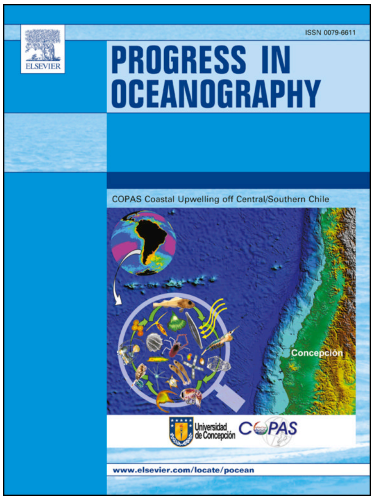

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Light and photosynthetic microalgae: A review of cellular- and molecular-scale optical processes

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Abstract

Light and its interaction with microalgae are essential concerns in the context of microalgae studies. The optical properties of microalgae have a great impact on the remote sensing ocean color, underwater light distribution and biomass accumulation, to mention some areas. A deep understanding of these processes requires knowledge on both the physical light interaction mechanisms with algae, and effects in cellular photophysiology and eventually primary production. Therefore, in this review we comprehensively explain the fundamental physical principles behind microalgae optical properties addressing the multidisciplinary microalgae community. We try to answer what happens with light in the microalgal cell on the cellular and molecular level, and explain the physical mechanisms of light absorption, scattering, fluorescence and diffraction. The current optical cell models that describe the absorbance and scattering properties of microalgae are compared and reviewed. The recent discoveries of the behavior of light in diatom frustules and coccolithophore coccoliths are represented, also showing the special role of these microalgae groups in terms of light interaction. Because microalgae and light are reciprocally interacting, we will briefly also view the photoacclimation and chromatic regulation associated with physical, metabolic and gene transcriptory changes. Finally, predictions and suggestions on the future research directions within oceanography, limnology, remote sensing and aqua culture are provided.

Contents

1. Introduction

Photosynthetic microalgae are one of the oldest life forms on Earth. Microalgae are eukaryotic, unicellular organisms ranging in size from few to hundreds of micrometers. The term 'microalgae' include highly diverse groups such as green algae, diatoms, dinoflagellates, and coccolithophores, and consist of an unknown number of species estimated to be tens or even hundreds of thousands (De Clerck et al. 2013; Guiry 2012; Mata et al. 2010). Microalgae are of vital importance to the Earth's ecosystem. They produce nearly half of the atmospheric oxygen together with cyanobacteria through photosynthesis and, therefore, are an important component of the global carbon cycle by sequestering the atmospheric and water dissolved carbon dioxide (Charpy-Roubaud and Sournia

1990; Field et al. 1998; Sayre 2010). Because of the efficient bio-fixation of CO_2 (conversion rate of CO_2 to organic compounds) there exists a great interest to utilize microalgae in carbon capturing and storage (Sayre 2010). Furthermore, they can be used in wastewater treatment and are of significant commercial interest as a renewable resource for lipids, pigments, hydrogen, proteins, emulsifiers, and gelling agents that are used in industries like pharmacy, bioplastics, nutrition, food, cosmetics, and last but not least, in sustainable energy production (Borowitzka 2013; Brennan and Owende 2010; Chauton et al. 2015; Fon Sing et al. 2013; Hallenbeck and Benemann 2002; Hamed 2016; Mata et al. 2010; Parlevliet and Moheimani 2014). Even the crude oil originates from microalgae and zooplankton sediment.

As being both economically and ecologically important, microalgae research extends over several fields including limnology, oceanography, remote sensing, and aqua-culturing. In all fields, one of the essential parameters are the optical properties of microalgae and the consequent interaction mechanisms with light. For example, interpretation of remote sensing optical signals from oceans relies largely on the knowledge of the optical properties of microalgae (Blondeau-Patissier et al. 2014; Werdell et al. 2013). Light absorption and scattering efficiency of microalgae determine the reflectance from ocean surface detected by satellites. The reflectance data is analyzed by inverse algorithms from which information on the chlorophyll *a* abundance and phytoplankton size distribution can be retrieved and used for predicting primary production, oceanic currents, fish occurrence, and production of greenhouse gases (Brewin et al. 2011; Klemas 2012; Klemas 2013).

Optical properties of microalgae determine the underwater light distribution that directly relates to growth (Bechet et al. 2013; Blanken et al. 2016). In natural waters, microalgae themselves together with water molecules, organic and inorganic compounds as well zooplankton modify the underwater light field via wavelength- and polarization-dependent scattering and via wavelength-dependent absorption (Hancke et al. 2014; Jonasz and Fournier 2007b). Due to these optical interaction processes the polarization properties (Cronin and Marshall 2011; Tonizzo et al. 2009) and the color (Fuente et al. 2017; Kirk 1994; Kuhl and Jorgensen 1994; Lassen et al. 1992; Palmisano et al.

1987) of propagating light are strongly altered. Light becomes partially polarized and loses intensity mostly at the red, yellow, and purple wavelengths when propagating in water.

When light reaches a microalgae cell after having travelled through the medium, the absorption efficiency of the cell together with the spectrum (wavelength dependent intensity distribution) of the incident light field determine the available amount of light for photosynthesis (Dubinsky et al. 1986). Absorbed electromagnetic light energy is then transformed into biochemical energy through photosynthesis, and used for cell respiration, growth and other metabolic processes (Masojidek et al. 2013). Light is often the limiting factor for microalgal growth: If the light intensity is too low, cell respiration consumes the high-carbon compounds at a higher rate than what is produced in photosynthesis and no new biomass is accumulated. On the other hand, if the light intensity is too high, the photo inhibition process in photosystem II produces free radicals leading into photo-oxidative damage and in severe cases, cell death. In addition to light, there are also other abiotic factors affecting microalgae growth including temperature, salinity, nutrients, CO_2, O_2 concentration, pH, and toxic chemicals (Mata et al. 2010).

Before entering the core chapters of this review, let us be reminded of the elementary notion of the wave-particle duality of light. Light is electromagnetic radiation and the duality implies that it can be described both as particles (photons aka light quanta) and as waves. Most of the light interaction phenomena (scattering, absorption, diffraction) in this review are explained by the wave description, whereas the particle description is used for fluorescence. Propagation of electric and magnetic fields and the interaction between them, is rigorously described by Maxwell's equations (Born and Wolf 1959) that are the foundation for mathematical treatment of light. Some of the main optical theories in the context of microalgae studies are derivations of them.

In this review we try to answer the question of what happens to light when it hits microalgae, and briefly also the other way around, how microalgae react to light exposure. The review focuses on the major optical phenomena absorption, scattering, diffraction and fluorescence and how they manifest in and interact with microalgae on molecular, cellular and suspension level. To achieve this, we describe the physics and provide examples of biological significance. Improved mechanistic understanding of light interactions in microalgae may be of use in e.g., bioproduction, treatment of remote sensing data, or modelling of primary production. In an optical sense, microalgae form a class of their own due to their unicellular structure, size range, and the composition of the photosynthetic apparatus, with diatoms and coccolithophorids as special cases due to their frustules and coccoliths. However, the fundamental physical principles represented in this review apply also to other photosynthetic microorganisms such as cyanobacteria, and we hope that this review will serve microalgae explorers across disciplines such as biology, oceanography and physics.

2. Light color and polarization

All the optical processes in microalgae are dependent on the wavelength of the incident light. Visible light covers the wavelengths between approximately 390 nm (violet) to 780 nm (red) of the electromagnetic spectrum, coinciding almost completely with the photosynthetically active radiation (PAR) range (400–700 nm). Different light sources, such as the sun, LED lamp or a fluorescent bulb, all have a unique wavelength-dependent intensity distribution (emission spectrum), see Fig.1. The color of light that finally reaches the microalgae cells is dependent on the spectrum of the light source and on the wavelength-dependent optical properties of the aquatic medium.

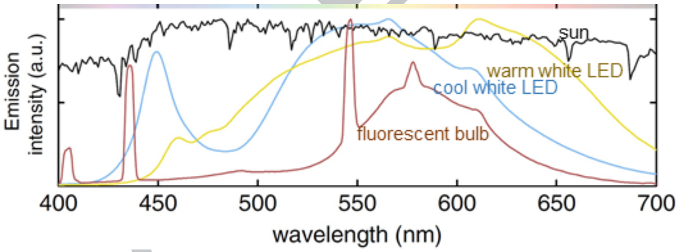


Figure 1. Example of different emission spectra with sunlight (black line) cool white LEDs (blue line), warm white LEDs (yellow line) and fluorescent bulbs (red line). Reproduced from (Ooms et al. 2016) under CC BY 4.0.

Another important characteristic of light is the polarization or "alignment" of the electric field relative to the propagation direction. Generally, the scattering and diffraction properties of microalgae are dependent on the polarization state of the incident light. Reciprocally, the polarization state of underwater light is dependent on the scattering properties of the microalgae. The term *linear* polarization indicates that the electric field of light oscillates on a single plane, which looks like a straight line when viewed along the propagation direction. For *unpolarized* light, the electric field is oscillating on several planes in an irregular manner over time. Underwater light field is predominantly partially linearly polarized (Sabbah and Shashar 2007) and it can be represented in terms of unpolarized and linearly polarized light.

