

PART I. ENVIRONMENT AND BIOTA OF THE TIKEHAU ATOLL (TUAMOTU ARCHIPELAGO, FRENCH POLYNESIA)

BY

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THE REGIONAL BACKGROUND

The islands of French Polynesia are scattered throughout a considerable oceanic area located on the eastern boundary of the Indo-Pacific Province. This area stretches from 134°28' W (*Temoe* Island) to 154°40' W longitude (*Scilly* Island), and from 7°50' S (*Motu one* Island) to 27°36' S latitude (*Rapa* Island). Out of the 118 islands constituting French Polynesia, 35 are high volcanic islands and 83 are low-relief islands or atolls. Altogether, the territory of French Polynesia represents an area of 4000 km² of dry land, 12,000 km² of lagoonal water and a huge Exclusive Economic Zone (EEZ) covering 5,500,000 km² of oceanic water (Gabrie and Salvat, 1985).

French Polynesia is divided into five archipelagos all oriented parallel to a northwest-southeast axis (Fig. 1). These are the Society archipelago, the Tuamotu archipelago, the Austral archipelago, the Marquesas archipelago and the Gambier archipelago.

The Tuamotu archipelago stretches over a distance of 1800 km. Its 76 atolls cover a total area of 13,500 km² of which 600 km² are dry land.

GEOLOGY OF THE TUAMOTU ARCHIPELAGO

As figured by Montaggioni (1985), the Tuamotu atolls cap the top of cone-like volcanoes which rise steeply from the floor of a huge ridge forming wide shelves ranging in depth from 1,500 to 3,000 m. Geomorphological and geochronological evidences support the fact that the formation of the Tuamotu chain is much older than that of other neighboring islands of French Polynesia. The foundations of extinct volcanoes appear to have been simultaneously, and not sequentially, active for at least the Northwestern Tuamotu chain. The existence of a massive submerged ridge and the lack of high volcanic islands are in accordance with average ages found out by the Deep Sea Drilling Project (summarized by Clague, 1981 and Schlanger, 1981) : reef debris of the early to late Eocene (50-51 mybp) have been sampled in two holes drilled on the northeastern flank of the Tuamotu archipelago and on the ridge itself. The occurrence of these fossils leads to the conclusion that vulcanism would have stopped between late Cretaceous and early Eocene for at least the northwestern part of the Tuamotu chain. The large number and the close-spacing pattern of the Tuamotu atolls are indicative of their origin in shallow waters close to the East Pacific ridge.

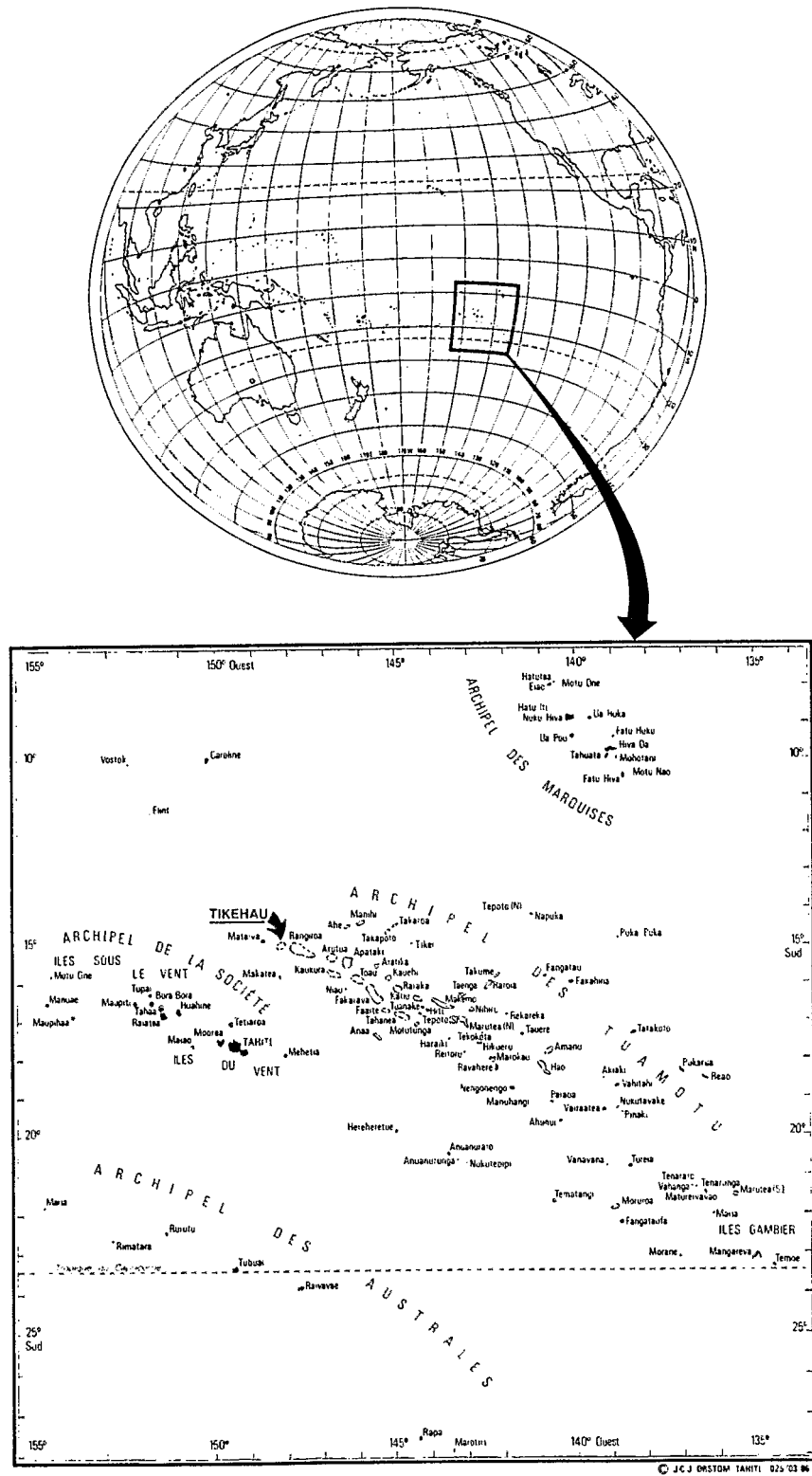


Fig. 1 : Map of French Polynesia and location of the Tikehau atoll, Tuamotu

In the northwestern Tuamotu, several atolls (including Tikehau), located in the vicinity of recently active volcanoes (Tahiti, Moorea, Mehetia), have been lifted up. Lambeck (1981) pointed out that the tectonic uplift of these atolls was a result of the loading effects of the nearby Tahiti volcanic complex. The magnitude of uplift was a few ten meters with respect to present sea level, without considering the unusual case of Makatea which, located near the center of the load, has its highest point 133 m above present sea-level. Since age dating of the oldest volcano (Moorea) is around 1.5 mybp, the tectonic uplift of atolls is thought to have been initiated in early Pleistocene.

At Tikehau, the magnitude of uplift can be related to the present day elevation of the numerous old reef remnants (locally termed *Feo*) that stand on the atoll rim (Plate 1). *Feo* are highly recrystallized and dolomitized old reef remnants, that witness a long period of subaerial weathering. Although there is insufficient evidence to accurately date the *Feo*, a comparison with analogous structures on Makatea confirms their emergence in the early Pleistocene (Pirazzoli and Montaggioni, 1985). On the southern shores of Tikehau, *Feo* can be as high as 12m above present sea-level. Many other lower *Feo* are located on the eastern and western reef flats.

Studies from Holocene fluctuations in sea level can be useful in interpreting individual reef histories. In Tikehau as well as in most of the islands of French Polynesia, cemented coral reef conglomerates, often found around islands and alongshore shallow channels, and notches, undercutting *Feo* near their bases are evidences to support a higher-than-present relative sea level between 5200 and 1200 ybp. This higher sea level may have been 0.9 m greater than the present sea level. In this region, the lowering of the sea level near to its present datum is thought to be a very recent phenomenon which has occurred not earlier than around 1200 ybp.

GENERAL OCEANOGRAPHY OF THE TUAMOTU ARCHIPELAGO

Current and oceanic water characteristics

Tikehau, as all the northwestern parts of the Tuamotu archipelago, resides in the South Equatorial Current. The current has a general westward drift between 40 to 50 cm s⁻¹ down to 200 m depth, steady throughout the year. The southern boundary of the current moves northward during the southern hemisphere summer and shifts back toward the south in winter. Currents near the atolls may vary in both speed and direction due to the dynamic topography and rather permanent eddies probably exist, though their occurrence has never been demonstrated in French Polynesia.

In the south of the northwestern part of the Tuamotu archipelago, variations in the current directions are considerable and may influence to some extent oceanographic patterns around Tikehau. Rougerie and Chabanne (1983) pointed out that during the summer, the current in the vicinity of Tahiti may be an extension of the South Equatorial Countercurrent which originates in the Solomon Sea and has a general eastward-southeastward drift. The salinity is low (34.8 ‰) reflecting the annual net rainfall in the South Pacific Convergence Zone (SPCZ) which occurs along a Solomon-Samoa-Tahiti line at this time of year. During winter, the SPCZ shifts northward and the trade winds strengthen somewhat over the Tahiti region. The current flows westward carrying high salinity water (36.4 ‰) drawn from the Central Pacific barren zone where evaporation exceeds precipitation by 50 cm per year (Rougerie, 1981).

Surface water temperature varies seasonally in a spread of 25.5°C to 29°C and reaches an average value of 28°C. The main thermocline is weak and is located between 400 and 600 m in depth with a temperature of 10°C at 400 m. By 1000 m, the temperature drops to 3°C.

Chemical data for ocean water (summarized in Table 1) show that the ocean surrounding the Tuamotu archipelago is nutrient-poor and is actually one of the poorest oceans in the world. For example, the average copepod surface population living in that oligotrophic environment is of 20 individuals m^{-3} near the surface while it is between 50 and 80 between New-Caledonia and Tonga, greater than 100 in the south of the Coral Sea, reaches 300 at the equator and exceeds 1000 to the south of Galapagos Islands.

Table 1 : Average chemical data for ocean water (0 to 100 m in depth) in the Tahiti zone. (DOM : Dissolved Organic Matter, chl a : Chlorophyll a, PProd : Primary Production, * : data measured during winter of southern hemisphere, ** : data measured in summer). Adapted from Rougerie and Wauthy (1985).

	Temp	Sal	PO4P	NO3N	SiO3	DOM	chl a	PProd
	(°C)	(‰)	(mmoles m^{-3})				$mg\ m^{-3}$	$gCm^{-2}g^{-1}$
Ocean	25.5*	36.4*	0.25	0.10	1.0	0.5	0.1	30
	29.0**	34.8**						

Waves and Tides

Waves in the Tuamotu archipelago are mostly from the east, a consequence of persistent trade winds. Waves are generally between 1 and 3 m high, breaking at a 6 to 9 s period. Swells from distant storms can reach the Tuamotu and create a different situation in which shores exposed to the swell (which can be either windward or leeward) are heavily pummeled, whereas the waves produced by the wind in the immediate area may be small. Northern hemisphere storms that occur in the Alaskan gulf during summer of the southern hemisphere generate waves from north-northwest which are generally about 4 m high and break at a period between 10 and 18 s on Polynesian shores. In winter, southern hemisphere storms generated in the lower southern latitudes may send associated waves to the Tuamotu zone. These 7 to 10 s period waves can exceed 3 m high and reach the southeast shores of the islands. Several cyclones and near-cyclones have passed by or over the Northwestern Tuamotu in 1982 and 1983. These storms have produced waves greater than 10 m high from various directions related to the storm track.

The tides at Tikehau are usually in good agreement with the French Navy (SHOM)* tide table established for Tahiti. However, ocean tide records at Tikehau show differences in timing. The time-lag between the tide at Tikehau and the tide at Tahiti is approximately 72 hours. The amplitude of spring tides is only 15 cm in the vicinity of Tikehau whilst neap tide amplitude is almost zero. Spring tides occur three days before the new moon and the full moon.

WEATHER AND CLIMATE

The Tuamotu archipelago lies in the tropical oceanic climate area. It has a distinct wet-dry annual cycle. The wet and hot season occurs from November through April and the dry and cold season from May to October. Since all of the islands are low and of a small area, they do not alter weather conditions by their presence. Data presented hereafter were provided by the National Meteorological Station of Rangiroa, except when otherwise mentioned as no weather records are available at Tikehau. Weather conditions have been recorded continuously from 1972 onward by this station.

Air Temperature

Average air temperature on a monthly basis for the 1972-1985 period ranges from 25.5 °C in August to 27.5 °C in March. There is little variation in these quantities through the year. Extreme temperatures have been recorded but provide little additional information since they rarely occur. The absolute minimum value recorded was 18 °C and the maximum 32 °C.

Wind

A summary of surface wind data is shown in Fig. 2. Tikehau is within the trade wind belt with a nearly consistent easterly wind. During much of the year, the wind blows from northeast to southeast 70 % or more of the time (*i.e.* 250 days/year). From June to September average wind speed increases slightly but rarely exceeds 6 of the Beaufort scale.

The occurrence of wind from west around to north is very low. The maximum frequency is in November, December and January when the South Pacific Convergence Zone is closest on the average and subsequently, disturbances most common.

Tropical storms and cyclones strike Tikehau infrequently, mostly during the wet season. An average of four cyclones per century is likely to occur in this area.

Precipitation, evaporation

The rainfall distribution throughout the year is shown in Fig. 3. The annual average rainfall of 1780 mm is not distributed uniformly throughout the year as about 65 % comes during the wet season. The maximum monthly average value is 229 mm in January and the minimum 75 mm in August. The variability of rainfall is high from year to year and data presented should be considered only as a general trend.

Evaporation reaches an average of 1800 mm a year and balances precipitation, as measured by the National Meteorological Station of Mururoa. Maximum evaporation takes place in December, January and February (179 mm, 193 mm and 188 mm), minimum values in June, July and August (109 mm, 109 mm and 124 mm).

