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The Photosynthetic Light Dispensation System: application to microphytobenthic primary production measurements

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ABSTRACT: Measurements of microphytobenthos primary production were carried out in the German Wadden Sea in order to test the application of a 'Photosynthetic Light Dispensation System', which was originally developed for photosynthetic research of higher plants. A description of the computer-controlled system, consisting mainly of a subunit providing the irradiance (photosynthetically active radiation, PAR), and a subunit equipped with a Clark-type electrode for measuring oxygen production and respiration processes is given. The system allows rapid and reproducible measurements of photosynthesis-irradiance (*P-E*) curves at light modes predetermined by the computer and simple, rapid data analysis. Additionally, *P-E* curves obtained by this system were compared to those received by simultaneously conducted ^{14}C measurements. Primary production measured by the oxygen method was on average 2.00 times higher than the values obtained by the ^{14}C method. Production rates varied between 1.7 and 4.1 mg C mg chl a^{-1} h^{-1} with a mean of 2.75 mg C mg chl a^{-1} h^{-1}

KEY WORDS: Photosynthetic Light Dispensation System · Primary production · Microphytobenthos · German Wadden Sea

INTRODUCTION

Phytoplankton and benthic microalgae are important primary producers in the water column and on the tidal flats of the Wadden Sea, respectively (Cadée & Hegeman 1974, Colijn 1984). A large number of investigations have focussed on the quantity of microphytobenthic biomass and primary production (Barranguet et al. 1996, McIntyre & Cullen 1996), on the role of the algae in sediment stabilisation processes (Paterson 1990, Yallop et al. 1994) and on the physiological reactions of the algae with changing environmental conditions (Colijn & van Buurt 1975, Admiraal 1977). Determination of microphytobenthic biomass and primary production is an important task in the monitoring of the Wadden Sea, because the algae provide up to a third of the total primary productivity, e.g. in estuarine systems (Sullivan & Montcreiff 1988, Pinckney & Zingmark 1993a, de Jonge 1995). However, due to the extremely heterogeneous distribution of algae, a large number of measurements is necessary to characterise a larger area on a monthly or annual basis, and therefore a quick and reliable measurement method is required. In the past, several methods for measuring primary production, such as the oxygen method (bell jars, microelectrodes) or the ^{14}C technique, have been used. The latter technique supplies data about the incorporated carbon, but an unknown amount of carbon is reassimilated, depending on the duration of incubation. The oxygen method using bell jars and oxygen electrodes provides net community production and community respiration data. During recent years, the use of microelectrodes has been established to measure 'in situ' benthic primary production (Hofman et al. 1991) providing the 'true' gross primary production (Revsbech & Jørgensen 1986), the total produced quantity of oxygen without deducting the losses of oxygen-consuming processes. However, this method does not allow

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reproducible measurements under controlled environmental conditions. These are considered to be important for comparing photosynthetic capacities of algal populations by Dubinsky et al. (1987), who describe a system for measuring phytoplankton photosynthesis in a defined irradiance field with an oxygen electrode. In the present study, a comparable system, a so-called 'Light Dispensation System' in combination with a Clark-type electrode, was used to determine oxygen production of benthic algae. The electrode subunit is connected to a computer-controlled subunit supplying irradiance (photosynthetically active radiation, PAR), which allows measurements of photosynthesis-irradiance (*P-E*) curves in reproducible irradiance conditions. For the photosynthetic parameters we have adopted the terminology of Sakshaug et al. (1997). The aim of this study was to test the application of the Photosynthetic Light Dispensation System to the measurement of benthic primary production, as up to now the system has only been used for photosynthetic research of higher plants and phytoplankton (E. Brammer pers. comm.). Additionally, we compared the results obtained by this method to data from simultaneous ^{14}C measurements.

MATERIAL AND METHODS

Sampling. Samples were taken in June 1996 on the tidal flats of Keitum, located on the east coast of the island of Sylt in the German Wadden Sea (8° 23' E, 54° 54' N). At several locations, thin layers of the muddy sediment surface were scraped with a small spatula and collected in a jar. Because the Photosynthetic Light Dispensation System was originally developed for the measurement of algal suspensions, the algae had to be separated from the sediment. Therefore, the thoroughly mixed sample was transferred into 20 × 30 cm containers and covered with 3 layers of lens tissue (Whatman 105).

