# Photosynthetic light curves in the Pomeranian Bay*

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## Abstract

Photosynthetic light curves at selected stations in the Pomeranian Bay were determined during four cruises undertaken in March and July 1996, and in May and October 1997. The mean assimilation numbers measured in particular seasons were as follows: spring – 2.46 mgC mgChl$^{-1}$ h$^{-1}$, summer – 3.99 mgC mgChl$^{-1}$ h$^{-1}$, autumn – 3.24 mgC mgChl$^{-1}$ h$^{-1}$ and winter – 2.17 mgC mgChl$^{-1}$ h$^{-1}$. A significant correlation was found between the assimilation number and water temperature over the entire period of study. In some seasons a dependence between the assimilation number and nutrient concentrations was also noted. Assimilation numbers in the areas adjacent to the Odra river months were higher than in the offshore zone.

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## 1. Introduction

Like other bays fed by large rivers, the Pomeranian Bay is exposed to discharges of pollutants and nutrients from land (Rybiński *et al.* 1992, Grelowski & Pastuszak 1996). Most of the nutrient loads introduced into the Baltic Sea are derived directly from land (approx. 67% of the nitrogen and 90% of the phosphorus); about 33% of the nitrogen enters as atmospheric deposition (HELCOM 1993, 1996). In Poland 80–90% of the total pollution load is discharged into the Baltic via rivers (HELCOM 1993), and 62% of the nitrogen and 46% of the phosphorus in this riverine run-off are leached from the drainage area (Rybiński *et al.* 1992). Nutrient concentrations in bays are thus higher than in open-sea waters, the difference lying primarily in the N:P ratios. These factors may exert a considerable influence on primary production. According to reports, both primary production and phytoplankton concentrations are higher in bays than in the open Baltic Sea (Renk 1991). To date, comparisons of primary production in the Pomeranian Bay and the Baltic Sea have been based on *in situ* measurements, therefore they are encumbered by a certain error arising from variability in irradiance. The results presented here refer to measurements of primary production carried out in an incubator under constant irradiance.

In recent years mathematical modelling has been applied in studies of primary production in various ecosystems. However, such an approach requires an appropriate database, which is not always available. Numerous researchers, *e.g.* Platt & Gallegos (1980), Dera (1995), and especially in the Baltic Sea by Renk (1983), Woźniak *et al.* (1989), Latała (1991a,b) and Renk & Ochocki (1998) have studied the relationship between light and the photosynthetic rate in the sea. This relationship is very complex owing to the fact that the light field in seawaters is subject to considerable diurnal and seasonal variability, and also to random fluctuations governed by hydro-meteorological conditions. Measured under natural conditions, the light-photosynthetic rate relationship can thus be relevant only to one particular region, and even then must be treated with caution. The primary production database of the Pomeranian Bay is much smaller than other such databases from elsewhere in the Baltic Sea. In order to fill the gaps in the primary production measurements, comprehensive oceanographic studies were carried out over the following periods of time: 10–20 March and 15–27 July 1996, 15–26 May and 19–27 October 1997. These studies involved the measurement of basic hydrochemical (Pastuszak *et al.* 1998) and hydrobiological parameters (Gromisz *et al.* 1999, Ochocki *et al.* 1999). Measurements of potential primary production in the Pomeranian Bay will now be discussed with reference to the effect of environmental parameters such as light, temperature and variability in nutrient concentrations on them.

## 2. Material and method

The determination of the photosynthetic light curve was based on measurements of primary production in an incubator under irradiance and temperature conditions similar to those in the natural environment, and on measurements of chlorophyll concentrations in water samples collected in the Pomeranian Bay from 2.5 m depth. The stations selected for the studies are shown in Fig. 1. A constant irradiance in the incubator of $250\,\mathrm{kJ\,m^{-2}\,h^{-1}}$ was provided by fluorescent lamps and by combinations of filters and mirrors to ensure the following scalar irradiances (PAR): 435, 186, 124, 62, 37 and $2.5\,\mathrm{kJ\,m^{-2}\,h^{-1}}$. A thermostat kept the water temperature the same as under natural conditions.

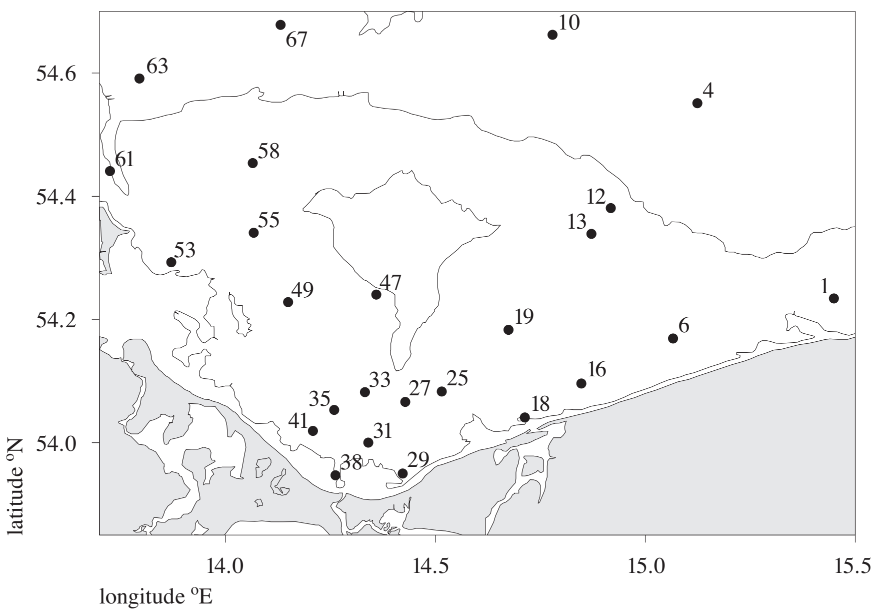


**Fig. 1.** Distribution of measuring stations

Chemical analyses were performed directly after sampling using standard BMP (Baltic Monitoring Programme) methods recommended for the Baltic Sea (Grasshoff *et al.* 1983, UNESCO 1983, BMEPC 1988). The photosynthetic intensity was determined radioisotopically (Steemann-Nielsen 1952, 1965, Aertebjerg-Nielsen & Bresta 1984) using $^{14}C$ with an activity of 150 kBq per incubated sample, the activity of phytoplankton samples after incubation being measured with a liquid scintillation counter. Inorganic carbon in water (essential for evaluating primary production) was determined by measuring the pH of the water before and after the addition of acid (0.01 N HCl in a volumetric ratio 1:4; BMEPC 1988). Chlorophyll concentrations were determined fluorimetrically by applying 24 h pigment extraction with 90% acetone solution in darkness at a temperature of *ca* 4°C (Evans *et al.* 1987).

