Optical absorption properties of phytoplankton in various seas

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Abstract

This is a review of the experimental data concerning the sea phytoplankton absorption properties. Basing on the own and the accessible from literature results, the spectral courses and the absolute magnitudes of the light absorption coefficients by phytoplankton, as well as their connections with the chlorophyll *a* concentration observed in the different areas of the World Ocean have been characterized.

Also analysed were the similarites and the differences in phytoplankton absorption properties measured "in vivo" and "in vitro" in acetone extracts of phytoplankton. In this way many empirical correlations between the "in vitro" and "in vivo" spectra were determined. This facilitated the development of a semiempiric, mathematical modelling of living phytoplankton absorption properties on the basis of the known optical properties of its extracts in acetone.

Using the above mentioned semiempirical modelling and the pigment distribution data for different seas (Woźniak and Ostrowska, 1990), the typical features of light absorption by phytoplankton in different biological types of seas were determined.

1. Introduction

This article is the fourth work in a row from the cycle devoted to sea phytoplankton optical properties and fluorometric methods of investigations on its photosynthesis. In the first article of this cycle (Ostrowska and Woźniak, in press a), the body luminescence phenomenon was generally discussed, and on this basis the sea water fluorescence and the accompanying processes were characterized. In particular, the phyto-

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plankton fluorescence as a part of the total sea water luminescence was analysed. In the two following articles (Woźniak and Ostrowska, 1990, in press) the individual optical properties (absorption and fluorescence) of various phytosynthetic pigments, and also the quantitative and qualitative analysis of these pigments' occurrence in sea phytoplankton for various ecological conditions were discussed. All these features determine the phytoplankton optical properties. That is why the subject of this and the next articles from the presented cycle are the optical properties of the sea phytoplankton.

The aim of this work is the characterization of the optical absorption properties of phytoplankton in various phytocenoses. However, the optical fluorescence properties of phytoplankton will be characterized in the next article (Ostrowska and Woźniak, in press b).

The assumed aim of this work was acomplished thanks to experimental data (our own and that available in literature) concerning the phytoplankton absorption properties in various seas. Moreover, an original attempt of systematization of these data, based on semi-empirical, mathematical modelling of these absorption properties in various ecological conditions has been presented.

2. Sea phytoplankton absorption properties in the light of experimental investigation

Determining the spectrum of the coefficient of light absorption by phytoplankton is a complex experimental problem. There are four main methods of absorption spectra determination $a_{pl}(\lambda)$ for phytoplankton. Following are the most important features of these methods:

Hydrooptical methods – they are of indirect character. Direct measurements of the global, real apparent optical properties are made[2]. Next, most often by means of approximate calculations, the absorption properties of various sea water components are determined, including the phytoplankton absorption spectra. These methods, in various versions, were utilized among others by Tyler (1975), Morel and Prieur (1977), Morel (1978). They are characterized by big errors and most often they are not suitable for a detailed analysis of the phytoplankton spectral properties.

[2]Systems of description of the properties of underwater fields of illumination using the apparent optical properties, and the elementary light absorption and dissipation phenomena in a medium based on the so-called inherent optical properties, are discussed in works by Jerlov (1976), Dera (1983).

Nonextract spectrophotometric methods – direct measurements of light absorption spectra in isolated phytoplankton "in vivo" samples or under conditions similar to "in vivo". Such measurements are made in concentrated or filtered samples of natural phytoplankton or cultivated cultures. In order to eliminate the scattered light, the spectrophotometers are equipped with integrating spheres or diffusers made of milky glass. The above listed methods were utilized and are described in works of Konovalov (1970, 1979, 1985), Lorenzen (1966, 1972), Kishino *et al.* (1984, 1986) and also in works with the authors contribution (Koblentz-Mishke *et al.*, 1985a).

Spectrophotometrical extraction methods – based on light absorption spectra measurements in extracts (mostly acetone) of the phytoplankton. In oceanological practice, they are widely applied as standard methods of pigment determination (Jeffrey and Humphrey, 1975; Lorenzen, 1968; Strickland and Parsons, 1968). The results obtained in this way, do not reflect the real absorption properties of the phytoplankton "in vivo". This is due to changes of individual absorption properties of the particular pigments in solvent, with respect to the "in vivo" conditions (Tabl. 2 in Woźniak and Ostrowska, in press). Phycobilins are not represented in the absorption spectra of phytoplankton organic extracts[3].

Fluorometric methods of phytoplankton spectra determination are based on determination of the spectra of its fluorescence. It is assumed that the fluorescence excitation spectra and the absorption spectra are similar (Fig. 4 in Ostrowska and Woźniak, in press b). The results must be recalibrated from the luminescence units to absorption coefficient units $[m^{-1}]$. In oceanological practice these methods are applied seldom and not for a long time, *e.g.* in Maske and Haardt work (1987).

From the discussed methods, the most appropriate for the "in vivo" analysis of the living phytoplankton optical properties are the spectra measured directly, using the non-extract, spectrophotometrical methods. It is connected however, with serious experimental problems. Due to this the number of the published in the world literature spectra of light absorption by phytoplankton "in vivo" is small. However, there is a rich experimental material concerning the absorption properties of phytoplankton extracts. As it was mentioned, in experimental practice they are obtained to some extent automatically, in a standard investigation

[3]Phycobilins are the only phytoplankton pigments, that are insoluble in organic solvents (acetone). Also opposite to the other pigments they dissolve in water very easily (Filipowicz and Więckowski, 1979, 1983).

procedure, because they are most often used for pigments concentration determination. Hence it is worth while to analyse the reverse method, *i.e.* the possibility of evaluation of the natural absorption properties of phytoplankton "in vivo", on the basis of data on absorption spectra of its extracts.

2.1. Comparison of nonextract (natural) and extraction spectra of light absorption by phytoplankton

Typical examples of spectra of light absorption by phytoplankton "in vivo" $a_{pl}(\lambda)$ and its extract in 90% acetone $a_{pl,e}(\lambda)$ are shown in Figure 1. The common feature of both these spectra is the occurrence of two main wide absorption bands in blue and red regions. However, the position of the maxima of these bands for both types of spectra is different: they are shifted for extracts for about $10 \div 15$ nm in the short wave direction, compared to their location for phytoplankton "in vivo". Moreover, different is also the sharpness of these bands. In the case of natural phytoplankton the bands are rather more broadened, and their half width is about two times bigger than in the case of the extracts spectra (Lorenzen, 1972). However, in the extracts spectra the band maxima are higher (sharper); lower is also the minimum occuring between these two bands. Apart from these two absorption bands, also the fine structure of these absorption spectra is observed. It is expressed by the existance of many local maxima of various height (Konovalov, 1979; Prieur and Sathyendranath, 1981; Koblentz-Mishke, 1985). These structures are sharper in $a_{pl}(\lambda)$ spectra, *i.e.* for phytoplankton in a natural state. This is related to the richer band structure of the absorption spectra of a living plant compared to the extract (Tabl. 2 in Woźniak and Ostrowska, in press).

The mentioned differences in the spectral courses of the $a_{pl}(\lambda)$ and $a_{pl,e}(\lambda)$ spectra do not allow to conclude about the fine structure of natural phytoplankton absorption spectra on the basis of the absorption spectra of its acetone extracts. Nevertheless, as it is shown among others in the works by Konovalov (1979) and Woźniak (in prepared), there exists a strong interdependence between the $a_{pl}(\lambda)$ and $a_{pl,e}(\lambda)$ spectra. It concerns the total phytoplankton absoroption ability in the visible range, and the colour index of both spectra.