3. Cell and molecular optics

The main electromagnetic interaction mechanisms are determined by the three size regimes: (1) When particles are *much smaller than the wavelength of light* (Rayleigh regime), the interaction can be characterized by scattering and absorption. The angular distribution of scattering is strongly dependent on the polarization state of the incident light (Bohren and Huffman 1983). For unpolarized light, such as the sun and incandescent lamp light, the angular distribution of scattering is approximately isotropic meaning that light is scattered equally backwards and forwards and less normal to the light beam, as depicted in Fig. 2a. Individual molecules fall into this category. (2) When the particle size *approaches the scale of the wavelength* (Mie regime) additional diffraction effects are introduced. The scattering pattern becomes forward peaking, regardless of the polarization state of the incident light, and only a small proportion of light will be backscattered (Fig. 2b). (3) When the diameter of a particle is *much larger than the wavelength* (geometrical or ray optics regime), the wave nature of light can be neglected and the interaction with light can be explained by the classical optical phenomena, refraction and reflection. Many of the larger cell organelles and the cell itself fall somewhere between the Mie and geometrical regimes with contributions from scattering, absorption, diffraction, refraction and reflection. The scattering pattern of algae is strongly forward peaking (Fig. 2c and 2d). Roughly 90 % of the scattered light is usually contained within a solid angle of 20 degrees around the optical axis in forward direction (Dauchet et al. 2015). Note, that the scattered field for unpolarized light (Fig. 2) is the average of the scattered fields for the two orthogonal linearly polarized states (parallel and perpendicular to the plane of incidence).

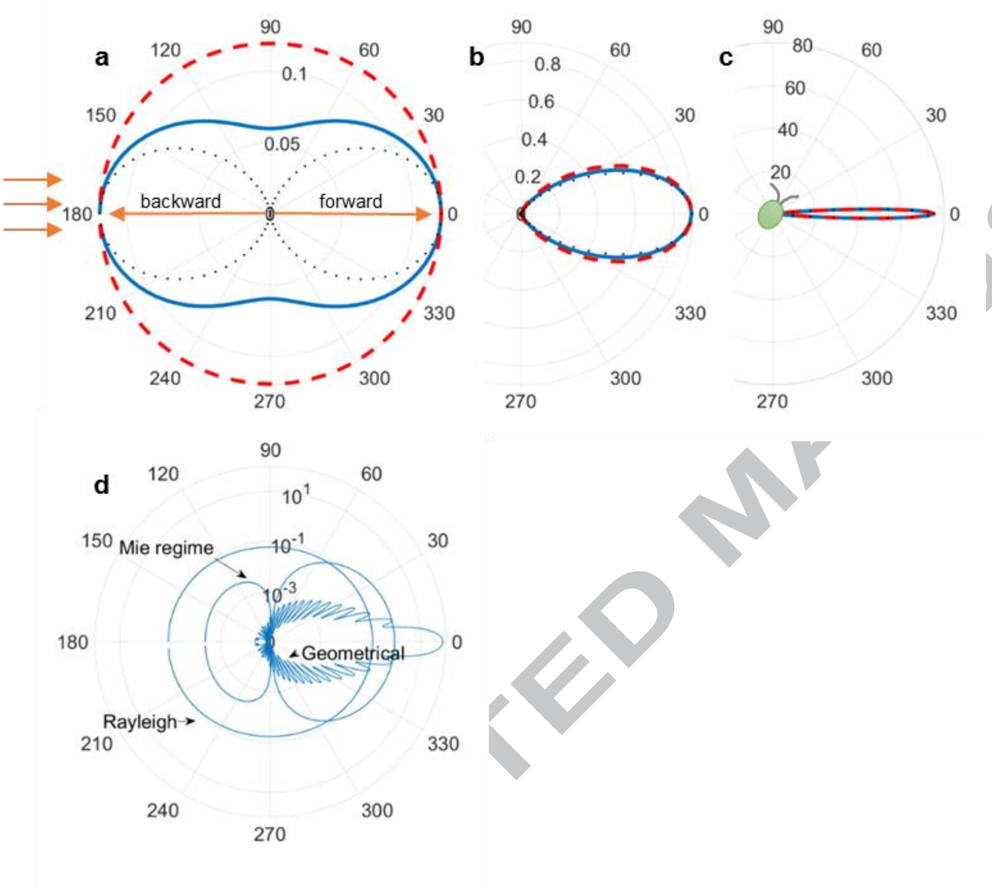


Figure 2. Scattering polar plot for a particle with a diameter of (a) 10 nm (Rayleigh regime), (b) 650 nm (Mie regime), and (c) 5 µm (Geometrical regime) when the refractive index of the particle is 1.37+0.005i and the surrounding medium is water. Solid blue lines represent unpolarized light, dashed red lines perpendicular and dotted black lines parallel linear polarization. (d) shows the logarithmic plot for all the three particle sizes for unpolarized light. Light enters from the left. Particle locates in the origin. Calculated with code available at http://omlc.org/calc/mie_calc.html (access date 24th Jan 2018) created by Scott Prahl.

3.1. Cell constituents

Generally, the optical properties of cell constituents are determined by the wavelength dependent refractive index (see below for explanation), the shape, and as already established above by the size compared to the wavelength. In the Rayleigh regime, particle shape does not contribute significantly to its electromagnetic properties. The shape does not become important until approaching the Mie regime and even at larger scale the importance of shape is less than that of the refractive index (Johnsen and Widder 1999).

The cell consists of several organelles of variable sizes and shapes embedded in the cytosol, e.g., chloroplasts, nucleus, nucleolus, mitochondria, lipid vesicles, gas or fluid filled vacuoles and pyrenoids (Fig. 3). Moreover, each organelle can further be divided into smaller constituents, namely molecules of water, proteins, lipids, pigments, and carbohydrates (Brown and Jeffrey 1992; Dunstan et al. 1992). Cell membranes and a complex cell wall surrounds the cell content. Each of these constituents have their own optical properties, and to which extent these structural details should be taken into consideration when describing the total optical response of the cell, will be clarified in the proceeding text.

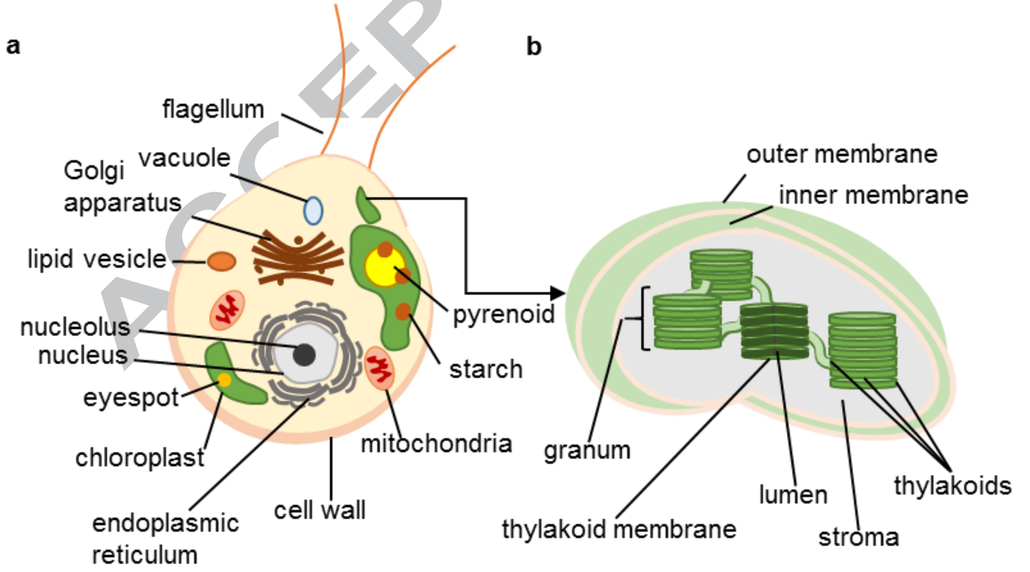


Figure 3. Illustration of (a) algal ultrastructure and (b) chloroplast in exemplified size proportions. Pigments locate on the thylakoid membrane of the chloroplast. The size and numbers of organelles, especially vacuoles and chloroplasts, may vary drastically between microalgae species and cells of the same species.

The several size scales and shapes of cell constituents make the optical modeling of microalgae a challenging task. Fortunately, the concept of complex refractive index brings simplicity in microalgal cell modeling. When molecules are packed close to each other such as in a cell, the mutual distance is much less than the wavelength of light and a destructive interference (the light waves have a phase difference that leads to destruction of each other) cancels the scattering effect of separate molecules (Johnsen and Widder 1999). Consequently, the molecular medium can be considered effectively as homogenous. This eliminates the need for considering the light interaction of individual molecules and we can use the complex refractive index to characterize the molecular medium instead. Even when the molecules are sparsely distributed, their scattering is negligible being a billion times weaker than that of organelles or the cell (Johnsen and Widder 1999). This leaves us with the cell organelles and the cell itself to be dealt with in further optical considerations.

The *real part of the refractive index* contains information on how the speed, direction and wavelength of light changes in the medium (in physics, ‘medium’ refers to the intervening substance). It is proportional to the density of the material. For microalgae the real part seems to relate to the carbon concentration (Jonasz and Fournier 2007a). Microalgae cells consist mostly of water, which has a refractive index of 1.33. Refractive index of different cell organelles varies between approximately 1.36 of cytoplasm to up to 1.51 of the chloroplast and cell wall (Bhowmik and Pilon 2016; Dauchet et al. 2015). At visible wavelengths, the refractive index of primary cellular constituents proteins, carbohydrates and fats are 1.6, 1.53, and 1.46, respectively (Aas 1996).

The imaginary part of the refractive index represents the absorption by the medium. For most of the cell constituents, the imaginary part (also called the extinction coefficient) is close to zero at the visible wavelengths, meaning that the light does not get absorbed. In fact, there is only one category of molecules in microalgae that significantly absorb the visible light – the pigments (Johnsen et al. 2011).

