Algal Blooms in High Turbidity, a Result of the Conflicting Consequences of Turbulence on Nutrient Cycling in a Shallow Water Estuary

R. Fichez[a] **T. D. Jickells**[b] **and H. M. Edmunds**[b]

[a]*Centre ORSTOM-Tahiti, B.P. 529, Papeete, Tahiti, French Polynesia and*
[b]*University of East Anglia, School of Environmental Sciences, NR4 7TJ
Norwich, England*

The fate of inorganic nutrients was studied together with the organic composition and chloropigment content of suspended particles in a shallow and well mixed estuary (Great Ouse, North Sea, England) from March 1990 to January 1991. Monthly sampling was made at high water neap tide yielding comparisons during a one year cycle. During early spring and summer phytoplankton development occurred inside the turbid estuary, chlorophyll *a* concentrations peaking above 100 µg l^{-1}, and nutrients displayed a non conservative behaviour related to the biological uptake. During autumn and winter the situation reversed, with low chlorophyll *a* concentration and more conservative behaviour of nutrients in the estuary. The reasons for the occurrence of phytoplankton blooms in turbid environment and their relation with turbidity and light-penetration are discussed. This study demonstrates that despite a thin euphotic zone and a totally mixed water column there is some convincing evidence for primary production development in shallow water estuary. It is possible to indeed rationalize the phytoplankton behaviour in terms of optical depth mixing approach. Photosynthetic uptake of nutrient inside estuaries may be of considerable important for understanding the fate of anthropogenic nutrients to the offshore waters, in this case the North Sea.

Introduction

The development of eutrophication events in estuaries and adjacent coastal environments in the past decades has emphasized our need for a better understanding of the fate of riverine nutrient inputs to the sea. While it is clear that there has been a significant increase in the gross nutrient inputs from rivers to the North Sea estuaries (Brockman *et al.*, 1988; Gerlach, 1988), the nature and importance of such an enrichment to the North Sea still has to be clarified (Postma, 1985; Gerlach, 1988; Duursma *et al.*, 1988).

In estuaries, primary production is influenced by a wide range of direct and indirect factors (Boynton *et al.*, 1982). In temperate areas such as the North Sea, temperature seems to play a secondary role (Gieskes & Kraay, 1975; Cadée & Hegeman, 1986) and

primary production is basically dependent on nutrient inputs and light supply. Many studies demonstrate that nitrogen is usually the limiting nutrient for phytoplankton production in estuarine and coastal waters (Ryther & Dunstan, 1972; Thayer, 1974; Boynton *et al.*, 1982). However, estuaries generally have high nutrient availability, especially at the end of winter and the development of phytoplankton blooms from early spring to summer is mainly light dependent. Beside the seasonal fluctuation in daily light exposure, turbidity is the main obstacle to the penetration of light in estuarine waters. Therefore, it is often assumed that turbid estuaries are unproductive ecosystems and that primary production is delayed relative to the clearer marine waters (Cadée & Hegeman, 1974; Milliman & Boyle, 1975; Parsons *et al.*, 1977; Wolff, 1980; McLusky, 1989). Indeed many studies have demonstrated that productivity in turbid estuaries is less than off-shore (Joint & Pomeroy, 1981; Oertel & Dunstan, 1981; Yoder & Bishop, 1985; Harding *et al.*, 1986; Randall & Day, 1987). Yet in almost all these cases, primary production occurs in turbid waters to some extent and very high rates of production have also been reported by several authors (Pomeroy *et al.*, 1972; Hobbie *et al.*, 1975; Oertel & Dunstan, 1981). Algal growth in turbid estuaries is related to the critical depth (Sverdrup, 1953; Grobbelaar, 1985) which depends on both mixing processes and light penetration. The criteria for net production have been considered in terms of a critical depth model (Wofsy, 1983; Cole & Cloern, 1984) showing that productivity is possible in turbid waters with phytoplankton moving rapidly through a fluctuating light regime, photosynthesising in the light and only respiring in the dark. The effect of such rapid changes on phytoplankton physiology is broadly predictable (Yoder & Bishop, 1985) since there is too little time for the phytoplankton to adapt to a particular light regime and hence the population is rather uniform in its adaptation. If the light regime will allow photosynthesis, there are several advantages for phytoplankton in such an environment. Clearly nutrient supply is large and also the processes that maintain suspended sediment in the turbidity maximum (Postma, 1980; McLusky, 1989) may also operate to maintain the phytoplankton within the estuary, hence allowing time for bloom development. As far as phytoplankton blooms and nutrient export are concerned, the retention time in the estuary may be a critical factor.

Studies were conducted at the University of East Anglia on the four estuaries (Great Ouse, Nene, Welland, Witham) draining to the Wash embayment that opens to the North Sea (Figure 1). This paper mainly focuses on the nutrients and chloropigments results from the Great Ouse estuary, the largest of the four estuaries, but mention of the other three estuaries (Witham, Welland, Nene) will be made where appropriate. Our study aimed at determining the influence of the turbidity and high water mixing rates on the nutrient uptake and the development of phytoplankton blooms.

Description of study area

The Great Ouse estuary (Figure 1) receives its main freshwater supplies from the Bedford Ouse and the Ely Ouse rivers and to a lesser extent from a few agricultural drains directly discharged to the estuary. The total catchment of the system is 8380 km^2 with an average freshwater flow of 38·5 m^3 s^{-1} (Gould *et al.*, 1986). Downstream of Denver Sluice, which forms a total barrier to upstream salt penetration, the tidal estuary is a 25 km long narrow (<70 m) and shallow (1 to 7 m at low water) channel opening to the marine embayment known as the Wash; we subsequently refer to the narrow region upstream of Kings Lynn as the canalised section of the estuary. A freshwater ditch follows the estuary from Denver Sluice to the vicinity of Kings Lynn where it is discharged into the estuary. The aim of this
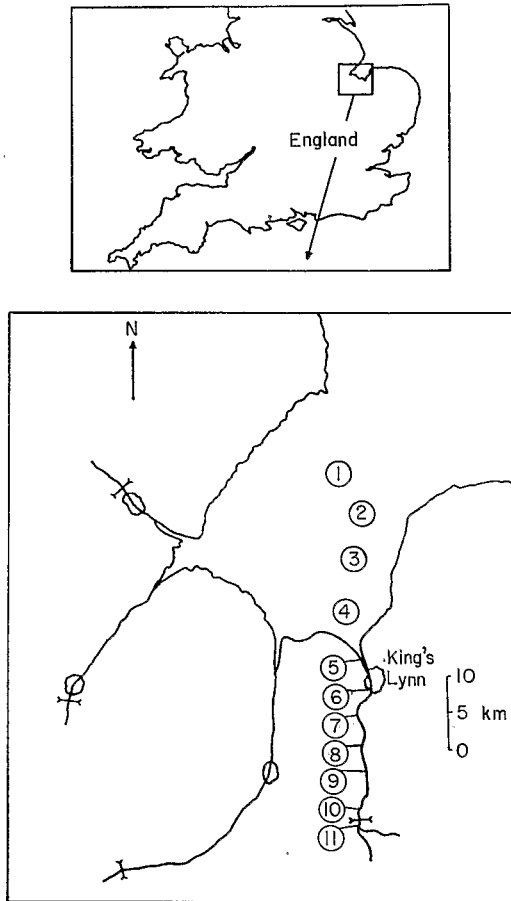
Figure 1. Location of the study site and of the sampling stations on the Great Ouse estuary, stations are numbered from 11 (river) to 1 (sea) and quoted as TO11 to TO1 in the text (TO standing for Trans-Ouse).

ditch is to regulate the flow at Denver Sluice, its effect being noticeable during high river flow regimes when a significant part of the fresh water can then be directly released in the middle estuary.