As a measure of the total absorption ability one can accept the respective integrals of light absorption coefficient spectra in the visible range, or their mean values:

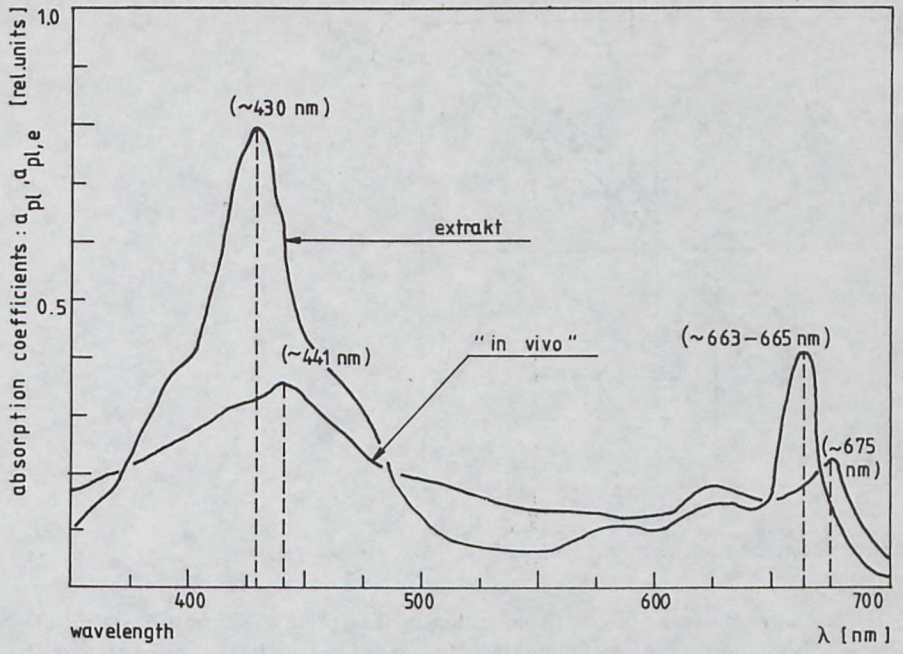

Figure 1: Comparison of spectra of light absorption by phytoplankton "in vivo" and its extract in 90% acetone

$$\widetilde{a_{pl}} = \frac{1}{350}\int_{400nm}^{750nm} a_{pl}(\lambda)d\lambda \quad \text{and} \quad \widetilde{a_{pl,e}} = \frac{1}{350}\int_{400nm}^{750nm} a_{pl,e}(\lambda)d\lambda. \qquad (1)$$

Figure 2 presents the exemplary comparison of the averaged coefficients for phytoplankton "in vivo" $\widetilde{a_{pl}}(\lambda)$ and for extract $\widetilde{a_{pl,e}}(\lambda)$. As one can see from this Figure, the values of both these coefficients are basicaly similar. There exists only a slight surplus of the mean phytoplankton absorption "in vivo" compared to such an absorption of its acetone extracts. This surplus seems to be of a systematic character, independent of the absolute absorption magnitude. The surplus is 14% and changes in a range of ±25%. In Woźniak (in prepared b) work, also the total non-extract and extraction spectra of light absorption by phytoplankton were compared, not in the entire visible range, but in two its subranges: 400 ÷ 600 nm and 600 ÷ 750 nm, connected with the two main absorption bands. In the case of the first of these subranges (400 ÷ 600 nm) they were similar as for the whole 400 ÷ 750 nm spectrum. However, for the red subrange (600 ÷ 750 nm) the systematic surplus of mean absorption for phytoplankton "in vivo" was higher compared to its extract by about 38%.

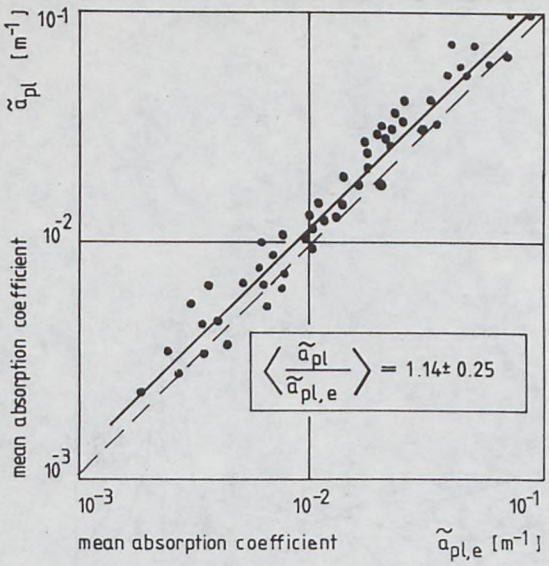

Figure 2: The observed dependence between the mean absorption coefficients in the visible light 400 ÷ 750 nm: $\widetilde{a_{pl}}$ – for phytoplankton "in vivo"; $\widetilde{a_{pl,e}}$ – for acetone extracts of phytoplankton. Broken line denotes the location of the points for which $\widetilde{a_{pl}} = \widetilde{a_{pl,e}}$, continous line illustrates the $\widetilde{a_{pl}} = f(\widetilde{a_{pl,e}})$ dependence, with an average slope $\left\langle \frac{\widetilde{a_{pl}}}{\widetilde{a_{pl,e}}} \right\rangle$ (Woźniak, in prepared b)

The existence of the above described surpluses of $\widetilde{a_{pl}}$ and $\widetilde{a_{pl,e}}$ can be caused by the lack of the phycobilins contribution to the total light absorption by phytoplankton extracts. There is also possible an increase in absorption of the natural phytoplankton samples because of their non-uniform internal structure[4], (optical non-homogeneities, as *e.g.* chloroplast or other intracellar substructures).

Finally, the differentiation between the absorption of the natural samples and phytoplankton extracts can be the consequence of systematic errors in the determination of both the absorption spectra. However, neglecting these difference, it is to conclude that the total (hence also mean) phytoplankton absorption in the visible range, and also in the 400 ÷ 600 nm and 600 ÷ 750 nm subranges is basicaly invariant with respect

[4]In such media the real optical path of quanta increases because of their repeated Mie type dissipation. The increase in the optical path leads in a consequence to an increase in the observed magnitudes of true absorption in discrete media compared to continuous media chemically filled with the same material (see, *e.g.* Morel and Bricaud, 1981; Zieliński *et al.*, 1986).

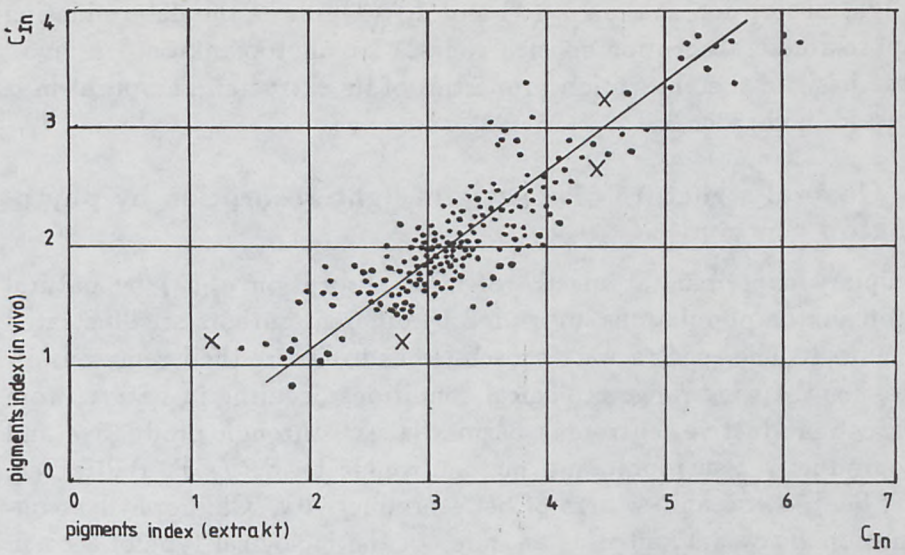

Figure 3: The observed dependence between the colour indexes of pigments: $C'_{In} = a_{pl}(441nm)/a_{pl}(675nm)$ – for spectra of light absorption by living phytoplankton. $C_{In} = a_{pl,e}(430nm)/a_{pl,e}(663nm)$ – for spectra of light absorption by acetone extracts of phytoplankton. Continous line – linear approximation according to equation (2) (Woźniak, in prepared b)

to their extracts in acetone. Only the systematic differences should be taken into account.

Interesting results gives also the comparison of colour indices of the pigments[5] indexes: C'_{In} – for phytoplankton "in vivo", and C_{In} – for the extract. These parameters are combined by an empirical interdependence (Fig. 3):

$$C'_{In} = 0,74C_{In} - 0.38 \tag{2}$$

The correlation coefficient for this dependence is $r = 0,83$. Hence, also in this case one can see strong, quantitative relationships between the $a_{pl}(\lambda)$ and $a_{pl,e}(\lambda)$ spectra.

[5]By the colour index of a pigment we understand the ratio of extinction or absorption for two main maximums of light absorption by phytoplankton. Hence, in the case of phytoplankton extracts, the colour index C_{In} is equal to:

$$C_{In} = a_{pl,e}(\lambda = 430nm)/a_{pl,e}(\lambda = 663nm)$$

while for phytoplankton "in vivo", the colour index C_{In} is:

$$C'_{In} = a_{pl}(\lambda = 441nm)/a_{pl}(\lambda = 675nm).$$

The existence of the discussed in this paragraph dependences between the light absorption spectra $a_{pl}(\lambda)$ and $a_{pl,e}(\lambda)$ allows the determination of approximate absorption spectra courses for phytoplankton "in vivo" on the basis of the absorption properties of its extracts. The problem is discussed in chapter 3.