3.2. Absorption by pigments

Plant pigments are the key components in photosynthesis. They act as an antenna by capturing light energy and funneling it into chlorophyll (chl) *a* molecules in the reaction center of the two photosynthetic units photosystem I (PSI) and photosystem II (PSII) (Mirkovic et al. 2017). Three main groups of pigments participate in light harvesting for photosynthesis: chlorophylls, carotenoids and phycobilins. Some carotenoids have a protective role against photodamage in high light intensities, by selectively quenching chl *a* triplet state and thus preventing the formation of singlet oxygen, which is a harmful reactive oxygen species (Faraloni and Torzillo 2017; Koyama et al. 1996).

The most common chlorophylls are chl *a*, chl *b* and chl *c*. Carotenoids include carotenes and a subgroup called xanthophylls that are oxygenated derivatives of carotenes (Jeffrey et al. 2011; Jin et al. 2003). The most common carotenoids are β-carotene, fucoxanthin and peridinin. Phycobilins are found only in the Rhodophyta and Cryptophyta divisions where the most common phycobilins are phycoerythrobilin, phycocyanobilin and allophycocyanin (Haxo et al. 1976; Jeffrey et al. 2011). The absorption of each pigment is strongly dependent on the wavelength of light (Fig. 4). This, together with wavelength selective scattering, gives a color to the algae when viewed with the naked eye. The absorption cross-section of in vivo chl *a* peaks at blue (440 nm) and red (675 nm) wavelengths (Bricaud et al. 1983; Lee et al. 2013; Röttgers et al. 2007). Optical (absorption or scattering) cross-section is the probability that a photon passing through a particle will be absorbed/scattered by that particle multiplied by the average cross-sectional area of the particle.

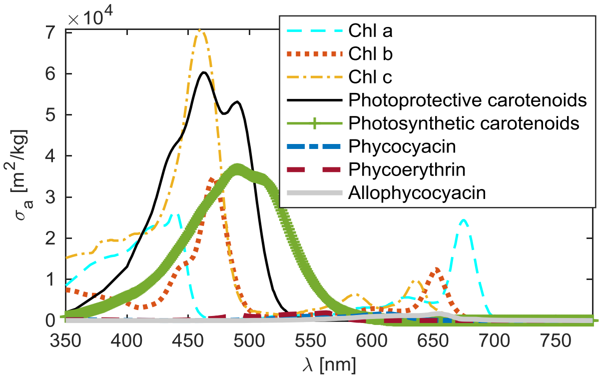


Figure 4: Absorption cross-section spectra of pigments. The spectra are measured for extracted pigments and compensated for the *in vitro* protein-bonding shifts. Data created by (Dauchet et al. 2015) available at http://edstar.lmd.jussieu.fr/databases (access date 24th Jan 2018).

It is important to notice that the *in vivo* absorption properties are different from those *in vitro* i.e., of pigment extracts (Bidigare et al. 1990; Charney and Brackett 1961; Duysens 1956). Inside the cells, pigments are contained in chloroplasts in an intricate molecular environment (see also section 6.1 on molecular plasticity related to acclimation). The reaction center is surrounded by core light harvesting complexes that, in turn, are bound to peripheral light harvesting complexes (Scholes et al. 2011). In the reaction center of PSII, two chl *a* molecules form a dimer called P680 with an absorption peak at 680 nm. PSI also has its own special pair of chl *a* with a slightly red-shifted absorption maximum, P700. Apo-proteins modify the absorption spectra by inducing a red shift and broadening of the absorption peaks (Johnsen and Sakshaug 2007), and in some cases adding complexity to the structure of the spectrum when compared to the absorption spectrum of the same pigments in an organic solvent (Butler 1962; Kirk 2011). The phenomenon is particularly pronounced for carotenoids, for which the redshift can be as large as 40 nm (Bidigare et al. 1990).

Absorption is an *inherent* optical property, but it is not a strictly additive property when pigments are contained within discrete packages. If the size of the microalgae cell is kept constant while increasing the cellular pigment concentration, the absorption does not increase linearly with pigment concentration. In addition, when the pigment concentration is kept constant and the size of the cell increases, the absorption per pigment decreases. This *package effect* is caused by the fact that as the size of any particle (chloroplast, cell) increases, the volume increases faster than the area (Kirk 1975; Morel and Bricaud 1981). This lessens the effectiveness with which the pigments collect light (Kirk 2011) and it is because of the package effect that the *in vivo* chl *a*-specific absorption is always lower than that of homogenous solution of the pigments (Hoepffner and Sathyendranath 1991).

3.3. The fate of non-absorbed light: fluorescence and scattering

Let us again consider the light harvesting by pigments. Absorption of photons excites an electron to an upper state, and energy from the excited electron is transferred from one pigment to another until it reaches the chlorophyll molecules in the reaction center. This energy of the excited electrons is only partially used by photosynthesis. The rest of the energy is dissipated either in the form of heat or by de-excitation to ground-state. The latter *inelastic* scattering process involving de-excitation from singlet state to the ground state, is called *fluorescence*. This process results in emission of a photon having lower energy than the absorbed photon. Fluorescence, heat, and photosynthesis are complementary processes. Therefore, by measuring the yield of chlorophyll fluorescence, information about the changes in the efficiency of photosynthesis and heat dissipation can be gained (Maxwell and Johnson 2000).

The energetic landscape of photosystems is such that only chl *a* molecules fluoresce considerably while other pigments transfer nearly 100 % of the absorbed photons to chl *a* (Babin 2008). A few out of hundred absorbed photons are re-emitted in the form of fluorescence by chl *a* (Mobley 1994). Fluorescence most often occurs between the first excited electron state and the ground state because at higher energies it is more likely that energy will be dissipated through internal conversion and vibrational relaxation into heat. As a result, the fluorescence emission spectrum of a molecule is independent on the excitation wavelength. Chlorophyll always has a major fluorescence band centered around 685 nm *in vivo* and a side band around 730 nm (see figure 7.6. in (Babin 2008)), regardless of the color of the excitation light (Mobley 1994; Suggett et al. 2011). The strength of the fluorescence signal, however, does depend on the excitation wavelength (Mobley 1994). The main and the side bands may be associated with the special pairs P680 and P700 of reaction center II and I, respectively, and also other side bands are known to occur corresponding to different molecular configurations of chl *a* and other pigments (Govindjee and Satoh 1986). In addition, phycoerythrin and phycocyanin fluoresce around 575 nm and 650 nm, respectively (Babin 2008).

The fluorescence radiation pattern is anisotropic for a single molecule at a certain time point. Molecular diffusion, however, is faster than fluorescence kinetics, which averages out the anisotropy. Consequently, in the length scales of standard spectroscopic measurements the fluorescent scattering pattern can be considered isotropic (Mobley 1994). Theoretically, phosphorescence (relaxation of the excited electron via triplet state) is an alternative de-excitation pathway (Hartzler et al. 2014; Sane et al. 1974). To our knowledge, this has so far not been observed for microalgae *in vivo*.

Laws of causality dictate that a change in the amplitude of an electromagnetic field (i.e., energy absorption) is followed by a change in the phase of the field, or *scattering*. This bidirectional connection between amplitude and phase change, or between absorption and scattering, is governed by Kramers-Kronig relations (Kramers 1927; Kronig 1926). Naqvi et al. (2004) showed that Kramers-Kronig relations are applicable to microalgae (Naqvi et al. 2004). They used the relations to derive pigment scattering spectra from measured absorption, and in some cases the scattering spectra of whole cells. Resulting from the causality, peaks in *in vivo* algal absorption spectra are accompanied by fluctuations in the magnitude of scattering (Latimer and Rabinowitch 1959) and, therefore, pigment scattering assumes an asymmetric line shape around the absorption peaks. On the short wavelength (blue) side of the absorption maximum there is a dip, and on the long wavelength (red) side there is a peak (Fig. 5a). A similar relationship is valid for the real and imaginary parts of the refraction index (Bricaud et al. 1983). Around the absorption peak, the refractive index is momentarily increasing along the wavelengths, which is the opposite to the regions where the medium is transparent, and therefore referred as ‘anomalous’ dispersion (Drude 1959; Zaneveld and Kitchen 1995).

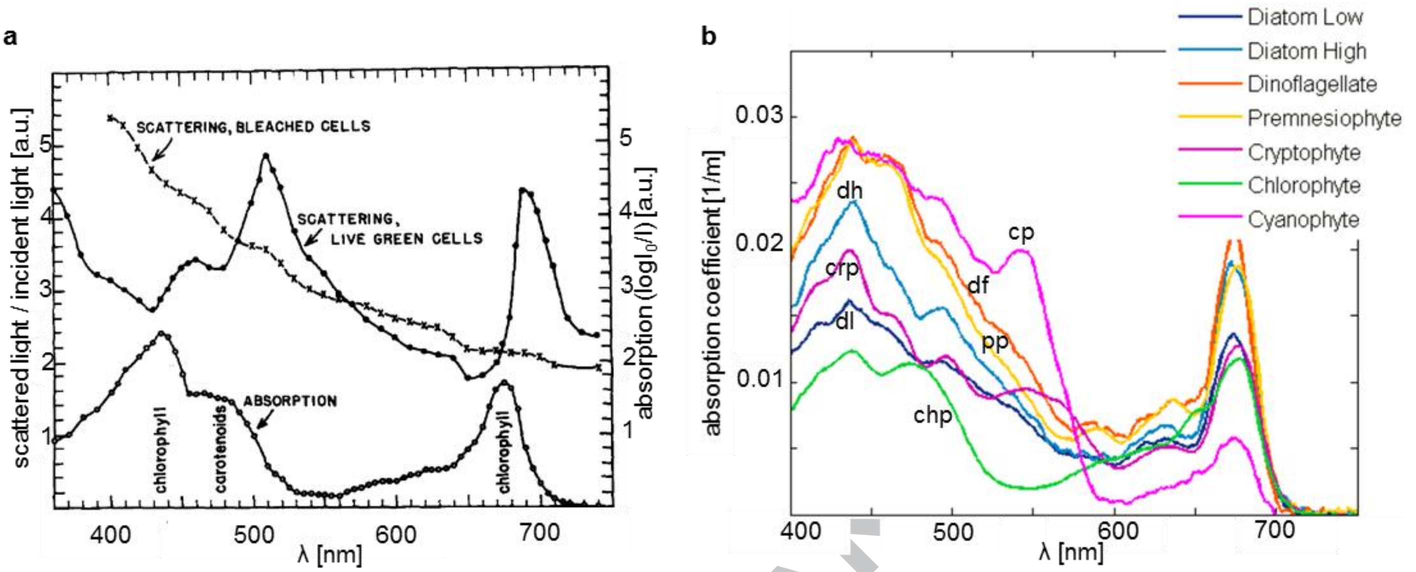


Figure 5. (a) *In vivo* absorption and scattering spectra of suspensions with live cells and cells without pigments (bleached) of green alga *Chlorella pyrenoidosa*. Reprinted from (Latimer and Rabinowitch 1959) Copyright (1959) with permission from Elsevier. (b) *In vivo* absorption spectra for suspensions of several microalgae classes. Reproduced from (Roesler (accessed 24th Jan 2018)), courtesy of Collin Roesler.

