

THE SIGNIFICANCE OF OBSERVED NUTRIENT CONCENTRATIONS IN THE DISCUSSION ABOUT NITROGEN AND PHOSPHORUS AS LIMITING NUTRIENTS FOR THE PRIMARY CARBON FLUX IN COASTAL WATER ECOSYSTEMS.

JOHAN SÖDERSTRÖM

SARSIA



SÖDERSTRÖM, JOHAN 1996 07 01. The significance of observed nutrient concentrations in the discussion about nitrogen and phosphorus as limiting nutrients for the primary carbon flux in coastal water ecosystems. – *Sarsia* 81:81-96. Bergen. ISSN 0036-4827.

Decisions about which of N or P limits the production in the marine environment, based on concentration ratios or enrichment experiments, have as a prerequisite that concentrations mirror nutrient availability. This is an assumption that lacks a theoretical background.

With the aid of a simple hydraulic model it is pointed out that concentrations in a steady state flux system, at a certain input, depend on the mechanisms that regulate the transports from the system. In a coastal water these mechanisms for the nutrient flux are water exchange and biological activities. Because the biological activities are not the same for nitrogen and phosphorus, the resulting N : P concentration ratios can not be expected to represent the ratios for the availabilities of the nutrients. Conclusions about N as the limiting nutrient, which are based on concentration ratios, or concentration dependent bioassays, can therefore not be accepted.

Examples from the monitoring of coastal waters in Sweden, show that, in accordance with the Redfield concept and the Smith & Hollibaugh concept of carbon controlled nitrogen cycling, the same concentrations of inorganic nutrients appear in areas with similar ecosystem structure, but different nutrient supplies and different primary productions. Concentrations depend more on ecosystem structure than on flux size.

Some observations from the Swedish west coast on C : N : P ratios in particles are described. The conclusion is that flux calculations involving Redfield ratios are meaningful tools in the assessment of the relative role of different nutrients in the flux of energy and matter in coastal ecosystems. An example is described, which explains the - seemingly incompatible - simultaneous occurrence of supply observations showing nitrogen surplus, and concentration-enrichment observations showing nitrogen deficiency.

With concentration ratios and enrichment experiments ruled out as methods for determining which of N and P limits plankton production in coastal waters, no valid arguments are left for N as the limiting nutrient in Swedish and Danish waters. Deliveries of nutrients to the Baltic Sea, and the Swedish and Danish coastal waters of Kattegat and Skagerrak, have a pronounced surplus of nitrogen in relation to the Redfield ratio for plankton. Evidently phosphorus is initially the limiting nutrient. This fact, together with the greatly improved knowledge in the last decades about the processes in the marine nitrogen cycle, makes it evident that the expensive measures against nitrogen output, imposed by Swedish and Danish authorities in order to diminish eutrophication in the coastal waters, are doomed to failure.

Johan Söderström, Box 3016, S-434 03 Vallda, Sweden.

KEYWORDS: N:P-ratios; bioassays; flux analysis.

INTRODUCTION

‘The distribution of inorganic nitrogen and phosphorus, and bioassay experiments, both show that nitrogen is the critical limiting factor to algal growth and eutrophication in coastal marine waters. About twice the amount of phosphate as can be used by the algae is normally present. This surplus results from the low nitrogen to phosphorus ratio in terrigenous contributions, including human waste, and from the fact that phosphorus regenerates more quickly than ammonia from decomposing organic matter. Removal

of phosphate from detergents is therefore not likely to slow the eutrophication of coastal marine waters, and its replacement with nitrogen-containing nitrilotriacetic acid may worsen the situation’.

This abstract from the much cited paper of RYTHER & DUNSTAN (1971) is still the best summing up of a concept that has dominated marine nutrient research and marine water management discussions for more than 20 years.

Before this paper arrived, the thinking expressed by REDFIELD (1958) and REDFIELD & al. (1963), was the basis for the then relatively few researchers in the

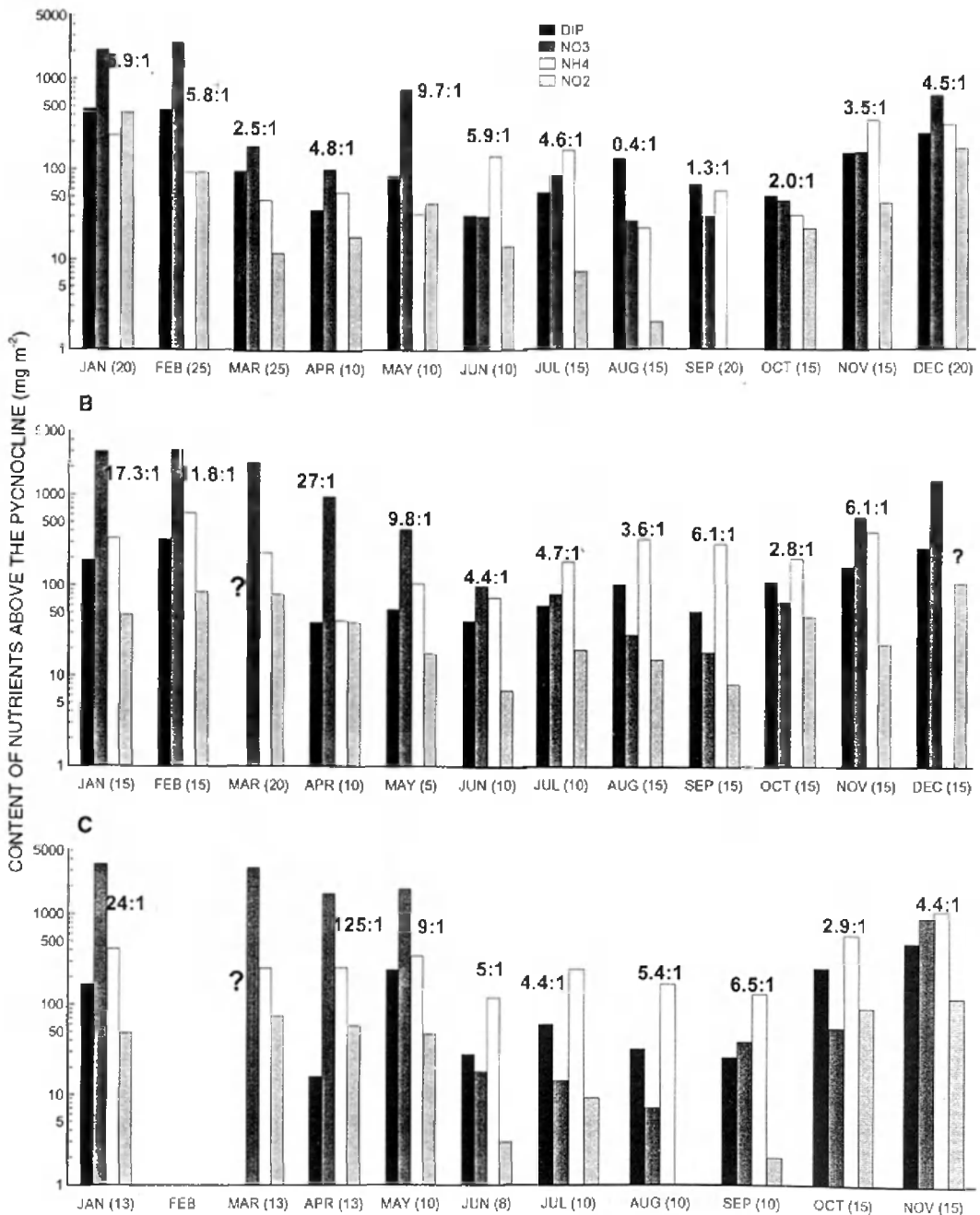


Fig. 1. Monthly water-column contents (mg m^{-2} above the pycnocline) in 1991 at one open-sea locality (A. Koster, Skagerrak) and two fjord localities (B. Galterø and C. Byfjorden). The approximate depth of the pycnocline is given in brackets on the x-axis. The seasonal DIN : DIP weight ratio is given above the bars. The annual mean DIN : DIP for the three localities was 4.2 : 1, 9.4 : 1 and 20.7 : 1, respectively.

field of marine eutrophication. The title from 1963, 'The influence of organisms on the composition of seawater', comprises these authors' inspiring new ideas.

Against Redfield's opinion that fixation would counteract deficiencies of nitrogen RYTHER & DUNSTAN wrote: 'It is certainly not effective locally or in the short run'. This was not based on measurements of the fixation, it was their logical conclusion since they interpreted low concentrations of inorganic nitrogen as evidence of nitrogen deficit in relation to phosphorus. However, to cite HOWARTH (1990): 'Unfortunately, N and P availabilities are not necessarily the same as concentrations'.

The new nitrogen thesis was adopted by a majority of marine biologists. The same methods, comparison of concentrations, and enrichment experiments, are still widely used as ground for the opinion that nitrogen is the limiting nutrient and therefore should be the aim of water protection measures (GRANELI & al. 1990, PEPPERZAK & PEETERS 1991).

From the beginning the concept formulated by RYTHER & DUNSTAN (1971) encountered criticism. A series of works by SCHINDLER (a summing up in 1988) might be mentioned in this connection. SMITH (1984) and SMITH & HOLLIBAUGH (1989) are important contributions. The reader is asked to observe that the controversy discussed here not is about which of nitrogen or phosphorus limits primary production, what is questioned is the conceptual framework, concentrated in the phrase 'twice the amount as can be used is present' as an argument for limitation.