The river Ouse drains freshwater from the agricultural lands and discharges at Denver Sluice which is the major input of nutrient to the estuary. Effluents located in the vicinity of Kings Lynn (middle estuary) are discharged during the ebbing tide, and thus have little impact on the canalised region of the estuary (Gould *et al.*, 1986).

Water was sampled at 1 m depth and at 11 fixed sampling points (TO1–11) on a 50 km transect across the estuary from Denver Sluice to the Roaring Middle buoy in the middle of the Wash. Sampling was done monthly close to high neap tide from March 1990 to February 1991. To keep close to the high tide it was necessary to shorten the sampling time, thus the 50 km transect was divided in two 25 km long complementary transects. Additional sampling was carried out during two tidal cycles (May, November) close to station TO2 in the Wash. On 3 occasions, JONUS (Joint Nutrient Study) cruises yielded more detailed surveys of the canalised estuary with water samples collected by boat at salinity intervals of approximately 2 psu.

Materials and methods

Water temperature and salinity were measured directly at each sampling point. Water samples were filtered in the laboratory on pre-ignited (4 h, 450 °C) Whatman GF.C glass fibre filters under moderate vacuum within a few hours of collection. Filter treatment and storage prior to suspended solids, particulate C and N and chlorophyll pigments analysis have been described in previous papers (Fichez, 1990; 1991).

Particulate carbon and nitrogen were measured on a Carlo Erba CHN/S analyser. Prior to analysis, filters were decarbonated by exposure to HCl vapours for 2 h and then dried overnight; the remaining amounts of carbon and nitrogen are considered to be organic (Dame *et al.*, 1986). Chloropigments were extracted in 90% acetone and analysed by spectrophotometry (Lorenzen & Jeffrey, 1980), or fluorimetry (Yentsch & Menzel, 1963) when concentrations were low (winter). The fluorimeter and the spectrophotometer were intercalibrated using a pure chlorophyll *a* standard.

Water samples for nutrient analyses were frozen within a few hours of collection and filtration. Samples were subsequently thawed thoroughly and analysed by standard auto-analyser techniques (Edmunds, 1991). Sampling conditions did not permit immediate analysis of samples and thus some form of preservation was necessary. Freezing is reported to adequately preserve samples for nutrient analysis (Strickland & Parsons, 1968) and we believe this to be the case for the Great Ouse estuary where nutrient concentrations are relatively high. Samples stored for varying length of time did not vary in concentration and this together with the internal consistency of our data (see later) led us to believe that sample collection, storage and analysis procedures were satisfactory.

During the course of this work, the need for measuring light penetration and its relation to SPM concentration arose in order to determine if phytoplankton development was possible in the natural light conditions encountered. The secchi disk depth was measured and multiplied by 2 to obtain 1% light penetration depth (euphotic depth); the use of 2 as a conversion factor may be considered as a minimum value, especially in turbid waters (Holmes, 1970).

The nutrient data from the estuary are presented as plots of concentrations against salinity to determine whether mixing is conservative or not (Liss, 1976). Turbidity maximum however is located close to the upstream limit of salt intrusion and the study of the behaviour of particulate matter must therefore be extended to the freshwater tidal reach. In this region salinity is not a useful tracer of mixing and data can only be reported against length along the estuary. This complexity of the processes occurring along an estuarine transect have required that we report some results plotted against salinity and some against distance.

Results and discussion

Temperature and salinity

Temperature in the river (Table 1) ranged between 21 °C in August and 3 °C in January. In the Wash, variations were slightly smaller, from 20 °C in August to 4 °C in December. Salinities within the estuary were highly variable (Figure 2). Fresh water extended through most of the canalized estuary in March–April, with the salinity then sharply increasing at the mouth of the estuary (Stations TO5 and TO4). The spring–summer low flow period showed a strong intrusion of marine water inside the tidal river with salinity of 11 psu recorded in August at TO9, 7 km downstream Denver Sluice. This trend reversed

TABLE 1. Water temperature (°C) in the Great Ouse estuary for the March 1990 to January 1991 survey and for each sampling station as defined in Figure 1

Date	TO11	TO10	TO9	TO8	TO7	TO6	TO5	TO4	TO3	TO2	TO1
20/03/90	11·40	11·40	11·39	11·33	11·30	11·28	10·61	9·42	9·03	8·52	8·49
17/04/90	10·04	10·01	9·97	9·90	9·84	9·40	9·18	8·93	8·76	8·50	8·45
17/05/90	14·79	14·45	13·74	12·85	12·00	11·34					
14/06/90	16·76	16·66	16·52	16·20	15·97	15·56	15·05	14·23	14·04	13·92	13·84
18/07/90	19·12	19·10	18·98	18·22	17·84	17·63	17·43	17·21	17·12	16·68	16·63
28/08/90	20·88	20·82	20·44	20·50	20·56	20·29	20·52	20·46	20·37	19·87	19·30
26/09/90	10·31	11·91	11·36	11·40	11·65	11·58	12·30	12·35	13·01	13·21	13·84
24/10/90	12·66	11·90	11·74	11·93	11·67	11·98	11·46	11·87	12·13	12·48	
26/11/90	5·81	5·02	5·00	5·41	5·49	5·90	5·51	6·12	7·20	7·50	7·01
08/12/90	4·25	3·74	4·03	4·34	4·48	4·73	4·82				
13/01/91	3·21	2·87	2·86	2·94	2·89	3·06	3·43	3·57	4·11	4·53	4·90

in September the freshwater progressively invading most of the tidal river. However, the location of the saltwater–freshwater interface moved upstream in December due to reduced rainfall and river flow (Gould *et al.*, 1986; NRA, unpublished data). The estuarine waters were well mixed even during the high river flow as the changes in the vertical salinity profiles were less than 2 psu for salinity and insignificant for temperature.

