In situ and *simulated in situ* primary production in the Gulf of Gdańsk

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Henryk Renk
Stanisław Ochocki
Sławomir Kurzyk
Sea Fisheries Institute,
H. Kołłątaja 1, PL–81–332, Gdynia, Poland;
e-mail: sochocki@mir.gdynia.pl

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Abstract

The method discussed in this article allows the *simulated in situ* primary production in the southern Baltic to be evaluated. To estimate the daily primary production at a given field station, the following parameters have to be measured: the coefficients AN and E_s (constants from the photosynthesis-light curve for phytoplankton), and the scalar irradiance attenuation coefficient (k), chlorophyll *a* concentration (Chl) and daily irradiation just below the sea surface (PAR). The results of *simulated in situ* primary production are in good agreement with the *in situ* measurements.

1. Introduction

Estimating the annual phytoplankton production in seas and oceans is not an easy task, particularly because of the limited number of possible measurements in time and space. Traditional oxygen and isotopic methods of measuring primary production require rather long *in situ* incubations, for example, a minimum of four hours in the case of the ^{14}C method. The additional preparatory operations may take up to two hours; therefore, conducting more than one measurement at one station per day is not possible (BMEPC 1988). This is because the daily *in situ* primary production should be measured around noon, when the irradiance usually reaches its maximum. Thus, the search for ways to obtain a higher frequency of measurements of the photosynthetic rate in seas continues (Li & Maestrini 1993). The search covers both well-tried methods (Lohrenz 1993, Tilzer *et al.* 1993) and recently introduced ones employing physical parameters, *e.g.* fluorescence, which can be measured quickly and easily, often with the use of remotely controlled electronic devices (Baretta *et al.* 1995) or satellite sensing systems (Sathyendranath & Platt 1993). But for now, the existing reliable methods have to suffice. They will still be used for a long time to come, particularly as a standard or reference, and to follow long-term changes in production.

At present, the possibilities of reducing the time needed to carry out a measurement are limited. With regard to the incubation method, the time can be reduced twofold, *i.e.* to two hours (Aertebjerg Nielsen & Bresta 1984), and if artificial light is used to maintain constant saturation irradiance, the measurement can be performed at any time of the day. Moreover, the reduced time spent by a boat at a sampling site means that a larger number of locations can be sampled in a day.

In the incubation method it is very important that the saturation irradiance and incubation temperature be equal or close to the ambient seawater temperature (Yentsch & Lee 1966). In a properly designed incubator it should be possible to attain these parameters. In addition, by using grey filters of various shades, the irradiance at different depths can be imitated, but not, however, the depth-related changes in the light spectrum. In any case, the variation in the light spectrum with depth probably does not significantly influence the measurements of phytoplankton production using the incubation method, because the phytoplankton collected at different depths – and therefore containing different quantities and types of pigments – is always exposed to the full light spectrum.

In this study an attempt was made to calculate the daily photosynthetic production of phytoplankton, based on the parameters of the photosynthetic light curves determined under artificial light conditions and at ambient temperature. The following parameters were required for the calculations: the daily irradiation or the 4-hour PAR irradiance at noon, the diffuse attenuation coefficient of downward irradiance (estimated from measurements of scalar irradiance under water), and the chlorophyll *a* content of the phytoplankton used for incubations (Lohrenz 1993). The primary production obtained in this way is called the *simulated in situ* primary production.

2. Materials and methods

The measurements were conducted in the Gulf of Gdańsk area at the locations shown in Fig. 1. Three types of primary production measurements were performed with the radiocarbon method (Steemann Nielsen 1952):

- *in situ* primary production at depths of 0.5, 2.5, 5, 10, 15 and 20 m,
- the potential primary production in water collected at depths as above, incubated under constant light intensity,
- the photosynthetic rates for establishing photosynthesis-light curves.

In situ primary production measurements were conducted during 4-hour incubations, preferably around noon. The onboard incubations for estimating potential primary production and photosynthetic rates were carried out for 2-hour periods.

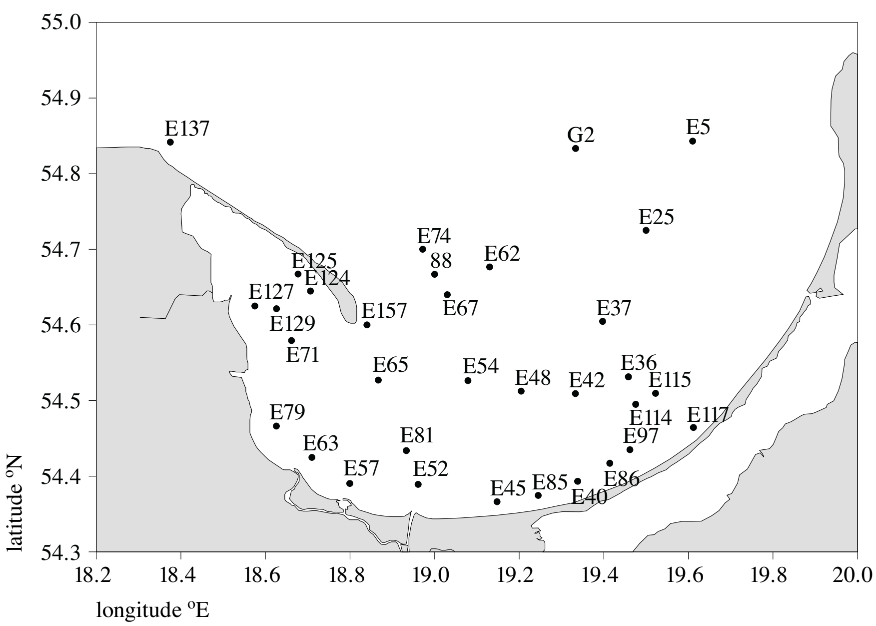

Fig. 1. Location of sampling sites

To obtain photosynthesis-light curves, the primary production for different light levels was measured mainly for the phytoplankton collected at 2.5 m. The chlorophyll content in phytoplankton was measured at the same time. In an incubator a constant irradiance of 250 kJ m^{-2} h^{-1} was supplied by fluorescent tubes. In addition, by using a system of filters and mirrors the following levels of light (PAR) were obtained: 435, 186, 124, 62, 37 and 2.5 kJ m^{-2} h^{-1}. The thermostat system ensured that the water temperature in the incubator was the same as the ambient temperature at the sampling depth.

