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Photosynthesis rates in cyanobacteria-dominated sub-tidal biofilms near Zanzibar, Tanzania

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Abstract

The surface cover (during 1998) and photosynthesis rates (measured intermittently between 1998 and 2000) of submerged cyanobacteria-dominated biofilms near a patchy reef in Zanzibar were determined using a line intercept transect method and pulse-amplitude modulated fluorometer (PAM), respectively. The biofilm surface cover ranged between 5 and 56% with an annual average value of 25%. Photosynthetic activity on deep-dwelling biofilms was low light adapted compared to shallow-dwelling biofilms. Biofilms also regulated their photosynthetic activity depending on the light regime over the day, manifesting high light utilization coefficient (α), light saturation index (E_k) and maximum electron transport rate (ETR_{max}) values at around noon compared to morning and evening measurements. We calculated carbon fixation rates of 0.05, 0.3 and 0.5 kg C m^{-2} y^{-1} for thin (~0.5 mm), medium (~1 mm) and thick (~2 mm) biofilms, respectively, and estimated an overall primary production rate of 0.14 kg C m^{-2} y^{-1} at depths of about 5 m. This study shows that biofilms in the area actively fix carbon and may contribute substantially to the primary productivity of coastal ecosystems. More experiments are required to precisely determine the absorption factor for robust determination of the ETR and to explain the significance of the biofilms on the overall productivity of coastal ecosystems.
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Keywords: microbial mats; biofilms; cyanobacteria; photosynthesis; Zanzibar; Tanzania

1. Introduction

Cyanobacteria often accumulate on coastal sediments, organic debris, coral reefs, rocks and other surfaces and may be the dominant structural and productive organisms on these surfaces (Stal, 1995). The release of photosynthetic products by cyanobacteria attracts other microbes such as sulfate reducing and methanogenic bacteria (Stal, 2001). These accumulations vary in appearance ranging from barely perceptible, mucilaginous coatings known as biofilms to well-developed multi-layered leathery carpets called microbial mats (Paerl et al., 1993). The border between the two forms is not well defined (Stal, 2001).

In recent years there has been an increased interest in biofilms and microbial mats that inhabit intertidal coastal areas and shallow sublittoral zones. This has been attributed to their functional significance in primary production and nutrient cycling (e.g. Underwood and Kromkamp, 1998; Stal, 2000). It is, for example, estimated that ~33% of the total primary production in Mississippi (USA) salt marsh benthic microalgal production comes from microphytobenthos (Sullivan and Moncreiff, 1988). Also, Sorokin (1993) estimated that 20–30% of the total primary production in coral reef systems is associated with microalgal production in

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sediments. In addition, primary productivity levels in some microbial mats are comparable to those in mangrove and rain forests (see Stal, 2000 and references therein).

Measurement of photosynthetic rates and primary productivity in sediment is, however, complicated by the high spatio-temporal variability (patchiness) and the migratory behaviour of the phototrophic organisms inhabiting these communities (e.g. Pinckney et al., 1994; Serôdio et al., 2001). In addition, there has been no common technique for measuring primary production in sediments. Methods used in determining primary production in sediments include the use of oxygen microelectrodes applied in situ (Revsbech and Jørgensen, 1983), photosynthesis chambers in combination with oxygen probes (Johnstone et al., 1990; Uthicke and Klumpp, 1998), ^{14}C-bicarbonate uptake techniques (Sundbäck et al., 1996; Hartig et al., 1998) and, recently, pulse-amplitude-modulated fluorometry (PAM; Hartig et al., 1998; Kromkamp et al., 1998; Barranguet and Kromkamp, 2000). All these methods have their own advantages and disadvantages as discussed by Kromkamp et al. (1998).

The aim of this work was to obtain basic ecophysiological information on cyanobacterial communities that dominate biofilms on reef sediments in the study area, and to establish their ecological role in the productivity of tropical lagoon ecosystems. For this purpose, we estimated biofilm surface coverage and its temporal variability using a line intercept transect method, and photosynthetic activity using PAM chlorophyll fluorescence. The PAM technique is non-destructive, as measurements are performed in situ without the need to remove the phototrophs from the substratum. It is a rapid method for assessing photosynthesis, and allows measurements over larger areas in a relatively short period of time compared to other conventional methods. In addition, parameters measured, such as the minimum chlorophyll fluorescence (F_o), maximum chlorophyll fluorescence (F_m) and the quantum yield of PSII (Y), provide useful information on the physiological status of the phototrophic organisms (Beer et al., 2001).

