ATOLL RESEARCH BULLETIN

NO. 452

INVESTIGATIONS ON THE SOFT BOTTOM BENTHOS IN A SOUTHWEST PACIFIC ATOLL LAGOON (UVEA, NEW CALEDONIA)

BY

CLAIRE GARRIGUE, JACQUES CLAVIER, AND CHRISTOPHE CHEVILLON

ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D.C., U.S.A.
SEPTEMBER 1998

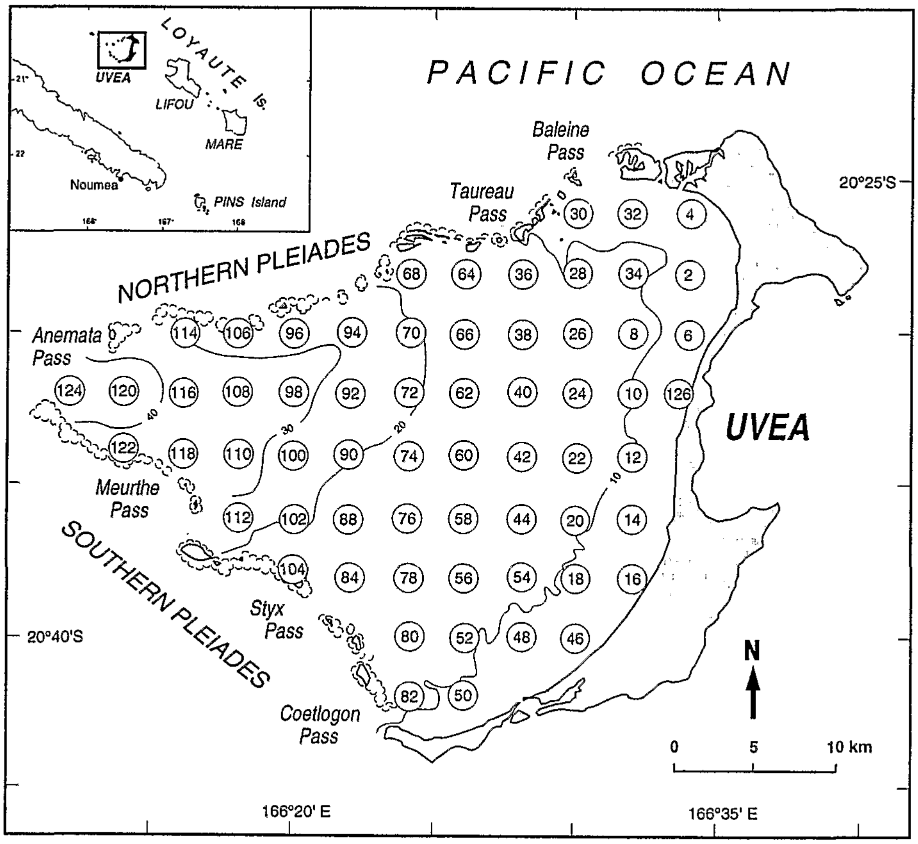

Figure 1. Location of the stations in Uvea Atoll.

INVESTIGATIONS ON THE SOFT BOTTOM BENTHOS IN A SOUTHWEST PACIFIC ATOLL LAGOON (UVEA, NEW CALEDONIA)

BY

Claire GARRIGUE[1], Jacques CLAVIER[2], and Christophe CHEVILLON[1]

ABSTRACT

Microbenthos and macrobenthos were quantitatively studied at 62 stations distributed regularly over the Uvea Atoll lagoon (850 km^2). Sampling was performed using both SCUBA and a 0.1 m^2 Smith McIntyre grab. Mean estimates of ATP, chlorophyll *a* and phaeopigments were 297.3 ng/cm^2, 77.01 mg/m^2 and 35.28 mg/m^2 respectively. The mean macrobenthic biomass was 4.14 gAFDW/m^2 of which the macrophytobenthos accounts for 39%. The benthic biomass decreased from the coast to the deepest parts of the lagoon. Macrophytes were most abundant in the coastal area and became progressively scarcer with increasing depth. By comparison, sessile species dominated on hard substrates in intermediate and deep zones. The abundance of the surface-deposit feeder group, that dominated the trophic structure of zoobenthos (33% of the macrofauna biomass), could be explained by a microphytic biomass six times higher than macrophytobenthic one in terms of carbon. Carnivores (32%) were mainly represented by necrophagous species, and filter-feeders (27%) by bivalves. Herbivores were rare. Four main benthic communities were identified on the basis of their macrobenthic assemblages using a Detrended Correspondence analysis. They corresponded to (1) a coastal zone, with the highest mud percentage in sediments, (2) an intermediate zone, with moderate depth and dominated by hard substrates, (3) a back reef zone, with thick sand layers, and (4) a deep zone dominated by hard substrates. Relative distribution of the trophic groups varied according to the different zones and suggests distinct functional characteristics for the different benthic assemblages. From a biogeographic point of view, this study highlighted the richness of the Uvea Atoll lagoon in terms of benthic species and biomass, compared to other central Pacific atoll lagoons.

INTRODUCTION

In coral reef areas most studies target community structure of the hard bottoms, focusing on the reef itself and the external slope surroundings. However, the soft bottoms, predominantly made up of carbonate sand and gravel, cover large surfaces and constitute the habitat of numerous organisms that are important in the coral ecosystem and cannot be neglected (Alongi, 1990 ; Jones et al., 1990). Of the studies

[1] ORSTOM B.P. A5, Nouméa, 98845 New Caledonia, South Pacific
[2] ORSTOM B.P. 70, 29280 Plouzané, France
Manuscript received 25 March 1998; revised 1 July 1998

carried out on atolls, very few have investigated soft-bottom benthic communities of the lagoon.

Of the few atolls in the southwest Pacific several belong to the Territory of New Caledonia : Uvea, Huon and Surprise in the north, and Chesterfield and Bellona in the west. Previous scientific data on these atolls are scarce. Some geology, geomorphology and sedimentology reports, and some descriptions and faunistic inventories can be found (Richer de Forges and Bargibant, 1985 ; Clavier and Garrigue, 1990 ; Richer de Forges, 1991; Chevillon et al., 1992 ; Chevillon, 1996), but the characteristics and communities of the soft bottoms of the lagoon are unknown.

In the present study we test the hypothesis that richness in terms of taxa and biomass is greater than in that found in central and eastern Pacific islands according to the biogeographic species dispersion theory (Eckman, 1953). More over due to the physical structure of this atoll situated on the slope of the lithospheric bulge (Dubois et al., 1977) we hypothesize that the spatial distribution of organisms will be different than that observed in a typical atoll. As the test, the composition, structure and biomass of the macrobenthos will be used. Other biological parameters such as ATP and photosynthetic pigment content in the sediments will be estimated in order to evaluate the quantity of micro + meiobenthos and microphytobenthos, respectively.