Suspended particulate matter (SPM)

SPM concentrations (Figure 2) were always less than 20 mg l^{-1} in the river peaked in the canalised estuary where the turbidity maximum occurred and decreased below 40 mg l^{-1} in the Wash. In March and April a low turbidity maximum (40 to 50 mg l^{-1}) extended from TO10 to TO6. From May to August SPM concentrations increased in the upper estuary, the maximum values being always located at TO10 and peaking at 141 mg l^{-1} in July. SPM load increased and the SPM maximum receded downstream in September (126 mg l^{-1} at TO9 and TO8) and October (370 mg l^{-1} at TO8). A bimodal SPM profile was displayed in October with a second peak in SPM concentration located at TO5 and reaching 129 mg l^{-1}. The SPM maximum moved upstream in November (335 mg l^{-1} at TO9) and December (399 mg l^{-1} at TO10) and downstream in January (337 mg l^{-1} at TO8). The location of the turbidity maximum was related to the freshwater inputs, moving downstream when the river flow was high. Suspended load values in the Wash were maximum in January ($\sim$ 40 mg l^{-1}).

Chloropigments

Chlorophyll *a* concentrations (Figure 3) in the river end member, above Denver Sluice, were 10 to 70 µg l^{-1} from March to July and below 2 µg l^{-1} in winter. The chlorophyll *a* maximum was always located in the canalised estuary, except for August when the maximum recorded value for chlorophyll *a* concentrations was located in the river. Concentrations in the chlorophyll *a* maximum were high from March to August (70–156 µg l^{-1} except for June (45 µg l^{-1}), decreased in September and were less than 20 µg l^{-1} during the following four months. In the Wash (TO1) concentrations were low (1 µg l^{-1}) in March-April and increased markedly in May (12·6 µg l^{-1}) when a phytoplankton bloom occurred in the whole Wash embayment. From late summer to January concentrations were low (0·5 µg l^{-1}) and almost steady in the Wash.
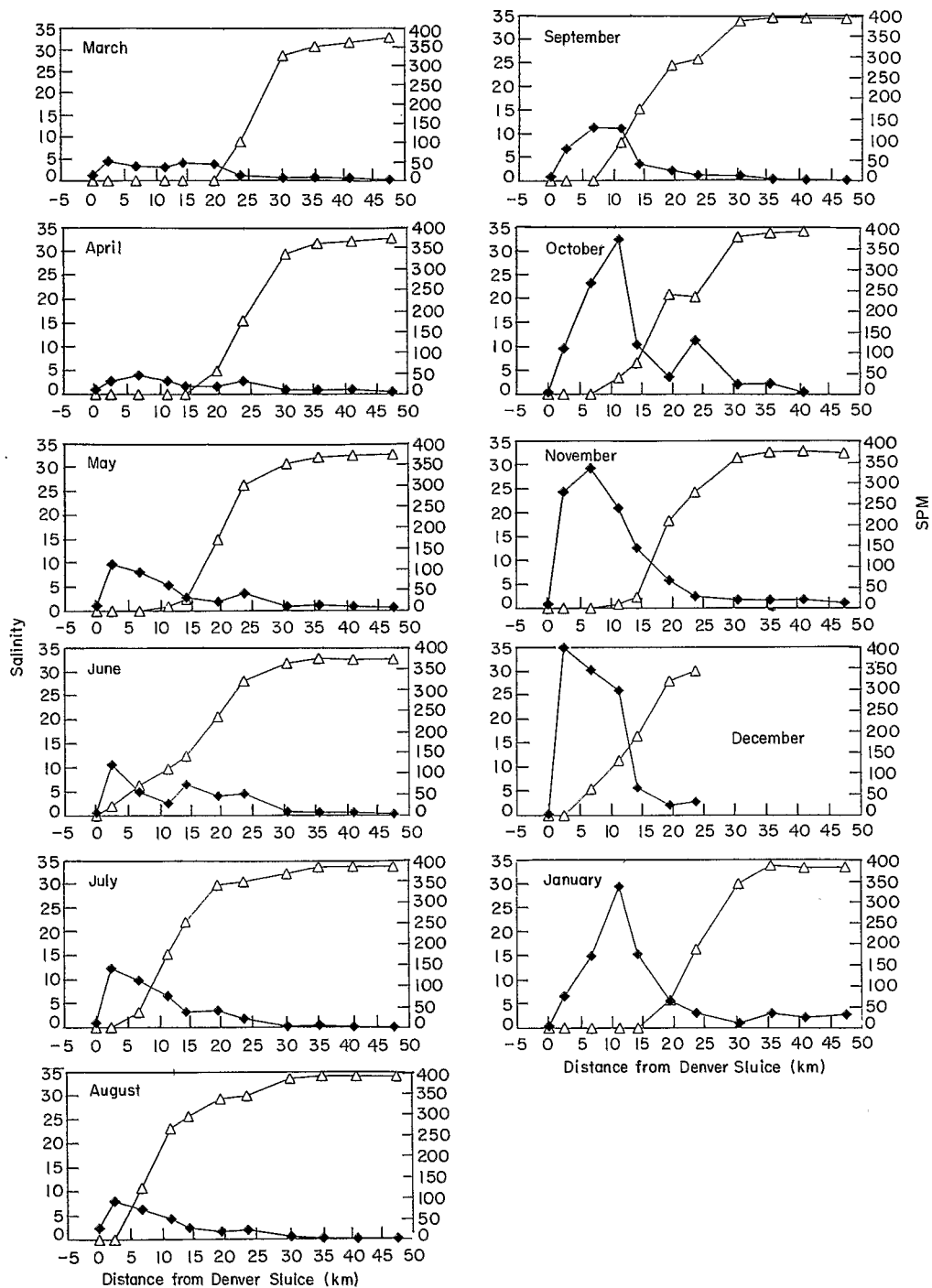
Figure 2. Time evolution of (△) salinity (psu) and (◆) SPM (mg l⁻¹) along the estuary from the sluice to the sea and for the period March 1990 to January 1991.
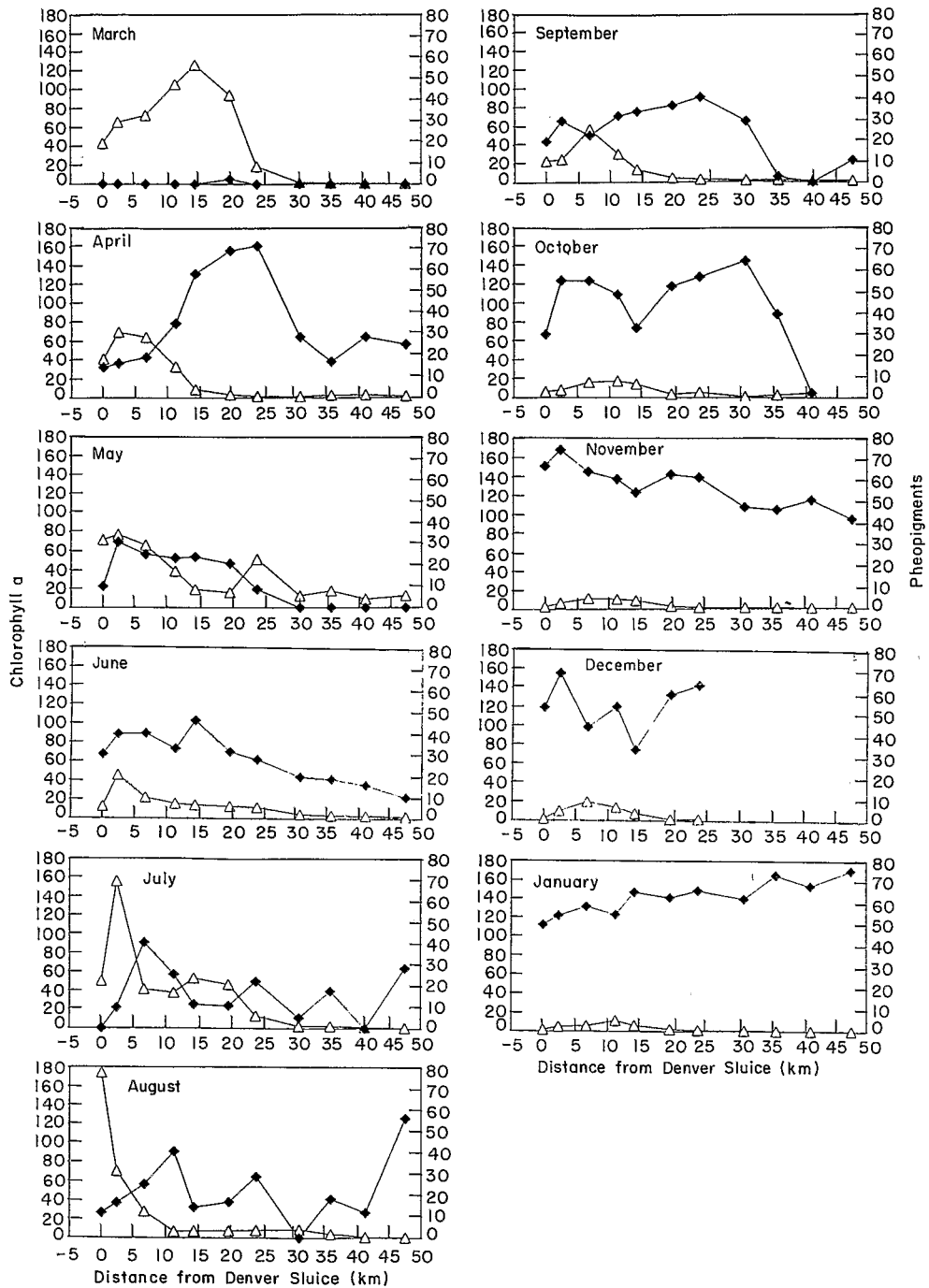
Figure 3. As figure 2 for ($\triangle$) chlorophyll *a* (μg l^{-1}) and ($\blacklozenge$) phaeopigments (% of total chloropigments).

