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Primary production of microphytobenthos in the Ems-Dollard Estuary*

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ABSTRACT: From 1976 through 1978 primary production of microphytobenthos was measured at 6 stations on intertidal flats in the Ems-Dollard estuary using the ^{14}C method. The purpose of the measurements was to estimate the annual primary production at different sites in the estuary and to investigate the factors that influence the rates of primary production. Therefore benthic chlorophyll *a* and a set of environmental factors were measured. Only primary production correlated significantly with chlorophyll *a* concentration in the superficial (0.5 cm) sediment layer; other factors (temperature, *in situ* irradiance) did not correlate with primary production, primary production rate or assimilation number. Annual primary production ranged from ca. 50 g C m^{-2} to 250 g C m^{-2} and was closely related to elevation of the tidal flat station. However, highest values were also recorded at the station closest to a waste water discharge point in the inner part of the estuary. Annual primary production can be roughly estimated from the mean annual content of chlorophyll *a* in the sediment. Use of different calculation methods results in annual primary production values that do not differ greatly from each other. Also productivity rates did not differ much over most of the estuary, except at the innermost station which showed a high production rate in combination with high microalgal biomass; this could not be explained by the high elevation of the station alone. A hypothesis is offered to explain the limited primary production of microphytobenthic vegetations.

INTRODUCTION

The radio carbon (^{14}C) method (Steemann Nielsen, 1952), although subject to several errors (cf. Colijn et al., 1983) (for review see Peterson, 1980), has been widely adopted to measure phytoplankton primary production in different habitats. With modifications, this method has also been used several times for the measurement of phytobenthos primary production in intertidal areas and shallow coastal seas (Grøntved, 1960; Steele and Baird, 1968; Gargas, 1970; Leach, 1970; Cadée and Hegeman, 1974, 1977; Plante-Cuny, 1978). In other, similar habitats, primary production has further been measured by means of the oxygen bell-jar technique (Pomeroy, 1959; Pamatmat, 1968; Van Es, 1982a; Lindeboom and De Bree, 1982). All these studies aimed essentially at estimating annual primary production and community respiration (in case of oxygen method) and at explaining how these processes are affected by abiotic and biotic factors.

The soft, sandy and muddy, sediments of the Ems-Dollard estuary do not harbour a conspicuous vegetation of macroalgae; however, a thin film of diatoms and cyanobacteria covers the sediment surface. These are the main primary producers on intertidal flats (Cadée and Hegeman, 1974; Admiraal, 1980; Colijn and Dijkema, 1981). The purpose of our study was to measure *in situ* photoautotrophic carbon fixation of sediments at different sites. The programme included measuring chlorophyll *a* content of the superficial layers of sediment; solar radiation; temperature; salinity; tidal emersion during daylight; and characterization of the type of sediment. Considerable effort was devoted to estimating the annual primary production, which can be calculated using a combination of data on tidal emersion and daylight periods. Physiological experiments and field investigations on benthic diatoms from the same estuary were made by Admiraal (1977a, b, c) and Admiraal and Peletier (1980). Results of recent measurements of primary production in the same estuary obtained with the oxygen method, were also available (Van Es, 1982a).

In addition to the factors that directly regulate prim-

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ary production – such as light and nutrients – we were also interested in the effects of indirect factors – such as grazing, burial, tansport, sedimentation, suspension and mortality of microphytobenthos and phytoplankton. Measurements of both phytoplanktic and microphytobenthic production (Colijn, 1978) should elucidate the quantitative importance of organic matter input derived from primary producers in the Ems-Dollard ecosystem as opposed to the allochthonic organic matter input from the North Sea (cf. de Jonge and Postma, 1974), the river Ems and the river Westerwoldsche A (Van Es, 1982b).

MATERIAL AND METHODS

Area and sampling stations

The Ems-Dollard estuary (Fig. 1) is one of the larger estuaries in the Wadden Sea. A particular feature of this estuary is the Dollard, a shallow protected embayment into which the Westerwoldsche A discharges only small amounts of freshwater, loaded with high concentrations of organic matter. For our research, measurements were regularly taken at 6 stations on intertidal flats (Fig. 1); all stations, except Station 2, were situated ca. 600 m from a larger tidal channel (Station 2: 50 to 100 m) to avoid the direct scouring influence of channel water. Stations 3, 5 and 6 were located in the Dollard, and Station 6 is in the direct vicinity of the wastewater outlet. The sediment type at each station has been described by Van Es (1982a: Table 1) and is fairly representative of the range of sediments found in the estuary. No macroalgal growth was found at the stations; however, diatoms with gelatinous tubes occasionally formed macroscopic tufts; their patchy distribution made adequate sampling difficult. All the sampling and measuring were done at low tide.

