

IMPORTANCE OF PHOTOSYNTHETIC PICOPLANKTON IN CORAL REEF ECOSYSTEMS

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PICOPLANKTON
CORAL REEFS
CYANOBACTERIA
GRAZING
NITROGEN FIXATION
NEW PRODUCTION

ABSTRACT. – The importance of photosynthetic picoplankton in coral reef ecosystems is discussed with regard to various oceans with a special focus on the Pacific Ocean for which recent data are more abundant (Tuamotu & Fiji). Picoplankton dominates the phytoplankton biomass of coral reef waters and *Synechococcus*, a small coccoid cyanobacterium, is the most important organism (abundance and biomass). The picoplankton is actively grazed by the coral reef community, and this capture of allochthonous particles has to be taken into account to estimate coral reef new production. In the future, special attention has to be paid to small nitrogen-fixing unicellular cyanobacteria, which can be important for allochthonous nitrogen supply and therefore have also to be taken into account for estimation of coral reef new production.

PICOPLANKTON
RÉCIFS CORALLIENS
CYANOBACTÉRIES
BROUTAGE
FIXATION D'AZOTE
PRODUCTION NOUVELLE

RÉSUMÉ. – L'importance du picoplancton dans les écosystèmes coralliens de différents océans est discutée avec un intérêt particulier pour l'Océan Pacifique où des données récentes sont disponibles (Tuamotu & Fiji). Le picoplancton domine la biomasse phytoplanctonique des eaux coralliennes. *Synechococcus*, une petite cyanobactérie unicellulaire, est l'organisme le plus important en termes d'abondance et de biomasse. Le picoplancton est brouté activement par la communauté corallienne. Cette capture de particules allochtones doit être prise en compte pour estimer la production nouvelle des récifs coralliens. Dans le futur, un intérêt particulier doit être porté sur les cyanobactéries unicellulaires fixatrices d'azote, dont la présence a été rapportée dans les écosystèmes coralliens, et dont la taille est proche de celle du picoplancton. Leur apport en azote allochtone doit aussi être considéré dans l'estimation de la production nouvelle des écosystèmes coralliens.

INTRODUCTION

Picophytoplankton in the global ocean

The discovery of picophytoplankton (i.e. the fraction of the phytoplankton composed of cells less than 2 μm in size) provided new insights into the productivity of the world's oceans (Stockner 1988). In tropical and subtropical oceanic waters, picophytoplankton account for ~80% of total chlorophyll *a* and phytoplankton biomass as well as ~70% of total primary production, e.g. (Li & Harrison 2001, Maranon *et al.* 2001).

Using flow cytometry (Olson *et al.* 1993), picophytoplankton can be accurately enumerated and discriminated into two main groups: picoeukaryotic algae and cyanobacteria, i.e. *Prochlorococcus* (Chisholm *et al.* 1988) and *Synechococcus* (Waterbury *et al.* 1979). These organisms have been studied extensively in oceanic waters of the Pacific (Campbell & Vaultot 1993, Campbell *et al.* 1994, Blanchot & Rodier 1996, Campbell *et al.* 1997), the Atlantic (Olson *et al.*

1990, Buck *et al.* 1996), the Indian Ocean (Zubkov & Quartly 2003) and Arabian Sea (Campbell *et al.* 1998). A review by Partensky *et al.* (1999) concluded that although *Synechococcus* and *Prochlorococcus* often co-occur, they have different types of adaptation with regard to biogeochemical conditions. *Prochlorococcus*, despite its narrower geographical distribution, seems to be more important than *Synechococcus* on a global scale since it is ca. 100 times more abundant (i.e. accounts for about 22 times more C) in warm oligotrophic areas, which correspond to a major part of the world ocean.

