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Nitrogen and phosphorus nutrition and productivity of two community forming seaweeds (*Fucus vesiculosus, Phycodrys rubens*) from the Western Baltic (Kiel Bight) in the light of eutrophication processes

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Abstract

Considerable amounts of nutrients enter as a result of human activity the Western Baltic Sea in the form of discharge or seepage from land or as atmospheric input. Benthic macrophytes which preferably inhabit the nutrient recipient shallow near-shore areas, and where they often constitute the major primary producers may thus play an important role in eutrophication processes by uptake and accumulation of nutrient elements, enhanced primary production and following degradation of the produced organic material. Nutrient uptake, binding capacity and limitation as well as nutrient dependent growth of the two community forming seaweeds *Phycodrys rubens* and *Fucus vesiculosus* have been investigated and related to the seasonal patterns of the nutrient conditions in their respective habitats. Nutrient concentrations, both phosphorus and nitrogen, in the algal beds are markedly higher than in the surface water of the open Kiel Bight. In general, the seaweeds seem not to be nutrient limited under natural conditions except for nitrogen in *Phycodrys* during summer. Nutrient tissue contents are saturated only for nitrogen during winter. The significance of these findings is discussed in view of the observed increasing nutrient levels and changes of the vegetation in the Kiel Bight.

Introduction

During the past decades, as a result of human activity, increasing quantities of inorganic nutrients have entered the Baltic Sea in the form of discharge or seepage from land or as atmospheric input (LARSSON et al. 1985, GERLACH 1986).

In the Kiel Bight (Western Baltic) alone, for example, the annual additional input has been estimated to amount to 1500 t phosphorus and 23000 t nitrogen which is equivalent to the total amount of inorganic phosphorus and which exeeds by far the amount of inorganic nitrogen (1430 t) contained in the water column during the winter maximum, respectively (GERLACH 1986).

While trend analyses revealed an increase of winter concentrations of dissolved phosphorus by 50 % during the past 30 years, the additional nitrogen input apparently did not alter the inorganic nitrogen levels in the seawter of Kiel Bight, and also the summer concentrations remained on the same low, sometimes undetectable level (BABENERD and ZEITZSCHEL 1985).

To explain this phenomenon and the possible fate of additional nutrient input, various pathways have been considered, including export by currents, denitrification by bacteria or binding by the sediment system (e.g. LARSSON et al. 1985, BALZER 1984).

One important aspect in this context is the role of primary producers in the nutrient budget of eutrophicated waters and the effects of additional nutrient loads on primary production.

Whereas the role of phytoplankton in the nutrient cycling of Kiel Bight has been discussed by several authors (BODUNGEN 1975, 1986, AERTEBJERG et al. 1981, GRAF et al. 1983, SMETACEK 1985), little is known about the role of benthic macrophytes and their response to the nutrient situation and eutrophication processes in the Baltic (FELDNER R., 1976, FELDNER, J. 1977. WALLENTINUS 1976, 1979, 1984, KAUTSKY 1982).

We may presume that benthic macrophytes, preferably occupying the shallow near shore waters, where they often constitute the major primary producers, on the first hand will be affected by nutrient land run-off and discharge.

Because of their well known potential for excess nutrient uptake and accumulation, in particular of phosphorus (e.g. LIN 1977, CHAPMAN and LINDLEY 1980, GERARD and NORTH 1981, WHEELER and NORTH 1981, BIRCH et al. 1981, SCHRAMM and BOOTH 1981, RYTHER et al. 1981, WALLENTINUS 1979, KUHL 1974), the macrophytobenthos thus may act as a biological filter or nutrient trap in the coastal ecosystem.

On the other hand, the possibly enhanced production of organic matter due to increased nutrient levels, subsequent down slope transport and decomposition of the macrophytic material may influence the nutrient and oxygen situation particularly in the deeper basins of the Western Baltic where oxygen depletion has been frequently observed during the past years (EHRHARDT and WENK 1984, GERLACH 1984, WEIGELT and RUMOHR 1986).

This work is concerned with the effects of nutrient concentrations and their changes in a range as observed in the Western Baltic on nutrient uptake and accumulation as well as on primary production of the two quantitatively important, community-forming perennial seaweeds *Fucus vesiculosus* and *Phycodrys rubens.* In addition, the nutrient situation in various habitats of these two species has been investigated.


Material and methods

Phycodrys rubens together with *Phyllophora-* and *Polysiphonia*-species constitute the major components of the red algal communities which below 6 m depth in the Kiel Bight make up the bulk of the macrophytic biomass (estimated 17000 t dry weight) according to recent surveys carried out in the frame of this project (BREUER and SCHRAMM 1988).

Fucus vesiculosus, on the other hand, is one of the characteristic community-forming seaweeds of the shallow near-shore areas of the Western Baltic above 6 m depth. Based on earlier investigations, the standing crop in the Kiel Bight has been estimated as 3600 t dry weight (GERLACH 1986), although more recent investigations indicate that *Fucus* has considerably declined and been replaced by filamentous red and brown algae (SCHRAMM, unpubl.).

For the laboratory experiments, *Fucus* was collected from 0.5 m and *Phycodrys* dredged from 8 m depth.

To characterize the seasonal nutrient situation in the *Fucus* and red algal communities, plant material and seawater samples have been collected usually twice per month from different *Fucus-* habitats along the German Baltic coast as well as from several red algal communities between 8 and 12 m depth (Fig. 1).
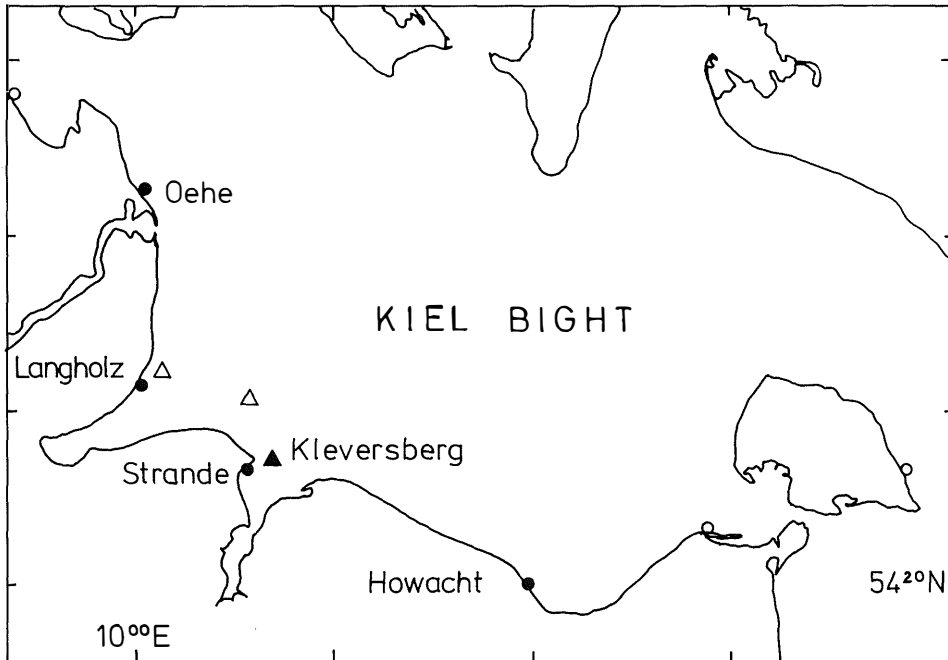
Figure 1

Kiel Bight (Western Baltic Sea). Sampling sites for *Fucus vesiculosus* (circles) and *Phycodrys rubens* (triangles) presented in this paper (closed symbols).

