

Fine-scale vertical resolution of chlorophyll and photosynthetic parameters in shallow-water benthos

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ABSTRACT: The vertical distributions of chlorophyll concentration and photosynthetic parameters of sediment-associated microalgae were measured with a resolution of 1 mm. Sediment and the overlying water were sampled at 3 sandy, shallow-water sites near Corpus Christi Bay, Texas, USA. All sediment samples had a floc in the surficial millimeter that contained as much as or more chlorophyll than the 0.2 to 0.6 m of water overlying them. The photosynthetic responses of the sediment-associated microalgae were comparable with those of the suspended phytoplankton. Below the surficial floc, constancy of chlorophyll concentration and photosynthetic-irradiance (*PI*) responses indicated the existence of a physically mixed layer in the underlying 8 to 15 mm. Photosynthetically competent algae were found below the mixed layer and well below the depth to which light penetrates the sediment (ca 1 mm). Primary production was more or less equally distributed between the surficial millimeter of benthos and the overlying water. The surficial floc and some of the underlying sediment may be readily resuspended so that 'benthic' microalgae can contribute significantly to both water column and benthic primary production.

KEY WORDS: Microphytobenthos · Phytoplankton · Photosynthesis · Production · Mixing

INTRODUCTION

The contribution of benthic microalgae to the carbon budgets of shallow-water systems has been extensively documented from a range of habitats, from mud-bottomed estuaries (Hopkins 1963, Admiraal et al. 1984) to sandy tidal flats (Pamatmat 1968, Steele & Baird 1968, Varela & Penas 1985) and salt marshes (Pomeroy 1959, Darley et al. 1981, Sullivan & Moncrieff 1988). When resuspended into the water column by wind mixing (Lukatelich & McComb 1986, Pejrup 1986, Demers et al. 1987) or tidal currents (Baillie & Welsh 1980, Shaffer & Sullivan 1988), benthic microalgae and detritus may be an important source of food for both macro- and microheterotrophs (Roman &

Tenore 1978, Wainright 1990, de Jonge & van Beusekom 1992). The microphytobenthos are also an important source of food for surface deposit feeders (Pace et al. 1979), some of which are able to switch between surface deposit feeding and suspension feeding, depending on water flow velocity (Miller et al. 1992).

Benthic microalgae have been divided into the 'epipellic' algae, those motile cells congregating at the surface of the sediment on which deposit feeders graze, and the 'epipsammic' fraction that are bound to the sediment (Round 1965). The utility of the distinction has been questioned because it is based not on taxonomic affinity but on a combination of the adhesive qualities of the cells and the degree of sediment sorting imposed by currents and waves (de Jonge 1985). Regardless of taxonomic distinction, though, flocculent assemblages are widespread and may be metabolically distinct from those in the underlying sandy sediment, having higher rates of both respiration and photosynthesis (Sweerts et al. 1986). Most studies of benthic production have examined the sedi-

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ment on vertical scales of centimeters, although these do not reflect the scale of 1 mm or less on which light is attenuated (Haardt & Nielsen 1980, Jørgensen & Des Marais 1986) nor the scale of hundreds of micrometers on which microphytobenthos are sorted in the sediment (Baillie 1987). We report the vertical distribution of microalgal chlorophyll and photosynthetic response at millimeter intervals from 3 sandy sites near Corpus Christi Bay, Texas, USA, and argue that this is the appropriate scale on which to study both production in the sediment *per se* and coupling of the benthos and overlying water.

Photosynthesis-irradiance (*PI*) responses of the benthic and suspended microalgae were determined from the incorporation of ^{14}C bicarbonate over a range of light intensities, using a technique developed by Lewis & Smith (1983). This allows direct comparison of the *PI* responses of the benthic microalgae and the microalgae suspended in the overlying water. The technique was modified for use with sediment samples by resuspending the sediment sample in filtered seawater from the sample site. The advantages and disadvantages of different methods of measuring benthic primary production have been debated previously (Revsbech et al. 1981, Jönsson 1991), and the technique presented here, relying as it does on disruption of the sediment, is inappropriate for compacted sediments. Unlike previous slurry techniques, reviewed critically by Jönsson (1991), the technique does correct for the attenuation of light in sediment. In common with other ^{14}C techniques, no correction is made for respiration, so it is not possible to measure net inputs of organic carbon to an ecosystem. The method has the advantage, though, that it allows direct investigation of the sediment on the spatial scale at which benthic microalgae are distributed (Baillie 1987). It allows rapid measurement of the photosynthetic parameters commonly used in production models, without lengthy (hours to day) enclosure of the sediment, which can cause profound changes in the flora. Last, the method permits direct comparison of the photosynthetic responses of the microalgae in the benthos and the overlying water, using a technique that is widely recognized in oceanography. Measurement of the distribution and photosynthetic responses of the benthic microalgae with this temporal and spatial resolution is useful in predicting the consequences of resuspension and redistribution of the sediment on the time-scales of change appropriate to many shallow-water systems. Given the existence of an abundant, photosynthetically active and readily resuspended surface floc, such a description is of crucial importance in understanding

the coupling between the sediment and water in these systems.