The photosynthetic rates were measured with the isotopic method (Steemann Nielsen 1952, 1965, Aertebjerg Nielsen & Bresta 1984) by using a ^{14}C solution at an activity level of 150 kBq per sample of incubated water. The activity of the phytoplankton samples after incubation was measured with a liquid scintillation counter. Inorganic carbon in water, a parameter necessary for calculating primary production, was measured by measuring the pH of the water before and after the addition of 0.01 N HCl in a ratio of 1:4 (BMEPC 1988).

The underwater irradiance measurements used for calculating the primary production were done with an underwater and a reference PAR irradiation sensor (a LI–COR LI–193SA sensor with an LI–1000 datalogger). The sensors were calibrated in absolute energy units. The daily irradiance dose was measured by the reference sensor, which was connected to an integrator.

Chlorophyll *a* concentrations were measured fluorometrically. The pigments were extracted with 90% acetone for 24 hours in the dark at 4°C (Evans *et al.* 1987).

3. Basic mathematical relationships

3.1. Mathematical description of the relationship between photosynthetic rate and irradiance

To describe the photosynthetic characteristics of phytoplankton with respect to light, a parameter called the photosynthetic rate, P_h, is used. This is the ratio of primary production in one hour PP_h to the chlorophyll *a* concentration Chl: $P_h = PP_h/\text{Chl}$. The photosynthetic rate P_h is influenced by numerous environmental factors, which usually undergo rather substantial changes during the measurements. One such factor is irradiance. A typical experimental graph of the photosynthetic rate versus irradiance is presented in Fig. 2. The highest rate of photosynthesis occurs at the saturation level of irradiance (Yentsch & Lee 1966) and is called the assimilation number AN_{exp} (Parsons & Takahashi 1973, Platt & Gallegos 1980).[1] The values of the assimilation number and saturation irradiance estimated from discrete experimental measurements are approximated (Fig. 2). More accurate values of the saturation irradiance and assimilation numbers can be obtained

[1] The assimilation number can also be defined as the daily primary production per unit of chlorophyll [mgC mgChl^{-1} d^{-1}] (Bannister & Laws 1980, Woźniak 1987, Woźniak *et al.* 1989).

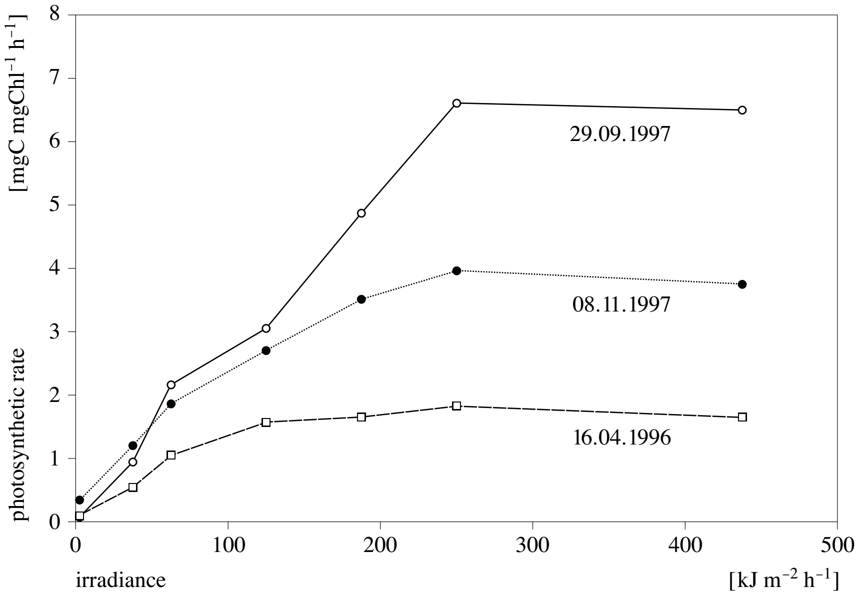

Fig. 2. Relationship between the rate of photosynthesis [mgC mgChl^{-1} h^{-1}] and irradiance [kJ m^{-2} h^{-1}] in water collected at a depth of 2.5 m in the Gdańsk Deep

by plotting photosynthesis-light curves, which relate the photosynthetic rate to irradiance, and are described by a mathematical equation.

A variety of models characterising the relationship between the photosynthetic rate and irradiance have been presented in the literature (Vollenweider 1965, Platt *et al.* 1977, Woźniak *et al.* 1989). The results of the investigations of the relationship for the Baltic Sea are best summarised by the following equation of Steele (1962), originally derived for the North Sea:

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

where
P_h – photosynthetic rate [mgC mgChl^{-1} h^{-1}],
E – scalar irradiance [kJ m^{-2} h^{-1}],
AN, E_s – constant parameters, AN [mgC mgChl^{-1} h^{-1}], E_s [kJ m^{-2} h^{-1}].
The physical significance of the parameters AN and E_s can be explained by calculating the extremum of the function (1). Thus, E_s is the level of irradiance, called the saturation irradiance, at which the photosynthetic rate achieves its maximum, and such a level of light can be assumed optimal for photosynthesis (Aalderink & Jovin 1997, Sakshaug *et al.* 1997). On the other hand, AN is the maximal value of the photosynthetic rate. Unlike

AN_{exp}, which is the maximal photosynthetic rate under the experimental conditions, AN is the real maximum of the function $P_h = f$ (irradiance).

