Geothermal endo-upwelling: a solution to the reef nutrient paradox?

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Abstract—Coral reef ecosystems have long been regarded as paradoxical because their high biomass and gross primary productivity far exceed that expected for ecosystems in tropical oligotrophic waters. Previous authors have explained the paradox by emphasizing efficient recycling, conservation and storage of nutrients within the reef ecosystem. However, the fact that reefs are net exporters of nutrients and organic matter means that for sustained productivity new nutrients must be imported.

Comparisons of the chemical properties of interstitial waters from shallow boreholes in atoll, barrier and lagoonal pinnacle reefs in French Polynesia indicate that their nutrient concentrations are similar or superior to those in Antarctic Intermediate Water (A.I.W.) at 500–1000 m depth. By the geothermal endo-upwelling process, A.I.W. enters the porous reef framework, is driven upward by the local geothermal gradient and emerges at the reef crest to provide nutrients to the flourishing algal–coral ecosystem.

Continuing research on the reef nutrient controversy suggests that there are several paths presently converging upon it's solution: among them the endo-upwelling model seems an adequate explanation for barrier reefs located in clear oligotrophic waters such as the Polynesian ocean.

1. REEFS: A BIOLOGICAL PHENOMENON

DUE TO their considerable size and complexity, the functional trophic aspects of reef ecosystems have been in nearly continuous dispute among researchers for decades. However, a few characteristics of reef ecosystems are rarely disputed today: (1) their biomass and gross productivity are among the highest of any natural ecosystem; (2) many reefs are located in areas noted for their very low concentrations of dissolved nutrients; and (3) their trophic complexity is related to their high taxonomic and ecologic diversity. Thus, reefs are truly "an oasis in a desert ocean" (ODUM, 1971) and a key to understanding their trophic functions lies in their ability to maintain this high biomass and productivity for thousands of years in nutrient-poor (oligotrophic) waters. These apparently contradictory characteristics and relationships have been regarded by many ecologists as paradoxical and so have stimulated much research (reviewed by LEWIS, 1981; ANDREWS and GENTIEN, 1982; KINSEY, 1985; LITTLER and LITTLER, 1985; HALLOCK and SCHLAGER, 1986; SOROKIN, 1990a; FAGERSTROM, 1987) directed towards the resolution of this "reef nutrient paradox".

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The data from this research indicate that flourishing reefs live in warm (18–30°C), shallow (0–100 m), clear, turbulent water, with abundant dissolved oxygen. These physical–chemical conditions are best satisfied in the tropical North and South Pacific and Coral Sea gyres where water clarity is at a maximum due to the lack of nutrients to support a significant phytoplankton biomass.

More than 25% of the papers in the most recent research status report on "Coral Reefs" (DUBINSKY, 1990) concern problems broadly termed biogeochemical. Many of the major conclusions reached by the authors of papers in this report, and in papers cited by them, deal with the nutrient paradox. They include the following.

(1) Despite their high gross productivity, net productivity is low. The traditional explanation for this difference is that gross productivity is sustained by efficient recycling and conservation of nutrients in both the reef framework and adjacent sediments (D'ELIA and WIEBE, 1990).

(2) In locations of high hydrodynamic flux, i.e. the crest and upper seaward slope, nutrients are exported from reef ecosystems making them nutrient limited whereas if the hydrodynamic flux is low, i.e. lagoons and reef flats, nutrients may be retained in concentrations adequate to locally sustain the gross productivity of the ecosystem (D'ELIA and WIEBE, 1990; EREZ, 1990).

(3) The biomass of bacteria is considerable and plays important roles in nitrogen fixation and in the processing and production of organic detritus, including coral mucus, for heterotrophic production by filter-feeders (DUCKLOW, 1990; SOROKIN, 1990b).

(a) *An autotrophic community*

Oligotrophy and accompanying water clarity provide the coral polyp endosymbionts, called zooxanthellae, with photochemical energy adequate to support high primary production (plant or autotrophic production) as well as rapid calcification of the reef framework. Of the various chemical elements required for reef biogeochemical cycles, dissolved inorganic nitrogen and phosphorus are commonly regarded as most limiting to reef growth (SMITH, 1984).

The overall "health" of a reef may be expressed as the ratio between photosynthesis/ production and respiration, or the ratio between oxygen production and oxygen consumption, commonly expressed as P/R. In healthy reef ecosystems measurements of $P/R = 1 \pm 0.1$ (D'ELIA and WIEBE, 1990); this includes the large and thick atolls and barrier reefs in the oligotrophic gyres where the productivities of reef ecosystems and that of the surrounding oceanic waters appear to be independent.