## 3. Results and discussion

The photosynthetic rate ($P_h$) – the ratio of the primary production during one hour ($PP$) to the chlorophyll concentration (Chl) – is a basic parameter used in this paper:

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

The photosynthetic rate ($P_h$) depends on numerous environmental parameters that varied considerably over the study period, *e.g.* irradiance. The highest photosynthetic rate occurring at optimal irradiance is called the

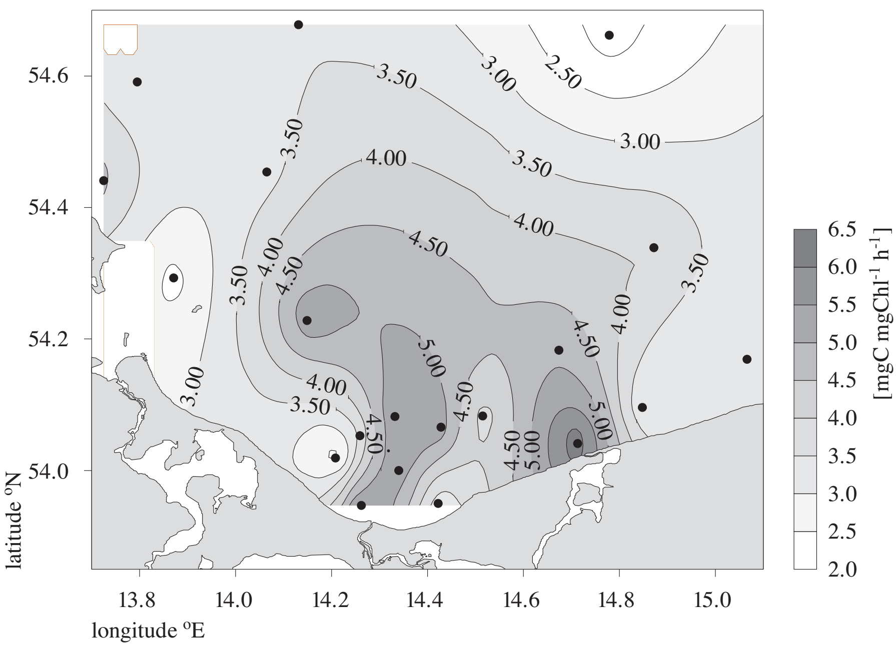


**Fig. 2.** Assimilation numbers [mgC mgChl$^{-1}$ h$^{-1}$] in the Pomeranian Bay in July 1996

**Table 1.** List of the most abundant phytoplankton species in the Pomeranian Bay

| Species | March 1996 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 4 | 29 | 27 | 12 | 63 | 55 | 47 | 41 | 18 |
| **microplankton** | | | | | | | | | |
| blue-green algae: | | | | | | | | | |
| *Aphanizomenon flos-aquae* | | | | | | | | | |
| *Gomphosphaeria* spp. | | | | | | | | | |
| *Microcystis* sp.//*Aphanothaece* sp. | | | | | | | | | |
| *Nodularia spumigena* | | | | | | | | | |
| diatoms: | | | | | | | | | |
| Centrales (*Coscinodiscus* sp., *Actinocyclus ehrenbergii*) | | | | | | | | | |
| *Cylindrotheca closterium* | | | | | | | | | |
| *Melosira arctica* | | x | x | x | x | x | x | x | x |
| Pennales (*Nitzschia* sp., *Fragilaria* sp., *Diatoma elongatum*) | | | | | | | | | |
| *Skeletonema costatum* | | | | | x | x | x | x | x |
| *S. subsalsum* | | | | | | | | | |
| green algae: | | | | | | | | | |
| *Pediastrum* (*duplex* + *boryanum*) | | | | | | | | | |
| dinoflagellates: | | | | | | | | | |
| *Peridiniella catenata* | x | | | x | | | | | x |
| **nanoplankton** | | | | | | | | | |
| diatoms: | | | | | | | | | |
| Centrales 5–10 $\mu$m (*Thallasiosira* spp.) | x | x | x | x | x | x | x | x | x |
| Centrales 10–20 $\mu$m (*Thallasiosira* spp., *Cyclotella* spp.) | | x | x | x | x | | x | x | x |
| green algae: | | | | | | | | | |
| *Monoraphidium contortum* | | | | | | | | | |
| dinoflagellates: | | | | | | | | | |
| *Katodinium rotundatum* | | | | | | | | | |
| Euglenophytes | | | | | | | | | |
| Cryptophytes | x | x | x | x | x | x | x | x | |
| Prasinophytes (*Pyramimonas* spp.) | | | | | | | | | |

