Available online at www.sciencedirect.com
SCIENCE DIRECT
Estuarine, Coastal and Shelf Science 64 (2005) 531–545
ESTUARINE COASTAL AND SHELF SCIENCE
www.elsevier.com/locate/ECSS

The impact of terrigeneous inputs on the Bay of Ouinné (New Caledonia) phytoplankton communities: A spectrofluorometric and microscopic approach

M.M.B. Tenório [a,*], R. Le Borgne [b], M. Rodier [b], J. Neveux [a]

[a] *UMR 7621, Laboratoire Arago, B.P. 44, F-66651 Banyuls sur mer Cedex, France*
[b] *UR99, Centre IRD, B.P. A5, 98848 Nouméa Cedex, New Caledonia*

Received 22 October 2004; accepted 3 February 2005
Available online 23 May 2005

Abstract

The impact of terrigeneous inputs on the phytoplankton composition was studied during a 2.5 months daily survey in the Bay of Ouinné, a deep cove on the south-eastern coast of New Caledonia. Surface waters benefited from nutrients originating from nearby land drainage and the Ouinné river outflow during periods of heavy rain. The nutrient composition mirrored the composition of the drained soils, with concentrations reaching 3–4 μM for nitrate and 0.13 μM for phosphate at the river mouth. In addition to nutrient inputs, significant quantities of particulate matter (inorganic and organic compounds) were discharged into the lagoon during heavy rain periods, resulting in transitory decreases of the photic layer depth and enrichments of the water column through remineralization processes. Changes in contributions of the main phytoplankton groups in response to terrigeneous inputs were shown by chlorophyll and phycobiliprotein spectrofluorometric analyses. While dry periods were marked by the dominance of pico- (*Prochlorococcus*, and high-phycourobilin (PUB) *Synechococcus*) and microcyanobacteria (*Trichodesmium* spp.), developments of various eukaryote populations resulted from land drainage occurring during the wet periods. This was indicated by the increase of accessory chlorophyll pigments that doubled at a depth of 15 m: chlorophyll *b* (chlorophytes), chlorophyll c_1+c_2 (associated with diatoms and dinoflagellates), chlorophyll c_3 (associated with c_1 and/or c_2 in prymnesiophytes, chrysophytes and/or pelagophytes). In addition, *Synechococcus* with a high phycoerythrobilin (PEB) content also appeared to be stimulated by river outputs. Finally, microscopic observations of the >35 μm net plankton confirmed the greater presence of diatoms and dinoflagellates during periods of rain compared to *Trichodesmium*, particularly in the surface layer.

Keywords: terrigeneous inputs; nutrients; phytoplankton; chlorophylls; phycoerythrins; spectrofluorometry; New Caledonia; Pacific Ocean

1. Introduction

As for other marine ecosystems, the lagoon ecosystem structure relies on the composition of the primary producer community. Thus, the kind of consumers that live on it, the structure of the rest of the trophic web, and the ecosystem yield, are determined by the phytoplankton taxonomic composition, size structure and physiology. Inputs of micro- and macro-nutrients of terrestrial origin, particularly where lagoons surrounding high islands are concerned, will affect the composition and biomass of phytoplankton communities and, therefore, the structure and the functioning of the lagoon ecosystem. Such an influence was suspected by Binet (1986) who observed a higher zooplankton biomass in NW New Caledonia (southwestern Pacific ocean). His interpretation was that the development of large phytoplankton cells with a silicon shell could result

* Corresponding author.
E-mail address: tenorio@obs-banyuls.fr (M.M.B. Tenório).

0272-7714/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.ecss.2005.02.030

from drainage of silica-rich soils (fersiallitic soils associated with podzols) in this part of the island. Such a hypothesis, however, could not be proved because of a lack of observations. The situation is similar for the other lagoons of New Caledonia. There are only two published papers or reports about these lagoons: Desrosières (1975) for an open ocean zone located near a channel through the reef, and Cardinal (1983) for the south-western lagoon. But neither of these two studies linked phytoplankton composition to nutrient data.

In the SW Pacific region, Revelante et al. (1982) worked in the Great Barrier Reef lagoon in Australia, and showed an inshore–offshore gradient in the composition of the phytoplankton community, with more diatoms near the shore and more dinoflagellates offshore. The authors ascribed this to a greater terrigeneous effect near the shore. Revelante et al. (1982) also pointed out that temporal variability exceeded the spatial one, with occurrences of the filamentous cyanobacteria *Trichodesmium* spp. during the austral summer (December–March) and the end of winter (August–September). Such temporal variations of *Trichodesmium* have often been linked to seasonal precipitation variations and related river effluxes (Bell et al., 1999; Navarro et al., 2000; Lugomela et al., 2002; Carpenter et al., 2004).

The primary objective of the present work was the study of the origin of filamentous cyanobacterial blooms. However, due to contrasting meteorological conditions, observations appeared later to lend themselves to the study of the effect of terrigeneous input on phytoplankton abundance and pigment composition. Data was collected from daily surveys made during the austral summer (January 3–March 14, 2002) in the Bay of Ouinné, located in the south east of New Caledonia's main island (Fig. 1). The survey consisted of environmental parameters (meteorological, hydrological, and nutrients) and phytoplankton composition and biomass measurements. The latter consisted of chlorophyll and phycobiliprotein (these being associated with cyanobacteria) pigment analyses made on total samples and on different size classes (>10 μm; 2–10 μm; <2 μm) within the whole community. Such a description was complemented by microscopic observations of net plankton (35 μm mesh).

2. Materials and methods

2.1. Study site

The bay of Ouinné is situated at the estuary of the Ouinné river. The river drains off modified and weathered ferralitic ferritic soils originating from ultramafic rocks, and in its lower part, eutrophic and magnesian brown soils (Latham, 1981). The bay is surrounded by steep mountains, and is 5 km long. Station 3 is at the entrance of the bay (Fig. 1) and was visited every morning with a small boat, 4.7 m long. Its position was 21°58.279′ S, 166°43.357′ E, and its depth, 50 m. There is no anthropic influence since the region is uninhabited.

2.2. Meteorology, hydrology and water sampling

Meteorological readings were taken twice a day at Météo-France's Ouinné station, located at the river's mouth. Water temperature and salinity were measured with a WTW® LF197 probe with a precision of 0.1 °C and 0.1, respectively during the periods 4/01–17/02 and 11–13/03. Because of technical problems with the salinity sensor, there were no measurements for this parameter for the period 18–24/02 and a SeaBird® SBE19 probe, with a precision of 0.001 °C and 0.001, was used during the period 25/02–10/03.

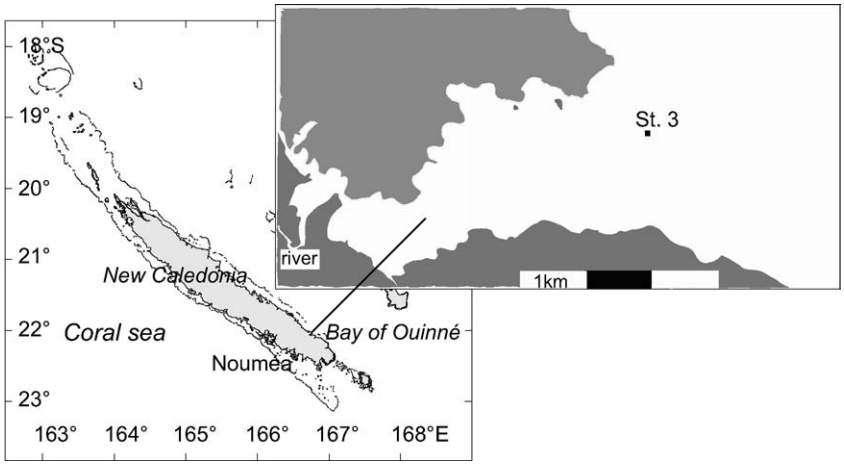

Fig. 1. Location of station 3 at the entrance of the bay of Ouinné, in the south east of New Caledonia, South Pacific.

Water for nutrient and pigment analyses was sampled with a 5 l Niskin bottle at 5, 15, 30 and 40 m for the former parameters and at 15 and 30 m for the latter. Samples at 0 m were collected directly with analytical flasks for both sets of parameters. Sampling was undertaken on a daily basis for nutrients and every 2 days for pigments.

2.3. Nutrient analyses

Samples were preserved by the addition of $HgCl_2$ (Kattner, 1999) and stored at 4 °C before analysis at the land laboratory. NO_3 and NO_2 were analysed with a Technicon® II autoanalyser, following the methods described in Strickland and Parsons (1972) for concentrations of NO_2 and $NO_3 > 1$ μM, and using the "high sensitivity" method of Raimbault et al. (1990) for concentrations of $NO_3 < 1$ μM. Soluble reactive phosphorus (PO_4) analyses were performed as described by Murphy and Riley (1962), using a CECIL® spectrophotometer equipped with a 10 cm cell and set at a wavelength of 885 nm. Analytical precision was 0.005 μM for NO_2 and NO_3 (high sensitivity) and 0.020 μM for PO_4 and NO_3 (low sensitivity).

2.4. Photosynthetic pigments

2.4.1. Chlorophylls and phaeopigments

Water samples (0.535 l) were filtered onto Whatman GF/F (diameter = 47 mm) for total pigment analyses, while 0.5 l samples were used for the size structure study. In the latter case, water sampled at 0 and 15 m (and 30 m in some instances), was fractionated by serial filtration on 10 μm and 2 μm polycarbonate filters and GF/F. For pigment extraction, GF/F filters were dipped in a centrifuge tube containing 5.4 ml of 100% acetone, ground with the freshly broken end of a glass rod, and left in the dark at 4 °C for a 12-h extraction. Polycarbonate filters, on the other hand, were just left in the dark at 4 °C for 24 h in 5 ml of 90% acetone.

