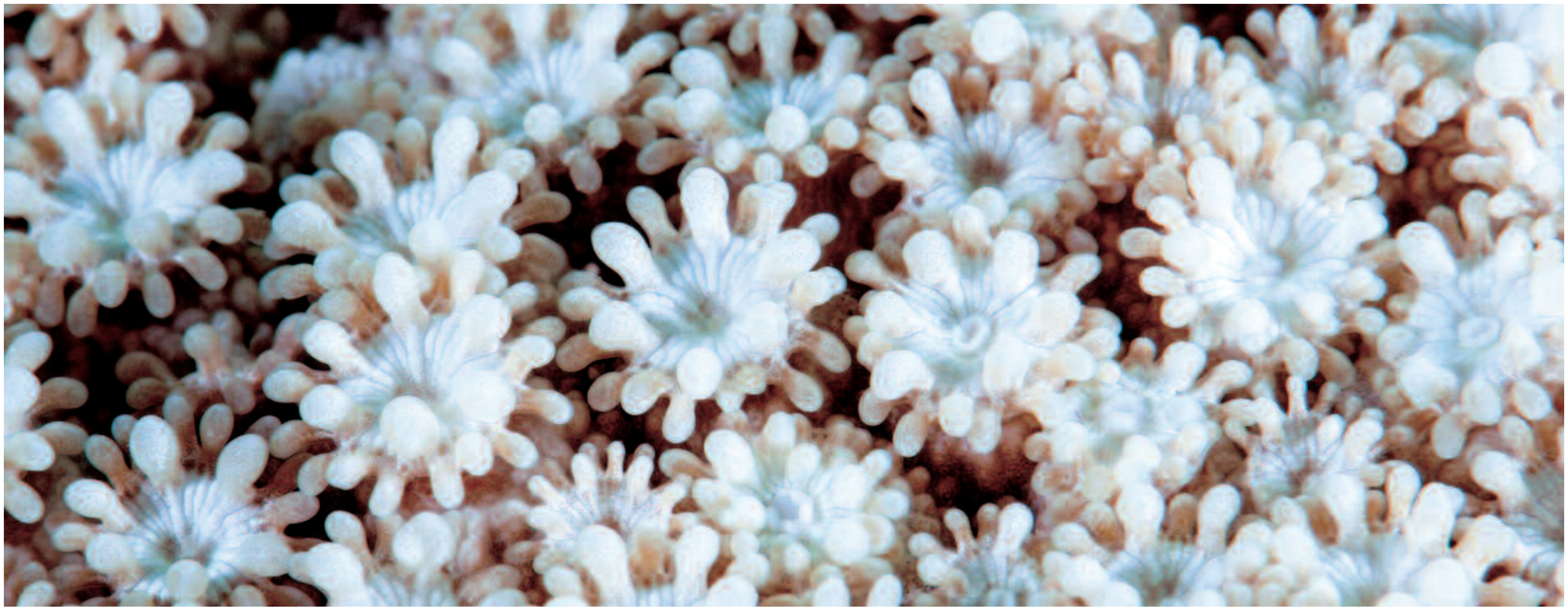
Chapter 7

The reefs' quest for diazotrophs

Valentine Meunier, Sophie Bonnet, Anne Lorrain, Mar Benavides, Mercedes Camps, Olivier Grosso and Fanny Houlbrèque



Deployed coral polyps searching for food. © G. Boussarie

Corals are voracious predators

Coral reefs are important diversity hotspots and major ecological reserves. Although corals develop in oligotrophic waters (poor in nutrients), they are recognized as the most productive ecosystems on our planet. Such a successful evolution is mainly due to their symbiotic relationship with microalgae. The symbiotic microalgae (*Symbiodinium*) present in the coral tissues provide their coral host with most of the carbon that they produce by photosynthesis.

However, in order to fulfill all their nutrient and energy needs, corals are also able to use a different nutrition mode: they are voracious predators that can feed on a wide range of preys (heterotrophic nutrition) (HOULBRÈQUE et FERRIER-PAGÈS, 2009). Their diet includes sediment particles, dissolved organic matter and plankton, which is present in the water column. Corals catch their prey in different ways. They can, for example, discharge stinging filaments (nematocysts) that contain toxic and paralyzing substances, produce mucus to which very small prey adhere, or use their tentacles to grab their prey and bring them to the buccal cavity.