3.4. Microalga cell models

As already discussed above, the molecular level is negligible when describing optical properties of microalgae cells if inelastic scattering is left aside. A simple approach is to model the cell as a homogenous sphere having an equal volume to the microalgae cell and consisting of material characterized by the effective complex refractive index (Bricaud and Morel 1986). Then, the optical properties can be calculated using Mie-theory (Mie 1908) that provides an exact solution of Maxwell’s equations in the form of series expansion of spherical waves. For such a model, the imaginary part of the complex refractive index is estimated from measurements of the spectral absorption coefficient (Bricaud and Morel 1986) or from measurements of pigment concentrations (Dauchet et al.

2015). The real part of the refractive index is obtained using dispersion theories such as the Kramers-Kronig relations or other consistent theories (Bricaud and Morel 1986; Dauchet et al. 2015). Dispersion theories are mathematical formulations that describe the wavelength dependent behavior of light, and thus, the relationship between the imaginary and real part of the refractive index. Alternatively, the refractive index can be found by inverse methods from experimental data of absorption and scattering cross-sections (Lee et al. 2013) or hemispherical transmittance and reflectance (Bellini et al. 2014; Qi et al. 2016). Typically, the effective refractive index assumes values of 1.35-1.41 for the real part, and 0.0000-0.01 for the imaginary part depending on the wavelength and species (Bricaud and Morel 1986; Lee et al. 2013; Qi et al. 2016; Stramski et al. 2001; Stramski and Mobley 1997). Because their refractive index is close to that of the surrounding aquatic medium, the microalgae cells are called optically soft particles.

The often used homogenous sphere model is simple and numerically effective yet lacks accuracy. The model is often sufficient in predicting absorption (Quirantes and Bernard 2004; Quirantes and Bernard 2006) but it underestimates the strength of backscattered light resulting in inaccurate angular scattering distribution (Gordon and Du 2001; Whitmire et al. 2010). The model is also insufficient in describing polarization properties of the scatted field. Two approaches have been suggested as a remedy for the poor backscattering predictions:

(1) Accounting for the cell heterogeneity by using sphere models with two or three layers that represent the optically most significant cell parts: the cell wall, chloroplast, and cytoplasm (Bellini et al. 2016; Bhowmik and Pilon 2016; Kandilian et al. 2016; Kitchen and Zaneveld 1992; Quirantes and Bernard 2004; Quirantes and Bernard 2006) (Table I). The coated sphere model is an improvement to the homogenous sphere model as it gives higher backscattering. Wu et al. noticed that the bare cell and nucleus dominate cell light scattering in the forward direction whereas subcellular structures, which were modelled as fractal continuous random medium, strongly affected the large angle scattering (Wu et al. 2007). The T-matrix method (Mishchenko et al. 2010; Waterman 1973) can be used for more detailed description of the microalgae cell. Bhowmik and Pilon (Bhowmik and Pilon

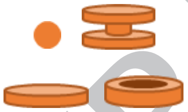
2016) distinguished the most relevant cell parts (nucleus, cytoplasm, mitochondria, cell wall, chloroplast and plasma membrane) and even accounted for metabolites such as lipid droplets and starch by using the T-matrix method. The model rendered optical properties that were consistent with experimental data.

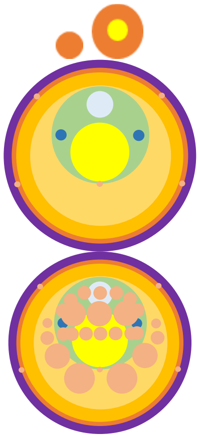
(2) Accounting for the shape (Table I): The spherical models have been used for microalgae species with rather spherical shape, including *Chlamydomonas reinhardtii, Chlorella vulgaris,* and *Aureococcus anophagefferens.* For species with more complex shape, the spherical models are not valid anymore (Clavano et al. 2007; Dauchet et al. 2015). Dauchet et al. compared the transmittance of prokaryotic cyanobacteria *Rhodospirillum rubrum*, *Arthrospira platensis* and eukaryotic microalga *Chlamydomonas reinhardtii* obtained from either spheroidal or cylinder models resembling actual cell shapes, or equivalent-volume spheres. In two out of three cases, models that considered the shape gave results that were closer to the experimental ones, compared to using a simple sphere approximation. In the third case, both the models and experiments gave similar results. As with the cell heterogeneity, the impact of shape is most prominent for backscattered light (Gibbs 1978; Gordon 2011). Near the forward direction, where the scattering is dominated by diffraction, non-spherical particles scatter similarly to area-equivalent spheres in general (Bohren and Huffman 1983). Gordon and Du concluded that multiple reflections within the particles makes the backscattering sensitive to shape in coccoliths of *Emiliania huxleyi* (Gordon and Du 2001). So far, to our knowledge, there are no studies where both the inner structure and the shape of the cell are included to the model when describing algal cells with complex shapes.

Table I: Illustration of microalga optical models and optical quantities compared with experiments. The model sizes are not proportional. Explanation for symbols:

λ=wavelength of light, θ = scattering angle, T = transmittance, T_{nh} = normal–hemispheric transmittance, R_{rs} = remote sensing reflectance, Q_a, Q_b, Q_c, Q_{bb} = efficiency factors (product of corresponding cross-section and geometrical cross-section of the particle) for absorption, scattering, extinction and backscattering, σ_a, σ_b, σ_c, σ_{bb} =

cross sections for absorption, scattering, extinction and backscattering, SPF = scattering phase function, VSF = volume scattering function (product of SPF and total scattering coefficient).

Reference	**Species**	**Model**	**Quantity compared with experiments**
Bricaud and Morel, 1986	*Platymonas suecica*		$Q_a(\lambda)$, $Q_b(\lambda)$, $Q_c(\lambda)$, $Q_{bb}(\lambda)$
”	*Skeletonema costatum*		$Q_a(\lambda)$, $Q_b(\lambda)$, $Q_c(\lambda)$, $Q_{bb}(\lambda)$
”	*Emiliana huxleyi*		$Q_a(\lambda)$, $Q_b(\lambda)$, $Q_c(\lambda)$, $Q_{bb}(\lambda)$
Kitchen and Zaneveld, 1992	Phytoplankton in Pacific central gyre		VSF(θ)
Gordon and Du, 2001	*Emiliana huxleyi coccoliths*		$\sigma_b(\lambda=550nm)$, $\sigma_{bb}(\lambda=550nm)$
Quirantes and Bernard, 2004	general marine algae		–
Quirantes and Bernard, 2006	*Aureococcus anophagefferens*		$R_{rs}(\lambda)$
Clavano et al., 2007	general marine-like particles		–
Dauchet et al., 2015	*Chlamydomonas reinhardtii*		T(λ)
Kandilian et al., 2016	*Chlamydomonas reinhardtii*		SPF(θ), $\sigma_a(\lambda)$, $\sigma_c(\lambda)$ $T_{nh}(\lambda)$
”	*Chlorella vulgaris*		SPF(θ), $\sigma_a(\lambda)$, $\sigma_c(\lambda)$, $T_{nh}(\lambda)$

Bhowmik and Pilon, 2016	*Chlorella vulgaris*		–
Bellini et al., 2016	*Isochrysis galbana*		T(λ)
”	*Phaeodactylum tricornutum*		T(λ)

4. Optics of cell suspensions

Until now, we have gone through the optical properties of the individual microalgae cells. Microalgae in suspension can be considered as a random distribution of discrete absorbing scatterers and the mathematical description of light propagation can be dealt with the radiative transport theory (sometimes called radiation transfer theory) (Ishimaru 1991; Pilon et al. 2011). By modeling the light propagation, one can predict the underwater light distribution. Radiative transport theory was considered to be a heuristic theory for decades until it was derived for the first time from electromagnetic Maxwell's equations (Mishchenko 2008). Transport theory regards a discrete medium as effectively homogenous and describes the transport of light power through the medium by effective scattering and absorption coefficients, and by the effective scattering phase function. The parameters can be determined by numerical simulations based on the above described optical models, or experimentally.

