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Vertical distribution of phytoplankton communities in open ocean: An assessment based on surface chlorophyll

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[1] The present study examines the potential of using the near-surface chlorophyll *a* concentration ($[\mathrm{Chl}a]_{surf}$), as it can be derived from ocean color observation, to infer the column-integrated phytoplankton biomass, its vertical distribution, and ultimately the community composition. Within this context, a large High-Performance Liquid Chromatography (HPLC) pigment database was analyzed. It includes 2419 vertical pigment profiles, sampled in case 1 waters with various trophic states (0.03–6 mg Chl*a* m^{-3}). The relationships between $[\mathrm{Chl}a]_{surf}$ and the chlorophyll *a* vertical distribution, as previously derived by Morel and Berthon (1989), are fully confirmed. This agreement makes it possible to go further and to examine if similar relationships between $[\mathrm{Chl}a]_{surf}$ and the phytoplankton assemblage composition along the vertical can be derived. Thanks to the detailed pigment composition, and use of specific pigment biomarkers, the contribution to the local chlorophyll *a* concentration of three phytoplankton groups can be assessed. With some cautions, these groups coincide with three size classes, i.e., microplankton, nanoplankton and picoplankton. Corroborating previous regional findings (e.g., large species dominate in eutrophic environments, whereas tiny phytoplankton prevail in oligotrophic zones), the present results lead to an empirical parameterization applicable to most oceanic waters. The predictive skill of this parameterization is satisfactorily tested on a separate data set. With such a tool, the vertical chlorophyll *a* profiles of each group can be inferred solely from the knowledge of $[\mathrm{Chl}a]_{surf}$. By combining this tool with satellite ocean color data, it becomes possible to quantify on a global scale the phytoplankton biomass associated with each of the three algal assemblages.

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1. Introduction

[2] A quasi-permanent monitoring of the algal content of the sunlit world ocean is only achievable by satellite observation of "ocean color." The sea spectral reflectance, as detected by a remote sensor, can provide an estimate of the chlorophyll *a* concentration, which is commonly used as an index of the algal biomass. This estimate, however, is restricted to the upper layer of the water column only [*Gordon and McCluney*, 1975]. Within the context of ecological studies dealing with the vertical distribution of algal species, as well as for biogeochemical applications involving primary production, such satellite information about the near-surface layer is insufficient. Indeed, the assessment of the algal biomass must be extended downward in order to encompass the entire depth range where algae can live and grow. For instance, the transformation of "chlorophyll maps" as obtained from spaceborne sensors into "primary production maps" [*Campbell et al.*, 2002], through the use of light-photosynthesis models, requires at least that the column-integrated algal biomass is known, and better, that the biomass vertical distribution within the decreasingly illuminated layers can be in some way described. The terms "known" or "described" actually mean "assumed" or "predicted" for each pixel of a satellite image with a sufficient degree of confidence. The creation of such a predictive capability was the main motivation of the first study carried out by *Morel and Berthon* [1989, hereinafter referred to as MB89].

[3] The heuristic hypothesis in MB89 was that the near-surface chlorophyll concentration is in some manner related to the column-integrated chlorophyll content, and even to the shape of the phytoplankton vertical distribution. The validity of this initial working hypothesis was amply demonstrated through the examination, and then the statistical analysis, of about 4000 vertical profiles of chlorophyll *a* concentration, determined in oceanic case 1 waters only [*Gordon and Morel*, 1983], and with near-surface concentrations varying over more than two orders of magnitude. The main conclusions of the MB89 study were as follows: (1) The integrated chlorophyll *a* biomass over the euphotic

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Table 1. Symbols Used in the Present Study and Their Significance

Symbol	Significance
Chl*a*	total chlorophyll *a* (chlorophyll *a* + divinyl chlorophyll *a* + chlorophyllid *a* + chlorophyll *a* allomers and epimers)
[Chl*a*]	Chl*a* concentration, mg m^{-3}
[P]	concentration of pigment P, mg m^{-3}
PAR	photosynthetically available radiation, W m^{-2}
Z_{pd}	penetration depth, m
$[Chla]_{surf}$	average total chlorophyll *a* within the surface layer $0-Z_{pd}$, mg m^{-3}
z	geometrical depth, m
Z_{eu}	depth of the euphotic layer, defined as the depth where the PAR is reduced to 1% of its surface value, m
ζ	depth normalized with respect to Z_{eu}: $\zeta = z/Z_{eu}$, dimensionless
$\langle Chla \rangle_{Zeu}$	Chl*a* column-integrated content, within the euphotic layer, mg m^{-2}
$\langle Chla \rangle_{1.5\ Zeu}$	Chl*a* column-integrated content, within the $0-1.5\ Z_{eu}$ layer, mg m^{-2}
$\overline{Chla}_{Zeu}$	average column-integrated content of total chlorophyll *a* within the euphotic layer, mg m^{-3}
$P(\zeta)$	concentration of pigment P, at (the dimensionless depth) ζ, mg m^{-3}
$p(\zeta)$	concentration of pigment P normalized with respect to $\overline{Chla}_{Zeu}$, $p(\zeta) = P(\zeta)/\overline{Chla}_{Zeu}$, dimensionless
micro-Chl*a*	total chlorophyll *a* associated to microplankton
nano-Chl*a*	total chlorophyll *a* associated to nanoplankton
pico-Chl*a*	total chlorophyll *a* associated to picoplankton
f_{micro}	fraction of Chl*a* associated to microplankton
f_{nano}	fraction of Chl*a* associated to nanoplankton
f_{pico}	fraction of Chl*a* associated to picoplankton
Z_m	depth of the mixed layer, m
$[P]_{max}$	maximum concentration on a considered P vertical profile, mg m^{-3}
Z_{max}	depth of $[P]_{max}$, m