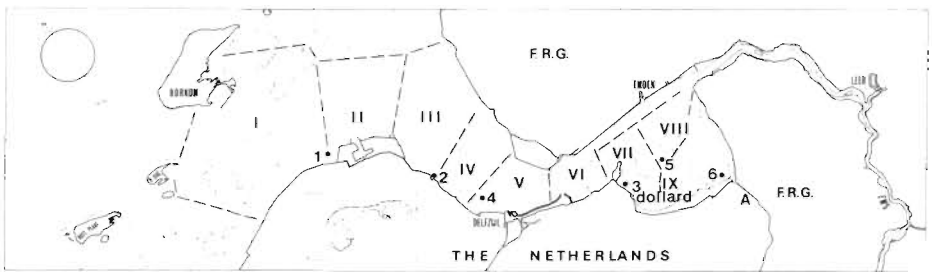

Fig. 1. Ems-Dollard estuary with location of sampling stations: A = Westerwoldsche A

Incubation techniques and sample preparation

Benthic primary production was measured in 3 perspex cylinders (2 light and 1 dark), each 6.0 cm in diameter and 15 cm long, as described by Leach (1970). Immediately after being mixed with 2 to 20 μC ^{14}C, 50 ml water was carefully added to each cylinder through a rubber cap. Remaining air was expelled by pressing the cylinders more deeply into the sediment. The incubators were kept in the sediment for 2 to 3 h. The incubation water was obtained from shallow pools on the tidal flats or from nearby gullies. Following the incubation period, the cylinders were brought to the laboratory or the research vessel in a dark box and processed within 1 h. Inorganic carbon was measured in the incubation water according to the method of Strickland and Parsons (1972). The added amount of ^{14}C was determined threefold. Light and dark serum bottles containing 50 ml of unfiltered incubation water were used as controls: fixation rates in these bottles were negligible and therefore no corrections were applied to fixation rates of the sediments itself. The temperature of the superficial sediments was measured at the beginning and end of the incubation period. For chlorophyll *a* analysis, 20 sediment samples were taken regularly distributed over a 50 × 50 m quadrat with a corer (internal diameter 2.4 cm) in the direct vicinity of the station. Chlorophyll *a* was measured (Colijn and Dijkema, 1981) according to Lorenzen's (1967) method with slight modifications: the upper 0.5 cm thick sediment layer was cut off and put into a centrifuge tube; all samples were deep-frozen and lyophilized to prevent inaccuracies resulting from differences in water content and to facilitate extraction; the dried sediments were extracted in 10 or 15 ml of aqueous aceton (90 %) with the addition of magnesium carbonate, centrifuged off and the supernatants measured in a colorimeter at 664 nm. No corrections for turbidity at 750 nm were made. A correction for pheopigments was made by acidification (Lorenzen, 1967). Irradiance in J cm^{-2} was measured continuously at 10 min intervals at Delfzijl (Fig. 1) with a Kipp solarimeter (Fig. 2).

Measuring ^{14}C activity

Uptake of label was measured as follows: incubation water with a little suspended sediment was filtered

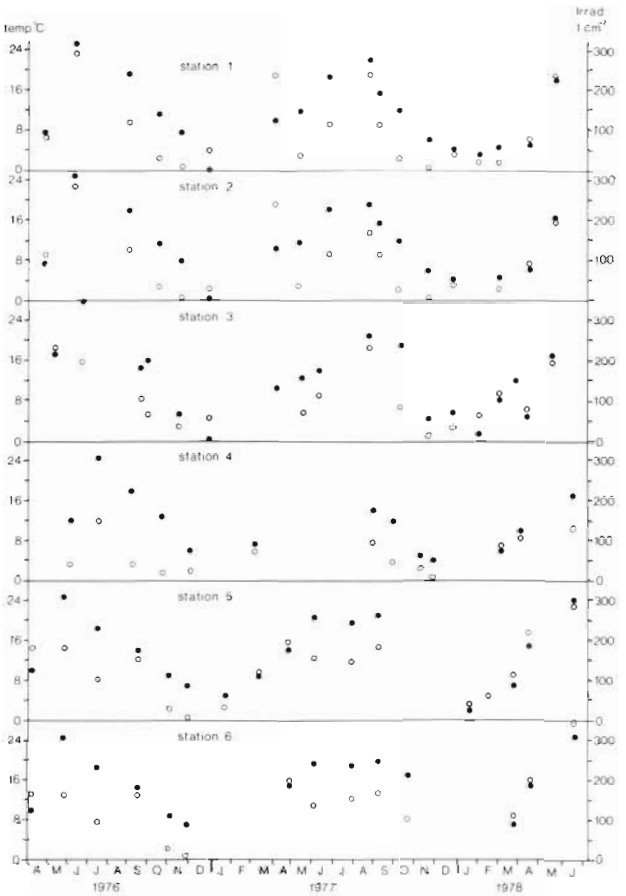

Fig. 2. Temperature (closed symbols) and irradiance (J cm^{-2} h^{-1}) (open symbols) during field incubations

through a GF/C filter (Fraction 1). Then a layer of sediment, 0.5 to 1.0 cm thick, was sliced off the sediment column. Approximately a quarter of this layer was used to make a slurry which was filtered (Fraction 2) and washed with filtered seawater to remove the added inorganic ^{14}C. Both fractions (1 and 2) and the remainder of the sediment were wrapped in weighted alufoils and immediately dried in a stove at 70 °C to prevent further biological activity. Excretion rate was not measured, because other researchers (Cadée and Hegeman, 1974; Darley et al., 1976) have shown that excretion in microphytobenthos is very low (a few % of the totally fixed carbon; see also Chapman and Rae, 1969; Hall and Fischer, 1982). To avoid problems in scintillation counting, a combustion method (Packard 306 Sample Oxidizer) was tested and used for dried sediments as well as for phytoplankton samples on filters loaded with sediment. The method was tested with labelled algae mixed with increasing amounts of sediment. In all cases the recovery of ^{14}C exceeded 95 % (cf. Revsbech et al., 1981). Drying at 70 °C did not result in loss of activity as compared with samples combusted immediately after filtration. Quench curves were made with hexadecane ^{14}C (by weight) as an internal standard, and later with the direct combustion of labelled methyl-methacrylate-^{14}C (New England Nuclear, 35 000 dpm) and paper strips with a ^{14}C standard which contained 5000 dpm (Radiochemical Centre). The scintillation mixture for counting the concentration of added ^{14}C in aqueous samples was composed of BBS-3 (Beckman) 20 % in toluene, and later in an Aquasol Phenethylamine mixture (5:1 v/v) (Iverson et al., 1976). The counting efficiencies were almost the same (ca. 80 %) in these 2 mixtures.