RYTHER & DUNSTAN (1971) assumed that the low N : P concentration ratios they observed were the result of terrigenous contributions (from New York waste water with N : P = 2.5 : 1). However, in multidisciplinary studies of a fjord at the Swedish west coast, similar low N : P concentration ratios, indicating nitrogen as the limiting nutrient, were found in the surface water

(DANIELSSON & al. 1975; SÖDERSTRÖM 1976) but extensive studies of water exchange (SVENSSON 1980) and nutrient deliveries to the fjord revealed a nutrient flux in which phosphorus clearly was the minimum nutrient. In Fig. 1 is shown DIN : DIP ratios near the Redfield ratio at the sea station, winter ratios at the fjord stations are high in accordance with the known deliveries of N and P. Very high ratios in April at the fjord stations indicate phosphorus limitation of the spring bloom. All stations have in the summer DIN : DIP ratios well below the Redfield ratio. It was evident that there was no simple correlation between delivery of nutrients and the concentrations in the fjord. GRANELI & al. (1986) found a surplus of N in the supply to the Laholm Bay, but DIN : DIP concentration ratios and enrichment experiments showed N as limiting. In the face of this dilemma they chose to rely on concentrations. It is not explained why they assumed the observed concentrations to show nutrient availability better than their flux computations.

RELATIONS BETWEEN FLUXES AND CONCENTRATIONS IN A HYDRAULIC SYSTEM

Fluxes in steady state systems, which is what constitutes ecosystems (REDFIELD & al. 1963), result in concentrations which are functions of both delivery and export. Low N : P ratios in the delivery and simultaneous low ratios in the concentrations, must, until otherwise shown, be considered as a coincidence. Enough attention has not always been paid to this and some elementary discussion of the relation fluxes/concentrations may be excused.

Fig. 2A shows a simple hydraulic model of a system where a continuous process is fed by fluxes of two fluid primary elements. The process is assumed to be constant. The primary elements are fed to the process through two

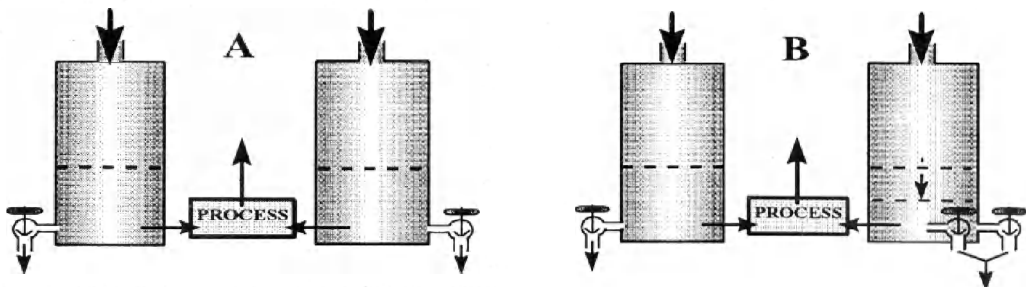


Fig. 2. A simplified hydraulic model with a constant delivery of two elements (left, right cistern) and a constant process utilizing the two elements. A. Identical taps in the two cisterns. B. Doubled tap capacity in the right cistern.

cisterns which function as buffering intermediate pools in the flux. It is directly seen that the level in the cisterns can be controlled by the taps at the bottom. On the other hand, with the taps constant, the level might also be regulated through changes in the delivery or in the process. In Fig. 2B the deliveries and the process are unchanged, but there are two taps on the right cistern, symbolizing that the tap opening is doubled. What happens now is that the level in the right cistern sinks until the pressure on the taps is decreased so that the same amount flows through two taps as before through one. The flux system is unchanged. The only change is in the level in the right cistern, a function of the tap opening. It should be evident that one who concludes from the position of this level, 'the amount present', that the flux in the right cistern is lower, is the victim of self-delusion. But this is just what is done when concentrations, directly or with bioassays, are used to determine which of nitrogen and phosphorus is limiting the production, the carbon/nitrogen/phosphorus fluxes, in an ecosystem.

A coastal water receiving nutrients from land functions in the same way. A continuous delivery of nutrients builds up a concentration gradient towards the surrounding areas until the specific water exchange makes possible a nutrient transport from the recipient of the same size as the delivery. This is exemplified in Scandinavian waters by the winter situation with its higher nutrient concentrations. However, in the spring concentrations decrease rapidly because a biological 'tap' is added to the hydrological. The flux through this tap is influenced by concentrations in a similar way as flux and pressure interact in the cisterns in Fig. 2. There is a feed-back system between biological activities and concentrations. With a constant nutrient flux the concentrations at steady state vary with the conditions for the biological exports. If biological exports function sufficiently at low concentrations, the result will be low concentrations in the ambient water, if they only function at high concentrations the ambient water gets high concentrations. Concentrations can consequently not be used as parameters for the availability of nutrients in an ecosystem. When biological transports function in the system the ambient concentrations can only show the relative availability of two nutrients if they have identical biological processes. The nitrogen cycle includes unique processes, as biological fixation and denitrification, and the relation flux/concentration can therefore not be the same as in the parallel phosphorus flux.

PRODUCTION VERSUS GROWTH OF PHYTOPLANKTON

One factor behind the nitrogen/phosphorus controversy is a diffuse distinguishing between production, the total flux from inorganic to organic forms, and the relative growth of plankton cells. This terminological problem was introduced already by RYTHER & DUNSTAN (1971) when they combined limitation of algal growth with eutrophication. THINGSTAD & SAKSHAUG (1990) recommended the term control, as distinguished from limitation, when whole systems are considered. The word control also suits the concept of growth. Growth is related to ambient concentrations in a way that usually is described with a so called Michaelis-Menten (or Monod) equation involving a half saturation coefficient (K_s) (DUGDALE & GOERING 1967, EPPLEY & THOMAS 1969, KILHAM & HECKY 1988). There is thus a gradual change in growth rate, not an absolute limit in the way that the amounts of necessary elements limit the quantity of biomass produced from the same elements. HECKY & KILHAM (1988) begin a discussion of the concept of limitation with a generalized equation for population growth rate. I should prefer to call this control of growth rate. I am certainly not prepared to follow them when they declare that cellular growth rate is a function of light, temperature and nutrient supply. The correct word here is nutrient *concentration*, and that must also in fact be what they mean since they refer to the Monod equation. The aim of the present paper is, however, to discuss questions of importance for practical decisions, the management of polluted waters. In that case we are concerned with negative effects of the production, e.g. anoxia in bottom waters caused by sedimentation of the organic material produced in the surface layer. This does not depend on the growth but on the net (export) production in absolute numbers. For this there is also an absolute limit, expressed as the rate of delivery of new nutrients.

For general comparisons of the relative importance of N and P for plankton production the Redfield ratios (REDFIELD & al. 1963) are commonly used. No doubt the N : P ratios in phytoplankton populations vary both with species composition and conditions in the environment (RYTHER & DUNSTAN 1971; SAKSHAUG & OLSEN 1986). Nevertheless the Redfield ratios, by atoms C : N : P = 106 : 16 : 1 and by weight (used in this paper) ca. 41 : 7.2 : 1, 'has withstood the test of time well' (HECKY & KILHAM 1988). However, when uptake rate, or growth, is discussed they have no meaning and one should instead consider the concept of half-saturation coefficients, K_s . The significance of K_s as a physiological characteristic of plankton populations, controlling ambient nutrient concentrations, and the use of Redfield ratios in flux studies, will be discussed in the following with the aid of examples from an extensive monitoring of the coastal water at the Swedish west coast.

A MONITORING PROGRAM AT THE SWEDISH WEST COAST

A monitoring program for the coastal water of the province of Göteborg and Bohus, Swedish west coast, was gradually started in the years 1982-1986 and the final presently ongoing program (AXELSSON & RYDBERG 1993) comprises 20 sampling stations along the coast of the province (Fig. 3). Samples are collected once a month from 0.5, 2, 5, 10, 15, 20, and where possible also from 30 and 40 m depth. Conventional parameters ($S_{\%}$, C° , O_2 , DIP, TP, NO_3^- , NO_2^- , NH_4^+ , TN, SiO_3 , and Chl-*a*) are analyzed in all samples, particulate carbon (POC) and particulate nitrogen (PON) in the samples from 5 and 20 m depth. Five m corresponds roughly to the depth limit for light saturation at noon in the summer. Twenty m is below the compensation depth (defined as the depth with an irradiance of $10^{15} Q \text{ cm}^{-2} \text{ s}^{-1}$), and also mostly below the pycnocline. The pycnocline is a result of the north going current of Baltic brackish water and a major characteristic of the coastal water along the Swedish west coast (cf. SVANSSON 1984 for a detailed description of the hydrography).

Chlorophyll-*a* has been analysed in every sample and thus the vertical distribution is well known for each occasion. A special computer program has been designed for the calculation of daily carbon flux from vertical chlorophyll-*a* profiles, daily irradiance, length of day, temperature and secchi depth. The program uses carbon uptake: chlorophyll ratios according to WILLIAMS & MURDOCH (1966), cf. also SÖDERSTRÖM & REX (1974) and GARGAS & al. (1980). Saturation light, (I_k) is calculated as a function of temperature mainly from measurements in Danish waters (G. Ærtebjerg-Nielsen, pers. commn). The principles were described in SÖDERSTRÖM (1986) cf. also COLE & CLOERN (1987).