Owing to the broad absorption peak of pigment-protein complexes and the overlapping of different pigment-protein absorption spectra, total absorption of the algae cell is a continuous function extending over the whole PAR region (Johnsen et al. 2011). Absorption spectra can be represented as a sum of Gaussian curves that correspond to the absorption bands of individual pigment classes (Hoepffner and Sathyendranath 1991), or the other way around, absorption spectra can be decomposed into absorption peaks of pigments by taking the fourth derivative of the total absorption spectrum (Aguirre-Gomez et al. 1995). The pigment content of individual cells is a highly dynamic variable, and cell-specific absorption is therefore affected by environmental factors such as nutrition, light quality and growth phase (Jeffrey et al. 2011). Pigment composition varies between phylogenetic groups and leads to differences between them in the *in vivo* absorption spectra (Fig 5b). This has been exploited as a tool (CHEMTAX) to identify phylogenetic groups from pigment samples (Mackey et al. 1996).

For microalgae in general, light scattering is higher than absorption efficiency by up to one order of magnitude (Ahn et al. 1992; Berberoglu et al. 2009; Merzlyak et al. 2008; Privoznik et al. 1978; Stramski and Mobley 1997). The *in vivo* scattering spectrum has contribution from all cell organelles. The non-absorbing components display a scattering spectrum that is monotonically decreasing as a function of wavelength from blue to red following the normal dispersion (Fig. 5a, bleached cells). Pigments, on the other hand, exhibit a strong wavelength-selectivity in their scattering spectrum (Charney and Brackett 1961; Latimer and Rabinowitch 1959), as demonstrated in Fig. 5a (live green cells). The dips and peaks in the scattering spectra are associated with absorption peaks within the framework of anomalous dispersion and Kramers-Kronig relations. Absorption and scattering properties of the cells in suspensions change depending on the refractive index of the surrounding medium. Typically, when the experimental results for absorption and scattering are represented, the contribution of the medium (fresh or saltwater with nutrients) has been removed by normalizing the scattering / absorption to that of medium. In principle, the absorption and scattering cross-sections of algal cells are different in seawater, by a very small amount, than in freshwater.

The scattering phase function describes the angular distribution of scattering at a given wavelength. Scattering phase function is mathematically defined as

$$\bar{\beta}(\theta,\lambda) = \frac{\mathrm{d}\,\Phi\,(\theta,\lambda)/\mathrm{d}\omega}{\frac{\Phi_0}{\mathrm{d}S}\,\mathrm{d}V\beta(\lambda)}$$

where $\Phi(\theta,\lambda)$ is the radiation flux (scattered energy per unit time [W]) into a direction of θ at a wavelength of λ, $\mathrm{d}\omega$ is the solid angle element, Φ_0 is the radiation flux incident on an area element $\mathrm{d}S$, $\mathrm{d}V$ is the volume element, and $\beta(\lambda)$ is the total scattering integrated over all angles (Kirk 2011). Scattering is azimuthally symmetric for suspensions with spherical cells and for suspensions with randomly oriented non-spherical cells (Clavano et al. 2007). The scattering phase function (Fig. 6) exhibits similar structure as the theoretical calculations in Fig. 2c and 2d, i.e., peaking in the forward direction and having a broad minimum at the sideward-angles. Oscillating resonance structures (seen in Fig. 2d) are not present in natural samples due to the polydispersity and non-spherical nature of the cells. Scattering strength can vary up to five orders of magnitude between the small and medium angles (Kandilian et al. 2016; Svensen et al. 2007; Zugger et al. 2008). The backscattering ratio of algal cells, a quantity of special importance in remote sensing, is typically < 3 % and often two or three orders of magnitude lower than the total scattered light (Ahn et al. 1992; Vaillancourt et al. 2004; Whitmire et al. 2010).

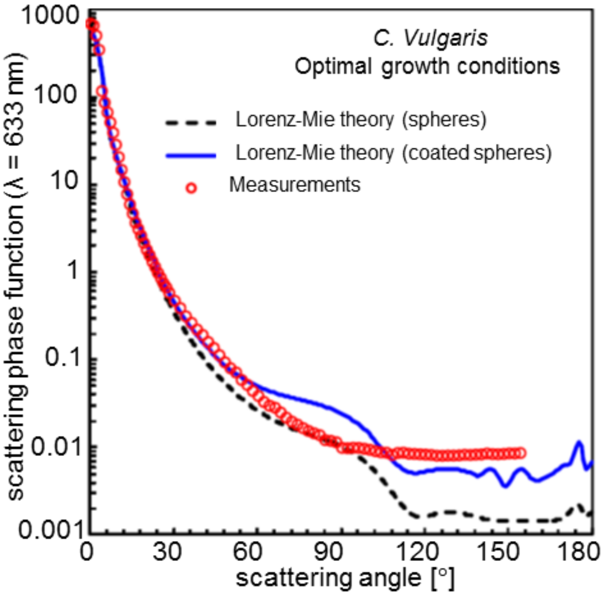


Figure 6. Scattering phase function for *Chlorella vulgaris*. Reprinted from (Kandilian et al. 2016) with permission from Elsevier.

Scattering phase functions measured for microalgae are almost always reported for unpolarized incident light. In nature, however, light reaching microalgae is not unpolarized as water and atmosphere modify the phase and amplitude of the electromagnetic field (Cronin and Marshall 2011; Kattawar et al. 2014). The dependence of scattering on polarization is described by the Müller matrix formalism: Müller matrix (**M**) is a 16-element matrix that transforms the incident electromagnetic field, represented by Stokes vector (**S**), into scattered electromagnetic field (**S**'=**MS**) in the vector form. In other words, the Müller matrix describes interaction of the sample upon light. For randomly oriented particles, the Müller matrix is of the form (Witkowski et al. 1998)

$$M = \begin{vmatrix} M_{11} & M_{12} & M_{13} & M_{14} \\ M_{12} & M_{22} & M_{23} & M_{24} \\ -M_{13} & -M_{23} & M_{33} & M_{34} \\ M_{14} & M_{24} & -M_{34} & M_{44} \end{vmatrix}.$$

Müller matrix is measured by determining the polarization for scattered light as a function of angle for varied input polarizations. Compared to the volume scattering function, Müller matrix of microalgae suspension contains more detailed information on the inner structure, size and shape of the cells (Quinby-Hunt et al. 1989; Witkowski et al. 1998; Witkowski et al. 1993; Volten et al. 1998). It has been shown that the elements M34, and M11 are sensitive to the size of the algae (Quinby-Hunt et al. 1989), the difference M22-M11 to the shape (Quinby-Hunt et al. 1989), and the elements M11, M12, M34 to the inner cellular structure (Quinby-Hunt et al. 1989; Witkowski et al. 1993; Volten et al. 1998). In addition, Witkowski et al (Witkowski et al. 1998) measured all elements of the Müller matrix and observed optical activity (or rotation of linearly polarized light) indicated by non-zero readings for M13, M14 and M24. Optical activity is caused by chirality in the system. An object is chiral when it is non-superimposable on its mirror image. In the case of algae, chirality could be a consequence of the organization of the inner structure in an asymmetric manner or of the chirality of the cell compartments themselves. Optical activity in biological system is not surprising, as nearly all molecules synthesized by living organisms are chiral (Smith 1989). The non-zero values were recorded for *Chlorella vulgaris* and *Chlorella kesleri* but not for *Chrococcus minor*, which indicates that the polarization properties may be dependent on the species or phylogenetic group.

5. Light diffraction in frustules and coccoliths

Over time, diatoms and coccolithophores have evolved sophisticated casings that are considered to function as a protection against grazers and pathogens and for buoyancy control (Borowitzka 2016; Young 1987). The casings might also have an evolutionary role in light manipulation. In the following, we will discuss the optical properties and photonic effects that make diatoms and coccolithophores a special group amongst microalgae. The photonic effects can be explained by light diffraction, which essentially is the interference of scattered light fields.

5.1. Diatoms

Diatoms carry a hard casing, called the frustule, consisting of hydrated silica (SiO2·2H2O) and organic material (protein, lipids, and carbohydrates) (Lopez et al. 2005; Tesson et al. 2009). It is generally thought that the frustule is of amorphous allotropic form, yet at least one species is reported to possess a crystalline structure (Goswami et al. 2012). The diatom frustule comprises two opposite halves with slightly different diameters so that they fall within each other, like the cover and bottom of a petri dish, enclosing the cell protoplasm inside. The frustule is patterned with quasi-periodic nano- and micro pores (aerola) and chambers between different SiO_2 layers, creating structural complexity that exceeds the capabilities of the modern nanofabrication techniques (Fig. 7). Diatoms are classified by the symmetry of the valve and spatial distribution of areolae into centric (radial symmetry) and pennate diatoms (usually bilateral symmetry). The shape and patterns of the valves are genetically determined, but environmental factors such as light, temperature, salinity and silicon availability will affect the final result.

