Papers

The assimilation of light energy by marine phytoplankton. Part 1. The light absorption capacity of the Baltic and Black Sea phytoplankton (methods; relation to chlorophyll concentration)

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Marine photosynthesis
Specific absorption of phytoplankton pigments
Baltic Sea
Black Sea

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Abstract

This paper discusses the significance of the light absorption capacity of marine phytoplankton as a measure of the photosynthetically active phytoplankton biomass, and as a means of calculating the energy flux at the input of the production process; its neccesity in evaluating the efficiency of phytoplankton photosynthesis and working out models of primary production in the sea is stressed.

The methods worked out by the authors of this paper and by other specialists are reviewed, and the values of light absorption by phytoplankton obtained during five cooperative cruises to the Baltic and Black Seas are compared with data published by other authors. These values demonstrate good agreement with the results of modelling light absorption by phytoplankton inhabiting waters of different productivity.

1. Introduction

Interest in the problems connected with light energy assimilation during marine photosynthesis in both Institutes arose long ago. Photosynthesis-light relationships have been studied since the late fifties and sixties (Koblentz-Mishke, 1960; Koblentz-Mishke and Ochakovskiy, 1966; Dera, 1971; Dera *et al.*, 1974; Hapter and Woźniak, 1977; Woźniak *et al.*, 1980).

From 1978 to 1990 specialists from the two Institutes of Oceanology carried out five joint cruises to the Black and Baltic Seas. Among other oceanological and hydrobiological research, they carried out a large series of measurements connected with the assimilation of light energy by marine phytoplankton. One of the most important aims of these investigations was to develop a practicable evaluation of the quantum yield of photosynthesis.

But until recently, the greatest obstacle in the way of measuring this parameter was the absence of routine methods for measuring the light absorption capacity (LAC) of phytoplankton in the natural environment.

At the present time such methods are well on the way to being worked out by the authors of this paper. In the course of the five above-mentioned expeditions, numerous LAC data were obtained.

The LAC data, gathered by the authors at the same time as measurements of hydrooptical and primary productivity parameters, enable not only the photosynthetic efficiency to be evaluated, but also bio-optical models of primary production to be worked out and algorithms for its indirect estimation to be suggested. The values obtained are compared with literature data and with the results of model computations by one of the authors (Woźniak, 1989; Woźniak and Ostrowska, 1990b).

The most important parameters discussed here are the average LAC coefficient of phytoplankton (in the 400–700 nm wavelength range) a_{pl}, and the specific coefficient of light absorption by phytoplankton a^*_{pl}, *i.e.* the ratio of a_{pl} to chlorophyll a + pheopigment concentration.

Measured under the conditions of a spectrally and energetically uniform light field, these characteristics, strictly speaking, reflect only the latent capacity of phytoplankton pigments to absorb light energy. Their real absorption *in situ* depends on the parameters of underwater light energy.

But their importance should not be overrated. In particular, a_{pl} is a more precise quantitative measure of the photosynthetically active biomass than the chlorophyll concentration (Koblentz-Mishke, 1979, 1980).

In the process of determining a_{pl}, the values of $a_{pl}(\lambda)$ are established. This leads to the possibility of calculating PUR (Morel, 1978), *i.e.* the absorption of radiant energy by phytoplankton *in situ*, which is a highly significant ecological parameter illustrating quantitatively the energy flux at the input of the production process. Evaluated by physical methods, PUR is estimated much more precisely than the analogous biological characteristics. Moreover, PUR is an essential component of the underwater light energy balance.

The exact determination of $a_{pl}(\lambda)$ and spectral PUR is essential for an accurate evaluation of the quantum yield of photosynthesis.

Generally speaking, the materials obtained on LAC allow for a better understanding of the regularities of the expansion and transformation of light energy in the sea, and enable primary production to be modelled successfully and reliable algorithms for its evaluation to be worked out.

1.1. Historical notes on the methods of LAC determination

The parameters characterising light absorption by marine phytoplankton have attracted the attention of many leading scientists, beginning with Steele (1962), who transferred parameter a from plant physiology to marine ecology, and Yentsch (1960, 1962), who laid the foundations of modern methods of measuring this parameter. Then during *ca* 20 years, attempts were made to work out the appropriate field methods to this end. Some dozens of articles appeared on this subject, reviewed in recent publications (*e.g.* Morrow *et al.*, 1989; Bricaud and Stramski, 1990; Babin *et al.*, 1993), so that there is no point in reiterating the literature survey on the methods for determining a_{pl}.

Briefly, there are two main approaches to the problem. The first, an indirect one, is based on hydrooptical *in situ* measurements (Tyler, 1975). Its discussion lies beyond the scope of the present article, but the results obtained using this approach are compared with our data (Tab. 1).

The second, direct approach entails two measurements of the absorption coefficient: of seston samples, concentrated mostly during filtration, and after the bleaching of pigments. In both measurements, the pathlength amplification factor β must be taken into account. The details of the direct method are very important in the context of this paper. A large set of data concerning spectral absorption by phytoplankton now exists, but methodological differences make comparison of results difficult.

Table 1. Some literature data on a^*_{pl} and a^{**}_{pl} [m^{-1} (mg chl a $m^{-3})^{-1}$]

Region or object	Phyto-cenosis	Literature	Method	a^*_{pl}	a^{**}_{pl}	Remarks
coastal phyto-plankton	eutrophic	Yentsch, 1960	direct	0.013		average from several samples
coastal phyto-plankton	eutrophic	Lorenzen, 1972	direct	0.0138		average from 26 populations
Saragasso Sea	oligo-trophic	Tyler, 1975	indirect hydro-optical		0.0415	average from many measure-ments in the 0–10 m layer
Atlantic, Maure-tanian upwelling region	meso-trophic	Morel and Prieur, 1977; Morel, 1978	indirect hydro-optical	0.0142	(0.014)	average in the surface layer
various seas and fresh-water basins and cultures	various	Bannister, 1974	various	(0.016 ± 0.003)	(0.016 ± 0.003)	global average in the surface layer
various sea basins	various	Atlas and Bannister, 1980	various		0.005 – 0.025	observed range for various depths
cultures		Morel and Bricaud, 1981	direct	0.0180 0.0397 0.0305		*Platymonas suecica* *Coccolithus huxleyi* *Chaetoceros protuberans*
cultures		Bannister and Weidemann, 1984	indirect calcula-tions		0.010 – 0.021	*Chlorella pyrenoidosae* *Coccolithus huxleyi*

Table 1. (continued)

Region or object	Phyto-cenosis	Literature	Method	a^*_{pl}	a^{**}_{pl}	Remarks
Plussea Edeberg-sea	eutrophic lakes	Meffert and Overbeck, 1985	indirect	0.0135 0.0124 0.0073		winter bloom spring bloom summer bloom
Pacific Ocean	oligo-trophic	Kishino *et al.*, 1986	direct	0.022 – 0.030	0.022 – 0.050	changes from surface to a depth of 100–150 m
Sargasso Sea	oligo-trophic	Smith *et al.*, 1989	direct		0.0144 – 0.0400	range in example profile
North Atlantic	0.1 – 8 mg m^{-3} chl *a*	Yentsch and Phinney, 1989	direct	0.049: $\lambda = 440$ nm 0.028: $\lambda = 670$ nm		mean from 10 cruises
cultures		Sakshaug *et al.*, 1991	direct		0.014* 0.0065 0.024* 0.028	*Thalassiosira nordenskioeldii* *Chaetoceros furcellatus*
cultures		Sosik and Mitchell, 1991	direct	0.027 ÷ 0.040 $\lambda = 436$ nm 0.019 ÷ 0.021 $\lambda = 668$ nm		*Dunaliella tertiolecta*
Grand Banks		Prasad and Hollibaugh, 1992	indirect	0.015		average in euphotic layer

