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REAPPRAISAL OF THE PRODUCTION AND IMPORT OF ORGANIC CARBON IN THE WESTERN WADDEN SEA

by

G. C. CADÉE

Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands

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I. INTRODUCTION

Primary production and import of organic carbon in the western part of the Dutch Wadden Sea (Fig. 1) were first estimated some 30 years ago (POSTMA, 1954). More recent estimates of the primary production of phytoplankton and phytobenthos were provided by POSTMA & ROMMETS (1970), CADÉE & HEGEMAN (1974a, 1974b, 1977, 1979), GOEDHEER (1977) and CADÉE (1978). VAN DEN HOEK, ADMIRAAL, COLIJN & DE JONGE (1979) reviewed the role of algae and seagrasses in the whole Dutch Wadden Sea. In the present paper a reappraisal will be presented of the available data on primary production and import of organic carbon in the western Dutch Wadden Sea and some new information on the input from the IJsselmeer will be given.

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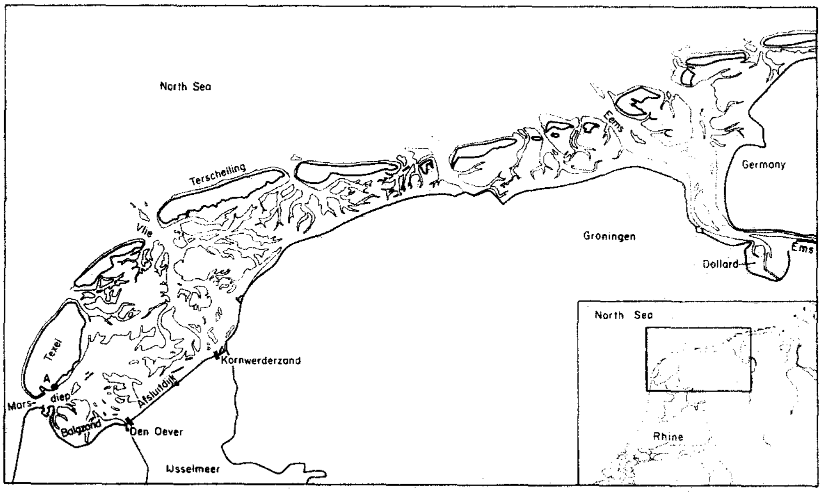

Fig. 1. Map of the Dutch Wadden Sea with low water line, geographical names mentioned in the text, and the tidal flat station A for which data are given in Figs 2b and 3.

II. PRIMARY PRODUCTION

a. PHYTOPLANKTON PRIMARY PRODUCTION IN THE TIDAL CHANNELS

Before the ^{14}C method became available POSTMA (1954) calculated phytoplankton primary production for the western Wadden Sea from chlorophyll a data and an estimated daily increase of phytoplankton of 30%. This rough method yielded values between 20 and 50 g $C \cdot m^{-2} \cdot a^{-1}$. POSTMA & ROMMETS (1970) introduced the ^{14}C method for phytoplankton primary production studies in the Wadden Sea and presented annual values for *in situ* measurements for 2 stations, one positioned centrally in the western Wadden Sea, the other in the Marsdiep inlet area, of 120 and 170 g $C \cdot m^{-2} \cdot a^{-1}$ respectively. CADÉE & HEGEMAN (1974a, corrected in 1979) estimated *in situ* phytoplankton primary production from incubator measurements under constant light for the western Wadden Sea at 200 g $C \cdot m^{-2} \cdot a^{-1}$. In the 1979 paper they published annual curves for one station in the Marsdiep tidal inlet area based on more frequent measurements which yielded a value of 145 g $C \cdot m^{-2} \cdot a^{-1}$.

In Fig. 2a three different curves of seasonal variation in phytoplankton primary production from the literature cited above are shown together. Although the annual estimates for primary production based by the authors on these curves vary from 145 to 200 g $C \cdot m^{-2} \cdot a^{-1}$, we have to conclude from their similarity that no differences in pattern or annual total between the 3 different years can be deduced from these data. The short term variations observed in the detailed 1974 curve, based on weekly measurements, could not be related to variations in daylight, but were largely a consequence of (unpredictable) variations in phytoplankton density (CADÉE & HEGEMAN, 1979).