To describe the relation between the photosynthetic rate and irradiance, a number of other equations have been used (Aalderink & Jovin 1997). The following hyperbolic equation is often used:

$$P_h = A\,\frac{E}{E + E_n}, \tag{2}$$

where

A – the asymptotic value of the photosynthetic rate equivalent to the saturation level of photosynthesis,

E_n – level of irradiance for which $P_h = \frac{A}{2}$.

The above equation does not account for the inhibition of photosynthesis that occurs at high intensities of irradiance.

3.2. Primary production at a given depth

To calculate the primary production at a given depth, eq. (1) is employed. In this equation the scalar irradiance at depth z can be expressed as:

$$E(z) = E(0)\ \times \exp[-k\ z], \tag{3}$$

where

$E(0)$ – irradiance just below the water surface,

k – attenuation coefficient of downward scalar irradiance. In the calculations we assume that k, the attenuation coefficient of downward scalar irradiance, does not change with depth. In this way, the photosynthetic rate at depth z can be written as:

$$P_h(z) = AN\ \frac{E(0)\ \exp(-k\ z)}{E_s} \times \exp\left[1 - \frac{E(0)}{E_s}\ \exp(-k\ z)\right]. \tag{4}$$

In the above equation $E(0)$ is a function of time. For simplicity, we shall assume that the changes in light intensity during the 'standard day' can be described by the following function (Vollenweider 1965):

$$E(t) = \frac{E_m}{2}\left(1 + \cos\frac{2\ \pi\ t}{\lambda}\right), \tag{5}$$

where

t – time measured since noon,

E_m – maximal irradiance at noon,

λ – length of day in hours. To calculate the maximal irradiance under the sea surface at noon $E_m(0)$ the daily dose of downward solar radiation just below the sea surface η_d was used; this takes into account the transmittance across the water surface (Dera 1995). By integrating eq. (5) over the range

$(-\frac{\lambda}{2}, \frac{\lambda}{2})$, that is, over the entire length of a 'standard solar day', one can obtain the daily solar irradiation η_d:

$$\eta_d = \int_{-\frac{\lambda}{2}}^{\frac{\lambda}{2}} \left(\frac{E_m(0)}{2} \left(1 + \cos \frac{2\ \pi\ t}{\lambda} \right) \right) dt. \tag{6}$$

Integrating the above equation yields $\eta_d = \frac{E_m(0)\ \lambda}{2}$, which can be rearranged as:

$$E_m(0) = \frac{2\ \eta_d}{\lambda}. \tag{7}$$

Substituting eq. (7) in eq. (5) we obtain

$$E(t) = \frac{\eta_d}{\lambda} \left(1 + \cos \frac{2\ \pi\ t}{\lambda} \right). \tag{8}$$

Therefore, the irradiance at depth z with respect to time can be expressed as:

$$E(z,t) = \frac{\eta_d}{\lambda} \times \exp(-k\ z) \left(1 + \cos \frac{2\ \pi\ t}{\lambda} \right). \tag{9}$$

To obtain the photosynthetic rate for time point t at depth z, eq. (9) has to incorporated into eq. (4):

$$P_h(z,t) = AN\ \frac{\eta_d\ \exp(-k\ z)\ (1 + \cos \frac{2\ \pi\ t}{\lambda})}{\lambda\ E_s} \times \\ \times \exp \left[1 - \frac{\eta_d\ \exp(-k\ z)\ (1 + \cos \frac{2\ \pi\ t}{\lambda})}{\lambda\ E_s} \right]. \tag{10}$$

The primary production at depth z can be calculated by multiplying eq. (10) by the chlorophyll a concentration:

$$PP_h(z,t) = AN\ \text{Chl}\ \frac{\eta_d\ \exp(-k\ z)\ (1 + \cos \frac{2\ \pi\ t}{\lambda})}{\lambda\ E_s} \times \\ \times \exp \left[1 - \frac{\eta_d\ \exp(-k\ z)\ (1 + \cos \frac{2\ \pi\ t}{\lambda})}{\lambda\ E_s} \right]. \tag{11}$$

3.3. Primary production under a 1 m^2 sea surface

The primary production per unit time in a column of water spanning the depth range from the surface to a depth H can be obtained by integrating eq. (11) over the depth range (0 to the limit of the euphotic zone H) as follows:

$$\mathrm{Prod}_h = \int_0^H AN\ \mathrm{Chl}\ \frac{\eta_d\ \exp(-k\ z)\ (1+\cos\frac{2\,\pi\,t}{\lambda})}{\lambda\ E_s} \times$$
$$\times \exp\left[1 - \frac{\eta_d\ \exp(-k\ z)\ (1+\cos\frac{2\,\pi\,t}{\lambda})}{\lambda\ E_s}\right] dz. \tag{12}$$

The formula expressing the daily primary production Prod_d in the water column is obtained by integrating eq. (12) over time from sunrise to sunset, that is from $-\frac{\lambda}{2}$ to $\frac{\lambda}{2}$:

$$\mathrm{Prod}_d = \int_{\frac{-\lambda}{2}}^{\frac{\lambda}{2}} \int_0^H AN\ \mathrm{Chl}\ \frac{\eta_d\ \exp(-k\ z)\,(1+\cos\frac{2\,\pi\,t}{\lambda})}{\lambda\,E_s} \times$$
$$\times \exp\left[1 - \frac{\eta_d\ \exp(-k\ z)\,(1+\cos\frac{2\,\pi\,t}{\lambda})}{\lambda\ E_s}\right] dz\ dt. \tag{13}$$

