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Population dynamics and environmental conditions affecting *Trichodesmium* spp.  
(filamentous cyanobacteria) blooms in the south-west lagoon of New Caledonia

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1 **Abstract.** The present description of *Trichodesmium* spp. population dynamics and associated  
 2 environmental variables is the first one using a very short sampling interval (2-3 days). Such a  
 3 strategy allows a fine description of changes involving the population density and characteristics. It  
 4 also lends itself to interpreting those changes from past environmental conditions. During the two  
 5 surveys, 2 and 5 month-long, *T. erythraeum* dominated the *Trichodesmium* population, with  
 6 temporary occurrence of *T. thiebautii* and five blooms could be described. These events appeared at  
 7 temperatures  $> 24^{\circ}\text{C}$  and followed, in all cases, nitrate, soluble reactive phosphorus and chlorophyll  
 8 *a* enrichments, with a 3-7 day time lag. Low wind speed ( $< 4\text{ m s}^{-1}$ ) was not a prerequisite for  
 9 *Trichodesmium* bloom developments as long as temperatures exceeded  $26^{\circ}\text{C}$ . As abundance  
 10 increased during the bloom, so did the number of filaments (trichomes) in colonies and their  
 11 buoyancy, leading to a clear positive biomass gradient from the bottom to the surface. A simple  
 12 model, using variable growth rates, showed trichome ascent would be responsible for 87-99% of  
 13 concentrations at 0.5m, with *Trichodesmium* net growth rates ranging from  $0.11$  to  $0.38\text{ d}^{-1}$ . Finally,  
 14 rapid trichome density declines could be ascribed to nutrient depletion and massive surface death  
 15 following ascent.

16

17

## 18 **1. Introduction**

19

20 High surface concentrations of the chain-forming diazotrophic cyanobacteria *Trichodesmium* spp.  
 21 have drawn attention, not only for their spectacular characteristics, but also for their potential  
 22 toxicity (Landsberg, 2002, ) and contribution to the carbon and nitrogen cycles in oligotrophic  
 23 regions via diazotrophy, i.e. di-nitrogen ( $\text{N}_2$ ) fixation (Karl et al., 2002). Such natural phenomena,  
 24 called "blooms" in most references, have often been observed in the south-west Pacific, both in the  
 25 open ocean (Dupouy et al., 2000) and coastal areas (Jones et al., 1982), as well as in other parts of  
 26 the tropical belt (Capone et al., 1997). While many causative mechanisms for bloom development

27 have been proposed in the past (Sellner, 1997), we still lack reliable descriptions of past  
28 environmental conditions that triggered their increase. The word "bloom" itself remains imprecise  
29 and is generally understood as corresponding to rapid and intense growth, as it does for other  
30 phytoplankters, although it is now admitted that aggregation may be responsible for many observed  
31 surface *Trichodesmium* concentrations. One of the reasons for such uncertainties is that many reports  
32 are based on instant observations, no account being provided on past characteristics, biomass and  
33 vertical distribution of the *Trichodesmium* population, as stressed by Carpenter et al. (2004).  
34 Therefore, the understanding of bloom dynamics and causes would benefit from high frequency  
35 observations of both cyanobacteria and environmental variables over the water column.

36 Such a strategy, involving very frequent sampling on a long period of time can virtually be made  
37 in coastal areas, only. Present knowledge, however, rely on rather low frequency observations with  
38 sampling being made every 7 – 15 days (Lugomela et al., 2002), 1 month (Post et al., 2002) or 10 –  
39 15 days (Muslim and Jones, 2003). While correlations between simultaneous data on *Trichodesmium*  
40 densities and environmental variables could be evidenced in these studies (Post et al., 2002; Muslim  
41 and Jones, 2003), effect of potential bloom triggers and environmental conditions that are required  
42 for bloom developments were not clearly proved because no information was collected in the few  
43 days preceding the start of the blooming event. For the same reason, causes of high surface  
44 aggregations remained hypothetical for lack of high temporal resolution surveys of *Trichodesmium*  
45 density along the water column, so that discriminating between effects of growth, vertical migrations  
46 and physical aggregation was impossible. Such considerations led to organizing “high” frequency  
47 sampling at the entrance of the Bay of Ste Marie (Noumea, New Caledonia) with two surveys made  
48 during the austral spring and summer, as both seasons are reported to be favourable for bloom  
49 development. Surveys lasted for 2.5 (Survey I: 9 October - 19 December 2003) and 5 months  
50 (Survey II: 15 November 2004 - 12 April 2005) with field measurements made at the same station,  
51 three times per week.

Here, we describe the *Trichodesmium* population, the changes in filament (trichome) density, degree of aggregation in colonies and vertical distribution during bloom development. From such a description and observed biovolume increase rates, we will show that high surface concentrations are due to growth and trichome ascent. Further, potential bloom triggers and favourable environmental conditions, will be identified from monitored environmental variables that prevailed between 2 and 7 days before. These variables were selected, taking into account results of the Muslim and Jones (2003) study in a similar shallow coastal site of the Great Barrier Reef (GBR, Australia): meteorology (wind strength and rainfall), hydrology (temperature and salinity), dissolved inorganic nutrients, turbidity, a proxy of suspended sediments, and chlorophyll, in addition to phytoplankton and zooplankton composition. Finally, one of the usual criticism of conclusions based on a solitary station deals with the effect of spatial heterogeneity on time-series data. This point will be considered taking into account observations made simultaneously at the entrance and 2.0 km off the bay.

## 2. Materials and methods

### 2.1. Sampling sites and general conditions (Fig. 1)

The study site, Sta. SM (22°18.86' S - 166°27.95' E, Fig. 1), was visited every Monday, Wednesday and Friday, between 07:00 and 09:00. While the station is away from inhabited areas and from urban inputs, it is protected from the prevailing SE trade winds and swell. A second station, Sta. O (22°19.80' S – 166°28.48' E) was visited in 2004-2005, weather permitting for comparison. Water column depth is 12 m and 28 m for Stas SM and O, respectively.

### 2.2. Meteorology, hydrology, and water sampling

Meteorological data were recorded at Faubourg Blanchot Meteo-France Station, 4.2 km away from the entrance of the Bay of Ste Marie.

CTD profiles (1 m to bottom) were obtained with a SeaBird<sup>®</sup> SBE 19 probe, fitted with pressure, temperature, salinity, turbidity, fluorescence and Photosynthetic Available Radiation (PAR) sensors.

Water samples were collected with 5 L-Niskin bottles at 0.5, 4, 7, and 10 m in 2003 and 0.5, 3, 6, and 10 m in 2004-2005. Niskin bottles were siphoned in the laboratory on land for nutrient and pigment analyses and *Trichodesmium* abundance, within one hour of sampling.

### 2.3. Nutrients and pigments

Nutrients were analyzed on HgCl<sub>2</sub>-preserved samples from 0.5 and 6-7 m. Nitrate (NO<sub>3</sub>) concentrations were determined by colorimetry using a Technicon<sup>®</sup> auto-analyzer and standard techniques (Strickland and Parsons, 1972), except for NO<sub>3</sub> < 0.1 μM, when the “high sensitivity” procedure of Raimbault et al. (1990) was used. Soluble reactive phosphorus (SRP) concentrations were measured with a Cecil<sup>®</sup> CE 1011 (10cm length-cell) spectrophotometer, using the molybdenum blue reaction (Murphy and Riley, 1962).

Chlorophyll *a* (Chl *a*) was measured on the < 20 and > 20 μm size fractions at all sampled depths, except for the > 20 μm fraction in 2004-2005, when analyses were only made at 3 and 10 m. For the < 20 μm Chl *a*, 200ml were prefiltered through a 20 μm nylon screen and collected on Whatman<sup>®</sup> GF/F filters. For the > 20 μm fraction, the whole Niskin bottle content was filtered through a 20 μm screen and gently rinsed off with filtered seawater onto GF/F filters. All filters were stored in liquid nitrogen until analysis within less than 2 weeks. Chl *a* was extracted in methanol and measured by fluorometry as described by Le Bouteiller et al. (1992).

### 2.4. *Trichodesmium* abundance and biometry

*Trichodesmium* were collected on 20 μm nylon screen from the total content of Niskin bottles (mean volume: 5.74 L) and transferred to a “sedimentation cell” with 5% formaldehyde. When trichomes did not sink, a few drops of pure acetic acid were added to the cell, in order to lower solution p<sub>H</sub> and break gas vesicles (Carpenter and Carmichael, 1995). Microscopic examinations and

enumeration were made 24 h later using a Leitz<sup>®</sup> Fluovert inverted microscope. Enumeration considered free trichomes and fusiform (tuft) and spherical (puff) aggregates, usually called “colonies” in the literature. The number of trichomes per colony was recorded and the volume of each trichome was calculated from its measured length and diameter, assuming a cylindrical shape for the organism. In this paper, *Trichodesmium* abundance has been expressed in terms of total number of trichomes (i.e. free and in colonies) per litre (trich. L<sup>-1</sup>), or as trichome biovolume per litre (μm<sup>3</sup> L<sup>-1</sup>). Integrated values have been computed by the trapezoidal method. While trichome density and biovolume are closely related (Fig. 2), due to the fact that biovolume data includes trichome numbers, biovolume is often preferred as it gives a better estimate of the biomass.

Two species of *Trichodesmium* were identified according to Carpenter and Carmichael (1995) and Janson et al. (1995). Individual cells of *T. thiebautii* Gomont are more long than wide and the trichome has a convex apex whereas *T. erythraeum* Ehrenberg cells are more wide than long and the trichomes have a flat apex. *T. erythraeum* colonies are usually darker than *T. thiebautii* colonies (Carpenter et al., 1993). Such morphological differences between the two species have also been confirmed by genetic finger prints of *Trichodesmium* spp. sampled in different areas of New Caledonia, considering the *hetR* and *rrs* encoding for 16S rDNA genes, the internal transcribed spacer (ITS) of the 16S-23S rDNA region and a highly iterated palindrome, HIP1 (Trottet, 2003).

121

## 122 2.5. *Trichodesmium* C, N and chlorophyll *a* contents

Plankton nets (35-μm mesh), towed at 1 m below the surface, were the source of 18-75 colonies hand-picked, using a plastic inoculation loop, and transferred onto 25 mm Whatman GF/F filters for Chl *a* measurements, or on pre-combusted filters for carbon (C) and nitrogen (N) analyses.

Filters for Chl *a* measurements were stored in liquid nitrogen and analyzed as described above. For C, N determinations, filters were dried at 60°C and kept in a dessicator until analysis with a Integra-CN PDZ EUROPA mass spectrometer. Single colonies were also selected for carbon

assimilation and nitrogen fixation experiments using  $^{13}\text{C}$  and  $^{15}\text{N}$  techniques (data not shown here, but reported in Le Borgne et al., 2006).

Carbon, N and Chl *a* contents are expressed per colony ( $\text{col}^{-1}$ ) and per trichome ( $\text{trich}^{-1}$ ). Since analyses were made on colonies originating from plankton nets, the mean number of trichomes per colony was obtained from microscopic observations of aliquots originating from the same catches and processed as described before.