Following extraction, the tubes were centrifuged for 5 min at 3500 rpm and the extracted fluorescence was measured with a HITACHI® F4500 spectrofluorometer. Concentrations of chlorophyll pigments (such as chlorophyll *a*, *b* and *c* (c_1+c_2; c_3); divinyl chlorophyll *a* and *b*) and phaeopigments derived from these different chlorophylls, were assessed using a modified version of Neveux and Lantoine's (1993) method. Modifications were as follows:

- Data acquisition was performed by recording the fluorescence emission spectra for each of 31 excitation wavelengths (3-nm increments from 390 to 480 nm). Emission spectra were recorded at 4-nm intervals from 615 to 715 nm, yielding 26 data points for each spectrum. Pigment concentrations were estimated from the resulting 806 data points (Neveux et al., 2003).
- Where the least squares approximation technique was constrained to discard negative solutions.
- A new standard, chlorophyll c_3 (DHI®, Denmark), was added to the ones described in Neveux and Panouse (1987) and Neveux and Lantoine (1993).

2.4.2. Phycobiliproteins

Three litres were filtered on Whatman GF/F (diameter = 47 mm) filters that were kept at −20 °C before extraction of phycoerythrins and phycocyanins, less than 2 weeks later. Filters were ground in 5 ml of phosphate buffer (NaH_2PO_4 0.1 M, pH = 6.5) and left for 12 h at 4 °C. Finally, after centrifugation at 3500 rpm for 20 min, the extracted fluorescence was measured using the technique described in Lantoine and Neveux (1997). Excitation spectra of phycoerythrin were recorded on the HITACHI® F4500 spectrofluorometer for the 450–580 nm range at an emission wavelength of 605 nm. Phycoerythrin concentration was inferred from the excitation spectrum area. Calibrations used *Synechococcus* phycoerythrin (Lantoine and Neveux, 1997) and such a procedure was validated by the observed association of this pigment with the <2 μm size class.

2.5. Net plankton (>35 μm)

Vertical (45–0 m) and surface (top of the net aperture was 50 cm deep) hauls were made with a plankton net, a description of which is presented in Blanchot et al. (1989). In brief, the net was 3.61 m long, with a 0.09 m^2 aperture and a 35 μm mesh size. The filtered water volume was measured with a TSK® flow meter. Plankton samples were kept in 5% formalin until processed for settled volume (Vsed) measurements and the counting of the main taxa. The latter were made on 14 sub-samples of the vertical hauls, selected regularly during the whole period. Sub-sampling was performed according to Frontier (1972): a known fraction of a balloon was drawn up with a bulb to obtain between 500 and 1000 filaments (or trichomes) of *Trichodesmium* spp. Counts refer to phyto- and zooplankton taxa and are expressed as numbers of individuals (or chains of diatoms and filaments of cyanobacteria) per cubic metre. Settled volumes are expressed in ml m^{-3}.

2.6. Statistical tests

Unless otherwise stated, all correlation coefficients, *r*, are Bravais–Pearson's and regression lines are least

squares. The mean comparison test in Table 2 is the *t*-test (Schwartz, 1963).

3. Results

3.1. Precipitation and hydrology

The sampling period was marked by three significant rain periods (Fig. 2). The first one was a thunderstorm (period A, Fig. 2) with 232 mm of rain in 24 h from 15–17/01. The second (period B) lasted from 22/01 to 15/02 and was associated with the presence of the South Pacific Convergence Zone. The rain fell almost continuously, with two main peaks on 27/01 (154 mm in 24 h) and 2/02 (105 mm in 24 h). Finally, a tropical depression (period C) brought 275 mm rain in 24 h from 6 to 7/03.

Except during periods of heavy rain, the salinity was >34.5 (Figs. 2 and 3), with temporary lower values (33.2–34.5) and temperatures above 27.6 °C within the first metre depth (Fig. 3). At this depth, however, sustained rainfall produced dramatic salinity decreases, with transient minimum levels (<15) associated with precipitation peaks. Thus, high vertical gradients occurred, since the salinity was only less than 30 above 1 m depth and less than 33 above 3 m. Decreases in surface temperature were associated with equivalent decreases in salinity, as on 4/02: the temperature and salinity were 24.5 °C and 7.7, respectively. Therefore, the surface stratification was mainly due to salinity decreases (Fig. 3).

3.2. Nutrients (NO_2, NO_3, PO_4)

Nutrient concentrations underwent important variations on both the temporal and the vertical scales (Fig. 4). Surface concentrations were very low, except during the rainy periods when they were linked to decreases in salinity. During period B, for example, NO_3 reached 3.6 μM in the five upper metres on 4/02 and

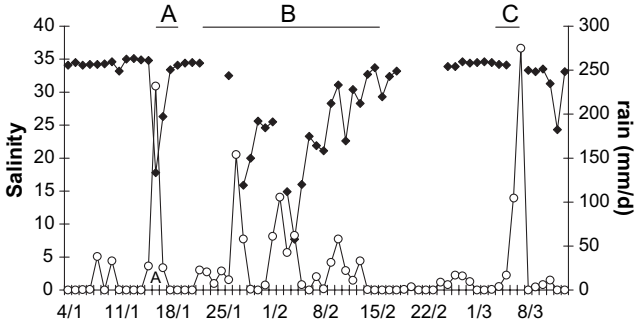

Fig. 2. Temporal variations of rainfall (dots) and surface salinity (diamonds). A, B and C refer to periods of heavy rain: 15–17/01, 22/01–15/02 and 6–7/03/2002.

PO_4, 0.17 μM on 28/01 (note that there was no variation in NO_2). The Ouinné river contributed to nutrient inputs with concentrations mirroring the low content of the drained soils, particularly for PO_4. Table 1 shows that the river concentrations were moderate for NO_3, nil for NO_2 and very low for PO_4. After the 8/02, lower NO_3 and PO_4 concentrations were observed, especially for the latter, probably indicating a thorough weathering of the soil during the periods of non-stop rain. Such a decrease may also be observed at station 3 (Fig. 4) with surface PO_4 concentrations of less than 0.080 μM, as from the 8/02. The link between nutrient concentrations and terrigeneous inputs was also illustrated by the inverse linear relationship between surface NO_3 and salinity ($S‰$): $NO_3 = -\ 0.124S‰ + 4.37$ ($r = -0.872$; $n = 60$ paired values). The correlation coefficient was less for PO_4 ($r = -0.567$; $n = 60$) and non-significant for the 5 m data because the waters at that depth were not affected by the water with a low saline content (Fig. 3).

There were generally more nutrients in the deep layers (30 and 40 m, Fig. 4), and the correlation coefficient was high between NO_3 and NO_2 ($r = 0.911$; $n = 85$) indicating possible nitrogen remineralization at the base of, or underneath, the photic zone. In spite of the lack of vertical light profiles, one may infer the depth of the photic zone from NO_2 vertical profiles, taking into account the normal association of the NO_2 maximum with the base of the photic layer in stratified environments. Given that our sampling grid was fairly lax in the vertical plane and using a 0.050 μM threshold for NO_2, the depth of the base of the photic layer appeared to be at a maximum of 40 m at the beginning of the study (until 26/01) and towards the end (26/02 and 5/03). During other periods it was at less than 30 m, except that during period B where it was at less than 15 m.

3.3. Photosynthetic pigments

Information about phytoplankton community biomass and structure was provided by chlorophyll and phycobiliprotein analysis, and its changes could be used to follow the phytoplankton response to meteorological disturbances.

3.3.1. Total chlorophyll a, an indicator of overall phytoplankton abundance

In general, total chlorophyll *a* (Tchl *a*), which is the sum of *Prochlorococcus* divinyl-chlorophyll *a* (dv-chl *a*) and chlorophyll *a* (chl *a*) of the other phytoplanktonic groups, had lower concentrations at 0 m than at deeper depths (Fig. 5; Table 2). Most of the time (72% of the samples), Tchl *a* was less concentrated at 15 m than at 30 m, while its concentrations were similar at these two depths (0.67 and 0.71 μg l^{-1}, respectively) the rest of the

