Light curves of marine plankton photosynthesis in the Baltic*

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Daily irradiation
Primary production
Rate of photosynthesis
Efficiency of photosynthesis
Baltic Sea

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Abstract

Empirical correlations between the intensity of photosynthesis of the marine phytoplankton and daily irradiation in Southern Baltic were analysed. The statistical 'light curves' of photosynthesis *in situ* and their seasonal changes for the Baltic were examined. Additionally, with the help of long-term statistical data of the irradiation field distribution in the Southern Baltic the characteristic depths of photosynthesis as well as their seasonal changes were determined.

1. Introduction

The primary production in the sea is governed by a complex group of biotic and abiotic factors influencing the photosynthesis process in marine plankton (Steemann-Nielsen, 1975). Among abiotic factors the most significant are: the underwater irradiance, content of biogenic substances in water and water temperature (Koblentz-Mishke and Vedernikov, 1977; Bougis, 1976).

The subject of this paper is discussion of the results of long-term investigations of the effect of underwater solar irradiance field on the photosynthesis in the Baltic. Due to time variability of solar irradiance, the diurnal doses of solar irradiance energy also called the daily irradiation $[J \cdot m^{-2} \cdot d^{-1}]$ are used (Jerlov, 1968).

The effect of irradiance field, as well as other factors, on the photosynthesis

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in the sea is very complex. This results from complexity of the process of the absorption of a broad spectrum of light by plant pigments and conversion of this light energy into chemical energy of the biomass (Govindjee, 1975), while the spectral composition and also the level of total energy of solar radiation in the sea are strongly time-dependent and diversified in water column. The light of wavelengths from 370 to 720 nm was found to be used by plant pigments in this process (Riley and Chester, 1972). Accordingly, the process of primary production in water column is most strongly dependent on the underwater irradiance field. The course of this dependence in vertical distribution in the sea is illustrated schematically in Figure 1, showing a typical vertical distribution of the solar irradiation in the upper layer of the sea (Fig. 1A) and the corresponding vertical distribution of the primary production (Fig. 1B). As seen

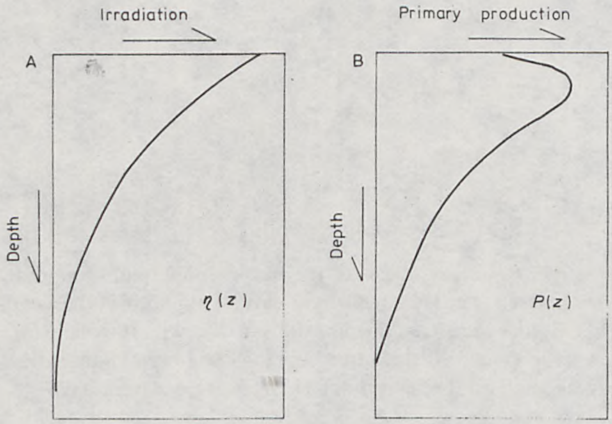

Fig. 1. Illustration of a typical vertical distribution of the diurnal dose of solar irradiance energy, *ie* daily irradiation in the sea (A) and the corresponding vertical photosynthesis profile (B)

from the figures, beginning from a defined, relatively small depth in the sea, the photosynthetic production decreases with depth in parallel with the lowering level of irradiation. The latter obviously pertains to total energy in a spectral region of photosynthetically active radiation (PhAR), *ie* in the wavelength range utilized by plant pigments given above*. Hence, light is the main factor determining vertical distributions of the primary production.

However, the absolute amount of produced biomas also depends on the composition and concentration of biogenic substances and on water temperature: biogenic substances constituting 'mineral feed' of phytoplankton and

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* The spectral range of PhAR reported in the literature is somewhat different (Hojerslev, 1978). For the Baltic, due to strong absorption of ultraviolet by the Baltic water, it can be practically assumed that this is visible light in the wavelength range from 400 to 700 nm.

temperature determining intensity of process in the ecosystem and also influencing species composition of phytoplankton (Riley and Chester, 1972). Both the above factors also exhibit – particularly in the Baltic – strong diversity in space and time variability. Consequently, in order to perform an analysis of the effect of irradiation alone on the photosynthesis, the influence of the factors in the investigations should be eliminated.

The effect of temperature on the primary production in the sea *in situ* can be eliminated by carrying out statistical analyses of this dependence under established thermal conditions. Approximately, such established conditions, *ie* fixed vertical distributions of temperatures can be assumed in southern part of the Baltic for individual months of the year. To eliminate in the studies the effect of biogenic substances let us note that as a result of slowness of changes in state of the ecosystem encountered in the nature we can assume in certain periods of time a relatively established dynamic equilibrium of phytocenosis. Under these conditions the biomass of phytoplankton is roughly proportional to concentration of biogenic elements. The intensity of photosynthesis related to concentration of phytoplankton at various depths is then practically independent of these established conditions of 'mineral feed' and depends only on the strongly variable irradiation field. Such understood intensity of photosynthesis is most frequently defined as a ratio of the primary production at a certain depth in the sea – $P(z)$, to the concentration of chlorophyll $a - B_a(z)$. Due to routinely performed measurements, the chlorophyll concentration B_a is most commonly employed as an indicator of phytoplankton concentration in the sea.

The ratio:

$$AN = \frac{P(z)}{B_a(z)} \quad (1)$$

is also called the assimilation number of the process of photosynthesis (Koblentz-Mishke, 1985).