## 2.6. *Microphytoplankton (>20 $\mu\text{m}$ ) and Macrosetella abundance*

Counts of the major phytoplankton taxa were conducted on samples from 2004-2005 survey. Selected taxa were diatoms, dinoflagellates and *Trichodesmium* spp. The two specific *Trichodesmium* spp. grazers, copepods *Macro-* and *Microsetella* spp. (Roman, 1978; O'Neil and Roman, 1994) were all enumerated on all samples. They were grouped into the "*Macrosetella*" taxon, since *Macrosetella gracilis* is the most abundant species in both our samples and lagoons of the west coast of New Caledonia (Binet, 1984).

## 2.7. *Trichodesmium biovolume net increase and carbon-specific growth rates*

Using observed *Trichodesmium* biovolume increases,  $\Delta V_i$ , exponential net increase rates,  $k_i$  (in  $\text{d}^{-1}$ ), can be calculated at depth,  $z_i$ :

$$\Delta V_i = V_{f,i} - V_{o,i} \text{ with } V_{f,i} = V_{o,i} e^{k_i t} \Rightarrow k_i = \ln(V_{f,i}/V_{o,i})/(t_f - t_o) \quad (1)$$

where  $V_{f,i}$  is the maximum biovolume of a peak period at time  $t_f$  and  $V_{o,i}$ , at the initial time  $t_o$ .

Biovolume-based doubling time,  $d'_{A,i}$  (in d), is equal to:

$$d'_{A,i} = \ln(2)/k_i = \ln(2) (t_f - t_o)/(\ln(V_{f,i}/V_{o,i})) \quad (2)$$



155 The carbon-specific growth rate for 0.5m depth,  $g_{C,0.5}$ , was obtained from  $^{13}\text{C}$  primary  
 156 productivity and elemental composition measurements, made on colonies in 2004-2005 (data  
 157 presented in Le Borgne et al., 2006). Calculations of  $g_{C,0.5}$  used the following equation:

$$158 \quad g_{C,0.5} = \ln((C_0 + p_C)/C_0) \quad (3)$$

160  
 161 where  $C_0$  is the initial carbon concentration,  $p_C$  is the daily rate of carbon fixation, and time is  
 162 understood as one day.

## 163 164 2.8. Data processing

165 Non-parametric and Gaussian statistics were used, following Snedecor and Cochran (1967).  
 166 Bravais-Pearson and Spearman's rank correlation coefficients are  $r$  and  $r_s$ , respectively, with level of  
 167 significance shown by \* and \*\* for  $p < 0.05$  and  $p < 0.01$  significance, respectively;  $n$  is the number of  
 168 data per series,  $s$ , the standard deviation and  $p$ , the probability of rejection in the Wilcoxon and sign  
 169 tests.

## 170 171 3. Results

### 172 173 3.1. *Trichodesmium* population dynamics: abundance, vertical distribution and net increase rates

174 *Trichodesmium* spp. were always present, at least at one of the sampled depths and made almost  
 175 the totality of the pelagic filamentous cyanobacteria, *Katagnymene* spp. being quasi-absent. *T.*  
 176 *erythraeum* was the dominant species in 2003 (99.0% of the 5,513 counts) and 2004-2005 (83% of  
 177 the 10,650 counts) with *T. thiebautii* making the remainder.

178 Amidst a background of low trichome concentration, several periods of abrupt increase and  
 179 decline were observed during the two surveys (Fig. 3 and 4). When the abundance exceeded 5  
 180  $\text{trich.L}^{-1}$  for at least two consecutive sampling times (i.e. 2-3 days), trichomes were considered as

181 thriving. Given the sharp variations, the term “bloom” will be used hereafter even though it is not  
 182 quite appropriate, in the sense that the *Trichodesmium* never dominated the microphytoplankton,  
 183 contributing a maximum of 27.7% of microphytoplankton counts.

184 Five blooms were observed with various features summarized in Table 1. Each bloom was  
 185 characterized by one peak abundance, except in 2003, when the 3 consecutive maxima were  
 186 interpreted as belonging to the same bloom (see Discussion). Peak amplitudes were variable from  
 187 one event to another and that of February 2005, although low, was considered as a bloom because  
 188 trichome densities were above  $5 \text{ L}^{-1}$  for 3 weeks. *T. erythraeum* was responsible for most of the  
 189 blooms, except in December 2004 and February 2005 when contribution of *T. thiebautii* was  
 190 significant. A striking point was the vertical distribution during the blooms, with a clear positive  
 191 gradient of trichome densities from deep to shallow depths (Fig. 3 and 4).

192 During the peak periods, the exponential net increase rate,  $k_i$ , (equation 1), ranged from 0.19 to  
 193  $1.51 \text{ d}^{-1}$  at 6-7 and 10m and from 0.52 to  $3.29 \text{ d}^{-1}$  at 3-4 and 0.5m (Table 2). These  $k_i$  values were  
 194 higher than carbon-specific growth rates,  $g_{C,0.5}$ , calculated from  $^{13}\text{C}$  uptake rates at 0.5m: 0.12-0.17  
 195  $\text{d}^{-1}$  (Le Borgne et al., 2006). Exponential net increase rate calculations from biovolume variations  
 196 were not possible outside the peak periods, while carbon-specific growth rates,  $g_{C,0.5}$ , provided by  
 197 the  $^{13}\text{C}$  uptake method were low,  $0.022 \text{ d}^{-1}$  on average (range:  $0.017 - 0.050 \text{ d}^{-1}$ ).

198 Finally, density variations were synchronized and of the same magnitude at stations SM and O  
 199 (Fig. 4) except from February 2005 on, when higher *Trichodesmium* densities were often found at  
 200 the latter site. Growth rates, estimated from the  $^{13}\text{C}$  experiments at both stations were similar (Le  
 201 Borgne et al., 2006).

202

### 203 3.2. *Trichodesmium* population features: trichome size, degree of aggregation and chemical

### 204 constituents

205 For both surveys, biovolume per trichome displayed quite a large range (Table 3), their length  
 206 variability was greater than the width one and *T. thiebautii* trichomes were significantly longer than

those of *T. erythraeum* ( $p < 0.001$ ). There was no significant size difference between trichomes from 0.5 and 6 m, as well as from Sta. SM and O (not shown) and between 2003 and 2004-2005 for both species.

During the two surveys, *Trichodesmium* population consisted mostly of free trichomes ( $65 \pm 22$  and  $63 \pm 15$  % in 2003 and 2004-2005, respectively) and colonies in tuft morphology prevailed (98% of the total number of colonies). Tufts were typically small, made of 2 to 34 trich. col<sup>-1</sup> while puffs of *T. thiebautii* were made up of 7 to 123 trich. col<sup>-1</sup>. As the number of free trichomes increased during the peak periods, so did the number of trichomes in colonies, leading to a significant correlation between the two forms ( $p < 0.01$ ; Fig. 5). Regression curves between densities of trichomes in colonies and free trichomes were calculated for each of the two periods, using a semi-log scale in order to take the anormal distribution of the free trichomes into account (Fig. 5).

*Trichodesmium* carbon, nitrogen and Chl *a* content data, presented in Table 4, were quite variable, likely due to different physiological or trophic states of filamentous cyanobacteria. Based on trichome densities and Chl *a* content, *Trichodesmium* Chl *a* was estimated as accounting for no more than 21% of total Chl *a*. Atomic C/N ratio averaged 6.2 (range: 4.6 - 7.4), a value close to the slope (6.75) of the C versus N regression line ( $r^2 = 0.96$ ,  $n=10$ ) and to the Redfield ratio.

To sum up, present surveys evidenced a shallower vertical distribution, higher growth rates and more trichome aggregation in colonies during *Trichodesmium* blooms. These are the result of environmental changes that are now considered.

### 3.3. General environmental conditions and causes of bloom developments (Fig. 6 and 7)

Both surveys started in austral spring, a season characterized by settled SE trade winds ( $> 6 \text{ m.s}^{-1}$ ) and low rainfall. Sea temperature increased gradually until the beginning of February (Survey II), reaching 29°C. Amidst this increasing trend, windy periods induced lower sea temperature and higher salinity in spring. In summer and autumn, however, effect of wind on salinity was the opposite, wind being associated to heavy rainfalls brought by tropical depressions, Kerry being one

of them in January 2005. Their major effect was high rainfall on the mainland and resulting lower lagoon salinity (<35.00).

Nutrient concentration increases followed local rainfall, as recorded at Noumea Met station in most instances. When they did not, they could be due, either to regional precipitation, not necessarily recorded by coastal stations, or to wind events leading to resuspension of shallow sediments and associated benthic nutrients (Muslim and Jones, 2003). The latter interpretation might indeed explain the nitrate peaks of November 2003 (Fig. 6) and March 2005 (Fig. 7) and the peak of SRP of January 2005, that took place during windy periods with no rainfall.

These increases in nutrient concentrations were not necessarily followed by total Chl *a* peaks for reasons probably linked to vertical mixing or trace metal inhibitions, as discussed later for *Trichodesmium*. Microphytoplankton contributed 15.9% ( $s = 8.0$ ;  $n = 119$ ) to total Chl *a* (>20  $\mu\text{m}$  + < 20  $\mu\text{m}$ ) in 2003 and 8.0% ( $s = 7.2$ ;  $n = 130$ ) in 2004-2005. Their main peak period occurred in February 2005, following January nutrient inputs (Fig. 7). Diatoms dominated the microphytoplankton, contributing 82% of the counts and dinoflagellates made most of the remainder (11%).

*Trichodesmium sp.* started thriving at a water temperature, ranging from 24.2 to 28.6°C (Fig. 6 and 7). The vertical temperature gradient was variable from one bloom event to the other (0.05 to 0.84°C) and, therefore, did not seem to affect *Trichodesmium* development. The same conclusion may be drawn for the vertical salinity gradient which ranged between 0.00 and 1.00.

A calm period (mean wind speed < 4  $\text{m s}^{-1}$ ) preceded development of *Trichodesmium* blooms, except in January 2005 (Fig. 7) when the bloom started and continued during a windy period (mean wind speed before the bloom commenced: 7.3  $\text{m s}^{-1}$ ). In this case, however, temperature was > 26°C. In the other instances, windy periods did prevent *Trichodesmium* growth, as observed in November-December 2003, for example. Higher turbidity was not systematically associated with wind speed and rather low turbidity was the rule most of the time. We conclude turbidity, as measured by the CTD sensor, is not a good descriptor of blooming conditions.

259 *Trichodesmium* always (5/5 cases) thrive after nutrient ( $\text{NO}_3$ , SRP) and Chl *a* concentration  
 260 increases, that occurred within 3-7 days before the peak abundance (Fig. 6 and 7). Since it happened  
 261 in all 5 cases, its occurrence was significant (sign test at  $p < 0.10$ ). In addition, amplitude of the peak  
 262 abundance at 0.5 m was significantly correlated ( $r_s = 0.879^*$ ) with  $\text{NO}_3$  concentration at the start of  
 263 the bloom (Fig. 8), but not with SRP.

264 In order to test the nutrient and Chl *a* trigger hypothesis, we have considered whether all of their  
 265 increases were followed by blooms. During the two surveys, there were only two exceptions (5-7  
 266 November 2003 and 10-14 January 2005) when nutrient enrichments did not lead to any  
 267 development. In those two cases, the nutrient-Chl *a* increases were followed by windy periods (Fig.  
 268 6 and 7) which could, therefore, prevent bloom development. However, as seen previously, the wind  
 269 factor alone may not explain the second exception (January 2005) since temperature was  $>26^\circ\text{C}$ . A  
 270 lower than usual salinity may be the direct or indirect reason for the lack of *Trichodesmium* bloom as  
 271 it was also for the lack of microphytoplankton biomass increase at the same period (Fig. 7).