MATERIAL AND METHODS

a. Study site

Uvea Atoll and its ''satellite'', Beautemps-Beaupré atoll, constitute the northern part of the Loyalty Archipelago, in the north east of New Caledonia. Uvea lagoon forms a vast equilateral triangle the sides of which are about 35 nautical miles long (Fig.1). It is bounded by the Northern and Southern Pleiades, a group of low coral islands set on top of a discontinuous barrier reef, and eastward by the main calcareaous island of Uvea. The lagoon is open to the ocean by numerous passes. Due to its situation on the slope of the lithospheric bulge (Dubois et al., 1977) the bottom of the lagoon slopes slightly westward reaching a maximum depth of about 40 m near Anemata Pass. The mean depth is 19 m. Hard susbtrates consist of a fairly smooth limestone tab with scattered small coral structures. Sediments are always of a light colour, have a high carbonate content, and a low percentage of mud. Sediment thickness is generally low with a mean depth of 5.4 cm and an average of 3.83% organic matter content (Chevillon et al., 1992 ; Chevillon, 1996).

The benthos was sampled from the *R.V. ALIS* during two cruises (August and September) in 1991. The zones investigated zone cover an area of 850 km². The study focused on lagoon bottoms, except for coral structures that represent only a small part of the total area (<5%). Sixty-two sampling stations were distributed regularly over a 2 nautical mile grid (Fig.1). Three benthic compartments were surveyed : the "small food web" (meio + microbenthos), the microphytobenthos and the macrobenthos (plant and animal benthos).

b. Sampling and analysis

Meio and microbenthos. ATP (Adenosin Triphosphate) is considered to be an estimate of living or metabolically active biomass (Pamatmat et al., 1981). We assumed that ATP is proportional to the "small food web" biomass (Chardy and Clavier, 1988). For convenience, we grouped under this category all the organisms smaller than 2 mm. This category included that part of the macrobenthos retained by a 1 mm mesh sieve but passing through a 2 mm mesh sa well as the meiobenthos and the microbenthos. Larger organisms can easily be seen and were removed from sediment cores prior to ATP extraction. Five 5.31 cm² cores were randomly collected by SCUBA at each sampling station except stations 112 and 124 where the sediment was too thin. On collection the top cm of each core was immediately and carefully separated. Extraction was accomplished with 10 ml of boiling NaHCO3 solution (0.1 M) (Bancroft et al., 1976), the extract was frozen for later analysis using the bioluminescence method (Strehler and Totter, 1952). The results were expressed in ng/cm².

Microphytobenthos. Biomass was indirectly assessed through measurement of sedimentary photosynthetic pigments, chlorophyll *a* and phaeopigments. Five 5.31 cm² cores were hand-collected by SCUBA at each sampling station. The top cm was carefully separated and frozen in darkness. According to the methods of Garrigue and Di Matteo (1991), the samples were later lyophilised and pigments were extracted with 90% acetone during an 18 to 24 h period. After filtration of the extract, optical densities were assessed using a spectrophotometer at 750 and 665 nm, both prior to and after acidification with 0.5N HCl. Lorenzen's (1967) equations were used to calculate functional chlorophyll *a* and phaeopigment concentrations. The results were expressed in mg/m².

Macrobenthos. Macrofauna (2 to 20 mm) and macroflora were sampled using a Smith McIntyre grab weighted down with an additional 60 kg of lead ballast. This gear collects the sediment from a 0.1 m² area. The depression left in the sediment is rectangular in shape, while the bite profile is elliptical with a maximal depth of 13 cm (Clavier, 1982). Zones with sediment layers greater than 10 cm were present in only 15% of the lagoon area, whereas thick sediment areas (>20 cm), where large organisms can be deeply burrowed, were seldom found and were mainly restricted to the north-western part of the lagoon (Chevillon et al., 1992). Thus, we consider that our sampling collected most of the benthic organisms and that biomass values are representative of the lagoon. A sampling unit of 1 m² area was collected using a 0.1 m² grab dropped ten times. The boat was anchored at the bow and was able to swing under the influence of wind. The 10 grab samples from the same station were combined and passed through 20, 5 and 2 mm mesh stacked sieves. On board, organisms were separated from the substrate, sorted by major taxonomic groups and preserved in 10% formalin neutralised with borax.

Epibenthic megafauna (> 20 mm) and large macrophytes were sampled using SCUBA. A 50 m rope was uncoiled on the bottom. The divers, using a 1 m pole, collected all large living organisms found to 1 m on each side of the rope, except those associated with coral structures. The resulting total area covered 100 m². Samples were frozen. In the laboratory, taxonomic determinations were carried out as precisely as possible using the available literature. The results per station have been expressed as number of taxa per sampling station and as densities (number of individuals per m² for each identified taxon). Dry weights were measured following oven-drying (60°C) to constant weight, and ash weight was measured after combustion at 550°C for 3 h. The ash free dry weight is the difference between these two values. Macrobenthic biomass was expressed in grams of ash free dry weight per m² (gAFDW/m²). These methods are similar to those used by Chardy et al. (1988) and Chardy and Clavier (1988) for the study of New Caledonia's SW lagoon macrobenthos.

The macrobenthic biomass was assessed for the whole lagoon and for each community. Calculations were first carried out on pooled data and then by taxonomic group. We considered the following categories : macrophytes, gastropods, bivalves, sponges, crustaceans and echinoderms. Other taxa were grouped as "others". Data were then organised by trophic groups according to the Chardy and Clavier (1988) classification, i.e. primary producers (macrophytes) (PP); suspension-feeders (S) mainly comprising sponges and filter bivalves; "deposit-feeders" divided into surface deposit-feeders (SDF) that take their food from the water-sediment interface, and deposit-swallowers (DS) that ingest the sediment, herbivores (H) feeding on macrophytes ; and carnivores (C) comprising both predators and necrophagous species.

*c. **Data analysis***

At the same time as the epibenthic megafauna sampling, the hard bottom cover was estimated at each station with a 10% precision according to the number of 0.1 m² grabs that were free of sediments. Because samples used for ATP and photosynthetic pigments measures were only taken from soft sediments, the results were amended to account for the percentage of hard bottom cover. Therefore the values calculated for ATP and photosynthetic pigments are over-estimated as meio, microbenthos or microphytobenthos were not sampled from hard substrate.