Nutrient uptake and growth experiments

Nutrient uptake and growth in relation to nutrient supply were investigated in laboratory batch experiments lasting two weeks. The experiments were carried out three times a year to characterize typical seasonal nutrient situations, i.e. in February/March during the winter maximum of nutrient concentrations in the seawater, in June during the summer minimum and in September at the end of the summer period with low nutrient levels.

Of the freshly collected seaweeds, samples of known weight (1g wet weigth *Fucus* or 0.5g wet weigth *Phycodrys* each) were kept in glass jars with 2 litres of seawater medium at ambient temperature ranging from 2° C in February to 10° C in June or 13° C in September, respectively.

Light (fluorescent lamps OSRAM daylight type) was about 100 $\mu Em^{-2}s^{-1}$ where growth is nearly light saturated in *Fucus* and above saturation in most red algae (LÜNING 1985).

Light/dark periods were 10/12 hours in February, 16/8 hours in June and 12/12 hours in September.

Prior to incubation, the material was cleaned as far as possible of epiphytes and epifauna and rinsed in N- and P-free medium. All jars were continuously aerated with air washing through concentrated sulfuric acid and distilled water, and passing through a glass wool filter.

The culture medium was artificial seawater adopted from the ASP12 recipe of PROVASOLI (1964), as described by GORDON et. al. (1981). Modifications were the adjustment to

15 % salinity and addition of $NaHCO_3$ to give an alkalinity similar to that in the Kiel Bight. Inorganic nitrogen was supplied as NH_4NO_3, since both N-species are present in the bottom water in Kiel Bight at comparable levels, and are utilized simultanously at similar rates (PRINCE 1974, WALLENTINUS 1984). Inorganic phosphorus was added as KH_2PO_4.

Two parallel experiments were run. One in which inorganic nitrogen (NO_2+NO_3, NH_4) varied (0,0.5,1,3,10 and 20 µmol N dm^{-3}) and phosphorus was supplied at constant levels (1 µmol dm^{-3}) corresponding to the average winter maximum in the Kiel Bight.

In the second experiment, phosphorus levels were 0,0.05,0.1,0.3,1 and 2 µmolP dm^{-3} while N was kept constant at 20 µmol dm^{-3}.

Nutrient concentrations were measured daily and adjusted to the desired levels. The medium was changed every second or third day. Nutrient uptake rates were determined on the first and the last two days of the experiments for two successive incubation periods per day, lasting 3–5 hours at daytime and 14–20 hours at night time, respectively. The results presented are the average of the day and night time measurements.

The nutrients were analyzed according to GRASSHOFF et. al. (1983), modified to a sample volume of 5 ml.

Total P content of the algal tissue was determined photometrically after combustin (550°C) and dissolution in HCl as described by SCHRAMM and BOOTH (1981).

Total nitrogen content was measured employing a C/H/N-analyzer (Carlo Erba).

Calculations

Because nutrient levels in the culture media fell during the uptake experiments, concentrations related to uptake rates, to growth or to tissue nutrient content were the average of intermediate nutrient levels observed during 3–5 successive incubation periods.

Relative daily growth rates (DGR) were determined for the first and the second five days of the culture experiment using the equation DGR (%)=[(lnW_1-lnW_0)/n-1]100, where n is the number of days of the experimental period, W_1 and W_0 are the final and initial weights of the sample, respectively.

Since mathematical approximations by employing e.g. the MONOD or MICHAELIS-MENTON equations, as commonly applied in nutrient kinetic studies, may give considerably deviating and often ecologically irrelevant results, depending on the hyperbolic model and the transformation used (GORDON et. al. 1981, WALLENTINUS 1984, MOREL 1987) we preferred visual fitting of the curves.

For comparison, however, the uptake rates versus substrate concentration were also analyzed employing the MICHAELIS-MENTEN equation to obtain Vmax– and Km-values.

Results

Uptake of nutrients

Uptake rates of nitrogen as well as of phosphorus increased with increasing substrate concentration and showed considerable variations with the season and to a certain extent also with the length of the culture period (Fig. 2,3).

The highest nutrient uptake rates were observed for the June material both in *Fucus* and *Phycodrys*, the lowest in February, except for phosphorus uptake by *Phycodrys* which was lowest in September at the end of its growing season.

Whereas phosphorus uptake rates at the end of the culture experiment were practically

saturated at 1.5–2 µmol dm^{-3} in the winter and autumn material of both seaweeds, nitrogen uptake rates reached saturation under given experimental conditions only in *Phycodrys* in February/March.
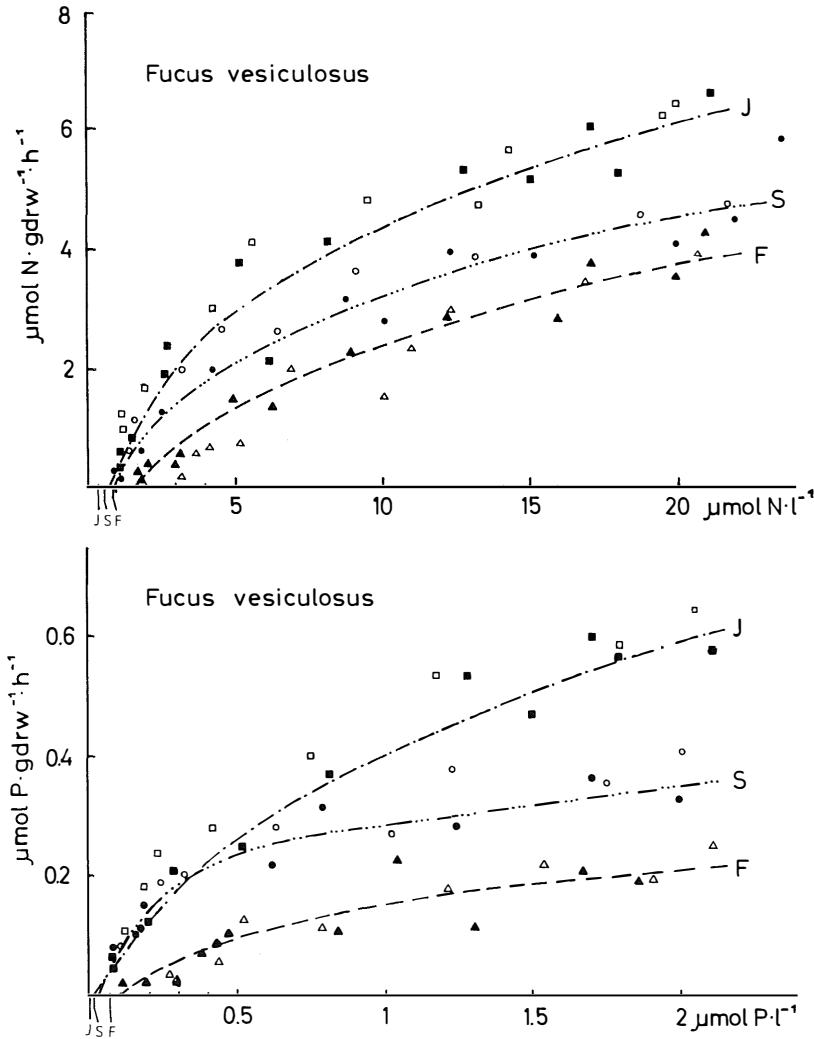
Figure 2

Inorganic nitrogen (NO_2, NO_3, NH_4) and phosphorus (PO_4) uptake rates (µmol $gdrw^{-1}$ h^{-1}) by *Fucus vesiculosus* as a function of mean nutrient concentrations (µmol dm^3) during laboratory batch experiments in February (F, triangles) at 2°C, in June (J, quadrats) at 10°C and in September (S, circles) at 13°C, respectively. Mean uptake rates during the first three days (open symbols) and the last three days (closed symbols) of the culture experiments. Curves visually fitted to the latter.