| Species | July 1996 | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 10 | 4 | 1 | 38 | 29 | 31 | 33 | 27 | 25 | 35 | 41 | 49 | 53 | 58 | 61 | 67 | 63 | 6 | 13 | 19 | 18 | 16 |
| **microplankton** | | | | | | | | | | | | | | | | | | | | | | |
| blue-green algae: | | | | | | | | | | | | | | | | | | | | | | |
| *Aphanizomenon flos-aquae* | x | x | x | | | x | x | x | x | x | | x | x | x | x | x | x | | x | x | | x |
| *Gomphosphaeria* spp. | x | x | x | x | | | | | | | | | x | | | x | x | | | | | |
| *Microcystis* sp.//*Aphanothaece* sp. | | | | | x | | | x | | | | | | | | x | x | x | x | | x | |
| *Nodularia spumigena* | | | | | | | | | | | | | x | | | | | | | | | x |
| diatoms: | | | | | | | | | | | | | | | | | | | | | | |
| Centrales (*Coscinodiscus* sp., *Actinocyclus ehrenbergii*) | | | | x | | x | | | | | x | | | | | | | | | | | x |
| *Cylindrotheca closterium* | | | | | x | x | | | | x | x | x | x | | | | | x | x | x | x | x |
| *Melosira arctica* | | | | | | | | | | | | | | | | | | | | | | |
| Pennales (*Nitzschia* sp., *Fragilaria* sp., *Diatoma elongatum*) | | | | x | | | | | | | | | | | | | | | | | | |
| *Skeletonema costatum* | | | | | | | | | | | x | | | | | | | | | | | |
| *S. subsalsum* | | | | x | | | | | | | | | | | | | | | | | x | |
| green algae: | | | | | | | | | | | | | | | | | | | | | | |
| *Pediastrum* (*duplex* + *boryanum*) | | | | x | | | | | | | | | | | | | | | | | | |
| dinoflagellates: | | | | | | | | | | | | | | | | | | | | | | |
| *Peridiniella catenata* | | | | | | | | | | | | | | | | | | | | | | |
| **nanoplankton** | | | | | | | | | | | | | | | | | | | | | | |
| diatoms: | | | | | | | | | | | | | | | | | | | | | | |
| Centrales 5–10 $\mu$m (*Thallasiosira* spp.) | | | | x | | | | | | | | | | | | | | x | x | | x | |
| Centrales 10–20 $\mu$m (*Thallasiosira* spp., *Cyclotella* spp.) | | | | | | | | | | | | | | | | | | | | | | |
| green algae: | | | | | | | | | | | | | | | | | | | | | | |
| *Monoraphidium contortum* | | | | | | | | | | | | | | | | | | | | | | |
| dinoflagellates: | | | | | | | | | | | | | | | | | | | | | | |
| *Katodinium rotundatum* | | | x | x | x | x | | x | x | x | x | x | | | x | | x | x | | | x | x |
| Euglenophytes | x | | | | | | x | x | | | | | | | x | | x | | | x | | |
| Cryptophytes | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x |
| Prasinophytes (*Pyramimonas* spp.) | x | x | x | | x | x | x | x | x | x | x | x | x | x | x | x | x | | | x | | x |

| Species | May 1997 | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 38 | 29 | 27 | 31 | 33 | 18 | 13 | 35 | 49 | 53 | 58 | 67 | 10 |
| **microplankton** | | | | | | | | | | | | | |
| blue-green algae: | | | | | | | | | | | | | |
| *Aphanizomenon flos-aquae* | | | | | | | | | | | | x | x |
| *Gomphosphaeria* spp. | x | x | x | x | x | | x | x | x | x | x | | |
| *Microcystis* sp.//*Aphanothaece* sp. | | | | | x | | x | | | x | x | | |
| *Nodularia spumigena* | | | | | | | | | | | | | |
| diatoms: | | | | | | | | | | | | | |
| Centrales (*Coscinodiscus* sp., *Actinocyclus ehrenbergii*) | | | | | | x | | | | | | | |
| *Cylindrotheca closterium* | | | | | | | | | | | | | |
| *Melosira arctica* | | | | | | | | | | | | | |
| Pennales (*Nitzschia* sp., *Fragilaria* sp., *Diatoma elongatum*) | x | | | | | x | | | | | | | |
| *Skeletonema costatum* | | | | | | | | | | | | | |
| *S. subsalsum* | | | | | | | | | | | | | |
| green algae: | | | | | | | | | | | | | |
| *Pediastrum* (*duplex* + *boryanum*) | x | | x | | | | | x | | | | | |
| dinoflagellates: | | | | | | | | | | | | | |
| *Peridiniella catenata* | | | | | | | | | | | | | |
| **nanoplankton** | | | | | | | | | | | | | |
| diatoms: | | | | | | | | | | | | | |
| Centrales 5–10 $\mu$m (*Thallasiosira* spp.) | | | | | | x | | | | | | | |
| Centrales 10–20 $\mu$m (*Thallasiosira* spp., *Cyclotella* spp.) | | | | | | | | | | | | | |
| green algae: | | | | | | | | | | | | | |
| *Monoraphidium contortum* | x | x | x | x | x | x | | x | | x | | | |
| dinoflagellates: | | | | | | | | | | | | | |
| *Katodinium rotundatum* | | x | | | | | | x | | x | | x | x |
| Euglenophytes | | | | | | | | | | | | | |
| Cryptophytes | x | x | x | x | x | x | x | x | x | x | x | x | x |
| Prasinophytes (*Pyramimonas* spp.) | x | x | x | x | x | | x | x | x | x | x | x | x |

assimilation number[1] (Parsons & Takahashi 1973, Platt & Gallegos 1980). The variability in the assimilation number in the Pomeranian Bay in June 1996 is illustrated in Fig. 2, which shows that assimilation numbers are higher in the vicinity of the Świna and the Dziwna mouths, draining over 80% of the Odra (Oder) waters, than in offshore waters. As a consequence, phytoplankton production is higher in areas close to the mouths of these straits. The high chlorophyll concentrations measured in inshore waters would suggest a high phytoplankton biomass; this was indeed linked to substantial concentrations of nutrients carried by riverine waters (Pastuszak *et al.* 1996, Pastuszak *et al.* 1998). With respect to the spatial distribution of photosynthetic rate, chlorophyll and nutrient concentrations, the situation was similar in other seasons of the period investigated. Such spatial differentiation was also noted in previous years with regard to chlorophyll and nutrient concentrations, and *in situ* primary production (Renk *et al.* 1976, Renk 1992, Ochocki *et al.* 1995).