2.2. General structure of spectra of light absorption by phytoplankton "in vivo"

Exemplary experimental spectra of light absorption $a_{pl}(\lambda)$ by natural phytoplankton populations, measured by different authors are illustrated in Figure 4. The spectra were chosen, so as to assure their representativeness for the wide range ecological conditions occuring in nature, from the most productive, eutrophic basins (lakes), through productive and mesoproductive, eutrophic and mesoeutrophic basins (*e.g.* Baltic Sea, Black Sea), to oceanic waters of little productivity. Chlorophyll *a* concentration Ba was adopted as an index of the biological type of a basin for the illustrated in Figure 4 $a_{pl}(\lambda)$ spectra.

The $a_{pl}(\lambda)$ absorptions occuring in nature differ in their absolute magnitudes, and also in the fine spectral structure. Both of these features are discussed furhter in this article. The attention will be concentrated herein on the general similarities of all these spectra.

As one can see from Figure 4, the general shape of the $a_{pl}(\lambda)$ spectra is preserved. They are basicly characterized by two main wide absorption bands. The first of them, higher and wider, is observed in the blue light range with the maximum most often at 435 ÷ 445 nm (on average 441 nm). Its half bandwidth often exceeds 100 m. The second of these bands is located in the red region with the absorption maximum at about 675 nm. It is narrower (half bandwidth 20–30 nm) and smaller. The occurrence of these main absorption maxima in spectra of light absorption by phytoplankton is related to the absorption properties of its pigments (Fig. 5 in Woźniak and Ostrowska, in press). Hence, chlorophyll *a* is mainly responsible for the occurrence of the absorption band in the red region. The share of chlorophyll *b* is very small because of its small concentration in phytoplankton. On the other hand, all the chlorophylls and carotenoides absorb blue or bluegreen light, so they have a contribution to light absorption in a large range of blue light. Yellow light is absorbed to a smaller extent, which is caused by a rather small, characteristic for most natural phytoplankton populations, amount of phycobilins.

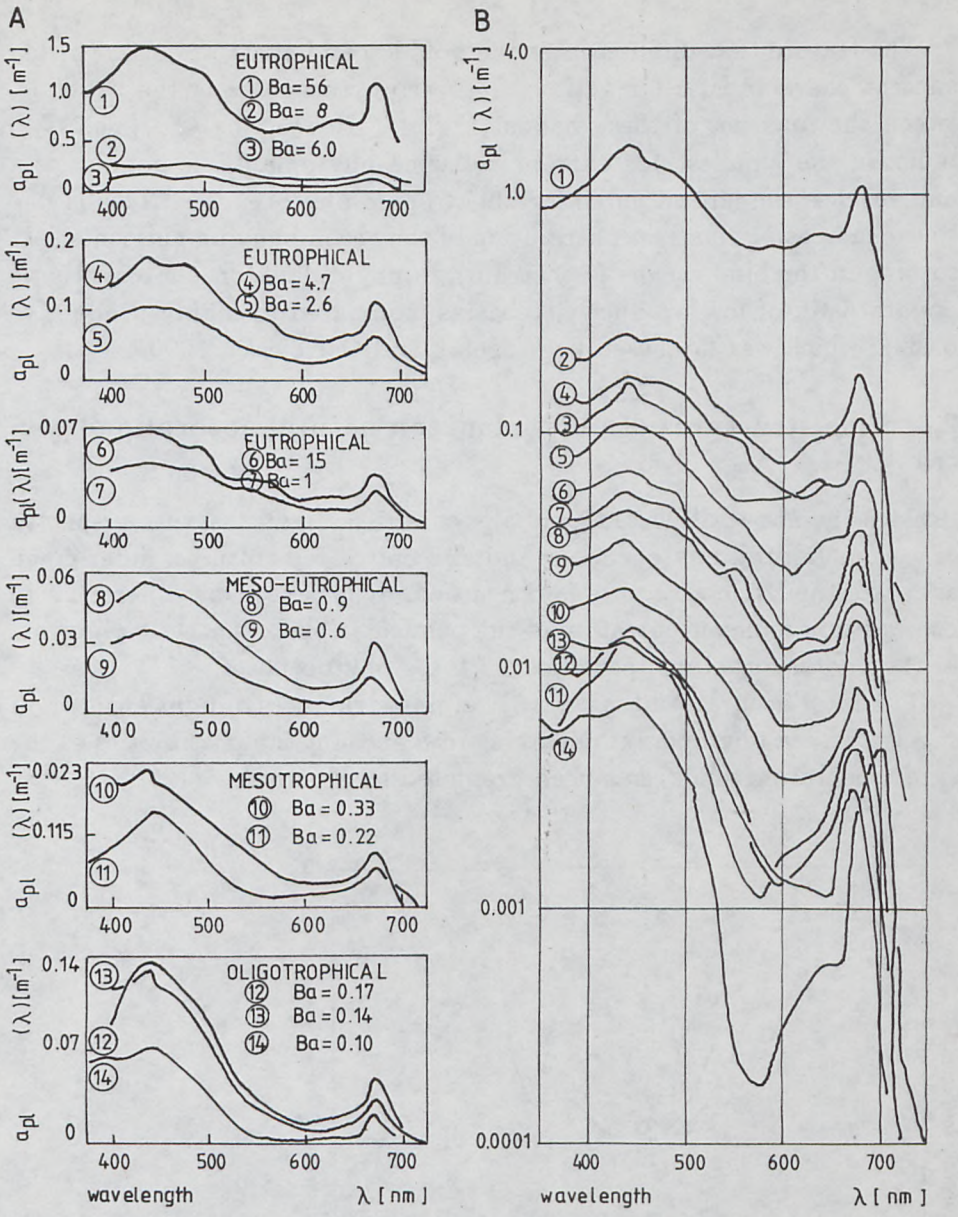

Figure 4: Experimental spectra of light absorption coefficients by phytoplankton $a_{pl}(\lambda)$, observed for various basins. A – a_{pl} coefficients in linear scale; B – a_{pl} coefficients in logarithmic scale; 1 – Fuki-ike Lake, Japan (Takematsu *et al.*, 1981); 3 – Kizaki Lake, Japan (Kishino *et al.*, 1984); 2, 4 ÷ 6 – Baltic Sea (Konovalov, 1985; Koblentz-Mishke *et al.*, 1985a); 7 ÷ 10, 12, 13 – Black Sea (Konovalov, 1985; Koblentz-Mishke *et al.*, 1985a); 11, 14 – Pacific Ocean (Kishino *et al.*, 1986). Note: In Figure 4A the corresponding concentrations of chlorophyll *a* Ba are given in units ($mg\,Chl\,a/m^3$)

The feature that differentiates the double band structure of the $a_{pl}(\lambda)$ spectra characteristic for various natural phytocenoses is the ratio between the maxima of these bands (Fig. 4). Hence, the C'_{In} (also C_{In}) index is the smallest for eutrophic basins phytoplankton populations, and reaches the largest value for oligotrophic phytocenoses. This is due to the increasing relative contribution of the accompanying pigments (absorbing in the blue range of spectrum), in phytoplankton photosynthetic apparatus in of low productivity basins, compared to highly productive basins, which was discussed by Woźniak and Ostrowska, 1990.

2.3. Fine structures of phytoplankton natural absorption spectra

Besides the above discussed general similarities, light absorption spectra of various natural phytocenoses, and also cultivated cultures, differ much as far as their fine structure is concerned. It is caused by differences in composition and concentration of the particular photosynthetic pigments in the photosynthetic apparatuses of these phytocenoses.

The most accurate characteristics of fine structures of light absorption spectra by sea phytoplankton (taking into account the possibilities of the experimental methods) has been presented by Konovalov (1979). He ba-

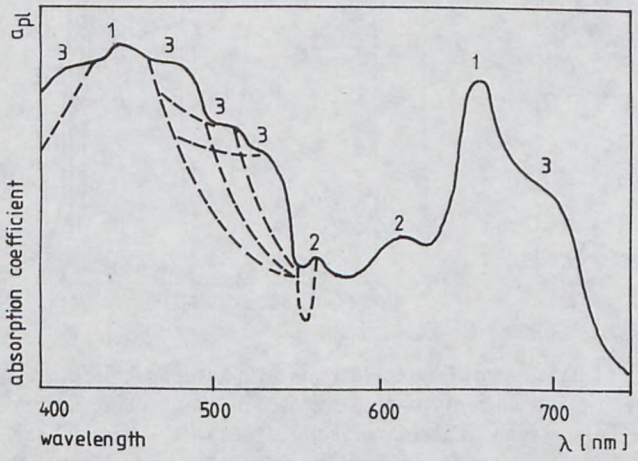

Figure 5: Location of maxima of location: first (1), second (2) and third (3) magnitude in the observed spectra of light absorption by phytoplankton (Konovalov, 1979)

Table 1: List of the possible characteristic points in the visible spectra of light absorption by phytoplankton. (Prepared on the basis of Konovalov, 1979)

Type of point	Number of points in the spectrum	Points location [nm]	Point is expressed as:
maximum of absorption band, 1st magnitude	2(1)	441±3 675±3	maximum, local maximum
maximum of absorption band, 2nd magnitude	0–2	587±3 637±3	local maximum
maximum of absorption band, 3rd magnitude	0–6	417±3 465±3 494±3 545±3 621±3 712±3	"hump"
transmission maximum	1–3	573±3 605±3 649±5	local minimum

sed his results on the analysis of about 1600 $a_{pl}(\lambda)$ spectra, determined for phytocenoses of various areas of the World Ocean. On the basis of those data, Konovalov distinguished many specific spectral features of the $a_{pl}(\lambda)$ spectrum. These features are shown in Table 1 and illustrated in Figure 5.

