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

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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 $3 \times 10^{-4}$ M for nitrate and $0.13 \times 10^{-6}$ M 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; phycerythrins; 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

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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 terrigenous 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 terrigenous 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.](image-url)
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 HgCl₂ (Kattner, 1999) and stored at 4 °C before analysis at the land laboratory. NO₃ and NO₂ were analysed with a Technicon® II autoanalyser, following the methods described in Strickland and Parsons (1972) for concentrations of NO₂ and NO₃ > 1 µM, and using the “high sensitivity” method of Raimbault et al. (1990) for concentrations of NO₃ < 1 µM. Soluble reactive phosphorus (PO₄) 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 NO₂ and NO₃ (high sensitivity) and 0.020 µM for PO₄ and NO₃ (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 (c₁+c₂; c₃); 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 c₃ (DHIC®, 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 (NaH₂PO₄ 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 m² 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
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 (NO₂, NO₃, PO₄)

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, NO₃ reached 3.6 μM in the five upper metres on 4/02 and PO₄, 0.17 μM on 28/01 (note that there was no variation in NO₂). The Ouinne river contributed to nutrient inputs with concentrations mirroring the low content of the drained soils, particularly for PO₄. Table 1 shows that the river concentrations were moderate for NO₃, nil for NO₂ and very low for PO₄. After the 8/02, lower NO₃ and PO₄ 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 PO₄ concentrations of less than 0.080 μM, as from the 8/02. The link between nutrient concentrations and terrigenous inputs was also illustrated by the inverse linear relationship between surface NO₃ and salinity (S_m): NO₃ = – 0.124S_m + 4.37 (r = –0.872; n = 60 paired values). The correlation coefficient was less for PO₄ (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 NO₃ and NO₂ (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 NO₂ vertical profiles, taking into account the normal association of the NO₂ 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 NO₂, 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
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. 3. Temporal variations of salinity, temperature (\( ^\circ \text{C} \)) and density (\( \sigma_\text{b} \)). 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 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 Ouiné, 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. 4. Temporal variations of nitrate, nitrite and phosphate (in µM). A, B and C refer to the same periods as in Fig. 2.](image1)

![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.](image2)

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

<table>
<thead>
<tr>
<th>Date</th>
<th>NO$_3$-N</th>
<th>NO$_2$-N</th>
<th>PO$_4$-P</th>
</tr>
</thead>
<tbody>
<tr>
<td>4/01</td>
<td>–</td>
<td>–</td>
<td>0.109</td>
</tr>
<tr>
<td>8/01</td>
<td>4.321</td>
<td>0.013</td>
<td>0.104</td>
</tr>
<tr>
<td>12/01</td>
<td>4.005</td>
<td>0.019</td>
<td>0.113</td>
</tr>
<tr>
<td>16/01</td>
<td>6.460</td>
<td>0.000</td>
<td>0.048</td>
</tr>
<tr>
<td>17/01</td>
<td>6.481</td>
<td>0.000</td>
<td>–</td>
</tr>
<tr>
<td>18/01</td>
<td>5.206</td>
<td>0.023</td>
<td>0.095</td>
</tr>
<tr>
<td>8/02</td>
<td>–</td>
<td>–</td>
<td>0.059</td>
</tr>
<tr>
<td>10/02</td>
<td>3.674</td>
<td>0.003</td>
<td>0.030</td>
</tr>
<tr>
<td>12/02</td>
<td>3.698</td>
<td>0.001</td>
<td>0.050</td>
</tr>
</tbody>
</table>
Table 2
Pigment concentrations (μg l⁻¹) and ratios at the three sampled depths during the heavy rain period B, and out of it

