Scattering properties of the dinoflagellates

Prorocentrum micans and P. minimum

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Abstract: The scattering properties of phytoplankton is one of the main factors needed to model light propagation in the water column. Light scattering by phytoplankton depends on cell size and intracellular materials. In order to characterize the effects, we examined the scattering efficiency of dinoflagellates with large cell sizes and high intracellular carbon contents. Scattering properties of the dinoflagellates Prorocentrum micans and P. minimum were examined in semi-continuous cultures under two light-saturated conditions. Scattering coefficients of the cells at 676 nm \(b_{ph}(676)\) were calculated as the difference between attenuation and absorption coefficients measured using a nine-wavelength absorption-attenuation meter. The \(b_{ph}(676)\) was normalized to the chlorophyll \(a\) (Chl \(a\); \(b_{ph}(676)\)) and cell concentrations \(b_{cell}(676)\). Lower \(b_{ph}(676)\) and higher \(b_{cell}(676)\) were observed for the larger \(P.\) micans compared with the smaller \(P.\) minimum. The \(b_{ph}(676)\) increased with the ratio of cellular carbon to Chl \(a\) \(\beta\) \(C : Chl a\). Both species indicated relatively high \(C : Chl a\) compared to other phytoplankton species. A reverse trend of \(b_{ph}(676)\) and \(b_{cell}(676)\) between the species could reflect a negative relationship between the equivalent spherical diameter \(d\) and intracellular Chl \(a\) content \(\beta\) \(Chl a\). A dimensionless efficiency factor for scattering at 676 nm \(Q_{ph}(676)\) was calculated experimentally from \(d\), Chl \(a\), and \(b_{ph}(676)\). The \(Q_{ph}(676)\) of both species was two-fold higher than theoretical values based on the anomalous diffraction approximation. The experimentally high \(Q_{ph}(676)\) might reflect the high \(b_{ph}(676)\). The significant relationship between \(b_{ph}(676)\) and \(C : Chl a\) suggests that \(C : Chl a\) could be a proxy for scattering efficiency in relation to intracellular materials.

Key words: absorption, ac-9, equivalent spherical diameter, ratio of cellular carbon to chlorophyll \(a\), scattering efficiency

Introduction

Light availability in natural assemblages of phytoplankton in the water column is fundamental to determining primary production. Light availability depends on the propagation of light in the water column and the propagation of light involves the absorption and scattering properties of biogeochemical constituents, including particulate matter. The relationships between particles and absorption or scattering properties are modeled as the “bio-optical state” (Smith & Baker 1978). The bio-optical model was developed based on the empirical relationships between chlorophyll \(a\) (Chl \(a\)) and the absorption coefficient of phytoplankton \(a_{ph}(\lambda)\) (Bricaud et al. 1995) and/or the scattering coefficient of phytoplankton \(b_{ph}(\lambda)\) (Morel & Ahn 1991). The relationships between Chl \(a\) concentration \(a_{ph}(\lambda)\) and \(b_{ph}(\lambda)\) are non-linear due to the geometric characteristics of phytoplankton, such as the cell size (Gordon & Morel 1983, Morel & Bricaud 1986). The relationship between cell size and \(a_{ph}(\lambda)\) and/or \(b_{ph}(\lambda)\) could be interpreted by changes in Chl \(a\)-specific \(a_{ph}(\lambda)\) \(a_{ph}(\lambda)\) and \(b_{ph}(\lambda)\) \(b_{ph}(\lambda)\) (Morel 1987, Ferreira et al. 2013). The \(a_{ph}(\lambda)\) decreases with increasing cell size as a result of the packaging effect of intracellular phytoplankton pigment (e.g., Morel & Bricaud 1981, Berner et al. 1989, Sathyendranath et al. 1989, Finkel 2001, Ciotti et al. 2002, Fujiki & Taguchi 2002). The significant characteristics of \(a_{ph}(\lambda)\) as a function of cell size are applied to distinguish cell class in natural phytoplankton assemblages (Ciotti & Bricaud 2006, Devred et al. 2006, Hirata et al. 2008, Brewin et al. 2011). However, to date, there have been only a few similar applications of the \(b_{ph}(\lambda)\) as a function of cell size (Morel 1987).