As one can see from Table 1 the $a_{pl}(\lambda)$ spectra can have even 10 absorption bands (not necessary max) for phytoplankton and up to three transmission maxima (*i.e.* local absorption minima). As far as the absorption bands are concerned, because of their contribution to the total absorption spectrum, one can distinguish three groups (Fig. 5). The first contains the discussed previously two main absorption bands, *i.e.* of the 1st magnitude. These bands are visible as high maxima in the $a_{pl}(\lambda)$ spectra.

The group of bands of second magnitude, consists of rather less intensive absorption bands. From 0 to 2 of these bands can occur together. When they occur, they always form local maxima in the $a_{pl}(\lambda)$ spectra.

The group of the 3rd magnitude bands consists of absorption bands giving the least contribution to the total absorption spectra. Moreover, they are always located in the areas of big slopes of the bands of the 1st and the 2nd magnitude. Therefore they never form separate maxima, and are visible only as a "hump" on the total spectrum background. Bands of this group can occur in a number from 0 to 6.

As one can see from Table 1, phytoplankton absorption spectra transmission maxima occur in a number from 1 to 3. These maxima are formed in the middle part of the spectrum, between the bands of the 1st and the 2nd magnitude.

The occurrence of the above characteristic features in the spectra of different phytoplankton samples i differentiated. The particular spectra vary with respect to both the quantity and the selection of the above listed absorption maxima and minima, and to their intensities. Nowadays it is impossible to give precise quantitative correlations and the conditions for the occurrence of the fine structure of $a_{pl}(\lambda)$, exept the main absorption bands. Further in the work we will limit ourselves to the general shape of the absorption spectra (*i.e.* their two main absorption bands) as a measure of the phytoplankton absorption abilities.

2.4. Spectra of specific coefficients of light absorption by phytoplankton

Spectral absorption abilities of phytoplankton in relation to the chlorophyll *a* concentration are described by the spectra of the specific absorption coefficients $K_c(\lambda)$. As the $K_c(\lambda)$ coefficient one takes the ratio of light absorption coefficient by phytoplankton $a_{pl}(\lambda)$ to the chlorophyll *a* concentration Ba, according to the dependence[6]

$$K_c(\lambda) = a_{pl}(\lambda)/Ba. \tag{3}$$

Exemplary $K_c(\lambda)$ spectra determined for the same natural phytoplankton populations as in Figure 4, are shown in Figure 6. As one can see from this Figure, the $K_c(\lambda)$ spectra are quite similar in the red, and also in the middle (green-yellow and orange) regions of the visible range. On the other hand, in the blue and the green ranges these spectra are different for different phytocenoses.

The similarity of the specific absorption coefficients in red is due to the dominant influence of chlorophyll *a* on the total light absorption in this range. Other pigments practically do not absorb in this region (except some phycobilins). Hence, the composition of pigments does not influence the longwave band of light absorption by phytoplankton. The values of

[6]Let us notice that it is not a very precise expression. Exactly the specific light absorption coefficient by the complete photosynthetic apparatus is the ratio of the $a_{pl}(\lambda)$ absorption to the sum of the concentration of all the pigments. In the case of only chlorophyll *a*, the specific absorption coefficient is equal to the ratio of the absorption component of this pigment to its concentration.

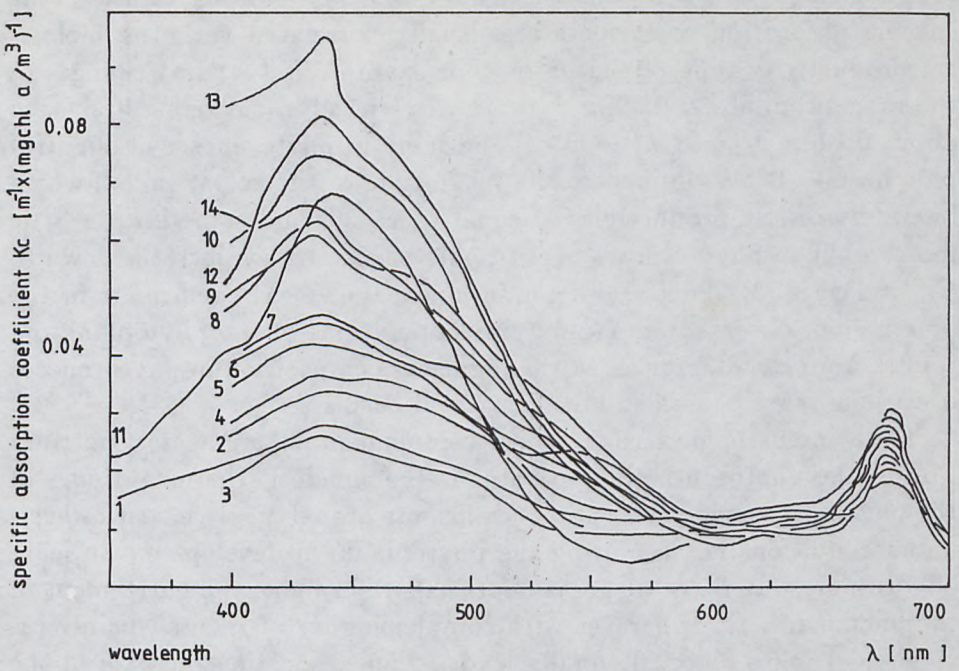

Figure 6: Experimental spectra of specific absorption coefficients by phytoplankton $K_c(\lambda)$, determined for various basins. Note: The numbers correspond to those in Figure 4

the specific absorption coefficients are relatively constant here. For the the 675 nm light, so for the maximum absorption of this band, the $K_c(675nm)$ coefficients range most often from 0.015 to 0.03$[m^{-1}/(mg\,Chl a\ m^{-3})]$ and are equal on average to $0.023 \pm 0.08[(m^{-1}/(mg\,Chl\,a \cdot m^{-3})]$ [7].

In the middle part of the spectrum (500–650 nm), so in its wide minimum the $K_c(\lambda)$ courses differentiation observed for various populations is relatively higher than in the red. This can be due to the phycobilins concentration, differing under varying conditions. Besides, it is the area of low absorption, hence the effect of the experimental errors is strong.

The greatest differences in the $K_c(\lambda)$ specific coefficients occuring in various natural populations and cultivated phytoplankton cultures, are ancountered in the main light absorption band with a maximum in the

[7] As one can see, these magnitudes are larger than the specific absorption coefficient characteristic for chlorophyll *a* $K_{cekst}(665) = 0.015m^{-1}$, in max. of its absorption band observed in acetone solution (Woźniak and Ostrowska, in press). Morel and Bircaud (1981), as well as Bannister and Weideman (1984) suggest that this absorption increase can be caused by an increase of the real optical path due to repeated light scattering (Mie type) effect, both outside and intracellutar. This effect concerns all the wavelengths. However, in the blue band it is less pronounced due to larger absorption.

blue region (Fig. 6). In this case, however, the observed values of the specific absorption coefficients are usually correlated with the biological productivity type of the basin. For example $K_c(441nm)$ changes in the range from about $0.02[m^{-1}/(mg\,Chl\,a \cdot m^{-3})]$ in eutrophic basins, to about $0.10[m^{-1}/(mg\,Chl\,a \cdot m^{-3})]$ and more in phytocenoses of oligotrophic basins. It also influences the magnitude of the colour index, which in waters of low productivity is equal to ca 3.5 and sometimes a little more, while in phytocenoses of eutrophic basins it may decrease down to $C_{In} = 1$ (Fig. 3). Such a differentiation of the $K_c(\lambda)$ coefficients in the blue region, observed among natural populations of the phytoplankton, results from the differences in the pigments composition in phytocenoses of various types of seas and other natural basins.

Thus, in eutrophic basins, where complementary pigments' contribution to the photosynthetic apparatus is the smallest, the magnitudes of the blue light specific absorption coefficients are relatively low. However, under conditions not favouring the phytoplankton development in lean, oligotrophic waters, or at great depths short in light, the enrichment of the photosynthetic apparatus with complementary pigments (mainly carotenoids) takes place. It finally leads to an absorption increase in the blue and green regions, which causes the $K_c(\lambda)$ increase, since it is a ratio of the absolute, total absorption coefficients to the concentration of only chlorophyll *a*.

