The Functioning of Coral Reefs and Atolls

From paradox to paradigm

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Feared and forever described by sailors as formidable boat-traps, coral reefs and atolls have also been the source of much debate amongst scientists. The first circumnavigators to cross the Pacific often paid their right of way through the Polynesian atolls with the loss of their ship. Thus it was for S. Del Cane, on one of the East Tuamotu atolls in 1520, and for Roggeveen (the "Magellan's Lieutenant discoverer" of Easter Island) on Takapoto Atoll in 1722.

At that time, naturalists held conflicting opinions on the biological nature of coral. J.A. Peysonnel (1694–1759) believed that coral belonged to the animal kingdom, which was vehemently contested by his colleagues at the Académie des Sciences who took it as read that "coral flowered under the sea" and thus belonged to the plant kingdom. Centuries earlier, the Greek geographer Strabon (58 BC – 21 AD) tended towards the latter view when he noticed that, on the dry shores of the Red Sea, "little sea trees grow all along the coast and down towards the depths, and are fully covered at high tide...".

Despite the still-growing number of wrecks impaled on coral reefs (one or two a year in Polynesia alone), the scientific community still has a number of fundamental questions to answer today, regarding, for example, the internal mechanisms which control coral metabolism and the growth of barrier reefs and atolls. In the middle of a monotonous ocean, these structures stand out as singular geomorphological entities, varying in size from 5 to 1600 km2 (Tuamotu atolls) and arbitrarily distributed.

THE FUNCTIONING OF CORAL REEFS AND ATOLLS

Within the Pacific Ocean, the barrier reefs and atolls of French Polynesia are biogeochemical peculiarities resulting from the growth and calcification of algo-coral colonies on a formerly volcanic basalt foundation. The fact that these reefs can thrive in the heart of a tropical ocean which is very poor in both nutritive salts and plankton is a paradox which can be explained using the geothermal endo-upwelling model of functioning (Rougerie and Wauthy, 1986–1993).

This model is based on deep ocean water rich in nutrients penetrating the interior of the reef structure, on its upward movement by thermo-convection and on its evacuation via the external reef crown which is exposed to and washed by the ocean swells. Other geochemical implications, such as phosphatogenesis, dolomitisation or the atoll-guyot (flooded atoll) evolutionary sequence, can be taken into account by this model, which could thus prove to be a generally applicable paradigm for all barrier reefs and atolls.

• The vast tropical oceanic desert

The geographical distribution of reef-building corals (hermaytpical) indicates that they belong to inter-tropical oceans, with a lower temperature limit around 18°C. The Polynesian ocean, where surface-layer temperatures range between 20° and 30°C depending on the season and especially the latitude, thus has favourable thermal characteristics for coral reef development, up to and including the area around the southernmost island, Rapa (28° S). Water salinity poses no problem, as the Polynesian zone falls between 36.5 and 35.5 psu (practical salinity unit). Large fluctuations can, however, be observed in the semi-closed or closed lagoons, depending on the balance of evaporation rainfall and local run-off.

As far as its richness in dissolved nutritive salts and its primary fertility are concerned, the Polynesian ocean ranks bottom on the world scale: the nutrient levels (phosphates, nitrates, silicates) of the sunlit layer, called the euphotic zone (0–150 m), are very low, only just detectable by analytical methods. However, without these nutrients, which are necessary for the production of any organic matter (autotrophic function), phytoplankton and zooplankton cannot develop. This nutrient deficiency, or oligotrophy, is indeed a general characteristic of tropical oceans and explains their clear waters: the Polynesian ocean is renowned for the crystal clarity of its waters, the famous "blue of the South Seas". But this blue means desert for the ocean, just as yellow–ochre does for the sand of the continental deserts.

