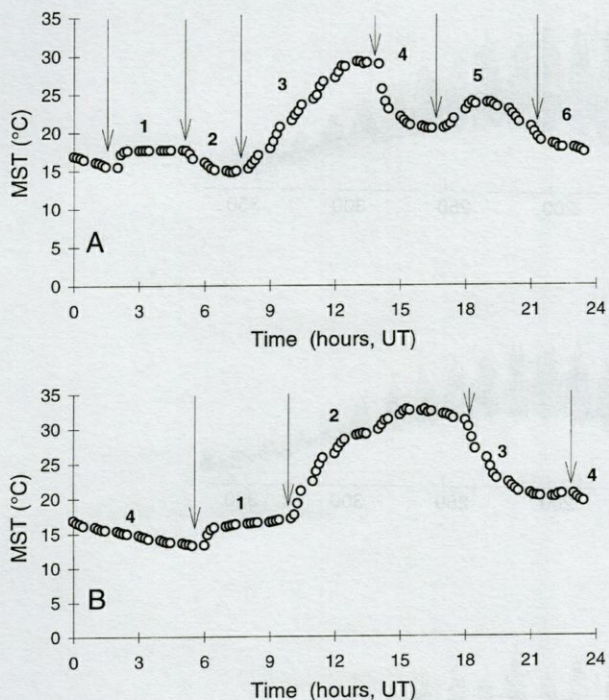


Fig. 3. – Schematic representation of MST short-term time scale dynamics. A : during neap tides, B : during spring tides. Numbers represent the different phases of MST variation cycle (see text for explanation).

where rM is the mass of mud per unit of volume (kg m^{-3}); CPM is the specific heat capacity of mud at constant pressure ($\text{J kg}^{-1} \text{K}^{-1}$); TM is the temperature of the mud ($^{\circ}\text{K}$); z is depth (m); t is time (s); the right-hand term is the Heat Energy Balance with (Fig. 4): the fluxes of radiation coming from the sun (R_s), from the atmosphere (R_{Atm} , infra red radiation), from the receiving surface (R_M), the sensible heat flux by conduction due to the difference between the temperature of mud and air ($S_{\text{Mud} \rightarrow \text{Air}}$), and the flux of evaporation (V_M) depending on the mud water content. During the submersion periods, the Heat Energy Balance is simply a sensible heat flux described as the product of thermal conductivity and of a finite-difference approximation of the temperature gradient between mud and overlying water.

Spatialization of the local equation is provided by an hydrodynamic model (Le Hir *et al.* 1993) which calculates the total water height variations over the intertidal area – and hence the duration of the emersion period.

Simulating long-term time series and large-scale spatial series

Modelling allows to work at scales relevant to the functioning of the ecosystem, that is simula-

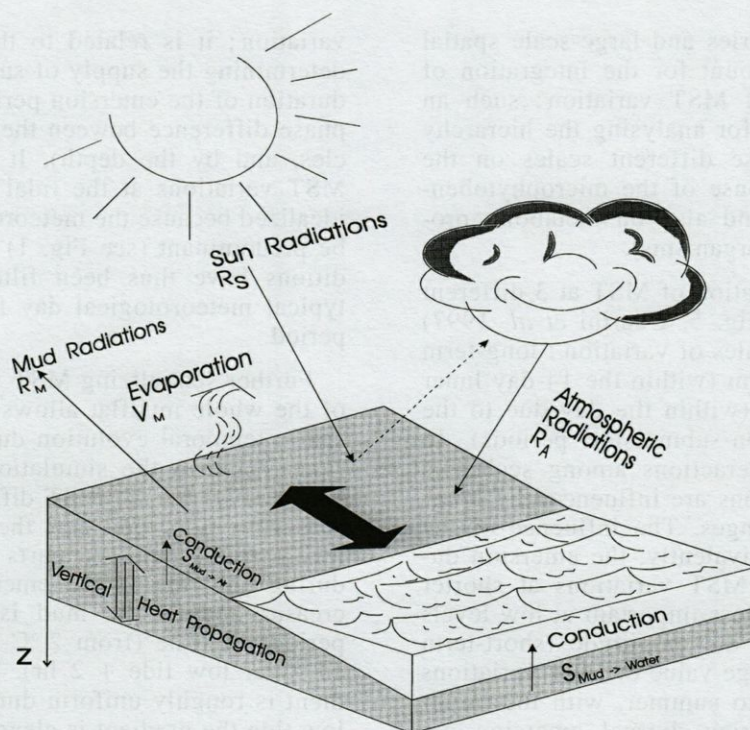


Fig. 4. – Diagrammatic representation of the thermodynamic MST model (from Guarini *et al.* 1997).

