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Bio-optical studies during the JGOFS-equatorial Pacific program: a contribution to the knowledge of the equatorial system

A. Bricaud^{a,*}, C.S. Roesler^b, J.S. Parslow^c, J. Ishizaka^d

^a *Laboratoire d'Océanographie de Villefranche, CNRS and Université Pierre et Marie Curie, BP 8, 06238 Villefranche-sur-Mer Cedex, France*

^b *Bigelow Laboratory for Ocean Sciences, P.O. Box 475, W. Boothbay Harbor, ME 04575, USA*

^c *Division of Fisheries, CSIRO, P.O. Box 1538, Hobart, Tasmania 7001, Australia*

^d *Faculty of Fisheries, Nagasaki University, 1-14 Bunkyo, Nagasaki 852-8521, Japan*

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Abstract

Bio-optical studies, pursued in the equatorial Pacific area during the International Joint Global Ocean Flux Study program, contributed to a better knowledge of this oceanic system. Besides the classical estimation of biogeochemical “core parameters” via optical measurements (e.g., Chl *a* concentration, particulate matter concentration, etc.), several original bio-optical studies included the estimation of the contributions from the various particulate pools and, within the algal pool, from the various phytoplanktonic communities, to the inherent optical properties (attenuation, scattering, absorption) and to stimulated Chl *a* fluorescence. New insights also were gained concerning the variations in these properties associated with the diel cycle, tropical instability waves, and Kelvin waves. Such studies are critical to improving the interpretation of the spatial and temporal variability of optical properties in terms of biogeochemical quantities. In addition, studies of diel variations of light attenuation by particles, of sun-stimulated fluorescence Chl *a*, and of the photophysiological parameters of phytoplankton to be used in bio-optical models, all contributed to a better assessment of primary production rates in the equatorial Pacific. © 2002 Elsevier Science Ltd. All rights reserved.

1. Introduction

The intensive study of biogeochemical processes in the equatorial Pacific was initiated in 1989 under the auspices of the Joint Global Ocean Flux Study program (JGOFS, 1990). Large field studies were conducted in this area by Australia (October 1990 to August 1997), Japan (August 1990 to January

1994), Canada (August–September 1992), United States (January 1992 to May 1996), and France (September–December 1994, October–November 1996), in various locations and biogeochemical conditions (Murray et al., 1995, 1997; Dandonneau, 1999; see also Table 1). These field programs capitalized, in particular, on the WEC88 cruise, which was one of the first major milestones in the study of this area (Barber, 1992 and references therein). The JGOFS program was mainly focused on the central and western equatorial Pacific, with the initial knowledge that it was a “high-nutrient,

*Corresponding author. Tel.: +33-493-7637-13; fax: +33-493-7637-39.

E-mail address: annick@obs-vlfr.fr (A. Bricaud).

Table 1
JGOFS cruises in the equatorial Pacific including bio-optical measurements

Country	Program/cruise	Dates	Location	Conditions at the equator
Australia	AUS-JGOFS	Oct. 2–17, 1990	155°E, 10°S–10°N	Warm pool area, moderate El Niño
	AUS-JGOFS	June 15–July 13, 1992	155°E, 10°S–10°N	Warm pool area, normal conditions
	AUS-JGOFS	Nov. 5–Dec. 1, 1993	155°E, 10°S–10°N	Warm pool area, normal conditions
	TROPICS	Aug. 5–17, 1997	144°E–152°E, eq.–4°S	Warm pool area, normal conditions
Japan	KH-90-2	Sep. 3–Oct. 25, 1990	180°, 160°W, 150°W; 20°N–20°S	Cold tongue area, moderate El Niño
	NOPACCS/NH-90-2	Aug. 22–Oct. 15, 1990	175°E, 45°N–8°S	Transition zone ^a , warm waters
	NOPACCS/NH-91-2	Aug. 9–Oct. 7, 1991	175°E, 48°N–15°S	Transition zone ^a , warm waters
	NOPACCS/NH-92-2	Aug. 7–Oct. 5, 1992	175°E, 48°N–15°S	Transition zone ^a , warm waters
	NOPACCS/NH-93-2	Aug. 7–Oct. 5, 1993	175°E, 48°N–15°S	Transition zone ^a , warm waters
	NOPACCS/NH-94-1	Apr. 14–June 11, 1994	175°E, 48°N–15°S	Transition zone, cold waters
Canada	(drifting buoys)	Aug. 29–Sep. 24, 1992	140°W–146°W, 6°N–6°S	Cold tongue area, normal conditions
USA	EqPac/TT007	Jan. 30–March 13, 1992	140°W, 12°N–12°S	Cold tongue area, El Niño
	EqPac/TT008	March 17–Apr. 20, 1992	140°W, eq.	Cold tongue area, El Niño
	EqPac/TT011	Aug. 5–Sept. 18, 1992	140°W, 12°N–12°S	Cold tongue area, normal conditions
	EqPac/TT012	Sept. 22–Oct. 25, 1992	140°W, eq.	Cold tongue area, normal conditions
	Zonal Flux	April 15–May 14, 1996	165°E–150°W, eq.	Warm pool area, moderate La Niña
France	Epope/FLUPAC	Sept. 24–Oct. 26, 1994	165°E, 15°S–6°N 165°E–150°W, eq.	Warm pool area, moderate El Niño Moderate El Niño
	Epope/OLIPAC	Nov. 3–Dec. 1, 1994	150°W, 16°S–2°N	Cold tongue area, weak El Niño
	EBENE	Oct. 21–Nov. 20, 1996	180°, 12°S–8°N	Cold tongue area, moderate La Niña

^a Transition zone between the warm pool and cold tongue areas.

low-chlorophyll (HNLC)'' area (Minas et al., 1986); i.e. this area was, in spite of high nutrient conditions due to the equatorial upwelling, mesotrophic within a latitudinal band around the equator (‘‘cold tongue area’’, ~4°N–4°S in normal conditions), and remained oligotrophic north and south of this band, as well as west of 170°E–180° (‘‘warm pool’’). It should be noted that the highly productive areas in the eastern part of the Pacific, such as the Peru upwelling or the Costa Rica dome, were not studied in this program. It was also well-known that the equatorial Pacific is a highly variable system, in particular because of the occurrence of El Niño–La Niña events, Kelvin waves and tropical instability waves, and that physical variability largely controls biological and biogeochemical variability.