272 In summary, according to the present observations, development of *Trichodesmium* blooms  
 273 would follow nutrient and Chl *a* concentration increases with a 3-7 day lag, provided temperature is  
 274  $>26^\circ\text{C}$  and no heavy and sustained rainfall occurs. The same conditions apply to  $> 24^\circ\text{C}$   
 275 temperatures, as long as wind speed is low ( $< 4 \text{ m s}^{-1}$ ).

276

## 277 4. Discussion

278

### 279 4.1. Sampling strategy: are conclusions drawn from one station valid?

280 Study of *Trichodesmium* population dynamics employed high frequency sampling at Sta. SM,  
 281 assuming the same watermass and planktonic population were sampled for a long enough period.  
 282 This implies a rather long residence time, which is supported by the study of Jouon et al. (2006).  
 283 Thus, the "e-flushing time", a proxy of the water residence time, is 15-25 days at the entrance of the  
 284 bay, for a  $\sim 8 \text{ m s}^{-1}$  (15.5 knots) SE wind velocity, and longer, of course, for lower wind speeds.

Besides, no significant tide effect was evidenced, especially in terms of salinity at 1m depth, because water exchanges proceed from both the south and the east of Sta. SM (Fernandez et al., 2006). Note also that *Trichodesmium* density and environmental parameter variations at Sta. SM displayed no erratic trends, at least at a period of a week. It appears, therefore, that this station lent itself to a satisfactory temporal description.

Moreover, present observations were representative of the surrounding lagoon waters, as seen for the following parameters: (1) *Trichodesmium* spp. densities and microplankton abundance at 0.5 m were in a fair agreement at the two stations even though *Trichodesmium* densities became higher out of the bay from February 2005 on. (2) Proportions of the two *Trichodesmium* species or of other microphytoplankton taxa were not significantly different at Sta. SM and O and (3) *Trichodesmium* spp. growth rates, as provided by the  $^{13}\text{C}$  method, were similar at the two stations. All these arguments support the view of a reasonable spatial homogeneity in the sampled area, which is the prerequisite to temporal variation descriptions.

#### 4.2. *Trichodesmium* population characteristics

*Density as compared to other studies.* Trichomes have been observed systematically during the two surveys and appeared to be a component of the usual phytoplankton population, as happens in the GBR where they would occur in 83% of the samples (Jones, 1992). However, they never made the bulk of the phytoplankton at Sta. SM, with their Chl *a* accounting for no more than 21% of the total. Similar contributions were reported by Letelier and Karl (1996) and Dupouy et al. (2000) for the open ocean of the tropical Pacific although higher values (11- 62%) were found in the Atlantic by Carpenter et al. (2004).

Maximum *Trichodesmium* abundances (240 and 244 trich.  $\text{L}^{-1}$  in 2003 and 2004, respectively) reported in this study, are rather modest compared to those found in the literature (Table 5) and this may be explained by differences in both methods and environmental conditions. Use of a 20 $\mu\text{m}$  mesh, trichome transfer from the silk into the sedimentation cell, insufficient trichome sinking

311 (Lugomela et al., 2002) or use of a 5.74 L sampling bottle instead of a net (Chang, 2000) may be  
 312 reasons linked to the methodology. In addition, present results refer to samples at 0.5m while some  
 313 of the reported densities in the literature refer to the very near-surface (i.e. 0m), where much higher  
 314 concentrations could be associated with discoloured waters and accumulations along fronts or  
 315 Langmuir cells. It remains some of the high densities found in literature refer to subsurface maxima  
 316 (e.g. 12-24 m of Carpenter et al., 2004) and not to the very top surface, leading us to look for  
 317 environmental-related reasons. Thus, an element may limit growth of the filamentous cyanobacteria  
 318 and it is probably not dissolved iron, given its very significant concentrations in the SW lagoon,  
 319 ranging between 2 and 5 nM (unpublished data). These values are much above 1 nM, the  
 320 concentration given by Sanudo-Wilhelmy et al. (2003) for areas of non Fe-limited diazotrophy in the  
 321 Atlantic ocean. Phosphorus, however, could be the limiting element of primary production,  
 322 considering that its two possible sources are phosphorus depleted: runoffs from lateritic soils of this  
 323 part of New Caledonia (Tenorio *et al.*, 2005) and exchanges with the surrounding oligotrophic ocean  
 324 (Van Den Broeck et al., 2004). This limitation could explain both the modest trichome density  
 325 maxima and the low Chl *a* ( $< 1 \text{ mg m}^{-3}$ ) concentrations (Fig. 6 and 7). Lastly, the observed positive  
 326 and significant correlation found between trichome and diatom densities ( $r_s = 0.395^{**}$ ;  $n = 41$ )  
 327 would suggest no negative effect of the main component of the microphytoplankton on  
 328 *Trichodesmium*. In conclusion, modest trichome density maxima of the present study might result  
 329 from a combination of different factors, the main one being possibly phosphorus limitation.

330 *Specific composition.* *T. erythraeum* was the dominant species with temporary occurrence of *T.*  
 331 *thiebautii*. The two species have distinct morphometric characteristics and they displayed much  
 332 higher length variations at Sta. SM (Table 3) than those reported by Post et al. (2002) in the Gulf of  
 333 Aqaba: 300 - 800  $\mu\text{m}$  for *T. erythraeum* and 1000 - 2000  $\mu\text{m}$  for *T. thiebautii*.

334 *T. erythraeum* dominance at Sta. SM, as in the GBR lagoon (Jones, 1992; Muslin and Jones,  
 335 2003) or the Tanzanian coast (Lugomela et al., 2002 ; Bryceson and Fay, 1981), the Mississippi  
 336 plume (Eleuterius et al., 1981) or the Bresilian coasts (Satô et al., 1963) might lead to the conclusion

337 it would be found more often in coastal areas than *T. thiebautii*. This seems to be corroborated by  
 338 observations made in the open ocean off the east coast of New Caledonia, where *T. erythraeum*  
 339 makes only 20-25% of the *Trichodesmium* filaments, while *T. thiebautii* and *T. tenue* would make  
 340 40-45% and 30% of the total, respectively (Tenorio, 2006). Actually, each of the two species is able  
 341 to prevail in the open ocean. It is *T. erythraeum* in the Coral Sea and *T. thiebautii* in the Caribbean  
 342 Sea (O'Neil et al., 1996 ), *T. thiebautii* in the Kuroshio area (Saino and Hattori, 1980) and the  
 343 Atlantic (Carpenter et al., 2004), but *T. erythraeum* in the north Indian Ocean (Capone et al., 1998).  
 344 Therefore, it seems unlikely that dominance of the two species would rely on the "hemisphere" as  
 345 suggested by Capone and Carpenter (1999), but rather on physiological and/or environmental  
 346 conditions, such as those prevailing in rather closed coastal areas, that seem to be more appropriate  
 347 to *T. erythraeum*. Such a feature may be explained by a lower diazotrophic capacity of this species  
 348 (Carpenter et al., 1993), which would imply its preference for less oligotrophic areas than *T.*  
 349 *thiebautii*, on the one hand, and by less resistance of its vacuoles to pressure, which means less  
 350 adaptation to deep environments, on the other hand (Carpenter et al., 1993).

351 *Contribution of trichomes in colonies to total.* Most (98%) of the colonies were of the tuft type  
 352 and made of < 20 trichomes, on average. Similar numbers were found for *T. erythraeum* by  
 353 Bryceson and Fay (1981) and Capone et al. (1998) with respectively, 5.5-10 and 10-30 trich. col<sup>-1</sup>.  
 354 But Carpenter et al. (2004), Letelier and Karl (1996) and Post et al. (2002) reported numbers > 100  
 355 for both *T. erythraeum* and *T. thiebautii*.

356 Also variable in the literature is the proportion of the number of aggregated trichomes to total  
 357 number of trichomes, or "bundleness" (Bryceson and Fay, 1981): ratios <20% were observed in the  
 358 North Pacific (Saino and Hattori, 1980 ; Letelier and Karl, 1996) and in the Atlantic (Orcutt et al.,  
 359 2001 ; Tyrell et al., 2003) while bundleness ranged from 25 to 90% off the Tanzanian coast  
 360 (Bryceson and Fay, 1981) and in the tropical Atlantic (Carpenter et al., 2004). Such variability is  
 361 discussed by the latter authors and could originate from damages to the colonies during the sampling  
 362 and sorting processes, too small a sampled volume, and/or a "fundamental difference in the state of



trichomes" between the different regions. Further, Orcutt et al. (2001), Fu and Bell (2003b) and Bell et al. (2005) suggest there would be more of free trichomes during the optimum growth phase, and more aggregation during the non optimum phases. Effect of wind speed and related water turbulence on bundleness is invoked by Bryceson and Fay (1981) and would be negative, although the present work does not support such a view, with bundleness not lower than usual during the windy January 2005 peak. More simply, present observations (Fig. 5) suggest bundleness would follow encounter probability law, i.e. the higher the trichome density, the higher the probability, thus agreeing with the view of Carpenter et al. (2004) of density-related bundleness. But, whatever the factors involved in colony formation, high bundleness seems to be typical of *Trichodesmium* blooms and responsible for higher nitrogen fixation rates (Saino and Hattori 1980; Bryceson and Fay, 1981; Letelier and Karl, 1998; Capone, 2001).

#### 4.3. *Trichodesmium* bloom features: respective roles of growth and ascent

A striking result in the present study and many other publications, is the intensity of *Trichodesmium* density increases, which appear to be inversely related to depth (Table 2): the shallower the level, the greater the increase. Moreover, doubling times  $d'_{A,i}$ , calculated on biovolume increases at 0.5, 3 - 4 and 6-7 m (Table 2), are much shorter than those reported in the literature for growth (Table 6), while  $d'_{A,10}$  at 10 m are in good agreement. From these observations, we conclude  $d'_{A,10}$  mainly result from growth and  $d'_{A,i}$  of shallower depths, result from growth plus another process. The latter is very likely the trichome ascent due to their positive buoyancy, a process which delivers them more or less rapidly to the surface as they grow and which would explain the observed vertical density gradient from the bottom to the surface (Fig. 3 and 4). Inversely, this gradient cannot be ascribed to trichome sinking because microscopic observations showed healthy trichomes at all depths and no or few trichomes were retrieved in sediment traps of the 2003 survey (Le Borgne et al., 2004).

388 *Trichodesmium* positive buoyancy is well known and *T. erythraeum* has been reported more  
 389 buoyant than *T. thiebautii* (Carpenter et al., 1993; Lugomela et al., 2002), which would explain the  
 390 modest increases of February 2005 at 0.5 m when *T. thiebautii* contribution was significant. Such  
 391 positive buoyancy, linked to the presence of gas vesicles (Capone et al., 1997), is different from that  
 392 governing daily up and down vertical motion, with diel variations of the carbohydrate to protein ratio  
 393 (Villareal and Carpenter, 2003).