According to the above assumption, to characterize the exclusive effect of irradiation on the photosynthesis process the analysis of the dependence of assimilation number at various depths in the sea on irradiation by sunlight getting through in the spectral range of PhAR should be carried out. Such dependences are called the light curves of photosynthesis (Koblentz-Mishke, 1985; Platt *et al*, 1980). An idealized shape of such curves is known (Steemann-Nielsen, 1964, 1974). It reveals the existence of three characteristic regions of the dependence – see Figure 2A. These are:

– the region of so-called light reactions *ie* reactions limited directly by an access of light (I),

– the region of dark reactions (of light saturation), *ie* reaction limited by enzymatic intracellular processes (II),

– the region of light inhibition (III).

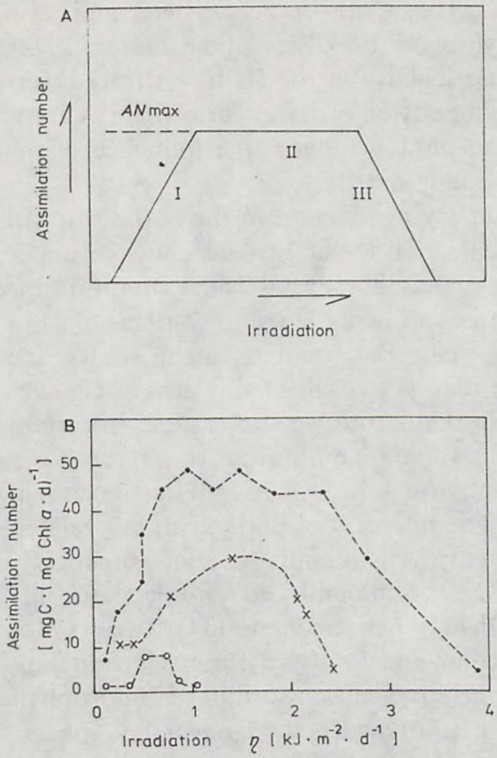

Fig. 2. Light curves of photosynthesis process
A – idealized according to the model, B – experimental, exemplary from an *in situ* measurement in the Baltic

In practice, however, the observed natural light curves of photosynthesis deviate from the ideal course (Fig. 2B) and exhibit variable diversity dependent on the time of observation and sea region. This results from the already mentioned diversity of spectral composition of irradiance penetrating water column, from changes in spieces composition of phytoplankton and from changes other than presented above, biotic and abiotic factors affecting marine photosynthesis. Consequently, the dependences of intensity of photosynthesis on the natural underwater irradiation for the whole phytoplankton in the sea is of statistical nature. It can be described only by averaged quantities, whose applicability depends on the choice of experimental material.

The main purpose of our investigation was the determination of typical shapes of light curves for the Southern Baltic. This goal was achieved by performing statistics in the seasonal context from long-term *in situ* measurements of photosynthesis and underwater irradiation fields.

Since irradiation determines vertical distributions of photosynthesis, the second important purpose of the investigations was the determination of statistical characteristics of vertical distributions of typical photosynthesis intensity in the Baltic for individual month of the year. This goal was accomplished by employing the results of statistical analyses of light curves and statistical characteristics of underwater irradiation fields in the Southern Baltic published earlier (Woźniak and Hapter, 1985; Dera *et al*, 1984).

The presented work is an attempt at recapitulation of long-term investigations of optical conditions of photosynthesis in the Baltic carried out by the group of physicists of the Institute of Oceanology of Polish Academy of Sciences in Sopot.

2. Experimental methods and materials

The work utilized the results of comprehensive hydrooptical and primary production measurements performed in 1972–1984 in various regions of the Southern Baltic. The investigations were carried out aboard Polish, Russian, and East German ships by the authors and their Polish co-workers and by foreign scientists: prof. O. I. Koblentz-Mishke from USSR and dr L. Gohs from GDR. Collected results of measurements and the methods of these investigations have been described in, among others, the following papers: Dera *et al*, 1974; Gohs *et al*, 1978; Koblentz-Mishke *et al*, 1985; Hapter, 1984; Woźniak and Hapter, 1985 and 1985a; Woźniak, 1987; Woźniak *et al*, 1975.

The present paper utilizes the experimental data concerning:

– $P(z)$, *ie* the diurnal primary production of biomas of the phytoplankton at different depths in the sea expressed in units of assimilated carbon in 1 m^3 of water [$mgC \cdot m^{-3} \cdot d^{-1}$];

– $B_a(z)$, *ie* the concentration of chlorophyll *a* at different depths in the sea expressed in units [$mgChl\ a \cdot m^{-3}$];

$\eta(z)$, *ie* the depth distributions in the sea of diurnal doses of solar irradiance energy (the daily irradiation) in the wavelength range 400–700 nm (PhAR) expressed in units [$kJ \cdot m^{-2} \cdot d^{-1}$].

The primary production was determined conventionally, *ie in situ* by the isotope method with carbon ^{14}C (Steermann-Nielsen, 1952, 1964). The so-called 'light factor' was also applied (Gargas, 1975; Gargas and Here, 1976). However, the concentration of chlorophyll in water samples taken from the sea was measured by a spectrophotometric method using the Strickland-Parsons' equation (Strickland-Parsons, 1968).

The optical measurements of the doses of solar irradiance energy in the sea were made *it situ* by spectrophotointegrator methods and instrumentation designed at the Institute of Oceanology of the Polish Academy of Sciences. The methods and construction of the instrumentation have been described by Woźniak *et al*, (1983), Woźniak and Montwiłł (1973).

Additionally, the rate of photosynthesis at different depths in the sea was analysed. The diurnal assimilation number, $AN(z)$, determined as a ratio of diurnal productions $P(z)$ to concentrations of chlorophyll *a*, $B_a(z)$, were adopted as a measure of these rates. The numbers $AN(z)$ are expressed in units $[\mathrm{mgC \cdot mgChl}\ a^{-1} \cdot \mathrm{d}^{-1}]$.