2. Materials and methods

The study was conducted around a patchy reef connected to a sand dune located north of Bawe Island, about 7 km from Zanzibar town, Unguja Island (Fig. 1). The sublittoral zones of this area were characterised by thin to dense biofilm patches ranging in size from as small as 1 cm^2 to about 20 m^2. Dominant photoautotrophs in the biofilms are cyanobacteria such as *Oscillatoria*, *Lyngbya* and *Anabaena* species (Lugomela et al., 2001). Other microphytobenthic organisms such as diatoms and dinoflagellates are also present but rarely dominate. In addition, animals like nematodes, ostracods and copepods are found intermingled among the photoautotrophs while sea urchins, starfishes, sea cucumbers and finfishes are found grazing on the biofilms.

Water samples for the determination of inorganic nutrients (PO_4^+ and NO_3^-) were taken from just above the bottom (~8 m deep) using a 1.5 l Niskin water bottle. After retrieval, the water samples were filtered through glass fiber filters (GF/F) into acid washed plastic vials and kept cool on ice for transport to the laboratory. In the laboratory, the samples were stored frozen at −20 °C. Analysis was done according to Parsons et al. (1984). Water temperature was determined in situ using a thermometer attached to the water bottle. A temperature logger was also used to monitor water temperature at the site for the whole year, in 1998. Light intensity at the sampling time was determined using a LI-COR (LI-189) photometer. In addition, light measurements over the day were taken on seven occasions at different seasons between 1999 and 2001 using a Stow away-LI light logger (Onset Computer Corporation, Massachusetts, USA). Rainfall and wind speed data were obtained from Zanzibar airport meteorological station.

Biofilm surface cover was quantified using a line intercept transect method (Gates, 1979) during 1998 in order to assess the temporal distribution in the area. Four replicate 10 m long permanent transects were established 5 m apart from each other on the eastern side of the reef. The abundance of visible biofilm patches was estimated by laying plastic fiber tapes on the substratum along transects. The lengths of biofilm cover intercepting the tape were recorded. The percentage cover of the biofilm was then calculated according to the following relationship:

$$\text{Cover}\ (\%) = \text{Total length of the biofilm intercepts} \times 100/\text{transect length} \quad (1)$$

Photosynthetic rates in biofilms were intermittently measured in situ on 20 occasions between September 1998 and April 2000 using a diving PAM (Walz, Germany). The PAM fiber optic was fixed in a 5 ml pipette tip with its tip end cut so as to position the fiber optic a consistent distance of about 2 mm from the sediment surface at an angle of 45°. The fiber optic assembly was then held by hand over the biofilm surface. For Rapid Light Curves (RLCs), the tip of the optic cable was fixed in the leaf clip adapter and held so that the tip of the cable was fixed at a distance of approximately 2 mm from the sediment surface, blocking out all light except that given from the PAM. Point measurements were taken simultaneously with Photosynthetic Photon Flux (PPF) measurements along depth

