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Response of phytoplankton communities to increased anthropogenic influences (southwestern lagoon, New Caledonia)

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ABSTRACT: We investigated the effects of changes in nutrient concentrations on phytoplankton biomass and community composition during 8 field trips performed during different seasons in the southwestern coral lagoon of New Caledonia. The lagoon is characterized by spatial variation in macronutrient concentrations, with locally elevated values in the bays bordering the city of Nouméa. Low DIN:DIP (dissolved inorganic nitrogen:dissolved inorganic phosphorus) and elevated Si:DIN ratios suggest that nitrogen is the macronutrient that likely drives phytoplankton community composition. Most of the microphytoplankton groups discriminated by inverted microscopy and the picoplankton groups distinguished by flow cytometry present significant and distinct relationships with inorganic nitrogen concentrations. Picophytoplankton-dominated assemblages are replaced by microphytoplankton-dominated assemblages with increasing DIN concentrations. Within the picophytoplankton, *Prochlorococcus* abundance dominates in the adjacent oceanic and southern lagoon shelf sites, and assemblages shift to *Synechococcus*-dominated populations in the bays, with an increasing proportion of picoeukaryotic phytoplankton. Within the microplankton, 142 species of microphytoplankton were identified, mainly represented by diatoms, dinoflagellates, and coccolithophorids. Nutrient enrichment in the bays favors large diatoms at the expense of coccolithophorids and dinoflagellates, which dominate in adjacent oceanic and southern shelf waters. Therefore, although moderate, the elevated nitrogen concentrations in the bays result in increased phytoplankton biomass, accompanied by important shifts in the phytoplankton community structure.

KEY WORDS: Size-fractionated chlorophyll · Picoplankton · Phytoplankton composition · Flow cytometry · Nutrients · Eutrophication · Coral reef lagoon

INTRODUCTION

The influence of macronutrient (N, P, Si) availability on phytoplankton species composition is well established in temperate waters (e.g. Olsen et al. 2001, Berg et al. 2003, Lee Chen et al. 2004), whereas oligotrophic tropical waters have received far less attention (Sakka et al. 1999, Van Duyl et al. 2002, Tada et al. 2003).

In tropical waters, coral reefs have often been considered to be mainly benthic ecosystems in which planktonic processes were negligible. Due to this relative lack of interest, planktonic studies in coral reef waters have mainly been focused on phytoplankton biomass and growth rate. Only a few studies have taken into account detailed information on phytoplankton composition, e.g. in French Polynesia (e.g. Delesalle et al. 1993, 2001, Dufour & Berland 1999), on the Great Barrier Reef (Revelante et al. 1982, Furnas & Mitchell 1986), or in the Caribbean (Van Duyl et al. 2002). Moreover, in most of the above studies, the relationships between nutrient concentrations and the phytoplankton community structure were not taken

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into account, with few exceptions (Sakka et al. 1999, Van Duyl et al. 2002).

Coral reef lagoons, like many coastal waters, are subjected to increased nutrient loads related to human activities and changes in nutrient concentrations, which have long been known to influence the composition of the phytoplankton community (Margalef 1978). These changes in the phytoplankton community structure, in turn, affect the nutrient cycling (Sakka et al. 2002) and the structure of the other compartments of the food web, either in temperate or in tropical waters (Niquil et al. 1999, Olsen et al. 2001). Due to their oligotrophic status, increased nutrient concentrations are expected to have a stronger impact on phytoplankton communities in coral reef waters than in meso- to eutrophic temperate waters. However, the influence of increased nutrient load of human origin on the phytoplankton community structure in tropical waters has only been documented in the study of Van Duyl et al. (2002) in the Caribbean.

Furthermore, changes in the structure of phytoplankton communities are known to have been involved in the increased frequency of phytoplankton blooms during the last decades in temperate waters (Smayda 1989), often with severe consequences for aquatic resources (Zingone & Oksfeldt-Enevoldsen 2000) and human health (Anderson et al. 2002). Planktonic harmful algal blooms in coral reef waters sometimes occur, but have seldom been documented (Guzman et al. 1990). Therefore, the consequences of an increased nutrient load of human origin on the phytoplankton community structure need to be considered in various coral reef environments of differing trophic status.

The aim of the present study was to investigate the effects of local changes in nutrient concentrations induced by human activities on the phytoplankton biomass and composition in the SW lagoon of New Caledonia. Very little is known about phytoplankton biomass (Rougerie 1985) and phytoplankton composition in this lagoon (Cardinal 1983), where several trophic gradients exist between the more-or-less anthropogenically impacted coastal regions and the oligotrophic ocean. Locally elevated nutrient concentrations observed in the coastal areas of metropolitan Nouméa are due to urban sewage, industrial, and/or agricultural wastes.

We studied the relationships between macronutrient concentrations and phytoplankton, first considering the global estimates of phytoplankton abundance, i.e. total and size-fractionated chlorophyll *a*, in order to allow comparisons with existing studies in coral reef waters. However, we focused mainly on the still largely unknown composition of the phytoplankton community, namely the pico- and microphytoplankton, and investigated in detail the relationships with macronutrient concentrations.

MATERIALS AND METHODS

Study area. The SW lagoon of New Caledonia covers approximately 2066 km^2, with a mean depth of 17.5 m (Fig. 1A). Three deep passes (60 m depth) bisect the barrier reef. Freshwater inputs are mainly provided by the Dumbéa, Boulari, and Pirogues Rivers. The dominant southeasterly trade winds govern the direction of the surface currents (Jouon et al. in press). Oligotrophic oceanic waters enter the lagoon through the open southern shelf, are driven into the study area by the trade winds, and then exit by the passes on the western shelf. Therefore, the shelf was divided into a western and a southern sector, the latter being generally the most oligotrophic area, as it is remote from the terrigeneous and anthropogenic influences.

The area of the lagoon studied encompasses the city of Nouméa, with a population of 146000 (63% of the total population of New Caledonia). Around Nouméa, 4 bays, which differ in terms of the predominant human activities, were examined (Fig. 1B). Sainte-Marie Bay receives urban waste waters from the Sainte-Marie area. Grande Rade Bay is also influenced by urban effluents, but, in addition, receives industrial effluents originating from the nickel industry. In contrast, Dumbéa and Boulari Bays are under terrigeneous influence from the Dumbéa and Pirogues Rivers, respectively. In addition, an oceanic station located 2 nautical miles offshore of the Dumbéa Pass was sampled (Fig. 1A). Thus, the investigated stations were arranged in 6 groups: southern shelf, western shelf, Sainte-Marie Bay, Grande Rade Bay, Dumbea Bay, and Boulari Bay, with the oceanic station being analyzed separately.

Sampling. Water samples were collected during 8 field trips that took place during different seasons between November 1999 and January 2003 (Table 1). A small speed boat was used for all field trips, except that of September 2000 during which work was done at 71 stations distributed throughout the whole SW lagoon; this sampling was conducted from the RV 'Alis' (Fig. 1A). In each bay and on the western shelf, transects of 6 stations, arranged along a trophic gradient, were sampled (Fig. 1B). Water samples were collected using acid-washed 5 l Niskin bottles at 3 m depth, in order to prevent contamination by occasional freshwater inputs following precipitation events. Previous work has shown that 3 m deep samples are, on average, representative of the whole water column (authors' unpubl. data). Samples were either immediately processed onboard (September 2000) or kept in Niskin bottles until return to the laboratory (within 1.5 h). Conductivity, temperature, *in vivo* fluorescence, and turbidity profiles were simultaneously recorded using a SeaBird SBE 19 profiler and Seapoint fluorometer and turbidity meter.