In Polynesian reefs, PICHON (1985) found P/R to be 1.04–2.00, a decisive indication of positive net production. This result is important because any reef with $P/R > 1$ may be a net organic exporter (KINSEY, 1985). Conversely, P/R ratios < 1 indicate a net loss of organic matter that must be quickly restored to prevent reef community death and cessation of calcification. In a critical review on the imbalances in energy, nutrients and carbonate budgets, SMITH and KINSEY (1988) concluded that there is no evidence that reefs require new nutrients. They assert that reef production is rather low and may be roughly equivalent to oceanic productivity. These contrasting views are central to controversial arguments in the reef literature and may simply reflect the difficulty in extrapolating figures obtained in a back-reef lagoon, which is essentially a sediment–nutrient trap, to a highly productive algal–coral reef crest bathed by an oligotrophic ocean.

(b) *The nutrient paradox*

On a large geographic scale the nutrient paradox is illustrated by the nature of reef communities. Particularly healthy reefs are found in the clearest and most oligotrophic parts of the tropical ocean, i.e. the North and South Pacific gyres and Coral Sea (WAUTHY, 1986). In contrast, reefs are absent or poorly developed, in the eastern intertropical nutrient-rich waters of the Atlantic and Pacific Oceans, i.e. the west coasts of the Americas and Africa.

Despite numerous attempts to resolve the nutrient budget problem by upwelling, this appears to be an exercise in futility for three reasons (reviewed by HALLOCK and SCHLAGER, 1986; HALLOCK, 1988):

(1) the temperature of coastal upwelling water can drop below the lethal limit of algal–coral ecosystems;

(2) nutrient-rich upwelling water should produce a bloom of both planktonic and benthic algae which should lead to a decrease in the input of light to the zooxanthellae–coral endosymbiotic system and eventually to eutrophication and coral polyp suffocation;

(3) increased destruction of reef frameworks by bioeroders whose abundance is related to the increasing benthic algal biomass.

WILDE *et al.* (1988) and LITTLER and LITTLER (1985) have also confirmed the reality of the paradox as did the addition of nutrient-rich sewage in Kanahoe Bay, Hawaii (SMITH *et al.*, 1981) which produced a bloom of algal macrophytes overgrowing the coral patches. Furthermore, total reef calcification may decrease from nutrient enrichment (KINSEY and DAVIES, 1979). Finally, algal blooms inhibit coral recruitment by competitive exclusion (BIRKELAND, 1977). To resolve the apparent nutrient paradox, HALLOCK and SCHLAGER (1986) suggested that "The primary carbonate sediment producers (*presumably algae and corals*) of the coral reef community are highly adapted to nutrient-deficient environments" (our italics).

2. REEFS AS EXPORTERS OF CARBONATE SEDIMENTS, NUTRIENTS AND ORGANIC MATTER

Rapid rates of calcification, of the order of several kg m^{-2} year^{-1} of carbonate (SMITH and PESRET, 1974; BARNES *et al.*, 1986) are characteristic of algal–coral reefs; the fact that calcification and photosynthesis displace the CO_2–carbonate system in opposite directions, clearly shows the link between these two processes. In periods without significant sea-level rise, part of the newly formed carbonate is commonly broken and displaced by oceanic wave energy in the form of sediment and sand, either toward the lagoon or down the outer reef slope.

(a) *Nutrient budgets in disequilibrium?*

Considerable evidence exists to suggest that reefs do in fact export both nutrients and organic matter (both dissolved and particulate as zooplankton and detritus; ODUM and ODUM, 1955; MARSHALL, 1965; JOHANNES, 1967; HATCHER, 1985). These data conflict with the requirement of a positive balance between the import and export of nutrients to support high levels of primary production in reef communities.

A second paradoxical feature occurs with the CO_2–carbonate system. In the photic zone of flourishing reef growth, the pH is usually high ($\bar{X} = 8.3$; thus, most inorganic carbon

occurs as $^-HCO_3$, not CO_2) and dissolved total CO_2 content is low ($\Sigma\ CO_2 = 2$ moles m^{-3}), limiting the availability of inorganic CO_2 for rapid growth of both zooxanthellae and benthic macroalgae. Dissolved free CO_2 is an important carbon source for translocation by the zooxanthellae to the coral polyp and coral skeleton. With such a high pH, the low concentration of free CO_2 is insufficient to sustain the high photosynthetic rates that characterize reef ecosystems (WEISS *et al.*, 1989). Despite that potential deficiency, important amounts of translocated carbon are released either as soluble or as particulate organic matter, zooxanthellae and mucus; important losses, up to 50% of the carbon fixed photosynthetically each day, have been reported by DAVIES (1984) and MUSCATINE *et al.* (1984).