In Fig. 4 is shown the calculated primary production for six stations in the monitoring program. The results for mean, minimum and maximum production demonstrate the influence of light on short time variations. The stations, 'Valö' and 'Koster' are open to Kattegat (Valö) and Skagerrak (Koster). 'Valö', to the south of Göteborg, is seldom influenced by waste water from Göteborg, due to the prevailing current system. Five stations (among them 'Instö Ränna') are situated in or nearby the two estuaries of the river Göta Älv (the biggest river in Sweden, TN : TP about 50 : 1) and represent influence from the sewage treatment plant of Göteborg on a descending scale. The capacity of this plant is equivalent to the waste water from 600 000 people. Since 1984 it combines biological treatment with chemical phosphorus precipitation and the outgoing water has a TN : TP ratio of 30 : 1. After the estuary mixing the delivery to the coastal surface water has a TN : TP ratio around 15 : 1 (SÖDERSTRÖM 1986). The station

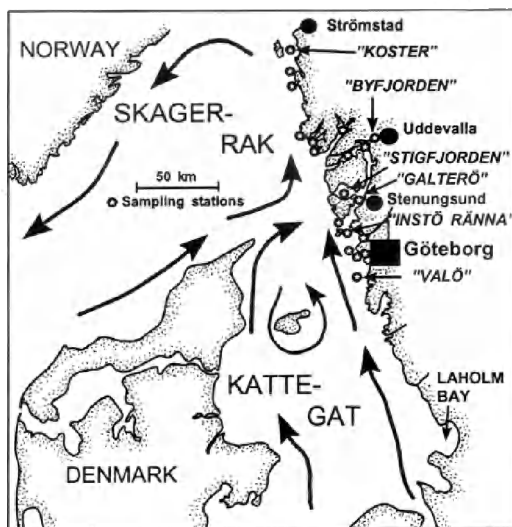


Fig. 3. Map of the Swedish west coast with the main currents in Skagerrak and Kattegat. Sampling stations in the monitoring program indicated, some of them also with their names.

'Galterö' is located to monitor effects of waste water (TN : TP = 50 : 1) from the industrial community of Stenungsund (petrochemical industries, inhabitants 20 000). The nearby station 'Stigfjorden' is shallow and has very little direct nutrient input. From the station 'Galterö' an average net current of $50 \text{ m}^3 \text{ s}^{-1}$ goes northwards through a series of sounds in which the station 'Havstens fjord' is situated. The station 'Byfjorden' represents a true fjord (SVANSSON 1980) connected with 'Havstens fjord' through a narrow and shallow sound, and eutrophicated by the waste water (TN : TP = 118 : 1) from the town of Uddevalla (Mixed industries, inhabitants 50 000). The water exchange is restricted as the tide in this area has an amplitude of only 0.1-0.2 m. Barometric changes are more important than the tide for the water exchange. In the area anoxic situations in the subpycnocline water occur regularly. Though known since the 1890s (PETTERSSON & EKMAN 1897), anoxia in the bottom water has obviously increased after 1950 together with a decreased transmittance in the surface water (SÖDERSTRÖM 1971). 'Byfjorden' showed the highest production in June whereas the other five stations had low production, probably due to an unusually dark period in June 1991. Further north along the coast, pollution is considered to be of less importance. However, and especially in late spring, water from Norwegian rivers occasionally reaches down to 'Koster', causing temporary increased nutrient concentrations, particularly of nitrate (SÖDERSTRÖM 1988).

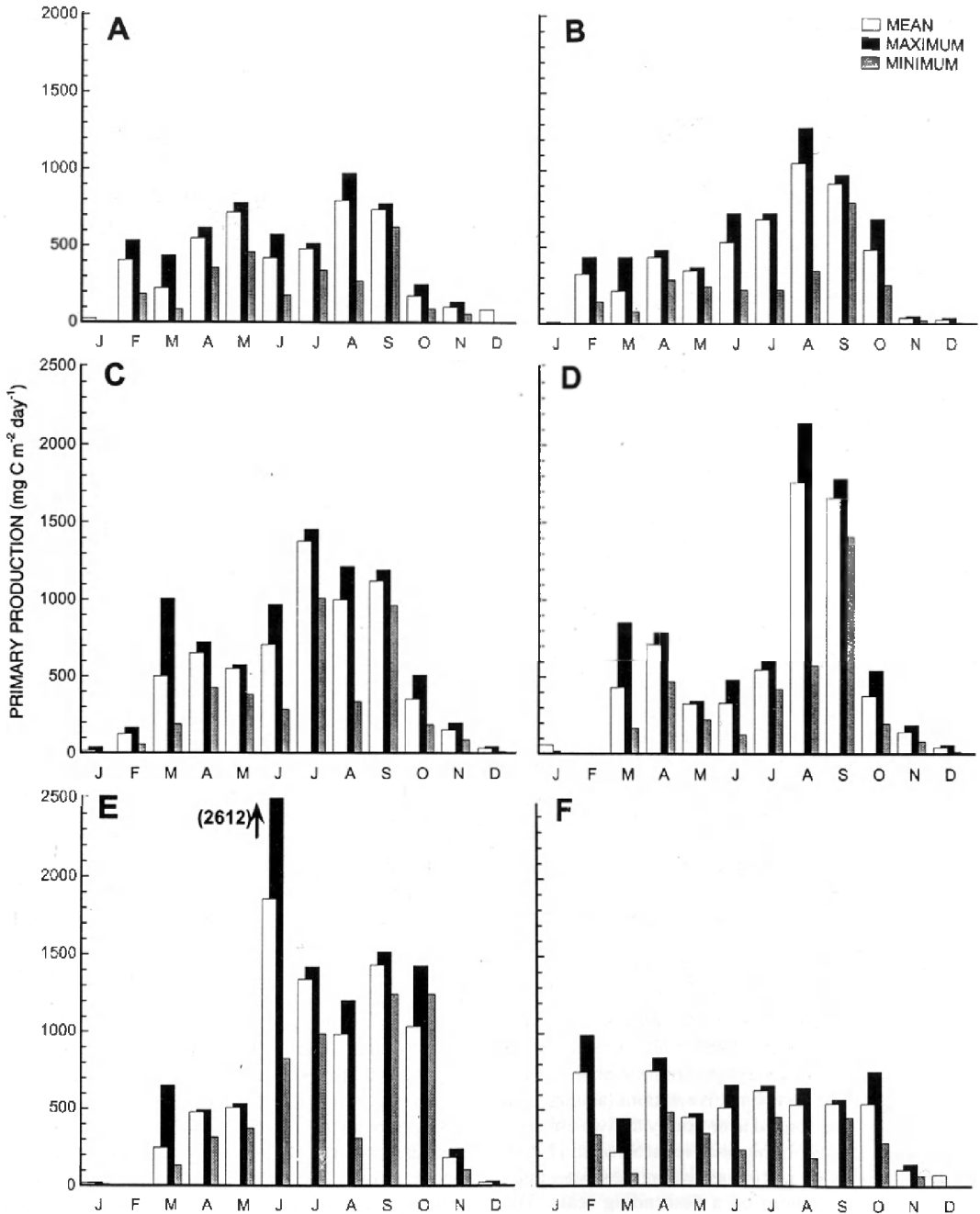


Fig. 4. Calculated daily carbon fluxes over the year for six stations in the monitoring program in 1991, based on the mean, minimum, and maximum daily irradiance during the week of sampling (see text). A. Valö. Annual production = 140 g C m⁻². B. Instö Ränna. Annual production = 153 g C m⁻². C. Galterö. Annual production = 200 g C m⁻². D. Stigfjorden. Annual production = 212 g C m⁻². E. Byfjorden. Annual production = 272 g C m⁻². F. Koster. Annual production = 154 g C m⁻².

K_s AS A FACTOR IN THE CONTROL OF AMBIENT NUTRIENT CONCENTRATIONS

The relation between growth rate (v) and ambient nutrient concentrations (S) has been described in relative terms with a Michaelis-Menten equation (EPPLEY & al. 1969, KILHAM & HECKY 1988).

$$v = V_{\max} \cdot S / (S + K_s)$$

Values for K_s and V_{\max} vary in the literature. For nitrate and ammonium values from 1.5 $\mu\text{g l}^{-1}$ to more than 100 $\mu\text{g l}^{-1}$ exist (EPPLEY 1969; EPPLEY & al. 1973; RÖMER 1983). For the discussion in this paper the essential is that the uptake rate of a nutrient by plankton algae decreases at specific concentrations. In this meaning the K_s concept has been used e.g. for comparisons of interactions between ammonium and nitrate uptake (DORTCH 1990).

There is unfortunately very little information on K_s for uptake of phosphate. From a work of McALLISTER & al. (1964) it seems to be below 1 $\mu\text{g P litre}^{-1}$. The same is indicated by conditions at the station 'Koster' (SÖDERSTRÖM 1988). The ratio $K_{sN} : K_{sP}$ could thus have values from 2 : 1 and upwards. This implies that ambient DIN : DIP ratios as low as 2 : 1 sometimes represent neutrality between N and P for the growth $\Delta \text{PON} : \Delta \text{POP} = 7 : 1$. The DIN : DIP ratios must be compared with the specific ratio $K_{sN} : K_{sP}$, not with the Redfield ratio, before anything can be said about which of N and P controls the growth of the cells.

