Photosynthetic rate and light curves of phytoplankton in the southern Baltic

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Abstract

The paper presents photosynthetic curves for the phytoplankton population at three stations located in the Polish Economic Zone of the Baltic Sea, *i.e.* in the Gdańsk and Bornholm Deeps and in the southern part of the Gotland Deep. Studies were carried out in 1995–1998. Assimilation numbers varied from 1.59 to 6.81 mgC mgChl^{-1} h^{-1}, the average value being 3.31 mgC mgChl^{-1} h^{-1}. Irradiation of photosynthesis saturation ranged from 216 to 673 kJ m^{-2} h^{-1}. The seasonal variations in assimilation number and its dependence on water temperature are described.

1. Introduction

The intensity of the photosynthetic production of organic matter in seawater is governed by numerous environmental factors, light being the most important one. Studies on the relationship between light and photosynthetic rate have been conducted by numerous researchers, *e.g.* Platt and Gallegos (1980), Dera (1995). This dependence is very complex owing to the fact that the light field in seawater is subject not only to considerable diurnal and seasonal time variability, but also to random fluctuations dependent on hydro-meteorological conditions. This means that the light/photosynthetic rate ratio measured under natural conditions can be referred only to a particular region, and even then must be treated with caution. For these obvious reasons, this relationship cannot be referred to phytoplankton populations in other study areas (Falkowski, 1980).

The light/photosynthetic rate ratios obtained for monocultures cannot always be used to describe the primary production of natural phytoplankton populations. The phytoplankton species composition and its physiological preferences, the highly time-variable hydrochemical conditions of the environment (Geider, 1993; Latała, 1991), and hydrodynamic processes such as vertical mixing (Marra, 1980), are thought to exert a significant influence on the primary production/light relationship.

The substantial progress already made in the mathematical modelling of phenomena in the marine environment calls for data on the relationship between photosynthesis and light under different environmental conditions (Baretta *et al.*, 1995; Savchuk and Wulff, 1993; Semovski and Woźniak, 1995). In the Baltic Sea this relationship has been studied by Renk (1983), Renk *et al.* (1983), Woźniak (1987) and Woźniak *et al.* (1989). Owing to the very variable environmental conditions in the Baltic, the photosynthetic process there is extremely complex and requires further study (Lohrenz, 1993; Tilzer *et al.*, 1993). The present results here are intended to fill this gap to some extent.

2. Materials and methods

Studies were conducted within the Baltic Monitoring Programme (BMEPC, 1988) at the following stations: P1 (54°50′N, 19°20′E) in the Gdańsk Deep, P5 (55°36′N, 19°59′E) in the Bornholm Deep, and P140 (55°36′N, 18°26′E) in the southern part of the Gotland Deep. In addition, occasional measurements were made in the Pomeranian Bay (ZP and B13) and in the Słupsk Furrow (SF). Measurements of primary production under different light conditions carried out in an incubator, and initial chlorophyll concentrations in the incubated water, usually collected at 2.5 m depth, enabled the photosynthetic light curves to be determined. The fluorescent lamps in the incubator provided a constant irradiation of 250 kJ m^{-2} h^{-1}, while the use of filters and mirrors ensured additional irradiation (PAR) of 435, 186, 124, 62, 37 and 2.5 kJ m^{-2} h^{-1}. A thermostat maintained the water temperature at the same level as that of the environment where the samples had been collected.

The photosynthetic intensity was determined radioisotopically (Steemann Nielsen, 1952, 1965; Aertebjerg Nielsen and Bresta, 1984), ^{14}C with 150 kBq activity per incubated water sample being used. The activity of phytoplankton samples after incubation was measured with a liquid scintillation counter. Inorganic carbon in water (essential for estimating primary production) was determined with a pH meter, the pH of the water being measured before and after acidification with 0.01 N HCl (1:4) (BMEPC, 1988). Chlorophyll concentrations were determined by fluorometric method using a 90% acetone solution and 24-h pigment extraction in darkness at a temperature of *ca* 4°C (Evans *et al.*, 1987). The chemical analyses of nutrients were done by a team from the Institute of Meteorology and Water Management, Gdynia, on board the research vessel directly after sampling using the standard analytical methods (Baltic Monitoring Programme) recommended for the Baltic Sea (BMEPC, 1988; UNESCO, 1983; Grasshoff *et al.*, 1983).