The species diversity of the phytoplankton was considerable; the dominant species are listed in Table 1. A detailed breakdown of particular phytoplankton size fractions and species compositions is given in Gromisz *et al.* (1999).

## Photosynthesis-light relationship

An example of the relationship between photosynthetic rate and scalar irradiance is given in Fig. 3; it is based on measurements made at station 27 on 16 May 1997. All the other cases are similar. Some mathematical models describing this dependence can be found in the literature, *e.g.* Vollenweider (1965), Platt & Gallegos (1980). Nevertheless, the model put forward by Steele (1962) best fits the conditions in the Pomeranian Bay:

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

where

$P_h$ – photosynthetic rate expressed as the ratio of primary production per hour to chlorophyll concentration,

$E$ – scalar irradiance [$\mathrm{kJ\,m^{-2}\,h^{-1}}$],

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

The physical significance of $AN$ and $E_o$ is as follows: $E_o$, the irradiance corresponding to the greatest photosynthetic rate (the so-called irradiance saturation), is assumed to constitute the optimal light conditions for

[1]Sometimes the assimilation number is defined as the daily primary production per chlorophyll unit [$\mathrm{mgC\,mgChl^{-1}\,day^{-1}}$] (Bannister & Laws 1980, Woźniak 1987, Woźniak *et al.* 1989).

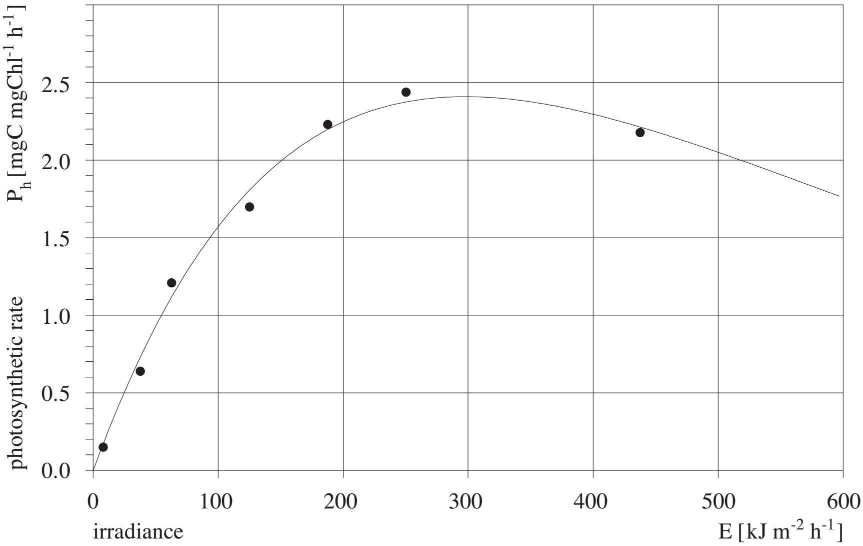


**Fig. 3.** Relationship between photosynthetic rate [mgC mgChl$^{-1}$ h$^{-1}$] and light intensity PAR [kJ m$^{-2}$ h$^{-1}$] at station ZP27 on 16 May 1997

photosynthesis, while $AN$, the assimilation number, is the maximum photosynthetic rate.

Apart from $AN$ determined from the photosynthetic light curve, there is also an assimilation number $AN_{\mathrm{exp}}$ which is the ratio of hourly primary production at optimal irradiance to chlorophyll concentration. Table 2 gives

**Table 2.** Coefficients of eq. (1) expressing the photosynthetic rate-irradiance relationship

| No. | Day | Station | $E_o$ [kJ m$^{-2}$ h$^{-1}$] | $AN$ [mgC mgChl$^{-1}$ h$^{-1}$] | $AN_{\mathrm{exp}}$ |
|---|---|---|---|---|---|
| | | | March 1996 | | |
| 1 | 10 | 4 | 413.3 | 2.93 | 3.46 |
| 2 | 12 | 29 | 328.0 | 2.27 | 2.01 |
| 3 | 14 | 27 | 250.2 | 3.06 | 3.28 |
| 4 | 15 | 12 | 321.7 | 1.99 | 2.46 |
| 5 | 16 | 63 | 185.2 | 1.98 | 2.04 |
| 6 | 17 | 55 | 225.9 | 2.04 | 1.97 |
| 7 | 18 | 47 | 246.5 | 1.82 | 1.71 |
| 8 | 19 | 41 | 177.7 | 1.66 | 1.46 |
| 9 | 20 | 18 | 259.3 | 1.77 | 1.63 |
| mean values in March | | | 257.5 | 2.17 | 2.22 |
| standard deviation | | | 72.1 | 0.50 | 0.71 |