Thus, despite some incompatibilities and mismatches in both temporal and spatial scales, most studies of reef biogeochemistry suggest that carbonate sediments, nutrients and organic matter are exported by reef ecosystems and are lost by turbulent transport to the surrounding ocean (ROUGERIE, 1986). These losses must be at least matched by imports that can only be provided in insignificant amounts by the adjacent oligotrophic waters.

This conclusion cannot be generalized to places where nutrients and/or plankton reach significant amounts, as along the equatorial belt, generally enriched by a moderate divergence–upwelling process. Atolls located inside the mesotrophic belt, such as Christmas (157°W), Tarawa (172°E) and New Guinea reefs, have adequate oceanic input of both dissolved and particulate matter, to balance their nutrient budgets and to export dissolved organic matter (SMITH *et al.*, 1984).

(b) *Pore-water recycling*: *constraints and limits*

Due to their high porosity (20–35%) and high permeability (1–10 Darcys) reefs contain a large and dynamic reservoir of interstitial water for bacterial degradation and remineralization of inorganic and organic matter. The hydrology and geochemistry of these waters are the keys to understanding reef metabolism and diagenesis (BUDDEMEIER and OBERDORFER, 1988). *In situ* nutrient regeneration occurs in pore waters in coral heads (RISK and MÜLLER, 1983) and sedimentary substrates (DI SALVO, 1974). Nutrients in larger reef cavities are easily exported by tidal currents (ANDREWS and MÜLLER, 1983; SZMANT-FROELICH, 1983; PARNELL, 1986); in the long term, such "leaks" produce significant shifts in the phosphorus balance whereas for nitrogen similar shifts can be partly compensated by its direct fixation by bacteria (WIEBE *et al.*, 1975; CAPONE and CARPENTER, 1982). However, within anaerobic reef pores, denitrification and nitrogen leakage can occur (D'ELIA, 1977); in fact, mass balance calculations for whole reefs have shown losses of fixed nitrogen nearly equal to the rates of nitrogen fixation (SMITH, 1984).

Between coral branches, reduced flow velocity and the organic matter released by the coral create a local environment different from and more or less independent of the nutritive level of the surrounding water. But in the long-term, regardless of its degree of efficiency, recycling of nutrients cannot sustain net ecosystem growth; for coral reefs, the loss terms are greater than the gain terms (EREZ, 1990). Atolls and barrier reefs surrounded by a turbulent ocean could hardly be expected to retain organics. In the absence of other imports, if such losses amount to only 1% year^{-1}, half of the biomass should be lost in just 70 years. Finally, analysis of reef biogeochemical processes and associated budgets indicate that reef exportation of inorganic nutrients and organic carbon

is not always balanced by imports from surficial oceanic or planktonic sources to support the long-term maintenance of high biomass and complex trophic relations recognized 150 years ago by Charles Darwin (1842).

3. GEOTHERMAL ENDO-UPWELLING PROCESS IN POLYNESIAN BARRIER REEFS

The sequence of steps between 1981 and 1986 that led to the formulation of the geothermal endo-upwelling concept, the main characteristics of its operation and the development of a convective circulation model have been described by ROUGERIE and WAUTHY (1986, 1988, 1992). It is the conjunction of a geothermal heat source and a porous and permeable structure which makes possible this process of geothermal endo-upwelling. Other pinpoint geothermal flow sources can be found on the ocean floor, such as hydrothermal springs in oceanic ridges or active volcanic seamounts, but they do not sustain "upwellings" because heat is progressively and regularly dissipated by eddy diffusion. Conversely, interstitial water within a porous limestone atoll structure in contact with volcanic basement is progressively heated; because of the cumulative build-up of heat, possible only in the absence of eddy diffusion, interstitial sea water loses density and a slow convective circulation is established in the permeable material. By this ascent, nutrient-rich deep ocean water is pushed toward the top of the atoll (Fig. 1) and issues along the most permeable paths, i.e. mainly through the algal reef crest groove and spur zone where sedimentation and clogging are prevented by ocean hydrodynamism.