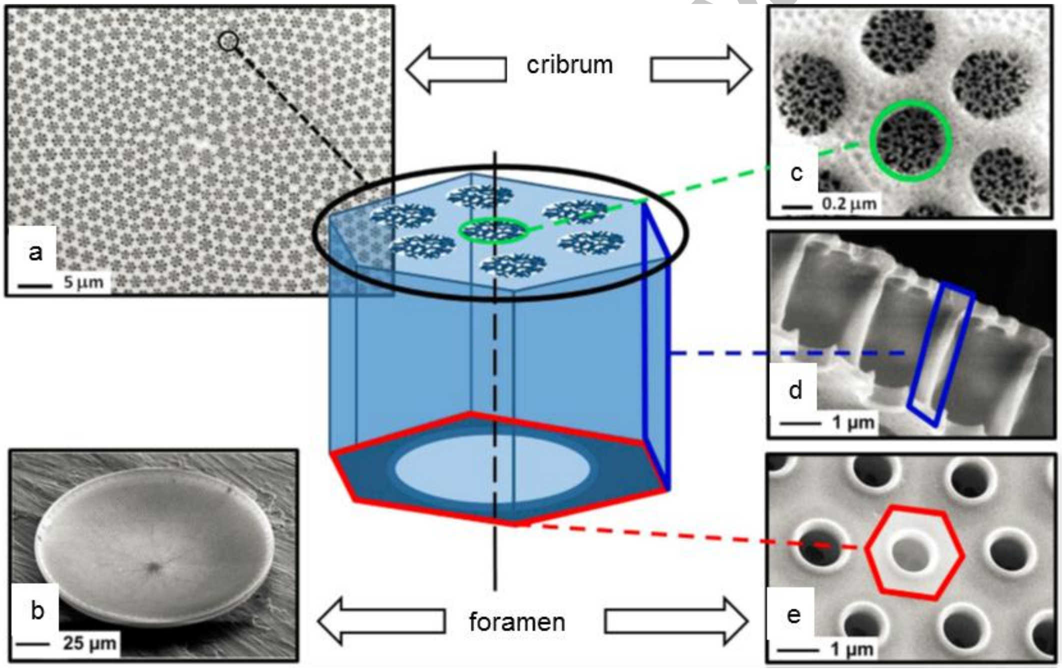


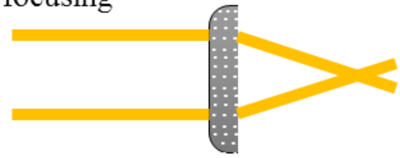
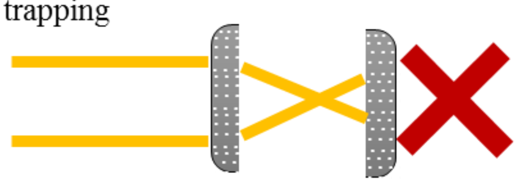
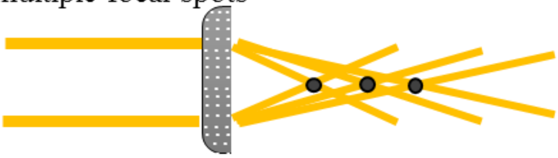
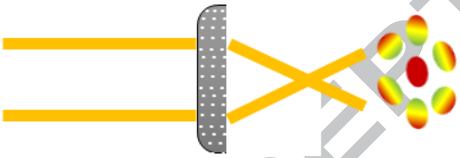
Figure 7. The micro- and nanostructures present in *Coscinodiscus centralis* valve and corresponding SEM images of (a) outer (cribrum) side of the valve, (b) interior (foramen) side pointing upwards, (c) details of cribrum, (d) areola side walls, and (e) foramen. Reproduced from (Romann et al. 2015a) under CC BY 4.0.

Being phototrophs, diatoms depend on light transport through the frustule and cytoplasm into the chloroplasts. The frustule is in principle glass-like being transparent to visible light. However, due to the size scale of rib and areola patterning, which is in the order of the wavelength of light, it interacts with light in a nontrivial manner. Indeed, the patterns induce modulation of light passing through the frustule, leading to phenomena such as transmission with strong wavelength dependency, light focusing, and light trapping. The transmission of light through the frustules cannot be interpreted by means of geometrical optics (refraction). Instead, a diffraction theory approach is implemented for accurate explanation of such effects (Di Caprio et al. 2014; Kieu et al. 2014; Noyes et al. 2008).

The light focusing effect was discovered by De Stefano et al. (De Stefano et al. 2007) in experiments with *Coscinodiscus wailesii*. They observed that when a red laser light (at 785 nm) was transmitted through a cleaned valve from the external (cribrum) side, the beam was focused at a distance of 104 µm from the valve. Later, the same focusing effect was confirmed by others (De Tommasi et al. 2010; Ferrara et al. 2014; Maibohm et al. 2015; Romann et al. 2015a; Romann et al. 2015b). In the opposite event, when light was incident from the interior (foramen) side, a major reduction in the transmittance was observed (Romann et al. 2015a; Romann et al. 2015b). Hence, light radiating in direction outwards of the valve is assumably reflected back towards the light source leading to a situation where light is trapped inside the cell. De Tommasi et al. showed that using structured light field (optical eigenmode decomposition) the spot size of the focused light can be squeezed under the diffraction limit of light (De Tommasi et al. 2014). Illustration and summary of the photonic phenomena in diatom frustules is given in Table II.

The focusing phenomenon can be explained by a constructive interference of scattered beams by the holes of the frustule (De Tommasi et al. 2010; Maibohm et al. 2015). In other words, it is a consequence of diffraction of light by the quasi-periodic structure. In some species instead of forming a singular focal point, light interferes constructively in a series (or a 'train') of hot spots on the optical axis of the valve, independent of the light incident angle (Ferrara et al. 2014; Maibohm et al. 2015; Romann et al. 2015b) (see Table II). The distance of the focal point from the valve depends on the pore distribution, on their diameter and mutual distance as well as on the wavelength of the illuminating light. Interestingly, for the short (UV/Blue) wavelengths, which are harmful for living cells, all the interference points occur far away from the valve outside the cell, as opposed to longer wavelengths (red) that are focused closer to the cell (De Tommasi et al. 2010; Ferrara et al. 2014; Maibohm et al. 2015).

Table II. Experimentally demonstrated photonic phenomena. All experiments have been conducted for centric diatoms.

Phenomenon	**Reference**
focusing 	De Tommasi et al., 2014 Romann et al., 2015a[a] Romann et al., 2015b[a] De Tommasi et al., 2010[a] De Stefano et al., 2007
trapping 	Romann et al., 2015a[a] Romann et al., 2015b
multiple focal spots 	Romann et al., 2015b[a] Ferrara et al., 2014 Maibohm et al., 2015
waveguiding 	Noyes et al., 2008 Fuhrmann et al., 2004[a]
diffraction pattern 	Noyes et al., 2008 Kieu at al., 2014

[a] Light source is less coherent broadband lamp. In other cases, the light source is laser.

The transmission of light through the frustules is strongly dependent on the wavelength of light (Kieu et al. 2014; Noyes et al. 2008; Romann et al. 2015a). It has been theoretically predicted that frustules could support band gaps, similarly to photonic crystals (Fuhrmann et al. 2004; Yamanaka et al. 2008), leading to a filtration of certain narrow wavelength bands. Alternatively, light could be coupled to the wave-guide modes of the frustule walls (Noyes et al. 2008; Romann et al. 2015a) and gradually leak out from the walls. In ref. (Noyes et al. 2008) red light was observed to have 80 % transmission, which was significantly higher than that for blue (22 %) and green (29 %). They estimated that the majority of the remaining 20 % of red light was reflected by the valve surface and a small portion (< 5 %) of the undetected red light was coupled to a wave-guide mode subsequently emerging outside the collection angle.

A high transfer efficiency of red wavelengths is consistent with the absorption bands of chlorophylls and photosystem reaction centers *in vivo*, and the wave-guide modes of the frustule could offer an opportunity to couple travelling light to chloroplasts located next to the cell wall. Interestingly, light quality dependent migration of chloroplasts toward the cortical cytoplasm was seen in the centric diatom *Pleurosira laevis* in green light (Shihira-Ishikawa et al. 2007) and in weak intensity white light (Di Caprio et al. 2014; Furukawa et al. 1998). Another noteworthy optical phenomenon regarding the diatom frustules is the photoluminescence. Diatom frustules are reported to emit blue or green light when excited by UV-light (Butcher et al. 2005; Goswami et al. 2012; Mazumder et al. 2010; Qin et al. 2008). More reading about diatom optics and their photonic application is found in ref. (De Tommasi 2016) and about diatom UV-optics in ref. (Ellegaard et al. 2016).

5.2. Coccolithophores

Coccolithophores are distinguished by having crystalline calcite ($CaCO_3$) plates, or scales, called coccoliths (Hagino and Young 2015). Initially, the coccoliths are attached to the cell wall but they drop off especially when growth ceases. Similarly to diatom valves, coccoliths have a regular nanopatterning (Fig. 8) whose purpose has not yet been fully understood (Paasche 2001).

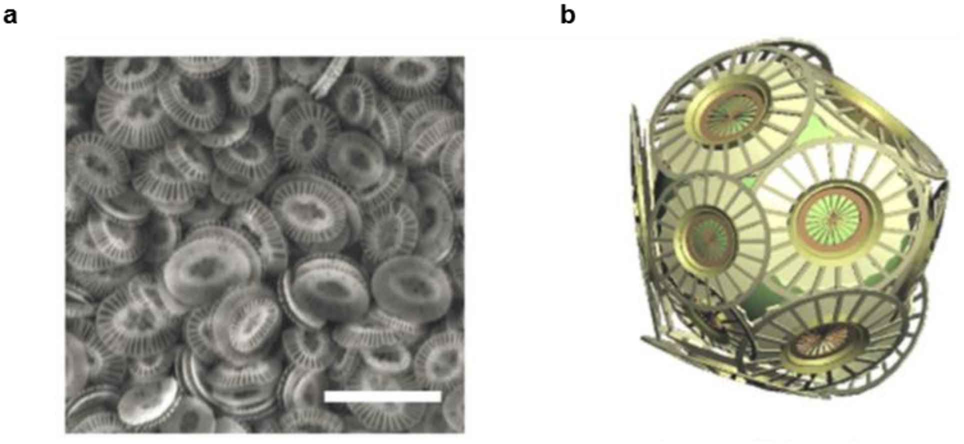


Figure 8. (a) SEM image of coccoliths of *Emiliania huxleyi* and a (b) model for coccolithophore *Emiliania huxleyi*. Bar length is 5 μm. Reproduced from (Mizukawa et al. 2015) under CC BY 4.0.