**Table 2.** (continued)

| No. | Day | Station | $E_o$ [kJ m$^{-2}$ h$^{-1}$] | $AN$ [mgC mgChl$^{-1}$ h$^{-1}$] | $AN_{\mathrm{exp}}$ |
|---|---|---|---|---|---|
| | | | July 1996 | | |
| 10 | 15 | 10 | 190.1 | 1.76 | 2.40 |
| 11 | 16 | 4 | 381.5 | 3.01 | 3.27 |
| 12 | 16 | 1 | 389.9 | 5.64 | 6.43 |
| 13 | 17 | 38 | 574.7 | 5.70 | 5.21 |
| 14 | 17 | 29 | 213.4 | 3.08 | 4.58 |
| 15 | 18 | 31 | 450.1 | 5.32 | 5.80 |
| 16 | 18 | 33 | 273.0 | 5.46 | 5.92 |
| 17 | 19 | 27 | 353.6 | 5.25 | 4.99 |
| 18 | 19 | 25 | 494.2 | 3.76 | 3.27 |
| 19 | 20 | 35 | 349.3 | 3.60 | 3.66 |
| 20 | 20 | 41 | 209.2 | 2.25 | 3.18 |
| 21 | 21 | 49 | 476.9 | 5.36 | 5.38 |
| 22 | 22 | 53 | 307.0 | 2.33 | 3.02 |
| 23 | 23 | 58 | 422.7 | 3.30 | 3.55 |
| 24 | 23 | 61 | 499.8 | 4.16 | 4.38 |
| 25 | 24 | 67 | 293.9 | 3.44 | 3.70 |
| 26 | 24 | 63 | 248.0 | 3.06 | 4.14 |
| 27 | 25 | 6 | 203.9 | 2.97 | 3.77 |
| 28 | 25 | 13 | 475.0 | 4.04 | 4.70 |
| 29 | 26 | 19 | 431.1 | 4.89 | 5.11 |
| 30 | 27 | 18 | 430.2 | 6.37 | 6.89 |
| 31 | 27 | 16 | 239.5 | 2.97 | 4.39 |
| mean values in July | | | 359.4 | 3.99 | 4.44 |
| standard deviation | | | 114.1 | 1.31 | 1.18 |
| | | | May 1997 | | |
| 32 | 15 | 38 | 357.3 | 3.13 | 3.06 |
| 33 | 15 | 29 | 311.4 | 2.12 | 2.07 |
| 34 | 16 | 27 | 297.6 | 2.41 | 2.44 |
| 35 | 17 | 31 | 278.9 | 2.13 | 2.19 |
| 36 | 17 | 33 | 264.9 | 1.70 | 1.65 |
| 37 | 18 | 18 | 348.7 | 2.79 | 2.62 |
| 38 | 20 | 13 | 331.0 | 2.17 | 1.98 |
| 39 | 21 | 35 | 247.0 | 2.15 | 1.91 |
| 40 | 22 | 49 | 285.8 | 2.86 | 2.69 |
| 41 | 23 | 53 | 359.2 | 2.14 | 2.08 |
| 42 | 24 | 58 | 336.1 | 2.80 | 2.69 |
| 43 | 25 | 67 | 318.5 | 3.21 | 3.12 |
| 44 | 26 | 10 | 302.2 | 2.41 | 2.29 |
| mean values in May | | | 311.2 | 2.46 | 2.37 |
| standard deviation | | | 35.4 | 0.46 | 0.45 |

**Table 2.** (continued)

| No. | Day | Station | $E_o$ [kJ m$^{-2}$ h$^{-1}$] | $AN$ [mgC mgChl$^{-1}$ h$^{-1}$] | $AN_{\mathrm{exp}}$ |
|---|---|---|---|---|---|
| | | | October 1997 | | |
| 45 | 19 | 38 | 501.5 | 3.66 | 3.41 |
| 46 | 19 | 29 | 450.1 | 3.14 | 2.93 |
| 47 | 20 | 31 | 380.0 | 3.52 | 3.65 |
| 48 | 21 | 27 | 414.8 | 3.58 | 3.27 |
| 49 | 22 | 41 | 487.0 | 3.49 | 3.07 |
| 50 | 23 | 49 | 500.1 | 4.17 | 3.40 |
| 51 | 24 | 61 | 348.7 | 3.04 | 3.11 |
| 52 | 24 | 58 | 354.1 | 2.81 | 2.66 |
| 53 | 25 | 63 | 349.2 | 2.62 | 2.42 |
| 54 | 25 | 67 | 335.6 | 3.27 | 3.12 |
| 55 | 26 | 4 | 422.3 | 3.43 | 3.15 |
| 56 | 26 | 1 | 378.4 | 2.93 | 2.75 |
| 57 | 27 | 13 | 363.7 | 2.43 | 2.43 |
| mean values in October | | | 422.0 | 3.24 | 3.03 |
| standard deviation | | | 69.6 | 0.48 | 0.38 |

values of $E_o$ and $AN$, determined by the least squares method (correlation coefficient $\mathrm{k} > 0.95$), and of $AN_{\mathrm{exp}}$, calculated directly from the primary production-to-chlorophyll ratio. Analysis of the data set indicates that

$$AN \cong AN_{\mathrm{exp}}$$

at a correlation coefficient of no less than 0.95.

It can be concluded from this table that average assimilation numbers and the average optimal irradiance for photosynthesis underwent seasonal changes, values being highest in summer and lowest in winter.

## Photosynthesis – temperature relationship

The relationship between assimilation numbers and temperature in oceanic waters is described *e.g.* by Eppley (1972). It is not the object of the present paper to scrutinise the complexity of this phenomenon or any of the limitations to which its evaluation is subject (Li 1980, Latała 1991b). We would, however, like to present the outcome of our calculations; the dependence between the assimilation number and temperature is shown in Fig 4. The data set in this figure encompasses all the measurements of assimilation number, regardless of season. The relationship is

$$AN_T = 1.765 + 0.138\,T \tag{2}$$

where $AN_T$ is the assimilation number at temperature $T$ [°C].