This international program emphasized that bio-optical oceanography, defined as ‘‘the study of the optical processes of the upper ocean as affected by biological processes and vice versa’’, would be an essential contribution to a better understanding of the various processes controlling

the fluxes of carbon and other biogeochemical elements (Dickey and Siegel, 1993). Optical properties are usually split into two categories: inherent optical properties, IOPs, and apparent optical properties, AOPs (Preisendorfer, 1961). The IOPs (such as the absorption, scattering and attenuation coefficients) are independent of the geometric structure of the light field, and depend only on the substances present in the medium; the contributions of these substances to the bulk optical coefficients are additive. The AOPs (such as diffuse attenuation coefficients or diffuse reflectance) are determined not only by the substances present in the medium but also by the light field. These properties are not additive and thus cannot be separated into component contributions. Both categories of optical properties are linked through the equation of radiative transfer (Preisendorfer, 1961; Mobley, 1994).

The interest in developing and including a bio-optical program in JGOFS was driven by the contributions such a program could provide,

specifically: (i) light propagation within the ocean is one of the essential parameters directly impacting the rate of carbon fixation by phytoplankton, and indirectly carbon export from the upper ocean; (ii) the IOPs constitute, via the radiative transfer theory, the essential link between biogeochemical quantities and AOPs, so that their knowledge provides the basis for the development of analytical bio-optical models and algorithms for ocean color interpretation; (iii) some IOPs also can (under certain conditions and with particular assumptions) be used as proxies of biogeochemical quantities, such as algal biomass or particulate matter concentration. This, in turn, prompted the development of bio-optical instrumentation for the measurement of both AOPs (e.g., spectroradiometers at discrete wavelengths, mostly designed for ocean color validation studies) and IOPs (particularly in situ profilers for measuring absorption, attenuation and backscattering at specified wavelengths). These profilers, which provide high-frequency measurements of some IOPs, are invaluable tools for studying the space and time variability of these properties.

Some in situ bio-optical techniques are commonly used to provide estimates of “bulk” biogeochemical parameters. The most classical examples are the continuous measurement of stimulated chlorophyll *a* (Chl *a*) fluorescence for deriving profiles of the Chl *a* concentration, or of the attenuation coefficient of particles (usually at 660 nm) for deriving vertical profiles of total particulate matter. Even if the approximate character of these estimates is well-known, the simplicity of these techniques explains why they are widely and routinely used during most cruises, and considered as operational for measuring the so-called “core parameters”. The results obtained with these techniques during the JGOFS cruises will not be discussed here. This paper will rather focus on some original contributions of bio-optical techniques, and on the progress they have brought in the knowledge of the equatorial Pacific system in several domains. It will be centered mainly on studies concerning the IOPs.

It is also well known that measurements of optical properties (both IOPs and AOPs) are important for estimating vegetal biomass and

primary production from space, and can be used with a view to developing ocean-color models or validating satellite data. These studies will not be described here, as they are discussed elsewhere (McClain et al., 2002). Finally, it should be recalled that optical properties affect the vertical distribution of heat flux in the upper ocean and possibly the ocean surface circulation. Lewis et al. (1990) showed that visible solar radiations penetrate to significant depth in the western Pacific Warm Pool, resulting in a reduction of the heat input into the upper mixed layer. Nakamoto et al. (2001) studied the effects of optical properties in a general circulation model and suggested that equatorial upwelling is enhanced by the presence of phytoplankton, which concentrate heat at the surface in the eastern equatorial Pacific.

The bio-optical studies reviewed in this paper can be split into two categories. The first deals with the bio-optical estimation of biomass and the interpretation of the corresponding optical properties, including: (i) the contributions of the various particulate pools to light attenuation, scattering and absorption; (ii) the contributions of the various phytoplanktonic communities to light absorption and fluorescence; and (iii) the issue of colored dissolved organic matter (CDOM). The second deals with bio-optical studies in relation to primary productivity estimates, including (i) the study of diel variations of light attenuation to estimate primary production rates, (ii) the use of natural (solar-stimulated) fluorescence of Chl *a*, (iii) the estimate of photosynthetic parameters of phytoplankton using various techniques, and (iv) the estimate of primary production via bio-optical models. We will review hereafter the achievements of these various bio-optical studies (as well as some still open questions) and their contribution to the knowledge of the equatorial Pacific system.

2. Methods of observation

2.1. *In situ* profilers

Various bio-optical properties, such as stimulated fluorescence of Chl *a*, but also attenuation,

absorption, and backscattering coefficients, are now accessible with ship-based profilers. Those which were most routinely measured during equatorial Pacific cruises were stimulated Chl *a* fluorescence and the attenuation coefficient of particles, using Sea Tech fluorometers (excitation at 425 nm, emission at 685 nm) and transmissometers (660 nm, 25-cm pathlength). In addition, some studies reported in this paper (Pegau, 1997; Simeon et al., submitted) were based on data provided by Wet Labs ac-9 (nine-wavelength absorption and attenuation meter) instruments.

Besides these now “conventional” profilers, a new generation of instruments recently has appeared, including hyperspectral transmissometers/absorptionmeters (e.g., Histar, Wetlabs, Inc.), fluorometers (e.g., Safire, Wetlabs, Inc.) and multiple-wavelength backscattering meters (e.g., Hydrosat-6, HOBI Labs, Inc.). Even now, however, the use of these sophisticated profilers is not yet considered as fully operational, and was still at an experimental stage at the end of field operations in the equatorial Pacific (1996–1997). Therefore, most of the bio-optical data for the equatorial Pacific were obtained from the classical profilers (associated, or not, with optical measurements on discrete samples).

