Tales of algae

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Macroalgal community typical of the Southern Lagoon. Woodin Channel, 2015. A golden brown and iridescent *Stypopodium* blade (center) mixes with the delicate red lace-like *Kallymenia*. © IRD/ C.E Payri

Algae, these funny organisms

Coral reef algae are a heterogeneous group of organisms, all capable of photosynthesis, but which have diverged during evolutionary history into several large and independent lineages. Although it has no taxonomic meaning, the term "algae" is generally used for convenience to refer to marine plants of various shapes and colors. They include unicellular microalgae of a few microns, or macroalgae, generally pluricellular, which can be several tens of centimeters in length (box. 9).

Nourishing seaweeds, protective algae

Macroalgae, also known as seaweeds, play an important role in the ecology of coral reefs. Like all photosynthetic organisms, they actively contribute to primary production. They are the main food source for a wide variety of herbivores living in reefs and lagoons (e.g., fish, crustaceans, mollusks) and are the very basis of the food web in coral ecosystems. The most consumed are the filamentous forms that cover dead corals and create an algal turf, which itself shelters a small and very rich mobile fauna loved by herbivorous fish. More coriaceous

Box 9 Microalgae





Microscopic view of zooxanthellae (*Symbiodinium*) in the polyp of the branching coral *Pocillopora damicornis*. Scale: 40 µm. © CNRS/V. Berteaux-Lecellier

Benthic diatoms. A: *Climacosphenia moniligera* (250 μm). B: *Navicula granulata* (90 μm). C: *Cocconeis* sp. (40-50 μm). A, B: © M. Ricard; C: © CRIOBE/B.Delesalle



Gambiersdiscus cultivated cell. These microalgae develop on other substrata, including macroalgae. When they graze on maroalgae, herbivorous fish also consume *Gambierdiscus*. These microalgae have toxins (ciguatoxins) which accumulate up the food chain and trigger an fooodborne sickness called ciguatera. © Louis Malardé Institute/M. Chinain

Microscopic unicellular forms of algae, or microalgae, generally live free in the water column and form the phytoplankton. However, several of them, such as some diatoms, have to be attached to a substratum in order to develop and form the first stages of "fouling". Others have forged a symbiotic partnership with animals; the most famous are zooxanthellae. They are found in the polyps of reefbuilding corals or in the mantle of giant clams. Zooxanthellae, or *Symbiodinium*, are dinoflagellates, such as *Gambierdiscus*. The latter is another microalga well known in coral reefs because it causes ciguatera, a food poisoning due to the consumption of certain reef fish species and large predators (e.g., barracudas and sharks). While *Symbiodinium* shelters in the tissues of its animal host, *Gambierdiscus* develops on the surface of dead corals or large macroalgae forms are rarely grazed. This is, for example, the leathery species of the brown macroalgae genus *Turbinaria*, or the calcareous algae that only parrotfish species or some mollusks are able to scrape with their powerful teeth, leaving very specific marks. The largest of them, such as the large brown algae *Sargassum*, form a canopy under which many species of invertebrate and fish escape predation, reproduce or live (box. 10).

In addition, massive and calcareous red algae play an essential role in the construction and consolidation of the reef structure. They cement the reef into a sturdy structure; the coral matrix alone would not be strong enough to withstand wave action and major events such as cyclones and tsunamis. On the most exposed sites of the barrier reef and the outer reef slope, they replace corals, which are less adapted to strong hydrodynamics. They form a compact pinkishbeige glaze, or rounded brain-shaped clusters or candles, such as in the Chesterfield or d'Entrecasteaux reefs.



Parrotfish grazing on turf and coralline algae. © M Juncker



A: Calcareous red algae (corallinales) are dominant in exposed sections of the external reef slopes where they build massive constructions, for example in the Chesterfield Islands. © IRD/G. Lasne B: Massive encrusting forms that cement the substratum. © IRD/C.E. Payri C: Candle-like forms of *Porolithon*. © IRD/C.E. Payri

