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Research Article

Chlorophylls and Phycoerythrins as Markers of Environmental Forcings Including Cyclone Erica Effect (March 2003) on Phytoplankton in the Southwest Lagoon of New Caledonia and Oceanic Adjacent Area

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Spatio-temporal variations of chlorophylls and phycoerythrins, inferred by spectrofluorometric methods, were studied from April 2002 to June 2003 in the southwest lagoon and oceanic waters of New Caledonia. Trade winds blew 75% of the time and appeared as the main factor influencing surface Tchl*a* (sum of monovinyl- and divinyl-chlorophyll *a*) variations in the ocean, near the barrier reef. Lagoon and oceanic waters differed in the composition of picoplanktonic cyanobacteria with a relative dominance of *Prochlorococcus* and high-phycourobilin *Synechococcus* in the ocean, and a relative dominance of high-phycoerythrobilin *Synechococcus* in the lagoon. Main pigment variations in the lagoon were associated with cyclone Erica in March 2003 and showed a 5-6 fold Tchl*a* increase around Nouméa. The cyclone stimulated mainly diatom growth as indicated by the high chlorophyll $(c_1 + c_2)$/chlorophyll *a* ratio and by the lowest values for the other pigment ratios. The relative importance of divinyl-chlorophyll *a* concentration and fluorescence excitation spectra of phycoerythrins appeared as useful tools for characterizing lagoon-ocean exchanges.

1. Introduction

Phytoplankton pigments (chlorophylls, carotenoids, phycobiliproteins) remain a major source of information on biomass, community structure, dynamic, and physiological state of phytoplankton. The old concept of chlorophyll *a* concentration as a proxy of phytoplankton biomass is now represented by the sum of two chemical entities (Tchl *a*): the monovinyl-chl *a* (chl *a*), associated to most of the photooxygenic organisms, and the divinyl chlorophyll *a* (dv-chl *a*) specifically associated to the cyanobacteria of the genus *Prochlorococcus*. The discrimination between these two pigments provides essential information about community structure in oligotrophic waters where *Prochlorococcus* often represents more than 50% of the Tchl *a* [1, 2].

Previous research on pigments in New Caledonian waters concerned mainly the south west lagoon (SWL, Figure 1) and was limited to bulk chl *a* concentration distribution and variations [3–10]. Early work reported increasing Tchl *a* concentration from the ocean through the coastal lagoon to the estuaries with maxima found after flooding and in urban effluent areas [3]. However, it did not provide

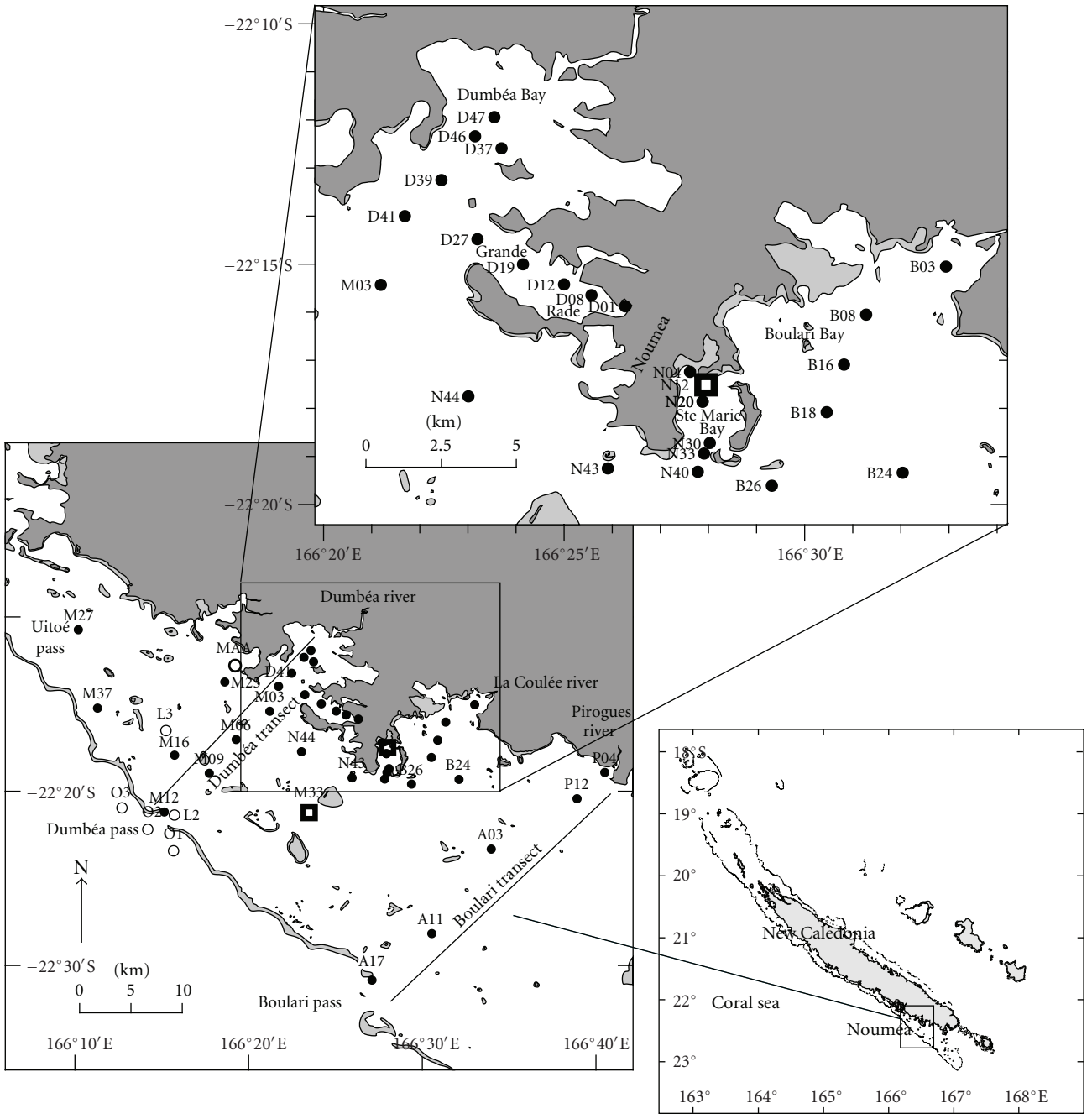

Figure 1: Map of the sampling locations. Stations sampled (1) at five depths with a mean frequency of 10.3 days (N12 and M33: open squares), (2) monthly at the surface (dark circles), (3) monthly (open circles) at the surface and near the bottom (lagoon: L2, L3, MAA) or at six depths from 0 to 100 m (ocean: O1), (4) during the tide cycles (O1, O2, O3, L2, L3).

any evidence of Tchl *a* temporal periodicity. More recent investigations highlighted the occurrence of clear daily and seasonal trends for Tchl *a* [9, 10]. The seasonal signal could also be extracted from a four-year long time series (1979–1983) by spectral analysis using wavelet methods [8]. Nevertheless, short-term fluctuations (1-2 weeks) related to local but usual meteorological event are in the same range than annual variations [9]. Winds, precipitations [9], anthropogenic activities [10], and hydrodynamics [11] are the main environmental factors that can explain the Tchl *a* variations in the SWL. A coupled three-dimensional physical-biological model was developed to simulate the Tchl *a* distribution in the SWL from freshwater input, trade winds intensity, and hydrodynamics [12]. This model demonstrated that eutrophication is limited to coastal bays and oligotrophic conditions prevailed in most part of the lagoon. In the ocean, results were relatively scarce. A general enrichment in chlorophyll of surface waters of the Coral Sea

Table 1: Sampling interval, period, and stations as well as physico-chemical (P-C. P.) and biological (B. P.) parameters measured during the different operations.

Period	Stations	interval	P-C. P.	B. P.
Apr 02-Apr 03 (S1)	N12, M33	10 ± 3.6 days	T., S., IF, Nut.[2]	Chl, PE, FC
Apr 02-May 03 (S2)	O1, L2, L3, MAA	Monthly	T., S., IF, Nut.[3]	Chl, PE, FC[4]
Sep 02-Apr 03 (S3)	Other stations[1]	Monthly	T., S., IF	Chl[5], PE[5]
13-14 June 03[6](S4)	O1, O2, O3, L2, L3	Tide cycles	T., S., IF, Nut.[3]	Chl, PE

T. = Temperature; S. = Salinity; IF = in vivo chl *a* fluorescence; Chl = chlorophylls; PE = phycoerythrins; FC = cell counts by flow cytometry; Nut. = nutrients. [1]28–30 stations in the south west lagoon according to weather conditions; [2]NO_3+ NO_2, PO_4, NH_4, $Si(OH)_4$; [3] NO_3+ NO_2, PO_4; [4]April 2003 only; [5]sampling at the surface only; [6]Diapalis 8 cruise.

until 20°S is observed during winter cooling and consecutive water column mixing [13]. Another increase of Tchl *a* near the barrier reef (Uitoé pass) seems related to nutrients and Tchl *a* ouput from the lagoon [14]. Nevertheless, during trade wind events, upwelling along the barrier reef could also enhance the phytoplanktonic production [15].

The bulk Tchl *a* concentration does not give information on the effect of environmental forcing on the structure of phytoplankton communities. Other phytoplankton pigments can help to determine this structure via more-or-less specific chemotaxonomic markers [16]. In the present work, spectrofluorometric methods were implemented to analyze the different chlorophylls [17, 18] and phycoerythrins [19, 20] in samples collected during several investigations in the SWL and in the adjacent oceanic area in 2002 and 2003. Outside the information on community structure, the spectrofluorometric chlorophyll analysis reduces pitfalls in the determination of Tchl *a* that are inherent to the classical fluorometric and spectrophotometric method [21].

The important question addressed in this study was how the community structure was affected by environmental forcing. For that, the objectives were (1) to examine temporal variability of phytoplankton biomass and community structure through pigment composition in relation to variations of environmental physico-chemical factors at the weekly, monthly, and seasonal scales, and (2) to analyze the effect of meteorological events as strong SE trade winds (mean 20 knots), heavy rains, cyclone on the pigment abundance, and distribution in the SWL. Another question was to assess if upwelling observed on the oceanic side of the barrier reef during trade winds events enriched surface waters in nutrients and promoted phytoplankton biomass and community structure changes. This phenomenon could also influence somewhat lagoon waters via exchanges with the ocean. Analysis of the cyanobacterial component of the photosynthetic community as a marker of water exchange between ocean and lagoon is discussed.

2. Material and Methods

2.1. Study Site. New Caledonia is an island located in the southwest Pacific Ocean (Coral Sea). It is surrounded by important barrier reefs delimiting a large lagoon area (4537 km^2 of reefs and 31.336 km^2 of non reef areas: lagoons, terraces, enclosed basins, and passages [22]). In the southwestern part, it is larger and separated from the ocean by a nearly continuous emerging barrier reef interrupted only by a few passages (Figure 1). At the southeast end, it is more open to the surrounding ocean and the main input of oceanic waters to occur there, especially when southeast trade winds are blowing [23]. Its mean depth is 17.5 m, but maximum depths of 60–70 m are observed in the narrow canyons located in front of the passes. Climatic conditions are characterized by periods of heavy rain in summer (200–600 mm per 24 h). River outflows and runoff from the steep slopes bordering the lagoon carry mineral and organic particulate matter as well as dissolved nutrients that can stimulate phytoplankton growth and productivity in the lagoon. Mining activities (nickel, chrome) also facilitate land erosion during runoff. The anthropogenic influence is also important in the SWL and is related to waste water and industrial effluents originating from the capital of New Caledonia, Nouméa [24], and its suburbs (nearly 160 000 inhabitants).

