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1 **Trichodesmium and other Planktonic Cyanobacteria in New Caledonian**  
2 **waters (South West Tropical Pacific) during an El Niño Episode**

3  
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23 KEY WORDS : *Trichodesmium*, Filamentous cyanobacteria, community structure,  
24 microscopy, picoplankton, pigments, Loyalty Islands, New Caledonia, coral-reef lagoon, ENSO

25  
26 ABSTRACT. Contributions of filamentous and picoplanktonic cyanobacteria to the  
27 phytoplankton community structure were examined in New Caledonian waters during the 2001-  
28 2003 El Niño period at three stations. Morphometric characteristics of diazotrophic filamentous  
29 cyanobacteria are given as well as the seasonal and inter-annual variations of their surface areas  
30 and integrated abundances. *Trichodesmium tenue* and *T. thiebautii* were the dominant species  
31 followed by *T. erythraeum*, altogether accounting for more than 51-80 % of the biomass of the  
32 free-living filamentous cyanobacteria. *Katagnymene* spp. accounted for a smaller percentage  
33 (<13.8 % at ocean stations, <3.6 % in the lagoon). *R. intracellularis* biomass was relatively small  
34 (<1 % of total surface area and volume of *Trichodesmium* trichomes) with the highest

35 concentration observed in summer (735 trichomes l<sup>-1</sup>). Colonies of unidentified cyanobacteria  
36 composed of spherical cells accounted on average for <1 % of the *Trichodesmium* biomass, with  
37 values exceeding 4000 cells l<sup>-1</sup>. Abundance of filamentous cyanobacteria varied according to  
38 environmental factors, with summer 2001-2002 characterized by low filamentous diazotroph  
39 abundance and summer 2003, occurring at the peak of the 2001-2003 El Niño, particularly rich  
40 in filamentous cyanobacteria (with a maximum *Trichodesmium* spp abundance of 4500 trichomes  
41 l<sup>-1</sup> in the Loyalty Channel). A similar variability pattern was observed for large diatoms and  
42 dinoflagellates, and for all picoeukaryotic populations. Different biomass estimators are provided  
43 as cell abundances, pigment concentrations including chlorophylls and phycoerythrin, and carbon  
44 content. The filamentous communities dominated in summer in oceanic waters while  
45 *Synechococcus* and picoeukaryote communities dominated in lagoon waters in winter at all  
46 stations.

47

## 48 INTRODUCTION

49

50 In the Oceans, most of the subtropical and tropical pelagic areas are dominated by  
51 oligotrophic conditions and picophytoplankton, which are best adapted to nutrient-poor  
52 environments (Buitenhuis et al. 2012a, Luo et al. 2012). Unicellular picoplanktonic cyanobacteria  
53 are certainly the most abundant photosynthetic group and distributed throughout the tropical  
54 Pacific Ocean (Le Bouteiller et al. 1992, Ishizaka et al. 1994, Buitenhuis et al. 2012b). Other  
55 marine cyanobacteria, comparatively patchier and less abundant, also play a pivotal role in N-  
56 limited ecosystems, combining primary production and dissolved N<sub>2</sub> fixation (diazotrophy). This  
57 cyanobacterial diazotrophic community includes unicellular, filamentous, and symbiotic forms  
58 (Luo et al. 2012, Bergman et al. 2013). Pelagic filamentous cyanobacteria consist mainly of the  
59 *Trichodesmium* genus with two more frequently reported and quantified species: *T. erythraeum*  
60 Ehrenberg and *T. thiebautii* Gomont. Three other *Trichodesmium* species (*T. tenue* Wille, *T.*  
61 *contortum* Wille and *T. hildebrandtii* Gomont), and two *Katagnymene* species (*K. pelagica* and  
62 *K. spiralis* Lemmerman) are more scarcely reported. Furthermore, *Richelia intracellularis* has  
63 been regarded as one of the main tropical filamentous diazotrophs in marine pelagic waters  
64 forming large blooms in some regions as parts of Diatom-Diazotrophic Associations (DDAs).  
65 This heterocystous cyanobacterium is usually observed as an endosymbiont of the *Rhizosolenia*  
66 (sometimes referred as Het1 or RR) and *Hemiaulus* (Het-2 or HR) (Venrick 1974, Janson et al.

67 1999) diatoms and has also been reported as an epiphyte of *Chaetoceros* spp. (Gómez et al. 2005)  
68 or a free-living filament. The epiphytic form was identified as a separate species, *Calothrix*  
69 *rhizosoleniae*, based on genetic characterization (Janson et al. 1999, Foster et al. 2010). It has  
70 also been reported in cohabitation with *Trichodesmium* puff-form colonies (Jabir et al. 2013,  
71 Momper et al. 2015, Giraud et al. 2016). Besides *Trichodesmium* and other filamentous  
72 cyanobacteria, free-living unicellular cyanobacteria (UCYN-A, -B, and -C) are also recognized  
73 as possible major diazotrophs in tropical and subtropical areas (Zehr & Bombar 2015), occupying  
74 different ecological niches.

75 N<sub>2</sub> fixation by filamentous cyanobacteria in the oceans is estimated at around 80 Tg N per  
76 year (Capone et al. 1997) for a global oceanic N<sub>2</sub> fixation of 100-200 Tg N per year (Karl et al.  
77 2002) and accounts for more than 70 % of global marine N<sub>2</sub> fixation (Luo et al. 2012, Bergman  
78 et al. 2013). The Southern Tropical Pacific is a region known for high N<sub>2</sub> fixation, as measured  
79 between New Caledonia and Vanuatu (Garcia et al. 2007, Masotti et al. 2007, Biegala et al. 2014),  
80 over a longitudinal transect at 17°S (Shiozaki et al. 2014) and in the lagoon (Biegala & Raimbault  
81 2008, Bonnet et al. 2016). Surface blooms are frequently observed in the region, mainly  
82 composed of filamentous cyanobacteria (Dupouy et al. 2011).

83 Identification and counts of filamentous cyanobacteria at the species level are nevertheless  
84 scarce (Campbell et al. 2005, Luo et al. 2012) as recent work relies only on *Nifh* gene counts  
85 (Moisander et al. 2010, Bonnet et al. 2015, 2016). Moreover, few studies address their temporal  
86 variability as reported at HOT in the Northern Pacific (Letelier & Karl 1996), BATS in the  
87 Northern Atlantic (Orcutt et al. 2001), and in the Indian Ocean (Lugomela et al. 2002).

88 By quantifying the different species abundances and their specific relationship with nutrient  
89 and physical environmental conditions, it should be possible to more precisely identify the main  
90 factors stimulating filamentous cyanobacterial growth and how they affect the community  
91 structure. Such data are essential for estimating global N<sub>2</sub> fixation more accurately, improving  
92 our understanding of how N<sub>2</sub> fixing species respond to their environment, and anticipating how  
93 the phytoplankton community will develop in the context of global climate change (Dutkiewicz  
94 et al. 2015, Gruber 2016). *In situ* abundance of filamentous cyanobacteria and their content in  
95 pigment are also needed to calibrate recent bio-optical models aiming to determine their  
96 abundance from light reflectance of surface mats (Dupouy et al. 2011, Gower et al. 2014,  
97 McKinna 2015) or medium concentration blooms (Westberry & Siegel 2006, De Boissieu et al.,  
98 2014).

99 A careful study of the seasonal and inter-annual variations of different filamentous  
100 cyanobacteria species abundances was undertaken in 2001-2003 (Diapalis program) in New  
101 Caledonian waters and tentatively analyzed based on changes in environmental conditions and in  
102 the abundance of other components of the autotrophic community, particularly picoplankton. For  
103 this paper, data were obtained at three stations: an open-ocean station (Loyalty Channel), a large,  
104 deep and open bay (Santal Bay, Lifou Island) and a lagoon station (Ouinne, southeast coral reef  
105 lagoon). Taxonomic identification, measurements and counts of filamentous species were carried  
106 out by microscopy while data on picoplankton were analyzed by flow cytometry. The various  
107 estimators for determining filamentous cyanobacterial biomass were also compared. Nutrient  
108 data (Van Den Broeck et al. 2004, Moutin et al. 2005) and all N<sub>2</sub> fixation rates measured under  
109 the Diapalis program had been published earlier (Garcia et al. 2007).

110

## 111 MATERIAL AND METHODS

112

113 **Sampling and environmental data.** Nine oceanographic cruises (Diapalis program: D1 to D9)  
114 lasting about a week each were conducted between October 2001 and October 2003 aboard IRD's  
115 R.V. *Alis* between 165°E and 168 °E and between 20°S and 23°S in the Eastern Coral Sea (Table  
116 1, Fig 1). Samples were taken at three stations: the first at 167°30'E 20°30'S in the deep Santal  
117 Bay which is broadly exposed to the ocean, on Lifou Island's west coast (bottom depth: 1050 m,  
118 ST1), the second in open ocean waters in the middle of the Loyalty Channel at 21°30'S 167°E  
119 (bottom depth: 2000 m, ST2), and the third (166°45'E 21°57'S) in the south eastern coral-reef  
120 lagoon of New Caledonia (bottom depth: 40 m, ST3). The sampling covered different seasons  
121 (Table 1): summers 2002 (D2 to D4) - 2003 (D7), winters 2002 (D6) - 2003 (D8) and transition  
122 periods (D1, D5, D9). A sample was also collected from a surface accumulation of  
123 *Trichodesmium erythraeum* located in New Caledonia's southwestern lagoon.

124 During cruises, CTD casts were carried out at each station with water sampling down to 200 m  
125 for the deepest stations and down to 30 m in the lagoon. Temperature (T°C) and salinity were  
126 measured with Sea-Bird SBE 911 and water samples were collected with 8L-Niskin bottles  
127 attached to a CTD-rosette system. Nitrate + nitrite (NO<sub>x</sub>) and phosphate (PO<sub>4</sub><sup>3-</sup>) were preserved  
128 in Nalgene bottles with HgCl<sub>2</sub> prior colorimetric assays on a Technicon autoanalyzer II  
129 (Raimbault et al. 1990). Ammonium was measured immediately on board by fluorometry (Turner  
130 Design TD-700) according to the procedure described in Holmes et al. (1999). More details on

131 the methods and the full data set Diapalis are available on <http://www.obs->  
132 [vlfr.fr/proof/vt/op/ec/diapazon/dia.htm](http://www.obs-vlfr.fr/proof/vt/op/ec/diapazon/dia.htm). The mixed layer depth (MLD) was estimated by taking  
133 the first depth where potential density ( $\sigma_t$ ) was  $0.03 \text{ Kg m}^{-3}$  greater than the density at 10  
134 meters, based on Montegut et al. (2004).

135  
136 **Filamentous cyanobacteria counting and morphometric characteristics.** Filamentous  
137 cyanobacteria were recovered from water samples taken at 4-6 depths down to 80 m, with a  
138 rosette of 8L Niskin bottles. Organisms were collected by filtering whole water bottles through a  
139  $10 \mu\text{m}$  Nuclepore polycarbonate membrane. The filter was then placed in a 20 mL glass bottle  
140 containing a 4 % formalin solution for preserving photosynthetic organisms. In the laboratory,  
141 the filter was rinsed with a plastic wash bottle containing filtered seawater in order to remove all  
142 the organisms from the filter and collect them in a 100 mL glass cylinder. After processing, the  
143 filter was checked for any remaining photosynthetic organisms. A suitable quantity of an acidic  
144 formalin solution (1/1 mixture of 40 % formalin and acetic acid) was then added to obtain  
145 organisms in a final 0.4 % formalin solution. From this solution, filamentous cyanobacteria and  
146 other large phytoplanktonic species were measured and enumerated with an inverted microscope  
147 (OLYMPUS IM.,  $100\times$  magnification) using a standard sedimentation technique (Utermöhl  
148 1931). According to Cronberg et al. (2004), the acetic acid breaks the gas vesicles facilitating the  
149 sedimentation of filaments in the sedimentation chambers. Sedimentation time was 24 hours in 5  
150 and 10 mL chambers and at least 48 hours for the 25 and 50 mL chambers, depending on cell and  
151 filament abundances. A total of 88 samples were examined for the 9 cruises. For surface  
152 accumulations of *Trichodesmium erythraeum*, samples were collected directly by hand with a  
153 small bottle (500 mL), which was then processed using the same method as described above.

154 Identification of the filamentous *Trichodesmium*, *Katagnymene* (see review in Bergman et  
155 al. 2013) and *Richelia* (Foster et al. 2010) was carried out based on their morphological  
156 characteristics. Cell shape and dimensions (particularly cell diameter) were the main criteria used  
157 for classifying and identifying them. The sample processing method used to facilitate  
158 enumeration and morphometric examination at trichome level could not be used for observations  
159 at colony level, because most of them had disintegrated. Trichome surface and volume were then  
160 calculated on the assumption that they had an elongated cylindrical morphology. For *T.*  
161 *erythraeum* and *T. thiebautii*, identification was confirmed by molecular biology studies (unp.  
162 data). Colonies of unidentified cyanobacteria composed of spherical cells were also observed and

163 enumerated.

164 **Photosynthetic pigment analysis by spectrofluorometry.** Chlorophylls including divinyl-chl *a*  
165 and *b* for *Prochlorococcus* were measured by spectrofluorometry (F4500 HITACHI  
166 spectrofluorometer) based on Neveux & Lantoine (1993) and Tenório et al. (2005). From 0.25 to  
167 0.5 L, water samples were filtered on 25 mm GF/F for the chlorophylls analysis in the total  
168 community. Chlorophylls were extracted in 90 % acetone after grinding the GF/F filter.  
169 Measurements in the >10 µm fraction of the community were also carried out by filtering a whole  
170 8L Niskin bottle through 47 mm Nuclepore polycarbonate membranes. In the latter case,  
171 chlorophylls were extracted in 90 % Dimethylformamide (DMF) without grinding the membrane.  
172 For convenience's sake, the abbreviations Chla, DV-Chla and TChla were used for monovinyl-  
173 chlorophyll a, divinyl-chlorophyll a and the sum of these two pigments (total chlorophyll a)  
174 respectively. Concentrations of cyanobacteria phycoerythrin (PE) were assessed by  
175 spectrofluorometry both on the overall and >10 µm community, after extraction/cell resuspension  
176 in a 50/50 mixture of glycerol/phosphate buffer based on Wyman (1992). 1 to 3 L water samples  
177 were filtered through 47 mm 0.4 µm polycarbonate membranes for total PE and 8L onto 10 µm  
178 membranes for size-fractionated PE. Details of the PE spectrofluorometric analysis are given in  
179 Lantoine & Neveux (1997), Neveux et al. (1999) and Neveux et al. (2006).

180

181 **Picoplankton and nanoplankton analysis by flow cytometry.** Subsamples (1 mL) were stored  
182 in cryovials, and fixed with paraformaldehyde (0.2 % final concentration, Campbell & Vaultot  
183 1993) and frozen in liquid nitrogen for a period of less than three months before flow cytometry  
184 analyses. Samples were counted on a Becton Dickinson FACSCan flow cytometer. For each cell,  
185 forward and side light scattering as well as red and orange fluorescence were quantified. The light  
186 signals were calibrated using 1.002 µm fluorescent beads (Polysciences Inc., Europe) as a  
187 reference. Four prevalent populations were distinguished and enumerated according to their  
188 scattering and fluorescence properties. Two of them belonged to picoplanktonic cyanobacteria,  
189 *Prochlorococcus* and *Synechococcus*, and two were eukaryotic groups, the smallest being deemed  
190 picoeukaryotes. Unicellular nanoplanktonic cyanobacteria such as *Crocospaera*, easily  
191 recognized by the fluorescence excitation spectra of their phycoerythrin and by their flow  
192 cytometric signature (Neveux et al. 1999), were not observed during the Diapalis cruises.

193 **Carbon biomass estimation.** Information on the relative size of each population within the total  
194 autotrophic biomass of the ecosystem was obtained by converting cell numbers into carbon units.

