Seasonal and interannual variability of ocean color and composition of phytoplankton communities in the North Atlantic, Equatorial Pacific and South Pacific.

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Abstract

Monthly averaged level-3 SeaWiFS chlorophyll concentration data from 1998 to 2001 are globally analyzed using Fourier's analysis to determine the main patterns of temporal variability in all parts of the world ocean. In most regions, seasonal variability dominates over interannual variability, and the timing of the yearly bloom can generally be explained by the local cycle of solar energy. The studied period was influenced by the late consequences of the very strong El Niño of 1997-98. After this major event, the recovery to normal conditions followed different patterns at different locations. Right at the equator, chlorophyll concentration was abnormally high in 1998, and then decreased, while aside from the equator, it was low in 1998, and increased later when equatorial upwelled waters spread poleward. This resulted in opposed linear trends with time in these two zones. Other noticeable examples of interannual variability in the open ocean are blooms of Trichodesmium that develop episodically in austral summer in the south-western tropical Pacific, or abnormally high chlorophyll concentration at 5°S in the Indian Ocean after a strong Madden-Julian oscillation. Field data collected quarterly from November 1999 to August 2001, owing to surface sampling from a ship of opportunity, are presented to document the succession of phytoplankton populations that underlie the seasonal cycles of chlorophyll abundance. Indeed, the composition of the phytoplankton conditions the efficiency of the biological carbon pump in the various oceanic provinces. We focus on the north Atlantic, Caribbean Sea, Gulf of Panama, equatorial Pacific, south Pacific subtropical gyre, and south-western tropical Pacific where these field data have been collected,. These data are quantitative inventories of pigments (measured by HPLC and spectrofluorometry), and picoplankton abundance (*Prochlorococcus*, *Synechococcus*, Picoeucaryotes and bacteria). There is a contrast between temperate waters where nanoplankton (as revealed by pigments indexes) dominate during all the year, and tropical waters where picoplankton dominate. The larger microplankton, that make most of the world ocean export production to depth, rarely exceed 20% of the pigment biomass in the offshore waters sampled by these cruises. Most of the time, there are large differences in the phytoplankton composition between cruises made at the same season on two different years.

1. Introduction

Marine primary production can be assessed directly using flux measurements in the field, such as ^{14}C fixation experiments. However, these measurements are expensive and time consuming, and world ocean data bases contain much more data of chlorophyll *a* concentration. The later e can easily be measured, and it is a key variable in models of photosynthesis. Errors in chlorophyll measurements are sometimes high, and often consist in biases caused by handling artifacts (for instance, too high filtration pressure, or poor conditions for preservation of samples) or by the measurement concept itself (chlorophyll *b* seen as pheophytin *a* in the fluorescence-acidification technique, or *in vivo* chlorophyll fluorescence taken as a proxy for the chlorophyll *a* concentration). The other important variables that force primary production are light, temperature, and nutrient concentrations, the variability of which are much better known and understood than that of chlorophyll concentration. As a consequence, in the past, we have learned more about variability of marine primary production by looking at the distribution of nutrients and coupled physical-biogeochemical models than from the numerous measurements of chlorophyll *a* concentration made at sea (Sverdrup, 1955; Dutkiewicz *et al.*, 2001).

The first series of satellite sea color data, provided by the Coastal Zone Color Scanner (CZCS), showed that chlorophyll *a* concentration could be estimated from space, and over sampled, under clear sky conditions. Unfortunately, the CZCS was not programmed for global coverage, and the 1978 to 1989 dataset has large gaps in many regions. Basing on these data however, it was possible to identify ecological provinces and to describe their annual cycle of phytoplankton (Longhurst, 1998). One decade later, the SeaWiFS sea color sensor was launched and is providing data that cover the global ocean at 9 km resolution (1 km for Local Area Coverage mode). This global dataset is not affected by cruise or method biases, unlike the *in situ* data sets. Furthermore, careful calibration of this instrument (Barnes *et al.*, 2001; Eplee *et al.*, 2001) may make it possible to detect possible long-term evolution of chlorophyll *a* concentration with time, a point of interest in the context of climate change. Algorithms that convert the signal seen by the satellite into chlorophyll *a* concentration are improving, and may provide estimates of new geophysical quantities in the future, such as other phytoplankton pigments or particulate organic carbon (Sathyendranath *et al*; 1994; Stramski *et al*., 1999; Loisel *et al*., 2001).

In this work, we used a simple and global analysis of the SeaWiFS data to describe the major patterns of seasonal and interannual variability over the period from January 1998 to

December 2001. An additional objective was to estimate how variations in chlorophyll concentration correspond to variations in composition of the phytoplankton. Indeed, the impact of primary production on marine geochemistry strongly depends on the species of phytoplankton that make photosynthesis. Well known examples are biocalcification by the Coccolithophorids, that reduces the alkalinity of seawater and thus modifies the dissolved carbonate equilibrium of (Robertson *et al*., 1994) or diazotrophy by the cyanobacteria *Trichodesmium* that increases the pool of reactive nitrogen through fixation of atmospheric N_2 (Capone *et al*., 1997). Aside from these extremes, the fraction of marine primary production that sinks to depth (export production) depends on the phytoplankton species that are present: the larger species (diatoms, dinoflagellates) are responsible for massive export of carbon while most of the production made by smaller species is rapidly recycled in place. Attempts have been made to detect some phytoplankton species from space (Brown and Yoder, 1994; Subramaniam *et al*., 1999) but these are limited to surface bloom conditions, and knowledge of the distribution of phytoplankton groups is still obtained from oceanographic cruises. Here, we used field data collected quarterly on a commercial shipping line that spans a wide range of latitude and oceanic conditions, as part of the GeP&CO and GeP&SIMBAD programs. GeP&CO (Geochemistry, Phytoplankton, and Color of the Ocean) is a component of the French program PROOF (PROcessus Océaniques et Flux), supported by the Institut National des Sciences de l'Univers, the Institut de Recherche pour le Développement, the Centre National d'Etudes Spatiales, and the Institut Français pour l'Exploration de la Mer. GeP&SIMBAD (GeP&CO and SIMBAD) is supported by the Centre National d'Etudes Spatiales.