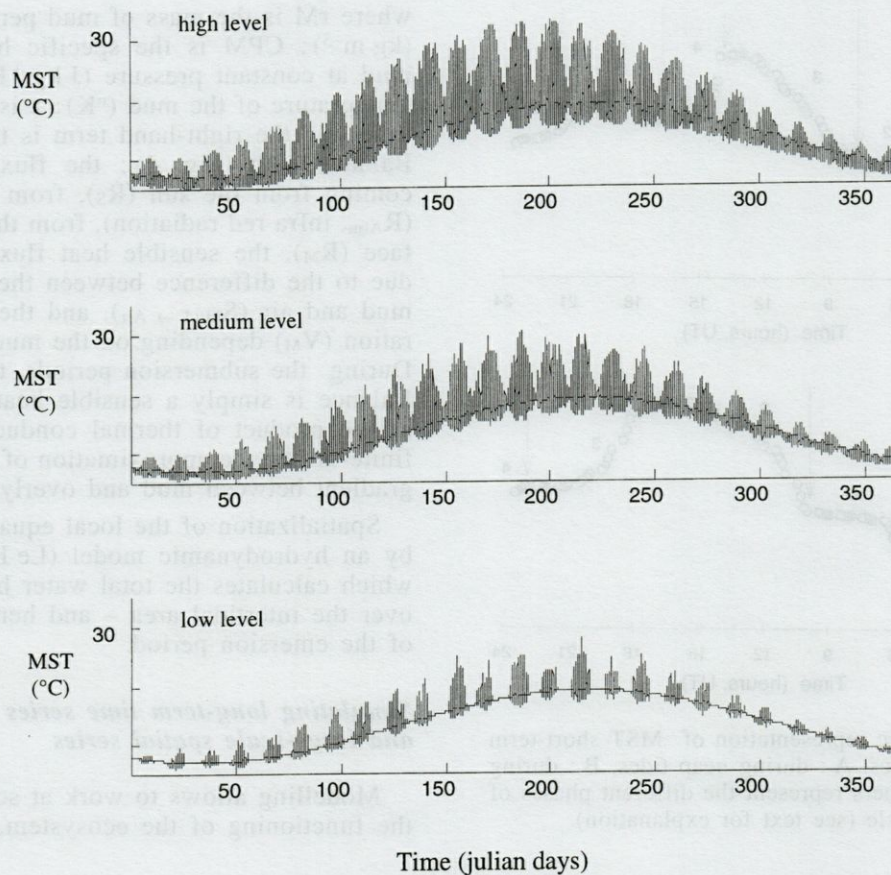


Fig. 5. – Whole-year simulation of MST at different levels (high, medium, low) on the Brouage mudflat in Marennes-Oléron Bay (along the French Atlantic coast) in 1996 (modified from Guarini *et al.* 1997).

ting long-term time series and large-scale spatial series in order to account for the integration of the different scales of MST variation; such an information is crucial for analysing the hierarchy of the effects of these different scales on the ecophysiological response of the microphytobenthic photosynthesis (and also on metabolic processes of all benthic organisms).

A whole-year simulation of MST at 3 different levels on a mudflat (Fig. 5, Guarini *et al.* 1997) clearly points out 3 scales of variation: long-term (seasonal), medium-term (within the 14-day lunar cycle) and short-term (within the day due to the succession of emersion-submersion periods). In addition, there are interactions among scales so that short-term variations are influenced by long- and medium-term changes. The influence of the topographic level (equivalently, the emersion duration) is also clear; MST variations at shorter time scales tend to be less important at low levels on the mudflat. Both the amplitude (short-term changes) and the average value of MST variations increase from winter to summer, with the larger changes occurring during diurnal emersion periods. At the scale of the tidal cycle, the major feature is the change of the amplitude of MST

variation; it is related to the temporal windows determining the supply of sunlight energy and the duration of the emersion period (controlled by the phase difference between the tidal and diurnal cycles, and by the depth). It is worth noting that MST variations at the tidal scale in figure 5 are idealized because the meteorological influence can be predominant (see Fig. 1); meteorological conditions have thus been filtered out by using a typical meteorological day for the corresponding period.

Further spatializing MST variations at the scale of the whole mudflat allows to describe the MST spatio-temporal evolution during an emersion period. Thus, in the simulation which we propose herein (Fig. 6), the MST difference in April 1996 at spring tide, between the highest and lowest levels of the emerged parts of the flat, increases during ebb tide as the emerged surface area increases and as the mud is exposed for longer periods of time (from 2 °C at low tide – 4 hr to 14 °C at low tide + 2 hr). The temperature gradient is roughly uniform during ebb tide. Then at low tide the gradient is clearly not uniform: MST tends to homogenize on high and mid-levels of the mudflat (where the highest MSTs are reached)