TABLE 2. POC *vs.* PON ratio (weight:weight) in the Great Ouse estuary for the March 1990 to January 1991 survey and for each sampling station as defined in Figure 1

Date	TO11	TO10	TO9	TO8	TO7	TO6	TO5	TO4	TO3	TO2	TO1
20/03/90	8·16	9·68	9·23	8·33	8·06	9·63	6·25	5·27	8·87	13·57	13·69
17/04/90	13·52	8·74	11·00	9·33	8·00	7·59	12·55	5·49	5·38	5·43	5·14
17/05/90	8·40	7·30	7·71	11·00	11·46	6·99	8·99	11·77	10·04	9·82	8·03
14/06/90	8·27	7·50	9·41	8·52	10·80	7·53	5·16	5·12	5·21	4·56	4·65
18/07/90	11·89	11·87	8·52	6·89	8·34	7·06	12·19	7·09	4·79	5·62	5·29
28/08/90	5·69	7·11	8·70	9·33	5·96	5·73	8·32	7·70	6·45	5·90	6·57
26/09/90	7·90	9·59	10·08	13·57	7·53	5·84	5·08	4·55	4·08	5·43	4·62
24/10/90	6·69	11·68	16·54	14·97	8·13	7·51	11·29	8·70	7·25	9·79	
26/11/90	7·89	9·14	9·66	8·87	7·48	6·39	7·03	6·83	6·71	7·67	6·24
08/12/90	7·86	10·59	9·22	7·77	6·45	6·16	6·53				
13/01/91	7·98	9·50	10·64	10·14	9·51	8·91	7·79	5·91	8·25	7·88	8·04

In both the river and the chlorophyll *a* maximum phaeopigments (Figure 3) were absent in March and below 39% of the total amount of chloropigments until August (12%). This ratio increased progressively up to 67% in November, stabilizing at 50–60% in December and January. Downstream of the chlorophyll *a* maximum, large variations appeared, the highest values being reached in January with degraded pigments accounting for 70% of total chloropigment concentration.

The most significant observation is the presence of high chlorophyll *a* concentrations with low degraded pigment contribution in the upper estuary despite relatively high SPM concentrations (<50 mg l^{-1}). This pattern was emphasized by the development of a large phytoplankton bloom in March.

Particulate organic carbon (POC) and nitrogen (PON)

Particulate organic carbon *vs.* particulate organic nitrogen (POC:PON) ratio (Table 2) ranged from 4·0 to 16·5. In the river, values were ∼8·0 for most of the year, peaking at 13·5 in April and 11·9 in July and decreasing to 5·7 in August. In the upper estuary the values of the ratio were around 10·0 except for October when high values (11·7 to 16·5) were recorded. In the chlorophyll *a* maximum, POC:PON ratio ranged from 5·7 (TO11, August) to 15·0 (TO8, October). Despite the occurrence of high active chlorophyll *a* concentration in March and May in the upper as well as in the middle estuary, high POC: PON ratios were recorded. Such ratios, corresponding with degraded organic material (Cauwet, 1981), may be related to the significant contribution of the river-borne complex organic matter to the bulk organic matter.

The process that concentrates particles forming the so-called turbidity maximum may result in a similar concentration of suspended chloropigments. The formation of the turbidity maximum is associated with an increase of the residence time of particles. Assuming the primary production to be inhibited by lack of light, the consequences would be the death and the degradation of the phytoplankton originating from the river, resulting in an increase in the relative importance of the degraded forms of chloropigments and in the POC:PON ratio. Such a pattern was actually observed during the autumn–winter period but during the spring–summer period degraded chloropigments were low and the POC:PON ratio decreased in the turbidity maximum.
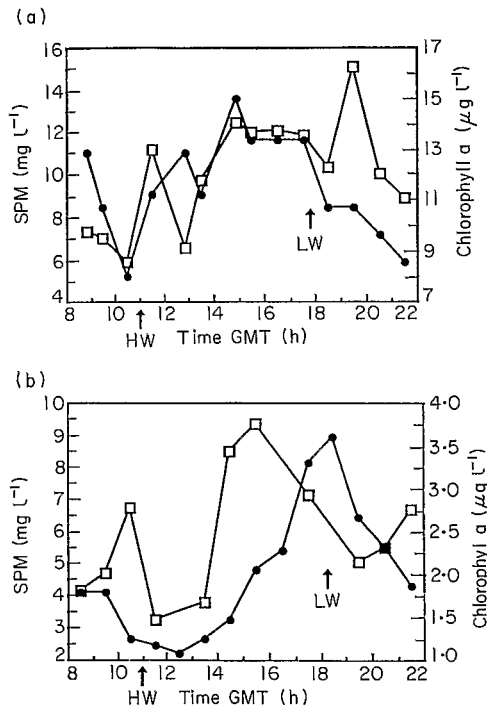
Figure 4. Tidal cycle for chlorophyll *a*, —●— and SPM —□— at station TO2. (a) 16 May 1990, (b) 16 July 1990. Arrows show low water (LW) and high water (HW) time.