The samples were pre-incubated at a constant irradiance of 70 µE m^{-2} s^{-1} during both day and night to stimulate algal migration and to enrich algal biomass on the tissues. Additionally, during the day some parallel samples were pre-incubated in the shade at 210 ± 10 µE m^{-2} s^{-1} and in full sunlight at 1760 ± 120 µE m^{-2} s^{-1}. The following morning, the lens tissue together with the part of the microphytobenthos which was able to migrate into the thin tissue (Eaton & Moss 1966) were harvested from the sediment. The algae in the upper 2 layers of the tissue (the lower layer was still contaminated with sediment) were resuspended in prefiltered (Whatman GF/C) water taken from small tide pools in the sampling area. The algal suspension was cleaned from tissue fibres by decanting over a small sponge in a funnel (Colijn & van Buurt 1975). All measurements were conducted using this concentrated cell suspension.

Photosynthetic Light Dispensation System. Net primary production was measured in the laboratory as oxygen production by the Photosynthetic Light Dispensation System developed by ILLUMINOVA, Sweden. The apparatus consists of a system of 3 subunits connected to a computer (Fig. 1). One subunit (pfd dispenser; pfd: photon flux density) contains a 150 W halogen lamp emitting irradiances over a potential range of 0 to 5000 µE m^{-2} s^{-1} (photosynthetic active radiation). The irradiance is controlled by 3 LI-189 quantum sensors (Li-Cor). The first one is located in this unit to control the emitted irradiance, and the

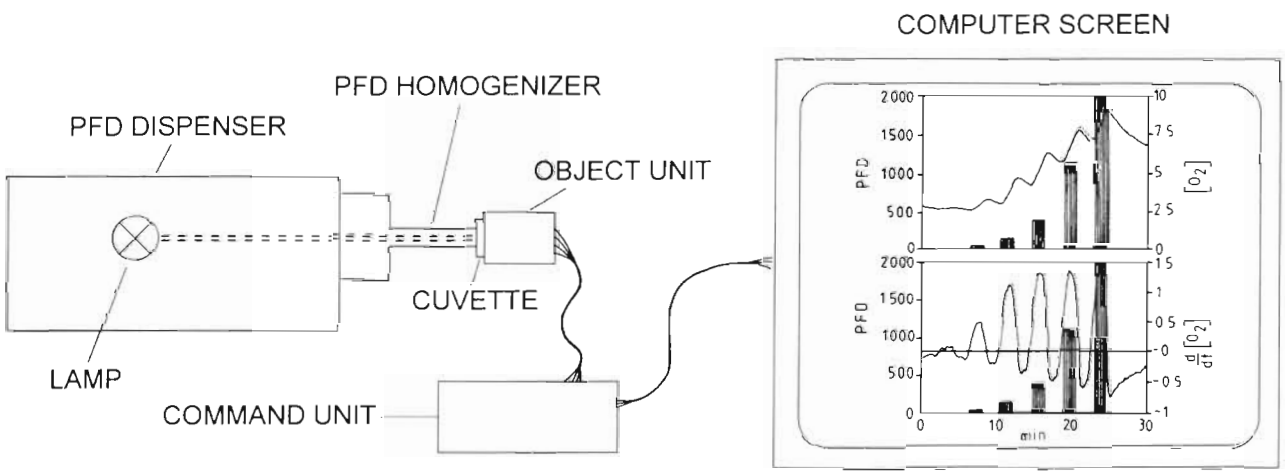

Fig. 1. Scheme of the Photosynthetic Light Dispensation System: pfd (photon flux density) dispenser with halogen lamp, object unit with measuring cuvette, command unit and computer screen showing an example of a measurements result, the absolute oxygen content and the change of the oxygen content per unit time at different irradiances