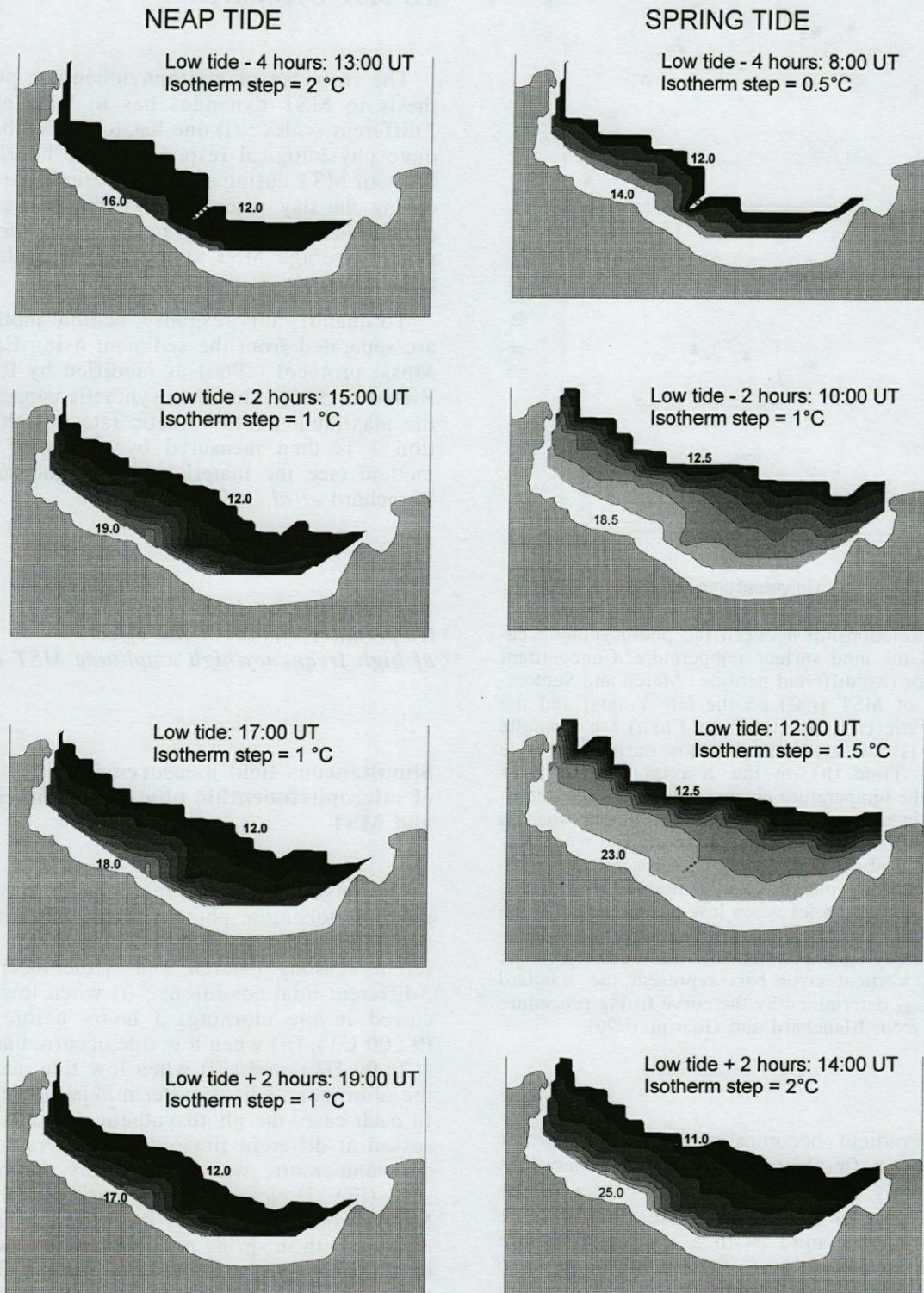


Fig. 6. – Spatial simulation of MST over an entire mudflat. Two situations are presented (spring and neap tides) at different times of low tide (at low tide – 4 h, at low tide – 2 h, at low tide and at low tide + 2 h) during a spring month in a mudflat of Marennes-Oléron Bay along the Atlantic French coast. The surface area is about 50 km² (modified from Guarini *et al.* 1997).