2.2. Stations. Several operations were conducted at different stations with various sampling interval using the R/V "Coris". They are summarized in Table 1.

From 4 April 2002 to 9 April 2003, morning sampling (S1) was realized at two stations with a mean (±SD) interval of 10.3 (±3.6) days (Figure 1, open squares). The objective was to compare a station submitted to untreated sewage input from Nouméa (N12 in the Sainte Marie Bay; sampling depths: 3, 4.75, 6.5, 8.25, and 10 m; bottom = 13 m) to a typical station of the central lagoon (M33; sampling depths: 3, 7, 11, 16, and 20 m; bottom = 23 m) more influenced by oligotrophic conditions. Temporal variability of phytoplankton abundance and primary production was examined in relation to variations of environmental physico-chemical factors [9, 25]. Counting of picophytoplanktonic populations by flow cytometry could be compared with specific pigment data (dv-chl *a* for *Prochlorococcus*; phycoerythrin for *Synechococcus*).

From April 2002 to June 2003, sampling every month (S2) at four stations: one oceanic station near the Dumbéa Pass (O1: sampling at 0, 20, 40, 60, 80, and 100 m depth, bottom > 300 m), one station inside the lagoon near the Dumbéa Pass (L2; bottom = 20 m), one station in the central lagoon northwest of M33 (L3, bottom = 30 m), and one station in the Maa Bay (MAA, bottom = 15 m). At these

three last stations, waters were taken at both the surface and from near the bottom. Days of sampling were chosen in order to reach the O1 and L2 stations around high tide in the morning (Figure 1, open circles). This program was conducted to compare temporal variations of pigment in the lagoon and oceanic waters and their relationship with physico-chemical parameters.

From September 2002 to April 2003, sampling every month (S3) at the surface of 30 stations (Figure 1, dark circles). This sampling was done over two consecutive days and included transects from the coast to the Dumbéa (M03, M06, M09, M12, D41, D39, D46, D47) and Boulari (A17, A11, A03, P12, P04) passes. It allowed rapid surveys of a large part of the central south west lagoon and to obtain more details on the different bays near Nouméa.

During the above operations, water samples for chlorophylls (0.25–0.5 L) and phycoerythrin (1–3 L) were stored in opaque plastic bottles and filtered at the laboratory, about 1–3 hours after sampling.

On 13-14 June 2003, the Diapalis 8 cruise (a component of the DIAPAZON program "Diazotrophy in the Pacific Zone": http://www.com.univ-mrs.fr/IRD/urcyano/bdd/diapazon/bddiapaz.htm) on the R/V Alis allowed us to sample L2 (Dumbéa pass), L3 (central lagoon) and a transect parallel to the reef of three oceanic stations: one located about 1.5 km in front of the Dumbéa Pass (O2) and the others 3km northwest (O3) and southeast (O1) of this station. The 5 stations were sampled (S4) at each high and low tide (±1h) during two tide cycles. Filtration for chlorophylls and phycoerythrins analysis was performed on board and the filters stored in liquid nitrogen. This operation was conducted to appreciate if picoplankton pigment could serve to the determination of ocean-lagoon exchanges.

2.3. Physico-Chemical Measurements. Temperature, salinity (conductivity), and pressure were measured with a CTD SEABIRD SBE 19 fixed on a stainless steel structure. This structure was also equipped with a Seapoint optical backscatter sensor and with a Seapoint fluorometer adapted for in vivo chlorophyll *a* fluorescence measurements.

For nitrate and phosphate determinations, samples taken at M33 and N12 were immediately frozen before analysis. During the other sampling programs, they were preserved by the addition of $HgCl_2$ [26] and maintained at 4°C before analysis. Nitrates were assayed with a Technicon II autoanalyzer following the method described in [27] for NO_3 concentrations $> 1\,\mu$M and the high sensitivity method for NO_3 concentrations $< 1\,\mu$M [28]. Soluble reactive phosphorus (PO_4) analyses were measured using a CECIL spectrophotometer equipped with a 10 cm cell and set at a wavelength of 885 nm [29]. Analytical precision was $0.005\,\mu$M for NO_2 and NO_3 (high sensitivity) and $0.020\,\mu$M for PO_4 and NO_3 (low sensitivity).

Ammonium concentration was assayed by fluorometry in 3 unfiltered 40 mL replicates on a Turner TD-700, using the *o*-phthaldialdehyde method [30] immediately after collection.

Silicates were determined on frozen samples according to [31].

2.4. Chlorophyll and Phaeopigments Analysis. Water samples were filtered onto 47 mm GF/F filters. The filters were dipped in 5.4 mL 100% acetone (final concentration ≈ 90% acetone taking into account water retention by the filter, i.e., 0.621 ± 0.034 mL) and ground with the freshly broken end of a glass rod for chlorophylls and phaeopigment extraction. Pigments were analyzed by spectrofluorometry according to the basic method described in [17] and using recent significant improvements in qualitative and quantitative analysis [18, 32]. Calibration of the instrument (HITACHI F4500 spectrofluorometer operating in ratio mode) was performed each two years with pure solutions of chl *a*, chl *b*, a mixture of chl c_1 and c_2 (chl $c_1 + c_2$), chl c_3, dv-chl *a*, dv-chl *b* and phaeopigments derived from each chlorophyll. Pigment concentrations were calculated from a 31×26 fluorescence excitation emission matrix (806 values) by nonnegative linear least squares approximation [18]. The method allows the discrimination between chl *a* and dv-chl *a*. It provides information on the relative proportion of chlorophyll *b*-(Chlorophytes) and chlorophyll *c*-(Chromophytes) containing eukaryotes, although chlorophyll *b* (chl *b*) is also synthesized by some strains of *Prochlorococcus* [33]

The significance of spectrofluorometric results is related both to the relative concentrations of the pigment in the extracts and to its quantum yield in the solvent used. Tchl *a* designation will be used for the sum of chl *a* and dv-chl *a*. Only a dv-chl *a* concentration which represented at least 8% of Tchl *a* will be considered significant. This does not mean necessarily that dv-chl *a* is absent, but that the accuracy of its determination is poor below this threshold. Similarly, thresholds for significant values of chl *b* and chl c_3 concentrations were fixed at 5% of Tchl *a* (2% for chl $c_1 + c_2$).

More recent sampling in the SWL (Bissecote cruise, February 2006) has enabled us to compare chlorophyll analysis by the current spectrofluorometric method (SPF) and by high-performance liquid chromatography (HPLC). Close correlations (Neveux, unpublished) were observed for each of the different chlorophylls. However, the mean absolute values for chl c_3 concentration were 3.0 ± 0.7 fold higher by SPF than by HPLC which suggested overestimation of this pigment and consequently of the chl c_3/chl ($c_1 + c_2$) ratio by SPF. Nevertheless, the relative changes of this ratio remain valid.

2.5. Phycoerythrin Analysis. In tropical waters, phycoerythrins (PE) are the dominant phycobiliproteins and are essentially associated to cyanobacteria. They exhibit spectral diversity related to their relative content in two chromophores, the phycourobilin (PUB) and the phycoerythrobilin (PEB) as well as to chromophore-chromophore interactions and chromophore-protein linkage [34]. This spectral diversity provides both qualitative and quantitative information on dominant populations of cyanobacteria in natural waters [35].

Water samples were filtered onto $0.4\,\mu$m Nuclepore polycarbonate membrane (47 mm diameter). Filters were dipped into a tube containing 4 mL glycerol-phosphate buffer (0.1 M NaH_2PO_4, pH = 6.5) mixture (50/50). The

Table 2: Distribution of chlorophylls in main algal classes (inspired from [37]).

Algal classes	Chl *a*	Dv-chl *a*	Chl *b*	Chl c_1	Chl c_2	Chl c_3	Dv-chl *b*
CHLOROPHYTES							
Chlorophyceae	X		X				
Prasinophyceae	X		X				
Euglenophyceae	X		X				
Eustigmatophyceae	X						
CHROMOPHYTES							
Bacillariophyceae[a]	X			X	X	X	
Prymnesiophyceae[b]	X			X	X	X	
Chrysophyceae	X				X	X	
Pelagophyceae	X				X	X	
Dinophyceae	X				X		
Cryptophyceae	X				X		
CYANOPHYTES							
Prochlorococcus		X	X				X
Others	X						

[a]chl c_3 replaces chl c_1 in some diatoms [37]
[b]Variable combinations of chl *c* pigments in this group [37]

tubes were shaken vigorously for resuspension of particles according to the in vivo Wyman's method [19]. Fluorescence excitation spectra of phycoerythrin were recorded between 450 and 580 nm (emission at 605 nm) on the HITACHI F4500 spectrofluorometer operating in ratio mode. Slit widths were 5 and 10 nm at the excitation and emission sides, respectively. Concentrations of phycoerythrin were assessed after blank subtraction from the area below the fluorescence excitation curves and using the calibration procedure described in [20]. Only the 450–560 nm range of the spectra is used for the calculation. The fluorescence in the 560–580 nm range indeed is significantly contaminated by an excitation light diffusion signal, particularly for samples high-loaded in particles and poor in cyanobacteria. For the determination of the PUB/PEB ratio (fluorescence ratio at the PUB and PEB excitation peaks), correction factors for excitation wavelength-dependent energy were determined by using Rhodamine B as quantum counter and applied to the recorded excitation spectra. This makes easier the comparison of PUB/PEB ratio in different field studies [13]. The PUB peak was generally located at 495±2 nm and the PEB peak at 550 ± 2 nm.

2.6. Flow Cytometry. Samples (2 mL) were preserved by addition of 40 μL of a 10% paraformaldehyde solution (0.2% final concentration) [36] and frozen in liquid nitrogen before storing at −80°C. Thawed samples were analyzed with a Becton Dickinson flow cytometer to obtain counts of *Prochlorococcus*, *Synechococcus,* and picoeukaryotes as well as light scatter (0°, 90°) and fluorescence (orange and red) properties of cells. Data were normalized using 1 μm Polysciences beads.

2.7. Meteorological Information. Precipitations and wind speed and direction were measured by Météo France at the Amédée Island station located near the Boulari Pass and by IRD the Maître Island station in the center of the lagoon (near M33).