Light curves of photosynthesis, AN *vs* η, relating to diurnal values of assimilation numbers and irradiance doses, were analysed in the paper.

3. Results

3.1. Light curves of photosynthesis

Earlier measurements in the already mentioned research groups resulted in a set of experimental plots of light curves of photosynthesis in the Southern Baltic for 120 days in various months of the year (Hapter, 1984; Woźniak and Hapter, 1985; Woźniak, 1985). At present, as a result of statistical analysis of these data a number of dependences presented below were found.

Namely, the light curve determined for the same months (irrespective of the year and region of investigations within open waters of the Southern Baltic) reveal considerable similarities. Their qualitative and quantitative diversity is significantly lower than in the case of a full set of data. Accordingly, we

Table 1. Multiannual mean values of numbers describing shapes of light curves of photosynthesis in the Southern Baltic in individual months of the year.

Month	No. of measurements	AN^{max} [mgC·(mg Chl *a*)·d^{-1}]	Values of irradiation η [kJ·m^{-2}·d^{-1}] for respective percentage of relative assimilation number AN/AN^{max}*									
			light reaction				light saturation			light inhibition		
			10%	30%	50%	70%	90%	100%	90%	70%	50%	30%
II	3	4.1	54	108	200	342	544	909	1060	.	.	.
		–	–	–	–	–	–	–	–			
III	20	4.83	74	180	346	632	1260	2140	2760	3500	4310	5950
		1.70	39	80	131	239	570	780	130	1480	–	–
V	12	46.6	180	582	1180	1950	2810	4090	5530	6740	8000	9500
		9.1	126	322	510	560	640	740	800	800	–	–
VI	10	26.4	280	607	1130	2150	3050	4900	6070	7330	9040	11300
		8.6	131	184	350	870	1340	1340	1720	2430	–	–
VII	21	24.0	88	271	628	1360	2810	4190	5480	7540	9210	13600
		5.5	40	139	255	560	760	1260	1380	1880	–	–
VIII	15	78.0	73	265	603	1180	2520	3540	4520	5610	7540	9630
		14.2	66	175	352	640	960	1090	1800	1760	–	–
IX	14	20.3	78	227	435	850	1280	1920	2470	3570	5480	7790
		12.4	32	69	147	230	390	500	620	980	–	–
X	11	14.7	41	149	331	528	858	1270	1700	2540	4170	5780
		4.0	22	111	228	356	444	360	420	700	–	–
XI	11	3.1	16	67	176	273	377	473	565	804	1200	.
		0.9	14	43	144	215	247	268	272	348	–	
XII	3	2.5	42	81	130	163	201	303	346	404	528	.
		–	–	–	–	–	–	–	–	–	–	

* Upper numbers – the irradiation, lower numbers – standard deviation

averaged these dependences for individual months in the year*. The results are presented in Table 1. The respective daily irradiation η (together with standard deviations) for which relative assimilation numbers, *ie* the ratios AN/AN^{max}, reach fixed values: 10, 30, 50, 70, 90, and 100%, are listed in columns 4–13. The curves are also illustrated in Figure 3. On the other hand, the average

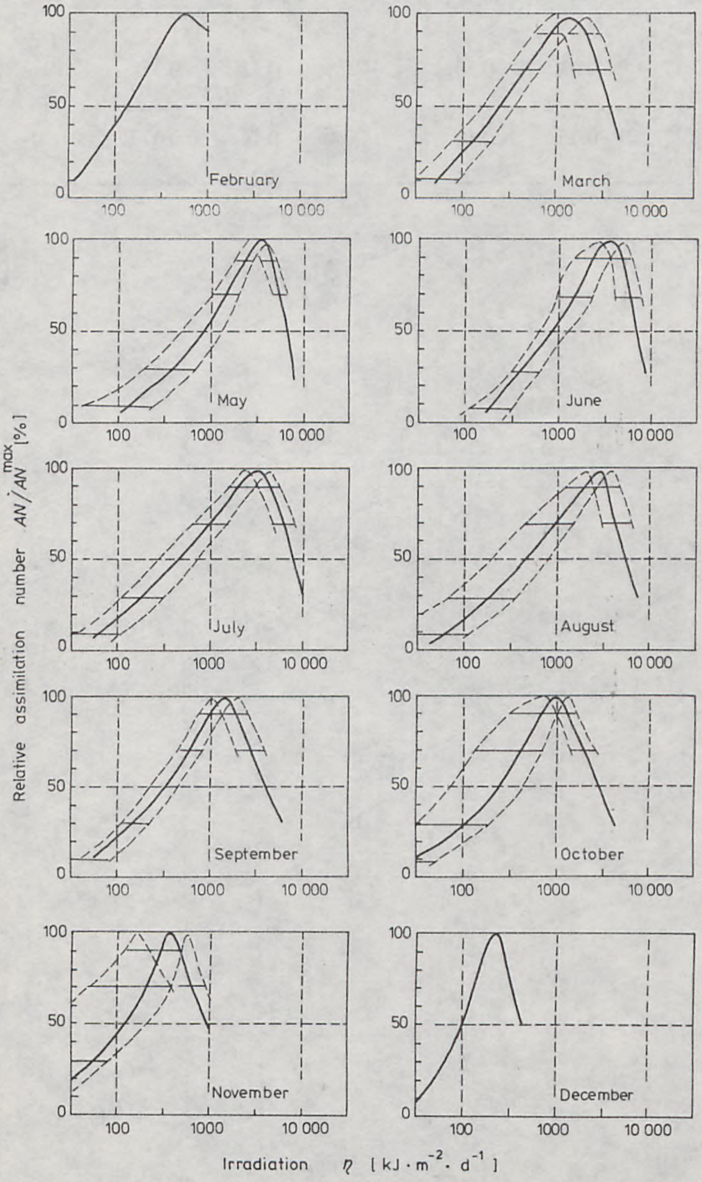

Fig. 3. Natural light curves of photosynthesis process in the Southern Baltic averaged for individual months on the basis of long-term data.
Broken lines illustrate the range of standard deviations

* Except for January and April when the measurements were not made.