Light scattering by large absorptive particles in water...
involves three processes: some of the light is reflected at the external surface, some passes through the particle and undergoes refraction, and some undergoes internal reflection and refraction (Kirk 2011). The scattering process for phytoplankton in water is not only influenced by cell size and refractive or reflective contents, such as intracellular carbon (Cᵢ), but also by absorptive contents, such as intracellular Chl a (Chl a₁) (Stramski 1999). The product of βₑᵃ(aₘ(λ)×Chl a₁) is mainly dependent on the geometric characteristics of the cell, such as cell size, and refractive index (Morel & Bricaud 1986). According to theoretical analysis based on the anomalous diffraction approximation (van de Hulst 1957), the association between the geometric characteristics of the cell, such as cell size, refractive index and absorbance (Morel & Bricaud 1986). Ahn et al. 1992). However, the βₑᵃ(aₘ(590) of the large-celled diatom Chaetoceros lauderi, with a cell diameter of 25.5 μm, was about 3-fold higher than that of the small naked flagellate Isochrysis galbana, with a cell diameter of 4.2 μm, perhaps due to its mineralized cell wall (Morel & Bricaud 1986, Kirk 2011). Dinoflagellates have a large C_i compared with other taxa of a similar cell size, and generally exhibit a high ratio of cellular C to Chl a (C : Chl a) (Chan 1980, Tang 1996). The high C : Chl a is expected to lead to a high βₑᵃ(λ); however their βₑᵃ(λ) as a function of C : Chl a has not yet been evaluated.

In addition to the βₑᵃ(λ) as an index of scattering efficiency, we experimentally calculated the dimensionless efficiency factor for scattering (Qₑ(λ)). The Qₑ(λ) relates scattering efficiency to cell size, and is the ratio of the scattering cross section to the geometrical cross section of the cell (Morel & Bricaud 1986). The Qₑ(λ) as a function of cell size can be theoretically estimated based on the Mie theory when the cell is assumed to be a homogeneous spherical cell (van de Hulst 1957). The Qₑ(λ) could differ large cells have a considerable capacity to modify the propagation of light because of the large scattering cross section per cell (Stramski & Mobley 1997). Most of the large cell species of phytoplankton are diatoms or dinoflagellates (Lalli & Parsons 1997). Diatoms with large cell sizes exhibit experimentally high βₑᵃ(λ). For example, the βₑᵃ(590) of the large-celled diatom Chaetoceros lauderi, with a cell diameter of 25.5 μm, was about 3-fold higher than that of the small naked flagellate Isochrysis galbana, with a cell diameter of 4.2 μm, perhaps due to its mineralized cell wall (Morel & Bricaud 1986, Kirk 2011). Dinoflagellates have a large C_i compared with other taxa of a similar cell size, and generally exhibit a high ratio of cellular C to Chl a (C : Chl a) (Chan 1980, Tang 1996). The high C : Chl a is expected to lead to a high βₑᵃ(λ); however their βₑᵃ(λ) as a function of C : Chl a has not yet been evaluated.

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| Symbol | Definition | Units |
|--------|------------|-------|
| aₑₘ(λ) | Absorption coefficient in suspension measured by ac-9 | m⁻¹ |
| aₑₛ(λ) | Temperature and salinity-corrected absorption coefficient in suspension measured by ac-9 | m⁻¹ |
| aₑₑ(λ) | Absorption coefficient of phytoplankton | m⁻¹ |
| aₑₛ(λ) | Absorption coefficient of reference seawater | m⁻¹ |
| aₑₑ(λ) | Chlorophyll a-specific absorption coefficient of phytoplankton | m² mg Chl a⁻¹ |
| bₑₑ(λ) | Cell specific scattering coefficient of phytoplankton | m² cell⁻¹ |
| bₑₑ(λ) | Scattering coefficient of phytoplankton | m⁻¹ |
| bₑₑ(λ) | Chlorophyll a-specific scattering coefficient of phytoplankton | m² mg Chl a⁻¹ |
| Chl a | Chlorophyll a | - |
| Chl a₁ | Intracellular chlorophyll a content | kg Chl a m⁻³ |
| [Chl a] | Chlorophyll a concentration in medium | mg Chl a m⁻³ |
| C : Chl a | Ratio of cellular carbon to cellular Chl a on a weight basis | g⁻¹ |
| Cᵢ | Intracellular carbon content | kg Carbon m⁻³ |
| cₑₘ(λ) | Attenuation coefficient in suspension measured by ac-9 | m⁻¹ |
| cₑₛ(λ) | Temperature and salinity-corrected attenuation coefficient in suspension measured by ac-9 | m⁻¹ |
| cₑₑ(λ) | Attenuation coefficient of phytoplankton | m⁻¹ |
| cₑₛ(λ) | Attenuation coefficient of reference seawater | m⁻¹ |
| d | Equivalent spherical diameter | μm |
| h | Height of cell | μm |
| l | Length of cell | μm |
| m | Refractive index (relative refraction to water) | - |
| [N] | Cell concentration | cell m⁻³ |
| Qₑ(λ) | Dimensionless efficiency factor for scattering | - |
| t | Width of cell | μm |
| V | Average cell volume in phytoplankton suspension | μm³ cell⁻¹ |
depending on the composition of the intracellular materials 
(Aas 1996), and therefore the \( Q_\lambda (\lambda) \) of the 
dinoflagellates could be high due to their high C : Chl \( a \).