In order to use the floral and faunal data, the densities of the taxa were coded into 5 classes, prior to analysis (Chardy et al., 1988). We omitted 148 taxa that were recorded only once or twice in our sampling, except those with more than 3 ind/m². A data matrix was then subjected to an ordination in reduced space in order to (1) identify the main benthic communities and to (2) determine the relationships between communities and environmental parameters. We used the "detrended correspondence analysis" (DECORANA), a variant of reciprocal averaging described by Hill (1979) and Hill and Gauch (1980). This method, previously used to define benthic assemblages (Marchant, 1990 ; Alongi and Christoffersen, 1992), allows the horseshoe effect to be avoided (Gauch, 1982). Stepwise multiple linear regression between stations (dependent variable) and environmental parameters (predictor variables) (Sokal and Rohlf, 1981) was then applied to interpret this distribution. Means of the biotic parameters (ATP and photosynthetic pigments) were calculated for each community. The homogeneity of means was tested using ANOVA and an *a posteriori* test (LSD) after verification of the normality of data (Shapiro and Wilk, 1965) and homogeneity of variances (Hartley, 1962), was performed.

RESULTS

a. Micro and meiobenthos and microphytobenthos.

The contents in the top cm of sediment for these 3 parameters are presented in Table 1. They are not evenly distributed within the lagoon ; the highest concentrations were observed on the eastern part of the lagoon and the lowest concentrations occurred near the Southern Pleiades.

Table 1. Mean and range of biological parameters (S.E. = standard error ; N = number of samples). ATP is expressed in ng/cm²; Chlorophyll *a* and Phaeopigments are expressed in mg/m².

Biological parameters	Range (min. - max.)	Mean	S.E.	N
ATP	5.0 - 620.5	297.3	21.5	60
Chlorophyll *a*	2.19 - 267.80	77.01	6.09	60
Phaeopigments	1.69 - 86.97	35.28	2.96	60
Number of taxa per sampling station	0 - 89	27.56	1.65	62
Biomass	0 - 63.48	4.14	1.03	62
Macrophytobenthic biomass	0 - 49.09	1.63	0.81	62
Macrozoobenthic biomass	0 - 14.40	2.51	0.32	62

For the correlation between these parameters and the environmental ones, see Table 2.

b. Macrobenthos.

Numerical analysis of taxa. A total of 3699 individuals from 341 taxa (22 flora and 319 fauna) were identified in the Uvea Lagoon (Clavier et al., 1992). The number of taxa per sampling station and the densities are in Table 1. These two parameters follow a decreasing gradient east-west, from Uvea Island to Anemata Pass. The correlation with the environemental parameters are presented in Table 2. Mean diversity (Shannon and Weaver, 1949) is H'=3.96 bits/ind (S.E.=0.10) and equitability (Pielou, 1969) is E=0.87 (S.E.=0.01). The distribution of zoological groups is presented in Figure 2A.

Biomass. The mean biomass of the macrobenthos is 4.14 gAFDW/m² (S.E.=1.03 ; N=62). The plant matter, which accounts for 39% of this biomass (Table 1), is mainly dominated by green algae (85%) and Cyanophyceae (14%). The macrofauna biomass is dominated by molluscs (Fig.2B), in particular gastropods (77% of macrofauna biomass). The distribution of the macrobenthic biomass in the lagoon follows a decreasing gradient from east to west. A high macrozoobenthic biomass in the western part of the Northern Pleiades is due to the presence of a thick sediment area.

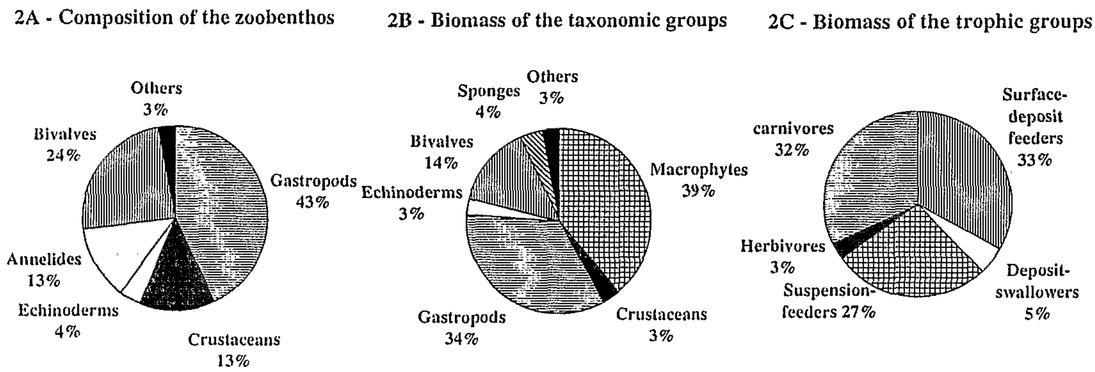

Figure 2. Composition and biomass of the benthos

While the high macrophytobenthic biomass in the centre of the lagoon, is a result of the high abundance of a cushion-shaped *Cyanophyceae spp.* at station 90. Animal biomass is significantly correlated with depth, and plant biomass with mud percentage (Table 2).

Table 2. Relations between biological parameters and environmental parameters (ATP in ng/cm² ; Chlorophyll *a* and Phaeopigments in mg/cm² ; Density in ind/m² ; Biomass in gAFDW/m² ; Mean grain size in mm ; % hard bottom = hard bottom cover percentage ; Depth in m ; Sediment thickness in cm ; % mud = percentage of grain size < 63 µm, r = coefficient of correlation, *P*= probability as follows : * : *P*<0.05, ** : *P*<0.01, ns : not significant).

	Mean grain size		% hard bottom		Depth		Sediment thickness		% mud	
	r	*P*	r	*P*	r	*P*	r	*P*	r	*P*
ATP	0.22	ns	-0.75	**	-0.20	ns	0.39	**	0.10	ns
Chlorophyll *a*	-0.20	ns	0.29	*	-0.02	ns	-0.17	ns	0.09	ns
Phaeopigments	-0.05	ns	0.42	**	-0.07	ns	-0.35	**	0.08	ns
Number of taxa per sampling station	0.36	**	-0.49	**	-0.50	**	0.35	**	0.30	*
Density	0.25	ns	-0.32	**	-0.47	**	0.15	ns	0.21	ns
Macrophytobenthic biomass	0.08	ns	0.06	ns	-0.23	ns	-0.08	ns	0.34	**
Macrozoobenthic biomass	0.04	ns	-0.22	ns	-0.36	**	0.02	ns	0.17	ns

Trophic structure. In the Uvea Lagoon, macrobenthic biomass is dominated by deposit-feeders (0.95 gAFDW/m² ; S.E.=0.18), particularly by surface deposit-feeders (Fig.2C). The gastropod *Cerithium sp.* (cf. *tenuifilosum*) represents more than 50% of the latter biomass. The dominant species of deposit-swallowers are the holothurians *Halodeima atra* and *Microthele nobilis* (95% of the total biomass). The second trophic group in the lagoon are carnivores (0.79 gAFDW/m², S.E.=0.13), dominated by necrophagous species (gastropods and pagurid crustaceans). Suspension-feeders (0.66 gAFDW/m², S.E. 0.17) include mainly bivalves (68%) and sponges (21%), the latter sessile species are found mostly on hard substrates. Bivalves comprise both scattered large species (*Trachycardium enode* and *Fimbria fimbriata)* and smaller but more abundant species (*Timoclea* [*Glycydonta*] *marica*, *Lunulicardia sp.*, *Circe sp.* and *Fulvia sp.*). Herbivores are unimportant (0.07 gAFDW/m², S.E.=0.02) comprising mainly three gastropod species (*Chrysostoma paradoxum*, *Monilea nucleus* and *Turbo chrysostoma*).