Table 2. Parameters of the averaged light curves of photosynthesis in the Southern Baltic approximated for various months by means of the Platt's formula (2).

Parameter	Month							
	III	V	VI	VII	VIII	IX	X	XI
$A\left[\frac{\text{mgC}}{\text{mgChl}a\cdot\text{d}}\right]$	11.8	145	49.5	64.2	438	48.3	25.5	6.51
$\alpha\left[\frac{\text{mgC}\cdot\text{cm}^2}{\text{mgChl}a\cdot\text{J}}\right]$	0.085	0.37	0.21	0.20	0.75	0.31	0.35	0.19
$\beta\left[\frac{\text{mgC}\cdot\text{cm}^2}{\text{mgChl}a\cdot\text{J}}\right]$	0.039	0.27	0.057	0.10	1.20	0.14	0.077	0.070

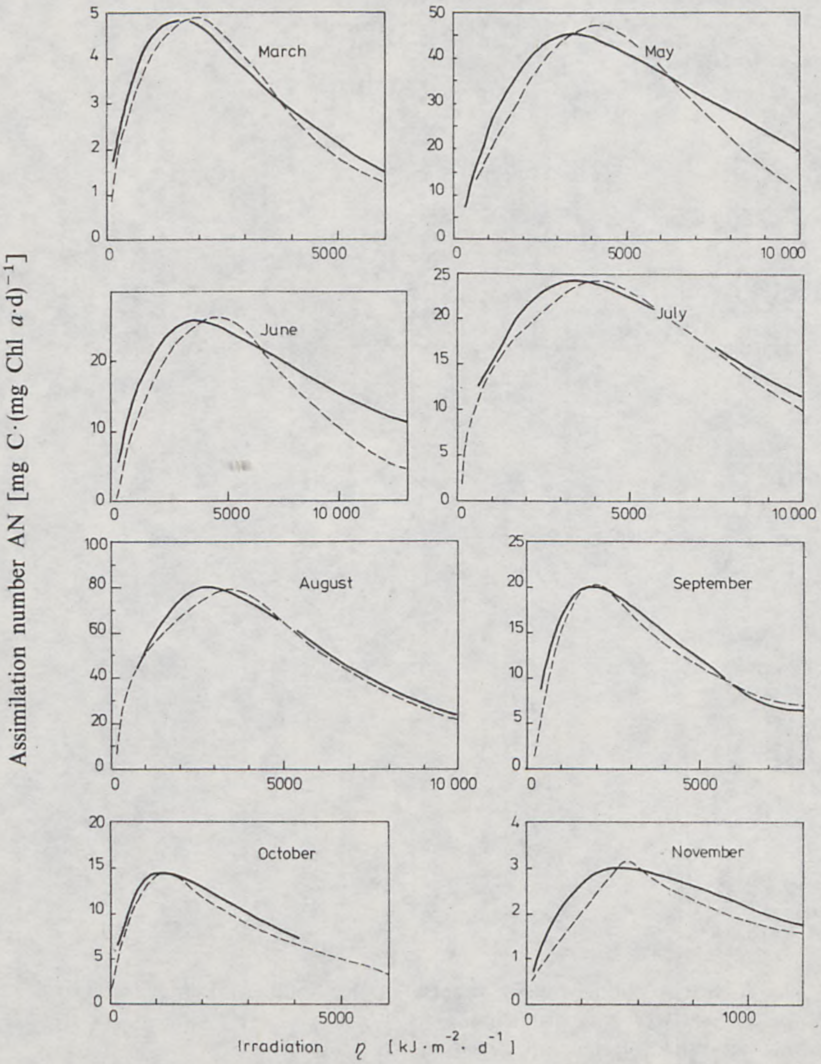

Fig. 4. Comparison of the averaged empirical light curves of photosynthesis in the Southern Baltic (broken lines) with theoretical curves (solid lines) described by the Platt's formula.

(together with standard deviations) absolute values of maximum assimilation numbers AN^{max*} for individual months are given in column 3 of Table 1.

The light curves of photosynthesis averaged for individual months were also approximated by a function. The expression postulated by Platt *et al* (1980), relating the rate of phytosynthesis to the irradiation, was employed in the following form:

$$AN = A\frac{1-e^{-\alpha\eta/A}}{e^{\beta\eta/A}}, \tag{2}$$

where A, α, β are parameters of the equation, distinguishing the light curves of photosynthesis.

The respective approximations were obtained using numerical methods of calculation of non-linear regressions. Their results are shown in Table 2. Apparently, the above equation approximates well the obtained averaged light curves of photosynthesis in the Southern Baltic. This is illustrated in Figure 4.

3.2. Distribution of the characteristic depths of photosynthesis in the sea

In order to find characteristic vertical distributions of intensity of photosynthesis in the sea, the results of two statistical generalizations were employed. These are:

(i) the set of averaged for individual months light curves of photosynthesis presented above (Fig. 3 and Table 1) $AN/AN^{max} = f_1(\eta)$,

(ii) the set of statistical distributions of daily irradiation in the Southern Baltic (see Table 3 and Fig. 5), published earlier by the authors (Woźniak and Hapter, 1985; Dera *et al*, 1984), $\eta = f_2(z)$.