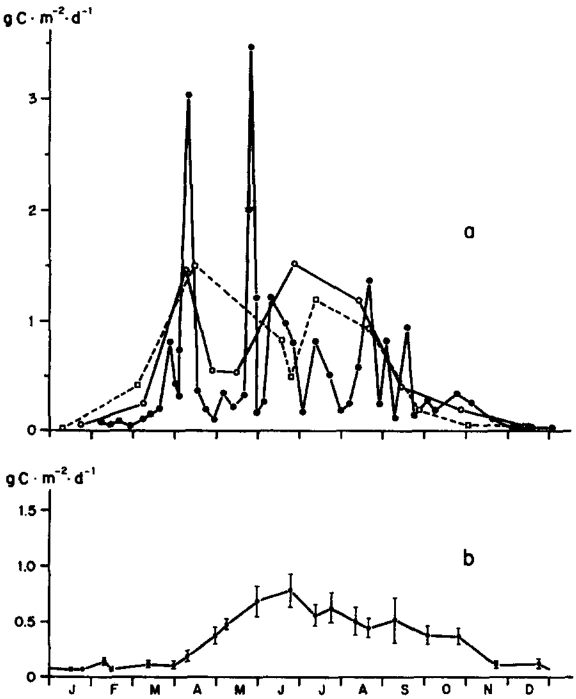

Fig. 2. a. Comparison of published seasonal curves for phytoplankton primary production (g $C \cdot m^{-2} \cdot d^{-1}$) from POSTMA & ROMMETS (1970: fig. 7; Marsdiep station 1, 1964–1966) (○); CADÉE & HEGEMAN (1974a: fig. 6; western Wadden Sea, 1972–1973) (□); and CADÉE & HEGEMAN (1979: fig. 3; Marsdiep, 1974) (●). b. Seasonal curve of microphytobenthos primary production (g $C \cdot m^{-2} \cdot d^{-1}$) on a tidal flat at station A, south of Texel in 1969 from CADÉE & HEGEMAN (1974b: fig. 4); bars indicate twice the standard deviation of the mean.

Therefore, it will be almost impossible to obtain a more precise estimate for phytoplankton primary production in the Marsdiep and western Wadden Sea than 150 ± 50 g $C \cdot m^{-2} \cdot a^{-1}$. In the more turbid inner parts of the western Wadden Sea primary production is probably lower; a comparable trend has been found for the Ems-Dollard estuary (CADÉE & HEGEMAN, 1974a; COLIJN, 1978; LUDDEN, 1980).

Apart from this spatial variation a year-to-year variation in primary production as observed in other areas (PLATT, 1971; RUSSELL, SOUTHWARD, BOALCH & BUTLER, 1971; LEHMUSLUOTO & PERSONEN, 1973; RIEMANN & MATHIESEN, 1977) will exist also in the Wadden Sea. However, without at least weekly measurements, it will be impossible to quantify such variations, and even so trends in primary production over a series of years have to be pronounced to be measurable. Most of the earlier data are insufficiently accurate for such trend studies.

b. MICROPHYTOBENTHOS PRIMARY PRODUCTION ON THE TIDAL FLATS

Data on primary production of microalgae living on the tidal flats in the western Wadden Sea are given by CADÉE & HEGEMAN (1974b, 1977). Short term variations appear to be less pronounced than in phytoplankton. Fig. 2b gives a seasonal curve based on 20 measurements of one day each. These days were chosen with alternating high and low water at noon to give maximum possible variations in available daylight at the tidal flat surface. These variations apparently did not affect the annual curve noticeably which may be explained by the fact that microphytobenthic algae reach their optimum in photosynthetic rate already at low light intensities and show little inhibition at high light intensities (CADÉE & HEGEMAN, 1974b; ADMIRAAL, 1977; COLIJN & VAN BUURT, 1975). Moreover, the biomass of microphytobenthos does not show such marked short term variations as observed in phytoplankton. During storms the tidal flat surface sediments may be eroded, but as benthic microflora occurs in considerable quantities below the sediment surface, down to at least 10 cm, removal of the surface layer of sediment has no large effect on algal biomass. At station A functional chlorophyll a at 5 cm depth amounted on average to 40% of the value found for the 0 to 1 cm layer (CADÉE & HEGEMAN, 1974a: fig. 10). Only heavy gales removing large quantities of tidal flat sediments may diminish microphytobenthic populations appreciably as documented by GRØNTVED (1965), CADÉE & HEGEMAN (1974b) and DIJKEMA (1975).

Fig. 3 gives a 12 years series of measurements of *in situ* primary production of microphytobenthos on a tidal flat near the Institute (station A in Fig. 1). Although the methods for measuring primary production changed during this 12 years period (short to long incubation periods, GM-counting to liquid-scintillation counting; CADÉE & HEGEMAN (1974b, 1977), each change in method was tested during a period in which both methods were used. Therefore, I suppose that these changes did not effect the annual values. The data of the first