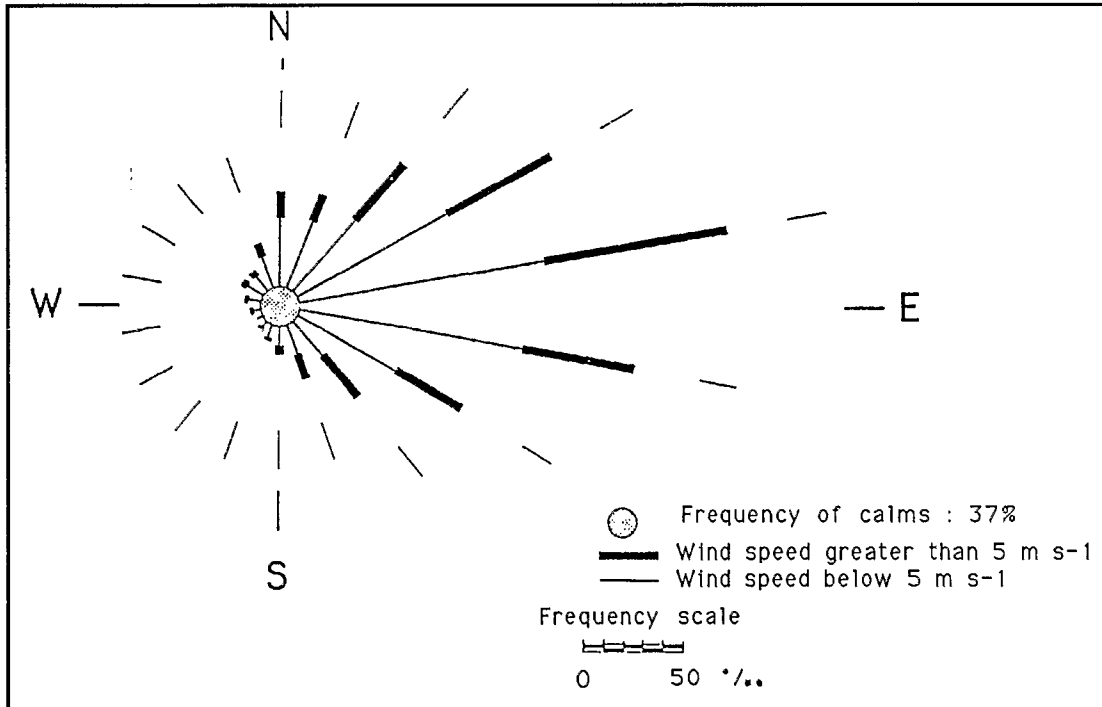


Fig. 2 : The yearly mean of surface wind data recorded at Rangiroa (Rangiroa is located 30 km to the east of Tikehau). Data provided by Meteorologie Nationale, Tahiti-Faaa.

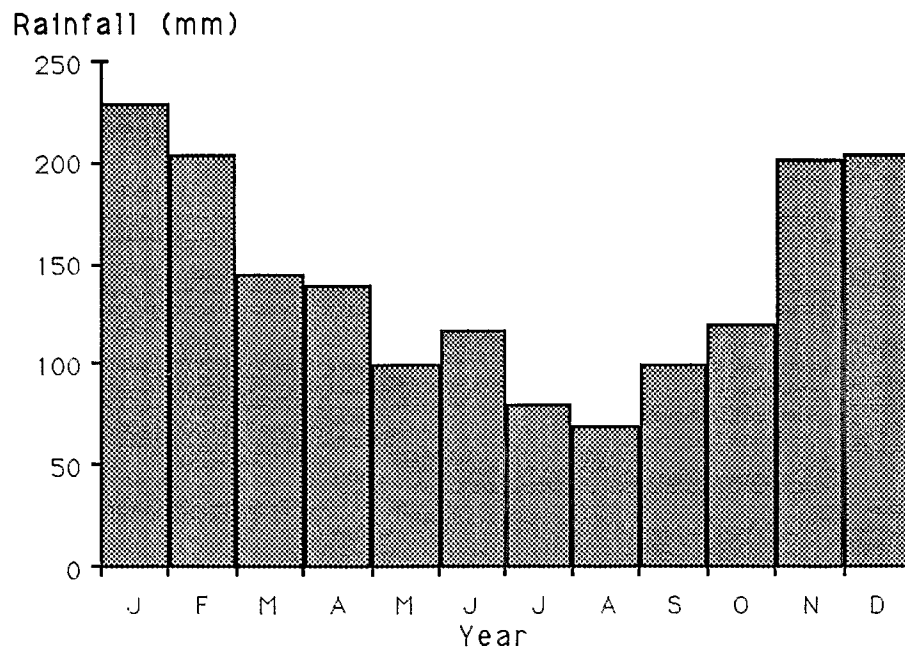


Fig. 3 : Average rainfall amounts for each month recorded at Rangiroa (Rangiroa is located 30 km to the east of Tikehau). Data provided by National Meteorological station of Tahiti-Faaa.

LOCATION AND SIZE OF TIKEHAU ATOLL

Atolls can be described as more or less continuous coral reefs (corals or other calcium carbonate producing organisms) which surround a deeper lagoon and drop steeply to oceanic depth on the seaward margin. All islands are typically low with soil derived primarily from reef rubble and sand.

Although almost identical in their general shape, atolls of the Tuamotu archipelago are different by the characteristics of their lagoon and the number of passes on which depends the amount of water circulation. As shown in Table 2, a few atolls have one or two passes and are termed **open atolls**, most have no pass and are termed **closed atolls**, four atolls have a dry lagoon, filled up by reef detritic and are termed **filled atolls**, one island, Makatea, has been uplifted by tectonic movements probably linked with the formation of Tahiti and is termed a **raised atoll**. Lastly, Portland is a **submerged atoll**.

Table 2 : Classification of the atolls of the Tuamotu archipelago based on the geomorphological characteristics of their lagoon.

Atoll group	Example
Open atolls with more than one pass	Rangiroa Fakarava Toau
Open atolls with one pass	Tikehau Mataiva Arutua
Closed atolls	Takapoto Hikueru Reao
Filled atolls	Akiaki Nukutavake Tikei
Raised atoll	Makatea
Submerged atoll	Portland

Tikehau has a large somewhat elliptically shaped lagoon, numerous shallow channels cutting the reef flat especially on the windward side, one pass between the lagoon and ocean, and narrow shelves dropping steeply into deep sea on all sides. A succession of small islands, locally termed *Motu*, constitute the dry land.

Tikehau is located in the northwestern Tuamotu archipelago with its center at 15°00'S and 148°10'W (Fig. 1). It is approximately 300 km from Tahiti to the south, 30 km from Rangiroa to the east and 20 km from Mataiva to the west. By French Polynesia standards, Tikehau is a relatively large elliptical atoll, about 20 km by 28 km in size, covering a total area of about 420 km². Among the 76 islands of the Tuamotu archipelago, Tikehau is the 11th largest. It is exceeded, among others, by Rangiroa (1640 km²), Fakarava (1220 km²) or Makemo (910 km²), the three largest islands. Small atolls are generally a pattern of the Tuamotu since 45 out of the 77 islands cover less than 100 km² (Mataiva : 50 km², Taiaro : 14 km², Tikei : 4 km²).

THE TERRESTRIAL ENVIRONMENT

Since few scientists conducted research in the terrestrial environment with respect to the marine environment of the Tikehau atoll, little is known about this part of the ecosystem. This section contains a review of what is known about atoll soils and associated vegetation, reports on the terrestrial fauna (birds and other vertebrates), and finally provides an overview of Tikehau human population evolution over the last century. Information is drawn from Jamet (1985) for soils, Florence (1985) for vegetation, Poulsen *et al.* (1985) for avifauna, and Sodter (1985) for human demography.

SOILS AND VEGETATION

Tikehau soils exclusively originate from the alteration of a mother rock made up of reef forming or reef living organisms. The micro-splitting of particles mostly through chemical processes leads to the formation of clay or carbonated silt in which the percentage can reach 40 % in sandy soils. Carbonates accumulate above the upper zone of the groundwater lens forming a calcareous crust. Organic matter is usually mixed with fine materials in a topsoil horizon fairly thick but it can also accumulate superficially in marshy depressions. Following these alteration processes, Tikehau atoll soils fall into four types :

- Rough mineral soils formed of accumulations of unaltered recent sediment.
- Weakly developed soils made up of coarse materials with low content of organic matter, found mostly on the oceanic shoreline of the island.
- Magnesium-calcite soils with a dark, developed A horizon more or less thick and with variable organic matter content. This kind of soils covers the majority of the islands at Tikehau.
- Marsh soils very rich in organic matter, located in island floor depressions (Plate 2).

Unlike high island soils, atoll soils almost lack silica, aluminium and iron. The mineralogy is almost exclusively calcium carbonate (80 to 95% of calcite and aragonite) which fine soluble particles represent 3 to 5 % in rough soils, more than 20 % in humus horizon, and exceed 30 % in marshes. Magnesium carbonate represents less than 1 %. Potassium and phosphorus content are generally less than 0.05 % in subsoils but fecal matter of birds and vegetation remains locally contribute to a ten fold increase in K and P concentrations of topsoils. Sodium concentration is lower (0.5 %) than expected in this kind of ecosystem.

The fertility of atoll soils is almost entirely dependant on the content of organic matter. Accounting for less than 2 or 3 % in rough soils, organic matter can reach 15 % in humus horizons and much more in marshy areas. Organic matter not only carries out the normal role of soil organic matter in storing and recycling nutrients, but it is also the major moisture storage component in the soils, since coral sands and rocks have an extremely limited moisture storage capacity. This is all important in atolls where evaporation exceeds precipitation eight months

of the year. Organic matter lowers pH which ranges between 8 and 9 in subsoils. The pH is almost neutral in topsoils, leading to a better nutrient assimilation.

Atoll soils have considerable influence on the composition of vegetation. There is a marked gradient from the beach toward the center of the island.

- Unaltered rough sediment soils are constantly rearranged and do not enable settlement of durable vegetation.

- Weakly developed soils constituted by coarse materials oceanward and fine sands lagoonward have a low organic matter content in the first 10 or 20 cm, forming patches or stretches. Two types of vegetation settled there :

Vegetation of the oceanic side of the island is a low and open assemblage of *Guettarda speciosa*, *Scaevola sericea* and *Tournefortia argentea*. Behind the beach, the assemblage gets richer with *Euphorbia atoto*, *Timonius polygamus* and *Pandanus tectorius*. On cemented coral substrata, *Pemphis acidula* forms bushes and on sand patches, *Suriana maritima* and *Lepturus repens* develop.

Vegetation of the lagoon side of the island is still well represented eastward the atoll whereas it was cleared by coconut plantations in other places. Bush assemblage is dominated by *Suriana maritima* and *Scaevola sericea*, but *Guettarda speciosa* and *Tournefortia argentea* occur sporadically. The herbaceous stratum is varied with *Triumfetta procumbens* and *Lepturus repens* dominating.

Magnesium calcite soils (found in the center of the island) cover the area of the forest. Although coconut plantation cleared much of the original vegetation, two facies can be distinguished :

- On weakly developed soils, *Pandanus tectorius* dominates the tree stratum along with *Tournefortia* and *Guettarda*. Among the bush, *Scaevola sericea*, *Pipturus argenteus* and *Timonius polygamus* were recorded. Herbaceous vegetation is rare : *Psilotum nudum*, *Cassytha filiformis* and *Nesogenes euphrasioides* were recorded nonetheless.

- On sandy soils, the original forest of *Pisonia grandis* has almost disappeared whereas *Guettarda speciosa* still occurs. Bushes are made up of *Pipturus argenteus*, *Morindia citrifolia* or *Euphorbia atoto*. The herbaceous stratum is varied with *Achyranthes velutina*, *Laportea ruderalis*, *Digitaria stenotaphrodes*, *Boerhavia tetrandra*.

Coconut plantations

Sand and gravel soils which are the most favourable for coconut agriculture have been planted mostly during the last century. The western coast has coarse substratum only allowing coconut trees to be planted on the lagoon side of the islands. From place to place, components of the original vegetation are encountered such as *Guettarda speciosa*, *Pisonia grandis* or *Pandanus tectorius* for trees, *Euphorbia atoto* or *Morinda citrifolia* for the bush, *Lepturus repens*, *Boerhavia tetrandra* and *Triumfetta procumbens* on the ground.

Feo vegetation

Feo are located north of the island supporting the main village and surrounded by coconut plantations. Being as high as 7 meters, they present a compact substratum with a low moisture storage capacity, and tiny soils in small caves. Tree stratum is composed of *Pandanus tectorius* and *Thespesia populnea*. Bush is made up of *Pipturus argenteus*, *Euphorbia atoto* and rarely *Capparis cordifolia*. On the ground, *Lepturus repens* and *Triumfetta procumbens* were recorded but also ferns such as *Asplenium nidus*, *Nephrolepis biserrata* or *Phymatosorus grossus*.

In a hydromorphic depression, vegetation is a Cyperaceous assemblage. *Cladium jamaicense* is so overwhelmingly dominating that the assemblage is almost monospecific, reaching 3 m high. On the edges of the marsh, *Mariscus pennatus* and *Eleocharis geniculata* are found.

THE TERRESTRIAL FAUNA

Avifauna

Sedentary terrestrial species widespread in all atolls are Tuamotu warbler (*Acrocephalus atypha*) of which 150 pairs were counted at Tikehau, at least 10 pairs of green pigeon (*Ptilinotus coralensis*), between 150 and 200 individuals of pacific reef heron (*Egretta sacra*). Tuamotu loriket (*Vini peruviana*) resides in a few atolls of western Tuamotu and breeds on Tikehau on western islands. About 20 pairs were counted. Sooty crane (*Porzana tabuensis*) was observed in the marshy area of the island supporting the village. New Zealand cuckoo (*Eudynamis taitensis*) is the only migrant species exclusively terrestrial sighted in autumn (May).