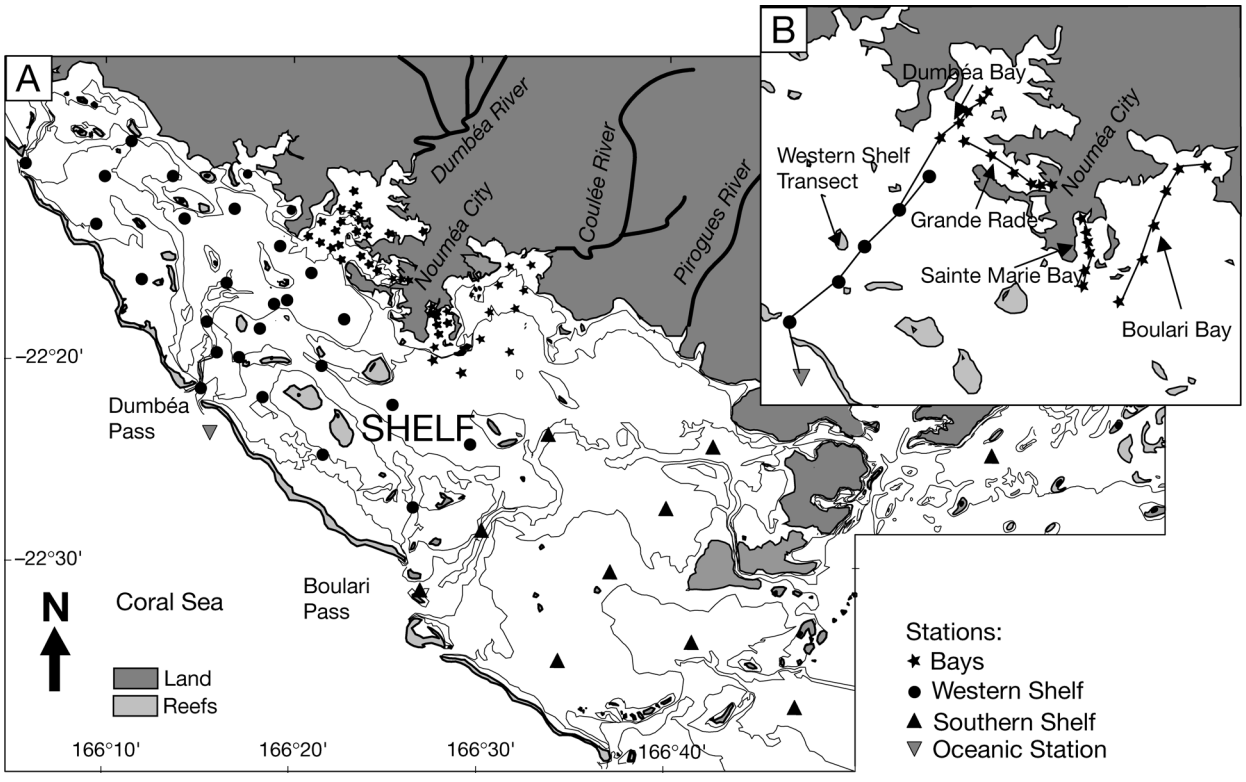

Fig. 1. (A) Map of the southwestern lagoon indicating sampling locations. Each group of stations is represented by a different symbol. (B) Stations sampled around Nouméa. Sainte-Marie Bay receives urban waste waters. Grande Rade receives urban waste waters and industrial effluents from the nickel industry. Dumbéa and Boulari Bays are under terrigeneous influence

Nutrient analyses. Ammonium concentration was fluorometrically determined in 3 unfiltered 40 ml replicates on a Turner TD-700, using the *o*-phthaldialdehyde method (Holmes et al. 1999) immediately after collection. This procedure gave a coefficient of variation (CV) between replicates ranging from 5 (eutrophic) to 30% (oligotrophic waters).

Unfiltered, replicate, 40 ml samples were immediately frozen pending nitrate + nitrite (NO_3 + NO_2) and phosphate (PO_4) analyses. NO_3 + NO_2 (CV 3 to 8%) and PO_4 (CV 6 to 11%) concentrations were determined on a Bran+Luebbe Autoanalyzer III according to Raimbault et al. (1990) and Grasshoff et al. (1983), respectively. Total silicates (i.e. dissolved and colloidal) were determined on one 60 ml subsample that was immediately frozen after sampling according to Grasshoff et al. (1983).

Phytoplankton abundance and composition. Chlorophyll *a* (chl *a*) concentration was fluorometrically determined on methanol extracts of replicate 300 ml samples filtered onto Whatman GF/F filters according to Holm-Hansen et al. (1965). The size-fractionated chl *a* concentrations were also determined on 90 replicate 300 or 500 ml samples, using 2 and 10 µm Nuclepore membranes. These samples were collected during the field trips in April 2002, August 2002, and January 2003.

Picophytoplankton, i.e. *Prochlorococcus*, *Synechococcus*, and picoeukaryotes, were enumerated by flow cytometry on 205 samples collected during the field

Table 1. Sampling period and number of stations sampled. A transect is a set of 6 stations located from the coast to the open sea (cf. Fig. 1B)

Period	No. of station	Site
Nov 1999	19	5 transects (1 in each of the 4 bays and 1 on the western shelf)
Sep 2000	71	Western and southern shelves, oceanic station, and bays
Nov 2000	9	Western shelf
Mar–Apr 2001	85	5 transects (1 in each of the 4 bays and 1 on the western shelf), 3 times
Jul 2001	21	4 transects (except Boulari Bay)
Apr 2002	30	5 transects (1 in each of the 4 bays and 1 on the western shelf)
Aug 2002	30	5 transects (1 in each of the 4 bays and 1 on the western shelf)
Jan 2003	30	5 transects (1 in each of the 4 bays and 1 on the western shelf)

trips in November 1999 to July 2001. Water samples (1.5 ml) were preserved with 7.5 µl glutaraldehyde (Sigma Grade II) at room temperature in the dark for 15 min before storage in liquid nitrogen pending analysis. Enumeration of picophytoplankton populations was conducted according to Blanchot & Rodier (1996) on a FACScan flow cytometer (Becton Dickinson) equipped with an air-cooled laser providing 15 mW at 488 nm and with a standard filter setup. Yellow fluoresbrite 0.95 µm beads were used as internal standards (size and fluorescence). The count rates per second never exceeded 500 optical events, in order to avoid underestimation of particle abundance. Glutaraldehyde-preserved picophytoplankton cannot be sized from a FACScan flow cytometer (FSC); picoplankton carbon was therefore computed using 0.053 pg C cell^{-1} for *Prochlorococcus* (Partensky et al. 1996), 0.25 pg C cell^{-1} for *Synechococcus* (Kana & Gilbert 1987), and 2.108 pg C cell^{-1} for picoeukaryotes (Campbell et al. 1994).

The abundance and biovolume of microalgae were estimated using inverted microscopy on a selection of 135 samples collected during field trips. Water samples (250 ml) were preserved in the dark with neutral formalin (2.5%, final concentration). Cell counts were carried out on the whole sample using the classical Utermöhl method with an inverted microscope (Wild M40 or Olympus IMT). Counting was done at a magnification of ×300, either on 1 cm^2 or on three 2.5 cm diameters of the settling chamber, depending on algal abundance. Higher magnification (×1500) was used for the identification of minute species. The inverted microscope usually does not allow the identification of most of the phytoplankton species, particularly the smallest specimens (e.g. coccolithophorids). In this study, phytoplankton was always identified at the class level, whereas the identification at the genus or species level was made whenever possible. Counts were expressed as numbers of individuals or filaments of cyanobacteria per liter. For chain-forming diatoms, each individual was counted, in order to calculate the biovolumes. Microalgal biovolumes were calculated using the standardized set of equations proposed by Hillebrand et al. (1999). The linear dimensions used for calculation were obtained either from microscopy measurements or from the literature (e.g. Tomas 1996). For each taxon, a unique mean volume was then applied to all samples in which this taxon was encountered. Finally, microplankton biovolume was converted into carbon units using the 2 carbon-to-volume relationships proposed by Menden-Deuer & Lessard (2000) for diatoms and flagellates, respectively.

Statistical tests. One-way ANOVA (analysis of variance) was used to compare nutrients and phytoplankton average data between the 7 areas of the SW lagoon. Data were normalized using $\log(x + 1)$ transformation. When the ANOVA test showed significant effects, an LSD (least significant difference) *a posteriori* Fisher's *t*-test was applied on paired groups of stations. Spearman rank correlation coefficients were used in order to characterize the gradients of nutrient concentrations along the stations of the transects (Fig. 1B). The correlation coefficients were tested by *a posteriori* Bonferroni test. Model II regression (Sokal & Rohlf 1995) was used on log-transformed data in order to analyze the relationships between nutrient concentrations and phytoplankton characteristics (i.e. total and size-fractionated chl *a* concentrations and pico- and microphytoplankton abundances). Regarding the microalgae, the limited precision of counts was circumvented by grouping algal abundances in a limited number of classes. All regression analyses of phytoplankton variables versus nutrients were performed on average values computed in 12 logarithmic classes of nutrient concentrations. Classes containing only 1 value were not considered in the regression analyses.

RESULTS

Physical characteristics

Temperature and salinity did not differ significantly along transects (data not shown). Water temperature ranged between 20.7°C (August 2002) and 28.8°C (January 2003), whereas salinity was generally (83% of the values) between 34.5 and 35.5.

Nutrients

The ANOVA analyses showed that DIN (dissolved inorganic nitrogen, ~0.15 µM) did not differ significantly between the ocean, the southern and western shelves, and Boulari Bay (Fig. 2). DIN concentrations were significantly elevated in the other bays, Sainte-Marie Bay being the most enriched (~0.95 µM).

Regarding phosphorus, Sainte-Marie Bay presented DIP concentrations (dissolved inorganic phosphorus, 0.12 µM) that were significantly higher than at all other sites, whereas Grande-Rade Bay (0.06 µM) displayed DIP concentrations that were greater than in Boulari Bay (0.03 µM) and on the western shelf (0.04 µM). Si concentration was significantly lower in the ocean and southern shelf (~1.04 µM) than on the western shelf (1.95 µM) and was significantly higher in the bays (2.5 to 5 µM) than in the adjacent ocean, western and southern shelves.