Macroalgae, a cabinet of curiosities

Between soft forms or stone-like masses, the architecture and colors of these organisms is astonishing. Red, green or brown, the macroalgae of tropical reefs and lagoons can take unbelievable shapes. They range from leaf-like appendages to branched, feathery, filiform, and articulated forms or to barely recognizable shapes when they adhere to the substratum. These adherent, or even encrusting species, whether brown like *Lobophora obscura*, green like *Codium lucasii* or red like Neogoniolithon or Peyssonnelia, appear like a lively and colorful painting on these otherwise dead coral debris and inert substratum. The khaki beret forms of *Codium saccatum* are as strange as the beads of its sister species *Codium globosum*, or the young specimens of *Halimeda cylindracea*, which spread out their segments like an outstretched hand. These three species are all made of a single giant tubular cell containing multiple nuclei, which is branched to form the body of the algae (box. 11). Even more unusual are these gelatinous and fluffy red algae, sometimes globular like *Gibsmithia*, sometimes branched like *Dudresnaya* or *Trichogloea*, which resist to strong currents, but dislocate when you try to pick them up.



Lobophora obscura. © IRD/C.E. Payri



Gibsmithia hawaiensis complex.© IRD/C.E. Payri



Cladophora sp. © IRD/C.E. Payri



Codium saccatum. © IRD/C.E. Payri



Trichogloea requinerii © IRD/C.E. Payri



Dictyota sp. © IRD/J.-L. Menou



Codium globosum. © IRD/C.E. Payri



Umbraulva sp. © IRD/C. Geoffray



Caulerpa cactoides. © IRD/C. Geoffray



Halimeda cylindracea. © IRD/C.E. Payri



Halymenia sp. © IRD/C.E. Payri



Sargassopsis decurrens. © IRD/J.-L. Menou





Halimeda minima complex. © IRD/C.E. Payri





Lithophyllum proliferum. © IRD/C.E. Payri



Padina melemele complex. © IRD/C. Geoffray

More classical, the fronds of some species can be thin foliaceous blades (*Umbraulva*), thick and digitate (*Halymenia*), or filamentous (*Cladophora*) forms, with simple branched (*Dictyota*) to more complex (*Caulerpa*) structures. The shapes of some species are even more complex and mimic the leaves and stems of terrestrial plants, like the brown macroalgae *Sargassum*.

While most macroalgae are fleshy and soft without a rigid structure, several groups can build a calcified skeleton by precipitating calcium carbonate from seawater into the inner walls of their cells. This is the case for the red coralline algae (over 100 different genera) or some green algae (about 20 genera) such as *Halimeda, Udotea*, or *Neomeris*. Only two genera of brown algae, *Newhousia* and *Padina*, precipitates a thin calcified layer in the fronds or on their surface, respectively.

Rhodoliths are even more singular. These free-living stony nodules that can be round or branched, are built by calcareous red algae. The algae develop in concentric layers, around a piece of coral debris (nucleus), as it rolls on the bottom under the action of a moderate current. They are purple-red to pink in color, and line parts of reef flats or form maerl fields at the bottom of lagoons swept by moderate currents.



Caulerpa taxifolia. © IRD/C.E. Payri



Avrainvillea sp. © IRD/C.E. Payri



Penicillus sp nov. © IRD/C.E. Payri

Box 10 Sargassum, the bush of the lagoon



Sargassopsis decurrens belongs to the Sargassaceae family. This species is easily recognized by its singular morphology in "fish bone" or Christmas tree. Vesicles (the "Christmas baubles") provide Sargassaceae species with a way of standing upright when attached to the bottom or to float at the surface when they detach (storms, senescence). © IRD/C. Geoffray





Sargassum bed in the Southern Lagoon. Sargassum spinuligerum is the most abundant species and can reach 1.5 to 2 m high. This underwater "bush" is an essential habitat for numerous species of other macroalgae, fish, invertebrates and mollusks. © IRD/C. Geoffray

look like brown mistletoe (e.g., *Sargassum ilicifolium*), while others resemble a flattened Christmas tree or even a fish bone (e.g., *Sargassopsis decurrens*)! They are found in a wide variety of habitats from coastal intertidal zones to barrier reefs. They form dense or scattered populations on coastal reef flats, on fringing reefs of islets, on lagoon bottoms to a depth of 30 m, and on the barrier reef to a depth exceeding 50 m (-56 m for *S. turbinarioides* at the Isle of Pines). They develop on all types of hard substrata, including more or less silted rocky bottoms (e.g., *S. polyphyllum*), coral debris (e.g., *S. polycycstum*), reef crevices or artificial riprap (e.g., *S. aquifolium*).

