



# Influence of photoacclimation on the phytoplankton seasonal cycle in the Mediterranean Sea as seen by satellite



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## ARTICLE INFO

### Article history:

Received 7 April 2015

Received in revised form 27 July 2016

Accepted 4 August 2016

Available online xxx

### Keywords:

Photoacclimation

Phytoplankton

Satellite data

Non-algal particles coefficient

Mediterranean Sea

## ABSTRACT

Photoacclimation is a cellular process that allows phytoplankton to change the intracellular chlorophyll-*a* concentration (*Chl*) in relation to environmental factors such as light and nutrients. This process is currently overlooked by standard operational ocean colour algorithms used to retrieve information about both the phytoplankton standing stock and production. Here, we describe the photoacclimation effect on the phytoplankton seasonal cycle through the chlorophyll to carbon ratio (*Chl:C*) over the Mediterranean Sea, using SeaWiFS (1998–2007) monthly data. Chlorophyll was calculated through a regionalized empirical algorithm and Carbon was estimated from the particle backscattering, after subtraction of the non-algal contribution ( $b_{bpNAP}$ ). Historically,  $b_{bpNAP}$  has been neglected or assumed constant, and only recently its space-time variability started to be taken into account. Here, bootstrapping simulations are used to compute the monthly  $b_{bpNAP}$ s over a former bio-regionalization map of the Mediterranean Sea, all highlighting significant space-time variability. Resulting *Chl:C* varies within a factor of three, demonstrating the important role that photoacclimation plays at seasonal and basin scales. Lowest *Chl:C* values ( $\sim 0.0013$ ) are observed during summer; this is due to the combined effect of high irradiation, shallow mixing and low nutrient concentration. Maximum values ( $\sim 0.031$ ) are observed in winter and spring dominated by both low solar radiation, deeper mixing and high nutrient availability. It emerges that a better view of the phytoplankton space and time variability can be achieved through the joint use of *Chl* and *C*.

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## 1. Introduction

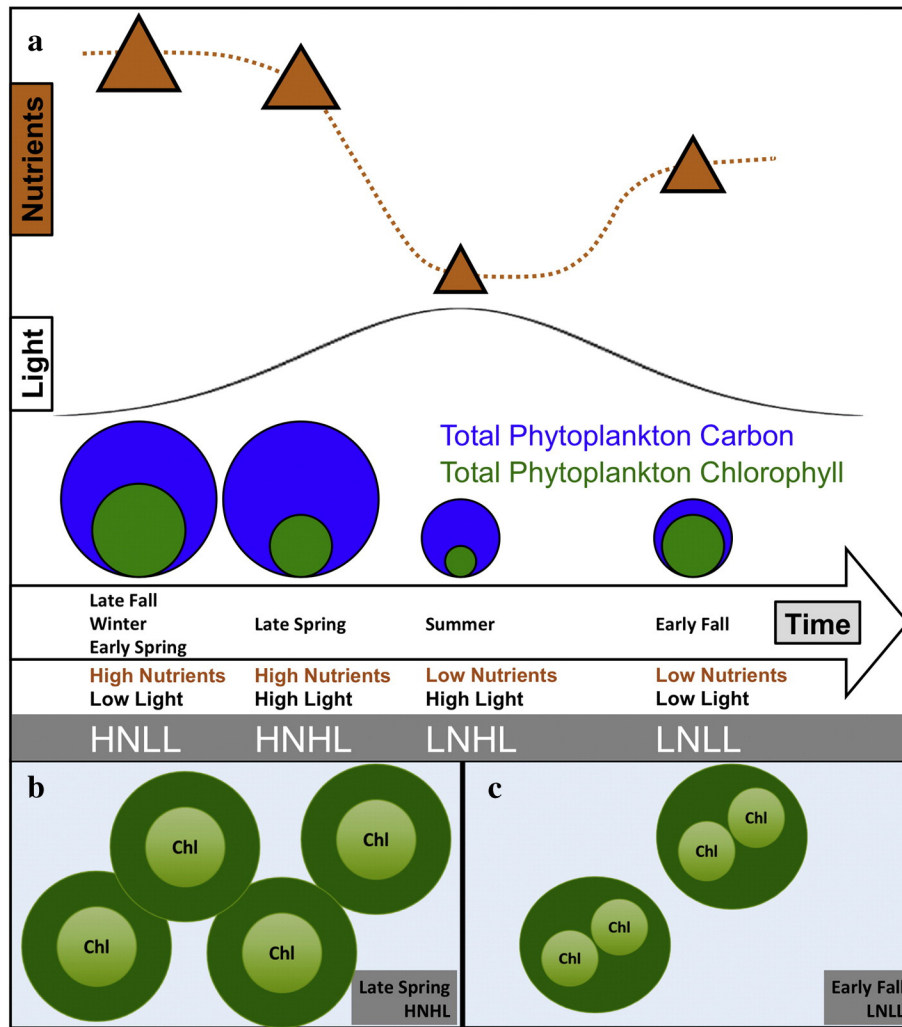
Light and nutrients are the most important environmental variables that drive the phytoplankton production and define the so-called “Integrated Growth Environment” (Behrenfeld et al., 2008). Phytoplankton cells respond to fluctuations in light and nutrients with physiological strategies that enhance the efficiency of light capturing and photosynthetic capacity, growth and persistence (Geider et al., 1997, 1998, 2009; MacIntyre et al., 2002; Behrenfeld et al., 2015). There are two different kinds of phytoplankton responses to light: photoadaptation and photoacclimation. The former describes changes that might happen at the genotype level, and are expected to occur on a long evolutionary time-scale (Moore et al., 2006). The latter identifies the short term phytoplankton phenotypic response to changes in irradiance conditions at the cellular level (Moore et al., 2006), and consists in the regulation of the pigment amounts (e.g. chlorophyll-*a*) and other components of the photosynthetic machinery (such as, electron transport chain, photosystem I and II, and their efficiency) in response to light intensity (Dubinsky and Stambler, 2009). Photoacclimation includes all the

