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THE REFRACTIVE INDEX OF
PHYTOPLANKTON

by

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The refractive index of phytoplankton is calculated from its metabolite composition. A reasonable mean value relative to sea water may be 1.03 ± 0.02 . The normal dispersion of the refractive index is negligible, but anomalous dispersion in the vicinity of strong absorption bands may be of importance for the light scattering properties of small phytoplankton.

CONTENTS

ABSTRACT	1
CONTENTS	2
1. CONCEPT AND ASSUMPTIONS OF THE MEAN REFRACTIVE INDEX	3
1.1. Some characteristics of phytoplankton	3
1.2. Definition of the refractive index	5
2. THEORY OF THE MEAN REFRACTIVE INDEX	10
2.1. The refractive index of mixtures	10
2.2. Difference between the indices due to choice of equation	15
3. THE COMPOSITION OF PHYTOPLANKTON	20
3.1. Dry mass composition	20
3.2. Water content	20
4. REFRACTIVE INDEX AND DENSITY OF THE CONSTITUENTS	22
4.1. Silica (opal)	22
4.2. Calcite.....	23
4.3. Protein	23
4.4. Carbohydrate	24
4.5. Fat	25
4.6. Pigment	25
4.7. Water	28
5. THE MEAN REFRACTIVE INDEX AND DENSITY OF PHYTOPLANKTON	29
6. COMPARISON WITH OTHER METHODS	32
7. NORMAL DISPERSION OF THE REFRACTIVE INDEX	34
8. ANOMALOUS DISPERSION OF THE REFRACTIVE INDEX ...	36
ACKNOWLEDGEMENTS	39
APPENDIX 1. THE MEAN REFRACTIVE INDEX OF A UNIAXIAL CRYSTAL	40
APPENDIX 2. THE THEORY OF ANOMALOUS DISPERSION	43
REFERENCES	52
FIGURES	59

1. CONCEPT AND ASSUMPTIONS OF THE MEAN REFRACTIVE INDEX

1.1. Some characteristics of phytoplankton

The phytoplankton is a transparent particle which as a single cell usually is so small that it becomes invisible, but which in greater concentrations is able to colour the sea. Its size is of an order of magnitude ranging from 1 to 1000 μm , or of an order 1 to 1000 compared with the wavelength of visible light. Colonial phytoplankton forms may obtain dimensions in the mm range.

The volume content of phytoplankton in sea water has in the eutrophic Oslofjorden been observed by KARL TANGEN (personal communication) to reach the extreme value $0.6 \text{ cm}^3/\text{l}$ (dinoflagellates), while normally a content of $1 \text{ mm}^3/\text{l}$ must be considered to be very high (see for instance the values quoted by JØRGENSEN, 1963, table 2.15). LISITZIN (quoted by PARSONS, 1963) gives an oceanic average of 0.8-2.5 mg/l of total particulate matter, and its organic fraction as 20-60%. The ratio between organic detritus and living phytoplankton cells will vary, but PARSONS (1963) suggest a ratio of order 10/2.

Thus less than 10^{-3} of the water volume and usually less than 10^{-6} , is likely to be occupied by phytoplankton. The values of LISITZIN and PARSONS indicate that the oceanic average may be in the range 10^{-8} - 10^{-7} . The meaning of these small numbers is better understood if one considers that a fractional volume of 10^{-6} corresponds to $1 \text{ mm}^3/\text{l}$.

Most of the phytoplankton volume consists of water. The main organic constituents or major metabolites are proteins, carbohydrates and fats. The pigment content is small, but is

still the only organic constituent with any significant light absorption.

Several cellular structures may be observed in the phytoplankton. Some species have an external silica shell, while others are covered with calcite scales. Internal silica structures may also occur. Organic cell walls may consist of cellulose, pectin or other substances.

In all algae, except the blue-green alga, the pigments are not evenly distributed, but concentrated in distinct parts of the cell called chloroplasts. Many species have only one or two chloroplasts per cell, but some may have numerous small chloroplasts.

Parts of the cell which are not filled with cytoplasm (including the chloroplasts), are called vacuoles. These are filled with a cell sap, which in composition may differ somewhat from sea water. Gas-filled vacuoles are rare in marine algae.

In some species the cell walls are covered with a mucilage layer, and some colonial forms may be completely embedded in this slime or jelly-like material.

For the present computation of the mean refractive index of the alga, however, the structure has been neglected and all constituents have been regarded as evenly distributed.

Another point which has not been taken into account here, is that the phytoplankton particle may aggregate with inorganic particles of sizes ranging from ionic dimensions to silt. The smaller particles may be taken up by the algae, and become a part of their structure.

VINOGRADOV (1953) quotes ferro oxide (Fe_2O_3) contents

from 0.5 to 2.0% in the dry matter of diatoms, and aluminium oxide (Al_2O_3) contents of the same order.

Since metallic minerals have absorption indices of order 1, similar to the absorption bands of pigments, it is possible that their influence on the optical properties of the plankton particle under certain conditions may equal that of the pigments. According to HARVEY (1937) particles of ferro hydroxide are readily adsorbed on the surface of diatoms, to such an extent that the algae may appear coated with the brown material.

It has, however, been assumed here that such cases are rare, and only the "pure" phytoplankton composition has been considered.

1.2. Definition of the refractive index

All matter consists partly of molecules or atoms and partly of empty space between the molecules. When a light wave enters such a medium, some of the light will interact with the molecules, and part of this light will be scattered and part of it absorbed, that is transformed to other forms of energy. The scattered light from a molecule or atom will interact with scattered light from the other molecules as well as with the undisturbed light wave. The total interaction will usually make the light wave proceed slower than if the space had been empty. The ratio between the phase velocity of light in vacuum and in the medium is termed the refractive index of the medium. The index is a function of the masses which participate in the interaction, and of the number of intermolecular bonds and their strength. This

relationship (which is briefly treated in Appendix 2) shall not be discussed here since we do not need to know it.

The absorption index may in certain calculations be regarded as the imaginary part of a complex refractive index. The refractive index is then written $m = n \pm i\kappa$, where n is the real part of the index, i is $\sqrt{-1}$ and κ is the absorption index. The \pm sign depends on how the phase of the light wave is written (Appendix 2, eq. 50).

In the sea the vertical attenuation of downward irradiance is influenced more by light absorption than by scattering. The absorption of a particle depends not only on its absorption index but also on its refractive index, and the scattering process too depends on both indices. So knowledge of both indices becomes necessary if one wants to estimate the optical properties of the particle and the influence of the particle on the light conditions.

If one is dealing with particles of irregular forms, like those found in the ocean, it may be practical to define a "significant" (ZANEVELD and PAK, 1973) refractive index. This is done by comparing the scattering properties of the natural particle with those of a homogeneous sphere of the same volume, and then see which refractive index the sphere must have in order to produce the same scattering. The basic idea or assumption behind this method is that a sample of irregular particles, oriented at random, will scatter light like spheres of the same volume or projected area.

The works of HODKINSON (1963), HOLLAND and GAGNE (1970, 1971) and PLASS and KATTAWAR (1971) are often referred to in support of this assumption. However, HOLLAND and GAGNE

TABLE 1

REFRACTIVE INDEX OF INORGANIC, MIXED AND ORGANIC MARINE PARTICLES

Ref.	Particles or area	Method	λ [nm]	m'
a	Quartz		589	1.15
"	Feldspar		"	1.13-1.18
"	Mica		"	1.15-1.25
"	Clay minerals		"	1.11-1.22
b	Near Japan Trench	scatterance	521,652	1.20-1.25
c	Sargasso Sea	"	633	1.20
d	"	"	"	(1.05-0.01 i)
e	" { D > 2.5 μ m D < 2.5 μ m	"	"	{ 1.15 (1.01-0.01 i)
f	" { "inorganic" "organic"	"	"	{ 1.15 1.05-1.075
g1	Mediterranean	"	"	1.20
h	Bahama Islands	"	436	1.15-1.20
i	Chesapeake Bay	attenuance	"	1.15
j	Central North Pacific	scatterance	436-578	1.03-1.05
k	Off Equador	"	436-546	1.01-1.05
g2	Baltic Sea	"	633	1.04
l	Different areas	"	"	1.02-1.05
m	Diatoms	immersion	"	1.087
n	"	"	589	1.060-1.067
o	Green alga cell wall	"	"	1.022
"	" cytoplasm exclusive chloroplast	phase contr.	"	1.015
"	" chloroplast	"	"	1.05-1.06
p	Golden-brown flagellates	scatterance	436	1.023-1.031
"	"	"	546	1.026-1.035
"	"	"	578	1.027-1.035
q	Spinach chloroplast	immersion	"	1.060
"	"	refractometer	"	1.030
"	"	scatterance	"	1.021
r	Phytoplankton	composition	589	1.03±0.02

a) WEAST, 1977, p.B-214-218
 b) SASAKI et al., 1960
 c) KULLENBERG, 1970
 d) GORDON and BROWN, 1972
 e) BROWN and GORDON, 1973a
 f) ZANEVELD et al., 1974
 g) KULLENBERG and BERG OLSEN, 1972
 h) BROWN and GORDON, 1973b
 i) BURT, 1955

j) SUGIHARA and TSUDA, 1979
 k) ZANEVELD and PAK, 1973
 l) MOREL, 1973
 m) HODGSON and NEWKIRK, 1975
 n) McCRONE et al., 1967
 o) CHARNEY and BRACKETT, 1961
 p) CARDER et al., 1972
 q) BRYANT et al., 1969
 r) This investigation

(1971) themselves draw the conclusion that "The limited results we have achieved so far..... do indicate large deviations between the scattering properties of spheres and our sample particles".

The "significant" refractive index defined by this method should then be regarded as what it is: A practical way of characterizing one of the optical properties of the marine particles.

Table 1 illustrates how the significant refractive index may vary with the applied particle size distribution. Ref. c,d,e and f have all used the same scatterance observations to calculate the refractive index which best reproduces the measurements. The real part of m' , which is the refractive index of the particles relative to sea water, is seen to vary between 1.20 and 1.05 in one-component systems, while the smallest of the real components in the two-component system varies between 1.01 and 1.05-1.075. Probably the significant indices of Ref. p and q are less uncertain, since they are based on observed scattering and size distributions from the same samples, which Refs. c-f had not at disposal.