394 In order to test whether trichome biovolume increases ( $\Delta V_i$ ) observed during the bloom periods,  
 395 resulted from both their net growth ( $G_i$ ) and ascent ( $A_i$ ) from deeper levels and in order to estimate  
 396 the respective contributions of the two processes, we used a simple model. Provided spatial  
 397 heterogeneity is negligible, as compared to temporal variability (see 4.1.), observed  $\Delta V_i$  at depth  $z_i$ ,  
 398 between  $t_0$  and  $t_f$  (see eqn (1)) may be ascribed to the sum of  $G_i$  and  $A_i$ :

$$400 \quad \Delta V_i = V_{f,i} - V_{o,i} = G_i + A_i \leftrightarrow \Delta V_i - (G_i + A_i) = 0 \quad (4)$$

401

402 with  $G_i = \sum_{t=t_0}^{t_f} V_{o,i} e^{g_i t} \Delta t$ ,  $g_i$ , being the exponential net growth rate,  $\Delta t$ , the time interval.

403 Corresponding doubling time,  $d_{A,i}$ , is equal to:  $d_{A,i} = \ln(2)/g_i$ . Now, assuming trichome ascent,  $A_i$ ,  
 404 would proceed at the same pace as growth and  $g_i$  be the same along the water column,  $A_i$  will be the

405 integral of  $G_i$  with depth:  $A_i = \sum_{z=12}^{z_i} G_i \Delta z = \sum_{t=t_0}^{t_f} \sum_{z=12}^{z_i} V_{o,i} e^{g_i t} \Delta t \Delta z$ , where  $\Delta z$  is the difference

406 between two sampled depths and 12 m, the Sta. SM depth.

407 Calculations of  $A_i$  and  $G_i$  have been made for  $z_i = 0.5$  m, with the following  $\Delta z$ : 12-10 m, 10-7  
 408 m, 7-4 m, 4-0.5 m in 2003 and 12-6 m and 6-0.5 m in 2004-2005. We solved equation (4), and  
 409 considered the realism of computed doubling times,  $d_{A,0.5}$  (Table 7). Except for the December 2004  
 410 event,  $d_{A,0.5}$  values (1.82 - 6.45 d) are within the range of the doubling times in the literature (Table  
 411 6) and include the December 2003 biovolume doubling time at 10m,  $d'_{A,10} = 2.9$  d (Table 2). The  
 412 December 2004 low  $d_{A,0.5}$  value (0.53 d) may be ascribed to an underestimated initial biovolume,

413  $V_{0.5}$ , which is used in equation 4. Estimates of  $A_{0.5}$  and  $G_{0.5}$  show that most (87 to 99%) of  
 414 biovolume increase observed at 0.5m ( $\Delta V_{0.5}$ ), would be due to  $A_{0.5}$ . Ascent contribution variability  
 415 might be linked to the mixing intensity of the water column, as illustrated by the windy January 2005  
 416 bloom, which had the lowest ascent contribution (Table 7).

417 In this type of calculation applied to peak periods, the growth rates ( $g_i$ ) varied from one peak  
 418 abundance to another ( $g_{0.5} = 0.11 - 0.38 \text{ d}^{-1}$ ). They varied also between non bloom and bloom  
 419 periods, as illustrated by the carbon-specific growth rates, provided by  $^{13}\text{C}$  uptake measurements.  
 420 Indeed, a ratio of 5.1 - 7.4 (see Results) between bloom and "normal" periods may be computed,  
 421 leading us to the next question: what is the origin of  $g_i$  variations leading to bloom developments?

#### 422 423 *4.4. Causes of bloom developments: favorable conditions and triggers*

424 These may be shared into necessary conditions which allow blooms to occur, and triggers that  
 425 effect  $g_i$ . The latter have been identified as nutrient increases during the 3-7 preceding days for all  
 426 the blooms, which supports observations made by Carpenter and Price (1977), Bell et al. (1999),  
 427 Muslim and Jones (2003) regarding a phosphate effect and Lugomela et al. (2002) about nitrate-  
 428 related blooms. Because diazotrophy is phosphorus-dependent (Sanudo-Wilhelmy et al., 2001; Fu  
 429 and Bell, 2003a; Mills et al., 2004), the role played by SRP in bloom developments seems to be  
 430 obvious. Less straightforward, however, may look the  $\text{NO}_3$  increase effect on diazotrophic  
 431 cyanobacteria growth. In fact, di-nitrogen fixation is usually low or absent when other nitrogenous  
 432 compounds are available since it is high energy demanding and repressed by  $\text{NH}_4$  (Mulholland and  
 433 Capone, 2000; Karl et al., 2002). At Sta SM, very low  $^{15}\text{N}_2$  fixation rates were indeed measured on  
 434 *Trichodesmium* colonies during the March-April 2005 bloom (Le Borgne et al., 2006), suggesting  
 435 most of their nitrogen needs were fulfilled by other compounds. Ammonium and very small  
 436 dissolved organic nitrogen (DON) molecules, which are released or produced by the microbial loop,  
 437 seem to be the best candidates, although such a statement cannot be proved for a lack of  
 438 measurements.

439 Then we get to the following scenario which fits observations at Sta SM. Observed Chl *a*  
 440 increases are very quick responses to NO<sub>3</sub> inputs. Part of the Chl *a* increases may be due to diatoms,  
 441 which have a higher NO<sub>3</sub> uptake capacity than most phytoplankters (Sarhou et al., 2005), and likely  
 442 respond immediately to nutrient inputs and lead to higher concentrations of ammonium and small  
 443 DON molecules through bacterial remineralization and microzooplankton grazing. These are taken  
 444 up eventually by filamentous cyanobacteria with a 3-7 d time-lag between NO<sub>3</sub> increases and  
 445 *Trichodesmium* bloom initiation. The direct relation between *Trichodesmium* and diatom densities  
 446 reported before may therefore be interpreted in this way.

447 The nutrient-related scenario suffers a troubling exception: the most important nutrient increase  
 448 of the two surveys, in January 2005, was followed nor by *Trichodesmium* nor by  
 449 microphytoplankton development, while the whole area was invaded by waters of lower than usual  
 450 salinity. The salinity may not be incriminated *per se*, considering maximum *Trichodesmium* growth  
 451 occurs in the 30 - 37 psu range (Fu and Bell, 2003b; Bell et al., 2005). It may rather indicate  
 452 important terrigenous inputs of suspended sediments and heavy metals and their possible inhibition  
 453 of microphytoplankton (including *Trichodesmium*) growth. Inhibition could proceed through light  
 454 limitation due to a heavy load of suspended particles. No significant increase in turbidity (data not  
 455 shown) was observed, however. Different could be the heavy metals inhibitory effect and Fernandez  
 456 et al. (2006) have shown Fe, Ni, Cr, Co, Mn, Cu and Sr are issued from laterite weathering, and  
 457 carried along from several estuaries, south of Noumea (e.g., La coulee, Fig. 1). There may be also an  
 458 impact of the amount and type of organic matter from terrigenous origin, on the microphytoplankton,  
 459 although this topic has not been documented, yet.

460 Bloom triggers work, provided necessary conditions are met, *i.e.* appropriate iron concentration,  
 461 temperature and wind velocity. As seen above, iron is probably non limiting in the present study, but  
 462 sunny and calm weather conditions may be necessary ones as invoked in the past by many authors  
 463 (Eleuterius et al., 1981; Jones et al., 1992; Sellner, 1997; Lugomela et al. (2002) ; Muslim and  
 464 Jones, 2003 ; Carpenter et al., 2004). However, calm weather is not sufficient a condition because

there may be blooms during long periods of wind, as illustrated by the January 2005 event. Based on this example, when temperature was  $\sim 26^{\circ}\text{C}$ , we conclude that blooms may occur during windy periods, only if sea temperature is above this threshold value, thus confirming the Carpenter and Capone (1992) analysis on bloom conditions. Inversely, below  $26^{\circ}\text{C}$ , a low wind velocity appears to be necessary for bloom development. The minimum temperature for them to occur is  $24^{\circ}\text{C}$  in the present study, which is less than the  $25^{\circ}\text{C}$  threshold of Chen et al. (2003). Combination of wind and temperature effects can be interpreted as the result of two antagonist actions on growth rates, positively correlated to temperature and negatively to wind induced-mixing. It follows that, when temperature reaches a threshold value, its effect on growth will overcome the negative effect of mixing.

#### 4.5. Decline origin

One of the striking points in the two surveys, was the brevity of the bloom decline phase, as for the growing one. Decline may be ascribed to mortality and to a recruitment diminution due to a growth rate slowdown as for any population, even though they might have common origins. In the present study, most blooms ended with very low nutrient concentrations ( $<0.030\ \mu\text{M NO}_3$  at the end of the December 2003 and February 2005 events and  $<0.030\ \mu\text{M SRP}$  for those of February and April 2005), which suggests nutrient exhaustion represents one of the decline causes, as mentioned already by Lenés et al. (2005) and Moutin et al. (2005). This process could reduce growth rates, in a way opposite to the nutrient increase effect described above, or induce mortality through a "Programmed Cell Death" (PCD) pathway (Berman-Frank et al., 2004, 2007). Viral lysis (Ohki, 1999) and PCD, caused by other factors than nutrient depletion, as listed by Berman-Franck et al. (2004), are other possible processes. Inversely, intense grazing is likely excluded, considering the low *Macrosetella* densities that were observed and their lack of relationship with trichome concentrations. But the present observations on trichome ascent and surface accumulation during bloom periods with no obvious sinking or downward migration do not exclude massive destruction

by solar radiation as infra-red or ultra-violet rays, independently of other processes. The solar effect is likely linked to the sea surface agitation, with a more rapid destruction during calm sea and low wind conditions. On the whole, apart from trichome viral lysis or PCD, abrupt decay could be the result of ascent to the very top surface, solar destruction and lack of new trichome formation for nutrient exhaustion.

#### 4.6. *Summary of Trichodesmium bloom dynamics as illustrated by the November - December 2003 event*

A summary of present conclusions on the bloom triggering factors (nutrient concentration increases), necessary conditions (combination of wind and temperature effects) and causes of bloom decay can be illustrated by the Nov-Dec 2003 event. Although it was made of three peak abundances, the following description shows it was only one event (Fig. 6).

An increase in nutrient concentrations was observed on 19 - 21 November for  $\text{NO}_3$  and 17 November for SRP. At that time, water temperature was around  $24^\circ\text{C}$  and development could not start before the wind velocity diminished. This occurred on the 23<sup>rd</sup> and was likely responsible for the observed trichome density and biovolume increase between 21 and 28 November. On 29 November, while temperature was now  $25^\circ\text{C}$ , but still  $< 26^\circ\text{C}$ , the wind started blowing again, which resulted in the first trichome density diminution between 28 November and 3 December. The wind slowed down between 4 and 5 December, allowing another *Trichodesmium* increase with a peak on the 5<sup>th</sup>. Calm weather conditions lasted until the 11<sup>th</sup>, allowing trichome ascent and mortality at 0m with the resulting biovolume decrease at all depths between 5 and 8 December and a small development between 10 and 12 December, once temperature had reached  $26^\circ\text{C}$ . The bloom ended when  $\text{NO}_3$  became exhausted ( $< 0.005 \mu\text{M}$  at 0.5m), i.e. from the 10<sup>th</sup>, on.