2.2. Measurements on discrete samples

Most optical measurements performed on discrete samples during the equatorial Pacific program have dealt with absorption by particulate matter. Such measurements are still needed because detailed spectral information is required when using absorption properties, either for tentatively analyzing the specific composition of phytoplankton, or for computing photosynthetic parameters. Such measurements were systematically performed, generally using the glass-fiber filter technique, during the NOPACCS program in spring 1994 (Harimoto et al., 1999), the FLUPAC and OLIPAC cruises in autumn 1994 (Allali et al., 1997; Dupouy et al., 1997), the Zonal Flux cruise in April–May 1996 (Dupouy and Simeon, 1997; Simeon et al., submitted), and the TROPICS cruise in August 1997 (Parslow et al., 1998).

Details of the methods are described in the mentioned references.

2.3. Moorings and drifters

Despite the fact that the use of optical instruments on moorings and drifters is limited by practical constraints (biofouling, power, data storage, interference between spatial and temporal variations for drifters, etc.), these systems are invaluable to obtain high-frequency time and space series which are inaccessible by ship sampling (e.g., Dickey et al., 1991, 1998). The EqPac study included high-resolution measurements of physical and bio-optical variables (Foley et al., 1997). These were mostly focused on the study of the influence of physical variability (equatorial longwaves: tropical instability waves (TIWs) and Kelvin waves) upon the variability of algal biomass and primary production during both El Niño and “normal” conditions. This study used the PROTEUS mooring, located at 0°, 140°W, and equipped with multi-variable moored systems (MVMS; Dickey et al., 1991) at four depths between 0 and 80 m, in addition to physical sensors (see complete description in Foley et al., 1997). Optical measurements included stimulated fluorescence of Chl *a*, beam transmission at 660 nm, PAR, downwelling irradiance at 488 nm ($E_d(488)$), and upwelled radiance at 683 nm ($L_u(683)$). In addition, expendable drifters, with optical sensors providing measurements of upwelling irradiances at six wavelengths corresponding to the SeaWiFS channels and at 683 nm, and downwelling irradiance at 490 nm (ESRs, Satlantic, Inc.), were deployed from aircraft at the same site. Data were used to estimate penetration of visible irradiance into the ocean, and the along-track pigment concentrations, using an ocean-color algorithm.

3. Main results and discussion

3.1. Bio-optical studies and biomass estimations

The IOPs can be used as proxies to assess the concentrations of various components of the

particulate or dissolved matter present in the ocean. Continuous bio-optical measurements, therefore, have to be combined with measurements on discrete samples in order to ensure a proper calibration. Inversely, they allow interpolation of discrete measurements, and give access to high spatial or temporal resolution for some biogeochemical variables. The prerequisite to such an approach, nevertheless, is the ability to interpret the optical properties in terms of biogeochemical quantities. This step is generally far from being straightforward, because the component-specific IOPs (i.e. normalized to component concentration)—scattering, absorption—or fluorescence, exhibit physical and/or physiological variability. Therefore, the interpretation of optical signals in terms of biological properties depends upon the knowledge (or the measurement) of the variability in the optical properties specific to each component or each category of components.

3.1.1. Contributions of the various particulate pools to light attenuation and scattering

At the beginning of the JGOFS program, it was already known that in the equatorial Pacific, micro-organisms smaller than 5 μm represented the dominant part of biomass and productivity (Chavez et al., 1990; Peña et al., 1990). This did not necessarily imply, however, that it was the case also for the bulk particle concentration, as determined from the beam attenuation coefficient of particles (c_p). The contributions of the various pools to c_p were poorly documented. Although c_p (usually measured at 660 nm, a wavelength of minimal absorption, and thus nearly equivalent to the scattering coefficient b_p) is frequently used as a descriptor of the bulk particle concentration, the various components of particulate matter do not contribute to total attenuation in proportion to their relative abundances. Their contribution is dependent upon their size distribution, complex refractive index (e.g., Van de Hulst, 1957; Morel and Bricaud, 1986; Kitchen and Zaneveld, 1990), and to lesser extent, particle shape and structure (e.g., Aas, 1984). Several bio-optical studies performed within the JGOFS program allowed the relative contributions of the various particulate pools to total attenuation and scattering to be

estimated and the temporal and spatial variation quantified. The variability in these relative contributions will have important implications in particular when interpreting the diel variations of beam attenuation for primary productivity estimates (see later).

Such studies were first developed by DuRand and Olson (1996) and Chung et al. (1996, 1998) during the EqPac cruises at 140°W from 12°N to 12°S, in February–March 1992 during El Niño conditions, and in August–September 1992 during cool surface-water conditions (see Table 1). These studies relied upon estimates of the scattering cross sections of the various particulate pools in the equatorial Pacific: *Prochlorococcus*, *Synechococcus* and autotrophic eukaryotes for the “algal compartment”, heterotrophic microorganisms and non-living detrital particles for the “non-algal compartment”. Various methods were used to estimate these cross sections: DuRand and Olson (1996) assessed them from a combination of laboratory calibrations and Mie theory, Chung et al. (1996) used published values, and Chung et al. (1998) derived them from flow-cytometric measurements, which led them to revise their previous estimates. The contribution of the non-algal compartment (or of the detrital compartment if that of heterotrophic organisms was directly assessed) was generally estimated by difference to the total cross section.

DuRand and Olson (1996), sampling at 140°W on the equator, found that the global contribution of the non-algal compartment was about 50% of c_p near the surface, and increased continuously with depth, with similar trends between El Niño and cool surface-water conditions. Within the algal compartment and in the upper 60 m, the major contribution was from picoeukaryotes (mostly 1–3 μm cells), while that of *Prochlorococcus* was small (9–12% of c_p in El Niño conditions, 4–6% in cool surface-water conditions) and that of *Synechococcus* was negligible. Chung et al. (1998), sampling between 12°N and 12°S at 140°W, found that the respective contributions to c_p were on average only 2% for picoeukaryotes, 7% for *Prochlorococcus*, and 1% for *Synechococcus*. For the non-algal compartment, they estimated the contributions of heterotrophic bacteria,

heterotrophic protists, and non-living detrital material to be, respectively, 16%, 20%, and 20–60% of c_p in surface waters.