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>0 m</th>
<th>15 m</th>
<th>30 m</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Out of B</td>
<td>B</td>
<td>Out of B</td>
</tr>
<tr>
<td>Tchl a</td>
<td>0.351</td>
<td>0.354</td>
<td>0.403</td>
</tr>
<tr>
<td>chl a</td>
<td>0.316</td>
<td>0.334</td>
<td>0.344</td>
</tr>
<tr>
<td>chl b</td>
<td>0.032</td>
<td>0.027</td>
<td>0.045</td>
</tr>
<tr>
<td>chl (c1+c2)</td>
<td>0.027</td>
<td>0.033</td>
<td>0.033</td>
</tr>
<tr>
<td>phe a</td>
<td>0.033</td>
<td>0.035</td>
<td>0.045</td>
</tr>
<tr>
<td>chl c3</td>
<td>0.023</td>
<td>0.022</td>
<td>0.036</td>
</tr>
<tr>
<td>PE</td>
<td>0.283</td>
<td>0.277</td>
<td>0.399</td>
</tr>
<tr>
<td>Dv-chl a</td>
<td>0.035</td>
<td>0.029**</td>
<td>0.058</td>
</tr>
<tr>
<td>%Dv-chl a</td>
<td>10.0</td>
<td>5.7**</td>
<td>14.9</td>
</tr>
<tr>
<td>chl b/chl a</td>
<td>0.099</td>
<td>0.089</td>
<td>0.127</td>
</tr>
<tr>
<td>Chl c1/2/chl a</td>
<td>0.086</td>
<td>0.096</td>
<td>0.097</td>
</tr>
<tr>
<td>chl c1/chl a</td>
<td>0.074</td>
<td>0.056</td>
<td>0.102</td>
</tr>
<tr>
<td>chl c2/chl c1</td>
<td>0.858</td>
<td>0.576*</td>
<td>1.066</td>
</tr>
<tr>
<td>PE/chl a</td>
<td>0.109</td>
<td>0.135</td>
<td>0.128</td>
</tr>
</tbody>
</table>

* Mean comparison test is significant at the 5% level.
** 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 (c1, c2, c3) 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 c3 and other chl c in variable proportions, depending on the species. In most cases, chl c1 and c2 are only present in diatoms and most dinoflagellates possess only chl c2. 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 (c1+c2) was distributed more or less equally among the three size groups, yet slightly more in the >10 μm fraction. Chlorophyll c3 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 c3/chl a ratios doubled while chl (c1+c2)/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 terrigenous 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 c3/chl (c1+c2) 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 c3 than for other chlorophyll c.
During period B, the chl \( c_3 / \text{chl} (c_1 + c_2) \) 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 \( c_3 / \text{chl} (c_1 + c_2) \) ratio of the \( >10 \mu\text{m} \) 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 \( >10 \mu\text{m} \) size class.

As most Trichodesmium filaments were retained on \( 10 \mu\text{m} \), their contribution to the overall chl \( a \) of the \( >10 \mu\text{m} \) 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 \( (r=0.99; \ n=26) \) was observed between chl \( a \) and chl \( (c_1 + c_2) \), leading to a mean chl \( (c_1 + c_2) / \text{chl} a \) 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 \( (c_1 + c_2) / \text{chl} a \) ratio of 0.2 for the \( >10 \mu\text{m} \) fraction, the concentrations of Trichodesmium associated chl \( a \) could be calculated. These values ranged from 0.003 (11–13/02) to 0.076 \( \mu\text{g} \text{ l}^{-1} \) (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 \( \mu\text{g} \text{ l}^{-1} \)) 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.

### 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 (c₁+c₂)/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 45–50 m water column

<table>
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<tr>
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<th>12/1</th>
<th>20/1</th>
<th>26/1</th>
<th>31/1</th>
<th>1/2</th>
<th>3/2</th>
<th>6/2</th>
<th>8/2</th>
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<th>9/3</th>
<th>13/3</th>
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<td>177</td>
<td>270</td>
<td>575</td>
<td>289</td>
<td>1001</td>
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<td>253</td>
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<td>794</td>
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</table>

Detritus amount: 0, none; +, a few detritus; ++, many detritus.
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 μM 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, Fe2O3 (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 PO₄ 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 NO₃ 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 PO₄.

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...
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 NO₂⁻ 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), N₂-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 𝑐₁ + 𝑐₂) 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 𝑐₃ into the analysis. This pigment, spectrally distinct from chl 𝑐₁ and 𝑐₂, 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 Emiliania 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 𝑐₃/(chl 𝑐₁ + 𝑐₂) 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 𝑐₃ (Stauber and Jeffrey, 1988) and some haptophytes do not have chl 𝑐₃ (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 \( \mu \)m) constituted 15–20% of Tchl \( a \), which was more than that for the 2–10 \( \mu \)m fraction. Finally, in the oligotrophic-type net plankton, colonial cyanobacteria were comprised of two *Trichodesmium* \( (\text{thiebautii}) \text{ and erythraeum} \) 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 \( \mu \)m 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 \( \mu \)m 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 \( \mu \)m 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 *Synechococcus*. 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; Örnölsdóttir 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 Mississippi 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 Ouinéé (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 Ouinéé 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.

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