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Seasonal distribution and succession of dominant phytoplankton groups in the global ocean: A satellite view

S. Alvain,^{1,3} C. Moulin,² Y. Dandonneau,⁴ and H. Loisel¹

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[1] Phytoplankton plays an important role in the global carbon cycle via the fixation of inorganic carbon during photosynthesis. However, the efficiency of this “biological pump of carbon” strongly depends on the nature of the phytoplankton. Monitoring spatial and temporal variations of the distribution of dominant phytoplankton groups at the global scale is thus of critical importance. Recently, an algorithm has been developed to detect the major dominant phytoplankton groups from anomalies of the marine signal measured by ocean color satellites. This method, called PHYSAT, allows to identify nanoeucaryotes, *Prochlorococcus*, *Synechococcus* and diatoms. In this paper, PHYSAT has been improved to detect an additional group, named phaeocystis-like, by analyzing specific signal anomalies in the Southern Ocean during winter months. This new version of PHYSAT was then used to process daily global SeaWiFS GAC data between 1998 and 2006. The global distribution of major phytoplankton groups is presented in this study as a monthly climatology of the most frequent phytoplankton group. The contribution of nanoeucaryotes-dominated waters to the global ocean varies from 45 to 70% depending on the season, whereas both diatoms and phaeocystis-like contributions exhibit a stronger seasonal variability mostly due to the large blooms that occur during winter in the Southern Ocean. Three regions of particular interest are also studied in more details: the Southern Ocean, the North Atlantic, and the Equatorial Pacific. The North Atlantic diatom bloom shows a large interannual variability. Large blooms of both diatoms and phaeocystis-like are observed during winter in the Southern Ocean, with a larger contribution from diatoms. Their respective geographical distribution is shown to be tightly related to the depth of the mixed-layer, with diatoms prevailing in stratified waters. *Synechococcus* and *Prochlorococcus* prevail in the Equatorial Pacific, but our data show also sporadic diatoms contributions in this region during La Niña. The observed seasonal cycle and interannual variability of phytoplankton groups in the global ocean suggest that the PHYSAT archive is suitable to study the impact of climate variability on the structure of marine ecosystems.

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1. Introduction

[2] Marine biology plays a major role in biogeochemical cycles in the oceans. More particularly, phytoplankton biological pump participates in regulating the amount of carbon in the atmosphere and is thought to be very sensitive to the forthcoming climate change [Cox *et al.*, 2000; Bopp *et al.*, 2001; Dufresnes *et al.*, 2002; Sarmiento

et al., 2004; Le Quéré and Metzl, 2004; Le Quéré *et al.*, 2006]. The intensity of both carbon fixation and export is however strongly dependent on the size and composition of phytoplankton cells. It is for example well known that diatoms, which are characterized by large cells with a heavy silicate skeleton, are particularly efficient for carbon export [Lochte *et al.*, 1993; Bopp *et al.*, 2005]. Most current global numerical models used to estimate the marine biological pump thus independently represent the main phytoplankton groups [Kamykowski and Janowitz, 1999; Aumont *et al.*, 2003; Gregg *et al.*, 2003; Moore *et al.*, 2004; Le Quéré *et al.*, 2005].

[3] The validation of these global models is crucial but also particularly difficult because of the lack of global data available on the geographical distribution of the main phytoplankton groups. Although it is well known that diatoms blooms occur every year in the North Atlantic and Pacific Oceans in the springtime and in

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the southern Ocean in winter [Lampitt, 1985; Knox, 1994; Dandonneau *et al.*, 2006], very little is known about their actual duration and location, and even less about their interannual variability. Several other groups have also significant impacts on biogeochemical cycles such as phaeocystis that produces atmospheric Dimethyl Sulfide compounds (DMS) [Belviso *et al.*, 2004]. As for diatoms, our knowledge on the spatial and temporal distributions of phaeocystis blooms, based only on sparse in situ measurements, is limited.

[4] Our current knowledge of the global distribution and seasonal variability of phytoplankton comes mainly from satellite observations: the first ocean color sensor, CZCS, has partially covered the 1979–1986 period, whereas its successors, OCTS, SeaWiFS and MODIS, have enabled a continuous monitoring of phytoplankton since 1997. The chlorophyll-a concentration (Chl-a), which is derived from these satellite observations using a bio-optical algorithm, is commonly used as a proxy of the phytoplankton concentration in surface waters because this photosynthetic pigment is dominant in most phytoplankton groups. Most of ocean color bio-optical algorithms [O’Reilly *et al.*, 1998] rely more or less on the same blue to green ratio of the normalized water leaving radiance (nLw), which quantifies the amount of light exiting the ocean surface. This chlorophyll-a concentration however does not provide any information about which phytoplankton group dominates in surface waters at the time of the measurement.

[5] Recently, a method called PHYSAT has been developed to identify the dominant phytoplankton group simultaneously with Chl-a [Alvain *et al.*, 2005] using ocean color data. This classification technique enables the identification of four major phytoplankton groups, i.e., nanoecaryotes, Prochlorococcus, Synechococcus, and diatoms. PHYSAT relies on the detection of spectral anomalies of nLw, which were associated to specific phytoplankton groups by using coincident in situ measurements of pigment inventories performed in the framework of the GeP&CO program [Dandonneau *et al.*, 2004]. It should be noted that in this work the nanoecaryote group replaces the haptophytes group defined by Alvain *et al.* [2005]. Indeed, when PHYSAT was developed, the phytoplankton group “haptophytes” was so denominated because it differed from other groups by abnormally high content of 19’hexanoyloxyfucoxanthin, which is usually considered as a diagnostic pigment for haptophytes [Jeffrey and Vesk, 1997]. This pigment however is abundant almost everywhere in the ocean, and in the GeP&CO data set, it covaries with violaxanthin, alloxanthin and 19’butanoyloxyfucoxanthin [Dandonneau and Niang, 2007], thus implying that the groups characterized by these carotenoid pigments are often found associated to the Haptophytes. These groups are formed by small nanoplanktonic flagellated algae which we now refer to “nanoecaryotes”.

[6] In this paper, we first show that PHYSAT can be extended to the detection of phaeocystis-like blooms, even if further validation is still needed. Then we analyze the monthly global climatology of the distribution of the five phytoplankton groups identified by PHYSAT, using

9 years (1998–2006) of daily SeaWiFS data. We finally present a more detailed analysis of the spatial and seasonal variability of phytoplankton group distribution for three contrasted regions of great importance in terms of biogeochemical cycles, i.e., the North Atlantic, the Equatorial Pacific and the Southern Ocean.

2. PHYSAT Method

2.1. Characteristics and Evolutions

[7] The PHYSAT approach is based on the identification of specific signatures in the nLw spectra measured by an ocean color sensor. It is described in detail by Alvain *et al.* [2005]. Briefly, this empirical method has been established by comparing two kinds of simultaneous and coincident measurements: SeaWiFS nLw measurements and in situ measurements of diagnostic phytoplankton pigments performed in the framework of the GeP&CO program [Dandonneau *et al.*, 2004]. GeP&CO cruises have sampled a wide range of water types, from the North Atlantic spring bloom to the oligotrophic subtropical south Pacific. In a first step, four dominant phytoplankton groups were identified within the GeP&CO data set based on the pigment inventories: diatoms, nanoecaryotes, Synechococcus and Prochlorococcus. Note that here, “dominant” has been defined by Alvain *et al.* [2005] as situations in which a given phytoplankton group is a major contributor to the total pigment. In a second step, coincident SeaWiFS nLw spectra between 412 and 555 nm were transformed into specific normalized water-leaving radiance (nLw*) spectra in order to evidence the second-order variability of the satellite signal. This was done by dividing the actual nLw by a mean nLw model (nLw^{ref}), which depends only on the standard SeaWiFS Chl-a.

