

# Factors controlling primary production and photosynthetic characteristics of intertidal microphytobenthos

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**ABSTRACT:** Microphytobenthic primary production and biomass were studied in an intertidal flat located in the Westerschelde (SW Netherlands) with a vertical resolution of 1 mm. Short-term variability of primary production and photosynthetic characteristics were compared during low tide in 2 types of sediment: sandy and muddy sands. The changes observed were compared with abiotic factors and the biomass abundance, which was dominated by benthic diatoms. <sup>14</sup>C uptake values obtained from incubations in a photosynthetron were used for the construction of P-I (photosynthesis-irradiance) curves. Annual averages indicate that both sediments were equally productive ( $34.5 \pm 23.6 \text{ mg C m}^{-2} \text{ h}^{-1}$  and  $41.1 \pm 11.6 \text{ mg C m}^{-2} \text{ h}^{-1}$  for the sands and muddy sands respectively), but production rates were highly variable on monthly time scales and were regulated by different mechanisms. Light and temperature played an important role in determining the production rates, especially in the muddy sediments, where changes in  $I_k$  (light saturation) were correlated with temperature.  $I_k$  showed seasonal changes, suggesting that algae adapted to the seasonal light conditions but there was not a significant correlation between the  $I_k$  and PAR (photosynthetic available radiation) at any of the stations. Vertical migration of the algae, as followed by spectroradiometric measurements, probably accounted for a general absence of photoinhibition. In the sandy sediments, production appeared to be limited by the low biomass of algae, due to resuspension and export. The fact that gross oxygen production rates measured on intact cores using microelectrodes were not lower than potential production obtained from <sup>14</sup>C fixation suggests that short-term limitation of production due to nutrients and/or carbon is not frequent in the microphytobenthos of the Westerschelde.

**KEY WORDS:** Microphytobenthos · Photosynthetic characteristics · Primary production · Tidal flats

## INTRODUCTION

The importance of benthic microalgae in shallow estuarine systems as oxygen producers, carbon fixers and food sources for grazers is now fully recognised and well documented (Heip et al. 1995 and references therein), but the mechanisms regulating microphytobenthos production on short time scales still need further study (Pinckney & Zingmark 1993).

In intertidal sediments, the microphytobenthos community has to adapt to a series of stressful factors, such as sediment transport, as well as steep gradients in light, temperature and nutrient concentrations. In tur-

bid estuaries, microphytobenthos production will be mainly restricted to the emersion period due to light limitation during flood tide (Colijn 1982). In turbid environments, benthic microalgae can be the principal input of organic matter in tidal flats (MacIntyre et al. 1996 and references therein). In temperate estuaries, microphytobenthic biomass is fairly constant throughout the year. However, the production shows both steep seasonal peaks and large variations on hourly time scales (Barranguet 1997 and references therein). Photoacclimation and vertical migration are some of the mechanisms which might be responsible for these changes in photosynthetic activities.

Blanchard & Cariou-Le Gall (1994) advocated the use of photosynthetic parameters (photosynthetic capacity and maximal photosynthetic efficiency) to

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better understand the mechanisms of adaptation of microphytobenthic algae to changing environmental conditions by photoacclimation.

We aimed to assess the rates of microphytobenthos production in a tidal flat of the Westerschelde (the Molenplaat, SW Netherlands) and the response of microalgal photosynthesis to environmental regulating factors. For that purpose, we used the photosynthetic parameters and production rates calculated from  $^{14}\text{C}$  P-I (photosynthesis-irradiance) curves, and gross oxygen production rates estimated with oxygen micro-electrodes. Both methods have their own advantages and limitations, and they have often been used for determining microphytobenthos production, but seldom simultaneously (Revsbech et al. 1981, Bott et al. 1997). In the Westerschelde estuary, microphytobenthos production rates show variability at seasonal and hourly scales (Kromkamp et al. 1995), and the annual estimate available so far is based on chlorophyll measurements (De Jong & De Jonge 1995), not on actual production measurements. This precludes the construction of accurate organic carbon budgets.

We have chosen to work with 2 sediment types differing in grain size distribution, euphotic zones and tidal energy to gain a better understanding of the factors affecting and limiting intertidal microphytobenthic production.

## MATERIAL AND METHODS

The Westerschelde is a macrotidal estuary located in the SW Netherlands (Fig. 1). Tidal flats occupy an important part of its area (20%), where microphytobenthos represents the main input of organic carbon to the sediments. A diverse assemblage of benthic microalgae also constitutes a large amount of biomass (Sabbe 1997). The composition of the microbenthic *community changes during the year, mainly in relation* to abiotic factors such as nutrient concentration, temperature and grain size (Barranguet et al. 1997). Two stations were sampled monthly: sediments at Stn A have on average 10% silt, 0.07 weight % organic C and are exposed to a high level of tidal energy; Stn B, with a higher percentage of silt (16%) and organic C (0.16 weight %), occupies a more elevated and protected part of the flat (Fig. 1).

