Light scattering by microorganisms in the open ocean

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Abstract — Recent enumeration and identification of marine particles that are less than 2μm in diameter, suggests that they may be the major source of light scattering in the open ocean. The living components of these small particles include viruses, heterotrophic and photoautotrophic bacteria and the smallest eucaryotic cells. In order to examine the relative contribution by these (and other) microorganisms to scattering, we have calculated a budget for both the total scattering and backscattering coefficients (at 550nm) of suspended particles. This budget is determined by calculating the product of the numerical concentration of particles of a given category and the scattering cross-section of that category. Values for this product are then compared to values for the particulate scattering coefficients predicted by the models of GORDON and MOREL (1983) and MOREL (1988).

In order to make such a comparison, we have estimated both the total scattering and backscattering cross-sections of various microbial components that include viruses, heterotrophic bacteria, prochlorophytes, cyanobacteria, ultrananoplankton (2-8μm), larger nanoplanlankton (8-20μm) and microplankton (>20μm). Such determinations are based upon Mie scattering calculations and measurements of the cell size distribution and the absorption and scattering coefficients of microbial cultures. In addition, we have gathered published information on the numerical concentration of living and detrital marine particles in the size range from 0.03 to 100μm.

The results of such a study are summarized as follows. The size distribution of microorganisms in the ocean roughly obeys an inverse 4th power law over three orders of magnitude in cell diameter, from 0.2 to 100μm. Thus, the size distribution of living organisms is similar to that for total particulate matter as determined by electronic particle counters. For representative values of refractive index, it appears that most of the scattering in the sea comes from particles less than 8μm in diameter, and that most of the backscattering comes from particles less than 1μm.

Among the microorganisms that are found in this size range, free-living heterotrophic bacteria may be often most important. These microbes account typically for 10 to 50% of the total particulate scattering and 5 to 20% of backscattering in oligotrophic waters that contain less than 0.5mg chlorophyll per m². The second most important source of microbial scattering is cyanobacteria (especially in tropical and temperate waters) and ultrananoplankton. Viruses, which may be very abundant, make little contribution because they have extremely small cellular scattering cross-sections. Large microorganisms, which include nanoplanlankton >8μm and microplankton and which efficiently scatter light, contribute little because of their low cellular concentrations.

While a significant fraction of the total scattering coefficient may come from the combined contributions of viable procaryotic and eucaryotic cells, only a small fraction of the backscattering appears to come from these microbes. Instead, it appears that the major source of particulate backscattering is small (<0.6μm), numerically abundant detrital particles. A recent description by electronic particle counting (KOIKE, HARA, TERAUCHI and KOGURE, 1990) of small detrital particles in the size range of 0.4 to 1μm satisfies the requirements for such a source of backscattering.
1. INTRODUCTION - OBJECTIVES AND PREVIOUS WORK

Light scattering by marine particulates is the subject of considerable importance to many research areas such as radiative transfer in the ocean, remote sensing of seawater components and determination of physical properties of particles. The scattering is dependent on the amount and composition of the suspended particles through their sizes, shapes and refractive indices. The relative significance of various particles is extremely difficult to quantify because of the great diversity of this material. The complexity of the problem remains even if the actual ensemble of irregularly shaped particles in random orientation is approximated as a collection of spherical particles.

Published assessments of the contribution of various particle size fractions to light scattering in the open ocean are rather conflicting. The prevailing opinion seems to be that particles large compared to light wavelength (i.e. >1-2μm) contribute most heavily to light scattering (JERLOV, 1968; KULLENBERG, 1968, 1974; MOREL, 1973; BROWN and GORDON, 1973). On the other hand, a few investigators suggested that a significant portion of the total scattering is derived from small particles less than 1μm in size (OCHAKOVSKY, 1966; BEARDSLEY, PAK, CARDER and LUNDGREN, 1970; MITCHELL and KIEFER, 1981).

Furthermore, there is no consensus as to whether the particles that account for most of the scattering in the oligotrophic ocean are organic or inorganic. A low index of refraction is generally associated with organic matter because of watery protoplasm in living cells, and a high index with inorganic particulates. However, some phytoplankters contain skeletal material characterized by a high refractive index. Detrital particles derived from microorganisms will thus likely have low and high refractive indices. Also, organic detritus occurring in seawater as aggregated masses are known to contain inorganic inclusions (RILEY, 1963; GORDON, 1970). Note that the term detritus is generally used to represent a large variety of all kinds of non-living particles which include fragments of microorganisms, decaying biogenous products of organic and inorganic nature, fecal pellets and excreta of organisms as well as terrigenous material consisting of minerals and organic debris.
Earlier investigations summarized by ZANEVELD, ROACH and PAK (1974) showed that if one value of the index of refraction is assumed to represent the bulk scattering properties of the entire collection of particles, then this value falls either in the range 1.15-1.25 or 1.01-1.05. This indicates that particle distributions are either dominated by inorganic and possibly skeletal material or by organic matter containing much water. BROWN and GORDON (1973) and ZANEVELD, ROACH and PAK (1974) have derived multi-component models of particulate scattering in clear oceanic water based upon Mie-scattering calculations, and concluded that the inorganic particles are the predominant scatterers. Specifically, BROWN and GORDON (1973) postulated that a low-index organic component contributes less than 10% to the total scattering by Sargasso Sea particles. KULLENBERG (1974) also postulated that the most representative value for the refractive index in the clear waters of the Sargasso Sea and the Mediterranean is high, between 1.15 and 1.20. In contrast, MOREL (1973) suggested a range of 1.02 to 1.05.

Such confusion is the result of a number of reasons. In many cases light scattering and the particle size distribution were measured neither at the same time nor at the same location. Furthermore, the various basic assumptions employed in the determination of the distribution of size and refractive index of particles from light scattering have been biased by an absence of complete information. Specifically, small particles have been traditionally ignored, or at best very crudely approximated, because conventional microscopic and electronic determinations of particle size distribution are restricted to particles larger than about 1μm. Furthermore, the composition of the particulate matter has not been ascertained experimentally, so the distribution of the index of refraction of the suspended particles is largely unknown. In the absence of a complete description of particle concentration, sizes and indices of refraction, solution to the inverse scattering problem may be ambiguous or meaningless.

Only recently have new techniques enabled researchers to demonstrate the quantitative importance of very small life forms, less than 2μm in size, in oceanic ecosystems. The discoveries of high abundance of photoautotrophic picoplankters (JOHNSON and SIEBURTH, 1979, 1982; WATERBURY, WATSON, GUILLARD and BRAND, 1979; CHISHOLM, OLSON, ZETTLER, GOERICKE, WATERBURY and WELSCHMEYER, 1988) and free-living heterotrophic bacteria (e.g. HOBIE, DALEY and JASPER, 1977; FUHRMAN, SLEETE, CARLSON and PROCTOR, 1989) have changed our understanding of pelagic food webs in which the microbial loop is now considered as a basic component (AZAM, FENCHEL, FIELD, GREY, MEYER-REID and THINGSTAD, 1983; SHERR and SHERR, 1988). High abundances of viruses, the smallest "living" particles, have also been reported recently in natural unpolluted waters (BERGH, BØRSHEIM, BRATBAK and HELDAL, 1989; PROCTOR and FUHRMAN, 1990). In addition, KOIKE, HARA, TERAUCHI and KOGURE (1990) have reported that non-living particles in the submicron region occur in the upper layers of the ocean in concentrations at least an order of magnitude higher than their living counterpart. All these findings seem to support the idea that enough small material is present in the oligotrophic ocean to cause a significant optical effect. The approximate abundances and sizes of major groups of microorganisms in the open ocean are shown in Fig.1.

Over the last decade there has also been significant progress in characterizing the optical properties of different groups of marine microorganisms. The bulk optical measurements on suspended phytoplankton cells (e.g. BRICAUD, MOREL and PRIEUR, 1983; BRICAUD and MOREL, 1986), the flow cytometric measurements of single phytoplankton cells (e.g. SPINRAD and BROWN, 1986; ACKLESON and SPINRAD, 1988) and the microphotometric analysis of individual particle absorption (ITURRIAGA, MITCHELL and KIEFER, 1988) were employed in this research. Most recently, fairly comprehensive descriptions based upon bulk measurements were presented for photoautotrophic cyanobacteria (STRAMSKI and MOREL, 1990) and heterotrophic bacteria (MOREL and AHN, 1990; STRAMSKI and KIEFER, 1990). STRAMSKI and KIEFER (1990) suggested that free-living bacteria are an important source for light scattering in oligotrophic waters.
In view of these recent advances in studying marine microbes, a further effort toward determining the relative significance of various suspended materials for light scattering in the ocean is warranted. In this paper, we estimate the contributions of various groups of microorganisms, covering the optically significant sizes from 0.03μm to 100μm, to the total particulate scattering and backscattering coefficients in the upper layers of the oligotrophic ocean. In such waters, which are in fact much of the world’s open ocean, the plankton stocks are low (concentrations of chlorophyll $a$ are typically less than 0.5mg m$^{-3}$). We combine Mie scattering theory with available data on the optical properties and concentrations of marine microorganisms. The central problem in our approach is the determination of cross-sections for total scattering and backscattering for each component of the planktonic community. By calculating the product of the numerical concentration of microorganisms of a given category and the scattering cross-section of that category, we determine a budget for both the total and backscattering coefficients of suspended particles. We also carry out calculations assuming idealized particle size distributions and various refractive indices in order to understand better how different size classes may contribute to the particulate light scattering.
2. BULK AND INDIVIDUAL PARTICLE SCATTERING - OUTLINE OF THE APPROACH

The total scattering coefficient, \( b \), and the backscattering coefficient, \( b_b \) (units are m\(^{-1}\)), are defined as:

\[
b(\lambda) = 2\pi \int_0^{\pi} \beta(\theta, \lambda) \sin \theta \, d\theta \quad (1)
\]

\[
b_b(\lambda) = 2\pi \int_{\pi/2}^{\pi} \beta(\theta, \lambda) \sin \theta \, d\theta \quad (2)
\]

where \( \lambda \) is the light wavelength (in vacuo), \( \beta(\theta, \lambda) \) the volume scattering function which describes the angular distribution of scattered radiation and \( \theta \) the scattering angle (e.g. PREISENDORFER, 1961). The bulk inherent optical properties \( \beta(\theta, \lambda) \), \( b(\lambda) \), \( b_b(\lambda) \) are all cumulative measures representing the sum of contributions by all particles suspended within the sample volume and water. All further considerations concern the particulate scattering unless specifically noted.

The collection of particles can be assumed to consist of \( M \) components, each characterized by a single value for the complex refractive index relative to the surrounding medium, \( m = n - in' \), and the density function of size distribution, \( F(D) \), such that \( F(D) dD \) is the number of particles per unit volume of seawater with diameters in the range \( (D, D+dD) \). The total bulk coefficients can be written:

\[
b = \sum_{j=1}^{M} (b_j) + b_w \quad \text{and} \quad b_b = \sum_{j=1}^{M} (b_b_j) + b_{bw} \quad (3)
\]

where \( b_w \) and \( b_{bw} \) are the scattering and backscattering coefficients of pure seawater, respectively. The sum of \( (b_j) \) and \( (b_b_j) \) is the total particulate scattering coefficient, \( b \), and the total particulate backscattering coefficient, \( b_b \), respectively.