Shorebirds : especially present in winter of southern hemisphere, the most readily observable species are lesser golden-plover (*Pluvialis dominica*), bristle-thighed curlew (*Numenius tahitiensis*), wandering tattler (*Heteroscelus incanus*). Less abundant though regular visitors of Tikehau, ruddy turnstone (*Arenaria interpres*), sanderling (*Calidris alba*) and pectoral sandpiper *Calidris melanotos* account.

Seabirds : Red-footed booby (*Sula sula*) forms some small nesting colonies in trees (*Pisonia grandis*). Brown booby (*Sula leucogaster*) and frigatebirds (*Fregata ariel* and great frigatebird *Fregata minor*) regularly occur but no breeding evidences were recorded. Terns are well represented with gray-backed tern (*Sterna lunata*) of which a 20 pairs nesting colony was sighted, sooty tern (*Sterna fuscata*) which seems only vagrant, great crested tern (*Sterna bergii*) of which about 50 pairs nest on the atoll, blue tern (*Procelsterna coerulea*) of which a few pairs are supposed to nest at Tikehau, the very common brown noddy (*Anous stolidus*) of which 1500 nests were censused in small trees (*Pemphis*, *Tournefortia*), 800 nests of black noddy (*Anous tenuirostris*) in trees (*Pisonia*, *Guettarda*), and lastly a nesting population of 3000 individuals of white tern (*Gygis alba*).

Other seabirds as petrel (*Pterodroma rostrata*) and skua (*Stercorarius pomarinus*) sometimes approach Tikehau.

Other vertebrates

Except marine green turtle (*Chelonia mydas*), reptiles reported to occur at Tikehau are lizards azure-tailed skink (*Lygosoma cyanurum*) which occurs in sunny forest floor, and house gecko (*Hemidactylus frenatus*). Among mammals, rodents are best represented with polynesian rat (*Rattus exulans*) and Norway rat (*Rattus norvegicus*). Some domestic cats returned to the wild were seen wandering in coconut plantations and marshes.

PEOPLE OF TIKEHAU, PAST AND PRESENT

Tikehau could have been one of the atolls discovered by Turnbull in February 1803 when he was sailing from Tahiti to Hawaii, but neither positions nor name were given. In 1816, Otto von Kotzebue, Russian master of the "Rurick" first identified the atoll of Tikehau and gave it the name of one of his shipmates : "Krusenstern". In May 1848, the atoll was once again described by a trader, Lucett. Given the poor knowledge of the danger of the island, none of those first discoverers attempted to land and as a result, nothing is known about the population during this period. However, archeological remains of the past (*marae*) attest that Tikehau was inhabited at the time of the Christ. In all probability, age dating of the sites would push the date for settlement of Tikehau further back in time.

The first information on the total number of inhabitants was given in 1862. Ten persons were counted but this total is probably unrealistic because the census method did not take into account the frequent seasonal movements of the population around the island.

In 1902, an official census made by French Authorities gives a total of 156 inhabitants for both Tikehau and Mataiva. The following census in 1911 gives a total of 95 inhabitants on Tikehau and 58 on Mataiva. Until the end of World War II, no information on Tikehau and Mataiva population is available. In 1946, 376 persons had been registered on both Mataiva and Tikehau.

From 1950 to 1983

From 1950 on, census at regular intervals allow to follow population variations. Census reliability depends however on how the important mobility of the population is taken into account. Census methods sometime tend to overestimate the population by counting a single person twice (in 1956 for instance).

As illustrated by information displayed in Table 3, the level of the population of Tikehau in 1983 is slightly the same as in 1951 though the total population of French Polynesia doubled meanwhile. Trends in population variation are difficult to analyse without precise individual information on place of birth and location of main home.

Table 3 : Variations of Tikehau, Mataiva, both Tikehau and Mataiva, and French Polynesia populations between 1946 and 1983. All census were made by French Authorities. Results of 1956 census are to be interpreted very cautiously since census method tends to over-estimate the actual population by counting some single person twice.

	1946	1951	1956	1962	1967	1971	1977	1983
Tikehau	--	259	349	275	287	246	266	279
Mataiva	--	126	241	162	138	147	178	183
Both	376	385	590	437	425	393	444	462
French Polynesia	55,424	62,678	76,327	84,551	98,378	119,168	137,382	166,753

The Population in 1983

A typical feature of the population of Tikehau , like of the population of French Polynesia, is the high proportion of young people : 28.7 % of the population is less than 10 years old and 52.7 % less than 20. The worker age class is very low, especially between 30 and 39 which represents only 5 % of the population.

The high migratory rate of the population, the main source of difficulties to accurately measure the population, is confirmed by the proportion of Tikehau inhabitants (21 %) having spent more than six months in a row in another district of French Polynesia. For 91 % of the people having moved, the island of Tahiti is the main destination, and 70 % of the 91 % go to Papeete.

The working population is composed by 90 persons, 76 men and 14 women. Among the 76 men, 50 put up with copra production, 14 are fishermen, 9 are artisans, 2 are employed by the government and 1 is administrative officer. Among women, 8 are administrative officers, 3 are shopkeepers and 3 are artisans ; 3 men and 33 women have declared to be looking for a job.

Conclusion

The main characteristics of Tikehau population are :

- High proportions of young people under 20 years old and, as a consequence, low proportions of people in the worker age class.
- High migratory rate.
- Men professional activities primarily oriented toward agriculture, especially copra production. Women professional activity is low but high employment request exists.

THE MARINE ENVIRONMENT

PHYSIOGRAPHY OF THE MARINE AREA

Definition of reef units

In order to classify reef units of the atoll, Faure and Laboute (1984) described three main types of reef units as follows :

- Compartments defined on a physiographic basis
- Zones assessed on a morphological basis
- Zones divided into biota according to bionomic field data

The three compartments are the **outer slope**, the **reef flat**, and the **lagoon formations**. A fourth virtual compartment termed **morphological discontinuities** grouping pass and shallow channels is also studied. Fig. 4 lists the different units classically found around an atoll.

BIOTA		ZONES		COMPARTMENTS	
Lower part	>60-70 m	Deep slope	25-75 m	OUTER SLOPE	
Middle part	35-60 m				
Upper part	25-35 m				
Lower part	15-25 m	outer terrace	10-25 m		
Upper part	0-15 m				
Fore reef platform	4-10 m	Fore reef area	0-10 m		REEF FLAT
Spur and groove zone	0-4 m				
Algal ridge					
Submerged reef flat		outer reef flat			
Inner flat					
Inner slope					
Down slope reef patches		inner reef flat			
Coral patches					
Upper zone	0-2 m				
Middle zone	2- 6 m	inner slope		LAGOON STRUCTURES	
Lower zone	6-15 m				
Pass					
Gutter (or Hoa)		Low depth coral patches			
		Pinnacles			
		Pass and Hoa			MORPHOLOGICAL DISCONTINUITIES

Fig. 4 : Inventory and repartition of the different atoll units (from Faure and Laboute, 1984).

The outer slope

The outer slope is the seaward part of an atoll which drops more or less steeply to oceanic depth. In Tikehau, the outer slope is divided into three zones :

- The **fore reef area** located between 0 and 10 m depth. This zone itself is subdivided into the **spur and groove zone** (0-4 m) and the **fore reef platform** (4-10 m). The spur and groove system is a succession of reef fingers projecting seaward where the waves break, oriented perpendicular to the reef front. Spurs are relatively flat on top. Their width ranges from 8 to 12 m with a low slope gradient of 2 to 4°. Grooves are shallow (1 to 3 m) and relatively narrow (2 to 3 m). The walls of the grooves are sub-vertical and their bases are floored with cobbles and dead coral boulders, precluding the development of any significant sessile benthic life (Plate 4). Just seaward of the spur and groove, the bottom flattens somewhat with the fore reef platform.

- The **outer terrace** begins at a depth of 10 m with a distinct change from a gentle slope of a few degrees to an angle of approximately 45°. It presents an irregular surface with small periodic shallow grooves oriented parallel to the slope direction, well distinguished from the spur and groove formations described above. This structure could be considered as an old spur and groove system (Chevalier, 1973).

- The **deep slope** (or drop off) begins below 25 m at an angle often greater than 45°. According to coral community distribution, the slope can be separated into three biota : the upper part (25-35 m), the middle (35-65 m) and the lower part from 70 m downwards.

The reef flat

The **outer reef flat** begins seaward by the **algal ridge** and ends lagoonward by the emerged conglomerate or the island. On leeward reef, the algal ridge is low (20 cm above low tide level) and has a width of 10 m while on windward shelves, the algal ridge is larger (30-40 m) and higher (40 cm above low tide level). Numerous deep grooves (1-3 m) extend across the windward algal ridge. Just inshore of this formation, a slight depression of the reef flat can occur, especially on the windward sides of the atoll. To this follows an emerged hardened conglomerate which can be considered as the remains of a past algal ridge. As shown in Fig. 5, the outer reef flat morphology varies considerably in different area, particularly between the windward and the leeward sides. Its width ranges from 150 to 180 m as measured on West-Southwest transects to 20 to 40 m on eastern shores. It consists of an area of rock pavement derived from an old conglomerate submerged under 10 to 50 cm of water with a rough bottom, pitted by small erosional pools. The floor is covered by a thin sedimental detritic layer that get thicker toward the beach.

The **inner reef flat** begins just lagoonward of the motu or the emerged conglomerate, and ends where the bottom starts to slope into the lagoon. The width of the inner reef flat varies considerably around the atoll rim. On windward shores, the inner lagoon margin flat is protected from trade winds by the outer reef flat, the motu and its associated vegetation. The inner reef flat is therefore somewhat dead and resembles a slight sandy slope. A different situation exists on the lagoon border in the lee of the atoll. Because of exposure to trade wind across the fetch of the lagoon, these areas are well-formed reef flats composed of an old conglomerate covered by a thin sedimental layer that gets thicker lagoonward.

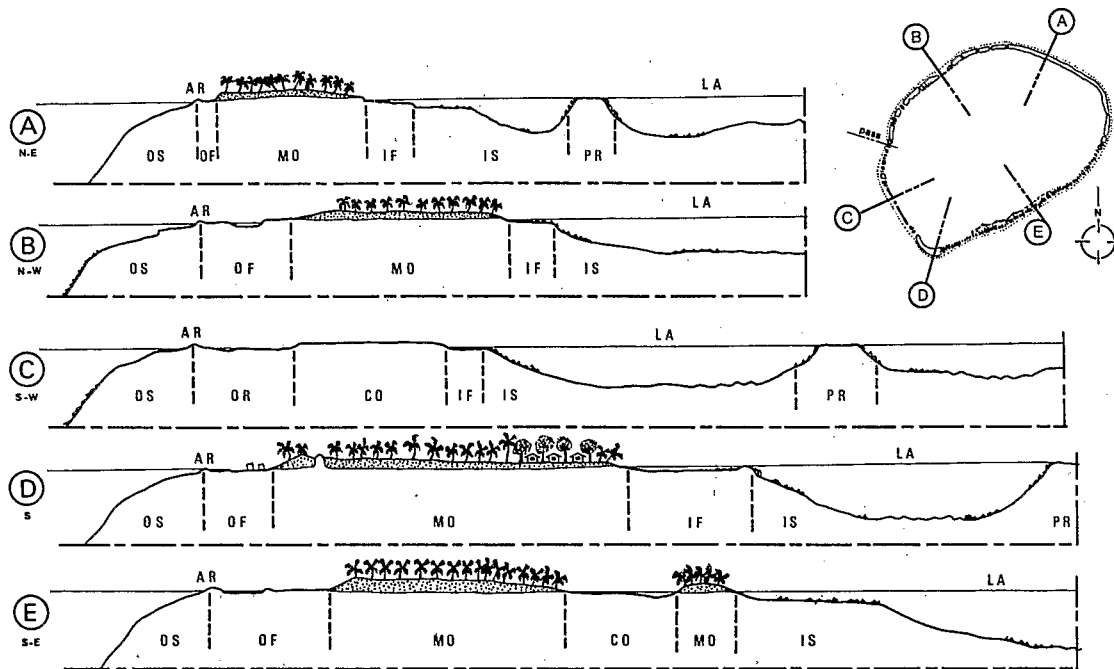


Fig. 5 : Cross atoll rim sections at various locations of the Tikehau atoll (OS : outer slope; AR : algal ridge; OF : outer reef flat; MO : island; CO : conglomerate IF : inner reef flat; IS : inner slope; LA : lagoon; PR : pinnacle reef) - from Harmelin-Vivien (1985).

Lagoon structures

Immediately after the inner reef flat, the lagoon inner slope is a relatively steep sediment and rubble slope which extends to depth of 2-6 m. When the slope begins to flatten out, numerous coral patches protrude from the sediment bottom. Where the water flow across the reef is unimpeded by islands, these coral colonies can be numerous and healthy. The lagoon floor is essentially flat with a low slope gradient. The bottom is primarily a fine sandy bottom. This is studied in more detail in a subsequent chapter of this volume.

Many coral pinnacles are scattered all over the lagoon. Up to 300 pinnacles visible from the surface (locally called *Karena*) have been counted. They are quite unevenly spaced throughout the lagoon since half of them can be found in the southwest part. Pinnacle reefs vary greatly in size, ranging from a few tens of meters to over 200 m in diameter for the largest.

The shape of the pinnacles can be roughly related to their size : the smaller the pinnacle reef's diameter, the steeper its slope. On small pinnacles, much of the slope is nearly vertical. The largest pinnacles are somewhat flat on top and an emergent one can support bushes or small trees. However, they still slope to the lagoon floor at an angle of at least 20°. Pinnacle reef shapes also vary considerably between the windward and the leeward sides. The windward side usually presents a steep subvertical slope whereas the leeward side of the pinnacle gently slopes to a detrital zone. Coral community zonation is rather regular among pinnacle reefs, and three biota may be recognized : the upper (0-2 m), middle (2-6 m) and lower zones (6 m downward).