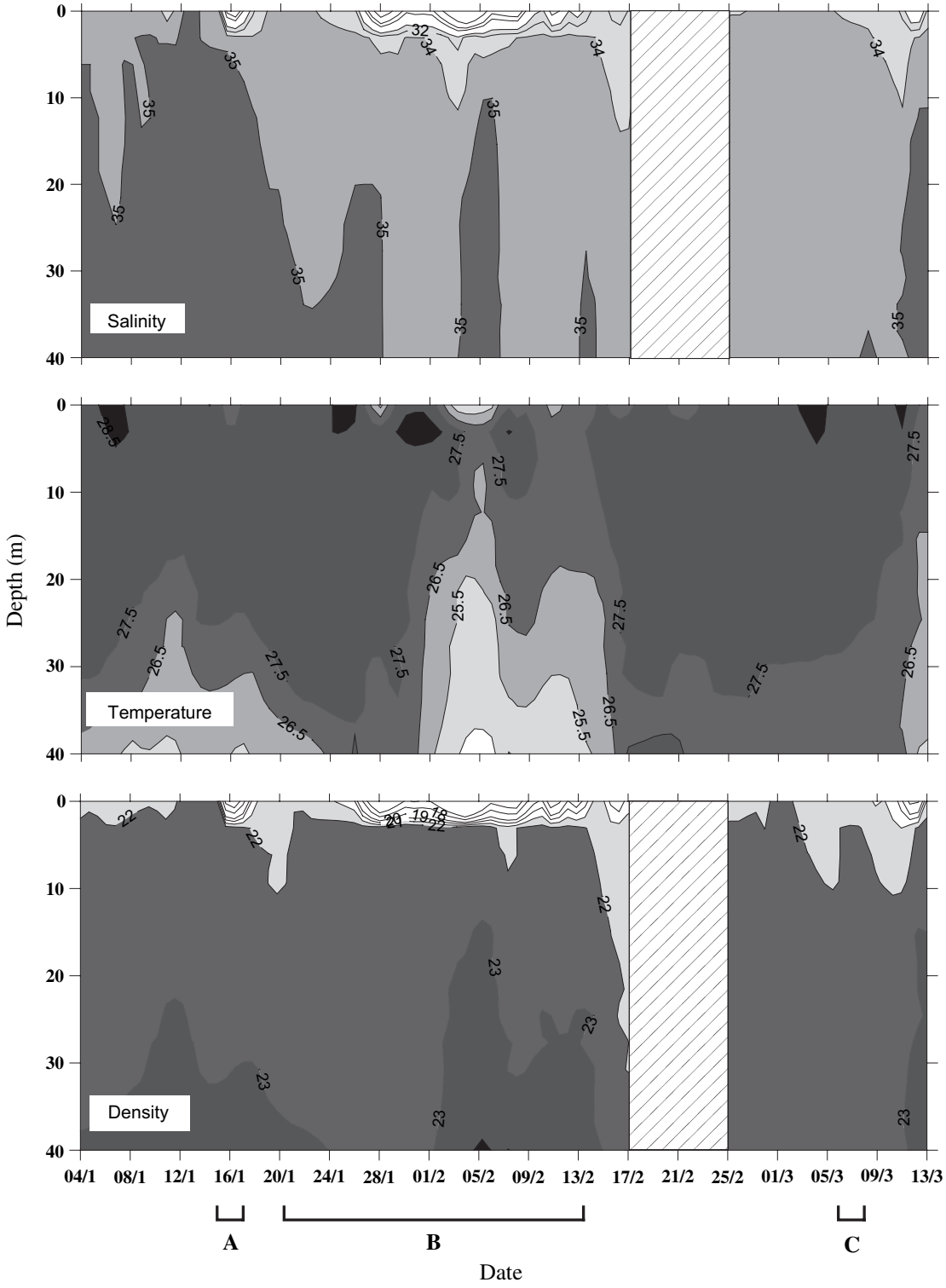

Fig. 3. Temporal variations of salinity, temperature (°C) and density (σ_0). A, B and C refer to the same periods as in Fig. 2.

time, i.e. mainly during period B. When Tchl *a* was considered at the depth of 15 m, a level where NO_2 was nearly depleted (Fig. 4) and therefore, lying in the photosynthetic layer, we obtained a higher mean concentration during period B (Table 2) when nutrient concentrations were at their maximum.

The 8-day long periodicity observed for the 30 m depth Tchl *a* (Fig. 5), particularly after the beginning of

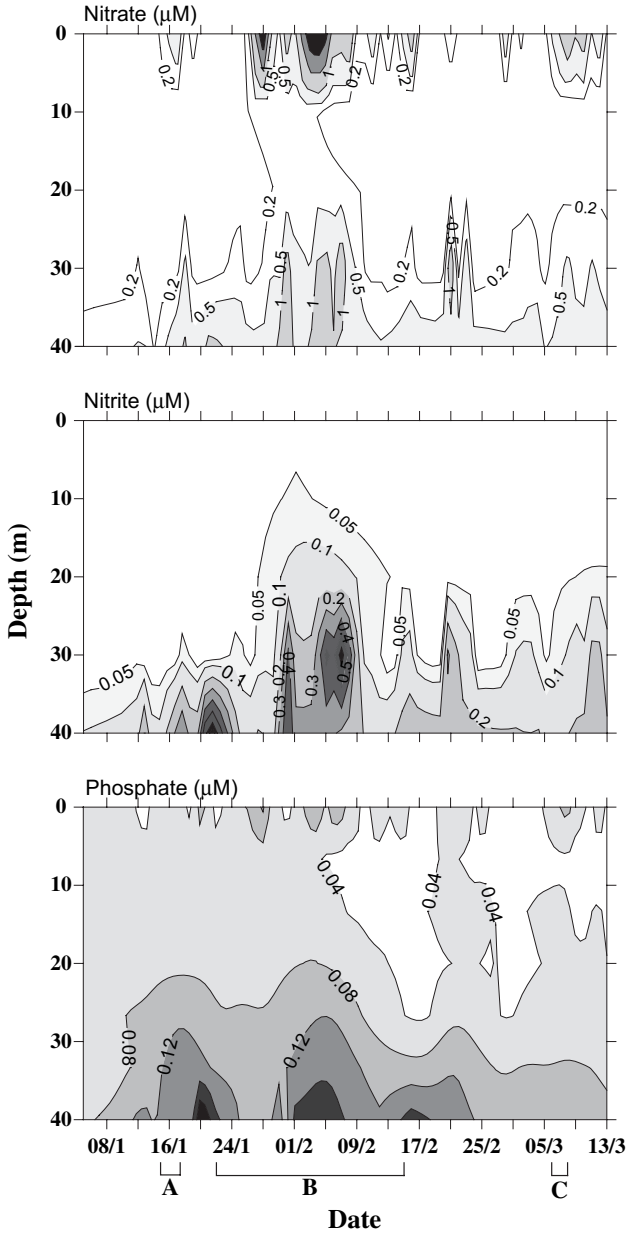

Fig. 4. Temporal variations of nitrate, nitrite and phosphate (in µM). A, B and C refer to the same periods as in Fig. 2.

period B is noteworthy. Such periodicity cannot be explained either by tidal or by rain and wind variabilities, although several Tchl *a* peaks arose 4–6 days after rainy periods.

Tchl *a* size structures for the 15 m and 0 m samples (Fig. 6) were quite similar, with respectively mean percentages of 28.1% and 23.0% for the >10 µm size class, 16.3% and 16.7% for the 2–10 µm class and 55.6% and 60.3% for the <2 µm class. This meant that most Tchl *a* belonged to the picoplankton (<2 µm) with its percentage component ranging from 35 to 75% at 0 m. The >10 µm size class Tchl *a* constituted around

Table 1
Nutrient concentrations (in µM) in the Ouinné river estuary (salinity = 0)

Date	NO_3-N	NO_2-N	PO_4-P
4/01	–	–	0.109
8/01	4.321	0.013	0.104
12/01	4.005	0.019	0.113
16/01	6.460	0.000	0.048
17/01	6.481	0.000	–
18/01	5.206	0.023	0.095
8/02	–	–	0.059
10/02	3.674	0.003	0.030
12/02	3.698	0.001	0.050

15–20% most of the time, but could exceed 40% in some cases, particularly during period B. The range of the 2–10 µm component was 9–27% at 0 m.

3.3.2. Divinyl-chlorophyll *a* and its percentage component: absolute and relative indices of the abundance of Prochlorococcus

Prochlorococcus constitutes the bulk (50%) of autotrophic communities of the oligotrophic open ocean, such as those living off New Caledonia's eastern lagoon. However, in the Bay of Ouinné, divinyl-chlorophyll *a* (dv-chl *a*) reached a maximum 24% of Tchl *a* and its highest proportions occurred at 15 m in 61% of the cases (Fig. 7). Whatever the depth, the lowest proportions and concentrations of dv-chl *a* were found during period B, a result which suggests that *Prochlorococcus* growth was not, or hardly, stimulated by terrigeneous inputs or precipitation (Table 2). At 15 m, in terms of concentration, the difference between period B and the rest of the time was less marked, however, in terms of proportions, the difference was quite clear (Table 2).

Dv-chl *a* was only present in the picoplankton size class. During rainy periods, dv-chl *a* constituted 10–30% of picoplankton Tchl *a* at 0 m and could exceed 50% at 15 and 30 m. These contributions became negligible at 0 m (<8%) and low (10–20%) at 15 m and 30 m during periods B and C.

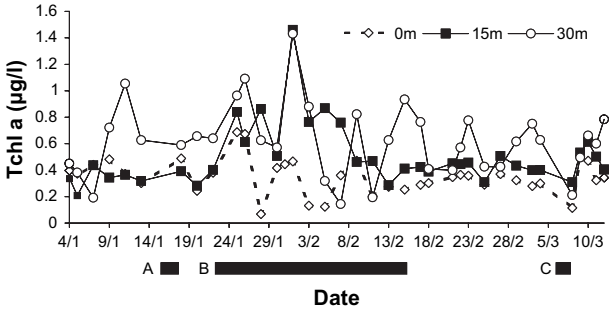

Fig. 5. Temporal variations of total chlorophyll *a* (Tchl *a*) at 0, 15 and 30 m. A, B and C refer to the same periods as in Fig. 2.

Table 2
Pigment concentrations (μg l^{-1}) and ratios at the three sampled depths during the heavy rain period B, and out of it

Depth (m)	0 m		15 m		30 m	
	Out of B	B	Out of B	B	Out of B	B
Tchl *a*	0.351	0.354	0.403	0.669*	0.574	0.711
chl *a*	0.316	0.334	0.344	0.615*	0.499	0.665
chl *b*	0.032	0.027	0.045	0.088*	0.112	0.119
chl (c_1+c_2)	0.027	0.033	0.033	0.067*	0.053	0.070
phe *a*	0.033	0.035	0.045	0.086*	0.074	0.117
chl c_3	0.023	0.022	0.036	0.080*	0.074	0.046
PE	0.283	0.277	0.399	0.479	0.425	0.472
Dv-chl *a*	0.035	0.020*,a	0.058	0.055	0.074	0.046*,a
%Dv-chl *a*	10.0	5.7*,a	14.9	9.2*	13.6	6.4*,a
chl *b*/chl *a*	0.099	0.089	0.127	0.138	0.211	0.186
Chl $c_{1,2}$/chl *a*	0.086	0.096	0.097	0.107	0.106	0.103
chl c_3/chl *a*	0.074	0.056	0.102	0.124	0.151	0.169
chl c_3/chl $c_{1,2}$	0.858	0.576*	1.066	1.163*	1.430	1.686*
PE/chl *a*	0.109	0.135	0.128	0.143	0.155	0.203

PE, phycoerythrin; chl $c_{1,2}$, chl (c_1+c_2). For other abbreviations see text.