Along transects, all nutrients showed significant gradients in Sainte-Marie and Grande Rade Bays, i.e. the bays located in the urbanized area (Table 2). In contrast, no significant gradients were detected for DIN and DIP

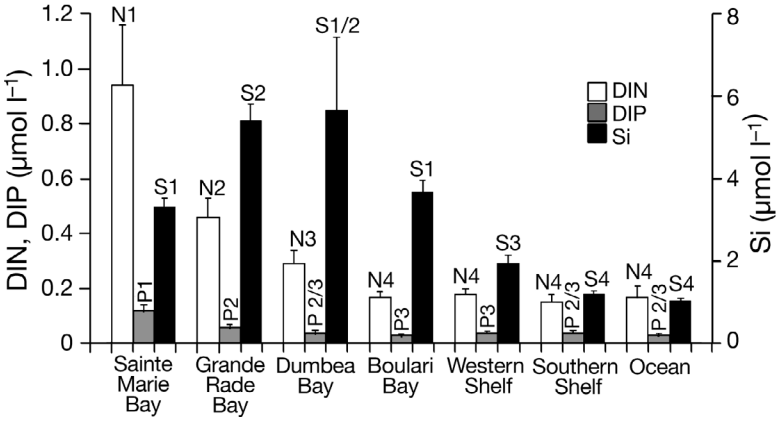

Fig. 2. Average nutrient concentrations for the different areas of the SW lagoon (DIN, DIP: dissolved inorganic nitrogen and phosphorus, respectively; Si: silicates). Error bars represent standard errors. Same letters and numbers indicate averages that are not significantly different (ANOVA, $p < 0.01$)

in the non-urbanized Dumbéa and Boulari Bays nor along the western shelf transect. Significant gradients in silicates were observed within all the transects.

The mean DIN:DIP ratio was 5.4 ± 0.9 (±SE, n = 241) for all samples. Low DIN and high Si concentrations resulted in high Si:DIN ratios (mean ± SE: 23.3 ± 2.1, n = 285). In general, there were no significant gradients in nutrient ratios within the bays. The only exceptions were Grande Rade Bay (Si:DIN) and Boulari Bay (NH_4^+:DIN).

Phytoplankton

The total chl *a* concentrations ranged from 0.1 to 2.4 µg l^{-1}. They did not differ between the ocean and the shelf, but significantly increased in the bays (Fig. 3). The chl *a* concentrations were significantly higher in Grande Rade and Sainte-Marie Bays than in Boulari and Dumbéa Bays, and coast-to-lagoon transects showed significant gradients within each bay (Table 2). The maximum contribution (88%) of the <2 µm fraction was observed in the ocean, whereas the maximum contribution (74%) of the >10 µm fraction was observed at the inner station of Grande Rade (Fig. 3).

The abundances of *Synechococcus*, *Prochlorococcus*, and picoeukaryotes varied by 2 orders of magnitude among sites. *Prochlorococcus* largely dominated picophytoplankton abundance at the oceanic station (87 ± 4%); it dropped to 40 and 31% on the southern and western shelves and exhibited minor contributions in the bays (Fig. 4). *Synechococcus* represented 12 ± 4% of picophytoplankton abundance in oceanic waters, and increased in proportion in shelf waters (57 to 66%) to reach up to 91% of picophytoplankton cells in the bays. Picoeukaryotic algal cells contributed little to picophytoplankton abundance, and increased from 1.2 ± 0.1% in oceanic waters up to 3.9 ± 0.6% on the shelf and 6.5 ± 0.6% in the bays.

Microalgal abundance varied by 3 orders of magnitude among sites, between 0.2 and 464 × 10^3 cells l^{-1}, whereas biovolume ranged between 2.0 × 10^5 and 3.3 × 10^9 µm^3 l^{-1}. The highest phytoplankton abundances and biovolumes were observed in Grande Rade and Sainte-Marie Bays, i.e. in the most urbanized bays (Fig. 5). Eight phytoplankton classes were identified (see below). However, diatoms, dinoflagellates, and coccolithophorids were predominant and together contributed 95.5% to total microalgal abundance. The mean (±SE) percentage of undetermined algae was 3.3 ± 0.5%. Microalgae were significantly

Table 2. Spearman's rank correlation coefficients between data and station distance from the coast. Correlations were computed with data from all transects (Fig. 1B) and not from Fig. 2 averages. Negative values indicate variables decreasing from the coast (**$p < 0.01$; *$p < 0.05$; otherwise not significant; DIN: dissolved inorganic nitrogen [$NH_4 + NO_3 + NO_2$]; DIP: dissolved inorganic phosphorus; Si: silicate; chl *a*: chlorophyll *a*)

	DIN	DIP	Si	Chl *a*
Sainte-Marie Bay	−0.52** (45)	−0.58** (50)	−0.39** (50)	−0.50** (50)
Grande Rade Bay	−0.55** (46)	−0.55** (46)	−0.62** (46)	−0.60** (46)
Dumbéa Bay			−0.70** (54)	−0.70** (54)
Boulari Bay			−0.51* (38)	−0.50* (40)
Western shelf transect			−0.39** (45)	−0.60** (45)

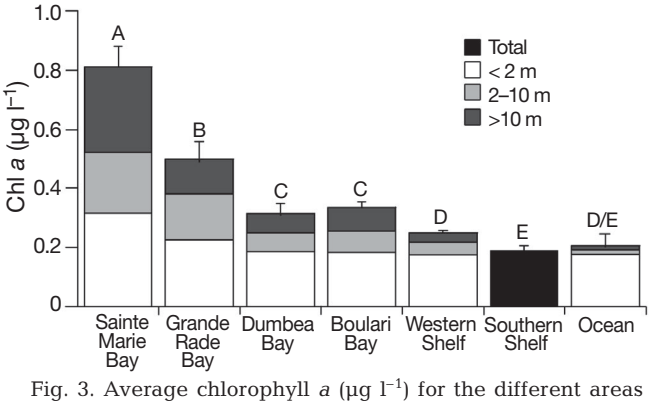

Fig. 3. Average chlorophyll *a* (µg l^{-1}) for the different areas of the SW lagoon of New Caledonia. Chl *a* concentrations always increased in the bays close to the coast. Error bars represent standard errors of the total chl *a* concentration. Same letters indicate averages of total chl *a* concentration that are not significantly different (ANOVA, $p < 0.01$)

more abundant ($p < 0.05$) in the bays than in the lagoon or ocean (Fig. 5). However, this higher abundance was mainly caused by an increase in the diatom numbers. This predominance of diatoms was observed in terms of both cell number and biovolume. The mean abundance and biovolume of diatoms ranged from ca. 1 to 3×10^3 cells l^{-1} and from 2.1 to 51.2×10^6 µm^3 l^{-1}, respectively, at the ocean and lagoon stations; in the bays, the cell number and biovolume always exceeded 20×10^3 cells l^{-1} and 311×10^6 µm^3 l^{-1}, respectively. In contrast, coccolithophorids showed a slight but significant decrease in the bays, whereas dinoflagellates did not significantly vary between the 7 sites (Fig. 5).

A total of 142 microalgal taxa belonging to 8 phytoplankton groups were identified (Appendix 1, see www.int-res.com/articles/suppl/m320p065_app.pdf). Diatoms, dinoflagellates, and coccolithophorids were the most diversified groups and contributed 50.7, 29.2, and 12.5% to the total number of taxa, respectively. Cyanophytes, prasinophytes, euglenophytes, cryptophytes, and dictyochophytes (silicoflagellata) were represented by few species, mainly because the identification of these taxa is difficult with the inverted microscope. Tropical species represented half of the identified species, the others being cosmopolite. Most of the species were truly planktonic species, <10 tychoplanktonic species (e.g. *Licmophora*, *Mastogloia* species, *Trachyneis aspera*) being observed. Regarding the ecological characteristics of the phytoplankton, oceanic species (e.g. *Oxytoxum* spp., *Podolampas spinifera*, *Dictyocha fibula*) were not restricted to the ocean and lagoon sites, but were occasionally observed in the bays. Similarly, some neritic species (e.g. *Diploneis bombus*, *Pleurosigma fasciola*, *Synedra* sp., *Prorocentrum micans*) were found on the western and southern shelves. Regarding the average abundance of the species, only 6 diatom species exceeded 10^3 cells l^{-1} (*Chaetoceros socialis*, *Bacteriastrum* spp., *Asterionellopsis glacialis*, *Bacteriastrum furcatum*, *Pseudonitzschia* sp., *Skeletonema costatum*; data not shown).