Tidal cycles

Two tidal cycle surveys were conducted in May and July (Figure 4) in the Wash embayment at the entrance of the Great Ouse channel (TO2). High concentrations of both SPM and chlorophyll *a* occurred close to low water while low concentrations occurred close to high water. However, beside this general trend, discrepancies between SPM and chlorophyll *a* profiles have to be emphasized. High SPM concentrations occurred before and after high water corresponding with water current velocities of 25–64 cm s^{-1}. At low tide SPM decreased and chlorophyll *a* increased concurrently with lowering of the water current velocity (<15 cm s^{-1}). SPM was clearly related to current speed through resuspension process while chlorophyll *a* was more related to tidal movement of water bodies.

Inorganic nutrients

Nitrate, silicate and phosphate in the river above the sluice (Figure 5) showed marked seasonality, though the pattern was different for each one. Nitrate had a maximum in winter, presumably after the soils had become sufficiently wet to allow wash out of soil nitrate. The decline in summer probably reflected biological uptake. Denitrification is an alternative explanation, but ammonium levels remained low ($<35\,\mu M$) when nitrate levels were low suggesting bio-chemical reduction processes were not of great significance. Silicate concentrations peaked earlier in the year than nitrate and then declined to very low levels in the spring before increasing from July onwards. We suggest that the spring decline results from a diatom bloom in the river system with a subsequent recovery
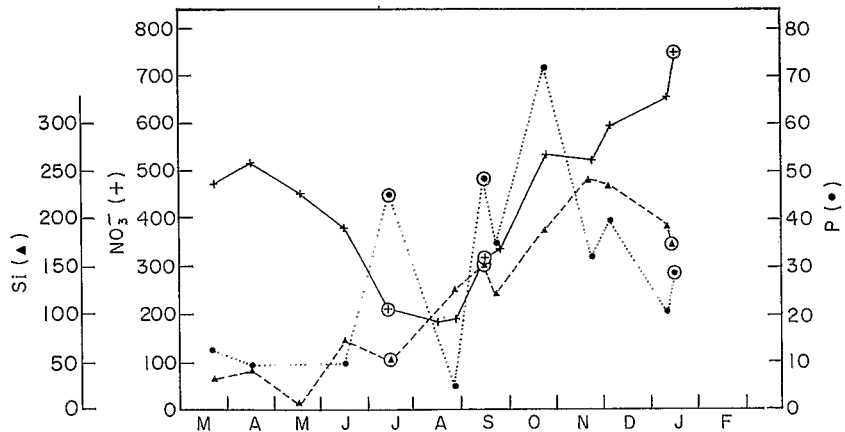
Figure 5. Seasonality of riverine (TO11) concentrations for silicates, nitrates and phosphates (μM l^{-1}). Results from the three JONUS cruises are circled.

of silicate concentrations as this bloom declined. Phosphate showed a somewhat more complex picture but was in general the inverse of nitrate. We suggest the phosphate seasonality reflects the dilution of fixed inputs to the river (possibly sewage) by varying river flows. These seasonal cycles and their interpretation are consistent with studies on the nearby river Yare (Edwards 1973*a,b*, 1974).

The results from the three JONUS cruises had a good precision because sampling was made as a function of the salinity gradient (Figure 6). We therefore selected these data to illustrate the different trends in nutrient behaviour.

In winter (JONUS 4), nitrate, silicate and phosphate behaviour was relatively conservative. Ammonium and nitrite were minor species in terms of the fixed nitrogen balance, but showed non conservative behaviour; ammonium was approximately constant along the estuary while nitrite showed a clear mid estuarine maximum. In autumn (JONUS 3), all nutrients showed somewhat more complex behaviour. Silicate was approximately conservative as was nitrate below while phosphate showed clear complex and non-conservative behaviour. Nitrite and ammonium behaved similarly to the survey described above. In summer (JONUS 2), marked and consistent non-conservative behaviour was observed, with substantial estuarine removal of silicate and phosphate, and to a lesser extent nitrate plus nitrite (nitrite was not measured separately on this occasion). There was a marked mid-estuarine maximum for ammonium.

The fixed point sampling strategy employed for the monthly survey, even if it gave less detailed information on the behaviour of nutrients, showed the evolution through the year. There was a relatively smooth transition between the different behaviours in the different seasons (data non-presented). Nitrate was non-conservative on a few occasions, phosphate generally non-conservative and silicate relatively conservative in the September to January period but not during the rest of the year.

The non-conservative behaviour of nutrients indicated significant nutrient uptake in the estuary. Denitrification in estuaries may be responsible for an important uptake of nitrate (Nixon, 1981; Smith *et al.*, 1985; Kemp *et al.*, 1990) but phosphate and silicate also displayed a non-conservative behaviour, demonstrating that another uptake process is involved. Furthermore, the calculated atomic N:P ratio for nutrient uptake in the estuary
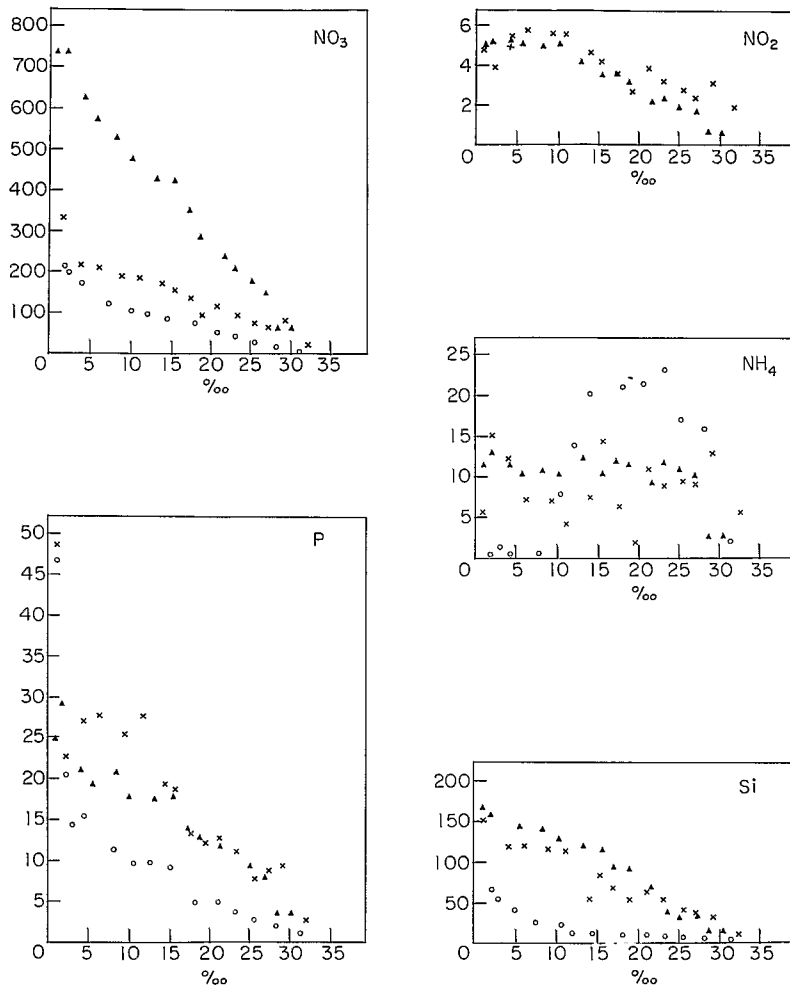
Figure 6. Nutrient concentration ($\mu M\ l^{-1}$) *vs.* salinity (psu) on (○) JONUS 2 (July 1990), (×) JONUS 3 (October 1990), and (▲) JONUS 4 (January 1991) cruises. NO_2 was not analysed during the JONUS 2 cruise.