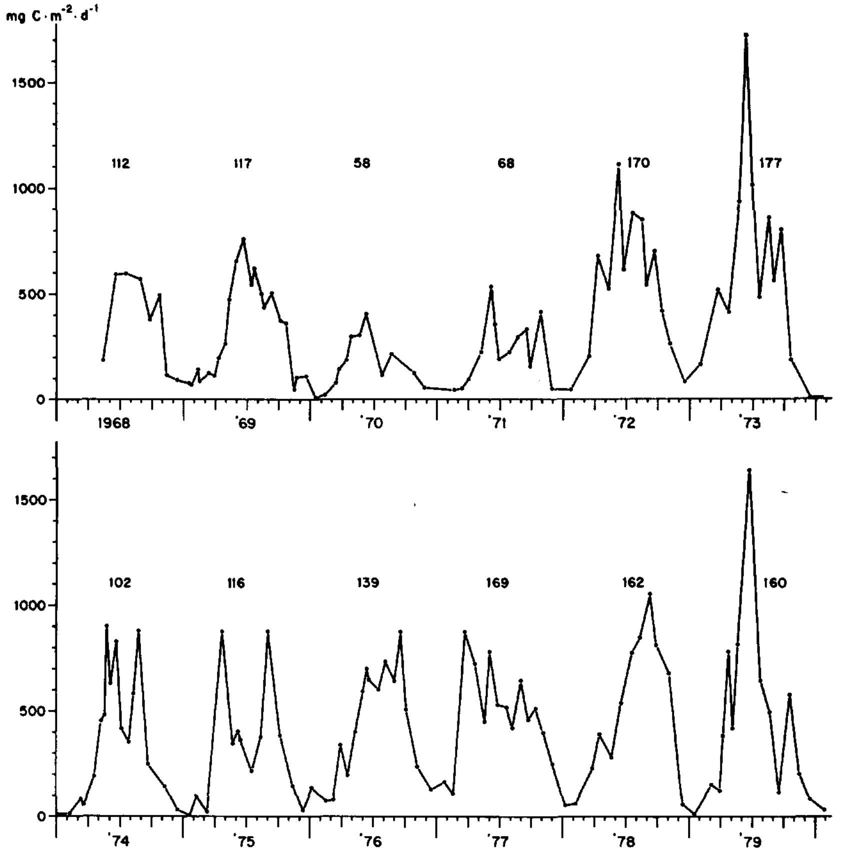

Fig. 3. Series of 12 years microphytobenthos primary production measurements (mg $C \cdot m^{-2} \cdot d^{-1}$) on a tidal flat at station A, south of Texel (same station as in Fig. 2b); year values (g $C \cdot m^{-2} \cdot a^{-1}$) indicated. Data for 1968 to 1972 already published in CADÉE & HEGEMAN (1974b: fig. 4).

5 years were already published (CADÉE & HEGEMAN, 1974b). The average annual value for the 12 years is 130 $\pm$ 40 (SD) and the range 58 to 177 g $C \cdot m^{-2} \cdot a^{-1}$. Year-to-year variations in temperature and solar radiation are too small to account for this large year-to-year variation in primary production. In the earlier paper an influence of grazing was suggested, and during a cooperative research program on a Balgzand tidal flat a remarkable correlation between a decrease in primary production and an increase of the gastropod *Hydrobia ulvae* with peak densities over 100 000 m^{-2} (counts by P. A. W. J. de Wilde and E. M. Berghuis) was found in summer. This suggests overgrazing, as a major part of the food of this gastropod consists of benthic diatoms

(MUUS, 1967). In experiments FENCHEL & KOFOED (1976) observed that the related *Hydrobia ventrosa* decreased primary production of microphytobenthos at densities above 30 000 m^{-2}. PACE, SHIMMEL & DARLEY (1979) observed that natural densities of the grazing gastropod *Nassarius obsoletus* reduced both algal biomass and productivity on a tidal mud flat on Sapelo Island, Georgia.

Another case of overgrazing but now affecting phytoplankton was observed in 1972 in an area with intensive mussel-culture south of Terschelling. Mussel grazing here decreased primary production to about 1/4 of the value found outside the area (CADÉE & HEGEMAN, 1974a: 256). Also chlorophyll a values were comparatively low in the area whereas MANUELS & POSTMA (1974) observed relatively low values for both ATP and organic carbon in suspended matter in the same area in the summer of 1971.

For a number of intertidal stations on the Balgzand tidal flat area, annual primary production was found to range from 29 to 188 g $C \cdot m^{-2} \cdot a^{-1}$, with a significant positive correlation with the tidal level of the stations (CADÉE & HEGEMAN, 1977).

Annual and spatial variations in microphytobenthos primary production make it difficult to give an annual figure for an average tidal flat in the western Wadden Sea, but as the tidal flat station near Texel has approximately an average level for the western Wadden Sea, I tentatively estimate microphytobenthic primary production at 130 ± 40 (SD) g $C \cdot m^{-2} \cdot a^{-1}$.

C. MACROPHYTOBENTHOS PRIMARY PRODUCTION

VAN DEN HOEK, ADMIRAAL, COLIJN & DE JONGE (1979) tried to estimate the primary production of *Zostera marina* in the period 1920 to 1932, *i.e.* before this species became nearly exterminated by the "wasting disease". They give a value of 10 to 50 g $C \cdot m^{-2} \cdot a^{-1}$ as a rough approximation for the whole western Wadden Sea. After 1932 the contribution of *Zostera marina* as well as that of the more littoral *Z. noltii* to the primary production is negligibly small.