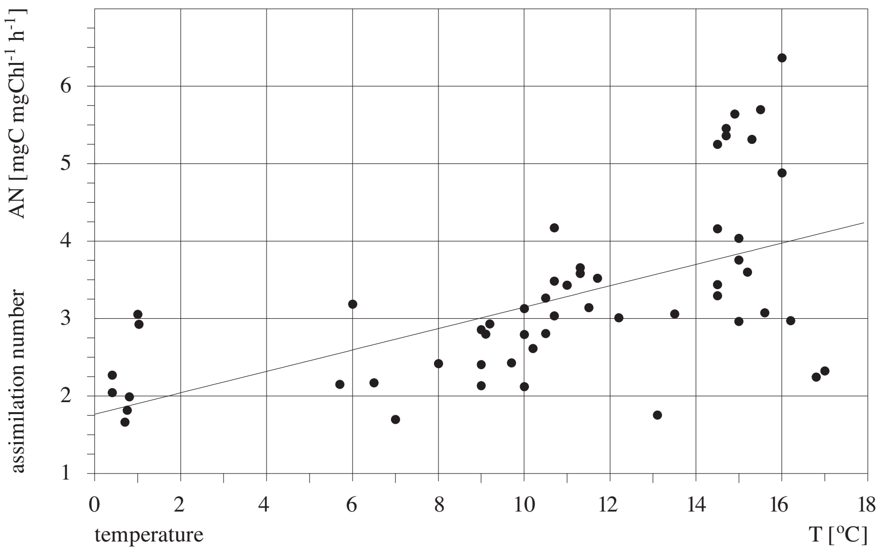


**Fig. 4.** Relationship between assimilation number [mgC mgChl$^{-1}$ h$^{-1}$] and temperature

**Table 3.** Dependence of assimilation number on temperature for various temperature ranges

| Period of cruises | Regression equations | Temperature [°C] | Mean $AN$* | Mean N:P |
|---|---|---|---|---|
| 10–20 March 1996 | $AN_T = 1.40+1.02\,T$ | 0.4–1 | 2.17 | 34.83 |
| 15–27 July 1996 | $AN_T = 2.00+0.13\,T$ | 12.2–17 | 3.99 | 2.94 |
| 15–26 May 1997 | $AN_T = 2.05+0.05\,T$ | 5.7–10 | 2.46 | 207.7 |
| 19–27 October 1997 | $AN_T = -1.00+0.40\,T$ | 9.2–11.7 | 3.24 | 3.77 |

* in [mgC mgChl$^{-1}$ h$^{-1}$]

The same dependence can be calculated with greater precision for particular cruises; Table 3 gives the regression coefficients. The seasonal measurements indicate that a temperature rise was accompanied by an increase in the irradiance at which photosynthetic saturation was reached.

Any variability in the mean assimilation number during particular cruises, and in the dependence of assimilation number on temperature may have arisen from the variable phytoplankton composition in the seasons studied. This is confirmed by literature findings (Ryther 1956, Li 1980, Latała 1991a,b).

## Photosynthesis – nutrient concentration relationship

The average nutrient concentrations (at the same depth at which photosynthesis was measured), their standard deviations (SD) and extreme values are set out in Table 4. Standard deviations of nutrient concentrations calculated for all the cruises usually exceeded the average values. Nutrient concentrations varied during the study period: they were around the detection limit in summer but very high in winter (March). Low nutrient concentrations were accompanied by low primary production (lowest $AN$); the converse was true in June. Table 5 lists the average nutrient concentrations for particular cruises. Nutrient concentrations are subject not only to seasonal variability but also to random fluctuations governed by the outflow of the Odra, and also by meteorological conditions, which play a key role in the transport of water masses in the Pomeranian Bay (Pastuszak *et al.* 1996, Siegel *et al.* 1996). Despite great spatial variability in the nutrient concentrations in the Pomeranian Bay, the highest values are always found near the mouths of the straits draining water from the Szczecin Lagoon,

**Table 4.** Average and extreme nutrient concentrations recorded in 1996–1997 in the Pomeranian Bay

| Parameter | Mean | SD | Maximum | Minimum |
|---|---|---|---|---|
| phosphates [mmol m$^{-3}$] | 0.22 | 0.25 | 0.95 | 0 |
| nitrates [mmol m$^{-3}$] | 2.53 | 5.04 | 22.6 | 0 |
| ammonia [mmol m$^{-3}$] | 0.65 | 1.30 | 6.90 | 0 |
| $\Sigma\,(NO_2 + NO_3 + NH_4)$ [mmol m$^{-3}$] | 3.34 | 6.42 | 28.2 | 0 |
| $AN$ [mgC mgChl$^{-1}$ h$^{-1}$] | 3.18 | 1.15 | 6.37 | 1.66 |
| $AN_{\rm exp}$ [mgC mgChl$^{-1}$ h$^{-1}$] | 3.30 | 1.26 | 6.89 | 1.46 |
| optimal irradiance [kJ m$^{-2}$ h$^{-1}$] | 346.6 | 99.4 | 574.7 | 177.7 |

**Table 5.** Average nutrient concentrations in particular periods [mmol m$^{-3}$]

| Period of cruises | $AN$* | | $NO_3$ | | $NH_4$ | | Nitrogen | | $PO_4$ | |
|---|---|---|---|---|---|---|---|---|---|---|
| | mean | SD | mean | SD | mean | SD | mean | SD | mean | SD |
| 10–20 March 1996 | 2.17 | 0.49 | 13.73 | 6.84 | 2.98 | 2.36 | 17.59 | 8.94 | 0.45 | 0.13 |
| 15–27 July 1996 | 3.99 | 1.31 | 0.16 | 0.53 | 0.21 | 0.69 | 0.39 | 1.26 | 0.11 | 0.19 |
| 15–26 May 1997 | 2.46 | 0.46 | 2.30 | 2.24 | 0.21 | 0.12 | 2.60 | 2.30 | 0.06 | 0.07 |
| 19–27 October 1997 | 3.24 | 0.48 | 1.18 | 1.96 | 0.66 | 0.70 | 1.94 | 2.57 | 0.39 | 0.30 |

* in [mgC mgChl$^{-1}$ h$^{-1}$],
SD – standard deviation.

part of the Odra estuary. Variability in nutrient concentrations between particular stations in the Bay are quite substantial and standard deviations are comparable with average values.

The N:P ratio is an important characteristic of the environment: according to Redfield *et al.* (1963) the atomic ratio of these elements in phytoplankton is 16:1. The N:P ratio in open Baltic water does not usually exceed 16 (Renk 1983, Trzosińska 1992), while in the Pomeranian Bay it displays temporal as well as spatial variability. The average N:P ratio in winter and particularly in spring is much higher than 16 (Table 3), while during the growing season it drops to well below 16. The inshore waters are characterised by a much higher N:P ratio as compared with the offshore zone. This feature had been observed earlier in the Pomeranian Bay and the Gulf of Gdańsk (Renk *et al.* 1976, Trzosińska *et al.* 1989).