In fact, there is an enormous reservoir of nutrients in the deep ocean, from 500 m downwards, but no mechanism exists, in Polynesia, to draw these rich waters up to the sunlit layer. When a large land mass is present (Peru) or along the equatorial line (divergence), the combined effects of wind and current allow the deep waters, rich in nutrients, to rise to the surface. This process is called "upwelling" and accounts for the very high primary production of these waters. In this way, upwelling zones are the source of 80 per cent of the production of the world's oceans, though they only occupy a small percentage of their surface area (Wauthy, 1986).

The Polynesian ocean cannot benefit from these upwelling enrichment processes because of its permanent stratification. The surface layer (9–150 m), heated by the sun, floats over the deeper waters and is separated from them by a thick density barrier which extends between 150 and 500 m, the depth from which the Intermediary Antarctic Water is found. The ocean is therefore in two layers: a warm, oligotrophic surface layer, clearly separated from the deep layer, which is both cold and rich in nutrients (Rancer and Rougerie, 1992).

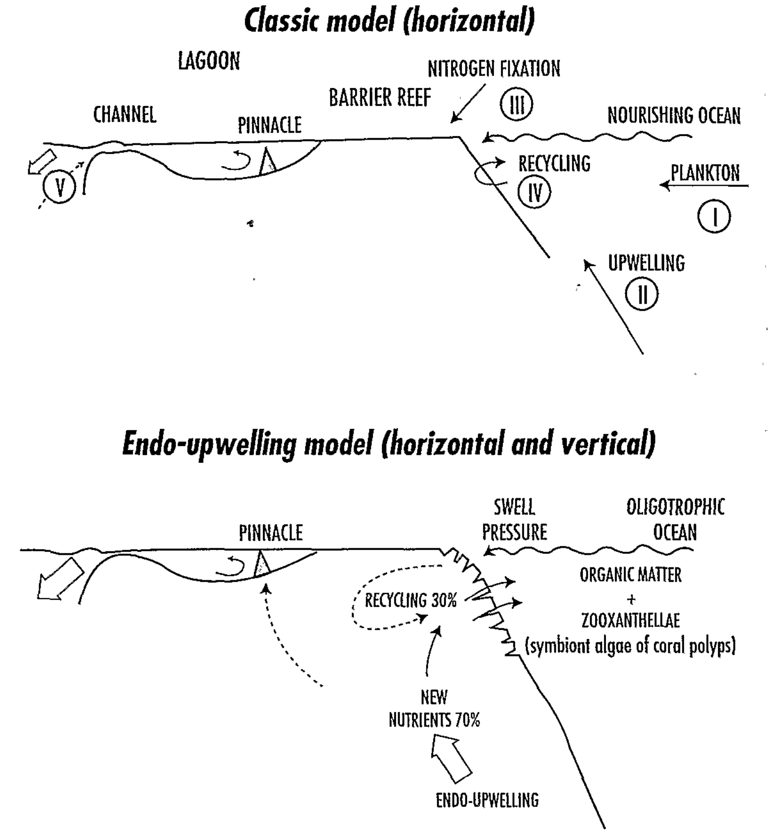
• Coral reefs and oasis-atolls

Coral colonies are found in banks of various sizes, where brown and green are the dominant colours. These colonies, consisting of roughly 40 different species in Polynesia, are created by the metabolism of the tiny coral polyps, whose tentacles can catch planktonic prey (heterotrophic function); they are indeed animals, as Peysonnel had surmised, but more particularly symbiotic animals, since each cubic centimetre of polyp houses millions of symbiont micro-algae, zooxanthellae, whose role determines colony growth. The photosynthesis of organic material, assured by the zooxanthellae, renders the autotrophic function definitively preponderant, especially when the ocean is poor in planktonic prey. Zooxanthella development is conditioned both by incidental light energy, and thus by the transparency of the reef waters, and by the nutrients available in the environment. The first condition is easily satisfied in Polynesian waters, but not the second, and yet reefs and atolls are abundant. There is moreover a close correlation between the rate of primary production of zooxanthellae and the speed of coral calcification, i.e. the construction speed of the external limestone skeleton (which continues to exist after the colonies have died). The figures showing this production are impressive and place coral reefs at the top of our planet's range of ecosystem production: 9.5 to 10 kg of organic matter fixed per m^2/year and 4 to 8 kg of limestone ($CaCO_3$) in the same period. The powerful reef walls and atolls built up in this way by algo-coral colonies are stunning oases of life for a highly diverse fauna (fish, crustaceans, echinoderms, etc.) which they provide with both food and refuge. Although the destruction and loss of matter due to swells, cyclones and storms are compounded by this biological predation, the reefs manage to grow permanently in order to remain "at wave level", and this in spite of the great poverty/oligotrophy of the surrounding ocean (Laboute et al., 1994).