(a) Nutrient concentrations: atoll reefs

To test the validity of the process for atolls and barrier reefs in oligotrophic oceanic waters of the South Pacific Gyre, borings were made at two locations in French Polynesia.
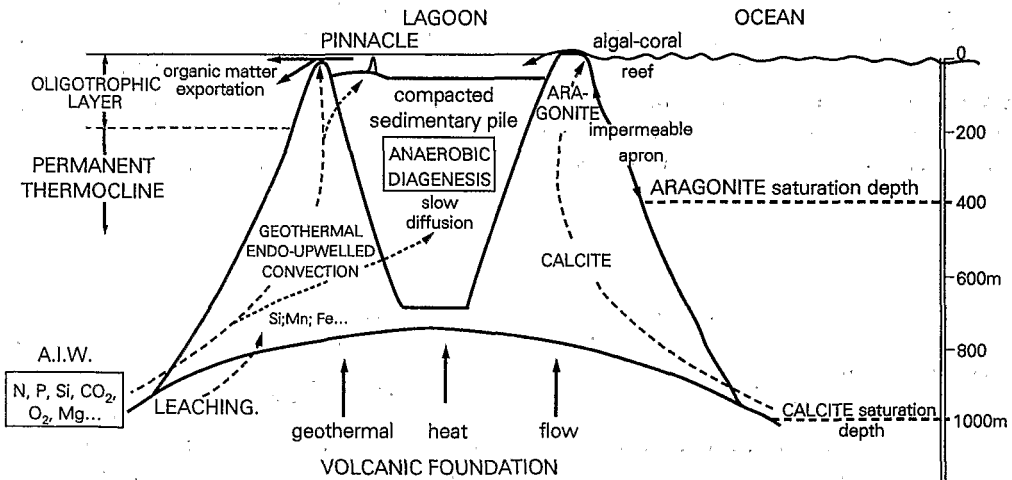

Fig. 1. Schematic diagram of geothermal endo-upwelling model showing convective paths and location of the various chemical (inorganic, diagenetic) and biological processes in mid-ocean atoll.
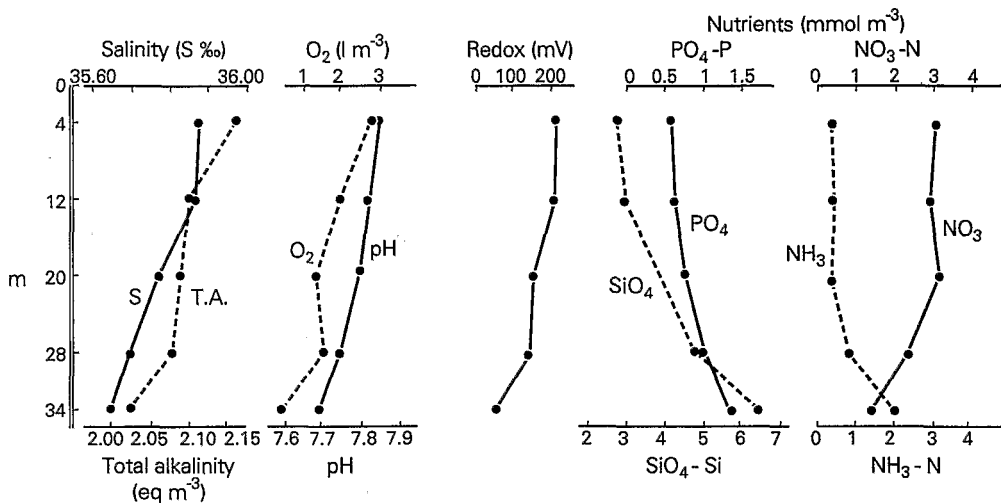
Fig. 2. Vertical profiles showing variation in chemical properties characteristic of interstitial water from boreholes located on the reef flat at Tikehau Atoll (148°W, 15°S), French Polynesia. Each point is the mean of 30 measurements.

First, four shallow (4–35 m) holes were drilled on the Holocene reef flat at Tikehau Atoll (148°W, 15°S) for the purpose of sampling and analysis of the interstitial waters. These analyses indicate that the interstitial water system is rich in dissolved nutrients and total CO_2, low in dissolved O_2 and of low pH (Fig. 2). In addition, the Apparent Oxygen Utilization (A.O.U.) within the framework cannot account for all of the nutrients present (Fig. 3a). There must be a source of new nutrients and the most probable source is the nutrient-rich Antarctic Intermediate Water entering the framework at depths of 500–1000 m and circulated to the living reef by endo-upwelling (Figs 1, 3b).

