

# Assessment of a brown tide impact on microalgal benthic communities in Baffin Bay (Texas) in 1990 using a primary production simulation model

Microphytobenthos  
Texas Brown Tide  
Primary Production  
Simulation  
Estuary

Microphytobenthos  
Efflorescence algale  
Production Primaire  
Simulation  
Estuaire

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## ABSTRACT

A primary production simulation model was used to assess the effect of a brown tide (Chrysophytes) on benthic microalgal photosynthesis. This model is based on the assumption that photosynthesis of microphytobenthos is primarily determined by irradiance at the sediment-water interface and by the photophysiological response of microalgae to changes of this irradiance. So, irradiance recordings at the sediment-water interface were used as the forcing variable. The simulation indicates that before the introduction of the brown tide, primary production of microphytobenthos was physically controlled. Light levels, hence primary production rates, were very variable ( $<1-132 \text{ mg C m}^{-2} \text{ d}^{-1}$ , CV = 80 %) because wind-induced resuspension generates turbidity within the water column. During the chrysophyte bloom, the mean production rate of microphytobenthos dramatically decreased by two orders of magnitude ( $0.25-1.31 \text{ mg C m}^{-2} \text{ d}^{-1}$ , CV = 46 %) due to shading by the planktonic compartment. Simulations further indicate that the indirect effects of this light reduction (decrease of P-I parameters and biomass) had a higher impact on microphytobenthic production rates than its direct effect (reduction of light energy at the surface of the sediment). As a result, the collapse of microphytobenthic productivity could partially explain the observed decrease of macrofaunal abundance in Baffin Bay, since microphytobenthos is an important food source for benthic invertebrates.

## RÉSUMÉ

Estimation de l'impact d'une efflorescence phytoplanctonique (chrysophytes) sur les communautés de microalgues benthiques (Baffin Bay, Texas) : utilisation d'un modèle de simulation de la production primaire

Un modèle de simulation de la production primaire a été utilisé pour estimer l'effet d'une efflorescence algale (chrysophytes) sur la photosynthèse des microalgues benthiques. Ce modèle suppose que la photosynthèse du microphytobenthos est principalement déterminée par l'intensité lumineuse et par la réponse photosynthétique de ces microalgues aux changements de cette intensité lumineuse. En conséquence, des enregistrements de lumière à l'interface eau-sédiment ont été utilisés comme variable forcante. La simulation met en évi-

dence, avant la « marée brune », que la production primaire microphytobenthique était physiquement contrôlée. L'intensité lumineuse et, par voie de conséquence, le taux de production primaire étaient très variables ( $<1-132 \text{ mg C m}^{-2} \text{ d}^{-1}$ ,  $\text{CV} = 80 \%$ ) à cause d'une forte remise en suspension du sédiment induite par le vent et engendrant une forte turbidité dans la colonne d'eau. Pendant le bloom de chrysophytes, la production moyenne du microphytobenthos a diminué d'un facteur 100 ( $0,25-1,31 \text{ mg C m}^{-2} \text{ d}^{-1}$ ,  $\text{CV} = 46 \%$ ) suite au phénomène d'ombrage provoqué par le compartiment phytoplanctonique. En outre, les simulations indiquent que les effets indirects de cette réduction de lumière (diminution des paramètres P-I et de la biomasse) ont sur la production primaire un impact supérieur aux effets directs (baisse de la quantité de lumière à la surface du sédiment). Il découle de ces simulations que l'effondrement de la productivité microphytobenthique pourrait expliquer en partie la baisse de l'abondance macrofaunique dans Baffin Bay car le microphytobenthos est une importante source de nourriture pour les invertébrés benthiques.

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## INTRODUCTION

A large, persistent bloom of an unknown chrysophyte species began in June 1990 in the tertiary bays of Baffin Bay, Texas. The bloom was characterized as a brown tide. The chrysophyte causing the bloom is both similar to and different from *Aureococcus anophagefferens* and *Pelagococcus subviridis*, and is probably a new species (Stockwell *et al.*, 1993). The alga, a Type III chrysophyte, 4-5  $\mu\text{m}$  in diameter, was very abundant during the monospecific bloom, reaching densities of  $2 \cdot 10^6 \text{ cells ml}^{-1}$ , with chlorophyll concentrations as high as  $80 \mu\text{g l}^{-1}$ . Brown tides in other areas of the world have had dramatic effects, particularly on benthic organisms (Shumway, 1990). In Texas, there was a decrease in mesozooplankton (Buskey and Stockwell, 1993), fish larvae (Scott Holt, pers. comm.) and benthic abundance and diversity (Montagna and Kalke, in preparation), while bivalves practically disappeared for a two-year period (Montagna *et al.*, 1993).