2.5. Review of experimental values of mean specific light absorption coefficient by phytoplankton

Besides the experimental investigations on the $K_c(\lambda)$ spectra, attention of the investigators has been for many years focused also on the determination of their mean values in the visible range:

$$\widetilde{K}_c = \frac{1}{350}\int_{400}^{750} K_c(\lambda)d\lambda. \tag{4}$$

Apart from the above $\widetilde{K}_c$ coefficient which, is just a mean value of the $K_c(\lambda)$ spectrum, often also similar average $\overline{K}_c$ coefficients are determined. These coefficients are averaged with a weight of underwater irradiation $E_o(\lambda)$, expressed as the amount of quanta:

Table 2: List of the quoted in the world literature mean specific light absorption coefficients $\widetilde{K}_c$ and $\overline{K}_c$ by phytoplankton

Region or object	Type of phytocenosis	Method	$\widetilde{K}_c$ $\left[\frac{m^{-1}}{mg\,Chl\,a/m^3}\right]$	$\overline{K}_c$ $\left[\frac{m^{-1}}{mg\,Chl\,a/m^3}\right]$	Remarks	Source
Coastal phytoplankton	eutrophic	direct	0.013		average from several samples	Yantsch, 1960
Coastal phytoplankton	eutrophic	direct	0.0138		average from 26 populations	Lorenzen, 1972
Sargasso Sea	oligotrophic	indirect hydrooptical		0.0415	average from many measurements in the 0–10 m layer	Tyler, 1975
Atlantic – Mauretan upwelling area	mesotrophic	indirect hydrooptical	0.0142	(0.014)	average in the surface layer	Morel and Prieur, 1977; Morel, 1978
Various seas & fresh water basins & cultures	various	various	(0.016 ± 0.003)	(0.016 ± 0.003)	global average in the surface layer	Bannister, 1974
Various sea basins	various	various		0.005 – 0.025	range of changes at encountered for various depths	Atlas and Bannister, 1980
Cultivated cultures	–	direct	0.0180 0.0397 0.0305		relate to platymonas suecica, coccolithus huxleyi, chaetoceros	Morel and Bricaud, 1981
Cultivated cultures	–	direct calculations		0.010 – 0.021	chlorella relate to pyrenoidsa, cancolothus huxleyi	Bannister and Weideman, 1984
Baltic (July, 1980)	eutrophic and mesoeutrophic	direct	0.023 ± 0.004		average from ca 130 measurements in the euphotic layer	Konovalov, 1985
Black Sea (September – October, 1978)	mesotrophic	direct	0.034 ± 0.004		average from about 100 measurements in the layer 0–80 m	Konovalov, 1985
Pacific Ocean	oligotrophic	direct	0.022 – 0.050	0.022 – 0.050	changes from surface to the depth 100–150 m	Kishino *et al.*, 1986

$$\overline{K}_c = \frac{\int_{400}^{750} K_c(\lambda) E_o(\lambda) d\lambda}{\int_{400}^{750} E_o(\lambda) d\lambda}. \tag{5}$$

The $\overline{K}_c$ coefficient is convenient for the analysis of energy absorbed by phytoplankton in a sea, and quantum efficiency of photosynthesis "in situ" (Woźniak, in prepared; Koblentz-Mishke *et al.*, 1985).

Let us notice that according to the above $\widetilde{K}_c$ and $\overline{K}_c$ definitions, these coefficients are convergent in the case of flat spectral distributions of $E_o(\lambda)$ irradiation. That is why the values of these two coefficients determined for surface layers of basins (where spectra of irradiation $E_o(\lambda)$ are rather flat) are similar.

Experimental coefficients $\widetilde{K}_c$ and $\overline{K}_c$ are more often determined than the $a_{pl}(\lambda)$ and $K_c(\lambda)$ spectra. Utilizing indirect hydrooptical methods, the specific absorption coefficients – especially $\overline{K}_c$, are determined easier that light absorption spectra by phytoplankton (Platt, 1969; Tyler, 1975; Morel and Prieur, 1977).

Table 2 presents a list of the quoted in the world literature average values of specific absorptions $\widetilde{K}_c$ and $\overline{K}_c$, determined by both indirect and direct (*i.e.* by integration of the directly measured $K_c(\lambda)$ spectra) methods. As one can see from this Table, the mean specific light absorption coefficients by phytoplankton, occuring under various natural conditions and in cultivated cultures are different. This is obviously due to the differentiation between the earlier presented $K_c(\lambda)$ spectra. In the case of $\overline{K}_c$, the additional differentiating factor is the spectral course of $E_o(\lambda)$ irradiation, strongly variable *e.g.* with depth in a sea.

3. Semiempiric, mathematical modelling of phytoplankton absorption properites for various types of seas

In the previous chapter a review of exemplary experimental data on phytoplankton absorption properites was made. These data are not systemized; especially they do not give quantitative characteristics of the differences in light absorption by phytoplankton under various ecological conditions. Presumably, the first attempts of such a systematization were made in works by Woźniak (in press a, b). Semiempiric, mathematical modelling of phytoplankton absorption properties gave a base for such a systematization. In this chapter we present the aims and assumptions of this modelling and some of the obtained results.

3.1. Main aims and modelling range

The main aims of phytoplankton absorption properties modelling are:

- quantitative determination of spectral and average (in the visible range) absorption abilities of phytoplankton in various basins and their presentation in an approximate analytical notation;
- characterization of the differences in phytoplankton absorption properties in relation to the biological type of a basin, observed in the World Ocean;
- utilitarian aim, *i.e.* elaboration of a method for the evaluation of absorption properties of phytoplankton "in vivo", on the basis of the measurements of phytoplankton acetone extracts absorption properties.

Accomplishment of the first two aims is basically possible on the basis of the statistics of direct light absorption spectra by phytoplankton "in vivo". However, the available experimental material concerning $a_{pl}(\lambda)$ and $K_c(\lambda)$ spectra is not extensive. On the other hand, the sets of spectra of light absorption by phytoplankton acetone extracts and the determined on their basis chlorophyll *a* Ba concentrations and magnitudes of the colour indexes C_{In} form a relatively richer material.

In such a situation, the optimal solution utilized in Woźniak works (in press a, b) was, to find the approximate analytical formulae for the dependence of the absorption spectra "in vivo" $a_{pl}(\lambda)$ on the Ba and C_{In} parameters. These formulae were found by means of nonlinear regression methods on the basis of several hundred experimental absorption spectra "in vivo" and the measured values of Ba and C_{In}. Next, the obtained analytical formulae were used for the determination of phytoplankton absorption properties typical for various biological types of waters.

3.2. Analytical description of phytoplankton absorption properties

As a result of an approximation, the following analytical expressions describing the phytoplankton absorption properties in relation to the chlorophyll *a* concentration Ba and the colour index of its acetone extracts C_{In}, were obtained:

spectra of specific absorption coefficients:

$$K_c(\lambda) = (1.87 \cdot 10^{-2} C_{In} - 1.1 \cdot 10^{-2}) e^{-1.2 \cdot 10^{-4}(\lambda - 441)^2} + 6.45 \cdot 10^{-3} e^{-3.5 \cdot 10^{-4}(\lambda - 608)^2} + 2.33 \cdot 10^{-2} e^{-1.4 \cdot 10^{-3}(\lambda - 675)^2}, \quad (6)$$

spectra of inherent absorption coefficients, $a_{pl}(\lambda) = K_c(\lambda) \cdot Ba$:

$$a_{pl}(\lambda) = Ba[(1,87 \cdot 10^{-2} C_{In} - 1.1 \cdot 10^{-2}) e^{-1.2 \cdot 10^{-4}(\lambda - 441)^2} + 6.45 \cdot 10^{-3} e^{-3.5 \cdot 10^{-4}(\lambda - 608)^2} + 2.33 \cdot 10^{-2} e^{-1.4 \cdot 10^{-3}(\lambda - 675)^2}], \quad (7)$$

average for visible light (400–750 nm), specific absorption coefficient:

$$\widetilde{K_c}(\lambda) = \frac{1}{350} \int_{400}^{750} K_c(\lambda) d\lambda = 6.41 \cdot 10^{-3} C_{In} - 2.13 \cdot 10^{-3}, \quad (8)$$

average for visible light (400–750 nm) absorption coefficient:

$$\widetilde{a_{pl}} = \frac{1}{350} \int_{400}^{750} a_f(\lambda) d\lambda = Ba(6.41 \cdot 10^{-3} C_{In} - 2.13 \cdot 10^{-3}). \quad (9)$$

The above presented analytical expressions describing the spectra of light absorption by phytoplankton (eqs. (6) and (7)) do not describe the fine structure of these spectra, but only the general tendencies. They contain three components described by Gaussian functions with maxima for 441, 675 and 608 nm. The first two components have a physical sense and relate to the two main maxima observed in the experimental absorption spectra of phytoplankton. The third component (608 nm), however, has only a quantitative meaning and is introduced as a correction in order to fit the observed light absorption spectra by phytoplankton to the model ones.