The relationships between the bulk optical coefficients and individual particle properties can now be used to evaluate the contributions of the \( j \)th component with a refractive index \( m_j \) and size distribution \( F_j(D) \) (VAN DE HULST, 1957; GORDON and BROWN, 1972):

\[
(b_j) = \int_{D_{\text{min}}}^{D_{\text{max}}} Q_b(\lambda, D, m_j) \left( \pi D^2/4 \right) F_j(D) dD \quad (4)
\]

\[
(b_{b,j}) = \int_{D_{\text{min}}}^{D_{\text{max}}} Q_{bb}(\lambda, D, m_j) \left( \pi D^2/4 \right) F_j(D) dD \quad (5)
\]

where \( Q_b(\lambda, D, m_j) \) and \( Q_{bb}(\lambda, D, m_j) \) are dimensionless efficiency factors for scattering and backscattering respectively of the individual particle having the sphere-equivalent diameter \( D \) and the refractive index \( m_j \). \( (\pi D^2/4) \) is the projected-area of the particle, and \( F_j(D) \) is the size distribution of the \( j \)th component which comprises particles with the refractive index \( m_j \). \( D_{\text{min}} \) and \( D_{\text{max}} \) delimit the size range of the particulate component. The efficiency factors \( Q_b \) and \( Q_{bb} \) depend on \( \lambda \), \( D \) and \( m \), and describe the fraction of radiative energy incident on the projected-area of the particle that has been scattered or backscattered. In (4) and (5), the particles are assumed to be spherical but analogous equations hold, in principle, for irregularly shaped particles (\( \pi D^2/4 \) must be replaced by the actual projected-area).

As yet, no simultaneous data on light scattering, size distribution and identity of oceanic particles are available. Therefore, an alternate method for estimating the contributions \( (b_j) \) and \( (b_{b,j}) \) must be considered. Finding these contributions will be here accomplished by determining the mean particle cross-sections for scattering, \( (\bar{\sigma})_s \), and backscattering, \( (\bar{\sigma})_{bb} \) (units are m\(^2\) per particle), for each component separately:
\[
(\bar{\sigma}_{b_j}) = \frac{D_{\text{max}}}{D_{\text{min}}} \int_{D_{\text{min}}}^{D_{\text{max}}} Q_b(\lambda, D, m_j) (\pi D^2/4) F_j(D) dD \quad (6)
\]

\[
(\bar{\sigma}_{bb_j}) = \frac{D_{\text{max}}}{D_{\text{min}}} \int_{D_{\text{min}}}^{D_{\text{max}}} Q_{bb}(\lambda, D, m_j) (\pi D^2/4) F_j(D) dD \quad (7)
\]

The values for \((\bar{\sigma}_{b_j})\) and \((\bar{\sigma}_{bb_j})\) represent a hypothetical "mean" particle of the jth component. Note that the knowledge of the shape of the size distribution \(F_j(D)\) is sufficient to apply Eqs (6) and (7); in other words \(F_j(D)\) can be expressed in terms of relative number of particles per unit volume per unit size bandwidth.

We define the particulate components in a way that size distributions and refractive indices appropriate to these components can be chosen, and also so that each of the components plays a specific role in oceanic ecosystem. Accordingly, such components of the microbial community are: virus (\(<0.2\mu m\) in size), free-living heterotrophic bacteria, prochlorophytes, photoautotrophic cyanobacteria, all falling into the size range of 0.2 to 2\(\mu m\), nanoplanckton (2-20\(\mu m\)) and microplankton (20-200\(\mu m\)). Heterotrophic bacteria, prochlorophytes and cyanobacteria are the predominant groups of the marine picoplankton. We follow the terminology based upon the logical sequence pico-nano-micro established by SIEBURTH, SMETACEK and LENCH (1978). All the specified microbial components cover the optically significant size range (\(<100\mu m\)) and are believed to account for nearly all scattering associated with living particulates in the open ocean.

The cross-sections given in Eqs (6) and (7) will be determined for each microbial component either by adopting values from previous studies or, if they are not available, by performing Mie scattering calculations after the particle size distribution and refractive index appropriate to the component under consideration have been chosen. All our Mie calculations are carried out for spherical, homogeneous particles using the algorithm given in BOHREN and HUFFMAN (1983).

Finally, in order to estimate the relative contribution of each microbial component to the total particulate light scattering, the values for \((b)\) will be compared with the model given by GORDON and MOREL (1983). Based on a large number of in situ measurements, these authors proposed a power law for describing the total scattering coefficient at 550nm as a function of pigment concentration in surface waters which yields:

\[
b_p(550) = 0.3C^{0.62} - b_w(550) \quad (8)
\]

where \(C\) is the chlorophyll \(a\) plus phaeopigment \(a\) concentration in mg m\(^{-3}\), and \(b_w(550) = 0.0019 m^2\) is the scattering coefficient for pure seawater at 550nm (see SMITH and BAKER, 1981). Two comments are in order with regard to Eq(8). First, this relationship was established for Case 1 waters in which the optical properties are primarily controlled by particulate and dissolved materials associated with primary productivity. Terrigenous and anthropogenic materials as well as resuspended sediments from bottom have negligible effect in such waters (MOREL and PRIEUR, 1977; GORDON and MOREL, 1983). Second, the relationship (8) is the best-fit regression to the empirical data which cover the range of chlorophyll concentrations greater than 0.01mg m\(^{-3}\), which occurs in the euphotic zone of all natural waters. Consequently, the use of Eq(8) for lower pigment concentrations is inappropriate.

The particulate backscattering, although essential to the modelling and interpretation of ocean colour, is still poorly documented. Using scarce data on backscattering by phytoplankton (MOREL and BRICAUD, 1981; BRICAUD and MOREL, 1986), two models of the particulate backscattering have been recently presented (GORDON, BROWN, EVANS, BROWN, SMITH, BAKER and CLARK, 1988; MOREL, 1988). We will estimate the significance of microbial components for backscattering by comparing our values of \((b_{b_j})\) with the model given in MOREL (1988):
\[ b_{sp}(\lambda) = [0.3C^{0.62} - b_w(550)] [0.002 + 0.02 \ (0.5 - 0.25 \log C) \ (550/\lambda)] \]  

As opposed to the original formulation, the first term in (9) is corrected for \( b_w(550) \) to account solely for particles (even though \( b_w(550) \) is generally \(<0.3C^{0.62}\)). While Eq(8) is empirical, Eq(9) is based upon a number of approximations. We also emphasize that \textit{in situ} measurements of backscattering integrated over all backward directions between 90 and 180 degrees are lacking. As shown in Fig.2, MOREL's model for backscattering yields similar results, especially in the green spectral region, to another model developed by GORDON, BROWN, EVANS, BROWN, SMITH, BAKER and CLARK (1988).

Our considerations will be mostly concentrated on the green spectral region (\( \lambda = 550 \text{nm} \)) for which the empirical Eq(8) has been established. The description of scattering over the entire visible spectral range would require a careful consideration of the effect of absorption by pigmented microorganisms. At \( \lambda = 550 \text{nm} \), the absorption is generally very weak, so it can be either neglected or included with a sufficient accuracy assuming reasonably small values for the imaginary part of the refractive index \( n' \).

![Graph](attachment:graph.png)

**FIG.2.** A semi-log plot of the spectral backscattering coefficient of oceanic particulates for several pigment (Chla + Phaeo a) concentrations \( C \) in sea water. The lines are the predictions obtained from MOREL (1988) and the points from GORDON, BROWN, EVANS, BROWN, SMITH, BAKER and CLARK (1988).
3. LIGHT SCATTERING BY PARTICLE SIZE FRACTIONS - THEORETICAL CONSIDERATIONS

We first present some predictions of Mie scattering theory, which will then aid in an assessment of the importance of microbial components to light scattering. The problem to which we direct ourselves now is to obtain information about the relative significance of various particle size fractions to light scattering and backscattering. This will be examined for hypothetical collections of particles, each characterized by a single value of refractive index and a single function for size distribution over the entire optically significant size range.

3.1 Basic information about calculations

Mie scattering calculations for homogeneous nonabsorbing spheres were made for a wavelength of light $\lambda = 550$ nm, for diameters $D = 0.002 (0.002) 0.3 (0.01) 2 (1) 20 (10) 100 \mu$m, where increment is given in parentheses, and for several values of the real part of the refractive index relative to water, $n = 1.025, 1.05, 1.075, 1.10, 1.125, 1.15$ and $1.20$. The values of $n$ cover the range one expects to find in oceanic particles (BURT, 1956; ZANEVELD, ROACH and PAK, 1974; AAS, 1981). The calculations yielded the scattering efficiency $Q_s(D,n)$ and the backscattering efficiency $Q_{bb}(D,n)$ for each diameter $D$ and refractive index $n$. The backscattering efficiency was obtained by integrating the Mie scattered intensity function between 90 and 180 degrees:

$$ Q_{bb}(D,n) = 2\pi^{-1} \int_{\pi/2}^{\pi} i(\theta, \alpha, n) \sin \theta \, d\theta $$

(10)

where $\alpha$ is the Mie size parameter ($= \pi D n_w / \lambda$), $n_w$ the refractive index of water ($= 4/3$) and $\theta$ the scattering angle. $Q_s(D,n)$ is given by similar formula with the exception that the lower limit of integration is 0. The angular intensity functions were calculated from 0 to 180 degrees with a 1 degree step.

By recalling Eq(4) and assuming that a collection of particles is characterized by a single value for refractive index and size distribution $F(D) \sim D^4$, the cumulative percent contribution to the particulate scattering coefficient from the size fraction of $D_{min}$ to $D$ is:

$$ C_s(D) = 100 \int_{D_{min}}^{D_{max}} Q_s(D,n) \, D^2 \, dD \, \left( \int_{D_{min}}^{D_{max}} Q_s(D,n) \, D^2 \, dD \right)^{-1} $$

(11)

Similarly, the cumulative percent contribution to the particulate backscattering coefficient is:

$$ C_{bb}(D) = 100 \int_{D_{min}}^{D_{max}} Q_{bb}(D,n) \, D^2 \, dD \, \left( \int_{D_{min}}^{D_{max}} Q_{bb}(D,n) \, D^2 \, dD \right)^{-1} $$

(12)

By replacing the integral in the numerator of (11) and (12) by its derivative, one obtains the differential percent contribution per unit particle diameter (per $\mu$m bandwidth) for total scattering and backscattering, respectively:

$$ C_i'(D) = 100 \int_{D_{min}}^{D_{max}} Q_i(D,n) \, D^2 \, dD \, \left( \int_{D_{min}}^{D_{max}} Q_i(D,n) \, D^2 \, dD \right)^{-1} $$

(13)

where subscript $i$ stands as substitute for $b$ or $bb$. In the limit as $\Delta D$ approaches zero, $C_i'(D)$ could alternatively be obtained from:

$$ C_i'(D) = \frac{C_i(D + \Delta D) - C_i(D)}{\Delta D} $$

(14)
3.2 Particle size distribution

The choice of the particle size distribution for these Mie calculations deserves some comment. Several formulations for parametrization of the size distribution of marine particles have been used in the past (BADER, 1970; CARDER, BEARDSLEY and PAK, 1971; PAK, ZANEVELD and BEARDSLEY, 1971; ZANEVELD and PAK, 1973; LAMBERT, JEHANNO, SILVERBERG, BRUN-COTTAN and CHESSELET, 1981). A power law, referred to as Junge-type distribution, is often a preferred parametrization (e.g. BADER, 1970; BRUN-COTTAN, 1971; GORDON and BROWN, 1972; McCAVE, 1975; LERMAN, CARDER and BETZER, 1977; JONASZ and ZALEWSKI, 1978). This is based primarily upon numerous measurements with electronic particle counters such as Coulter counters. These measurements showed that a cumulative size distribution in the size range from about 1 μm to a few tens of micrometers (possibly up to 100 μm) is closely approximated by:

\[ N_{>D} = k D^{-\gamma} \]  \hspace{1cm} (15)

where \( N_{>D} \) is the number of particles per unit volume with equivalent spherical diameters larger than \( D \), \( k \) is the concentration of particles larger than 1 μm, and \( \gamma \) is the slope of the distribution. The differential size distribution, \( F(D) \), which is the negative derivative of the cumulative distribution, is also a power function, and has the slope \( -(\gamma+1) \). The slope of the differential distribution will be thereafter denoted by \( s \). In most cases, either one value of \( k \) and \( \gamma \) or the segmented (bivariate) description is required for a good fit to the Coulter counter data.