METHODS

Sediment and water were sampled at 3 sites (Fig. 1) near Port Aransas, Texas, over a period of 14 d in June 1986. Sediment at each site was sampled where there was 0.4 m of overlying water. Sediment was collected along with a small quantity (50 to 100 ml) of supernatant water in 20 to 25 acrylic cores (32 mm inner diameter) that were pushed into the sediment in a 40 × 40 cm grid. Water from immediately below the surface of the water column was collected in acid-washed polycarbonate bottles. The samples were transported by boat to the Marine Science Institute (University of Texas) in Port Aransas for analysis. Travel time was less than 15 min, during which the samples were held in the dark. Cores were assigned randomly to pigment, *PI* and light attenuation measurements based on their location in the 40 × 40 cm sampling grid, using a random number table. The sediment was prepared for analysis by careful removal of the supernatant by aspiration, after which the cores were sectioned in 1 mm slices with a methanol-rinsed razor blade. Sediment was extruded from the core using a micromanipulator to advance the piston (Joint et al. 1982). Care was taken to ensure that the sediment surface was perpendicular to the long axis of the cores to minimize unevenness in the thickness of the surficial millimeter.

Sections of sediment were placed in 10 ml of 90% acetone (cf. Phinney & Yentsch 1985) and pigments extracted for 24 to 48 h in the dark at -4°C . After extraction, each sample was centrifuged at 5000 rpm for 5 min and diluted with 90% acetone. Chlorophyll a concentrations in the supernatant were determined fluorometrically, after nominal correction for degradation products (Holm-Hansen et al. 1965). Pigment

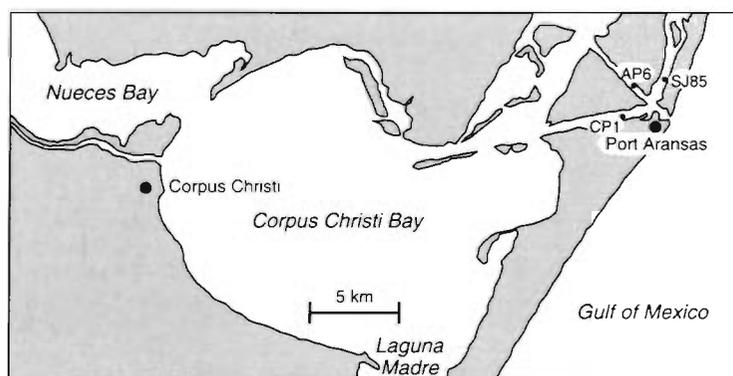


Fig. 1. Map of Corpus Christi Bay, Texas, USA, showing the 3 sample sites (SJ85, AP6 and CP1)

determinations were made on sequential 1 mm sections of 3 to 5 cores. Aliquots of the water samples were filtered through Whatman GF/F filters for determination of suspended chlorophyll. Extraction and analysis were as for the sediment samples, except that centrifugation was omitted. For ease of comparison, chlorophyll concentrations are reported in $\mu\text{g dm}^{-3}$ and mg dm^{-3} . In the case of the suspended algae, $\mu\text{g dm}^{-3}$ is equivalent to the more conventional $\mu\text{g l}^{-1}$. For the benthos, 1 mg dm^{-3} is equivalent to 1 mg m^{-2} for a layer of sediment 1 mm thick.

PI curves of both the suspended and benthic assemblages were constructed by measuring ^{14}C -bicarbonate uptake in a 'photosynthetron' (Lewis & Smith 1983). The technique was modified for sediment samples as follows. A 1 mm thick section of sediment was suspended in 50 ml of GF/F-filtered water from the sample site. The sample was then inoculated with ^{14}C -bicarbonate (final activity ca $0.5 \mu\text{Ci ml}^{-1}$) and 18 aliquots of 1 ml dispensed into scintillation vials in the incubator. Two aliquots were dispensed into vials containing 50 μl of borate-buffered formalin as time-zero controls. To prevent settling of sediment during dispensing, the suspension was mixed continuously while the aliquots were being dispensed. The concentration of ^{14}C -bicarbonate in the suspension was measured by subsampling into 10 ml of counting cocktail (RPI Corp. 3a70B Complete Counting Cocktail) containing 0.2 ml of phenylethylamine. Light in the incubator was provided by 4 ENH projector lamps and was measured with a Biospherical QSL-100 4π quantum sensor inserted into a scintillation vial. The samples were incubated for 20 min at the ambient temperature of the water at the sample site (29 to 30°C) and then killed with 50 μl of borate-buffered formalin. Inorganic carbon was expelled before counting ^{14}C incorporation by acidifying each aliquot with 0.25 ml of 6 N HCl and shaking for 2 h. Photosynthesis rates were not corrected for isotope discrimination. Chlorophyll and inorganic carbon concentrations in the slurry were measured before adding the radioactive label. The concentration of inorganic carbon in the suspension was determined conductometrically, as described by Cameron (1986). Two independent series of incubations were performed on each stratum examined.