• Darwin's paradox

Coral thus seems to proliferate when ocean waters are warm, poor, clear and agitated, a fact which Darwin had already noted when he passed through Tahiti in 1842.

This constitutes a fundamental paradox, shown quantitatively by the apparent impossibility of balancing input and output of the nutritive elements which control the coral polyp metabolism. Recent oceanographic research has brought to light the reality of this paradox by confirming that the oligotrophy of the ocean euphotic zone persists right up to the swell-battered reef crest. When you approach the reef edges and atolls from the quasi-desert of the open sea, the near absence of living matter suddenly becomes a plethora of life, without transition. So why is there something rather than nothing, and more precisely, where do the necessary nutrients for the functioning of this extraordinary coral-reef machine come from ? (Fig. 1)



The classic horizontal model does not explain the huge productivity of reefs within an ocean which is extremely poor in nutritive salts and plankton.
On the other hand, the model based on the geothermal endo-upwelling process allows for compensation of atoll-oasis losses by ensuring an overall positive production for the coral ecosystem, recognised as being essentially autotrophic, i.e. producing organic matter from dissolved minerals and nutrients.

Fig. 1 - Functional models of atolls and barrier reefs

• The geo-thermal endo-upwelling solution

Drilling carried out since 1988 through the reef crowns at Tikehau Atoll (Tuamotus) and on the Tahitian barrier reef has provided good clues for answering this question: analysis of the interstice waters of the drillings (at a depth of between 5 and 50 m) has shown the presence of high levels of dissolved nutrients, directly usable by symbiont zooxanthellae. The discovery of this interstice nutrient reserve inside the highly permeable/porous reef limestone (30 to 50%) confirms similar results obtained at Mururoa Atoll in the early 1980s. Analysis of deep oceanic tracers and markers (salinity, helium-3, freon) has shown that these nutrients originated in the deep ocean (Intermediary Antarctic Water). At the same time, several American and French authors who had worked on deep drilling in the atolls of Eniwetok (Marshall Islands) and Mururoa (Tuamotus) concluded that a circulation by thermal convection existed within these atolls, under the action of the geothermal flow originating from the once-volcanic basalt bedrock (Guille et al., 1993). By combining these data, we have been able to propose a model for reef functioning by "geothermal endo-upwelling" (Fig. 2): the deep oceanic water, both cold and rich in nutrients, which enters at the base of the reef or atoll is slightly warmed by the geothermal flow and rises by thermal convection (lowering of density) to the top of the structure; this "endo-upwelled" water leaves by way of the external reef crown, which is exposed to and washed by the swells, thus preventing the plugging of the porous network (Rougerie and Wauthy, 1990).

Secondary points of exit can exist in the lagoons, depending on the presence of fractures and fissures under the lagoon. This would explain the presence and random distribution of coral heads and pinnacles (Guilcher, 1988). These coral structures in the shape of stalagmites are occasional oases of life within lagoon basins that

In this recently-proposed model, which is being tested, the deep oceanic waters, rich in CO_2 and nutritive salts, penetrate the limestone slopes of the atoll and, warmed by the geothermal flow from the basalt bedrock, rise by thermal convection through the porous reef limestone. These interstitial waters tend to emerge slowly around the atoll's coral crown, where the action of the swells thoroughly cleans the porous substratum. The symbiont algae (zooxanthellae) of the coral polyps thus benefit from a constant supply of nutritive salts, allowing a strong primary production. This is at the base of the richness of the reef, and thus atoll, ecosystem.