195 Conversion factors [ $\text{fg C cell}^{-1}$ ] for *Prochlorococcus* (36), *Synechococcus* (255) and  
196 picoeukaryotes (2590) were used according to Buitenhuis et al. (2012b) and for *Richelia* (10) from  
197 Luo et al. (2012). For all filamentous cyanobacteria, the carbon conversion factor determined in  
198 this study on *Trichodesmium erythraeum* was applied ( $17.22 \text{ ng C trichome}^{-1}$ ; see Table 8). The  
199 integrated carbon content of each group and their relative percentages were calculated for the  
200 upper layer (0-60 m ST1 and ST2, 0-30 m at ST3). Note that diatoms and dinoflagellates in the  
201  $>10 \mu\text{m}$  fraction were not included in the analysis, since mean cell size or cell volume was not  
202 determined.

203

## 204 **RESULTS**

205

### 206 **Environmental conditions during the 9 Diapalis cruises**

207

208 The New Caledonia region (Fig. 1) is typical of the tropical regime in the South West  
209 Tropical Pacific with clear-air temperature and precipitation seasonality (Fig. 2). The Diapalis  
210 period (2001-2003) coincided with the 2002-2003 El Nino build-up, with a first period (2001)  
211 marked by a Neutral Multivariate El Nino Index (MEI) and the second (2003) by a stronger  
212 positive MEI, indicative of a strong Central Pacific El Nino during D7-D9 (Fig. 2). On New  
213 Caledonia's east coast, precipitations were more abundant during summer 2001-2002, with a  
214 peak of cumulative rain in January-March 2002, while summer 2003 was drier, except for the  
215 passage of Tropical Storm Beni, which crossed the area just before the February 2003 cruise.  
216 Beni reached peak intensity on January 29 with winds of 125 mph (205 km/h), before rapidly  
217 weakening, and dissipating on February 5. It brought heavy precipitation and floods lasting 6  
218 days.

219 During the austral summer, seawater temperature increased to  $27 \text{ }^{\circ}\text{C}$  at ST1 and ST2 and  
220 up to  $28^{\circ}\text{C}$  in the lagoon at ST3 (Fig. 3, left panel), leading to a vertical stratification and the  
221 formation of a pronounced thermocline (Fig. 4). During the winter, cooling of surface waters  
222 induced vertical mixing in the water column at least down to the deepest sampling level, e.g. 90-  
223 100 m in Aug 02 at ST2. Minimum temperatures in the upper layer were  $23.4 \text{ }^{\circ}\text{C}$  at ST1 and ST2  
224 and  $22.8 \text{ }^{\circ}\text{C}$  at ST3. The highest salinities (around 35.4) were measured in Oct 03 at all three study  
225 sites, and the lowest during the wet summer season, in Apr 02 (from 34.47 at ST3, close to the  
226 mouth of the Ouinne River to 34.86 at ST1). Mean salinities were similar at ST1 and ST2 stations,



227 but lower in summer 2002 than summer 2003, due to different precipitation regimes linked to the  
228 El Nino episode (Fig. 2). Mean phosphate ( $\text{PO}_4^-$ ) concentrations in the upper layer (Fig. 3, right  
229 panel) were weak throughout the sampling period, reaching maximum values of 0.06-0.12  $\mu\text{mol}$   
230  $\text{l}^{-1}$  in Oct 01 and Oct 03 during the transition periods and the minimum of 0.02  $\mu\text{mol l}^{-1}$  in summer.  
231 A small increase was observed in winter in Aug 02 due to a deepest MLD (Fig. 4). In wide Santal  
232 Bay (ST1),  $\text{NO}_x$  concentrations were also very low, except in Aug 02, when they reached 0.08  
233  $\mu\text{mol l}^{-1}$ , linked to the deep winter mixing. The upper layer waters at ST2 oceanic station were  
234  $\text{NO}_x$  poor with concentrations always  $<0.06 \mu\text{mol l}^{-1}$  (Fig. 3), even during deep vertical winter  
235 mixing as in Aug 02. Small maxima (0.05  $\mu\text{mol l}^{-1}$ ) were observed in Oct 03 as in Feb 03 despite  
236 warmer, saltier waters. At ST3 lagoon station, the  $\text{NO}_x$  concentrations varied from 0.01 to a  
237 maximum of 0.07  $\mu\text{mol l}^{-1}$  in Jan 02.  $\text{NH}_4^+$  concentrations (data not shown) at ST1 and ST2 were  
238 generally low  $<0.04 \mu\text{mol l}^{-1}$  and often close to the detection limit 0.01  $\mu\text{mol l}^{-1}$ . Higher  
239 concentrations were observed only in Feb 03 at both stations (0.11 and 0.19  $\mu\text{mol l}^{-1}$  at ST1 and  
240 ST2, respectively). In the lagoon, concentrations were on average slightly higher: up to 0.30  $\mu\text{mol}$   
241  $\text{l}^{-1}$ .

242

### 243 **Filamentous cyanobacteria**

244 **Specific composition:** Five species of the *Trichodesmium* genus were observed (Fig. 5-6) and  
245 identified by their morphology and morphometric characteristics (Table 2). Three of them, *T.*  
246 *erythraeum*, *T. thiebautii* and *T. tenue* (Fig. 5A, B, H) were the most frequently observed at all  
247 three sampling sites. *T. contortum* was seldom observed (3 samples). *Katagnymene* (Fig. 5E, F,  
248 G) and *Richelia/Calothrix* (Fig. 6) genera were common (in 50 % and 75 % of samples,  
249 respectively), but generally in low abundance. *Richelia* was observed as an endosymbiont of  
250 *Rhizosolenia* and *Hemiaulus* and *Calothrix* as an epibiont on *Chaetoceros sp.* During the May  
251 02 cruise, west of Lifou, we observed unidentified filaments very similar to *Trichodesmium*, but  
252 differing in their very small cellular diameter (2.7-3  $\mu\text{m}$ ). We also observed colonies of  
253 unidentified cyanobacteria (Fig. 5C, D), which formed clusters sometimes made up of several  
254 dozen cells. All filamentous species during Diapalis had dimensions (cell length and cell  
255 diameter) within the range published in the literature (Table 3 and 8) and the sizes of *T.*  
256 *thiebautii* and *T. erythraeum* species were in the low part of the size range.

257 ***Trichodesmium* and *Katagnymene* abundance:** At ST1 and ST2, the highest abundances of  
258 filamentous cyanobacteria in the 0-60 m upper layer were noted in summer (Feb 03; Fig. 7), i.e.

259 3000-4500 trichomes l<sup>-1</sup> and 1000-3000 trichomes l<sup>-1</sup> between 5 and 10 m, respectively. However,  
260 the concentrations and vertical distribution could be highly variable from one day to another, as  
261 shown at ST1 in Feb 03 (Fig. 7). Some vertical profiles showed maximum concentrations at 40  
262 m as at ST2 (mostly due to *T. erythraeum*). Vertical distributions were quite homogeneous at the  
263 period of low abundance, i.e. in the austral winter (Aug 02 and Jun 03). At ST3 (Fig. 7),  
264 concentrations did not exceed 1000 trichomes l<sup>-1</sup>. Tables 4 to 6 give general statistics on the  
265 abundances of the different filamentous cyanobacteria enumerated by inverted microscopy  
266 during Diapalis cruises 1-9 for each station. Filamentous cyanobacteria were extremely rare in  
267 Oct 03 regardless of depth.

268 Assuming that *Trichodesmium* can migrate vertically within one day (Villareal & Carpenter  
269 2003), using integrated abundance seemed more appropriate for gauging their seasonal variations  
270 in the water column (Fig. 4). Thus, at ST2, 0-60 m integrated abundance showed a 500-fold  
271 variation between minimum in Oct 03 (<0.5 10<sup>6</sup> trichomes m<sup>-2</sup>) during the transition periods and  
272 maximum in summer (Feb 03: 235 10<sup>6</sup> trichomes m<sup>-2</sup>). At ST1, the seasonal variations appeared  
273 similar but the variation range (x 150) and the maximum summer concentrations (73 10<sup>6</sup> trichomes  
274 m<sup>-2</sup>) were lower than at ST2. At both stations, maximum abundance in summer 2003 was  
275 coincident with a shallow MLD, but low abundances were also observed in summer 2002 with a  
276 similar thermohaline structure. At ST3 station (Fig. 4), integrated concentrations (0-30 m only)  
277 were 15 times lower and varied from 0.9 10<sup>6</sup> trichomes m<sup>-2</sup> to 13.5 10<sup>6</sup> trichomes m<sup>-2</sup>, although  
278 ST3 was not sampled in Feb 03.

279 The three main *Trichodesmium* species together accounted for 85-100 % of the integrated  
280 biomass of filamentous cyanobacteria in terms of trichome numbers and always more than 51 %  
281 in terms of trichome volume (Fig. 8). *Trichodesmium tenue* and *T. thiebautii* were generally the  
282 dominant species followed by *T. erythraeum*. Their mean cell numbers per trichome were  
283 relatively similar (Table 7). As expected, the percentage contribution of slender *T. tenue* was  
284 higher in terms of total trichome number than total volume (40-49 % vs 33 %). Its percentage  
285 contribution (trichome numbers) was minimum at ST2 in Feb 03 (23 %) and maximum (>70 %)  
286 in Dec 01 at ST2 and ST3. *T. thiebautii* reached >40 % of the total trichome number in 65 % of  
287 the samples with minimal contributions in Dec 01 and May 02 at ST2 (<14 %) and a fairly stable  
288 one at ST1 and ST3 (37-47 %).

289 In terms of volumes, *T. thiebautii* contributions (reaches 50 % at ST2) were more variable,  
290 linked to a trichome length changes along the annual cycle. The third main species, *T.*

291 *erythraeum*, represented less than 18 % of total trichomes on average, with the minimum  
292 contribution at ST3 (<7 %) and maximum at ST1 and ST2 in Feb 03 during the peak abundance  
293 (Tables 4 to 6). Its relative importance increased as expressed in volume, especially in Feb 03 at  
294 the two open ocean stations (22-28 %). *T. contortum* and *T. hildebrandtii* (given as “others” in  
295 Fig. 8), contributed <3 % to total trichome number or volume. The unidentified trichomes  
296 observed in May 02 further north than ST2 represented less than 1 % of the integrated biomass.

297 The two *Katagnymene* species (*K. spiralis* and *K. pelagica*) were not numerous, but their  
298 contribution in terms of volume was significant. Each form accounted for less than 4 % of the  
299 total number of trichomes, except *K. spiralis* at ST1 in Oct 01 (10 %). *K. spiralis* was observed  
300 in 50 % of samples. Its highest contributions to the total volume of trichomes occurred at ST1 in  
301 Oct 01 (28 %) and Feb 03 at ST2 (12 %). The contribution of *K. pelagica* was around 20 % of  
302 the total volume in Feb 03 at ST1 and ST2, 15 % at ST2 in Oct 01, and was not observed at  
303 ST3. The relative abundance of species could change along depth. For example, during cruises  
304 D4 and D5 (Apr-May 02), *T. thiebautii* and *T. tenue* were numerous in the upper layer (60 %)  
305 and disappeared at 50 meters while *T. erythraeum* peaked at this depth. Obviously, the relative  
306 abundance depends on the biomass criteria considered. For example, at ST2 in Apr 02, *T.*  
307 *erythraeum* contributions at 30 to 50 m decreased in terms of trichome number (6 %) but  
308 increased (41 %) in terms of total volume, because trichome size increased. The opposite trend  
309 was observed for *T. thiebautii*.

310  
311 ***Richelia intracellularis/Calothrix rhizosolenia (RC) from DDAs and unidentified***  
312 ***cyanobacteria abundance:*** *RC* (Tables 4 to 6) were observed in 75 % of samples, but their  
313 abundance was never very high. The highest *RC* abundances were recorded in Feb 03 at both  
314 ST1 and ST2 (64 trichomes l<sup>-1</sup> and up to 735 trichomes l<sup>-1</sup>, respectively), accounting for less than  
315 1 % of total *Trichodesmium* trichome surface area and volume. Conversely, at ST3, peak  
316 abundance was observed for *R. intracellularis* in Oct 01 (up to 117 trichomes l<sup>-1</sup> at the surface)  
317 equivalent to 4.3 % of *Trichodesmium* trichome volume. In our samples, *RC* in DDAs  
318 experienced a considerable variation in filament length (10-88 µm) and cell diameter (vegetative  
319 cells 2-7 µm; heterocyst 3-10 µm) or trichomes per host cell (1-22). We also noted that in most  
320 cases, the host cell was almost empty. Apart from *Richelia*, other symbiotic coccoid-form  
321 cyanobacteria (not necessarily diazotrophs) were also observed in *Climacodium* sp. and  
322 *Ornithocercus* sp., though only in the New Caledonian lagoon.

323 Colonies of unidentified cyanobacteria composed of round-shaped cells observed in some  
324 samples reached less than 1 % of *Trichodesmium* biomass on average (Tables 4 to 6, Fig 5C, D).  
325 The highest concentrations were observed at ST2 during Jan 02 and May 02 with values exceeding  
326 4000 cells l<sup>-1</sup>, which was equivalent to less than 1.6 % of *Trichodesmium* trichome volume. At  
327 ST1, these organisms were rarely observed and only at very low concentrations, i.e. <20 cells l<sup>-1</sup>.  
328 At ST3 they were observed only in Jan 02 with a maximum value at 10 m of 429 cells l<sup>-1</sup>. Tracking  
329 *Crocospaera* (2-10 µm cell size) by flow cytometric and phycoerythrin signatures was  
330 unsuccessful during Diapalis although it has been reported in the region (Saito et al. 2010 and  
331 references therein). However, Diapalis samples showed relatively high N<sub>2</sub> fixation in the <10 µm  
332 fraction, particularly in Oct 03 (Garcia et al. 2007), but it was not possible to link this fixation to  
333 specific organisms or biomass indicators.

334

335

### Abundance of other phytoplankton groups

336

337 **Picoplankton abundance:** *Prochlorococcus* concentrations at ST1 and ST2 (Tables 4-5 and Fig.  
338 9A) was maximum (10-13 10<sup>12</sup> cells m<sup>-2</sup>) during the warm season (Dec 01-Apr 02 and in Feb 03).  
339 During transition periods, concentrations were lower by a factor of 3 with 3.5-3.9 10<sup>12</sup> cells m<sup>-2</sup>  
340 at ST2 (Oct 01 and Oct 03, respectively), while at ST1 the minimum concentration (4.5 10<sup>12</sup> cells  
341 m<sup>-2</sup>) was observed during winter. At these two oceanic stations, the vertical distribution of  
342 *Prochlorococcus* was quite similar, with a marked maximum below the thermocline (40-80 m)  
343 in summer and a more homogeneous distribution down to 60-80 m in winter. At ST3,  
344 *Prochlorococcus* abundance was much lower than at the oceanic stations, with values <2.3 10<sup>12</sup>  
345 cells m<sup>-2</sup> through 0-30 m (max 70 10<sup>3</sup> cells ml<sup>-1</sup>), except in Dec 02 when they reached 4.8 10<sup>12</sup>  
346 cells m<sup>-2</sup> (max 225 10<sup>6</sup> cells ml<sup>-1</sup> at depth).

347 Unlike *Prochlorococcus*, integrated abundance of *Synechococcus* (Tables 4 to 6, Fig. 9B),  
348 was on average 5 to 14 times higher at the lagoon station (ST3) than offshore (ST1 and ST2),  
349 except during the austral winter (Aug 02) when they were 24 % higher in oceanic waters at ST2  
350 (1.91 10<sup>12</sup> cells m<sup>-2</sup>). This winter maximum was linked to thoroughly-mixed cool waters down to  
351 >60 m. The maximum *Synechococcus* abundance at the oceanic stations was generally located  
352 shallower than that of *Prochlorococcus*, i.e. in the upper mixed layer or at the top of the  
353 thermocline, except during the Oct 03 cruise when it peaked at the same depth (between 75 and  
354 110 m).