3. Mathematical description of the relationship between the rate of photosynthesis and irradiation

A parameter called the photosynthetic rate P_h is used to determine the light curves of Baltic phytoplankton; it is the ratio of primary production (PP) during one hour to the chlorophyll concentration (Chl)

$$P_h = \frac{PP}{\mathrm{Chl}}. \tag{1}$$

The photosynthetic rate (P_h) depends on numerous environmental factors, irradiation included. The highest photosynthetic rate, occurring at saturation irradiation (Yentsch and Lee, 1966), is called the assimilation number (AN) (Parsons and Takahashi, 1973; Platt and Gallegos, 1980)[1]. The experimental determination of AN is usually done at discrete irradiation values; therefore, the irradiation value assumed as saturation irradiation is an approximate value, hence the AN_{exp} determined in this manner are approximate too. A more exact value of the saturation irradiation and more precise AN can be obtained by drawing so-called light curves of the photosynthetic rate and irradiation, which are expressed by a mathematical formula. There are several models describing the dependence between photosynthetic rate and irradiation *e.g.* by Vollenweider (1965) and Platt *et al.* (1977). However, as far as the Baltic Sea is concerned, the equation proposed by Steele (1962) for the North Sea fits best (Renk *et al.*, 1983):

$$P_h = AN\,\frac{E}{E_o}\,\exp\left(1 - \frac{E}{E_o}\right), \tag{2}$$

where

P_h – photosynthetic rate expressed as a ratio of primary production over one hour to chlorophyll concentration,

E – irradiation [kJ m^{-2} h^{-1}],

[1] The assimilation number is sometimes defined as the daily primary production per chlorophyll unit [mgC mgChl^{-1} day^{-1}] (Bannister and Laws, 1980; Woźniak, 1987; Woźniak *et al.*, 1989).

AN and E_o – constants; AN [mgC mgChl^{-1} h^{-1}], E_o [kJ m^{-2} h^{-1}].

The physical significance of AN and E_o is as follows:

E_o is the irradiation at which the photosynthetic rate is highest (the so-called saturation value); it can be assumed to be the optimum irradiation for photosynthesis,

AN is the maximum photosynthetic rate, *i.e.* the assimilation number. AN corresponds to the real maximum of function $P_h = f$ (irradiation), which, in contrast to AN_{exp}, describes the photosynthetic rate at the assumed optimum irradiation.

4. Results

An example of a light curve for phytoplankton in water collected at the depth of 2.5 m is given in Fig. 1, while the values of the constants E_o and AN, determined using the least square method (at a correlation coefficient of $k > 0.95$), and of AN_{exp}, calculated directly from the ratio of primary production to chlorophyll, are presented in Tab. 1. Analysis of the data shows that $AN \cong AN_{\mathrm{exp}}$ at a correlation coefficient no lower than 0.95.