The aim of this study was to investigate the scattering 
properties and C : Chl \( a \) of the different sized 
dinoflagellates \( Prorocentrum micans \) and \( P. minimum \). The 
scattering properties were investigated under two lighting 
conditions, saturated and supra-saturated light. The two 
light intensities could induce differences in C : Chl \( a \) (Ma-
clinty et al. 2002). To evaluate the scattering properties of 
\( P. micans \) and \( P. minimum \), we enumerated the scattering 
coefficients of various phytoplankton species from previous 
sto studies. Scattering properties as a function of C : Chl 
\( a \) could provide a more accurate estimation of the scatter-
ing efficiency of phytoplankton. Scattering properties were 
assessed at 676 nm, where Chl \( a \) was a major cause 
of absorption and Chl \( a \) fluorescence was excited. Error 
due to Chl \( a \) fluorescence emission for the measurement of 
\( b_{\text{ph}} (676) \) should be negligible because emission is mainly 
at 681 nm. The light scattering properties of dinoflagellates 
with different cell sizes and C : Chl \( a \) could provide an 
understanding of the effect of intracellular materials on 
the light scattering efficiency of phytoplankton. Furthermore, 
data on the light scattering properties of phytoplankton as 
a function of cell size or C : Chl \( a \) could assist in the evalua-
tion of light propagation in the water column. A list of 
definitions used in this paper is provided in Table 1.

Materials and Methods

Culture and growth conditions

The dinoflagellates \( Prorocentrum micans \) Ehren-
berg (NIES-218) and \( P. minimum \) Pavillard (NIES-237) 
were obtained from the microbial culture collection at 
the National Institute for Environmental Study (NIES), 
Japan. All cultures were grown in 4L sterilized screw-
top polycarbonate bottles in f/2 medium (Guillard & Ry-
ther 1962), without silicate, using aged filtered seawater 
(temperature \( 20 \degree C \), salinity \( 35 \) \)) collected from Manazu-
rui Bay, Japan. Irradiance of 600 \( \mu \text{mol} \text{ photons m}^{-2} \text{ sec}^{-1} \) (HL) and 300 \( \mu \text{mol} \text{ photons m}^{-2} \text{ sec}^{-1} \) (LL) was provided 
by cool fluorescent lamps (FL40SW; Panasonic Corpora-
tion, Osaka, Japan) on a 12 : 12 h light-dark cycle. To ac-
climate phytoplankton to the growth conditions prior to 
the experiment, the cells were preconditioned in semi-contin-
uous culture by transferring half of the volume every 2 
days. In the middle of the exponential growth phase (usu-
ally day 2), subsamples were taken from each experimental 
bottle at the mid-point of the light phase.

Equivalent spherical diameter

The shapes of \( P. micans \) and \( P. minimum \) were assumed 
to be ellipsoid. The average cell volume \((V; \mu \text{m}^3)\) of 50 
cells was determined by measuring cells under a micro-
scope (LH50A; Olympus, Tokyo, Japan) with an ocular 
ruler, calibrated with a micrometer, and calculated us-
ing the following formula described by Hillebrand et al. 
(1999):

\[
V = (\pi/6)lth
\]  

(1)

where \( l \) is the apical axis (length), \( t \) is the trans-apical axis 
(width), \( h \) is height, and \( \pi \) refers to the circular constant. 
The average \( d (\mu \text{m}) \) was calculated from \( V \), assuming that 
the cells were spherical.