Coral reef ecosystems

Coral reef ecosystems are located worldwide between 30°N and 30°S latitude in optically clear, oligotrophic tropical seas (Lesser 2004). The most extensively studied coral reef ecosystems for phytoplankton are the French Polynesian atolls (Sournia & Ricard 1975, Charpy & Charpy Roubaud 1990, Charpy *et al.* 1992, Charpy 1996,

Charpy & Blanchot 1996, Charpy *et al.* 1997, Charpy & Blanchot 1998, Gonzalez *et al.* 1998, Charpy & Blanchot 1999b, Loret *et al.* 2000, Delesalle *et al.* 2001, Ferrier-Pagès & Furla 2001, Sakka *et al.* 2002), Moorea, French Polynesia (Legendre *et al.* 1988), the Great Barrier reef lagoon (Furnas & Mitchell 1986, Furnas 1987, Furnas & Mitchell 1987, Furnas 1990, Furnas *et al.* 1990, Furnas 1991, Ayukai 1992, Crosbie & Furnas 1999, Furnas & Crosbie 1999, Crosbie & Furnas 2001b, 2001a, Pile 2005), the Great Astrolabe reef (Charpy & Blanchot 1999a, Torretton 1999), Kaneohe Bay, Hawaii (Ribes *et al.* 2003, 2005) and the Red Sea (Shaikh *et al.* 1986, Gradinger *et al.* 1992, Veldhuis & Kraay 1993, Lindell & Post 1995, Reckermann & Veldhuis 1997, Veldhuis *et al.* 1997, Lil *et al.* 1998). Other studies were recently conducted in Okinawa Islands, Japan (Casareto *et al.* 2000, Tada *et al.* 2003).

In this paper, I will describe the contribution of each of the three picoplankton groups to phytoplankton biomass and production in atolls (Tuamotu), high island lagoon (Great Astrolabe reef, Fiji) and other coral reef ecosystems.

ENVIRONMENTAL CONDITIONS

Nutrient concentrations are low in coral reef ecosystems and significantly different compared to oceanic waters. In Tuamotu, nutrient concentrations in surrounding oceanic waters were on average $0.023 \pm 0.004 \mu\text{M}$ DIN and $0.21 \pm 0.01 \mu\text{M}$ DIP. In 12 atoll lagoons, DIN was higher ($0.1\text{--}0.8 \mu\text{M}$ in average) and DIP generally lower ($0.01\text{--}0.1 \mu\text{M}$) with some exceptions in very shallow and open lagoons (Dufour *et al.* 2001). In atoll lagoons, nitrogen fixation by benthic cyanobacteria is high (Charpy-Roubaud *et al.* 2001) and appears to constitute an important source of nitrogen for lagoonal waters (Charpy-Roubaud *et al.* 1990). The increase of DIN may explain the decrease in PO_4 by a shift from N limitation to P limitation for shallow, enclosed lagoons (Dufour *et al.* 2001).

In the Great Astrolabe reef (Fiji) lagoon, nutrient concentrations ($0.61 \pm 0.05 \mu\text{M}$ DIN, $0.18 \pm 0.02 \mu\text{M}$ DIP, $N = 48$) were higher than in atolls, due to the input of freshwater in the vicinity of the islands located inside the lagoon (Charpy & Blanchot 1999a).

On the Central and Southern Great Barrier reef, Crosbie & Furnas (1999) reported DIN concentrations ranging between 0.02 and $0.16 \mu\text{M}$, with concentrations on some occasions (post cyclone), reaching $2.3 \mu\text{M}$. In a recent paper, Furnas *et al.* (2005) have summarized nutrient data. They consider that DIN concentrations are usually of the order of $0.1 \mu\text{M}$ but exceptions occur when nearshore waters are affected by river flood plumes, during

sediment resuspension events caused by strong winds and at the shelfbreak during upwelling events. However, DIN is quickly taken up by the phytoplankton community.

In a transect across a coral reef in the Gulf of Aqaba, Rasheed *et al.* (2002) reported average nutrient concentrations ranging from $0.35 \mu\text{M}$ DIN and $0.06 \mu\text{M}$ DIP in summer to $0.65 \mu\text{M}$ DIN and $0.09 \mu\text{M}$ DIP in winter. In offshore waters, during the same period, average nutrient concentrations ranged from $0.13 \mu\text{M}$ DIN and $0.02 \mu\text{M}$ DIP in summer to $0.58 \mu\text{M}$ DIN and $0.07 \mu\text{M}$ DIP in winter.