After drying and mixing well in a mortar, 3 sediment subsamples were weighed (ca. 100 mg) and each combusted separately in a piece of filter paper. For all calculations of the total ^{14}C uptake, the weight of the sediment fraction was used, together with the radioactivity of the two filters and in both fractions (1 and 2). All data were expressed in mg C m^{-2} h^{-1}.

Calculations

Hourly fixation rates (Fig. 3B) (not corrected for dark uptake of ^{14}C) were assumed to reflect the net assimilation rates (Williams et al., 1979). These rates were multiplied by the actual emersion period of the day on which these samples were taken, to calculate the daily production (Fig. 3A). The emersion period was determined from the actual recorded tidal curves (Rijkswaterstaat, Meet- en Adviesdienst, Delfzijl) and the elevation of each station. Five different methods were used to estimate annual production (Table 1) and to evaluate possible differences in annual production caused by different calculation methods.

Table 1. Methods for calculation of annual primary production. Effective photoperiod = emersion during daylight

Method I:	Interpolation of hourly rates between measurements × effective photoperiods for all days = production value per day; summation of all daily values gives annual production
Method II:	Hourly rate × effective photoperiod = production value per measuring day; planimetry of resulting annual graph (Fig. 3A)
Method III:	Hourly rate × mean annual emersion period (%) × daylength of measuring day = production value per day; planimetry of resulting annual graph
Method IV:	Monthly average of hourly rates (Stations 1 to 5 and 6) × actual monthly effective photoperiods = monthly production value; summation of monthly values
Method V:	Monthly average of hourly rates (Stations 1 to 5 and 6) × calculated monthly effective photoperiod from model = monthly production value; summation of monthly values

For these calculations average emersion periods during daylight for each station were calculated from a linear regression of the measured annual effective photoperiods against the elevation of the stations (Table 3). Annual production per station was taken as the means of the values over two successive years. Effective photoperiods in Method V were derived from the interaction of daylength and tidal emersion (Colijn, 1982). For all calculations given, we assumed that no irradiance reached the surface of the sediment during submersion (see 'Discussion').

RESULTS

Production and chlorophyll *a* measurements

Daily production values (mg C m^{-2}) and mean chlorophyll *a* data (mg m^{-2}) are given in Fig. 3A, and the actual hourly rates are given in Fig. 3B. Production values per day were calculated by multiplying the hourly rate by the actual effective photoperiod on the day of measurement. Low daily values were found at all stations in winter, especially in November and December. High daily values were recorded both in spring and summer. The measurements at Station 6 were atypical: both chlorophyll *a* and production showed comparatively high values during a large part of the year. The mean hourly rates per month showed a large month-to-month variation in these fixation rates; hourly rates were lowest in November and December, and during the rest of the year higher fixation rates were found almost irrespective of the season. However, if the data from Station 6 were omitted, the mean hourly rate was highest in April.

The fixation rates at Station 6 reached values of up to 100 mg C m^{-2} h^{-1}, or 1300 mg C m^{-2} d^{-1}. The mean hourly rate for all stations over 2 yr was ca. 37 mg C m^{-2} h^{-1}. However, this mean hourly rate was twice as high at Station 6. The mean assimilation number (production rate per unit of chlorophyll *a*, mg C mg chl a^{-1} h^{-1}) for all measurements was 0.67. The maximum mean value (0.49) per station was found at Station 2, the minimum mean value (0.43) at Station 6. However, owing to the wide range in assimilation numbers per station, these mean assimilation numbers per station did not differ significantly from each other (ANOVA, F_o (5,89) = 2,57; $0.05 > P_r > 0.025$). Chlorophyll *a* concentration ranged from low winter values of 10 mg m^{-2} at Station 2 to high summer values of up to 400 mg m^{-2} at Station 6. At the other stations, values above 100 mg m^{-2} were occasionally measured during short blooms. Mean values ranged from ca. 30 mg m^{-2} at Station 2 to ca. 190 mg m^{-2} at Station 6. Stations 1 to 4 showed approximately the same average value, whereas Station 5 showed a higher value, intermediate between those of Stations 1 to 4 and Station 6. A linear regres-