355 Picoeukaryotes were the least abundant picoplankton organisms (Tables 4 to 6, Fig. 9C).  
356 Integrated abundances were more variable at ST2 (factor 6; 0.02 to 0.12  $10^{12}$  cells  $m^{-2}$ ) than at  
357 ST1 (0.07 to 0.14  $10^{12}$  cells  $m^{-2}$ ). At ST3, integrated abundances changed from 0.08 to 0.17  $10^{12}$   
358 cells  $m^{-2}$ . Picoeukaryote maxima were consistently found below the thermocline and, therefore,  
359 deeper than the *Synechococcus* maxima, even in Aug 02.

360

361 **Large eukaryotes:** Large eukaryotes ( $>10$   $\mu m$ ) described by microscopy and made up of  
362 dinoflagellates and diatoms (Fig. 10) were generally found together with *Trichodesmium* in open  
363 ocean waters at ST1 and ST2 and, to a lesser extent, at ST3 coastal site. Dinoflagellates showed  
364 a maximum of 60  $10^6$  cells  $m^{-2}$  during the maximum *Trichodesmium* abundance in Feb 03 at ST1  
365 and ST2 and low abundance ( $<30$   $10^6$  cells  $m^{-2}$ ) at other periods. Diatoms also showed a maximum  
366 concentration (412  $10^6$  cells  $m^{-2}$ ) in Feb 03 at ST2 and, to a lesser extent, at ST1. At ST3 coastal  
367 site, no data were available in Feb 03, but there was a considerable maximum for both groups (17  
368  $10^6$  cells  $m^{-2}$  for dinoflagellates; 240  $10^6$  cells  $m^{-2}$  for diatoms) in winter (Aug 02). The main  
369 diatoms belonged to 1) the *Navicula*, *Nitzschia* and *Pseudo-nitzschia* genera at ST1, 2) the  
370 *Chaetoceros*, *Navicula* and *Pseudo-Nitzschia* genera at ST2, 3) the *Chaetoceros*, *Navicula* and  
371 *Rhizosolenia* genera at ST3. *Rhizosolenia* was the main RC host. Among dinoflagellates,  
372 protoperidinians were represented at all stations, but few larger cells were found as *Ceratium* and  
373 *Amphisiolena* species at ST3 in Oct 01.

374

### Chlorophyll and phycoerythrin distribution

375 Pigment content (Chla, PE) per cell or per trichome (Table 8) was calculated for Diapalis  
376 samples during the Feb 03 cruise at ST1 and ST2, and for a pure sample of *T. erythraeum*. Mean  
377 Chla concentration per trichome was 99 pg cell $^{-1}$  for pure *T. erythraeum* while the relationship  
378 between trichome numbers and Chla in the  $>10$   $\mu m$  fraction suggested an upper limit for the mean  
379 Chla concentration per trichome of 43 pg for the mixed community of *Trichodesmium* (Table 8).  
380 Considering the diatoms and dinoflagellates in the  $>10$   $\mu m$  fraction revealed by microscopy and  
381 by the presence of a significant quantity of Chlc, the Chla per trichome would be approximately  
382 10 % lower (assuming a constant Chlc/Chla ratio of 0.2 for diatoms and dinoflagellates) than this  
383 upper limit. Similarly, the PE per trichome (Table 8) was 251pg trichome $^{-1}$  for pure *T. erythraeum*  
384 and 197 pg trichome $^{-1}$  for mixed *Trichodesmium* (Table 8).

385 Regarding phycoerythrin (PE), its fluorescence excitation spectra were typical of PE-

386 cyanobacteria according to Neveux et al. (2006) with either PE-*Synechococcus* or PE-  
387 *Trichodesmium* dominating or a clear mixture of both PEs. At ST1 and ST2 stations, PE-  
388 *Trichodesmium* dominated the community in Dec 02 and Feb 03. Integrated Total Chla change  
389 showed much less variation across cruises than trichome abundance (Fig. 11). The integrated  
390 proportion of Dv Chla to TChla was generally around 20 % in lagoon waters (ST3), 40 %-50 %  
391 at ST1 and over 50 % in the Loyalty Channel (ST2). The highest integrated values of PE at ST1  
392 and ST2 in Feb 03 (69 mg.m<sup>-2</sup>, Fig. 11) was linked to the high abundance of *Trichodesmium* at  
393 the surface while the high value in Oct 03 at ST1 was related to a deep maximum of  
394 *Synechococcus*. In Feb 03, PE maxima measured in the upper layer were 4 to >10 times higher  
395 than during the other cruises, ranging from 0.61 µg l<sup>-1</sup> at ST1 to 1.27 µg l<sup>-1</sup> at ST2. In the >10 µm  
396 fraction, the PE in the upper layer (data not shown) was exclusively related to filamentous  
397 cyanobacteria, mainly *Trichodesmium*. At ST3 station (Fig. 11), PE was essentially related to  
398 *Synechococcus* and concentrations varied between 0.10 (Apr 02) and 0.62 µg l<sup>-1</sup> (Aug 02) at the  
399 surface with fairly even vertical distribution. The integrated concentrations varied from 4.30 (Apr  
400 02) to 29.26 mg m<sup>-2</sup> (Aug 02). The integrated N<sub>2</sub> fixation rate for all species (Garcia et al. 2007)  
401 roughly followed the integrated PE pattern (Fig. 11) and are correlated with the integrated  
402 trichome concentrations ( $r^2=0.73$ , N=11).

403

404

### **C biomass distribution in the microbial community**

405

406 The relative contribution of *Trichodesmium* + *Katagnymene* (TK) to C biomass of total  
407 picoplankton and filamentous cyanobacteria (Fig. 12) was generally high at ST2 with maxima in  
408 summer (80 % in Feb 03) and minima in winter (6 % in Aug 02), where TK was replaced by  
409 *Synechococcus* as the major contributor and in Oct 03 with only a few filaments observed.  
410 Comparatively, the contribution of TK at ST1 was lower, with a maximum of ~ 50 % in Feb 03.  
411 At ST3, *Synechococcus* was the main contributor to C biomass and the contribution of TK was  
412 generally low. At all stations, the contribution of RC to C biomass was negligible over the whole  
413 sampling period. Picoeukaryotes may account for a significant portion of the biomass in the  
414 lagoon near Quinne and in winter at all stations.

415

### **Correlations between groups and environmental variables**

416

417 To determine the impact of environmental variables on the abundance variations of the  
418 different phytoplanktonic groups and species, Spearman correlations were calculated between  
419 integrated abundances of each filamentous species, integrated nutrients, and depth-averaged  
420 temperature and salinity, at each station/cruise (Table 9). Significant positive correlations were  
421 found between total trichome abundance, temperature and ammonium and a negative correlation  
422 with phosphate, but no significant correlation with MLD (see also Fig. 4). At the species level,  
423 *RC* showed a strong positive correlation with MLD and ammonium, but *K. pelagica* only with  
424 phosphate, while *K. spiralis* was strongly correlated with all the analyzed nutrients (NO<sub>x</sub>,  
425 phosphate and ammonium). Diatom and picoplanktonic species did not show any correlation with  
426 environmental parameters. Inter-species correlations revealed that *RC* was positively correlated  
427 with *T. thiebautii* and *K. spiralis*, but not with *T. tenue* (inversely correlated with *T. thiebautii*).  
428 Dinoflagellates were closely correlated with total trichome abundance and *T. erythraeum*, but  
429 inversely with *K. pelagica*. No correlations were evidenced between diatoms and the other groups.  
430 Finally, *Synechococcus* and picoeukaryotes showed a positive correlation.

431

432

## DISCUSSION

433

### **Influence of methodology on enumeration and biomass estimates**

434

435  
436 As part of the effort of collecting biomass and metabolic rates specific to different  
437 phytoplankton functional groups, a database on diazotrophic organisms in the global pelagic  
438 upper ocean was built by Luo et al. (2012). Variability in counting and sampling procedures,  
439 however, hamper comparisons between studies around the world, especially for filamentous  
440 cyanobacteria. Significant error in the accuracy of low abundance measurements occurs  
441 depending on the sampling mode. In this case, the use of a plankton net increased the detection  
442 of *Trichodesmium* (0.1 against 1 trichome. l<sup>-1</sup>) by a factor of 10 compared to water samples  
443 collected with 2.5 L GO FLO bottles (Chang et al. 2000). When bottle sampling, it is essential to  
444 filter all the contents to prevent uneven distribution of *Trichodesmium*, which can occur when  
445 trichomes (and colonies) migrate due to cell-controlled or uncontrolled buoyancy (Bergman et al.  
446 2013). When tightly-packed filaments of *T. erythraeum* are observed at the surface, manual  
447 sampling within the first few millimeters of depth with narrow-necked plastic bottles provides a  
448 fairly accurate picture of trichome abundance, despite the somewhat uneven distribution.

449 Abundance data are usually expressed as cell, trichome or colony numbers with or without  
450 specific information on the taxonomic composition of filamentous cyanobacteria. Conversion  
451 factors from one unit to another are, however, vague and based on the morphometric variability  
452 of filamentous diazotrophs (Luo et al. 2012), such as the number of trichomes per colony, cell  
453 numbers per trichome, and trichome dimensions, which are quite variable. For the Diapalis data  
454 set, trichome counts of mixed species were linearly correlated (Spearman's rank coefficient >  
455 0.95,  $p < 0.001$ ) with the estimates of entire surface and total volume of trichomes, as previously  
456 pointed out by Neveux et al. (2006). So, replacing trichome numbers with trichome surface areas  
457 or volumes did not greatly modify the qualitative vertical distributions or seasonal trends in the  
458 filamentous biomass. This indicated a relatively constant composition of the filamentous  
459 community. Also, mean *T. erythraeum* carbon content per trichome (17.22 ng) and per cell (290  
460 pg) were determined by our microscope counts. These values were in the upper range of the  
461 approximate cell carbon content previously published for *Trichodesmium* species assuming 100  
462 cells trichome<sup>-1</sup> (110-250 pg C cell<sup>-1</sup>; Luo et al. 2012). Taking the measured value of 290 pg C  
463 cell<sup>-1</sup> of *T. erythraeum* (Table 8), TK accounted for up to 80 % of C cyanobacteria biomass in  
464 summer at the oceanic station of the Loyalty Channel, which confirms the essential role of  
465 filamentous cyanobacteria for the global food chain (Bergman et al. 2013) and in the south  
466 western tropical Pacific Ocean (SWTP) (Biegala et al. 2014, Bonnet et al. 2015).

467

#### 468 **Comparison of *Trichodesmium* abundance with other studies**

469

470 During the Diapalis program, *Trichodesmium* spp. abundance in the ocean varied from 1 to  
471 4578 trichomes l<sup>-1</sup> found at 0 to 60 meters (average 586 trichomes l<sup>-1</sup>,  $n = 88$ ), which was much  
472 higher than previously published data in New Caledonian waters at the end of the summer (250-  
473 1000 trichomes l<sup>-1</sup> in April 1998; Campbell et al. 2005). The only other abundance data available  
474 for our region around New Caledonia are *nifH* gene copies (Moisander et al. 2010). In Ouinne  
475 lagoon, a maximum of 1200 trichomes l<sup>-1</sup> was found in summer 2007 and more than 10,000  
476 trichomes l<sup>-1</sup> in accumulations (Rodier & Leborgne 2010). These concentrations are, however,  
477 lower than measured in a surface accumulation in the Southwest Lagoon, namely up to 30 10<sup>6</sup>  
478 trichomes l<sup>-1</sup> for a Chla value of 3 mg. l<sup>-1</sup> (Neveux et al. 2009), the highest values reported for the  
479 region. Such surface accumulations (>10,000 trichomes l<sup>-1</sup>) of mixed *Trichodesmium* species  
480 were collected 98 times in summer between New Caledonia and Vanuatu (1998 to 2010: Dupouy



481 et al. 2011, 2017). In the southernmost part of the SWTP at 28°S in the austral summer, Law et  
482 al. (2011) observed comparatively low surface *Trichodesmium* abundance, averaging 11  
483 trichomes l<sup>-1</sup> in the upper 10 m to 6 trichomes l<sup>-1</sup> at 35-50 m. Some high values were found in the  
484 Solomons Islands, expressed as trichome number (7700 trichomes l<sup>-1</sup>; Giraud et al. 2016) or *NifH*  
485 copies (Bonnet et al. 2015). In the Western North Pacific Ocean, abundance was between 1 and  
486 400 trichomes l<sup>-1</sup> (Marumo & Asaoka 1974, Marumo & Nagasawa 1976, Chen et al. 2003,  
487 Shiozaki et al. 2015) with some high values in accumulations (>20,000 filaments l<sup>-1</sup>) near the  
488 Miyako Islands (Shiozaki et al. 2015).

489 Comparing the Diapalis program with other time series conducted on *Trichodesmium* in  
490 subtropical waters raises a number of problems, as a different sampling strategy and sample  
491 processing method were used. During the Hawaiian (HOT) and Bermuda Atlantic Time-Series  
492 (BATS), *Trichodesmium* abundance was studied at approximately monthly intervals (HOT=  
493 October 1989-December 1992, Letelier & Karl 1996; BATS = 1995-1997, Orcutt et al. 2001) and  
494 free trichomes (water filtration sampling) and colonies (net sampling) were counted separately.  
495 So, a conversion factor of 200 trichomes per colony used in Orcutt et al. (2001) was applied to  
496 HOT and BATS counting data for comparisons with the Diapalis values, as in our study colonies  
497 were not counted (disintegrated during the counting) and only trichome abundance is available.  
498 This showed that trichome abundances in New Caledonian waters were generally higher than  
499 those observed at HOT and BATS stations. In fact, the integrated maxima observed in Feb 03 in  
500 the Loyalty Channel (240 10<sup>6</sup> trichome m<sup>-2</sup>) were 70 times and 400 times higher than at HOT (3.5  
501 10<sup>6</sup> trichome m<sup>-2</sup>) and BATS (0.64 10<sup>6</sup> trichome m<sup>-2</sup>), respectively. Moreover, mean cell numbers  
502 per trichome were generally lower in Diapalis samples (50-60) than at HOT (100). At HOT, apical  
503 cells were counted and divided by two to obtain the trichome number (Letelier & Karl 1996). This  
504 precaution was not applied to Diapalis samples, leading to a possible overestimation of trichome  
505 numbers due to trichome breaking during sample processing. HOT and BATS studies have shown  
506 a maximum abundance in summer and relatively strong inter-annual variability, even if free  
507 trichome variations at BATS seemed identical from one year to another. At BATS, however,  
508 interannual variations deduced from only 7 integrated depth profiles for 3 years fitted by a third-  
509 degree polynomial function of Julian days (Fig 1A in Orcutt et al. 2001), are questionable.

510 **Filamentous diazotroph species and their relationship with environmental factors**

511

512 The SWTP around New Caledonia is a typical warm low-nutrient low-chlorophyll  
513 (LNLC) region (Ceccarelli et al. 2013), with phosphate recharged annually (presumably other  
514 nutrients as well) in the euphotic zone during the transition periods (Moutin et al. 2005). The  
515 phosphate can limit the growth of diazotrophs species and consequently controls nitrogen  
516 fixation rates in the ocean (Karl et al. 2002). In LNLC, diazotroph species such as  
517 *Trichodesmium* are better adapted as they are able to use atmospheric N<sub>2</sub> (Bergman et al. 2013).  
518 Diazotrophs are likely responsible for the lower phosphate concentrations in summer in the  
519 region due to their PO<sub>4</sub> uptake (Moutin et al. 2005, Shiozaki et al. 2014), which corroborates the  
520 negative correlation between *Trichodesmium* and phosphate found in this study. During  
521 Diapalis cruises the ammonium concentrations at ocean stations were only high in February  
522 2003 coinciding with the highest concentrations of trichomes, PE and cyanobacteria carbon. The  
523 ammonium concentrations also were positively correlated to *Trichodesmium* densities.  
524 Therefore, the relatively high ammonium concentrations may be attributed partially to direct or  
525 indirect release of this nutrient by the diazotrophs (Mulholland 2007; Bergman et al. 2013). We  
526 did not find any correlation between *Trichodesmium* abundance and MLD. As stated by Hood et  
527 al. (2004), increased *Trichodesmium* concentrations are linked to a shallow MLD (resulting in  
528 high mean light levels) and low dissolved inorganic nitrogen (DIN) concentrations for extended  
529 periods of time. The relationship between nitrogen fixation rates in plankton net samples and  
530 MLD depth was significantly fitted by a hyperbolic function in the Atlantic Ocean ( $r^2 = 0.31$ ,  $p$   
531  $< 0.05$ ,  $n = 18$ , Agawin et al. 2013).