According to the Redfield principle, one should consider K_s not as a concentrationcontrolling the activity of algae, but instead as an inherent physiological quality, that is a critical part of the mechanism for the biological regulation of the ambient nutrient concentrations.

The spring bloom in Scandinavian waters is triggered by the return of light. The high nutrient concentrations (S) built up during the winter imply that the algae are able to grow at V_{\max} for the actual light conditions. The biomass (M) increases rapidly and simultaneously the production ($v \cdot M$) and the biological export (E). When $v \cdot M$ has increased to a size that represents a bigger flux of nutrients than the continuous external delivery (D) to the production layer, the process goes on for a while using the store represented by the high winter concentrations of inorganic nutrients. A period of decreasing concentrations follows. When S approaches K_s for the current planktonpopulation, v decreases until the biological flux is in balance with the continuous delivery, $D = v \cdot M$.

Any reference to concentrations, for an estimate of potential production, is meaningless in this state. As shown in Fig. 1 the 'amount present', e.g. of DIP in April, is only

enough for some few days of a normal summer production between 500 and 1000 $\text{mg C m}^{-2} \cdot \text{day}^{-1}$, i.e. 12-24 $\text{mg P m}^{-2} \cdot \text{day}^{-1}$.

In a closed system, as e.g. a bottle experiment, a continuous nutrient delivery would cause continuously increasing concentrations. An open system, with dominant biological flux and a delivery D , strives towards a steady state when $D = v \cdot M = E$. Since v is a function of S , steady state implies a specific S .

In the early spring sinking of algal cells is the main biological export besides the export through water exchange. With decreasing S the water exchange export decreases, and sedimentation becomes the important factor. With a low sinking rate, M must be correspondingly bigger to make $E = D$ possible and v must decrease to make $v \cdot M = D$. If $v \cdot M > D$ still more of the nutrient store must be used with lowered S , and finally v , as the consequence. If the sinking rate is high a smaller M is sufficient to keep $E = D$ and v must be proportionally higher to make $v \cdot M = D$. Two physiological qualities of the plankton thus combine in a spring bloom to control the ambient nutrient concentrations at a continuous nutrient delivery, the quality K_s and the quality sinking rate (EPPLEY & al. 1968, LÄNNERGREN 1979, BIENFANG & HARRISON 1984).

If D increases, but the active population has unchanged qualities, an increase in S and thus in $v \cdot M$, could at first balance the bigger D . However, when biological export dominates, the requirement $E = D$ can only be met with by an increased M . Increased D should thus generate a new steady state system with increased M , but unchanged S in the neighborhood of K_s .

In the summer the system becomes apparently more complicated by the introduction of a production based on nutrients from regeneration in the production layer. However, the basic requirements for steady state are unchanged. To sinking rates, as a factor for E , is now added the growth of grazers, and their fast sinking pellets. Effective grazers may keep $E = D$ in a situation with high v and low M . The increase in v may be brought about either by increased S or by a change of the phytoplankton composition to species with a higher v at the same S . This is a main factor in the competition strategies discussed by SAKSHAUG & OLSEN (1986).

For the present discussion the important fact is that the ambient nutrient concentrations in a steady state flux are functions of physiological qualities of the organisms in the produced biomass, and thus cannot be expected to correlate with the delivery.

* $K_{sP} = K_s$ for phosphorous; $K_{sN} = K_s$ for nitrogen.

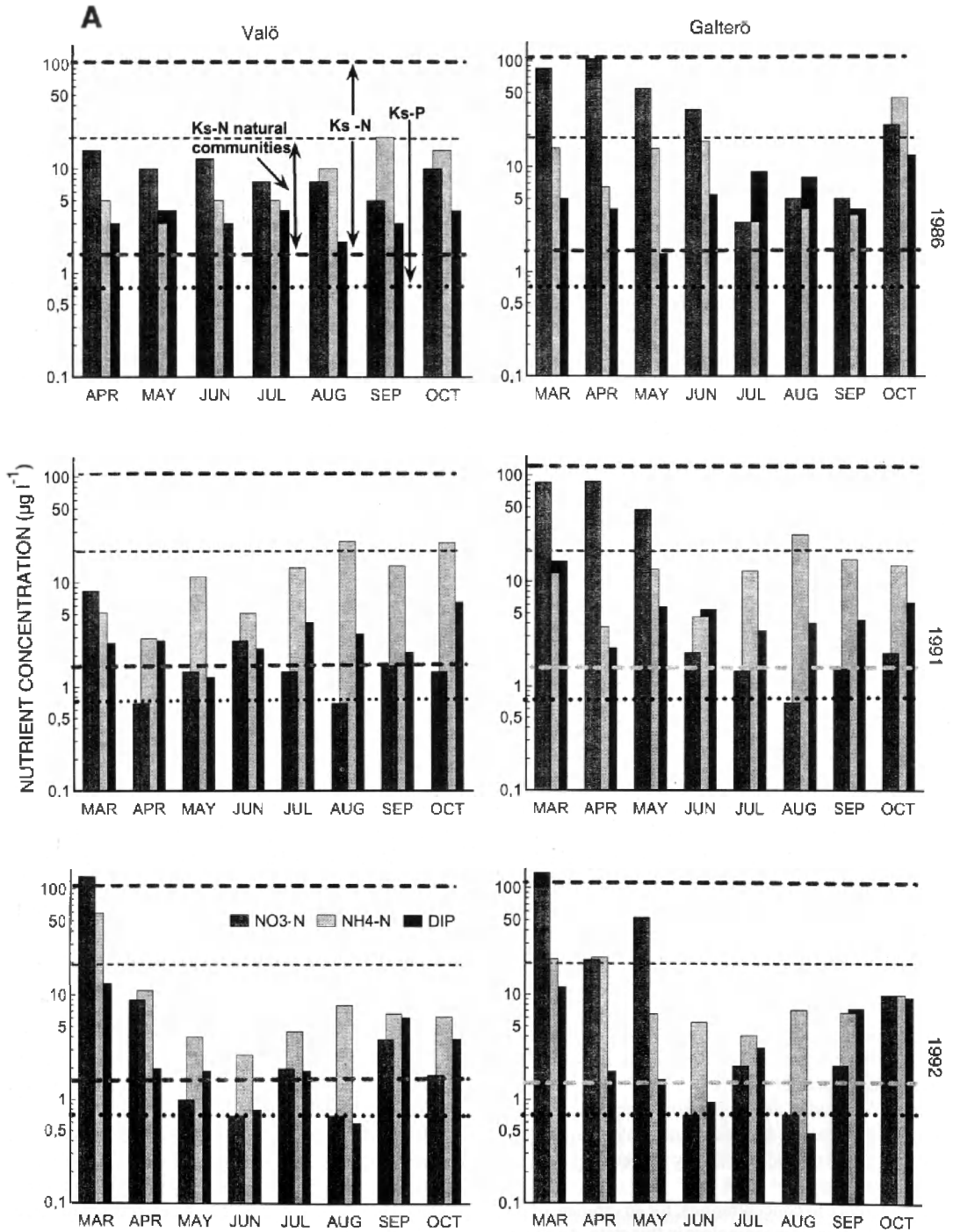


Fig. 5. Concentration of nitrate, ammonium and inorganic phosphate (DIP) in the surface water (0-5 m depth) during the productive season in 1986, 1991, and 1992. Limits for K_s (nitrogen) according to EPPLEY & al. (1969 and 1973) and the expected value for K_s (phosphate) are shown. A. The Kattegat station Valö and the eutrophicated fjord station Galterö.