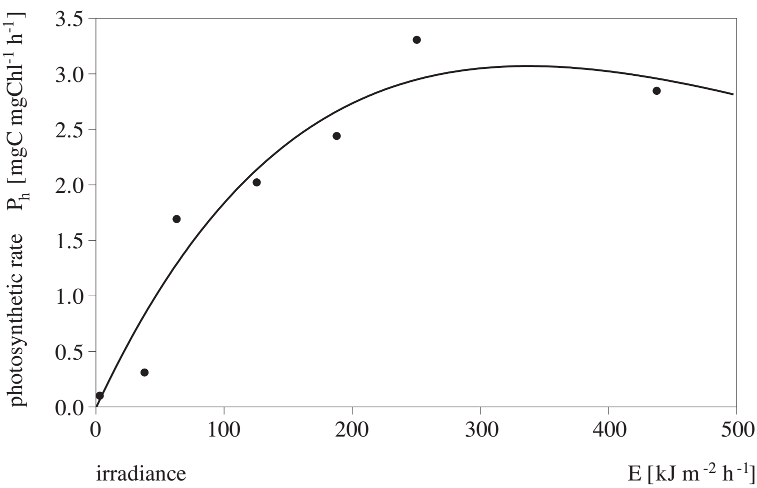


Fig. 1. Relationship between photosynthetic rate [mgC mgChl^{-1} h^{-1}] and irradiation [kJ m^{-2} h^{-1}]

It can be concluded from the table that the assimilation numbers and average irradiations, optimum for photosynthesis, displayed seasonal variability. Assimilation numbers (6 mgC mgChl^{-1} h^{-1}) were highest in summer, while the lowest, winter values were no greater than 2 mgC mgChl^{-1} h^{-1}. It can be seen from Tab. 1 that for the open Baltic waters, that is for stations P1, P5 and P140, the values of AN and E_o increase with increasing water

Table 1. Coefficients of eq. (1) expressing the interdependence between photosynthetic rate and irradiation

Date	Station	AN [mgC mgChl^{-1} h^{-1}]	AN_{exp}	E_o [kJ m^{-2} h^{-1}]	r Correlation coefficient
24.09.1995	P1	5.54	4.69	662.56	0.978
25.09.1995	P140	3.84	3.00	607.45	0.990
25.09.1995	P5	4.17	4.03	448.79	0.985
16.04.1996	P1	1.69	1.71	218.09	0.989
17.04.1996	P5	1.59	1.90	260.31	0.967
18.04.1996	P140	1.96	1.49	294.68	0.990
04.08.1996	P1	6.12	6.53	451.10	0.962
05.08.1996	P140	3.18	3.18	348.70	0.974
06.08.1996	P5	4.66	4.81	481.11	0.964
25.09.1996	P1	4.82	5.58	400.51	0.951
26.09.1996	P140	4.25	4.33	261.74	0.995
27.09.1996	P5	4.38	5.62	276.99	0.895
21.03.1997	P1	1.83	1.95	262.04	0.984
22.03.1997	P140	1.84	2.04	261.10	0.948
23.03.1997	P5	2.88	2.98	336.19	0.994
24.03.1997	SF11	2.54	2.49	360.28	0.995
25.03.1997	SF16	3.61	3.93	216.94	0.979
23.04.1997	P1	2.46	2.47	382.90	0.978
25.04.1997	B13	3.76	3.52	358.96	0.984
26.04.1997	P5	3.08	3.32	337.04	0.963
27.04.1997	P140	2.55	2.66	261.76	0.943
06.06.1997	P1	4.84	4.25	672.94	0.944
07.06.1997	P140	3.75	4.01	427.47	0.986
08.06.1997	P5	3.96	3.65	430.76	0.997
09.06.1997	B13	3.15	3.02	349.40	0.997
11.06.1997	P1	2.85	3.19	344.69	0.983
26.09.1997	P1	6.81	6.61	472.84	0.985
08.11.1997	P1	3.98	3.96	348.96	0.985
09.11.1997	P140	3.40	3.19	385.22	0.998
10.11.1997	P5	4.18	4.02	410.44	0.996
11.11.1997	ZP38	1.85	1.69	332.34	0.987
11.11.1997	ZP31	2.12	1.96	248.14	0.990
25.01.1998	SF	2.02	2.01	242.84	0.95
25.01.1998	P5	1.99	1.86	235.17	0.94
02.02.1998	P1	1.80	1.77	273.20	0.98
05.02.1998	P140	1.80	1.72	228.32	0.80
average		3.31	3.31	358.22	