Calcium carbonate is a birefringent material, meaning that the optical properties are dependent on the direction of light propagation and polarization (Gordon and Du 2001). The refractive index of calcium carbonate is relatively high (n = 1.64, (Fournier and Neukermans 2017)), making the coccoliths strong light scatterers in water. The strength of scattering of an individual coccolith is dependent on its orientation (Mizukawa et al. 2015). In natural waters the randomly oriented coccoliths form “white” waters during the bloom (Tyrrell et al. 1999). Indeed, the scattering leads to bright surface waters and reduced penetration of light into deeper water (Balch et al. 1996; Tyrrell et al. 1999), which shades the competing species from growing in deeper layers (Hovland et al. 2014).

One of the purposes for the regular patterning might be mitigation of UV-induced stress. Xu *et al.* (Xu et al. 2016) reported 3.5 higher growth rates of calcified *Emiliania Huxleyi* cells compared to naked cells when exposed to outdoor conditions. Quirento-Torres et al. modelled the back-scattering properties of *Calcidiscus leptoporus* and *Helicosphaera carteri* and concluded that the periodical nano-structures increased the scattering of UV-light compared to a similar amorphous structure (Quintero-Torres et al. 2006). In addition, the periodicity seemed to reduce the back-scattering of PAR light. However, the nanopatterning is not always essential for the high backscattering, especially for structures with dimensions smaller than the wavelength of light (Gordon 2006). Hence, coccoliths with sub-wavelength structures may have more important role in the management of UV rather than visible light.

6. Photoacclimation and chromatic regulation

Microalgal cells react to variations in light on transcriptional, physiological and metabolic levels, which further manifests as a change in optical properties and photosynthetic capacity of the cell. The series of adjustments in the cell as a response to the change in light intensity or color are referred to as photoacclimation or chromatic acclimation, respectively. The term *acclimation* refers to a phenotypic response and it occurs within minutes or hours. In studies regarding color of light, it often remains unclear whether the cell exhibits phenotypic or genotypic response. In the latter case, chromatic *adaptation* corresponding to evolutionary time scales would be the correct term. For this reason, we have decided to use the term chromatic *regulation* to indicate the possibility that both chromatic adaptation and acclimation may occur. We would also like to note, that the physics term *intensity* is here the same as irradiance in radiometry, with a unit [W/m^2] that can be converted to [photons / m^{2}s].

Photoacclimation and chromatic regulation are dynamic changes, with time-scales from minutes to days. That may inflict problems for an experimentalist measuring the light-dependent radiative properties of algae by optical means, or in remote sensing where the interpretation of the backscattered signal depends on the time of the day. On the other hand, acclimation offers an opportunity for light-controlled modifications in, for example, adjusting the metabolic composition in the context of aqua-culturing or tailoring the morphology for photonic applications.

6.1. Intensity

The natural day-night cycle (diel) and the following change in light intensity concurs with cyclic variations in the phytoplankton pigmentation and cell diameter (Fig. 9). Stramski and Reynolds (Stramski and Reynolds 1993) reported the cellular chl *a* amount increasing towards the end of the bright period and a decreasing during the dark period (night) for the marine diatom *Thalassiosira pseudonana*. The cell diameter reached a maximum around noon and minimum during the night. Mercado et al. found similar trends for chl *a* in field studies in the Alborán Sea (Mercado et al. 2006). Phytoplankton pigment concentration and cell size can vary by as much as about 100 % during the day (Mas et al. 2008; Stramski and Reynolds 1993).

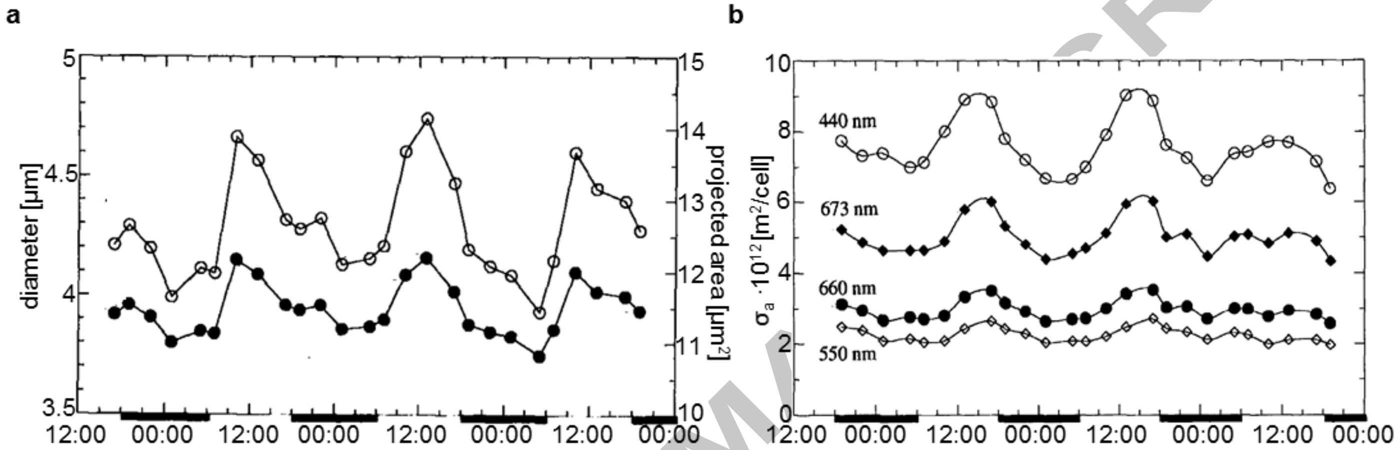


Figure 9. Diel variations in *Thalassiosira pseudonana*. (a) Mean cell diameter (white circles) and projected cell area (black circles) and (b) absorption cross-section at indicated wavelengths. Black bars on the time axis indicate darkness. Reproduced from (Stramski and Reynolds 1993), with permission from Wiley.

Diurnal changes have a direct impact on the complex refractive index and consequently on the absorption and scattering properties of the cells (Fig. 9b). The absorption cross-section was greatest in the afternoon and lowest during the night in papers by (Ohi et al. 2002; Stramski and Reynolds 1993). The scattering cross-section had a daytime maximum and a minimum before the sunrise in (DuRand et al. 2002; Stramski and Reynolds 1993). The shape of the absorption spectrum did not have diurnal variations in a study using *Micromonas pusilla* (DuRand et al. 2002), whereas in papers by (Mercado et al. 2006; Ohi et al. 2005) the blue-to-red (440 nm and 490 nm to 675 nm) absorption band ratios increased in the afternoon indicating accumulation of carotenoids relative to chl *a*. The discrepancies in the diurnal variations remind us that there exists different photoacclimation strategies between microalgae classes and even between strains (Suggett et al. 2007).

A similar photoacclimation process occurs in photobioreactors when the cell concentration increases in a finite reactor volume under a constant intensity. Less light penetrates through the high-density cell culture, followed by regulation in the amount of pigments and a change in the absorption and scattering spectra (Heng and Pilon 2014). Generally, low light intensity conditions result in increase of light-harvesting pigments and decrease in photo-protective pigments (carotenes), whereas the opposite takes place under high light intensity (Dubinsky and Stambler 2009). Interestingly, at least for one species, the diatom model organism *Phaeodactylum tricornutum*, the ratio between different light-harvesting pigments remain the same in the acclimation process (Nymark et al. 2013). This corroborates the latest model (Premvardhan et al. 2010) suggesting that the apo-protein backbone (fucoxanthin-chlorophyll) always binds the same number of chl *a*, fucoxanthin and chl *c*. A photoacclimated photosynthetic apparatus with modified pigment composition in turn affects the growth rate, the quantum yield (i.e., ratio of oxygen evolution per absorbed photon), dark respiration and division rate (Fisher et al. 1996).

An important molecular mechanism in photoacclimation is the state transitions, which involves reorganization of the photosynthetic apparatus by relocating light harvesting complex II proteins. This balances the excitation levels between PSI and PSII and, thus, optimizes the electron flow for efficient photosynthesis (Minagawa 2011). The fluorescence and absorption properties differ between the two states (Drop et al. 2014). The exact molecular mechanism for controlling the pigment amount in biosynthesis is not known, but it is speculated that transcriptional regulation also plays an important role (Cazzonelli and Pogson 2010; Laroche et al. 1991). Changes in the genes encoding light harvesting machinery and reactive oxygen species occur within 30 minutes of exposure to higher light intensity (Nymark et al. 2009; Nymark et al. 2013). The same applies for regulation of genes related to carbohydrate and lipid metabolism (Chauton et al. 2013). The metabolic changes in *Nannochloropsis oculata* as a consequence of photoacclimation were indicated in a paper by (Heng and Pilon 2014). They suggested that high intensity leads to increased synthesis of carbohydrates and proteins at the expense of lipids. Since carbohydrates and proteins have higher refractive index than lipids, the total refractive index of the cell increased, leading to higher scattering. The changes in the scattering properties were attributed mostly to variations in the cell size (DuRand et al. 2002; Kandilian et al. 2013) .

6.2. Color

Recently, metabolic changes as a response to the color of light (spectrum) has attracted a lot of interest in the context of utilization of microalgae as bio-crudes. Many studies have focused on the special role of blue light in metabolism (Kula et al. 2014; Marchetti et al. 2013; Mercado et al. 2004; Sanchez-Saavedra and Voltolina 1996; Shu et al. 2012). There are many reasons why blue light is particularly interesting. Firstly, chl *a* has a pronounced absorption peak in the blue part of the light spectrum. Secondly, blue light penetrates deeper into clear waters than any other color. Thirdly, blue light influences gene expression, activation of enzymes and metabolic pathways in microalgae via the blue-light photoreceptors cryptochromes, aureochromes and phototropins.