* Mean comparison test is significant at the 5% level.

[a] dv-chl *a* measurement precision decreases at this percentage level, so actual values may be even lower.

3.3.3. Accessory chlorophylls and pigment ratios: absolute and relative indices of eukaryotic components of phytoplankton communities

While Partensky et al. (1993) showed part of chlorophyll *b* (chl *b*) could be associated with *Prochlorococcus* in the <2 μm size fraction, no significant correlation between dv-chl *a* and chl *b* was evident in our study. This would indicate that at all sampled depths, chl *b* was mainly due to eukaryotes. Generally, chl *b* and chlorophylls *c* (c_1, c_2, c_3) characterize distinct phytoplankton taxa. The former pigment is specific to prasinophytes, chlorophytes, trebouxiophytes and euglenophytes, while chl *c* characterizes the other groups. Prymnesiophytes, chrysophytes and pelagophytes possess both chl c_3 and other chl *c* in variable proportions, depending on the species. In most cases, *chl* c_1 and c_2 are only present in diatoms and most dinoflagellates possess only *chl* c_2. During our survey, all accessory chlorophylls were co-varying and varied also with chl *a* and Tchl *a*. Concentrations of all pigments were significantly higher at 15 m during period B (Table 2). As in the case of Tchl *a* at 30 m, an 8-day periodicity was noted for the other pigments throughout the survey.

An average of 65% of chl *b* was found in the picoplankton, while only 5% was found in the larger size fraction. Unlike chl *b*, chl (c_1+c_2) was distributed more or less equally among the three size groups, yet slightly more in the >10 μm fraction. Chlorophyll c_3 was more specific to the two smaller size classes.

Variation in the accessory chlorophylls to chl *a* ratio was not only linked to taxonomic changes occurring within the phytoplankton community, but also to photoacclimation processes that affect the cell content of any one pigment in each particular taxa. As a result, the accessory pigment to chl *a* ratio increased with depth (Table 2), contrary to the mean light intensity, thus confirming the role played by photoacclimation processes. Between surface samples and the deepest ones, chl *b*/chl *a* and chl c_3/chl *a* ratios doubled while chl (c_1+c_2)/chl *a* ratios only increased on average by 15%. During period B all ratios were a little higher at 15 m (Table 2), a result which may be ascribed to the low water transparency due to the heavy particle load of terrigeneous origin; the Tchl *a* increase observed during that same period may therefore reflect a combined photoacclimation process and an increase of phytoplanktonic biomass. However, differences between the ratio of mean values during and outside period B were not significant (Table 2), except for the chl c_3/chl (c_1+c_2) ratio.

Because this latter ratio increased with depth, the photoacclimation effect is suspected, which as light intensity diminishes, would produce a larger intracellular increase for chl c_3 than for other chlorophyll *c*.

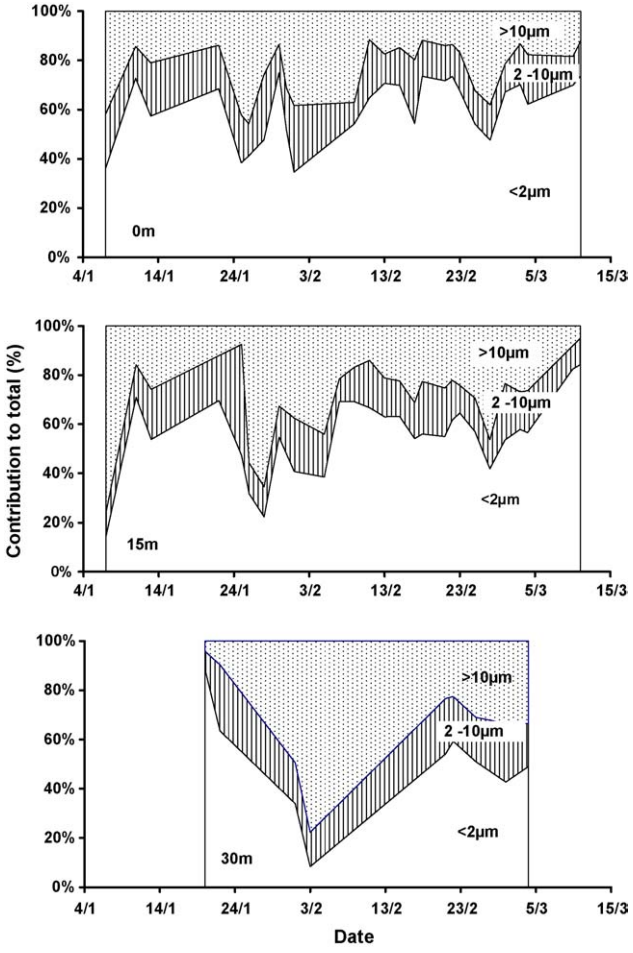

Fig. 6. Total chlorophyll *a* (Tchl *a*) size distribution: temporal variations at 0, 15 and 30 m.

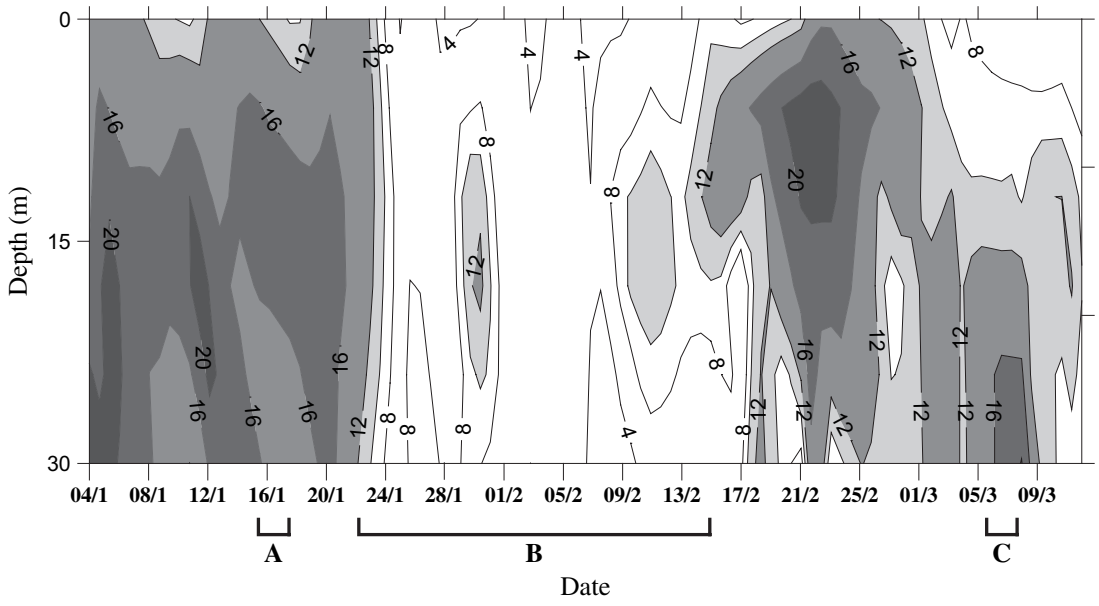

Fig. 7. Temporal variations of the percentage contribution of divinyl-chlorophyll *a*. A, B and C refer to the same periods as in Fig. 2.

During period B, the chl c_3/chl (c_1+c_2) ratio increased significantly at 15 and 30 m while it decreased at the surface during the same period (Table 2, Fig. 8). Such an observation can be ascribed to fluctuations in the relative amounts of the different types of chl c_3-containing algae compared with the other chromophytes.

The chl c_3/chl (c_1+c_2) ratio of the >10 μm size fraction was generally low (<0.8), or nil for surface samples collected during the periods of rain, suggesting a dominance of dinoflagellates and diatoms in that size class. However, it was larger (around 1) in the smaller size fractions and increased with depth for all fractions. However an exceptional value of 3.7 was observed at 30 m on 1/02 in the >10 μm size class.

As most *Trichodesmium* filaments were retained on 10 μm, their contribution to the overall chl *a* of the >10 μm size could be assessed by considering the pigment characteristics in this fraction. The main accessory pigment of this size class was chl (c_1+c_2), since chl *b*-containing algae were negligible. A strong correlation

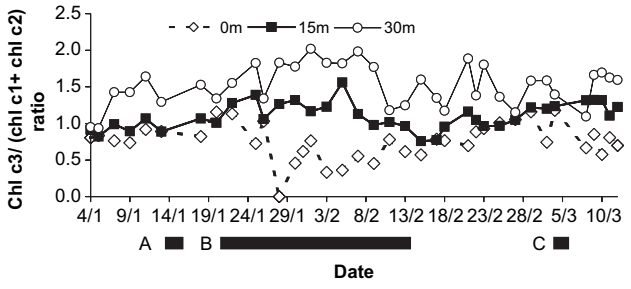

Fig. 8. Temporal variations of the chl c_3/chl (c_1+c_2) ratio. A, B and C refer to the same periods as in Fig. 2.

($r=0.99$; $n=26$) was observed between chl *a* and chl (c_1+c_2), leading to a mean chl (c_1+c_2)/chl *a* ratio of 0.144. Such a ratio may well indicate a diatom species, although it varied from 0.10 on 3/03 to 0.19 on 10/03. Knowing that *Trichodesmium* has no accessory chlorophyll pigments and assuming a constant chl (c_1+c_2)/chl *a* ratio of 0.2 for the >10 μm fraction, the concentrations of *Trichodesmium* associated chl *a* could be calculated. These values ranged from 0.003 (11–13/02) to 0.076 μg l^{-1} (26/01) which represented a little more than 10% of Tchl *a* in the upper part of the range.