4. Results

4.1. Photosynthesis-light curves for phytoplankton in the Gulf of Gdańsk

The results of the measurements of photosynthetic rate with respect to irradiance in the Gulf of Gdańsk were assigned to the curves described by eqs. (1) and (2). A few examples of the photosynthetic rate versus irradiance relationship derived from these measurements, including the curves described by eqs. (1) and (2), are shown in Fig. 3. Correlation coefficients for the raw data and the values fitted from eq. (1) ranged from 0.95 to 1; for eq. (2) they were, on average, lower by 0.02. As demonstrated in Fig. 3, eq. (2) turned out to be a good model of the photosynthetic rate vs. irradiance relationship for low irradiances; however, for high irradiance levels the fit of the data to the model was poor. It should be emphasised that in summer, it is the high level of irradiance that drives the whole process of photosynthesis and primary production in the euphotic zone. In further calculations, eq. (1) was used to simulate primary production, especially as it accounts for the inhibitive effect of excessive irradiance. The coefficients of eq. (1), estimated by the least squares method from the photosynthesis-light curves for the phytoplankton in the

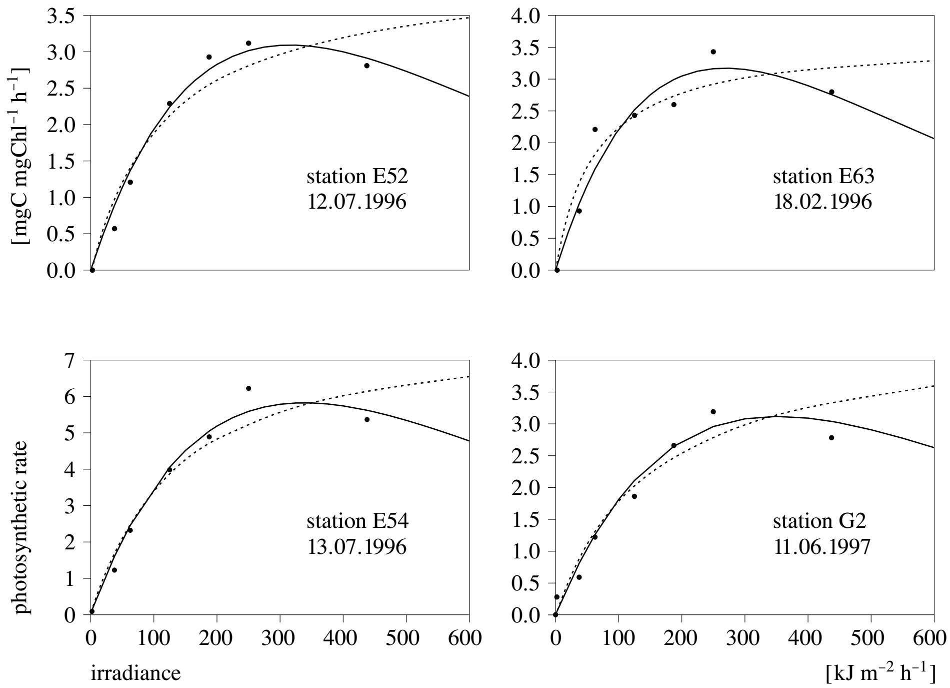

Fig. 3. Photosynthesis-light curves representing the relationship between the photosynthetic rate [mgC mgChl^{-1} h^{-1}] and irradiance [kJ m^{-2} h^{-1}]. The solid line is described by eq. (1), the dashed line by eq. (2)

Gulf of Gdańsk, are shown in Table 1. The assimilation numbers for the Gulf of Gdańsk, estimated from the photosynthetic curves, ranged from 1.70 to 8.22 [mgC mgChl^{-1} h^{-1}]. Assimilation numbers were lowest in February and May, and highest in July.

4.2. Vertical distribution of primary production

Selected data sets of the vertical distribution of primary production are shown in Fig. 4. The curves represent the hypothetical vertical distributions calculated from eq. (11). The raw data used in the calculations are shown in Tables 1–3. The curves show a good fit of the model to the values measured *in situ*. Fig. 5 illustrates the correlation between the calculated and *in situ* primary production measured for 1 hour in 1 m^3 of water. It is clear that deviations between the *in situ* results and those obtained using the eq. (11) are small. The correlation coefficient for this relationship is 0.98.