The *PI* curve was constructed by fitting the data to the following equation (Webb et al. 1974) by the least squares method:

$$P = P_m \left[1 - \exp\left(\frac{-\alpha I}{P_m}\right) \right] + P_0 \quad (1)$$

where P is the rate of photosynthesis normalized to chlorophyll [$\text{g C (g chl)}^{-1} \text{ h}^{-1}$] at light intensity I ($\mu\text{mol m}^{-2} \text{ s}^{-1}$); P_m is the maximum rate of photosynthesis [$\text{g C (g chl)}^{-1} \text{ h}^{-1}$]; α is the initial slope of the *PI* curve [g C

$(\text{g chl)}^{-1} \text{ h}^{-1}$ ($\mu\text{mol m}^{-2} \text{ s}^{-1})^{-1}$]; and P_0 is an intercept term [$\text{g C (g chl)}^{-1} \text{ h}^{-1}$]. Although the photosynthetic parameters are normalized to chlorophyll concentration, the superscript B (Platt et al. 1980) has been suppressed for simplicity. The parameter P_0 is not a reliable estimate of respiration because of the limitations of tracer methodology (Jassby & Platt 1976, Peterson 1980). Rather it is used to increase the amount of variability explained and to improve the distribution of residuals. It is subtracted from P so that modeled gross photosynthesis in the dark is always zero.

Light extinction through the water column was estimated from measurements made immediately below the water surface and at the sediment-water interface, obtained with a Biospherical Instruments QSL-100 4π quantum sensor. Four pairs of readings were taken for each estimate. A diffuse attenuation coefficient, k (m^{-1}), was calculated as:

$$k = \frac{\left(\ln \frac{I_0}{I_z} \right)}{z} \quad (2)$$

where I_z is the scalar irradiance at the sediment-water interface ($\mu\text{mol m}^{-2} \text{ s}^{-1}$); I_0 is the light intensity just below the water surface ($\mu\text{mol m}^{-2} \text{ s}^{-1}$); and z is the depth of the water column (m). Winds were low ($<5 \text{ m s}^{-1}$) at the time of sampling; the resulting low swell occasioned little variability between pairs of measurements. The skies were clear and light intensities at the sediment-water interface were typically 400 to $700 \mu\text{mol m}^{-2} \text{ s}^{-1}$.

The extinction of light within the sediment was calculated by measuring the transmission through reconstituted sediment. Sections of the surficial millimeter of sediment were settled in GF/F-filtered water in a glass-bottomed, opaque cylinder of the same inner diameter as the sample core. The sample was illuminated from above with a General Electric ENH projector lamp. Spectral transmission at 50 nm intervals between 400 and 750 nm was measured using an ISCO Model SR Spectroradiometer with the sensor held 1 cm below the sample. Transmission through the sediment was compared to that through filtered seawater alone. A diffuse attenuation coefficient, k (mm^{-1}), was calculated at each wavelength according to Eq. (2), where I_z is the downwelling irradiance measured through the reconstituted sediment ($\mu\text{W cm}^{-2}$); I_0 is the downwelling irradiance measured through the water alone ($\mu\text{W cm}^{-2}$), and z is the thickness of the reconstituted sediment (1 mm). The attenuation coefficient used in calculating rates of photosynthesis in the sediment was obtained by averaging the values of k over the range 400 to 750 nm. There was less than 3% transmission through the surficial millimeter of sediment in all cases.

Production was calculated by integration of photosynthetic rates with depth and over time (Jitts et al. 1976). Depth profiles of photosynthesis were constructed by using the vertical profile of light intensity as an input and a *PI* curve as a transform function. The light profile was established from incident light intensity, averaged over the time of sample collection, and the attenuation coefficient in either the water column or the surficial millimeter of sediment. [Subsequent research (Kühl & Jørgensen 1994, Kühl et al. 1994) has shown that backscatter of light in sandy sediments can elevate the integral light intensity at the sediment surface to 180–280% of the downwelling irradiance incident on it, depending on sediment granulometry and pigment content. The attenuation coefficients in the sediment presented here, which are insensitive to backscatter, are therefore likely to cause an underestimation in benthic production. Conversely, attenuation coefficients in the water column, which were sensitive to backscatter, are likely to cause an overestimation of planktonic production.] The light profiles were used to calculate depth profiles of photosynthesis, which were summed by trapezoidal integration using 1 cm intervals in the water and 50 μm intervals in the sediment. The resulting depth integrals were summed by inte-

gration between samples where a daily rate was calculated:

$$P_{\text{Total}} = \sum_{t=0}^{t=t_m} \left(\sum_{z=0}^{z=z_m} P(z,t) \Delta z \right) \Delta t, \quad (3)$$

where

$$P(z,t) = \text{chl}(t) \times P_m(t) \left(1 - \exp \frac{\alpha(t) I(z,t)}{P_m(t)} \right) \quad (4)$$

and

$$I(z,t) = I_0(t) \exp[-k(t)z]. \quad (5)$$

Areal photosynthesis in either the water column or the sediment, $P_{z,t}$, is integrated with respect to depth and time, denoted by the suffices z and t . The limits of integration with respect to depth ($z = z_m$) were the depth of the water column and 1 mm for the sediment. The limit with respect to time ($t = t_m$) was the length of daylight.