## 5. Conclusion

516        Photosynthetic filamentous cyanobacteria of the *Trichodesmium* genus, display the same  
 517 physiological processes as the other co-occurring phytoplankton and have the same requirements. In  
 518 particular, dissolved nutrients are primarily involved in their growth processes. But the present  
 519 surveys have shown major differences, with very steep density variations and changes in the  
 520 cyanobacterial vertical distribution during the blooms, both being the result of the trichome positive  
 521 buoyancy. This characteristic has two consequences: (1) most of the biomass accumulation will  
 522 happen at 0m and not in the water column; (2) once they have reached the very top surface,  
 523 trichomes will remain there, and eventually be destroyed. In addition, because of their toxicity, the  
 524 grazing control of the *Trichodesmium* population appears to be restricted to a few species, like  
 525 harpacticoid copepods (Hawser et al., 1992) and these were not abundant in the studied area. These  
 526 two features of the *Trichodesmium* population dynamics, i.e. effects of positive buoyancy and low  
 527 grazing losses, make it quite different from what happens to the rest of the phytoplankton  
 528 community. Such a statement, however, is based on observations of a *T. erythraeum* dominated  
 529 population, which is known to be more buoyant and less diazotrophic than *T. thiebautii*. Therefore,  
 530 bloom causes and characteristics of *T. thiebautii* populations might be different to some extent and  
 531 would deserve a similar study, related to the toxicity issue, this species being considered as more  
 532 toxic than *T. erythraeum* (Sellner, 1997; Landsberg, 2002).

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## References

- Bell, P.R.F., Elmetri, 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. Mar. Ecol. Prog. Ser. 186, 119-126.
- Bell, P.R.F., Uwins, P.J.R., Elmetri, I., Phillips J.A., Fu, F.X., Yago, A.J.E., 2005. Laboratory culture studies of *Trichodesmium* isolated from the Great Barrier Reef Lagoon, Australia. Hydrobiologia 532, 9-21.
- Berman-Frank, I., Bidle, K. D., Haramaty, L., Falkowski, P., 2004. The demise of the marine cyanobacterium, *Trichodesmium spp.*, via an autocatalyzed cell death pathway. Limnol. Oceanogr. 49, 997-1005.
- Berman-Frank, I., Rosenberg, G., Levitan, O., Haramaty, L., Mari, X., 2007. Coupling between autocatalytic cell death and transparent exopolymeric particle production in the marine cyanobacterium *Trichodesmium*. Environ. Microbiol. doi. : 10.1111/j. 1462-2920.2007.01257.x.
- Binet, D., 1984. Copépodes planctoniques du lagon de Nouvelle-Calédonie: facteurs écologiques et associations d'espèces. Mar. Biol. 82, 143-156.
- Bryceson, I., Fay, P., 1981. Nitrogen fixation in *Oscillatoria (Trichodesmium) erythraea* in relation to bundle formation and trichome differentiation. Mar. Biol. 61, 159-166.
- Capone, D. G., Carpenter, E. J., 1999. Nitrogen fixation by marine cyanobacterium : historical and global perspectives. Bull. Inst. Océanogr. Monaco 19, 235-256.
- Capone, D. G., Zehr, J. P., Paerl, H. W., Bergman, B., Carpenter, E. J., 1997. *Trichodesmium*, a globally significant marine cyanobacterium. Science 273, 1221-1229.



- Capone, D. G., Subramaniam, A., Montoya, J. P., Voss, M., Humborg, C., Johansen, A. M., Siefert, R. L., Carpenter, E. J., 1998. An extensive bloom of N<sub>2</sub>-fixing cyanobacterium *Trichodesmium erythraeum* in the central Arabian Sea. Mar. Ecol. Prog. Ser. 172, 281-292.
- Carpenter, E. J., Price, C. C., 1977. Nitrogen fixation, distribution, and production of *Oscillatoria* (*Trichodesmium*) spp. in the western Sargasso and Caribbean Seas. Limnol. Oceanogr. 22, 60-72.
- Carpenter, E.J., Romans, K., 1991. Major role of the cyanobacterium *Trichodesmium* in nutrient cycling in the North Atlantic ocean. Science 254, 1356-1358.
- Carpenter, E. J., Capone, D. G., 1992. Nitrogen fixation in *Trichodesmium* blooms. In: Carpenter, E. J., Capone, D. G., Rueter, J. G. (Eds.), Marine Pelagic cyanobacteria: *Trichodesmium* and other Diazotrophs. Kluwer Academic Publishers, Dordrecht, pp. 211-217.
- Carpenter, E. J., Carmichael, W. W., 1995. Taxonomy of Cyanobacteria,. In: Hallegraeff, G. M., Anderson, D. M., Cembella, A. D. (Eds), Manual on Harmful marine algae. UNESCO, Paris, pp. 373-380.
- Carpenter, E. J., O'Neil, J. M., Dawson, R., Capone, D. G., Siddiqui, P. J. A., Roenneberg, T., Bergman, B., 1993. The tropical diazotrophic phytoplankter *Trichodesmium* : biological characteristics of two common species. Mar. Ecol. Prog. Ser. 95, 295-304.
- 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 Res. I 51, 173-203.
- Chang, J., 2000. Precision of different methods used for estimating the abundance of the nitrogen-fixing marine cyanobacterium, *Trichodesmium* Ehrenberg. J. Exp. Mar. Biol. Ecol. 245, 215-224.
- Chen, Y-B. L., Chen, H-Y., Lin, Y-H., 2003. Distribution and downward flux of *Trichodesmium* in the South China Sea as influenced by the transport from the Kuroshio Current. Mar. Ecol. Prog. Ser. 259, 47-57.

- Dupouy, C., Neveux, J., Subramaniam, A., Mulholland, M. R., Montoya, J. P., Campbell, L., Carpenter, E. J., Capone, D. G., 2000. Satellite captures *Trichodesmium* blooms in the southwestern tropical Pacific. *Eos* 81, 15-16.
- Eleuterius, L., Perry, H., Eleuterius, C., Warren, J., Caldwell, J., 1981. Causative analysis on a nearshore bloom of *Oscillatoria erythraea* (*Trichodesmium*) in the Northern Gulf of Mexico. *Northeast Gulf Science* 5, 1 -11.
- Fernandez, J-M., Ouillon, S., Chevillon, C., Douillet, P., Fichez, R., Le Gendre, R., 2006. A combined modelling and geochemical study of the fate of terrigenous inputs from mixed natural and mining sources in a coral reef lagoon (New Caledonia). *Mar. Pollut. Bull.* 52, 320-331.
- Fu, F.-X., Bell, P. R. F., 2003a. Factors affecting N<sub>2</sub> fixation by the cyanobacterium *Trichodesmium* sp. GBRTLI101. *FEMS Microbiol. Ecol.* 45, 203-209.
- Fu, F.-X., Bell, P. R. F., 2003b. Effect of salinity on growth, pigmentation, N<sub>2</sub> fixation and alkaline phosphatase activity of cultured *Trichodesmium* spp. *Mar. Ecol. Prog. Ser.* 257, 69-76.
- Hawser, S.P., O'Neil, J.M., Roman, M.R. Codd, G.A., 1992. Toxicity of blooms of the cyanobacterium *Trichodesmium* to zooplankton. *J. Applied Phycol.* 4, 79-86.
- Janson, S., Siddiqui, P. J. A., Walsby, A.E., Romans, K.M., Carpenter, E. J., Bergman, B., 1995. Cytomorphological characterization of the planktonic diazotrophic cyanobacteria *Trichodesmium* spp. from the Indian Ocean and Caribbean and Sargasso Seas. *J. Phycol.* 31, 463-477.
- Jones, G. B., 1992. Effect of *Trichodesmium* blooms on water quality in the Great Barrier Reef Lagoon,. In: Carpenter, E. J., Capone, D. G., Rueter, J. G. (Eds.), *Marine Pelagic Cyanobacteria: Trichodesmium and other Diazotrophs*. Kluwer Academic Publishers, Dordrecht, pp. 273-287.

- Jones, G.B., Burdon-Jones, C., Thomas, F.G., 1982. Influence of *Trichodesmium* red tides on trace metal cycling at a coastal station in the Great Barrier Reef Lagoon. *Oceanol. Acta Special Publication*, 319-326.
- Jouon, A., Douillet, P., Ouillon, S., Fraunié, P., 2006. Calculations of hydrodynamic time parameters in a semi-opened coastal zone using a 3D hydrodynamic model. *Cont. Shelf Res.* 26, 1395-1415.
- Karl, D., Michaels, A., Bergman, B., Capone, D. G., Carpenter, E.J., Letelier, R., Lipschultz, F., Paerl, H., Sigman, D., Stal, L., 2002. Dinitrogen fixation in the world's oceans. *Biogeochemistry* 57/58, 47-98.
- Landsberg, J.H., 2002. The effects of harmful algal blooms on aquatic organisms. *Rev. Fish. Sci.* 10, 113-390.
- Le Borgne, R., Faure, V., Raimbault, P., Rodier, M., 2004. Suivi de l'abondance de *Trichodesmium* spp. (cyanobactéries filamenteuses) et des paramètres du milieu lagunaire en Baie de Sainte-Marie (Nouméa, Nouvelle-Calédonie): 7 octobre - 19 décembre 2003. *Arch. Sc. Mer IRD/Nouméa* 6, 1-50.
- Le Borgne, R., Mazzeo, I., Raimbault, P., Rodier, M., Rouchon, C., 2006. Suivi de *Trichodesmium* spp. (cyanobactéries filamenteuses) et des paramètres du milieu lagunaire en baie de Sainte-Marie, Nouméa, Nouvelle-Calédonie. 3 novembre 2004 - 12 avril 2005. *Arch. Sc. Mer IRD/Nouméa* 8, 1-55.
- Le Bouteiller, A., Blanchot, J., Rodier, M., 1992. Size distribution patterns of phytoplankton in the western Pacific: towards a generalization for the tropical ocean. *Deep-Sea Res* 39, 803-823.
- Lenes, J.M., Walsh, J.J., Otis, D.B., Carder, K.L., 2005. Iron fertilization of *Trichodesmium* off the west coast of Barbados: A one-dimensional numerical model. *Deep-Sea Res. I* 52, 1021-1041.
- Letelier, R. M., Karl, D. M., 1996. Role of *Trichodesmium* spp. in the productivity of the subtropical North Pacific Ocean. *Mar. Ecol. Prog. Ser.* 133, 263-273.

- 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.
- Mills, M. M., Ridame, C., Davey, M., La Roche, J., Geider, R. J., 2004. Iron and phosphorus co-limit nitrogen in the tropical North Atlantic. *Nature* 429, 292-294.
- Moutin, T., Van Den Broeck, N., Beker, B., Dupouy, C., Rimmelin, P., Le Bouteiller, A., 2005. Phosphate availability controls *Trichodesmium* spp. biomass in the SW Pacific Ocean. *Mar. Ecol. Prog. Ser.* 297, 15-21.
- Mulholland, M. R., Capone D. G., 2000. The nitrogen physiology of the marine N<sub>2</sub>-fixing cyanobacterium *Trichodesmium* spp.. *Trends Plant Sci.* 5, 148-153.
- Mulholland, M. R., Bernhardt, P. W., 2005. The effect of growth rate, phosphorus concentration, and temperature on N<sub>2</sub> fixation, carbon fixation, and nitrogen release in continuous cultures of *Trichodesmium* IMS 101. *Limnol. Oceanogr.* 50, 839-849.
- Murphy, J., Riley, J.P., 1962. A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta* 26, 31-36.
- Muslim, I., Jones, G.B., 2003. The seasonal variation of dissolved nutrients, chlorophyll *a* and suspended sediments at Nelly Bay, Magnetic Island. *Estuar. Coastal Shelf Sci.* 57, 445-455.
- Negri, A.P., Bunter, O., Brian, J., Llewellyn, L., 2004. Effects of the bloom-forming alga *Trichodesmium erythraeum* on the pearl oyster *Pinctada maxima*. *Aquaculture* 232, 91-102.
- Ohki, K., 1999. A possible role of temperate phage in the regulation of *Trichodesmium* biomass. *Bull. Inst. Océanogr. Monaco* 19, 287-291.
- O'Neil, J. M., Roman M. R., 1994. Ingestion of the cyanobacterium *Trichodesmium* spp. by pelagic harpacticoid copepods *Macrosetella*, *Miracia* and *Oculosetella*. *Hydrobiologia* 292/293, 235-240.