Morphological discontinuities

Passes can be defined as major deep channels between the ocean and the lagoon. In Tikehau, the only pass, called *Tuheiava*, is located at the western part of the atoll. Localisation of the pass on the leeward side of atolls appears to be a general trend of the Tuamotu archipelago. Minimal depth of the pass is about 4 m and is sufficient for a small boat to traverse. The bottom, of bare eroded flagstone, slopes steeply seaward and gradually deepens lagoonward until it merges with the lagoon floor. Current direction in its vicinity reverses, depending on the tide and on the height of water in the lagoon. When tidal currents run against the trade winds, steep standing waves can occur in the pass, hampering sailing and fishing activities. When sea-level is high in the lagoon, the current is mostly unidirectional out of the lagoon. This occurs frequently when storm associated waves break on windward reef and drive large quantities of water into the lagoon. On an annual basis, the net flow through the pass is an outflow. Main features of water circulation at Tikehau are studied out in details in a subsequent chapter of this volume.

Hoa, also termed rips or gutters, are shallow channels which cut the reef flat superficially. They draw their flow from the shallow reef flat and channelize the flow of water into the lagoon between the motu (Plate 5). In Tikehau, their width ranges from a few tens of meters to 500 m. When currents can freely flow through *hoa* across the atoll rim, *hoa* are termed **open or functional *hoa***. On the contrary, when currents do not flow or flow only when a storm occurs because the channel is obstructed by boulders on the outer flat and/or is closed by littoral sand shoals or rubble accumulations lagoonward, *hoa* are termed **closed or non functional *hoa***. The shape of these channels is subject to major changes owing to sedimentation and high erosion. *Hoa* are shallow on the outer reef flat (10 to 20 cm) but deepen towards the lagoon (1-3 m). On their lagoonward end where current flow slows down, *hoa* usually have shallow sand shoals. *Hoa* have sandy bottoms sculptured by current fluxes with more or less patch reefs. The amount of patch reefs are directly related to the intensity of water circulation through them.

Up to 150 *hoa* have been counted around the atoll rim. More than 100 are concentrated on the southeast coast and are mostly open channels. The current flow through them is almost unidirectional, from ocean into the lagoon, depending on water level in the lagoon. The 50 other *hoa* are principally located on the northwest coast. A few of them are functional.

Hoa, as well as the pass, are the major source of water movements between the ocean and lagoon.

BATHYMETRY OF THE LAGOON

Knowledge of the bathymetry of the lagoon is basic data for all marine research carried out on the lagoon. There is no detailed marine chart of the lagoon available and an attempt to map the Tikehau lagoon bottom from the satellite LANDSAT proved to be unsuccessful. The main cause was the high and uneven turbidity of the water in the lagoon which prevented LANDSAT from mapping the bottom efficiently. The bathymetry of the lagoon of Tikehau was mapped using field measurements (Lenhardt, 1987). A SIMRAD EY-M echo-sounder (frequency 70 khz, range 0-60m) was used on board a motor boat and depth continually recorded on eight transects across the lagoon. The boat was steaming at a regular speed of 3.2 knots on the magnetic North-South axis (declination : 13 °). Results obtained have been cross-checked with results from five other transects. To discretize the continuous series of data, one depth measure was taken every 80 m and raw data smoothed to eliminate numerous local minor unevenness of the bottom.

Pass morphology was studied by recording depth on three transects, one through and two across the pass.

Bathymetric map

Smoothed depths recorded on transects were contoured to map the bathymetry of Tikehau (Fig. 6). The greatest depth recorded was 38 m in the central northeastern part of the lagoon. The main lagoon basin appears to be a relatively flat area with gentle slopes.

Depth histogram

The histogram presented on Fig. 7 shows that the general shape of the lagoon is that of a basin with steep walls. Depths between 0 and 15 m represent only 7 % of the total surface of the lagoon ($S = 420 \cdot 10^6$ square meters).

Other geometric data

The mean depth P as well as the total volume V of the lagoon is of great interest for other studies. Mean depth is calculated by computing the mean depth of each transect with mean length and width of each transect. The result is an average depth of $P = 25$ m. The total volume of the lagoon is calculated by multiplying the total surface of the lagoon by its mean depth. The result is $V = 10^{10}$ cubic meters. The confidence interval of those data is about 5% which meets the requirement for precision of other research.

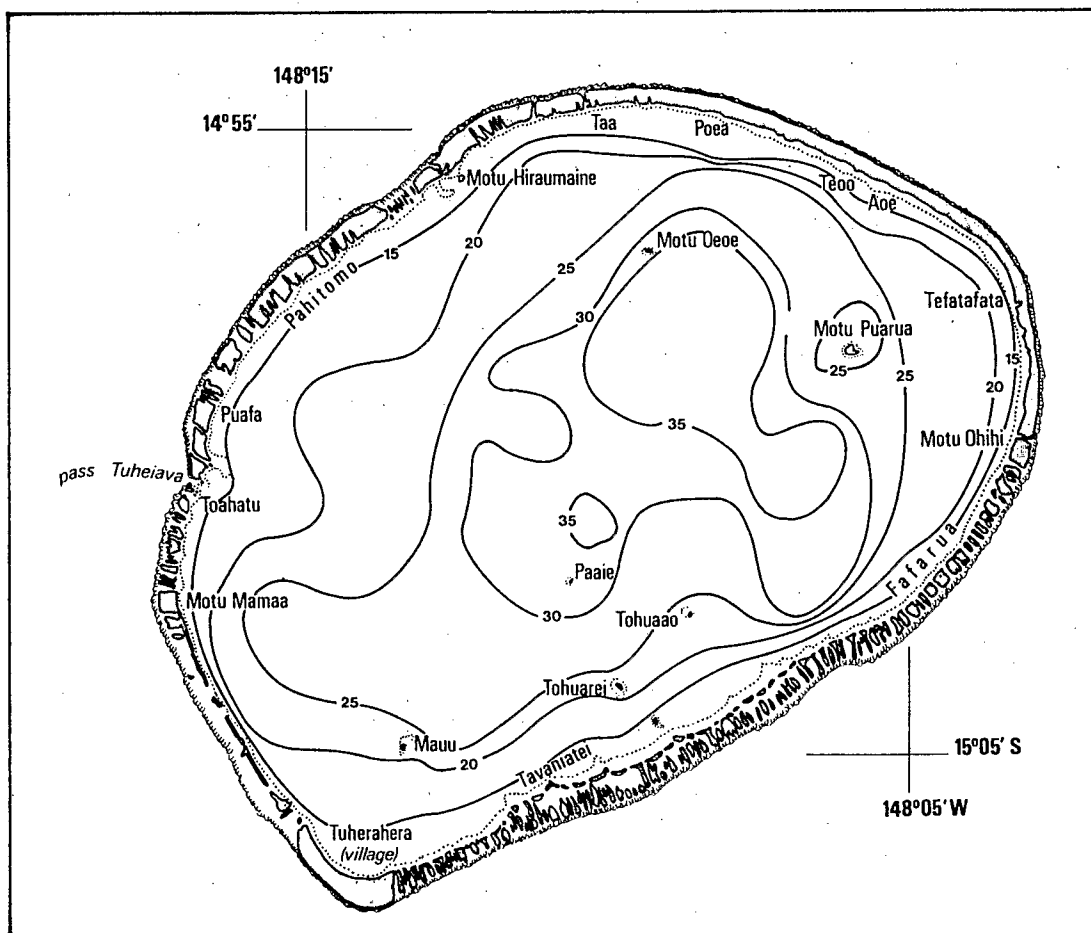


Fig. 6 : Contoured depths (in m) in the lagoon of Tikehau.

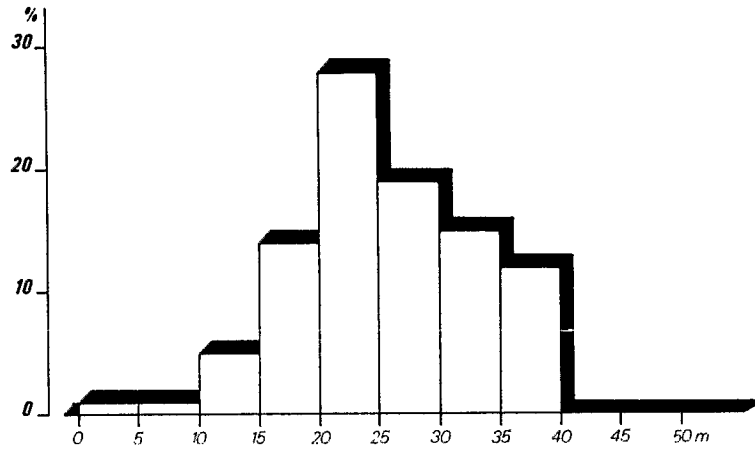


Fig. 7 : Average Tikehau lagoon surface per 5 m depth intervals expressed as a percentage of total lagoon surface .

Characteristic of the pass

Fig. 8 shows the bathymetric map of the pass, transects to record the depth and the smoothed shape of the bottom. The minimal depth recorded in the pass is 4 m. For further modelisation of the flow through this channel and water circulation in the lagoon, the mean section of the pass is estimated at 1000 square meters and average length at 600 m.

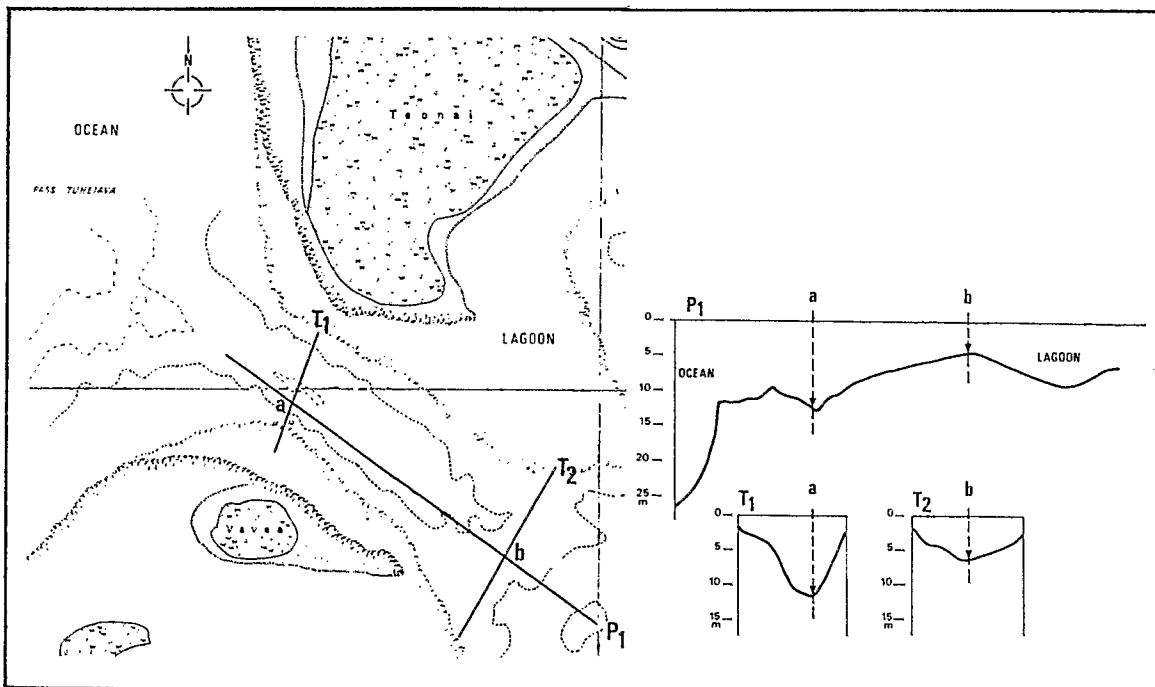


Fig. 8 : Bottom profile of Tikehau atoll pass.

NATURE AND DISTRIBUTION OF LAGOON SEDIMENTS

The bottom sediments of the Tikehau lagoon were characterized by Intes and Arnaudin (1987). Fifty four samples of bottom sediment were taken in various location of the lagoon and subsequently sorted and analyzed in the laboratory.

Findings were that the sediments are all calcareous organic sands. They consist of the following chief components : *Halimeda* segment sand, Foraminifera (family *Miliolidae*) test sand, mollusc shell sand and miscellaneous debris.

Halimeda segment sand is the first common material. It is present in almost all samples and predominates in most of them, especially in samples taken in the western part of the lagoon. As shown on Fig. 9, *Halimeda* segment distribution follows an horizontal west-east gradient and a vertical gradient since its abundance decreases steadily below a 20 m depth. Foraminifera test is the second most common material. Large stretches of foram sand occur on shallow bottoms less than 10 m deep along the southern and southeastern lagoon margin. Moreover, a large foram sand patch extends in the northern central part of the lagoon between a depth of 20 and 35 m. Mollusc shell sand and gravel are never abundant and never dominate the sediment composition.