3.3.4. Phycoerythrins as an abundance index for non-Prochlorococcus cyanobacteria

Concentrations of phycobiliproteins (phycoerythrins and phycocyanins), which are accessory photosynthetic pigments, may be used to assess the abundance of cryptophytes, rhodophytes and cyanobacteria. Moreover, their spectral properties (absorption and fluorescence) rely on the protein structure and the composition of their prosthetic compounds. In fact, variations are marked for phycoerythrins which have two prosthetic compounds in variable proportions, i.e. phycourobilin (PUB) and phycoerythrobilin (PEB), which show absorption peaks of around 495 and 540–560 nm, respectively. During our survey only phycoerythrins presented significant concentrations, with two peaks in their fluorescence excitation (=absorption) spectrum, at 495 and 546 nm, and one peak at 565 nm in their emission spectrum. Such characteristics were indicative of a systematic occurrence of *Synechococcus*, sometimes in great quantities (Ong et al., 1984; Wood et al., 1985; Lantoine and Neveux, 1997). The highest surface concentrations (0.5–0.6 μg l^{-1}) were measured during

period B from 25 to 30/01, but there were zero values during precipitation peaks (28/01 and 3/02).

Generally, concentrations were higher at 15 and 30 m than at 0 m, and reached 1 μg l^{-1} (Fig. 9) on three distinct dates (11/1, 1/02, 10/3). Concentrations are rather low (<0.4 μg l^{-1}) between periods B and C. In addition, an evolution in fluorescence excitation spectrum characteristics was observed for phycoerythrins. The PUB/PEB ratio, which is the ratio between fluorescence intensities measured at 495 nm excitation wavelengths and those at 546 nm, often increased with depth. Furthermore, this ratio tended to decrease at the three sampled depths throughout the survey. For example, at 0 m, it was often >1 in January (mean: 1.22 between 4 and 26/01; $n=11$; maximum: 1.4) and dropped as low as 0.5–0.6 in the middle of period B, and at the end of the survey (mean: 0.86; $n=27$).

Finally, no significant phycoerythrin concentrations could be detected in the *Trichodesmium* size class (>10 μm), thus showing that almost all of this pigment was associated with the picoplankton.

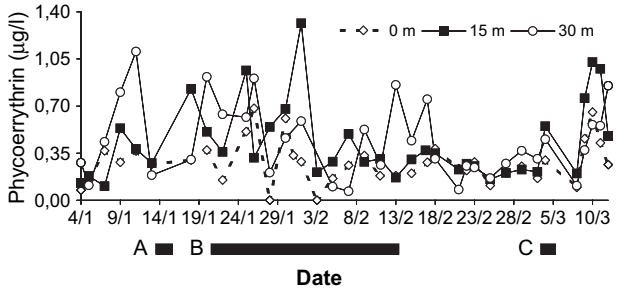

Fig. 9. Temporal variations of phycoerythrins at 0, 15 and 30 m. A, B and C refer to the same periods as in Fig. 2.

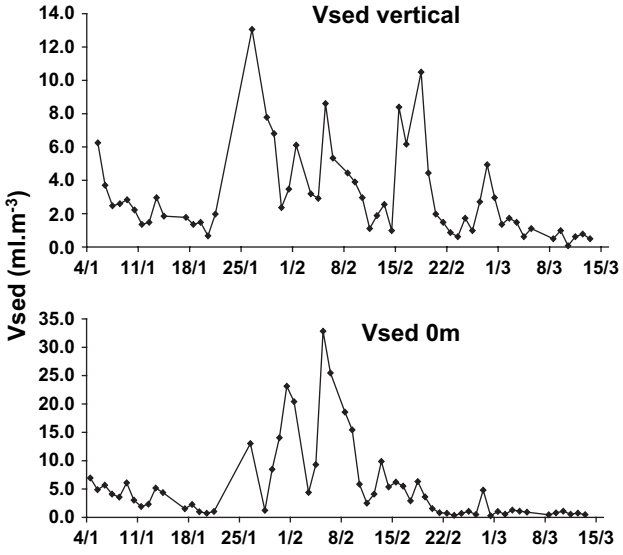

Fig. 10. Temporal variations of planktonic settled volume (Vsed, ml m^{-3}) at 0 m (Vsed 0 m) and for the 0-45 m water column (Vsed vertical).

3.4. Net plankton (>35 μm) observations

Settled volumes of vertical net samples showed peak values between 26/01 and 19/02 and on the 27/02, with clear temporary minima in the meantime (Fig. 10). The same peaks were observed for the surface samples, with even more marked minima (Fig. 10). Actually, in terms of settled volumes per cubic meter, both vertical and surface samples were correlated (Spearman rank correlation coefficient is equal to 0.723; $n=56$), thus indicating that surface hauls gave a fair estimate of the whole water column biovolumes. On average, surface ones were 1.71 times larger, and there was a great variability (standard error=1.51). The horizontal to vertical ratio was systematically > 1.71 during period B and in 10% of the total cases, with a more superficial distribution during the rain period.

The Spearman correlation coefficient of the surface biovolume/Tchl *a* relationship was significant at the 5% level ($r=0.436$; $n=33$) when all data, except those of 5/02, are considered. It was significant at the 1% level ($r=0.818$; $n=10$) for period B. The anomalous ratio found for data on the 5/02 may be due to a sampling problem: while water for Tchl *a* measurement was collected with a flask at 0 m, the plankton net was operating deeper, between 0.5 and 1 m. As there was a sharp salinity gradient on the 5/02 (16.0 at 0 m, 29.6 at 1 m), the two sampling means might have worked on two different populations.

Biovolumes of the vertical net samples ranged from 1 to 176, as compared to Tchl *a*, which ranged from 1 to 5. Moreover, there was no significant correlation between the two parameters probably for two reasons: (1) biased integrated Tchl *a*, resulting from the small number of sampled depths along the water column and (2) biovolumes influenced by non-phytoplanktonic particles collected by plankton nets.

Phytoplankton taxa numbers per cubic meter (Table 3) undergo important variations from one sample to another, and no clear conclusions can be drawn about their temporal variability, except for numbers of trichomes that decrease dramatically during the rainy period (31/01–8/02). Yet, one gets a clearer view for the diatom, dinoflagellate or *Trichodesmium* contributions to the total (Fig. 11): there are more diatoms and dinoflagellates during period B and at the beginning and the end of the survey, which agrees with the slight increase of the >10 μm chl (c_1+c_2)/chl *a* ratio observed after the rain (0.11–0.14 to 0.14–0.18). Proportions of *T. erythraeum* to total (i.e. *T. erythraeum* and *T. thiebautii*) follow the same trend (Fig. 11).

Copepod numbers follow a decreasing trend throughout the survey (Table 3) with *Macrosetella* sp. being found in all samples and more particularly during period B. Since this was the time of low *Trichodesmium*

Table 3
Concentrations (in numbers per cubic meter) of the major taxa collected by the 35 μm net in the 45–0 m water column

Taxa		7/1	12/1	20/1	26/1	31/1	1/2	3/2	6/2	8/2	14/2	21/2	1/3	9/3	13/3
Diatoms	*Nitzschia* spp.	273	177	270	575	289	1001	248	253	786	171	180	216	707	83
	Chaetoceros spp.	2560	1478	594	1933	220	794	203	364	912	35	207	79	220	133
	Rhizosolenia spp.	533		84	3929		1108	465	347	1698	14	173	108	1613	230
	Other diatoms	80	0	36	200	509	328	128	57	222	2	153	79	107	49
Dinoflagellates	*Ceratium* spp.	1607	1574	1716	1509	362	1711	713	479	1422	677	627	395	2633	346
	Other dinoflagellates	1047	1440	1068	1142	289	2353	533	168	546	457	720	432	840	100
Trichodesmium	*T. thiebautii* trichomes	3760	8827	11636	29165	3834	4973	1316	829	1154	6274	15915	7605	9817	583
	T. erythraeum trichomes	5733	3381	6496	16835	1820	5752	1170	1881	2391	6913	12196		13869	671
	Tufts	0	0	0	0	6	0	0	0	0	7	0	0	28	3
	Puffs	0	0	0	0	0	0	0	0	0	0	14	0	0	0
Radiolaria–Acantharia		100	80	6	40	29	115	15	38	108	52	100	17	127	29
Foraminifera		33	9	0	16	0	0	8	4	6	3	7	2	0	0
Tintinnoinea		67		750	96		8	0	6	6	282	100	0	27	0
Copepoda	*Microsetella/Macrosetella*	40	28	24	8	3	69	19	17	78	33	67	32	27	9
	Harpacticoids	60	1009	198	232	420	367	413	801	990	202	1373	1041	313	133
	Other copepods	9067	11407	5436	5558	4184	6386	3311	3614	5952	1253	4720	3972	4800	2378
	Nauplii	8227	9638	6978	8521	3400	11229	5115	6038	10026	1093	5620	1546	10993	1591
Ostracoda		0		6	8		31	15	4	6		7	8	7	0
Larval Cirrhipedae		167	278	114	120	12	237	45	69	120	188	33	42	140	39
Cladocera		47	49	36	40	26	31	23	8	24	6	13	8	0	9
Larval Euphausiacea		0	6	0	0	0	0	0	1	0	3	7	2	0	0
Larval Decapods	Zoe Brachyura	0	23	6	8	12	8	0	0	6	0	7	0	0	0
	Miscellaneous	27	9	12	24	0	8	15	19	36	6	13	8	60	5
	Peneids	0	2	0	0	0	0	0	0	0	0	0	0	0	0
	Sergestids	0	2	0	8	0	8	0	0	12	5	0	3	13	2
Larval Echinodermata		60	15	0	32	17	8	8	1	6	3	0	3	13	2
Larval Polychaeta		60	2	18	72	38	61	8	17	18	6	20	9	27	34
Larval Gasteropoda		373	235	354	559	150	367	210	192	126	65	213	74	67	15
Larval Lamellibranchiata		780	602	528	1517	0	2101	773	599	1176	60	560	398	1480	133
Pteropoda	*Creseis* sp.	193	34	5562	870	15	53	0	35	198	88	240	14	273	6
Polychaeta		100	125	72	208	133	260	113	42	114	82	53	56	227	23
Appendicularia		347	49	156	958	177	565	315	83	312	31	113	108	193	193
Chaetognatha		13	51	42	72	119	61	38	61	18	74	40	48	147	26
Hydromedusae		0	5	18	0	0	0	0	0	0	3	0	0	7	3
Siphonophorae		0	2	0	0	0	0	0	0	0	0	0	0	0	0
eggs		820		594	918	113	1001	1035	506	906	91	1520	386	1127	216
Fish eggs		7		0	0		0	0	0	6		0		0	2
Detritus		+		++	+		0	+	+	0	++	+	+	+	+

Detritus amount: 0, none; +, a few detritus; ++, many detritus.