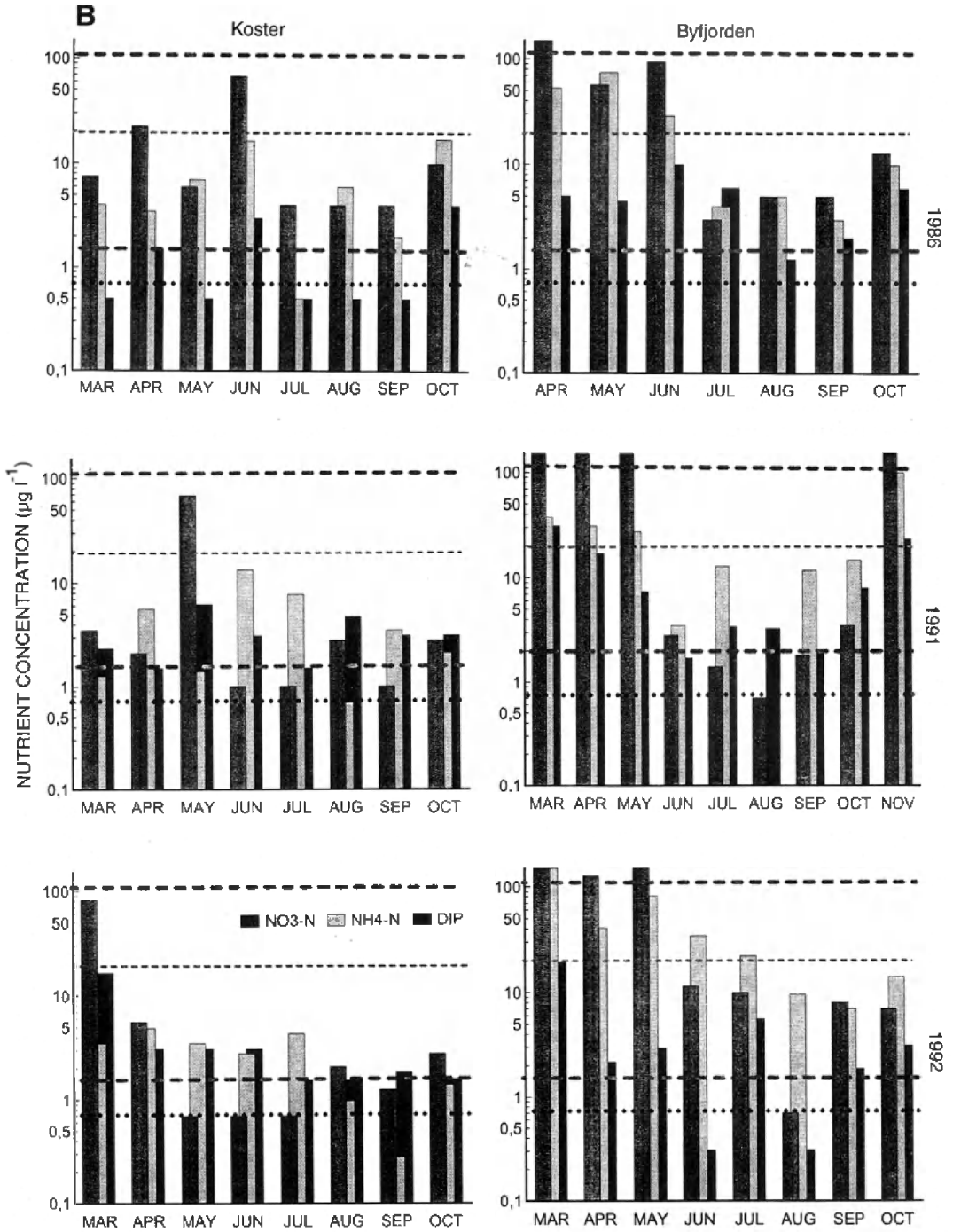


Fig. 5 (continued). B. The open sea station Koster and the station Byfjorden, which is influenced by waste water from the town Uddevalla.

TEST OF THE DESCRIBED MODEL

The practical test of the described concept can not be made with the aid of experiments. The whole ecosystem, including hydrographical conditions, must be present. One possible test is to compare S in water areas with different nutrient delivery but a reasonably similar structure in their ecosystems due to geographic location. Such a test is shown in Fig. 5, based on data from the monitor program. As expected there are small differences between the eutrophicated fjord stations and the unpolluted stations during the steady state period. The comparisons are complicated by the simultaneous presence of ammonium and nitrate. There are reports that the algae under some conditions prefer ammonium as a nitrogen source (RÖNNER 1983, DORTCH & CONWAY 1984, CARPENTER & DUNHAM 1985, SAHLSTEN 1987) but the inhibition of nitrate uptake is seldom complete (DORTCH 1990). However, it is evident that ammonium and nitrate must be treated separately and not together as DIN. Some very low concentrations of nitrate are not necessarily the result of uptake through photosynthesis. They could instead mirror conditions for other fluxes in the nitrogen cycle, nitrification, reduction of nitrate to ammonium, or denitrification. It is more and more evident that nitrate reductions are important activities also in well oxygenated surface waters (McCARTHY & al. 1984, SÖDERSTRÖM 1988). The DIN : DIP ratio in the field is clearly not a simple result of delivery and plankton production.

It is evident that concentrations can not be parameters of nutrient availability or of potential production. One must therefore try to calculate the real availability (the delivery flux from all sources) of both P and N to the production layer. With some knowledge of the terrestrial and atmospheric nutrient inputs, water exchange, average nutrient concentrations, and a use of the Redfield ratios C : N : P for a ^{14}C -determined production, it should be possible to get an insight into the nutrient fluxes in the phototrophic layer, and understand which nutrient is limiting. Such a task may be difficult, and perhaps even require some guessing, but it is under all circumstances a more reliable way to understand the relative importance of N and P in the plankton

production, than the principally wrong way of direct judging from ever so exactly measured concentration ratios or statistically controlled bottle experiments.

POC : PON : OP RATIOS IN THE COASTAL WATER, PROVINCE OF GÖTEBORG AND BOHUS

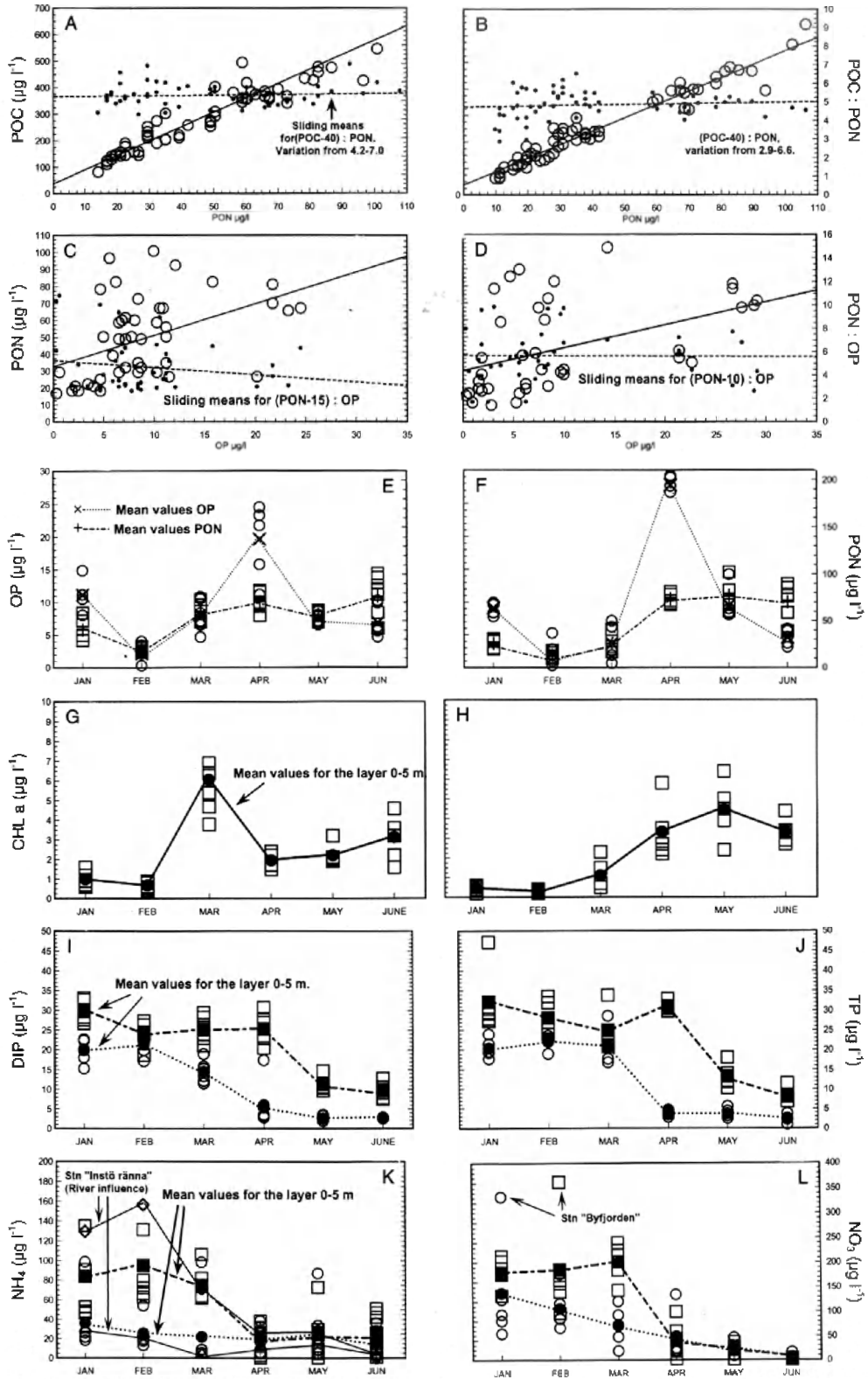
There is a good correlation ($r = 0.92$ and 0.97 , respectively) between POC and PON concentrations in the two categories of sampling sites (Fig. 6A, B) and the intercept of the regression lines is below $50 \mu\text{g C litre}^{-1}$. The slope of the regression lines show $\Delta \text{POC} : \Delta \text{PON}$ ratios of 5.4 and 5.1 by weight, only slightly lower than the expected Redfield ratio of 5.7.

Unfortunately particulate phosphorus has not been measured together with particulate organic nitrogen. OP, the difference between total phosphorus and DIP, has been tried as a substitute (Fig. 6C, D). The amount of DOP that is excreted from growing algae varies (KUENZLER 1970). From the north Pacific ORRET & KARL (1987) report that DOP comprised 18 - 40 % of the total dissolved phosphorus pool. Production of DOP was highest in the lower part of the photic layer. OP may not represent POP very well. However PON and OP are not so independent of each other as Fig. 6C, D indicates. The variations during the spring follow a regular pattern that can be biologically understood (Fig. 6E, F).

