

Oxygenic photosynthesis and light distribution in marine microbial mats

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Introduction

Marine intertidal sediments are often colonized by dense populations of phototrophic microorganisms forming stratified communities with diatoms at the very surface and an underlying population of cyanobacteria (Stal et al. 1985). Underneath the layers of oxygenic phototrophs, purple and green sulfur bacteria frequently form additional colored bands (Nicholson et al. 1987). Microalgae in the top layers shade the underlying sediment of those regions of the light spectrum which they preferentially absorb (Jørgensen et al. 1987; Pierson et al. 1987; Lassen et al. 1992b; Ploug et al. 1993). The distinct stratification, which is often observed for different types of phototrophic organisms, may thus be strongly influenced by their complementary utilization of the light spectrum. Below the layers of the oxygenic phototrophs, scalar irradiance in the visible spectrum (400-700 nm, PAR) is depleted 10-100 times more than light in the near infrared spectrum (NIR) (Pierson et al. 1990; Lassen et al. 1992b; Kühl and Jørgensen 1992). The NIR absorption bands of the bacteriochlorophyll-protein complexes of the anoxygenic phototrophs are essential for the presence of the dense populations of these organisms underneath the oxygenic phototrophs.

It is not known to what extent complementary spectral utilization of the incident light has an ecological significance for the zonation of the oxygenic phototrophs. The extension of the euphotic zone of oxygenic photosynthesis in microbial mats is often only about 1 mm. The aim of the present study was to quantify the efficiency by which available light in sediments is used for photosynthesis, to measure action spectra for photosynthesis and from these data to estimate the extent to which changes in the spectral light composition was of competitive advantage to cyanobacteria over diatoms.

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Photosynthetic efficiency

The investigated microbial mats were collected in August 1990 and 1991 at sheltered sandy sediments of Limfjorden, Denmark, in areas periodically desiccated. Light gradients in the sediments were measured by 70 μm wide fiber-optic scalar irradiance (4π) sensors (Lassen et al. 1992a). Gross oxygenic photosynthesis was measured by the light-dark-shift technique (Revsbech and Jørgensen 1983) using oxygen microelectrodes with a 90% response time of 0.3–0.4 s (Revsbech 1989).

When illuminated at high irradiance, the depth distribution of photosynthesis exhibited a maximum at the very surface and a secondary maximum at 1.0 mm, reflecting the zonation of the dominant oxygenic phototrophs (Fig. 1). At the depth of the secondary maximum, PAR was only 12 $\mu\text{E m}^{-2}\text{s}^{-1}$ i.e. less than 2% of incident irradiance. The efficiency by which the available light was utilized for oxygenic photosynthesis could be calculated by dividing the photosynthetic rates for each depth interval by the scalar irradiance (PAR) at the top of the interval (Fig. 2). At the secondary maximum, the efficiency was 10-fold higher than the efficiency in the upper 0.0–0.6 mm of the sediment when the sediment was illuminated at high irradiance (60% of *in situ* irradiance on a clear day).

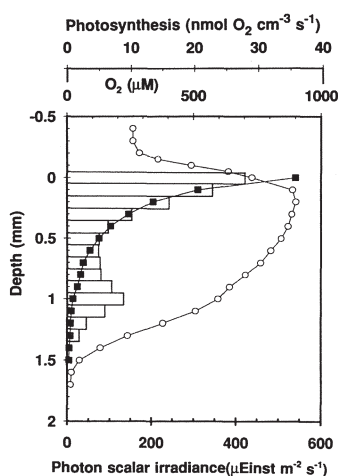


Fig. 1. Depth profiles of photosynthesis (bars), O₂ concentration (○) and photon scalar irradiance (■) in a microbial mat with a dense surface layer of pennate diatoms and an underlying layer of *Oscillatoria* spp. Incident irradiance was 740 $\mu\text{E m}^{-2}\text{s}^{-1}$. Reproduced from *Limnology and Oceanography* (Lassen et al. 1992 b).

The efficiency as calculated here is an ecological parameter and will both depend on the concentration of phototrophs and the efficiency by which the absorbed light is used for photosynthesis. The latter depends on the intensity of incident light and will decrease as the

intensity exceeds the saturation onset parameter, E_k , of the population of phototrophs (4π). At lower irradiances the efficiency will thus increase. The local maximum of photosynthesis and the maximum photosynthetic efficiency at $12 \mu\text{E m}^{-2} \text{s}^{-1}$ were probably an effect of the observed accumulation of cyanobacteria at this depth.

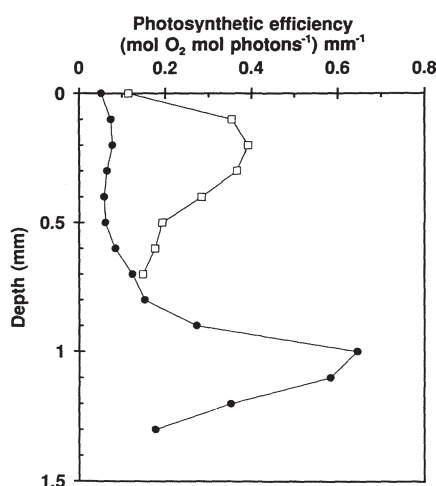


Fig. 2. Photosynthetic efficiency at 740 (●) and $55 \mu\text{E m}^{-2} \text{s}^{-1}$ (□). Data (●) calculated from Fig. 1. Reproduced from (Lassen et al. 1992 b) with permission from the publisher.