RESULTS

The sediment at the 3 study sites was well sorted and dominated by very fine (63 to 125 μm diameter) and fine (125 to 250 μm diameter) sand, which constituted >97% of the dry weight. Microscopic examination

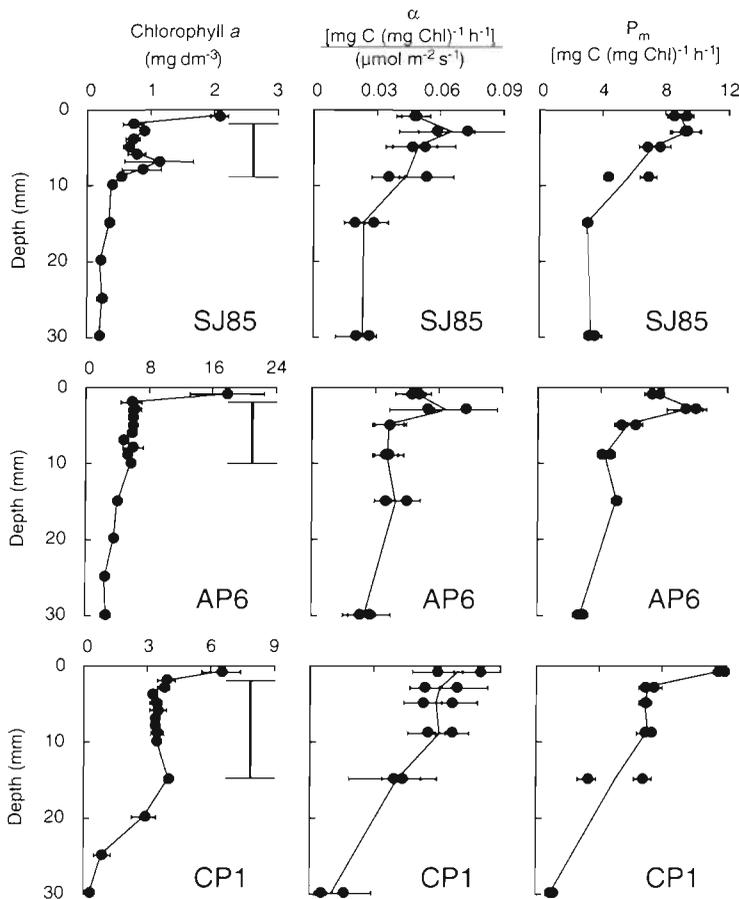


Fig. 2. Vertical profiles of chlorophyll concentration and the photosynthetic parameters α and P_m at Sites SJ85, AP6 and CP1 on 3 consecutive days (16 to 18 July 1986). Note different scales on the 3 plots of chlorophyll concentration. Chlorophyll concentrations are expressed in mg dm^{-3} , which are equivalent to mg l^{-1} or to mg m^{-2} for a sample 1 mm thick. Error bars on plots of chlorophyll are SDs of 3 measurements. Two independent estimates of P_m and α were made at each depth tested. Error bars on the photosynthetic parameters are the 95% confidence limits for each non-linear curve fit. Note that these do not indicate photosynthesis *in situ*, which is confined to the surficial millimeter of sediment. Vertical bars on plots of chlorophyll indicate layer of homogeneous concentration ($p < 0.05$)

showed that the flora in the surface sediment was dominated by small (3 to 5 μm) pennate diatoms and an unidentified flagellate (2 to 3 μm in diameter). Cells smaller than 1 μm were not detected.

The sediment at each of 3 sites, sampled on consecutive days, had a surficial floc with high and variable chlorophyll concentration, beneath which there was a zone of 8 to 15 mm in which there was no significant difference in concentration ($p < 0.05$, as determined by the Kruskal-Wallis analysis of variance, with depth as the independent variable; Fig. 2). Below this homogeneous layer, the pigment content of the sediment declined steadily. The chlorophyll concentration in the floc may have been biased by settling of suspended material from the water overlying the core between sampling and processing of the cores. Rough calculation, based on the assumption that *all* of the chlorophyll in the water overlying the sediment in the core would settle out, indicates that the overestimate was at most 5 to 12%, less than the difference between the floc and the underlying sediment.

Light was attenuated rapidly in the sediment: the attenuation coefficient varied between 3.5 and 5.6 mm^{-1} , so that light was reduced to 1% of incident in 0.8 to 1.3 mm. The coefficient varied inversely with wavelength over PAR (photosynthetically active radiation), being 35 to 40% higher at 400 nm than at 700 nm (data not shown). There was no significant ($p < 0.05$) difference between sites nor was there any correlation between the mean attenuation coefficient and the

chlorophyll concentration in the sediment. As expected, the attenuation coefficients determined here are similar in magnitude to those reported elsewhere for resettled sediments of comparable grain size (Haardt & Nielsen 1980, Colijn 1982) but are very much lower than measurements made on organic-rich, silty sediments that were either reconstituted (Colijn 1982, Baillie 1987) or undisturbed (Jørgensen & Des Marais 1986).