3. Results

3.1. Normal Spatial Surface Distribution in the Southwest Lagoon. Surface sampling every month at 30 stations from September 2002 to April 2003 (S3) provided synthetic information on the spatiotemporal distribution of phytoplankton in the SWL (Figure 2). Under normal conditions, the highest Tchl *a* concentration was always found at coastal stations and particularly in the different bays near Nouméa (Sainte-Marie: 1–2.9 μg L^{-1}; Grande Rade: 1–2.2 μg L^{-1}). From Nouméa to the barrier reef, the Tchl *a*, accessory chlorophylls and PE decreased whereas dv-chl *a* increased. Considering chlorophylls distribution in the main groups of marine pelagic algal classes (Table 2), Tchl *a* decrease was associated to relative increase of *Prochlorococcus* (dv-chl *a* percentage) and chlorophytes (chl *b*/chl *a* ratio) abundance and reduction of chromophytes populations. Additionally, changes within the community of chromophytes emerged from the increase of chl c_3/ (chl c_1 + c_2) ratio with a relative increase of chl c_3-containing groups (Chrysophyceae, Prymnesiophyceae, Pelagophyceae) compared to those containing chl c_1 + c_2 (diatoms, although chl c_3 replaces chl c_1 in some diatoms [37]) or only c_2 (Dinoflagellates, Cryptophytes). The fluorescence excitation spectra of PE showed typical characteristics of cyanobacteria belonging to the *Synechococcus* genus. The PUB/PEB ratio was generally higher in the central lagoon than in the bays. This suggested a relative increase of high-PUB *Synechococcus* with regard to high-PEB *Synechococcus*. However, one outlier value of Tchl *a* (October 2002: 8 μg L^{-1}) was associated to high concentration of PE (> 15 μg L^{-1}) with excitation spectra typical of *Trichodesmium erythraeum*.

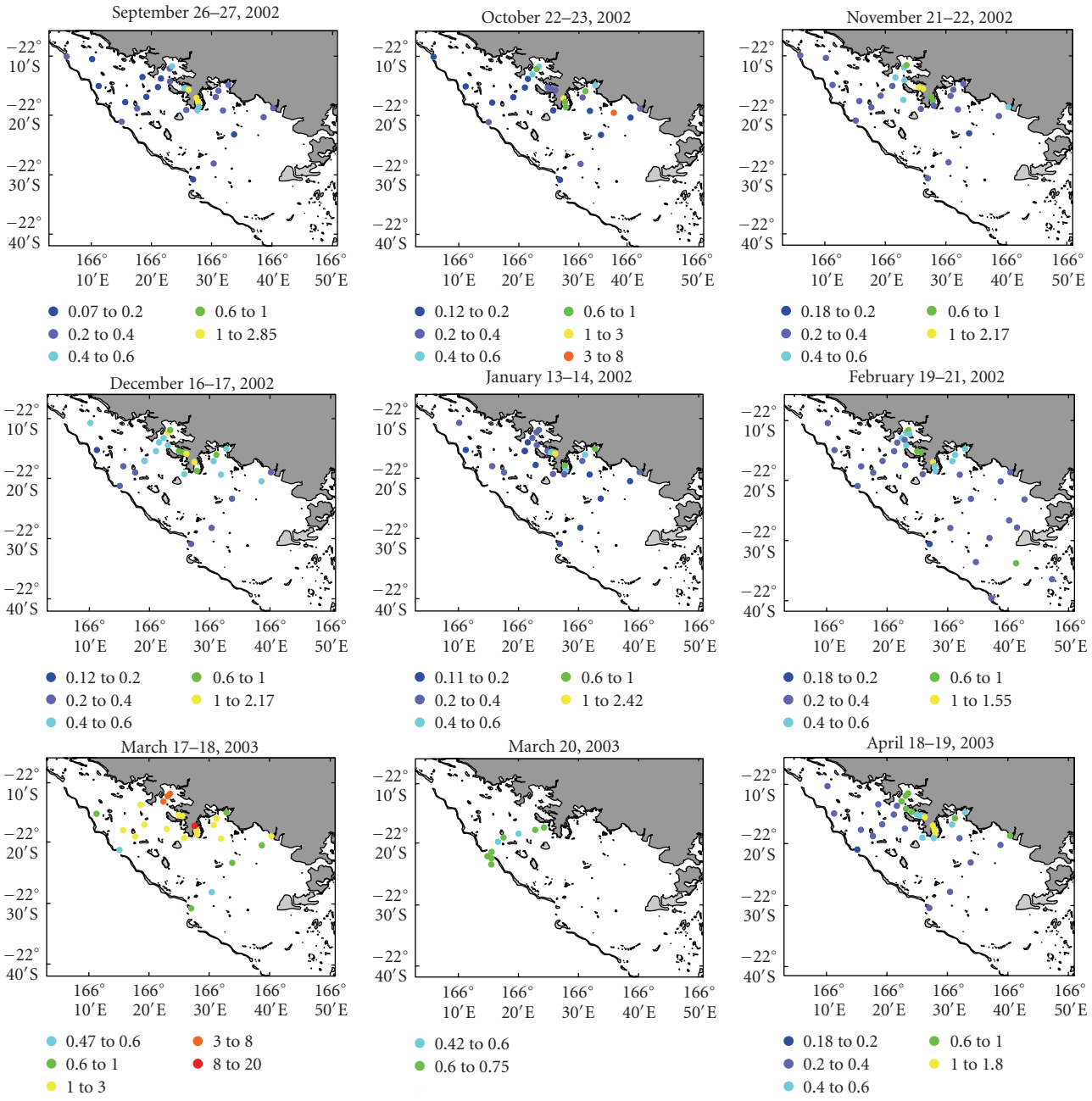

Figure 2: Spatial distribution of Tchl *a* (μg L^{-1}) in the southwest lagoon, each month from October 2002 to April 2003.

Percentage of phaeopigments *a* (%phae *a* = phaeopigments *a**100/Tchl *a*) were generally lower than 10% (86% of data). Maximum values (20–30%) occurred at shallow stations (< 15 m) and more particularly at M37 and N04.

Mean Tchl *a* surface concentration deduced from all the 30 stations was relatively stable all along the sampling period, around 0.48 ± 0.10 μg L^{-1} (Table 3). The Tchl *a* concentrations in the central part of the lagoon were in the 0.2–0.4 μg L^{-1} range, but could decrease to less than 0.2 μg L^{-1}, as in October 2002 or January 2003 (Figure 2). The mean dv-chl *a* percentage was always lower than 10% (Table 2), but it could reach 40% at stations near the passes (A17, M12: September 2002; December 2002 to February 2003) and along the barrier reef (M37: December 2002). The chl *b*/chl *a* ratio showed maximum values (0.2–0.3) near the passes (M12, A17, L2: September and February). However, some high values (0.15–0.20) could also be noted in the Dumbéa bay (September) and the "Grande Rade" (February). The mean and maximum concentrations of *Synechococcus*-PE concentration were around 1–1.5 μg L^{-1}and 5 μg L^{-1}, respectively. The PE/chl *a* ratio was higher in summer than in other seasons which indicated a higher

Table 3: Variations of mean ± (standard deviation) pigment characteristics during the spatiotemporal sampling in the southwest lagoon of New Caledonia; total chl *a* (Tchl *a*) and phycoerythrin (PE) concentrations, dv-chlorophyll *a* percentage (dv-chl *a* * 100/Tchl *a* = %dva), and chlorophyll ratios.

Date	Tchl *a* (μg L^{-1})	$\frac{chl\ b}{chl\ a}$	$\frac{chl\ (c_1+c_2)}{chl\ a}$	$\frac{chl\ c_3}{chl\ (c_1+c_2)}$	%dva	PE (μg L^{-1})	$\frac{PE}{chl\ a}$	$\frac{PUB}{PEB}$
26-27 September	0.43	0.121	0.125	1.0	7.9	0.33	1.24	1.02
	(0.54)	(0.033)	(0.012)	(0.2)	(9.3)	(0.15)	(0.57)	(0.21)
22-23 October	0.35	0.103	0.099	0.7	9.5	0.39	2.01	0.82
	(1.48)	(0.045)	(0.037)	(0.25)	(10.2)	(0.35)	(0.87)	(0.24)
21-22 November	0.47	0.140	0.105	0.8	5.2	0.65	1.87	0.88
	(0.40)	(0.033)	(0.011)	(0.22)	(3.3)	(0.21)	(0.97)	(0.32)
16-17 December	0.66	0.105	0.102	0.4	7.9	1.46	3.51	0.77
	(0.48)	(0.025)	(0.019)	(0.36)	(6.7)	(0.70)	(1.61)	(0.22)
13-14 January	0.42	0.080	0.094	1.0	6.9	0.72	2.56	0.81
	(0.49)	(0.020)	(0.016)	(0.34)	(8.3)	(0.37)	(0.97)	(0.19)
19-20 February	0.48	0.139	0.105	0.9	7.9	1.01	2.8	0.71
	(0.33)	(0.040)	(0.011)	(0.35)	(9.0)	(0.30)	(0.96)	(0.19)
17-18 March	2.95	0.079	0.123	0.4	2.8	1.28	0.96	0.60
	(4.53)	(0.028)	(0.018)	(0.33)	(2.5)	(0.42)	(0.55)	(0.09)
17-18 April	0.57	0.112	0.099	0.8	6.1	1.48	3.16	0.64
	(0.40)	(0.020)	(0.017)	(0.26)	(9.1)	(0.77)	(1.17)	(0.09)

proportion of cyanobacteria in the community, except in January 2003 (Table 3).

3.2. Study of the Seasonal Cycle. The seasonal variations were studied during S1 and S2 sampling (Table 1). S1 compared two stations which differed by the relative anthropogenic influence of the city of Nouméa: N12 in the Sainte Marie Bay and M33 in the central lagoon. S2 compared two stations which differed by their position with regard to the barrier reef: the oceanic station O1 and the lagoon station L2, both located near the Dumbéa pass.

3.2.1. The Sainte Marie Bay (N12) and Central Lagoon (M33) Stations. Between August and September 2002 (austral winter) and February to March 2003 (austral summer), surface water temperature shows clear seasonal variations (21–28.8 °C at N12, 21.1–27.9°C at M33) compared to other physical, chemical, and biological parameters [5, 25]. Salinity tended to increase from April to December 2002 (35.1–35.6 at M33; 34.8 to 36.0 at N12), then decreased until April 2003 (35.3 at M33; 35.1 at N12) in connection with rainfall that was more important in summer than in winter. These observations can be extended to all stations in the SWL, although salinity was more variable at stations located near the mouth of the main rivers. Nutrient concentrations were generally higher at N12 than at M33 with an average factor of 5, 3, and 6 for NO_3 + NO_2, NH_4, and PO_4, respectively (Table 4). Phosphate did not show clear seasonal patterns at the two stations. For dissolved inorganic nitrogen, peaks of short duration were observed between April and August [9]. A significant negative Spearman correlation coefficient was found between each nutrient (at N12 and M33) and salinity indicating the influence of terrestrial and sewage inputs via runoff on the enrichment of the lagoon waters.