The number of taxa observed at each site varied from 40 in Boulari Bay and 48 in the ocean up to 100 in Dumbéa Bay and 114 on the western shelf, the other sites showing intermediate values of ca. 60 to 70 taxa (Appendix 1). These variations were mainly related to the number of diatom species identified, which varied 4-fold between the ocean and the western shelf. However, despite several statistical analyses, it was not possible to describe a consortium of species restricted to a given site nor to identify specific phytoplankton in the bays versus the lagoon or the ocean. In fact, only 32 species were observed exclusively at 1 site (Appendix 1). Furthermore, most of the 32 species occurred on only 1 or 2 occasions, with abundances never exceeding 3×10^3 cells l^{-1}, except *Cyclotella* sp. (8.6×10^3 cells l^{-1}). Similarly, only 23 species were observed in the bays but not in the lagoon or ocean, and they occurred in <10% of the samples, except for *Asterionellopsis glacialis* and *Leptocylindrus danicus* (Appendix 1). In the bays, 3 spe-

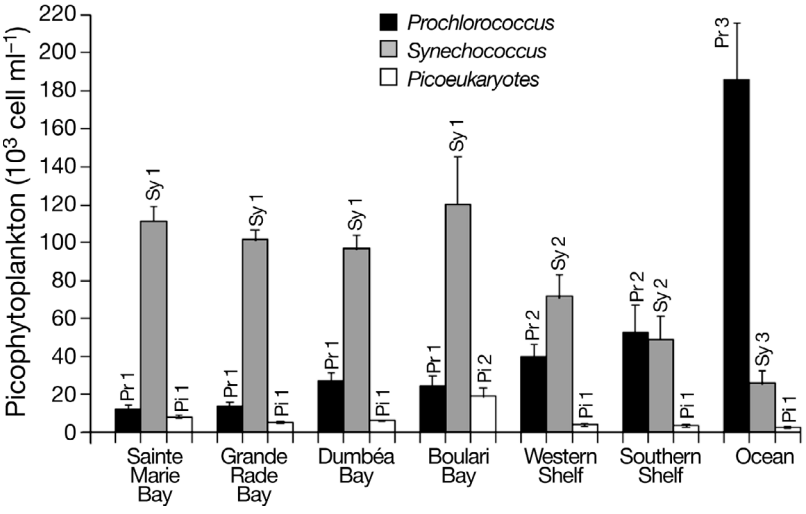

Fig. 4. Picophytoplankton average abundance in different lagoon areas. Error bars represent standard errors. Same letters and numbers indicate that averages are not significantly different (ANOVA, $p < 0.01$)

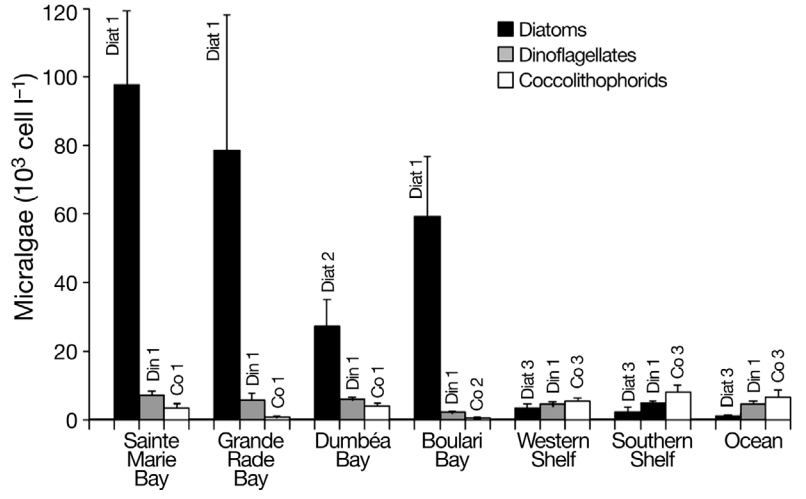

Fig. 5. Microalgal average abundance in different lagoon areas. Error bars represent standard errors. Same letters and numbers indicate averages that are not significantly different (ANOVA, $p < 0.01$)

Table 3. Mean and maximum abundances (cells l^{-1}) and frequency of occurrence (%) of potentially toxic microphytoplankton species. Species are arranged according to decreasing mean abundances

Potentially toxic species	Abundance (cells l^{-1}) Mean	Max.	Occurrence (%)
Pseudonitzschia sp. H. Peragallo	11332	187259	41
Prorocentrum micans Ehrenberg	432	4560	20
Gymnodinium sp. Stein	265	1053	15
Oscillatoria sp. Vaucher Ex Gomont	235	877	20
Prorocentrum aff. *mexicanum* Tafall	233	1909	12
Gyrodinium sp. 1 Stein	203	912	49
Prorocentrum dentatum Stein	201	909	8
Prorocentrum spp. Ehrenberg	150	785	11
Gyrodinium sp. 2 Stein	101	197	9
Dinophysis caudata Saville-Kent	98	206	4
Pronoctiluca acuta (Lohmann) Schiller	96	303	14
Amphidinium sp. Clarapède & Lachmann	92	95	2
Cochlodinium sp. Schütt	77	303	11
Gonyaulax sp. Diesing	73	197	13
Lingulodinium polyedrum (Stein) Dodge	54	77	3
Dinophysis sp. Ehrenberg	52	155	8
Gonyaulax kofoïdii Pavillard	18	18	1

cies showed significant mean abundances: *Asterionellopsis glacialis* and *Skeletonema costatum* (24×10^3 cells l^{-1}) and *Cyclotella* sp. (8.6×10^3 cells l^{-1}).

Finally, it has to be noted that the possibly toxic genus *Pseudonitzschia* was observed in 40% of the samples, with a mean abundance of 11×10^3 cells l^{-1} and a maximum of 187×10^3 cells l^{-1} (Table 3). Identification of the species of *Pseudonitzschia*, required because only some species of the genus are toxic, was impossible as it necessitated SEM (scanning electron microscope) examinations. Several possibly toxic dinoflagellates, e.g. *Prorocentrum* aff. *mexicanum* or *Dinophysis caudata*, were also observed, but their abundances never reached 2×10^3 cells l^{-1}, except for *Prorocentrum micans* (4.6×10^3 cells l^{-1}) (Table 3).

DISCUSSION

Few studies have investigated the relationships between the nutrient concentrations and phytoplankton in coral reef waters. Most of them focused on the global estimates of phytoplankton abundances, i.e. total or size-fractionated chl *a* (e.g. Charpy & Blanchot 1999), while the effects of nutrients on the structure of the phytoplankton communities were seldom considered (Sakka et al. 1999, Van Duyl et al. 2002). Treating the phytoplankton as a single ecological and physiological unit does not allow the study of the varying impacts of different phytoplankters on matter and energy cycles in the ocean. Although size fractionation captures some of the functional differences between groups of phytoplankters (Agawin et al. 2000), it is useless as a tool to discriminate between groups of similar size. Indeed, diatoms and dinoflagellates, which are the major groups of large phytoplankters, exhibit important physiological and ecological differences (Goericke 2002), and, among picophytoplankton cells, *Prochlorococcus* and *Synechococcus* may utilize different nitrogen sources (Moore et al. 2002) and be consumed by flagellates at different rates (Christaki et al. 2002). Thus, the effects of nutrients on the phytoplankton in the SW lagoon of New Caledonia were considered not only as total chl *a*, but also as a range of variables describing the phytoplankton community structure, i.e. size-fractionated chl *a*, picophytoplankton abundance, composition and biovolumes, and abundance, composition, and biovolumes of nano- and microphytoplankton.

Limiting nutrient

The median value of the DIN:DIP ratio (4.5:1) was considerably lower than the classical (16:1) Redfield ratio, whereas, in contrast, the Si:DIN ratio (median: 23.3) by far exceeded the Redfield ratio (1:1). However, the nutrient status of phytoplankton cannot be assessed by the N:P ratio alone, but requires comparison of nutrient concentrations with threshold literature values (Dortch & Whitledge 1992). Using literature threshold values (DIN ≤ 1 µM, DIP ≤ 0.1 µM, and SiO_2 ≤ 2 µM; Justic et al. 1995) and according to the criteria by Justic et al. (1995), P is limiting if Si:DIP > 22 & DIN:DIP > 22, N is limiting if DIN:DIP < 10 & Si:DIN > 1, and Si is limiting if Si:DIP < 10 & Si:DIN < 1.

Therefore, nutrient values strongly suggest that N was the limiting nutrient in the large majority of the samples in New Caledonia's SW lagoon (Table 4). This N limitation is in agreement with the much shorter turnover time (concentration:uptake rate) for ammonium than for DIP in the same area (J.-P. Torréton pers. comm.). This limitation by nitrogen is not surprising, since coral reef waters have often been considered N limited. Indeed, N limitation has been reported in the tropical Pacific waters of most of the 12 Tuamotu Atoll lagoons studied (Dufour & Berland 1999, Torréton et al.

Table 4. Percentage of samples in which nutrient ratios and concentrations suggest nutrient limitation (n: number of samples)

	Ocean (n = 10)	Southern shelf (n = 15)	Western shelf (n = 50)	Boulari Bay (n = 35)	Dumbea Bay (n = 59)	Grande Rade (n = 49)	Sainte-Marie Bay (n = 47)
P limiting	0	20	2	6	10	4	9
N limiting	86	80	88	77	75	69	64
Si limiting	0	0	0	0	0	0	0
None of the above	14	0	10	17	15	27	27

2000), and in the Caribbean (Van Duyl et al. 2002). In the SW lagoon of New Caledonia, the distribution of phytoplankton variables can thus be examined versus DIN concentrations, without taking into account the other macronutrients. It can be argued that Fe concentrations may limit phytoplankton development, as observed in HNLC (high nutrient, low chlorophyll) areas. However, Fe limitation is very unlikely in New Caledonia lagoons, where the soils are known for their richness in several metals including Fe (Latham 1981). Indeed, Fe concentrations are 0.6 to 2 nM in the Loyalty Channel on the east coast of New Caledonia (M. Rodier pers. comm.), far exceeding the limiting Fe concentrations of 0.13 nM in the Equatorial Pacific (Coale et al. 1996). The SW lagoon of New Caledonia receives considerably higher terrigeneous inputs than Loyalty Channel (Ambatsian et al. 1997), and, therefore, Fe limitation is very unlikely to occur.