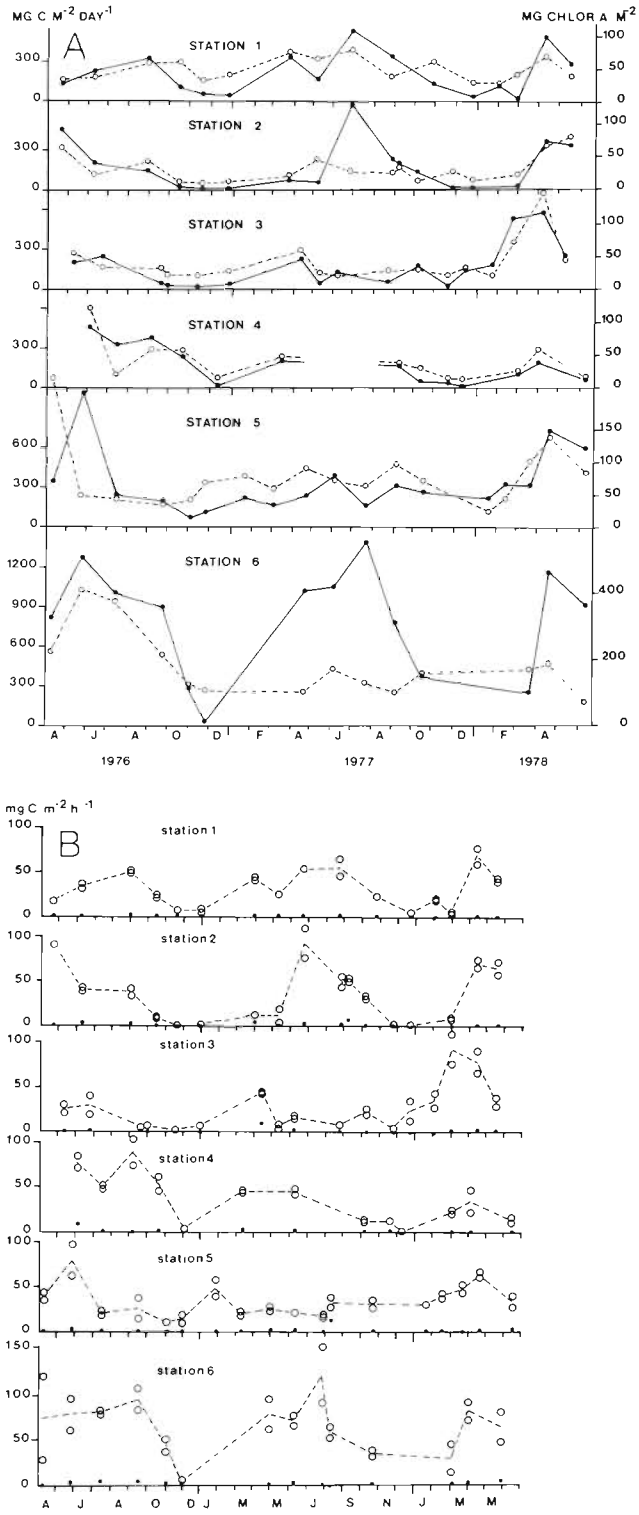

Fig. 3 (A). Daily primary production and chlorophyll *a* at the 6 stations (• mg C m^{-2} d^{-1}; ○ mg chl *a* m^{-2}) (B) Primary production rates and dark uptake rates (mg C m^{-2} h^{-1}). Mean of light values (open symbols) are connected; dark values (small dots)

sion of all production rates against all chlorophyll *a* concentrations revealed a positive correlation between these 2 variables ($r = 0.5515$, $n = 95$, $p < 0.001$, Fig. 4).

A positive correlation was also found between these variables for each of the Stations 1 to 4, but not for Stations 5 and 6 (Table 2). This special feature of Stations 5 and 6 is caused by the comparatively low fixation rates at high chlorophyll *a* concentrations (Fig. 4) which suggests that carbon fixation reached saturation values at higher chlorophyll *a* values.

Table 2. Regression of primary production rate against chlorophyll *a* concentration in the top 0.5 cm of sediment, for each of the 6 stations

Station	N	Slope	Y intercept	R^2	P
1	16	0.6652	−1.98	0.3351	0.05
2	17	0.9938	1.26	0.4465	0.01
3	17	0.6431	−0.38	0.6416	0.01
4	13	0.6871	7.99	0.5826	0.01
5	18	0.1043	25.95	0.0811	n.s.
6	14	0.0854	50.54	0.0846	n.s.
1–6	95	0.2220	21.74	0.3042	0.01
1–4	63	0.6705	4.01	0.4422	0.001

Temperatures and irradiances measured simultaneously with the field incubations are presented in Fig. 2. Both temperature and irradiance reflected seasonal changes and showed a weak positive correlation ($r = 0.4487$), which was statistically significant ($p < 0.001$). Both factors correlated positively, but weakly with the hourly production rate ($r = 0.3843$ and 0.3643, $n = 95$, $p < 0.01$, respectively). This correlation was not significant for the data of each individual station, because of the marked variation in production rates and the paucity of observations.

Also, the assimilation number did not show a significant correlation, either with irradiance, or with temperature.

Annual production

The estimates of annual production as calculated by the 5 methods described above are presented in Table 3. Methods, I II and III gave almost identical results. Surprisingly, annual production values based on the accurately determined photoperiods (I) were almost the same as those based on the rougher Methods II and III. The results obtained by Methods IV and V were in close agreement with each other but differed from the results obtained by Methods I to III: at all stations except at Station 3, annual production on the basis of mean monthly production values mg C m^{-2} h^{-1}) was lower than on the basis of actually measured production values. The differences in annual production values calculated by Methods IV and V are completely determined by the elevation of the stations and the tidal range, in other words, by the effective photoperiod. The percentual agreement between the results obtained by Methods IV and V proves that the calculation of the effective photoperiods with the model is in accord with actually measured photoperiods (Table 3, Methods IV and V).