PAR (photosynthetic available radiation) was measured during the emersion period with a cosine sensor LI 192 (Q 17079) connected to a Licor Data Logger LI-1000. Data were integrated every 10 min. Spectral reflectance at the sediments surface was measured with a MACAM SR9910 spectroradiometer on sediment cores exposed to an irradiance level of  $800 \mu\text{mol m}^{-2} \text{s}^{-1}$  by means of a Schott KL 1500 light source.

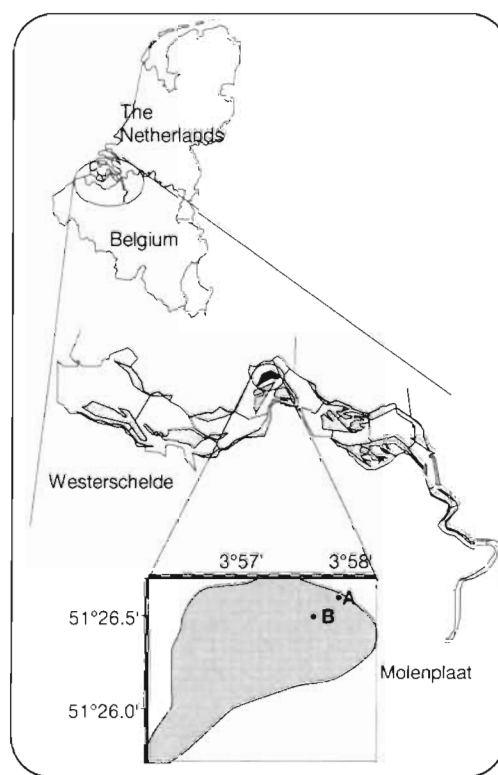


Fig. 1. Study site and location of the stations at the Molenplaat

Temperature was recorded in the field with an RD-Temp Omega temperature data logger at 5 min intervals. Samples were always taken during ebb tide (between 3 and 5 h of emersion) once a month on dates when the minimum water level was around noon. Cores for chlorophyll and production measurements (inner diameter 2.5 cm) were taken 3 times during ebb tide. The sediment was extruded from the core in 1 mm slices with a piston manipulated with a screw, with one whole turn equivalent to 1 mm. The samples for chl *a* were frozen on board until analyses. Pigments were extracted from freeze-dried samples with methanol (95%) buffered with ammonium acetate (5%) and were sonicated for 10 min. Chl *a* was analyzed by HPLC as in Barranguet et al. (1997). The results are expressed in  $\text{mg chl } a \text{ m}^{-2}$  for the first mm of sediment.

**Primary production measurements. Carbon uptake:** Microphytobenthic potential production, calculated as  $^{14}\text{C}$  bicarbonate uptake, was measured in a photosynthetron (Lewis & Smith 1983). Duplicate samples were incubated in the dark and at 32, 43, 91, 203, 328, 614 and  $864 \mu\text{mol m}^{-2} \text{s}^{-1}$  during the first months, and then at 58, 72, 154, 332, 614, 1038,  $1536 \mu\text{mol m}^{-2} \text{s}^{-1}$  the rest of the year. Photoinhibition was never observed in any of the measurements.

The incubation procedure followed that of McIntyre & Cullen (1995), with small modifications. The

superficial mm of 2 sediment cores was diluted in 50 ml of filtered sea water, and aliquots of 2.5 ml were taken while the sample was agitated, producing a homogeneous slurry. The aliquots were placed in glass scintillation vials and 50  $\mu\text{l}$  of  $\text{NaH}^{14}\text{CO}_3$  (Amersham) was added to each sample for a final activity of 0.0185 MBq  $\text{ml}^{-1}$ . The samples were incubated at *in situ* temperature. When an increase in sediment temperature was measured during emersion, the temperature was adjusted in the incubator. The carbon incorporation was stopped with 100  $\mu\text{l}$  of concentrated HCl, which removes all the non incorporated inorganic carbon, as proved by dark and control incubations. The incubation time was short (30 min) so as to obtain production values as close as possible to gross production (Williams 1993). The samples were counted using a Beckman LS 5000TD scintillation counter including quenching correction, after the addition of 17.5 ml of Dynagel (Baker Analyzer Reagent).

The values of production for each light intensity (2 replicates), expressed per unit area ( $\text{mg C m}^{-2} \text{h}^{-1}$ ), were normalized for chlorophyll units and fitted according to 5 different models for primary production. The model with the best fits (Platt & Jassby 1976) was adopted to calculate the photosynthetic parameters  $\alpha^B$ ,  $P_{\text{max}}^B$  and  $I_k$ .  $\alpha^B$  is the initial slope of the P-I curve (photosynthesis rate at sub-saturating light, in  $\text{mg C mg chl a}^{-1} [\mu\text{mol m}^{-2} \text{s}^{-1}]^{-1} \text{h}^{-1}$ ).  $P_{\text{max}}^B$  is the maximum photosynthetic capacity at saturating irradiances ( $\text{mg C mg chl a}^{-1} \text{h}^{-1}$ ).  $I_k$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), the light saturation parameter, is calculated as  $P_{\text{max}}^B/\alpha^B$  and is normally used as a photoacclimation index.