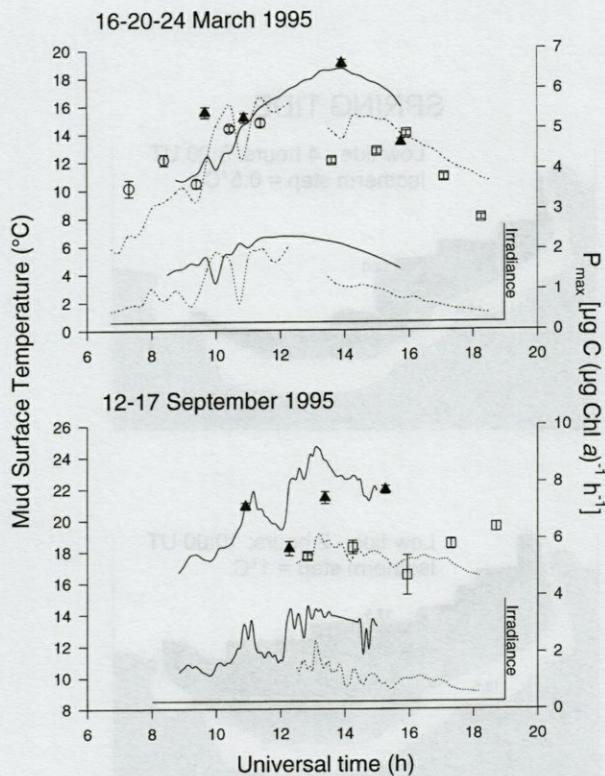


Fig. 7. – Relationship between the photosynthetic capacity and the mud surface temperature. Concomitant changes (for two different periods : March and September 1995) of MST [$^{\circ}\text{C}$] on the left Y-axis] and the photosynthetic capacity [$\mu\text{g C } (\mu\text{g Chl } a)^{-1} \text{ h}^{-1}$] on the right Y-axis] of microphytobenthos during low tide [Universal Time (h) on the X-axis]. Dotted lines represent the temperature change when low tide occurred either in the morning or in the afternoon, whereas solid lines represent the temperature change when low tide occurred at midday. Symbols represent the photosynthetic capacity measured at different times during emersion : empty circles when low tide occurred in the morning, full triangles when low tide occurred at midday, and empty squares when low tide occurred in the afternoon. Vertical error bars represent the standard error on P_{max} determined by the curve fitting procedure (modified from Blanchard and Guarini 1996).

and the gradient becomes steeper at the water front. During flood tide, the gradient becomes again roughly uniform : MST gets colder in the mid-level part of the flat and the flooding tide cools the surface mud (with a short equilibrium period) in the lowest part of the mudflat. At neap tide, there are several differences with the spring tide pattern because the phase difference between the tidal and diurnal cycles is maximum : (i) the maximal MST reaches only 19°C in the highest part of the emerged flat at 15 : 00 UT during ebb tide, (ii) MST starts to decrease before low tide and (iii) the MST gradient is not uniform and becomes steeper landwards instead of seawards.

RESPONSE OF MICROPHYTOBENTHOS PHOTOSYNTHETIC CAPACITY TO MST DYNAMICS

The response of microphytobenthos photosynthesis to MST dynamics has to be analysed at 2 different scales : (i) one has to assess the immediate physiological response to the hourly variability of MST during emersion periods particularly during the day when photosynthesis occurs, and (ii) one has also to evaluate how long-term changes in average MST (the seasonal cycle) affect this immediate response.

To quantify this response, benthic motile algae are separated from the sediment using Eaton and Moss' protocol (1966) as modified by Riera and Richard (1996). The photosynthetic capacity – i.e. the maximum photosynthetic rate at light saturation – is then measured by means of the ^{14}C method (see the material and method section in Blanchard *et al.* 1996).

The response to short-term time scale temperature changes : the effect of high frequency/high amplitude MST changes

Simultaneous field measurements of microphytobenthic photosynthetic capacity and MST

We have studied the relationship between the microphytobenthic photosynthetic capacity (P_{max}) and MST (Blanchard & Guarini 1996) at 2 different seasons (March and September) and in 3 different tidal conditions : (i) when low tide occurred in the morning, 3 hours before midday (9 : 00 UT), (ii) when low tide occurred at midday (12 : 00 UT), and (iii) when low tide occurred in the afternoon, 3 hours after midday (15 : 00 UT). In each case, the photosynthetic capacity was assessed at different times of the emersion period, and temperature was continuously recorded. Results (Fig. 7) clearly show a marked difference in MST recordings between the different tidal conditions, both in spring and autumn ; measurements of the photosynthetic capacity further show that there is a good agreement with MST changes. The highest values tend to occur around midday when there is the maximum supply of sunlight energy, while the lowest values occur early in the morning or late in the afternoon. It thus turns out that microphytobenthic photosynthesis at the surface of the sediment during diurnal emersions is related to MST dynamics.

Experimental determination of the short-term temperature effect on P_{\max} and mathematical formulation

Because there seems to be a relationship between MST changes in the field and the photosynthetic capacity of natural assemblages of benthic microalgae, it was necessary to assess and quantify the physiological response of microphytobenthos to a temperature change (Blanchard *et al.* 1996). As a first step, the photosynthetic capacity was measured in the laboratory at different temperatures: the effect of an increase in the range 5-35 °C at a rate of 3 °C h⁻¹ – similar to what occurs in the field – was tested. Results (Fig. 8) show that the shape of the relationship is typical of a short-term temperature effect on light-saturated photosynthesis (Davison 1991): a progressive increase up to an optimum temperature, beyond which P_{\max} declines rapidly. We have proposed an original non-linear model to fit those experimental data:

$$P_{\max}(T) = P_{\max} \left(\frac{T_{\max} - T}{T_{\max} - T_{\text{opt}}} \right)^{\beta} \exp \left\{ -\beta \left(\frac{T_{\max} - T}{T_{\max} - T_{\text{opt}}} - 1 \right) \right\}$$

where T (°C) is temperature; P_{\max} is the photosynthetic capacity ($\mu\text{g C } \mu\text{gChl } a^{-1} \text{ h}^{-1}$); P_{\max} ($\mu\text{g C } \mu\text{gChl } a^{-1} \text{ h}^{-1}$) is the maximum value of P_{\max} at the optimum temperature, T_{opt} (°C); T_{\max} (°C) is the lethal temperature at which P_{\max} decreases to zero; β is a dimensionless shape parameter.