Table 3. Annual primary production in g C m^{-2} at 5 stations in the Ems-Dollard Estuary as based on 1 set of data and 5 different methods of calculation ('Material and Methods'), together with the mean chlorophyll *a* concentration and the mean emersion period (as % of tidal cycle) of each station. All annual production values are exclusively based on the emersion periods of the stations. NAP = approx. mean sea level

Method	Station					
	1	2	3	4	5	6
I	81	62	62	62	99	245
II	77	56	59	61	106	256
III	76	57	67	58	101	245
IV	73	57	82	53	99	200
V	70	54	84	51	98	214
Mean chlorophyll *a* (mg m^{-2})	49	33	42	40	77	184
Station elevation (m NAP)	0	−.4	+.3	−.5	+.7	+1.1
Average annual emersion (%) during daylight	49	37	57	35	69	80

The linear extrapolation of the tidal emersion effect (Table 3, Methods IV to V) would result in an expected production of ca. 110 g C m^{-2} yr^{-1} at Station 6. The actual value was roughly twice as high, because of the much higher production rate at this station, notwithstanding the relatively low mean assimilation number. The atypicality of this station in the estuary is also reflected by the very high chlorophyll *a* values (Fig. 3A).

Dark ^{14}C fixation values (Fig. 3B) showed no correlation with production rate, temperature, or station number. The mean value was 2.09 mg C m^{-2} h^{-1}, which is 5.6 % of the mean hourly production rate. As pointed out under Material and methods we assumed that primary production only occurred during emersion. Obviously, this holds for the turbid inner part of the estuary, but not for the outer part with much clearer waters. Therefore, we calculated, using the characteristic values of Station 1, the effective light period which is defined now as the emersion period plus the submersion time, when photosynthetic active radiation (PAR) at the sediment surface exceeded 25 W m^{-2}. This value is assumed to equal the saturation irradiance (Colijn and Van Buurt, 1975). With these assumptions the total effective light period increases by 25 %. For

Station 1 this would increase the annual primary production from 70 to 89 g C m^{-2} (Method V). Although we had no measurements during submersion to check this estimate, it seems to be realistic (cf. Cadée and Hegeman, 1974).

DISCUSSION

Methodology

The problem of self-absorption normally encountered when one determines radiocarbon in sediment samples can be solved in several ways. In liquid scintillation counting, high counting efficiences are easily obtained by suspending the sediment in a gelling scintillation cocktail (Skauen et al., 1971; Cadée and Hegeman, 1974, 1977). However, only small amounts of sediment can be subjected to this procedure, especially as the sediment contains silt with high quenching properties. The acid digestion method (Van Raalte et al., 1974) has proved to be unsuccessful, because of an unexplained low recovery. The combustion method which we adopted lacks the above disadvantages. Thus we could process samples of up to a few 100 mg of dry sediment with almost 100 % recovery and reach counting efficiencies of ca. 75 %. However, the non-uniform distribution of the labelled incubation solution in the upper sediment layer is a problem (cf. Colijn and Van Buurt, 1975). Also, the concentrations of inorganic carbon in the upper sediment layers may differ from the concentration in the incubation water (Klein, 1981; Revsbech et al., 1981; Lindeboom and De Bree, 1982). A few measurements of the concentration of total inorganic carbon showed (unpubl. own results) that the surface water film and the 0 to 2 mm deep layer had minor differences in inorganic carbon content (cf. Revsbech et al., 1981). Because we did not measure the specific activity of $H^{14}CO_3^-$ in the upper sediment layers, there is some uncertainty about the actual fixation rates in these layers. According to Revsbech et al., (1981) this may cause an underestimation of the fixation rate in deeper layers up to a factor of 2 to 5. The very small light penetration in our sediments (Colijn, 1982) may well reduce this error, because the maximal photosynthetic rates take place within a layer of only 0.5 mm (Revsbech and Jörgensen, 1983). An advantage of the *in situ* method is that the sediment with the microalgal layer stays intact and that the flux of nutrients including bicarbonate from the deeper sediment layers is not disrupted. Measurements of nutrient concentrations in channel waters in the Dollard have shown that these nutrient concentrations usually are high (de Jonge and Postma, 1974; Rutgers van der Loeff et al., 1981). Nutrient limitation is not necessarily occurring in the thin film of water overlying the mudflat since nutrient uptake and photosynthesis are not always coupled (Eppley, 1981). We think that, generally, nutrients will not act as a limiting factor for the growth of the microphytobenthic vegetation in the Ems-Dollard estuary (cf. Admiraal et al., 1982).

In our investigation, the sample surface (ca. 28 cm^2) was large enough to prevent 'edge effects' from playing an important role, as can easily occur with very small samples (Marshall et al., 1973; cf. Cadée and Hegeman, 1974). The water flow, which is an inevitable consequence of the bell-jar technique (Van Es, 1982a), creates a major problem. Generally, stirring stimulates both macroalgae and sediment-inhabiting microalgae to give higher production values (UNESCO manual, 1973; Boynton et al., 1981; Revsbech et al., 1981), possibly by improving CO_2 exchange (Admiraal et al., 1982), or by removing inhibiting O_2, or by suspending algae and thereby increasing their average illumination. An increase in production, however, is not always found (Hargrave et al., 1983). In our view, microphytobenthos on intertidal flats is not subjected to any appreciable water flow during emersion, and therefore the best imitation of the natural emerged environment should be a non-stirred incubator. Not even such a non-stirred incubator fully reproduces conditions on a natural emerged sand- or mudflat (Darley et al., 1976). However, Darley et al. found that during 1 h experiments air-incubated samples showed a linear uptake of label at a rate comparable with that shown by submerged samples. A recent study (Holmes and Mahall, 1982) revealed that flooding with a 1 to 2 mm layer of agitated water reduced net photosynthetic rates by ca. 50 %. Although the cause of this reduction was not given, it is reasonable to infer that the reduction was the result of the microalgae migrating into deeper layers. During our measurements we never observed a visual downwards migration of diatoms.