Identification of benthic communities. The results from the detrended correspondence analysis are presented in Figure 3. Axis 1 is significantly correlated to hard bottom cover percentage, depth and mean grain size while axis 2 is only significantly correlated to depth and sediment thickness (Table 3).

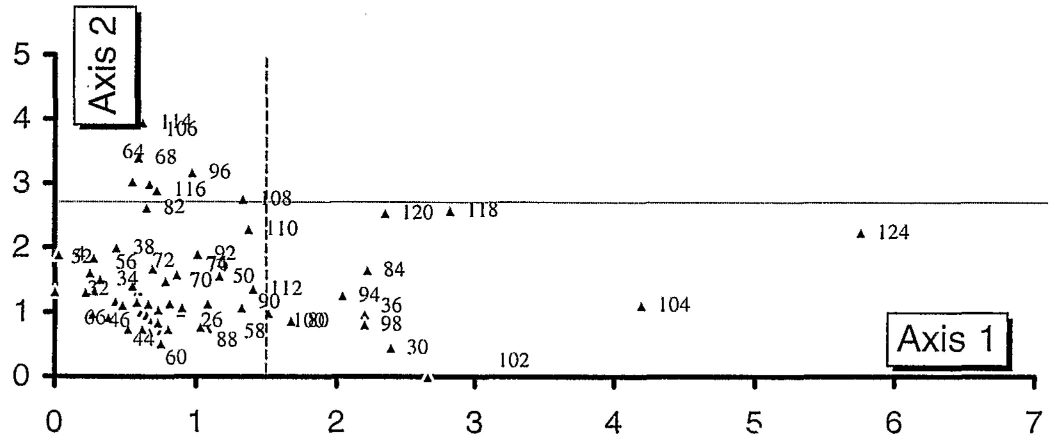

Figure 3. Results of the detrended correspondence analysis

In both cases predictor variables explain more than two thirds of the variance. Comparison of station distributions in the first factorial plane and their geographic positions allows four main groups to be identified (Figs. 3 and 4).

Table 3. Stepwise regression between station co-ordinates according to DECORANA analysis and environmental parameters. Only the parameters accepted by the regression are presented with their coefficient and t value. ** P< 0.01, r^2 is the coefficient of determination.

	Parameters	Coefficient	*t*	r^2
Axis I	Hard bottom cover percentage	0.015	6.30 **	
	Depth	0.048	6.28 **	
	Mean grain size	0.099	4.57 **	0.736
Axis II	Sediment thickness	0.058	8.47 **	
	Depth	0.037	5.60 **	0.680

Furthermore, the joint increase of station co-ordinates along the two axes corresponds to a depth gradient related to the distance from the Uvea coast line. Each group can be distinguished by the characteristics of the environmental and biotic parameters (Table 4).Group I corresponds to shallow areas, with a relatively thin layer of medium to coarse sand. Group II mostly corresponds to hard substrates at medium depths; when present, the sediment consists of very coarse sand. Group III also corresponds to intermediate depths but with a relatively thick medium-to-coarse sand cover. Lastly, Group IV corresponds to deep hard bottoms almost baren of sediments.

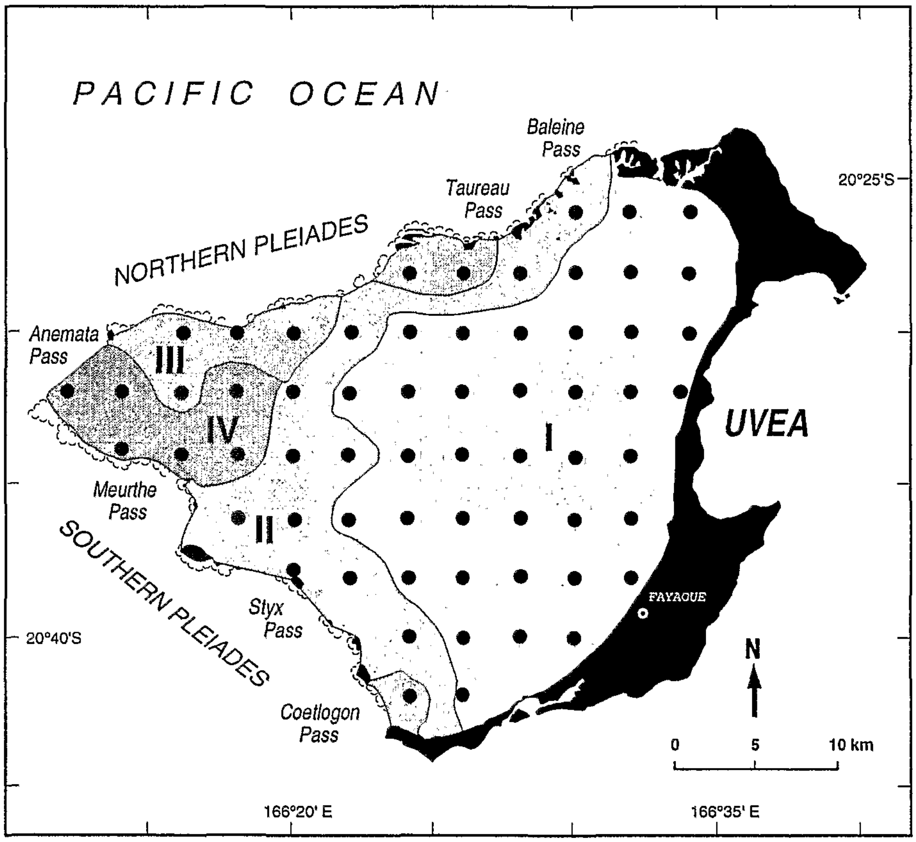

Figure 4. Location of the stations following tthe results of DECORANA analysis.

The means of biotic parameters in Group I are significantly greater than those of Group II, which are not significantly different from those calculated for Group IV characterised by a high percentage of hard ground cover. Group III has high mean values for ATP, chlorophyll *a* and organic matter. Because the organic matter content in sediment was measured from a 4 cm layer, its value is greatly dependent on the sediment thickness. This explains the low mean values for Groups II and IV. The distribution of the biomass by benthic community is heterogeneous (Table 4). Group I stations show the richest biomass. Algae are abundant (Fig.5) in particular *Halimeda melanesica* and *H. cylindracea.* The gastropod *Cerithium sp.* (cf. *tenuifilosum*) dominates animal biomass together with other gastropods such as *Vasum turbinellus* and *Rhinoclavis aspersa*, bivalves *Cardium enode* and *Arcopagia (Pinguitellina)* *robusta*, and the holothurian *Halodeima atra.* In Group II, plants only represent 25% of the total biomass, largely dominated by *Cyanophyceae* attached to hard substrate.