So far, this mathematical relationship has been parameterized for an increase in temperature in the range 5-35 °C (Blanchard *et al.* 1996), but a different set of parameters might then be necessary for describing the response of P_{\max} to the decrease in temperature. This possibility has not been tested yet, although it is crucial for assessing the complete response of microphytobenthic photosynthesis to short-term time scale MST dynamics. Therefore, we think that additional research is required on the following issues: (i) in the range of suboptimal temperatures ($T < T_{\text{opt}}$), is the photosynthetic response to the decrease in temperature (from T_{opt} downwards) symmetrical to that of the increase (towards T_{opt})? (ii) does an exposure to supraoptimal temperatures (but still sublethal, $T_{\text{opt}} < T < T_{\max}$) impair the photosynthetic response in the suboptimal range, and if so, to what extent? (iii) in case of an impairment, what is the ability of the microphytobenthic community to resume its initial photosynthetic capacities? Although far from being exhaustive, these issues represent the minimum basis to investigate accurately the complete response of microphytobenthic photosynthesis to short-term time scale MST dynamics.

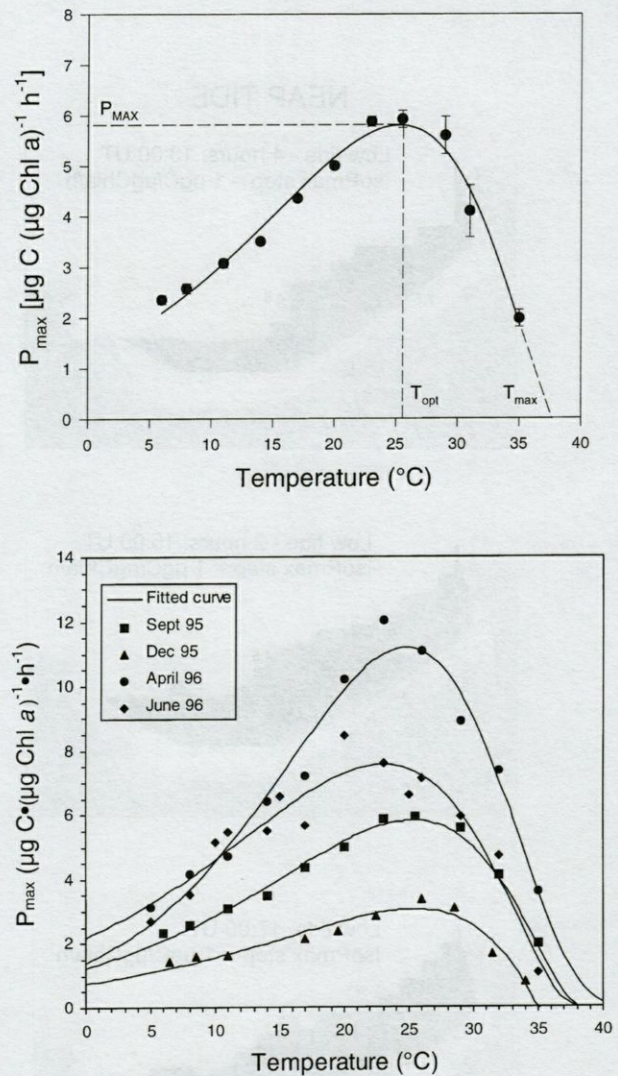


Fig. 8. – Above, response of the photosynthetic capacity P_{\max} to a rapid increase in temperature. Experimental data from September 1995 (symbols) and the fitted curve (solid line) are presented. T_{opt} is the optimum temperature for photosynthesis, P_{\max} is the maximum value of P_{\max} at T_{opt} , T_{\max} is the lethal temperature when P_{\max} drops to 0 (modified from Blanchard *et al.* 1996). Below, seasonal influence on the relationship between the photosynthetic capacity and temperature. Squares for September 1995, triangles for December 1995, circles for April 1996, diamonds for June 1996, and the solid line represents the model equation fitted to each data series (from Blanchard *et al.* 1997).