Box 11 Amazing siphonous algae!



Avrainvillea sp nov. © IRD/C.E. Payri



Rhipilia penicilloides. © IRD/C.E. Payri





Rhipilia sp nov. © IRD/C.E. Payri

Chlorodesmis sp. © IRD/C.E. Payri

Who would have thought that these algae are one single cell? This is characteristic of species belonging to the order Bryopsidales. Despite this simple structure, their morphological diversity is unbelievable. Specimens can reach over 10 cm in height, and are capable of forming very different body shapes depending on the family to which they belong. Some are so complex (rhizoids, stipe and blades comparable to the roots, stem and leaves of terrestrial plants) that it is difficult to believe they are unicellular organisms. However, these algae are made up of a single, plurinucleate and tubular cell called a siphon, which divides into several branches that share the same cytoplasm. The arrangement and organization of these siphons (which can intertwine, be perfectly aligned, even coalesce, or remain free) is very different from one species to another and creates an important morphological diversity, which is visible to the naked eye. In New Caledonia, all macroalgae are benthic organisms. It means that they attach to a support, which can be as tiny as a grain of sand. To date, only two macrophyte species are known to develop without ever being fixed. They are two species of the brown algae *Sargassum*, found in the Sargasso Sea, in the North Atlantic. These pelagic algae can form very large rafts, which are very important ecologically. For a few years now, the Caribbean islands and the coasts of Brazil and West Africa have been experiencing massive stranding of these pelagic *Sargassum*, but no one has yet been able to identify their origin or explain this recent phenomenon.

In the lagoon of New Caledonia, it is common to see *Sargassum*, which after having been detached from their substratum, float (thanks to small air vesicles) and drift according to currents before stranding on beaches or disappearing into the depths, marking the end of their life.

A world of colors

Macroalgae are commonly referred to as red, green and brown algae - here, we do not consider the so-called "blue-green algae", which are bacteria (cyanobacteria), or seagrasses which belong to a completely different evolutionary lineage: the phanerogams. For macroalgae, the three broad categories of colors refer to three main taxonomic divisions, rhodophytes (red algae) and chlorophytes (green algae), which form two evolutionary divergent lineages but belong to the same "green lineage", and the phaeophytes (brown algae), the "brown lineage", which is evolutionarily distinct from the previous one. Three types of pigments, chlorophylls (green pigments), carotenoids (orange and yellow pigments) and phycobilins (red and blue pigments) are sufficient to create a whole range of colors depending on their concentration, sometimes causing confusion. Red algae can appear brown, while brown algae can take on greenish colors... But the different combinations of pigments are not the only criteria on which taxonomy and phylogeny are based. The various products of photosynthesis, cell walls, the shape and number of flagella in unicellular cells or reproductive organs in pluricellular organisms, and cellular organelles, such as plasts, are also taken into account.



Caulerpa chemnitzia. © IRD/C.E. Payri



Codium taylorii. © IRD/C.E. Payri



Padina melemele. © IRD/C.E. Payri



Platoma sp. © IRD/C.E. Payri



Dictyosphaeria cavernosa. © IRD/G. Lasne



Distromium didymotrix. © IRD/C.E. Payri



Melanthalia vieillardii. © IRD/C.E. Payri



Callophycus serratus. © IRD/C.E. Payri

They are everywhere...

Macroalgae are everywhere: from mangrove forests, where the small red algae *Bostrychia* nests on mangrove roots, to coastal meadows, where grow many species of brown algae such as *Padina*, red algae such as *Dichotomaria*, and green algae such as *Caulerpa*. The latter has fronds that can be digitate (e.g., *Caulerpa cupressoides*), feather-like (e.g., *Caulerpa sertularioides* or *C. taxifolia*), or like a bunch of grapes (e.g., *Caulerpa racemosa* and *C. chemintzia*).

On the bottom of the lagoon, several species of green algae are anchored in grey sand with their compact rhizoidal bundle: *Halimeda*, recognizable for its small calcified segments, the tender green and fan-shaped *Udotea*, and the dark green *Avrainvillea*, whose frond, devoid of calcified structures, has a velvet touch.