[8] Alvain *et al.* [2005] showed that every dominant phytoplankton group sampled during GeP&CO is associated with a specific nLw* spectrum. They defined a set of criteria to characterize each group in function of its nLw* spectrum. These criteria can be applied to global daily SeaWiFS GAC archive to get global monthly maps of the most frequent group of dominant phytoplankton, as shown in Figure 1a for January 2002. When no group prevails over the month, the pixels are associated with an “unidentified” phytoplankton group. The only difference between the PHYSAT method used in this study and that of Alvain *et al.* [2005] is the use of a new nLw^{ref} model. The former model was indeed calculated from a large SeaWiFS data set extracted along the GeP&CO ship track for 2001, whereas the new one was obtained by taking into account all SeaWiFS data available for all the geographical areas of the same year, so that it includes data from the Southern Ocean. This modification led to slight changes of the criteria used to identify the four initial phytoplankton groups, as shown in Table 1. Global results for nanoecaryotes, Prochlorococcus, Synechococcus and diatoms presented in Figure 1b are very close to that obtained with the original PHYSAT method shown in Figure 1a. The main difference between Figures 1a and 1b is that diatom blooms are more

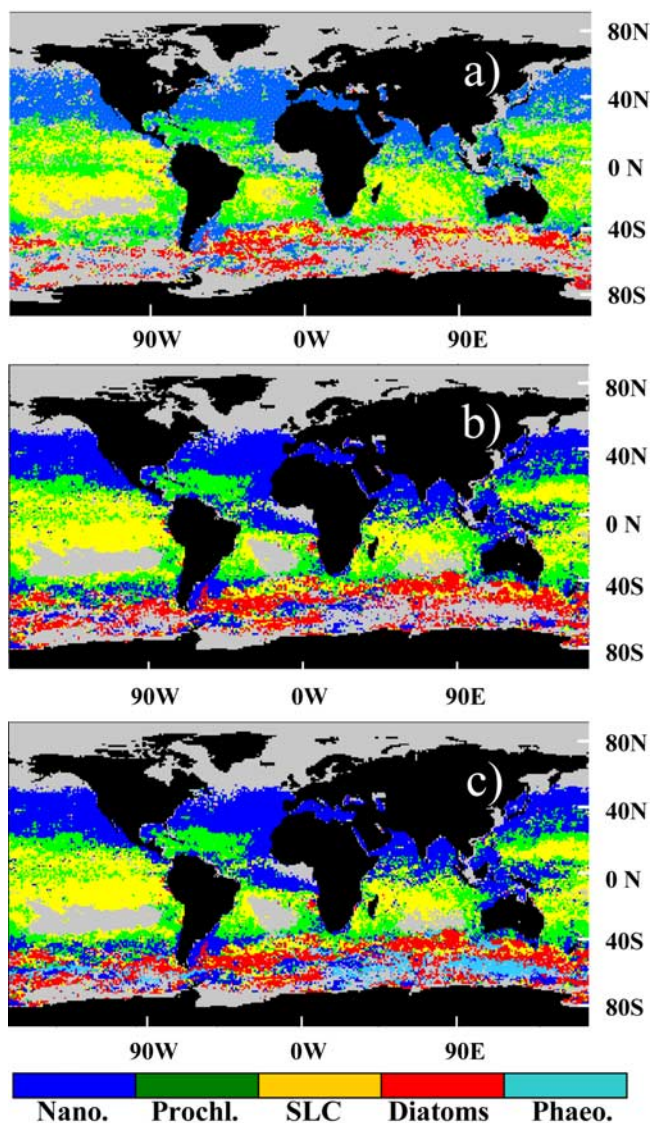


Figure 1. Maps of the dominant phytoplankton group for January 2002 obtained from (a) the standard PHYSAT method of *Alvain et al.* [2005], (b) the improved PHYSAT method used in this study, and (c) the improved PHYSAT method with the additional phaeocystis-like group.

pronounced in the Southern Ocean as well as in upwelling regions when the new PHYSAT is applied.

2.2. Phaeocystis-Like: An Additional Phytoplankton Group for PHYSAT

[9] Figures 1a and 1b show that some regions are characterized by a large number of unidentified pixels. This can be easily explained at high latitude in the Northern Hemisphere because of the low sun angles, in the equatorial Atlantic where the aerosol optical thickness due to Saharan dust plumes is often above 0.15 (the maximum value allowed by PHYSAT), as well as in the ultra-oligotrophic subtropical gyres in the southern Pacific and Atlantic where Chl-a values are often below 0.04 mg.m^{-3} (the minimum value allowed in PHYSAT). On the contrary, the large number of unidentified pixels is surprising in the southern Ocean during summer because all selection criteria are fulfilled for most pixels in this region. Considering the coherence of these spatial structures, it is likely that they correspond to a specific phytoplankton group or at least to a given ecosystem structure. Unfortunately, the GeP&CO cruises have not sampled these waters. Several other campaigns in the Southern Ocean have however highlighted the frequent occurrence of phaeocystis blooms [*Goffart et al.*, 2000; *Smith et al.*, 2003; *Croot et al.*, 2004; *Schoemann et al.*, 2005]. Phaeocystis is known for its particular optical properties due to the white mucus exuded by cells during the blooming season.

[10] We examined the unidentified nLw* spectra in this region and we found that most of them are very similar in both amplitude and spectral shape. The mean spectrum of these unclassified pixels is characterized by nLw* values close to those of diatoms at 443 nm, higher between 490 and 555 nm, and lower at 412 nm, as shown in Figure 2. Similarly to what was done by *Alvain et al.* [2005], we have defined in Table 1 a range of acceptable nLw* values for this new class of spectra. These criteria were added to the new PHYSAT method to process the global SeaWiFS archive. Figure 1c shows in light blue the location of these supplementary classified pixels for January 2002. This figure confirms that large parts of the Southern Ocean have optical properties that belong to this additional class of nLw* spectrum. These spectra are also detected during summer in more restricted area like in the North Sea, where

Table 1. Characteristics of nLw* Spectra for the Six Phytoplankton Groups Detected With PHYSAT

	412 nm	443 nm	490 nm	510 nm	555 nm	Additional Criteria
Nanoec. min.	0.4	0.55	0.6	0.6	0.6	nLw*412 < nlw*443
Nanoec. max.	0.8	0.9	0.95	1.0	1.0	nLw*443 < nlw*490
Prochloroc. min	0.8	0.9	0.9	0.9	0.9	...
Prochloroc. max	1.0	1.0	1.0	1.0	1.0	...
Synechococcus min.	1.0	1.0	1.0	1.0	1.0	...
Synechococcus max.	1.2	1.2	1.15	1.15	1.15	...
Diatoms min.	1.2	1.2	1.15	1.15	1.15	nLw*412 > nlw*490
Diatoms max.	2.2	1.8	1.5	1.4	1.4	nLw*555 < nlw*490
Phaeocystis-like min.	1.3	1.4	1.4	1.4	1.4	nLw*412 < nlw*443
Phaeocystis-like max	1.5	1.6	1.6	1.6	1.6	nLw*443 < nlw*490 nLw*510 > nlw*555
Coccolithes. - bloom min.	2.5	2.5	2.5	2.5	2.5	
Coccolithes. - bloom max.	6.0	6.0	6.0	6.0	6.0	

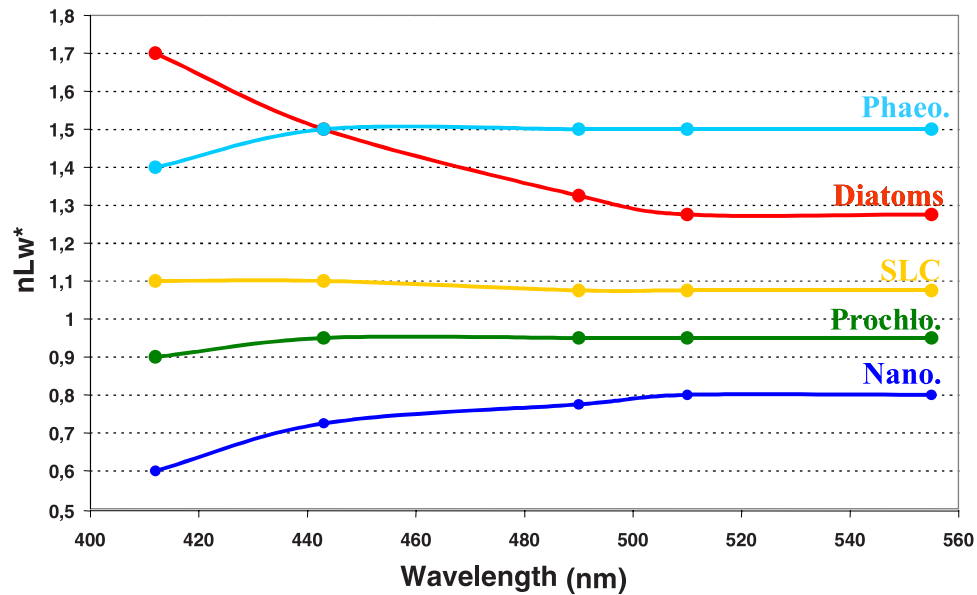


Figure 2. Mean nLw^* spectra for the five PHYSTAT phytoplankton groups: diatoms in red, nanoeucaryotes in blue, Synechococcus in yellow, Prochlorococcus in green, and phaeocystis-like in light blue.

limited but intense phaeocystis blooms are often observed [Lancelot *et al.*, 1994], and the North Pacific, and from time to time in the North Atlantic in spring and summer.