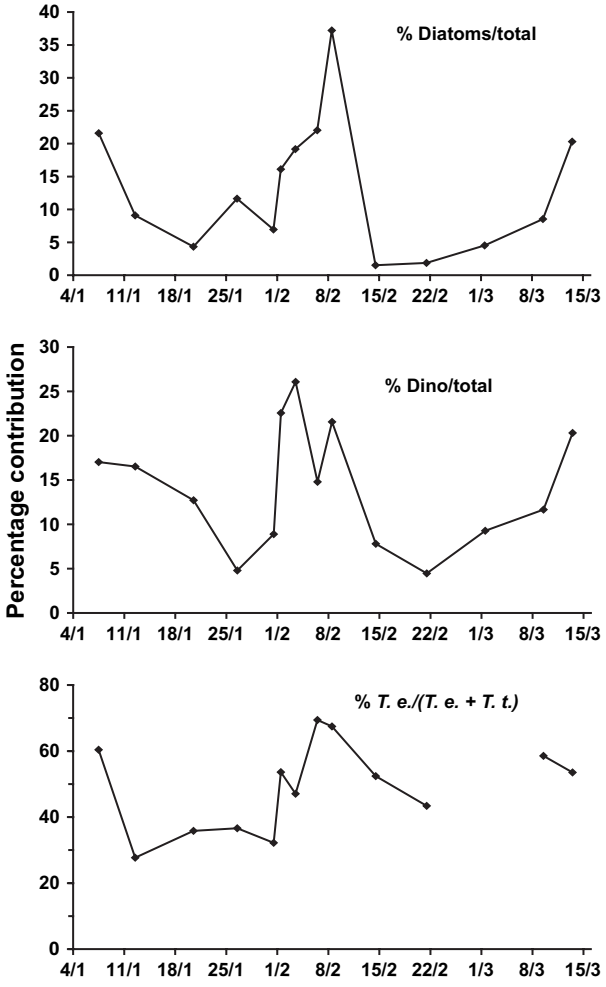

Fig. 11. Temporal variations of percentage contributions of diatoms (% Diatoms/total) and dinoflagellates (%Dino/total) with respect to total phytoplanktonic numbers in vertical hauls of the 35 μm net and variations of *Trichodesmium erythraeum* (*T. e.*) with respect to total *T. e.*+*T. thiebautii* (*T. t.*).

concentrations, one might ascribe such a decrease to grazing by *Macrosetella*, one of the rare planktonic species able to feed on *Trichodesmium* (Roman, 1978; O'Neil et al., 1996). No *Miracia* sp., another possible grazer, was found in net samples.

From the numbers of trichomes per cubic meter and a mean chl *a* concentration per trichome of 101 pg found by Tenório et al. (unpublished data) in a bloom event which occurred in the SW lagoon of New Caledonia, a maximum of 0.005 μg l^{-1} can be calculated for the 26/01 sample. However, such an estimate is far below that based on the hypothesis that the chl (c_1+c_2) ratio in the eukaryotes of the >10 μm fraction is constant and equal to 0.2 (see above). The difference between the two may be ascribed to uncertainties on *Trichodesmium* abundance estimates, resulting from different sampling methods (Chang, 2000). It can also mean that, either the supposed constancy of the chl (c_1+c_2)/chl *a* ratio is not a valid hypothesis for eukaryotes, or that it is >0.2.

4. Discussion

4.1. Characteristics of terrigeneous inputs

As illustrated in Table 4, nutrient concentrations were very low in the lagoon off the Bay of Ouinné during dry periods, when salinity was >34.5. Similar concentrations were found at station 3 during the 5–21/01 period, except during period A. In such an environment, the only possible enrichment originates from land effluxes that follow precipitation. In those cases, the longer the precipitation period, the steeper the surface salinity decrease as observed during period B. A decrease in salinity results from the combined effect of the Ouinné river outflow and run-off from the steep slopes surrounding the Bay of Ouinné. The river drains modified ferralitic ferritic soils from its basin, while run-off introduces eutrophic and slightly modified brown soils (Latham, 1981). The former type of soil is almost depleted in available phosphate, has low silicon concentrations but plenty of ferrous oxide, Fe_2O_3 (Table 5). Brown soils, on the other hand, contain more silicon and available phosphate than the modified ferralitic ferritic soils. Present results for the Ouinné river and station 3 (maximum 0.127 μM PO_4 on 28/01; Fig. 4) confirm the very low phosphate levels of the soils (Table 5). Nitrate concentrations were moderate with a maximum of 6.5 μM in the river and 3.6 μM at station 3. There are no data on NO_3 soil concentration, which is a function of the vegetal cover and its diazotrophic capacity (Jaffré, 1992). Finally, land drainage deposits very significant amounts of iron and silicate (Table 5) into the Bay, although no data of seawater concentrations are available. To sum up, terrigeneous inputs are the source of most nutrients, except for PO_4.

Since these nutrients are associated with freshwater, their effect is felt mainly at the surface, and communities living in the deeper and saltier depths (5–20 m) are hardly influenced directly. Thanks to mixing processes and to high light levels, part of the nutrients may be taken up quickly by phytoplankton communities living at the interface between the surface and the underlying layers of water. Because the lower light intensities limit

Table 4
Mean nutrient concentrations (μM) in the 0–30 m water column of DIAPALIS cruises Ouinné station (1.8 nautical miles offshore from station 3 of the present study) and of station 3 (during the dry period preceding the rainy period A)

	NO_2-N	NO_3-N	PO_4-P	NH_4-N
DIAPALIS				
December 2001	0.030	0.016	0.073	0.103
January 2002	0.018	0.053	0.038	0.055
April 2002	0.022	0.150	0.037	0.058
Station 3	0.011	0.083	0.066	

Table 5
Percentage contributions of silicate (SiO_2), ferrous oxide (Fe_2O_3) and phosphate (P_2O_5) in the soils of the region of Ouinné (from Latham et al., 1978)

	SiO_2	Fe_2O_3	P_2O_5
Modified ferralitic ferritic soils	1.13	75.66	0.02
Eutrophic and slightly modified brown soils	24.10	10.85	0.10

photosynthesis at deeper levels, as shown by the significant nitrite concentrations, nutrient concentrations increase with depth (30–40 m; Fig. 3). For the same reason, the rise of the 0.05 μM NO_2 isoline during the rain episodes (Fig. 3), may be interpreted as being due to a reduction of the photic layer depth, following inputs of fine particles from land drainage. In addition, these particles are likely to sink, become mineralized and their inorganic compounds be eventually taken up by phytoplankton. There may be a time lag following rainy periods, between nutrient availability and their consumption when water transparency conditions are not satisfactory. In such a case, the lag will depend on the particle load and its sinking rate.

4.2. Pigment analysis by spectrofluorometry and community structure

Spectrofluorometry measurements dealt with two categories of photosynthetic pigments, chlorophylls and phycobiliproteins, which provide taxonomical information: dv-chl *a* concentrations are specific to *Prochlorococcus* cyanobacteria, and phycobiliproteins mainly indicate other cyanobacteria. Moreover, phycobiliprotein spectral diversity makes it possible to discriminate between different cyanobacterial types: various *Synechococcus* (Ong et al., 1984; Wood et al., 1985; Lantoine and Neveux, 1997), N_2-fixing filamentous cyanobacteria (Fujita and Shimura, 1974; Haxo et al., 1987), and less well-known cyanobacteria (Neveux et al., 1999). Spectrofluorometry is also useful for differentiating prokaryotes from eukaryotes, and information about eukaryotic composition can be drawn from concentrations of the different accessory chlorophylls: chl *b* for chlorophytes, and chl *c* for chromophytes. The original spectrofluorometric method of Neveux and Lantoine (1993) only took chl *b*, dv-chl *b* and chl *c* (as c_1+c_2) fluorescence into account and only used measurements provided by 24 coupled wavelengths (excitation, emission). Currently, use of 806 data points from a 3D-fluorescence spectrum has improved the spectral resolution and quantification of individual chlorophylls (Neveux et al., 2003). The latest improvement has been the introduction of chl c_3 into the analysis. This pigment, spectrally distinct from chl c_1 and c_2, represents one of the three major pigments of the chl *c* family, which includes 11 distinct pigments (Zapata et al., 2004). It was first described in *Emiliana huxleyi* (Jeffrey and Wright, 1987) and represents an important component of most haptophytes (Zapata et al., 2004), chrysophytes and pelagophytes (Vesk and Jeffrey, 1987). However, interpretation of the chl c_3/(chl c_1+c_2) ratio as an index of the relative abundance of the three latter groups with regard to diatoms and dinoflagellates, has to be used with caution since some tropical pennate diatoms contain significant quantities of chl c_3 (Stauber and Jeffrey, 1988) and some haptophytes do not have chl c_3 (Zapata et al., 2004). Nevertheless, spectrofluorometry appears to be a useful tool when the main fluorescing photosynthetic pigment concentrations need to be measured in the field, particularly in tropical and equatorial waters where *Prochlorococcus* is often a major component. In addition, it is convenient for high-frequency sampling analysis and it is cheap. However, high-performance liquid chromatography is required for more detailed qualitative and quantitative information on algal pigments including carotenoids which do not have significant fluorescence (Mantoura and Llewellyn, 1983).