Rocky bottoms are generally covered by *Sargassum* meadows. Their small floats pull their long fronds towards the surface. They shelter under their canopy other species of brown algae *(Lobophora, Dyctyopteris, Hormophysa...)*, which together form a particularly productive ecosystem. On intermediate reefs and barrier reefs, soft macroalgae are more modest, although they are still many. It is the realm of the green algae *Rhipilia* and *Chlorodesmis*, which form small pompon balls, of an intense green, at the top of coral colonies. Next to them, *Halimeda* spreads out in long curtains along the walls of massive corals, or hide in coral interstices with other strange species, such as *Valonia ventricosa* (large green marbles) or *Dictyosphaeria cavernosa* (compact cupules). In these areas, the slightest hard substrata are cemented by crustose coralline algae which consolidate the reef.

On the outer reef slope, algae are distributed according to depth and water movements, forming communities down below 100 m deep. Regardless of their color, they are strongly attached to hard substrata. Species with erect fronds sway in the endless movement of water; this is most red algae, such as *Gibsmithia, Dudresnaya, Predaea, Platoma* and species of Liagorales. Others spread out over the substratum, like the thin, golden-brown and rounded blades of the brown algae Dictyotales (e.g., *Distromium, Lobophora, Homeostrichus*). Green algae are mainly represented by *Halimeda* and *Codium*, the latter is sometimes branched and erect, sometimes strongly adhering to corals. Many species live under overhangs or line the walls of caves: they are the numerous *Peyssonnelia* species, some encrusting, others forming large rounded blades of a very dark red. They are easily distinguishable from calcareous coralline algae, which form crusts over any available surfaces, creating artistic mosaics of warm colors in this relatively dark universe.

Contrasting with the large red algae are the tiny and delicate green species, of only a few millimeters high, whose diversity is inversely proportional to their size. This is the world of the *Rhipidosiphon* (calcified), *Rhipiliopsis* and *Rhipiliella* (uncalcified) species, many of which are still to be described. Macroalgae are everywhere, they even live inside coral skeletons or other carbonate substrata, they are called "endoliths". Through their perforating action, along with other perforating organisms such as bivalves, sponges and worms, these algae cause a superficial decay in the rock which affects the morphology of the reef.

Although they are dependent on light, macroalgae also colonize the mesophotic zone, this section of the reef between 70 and 125 m deep, which some experienced divers have explored equipped with recyclers powered by suitable gas mixes. Algae in this area are not very well know and each new dive brings back new species, including some of the brown *Distromium*, the red *Delisea*, and the green *Phacelocarpus* and *Halimeda*.

How many algae species in New Caledonia?

The total number of macroalgae species in world has been estimated to be between 7,000 and 15,000. In New Caledonia, the first estimate, published in a compendium in 2007, totalized 443 species. However, this is a very preliminary estimate, because it is based on relatively limited collections and mainly morphological observations. This number keeps growing with additional collection campaigns, repeated surveys between 40 and 60 m deep, and

Macroalgae from the mesophotic zone



Phacelocarpus neurymenioides (80 m deep) © IRDJ.-L. Menou



Distromium sp.(85 m deep) © Biocénose/G. Lasne



Halimeda minima complex (100 m deep) © IRD/J.-L. Menou

genetic analyses. It is likely to reach or even exceed 1,000 species. It would be pretentious to think that the inventory of New Caledonia's macroalgae has been completed. This is because despite the prospecting effort developed throughout the archipelago over the last 15 years, sites have not been prospected in a comparable manner and, as a matter of fact, the large Southwestern Lagoon region remains the best known to date.

While marine macrophytes are increasingly being studied, a large number of species are still waiting to be named according to the code of botanical nomenclature (i.e., a genus name followed by a species name). As DNA and genetic barcoding analyses become more common, the discovery of new species has increased at a rate much higher than the time required to formally describe these species. For example, only two species of the genus *Lobophora* (brown algae) were recorded in New Caledonia until 2007, but it now has nearly 30 species, 10 of which are new to science. Globally, this genus accounts for more than 100 species, but only about 30 have been described and named; the others are indexed by DNA sequences linked to reference specimens. The situation is similar for most groups, supporting the idea that the total number of species will never be known!