The high densities of the Texas brown tide alga caused dramatic reductions in the amount of light reaching the bottom. In 1990, light levels at the sediment-water interface were only 20 % as high as they had been prior to the brown tide (Dunton, pers. comm.). This caused great concern with regard to the potential impact on the luxurious seagrass beds in Laguna Madre. Moreover, the drop in light levels caused a significant decrease in the photophysiological parameters (the photosynthetic efficiency  $\alpha^B$  and the photosynthetic capacity  $P_m^B$ ) of microphytobenthos in the usually turbid Baffin Bay, where seagrass beds are absent (Blanchard and Montagna, 1992). Microphytobenthos is an important food source for benthic meiofauna (Montagna, 1984; Plante-Cuny and Plante, 1986; Montagna and Yoon, 1991) and macrofauna (Pace *et al.*, 1979; Plante-Cuny and Plante, 1986) and possibly even for zooplankton in early spring (de Jonge and van Beusekom, 1992). If the brown tide caused a decrease in light levels that could inhibit primary production by microphytobenthos, then benthos could become food-limited during the

peak of a phytoplankton bloom. Loss of microphytobenthic production could thus explain, at least partially, the loss of macrobenthic productivity that is associated with the brown tide, even though many macrofauna species are able to change from deposit-feeding to filter-feeding.

Unfortunately, actual measurements of benthic primary production could not be planned either before or during the brown tide, because such an event is unpredictable. Although it is intuitively easy to conceive a decrease in microphytobenthos production, it is nevertheless necessary to quantify this decrease and to assess to what extent the brown tide was responsible. For that purpose we used a primary production simulation model with the light level measured at the sediment-water interface as the forcing variable, since benthic primary productivity is positively correlated with irradiance (Van Raalte *et al.*, 1976; Colijn, 1982; Whitney and Darley, 1983; Sundbäck and Granéli, 1988). The model is based on the assumption that photosynthesis is primarily determined by irradiance and by the photophysiological response of microalgae to changes of this irradiance (Blanchard and Montagna, 1992). Furthermore, the model also takes into account the light attenuation within the sediment, so that only the photosynthetically active chlorophyll contributes to total production. Photosynthetic rates were determined using Photosynthesis-Irradiance curves calculated in a previous study (Blanchard and Montagna, 1992). This simulation of microphytobenthic primary production in Baffin Bay was performed during two different 20-day periods: the first in May 1990 before the beginning of the brown tide and the second in June-July 1990 following its development. The aim of the model was threefold: (i) to simulate the daily production based on reasonable assumptions; (ii) to test the effect of different light attenuation coefficients in the sediment on these production rates; and (iii) to separate the respective effects of the decrease in light levels, P-I parameters and Chl *a* content of the sediment on microphytobenthos production.

## MATERIAL AND METHODS

The study was conducted at a subtidal site (2.4 m deep) in the hypersaline Baffin Bay, Texas (97°26' W, 27°18' N) (Fig. 1). The sediment composition of the upper 3 cm was: 7 % rubble (>2000  $\mu\text{m}$ ); 4 % sand (62.5-2000  $\mu\text{m}$ ); 34 % silt (3.9-62.5  $\mu\text{m}$ ); and 55 % clay (< 3.9  $\mu\text{m}$ ). Turbidity of the water column is usually variable: from ~ 10 to ~ 60 NTU (Hach photometer), which represents 0.46 to 2.36  $\text{g l}^{-1}$  of suspended sediment.

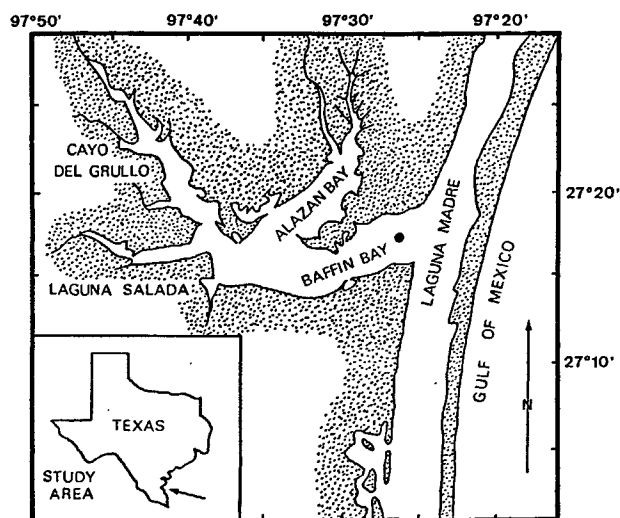


Figure 1

Baffin Bay, Texas. (•) indicates the study site (97°26' W, 27°18' N), and the insert map locates the study area on the Texas coast.