A 17 m deep borehole was drilled in a lagoonal pinnacle (Fig. 1) at Tikehau and it also contains nutrient- and CO_2-rich interstitial waters. However, it differs from the reef flat pore waters in being anoxic, with $O_2 < 0.2 \, ml \, l^{-1}$ and negative Redox potential (Fig. 3a); we interpret this anoxia as the consequence of the lack of wave-driven turbulence in the lagoon to force oxic waters into the pinnacle pores. In addition, the location and growth of

Fig. 3. (a) Comparison of chemical characteristics for oceanic and interstitial borehole waters. Theoretical mixing line is between Antarctic Intermediate Water (A.I.W.) and Tropical Oligotrophic Water (T.O.W.). The deviation of the borehole waters from the theoretical mixing line (A.O.U.) represents the degree of oxygen use by bacteria for decay of organic matter. Mean value for salinity of borehole water = 35.7‰.

Fig. 3. (b) Comparison of dissolved inorganic phosphate concentrations in oceanic and interstitial borehole waters. Phosphate concentration in all borehole waters exceeds $0.65 \, mmole \, m^{-3}$, which is the theoretical concentration of mixed A.I.W. and T.O.W. This indicates that the chief phosphate sources are A.I.W. plus *in situ* remineralization of organic matter in the interstitial borehole waters. Salinity difference between interstitial water (S = 35.7‰ ± 0.1) and tropical oceanic water (S = 36.2‰ ± 0.2) is 0.5‰ on a 2 year long basis (1989–1990).

(a)
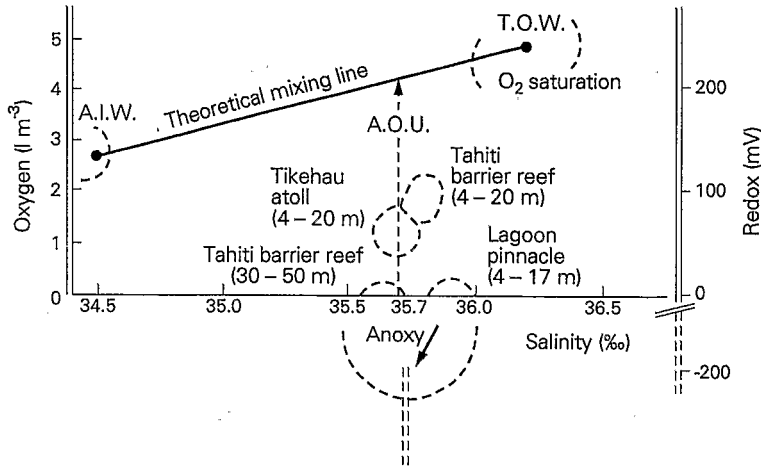
(b)
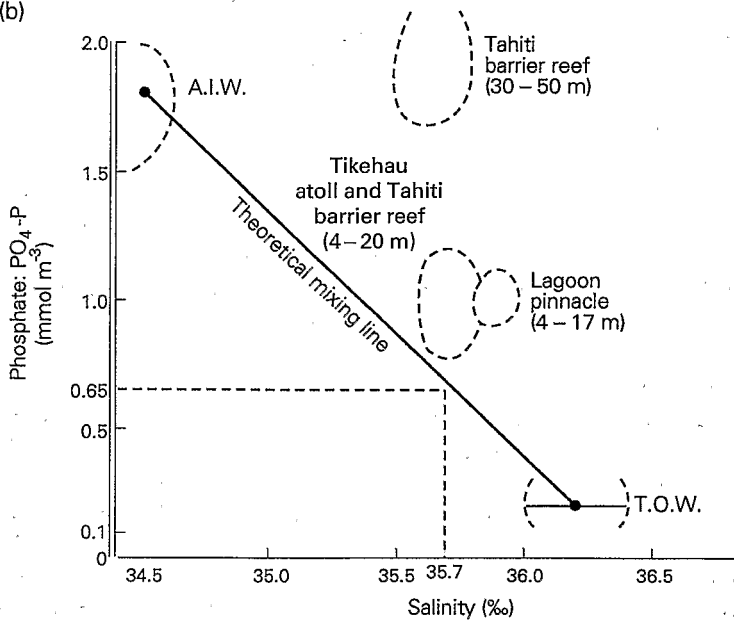
A.O.U. Apparent Oxygen Utilisation
T.O.W. Tropical Oligotrophic Water (0 – 100 m)
A.I.W. Antarctic Intermediate Water (0.5 – 1.5 km)

lagoonal pinnacle reefs appears to be controlled by the presence of sub-lagoonal fractures along which nutrient-rich waters could seep (GUILCHER, 1991).