second at one side of the measuring cuvette (part of the second subunit: object unit) to measure the quantity of light not reaching the cuvette. The third is located at the bottom of the cuvette to measure the absorbance of irradiance by the sample. Irradiance absorbance of the algal suspensions in the cuvette was always less than 10%. Uniform illumination of the cuvette window was achieved by a light homogenizer, a polished aluminium tube which connects the pfd dispenser to the cuvette in such a way that all supplied light reached the cuvette window. The object unit contains the cuvette into which the 3 ml sample is injected by a small syringe. The algal cells in the cuvette are kept in suspension by a small magnetic stirrer, driven by a 24 V motor located behind the cuvette. Oxygen concentration was measured by a Clark-type electrode MI-730 (response time <20 s; Microelectrodes Inc., USA), inserted at the back of the cuvette. The temperature of the measuring suspension was controlled by a connected refrigerated water bath. The third command unit connects the other subunits to the computer and is fitted with several controlling devices, e.g. for regulating the stirrer's velocity, to change between manual or computer-controlled measurements, and for calibration procedures, e.g. for adjusting zero and 100% oxygen saturation, as well as several vacant spaces for external light and pH meters.

Measuring procedure. Each day prior to the measurements the system was calibrated against air-saturated seawater at the experimental temperature (= 100%), and against a 0% oxygen solution using a saturated Na_2SO_3 solution. One measurement of a *P-E* curve took about 40 min, and 2 parallel measurements of each sample were performed. Measurement started with 2 min of darkness, followed by a stepwise, successive increase of irradiance. Each irradiance step lasted for about 3 min, and the samples were subjected to another 2 min of darkness at the end of the measurement to determine the respiration rate. Two different schemes of irradiance steps were tested: 7, 12, 20, 40, 55, 80, 125, 220, 335, 400 and 595 µE m^{-2} s^{-1} to obtain fine resolution of the initial slope of the curve, and 40, 90, 135, 185, 325, 460, 695, 930, 1160, 1400 and 1870 µE m^{-2} s^{-1} to span the range of maximum natural irradiances. The sample temperature during the measurement was held constant at 18 ± 0.1°C. All measured data (oxygen concentration and changes with time, e.g. production as well as respiration, temperature, velocity of the stirrer, emitted irradiance by the pfd dispenser and irradiance measured at the bottom of the cuvette) were transferred immediately to the computer, allowing online-monitoring of the measurement in process. Data analysis was performed immediately afterwards using specifically developed software. Oxygen production was converted to carbon units using a factor of 0.32, assuming a photosynthetic quotient (PQ) of 1.2 (Asmus 1982, Mills & Wilkinson 1986), in order to compare the results to those obtained by the ^{14}C method (see 'Discussion').

^{14}C measurements. Aliquots (2.5 ml) of the algal suspension were incubated simultaneously in a photosynthetron at 18 ± 1°C (for more detailed description see Hartig et al. 1998, this volume). Irradiance was supplied by a quartz-halogen lamp, and the gradient of 11 different irradiances was generated by metal netting. Radioactive $NaH^{14}CO_3$ (0.5 µCi) was added to glass vials containing the algal suspension and a known inorganic carbon content. After a 1 h incubation, the suspensions were filtered over a membrane filter of 0.45 µm pore-size. Uptake of radioactive carbon was measured by a Tri-Carb 1900 TR, Packard Instruments, liquid scintillation counter.

All photosynthetic rate data (O_2 and ^{14}C) were normalised to chlorophyll *a*. Photosynthetic efficiency (α) and the light saturation constant (E_k) were calculated according to Megard et al. (1984).

Physical and chlorophyll measurements. Water temperature, pH and salinity were measured in small tide pools near the sampling locations. *In situ* irradiance was measured by a 2π LI Q 12331 quantum sensor connected to a LI-1000 data-logger (Li-Cor, USA).

Water content of the sediment samples (in %) was calculated by subtracting the sediment dry weight from the wet weight, dividing this value by the wet weight, and multiplying the resulting value by 100. Dry weight was determined after drying the samples at 60°C for 24 h. The organic content was calculated as loss on ignition (in %) after combustion at 500°C for 2 h (Greiser 1988). As an index of algal biomass, chlorophyll *a* was determined using a Thermo Separation Products HPLC system according to the method of Mantoura & Llewellyn (1983), as modified in Hartig et al. (1998).

In order to relate algal primary production to the dominant algal species, samples were inspected by light microscopy. To enable identification of the diatom species, organic cell compounds were removed by a treatment with sulphuric acid, potassium permanganate and oxalic acid (Hasle & Fryxell 1970) and embedded in Naphrax.