The theoretical kinetic constants Vmax and Km computed on the basis of MICHAELIS-MENTEN kinetics, are given in Tab. 1.

Table 1

The kinetic parameters Km (μmol dm^{-3}) and Vmax (μmol g drw^{-1} hr^{-1}) for *Fucus vesiculosus* and *Phycodrys rubens*, respectively, at different times of the year. Values obtained on the basis of laboratory batch experiments, employing the MICHAELIS-MENTEN equation and linearization s/v=f(s) (DeBOER plot; in parenthesis: s=f(s/v); WOOLF plot).

		Fucus vesiculosus			*Phycodrys rubens*		
		Febr. 2°C	June 10°C	Sept. 13°C	Febr. 2°C	June 10°C	Sept. 13°C
Inorg.N	Vmax	5.05 (9.43)	6.75 (9.80)	6.56 (7.75)	6.05 (6.80)	10.26 (10.65)	10.56 (12.34)
	Km	10.48 (31.04)	4.7 (12.06)	9.60 (13.80)	3.31 (5.73)	7.49 (8.13)	11.56 (15.06)
	r	0.73	0.83	0.92	0.94	0.98	0.93
Inorg.P	Vmax	0.10 (0.18)	0.75 (0.91)	0.35 (0.38)	0.59 (0.89)	0.97 (1.12)	0.94 (0.39)
	Km	0.51 (0.03)	0.76 (1.14)	0.1 (1.51)	1.16 (2.29)	0.87 (1.12)	0.36 (0.53)
	r	0.75	0.95	0.97	0.81	0.94	0.94

Similarly, the lower limits for nutrient uptake varied with the season. The lowest concentration at which phosphorus were taken up ranged from undetectable levels for both seaweeds in June to 0.05 to 0.08 μmolP dm^{-3} in winter for *Fucus* and *Phycodrys,* respectively. The lower limiting concentrations for nitrogen uptake were higher, i.e. 0.3 – 0.4 μmol N dm^{-3} in June or 0.8 – 0.9 μmolN dm^{-3} in winter for *Fucus* and *Phycodrys,* respectively.

During the time course of the incubation experiments, uptake rates changed, obviously reflecting the nutrient situation in situ and the internal nutrient status of the seaweeds. In winter, when external as well as internal nutrient levels were high, uptake rates particularly at low nutrient levels were lower at the beginning of the experiment and increased with progressive depletion of internal nutrient reserves towards the end of the culture period.

In June and September, on the other hand, when nutrient concentrations in situ were low, the uptake rates of the initially nutrient depleted algae decreased with increasing nutrient saturation during the culture experiment.

Tissue nutrient content versus substrate nutrient concentration

The relationship between nutrient concentration in the culture media and the content of the algal tissue at the end of the culture experiments is shown in Fig. 4.

Whereas nitrogen content approached saturation levels between 10 and 20 μmol N dm^{-3} both for *Fucus* and *Phycodrys* within the culture period, tissue phosphorus content obviously was not saturated under given experimental conditions.

The maximum tissue nutrient level as obtained in our experiments was observed in situ only for nitrogen during the winter months, indicating nitrogen satiation under natural conditions.
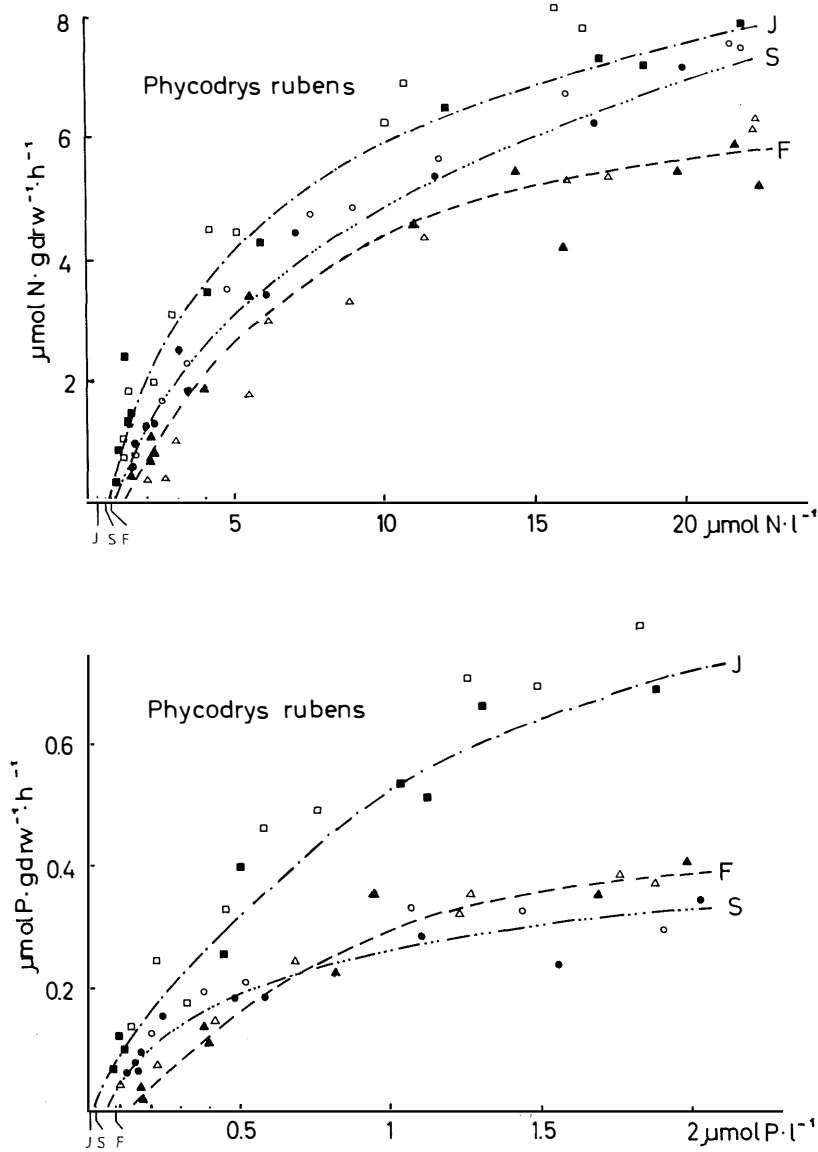
Figure 3

Inorganic nitrogen (NO_2, NO_3, NH_4) and phosphorus (PO_4) uptake rates (μmol . gdrw^{-1} h^{-1}) by *Phycodrys rubens* as a function of mean nutrient concentrations (μmol dm^{-3}). For further explanation cf. Fig. 2

Growth versus nutrient concentration in the culture medium

Relative growth rates in relation to substrate nutrient concentrations during the first and second 5 days of the culture experiments are shown in Fig. 5.