[11] This additional group is of strong interest for climate studies since phaeocystis blooms can be as effective as diatoms blooms in exporting carbon toward the deep ocean [DiTullio *et al.*, 2000]. They are also important producers of Dimethyl Sulfide (DMS), the precursor of secondary sulfate aerosols [Belviso *et al.*, 2004]. Despite the lack of direct

validation, we propose here to add the identification of a “phaeocystis-like” group to this new version of PHYSTAT.

2.3. Coccolithophorids Blooms

[12] Coccolithophorids were the first phytoplankton group detected from space [Brown and Yoder, 1994]. Indeed, coccolithophorid cells have a spherical shape made of an assemblage of calcium carbonate plates. When the cell dies, these plates are released and produce the well known milky turquoise color in ocean color imagery. This is

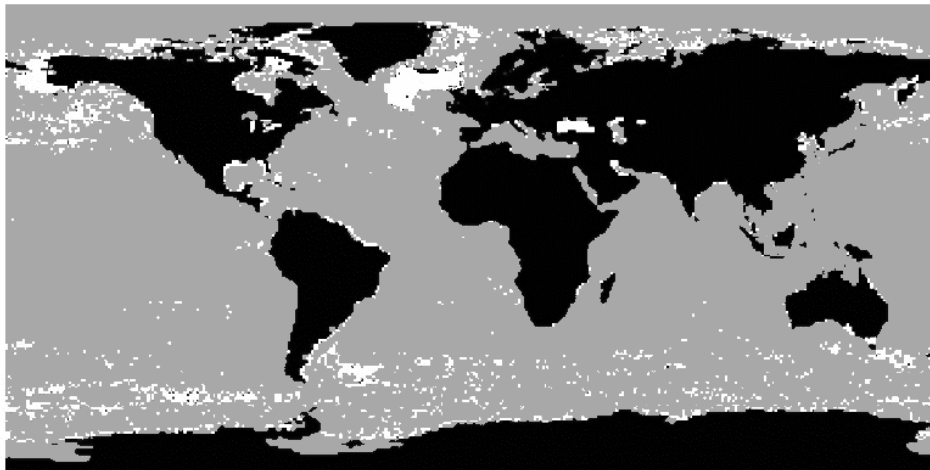


Figure 3. Occurrence of Coccolithophorid blooms (in white) obtained with PHYSTAT from SeaWiFS data over the 1997–2006 period, using the cumulative approach used by Iglesias-Rodríguez *et al.* [2002]. Each pixel that has been identified once or more as a Coccolithophorid bloom over the 10-year period is displayed in white.

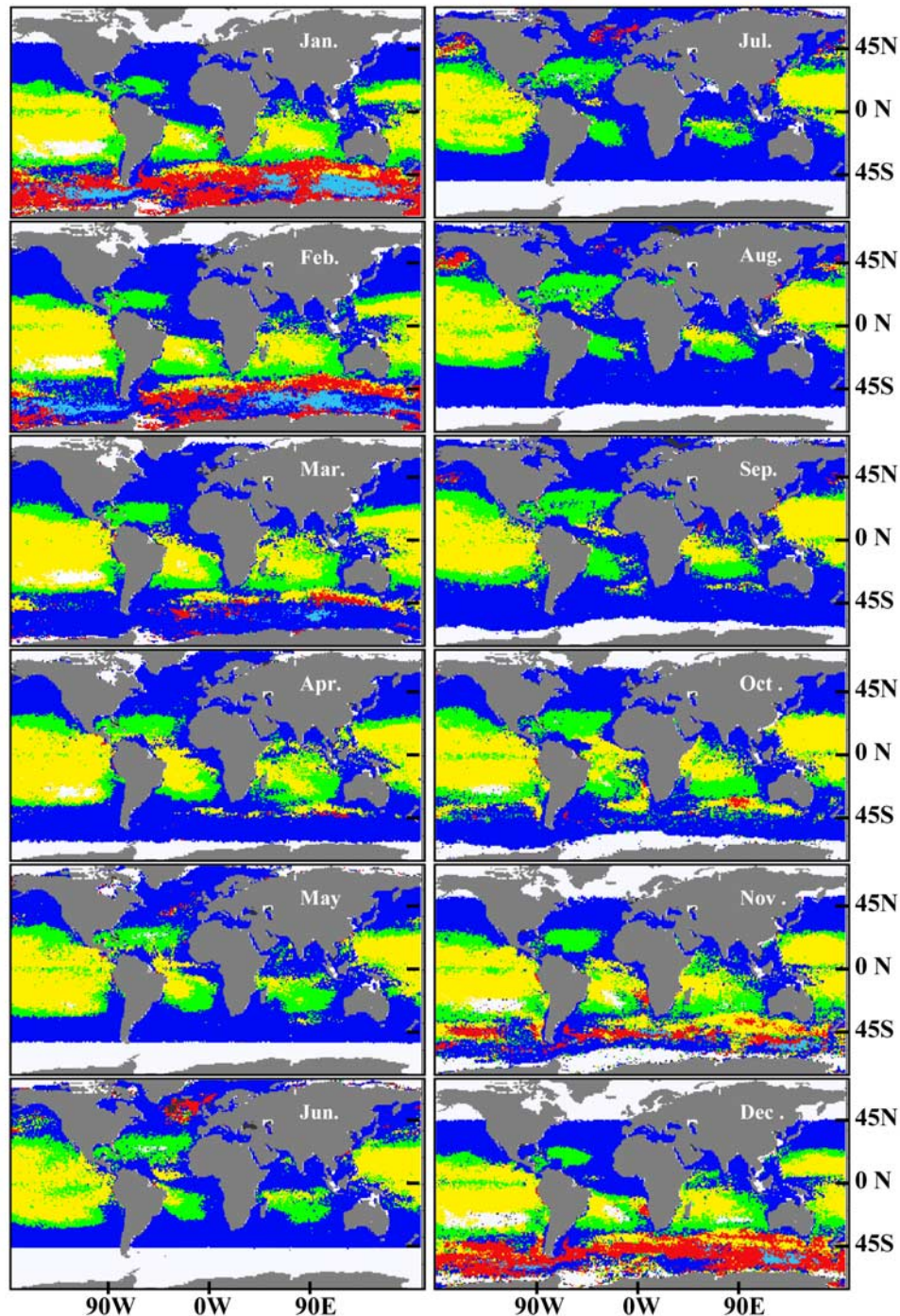


Figure 4. Monthly climatology (1998–2006) of the dominant phytoplankton group.

particularly the case for the “*Emiliana huxleyi*” species, which is capable of forming large blooms, from over hundred kilometers scale. Those blooms are significant in terms of both climate impact via the export of carbonate and biogeochemical cycles through the emission of chemical compounds.