Baffin Bay, Texas. (•) indique le site de l'étude (97°26' W, 27°18' N) et l'encart positionne la zone d'étude le long de la côte texane.

Photosynthetic Active Radiation (PAR, 400-700 nm) was continually recorded with a LI-1000 DataLogger (LI-COR Inc., Lincoln, Nebraska) connected to a LI-193SA spherical ( $4\pi$ ) quantum sensor ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) at the sediment-water interface. Light measurements were averaged over one-hour intervals throughout the day during two 20-day periods: 12-31 May and 15 June - 4 July 1990. The irradiance regime was dramatically different between these

periods because the brown tide (chrysophytes) bloom appeared in June (Fig. 2). In May, incident irradiance was up to 578  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , with very large variability of the maximum daily irradiances, while it never exceeded 68  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in July.

Light attenuation is highly variable in sediments and exhibits an inverse relationship with the grain size. For example, Fenchel and Straarup (1971) measured an attenuation coefficient ( $K_z$ ) of 1.06  $\text{mm}^{-1}$  for white light in a bleached and rinsed sand, while Haardt and Nielsen (1980) observed values from 1.9  $\text{mm}^{-1}$  for sand to 12.2  $\text{mm}^{-1}$  for mud. Colijn (1982) detected an even wider range (ca. 2-33  $\text{mm}^{-1}$ ) for a variety of sediments. We did not measure  $K_z$  in the present study; but we used a range of values ( $K_z = 8$  to 16  $\text{mm}^{-1}$ ), taken from the literature and representative of muddy sediments (see references above), to test the sensibility of this parameter on the simulation of benthic primary production. In addition, we used  $K_z = 12 \text{ mm}^{-1}$  (as representative of mud; Haardt and Nielsen, 1980) to test the sensibility of the other parameters (Chl *a* content of the sediment, the light level, P-I parameters).

We used the Photosynthesis-Irradiance curves as determined by Blanchard and Montagna (1992) using the photoinhibition equation of Platt *et al.* (1980). As the P-I parameters were measured at different times of day, we calculated the averaged value over that day: on 8 May (just before the selected period in May) and on 7 July 1990 (just after the selected period in June); they are reported in Table 1. Concerning the P-I parameters from July, they probably reflect a mixed photosynthetic response of microphytobenthos and sedimented planktonic cells.

Chl *a*, as an index of microphytobenthic biomass, was measured fluorometrically (Lorenzen, 1966). Five sediment cores of 3.8  $\text{cm}^2$  were sampled once in May and once in July. Chl *a* from the top 5 mm was extracted in 90 % acetone for 24 h in the dark. Although Chl *a* is present at depths to several cm (Steele and Baird, 1968; Fielding *et al.*, 1988; Delgado, 1989; Cariou-Le Gall and Blanchard, 1994; De Jonge and Colijn, 1994), the strong attenuation of light in mud suggests that only Chl *a* in the top mm of the sediment is receiving enough light to be photosynthetic.

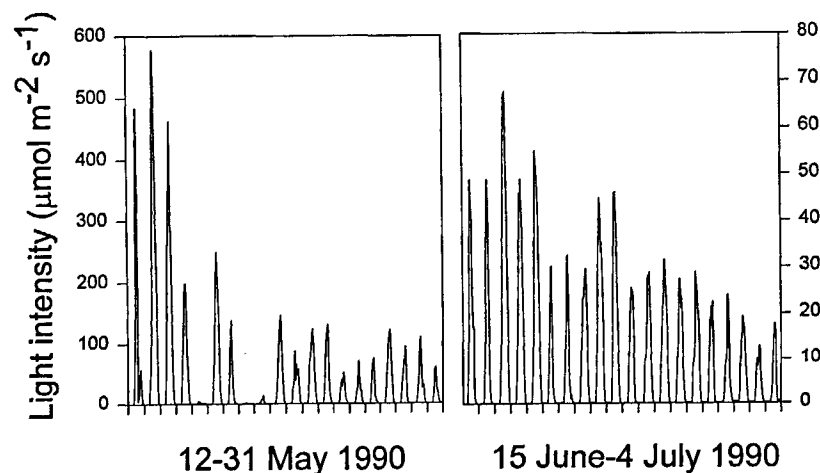


Figure 2

Light measurements ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) at the sediment-water interface during the two 20-day periods: 12-31 May and 15 June-4 July 1990. PAR was continually recorded and averaged over 1-hour intervals.