was about 10:1 in July (based on deviations from conservative mixing), being close to the Redfield ratio of 16:1 (Redfield, 1958) and in the 10:1 to 20:1 range given for phytoplankton uptake (Parsons *et al.*, 1961; Rhee, 1978). All this evidence is consistent with phytoplankton development taking place in the turbid estuary resulting in a significant photosynthetic transformation of inorganic nutrient to particulate organic material. Because of the anthropogenic enrichment of river waters with nitrate and to a lesser extent phosphorus, but not with silica, the biological removal is seen most clearly for phosphate and silica. The occurrence of an extensive bloom in May can explain the general decrease in chlorophyll *a* concentrations in June as a consequence of the exhaustion of nutrient silicate, assuming that the estuarine algal blooms were dominated by diatoms. We do not have detailed photoplankton information but preliminary sampling in September suggested a mixed algal culture including diatoms (Malin Pers. comm.).
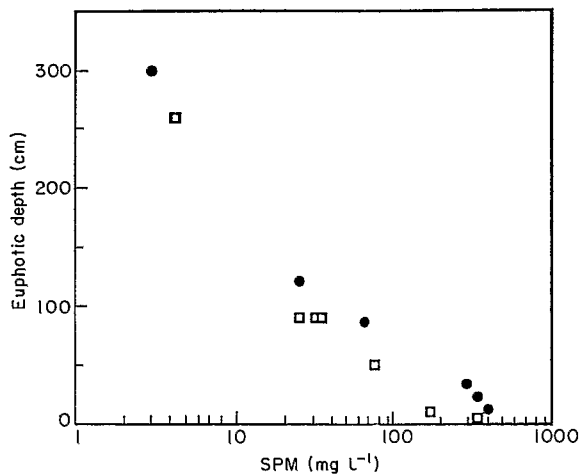
Figure 7. Light penetration *vs.* SPM (log scale) for two sampling occasions. Light penetration was calculated as 2 times the Secchi depth (see text). □, 18 December 1990; ●, 13 January 1991.

Light penetration

Euphotic depth (2 Secchi depth) was plotted against SPM concentration for the last two months of sampling (Figure 7). The resulting exponential relationship showed that a dramatic increase in light penetration (> 100 cm) corresponded with SPM concentrations decreasing below 25 mg l^{-1}, such a situation being mainly encountered in the river or in the marine end member during spring and summer. In the estuary, SPM concentrations above 100 mg l^{-1} reduced light penetration to depth less than 20 cm. While these measurements were only conducted in the winter of 1990/1991, in the absence of other data we assumed that the relationship in Figure 6 applies throughout the year. This is an unsatisfactory assumption because light penetration will vary seasonally as a consequence of the solar angle and the light scattering. SPM is mainly responsible for such light scattering but dissolved coloured substances may also play a significant role and show wide seasonal variations (Randall & Day, 1987; Grobbelaar, 1989; Gallegos *et al.*, 1990), especially in estuarine waters where dissolved humic substances abound (Ewald, 1985; Gough & Mantoura, 1990). However, we estimated that the approximation we made was not weakening our final conclusions, especially as the increase in the solar angle from January to June would increase light penetration.

Estuarine waters are characterized by a thin euphotic zone (> 1% of surface irradiance) and a thick aphotic zone. The determinant factor for phytoplankton development in natural environment is the time alternatively spent in the dark and in the light by the algae and the subsequent balance between respiration and photosynthesis. If water mixing exceeds a critical mixing depth (Sverdrup, 1953; Talling, 1957) photosynthesis cannot compensate for respiration losses and algal population degenerates. Due to the relative thinness of the euphotic zone, mixing depth was assumed to be the main factor influencing phytoplankton production in turbid systems (Grobbelaar, 1985). Production processes in these environments depends on sequential exposure to the light due to the turbulent mixing (tide + freshwater flow) that carries algal cells up and down the water column. In the case of the Great Ouse estuary the absence of stratification demonstrated that, in the

canalised estuary, the whole water column was well mixed, the mixing depth being therefore equal to the water depth. Consequently, phytoplankton development is possible if the critical depth is more than the water depth. Critical depth can be calculated as a simple function of the euphotic layer. According to various authors the minimum ratio for the critical depth compared to the euphotic zone ranges from 6 (Cole & Cloern, 1984; Grobbelaar, 1985) to 10 (Wofsy, 1983). More recently, Grobbelaar (1990) modelling productivity in turbid waters found the critical mixing depth to be 20 time the euphotic depth. Assuming an average depth of 5 m at high tide for the canalised estuary and a critical depth *vs.* euphotic depth ratio of 10 it is possible to broadly estimate a threshold SPM concentration of 70 mg l^{-1} to correspond with a light penetration depth of 50–60 cm which would then allow phytoplankton growth. At low tide the increase in SPM concentration which will result in decreasing light penetration could be compensated by the concurrent decrease in water depth (average 2 m).

It must be emphasized that light penetration is not the only influencing factor, daily time of sunlight exposure, salinity stress and nutrient availability also significantly affect production. Nevertheless, this simple assessment confirms that important phytoplankton development is possible in turbid and well-mixed shallow water ecosystems as long as critical depth is more than water depth. The processes observed in the Ouse are probably not unique to this estuary in this year. In July, a survey of all four estuaries draining to the Wash revealed non conservative behaviour of nitrate, phosphate and silicate and oxygen supersaturation, consistent with algal blooms.