intra-cellular processes aimed at optimizing photosynthesis and growth, and involves changes in the cellular size and shape, in the number of vacuoles or of thylakoids per grana (Berner et al., 1989; Fisher et al., 1998), in the electron chain activity, and alteration in the reaction centres of photosystems I and II (Osmond and Forster, 2008). The most important and easily observable effect due to photoacclimation is the variation of the cellular concentration of photosynthetic pigment such as chlorophyll-*a* (*Chl*). The photoacclimation-induced cellular changes can be observed on the time scale ranging from minutes to seasons (MacIntyre et al., 2000; Halsey and Jones, 2015), and can therefore be detected and quantified using space-borne observations. Photoacclimation can be accounted for in terms of the variation of the chlorophyll-*a* to carbon ratio (*Chl:C*) (Geider, 1987; MacIntyre et al., 2002; Halsey and Jones, 2015), consistent with the physiological adjustments to environmental factors. It is generally accepted that *Chl:C* is an important property in evaluating the phytoplankton community dynamics and its seasonality (Laws and Bannister, 1980; Halsey and Jones, 2015).

The seasonal variability of *Chl* and total phytoplankton carbon (*C*) at community scale, under different light and nutrient regimes (adapted from Behrenfeld et al., 2004), is conceptually outlined in Fig. 1a. Despite the natural phytoplankton population variability (e.g., health of the cells, life stages and so on), here, all phytoplankton cells are assumed

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**Fig. 1.** a) Schematics of the annual cycle of chlorophyll and total phytoplankton carbon under different nutrient and light conditions (adapted from Behrenfeld et al., 2004). Blue circles represent the total phytoplankton carbon available in a unit volume of water, while green circles account for total chlorophyll concentration in the same volume. The annual cycles of light (black line) and nutrients (brown dotted line and triangles) are also depicted. Two different scenarios with the same chlorophyll concentration are illustrated for late spring (b) and early fall (c). The total phytoplankton carbon and abundance present in b) is higher than in c) making *Chl* an ambiguous proxy. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

to behave the same way. Phytoplankton cells need to produce an amount of *Chl* in relation to the nutrient concentration and light availability in order to optimize photosynthesis. Over the annual cycle, changes in nutrients and light conditions have an impact on the phytoplankton standing stock and on the cellular chlorophyll concentration. However, *Chl* and *C* do not covary over the entire seasonal cycle; for example, from early to late spring, *Chl* decreases while *C* does not. Similarly, phytoplankton abundance is not expected to increase significantly from summer to the beginning of autumn, whereas *Chl* does. Four different scenarios are illustrated in Fig. 1a. In late fall to early spring, under high nutrients and low light (HNLL), both *Chl* and *C* show their maximum values. In late spring, light intensity increases and there is no longer a need for the cells to produce and sustain large amounts of the energetically expensive *Chl* pigment. Under these conditions, phytoplankton cells exploit the nutrients still present in the sunlit layer. This, together with the more stable light conditions provided by the increased stratification allows phytoplankton to grow, despite *Chl* concentration decreases. During summer, the strong increase of light determines the decrease of phytoplankton pigment demand, while low nutrient concentrations limit phytoplankton population growth and division rate. In this period, under low nutrients (period of highest stratification) and high light conditions (LNHL), both *Chl* and *C* are at their minima. Later on, during early fall, as light starts to decrease and

mixing starts to occur again, phytoplankton allocate the energy from the newly available nutrients (at least part of it) into the production of chlorophyll, limiting their growth rate (LNLL). Following this scheme and despite some similarities (e.g., HNLL and LNHL), it is clear that during the year and at community scale, *Chl* and *C* have different seasonal behaviours in relation to light and nutrients. Their different temporal behaviour is reflected in the temporal variability of the *Chl*:*C* which accounts for the combined effect of the changes in light and nutrients. Numerous laboratory studies have shown that phytoplankton respond to light and nutrient variations by adjusting the cellular pigment levels, making the chlorophyll to carbon ratio a useful index to evaluate phytoplankton physiology from space (Behrenfeld et al., 2005). It is worth mentioning that the above discussion only considers bottom-up processes (such as those associated with light and nutrient availability) and does not consider the role played by top-down processes (such as zooplankton grazing or natural mortality) similarly known to control phytoplankton space-time distribution.

Historically, in satellite oceanography, *Chl* has been the only available proxy of the algal biomass concentration (Siegel et al., 2013). However, *Chl* retrieval does not take into account the physiological adjustments that phytoplankton undergoes in response to changes in light and nutrient conditions (Halsey and Jones, 2015). The comparison of Fig. 1b and Fig. 1c provides an indication of the circumstances (as

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