- O'Neil, J.M., Metzler, P.M., Glibert, P.M., 1996. Ingestion of  $^{15}\text{N}_2$ -labeled *Trichodesmium* spp. and ammonium regeneration by the harpacticoid copepod *Macrosetella gracilis*. Mar. Biol. 125, 89-96.
- Orcutt, K. M., Lipschultz, F., Gundersen, K., Arimoto, R., Michaels, A. F., Knap, A. H., Gallon, J. R., 2001. A seasonal study of the significance of  $\text{N}_2$  fixation by *Trichodesmium* spp. at Bermuda Atlantic Time-series Study (BATS) site. Deep-Sea Res. II 48, 1583-1608.
- 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., Mar. Ecol. Prog. Ser. 239, 241-250.
- Prufert-Bebout, L., Paerl, H.W., Lassen, C., 1993. Growth, nitrogen fixation and spectral attenuation in cultivated *Trichodesmium* species. Appl. Environ. Microbiol. 59, 1367-1375.
- 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, Mar. Biol. 104, 375-351.
- Revelante, N., Gilmartin, M., 1982. Dynamics of phytoplankton in the Great Barrier Reef Lagoon. J. Plankton Res. 4, 47-76.
- Riedel, G.F., J. G. Sanders, Breitburg, D. L., 2003. Seasonal Variability in Response of Estuarine Phytoplankton Communities to Stress: Linkages between Toxic Trace Elements and Nutrient Enrichment. Estuaries 26, 323-338.
- Roman, M.R., 1978. Ingestion of the blue-green algae *Trichodesmium* by the harpacticoid copepod, *Macrosetella gracilis*. Limnol. Oceanogr. 23, 1245-1255.
- Saino, T., Hattori, A., 1980. Nitrogen fixation by *Trichodesmium* and its significance in nitrogen cycling in the Kuroshio area and adjacent waters. In: Takenouti, A.Y. (Ed), The Kuroshio. Saikon Publishing, Tokyo, pp. 697-709.

- Sanudo-Wilhelmy, S. A., Kustka, A. B., Gobler, C. J., Hutchins, D. A., Yang, M., Lwiza, K., Burns, J., Capone, D. G., Raven, J. A., Carpenter, E. J., 2001. Phosphorus limitation of nitrogen fixation by *Trichodesmium* in the central Atlantic Ocean. *Nature* 411, 66-69.
- Sarthou, G., Timmermans, K. R., Blain, S., Tréguer, P., 2005. Growth physiology and fate of diatoms in the ocean: a review. *Journal of Sea Research* 53, 25-42.
- Satô, S., Paranagua, M.N., Eskinazi, E., 1963. On the mechanism of red tide of *Trichodesmium* in Recife, northeastern Brazil, with some considerations of the relation to the human disease "Tamandare fever". *Trab. Inst. Oceanogr. Univ. Recife* 6/7, 7-49.
- Sellner, K.G., 1997. Physiology, ecology and toxic properties of marine cyanobacteria blooms. *Limnol. Oceanogr* 42, 1089-1104.
- Snedecor, G.W., Cochran, W.G., 1967. Statistical methods, 6th ed.. Iowa State Univ. Press.
- Strickland, J., Parsons, T., 1972. A practical handbook of seawater analysis, Fish Res. Bd Can. Bul. 167.
- Tenório, M. M. B., Le Borgne, R., Rodier, M., Neveux, J., 2005. The impact of terrigenous inputs on the Bay of Ouinné (New Caledonia) phytoplankton communities : a spectrofluorometric and microscopic approach. *Estuar. Coastal Shelf Sci.* 64, 531-545.
- Tenório, M. M. B., 2006. Les cyanobactéries pélagiques en milieu tropical oligotrophe: occurrence, distribution et dynamique. Univ. Paris VI Thesis, 1-359.
- Trottet, A., 2003. Biodiversité des cyanobactéries filamenteuses du genre *Trichodesmium* dans l'océan Pacifique tropical sud-ouest. Mémoire DEA Univ. Paris VI, 1-26.
- Tyrell, T., Maranon, E., Poulton, A. J., Bowie, A. R., Harbour, D. S., Woodward, E. M. S., 2003. Large-scale latitudinal distribution of *Trichodesmium* spp. in the Atlantic Ocean. *J. Plankton Res.*, 25, 405-416.
- 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. *Mar. Ecol. Prog. Ser.* 268, 1-12.

Villareal, T. A., Carpenter, E. J., 2003. Buoyancy regulation and potential for vertical migration in the oceanic cyanobacterium *Trichodesmium*. Microb. Ecol., 45, 1-10.

## Tables

Table 1

Main characteristics of the five *Trichodesmium erythraeum* blooms (\* denotes presence of *T. thiebautii*).

Period	Number of peaks	Difference in time evolution at 6 and 0.5 m	Total duration (d)	Maximum at 0.5 m (trich. L <sup>-1</sup> )	Maximum at 6-7 m (trich. L <sup>-1</sup> )
24 Nov - 14 Dec 2003	3	No	18	238.7	47.4
13 - 20 Dec 2004*	1	at 6m, 2 d before	7	244.6	20.7
3 - 14 Jan 2005	1	No	11	81.5	14.8
4 - 18 Feb 2005*		No	14	10.1	19.4
29 Mar - 7 Apr 2005	1	at 6m, 4 d before	9	156.5	44.3



Table 2

Exponential net increase rates ( $k_i$  in  $d^{-1}$ ) and corresponding doubling times ( $d'_{A,i}$  in d) in parentheses, from changes in *Trichodesmium* population biovolume, at different depths (equations 1 and 2).

2003	<i>T. erythraeum</i>				2004-2005	<i>T. erythraeum</i>		<i>T. thiebautii</i>	
	10m	7m	4m	0.5m		6m	0.5m	6m	0.5m
24-30 Nov		0.36 (1.9)	0.43 (1.6)	0.36 (1.9)	13-12 Dec	0.39 (1.8)	3.29 (0.2)	1.51 (0.5)	2.20 (0.3)
3-9 Dec	0.24 (2.9)	0.68 (1.0)	0.61 (1.1)	0.72 (1.0)	3-14 Jan	0.98 (0.7)	1.13 (0.6)		
11-14 Dec			0.15 (4.6)	0.40 (1.7)	4-18 Feb	0.19 (3.7)	0.52 (1.3)	0.23 (2.9)	0.94 (0.7)
					29 Mar - 4 Apr	0.67 (1.0)	0.59 (1.2)		

Table 3

Sizes of *T. erythraeum* and *T. thiebautii* during the 2003 and 2004-2005 surveys at Sta SM. Means  $\pm$  standard deviations, and range (in parenthesis) of size parameters for  $n$  observations.

		Width ( $\mu\text{m}$ )	Length ( $\mu\text{m}$ )	Volume ( $10^3 \mu\text{m}^3$ )
<i>T. erythraeum</i>				
2003	0.5m - 10 m	$11.0 \pm 0.6$	$477 \pm 190$	$45.3 \pm 20.7$
	$n = 2612$	(5.5 - 22.0)	(56-1489)	(5.3-426.1)
2004-2005	0.5m - 6 m	$10.5 \pm 1.4$	$550 \pm 344$	$48.4 \pm 34.8$
	$n = 6362$	(5.5 - 22.0)	(60 - 2675)	(4.1 - 448.6)
<i>T. thiebautii</i>				
2003	0.5m – 10m	$11.3 \pm 2.3$	$822 \pm 499$	$67.1 \pm 26.0$
	$n=8$	(8.2 - 16.5)	(440 -2031)	(25.6 - 96.9)
2004-2005	0.5m – 6m	$5.7 \pm 1.0$	$847 \pm 440$	$22.0 \pm 16.4$
	$n = 1618$	(5.5 - 11.0)	(57 – 3386)	(1.3 - 186.4)

Table 4

*Trichodesmium* carbon, nitrogen and chlorophyll *a* content of the 2004-2005 survey: means, standard deviations (sd) and ranges.

	Per colony			Per trichome			Ratio	
	Chl <i>a</i>	C	N	Chl <i>a</i>	C	N	C/N	C/Chl <i>a</i>
	(ng)	( $\mu$ g)	( $\mu$ g)	(ng)	(ng)	(ng)	(mol/mol)	(g/g)
Mean $\pm$ sd	7.84 $\pm$ 5.16	1.25 $\pm$ 0.29	0.20 $\pm$ 0.12	0.44 $\pm$ 0.26	103.1 $\pm$ 36.1	16.8 $\pm$ 5.7	6.2 $\pm$ 0.8	265.1 $\pm$ 161.5
Range	2.41 – 14.9	0.79 – 1.57	0.15 – 0.39	0.17 – 0.92	61.5 – 191.0	10.7 – 28.0	4.6 – 7.4	87.0 – 486.5

Table 5

*Trichodesmium* spp. densities (as trich. L<sup>-1</sup>) literature review (Note: references considering colony abundance are not presented. Specific difference between *T. erythraeum* (§) and *T. thiebautii* (\*) are reported when available. m: mean value; max: maximum value.

Region	Depth	Density	Author(s)
Sargasso and Caribbean seas	0 m (range) 15-200 m (range)	0-49* 0-294*	Carpenter and Price (1977)
Kuroshio (Japan)	0-100 m (max)	40 – 50000	Saino and Hattori (1980)
Great Barrier Reef lagoon	bloom (max)	50,000	Revelante and Gilmartin (1982)
Cleveland Bay (Australia)	inshore "blooms" (m) offshore "blooms" (m)	8515§ 3300§	Jones (1992)
HOT Station (Hawaii)	0-45 m (range)	11 – 84	Letelier and Karl (1996)
Southwest tropical Pacific	0 m - Fiji (max) 0 m New Caledonia ( max)	10,000 1000	Dupouy et al. (2000)
Tanzania coast	0 m "bloom" (range) 0 - 20 m (range)	38,000 - 120,000§ 0 - 63,000§	Lugomela et al. (2002)
Gulf of Aqaba	0-90 m (range)	0.05 - 2	Post et al. (2002)
South China Sea	0 m (m, range)	77 (0 - 962)	Chen et al. (2003)
Magnetic island (Australia)	surface (range) 15 m (m)	9 - 102,000 13,000	Muslim and Jones (2003)
North and South Atlantic	7 m (m) (max)	300 2200	Tyrell et al. 2003
Dampier Archipelago (Australia)	0-20 m (m)	1800§	Negri et al. (2004)
North tropical Atlantic	"surface" (m) "surface", peak period (m)	222 – 292* 2250 (up to 10867)*	Carpenter et al. (2004)
Bay of Ouinné (New Caledonia)	0 - 45 m (m)	0.7 - 17§ ; 0.6 – 29*	Tenório et al. (2005)
Loyalty channel (New Caledonia)	0 - 60 m (range)	0 - 1011§ ; 4 – 2450*	Tenorio (2006)
Bay of Sainte Marie (New Caledonia)	0.5 m (range) 6 m (range)	0 - 240§ ; 0 – 34* 0 - 47§ ; 0 – 18*	Present study

Table 6

Literature review of *Trichodesmium* carbon-specific doubling times (d).