RESULTS

Environmental conditions, microphytobenthic biomass and dominant algal species

Environmental conditions, e.g. temperature, salinity and pH of the small tide pools as well as water content and loss on ignition as a parameter for the organic con-

Table 1 Environmental data from the sampling site at Keitum, Sylt, Germany

Date	Water temperature (°C)	Salinity	pH	Water content (%)	Loss on ignition (%)
June 6, 1996	26	24.5	8.17	68.9	11.3
June 7, 1996	26	29.3	7.96	69.3	11.8
June 8, 1996	25	35.9	8.06	69.7	12.5
June 9, 1996	20	31.6	8.0	55.2	8.9

tent of the sediment, are presented in Table 1. Water content and the content of organic matter were very high, representative of muddy sediments (Figge et al. 1988). Concentrations of chlorophyll *a* in the algal suspensions obtained using the lens tissue technique, ranged between 0.138 and 2.587 mg l^{-1} (Table 2), but these values do not reflect natural conditions. Due to this technique, the suspension contained only motile algae, which were able to migrate into the tissues. Dominant algae of this suspension were *Gyrosigma acuminatum* and *Navicula flanatica*, followed by *Amphora coffaeformis* and *Navicula digitoradiata*, which together amounted to approximately 90% of the total algal cells.

Photosynthetic parameters

Maximal photosynthetic rates normalised to chlorophyll *a* (P^B_{max}), measured by the oxygen method in the laboratory, varied between 1.7 and 4.1 mg C mg chl a^{-1} h^{-1} (mean of 2.75 ± 0.69 mg C mg chl a^{-1} h^{-1}) (Table 2), with the exception of 1 extremely high value of 11.1 mg C mg chl a^{-1} h^{-1} on June 6 (omitted). Results obtained with the ^{14}C technique ranged between 0.66 and 1.72 mg C mg chl a^{-1} h^{-1} (mean of 1.23 ± 0.46 mg C mg chl a^{-1} h^{-1}). Maximal photosynthetic rate occurred between 350 and 500 µE m^{-2} s^{-1}.

A few examples of the measured *P-E* curves are shown in Fig 2. Measurements of *P-E* curves were performed using a maximum provided irradiance of approximately 600 µE m^{-2} s^{-1} and additionally, a maximum of approximately 1900 µE m^{-2} s^{-1}, to span the range of natural maximum irradiances from 924 to 1933 µE m^{-2} s^{-1}. The curves of both experiments mostly show a saturation of primary production between 300 and 500 µE m^{-2} s^{-1} A slight photoinhibition, e.g. decreasing oxygen production with increasing irradiance, mostly took place at irradiances above 400 µE m^{-2} s^{-1}, which can be observed more clearly in Fig. 2B. Production rates showed a considerable variability during all days and did not seem to be influenced by lower light intensities and temperatures on June 9.

Community respiration (only algae and bacteria due to the lens tissue method) was measured at the end of each incubation and varied between 0.25 and 4.058 mg C mg chl a^{-1} h^{-1} which amounts to between 6 and 99% of primary production.

Physiological parameters of the algal suspensions, such as the photosynthetic efficiency (α) and the light saturation constant (E_k), are listed in Table 3. α, an indicator of efficient use of irradiance by algae, varied between 0.007 and 0.057 (µg C µg chl a^{-1} h^{-1}) (µE m^{-2} s^{-1})$^{-1}$, showing the lowest values [0.007 to 0.023 (µg C µg chl a^{-1} h^{-1}) (µE m^{-2} s^{-1})$^{-1}$] on the first 2 sampling days and higher values [0.016 to 0.057 (µg C µg chl a^{-1} h^{-1}) (µE m^{-2} s^{-1})$^{-1}$] on the last 2 sampling days, the latter being related to measurements up to a maximum irradiance of approximately 1900 µE m^{-2} s^{-1}. E_k was between 55.82 and 297.48 µE m^{-2} s^{-1} and did not show any relationship to the different irradiances. It was, however, interesting that the values decreased after June 7.