The vertical profiles of chlorophylls and PE were relatively homogeneous at the N12 and M33 stations. Consequently, the results can be presented as time variations of integrated concentration over the water column (10 m for N12 and 20 m for M33). The Tchl *a* integrated concentration was generally higher in Sainte-Marie Bay than in the central lagoon (Figure 3(a)). Mean and maximum values were 11 and 23 mg m^{-2} at N12, respectively (6 and 12 mg m^{-2} at M33). Temporal changes showed a 4-5 fold maximal amplitude with peaks of abundance rather observed in austral summer and autumn at the two stations (March-May). However, only the station N12 exhibited a relatively important peak in December 2002 and there was no significant Spearman correlation ($r = 0.30$; $P = .11$) between the Tchl *a* variations observed at the two stations. At N12, the relative integrated concentration of dv-chl *a* was never significant (<8% of Tchl *a*), however, at M33, it reached sometimes a significant proportion (between 8% and 16%) of Tchl *a* (Figure 3(b)) particularly in May-June 2002 and December 2003. Considering pigment ratios, the chl *b*/chl *a* ratio was generally higher at M33 (0.13 ± 0.03) than at N12 (0.10 ± 0.05; Figure 3(c)) while the contrary was true for the chl (c_1 + c_2)/chl *a* ratio (M33: 0.095 ± 0.015; N12: 0.125 ± 0.035; Figure 3(d)). At N12, variations of the chl *b*/chl *a* ratio mirrored that of the chl (c_1 + c_2) ratio with a significant negative Spearman correlation coefficient between the two ratios ($r = -0.71$; $n = 30$; $P = .00001$). Tchl *a* was positively correlated with chl (c_1 + c_2)/chl *a* (0.66; $P = .001$) showing that peaks of Tchl *a* were rather associated to chromophytes. At M33, chl (c_1 + c_2)/chl *a* and chl *b*/chl *a* were positively correlated ($r = 0.39$; $n = 30$; $P = .033$) but no significant

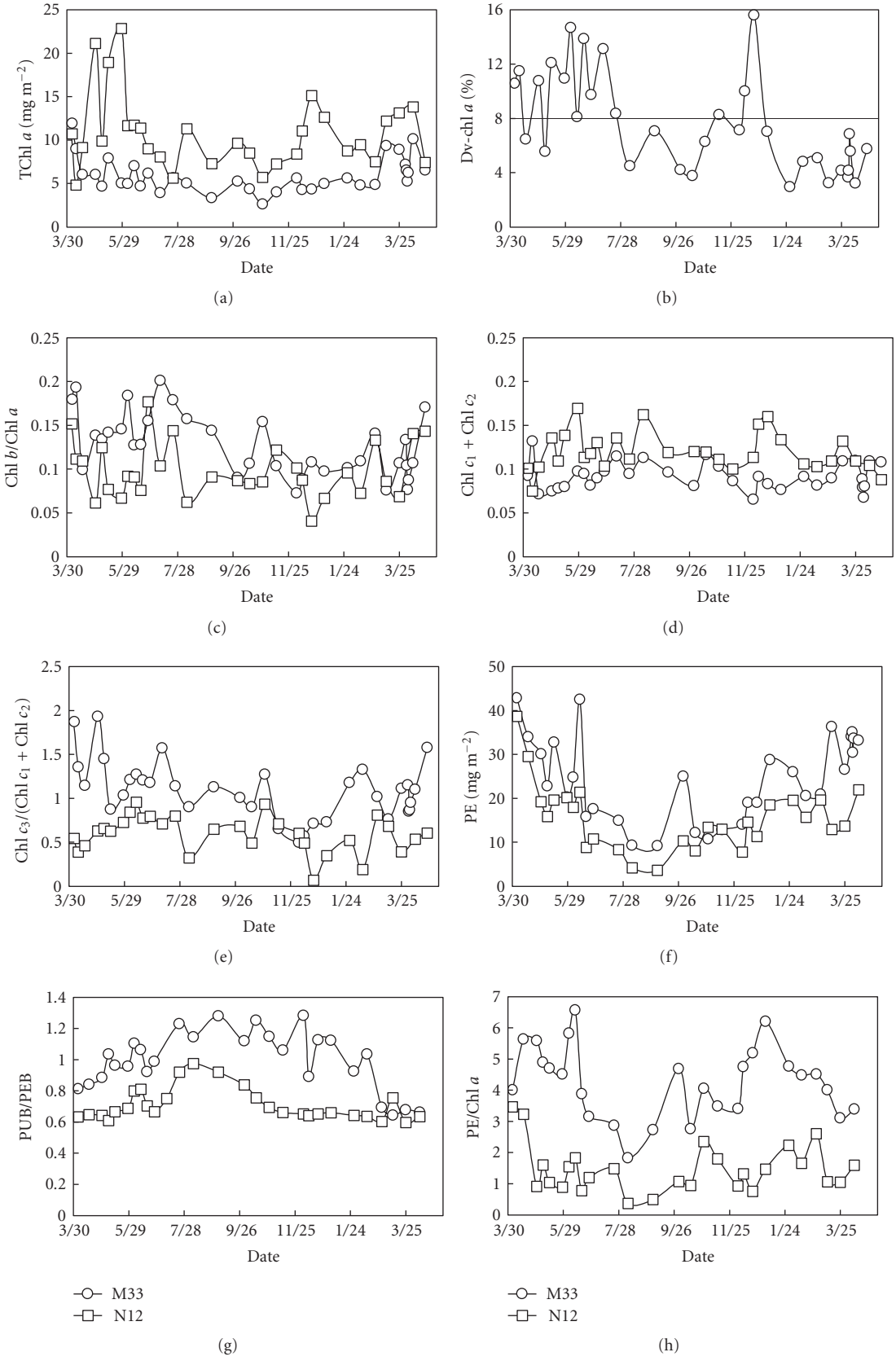

Figure 3: Time series at N12 and M33. Seasonal variations of integrated (a) Tchl a (= chl a + dv-chl a), (b) dv-chl a percentage [= 100(dv-chl a/(dv-chl a + chl a)], (c) chl b/chl a ratio, (d) chl (c_1 + c_2)/chl a ratio, (e) chl c_3/(chl c_1 + c_2) ratio, (f) Phycoerythrin (PE), (g) PUB/PEB ratio, (h) PE/chl a.

correlation was observed between these ratios and Tchl *a* concentration. The difference in chl c_3/ (chl c_1 + c_2) ratio confirmed the results obtained during the spatiotemporal survey with higher chl c_3-containing species in the central lagoon than in the bays (Figure 3(e)). At N12, this ratio did not exhibit maximum coinciding with Tchl *a* peaks.

The integrated PE concentration (Figure 3(f)) was generally higher at M33 (9–42 mg m^{-2}) than at N12 (3–38 mg m^{-2}), but the mean PE concentration was slightly higher at N12. The integrated PE concentration tended to decrease from April to August 2002 then to increase until April 2003. The PUB/PEB ratio was low and relatively constant at N12 (0.6-0.7) 75% of the total time series duration, but reached slightly higher values during the austral winter (0.83–0.98: Figure 3(g)). At M33, this ratio was 1.4 fold higher on average than at N12 with minimum values in March. Variations of PUB/PEB ratio could reflect the nutrient status of waters and the relative influence of the oligotrophic ocean (high ratio) with regard to the terrestrial or/and anthropogenic nutrient input (low ratio). The PE/chl *a* ratios were also higher at M33 than at N12, suggesting that cyanobacteria represented a higher proportion of the community at M33 and confirming spatial distribution results (Figure 3(h)). At the two stations, the PE/chl *a* ratio was negatively correlated with the chl (c_1 + c_2)/chl *a* ratio (-0.74, $n = 27$, $P = .00001$ for N12; -0.77, $n = 27$, $P < .00001$ for M33). In contrast, the chl *b*/chl *a* ratio was positively correlated with the PE/chl *a* ratio at N12 (0.61, $n = 27$, $P = .00075$) but uncorrelated at M33. The %phae *a* was on average (±SD) 7.9 ± 1.3% and 10.8 ± 1.5% at M33 and N12, respectively.

If pigment ratios and their variations allow analyzing spatiotemporal changes in phytoplankton community structure, they do not give information on the relative contribution of the different groups to the Tchl *a* concentration. Considering that contribution of *Prochlorococcus* was assessed by the concentration of dv-chl *a*, the problem was to determine the contribution of chl *a*-containing groups to chl *a*. To achieve this goal, several hypotheses were advanced: (1) Chl *a* belonged to three main groups: chlorophytes, chromophytes, and cyanobacteria; (2) each group was represented by an independent variable: chl *b*, chl (c_1 + c_2) and PE, respectively; (3) pigment ratios were relatively constant within these groups. From these hypotheses, a linear multiregression analysis was performed on integrated concentration to determine pigment ratio in each population, separately at N12 and M33:

$$\text{Chl } a = (K_1 \times \text{Chl } b) + (K_2 \times \text{Chl } c_1 + c_2) + (K_3 \times \text{PE}) + K_4, \quad (1)$$

where K_1, K_2, K_3 represent the inverse of the chl *b*/chl *a*, chl (c_1 + c_2)/chl *a* and PE/chl *a* ratios.

Estimated mean coefficients were relatively similar for the two stations (Table 5) and comparable with values published from cultures for chl *b*/chl *a* (0.2–1.0 in Chlorophyceae and Prasinophyceae), and for chl (c_1 + c_2) (0.1–0.3 in diatoms and dinoflagellates). For PE/chl *a* ratio in field samples or from a culture, little information is available. In the CHEMTAX software [38], this ratio is fixed at 7 (H. Higgins,

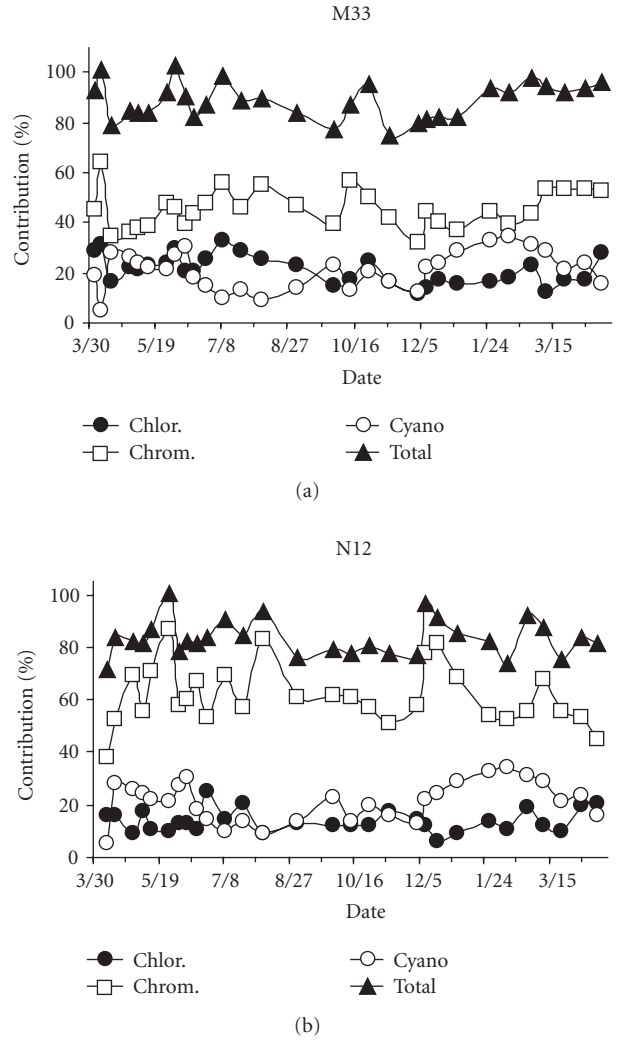

Figure 4: Estimates of the relative contribution of chlorophytes, chromophytes, and cyanobacteria in the global phytoplankton communities during the time series at M33 (a) and N12 (b).

personal communication), which represents half of the mean coefficient determined here. From the mean values, it was possible to calculate at N12 and M33 the contribution of the different groups to chl *a* during the time series (Figure 4). The temporal variations of this contribution matched strictly that of the observed pigment ratio (Figure 3). At N12, the mean contribution to chl *a* was 61 ± 11% for chl (c_1 + c_2)-containing algae, 15 ± 5% for chl *b*-containing algae and 8 ± 5% for PE-containing cyanobacteria (residual = 13%). At M33, the mean contribution of chl (c_1 + c_2) containing-algae was reduced to 45 ± 7%, and that of the two other increased to 21 ± 6% (chl *b* species) and 22 ± 7% (cyanobacteria; residual 11%).