GOEDHEER (1977) studied primary production of macrobenthic algae on some relatively sheltered tidal flats near Texel. He found annual values ranging from 5 to 26 g $C \cdot m^{-2} \cdot a^{-1}$. On more exposed flats (not studied by him) no macroalgae can maintain themselves in most summers, hence macrobenthic primary production is generally absent. Even on the most sheltered tidal flats, part of the macroalgae will be removed during gales. They will float and continue primary production as long as they remain in the euphotic zone. Part of these floating algae will accumulate in the tidal channels below euphotic depth or above the high water line along the shores. It is nearly impossible to estimate biomass and primary production of these floating macroalgae. Although locally macroalgae (particularly *Ulva* and *Enteromorpha*) may form a dense vegetation on some sheltered tidal flats during summer, their contribution to the primary production of the Wadden Sea is probably low. VAN DEN HOEK, ADMIRAAL, COLIJN & DE JONGE (1979) come to the same conclusion.

d. TOTAL PRIMARY PRODUCTION IN THE WESTERN WADDEN SEA

In the tidal channels phytoplankton is the only primary producer, and annual primary production amounts to 150 ± 50 g $C \cdot m^{-2} \cdot a^{-1}$. On tidal flats microphytobenthic algae are the main producers, producing annually about 130 g $C \cdot m^{-2}$. During high water phytoplankton primary production too is possible above the tidal flat and locally macrophytobenthic may also contribute. CADÉE & HEGEMAN (1974b: 269) measured during one year phytoplankton primary production above a tidal flat and arrived at an estimate of 20 g $C \cdot m^{-2} \cdot a^{-1}$. Macrobenthic algae primary production is probably between 1 and 10 g $C \cdot m^{-2} \cdot a^{-1}$ (GOEDHEER, 1977; VAN DEN HOEK, ADMIRAAL, COLIJN & DE JONGE, 1979). A rough estimate of total primary production on and above a tidal flat will be the sum of these values and amount to 150 ± 50 g $C \cdot m^{-2} \cdot a^{-1}$. This means that primary production on and above the tidal flats is the same as in the tidal channels.

Tidal marshes were not considered in this paper to belong to the Wadden Sea. Moreover, most of the organic matter produced in these areas remains on the tidal marshes and is not transported to the Wadden Sea; their contribution is certainly less than 5 g $C \cdot m^{-2} \cdot a^{-1}$ (VAN DEN HOEK, ADMIRAAL, COLIJN & DE JONGE, 1979).

With the shortcomings mentioned in this and the previous sections, primary production in the western Wadden Sea is estimated at 150 g $C \cdot m^{-2} \cdot a^{-1}$, probably ranging between 100 and 200 g $C \cdot m^{-2} \cdot a^{-1}$. Due to the large annual and spatial variations a more precise figure would be unwarranted.

III. IMPORT OF ORGANIC CARBON FROM OUTSIDE THE AREA

a. IMPORT FROM THE NORTH SEA

Estimates for an import of organic matter from the North Sea were based on phosphate measurements (POSTMA, 1954; DE JONGE & POSTMA, 1974). Concentrations of dissolved P are on average higher in the Wadden Sea than in the North Sea; this will result in a transport of dissolved P from the Wadden Sea to the North Sea. The amount of Wadden Sea water exchanged per tide with the North Sea can be derived from the amount of IJsselmeer water present in the Wadden Sea, by dividing this amount by the fresh water supply per tide through the sluices at Den Oever and Kornwerderzand (POSTMA, 1954; ZIMMERMAN, 1976). Therefore, knowing the excess of dissolved P content of the Wadden Sea as compared with the North Sea, one can estimate the transport of dissolved P from this area to the North Sea. For 1950, POSTMA (1954) calculated a transport of 2400 kg P per tide of which 500 kg P were contributed by fresh water from the harbour of Den Helder (the 200 kg P per tide contributed by the IJsselmeer was neglected; POSTMA, 1954: 82). The loss of the remaining 1900 kg of dissolved P was assumed to be neutralized by the counter transport of a similar amount in the form of particulate organic P, incorporated in organic matter transported from the North Sea to the Wadden Sea. From the measured C/P ratio of this particulated organic matter (POC) of 40/1, POSTMA estimated the transport per tide and, taking into account the 700 tides per year and the total area of the western Wadden Sea (0.69×10^9 m^2), a transport of 80 g C·m^{-2}·a^{-1} was found. DE JONGE & POSTMA (1974) recalculated this North Sea input on the basis of data they collected in 1970 and came to the conclusion that the input had increased threefold in the 20 years between 1950 and 1970 to 240 g C·m^{-2}·a^{-1}. Only a North Sea origin for this particulate organic matter was assumed.

A tidal mechanism to accumulate (organic) particles from the North Sea in the Wadden Sea has been described by POSTMA (1954, 1961a). Particles are carried into the Wadden Sea with the flood current. Towards high tide, when current velocity decreases, nearly all material sinks to the bottom. These particles are brought in suspension again by the returning ebb current not before the latter has reached a velocity considerably higher than that of the flood current at the moment of deposition. In this manner the material is resuspended in a water mass the relative position of which is farther inward than that of the water mass which carried the particles during the flood. At low tide a considerable part of the material remains in suspension and is not subjected to a process similar to that at high tide. As a result particles over a full tidal cycle undergo a net inward displacement.