The table also illustrates the importance of the chosen method. By the immersion method the particle is immersed in liquids of different indices, until a liquid is found where the contours of the particle disappear. The liquid will then have the same refractive index as the particle, or vice versa. The method is obviously less good for inhomogeneous particles, in particular those with shells, since the shells seem to dominate the index (Ref. m and n).

Phase contrast methods are microscope techniques based on the same principles as the immersion method. In the refractometer the phase difference of the light passing through the test liquid and a reference medium is observed, and the refractive index may be calculated. The measurements on spinach chloroplast by Ref. q give three different indices of which the one obtained by the immersion method is the greatest, 1.06, and the one calculated from scatterance measurements is the smallest, 1.02.

One may then ask whether the concept of a mean refractive index has any unic meaning for an inhomogeneous particle. The right answer is probably that the concept "mean" depends on the type of measurement it is calculated from. In this work it has been tried to estimate the "mean" refractive index of phytoplankton and its most likely variations by an indirect method, that is from its "mean" metabolite composition.

While each water molecule within a raindrop scatters light, the molecular scatterance is negligible compared with the scatterance of the raindrop as a whole. Similarly it is thought here that while a phytoplankton particle may consist of different parts with different properties, these differences can be neglected compared with the integrated properties of the particle. That is, it is assumed that the particle can be regarded as homogeneous.

A more important factor for the optical behaviour than the internal variation, may be the shape of the particle, as already suggested, but this problem shall not be further delt with here.

Chapters 2 - 6 in this work are concerned with the real part of the refractive index. Since the imaginary part is linked theoretically together with the real part, the magnitude of its influence on the real part should be estimated too. This is done in Chapters 7 - 9.

2. THEORY OF THE MEAN REFRACTIVE INDEX

2.1. THE REFRACTIVE INDEX OF MIXTURES

A simple equation for the refractive index of a mixture, supported by experiments with liquids, was proposed in 1863 by GLADSTONE and DALE:

$$\sum_j (n_j - 1)V_j = \frac{(\sum_j V_j \rho_j)}{\rho_m} (n_m - 1) = V_m (n_m - 1) \quad (1)$$

The subscript j refers to the j -th component, while m refers to the homogenous mixture. n is refractive index, ρ is density, and V is volume. This equation takes into account the possibility that

$$\sum_j V_j \neq V_m \quad (2)$$

For the case that

$$\sum_j V_j = V_m \quad (3)$$

and by means of the partial volume

$$v_j = \frac{V_j}{V_m} \quad (4)$$

eq. 1 reduces to

$$\sum_j n_j v_j = n_m \quad (5)$$

For a two-component system the last equation yields

$$n_m = n_1 v_1 + n_2 v_2 = n_1 (1 - v_2) + n_2 v_2 = n_1 + (n_2 - n_1) v_2 \quad (6)$$

By introducing the concentration C of the second component

$$C = v_2 \rho_2 \quad (7)$$

eq. (6) may be written

$$n_m = n_1 + \left(\frac{n_2 - n_1}{\rho_2} \right) C = n_1 + \alpha C \quad (8)$$

In this form the Gladstone-Dale equation is used by cell biologists to determine the concentration of cellular constituents (e.g. ROSS, 1967). α is called the specific refraction increment.

Some years after the Gladstone-Dale equation another relation was derived theoretically by LORENZ (1880) and LORENTZ (1880):

$$\sum_j \frac{n_j^2 - 1}{n_j^2 + 2} V_j = \frac{n_m^2 - 1}{n_m^2 + 2} V_m \quad (9)$$

LORENTZ (1915) says that "This equation is found to hold as a rough approximation for various liquid mixtures", and adds that the same may be said of the Gladstone-Dale equation. Many textbooks, however, describes eq. 9 as superior to eq. 1.

One of the advantages of the Lorenz -Lorentz-equation is that it may be used to estimate the refractive index of a chemical compound. It will then have the form

$$\sum_j \frac{n_j^2 - 1}{n_j^2 + 2} \frac{M_j}{\rho_j} = \sum_j R_j = \frac{n_m^2 - 1}{n_m^2 + 2} \frac{M_m}{\rho_m} = R_m \quad (10)$$

M is the molecular or atomic weight of the constituent.

The term R_j , defined by

$$R = \frac{n^2 - 1}{n^2 + 2} \frac{M}{\rho} \quad (11)$$

is called the molar refraction. Some values of R are listed by "The Handbook of Chemistry and Physics" (WEAST, 1977). Eq. 10 will be applied later in Chapter 4.6.

Eqs. 1 and 9 were criticised by WIENER (1912).

According to him, a mixture of spheres with refractive index n_2 in a liquid of index n_1 , should have a mean refractive index n_m given by the relation

$$\frac{n_m^2 - n_1^2}{n_m^2 + 2n_1^2} = v_2 \frac{n_2^2 - n_1^2}{n_2^2 + 2n_1^2} \quad (12)$$

For fibers (n_2) in a liquid (n_1) he obtained that

$$\frac{n_{mn}^2 - n_1^2}{n_{mn}^2 + n_1^2} = v_2 \frac{n_2^2 - n_1^2}{n_2^2 + n_1^2} \quad (13)$$

when the direction of the electrical vector in the polarized light is normal to the optical axes, that is normal to the fiber axes, and

$$n_{mp}^2 = v_1 n_1^2 + v_2 n_2^2 \quad (14)$$

when the direction is parallel with the optical axes.

If the constituents are arranged in parallel layers, and the electric vector of the polarized light is normal to the optical axes, that is, parallel with the layers, WIENER obtained

$$n_{mn}^2 = v_1 n_1^2 + v_2 n_2^2 \quad (15)$$

When the electric vector is parallel with the optical axes (normal to the layers), the relation is

$$\frac{1}{n_{mp}^2} = \frac{v_1}{n_1^2} + \frac{v_2}{n_2^2} \quad (16)$$

WIENER's equations require that eq. 3 is valid, but on a molecular scale this is not necessarily true. In his

criticism of eq. 9 he seems to have overlooked that he is working on a dimensional scale quite different from that of LORENZ and LORENTZ. His structures consist of ordered arrangements of optically isotropic material, with dimensions small compared with the wavelength of light, but still large compared with the size of molecules. LORENZ and LORENTZ on the other hand, are working on the atomic scale. The distinction between spheres and liquid in WIENER's eq. 12 for instance, becomes meaningless when the spheres are of molecular size. However, his eqs. 13 and 14 have proven to describe the so-called textural (OSTER, 1955) or form (BORN and WOLF, 1975) birefringence of fibers. Some calculation gives that

$$n_{mp}^2 - n_{mn}^2 = \frac{v_1 v_2 (n_2^2 - n_1^2)^2}{(v_2 + 1)n_1^2 + v_1 n_2^2} > 0 \quad (17)$$

that is

$$n_{mp} > n_{mn} \quad (18)$$

(OSTER, 1955). In fact, for natural cellulose fibers it has been observed that $n_{mp} = 1.58-1.60$, while $n_{mn} = 1.53-1.54$ (FREY, 1926, McCURONE et al., 1967). In an analysis of eleven phytoplankton species, PARSON et al. (1961) found that 0.3 - 14%, with a mean value of 3%, of the total dry mass content were crude fibres. Birefringence effects due to fibers should then be negligible.

(The formulae become far more complicated if one of the constituents is light absorbing (WIENER, 1927), but such cases shall not be discussed here).

Textural birefringence behaves like the birefringence

of uniaxial crystals, with an "ordinary" refractive index ω and an "extraordinary" refractive index ϵ . n_{mn} corresponds to ω and n_{mp} to ϵ .

It may be shown (Appendix 1) that for arbitrary orientations of uniaxial crystals, the mean refractive index will be approximately

$$\bar{n} \approx (2\omega + \epsilon)/3 \quad (19)$$

Biaxial crystals like aragonite, with refractive indices α , β and γ , will have the mean refractive index (DANA, 1950):

$$\bar{n} \approx (\alpha + \beta + \gamma)/3 \quad (20)$$

Refractive indices, if not otherwise stated, are usually given at the yellow D-line (589 nm).

2.2. Difference between the indices due to choice of equation

A refractive index $n_2 = 1.55$ of particle dry mass was used together with $n_1 = n_w = 1.34$ of water, in order to compute the mean refractive index as a function of the partial water volume $v_1 = v_w$. Eqs. 6,9,12-16 of the last chapter were applied. The partial volumes were assumed to be additive (eq.3). The results are presented in Fig. 1. GD and LL refer to the Gladstone-Dale and the Lorenz-Lorentz equation respectively. In the actual range of v_w , 0.7-0.9, there is an almost linear relation between the refractive index and v_w .

If we can assume that the incident light is unpolarized and that the internal structures are oriented at random, so that the textural birefringence effects are meaned,

then the maximum difference between the indices, resulting from the different equations or internal structures is about 0.003.

TABLE 2
THE DRY MASS COMPOSITION OF PHYTOPLANKTON
ALGAE WITH ORGANIC SURFACE

Reference (and series of measurement)	Species	Prot.	Carb.	Fat	Pigm.
		[% of dry mass]			
	DINOFLAGELLATES				
a (An. IV)	Mainly <u>Ceratium</u>	52	45	3	
" (" X)	" "	82	12	6	
" (" XIa)	" "	79	13	8	
" (" b)	" "	84	8	8	
" (" c)	" "	78	14	8	
" (" d)	" "	73	19	8	
" (" e)	" "	73	18	9	
b	<u>Amphidinium carterae</u>	35	39	23	3
"	<u>Exuviaella</u> sp.	37	44	18	1
	BROWN FLAGELLATES				
"	<u>Monochrysis lutheri</u>	53	34	12	1
	BLUE-GREEN ALGAE				
"	<u>Agmenellum quadruplicatum</u>	44	38	16	2
	GREEN ALGAE				
c	<u>Chlorella pyrenoidosa</u>	48	27	25	
"	<u>Chlorella vulgaris</u>	48	32	20	
d (Day 11)	" "	30	44	23	3
" (" 18)	" "	21	48	28	3
" (" 25)	" "	21	46	31	2
" (" 32)	" "	15	49	34	2
b	<u>Tetraselmis maculata</u>	72	21	4	3
"	<u>Dunaliella salina</u>	58	32	7	3
	RED ALGAE				
d (A8)	<u>Porphyridium cruentum</u>	40	47	10	3
" (A20)	"	33	55	10	2
" (A26)	"	39	45	14	2
" (B20)	"	26	65	8	1

TABLE 2 (cont.)