A similar approach was applied by Claustre et al. (1999) during the OLIPAC cruise along 150°W in November 1994 (see Table 1). They computed the scattering cross sections from published values of size for the various algal components, assuming a refractive index of 1.05 for all organisms. Consistent with DuRand and Olson (1996), their results suggest that in the upper 60 m at the equator, the contributions of algal and non-algal compartments were similar. In the algal compartment, picoeukaryotes were the main contributor (about 30% of the total c_p), while contributions by *Prochlorococcus* and *Synechococcus* were minor (about 10% and 5%, respectively); in the non-algal compartment, the contributions of detrital material and heterotrophic organisms (bacteria and protists) represented 30% and 20% of the total c_p .

In spite of some disagreements in the precise contributions of the various components, these studies led to some converging results. The algal and non-algal pools appear to contribute similarly to c_p in the upper layer at the equator, while at depth the non-algal signal becomes dominant. Within the non-algal compartment, detrital particles are likely to provide the main contribution to c_p . Within the algal compartment, the contribution of *Synechococcus* is always recognized as minor or negligible, while that of *Prochlorococcus* is variable, being more important during El Niño conditions than in normal conditions, consistent with other observations (Bidigare and Ondrusek, 1996). This trend, however, appears more clearly in the results of DuRand and Olson (1996) than those of Chung et al. (1998). Note that these observations are specific to the equatorial area: in the subtropical gyre at 16°S (see Claustre et al., 1999), the contributions of the non-algal and algal compartments are quite different (respectively, 80% and 20% of the total c_p), and within the algal compartment, *Prochlorococcus* dominates the c_p signal down to the deep chlorophyll maximum, a situation that is likely similar to that of the oligotrophic “warm pool”.

Some noticeable differences remain between the results of these studies, e.g., the contribution of

picoeukaryotes to the total c_p . These may originate partly from differences in spatial and temporal sampling, in an area where, even outside El Niño conditions, seasonal and interannual biological variability is known to be dramatically high (see e.g., McClain et al., 1999) and largely affected by physical forcings such as Kelvin waves and tropical instability waves (e.g., Walsh et al., 1997; Foley et al., 1997). In addition, the use of different methods for estimating scattering cross sections, each with its own limitations, also certainly contributes to this variability. In particular, Claustre et al. (1999) have emphasized the uncertainties concerning the average size, and consequently the scattering cross section of picoeukaryotes. Specific optical studies concerning this picoplanktonic group, which still remains poorly documented, would provide useful information to interpret transmissometry measurements, and could help to reconcile the estimates of the contributions of the various components to c_p . Further work also is needed concerning the non-algal detrital compartment, which appears to be one of the main contributors to c_p , and nevertheless remains largely unknown. Viruses and particles below 0.6 μm , which have been recognized to be extremely abundant in most waters (Koike et al., 1990) and to contribute significantly to backscattering, have low overall contributions to scattering because of their tiny size (Morel and Ahn, 1991; Stramski and Kiefer, 1991). More likely the contribution is originating from “large” (a few μm or more) biogenous particles that can undergo rapid cycling in surface waters due to aggregation/disaggregation processes.

The possible contribution of coccolithophores to total scattering also should be mentioned. During the EqPac TT011 cruise, Balch and Kilpatrick (1996) made underway measurements of light scattering at 90° using a flow-through system, before and after acidification (the difference in signals being converted into particulate calcite), along with measurements on samples (counts of coccolithophore cells and detached coccoliths, particulate calcite, etc.). Although some difficulties appeared in the quantitative interpretation of these optical measurements (the

acid-labile scattering values were noisy and sometimes negative), calcite-producing populations near the equator and down to 9°S were detected unambiguously. The presence of these populations, which was not explicitly considered in the above studies, may have introduced some bias when evaluating the relative contributions of the various components to scattering or attenuation.

3.1.2. Contributions of the algal and non-algal particulate pools to light absorption

Absorption measurements, usually performed by filtering samples on a glass-fiber filter and measuring the spectral optical densities with reference to a blank wet filter, give access to absorption coefficients of the whole particulate pool. By using either experimental methods (extraction in methanol, Kishino et al., 1985, and subsequent extraction with hot water or phosphate buffer to remove phycobilipigments, Roesler and Perry, 1995) or numerical decomposition methods (e.g., Morrow et al., 1989; Roesler et al., 1989; Bricaud and Stramski, 1990), it is then possible to separate the “algal” and “non-algal” fractions. Note, however, that the algal fraction is that due to phytoplankton-derived pigments *in vivo*, and the non-algal fraction includes all other living and detrital particulate material.

Absorption measurements performed during the OLIPAC and FLUPAC cruises (see Table 1) have shown a remarkably low contribution of non-algal particles to total absorption (Allali et al., 1997). Total absorption spectra tended to resemble those of detritus-free cultures grown in laboratory; at 440 nm (the wavelength of maximal pigment absorption), for instance, the non-algal-to-algal absorption ratio was on average 0.1 near the surface and 0.17 at the bottom of the euphotic layer. These figures were virtually identical in the equatorial zone and in the subequatorial area down to 13°S. Ratios of 0.1 also were observed on the TROPICS cruise in the Western equatorial Pacific (Parslow et al., 1998), and similar values (around 0.14 in the euphotic layer) were obtained during the FLUPAC cruise (Dupouy et al., 1997), as well as during Zonal Flux (Dupouy, unpublished results). Such values are exceptionally low when compared with other oceanic waters with

similar pigment contents (see Fig. 2 in Bricaud et al., 1998). These results are consistent with the particularly high reflectance values observed by Morel and Maritorena (2001) in the blue-UV domain (300–450 nm) for the oligotrophic sub-equatorial area. These values are higher (by about 50% at 400 nm) than those observed for similar pigment contents in the Atlantic Ocean and in the Mediterranean Basin.

The weak contribution of non-algal particles to total absorption in the equatorial Pacific is not necessarily in contradiction with the fact that the contribution of these non-algal particles to c_p was found to be much larger (approximately 50%). This may indicate that these particles, even if they contribute largely to scattering because of their high concentration, large average size or high refractive index (or any combination of these factors), are very weakly colored. This geographical specificity points out, however, the difficulty in proposing a general optical model for the non-algal compartment.