Mesure de la lumière à l'interface eau-sédiment pendant les deux périodes de 20 jours : 12-31 mai et 15 juin-4 juillet 1990. L'intensité lumineuse (PAR) a été enregistrée en continu et moyennée sur des périodes d'une heure.

Table 1

*P-I* parameters used to calculate benthic primary production rates from light intensity recorded at the sediment-water interface. These parameters are from the equation of Platt *et al.* (1980) and are the mean of data from Table 1 in Blanchard and Montagna (1992).  $P_s^B$  (mg C mg Chl  $a^{-1} h^{-1}$ ) is the maximum photosynthetic rate in the absence of photoinhibition and numerically equals  $P_{max}^B$  (mg C mg Chl  $a^{-1} h^{-1}$ ) when  $\beta^B$  is zero,  $\alpha^B$  (mg C mg Chl  $a^{-1} h^{-1} (\mu\text{mol } m^{-2} s^{-1})^{-1}$ ) is the photosynthetic efficiency corresponding to the initial linear part of the *P-I* curve, and  $\beta^B$  (mg C mg Chl  $a^{-1} h^{-1} (\mu\text{mol } m^{-2} s^{-1})^{-1}$ ) is the parameter describing photoinhibition. Superscript  $B$  indicates that *P-I* parameters are normalized to Chl *a* (mg C  $m^{-2} 5 \text{ mm}^{-1}$ ).

Paramètres *P-I* utilisés pour calculer les taux de production primaire benthique à partir de l'intensité lumineuse enregistrée à l'interface eau-sédiment. Ces paramètres sont issus de l'équation de Platt *et al.* (1980) et représentent la moyenne des données du tableau 1 dans Blanchard et Montagna (1992).  $P_s^B$  (mg C mg Chl  $a^{-1} h^{-1}$ ) est le taux de photosynthèse maximal en l'absence de photoinhibition et équivaut à  $P_{max}^B$  (mg C mg Chl  $a^{-1} h^{-1}$ ) quand  $\beta^B$  est égal à zéro,  $\alpha^B$  (mg C mg Chl  $a^{-1} h^{-1} (\mu\text{mol } m^{-2} s^{-1})^{-1}$ ) est l'efficacité photosynthétique correspondant à la partie initiale linéaire de la courbe *P-I* et  $\beta^B$  (mg C mg Chl  $a^{-1} h^{-1} (\mu\text{mol } m^{-2} s^{-1})^{-1}$ ) est le paramètre décrivant la photoinhibition. L'exposant  $B$  indique que les paramètres *P-I* sont standardisés par la Chl *a* (mg C  $m^{-2} 5 \text{ mm}^{-1}$ ).

<i>P-I</i> Parameters	12-31 May	15 June-4 July
$P_s^B$	15.54	3.69
$\alpha^B$	0.019	0.017
$\beta^B$	$4.27 \cdot 10^{-3}$	$6.88 \cdot 10^{-4}$
$P_{max}^B$ *	13.15	3.10
Chl <i>a</i>	35.50	9.75

$$*P_{max}^B = P_s^B \cdot (\alpha^B / (\beta^B + \alpha^B)) \cdot (\beta^B / (\alpha^B + \beta^B))^{(\beta^B / \alpha^B)}$$

Primary production rates ( $P_z$ ) at depth *z* were calculated with the equation of Platt *et al.* (1980) using irradiance data ( $I_z$ ) at that depth, *P-I* parameters and Chl *a* concentration (Tab. 1):

$$P_z = [P_s^B \cdot [1 - \exp(-\alpha^B I_z / P_s^B)]] \cdot \exp(-\beta^B I_z / P_s^B) \cdot \text{Chl } a \quad (1)$$

with

$$I_z = I_0 \cdot \exp(-K_z \cdot z) \quad (2)$$

in which  $P_z$  = primary production rate (mg C  $m^{-2} h^{-1}$ ) at depth *z* (mm) and at light intensity at depth *z*  $I_z$  ( $\mu\text{mol } m^{-2} s^{-1}$ ), while  $I_0$  is the light intensity at the surface of the sediment,  $P_s^B$  is the maximum photosynthetic rate in the absence of photoinhibition (mg C mg Chl  $a^{-1} h^{-1}$ ),  $\alpha^B$  is the photosynthetic efficiency (the slope of the linear part of the *P vs. I* curve) (mg C mg Chl  $a^{-1} h^{-1} (\mu\text{mol } m^{-2} s^{-1})^{-1}$ ),  $\beta^B$  is the photoinhibition parameter (mg C mg Chl  $a^{-1} h^{-1} (\mu\text{mol } m^{-2} s^{-1})^{-1}$ ), and Chl *a* (mg  $m^{-2} 50 \mu\text{m}^{-1}$ ).