JONASZ (1983) summarized the data on the slopes of the particle size distribution measured with Coulter counter by several investigators in various oceanic regions. If two hyperbolic distribution segments appear to be the satisfactory formulation, then the smaller size range is characterized by slopes, \( s \), ranging typically between -3 and -4, and larger size range by steeper slopes, from about -4.5 to less than -5. The “knee” separating these segments is usually between 4 and 8 μm. A single slope often provides a very good fit over the entire size range measured with a Coulter counter, and the value of \( s \) for this fit is typically between -3.5 and -4.5. In the upper layers of the ocean, some irregularities are often superimposed on this hyperbolic pattern, mostly as a result of biological processes (KITCHEN, MENZIES, PAK and ZANEVELD, 1975; JONASZ, 1983).

Given this information we will employ the differential size distribution, \( F(D) \), approximated by one hyperbolic segment with a slope of -4 between limits \( D_{min} = 0.002 \) μm and \( D_{max} = 100 \) μm. An upper size cutoff is chosen so that the contribution to light scattering by particles larger than \( D_{max} \) is negligible. Previous models on particle scattering in seawater suggest that even lower values for the upper size cutoff (in the range of 20 to 40 μm) can safely be assumed (GORDON and BROWN, 1972; ZANEVELD, ROACH and PAK, 1974; JONASZ and PRANDKE, 1986).

The choice of the lower size cutoff \( D_{min} \) must also be considered. The particle size distribution is governed by physico-chemical processes (sedimentation, flocculation, adsorption, dissolution) and biological processes. As a consequence, it can be expected that below a certain very small size, the particle number no longer continues to increase, which invalidates the use of hyperbolic distribution with negative slope. Unfortunately, the form of the size distribution below 1 μm is poorly known. Only very few and rather conflicting data are available for this small size range. Some of Coulter counter measurements in the clear coastal waters near Bahama Islands indicated that the slope \( s \) may become very steep (about -6) for diameters between 0.65 and 1 μm (BROWN and GORDON, 1974). For deep oceanic waters, a study by using transmission electron microscopy yielded hyperbolic distribution \( F(D) \sim D^{-2.65} \) in the diameter range of 0.02 to 2 μm (HARRIS, 1977),
and a scanning electron microscopy study suggested the log-normal distribution with a decrease of particle concentration below ~ 0.5μm (LAMBERT, JEHANNO, SILVERBERG, BRUN-COTTAN and CHESSELET, 1981).

Clearly, further investigations are needed to ascertain the shape of the particle distribution in the small size range. As yet, one is forced to make assumptions, and we believe that the extrapolation of the hyperbolic distribution F(D) ~ D^4 down to diameters of the order of 0.01μm is a judicious choice. In support of this we note that the observed particle scattering in the Sargasso Sea was reproduced by Mie calculations using F(D) ~ D^4 down to D=0.1μm (GORDON and BROWN, 1972; BROWN and GORDON, 1973) and F(D) ~ D^{3.6} down to 0.04μm (ZANEVELD, ROACH and PAK, 1974). Similarly, the particle scattering in the Baltic was best simulated using F(D) ~ D^{3.8} in the diameter range of 0.02μm to 2μm (REUTER, 1980) and F(D) ~ D^{-4.1} for D between 0.1μm (or 0.01μm) and 2μm (JONASZ and PRANDKE, 1986). The size analysis of ocean-bottom sediments yielded the maximal numerical concentration of particles at a diameter of 0.01μm (PAK, ZANEVELD and BEARDSLEY, 1971). In addition, in section 4.4 (Fig.15) we will discuss further evidence supporting the validity of an inverse 4th power law for microorganisms ranging in size from 0.2 to 100μm.

No physical significance should be attached to the value of 0.002μm for the lower size cutoff. Importantly, all predictions from Eqs(11), (12) and (13), which are presented in the next section, are virtually insensitive to the choice of D_{min} between 0.002 and 0.03μm. The latter value roughly corresponds to the size of smallest viruses.

3.3 Predictions of Mie theory for an inverse 4th power law of size distribution

The contribution to the particulate scattering coefficient at λ=550nm, determined as described above, is shown in Fig.3. The maximum differential contribution occurs at 0.5μm for the ensemble of high-index particles with n=1.20 (Fig.3a). This maximum broadens and shifts toward larger sizes if particles with lower indices are considered, but always remains in the small diameter range <2μm. For the collection of particles with n=1.05, which probably best represents living microorganisms, the curve still peaks at a very small diameter D=1μm.

The cumulative curves in Fig.3b indicate that 50% of scattering is caused by particles smaller than 0.9μm, 3μm and 6μm for n=1.20, 1.05 and 1.025, respectively. Less than 1% comes from the diameter range <0.1μm, even for high-index particles. Also, less than 1% is contributed by particles larger than 30μm, 60μm and 80μm for n=1.20, 1.05 and 1.025, respectively. Our cumulative curve for n=1.15 is consistent with that calculated by PAK, ZANEVELD and BEARDSLEY (1971) for a nepheloid suspension over a red clay sediment in the North Pacific. Whereas they concluded that the middle 90% of the total scattering is caused by particles between 0.5 and 8.5μm (with 5% contribution beyond each end-point of this size range), our calculations yield a similar size range of 0.25μm to 8.3μm. As a general statement, the scattering coefficient is determined largely by particles less than 10μm in size, which already has been postulated by MOREL (1973).

The most significant feature of the differential contribution to the backscattering coefficient is a maximum located at about 0.16μm regardless of the refractive index (Fig.4a). Hence, the bulk of the backscattering effect is caused by very small particles <1μm, which is also evidenced by the cumulative percentages shown in Fig.4b. For low-index particles with n=1.025 or 1.05, 50% of backscattering is caused by particles <0.2μm. For n=1.20, 50% of the cumulative contribution is reached at 0.33μm. The contribution by particles larger than 10μm is less than 5% (except for n=1.075 when it slightly exceeds this percentage).
FIG. 3. The percent contribution to the particulate scattering coefficient $b(550)$ per micrometer bandwidth (panel a) and the cumulative percent contribution (panel b) as a function of particle diameter (abscissa in log scale). The curves represent particle ensembles with various values of the refractive index $n$: 1.025, 1.05, 1.075, 1.1, 1.125, 1.5, 1.2. The particle size distribution is $F(D) \sim D^4$, and the imaginary part of the refractive index is zero. The extreme curves are labelled with values for $n$. 
The size dependence of total scattering and backscattering are governed by the product of the scattering efficiency $Q_b$, or backscattering efficiency $Q_{bb}$, and the particle projected-area concentration in seawater (Eq.13). For $F(D)\sim D^4$, the concentration of particle projected-area increases with decreasing particle size as $D^{-2}$. The efficiencies $Q_b$ and $Q_{bb}$ as a function of $D$ are shown in Fig.5. A decrease in the differential contribution in the small size range located to the left of the maximum (Figs 3a and 4a) results from the fact that $Q_b$, or $Q_{bb}$ respectively, decreases faster with decreasing diameter than the corresponding increase in the concentration of particle projected-area. For larger sizes, located to the right of the maximum contribution, increases in $Q_b$ or $Q_{bb}$, if any, are not large enough to compensate for decreases in the concentration of projected-area; hence, the differential contribution decreases with size.
The difference in the patterns of $Q_b$ and $Q_{bb}$ lead to two important points. First, a predominance by small particles is much more pronounced for backscattering, for which the submicron region is of primary importance. Second, while the contribution by small size fraction to the total scattering becomes increasingly important when particles become more refringent, the opposite holds for backscattering (Figs 3b and 4b).

The results of the Mie calculations for $F(D)\sim D^{-4}$ and selected values of $n$ are summarized in pie graphs (Figs 6 and 7). These graphs show the relative contributions to the particulate scattering and backscattering coefficients integrated over equal size bands of 1μm width for D<8μm. For larger particles, the contributions are integrated over bands of 8-20μm and 20-100μm. For very low-index particles (n=1.025), the contribution to total scattering is uniformly distributed for
D<8μm, with the smallest size fraction <1μm as important as any other 1μm wide class (Fig.6). For n=1.05, more than half of the scattering is caused by particles <4μm. The contribution by each 1μm wide class in this region is very similar. The importance of the smallest fractions, 0-1μm and 1-2μm, continues to increase with increasing refractive index, so the total scattering by high-index particulates is clearly dominated by these small particles. The pie graphs in Fig.7 expressively demonstrate that most of the backscattering effect (70-90%) is caused by the smallest fraction (<1μm) for both low- and high-index particles.

FIG.6. Pie graphs showing the contribution to the scattering coefficient, b(550), by various particle size classes for several values of the refractive index n. Other assumptions as in Fig.3.
Some comment is in order to summarize the simple scattering model outlined here. First, the particulate matter in the ocean is a mixture of organic and mineral components with different indices of refraction. Unfortunately, the quantitative information about proportions between individual components and their size distributions is scarce. Yet, one can expect that the contributions to scattering by size fractions in many realistic situations will correspond to our predictions for $n$ ranging between 1.05 and 1.15.

Second, our assumption that there is no absorption by marine particles is, in a first approximation, reasonable for $\lambda=550\text{nm}$. Because of phytoplankton pigments, the effect of absorption on scattering for most wavelengths over the visible spectrum cannot be ignored, however. This effect would be difficult to include in a simple model because of the variability in the spectral values of the imaginary part of the refractive index between phytoplankton species and even within any single species which changes its physiological status. Nevertheless, it can generally be anticipated that with increasing wavelength toward the blue region of the spectrum, the small particulate fraction becomes increasingly important for scattering. As an example, for $\lambda=440\text{nm}$, the contribution maxima in Figs 3a and 4a would be shifted to particle diameters which are 0.8 times those for $550\text{nm}$, so that the ratio $D/\lambda$ remains unchanged. In addition, if one considers the particulates that absorb strongly in the blue spectral region such as phytoplankton, the predominance of small-sized fraction in the scattering of blue light will be further enhanced because a reduction of scattering by absorption is more pronounced for large particles than for small ones (BRICAUD and MOREL, 1986; MOREL and BRICAUD, 1986).