[13] As the location of major coccolithophorid blooms are well-known (e.g., south of Iceland in summer or in the

Baltic Sea), we searched for specific nLw^* anomalies in these regions, as we did for phaeocystis in the previous section. We found that coccolithophorid blooms are associated to very high nLw^* values at all the wavelengths (see Table 1), which is an expected result for those very bright cells. Figure 3 shows that the use of these criteria within PHYSAT leads to global maps that are exactly the same as those obtained with former methods [e.g., *Iglesias-Rodríguez*

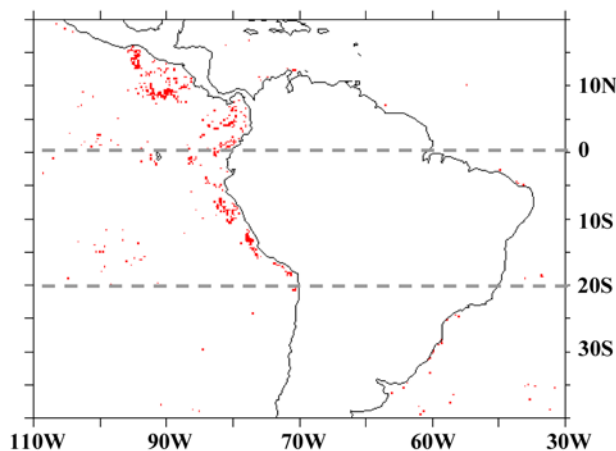


Figure 5. Detection of diatom blooms in the Peru-Chile upwelling in June 2001 using PHYSAT at a $\frac{1}{4}^\circ$ resolution.

et al., 2002]. However, it turned out that the SeaWiFS data used by the PHYSAT method, i.e. Level 3 daily GAC products, are screened to remove coccolithophorid blooms using a threshold on nLw during the data processing, so that our PHYSAT results, as former methods, likely underestimate the actual size of coccolithophorid blooms. Note that information about the coccolithophorid screening are not available in Level 3 GAC products and that a complete reprocessing of the SeaWiFS Level 2 archive would be necessary to overcome this problem. We have thus decided to not include this group to our climatology.

2.4. Data Processing

[14] The new PHYSAT defined above has been applied to all SeaWiFS daily L3-binned GAC data between 1998 and 2006 (processing version 5.2). These data were available from the NASA/GSFC/DAAC web site (<http://oceancolor.gsfc.nasa.gov/>). Daily phytoplankton group maps at a resolution of $1/12^\circ$ were used to generate monthly maps of most frequently identified dominant phytoplankton group at a 1° resolution by selecting the group that had been retrieved for at least half of the valid (including unidentified) pixels within each $1^\circ \times 1^\circ$ grid box. Note that no phytoplankton group is assigned to a grid box for which no phytoplankton group dominates or for which unidentified pixels prevail. PHYSAT data used in this work are available at <http://log.univ-littoral.fr/Physat>.

3. Global Climatology of Phytoplankton Groups

3.1. Geographical Distribution

[15] Figure 4 shows the monthly climatology (1998–2006) of the most frequent phytoplankton groups. These global results show well-defined and persistent patterns of phytoplankton that are similar to those obtained by *Alvain et al.* [2005] for the year 2001. *Prochlorococcus* and *Synechococcus* are mostly detected in oligotrophic tropical waters because the small size of these pico-plankton cells, and hence their large surface-to-volume ratio, makes them less sensitive to nutrient limitation than larger phytoplankton groups [*Longhurst, 2007*].

[16] *Prochlorococcus* are nevertheless preferentially observed between 25° and 35° N and between 20° and 35° S, whereas *Synechococcus* prevail in equatorial waters. *Prochlorococcus* and nanoeucaryotes prevail in the North Atlantic with a *Prochlorococcus* shift northward in summer and fall as observed at the BATS station in the Sargasso Sea [*DuRand et al., 2001*]. *Prochlorococcus* and *Synechococcus* seem also to vary more in space in the Pacific Ocean. For example, *Synechococcus* is seldom dominant during northern summer in the Atlantic where it is replaced by both *Prochlorococcus* and nanoeucaryotes. These results are coherent with analysis of Atlantic Meridional Transect (AMT) transects data by *Zubkov et al.* [2000]. Several processes are likely controlling this difference in phytoplankton group succession in the two tropical oceans. *Zubkov et al.* showed that *Prochlorococcus* and *Synechococcus* are associated with different surface temperature water, but other elements such as iron availability due to differences in aerosol deposition (desert dust in the Atlantic), river inputs (Amazon and Congo in the Atlantic) and vertical mixing are also proposed by *Longhurst* [2007]. Nanoeucaryotes are also widely present at middle- and high-latitude waters. They can also be found in the southeastern Pacific Ocean during spring and summer, as well as in the northeastern Indian Ocean.

[17] As expected, a diatoms bloom is observed in the North Atlantic Ocean during spring. This bloom starts in the South-East of the basin in May around 40° N and moves northward up to 60° N in August. A similar evolution of the North Pacific diatoms bloom is observed, but delayed by 1 month.

[18] During the austral summer, large blooms of both diatoms and phaeocystis-like are observed in the southern Ocean. As in the Northern Hemisphere, diatoms blooms move poleward from November to January. These blooms will be discussed in more details in section 4. Finally, diatoms are also frequently observed, in area characterized by strong upwelling conditions, even from climatology monthly maps at a 1° resolution. Thus diatoms are dominant near Angola or Namibia coasts in the Atlantic or along the Equator and Peru coasts in the Pacific. Note that the observation of coastal diatoms bloom due to upwelling conditions are not optimal at $1 \times 1^\circ$ of resolution because of the limited spatial extension of these blooms. A spatial resolution of $\frac{1}{4}^\circ$ or less at one month scale maximum would be more adapted as shown in Figure 5. This is why diatoms bloom in the upwelling area are not always visible on the climatology maps in Figure 4.

3.2. Validation

[19] The geographical distributions and seasonal successions of major phytoplankton groups showed in Figure 4 are in good agreement with previous studies [e.g., *Dandonneau et al., 2004*; *Zubkov et al., 2000*; *Marty and Chiavèrini, 2002*; *DuRand et al., 2001*; *Steinberg et al., 2001*; *Longhurst, 2007*], as already discussed by *Alvain et al.* [2005] from the analysis of year 2001. We present here a tentative validation of the global monthly PHYSAT products using the two main consistent global pigment inventories data sets available: NOMAD [*Werdell and Bailey, 2005*] and GeP&CO

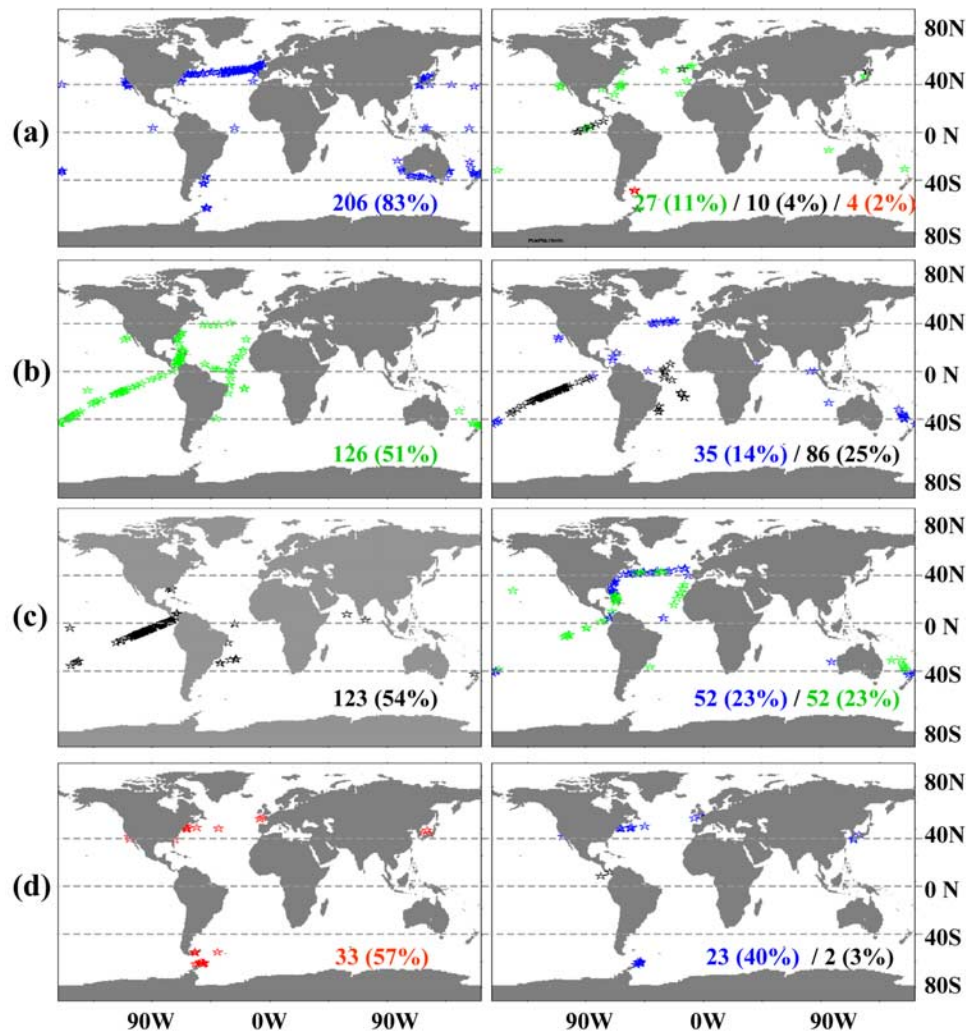


Figure 6. Validation of PHYSAT using GeP&CO and NOMAD data sets (see text): Each map displays the localization, the number and the percentage of valid (left column), and wrong (right column) PHYSAT identifications for (a) nanoeucaryotes, (b) *Prochlorococcus*, (c) *Synechococcus*, and (d) diatoms. Wrong identifications are separated by groups (blue for nanoeucaryotes, green for *Prochlorococcus*, black for *Synechococcus*, and red for diatoms).