2. Data and methods

This study is based on monthly averaged level-3 binned SeaWiFS chlorophyll data issued by the third reprocessing. Data are first averaged on a 0.5° longitude × 0.5° latitude grid, and each time series in all grid elements was analyzed using Fast Fourier Transform (FFT). The grid elements where the surface of the ocean was not seen by SeaWiFS during more than two consecutive months, or more than twelve months over the 1998-2001 period, were removed from the analysis. Missing months were interpolated using previous and posterior available data at the same location. The counterpart of this treatment is that it excludes many pixels at high latitudes where cloud coverage often hinders observation of sea

color by satellites. It is balanced by the simplicity and efficiency of FFT to analyze the variance of periodic signals. Prior to FFT, the data in each grid element were corrected for possible linear trend. Once this linear trend was subtracted, FFT was applied on each 0.5 x 0.5 degree pixel time series from January 1998 to December 2001. The linear trend, as well as the first harmonics at 48, 24 and 16 months, account for interannual variability. The harmonics corresponding to 12 and 6 month periods summarize the seasonal cycle. We checked that other harmonics have small amplitude and thus, they were neglected.

The field data that document the variability of phytoplankton populations originate from the GeP&CO cruises (http://www.lodyc.jussieu.fr/gepco) on a ship of opportunity, MS Contship London. These cruises sailed from Le Havre (France) to Nouméa (New Caledonia) every 3d month since October 1999. A scientific observer onboard sampled surface seawater from every 4 hours. Filtrations were made immediately on Whatman GF/F filters and filters were stored at -80 °C until analysis in the laboratory after the cruises. The analysis of photosynthetic pigments was made by spectrofluorometry for chlorophyll *a*, *b*, *c1+c2* and *c3*, divinyl-chlorophyll *a* and *b*, and related pheopigments, according to Neveux and Lantoine (1993), and by High Performance Liquid Chromatography (HPLC) for peridinin, 19'butanoyloxyfucoxanthin (19'BF), fucoxanthin, 19'hexanoyloxyfucoxanthin (19'HF), prasinoxanthin, violaxanthin, diadinoxanthin, alloxanthin, zeaxanthin and β-caroten (Mantoura and Llewellyn, 1983). Our HPLC equipment also measures the chlorophyllous pigments giving results that generally agree with results from spectrofluorometry, but show a greater dispersion. Comparisons of field and satellite data use the sum chlorophyll *a* + divinyl-chlorophyll *a*, and the SeaWiFS level-3 chlorophyll data issued by the third reprocessing, hereafter mentioned as GeP&CO Chl and SeaWiFS Chl. The logarithms of co-localized SeaWiFS and GeP&CO Chl data are tightly correlated (R = 0.93), as shown in Fig. 1. For the purpose of diagnosing the regional and seasonal composition changes of the phytoplankton, we used pigments indexes proposed by Bidigare *et al.* (1990) and Claustre (1994). These indexes are based on the observation that fucoxanthin generally characterizes the diatoms, peridinin the dinoflagellates, 19'HF, 19'BF, alloxanthin and chlorophyll b the nanoflagellates, zeaxanthin and divinyl-chlorophyll *b* the picoplankton. The phytoplankton can thus be distributed into size classes as follows:

microplankton will be represented by *Micro* = (peridinin + fucoxanthin) / Σdiagpigs,

nanoplankton by *Nano* = (19'HF + 19'BF + alloxanthin + chlorophyll *b*) / Σdiagpigs,

picoplankton by *Pico* = (zeaxanthin + d-chlorophyll *b*) / Σdiagpigs,

where Σdiagpigs is equal to peridinin + fucoxanthin + 19'HF + 19'BF + alloxanthin + chlorophyll *b* + zeaxanthin + d-chlorophyll *b*.

Counts of picoplankton cells are also routinely made on the GeP&CO cruises using flow Cytometry. We thus obtain the abundances of Cyanobacteria *Prochlorococcus* and *Synechococcus*, and of picoeucaryotes (Partensky *et al.*, 1996; Blanchot and Rodier, 1996). Detection and counting of genus *Synechococcus* is based on the yellow-green and orange fluorescence of its dominant pigment phycoerythrin (PE). This pigment however exists in other Cyanobacteria such as *Synechocystis* (Neveux *et al.*, 1999), or red algae, and the term *Synechococcus* in this work may sometimes be inappropriate. The general term "PE-containing picocyanobacteria" is thus preferred (Wood *et al.*, 1999). These counts together with the pigments indexes are used here to qualitatively describe the biomass observed by SeaWiFS in the regions sampled by GeP&CO.