*two values for a different growth ratio

In order to distinguish light absorption by pigments from that by other absorbent materials, direct and numerical procedures have been proposed, the latter initially by Kiefer and Soo Hoo (1982). This was later improved

and combined with the measurements of phytoplankton fluorescence excitation spectra (Mitchell and Kiefer, 1984, 1988; Morrow *et al.*, 1989). Bidigare *et al.* (1989) reconstructed an absorption spectrum from published absorption coefficients of the main pigments. Bricaud and Stramski (1990) proposed another method, based on the assumption that the absorption spectrum of detritus changes logarithmically with wavelength.

The most promising modern method is based on the microphotometering of individual algal cells (Iturriaga and Siegel, 1989), but unfortunately its present modification is too laborious for field conditions.

The direct method for a_{pl} discrimination has been adopted in our investigations since 1966 (Konovalov and Bekasova, 1969). In principle, it involves the determination of the light absorption coefficients of seston on the filters before and after removal of pigments. These can be removed by oxidation

Table 2. The most important details of the methods for measuring $a_{pl}(\lambda)$ during the various expeditions

Vessel, expedition year	Filters, pore size, $\bar{\rho}_f$	Spectrophotometers, regime of measurements	Corrections	Pigment removal method
'Vityaz' 64 1978	SYNPOR N4 + $BaCO_3$ layer 0.85 μm $\bar{\rho}_f = 0.75$	SF–14 Sample and reference filters at the middle of Ulbricht's sphere	K factor eq. (6)	$UV + H_2O_2$
'Profesor Siedlecki' 14 1980	Nucleopore 1 μm $\bar{\rho}_f = 0.20$	Specord UV–VIS Shibata *et al.*, 1954	for the number of filter layers	freezing solvents alkali
'Akademik Kurchatov' 39 1984	SYNPOR N5 + $BaCO_3$ layer 0.65 μm $\bar{\rho}_f = 0.75$	SF–18 Sample and reference filters at the middle of Ulbricht's sphere	$\beta(\lambda, D)$ Konovalov, 1992 eq. (4)	$UV + H_2O_2$
Sopot'87 experiment 1987	GF/C 1.2 μm $\bar{\rho}_f = 0.465$	see 'Akademik Kurchatov'	$\beta(\lambda, D)$ Konovalov, 1992 eq. (5)	$UV + H_2O_2$
'Professor' Shtokman' 25 1990	GF/F 0.6 μm $\bar{\rho}_f = 0.60$	see 'Akademik Kurchatov'	$r\beta(\lambda, D)$ Konovalov, 1992 eq. (5)	$Ca(OCl)_2$ 2% solvent

or by solvents. During most of our cruises, pigments were oxidised by H_2O_2 and UV or by $Ca(OCl_2)$ (Tab. 2).

Kishino *et al.* (1985) used methanol for dissolving pigments.

In both the Konovalov and the Kishino methods of pigment removal there exist sources of error. In the former, excessive bleaching may result in removing from the filters both the extractable pheopigments and the detrital carotenoids present in the debris. In the case of methanol, water-soluble pigments remain unextracted.

The pathlength amplification of the light beam, or the 'β factor', was introduced into the results of early publications as a constant value for the whole spectrum range and for all samples, (*e.g.* Kiefer and Soo Hoo, 1982); later, however, the dependence of β on the optical density of samples was noticed and corresponding formulae were proposed (Mitchell and Kiefer, 1984, 1988). Konovalov (1992) also established the dependence of β on the clean filter reflectance coefficient $\bar{\rho}_f$ and on the wavelength.

It should be mentioned that Konovalov's experiments on the regularities of β formation took many years. They were also performed during several cruises in the highly productive waters of the Pacific and Atlantic oceans. They involved the comparison of the optical density of phytoplankton samples spectrophotometered both in suspension and after filtration.

2. Material and methods

The basic information about the joint expeditions are presented in Vinogradov (1980), Koblentz-Mishke *et al.* (1985), Koblentz-Mishke and Belayeva (1987), Konovalov *et al.* (1990).

Some data on the experimental points are given in Tab. 3. Fig. 1 shows the position of the stations.

Table 3. Data on experimental points and the ecological conditions obtaining there (explanation of symbols below table)

Station	Date	Lat. °N	Long. °E	$C_a(0)$	P_{tot}	ε_{tot}	η_0
r/v 'Vityaz' 64th cruise (Black Sea):							
7894/1	1978.09.26	44°25′	37°48′	0.23	224	0.208	10.43
7894/2	1978.09.28	44°25′	37°44′	0.28	348	0.182	18.48
7896	1978.09.29	44°25′	37°57′	0.17	603	0.38	15.34
7897/1	1978.10.04	44°08′	37°23′	0.16	368	0.233	15.25
7897/2	1978.10.05	44°08′	37°22′	0.16	295	0.192	14.83
7898/2	1978.10.09	43°31′	36°51′	0.18	437	0.282	14.96
7899/1	1978.10.11	43°11′	36°15′	0.13	518	0.332	15.08

Table 3. (continued)