3.1.3. Contributions of the various phytoplanktonic groups to light absorption

Algal absorption measurements are most often used for determining photosynthetic parameters such as the maximum quantum yield for carbon fixation (Lindley et al., 1995; see also Section 3.2.3) and, more generally, when modeling primary production (Behrenfeld and Falkowski, 1997, and references therein). In addition, they also may provide information about the taxonomic composition and photoadaptive status of phytoplankton. Spectral variations are associated with different pigment suites and the flattening of absorption peaks, associated with the package effect. This effect is caused by increases in the intracellular pigment concentrations, a response to limiting light conditions, and/or in the cell size (Morel and Bricaud, 1981). A measure of the absorption efficiency used to compare algal communities is the chl-specific absorption, which varies with pigment composition, cell size, and intracellular pigment concentrations.

Therefore, absorption properties of phytoplankton often behave as an indicator of the trophic regime. Allali et al. (1997), from measurements

made during the OLIPAC cruise, showed that chl-specific absorption of phytoplankton decreased from the oligotrophic waters of the subequatorial area (south of 1°S) to the mesotrophic waters of the equatorial system (~1°S–1°N, in weak El Niño conditions). This decrease was mainly originating from (i) a decrease in the concentrations of non-photosynthetic pigments, and (ii) an increase in the package effect. Both effects mostly resulted from latitudinal changes in the taxonomic composition of populations. These changes were evidenced both by flow-cytometric measurements (which revealed a decreasing abundance of *Prochlorococcus*, and therefore of zeaxanthin, toward the equator) and of HPLC measurements (which showed, in addition, an increasing presence of fucoxanthin, characteristic of large cells such as diatoms). Similarly, Dupouy et al. (1997) observed, during the FLUPAC cruise along the equator between 165°E and 150°W, very contrasted bio-optical properties between the “warm pool” west of 170°W (with spectra characteristic of oligotrophic waters), and the upwelling area east of 170°W. Performing EOF analyses of phytoplankton absorption spectra measured along 175°E (from 48°N to 15°S) during the Northwest Pacific Carbon Cycle Study (NOPACCS) in spring 1994, Harimoto et al. (1999) also evidenced large regional differences in absorption properties. In their dataset, absorption spectra of equatorial samples, under weak upwelling conditions, showed the highest values (in association with the highest concentrations of non-photosynthetic pigments and the likely high abundance of *Prochlorococcus*). Parslow et al. (1998) reported strong contrasts in phytoplankton absorption spectra and pigment composition between samples from the mixed layer and the deep chlorophyll maximum (DCM) in the Western equatorial Pacific (warm pool) in August 1997. Samples taken from the mixed layer showed very high chlorophyll-specific absorption coefficients around 440 nm, and pigment composition indicative of small picoeukaryotes or cyanobacteria, while samples from the deep chlorophyll maximum showed a double absorption peak at 440 and 470 nm, and pigment composition indicative of prochlorophytes, with a large divinyl-chl *b* contribution.

Therefore, the four studies mentioned above provided very consistent results, showing that the absorption properties of phytoplankton, strongly influenced by its taxonomic composition, are contrasted in the different trophic regimes. Chl-specific absorption spectra reveal a high concentration of non-photosynthetic carotenoids and a low package effect (both characteristics leading to high chl-specific absorption coefficients) in the oligotrophic waters of the “warm pool”, and south of the equatorial upwelling area. Consistently, they show inverse characteristics in the mesotrophic waters of the equatorial area east of 170°W. In addition, absorption measurements performed on different size fractions during the Zonal Flux cruise, in moderate La Niña conditions, have shown that near the surface, 75–82% of total particulate absorption at 440 nm was attributable to the fraction <3 µm and 15–20% to the fraction 3–10 µm, the fraction > 10 µm being virtually absent (or <5%) in this area (Simeon et al., submitted).

It is important to mention that the variability in chl-specific absorption observed for the different trophic regimes is greatly reduced when considering the absorbed energy available for photosynthesis. Both Allali et al. (1997) and Dupouy et al. (1997) showed that the spatial (horizontal and vertical) variations of absorption by photosynthetic pigments were much lower than those of total phytoplanktonic absorption. Therefore, the variability of absorption by phytoplankton in equatorial waters is expected to have a limited impact upon its photosynthetic performances, which are mostly controlled by other factors (see Section 3.2.3).

3.1.4. Contributions of the various phytoplanktonic groups to fluorescence

Like beam attenuation for total particulate matter, the stimulated fluorescence of Chl *a*, as measured with an in situ fluorometer, often has been used as a proxy of algal biomass. It is well-known, however, that the ratio of Chl *a* fluorescence to Chl *a* concentration is highly variable, not only spatially but also temporally (e.g., Falkowski and Kiefer, 1985). Dandonneau and Neveux (1997) observed a clear diel cycle in in situ

stimulated fluorescence of Chl *a*, which was attributed to physiological rhythms of phytoplanktonic cells at depth superimposed on non-photochemical quenching near the surface. This diel cycle was reproducible over five transects through the equatorial Pacific (but was not observed in other areas, including the southern tropical Pacific), which the authors attributed to a very low mesoscale activity of the equatorial Pacific. Obviously such diel variations (also observed by Claustre et al., 1999, during the OLIPAC cruise) have direct implications when using in situ fluorescence as a tool to estimate the Chl *a* concentration.

The interpretation of Chl *a* fluorescence also can be refined by attempting to distinguish the contributions of the various groups to total Chl *a*, which is not feasible by any direct technique. Combining the measurements provided by an in situ fluorometer with the fluorescence signals associated to each group as measured by flow-cytometry, Claustre et al. (1999) estimated the contributions of the various phytoplanktonic groups to total Chl *a*. They concluded that picoeukaryotes represent the main contribution from the surface down to 200 m at the equator (whereas in the oligotrophic waters at 16°S, *Prochlorococcus* would be the main contributor to Chl *a* near the surface). This approach, which could provide new information upon the repartition of algal biomass among the various components, relies, however, on the hypothesis that the fluorescence-to-Chl *a* ratio is identical for the various groups (and in addition, varies similarly with depth), which is very likely an approximation (Sosik et al., 1989). Fundamental studies of the fluorescence and photoacclimation properties of the various picoplanktonic groups would allow such an approach to be refined.