Intracellular Chl \( a \) and C

Subsamples for cellular pigment analysis were filtered 
onto 25 mm Whatman GF/F glass fiber filters and stored 
at \(-80\degree C\) until analysis. The cells collected on the 
filters were homogenized in 2 ml of 90% acetone in a 15 ml cen-
trifuge tube on ice using an ultrasonic homogenizer (UH-
50; SMT Co., Ltd., Tokyo, Japan) and allowed to extract 
in the dark at \(-20\degree C\) for 24 h, as described by Wright et al. 
(1997). The extract was then centrifuged at 1000 rpm for 
5 min and the supernatant was filtered through a 0.20 \( \mu \text{m} \) 
filter unit (Millex-LG; Merck Millipore, Billerica, MA, 
USA). Finally, the extracts were run on a high performance 
liquid chromatography system (168 Diode Array Detecto-
c, C18 reversed-phase Ultrasphere 3 mm column; Beck-
man Coulter Instruments, Inc., Fullerton, CA, USA) using 
a solvent gradient with solvent A (80% methanol and 20% 
0.5M [v/v] ammonium acetate) and solvent B (70% metha-
nol and 30% ethyl acetate), as described by Wright et al. 
(1997). The peaks were quantified using pure Chl \( a \) stan-
dard from the Danish Hydraulic Institute. The Chl \( a \) (kg 
Chl \( a \) \( m^{-3} \)) was estimated by dividing Chl \( a \) concentra-
tion (kg \( m^{-3} \)) by cell volume concentration in phytoplankton 
suspension (m\(^3 \) m\(^{-3} \)).

Subsamples for cellular C analysis were filtered onto 
25 mm Whatman GF/F filters, pre-combusted at 500\degree C 
for 2 h. Cells on the filters were oven-dried at 60\degree C for 24 h 
and stored in a desiccator until analysis. Cellular particu-
late organic C was measured using an elemental analyzer 
(Thermo Fisher Scientific, MA, USA) with reference to ac-
etanilide as the standard (Nagao et al. 2001). The Ci (kg 
C \( m^{-3} \)) was estimated by dividing C concentration (kg \( m^{-3} \)) 
by cell volume concentration in phytoplankton suspension 
(m\(^3 \) m\(^{-3} \)). The C : Chl \( a \) was calculated on a weight basis.

Scattering properties

The absorption and attenuation coefficients of phyto-
plankton at nine wavelengths (412, 440, 488, 510, 532, 555, 
650, 676, and 715 nm) were measured using an absorp-
tion-attenuation meter with a 25 cm path length (ac-9; WET 
Labs, Philomath, OR, USA). The absorption and attenua-
tion coefficient of the phytoplankton suspension was mea-
sured using reflective and non-reflective flow tubes, re-
spectively. The ac-9 was set up as a bench-top instrument 
in a fixed tilt position at 45\degree to avoid trapping air bubbles 
in the flow tubes (WET Labs, Inc. 2013). Two reservoirs 
were attached with tubing to the inlet and outlet of the flow
Scattering properties of the dinoflagellates *Prorocentrum micans* and *P. minimum*

The mean \(d\) indicated an approximately 2-fold difference between the large celled *Prorocentrum micans* and the small celled *P. minimum*, but did not differ between HL and LL within the same species (Table 2). The \(d\) of *P. micans* and *P. minimum* under both light conditions was 25.0 ± 0.22 \(\mu\)m and 12.6 ± 0.24 \(\mu\)m, respectively. The Chl \(a_i\) and \(C_i\) of both species was higher compared with diatoms because the dinoflagellates are significantly more carbon-dense than diatoms (Strathmann 1967, Menden-Deuer & Lessard 2000). Thus the scattering properties of the species are confirmed to be a function of both cell size and intracellular Chl \(a\) and \(C\).