Production rate, algal biomass and environmental factors

Possible relationships between primary production and environmental factors can be established by applying stepwise multiple regression analysis (Van Es, 1982a). This analysis showed that only chlorophyll *a* values explained the variation in production values for all station, but other factors (temperature und irradiance) made a very inconsistent contribution to the variance. Although the main goal of our study was to establish the annual primary production in the Ems-Dollard estuary (with an area of ca. 500 km^2), knowledge on the factors regulating this production is also important. The significant positive correlation between algal biomass (expressed as mg chl *a* m^{-2}) and

the production rate (Colijn and Venekamp, 1977; Plante-Cuny, 1978) should enable us to make rough estimates of the primary production over greater areas without time consuming production measurements. A statistically significant correlation was found between mean annual production (Method I) and mean chlorophyll *a* concentration over the same period ($r = 0.9973$, $n = 6$, $p < 0.001$; without Station 6: $r = 0.9689$, $n = 5$, $p < 0.01$) (Table 2, Fig. 5).

A similar, close correlation between mean annual chlorophyll *a* content and annual production was found by Cadée and Hegeman (1977) in the Western

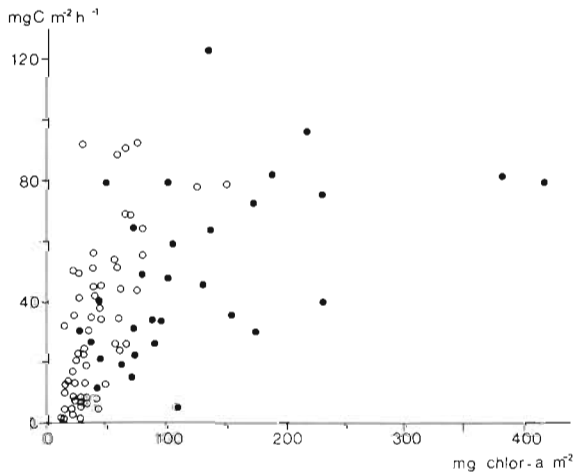

Fig. 4. Relation between chlorophyll *a* concentration and production rate. Open symbols: Stations 1 to 4; closed symbols: Stations 5 and 6

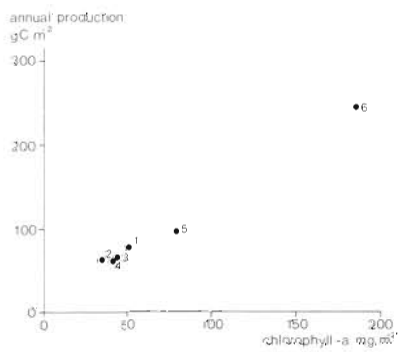

Fig. 5. Relation between annual mean chlorophyll *a* concentration and annual primary production for the 6 stations studied

Wadden Sea. However, the slope of their regression line is less steep than ours; the reason for this difference is that their chlorophyll *a* measurements included sediment to a depth of 1 cm, while ours included sediment only to a depth of 0.5 cm. Thus, we agree with Cadée und Hegeman, that the annual microphytobenthic production can be estimated on the basis of relatively few chlorophyll *a* samples distributed over the year. On the other hand, this method yields only a limited insight into the year-round variability of the primary-produced organic carbon available for estuarine processes of grazing, burial, transport and mortality. Daily production rates and chlorophyll *a* concentrations were expected to increase with increasing elevation of the stations. However, biomass only increased in this way at Stations 5 and 6, and production rates were only relatively high at Station 6. A significant positive correlation between primary production and tidal level was also found by Cadée and Hegeman (1977), and we agree that this is caused by the longer effective photoperiods on the more elevated tidal flats. This is supported by Admiraal (1977a) who investigated the minimum irradiance requirement of benthic diatoms in culture. Extrapolation of these and other literature data (Colijn, 1982) shows that a minimum irradiance for saturating diatom growth occurs during most of the year; only during winter may irradiance be limiting (Colijn and Dijkema, 1981; Colijn, 1982) through the combination of low solar irradiance and short effective photoperiods. Field observations (Admiraal and Peletier, 1980) have also shown that the starting point in spring of the growth of natural diatom vegetations on a short transect with 3 stations at different tidal levels correlated with the duration of emersion; the higher stations exhibited an earlier start than the lower stations. The high primary production rate at Station 6 largely resulted from that station's high elevation. The high chlorophyll *a* concentration accorded with the high primary production. As mentioned before, the influence of elevation alone could not account for the high production level; other factors may have enhanced this production: the sheltered position of Station 6, the lack of macrofaunal grazers (Van Es et al., 1980), the high nutrient concentration in the tidal water and in the pore water (De Jonge, unpubl.), combined with the high mineralization rate of allochthonic organic material (Van Es, 1982b) that supplies inorganic carbon. The population of benthic algae mostly consisted of diatoms, but it also contained blue-green algae and Euglenophyceae, particularly in summer. This vegetation had a lower specific production rate than the diatom vegetations of the other stations. However, interpreting the assimilation numbers raises problems, the depth of the photic layer in the sediment strongly depends on the composition of the sediment (Colijn, 1982). When the specific production rates were calculated from the chlorophyll *a* contents of the top 0.5 cm of sediment, it was assumed that all chlorophyll in this layer contributes to the primary production, because it was impossible to measure chlorophyll *a* in the photic layer properly. Consequently, the assimilation number was always underestimated. The absence of a significant correla-

tion between primary production rate and temperature or irradiance was surprising at first sight. Laboratory experiments with small cores (Colijn and van Buurt, 1975) have shown that both temperature and irradiance enhance the primary production rate unless irradiance reaches saturation levels. That no correlation between irradiance and photosynthetic rate, and assimilation number was found can be explained by the incubation irradiances, which nearly always exceeded a saturation level of 11–25 W m^{-2} (PAR) (recalculated from Colijn and van Buurt, 1975). Our field incubations in November, December, January and February were performed with lower irradiance values only.