Third, we examined the sensitivity of our predictions to the slope of the hyperbolic size distribution. For the slope $s=4.5$, the importance of small particles is naturally more pronounced. As an example, for particles with $n=1.05$, the contribution of the $<2\mu\text{m}$ size fraction to the total scattering increased to 53%, as compared to 36% for $s=4$. The opposite trend was tested assuming
s=-3.5. The Mie calculations had to be extended to a diameter of 1000\(\mu\)m to obtain a reasonable levelling off in the cumulative contribution at the large diameter side of the size spectrum. The contribution by relatively large particles >8\(\mu\)m was found to be significant even for backscattering. This size fraction contributed 16 to 36% to backscattering, and 18 to 63% to total scattering with higher percentages for low-index particles in both cases. Yet, contrary to KULLENBERG's (1984) argument that the small volume of water processed in Coulter counter leads to an underestimation of numbers of large particles because of their scarcity, the slope as small as -3.5 seems rather atypical for particles larger than 8\(\mu\)m. One of the most careful studies to date on the size distribution of coarse particles, which combined microscopic analysis with large volume filtrations, showed that the slopes are steeper than -5 for fecal materials and Foraminifera, the major components of large particle fraction >50\(\mu\)m (BISHOP, EDMOND, KETTEN, BACON and SILKER, 1977; BISHOP, KETTEN and EDMOND, 1978).

It is instructive to summarize this sensitivity analysis by providing the information on how the 50% point of the cumulative curves in Figs 3b and 4b would change if the slope of the size distribution varied between -3.5 and -4.5. For the total scattering by low-index particles (n=1.05), the 50% point corresponds to the particle diameter \(D\) of about 5.7, 3.2 and 1.85\(\mu\)m for slopes of -3.5, -4 and -4.5, respectively. For high index particles (n=1.20) the 50% point is located at \(D\) of 1.5, 0.92 and 0.64\(\mu\)m respectively. Thus, the change in slope between -3.5 and -4.5 causes a few-fold variation in the 50% point. Note that the extent of such change is comparable to the effect of changing the refractive index between 1.05 and 1.20 for a given slope of the size distribution. In the case of backscattering by particles with n=1.05, the 50% contribution is reached at \(D\) of 1.2, 0.2 and 0.16\(\mu\)m for \(s=\)-3.5, -4 and -4.5, respectively. For particles with n=1.20, the 50% point corresponds to \(D\) of 1.7, 0.33 and 0.17\(\mu\)m, respectively. Again, as with total scattering, there is a significant shift of the 50% point toward smaller size ranges if the slope of a size distribution becomes steeper than -3.5.

Finally, it is clear that an ideal approach would be to use a large number of very narrow size distributions, each characterizing a component with a specific refractive index, rather than a broad composite distribution. By assuming a tractable number of components representing various groups of marine microbes as described in the preceding section, the following is a step toward such an approach.

4. CROSS-SECTIONS, CONCENTRATIONS AND BULK SCATTERING BY DIVERSE MICROBES

4.1 Viruses

Recent electron microscopic studies demonstrated that the concentration of viruses in the ocean is much larger than thought previously (BERGH, BØRSHEIM, BRATBAK and HELDAL, 1989; BRATBAK, HELDAL, NORLAND and THINGSTAD, 1990; PROCTOR and FUHRMAN, 1990), but the potential effect of these smallest "living" particles on ocean optics has not been considered yet. In order to model the optical properties of viruses, we adopted a size distribution (Fig.8) from ACKERMANN and DUBOW (1987). This differential distribution is expressed in terms of relative number of particles per unit volume per unit size bandwidth; a similar representation is also used below for heterotrophic bacteria and cyanobacteria (see Figs 11 and 13).
FIG. 8. The size distribution of isometric viral heads after ACKERMANN and DUBOW (1987). The relative frequency of occurrence is normalized to unity at its maximum.

The distribution in Fig. 8 represents isometric heads of tailed viruses, and was obtained from about 180 “species” that infect various bacteria including cyanobacteria. Such a description of sizes is a reasonable choice because the tailed bacterial viruses (bacteriophages) are the most numerous of all viruses, moreover many virions (i.e. free-floating viral particles) in marine environments are similar to known tailed bacteriophages with polygonal heads (PROCTOR and FUHRMAN, 1990). Figure 8 shows that bacteriophages are most frequently in the 55 to 65nm size range. This is consistent with observations that oceanic viruses are generally dominated by forms which are somewhat smaller than 60nm (BERGH, BØRSHIEIM, BRATBAK and HELDAL, 1989; BRATBAK, HELDAL, NORLAND and THINGSTAD, 1990). The distribution is slightly skewed with the average diameter $\bar{D}$ of 71.5nm. The value of $\bar{D}$ satisfies the condition $\bar{G} = \pi \bar{D}^2/4$, where $\bar{G}$ is the average projected-area obtained from:

$$\bar{G} = \frac{\pi}{4} \int_{D_{min}}^{D_{max}} D^2 F(D) dD \left( \int_{D_{min}}^{D_{max}} F(D) dD \right)^{-1}$$  \hspace{1cm} (16)

where $F(D)$ is the function shown in Fig. 8.

In the determination of scattering properties, the tails of the viruses will be neglected. The length of a tail can vary greatly from tenths to hundreds of nanometers and their minor dimensions fall in the range of 7 to 25nm (ACKERMANN and DUBOW, 1987). Assuming that viruses are randomly oriented and have cylindrical tails, we estimate that the intra-specific variation in the projected-area of the tails (one fourth of the cylindrical surface area, see VAN DE HULST, 1957) can vary in the range of 700 to 3300nm$^2$. This suggests that the tails are much less important for light scattering than the heads, which have the average projected-area of 4000nm$^2$. In addition, bacteriophages without visible tails may dominate, as observed in coastal Norwegian waters (BRATBAK, HELDAL, NORLAND and THINGSTAD, 1990). Hence the effect of neglecting the tails
will be relatively trivial.

The internal volume of viral heads is filled with DNA (25%) and water (75%) and enclosed by a thin rigid protein shell (EARNSHAW, KING and EISERLING, 1978). The ratio of the DNA to protein content is typically 50:50, which yields an overall density of viral solids of 1.5 g cm\(^{-3}\) (ACKERMANN and DUBOW, 1987). Using these data we estimate the refractive index of viral particle from (BARER and JOSEPH, 1954; ROSS and BILLING, 1957):

\[
(n-1) n_w = 0.18 \rho_s v_s \tag{17}
\]

where \(\rho_s\) is the density of solids in g cm\(^{-3}\) and \(v_s\) the partial volume occupied by solids (0.25 in this case). This formula is based on the observation that the increment in refractive index, \((n-1)n_w\), of living cells is usually very close to 0.18 when the intracellular concentration of solids, \(\rho_s v_s\), is increased by 1 g cm\(^{-3}\). Accordingly, our estimate of the refractive index for viral particle is \(n=1.05\).

The size distribution from Fig.8 and refractive index \(n=1.05\) were used in Mie scattering calculations for viruses with the assumption of no absorption \((n'=0)\). The spectral values of cross-sections \(\sigma_b\) and \(\sigma_{bb}\) for a "mean" viral particle, as determined from Eq(6) and Eq(7), are shown in Fig.9. The rapid increase of scattering with decreasing wavelength and high backscattering ratio \(\beta_b = b_b/b\) (or equivalently \(\sigma_{bb}/\sigma_b\)) indicates that viruses approach the domain of Rayleigh scattering \((D<<\lambda)\). The scattering in this domain is characterized by \(\lambda^{-4}\) dependence and \(\beta_b = 0.5\) (e.g. VAN DE HULST, 1957). Figure 10 shows that the volume scattering function of a particle with \(D=60\) nm is fairly close to the symmetric pattern of Rayleigh scattering at 550 nm. Viruses have thus the highest backscattering ratio amongst the living particles in the ocean.

The values for cross-sections at a wavelength of 550 nm together with bulk properties are listed in Table 1, which also includes similar data for other microbial components. The bulk coefficients of scattering and backscattering are shown for selected particle concentrations, which were chosen to cover a range of values typically observed in the open ocean. The small amounts of data now available from unpolluted marine environments indicate a broad variation in virion abundance within 5 orders of magnitude, with lowest numbers observed in the Sargasso Sea and highest numbers in the Gulf Stream (PROCTOR and FUHRMAN, 1990). Whether the virions do occur at concentrations as high as \(10^{14}\) m\(^{-3}\) in the open ocean is uncertain, because such a high value has been reported only once. Associated with changes in the concentration, is the variability in the bulk scattering and backscattering coefficients of viruses. For virion abundances on the order of \(10^{12}\) m\(^{-3}\) or less, these coefficients remain very low, however.

Further studies are needed to ascertain not only the concentrations of virions but also their sizes in the ocean. The potential changes in the size distribution of virus populations are of critical importance from the optical viewpoint. This is because the scattering efficiency varies very rapidly with diameter in the viral size range. The bulk scattering coefficients would increase approximately 7-fold if virions of 100 nm in size dominate rather than 70-nanometer virions. Although our size distribution is likely representative of most oceanic conditions, virions >100 nm in diameter have been found occasionally to be as important as smaller forms (BRATBAK, HELDAL, NORLAND and THINGSTAD, 1990).
FIG. 9. The cross-section for scattering (panel a) and backscattering (panel b) of viruses as a function of light wavelength.
FIG. 10. Comparison of the volume scattering function, $\beta(\theta)$, produced by a spherical particle of 60nm in diameter (Mie solution) with Rayleigh pattern. The $\beta(\theta)$ function is normalized so that its integral over the entire angular range is unity.