Relationships between nutrients and phytoplankton variables

Since nitrogen is the main limiting factor, we examined the relationships between phytoplankton variables and DIN concentrations. The Model II regressions (Table 5) showed that all phytoplankton variables displayed significant relationships with all forms of DIN. The only exceptions were dinoflagellate and coccolithophorid abundances versus $NO_3 + NO_2$. All relationships were positive, except for *Prochlorococcus*, for which abundance decreased with increasing nitrogen concentrations.

Phytoplankton size classes

The slope was significantly lower for the <2 µm fraction than for the 2 other size fractions (Table 5). The relative contribution of <2 µm phytoplankton to total biomass (in terms of chl *a*), therefore, decreases with increasing trophic status (Fig. 3). A similar trend was observed by Tenório et al. (2005) in the Bay of Ouinne on the east coast of New Caledonia: phytoplankton was dominated by picophytoplankton and microcyanobacteria during dry seasons, corresponding to low freshwater inputs and low nutrient concentrations, and by larger eukaryotic populations during wet seasons. This trend is in agreement with meta-analyses of data from various marine (e.g. Chisholm 1992, Agawin et al. 2000) and freshwater environments (Bell & Kalff 2001), although some of these trends may be corrupted by spurious correlations when chlorophyll is used to define the trophic status (Berges 1997). Several hypotheses have been formulated to explain the shift from smaller to larger cells with increasing trophic conditions. Firstly, it could be linked to a higher NH_4:DIN ratio in oligotrophic systems (Chisholm 1992) and to a higher affinity of picophytoplankton for NH_4 than for nitrate (Laws et al. 2000). This preference was, however, not observed by Sherr et al. (1982) or Furnas (1983), nor is it supported by our results. Indeed, in the SW lagoon of New Caledonia, the NH_4:DIN ratio is rather high (0.69 on average), but does not vary significantly with distance from the coast (Table 2). In addition, no significant relationship can be outlined between the relative contribution of picoplankton to total phytoplankton and the NH_4:DIN ratio (data not shown). Secondly, the shift to larger cells with increasing DIN concentrations can be explained by the larger surface to volume ratio of smaller cells, leading to a more efficient uptake of nutrients in oligotrophic waters (Legendre & Rassoulzadegan 1995) together with a better molecular diffusion (Chisholm 1992). Alternatively, the intrinsic capacity of larger cells to multiply faster than smaller cells when they are not limited by nutrient diffusion has been demonstrated (Agawin et al. 2000, Fernández et al. 2003). However, in the SW lagoon of New Caledonia the ratio of primary production to chl *a* is not significantly higher for the largest size fractions (authors' unpubl. data). This suggests that increasing contributions of 2 to 10 µm and >10 µm size classes with increasing DIN concentrations are not due to higher growth rates. A final hypothesis is advanced by Samuelsson et al. (2002) that phytoplankton develops faster in enriched conditions than mesozooplankton does. A lower predation pressure on larger cells could indeed explain this dominance of larger cells in enriched conditions. Unfortunately, we have no data to test this hypothesis.

These changes in phytoplankton size classes in response to nutrient enrichment may have important consequences, especially in terms of carbon flow towards upper trophic levels. The contribution of picoplankton and microplankton in terms of carbon (see 'Materials and methods') was computed for the bays, the lagoon, and the ocean. This calculation results in an obvious predominance of microphytoplankton in the bays, as the picoplankton and microphytoplankton represented 46.1 and 56.7 µg C l^{-1}, respectively, compared to the lagoon and the ocean, where picoplankton represented 26.8 and 20.7 µg C l^{-1}, respectively, and microplankton represented 13.5 and 5.9 µg C l^{-1}, respectively. Since the number of predation steps necessary to reach mesozooplankton is expected to be lower for microphytoplankton than for picophytoplankton, the percentage of carbon losses should be lower in the microphytoplankton-dominated populations from the bays. As a consequence, the effect of nutrient enrichment should theoretically favor mesozooplankton production (and therefore the production of higher trophic levels) more than could be expected from bulk primary production due to these changes in size classes.

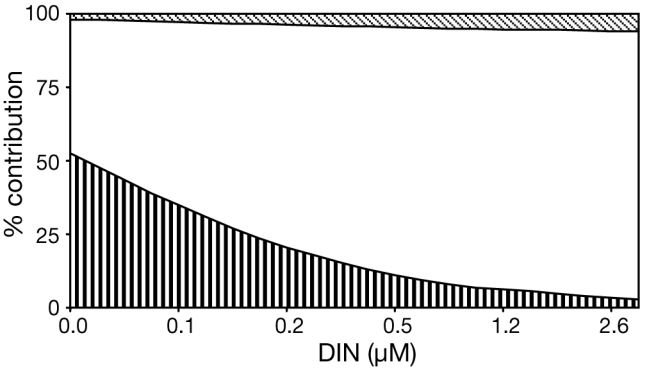

Fig. 6. Percent contributions of *Prochlorococcus* (vertical stripes), *Synechococcus* (white), and picoeukaryotes (diagonal stripes) to total picophytoplankton abundance versus DIN concentrations. Values computed from Table 5 relationships

Picophytoplankton groups

In the whole lagoon, except for Sainte-Marie Bay, the <2 µm fraction predominated in numbers and was mainly constituted of *Synechococcus*. This pattern in phytoplankton size fraction has often been observed in oligotrophic coral reef waters (e.g. Charpy & Blanchot 1999, Sakka et al. 1999, Van Duyl et al. 2002, Tada et al. 2003). The 3 components of the picoplankton compartment, i.e. *Prochlorococcus*, *Synechococcus*, and picoeukaryotes, behaved differently according to the DIN concentrations (Fig. 6). As shown by the regressions in Table 5, a significant shift from *Prochlorococcus* to *Synechococcus* dominance was observed with increasing DIN concentrations (0.03 to 3.24 µM). The *Prochlorococcus* dominance at the most oligotrophic stations agrees with similar observations in the tropical Pacific Ocean (Blanchot & Rodier 1996) and in the tropical Atlantic Ocean (Partensky et al. 1996). Similarly, a higher abundance of *Synechococcus* in relatively enriched waters was reported by Campbell et al. (1994) in the Pacific area and by Partensky et al. (1999) in the Atlantic Ocean. The slightly decreasing ratio between cyanobacteria and picoeukaryotes with increasing DIN concentrations (Fig. 6) could be related to both the greater size of picoeukaryotes modifying nutrient uptake abilities and/or grazing efficiencies, and photosynthetic content modifying adaptation to ambient light for picoeukaryotes (Partensky et al. 1999).

Microphytoplankton groups

Our results show consistent changes of phytoplanktonic communities as a function of DIN concentration. This study shows, moreover, that inside each main

Table 5. Model II log–log regressions of chlorophyll *a* (chl *a*) in size classes and phytoplankton groups versus DIN, NH_4, and NO_3 + NO_2 (*a*: log–log slope [95% CL in parentheses]; *b*: intercept; r: determination coefficient; ***p < 0.001; **p < 0.01; *p < 0.05; NS: not significant). Units are µg l^{-1}, 10^6 cells l^{-1}, cells l^{-1}, and µM for chl *a*, picoplankton, microalgae, and nutrients, respectively

	vs. DIN				vs. NH_4				vs. NO_3 + NO_2			
	a	*b*	r	p	*a*	*b*	r	p	*a*	*b*	r	p
Total chl *a* (GF/F)	0.38 (0.27–0.49)	−0.15	0.95	***	0.34 (0.18–0.52)	−0.12	0.87	**	0.25 (0.18–0.32)	−0.00	0.92	***
Chl *a* (<2 µm)	0.14 (0.04–0.24)	−0.65	0.77	*	0.11 (0.01–0.21)	−0.64	0.69	*	0.18 (0.12–0.24)	−0.52	0.92	***
Chl *a* (2–10 µm)	0.81 (0.58–1.10)	−0.33	0.96	***	0.77 (0.45–1.22)	−0.20	0.93	**	0.44 (0.17–0.76)	−0.41	0.81	**
Chl *a* (>10 µm)	0.87 (0.50–1.43)	−0.24	0.94	**	0.51 (0.14–1.04)	−0.32	0.86	*	0.35 (0.26–0.46)	−0.58	0.95	***
Prochlorococcus	−0.63 (−0.82 to −0.46)	0.91	0.96	***	−0.78 (−1.10 to −0.54)	0.79	0.97	***	−0.42 (−0.61 to −0.25)	0.62	0.89	***
Synechococcus	0.16 (0.05–0.27)	2.02	0.81	**	0.17 (0.06–0.30)	2.06	0.86	**	0.06 (0.05–0.08)	2.09	0.96	***
Picoeukaryotes	0.26 (0.20–0.33)	0.79	0.97	***	0.24 (0.16–0.32)	0.82	0.96	**	0.16 (0.11–0.21)	0.89	0.90	***
Diatoms	1.32 (0.73–2.74)	4.58	0.82	**	1.13 (0.61–2.18)	4.57	0.84	**	0.69 (0.23–1.50)	4.95	0.69	*
Dinoflagellates	0.41 (0.21–0.64)	3.91	0.87	**	0.34 (0.16–0.54)	3.90	0.85	**			0.26	NS
Coccolithophorids	0.82 (0.48–1.33)	4.02	0.92	**	0.42 (0.19–0.70)	3.78	0.86	**			0.24	NS