3. Interannual variability

3.1. Linear trend

Prior to the FFT analysis, a linear trend $p \times t$, where p is the chlorophyll per month increase, and t is time in months from January 15, 1998 to December 15, 2001, was subtracted from the SeaWiFS monthly chlorophyll concentrations in each 0.5° x 0.5° grid elements. The distribution of p in the world ocean is shown on Fig. 2. Rapid increases (greater than 0.004 mg m^{-3} month^{-1}) in chlorophyll concentration can be seen in some restricted areas. Among these are the Costa Rica Dome region, the plumes of Amazon and Rio de la Plata rivers, the east of the Kerguelen islands, upwelling off Somalis, and tropical eastern boundary upwellings (California, Humboldt, Mauritania, Benguela) where high year to year differences in the area influenced by upwelling have been shown by Carr (2002),. Regions in which a rapid decrease (faster than 0.004 mg m^{-3} month^{-1}) is observed are mostly the subtropical front east of Cape Agulhas, east of new Zealand, and east of Cape Horn, and small spots in coastal areas, except along the eastern coast of North America where the decrease affects most of the coastline. These strong trends in restricted places generally correspond to very dynamic areas for which a climatology established on a 4 year time series is not yet stabilized. They are caused by year to year variability in local dynamics, and understanding all the phenomenon that gave rise to these anomalies is beyond the scope of this study. In all other parts of the

ocean, this linear trend is less than 0.004 mg Chl m^{-3} month^{-1} in absolute value. Positive and negative trends evidenced in Fig. 2 however seem to be organized by large regions rather than randomely, and thus deserve attention. The trends in the equatorial Pacific can be explained by the recovery from the 1997-98 El Niño. The equatorial Pacific is known as a HNLC area (high nutrient – low chlorophyll) where the growth of phytoplankton is limited by lack of iron, and by equilibrium between grazers and phytoplankton that prevents exponential growth of the later (Landry *et al.*, 1997). At the end of this warm episode (early 1998), the entire equatorial tongue of water had a low chlorophyll concentration. When upwelling started again, the biological response was immediate and intense, in the form of a sharp chlorophyll maximum right at the equator (Murtugudde *et al.*, 1999; Radenac et al., 2001). Certainly, the zooplankton populations had been submitted to food shortage and high mortality during the El Niño episode, and when upwelling was restored, grazing pressure was low (tropical copepods have a generation time of about three weeks) and could not restrain the exponential growth of the phytoplankton. It is possible too that iron supply has been enhanced during this period, but we know no report of such supply. Later, chlorophyll concentrations decreased to their usual values, as seen by the decrease in 1998-2001 right at the equator in the Pacific (Fig. 2). Aside from the equator, in the equatorial tongue of upwelled water, the chlorophyll concentration was low in 1998 after the El Niño, and increased later when upwelling started again and upwelled waters spread over the region. A Chl increase with time was observed at equatorial latitudes in the Atlantic and Indian Oceans, and also at latitudes greater than 45° in all oceanic basins. Oppositely, oligotrophic gyres between 20 and 40° in latitude, as well as the western Pacific warm pool, showed a slight decrease in chlorophyll concentration. Obviously, the strong 1997-98 El Niño had a profound impact on the equatorial Pacific, and also on the Indian Ocean (Mutugudde *et al.*, 1999). It resulted in abnormal conditions in most of the tropics, and affected the first year of our studied period. The following years were a priori normal years, in such a way that the period from 1998 to 2001 includes a regime change which can explain many of the observed linear trends. In other regions where SeaWiFS chlorophyll concentration changed linearly with time since January 1998, a possible effect of drift in the calibration of the instrument can not be absolutely excluded. For instance, in our analysis, the Mediterranean Sea shows a decrease in Chl over the studied period. Bricaud *et al.* (2002) also found high interannual variability in this region, and drew attention to the many sampling and technical artefacts that may invalidate such conclusions. The occurrence of spatially well-organized positive and negative trends gives confidence to the hypothesis that Chl responded to climatic forcing on a multiyear time scale. The question of a change in

Chl caused by long-term global warming cannot be answered using such a short time series which, in addition, includes a major event such as the 1997-98 El Niño.

3.2. Interanual vs seasonal variability

The above linear trend and the various terms issued from the FFT analysis account for the variance of Chl at different frequencies. The variance Vs that corresponds to the seasonal cycle can be estimated as half of the sum of squares of amplitudes of 12, 6, 4, 3, 2.4 and 2 month harmonics, i. e. $Vs = 1/2 \ (a_4^2 + a_8^2 + a_{16}^2 + a_{20}^2 + a_{24}^2)$. In fact, only a_4 and a_8 were considered, the terms at smaller periods being negligible. Similarly, the interannual variance can be computed as the sum of a periodic component: $1/2 \ (a_1^2 + a_2^2 + a_3^2 + a_5^2 + ...)$, to which the variance caused by the linear evolution must be added, i. e. $1/3 \ (48 \ p/2)^2$, where p is the average monthly increase in chlorophyll over the 48 month analyzed period. Here too we neglected the terms a_5 (9.6 month) and further ones, which are very small. Fig. 3 presents the distribution of the ratio of interannual to total variance:

$$V_i / V = (1/3(24p)^2 + 1/2(a_1^2 + a_2^2 + a_3^2)) \ (1/3(24p)^2 + 1/2(a_1^2 + a_2^2 + a_3^2 + a_4^2 + a_8^2))^{-1} \quad (1)$$

The global map of V_i/V is heavily marked by a large area in the equatorial Pacific and eastern Indian Ocean where interannual variance is higher than seasonal variance. This region is well-known for interannual variability caused by ENSO, but it appears here with a size that is much larger than the equatorial Pacific cold water tongue, i. e. as a triangle from 20°S to 30°N in the eastern pacific, with a tip at the equator, 80°E in the Indian Ocean. Inside this huge area where interannual variability dominates over seasonal variability, there are zonal stripes where seasonal variability still dominates. Since the studied period (1998-2001) started from abnormally warm conditions caused by the 1997-98 El Niño, it is tempting to explain the interannual variance by this warm event that cut off the huge equatorial upwelling source of nutrients. We have mentioned above that recovery from nutrient poor El Niño conditions at the beginning of 1998 leading to normal nutrient rich conditions later could explain the positive linear trend observed away from the equator over the period (Fig. 2). North of the equator, at $4° – 5°$ N and east of $160°$ W, the zone affected by tropical instability waves also varies more on an interannual basis than on a seasonal one. Indeed, tropical instability waves that strongly impact the distribution of chlorophyll at the sea surface (Murray *et al.*, 1994; Strutton *et al.*, 2001) do not occur during El Niño episodes. Consequently, this area had low