The dv-chl *a* estimates related to abundance of *Prochlorococcus* were often at the limit of significance by the spectrofluorometric method and bulk PE, mainly attributed to *Synechococcus* population could be affected by other PE-containing species. Consequently, it seemed useful to appreciate the coherence between flow cytometry and

Table 4: Mean (± standard deviation) and maximum values of nutrients during the time series at stations N12 (Sainte Marie Bay) and M33 (center of the lagoon in front of Nouméa).

	NO_3+NO_2 μM		NH_4 μM		PO_4 μM		$Si(OH)_4$ μM	
	mean	max	Mean	max	mean	max	mean	Max
M33	0.055 ± 0.095	0.57	0.098 ± 0. 064	0.286	0.020 ± 0.012	0.066	1.75 ± 0.60	3.92
N12	0.255 ± 0.320	1.45	0.300 ± 0.296	1.157	0.113 ± 0.054	0.32	3.00 ± 1.48	7.73

pigment data. At M33, time variations of integrated cell number of *Prochlorococcus* and integrated dv-chl *a* were in good agreement with a significant linear relationship even including samples where the percentage of dv-chl *a* was less than 8% ($R^2 = 0.83$; $n = 21$; Figure 5(a)). Concentration of dv-chl *a* per cell was estimated as 1.12 ± 0.35 fg in average. At N12, dv-chl *a* concentration was always insignificant (< 8% Tchl *a*). However, flow cytometry showed, in 50% of the samples, a small population with cell characteristics of *Prochlorococcus* (peaks of 10–15 10^3 cell mL^{-1} in April–July 2002; not shown). Nevertheless, an unknown population of picoplanktonic cells could be present in the Sainte Marie Bay which is influenced by sewage input and is probably not a good environment for the development of *Prochlorococcus*.

A significant linear relationship was also observed between the integrated concentration of *Synechococcus* and that of PE at M33 ($R^2 = 0.67$; $n = 21$; Figure 5(b)), but not at N12 ($R^2 = 0.28$; $n = 23$; Figure 5(c)). Some discrepancies appeared attributable to change in cellular PE concentration related to (1) the presence of different strains of *Synechococcus*, (2) cells at different stages of the cell cycle, (3) photoacclimation. At M33, but not at N12, a higher determination coefficient ($R^2 = 0.76$) was found taking into account total fluorescence of *Synechococcus* (cellular fluorescence by cell number) instead of cell number. At N12, the possible presence of phycoerythrin-containing population (cyanobacteria, Cryptophyceae) of higher cell size than *Synechococcus* (not seen by flow cytometry) could explain the bad PE-fluorescence linear relationship and the highest PE/cell ratio observed in May-June 2002 and January 2003. However, PE fluorescence excitation and emission spectra (max around 567 ± 2 nm) did not vary dramatically during the overall time series at N12 with a mean PUB/PEB ratio of 0.72 (coefficient of variation = 14%).

3.2.2. The Oceanic (O1) and Near Dumbéa Pass Lagoon (L2) Stations. The survey at station O1 showed homogeneity in the physical parameters of the 0–100 m layer during the austral winter dry season (Figures 6(a)–6(c)). In summer (April–June 2002 and December2002–May 2003) a strong stratification occurred mainly related to the seasonal increase of temperature to nearly 27°C (Figure 6(a)). Salinity generally ranged between 35.35–35.50, with a minimum (35.20) in June 2002 (Figure 6(b)).

In winter (July-August 2002), water cooling and mixing beyond the maximum sampling depth (100 m) enriched the euphotic zone (NO_3 + NO_2 = 0.25–0.4 μM). Then, the NO_3 + NO_2 concentration in the upper layer decreased to very

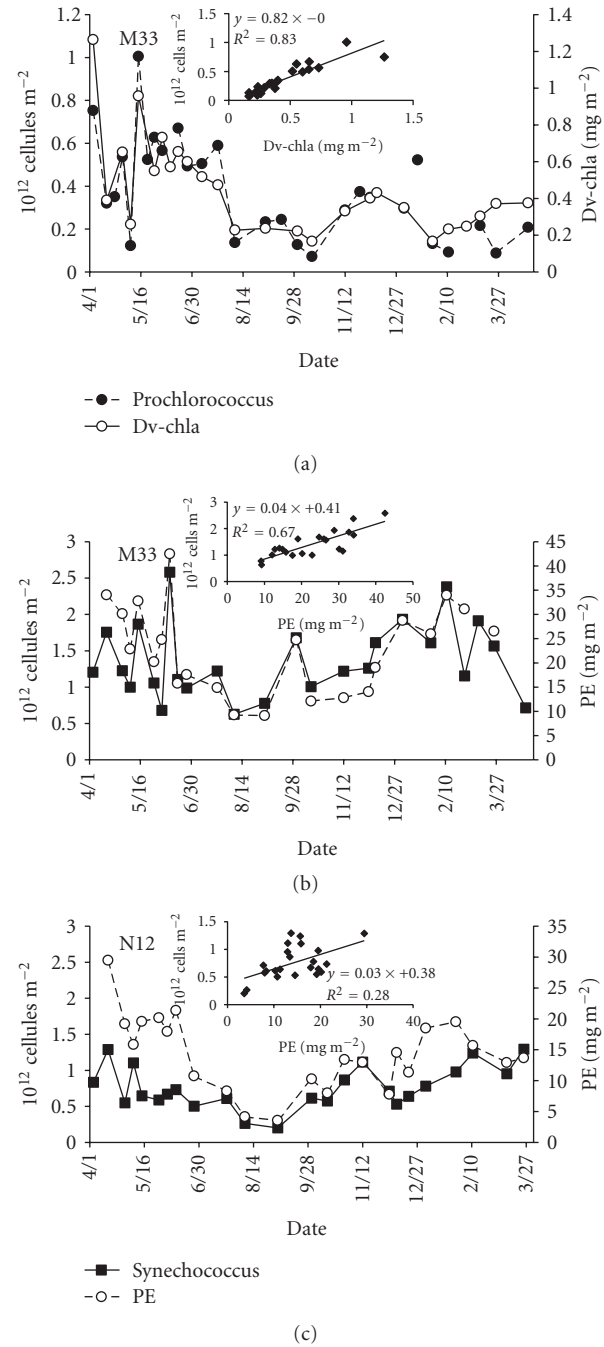

Figure 5: Seasonal variations of integrated (a) dv-chl *a* and *Prochlorococcus* abundance at station M33, (b) and (c) phycoerythrin (PE) and *Synechococcus* abundance, at N12 (bottom = 13 m) and M33 (bottom = 23 m), respectively. Inserts are the linear regression between the two parameters.

Table 5: Multiregression between chl *a* and photosynthetic accessory pigments for data of the time series at N12 and M33: chlorophyll *b* (chl *b*), chlorophyll c_1+c_2 (chl c_1+c_2), and phycoerythrin (PE). K_1, K_2, K_3 represent the partial regression coefficients and K_4 residual chl *a* when accessory pigments are null. The inverse of K_1, K_2, K_3 represent the mean estimate of the different pigments/chl *a* ratios. C_x = mean estimates of pigment ratio for chlorophytes ($x = 1$), chromophytes ($x = 2$), and cyanobacteria ($x = 3$).

N12 ($n = 27$)	Residual chl *a*	chl *b*	chl $c_1 + c_2$	PE
Mean coeff. (± SD)	$K_4 = 1.38$ (± 0.55)	$K_1 = 1.43$ (± 0.60)	$K_2 = 5.11$ (± 0.24)	$K_3 = 0.086$ (± 0.032)
P	.019	0.026	.000	.014
$R^2 = 96.1\%$				
C_x (1/mean coeff)		$1/K_1 = 0.55$	$1/K_2 = 0.19$	$1/K_3 = 15.4$
C_x + SD		0.41	0.18	10.2
C_x – SD		0.83	0.20	31.2
M33 ($n = 27$)	Residual chl *a*	chl *b*	chl $c_1 + c_2$	PE
Mean coeff. (± SD)	$K_4 = 0.63$ (± 0.17)	$K_1 = 1.62$ (± 0.30)	$K_2 = 4.87$ (± 0.55)	$K_3 = 0.069$ (± 0.011)
P	.002	.000	.000	.000
$R^2 = 97.4\%$				
C_x (1/mean coeff)		$1/K_1 = 0.61$	$1/K_2 = 0.20$	$1/K_3 = 14.3$
C_x + SD		0.51	0.18	12.3
C_x – SD		0.75	0.23	17.2

low levels from September 2002 to January 2003 (<0.05 μM) with increasing physical stratification. The mixed layer depth calculated as the depth where the σ_θ gradient exceeded 0.005 kg m^{-4} varied from 85 m in September to 15 m in January. During summer, reduced stratification (oscillation of the mixed layer depth from 10 to 60 m) and parallel slight increases of $NO_3 + NO_2$ at the surface were observed (Figure 7). The most important increases were on 6 May 2002, 20 March and 13 June 2003. It appeared consecutive to the SE strong wind events (> 8 m s^{-1} ≈ 16 knots) which preceded the sampling date (Figure 7).

Tchl *a* concentrations did not exhibit clear seasonal variations. At the surface, it varied between 0.11 and 0.67 μg L^{-1} with maxima in May 2002 and March–June 2003 (Figure 8). Maximum values coincided with the $NO_3 + NO_2$ maxima. Vertical profiles showed a deep Tchl *a* maximum that was particularly sharp in November-December 2002 at 60–80 m. On July-August 2002, the Tchl *a* concentration (0.20–0.25 μg L^{-1}) was homogeneous in agreement with physical conditions. The Tchl *a* concentration was generally higher than 0.15 μg L^{-1} at 100 m depth, but in June 2003, it was relatively high (0.3-0.4 μg L^{-1}) and homogeneous in the 0–40 m surface layer, decreasing rapidly with depth (only 0.02 μg L^{-1} at 100 m).