VERWEY (1952, 1966) stressed the importance of biological accumulation of particles in the Wadden Sea besides the mechanism of tidal transport. He pointed to the part played by the enormous quantities of filter-feeding cockles (*Cerastoderma edule*) and mussels (*Mytilus edulis*). He assumed that nearly all the suspended matter present in the water can be retained by the gills of the filter feeders

(VERWEY, 1952: 199), and calculated that the mussels present in the western Wadden Sea filtrate the total volume of water in this basin (5 km^3) within a period of 2 weeks. The cockle was thought to be a filter-feeder of about equal importance (VERWEY, 1966). The suspended material filtered from the water is deposited as faeces and pseudofaeces, *i.e.* is concentrated in particles that are larger than the original ones and less easily transported back to the North Sea again.

It must be emphasized that the gradient in dissolved P between Wadden Sea and North Sea is only present during summer when mineralization of organic matter in the Wadden Sea reaches its peak (DE JONGE & POSTMA, 1974). Although there is no reason to suppose that the tidal mechanism for accumulation of (organic) particles from the North Sea in the Wadden Sea is restricted to the summer, there are indications that it is more effective in summer than in winter. Settling of particles during high water, necessary for the accumulation process, will be prevented during strong winds and storms which occur more often in winter than in summer. Therefore, the amount of suspended matter is on average higher in winter than in summer (POSTMA, 1954: 54; CADÉE & HEGEMAN, 1979: 231). Also biological accumulation by filter-feeders will be more effective during their growing season than during winter.

There are several indications pointing even to a reversal of the direction of transport of suspended matter (including organic particles) during or shortly after storms. REINECK, DÖRJES, GADOW & HERTWECK (1968: 291, fig. 13) observed storm sand layers in the North Sea between Büsum and Helgoland, the material of which apparently originated from the Wadden Sea as indicated by the occurrence of the small gastropod *Hydrobia ulvae* which lives on tidal flats in the Wadden Sea, not in the North Sea. As the animals had made escape burrows through the sand layers they must have been transported alive from the Wadden Sea after a storm period together with large amounts of sediment. Also WINKELMOLEN & VEENSTRA (1980) point to the importance of storms for the transport of Wadden Sea tidal flat material towards the North Sea. They stress the influence of wind stowage as a consequence of strong NW winds. During storms water does not recede from the tidal flats at low water, and the highly agitated water causes large-scale erosion. The first ebb after the storm will bring large quantities of Wadden Sea sediment to the North Sea. This is illustrated by a long turbidity recording given by POSTMA (1980: 164, fig. 8). After a storm had subsided the water was clearly more turbid during ebb than during flood.

Direct evidence for the alternation between accumulation of sediment during summer and erosion during winter was observed by KAMPS (1950). The clay content of tidal flat sediments off Groningen increased during spring and summer but showed a sudden rapid decrease after a storm period in autumn. COLES (1979) and FROHSTICK & MCCAVE (1979) observed accretion of high tidal flats during summer and erosion during winter in areas comparable to the Wadden Sea. An accumulation-erosion cycle apparently also causes a cycle in the organic carbon contents of high tidal flat sediments as we (CADÉE & HEGEMAN, 1977) observed an increase in contents of the top layer during spring and early summer that exceeded *in situ* primary production 2 to 3 times. This was a direct indication of import of organic matter from elsewhere. After the summer peak organic carbon content decreased regularly to lowest values during winter and an increase starts again in early spring. This increase coincides with the phytoplankton spring bloom occurring every year in the North Sea Coastal Water (CADÉE, 1978).

In conclusion it may be stated that physical and biological mechanisms for accumulating particulate organic matter in the Wadden Sea are most effective during spring and summer. During storms, occurring especially in winter, transport will temporarily be reversed, suspended matter including organic matter being transported from Wadden Sea to North Sea.

b. IMPORT FROM THE IJSSELMEER

In earlier papers (POSTMA, 1954; DE JONGE & POSTMA, 1974) import of particulate organic carbon from the IJsselmeer was considered to be of minor importance and therefore neglected. Only DUURSMA (1961: 39) estimated dissolved organic carbon transport from the IJsselmeer into the Wadden Sea from dissolved organic P data and a C/P ratio. His estimate amounted to $105 \cdot 10^3$ kg C per tide or about 105 g $C \cdot m^{-2} \cdot a^{-1}$.

From September 1978 on, both dissolved (DOC) and particulate (POC) organic carbon content were measured regularly in samples of IJsselmeer water collected near the sluices at Den Oever. POC and DOC were separated using precombusted Whatman GFF filters, and were determined with the "Total Carbon System" of Oceanography International Corp., Texas, USA using the wet oxidation method with $K_2S_2O_8$ of MENZEL & VACCARO (1964).