Conclusions

The biogeochemical cycling in the Great Ouse estuary can be broadly separated into two periods. During the first period (September–January), phytoplankton development was inhibited by high SPM loads (>100 mg l^{-1}) which were presumably responsible for a decrease in light penetration. This is consistent with the low values of chlorophyll *a*, the increase in POC:PON ratio and the conservative pattern of nitrate and silicate in the canalised estuary and corresponds with a classical pattern of phytoplankton inhibition in estuaries with turbid well mixed waters (Cloern *et al.*, 1985; Pennock & Sharp, 1986; Fisher *et al.*, 1988; Garcia-Soto *et al.*, 1990). During the second period (March–August) phytoplankton bloom events occurred. Clear evidence for the March-bloom arose from the high level of chlorophyll *a* and the absence of degraded pigments. The bloom extended through the whole estuary length, maximum chlorophyll *a* concentration together with minimum POC:PON ratio occurring at TO7, 14 km downstream the tidal sluice. Chlorophyll *a* concentrations dramatically decreased in the Wash part of the transect together with an increase of POC:PON ratio demonstrating the phytoplankton development to be confined to the estuary.

The present work identified large scale blooms in the relatively turbid waters of the shallow Great Ouse estuary. The occurrence of significant primary production in this environment can be explained reasonably well in terms of a critical depth model. The productivity of non stratified estuarine waters cannot be neglected on the sole account of turbidity because of the possible dependence of algal cells to the sequential exposure to the light.

The occurrence of significant primary production at the continent-ocean boundary will have a major effect on the cycling and the flux of nutrients. Environmental conditions specific to estuaries have certainly been neglected in most of the studies on primary

production, especially the problems of fluctuating light regimes. This conclusion agrees with recent studies which emphasized the importance of the tidal freshwater reaches as potential location for significant primary production and biogeochemical reactions (Anderson, 1986; Schuchardt & Schrimer, 1991).

Our results suggest that algal developments in shallow water estuaries can play a significant role in the regulation of the release of anthropogenic nutrients to the sea and in the eutrophication of coastal waters. In particular it seems the riverine and estuarine blooms pre-date the offshore blooms and thus the estuarine input to the North Sea is depleted in nutrients, particularly silica, during the offshore spring bloom. This may act to select against diatom blooms in such offshore waters. The transformation of a large fraction of the pool of dissolved inorganic nutrient to organic particulate material in the estuary certainly may significantly influence the export of nutrients, although the subsequent fate of this algal material is uncertain. However, the phytoplankton activity in the freshwater reach of estuaries should be considered in modelling the biogeochemical cycle of nutrients in the North Sea.

Acknowledgements

References

Anderson, G. F. 1986 Silica, diatoms, and freshwater productivity maximum in Atlantic coastal plain estuaries. Chesapeake Bay. *Estuarine, Coastal and Shelf Science* **22**, 183–197.

Boynton, W. R., Kemp, W. M. & Keefe, C. W. 1982 A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. In *Estuarine Comparisons* (Kennedy, V. S., ed.). New York: Academic Press, pp. 69–90.

Brockmann, U., Billen, G. & Gieskes, W. W. C. 1988 North Sea nutrients and eutrophication. In *Pollution of the North Sea an assessment* (Salomons, W., Bayne, B. L., Duursma, E. K. & Förstner, U., eds). Berlin: Springer-Verlag, pp. 348–389.

Cadée, G. C. & Hegeman, J. 1974 Primary production of phytoplankton in the Dutch Wadden Sea. *Netherland Journal of Sea Research* **8**, 240–259.

Cadée, G. C. & Hegeman, J. 1986 Seasonal and annual variation in *Phaeocystis pouchetii* (Haptophyceae) in the westernmost inlet of the Wadden Sea during the 1973 to 1985 period. *Netherland Journal of Sea Research* **20**, 29–36.

Cauwet, G. 1981 Non-living particulate matter. In *Marine organic chemistry*. Evolution, composition, interactions and chemistry of organic matter in sea water. (Duursma, E. K. & Dawson, R. eds.). Amsterdam: Elsevier, pp. 71–90.

Cole, B. E. & Cloern, J. E. 1984 Significance of biomass and light availability to phytoplankton productivity in San Francisco Bay. *Marine Ecology Progress Series*, **17**, 15–24.

Cloern, J. E., Cole, B. E., Wong, R. L. J. & Alpine, A. E. 1985 Temporal dynamics of estuarine phytoplankton: a case study of San Francisco Bay. *Hydrobiologia* **129**, 153–176.

Dame, R., Chrzanowski, T., Bildstein, K., Kjerfve, B., McKellar, H., Nelson, D., Spurrier, J., Stancyk, S., Stevenson, H., Vernberg, J. & Zingmark, R. 1986 The outwelling hypothesis and North Inlet, South Carolina. *Marine Ecology Progress Series* **33**, 217–229.

Duursma, E. K., Beukema, J. J., Cadée, G. C., Lindeboom, H. J. & Wilde, P. A. W. J. 1988 Assessment of environmental impact of nutrients. In *Environmental protection of the North Sea* (Newman, P. J. & Agg, A. R., eds). Oxford: Heineman Professional Publishing, pp. 176–188.

Edmunds, H. M. 1991 The seasonal cycle of dissolved inorganic nutrient in the southern North Sea during 1988/1989. MPhil Thesis, University of East Anglia, submitted.

Edwards, A. M. C. 1973a Dissolved load and tentative solute budgets of some Norfolk catchments. *Journal of Hydrology* **18**, 201–217.

Edwards, A. M. C. 1973b The variation of dissolved constituents with discharge in some Norfolk rivers. *Journal of Hydrology* **18**, 219–242.

Edwards, A. M. C. 1974 Silicon depletion in some Norfolk rivers. Freshwater Biology **4**, 267–274.

Ewald, M., Berger, P. & Belin, C. 1985 Substances humiques du dissous et du particulaire en milieu estuarien: dosage et échange. *Océanis* **11**, 437–442.

Fichez, R. 1990 Les pigments chlorophylliens: indices d'oligotrophie dans les grottes sous-marines. *Comptes rendus de l'Académie des Sciences*, Paris (ser. III) **310**, 155–161.

Fichez, R. 1991 Particulate organic matter in a Mediterranean submarine cave. *Marine Biology* **108**, 167–174.

Fisher, T. R., Harding, L. W. Jr, Stanley, D. W. & Ward, L. G. 1988 Phytoplankton, nutrients, and turbidity in the Chesapeake, Delaware, and Hudson estuaries. *Estuarine, Coastal and Shelf Science* **27**, 61–93.

Gallegos, C. L., Correll, D. L. & Pierce, J. W. 1990 Modeling spectral diffuse attenuation, absorption and scattering coefficients in a turbid estuary. *Limnology and Oceanography* **35**, 1486–1502.

Garcia-Soto, C., De Madariaga, I., Villate, F. & Orive, E. 1990 Day-to-day variability in the plankton community of a coastal shallow embayment in response to changes in river runoff and water turbulence. *Estuarine, Coastal and Shelf Science* **31**, 217–229.

Gerlach, S. A. 1988 Nutrients—an overview. In *Environmental protection of the North Sea* (Newman, P. J. & Agg, A. R., eds) Oxford: Heineman Professional Publishing, pp. 147–175.