As primary production was simulated over the full photic zone,  $I_z$  and  $P_z$  were calculated (equations 2 and 1, respectively) every 50  $\mu\text{m}$  from the sediment surface down to 500  $\mu\text{m}$  (to obtain a series of linear segments along the exponential attenuation of light in the sediment), this depth corresponding to the photic zone. A trapezoidal integration was performed on each sediment layer before being sum-

med to give the hourly production ( $P_{zh}$ ), and daily rates ( $P_{zd}$ ) were obtained by summation of these hourly rates:

$$P_{zh} = \sum_{i=0}^{i=10} [(P_{zi,50\mu\text{m}} + P_{(zi+1),50\mu\text{m}}) / 2] \quad (3)$$

$$P_{zd} = \sum P_{zh} \quad (4)$$

This production simulation model is based on several reasonable assumptions, namely: (i) that *P-I* parameters (obtained at different times of single days) were representative of the two simulated periods because the light levels recorded during those sampling days encompassed the light levels recorded during the whole simulated periods; (ii) that *P-I* parameters were estimated on the first 5 mm, and that they are homogeneous in this layer. (This assumption is realistic since Blanchard and Cariou-Le Gall (1994) show no difference in *P-I* parameters between the top 2.5 mm and the underlying aphotic 2.5 mm on an intertidal mudflat. Gargas (1971) also observed no change in the

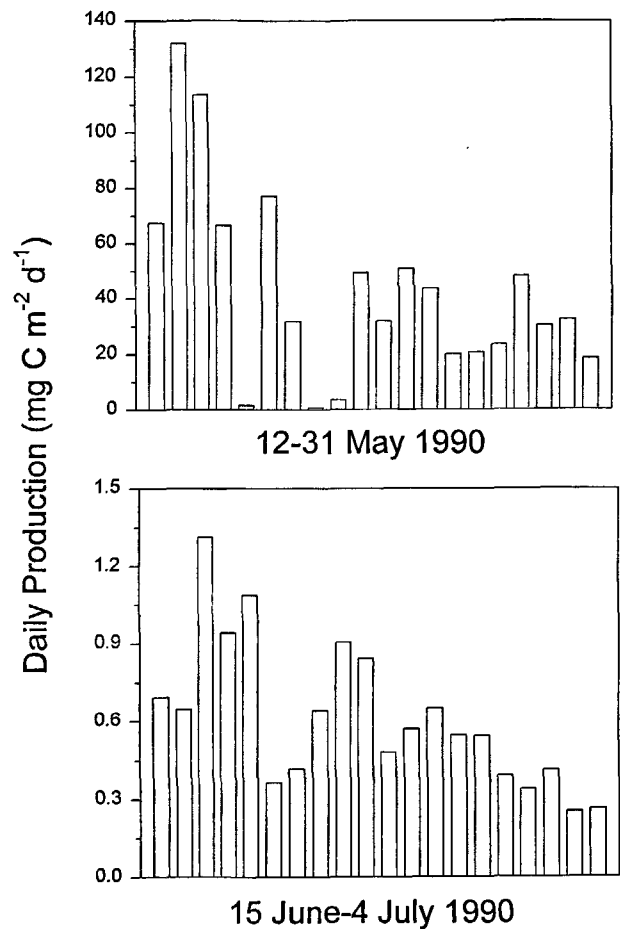


Figure 3

Simulated daily production rates of microphytobenthos (mg C  $m^{-2} d^{-1}$ ), with a light attenuation coefficient  $K_z = 12 \text{ mm}^{-1}$ , for the two 20-day periods: 12-31 May and 15 June-4 July 1990.

Simulation du taux de production journalière du microphytobenthos (mg C  $m^{-2} d^{-1}$ ), avec un coefficient d'atténuation lumineuse  $K_z = 12 \text{ mm}^{-1}$ , pour les deux périodes de 20 jours : 12-31 mai et 15 juin-4 juillet 1990.

state of microphytobenthos photoacclimation between surface and deeper sediment layers because of homogenization by resuspension). (iii) that Chl *a* is homogeneously distributed within the photic zone of the sediment (which is very thin, *ca.* 500  $\mu\text{m}$ ). (There is indeed a constant mixing of the superficial sediment due to resuspension and bioturbation); and (iv) that  $K_z$  was constant throughout the photic zone of the sediment.