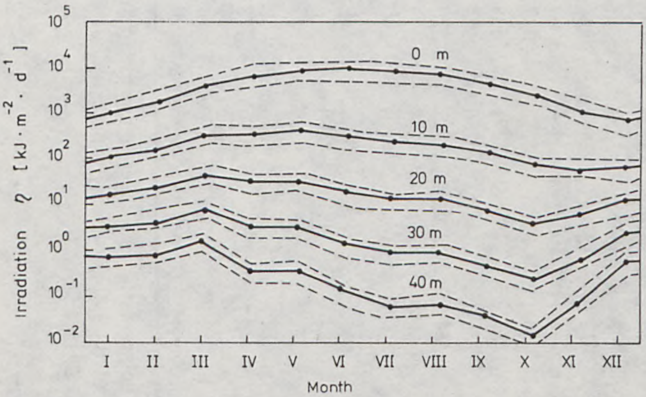

Fig. 5. Averaged seasonal changes of the daily irradiation at various depths in the Southern Baltic in the PhAR spectral region (400 – 700 *nm*)
Broken lines denote the values at small cloudiness, 0–2 in a 1–10 scale (above the soild line) and at large cloudiness, *ie* 8 – 10 (below the solid line)

* AN^{max} denotes a maximum of the light curve, *ie* it corresponds to an optimum irradiation

Table 3. Multiannual mean daily solar irradiation of visible light (400–700 nm) for every month at different depths in Southern Baltic* (Dera *et, al,* 1984) $\eta\,[kJ \cdot m^{-2} \cdot d^{-1}]$

Depth h [m]	Month											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
0	804	1628	3851	5989	8182	9475	8270	7134	4275	2416	955	572
0.05	793	1605	3797	5887	8035	9276	8096	6984	4194	2368	939	561
0.1	782	1582	3743	5785	7896	9087	7931	6842	4113	2319	923	550
0.25	751	1514	3501	5492	7487	8528	7443	6421	3877	2179	878	518
0.5	702	1408	3331	5037	6848	7675	6699	5779	3523	1967	807	471
1	613	1218	2877	4234	5727	6216	5425	4680	2898	1602	681	3088
1.5	535	1052	2484	3563	4795	5031	4391	3788	2390	1305	577	319
2	463	921	2153	2989	3944	4036	3523	3039	1949	1056	484	263
4	287	555	1271	1605	2037	1914	1646	1448	936	495	265	166
6	186	348	786	904	1113	966	817	735	475	246	152	109
8	124	226	501	529	629	517	426	392	247	127	90.1	74.4
10	84.4	151	327	317	366	285	229	215	133	67.4	54.8	52.6
12	58.9	103	216	193	217	161	127	121	73.5	36.7	33.9	37.8
14	41.4	70.5	145	120	131	93.1	70.7	69.1	41.5	20.3	21.1	26.9
16	29.3	49	99	74.9	79.6	54.4	40.1	39.9	23.6	11.3	13.7	19.4
18	21.0	34.4	67.8	47.1	49.0	32.2	23.1	23.3	13.6	6.43	8.72	14.3
20	15.1	24.1	46.6	30.1	30.3	19.2	13.2	13.3	7.95	3.67	5,64	10.4
25	6.79	10.3	18.8	9.94	9.33	5.46	3.48	3.69	2.11	0.92	1.95	5.37
30	3.16	2.46	7.74	3.35	2.96	1.6	0.93	1.03	0.58	0.24	0.69	2.87
40	0.69	0.88	1.37	0.40	0.31	0.14	0.07	0.08	0.04	0.02	0.09	0.75

* The presented data differ somewhat from those published earlier by the authors. It results from increasing amount of statistical data about the radiant energy transfer through the atmosphere and through the water column as well as from improvements of the empirical formulas

Using both statistical sets of data mentioned above, the depths characteristic for photosynthesis in the Southern Baltic were determined. Appropriate computations amounted here to formal reduction of the variable η from the system of dependences:

$$AN/AN^{max} = f_1(\eta),$$

$$\eta = f_2(z),$$

and determination of the relationship

$$z = f_3(AN/AN^{max}) \equiv f_2^{-1}(f_1^{-1}(z)).$$

The results of the above calculations are given in Table 4. It contains, determined for individual months, depths z at which relative assimilation number reach the values AN/AN^{max} equal to: 100%, 90%, ..., 10%. The

Table 4. Averaged characteristic depths corresponding to fixed values of the relative assimilation number in Southern Baltic in individual months