[Dandonneau *et al.*, 2004]. We removed from the latter data set the 15% of data that were used for developing the PHYSAT method (see Alvain *et al.* [2005] for details). These two data sets contain the seven essential pigments used to labelize phytoplankton groups (Chlorophyll-*a*, Phaeophytin-*a*, Divinyl Chlorophyll-*a*, Peridinin, Fucoxanthin, 19'-hexanoyloxyfucoxanthin and Zeaxanthin), and 1286 pigments inventories \pm 378 from NOMAD and 908 from GeP&CO) satisfying our quality criteria, i.e., case 1 waters from Patt *et al.* [2003], Chl-*a* concentration values between 0.04 and 4 mg·m⁻³ and Phaeophytin-*a* relative concentration lower than 0.3, were selected. Over these 1286 inventories, 986 were successfully associated with one dominant phytoplankton group using the criteria on pigments of Alvain *et al.* [2005]. 779 of these inventories (233 from NOMAD and 546 from GeP&CO) were successfully associated with a phytoplankton group in the PHYSAT

monthly archive (1997–2006) for the month and the 1° × 1° grid cell that corresponds to the measurement. These inventories contain 247 water samples dominated by nanoeucaryotes, 247 by *Prochlorococcus*, 227 by *Synechococcus* and 58 by diatoms.

[20] Figure 6 provides a synthetic view of this validation exercise, by showing, for each of the four PHYSAT original groups, the localization, the number and the percentage of data properly (on the left) and erroneously (on the right) identified by PHYSAT. 87% of the pigments inventories corresponding to nanoeucaryotes are associated with the same phytoplankton group in the PHYSAT monthly product. PHYSAT leads to only a limited number of wrong identifications, mostly *Prochlorococcus* in the Northern Hemisphere and *Synechococcus* from one campaign in the Equatorial Pacific.

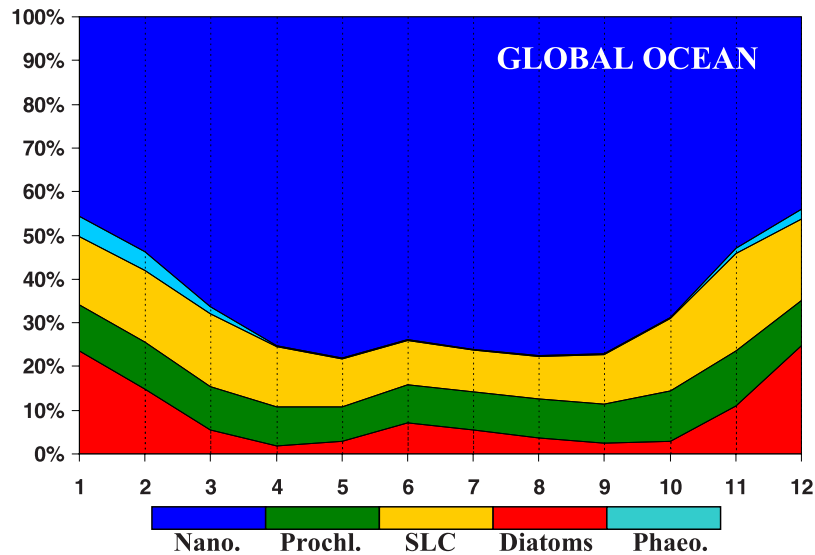


Figure 7. Mean seasonal evolution over the 1998–2006 period of the relative contribution of each phytoplankton group to the mean chlorophyll-a concentration for the global ocean, as obtained from the monthly climatology in Figure 4.

[21] The result of this validation is less satisfactory for both *Prochlorococcus* and *Synechococcus*, with slightly more than 50% of proper identification in the PHYSAT monthly products. Interestingly, most erroneous identifications for one of these two groups is associated with the other group, which suggests that there is an uncertainty in PHYSAT between *Prochlorococcus* and *Synechococcus*. This particularly the case in the Equatorial Pacific, where the two groups can be found. Note that this result is not surprising considering the close characteristics (geographical distribution, size and specific signal in PHYSAT) of these two groups.

[22] A significant fraction (57%) of Diatom pigment inventories are properly identified in $1 \times 1^\circ$ monthly PHYSAT products of dominant groups. Most erroneous identifications are associated with nanoeucaryotes and are found in waters which are shown in Figure 4 to be alternatively dominated by nanoeucaryotes and diatoms, essentially in the North Atlantic and Pacific and in the Southern Ocean. The temporal and spatial resolution used for this validation likely explains this result for a blooming phytoplankton group as diatoms. Another explanation for this result is that PHYSAT does not apply to pixels with Chl-a above $4 \text{ mg}\cdot\text{m}^{-3}$. This validation suggests that our global PHYSAT monthly climatology products certainly underestimates the diatom abundance.

3.3. Seasonal Succession

[23] Figure 7 shows the climatological (1998–2006) monthly mean evolution of the fraction of the global mean Chl-a for the various PHYSAT groups. To do so, every daily pixel of the 9-year SeaWiFS archive for which a dominant group is detected has been associated with its corresponding Chl-a to allow the computation of the monthly climatological mean Chl-a of each group. This figure shows that nanoeucaryotes are prevailing all yearlong, and contribute

for more than 70% during spring and summer months to almost 50% during winter. *Prochlorococcus* account for slightly less of the global Chl-a (maximum of 10%) than *Synechococcus* (15 to 20%), mostly because this latter group is usually associated with slightly higher Chlorophyll-a [Alvain *et al.*, 2005]. There is no significant seasonal variation in the contribution of these two groups, even if *Synechococcus* seems to be more abundant in winter than in summer (from 10 to 15%). On the contrary, the Diatom's contribution shows a significant seasonal cycle. The contribution of this group reaches at least 20 to 25% of the global Chlorophyll-a (considering the diatoms PHYSAT and chlorophyll a underestimation see Alvain *et al.* [2006]) during winter when the southern Ocean is blooming but accounts for less than 5% in April, May, September and October. The contribution of phaeocystis-like is much smaller (<5%) than that of diatoms, but follows a similar seasonal cycle.