Both average assimilation numbers and nutrient concentrations display evident seasonal variability, so it is interesting to discover which of the nutrients could play a decisive limiting role with respect to carbon assimilation, and thus phytoplankton production. In Baltic waters the N:P ratio is $< 16$; thus nitrogen is used up earlier than phosphorus (Sen Gupta 1972, Renk *et al.* 1992). In the Pomeranian Bay, by contrast, particularly in areas adjacent to the outlets of the straits, N:P is $> 16$, and sometimes (in spring) this figure is even higher than 100. In these areas, therefore, nitrogen is in excess and phosphorus may well be the factor limiting primary production.

In order to substantiate this suggestion, several analyses demonstrating the interdependence between assimilation number and nitrate, nitrite, N-inorg. (sum of $NO_3 + NO_2 + NH_4$), and phosphate were performed, and to that end the Michaelis-Menten equation was invoked (Dugdale 1967, Eppley *et al.* 1968, MacIsaac & Dugdale 1969):

$$AN = AN_o \frac{x}{k_s + x}, \tag{3}$$

where

$AN$ – assimilation number [$\mathrm{mgC\,mgChl^{-1}\,h^{-1}}$],

$AN_o$ – assimilation number at very high nutrient concentrations (no limitation of primary production),

$x$ – nutrient concentration,

$k_s$ – nutrient concentration at which assimilation number equals $\frac{AN_o}{2}$.

The dependence between the assimilation numbers and phosphate concentrations described by the Michaelis-Menten equation is illustrated in Fig. 5 for the May and October 1997 data. The coefficients in eq. (3), calculated by the least squares method, indicate that in the case of nutrient depletion

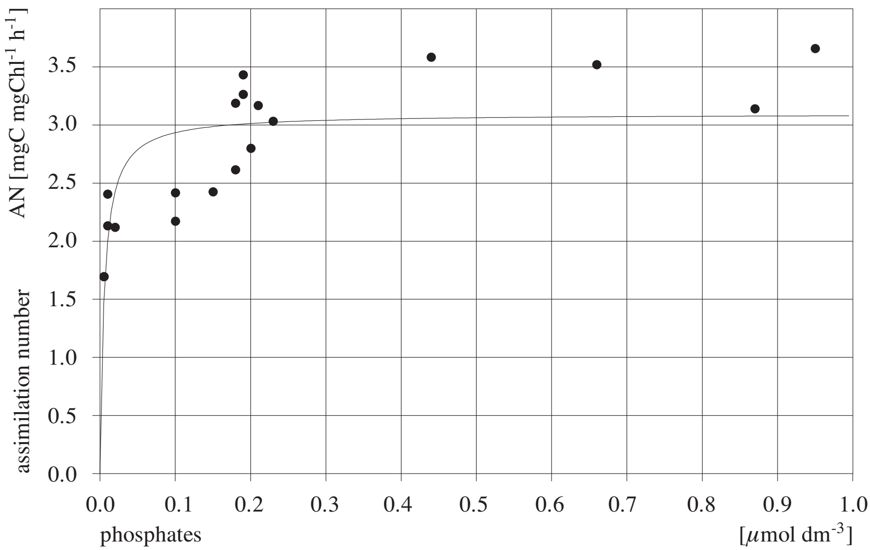


**Fig. 5.** Relationship between assimilation number [mgC mgChl$^{-1}$ h$^{-1}$] and phosphate concentrations [$\mu$mol dm$^{-3}$] in the Pomeranian Bay in May and October 1997

the assimilation numbers do not begin to decrease visibly before phosphate reaches concentrations $< 0.0055$ mmol m$^{-3}$. Assimilation numbers do not depend on higher phosphate concentrations (as was demonstrated in our studies) and oscillate around the average of 3.097 mgC mgChl$^{-1}$ h$^{-1}$. In the other cases, the dependence described by the Michaelis-Menten equation displays a stronger correlation.

Since to the fact that assimilation numbers are temperature-dependent, it seems reasonable to show the relationship between the assimilation number and phosphate concentration for narrower temperature ranges; Fig. 6 illustrates such a dependence for an incubation temperature of $> 11°$C. Table 6 shows the calculated coefficients of the Michaelis-Menten equation for the temperature ranges $t < 10°$C, $10°\text{C} < t < 14°$C and $t > 14°$C. It emerges from Tables 5 and 6 that the coefficients $k_s$ for phosphorus are much lower than the average phosphate concentrations usually recorded in the Pomeranian Bay. This suggests that only in some cases, most often in spring, does some limitation of primary reduction due to phosphorus deficiency occur.

When the N:P ratio exceeded 16, *i.e.* in March 1996 and May 1997, there was no correlation between assimilation numbers and concentrations of inorganic compounds of nitrogen or their sum. In July 1996 and October 1997 the N:P ratio was on average $< 16$ and for these periods the correlation

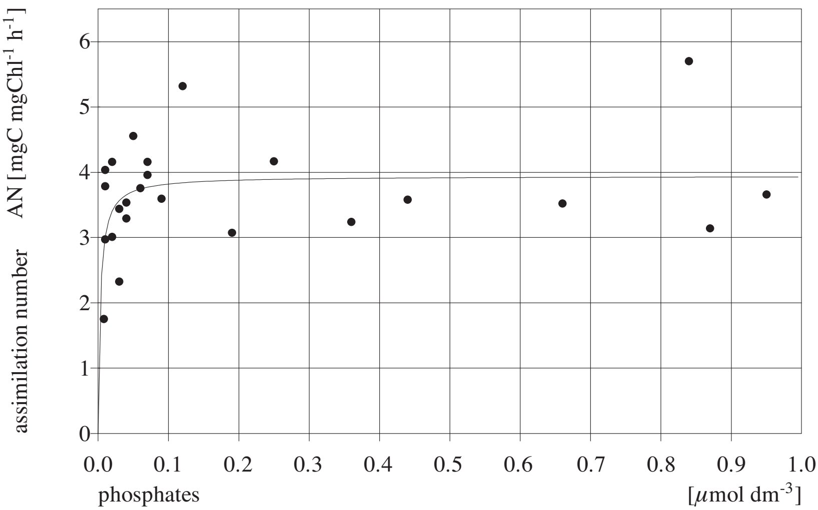


**Fig. 6.** Relationship between assimilation number [mgC mgChl$^{-1}$ h$^{-1}$] and phosphate concentrations [$\mu$mol dm$^{-3}$] in the Pomeranian Bay at incubation temperature $> 11°$C

between assimilation numbers and ammonia concentrations was significant (Table 6). A significant correlation was also noted between AN and the sum of inorganic nitrogen in October 1997 (Fig. 7). At that time, ammonia was