## RESULTS AND DISCUSSION

According to the simulation using a light attenuation coefficient for mud ( $K_z = 12 \text{ mm}^{-1}$ ) in May (fig. 3), the averaged daily production rate was  $43.17 \text{ mg C m}^{-2} \text{ d}^{-1}$ . This is low in comparison with previous estimates reported in the literature (Pomeroy *et al.*, 1981; Colijn and De Jonge, 1984; Knox, 1986; McLusky, 1989), mainly because our site was subtidal and subjected to sediment resuspension which strongly reduces the quantity of light reaching the sediment-water interface. The attenuation of light within the sediment was also strong since it was a muddy site (Fig. 4); the photic zone was less than 500  $\mu\text{m}$  with  $K_z = 12 \text{ mm}^{-1}$ . As this choice of  $K_z$  was somewhat arbitra-

ry, albeit based on published results, we have tested the effect of this coefficient (in the range  $8\text{-}16 \text{ mm}^{-1}$ ) on the averaged daily production rate (Fig. 4). It increases up to  $63.07 \text{ mg C m}^{-2} \text{ d}^{-1}$  (46 % increase) and decreases down to  $32.73 \text{ mg C m}^{-2} \text{ d}^{-1}$  (24 % decrease) with attenuation coefficients of 8 and  $16 \text{ mm}^{-1}$ , respectively. This sensitivity analysis indicates that the value of  $K_z$ , hence the grain size, has a significant influence on the production rates. It is therefore very important to have an accurate estimate of  $K_z$  when the establishment of a carbon budget is necessary; otherwise, there is a risk of over- or underestimating microphytobenthic production. On the other hand,  $K_z$  does not affect the variability of production rates and their comparison from the same site between two different periods, provided the grain size remains unchanged. In May, the range of production rates was very large ( $<1\text{-}132 \text{ mg C m}^{-2} \text{ d}^{-1}$ , CV = 80 %) because the simulations were directly influenced by the availability of light at the sediment-water interface. In Baffin Bay, light energy, and consequently primary production, were primarily controlled by wind-induced resuspension. In this shallow subtidal area, resuspension events are likely to decrease microphytobenthic production by displacing sediment and microalgal biomass into the water column and reducing the availability of light at the sediment-water interface.

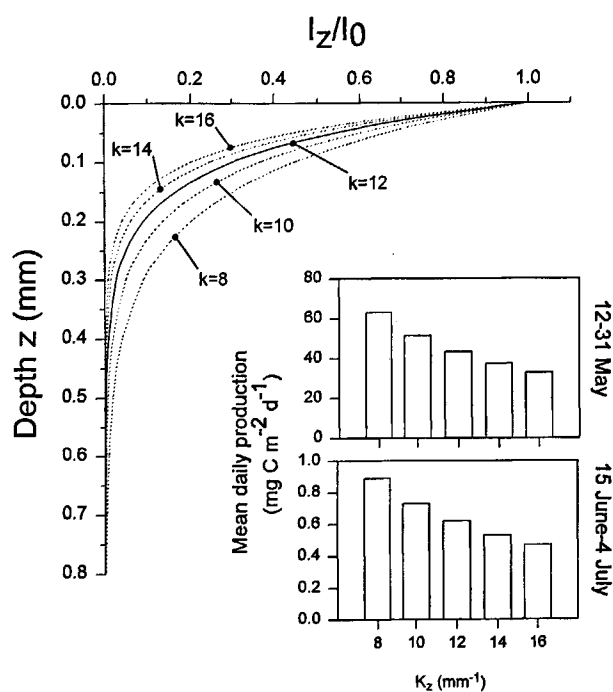


Figure 4

Light attenuation in the sediment.  $I_z/I_0$  is the proportion of the incident light at the sediment-water interface ( $I_0$ ) present at depth  $z$  ( $I_z$ ) as a function of depth (mm) for different light attenuation coefficients (in the range  $8\text{-}16 \text{ mm}^{-1}$ ). Bar diagrams show the mean daily production ( $\text{mg C m}^{-2} \text{ d}^{-1}$ ) as a function of  $K_z$  ( $\text{mm}^{-1}$ ) for the two 20-day periods: 12-31 May and 15 June-4 July 1990.

Atténuation lumineuse dans le sédiment.  $I_z/I_0$  est la proportion de lumière incidente à l'interface eau-sédiment ( $I_0$ ) présente à la profondeur  $z$  ( $I_z$ ) en fonction de la profondeur (mm) pour différents coefficients d'atténuation lumineuse (dans la gamme  $8\text{-}16 \text{ mm}^{-1}$ ). Les diagrammes en barres montrent la production journalière moyenne ( $\text{mg C m}^{-2} \text{ d}^{-1}$ ) en fonction de  $K_z$  ( $\text{mm}^{-1}$ ) pour les deux périodes de 20 jours : 12-31 mai et 15 juin-4 juillet 1990.