### Results and Discussion

#### Cell size and intracellular Chl \(a\) and \(C\)

The mean \(d\) indicated an approximately 2-fold difference between the large celled *Prorocentrum micans* and the small celled *P. minimum*, but did not differ between HL and LL within the same species (Table 2). The \(d\) of *P. micans* and *P. minimum* under both light conditions was 25.0 ± 0.22 \(\mu\)m and 12.6 ± 0.24 \(\mu\)m, respectively. The Chl \(a_i\) and \(C_i\) of both species was higher compared with diatoms because the dinoflagellates are significantly more carbon-dense than diatoms (Strathmann 1967, Menden-Deuer & Lessard 2000). Thus the scattering properties of the species are confirmed to be a function of both cell size and intracellular materials.

The Chl \(a_i\) of both *P. micans* and *P. minimum* exhibited a 1.5-fold difference between the two light conditions \((p<0.05)\), but the \(C_i\) did not differ between the light conditions (Table 2). The Chl \(a\) \((g\ g^{-1})\) of the small celled *P. minimum* was more strongly influenced by irradiance in terms of the reduction in cellular Chl \(a\) and consequently the 1.7-fold higher C : Chl \(a\) under HL compared with LL \((p<0.001)\). The large celled *P. micans* exhibited a 1.5-fold higher C : Chl \(a\) under HL compared with LL \((p<0.01)\). The dependence of Chl \(a\) on irradiance has been suggested to reflect photoacclimation due to the change in cellular Chl \(a\) content (Geider 1987, MacIntyre et al. 2002). The Chl \(a\) of dinoflagellates is considerably higher compared with other species of a similar cell size (Tang...
Scattering properties

The trend in the $b_{\text{cell}}^{*}(676)$ of the large celled $P$. micans and the small celled $P$. minimum (Table 3) confirms dependence of the $b_{\text{cell}}^{*}(676)$ on cell size, as suggested by Stramski et al. (2001). However, means of the $b_{\text{cell}}^{*}(676)$ for $P$. minimum were 1.4-fold higher than those for $P$. micans under both light conditions ($p < 0.001$, Table 3). The reverse trend of $b_{\text{cell}}^{*}(676)$ and $b_{\text{cell}}^{*}(676)$ with cell volume could reflect the reverse relationship between cell size and Chl $a$ (Augusti 1991). In previous studies, the $b_{\text{cell}}^{*}(676)$ of phytoplankton with $d < 10 \mu m$ has ranged from 0.042 m$^2$ mg Chl $a^{-1}$ for chlorophytes to 0.51 m$^2$ mg Chl $a^{-1}$ for haptophytes, while the $b_{\text{cell}}^{*}(676)$ of phytoplankton with $d > 10 \mu m$ ranged from 0.032 m$^2$ mg Chl $a^{-1}$ for chlorophytes to 0.17 m$^2$ mg Chl $a^{-1}$ for diatoms (Table 4, Fig. 1). The high $b_{\text{cell}}^{*}(676)$ of haptophytes and diatoms could be due to the mineralized cell wall of haptophytes such as coccoliths indicated a higher carbon-specific scattering coefficient than that of the cells themselves (Balch et al. 1996). Although there is no effect due to a mineralized cell wall on the $b_{\text{cell}}^{*}(676)$ of both species under LL was significantly different between those of diatoms and haptophytes of similar or smaller size (Table 4). For the dinoflagellates, the high $b_{\text{cell}}^{*}(676)$ as a function of cell size is presumably due to the high C content.

Table 2. Average ± one standard deviation of $d$, Chl $a$, $C$, and $C: Chl a$ of Prorocentrum micans and $P$. minimum under HL (irradiance of 600 µmol photons m$^{-2}$ sec$^{-1}$) and LL (irradiance of 300 µmol photons m$^{-2}$ sec$^{-1}$). $n$ indicates the number of samples.

Table 3. Average ± one standard deviation of $b_{\text{ph}}^{*}(676)$, $b_{\text{cell}}^{*}(676)$ and $Q_{s}(676)$ of Prorocentrum micans and $P$. minimum under HL (irradiance of 600 µmol photons m$^{-2}$ sec$^{-1}$) and LL (irradiance of 300 µmol photons m$^{-2}$ sec$^{-1}$). $n$ indicates the number of samples.
Table 4. Literature values of optical, biological, and chemical properties of phytoplankton species used to evaluate the dinoflagellates in this study. The $d$, Chl $a$, and $b^a_{ps}(676)$ of phytoplankton species during the exponential growth phase were obtained from Bricaud et al. (1983), Morel & Bricaud (1986), Bricaud et al. (1988), and Ahn et al. (1992). The $d$, Chl $a$, and $b^a_{ps}(676)$ of the chlorophyte Dunaliella tertiolecta under fluctuating high light and constant high light conditions were obtained from Stramski et al. (1993). The $d$, Chl $a$, $b^a_{ps}(676)$, and $C_i$ of the prasinophyte Micromonas pusilla were obtained at two time points, dawn and dusk, from DuRand et al. (2002). The $C_i$ of the other species, except those studied by DuRand et al. (2002), were calculated from the $d$ following Strathmann (1967). The $Q_{st}(676)$ was calculated using the $d$, Chl $a$, and $b^a_{ps}(676)$ using equation (7).