Spatializing the photosynthetic response at the scale of the ecosystem

By combining the equation describing the physiological response of microphytobenthos to short-term temperature changes with the thermodynamic model of MST (§1.2.), it becomes possible to

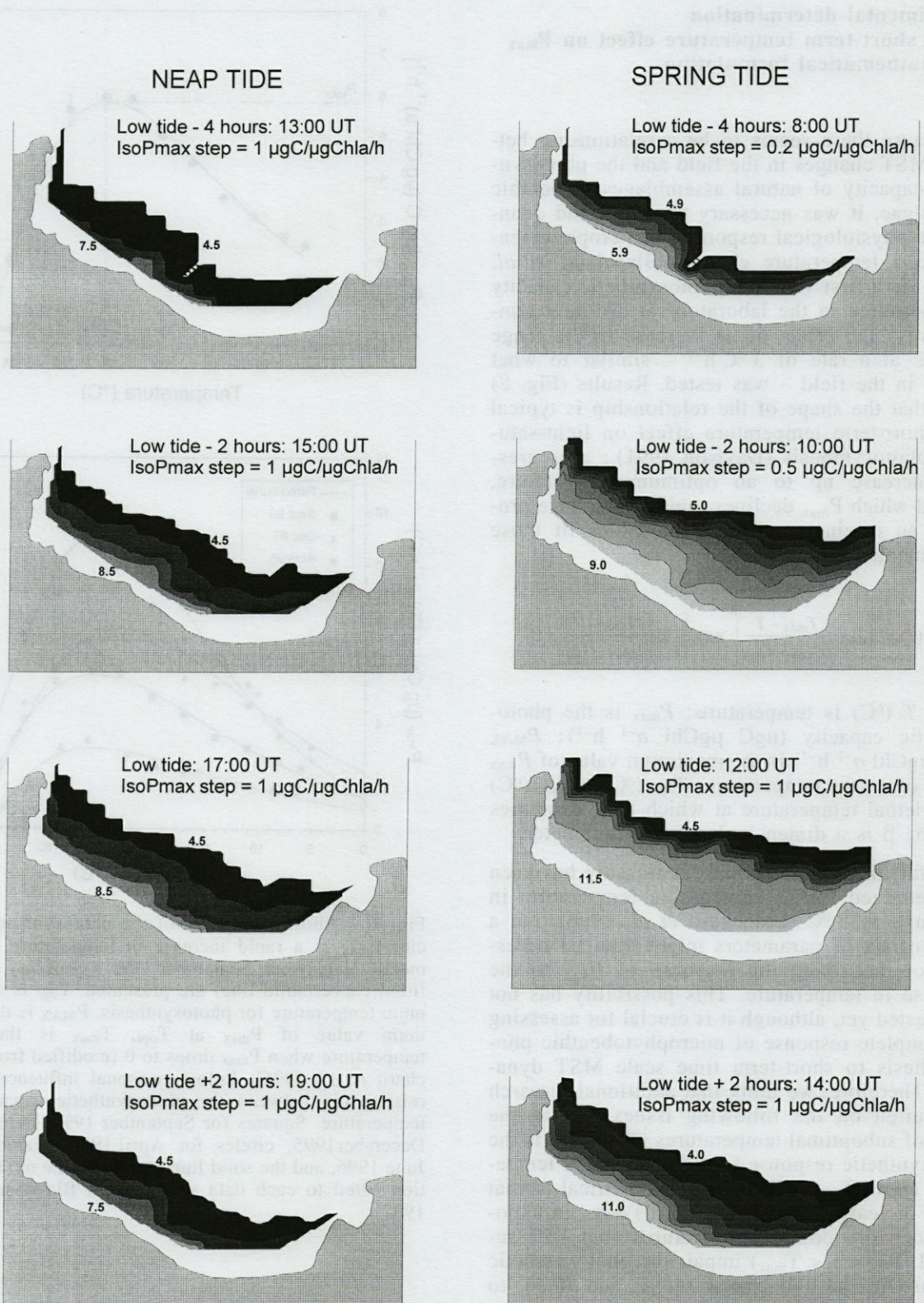


Fig. 9. – Simulation of the spatio-temporal dynamics of P_{\max} in April 1996 at spring tide (left-hand side) and neap tide (right-hand side). Spatialized series are provided at 4 different times during a diurnal emersion period : at low tide - 4 h, at low tide - 2 h, at low tide and at low tide + 2 h. The iso- P_{\max} steps are also provided (modified from Guarini *et al.* 1997).