Table 4. Mean values of the environmental and biotic parameters for the four benthic communities defined using DECORANA (Surface in %; % mud = mud percentage; Mean grain size in mm; Sediment thickness in cm ; % hard bottom = hard bottom cover percentage; Depth in m ; ATP in ng/cm²; Chlorophyll *a* and Phaeopigments in mg/m²; Organic matter calculated on a maximum layer of sediment of 4 cm in g/m²; Macrobenthic biomass in g/m²; standard errors are in brackets).

	Group I	Group II	Group III	Group IV
Surface represented (%)	61	18	11	10
% mud	5.43	2.27	2.39	2.73
Mean grain size	0.38	3.97	0.40	1.40
Sediment thickness	4.34	2.31	24.79	2.92
% hard bottom	18.38	64.58	13.57	56.33
Depth	14.01	22.43	24.99	35.40
ATP	349.89 (23.05)	131.10 (42.40)	331.29 (71.77)	182.29 (54.21)
Chlorophyll *a*	93.33 (7.37)	42.99 (13.00)	58.37 (11.46)	47.12 (16.76)
Phaeopigments	42.74 (2.43)	19.42 (6.28)	23.58 (3.75)	26.67 (8.13)
Organic matter	1853 (117)	632 (196)	1795 (298)	982 (349)
Macrobenthic biomass	5.72 (1.63)	1.87 (0.33)	2.05	0.75 (0.04)

The animal community is similarly dominated by sessile species such as *Sarcophyton sp.* and sponges, together with the holothurian *Microthele nobilis* and the gastropod *Cerithium sp.* (cf. *tenuifilosum*). The biomass of Group III is almost entirely composed of macrofauna (Fig.5); algae are very scarce. Five species form more than 70% of the total biomass, i.e. the bivalves *Fimbria fimbriata* and *Trachycardium enode*, the gastropods *Rhinoclavis fasciata* and *Strombus gibberulus* and the fish *Callechelys sp.*. The biomass of Group IV is contributed to by sessile species such as the sponges *Pseudaxinissa cantharella* and *Spirastrella sp.*, and the cnidarian *Sarcophyton sp.*. Free living species are represented by the gastropods *Rhinoclavis fasciata, Cerithium sp.* (cf. *tenuifilosum*) and *Rhinoclavis articulata* distributed on hard substrates. Algae are almost absent. In terms of biomass, Group IV appears the poorest in the lagoon. Relative distribution of trophic-group biomass clearly differs among the four communities (Fig.6). Groups I, II and IV show a similar pattern of progressive decrease in the biomass of primary producers, carnivores and herbivores, and an opposite increase of suspension-feeder percentages. However, Group II is noteworthy for the relative proportions of the two deposit-feeder categories, surface deposit-feeders being abundant due to the holothurian *Microthele nobilis.* In comparison, Group III shows a different trophic structure, limited to three categories with a similar biomass : surface deposit-feeders, carnivores, and suspension-feeders and is intermediate between the Groups II and IV.

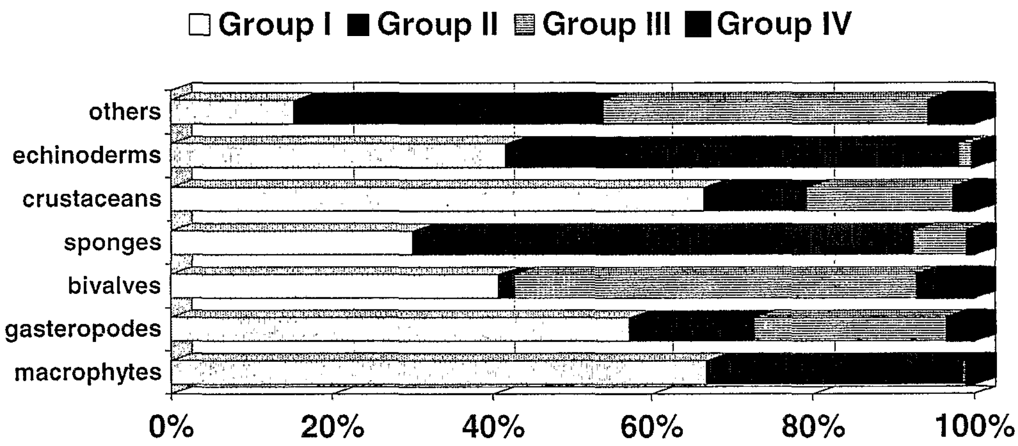

Figure 5. Biomass of the taxonomic groups for the benthic communities

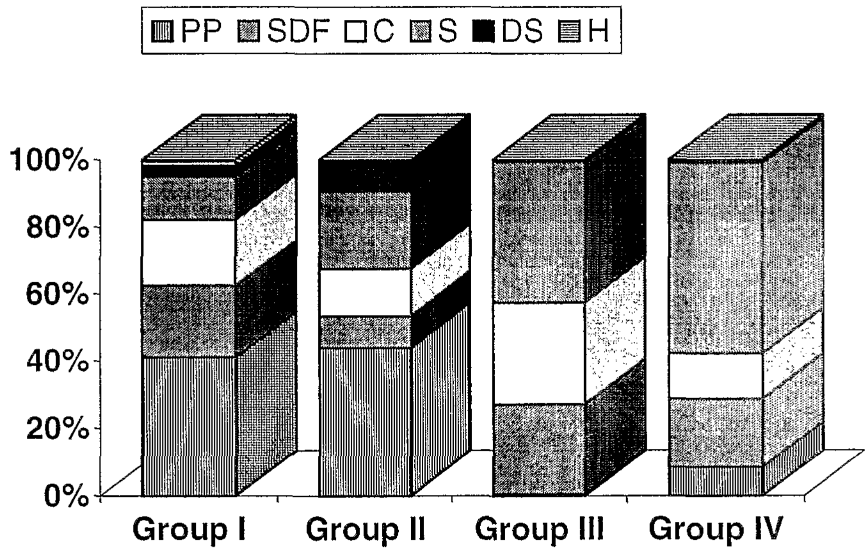

Figure 6. Biomass of the trophic groups for the benthic communities. (PP : primary producers ; DS : deposit-swallowers ; C : carnivores ; S : suspension-feeders ; SDF : surface deposit-feeders ; H : herbivores).

DISCUSSION

a. Micro and meiobenthos.

The mean ATP value in the Uvea Lagoon does not differ significantly from ATP values (294.1 ng/cm²) obtained for the same season and with similar methods by Garrigue et al. (1992) in the SW lagoon of New Caledonia (t test, P=0.95). However, our results are lower than Charpy-Roubaud's findings (1986) in Tikehau atoll (French

Polynesia) : 360 ng/cm², accepting a constant concentration over the top centimetre of sediment.

b. Microphytobenthos.