3.1.5. *The contribution of colored dissolved organic matter to light absorption*

As a general rule, information concerning the distribution of colored dissolved organic matter (CDOM) in the open ocean are very scarce, and the existence (or not) of relationships between its concentration and those of other components remains largely unknown; this statement fully

applies to equatorial Pacific waters. Although CDOM, which in the open ocean originates from the decay of phytoplankton, remains in low concentration (actually, often hardly measurable in the visible with conventional spectrophotometric techniques), its effect on bio-optical properties of waters in general cannot be neglected. Prieur and Sathyendranath (1981), from measurements in various waters, stated that CDOM absorption at 440 nm covaries with, and is on average 20% of, total absorption, while other authors (e.g., Kopelevich and Burenkov, 1977) suggest that in oceanic waters, CDOM is a pool accumulated over a long period, weakly affected by changes in biomass, and therefore poorly correlated with the bulk absorption properties of the water mass.

Various studies within the JGOFS program have dealt with the contribution of DOC to carbon fluxes in the equatorial Pacific waters (Murray et al., 1994, 1996). These results, however, are not directly applicable to CDOM, as the CDOM:DOM and DOM:DOC ratios are highly variable regionally (Mueller and Lange, 1989). Parslow et al. (1998) measured CDOM absorption spectra along with particulate absorption spectra for samples near the Sepik River plume north of Papua New Guinea, as well as in open ocean waters along the equator between 146° and 152°E. CDOM-to-total absorption ratios in this region were around 0.5 (at 440 nm), and did not differ significantly between coastal and ocean waters. Pegau (1997), from ac-9 measurements performed along the equator between 150°W and 165°E (Zonal Flux cruise), concludes that the CDOM contribution to total absorption could be important even in the surface layer. Simeon et al. (submitted), using spectrophotometric measurements on discrete samples during the same cruise, determined that the fraction of matter passing GF/F filters (i.e. operationally CDOM) contributed to total absorption at 440 nm for nearly 50% in the surface layers and 100% below the DCM. In addition, the separation of this fraction into <0.2 and >0.2 μm ranges evidenced a very clear spatial pattern, with the >0.2 μm fraction dominating the upper 50 m of the water column and negligible below, while the <0.2 μm fraction was nearly

uniform in the upper 100 m and increasing with depth (Simeon et al., submitted). Although dissolved matter is generally defined as the matter passing a 0.2- μm membrane (Mueller and Austin, 1995), a significant part of CDOM might be contained as colloidal material in the $>0.2\text{-}\mu\text{m}$ fraction passing through GF/F filters (picoplankton is virtually absent in this fraction, see Chavez et al., 1995). Simeon et al. (submitted) suggested that based upon the distributions and the spectral shape of the absorption curves (Carder et al., 1989), the larger fraction ($>0.2\text{ }\mu\text{m}$) is most likely comprised of the newer labile organic material while the smaller fraction ($<0.2\text{ }\mu\text{m}$) is that of the older more refractory material described by Archer et al. (1997).

Information concerning the CDOM concentration, however, remains relatively scarce. This emphasizes the need for systematic measurements of CDOM absorption, in conjunction with measurements of particulate absorption and other bio-optical parameters. Such need, critical in particular for the purpose of bio-optical modeling, could be fulfilled with the increasing use of two multiwavelength absorptionmeters (one being equipped with a filter) used simultaneously.

3.2. Bio-optical measurements and primary productivity studies

3.2.1. Diel cycles of light attenuation by particles

Diel variations of beam attenuation have been used in several studies to estimate primary production, with the implicit hypothesis that these variations reproduce those of particulate organic carbon (POC), i.e. that the carbon-specific beam attenuation coefficient (c_c^*) is constant throughout the day (Siegel et al., 1989). Cullen et al. (1992) used this technique in the equatorial Pacific during the WEC88 cruise (150°W , 15°N – 15°S) and obtained encouraging results. Walsh et al. (1995) also applied this method during the EqPac cruises TT008 and TT012, and obtained estimates much lower than the corresponding ^{14}C uptake-based estimates, which they explained by the influence of in situ removal processes (grazing and aggregation). Their estimates may have been biased also

because they were based on a POC-to-particulate matter concentration ratio derived from North Atlantic waters, which was a factor of two lower than that observed during the TT012 cruise (see Claustre et al., 1999). Other sources of error, however, are likely to affect such estimates. Cullen et al. (1992) emphasized that the constancy of c_c^* throughout the day was probably questionable, which was confirmed later by Stramski et al. (1995), who observed, from laboratory experiments on *Synechococcus*, an increase in c_c^* by approximately 30% from dawn to dusk. Therefore, assuming a constant c_c^* should provide primary production rates overestimated by the same amount. Bishop (1999), reanalyzing c_p and POC data collected (between 0 and 1000 m) during the TT007 and TT011 cruises, observed a high correlation in the c_p vs. POC relationship (with a slope virtually independent of location, season and depth), which suggests that c_c^* could be considered as constant. This conclusion, however, might not be relevant to the diurnal scale, because diel variations of c_c^* may have been obscured by the large variation ranges of c_p and POC values in this data set.

Cullen et al. (1992) also pointed out that specific growth rates of phytoplankton cannot be reliably determined from changes in c_p if the relative contributions of phytoplankton, heterotrophic organisms and detrital particles to this coefficient are not known. As the non-algal part of c_p is expected to vary much less than the algal part throughout the day, assuming that 100% of the c_p signal is originating from phytoplankton will lead to underestimates of growth rates and primary production rates. The previously mentioned studies by DuRand and Olson (1996), Chung et al. (1996, 1998) and Claustre et al. (1999) demonstrated that the actual contributions can be determined with a reasonable accuracy, and vary according to local biogeochemical conditions within the equatorial Pacific. Using these estimates, Claustre et al. (1999) obtained primary production rates of $0.85 \pm 0.27 \text{ gC m}^{-2} \text{ d}^{-1}$ at 5°S , which compared well with ^{14}C uptake-based estimates ($0.65 \pm 0.22 \text{ gC m}^{-2} \text{ d}^{-1}$) (note that taking into account a 30% increase in c_c^* would still improve the agreement).