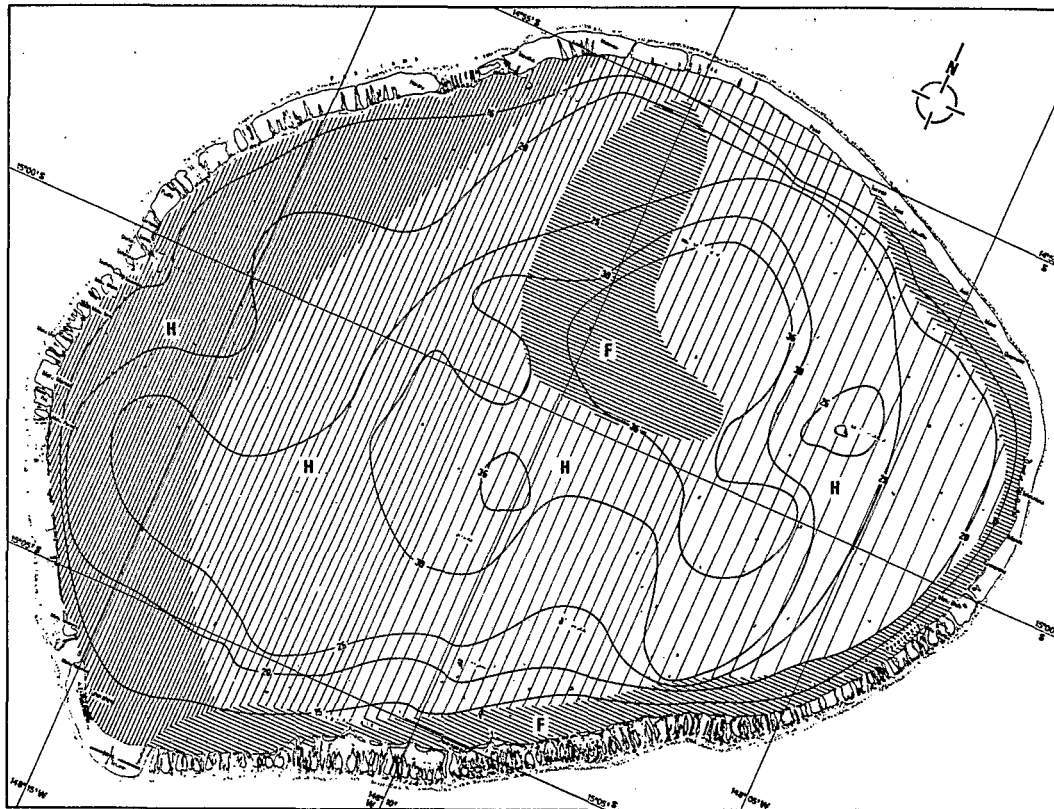


Fig. 9 : Contoured bottom sediment data of Tikehau lagoon characterized by their chief components (H : *Halimeda* sands, F : Foraminifera sands).

The mean size of the sand taken in every sample was estimated by sieving in order to classify the sediment into three size classes : very fine sand (STF - less than 0.25 mm), fine sand (SF - between 0.25 and 0.50 mm) and medium sand (SM - greater than 0.50 mm). Sediment smaller than 0.04 mm was not studied. Contoured data (Fig 10) show that lagoon sediments are mostly fine sand, found in a wide range of depths. However, a large stretch of very fine sand was found in the central northern part of the lagoon between 15 and 30 m, and on an irregular discontinuous strip located 20 to 30 m leeward the eastern and southern reef at depth between 9 and 30 m. Some small medium sand patches are scattered along the lagoon margin down to a 10-15 m depth and a large stretch occurs across the deep central basin of the lagoon.

Most of the materials of the sand sample taken proved to be quite heterogeneous with a large size range and a symmetric distribution, except for foram medium sands that are homogeneous. Sands easily driven by currents are logically found in area of important water transport (*i.e.* lagoonward *hoa*, in the vicinity of the pass) and unexpectedly at a 34 m depth in the center of the lagoon which is an area thought to be calm.

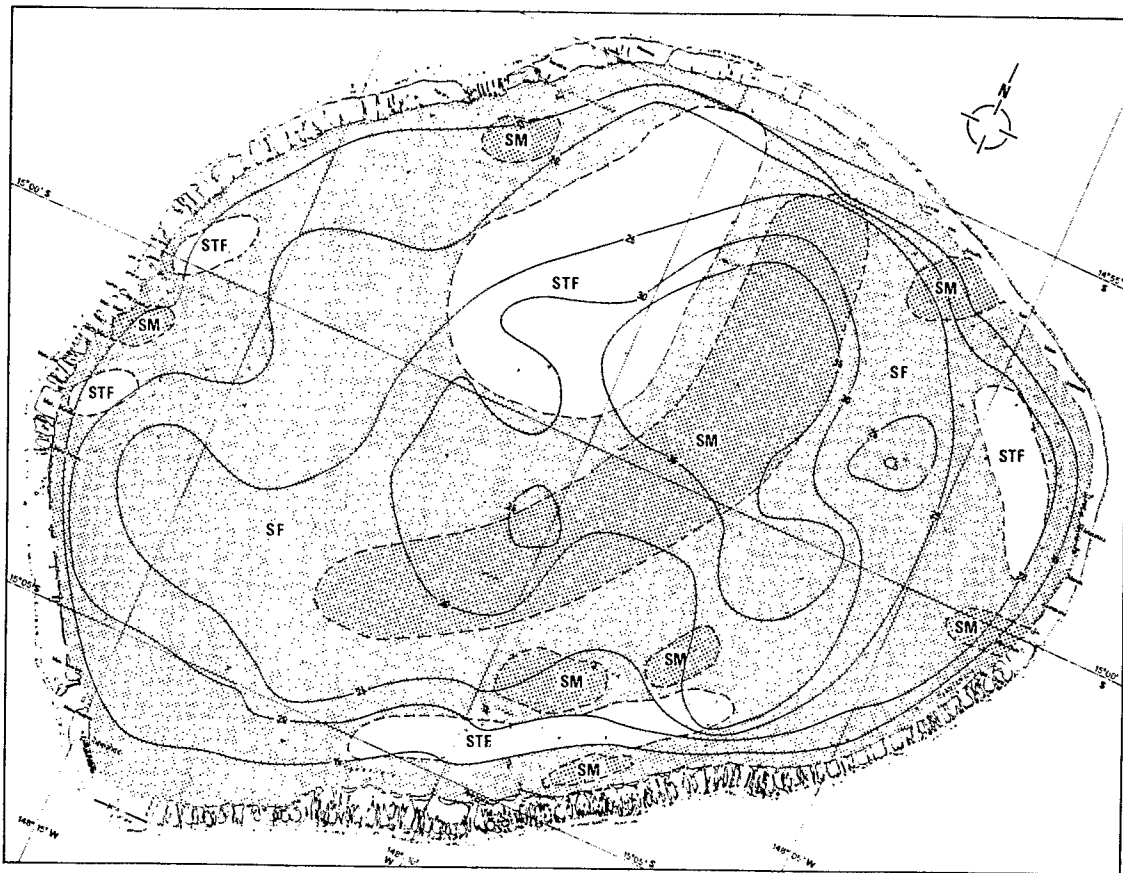


Fig. 10 : Contoured bottom sediment data of Tikehau lagoon characterized by mean sand size (STF : very fine sand, SF ; fine sand; SM medium sand; see text for definition of size-classes).

BIOLOGICAL COMMUNITIES OF THE OUTER SLOPE

This chapter, as well as the following ones, does not attempt to provide a comprehensive description of the fauna in Tikehau but descriptive information about marine habitat. Determination of many coral and sponge species is still underway and furthermore, fauna description is limited to the first 90 m in depth. Depths below are unpractical for sustained SCUBA diving operations and should be sampled remotely. The information presented hereafter has been drawn from publications of Faure and Laboute (1984) for coral species census and distribution, Peyrot-Clausade (1984) for cryptofauna distribution and unpublished data of Intes for zoobenthos of sediments. Fish fauna distribution will be studied in a subsequent chapter of this volume.

The fore reef area

In the spur and groove zone (0-4 m), corals are largely dominated by calcareous algae which become increasingly dominant as exposure to trade wind increases. Total coral coverage rate ranges from 5 to 25 %. Spur and groove have on them coral adapted to withstand this high energy environment. The top of the spur and the parts of the wall of the grooves are colonized by small branching *Pocillopora* (*P. verrucosa*, *P. meandrina*, *P. damicornis*); small massive *Favia rotumana*, *F. stelligera*, *Montastrea curta*, *Pavona clavus*; encrusting forms of *Montipora caliculata*, *Acropora robusta*, *Millepora platyphylla* and *Acropora abrotanoides*.

Algae are the major component of this substrate. The main species are green algae *Halimeda opuntia*, *H. discoidea*, *Caulerpa pickeringii*, *C. seuratii*, *Neomeris van bosse*, *Microdyction* and the red algae *Dasya* to some extent.

Sessile cryptofauna is abundant, sheltering among coral branches or small grooves in the rock. The highest richness is reached on overhangs and in small caves as noticed on the south southeast coast (Sponges, Hydroids *Solanderia*, Bryozoans, Stylasterids, Dendrophiliids, Didemnid and Polyclinid Ascidians). An important motile cryptofauna occurs in this zone. Polychaetes and Crustaceans dominate and borers (mainly Sipunculids) are rare.

On the fore reef platform (4-10 m), the amount of coral coverage increases (60-80%) as well as its diversity. The most conspicuous coral species are short bunches of *Acropora humilis*, *A. digitifera*, *A. variabilis*, *Astreopora myriophthalma*, the first noticed Fungid (*Fungia fungites* and *F. scutaria*), and all the coral species cited above. On the northwest shelves where the platform is wide, the fore reef platform is also highly colonized by algae of the genus *Microdyction*, *Halimeda* and *Caulerpa*.

Cryptic community biomass decreases slightly, still dominated by Polychaetes and Crustaceans.

The outer terrace

Between 10 and 15 m depth, grooves floored with rubbles alternate with coral ridges. Communities are made up of *Favia stelligera*, *Pocillopora eydouxi*, *Astreopora myriophthalma*, *Acropora abrotanoides*, *Platygyra daedalea*, *Porites lobata*, *Favia rotumana*, *Millepora platyphylla*. Coral coverage rate is about 60 %. From 15 m to 25 m, *Porites lobata* progressively dominate followed in, order of abundance, by *Pocillopora eydouxi*, *Favia stelligera*, *F. rotumana*, *Astreopora myriophthalma*, *Acanthastrea echinata*, *Pavona varians*, *Herpolitha limax* and *Acropora sp.*

Calcareous algae *Porolithon* and *Peyssonnelia* along with soft algae colonize the outer terrace bottom to depth of 25 m. On the windward coast, algae coverage can be important to some extent.

Sessile fauna, except for some sponges as *Astroclera sp.*, shelter among coral patches and is rather scarce. Echinoderms, Molluscs and Crustaceans are abundant but remain hidden during daytime. The only occurrence of the invertebrate coral predator, the crown-of-thorn starfish *Acanthaster planci*, was recorded in this zone. Its population level seems to be very low and no evidence of an extensive coral predation was found.

Motile cryptofauna is dominated by Polychaetes and Crustaceans. Its biomass is low and is reduced by half between 10 and 20 m in depth.

The deep slope

The living coral coverage rate of the deep slope is high ranging from 50 to 100 %. At these depths, the amount of light energy reaching the bottom decreases steadily, inducing a colonization of the bottom by coral species fitted to dim recess conditions. The plate-like *Pachyseris speciosa* is thus the major component of the coral fauna, so much that this zone is termed the "*Pachyseris speciosa* area". In the **upper zone** (25-35 m), most of the dominant species of the previous zone (*Porites lobata*, *Pocillipora eydouxi*, *Favia stelligera* and *Acropora sp.*) are progressively replaced by species more shade-tolerant as *Gardinoseris planulata*, *Lobophyllia sp.*, *Coscinarea sp.* and small colonies of *Pachyseris speciosa* are located in the shade of large vasiform coral species. The live coral coverage rate is above 50 %. In the **middle zone** (35 to 60-70 m), *Pachyseris speciosa* sharply predominates colonies of *Porites lobata*, *Pavona varians*, *Leptoseris incrustans*, *Gardinoseris planulata* and *Echinophyllia aspera*. In the **lower zone** (from 60-70 m downwards), numerous colonies of *Leptoseris* (*Leptoseris hawaiiensis*, *L. scabra*, *Leptoseris sp.*) and *Echinophyllia* (*E. aspera*, *E. echinata*) appear among well-developed colonies of *Pachyseris speciosa* with a nearly flat upper surface well adapted for best capturing sunlight. *Stylaster* and especially the red coral *Stylaster sanguineus* are common species below 60 m but they are already found from 40 m downward in places well protected from light (*i.e.* : on overhangs, in small caves or in the shade of larger species). No SCUBA diving investigations were made below 85 m but given the transparency of the water, it has been observed that the *Pachyseris-Leptoseris* population is still developing with the same energy below a depth of 90 m.

Algae zonation is not restricted to the upper strata of the slope. When a dead coral leaves a living site, the vacated space can be reoccupied by *Caulerpa urvilliana* (to depths of 65 m), *Caulerpa seuratii* (15-70 m), *Caulerpa bikinensis* (to depths of 75 m and probably below), *Microdyction sp.*, (1-65 m) or an unidentified species of *Halimeda*.

The black sponge *Astroclera sp.* remains the most conspicuous species among the 25 observed sponge species. It reaches its maximum density at a depth of 40 m but is still abundant in small colonies at 70 m. The paucity of other sessile invertebrates like Gorgonians, Anthipatharians or large Hydroids is noteworthy. Unlike many Indo-Pacific coral reefs, this is a common feature of outer slope of atoll in the Tuamotu archipelago.

BIOLOGICAL COMMUNITIES OF THE REEF FLAT

In all aspects, the reef flat is quite variable. Various authors have described this zone at Tikehau, usually in combination with a description of cross-reef flat transects on several parts of the atoll rim.

The algal ridge

The algal ridge is mostly built by calcareous algae of genus *Porolithon* and *Chevaliericrusta* along with *Pocockiella variegata* and algal turf made of *Caulerpa*, *Halimeda*, *Microdyction* and *Liagora*.

Coral coverage rate is low, less than 2 % on windward reef and less than 10 % on leeward shelf. Coral colonies generally flourish on the wall of the grooves which are emergent only when low spring tide occurs. Coral species are short, small and blunt ecomorphs fit to withstand the high-energy environment generated by wave action. The main components of this community are : *Pocillipora damicornis*, *Porites lobata*, *Pocillipora verrucosa*, *Montipora caliculata*, *Acropora humilis*, *A. digitifera* and *Millepora platyphylla*.