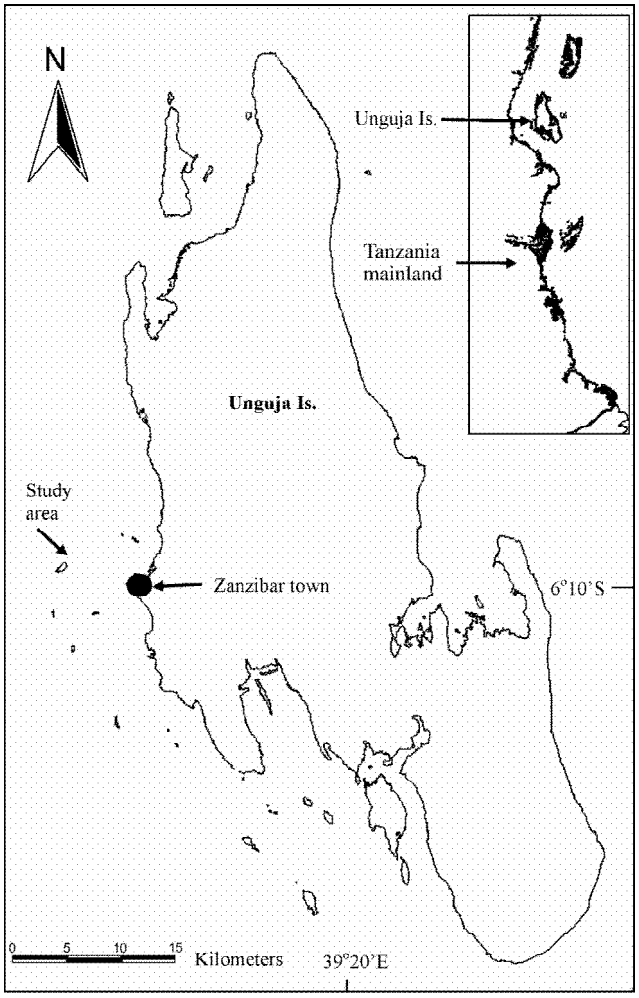


Fig. 1. Map of Unguja Island (Zanzibar) showing the study area (arrow), insert map shows the coastal line of Tanzania mainland.

gradients of 5–20 m. In addition, rapid light curves (three replicates) and 50 point measurements were taken at regular intervals within subdivisions of a 1 m^{-2} quadrat placed on sediments at approximately 5, 10 and 20 m depths. Rapid light curves (three replicates) and 50 point measurements were also taken over the day at the same spots (within subdivisions of a 1 m^{-2} quadrat) at a depth of ~5 m.

In order to determine the relationship between oxygen evolution and electron transport rate, 1 cm^{-2} biofilm samples were enclosed in a Hansatech O_2 electrode chamber. O_2 evolution was measured simultaneously with the quantum yield by inserting the PAM fiber optic connection in the Hansatech chamber above the sample. Light intensities were varied using neutral density filters. Following this, the amount of chlorophyll *a* was determined to get the estimate of the sample biomass.

In order to determine the absorption factor of cyanobacterial biofilms with different thickness subjectively categorized as thin (~0.5 mm thick), medium (~1 mm thick) and thick (~2 mm thick) biofilms in relation to the amount of chlorophyll *a*, light absorbance, transmittance and biomass (Chl *a*) were measured on biofilm sections (1 cm^{-2}) using an Oceanoptics spectrometer (USA).

The effective quantum yield in actinic irradiance (Y) is calculated according to Genty et al. (1989) as follows:

$$Y=(F'_m-F)/F'_m=\Delta F/F'_m \quad (2)$$

where F'_m is the maximum fluorescence in actinic light, F_s is steady-state fluorescence in actinic light, and ΔF is variable fluorescence in actinic light. If the effective quantum yield is measured together with the irradiance, the amount of electrons moving between the PSII and PSI can be calculated. This is termed Electron Transport Rate (ETR) and considered a good parameter for measuring photosynthetic rates in aquatic organisms (see e.g. Beer et al., 2001). In this study ETR were calculated as $\Delta F/F'_m$ multiplied by the incident PPF (measured with the Diving-PAM's quantum sensor), 0.5 and a factor for the proportion of light absorbed by the photosynthetic tissue (AF; see e.g. Beer et al., 2001). For

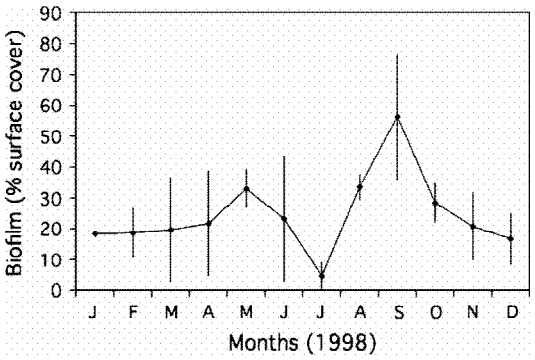


Fig. 2. Temporal variations on the surface coverage of cyanobacterial biofilms at the study site (error bars = SD, $n = 4$).

further explanations of the use and limitations of PAM fluorometry in marine photosynthesis estimations, see e.g. Beer et al. (2001), Beer and Axelsson (2003) and Carr and Björk (2003).