The photosynthetic parameters P_m and α declined with depth, except that the surficial floc had values of P_m that were variously higher, lower or no different than the deeper assemblages (Fig. 2). Estimates of P_m and α were not different (95% confidence intervals of the estimates) between independent determinations from the same stratum, except for 1 sample each from Sites SJ85 and CP1. These were both from the bottom of the homogeneous chlorophyll layer, suggesting that there was lateral heterogeneity within this layer on the scale of the sample grid (40 \times 40 cm). Although there was wide variation in the range of chlorophyll concentrations between the 3 sites, there was comparatively little difference in the photosynthetic parameters. There was no inhibition of photosynthetic rates at high light intensities, consistent with other studies (Taylor 1964, Cadée & Hegeman 1974, Colijn & van Buurt 1975). Representative PI curves, from the surficial floc and the deepest samples taken, are shown in Fig. 3.

To assess the importance of mixing in maintaining the layer of homogeneous chlorophyll content, we

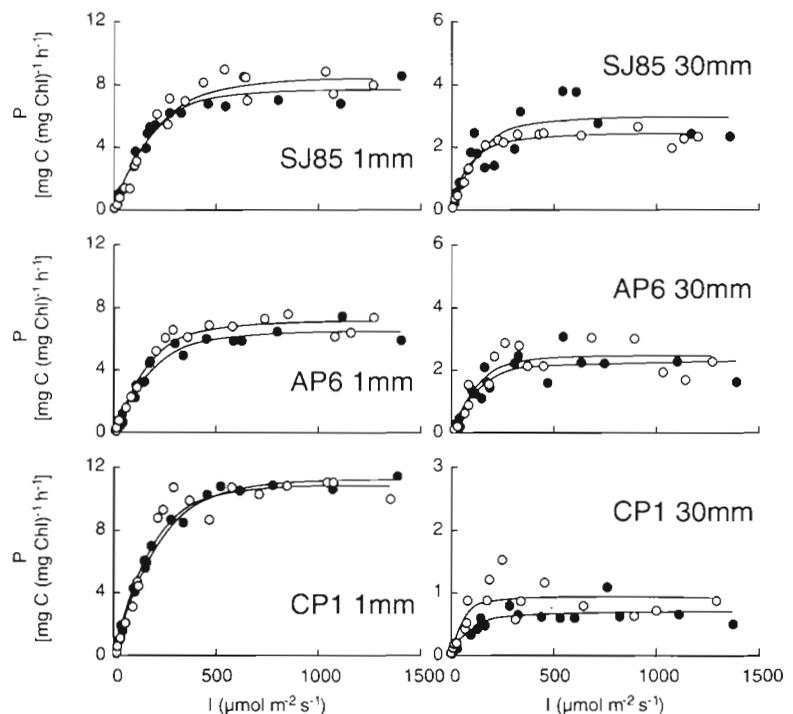


Fig. 3. Representative photosynthesis-irradiance (PI) curves for the sediment samples. The curves are the surficial and deepest sample from each of the profiles shown in Fig. 2. Each panel shows 2 independent curves (\bullet and \circ) and the best-fit lines for Eq. (1). Note that the scales differ between panels

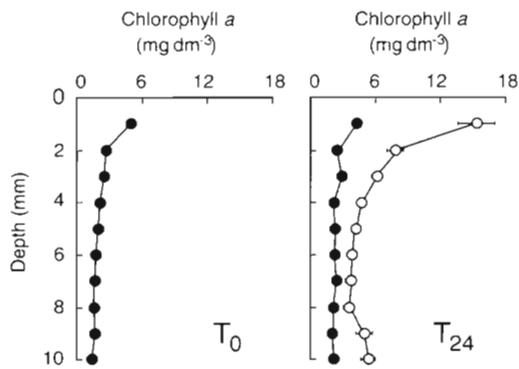


Fig. 4. Vertical profiles of chlorophyll in control (●) and enclosed (○) sediment at Site SJ85 on 28 July 1986, the date on which the cores were deployed (T_0 , left panel), and 24 h later (T_{24} , right panel)

enclosed sediment at Site SJ85 and compared the vertical profiles of chlorophyll content in the enclosed and control sediment. Sediment was enclosed in acrylic cores (32 mm inner diameter) that were pushed into the sediment so that between 6 and 7 cm protruded above the sediment surface. The cores were open at either end. The control was the surrounding sediment that was not enclosed. After 24 h, there was a well-developed discontinuity at about 10 mm in the enclosed samples, below which the sediment was black in color and sulfidic in odor. The sediment above this was highly cohesive, odorless and golden brown in color. In marked contrast, the control was friable, odorless and apparently colorless to a depth of at least 6 to 7 cm. There was a significant increase ($p < 0.05$) in the chlorophyll content in the enclosed cores (Fig. 4). This was most marked at the surface but was evident to 10 mm. The homogeneous vertical distribution of chlorophyll in the control sediment was not maintained in the enclosed samples.