4. Regional Studies

4.1. North Atlantic (40°N – $70^\circ\text{N}/10^\circ\text{W}$ – 60°W)

[24] The North Atlantic phytoplankton community is dominated all yearlong by nanoeucaryotes, as shown in Figure 8a. The diatom dominant contribution however increases significantly during the spring bloom, between May and August. Figure 8b shows that the North Atlantic Chl-a starts to increase in February, following the stratification of waters and the increase of sea surface temperature as shown in Figure 8c. Note that the temperature start to increase in March–April, as diatoms, after the beginning of the Chl-a increase. This observed shift is also certainly due to the specificity of PHYSAT, which allows to detect a group only when it become dominant, i.e., accounts for more than 60% of the whole phytoplankton [Alvain *et al.*, 2005]. The onset of the North Atlantic spring bloom is thus

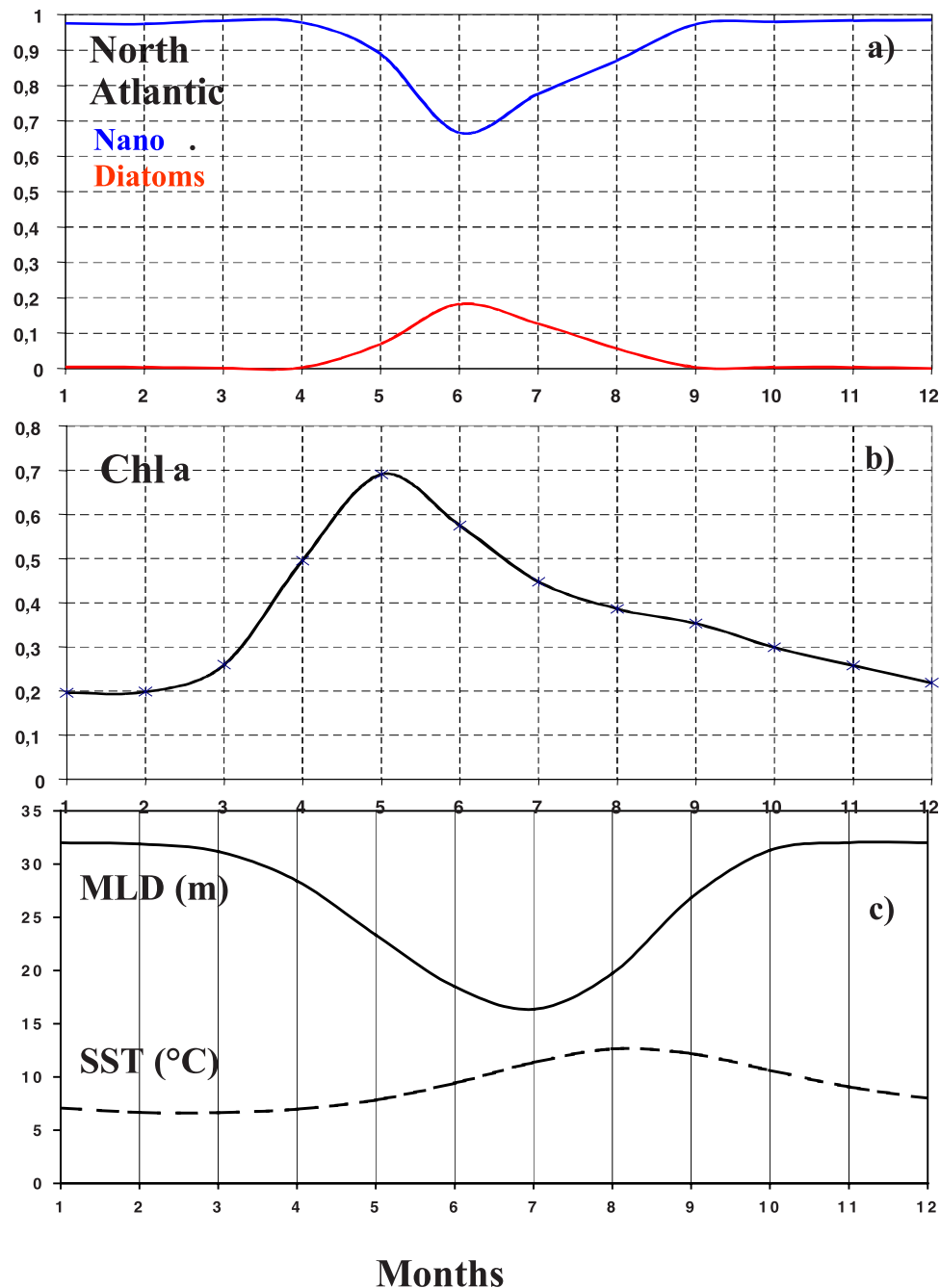


Figure 8. Mean seasonal evolution over the 1998–2006 period of: (a) the relative contribution of each phytoplankton group to the mean chlorophyll-a concentration for the North Atlantic Ocean (40°N – $70^{\circ}\text{N}/60^{\circ}\text{W}$ – 20°W), (b) the mean global chlorophyll-a concentration, and (c) the mean mixed layer depth [Le Quéré *et al.*, 2006] and the mean sea surface temperature (from ICDOADS -<http://www.cdc.noaa.gov>). Only groups that contribute for more than 5% for at least 1 month in the year are shown in this figure.

likely in March, certainly in waters with diatoms but not dominant in terms of PHYSAT criteria until April.

[25] Figure 9 shows that behind the general patterns evidenced by the climatology (see Figure 4), there is an important interannual variability in the amplitude and evolution of this diatom spring bloom. In addition to start and end later in 2001 than in 2005, the spring bloom has also

very different patterns with more diatoms detected between 40°N and 50°N in 2001 and between 50°N and 60°N in 2005. This variability is likely controlled by differences in water stratification and nutrient availability, as well as in light and temperature conditions from one year to another [Leblanc *et al.*, 2005]. Another implication of this strong geographical variability of the bloom is that the diatoms contribution

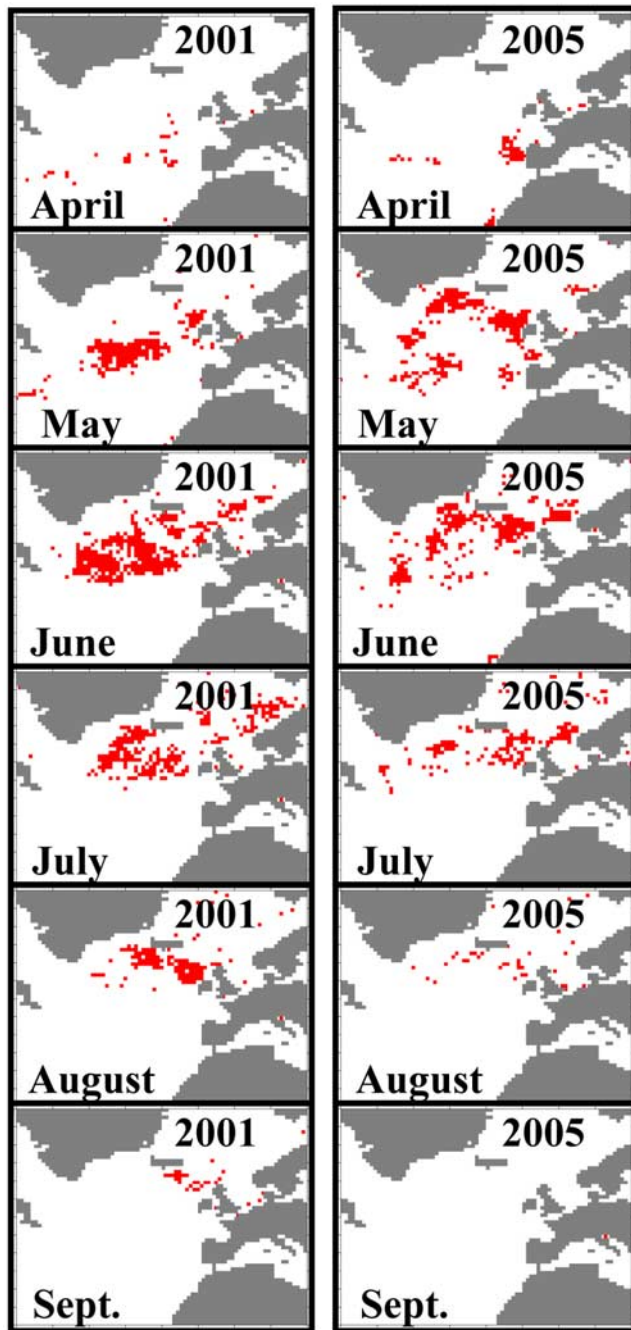


Figure 9. Comparison of evolution of the North Atlantic diatoms spring bloom (in red) for years 2001 and 2005.

deduced from the climatology in Figure 4 is probably underestimated.