(Rougerie and Wauthy, 1986)

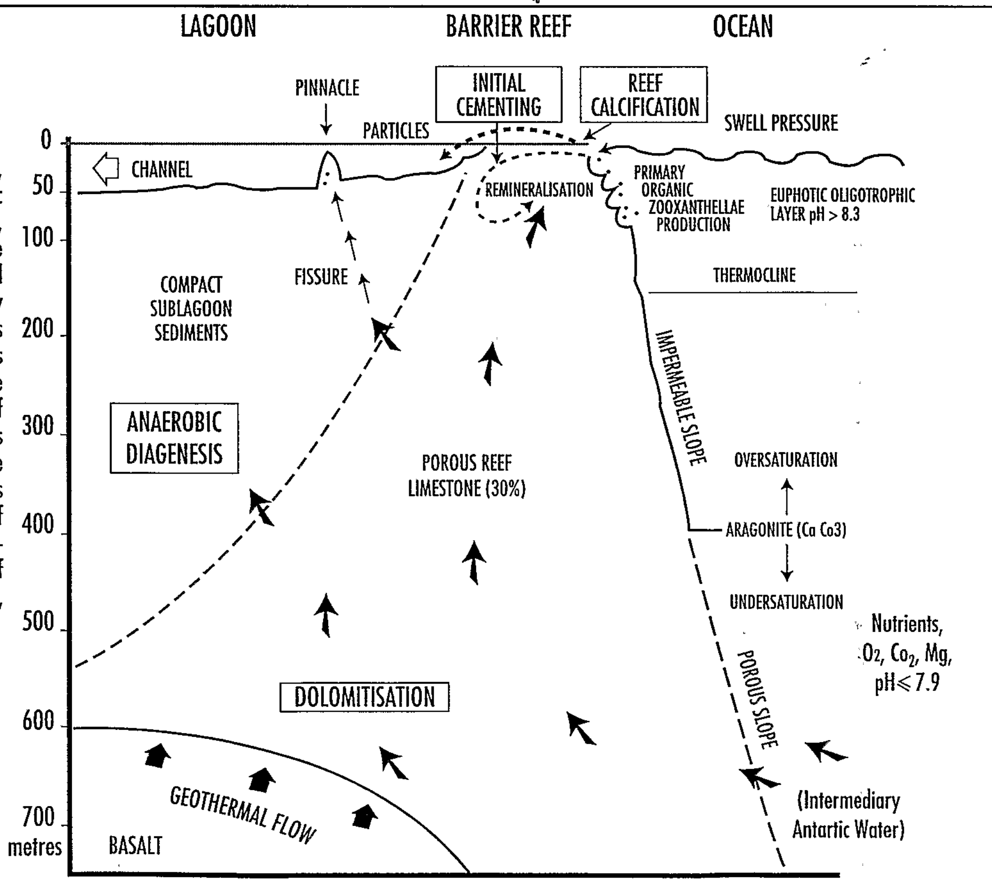
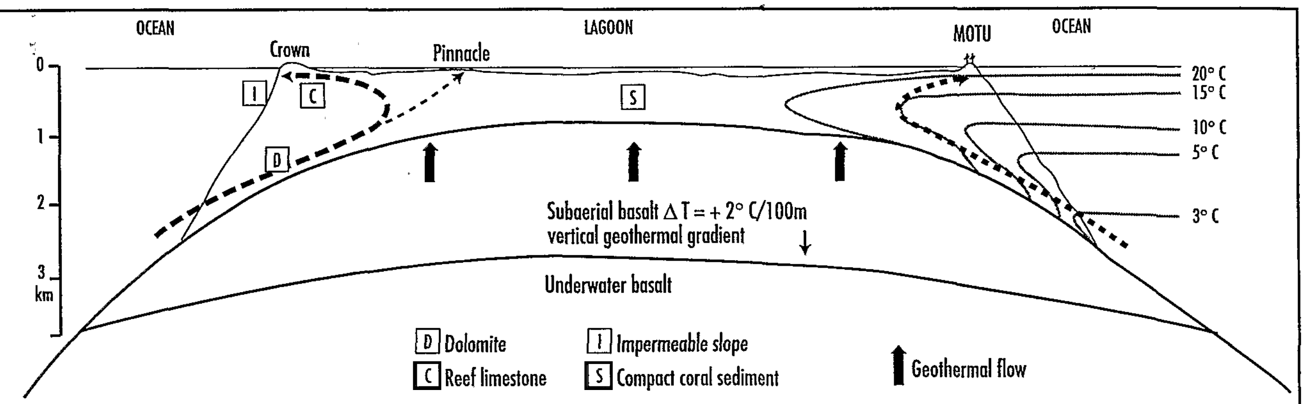