| Class       | Species                        | Irradiance ($\mu$mol photons m$^{-2}$ s$^{-1}$) | $d$ (µm) | Chl $a$ (kg Chl $a$ m$^{-3}$) | $C_i$ : Chl $a$ ($g$ Chl $a^{-1}$) | $b^a_{ps}(676)$ (m$^2$ mg Chl $a^{-1}$) | $Q_{st}(676)$ | References         |
|-------------|--------------------------------|-----------------------------------------------|----------|-----------------------------|---------------------------------|----------------------------------------|----------------|-------------------|
| Haptophyte  | Hymenomonas elongata           | 400                                           | 13.6     | 2.9                         | 132                             | 0.073                                 | 1.94           | Bricaud et al. (1983) |
| Prasinophyte| Platymonas sp.                 | 400                                           | 6.8      | 1.9                         | 175                             | 0.180                                 | 1.53           | Bricaud et al. (1983) |
| Prasinophyte| Tetraxelminis maculata         | 400                                           | 8.5      | 1.6                         | 160                             | 0.169                                 | 1.55           | Bricaud et al. (1983) |
| Haptophyte  | Coccolithus huxleyi            | 400                                           | 3.4      | 1.1                         | 231                             | 0.510                                 | 1.32           | Bricaud et al. (1983) |
| Diatom      | Skeletonema costatum           | 300–400                                       | 5.5      | 0.9                         | 128                             | 0.443                                 | 1.48           | Morel and Bricaud (1986) |
| Prasinophyte| Platymonas suecica             | 300–400                                       | 3.4      | 6.4                         | 232                             | 0.159                                 | 2.27           | Morel and Bricaud (1986) |
| Diatom      | Chaetoceros curvisetum         | 400                                           | 7.5      | 1.4                         | 102                             | 0.216                                 | 1.46           | Bricaud et al. (1988) |
| Diatom      | Chaetoceros lauderi            | 400                                           | 25.5     | 0.3                         | 42                              | 0.168                                 | 0.91           | Bricaud et al. (1988) |
| Haptophyte  | Pavlova pinguis                | 400                                           | 3.6      | 4.3                         | 226                             | 0.136                                 | 1.42           | Bricaud et al. (1988) |
| Haptophyte  | Pavlova luheri                 | 400                                           | 4.5      | 2.6                         | 207                             | 0.314                                 | 2.47           | Bricaud et al. (1988) |
| Haptophyte  | Pyrnesium parvum               | 400                                           | 5.7      | 2.6                         | 188                             | 0.202                                 | 1.97           | Bricaud et al. (1988) |
| Chlorophyte | Dunaliella salina              | 400                                           | 10.2     | 6.2                         | 149                             | 0.032                                 | 1.33           | Bricaud et al. (1988) |
| Red algae   | Porphyridium cruentum          | 400                                           | 4.9      | 4.3                         | 200                             | 0.159                                 | 2.21           | Bricaud et al. (1988) |
| Cyanophyte  | Synechococcus sp.              | 20                                            | 1.6      | 2.2                         | 313                             | 0.095                                 | 0.22           | Bricaud et al. (1988) |
| Cyanophyte  | Synechocystis sp.              | 200                                           | 1.5      | 1.4                         | 321                             | 0.136                                 | 0.20           | Bricaud et al. (1988) |
| Cyanophyte  | Synechocystis sp.              | 16                                            | 1.5      | 2.2                         | 321                             | 0.091                                 | 0.20           | Bricaud et al. (1988) |
| Chlorophyte | Dunaliella bioculata           | 100                                           | 6.7      | 14.1                        | 176                             | 0.042                                 | 2.64           | Ahn et al. (1992)    |
| Haptophyte  | Emiliania huxleyi              | 100                                           | 4.9      | 3.7                         | 199                             | 0.260                                 | 3.19           | Ahn et al. (1992)    |
| Haptophyte  | Isochrysis galbana             | 100                                           | 4.5      | 6.9                         | 207                             | 0.113                                 | 2.30           | Ahn et al. (1992)    |
| Dinoflagellate| Prorocentrum micans           | 100                                           | 27.6     | 2.3                         | 100                             | 0.036                                 | 1.49           | Ahn et al. (1992)    |
| Cryptomonad | Chroococcus fragaroides        | 100                                           | 5.6      | 3.6                         | 190                             | 0.169                                 | 2.24           | Ahn et al. (1992)    |
| Cyanophyte  | Synechococcus sp.              | 100                                           | 1.1      | 2.0                         | 371                             | 0.140                                 | 0.19           | Ahn et al. (1992)    |
| Cyanophyte  | Synechocystis sp.              | 100                                           | 1.4      | 2.5                         | 331                             | 0.203                                 | 0.47           | Ahn et al. (1992)    |
| Cyanophyte  | Anacystimorina                 | 100                                           | 1.4      | 3.4                         | 327                             | 0.160                                 | 0.52           | Ahn et al. (1992)    |
| Chlorophyte | Dunaliella tertiolecta         | 830                                           | 8.3      | 3.2                         | 162                             | 0.075                                 | 1.33           | Stramski et al. (1993) |
| Chlorophyte | Dunaliella tertiolecta         | 790                                           | 7.9      | 3.9                         | 165                             | 0.086                                 | 1.75           | Stramski et al. (1993) |
| Prasinophyte| Micromonas pusilla             | 120                                           | 1.4      | 8.6                         | 262                             | 0.063                                 | 0.52           | DuRand et al. (2002) |
| Prasinophyte| Micromonas pusilla             | 120                                           | 1.8      | 7.7                         | 253                             | 0.088                                 | 0.81           | DuRand et al. (2002) |
| Dinoflagellate| Prorocentrum micans           | 600                                           | 25.1     | 1.2                         | 183                             | 0.142                                 | 2.95           | Present study        |
| Dinoflagellate| Prorocentrum micans           | 300                                           | 24.8     | 1.8                         | 178                             | 0.140                                 | 4.16           | Present study        |
| Dinoflagellate| Prorocentrum minimum           | 600                                           | 12.4     | 1.8                         | 323                             | 0.250                                 | 3.61           | Present study        |
| Dinoflagellate| Prorocentrum minimum           | 300                                           | 12.8     | 2.8                         | 307                             | 0.192                                 | 4.65           | Present study        |