Monthly averages of DOC and POC (Fig. 4a) were read from smoothed curves, fitted by eye, which were multiplied with the monthly fresh water discharges from the IJsselmeer at Den Oever and Kornwerderzand (Fig. 4b; data of Rijkswaterstaat, Directie Zuiderzeewerken, Lelystad). This yields monthly discharged amounts of POC and DOC (Fig. 4c). In 1979 about $46 \cdot 10^9$ g POC and $88 \cdot 10^9$ g DOC were discharged, or about 65 g POC per m^2 and 125 g DOC

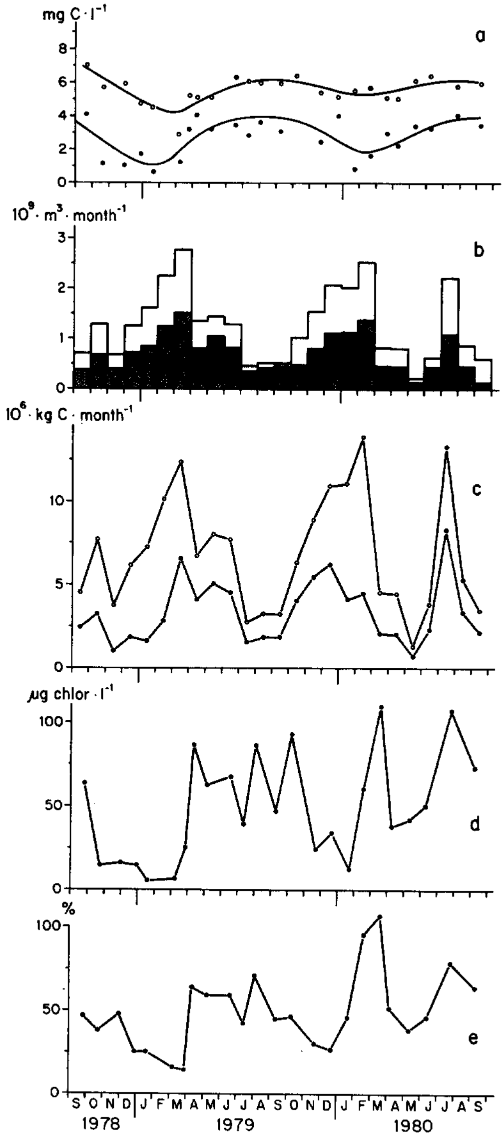

Fig. 4. Seasonal variation in properties of IJsselmeer water samples collected near the sluice at Den Oever and data on discharge from the IJsselmeer to the western Wadden Sea. a. Concentrations of DOC (○) and POC (●), smoothed curves fitted by eye ($mg\ C \cdot l^{-1}$). b. IJsselmeer fresh water discharged at Den Oever (hatched) and Kornwerderzand (white) ($10^9 \cdot m^3 \cdot month^{-1}$); data from Rijkswaterstaat directie Zuiderzeewerken, Lelystad. c. Amounts of DOC (○) POC (●) discharged from the IJsselmeer at Den Oever and Kornwerderzand ($10^6 \cdot kg\ C \cdot month^{-1}$). d. Concentrations of functional chlorophyll a ($\mu g \cdot l^{-1}$). e. Percentage of living algal carbon of total POC in IJsselmeer water, calculated as chlorphyll $\times$ 30 = algal carbon.

per m^2 (total area of the western Wadden Sea taken at $0.69 \cdot 10^9$ m^2 in accordance with POSTMA, 1954: table II). This DOC import value is of the same order of magnitude as the estimation of DUURSMA (1961), but it must be kept in mind that this author used a different wet oxidation method and method of separation of DOC, DOC being in his paper the fraction of organic substances that over a period of at least 24 hours does not settle in water acidified to pH 0.9 to 1.1.

These data indicate that the POC plus DOC discharged into the western Wadden Sea is by no means negligible and exceeds *in situ* primary production. Although some forms of dissolved organic matter are absorbed by marine invertebrates, phytoplankton and bacteria (PÜTTER, 1909; SEPERS, 1977; STEWART, 1979), a large part of the IJsselmeer DOC will consist of refractory organic matter with little value as food. The stable character of IJsselmeer DOC components in the Wadden Sea can be deduced from the fairly conservative mixing lines in DOC-salinity diagrams (DUURSMA, 1961; LAANE, 1980), although as remarked by DUURSMA (1961: 31) decomposition and formation of DOC in the Wadden Sea might be in the same order of magnitude. Moreover, the IJsselmeer water remains only for a short period in the western Wadden Sea, only 15 to 31 tidal periods (of 12 h 25 min) (ZIMMERMAN, 1976).

IJsselmeer POC is probably a good food source for Wadden Sea invertebrates as a high percentage of POC consists of living phytoplankton. For converting chlorophyll a data to organic carbon a factor 30 was used (STRICKLAND, 1960). On average 50% of the POC consists of living algae (Fig. 4d and e).

Estimates of import of POC from the North Sea (POSTMA, 1954; DE JONGE & POSTMA, 1974) were based on balance studies in which all POC imported to the Wadden Sea was supposed to have North Sea origin, neglecting IJsselmeer import. As a consequence IJsselmeer POC import should be subtracted from the values given for North Sea import. Than this import would be about 1/4 lower than the 240 g $C \cdot m^{-2} \cdot a^{-1}$ given by DE JONGE & POSTMA (1974).