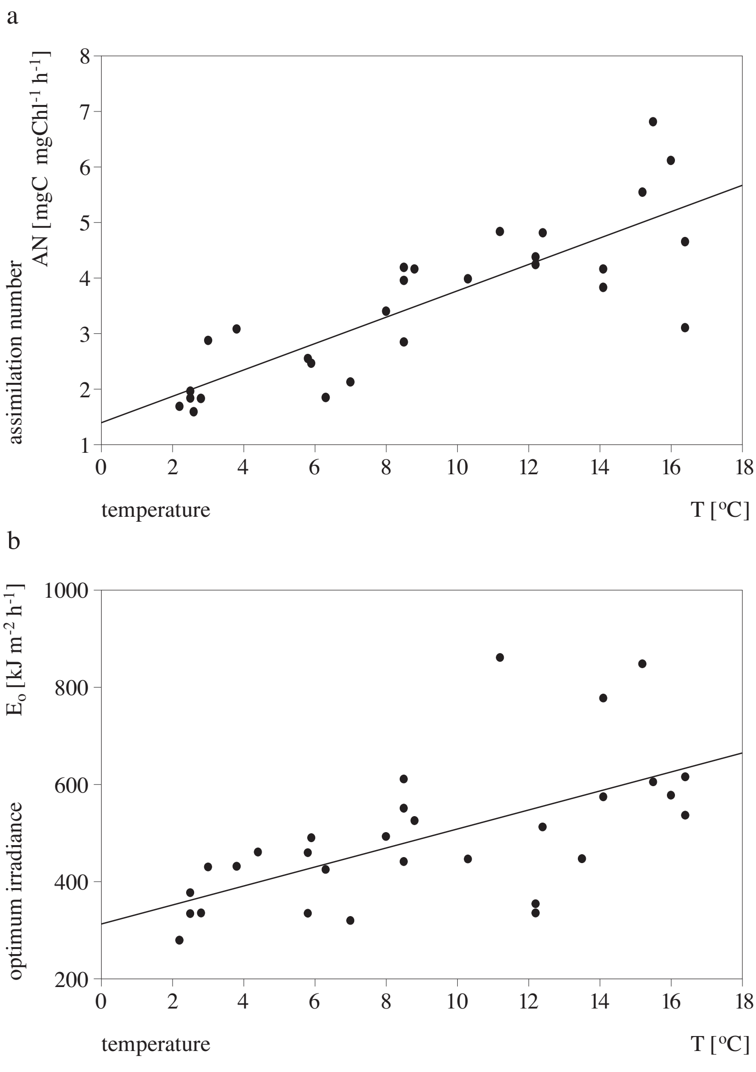


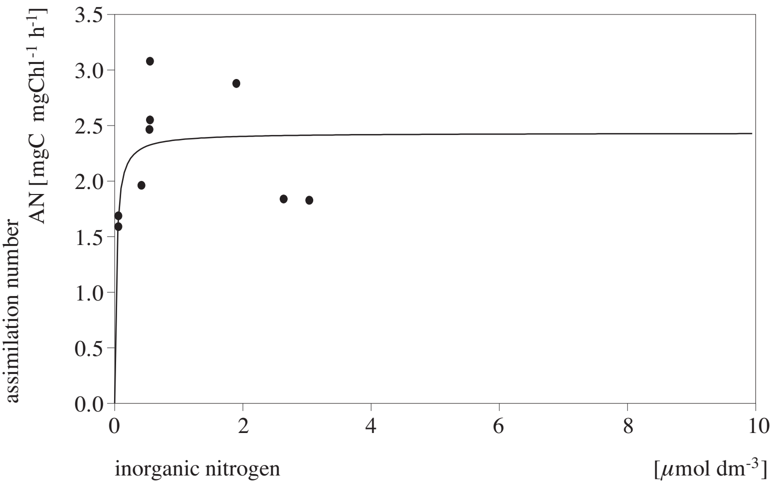
Fig. 2. Relationship between assimilation number [mgC mgChl^{-1} h^{-1}] (a), coefficient E (b) and temperature T [°C] in the southern Baltic