Table 2. Chlorophyll *a* content in the suspension and a comparison of photosynthetic rates (P^B_{max}) measured using the ^{14}C and O_2 techniques (net O_2 production data are mean values of 2 parallel measurements)

Sample		Pre-incubation irradiance of the sample (µE m^{-2} s^{-1})	Chlorophyll *a* (mg l^{-1})	^{14}C P^B_{max} (mg C mg chl a^{-1} h^{-1})	O_2 P^B_{max} (mg C mg chl a^{-1} h^{-1})	Ratio (O_2/^{14}C)
June 6, 1996	a	70	0.175	0.96	1.70	1.77
	b	210	1.608	1.38	2.1	1.52
	c	70	0.138	0.66	2.3	3.48
	d	210	1.608	1.62	2.56	1.58
	e	210	1.608	1.67	2.60	1.56
June 7, 1996	a	70	0.420	1.59	2.83	1.78
	b	1760	2.587	0.85	2.10	2.47
June 8, 1996	a	70	0.192	0.67	3.63	5.42
	b	70	0.192	0.66	4.10	6.21
June 9, 1996	a	70	1.132	1.61	3.22	2.00
	b	70	1.132	1.72	3.16	1.84

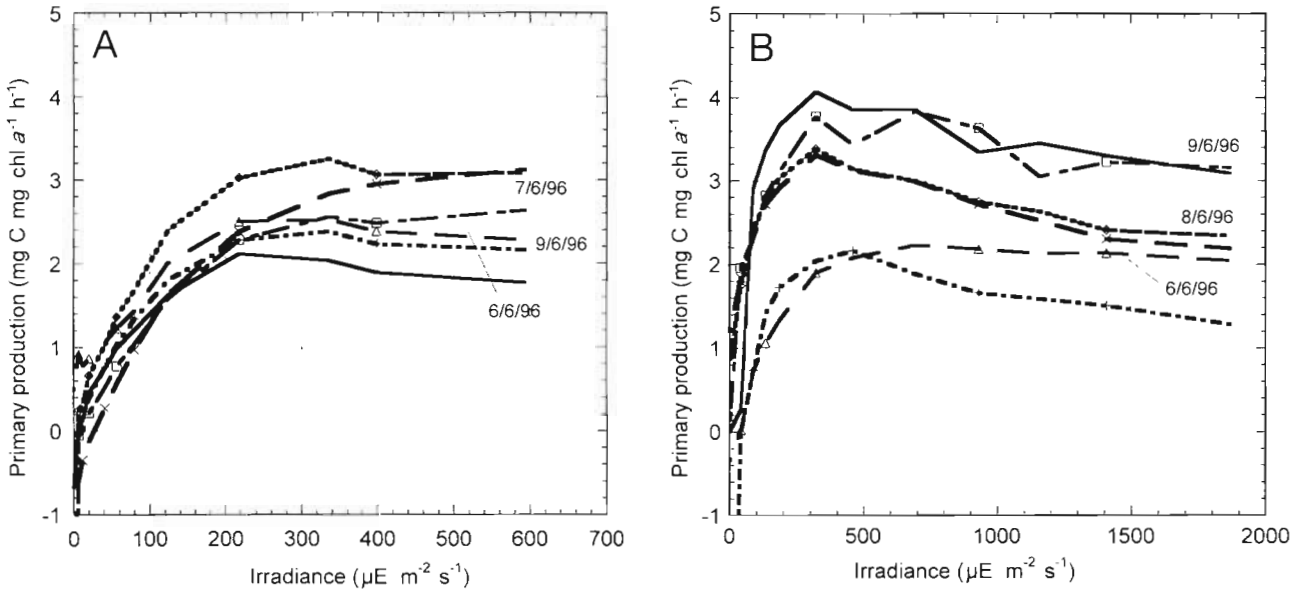

Fig. 2. Microphytobenthos primary production rates (O_2 technique) vs irradiances (A) from 0 to 595 µE m^{-2} s^{-1} and (B) from 0 to 1870 µE m^{-2} s^{-1} Dates given as day/month/year

Table 3. Data of initial slope (α) of the photosynthesis-irradiance *P-E* curves and the light saturation constant (E_k). (*): values are related to measurements at the maximum irradiance of 1900 µE m^{-2} s^{-1}