At the surface, the dv-chl *a* concentration varied between 0.02 and 0.18 μg L^{-1} (mean = 0.08 μg L^{-1}) with maximum values on 7 April (0.18 μg L^{-1}) and 14 May (0.13 μg L^{-1}) 2003 (Figure 9). The mean dv-chl *a* percentage represented 34% of Tchl *a* (Figure 9(a)). The vertical distribution of dv-chl *a* concentration indicated either a deep maximum (60–80 m) or a relative homogeneity (Figure 9(b)). Sometimes, the deep maximum coincided with a maximum of chl *a* (as in December 2002, 80 m: Figures 9(b)-9(c)). In other cases, it could be located below (60 m) the chl *a* maximum which occurred in the 0–40 m surface layer as in March 2003. The mean dv-chl *a* percentage in the 0–100 m water column ranged from 12% in June 2003 to 40–48% in June and September 2002, and in January and April 2003.

The surface PE concentration exhibited high variations, from 0.08 to 1.19 μg L^{-1}. Maxima were observed on 6 May 2002 and 7–20 March 2003. From June to December 2002, they were lower than 0.3 μg L^{-1} (Figure 10(a)). The PUB/PEB ratio (Figure 10(b)) ranged between 0.76 and 1.82 (mean = 1.22). During winter (June–October 2002), it exceeded 1.3 and was rather homogeneous along the water column. This coincided with the lowest PE concentration. At other periods, the ratio was lower at the surface and increased with depth. Sometimes it was influenced at the surface by the presence of a significant proportion of PE related to *Trichodesmium* species, particularly as was observed on 7 April 2003.

Samplings at O1 and L2 were generally done at high tide and the dv-chl *a* concentration and percentage at the surface were similar at the two stations during two periods (June–August 2002; December–February 2003). At most other times, dv-chl *a* percentage was more important in the ocean. However, on 7 March 2003, it was unexpectedly and clearly higher at L2 (47%) than at O1 (< 8%).

3.3. Influence of Environmental and Climate Forcing. In normal conditions, precipitations and winds are the main environmental factors driving the spatiotemporal variations of phytoplankton biomass in New Caledonian waters [11, 12] although anthropogenic influences could affect it locally, particularly around Nouméa [5, 10]. From April 2002 to April 2003, trade winds blew over 75% of the time and, in agreement with the Douillet et al. model [23], they created a northwest circulation in the SWL with output of lagoon waters by the different passes (Dumbéa, Boulari). Furthermore, trade winds provoked also transitory upwelling along the oceanic side of the barrier reef [15]. At the surface of the oceanic station O1, cooling of waters (1.5°–3°C)

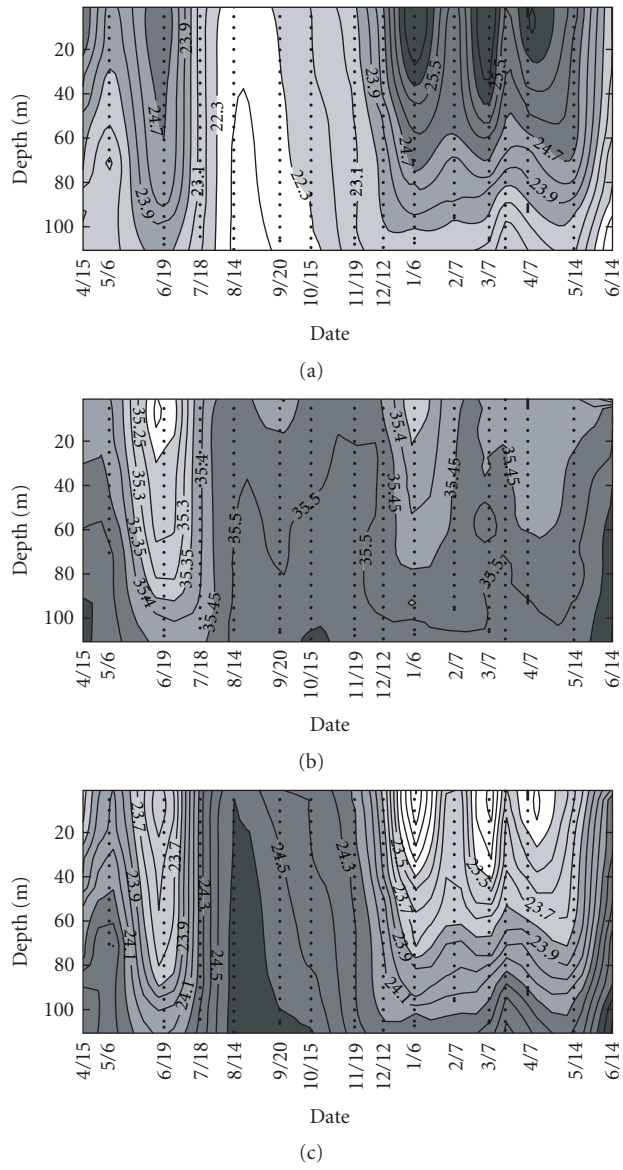

Figure 6: Seasonal variations of (a) temperature (°C), (b) salinity, and (c) density (σ_θ) at the oceanic station (O1) deduced from monthly sampling. Dotted vertical lines show date and depths of sampling.

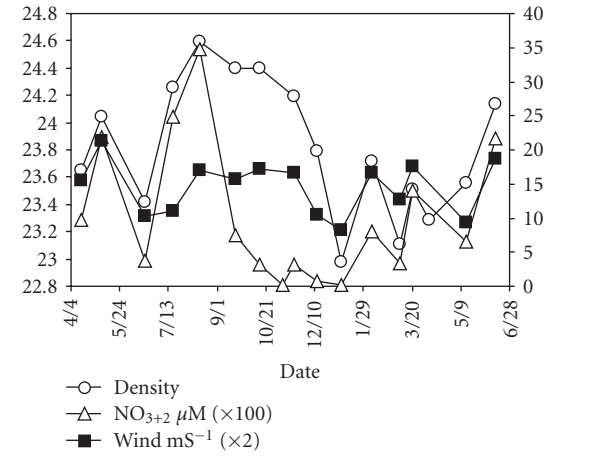

Figure 7: Seasonal variations of density (σ_θ) and nitrates (NO_3) + nitrites (NO_2) in the 0–20 m surface layer, deduced from monthly sampling at the oceanic stations O1, and their relationship with trade wind intensities. The wind speed corresponds to the mean intensity of trade winds blowing during the previous seven days before sampling.

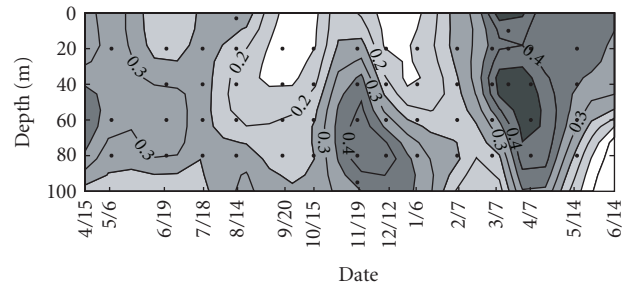

Figure 8: Seasonal variations of Tchl *a* (μg L^{-1}) deduced from monthly sampling at the oceanic station O1.

during the summer wet season coincided with trade wind episodes, Tchl *a* maxima, and significant enrichment in NO_3 + NO_2 (Figure 7). The question was that did these enrichments result from an output of lagoon waters or an arrival of oceanic upwelled deep waters. Only the main NO_3 + NO_2 increase (June 2003) seemed associated with recently upwelled waters. The surface NO_3 + NO_2 concentrations were 6–10 fold higher in the ocean (0.21 μM on average in the 0–40 m layer) than in the lagoon (PO_4 concentrations were only two fold higher: 0.08 μM compared to 0.04 μM). On this occasion, samples were taken at L2 (S4) to visualize water exchanges through the Dumbéa pass from variations in pigments of cyanobacteria. Unusually, ocean and lagoon were both poor in dv-chl *a* and precluded to visualize significant exchanges. As contrary, the PUB/PEB ratio oscillated clearly at L2 with maximum (1.1) and minimum (0.75) values at high and low tide, respectively (not shown). The oscillation varied in phase with salinity. At the oceanic (1.18 ± 0.06: O1) and the central lagoon (0.67 ± 0.02: L3) stations, there were only few variations. Although the balance between output and input flows was not estimated, it appeared that tidal current could occasionally transport nutrients in the lagoon and feed coral reefs.

Other enrichments appeared more related to output of lagoon waters since they concerned a small thickness of surface water and exhibited nutrient concentrations similar to that in the lagoon. During the dry season (October-November 2002), trade wind episodes were not accompanied by surface nutrient enrichment at the oceanic station. This difference could be explained by the relative increase of main river flows (Dumbéa, La Coulée, Pirogues) and urban activities during summer and simultaneous increase of nutrient supply to the lagoon.

The major environmental forcing of the 2002-2003 period was the cyclone Erica. Characterized by a short duration (4 hours), heavy rain (200–250 mm), and strong

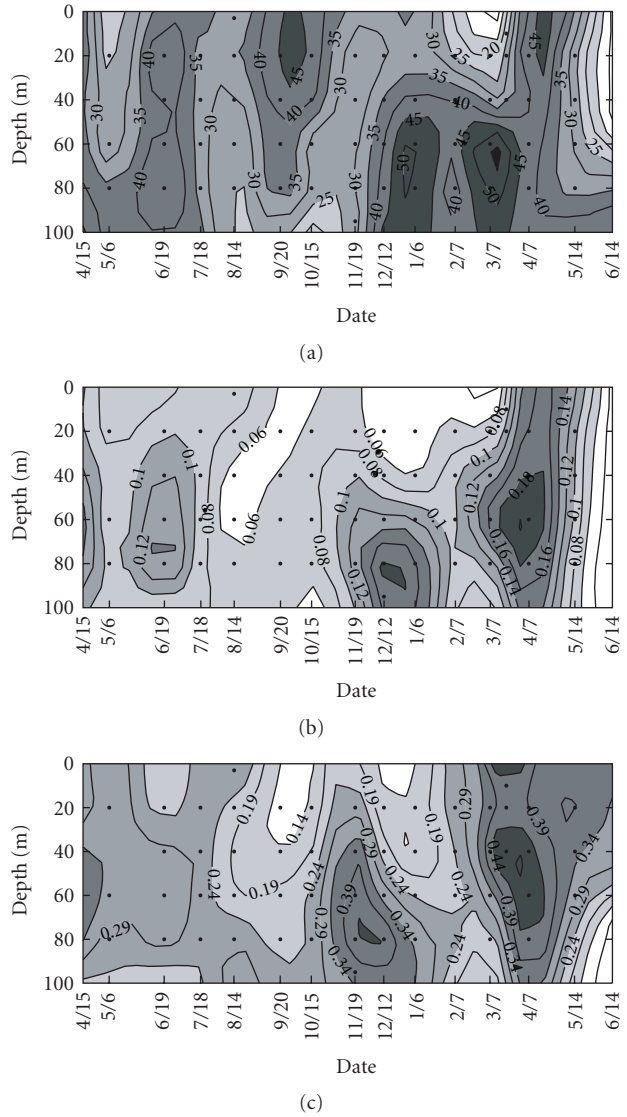

Figure 9: Seasonal variations of (a) dv-chl *a* percentage, (b) dv-chl *a*, and (c) chl *a* concentrations deduced from monthly sampling at the oceanic station O1.