Station	Date	Lat. °N	Long. °E	$C_a(0)$	P_{tot}	ε_{tot}	η_0
7899/2	1978.10.12	43°02′	36°15′	0.19	478	0.324	14.25
7903/1	1978.10.24	43°17′	31°25′	0.31	228	0.389	5.66
7903/2	1978.10.25	43°10′	31°18′	0.35	434	0.403	10.35
7904	1978.10.27	43°00′	34°00′	0.45	355	0.694	4.94
r/v 'Profesor Siedlecki' 14th cruise (Baltic):							
B–2	1980.07.07	55°14′	17°01′	0.89	377	0.147	22.00
B–2	1980.07.08	55°14′	17°01′	1.12	394	0.141	23.42
B–2	1980.07.11	55°14′	17°01′	1.71	525	0.196	23.84
B–2	1980.07.12	55°14′	17°01′	1.15	417	0.153	23.72
B–2	1980.07.13	55°14′	17°01′	1.29	356	0.333	9.47
B–2	1980.07.14	55°14′	17°01′	1.99	503	0.163	26.73
2	1980.07.18	54°36′	19°06′	7.98	829	0.531	13.49
2	1980.07.19	54°36′	19°06′	4.58	632	0.471	11.56
G–2	1980.07.21	54°50′	19°20′	6.27	364	0.631	4.94
G–2	1980.07.23	54°50′	19°20′	5.95	898	0.479	21.20
G–2	1980.07.24	54°50′	19°20′	4.22	498	0.417	12.86
G–2	1980.07.25	54°50′	19°20′	3.77	610	0.404	17.77
r/v 'Akademik Kurchatov' 39th cruise (Baltic):							
4174	1984.05.17	55°52′	18°51′	2.78	659	0.328	21.24
4178	1984.05.18	56°12′	20°42′	3.37	630	0.307	19.01
4179	1984.05.19	56°54′	17°28′	0.72	208	0.099	19.38
4180	1984.05.20	57°13′	20°57′	1.36	505	0.206	23.23
4181/1	1984.05.22	57°18′	20°58′	2.25	504	0.228	19.66
4195/1	1984.05.25	56°43′	19°46′	4.27	602	0.272	25.08
4195/2	1984.05.25	56°44′	19°37′	1.02	379	0.171	17.68
4201/1	1984.05.27	58°01′	19°55′	2.55	304	0.344	8.22
4201/2	1984.05.27	58°02′	19°56′	1.53	241	0.272	8.70
4208/1	1984.05.29	58°25′	20°04′	1.13	422	0.244	15.63
4208/2	1984.05.29	58°29′	20°06′	0.64	270	0.156	16.97
4216	1984.06.05	59°37′	22°42′	1.38	481	0.183	27.31
4223/1	1984.06.07	59°58′	21°14′	1.32	300	0.124	26.97
4223/2	1984.06.07	59°53′	21°31′	1.06	329	0.136	20.28
Sopot'87 experiment (Gulf of Gdańsk):							
G–2	1987.05.01	54°50′	19°20′	14.8	943	0.444	20.88
G–2	1987.05.02	54°50′	19°20′	19.6	1151	0.583	19.75
G–2	1987.05.02	54°50′	19°20′	13.6	1031	0.523	19.75
G–2	1987.05.03	54°50′	19°20′	11.0	699	0.536	12.79
Z	1987.05.05	54°32′	18°50′	19.7	589	0.416	13.64
Z	1987.05.05	54°32′	18°50′	23.0	853	0.602	13.64
Z	1987.05.06	54°32′	18°50′	19.5	968	0.482	20.11
Z	1987.05.06	54°32′	18°50′	17.4	730	0.364	20.11

Table 3. (continued)

Station	Date	Lat. °N	Long. °E	$C_a(0)$	P_{tot}	ε_{tot}	η_0
r/v 'Professor Shtokman' 25th cruise (Baltic):							
2603	1990.01.31	55°21′	16°00′	0.40	154	0.737	2.07
2605/1	1990.02.01	55°36′	15°05′	0.59	142	0.575	2.45
2605/2	1990.02.01	55°36′	15°05′	0.80	120	0.489	2.45
2609/1	1990.02.03	55°14′	17°04′	0.78	140	0.421	3.39
2609/2	1990.02.03	55°14′	17°04′	0.71	174	0.524	3.39
2623/1	1990.02.06	55°54′	18°56	0.26	68	0.141	5.01
2623/2	1990.02.06	55°54′	18°56′	0.60	167	0.345	5.01
2632	1990.02.10	58°56′	20°59′	0.42	56	0.203	2.77
2634/1	1990.02.11	59°25′	21°22′	0.40	62	0.248	2.50
2634/2	1990.02.11	59°25′	21°22′	0.44	70	0.281	2.50
2635/1	1990.02.16	58°40′	18°36′	0.45	111	0.358	3.12
2635/2	1990.02.16	58°40′	18°36′	0.62	76	0.246	3.12
2636	1990.02.17	57°23′	20°06′	0.79	118	0.577	2.01
2646	1990.02.18	57°25′	19°56′	0.46	61	0.481	1.24
2661/1	1990.02.21	57°39′	19°27′	0.24	89	0.307	2.96
2661/2	1990.02.21	57°39′	19°27′	0.38	90	0.310	2.96
2672/1	1990.03.02	55°23′	18°02′	0.78	152	0.450	3.39
2672/2	1990.03.02	55°23′	18°02′	1.08	155	0.459	3.39

Symbols:

$C_a(0)$ – chlorophyll *a* concentration at the sea surface [mgC m^{-3}],
P_{tot} – diurnal total primary production in the water column [mgC m^{-2} day^{-1}],
ε_{tot} – photosynthetic index [%],
η_0 – diurnal dose of solar energy over the whole spectrum range at the sea surface [MJ m^{-2} day^{-1}].

Four of the five expeditions reported on here were conducted in the Baltic Sea, only the first having been in the Black Sea. The Baltic Sea is being used as a reference area for developing approaches to the general problem and for methodological studies.

2.1. Sampling

Sampling was accompanied by continuous measurements of CTD, water transparency and fluorescence, which facilitated the choice of the sampling depths.

Chlorophyll and a_{pl} were determined in sample aliquots of 5 to 30 l from large water bottles. The remainder of the sample volume was used for measuring the primary production and the other parameters.