Date		α [(µg C µg chl a^{-1} h^{-1} (µE m^{-2} s^{-1})$^{-1}$]	E_k (µE m^{-2} s^{-1})
June 6, 1996		0.017	136.77
		0.012	192.19
	(*)	0.009	190.05
	(*)	0.007	227.80
June 7, 1996		0.023	138.44
		0.011	297.48
June 8, 1996	(*)	0.044	93.8
	(*)	0.055	65.46
June 9, 1996	(*)	0.057	56.65
	(*)	0.056	55.82
		0.016	147.34
		0.038	63.58

DISCUSSION

Application of the method

The prime objective of our study was to test the application of the Photosynthetic Light Dispensation System to the measurement of primary production of microphytobenthos in its natural habitat. Several methods to measure microphytobenthic primary production are available. They all have their advantages and limitations, which are discussed elsewhere (Revsbech et al. 1981, Gätje 1992, Wiltshire et al. 1996). During this study, the limitation of the Photosynthetic Light Dispensation System was that only measurements on suspensions, obtained by the lens tissue method, could be conducted. Using this method to harvest microphytobenthos for the measurement of

Table 4. Maximum microphytobenthic photosynthesis rates from different areas

Investigated area	P^B_{max} (mg C mg chl a^{-1} h^{-1})	Method	Source
Ems-Dollard Estuary, Germany	3.4–13	O_2 (Clark-electr.) Lens tissue	Admiraal & Peletier (1980)
Baffin Bay, Texas, USA	2.98–20.01	^{14}C Sediment core	Blanchard & Montagna (1992)
Ems-Dollard Estuary, Germany	0.49	^{14}C Sediment core	Colijn & de Jonge (1984)
Elbe Estuary, Germany	3.94	O_2 (Microelectr.) Sediment core	Gätje (1992)
Bay of Fundy, Nova Scotia, Canada	0.1–7	O_2 (Clark-electr.) Sediment core	Hargrave et al. (1983)
River Avon, Great Britain	3.74	O_2 (Clark-electr.) Lens tissue	Mills & Wilkinson (1986)
Sylt, German Wadden Sea	0.65–1.8, 1.7–4.1	^{14}C O_2 (Clark electr.) Lens tissue	This study

Table 5. Comparison of the ratios of photosynthetic rates (P^B_{max}) measured by ^{14}C and O_2 techniques using a PQ of 1.2 and 1.8

Sample	Pre-incubation irradiance of the sample (µE m^{-2} s^{-1})	Ratio (O_2/^{14}C), PQ = 1.2	Ratio (O_2/^{14}C), PQ = 1.8
June 6, 1996 a	(70)	1.77	1.16
b	(210)	1.52	1.00
c	(70)	3.48	2.29
d	(210)	1.58	1.04
e	(210)	1.56	1.02
June 7, 1996 a	(70)	1.78	1.17
b	(1760)	2.47	1.62
June 8, 1996 a	(70)	5.42	3.56
b	(70)	6.21	4.08
June 9, 1996 a	(70)	2.00	1.31
b	(70)	1.84	1.21

their primary production capacity is only an approximation of true 'in situ' conditions because it is not possible to measure the production of the whole community. The number of cells and species obtained by this method varies depending on the population composition. To estimate *in situ* rates, there is no alternative to measuring in undisturbed sediment cores. This has already been done by several workers (Revsbech & Jørgensen 1986, Brotas et al. 1990, Gätje 1992) using microelectrodes.

The advantages of the Photosynthetic Light Dispensation System over the microelectrode method and the bell jar technique, however, is the precise control of environmental conditions such as irradiance and temperature, the supply of reproducible, rapid measurements of *P-E* curves and the measurement of physiological parameters in all requested light modes, predetermined by the computer. The latter is a new function, not included in a similar system described by Dubinsky et al. (1987). Additionally, there is the advantage of online-monitoring of the measurements, and data analysis is quite simple and rapid, because all data are immediately transferred to the connected computer, on which they are analysed by the integrated software and can be further processed by common calculation programs. Therefore, many measurements, e.g. using cultures of isolated microphytobenthic species, can be conducted very fast to study the physiology of the single species. The disadvantage of the oxygen method in comparison to the ^{14}C technique is the low sensivity of the Clark-electrode. The algal biomass of 0.138 mg chl *a* l^{-1} in the measurements conducted on June 6 is considered to be a minimum if reliable production values are to be obtained. Therefore, the system cannot be used in conditions of lower algal biomass and when there is no possibility of enriching the algal suspensions. However, new, more sensitive electrodes may emerge on the market which could be combined with the described system.