Month	Depth z[m] for respective percentage of the relative assimilation number AN/AN^{max}									
	light inhibition			light saturation			light reaction			
	30%	50%	70%	90%	100%	90%	70%	50%	30%	10%
	The average in the month									
II				1.1	1.6	3.6	5.6	8.1	11.2	14.8
III			0.1	0.9	1.8	3.8	6.6	9.4	12.5	17.1
IV			0.3	0.9	1.7	2.9	4.0	5.7	8.2	12.7
VI			0.4	0.9	1.4	2.6	3.5	5.4	7.3	9.9
VII			0.1	0.8	1.4	2.4	4.4	6.6	9.2	13.0
VIII			0.4	0.9	1.5	2.3	4.4	6.4	9.0	13.5
IX			0.2	1.1	1.8	2.9	4.5	5.9	7.9	11.4
X				0.6	1.3	2.3	3.6	4.9	7.2	11.3
XI			0.1	1.2	1.7	2.4	3.5	5.0	8.7	14.8
XII		0.5	1.2	1.5	1.9	3.6	4.6	5.7	8.2	12.0
	The average for days with small cloudiness (0–2 in 1 to 10 scale)									
II				3.5	4.2	6.4	8.6	11.3	14.6	18.2
III		0.8	1.5	2.4	3.3	5.5	8.5	11.4	14.7	19.6
V	0.5	1.0	1.5	2.1	3.0	4.1	5.4	7.1	9.7	14.4
VI	0.2	1.0	1.2	1.6	2.2	3.4	4.4	6.3	8.3	10.9
VII		0.5	1.0	1.7	2.4	3.4	5.5	7.8	10.5	14.4
VIII	0.0	0.6	1.3	1.8	2.5	3.4	5.5	7.6	10.4	15.0
IX		0.1	1.2	2.2	2.9	4.0	5.2	7.2	9.3	12.9
X			0.8	1.7	2.5	3.5	4.9	6.2	8.6	12.9
XI		1.1	2.3	3.5	4.1	4.9	6.1	7.7	11.7	18.0
XII		1.6	2.5	3.1	3.7	5.7	6.8	8.0	10.7	14.6

Table 4. (continued)

Month	Depth z[m] for respective percentage of the relative assimilation number AN/AN^{max}									
	light inhibition			light saturation			light reaction			
	30%	50%	70%	90%	100%	90%	70%	50%	30%	10%
	The average for days with large cloudiness (8–10)									
II				0.3	0.9	2.8	4.7	7.1	10.0	13.7
III					0.2	2.0	4.6	7.2	10.2	14.7
V					0.3	1.3	2.4	3.9	6.3	10.6
VI						1.0	1.8	3.5	5.3	7.7
VII					0.1	1.1	2.8	4.9	7.5	11.1
VIII					0.2	1.0	2.9	4.8	7.3	11.6
IX					0.5	1.5	2.6	4.5	6.4	9.8
X					0.3	1.3	2.5	3.7	6.0	10.0
XI				0.9	1.4	2.1	3.1	4.7	8.3	14.3
XII					0.1	1.2	1.7	2.5	4.6	8.0

results are reported for three different irradiation conditions: the average encountered in the Southern Baltic, extremely strong irradiation (for sunny days with cloudiness 0–2 in a ten degree scale) and extremely weak irradiation corresponding to days with a large degree of cloudiness (8–10 degrees).

4. Discussion and conclusions

4.1. Seasonal variability of light curves of photosynthesis

The results presented in paragraph 3.1 demonstrate a strong correlation between the irradiation at various depths in the sea and the intensity of photosynthesis observed there. However, the shapes of light curves of photosynthesis for particular months differ qualitatively and quantitatively.

Seasonal changes of the determined various statistical quantities and parameters characterizing light curves of photosynthesis in the Baltic are illustrated by the plots in Figure 6. All these quantities exhibit non-random variability in time. For example, it is evident from Figure 6A that the largest assimilation numbers of photosynthesis in the Southern Baltic has phytoplankton in May and August. This coincides more or less with the periods, noted by various authors, of spring and summer–autumn plankton blooming in this region of the Baltic (*eg* Renk, 1973, 1974; Torbicki, 1975). Interesting conclusions follow also from Figure 6B. As seen from this figure, the respective irradiation optimum for photosynthesis (see curve 1) is considerably lower in winter than in summer. For example, the dose for December is 14 times lower

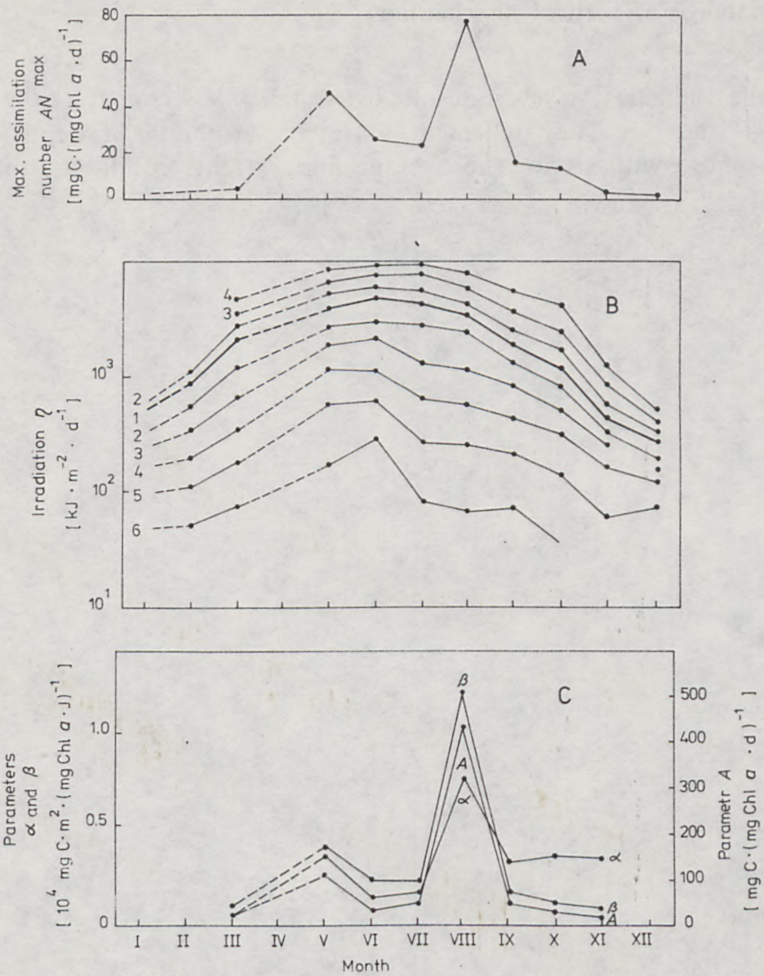

Fig. 6. Seasonal variability of maximum assimilation numbers AN^{max} (A) and the daily irradiation η corresponding to defined, relative values of assimilation numbers AN/AN^{max} in the Southern Baltic (B). Part (C) represents changes in values of light curve parameters approximated according to the Platt's formula (see Table 2)