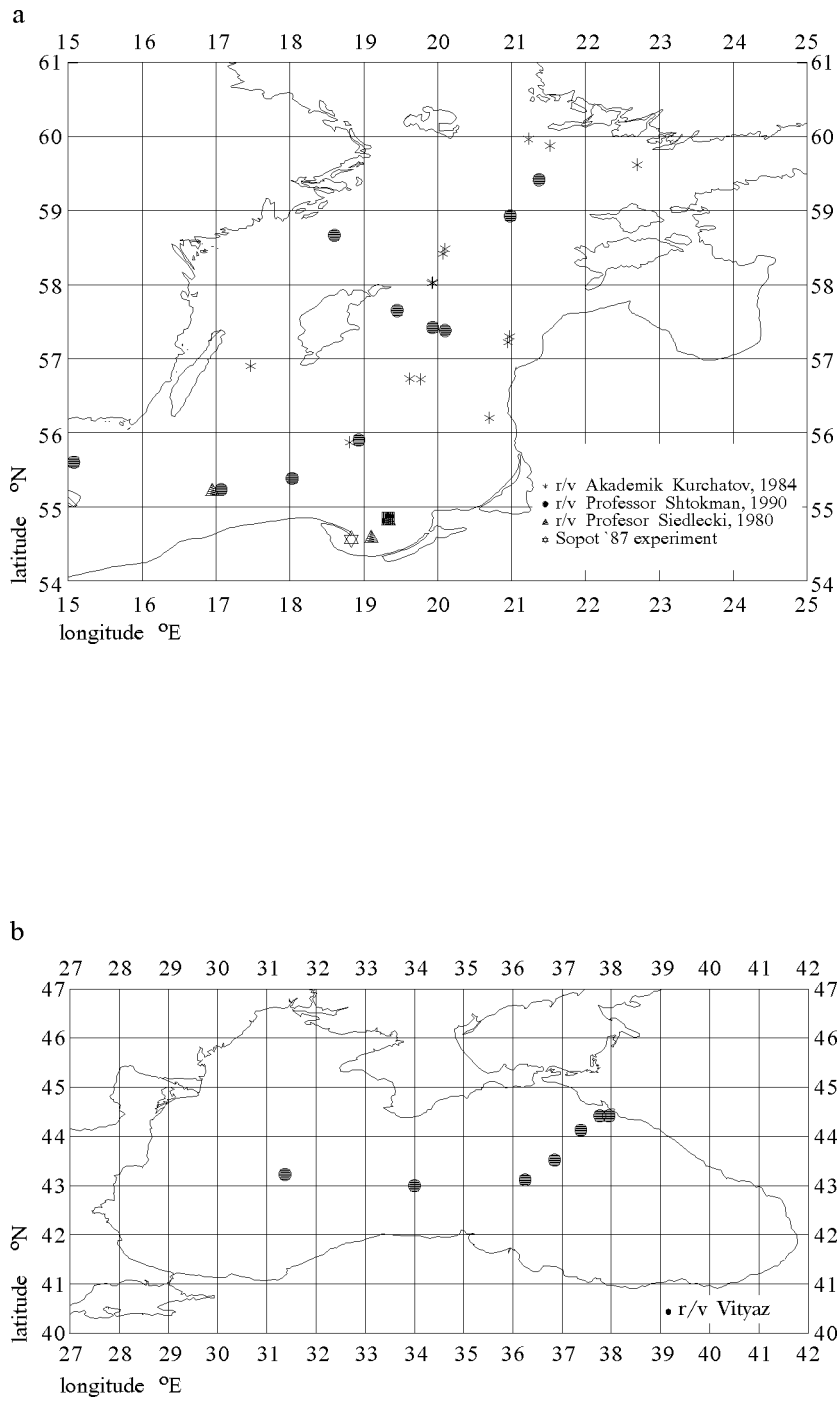

Fig. 1. Positions of experimental points: the Baltic Sea (a), the Black Sea (b)

2.2. Chlorophyll *a* concentration

The determinations of chlorophyll concentration were performed by the extracting spectrophotometric method (SCOR–UNESCO, 1966) in various modifications described in the papers reporting on the relevant cruises. The most important differences between these modifications arose during the filtering of water samples.

In the 'Vityaz' cruise 64 and the 'Akademik Kurchatov' cruise 39, acetone-soluble SYNPOR membrane filters No. 4 or 5 (pore size 0.85 and 0.65 mm) with a finely-dispersed $BaCO_3$ powder cover were utilised. Before pigment extraction this layer, together with the phytoplankton settled on the powder surface, was detached from the filter surface and transferred to the centrifugal vials.

In the remaining cases filters without $BaCO_3$ were used. In the 'Profesor Siedlecki' cruise Nucleopore filters were adopted (pore size 1 μm). In the Sopot'87 experiment use was made of GF/C fibreglass filters (1.2 μm pores), whereas in the 'Professor Shtokman' cruise 25 GF/F filters (0.6 μm pores) were employed.

Pigments were extracted with 90% acetone.

The extracts were spectrophotometered in the following types of spectrophotometers: two-beam Specord UV–VIS ('Profesor Siedlecki', Sopot'87), two-beam SPh–14 ('Vityaz'), single-beam SPh–4a ('Akademik Kurchatov'), and two-beam SPECORD M40 ('Professor Shtokman'). The computations using the Jeffrey and Humphrey (1975) formulae yielded the total chlorophyll and pheophytin *a*.

An example of the optical density spectrum of the acetone extract is shown in Fig. 2 (curve 1).

Additionally, the highly informative but unreasonably forgotten parameter, namely the pigment index, P_i, (Margalef, 1960) was calculated, as usual since 1968, at the P. P. Shirshov Institute.

2.3. Light-absorbing capacity of phytoplankton pigments *in vitro*

As mentioned earlier, we improved and later applied in the expeditions the direct spectrophotometric *in vitro* method for determining a_{pl} proposed by Yentsch (1962). It entails

a) filtering water samples (see previous section);

b) spectrophotometering wet filters with particulate material, including the phytoplankton settled on them in the process of filtering.

During the 'Profesor Siedlecki' cruise this was done using a 'Specord UV–VIS' spectrophotometer fitted with an opal glass. To maximise the spectral absorption signals, the sample filter was cut into a number of strips

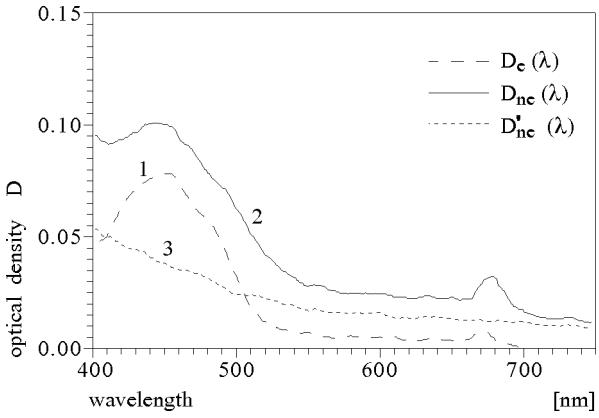

Fig. 2. An example of initial extinction spectra for calculations of a_{pl}: $D_e(\lambda)$ – in a pigment extract, $D_{ne}(\lambda)$ – wet filter with suspended matter containing phytoplankton, $D'_{ne}(\lambda)$ – the same filter after removal of pigments

which were stacked in layers of 2–4. The nonlinearity of the results of such stacking was established by special measurements and taken into account in the calculations (Konovalov, 1985), *i.e.* the light absorption by seston settled on a single Nucleopore filter layer was used as the input parameter for further calculations.

In the remaining cases SF–14 or SF–18 spectrophotometers equipped with an Ulbricht light-scattering sphere, in the middle of which a sample and a blank filter were placed, were used. An example of the resulting curve is shown in Fig. 2 (curve 2).

c) removal of pigments from filters.

For this purpose filters with settled material during the 'Profesor Siedlecki' cruise were frozen for 30 minutes, treated with 90% acetone and then with 0.15 N NaOH for several minutes. The remaining pigments were removed with a 1:3 ethanol-acetone mixture. The filters were successively transferred into Petri dishes containing small amounts of the above reagents; the filters floated on their surface. Between each treatment they were dried with filter-paper.

During the 'Vityaz' and 'Kurchatov' cruises as well as during the Sopot'87 experiment the removal of pigments was effected by UV radiation in Petri dishes, at the bottom of which there was a filter paper immersed in hydrogen peroxide (H_2O_2) solution.

Another technique of pigment removal was used during the 'Professor Shtokman' cruise. The filters were placed in special small boxes folded from hemi-blotting paper and kept afloat for 2 hours on the surface of a 2% solution of $Ca(OCl)_2$ poured out into a wide vessel covered by a lid.

After pigment removal, the filters were spectrophotometered repeatedly, which process yielded curve 3 in Fig. 2. The most important details of the methods for measuring $a_{pl}(\lambda)$ are presented in Tab. 2.

d) computations of the light absorption coefficient by pigments.

The spectral light absorption coefficient by pigments, $a_{pl}(\lambda)$ was computed from the formula

$$a_{pl}(\lambda) = \frac{D_{ne}(\lambda)\ S}{\beta(\lambda)\ V} - \frac{D'_{ne}(\lambda)\ S}{\beta(\lambda)\ V}, \tag{1}$$

where

S – the filter surface area,
V – the volume of the filtered sample,
$D_{ne}(\lambda)$,
$D'_{ne}(\lambda)$ – the respective optical densities of the seston before and after pigment removal,
β – the pathlength amplification factor.