Fig. 2 - Schematic representation of the principle of atoll functioning by geothermal endo-upwelling

are unproductive and filling up with limestone sands from the reef crest. Numerous Polynesian lagoons are already closed in, filled and uplifted, without any alteration in the geomorphological characteristics of the reef wall which encloses them. Whilst playing an important role in the harmony of Polynesian and Paumotu society, lagoons, with respect to the overall functioning of atolls, are secondary features, condemned to disappear through drying up when sea-levels fall or tectonic plates rise (Makatea). The algo-coral crest and the external reef slope are the essential structure, the primary feature, whose durability depends entirely on the flow of interstice water rising slowly to its level; this flow, thanks to its richness in nutrients, maintains the strong reef productivity/calcification but has no effect on the ionic composition of the surface ocean, as it is so very diluted. It has to be remembered that persistence of the oligotrophy in the euphotic layer, and thus of the clearness of the water, is vital in that it provides the zooxanthellae with optimal light energy. Interstice water, on reaching the upper part of the reef structure, undergoes a rapid drop in pressure and thus loses CO_2. The CO_2-carbonate balance is shifted, which favours early reinforcing of the coral mass by the fusion of detrital coral boulders; without this early "cementing", a reef would be similar to a building erected without reinforced concrete: it would not last long. Other geochemical and diagenetic phenomena affect the reef matrix, depending on the intensity and ionic composition of the interstice water flow. We can therefore consider that a barrier reef or an atoll is a bio-geochemical signal determining the exit sites of endo-upwelled waters: this model (Fig. 3) is a necessary and sufficient solution to Darwin's paradox (Rougerie and Wauthy, 1993).



The limestone substratum is 1km thick at the centre of the atoll and can reach 2.5km at its walls. These figures apply to atolls which are at least 20 million years old, such as those located in the western Tuamotus. The geothermal flow emitted by the once-volcanic basalt substratum maintains the thermal convection of the incoming oceanic water. The first measurements of vertical thermal profiles were carried out in the deep drillings at Bikini and Eniwetok (1955), then at Mururoa from 1965 by the CEA, and these have provided the physical base for the geothermal mechanism of endo-upwelling (Samaden et al., 1984).