The import of IJsselmeer POC is, however, not evenly distributed over the year (Fig. 4c), POC values are lowest in winter when discharge of fresh water is at a maximum. For the 2-year period over which data are available about half of the organic carbon import from the IJsselmeer occurred in the period March to September (inclusive), *i.e.* within the period in which it can be used by Wadden Sea invertebrates. Assumed that all the import from the North Sea takes place in summer, we have to subtract only half of the IJsselmeer import from the total import to obtain the net North Sea import.

With regard to the POC import from the IJsselmeer two questions may arise: Were POC values in the IJsselmeer formerly lower so that earlier authors were right in neglecting this source and, secondly, are there any indications of accumulation of IJsselmeer POC in the Wadden Sea?

Earlier estimates of POC in northern IJsselmeer water can be derived from Postma (1954: 79). He measured total suspended matter and ignition loss to obtain a measure for particulate organic matter (POM). POM varied from 12% in winter to 45% in summer, average about 25 $mg \cdot l^{-1}$. For conversion of POM to POC Postma (1954) used a factor 1/2.3, giving an average POC value of 2.7 $mg \cdot l^{-1}$. Manuels & Postma (1974: 300) observed 20 years later a variation of POC of 0.8 to 7 $mg \cdot l^{-1}$, average 2.7 $mg \cdot l^{-1}$. From September 1978 to October 1980 I measured POC content to vary from 0.6 to 6.1 $mg \cdot l^{-1}$, average 2.8 $mg \cdot l^{-1}$. Although we have to keep in mind that POC was measured by 3 different methods (respectively ignition loss, dry combustion and wet oxidation), the conclusion that POC values in the northern IJsselmeer probably did not alter considerably during the last 30 years seems to be warranted. Particulate P in northern IJsselmeer water, however, almost doubled from 7.0 in 1950 to 13.2 μmol per 100 mg suspended matter in 1970 (de Jonge & Postma, 1974: 149). This casts some doubts on the use of particulate P as a measure for organic matter. As already mentioned by Postma (1954: 87) particulate P may contain a small quantity of inorganically bound P. In the northern IJsselmeer this inorganic fraction might have increased during the last 20 years. Water in the IJsselmeer largely has Rhine origin. Salomons & Gerritse (1981) observed an increase of total P in Rhine sediments since 1923 by a factor 8, whereas organic P increased only by a factor 2. This increase therefore is largely due to inorganic P. This makes an increase of inorganic P in suspended matter of the IJsselmeer probable.

For an answer to the second question, that about accumulation of IJsselmeer POC in the Wadden Sea, *Scenedesmus*, a fresh water phytoplankton alga belonging to the Chlorococcales having a very resistant cell wall, was chosen as a tracer for IJsselmeer POC. Colonies of *Scenedesmus* are abundant throughout the year in IJsselmeer phytoplankton, the size of the colonies, nearly always consisting of 4 cells, is 10 to 20 μm. *Scenedesmus* colonies are supposed to be a reliable tracer for IJsselmeer POC; although colonies collected in the Marsdiep sometimes still show fluorescence of their chlorophyll under the microscope, and therefore are probably alive, it is unlikely that they continue dividing after a salinity shock from 0‰ in the IJsselmeer to about 20‰ in the Wadden Sea.

For 1972–1973 we have a set of phytoplankton counts for IJsselmeer and Marsdiep from 11 cruises distributed over the year. During one of these cruises (7 to 11 August 1972) we collected samples at 13 stations in the mixing area in the western Wadden Sea and 2 in the IJsselmeer near the sluices at Kornwerderzand and Den Oever. The numbers of *Scenedesmus* cells present in the Wadden Sea expressed as percentage of the numbers present in an equal volume IJsselmeer water plotted against salinity (Fig. 5), do not follow the mixing line

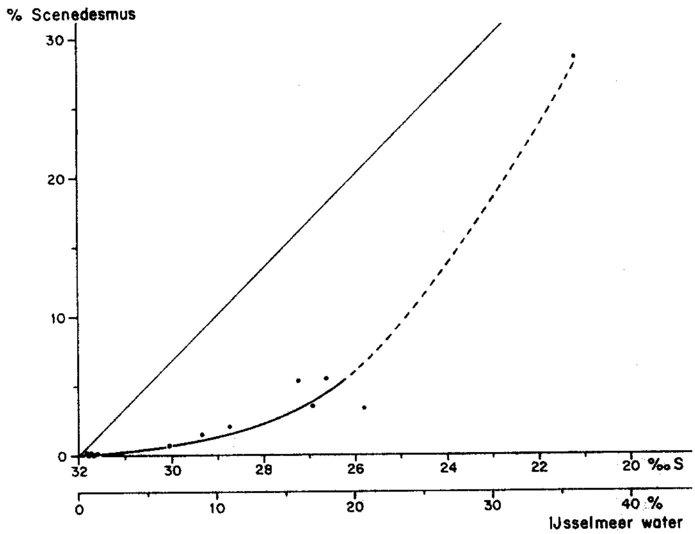

Fig. 5. Number of IJsselmeer *Scenedesmus* cells present at 13 stations in the western Wadden Sea (7 to 11 August 1972) expressed as percentage of the number present in the northern IJsselmeer plotted against salinity (‰ S) as a measure for the percentage IJsselmeer water. Following ZIMMERMAN (1976: 162) 0% IJsselmeer water corresponds to 31.5‰ S in the Marsdiep tidal inlet area and 32.5‰ S in the Vlie inlet area.