ALGAE WITH MINERALIZED SURFACE

Reference and series of measurement	SILICA SHELL Species	Silica	Prot. Carb. Fat Pigm.			
			[% of dry mass]			
DIATOMS						
a (An.III)	Mainly <u>Rhizosolenia</u>	46	30	20	4	
" (" V)	" <u>Skeletonema & Thalassiothrix</u>	41	48	5	6	
" (" VI)	" <u>Skeletonema</u>	28	32	33	7	
" (" VII)	" "	24	42	27	7	
" ("VIIIa)	" diatoms	35	57	1	7	
" (" b)	" "	37	49	1	13	
" (" c)	" "	29	63	2	6	
" (" d)	" "	23	64	5	8	
b	<u>Skeletonema costatum</u>	32	39	22	5	2
"	<u>Coscinodiscus</u> sp.	67	24	6	2	1
"	<u>Phaeidactylum tricorutum</u>	1	49	36	10	4
e (Day 12)	Mainly diatoms	49	31	11	6	3
" (" 15)	" "	47	21	23	6	3
f (Day 12)	Mainly diatoms	30	59	5	4	2
" (" 14)	" "	36	51	6	4	3
" (" 16)	" "	42	38	12	6	2
" (" 18)	" "	40	32	21	6	1
" (" 20)	" "	40	30	21	8	1
CALCITE SCALES		Calcite	Prot.	Carb.	Fat	Pigm.
b	COCCOLITHOPHORIDS <u>Syracosphaera carterae</u>	23	54	17	5	1

a) BRANDT & RABEN, 1920

d) COLLYER & FOGG, 1955

b) PARSONS et al., 1961

e) McALLISTER et al., 1961

c) KETCHUM & REDFIELD, 1949

f) ANTIA et al., 1963

TABLE 3

THE WATER CONTENT OF ALGAE

Ref.	Species	m_d	$\overset{c}{c}$ [g cm ⁻³]	v_w
a	Sea weeds <u>Fucus, Laminaria</u>)	0.18-0.24	(0.19-0.25)	(0.80-0.86)
b	diatoms	(0.43-0.66)	0.50-0.85	(0.43-0.67)
"	other species	(0.19-0.37)	0.20-0.40	(0.69-0.85)
c	mixed population	(0.35)	0.39	(0.72)
"	organic part	(0.26)	0.28	(0.79)
d	green algae	(0.22±0.03)	0.23±0.03	(0.82±0.03)
e	green algae	0.25	(0.27)	(0.80)
f	green algae (usual range)	0.20-0.33	(0.21-0.36)	(0.73-0.84)
g	mainly diatoms	0.16±0.06	(0.17±0.07)	(0.89±0.05)
	Mean value	0.3	0.3	0.8
	Standard deviation	0.1	0.2	0.1
<p>a) Quoted by ATKINS (1923) d) KETCHUM and REDFIELD (1949)</p> <p>b) GRIM (1939) e) MYERS and JOHNSTON (1949)</p> <p>c) RILEY (1941) f) SPOEHR and MILNER (1949)</p> <p>g) HARRIS and RILEY (1956)</p>				

3. THE COMPOSITION OF PHYTOPLANKTON

3.1. Dry mass composition

Table 2 gives some examples of the major metabolite composition of phytoplankton. (The original taxonomy has been retained). The table does not pretend to show all possible variation, but it is hoped that some idea about the mean values may be obtained from the numbers. An interesting result is that the total pigment content in these examples only varies between 1 and 3% of the dry mass.

The content of inorganic material, except silica and calcite, has been neglected. The ash content of many marine algae does not exceed 10% of the dry mass, and consist mainly of sea salts (STRICKLAND, 1960), which here has been supposed to be included in the water content.

3.2. Water content

The water content is the greatest factor of uncertainty in our estimates of the refraction index. Table 3 gives some observations of water and dry mass content. Numbers without parentheses are observed, while numbers in parenthesis have been calculated. Dry mass has been converted to volume and vice versa by assuming that the dry mass of diatoms has density $\rho_d = 1.5 \text{ g cm}^{-3}$, that other species have density 1.3 g cm^{-3} , and that mixed populations have density 1.4 g cm^{-3} (see Table 8). The relations between m_d , C and v_w of Table 3 are

$$m_d = \frac{\text{dry mass}}{\text{total mass}} = \left(\frac{1}{C} - \frac{1}{\rho_d} + 1 \right)^{-1} \quad (21)$$

$$C = \frac{\text{dry mass}}{\text{total volume}} = \left(\frac{1}{m_d} + \frac{1}{\rho_d} - 1 \right)^{-1} \quad (22)$$

$$v_w = \frac{\text{water volume}}{\text{total volume}} = \left(1 + \frac{m_d}{(1-m_d)\rho_d}\right)^{-1} \quad (23)$$
$$= 1 - C/\rho_d$$

A factor of uncertainty is that sea salts may be included in the dry mass, but the error, as mentioned earlier, is probably not great.

The mean value of m_d in Table 3 is about 4 times the value once recommended by ICES (CUSHING et al., 1958), but the latter seem to have largely overestimated the water content.

The problem of measuring the true "wet weight" or total mass of algae has been discussed by STRICKLAND (1960). According to him, the experimental wet weight will rarely be less than twice the true algal weight, due to the presence of interstitial water. However, his own guess of a mean dry mass concentration C is 0.35 g cm^{-3} , which is in agreement with the mean value 0.3 g cm^{-3} obtained in Table 3 without any corrections.

JØRGENSEN (1966) has discussed the problem too, and quotes some additional data in the same range as Table 3.

4. REFRACTIVE INDEX AND DENSITY OF THE CONSTITUENTS

4.1. Silica (opal)

Diatom cells are enclosed in walls composed of hydrated amorphous silica (LEWIN, 1962a). Silica in this form ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$) is called opal. Some data for the density ρ and refractive index n of opal and quartz (SiO_2), as well as of diatoms, are presented in Table 4.

Ref.	Silica form	ρ [g cm ⁻³]	n
a	opal		1.406
b(p.B-155)	"	2.17-2.20	1.41-1.46
"(p.B-217)	"	1.73-2.16	1.41-1.46
c	diatom opal	2.00-2.07	1.40-1.43
d	diatoms	ca. 2.0	1.42-1.43
e	skeletonema		1.457
d	devitr.diat.	ca. 2.7	ca.1.486
f	vitr.quartz		1.458
b(p.B-155)	crystal quartz	2.64-2.66	1.547

a) FORSYTHE (1954)	d) McCURNE et al. (1967)
b) WEAST (1977)	e) HODGSON and NEWKIRK (1975)
c) quoted by LEWIN (1962a)	f) JENKINS and WHITE (1957, p.465).

The values $\rho = (2.07 \pm 0.10) \text{ g cm}^{-3}$ and $n = 1.43 \pm 0.03$ have been chosen to represent opal.

4.2. Calcite

Some algae bear small scales of anhydrous crystalline CaCO_3 , called coccoliths. Usually each coccolith comprises only one crystal type, either uniaxial calcite or biaxial aragonite (LEWIN, 1962b). Table 5 gives densities and mean refractive indices of these crystal forms.

TABLE 5			
DENSITY AND REFRACTIVE INDEX OF CaCO_3			
Ref.	Form	ρ [g cm ⁻³]	\bar{n}
a	calcite	2.71	1.601
b(p.B-99)	"	2.71	1.601
"(p.B-215)	"	2.72-2.94	1.601-1.677
a	aragonite	2.94	1.633
b(p.B-99)	"	2.93	1.632
"(p.B-215)	"	2.94-2.95	1.632-1.633
a) McCrone et al. (1967)		b) Weast (1977)	

The values $\rho = (2.71 \pm 0.01) \text{ g cm}^{-3}$ and $\bar{n} = 1.60 \pm 0.01$ have been chosen to represent the calcite of the coccolithophorids of Table 2.

4.3. Protein

ARMSTRONG et al. (1947) found that lipid-free proteins had a refractive index $n = 1.60$, while proteins with 75% lipid content had $n = 1.51$.

From the indices of ARMSTRONG et al., compared with densities of ONCLEY et al. (1947), the values $n = 1.60 \pm 0.01$ and $\rho = (1.33 \pm 0.02) \text{ g cm}^{-3}$ have been chosen.

Protein and non-protein indices of cellular constituents have been discussed by BARER (1966) and ROSS (1967).

4.4. Carbohydrate

Table 6 gives densities and refractive indices of some algal carbohydrate forms: cellulose and starch ($(\text{C}_6\text{H}_{10}\text{O}_5)_n$), sucrose ($\text{C}_{12}\text{H}_{22}\text{O}_{11}$) and glucose ($\text{C}_6\text{H}_{12}\text{O}_6$). The values which have been chosen to represent all carbohydrate, are $\rho = (1.53 \pm 0.04) \text{ g cm}^{-3}$ and $n = 1.55 \pm 0.02$.

TABLE 6			
DENSITY AND REFRACTIVE INDEX OF CARBOHYDRATE			
Ref.	Carbohydrate form	ρ [g cm ⁻³]	\bar{n}
a(p.C-242)	cellulose, cryst.	1.27-1.61	
b	" "		1.55
c	" , amorph.	1.482-1.489	
d	" , fibers	1.48-1.55	1.563-1.573
d	starch	1.53	1.53-1.56
e	"	1.50	1.53
a(p.F-1)	"	1.53	
f	"		1.53
g	"		1.51-1.54
a(p.C-504)	sucrose	1.581	1.538
e	"	1.588	1.558
d	"	1.588	1.56
f	"		1.557
a	glucose	1.562	
d	"	1.544	1.55

a) WEAST (1977) d) McCrone et al. (1967) g) CHAMOT and
 b) STECHER (1968) e) DAVIES et al. (1954) MASON (1944)
 c) TREIBER (1955) f) GIBBS (1942)

4.5. Fat

Mean values and standard deviations of the densities and refractive indices of plant oil quoted by WEAST (p.0-216) have been calculated, neglecting temperature effects since the coefficient of volume expansion only is about $0.0007 (^{\circ}\text{C})^{-1}$ (CLARK, 1962, p.53). The results are $\rho = (0.93 \pm 0.02) \text{ g cm}^{-3}$ and $n = (1.47 \pm 0.01)$, and these values have been chosen to represent the algal fat.