In general, growth rates of both seaweeds were highest in June when nutrient concentrations were higher than 3μmol N dm^{-3} and 0.3 umol P dm^{-3}, respectively.
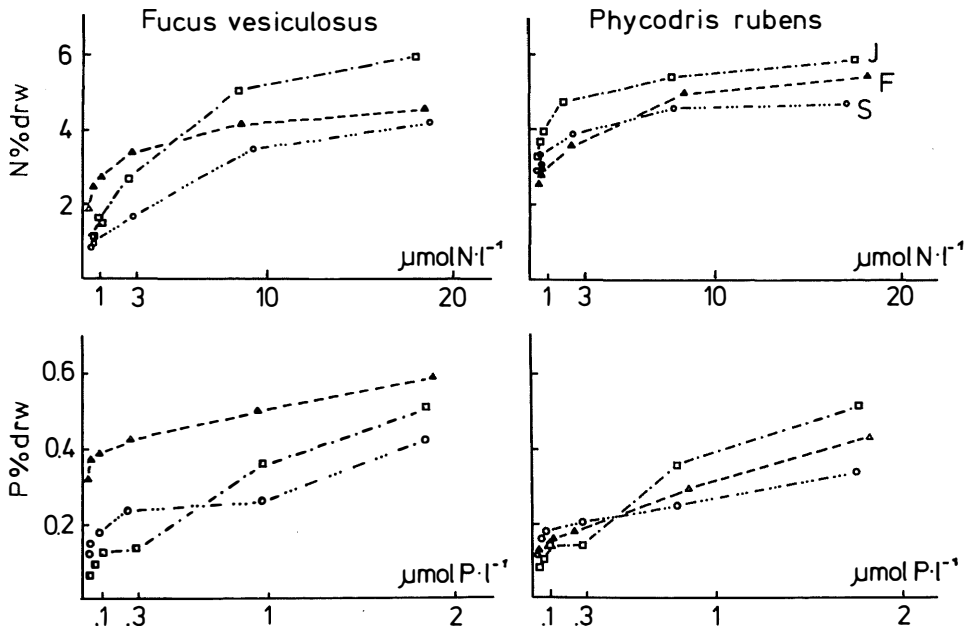
Figure 4

Total nitrogen and total phosphorus contents (% dry weight) in the tissue of *Fucus vesiculosus* and *Phycodrys rubens* as a function of mean substrate concentrations (μmol dm⁻³). For further explanation cf. Fig. 2.

Below these concentrations, growth rates of the winter material were relatively higher, however, less stimulated at higher ambient nutrient levels, obviously due to higher internal nutrient reserves.

In the further time course till the end of the experiments, growth rates declined when nutrients were maintained below 10 μmol N dm⁻³ or 1 μmol P dm⁻³, most rapidly in June and September, whereas above these concentrations growth always remained saturated.

Growth versus tissue nutrient levels

Growth rates at the end of the culture experiments plotted against corresponding tissue nutrient levels as obtained under given culture conditions are shown in Fig. 6.

Extrapolation of the curves renders estimates of upper critical nutrient contents at which growth is saturated or lower limiting ("minimum viable") levels where growth ceases.

While the upper critical nitrogen as well as phosphorus levels for *Fucus* were highest in February, the lowest values were obtained for nitrogen in September and for phosphorus in June.

In *Phycodrys* similar seasonal differences were observed for phoshorus dependent growth, whereas critical nitrogen levels were considerably higher in June and September compared to February.

The lower growth limiting levels extrapolated from our results can only be crude estimates, because growth rates were still considerably high in our experiments, even at the lowest levels applied. We may presume, however, that the lower critical nutrient levels are higher in winter for both seaweeds, except for *Phycodrys* where limiting nitrogen levels did not
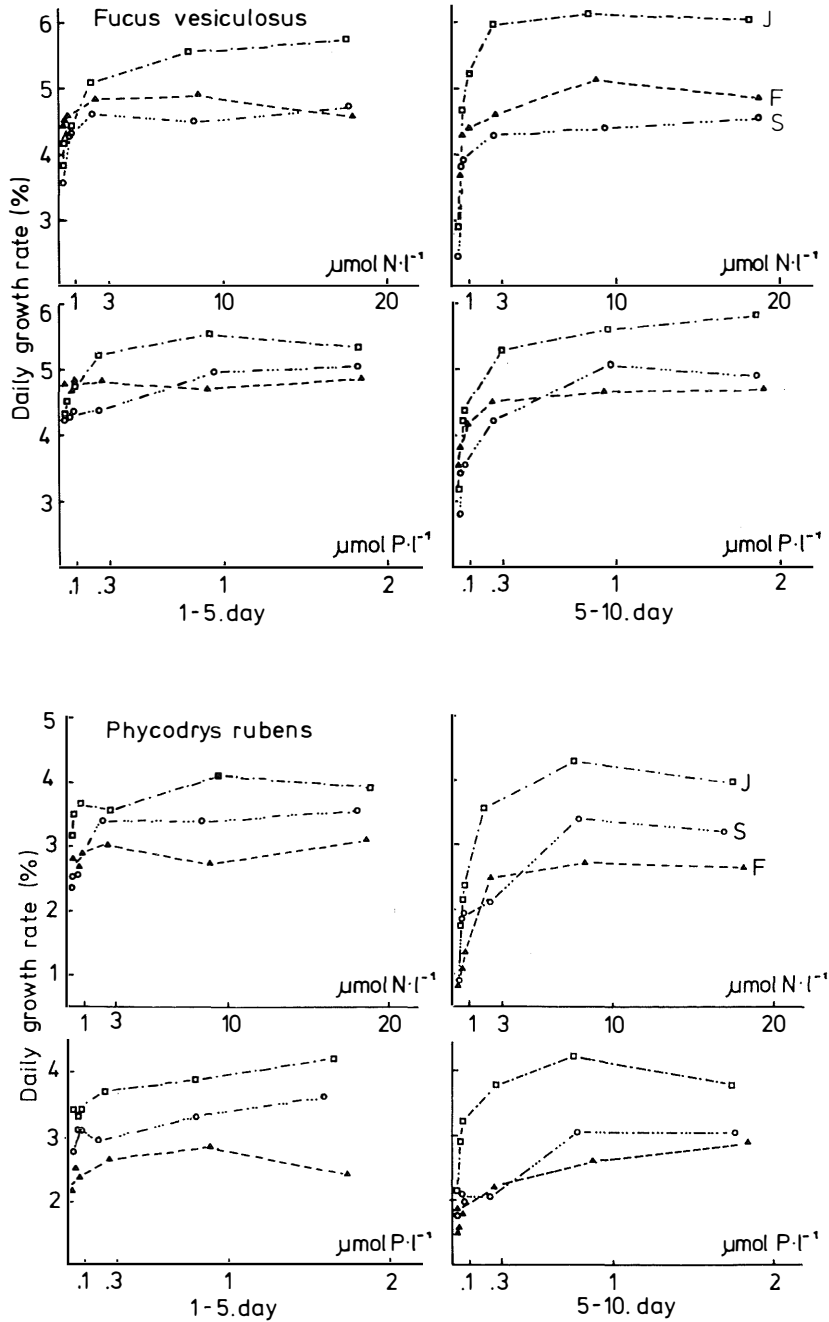
Figure 5