DANIELSSON & al. (1975) measured particulate nitrogen and phosphorus in 'Havstens fjord' and 'Byfjorden' at 20 occasions from January 1973 to June 1974. For the surface (1 m depth) they found a considerable variation in the PON : POP ratios but the mean value was near the Redfield ratio.

In Fig. 6C, D the lowest OP concentrations occur simultaneously with PON between 10 and $20 \mu\text{g N litre}^{-1}$. This is deducted as phosphorus depleted detritus. The mean PON : OP ratios obtained thus are from 3 : 1 to 6 : 1. If, as an average, 1/3 of OP is assumed to be DOP, the ratio PON : POP would be from 4.5 : 1 to 9 : 1 and thus cover the Redfield ratio of 7.2 : 1 by weight.

Fig. 6. (next page) Hydrochemical data for the period January-June 1993 from seven stations in the vicinity of Göteborg (A, C, E, G, I, K) and six fjord stations (excluding anoxic water) north of Göteborg (B, D, F, H, J, L). A, B. Ambient POC concentration at 5 and 20 m depth as a function of PON concentration (open circles) and the corresponding POC : PON ratios (small dots). A: $y = 36.4 + 5.4 x$; $n = 59$; $r = 0.92$. B: $y = 37.5 + 5.1 x$; $n = 60$; $r = 0.97$. C, D. Ambient PON concentration (open circles) at 5 and 20 m depth as a function of OP concentration and the corresponding PON : OP ratios (small dots). C: $y = 33 + 1.9 x$; $n = 45$; $r = 0.46$. D: $y = 30 + 1.35 x$; $n = 39$; $r = 0.45$. E, F. Monthly concentration of OP and PON at 5 m depth. G, H. Monthly concentration of chlorophyll *a* in the 0-5 m layer (mean of 0.5, 2 and 5 m depth). I, J. Monthly concentration of DIP (open circles) and TP (open squares) in the 0-5 m layer (mean of 0.5, 2 and 5 m depth). K, L. Monthly concentration of ammonium (open circles) and nitrate (open squares) in the 0-5 m layer (mean of 0.5, 2 and 5 m depth).



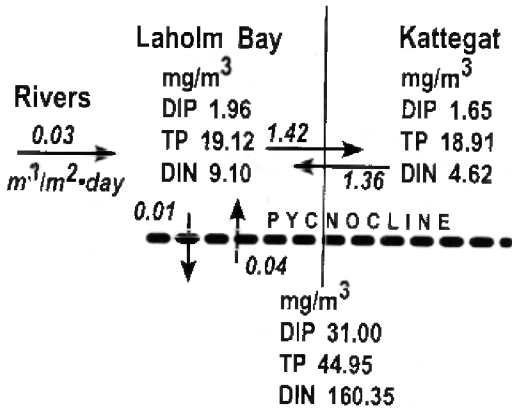


Fig. 7. The basis for the calculation of vertical and horizontal nutrient transports in the Laholm Bay. Mean values for March-August 1982-84.

The same pattern for changes in OP (Fig. 6E, F) appears in the two areas, the vicinity of Göteborg and the fjords, in spite of a difference in the spring bloom. In the Göteborg area a classical spring bloom was observed at all stations as a distinct chlorophyll-*a* maximum in the month of March (Fig. 6G, H). In the fjords the chlorophyll-*a* concentrations increased slowly to a maximum in May. The decrease in the pools of DIP and DIN also shows a later development of the plankton in the fjords (Fig. 6I, J). Both areas showed about the same apparent uptake of nutrients. This uptake had an N : P ratio of about 10 : 1. However, considering the simultaneous deliveries, hydrological exports, and possible denitrification (RYDBERG & SUNDBERG 1988), it is permissible to assume that the periods real uptake in plankton followed Redfield ratios.

Based on these results the biogenic particles at the Swedish west coast may be estimated to have an average weight ratio C : N : P 35 : 6.8 : 1. This is close enough to the Redfield ratios to allow the conclusion that they may be used for computing average nutrient fluxes in Swedish coastal water.

A STEADY-STATE FLUX BUDGET FOR THE LAHOLM BAY, SOUTH KATTEGAT

According to ambient DIN : DIP concentration ratios below 7 : 1, and results of bioassays, the Laholm Bay was considered to be nitrogen limited in spite of supply ratios N : P of the magnitude 10-20 : 1 (GRANELI & al. 1986). A flux analysis shows that a conclusion that P is the limiting nutrient not is contrary to the low concentration ratios (SÖDERSTRÖM 1988).

Transports of nutrients in the bay have been computed on the basis of informations about mean concentrations for TP, DIP, and DIN for the period March-August 1982-1984 (GRANELI & al. *ibid.*), and water exchange in the bay (RYDBERG & SUNDBERG 1986a, b) (Fig. 7).

The external deliveries of N and P are reported by RYDBERG & SUNDBERG (*ibid.*) and by STIBE & FLEISCHER (1986). ¹⁴C-determinations of the primary carbon flux were made by EDLER (1986). Input of phosphorus includes TP from rivers, waste water plants, transport from the deep water, and precipitation. All delivered phosphorus is supposed to be available in the time scale of the scheme. The flux budget (Fig. 8) indicates that remineralized P accounts for 80 % of the flux through phytoplankton. With this rate of remineralization more than 90 % of the new delivery of total P should be available on a 24 hour time scale. At least the use of total P does not underestimate the delivery.

Total N includes some forms of N probably not available for plankton photosynthesis, e.g. humic substances, but also forms that might serve as nitrogen sources for plankton, e.g. aminoacids and urea (BRONK & al. 1994). However, only the sum of nitrate and ammonium (DIN) was obtainable for the scheme and the delivery of usable N is most probably underestimated.

Starting with the known carbon flux the simultaneous uptake of N and P is calculated from Redfield ratios (Fig. 8). The difference between the requirements of P and the total external input, is the size of the remineralization in the 10-15 m deep production layer.

Exports of TP and DIP are calculated from reported concentrations and water exchange (Fig. 7). The export through sedimentation (also including other possible biological exports) is derived from the difference between input of TP and export through water exchange. Sedimentation of N is then calculated from this value with the Redfield ratio. Unfortunately neither particulate P nor dissolved organic P were measured in the bay. The division of the organic P had therefore to be estimated from other parts of the coast (cf. also ORRET & KARL 1987).

A mass balance for total N made from data in RYDBERG & SUNDBERG (1986a) implied a N : P weight ratio for sinking particles as low as 4.5 : 1. This should have resulted in a still higher N surplus and denitrification in the scheme, than the use of the Redfield ratio for the sedimentation. The export of TN is therefore calculated from the DIN data. All delivered P passes the plankton photosynthesis and the export flux of 1.43 $mg/m^2 \cdot day^{-1}$ TP should thus have a parallel TN flux of 10.37. However the DIN export calculated this way is less than the one directly calculated from the water exchange. The difference is added as a separate export directly from the input.

There is now an unaccounted rest of N in the flux of 5.34 $mg N m^{-2} \cdot day^{-1}$. This is explained as denitrification. SAHLSTEN & SÖRENSON (1986) reported 3.5 $mg N m^{-2} \cdot day^{-1}$

¹ from sediments at a depth of 17-20 m. RYDBERG & SUNDBERG (1988) computed denitrification in the Laholm area in March 1984. They report $26 \text{ mg N m}^{-2} \text{ day}^{-1}$. The denitrification in the flux scheme is about 20 % of the total input. SEITZINGER (1988) reports 20-50 % as normal for American estuaries.

A parallel arrow in the remineralization, corresponds to the requirements of organic material as energy source for denitrification (RICHARDS & al. 1965), and completes the scheme. In the scheme denitrification uses 1 % of the primary production. The same has been reported from Tomales bay, California, by SMITH & HOLLIBAUGH (1989).

The average weight ratio DIN : TP for the total new delivery to the Laholm Bay during the period in question is in the scheme 10.3 : 1, and for DIN : DIP 16.6 : 1. GRANIELI & al. (1986) report the N : P ratio in the total nutrient supply for the period May-August to be 11.2 : 1 while the concentration ratio DIN : DIP averages 5 : 1 and in July-August goes down to nearly 1 : 1. These low concentration ratios (which, as pointed out above, still may represent neutrality between N and P for a growth with $\Delta \text{PON} : \Delta \text{POP} = 7 : 1$), accordingly result in enrichment experiments indicating nitrogen limitation. Concentrations imply an average deficit of N relative to the Redfield ratio of about 25 % (and even as much as 80 % in the middle of the summer period) while the flux scheme, built on the same data, points to an average N-surplus of 30 %!

Replacing the denitrification with hydrological transport implies for retained flux balance that the mean DIN concentration in the bay (Fig. 7) has to be increased from the reported 9.1 to 12.9, with the DIN : DIP ratio then changing from 4.6 : 1 to 6.6 : 1. With this presumption the DIN : DIP ratio would thus be close to the Redfield ratio, and enrichment experiments would no longer show N as limiting. It is not export *per se*, but export just as denitrification, that in the Laholm bay causes the low N : P ratios mistakenly interpreted as showing N-limitation and giving N-limitation as the false result of bottle experiments.

It is easy to criticize the proposed flux scheme in details. What is important is, however, not the reliability of the data emanating from the research in the Laholm bay, but the fact that the same data generate completely opposite conclusions if they are used directly as concentration ratios or indirectly for a flux analysis. The low DIN : DIP ratios and the results of enrichment experiments are not contrary to the P-limitation shown by the flux calculation, they are the necessary result of the nature of the biological processes which constitute the flux system.