chlorophyll concentrations at the beginning of 1998. In addition, tropical instability waves were exceptionally strong in January-March 2000, resulting in chlorophyll concentrations much higher than during the same period in 1999 and 2001. The tropical Pacific Warm Pool is a region known as permanently oligotrophic and thus with low chlorophyll concentration and low variability. It is marked by a zonal stripe at about 13°N, from 145°E to 160°W, where interannual variance represents more than 70% of the total variance. West of this zone, the interannual anomaly consists mainly in a chlorophyll maximum during the beginning of 1998, at the end of the El Niño. Such chlorophyll maxima when the Warm Pool waters have been drained eastwards by the North Equatorial Counter Current have already been observed after strong El Niño episodes (Dandonneau, 1992). Farther east in this stripe, the variations with time are quite different, with irregular patterns and a maximum generally in 1999. Here, interannual variability dominates over seasonal variability primarily because the later is very small. At the western tip of this triangle, the area at about 5°S between 70°E and 90°E in the Indian Ocean has a high interannual variability. The strong chlorophyll maximum that happened in January and February 1999 is not a response to the 1997-98 El Niño. This anomaly could rather be a response to a very strong Madden-Julian oscillation that occurred at this time inducing a cooling of sea surface temperature by more than one degree through Ekman pumping and brought nutrients to the photic layer (Jérome Vialard, personal communication).

The southwestern tropical Pacific, between New Caledonia, Vanuatu and the Fiji Islands also shows higher interannual than seasonal variability. This is an area where *Trichodesmium sp.* is known to occur frequently, but irregularly, in summer (Dandonneau and Gohin, 1984; Dupouy *et al.*, 2000). At the same latitude and western position in the Indian Ocean, at the southeast of Madagascar, an area with similarly high interanual variability caused by blooms in summer in tropical stratified waters, that Longhurst (2001) attributed to input of nutrients by mesoscale activity, might too have its origin in *Trichodesmium* blooms.

At high latitudes (>40°), especially in the Southern Ocean, there are many places along the subtropical convergence where interannual variability has been higher than the seasonal variability. In this frontal system, limitation by iron and lack of vertical stability is thought to maintain the chlorophyll concentration at low levels (HNLC conditions). Interannual variability here probably corresponds to localized episodes of exponential growth of the phytoplankton triggered by iron inputs and by the strong mesoscale dynamics and eddies that characterize this zone (Banse, 1996).

Generally, many structures observed in Fig. 2 also appear in Fig. 3. This was expected since the linear trend p is used to compute V_i/V (equation 1). However, the periods at 48, 24 and 16 month also contribute to this estimate. It is remarkable that the oligotrophic subtropical gyres where Chl is low all year are nevertheless dominated by the seasonal cycle (Fig. 3). The Chl linear decrease in these later regions merits attention, and should be re-examined on a longer time-series.

4. Occurrence time of the seasonal chlorophyll maximum

The chlorophyll concentration at the sea surface generally responds to the seasonal cycle of solar energy that strongly impacts the timing and intensity of vertical nutrient flux, and vertical stability. Hence, at 50°S, the peak of biomass occurs in November, December or January, i. e. at the season where light and vertical stability combine to trigger growth of phytoplankton (Fig. 4). At lower latitudes, the chlorophyll maximum occurs earlier, as soon as July (i. e. in austral winter) at about 20°S. The dominant scheme is thus a transition from a high latitude system where the bloom is triggered by higher temperature, light and vertical stability conditions (Sverdrup, 1953; Siegel *et al.*, 2002), to a low latitude system where it is triggered instead by less vertical stability that allows deeper nutrients to fuel the permanent warm, nutrient exhausted mixed layer (Dandonneau and Gohin, 1984). Starting for instance from 20°S, 100°W in the south Pacific, the peak of chlorophyll occurs in July ; at 40°S, it occurs in August, and is more and more delayed when moving southwards, until it occurs in December at 50°S . In the north Atlantic, a symmetrical scheme is found with a maximum in January at 20°N, 20°W, shifting progressively to May at 50°N. A similar transition can be seen in the north Pacific, but north of 40°N, there is an abrupt change from a maximum in spring to a fall maximum in September and October. Identically, there is an abrupt transition between 70°E and 135°E in the southern hemisphere from a chlorophyll maximum in austral spring, north of the south subtropical convergence at about 40°S, to a maximum as late as March immediately south of this convergence, as if starting of the annual bloom in spring was inhibited.

These two areas in the northern Pacific and Southern Ocean are known to have iron limitation that prevents rapid use of the nutrients that are made available after winter mixing and stratification in spring. The heterogeneity that can be seen south of 40°S may result from the interaction of sporadic atmospheric iron inputs and episodes during which the upper water

column is stabilized, thus making earlier or delaying the annual bloom of phytoplankton by several months.

At lower latitudes near the equator, the maximum occurs from August to October, caused by intensification of the equatorial upwelling after the northward migration of the Inter Tropical Convergence Zone in boreal summer, and this feature develops farther to the south than to the north in both the Pacific and the Atlantic Ocean. A large area centred at 115°W, 15°S instead shows a maximum at the beginning of the year. This corresponds to an anomaly caused by a strong negative chlorophyll concentration anomaly through 1998. This area indeed presents a very high interannual to seasonal variability ratio (Fig. 3). The seasonal pattern is different in the Indian Ocean where the winter monsoon north-easterly winds are favourable to upwelling and trigger seasonal chlorophyll maximum in September to November as previously described by Banse and McClain (1986).