To calculate production for the whole photic zone, attenuation between 400 and 700 nm in the first mm of sediment was measured with reconstituted sediment as in MacIntyre & Cullen (1995), assuming an exponential decrease of light intensity in the sediments, according to the formula:

$$I_z = I_0 \cdot e^{-kz}$$

Although scatter may cause an increase of light in the first mm with respect to the exponential model (Kühl & Jørgensen 1994), the sediments at the Molenplaat do not have features favorable for a high scatter, like white quartz sands. This is not the only potential error in vertical fine scale: the algal biomass within the first mm of sediment (chl *a*) is assumed to be constant, while algae stratify vertically in tenth-of-millimetre scales (Taylor & Paterson 1998).

Incident light intensity was averaged for the 1.5 h period between each measurement and, with 3 P-I curves, 3 estimates of carbon fixation were obtained per sampling day.

Production was calculated at each depth with a resolution of 0.1 mm as:

$$P_z = \text{chl } a \cdot P_{\text{max}}^B \cdot \tanh(\alpha^B \cdot I_z / P_{\text{max}}^B)$$

The production at each layer was added up for the whole photic zone, assuming a constant chl *a* content with depth in the photic zone. Two-way ANOVAs were performed to test the significance of the short-term (hours) and monthly variations of chl *a* contents, primary production, and photosynthetic parameters ( $P_{\text{max}}^B$ ,  $\alpha^B$  and  $I_k$ ) at both stations. To compare these values with oxygen derived values of gross production, the production values were also calculated assuming a constant incident light intensity of 800  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .

**Oxygen production:** Microphytobenthic gross production was measured by oxygen production in sediment cores (i.d. 6 cm) at ambient temperature with a fixed irradiance of approximately 800  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . The cores were transported to the ship, then successive measurements were made on board during the emersion period. The cores were cooled in the winter to avoid large differences of temperature from those in the field;  $\Delta T$  between the sediments in the field and the core were 1 or 2°C only. In March 1996, at Stn B, the difference was 4°C, and the values of production were corrected.

Oxygen concentration was measured with Diamond glass microelectrodes (737 GC Clark Style). The microelectrodes (duplicates) were lowered via an electrically driven micromanipulator connected to a data logger that controlled the light and dark intervals as well as the distance between measurements.

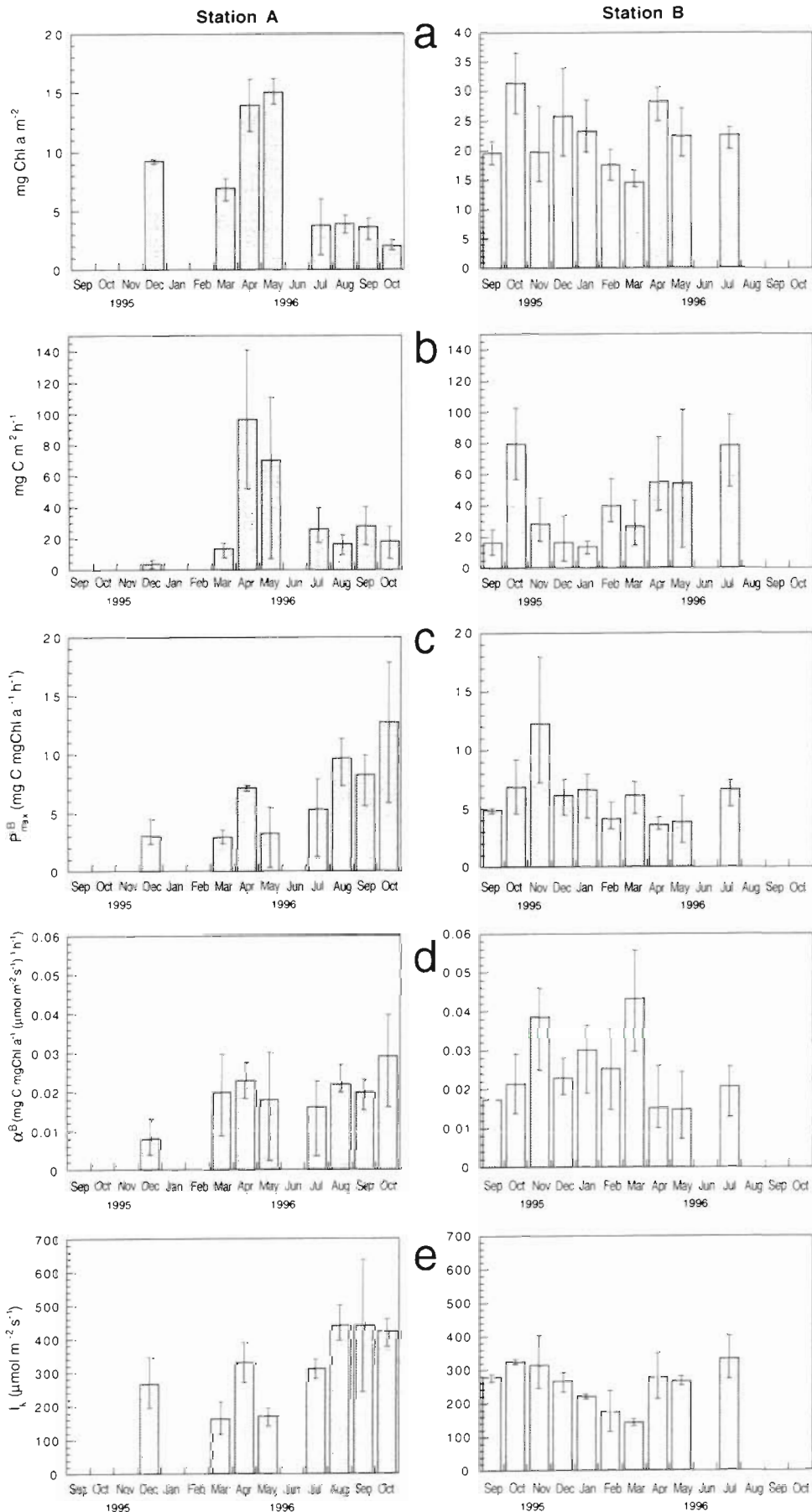
The electrodes were calibrated after each set of measurements, with air saturated water, and the anoxic layer of the cores was calibrated for 0% oxygen.