Indeed, it is mainly blue light that promotes the synthesis of ribulose-l,5-bisphosphate carboxylase (RuBisCo) (Roscher and Zetsche 1986) and carbonic anhydrase (Dionisio et al. 1989), that are enzymes affecting the carbon dioxide fixation rates and ultimately accumulation of lipids (Sayanova et al. 2017). Consequently, blue light has been reported to increase lipid contents in the algal cells compared to other colors or white light (Atta et al. 2013; Chen et al. 2013; Perez-Pazos and Fernandez-Izquierdo 2011; Shu et al. 2012). A summary of the impact of colored LED light on biochemical composition is presented in ref. (Schulze et al. 2014). Due to the pigment composition and the resulting absorption spectra, red and blue light produce generally higher growth rates and biomass accumulation than yellow and green light for microalgae, expect for species with phycobilins that efficiently utilize yellow, green and red light waves. It is noteworthy that also far-red light (720 nm) influences the metabolism and the chemical composition of algae via far-red-light receptors, or phytochromes (Fortunato et al. 2016; Kula et al. 2014).

So far, solid evidence for chromatic *acclimation* in the photosynthetic apparatus has been found only for the cyanobacteria among phytoplankton (Dubinsky and Stambler 2009). However, microalgae do *regulate* their photosynthetic apparatus as a response to light color. Exposing microalgae to red light conditions leads to slow increase in the red light absorption (around 710 nm) and in reorganization of the thylakoid membrane architecture (Herbstova et al. 2017; Kotabova et al. 2014). Also, in a study by Valle et al. the *in-vivo* fluorescence excitation spectrum was dependent on the color of the incident light after more than 30 minutes exposure, which suggests color-dependent energy transfer efficiency for diatom *Phaeodactylum tricornutum* (Valle et al. 2014). They also reported changes in the gene expression profiles of electron transport chain components and proteins involved in photoprotection after 30 minutes of exposure. These changes were color dependent, although, lasting for a limited period of six hours.

In addition, there exists some interesting physiological changes as a response to wavelength of light. The synthesis of diatom frustule structure has been reported to depend on light intensity and color (Su et al. 2017; Su et al. 2015). In ref. (Su et al. 2015) diatoms grown under red, yellow, green and blue light at high intensity (300 µmol / m^{2}s) expressed decreased foramen density, relative to white light. Cells grown under high intensity colored light had decreased foramen density relative to low intensity (100 µmol / m^{2}s), whereas the opposite was true for white light. Finally, germination of resting spores has a color-dependent activity (Shikata et al. 2011).

Summary and outlook

Light and microalgae cells form a reciprocally interacting pair: cells modify the light field and light modifies the cells. Light exposure triggers a set of physiological processes in the algae cells, on both transcriptional and metabolic levels. These processes shape the chemical composition of the cell, which further affects the optical properties of the cell. Therefore, optical properties and the size of the cells are not constant, but constantly changing as a response to variations in light intensity and color, among other factors. The scattering and absorption cross section and the size of the cells can vary as much as ~100 % during the natural daylight cycle. This has a great significance on the interpretation of optical signals measured.

The behavior of light within a microalgal cell is not simply envisioned. It would be tempting to visualize light by bundle of rays that refract and reflect from the cell, but this is not sufficiently accurate for microalgae that have feature sizes close to the wavelength of visible light. Instead, one needs to implement more rigorous models and consider light as electromagnetic waves with a certain phase, intensity and polarization state. Then, the sum of scattering and absorption from all the cell parts and the mutual interaction between the light fields, determines the total optical response of the cell.

Diatoms and coccolithophores form a special case among microalgae when it comes to the behavior of light on the cell surface. Diatom frustules are photonic structures with quasi-periodic patterns with feature sizes comparable to the wavelength of light. Frustules modify the color of light that enters the cell and potentially enhances light absorption in chloroplasts. Frustules also focus light towards the cell interiors, and the frustule may trap light by letting light enter in but not out from the cell. Frustules also seem to act as wave-guides by coupling light into modes propagating on the frustule structures and gradually leaking out. Studies on the optical role of coccolith structures are much scarcer and, hence, there is plenty of room for future studies on the subject.

The molecular medium of microalgae cells is satisfactorily characterized as homogenous having a complex refractive index. However, the heterogeneous nature of the cells needs to be considered on the organelle level. Describing cells as homogenous leads to underestimation in algae backscattering, although it may give correct results for absorption. Similarly, the shape of the particle is important especially in the backscattering predictions. Fluorescence is a form of inelastic scattering in all photosynthetic algae, and the physical explanation of fluorescence requires acknowledgement of light's particle nature. In this case, neither electromagnetic waves nor the complex refractive index describes the phenomenon. Fluorescence is usually weak, but it can be of the same strength as elastic backscattering. Hence, it is an important factor in analysis of remote sensing reflectance and in angular distribution measurements of scattering.

Microalgae optical properties have been studied for several decades (Emerson and Lewis 1943; Latimer 1959; Shibata et al. 1954). It is intriguing that even today the optical model for microalgal cell is not complete and new discoveries, such as the photonic effects in frustules and coccoliths, are still made. It is likely that new optical phenomena await to be revealed, for example, in studies of microalgae's ability to manipulate the polarization of light. Müller matrix measurements have already showed that polarized light gives information on the structure, size and shape that are unavailable in studies that use unpolarized light. Chloroplasts and the calcite of coccoliths are birefringent and chirality is introduced by the molecules and, possibly, by the intracellular organization. Hence, polarization dependent measurements are strongly encouraged in the future microalgae characterizations. In addition, some microalgae species can form chain-like assemblies, which has not been studied in the optical context. Due to the periodicity of such structures, these chains could possess some interesting optical properties.

Light has always been and will continue to be an important aspect in development of microalgae related research fields. Currently, the interests in aqua culture are directed towards light distribution optimization and control of metabolic products by light quality. Albeit computationally complex, accounting for the polarization state in the radiative transfer theory should yield in more truthful light distribution predictions. Remote sensing of natural waters is quickly evolving field, and the inverse ocean color algorithms are constantly under improvement for more accurate analysis of the phytoplankton community, which further finds applications in limnology and oceanography. It would seem reasonable that in the near future, efforts will be dedicated to detailed optical modeling of the microalga cell. Incorporating the shape and structure into the theoretical model will benefit the inverse algorithms and estimations of phytoplankton size distribution and growth. In any case, future studies of microalgae should always see them in a new light.

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HIGHLIGHTS:

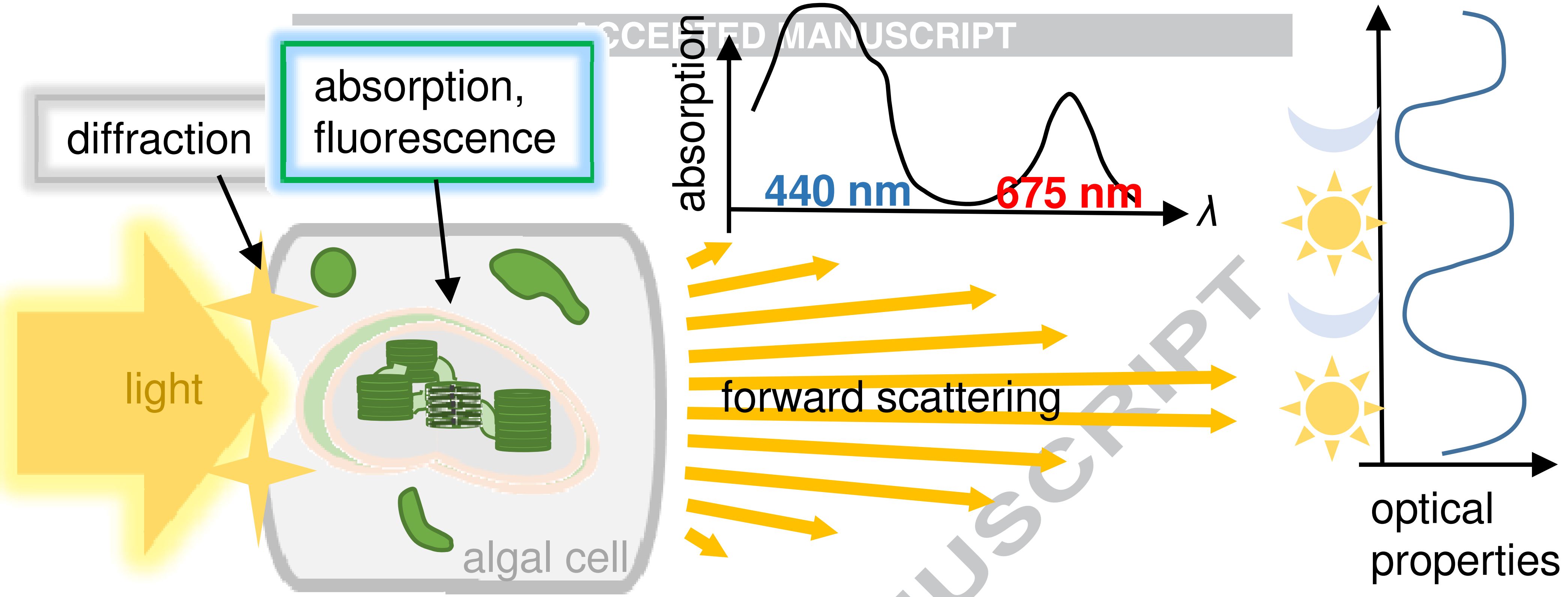
-Cellular and molecular level optical properties of algae are viewed

-The physics of scattering, absorption, and fluorescence are explained

-Photonic effects of diatoms and coccolithophores are represented

-Numerical algal cell models are compared

-Photoacclimation and chromatic regulation are discussed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