Species communities can be described according to large habitat types or their biogeographic affinities. As an indication, the few hundred species that have been recorded to date represent 63 families and 185 genera unevenly distributed among the three major divisions. Red algae account for more than half of the species, followed by green algae, with a very strong dominance of Bryopsidales, and brown algae, which account for less than one-fifth of the species, but represent the largest biomass. Nine families account for more than half of the species, while many others have a small number of representatives. In addition, many species are relatively rare. The biological and ecological scarcity that have been reported for fish, mollusks and other invertebrates appears to be a rule. Similarly, endemism in algae is less than 3%, which is similar to most other biological groups.

Box 12 Similar... but different!



Lobophora rosacea. © IRD/C. Vieira



L. hederacea. © IRD/C. Vieira







L. hederacea. © IRD/C. Vieira

L. hederacea. © IRD/C. Vieira

L. obscura. © IRD/C. Vieira

The identification of biological diversity units is essential in fundamental ecology, for the quantification of biodiversity, but also for conservation biology. However, this identification is made difficult by the presence of cryptic species, which are species that are genetically distinct but morphologically similar.

The development of molecular biology has led to the discovery of a particularly important cryptic diversity in the marine environment. This cryptic diversity is only starting to be explored

in marine algae. For example, more than a hundred species were hiding under the name *Lobophora variegata*, a small brown alga growing in coral reefs and assumed to be present in all warm seas.

The situation is similar for the red algae *Portieria hornemannii*, which in fact includes over 90 distinct genetic entities. The recent discovery of this cryptic flora calls for a re-evaluation of the algal biodiversity, particularly in tropical regions where this interspecific biodiversity reaches its maximum.

When geological history and geography govern diversity

Mediterranean Sea, yet for a much smaller area. There are several reasons for this. First is the proximity of the coral triangle (Philippines, Indonesia, and Papua New Guinea), an area that concentrates the world's highest marine biodiversity. Second is an exceptional diversity of habitats with more than 150 geomorphological units. Last is the oceanographic and climatic context, with a gradient ranging from tropical to subtemperate, or even temperate, from north to south. Although the southwest region is influenced by cold-water upwelling, the water temperature at the coast is a few degrees higher. As a consequence of this geographical and climatic setting, the Loyalty Islands share less than 25% of their macroalgae species with the rest of the archipelago, but have a very strong affinity with the flora of Vanuatu, the Solomon Islands and Papua New Guinea. In contrast, the



Bellotia simplex described from the bay of Saint Vincent, west coast of Grande Terre. Woodin Channel, 2015. © IRD/J.-L. Menou

Southern Lagoon, which includes Isle of Pines and Corne Sud, harbors species, characteristic of subtemperate coral reefs, which are also recorded from Lord Howe Island and the west coast of Australia. Some genera, such as *Melanthalia*, a large red macroalgae, have a distribution restricted to the south of New Caledonia, the south of Australia, and the north of New Zealand. This sub-regional endemism has been interpreted as a vestige of Gondwana.

Each region of the New Caledonian archipelago has a few characteristic taxa that are only found there. The genus Penicillus, a brush-like green algae, has only been observed on the sandy bottoms of the Chesterfield atolls; whereas Apjonhia, a fir-shaped green alga, is only found at the Isle of Pines. The order Sporochnales (e.g., Bellotia, Nereia) testifies for the similarity of the New Caledonian and Australian marine flora. They are very elegant brown algae with small pompon-like tips and a slimy touch, very diverse in genera and species, and which are found in bays rich in terrigenous sediments. There is also a whole selection of species in common with the Ryukyu archipelago in southern Japan. Most of these species, which prefer shallower habitats in Japan, develop in deeper habitats (30 m) in New Caledonia, where they find a matching water temperature. The best example is Padina stipitata, which grows at the Gail Bank south of Grande Terre, and whose DNA sequences are strictly the same than those of specimens from the type locality in Japan.

The taxonomic data available for the Pacific is too fragmented to draw conclusions about the exact limits of the geographic range of algal species. However, results of molecular phylogenetic studies, carried out for some groups, show that the New Caledonian marine flora belongs to a Southwest Pacific biogeographic region, which includes the Coral Sea to the west and, the Melanesian arc to the east, stretching from the Solomon Islands to Fiji. New Caledonia also shares part of its biodiversity with other regions in the Pacific Basin.