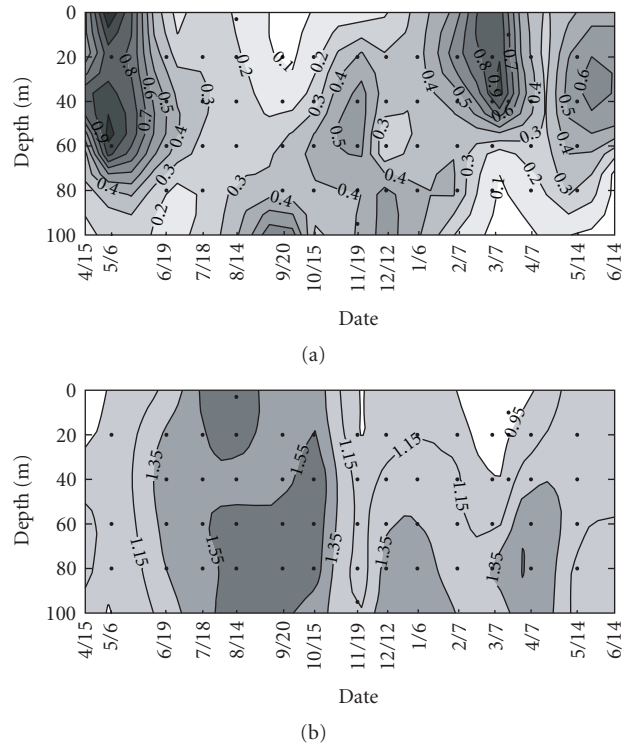

Figure 10: Seasonal variations of (a) phycoerythrin (μg L^{-1}) concentration and (b) PUB/PEB ratio, deduced from monthly sampling at the oceanic station O1.

winds (average > 110 km/h with gusts at 236 km/h), it led to a 5-6 fold increase of the Tchl *a* concentrations on average (Table 3). The Tchl *a* concentrations reached 3–6 μg L^{-1} in Dumbéa Bay and until 20 μg L^{-1} at the bottom of the Sainte-Marie Bay (17-18 March: Figure 2). In the central lagoon, in front of Nouméa (Dumbéa transect), the Tchl *a* concentrations were 1-2 μg L^{-1}. South of Nouméa, the Boulari transect showed concentrations higher than usual but generally below 1 μg L^{-1}. The dv-chl *a* percentage was insignificant (2.8% of Tchl *a*, on average) except at the Boulari Pass station (13% at A17). The chl (c_1 + c_2)/chl *a* ratio showed maximal values on the axis of the Dumbéa transect (0.14–0.17) and decreased southward reaching 0.05–0.1 on the Boulari transect except at the Boulari Pass. On the contrary, the chl *b*/chl *a* ratio was higher (0.10–0.15) on the Boulari transect than anywhere else, indicating a relative increase of chlorophytes in this part of the lagoon. The chl c_3/(chl c_1 + c_2) ratio was the lowest observed during the whole sampling period with insignificant chl c_3 concentration in the bays. The excitation spectra of *Synechococcus* PE always showed a low PUB/PEB ratio (around 0.6) except at the Boulari Pass (0.9) where the minimum PE concentration (0.59 μg L^{-1}) was observed. The mean PE concentration was 1.28 μg L^{-1}.

After Erica, on 20 March, Tchl *a* and PE concentrations decreased to around 0.63 and 0.56 μg L^{-1} for the two pigments, respectively, on the Dumbéa transect, as did the chl (c_1+ c_2)/chl *a* ratio, and the dv-chl *a* remained insignificant (5% in average). The output of surface lagoon waters provoked an increase of the NO_3 + NO_2 concentration (0.14 μM) at the surface of the oceanic waters.

It is clear that the impact of the cyclone on biomass and community structure of phytoplankton was missed by the time series at N12 and M33, which included a fourteen day gap between sampling dates, that is, sampling three days before (March 11, 2003) and eleven days after (March 25, 2003) the cyclone. This underscores the rapid response of the ecosystem to an important disturbance and the subsequent rapid return to normal condition in the lagoon.

4. Discussion

The implementation of spectrofluorometric methods was intended to provide new information on phytoplankton

biomass and community structure in New Caledonian waters in relation with environmental forcing. Although spectrofluorometric chlorophyll analysis improved the estimation of Tchl *a* compared to that obtained by methods used in previous works, it did not modify main views concerning its spatial distribution in the SWL and its relationship with rain and winds in normal weather conditions for the region. The Tchl *a* concentration was maximum in the bays adjacent to Nouméa and decreased from the coast to the barrier reef. The seasonal signal was weak with peaks in April-June, period where nutriments were roughly more abundant. Moderate trade winds (20 knots or less) did not seem an important factor to stimulate the productivity of the lagoon. However, they promoted surface water transport that could favour the productivity of the northern part of the SWL by advection to the northwest of nutriments discharged by the main rivers. This transport could explain the highest chl *a* concentration generally observed on the Dumbéa transect than on the Boulari one. It could also explain most increase of surface Tchl *a* in the ocean near the barrier reef. However, the present study showed more original data on (1) the consequence of the cyclone Erica for the phytoplankton community, and (2) the occurrence of significant oceanic enrichment related to upwelled waters drove by trade winds. In the following, discussion will concern more particularly (1) advantages and disadvantages of spectrofluorometric analysis of pigments, (2) the eutrophication of lagoon, (3) the occurrence of *Trichodesmium erythraeum* bloom, (4) the effect of climatic events on phytoplankton, (5) the interest of pigments of cyanobacteria to characterize water masses and water exchanges between ocean and lagoon, and (6) the importance of the ocean in the development of coral reefs.

4.1. Advantages and Disadvantages of Spectrofluorometric Pigment Analysis. Previously, Tchl *a* has been measured in the SWL with different techniques: (1) in vivo fluorescence [3], (2) fluorescence of particles on GF/F filters [4] according to the Dandonneau's method [39], (3) fluorescence before and after acidification [40] to eliminate interference of phaeopigments *a* (phae *a*) in the determinations. All these techniques are not equivalent and the relative accuracy of each one can be discussed in function of various interference problems but overall they converge to approximately the same conclusions regarding the spatiotemporal variations in the SWL, except that Rougerie [3] failed to observe seasonal variations. The interest of spectrofluorometric method is to reduce pitfalls inherent to the above methods. For example, the fluorometric method of Holm-Hansen et al. [40] is currently used in field studies, but chl *b* interference could significantly underestimate Tchl *a* and overestimate phae *a* [41]. In the present study, the mean phae *a*/chl *a* ratio was around 0.08 in the SWL while this ratio determined previously by the fluorometric method in the same region was ten-fold higher (mean around 0.75–0.90, [10]). In addition, spectrofluorometric determination of chlorophylls and PE provides useful information on phytoplankton community structure. The contribution of *Prochlorococcus* to Tchl *a* is easily obtained by the dv-chl *a* concentration. The other contributions can be assessed by linear multiregression analysis assuming three major chl *a*-containing autotrophic groups (chromophytes, chlorophytes, and PE-containing cyanobacteria), each associated to independent pigment variables (chl *b*, chl $(c_1 + c_2)$, PE) and assuming roughly the constancy of the pigment/chl *a* ratios in these groups. A priori, the independence of the three pigments is expected since chl *b*, chl $(c_1 + c_2)$, and PE are mutually exclusive in individual cells. Nevertheless, the groups containing these pigments are not completely independent in water samples. Furthermore, the pigment/chl *a* ratio in each group can vary according to species and environmental factors as nutrients and light conditions. In spite of these restrictions, the relative similitude of the pigment ratios determined at N12 and M33 and their compatibility with observations in algal cultures suggest a certain confidence in the estimation of contribution to Tchl *a* of the three major groups. For a complete analysis of community structure from pigments, high performance liquid chromatography is required. Contrary to spectrofluorometry, this method provides more analytical capabilities for chlorophyllous pigments and information on carotenoids that are used to discriminate different groups within chlorophytes and chromophytes [16].

4.2. Natural and Anthropogenic Eutrophication. In normal condition, temporal variations of Tchl *a* in the SWL are similar to those described by Binet and Le Borgne [4] during a weekly time series at a station near N43 (see Figure 1) from 1979 to 1983. The Tchl *a* maxima are comparable and occur in April–July, but some peaks could also be observed from December to February associated to peaks in primary production [9]. This suggests that the impact of eutrophication on the phytoplankton abundance is not more important at present than during the 1980s, despite the expansion of Nouméa. The Tchl *a* concentrations in the SWL are closely related to those observed in a tropical lagoon not subject to eutrophication [42, 43]. On the Australian Great Barrier Reef, Revelante and Gilmartin [42] observe a temporal pattern similar to that in the SWL with maximum integrated concentrations between April and June associated with diatom population. The mean value in the center of the Australian lagoon (9 mg m^{-2}) is in the same range as that of M33 (6 mg m^{-2}), after the different thicknesses of the integrated layers (32 m in the lagoon of the Great Barrier Reef and 20 m at M33) are accounted for.

The eutrophication could be higher in more enclosed bays. Discrimination of natural trophic enrichment along the offshore-inshore gradient from anthropogenically induced eutrophication is highlighted by principal component analysis [10]. Chronic eutrophication related to increasing human being activities is added on transitory natural eutrophication related to meteorological event. Tchl *a* concentration represents a good indicator of nutrient status [10] and quality [44] of lagoon and coral reef waters. An annual mean concentration of 0.5 μg L^{-1} Tchl *a* seems a threshold tolerance to protect coral reefs from invaders, particularly in region characterized by low flushing time like embayments and calmer lagoon sector [44]. In the Grande Rade and the Sainte-Marie Bay, the Tchl *a* concentrations are generally

higher than this threshold (1-2 μg L^{-1}). Protection of Coral Reef implies reduction of eutrophication by tertiary sewage treatment (reduction of nutrient stimulating algal growth). Outside the Bays, the lagoon of New Caledonia does not seem at this time threatened by excessive eutrophication (mean annual Tchl $a < 0.5\,\mu$g L^{-1}).

4.3. Accumulations of Trichodesmium. Accumulations or "blooms" of *T. erythraeum* were sometimes noted during the sampling program (October 2002) but the most important ones were observed independently and sampled specifically. They occurred as more or less wide spots (Sainte-Marie Bay: 23–25 October 2002; Boulari Bay: 13 December 2002) or lines 2-3 m in width and several hundreds meters long (central lagoon: May 14, 2003). A maximum of 3 mg L^{-1} Chl *a* was measured in the 2 cm surface layer of the Boulari Bay on December 13, 2002. It corresponded to a population of about 30 10^6 trichomes L^{-1}. This observation was not preceded by an important rainy episode (nutrient inputs by run-off). Accumulation seemed rather related to the decay of the *Trichodesmium* population than to intense local growth and mainly the result of physical processes (positive buoyancy of colonies, hydrodynamics). Nevertheless, high-frequency sampling in the Sainte Marie Bay shows that increase in the *T. erythraeum* population is often consecutive to dissolved combined nitrogen (NO_3^-) pulses with a 3–7 day time lag [45]. Accumulations of *T. erythraeum* are also frequent in the lagoon of the Australian Great Barrier Reef [42] and other coastal regions (i.e, Brazil, [46]; India [47], Canary Island [48]). The population decay can provide readily available organic material for the other phytoplankton components and coral reef. Development of Diatoms is reported following *Trichodesmium* accumulations [42]. However, planktonic *Trichodesmium* could also have negative impact by smothering of corals [49]. Accumulations appear during calm weather. Significant negative linear correlations are observed between the intensity of winds and *Trichodesmium* concentration [45, 50].