4.3. The effect of precipitation on phytoplankton biomass

With respect to the effect of precipitation, two distinct layers must be considered: the surface, which receives nutrient inputs immediately, and the rest of the water column. During period B, for instance, there was a general increase of planktonic (>35 μm) biomass in the water column, but transitory surface minima coinciding with Tchl *a* minima, were observed each day following precipitation peaks. In those instances, strong salinity gradients occurred within the first upper metre.

The surface biomass minima may be ascribed to the dilution effect of sea water by the plankton-free freshwater, or equally the elimination of some marine species by osmotic stress or growth disturbance. Finally, the observed anomalous ratio between Tchl *a* and surface plankton biomass of 5/02 (cf. Section 3.4) stresses the importance of sampling depth: collecting water at the depth of 1 m rather than at 0 m, would probably have given higher Tchl *a* values and therefore, led to no minima during period B. During the same period, but at 15 m, Tchl *a* increased significantly by 50%, partly because of photoacclimation in a more turbid environment. Tchl *a* also increased at 30 m, although not significantly (5% level; Table 2), by 25%. Part of these increases originated from surface enrichment, which poses the problem of the nutrient transfer down to the deeper levels through density gradients. Most likely, mixing happened progressively,

thanks to water mixing and to the reduced thickness of the surface layer of low salinity. Most of the time, this was shown by the small density gradient observed.

4.4. The effect of precipitation on phytoplankton composition

During dry periods, phytoplankton communities of the Bay of Ouinné were dominated by the picoplankton. This feature is typical of oligotrophic ecosystems that characterize the nearby open ocean and can be explained by the easy exchanges of water between the open ocean and the lagoon. As a result, the lagoon of the east coast barrier reef, which is discontinuous and not as shallow as the west coast one, is much more open to the nearby deep sea. Concerning picophytoplankton, pigment analyses showed that dv-chl *a* constituted 10–30% of Tchl *a* at 0 m, and 20–50% at 15 and 30 m. In addition, most of the chl *b*, a pigment associated with picoeukaryotes of the prasinophyte and chlorophyte groups, part of the chl *c* associated with the other eukaryote taxa, and almost all phycoerythrins of the *Synechococcus* species originated from the picophytoplankton. The larger size class (>10 μm) constituted 15–20% of Tchl *a*, which was more than that for the 2–10 μm fraction. Finally, in the oligotrophic-type net plankton, colonial cyanobacteria were comprised of two *Trichodesmium* (*thiebautii* and *erythraeum*) species in equal proportion and they made up the bulk of the population (60–93%).

During periods of sustained rain, the phytoplankton community changed and became more typical of nutrient-rich ecosystems. As for the biomass (cf. Section 4.3), the surface layer and the water column need to be considered separately. During the surface biomass minima of period B, when surface salinity was low, there were no dv-chl *a*, no phycoerythrins and no chl c_3, suggesting the absence of pico- or filamentous cyanobacteria and chl c_3-containing eukaryotes. Apart from these minima, observed Tchl *a* increases were linked to those of the chl *a* (80% mean increase at 15 m), since dv-chl *a* concentrations were reduced. This can be interpreted as an increase of the eukaryote population biomass, also supported by the doubling of the accessory chlorophylls at 15 m. During those periods, *Synechococcus* phycoerythrin mean concentrations appeared to be unaffected by nutrient inputs, although a decrease of the PUB/PEB ratio was noted, and presumably indicates the occurrence of various *Synechococcus* clones in variable proportions. In fact, high PUB/PEB cyanobacteria are often present in oligotrophic open-ocean ecosystems, while the low PUB/PEB clones are mainly encountered in nutrient-rich environments (Lantoine and Neveux, 1997). This is illustrated by period B, with nutrients being introduced from the land and leading to a higher concentration of low PUB/PEB cyanobacteria. Part of the PUB/PEB ratio changes could be ascribed to environmental changes, particularly light intensity. Indeed, some *Synechococcus* clones are able to change their phycoerythrin spectral properties in accordance with light conditions (Palenik, 2001) and some *Prochlorococcus* strains found at depth possess a phycoerythrin pigment (Hess et al., 1996), the latter being unobserved in our samples. Finally, Tchl *a* contribution of the >10 μm size class increased during the rainy periods, representing >40% between 25/01 and 1/02. At the same time, trichome numbers underwent a dramatic drop, whereas diatom chains and dinoflagellates made up the bulk of the >35 μm phytoplankton.

In summary, in spite of reduced sampling on the vertical scale, this study clearly showed two types of phytoplankton communities: one was specific to oligotrophic waters that was dominated by picocyanobacteria (*Prochlorococcus* and *Synechococcus*) and *Trichodesmium* in the >35 μm fraction; the other one, occurred when lagoon waters were fertilized by nitrate, and presumably silicate (as inferred from the drained soil composition), and was dominated by eukaryotes, with a very significant reduction of the cyanobacterial biomass and a shift from high PUB to high PEB *Synechoccocus*. The origin of such changes within the phytoplankton community may lie in differences in the metabolic properties of any one taxa and in their adaptation capacity in response to environmental changes. Although some *Prochlorococcus* strains are known to use oxidized nitrogen compounds (Partensky et al., 1999), it is generally recognized that these picocyanobacteria work on nitrogen ions which are regenerated within the photic zone. Diatoms, on the other hand, may respond to nitrate inputs very quickly thanks to their high growth rate (Eppley, 1972; Furnas, 1990; Örnólfsdóttir et al., 2004). This is not the case for *Trichodesmium* where the turn over time is, at least, 3–4 days at 26 °C (Mulholland and Capone, 1999). From the growth rate difference, it follows that *Trichodesmium* coexists with the rest of the phytoplankton taxa with no actual competition, as noted by Eleuterius et al. (1981) in the Mississipi plume or in the results of Post et al. (2002) for the Gulf of Aqaba. Coexistence stops when nitrate becomes depleted and eukaryotes (diatoms, dinoflagellates, coccolithophorids, etc.) vanish. They are replaced by picocyanobacteria working on regenerated production and diazotrophic microcyanobacteria (Capone et al., 1997, for review). Considering the soil composition of the region, diazotrophy is most likely limited by phosphorus rather than by iron, as shown also by Van den Broeck et al. (2004) for the nearby open ocean and Muslim and Jones (2003) at Magnetic Island (Great Barrier Reef).

Changes in the phytoplankton community should affect the grazer community with more copepods during

diatom and dinoflagellate developments. However, such a pattern was not found in the present survey made at the entrance of the Bay of Ouinné (station 3). A possible reason is the spatial and temporal evolution of planktonic communities that drift offshore, particularly during heavy river outflows. Using this hypothesis, one might expect to find more mature communities off station 3, with more grazers and zooplankton in general. Binet (1986) speculated on the diatom origin of higher zooplankton biomasses in northern New Caledonia. From the Ouinné survey, we recognize the land-based origin of diatom developments, but we lack observations on their effect on the zooplankton. In any case, diatom blooms are likely to be limited, taking into account the poverty of the soils in terms of nitrogen and above all phosphorus.

Acknowledgments

This study benefited from the financial support of the IRD (Institut de Recherche pour le Développement - ex ORSTOM) Research Unit 99 (Cyano) and the PNEC (Programme National sur l'Environnement Côtier) New Caledonia field site. We are particularly indebted to "Société Minière Georges Montagnat" for their free logistical support and to Mr André Puech for his precious help and for providing us with the meteorological data. Thanks are due to John Butscher, Francis Gallois, Miguel Clarque, and Barbara Planche for their technical assistance. Marcio Tenório thanks the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) of the Brazilian Government for the PhD scholarship. The contribution of Jacques Neveux resulted from a joint agreement between the Directions of IRD and CNRS (UMR 7621). Finally we thank Dr Nyree West for improving our English text.

References

Bell, P.R.F., Ulmetri, I., Uwins, P., 1999. Nitrogen fixation by *Trichodesmium* spp. in the Central and Northern Great Barrier Reef lagoon: relative importance of the fixed-nitrogen load. Marine Ecology Progress Series 186, 119–126.

Binet, D., 1986. Note sur l'hypothèse d'une influence de la nature géologique et pédologique des terrains côtiers sur la biomasse zooplanctonique dans le lagon de Nouvelle-Calédonie. Océanographie Tropicale 21 (1), 1–110.

Blanchot, J., Charpy, L., Le Borgne, R., 1989. Size composition of particulate organic matter in the lagoon of Tikehau atoll (Tuamotu archipelago). Marine Biology 102, 329–339.

Capone, D.G., Zehr, J.P., Paerl, H.W., Bergman, B., Carpenter, E.J., 1997. *Trichodesmium* a global significant marine cyanobacterium. Science 276, 1221–1229.

Cardinal, M., 1983. Etude des populations phytoplanctoniques sur la côte sud-ouest de la Nouvelle-Calédonie durant les années 1977–1978–1979. Bulletin de liaison SEPANRIT 12, 167–172.

Carpenter, E.J., Subramaniam, A., Capone, D.G., 2004. Biomass and primary productivity of the cyanobacterium *Trichodesmium* spp. in the tropical N Atlantic ocean. Deep-Sea Research I 51, 173–203.