<table>
<thead>
<tr>
<th>Microbial component</th>
<th>Cross-sections at 550nm (m$^2$ per particle)</th>
<th>Numerical concentration (m$^2$)</th>
<th>Bulk coefficients at 550nm (m$^3$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$(\tilde{\sigma}_{i})$</td>
<td>$(\tilde{\sigma}_{\infty})$</td>
<td>$(b)_i$</td>
</tr>
<tr>
<td>Viruses</td>
<td>$2.07 \times 10^{-18}$</td>
<td>$0.85 \times 10^{-18}$</td>
<td>$3.0\times 10^9$</td>
</tr>
<tr>
<td></td>
<td>$4.6 \times 10^{14}$</td>
<td></td>
<td>$4.6 \times 10^{14}$</td>
</tr>
<tr>
<td>Heterotrophic bacteria</td>
<td>$3.84 \times 10^{-14}$</td>
<td>$2.44 \times 10^{-16}$</td>
<td>$3.0 \times 10^{11}$</td>
</tr>
<tr>
<td></td>
<td>$1.5 \times 10^{12}$</td>
<td></td>
<td>$1.5 \times 10^{12}$</td>
</tr>
<tr>
<td>Prochlorophytes</td>
<td>$1.08 \times 10^{-13}$</td>
<td>$7.01 \times 10^{-16}$</td>
<td>$3.0 \times 10^9$</td>
</tr>
<tr>
<td></td>
<td>$5.0 \times 10^{10}$</td>
<td></td>
<td>$5.0 \times 10^{10}$</td>
</tr>
<tr>
<td></td>
<td>$1.0 \times 10^{11}$</td>
<td></td>
<td>$1.0 \times 10^{11}$</td>
</tr>
<tr>
<td>Cyanobacteria</td>
<td>$8.06 \times 10^{-13}$</td>
<td>$1.84 \times 10^{-15}$</td>
<td>$3.0 \times 10^9$</td>
</tr>
<tr>
<td></td>
<td>$5.0 \times 10^{10}$</td>
<td></td>
<td>$5.0 \times 10^{10}$</td>
</tr>
<tr>
<td></td>
<td>$1.0 \times 10^{11}$</td>
<td></td>
<td>$1.0 \times 10^{11}$</td>
</tr>
<tr>
<td>Ultrananoplankton (2-8µm)</td>
<td>$1.60 \times 10^{-11}$</td>
<td>$7.59 \times 10^{-15}$</td>
<td>$3.0 \times 10^8$</td>
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<td></td>
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<td></td>
<td>$5.0 \times 10^8$</td>
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<tr>
<td></td>
<td>$1.0 \times 10^9$</td>
<td></td>
<td>$1.0 \times 10^9$</td>
</tr>
<tr>
<td>Larger nanoplankton (8-20µm)</td>
<td>$1.73 \times 10^{-10}$</td>
<td>$1.90 \times 10^{-13}$</td>
<td>$4.5 \times 10^6$</td>
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<tr>
<td></td>
<td>$7.5 \times 10^6$</td>
<td></td>
<td>$7.5 \times 10^6$</td>
</tr>
<tr>
<td></td>
<td>$1.5 \times 10^7$</td>
<td></td>
<td>$1.5 \times 10^7$</td>
</tr>
<tr>
<td>Microplankton</td>
<td>$1.20 \times 10^9$</td>
<td>$2.90 \times 10^{12}$</td>
<td>$3.0 \times 10^5$</td>
</tr>
<tr>
<td></td>
<td>$1.0 \times 10^6$</td>
<td></td>
<td>$1.0 \times 10^6$</td>
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<td>$5.0 \times 10^6$</td>
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<td>$5.0 \times 10^6$</td>
</tr>
</tbody>
</table>
4.2 Heterotrophic bacteria

Heterotrophic bacteria are the most numerous microbes of the oceanic picoplankton which include microorganisms in the size fraction 0.2-2μm. The optical properties of bacteria adapted here will be those measured in our previous experiments with naturally derived free-living bacterioplankton grown in unenriched seawater (STRAMSKI and KIEFER, 1990). Briefly, the measurements of beam attenuation coefficient, absorption coefficient, and size distribution of cell suspensions were used to calculate the optical efficiency factors and refractive index of bacteria. The computational scheme of the approach was based primarily upon Mie theory.

In three separate experiments, the real part of the bulk refractive index of bacterial cells varied between 1.04 and 1.07, and was more or less wavelength independent between 350 and 750nm. The values for the imaginary part across the spectrum were on the order of $10^{-4}$ or less, with a maximum related to absorption by respiratory cytochromes at about 410nm. An example of size distribution of bacterial cells is shown in Fig.11. Most of the bacterial cells could not be categorized as spheres, and we attempted to account for this fact by measuring length and width of cells. Generally, the cells with length <1μm and width <0.5μm predominate in the population (Fig.11a). Two shapes, a prolate spheroid and a cylinder, were used to transform the nonspherical cells into spheres with equivalent projected-area. The result is that the cells having an equivalent diameter $D$ of 0.3 to 0.6μm occur most frequently, and the average cell diameter $\bar{D}$ is 0.55μm (Fig.11b). $\bar{D}$ varied from only 0.53 to 0.58μm between experiments. Also the range of diameters was more or less constant from one experiment to another; the smallest cells had $D$ of about 0.15μm, and the biggest of 1.3μm. Given the size distribution and morphological diversity, the unenriched cultures in our experiments are believed to resemble closely the natural populations of heterotrophic bacteria.

![Fig.11](image-url)  
**FIG.11.** The size distribution of heterotrophic bacteria. (a) a contour plot showing the relative frequency of occurrence of cells having a particular length and width. The frequency is normalized to unity at its maximum as indicated on the scale. The straight line on the graph represents a spherical shape. (b) the relative frequency of occurrence of bacterial cells after transformation into spheres with equivalent projected-area.
We found that the efficiency factor for scattering, $\bar{Q}_b$, of bacteria vary with light wavelength approximately in proportion to $\lambda^{-2}$. The values of $\bar{Q}_b$ at 400nm ranged between 0.3 and 0.45 in the three experiments. The backscattering efficiency, $\bar{Q}_{bb}$, showed no significant spectral trends and ranged from about 6 $10^{-4}$ to 2 $10^{-3}$ in response to increased refractive index. Similarly to cross-section $\sigma$, the bar above $Q$ indicates that the efficiency factor represents a hypothetical "mean" cell from a polydispersed assemblage (see BRICAUD and MOREL, 1986; MOREL and BRICAUD, 1986). Our estimates of efficiency factors for bacteria are consistent with results of another recent study (MOREL and AHN, 1990).

The cross-sections for scattering and backscattering of bacteria, as averaged from our three experiments, are plotted as a function of light wavelength in Fig. 12. These spectral curves follow the above described behaviour of $\bar{Q}_b(\lambda)$ and $\bar{Q}_{bb}(\lambda)$. The data for $\lambda=550$nm in Table 1 indicate that the bulk coefficients of scattering and backscattering by bacteria are typically a few orders of magnitude higher than those associated with viruses. This results from a significant increase in optical cross-sections $\bar{\sigma}_b$ and $\bar{\sigma}_{bb}$ of bacteria, which far more than compensates for their lower abundances. Note that the contributions to backscattering by viruses and bacteria may only become comparable when viruses are extremely abundant.

The values chosen to represent bacterial abundance in Table 1 are taken from CHO and AZAM (1990). They demonstrated an interesting feature of bacterial abundance in the upper layers of the oligotrophic oceans is its relatively narrow range of $3 \times 10^{11}$ to $1.5 \times 10^{12}$ cells m$^{-3}$, and apparently locked covariation with chlorophyll $a$ at concentrations less than 0.5mg m$^{-3}$. Thus light-scattering by bacteria will become progressively more significant relative to chlorophyll-bearing phytoplankton with increasingly oligotrophic conditions. They also showed that only for Chl $a > 1$mg m$^{-3}$, that is in mesotrophic to eutrophic waters, is there a significantly positive relationship between bacterial abundance and chlorophyll concentration.

4.3 Photoautotrophic picoplankton

The most ubiquitous and abundant photoautotrophs in the picoplankton size fraction are the chroococcoid cyanobacteria (JOHNSON and SIEBURTH, 1979; WATERBURY, WATSON, GUILFORD and BRAND, 1979) and prochlorotrich cells believed to be prochlorophytes (CHISHOLM, OLSON, ZETTLER, GOERICKE, WATERBURY and WELSCHMEYER, 1988). The widespread occurrence of tiny eucaryotic phototrophs, including prasinophytes, chlorophytes and eustigmatophytes, was also documented, but no eucaryotic heterotrophs were observed in the picoplankton samples (JOHNSON and SIEBURTH, 1982; MURPHY and HAUGEN, 1985; CHAVEZ, BUCK and BARBER, 1990). The few data now available on eucaryotic picoplankters show that their numbers generally range one order of magnitude below those for the cyanobacteria; the maximal concentrations of these eucaryotic microalgae appear to be between $10^9$ and $10^{10}$ cells per m$^3$, which corresponds to rather low abundances of cyanobacteria and prochlorophytes. Therefore, the examination of light scattering by photoautotrophic picoplankton can, in a first approximation, be limited to numerically dominant components; cyanobacteria and prochlorophytes.

The optical characterization of cyanobacteria will be here based upon a fairly comprehensive description of the absorptive and scattering properties of a phycocyanin-rich cyanobacterium Synechocystis given in STRAMSKI and MOREL (1990). In their experiments, the size distribution of nearly spherical Synechocystis peaked typically at about 1.14$\mu$m (Fig. 13). The real part of the refractive index ranged from 1.045 to 1.06. The lower values of $n$ characterized cells adapted to low intensity of growth irradiance (20$\mu$mol quanta m$^{-2}$s$^{-1}$), and higher $n$ was associated with high-light adapted cells (700$\mu$mol quanta m$^{-2}$s$^{-1}$). The imaginary part of the refractive index, $n'$, showed
distinct spectral signatures of absorbing pigments present in *Synechocystis*. The values for $n'$ extended to 0.006 in the blue Soret band of chlorophyll $a$ for low-light adapted cells, but remained below 0.001 at 550nm regardless of the physiological status of the cyanobacterium.

![Diagram](image)

**FIG.12.** The cross-section for scattering (panel a) and backscattering (panel b) of heterotrophic bacteria as a function of light wavelength.
In accordance with Mie theory, such values of the refractive index together with cell sizes near 1μm yield characteristic spectral patterns of scattering, $\bar{Q}_b(\lambda)$, and backscattering, $\bar{Q}_{bb}(\lambda)$, efficiencies. STRAMSKI and MOREL (1990) demonstrated that while $\bar{Q}_b$ of cyanobacteria exhibits a general trend to increase with decreasing wavelength, the opposite behaviour is observed for $\bar{Q}_{bb}$. In order to obtain the cross-sections $\bar{\sigma}_b$ and $\bar{\sigma}_{bb}$ for *Synechocystis*, we multiplied the values of $\bar{Q}_b$ and $\bar{Q}_{bb}$ by the averaged projected-area, $\bar{G}$, derived from the size distribution shown in Fig.13 according to Eq(16). This average projected-area represents a cell with a diameter $\bar{D} \equiv 1.3μm$. In accord with the behaviour of $\bar{Q}_b$ and $\bar{Q}_{bb}$, the spectral curves of $\bar{\sigma}_b(\lambda)$ and $\bar{\sigma}_{bb}(\lambda)$ exhibit the general trends, on which the features related to the depressive effect of absorption are superimposed (Fig.14). These effects are more pronounced for backscattering in agreement with theoretical predictions (MOREL and BRICAUD, 1981, 1986). Figure 14 also shows that cross-sections $\bar{\sigma}_b(\lambda)$ and $\bar{\sigma}_{bb}(\lambda)$ for this species vary considerably with differences in growth irradiance.

In our further considerations of scattering budget at 550nm we will assume the average values based on data for low-light and high-light adapted cells.

Although *Synechocystis* has specific absorption signatures, its scattering properties are likely to be representative of other species of cyanobacteria which are more abundant in open ocean environments. These dominant species belong to the genus *Synechococcus* and, like *Synechocystis*, are ~1μm in size (e.g. WATERBURY, WATSON, VALOIS and FRANKS, 1986). In addition, the most common *Synechococcus* strains in the open ocean are characterized by having high contents of phycourobilin relative to phycoerythrobilin (CAMPBELL and ITURRIAGA, 1988; OLSON, CHISHOLM, ZETTLER and ARMBRUST, 1990). The former pigment absorbs primarily at 495nm (ONG, GLAZER, and WATERBURY, 1984) and the latter at 545nm (WATERBURY, WATSON, VALOIS and FRANKS, 1986). Therefore, the oceanic-type *Synechococcus* is characterized by weak absorption at 550nm, and likely will have values of $n'(550)$ similar to those of *Synechocystis*.