temperature T (Fig. 2). The regression lines in Fig. 2 are described by the following formulas:

$$E_{ot} = 313.64 + 19.56\,T, \tag{3}$$

$$AN_t = 1.385 + 0.238\,T. \tag{4}$$

The scatter of the experimental points around the regression lines (in particular at higher temperatures) suggests that AN and E_o also depend on some other environmental factors. This inclined the authors to a



b

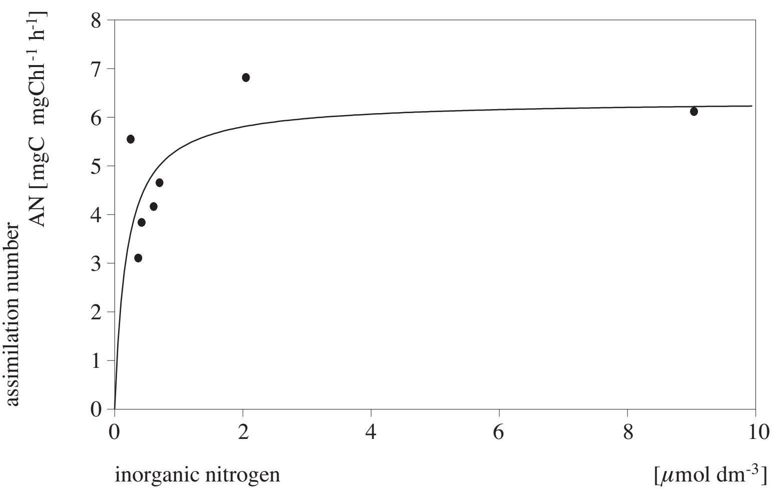


Fig. 3. Relationship between assimilation number [mgC mgChl^{-1} h^{-1}] and inorganic nitrogen $\Sigma\,(NO_3+NO_2+NH_4)$ [μmol dm^{-3}] in seawater. The upper figure (a) refers to the temperature range 4–6°C, the lower figure (b) to 14–17°C

analyse the interdependence between the assimilation numbers and nutrient concentrations, in particular phosphate, nitrate, ammonia and the total $(NO_3+NO_2+NH_4)$ concentrations. The open waters of the Baltic Sea did not reveal any statistically significant correlation between AN and phosphate concentrations; the same applies to E_o. In contrast, there was a correlation between the assimilation numbers and the total inorganic nitrogen $(NO_3+NO_2+NH_4)$. The quantitative dependence between the latter parameters was tested by the Michaelis-Mentens equation describing the kinetics of nutrient uptake (Dugdale, 1967; Eppley and Coatsworth, 1968; Eppley *et al.*, 1969):

$$AN = AN_o \frac{X}{k + X}, \tag{5}$$

where

AN – assimilation number,

AN_o – assimilation number at very high nutrient concentrations (saturation value of the assimilation number),

k – half-saturation Michaelis-Menten constant – concentration of limiting nutrient at which $AN = AN_o/2$,

X – concentration of the nutrient limiting primary production.

An example of the dependence between the assimilation number and the inorganic nitrogen concentration for two temperature ranges (4–6°C and 14–17°C) is illustrated in Fig. 3. Tab. 2 shows the coefficients AN_o and k of the Michaelis-Menten equation determined for various temperature ranges.

Table 2. Coefficients of the eq. (2) – half-saturation constans for nitrogen uptake by phytoplankton

Temperature range [°C]	AN_o	k
14–17	6.349	0.188
12–14	4.377	0.008
10–12	2.897	0.005
8–10	2.764	0.012
6–8	2.433	0.023
4–6	2.433	0.026
2–4	2.362	0.024

Like temperature, assimilation numbers are subject to seasonal fluctuation: these are highest in summer and lowest in winter. The seasonal variability of average assimilation numbers are presented in Fig. 4.