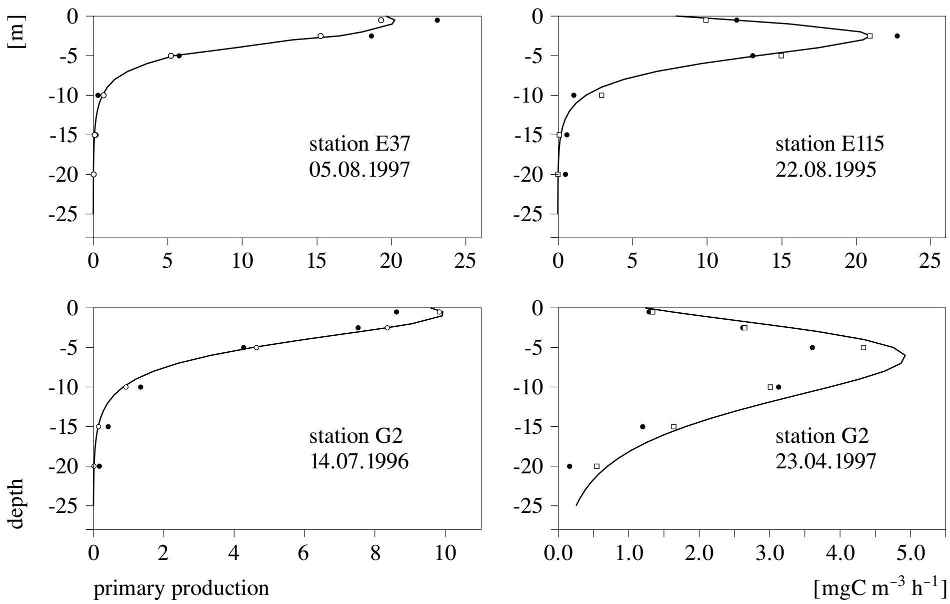

Fig. 4. Vertical distribution of primary production. The points indicate *in situ* measurements. The curves were constructed from eq. (1) and the circles (explained in the Discussion) represent calculated values, including potential primary production

4.3. A comparison of the *in situ* primary production in a column of water measured for 4 hours and the calculated primary production

The production per unit time in a water column extending from the surface to the boundary of the euphotic zone is described by eq. (12). In the calculations, mean chlorophyll a concentrations for the euphotic zone were used under the assumption that these concentrations do not vary with depth. The values of primary production calculated by integrating eq. (12) over a four-hour time interval were compared with the *in situ* values. The integrated equation took the form

$$\mathrm{Prod}_{\Delta t} = \int\limits_{t1}^{t2} \int\limits_{0}^{H} AN \ \mathrm{Chl} \ \frac{\eta_d \ \exp\left(-k \ z\right)\left(1 + \cos \frac{2\ \pi \ t}{\lambda}\right)}{\lambda \ E_s} \times$$

$$\times \exp \left[1 - \frac{\eta_d \ \exp\left(-k \ z\right) \ \left(1 + \cos \frac{2\ \pi \ t}{\lambda}\right)}{\lambda \ E_s}\right] dz \ dt.$$

Table 1. Coefficients of eq. (1) for phytoplankton in the Gulf of Gdańsk

Date	Station	AN [mgC mgChl^{-1} h^{-1}]	E_s [kJ m^{-2} h^{-1}]	AN_{exp} [mgC mgChl^{-1} h^{-1}]
22.08.1995	E115	2.84	365.4	2.66
23.08.1995	E137	4.14	381.0	3.88
28.08.1995	E71	3.55	306.6	3.93
29.08.1995	E65	4.05	382.8	4.65
31.08.1995	E125	4.60	332.6	4.62
August 1995	mean	3.84	353.7	3.95
	SD	0.67	33.1	0.81
13.02.1996	E40	2.81	264.8	3.77
15.02.1996	E54	2.97	548.5	2.67
16.02.1996	E157	2.12	290.1	1.69
18.02.1996	E63	3.16	268.8	3.43
February 1996	mean	2.76	343.1	2.89
	SD	0.45	137.4	0.92
11.07.1996	E71	8.22	329.0	7.71
12.07.1996	E52	3.10	315.6	3.12
12.07.1996	E63	5.37	312.3	5.97
13.07.1996	E40	5.10	425.7	
13.07.1996	E54	5.83	338.2	6.22
14.07.1996	G2	5.29	444.4	5.09
July 1996	mean	5.49	360.9	5.62
	SD	1.64	58.5	1.69
06.05.1997	E65	1.70	352.3	2.1
07.05.1997	E54	2.43	338.4	2.65
07.05.1997	E63	4.25	383.2	4.26
08.05.1997	E37	3.21	506.7	2.49
08.05.1997	E115	2.52	339.5	2.48
09.05.1997	E52	3.91	418.4	3.75
09.05.1997	E45	1.79	388.5	1.77
10.05.1997	E40	2.98	384.9	2.97
11.05.1997	G2	3.00	431.9	2.67
11.05.1997	E42	2.26	448.4	2.13
12.05.1997	E88	1.95	435.3	2.11
13.05.1997	E79	3.05	445.5	2.96
13.05.1997	E124	2.10	522.1	2.14
May 1997	mean	2.67	402.5	2.65
	SD	0.77	71.7	0.71

Table 2. Comparison of the primary production measured *in situ* in a column of water during 4 hours and the primary production calculated from the eqs. (13) and (14)