Relative daily growth rates (mean % biomass increase per day) of *Fucus vesiculosus* and *Phycodrys rubens* as a function of mean nutrient concentrations (μmoldm^{-3}) of inorganic nitrogen (NO$_2$, NO$_3$, NH$_4$) and phosphorus (PO$_4$) during the first and last five days of the culture periods respectively. For further explanation cf. Fig 2.
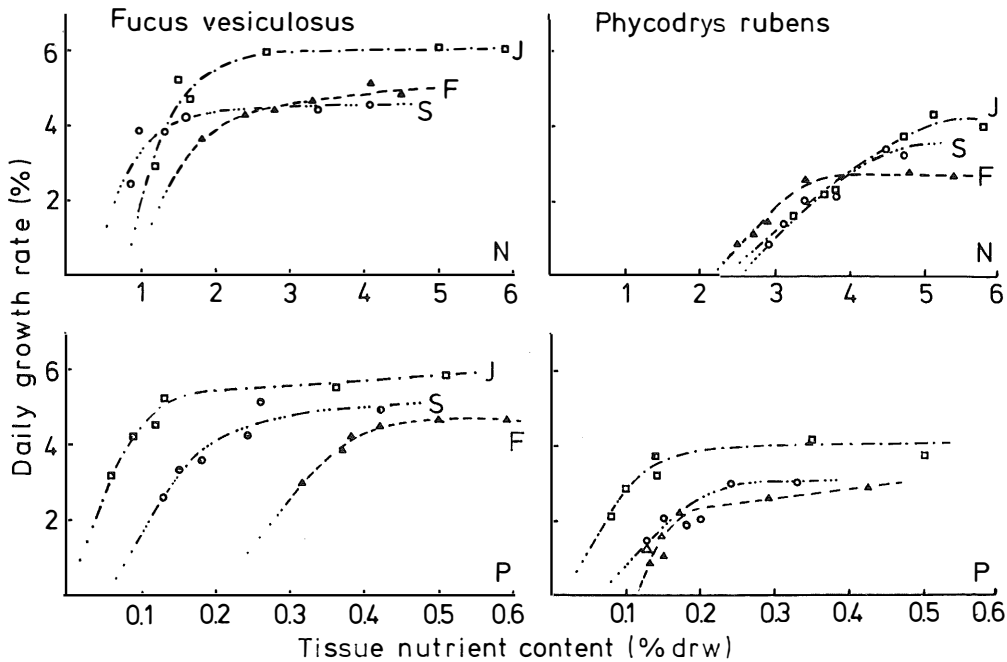
Figure 6

Relative daily growth rates (mean % biomass increase per day) of *Fucus vesiculosus* and *Phycodrys rubens* as a function of total nitrogen and total phosphorus contents in the algal tissue (% dry weight). For further explanation cf. Fig. 2

differ from season to season, and were considerably higher (2–3 % N) compared to *Fucus* (<1 % N).

The in-situ nutrient situation

From the *Fucus*-habitats investigated, four examples of the seasonal variations of inorganic nutrient concentration are shown in Fig. 7.

The typical situation for a red algae community at 8 m depth as well as in the surface water from the same location is given in Fig. 8.

From September to June, the nutrient concentrations in the interalgal seawater were considerably higher in almost all nearshore *Fucus*-communities and slightly higher in the off-shore red algal bed (Kleversberg) compared to the surface water of the same location, the latter showing the same levels as reported for the open Kiel Bight in the previous years (STIENEN 1986).

An exception was the station Oehe (Fig. 7) with significantly lower concentrations comparable to those in the open sea, possibly due to a particular hydrographic condition (e.g. advection of nutrient depleted surface water from the open sea?).
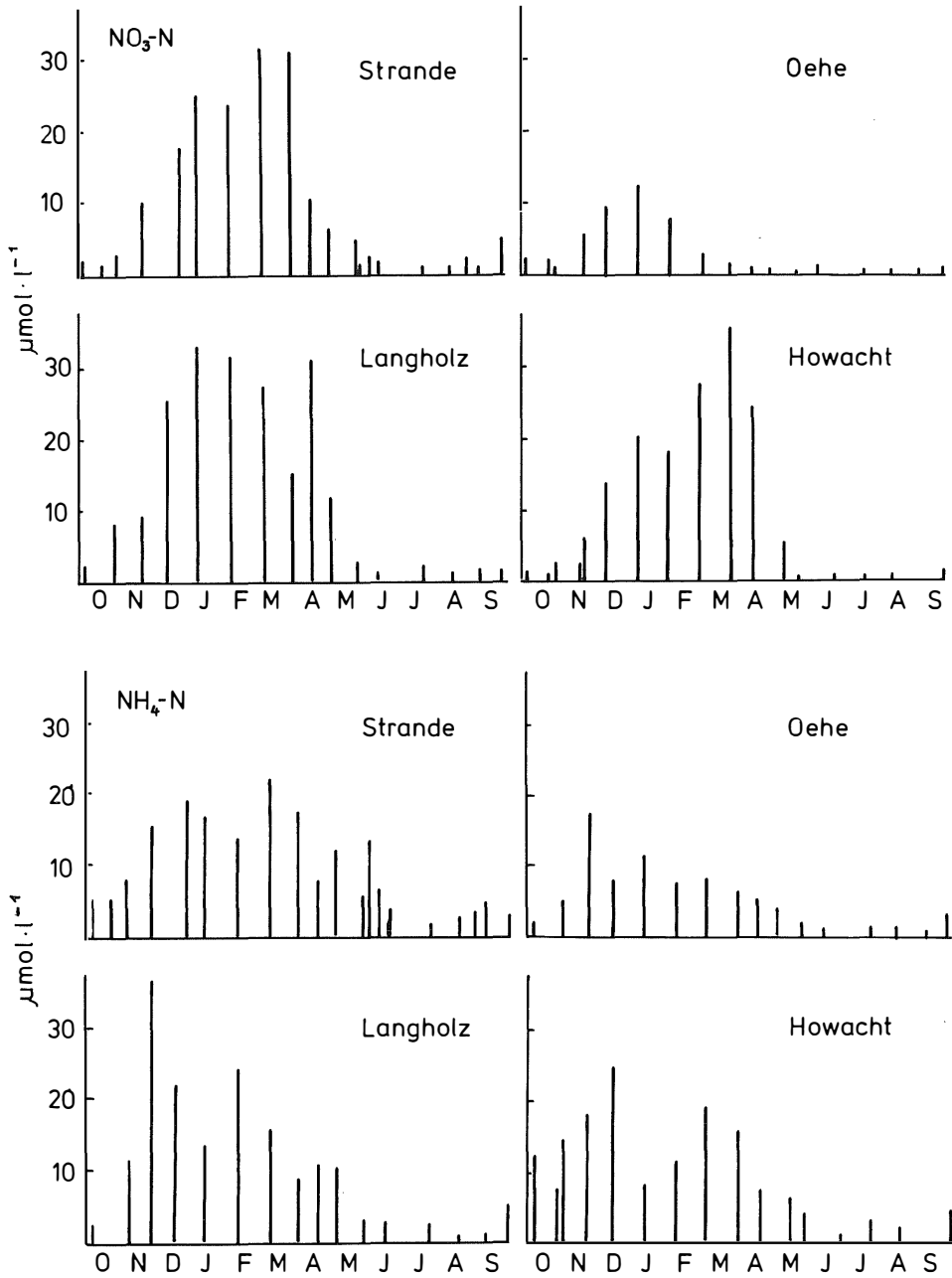
Figure 7