4.6. Pigment

Very little information about densities and refractive indices of pigments is given in the literature. The few obtainable data are presented in Table 7. The numbers in parentheses are "educated guesses", which have been obtained in this way:

The molecular structure of xantophyll or luteol ($\text{C}_{40}\text{H}_{56}\text{O}_2$) is very similar to β -carotene ($\text{C}_{40}\text{H}_{56}$). (e.g. RABINOWITCH, 1945). Roughly speaking, the difference is an oxygen atom added at each end of the molecule. If the volume remains practically the same, the ratio between the densities should be equal to the ratio between the molar masses, and the density of xantophyll should be $\rho = (1.00 \text{ g cm}^{-3})569/537 = 1.06 \text{ g cm}^{-3}$.

The refractive index of chlorophyll a ($\text{C}_{55}\text{H}_{72}\text{Mg N}_4\text{O}_5$) is obtained by observing that the molecule consists of a phytol tail ($\text{C}_{20}\text{H}_{40}\text{O}$) and a head ($\text{C}_{35}\text{H}_{32}\text{Mg N}_4\text{O}_4$). The tail has molar mass 297 g, density 0.85 g cm^{-3} , refractive index 1.460 (WEAST, p. C-439), and consequently a molar refraction (eq. 12) of $R = 95.7 \text{ cm}^3$.

TABLE 7			
DENSITY AND REFRACTIVE INDEX OF PIGMENT			
Ref.	Pigment	ρ [g cm ⁻³]	n
a(p.C-241)	α -carotene	1.00	
b	"		1.451
a(p.C-241)	β -carotene	1.00	
b	"		1.453
b	xantophyll		1.448
see text	"	(1.06)	
c	chlorophyll <u>a</u>	1.11	
see text	"		(1.52)
"	chlorophyll <u>b</u>	(1.13)	(1.52)
"	chlorophyll <u>c</u>	(1.31)	(1.54)

a) WEAST (1977)
 b) EULER and JANSSON (1931)
 c) KETELAAR and HANSON (1937)

The constituents of the head (WOLKEN, 1973) have the R-contributions (WEAST, p. E-223)

C ₃₅	2.591 cm ³	x 35 =	90.7 cm ³
H ₃₂	1.028 "	x 32 =	32.9 "
aromatic N ₄	3.550 "	x 4 =	14.2 "
double bond O ₂	2.122 "	x 2 =	4.2 "
single bond O ₂	1.643 "	x 2 =	3.3 "
Mg	3 ?	" x 1 =	3.0 "
		R _{head}	<u>148.3 cm³</u>

Since

$$R_{\text{total}} = R_{\text{head}} + R_{\text{tail}} = 138.3 \text{ cm}^3 + 95.7 \text{ cm}^3, \text{ that is}$$

$$\frac{n^2-1}{n^2+2} \frac{894 \text{ g}}{1.11 \text{ g cm}^{-3}} = 244 \text{ cm}^3,$$

we obtain for chlorophyll a that $n = 1.52$.

If chlorophyll b ($C_{55}H_{70}MgO_6N_4$) occupies the same volume as chlorophyll a, the ratio between their densities should equal the ratio between their molar masses, and the density of chlorophyll b should be $\rho = (1.11 \text{ g cm}^{-3})907/893 = 1.13 \text{ g cm}^{-3}$. In the same way as for chlorophyll a, the refractive index of chlorophyll b may be estimated to $n=1.52$.

Chlorophyll c is a mixture of $C_{35}H_{28}Mg N_4O_5$ and $C_{35}H_{30}Mg N_4O_5$. (DOUGHERTY et al., 1966) and its structure resembles the head of chlorophyll a. It is then not unlikely that it will also occupy approximately the same volume. If the volumes of the head and tail of chlorophyll a are additive, that is

$$\left(\frac{M}{\rho}\right)_{\text{total}} = \left(\frac{M}{\rho}\right)_{\text{head}} + \left(\frac{M}{\rho}\right)_{\text{tail}},$$

we find that the molar volume of the head should be

$$\left(\frac{M}{\rho}\right)_{\text{head}} = 464 \text{ cm}^3.$$

Since the molar mass of chlorophyll c are about 609 g, its density should be about 1.31 g cm^{-3} . As for chlorophyll a, we may estimate its R value to about 146.4 cm^3 , and its refractive index should then be 1.54.

In an investigation by ANTIA et al. (1963) of a population of mainly diatoms, the ratios chlorophyll a: chlorophyll c: carotenoids were ca. 1: 0.5 : 1. By means of Table 7 the values $\rho \approx (1.12 \pm 0.06) \text{ g cm}^{-3}$ and $n = 1.50 \pm 0.04$ have then been chosen to represent pigment. It should be noted, however, that due to the small pigment content, the

chosen values have little influence on the total refractive index of the algae.

The absorption bands of the pigments and their influence on the refractive index, is discussed in Chapter 8.

4.7. Water

It has been assumed that the water of the algae has the same density and refractive index as sea water. Values of these can be found in most textbooks, and the ones used here are $\rho = 1.025 \text{ g cm}^{-3}$ and $n = 1.34$.

5. THE MEAN REFRACTIVE INDEX AND DENSITY OF PHYTOPLANKTON.

By means of the densities and refractive indices chosen in the last chapter, the Lorenz-Lorentz equation (eq.9) has been applied to calculate the mean refractive index of the phytoplankton. The relative dry mass composition of Table 2, and a varying water content were used to obtain the values presented in Fig. 2 and Table 8. The density ρ of the phytoplankton was, by means of eq.3, calculated from

$$\rho = \sum \rho_j v_j = \rho_d - (\rho_d - \rho_w) v_w \quad (24)$$

ρ_d and ρ_w are the densities of dry mass and water respectively. The subscript m of n_m is omitted in the following discussion.

TABLE 8							
REFRACTIVE INDEX AND DENSITY OF PHYTOPLANKTON							
(mean values based on Table 2)							
Species	v_w	\bar{n}			$\bar{\rho}$ (g cm ⁻³)		
		0	0.5	1	0	0.5	1
Coccolithophorids		1.562	1.446	1.340	1.426	1.226	1.025
Dinoflagellates		1.552	1.442	"	1.240	1.133	"
Brown flagellates		1.548	1.439	"	1.258	1.142	"
Red algae		1.545	1.437	"	1.317	1.171	"
Blue-green algae		1.541	1.437	"	1.252	1.139	"
Green algae		1.535	1.434	"	1.229	1.127	"
Diatoms		1.520	1.429	"	1.451	1.238	"
Mean from Table 2		1.547	1.434	"	1.306	1.183	"
Standard deviation		0.023	0.011		0.046	0.018	

It should be noted that the "mean values" presented here are the mean values of Table 2, and not necessarily the mean values found in nature. It is hoped, however, that the

numbers represent at least some of the natural values most likely to occur.

Fig. 2 illustrates that for values of v_w greater than 0.5, \bar{n} becomes an almost linear function of v_w . For partial water volumes in the range 0.7 - 0.9, the refractive index of the figure varies between 1.403 and 1.357, that is about 1.05 and 1.01 relative to water. The lines of the figure are described by

$$\bar{n} \approx (1.54 \pm 0.02) - (0.20 \pm 0.02)v_w$$

If a reasonable mean value of v_w is 0.8 (Table 3), the corresponding mean value of n might be 1.38, according to the last equation, that is 1.03 relative to water. Thus perhaps a reasonable variation of \bar{n} for living phytoplankton particles is 1.03 ± 0.02 . The corresponding density becomes $(1.09 \pm 0.05) \text{ g cm}^{-3}$. If only species with organic surfaces are regarded, the density will be $(1.07 \pm 0.03) \text{ g cm}^{-3}$, which is in good agreement with the often quoted density range 1.03 - 1.10 g cm^{-3} of cytoplasm (e.g. BONEY, 1975, p. 42).

The few calculated values given in Table 8, show that there is a better correlation between refractive index and partial water volume than between refractive index and density.

In Chapter 2.2 the maximum difference in n resulting from the use of different equations, was estimated to be about 0.003. The possible error in n , due to errors in refractive index and density of the algal constituents, is higher. With the standard deviations or possible errors

estimated in Chapter 4, it can be calculated by means of Table 2 that the standard deviation of n , at a partial water volume of 0.8, has a mean value about 0.008. The standard deviation of n due to the individual differences in composition, is likewise found to be about 0.007. The variation due to species seems to be less important, since the standard deviation of \bar{n} of the species is about 0.003 when $v_w = 0.8$.

The greatest factor of uncertainty in our estimate of \bar{n} , however, is the algal water content. Earlier in this chapter we have estimated the combined variation in \bar{n} , due to species and water content, to be about ± 0.02 .

6. COMPARISON WITH OTHER METHODS

Table 1 presents some refractive index determinations of marine particles. The common minerals have indices in the range 1.11-1.25 relative to water, and some of the scatterance measurements (Ref. b,c,g1,i) indicate that this inorganic type of particles, with $m' = 1.15-1.25$, is dominating. Other measurements of scatterance in other areas (Ref. j,k,g2,l) suggest that the dominating type of particles is organic, with $m' = 1.01-1.05$.

Very few refractive index measurements on pure algal cultures seem to have been made. The indices of diatoms obtained by the immersion method (Ref. m and n) probably are dominated more by the silica shell than they should according to the percentage silica content. The spherical flagellate Isochrysis galbana (Ref. p) seems from scatterance observations to have the mean refractive index $m' = 1.031 \pm 0.004$, which lies at the center of the range 1.03 ± 0.02 estimated in the present investigation. Phase contrast measurements on the spherical green alga Chlorella pyrenoidosa (Ref. o) give that the chloroplast has a refractive index $1.05-1.06$ while the rest of the cytoplasm has the index 1.015. If about 1/3 to 1/2 of the cell is occupied by the chloroplast, the mean refractive index of the total cytoplasm will be in the range 1.027-1.038. If the refractive index of the cell wall, 1.022, is included, the mean index of the alga becomes slightly lower, and in good agreement with the earlier estimated "mean" value of 1.03.