Until now this system has been used for photosynthesis studies on higher plants or macroalgae, but not for sediment-dwelling microalgae (E. Brammer pers. comm.). Additionally, the lens tissue technique had to be used during this study, because fluorescence induction kinetics of the microphytobenthos were measured at the same time by the pulse-amplitude modulated (PAM) fluorescence technique (Hartig et al. 1998). Both methods, the Photosynthetic Light Dispensation System and the PAM technique, were developed for photosynthetic research of higher plants or phytoplankton (Dubinsky et al. 1987, Edwards & Baker 1993, Schreiber & Bilger 1993) and were tested here for the first time for studies on microphytobenthic communities.

Future development steps would be to bring a known amount of sediment containing epipelic as well as epipsammic species into the cuvette to obtain information on physiological parameters of the total algal population. Moreover, it is an advantage to sample sediments of larger areas to get a mixed sample with an average value which could serve as baseline data for modelling microphytobenthic primary production.

Comparison of the production rates and the photosynthetic parameters with data of other studies

It is generally very difficult to compare data of microphytobenthic production obtained by different authors, because different methods (O_2, ^{14}C), various incubation times, and *in situ* and laboratory incubations are used and also because in some studies primary production of the total algal population is investigated, whereas in others only that of the motile, epipelic algae is examined.

Nevertheless, it is common to compare primary production rates of different areas, despite the absence of a standardisation of the method (Gätje 1992, Pinckney & Zingmark 1993b). The obtained production rates of this study were in the same range as those obtained by other authors using different methods and different algal composition (Table 4). In the present study, maximum photosynthetic rates of 1.7 to 4.1 mg C mg chl a^{-1} h^{-1} (with one exception of 11.1 mg C mg chl a^{-1} h^{-1}) were measured with the oxygen method. These values are somewhat lower than the maximum photosynthetic rates found by Admiraal & Peletier (1980)

(3.4 to 13 mg C mg chl a^{-1} h^{-1}) which were also obtained on algae collected using the lens tissue method. In our study, mean maximum photosynthetic rate (O_2 method, data were converted to carbon by using a factor of 0.32 assuming a PQ of 1.2) was 2.75 ± 0.69 mg C mg chl a^{-1} h^{-1} (^{14}C technique: 1.23 ± 0.46 mg C mg chl a^{-1} h^{-1}). The photosynthetic rates found by Mills & Wilkinson (1986), which were also obtained with algal suspensions harvested using the lens tissue method, were slightly higher than our data, which had a mean of 3.53 mg C mg chl a^{-1} h^{-1}. These elevated rates could be caused by the higher temperature during their measurements. The influence of temperature upon the rate of primary production has already been shown by MacIntyre et al. (1996) and Blanchard et al. (1996). Pre-incubation at different irradiances, e.g. in the shade or in full sunlight, seemed to have no influence on the rate of primary production.

Primary production measured with the oxygen method was always higher than that measured with the ^{14}C method. The mean ratio of O_2 and ^{14}C was 2.00 ± 0.59, excluding the extremely variable high ratios of June 8. The relatively high production rates based on the oxygen method in comparison to the ^{14}C technique could be influenced by using a conversion factor of 0.32 (mg oxygen to mg carbon; Asmus 1982, Mills & Wilkinson 1986) and by the chosen PQ of 1.2. The choice of a higher PQ value, common in studies on phytoplankton production (Garcia & Purdie 1994), would lead to a smaller difference; therefore, additional calculations using a PQ of 1.8 were conducted, resulting in less differences between the 2 methods (Table 5) with a mean ratio of O_2 to ^{14}C of 1.31 ± 0.39. However, a lower PQ than 1.8 was chosen by most authors for microphytobenthic primary production, e.g. 1.0 (Hargrave et al. 1983, Barranguet et al. 1994), 1.2 (Asmus 1982, Mills & Wilkinson 1986, Gätje 1992) and 1.3 (Colijn et al. 1983). The nitrogen source is important for the choice of PQ: a higher PQ (1.5 to 1.8) should be taken when nitrate is assimilated and a lower value of approximately 1.25 should be used when ammonia is assimilated (Williams et al. 1979). The latter was true for the algal population at the sampling site of Keitum (R. Asmus pers. comm.).