CONCLUSIONS.

The nitrogen-phosphorus controversy has two sides. One is about the Redfield thesis that biofixation of N_2 counter-

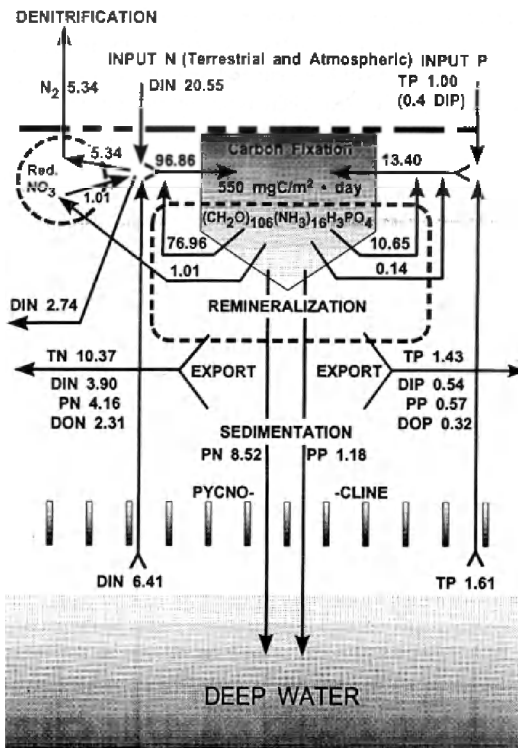


Fig. 8. Calculated average nutrient fluxes ($\text{mg m}^{-2} \text{ day}^{-1}$) in the Laholm Bay during the period March-August 1982-1984. (Redrawn from SÖDERSTRÖM 1988).

acts any deficiency of nitrogen in relation to the availability of phosphorus (REDFIELD 1958). RYTHER & DUNSTAN (1971) opposed Redfield on basis of observations of DIN : DIP concentration ratios below the Redfield ratio. With the coupling concentration-availability rejected, there is no reason not to follow SMITH (1984) who showed, for lagoons where the delivery had N : P ratios well below the requirements of plants, that fixation made phosphorus the limiting nutrient. Smith concluded: 'The minimum time scale for phosphorus limitation in the marine environment remains unclear, but it is short enough to be significant to the understanding and management of marine ecosystems'.

There has been a reversed version of this discussion in Sweden (GRANELI & al. 1986) where the failure to detect fixation in the Laholm Bay has been put against the use of SMITH's thesis of phosphorus limitation. However, unless one interprets low DIN : DIP ratios to show N limitation in spite of the reported N-surplus in the nutrient supply, there is no reason to expect fixation in the Laholm Bay.

The biological compensation process to be expected in the nutrient fluxes in the Laholm Bay, as well as in the Baltic and the coastal waters of Kattegat and Skagerrak, is not fixation but denitrification. There is no controversy about the fact that the N : P ratios of the deliveries to these areas, even when all sources are counted, are significantly above the Redfield ratio (GRANELI & al. 1986, 1990; WULFF & STIGEBRANDT 1989). Nor is there any doubt that denitrification in coastal waters and estuaries has about the same time scale as the delivery of nitrogen (RÖNNER 1983, SEITZINGER 1988). The delivery of nutrients to the waters discussed here, with a N : P weight ratio usually about 15 : 1, thus forces two dominant biological nitrogen fluxes, one through photosynthesis and one through denitrification. Compare this with Fig. 2B. There the buffering store, 'the amount present', is determined by the physical laws for the relation pressure/tap-opening/flux. In the same way the store of DIN is determined by the biological laws for the relation concentration/ K_s /flux, K_s here used in a broad sense for specific physiological qualities of the organisms controlling their interactions with ambient conditions. The low DIN : DIP ratios in the ambient concentrations are accordingly not signs of a nitrogen deficit relative the phosphorus flux, on the contrary, they are the unavoidable result of a surplus in nitrogen availability in a productive water which favours denitrification. Denitrification does not cause or enhance N limitation (GRANELI & al. 1986), it is a flux showing a surplus of N in relation to P. The denitrification functions in low ambient DIN concentrations, and causes the low ambient concentrations in the same way as the double tap in Fig. 2B causes a lowered level in the cistern. This does not change the availability of nitrogen for photosynthesis. Though low enough to result in DIN : DIP ratios much below the Redfield ratio, the DIN concentrations are not low enough, in comparison with K_s for nitrate and ammonium, to be a serious hindrance for an uptake in the algae corresponding to the availability of phosphorus.

This whole concept is based on REDFIELD (1958, 1963) and is also in accordance with the carbon controlled nitrogen cycling described by SMITH & HOLLIBAUGH (1989). It is true that the last mentioned describe denitrification as causing N limitation of primary production, but it is an apparent limitation, not a real. Their recommendation for water management in such cases as the Swedish and Danish coastal waters exemplify, is not to reduce nitrogen loading, but to reduce organic loading, either directly or by reducing DIP loading.

Enrichment experiments make the other side of the controversy. Such experiments, when performed in isolated volumes, cannot show anything more than what is related to the concentrations in the original sample. This is a fundamental restriction that is valid either one uses small volumes or bigger, eventually called 'mesocosm' (KIVI & al.

1993) or 'microcosm' (FONG & al. 1993). If concentration ratios lie about the availability ratios, enrichment experiments must also be ruled out as arguments for which of N and P limits production in a water area.

In aquatic ecosystems there are several biological processes which reduce an imbalance between N and P availabilities relative to the needs of plankton (BRATTBERG 1980; BRONK & al. 1994; DORTCH & CONWAY 1984; DYRSSEN & GUNDERSEN 1976/77; HOWARTH 1990; MC CARTHY & al. 1984; NIEMI 1979; PAERL 1985; PAERL & al. 1987; RÖNNER 1983; SCHINDLER 1988; SEITZINGER 1988; SMITH 1984; SMITH 1990; WOOD 1965). WILLIAMS & von BODUNGEN (1989) report from a group work on 'new production': 'We now realize that cyanobacteria are ubiquitous in the sea - Have we seriously underestimated N_2 -fixation?'. BRONK & al. (1994) declare with reference to KARL & al. (1992) that rates of N fixation are increasingly recognized as higher than previously thought. The coupling between phosphorus availability and fixation by Cyanophyta was given a practical demonstration in the 1970s for the archipelago of Stockholm (Baltic sea, brackish water) (BRATTBERG 1980). 75 % decrease in the phosphorus load was followed by 90 % decrease in heterocyst activity. However, with N-surplus in the supply to Swedish coastal waters, denitrification should normally be expected, and without doubt it is a major process in the Baltic (RÖNNER 1983).

Coastal ecosystems thus have built-in possibilities to regulate the nitrogen availability, while for phosphorus they are completely dependent on the terrigenous deliveries. Considering the surplus of nitrogen in the nutrient deliveries to Swedish and Danish coastal waters, as well as the whole Baltic area, and the nature of the biological nitrogen transformations, the recommendation to remove nitrate, from waste water and influx to rivers, in order to counteract eutrophication, has no tenable scientific basis.

REFERENCES

- Axelsson, R. & L. Rydberg 1993. Utvärdering av Bohusläns kustvattenkontrollprogram för perioden 1990-92. Hydrografi och näringsämnen. - *Oceanografiska Inst. Göteborgs universitet, Röda serien* 19.
- Bienfang, P.K. & P.J. Harrison 1984. Sinking-rate response of natural assemblages of temperate and subtropical phytoplankton to nutrient depletion. - *Marine Biology* 83:293-300.
- Brattberg, G. 1980. Kvävefixering i marin miljö - Östersjön. - Pp. 95-103 in Rosswall, Th. (ed.): *Processer i kvävet kretslopp*. SNV PM 1213 Stockholm.
- Bronk, D.A., P.M. Glibert and B.B. Ward 1994. Nitrogen uptake, Dissolved organic nitrogen Release, and New production. - *Science* 265:1843-1846.
- Carpenter, E.J. & S. Dunham 1985. Nitrogenous nutrient uptake, primary production, and species composition of