The two above mentioned places with high interannual variability in the southwest tropical Pacific and southwest tropical Indian Ocean (respectively, between New Caledonia and Fiji Islands, and southeast of Madagascar) stand out here too as the chlorophyll maximum occurs in austral summer. In this period, the photic layer exhausted in nutrients, combined with strong vertical stratification, do not favour phytoplankton growth. Blooms of Trichodesmium are frequent in austral summer in the first area (Dandonneau and Gohin, 1984; Dupouy *et al.*, 2000). This species can fulfil its nitrogen requirements using N_2 from the atmosphere (Carpenter and McCarthy, 1975) and might be responsible for the bloom near Madagascar that occurs under similar low nutrient and high vertical stability conditions.

This description is generally in agreement with the detailed, province by province, analysis by Longhurst (1998), based on the data collected by the Coastal Zone Color Scanner and on published data. He identified 51 provinces. Comparison could not be made for 10 provinces which were excluded from our analysis due to cloudy conditions. In 32 provinces, the seasonal chlorophyll maximum occurs at the same months as in our analysis of the four first years of SeaWiFS data. Exceptions to this overall excellent agreement are listed in table 1. In some cases, the synthesis by Longhurst and the present analysis differ by only a few months. This is the case for the Eastern India Coast, for the North Pacific Subtropical Gyre, and for the Pacific Equatorial Divergence. In some other cases, there is nearly a phase opposition between our respective results: the Red Sea, the Tasman sea, and the Subantarctic Water Ring. In these provinces, a spring bloom when the surface mixed layer is formed, and an autumn bloom when it deepens and entrains deeper nutrients rich water may occur each year, separated by about six months. The stronger of the two events determines the yearly

maximum, but it may alternate from year to year. The other provinces listed in Table 1 exhibit a high variability in Fig. 4. Analysis on a longer time series is needed to ascertain the conclusions of this study. The chlorophyll maximum in the Indian Ocean Monsoon Gyres occurs in August over most of this province, but it occurs in December to March in a zone slightly south of the equator. As previously mentioned, this might be caused by Madden-Jullian Oscillations that strongly impact this region during the winter monsoon.

5. Large scale ecosystem observations by GeP&CO

Marine primary production can be estimated from chlorophyll satellite data with acceptable accuracy (Morel, 1991, Behrenfeld and Falkowski, 1997). However, what is pertinent in global carbon geochemistry is new production. The fraction of primary production that corresponds to new production, i. e. the f ratio (Dugdale and Goering, 1967), is strongly dependent on the population of phytoplankton. The general consensus is that large diatoms grow on nitrate and rapidly export large amounts of carbon, corresponding to high f values, while most of production by small picoplankton is tightly coupled to grazing and is recycled in the photic layer. The information on phytoplankton populations is available only from oceanographic cruises, and thus, only exists at given places and time. Ecological provinces have been proposed in the ocean (Longhurst, 1998) inside which it is expected that these populations are homogeneous. We examine here those provinces where we have collected pigment data and cells counts of picoplankton during quarterly sampling on eight GeP&CO cruises from November 1999 to August 2001 (Fig. 5).

5.1. The North Atlantic Drift Province

This region is well known for its phytoplankton bloom in spring and was the site of the first JGOFS process study : the North Atlantic Bloom Experiment (Lochte *et al.*, 1993). It is also the place where Sverdrup (1953) has developed his theory on the conditions of light and vertical stability that are needed for the blooming of phytoplankton, recently completed by Siegel et al. (2002) to account for grazing and other aspects of the ecosystem. Fig. 6$_a$ shows the results from the GeP&CO cruises, superimposed on the results of our analysis of SeaWiFS data (linear trend, plus harmonics at 48, 24, 16, 12 and 6 months). The quantitative agreement between the two sets of data is generally good, with SeaWiFS chlorophyll however slightly

higher than GeP&CO field results at most cruises, except in April 2001. The maximum occurs in spring on both data sets, and an autumn maximum can also be seen. Minima are in winter and summer. At all time, the nanoplankton, estimated using pigments indexes, exceeds 70% of the biomass. The microplancton (that mostly represents diatoms, indicated by fucoxanthin, since peridinin was never abundant in our samples) is found in moderate amounts (20 to 30% of the pigments biomass) in April 2000 and 2001, and also in July 2000. Picoplankton was only abundant in July and October 2000, while cells counts of picoplankton detected maximum abundance of PE-containing picocyanobacteria and Picoeucaryotes in samples from the April 2001 bloom: picoplankton had its maximum abundance during this bloom but was still dominated by the other phytoplankton size (pigments) classes. *Prochlorococcus* abundance was highest in autumn, and this genus was not observed in spring and summer. While the absence of *Prochlorococcus* in spring is plausible, it may be an artefact in summer caused by very low fluorescence of *Prochlorococcus* cells under high irradiance and oligotrophic conditions in summer, which made them undetectable by our flow cytometer. Indeed, GeP&CO pigments data indicate that divinyl-chlorophyll a, which replaces chlorophyll a in *Prochlorococcus*, was about 20 % of total chlorophyll during these summer cruises.

5.2. The Northwest Atlantic Shelves

The GeP&CO measurements made along the eastern coast of North America are not considered here, while the province delineated by Longhurst (1998) includes this coastline. They often represent coastal waters in the vicinity of harbours, and exhibit very high pigments concentrations and variability. As in the former province, a strong seasonal cycle of chlorophyll concentration is observed in this province. The annual maximum also occurs in April – May in the analysis of SeaWiFS data, and a marked minimum occurs in July – August. Concentration increases in October, and there is no strongly marked winter minimum between this autumn bloom and the spring bloom. This is different from the previous region where a marked minimum was detected in January. Instead, here, the GeP&CO data show high chlorophyll concentration (up to about 2 mg m^{-3}) in January of both 2000 and 2001 (Fig. 6$_b$). While dominated in all cases by nanoplankton, the phytoplankton populations in the Northwest Atlantic Shelves are much more contrasted than in the previous region. There is a clear oscillation between winter and spring populations; in spring, microplankton (mostly

diatoms) represents 20 to 40% of the pigments biomass, while in summer and autumn populations, it represents only about 5%. Oppositely, the picoplankton accounts for about 30 to 40% of this biomass in October of 2000 and July of 2001, and more than 50% in July 2000. The abundance of picoeucaryotes increases from July to April, mirroring that of chlorophyll. PE-containing picocyanobacteria cells are present all the time, with numbers between 5000 and 30 000 cells ml^{-1}, and do not show any clear seasonal cycle. *Prochlorococcus* culminate in summer and autumn, especially in 2000. They were not detected in July 2001, probably because of weak fluorescence and instrumental limits, as mentioned for the previous province.