phytoplankton group species may have different response levels to nutrient inputs. However, these trends did not result in the establishment of specific phytoplankton populations in the bays. Similarly, it does not seem that the eutrophication gradient influences the phytoplankton diversity. It must be kept in mind that since not all phytoplankters can be distinguished at the species level and the method used for microplankton examination did not produce an exhaustive list of species, diversity and evenness indices cannot be computed from our data set. The failure to observe specific phytoplankton populations on the lagoon shelf and in the bays may be explained by the continual water renewal in the SW lagoon. Indeed, the lagoon circulation, mostly driven by southeasterly trade winds, is dominated by a heavy flow of oligotrophic oceanic waters entering from the southeast and exiting the lagoon in the northwest, and the residence time of water has been estimated to be <7 d on average (Jouon et al. in press). This could explain the regular presence of oceanic species (e.g. *Oxytoxum* spp., *Podolampas spinifera*, *Dictyocha fibula*) in the bays.

The community composition of nano- and microalgae, however, displayed drastic changes with varying DIN concentrations (Fig. 7). Regression fits show that cells >10 µm are responsible for a large part of the increase in phytoplankton biomass at higher DIN concentrations and that this increase was due to diatoms. Indeed, dinoflagellates and coccolithophorids were replaced by diatoms when DIN concentrations increased from 0.03 to 2.65 µM. In addition, diatoms were the only microalgal group showing a positive correlation with nitrates (Table 5).

Similar relationships between diatoms and DIN were reported in other coral reef environments (Revelante et al. 1982, Furnas & Mitchell 1986, Van Duyl et al. 2002).

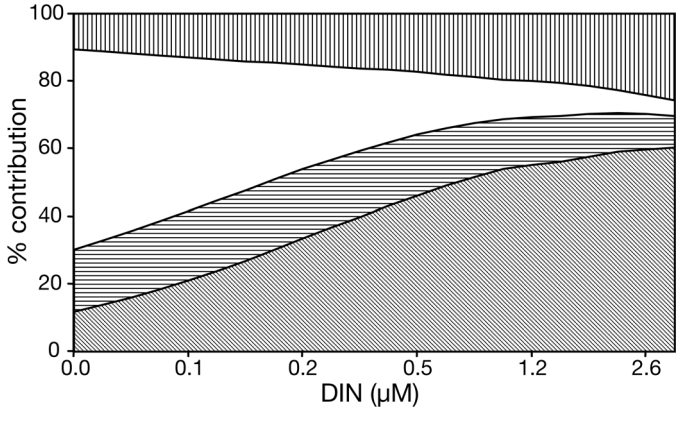

Fig. 7. Percent contributions of diatoms (diagonal stripes), coccolithophorids (horizontal stripes), dinoflagellates (white), and others (vertical stripes) to total microphytoplankton abundance as a function of DIN concentration. Values computed from Table 5 relationships

Short-term nutrient enrichments, either natural following a cyclone (Delesalle et al. 1993) or experimental (Sakka et al. 1999), also resulted in a predominance of diatoms in atoll environments. Therefore, as Chisholm (1992) already noted for temperate waters, diatoms play a primary role in increasing the phytoplankton biomass in these tropical environments.

The silicate concentrations are critical for diatom growth (Egge & Aksnes 1992), and a silicate deficiency can lead to dinoflagellate blooms if DIN is available (Officer & Ryther 1980). During enrichment experiments, Egge & Aksnes (1992) determined a threshold of 2 µM Si beyond which diatoms become dominant. In the present study, 63% of the silicate concentrations exceeded this threshold. These concentrations above the threshold were essentially encountered in the bays. Therefore, the predominance of diatoms in the bays in response to higher DIN concentrations was likely favored by correspondingly higher Si concentrations. Correspondingly, a significant statistical relationship could be observed between diatom numbers and silicate concentrations [log(diatoms) = 2.41 log(Si) + 2.94, $r = 0.87$, $p < 0.001$].

Taxon-specific relationships with DIN

The trends linking abundances of large phytoplankton groups with the DIN concentrations determined in this study are in agreement with the results of Berg et al. (2003), who determined taxon-specific nitrogen uptake rates in the Baltic Sea. However, they only considered relatively high taxonomic levels (e.g. diatoms, dinoflagellates, etc.). In the present study, we were able to investigate the possible relationships between phytoplankton taxa and DIN concentrations at the genus or species level.

Among the 72 diatoms identified, 22 were abundant enough over a range of DIN concentrations to allow the determination of specific trends of abundance versus DIN (Fig. 8). Among those, *Rhizosolenia imbricata* did not show any significant trend versus DIN, i.e. abundance did not vary significantly with DIN concentration (369 ± 69 cells l^{-1}). Ten species presented slopes exceeding 1.00; *Thalassiosira* sp. exhibited the largest log–log slope (2.52 ± 0.28), immediately followed by *Guinardia striata* (2.12 ± 0.36) and *Rhizosolenia setigera* (1.67 ± 0.14; Fig. 8).

Similarly, among the dinoflagellates, 41 species were identified and 10 were abundant enough over a range of DIN concentrations to allow the examination of trends versus DIN. Among these, *Prorocentrum gracile* displayed nearly constant abundance independent of DIN concentration (388 ± 43 cells l^{-1}). *Gymnodinium* sp. (1.29 ± 0.37) and *Prorocentrum* sp. (1.03 ± 0.09)

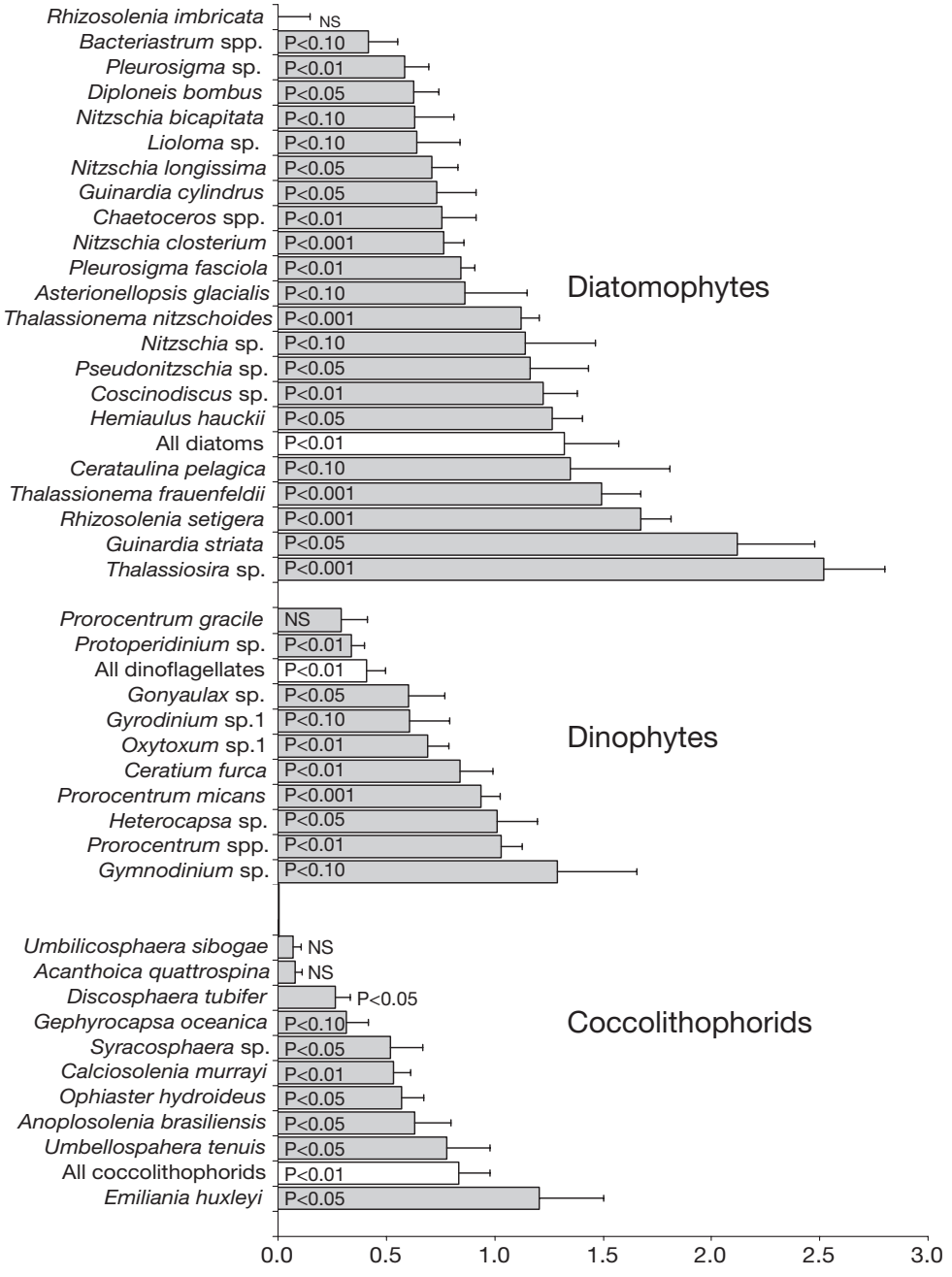

Fig. 8. Log-log slopes of abundance (cells l^{-1}) versus DIN (µM) for taxa belonging to diatomophytes, dinophytes, and coccolithophorids. Error bars are standard errors. Probabilities given for each regression (NS: not significant)

exhibited much larger slopes (1.03 to 1.29; Fig. 8); however, these were usually lower than for diatoms.