Three echinoderms, *Heterocentrus mammillatus*, *Colobocentrotus pedifer*, *Actinopyga mauritania* and lesser number of juvenile sea-urchins sheltered in holes with *Echinometra sp.*, are often abundant. Among molluscs, the most seaward species is *Platella flexuosa* followed lagoonward by *Drupa ricinus*, *D. morum*, *Turbo setosus*, *Morula uva* and two species of Vermetid.

The algal ridge structure provides numerous small cavities which afford protection from the wave surge (and predation) to motile cryptofauna. Its biomass is high and mostly consists of Polychaetes and Crustaceans. Sessile cryptofauna has a high species richness index but since its living space is restricted by the availability of cavities always submerged, the total biomass is low.

The outer reef flat

The coral community of the outer reef flat is extremely poor with only two species censused, *Pocillipora damicornis* and *Porites lobata*, covering less than 1 % of the area. Algae are scarce.

Among the most conspicuous molluscs, *Drupa grossularia*, *Conus sponsalis*, *C. ebraeus*, *Erosaria moneta*, *Cerithium alveolus*, young *Tridacna maxima* and *Chama imbricata* are frequently encountered.

The conglomerate has evidence of extensive rock boring by numerous Lithophagids (up to 50 individuals m⁻²). Various sessile invertebrates shelter under blocks and in cavities but their abundance is quite low. Motile cryptofauna is scarce and of low biomass, dominated by Polychaetes and Molluscs.

The inner reef flat

Algae are the main components of the innermost part of the reef flat. The primarily fine sandy bottom is colonized by *Halimeda opuntia*, *Caulerpa serrulata* and *C. urvillana*. Many sand mounds of the mud shrimp *Callinectes armatus* are scattered all over this area, attesting an important burrowing activity.

Lagoonward the inner reef flat and down to a 2 m depth, the coral community consists of *Pocillipora damicornis*, *Acropora digitifera*, *A. abrotanoides*, *A. corymbosa*, *A. humilis*, *Favia stelligera*, *Montastrea curta*, *Platygyra daedalea*. Live coral fauna covers about 25 % of the substrate.

Algae coverage is high over blocks and sites left by dead coral colonies. Species identified are Dictyotales, *Halimeda sp.*, *Mycrodyction sp.*, *Pocockiella sp.* and a thick algal turf. A great abundance of *Cerithium alveolus* and *Erosaria moneta* is remarkable.

Shapes and extensions of dead coral colonies provide a lot of space for a motile cryptofauna settlement. As a consequence, its biomass is high, dominated by motile and boring Molluscs and Sipunculids which account for more than 30 % of the total cryptofauna biomass. Main species of Ascidiaceans are from the families of Didemnidae and Polycitoridae.

BIOLOGICAL COMMUNITIES OF THE LAGOON

The lagoon slope

The important sedimental layer of the inner slope hampers somewhat the development of coral communities. Live coral coverage rate is less than 10 % and consists of *Pocillipora sp.* mostly settled in the shallowest part of the slope, followed downward by massive and encrusting forms of *Porites lobata*, *Leptastrea purpurea*, *Pavona varians*, *Platygyra daedalea*, *Montipora verilli* and *Fungia sp.*

Algae are generally scarce. *Microdyction* have colonized hard substrate on the windward side of the atoll. On the west coast, not far from the pass, an algal flat community dominated by *Caulerpa sp.* extends on the slope with some *Halimeda sp.* found where the slope flattens out and merges with the lagoon bottom.

Invertebrates occur sporadically in this barren area.

Between 6 and 12 m depth, the lagoon margin has areas of abundant patch reefs. Particularly in places exposed to an abundant water circulation but protected from sediment overwash, lagoon margin patch reefs have well developed coral communities which can be either multispecific coral heads of *Pseudocolumastrea pollicata*, *Platygyra daedalea*, *Leptastrea purpurea*, *Pavona varians*, *P. minuta*, *Stylocoeniella sp.*, *Astreopora sp.*, *Fungia ssp.*, *Porites lutea*, *Stylophora pistillata*, *Montipora verrucosa*, *M. verrilli* or paucispecific bunches of *Acropora formosa* and *Acropora vaughani*.

A few sessile bivalves grow on the sides of the patch reefs. The most frequently encountered species are *Arca ventricosa*, *Pinctada maculata* and rarely the pearl oyster *Pinctada margaritifera*. In addition to some echinoids hidden in shelters provided by coral patches, beche-de-mer *Halodeima atra*, *Thelenota ananas* and several species of synaptid commonly feed in this area.

The lagoon bottom

The nature of lagoon bottom substrate has not been studied in detail but obviously, soft sediment substrata overwhelmingly dominate hard coral substratum. The lagoon floor can be characterized as large stretches of sand with occasional patch reefs. Wide areas of soft bottom are covered with a thin algal mat of brown Cyanophyceae. Other Cyanophyceae are visible on the sediment as large red balls. Species of *Halimeda* (principally *H. opuntia*) and *Caulerpa* (*C. serrulata*, *C. urvilliana*) can build up large algal flat areas. *Caulerpa sp.* grows via rhizomes, spreading out over the bottom in easily distinguishable patterns. Sea grass beds of the marine phanerogame *Halophila ovalis* reach high density in some places.

Little is known on the fauna buried in, or on, sediments. Epifauna is composed mostly of sponges (*Echinodictyon*, *Axinella*) scattered over sediment surface. From place to place, some bivalves of the genus *Pinna* raise from the sediment. Holothurian *Halodeima atra* concentrates in great numbers, up to 10 individuals per square meter in the shallowest sandy areas. Polychaetes and Molluscs alternatively dominate the endofauna. Sedentary Polychaetes are well represented mostly by the families of Spionidae (*Prionospio sp.*, *Aonides oxycephala*), Maldanidae (*Axiothella sp.*), Capitellidae (*Dasybranchus* and *Notomastus*) and Terebellidae. A few errant species live in the sediments ; they belong to the families of Glyceridae, Eunicidae and Nephtyidae. Molluscs are essentially little bivalves like Tellinidae but some carnivorous gastropods exist (Naticidae, Strombidae). Among Echinoderms, only a few ophiuroids may be encountered. Very motile crustaceans as Portunid crabs may bury in sediments. Lancelets are locally abundant, especially in coarse sands. Small conical mounds disrupting the sediment surface are evidences of the presence of mud-shrimps. Their density is quite high, approximately 15 mounds per ten square meters. Mounds can be as large as 50 cm diameter on bottom of deep zones.

Stretches of hard bottom are found down to a 20 m depth. They are often restricted to areas of a few square meters but around the largest pinnacle reefs, they can cover areas of hundreds of square meters. Coral communities are made up of either multispecific patches of *Porites lobata*, *Psammocora* sp., *Montipora* sp. *Astreopora* sp., or paucispecific bunches of *Acropora* spp.. Macroalgae, particularly species of *Halimeda*, are often found among the corals.

Pinnacle reefs

The pinnacle reefs of Tikehau cover only a few percent of the lagoon bottom area but concentrate a great biological diversity, harbouring a wealth of various organisms. The **upper zone** (0-2 m) can be emergent at low tide. The center of the largest pinnacle reefs is rugged with sediment and rubble, colonized by algae *Halimeda*, *Pocockiella*, *Caulerpa*, *Padina* and *Lobophora*. On the windward side, very large colonies (6 to 8 meters) of *Porites lutea* and *Millepora platyphylla* grow along with a few *Pocillipora meandrina* and *Acropora abrotanoides*. The leeward side supports branched colonies dominated by *Acropora variabilis*, *A. hyacinthus*, *A. hemprichi* and *Montipora* spp..

The motile cryptofauna of the upper zone is rich and dominated by Molluscs. Borers are rare.

The bottom of the **middle zone** (2-6 m) is largely a rocky substrate with shelves on which considerable quantities of sediment and rubble are retained, promoting the development of *Halimeda* and *Caulerpa* algal flat. Some coral heads of *Montipora verrucosa*, *Astreopora* sp., *Psammocora* sp., *Porites lobata*, *Platygyra daedalea* and *Pavona varians* intersperse among sediment stretches.

Cryptofauna abundance decreases somewhat, being still dominated by Molluscs. Boring invertebrates, mostly Molluscs and Sipunculids, represent almost 40 % of the total biomass. The important sediment deposition in this zone precludes the development of any significant sessile fauna.

The **lower zone** (6-15 m) of the pinnacle reef is covered by coral patches of *Montipora verrucosa*, *Stylocoenilla* sp., *Platygyra daedalea* and branched forms of *Acropora formosa*, *Stylophora pistillata* and *Favia favius*. Below 15 m, coral colonies vanish under the sediment.

BIOLOGICAL COMMUNITIES OF MORPHOLOGICAL DISCONTINUITIES

The pass

Numerous live coral ridges oriented parallel to the pass axis are scattered over the bottom of the pass. These colonies are characterized by an outstanding development of *Pocillipora* (*P. meandrina*, *P. verrucosa*, *P. eydouxi*, *P. damicornis*) measuring up to 3 m. Live coral coverage rate is about 80 % and reaches 100 % alongshore. Small colonies of *Leptastrea purpurea*, *Montipora* sp. *Fungia fungites*, *F. scutaria* and *Millepora platyphylla* are found protected from current on the flagstone between ridges.

Algae and invertebrates are rare in the pass owing to extremely rough current conditions. Some sponges (*Aurora* sp.), beche-de-mer (*Thelenotia ananas*) or Asterids settled there nonetheless.

Hoa

The seaward bare bottom of *hoa* is colonized by a great number of *Cerithium alveolus* and often bored by numerous lithophagid. The top of many dead coral blocks is covered with the black Cyanophyceae *Hassalia byssoides*. Pink sands rich in Cyanophyceae and bacteria have accumulated alongside the edge of the channel. Coral patches of *Porites lobata*, *Leptastrea purpurea*, *Porites* cf *andrewsi* and *Platygyra daedalea* appear lagoonward, downcurrent of the reef where sediment overwash is weaker. Echinoid species (*Echinometra*,

Echinothrix, *Diadema*) are concentrated in some numbers around these coral heads. Some bivalves *Tridacna* grow on top of them.

The motile cryptofauna dominated by Crustacean and Polychaetes is poor due to the paucity of suitable substrates.

OCEANOGRAPHY OF THE TIKEHAU LAGOON

The understanding of lagoonal water circulation is of primary interest for all biological and chemical studies carried out in the lagoon. Current data were recorded by four current meters set in the *hoa* of the windward reef, of the southwestern reef, of the northwestern reef, and in the pass. A tide gauge continually recorded water height in the lagoon. Modeling of the lagoon circulation was furthermore attempted.

Pass currents

The pass current is reversing. Its speed and timing are in phase with the tide. Data from Lenhardt (1991) show that the current speed usually ranges from 0 to 120 cm s⁻¹, increasing from 0 to maximum speed in about 3 hours and then decreasing to slack water in another 3 hours. The period of slack water in the pass is only a few minutes. When water level is high in the lagoon, the pass has a nearly continuous outflow. The current speed may exceed 3 m s⁻¹ under these frequent conditions and can last from 3 to 10 days.

The volume of transport of the pass current varies between neap and spring tide and more importantly with water height figures in the lagoon. Data available did not enable us to estimate the outflow through the pass but the average inflowing water transport was estimated to be 400 m³ s⁻¹ over a tidal cycle. It was furthermore estimated that the net transport volume of the pass is approximatively zero over a tidal cycle under normal lagoon water level conditions.

Hoa currents

Hoa currents or cross-reef currents involve a shallow flow over the reef margins. *Hoa* draw their flow from the outer reef flat and channelize the water off the reef into the lagoon between islands. *Hoa* currents are a result of breaking waves over the algal ridge on the windward reef. They vary in response to surf height and therefore to regional oceanographic patterns. Lenhardt (1991) pointed out that *Hoa* currents do not reverse direction at Tikehau, they always flow from ocean to lagoon even when water level is high in the lagoon.

Cross-reef currents do not flow in any well developed pattern as summarized in Table 4. The average current speed is low, generally less than 30 cm s⁻¹. It ranges from 0 to 120 cm s⁻¹ when high surf occurs. Current speed also varies seasonally, it is highest in *hoa* of the northwestern coast in summer of southern hemisphere while it is maximum in *hoa* of southeastern and southwestern reefs in winter. Table 4 shows that volume transport across the windward reef (southeast shore) accounts for more than 60 % of cross-reef water input whereas southwestern water transport accounts for 31 % and northwestern reef for 9 %. Average inflow per unit length of open coast (hereafter expressed lineic flow rate in m³ s⁻¹/m or m² s⁻¹) is an useful data. Its variations over the year are summarized in Fig. 11. Bases for calculation are : length of South-East coast 23 km; length of South-West coast 11 km; length of North-West coast 11 km.

Table 4 : Estimates of monthly inflowing current speed and associated water transport in hoa and pass of the Tikehau atoll. Sse : current speed in southeastern channels, Ssw : current speed in southwestern channels, Snw : current speed in northwestern channels, Tse, Tsw and Tnw : relevant water volume transport. Rt : residence time. Bases for calculation : equivalent section of southeastern reef front : 5000 m^2 , southwestern reef : 2600 m^2 , northwestern reef : 80 m^2 . Total inflow is the sum of inflow through pass and hoa.