Chang, J., 2000. Precision of different methods used for estimating the abundance of the nitrogen-fixing marine cyanobacterium, *Trichodesmium* Ehrenberg. Journal of Experimental Marine Biology and Ecology 245, 215–224.

Desrosières, R., 1975. Quelques observations sur le phytoplancton océanique des abords de la Nouvelle Calédonie (Océan Pacifique sud-ouest). Norwegian Journal of Botany 22, 195–200.

Eleuterius, L., Perry, H., Eleuterius, C., Warren, J., Caldwell, J., 1981. Causative analysis of a nearshore bloom of *Oscillatoria erythraeum* (*Trichodesmium*) in the northern Gulf of Mexico. Northeast Gulf Sciences 5, 1–11.

Eppley, R.W., 1972. Temperature and phytoplankton growth in the sea. Fishery Bulletin 70, 1063–1085.

Frontier, S., 1972. Calcul de l'erreur sur un comptage de zooplancton. Journal of Experimental Marine Biology and Ecology 8, 121–132.

Fujita, Y., Shimura, S., 1974. Phycoerythrin of the marine blue-green alga, *Trichodesmium thiebautii*. Plant and Cell Physiology 15, 939–942.

Furnas, M.J., 1990. In situ growth rates of marine phytoplankton: approaches to measurement, community and species growth rates. Journal of Plankton Research 12, 1117–1151.

Haxo, F.T., Lewin, R.A., Lee, K.W., Li, M., 1987. Fine structure and pigments of *Oscillatoria* (*Trichodesmium*) aff. *thiebautii* (Cyanophyta) in culture. Phycologia 26, 443–456.

Hess, W., Partensky, F., Van der Staay, G.W.M., Garcia-Fernandez, J.M., Börner, T., Vaulot, D., 1996. Coexistence of phycoerythrin and a chlorophyll a/b antenna in a marine prokaryote. Proceedings of the National Academy of Sciences USA 93, 11126–11130.

Jaffré, T., 1992. Floristic and ecological diversity of the vegetation on ultramafic rocks in New Caledonia. In: Baker, A.J.M., Proctor, J., Reeves, R.D. (Eds.), The vegetation of ultramafic (serpentine) soils. Intercept, Hampshire, UK, pp. 101–107.

Jeffrey, S.W., Wright, S.W., 1987. A new spectrally distinct component in preparation of chl *c* from the microalgae *Emiliana huxleyi* (Prymnesiophyceae). Biochimica et Biophysica Acta 894, 180–188.

Kattner, G., 1999. Storage of dissolved inorganic nutrients in seawater: poisoning with mercuric chloride. Marine Chemistry 67, 61–66.

Lantoine, F., Neveux, J., 1997. Spatial and seasonal variations in abundance and spectral characteristics of phycoerythrins in the tropical northeastern Atlantic Ocean. Deep-Sea Research I 44, 223–246.

Latham, M., 1981. Aptitudes culturales et forestières. In Atlas de la Nouvelle-Calédonie et dépendances. Editions ORSTOM, Bondy, France, 222 pp.

Latham, M., Quantin, P., Aubert, G., 1978. Etude des sols de la Nouvelle-Calédonie. Nouvel essai sur la classification, la caractérisation, la pédogénèse et les aptitudes des sols de Nouvelle-Calédonie. Carte pédologique de la Nouvelle-Calédonie à 1/1000000. Carte d'aptitudes culturale et forestière des sols de Nouvelle-Calédonie à 1/1000000. Notice explicative No. 78. ORSTOM, Paris, 138 pp.

Lugomela, C., Lyimo, T.J., Bryceson, I., Semesi, A.K., Bergman, B., 2002. *Trichodesmium* in coastal waters of Tanzania: diversity, seasonality, nitrogen and carbon fixation. Hydrobiologia 477, 1–13.

Mantoura, R.F.C., Llewellyn, C.A., 1983. The rapid determination of algal chlorophyll and carotenoid pigments and their breakdown products in natural waters by reverse-phase high-performance liquid chromatography. Analytica Chimica Acta 151, 297–314.

Mulholland, M.R., Capone, D.G., 1999. Nitrogen fixation, uptake and metabolism in natural and cultured populations of *Trichodesmium* spp. Marine Ecology Progress Series 188, 33–49.

Murphy, J., Riley, J.P., 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta 26, 31–36.

Muslim, I., Jones, G., 2003. The seasonal variation of dissolved nutrients, chlorophyll *a* and suspended sediments at Nelly Bay, Magnetic Island. Estuarine, Coastal and Shelf Science 57, 445–455.

Navarro, A., Corredor, J.E., Morell, J.M., Armstrong, R.A., 2000. Distribution of the cyanophyte *Trichodesmium* (Oscillatoriaceae) in the eastern Caribbean Sea: influence of the Orinoco river. Revista de Biologia Tropical 48 (Suppl. 1), 115–124.

Neveux, J., Panouse, M., 1987. Spectrofluorometric determination of chlorophylls and pheophytins. Archiv für Hydrobiologie 109, 567–581.

Neveux, J., Lantoine, F., 1993. Spectrofluorometric assay of chlorophylls and phaeopigments using the least squares approximation technique. Deep-Sea Research Part A 40, 1747–1765.

Neveux, J., Lantoine, F., Vaulot, D., Marie, D., Blanchot, J., 1999. Phycoerythrins in the southern tropical and equatorial Pacific Ocean: evidence for new cyanobacterial types. Journal of Geophysical Research 104 (C2), 3311–3321.

Neveux, J., Dupouy, C., Blanchot, J., Le Bouteiller, A., Landry, M.R., Brown, S.R., 2003. Diel dynamics of chlorophylls in HNLC waters of the equatorial Pacific (180°): interactions of growth, grazing, physiological responses and mixing. Journal of Geophysical Research 108 (C12), 8140, doi:10.1029/2000JC000747.

O'Neil, J.M., Metzler, P.M., Glibert, P.M., 1996. Ingestion of ^{15}N-labelled *Trichodesmium* spp. and ammonium regeneration by the harpacticoid copepod *Macrosetella gracilis*. Marine Biology 125, 89–96.

Ong, L.J., Glazer, A.N., Waterbury, J.B., 1984. An unusual phycoerythrin from a marine cyanobacterium. Science 224, 80–83.

Örnólfsdóttir, E.B., Lumsden, S.E., Pinckney, J.L., 2004. Nutrient pulsing as a regulator of phytoplankton abundance and community composition in Galveston Bay, Texas. Journal of Experimental Marine Biology and Ecology 303 (2), 197–220.

Palenik, B., 2001. Chromatic adaptation in marine *Synechococcus* strains. Applied and Environmental Microbiology 67, 991–994.

Partensky, F., Hoepffner, N., Li, W.K.W., Ulloa, O., Vaulot, D., 1993. Photoacclimation of *Prochlorococcus* sp. (Prochlorophyta) strains isolated from the North Atlantic and the Mediterranean Sea. Plant Physiology 101, 295–296.

Partensky, F., Hess, W.R., Vaulot, D., 1999. *Prochlorococcus*, a marine photosynthetic prokaryote of global significance. Microbiology and Molecular Biology Reviews 63, 106–127.

Post, A.F., Dedej, Z., Gottlieb, R., Li, H., Thomas, D.N., El-Absawi, M., El-Naggar, A., El-Gharabawi, M., Sommer, U., 2002. Spatial and temporal distribution of *Trichodesmium* spp. in the stratified Gulf of Aqaba, Red Sea. Marine Ecology Progress Series 239, 241–250.

Raimbault, P., Slawyk, G., Coste, B., Fry, J., 1990. Feasibility of using an automated colorimetric procedure for the determination of seawater nitrate in the 0 to 100 nM range: examples from field and culture. Marine Biology 104, 347–351.

Revelante, N., Williams, W.T., Bunt, J.S., 1982. Temporal and spatial distribution of diatoms, dinoflagellates and *Trichodesmium* in waters of the Great Barrier Reef. Journal of Experimental Marine Biology and Ecology 63 (1), 27–45.

Roman, M.R., 1978. Ingestion of the blue-green alga *Trichodesmium* by the harpacticoid copepod, *Macrosetella gracilis*. Limnology and Oceanography 23 (6), 1245–1248.

Schwartz, D., 1963. Méthodes statistiques à l'usage des médecins et des biologistes. Editions Médicales Flammarion, France, 318 pp.

Stauber, J.L., Jeffrey, S.W., 1988. Photosynthetic pigments in fifty-one species of marine diatoms. Journal of Phycology 24, 158–172.

Strickland, J., Parsons, T., 1972. A practical handbook of seawater analysis. Bulletin 167. Fisheries Research Board of Canada, 310 pp.

Van den Broeck, N., Moutin, T., Rodier, M., Le Bouteiller, A., 2004. Seasonal variations of phosphate availability in the SW Pacific Ocean near New Caledonia. Marine Ecology Progress Series 268, 1–12.

Vesk, M., Jeffrey, S.W., 1987. Ultrastructure and pigments of two strains of the picoplanktonic alga, *Pelagococcus subviridis* (Chrysophyceae). Journal of Phycology 23, 332–336.

Wood, A.M., Horan, P.K., Muirhead, K., Phinney, D.A., Yentsch, M., Waterbury, J.B., 1985. Discrimination between types of pigments in marine *Synechococcus* sp. by scanning spectroscopy, epifluorescence microscopy, and flow cytometry. Limnology & Oceanography 30, 1303–1315.

Zapata, M., Jeffrey, S.W., Wright, S.W., Rodriguez, F., Garrido, J.L., Clementson, L., 2004. Photosynthetic pigments in 37 species (65 strains) of *Haptophyta*: implications for oceanography and chemotaxonomy. Marine Ecology Progress Series 270, 83–102.