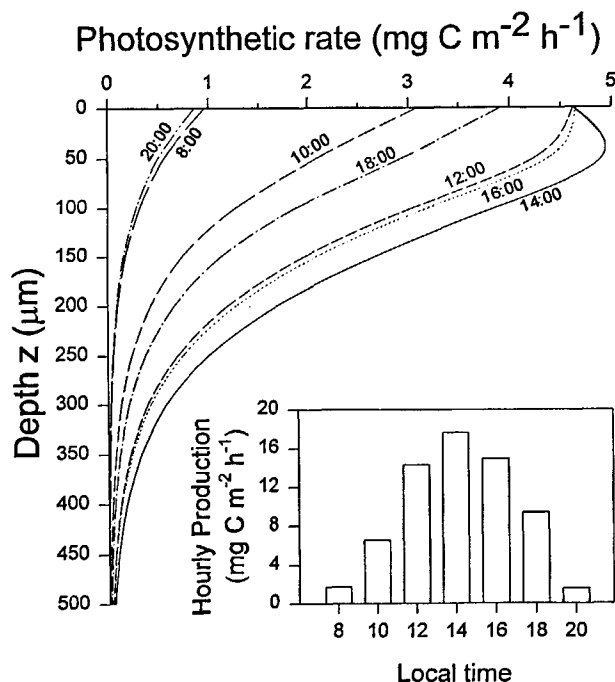


Figure 5

Simulated hourly primary production rates ( $\text{mg C m}^{-2} \text{ h}^{-1}$ ) as a function of depth  $z$  ( $\mu\text{m}$ ) at different times of day (13 May 1990, as an example) with a light attenuation coefficient  $K_z = 12 \text{ mm}^{-1}$ . Bar diagram shows the hourly production integrated over the full photic zone at different times of the day.

Simulation du taux de production horaire ( $\text{mg C m}^{-2} \text{ h}^{-1}$ ) en fonction de la profondeur  $z$  ( $\mu\text{m}$ ) à différentes heures de la journée (par exemple, le 13 mai 1990) avec un coefficient d'atténuation lumineuse  $K_z = 12 \text{ mm}^{-1}$ . Le diagramme en barres montre la production horaire intégrée sur toute la zone photique à différentes heures de la journée.

In contrast, the production pattern was less variable in the June-July period (in the range 0.25-1.31 mg C m<sup>-2</sup> d<sup>-1</sup>, CV = 46 %), and the average rate was very low (0.62 mg C m<sup>-2</sup> d<sup>-1</sup>). This dramatic change, due to the chrysophyte bloom, appeared in June 1990 in lower Baffin Bay and upper Laguna Madre (Texas). The enhanced planktonic biomass and production strongly reduced the penetration of light to the bottom, and subsequently decreased sediment production rates. Integrated Chl *a* concentration in the water column increased from 19.68 µg m<sup>-2</sup> in May to 83.49 µg m<sup>-2</sup> in July, and daily integrated phytoplanktonic primary production from 2.29 g C m<sup>-2</sup> d<sup>-1</sup> in April to 6.93 g C m<sup>-2</sup> d<sup>-1</sup> in July (Stockwell, unpubl.). This seems to indicate that light levels at the sediment-water interface and benthic primary production were mainly controlled by shading induced by the plankton bloom. Meanwhile, chlorophyll concentration in the sediment decreased from 35.50 ± 1.73 mg Chl *a* m<sup>-2</sup> 5 mm<sup>-1</sup> in May to 9.62 ± 0.87 mg Chl *a* m<sup>-2</sup> 5 mm<sup>-1</sup> in June, probably because of grazing by benthic invertebrates which was no longer balanced by production.

According to the simulations ( $K_z = 12 \text{ mm}^{-1}$ ), the hourly primary production rate integrated over the full photic zone of the sediment on 13 May 1990 (fig. 5) was the highest at midday (14:00 local time), reaching 17.64 mg C m<sup>-2</sup> h<sup>-1</sup>. The model even predicts a photoinhibition effect in the top 50 µm of the sediment at midday, which is the consequence of the parameter  $\beta^B$  in the equation of Platt *et al.* (1980), even if its value was very low (Tab. 1). As a result, the model seems to be very sensitive to this potential photoinhibitory effect, accurate measurement of which requires additional work. A recent study (Blanchard and Cariou-Le Gall, 1994) has indeed shown that intertidal microphytobenthos probably does not experience photoinhibition *in situ*, but is sensitive to it in artificial conditions.