The mean light absorption coefficient a_{pl}, in the PAR range was computed from the formula

$$a_{pl} = \frac{1}{300}\int_{400}^{700} a_{pl}(\lambda)d\lambda. \tag{2}$$

As was shown by special experiments (Konovalov, 1992), coefficient β exhibits a complicated dependence on three parameters: the filter reflectance coefficient ρ, the optical density of the seston D and the wavelength λ. The complicated nonlinear dependences of any of these parameters (when the others are constant) are very difficult to express mathematically. Konovalov recommended measuring D in the $0.05 < D < 0.4$ range. When $D > 0.4$ the pathlength amplification factor increases sharply and is hard to determine; when $D < 0.05$ the errors associated with the low signal level and backscattering become excessive.

The general formula for $0.05 < D < 0.4$ is

$$\beta = mD + n, \tag{3}$$

where

$m = a_m\lambda + b_m$,
$n\ = a_n\lambda + b_n$.

Konovalov (1992) found coefficients a_m, b_m, a_n, b_n for different types of filters. From his work two formulae were used for corrections of β:

$$\beta(\lambda) = (0.0021\ \lambda - 6.35)\ D + 0.00073\ \lambda + 4.38 \tag{4}$$

and

$$\beta(\lambda) = (0.00234\ \lambda - 4.54)\ D + 0.00033\ \lambda + 2.92, \tag{5}$$

where D is the optical density of the sample on the filter and λ is expressed in nanometers.

Formula (4) was used in calculations of the results during the 'Professor Kurchatov' cruise (SYNPOR N5 filters + $BaCO_3$ layer) and expression (5) for the results of the 'Professor Shtokman' cruise (GF/F) and the Sopot'87 experiment (GF/C filters).

In the case of the 64th 'Vityaz' cruise the corrections for the internal scattering of the filter material and sediment was based on the assumption that the optical density integrals in the PAR range of the phytoplankton settled on the filter and its extract are practically equal. Now it has become clear that such an assumption is not quite correct. Nevertheless, for the materials of the 'Vityaz' cruise the correction (β') was introduced:

$$\beta' = \frac{\int_{400}^{700} a_{pl}(\lambda)\ d\lambda}{\frac{V_e}{V_p\ l} \int_{400}^{700} D_e(\lambda)\ d\lambda}, \tag{6}$$

where

$D_e(\lambda)$ – optical density of acetone extracts of phytoplankton,
V_e – volume of acetone extract,
V_p – volume of sample,
l – length of the absorption cell.

The utilisation of the constant coefficient β' instead of $\beta(\lambda)$ during the 'Vityaz' cruise leads both to the misrepresentation of the real spectrum of $a_{pl}(\lambda)$ and to the overestimation of a_{pl}. This, in turn, results in an underestimation of the energetic efficiency of photosynthesis.

3. Results and discussion

The statistical dependence of a_{pl} on C_a, derived from the experimental data listed in Tab. 3, shows very clearly (Tab. 4 and Fig. 3) that the mean light absorption by pigments a_{pl} grows with increasing chlorophyll concentration, as might be expected, but that a direct proportionality between these parameters exists only from a level slightly exceeding 1 mg m^{-3} of chlorophyll. Within the euphotic layer of mesotrophic and eutrophic waters examined in the Baltic and Black Seas this coefficient fluctuates in the range from *ca* 0.002 to *ca* 0.35 [m^{-1}], *i.e.* 175 times. This fluctuation corresponds to a range of chlorophyll concentration from *ca* 0.1 to *ca* 13 [mg m^{-3}]; within that range the quantity of chlorophyll increases 130 times.

Analysis of the relation between the specific light-absorbing capacity of pigments a^*_{pl} and the chlorophyll concentration C_a (Tab. 5 and Fig. 4) shows clearly the decrease of a^* at higher chlorophyll concentrations, especially when a^*_{pl} takes low values; however, it follows from Fig. 4 that the

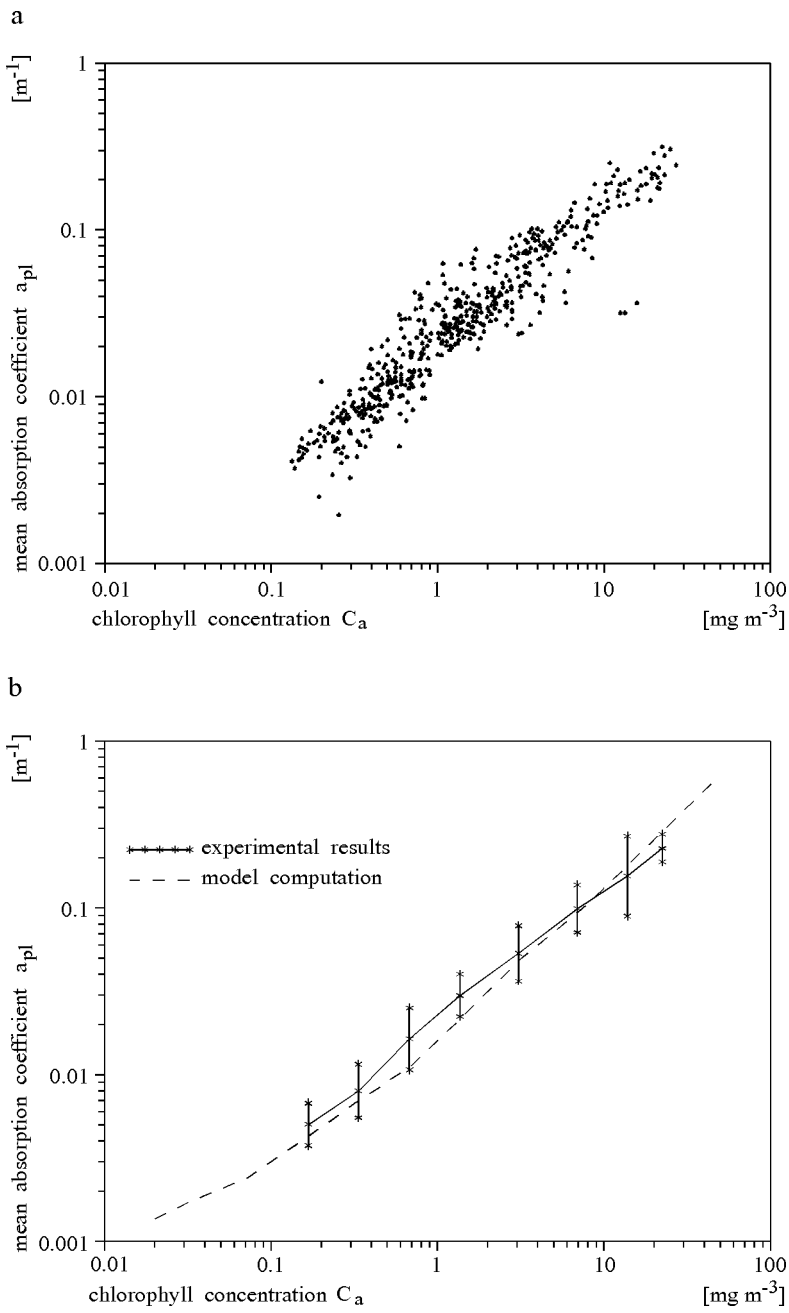

Fig. 3. Correlation between the mean light absorption coefficients by phytoplankton pigments in the PAR (400–700 nm) range a_{pl} [m^{-1}] and chlorophyll concentrations C_a [mg m^{-3}]: experimental points (a), curves (b): averaged experimental results and standard deviations (solid line), results of calculations using Woźniak's model (Woźniak *et al.*, 1992) (dashed line)