Regional differences in assimilation numbers were also observed: as a rule, the assimilation numbers were highest in the Gdańsk Deep, lower in the Bornholm Deep and lowest in the Gotland Deep (Tab. 1). These differences may be due to the different environmental conditions at the stations in question, in particular as regards temperature and nutrient concentrations.

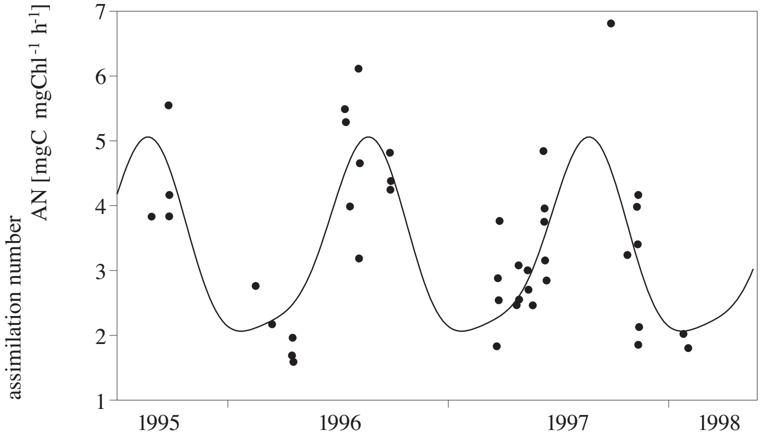


Fig. 4. Seasonal variability in the assimilation number in the southern Baltic

5. Discussion

A clearer picture of the seasonal variability of assimilation numbers can be obtained by applying the average values determined during particular cruises (arithmetic means of the results from stations P1, P5 and P140). The seasonal variability of the average assimilation number in the southern Baltic was approximated by a curve described using a trigonometric series (Renk, 1989):

$$AN = 3.544 - 1.828 \sin(2\pi\, x + 0.791) + 0.318 \sin(4\pi\, x + 0.880), \quad (6)$$

where

x – date expressed by a decimal fraction of a calendar year.

Coefficients of the series were calculated with the least squares method. The average assimilation numbers determined for particular cruises, as well as the curve corresponding to eq. (5), are presented in Fig. 5. The above equation allows the probable assimilation number in the Baltic Sea to be forecast for any day of the year.

As can be seen from Fig. 5, the average assimilation number in the open waters of southern Baltic is equal to 3.5 mgC mgChl^{-1} h^{-1}, while the average amplitude of seasonal changes is 1.8 mgC mgChl^{-1} h^{-1}. Tab. 1 shows the arithmetic mean of all the measurements – 3.31 mgC mgChl^{-1} h^{-1}. Both these values are slightly higher than the arithmetic mean determined for the Pomeranian Bay (3.18 mgC mgChl^{-1} h^{-1}), (Renk *et al.*, in preparation). It is generally thought that both primary production and chlorophyll concentration in the Bay waters are higher as compared to values in open-sea waters. This statement cannot be directly referred to the assimilation number, which is the ratio of primary production to chlorophyll. In Tab. 3,

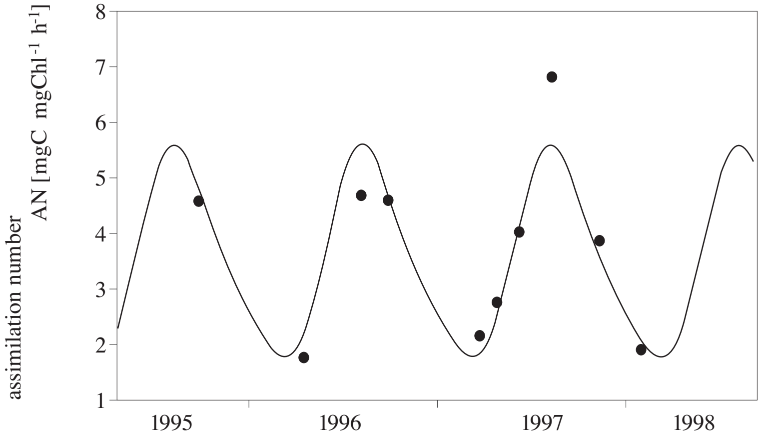


Fig. 5. Seasonal variations in the assimilation number [mgC mgChl^{-1} h^{-1}] in the southern Baltic. The dots indicate the average values of three measurements made at stations P1, P5, P140. The curve corresponds to eq. (5)