532 *T. thiebautii* and *T. tenue* were the predominant species in the oceanic waters around New  
533 Caledonia and in the open lagoon of the east coast, as previously stated in Rodier & Leborgne  
534 (2010). By contrast and according to these authors, *T. erythraeum* dominate in the SW lagoon of  
535 New Caledonia, which is a semi-closed and larger lagoon than the SE lagoon. Generally, *T.*  
536 *thiebautii* and *T. tenue* are poorly represented in coastal regions (Relevante & Gilmartin 1982).  
537 They dominate in the oligotrophic gyre of the Northern Pacific, Western Pacific (Marumo &  
538 Nagasawa 1976) and eastern part of the China Sea (Marumo & Asaoka 1974) and are likely better  
539 adapted to low-nutrient conditions than *T. erythraeum*. In our study, *T. tenue* was inversely  
540 correlated with *T. thiebautii*, which suggests competition between the two species for an  
541 apparently similar environment. According to Romans et al. (1994), *T. tenue* is a common species  
542 often confused with *T. thiebautii* in optical microscopy, which can explain the lack of information  
543 on the species' distribution and quantification. The predominance of *T. tenue* observed on

544 occasion during the Diapalis cruises is a relatively original finding. In this study around New  
545 Caledonia, *T. contortum* and *T. hildebrandtii* occur in very low densities as in most oceans  
546 (Bergman et al. 2013).

547 Information on *Katagnymene* species in the field is very scarce. They are mentioned in the  
548 Southwestern Pacific (Lundgren et al. 2001, Dupouy et al. 2011, Giraud et al. 2016). Both  
549 *Katagnymene* species, *K. pelagica* and *K. spiralis*, should now be considered as two  
550 morphological forms of the same species (Lundgren et al. 2005). In our study, both forms are  
551 frequently observed, but always in low abundance <284 trichomes l<sup>-1</sup>. The strongest  
552 concentrations were observed in the first 40 meters, although a deeper maximum (60 m) was  
553 found in the Loyalty Channel in Feb 03. At this maximum, the *K. spiralis* form accounts for 81  
554 % of the *Katagnymene* genus. Along the Revelle cruise track between New Caledonia and the Fiji  
555 Islands (April 1998), Lundgren et al. (2001) found both *Katagnymene* forms at 34 of the 51  
556 stations and counted up to 400 trichomes l<sup>-1</sup> of *Katagnymene* in the 0-25 m layer, with 89 % *K.*  
557 *pelagica*. It should be noted that *Katagnymene* trichomes are generally long (1 cm) and extremely  
558 fragile and can be broken up by handling before counting; hence the recommended use here of  
559 surface and total volume for biomass estimates. The significant relationship of *K. spiralis* with all  
560 nutrients, while *K. pelagica* was correlated only with phosphate, may indicate a different  
561 ecological niche for these two species.

562 Like *Trichodesmium* and *Katagnymene*, the heterocystous *Richelia intracellularis* is  
563 widespread in warm tropical and subtropical waters (Luo et al. 2012, Bonnet et al. 2015), whereas  
564 *Calothrix rhizolenia*, as epibionts of *Chaetoceros*, have been observed in the Indian and  
565 Western Pacific Oceans (Sarma 2012, Giraud et al. 2016). Around New Caledonia in this study,  
566 both *Richelia* and *Calothrix* species (*RC* groups) were sometimes present as free-living  
567 organisms, but more frequently in endosymbiotic association with diatoms (mainly in  
568 *Rhizolenia* sp.). *RC* were present in all seasons with a maximum (>700 trichomes l<sup>-1</sup>) in the  
569 Loyalty Channel in summer (Feb 03), as was *Trichodesmium*. Based only on samples where *RC*  
570 was detected, its biomass correlated with the number of diatoms in the >10 µm fraction (Spearman  
571 rank correlation between 0.52 and 0.57,  $p < 0.0001$ ; data not shown). In endosymbiosis, the host  
572 cell provides a protective micro-environment and positive buoyancy to the symbiont, which  
573 enables the cell to remain in the euphotic layer, as, unlike *Trichodesmium*, this species does not  
574 have gas vacuoles (Janson et al. 1999). *Richelia* has a very uneven space distribution in the oceans,  
575 like *Trichodesmium*, depending on whether the environment is conducive to their growth. Both

576 genera often inhabit the same types of ecosystems, as they have similar physiological properties,  
577 like all diazotrophs (Bergman et al. 2013 and references therein). In the case of cyanobacteria-  
578 diatom associations, environmental conditions must meet the needs of both organisms, and  
579 particularly sufficient silicate concentration for the diatom host growth. Iron and silica were not  
580 limiting factors in our area of study and are provided by leaching from terrestrial soils (Shiozaki  
581 et al. 2014). In our study, *RC* was more correlated with *T. thiebautii* and *K. spiralis*, and its  
582 positive dependence on the density structure of the water column (MLD) and ammonium needs  
583 to be further explored. In the Northern Pacific Gyre, the greatest abundance in *Richelia*  
584 *intracellularis* is also observed in summer, when the species can form blooms of about  $10^4$   
585 filaments per liter (Venrick 1974), values which are thus greater than ours (max 734 filaments l<sup>-1</sup>).  
586 Around the Hawaiian Islands (Sohm et al. 2011), a high abundance of all three groups, i.e.  
587 *Trichodesmium*, *Katagnymene* and *Richelia*, was reported in late boreal summer 2002 (Sep-Oct)  
588 and summer 2003 (July-Aug), with *Richelia*-diatom associations more abundant to the south of  
589 the islands. The high variability in *Richelia* size in our samples is another reason to underline the  
590 inaccuracy of biomass measurements in terms of filament numbers rather than total filament  
591 surface area or volume. The contribution of *RC* in terms of volume (or carbon) was minor (<1 %)  
592 but must not mask the great impact of this species on carbon sequestration by DDA's as shown  
593 in the North Tropical Pacific (Dore et al. 2008, Karl 2014; Karl & Church 2014).

594 In our study, large diatoms did not show significant correlations with any of the other groups  
595 enumerated nor with any of the environmental variables. Dinoflagellates correlated positively  
596 with total trichome abundance. Their positive correlation with the percentage of *T. erythraeum*  
597 and their negative correlation with the percentage of *K. pelagica*, suggested affiliation to more  
598 coastal than oceanic environments. The diversity of trophic status in dinoflagellates  
599 (photosynthetic, mixotroph, heterotroph) was, nevertheless, not considered in the analysis. In the  
600 Northern Tropical Pacific, the dinoflagellate group revealed no specific ecological pattern nor any  
601 characteristic assemblages (Giraud et al. 2016). During the Diapalis cruises, the picoplanktonic  
602 groups did not show any correlation with environmental parameters (Table 9), which was  
603 surprising, as *Synechococcus* and *Prochlorococcus* have distinct ecophysiology, *Synechococcus*  
604 being better adapted to mesotrophic conditions and *Prochlorococcus* to oligotrophic conditions  
605 (Partensky et al. 1996). This could be explained for *Prochlorococcus* by the fact that their  
606 abundance varied little over the annual cycles. *Prochlorococcus* never dominated the  
607 phytoplankton C biomass, but were often the second contributor to C biomass after filamentous

608 cyanobacteria in oceanic waters (Fig. 12). All phytoplankton share a requirement for light and  
609 nutrients. A more specific mechanism underlying the covariation between *Synechococcus* and the  
610 picoeukaryotes, as opposed to *Prochlorococcus*, is that they have a larger cell size than the latter,  
611 and are able to use nitrate. This could explain they tend to respond positively to enhanced nutrient  
612 supply as observed mostly in the lagoon station and at Santal Bay. The covariation between  
613 *Synechococcus* and the picoeukaryotes has been described before in the Atlantic subtropical gyres  
614 (Marañón et al. 2003) and in the Pacific Ocean (Worden et al. 2004). The significant positive  
615 correlation between *Synechococcus* and picoeukaryotes may also occur due to similarities in  
616 favorable light conditions (Gutiérrez-Rodríguez et al. 2016). *Synechococcus* and picoeukaryotes  
617 dominated the C biomass in the lagoon, but may also be large contributors in oceanic waters, as  
618 observed in winter (Fig. 12).

619

620

### 2001-2003 Inter-annual variability

621

622 The difference in large diazotroph abundance (and nitrogen fixation rates, Garcia et al.  
623 2007; Fig. 12C) observed between the summers of 2001-2002 and 2002-2003 could be the result  
624 of a relatively low *in situ* sampling frequency. Satellite imagery nevertheless confirmed the very  
625 low chlorophyll values during summer 2001-2002 compared to summer 2003 (Dupouy et al.  
626 2011). Moreover, satellite-classified *Trichodesmium* pixels in the region 5°S-25°S, 160°E-170°W  
627 determined using the TRICHOSAT model were clearly lower in summer 2001-2002 (La Niña  
628 years) than summer 2003 (an El Niño year). The spectral fluorescence signature of surface blooms  
629 as measured by the MERIS sensor (Gower et al. 2014) was also high during El Niño summers  
630 (2003, 2007, 2010) but low during La Niña summers. The difference in cumulative precipitation  
631 between 2001-2002 and 2003 summers is striking, with 2003 being drier despite the occurrence  
632 of two tropical storms, namely Beni in January 2003 and Erica in March 2003 (Neveux et al.  
633 2009). Law et al. (2011) reported that nitrogen fixation increased owing to an iron supply from a  
634 wet-dust deposition 8 days after Tropical Cyclone Wati in the Tasman Sea. Australian dust  
635 peaking in 2001 and 2002 was cited as a potential factor in increasing occurrence in the seas to  
636 the east of Australia (estimated by satellite) in 2001-2005 (Mackie et al. 2008). The regional  
637 distribution of aerosols was probably also influenced by the continuous passive (non-explosive)  
638 volcanic degassing of the Melanesian Volcanic Arc, as indicated by sulfur dioxide (SO<sub>2</sub>), the  
639 composition of which has been analyzed using satellite data and modelling (Lefèvre et al. 2015).

640 Likewise, Sahara dust deposition at BATS corresponded to an increased abundance of  
641 *Trichodesmium* colonies as well as changes in their chemical composition, even though it did not  
642 enhance the N<sub>2</sub> fixation rate per colony (Orcutt et al. 2001). At BATS, inter-annual variability  
643 could also be related to the relative extent of vertical mixing from one year to another, including  
644 the effects of hurricane frequency, which would reduce *Trichodesmium* abundance (Orcutt et al.  
645 2001). During the Diapalis program, this negative vertical-mixing effect was not confirmed, as  
646 the highest *Trichodesmium* abundance occurred just after Tropical Storm Beni struck New  
647 Caledonia in Late January 2003. Inter-annual variability would also have been related to changes  
648 in main-current transports, i.e. a westward Sverdrup transport and trade winds enhanced during  
649 El Niño periods as against falling Sverdrup transport and strengthening northwesterly winds  
650 during La Niña (Kessler & Cravatte 2013; Cravatte et al. 2015). Wind regime, which may impact  
651 mixed-layer formation is known to alternate around New Caledonia with a trade-wind regime  
652 during El Niño and more westerly winds during La Niña, which may increase surface currents in  
653 the Loyalty Channel (Lefèvre et al. 2010). How such large-scale current variability or atmospheric  
654 composition influence total biomass and *Trichodesmium* abundance in New Caledonia is not clear  
655 yet.

## 657 CONCLUSION

658  
659 In 2001-2003, the seasonal and inter-annual variations in cyanobacteria abundance were  
660 investigated in New Caledonian waters during the 9 Diapalis program cruises. Three sites  
661 representative of different biotopes were sampled, i.e. open ocean (Loyalty Channel), coastal  
662 (lagoon off the Ouinne River estuary) and deep bays (Santal Bay at Lifou). Abundance was  
663 determined at the species level for diazotrophic filamentous cyanobacteria. Our description of the  
664 organisms (*RC* and diatoms) in symbiotic associations was well detailed. Filamentous  
665 cyanobacteria were practically always present throughout the year, but with relatively high  
666 variations. The highest abundances occurred during the summer seasons. The dominant species  
667 were *Trichodesmium thiebautii* and *T. tenue*, followed by *T. erythraeum*. *Katagnymene* as well as  
668 *Richelia* species (mainly endosymbiotic in diatoms), which were consistently present in low  
669 abundance. Microscopic examination also revealed the presence of unknown filamentous species  
670 formed by round-shape cells not yet described by molecular tools. Picoplanktonic cyanobacteria  
671 (*Prochlorococcus* and *Synechococcus*) were consistently present in abundance with less

672 pronounced seasonal variations than filamentous cyanobacteria. *Trichodesmium* dominated in  
673 terms of carbon content in the Loyalty Channel and Santal Bay in summer, while *Synechococcus*  
674 dominated at the Ouinne station and in winter at all the three stations. The comparison of the 2002  
675 and 2003 summers showed major inter-annual variability. Environmental factors that could  
676 explain this variability were not clearly identified. One hypothesis could be the effects of  
677 alternation between La Niña and El Niño with maximum diazotrophs and *Trichodesmium*  
678 abundance during a well-established El Niño. Some hypotheses relating to the El Niño/La Niña  
679 cycle need verifying, i.e. dust inputs and links with precipitations, winds, vertical movements and  
680 horizontal circulation within the upper 200-meter layer, gyre formation in relation to wind  
681 strength and direction and increased mesoscale circulation.

682

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693

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TABLES

**Table 1:** Dates of the 9 Diapalis cruises

Diapalis cruises	Dates	Austral Season
D1	22-31 October 2001	transition period
D2	10-22 December 2001	Austral summer
D3	15-22 January 2002	Austral summer
D4	2-9 April 2002	Austral summer
D5	21-28 May 2002	transition period
D6	6-13 August 2002	Austral winter
D7	1-10 February 2003	Austral summer
D8	10-14 June 2003	Austral winter
D9	7-16 October 2003	transition period

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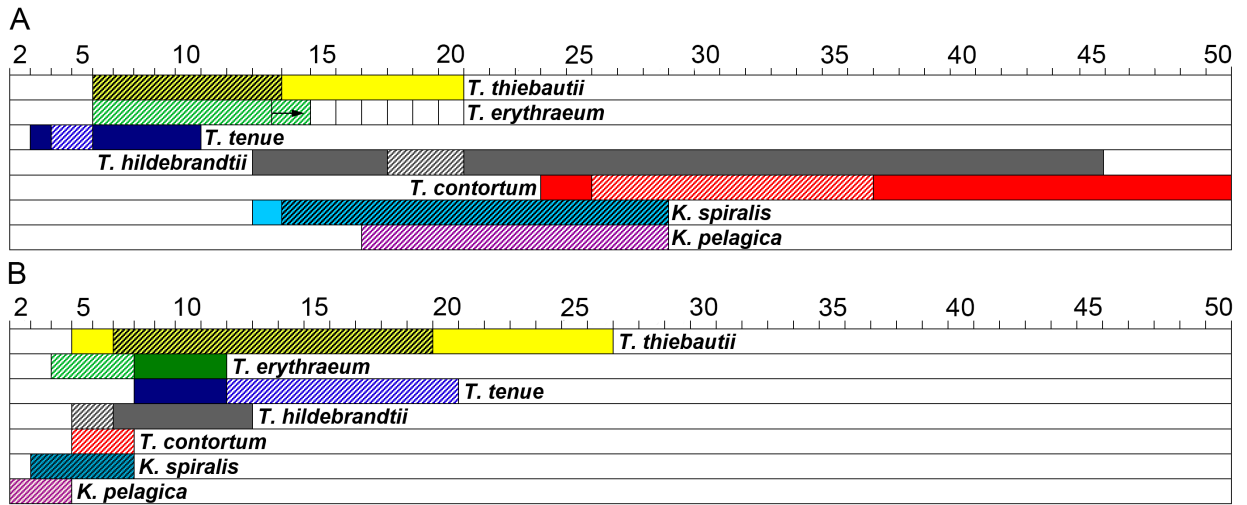
**Table 2:** Morphometric characteristics of filamentous cyanobacteria, in the >10 µm size fraction, encountered during the Diapalis cruises. NDO: not distinctly observed.