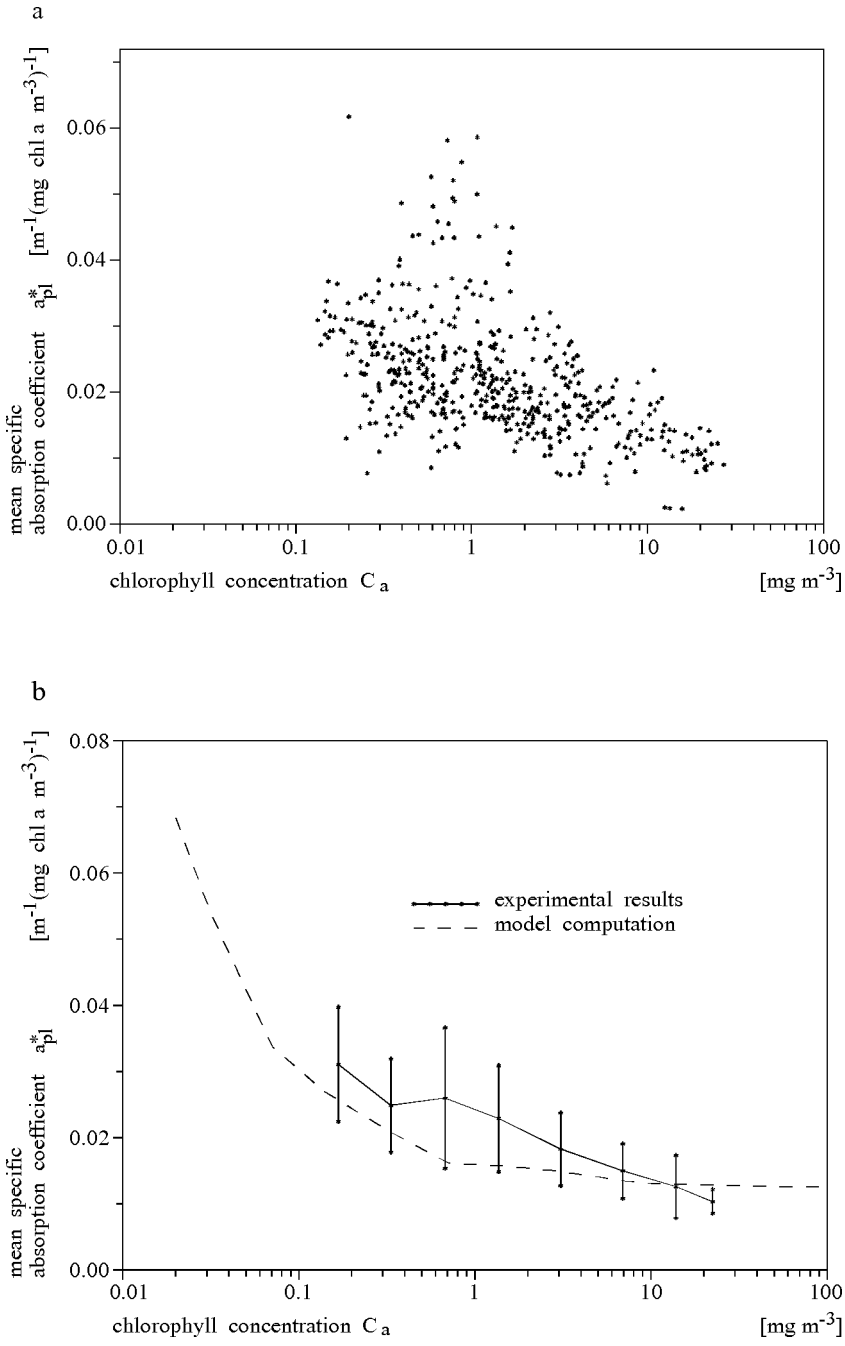

Fig. 4. Correlation between the mean specific absorption coefficients by pigments in the PAR range a^*_{pl} [m^{-1} (mg chl a m^{-3})$^{-1}$] and chlorophyll concentrations (for explanation – see Fig. 3)

Table 4. Statistical dependence of light absorption coefficient a_{pl} [m^{-1}] (mean for PAR range) on chlorophyll a (+ pheophytin) concentration, C_a [mg m^{-3}] (Woźniak *et al.*, 1992)

Trophic type	Range of chlorophyll a + pheophytin concentration C_a	Logarithmic mean $< a_{pl} >$	Range of standard deviation $a_{pl,\min} - a_{pl,\max}$	Number of data
O–III	0.1 – 0.2	0.00502	0.00376 – 0.00672	20
M	0.2 – 0.5	0.00797	0.00551 – 0.0116	109
I	0.5 – 1.0	0.0164	0.0107 – 0.0251	199
E–I	1 – 2	0.0298	0.0222 – 0.0400	110
E–II	2 – 5	0.0535	0.0365 – 0.0782	106
E–III	5 – 10	0.0991	0.0716 – 0.137	36
E–IV	10 – 20	0.155	0.0895 – 0.270	29
E–V	20 – 30	0.229	0.189 – 0.278	11

Trophic type symbols:

O – oligotrophic waters,
M – mesotrophic waters,
I – intermediate waters,
E – eutrophic waters.

Table 5. Statistical dependence of specific absorption coefficient a^*_{pl} [m^{-1} (mg chl a $m^{-3})^{-1}$] (mean for PAR range) on chlorophyll a (+ pheophytin) concentration, C_a [mg m^{-3}]

Trophic type	Range of chlorophyll a + pheophytin concentration C_a	Mean $< a^*_{pl} >$	Standard deviation $\sigma_{a^*_{pl}}$	Number of data
O–III	0.1 – 0.2	0.0311	0.00862	20
M	0.2 – 0.5	0.0249	0.00705	109
I	0.5 – 1.0	0.0260	0.0106	99
E–I	1 – 2	0.0229	0.008	110
E–II	2 – 5	0.0183	0.00551	106
E–III	5 – 10	0.0150	0.00411	36
E–IV	10 – 20	0.0126	0.00473	29
E–V	20 – 30	0.0104	0.00179	11

decreasing trend will also be maintained at chlorophyll concentrations exceeding 1 mg m^{-3}.

The specific absorption coefficient a^*_{pl} falls by a factor of *ca* 60, *i.e.* three times less than a_{pl} does. Though still very considerable, this fluctuation confirms the above results of the considerable variability of this parameter, which twenty years ago was taken to be constant (Bannister, 1974).