Reference	Conditions	Temperature (°C)	Doubling time (d)
Carpenter and Romans (1991)	natural populations, tropical -subtropical Atlantic	26.5 - 28	1.8 - 18
Carpenter and Capone (1992)	Review	>27	3 - 6
Carpenter et al. (1993)	natural populations <i>T. erythraeum</i>	26.5 - 28	3.8
	<i>T. thiebautii</i>		3.0
Prufert-Bebout et al. (1993)	Cultures		3.0*
Mulholland and Capone (2000)	Cultures		2.2
	natural populations		3.8 - 198
Orcutt et al. (2001)	natural populations, Bermuda		2
Bell et al. (2005)	Cultures	25 ± 3	2.3 – 3.5
Mulholland and Bernhardt (2005)	continuous culture	28	3 - 10
Le Borgne et al. (2006)	natural populations, bloom, Bay of Ste Marie,	27 - 29	4.1 - 5.8
	<i>idem</i> , non-bloom conditions	27 - 29	13.9 - 40.8

\* inferred from their 0.23 division d<sup>-1</sup> growth rate

Table 7

Values of the trichome exponential net growth rate ( $g_{0.5}$ ) and their corresponding doubling time ( $d_{A, 0.5}$ ) satisfying equation 4, for  $z = 0.5$  m. Percent contributions of net growth ( $G_{0.5} / \Delta V_{0.5}$ ) and ascent from deeper levels ( $A_{0.5} / \Delta V_{0.5}$ ) to observed biovolume increases at 0.5 m,  $\Delta V_{0.5}$ .

Period	$g_{0.5}$ ( $d^{-1}$ )	$d_{A, 0.5}$ (d)	$A_{0.5} / \Delta V_{0.5}$ (%)	$G_{0.5} / \Delta V_{0.5}$ (%)
24-28 Nov 2003	0.18	3.86	87.3	12.5
3-5 Dec 2003	0.38	1.82	97.6	2.4
10-12 Dec 2003	0.12	5.57	87.3	12.6
13-15 Dec 2004	1.32	0.53	98.2	1.8
3-5 Jan 2005	0.11	6.45	87.0	13.0
25 Mar - 4 Apr 2005	0.17	4.14	98.9	1.1

### Figure captions

Fig. 1. Sampling station locations at the entrance (Sta. SM) and off (Sta. O) the Bay of Ste Marie.

Fig. 2. *Trichodesmium* abundance as trichome numbers versus biovolume during the 2003 and 2004-2005 surveys. Slopes (b) of the linear regressions are :  $b = 44240$  in 2003 and  $b = 45084$  in 2004-2005, respectively.

Fig. 3. Temporal variations in *T. erythraeum* biovolume at Sta. SM four sampled depths, during Survey I (2003). Note : *T. thiebautii* densities, contributing for <1% of the total, have not been represented on the figure.

Fig. 4. Temporal variations in *T. erythraeum* and *T. thiebautii* biovolume at Sta SM two sampled depths, during Survey II (2004-2005). Less frequent observations were made at Sta. O, 0.5 m

Fig. 5. Relationships between trichome in colony (y) and free trichome (x) densities during the 2003 and 2004-2005 surveys.

Fig. 6. Temporal variations of environmental variables and *Trichodesmium* spp. densities at Sta. SM during Survey I. Temperature and salinity refer to the 1 m depth. Nitrate ( $\text{NO}_3$ ), Soluble Reactive Phosphorus (SRP) and chlorophyll *a* (Chl *a*) concentrations are averaged through the 0-12 m water column, wind velocities, on 24 h. Significant rainfall ( $>10\text{mm d}^{-1}$ ) are indicated by vertical arrows. *Trichodesmium* spp. abundances are integrated over 10m.

Fig.7. Same as Fig. 3, but for Survey II.

Fig. 8. *Trichodesmium* peak amplitude versus nitrate concentration at the beginning of the five blooms.