5.3. The Caribbean Sea

Chlorophyll concentrations are low all the year round in the Caribbean Sea (less than 0.5 mg m-3) both in the SeaWiFS and in the GeP&CO data which are in overall agreement (Fig. 6$_c$). A maximum occurs in winter (0.15 to 0.20 mg m^{-3}), triggered by winter vertical mixing and a minimum in summer (about 0.10 mg m^{-3}). The picoplankton represents more than 50% of the pigments biomass at all eight cruises, as generally observed in oligotrophic areas. It is always dominated by *Prochlorococcus* which is very abundant in this region, generally over 100 000 cells ml^{-1}. PE-containing picocyanobacteria and picoeucaryotes are in small numbers, less than 5000 cells ml^{-1}. The microplankton represents generally less than 5% of the plankton biomass. As this group is considered as the main responsible of new production, this is an indication of very low biological carbon export in this province.

5.4. The North Pacific Equatorial Countercurrent

Vertical velocity at the thermocline depth caused by maximum wind curl was retained by Longhurst (1998) to explain a winter maximum in the area of the Pacific North Equatorial Countercurrent. The GeP&CO field data and the 1998-2001 SeaWiFS data in the eastern Pacific do not suggest such a clear pattern (Fig. 6$_d$). Indeed, this region is also influenced by rivers outflows that culminate in northern summer, when the atmospheric Inter Tropical Convergence Zone (ITCZ) has its northernmost position. It is also located near the Niño1 region and may thus be influenced by ENSO events. SeaWiFS chlorophyll estimates lie around 0.3 to 0.6 mg m^{-3}, and tend to increase during the 1998 to 2001 period, as mentioned

in the section on linear trend. The chlorophyll concentrations from GeP&CO cruises are generally lower, about 0.1 to 0.5 mg m^{-3}, except a few high values in January 2000 and 2001 and April 2001. In the 1998-2001 period, these moderately enriched tropical waters thus have an uncertain seasonal variability. The composition of the phytoplankton is also relatively constant, with a high contribution of nano- and picoplankton at all times. Counts of *Prochlorococcus* and PE-containing picocyanobacteria indicate high numbers, respectively around 200 000 and 100 000 cells ml^{-1}. The picoplankton contribution to pigments biomass is slightly higher in January 2000 and 2001, indicating that this period of the year is dominated by the microbial loop and has low new production. Microplankton represents 1 to 5% of the pigments biomass.

5.5. The Pacific Equatorial Divergence

Basing on previous studies (Dandonneau and Eldin, 1987) and SeaWiFS imagery, we have extended this zone to 12°S in the eastern Pacific, while Longhurst (1998) limited it at 5°S. This region was affected by the 1997-98 El Niño, and strongly responded to the 1998 La Niña conditions by high chlorophyll concentrations detected by SeaWiFS (Fig. 6$_e$). Seasonal variability is low in this area (Fig. 3). It is often suggested that chlorophyll concentration should respond to the yearly maximum of upwelling intensity in the second half of the year, but such a pattern is only partly confirmed by our analysis of SeaWiFS data (Fig. 4). The GeP&CO field data do not show seasonal variability. The High Chlorophyll – Low Nutrients character of these waters, which results from delayed use of the nutrients by the phytoplankton, probably explains that chlorophyll concentration does not respond closely to upwelling velocity. Chlorophyll concentration lies between 0.15 and 0.4 mg m^{-3} (SeaWiFS) or 0.1 to 0.4 mg m^{-3} (GeP&CO). Compared to the North Pacific Equatorial Countercurrent, the Pacific Equatorial Divergence has a higher nanoplankton contribution to pigments biomass, and relatively high picoeucaryotes cells counts, in conformity with the important role of this area for global new production. The microplankton contribution is small at all eight GeP&CO cruises. *Prochlorococcus* cells are abundant in the region.

5.6. The South Pacific Subtropical Gyre

The SeaWiFS and the GeP&CO data agree to describe this area as a permanently oligotrophic one. Chlorophyll concentrations are generally less than 0.15 mg m-3 all the year round, with nevertheless a slight maximum in austral winter in both datasets (Fig. 6$_f$), which can be explained either by winter cooling that favours vertical mixing of the surface mixed layer with deeper nutrients – rich waters, or as a response of pigments antennas to decreased irradiance. These slight maxima in August 2000 and 2001 have relatively high number of picoeucaryotes, around 5000 cells ml-1, while only a few hundreds to 1000 were found on the other cruises. Picoplankton represents always more than 50% of the pigments biomass, and *Prochlorococcus* is the main contributor. Absence of this genus in November 1999 and January 2000 (i. e. in austral summer) is probably an artefact caused by low fluorescence of these cells under high irradiance, as mentioned earlier for the North Atlantic.