3. Results

A temporal distribution in biofilm cover was noted at the study site (Fig. 2) with a mean ranging from 5% during July to a maximum value of 56% recorded in September. The annual average biofilm coverage was 25%. Environmental parameters recorded during 1998 are shown in Table 1. Water temperature ranged between 26.4 °C in August to 29.5 °C in February. Surface light intensity at the time of sampling varied between 60 μmol photons $m^{-2}s^{-1}$ in March to 1958 μmol photons $m^{-2}s^{-1}$ in September. Wind speed was minimum in February (6 knots) and a maximum of 10 knots was recorded in January, March, April and December. Rainfall in the area was lowest in August, with a total monthly value of 3.8 mm and highest in April, with a total monthly value of 596 mm. Nitrate concentration was not detected in October and November, while the highest level was 1.8 μg l^{-1} recorded in April. Phosphate concentrations were lowest in June and November with a mean of 0.3 μg l^{-1}. A maximum phosphate level of 0.5 μg l^{-1} was recorded in February and March. The data obtained showed a weak positive correlation between the biofilm cover and phosphate concentration ($r^2 = 0.034$, $p = 0.590$, $n = 11$), and between biofilm cover and surface light intensity ($r^2 = 0.053$, $p = 0.552$, $n = 10$). However, a weak negative correlation was observed between biofilm cover and nitrate concentration ($r^2 = 0.059$, $p = 0.425$, $n = 12$), between biofilm cover and water temperature ($r^2 = 0.135$, $p = 0.241$, $n = 12$), and between biofilm cover and wind speed ($r^2 = 0.090$, $p = 0.677$, $n = 12$). Also a weak negative correlation was observed between the biofilm cover and rainfall in the area ($r^2 = 0.003$, $p = 0.867$, $n = 12$).

Variations in ETR and PPF values over a depth profile are shown in Fig. 3. ETR values decreased with depth, mainly as a result of decrease in PPF. As expected, the effective quantum yield of PSII (Y) tended to increase with depth as PPF values decreased and more PSII reaction centres become available (Fig. 4). As expected also, the biofilms at 5 m depth were apparently adapted to higher light intensities compared to those found at 20 m depth as the latter were light saturated and inhibited at relatively lower intensities (Fig. 5). In addition, deep-dwelling biofilms had lower ETR_{max} values. Also, biofilms at deeper depths were more efficient in utilizing low irradiances (i.e. had low light utilization coefficient, α) as compared to those found in shallower areas.

On a diurnal basis, the ETR values also closely followed PPF values over the day while tidal amplitudes seemed to have little effect on both PPF and ETR variations at depths of about 5–8 m (Fig. 6). The

Table 1
Environmental parameters recorded in association with cyanobacterial biofilm coverage at the study site during 1998

Month	PO_4	NO_3	Rainfall	Wind	Temperature	Light
January	nd	1.6	311.2	10	27.8	nd
February	0.48	1.2	177.4	6	29.5	nd
March	0.48	1.4	81.4	10	28.2	60
April	0.33	1.8	595.7	10	29.0	1120
May	0.36	1.2	208.4	8	28.3	866
June	0.30	0.9	44.4	8	28.0	450
July	0.34	0.8	25.9	8	27.0	1719
August	0.33	0.6	3.8	9	26.4	1818
September	0.44	0.6	95.5	8	26.7	1958
October	0.33	0.0	318.4	8	27.9	1875
November	0.30	0.0	354.7	8	28.0	1880
December	0.36	0.8	44.2	10	28.0	1550

Nutrient concentrations (PO_4 and NO_3) are given in μg l^{-1}, rainfall in mm, surface wind speed in knots, water temperature in °C, and surface light intensity in μmol photons $m^{-2}s^{-1}$, nd = not determined.