4.4. Climatic Events and Phytoplankton. According to [11], Tchl *a* in the SWL is low all year because the nutrient inputs and the river flow are relatively low. Even the effect of short heavy rain periods provoke only a local increase of Tchl *a* and does not seem to strongly impact the community of the central lagoon. However, a three-week cumulative rainfall (500 mm) leads to a doubling of Tchl *a* at the mouth of the Bay of the Ouinné river (eastern coast of New Caledonia [18]). In the Gulf of Carpentaria, the Tchl *a* concentration peaks occur during periods of heavy rain and elevated temperature [43]. Strong winds can also stimulate phytoplankton growth from resuspension of nutrient-rich sediment related to intense vertical mixing as observed in the shallow waters of the Great Barrier Reef [51, 52]. In 2003, the cyclone Erica that had a short duration (4 hours) combined strong winds and heavy rain. It lead to a 5-6 factor increase of total phytoplankton biomass (Tchl *a*) at the surface of the whole study area for several days. Although nutrient concentrations were not measured during this operation, such an increase could not be envisaged without an important enrichment of waters, resulting from an increase in river discharges and from resuspension of bottom sediment. The %phae *a* being higher in sediments (50–900%: [24]) than in the water column, it could serve to visualize an effect of resuspension. However, the time lag between the cyclone and sampling was probably too high to observe increase in %phae *a*. Rapid settling of particles and photooxydation of phae *a* could explain that significant effect be overlooked. During the overall sampling program, the highest %phae *a* was generally observed at two shallowest stations (M37, N04) that are very different in location. They could result from sediment resuspension and water mixing driving by winds and hydrodynamics.

Increase of total phytoplankton biomass after a cyclone event was previously noted by direct in situ measurements [53–56] and satellite observations [57]. However, this increase could vary according to the type of environment studied and to the relative importance of rainfall during the event [55].

In the SWL, the cyclone-stimulated growth of chl (c_1 + c_2)-containing chromophytes lead to the lowest chl *b*/chl *a* and chl c_3/chl (c_1 + c_2) ratios measured during the present study. The PE concentration was similar to that observed in February or April 2003 and associated to high-PEB *Synechococcus*. These characteristics were compatible with general observation of increase of diatoms associated to nutrient enrichment in the Bay of Ouinné [18] and the SWL [5]. Classically, the increase of diatoms is observed when nutrient input from freshwater occurs in tropical [53–55] and temperate waters [58, 59]. Under normal conditions, the microplankton in the bays around Nouméa is mainly dominated by diatoms while in the central lagoon, the coccolithophorids (Prymnesiophyceae) become relatively more important. [5]. This is consistent with the present observation of a higher chl c_3/chl ($c_1 + c_2$) ratio in the central lagoon than in the bays.

4.5. Pigments of Synechococcus and Prochlorococcus as Marker of Water Masses. The picoplankton fraction (cell $\leq 2\,\mu$m) generally dominates in the phytoplankton community of New Caledonian lagoon and adjacent oceanic waters [5, 18]. However, these two types of water differ in the composition of picoplanktonic cyanobacteria with a relative dominance of *Prochlorococcus* and high-PUB *Synechococcus* in the ocean and a dominance of high-PEB *Synechococcus* in the lagoon. These features are similar to results reported in the regions of the Australian Great Barrier Reef [56] and of French Polynesian atolls [60]. Furthermore, *Synechococcus* abundance is generally higher in the lagoons than in the ocean as has been previously observed (SWL [5]; Great Barrier Reef Lagoon [56]; Takapoto and Great Astrolabe Lagoons [61]; Sesoko Island [62]). Consequently, the composition and abundance of cyanobacteria can characterize the nutrient status of waters and provide a mean to appreciate ocean-lagoon exchanges. Intrusion of oceanic waters in the lagoon can be traced by biological parameters like the dv-chl *a* percentage and the PUB/PEB ratio. During the present studies, main intrusion appeared to intervene through the passes. At high tides, both dv-chl *a* percentage and PUB/PEB

ratio were generally higher in the Dumbéa Pass (L2) and oceanic (O1) stations than in the central lagoon. They were also high at the surface of stations relatively far from the passes but near to the barrier reef (M37) which are subjected to breaking of waves over the reef [63]. Furthermore, relatively high dv-chl *a* percentage (48%) and concentration ($0.14\,\mu g\ L^{-1}$) were observed near the bottom (50–55 m) of the Boulari Canyon (stn. A11 on January 2003). This suggested inflow of oceanic waters under the surface layer relatively far inside the lagoon through the Boulari Pass. The lower temperature, comparable to that of the ocean at 20 m depth (O1) supported this hypothesis. On the contrary, the presence of high-PEB *Synechococcus* in the ocean seemed to be the consequence of output of lagoon waters like on March 7 and 20, 2003. Fluorescence excitation spectrum of phycoerythrin is a potential tool to characterize water masses [20, 64, 65] as well as the dv-chl *a* percentage.

4.6. Nutrient and Chlorophyll Variation in the Ocean along the Barrier Reef. According to [23], the trade winds push SWL surface waters in the northwest direction with output through the passes. In 1983-1984, off the Uitoé Pass (northwest of the Dumbéa Pass, see Figure 1), increases of chl *a* in the ocean are attributed to output from the lagoon [14]. In the present study, most of the increases in NO_3 + NO_2 and Tchl *a* concentrations in the ocean appeared also related to output of lagoon waters (except during cooling and homogenization of water column in winter). However, the enrichment observed on June13-14, 2003 could have an upwelled origin. At this time, exchanges between the ocean and the lagoon related to tidal currents could be seen in the Dumbéa pass from changes in salinity and PUB/PEB ratio. A slight increase of NO_3 + NO_2 concentration could also be observed at high tide in the lagoon. A more recent study (EMERLIS cruises [66]) showed the occurrence of similar enrichment of surface waters during a strong trade wind event [66]. However, coincidence between enrichment of surface oceanic waters and trade wind event were not always observed. In October-November 2002, the strength of trade winds was similar to that in June 2003 and an increase of surface Tchl *a* was noted in November but without significant enrichment. Observations of enrichment could be the result of a combination of several factors including local circulation. Andrews and Gentien [67] identify a broad scale of physical mechanisms which combine to deliver nutrient from the ocean to the Great Barrier Reef. In the three-dimensional-coupled physical-biological model, the ocean is considered as an oligotrophic vector for the SWL and productivity increase essentially associated to terrestrial and/or anthropogenic inputs [12]. This notion could be revised by an increase of research effort to identify more precisely climatic conditions which could enhance the role of the ocean in lagoon and coral reef productivity. Internal waves related to tidal period upwelling can enrich the continental shelf as, for example, at the entrance of Raine Island (Great Barrier Reef [68]). During the Echolag cruise (February-March 2007), intrusion of nutrient rich oceanic waters during trade wind events affected clearly mid- and bottom waters above the continental shelf at the southeastern end of the Grande Terre which is characterized by two horn reefs (Neveux et al., unpublished). However, the possible impact of this intrusion on the productivity of the SWL remains to be determined. Furthermore, coral reefs all around New Caledonia could also benefit of upwelling related-intrusion of nutrient-rich oceanic waters. Occasional strong west and northwest winds may induce upwelling on the east coast of New Caledonia [15].

5. Summary

Spectrofluorometric methods for chlorophylls, phaeopigments, and phycoerythrin analysis were implemented during the 2002-2003 years in several operations conducted in the Southwest lagoon (SWL) of New Caledonia and its adjacent oceanic area. These methods allowed (1) to determine Tchl *a* and phe *a* avoiding pitfalls related to spectrophotometric or fluorometric methods which were used previously to analyze New Caledonian waters, (2) to add information on the phytoplankton community structure.

Overall, the main characteristics of spatiotemporal variations of Tchl *a* are consistent with the results of previous work. In the SWL, the highest Tchl *a* concentration occurred in the Bays near Nouméa and seasonal variations appeared weak in both eutrophicated bays and oligotrophic central lagoon. However, the effect of the cyclone Erica largely exceeded that of more usual meteorological event with a general mean 4–6 factor increase of Tchl *a* in a large area of the SWL.

The temporal variations at the Sainte Marie Bay showed that peaks of Tchl *a* in April–June and December 2002 were mainly associated with chl ($c_1 + c_2$)-containing species (chromophytes). Comparing to the bay, the increase of the chl c_3/ (chl $c_1 + c_2$) ratio in the central lagoon indicated modification of the chromophyte populations with higher proportion of chl c_3-containing species. The proportion of chl *b*-containing species (chlorophytes) and cyanobacteria (*Prochlorococcus*, *Synechococcus*) were also relatively more abundant in the central lagoon. The cyclone favored the development of chl ($c_1 + c_2$)-chromophytes in most part of the sampling area (probably Diatoms).

Accumulation of the filamentous *Trichodesmium erythreum* occurred frequently in the different bays around Nouméa and the central lagoon all along the year, but the highest abundances were most often observed in summer.

Outside the bays, the phytoplankton was generally dominated by the picoplanktonic fraction (cell diameter $< 2\,\mu$m). *Prochlorococcus* and high-PUB *Synechococcus* generally dominated picoplankton in the ocean whereas picoeukaryotes and high-PEB *Synechococcus* dominated in the lagoon. This difference appeared useful to characterize ocean-lagoon water exchanges and nutrient status of lagoon waters. Relative increase of *Prochlorococcus* abundance in the lagoon can reflect the intrusion of oceanic water as high-PEB *Synechococcus* an output of lagoon waters in the ocean. Stations influenced by terrestrial and anthropogenic nutrient input were characterized by low PUB/PEB ratio contrary to those sustaining oligotrophic conditions.

The impact of southeast trade winds in the increase of the surface Tchl *a* concentration of the ocean seemed most often related to output of lagoon waters. As contrary, nutrient enrichment on 13-14 June seemed rather associated to upwelled waters. However, strong trade winds did not lead always to enrichment of oceanic surface waters. A combination of several factors could be required to observe a significant enrichment.

In the last fifteen years, research effort was essentially focused on the influence of terrestrial and anthropogenic nutrient inputs and winds on the SWL productivity. In this context, the ocean is frequently considered as an oligotrophic vector. This notion could be revised by an increase of research effort to evaluate the role of climatic conditions on the ocean hydrodynamics, the enrichment of the continental shelf and the growth of coral reef all around New Caledonia. The quantification of upwelling-related intrusion of Coral Sea waters on the shelf (and associated nutrient fluxes) of New Caledonian reefs could be achieved by installation of mooring systems equipped with CTD probe, in situ fluorometer, and automatic in situ nutrient analyzer.

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