Fig. 3 - Section of an atoll raised over the ocean floor

• The enigma of atoll phosphates

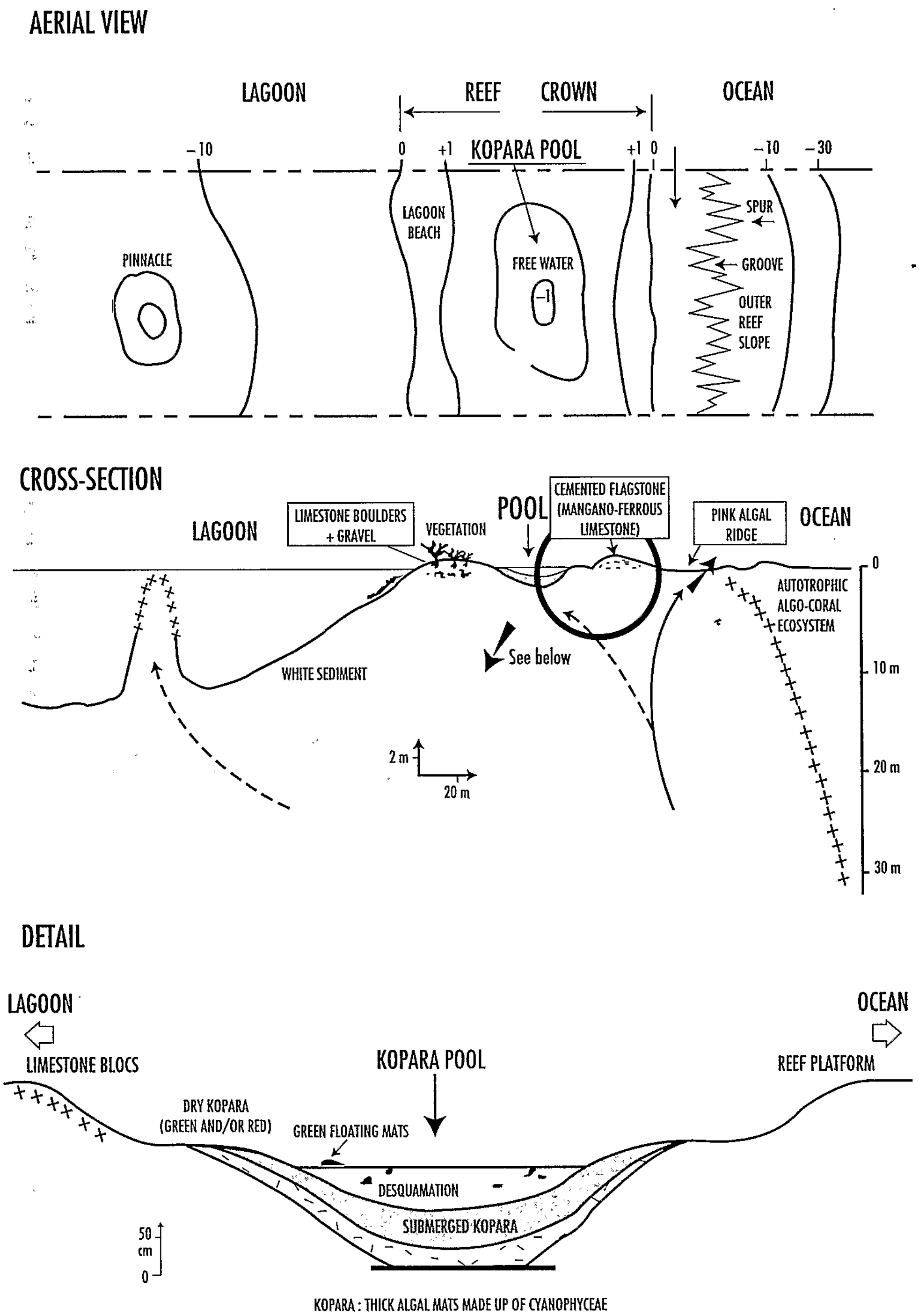
Phosphate deposits possibly exceeding several tens of millions of tonnes occupy the summits of certain filled or raised atolls. These deposits, which have been exploited since the beginning of the century and which in some cases are now exhausted (Makatea), are composed of insoluble fluor-apatite containing up to 35 per cent P_2O_5. Faced with the problem of the origin of these atoll or insular phosphates, those who first came across the deposits could only suggest an avian origin, by analogy with what they already knew, i.e. guano deposits. The latter deposits evidently resulted from the accumulation of seabird excrement in highly-productive marine zones; these zones benefit from the rising of deep waters rich in nutritive salts (upwelling), giving rise to a proliferation of plankton that maintains large fish populations (anchovies, sardines) which are themselves subject to predators, including birds. The bird populations of upwelling zones can be enormous (tens of millions of birds) and therefore produce substantial layers of guano. Thus, Chilean guano was exploited on a large scale and imported to Europe as a source of nitrate fertiliser and explosive until the 1920s. (Then the electric synthesis of ammonia from atmospheric nitrogen was discovered and the explosives became nuclear!)