but all points are below this line, indicating removal (deposition) of *Scenedesmus* cells in the Wadden Sea. At 26‰ salinity the amount of IJsselmeer water was about 20%, but only 5% of the IJsselmeer *Scenedesmus* cells were still present. Combining all *Scenedesmus* counts made for the Marsdiep tidal inlet area from 1972 and 1973, on average 0.34% of IJsselmeer *Scenedesmus* was found at an average salinity of 30.3‰, pointing to about 3.5% IJsselmeer water according to ZIMMERMAN (1976: 176). This also indicates removal of IJsselmeer POC and most probably deposition in the Wadden Sea. *Scenedesmus* colonies frequently occur in the top layer of tidal flat sediments in the western Wadden Sea.

Accumulation of particles by the tidal process as described by POSTMA (1961a) depends on grain size. Only particles below the fraction of 64 to 128 μm are accumulated and part of the fraction below 8 μm did not settle at high water and therefore escape the accumulation process. There is a difference between "true" grain size as measured under the microscope and "settling" grain size as determined by settling velocity measurements assuming that all material behaves like quartz spheres (POSTMA, 1961b). Differences are large when the material is organic instead of inorganic because of the lower specific gravity and a high water content. Depending on water contents of 80 to 95%, POSTMA (1961b: 366) argues that "true" grain size may be 5 to 9 times the "settling" grain size. This makes it understandable that the fraction smaller than 8 μm remaining suspended during high tide, consists mainly of finely divided organic matter, among which living phytoplankton (POSTMA, 1961a: 174), and that on the other hand only part of the *Scenedesmus* colonies are retained in the Wadden Sea.

Also biological accumulation depends on grain size. VERWEY (1952: 199) assumes that nearly all the suspended matter present in Wadden Sea water can be pumped in by the filter feeders *Cerastoderma edule* and *Mytilus edulis*. DRAL (1967), however, observed a lower limit of 3 μm at low pumping rates and 6 μm at high pumping rates for *Mytilus edulis*. Both values relate to "true" grain size. Mussels can vary their retention of small particles at will; only particles larger than 30 to 40 μm are 100% retained (see also TAMMES & DRAL, 1955).

Fresh water algae used as a natural tracer of IJsselmeer POC indicate that not all IJsselmeer POC is trapped in the Wadden Sea. Part of it escapes the tidal accumulation process because the particles are to small to settle during high tide. Particles may escape biological accumulation if they remain in the tidal channels and come not in contact with the filter feeders which live in the shallow areas and on the tidal flats.

In conclusion we can state that the IJsselmeer contributes a considerable quantity of POC to the western Wadden Sea, but it is difficult to estimate which part of it is used and mineralized in the Wadden Sea and contributes to the higher phosphate values as compared with the North Sea.

IV. SUMMARY

Annual phytoplankton primary production in the tidal channels of the western Wadden Sea cannot be estimated more precise than 150 ± 50 g $C \cdot m^{-2} \cdot a^{-1}$, because of large spatial and short-term temporal variations.

This implies that year-to-year variations and possibly long term trends have to be very pronounced to be measurable even with a weekly sampling program.

Short-term temporal variation in primary production of microphytobenthos living on the tidal flats is less pronounced but spatial variation is large. Primary production on high tidal flats is larger than on flats lower in the tidal zone. Year-to-year variation on a tidal flat station occupied now for 12 years is large. This variation cannot be explained by year-to-year variations in nutrients, light or temperature, but probably by year-to-year variations in grazing. Macrophytobenthic primary production plays a subordinate role in the western Wadden Sea. It is difficult to give one figure for annual primary production for an "average" tidal flat for reasons mentioned. Tentatively microphytobenthic plus macrophytobenthic plus phytoplanktonic primary production on and above an average tidal flat is estimated at 150 ± 50 g $C \cdot m^{-2} \cdot a^{-1}$, *i.e.* the same as given for phytoplankton production in the tidal channels.

The western Wadden Sea receives a considerable amount of particulate organic carbon from outside the area, estimated at 240 g $C \cdot m^{-2} \cdot a^{-1}$. Formerly the North Sea was thought to be the only source. New data also indicate an important input from the IJsselmeer. This import of organic carbon, particulate plus dissolved, surpasses *in situ* primary production. IJsselmeer DOC is probably not used to a considerable extent in the Wadden Sea. IJsselmeer POC, however, consisting for 50% on average of living phytoplankton cells, may form a suitable food source for Wadden Sea invertebrates. Cell counts of the freshwater alga *Scenedesmus* showed that at least part of the IJsselmeer POC is retained in the western Wadden Sea. The importance of particle size in tidal as well as biological accumulation processes of POC in the Wadden Sea is stressed. There is no indication that POC content of the northern IJsselmeer has changed during the last 30 years.

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