Station	Date	Depth [m]	η_d (PAR) [kJ m^{-2} d^{-1}]	$\eta_{\Delta t}$ (PAR) [kJ m^{-2} Δt^{-1}]	k [m^{-1}]	Chl [mg m^{-3}]	Prod$_{\Delta t\,\text{meas.}}$ [mgC m^{-2} Δt^{-1}]	Prod$_{\Delta t\,\text{cal.}}$ [mgC m^{-2} Δt^{-1}] eq. (14)	Prod$_{\text{meas.}}$/ (Prod$_{\text{cal.}}$)	Prod$_{d\,\text{cal.}}$ [mgC m^{-2} d^{-1}] eq. (13)
E115	22.08.1995	59	9891	4536	0.40	6.35	534.7	468.0	1.14	1192.8
E137	23.08.1995	12	9073	4092	0.36	1.86	218.9	208.3	1.05	524.0
E65	29.08.1995	68	1008	281	0.40	5.74	116.4	105.9	1.10	362.2
E40	13.02.1996	19	2404	1608	0.26	0.55	38.6	49.0	0.79	80.4
E54	15.02.1996	73	1715	1288	0.28	0.63	28.6	32.0	0.90	45.3
E157	16.02.1996	48	1288	1044	0.28	0.51	20.3	24.5	0.83	34.3
E63	18.02.1996	10	2045	1260	0.38	0.82	25.6	40.8	0.63	71.0
E71	11.07.1996	34	6834	3986	0.39	3.33	571.1	721.1	0.79	1859.7
E52	12.07.1996	22	6970	3904	0.48	6.47	435.9	430.6	1.01	1132.4
E40	13.07.1996	19	12076	5160	0.40	3.73	654.9	488.6	1.34	1402.4
G2	14.07.1996	110	6471	1396	0.37	2.43	218.9	204.3	1.07	777.2
E37	08.05.1997	83	4475	1348	0.35	7.50	397.9	362.3	1.10	1117.9
E52	09.05.1997	21	3366	1100	0.34	2.29	85.8	137.8	0.62	402.9
E40	10.05.1997	19	8464	3484	0.46	4.62	359.9	338.1	1.06	893.2
G2	10.05.1997	110	11026	4736	0.35	2.84	260.7	247.3	1.05	669.0
88	12.05.1997	86	8607	2700	0.27	3.54	313.3	213.2	1.47	642.0
E79	13.05.1997	10	4869	1260	0.31	1.02	62.5	51.9	1.21	174.9
G2	23.04.1997	110	9953	4376	0.25	1.99	175.1	199.1	0.88	514.4
G2	11.06.1997	110	11496	4578	0.24	1.22	162.6	160.4	1.01	480.2
G2	08.11.1997	110	824	503	0.20	0.98	57.8	57.9	1.00	94.5

The calculated primary production values and *in situ* measurements for a four-hour period are shown in Table 2. The ratio of calculated primary production to its *in situ* values ranged from 0.63 to 1.47 with a mean of 1.01. Fig. 6 illustrates the relationship between the primary production in a column of water during 4 hours and the *in situ* production measured at

Table 3. Primary production calculated from eq. (13)

Station	Date	Depth [m]	*AN* [mgC mgChl^{-1} h^{-1}]	E$_m$ [kJ m^{-2} h^{-1}]	η_d [kJ m^{-2} d^{-1}]	*k* [m^{-1}]	Chl [mg m^{-3}]	Prod$_{d\,\text{cal.}}$ [mgC m^{-2} d^{-1}]	Prod$_{d\,\text{meas.}}$ [mgC m^{-2} d^{-1}]
E86	08.04.1994	30	2.15	335	6802	1.74	38.75	1120.1	
E97	08.04.1994	12	2.15	335	6802	1.61	35.3	1092.6	
E85	09.04.1994	15	2.17	335	8276	1.48	31.6	1146.6	
E114	09.04.1994	59	2.17	335	8276	1.04	14.28	737.3	
E52	21.07.1994	21	5.53	361	11656	0.61	6.47	1772.1	1867
E54	21.07.1994	73	5.53	361	11656	0.46	3.53	1282.2	
E40	22.07.1994	19	5.54	361	11999	0.64	7.62	2005.1	2068
E42	22.07.1994	71	5.54	361	11999	0.35	4.80	2309.4	
E36	23.07.1994	69	5.55	361	12003	0.40	3.20	1346.7	1243
E117	23.07.1994	13	5.55	361	12003	0.86	6.55	1282.0	
E25	24.07.1994	98	5.56	361	11405	0.36	5.03	2319.0	2297
E5	24.07.1994	25	5.56	361	11405	0.46	3.88	1400.0	
E74	25.07.1994	89	5.57	361	11471	0.45	4.22	1558.2	
G2	25.07.1994	110	5.57	361	11471	0.44	4.22	1593.6	1506
E71	28.07.1994	34	5.59	361	9693	0.90	4.47	783.4	786
E127	28.07.1994	9	5.59	361	9693	0.72	6.59	1437.9	
E57	04.11.1994	11	3.58	381	2923	0.46	3.89	368.8	
E52	04.11.1994	21	3.58	381	2923	0.38	5.76	667.8	
E42	05.11.1994	71	3.55	381	2973	0.66	7.57	504.4	
E45	05.11.1994	16	3.55	381	2973	0.42	3.96	413.8	
E81	06.11.1994	37	3.53	381	2322	0.44	6.28	539.7	
E125	30.08.1995	24	5.37	354	1245	0.39	3.67	402.2	595
E115	13.02.1996	59	1.93	343	1811	0.36	0.48	25.6	
E48	14.02.1996	75	1.92	343	2408	0.38	0.53	32.0	
E62	15.02.1996	91	1.91	343	1717	0.30	0.44	27.0	
E52	16.02.1996	21	1.90	343	1290	0.44	0.66	22.4	
E79	17.02.1996	10	1.90	343	789	0.28	0.94	31.5	32
129	17.02.1996	29	1.89	343	789	0.33	0.99	30.1	
E57	18.02.1996	11	1.88	343	2048	0.67	1.35	41.3	
E63	12.07.1996	10	5.37	312	6970	0.40	4.14	1453.0	
E54	13.07.1996	73	5.83	338	12076	0.40	4.05	1221.1	
E71	06.05.1997	34	2.96	403	7181	0.29	2.03	491.6	502
E65	06.05.1997	68	1.70	352.3	7181	0.39	3.28	358.6	
E115	08.05.1997	59	2.52	339.5	4475	0.43	7.33	884.7	
E45	09.05.1997	16	1.79	388.5	3366	0.38	3.08	232.3	
E42	11.05.1997	71	2.26	448.4	11026	0.54	6.02	684.2	
E124	13.05.1997	35	2.10	522.1	4870	0.30	1.42	168.4	

the same time. Both the linear relationship in the graph and the results in Table 3 demonstrate the good fit of the model. The aforementioned calculations indicate that the incubation-based method chosen here to estimate the primary production could possibly replace the *in situ* measurements.