4.2. Southern Ocean (40°S–70°S/180°W–180°E)

[26] The particularities of this region are a seasonal ice-cover and strong physical forcing. These specificity, associated with the absence of coastline and a specific topography, induce strong currents and nutrient inputs as well as large discontinuity front areas. All these characteristics associ-

ated with seasonal light variability allow large phytoplankton blooms in spring and summer. As shown in the climatology of Figure 4, these conditions facilitate the development of large blooms of both diatoms and phaeocystis-like. The diatoms blooms start and finish in the convergence zone around 40°S, respectively in October and April [Tremblay et al., 2002], while they cover most of the southern Ocean in December and January [Smetacek et al., 1990]. From November to March, diatoms blooms move similarly than in the Northern Hemisphere, i.e., from low to high latitudes, following the apparition of favorable conditions. In December and January, diatoms are detected also near the melting zone and along the stratified marginal ice zone as observed in the Ross Sea [Mangoni et al., 2004; Goffart et al., 2000; Smith et al., 2003]. The widest phaeocystis-like blooms are detected in January and February, after diatoms blooms, mostly in the southern Indian Ocean and South of Patagonia. Large patches of *Synechococcus* are also detected in association with diatoms in the convergence zone between 40°–50°S, as reported by Zubkov et al. [2000]. They are known to appear when conditions are not or no more favorable to diatoms, for example when the silicate concentration, which is essential to diatoms, is reduced to limiting values [Peeken, 1997; Selph et al., 2001].

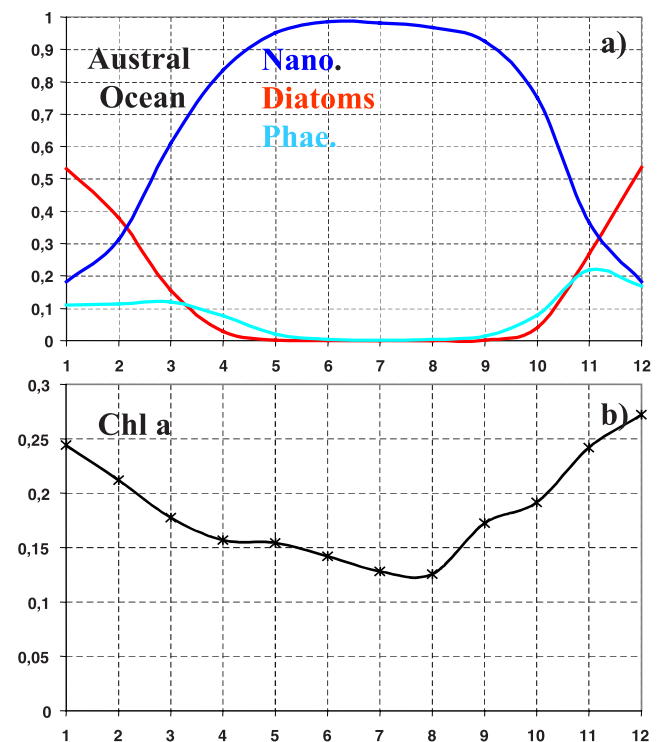


Figure 10. Mean seasonal evolution over the 1998–2006 period of: (a) the relative contribution of each phytoplankton group to the mean chlorophyll-a concentration for the Southern Ocean (40°S–70°S/180°W–180°E) and (b) the mean global chlorophyll-a concentration. Only groups that contribute for more than 5% for at least 1 month in the year are shown in this figure.

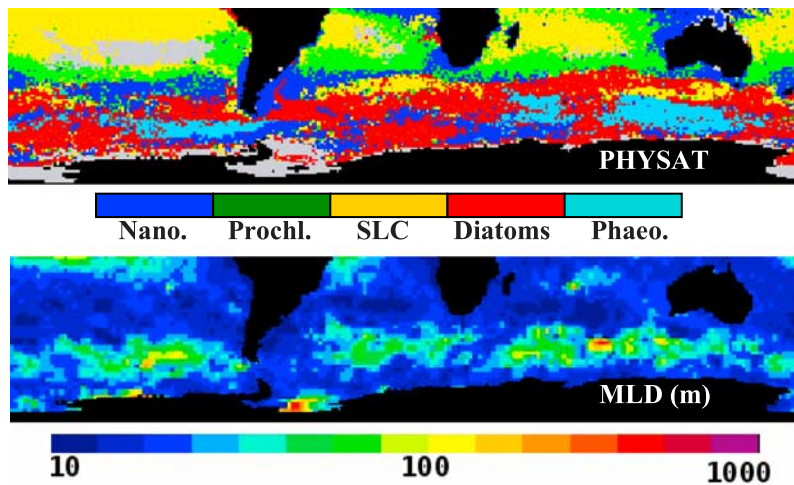


Figure 11. Comparison for the month of January of the climatology of the dominant phytoplankton group with the climatology of the mixed layer depth (in meters) from *de Boyer Montégut et al.* [2004].

[27] Figure 10 shows the strong seasonal cycle in the group contribution to the chlorophyll-*a*. Nanoecaryotes are responsible for most of the chlorophyll-*a* in the southern Ocean from March to October, but their contribution drops down to less than 50% from November to January when phaeocystis-like and diatoms are blooming to reach respectively 20% and 50% of the chlorophyll-*a*. According to PHYSAT, diatoms and to a lesser extent phaeocystis-like are thus the two main groups dominant in winter. This is in agreement with our current knowledge about the distributions of diatoms and phaeocystis-like, which are known to be major phytoplankton groups in winter in the nutrient-rich southern Ocean [Longhurst, 2007]. As in the North Atlantic, and likely for the same methodological reason, Figure 7 shows that Chl-*a* starts to increase before PHYSAT detects an increase in the diatoms and phaeocystis-like coverage. It is also known that the geographical distribution of these two groups is strongly controlled by the thickness of the mixed layer. diatoms are found preferentially in stratified waters which allow the bloom development [Weber and El-Sayed, 1987; Jochem et al., 1995], whereas phaeocystis-like usually prevails in regions of deep mixed layer [Arrigo et al., 1999; Goffart et al., 2000; Mangoni et al., 2004]. The comparison of the PHYSAT climatological map with a climatology of the mixed layer depth [de Boyer Montégut et al., 2004] for January shown in Figure 11 confirms this environmental control of the dominance of each group, mainly in the southern Indian and Pacific Oceans.

4.3. Equatorial Pacific (5°S–5°N/80°W–170°W)

[28] The eastern Equatorial Pacific is of special interest for the global carbon cycle because it behaves both as a large natural source of CO₂ for the atmosphere and as a sink through primary production, which induces atmospheric CO₂ uptake [Murray et al., 1995]. The equatorial Pacific is characterized by high nutrient concentrations, brought up by the quasi-permanent upwelling. However, Chl-*a* remains

relatively low, so that this region has been described as having High Nutrients-Low Chlorophyll characteristics (HNLC [Thomas, 1979]). This apparent paradox is explained by the steady upwelling conditions, that favor high level of grazer population, and thus limit the growth of the phytoplankton [Walsh, 1976; Cullen, 1991], or by the lack of iron [Coale et al., 1996], or by both factors [Landry et al., 1997].

[29] The PHYSAT climatology in Figure 4 shows a large dominance of *Synechococcus* and *Prochlorococcus* in the Equatorial Pacific all yearlong, in agreement with available observations which show that phytoplankton community in this region is dominated by small cells, less than 5 μm in diameter [Chavez et al., 1999]. Even with PHYSAT uncertainty explain in section 1.3 about *Synechococcus* and *Prochlorococcus* distinction in this region, the *Synechococcus* contribution to the total Chl-*a* seems to be higher (be 3 to 8 times) than that of *Prochlorococcus*, as shown in Figure 12a. Figure 12b shows that there is no clear correlation between the variation of the contribution of these two groups and the variation of the total Chl-*a* over the area. On the contrary the seasonal evolution of the diatoms contribution in the Equatorial Pacific resembles that of the total Chl-*a* (Figure 12c). It is generally admitted that diatoms do not contribute to more than 20 % of phytoplankton biomass [Blanchot et al., 2001; Kobayashi and Takahashi, 2002; Dandonneau et al., 2004] in this region, but blooms however have been exceptionally reported in this area [Bender and McPhaden, 1990; Chavez et al., 1990; Archer et al., 1997]. How common are such diatoms blooms in the Equatorial Pacific remains unknown because of the paucity of in situ measurements. They may break out when equatorial upwelling is intense and non limited to the coastal region, as shown in Figure 13, corresponding to “La Niña” event of 1998 bringing large amounts of nutrients into the photic layer [Strutton and Chavez, 2000; Ryan et al., 2002]. Iron limitation is especially important for diatoms, which