The relative contributions of the benthic and suspended microalgae to areal production were assessed from measurements of chlorophyll, light intensity and PI parameters at SJ85 over the course of a day. Production was calculated in 2 ways. In the first, production was distributed between 2 compartments, the sediment and overlying water. However, much of the production in the water column in shallow systems may be due to displaced benthic diatoms (Shaffer & Sullivan 1988, de Jonge & van Beusekom 1992). Therefore, production was also modeled in 3 compartments, the sediment and the 'phytoplanktonic' and 'resuspended' fractions of the overlying water. Because less than 3% of incident light is transmitted through the sediment, we assume that production in the sediment is confined to the surficial millimeter, dominated by the floc. The water at the study site was 0.3 to 0.6 m deep, and light intensities at the sediment-water interface reached

$1200 \mu\text{mol m}^{-2} \text{s}^{-1}$. The sky was clear and winds were low ($< 5 \text{ m s}^{-1}$). Chlorophyll and attenuation coefficients in the water column were measured 9 times from dawn to dusk. Benthic pigment and light attenuation coefficients were measured at dawn, midday and dusk, as were the PI responses of both the suspended and benthic algae. Production was calculated from interpolated values of these parameters at the remaining sample times. Of the parameters measured, only the suspended chlorophyll content, the attenuation coefficient in the water and P_m of the suspended algae showed significant ($p < 0.05$) diel variation (Fig. 5a, b, c). Changes in chlorophyll concentration were only

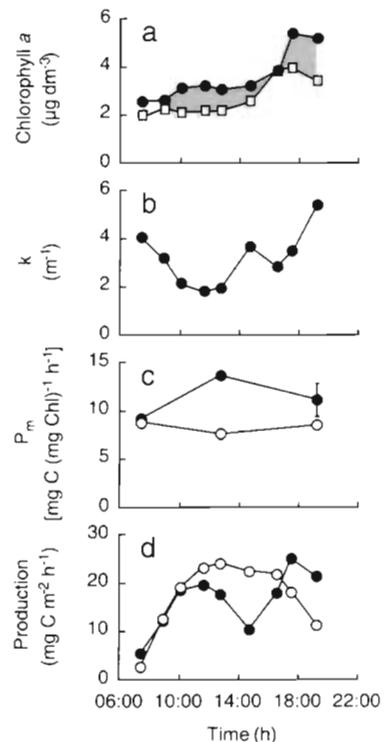


Fig. 5. Diel variation of the parameters used to model production in the surficial millimeter of sediment (○) and the water column (●) at Site SJ85 on 28 July 1986. (a) Suspended chlorophyll at the sample site (●) and at a 3 m deep site 10 m distant (□). Stippled area between curves is the 'resuspended' fraction in the 3-compartment model of production (see 'Results'). The SDs of triplicate estimates are smaller than the symbols plotted. The chlorophyll concentration in the sediment compartment was 5 mg dm^{-3} , 3 orders of magnitude higher than the concentrations shown for the water column. (b) Diffusion attenuation coefficients (k) in the water column. The SDs of quadruplicate estimates are smaller than the symbols plotted. The attenuation coefficient in the sediment was 4.7 m^{-1} , 3 orders of magnitude higher than that in the water column. (c) Photosynthetic capacity, P_m , in the water column and surficial sediment. Error bars are the range of 2 independent estimates. (d) Hourly rates of production, expressed per unit area, in the water and surficial sediment, in the 2-compartment model. Areal production, $P(z,t)$ (Eq. 3), is the area under each curve

weakly correlated ($R^2 = 0.23$) with changes in the attenuation coefficient. The chlorophyll concentration and light attenuation coefficient in the surficial sediment were 3 orders of magnitude higher than in the water: mean chlorophyll concentrations were $5.0 \text{ mg chl dm}^{-3}$ vs $3.1 \text{ } \mu\text{g chl dm}^{-3}$, and mean attenuation coefficients were 4.7 mm^{-1} vs 3.0 m^{-1} in the sediment and water, respectively. The *PI* responses of the benthic and suspended microalgae were similar (Fig. 5c).

When production was assigned to the sediment and water column in the 2-compartment model, the photosynthetic rates in the 2 compartments were similar (Fig. 5d), as were rates of daily gross production (Table 1). However, it is likely that much of the chlorophyll in the water at the sample site was resuspended from the benthos: chlorophyll concentrations measured in water 3 m deep, 10 m distant from the sample site, were on average 35% lower than at the sample site (Fig. 5a). We assume that the difference between chlorophyll concentrations in the deeper water and at the sample site is due to resuspension of benthic microalgae at the sample site. As a first approximation, then, we partitioned production into 3 compartments, distributing production in the water between the 'phytoplanktonic' fractions (the chlorophyll at the deeper subsite) and the 'resuspended' fraction (the difference in chlorophyll concentration between the shallow and deeper subsites, shown as the stippled area in Fig. 5a). When production was distributed in the 3-compartment model, the contribution of the benthic microalgae to total areal production rose from 53 to 64% (Table 1). As there was a bias in the measurements of light attenuation in both sediment and water column (see 'Methods') and as some undetermined fraction of the 'phytoplankton' at the deeper site are probably resuspended benthos, this is likely still a conservative estimate of the role of benthic microalgae.