layer (mg m^{-2}) and the near-surface chlorophyll *a* concentration (mg m^{-3}) are highly correlated, albeit in a nonlinear fashion. (2) The vertical chlorophyll *a* profiles in stratified waters can be orderly sorted into several ‘‘trophic categories,’’ on the basis of the near-surface chlorophyll *a* concentration, and (3) each of these categories exhibits, in a statistical sense, a typical chlorophyll *a* vertical profile, which generally includes a somewhat pronounced, and more or less deep, chlorophyll *a* maximum; (4) for such vertically stratified waters, a parameterization was proposed which allowed the vertical structure of the chlorophyll *a* profiles to be predicted in a continuous manner from the near-surface chlorophyll *a* value alone; and finally, (5) the separate statistical analysis of vertically well mixed waters (essentially in high latitudes and in winter) showed that the vertical chlorophyll *a* profiles are essentially uniform (as intuitively expected).

[4] The present study is chiefly motivated by the considerable improvement brought by the introduction, and systematic use, of High-Performance Liquid Chromatography (HPLC) for determining the concentration of marine pigments. Indeed, in the frame of national and international programs such as Joint Global Ocean Flux Study (JGOFS), HPLC pigment analyzes have been systematically carried out during at least the last decade; once merged, these data constitute an incomparable set for global ocean studies like the present one. Before proceeding further, the logical first goal of the present study is, therefore, to check the validity of the initial working hypothesis of MB89, and to confirm or modify the global description they proposed, by considering another data set, which is based on another analytical method.

[5] Beyond this first objective, it is now possible to delve deeper into the analysis. Indeed, it becomes increasingly obvious that the use of only chlorophyll *a* as a proxy for the algal biomass remains insufficient, as far as oceanic biogeochemical cycles are to be studied and ultimately modeled. In effect, the ‘‘quality’’ of the phytoplankton populations (in particular their taxonomic composition) impacts on, or reciprocally, is a signature of, specific biogeochemical processes. For example, tiny phytoplankton are preferentially associated with the presence of regenerated forms of the nutrients they are able to utilize, whereas large phytoplankters (diatoms), which are more involved in so-called new production, develop preferentially when fresh nutrients become available [*Eppley and Peterson*, 1979; *Malone*, 1980; *Goldman*, 1993]. A relationship between the (instantaneous) trophic status of a water body, as locally depicted by the near-surface chlorophyll *a* content, and the local taxonomic composition of the algal assemblage can reasonably be expected [*Claustre*, 1994], and is worth pursuing.

[6] The HPLC method allows the assessment of the so-called ‘‘total’’ chlorophyll *a* concentration; this quantity will be simply noted [Chl*a*] (see Table 1 for a list of symbols). More importantly, the HPLC method also allows a suite of accessory pigments (carotenoids and chlorophylls) to be determined. Many of these pigments are specific of individual phytoplanktonic taxa or groups [*Jeffrey and Vesk* 1997]. They can thus be used as biomarkers of various phytoplankton groupings [e.g., *Gieskes et al.*, 1988; *Prézelin et al.*, 2000], and with some cautions assigned to different size classes, such as microphytoplankton, nanophytoplankton and picophytoplankton [*Vidussi et al.*, 2001]. Consequently, the column-integrated biomasses of each of the algal classes, as well as their vertical profiles, can be determined from the details of the vertical distribution of the pigment composition. As a result, the respective contribution of each class to the total standing algal stock can be assessed. The second objective of the present study is, therefore, to examine, on the basis of the analysis of HPLC data, whether some generic properties regarding the composition and vertical distribution of the various phytoplankton assemblages may be predicted from the near-surface total chlorophyll *a* concentration (hereinafter denoted $[Chla]_{surf}$).