Consecutive curves (1–6) express the daily irradiation corresponding to relative values of assimilation numbers AN/AN^{max} equal to: 1–100%, 2–90%, 3–70%, 4–50%, 5–30%, and 6–10%

than that for June (303 $kJ \cdot m^{-2} \cdot d^{-1}$ and 4900 $kJ \cdot m^{-2} \cdot d^{-1}$, respectively). This demonstrates high adaptability of natural cultures of the Baltic photosynthesis for diversified irradiance conditions in the sea in different seasons of the year. The adaptation involves a change in species composition of the phytonplankton and, consequently, the composition of its pigments, which has been demonstrated in the paper by Woźniak (1985).

4.2. Seasonal variability of vertical distributions of zones of photosynthesis

A direct graphical illustration of the results listed in Table 4 constitute the plots in Figure 7 and 8*. They represent seasonal variability of depths characteristic for photosynthesis for the average and extreme conditions of

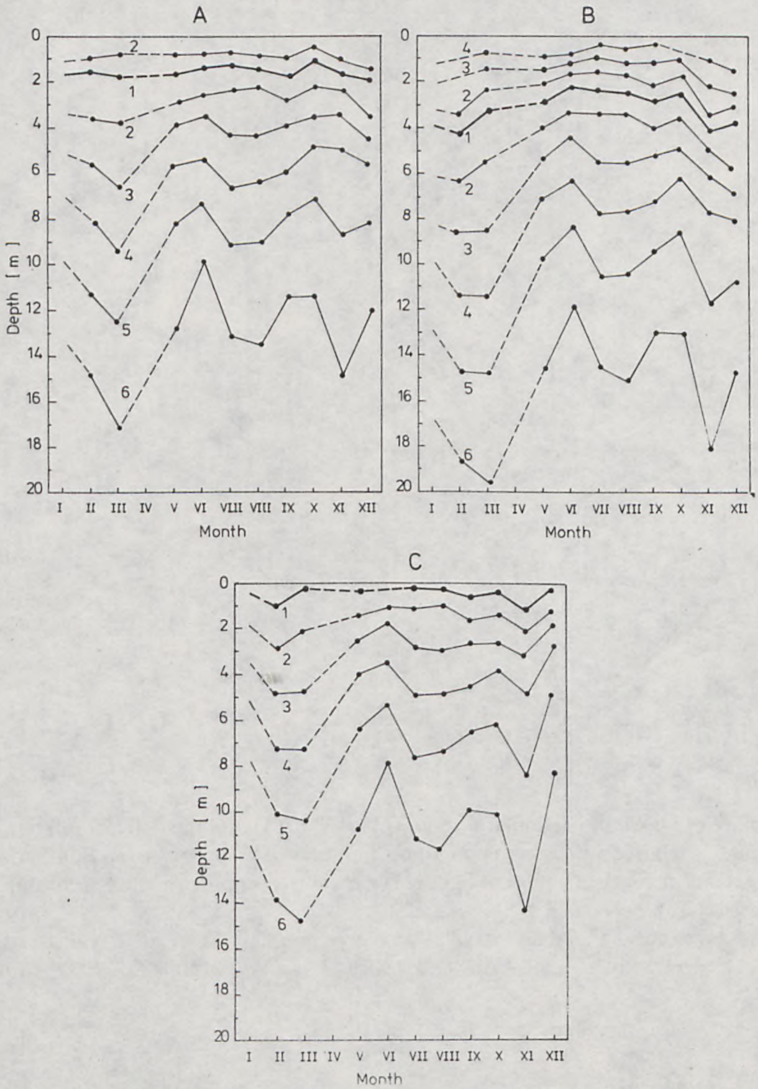

Fig. 7. Averaged seasonal changes in depth of fixed relative assimilation numbers AN/AN^{max} isolines in the Southern Baltic

A – for the average irradiance conditions, B – at small cloudiness (0 – 2) in a 1 to 10 scale), C – at large cloudiness (8 – 10). Consecutive curves (1 – 6) express the AN/AN^{max} values: 1 – 100%, 2 – 90%, 3 – 70%, 4 – 50%, 5 – 30%, and 6 – 10%.

* The plot in Figure 8 illustrates changes in location of individual photosynthesis zones with an assumption that the depths delimiting the regions: III (inhibition, *ie* over saturation with light), II (optimum irradiation), and I (undersaturation) are depths at which $AN/AN^{max} = 90\%$.