The Tikehau pore-water data and our interpretations are consistent with those of SANSONE *et al.* (1990) who also found patch reef porewaters to be rich in nutrients and inorganic carbon, anoxic and of low pH (7.5–7.9). They concluded that anaerobic diagenesis involving bacterial degradation of organic matter is a common process in lithified marine carbonates and that they can be sources of methane and/or ammonia to adjacent seawater with subsequent utilization by aerobic chemolithotrophs (TRIBBLE *et al.*, 1990).

(b) *Nutrient concentrations*: *high island barrier reefs*

Secondly, by means of a 50 m deep hole drilled in April 1990 on the crest of the barrier reef at Tahiti (17°30'S, 150°W) additional sampling and analyses of interstitial waters were made for comparison with those from Tikehau. The results of 10 data sets (Fig. 4a) indicate that the Tahitian waters are also nutrient- and CO_2-rich compared to the adjacent oceanic mixed layer (0–100 m) waters and their nutrient concentrations are equivalent to those at Tikehau in the upper 20 m (ROUGERIE *et al.*, 1991; Table 1). Below 20 m, Tahitian interstitial waters are anoxic and contain abundant phosphate, silica and dissolved inorganic nitrogen.

There are five aspects of the upper interstitial waters that are important to the present discussion.

(1) A main source for these waters is clearly from oceanic wave surge on the reef crest. This Tropical Oligotrophic Water (T.O.W.) penetrates the inner reef with its high O_2–low nutrient content. The highly porous nature of the crest relative to the high wave turbulence was demonstrated by ROBERTS *et al.* (1988) at St Croix, U.S. Virgin Islands; they observed a nearly instantaneous hydraulic response in wells to the high frequency wave surge. Jets of clear ocean surface water prevent clogging of pores in the living reef crest by sediment or algae and the high O_2 content promotes bacterial degradation and remineralization.

(2) From the upper part of the framework (above 20 m) to the 20–50 m depth there is a rapid shift in dissolved oxygen from oxic to anoxic in the interstitial waters, which is confirmed by the shift of the Redox potential from positive to negative values (Figs 3a and 4a); above 20 m, reductive molecules such as NH_3 and H_2S are oxidized. Thus, the toxic, H_2S-rich anoxic interstitial waters present below 20 m are not in direct contact with the living algal–coral veneer.

(3) The main source of the nutrients and CO_2 in the interstitial water is postulated to be, just as for the atoll, the A.I.W. entering the island basement below 500 m. The theoretical mixing line drawn between A.I.W. and T.O.W. indicates that phosphate in borehole waters represents a mixing of these two sources (Fig. 3b) with, above 20 m, phosphate values of 1 ± 0.2 mmole m^{-3}, a content equivalent to that found in atoll boreholes. The excess of phosphate (and other nutrients) can be partly explained by remineralization of organic matter inside the reef matrix. This remineralization is accompanied by an A.O.U. of nearly 3 ml l^{-1} between 0 and 20 m (Fig. 3a). Below 30 m oxygen is totally consumed for mineralization of organic compounds and other oxidized molecules such as SO_4^- and NO_4^-, play the role of oxydant to sustain anaerobic bacterial activity.