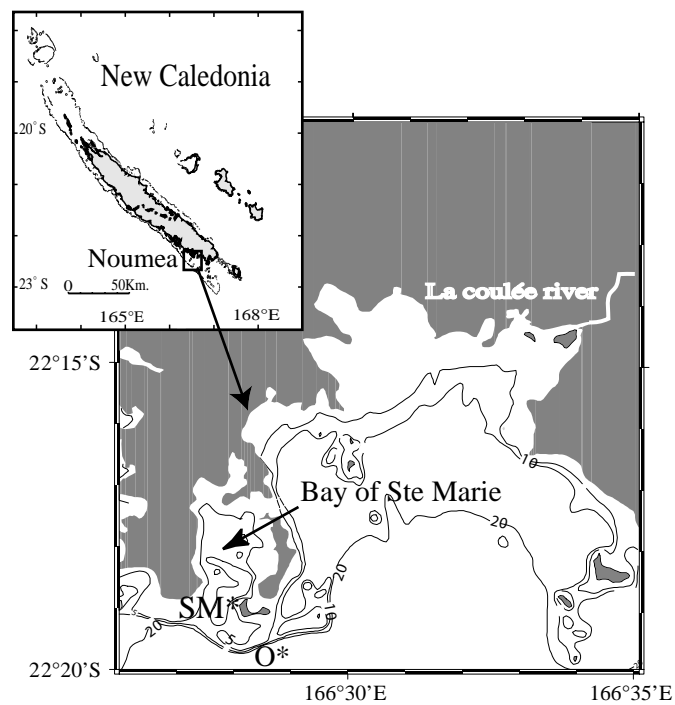


Fig. 1



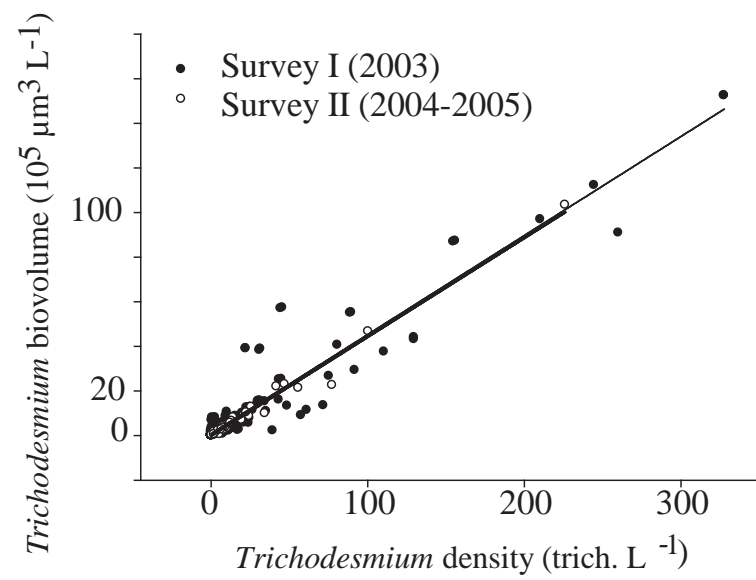


Fig. 2

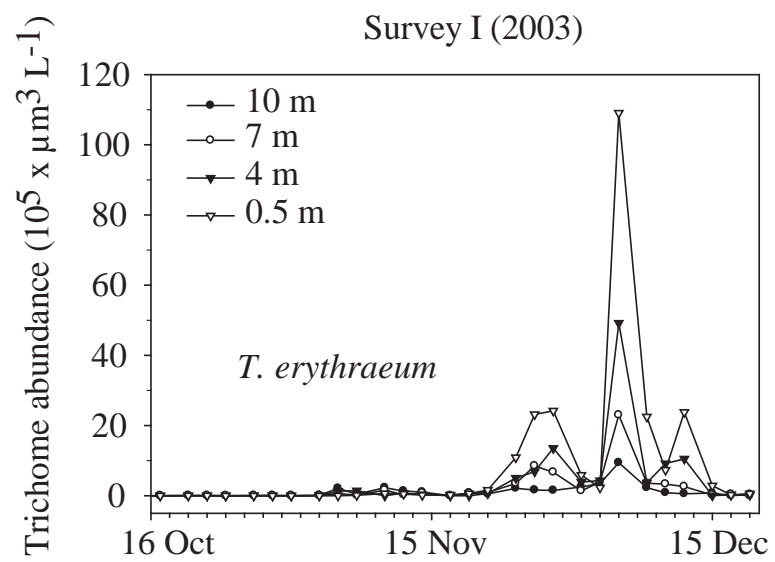


Fig. 3

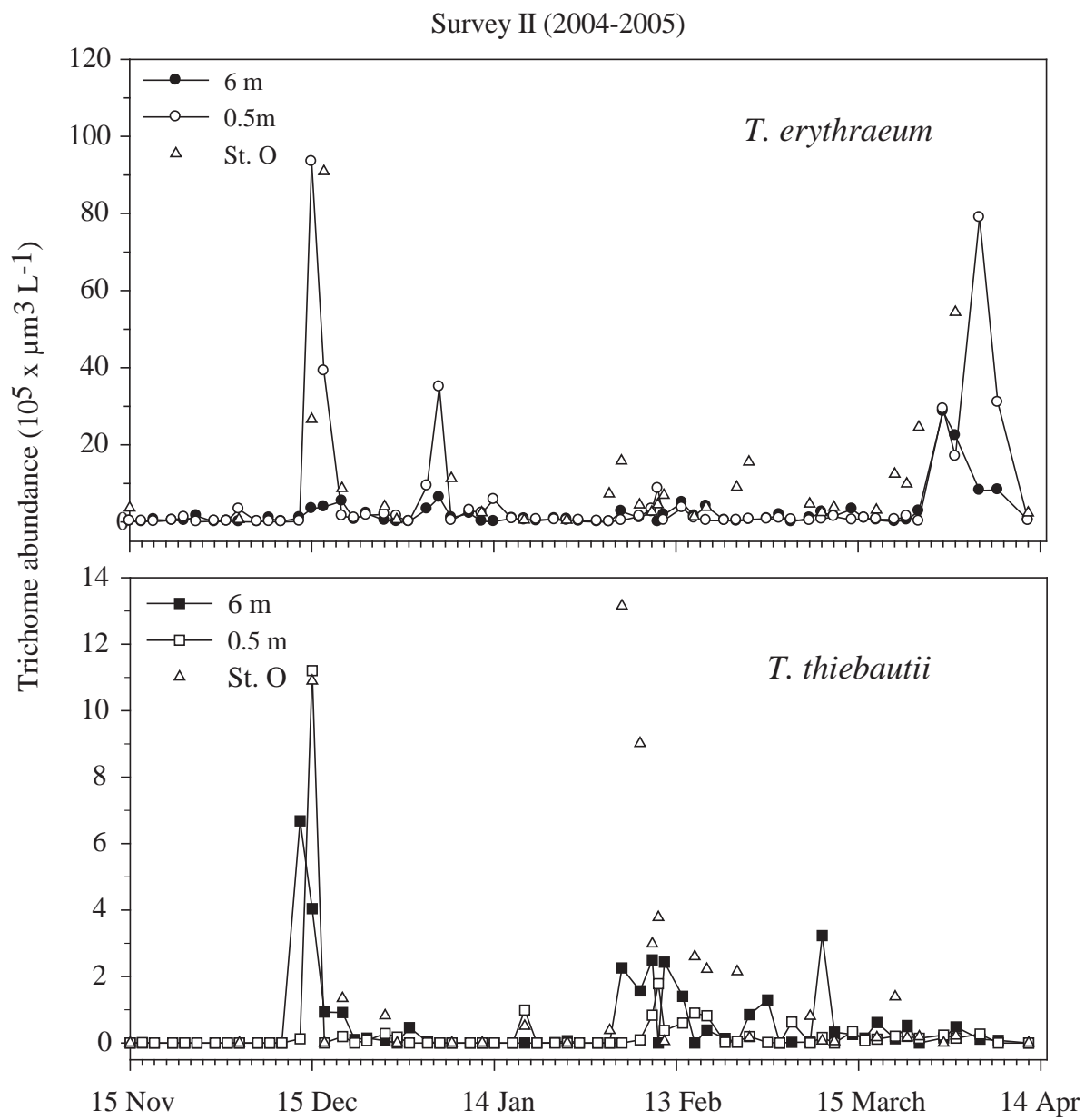


Fig. 4

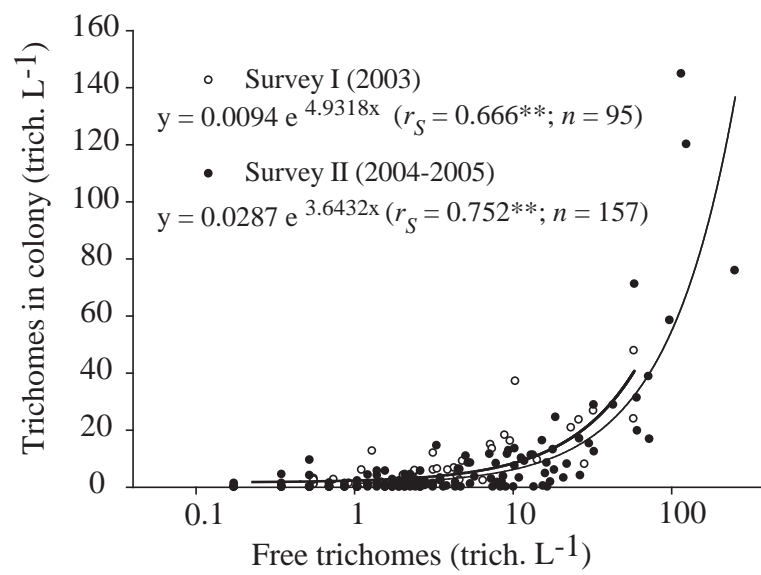


Fig. 5

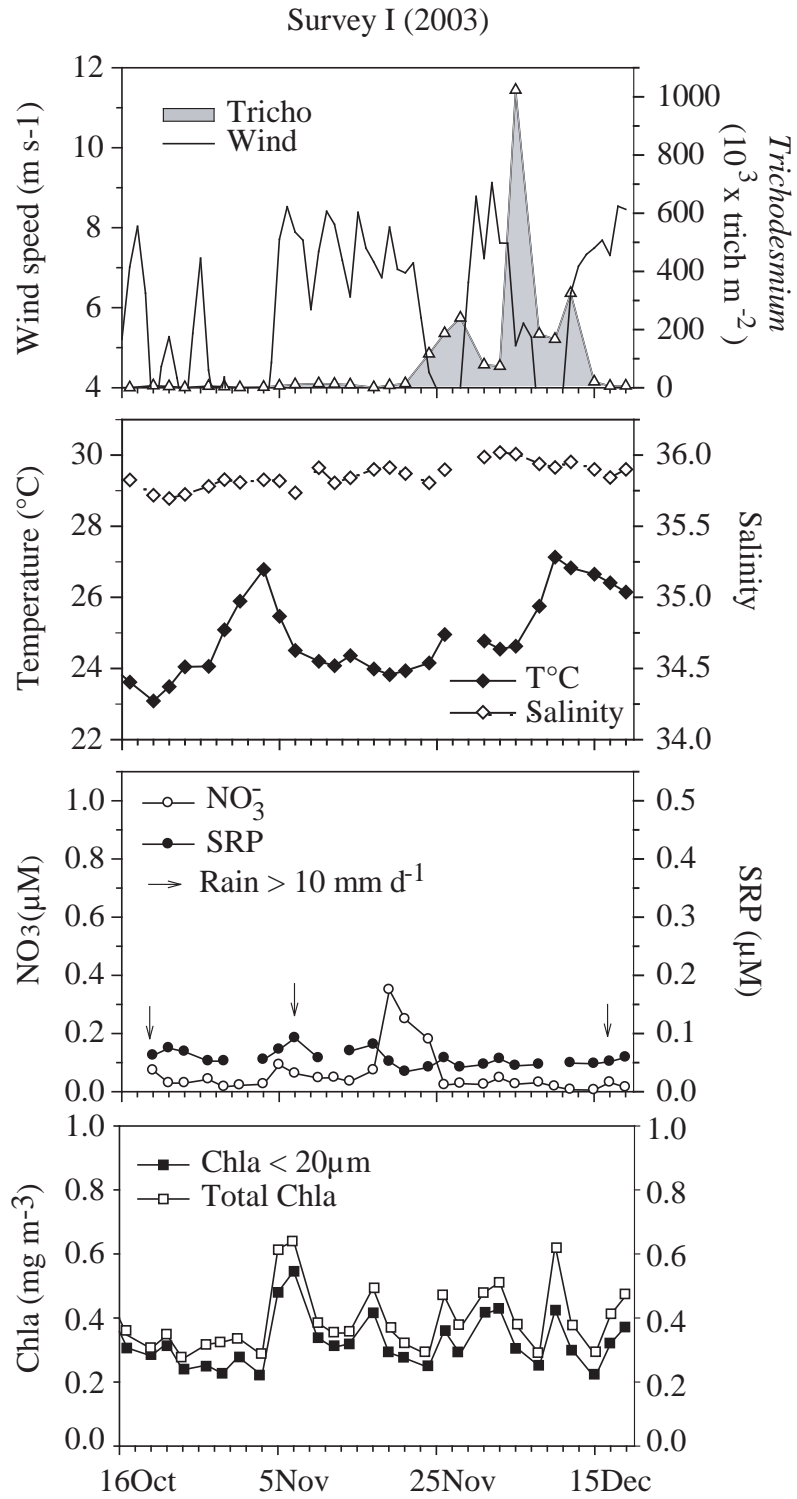


Fig.6

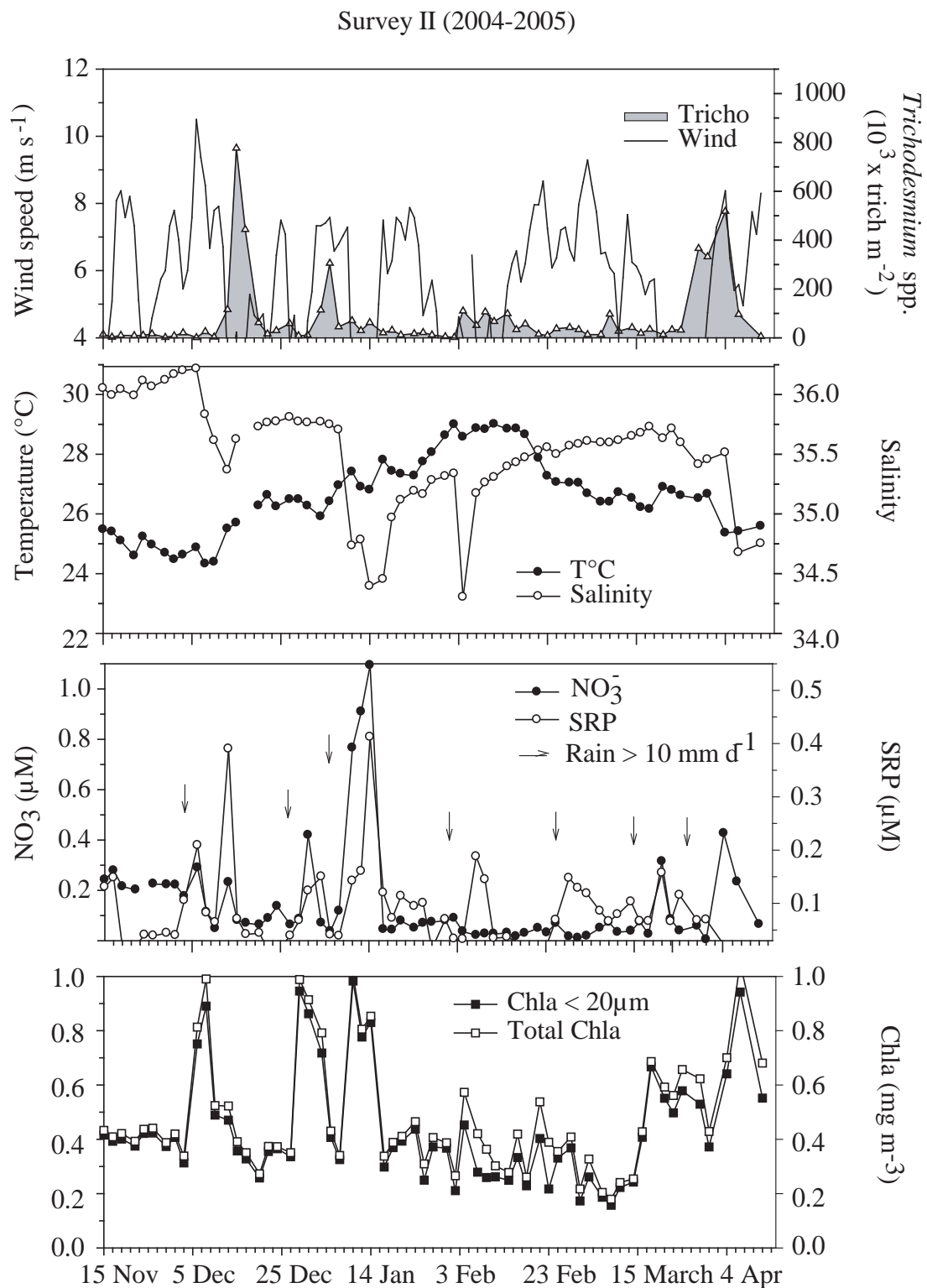


Fig. 7

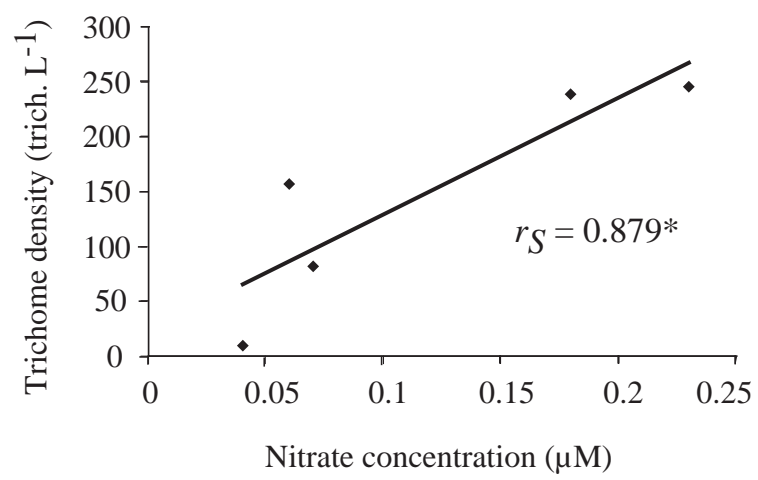


Fig. 8