Month	Cross-reef current and transport						Pass inflow	Total inflow	Rt
	Sse cm s^{-1}	Tse $\text{m}^3 \text{ s}^{-1}$	Ssw cm s^{-1}	Tsw $\text{m}^3 \text{ s}^{-1}$	Snw cm s^{-1}	Tnw $\text{m}^3 \text{ s}^{-1}$			
January	5.5	270	2.5	65	18	15	260	600	
February	3.0	140	3	75	21	18	180	400	230
March			4	100	17	14	150		
April			7.5	200	28	18	250		
May	15	800	10.5	280	9	7	100	1200	
June	20	1000	6	160	13	11	70	1200	105
July	11	550	7.5	190	3	2	100	900	

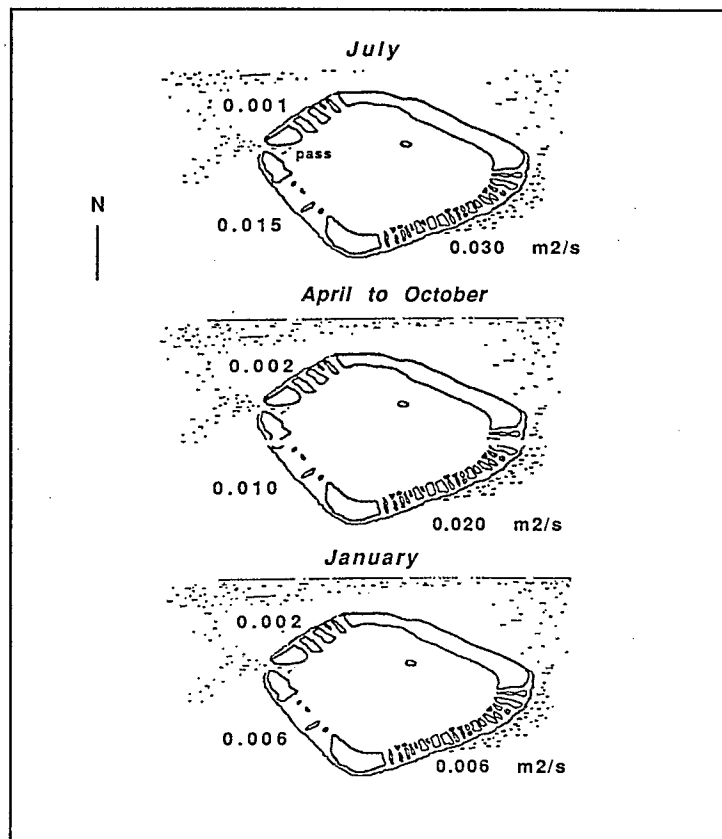


Fig 11 : Variations of lineic flow rate through *hoa* of Tikehau over the year.

Lagoon currents

Suspended acoustic drifter releases at a 4 m depth, in various points of the lagoon, show that the surface current in the lagoon is primarily wind-driven. The general surface drift is downwind (or roughly westerly) at a speed of approximately 1 % of the wind speed. Lagoon currents in the vicinity of pass and *hoa* is strongly altered by local current conditions. Current patterns were found to vary with depth. Current in the deep layers of the lagoon is upwind and flows at about one half of the surface current speed.

Water budget and residence times

Because the cross-reef currents never reverse, the volume transport over the reef through *hoa* represent a net input of water into the lagoon. Water furthermore flows into the lagoon from the pass. The water can flow out of the lagoon only from the pass. As the quantity of water entering the lagoon and the quantity of water exiting out of the lagoon must be balanced, the net inflow must exit as outflow out of the pass. Thus, water transport in the pass is indicative of water budget figures in the lagoon. The volume transport Q ($\text{m}^3 \text{s}^{-1}$) flushing in the pass was found to be a simple function of the difference in m between height of lagoon (h) and ocean (z) according to :

$$Q = \varepsilon 3000 \sqrt{|h-z|}$$

ε being -1 if water flows out of the lagoon, +1 if water flows in.

The average residence time of water in the lagoon can be estimated by dividing the lagoon volume (*i.e.* $10 \cdot 10^9 \text{ m}^3$) by the net rate of water input presented in Table 4. Under these very simple assumptions, the calculation yields a residence time of 230 days in summer and 105 days in winter, the yearly average value being 170 days. Because the water entering the southeastern lagoon must transit the entire lagoon before exiting through the pass and because it probably undergoes mixing by the wind-driven circulation, during that transit, the residence time of this part of the inflow will be longer. Conversely, water inflowing through northwestern channels will be expected to have a residence time shorter than the average. The residence times estimated at Tikehau can be compared to those estimated in the lagoon of a high island (Moorea, 6.5 hours) and in the lagoon of a closed atoll (Takapoto, between 4 and 5 years).

Circulation model

Lagoon circulation can be explained as a response to three sources of energy : the tide, the surf on the ocean reef and the wind. Lenhardt (unpublished data) proposed a bi-dimensional finite difference model using vertically integred Navier-Stockes equations to model the response of lagoon circulation to these three sources of energy taken separately then altogether.

Fig. 12a shows the residual tide-induced circulation in the lagoon. Tidal currents influence the flow of water only in the immediate area of the pass. Current speed is greater than 1 cm s^{-1} only within 4 km of the pass. Elsewhere in the lagoon, tidal current speed is very low (a few mm s^{-1}) and can hardly be measured. The tide generates a conspicuous clockwise local eddy south to the pass and a weak counter clockwise eddy north of the pass.

Fig. 12b shows the circulation induced by the surf on the windward reef. The oceanic water spreads into the lagoon, moving downwind toward the pass. Currents are significant only in the southern part of the lagoon with speed of about 1 cm s^{-1} . The northern part of the lagoon appears to be poorly affected by this circulation with modeled current speed less than 0.5 cm s^{-1} .

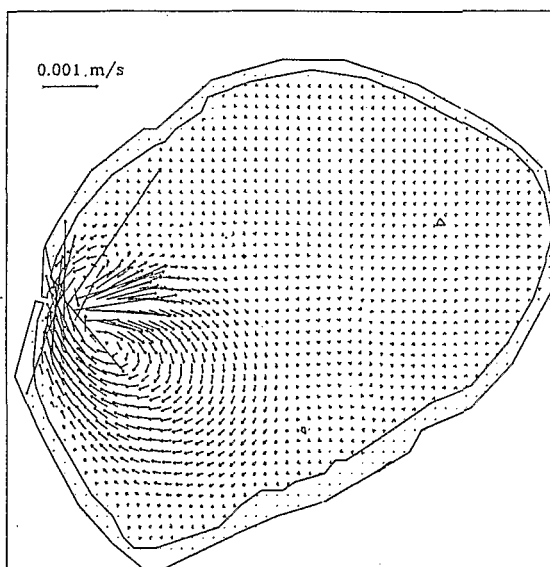


Fig 12a : Lagoon residual circulation generated by the tide at Tikehau (amplitude 10 cm ; arrows : current vectors).

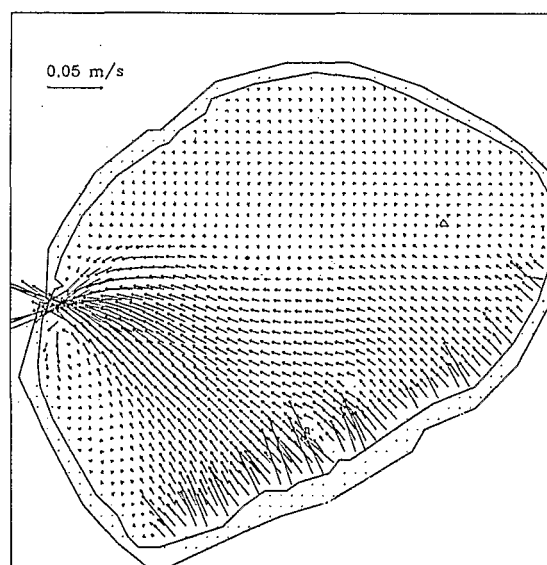


Fig 12b : Lagoon circulation generated by surf on the windward reef of Tikehau (lineic flowing current : $0,3 \text{ m}^3 \text{ s}^{-1} / \text{m}$).

Fig. 12c shows the circulation generated by a constant, unidirectional easterly windstress of 10 m s^{-1} (about 20 knots). Closed and impermeable boundaries were set to the atoll rim in order to avoid effects of water inflow for modelisation purposes. As measured by drogue releases, current speeds are strongly related to wind speeds (e.g. current speed is 1 to 2 % of the wind speed). In shallow part of the lagoon, the wind creates a downwind drift and an upwind drift in the deepest area. The wind-driven circulation induces two large conspicuous counter-rotating bodies of water, a counter clockwise northern eddy and another clockwise southern eddy.

Fig.12d shows the connection the effects of the three sources of energy, the tide, the surf and the wind. Given the low current speed of the tide-induced circulation, the connection of the three sources is actually the sum of the wind and surf-driven circulation. Fig. 12d shows a general downwind drift toward the pass in the southern lagoon and a weak water circulation in the northern lagoon.

The relevance of the model is somehow limited by the fact that it is bi-dimensionnal. The model gives only an average of the current speed and direction over the whole water layer and cannot take into account changes in current with depth. In all probability, and as confirmed by acoustic drogue releases and current speed records at various depths, the pattern of circulation in the lagoon must be a general downwind surface drift oriented toward the pass, balanced by an upwind low-depth drift. Moreover, the lagoon rim is closed neither to the pass nor windward. Large quantities of water are introduced along the windward edge and flushed out of the pass, and considerably modify wind-driven current patterns in the lagoon. Further circulation models should therefore be developed in three dimensions though information supplied by the bi-dimensional model meets biological research requirements.

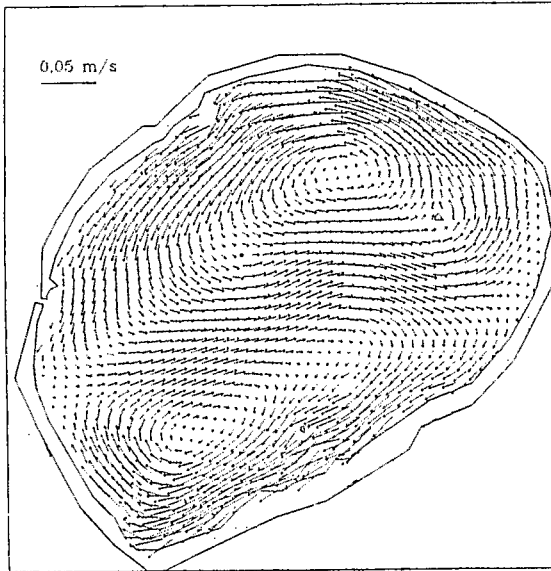


Fig 12c : Lagoon circulation generated by a constant 10 m s^{-1} easterly wind at Tikehau.

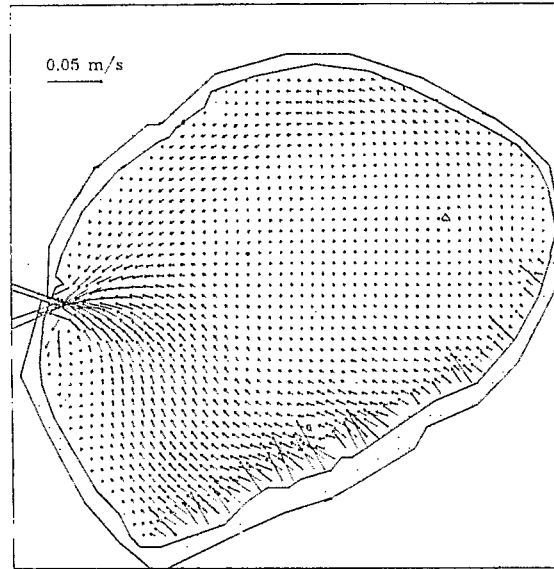


Fig. 12d : Lagoon circulation generated by the connection of the three sources of energy (tide : 10 cm, surf : $0,3 \text{ m}^3 \text{ s}^{-1}/\text{m}$ and wind : 4 m s^{-1}) at Tikehau.

AN EXAMPLE OF MAJOR DISTURBANCE : CYCLONES

About four cyclones per century are likely to occur in the Tuamotu archipelago but during the hot season 1982-1983, no less than four cyclones (Orama, Reva, Veena and William) and a tropical storm (Lisa) ravaged French Polynesia, causing severe damages to human installations, vegetation and coral reef ecosystems. This meteorological phenomenon of an outstanding frequency and intensity induced waves measuring more than 10 meters, a sea-level rising of 3 meters above predicted tidal levels, and a wind blowing in excess of 160 km per hour with gusting to over 200 km per hour. In particular, the cyclone Veena occurred in the vicinity of Tikehau between the 6th and 13th of April 1983. SCUBA Dive surveys carried out on the same transects before and after that disaster allow to assess the magnitude of damage caused to coral communities, and to explain destruction mechanisms. Two years later, SCUBA Dive surveys carried out on the same transects showed that time of recovery is very long. It will take at least five decades to have the coral communities in the state observed prior 1983.

Damage assessment

Damaged area (SD) is assessed by multiplying the length of destroyed reef (L) by 200 m (this value is the average length l of the outer slope between the depth of 0 and 90 m where hermatypic corals live). L is an estimation based on field observations made during 22 SCUBA Dive surveys around the atoll rim. In Tikehau, an area of 13 million square meters is estimated to have been damaged. This represents 80 % of the outer slope (Laboute, 1985). The area located windward of the atoll (from the north around to the south-west through the east) has been destroyed to a magnitude exceeding 90 %. Areas located north-north-west and west have been damaged to a magnitude varying between 30 and 80 %. The western side of the atoll remained intact.

Destruction mechanisms

Based on the outer slope morphology, three types of destruction mechanism were figured by Laboute (1985) and Harmelin-Vivien and Laboute (1986) following field observations. These theoretical processes are subject to variations with local details of the slope.

The reef flat is narrow, the fore reef area above a depth of 15 m and the slope very steep ($> 45^\circ$) as on the western coast of the atoll. Between 0 and 15 m, plate-like and branching madreporic species are abundant. They are of the genus of *Pocillipora*, *Acropora*, *Montipora*, *Astreopora*, *Favia* and *Pavona*. All those species are fragile and have been uprooted then reduced to rubble by the strength of the swell. The remains have contributed to destroy more resistant species by recurrent impacts and abrasion. Most of the remains have been thrown up on the reef flat.