Although the mean refractive index of phytoplankton is likely to vary with depth and position in the sea, the

value 1.03 is perhaps closer to a true mean than the "significant" refractive indices given by Ref. e and f in Table 1. The former reference assumes that the particle fraction with diameter less than 2.5 μm is "organic" with the complex index $1.01 - 0.01 i$, and the latter obtains by another method an index in the range 1.05 - 1.075.

7. NORMAL DISPERSION OF THE REFRACTIVE INDEX

The refractive index, or the velocity of light, may be influenced by two factors: The change of phase and the change of amplitude of the electric vector as compared with the undisturbed light wave. So far we have been discussing the refractive index at the wavelength 589 nm, and only as a result of alterations of phase velocity. However, most natural transparent matter will be less transparent in the UV region, that is absorption will diminish the amplitude. This process will not only influence the refractive index in the UV region, but it will make the refractive index decrease monotonously from UV towards the red part of the spectrum. This behaviour is called the normal dispersion of the refractive index. If the matter has absorption bands in the visible part of the spectrum, the refractive index in this region will vary in a way which is called the anomalous dispersion of the coefficient. The classical theory of the relation between absorption coefficient and refractive index was given by HELMHOLTZ (1875) and is discussed in Appendix 2.

The normal dispersion may be described by the SELLMIEIER equation in its most simple form:

$$n^2 = 1 + \frac{\lambda^2 A}{\lambda^2 - \lambda_1^2} \quad (25)$$

where A and λ_1 are constants, $\lambda_1 < \lambda$. As shown by JENKINS and WHITE (1957, p.473), the equation can be expanded to give the CAUCHY equation

$$n = P + \frac{Q}{\lambda^2} + \frac{R}{\lambda^4} \quad (26)$$

where P , Q and R are constants. In the visible region it may suffice with the two first terms on the right side to describe the dispersion.

The refractive index relative to water may be written

$$n' = \frac{n}{n_w} = P' + \frac{Q'}{\lambda^2} \quad (27)$$

Some values of P , P' , Q and Q' are given in Table 9. The relative refractive index n' as a function of λ is shown in Fig. 3. The difference $n'(300 \text{ nm}) - n'(700 \text{ nm})$ has a maximum of 0.025 for protein, for the other constituents the difference is less than 0.008. When about 80% of the phytoplankton consists of water, the difference for the alga will be less than 0.005. This variation of n' is small compared with the variation of the wavelength, and for many problems may be neglected (see for instance Chapter 8, eqs. 30 - 31).

TABLE 9					
DISPERSION OF THE MAIN CONSTITUENTS					
Based on data from	Constituent	P	Q	P'	Q'
a	Protein	1.578	7530 nm ²	1.192	2840 nm ²
b	Calcite	1.584	6070 "	1.197	1720 "
c	Carbohydrate	1.517	4410 "	1.146	590 "
d	Fat	1.457	4530 "	1.101	790 "
e	Opal	1.420	3510 "	1.073	90 "
f	Water	1.324	3170 "	1	0 "

a) TIMASHEFF (1976)	d) WASHBURN (1927)
b) WEAST (1977, p. E-223)	e) JENKINS and WHITE (1957, p.465)
c) KORITNIG (1962)	f) quoted by JERLOV (1976).

8. ANOMALOUS DISPERSION OF THE REFRACTIVE INDEX

A simplified relation between the absorption index κ and the refractive index n in the vicinity of an absorption band is

$$n \approx N + \frac{2\kappa_1 G(\lambda - \lambda_1)}{4(\lambda - \lambda_1)^2 + G^2} \quad (\text{eq.80, Appendix 2})$$

N is the mean refractive index outside the absorption region, κ_1 is the peak value of the absorption index at the wavelength λ_1 , and G is the width of the absorption band where κ is $\kappa_1/2$. The extreme values of n occur at $\lambda = \lambda_1 \pm G/2$ and is $n = N \pm \kappa_1/2$. The variation of the refractive index is thus equal to half the peak value of the absorption index. The relation between absorption index κ and the absorption coefficient a is

$$\kappa = \frac{a\lambda}{4\pi} \quad (\text{eq.49, Appendix 2})$$

Theoretically κ should be approximately symmetric around κ_1 , given by

$$\kappa = \frac{\kappa_1 G^2}{4(\lambda - \lambda_1)^2 + G^2} \quad (\text{eq.77, Appendix 2})$$

Fig. 4 gives absorption indices for chlorophyll a and b in ethyl ether, at a concentration of 10 g liter⁻¹ or 10 mg cm⁻³ (RABINOWITCH, 1951, p.605-610), as well as the variation of $n-N$, according to eq. 30. From Tables 1 and 2 it may seem as if usual cell concentrations of total pigments are about 0.5-1% of the total mass volume, or 5-10 mg cm⁻³. This may perhaps correspond to a chlorophyll a content of 2-10 mg cm⁻³. RABINOWITCH (1945, p. 411) quotes as an extreme value of chlorophyll a the concentration

1.7% of the total mass, or 17 mg cm^{-3} . The variation of the refractive index due to chlorophyll a is then likely to be about 0.001-0.005, in extreme cases 0.008.

If the pigments are not homogeneously distributed within the particle, "sieve effects" will occur (DUYSEN, 1956) and the total influence of the pigments will be reduced. Such effects are neglected here.

If there are p particles of equal size and shape per volume unit, and their geometrical cross section is G , then their scattering efficiency Q_b is defined as

$$Q_b = \frac{b}{pG} \quad (28)$$

where b is the scattering coefficient due to the particles. Similarly the absorption efficiency Q_a is defined as

$$Q_a = \frac{a}{pG} \quad (29)$$

VAN DE HULST (1957, p.174-182) has derived some approximate expressions for Q_a and Q_b of spheres, for the case that the refractive index of the spheres is close to that of the surrounding medium, and the diameter is much greater than the wavelength. Even when the particles are not much greater than the wavelength the expressions may be used with not too serious errors. The results applied here have been checked with the more complicated "Mie"-theory.

The expressions of VAN DE HULST may be written:

$$Q_a = 2\left(\frac{1}{2} + \frac{e^{-2\gamma}}{(2\gamma)^2} (2\gamma + 1) - \frac{1}{(2\gamma)^2}\right) \quad (30)$$

$$Q_b = 4\text{Re} \left\{ \frac{1}{2} + \frac{e^{-i\rho^*}}{(i\rho^*)^2} (i\rho^* + 1) - \frac{1}{(i\rho^*)^2} \right\} - Q_a \quad (31)$$

where $\rho^* = \rho - i\gamma$

$$\rho = \frac{2\pi D}{\lambda} (n - n_w)$$

$$\gamma = \frac{2\pi D}{\lambda} \kappa$$

D is the particle diameter.

The features of chlorophyll a of Fig. 4 can be used to illustrate the influence of the different coefficients. We set $\kappa_1 = 0.012$, $\lambda_1 = 662$ nm, $G = 22$ nm, $N = 1.38$ and $n_w = 1.34$. Eqs. 30 - 31 then give the solid lines of Fig. 5. With a particle diameter of 1 μ m the scattering efficiency has a minimum at the short wavelength side and a maximum at the long wavelength side of the absorption peak. A similar selective scattering from the green alga Chlorella ($D = 2-5$ μ m), as well as from other algae, has been observed (LATIMER and RABINOWITCH, 1959, CHARNEY and BRACKETT, 1961).

This effect depends entirely on the anomalous dispersion of the refractive index. If n is assumed constant ($n = N$), but κ is allowed to vary as before, a monotonous decrease of the scattering efficiency with increasing wavelength will be the result, as shown by the dotted line of Fig. 5. In fact, at this small particle diameter (1 μ m), the absorption index has practically no influence on the scattering efficiency. The hatched curve, which gives Q_p when n is assumed constant and κ zero, is seen to coincide with the former curve. Another way to express this, is to say that the amplitude decrease of the ray passing through the sphere is too small to influence the scattering.

With increasing size, the absorption, which is an exponential function of the diameter, becomes more pronounced.

When the diameter is 10 μm and κ_1 is 0.012, like in Fig. 5, absorption has become the dominating effect, and the dispersion of the refractive index can be neglected.

If the concentration of chlorophyll a is reduced to 1 mg cm^{-3} , so that $\kappa_1 = 0.0012$, the scattering efficiency will be almost the same as in the nonabsorbing case, as shown by Fig. 6. Only for large phytoplankton, with diameter 100 μm , is a small influence of the absorption band found.

We may then conclude that the anomalous dispersion of the refractive index will probably only influence the scattering properties of small phytoplankton in the vicinity of strong absorption bands.

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APPENDIX 1. THE MEAN REFRACTIVE INDEX OF A UNIAXIAL CRYSTAL.

A ray of polarized light with the electric vector parallel with the optical axis of a uniaxial crystal will have the phase velocity

$$v_{\epsilon} = c/\epsilon \quad (32)$$

c is the velocity of light in air (or vacuum) and ϵ is the extraordinary refractive index. The ray and the optical axis define a plane. For another ray in this plane, normal to the first ray and with the electric vector in the plane, the electric vector will be normal to the optical axis. The velocity of this ray will be

$$v_{\omega} = \frac{c}{\omega} \quad (33)$$

ω is the ordinary refractive index. For all other directions where the electric vector lies in this plane, the velocity will be

$$v_{\phi} = ((v_{\epsilon} \cos \phi)^2 + (v_{\omega} \sin \phi)^2)^{\frac{1}{2}} \quad (34)$$

where ϕ is the angle between the electric vector and the optical axis. The velocity vector of v_{ϕ} will then describe an ellipses with halfaxes v_{ϵ} and v_{ω} .