- phytoplankton in the Carmans river estuary, Long Island, New York. – *Limnology and Oceanography* 30:513-526.
- Cole, B.E. & J.E. Cloern 1987. An empirical model for estimating phytoplankton productivity in estuaries. – *Marine Ecology Progress Series* 36:299-305.
- Danielsson, L.G., D. Dyrssen, T. Johansson & G. Nyquist 1975. Byfjorden - Kemiska undersökningar. – *SNV PM* 609 (Stockholm).
- Dortch, Q. & H.L. Conway 1984. Interactions between nitrate and ammonium uptake: variation with growth rate, nitrogen source and species. – *Marine Biology* 79:151-164.
- Dortch, Q. 1990. The interaction between ammonium and nitrate uptake in phytoplankton. – *Marine Ecology Progress Series* 61:183-201.
- Dugdale, R.C. & J.J. Goering 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. – *Limnology and Oceanography* 12:196-206.
- Dyrssen, D. & K. Gundersen 1976/77. *Kvävebalansen i havet - en av naturvetenskapens stora gåtor*. – NFR årsbok 'Kretslopp':137-152.
- Edler, L. 1986. Västplanktonproduktionen i Laholmsbukten. – *SNV rapport* 3272:66-71. (Stockholm)
- Eppley, R.W., R.W. Holmes & J.D.H. Strickland 1968. Sinking rates of marine phytoplankton measured with a fluorometer. – *Journal of Experimental Marine Biology and Ecology* 1:191-208.
- Eppley, R.W. & W.H. Thomas 1969. Comparison of half saturation constants for growth and nitrate uptake of marine phytoplankton. – *Journal of Phycolgy* 5:375-379.
- Eppley, R.W., J.N. Rogers & J.J. McCarthy 1969. Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton. – *Limnology and Oceanography* 14:912-920.
- Fong, P., J.B. Zedler & R.M. Donohoe 1993. Nitrogen vs. phosphorus limitation of algal biomass in shallow coastal lagoons. – *Limnology and Oceanography* 38: 906-923.
- Gargas, E., S. Mortensen & G. Ærtebjerg Nielsen 1980. Production and photosynthetic efficiency of phytoplankton in the open Danish waters 1975-77. – *Ophelia*, Suppl. 1:123-144.
- Graneli, E., W. Graneli & L. Rydberg 1986. Nutrient limitation at the ecosystem and the phytoplankton community level in the Laholm Bay, south east Kattegat. – *Ophelia* 26:181-194.
- Graneli, E., K. Wallström, U. Larsson, W. Graneli & R. Elmgren 1990. Nutrient limitation of primary production in the Baltic Sea area. – *Ambio* 19:142-151.
- Hecky, R.E. & P. Kilham 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effects of enrichment. – *Limnology and Oceanography* 33:796-822.
- Howarth, R.W. 1990. Nitrogen-fixing cyanobacteria in the plankton of lakes and estuaries: A reply to the comment by Smith. – *Limnology and Oceanography* 35:1859-1863.
- Kilham, P. & R.E. Hecky 1988. Comparative ecology of marine and freshwater phytoplankton. – *Limnology and Oceanography* 33:776-795.
- Kivi, K., S. Kaitala, H. Kuosa, J. Kuparinen, E. Leskinen, R. Lignell, B. Marcussen & T. Tamminen 1993. Nutrient limitation and grazing control of the Baltic plankton community during annual succession. – *Limnology and Oceanography* 38:893-905.
- Kuenzler, E.J. 1970. Dissolved organic phosphorus excretion by marine phytoplankton. – *Phycologia* 6:7-13.
- Lännergren, C. 1979. Buoyancy of natural populations of marine phytoplankton. – *Marine Biology* 54:1-10.
- McAllister, C.D., N. Shah & J.D.H. Strickland 1964. Marine phytoplankton photosynthesis as a function of light intensity: A comparison of methods. – *Journal of the Fisheries Research Board of Canada* 21:159-181.
- McCarthy, J.J., W. Kaplan & J.L. Nevins 1984. Chesapeake Bay nutrient and plankton dynamics. 2. Sources and sinks of nitrite. – *Limnology and Oceanography* 29:84-98.
- Niemi, Å. 1979. Blue-green algal blooms and N:P ratio in the Baltic sea. – *Acta Botanica Fennica* 110:57-61.
- Orrett, K. & D.M. Karl 1987. Dissolved organic phosphorus production in surface seawaters. – *Limnology and Oceanography* 32:383-395.
- Paerl, H.W. 1985. Microzone formation: Its role in the enhancement of aquatic N fixation. – *Limnology and Oceanography* 30:1246-1252.
- Paerl H.W., K.M. Crocker & L.E. Prufert 1987. Limitation, of N fixation in coastal marine waters: Relative importance of Molybdenum, Iron, Phosphorus, and organic matter availability. – *Limnology and Oceanography* 32:525-536.
- Peperzak, L. & J.C.H. Peeters 1991: Bioassay of nutrient pollution in the North Sea. – *Water Science and Technology* 24:319-320.
- Pettersson, O. & G. Ekman 1897. De hydrografiska förändringarna inom Nordsjöns och Östersjöns område under tiden 1893-1897. – *Kungliga Svenska Vetenskaps Akademiens Handlingar* (Stockholm) NF 29:5.
- Redfield, A.C. 1958. The biological control of chemical factors in the environment. – *American Scientist* 46: 205-222.
- Redfield, A.C., B.H. Ketchum & F.A. Richards 1963. The influence of organisms on the composition of sea water. – Pp. 26-77 in: Hill, M.N. (ed.) *The Sea*. New York.
- Richards, F.A., J.D. Cline, W.W. Broenkow & L.P. Atkinson. 1965. Some consequences of the decomposition of organic matter in lake Nitinat, an anoxic fjord. – *Limnology and Oceanography* Suppl. 10:R185-R201.
- Rönner, U. 1983. *Biological nitrogen transformations in marine ecosystems with emphasis on denitrification*. – Dissertation Ph.D. Inst. Mar. Microbiol. University of Göteborg.
- Rydberg, L. & J. Sundberg 1986a. Seasonal nutrient supply to coastal waters. Elsevier – *Oceanography Series* 42:467-488.
- 1986b. Hydrografi, syrgas och närsaltförhållanden i SÖ Kattegat. Tillförsel av näringsämnen från omgivande havsområden. – *SNV rapport* 3272:11-13;34-42. (Stockholm).
- 1988. An estimate of oxygen consumption and denitrification in coastal waters of the Swedish west coast using indirect methods. – *Estuarine, Coastal and Shelf sciences* 26:269-284.
- Ryther, J.H. & W.M. Dunstan 1971: Nitrogen, phosphorus, and eutrophication in the coastal marine environment. – *Science* 171:1008-1013.

- Sahlsten, E. 1987. Nitrogenous nutrition in the euphotic zone of the Central North Pacific Gyre. – *Marine Biology* 96:433-439.
- Sahlsten, E. & F. Sörensson, 1986. Kväveomsättande processer. – *SNV rapport* 3272:75-82.
- Sakshaug, E. & Y. Olsen 1986. Nutrient status of phytoplankton blooms in Norwegian waters and algal strategies for nutrient competition. – *Canadian Journal of Fisheries and Aquatic Science* 43:389-396.
- Schindler, D.W. 1988. Experimental studies of chemical stressors on whole lake ecosystems. – *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* 23:11-41.
- Seitzinger, S.S. 1988. Denitrification in freshwater and coastal marine ecosystems: Ecological and geochemical significance. – *Limnology and Oceanography* 33:702-724.
- Smith, S.V., 1984. Phosphorus versus nitrogen limitation in the marine environment. – *Limnology and Oceanography* 29:1149-1160.
- Smith, S.V. & J.T. Hollibaugh 1989. Carbon-controlled nitrogen cycling in a marine 'macrocosm': an ecosystem model for managing cultural eutrophication. – *Marine Ecology Progress Series* 52: 103-109
- Smith, V.H. 1990. Nitrogen, phosphorus, and nitrogen fixation in lacustrine and estuarine ecosystems. – *Limnology and Oceanography* 35:1852-1859.
- Söderström, J. 1971. The capacity of coastal waters to use nutrients in Bohuslän, Sweden. – *Botanica Marina* 14:39-52.
- 1976. Ekologiska studier i en eutrofierad fjord. In: Byfjorden - marinbotaniska undersökningar. – *SNV PM* 684:5-66 (Stockholm).
- 1986. *Kustvattnet i Göteborgsregionen 1982-84*. Miljöfakta i Göteborgs och Bohus län 1986:5: I-IV, 1-79 (Göteborg).
- 1988. *Phytoplankton production in Swedish coastal waters, a steady state system controlled by the availability of phosphorus*. – Report from the Province administration, Province of Göteborg and Bohus, to the Environment Department, Stockholm, 9 Nov. 1988:1-53.
- Söderström, J. & M. Rex 1974. Carbon uptake:Chlorophyll-a ratios in two Swedish fjords. – *Botanica Marina* XVII:196-203.
- Stibe, L. & S. Fleischer 1986. Närsalter - tillförsel och utbyte. Atmosfärisk deposition. – *SNV rapport* 3272:26-33. (Stockholm)
- Svansson, A. 1984. Hydrographic features of the Kattegat. – *Rapport et procès-verbaux des réunions. Conseil international pour l'exploration de la mer*. 185:78-90.
- Svensson, T. 1980. *Water Exchange and Mixing in Fjords*. – Mathematical Models and Field Studies in the Byfjord. Report Series A:7, Department of Hydraulics, Chalmers University of Technology. 1-266.
- Thingstad, T.F. & E. Sakshaug 1990. Control of phytoplankton growth in nutrient recycling ecosystems. Theory and terminology. – *Marine Ecology Progress Series* 63:261-272.
- Williams, R.B. & M.B. Murdoch 1966. Phytoplankton production and chlorophyll concentration in the Beaufort Channel, North Carolina. – *Limnology and Oceanography* 11:73-82.
- Williams, P.J. leB. & B. von Bodungen 1989. Export productivity from the photic zone. – Pp. 99-115 in: Berger, W.H., V.S. Smetacek & G. Wefer (eds). *Productivity of the ocean: Present and past*.
- Wood, E.J. Ferguson, 1965. *Marine Microbial Ecology*. London/New York.
- Wulff, F. & A. Stigebrandt 1989. A time dependent budget model for nutrients in the Baltic sea. – *Global Biochemical Cycles* 3:63-78.

Accepted 11 February 1996.