**Table 6.** Coefficients of the Michaelis-Menten equation expressing the interdependence between assimilation numbers and nutrient concentrations

| Parameter | Temperature [°C] | Period of observation | $AN_o$* | $k_s$** | Mean N:P |
|---|---|---|---|---|---|
| $PO_4$ | 0.4–1 | March 1996 | 2.42 | 0.025 | 34.8 |
| $PO_4$ | 12.2–17 | July 1996 | 4.37 | 0.0051 | 2.94 |
| $PO_4$ | 5.7–10 | May 1997 | 2.58 | 0.0006 | 207.7 |
| $PO_4$ | 10.2–11.7 | October 1997 | 3.72 | 0.039 | 3.77 |
| $PO_4$ | $t > 14$ | 1996–1997 | 4.66 | 0.0032 | >15 |
| $PO_4$ | $10 < t < 14$ | 1996–1997 | 3.36 | 0.0023 | >15 |
| $PO_4$ | $t < 10$ | 1996–1997 | 3.35 | 0.0415 | >15 |
| $NH_4$ | 12.2–17 | July 1996 | 4.29 | 0.0019 | |
| $NH_4$ | 10.2–11.7 | October 1997 | 3.34 | 0.011 | |
| nitrogen compounds | 10.2–11.7 | October 1997 | 3.75 | 0.113 | |

* in [mgC mgChl$^{-1}$ h$^{-1}$],
** in [$\mu$gat dcm$^{-3}$].

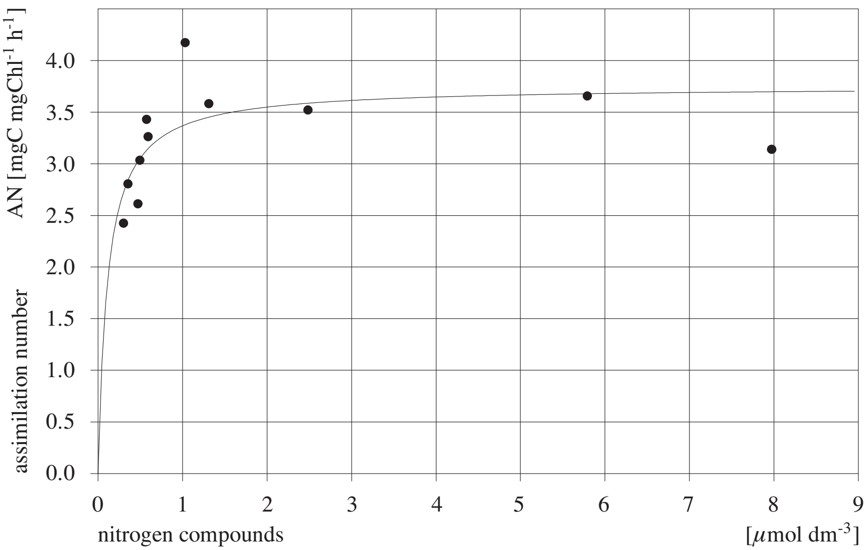


**Fig. 7.** Relationship between assimilation number [$mgC\,mgChl^{-1}\,h^{-1}$] and concentrations of inorganic nitrogen compounds [$\Sigma\,(NO_2 + NO_3 + NH_4)$] [$\mu mol\,dm^{-3}$] in the Pomeranian Bay in October 1997

the parameter limiting photosynthesis. The situation observed in summer and autumn in the Pomeranian Bay is similar to that in the open Baltic waters after the spring phytoplankton bloom. The Bay and the Baltic display similarities, particularly in summer and autumn when nitrogen compounds are the factor limiting photosynthesis (Graneli *et al.* 1990, Renk *et al.* 1992). In late autumn and in winter intense water mixing in the isohaline layer of open waters leads to enrichment of the euphotic layer with nitrogen compounds. By contrast, the shallow areas of the Pomeranian Bay are under the impact of outflowing riverine waters rich in nitrogen compounds, nitrates in particular (Pastuszak *et al.* 1998).

## 4. Conclusions

- The average assimilation number for the Pomeranian Bay was 3.18 $mgC\,mgChl^{-1}\,h^{-1}$ and its variability coefficient was 36%.
- The assimilation numbers displayed distinct seasonal variability and their average values for particular seasons were: spring – 2.46 $mgC\,mgChl^{-1}\,h^{-1}$, summer – 3.99 $mgC\,mgChl^{-1}\,h^{-1}$, autumn – 3.24 $mgC\,mgChl^{-1}\,h^{-1}$, and winter – 2.17 $mgC\,mgChl^{-1}\,h^{-1}$.

- The average irradiance, optimal for photosynthesis in the Pomeranian Bay, was estimated at around 311 kJ m$^{-2}$ h$^{-1}$. This figure was lower in winter but higher in summer and autumn.
- Assimilation numbers were found to be temperature-dependent. The assimilation number rises with increasing water temperature.
- Nutrient concentrations recorded during cruises were usually higher than the value of $k_s$ at which primary production drops to half its maximum value.
- No significant correlation between inorganic nitrogen compounds and assimilation numbers were found in winter or spring in the Pomeranian Bay. In autumn, when N:P ratios are low, assimilation numbers dropped to half their maximum values at ammonia concentrations of around 0.01 mmol m$^{-3}$.

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