5.7. The Archipelagic Deep Basins

In this region that lies in the same latitude range as the previous one, a clear seasonal cycle is evidenced by the FFT analysis of SeaWiFS data, and confirmed by the GeP&CO field data that follow remarkably well the signal seen by the satellite (Fig. 6$_g$). Unlike Longhurst (1998) who extended this province northward to the Bismark Sea close to the equator, our GeP&CO data are limited to the south of 23°S, and thus do not include the many islands that characterize this province. The denomination "Archipelagic" thus is not well suited. A yearly maximum in austral winter in June through October of about 0.20 to 0.30 mg m^{-3} is in agreement with the seasonal cycle described by Dandonneau and Gohin (1984). This maximum was explained by entrainment of deeper, nutrients–rich waters after the winter cooling of the surface mixed layer. This cycle is reflected in the size classes composition of the phytoplankton deduced from pigments indexes: chlorophyll–rich waters have 50% or more of the biomass in nanoplankton, while more than 70% was observed in the picoplankton during the cruises in austral summer. Significant amounts of microplankton were detected on most cruises, except the austral summer ones in January 2000 and 2001. *Prochlorococcus* was found to be abundant (more than 150 000 cells ml^{-1}) most of the time. Very high numbers of PE-containing picocyanobacteria, that are known to respond positively to nutrients input (about 150 000 cells ml^{-1}), were found in November 1999 and in August 2000. Neveux *et al.*

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(1999) found new types of phycoerythrin precisely in this region. Picoeucaryotes were abundant in November 1999, in August 2000 and in May 2001.

6. Conclusion

This analysis of SeaWiFS data was limited to places where time gaps, caused by clouds, did not exceed 2 consecutive months and amounted to less than 12 months for the entire1998 to 2001 period. This constraint excluded high latitudes where the seasonal bloom of phytoplankton is known to force a major export flux of oceanic carbon to depth. The remaining low and mid latitudes represent however about 4/5 of the world ocean. The chlorophyll concentrations collected by SeaWiFS (third processing) are in overall agreement with field data collected at the surface of the ocean, and provide a new vision of phytoplankton biomass at sea, and of its coupling with ocean circulation. Until now, attention has been mostly focused on mesoscale features (McGillicudy *et al.*, 1998; Machu and Garçon, 2001) but the long life length of SeaWiFS, and the rapid processing and availability of data offer the possibility to investigate the variability of phytoplankton biomass at large space and time scales (Murtugudde *et al.*, 1999). Long term variability studies require that drifts of the sensor are carefully checked. Comparisons of remote areas need that algorithms perform identically at different latitudes and under different atmospheric conditions. SeaWiFS started in 1997 during a strong El Niño event, and the recovery of the Pacific ecosystem after this event resulted in significant interannual variability over a large part of the world ocean. Other minor events caused interannual variability, such as the episodic blooms of Trichodesmium in the South-western Tropical Pacific, or the strong Madden-Julian oscillation in early 1999. Over most of the world ocean, chlorophyll exhibits a seasonal cycle, and the timing of the yearly maximum is strongly modulated by the seasonal cycle of solar energy. Exceptions to this pattern originate from limitations by micronutrients that delay the timing of the seasonal blooms of phytoplankton.

Determining the fate of carbon fixed by photosynthesis is an important goal for understanding the global marine carbon cycle. Different ecosystems and different phytoplankton populations may make completely different use of photosynthesized carbon. A correct answer requires knowledge of the composition of the phytoplankton. Field data that provide insight into the diversity of phytoplankton populations show that these populations are highly variable in space and time. A dominant feature is the dominance of nano- or even

microplankton at high latitudes, and of picoplankton in tropical waters. During the two first years of GeP&CO cruises, we did not encounter blooms of *Trichodesmium sp.* or Coccolithophorids that would significantly impact the chemistry of the ocean. However, we did observe an important variability of accessory pigments and picoplankton categories that often does not reproduce from year to year. Since the ability of the ecosystem to export carbon depends on the phytoplankton composition, efforts should be made to derive information relative to these ecosystems from space, in addition to the now widely used chlorophyll.

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Province	Occurrence of chl maximum	
	Longhurst (1998)	this study
Indian Ocean Monsoon Gyres	July – September	In some parts : December to March
Red Sea	July – October	January – February
Eastern India Coastal Province	July – August	October November
North Pacific Transition Zone	January	April – May, or October
Tasman sea	May	September
North Pacific Tropical gyre	September – November	November – January
Pacific Equatorial Divergence	October (not well defined)	August – September
New Zealand Coastal Province	May – June	March (south) or October (north)
Subantarctic Water Ring	May – June	October - March

Table I : list of oceanic provinces where the timing of the annual bloom differs in the 1978 – 1986 Coastal Zone Color Scanner data set, and in the 1998-2001 SeaWiFS data set

Figures captions

Fig. 1 : comparison of SeaWiFS (third processing) and GeP&CO Chl concentration at co localized points.

Fig. 2 : Monthly increase in chlorophyll concentration over the period from January 1998 to December 2001.

Fig. 3 : Ratio of interanual (Vi, caused by linear trend + harmonics at 48, 24 and 16 month) to total variance (Vi + harmonics at 12 and 6 month) for the period from January 1998 to December 2001.

Fig. 4 : Occurrence time of chlorophyll seasonal cycle maximum

Fig. 5 : positions of the observations made during the first eight GeP&CO cruises, and subsets representative of oceanic provinces: North Atlantic Drift Province (NADR), Northwest Atlantic Shelves (NWCS), Caribbean Sea (CARB), Pacific North Equatorial Countercurrent (PNEC), Pacific Equatorial Divergence (PEQD), South Pacific Subtropical Gyre (SPSG), and Archipelagic Deep Basins (ARCH).