The refractive index n_{ϕ} is defined by

$$\begin{aligned} n_{\phi} &= \frac{c}{v_{\phi}} = c((v_{\epsilon} \cos \phi)^2 + (v_{\omega} \sin \phi)^2)^{-\frac{1}{2}} \\ &= (\cos^2 \phi / \omega^2 + \sin^2 \phi / \epsilon^2)^{-\frac{1}{2}} \\ &= \epsilon (1 - \frac{\omega^2 - \epsilon^2}{\omega^2} \cos^2 \phi)^{-\frac{1}{2}} \end{aligned} \quad (35)$$

We shall assume that the difference between ϵ and ω is small, so that the term $(\omega^2 - \epsilon^2) \cos^2 \phi / \omega^2$ is a number

less than 1, and make the approximation

$$\begin{aligned}
 n_{\phi} &\approx \epsilon \left(1 + \frac{1}{2} \frac{\omega^2 - \epsilon^2}{\omega^2} \cos^2 \phi \right) \\
 &= \epsilon \left(1 + \frac{1}{2} \frac{\omega - \epsilon}{\epsilon} \frac{\epsilon \omega + \epsilon^2}{\omega^2} \cos^2 \phi \right) \\
 &\approx \epsilon \left(1 + \frac{1}{2} \frac{\omega - \epsilon}{\epsilon} 2 \cos^2 \phi \right) \\
 &= \epsilon + (\omega - \epsilon) \cos^2 \phi
 \end{aligned} \tag{36}$$

The mean value of n_{ϕ} is obtained by integrating over all possible directions in a hemisphere:

$$\begin{aligned}
 \bar{n}_{\phi} &= \frac{1}{2\pi} \int_{2\pi} n_{\phi} d\Omega = \frac{2\pi}{2\pi} \int_0^{\frac{\pi}{2}} n_{\phi} \sin\phi d\phi \\
 &= \int_0^{\frac{\pi}{2}} (\epsilon + (\omega - \epsilon) \cos^2 \phi) \sin\phi d\phi \\
 &= \frac{2\epsilon + \omega}{3}
 \end{aligned} \tag{37}$$

This is the mean refractive index for all light with the electric vector in the plane through the ray and the optical axes. For all light with the electric vector normal to this plane, that is normal to the optical axes, the index will be

$$n_n = \omega \tag{38}$$

The mean refractive index of unpolarized light will than be

$$\bar{n} = \frac{1}{2} (\bar{n}_{\phi} + n_n) = \frac{1}{2} \left(\frac{2\epsilon + \omega}{3} + \omega \right) = \frac{2\omega + \epsilon}{3} \tag{39}$$

This result can also be obtained as follows:

Let the z axes of a coordinate system be parallel with the optical axis. Unpolarized light incident along

the x axis will then have the mean refractive index $(\omega+\epsilon)/2$, and similarly for light incident along the y axis. Light along the z axis will have the refractive index ω , and the mean value for light along the three axes will give the result of eq. 39. The mean refractive index of a biaxial crystal, eq. 20, may be deduced quite similarly.

APPENDIX 2. THE THEORY OF ANOMALOUS DISPERSION.

In 1875 HELMHOLTZ presented a theory which gave a relation between the absorptions bands and the anomalous dispersion of the refractive index. His theory was based on a mechanical analogy. For the free "ether" he assumed that the equation of motion could be written

$$\rho \frac{\partial^2 \xi}{\partial t^2} = \alpha \frac{\partial^2 \xi}{\partial y^2} \quad (40)$$

ρ is the "density" of "ether", and α is an elasticity constant per volume unit of the ether, ξ is the displacement along the y axis of a parcel of ether from its mean position. If the motion has the character of a free, progressive harmonic wave along the y axis, it may be described by

$$\xi = \xi_0 e^{i \frac{2\pi}{\lambda}(y-ct)} \quad (41)$$

ξ_0 is then the amplitude of the wave, λ is the wavelength and c the phase velocity. Inserting eq. 41 in 1, we obtain the relation

$$c^2 = \alpha/\rho \quad (42)$$

When molecules are present, HELMHOLTZ thought that there are a Hook type of elastic force between each atom of the molecule and the ether, that is of the form

$$\beta(x-\xi),$$

where β is the Hook constant, and x is the displacement of the atoms from their mean position. The equation of motion for the ether then becomes

$$\rho \frac{\partial^2 \xi}{\partial t^2} = \alpha \frac{\partial^2 \xi}{\partial y^2} + \beta(x-\xi) \quad (43)$$

If there are j different types of atoms present, the equation should read

$$\rho \frac{\partial^2 \xi}{\partial t^2} = \alpha \frac{\partial^2 \xi}{\partial y^2} + \sum \beta_j (x_j - \xi) \quad (44)$$

For the j -th type atoms with mass r_j the equation of motion is

$$r_j \frac{\partial^2 x_j}{\partial t^2} = -f_j x_j + \beta_j (\xi - x_j) - g_j \frac{\partial x_j}{\partial t} \quad (45)$$

The first term on the right side of the equation is the intermolecular Hook force which results from the displacement of the atom within the molecule. The molecule as a whole is supposed to be at rest. The second term is the reactio of the actio in eq. 44, and the third term describes the dissipation of energy, which is supposed to be proportional with the velocity of the oscillating atoms.

A light wave passing through this medium must then have a term which accounts for the dissipation or absorpction effect. Instead of eq. 41 we should write

$$\xi = \xi_0 e^{i \frac{2\pi}{\ell}(y-vt) - \frac{a}{2} y} \quad (46)$$

and x should be of the form

$$x_j = x_{j0} e^{i \frac{2\pi}{\ell}(y-vt) - \frac{a}{2} y} \quad (47)$$

ℓ and v are the wavelength and velocity of the wave in this medium, and $a/2$ is the absorpction coefficient of the amplitude. (Since the energy is proportional with

the square of the amplitude, the absorption coefficient of the energy is then a).

The exponents of the eqs. 46-47 may be written

$$i \frac{2\pi}{\ell} \left((1 + i \frac{a\ell}{4\pi})y - vt \right).$$

By introducing the refractive index of the medium relative to ether

$$n = \frac{c}{v} = \frac{\lambda}{\ell}, \quad (48)$$

and the absorption index

$$\kappa = \frac{a\lambda}{4\pi} \quad (49)$$

the exponent becomes

$$i \frac{2\pi}{\lambda} \left((n + i\kappa)y - ct \right).$$

The complex refractive index m may in this context be defined as

$$m = n + i\kappa \quad (50)$$

(The phase in eq. 46 may just as well be expressed by $vt - y$ instead of $y - vt$. m will then be defined as $n - i\kappa$. It should also be noted that both n and κ are indices relative to the refractive index of the medium in which λ is the wavelength). The eqs. 46-47 now become

$$\xi = \xi_0 e^{i \frac{2\pi}{\lambda} (my - ct)} \quad (51)$$

$$x_j = x_{j0} e^{i \frac{2\pi}{\lambda} (my - ct)} \quad (52)$$

Inserting these functions in eqs. 44-45, we obtain

$$-\rho \left(\frac{2\pi}{\lambda} c \right)^2 \xi_0^2 = -\alpha \left(\frac{2\pi}{\lambda} m \right)^2 \xi_0^2 + \Sigma \beta_j (x_{j0} - \xi_0) \quad (53)$$

$$-r_j \left(\frac{2\pi}{\lambda} c \right)^2 x_{j0} = -f_j x_{j0} + \beta_j (\xi_0 - x_{j0}) + i g_j \frac{2\pi}{\lambda} c x_{j0} \quad (54)$$

The last equation may be solved for x_{j0} , and substituting this into eq. 53, the result becomes after some ordering

$$m^2 = \frac{\rho}{\alpha} c^2 - \frac{1}{\alpha} \left(\frac{\lambda}{2\pi} \right)^2 \Sigma \beta_j + \frac{1}{\alpha} \left(\frac{\lambda}{2\pi} \right)^2 \Sigma \frac{\lambda^2 \beta_j^2}{\lambda^2 (\beta_j + f_j) - 4\pi^2 c^2 r_j - i 2\pi c \lambda g_j} \quad (55)$$

The first term on the right side of eq. 55 is 1, according to eq. 42.

The second term is a constant, $\Sigma \beta_j / 4\pi^2 \alpha$, multiplied with λ^2 . It will make m^2 decrease monotonously as λ increases, and consequently does not describe the phenomenon of anomalous dispersion. Probably the term is very small or is compensated for by the third term, otherwise m^2 would soon acquire very unreasonable values outside the absorption bands, due to the λ^2 influence. We shall then omit this term here.

The third term gives rise to the anomalous behaviour of m^2 . If we assume that the influence of each j -contribution is restricted to a very small wavelength interval, so that the factor λ^2 before the Σ sign may be regarded as a constant for each j -term, we may as a first approximation write

$$A_j = \frac{1}{\alpha} \left(\frac{\lambda}{2\pi} \right)^2 \beta_j^2 / (\beta_j + f_j) \quad (56)$$

It will also be convenient to write

$$\lambda_j^2 = 4\pi^2 c^2 r_j / (\beta_j + f_j) \quad (57)$$

and

$$G_j = 2\pi c g_j / (\beta_j + f_j) \quad (58)$$

Eq. 55 then becomes

$$m^2 = 1 + \Sigma \frac{\lambda^2 A_j}{\lambda^2 - \lambda_j^2 - i\lambda G_j} \quad (59)$$

This equation may be separated into its real and imaginary parts:

$$n^2 - \kappa^2 = 1 + \Sigma \frac{\lambda^2 (\lambda^2 - \lambda_j^2) A_j}{(\lambda^2 - \lambda_j^2)^2 + \lambda^2 G_j^2} \quad (60)$$

$$2n\kappa = \Sigma \frac{\lambda^3 A_j G_j}{(\lambda^2 - \lambda_j^2)^2 + \lambda^2 G_j^2} \quad (61)$$

These are the equations presented by JENKINS and WHITE (1957, p. 476) as resulting from the theory of HELMHOLTZ.

An interesting point is that a later model by LORENTZ (1915), based on electromagnetic theory, gives a formula of the type

$$\frac{m^2 - 1}{m^2 + 2} = \Sigma \frac{\lambda^2 A_j}{\lambda^2 - \lambda_j^2 - i\lambda G_j} \quad (62)$$

(LORENTZ gives the formula explicit for a non-absorbing mixture (page 311, note 58)). If the relative variation of $m^2 - 1$ is much greater than the relative variation of $m^2 + 2$, that is, m is close to 1, then $m^2 + 2 \approx 3$ and eqs. 59 and 62 become of identical form.