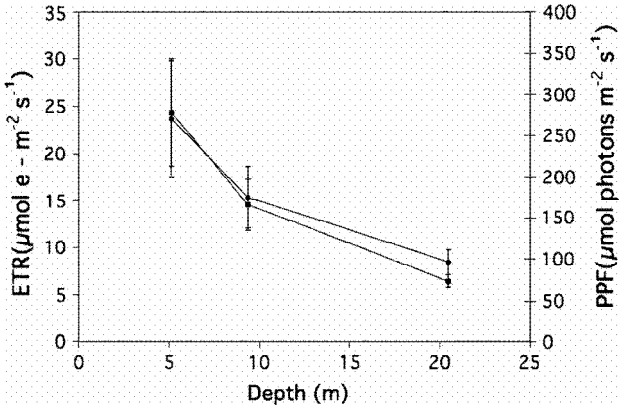


Fig. 3. Variations in ETR (circles) and PPF (squares) as a function of depth on sub-tidal cyanobacterial biofilms in Zanzibar coastal waters (error bars = SD, $n = 50$).

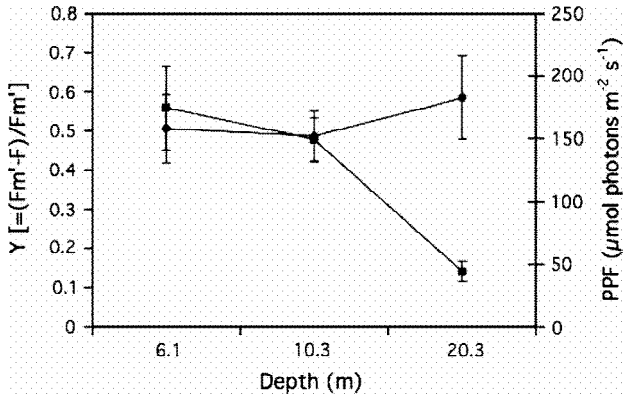


Fig. 4. Variations in the effective quantum yield (Y) of PSII (circles) and PPF (squares) as a function of depth on sub-tidal cyanobacterial biofilms in coastal waters of Zanzibar (error bars = SD, $n = 50$).

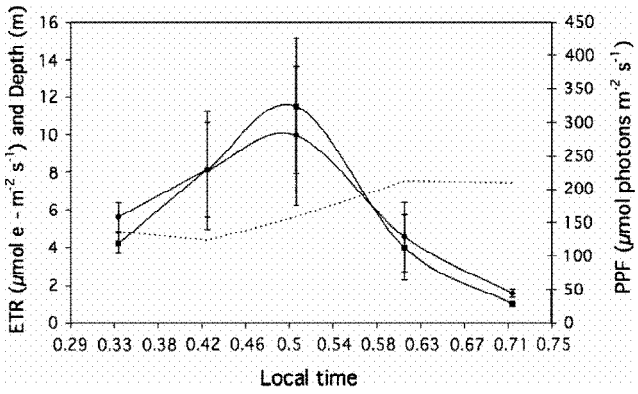


Fig. 6. Variations in ETR (circles), PPF (squares) and tidal amplitude (dashed line) over the day on sub-tidal cyanobacterial biofilms in Zanzibar coastal waters (error bars = SD, $n = 50$).

effective quantum yield of PSII (Y) decreased with increasing irradiance, being high in the morning, declining to minimal values at noon, and eventually increasing to higher values towards dusk (Fig. 7). ETR based PE-curves over the day are shown in Fig. 8. At around mid-day, the biofilms were light adapted, being saturated at higher irradiances, showing higher maximal activity (ETR_{max}) and being inhibited at higher irradiances compared to the morning and dusk measurements. Morning and dusk measurements had a lower light utilization coefficient, α, compared to measurements taken at mid-day. Variations in photosynthetic parameters taken during different sampling days were observed but the general trend remained the same (data not shown).