The lack of correlation between production rate and assimilation number with temperature contrasts with results obtained by Admiraal and Peletier (1980). They observed that doubling rates of cultures in enclosed incubators increased from ca. 0.2 d^{-1} in winter to more than 2 d^{-1} in late spring. However, simultaneously observed doubling rates of natural populations were always much lower (max. 0.1 d^{-1}) even under high (> 20 °C) temperatures. Apparently, in our field incubations the effect of temperature on production rate is obscured by other factors. The observed low doubling rates (Admiraal and Peletier, 1980) and the relatively low chlorophyll *a* concentrations at Stations 1 to 4 are probably caused by grazing, burying and transport. In other studies, the removal of epibenthic grazers resulted in a significant increase in algal biomass and productivity (Pace et al., 1979; Darley et al., 1981). These results, however, are not in accordance with those obtained by Connor et al. (1982), who observed a positive feedback between grazing by mud snails and the chlorophyll standing stock, at least at low animals densities. If the microcosms were raked daily and densities of snails were high, the algal biomass and rates of photosynthesis fell. Also the removal of a proportion of the actively growing diatoms from the photic zone into the aphotic sediment layers (De Jonge and Colijn, in prep.) and suspension and transport by tidal currents (Cadée and Hegemann, 1974; Ballie and Welsh, 1980; de Jonge, 1983) can keep the benthic diatom population at a low level.

High primary production and chlorophyll *a* concentrations at Station 6 probably form the limit for microphytobenthic vegetations. This limit can be set by high concentrations of O_2, low diffusion flux of CO_2 into the microalgal layer (Admiraal et al., 1982) and absorption of PAR by chlorophyll *a* and fine sediment particles (Fenchel and Staarup, 1971; Colijn, 1982). This hypothesis is supported by the saturation of production rate (Fig. 4) and by the low assimilation numbers at very high chlorophyll concentrations at Station 6 during favourable conditions of temperature and irradiance: 0.19 and 0.20 mg C mg chl a^{-1} h^{-1} were measured at Station 6 on 25. V. and 14. VII. 1976, respectively, as opposed to a mean value of 1.37 for 8 other measurements at temperatures above 19 °C, irradiance > 150 W m^{-2}, and chlorophyll *a* concentrations below 50 mg m^{-2}.

Recently, Admiraal et al. (1983) have discussed 2 different interpretations of the term primary production; the first was based on the photosynthetic rate on an hourly basis, as in this study, the second on the biomass increase over 24 h periods. They showed that in the latter case at a biomass density of 4 g C m^{-2} (roughly equivalent to 100 mg chl *a* m^{-2}) biomass net production might be as low as zero. That we were still able to measure positive fixation rates reflects the inherent property of the ^{14}C method that neither excretion nor respiration rates are subtracted from the fixation rates on a 24 h basis. Thus it is still not clear how much fixed carbon is available for primary consumers per year.

Comparison with other areas

Data on primary production form intertidal flats and shallow coastal areas around the world have been compiled in Table 4. Two important results are obvious from this table: Firstly, the annual production data measured with a bell-jar technique in the Ems-Dollard estuary and partly during the same period (Van Es, 1982a) fit in with ^{14}C fixation rates: $r = 0.9699$, $n = 6$, $p < 0.01$, (slope = 1.27). Thus both techniques give roughly identical estimates of annual primary production (Hunding and Hargrave, 1973). However, the individual, actually measured hourly rates per station showed large variations, probably because the measurements could not be performed at exactly the same spot; patchy distribution of microalgae (Van den Hoek et al., 1979) can lead to a 2- to 10-fold difference in chlorophyll *a* concentration and cell numbers over a distance of a few centimetres (De Jonge and Colijn, in prep.). Secondly, the values for annual primary production at stations in the Western Wadden Sea (Cadée and Hegeman, 1974, 1977) are in the same range as the data from our Stations 1 to 5, again with the exception of our Station 6, with higher values than those of their Station 1 (188 g C m^{-2} yr^{-1}). Leach (1970) showed that with relatively high chlorophyll *a* values (400 to 600 mg m^{-2}) the annual production was rather low (31 g C m^{-2} yr^{-1}). This might be caused by the muddy sediments (Station 3) with a thin photic layer and a high chlorophyll *a* content in the deeper sediment layers. Surprisingly, as Table 4 shows, on a more global scale most of the annual production values are within a narrow range from 50 to 200 g C m^{-2}, even though they were determined at very different geographical

Table 4. Comparison of annual production rates in intertidal and shallow coastal sediments. Upper part: ^{14}C-values; lower part: O_2-values