Gross production was estimated by the light-dark shift method described by Revsbech et al. (1981) and Revsbech & Jørgensen (1986): after a steady state in oxygen concentration is reached during illumination, the observed decrease in oxygen concentration during the first seconds of darkness will be equal to the rate of gross photosynthesis. Microphytobenthic production was assessed in steps of 0.2 mm. The obtained results were integrated over the euphotic zone to estimate the total gross primary production. The mean values of several profiles were averaged to get an average hourly production per emersion period.

A photosynthetic quotient ( $\text{PQ} = \Delta\text{O}_2/\Delta\text{C}$ ) of 1 was used to transform the oxygen values into carbon (Hargrave et al. 1983).

## RESULTS

During the sampling period, incident light intensities ranged from 25 to 1700  $\mu\text{mol m}^{-2} \text{s}^{-1}$  with high seasonal variability and hourly variability due to cloudiness.



Temperature at the sediment surface was also highly variable according to the season, with sharp changes also detected on daily time scales. The minimum was 4°C in February 1996 and the maximum temperature recorded was 23°C in September 1996. Increases in sediment temperature of 3.5°C were recorded during emersion periods on our sampling dates in September and October; in winter, or with cloudy skies, temperatures remained constant at the sediment surface during the whole emersion period.

The calculated depth of the photic zone differed at both stations, due to differences in grain size and silt content and attenuation coefficients showed small variations between the 3 measurements made in March, May and October (1995):  $1.98 \pm 0.07$  and  $4.24 \pm 0.10 \text{ mm}^{-1}$  for Stns A and B respectively.

Microphytobenthos was more abundant at Stn B than at Stn A (annual mean for 1995,  $5.9 \pm 3.2 \text{ mg chl } a \text{ m}^{-2}$  for the top mm at Stn A and  $17.3 \pm 6.7 \text{ mg chl } a \text{ m}^{-2}$  for Stn B). A description of the chlorophyll content and microphytobenthic community composition at the eastern part of the Molenplaat was made in Barranguet et al. (1997). The spatial heterogeneity of chl *a* was less pronounced at Stn A than at Stn B, typical of more agitated sediments. The maximum chl *a* concentration and primary production were recorded in April and May 1996 for Stn A (Fig. 2). At Stn B, the variability in chl *a* content during the year was less pronounced and the maximums occurred in October 1995 and April 1996. The classically observed 2 annual peaks in primary production occurred in September 1995 and spring 1996 (March, April and May) (Fig. 2).

Averaging potential hourly production over the entire year ( $^{14}\text{C}$  data), using the recorded incident irradiance, there was no significant difference between

rates at both stations (paired *t*-tests, 2-tailed), with  $34.5 \pm 23.6 \text{ mg C m}^{-2} \text{ h}^{-1}$  for Stn A and  $41.1 \pm 11.6 \text{ mg C m}^{-2} \text{ h}^{-1}$  for Stn B. At Stn B, the maximum potential production obtained from C fixation measurements ( $P_{\text{max}}$ , not shown) occurred in November ( $267 \text{ mg C m}^{-2} \text{ h}^{-1}$ ). The correlation between chl *a* and  $P_{\text{max}}$  was not significant at Stn B. For Stn A, the maximum potential production was recorded in April ( $119 \text{ mg C m}^{-2} \text{ h}^{-1}$ ), and  $P_{\text{max}}$  was significantly correlated with chl *a* ( $r = 0.58$ ;  $n = 23$ ;  $p < 0.01$ ).