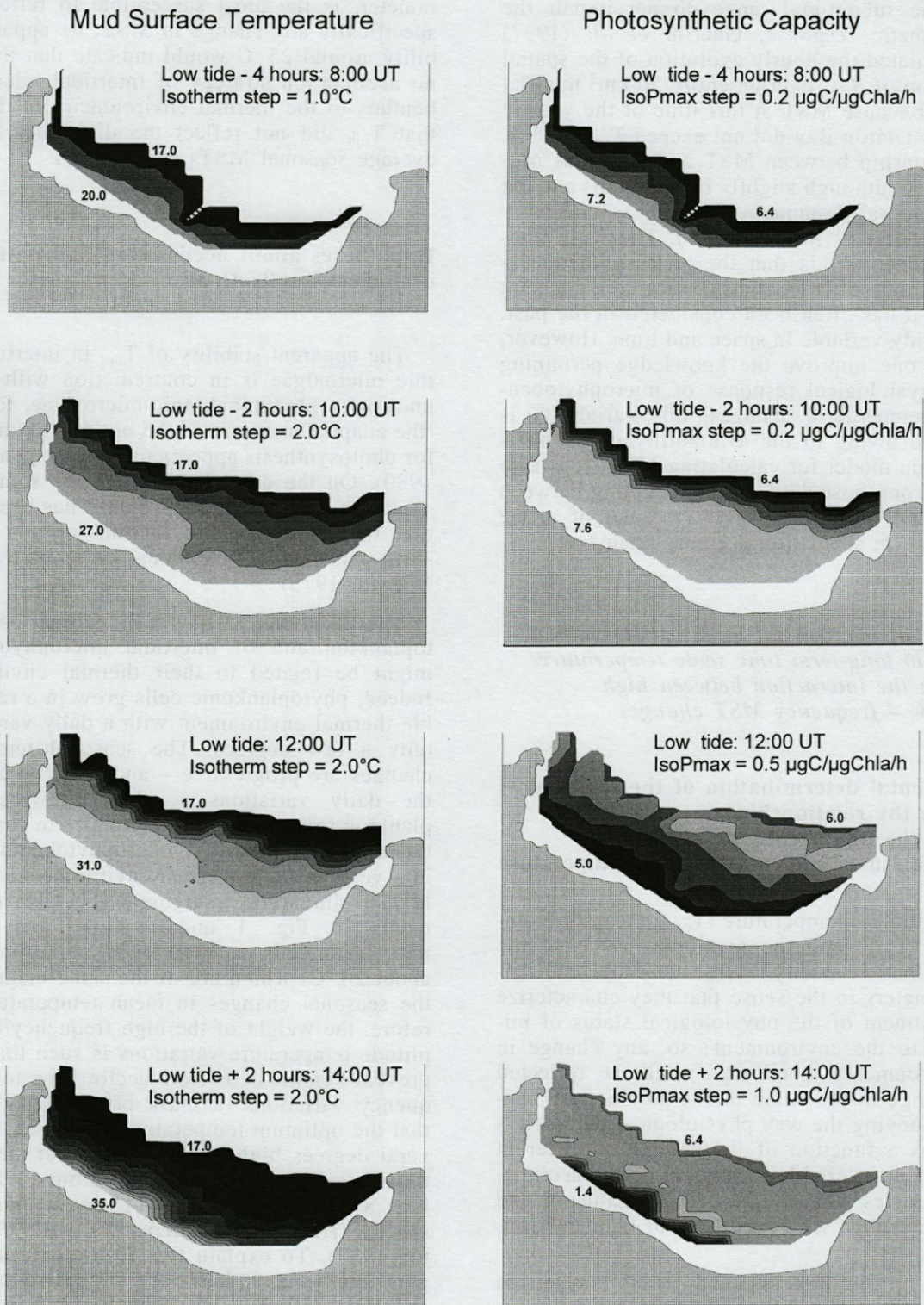


Fig. 10. - Simulation of the spatio-temporal dynamics of MST (left-hand side) and P_{max} (right-hand side) in June 1996, spring tide (from Guarini *et al.* 1997).

analyse the spatio-temporal dynamics of microphytobenthic P_{\max} at the scale of a whole mudflat. For instance, assuming that any temperature changes in the suboptimal range do not impair the photosynthetic response, Guarini *et al.* (1997) have simulated the hourly evolution of the spatial distribution of P_{\max} over an entire 50 km² mudflat (Fig. 9). Because MST at this time of the year in Marennes-Oléron Bay did not exceed T_{opt} (25 °C), the relationship between MST and P_{\max} was roughly linear (although slightly exponential) and the spatio-temporal dynamics of P_{\max} was thus very similar to that of MST (Fig. 6). The main conclusion, therefore, is that the photosynthetic capacity of microphytobenthos cannot be a constant value, as it has often been considered in the past, but is highly variable in space and time. However, provided one improve the knowledge pertaining to the physiological response of microphytobenthos to temperature changes, this variability is predictable owing to the availability of the thermodynamic model for calculating MST. It is also obvious from those data that the coupling between physics and biology is very tight and of prime importance in such littoral environments.

Response of microphytobenthos photosynthetic capacity to long-term time scale temperature changes : the interaction between high – and low – frequency MST changes

Experimental determination of the seasonal effect on the relationship between the photosynthetic capacity of intertidal microphytobenthos and temperature

The optimum temperature (T_{opt}), the lethal temperature (T_{max}) and the maximum value of the photosynthetic capacity (P_{MAX}) are ecophysiological parameters in the sense that they characterize the adjustment of the physiological status of microalgae to the environment; so, any change in the environmental conditions might be reflected by a change in the value of the parameters. Therefore, studying the way physiological parameters change as a function of the change of different environmental variables allows to define acclimation strategies, that is the way organisms and populations cope with variations of their environment.