The two issues discussed above (diel variations of c_c^* , contributions of the various constituents to c_p) therefore have to be considered, even if the corresponding errors may partially compensate each other. As emphasized by DuRand and Olson (1996), this clearly illustrates the need for a characterization of the phytoplankton community when using diel variations of beam attenuation as a tool to estimate primary production. With this regard, the bio-optical studies performed in the equatorial Pacific have therefore largely contributed to improve the interpretation of c_p variations.

It is also important to mention that a significant part of the diel changes in c_p could be accounted for by variations in the surface mixed-layer depth (Gardner et al., 1995). These authors observed, during the EqPac TT008 cruise (cool surface-water conditions) at the equator, an increase in mixed-layer depth from approximately 20 m during the day to 70 m at night, and found that approximately 50% of the decrease in c_p at night could simply result from the dilution of surface water with particle-depleted, deeper water. This mixing process (which also may influence the optical properties of phytoplankton via photoadaptation of cells to varying light levels), therefore has to be considered when estimating primary production from c_p diel changes. Finally, such mixing may also induce diel changes in photosynthetic parameters (see Section 3.2.3).

3.2.2. Primary production estimates from solar-stimulated fluorescence

Many studies have been dedicated to the potentialities of natural (sun-stimulated) fluorescence of Chl *a* for estimating primary production (e.g., Topliss and Platt, 1986; Kiefer et al., 1989). This technique relies upon the hypothesis that the ratio of quantum yields for carbon fixation and fluorescence is constant, or at least predictable (Chamberlin et al., 1990). Measurements performed during the WEC88 cruise (15°N to 15°S, along 150°W) by Stegmann et al. (1992), combined with a linear production–fluorescence model, allowed the variability of this ratio to be estimated. These measurements revealed that (i) this ratio was relatively low in the investigated area, possibly as a result of light-induced or other physiological

stress, (ii) it showed latitudinal variations, with the highest values occurring in the equatorial zone, (iii) the largest variations were diurnal, with a drop by almost a factor of 2 between morning and evening. Stegmann et al. (1992) concluded that a large part of variability was still unexplained, and that the influence of environmental factors upon the variability of these quantum yields would have to be better understood.

Within the JGOFS-equatorial Pacific program, even if to our knowledge the production–fluorescence relationships have not been reexamined, several studies concerning the corresponding quantum yields have been conducted. Those dealing with the maximum quantum yield for carbon fixation reveal that it exhibits large spatial and diel variations (see below). As for the quantum yield for fluorescence, experimental determinations were made in a recent study (Maritorena et al., 2000) from measurements performed with a LICOR spectroradiometer and a Biospherical PNF profiler during the OLIPAC cruise. The quantum yield, determined around noon, was found to vary by almost a factor of 3 (from 0.34% to 0.92%) near the surface between 5°S and 1°N, with no apparent latitudinal trend. Therefore, both the spatial and diel variations of the quantum yields for carbon fixation and fluorescence still appear to be serious limitations to reliable estimates of primary production from natural fluorescence of Chl *a*.

3.2.3. Bio-optical properties and estimation of photosynthetic parameters

Several studies in the equatorial Pacific were dedicated to the determination of photosynthetic performances of phytoplanktonic populations, mostly with the objective of explaining the high-nutrient, low-chlorophyll situation, i.e. “why the equator is not greener” (Barber, 1992). Some of these included bio-optical measurements.

When determining the photosynthetic parameters of phytoplankton from measurements of photosynthesis–irradiance (“*P* vs. *E*”) curves, measurements of bio-optical (absorption) properties are involved only when converting the initial slopes of the curves, α , into maximum quantum yields for carbon fixation, Φ_m . Prior to the JGOFS program (WEC88 cruise), Cullen et al. (1992)

determined the photosynthetic characteristics of phytoplankton, and suggested that grazing was the major factor controlling phytoplankton growth. In their study, P vs. E curves were not associated with absorption measurements, so that results were discussed in terms of initial slopes α and assimilation numbers P_{\max} (these latter being found relatively low, in spite of high growth rates, possibly because of low C:Chl ratios).

During the EqPac TT011 cruise, Lindley et al. (1995) derived Φ_m from measurements of photosynthesis–irradiance curves. Absorption spectra of phytoplankton were not measured, but reconstructed from HPLC-determined pigment concentrations, assuming a negligible packaging effect (but see Sosik and Mitchell, 1991). They observed an increase of Φ_m when approaching the equator, although the values remained much lower than for nutrient-replete populations (around 0.010 – $0.015 \text{ mol C (mol quanta)}^{-1}$ near the surface). As mentioned by the authors, direct determinations of particulate absorption during this cruise (Cleveland, 1994) suggest that the reconstructed absorption values were overestimated near 2°N where diatoms were abundant, indicating that the packaging effect was not negligible (see also Allali et al., 1997), and that Φ_m could be underestimated around the equator. Such a bias would still reinforce the latitudinal patterns observed by Lindley et al. (1995). Sadoudi et al. (1997), from measurements of photosynthesis–irradiance curves and absorption spectra during the OLIPAC cruise, also observed a maximum of Φ_m near the surface at the equator, with values in the same range (around $0.010 \text{ mol C (mol quanta)}^{-1}$).

Additional information was obtained by computing the quantum yield for carbon fixation with respect to photosynthetically usable absorption instead of total phytoplanktonic absorption (i.e. by removing the contribution of non-photosynthetic pigments). Lindley et al. (1995) found that the quantum yields so computed (hereafter called $\Phi_{m,ps}$) followed spatial patterns quite different from those of Φ_m , with a continuous decrease from 12°N to 12°S , which they explained by a combination of N and Fe limitations (macronutrient limitation north and south of the

equatorial band, and an increasing Fe limitation from 12°N to 12°S , which the authors related to the concomitant decrease of the atmospheric deposition of iron-rich Asian dusts). Coale et al. (1996), however, showed that the source of iron at the equator is primarily upwelling from the equatorial Undercurrent, rather than the atmosphere. Sadoudi et al. (1997) deriving the $\Phi_{m,ps}$ values from simultaneous measurements of photosynthesis–irradiance curves and absorption spectra during the OLIPAC cruise, did not observe such a latitudinal trend, presumably because during this period the equatorial Undercurrent was about 50 m deeper than the mean (R. Barber, pers. comm. to M. Babin) and the upwelling regime was weakened.