The theoretical $Q_{st}(676)$, based on the anomalous diffraction approximation, indicates oscillations with cell size and convergence to 1 when the dimensionless efficiency factor for absorption at 676 nm converges to 1 (Morel & Bricaud 1986). The experimental $Q_{st}(676)$ in previous studies (Bricaud et al. 1983, Bricaud et al. 1988, Ahn et al. 1992, Stramski et al. 1993, DuRand et al. 2002) was similar to or lower than the theoretical values of the real part of $m=1.06$, which was the average index of pure phytoplankton cultures (Aas 1996). However, the $Q_{st}(676)$ of $P$. micans and $P$. minimum was 2-fold higher than the theoretical values.
for similar cell sizes. When similar cell sizes are compared, the \( Q_b(676) \) could be similar. The high experimental \( Q_b(676) \) suggests that the scattering efficiency in dinoflagellates is not simply the result of cell size or geometrical area and refractive index, but may be the result of complex interactions with cell size, shape and refractive index. Furthermore, the higher experimental \( Q_b(676) \) compared to \( Q_h(676) \) as a function of \( \rho \) suggests that the C : Chl \( a \) implies the potential contribution of natural assemblages of phytoplankton. Furthermore, the relationship between C : Chl \( a \) and the \( Q_h(676) \) can be directly estimated from the scattering properties of phytoplankton, the estimates can provide a more accurate estimation of the physiological properties of natural assemblages of phytoplankton. Furthermore, the relationship between C : Chl \( a \) and the \( Q_h(676) \) may lead to a better understanding of light propagation in phytoplankton assemblages.

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