Experimental verification of presented model has been also carried out. It cousisted in a comparison of 370 calculated (according to the modelling equations, on the basis of the measured Ba and C_{In}) absorption coefficients spectra with the directly measured spectra. In this way the relative errors for the particular individual cases were determined:

$$\varepsilon(\lambda) = \frac{K_c(\lambda)_c - K_c(\lambda)_m}{K_c(\lambda)_m}, \quad (10)$$

where:
$K_c(\lambda)_m$ – measure absorption coefficients,
$K_c(\lambda)_c$ – calculated absorption coefficients.

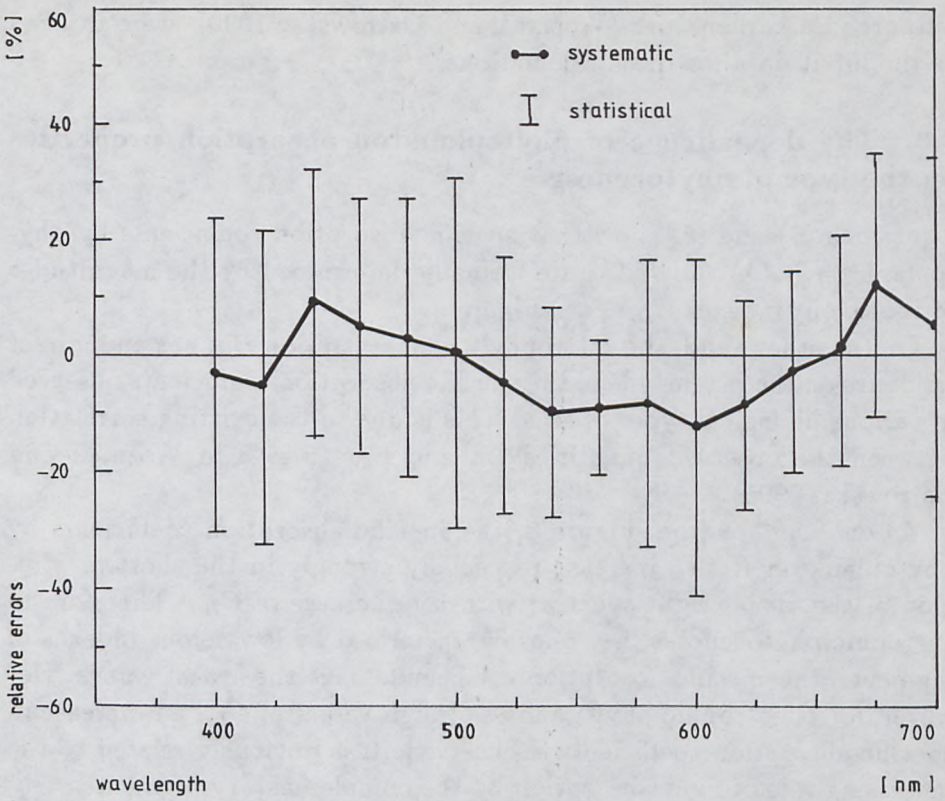

Figure 7: Error spectrum of the coefficients of light absorption by phytoplankton, determined from model equations (6) and (7) (Woźniak, in press a, b)

The mean $< \varepsilon(\lambda) >$ errors for the set of 370 spectra couples have the sense of a systematic error of the model. The observed in this set standard deviations of error σ_ε, can be accepted as the statistical modelling error. The results of verifications are shown in Figure 7. It follows from this Figure that the magnitudes of these errors are comparable with the inaccuracies of the experimental methods of measurements of light absorption by phytoplankton. One can assume therefore that this model is usefull for the approximate determination of the absorption properties of phytoplankton.

Hence, the expressions 3.1 $\div$ 3.4 were used for the determination of phytoplankton absorption characteristics, typical for various ecological conditions. The more important results of the model calculations are presented in two following paragraphs. The results of the statistics concerning the Ba and C_{In} distributions in various seas, presented by the

authors in a earlier work (Woźniak and Ostrowska, 1990), were utilized as the input data for these calculations.

3.3. The dependence of phytoplankton absorption properties on the type of phytocenosis

Equations (6) and (8) show that specific absorption coefficients by phytoplankton $K_c(\lambda)$ and $\widetilde{K}_c(\lambda)$ are formally determined by the magnitudes of the colour indexes C_{In} – see Figure 8.

On the other hand, the chlorophyll *a* concentration Ba, has an indirect influence on the magnitude of the specific absorption coefficients observed in various biological types of seas. This is due to the existing correlation between the observed quantities Ba and C_{In} (Fig. 8 in Woźniak and Ostrowska, 1990).

As one can see from Figure 8, the specific absorption coefficients by phytoplankton $K_c(\lambda)$, increase (especially strongly in the shortwave region of the visible light spectra) with the increase of C_{In}. Therefore in eutrophic phytocenoses, *i.e.* ones characterized by low colour indexes of pigments, the specific absorption coefficients have the lowest values. However, for oligotrophic phytocenoses of high values of C_{In}, an increase in specific absorption coefficients is observed. It is obviously related to the increasing role of light absorption by the complementary pigments.

According to equations (7) and (9), the chlorophyll *a* concentration directly influences the differences in the magnitude of the absorption $a_{pl}(\lambda)$ and $\widetilde{a_{pl}}$. This is illustrated in Figure 9, presenting the typical for various phytocenoses ranges of characteristic spectral absorption coefficients $a_{pl}(\lambda)$.

A good illustration of the phytocenosis type influence on the phytoplankton properties is also provided by the interdependence of the mean in visible range coefficients of $\widetilde{a_{pl}}$ – absorption and $\widetilde{K}_c$ – specific absorption on the chlorophyll *a* concentration Ba. These interdependence is shown in Figure 10. As one can see, the $\widetilde{K}_c$ coefficient decreases with the Ba concentration increase, from the value of about $0.07[m^{-1}/(mg\,Chl\,a \cdot m^{-3})]$ in oligotrophic basins to ca $0.013[m^{-1}/(mg\,Chl\,a \cdot m^{-3})]$ in eutrophic phytocenoses. It is caused by the colour index magnitude decrease in eutrophic seas compared to oligotrophic seas (Fig. 8 in Woźniak and Ostrowska, 1990). On the other hand, in the case of total absorption $\widetilde{a_{pl}}$, the situation is the opposite. Their values increase to about $0.0013(m^{-1})$ in oligotrophic basins with $Ba = 0.02mg/m^3$, to about $0.13(m^{-1})$ in