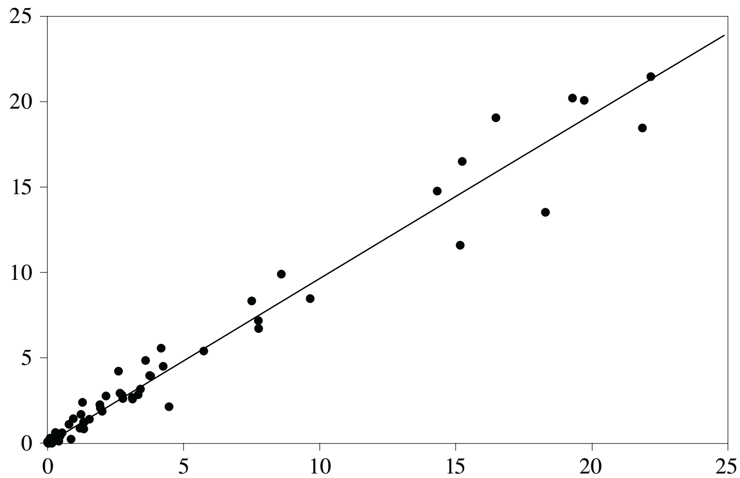

Fig. 5. Correlation between the primary production [mgC m^{-3} h^{-1}], calculated from eq. (1), and the primary production [mgC m^{-3} h^{-1}] measured *in situ* in 1 m^3 of water for 1 hour. The lines are described by the equation $PP_{h\,\mathrm{cal.}} = 0.961\ PP_{h\,in\,situ}$

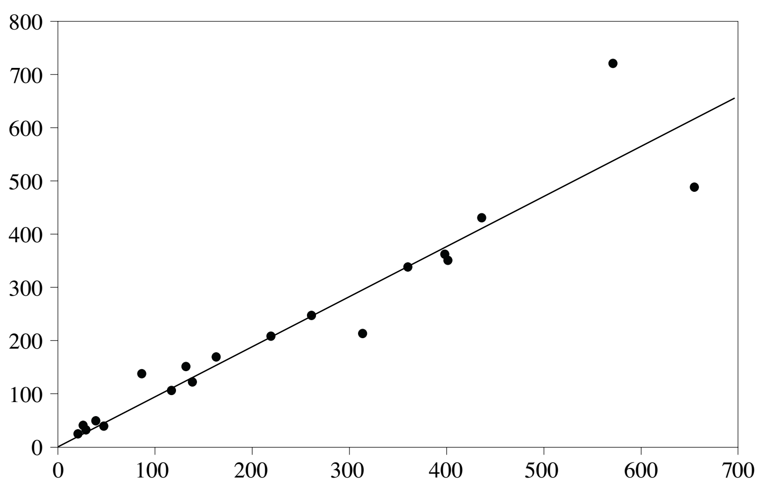

Fig. 6. Correlation between the primary production [mgC m^{-2} $4h^{-1}$] in a column of water under a 1 m^2 surface area, calculated from eq. (14), and primary production [mgC m^{-2} $4h^{-1}$] measured *in situ* during the 4 hours around noon

4.4. Daily primary production in a column of water extending from the surface to the boundary of the euphotic zone

The daily primary production in a water column from the surface to the limit of euphotic zone is described by eq. (13). As in the previous section, it was assumed in the calculations that chlorophyll *a* concentrations do not vary with depth. Some daily primary production values are presented in Tables 2 and 3. In cases where actual *in situ* primary production values are available, the correlation between the measured and calculated primary production under 1 m^2 of water is presented graphically. The line in Fig. 7 is described by the equation

$$\mathrm{Prod}_{d\ \mathrm{cal.}} = 1.005\mathrm{Prod}_{d\,in\,situ}.$$

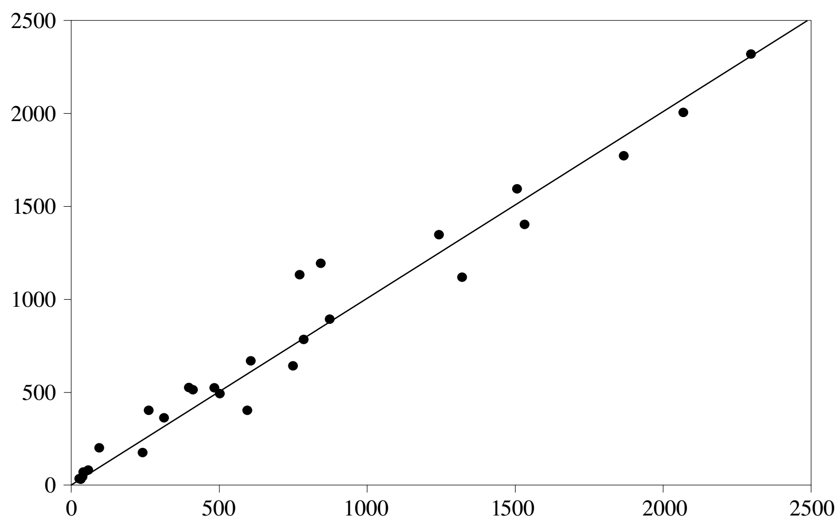

Fig. 7. Correlation between the daily primary production under a 1 m^2 surface area [mgC m^{-2} d^{-1}], calculated from eq. (13), and the daily primary production measured *in situ*

5. Discussion

Of the two types of curves shown in Fig. 3, the one described by eq. (1) (the solid curve on the graph) was chosen. The curve well describes the decrease in photosynthetic rate under a very high level of irradiance. On the other hand, the curve described by eq. (2) (the broken curve on Fig. 3) approaches the asymptote at high irradiance levels; this corresponds to photosynthetic saturation. This means that the curve does not model well the photosynthetic inhibition under excessive light conditions in the Gulf of Gdańsk.