At 12-15 m on the fore reef area, massive and heavy madreporic species like *Porites lobata* and *Montipora* prevail. As above, those species have been uprooted by the swell but since they were growing near or on high-angle substrates, remains rolled down the steep slopes weeping deeper colonies often more fragile, such as the plate-like *Pachyseris speciosa*, the dominant species below 40 m. Destructive effects of this underwater avalanche increased with depth as shown in Fig. 13. It is likely that coral blocks accumulated at some level between 300 and 500 m where the slope begins to flatten out, contributing to the formation of a detrital cone surrounding the atoll (Harmelin-Vivien and Laboute, 1986).

So far, this avalanche phenomenon has never been described elsewhere. All previous hurricane effect descriptions were done for islands without this typical steep outer slope and as a result, cyclone damages were thought to be limited to the upper level of the ecosystem.

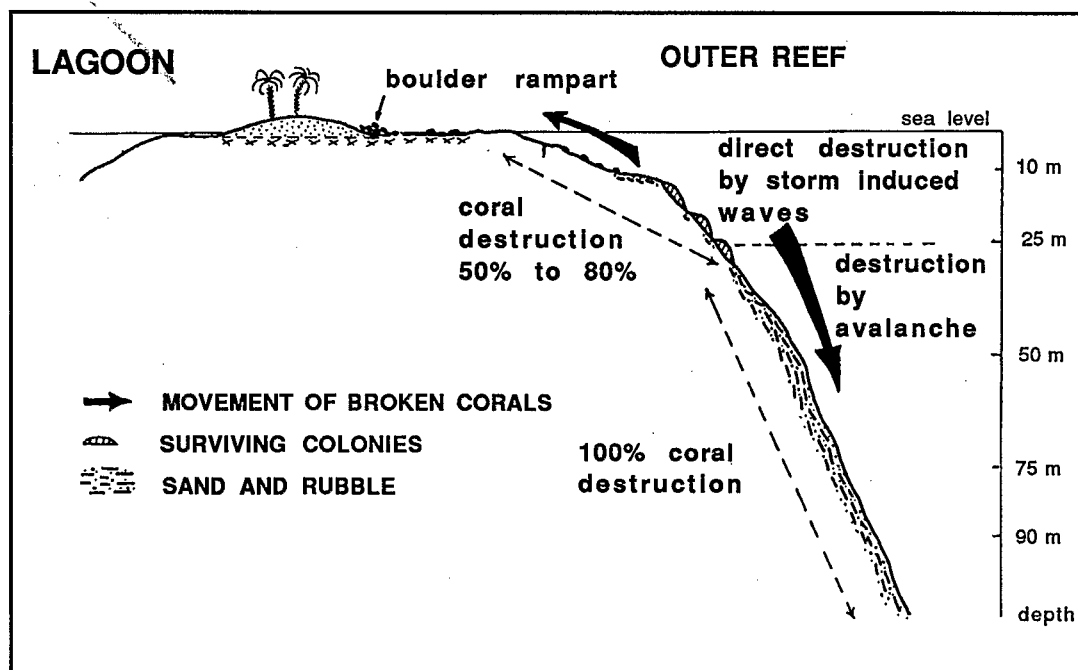


Fig. 13 : Cross section of the west coast of Tikehau with explanatory hypothesis of deep coral destruction : direct coral destruction by storm-induced waves occurred between the surface and 20 to 22 m depth. Most remains of broken coral rolled down the slope breaking fragile deeper colonies (after Harmelin-Vivien and Laboute, 1986).

The reef flat is large with a low slope gradient, the fore reef area deeper (25 m) and the outer slope less steep ($< 45^\circ$) as on the northern coast of the atoll. Coral colonies have been broken down to 15 m. Part of their remains were thrown up on the reef flat, the other part remaining on the same area. Many coral skeleton were covered by algae (genus *Microdyction* and calcareous algae). Massive species between 15 and 25 m have been uprooted too but given the distance to the steep slope, no avalanche occurred and therefore deeper colonies remained undamaged.

The reef flat is equally large or narrow but there is a depression or a very low-angled zone just before the fore reef area. Madreporic species located above a depth of 15 m have been destroyed following the previous process, but part of their remains have been trapped in that depression, preventing an avalanche. Thus, *Porites lobata* and *Pachyseris speciosa* colonies of deeper zones have been preserved.

Whatever the shape of the deep slope is a shallow fore reef coral community (composed of small colonies well adapted to withstand high energy level environment) suffered less than deeper reef communities. Coral destruction, estimated at 50 %, resulted primarily from abrasions by dislodged material, rolling remains and scouring sand.

Destruction mechanism in the pass and in the vicinity is of a particular nature. The Tikehau pass, located at the west of the atoll, was colonized by numerous species of the genus *Pocillopora* (*P. meandrina*, *P. verrucosa*, *P. eydouxi* and *P. damicornis*). The live coral covering rate was high, reaching 80 % to 100 % alongside the edge of the pass, between 2 and 8 meters. Those colonies remained intact as observed during SCUBA Dive surveys carried out six months after the cyclone Veena. More than one year later, all species were dead and skeleton still in place. This can be explained by the following observations : after the cyclone, the sea-level in the lagoon was high and currents constantly flowed out of the lagoon. Water was loaded with a considerable amount of suspended particulate matter and was, as a result, very turbid. Sedimentation was very important in the vicinity of the pass and therefore the amount of light energy reaching the bottom decreased dramatically and subsequently, corals died.

In all cases, most of the coral associated fauna (sessile fauna and fish) disappeared owing to a high mortality rate and to a lack of food and shelter.

Recovery processes

Coral resettlement became visible only one year after the cyclone in an area restricted to the upper 15 m as pointed out by Laboute (1985). In May 1984 *Pocillopora* (measuring between 2 and 4 cm) were dominating followed by encrusting forms of *Favia stelligera*, *Acropora* (size range : 2-7 cm), *Millepora platyphylla* and to some extent, small colonies of *Pavona minuta* and *Favia rotumana*. In the ravaged areas, no new madreporic colonies were seen below 15-20 m.

In February-March of 1985, an important madreporic and algae resettlement could be seen on the West coast of the atoll between 3 and 15 m. Species inventoried were : *Pocillopora* - obviously the most numerous - (size range : 1-20 cm), *Montipora caliculata*, *Montipora verrilli*, *Astreopora myriophthalma* (size range : 10-30 cm), *Favia stelligera* (size range : 2-12 cm), algae *Halimeda taenicola*, *Microdyction* and *Caulerpa uvilliana*.

In June of 1985, algae and madreporic species were still resettling on the outer slope especially between 3 and 15 m. Species were : *Pocillopora* (size range : 4-23 cm), two or three species of *Acropora* (4-20 cm), *Favia rotumana* (4-15 cm), *Porites lobata* (2-11 cm), *Pavona minuta* (5-9 cm), *Millepora platyphylla* (15-50 cm). Algae *Halimeda taenicola*, *Microdyction* and *Caulerpa uvilliana* were as abundant as before the cyclone. In the area partly damaged and below a depth of 15 m, madreporic resettlement seemed to be faster owing to the presence of some sparse colonies which survived the cyclone. For instance :

At 20 m *Acropora robusta* was 60 cm large but still very encrusting except on its edge, *Favia stelligera* numerous in some place (size range : 10-40 cm), sparse *Porites lobata* (6-17 cm).

At 30 m, numerous *Fungia fungites* (size range : 8-10 cm), *Millepora platyphylla* as large as 1 m but still thin and encrusting.

At 40 m, *Astreopora myriophthalma* measuring between 8 and 35 cm, sparse 17 cm *Porites lobata* very thin which had settled on previous base of same species.

At 50 m, rare *Fungia* sp. of 3 cm and *Pachyseris speciosa* (size range : 4-7 cm).

The impact of cyclones on fish fauna has been studied in detail and the results are presented in a later number of this issue.

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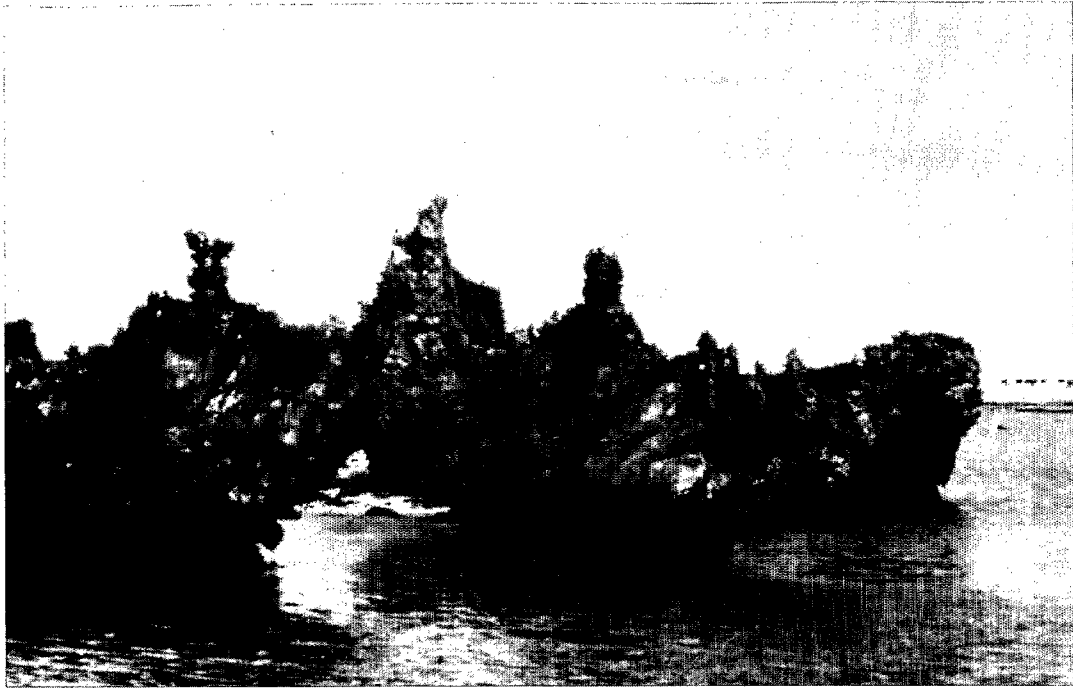


Plate 1 : Uplifted reefs, locally known as "FEO", are distributed along the northern coast of the atoll. Some of them, basally notched, may be seen on the outer reef flat. (Photo Intes)



Plate 2 : The marshy depression is covered with the cyperaceous assemblage dominated by *Cladium jamaicense*. (Photo Intes)



Plate 3 : Local popular game of javelin throwing. (Photo Intes)



Plate 4 : The spur and groove zone (eastern coast, 4 m). (Photo Laboute)



Plate 5 : The ocean water flows into the lagoon through shallow channels called "Hoa". (Photo Intes)

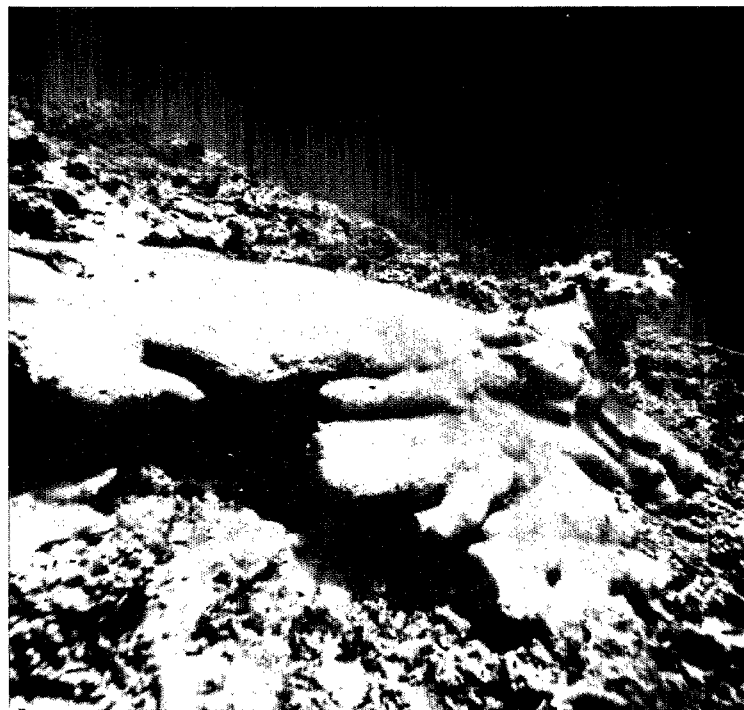


Plate 6 : A large *Acropora* colony overturned by the wave action induced by the hurricane "Veena" in April 1983 (eastern outer slope, 8 m). (Photo Laboute)



Plate 7 : The avalanche effect may destroy 100% of the corals of the outer slope (eastern outer slope, 22 m). (Photo Laboute)



Plate 8 : Recolonisation of the fore reef platform two years after hurricane "Veena" (eastern coast, 8 m). (Photo Laboute)

ATOLL RESEARCH BULLETIN

NO. 415

TIKEHAU

AN ATOLL OF THE TUAMOTU ARCHIPELAGO (FRENCH POLYNESIA)

**PART I. ENVIRONMENT AND BIOTA OF THE TIKEHAU (TUAMOTU ARCHIPELAGO,
FRENCH POLYNESIA)
BY A. INTES AND B. CAILLART**

**PART II. NUTRIENTS, PARTICULATE ORGANIC MATTER, AND PLANKTONIC AND
BENTHIC PRODUCTION OF THE TIKEHAU ATOLL (TUAMOTU ARCHIPELAGO,
FRENCH POLYNESIA)
BY C.J. CHARPY ROUBAUD AND L. CHARPY**

**PART III. REEF FISH COMMUNITIES AND FISHERY YIELDS OF TIKEHAU ATOLL
(TUAMOTU ARCHIPELAGO, FRENCH POLYNESIA)
BY B. CAILLART, M.L. HARMELIN-VIVIEN, R. GALZIN, AND E. MORIZE**

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