As the decrease of benthic primary production is due to several factors (light, P-I parameters, Chl *a* content of the

Table 2

*Benthic primary production simulation as a function of different parameter sets for Chl a, light and P-I parameters (see Tab. 1 and Fig. 2). M represents the value for the 12-31 May period and J the value for the 15 June-4 July period. The daily mean (mg C m<sup>-2</sup> d<sup>-1</sup>) is reported for each simulation as well as the percentage of decrease from May to June due to a specified parameter.*

Simulation de la production primaire benthique en fonction des différentes séries de paramètres pour la Chl *a*, l'intensité lumineuse et les paramètres P-I (voir Fig. 2). M représente la valeur d'un paramètre pour la période du 12-31 mai et J la valeur pour celle du 15 juin-4 juillet. La moyenne journalière (mg C m<sup>-2</sup> d<sup>-1</sup>) est reportée pour chaque simulation ainsi que le pourcentage de décroissance entre mai et juin, dû à un facteur particulier.

Benthic primary production simulations					
	M	M	J	M	J
Chl <i>a</i>	M	M	J	M	J
Light	M	J	M	M	J
P-I parameters	M	M	M	J	J
<b>Daily mean</b> (mg C m <sup>-2</sup> d <sup>-1</sup> )	<b>43.17</b>	<b>14.42</b>	<b>11.86</b>	<b>7.20</b>	<b>0.62</b>
%	<b>0</b>	<b>68</b>	<b>74</b>	<b>85</b>	<b>100</b>

sediment), Table 2 presents the result of different simulations which assess their respective effects. The mean daily production rate has been calculated with the different parameters from May; then, we have simulated what would have been the mean daily rate if only one of these parameters was replaced by its June value. The consecutive decrease has also been expressed as a percentage of the difference between the May and June simulations. It turns out (Tab. 2) that the decrease of the P-I parameters from May to June had the highest impact on the decrease of the mean daily production rate (85 %), while the effect of biomass alone was also important (74 %), and that of light was the lowest (68 %). Consequently, these simulations indicate not only that the direct effect of the decrease in light intensity is not sufficient to explain the total decrease in production rates, but also that this is not the main effect. Instead - as light, P-I parameters and biomass are not independent - there was in all likelihood an indirect effect of the decrease of light on the decrease of P-I parameters and biomass which, in turn, greatly affected production rates. From a practical standpoint, this implies that more attention should be paid to the measurement of P-I parameters and biomass, since the model seems to be very sensitive to them and because we already have a very good temporal resolution in the measurement of light levels at the sediment-water interface. Furthermore, we worked with daily averaged P-I parameters although we know that they are variable at an hourly scale (Blanchard and Montagna, 1992; Blanchard and Cariou-Le Gall, 1994) but no clear pattern of variation as yet exists that can be included in the calculations. It is clear, however, that these short-term variations of microphytobenthos P-I parameters will have to be taken into account in the future refinement of our simulations.

Temperature was not included in the model because, unlike light, it was not continuously recorded *in situ*. However, temperature explained only a minor part of  $\alpha^B$  and  $P_s^B$  variability (8 % and 2 %, respectively; Blanchard and Montagna, 1992), but might be expected to have a more important role where and/or when temperature changes are more pronounced.

In conclusion, the results of this modelling exercise are in agreement with what we would have intuitively imagined, namely a decrease of the mean daily production due to the brown tide. However, what would not have been thrown into relief without this modelling is the predominance of the indirect effects of light (decrease in P-I parameters and biomass) on the collapse in microphytobenthos production. Moreover, by enhancing the importance of the benthic P-I parameters, the model indicates the need for a complete understanding of the different scales of variability in these parameters, the objective being to integrate the pattern of variation in a more complete model. Finally, to achieve more accurate estimates on long-term simulations and on different sites, it would appear necessary to increase the temporal resolution in the measurement of biomass and to estimate with precision the attenuation of light within the different sediments. Concerning light measurements, Kühl *et al.* (1994) have shown that the classical measurement of downwelling photon irradiance can underestimate the total light intensity available for microphyto-

benthos because of intense scattering; the light attenuation coefficient has thus to be assessed using scalar irradiance fibre-optic microprobes.

While the short-term variability seemed to be controlled by resuspension, occasional events such as phytoplankton blooms strongly affected benthic production on a medium-term scale in Baffin Bay, resulting in the control of the microphytobenthic compartment by the phytoplanktonic compartment of this estuarine ecosystem. This control takes the form of an inhibition by shading. So, as an alternative to a direct toxic effect, this decrease of the microphytobenthic biomass and production could be a plausible cause of the decrease in the macrofaunal abundance (Mon-

tagna *et al.*, 1993) if the chrysophyte bloom was consumed neither by the filter-feeders, nor by the deposit-feeders after sedimentation.

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