Species	Cell diameter (µm)	Cell length (µm)	Cell shape
<i>T. erythraeum</i>	8 to 13.6	4 to 7	as wide as or up to twice as wide as long
<i>T. thiebautii</i>	6 to 14	7 to 19	as long as or up to twice as long as wide
<i>T. tenue</i>	4 to 5	12 to 20	3 to 4 x longer than wide
<i>T. contortum</i>	26 to 36	5 to 7	5 to 6 x wider than long
<i>T. hildebrandtii</i>	18-20	5 to 6	2.7 to 3 x wider than long
Unidentified filaments	2.7 to 3	NDO	NDO
<i>K. spiralis</i>	14 to 28	3 to 8	2.2 to 4.8 x wider than long
<i>K. pelagica</i>	17 to 28	2.5 to 3.5	4 to 14 x wider than long
<i>R. intracellularis/C. rhizosoleniae</i> group	cell 2-7 Ø heterocyst 3-10 Ø	-	-
Colonies of unidentified cyanobacteria (spherical cells)	type 1: 2.7-3 Ø type 2: 6 Ø	-	-

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**Table 3:** A) Cell diameter (µm) and B) cell length (µm) of *Trichodesmium* and *Katagnymene* species. The colored areas represent size ranges published in the literature and shaded areas part

929 of the size range observed during the Diapalis cruises in the New Caledonian Lagoon. A black  
 930 arrow indicates observation of a few *T. erythraeum* trichomes with a slightly wider diameter  
 931 than previously published.



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947 **Table 4.** Statistical data for the different groups enumerated by inverted microscopy in the  
 948 >10  $\mu\text{m}$  fraction and by flow cytometry in the picoplanktonic fraction (trichome number for  
 949 identified filamentous cyanobacteria and cell number for all other groups and the colonies  
 950 of unidentified cyanobacteria with spherical cells), at ST1, the Santal Bay station, during the  
 951 9 Diapalis cruises (2001-2003). Concentrations taken at 4-6 depths down to 60 m ( $\text{l}^{-1}$ ) and  
 952 integrated values ( $\text{m}^{-2}$ ) in the 0-60 m layer. Trichomes: sum of *Trichodesmium* and  
 953 *Katagnymene* trichomes.

ST1 Diapalis 01-09	min	max	average	stdev	n
Trichomes $\text{l}^{-1}$	1	2929	651	648	50
$10^6$ Trichomes $\text{m}^{-2}$	0.06	89	38	30	12
$10^6 \mu\text{m}^3$ Trichomes $\text{l}^{-1}$	0.59	49.22	11.46	12.70	25
$10^9 \mu\text{m}^3$ Trichome $\text{m}^{-2}$	0.16	1.15	0.52	0.37	7
<i>R. intracellularis</i> / <i>C. rhizosoleniae</i> group $\text{l}^{-1}$	0	64	8	16	25
$10^3 \mu\text{m}^3$ <i>R. intracellularis</i> / <i>C. rhizosoleniae</i> group $\text{l}^{-1}$	0.00	12.76	1.13	2.74	24
Unidentified cyanobacteria with spherical cells (cell $\text{l}^{-1}$ )	0	20	1	5	25
Dinoflagellates $\text{l}^{-1}$	22	1927	322	405	31
Diatoms $\text{l}^{-1}$	14	4516	640	1096	31
<i>T. tenue</i> $\text{l}^{-1}$	20	947	285	255	28
<i>T. erythraeum</i> $\text{l}^{-1}$	3	621	145	159	28
<i>T. thiebautii</i> $\text{l}^{-1}$	18	1351	335	353	28
<i>K. spiralis</i> $\text{l}^{-1}$	0	199	29	49	28
<i>K. pelagica</i> $\text{l}^{-1}$	0	61	6	14	28
$10^6 \mu\text{m}^3$ <i>T. tenue</i> $\text{l}^{-1}$	0.09	7.82	2.20	2.25	27
$10^6 \mu\text{m}^3$ <i>T. erythraeum</i> $\text{l}^{-1}$	0.02	15.41	2.46	3.66	27
$10^6 \mu\text{m}^3$ <i>T. thiebautii</i> $\text{l}^{-1}$	0.18	13.90	3.67	3.64	27
$10^6 \mu\text{m}^3$ <i>K. spiralis</i> $\text{l}^{-1}$	0.00	6.90	1.33	1.98	27
$10^6 \mu\text{m}^3$ <i>K. pelagica</i> $\text{l}^{-1}$	0.00	31.40	1.54	6.04	27
$10^4$ <i>Prochlorococcus</i> $\text{ml}^{-1}$	3.73	46.21	13.37	8.13	76
$10^4$ <i>Synechococcus</i> $\text{ml}^{-1}$	0.22	3.58	1.50	0.86	76
$10^4$ Picoeukaryotes $\text{ml}^{-1}$	0.06	0.47	0.18	0.08	76
$10^{12}$ <i>Prochlorococcus</i> $\text{m}^{-2}$	3.41	14.80	8.76	3.96	11
$10^{12}$ <i>Synechococcus</i> $\text{m}^{-2}$	0.19	1.75	0.94	0.49	11
$10^{12}$ Picoeukaryotes $\text{m}^{-2}$	0.06	0.17	0.11	0.04	11

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966 **Table 5.** Statistical data for the different groups enumerated by inverted microscopy in the  
 967 >10  $\mu\text{m}$  fraction and by flow cytometry in the picoplanktonic fraction (trichome number for  
 968 identified filamentous cyanobacteria and cell number for all other groups and the colonies  
 969 of unidentified cyanobacteria with spherical cells), at the ST2, Loyalty Channel station,  
 970 during the 9 Diapalis cruises (2001-2003). Concentrations taken at 4-6 depths down to 60 m  
 971 ( $\text{l}^{-1}$ ) and integrated values ( $\text{m}^{-2}$ ) in the 0-60 m layer. Trichomes: sum of *Trichodesmium* and  
 972 *Katagnymene* trichomes  
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ST2 Diapalis 01-09	min	max	average	stdev	n
Trichomes $\text{l}^{-1}$	4	4578	676	1089	45
$10^6$ Trichomes $\text{m}^{-2}$	0.46	235	44	66	11
$10^6 \mu\text{m}^3$ Trichome $\text{l}^{-1}$	0.03	62.22	9.53	15.29	36
$10^9 \mu\text{m}^3$ Trichome $\text{m}^{-2}$	0.16	3.05	0.63	0.92	9
<i>R. intracellularis</i> / <i>C. rhizosoleniae</i> group $\text{l}^{-1}$	0	735	36	121	41
$10^3 \mu\text{m}^3$ <i>R. intracellularis</i> / <i>C. rhizosoleniae</i> group $\text{l}^{-1}$	0.00	117.33	7.22	21.64	30
Unidentified cyanobacteria with spherical cells (cell $\text{l}^{-1}$ )	0	4934	224	833	40
Dinoflagellates $\text{l}^{-1}$	8	1205	289	306	40
Diatoms $\text{l}^{-1}$	5	9969	834	2190	40
<i>T. tenue</i> $\text{l}^{-1}$	13	1053	209	250	36
<i>T. erythraeum</i> $\text{l}^{-1}$	2	417	50	78	36
<i>T. thiebautii</i> $\text{l}^{-1}$	3	635	136	150	36
<i>K. spiralis</i> $\text{l}^{-1}$	0	31	3	6	36
<i>K. pelagica</i> $\text{l}^{-1}$	0	11	2	3	36
$10^6 \mu\text{m}^3$ <i>T. tenue</i> $\text{l}^{-1}$	0.04	17.28	2.88	3.49	32
$10^6 \mu\text{m}^3$ <i>T. erythraeum</i> $\text{l}^{-1}$	0.01	17.97	1.99	3.88	32
$10^6 \mu\text{m}^3$ <i>T. thiebautii</i> $\text{l}^{-1}$	0.13	21.03	2.92	4.66	32
$10^6 \mu\text{m}^3$ <i>K. spiralis</i> $\text{l}^{-1}$	0.00	15.89	0.82	2.90	32
$10^6 \mu\text{m}^3$ <i>K. pelagica</i> $\text{l}^{-1}$	0.00	2.07	0.18	0.46	32
$10^4$ <i>Prochlorococcus</i> $\text{ml}^{-1}$	2.59	29.02	13.05	5.95	111
$10^4$ <i>Synechococcus</i> $\text{ml}^{-1}$	0.05	4.58	0.99	1.24	111
$10^4$ Picoeukaryotes $\text{ml}^{-1}$	0.03	0.67	0.11	0.08	111
$10^{12}$ <i>Prochlorococcus</i> $\text{m}^{-2}$	3.53	14.87	8.76	3.59	17
$10^{12}$ <i>Synechococcus</i> $\text{m}^{-2}$	0.08	2.55	0.62	0.79	17
$10^{12}$ Picoeukaryotes $\text{m}^{-2}$	0.02	0.15	0.07	0.04	17

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985 **Table 6.** Statistical data for the different groups enumerated by inverted microscopy in the  
 986 >10 µm fraction and by flow cytometry in the picoplanktonic fraction (trichome number for  
 987 identified filamentous cyanobacteria and cell number for all other groups and the colonies  
 988 of unidentified cyanobacteria with spherical cells), at ST3, the Quinne station, Eastern  
 989 Lagoon, during the 9 Diapalis cruises (2001-2003). Concentrations taken at 4-6 depths down  
 990 to 30 m (l<sup>-1</sup>) and integrated values (m<sup>-2</sup>) in the 0-30 m layer. Trichomes: sum of  
 991 *Trichodesmium* and *Katagnymene* trichomes.

ST3 Diapalis 01-09	min	max	average	stdev	n
Trichomes l <sup>-1</sup>	10	854	172	219	32
10 <sup>3</sup> Trichomes m <sup>-2</sup>	0.38	15.00	4.74	5.30	9
10 <sup>6</sup> µm <sup>3</sup> Trichomes l <sup>-1</sup>	0.07	10.19	2.67	2.81	20
10 <sup>9</sup> µm <sup>3</sup> Trichome m <sup>-2</sup>	0.01	0.18	0.09	0.07	5
<i>R. intracellularis</i> / <i>C. rhizosoleniae</i> group l <sup>-1</sup>	0	117	15	25	25
10 <sup>3</sup> µm <sup>3</sup> <i>R. intracellularis</i> / <i>C. rhizosoleniae</i> group l <sup>-1</sup>	0	64.90	7.25	14.36	23
Unidentified cyanobacteria with spherical cells (cell l <sup>-1</sup> )	0	429	22	88	24
Dinoflagellates l <sup>-1</sup>	82	1000	344	251	22
Diatoms l <sup>-1</sup>	26	16893	2458	4345	22
<i>T. tenue</i> l <sup>-1</sup>	5	868	136	228	29
<i>T. erythraeum</i> l <sup>-1</sup>	0	132	16	28	29
<i>T. thiebautii</i> l <sup>-1</sup>	2	147	43	40	29
<i>K. spiralis</i> l <sup>-1</sup>	0	9	0	2	29
<i>K. pelagica</i> l <sup>-1</sup>	0	8	0	2	29
10 <sup>6</sup> µm <sup>3</sup> <i>T. tenue</i> l <sup>-1</sup>	0.08	6.09	1.61	2.10	18
10 <sup>6</sup> µm <sup>3</sup> <i>T. erythraeum</i> l <sup>-1</sup>	0.00	4.79	0.66	1.14	18
10 <sup>6</sup> µm <sup>3</sup> <i>T. thiebautii</i> l <sup>-1</sup>	0.02	2.41	0.89	0.68	18
10 <sup>6</sup> µm <sup>3</sup> <i>K. spiralis</i> l <sup>-1</sup>	0.00	0.50	0.03	0.12	18
10 <sup>6</sup> µm <sup>3</sup> <i>K. pelagica</i> l <sup>-1</sup>	0.00	1.42	0.10	0.35	18
10 <sup>4</sup> <i>Prochlorococcus</i> ml <sup>-1</sup>	1.01	24.17	7.28	4.40	66
10 <sup>4</sup> <i>Synechococcus</i> ml <sup>-1</sup>	1.14	13.82	6.60	2.91	66
10 <sup>4</sup> Picoeukaryotes ml <sup>-1</sup>	0.13	1.74	0.34	0.26	66
10 <sup>12</sup> <i>Prochlorococcus</i> m <sup>-2</sup>	0.48	4.75	2.13	1.05	11
10 <sup>12</sup> <i>Synechococcus</i> m <sup>-2</sup>	0.82	3.27	1.92	0.79	11
10 <sup>12</sup> Picoeukaryotes m <sup>-2</sup>	0.06	0.17	0.10	0.04	11

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 995 **Table 7:** Cell number per trichome of each *Trichodesmium* and *Katagnymene* species during the  
 996 Diapalis cruises.

	<i>T. tenue</i>	<i>T. thiebautii</i>	<i>T. erythraeum</i>	<i>T. hildebrandtii</i>	<i>T. contortum</i>	<i>K. spiralis</i>	<i>K. pelagica</i>
min	3	3	4	16	19	2	10
max	206	209	235	132	62	140	334
Mean	54	55	64	62	40	42	57
STD	36	38	45	40	22	34	77
N	584	469	322	9	3	49	18

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**Table 8:** Morphometric characteristics of *Trichodesmium* and *Katagnymene* species at the *Trichodesmium* peak abundance in February 03 (Diapalis 7). Their chlorophyll *a* (Chla), phycoerythrin (PE), carbon (C) content per trichome and volume of trichome. Comparison with cellular characteristics, pigments and carbon content obtained with *T. erythraeum* in New Caledonian waters (West Coast). TK: sum of *Trichodesmium* and *Katagnymene* trichomes.