The richness of avian guano thus came (as it still does) from its high level of nitrogenous components (ammonium or nitrate) whilst its phosphate content is low (less than a few percent). Chemical analysis of the guanos does not even show the range of elements which accompany the phosphorus of the fluor-apatites: only a trace of fluorine is found and other characteristic elements, such as zinc, titanium and boron, are absent. What is more, one point which particularly disproves the bird-guano model is the fact that birds appeared in the Jurassic period (120 million years ago), directly descended from their famous ancestors, the flying dinosaurs.

Given the hugeness of the phosphate deposits dating from the Cambrian period and beyond, and their geochemical resemblance to the more recent deposits, it is clear that the classic bird-guano model is heading for a nose-dive. And we must remember also that the inter-tropical Pacific Ocean zone has very unproductive waters, which can only support very small bird populations. This situation, which can be seen at Makatea (16° S) and even at Nauru (170° E, 0°), has remained unchanged for several tens of millions of years and probably since the start of the Oligocene epoch (36 million years ago).

Another phosphatogenesis model is based on the dissolving of basalt or pumice, a process which could indeed produce certain elements of the geochemical range, but not all (boron and fluorine would be lacking). Furthermore, as far as quantity is concerned, the inadequacy of this model is evident: you would have to dissolve or alter a layer of rocks more than 500 m thick to obtain a few decimetres of phosphates. The problem of carbonate–phosphate association and of their diagenesis is no less worrying. However the conceptual void created by the limits of these classic models seems to be readily filled by taking into account the reef-functioning model based on endo-upwelling. Although most of the flow of dissolved nutrients (notably nitrates and phosphates) is used by the algo-coral ecosystem at the reef crest and on the outer reef slope, a fraction of it could reach the lagoons and the ground water situated under the atoll *motu* (islets), thus maintaining the high productivity of vegetation and of the coconut grove.

In lagoons which are open to the ocean, turbulent exchanges of water and strong channel currents constantly dilute the freed interstice nutrients, thus leaving the lagoon waters limpid. In closed lagoons and slightly raised atolls, nutrient levels increase with time, the lagoon undergoes a process of eutrophisation, the coral disappears and thick carpets of seaweed develop on the lagoon floor. A fluor-apatite precipitation can then begin amongst the cyanobacterial seaweed detritus (called *kopara* in Paumotu), as is happening in the Niau lagoon (Tuamotus) (Fig. 4). The apatite-rich layer will grow as long as deep phosphorus is supplied by the process of endo-upwelling and the accumulation of *kopara* is thus maintained. A deposit therefore develops from organic lagoon sediments (Mataiva lagoon), a deposit which could possibly be exposed to the open air if the whole atoll were uplifted, as at Makatea, Nauru, Christmas Island (Indian Ocean), etc. (Jehl and Rougerie, 1993).



Kopara ponds can only exist in zones which are protected from the ocean and lagoon swells. They thus occupy relative declivities (–1 metre) of atoll ridges, emerged areas and islets (motu). The ponds are brackish, green in colour (chlorophyll pigments) and/or red (carotenoid pigments) and constitute open "windows" onto the interstitial and groundwater reef environment. Their colonisation by Cyanophyceae algae (Kopara) can be total and date back over 1000 years; the thickness of Kopara (living and detritical) can be over one metre.