Prochlorophyte picoplankton have been less well studied so far, perhaps because they were
FIG. 14. The cross-section for scattering (panel a) and backscattering (panel b) of cyanobacterium *Synechocystis* as a function of light wavelength, obtained from STRAMSKI and MOREL (1990). The values for growth irradiance in μmol quanta m$^{-2}$s$^{-1}$ are indicated.

discovered only a few years ago and are difficult to isolate. Even the identity of these cells is still not definitively established (CHISHOLM, OLSON, ZETTLER, GOERICKE, WATERBURY and WELSCHMEYER, 1988; OLSON, CHISHOLM, ZETTLER, ALTABET and DUSENBERRY, 1990). We will assume that cross-sections for scattering and backscattering, as calculated from Mie theory for a spherical cell with refractive index $n = 1.055$ and a diameter $D = 0.8\mu$m, are representative of prochlorophytes. The chosen value for $n$ is consistent with the data for the cyanobacterium *Synechocystis*, and the diameter of 0.8μm with microscopic observations of prochlorophytes (CHISHOLM, OLSON, ZETTLER, GOERICKE, WATERBURY and WELSCHMEYER, 1988). The calculated cross-sections at $\lambda = 550$nm with the assumption that $n'(550)=0$ are given in Table 1. Ignoring absorption by prochlorophytes at 550nm is not critical because $\sigma_b$ and $\sigma_{bb}$ would decrease only by 0.7% and 1.4%.
respectively, if one assumes \( n'(550) = 0.001 \). Such a value for \( n'(550) \) is likely very close to a maximum in this spectral region, as suggested by studies with *Synechocystis*. A prediction of light scattering by prochlorophytes across the visible spectral region is now hindered by a lack of information on spectral absorption of these species.

As shown in Table 1, prochlorophytes have scattering cross-sections that are lower than cyanobacteria but higher than heterotrophic bacteria. The concentrations of prochlorophytes and cyanobacteria are variable in time and space, and in the open ocean their abundances span typically two orders of magnitude from \( 10^9 \) to \( 10^{11} \) cells m\(^{-3} \) (ITURRIAGA and MARRA, 1988; OLSON, CHISHOLM, ZETTLER, ALTABET and DUSENBERY, 1990; OLSON, CHISHOLM, ZETTLER and ARMBRUST, 1990). Flow cytometric measurements by OLSON, CHISHOLM, ZETTLER, ALTABET and DUSENBERY (1990) indicates that the coincidence of very high concentrations (~\( 10^{11} \) cells m\(^{-3} \)) of these two picoplankters is unlikely. Generally, these microbes have seasonal variations in abundance that are opposite in direction. Another important distinction between the two taxa is that prochlorophytes can form pronounced, seasonal subsurface maxima with relatively few cells at the surface, while cyanobacteria are usually more uniformly distributed throughout the upper water column.

The numerical abundances and associated bulk coefficients \( b(550) \) and \( b_s(550) \) for prochlorophytes and cyanobacteria were chosen in Table 1 to cover a wide range of values expected in the oligotrophic waters. Only when the total abundance of phototrophic picoplankters is very high \( \geq 5 \times 10^{10} \) cells m\(^{-3} \), is their contribution to scattering coefficient \( b(550) \) comparable to that of heterotrophic bacteria. Most frequently, when there is no "bloom", the numbers of prochlorophytes and cyanobacteria are close to \( 10^{10} \) cells m\(^{-3} \) or less. In such common situations, the heterotrophic bacteria are numerous enough to compensate for lower scattering cross-sections. Consequently, they appear to be the most important component of picoplankton for light scattering. This predominance of heterotrophic bacteria is especially well pronounced for backscattering.

### 4.4 Nanoplankton and microplankton

The nanoplankton (2 to 20\( \mu \)m in size) and microplankton (20 to 200\( \mu \)m) include diverse taxa of autotrophs and heterotrophs. Because the information on the separate abundances of various components of these assemblages is scarce, we will use a composite size distribution encompassing all the microorganisms larger than 2\( \mu \)m. In addition, we will separate photosynthetic forms from heterotrophs only on the basis of their proportion of total cell numbers. The nanoplankton fraction will be divided into two groups: ultranoplankton (2 to 8\( \mu \)m in size) and larger nanoplankton (8 to 20\( \mu \)m). The term "ultraplankton" has been used historically to describe plankters <5-10\( \mu \)m (MURPHY and HAUGEN, 1985).

The data collected by TAKAHASHI and BIENFANG (1983) in subtropical Hawaiian waters (Chla concentration about 0.12mg m\(^{-3} \)) are used to construct a size distribution of phytoplankton larger than 2\( \mu \)m. These authors enumerated phytoplankton cells, distinguished according to size and taxonomic groups. Their data along with the fitted hyperbolic cumulative distributions in the size range >2\( \mu \)m (\( r^2=0.97 \)) are shown in Fig. 15. While one of the regression curves (solid line) includes the data point for \( D=100\mu \)m, the dashed line omits this point because larger uncertainty may be associated with counts of less abundant cells >100\( \mu \)m. The respective hyperbolic approximations are 2.2 \( 10^9D^{-2.86} \) and 5.0 \( 10^9D^{-3.37} \). Note that both values for the slope parameter are close to -3, hence the slope of the differential distribution is about -4.
FIG. 15. A logarithmic plot of the cumulative size distribution of phytoplankton in the $>2\mu m$ range obtained from TAKAHASHI and BIENFANG (1983). The solid and dashed lines represent the best-fit hyperbolic approximations to the data points. The dotted line is plotted to suggest the generality of a slope of -3 in the broad size range between 0.2 and 100$\mu m$. The open circle is the expected concentration of heterotrophic bacteria and other larger microorganisms in these waters.

In addition, we suggest that such a slope appears to be also valid for microbes in the picoplankton size range. To support this suggestion, in Fig. 15 we have plotted a dotted line which begins at a diameter of 0.2$\mu m$ and has a slope of -3. This line is not intended to convey any specific quantitative information, and we have chosen a value of $7 \times 10^{11}$ cells m$^{-3}$ to represent a number of organisms $>0.2\mu m$. This choice is consistent with typical concentrations of heterotrophic bacteria which decisively dominate the numbers of marine organisms in the size range $>0.2\mu m$. Thus, to a first approximation, i.e. neglecting transient features associated with enhanced growth of certain species, marine microorganisms appear to obey an inverse 4th power law over three orders of magnitude in cell diameter, covering pico-, nano- and microplankton size ranges. This fact can substantially aid in understanding and modelling the microbial food webs in the ocean. The above suggestion about the generality of a slope of -4 for the size distribution $F(D)$ is different from previous work with Coulter counter, because here we refer specifically to living microorganisms and not to total particulate material. Such general power law for microorganisms was in fact hypothesized two decades ago by SHELDON, PRAKASH and SUTCLIFFE (1972). They postulated that in a unit volume of seawater roughly equal volumes of living material occur in logarithmically equal size intervals within the range from bacteria to whales. This in turn implies a slope of -4 for the $F(D)$ distribution. Such size spectra are expected to dominate in oceanic waters characterized by relatively low primary productivity during periods when no plankton blooms are occurring.

The cross-sections for scattering, $\sigma_s$, and backscattering, $\sigma_{bb}$, of nanoplankton and microplank-
ton were obtained from Eq(6) and Eq(7) for \( \lambda = 550 \text{nm} \) by using the size distributions from Fig.15 (solid and dashed lines) over appropriate size ranges. We assumed that \( n = 1.05 \) and \( n' = 0.001 \). The values shown in Table 1 are averages based upon the two size distributions. Note that \( \bar{b}_n \) and \( \bar{b}_b \) for nanoplancton and microplankton are increased by several orders of magnitude as compared to smaller picoplanktonic microbes.

It is instructive to examine how the cross-sections of nano- and microplankton depend on the choice of size distribution and refraction index. Little effect is caused by the slope of the size distribution if it varies within the limits shown in Fig.15. The use of one of the power functions would change the mean values of \( \bar{b}_n \) and \( \bar{b}_b \) shown in Table 1 by less than 10% for any component of the >2\( \mu \text{m} \) size fraction. An order of magnitude change in \( \bar{b}_b \) for nano- or microplankton is, however, caused by the variation in the real part of the refractive index from 1.03 to 1.07. The cross-section for total scattering is less sensitive to such variation in \( n \) (\( \bar{b}_b \) undergoes about two-fold change for nanoplancton and only 10% change for microplankton). Understanding of these effects is aided by the analysis of the size dependence of \( \sigma_n \) and \( \sigma_b \) in the >2\( \mu \text{m} \) fraction for individual spherical particles having various indices of refraction (Fig.16). We recall that these cross-sections of individual particles are weighted by size distribution and integrated over appropriate size range to yield ultimate estimates of \( \bar{b}_n \) and \( \bar{b}_b \) (see Eq(6) and Eq(7)).

Changes in abundance of microorganisms larger than 2\( \mu \text{m} \) in oligotrophic ocean are limited to a fewfold or less. The average abundances of all microorganisms including heterotrophs in the size fraction of 2 to 200\( \mu \text{m} \) ranged between 3.3 \( 10^8 \) and 6.0 \( 10^8 \) per m\(^3\) throughout a year in the euphotic zone of the North Pacific central gyre (BEERS, REID and STEWART, 1982). CHAVEZ, BUCK and BARBER (1990) reported that the mean abundances ranged between 3.5 \( 10^8 \) and 10\(^8 \) per m\(^3\) at the surface in the equatorial Pacific. In addition, their data suggest that heterotrophs can account for 10-50% of the population larger than 2\( \mu \text{m} \) in size; typically their contribution is 20-30%. The numbers of phytoplankton >2\( \mu \text{m} \), derived from hyperbolic distributions in Fig.15, range between 3.1 \( 10^8 \) and 4.8 \( 10^8 \) cells m\(^3\), so they are consistent with the studies cited above. More than 99.5% of the cells larger than 2\( \mu \text{m} \) are in the nanoplanckton size fraction. In addition, ultrananooplankton cells comprise about 98% of the size fraction >2\( \mu \text{m} \). This discounts the importance of microplankton and even much of the nanoplanckton size class.

Accordingly, the abundances of nanoplancton shown in Table 1 range from 3 \( 10^8 \) to 10\(^9 \) cells m\(^3\). The associated values of the scattering coefficient are on the order of \( 10^{-3} \) or 10\(^{-2}\) m\(^{-1}\). The bulk of the effect (~87%) in the size range of 2 to 20\( \mu \text{m} \) is caused by ultrananooplankton, which also dominates backscattering (~75%).

Microplankton numbers in Table 1 were also chosen to cover a range one can expect in oligotrophic waters. The lowest value is 0.1% of its counterpart for nanoplanckton, which is consistent with the slope \( s = 4 \) of the size distribution. The choice of the highest value for microplankton abundance is based upon the data from Southern California nearshore waters; specifically from locations or depths where Chl\( \alpha \) + Phaeo\( \alpha \) concentration was less than 0.5 mg m\(^{-3}\) (BEERS, REID and STEWART, 1980). This highest value corresponds to 0.5% of its counterpart for nanoplanckton. In such a case, the microplankton would scatter about 30% of the amount of radiant energy scattered by nanoplanckton and somewhat larger amount in backward directions. However, the typical slope of size distribution implies that the proportion of microplankton in the >2\( \mu \text{m} \) size fraction is usually lower than 0.5%. Thus, the coefficients \( b_n \) and \( b_b \) for microplankton will be a fewfold to an order of magnitude lower than those for nanoplanckton.