At Sesoko Island (Okinawa, Japan), Tada *et al.* (2003) found average nutrient concentrations ranging from $0.99 \mu\text{M}$ DIN and $0.32 \mu\text{M}$ DIP in 1998 to $0.69 \mu\text{M}$ DIN and $0.06 \mu\text{M}$ DIP in 1999.

In some coral reef ecosystems, groundwater seepage increases the nutrient concentrations (Kawahata *et al.* 2000, Wood 2001, van Duyl *et al.* 2002).

PICOPLANKTON BIOMASS

The contribution of unicellular cyanobacteria to phytoplankton biomass and production varies according to the coral reef ecosystem and the sampling periods.

In Tuamotu, wide differences in relative picoplankton group abundance were observed between the two sampling periods in some lagoons. *Prochlorococcus* were particularly abundant in Hiti lagoon (281×10^3 cells ml^{-1}) during the rainy season and in Haraiki (210×10^3 cells ml^{-1}) during the dry season. *Synechococcus* were very abundant in Haraiki lagoon during both seasons but especially in March when average abundance reached 370×10^3 cells ml^{-1} . A large number of *Synechococcus* were also observed in Tepoto Sud lagoon in November 1995 (278×10^3 cells ml^{-1}). Highest picoeukaryote abundance was recorded in Taiaro during both seasons, particularly in March (7.4×10^3 cells ml^{-1}). *Prochlorococcus* dominated the picoplankton biomass in only one lagoon: Hiti in November (73% of chl *a* and 52% of C). The contribution of *Synechococcus* to picoplankton biomass was important in all lagoons except Reka-Reka, Taiaro and Tekokota. Its contribution was also strong in Tepoto Sud but only in November, when they contributed 73% of chl *a* and 84% of C. Picoeukaryotes dominated the picoplankton biomass at Reka-Reka, Taiaro, Takapoto (in surface water) and Tekokota. They also dominated the picoplankton biomass at Tepoto Sud in March (96% of chl *a* and 65% of C) (Charpy & Blanchot 1998).

On the two largest atolls of Tuamotu (Fakarava & Rangiroa), picoplankton biomass was also pre-

dominant, with cyanobacteria as the most important group. *Prochlorococcus* contributed only 5 to 9% of the total chlorophyll *a* (Ferrier-Pagès & Furla 2001).

In the Great Astrolabe Reef lagoon (Fiji), *Synechococcus* were the most abundant group whatever the station. *Prochlorococcus* were less abundant but were of the same order of magnitude as the *Synechococcus*. Picoeukaryotes were an order of magnitude less abundant. The abundances of the three picoplankton groups varied significantly between stations while depth had a significant effect only on *Prochlorococcus* abundance. The maximum picoplankton abundance was $140 \pm 4 \times 10^3$ *Prochlorococcus* ml⁻¹, $180 \pm 14 \times 10^3$ *Synechococcus* ml⁻¹ and $5.3 \pm 0.3 \times 10^3$ picoeukaryotes ml⁻¹. On average, *Prochlorococcus*, *Synechococcus* and picoeukaryotes contributions to picoplankton chl *a* were $2.0 \pm 0.1\%$, $90.5 \pm 0.5\%$ and $7.5 \pm 0.5\%$, respectively. The major contribution of *Prochlorococcus* was windward of the lagoon where water exchange with the ocean is at a maximum. The contributions of the 3 groups to the total chl *a* were in average \pm SD $0.9 \pm 0.1\%$, $42.0 \pm 1.9\%$ and $3.3 \pm 0.2\%$, respectively (Charpy & Blanchot 1999a).

In the Great Barrier Reef, Ayukai (1992) reported average abundance of cyanobacteria (*Synechococcus*) ranging between 0.16 and 2.41×10^4 cells ml⁻¹. Later, Crosbie & Furnas (2001a) using a flow cytometer, observed that *Synechococcus* was more abundant and had a greater biomass than *Prochlorococcus* at most inshore and mid-shelf sites in the central (17°S), and at all shelf sites in the southern (20°S). *Synechococcus* and *Prochlorococcus* abundance was better correlated with salinity, shelf depth and chlorophyll *a* concentration, than with nutrient concentrations.