The photosynthetic performances of phytoplankton in the equatorial Pacific also have been examined by active fluorescence (Falkowski et al., 1992), which can be considered also as a “bio-optical technique”. In this approach (which includes pump-and-probe and fast repetition rate fluorometry), the measured quantity is the maximum change in the quantum yield of in vivo chlorophyll fluorescence ($\Delta\Phi_m = F_v/F_m$, where F_v is the variable fluorescence and F_m is the maximum fluorescence, when all reaction centers are closed), which represents the efficiency of photochemical energy conversion. The first results obtained using this technique in the equatorial Pacific, obtained by Greene et al. (1994) during the FeLINE II cruise in spring 1992, showed, consistent with those of Lindley et al. (1995), a decrease of $\Delta\Phi_m$ from 12°N to the equator. During the JGOFS program, measurements by FRR fluorometry were also performed during the OLIPAC cruise. Sadoudi et al. (1997) observed spatial patterns similar to those observed for $\Phi_{m,ps}$ (particularly in their depth dependence). Behrenfeld and Kolber (1999) observed during the same cruise a strong diel pattern in $\Delta\Phi_m$ in the upper layer, and stated, from further laboratory and in situ (IronEx II) experiments, that this pattern was induced by iron limitation. Consistently, Gardner et al. (1995) suggested that the strong increase in the mixed-layer depth observed at night during cool surface-water conditions (see Section 3.2.1) could introduce micronutrients from deep waters to the

surface (and possibly iron from the equatorial Undercurrent), which could induce diel changes in $\Delta\Phi_m$.

Even if the origin of these diel changes is still controversial (they also were observed in areas where no iron limitation occurs; M. Babin, pers. comm.), the evidence of a physiological limitation of phytoplankton growth by iron seems to be now established, as one of the major causes of HNLC conditions in the equatorial Pacific (Greene et al., 1994; Coale et al., 1996; Barber et al., 1996). The above-mentioned studies, based on bio-optical measurements, therefore contributed to support this hypothesis. In addition, spatial and temporal sampling of photosynthetic parameters should in the future provide bases for feeding primary production models with realistic inputs, instead of standard sets of parameters. The above studies suggest that parameterizations at a regional scale might be insufficient, and that the scales of spatial and temporal variability in nutrient supply, species composition, and algal size also should be considered.

3.2.4. Estimate of primary production rates via bio-optical models

Bio-optical variables can be used as input parameters into light-photosynthesis models with a view to estimating primary production rates (see e.g., Bidigare et al., 1992). In the equatorial Pacific, this approach was used in particular by Foley et al. (1997) to predict the temporal changes in primary production from the continuous measurements acquired from the PROTEUS mooring (at 0°, 140°W). They used a simple bio-optical model, with chlorophyll concentration (derived from in situ fluorescence), PAR, and shipboard measurements of assimilation numbers (P_{\max}) as input parameters. Using these estimates in conjunction with physical parameters, they were able to show evidence that primary productivity variations were largely controlled by the physical variability associated with the passage of equatorial longwaves (including TIWs and Kelvin waves) and to the depth of the equatorial Undercurrent as related to ENSO phase.

4. Summary and conclusions

The bio-optical studies performed during the JGOFS-equatorial Pacific program have contributed to the knowledge of this oceanic region in various aspects. Some of these studies allowed the temporal and spatial variations of inherent optical properties to be quantified, and the relative contributions of the various particulate pools (and within the algal pool, of the various phytoplanktonic groups) to these properties to be estimated. Such continuous bio-optical measurements were complementary to (and enhanced the value of) discrete measurements of biological or biogeochemical variables (necessary for a proper calibration); in turn, they gave access to higher spatial and temporal resolution for these variables, and therefore to a better characterization of the various pools, and of the phytoplankton community itself. These studies thus provided useful information for bio-optical models to be developed for this oceanic area, e.g., the large contribution of non-algal particles to total scattering or attenuation (approximately 50%), their weak contribution to particulate absorption (approximately 10% at 440 nm), and the large contribution of CDOM to total absorption (approximately 50% at 440 nm in the surface layer). The direct influence of physical conditions upon the bio-optical and biogeochemical variability of equatorial Pacific waters, however, also was clearly evidenced, as well as the diel variability of some optical properties such as light attenuation and stimulated fluorescence of Chl *a*.

Bio-optical measurements also contributed to a better assessment of primary production rates in the equatorial Pacific, mostly via (i) the determination of diel variations of light attenuation by particles (c_p), (ii) the estimate of quantum yields for carbon fixation by phytoplankton, and (iii) the combined use of bio-optical mooring time series and models. The interpretation of c_p variations was greatly improved by the characterization of the particulate pools as mentioned above, although it still needs to be refined through a better knowledge of the variations in the carbon-specific attenuation coefficient of particles. Quantum yields of carbon fixation by phytoplankton

were confirmed to be lower in the equatorial upwelling band than those expected for nutrient-replete populations, consistent with the current hypothesis of iron limitation in this oceanic area.

Information concerning the bio-optical properties of equatorial Pacific waters acquired during the JGOFS program was still limited in many situations, because all the pertinent variables were not systematically determined (e.g., CDOM absorption concurrently to particulate absorption, etc.), some variables were still inaccessible (e.g., particulate backscattering), and because in situ profilers had limited capacities (i.e. provided measurements at only one wavelength) at the time of field operations. The development of multiple-wavelength or hyperspectral attenuation/absorption meters, backscattering meters and fluorometers is therefore likely to contribute to a better knowledge of the equatorial Pacific system in the upcoming years. Time series of bio-optical variables, as acquired from moorings within the Tropical Atmosphere Ocean (TAO) array during the JGOFS EqPac program (Foley et al., 1997) and subsequently by Chavez et al. (1999), also have been shown to provide valuable information for studying the processes driving the biological and biogeochemical variability of the equatorial Pacific system, and should become more widely used in the future.

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