The mean values of chlorophyll *a* in Uvea Lagoon are significantly greater than the values found in the southwest lagoon of New Caledonia (47.16 mg/m²; Garrigue, 1995) and in the lagoon of Tikehau, French Polynesia (9.6 mg/m²; Charpy-Roubaud, 1988) (t test, P=0.005 and P<0.001, respectively). However, our findings are lower than the values found in Takapoto, French Polynesia (236 to 907 mg/m²; Sournia, 1976) for shallow foraminifera sands containing symbiontic algae. In contrast, the mean value of phaeopigments in Uvea Lagoon is significantly lower than that found in the southwest lagoon of New Caledonia (78.41 mg/m²) (t test, P<0.001). As a consequence of the high chlorophyll *a* content and the low phaeopigment content, there is a high percentage of chlorophyll *a* to total pigments (mean = 67.2%) in the lagoon of Uvea, this suggests a high microphytobenthic production. The importance of phaeopigment contents along Uvea island may be partly related to the disintigration of macroalgae that are found in great quantity at the coastal stations. The significant correlation between phaeopigment content, hard bottom cover and the sediment thickness indicate a preferential accumulation of seaweed detritus in areas of low sediment thickness. In this biotope, sand patches are located in substrate depressions or close to coral formations where organic debris concentrates. As there is no relation between organic matter content in the sediment and sediment thickness (r=0.03, P=0.82), we deduce that there is no accumulation of organic matter in these areas. Furthermore, ATP content and sediment thickness are significantly correlated. These facts suggest that organic matter is rapidly degraded by microbenthos and that areas with a thin sediment layer are the most important of the lagoon in terms of production.

c. Macrobenthos.

Using similar sampling methods, Chardy et al. (1987) identified 387 taxa from 35 stations in the SW lagoon of New Caledonia. This value is close to Uvea global richness. However, the number of taxa per sampling station (SW lagoon : 39.5 ; Uvea : 27.56) and the macrobenthic mean density (SW : 117 ind/m² ; Uvea : 59.66 ind/m²) were significantly greater in the SW lagoon (t tests, P<0.00 and P=0.01 respectively). Conversely, the mean diversity H' and the equitability E in Uvea Lagoon are slightly greater (Chardy et al., 1988). With 319 taxa, Uvea Lagoon has a high faunistic richness compared to that of Fiji's Great Astrolabe Lagoon (186 taxa; Clavier et al., 1996) and some Polynesian atolls such as Reao (less than 100 taxa ; Salvat, 1972), Tikehau (80 taxa ; Charpy and Charpy-Roubaud, 1994) or Mururoa (55 taxa ; Bablet et al., 1995). This richness could result from the biogeographic dispersion of species in the Pacific ocean decreasing from west to east (Eckman, 1953). In addition, Uvea Lagoon is of a greater size and due to numerous large passes (e.g. Anemata and Styx) is open to the oceanic circulation.

Hierarchy of the different zoological groups is fairly constant in Pacific soft bottom communities (Long and Poiner, 1994, Newell and Clavier, 1997, Baron et al., 1993), with a dominance of molluscs, followed by annelids and crustaceans. However, this composition is valid only for large macrofauna (>2mm), polychaetes being more abundant in 0.5-2 mm size class (Riddle, 1988, Newell and Clavier, 1997). The outstanding feature of Uvea Lagoon is the relative importance of gastropods species (Clavier et al., 1992).

The mean macrobenthic biomass in Uvea Lagoon is very similar to Fiji's Great Astrolabe Lagoon (4.70 gAFDW/m^2; Newell and Clavier, 1997) but almost six times smaller than that of the New Caledonia South West Lagoon (23.6 gAFDW/m^2; Chardy and Clavier, 1988). Conversely, macrobenthic biomass is higher than Central Pacific atolls : 0.009 to 2.04 gAFDW/m^2 in Mururoa Lagoon (Villiers, 1988) and 0.001 to 3.5 gAFDW/m^2 in Tikehau Lagoon (Bablet et al., 1995).

Taxonomic group biomass distributions, are the same in the three West Pacific lagoons. Of the macrofauna, molluscs dominate the biomass both in Tikehau, and in Uvea Lagoons whereas in Mururoa the polychaetes constitute the greatest part of the biomass with the molluscs representing just 10% of which only 2% are gastropods (Villiers, 1988). In Uvea the polychaetes are a minor group, and in Tikehau Lagoon they constitute only 9%. Two other minor zoological groups in Uvea, are important in Tikehau : the sipunculids (25%) and the sponges (27%) (Charpy and Charpy-Roubaud, 1994). The free-living cnidarian *Heteropsammia cochlea*, together with the commensal sipunculian *Aspidosiphon jukesi*, forms a major part of zoobenthic biomass in the SW lagoon of new Caledonia whereas they are seldom found in Uvea Lagoon.

The importance of the macrophytic primary producers is highlighted in the trophic structure of the Uvea Lagoon. Comprising roughly 40% of the overall macrobenthic biomass, they dominate the system. The same pattern has been found in Fiji's Great Astrolabe Lagoon and in the SW Lagoon of New Caledonia (Chardy and Clavier, 1988 ; Garrigue, 1995 ; Newell and Clavier, 1997). In the Central Pacific, the macrophytes represent a greater proportion of the total biomass in Tikehau lagoon (60 %). The primary produce group could be enlarged by adding the other categories of photosynthetic organisms : microphytobenthos, phytoplankton, endolithic algae and symbiotic algae. Endolithic algae, symbiotic algae and phytoplankton were not studied in the present work, however microphytobenthos were measured using benthic chlorophyll *a*.

To evaluate the relative importance of microphytobenthos to macrophytobenthos we have expressed the results in carbon, assuming that carbon represents 40% of the ash-free dry weight biomass (Steele, 1974) and that the ratio of carbon / chlorophyll *a* = 50 (Charpy and Charpy-Roubaud, 1990). From this evaluation, the biomass of microphytobenthos (3.85 gC/m^2) is six times greater than the biomass of macrophytobenthos (0.62 gC/m^2) in the Uvea Lagoon, whereas it represents only half of the macrophytobenthos (micro : 2.4 gC/m^2 and macro : 5.2 gC/m^2) in the SW Lagoon of New Caledonia (Garrigue, 1995). This is partly due to the scarcity of macrophytes in Uvea Lagoon but more specifically to the importance of the microphytobenthos on the bottom of Uvea Lagoon. The significance of microphytobenthos explains the importance of the surface deposit-feeders biomass, especially that of the gastropod *Cerithium sp.* (cf. *tenuifilosum*) that dominates this group. This species preferentially lives in areas with low sediment thickness and feeds on a microphytobenthic film that covers the substrate surface. Compared to the other trophic groups, the carnivores seem to be abundant, but their biomass represents only two-thirds of that measured in the SW Lagoon, where this group was considered to be of minor importance. The overabundance of necrophagous species compared to other benthic fauna suggests an exogenous input of organic matter such as decayed fishes from the lagoon.