(4) The high concentration of silica in the borehole waters and its increase with depth indicate that these waters have had significant contact with the underlying volcanic rocks
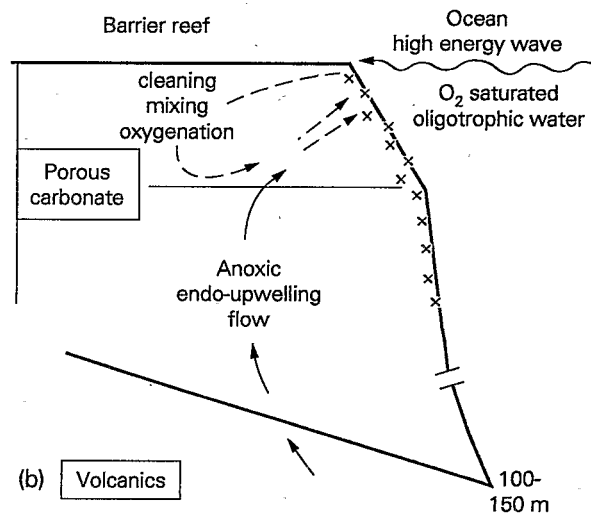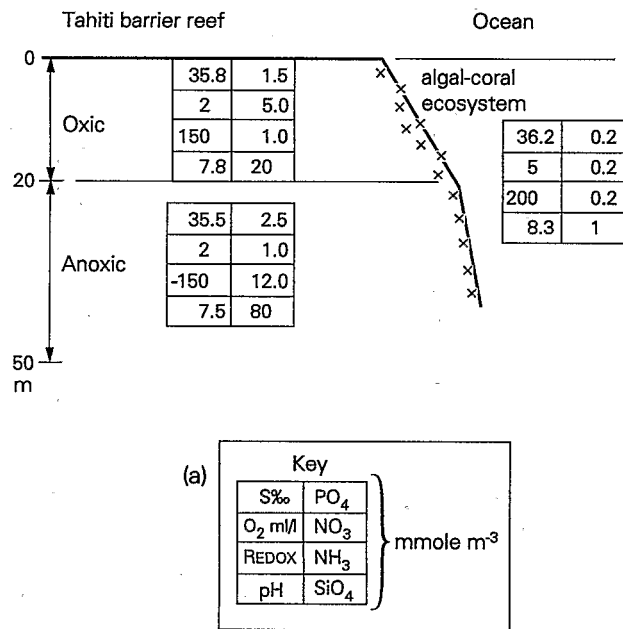
Tahiti barrier reef   Ocean

0

35.8	1.5
2	5.0
150	1.0
7.8	20

Oxic

× algal-coral
× ecosystem
×
×
×
×

36.2	0.2
5	0.2
200	0.2
8.3	1

20

35.5	2.5
2	1.0
-150	12.0
7.5	80

Anoxic

50
m

(a)

Key	
S‰	PO$_4$
O$_2$ ml/l	NO$_3$
REDOX	NH$_3$
pH	SiO$_4$

} mmole m^{-3}

Barrier reef   Ocean
                    high energy wave

cleaning
mixing
oxygenation

O$_2$ saturated
oligotrophic water

Porous
carbonate

Anoxic
endo-upwelling
flow

(b)   Volcanics

100-
150 m

Fig. 4. (a) Chemical properties of interstitial borehole (0–50 m) and open ocean waters, Tahiti (150°W, 17°30′S), French Polynesia. Each datum is a mean of 10 measurements collected every 10 m. (b) Schematic diagram of geothermal endo-upwelling model for Tahiti barrier reef based on interpretation of data in (a).

which occur only about 100–150 m below the bottom of our borehole (DENEUFBOURG, 1967). Thus, we believe that the barrier reef thermally driven endo-circulation involves both the volcanic foundation and the overlying porous framework (Fig. 4b). Similar thermo-convection of oceanic water through the volcanic foundation, alleged to be porous as a consequence of its past aerial exposure, has been described at Oahu, Hawaii by MINK (1964) and SOUZA and VOSS (1987).

(5) As silica is less critical than other nutrients in sustaining the algal–coral ecosystem, it can be not totally consumed, the excess possibly "spiking" the adjacent ocean waters with silica. However, a vertical flow of $1 \, \text{cm} \, \text{h}^{-1}$ (range for coastal upwellings is $1 \, \text{cm} \, \text{h}^{-1}$ to $10 \, \text{cm} \, \text{h}^{-1}$) would give a total of $10 \, \text{l} \, \text{h}^{-1} \, \text{m}^{-2}$ of interstitial water seeping out of the reef surface for turbulent mixing with the oceanic system. Using a realistic horizontal advection of $0.3 \, \text{m} \, \text{s}^{-1}$ for oceanic currents, the dilution factor is 10^5, which makes any silica enrichment undetectable. An analogy can be made with the deep hydrothermal vents; for active black smokers, enrichment in Mn and Fe is detectable only in the close vicinity of the vents and for cold seep systems, nothing is measurable, except for the biological signal (SIBUET *et al.*, 1988).

(c) *Helium-3 anomaly*

Our final evidence in support of the endo-upwelling model is the presence of a positive Helium-3 anomaly in the Tikehau interstitial waters (ROUGERIE *et al.*, 1991). Previous research on the large scale distribution of He-3 in the deep Pacific Ocean (LUPTON and CRAIG, 1981) shows that the positive anomaly originates from hydrothermal vents on the crest of the East Pacific Rise at a depth of about 2500 m and spreads westward as a plume into the central Pacific where it is entrained in Antarctic Intermediate Water (A.I.W.) at 500–2000 m depths.