In order to explain its exceptional biodiversity, one must go back in time to periods when sea level was lower. At that time, it is likely that the New Caledonian archipelago was a biodiversity refuge, similar to the coral triangle, where numerous coral reef species accumulated over time.

Box 13 A complex chemistry, a fragile equilibrium



Metabolomic profile of the brown macroalgae *Lobophora rosacea*, a common species in the lagoon of New Caledonia, often associated with branching corals. @ IRD/C. Vieira

Within coral ecosystems, interactions are widely mediated by chemicals, especially between benthic organisms. Marine animals use chemical signals, for example in the regulation of social and reproductive behaviors, or for the recognition of food. In order to avoid, minimize or tolerate the damages caused by herbivores, macroalgae have adapted to reduce their attractiveness, and chemical defenses are one of the most common strategies used by tropical algae. With their arsenal of chemical substances, macroalgae can create a chemical barrier against aggressors (herbivores, bacteria, epiphytes, and pathogens), but they can also use them as a "weapon" while competing for space with other benthic organisms such as corals, particularly when the ecosystem is weakened by disturbances. Like in corals, chemical interactions play an important role in the reproduction and recruitment of algae. However, this is only the visible part of the iceberg, and further research is needed to understand the biological and ecological functions of chemical compounds in macroalgae.

Good or bad algae?

Macroalgae are often wrongly associated with environmental degradation. As mentioned above, they are so essential to the system that it would be more accurate to call these ecosystems "algo-coral" reefs. However, ecological imbalance sometimes leads to the abnormal proliferation of some algal communities, which can, in some instances, take over living corals. Are algae the cause or the result of coral disappearance? This is a major question in the context of global change, and as the international community is warning about the regression of coral reefs. The community changes that have been described in many parts of the world seem to have spared the New Caledonian coral reef ecosystem, but for how long? Human populations and their activities at the coast are increasing.

While the coral reefs of New Caledonia still are in a good (even excellent) health for the majority of them, near peri-urban areas, reefs show some stigmas of degradation. In some instances, these stigmas are biological interactions between algae and corals to the detriment of the latter. Algae have much higher growth and reproductive capacities than corals. When for various reasons coral colonies die, a new substratum is available for algae to colonize. Coral bleaching, coral diseases, and smothering of coral polyps by terrigenous particles are all causing coral death. If environmental conditions have changed to a point that algal growth is promoted, the coral recruitment will be affected, and then, algal blooms may be associated with reef degradation (box. 13).

However, there are no good or bad algae; they all have a role and function in coral reef ecosystems. Like all other organisms, they have, during their own evolutionary history, developed functional biological traits that allow them to live in their specific environment. Algae are an invaluable reservoir of bioactive substances. The way they interact with their environment is not easy to comprehend, but chemical ecologists have shown that these substances are pathways of communication for biological interactions. Many Dictyotales produce polyphenols that keep predators at bay, others cause the death of coral polyps, such as *Lobophora hederacea* in New Caledonia.

While some red calcareous algae are known to kill the corals with which they compete for space occupation (e.g., *Pneophyllum conicum*), others from the same group (*Titanoderma*) play an important role in the fixation of coral larvae. The mechanisms that are involved are not well known, but there could be a production of attractive molecules.

Algae, a source of inspiration

With an estimated thousand or more macroalgal species, the lagoons and reefs of New Caledonia provide an exciting playground for phycologists. Since the early work of missionaries and amateur naturalists in the late 19th century important knowledge has been accumulated. Different aspects of this diversity have been revealed throughout various disciplines and methodological approaches. Adding on to the taxonomic work needed to understand what is being protected, other studies have shed light on the issues surrounding the future of these communities in the context of global change. At present, phycologists (box 14) investigate the evolutionary history of macroalgae, analyze their biological interactions with other reef organisms, and also look for molecules of interest to man in this reservoir of complex substances produced by algae to grow, defend and reproduce.

Box 14 Etymology

Scientists who study algae are called "phycologists", and not "algologists" who study the science of pain! In English, "algae" comes from the Latin "algae", while "algologist" and "phycologist" come from the ancient Greek. In Greek "algos" means "pain" (e.g., also found in "analgesic"), "phycos" means "algae", and "logos" means "study or knowledge" (e.g., also found in "musicologist").

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New Caledonia World of corals

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