The high occurrence of *Cyanophyceae* noticed during most of the investigations carried out on the lagoons (Chevalier et al., 1968 ; Colin, 1987 ; Intes and Caillart, 1994), suggests that microphytobenthos is a characteristic of the lagoons of the atoll. For example, one of the four communities has been described in Enewetak Lagoon as ''sand substrate with visible algal mat''. This mat can reach 1 m in diameter (Colin, 1987). At the same time, the great abundance of *Cerithidae* in the lagoon of Mururoa (Salvat and Renaud-Mornant, 1969), *Strombus luhuanus* in Enewetak (Colin, 1987) and the dominance of deposit-feeders in Tikehau lagoon (46% of biomass ; Charpy and Charpy-Roubaud, 1994) could suggest the importance of the role played by deposit-feeders.

CONCLUSIONS

Due to its situation on the slope of the lithospheric bulge Uvea Atoll presents a depth gradient that increases regularly from Uvea Island in the east to Anemata Pass on the west, and a thin layer of sediment associated with a high proportion of hard substrate. The decrease in the sediment thickness is probably a result of hydrodynamic turbulence coming from large passes that open widely to the surrounding ocean. These two phenomena could explain most of the observed structures. The spatial distributions of organisms were different than those observed in a typical atoll, the center of which constitute a sink where organisms are scarce. In Uvea, the main part of the benthos is found in the shallow waters close to the island. The deterioration of benthic communities follows a decrease of sediment thickness and an increase in depth. Our approach allows us to describe four main benthic communities in the Uvea Lagoon. Such a classification is essentially a convenient model of a more complex situation. In fact, sampling stations are distributed along gradients and their allocation to one group or another is sometimes uncertain.

Uvea Island and its lagoon exhibit the geomorphological characteristics of an atoll. From a sedimentological point of view, the sediment is exclusively carbonates with a low mud content (Chevillon et al., 1992 ; Chevillon, 1996). Biologically, numerous features allow the distinction between the lagoon of an atoll and a coastal lagoon that is under the influence of terrigenous inputs. Compared to the coastal SW Lagoon of New Caledonia, the macrobenthos of the Uvea Lagoon is both low in abundance and biomass, but the high percentage of active chlorophyll *a* suggests a high microphytobenthic production, which enters into the trophic system directly or indirectly via bacteriological transformation. It represents an important source of food for the deposit-feeders which could explain the preponderance of this trophic group in the trophic structure of the lagoon.

From a biogeographic point of view, this study demonstrates the richness of the lagoon of Uvea Atoll, in terms of benthic species and biomass, compared to other central Pacific atoll lagoons. For Uvea Lagoon itself, these results highlight the existence of an east to west gradient between Uvea Island and Anemata Pass.

ACKNOWLEDGEMENTS

Uvea Atoll is part of the Province Iles. This study was carried out under an agreement between ORSTOM, the State and Province Iles, as part of a multidisciplinary program on fish resources of the lagoon of Uvea. We thank the crew of *R. V. Alis*, the divers and the technicians for their help at sea.

REFERENCES

Alongi, D.A. 1990. The ecology of tropical soft-bottom benthic ecosystems. Oceanogr. Mar. Biol. Annu. Rev., *28*, 381-496.

Alongi, D.A. and P. Kristoffersen. 1992. Benthic infauna and organism-sediment relations in a shallow, tropical coastal area: influence of outwelled mangrove detritus and physical disturbance. Mar. Ecol. Progr. Ser., *81*, 229-245.

Bablet J.P., B. Goût and G. Goutiere. 1995. Les atolls de Mururoa at de Fangataufa (Polynésie Française). III. Le milieu vivant et son évolution. Direction des Centres d'expérimentations nucléaire. 306 p.

Bancroft K., E.A. Paule and W.J. Wiebe. 1976. The extraction and measurements of adenosine triphosphate. Limnol.Oceanogr., 1, 473-480.

Baron J. , J. Clavier and B.A. Thomassin. 1993. Structure and temporal fluctuations of two intertidal seagrass-bed communities in New Caledonia (SW Pacific Ocean). Mar. Biol., 117, 13-144.

Chardy P., J. Clavier, P. Gerard, P. Laboute, A. Martin and B. Richer De Forges. 1987. Etude quantitative des fonds meubles du lagon sud-ouest de Nouvelle Calédonie. Liste taxonomique, densités et biomasses. Noumea : ORSTOM. Rapp. Sci. Tech. Sci. Mer Biol. Mar., 44, 81 p.

Chardy P., C. Chevillon and J. Clavier. 1988. Major benthic communities of the southwest lagoon of New Caledonia. Coral Reefs, 7, 69-75.

Chardy P. and J. Clavier. 1988. Biomass and trophic structure of the macrobenthos in the southwest lagoon of New Caledonia. Mar. Biol., 99, 195-202.

Charpy-Roubaud C. 1986. Le microphytobenthos du lagon de Tikehau (archipel des Tuamotu Polynésie française): I. Biomasse (premiers résultats). Tahiti : ORSTOM. Notes Doc. Océanogr., 28, 1-49.

Charpy-Roubaud C.J. 1988. Production primaire des fonds meubles du lagon de Tikehau (atoll des Tuamotu, Polynésie française). Oceanologica Acta, 11, 241-248.

Charpy L.. and C. Charpy-Roubaud. 1990. Trophic structure and productivity of the lagoonal communities of Tikehau atoll (Tuamotu archipelago, French Polynesia). Hydrobiol., 207, 43-52.

Charpy L. and C. Charpy-Roubaud. 1994. Nutrients, particulate organic matter and planktonic and benthic production of the Tikehau atoll (Tuamotu Archipelago, French Polynesia). In An atoll of the Tuamotu archipelago (French Polynesia). Atoll Res. Bull., 415, 30 p.

Chevallier J.P., M. Denizot, J.L. Mougin, Y. Plessis and B. Salvat. 1968. Etude géomorphologique et bionomique de l'atoll de Mururoa (Tuamotu). Cah. Pac., 12, 1-144.

Chevillon C., J. Clavier and C. Garrigue. 1992. Preliminary data on the sediments of the Uvea lagoon (New Caledonia). Proc. 7th Int. Coral Reef Symp., 2, 1115-1120.

Chevillon C. 1996. Skeletal composition of modern lagoon sediments in New Caledonia : coral, a minor constituent. *Coral Reefs*, *15*, 199-207.

Clavier J. 1982. Efficacité comparées d'un carottier manoeuvré en plongée et de deux bennes, sur substrat de sables fins vaseux. Bulletin de la Société Scientifique de Bretagne, 55, 1-4.