Seasonal variations of nutrient concentrations (NO_3-N, NH_4-N, PO_4-P µmol dm^{-3} in the interalgal seawater of some *Fucus vesiculosus*- communities in the Kiel Bight (Western Baltic Sea). Location of the sampling sites cf. Fig. 1.
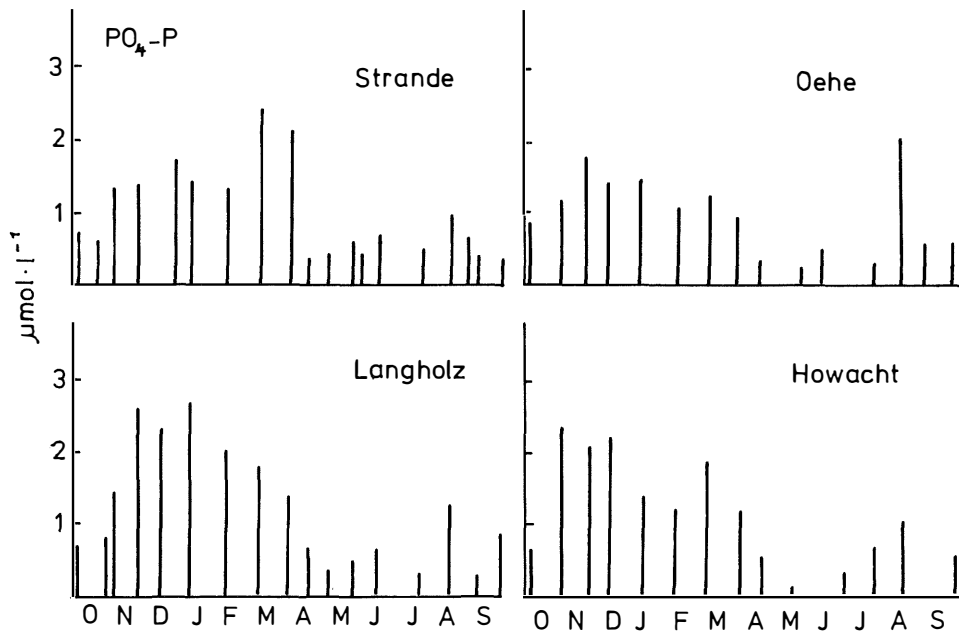
Figure 7   Continued
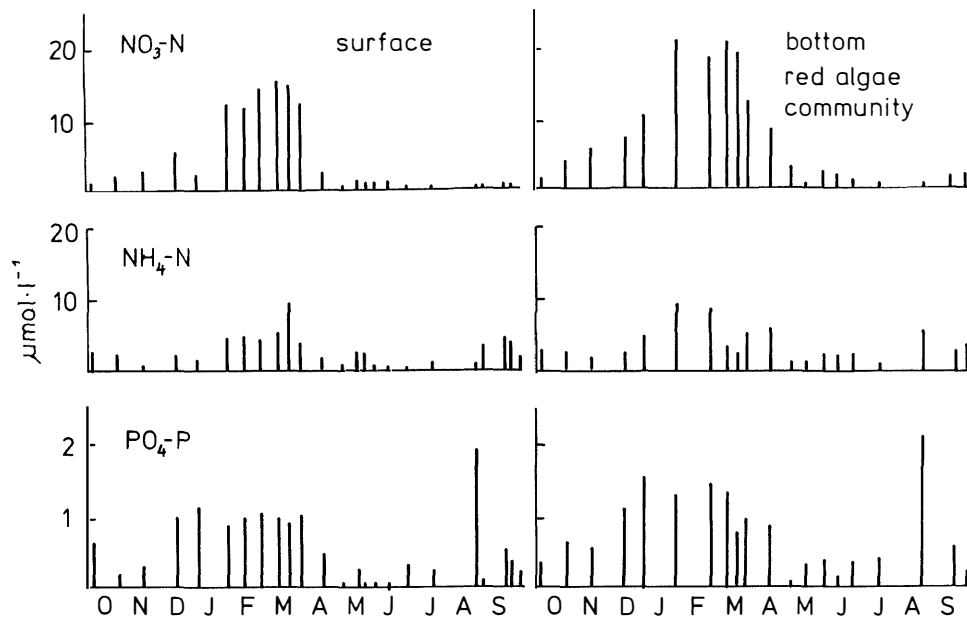
Figure 8

Seasonal variations of nutrient concentrations (NO_3-N, NH_4-N, PO_4-P µmol dm^{-3}) in the interalgal seawater (right) of a red algal community (8 m depth) and in the overlaying surface water (left) in the Kiel Bight (Western Baltic Sea). Location of sampling site Kleversberg, cf. Fig. 1.

Only from June to September, the nitrate levels fell to comparable low levels as in the open Kiel Bight, whereas the PO_4- and NH_4-concentrations were markedly higher, particularly in the *Fucus*-communities.

Seasonal variation of N content of the seaweeds from the various sampling sites followed more or less the ambient N concentrations, whereas P contents were relatively higher in early summer, possibly due to P reserves accumulated during the winter and early spring months when P levels were high (Fig. 9). Reduction of tissue nutrient content indicates that internal reserves are utilized during the summer months.
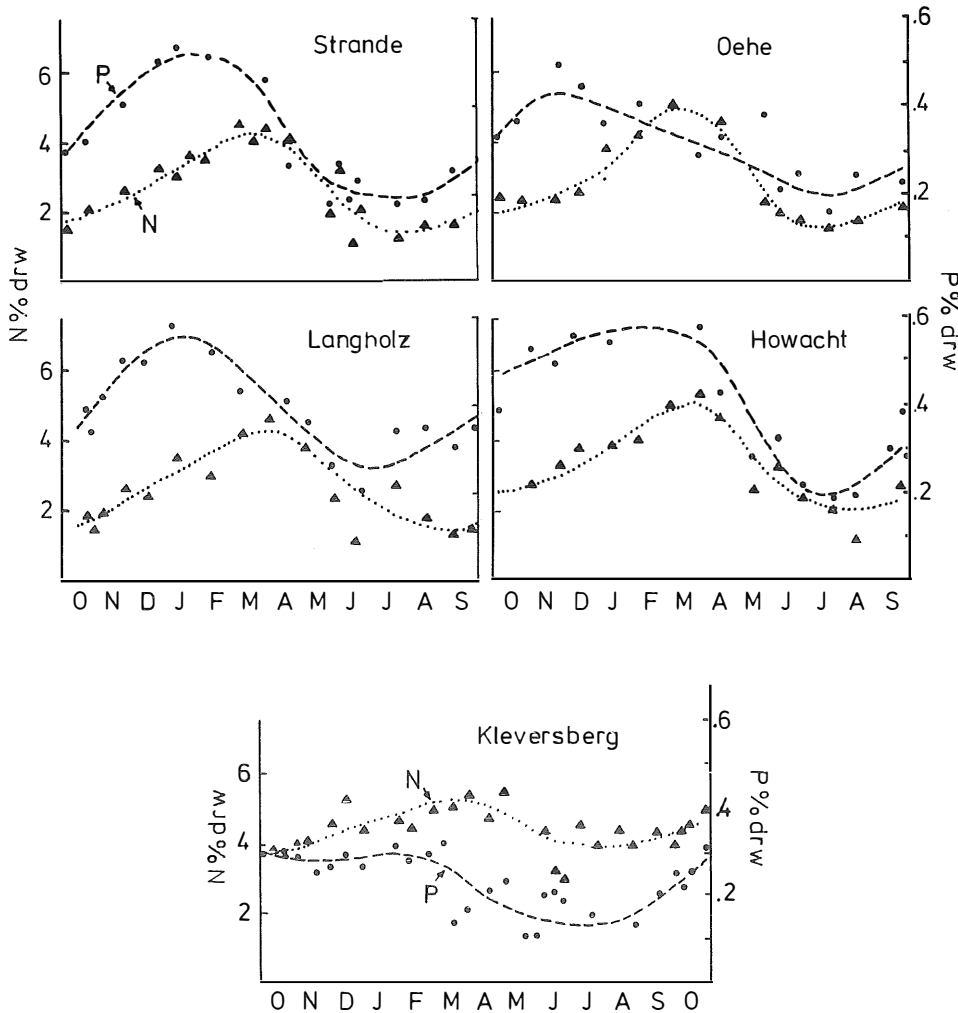
Figure 9

Seasonal variations of total nitrogen and phosporus contents (% dry weight) in the tissue of *Fucus vesiculosus* and of *Phycodrys rubens* from various locatities in the Kiel Bight (Western Baltic Sea). Location of the sampling sites cf. Fig. 1.