In Sesoko Island (Okinawa, Japan), Tada *et al.* (2003) found that picoplankton dominated the phytoplankton community with an average contribution to the total Chl *a* biomass of 52%.

At Miyako Island (Okinawa, Japan) the contribution of picophytoplankton to total phytoplankton biomass varied between 45 and 100% (Ferrier-Pagès & Gattuso 1998). In another study, Casareto *et al.* (in press) found a picophytoplankton contribution to total chlorophyll varying between 32 and 73%. *Prochlorococcus*, *Synechococcus*, and picoeukaryote abundance was on average 64 ± 11 , 12 ± 2 and $4 \pm 0.7 \times 10^3$ cells ml⁻¹, respectively. Their contribution to picoplankton biomass was 10, 49 and 41%, respectively.

PICOPLANKTON GRAZING

In coral reef ecosystems, picoplankton can be grazed by planktonic and benthic organisms.

Grazing by plankton

Very few studies concern the grazing of picoplankton in coral reef waters. In Tikehau lagoon (Tuamotu), Gonzalez *et al.* (1998) showed that phagotrophic nanoflagellates were the major grazers of picocyanobacteria. Ciliates, and heterotrophic dinoflagellates, appeared to be grazing mostly on nanoplankton, both autotrophic and heterotrophic cells.

In Takapoto (Tuamotu), the grazing rates of <200 µm protozoa on picocyanobacteria represented 74% of their growth rates (Sakka *et al.* 2000). In the lagoonal waters of the two largest atolls of French Polynesia (Fakarava & Rangiroa), 75% of the cyanobacterial productions were consumed by the <10 µm fractions. This is equal to 0.05 to 0.5 10⁴ cyanobacteria ml⁻¹ h⁻¹ ingested (Ferrier-Pagès & Furla 2001).

In the water over a fringing coral reef at Miyako Island (Japan), 30-50% of the picocyanobacteria production was grazed by the heterotrophic flagellates and ciliates, which themselves were grazed (50-70% of the production) by the higher trophic levels (Ferrier-Pagès & Gattuso 1998).

Grazing by the reef benthos

The estimation of coral reef new production is a challenge for the coral reef scientist. New production is the proportion of excess production that utilizes allochthonous nutrients in the synthesis of organic material. Nutrients are assimilated either directly or after the capture and in situ remineralisation of particulates (Charpy 2001). Despite the potential importance of this capture, few quantitative data are available on natural prey capture, and most of the studies have concentrated on the ingestion of meso- and macrozooplankton over time scales of hours and few studies have investigated the ability of coral reef communities to feed on picoplankton (Houlbrèque *et al.* 2004).

Sorokin (1973) was one of the first to suggest that corals are able to consume planktonic bacteria. The demonstration that benthic organisms of coral reef ecosystems can feed on picoplankton has now been achieved for different ecosystems.

On the Great Barrier Reef, Moriarty *et al.* (1985) showed that pico- and nanoplankton were actively removed from the water flowing above reef flats. Also on the Great Barrier Reef, Ayukai (1995) showed that coral reefs were able to retain planktonic microbes. The retention value is virtually equal to estimates of net community production of the reefs studied. This allochthonous organic subsidy may help maintain a positive carbon balance on both Davies and Myrmidon Reefs on the Great Barrier Reef.