Although we do not specifically model the scattering by heterotrophic nano- and microplankton, the bulk coefficients in Table 1 can be, in a first approximation, viewed as representative of all microorganisms in the >2\( \mu \text{m} \) fraction. The proportions of numbers of heterotrophs and autotrophs, as mentioned above, favour the predominance of autotrophs.
FIG. 16. A logarithmic plot of the size dependence of the cross-section for scattering (panel a) and backscattering (panel b) of individual particles in the >2μm range. The curves represent Mie solutions for various values of the refractive index as indicated; the imaginary part of the index is zero, and the light wavelength is 550nm.
5. CONTRIBUTIONS BY MICROBIAL COMPONENTS TO LIGHT SCATTERING

5.1 The total scattering coefficient

The percent contributions of microbial components to the total particulate scattering at 550nm in oligotrophic ocean is shown in Fig.17. For each component, the values of \( b_p \), listed in Table 1 for the three different cell abundances were divided by the total coefficient, \( b_p \), given in Eq(8). Because the total \( b_p(550) \) is expressed as a function of chlorophyll \( a \) and phaeopigment \( a \) concentration, \( C \), so are the percent contributions in the figure. Several precautions must be taken when interpreting these plots.

First, some of the curves reach unrealistically high percentages, exceeding even 100%, which means that the corresponding combination of cell numbers, pigment concentration and total scattering coefficient does not occur in the natural environments. Note the shaded regions in Fig.17 indicate typical conditions. Second, although Eq(8) can be considered as a good representation for surface waters, the individual data points describing \( b_p(550) \) versus pigment concentration, \( C \), are widely scattered and vary threefold for a given pigment concentration (Gordon and Morel, 1983; Morel, 1987). As a result, the total particulate scattering, \( b_p(550) \), at any pigment concentration can vary between 50 and 150% of the central value assumed for calculating the plots. Finally, each of our curves represents a constant cell concentration for a given microbial component although, in reality, the cell numbers, the total scattering, \( b_p \), and pigment concentration, \( C \), may vary. Nevertheless, Fig.17 provides some very useful information about the significance of various microbial components for light scattering. The shaded regions are believed to indicate typical conditions in surface oligotrophic waters, where pigment concentrations range between 0.03 and 0.5mg m\(^{-3}\).

Viruses are not included in Fig.17 because even at the highest abundances reported so far (on the order of \( 10^{14} \) virions m\(^{-3}\) in the Gulf Stream; Proctor and Fuhrman, 1990), these particles will contribute less than 1 or 2% to the total particulate scattering at 550nm. We expect that in the blue spectral region, where scattering by viruses is increased 3 to 4-fold as compared to 550nm (see Fig.9), their contribution will usually be insignificant as well. The most striking feature of our assessment is the importance of free-living heterotrophic bacteria. Their contribution appears to range typically from 10 to several tens of percent. In certain situations, more than a half of the light scattering may be associated with these microbes. The shaded region on the graph suggests that the relative contribution by bacteria tends to increase with decreasing pigment concentration. This is consistent with the observation that bacterial abundance does not covary with pigments under increasingly oligotrophic conditions (see section 4.2).

The numbers of autotrophic cyanobacteria typically remain <2 \( 10^{10} \) cells m\(^{-3}\) (Olson, Chisholm, Zettler and Armbrust, 1990), so normally they are expected to contribute less than 25% of the light scattering, and frequently less than 10%. The bloom situations illustrated by the two upper curves on the relevant graph, can lead to higher percentages, exceeding perhaps 50%. Note that in Fig.17 the shaded regions for cyanobacteria (and other chlorophyll-bearing components), extend approximately in parallel to the horizontal axis. We choose to show such a pattern because cell numbers of photosynthetic microbes and pigments concentration in sea water are expected to covary. Prochlorophytes seem to make the least important contribution to the picoplanktonic component of the total light scattering in surface waters - generally less than 10%. However, it seems possible that in the lower part of the euphotic zone, prochlorophytes will occasionally make a higher contribution than other picoplankters, for example, in the characteristic subsurface maxima of prochlorophytes in which the proportions in numerical abundance of different groups of microbes are changed.
Ultrananoplankton are expected typically to contribute 10 to 20% to the total particulate scattering, with at least one half of this contribution being associated with photoautotrophs. Larger nanoplankton (>8μm) and microplankton are predicted to have a small effect, typically contributing less than 5%, and quite frequently a negligible amount (<1%).

In summary, small microbes in the size range 0.2-8μm, are responsible for the largest proportion of the light scattering by living organisms. This is consistent with the predictions of our simplified model for particle collections with lower indices of refraction (Figs 3 and 6). In addition Fig.17 suggests that the overall effect of living microorganisms on the light scattering in the open ocean is never negligible. It appears that the suggestion by BROWN and GORDON (1973) that organics in the Sargasso Sea contribute less than 10% to particulate scattering is very unlikely,
except perhaps when Saharan dust influxes are occurring (CARDER, STEWARD, BETZER, JOHNSON and PROSPERO, 1986). We expect that all microorganisms will contribute at least 20% to the total particulate scattering in the open ocean. This is supported by the fact that the abundance of heterotrophic bacteria in surface waters rarely drops below $3 \times 10^{11}$ cells m$^{-3}$. In waters where there is a bloom of picophytoplankton or concentration of heterotrophic bacteria approaches $10^{12}$ cells m$^{-3}$, the microorganisms may dominate light scattering, accounting for $>50\%$ of its total magnitude.

5.2 The backscattering coefficient

The significance of microbial contributions to particulate backscattering is presented on similar graphs in Fig. 18. The reference values for the total particulate backscattering coefficient, $b_{bp}(550)$, were obtained from Eq.(9). The most striking feature is that the microorganisms larger than 2$\mu$m have a negligible effect on backscattering. The smallest living particles, viruses, will only be an important source for backscattering at extremely high abundances, e.g. $\sim 10^{14}$ virions m$^{-3}$; so far such abundances have been reported only once in unpolluted, open ocean waters (PROCTOR and FUHRMAN, 1990), so we have chosen not to shade any region on the graph for viruses in Fig. 18. If in future normal virion abundances are confirmed as being of the order of $10^{12}$ m$^{-3}$ or less, then these particles must be considered insignificant sources of backscattering. Note that, as with total scattering, the contribution of viruses to backscattering in the shortwave side of the visible spectrum is expected to increase a few-fold as compared to 550nm. Also note that a slight increase in virion size may increase the scattering or backscattering many-fold.

As is generally true for the total particulate scattering, the heterotrophic bacteria are most important microorganisms contributing to the particulate backscattering. It even appears that bacteria comprise the only microbial component which remains significant for backscattering throughout much of the year in the surface oligotrophic ocean. Nonetheless, the contribution of bacteria to $b_{bp}(550)$ is relatively small, ranging typically from a few to about 30%. The photoautotrophic picoplankters contribute significantly to $b_{bp}(550)$ (as much as 15% or so) only under bloom conditions, when cell abundances are $\geq 5 \times 10^{10}$ m$^{-3}$. Otherwise, both prochlorophytes and cyanobacteria are expected to make contributions on the order of a few percent at the most.

5.3 Detrital particles and scattering

From the above discussion it is evident that most of the particulate backscattering must be associated with non-living (detrital) suspended materials. In addition, the total contribution by all chlorophyll-containing components is very small, typically <5%. This conclusion is consistent with the previous assessment by MOREL and BRICAUD (1981) that the bulk of particulate backscattering originates from detritus.

Another intriguing feature which emerges from comparison of Figs 17 and 18 is that microorganisms seem to contribute significantly smaller percentages to the particulate backscattering than to the total scattering coefficient. As an example, for waters with a pigment concentration of 0.1mg m$^{-3}$, all microorganisms contribute about 66% to $b_{bp}(550)$ and only 18% to $b_{bp}(550)$. In these tentative calculations, we assumed the middle values for microbe abundances from Table 1, with the exception that numbers for prochlorophytes and cyanobacteria were taken as $10^{10}$ rather than $5 \times 10^{10}$ cells m$^{-3}$ to represent better "no bloom" conditions. It is difficult to ascertain at the moment whether the difference in the percent contribution by microbes to the total scattering and backscattering is real or an artefact resulting from an inadequacy of Eq.(9) or an inaccuracy in our estimates of scattering cross-sections. If real, the optical components consisting of detrital particles that contribute heavily to backscattering but considerably less to the total scattering must be found.
Identification of such detrital components can be aided by estimating the backscattering ratio. The total particulate coefficients for scattering and backscattering can be written:

\[ b_p(550) = N_x (\bar{\sigma}_b)_x + \sum_{j=1}^{7} N_j (\bar{\sigma}_b)_j \]  
\[ b_{bp}(550) = N_x (\bar{\sigma}_{bb})_x + \sum_{j=1}^{7} N_j (\bar{\sigma}_{bb})_j \]  

where \( N \) is the number of particles per unit volume of seawater, the subscript \( j \) describes one of the seven microbial components (see Table 1), and \( x \) the unknown detrital component. In order to solve Eqs(18) for the backscattering ratio, \( (\bar{\sigma}_{bb})_x/(\bar{\sigma}_b)_x \), we use the example given above, in which all microorganisms contribute 66% to \( b_p(550) \) and 18% to \( b_{bp}(550) \). According to Eqs(8)
and (9), the values for $b_0(550)$ and $b_{sp}(550)$ are 0.07$m^{-1}$ and 0.0012$m^{-1}$ respectively if $C=0.1$mg m$^{-3}$. Thus, the required value for the backscattering ratio is 0.041. This value is high when compared to most microorganisms; heterotrophic bacteria are characterized by the values on the order of $10^{-3}$ (MOREL and AHN, 1990; STRAMSKI and KIEFER, 1990) and larger microbes by even smaller values (BRICAUD, MOREL and PRIEUR, 1983; STRAMSKI and MOREL, 1990). Importantly, our estimate for the detrital component is consistent with MOREL’s (1988) description of particulate backscattering, which also requires a large detrital component with the comparatively high backscattering ratio of about 0.02. The Mie calculations described earlier, point to two categories of particles that have a backscattering ratio of about 0.04. First, there are fine particles of diameter near 0.3$\mu$m, with an unconstrained refractive index, $n$, because the backscattering ratio is practically independent of $n$ in this small size range. The second category includes high-index particles ($n = 1.15$ to 1.2) ranging approximately between 2 and 10$\mu$m in size.

There is circumstantial evidence which points to fine, low-index particles as being the major backscatterers in the ocean. Recently, KОIKE, HARA, TERAUCHI and KOGURE (1990) have counted electronically particles in the size range 0.38-1$\mu$m, at concentrations on the order of $10^{13}$ m$^{-3}$ in surface oceanic waters. More than 95% of these submicron particles were non-living, and less than 0.6$\mu$m in size. They suggested that such particles are fragile, have a high water content, and are associated with the grazing of the microzooplankton. MELNIKOV (1976b) also suggested that the dominant contribution to particulate organic carbon in the ocean was of submicron detritus.