The photosynthetic activity varied during low tide; however, we could not see any consistent trend in the parameters  $P_{\text{max}}^{\text{B}}$  and  $\alpha^{\text{B}}$ . This is in contrast to results obtained earlier (Kromkamp et al. 1995). The ANOVA tests showed that the short-term variations (hours) of the variables studied (chl *a*, carbon production and photosynthetic parameters  $P_{\text{max}}^{\text{B}}$ ,  $\alpha^{\text{B}}$  and  $I_k$ ) were not significant for both stations (Table 1).

Nevertheless, production showed consistent seasonal patterns at both stations. Chl *a* concentrations, carbon production and  $P_{\text{max}}^{\text{B}}$  changed significantly at Stn A for the different months sampled, whereas  $I_k$  and  $\alpha^{\text{B}}$  did not (Table 1).  $P_{\text{max}}^{\text{B}}$  was positively correlated to temperature ( $r = 0.588$ ;  $p < 0.01$ ).

For Stn B, the monthly variations of chl *a*, carbon production rates and  $I_k$  were significant (Table 1). Both carbon production and  $I_k$  were correlated with temperature ( $r = 0.439$ ,  $p < 0.05$  and  $r = 0.754$ ,  $p < 0.01$  respectively). These correlations between the photosynthetic parameters and primary production rates and temperature suggest an adaptation of the microphytobenthic communities to the seasonal changes of light and temperature in the silty sediments. Low rates of production were recorded from October to February at Stn B, hinting at a better photoacclimation at Stn B. At Stn B,  $I_k$  showed seasonal changes, suggesting that algae

Table 1. Analysis of variance for chlorophyll concentrations, carbon production rates and photosynthetic parameters, for Stns A and B. Significant probabilities are underlined

	df	Month F-ratio	p	df	Hour F-ratio	p
<b>Stn A</b>						
Chl <i>a</i> ( $\text{mg m}^{-2}$ )	7	38.84	<u>0.000</u>	2	2.041	0.170
Prod. rates ( $\text{mg C m}^{-2} \text{ h}^{-1}$ )	7	3.19	<u>0.034</u>	2	1.79	0.206
$P_{\text{max}}^{\text{B}}$ ( $\text{mg C mg chl } a^{-1} \text{ h}^{-1}$ )	7	3.36	<u>0.032</u>	2	0.383	0.690
$\alpha^{\text{B}}$ ( $\text{mg C mg chl } a^{-1} [\mu\text{mol m}^{-2} \text{ s}^{-1}] \text{ h}^{-1}$ )	7	1.53	0.247	2	0.221	0.805
$I_k$ ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )	7	1.22	0.362	2	0.371	0.291
<b>Stn B</b>						
Chl <i>a</i>	8	3.02	<u>0.027</u>	2	1.863	0.186
Prod. rates	8	3.29	<u>0.018</u>	2	0.309	0.738
$P_{\text{max}}^{\text{B}}$	8	1.54	0.214	2	0.465	0.636
$\alpha^{\text{B}}$	8	2.17	0.085	2	0.009	0.991
$I_k$	8	4.77	<u>0.003</u>	2	1.689	0.214



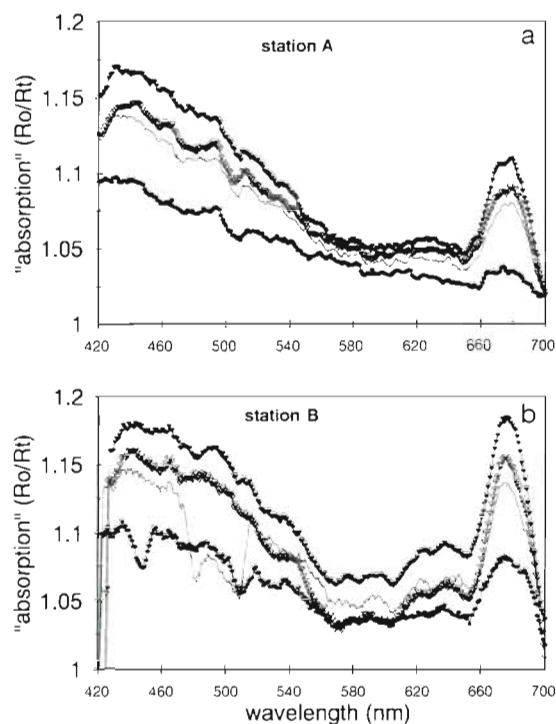


Fig. 3. Spectrum of the light absorbed by the sediments at Stns A and B during different times of low tide (September) showing vertical upwards migration of microphytobenthic algae by continuous increase of absorption at 680 nm. (a) ● 11:43 h; — 12:36 h; ▽ 12:54 h; ▼ 13:47 h. (b) ● 10:08 h; — 10:38 h; ▽ 12:08 h; ▼ 12:38 h

adapted to the seasonal light conditions (Fig. 2), but there was no significant correlation between the  $I_k$  and PAR, at any of the stations. Blanchard & Cariou-Le Gall (1994) also found the same pattern of increasing  $I_k$  from March to July in muddy sediments as that which we found.