Nitrogen at any price!

Nitrogen is essential to the development of corals. It is particularly important for the synthesis of proteins, molecules which are present in all living organisms. To meet their daily nitrogen requirement, corals use various mechanisms (Fig. 1): they host bacteria and cyanobacteria in their tissues that can fix atmospheric dinitrogen (N_2); with the help of their *Symbiodinium*, they can uptake dissolved inorganic nitrogen (DIN: nitrate NO_3^- and ammonium NH_4^+) and dissolved organic nitrogen (DON: urea and amino acids) in the surrounding seawater and nitrogen is also supplied by ingested prey and particles.

The Western Tropical South Pacific Ocean is known as a hotspot for atmospheric dinitrogen fixation. Around Melanesian archipelagos, and particularly in New Caledonia, the rates of dinitrogen fixation are some of the highest in the world (BONNET *et al.*, 2017). This is mainly due to abundant quantities of planktonic nitrogen-fixing bacteria and cyanobacteria. These "diazotrophic" organisms are able to fix N_2 dissolved in the surface layer of the ocean, and to transform it into ammonium to satisfy their nitrogen requirements. Part of this nitrogen is released in the surrounding environment and transferred to other planktonic organisms that do not have the same ability (BONNET *et al.*, 2016). During summer, nitrogen fixation supports most of the new planktonic production in the New Caledonian lagoon (BERTHELOT *et al.*, 2015). Furthermore, it has also been shown that an important part of this plankton is rapidly exported to the bottom of the reef, which potentially benefits benthic organisms such as corals.

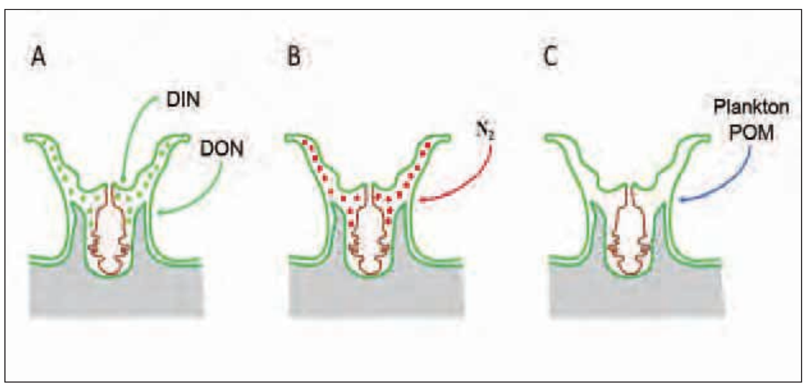


Figure 1: Major nitrogen uptake strategies of corals.
A: In dissolved organic or inorganic forms (DON or DIN), by coral tissues and *Symbiodinium* (green dots).
B: In the form of N_2 by bacteria and cyanobacteria inside coral tissues (red dots).
C: In the form of particulate organic matter (POM) and plankton, by corals.

Diazotrophs for corals

Corals are very important predators of plankton so dinitrogen-fixing organisms or plankton which have benefited from dinitrogen fixation could constitute food sources for corals, through heterotrophic nutrition. However, to date, the role of planktonic dinitrogen fixation in the nutrition of corals has been little investigated. A team from the IRD research center in Nouméa, traced nitrogen from the atmosphere, through plankton and all the way to its ingestion by corals.

Natural N_2 in the Earth's atmosphere is a mixture of two stable isotopes: ^{14}N and ^{15}N. The latter is widely used as an isotopic tracer to monitor the flow of matter in the environment. In order to follow the transfer of nitrogen resulting from diazotrophy, ^{15}N plankton isotopic labelling has been carried out. Small colonies of the coral species *Stylophora pistillata*, which is very common and abundant in the New Caledonian lagoon, were incubated for 12 hours in seawater containing ^{15}N-prelabelled plankton. The concentration of plankton was measured before and after the incubation in order to quantify the ingestion rates by corals.