Fig. 6 : Summary of GeP&CO observations in the oceanic provinces indicated on Fig. 5. The content of each panel is listed hereafter, from top to bottom. The distribution of biomass into pico-, nano- or microplankton (rectangles) is based on pigments indexes (see material and methods), and scaled in the bottom left corner, where it corresponds to 1/3 for each size class. Picoplankton abundance (Picoeucaryotes = triangles, PE-containing Cyanobacteria, mentioned as "*Synechococcus* = stars, and *Prochlorococcus* = circles) corresponds to the median value found for each GeP&CO cruise. The cells numbers are proportional to the size of the symbols, scaled in the bottom left corner. Note that null or quasi null abundance of *Prochlorococcus* may result from instrumental artefacts, since our flow cytometer could not detect weakly fluorescent cells in summer in oligotrophic conditions. Chl concentration (left scale) measured *in situ* on GeP&CO cruises (bold crosses) are superimposed to SeaWiFS Chl estimates issued from the FFT analysis in all grid elements in the areas shown on Fig. 5.All data are plotted versus time, and the dates of the GeP&CO cruises can be inferred from the position of the bold crosses.
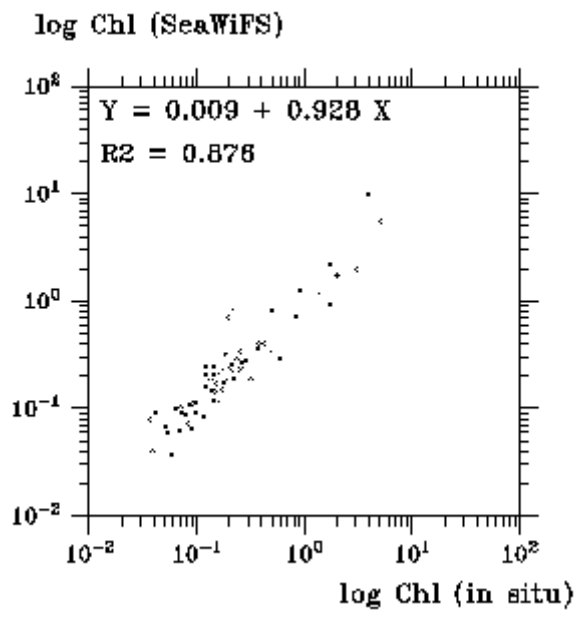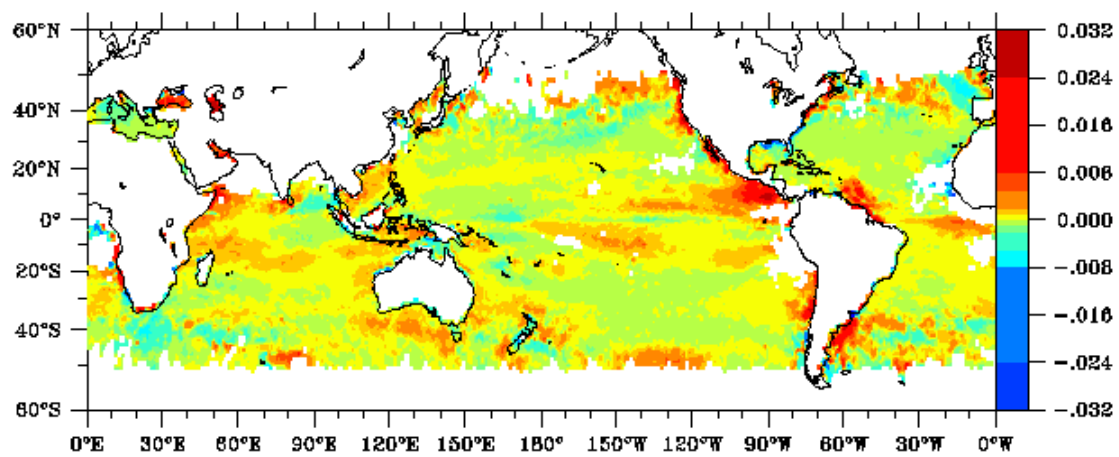
Fig. 1

log Chl (SeaWiFS)
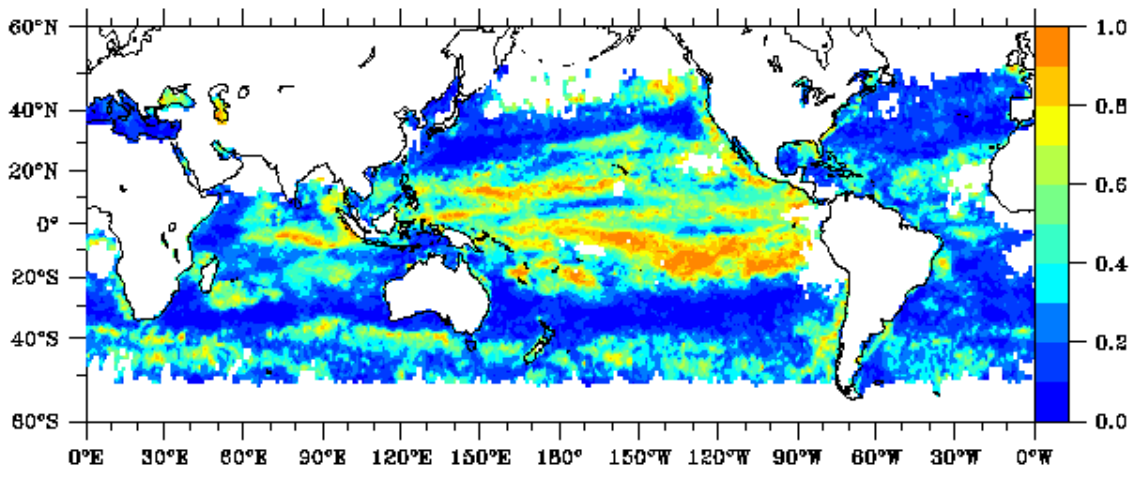
Y = 0.009 + 0.928 X

R2 = 0.876

log Chl (in situ)

Fig. 2

Fig. 3

Fig.4

Fig.5

Fig. 6