A certain part of this dispersion, however, may be related to the *in vitro* absorption of light energy by detritus or by other kinds of non-photosynthetic pigments. This is confirmed by Figs. 5a,b,c, where the curves of $a_{pl}(\lambda)$ normalised for $\lambda = 675$ nm obtained during the winter cruise of the 'Professor Shtokman' are grouped according to three water layers. One can see that below 15 m, where no photosynthesis was recorded, the dispersion of light absorbance by accessory pigments at short wavelengths is significantly higher than in the middle part of the photosynthetic layer, which leads to a corresponding increase in the average a_{pl}. The same phenomenon is reflected by the spectrograms of the blanched filters, but it is less strongly expressed (Fig. 5d,e,f), so that subtracting the light absorption due to the blanched seston from that due to the unblanched seston does not seriously change the general picture.

Almost the same phenomenon is seen on the curves for the upper water layer but here the reason for it is the increased content of protective pigments, the peaks of which are visible on the spectra.

Another aim of this section is to compare the measured values of a_{pl} and a^*_{pl} in the Black and Baltic Seas with the relevant literature data and with the final results of model computations by Woźniak (1989).

The early measurements of LAC were evaluated on cultures, or on dense coastal phytoplankton populations (Yentsch, 1960; Lorenzen, 1972; Bannister, 1974) which are in initial succession stages (Margalef, 1960). Typically they have a low carotenoid content as compared to chlorophyll, and correspondingly low pigment indices P_i and P'_i. The measurements on such cultures and populations yield a roughly constant value of a^*_{pl}, but which is inapplicable to phytocoenoses at higher stages of succession. Thus in summarising the data on a^*_{pl} in rich marine and freshwater plant communities and that in cultures, Bannister (1974) found that these coefficients might be assumed constant: $a^*_{pl} = 0.016 \pm 0.003$ m^{-2} mg^{-1}. By contrast, the authors working on plant communities sharply distinguished by productivity, obtained values of a^*_{pl} differing from each other by 1–2 orders of magnitude (Platt and Jassby, 1976; Morel and Prieur, 1977; Morel, 1978; Atlas and Bannister, 1980; Koblentz-Mishke, 1980; Morel and Bricaud, 1981; Kishino *et al.*, 1986; Iturriaga and Siegel, 1989; Yentsch and Phinney, 1989). As can be seen in Fig. 4 and Tab. 5, this also applies to our own data.

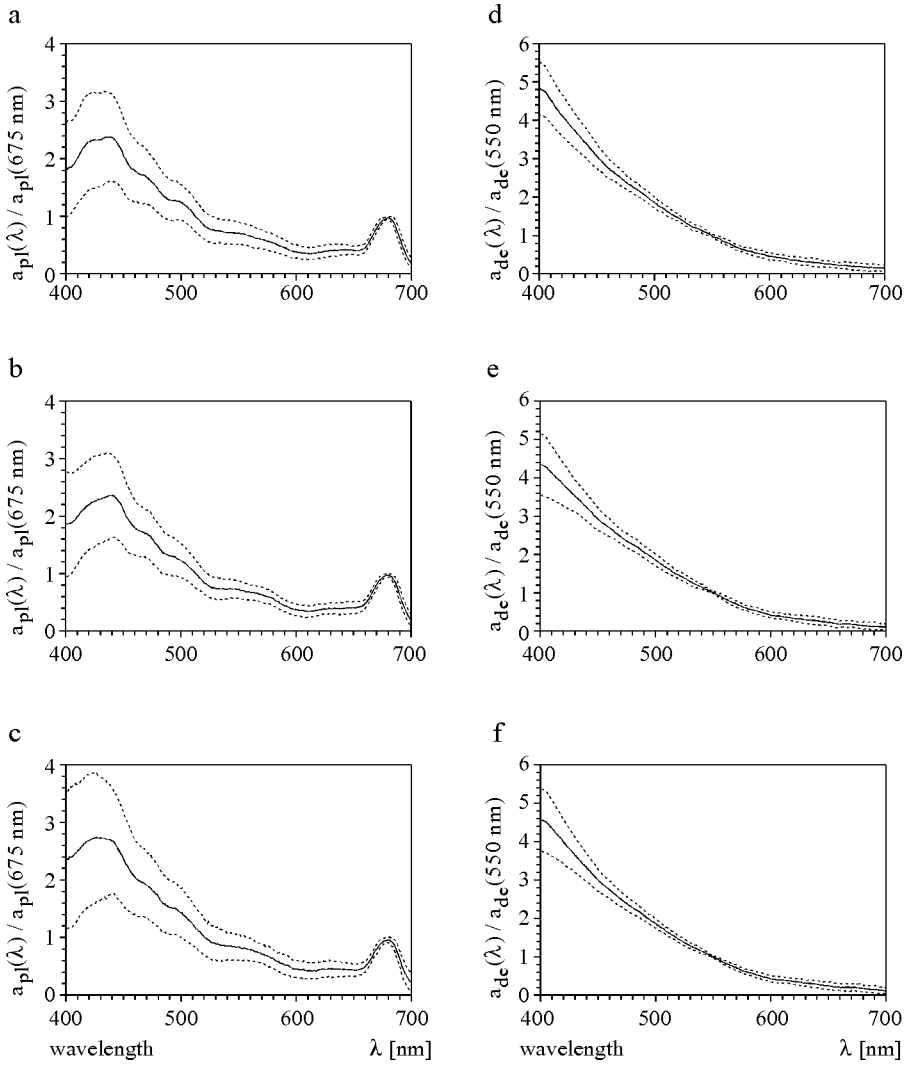

Fig. 5. The spectra of light absorption coefficients by pigments and by detritus. Data obtained during the 'Professor Shtokman' cruise in 1990 (solid line – mean values, dashed lines – range of standard deviation): phytoplankton pigments, spectra normalised to the value at 675 nm (a), (b), (c); detritus, spectra normalised to the value at 550 nm (d), (e), (f); (a) and (d) – mean in surface layer 0–5 m (55 spectra); (b) and (e) – mean in 5–15 m layer (56 spectra); (c) and (f) – mean in 15–50 m layer (50 spectra)

Tab. 1 lists some literature sources concerning light absorption by phytoplankton, measured by different methods under natural and laboratory conditions. As is evident, with some exceptions, a^*_{pl} and a^{**}_{pl} measured in the natural phytoplankton are higher than those measured in cultures. However, this comparison does not provide an adequate idea of the ecological role of the variability of the parameters related to light absorption by pigments. More ideas on these relationships may emerge from model computations.