A close linear relationship between oxygen evolution and ETR values was observed at lower light intensities, while at higher light intensities the linearity tended to deviate (Fig. 9). At even higher intensities, both oxygen evolution and ETR declined, suggesting that there was photo-inhibition. At low light intensity, the ratio of O_2 evolution to electron transport was close to the theoretical value of 0.25, while at higher light intensities, this ratio tended to increase. Our data also show a significant positive correlation ($r^2 = 0.448$, $p < 0.001$, $n = 24$) between the biomass (Chl a) of biofilms and light absorbance (Fig. 10). The equation obtained from this relationship was used to calculate the absorption factor (AF) for biofilms with different biomass categorized as thin, medium and thick biofilms, i.e.:

$$AF = 0.0774x - 0.6092 \quad (3)$$

where x is the biomass (Chl a) for the different biofilm categories. This gave us AF values of 0.03, 0.17 and 0.25 for the three different categories, respectively. From these values, we calculated the daily ETR rate according to Eq. (4) as follows:

$$ETR = Y \times PPF \times AF \times 0.5 \quad (4)$$

where Y is the mean quantum yield obtained over the day from our diel measurement at 5 m depth, PPF is the total photosynthetic photon flux measured over the day; AF is the calculated absorption factor for the different biofilm categories, a factor 0.5 being the assumed light

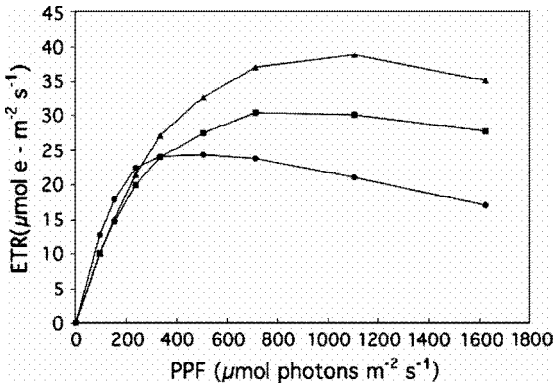


Fig. 5. Variations in PE-curves with depth in sub-tidal cyanobacterial biofilms in Zanzibar coastal waters, symbols: circles = 20.5 m, squares = 9.4 m, triangles = 5.1 m (each curve is a mean of three measurements).

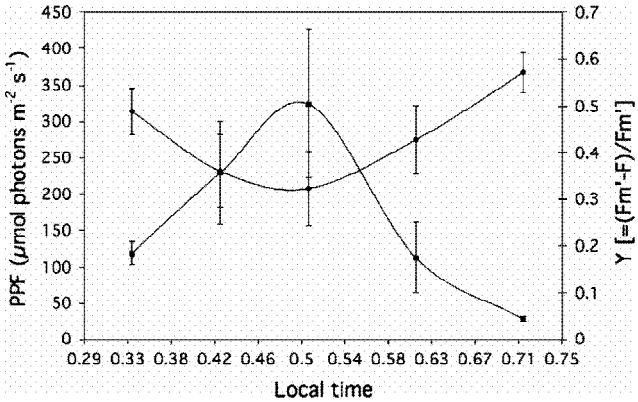


Fig. 7. Variations in the effective quantum yield (Y) of PSII (circles) and PPF (squares) over the day on sub-tidal cyanobacterial dominated biofilms in Zanzibar coastal waters (error bars = SD, $n = 50$).

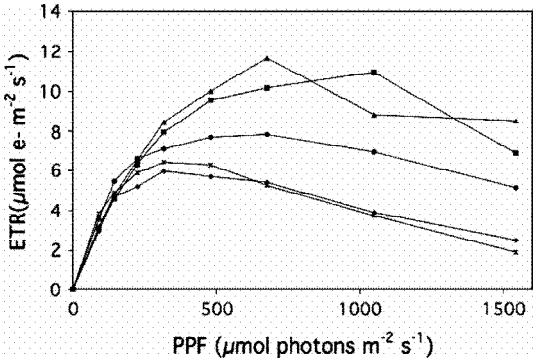


Fig. 8. Variations in the PE-curves over the day on sub-tidal cyanobacterial biofilms in Zanzibar coastal waters, symbols: circles = 0816 hours, squares = 1020 hours, triangles = 1225 hours, diamonds = 1449 hours, stars = 1712 hours (each curve is a mean of three measurements).

absorption of PSII relative to PSI. Assuming the theoretical ratio of 0.25 mol of O_2 evolved per mol of electron transport between PSII and PSI, and assuming a 1:1 ratio between O_2 evolution to CO_2 fixation, we calculated carbon fixation rates of 0.05, 0.32 and 0.48 kg C m^{-2} y^{-1}, for thin, medium and thick biofilms, respectively. Pooling together the medium and dense biofilm fractions as visible biofilm coverage and assuming thin biofilm as equivalent to non-visible biofilms coverage, we extrapolated our production rates to the measured annual visible biofilm coverage of 25% and non-visible biofilm coverage of 75%. This gave us an overall production rate of 0.14 kg C m^{-2} y^{-1} at depths of about 5 m.