For coccolithophorids, 10 species of the 18 identified were abundant enough to permit determination of trends versus DIN. Among these species, *Emiliania huxleyi* exhibited the highest increase (1.20 ± 0.30; Fig. 8) with increasing DIN concentrations, whereas *Umbilicosphaera sibogae* and *Acanthoica quattrospina* displayed nearly constant abundances independent of DIN concentration (365 ± 70 and 122 ± 13 cells l^{-1}, respectively).

With respect to taxonomic level, Fig. 8 shows that the slopes markedly differed between total abundance and the identified genus or species. Thus, taking only total abundance into account would suppress various trends involving DIN concentrations that are revealed at a more precise level. This can be rather useful when dealing with putatively toxic species (e.g. *Pseudonitzschia*).

Several potentially toxic and bloom-forming species were observed (Table 3), some of which, e.g. *Dinophysis caudata* and *Lingulodinium polyedrum*, are known to cause fish and shellfish mortality events (Bruno et al. 1990). None of them, however, exhibited high abundances, nor a significant relationship with DIN concentrations, except *Pseudonitzschia* sp., and no toxic event due to planktonic algae has ever been reported from New Caledonia. This might be related to the absence of aquaculture of filter feeders in New Caledonia. This may, however, change in the future if oyster mariculture is further developed in the bays. At present, there is only 1 oyster farm in Dumbea Bay (Kulbicki pers. comm.), and the most frequent disease is ciguatera fish poisoning, which is caused by the benthic dinoflagellate *Gambierdiscus toxicus*.

Comparison with previous studies

The mean chl *a* concentration (0.45 ± 0.02 µg l^{-1}) determined in this study is similar to values obtained in various other coral reef lagoons throughout the world, e.g. on the Great Barrier Reef (Furnas & Mitchell 1986), in French Polynesia (Dufour & Berland 1999, Delesalle et al. 2001), in the Fiji Islands (Charpy & Blanchot 1999), at Curaçao Island (Van Duyl et al. 2002), or at Okinawa Island (Tada et al. 2003).

The chlorophyll concentrations observed in the present study can be compared to the results obtained by Rougerie (1985) from the same area in order to evaluate the temporal evolution of the phytoplankton biomass over 25 yr. The average chlorophyll concentration computed by Rougerie (1985) from ca. 20000 samples collected between 1976 and 1979 throughout the whole SW lagoon is very similar to ours (0.57 ± 0.18 vs. 0.47 ± 0.02 µg chl *a* l^{-1}). He observed a decrease in chl *a* concentrations with the distance from the coast, similar to our results, and also reported similar average chl *a* values in the bays near Nouméa (0.72 vs. 0.60 to 0.82 µg chl *a* l^{-1} in our study). The DIN concentrations were also comparable (0.87 vs. 0.94 µM) in the bays near Nouméa. Since Rougerie's (1985) study, the population of Nouméa City has increased by ca. 90%, and the sewage treatment is still insufficient. At first glance, increased urbanization does not seem to result in either higher mean phytoplankton biomass or higher mean nutrient concentrations in the coastal part of the lagoon. As already mentioned, this may be explained by the substantial water renewal in the SW lagoon. It should be noted, however, that the maximum concentrations of both nitrogen and chl *a* differed significantly between the 1970s and our study. Rougerie (1985) reported a maximum chl *a* value of 1.01 µg l^{-1}, whereas we measured more than twice this value (2.4 µg l^{-1}).

In summary, the 7 areas studied in the SW lagoon of New Caledonia are characterized by distinct macronutrient concentrations, with the bays in the urbanized area showing the largest departure from average lagoon conditions. Examination of the nutrient ratios shows that nitrogen is likely the macronutrient that drives phytoplankton community composition. In agreement, we found significant statistical relationships between abundance of the major phytoplankton groups and DIN concentrations. We have shown that, although moderate, local nutrient enrichments increase phytoplankton biomass and induce significant shifts in the phytoplankton community structure. These changes are not restricted to changes in phytoplankton size. Regarding picoplankton, the *Prochlorococcus*-dominated consortia in the surrounding oceanic and southern lagoon shelf waters are replaced by *Synechococcus*-dominated populations in the bays, combined with an increasing proportion of picoeukaryotic phytoplankton. Regarding microphytoplankton, nutrient enrichment in the bays favors large diatoms.

The present work can also be considered as a first and necessary step in the study of the consequences of metal inputs into the marine food web. Indeed, the SW lagoon of New Caledonia is subjected to large inputs of toxic trace metals, such as nickel, cadmium, copper, and zinc, from both mining and urban activities. Knowledge of the phytoplankton community structure is essential to study the pathways of metal integration into marine food webs. Evaluating the effect of nutrient enrichment on phytoplankton community structure was a prerequisite to assessing the effects of other inputs, like metals.

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The following appendix accompanies the article

Response of phytoplankton communities to increased anthropogenic influences (southwestern lagoon, New Caledonia)

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Appendix 1. List of the 142 microalgal taxa identified in the 135 samples and the areas in which they were found (grey rectangles) in the SW lagoon. Letters indicate the usual distribution of species: tropical warm waters (W), temperate waters (T), or cosmopolitan (C)

		Sainte Marie Bay	Grande Rade Bay	Dumbéa Bay	Boulari Bay	Western shelf	Southern shelf	Ocean
DIATOMOPHYTES								
Amphora sp. Ehrenberg	C	■		■		■		
Asterionellopsis glacialis (Castracane) Round	C	■	■	■		■		
Asterionellopsis kariana (Grunow) Round	T					■		
Asteromphalus heptactis (Brébisso) Ralfs	T					■		
Bacteriastrum furcatum Shadbolt	T		■	■		■		
Bacteriastrum hyalinum Lauder	T	■	■	■		■		
Bacteriastrum spp. Shadbolt		■	■	■	■	■	■	■
Cerataulina pelagica (Cleve) Hendey	C	■	■	■		■		
Chaetoceros anastomosans Grunow in Van Heurck	W,T					■		
Chaetoceros atlanticus Cleve	C		■	■		■		
Chaetoceros coarctatus Lauder	W			■	■			
Chaetoceros curvisetus Cleve	C	■	■	■		■		
Chaetoceros decipiens Cleve	C	■	■	■		■		
Chaetoceros didymus Ehrenberg	W,T		■	■		■	■	■
Chaetoceros laciniosus Schütt	T	■	■	■		■		
Chaetoceros peruvianus Brightwell	W,T	■	■	■		■	■	
Chaetoceros socialis Lauder	C	■	■	■		■		
Chaetoceros spp. Ehrenberg		■	■	■	■	■	■	■
Climacodium frauenfeldianum Grunow	W					■		
Corethron criophilum Castracane	C					■		
Coscinodiscus sp. Ehrenberg emend. Hasle & Sims		■	■	■		■		
Cyclotella sp. (Kützing) Brébisson				■				
Dactyliosolen fragilissimus Bergon (Hasle)	C	■						
Diploneis bombus Ehrenberg	W,T		■	■	■	■	■	■
Diploneis sp. Ehrenberg		■		■			■	■
Entomoneis alata (Ehrenberg) Ehrenberg	W	■	■	■		■		
Eucampia cornuta (Cleve) Grunow	W	■					■	
Eucampia zodiacus Ehrenberg	C					■		
Guinardia cylindrus (Cleve) Hasle	W	■	■	■	■	■		■
Guinardia flaccida (Castracane) Peragallo	C	■				■		
Guinardia striata (Stolterfoth) Hasle	C	■	■	■	■	■		
Gyrosigma sp. Agardh						■		
Hemiaulus hauckii Grunow in Van Heurck	W,T		■	■		■		■
Hemiaulus sinensis Greville	W,T	■	■	■		■		
Lauderia annulata Cleve	W,T	■			■	■		
Leptocylindrus danicus Cleve	C	■		■		■		
Licmophora sp. Agardh				■		■		
Lioloma sp. Hasle	W,T			■	■	■	■	■
Mastoglioa binotata (Grunow) Cleve	W,T					■		

Appendix 1 (continued)