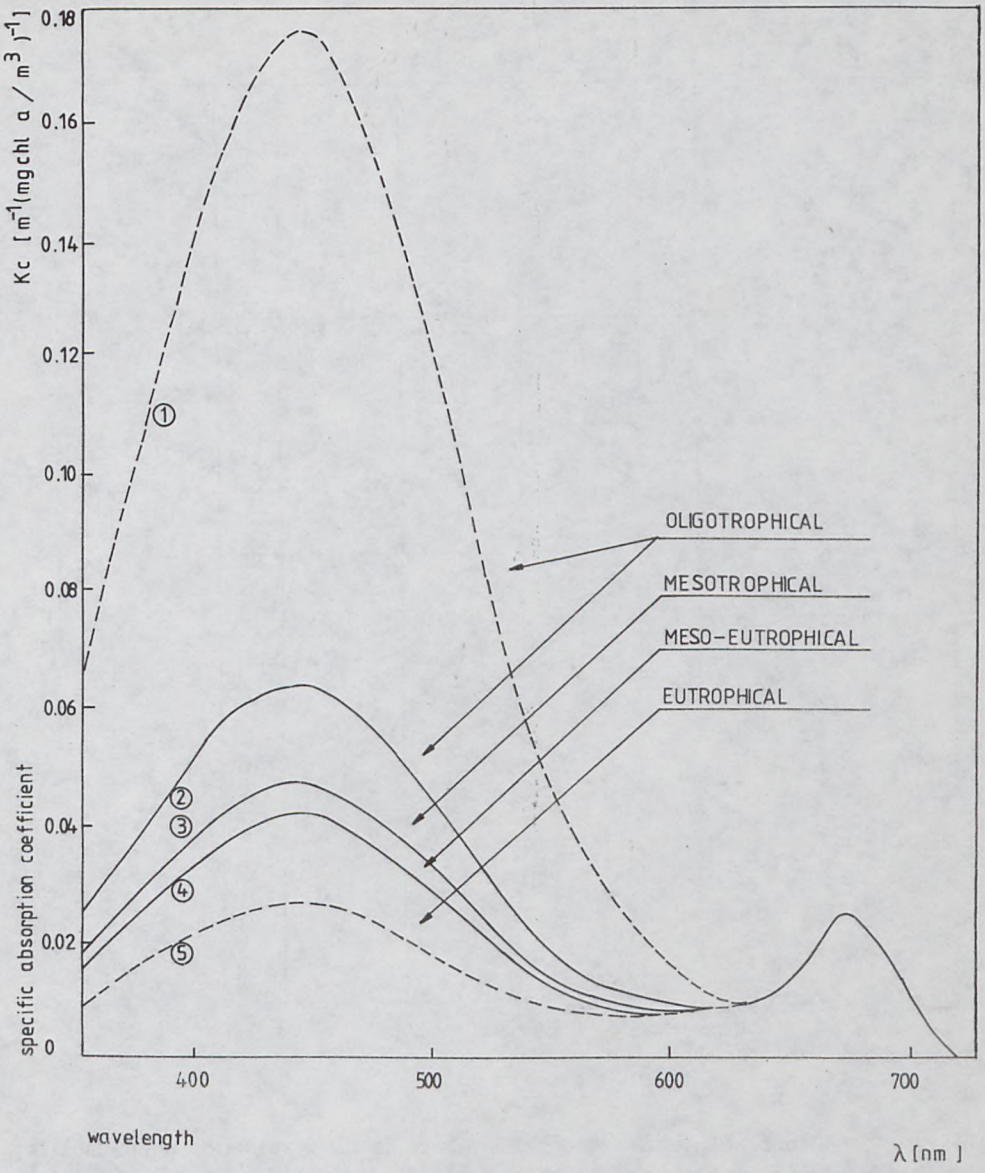

Figure 8: Theoretical spectra of the coefficients of specific absorption by phytoplankton $K_c(\lambda)$ determined on the basis of equation (6) for various phytocenoses of various magnitudes of the colour index C_{In} (for extracts): $1 - C_{In} = 10$; $2 - C_{In} = 4$ (conventional border between the oligotrophic and mesotrophic types); $3 - C_{In} = 3.1$ (conventional border between the mesotrophic and meso-eutrophic types); $4 - C_{In} = 2.8$ (conventional border between the meso-eutrophic and eutrophic types); $5 - C_{In} = 2$

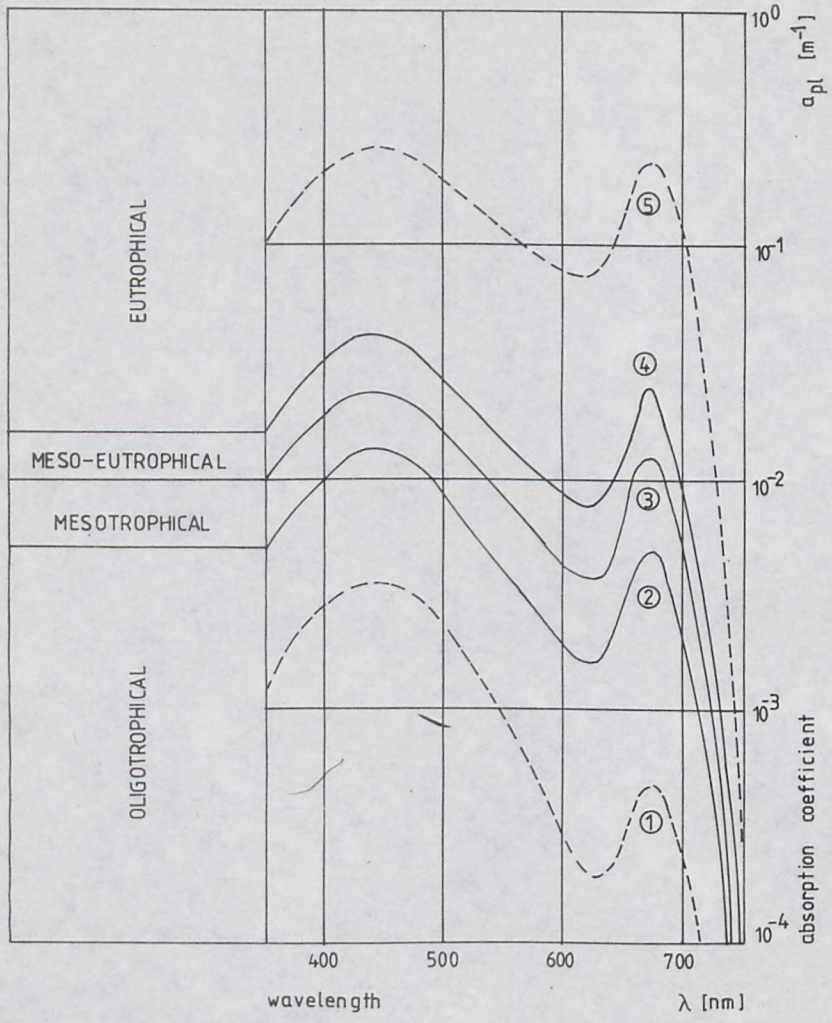

Figure 9: Theoretical spectra of the coefficients of light absorption by phytoplankton, $a_{pl}(\lambda)$, determined on the basis of equation (7), for various phytocenoses of different chlorophyll *a* concentration Ba and colour index C_{In} (for extracts): $1 - Ba = 0.02\ mg/m^3$, $C_{In} = 10$; $2 - Ba = 0.2\ mg/m^3$, $C_{In} = 4$ (conventional border between the oligotrophic and mesotrophic types); $3 - Ba = 0.5\ mg/m^3$, $C_{In} = 3.1$ (conventional border between the mesotrophic and meso-eutrophic types); $4 - Ba = 1\ mg/m^3$, $C_{In} = 2.8$ (conventional border between the meso-eutrophic and eutrophic types); $5 - Ba = 10\ mg/m^3$, $C_{In} = 2$

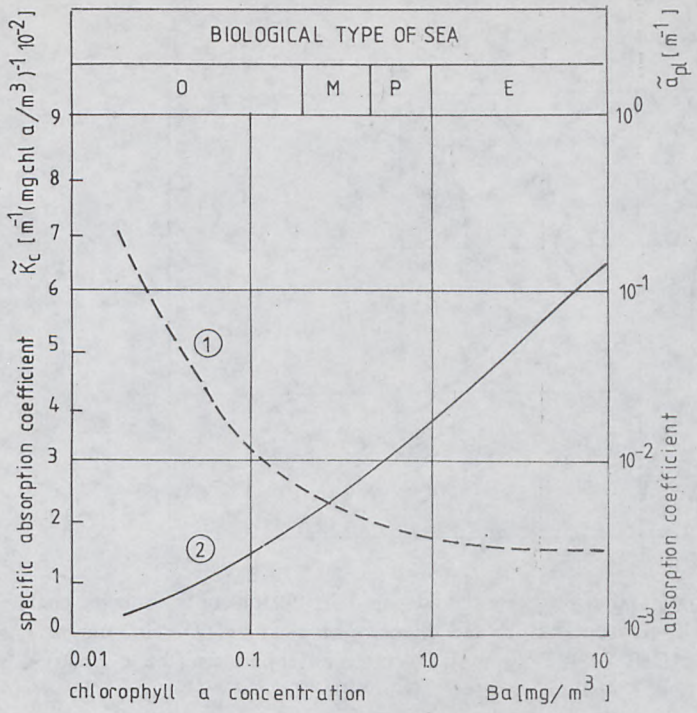

Figure 10: Model dependence of the mean coefficients of light absorption by phytoplankton in the 4000 ÷ 750 nm band: specific – $\widetilde{K}_c$ (curve 1) and inherent $\widetilde{a_{pl}}$ (curve 2) on the biological type of a basin, represented by the chlorophyll *a* concentration *Ba*. Denotations: O – oligotrophic, M – mesotrophic, P – meso-eutrophic, E – eutrophic

eutrophic seas with $Ba = 10\ mg/m^3$ which is related to the decisive influence of the *Ba* concentration on the absorption coefficients $a_{pl}(\lambda)$ and $\widetilde{a_{pl}}$. However, as one can see from Figure 10, curve 2 – the increase in the $\widetilde{a_{pl}}$ absorption is not proportional to the *Ba* concentration increase – it proceeds slower[8]. This results from the above described decrease in the specific absorption coefficient value in rich in chlorophyll *a* photocenoses compared to biologically lean phytocenoses.