Woźniak (Woźniak, 1989; Woźniak and Ostrowska, 1990b) has produced a semi-empirical model of the light-absorbing capacity of pigments in various ocean areas differing in their ecological conditions and productivity. On the basis of experimental data (Haga and Matsuike, 1981; Konovalov, 1985; Kishino *et al.*, 1984, 1986; Morel and Bricaud, 1981; Takematsu *et al.*, 1981) on C_a, P_i and $a_{pl}(\lambda)$ for different areas of the World Ocean, the following expression describing the dependence of a_{pl} on C_a and P_i, has been derived:

$$a_{pl}(\lambda) = C_a\,[(1.87 \times 10^{-2}\ P_i - 1.1 \times 10^{-2})e^{-1.2\times10^{-4}(\lambda-441)^2} + \\ + 6.45 \times 10^{-3}e^{-3.5\times10^{-4}(\lambda-608)^2} + 2.33 \times 10^{-2}e^{-1.4\times10^{-3}(\lambda-675)^2}]. \quad (7)$$

From this formula two other equations can be derived, enabling a_{pl} and a^*_{pl} to be evaluated:

$$a_{pl} = \frac{1}{350}\int_{400}^{750} a_{pl}(\lambda)\ d\lambda = C_a(6.41 \times 10^{-3}\ P_i - 2.13 \times 10^{-3}), \quad (8)$$

$$a^*_{pl} = \frac{1}{350}\int_{400}^{750} a^*_{pl}(\lambda)\ d(\lambda) = 6.41 \times 10^{-3}\ P_i - 2.13 \times 10^{-3}. \quad (9)$$

Later Woźniak and Ostrowska (1990a) analysed the statistical dependence of P_i on C_a evaluated from the same data set, by making use of 1300 determinations by numerous workers in different parts of the Ocean. Some of the results of this analysis are given in Tab. 6 and Fig. 6.

By combining the data from Tab. 6 and eqs. (8) and (9) it is possible to arrive at model values of coefficients a_{pl} and a^*_{pl} for different chlorophyll *a* concentrations. The results are presented in Tab. 6 and Figs. 3 and 4 (dashed lines).

On examining Figs. 3 and 4 it is easy to see that, despite the differences in the methods employed, our experimental data on a_{pl} and a^*_{pl} are in good agreement with those of other workers (Woźniak and Ostrowska, 1990a).

The general trend towards higher a_{pl} and lower a^*_{pl} with higher chlorophyll concentration stands to reason, since it is known that in waters of higher productivity the pigment index P_i is lower than in less productive ones (Margalef, 1960). This is due to the lower ratio of additional yellow and red pigments to chlorophyll.

Table 6. Coefficients P_i, a_{pl} and a^*_{pl} in Woźniak's model in relation to the chlorophyll concentration in various ocean areas (Woźniak (1989), Woźniak, *et al.* (1992))

C_a [mg m^{-3}]	P_i	a_{pl} [m^{-1}]	a^*_{pl} [m^{-1} (mg chl a m^{-3})$^{-1}$]
0.0316	11.50	0.00273	0.0865
0.0707	8.30	0.00443	0.0627
0.141	5.00	0.00538	0.0382
0.316	3.90	0.00948	0.0300
0.707	3.50	0.0191	0.0270
1.41	3.00	0.0328	0.0233
3.16	2.70	0.0666	0.0211
7.07	2.40	0.133	0.0188
14.1	2.30	0.255	0.0181

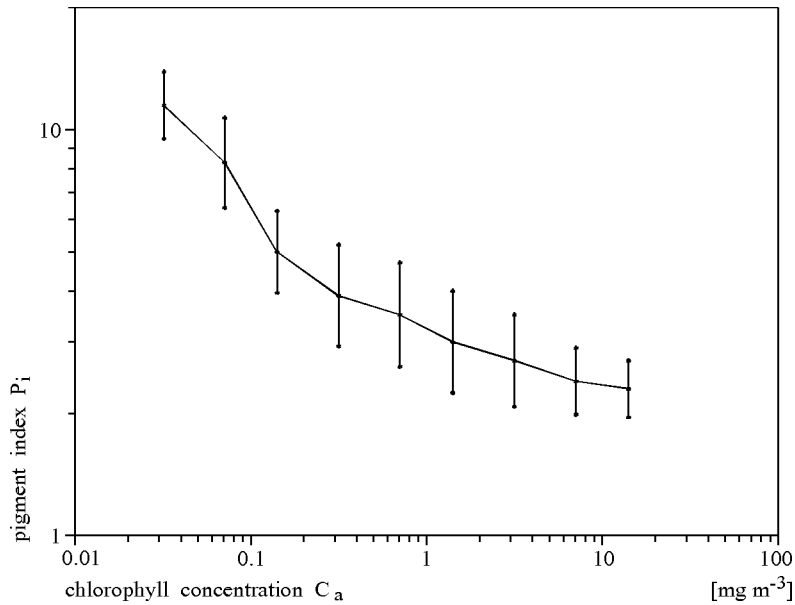

Fig. 6. Dependence of pigment index P_i (D_{430}/D_{663}) on chlorophyll concentration C_a [mg m^{-3}]

In turn, the increase in the quantity of additional pigments results from a poor mineral supply and the lighting conditions. Consequently, the pigment index displays an inverse relationship with the chlorophyll concentration, which is illustrated by Fig. 6 and Tab. 6.

4. Conclusion

In this paper we have concentrated on the methodological aspects of studying the light absorbing capacity of phytoplankton, and have accorded less attention to the nature of the phenomena involved in the absorption of light by photosynthetic pigments. This problem is the object of our studies. It is worth stressing the significance of this problem in the context of research into the efficiency of marine photosynthesis, a subject we shall be returning to in our next paper.

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Symbols and abbreviations

LAC – light absorption capacity of phytoplankton pigments

PAR – photosynthetically available radiation (in 400–700 nm spectral range)

PUR – photosynthetically usable radiation (in 400–700 nm spectral range)

C_a – chlorophyll concentration [mg m^{-3}]

$a_{pl}(\lambda)$ – spectral light absorption coefficient by phytoplankton [m^{-1}]

a_{pl} – mean absorption coefficient over the PAR range [m^{-1}], (eq. 2)

a^*_{pl} – specific light absorption coefficient by phytoplankton averaged over the PAR range [m^{-1} (mg chl *a* $m^{-3})^{-1}$]: $a^*_{pl} = a_{pl}/C_a$

a^{**}_{pl} – mean specific light absorption coefficient by phytoplankton over the PAR range, (irradiance weighted) [m^{-1} (mg chl *a* $m^{-3})^{-1}$]:

$$a^{**}_{pl} = \frac{\int_{400}^{700} a_{pl}(\lambda)\ E_d(\lambda)\ d\lambda}{\int_{400}^{700} E_d(\lambda)\ d\lambda}$$

E_d – downwelling irradiance [W m^{-2}]

η_0 – diurnal dose of solar energy over the whole spectral range at the sea surface [MJ m^{-2} day^{-1}]

P_{tot} – diurnal total primary production in the water column [mgC m^{-2} day^{-1}]

ε_{tot} – photosynthetic index [%], *i.e.* the total diurnal primary production per diurnal PAR energy dose entering the sea $\eta_{\mathrm{PAR}}(0)$, defined as

$$\varepsilon_{tot} = \frac{K_{E/P}\ P_{tot}}{\eta_{\mathrm{PAR}}(0)}$$

where $k_{E/P} \cong 40$ kJ/g C – the energy equivalent of the mass of assimilated carbon

P_i – pigment index of acetone extracts of phytoplankton $= D_{430}/D_{663}$

P'_i – pigment index for phytoplankton *in vivo* $= D_{441}/D_{675}$

λ – wavelength [nm]

$D(\lambda)$ – light extinction for wavelength λ

D_{ne} – extinction for light absorption by seston, including living phytoplankton

D_e – extinction for acetone extracts of phytoplankton

D'_{ne} – extinction of filter after removal of pigments

β – light pathlength amplification factor

$\bar{\rho}_f$ – filter reflectance coefficient