Table 1. Distribution of production between the sediment and water column at SJ85, 28 July 1986. Production is calculated in 2-compartment and 3-compartment models, as described in 'Results'. Areal production [$P(z,t)$] was calculated according to Eq. (3). Total areal production is the sum of production in the 2 or 3 compartments

Model Compartment	Areal production ($\text{mg C m}^{-2} \text{ d}^{-1}$)	% Total areal production
2-compartment		
Benthos	220	53
Suspended microalgae	193	47
3-compartment		
Benthos	220	53
Resuspended benthos	45	11
Other suspended microalgae	148	36

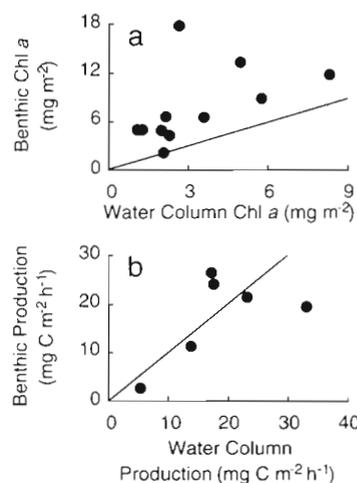


Fig. 6. Comparison of chlorophyll content and production rates in the surficial millimeter of sediment and the overlying water. Lines represent 1:1 relationships. (a) Chlorophyll data collected at all 3 sites between 16 July and 30 July 1986. (b) Production rates of samples from Site SJ85, collected between 28 and 30 July 1986. Only samples on which photosynthesis-irradiance (*PI*) curves were measured (as opposed to those for which *PI* parameters were interpolated) are shown

A comparison of the biomass and productivity associated with the benthos and water column in these shallow-water environments, as calculated by the 2-compartment model, is given in Fig. 6. The chlorophyll content of the surficial millimeter of sediment is equal to or exceeds that of the overlying water (depth 0.2 to 0.6 m). Hourly production rates in this surficial millimeter are comparable to those in the overlying water, the much greater abundance of algae in the sediment being offset by the reduced availability of light. Although we present only a small number of comparisons, equal partitioning of production between the sediment and water or a higher contribution by the benthos has been demonstrated in other environments (Grøntved 1960, Cadée & Hegeman 1974, Hargrave et al. 1983, Varela & Penas 1985).

DISCUSSION

The presence of photosynthetically competent algae well below the depth to which light penetrates the sediment has been documented previously (Pamatmat 1968, Steele & Baird 1968, Gargas 1970, 1971, Hunding 1971, Cadée & Hegeman 1974, Riaux-Gobin et al. 1993). However, this is the first study in which the vertical distribution of chlorophyll concentration and photosynthetic response has been examined on a millimeter length scale. Intercomparison of published reports of benthic pigment concentration is difficult because of the uneven distribution of pigment: various studies

have reported concentrations in the uppermost 0.3, 0.5, 1, 1.3 and 2 cm of sediment. However, the chlorophyll concentrations reported here, when expressed in terms of comparable volumes of sediment, are among the lowest reported in 21 studies on estuarine systems (reviewed in MacIntyre 1988). They are comparable with those reported from northern Spain (Varela & Penas 1985, Delgado 1989) and an order of magnitude lower than those from the northeast United States and Canada (Sanders et al. 1962, Hargrave et al. 1983) and Holland (Cadée & Hegeman 1974, Colijn & de Jonge 1984).

The vertical distribution of microalgae in the sediment can be ascribed to migration and/or physical transport. Benthic diatoms are capable of migrating at speeds of 10 to 27 mm h⁻¹ (Hopkins 1963), reaching depths of 5 cm or more in undisturbed sediment over a period of 2 to 20 d (Fenchel & Straarup 1971, Cadée & Hegeman 1974, Admiraal et al. 1982). Phototactic migration, with species-specific differences in response, can result in a surface maximum and microzonation by species and size (Hopkins 1963, Round 1979a, b, Admiraal et al. 1984, Baillie 1987). Migration alone, therefore, could account for both the presence of algae well below the illuminated layer of sediment and the floc at the surface. Alternatively, the vertical distribution could be caused by physical mixing of the sediment and associated algae by the overlying water. Mixing to a depth of 5 cm in 24 h has been demonstrated under controlled conditions, with a current velocity of 20 cm s⁻¹ at 15 cm above the sediment surface (Jennes & Duineveld 1985). Different rates of resuspension and resettling of algae and sediment have been demonstrated under controlled (de Jonge & van den Bergs 1987, Delgado et al. 1991) and field conditions (Baillie & Welsh 1980, de Jonge 1985). Such a mechanism could account for the observed vertical distributions of chlorophyll and photosynthetic responses by overwhelming any migration. The fraction of sediment and associated flora that was reworked regularly would constitute the layer of homogeneous chlorophyll content. That fraction of the algae with a rate of settling slower than the sediment would constitute the surficial floc. The presence of viable microalgae below the mixed layer would reflect either downward migration out of the mixed layer or deposition by stronger episodic mixing, followed by grazing or chlorosis in response to prolonged darkness.