Locality (Lat.)	Sediment typ, depth (m)	Method	Annual production (g C m^{-2})	Production rate (mg C m^{-2} h^{-1}) range; mean	Chlorophyll (mg m^{-2})	Dominating microphytes	References
Danish fjords (55° N)	Littoral sand & mud, 0.2–1.8 m	^{14}C	116	25–90; 60	n.d.	Pennate diatoms	Grøntved (1960)
Danish Wadden Sea (55° N)	Intertidal sands	^{14}C	571 (sheltered) 892 (exposed)*	25–300 25–500	n.d.	Pennate diatoms	Grøntved (1962)
Loch Ewe, Scotland (57° 50′ N)	Sandy beach	^{14}C	4–9	0.14–1.78 mg C mg Chl^{-1} h^{-1}	3–20 μg g^{-1} dry sediment	Sand-attached diatoms	Steele and Baird (1968)
Ythan estuary, Scotland (57° N)	Intertidal muds	^{14}C	31	4–26; 10	25–34 μg g^{-1} dry sediment	Motile pennate diatoms	Leach (1970)
South New England, USA (41° N)	Intertidal mixed sediment	^{14}C	81	8.2–30.8; 20.1	100	Pennate diatoms dinoflag., filamentous algae	Marshall et al. (1971)
Niva Bay, Øresund, Denmark (56° N)	Shallow sands, 0.5 m	^{14}C	n.d.	125–300*	n.d.	Free-living and attached diatoms	Gargas (1970)
Madagascar (13° S)	Marine sands, 5–60 m	^{14}C	150 (5 m) 66 (mean)	9.22	38,78	Cyanophyceae, diatoms, symbiotic dinoflag	Plante-Cuny (1978)
Madagascar (13° S)	Marine sands, 5–38 m	^{14}C	n.d.	(5m) 410 mg C m^{-2} d^{-1} (15) 232 mg C m^{-2} d^{-1} (25) 40 mg C m^{-2} d^{-1} (38) 9 mg C m^{-2} d^{-1}	3–34	Ditto	Plante-Cuny (1973)
Mediterranean coast, France (43° N)	Marine sands, up to 12 m	^{14}C	n.d.	120–194 mg C m^{-2} d^{-1}	24–64	n.d.	Colocoloff (1972)
Falmouth Bay, USA (41° N)	Salt marsh muds	^{14}C	105.5±12.5	5–80	n.d.	n.d.	van Raalte et al. (1976)
Chuchi Sea, USA (71° N)	Fine muds and sands, 5 m	^{14}C	5	0.5–57	40–320	Diatoms and Euglenophyceae	Matheke and Horner (1974)
Wadden Sea, Netherlands (53° N)	Intertidal flats (sandy-mud)	^{14}C	100±40	50–100 (winter) 100–1100 (summer)	7.1 μ g^{-1} dry sediment 100; 40–400	Attached and suspendable diatoms	Cadée and Hegeman (1974)
River Lynher estuary, SW England (50° N)	Intertidal mudflats	^{14}C	143	5–115	30–80 μg g^{-1} dry sediment	n.d.	Joint (1978)
Balgzand, Wadden Sea (53° N)	Intertidal flats, 4 transects	^{14}C	85 (29–188) (15 stations)	0–900 (d^{-1})	3–13 μg g^{-1} dry sediment	Diatoms	Cadée and Hegeman (1977)
Bolsa, Bay, USA (34° N)	Barren estuarine mudflats	^{14}C	115–246	26–59 (4 stations)	185–385 (annual mean)	Motile & non-motile diatoms, bluegreens, dinoflagellates	Riznyk et al. (1978)
Ems-Dollard estuary (53° N)	Intertidal mudflats	^{14}C	62–276 (6 stations)	1–120; 37.0	33–184 (annual mean)	Diatoms, occ. Euglenophyceae bluegreens	This study
Ems-Dollard estuary (53° N)	Intertidal mudflats	O_2	69–314 (6 stations)	0–1900 mg C m^{-2} d^{-1}	n.d.	Diatoms, occ. Euglenophyceae bluegreens	van Es (1982a)
False Bay, USA (48° N)	Intertidal sandflats	O_2	143–226 (3 stations)	0–100	30–70 μ g^{-1} dry sediment	Diatoms (*Navicula* spp.)	Pamatmat (1968)
Georgia salt marshes, USA (31° N)	Intertidal mudflats	O_2	200	5–140	n.d.	Pennate diatoms flagellates, bluegreens, dinoflagel.	Pomeroy (1959)
Bay of Fundy, Canada (45° N)	Intertidal flats	O_2	47–83	10–800	10–500	Microalgae	Hargrave et al. (1983)

n.d. = not determined; * = potential rates

latitudes. An exception are the data obtained by Steele and Baird (1968) who found a very low annual production, probably a result of the washout of free-living diatoms from their wave-exposed sands and the dispersal of viable cells to at least 20 cm depth. Other very low values have been found in polar regions and can be ascribed to the short growing season (Matheke and Horner, 1974). The high values given by Grøntved (1962) are based on potential measurements and do not reflect *in situ* production conditions.

As pointed out also by Cadée and Hegeman (1974), the spreading of small sediment cores results in much higher primary production. There is a possible explanation for the small range of annual production values. The abiotic environment in tidal areas largely precludes the existence of stable, permanent microalgal vegetations, because the cells are continually being suspended and removed. Moreover, the photic layer in sediments is too thin to enable all availabe cells to contribute optimally to the process of primary production. Thirdly, if an algal layer is formed, its growth is reduced through its own photosynthesis products or because the diffusion of carbon dioxide and nutrients is hampered in the algal film. All these processes limit the formation of a considerable microalgal biomass and restrict the concomitant net primary production.

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