	Mean	STD	Number
<b>D7 Cruise</b>			
pg Chla trichome <sup>-1</sup>	43.23	18.86	30
µg Chla mm <sup>-3</sup> trichome	3.47	1.71	23
pg PE trichome <sup>-1</sup>	196.86	58.34	30
µg PE mm <sup>-3</sup> trichome	16.71	7.94	24
TK trichome diameter (µm)	6.64	3.32	1884
TK trichome length (µm)	360	302	1884
TK trichome volume (µm <sup>3</sup> )	12808	28847	1884
<i>T. contortum</i> trichome diameter (µm)	33.00	-	2
<i>T. contortum</i> trichome length (µm)	128	-	2
<i>T. erythraeum</i> trichome diameter (µm)	8.01	1.11	402
<i>T. erythraeum</i> trichome length (µm)	320	245	402
<i>T. hidelbrandtii</i> trichome diameter (µm)	16.00	2.49	9
<i>T. hidelbrandtii</i> trichome length (µm)	269	308	9
<i>T. tenue</i> trichome diameter (µm)	4.49	0.57	530
<i>T. tenue</i> trichome length (µm)	472	357	530
<i>T. thiebautii</i> trichome diameter (µm)	6.06	0.28	735
<i>T. thiebautii</i> trichome length (µm)	327	273	735
<i>K. pelagica</i> trichome diameter (µm)	24.00	5.10	5
<i>K. pelagica</i> trichome length (µm)	403	558	5
<i>K. spiralis</i> trichome diameter (µm)	20.00	3.95	65
<i>K. spiralis</i> trichome length (µm)	170	189	65
<b><i>T. erythraeum</i></b>			
pg Chla cell <sup>-1</sup>	1.58	0.26	5
pg Chla trichome <sup>-1</sup>	99.00	14.62	5
ng Chla mm <sup>-3</sup> trichome	3.31	3.86	5
pg PE cell <sup>-1</sup>	4.01	0.76	5
pg PE trichome <sup>-1</sup>	251.57	41.26	5
µg PE mm <sup>-3</sup> trichome	8.37	1.21	5
pg carbon cell <sup>-1</sup>	289.89	-	2
ng carbon trichome <sup>-1</sup>	17.22	-	2
µg carbon mm <sup>-3</sup> trichome	588.06	-	2
PE/Chla	3.81	1.79	13
Carbon/Chla	173.21	55.96	9
Carbon/PE	71.15	33.54	6
Cell diameter (µm)	9.6	0.5	1849
Cell length (µm)	6.3	0.7	1849
Cell volume (µm <sup>3</sup> )	456	76	1849
Trichome length (µm)	402	157	1849

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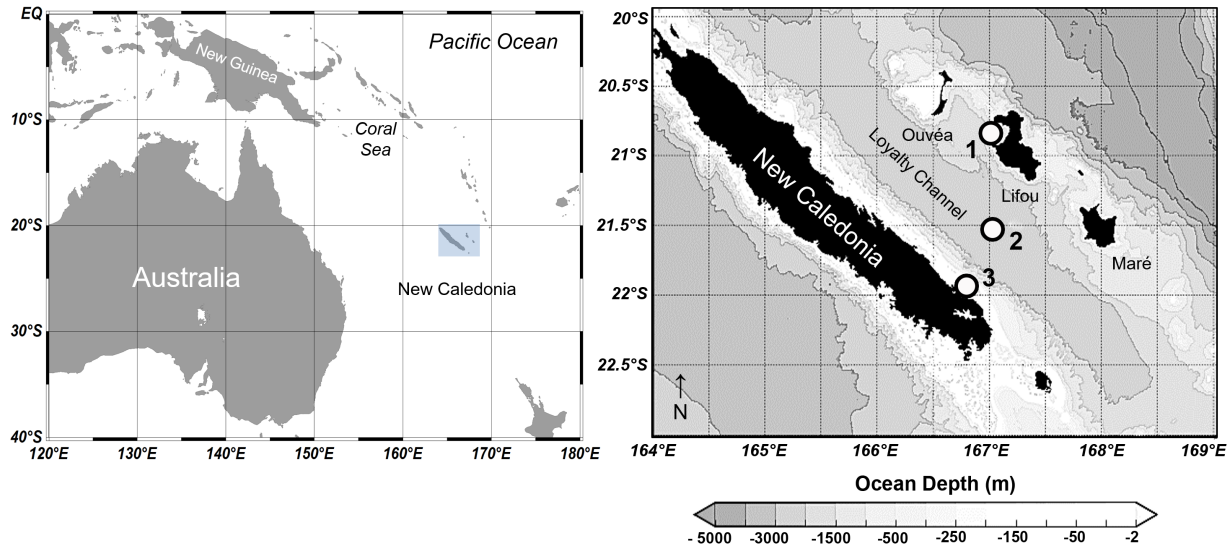
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**Table 9.** Spearman's correlation coefficient for the relationships between integrated abundance (cell or trichomes m<sup>-2</sup> over 60 m for ST1 and ST2 and 30 m for ST3) of autotrophic groups, the percentage of the different species of filamentous cyanobacteria and environmental parameters (n = 28). Data from the Diapalis cruises (2001-2003). \*p < 0.01, \*\*p < 0.05, ns: not significant; TK: sum of *Trichodesmium* and *Katagnymene* trichomes; Din: Dinoflagellates; Diat: Diatoms; *Rich*: *Richelia*; *Proc*: *Prochlorococcus*; *Syn*: *Synechococcus*; *Peuk*: Picoeukaryotes; *T.t*: *T. tenue*; *T.e*: *T. erythraeum*; *T.th*: *T. thiebautii*; *K.s*: *K. spiralis*; *K.p*: *K. pelagica*; MLD: mixed layer depth; T(°C): Temperature; Sal: Salinity.

Variables	Din	Diat	TK	<i>Rich</i>	<i>Proc</i>	<i>Syn</i>	<i>Peuk</i>	% <i>T.t</i>	% <i>T.e</i>	% <i>T.th</i>	% <i>K.s</i>	% <i>K.p</i>	MLD	T(°C)	Sal	NO <sub>x</sub>	NH <sub>4</sub>	PO <sub>4</sub>	
Din	1	0.46**	0.63**	ns	ns	ns	ns	ns	0.50**	ns	ns	-0.57**	ns	ns	ns	ns	ns	ns	ns
Diat		1	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
TK			1	ns	0.65*	ns	ns	ns	ns	ns	ns	ns	ns	0.62*	ns	ns	0.51**	-0.48**	
<i>Rich</i>				1	ns	ns	ns	ns	ns	0.61*	0.69*	ns	0.60**	ns	ns	ns	0.85*	ns	
<i>Proc</i>					1	-0.42**	ns	ns	ns	-0.50**	ns	ns	ns	ns	ns	ns	ns	ns	ns
<i>Syn</i>						1	0.52**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
<i>Peuk</i>							1	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
% <i>T.t</i>								1	ns	-0.65*	-0.59**	ns	ns	0.49**	ns	ns	-0.57**	ns	
% <i>T.e</i>									1	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
% <i>T.th</i>										1	ns	ns	ns	ns	ns	ns	ns	ns	ns
% <i>K.s</i>											1	ns	ns	ns	ns	0.64**	0.55**	0.59**	
% <i>K.p</i>												1	ns	ns	ns	ns	ns	0.63**	
MLD													1	ns	ns	-0.46**	ns	ns	
T(°C)														1	-0.63*	ns	ns	-0.55*	
Sal															1	ns	ns	0.52**	
NO <sub>x</sub>																1	ns	0.48**	
NH <sub>4</sub>																	1	ns	
PO <sub>4</sub>																			1

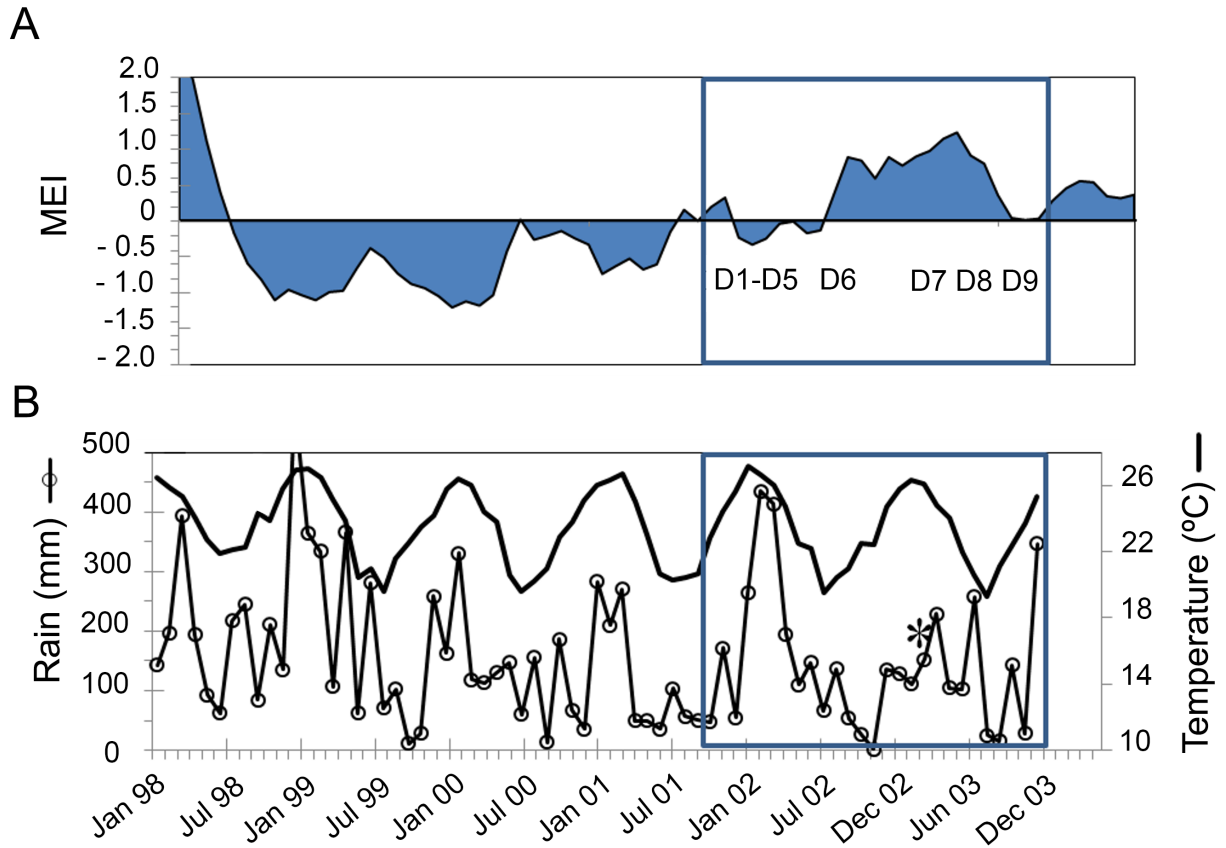
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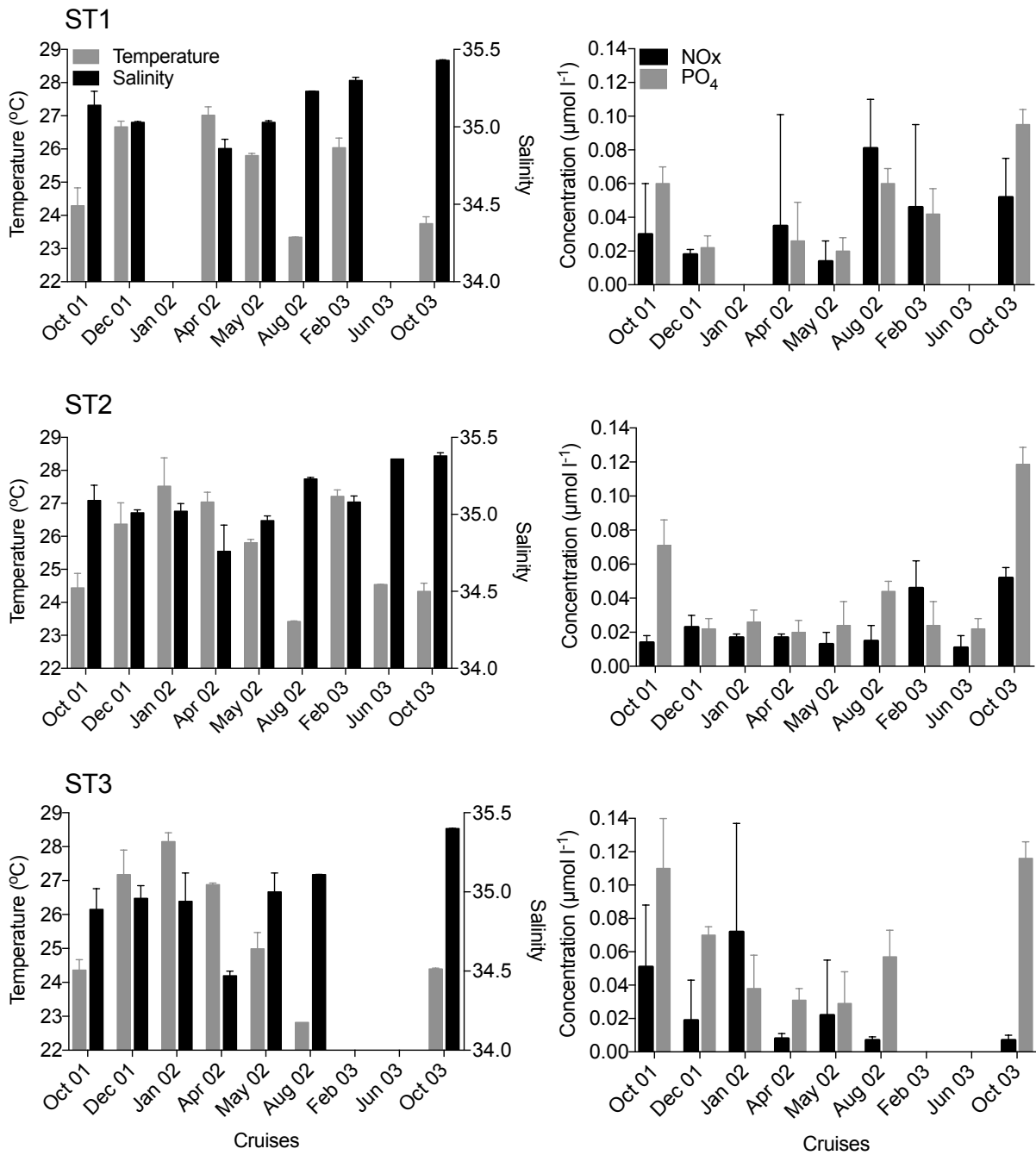
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**Figure 1.** Location of the 3 main stations sampled during the nine Diapalis cruises in the New Caledonian waters: ST1 (Santal Bay) on Lifou Island ( $167^{\circ}04'E$   $20^{\circ}51'S$ , 1050 m depth), ST2 (Loyalty Channel,  $167^{\circ}E$   $21^{\circ}30'S$ , 2100 m depth) and ST3 (Ouinne station) in the East Coast lagoon ( $166^{\circ}45'E$   $21^{\circ}57'S$ , 35 m depth). Figure Courtesy J. Lefèvre.



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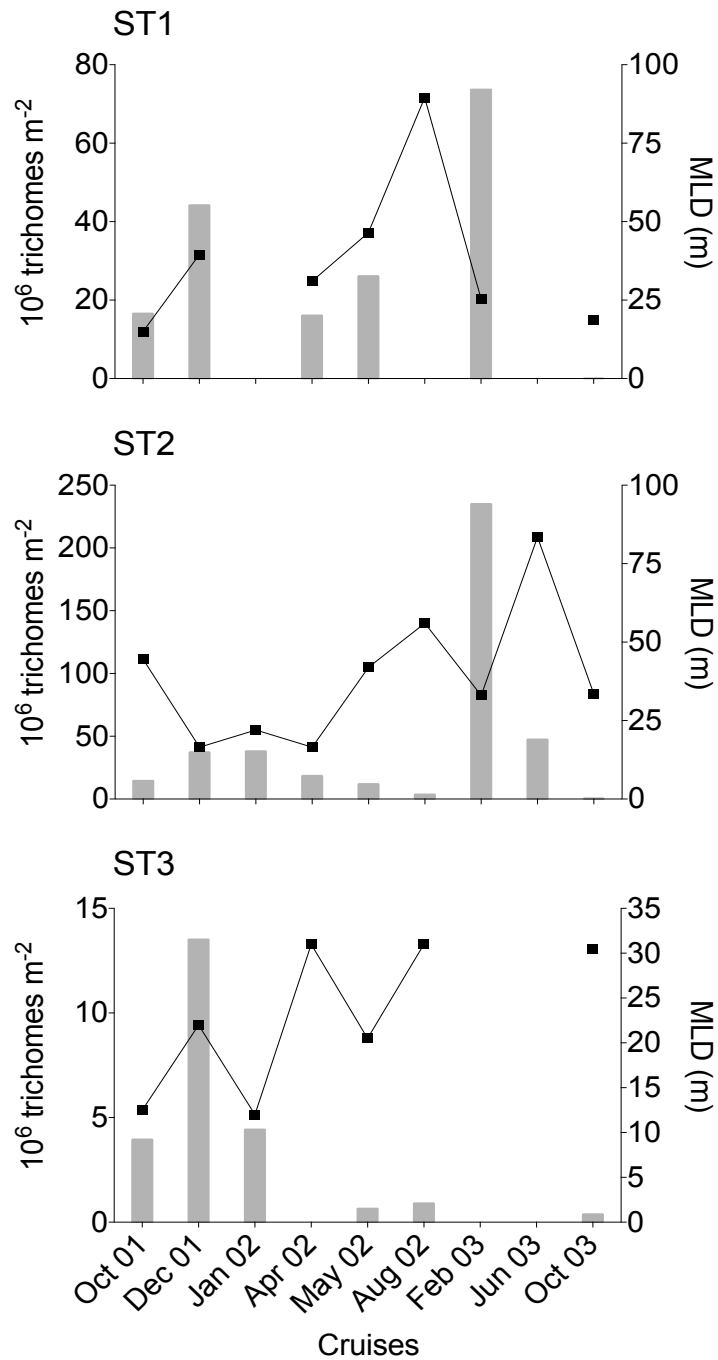
**Figure 2.** (A) Multivariate El Niño Index, (B) air temperature and (T °C) and monthly cumulative precipitation (mm) for 1998-2003 on New Caledonia's east coast (Thio station). The framed area represents the Diapalis sampling period. Tropical Storm Beni (29 Jan - 5 Feb 2003) is indicated as (\*). See Table 1 for the dates of the cruise.