Table 3. Average assimilation numbers in particular seasons

Season	Southern Baltic		Pomeranian Bay	
	AN	SD	*AN*	SD
spring	2.73	0.95	2.46	0.46
summer	4.90	1.05	3.99	1.31
autumn	3.85	0.41	3.24	0.48
winter	2.10	0.43	2.17	0.49
average	3.31		3.18	

SD – standard deviation.

assimilation numbers from the open Baltic waters are compared with those from the Pomeranian Bay. This shows that the assimilation numbers in offshore Baltic waters in spring, summer and autumn are higher than in the Pomeranian Bay, but that in winter the assimilation numbers of both regions are almost the same. The amplitudes of the seasonal variations of assimilation numbers in open Baltic waters are greater than those from the Pomeranian Bay. Standard deviations (SD) of assimilation numbers are highest in summer, and moreover, the summer SD of assimilation numbers are higher in the Pomeranian Bay than in the open Baltic waters. This is due to the considerable differentiation of the entire Pomeranian Bay, which is strongly influenced by riverine waters (Ochocki *et al.*, in preparation;

Pastuszak *et al.*, 1996). Riverine waters, rich in nutrients, considerably affect the N:P ratio in the Pomeranian Bay and bring in substantial amounts of freshwater phytoplankton species, which at higher salinities may display reduced photosynthetic activity, and therefore lower assimilation numbers.

The interdependence between assimilation number and temperature, also observed in the Pomeranian Bay, is similar in nature to that observed in other regions (Yentsch and Lee, 1966). Within the recorded temperature ranges it can be approximately described by a linear function. However, it has been stressed in many papers that this dependence is complex and is governed by numerous environmental factors (Eppley, 1972; Li, 1980).

The N:P ratio is significant with respect to nutrient requirements in primary production. In plants the atomic N:P ratio is equal to 16:1 (Redfield *et al.*, 1963). In the open Baltic waters the N:P ratio does not usually exceed 16 (Nehring, 1982; Trzosińska *et al.*, 1989; Trzosińska, 1992), and occasionally inorganic nitrogen becomes depleted during summer, which limits primary production. The Michaelis-Menten constants for nitrogen uptake by the phytoplankton of the southern Baltic are presented in Tab. 2. In the 14–17°C temperature range, the Michaelis-Menten half-saturation constant for inorganic nitrogen $\Sigma\,(NO_2 + NO_3 + NH_4)$ is $k = 0.188$ μmol dm^{-3}. This means that at a concentration of nitrogen $k = 0.188$ the assimilation numbers drop to half their maximum values. The earlier in situ studies conducted in 1983–1993 showed that $k = 0.18$ (Renk, 1997). At lower temperatures, the value of k also falls.

In bay waters (Gulf of Gdańsk, Pomeranian Bay) the N:P ratio is subject to temporal and spatial fluctuations. The average N:P ratio in winter, and in spring is > 16, but over the growing season it drops to values below 16 (Trzosińska, 1992; Renk *et al.*, in preparation). In particular, waters close to river mouths are characterised by a higher N:P ratio as compared with the open Baltic waters (Renk *et al.*, 1976). The N:P ratio in the areas directly influenced by riverine waters is > 16, and sometimes (especially in spring) it is even in excess of 100. This means that in these cases nitrogen is in excess, and the scarcity of phosphorus may cause the latter to become the factor limiting primary production (Renk *et al.*, in preparation).

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