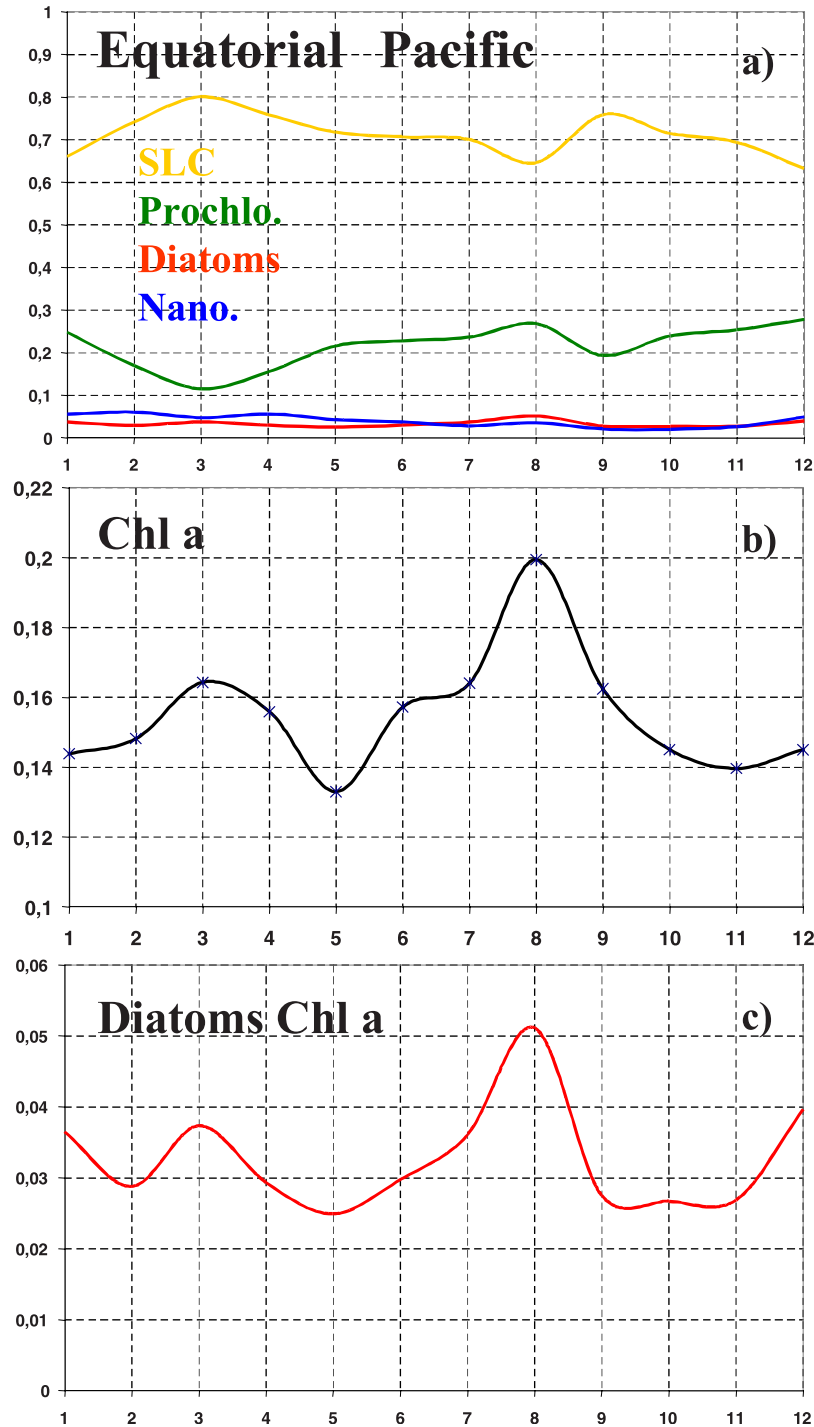


Figure 12. Mean seasonal evolution over the 1998–2006 period of: (a) the relative contribution of each phytoplankton group to the mean chlorophyll-a concentration for the Equatorial Pacific (5°S – 5°N / 170°W – 80°W), (b) the mean chlorophyll-a concentration, and (c) the mean chlorophyll-a concentration associated with diatoms. Only groups that contribute for more than 5% for at least 1 month in the year are shown in this figure.

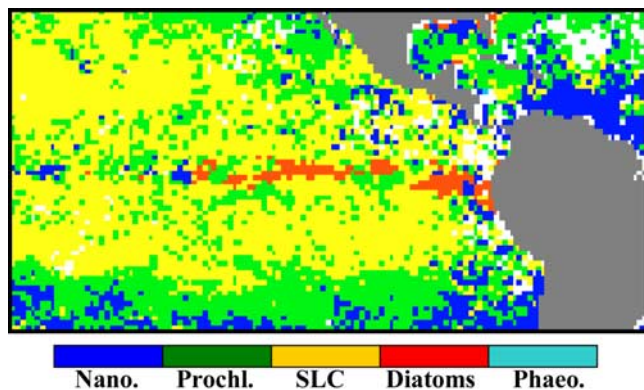


Figure 13. The unusual diatom bloom in the Equatorial Pacific region in August 1998.

need high iron concentration to achieve maximum growth rates. When nutrients and iron are abundant in the photic layer, diatoms grow rapidly, dominate the phytoplankton population, and give rise to massive exports of organic carbon to the sediment as shown by *Greene et al.* [1991], *Cavender-Bares et al.* [1999], and *Boyd et al.* [1998].

5. Conclusion

[30] PHYSAT [*Alvain et al.*, 2005] is a classification technique that allows to identify four major phytoplankton groups (diatoms, Prochlorococcus, Synechococcus, nanoeucaryotes) from the spectral shape of the normalized water-leaving radiance (nLw) of the SeaWiFS ocean color sensor. In this paper, we have slightly modified PHYSAT by improving the nLw normalization technique. The identification of an additional group, phaeocystis-like, is also discussed.

[31] This new version of PHYSAT has been applied to the SeaWiFS archive (1998–2006) of daily global level-3 products. A validation of PHYSAT monthly maps are presented using GeP&CO and NOMAD pigments data set. Percentage of valid and wrong diagnostics are detailed according to each group. PHYSAT monthly maps were next used to derive a monthly climatology of the distribution of dominant phytoplankton groups in the world ocean. The climatology shows that nanoeucaryote is the dominant species at the global scale. Its contribution to the global biomass varies between 45% in winter and 75% in summer. This group is mostly observed at mid and high latitudes, whereas Prochlorococcus and Synechococcus prevail in tropical waters. Synechococcus contribute to about 15% of the global biomass and is mostly observed in highly oligotrophic waters, whereas Prochlorococcus are found in more productive regions, even if they contribute only to about 10%. In summertime, diatoms invade almost entirely the Southern Ocean, as phaeocystis-like to a lesser extent.

[32] A regional analysis of the climatology highlights the major role of diatoms on the seasonal cycle of the primary production at high latitudes. Their contribution accounts for up to 20% (respectively 50%) of the total Chl-a in the North Atlantic (respectively Southern Ocean) in June (respectively in January and December). The North Atlantic diatoms

bloom shows a very large interannual variability, in terms of both timing and geographical location. Large phaeocystis-like blooms are also detected in the Southern Ocean, with a maximum contribution of 20% of the total Chl-a in November and December, i.e., one month before the period of maximum diatoms contribution. A comparison with a climatology of the mixed-layer depth [*de Boyer Montégut et al.*, 2004] reveals that phaeocystis-like have affinities with deep mixed-layers and diatoms prevailing in the more stratified waters.

[33] The last region that has been studied in details in this paper is the Equatorial Pacific. Synechococcus and Prochlorococcus, prevail in this region, but our archive shows that the ecosystem structure is sensitive to climate variability. Thus when nutrients and iron are abundant in the photic layer, diatoms can also grow rapidly and dominate the phytoplankton population.

[34] These regional analyses demonstrate the importance of the PHYSAT archive presented in this paper to improve our knowledge on the temporal and geographical distribution of the major phytoplankton groups at the global scale, but also to study the impact of climate variability on ecosystems. More detailed analyses of the mechanisms responsible for these controls should allow to a better prediction of the impact of ongoing climate change on the composition of marine ecosystems.

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