The indices n and κ may be found from eqs. 60-61, but the resulting expressions are complicated. To simplify the discussion we shall just look at the behaviour around one of the absorption bands. We will further assume that the other bands contribute to a rather constant refractive index N outside the actual band, and that their absorption

is practically zero at these wavelengths. The eqs. 60-61 then become

$$n^2 - \kappa^2 = N^2 + \frac{\lambda^2(\lambda^2 - \lambda_1^2)A}{(\lambda^2 - \lambda_1^2)^2 + \lambda^2 G^2} \quad (63)$$

$$2n\kappa = \frac{\lambda^3 A G}{(\lambda^2 - \lambda_1^2)^2 + \lambda^2 G^2} \quad (64)$$

From eq. 64 it is seen that if n is fairly constant, κ will have its greatest values around λ_1 . We shall now again make use of the earlier assumption that the influence of the absorption is restricted to a small interval, so that λ may be regarded as constant compared with $(\lambda - \lambda_1)$, and write

$$\lambda^2 - \lambda_1^2 = (\lambda - \lambda_1)(\lambda + \lambda_1) \approx (\lambda - \lambda_1)2\lambda_1 \quad (65)$$

$$\lambda^2 \approx \lambda_1^2 \quad (66)$$

$$\lambda^3 \approx \lambda_1^3 \quad (67)$$

Further we shall assume that the absorption index κ is small compared with the refractive index n , but that its relative variation is greater, that is

$$\kappa \ll n \approx N \quad (68)$$

$$\left| \frac{1}{\kappa} \frac{d\kappa}{d\lambda} \right| \gg \left| \frac{1}{n} \frac{dn}{d\lambda} \right| \quad (69)$$

With these assumptions eqs. 63-64 may be written

$$n^2 \approx N^2 + \frac{\lambda_1^2(\lambda - \lambda_1)2\lambda_1 A}{(\lambda - \lambda_1)^2 4\lambda_1^2 + \lambda_1^2 G^2} \quad (70)$$

$$2N\kappa \approx \frac{\lambda_1^3 A G}{(\lambda - \lambda_1)^2 4\lambda_1^2 + \lambda_1^2 G^2} \quad (71)$$

We may simplify eq. 70 further by observing that

$$n^2 - N^2 = (n-N)(n+N) \approx (n-N)(2N) \quad (72)$$

If we write

$$B = A/2N \quad (73)$$

eqs. 70-71 become

$$n \approx N + \frac{2\lambda_1(\lambda - \lambda_1)B}{4(\lambda - \lambda_1)^2 + G^2} \quad (74)$$

$$\kappa \approx \frac{\lambda_1 B G}{4(\lambda - \lambda_1)^2 + G^2} \quad (75)$$

These expressions are more suitable for discussions than eqs. 60-61.

We see from eq. 75 that κ will have its peak value κ_1 for $\lambda = \lambda_1$:

$$\kappa_1 = \frac{\lambda_1 B}{G} \quad (76)$$

Solving for B and substituting the expression for B in eq. 75 gives

$$\kappa = \frac{\kappa_1 G^2}{4(\lambda - \lambda_1)^2 + G^2} \quad (77)$$

It should be noted that κ is a symmetric function around λ_1 .

There are two wavelengths λ_2 where κ has the value $\kappa_1/2$. From

$$\frac{\kappa_1}{2} = \frac{\kappa_1 G^2}{4(\lambda_2 - \lambda_1)^2 + G^2} \quad (78)$$

it is obtained that these wavelengths are

$$\lambda_2 = \lambda_1 \pm \frac{G}{2} \quad (79)$$

Thus G is the width of the absorption band where κ has half of its peak value.

With the substitution of B from eq. 76, eq. 74 becomes

$$n = N + \frac{2\kappa_1 G(\lambda - \lambda_1)}{4(\lambda - \lambda_1)^2 + G^2} \quad (80)$$

It is seen that $n - N$ is antisymmetric around $\lambda = \lambda_1$. For $\lambda = \lambda_1$, $n - N = 0$, or $n = N$.

By differentiating the last equation with regard to λ , one obtains

$$\frac{dn}{d\lambda} = \frac{2\kappa_1 G(G^2 - 4(\lambda - \lambda_1)^2)}{(4(\lambda - \lambda_1)^2 + G^2)^2} \quad (81)$$

This expression is zero for

$$\lambda = \lambda_1 \pm \frac{G}{2} \quad (82)$$

that is for $\lambda = \lambda_2$. At these wavelengths eq. 74 gives that

$$n = N \pm \frac{\kappa_1}{2} \quad (83)$$

The approximate model described by eqs. 74-75 thus gives that n will have a minimum value at $\lambda_1 - \frac{G}{2}$, cross its mean value N at λ_1 , and obtain its maximum at $\lambda_1 + \frac{G}{2}$. The difference between the maximum and minimum value of the refractive index equals the peak value of the absorption curve.

An interesting point is that if we have just one absorption band, and we are far from it, at the long wavelength side, then

$$\lambda \gg \lambda_1 \quad (84)$$

$$\lambda^2 G^2 \ll (\lambda^2 - \lambda_1^2)^2 \quad (85)$$

and eq. 60 may be written

$$n^2 = 1 + \frac{\lambda^2 A}{\lambda^2 - \lambda_1^2} \quad (86)$$

which is identical with the SELLMEIER equation presented in Chapter 7.

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Fig.1. The refractive index of a two-component system, based on different equations, as a function of the partial water volume.

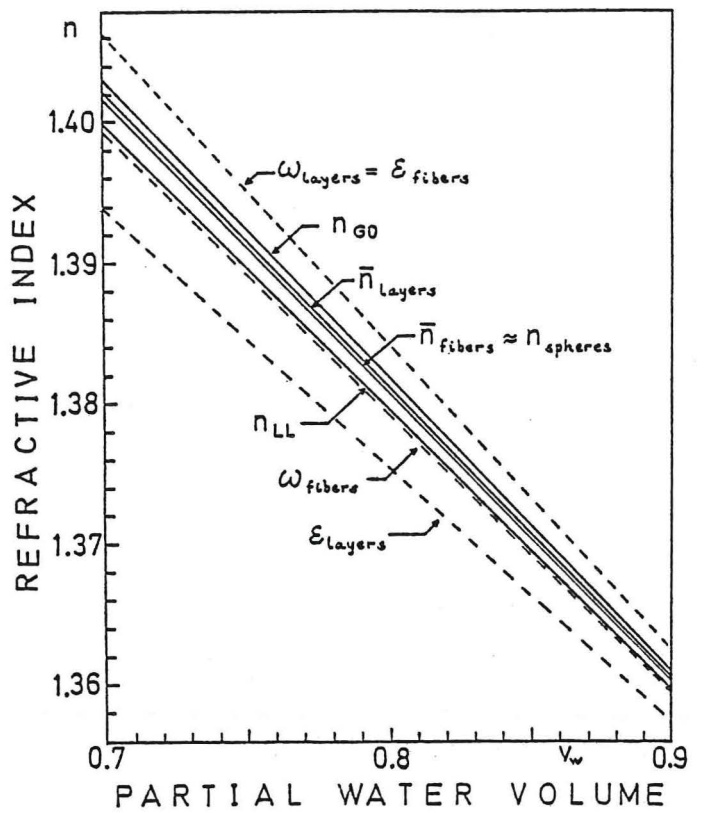


Fig.2. The mean refractive index of different plankton species, based on Table 2, as a function of the partial water volume.

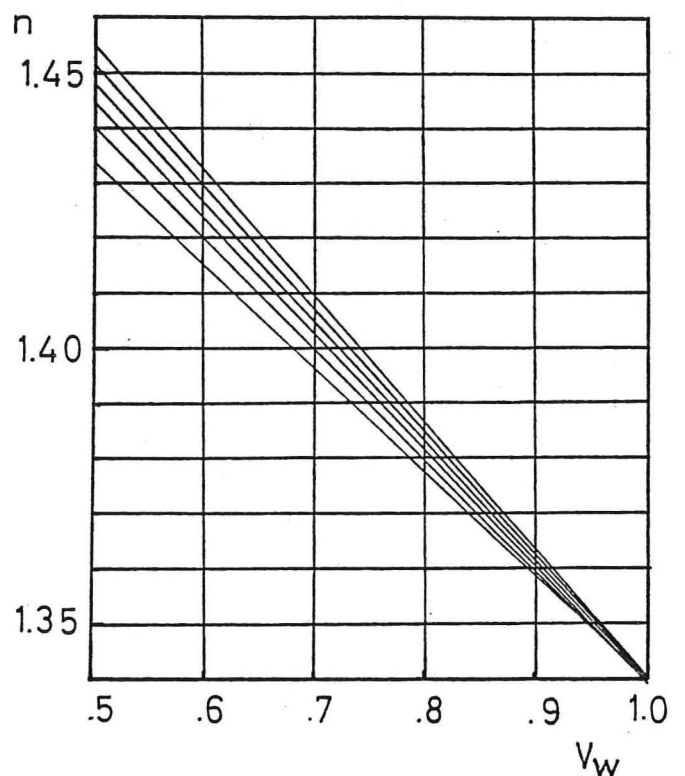


Fig.3. Dispersion of the main algal constituents, relative to water.