Clavier J. and C. Garrigue. 1990. Etude quantitative du macrobenthos dans le lagon des îles Chesterfield. Liste taxonomique, densités et biomasses. Nouméa : ORSTOM. Rapp. Sci. Tech. Sci. Mer Biol. Mar., 59, 100 pp.

Clavier J., P. Newell, C. Garrigue, B. Richer de Forges and A. Di Matteo. 1996. Soft substrate macrobenthos of Fiji's Great Astrolabe lagoon. List of taxons, densities and their biomass. ORSTOM : Tahiti. Notes et Doc. Océanogr., 46, 17-46.

Clavier J., C. Garrigue, G. Bargibant, A. Di Matteo, P. Hamel, M. Kulbicki and R. Urbain. 1992. Etude quantitative du benthos dans le lagon d'Ouvéa. Liste taxonomique, densités et biomasses du macrobenthos, ATP, pigments photosynthétiques et matière organique dans le sédiment. Nouméa : ORSTOM. Rapp. Sci. Tech. Sci. Mer Biol. Mar., 64, 72 pp.

Colin P.L . 1987. Subtidal environments and ecology of Enewetak atoll. In The natural history of Enewetak atoll. I - The ecosystem : environments, biotas, and processes. United States Department of Energy, 91-138.

Dubois J., J. Launay, J. Récy and J. Marshall. 1977. New Hebrides trench:subduction rate from associated lithospheric bulge. Can. J. Earth Sci., 14, 250-255.

Eckman S. 1953. Zoogeography of the sea. Sidwick and Jackson Ltd, London, 417 pp.

Garrigue C. and A. Di Matteo. 1991. La biomasse végétale benthique du lagon sud-ouest de Nouvelle-Calédonie. Résultats bruts : liste taxonomique, biomasses, pigments chlorophylliens. Nouméa : ORSTOM. Arch. Sci. Mer Biol. Mar., 1, 143 pp.

Garrigue C., J. Clavier J, G. Boucher G, P. Gérard and J.L. Menou. 1992. Flux d'oxygène et de gaz carbonique à l'interface eau-sédiment dans le lagon sud-ouest de Nouvelle-Calédonie. Méthodes et recueil des données. Nouméa : ORSTOM. Rapp. sci. tech. Sci. Mer Biol. mar., 62, 21 pp.

Garrigue C. 1995. Macrophytes associations on the soft bottoms of the southwest lagoon of New Caledonia : description, structure and biomass. Bot. Mar., 38, 481-492.

Gauch H.G. 1982. Multivariate analysis in community ecology. Cambridge Studies in Ecology 1. Cambridge University Press, Cambridge, London, New York, New Rochelle, Melbourne, Sydney, 298 pp.

Hartley H.P. 1962. Analysis of variance. In : Ralston A, Wilf HS (eds.) Mathematical methods for digital computers, Vol 1. Wiley, New York, 221-230.

Hill M.O. 1979. DECORANA - A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ecology and systematics, Cornell University, Ithaca, New York, 14850, 52 pp.

Hill M.O. and H.G. Gauch. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio, 42, 47-58.

Intes A. and B. Caillart. 1994. Environment and biota of the Tikehau atoll (Tuamotu archipelago, French Polynesia). In An atoll of the Tuamotu archipelago (French Polynesia). Atoll Res. Bull., 415, 34 p.

Jones G.P., D.J. Ferell and P.F. Sale. 1990. Spatial pattern in the abundance and structure of mollusc populations in the soft sediments of a coral reef lagoon. Mar. Ecol. Prog. Ser., 62, 109-120.

Long B.G. and I.R. Poiner. 1994. Infauna benthic community structure and function in the Gulf of Carpentaria, Northern Australia . Austr. J. Mar. Freshwat. Res., 45, 293-316.

Lorenzen C.J. 1967. Determination of chlorophyll and pheo-pigments : spectrophotometric equations. Limnol. Oceanogr., 12, 343-346.

Marchant R. 1990. Robustness of classification and ordination techniques applied to macroinvertebrate communities from La Trobe river, Victoria. Austr. J. Mar. Freshwat. Res., 41, 493-504.

Newell P. and J. Clavier 1997. Quantitative structure of soft substrate macrobenthos of Fiji's Great Astrolabe lagoon. Proc. 8th Int. Coral Reef Symp. 1 : 455-458.

Pamatmat M.M., G. Graf, W. Bengtsson and C.S.Novak. 1981. Heat production, ATP concentration and electron transport activity of marine sediments. Mar. Ecol. Progr. Ser., 4, 135-143.

Pielou E.C. 1969. An introduction to mathematical ecology. Wiley-Interscience : New York (USA), 286 pp.

Richer de Forges B. and G. Bargibant. 1985. Le lagon nord de la Nouvelle-Calédonie les atolls de Huon et Surprise. Noumea : ORSTOM. Rapp. Sci. tech. Sci. Mer Biol. Mar., 37, 23pp.

Richer de Forges B. 1991. Les fonds meubles des lagons de Nouvelle-Calédonie : généralités et échantillonnages par dragages. *In* Richer de Forges B. (ed.) Etudes et Thèses ORSTOM : Paris. Le benthos des fonds meubles des lagons de Nouvelle-Calédonie, Vol. *1*, 7-148.

Riddle M.J. 1988. Patterns in the distribution of macrofaunal communities in coral reef sediments on the central Great Barrier Reef. Mar. Ecol. Prog. Ser., 47, 281-292.

Salvat B. 1972. La faune benthique du lagon de Reao (Tuamotu, Polynésie). Cah. Pac., 16, 31-109.

Salvat B. and J. Renaud-Mornant. 1969. Etude écologique du macrobenthos et du meiobenthos d'un fond sableux du lagon de Mururoa. Cah. Pac., 13, 159-179.

Shannon C.E. and W. Weaver. 1949. The mathematical theory of communication. Urbana Illinois Press (USA), 117 pp.

Shapiro S.S. and M.B. Wilk. 1965. An analysis of variance test for normality (complete samples). Biometrica, 52, 591-911.

Sokal R.R. and F.J. Rolf. 1981. Biometry. Freeman and company, New York, 859 pp.

Sournia A. 1976 Primary production of sands in the lagoon of an atoll and the role of Foraminiferan symbionts. Mar. Biol., 37, 29-32.

Steele J.H. 1974. The structure of marine ecosystems. Harvard University Press, Cambridge, Mass.

Strehler B.L. and J.R. Totter. 1952. Firefly luminescence in the study of energy transfer mechanism. I. Substrate and enzyme determination. Archs. Biochem. Biophys., 40, 28-41.

Villiers L. 1988. Density and biomass of macro - and meio-fauna in lagoon sands at Mururoa atoll, French Polynesia. Proc. 6th Int. Coral Reef Symp., 2, 45-51.