Desalinated lagoons such as Niau or Mataiva function (or have functioned) as gigantic Kopara ponds, where the accumulation (in anoxic conditions) can represent millions of t of organic matter. The uncovered reef flats of high islands can also be rich in Kopara basins (Maiao, Tahaa, Moorea islands...).

Fig. 4 - Position and functioning of a Kopara pool

• Other geographical implications

The phenomenological advantages of the endo-upwelling–*kopara*–phosphate solution are thus clear, both qualitatively and quantitatively, since the deep ocean constitutes an enormous reservoir of phosphorus and fluorine and the whole geo-chemical range is present. Tests to validate this theory are under way on Tikehau Atoll and on the Tahitian barrier reef, particularly by way of medium-depth drillings (15, 30, 50 and 150 m). They tend to corroborate the pertinence and soundness of the endo-upwelling functioning model. Generalising for carbonate formations along coastal zones and continental fringes poses no specific problem, especially in Florida, where circulation by thermo-convection was suggested as a model 25 years ago. Other questions regarding the nature and evolution of carbonate structures can be tackled from a new angle; the process of dolomitisation, for example, which transforms limestone (calcium carbonate) into dolomite (calcium and magnesium carbonate) can logically result from the thermo-convective circulation of interstice water: this water, thanks to its low pH, can dissolve the softest limestone whilst at the same time providing magnesium, abundant in the deep ocean, thus leading to dolomite formation. These rocks, which are more resistant and porous than the original limestone, are known to be excellent oil traps/reservoirs. In this connection, we have been able to show the existence of traces of hydrocarbons in the interstice waters of Tikehau atoll, thus establishing the possibility that the reef and sub-lagoon limestone sediment systems could function as biological reactors. Even if the present production of the Tuamotu atolls is not quantitatively significant, a favourable tectonic and geomorphological evolution could eventually lead to an accumulation/trapping of hydrocarbon compounds: this can be seen, for example, on one of the Tongan atolls, which is rich in bitumen and naphtha. The processes of thermo-convection, of maturation of organic matter and of interactions between the reef matrix and the interstice water lead to modifications in the latter's chemical composition, making it quite different from what it was (deep oceanic water) when it entered the structure: thus it all boils down to a low-energy hydro-thermal process. Atolls and barrier reefs are hydro-thermal oceanic oases, whose functioning is ensured by an internal convection unit specific to each structure. This finding can be used to explain the presence of flooded atolls or guyots, which occur at a depth of several hundred metres, or even kilometres. These former atolls have obviously lost the battle to remain on the surface and have thus inevitably been engulfed by the structure's subsidence. We suggest that their death is brought about by a stop in the growth/calcification of their reef crown, due to a reduction in the endo-upwelling flow, following a sudden weakening of the geothermal flow in the basaltic bedrock.

• Towards a new paradigm

We are therefore looking at a wide range of biological, geo-chemical, dia-genetic and geological implications, dependent upon a single thermo-convective process based on 3 constraints: a porous, permeable structure; an underlying geothermal flow; and a contiguous deep ocean (rich in nutrients). Although initially proposed to account for the biological paradox presented by the existence of highly productive coral reefs within a tropical oceanic desert, the endo-upwelling model thus leads to a far broader concept and could eventually constitute a genuine paradigm. The future will tell whether the results of research on the reef systems and atolls outside French Polynesia tend to confirm, or refute, the conclusion that has been drawn from the French Polynesian reefs and atolls.

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This is an important contribution to our understanding of the geography of the Pacific Island countries. It consists of studies on the French-speaking Pacific Territories (Vanuatu, New Caledonia, French Polynesia, Wallis and Futuna), the greater part of which are the fruit of entirely new and original work. It both constitutes an in depth presentation of these territories, their particularities, their problems, and contains much food for thought in its analyses of the natural (terrestrial and marine) and the human (socio-cultural and economic) environments of these islands.

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