Our measurements show anomalously high values of He-3 in the atoll reef interstitial waters. These values, compared to the adjacent oceanic He-3 profile, indicate a "recharge" depth of about 700–800 m for the A.I.W. penetrating the atoll, which is in good agreement with the nutrient data discussed above. Thus, the presence of the He-3 tracer in Tikehau borehole waters provides quasi-absolute evidence of endo-upwelling circulation of A.I.W. through the reef framework to the reef surface.

(d) *Future research directions*

To provide additional data regarding the endo-upwelling process, the following projects have been or will be undertaken.

(1) Chlorofluorocarbon (CFC). CFC and He-3 constitute opposite constraints because of their opposite boundary conditions: the He-3 source is the deep ocean, the CFC source is the atmosphere. The first measurements made in 1991 show CFC-11 and CFC-12 to be present in oceanic waters around Tahiti from the surface to 500 m. Using identical sampling and analytical techniques, CFC were absent or with significant negative anomaly inside borehole interstitial waters. This deficit of CFC may be regarded as a clue similar to the He-3 anomaly, but for the opposite reason.

(2) Heavy metals and limiting ions. The first sets of measurements in Tahiti interstitial waters show Fe amounts to be 300 times higher than in surrounding oceanic surface water and Mn and Cd to be 10 and 30 times higher, respectively. Conversely, Mg is less

concentrated (5–15%) in borehole waters than in the ocean. These data appear to confirm the circulation of endo-upwelled water within reef basalt foundation.

(3) Geothermal gradient. Direct measurements are planned in atoll and barrier reef boreholes as they have been done in Eniwetok (SWARTZ, 1958) and Mururoa Atolls in 1975–1980.

(4) Water convective flow rate will be directly measured by the self potential method, using permanently inserted electrodes.

(e) Limitations of the model

As the endo-upwelling model requires the conjunction of an abnormally high geothermal flux, a porous reef framework and a deep water source of dissolved nutrients, it may not be a universal reef nutritive process. Although we have no data to prove or disprove its presence in such areas as the continental shelves on the east coast of Brazil, west coast of Panama or the east coast of Africa, we do not believe that endo-upwelling is important there. In addition, the importance of weaker endo-upwelled currents, if present, would be diminished in areas of moderate coastal enrichment or equatorial upwelling (see Section 2a above). Ocean currents can play an important role at both local and regional scales in perturbating the oligotrophic pattern. Studies by WOLANSKI et al. (1986) along the Great Barrier Reef have revealed vertical oscillations, wake and tidal jet effects in reef passages, that allow nutrient rich water from below the thermocline to spill on to the continental shelf.

4. SUMMARY

Endo-upwelling is a well-balanced diapycnal process that does not lead to any of the dire consequences envisioned by HALLOCK and SCHLAGER (1986) and HALLOCK (1987) for coastal upwelling. Furthermore, the endo-upwelling model is completely compatible with the trophic relations and energy transformations outlined by LEWIS (1981).

(1) In oligotrophic regions, endo-upwelling can provide the new nutrients to sustain the net primary production by the zooxanthellae–coral symbiosis.

(2) Such primary production in turn supports coral skeletogenesis, microbial production and internal recycling of detrital organic matter injected into the reef matrix by wave energy.

(3) Both the excess production and recycling of inorganic nutrients and organic carbon (chiefly zooxanthellae, mucus and dissolved organic matter) are exported to the adjacent ocean. Excess zooxanthellae are purged in enormous numbers by the coral polyps (WILKINSON, 1987) and may be consumed by the zooplankton and benthos, the first links of the reef food chain. This food chain, centered around atoll and barrier reef crests may explain the high biomass and secondary production observed in these oceanic oases.

Finally, a permanent endo-upwelling can bring new nutrients to the surficial autotrophs, supporting the long-term growth and exportation of the ecosystem. Endo-upwelling convection also bypasses the problems of coastal upwelling noted above, i.e. there is no cooling below the coral lethal limit and no oceanic plankton bloom to increase turbidity. In short, there is no eutrophication pattern to imperil or destroy the reef community. So this model seems to be the sufficient and necessary response to the paradox of the huge coral productivity in clear oligotrophic waters.

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