3.4. Changes of phytoplankton absorption properties with depth

The concentration and composition of phytoplankton photosynthesis pigments differ not only depending on the biological type of a basin, but also

[8]This is evidenced by the slope of the $\log \widetilde{a_{pl}} = f(\log Ba)$ dependence, which is lower than 45^o within the entire *Ba* variability region.

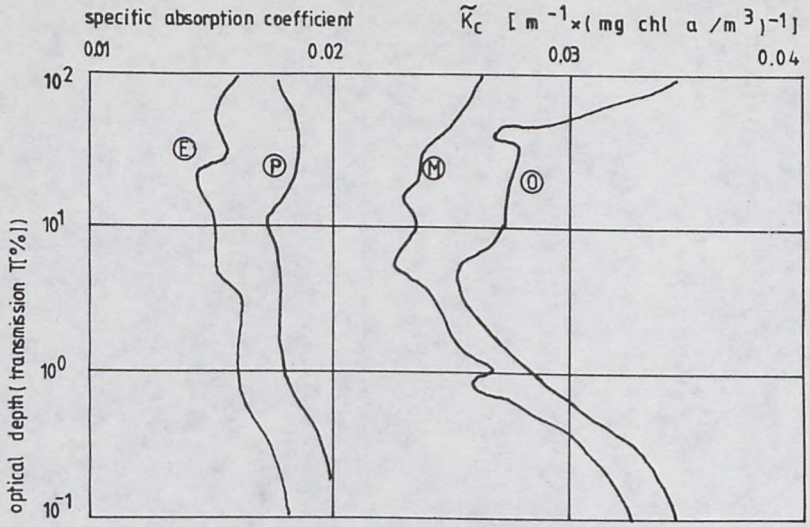

Figure 11: Mean for the particular sea types model depth distributions of the specific coefficients of light absorption by phytoplankton: O – oligotrophic sea ($Ba(O) < 0.2\ mg/m^3$); M – mesotrophic sea ($0.2 < Ba(0) < 0.5\ mg/m^3$); P – meso-eutrophic sea ($0.5 < Ba(0) < 1\ mg/m^3$); E – eutrophic sea ($BA(0) > 1\ mg/m^3$)

on the depth in a sea (Woźniak and Ostrowska, 1990). It causes depth changes of absorption properties of phytoplankton, which is illustrated in Figures 11 and 12.

Figure 11 illustrates the model depth profiles of the mean for the visible range specific absorption coefficient $\widetilde{K}_c$, in various biological types of the seas. They presented versus the optical depth in the sea. As a measure of this optical depth we accepted the PhAR transmission T[9]. Similar changes with the optical depth of the mean total absorptiona $\widetilde{a_{pl}}$ determined for seas of various surface chlorophyll a concentration are shown in Figure 12A. Figure 12B illustrates the changes of the same $\widetilde{a_{pl}}$ versus the real depth in a sea $z[m]$.

It follows from Figure 11 that for all the types of seas the depth profiles of the specific absorption coefficient $\widetilde{K}_c$ are characterized by an occurance of a minimum at particular depths in the sea. Above and below these depths an increase in the $\widetilde{K}_c$ value is observed. Such a character the $\widetilde{K}_c(T)$ profiles is hence correlated with the depth profiles of the colour index $C_{In}(T)$ (Fig. 10 in Woźniak and Ostrowska, 1990) and is also caused by

[9]See reference one on page 18 in Woźniak and Ostrowska, 1990.

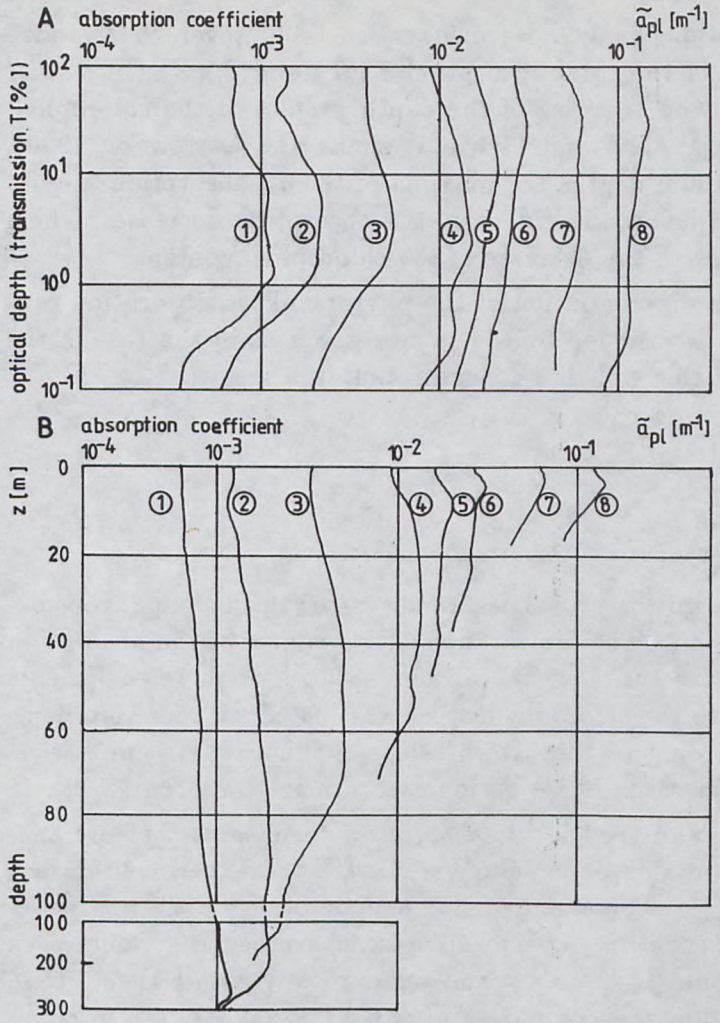

Figure 12: Examples of model, depth distributions of the coefficient of light absorption by phytoplankton. Oligotrophic seas: 1 – with surface chlorophyll *a* concentration, $Ba = 0.02\ mg/m^3$; 2 – with surface chlorophyll *a* concentration, $Ba = 0.035\ mg/m^3$; 3 – with surface chlorophyll *a* concentration, $Ba = 0.1\ mg/m^3$. Mesotrophic seas: 4 – with surface chlorophyll *a* concentration, $Ba = 0.35\ mg/m^3$. Meso-eutrophic seas: 5 – with surface chlorophyll *a* concentration, $Ba = 0.75\ mg/m^3$. Eutrophic seas: 6 – with surface chlorophyll *a* concentration, $Ba = 1.5\ mg/m^3$; 7 – with surface chlorophyll *a* concentration, $Ba = 3.5\ mg/m^3$; 8 – with surface chlorophyll *a* concentration, $Ba = 7.5\ mg/m^3$. Depth distributions are related to: A – optical depth (expressed in PhAR transmission scale; B – real depth $z[m]$

pigments' composition changes. Reverse tendencies however, characterize the depth profiles of the total absorption $\widetilde{a_{pl}}(T)$ and $\widetilde{a_{pl}}(Z)$ (Figs. 12A and 12B). Similarly to the case of the depth profiles of the chlorophyll *a* concentration (Figs. 11A and 11B in Woźniak and Ostrowska, 1990), at particular, optimum depths the maxima of the $\widetilde{a_{pl}}$ absorption are observed. Above and below these depths, the absorption decreases, which correlates directly with the decrease of the chlorophyll content.

Thus, the depth differentiation of the phytoplankton absorption properties in a sea is determined by the same reasons as in the case of the colour indexes and chlorophyll *a* concentration in a sea.

4. Conclusions

Phytoplankton absorption properties are discussed in this paper considering two main aspects. The first is the spectra course of the absorption coefficients, while the second – the absolute values of these coefficients and their relation to the chlorophyll concentration. Both these problems are discussed according to the present state-of-the-art. We emphasize, however, that in the second case basic misaccuracies can occur.

Variability ranges of the specific absorption coefficients that are analyzed and quoted in this paper agree well with the experimental data of most the authors. For example, for a light of $\lambda = 675\ nm$ wavelength, the $K_c(\lambda = 675\ nm)$ coefficient has on average the value of ca $0.023 \pm 0.08[m^{-1}/(mg\,Chl\,a \cdot m^{-3})]$ and varies mostly within the $0.015 \div 0.030$ range (same units) – compare Figure 6.

However, some author think that the above mentioned values are too high due to systematical methodical errors. For example in works by Privoznik *et al.* (1978), as well as Haardt and Maske (1978), the values of the specific absorption coefficient for the red light falling within the range from 0.0043 to $0.0174[m^{-1}/(mg\,Chl\,a \cdot m^{-3})]$ are quoted. The future experimental and theoretical investigations will show which of these ranges is correct.

The previously mentioned uncertainity in the evaluation of the absolute variability ranges of the absorption coefficients does not influence the remaining regularities of the process of light absorption by phytoplankton in a sea, discussed in this paper.

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