Analyses were carried out to assess the exact isotopic composition of coral tissues and their symbionts and the results highlighted a significant ^{15}N enrichment in *Symbiodinium*, meaning that diazotroph-derived nitrogen is assimilated by these symbionts and directly allocated and stored into these cells. The ingestion of planktonic diazotrophs or plankton derived from diazotrophy would provide six times more nitrogen than the daily ingestion of small plankton. The abundance and activity of diazotrophs in the New Caledonian lagoon suggest that these organisms are an important nitrogen source for tropical corals (BENAVIDES *et al.*, 2016).

Branching *Acropora* massif, Larégnère Reef, damaged during the massive bleaching event in February 2016. © IRD/F. Houlbrèque

However, further research is needed to understand how the diazotrophic nitrogen is transferred into corals, and in order to investigate its preferential use by symbionts.

Nitrogen to the rescue!

For the last 30 years, repeated beaching events have struck the world's coral reefs with increasing frequency. Although they had been previously spared, the New Caledonian fringing and intermediate reefs were heavily damaged in February 2016 by a massive beaching event which also hit most of the world's coral reefs (chap. 25). When corals are bleached, they lose their *Symbiodinium*. Their colors fade and they lack their main source of energy. Several studies have shown that, during environmental stress such as seawater warming events, corals were capable of increasing their feeding rates on plankton and dead organic matter (PALARDY *et al.*, 2008). This raises the hypothesis that corals could benefit from the presence of diazotrophic plankton to fulfill their nitrogen demand during bleaching events. Preliminary experiments have demonstrated the capacity of *Stylophora pistillata* to increase its feeding rates on diazotrophic plankton or to incorporate more diazotrophic compounds in its diet, during a bleaching event. Hence, bleached corals could compensate for the lack of energy and nitrogen linked to the loss of their symbionts. However, it is not known if this nitrogen intake can, over the long term, increase the resilience of corals after a bleaching event.

References

BONNET S. *et al.,* 2016 Diazotroph derived nitrogen supports diatoms growth in the South West Pacific: a quantitative study using nanoSIMS. *Limnology and Oceanography.* doi : 10.1002/lno.10300.

BONNET S. *et al.*, 2017 Hot spot of N_2 fixation in the western tropical South Pacific pleads for a spatial decoupling between N_2 fixation and denitrification. *Proceedings of the National Academy of Sciences of the United States of America.*, 114 (14) : E2800-E2801.

BENAVIDES M. *et al.*, 2016 Diazotrophs : a non-negligible source of nitrogen for the tropical coral Stylophora pistillata. *Journal of Experimental Biology*, 219 (17) : 2608-2612.

BERTHELOT H. *et al.*, 2015 Dinitrogen fixation and dissolved organic nitrogen fueled primary production and particulate export during the Vahine mesocosm experiment (New Caledonia lagoon). *Biogeosciences*, 12 : 4099-4112.

HOULBREQUE F., FERRIER-PAGES C., 2009 Heterotrophy in tropical Scleractinian corals. *Biological Reviews.* 84 : 1-17.

PALARDY J. E., RODRIGUES L. J., GROTTOLI A. G., 2008 The importance of zooplankton to the daily metabolic carbon requirements of healthy and bleached corals at two depths. *Journal of Experimental Marine Biology Ecology*, 367 : 180-188.

New Caledonia
World of corals

Scientific direction: Claude E. Payri

IRD Editions
French National Research Institute for Sustainable Development, Marseilles, 2018
Editions Solaris

Translation: Lydiane Mattio
Editorial coordination: Claude E. Payri
Page and cover layout : Pierre-Alain Pantz - Editions Solaris
Printing: Winson Press, Singapour

Cover illustrations

Cover page 1 (from top to bottom):
Bay of Upi, Isle of Pines. © P.-A. Pantz
Coral biodiversity of Larégnère reef. © IRD/S. Andréfouët

Cover page 4 (from left to right):
Loading of a mïkwaa net on a decked pirogue at Pwadèwia, St. Joseph Bay, Isle of Pines, 2017. © M. Juncker
Clown fish eggs. © G. Boussarie
Incubation of coral colonies in benthic chambers. © CNRS/E. Amice
Flying Red-footed booby *(Sula sula)*. © M. Juncker

ISBN : 978-2-7099-2677-5

Recommended citation:
Payri, C.E. (dir.), 2018 – New Caledonia: world of corals. IRD Editions/Solaris, Marseilles/Nouméa, 288 pp.