Gieskes, W. W. C. & Kraay, G. W. 1975 The phytoplankton spring bloom in Dutch coastal waters of the North Sea. *Netherland Journal of Sea Research* **9**, 166–196.

Gough, M. A. & Mantoura, R. F. C. 1990 Advanced analytical methods for the characterisation of macro-molecular marine organic matter. In *Mass spectrometry of large non volatile molecules for marine organic chemistry* (Hilf, E. & Tuszynski, D., eds). World Scientific in press.

Gould, D. J., Dyer, M. F. & Tester, D. J. 1986 Environmental quality and ecology of the Great Ouse estuary. *Water Pollution Control* **1**, 84–103.

Grobbelaar, J. U. 1985 Phytoplankton productivity in turbid waters. *Journal of Plankton Research* **7**, 653–663.

Grobbelaar, J. U. 1989 The contribution of phytoplankton productivity in turbid fresh waters to their trophic status. *Hydrobiologia* **173**, 127–133.

Grobbelaar, J. U. 1990 Modelling phytoplankton productivity in turbid waters with small euphotic to mixing depth ratios. *Journal of Plankton Research* **12**, 923–931.

Harding, L. W., Meeson, B. W. Jr & Fisher, T. R. Jr 1986 Phytoplankton production in two East Coast estuaries: Photosynthesis-light functions and patterns of carbon assimilation in Chesapeake and Delaware bays. *Estuarine, Coastal and Shelf Science* **23**, 773–806.

Hobbie, J. E., Copeland, B. J. & Harrison, W. G. 1975 Sources and fates of nutrients of the Pamlico River estuary, North Carolina. In *Estuarine Research* vol. 1 (Cronin, L. E., ed.). New York: Academic Press, pp. 287–302.

Holmes, R. W. 1970 The Secchi disk in turbid coastal waters. *Limnology and Oceanography* **15**, 688–694.

Joint, I. R. & Pomeroy, A. J. 1981 Primary production in a turbid estuary. *Estuarine, Coastal and Shelf Science* **13**, 303–316.

Kemp, W. M., Sampou, P., Caffrey, J., Mayer, M., Henriksen, K. & Boynton, W. R. 1990 Ammonium recycling *vs.* denitrification in Chesapeake Bay sediments. *Limnology and Oceanography* **35**, 1545–1563.

Liss, P. S. 1976 Conservative and non-conservative behaviour of dissolved constituents during estuarine mixing. In *Estuarine Chemistry* (Burton, J. D. & Liss, P. S., eds). London: Academic Press, pp. 93–130.

Lorenzen, C. J. & Jeffrey, S. W. 1980 Determination of chlorophyll in seawater. Unesco technical papers in marine Science 35, 20 pp.

McLusky, D. S. 1989 The estuarine ecosystem. Glasgow: Blackie & Sons, 215 pp.

Milliman, J. D. & Boyle, E. 1975 Biological uptake of dissolved silica in the Amazon river estuary. *Science* **189**, 995–997.

Nixon, S. W. 1981 Remineralization and nutrient cycling in coastal marine ecosystems. In *Nutrient Enrichment in Estuaries* (Neilson, B. J. & Cronin, L. E., ed). Clifton, New Jersey: Humana Press, pp. 111–138.

Oertel, G. F. & Dunstan, W. M. 1981 Suspended-sediment distribution and certain aspects of phytoplankton production off Georgia, USA. *Marine Geology* **40**, 171–197.

Parsons, T. R., Stephens, K. & Strickland, J. D. H. 1961 On the chemical composition of eleven species of marine phytoplankton. *Journal of the Fisheries Research Board Canada* **18**, 1001–1016.

Parsons, T. R., Takahashi, M. & Hargrave, B. 1977 Biological oceanographic processes. Pergamon Press, Oxford, 332 pp.

Pennock, J. R. & Sharp, J. H. 1986 Phytoplankton production in the Delaware estuary: temporal and spatial variability. *Marine Ecology Progress Series* **34**, 143–155.

Pomeroy, L. R., Shenton, L. R., Jones, R. D. H. & Reimold, R. J. 1972 Nutrient fluxes in estuaries. In *Nutrients and Eutrophication. ASLO Special Symposium* vol. 1, pp. 274–291.

Postma, H. 1980 Sediment transport and sedimentation. In *Chemistry and biochemistry of estuaries* (Olausson, E. & Cato, I., eds). Chichester: Wiley & Sons, pp. 153–186.

Postma, H. 1985 Eutrophication of Dutch coastal waters. Netherland Journal of Sea Research **11**, 334–364.

Randall, J. M. & Day, J. W. Jr 1987 Effects of river discharge and vertical circulation on aquatic primary production in a turbid Louisiana (U.S.A.) estuary. *Netherland Journal of Sea Research* **21**, 231–242.

Redfield, A. C. 1958 The biological control of chemical factors in the environment. American Journal of Science **46**, 205–221.

Rhee, G. Y. 1978 Effects of N:P atomic ratio and nitrate limitation on algal growth, cell composition, and nitrate uptake. *Limnology and Oceanography* **23**, 10–25.

Ryther, J. H. & Dunstan, W. M. 1971 Nitrogen, phosphorus, and eutrophication in the coastal marine environment. Science **171**, 1008–10013.

Schuchardt, B. & Schirmer, M. 1991. Phytoplankton maxima in the tidal freshwater reaches of two coastal plain estuaries; *Estuarine, Coastal and Shelf Science* **32**, 187–206.

Smith, C. J., De Laune, R. D. & Patrick, W. H. Jr, 1985 Fate of riverine nitrate entering an estuary: I. Denitrification and nitrogen burial. *Estuaries* **8**, 15–21.

Strickland, J. D. H. & Parsons, T. R. 1968 A practical handbook of seawater analysis. *Bulletin of the Fisheries Research Board Canada* **167**, 311 pp.

Sverdrup, H. W. 1953 On conditions for the hivernal blooming of phytoplankton. *Journal du Conseil International pour l'Exploration de la Mer* **29**, 130–135.

Talling, J. F. 1957 The phytoplankton population as a compound photosynthetic system. *New Phytologist* **56**, 133–149.

Thayer, G. W. 1974 Identity and regulation of nutrients limiting phytoplankton production in the shallow estuaries near Beaufort, N.C. *Oecologia* **14**, 75–92.

Wofsy, S. C. 1983 A simple model to predict extinction coefficients and phytoplankton biomass in eutrophic waters. Limnology and Oceanography **28**, 1144–1155.

Wolff, W. J. 1980 Biotic aspects of the chemistry of estuaries. In *Chemistry and Biochemistry of Estuaries* (Olausson, E. & Cato, I., eds). Chichester: Wiley & Sons, pp. 261–295.

Yentsh, C. S. & Menzel, D. W. 1963 A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep Sea Research **10**, 221–231.

Yoder, J. A. & Bishop, S. S. 1985 Effects of mixing-induced irradiance fluctuations on photosynthesis of natural assemblages of coastal phytoplankton. *Marine Biology* **90**, 87–93.