Upward algal migration was detected by the spectroradiometer measurements at both stations from the beginning of emersion onwards. The amount of light absorbed by chlorophyll (around 670 to 680 nm) increased sharply during the first hour of emersion (Fig. 3). No significant differences in the change of light absorbed were detected between the 2 stations for the whole emersion period, although the mean  $\Delta R$  (reflectance) was higher at Stn B.

The gross production rates calculated with the microelectrodes were often in good agreement with the carbon uptake values, with the only large discrepancies found in periods with the highest production rates in spring-summer 1996. At this time, gross oxygen production was much higher than the  $^{14}\text{C}$  uptake (Fig. 4).

During spring and summer, a station located on a tidal flat in the Oosterschelde was also sampled. The water of the Oosterschelde is much poorer in nitrogen

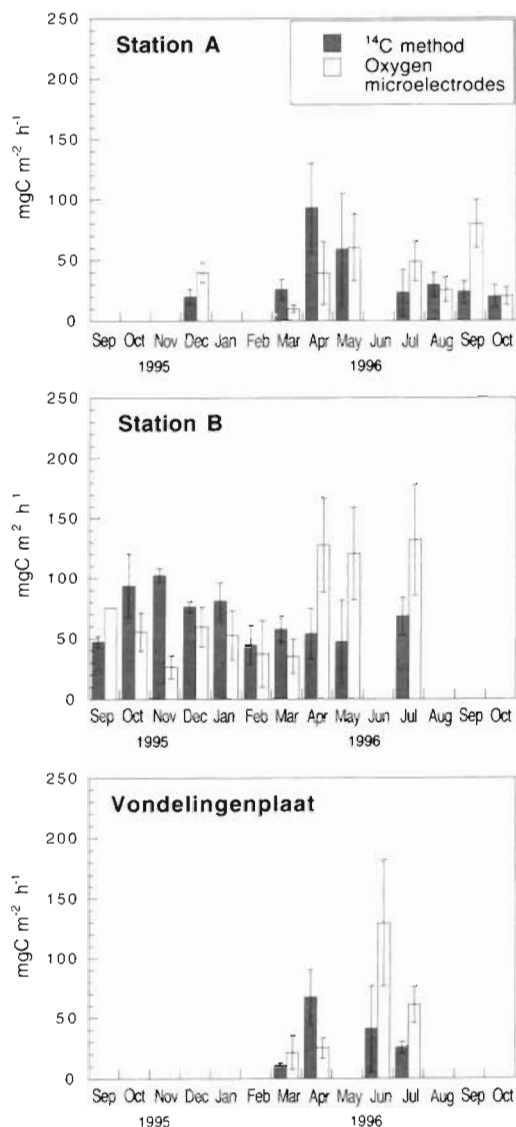


Fig. 4. Gross microphytobenthic production measured with oxygen microelectrodes with an incident light intensity of  $800 \mu\text{mol m}^{-2} \text{s}^{-1}$  and potential production from the photosynthetic parameters issued from the  $^{14}\text{C}$  incubations, calculated for a similar incident light. Stns A and B are located at the Molenplaat in the Westerschelde, and Vondelingenplaat is located in the Oosterschelde

and silicate than that of the Westerschelde (Wetsteyn & Kromkamp 1994). We also measured oxygen production and carbon uptake to determine any differences in photosynthesis during the periods of maximal productivity that could hint at a nitrogen or silicate limitation during ebb tide. The production rates were slightly lower than in the Westerschelde, and the same discrepancy between oxygen and  $^{14}\text{C}$  arose in June for the microphytobenthos in the Oosterschelde (Fig. 4).

## DISCUSSION

Part of the complexity in attributing changes in microphytobenthos production to seasonal factors can be explained by the mixed microphytobenthic composition of motile and non motile fractions with different ecological strategies. Sabbe (1997) already pointed out the complexity of the microphytobenthic diatom community in the Westerschelde, as temporal patterns are subordinate to spatial ones. He found that the proportion of motile and non motile fractions varied depending on the kind of sediments present and that both fractions had a different seasonal evolution.

In the Molenplaat, the sandy sediments (Stn A) contained proportionally more epipsammic than epipellic algae (Barranguet et al. 1997). The epipsammic fraction is composed of diatoms showing low motility which are firmly attached to the sand grains (De Jonge 1985), and hence more resistant to export, but do not present the functional advantages of the motile fraction, which can vertically migrate in the sediments: migration ensures protection from photoinhibition and desiccation and facilitates access to nutrients and organic and inorganic carbon deeper in the sediments. The spectroradiometer measurements showed vertical algal migration at both stations, but it is difficult to compare quantitatively the amount of the migrating fraction at the 2 stations. First, it is not possible to estimate accurately from which depth the light signal is coming at each of the stations. Second, if the detrital part of the sediment in the beginning of the exposure is already absorbing light in the chlorophyll region, then the normalisation will give lower results of migration than in a sediment without algae. Stn B was richer in degradation pigments of chl *a* than Stn A (Barranguet et al. 1997), and the measured change in *R* at both stations was in the same range, implying that the proportion of migratory algae is larger at Stn B.