4. Discussion

A fluctuation of the biofilm cover without a clear seasonal trend was noted over the study period. This variation showed no significant correlation with any of the measured environmental parameters. The reason for

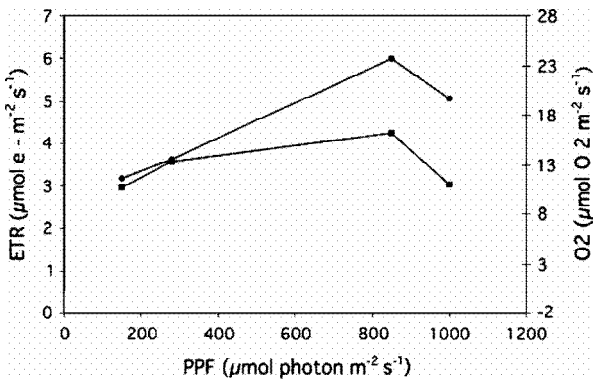


Fig. 9. Relationship between ETR (cycles) and oxygen evolution (squares) on cyanobacterial biofilms collected from Zanzibar coastal waters.

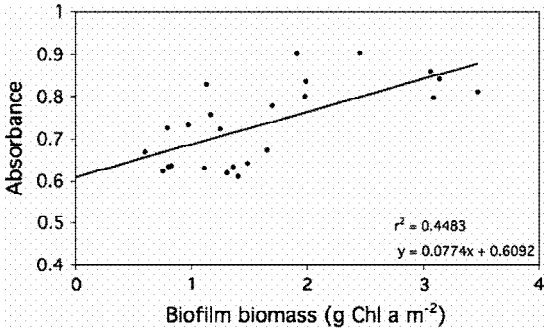


Fig. 10. Relationship between light absorbance and biomass (Chl *a*) by cyanobacterial biofilms collected from Zanzibar coastal waters.

this variation is unclear, though it may be attributed to other parameters such as physical disturbances of biofilms as a result of grazing or water movements and/or bioturbation induced by animals. These factors were not assessed in the current study. Grazing pressure has, in many cases, been reported to be a key factor preventing the development of conspicuous cyanobacterial mats (e.g. Fenchel, 1998; Stal, 2000). Field observation at the study site showed a myriad of animals such as sea urchins, starfishes, and sea cucumbers as well as finfishes grazing on the biofilms (Lugomela, pers. obs.). The high standard deviations observed between different transects measured within a day are due to the high patchiness characterising the development of biofilms in the study area.

The negative correlation between the biofilm cover and nitrate concentration may suggest that the biofilms use molecular nitrogen to supplement their nitrogen requirement. Indeed, Lugomela (2002) reported positive nitrogenase activity on biofilms at the study area. The ability of some cyanobacteria to fix di-nitrogen has been reported to provide them with a competitive advantage, allowing them to flourish during times of extreme low nutrient concentrations (Bautista and Paerl, 1985; Stal and Krumbein, 1985; Joye and Paerl, 1993). In a study in which combined nitrogen was added to microbial mats, the primary production was stimulated (Paerl et al., 1993), suggesting that new sources of biologically available nitrogen are both in high demand and readily utilized to support primary production.

Photo-acclimation of the biofilms to different light intensities were indicated by changes in ETR based PE-curve parameters such as α, E_k, and ETR_{max}. Differences in species composition may have resulted in differences in the light absorption and, consequently, on the observed photosynthetic parameters such as the initial slope of the PE-curves in the light limited range (α). Similar observations have been reported for different phytoplankton species (Geel et al., 1997). However, α differences observed in this study indicate the ability of the biofilms to quickly respond to changes in irradiance. This may be achieved by regulating their

intrinsic functional absorption cross-section of Photosystem II (σ_{PSII}). σ_{PSII} has been shown to be dependent on irradiance and may change rapidly in fluctuating light by means of state transition (Kroon, 1994). Other factors such as variability in species composition might have contributed to the observed variability in photosynthetic parameters, especially on measurements taken along a depth gradient. In addition, vertical migration of microphytobenthos as observed by Serôdio et al. (2001) might have contributed to the observed differences in photosynthetic parameters as a result of redistribution of the photoautotrophs that experienced different light histories.