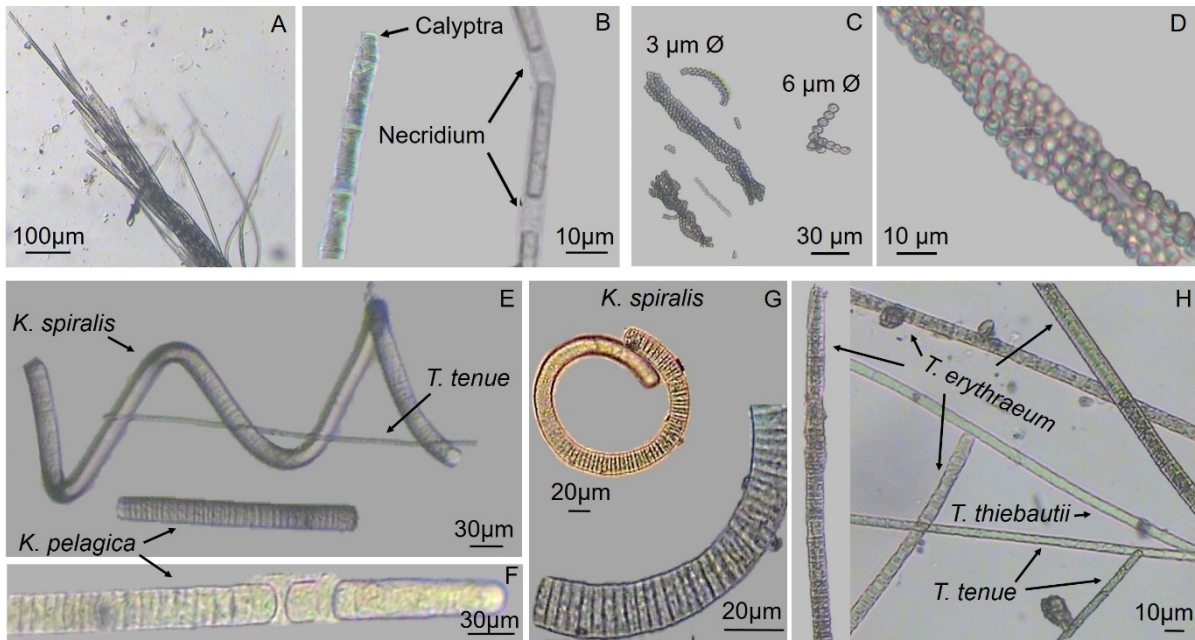
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**Figure 3.** Mean temperature, salinity (left panel) and nutrients (NO<sub>x</sub>, PO<sub>4</sub><sup>-</sup>) (right panel) during the Diapalis cruises. Values are averaged from 0-60 m at ST1 and ST2 and 0-30 m at ST3. ST3 was not sampled in Feb 03 and Jun 03.



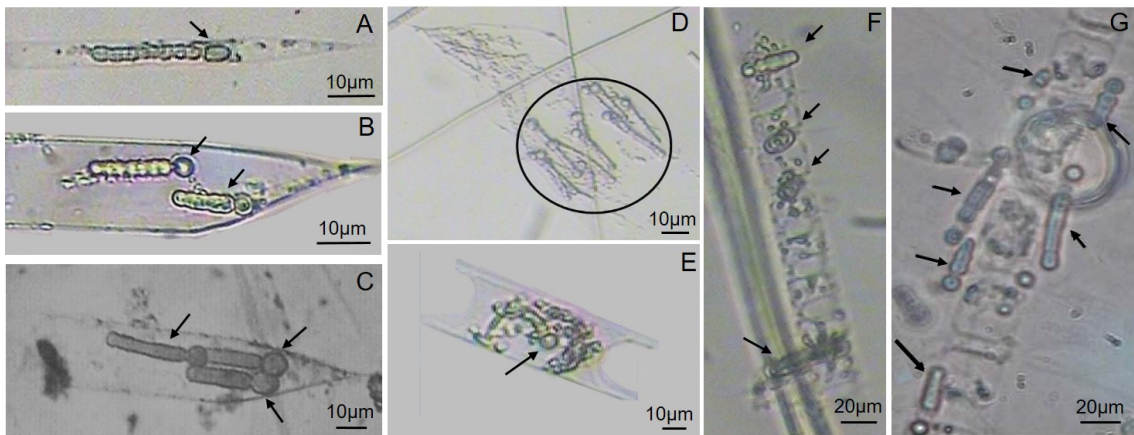


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 1047 **Figure 4.** Integrated concentrations of the total filamentous cyanobacteria (trichomes  $\text{m}^{-2}$ ) in  
 1048 the  $>10 \mu\text{m}$  fraction (*R. intracellularis* and *C. rhizosoleniae* not included) (bars) and the  
 1049 mixed layer depth (MLD) (lines) during the Diapalis cruises. Integration depths: 0-60 m at  
 1050 ST1 and ST2 and 30 m at ST3.  
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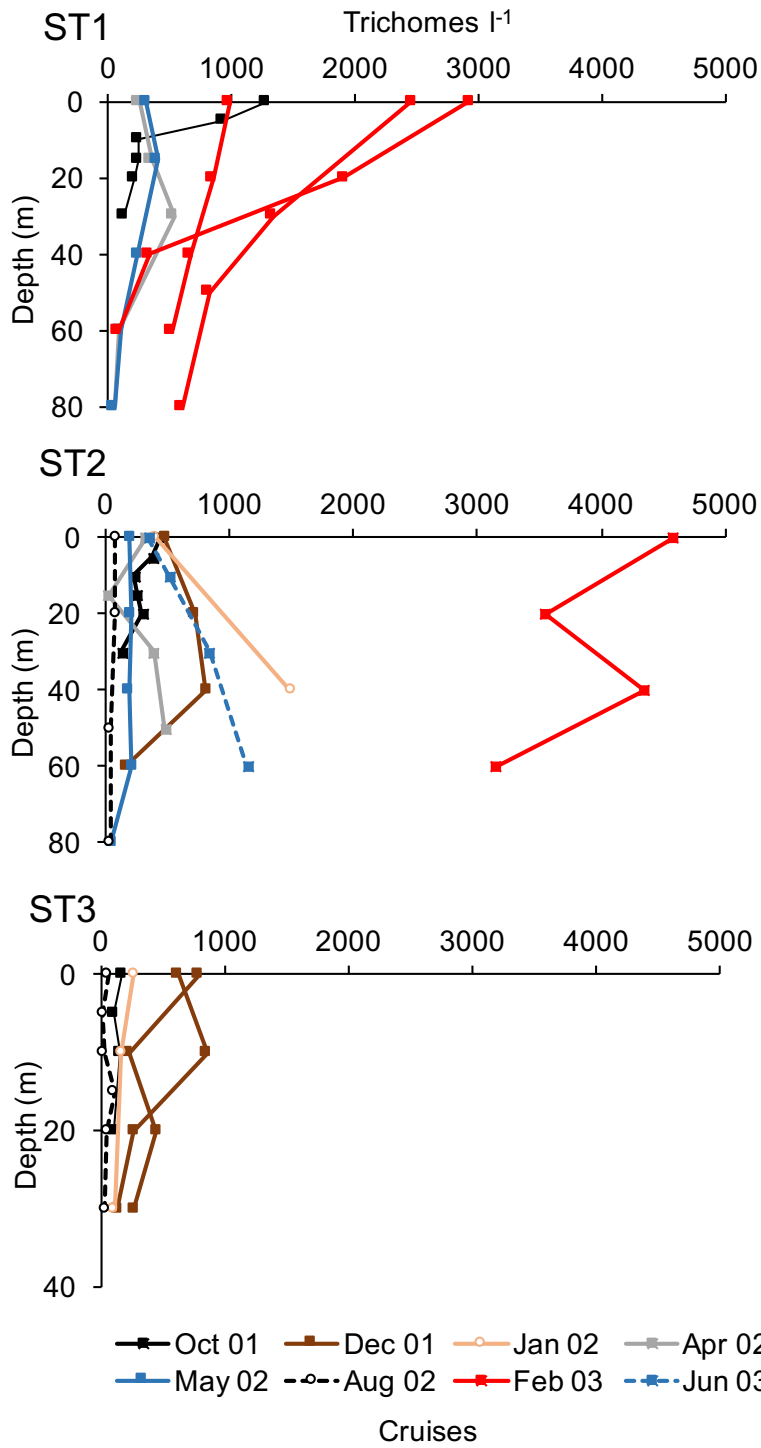
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**Figure 5.** Photomicrographs of filamentous cyanobacteria obtained from the Diapalis cruises. A) *Trichodesmium tenue*, B) Details of *T. tenue* trichomes: note that cell length is about 3 times longer than wide; the calyptra (formation at the tip of the trichome) and the necridium (structure formed from a dead cell which constitutes a fracture point of the filament). C) Colonies of unidentified cyanobacteria composed of round-shaped cells. Type 1, 3 $\mu\text{m}$   $\varnothing$  and Type 2, 6 $\mu\text{m}$   $\varnothing$  and D) details of Type-1. E-G) *Katagnymene spiralis* and *Katagnymene pelagica*. Note the size difference between *Katagnymene* spp. and *T. tenue*. H) Mix of major species (*T. erythraeum*, *T. tenue*, *T. thiebautii*).



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**Figure 6.** A-D) *Richelia intracellularis* symbiotic with *Rhizosolenia* spp. and E) *Hemiaulus* sp.; F-G) *Calothrix rhizosoleniae* epiphyte on *Chaetoceros* sp. Size and number of *Richelia* vary based on the size of the host. Photomicrographs obtained from the Diapalis cruises.