The assimilation numbers for the Gulf of Gdańsk ranged between 1.69 and 8.22. The mean values obtained during cruises were as follows: 3.84 in August 1995, 2.76 in February 1996, 5.19 in July 1996, and 2.67 in May 1997. As we see, the values are indicative of a seasonal variability. Assimilation numbers in the Pomeranian Bay and the open waters of the southern Baltic are also known to fluctuate (Renk & Ochocki 1998). Seasonal changes in the mean assimilation number for the waters of the Gdaśk Deep were described by the following function:

$$AN = 3.57 - 2.18 \sin(2\pi x + 0.69) + 0.55 \sin(4\pi x - 0.48), \tag{14}$$

where
x = day of the year.
The above equation allows the mean assimilation number for a given day of the year to be estimated and thus, the primary production in the Gulf of Gdańsk to be calculated. In summer, inhibition is known to occur around noon over the depth range from 0 to 6 m (Fig. 4), (Renk 1983, 1997). Hence, a function of the type described by eq. (1) adequately models the relationship between the photosynthetic rate and irradiance in the southern Baltic. Similar conclusions were formulated earlier by Woźniak *et al.* (1989) and Renk & Ochocki (1998).

As Fig. 4 shows, not all the measured values of the primary production lie close to the fitted curve described by eq. (11). On analysing this equation, it becomes obvious that the considerable deviation from the model is caused by the variable irradiance and chlorophyll concentrations, and by parameters such as the light attenuation coefficient, AN and E_s. All these values are biased because of the random error associated with the experimental technique by which they are being measured. In particular, the following should be considered:

(1) It can be seen in Fig. 3 that, quite frequently, the values of the maximal photosynthetic rate lie above the photosynthesis-light curves. This could result in a certain decrease of the calculated primary production within the depth range for which the maximal photosynthetic rate occurs. Figure 4 confirms this finding.

(2) In eqs. (4) and (11), which describe the vertical distribution of primary production, it was assumed for the sake of simplicity that the downwelling irradiance attenuation coefficient k is constant with depth. This assumption could introduce a certain bias into both the

vertical distribution of primary production and the calculated daily primary production.

(3) In calculations involving eq. (13) it was assumed that chlorophyll *a* concentrations are not depth-dependent. However, such an assumption is not always correct, especially during the spring bloom.

(4) It was assumed in eq. (11) that AN and E_s do not depend on depth, and that parameter values for a depth of 2.5 m were used in the calculations. This means that the photochemical properties of phytoplankton and the chemical characteristics of the environment have not been considered.

It has been shown that the above parameters depend on the temperature and concentration of nutrients (Renk & Ochocki 1998, Renk *et al.* 1999). The photochemical properties of phytoplankton and the chemical characteristics of the environment for the discrete levels can be taken into account by multiplying the primary production calculated from the model (11) by a parameter ε (Sorokin 1960). Parameter ε is the ratio of the potential primary production at a given depth to the potential primary production at a depth of 2.5 m. Such corrected values of the primary production, calculated according to model (11), which account for the real chlorophyll *a* concentrations as well as the photochemical properties of phytoplankton, are shown as circles in Fig. 4. For discrete levels the corrected results are closer to the *in situ* measured values. However, the method cannot be used to plot the vertical distribution of primary production (continuous function).

Another source of deviation of the calculated daily primary production from the *in situ* values is due to the fact that the latter is estimated, as suggested by the BMEPC (1988), from the four-hour measurements of primary production. According to this method, the daily primary production is calculated by multiplying the four-hour production by a so-called 'light factor', which is the ratio of the daily dose of solar irradiation to the energy emitted during four hours. The assumption is made about the proportional correlation of primary production in a column of water and the dose of solar irradiation entering the sea. Nevertheless, these detailed studies have demonstrated that such a relationship is not always linear, and a certain error in the estimate of the daily primary production with the method proposed by the BMEPC (1988) may occur.

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Appendix

List of symbols

Symbol	Denotes	Units
PP_h	primary production per unit time in unit volume of water	mgC m^{-3} h^{-1}
Chl	chlorophyll *a* concentration	mgChl m^{-3}
P_h	photosynthetic rate determined as the ratio $\frac{PP_h}{\mathrm{Chl}}$	mgC mgChl^{-1} h^{-1}
AN	assimilation number evaluated from the photosynthetic light curve	mgC mgChl^{-1} h^{-1}
AN_{exp}	assimilation number determined as the measured maximal ratio $\frac{PP_h}{\mathrm{Chl}}$	mgC mgChl^{-1} h^{1}
Prod_h	primary production in the water column per hour	mgC m^{-2} h^{-1}
$\mathrm{Prod}_{\Delta t}$	primary production in the water column during Δt	mgC m^{-2} Δt^{-1}
Prod_d	daily primary production in the water column	mgC m^{-2} d^{-1}
E	PAR irradiance	kJ m^{-2} h^{-1}
E_s	PAR irradiance at which photosynthetic saturation is achieved	kJ m^{-2} h^{-1}
η_d	daily PAR irradiation (daily irradiance dose) just below the sea surface	kJ m^{-2}
$\eta_{\Delta t}$	PAR irradiance dose during Δt hours just below the sea surface	kJ m^{-2}
k	diffuse attenuation coefficient for scalar PAR irradiance	m^{-1}
λ	length of day	h
H	thickness of euphotic layer	m