Discussion

For the assessment of possible effects of increasing nutrient levels as apparent in the open Kiel Bight on nutrient uptake and productivity of marine macrophytes, it must be emphasized that the nutrient situation in the algal habitats differs significantly from the water column in the open bight which is commonly considered to characterize the eutrophication level. Figs. 10 and 11 show the seasonal variation of nutrients in the interalgal seawater and in the seaweed tissue for a typical *Fucus-* community (Strande) and a red algal bed (Kleversberg) in Comparison to the average nutrient concentration in the open Kiel Bight, based on own measurements and data from STIENEN (1986).

To faciliate the interpretation of our results, the field observations and the critical nutrient levels as obtained from our laboratory experiments are composed in the graphs.

Elevated nutrient concentrations within the phytobenthic communities have been frequently reported (KAUTSKY and WALLENTINUS 1980, BIRCH et.al. 1981, SCHRAMM and BOOTH 1981, GERARD 1982).

Mostly they have been attributed to biological activities such as excretion by associated animals, enhanced bacterial regeneration or release from the sediments.

It is not clear, wether and to what extent direct run-off or seepage from land will affect nutrient concentration, particularly in near-shore habitats.
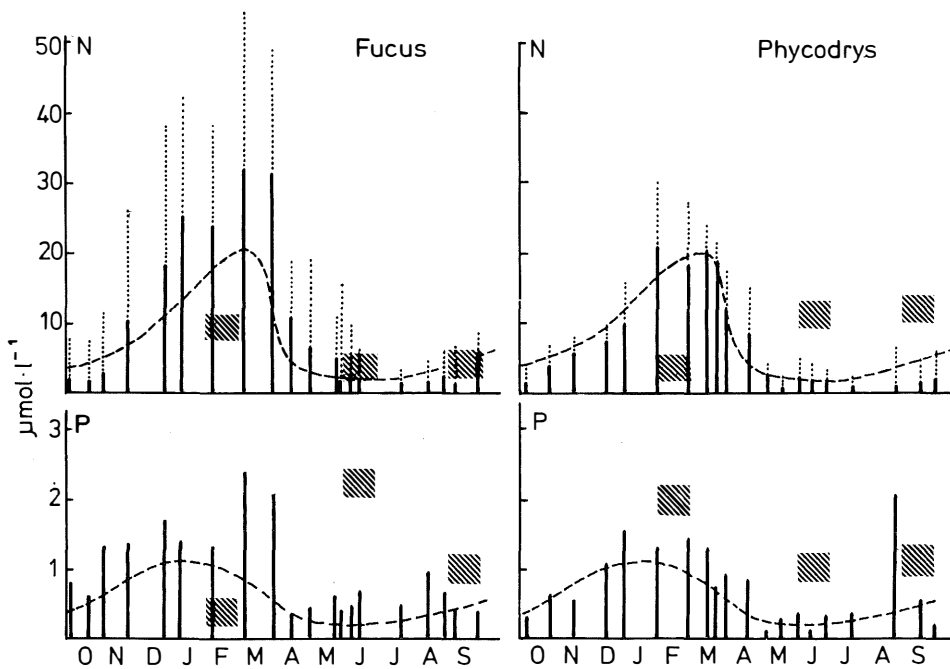
Figure 10

Seasonal variations of inorganic nitrogen (NO_2+NO_3-N:solid bars, NH_4-N: pointed bars) and phosphorus (PO$_4$-P) concentrations in the interalgal seawater of the *Fucus*-community in Strande and the red algal community (*Phycodrys*) at Kleversberg in relation to growth saturating nutrient concentrations during different times of the year (hatched areas). The curves (broken line) represent the mean variations of nutrient concentrations in the surface water of the open Kiel Bight according to STIENEN (1986) and own measurements.
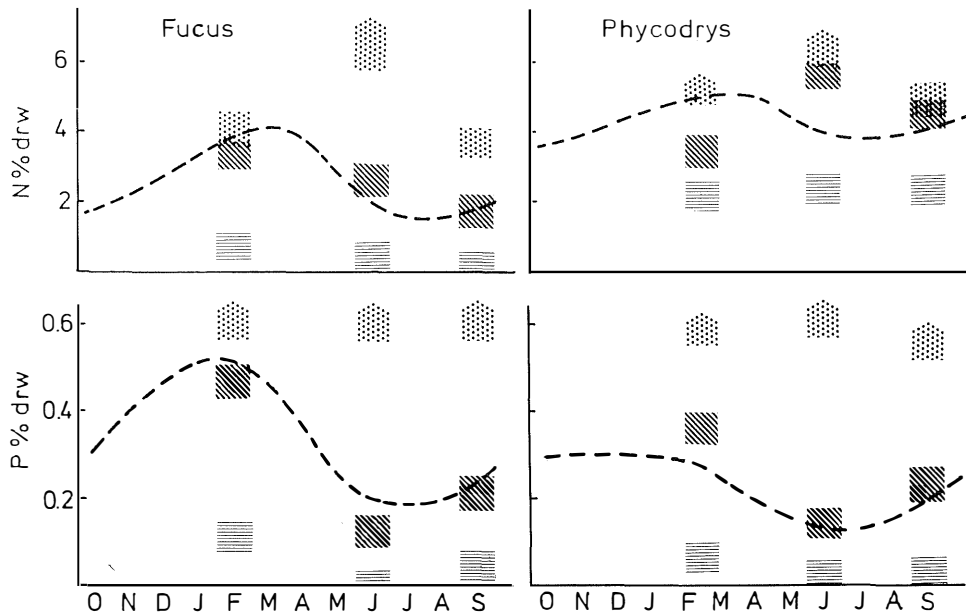
Figure 11

Seasonal variations of total nitrogen and phosphorus contents in the tissue of *Fucus vesiculosus* and *Phycodrys rubens* (broken curves) in relation to saturated nutrient contents (dotted areas), and to nutrient contents at which growth is satiated (diagonal hatching) or where growth ceases (horizontal hatching).

Control measurements in nearshore areas without macrophytic vegetation gave usually nutrient concentrations slightly higher than in the open bight, but lower than in the algal beds.

The significantly higher nutrient concentrations as observed in "polluted" sampling sites which have not been presented here (e.g. Flensburg Fjord) may be also caused by less exposure to wave action or reduced water exchange which favours the deposition and remineralization of organic material or the formation of concentration gradients between the algal beds and the overlaying water column.

Relating the in situ nutrient concentrations to our laboratory results on nutrient uptake rates and tissue contents (cf. Figs. 10, 11, 2–6), we may assume that in the field, saturation will probably be reached only for nitrogen during the winter nutrient maximum.

The discrepancy that *Fucus* did not reach satiated tissue N-content in early summer, although seawater concentrations were sufficient for saturated uptake, may be due to competitive nutrient uptake by the *Fucus*-epiphytes which show maximal development during this season. The concentrations where uptake rates were practically saturated as estimated by graphical extrapolation, differ considerably from our as well as from WALLENTINUS' (1984) results calculated on the basis of MICHAELIS-MENTEN kinetics (Tab. 1).