The comparison of hourly changes in the photosynthetic parameters during each of the emersion periods studied did not give any additional information regarding a consistent pattern of change at the 2 stations. However, the migration during ebb tide appears to be responsible for the changes in the vertical profiles of production shown in Fig. 5, where the maximum photosynthesis rates progress upwards during the emersion period.  $^{14}\text{C}$  calculations of primary production consider the amount of biomass vertically constant in the photic zone, so production will exponentially decrease downwards with decreasing irradiance, without taking into account heterogeneous biomass or vertical migration. In the  $^{14}\text{C}$  profile, production decreases exponentially with depth, while in consecutive profiles of oxygen production we see that the maximum production is not located at the surface layer of the sediment

but, as also shown by the spectroradiometer measurements, migrates upwards during ebb tide. This could partly explain the discrepancies found between measurements in summer using carbon and oxygen methods. Oxygen profiles show the skewed vertical profile of production, with a maximum biomass located in the subsurface and upward migration during emersion (Fig. 5).

The other reason for a discrepancy between  $^{14}\text{C}$  incorporation and oxygen production on those occasions is the apparent wider euphotic zone in the oxygen profiles than the one calculated using the attenuation coefficients of 1995. If there was an enrichment in sand contents in those months, the light intensity penetrating the sediments used to calculate integrated

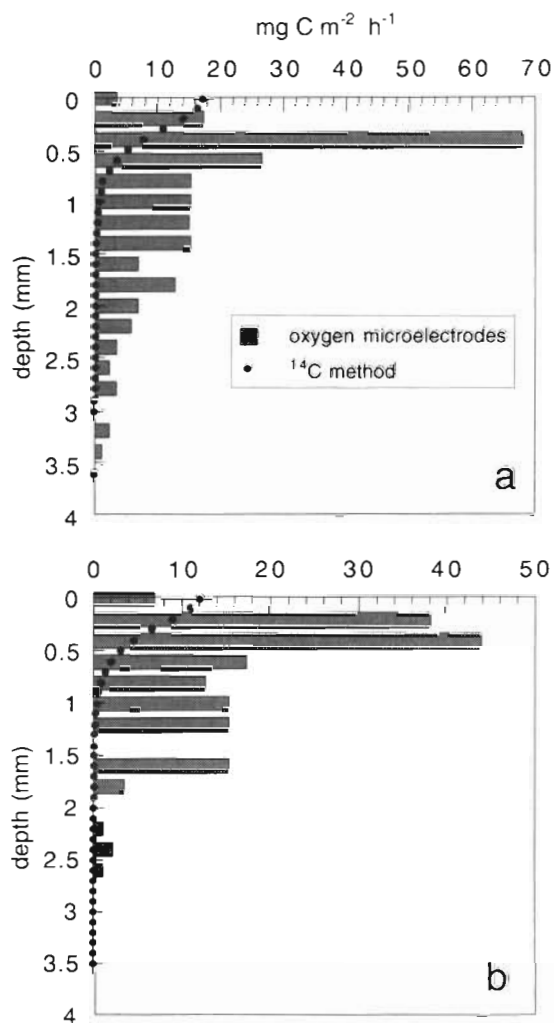


Fig. 5. Vertical profiles of production at Stn B (4 July 1996, ebb tide at 12:16 h) with  $800 \mu\text{mol m}^{-2} \text{ s}^{-1}$  incident irradiance, measured with oxygen microelectrodes (bars) with 0.2 mm resolution and  $^{14}\text{C}$  incorporation (●), calculated with 0.1 mm resolution. (a) Oxygen profile at 10:20 h,  $^{14}\text{C}$  P-I curve started at 10:30 h. (b) Oxygen profile at 12:45 h,  $^{14}\text{C}$  P-I curve started at 12:30 h

production was underestimated, indicating that light attenuation should be measured on each sampling occasion.

For most of the measurements, given the limitations of the 2 very different procedures, there was an acceptable agreement between oxygen and carbon results, suggesting that no marked nutrient limitation occurred at either station. Carbon incorporation values measure potential production, because the algae are resuspended and all the nutrient gradients destroyed, whereas oxygen gross production is measured in intact cores. Therefore, when values measured by the 2 methods are in agreement, as seen in this study, nutrient limitation is not probable. That is, if severe nitrogen or carbon limitation existed,  $^{14}\text{C}$  production rates would be much higher than oxygen production measured in an intact core, since during  $^{14}\text{C}$  incubations a very small amount of the algae is in contact with an excess of nutrients in the water. Also, nitrate concentration in Westerschelde waters is very high: 185.1  $\mu\text{M}$  in June 1996 and an average concentration of 161  $\mu\text{M}$  in 1995/96 for the Molenplaat area (Sinke pers. comm.).