In addition, Figs 6 and 7 suggest that submicron particles of low refractive index possess the necessary characteristics for them to make a larger contribution to backscattering than to total scattering, as in the example given above, in which all microorganisms contribute 66% to $b_0(550)$ but only 18% to $b_{sp}(550)$. The addition of 0.7 $10^{13}$ particles per m$^3$ with a diameter of 0.5$\mu$m and 5 $10^{13}$ particles per m$^3$ with a diameter of 0.2$\mu$m, all having $n=1.025$, would explain the required 34% of total scattering and 82% of backscattering in this example. Thus, the detrital particles with $n<1.03$ and $D<0.6\mu$m may be the major component required to explain the portions of total particulate scattering and backscattering, which are unaccounted for by microorganisms.

How such submicron detritus with very low refractive index can be formed will have to remain conjectural because these particles have not been physically or chemically characterized. We can postulate two simple pathways whereby such particles may be formed. The first pathway would be through the successive fragmentation of larger detritus which include fecal material egested by grazers, aggregated particulates and fragments of dead organisms. Processes leading to this fragmentation would be the microbial decomposition of the organic matrix (e.g. BIDDANDA AND POMEROY, 1988), the activities of both of the colonizing microbes that utilize the substrates, and the protozoan grazing on attached bacteria which would result in mass loss of the particle proper, and hence would decrease the refractive index. As the structural integrity of the organic matrix weakens, the particles disintegrate into finer particles. Physical forces will also contribute to the disaggregation (JOHNSON, KRANCK and MUSCHENHEIM, 1990). Many of the disintegration products may be highly hydrated and submicron in size. The second pathway may be associated with abiotic formation of particles from dissolved organic matter by flocculation and adsorption on surfaces (BADER, HOOD and SMITH, 1960; JOHNSON and COOKE, 1980; JENSEN and SØNDERGAARD, 1982; BOWEN, 1984). Primary producers and grazers may play an indirect role in this pathway through their release of the dissolved organic matter into the water. Again particle processing by microbes may also contribute to the production of very fine, highly hydrated particles because particles formed abiotically will be comprised largely of labile organic compounds that are susceptible to breakdown by digestive enzymes.

It is still premature to generalize about the significance of submicron detritus to light scattering, and specifically we cannot rule out the possible role of particles with higher refractive index. A better knowledge of chemical composition, numbers and size distributions for detrital particles over the entire range of optical significance is prerequisite to a good understanding of optical
processes involving particulate matter. Unfortunately, too few relevant data are available for optical modelling of detritus, because of the diversity of detritus and problems associated with separating detritus from living microorganisms. In addition, the detrital material is often inextricably associated with live bacteria which grow on particle surfaces. The question whether the detritus-microbe particulate complexes are important to ocean optics remains to be answered.

Figure 19 shows some data from microscopic analysis and electronic counting of detrital particles in different oceanic regions. The slope of the size distribution for detritus from the shallow waters of the Baltic tends to decrease with decreasing particle size (LENZ, 1972). This was one of the most careful set of measurements achieved so far, but it was limited to particles larger than 10μm from a coastal environment. There is no consistent pattern emerging from the sparse data available for detritus in the open ocean. The indirect evidence for the submicron particles being extremely abundant, needs to be constantly evaluated. The concentrations of detrital particles larger than 5μm, as determined by microscopic analysis, appear to range from about 2 \times 10^7 to over 10^8 per m^3. For comparison, the average numbers obtained with a Coulter counter in the >5μm size range, were about 2 \times 10^6 particles m^-3 in the Sargasso surface waters (GORDON and BROWN, 1972). The number of phytoplankton >5μm in Fig.15 is about 2.2 \times 10^7 cells m^-3. These data seem consistent with the long recognized fact that the reserves of detrital matter are usually greater than the stocks of microorganisms.

![Graph showing detrital particle concentrations](image)

**FIG.19.** Summary of published data on the concentration of detrital particles with diameters larger than D in the upper layers of the ocean. The methods used by various investigators include particle electronic counting and microscopic analysis.

Open ocean:
- □ Northwestern Pacific (KOIKE, HARA, TERAUCHI and KOGURE, 1990)
- ○ Southeastern Pacific (MELNIKOV, 1976a)
- ◆ Sargasso Sea (GORDON, 1970)

Coastal waters:
- ▲ Western Baltic, Kiel Bight (KREY, 1961)
- • Western Baltic, Kiel Bight (LENZ, 1972)
6. CONCLUDING REMARKS

Our multi-component description of particulate scattering is distinctive from similar work reported in the past. We have precisely defined microbial components that are known to play specific roles in the functioning of marine ecosystem. We have then quantified the cellular scattering cross-sections and contributions of these components to light scattering in the ocean. This we believe remedies the main deficiency in previous work which, by solving the inverse scattering problem, yielded the dominant particulate components that were defined only on the basis of their physical properties (e.g. GORDON and BROWN, 1972; BROWN and GORDON, 1973, 1974; ZANEVELD, ROACH and PAK, 1974). Specifically, in this earlier work, various categories of particles known to play different roles in the ecosystem (e.g. detrital organics, living autotrophs and heterotrophs), have been considered to be a single component covering a broad range of particle sizes within the trophic continuum.

The present approach offers a promising analysis because it identifies bio-optical relationships and details. Our estimates of the cellular scattering cross-sections can be refined as more information on the parameters controlling the cellular optics becomes available. Specifically, for any given group of microorganisms the variability of scattering cross-sections is insufficiently characterized to enable a definitive and precise evaluation of its importance to the scattering budget. In addition, we have not considered certain groups of microorganisms which exhibit specific properties such as enhanced backscattering caused by the presence of external calcified plates in coccolithophore phytoplankton (HOLLIGAN, VIOLLIER, HARBOUR, CAMUS and CHAMPGNE-PHILIPPE, 1983) or the intracellular gas vacuoles in cyanobacteria Oscillatoria (VAN BAALEN and BROWN, 1969). As more data become available our approach may be refined by defining more microbial categories, especially in the >2μm size range, and extending it to other light wavelengths.

Several major conclusions of our study are consistent with a paper by MOREL and AHN (1991) which was published just after the initial submission of our manuscript for publication. It is worthwhile to reiterate the conclusions which are common to the two studies: (i) particles up to 10μm in size dominate the total scattering and particles <1μm dominate backscattering; (ii) microorganisms have relatively little contribution to particulate backscattering but dominate the total scattering coefficient in the open ocean; (iii) heterotrophic bacteria are most important backscatterers among microorganisms; and, (iv) submicron detritus may be a major particulate backscatterer in the ocean.

In addition, MOREL and AHN suggest that while algal cells are most important microorganisms for the total scattering coefficient in the oligotrophic ocean, heterotrophic bacteria make considerably less contribution (typically ~14% at 550nm). Such a small contribution of bacteria results from their assumption that these microbes occur at relatively low concentrations, e.g. 2.7 \(10^{11}\) cells m\(^{-3}\) when chlorophyll concentration is 0.1mg m\(^{-3}\). MOREL and AHN rely on the empirical relationship between bacterial abundance and chlorophyll concentration (COLE, FINDLAY and PACE, 1988) which does not include data from waters where Chl a is less than 0.2mg m\(^{-3}\). In our budget, we assert that bacterial abundances in the upper part of the euphotic zone in oligotrophic waters may often be a few-fold higher than those obtained by the extrapolation of COLE, FINDLAY and PACE's regression (see data in FUHRMAN, SLEEGER, CARLSON and PROCTOR, 1989; CHO and AZAM, 1990). Therefore, we feel that the values for the contribution of bacteria to the total scattering coefficient, \(b_p(550)\), in the range of 20 to 40% are both reasonable and common. Such bacterial contributions may often be either comparable or even higher than those attributed to photoautotrophic microorganisms. It must be kept in mind, however, that various scenarios are possible depending on the relative proportions of bacterial and algal abundances. More data from
different regions and times of the year will be needed before it is sensible to make further generalizations about the relative contributions by these microorganisms to light scattering in the open ocean.

In conclusion, we point to three directions that are priorities for future work. First, the spectral scattering and absorption of various categories of microorganisms, such as prochlorophytes, auto-, mixo- and heterotrophs from the nanoplanктон size range, need to be further investigated. The variability of the optical properties with changing physiological status of microorganisms should be included into the experimental framework. Second, the properties of detrital particles, their variability and significance to ocean optics must be characterized more thoroughly. Finally, there should be simultaneous acquisition of in situ data on light scattering and absorption, as well as concentrations and origins of the various categories of particles. When such data become available, there will be a potential for deriving the multi-component, spectral optical description of oceanic particulates, which then can be of more practical value. In addition to absorption, backscattering deserves particular attention because it is also a component necessary for an analysis of satellite ocean colour imagery.

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8. REFERENCES


9. APPENDIX

Significant symbols:

- \( b \) Total scattering coefficient, m\(^{-1}\)
- \( b_b \) Total backscattering coefficient, m\(^{-1}\)
- \( b_p \) Particle scattering coefficient, m\(^{-1}\)
- \( b_{bp} \) Particle backscattering coefficient, m\(^{-1}\)
- \( b_w \) Water scattering coefficient, m\(^{-1}\)
- \( b_{bw} \) Water backscattering coefficient, m\(^{-1}\)
- \( b_j \) Scattering coefficient caused by jth particulate component, m\(^{-1}\)
- \( b_{bj} \) Backscattering coefficient caused by jth particulate component, m\(^{-1}\)
- \( b \) Backscattering ratio
- \( \beta(\theta) \) Total volume scattering function, m\(^{-4}\)sr\(^{-1}\)
- \( C \) Chlorophyll \( a + \) Phaeopigment \( a \) concentration, mg m\(^{-3}\)
- \( D \) Particle diameter, \( \mu m \) or nm
- \( \bar{D} \) Average diameter of particles from a given polydisperse assemblage, \( \mu m^2 \) or nm\(^2\)
- \( F(D) \) Particle size distribution, number of particles per unit volume per micrometer bandwidth
- \( F(D)_j \) Size distribution for the jth particulate component
- \( G \) Average projected-area for particles from a polydisperse assemblage, \( \mu m^2 \) or nm\(^2\)
- \( j \) Subscript used to distinguish a specific assemblage of particles all having the same complex refractive index and obeying a characteristic size distribution
- \( \lambda \) Light wavelength in vacuo, nm.
- \( m \) Complex index of refraction of a particle relative to water
- \( n \) Real part of the refractive index of a particle relative to water
- \( n' \) Imaginary part of the refractive index of a particle relative to water
- \( N_{>D} \) Cumulative size distribution, number of particles with a diameter larger than \( D \) per m\(^3\)
- \( Q_b \) Efficiency factor for light scattering by a particle
- \( Q_{bb} \) Efficiency factor for light backscattering by a particle
- \( Q_b \) Mean efficiency factor for light scattering by a given polydisperse assemblage of particles
- \( Q_{bb} \) Mean efficiency factor for light backscattering by a given polydisperse assemblage of particles
- \( s \) Slope of the size distribution \( F(D) \)
- \( \sigma_b \) Scattering cross-section of a particle, m\(^2\) per particle
- \( \sigma_{bb} \) Backscattering cross-section of a particle, m\(^2\) per particle
- \( \langle \sigma_b \rangle_j \) Mean scattering cross-section for the jth particulate component, m\(^2\) per particle
- \( \langle \sigma_{bb} \rangle_j \) Mean backscattering cross-section for the jth particulate component, m\(^2\) per particle