The differences between the 2 methods could also be caused by the fact that the medium was kept in motion by a stirrer as opposed to the ^{14}C measurements (Hartig et al. 1998). Colijn & de Jonge (1984) and Gould & Gallagher (1990) proposed that the production of microalgae could be enhanced by stirring the overlying water over a sediment core. Also, H. Lindeboom in Colijn et al. (1983) observed a 4.3 to 8.8 higher production measured with the oxygen method (microelectrodes) compared to the ^{14}C technique. It also has to be considered that in this investigation the values obtained by the ^{14}C technique have to be regarded as gross production values because the incubation time was only 1 h (Fast 1993), whereas the results of the oxygen method of this study are net values. The differences in the results of the 2 methods could also be due to the different incubation procedures. During the measurements with the oxygen method, the sample was incubated for 40 min with successively increasing steps of irradiance. For the measurements using the ^{14}C technique, single incubations were conducted, i.e. each subsample was incubated for 1 h at a constant light intensity. In this context, Weger et al. (1989) mentioned that net photosynthetic oxygen evolution is higher when the cells are exposed to increasing irradiance levels than when they are exposed at constant irradiances.

In this study, the *P-E* curves showed a steep initial slope, serving as an indicator of to what extent the algae may use low irradiances. This observation shows the very effective use of low irradiances by the algae. Photosynthetic efficiency α varied between 0.007 and 0.057 (µg C µg chl a^{-1} h^{-1}) (µE m^{-2} s^{-1})$^{-1}$, the latter being slightly higher than the values obtained by Blanchard et al. (1994) of between 0.01 and 0.02 (µg C µg chl a^{-1} h^{-1}) (µE m^{-2} s^{-1})$^{-1}$, but lower than the values [0.04 to 0.08 µg C µg chl a^{-1} h^{-1}) (µE m^{-2} s^{-1})$^{-1}$] obtained by Pinckney & Zingmark (1993a). The light saturation constants E_k of the latter studies were much higher (258 to 648 µE m^{-2} s^{-1} and 581 to 834 µE m^{-2} s^{-1}, respectively) than those calculated during this investigation (56 to 297 µE m^{-2} s^{-1}). Reaching a saturation plateau at lower irradiances may be considered to indicate that the algae are well adapted to low light conditions, which could be due to the pre-incubation at low irradiances. Another explanation may be that another factor was limiting photosynthesis, e.g. carbon dioxide, which could be possible due to the duration of a measurement and the small volume of the measuring cuvette. Differences between the parallel measurements (Table 3) may be caused by the inhomogeneity of the algal suspension or by the calculation program drawing the fit through the measured values.

It has to be considered that our production rates are related only to the motile, epipelic fraction of the algae, which could be caught by the lens tissue method. Therefore, the values should not be used as absolute values to characterise production capacities of this sampling station. When comparing the ratio of epipelic/epipsammic algae of the total community, the various sediment types have to be considered. According to Varela & Penas (1985), 60 to 75% of the total production of the algal population is due to epipsammic algae, whereas Brotas & Catarino (1995) found that the epipelic biomass produce 8 to 87% of total chlorophyll *a*. However, MacIntyre et al. (1996) assume that

migrating algae are likely to dominate microphytobenthic biomass and productivity. Species composition of the total algal population was not investigated, but at this sampling site migrating, epipelic algae dominate (K.-H. van Bernem pers. comm.). This is in agreement with the findings of Epping (1996), who concluded that epipelic diatoms inhabit the mud whereas epipsammic diatoms grow firmly attached to sand grains.

In conclusion, successful application of the Photosynthetic Light Dispensation System depends on the kind of investigations performed. For *in situ* measurements, the Photosynthetic Light Dispensation System may be problematic because of the described uncertainties. However, it proved to be useful for comparative purposes, e.g. investigation of seasonal variation of primary production. Especially for measurements of photosynthetic characteristics of algae, also of microphytobenthos, it seems to be a very suitable tool.

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