The „half" saturation constants (Km) for maximal nutrient uptake e.g. for *Fucus vesiculosus* from Askö (Swedish east coast) at 3°C were as high as 45 μmol PO_4-P dm^{-3}, 271 μmol NO_3-N dm^{-3} and 508 μmol NH_4-N dm^{-3}, respectively.

As WALLENTINUS (1984) could demonstrate, employing MICHAELIS-MENTEN kinetics may give strongly variable and ecologically irrelevant kinetic constants depending on the

linear transformation used, when nutrient uptake rates do not fit the hyperbolic model (cf. also DOWD and RIGGS 1965, EPPLEY et. al. 1969, D'ELIA and DeBOER 1978).

The inaccuracy in estimating Km-values for nutrient uptake rates, particularly at low substrate concentrations, has also been pointed out by e.g. TOPINKA (1978) or HANISAK and HARLIN (1978). Another source of error in the application of phenomenological equations lies in the different chemical species, as for example, nitrogen which in several inorganic and possibly organic forms may be taken up simultaneously at different rates (MOREL 1987).

Growth saturating nitrogen concentrations were considerably lower and are likely to be met in the field for *Fucus* throughout the year, for *Phycodrys* during the winter months (Fig. 10).

In contrast, in situ PO_4-concentrations were mostly below growth saturating levels, except for *Fucus* in winter.

This does not take into account, however, the possibility of a steady state between continuous nutrient supply (for example, through excretion and regeneration of nutrients by closely associated animals and bacteria or release from the sediment) and the immediate and continuous uptake by the plants, possibly sufficient to support maximal growth.

Another interesting aspect is, that during summer in *Fucus*- as well as seagrass communities pronounced diurnal fluctuations of seawater nutrient concentrations could be observed, with strong pulses of nutrients which may be rapidly absorbed by the seaweeds to maintain growth over days or even weeks, as shown, for example, for *Gracilaria* or *Ulva* in culture experiments (RYTHER et. al. 1981, DeBUSK et. al. 1986).

Little information is available about such processes (e.g. KAUTSKY and WALLENTINUS 1980), the study of which certainly would open new aspects for the understanding of the role of benthic systems in the nutrient cycling within marine ecosystems.

The observed variations in critical nutrient levels for uptake as well as growth, independent from ambient nutrient conditions, may reflect variations in other essential factors.

Besides changing environmental factors, such as light, temperature or water movement, and the physiological or developing stage of the plants (e.g. TOPINKA 1978, HANISAK and HARLIN 1978, GORDON et al. 1981, PROBYN 1984, ROSENBERG et al. 1984), the internal nutrient levels in particular may strongly influence nutrient kinetics as well as productivity, and have therefore frequently been suggested to be a more relevant measure of the nutrient situation of marine plants (BUGGELN 1978, CHAPMAN et al. 1978, HANISAK 1979, LAPOINTE and RYTHER 1979, BIRD et al. 1981, GERARD 1982, MANLEY and NORTH 1984).

MOREL (1987) has recently discussed the theoretical aspects of the large differences which exist between nutrient saturation constants for growth and short-term uptake in microalgae. He suggests that due to acclimation capabilities of the algae, growth can be maintained by modulating both their internal (cellular) nutrient quota and uptake rates in response to the external nutrient supply.

The observed seasonal changes of internal nutrient levels following in principle ambient nutrient concentrations, are typical for perennial seaweeds (BLACK 1949, JACOBI 1954, CHAPMAN and CRAIGIE 1977, BUGGELN 1978, WALLENTINUS 1979, BIRCH et al. 1981, KORNFELDT 1982; cf. Figs. 14,15,17). Also the less pronounced fluctuations in *Phycodrys* with higher N- and lower P-levels compared to *Fucus,* seem to be a distinctive characteristic for red and brown algae (NIELL 1976, KORNFELDT 1982).

While the range of nutrient contents in the two seaweeds from Kiel Bight is comparable to that of *Phycodrys rubens* from the Swedish west coast at Kullen (KORNFELDT 1982) or of *Fucus vesiculosus* from the inner archipelago at Askö (Baltic proper), the P- and N-levels in *Fucus* from the outer archipelago near Askö was markedly lower (0.096-0.34 % P, 0.61-3.86 % N; WALLENTINUS 1979), possibly reflecting the different degree of eutrophication in these areas at that time.

V. WACHENFELDT (pers.comm.) compared herbarium material of *Fucus vesiculosus* and *Fucus serratus* from the Swedish coast (Kattegatt, Sound, Baltic proper) and found that N- and P-levels have steadily increased from the 1930th until now by a factor up to 2–3.

The „minimum viable" levels, i.e. tissue nutrient contents at which growth is likely to cease, were always below the levels observed under natural conditions. While our estimates for nitrogen in *Fucus* are comparable with figures for e.g. *Macrocystis pyrifera* (0.7 %; GERARD 1982), *Cladophora albida* (1.2 %; GORDON et al. 1981) or *Fucus distichus* (0.6 %; ROSENBERG et al. 1984), minimum levels for *Phycodrys* are conspicuously higher, suggesting that internal nitrogen sources are less readily available in this red alga.

Critical nutrient levels for saturated growth of *Fucus* were always close to the observed internal N- and P-levels, which implies that in the *Fucus* habitats phosphorus is not limiting, while nitrogen possibly slightly so only in early summer.

On the other hand, *Fucus,* although having the capacity, showed only little excess uptake during winter, as reported for other seaweeds (CHAPMAN et al. 1977, CHAPMAN and CRAIGIE 1978, HANISAK 1978, WALLENTINUS 1979, BIRCH et al. 1981, SCHRAMM and BOOTH 1981, GERHARD 1982).

Another situation is given in *Phycodrys,* where nitrogen, although taken up in excess during winter, is limiting growth in June and possibly also in September. Phosphorus, on the other side, is perhaps growth limiting in winter, however, not in summer and autumn.

In view of the possible response of seaweeds to increased nutrient levels as observed in the Kiel Bight, and considering the role of benthic macrophytes in eutrophication processes, either by fixation of nutrient elements or by enhanced production, we may draw provisional conclusions from our findings. An increase of nitrogen concentrations in the interalgal seawater would probably lead to higher uptake rates and N-levels both in *Fucus* and *Phycodrys* only during summer and autumn. Production might be enhanced only in *Phycodrys* during summer, possibly also in autumn.

Additional phosphorus could be taken up by *Fucus* as well as *Phycodrys* throughout the year, however, would increase productivity only in *Phycodrys* during winter.

Altogether, it appears that increasing nutrient supply would be more advantageous to *Phycodrys* than to *Fucus*.

The different response to nutrients may be another explanation beside the suggested changes in the light climate and the substrate situation for the observed spreading of red algae, in particular of *Phycodrys,* into the shallower waters above 12 m depth and the decline of *Fucus serratus* and *Fucus vesiculosus* along the German Baltic coasts during the past years (BREUER and SCHRAMM 1988, SCHRAMM, unpubl. data).

We are aware of the fact that deduction from laboratory results like ours to in situ conditions must be looked at very critically. More research, for example on competitive advantages in nutrient uptake by annual filamentous algae (WALLENTINUS 1984), on the role of internal coupling for the nutrient cycling in benthic systems or the influence of changes in substrate conditions (BREUER and SCHRAMM 1988) is certainly needed.

Acknowledgements

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