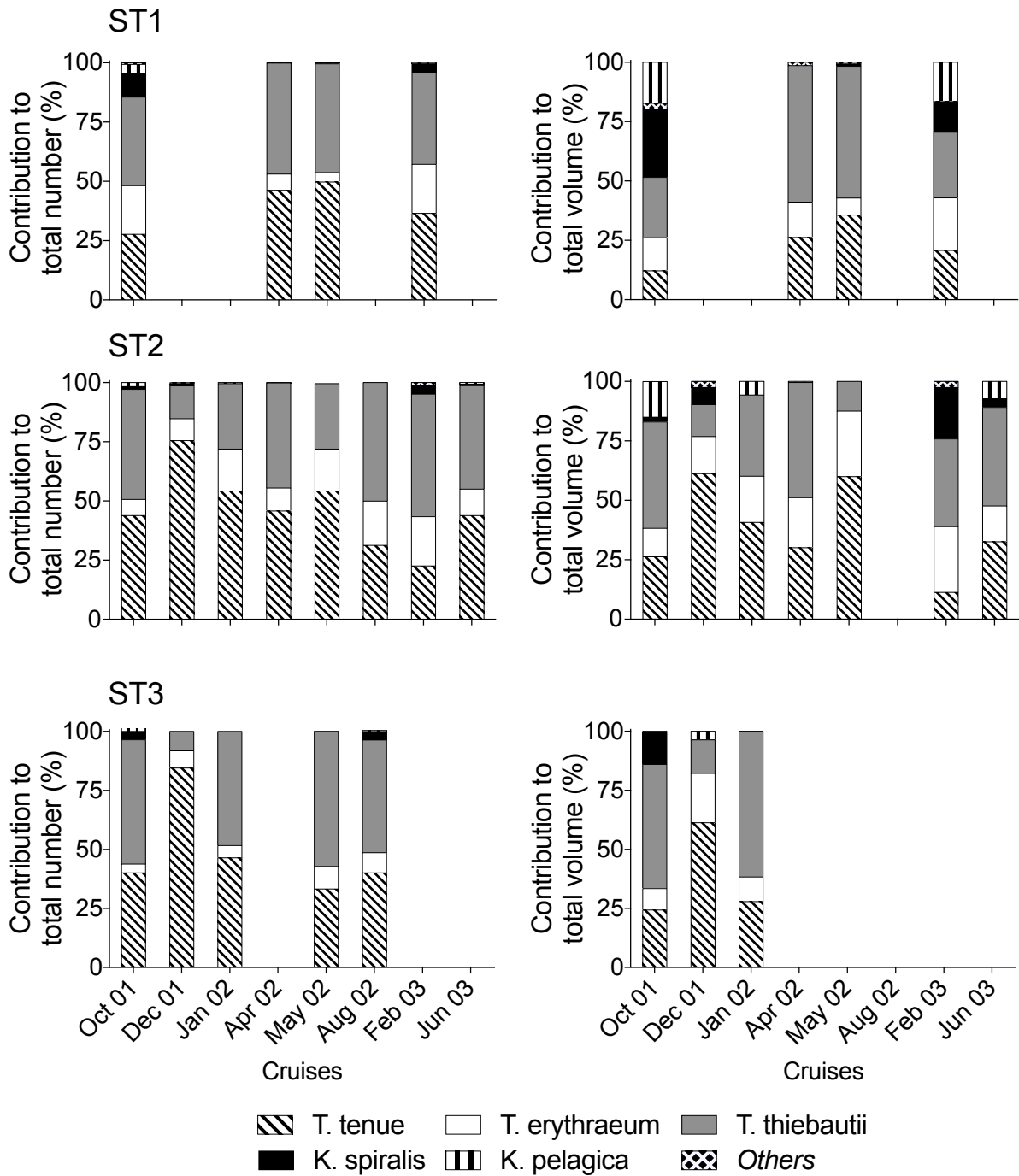


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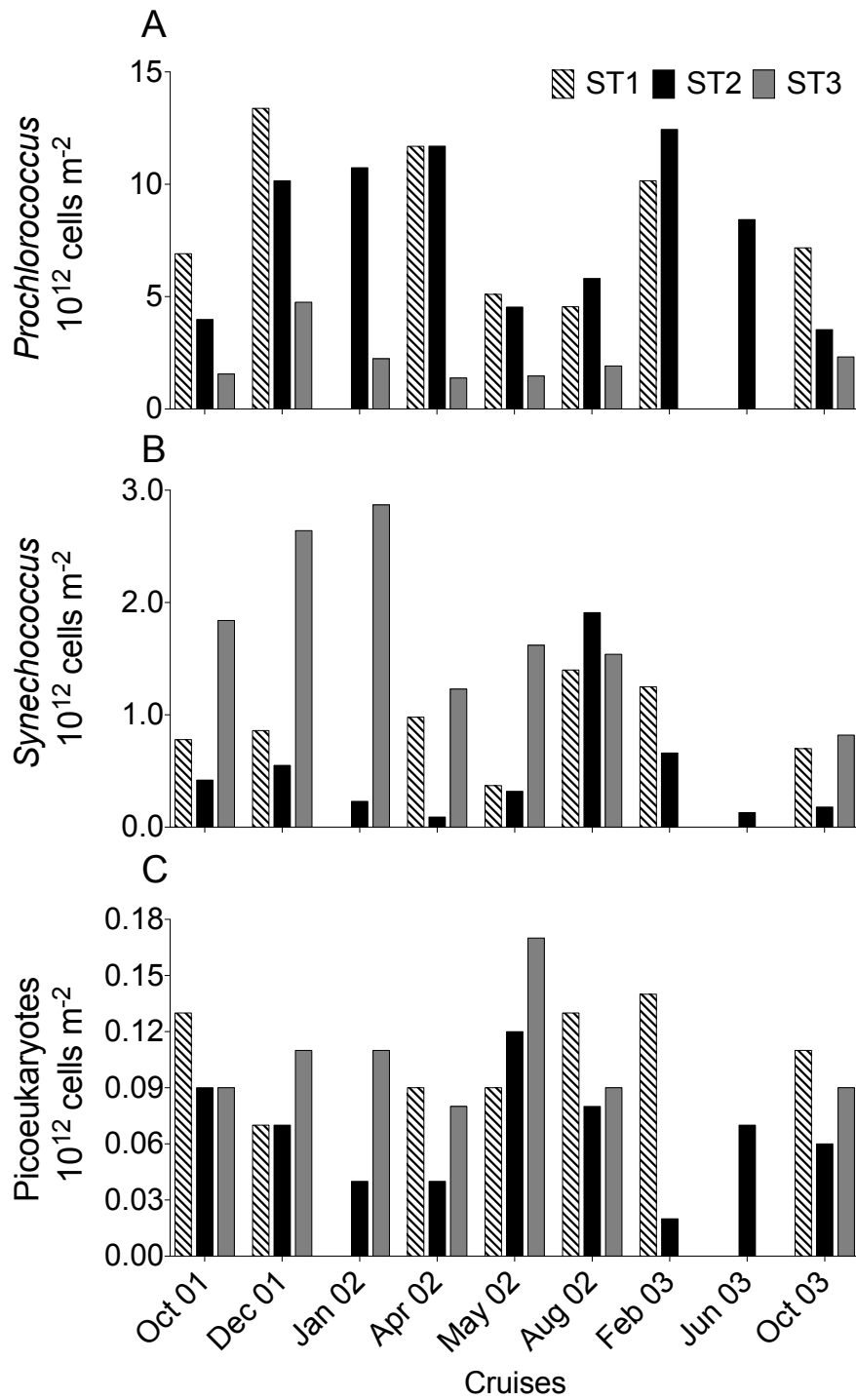
1074 **Figure 7.** Vertical profiles for filamentous cyanobacteria abundance (Trichomes l<sup>-1</sup>) (except  
 1075 *R. intracellularis* and *C. rhizosoleniae*) during the Diapalis cruise stations. ST2 (open ocean,  
 1076 Loyalty Channel) is well representative of the seasonal variations (some cruises are missing  
 1077 at ST1 and ST3). Note that at ST1 in February 2003, 3 profiles were performed with intervals  
 1078 of approximately 24h.

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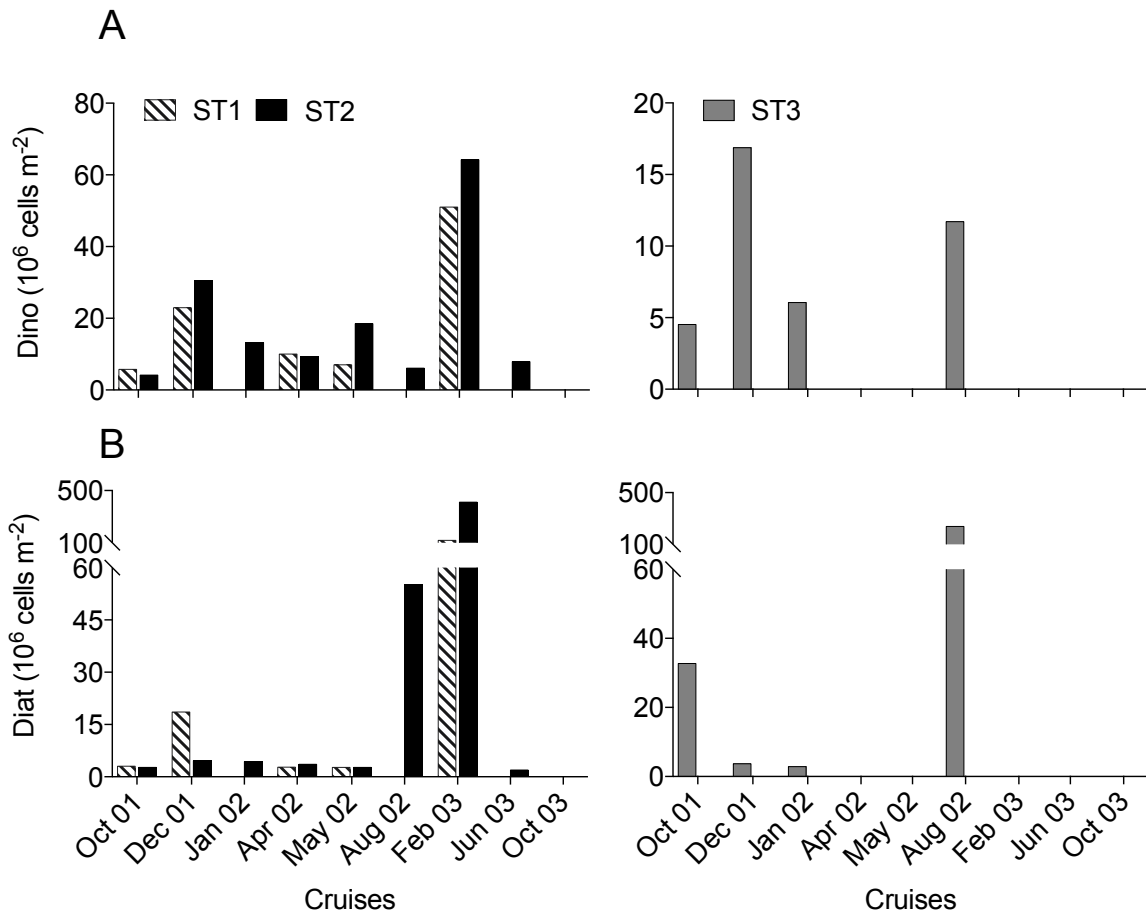


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**Figure 8:** Contributions of the various species (%), in terms of trichome number (left panels) and trichome volume (right panel) to the total community of filamentous cyanobacteria (*R. intracellularis* and *C. rhizosoleniae* not included) at the three stations sampled during the Diapalis cruises. Integration depths: 0-60 m at ST1 and ST2; 0-30 m at ST3. At ST1 “Others” = *T. hildebrandtii* (October 2001, May 2002 and February 2003) or *T. contortum* (October 2001); At ST2 “Others” = *T. hildebrandtii*. At ST2, species contributions were determined at each cruise, except in August 2002 for the *Trichodesmium* volume contribution. Some cruises are missing at ST1 and ST3.



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 1093 **Figure 9.** Integrated concentrations of (A) *Prochlorococcus*, (B) *Synechococcus*, and (C)  
 1094 picoeukaryotes at the three stations sampled during the Diapalis cruises. Integration depths: 0-  
 1095 60 m at ST1, ST2; 0-30 m at ST3.



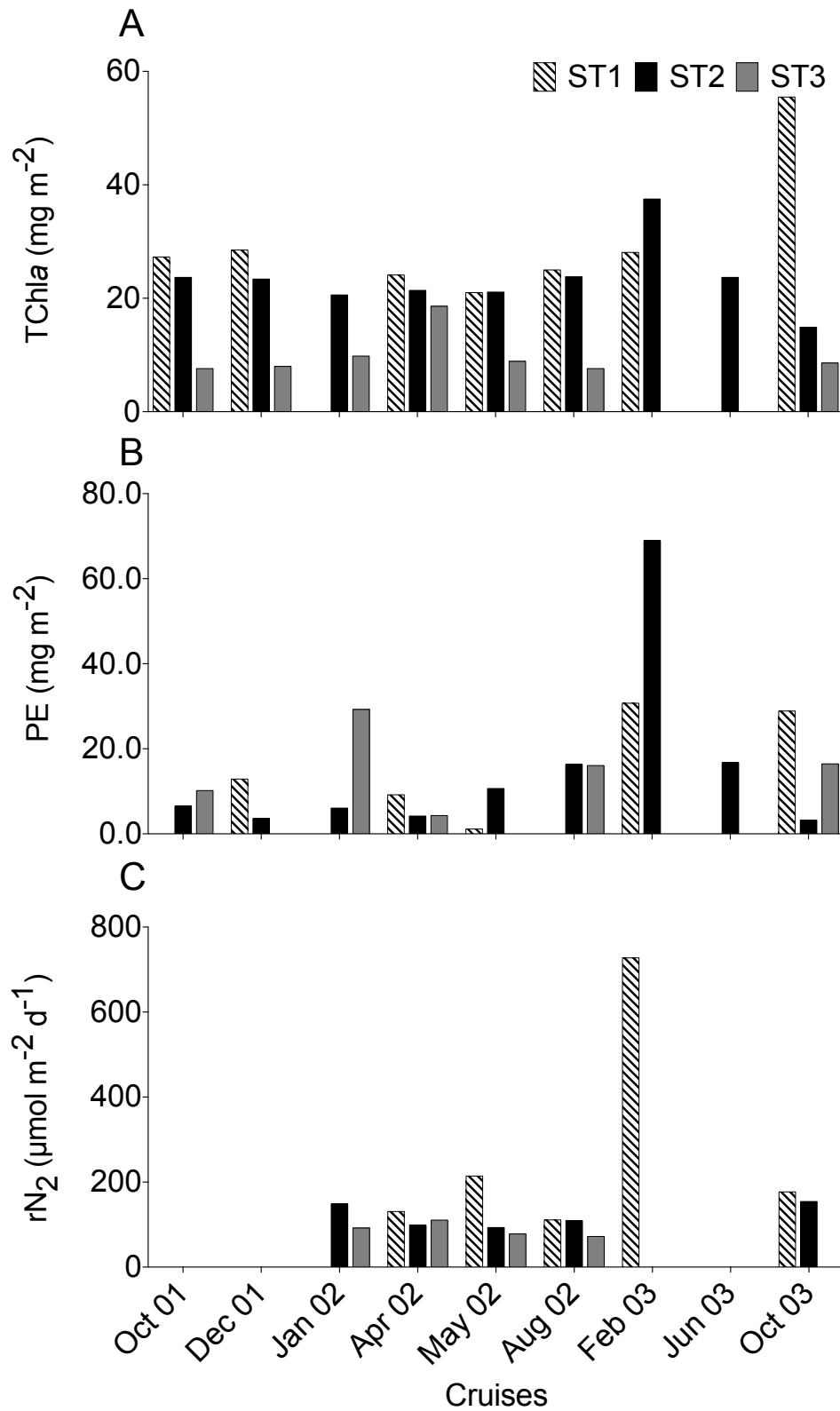
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1098 **Figure 10.** Integrated concentrations of (A) dinoflagellates (Dino) and (B) diatoms (Diat) in the  
 1099  $>10 \mu m$  fraction. Enumeration was carried out by inverted microscopy at the three stations  
 1100 sampled during Diapalis cruises. Integration depths: 0-60 m at ST1, ST2; 0-30 m at ST3. At ST2,  
 1101 integrated concentrations were determined at each cruise, except in August 2002. October 2003  
 1102 abundance was too low for enumeration. Some cruises are missing at ST1 and ST3.

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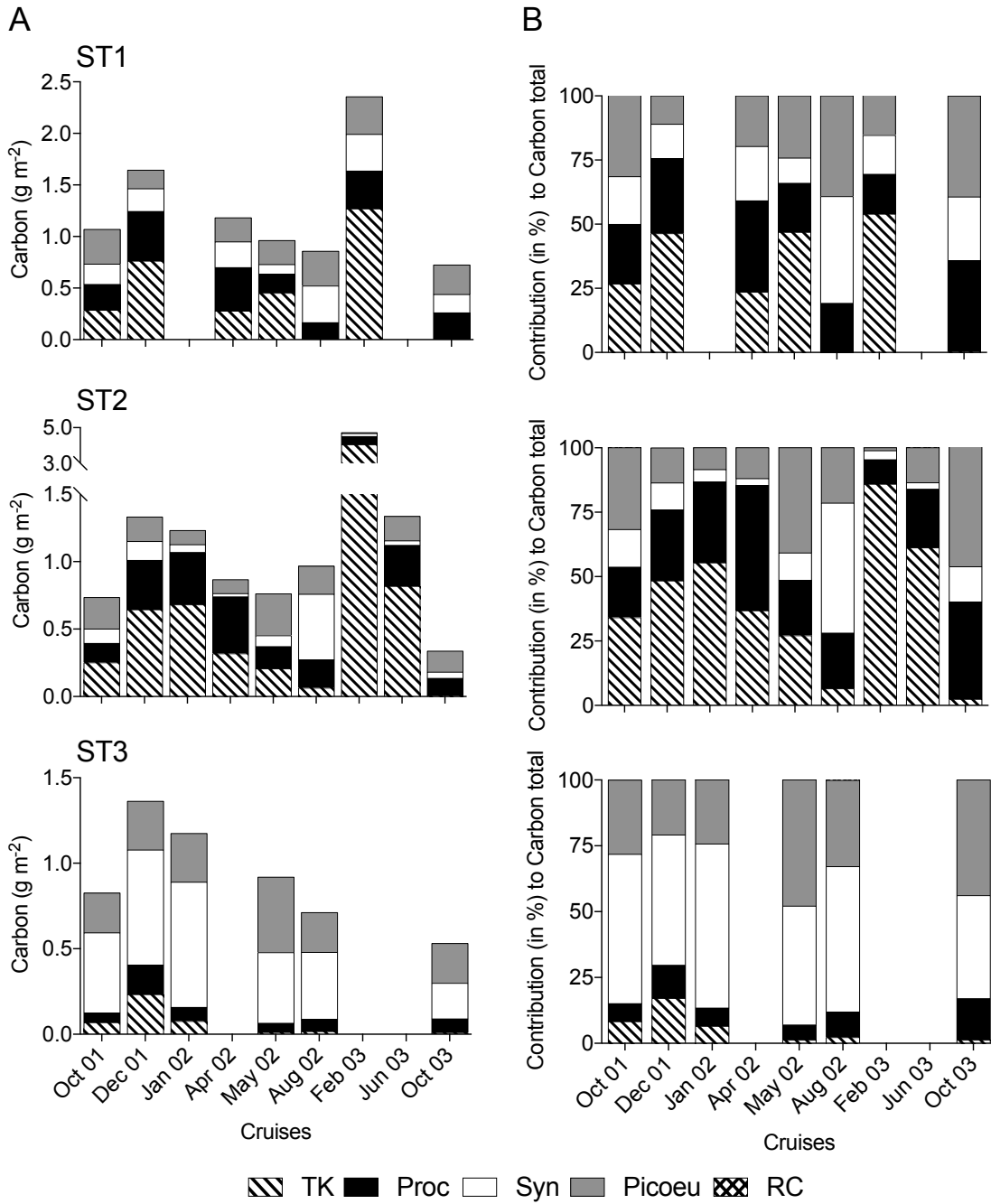
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1106 **Figure 11.** Integrated Tchl<sub>a</sub> (A) and phycoerythrin (B) concentrations and (C) N<sub>2</sub> fixation rates  
 1107 (Garcia et al. 2007) at the three stations sampled during the Diapalis cruises: Integration depths:  
 1108 0-60 m at ST1 and ST2, and 0-30 m at ST3.

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1113 **Figure 12.** A) Carbon biomass of picoplankton and filamentous cyanobacteria at the three  
 1114 stations sampled during the Diapalis cruises. The conversion factors were (fgC cell<sup>-1</sup>):  
 1115 *Prochlorococcus* – Proc (36), *Synechococcus* - Syn (255), picoeukaryotes - Picoeu (2590),  
 1116 *Richelia* - RC (10), sum of *Trichodesmium* and *Katagnymene* – TK (17.22 10<sup>6</sup> fgC trich<sup>-1</sup>). B)  
 1117 Contribution of each group to the total carbon shown in A).