Based on this principle and on the analysis of the simulation of whole-year temperature variations (Fig. 5), we have measured the response of microphytobenthic P_{\max} to a rapid increase in temperature (such as in Fig. 8, above) at the 4 different seasons (Blanchard *et al.* 1997). Results (Fig. 8, below) show that the photosynthetic response changed between seasons, but the only pa-

rameter which changed significantly was the maximum value of P_{\max} ; T_{opt} and T_{max} did not change throughout the year. Since T_{opt} , as a parameter, is the most susceptible to reflect more specifically any change in MST, its apparent stability around 25 °C would indicate that there was no acclimation strategy of intertidal microphytobenthos to the thermal environment, in the sense that T_{opt} did not reflect the difference between average seasonal MSTs (see Fig. 5).

Hypotheses about acclimation and potential ecological implications

The apparent stability of T_{opt} in intertidal benthic microalgae is in contradiction with what is known for phytoplanktonic microalgae, for which 'the adaptive nature of the optimum temperature for photosynthesis appears to be quite general' (Li 1980). On the other hand, there are some analogies with macroalgae for which it has been shown that the photosynthetic thermal optima did not shift seasonally (Yokohama 1972, Mathieson & Norwall 1975).

The difference in seasonal acclimation of phytoplankton and of intertidal microphytobenthos might be related to their thermal environment. Indeed, phytoplanktonic cells grow in a rather stable thermal environment with a daily variation of only a few degrees. The seasonal temperature changes are progressive – and large compared to the daily variations –, thus allowing phytoplankton to acclimate to the long-term change. On the opposite, intertidal microphytobenthos grow in a very unstable thermal environment; the whole-year simulation in figure 8 (but also measurements in Fig. 1 and 2) shows that benthic microalgal cells undergo daily variations (up to about 20 °C) which are of the same magnitude as the seasonal changes in mean temperature. Therefore, the weight of the high frequency/high amplitude temperature variations is such that it may prevent benthic cells from acclimating to low frequency variations (a mask effect): the result is that the optimum temperature ($T_{\text{opt}} = 25$ °C) is several degrees higher than the highest mean monthly seawater temperature (around 18-19 °C, Fig. 8), like in the case of several macroalgal species (Healey 1972, Mizusawa *et al.* 1978, Bolton 1983). To explain this feature of macroalgal photosynthesis, it has been suggested by Zupan and West (1990) – based on Berry & Bjorkman' review (1980) on higher plants – that the energy expenditure required for lowering the photosynthetic temperature optimum to a relatively low growth temperature may not be compensated by the increase in photosynthetic rate at that lower temperature.

The apparent stability of T_{opt} has important ecological implications. The whole-year simulation of MST (Fig. 5) clearly points out that MST exceeds T_{opt} ($T > 25\text{ }^{\circ}\text{C}$) during diurnal emersion periods in spring tide conditions in the summer time at the highest levels on a mudflat. This implies that microphytobenthic photosynthesis is potentially thermo-inhibited during these periods. To account for the spatial extend of this thermo-inhibition, we provide a simulation of MST and P_{max} over an entire mudflat in Marennes-Oléron Bay, at different times of low tide in spring tide conditions in June 1996 (Fig. 10). MST exceeds T_{opt} in the highest part of the mudflat 2 hours before low tide and reaches $35\text{ }^{\circ}\text{C}$ two hours after low tide. As a consequence, P_{MAX} (the maximum value of P_{max} at $T_{opt} = 25\text{ }^{\circ}\text{C}$) is achieved rapidly at the beginning of low tide; afterwards, the supraoptimal MSTs on the major part of the surface area induce thermo-inhibition of photosynthesis, with extreme values at high levels on the flat in the second half of the emersion period: the higher the topographic level – and hence the emersion duration – the stronger the inhibition. At the time of maximum inhibition, about 75% of the surface area is expected to be inhibited with a photosynthetic rate being reduced down to 30% of its optimal value. Therefore, by comparing with a Spring situation where no thermo-inhibition occurs ($MST < T_{opt}$), the spatial pattern of P_{max} distribution is characterized by an inverse gradient with the highest values in the lowest parts of the mudflat, and the lowest values in the highest parts (Fig. 10).

CONCLUSION

On the whole, it seems that the combination between modelling and the use of an ecophysiological approach to analyse the potential effect of a physical variable on a metabolic rate at different scales – in the present case, the effect of temperature on photosynthesis – is very promising. It has already been established that MST dynamics controls intertidal microphytobenthic photosynthesis at a very short-term time scale. In that respect, this finding clearly points out that the dynamics of the primary production system of intertidal microphytobenthos differs from that of phytoplankton where the control by temperature occurs at longer time scales.

However, data accumulated so far on this topic are scarce and only represent the first steps of what should be, in our opinion, a more important and systematic approach. Indeed, many uncertainties remain about the photosynthetic response of intertidal benthic microalgae to temperature dynamics, at the different time scales.

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