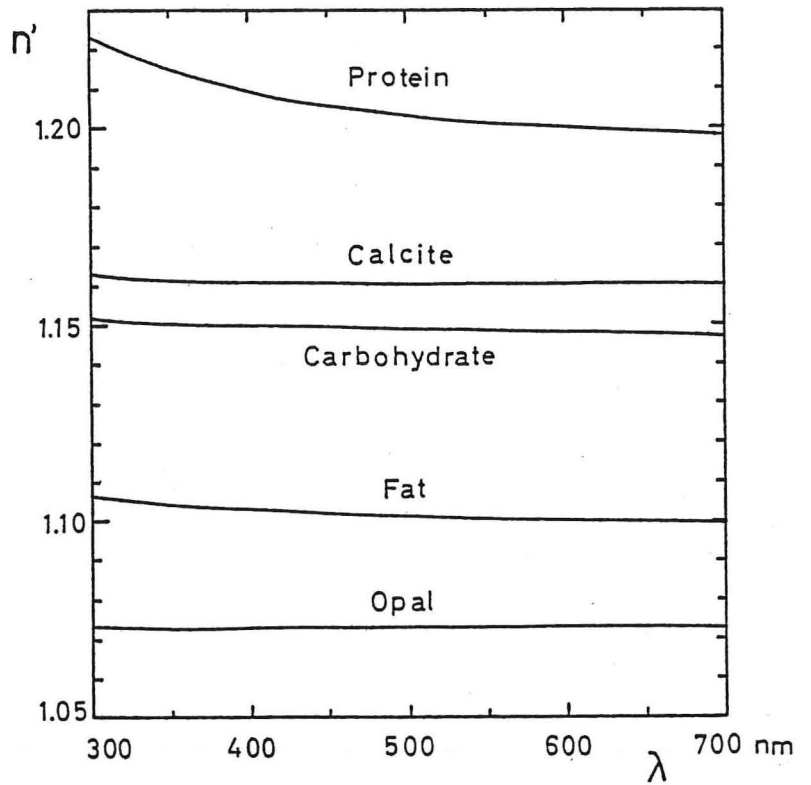


Fig.4. Absorption index κ and refractive index n of an idealized homogeneous alga, due to chlorophyll a and b.

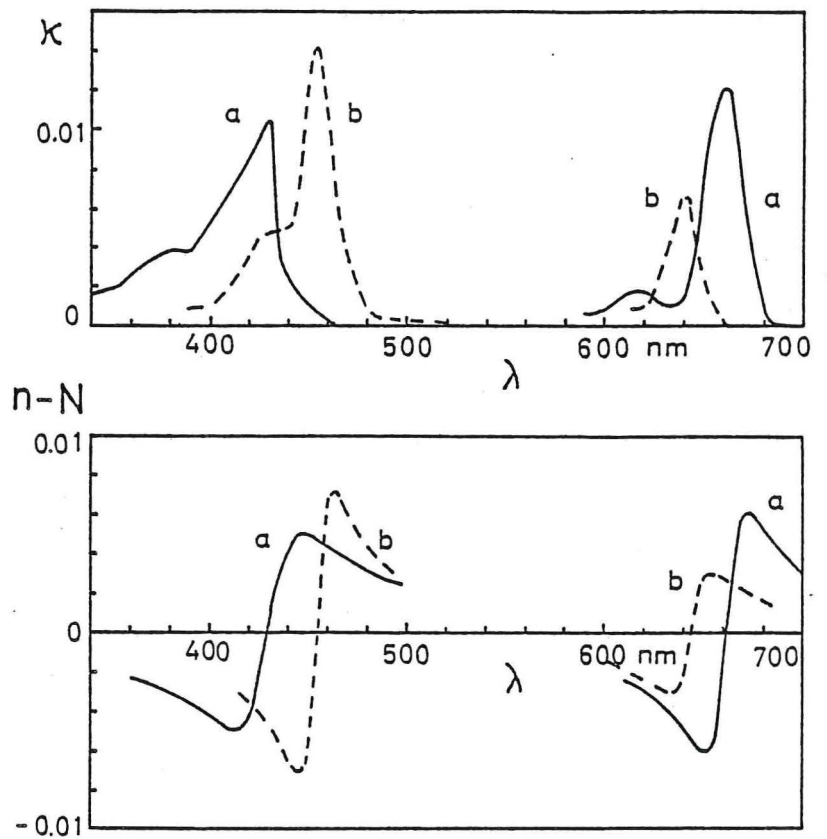


Fig.5. Absorption and scattering efficiencies for different diameters, when the chlorophyll a content is 10 mg cm^{-3} .

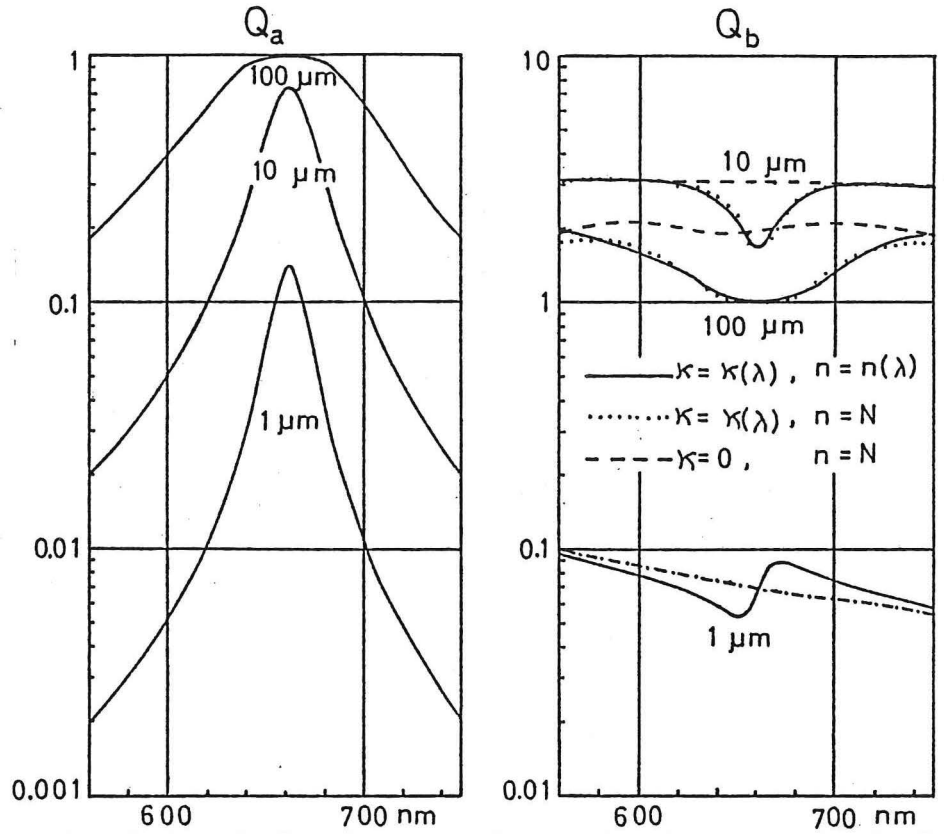
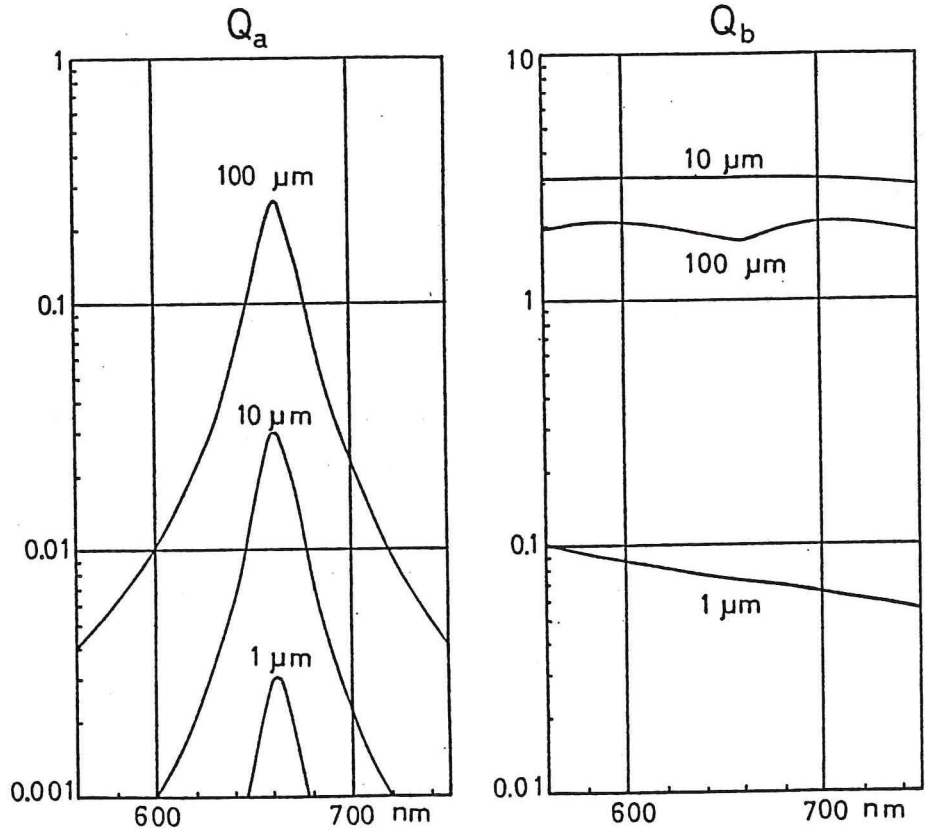


Fig.6. Absorption and scattering efficiencies for different diameters, when the chlorophyll a content is 1 mg cm^{-3} .



COMMENTS AND CORRECTIONS TO REPORT NO.46:

THE REFRACTIVE INDEX OF PHYTOPLANKTON

Chapter 4.1, page 22

The waterish type of opal, with $\rho=2.07 \text{ g cm}^{-3}$ and $n=1.43$, was chosen for the calculations since the opal of the phytoplankton contains water. However, the relative mass concentrations of silica given in Table 2 (page 18) probably represents dry SiO_2 without any water content. More correct values for the calculations are then perhaps $\rho=2.65$ and $n=1.486$.

This change leads to some corrections. Two of the lines in Table 8 (page 29) should now be

Diatoms	1.538	1.438 "	1.536	1.281 "
Mean from Table 2	1.555	1.438 "	1.342	1.201 "

Line no.9 on page 30 should read:

$$\bar{n} \approx (1.55 \pm 0.01) - (0.21 \pm 0.01)v_w$$

and line no.15:

density becomes $(1.10 \pm 0.05) \text{ g cm}^{-3}$. If only species with

Fig.2 consists of six curves for n as a function of c_w . The lowest of these curves, for diatoms, should now be omitted, since the new curve for diatoms will coincide with the one for blue-green algae.