However, carbon production rates much higher than oxygen gross production, suggesting a nutrient or carbon limitation, have been observed during spring measurements in very thick mats located in the south of the tidal flat (Barranguet & Peene 1996), which has a biomass about double that of the northern part. The shape of the P-I curves did not indicate that the microalgae were limited by nutrients or inorganic carbon as there was no decrease in photosynthetic activity during low tide. It can be concluded that under the average concentrations of algal biomass in the Molenplaat, there was no nutrient limitation for microphytobenthic production during the studied period.

Changes in the pattern of photosynthetic parameters during emersion can also be related to environmental factors other than nutrients. Blanchard & Cariou-Le Gall (1994) found highly variable hourly photosynthetic rates in intertidal microphytobenthos during March and July in Marennes-Oléron Bay which were attributed to the high adaptive capacity of the algae to short-term variations in field conditions (Blanchard & Montagna 1992).

Specific adaptation to light and temperature has been often suggested in correlative field studies in intertidal environments (Cadée & Hegeman 1974, Rasmussen et al. 1983, Grant 1986, Blanchard et al. 1996), as intertidal areas are subject to large fluctuations of temperature, and seasonal increases in temperature are closely accompanied by an increase in PAR. In subtidal environments, microphytobenthos production is more directly linked to light than to temperature (Blanchard & Montagna 1992, Cahoon & Cooke 1992, Moncreiff et al. 1992, Barranguet 1997).

Furthermore, photoinhibition is generally not encountered in intertidal microalgae (Cadée & Hegeman 1974, Cadée 1980, Rasmussen et al. 1983, Colijn & de Jonge 1984). Some studies on subtidal sediments have, however, shown photoinhibition (Davis & MacIntyre 1983, Sundbäck & Jönsson 1988, Barranguet 1997). An intermediate situation was described by Gargas & Gargas (1982) in very shallow sediments (0.5 to 0.7 m) where photosynthesis seemed to be regulated by both temperature and light, although temperature was the dominant factor.

In our study,  $P_{\text{max}}^{\text{B}}$  at Stn A and  $I_k$  at Stn B showed clear seasonal trends, such as a marked correlation with light and temperature, in agreement with the results of Blanchard et al. (1996). MacIntyre & Cullen (1996) also found a link between  $P_{\text{max}}^{\text{B}}$  and temperature in shallow water sediments in San Antonio Bay.

Changes in  $P_{\text{max}}^{\text{B}}$  may be explained by changes in algal community composition, which may have varying photosynthetic features: diatoms have a high  $P_{\text{max}}^{\text{B}}$  when blooming (Kirk 1986) and the microphytobenthic community in the Molenplaat is composed principally of diatoms during the blooming periods of spring and autumn (Barranguet et al. 1997).

The high correlation between  $I_k$  and temperature and the significant seasonal changes suggests that the main factors regulating microphytobenthic production in the silty sediments were temperature and, indirectly, light conditions. With a narrower euphotic zone, a higher biomass per unit area and no clear nutrient limitation, microalgae at Stn B appeared to be light limited.

At Stn A, however, the regulating factors seemed to be of a different nature than at Stn B. Station A is subjected to a high hydrodynamic energy level, resulting in a constant export of microphytobenthic biomass (Barranguet et al. 1997).  $P_{\text{max}}^{\text{B}}$ , chlorophyll and production rates vary significantly over the year, with biomass and production being correlated. The absence of large fluctuations in  $\alpha^{\text{B}}$  and the lesser dependence of  $I_k$  variance on temperature suggest that the amount of microphytobenthos biomass is determining how much carbon is produced. Resuspension and horizontal transport will result in continuous export of microalgal biomass in sediments at the margins of the Molenplaat, making algal biomass the critical factor lowering production.

Therefore, the factors regulating the production in the 2 types of sediments differed, as did the response of the community. However, the amount of production was of the same order of magnitude in both sediments.

On an annual basis, estimates of intertidal microphytobenthos production fall always around 100  $\text{g C m}^{-2} \text{ yr}^{-1}$  (Pomeroy 1959, Gargas 1970, Davis & Lee 1983, Rasmussen et al. 1983, Colijn & de Jonge 1984, Varela



& Penas 1985, Shaffer & Cahoon 1987, Shaffer 1988, Sullivan & Moncreiff 1988, Cammen 1991, Steward et al. 1992). The same annual rate of production can be reached by very different mechanisms, resulting in yearly averages which are rather constant. Photosynthesis in microalgae appears to be regulated by very diverse environmental variables; the forcing factors can be as varied as nutrient limitation, light, temperature or sediment grain size and stability.

Our results point to the strong influence of light and sediment stability on microphytobenthos production in the Molenplaat and the important role of migration during ebb tide in determining photosynthesis rates, as well as the bias that can occur in primary production estimations if this process is not considered, especially during periods of high production rates, like blooms, in which biomass is composed mainly of epipellic algae.

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