On Conch Reef, Florida Key, Pile (1997) demonstrated that picoplankton was actively grazed by sponges. In the Gulf of Aqaba, Yahel *et al.* (1998) found that phytoplankton grazing is an important component of benthic-pelagic coupling in coral reefs with a strong contribution of picoplankton (up to 70% of the total depleted carbon). Fabricius & Dommissé (2000) studied the depletion of suspended particulate matter over coastal reef communities dominated by zooxanthellate soft corals. They found that detritus and other small particles with a size <10 µm are an important food source for alcyoniid-dominated reef communities. In the Red Sea, Richter *et al.* (2001) demonstrated using endoscopic exploration that the sponge-dominated coelobite community removed more than 60% of the phytoplankton in the course of its less than 5-minute passage through the crevices. They concluded that mineralization of the largely allochthonous organic material is a principal source of nutrients supporting coral and algal growth. Yahel *et al.* (2003) demonstrated that the symbiont-bearing sponge *Theonella swinhoei* removed 85-95% of live picoplankton in the Gulf of Aqaba, Red Sea. Using an experimental flume, Ribes *et al.* (2003) demonstrated that picoplankton is a major source of nitrogen for the Kaneohe Bay reef flat. Under experimental conditions (Monaco aquarium), Houlbrèque *et al.* (2004) showed that ingestion rates of 3 coral species were proportional to prey concentrations. In terms of carbon, nanoflagellates represented the most important contribution, amounting to 84-94% of the total carbon ingested. Bacteria, cyanobacteria and picoflagellates accounted only for 1-7% of the ingested carbon. They concluded that pico- and nanoplankton may constitute an important food source for these corals. At Orpheus Island, Great Barrier Reef, Pile (2005), showed that retention efficiency for sponges was generally high, 85%-93%, for all types of ultraplankton, but in contrast, the retention efficiency of *Prochlorococcus* sp. by ascidians was more variable and lower than that of sponges. In Kaneohe Bay, Ribes *et al.* (2005) observed that *Synechococcus* and heterotrophic bacteria were the major sources of particulate organic nitrogen and that PON removed by rubble and live coral assemblage was directly related to sponge and ascidian biomass on the coral and coral rubble.

IS PHOTOSYNTHETIC PICOPLANKTON ABLE TO FIX NITROGEN?

N₂-fixing coccoid cyanobacteria and bacteria were recently discovered in the North Pacific subtropical gyre (Zehr *et al.* 2001). Direct measurements of ¹⁵N₂ fixation by small diazotrophs in various parts of the Pacific Ocean, including the waters off Hawaii where the unicellular diazotrophs were

first characterized, show that N₂ fixation by unicellular diazotrophs can support a significant fraction of total new production in oligotrophic waters (Montoya *et al.* 2004). However, these organisms seem to have a size greater than 3 µm and a low biomass (LaRoche & Breitbart 2005).

The first report of nitrogen fixation by small unicellular cyanobacteria in coral reef ecosystems was in Tikehau atoll lagoon (Charpy-Roubaud *et al.* 2001). In the coral reef lagoon of Mayotte (Indian Ocean), we found a nitrogen-fixing unicellular cyanobacteria with a size <10 µm, phylogenetically related to *Synechocystis* (unpublished data). In New Caledonia coral reef lagoon, N₂ fixation rate by unicellular cyanobacteria (<10 µm) was between 0.1 and 0.5 nM N₂ L⁻¹ h⁻¹, equivalent to 20 to 40% of the new production (Rimbaud, unpublished data).

SUMMARY

Picoplankton dominates phytoplankton biomass in coral reef waters like in oligotrophic oceanic waters. *Synechococcus* is the most abundant organism, contributing up to 90% of picoplankton biomass. The relation between environmental conditions and picoplankton composition is still unclear. *Prochlorococcus* sp. is generally uncommon in coastal coral reef waters but can be abundant in some oceanic coral reefs (atolls). However, we don't know if this paucity is real or due to problem in quantitatively detecting *Prochlorococcus* in high illuminated waters.

In spite of their small size, picoplankton organisms are actively grazed by sponges, ascidians, zooxanthellate soft corals and scleractinian. This allochthonous organic subsidy may help maintain a positive carbon balance on coral reefs. Therefore picoplankton availability and grazing rate by benthic community has to be taken into account when estimating the new production of coral reef ecosystems.

The new discovery of small unicellular diazotrophs in oligotrophic waters in general and in coral reef lagoons in particular, may be of major importance for estimating nitrogen budget in coral reef ecosystems. However, to date, the size of the first characterized unicellular diazotrophs is greater than the picoplankton size. Their study in coral reef ecosystems is a very exciting challenge for the future.

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