Seasonal changes in ETR_{max} and E_k have been reported for temperate microphytobenthos from Westerschelde estuary, SW Netherlands (Kromkamp et al., 1998). The authors did not, however, observe any apparent seasonality in maximum PSII quantum efficiency. Nutrient limitations have been noted to decrease the photosynthetic energy conversion efficiency in marine microalgae (Kolber et al., 1988). In the current study, we noted a variation in the ETR_{max} values taken during different sampling dates. This variation may be related to variability in environmental factors such as light, temperature and NO_3 concentrations. It is also possible that this variability resulted from different populations with different absorption cross-sections as a result of differences in biomass or species composition.

The observed non-linearity between oxygen evolution and ETR at higher light intensities is possibly due to the presence of other electron sinks such as photorespiration and Mehler-type oxygen reduction. This situation has been reported before for phytoplankton (Geel et al., 1997) and macro algae (Beer and Axelsson, 2003; Carr and Björk, 2003).

The relationship between the efficiency of PSII electron transport (Y) and CO_2 uptake has been examined under a variety of conditions in higher plants and green algae. A linear relationship in these parameters was found in C4 plants (Krall and Edwards, 1990) and in several C3 plants under non-photorespiration conditions (Harbinson et al., 1990). In the presence of 20% oxygen, a non-linear relationship was observed in C3 plants (Harbinson et al., 1990). Öquist and Chow (1992) reported a curvilinear relationship at high CO_2 levels where photorespiration is reduced but where Mehler-type oxygen reduction still might occur. Measurement taken on microphytobenthos showed a high correlation for maximal production (P_{max} values) between ^{14}C- and fluorescence-based production rates (Hartig et al., 1998). However, the authors observed differences between the two methods for other photosynthetic parameters like α and E_k. Also, Barranguet and Kromkamp (2000) observed a linear relationship between ^{14}C fixation and ETR from PAM measurement at low irradiances. However, at saturating irradiances, the authors observed a non-linear relationship and explained this observation as being due to vertical migration of epipelic diatoms. It will also be of interest in future to compare PAM measurements and ^{14}C fixation in the study area so as to have a better picture of the validity of PAM measurements in carbon fixation in tropical microphytobenthos.

Our results on primary production on thin and thick biofilms are lower compared to those reported by Stal (2000) for microbial mats from Mellum Island, North Sea, and Solar Lake, Sinai, of 1.83 and 2.26 kg C m^{-2} y^{-1}, respectively. This is possibly due to the low biomass of the biofilms in our case as compared to the well-developed microbial mats in the other studies. Our overall primary production estimate (0.14 kg C m^{-2} y^{-1}) is, however, comparable to the gross primary production values ranging from 0.09 to 0.16 kg C m^{-2} y^{-1} reported for fine and coarse sediments, respectively, from the Great Barrier Reef lagoon, Australia (Johnstone et al., 1990). Also, Uthicke and Klumpp (1998) reported net primary production values of 0.17 kg C m^{-2} y^{-1} in microphytobenthic communities from Great Barrier Reef. We believe that the microphytobenthic production benefited the heterotrophic meiobenthos and macrobenthos and pelagic deposit feeders that were seen in association with the biofilms. Microphytobenthos may also be easily suspended in the water column (Varela and Penas, 1985), benefiting other pelagic feeders within the area and/or adjacent biotopes (Ribelin and Collier 1979).

The current study confirms that cyanobacterial dominated biofilms on sediment in the study area are photosynthetically active and may be contributing substantially to the productivity of shallow marine habitats such as coral reef lagoons. This is the first study to employ the PAM technique in measuring microphytobenthic primary production in sediments in the western Indian Ocean. In general this approach has yielded promising results and the instrument can indeed be used to assess primary production in microphytobenthos in tropical coastal areas. More experiments are required, however, to verify the current results and compare them with other conventional methods for measuring carbon fixation in microphytobenthic habitats.

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