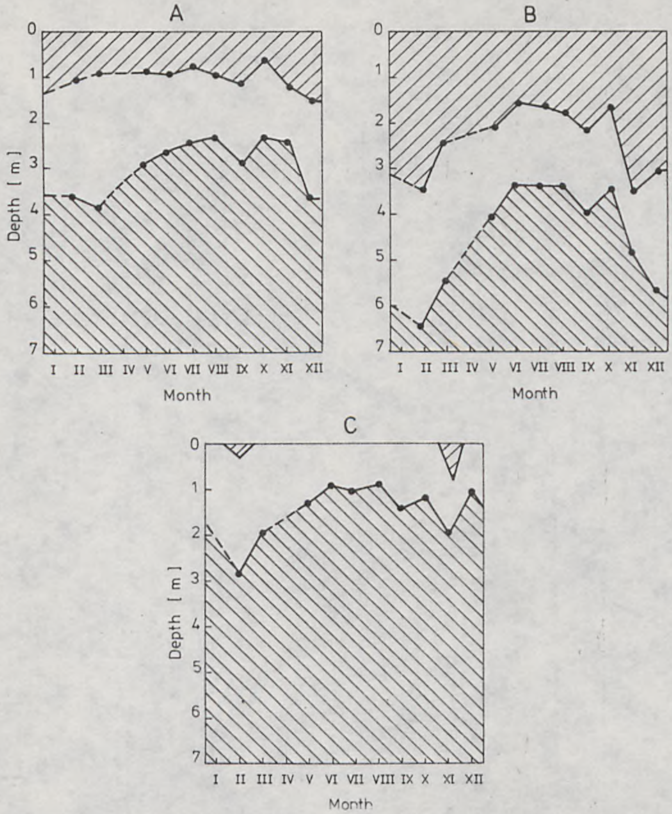

Fig. 8. Seasonal changes of particular zones of photosynthesis (oversaturated with light – the upper one, optimally irradiated – the white one, undersaturated with light – the lower one) in the Southern Baltic

A – for the average irradiance, B – for days with small cloudiness (0 – 2), C – for days with large cloudiness (8 – 10)

cloudiness. On the other hand, Figure 9 illustrates these results in the form of typical of individual months depth profiles of relative intensity of photosynthesis $AN/AN^{max} = f_3(z)$.

Apparently, in the case of average irradiance and small depths (Fig. 7A) the profiles of relative intensity are similar for all months. Particular zones of photosynthesis occur most frequently at the depths (Fig. 8A): 0 – 1 m (the zone of light inhibition), 1 – 3 m (the zone of light saturation) and below 3 m (the zone of undersaturation with light, *ie* light reactions region). These depths are similar despite the fact that in different seasons considerable differences in the level of irradiation occur there (Fig. 5). The stability of vertical distributions of relative intensity of photosynthesis presented above indicates the already mentioned high adaptability of natural phytocenoses to diversified irradiance conditions in various seasons of the year.

In spite of similarities in the surface layer, a seasonal diversity of location of the AN/AN^{max} isolines, increasing with depth, is observed in the zone of

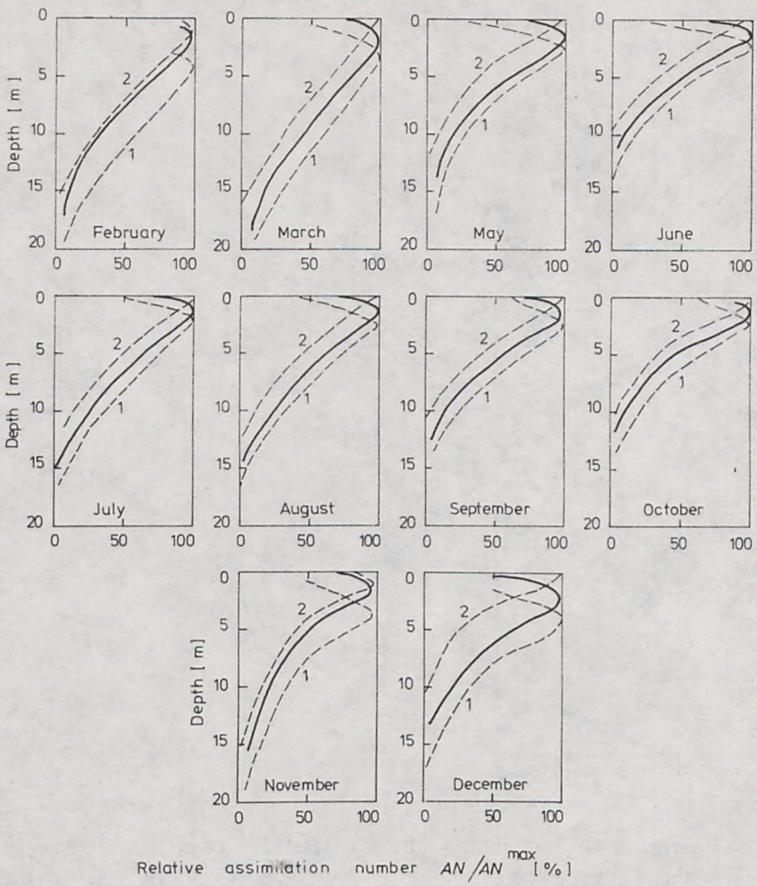

Fig. 9. Averaged vertical distributions of relative values of assimilation numbers AN/AN^{max} in the Southern Baltic in individual months
Solid curves – for the average irradiance conditions; broken curves: 1 – for days with small cloudiness (0–2), 2 – for days with large cloudiness (8–10)

undersaturation with light (*eg* see curves with indices $\geqslant$ 5 in Figure 7A). It consists in somewhat larger 'breadths' of the productive zones during the winter–spring period compared to summer and fall.

Comparison of the distribution of photosynthesis zones characteristic of the average irradiance conditions (Figs. 7A and 8A) with those for the days with large and small cloudiness (Figs. 7B, C and 8B, C, respectively) reveals that the weather changes strongly affect the depth distribution of the intensity of photosynthesis. Thus, in the case of small cloudiness an increase af all characteristics for photosynthesis depths is observed compared to the average irradiance conditions, most often by about 1–3 m. On the other hand, in the case of cloudy days particular zones of photosynthesis are shifted upwards relative to the average locations by about 2 m. Under the circumstances, the light saturation zone appears already just below the water surface, while the light inhibition zone does not occur at all.

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