Sediment at the 3 sites described here is subjected to strong tidal action because of proximity to the Aransas Pass, which links Corpus Christi Bay and the Laguna Madre with the Gulf of Mexico. Further strong currents are generated at CP1 by the passage of oil tankers en route to Corpus Christi. Consequently, these sediments are probably subjected to greater

shear stress than those in more sheltered locations. However, we have found similar homogeneous distributions in San Antonio Bay, Texas (MacIntyre & Cullen unpubl. data), in which tidal currents are less focused and boat traffic less prevalent than near Aransas Pass. The experimental enclosure of sediment at SJ85 suggests that physical mixing over periods of less than 24 h is responsible for maintaining the characteristically homogeneous vertical profiles of chlorophyll concentration. Although the cores interrupt the flow regime of the overlying water and would restrict the activity of grazers, it is unlikely that these would cause the observed increase in chlorophyll to a depth of 10 mm in the sediment. We attribute this to migration in the absence of strong physical mixing.

The depth profiles of the photosynthetic parameters are similar to those of chlorophyll, although P_m shows some vertical differentiation not seen in the pigment profiles at SJ85 and AP6. It is possible that the observed depth profiles of photosynthetic parameters arise as a consequence of the technique used to estimate chlorophyll concentrations, which were nominally corrected for 'phaeopigments' by acidification. While this technique can distinguish between chlorophyll and phaeophorbide or phaeophytin, it cannot distinguish between chlorophyll and chlorophyllide, which may be a major breakdown product (Lorenzen & Jeffrey 1980). If there were any variation in the proportion of chlorophyll to chlorophyllide with depth, the values of P_m and α (which are normalized to chlorophyll plus chlorophyllide) would appear to vary with depth in the absence of any real differences (i.e. as normalized to chlorophyll alone). Assuming, though, that physical mixing is responsible for the vertical profiles, there are 2 mechanisms that could give rise to this. The first of these, discussed above, is sorting with depth in the sediment. If the microalgae were sorted with resuspension and deposition of the benthos and if there were species-specific differences in photosynthetic response, there would be a vertical differentiation of photosynthetic efficiency and capacity in the sediment. It is likely that this is the mechanism responsible for the variable patterns of photosynthetic response in the flocculent surficial millimeter of the sediment. The second mechanism that might cause the vertical differentiation is a progressive physiological response to darkness. Many microalgae, and in particular diatoms, are able to survive long periods (days to weeks) of darkness (Smayda & Mitchell-Innes 1974) but show a progressive reduction in both P_m and α (Yentsch & Reichert 1963, MacIntyre & Cullen unpubl. data). The reduction in these 2 parameters in the deeper sediment could reflect an increasing duration of burial with depth. Variability of photosynthetic responses within the layer of homogeneous chloro-

phyll concentration, as occurred with P_m at SJ85 and AP6, could reflect different time-scales of change in cellular chlorophyll content and photosynthetic response (cf. Lewis et al. 1984, Cullen & Lewis 1988). Post et al. (1985) have demonstrated that cellular chlorophyll quota is slower to respond to a reduction in light intensity than photosynthetic efficiency or the turnover time of photosynthesis (hence photosynthetic capacity) in the diatom *Thalassiosira weissflogii*; a similar suite of response times may characterize responses to darkness.

The effects of current-induced mixing extend beyond the distribution of microalgae within the benthos. Although there is a vast reservoir of photosynthetically competent algae within the benthos, the very rapid attenuation of light in sediment restricts their potential for photosynthesis to the upper millimeter of sediment. This disproportionate fraction of the microalgae contributed only 50% of total areal production under optimal conditions for benthic production, where the overlying water was shallow and clear so that the sediment was well illuminated. Although Corpus Christi Bay and most of the other bays along the coast of Texas are shallow (1 to 3 m in depth), most are also very turbid, so benthic production (*sensu stricto*) is restricted to those sediments at the margins, where light reaches the bottom. The contribution of the microphytobenthos when resuspended is potentially more important to total areal productivity. If benthic microalgae alone were resuspended into the comparatively well-lit water column, total areal productivity would rise. However, any sediment that is resuspended will offset this trend because of the increased turbidity of the water. The effect of resuspension on areal productivity will depend on the relative magnitude of these opposing factors. Although it is not possible simply to separate advection from resuspension, it is clear that there can be profound changes in suspended chlorophyll and light attenuation over a period of hours. Moreover, changes in chlorophyll concentration may be only weakly correlated with changes in turbidity. Therefore, it is not possible to predict the effect of resuspension on total areal production without a better understanding of the complex dynamics of resuspension of microalgae and sediment.

CONCLUSION

We have presented a method for examining the photosynthetic responses of benthic microalgae in well-worked sediments, on spatial scales appropriate to their distribution in the sediment. A small number of observations suggest that photosynthesis by microphytobenthos *in situ* is confined to a flocculent surficial

layer and that this flocculent layer may contribute significantly (up to or more than 50%) to system primary production in the very shallow (< 1 m) waters of Corpus Christi Bay. Microalgae in the floc have photosynthetic responses comparable to those of algae suspended in the overlying water and may have an important role in photosynthesis when resuspended into the water column.

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