		Sainte Marie Bay	Grande Rade Bay	Dumbéa Bay	Boulari Bay	Western shelf	Southern shelf	Ocean
Mastoglioa fimbriata (Brightwell) Cleve	W,T			▬				
Mastoglioa sp. Thwaites in Wm. Smith	W,T			▬		▬		
Melosira granulata (Ehrenberg) Ralfs	C					▬		
Melosira sp. Agardh	C		▬	▬				
Navicula sp. Bory de St. Vincent		▬	▬	▬	▬	▬	▬	▬
Nitzschia bicapitata Cleve	W,T	▬	▬	▬	▬	▬	▬	▬
Nitzschia closterium (Ehrenberg) Wm. Smith	C	▬	▬	▬	▬	▬	▬	▬
Nitzschia distans Gregory				▬				
Nitzschia longissima (Brébisson) Ralfs	C	▬	▬			▬		
Nitzschia maxima Grunow		▬				▬		
Nitzschia punctata var. *coarctata* (Grunow) Diaz-Ramos		▬						
Nitzschia sp. Hassall		▬	▬	▬		▬		
Odontella sinensis (Greville) Grunow	C		▬					
Pleurosigma angulatum (Quekett) Wm. Smith	C			▬	▬	▬		
Pleurosigma fasciola Wm. Smith	C	▬		▬		▬		
Pleurosigma sp. Wm. Smith	C	▬	▬	▬	▬	▬	▬	
Proboscia alata (Brightwell) Sundström			▬	▬		▬		
Pseudonitzschia sp. H. Peragallo		▬	▬	▬	▬	▬	▬	▬
Pseudosolenia calcar-avis (Schultze) Sundström	W	▬	▬	▬	▬	▬	▬	
Rhabdonema adriaticum Kützing	W,T					▬		
Rhaphoneis sp. Ehrenberg	C	▬						
Rhizosoleia imbricata Brightwell	C	▬	▬	▬	▬	▬	▬	
Rhizosolenia robusta Norman in Pritchard	W			▬				
Rhizosolenia setigera Brightwell	C	▬	▬	▬	▬	▬		
Rhizosolenia sp. Brightwell		▬	▬	▬				
Rhopalodia gibba (Ehrenberg) O. F. Müller				▬				
Skeletonema costatum (Greville) Cleve	C	▬		▬		▬		
Surirella sp. Turpin				▬				
Synedra sp. Ehrenberg			▬			▬		
Thalassionema frauenfeldii (Grunow) Hallegraeff	W,T	▬	▬	▬	▬	▬	▬	▬
Thalassionema nitzschoides (Grunow) Mereschkowsky	C	▬	▬	▬	▬	▬	▬	▬
Thalassiosira sp. Cleve		▬	▬	▬		▬	▬	
Trachyneis aspera (Ehrenberg) Ehrenberg	W,T		▬	▬				
DINOPHYTES								
Amphidinium sp. Clarapède & Lachmann				▬		▬		
Ceratium breve (Ostenfeld & Schmidt) Schröder	W					▬		
Ceratium candelabrum (Ehrenberg) Stein	W						▬	
Ceratium furca (Ehrenberg) Clarapède & Lachmann	W,T	▬	▬	▬	▬	▬	▬	
Ceratium fusus (Ehrenberg) Dujardin	C		▬	▬		▬		
Ceratium pentagonum Gourret	W	▬		▬		▬		
Ceratium tripos (O. F. Müller) Nitzsch	C			▬	▬			▬
Ceratium sp. Schrank			▬					
Cochlodinium sp. Schütt	W,T		▬	▬	▬	▬	▬	
Corythodinium tesselatum (Stein) Loeblich Jr. & Loeblich III	W	▬	▬	▬		▬	▬	
Dinophysis caudata Saville-Kent	W		▬	▬				
Dinophysis sp. Ehrenberg			▬	▬		▬	▬	▬
Gonyaulax kofoïdii Pavillard	C		▬					
Gonyaulax sp. Diesing		▬	▬	▬	▬	▬	▬	▬
Gymnodinium sp. Stein		▬	▬	▬		▬		
Gyrodinium sp. 1 Stein		▬	▬	▬	▬	▬	▬	▬
Gyrodinium sp. 2 Stein						▬	▬	▬
Heterocapsa sp. Stein		▬	▬	▬	▬	▬		▬
Histioneis sp. Stein	W					▬		
Lingulodinium polyedrum (Stein) Dodge	W		▬	▬				
Micracanthodinium sp. Deflandre	W					▬		▬
Ornithocercus magnificus Stein			▬	▬		▬		
Oxytoxum scolopax Stein	W					▬		▬
Oxytoxum subulatum Kofoid	W			▬		▬	▬	
Oxytoxum sp. 1 Stein		▬	▬	▬	▬	▬	▬	▬
Oxytoxum sp. 2 Stein			▬			▬	▬	▬
Oxytoxum spp. Stein					▬	▬	▬	▬
Podolampas bipes Stein	W		▬			▬	▬	

Appendix 1 (continued)

		Sainte Marie Bay	Grande Rade Bay	Dumbéa Bay	Boulari Bay	Western shelf	Southern shelf	Ocean
Podolampas spinifera Okamura	W			▬		▬	▬	
Polykrikos kofoidii Chatton	W,T						▬	
Pronoctiluca acuta (Lohmann) Schiller	W,T			▬	▬	▬	▬	▬
Prorocentrum dentatum Stein	C	▬		▬		▬	▬	
Prorocentrum gracile Schütt	C	▬	▬	▬	▬	▬	▬	▬
Prorocentrum aff. *mexicanum* Tafall	W	▬	▬	▬		▬		
Prorocentrum micans Ehrenberg	C	▬	▬	▬	▬	▬	▬	
Prorocentrum spp. Ehrenberg		▬	▬	▬	▬	▬	▬	▬
Protoperidinium bispinum Schiller	C					▬		
Protoperidinium elegans (Cleve) Balech	W		▬	▬				
Protoperidinium globosum (Dangeard) Balech	C			▬	▬			
Protoperidinium oceanicum (Van Höffen)	W,T		▬					
Protoperidinium sp. Berg		▬	▬	▬	▬	▬	▬	▬
COCCOLITHOPHORIDS								
Acanthoica quattrospina Lohmann	C	▬		▬		▬	▬	▬
Algirosphaera sp. Schlauder	W,T					▬	▬	
Anoplosolenia brasiliensis (Lohmann) Deflandre	C	▬	▬	▬	▬	▬	▬	▬
Calciosolenia murrayi Gran	C	▬		▬		▬	▬	
Discosphaera tubifer (Murray & Blackman) Ostenfeld	C			▬		▬	▬	▬
Emiliania huxleyi (Lohmann) Hay & Mohler	C	▬	▬	▬	▬	▬	▬	▬
Gephyrocapsa oceanica Kamptner	C	▬	▬	▬	▬	▬	▬	▬
Halopappus adriaticus Schiller, emend. Manton, Bremer & Oates	C			▬		▬	▬	
Helicosphaera carteri (Wallich) Kamptner	C			▬		▬		
Helladosphaera sp. Kamptner	C			▬	▬	▬	▬	▬
Michaelsarsia elegans Gran, emend. Manton, Bremer & Oates	C			▬		▬	▬	▬
Ophiaster hydroideus (Lohmann) Lohmann, emend. Manton & Oates	C	▬	▬	▬		▬	▬	▬
Pontosphaera sp. Lohmann	C					▬		
Rhabdosphaera sp. Haeckel	C					▬	▬	▬
Syracosphaera sp. Lohmann	C	▬		▬		▬	▬	▬
Umbellosphaera irregularis Paasche	C			▬		▬	▬	▬
Umbellospahera tenuis (Kamptner) Paasche	C					▬	▬	▬
Umbilicosphaera sibogae (Weber-van-Bosse) Gaarder	C	▬		▬		▬	▬	▬
CYANOPHYTES								
Anabaena sp. St. Vincent, ex Bornet & Flah	C					▬		
Lyngbya sp. Agardh ex Gomont	C					▬		
Oscillatoria sp. Vaucher ex Gomont	W,T			▬	▬	▬	▬	▬
Pseudanabaena sp. Lauterborn	C						▬	
Richelia intracellularis Schmidt in Ostenfledt & Schmidt	W,T		▬	▬	▬	▬		
PRASINOPHYTES								
Pachysphaera sp. Ostenfeld	C					▬	▬	▬
Pyramimonas sp. 1 Schmarda	C	▬		▬		▬		▬
Pyramimonas sp. 2 Schmarda	C	▬	▬	▬		▬	▬	▬
EUGLENOPHYTES								
Euglena sp. Ehrenberg	C	▬	▬	▬		▬	▬	
CRYPTOPHYTES								
Undetermined		▬	▬	▬	▬	▬	▬	▬
DICTYOCHOPHYTES								
Dictyocha fibula Ehrenberg	C		▬	▬		▬	▬	▬
Number of taxa								
DIATOMOPHYTES		41	38	52	18	56	18	14
DINOPHYTES		14	24	27	14	31	21	15
COCCOLITHOPHORIDS		8	4	14	4	18	16	13
OTHERS		5	5	7	3	9	7	6
TOTAL		68	71	100	39	114	62	48