Light quality

To analyze the ecological significance of measured differences in spectral photosynthesis for the zonation of diatoms and cyanobacteria, the relative quality of the ambient light was calculated for the two populations as a function of depth (Ploug et al. 1993). The relative light quality was calculated from measured action spectra for photosynthesis for the two populations and the spectral distribution of scalar irradiance in the sediment. At the top of the sediment, the spectral distribution of scalar irradiance changed dramatically due to absorption by diatom photopigments, and the spectral window of 550-650 nm constituted an increasing part of the available light with depth (Fig. 3). Light in this part of the spectrum was efficiently used for photosynthesis by the cyanobacteria. Relative to the quality of PAR incident at the surface, the light quality for the diatoms decreased to 85% at 1 mm depth whereas the relative light quality for the cyanobacteria increased to 107% at this depth (Fig 4). In other words, the cyanobacteria at the lower boundary of the euphotic zone had a competitive advantage of 26% over the diatoms due to their relatively more efficient utilization of the light spectrum available at this depth.

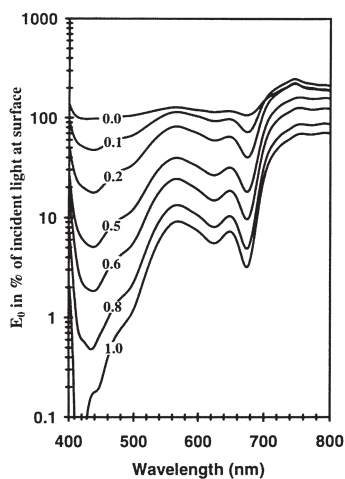


Fig. 3. Depth distribution of scalar irradiance, E_0 , normalized to the incident light at the sediment surface, E_{0d} . The numbers on the curves indicate the depth in the sediment in mm. Reproduced from FEMS Microbiology Ecology (Ploug et al. 1993) with permission from the publisher.

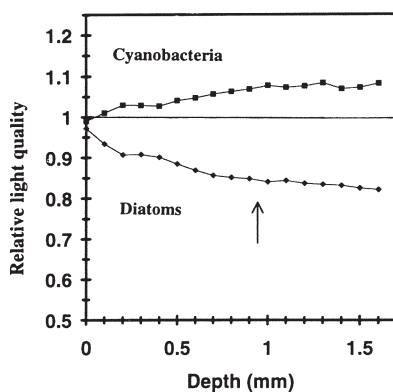


Fig. 4. Changes in the relative light quality with depth calculated from the depth distribution of spectral scalar irradiance (400-700 nm) and the action spectra for photosynthesis of the two phototrophic populations. The value 1 equals no change in relative light quality. The arrow indicates the lower boundary of the euphotic zone. Reproduced from FEMS Microbiology Ecology (Ploug et al. 1993).

The results indicate that complementary utilization of the spectral light can only be one of several factors explaining the zonation of the oxygenic phototrophs. The zonation of the cyanobacteria is probably determined by the combined effect of light and chemical microgradients.

High resolution photosynthesis measurements

Gross photosynthesis was in these studies measured by the light-dark-shift method using a strip chart recorder. The extension of the zone of oxygenic photosynthesis in these microbial mats was only about 1 mm resulting in steep gradients of O_2 between the most active regions and the surroundings. After the onset of darkness, the diffusional fluxes of O_2 will therefore change very fast. By computer simulation it has been shown that the photosynthesis profile as measured by this method will underestimate the photosynthetic rates in the most active layers and overestimate the rates in adjacent layers (Revsbech et al. 1986; Glud et. al 1992). For this reason, an improved method was developed where initial rates of oxygen decrease after darkening were estimated from 3rd order polynomial fits to the oxygen curve within the first 0.3-4.0 s after darkening recorded by a personal computer (Lassen et al., in preparation). The initial rate of oxygen decrease was calculated as the slope of the polynomial in 0.3 s (90% response time of the electrode).

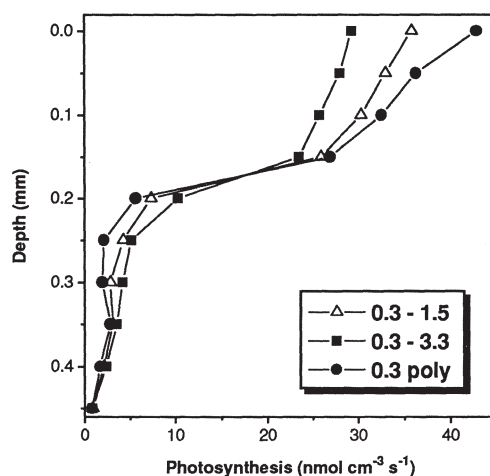


Fig. 5. Gross photosynthesis in cyanobacterial mat from Limfjorden, Denmark. The photosynthetic rates were calculated from 3rd order polynomial fit to the interval 0.3-3.0 s after darkening (0.3 poly) or from linear regression to the indicated intervals (s). The water flow above the sediment was 4-5 $cm s^{-1}$. Adapted from Lassen et al, manuscript in preparation

In a microbial mat with a dense surface layer of cyanobacteria, maximum photosynthetic rates calculated from the polynomial were 18% higher than the rates calculated from linear regression to the interval 0.3-1.5 s (Fig 5). Just below the highly photosynthesizing layer, photosynthesis calculated from the linear regression was in contrast 98% higher than the rates calculated from the polynomial. These differences reflect the different spatial resolutions of the two methods, and the underestimation of the rates in one layer using linear regression is to

some extent counterbalanced by an overestimation in other layers. But due to diffusion of O₂ from the sediment to the water, the depth integrated photosynthesis will systematically be underestimated by the linear regression method. In these measurements the depth integrated photosynthesis calculated from the polynomial was 5% higher than calculated from linear regression. For detailed studies of light-photosynthesis properties in microbial mats, the higher resolution of the photosynthesis measurements when polynomial fits are used, can be essential.

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