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Community structure of harpacticoid copepods in a tropical reef lagoon (Fangataufa Atoll - French Polynesia)

Harpacticoid copepods
Assemblages
Reef lagoon
French Polynesia

Copépodes harpacticoïdes
Peuplements
Lagon récifal
Polynésie française

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ABSTRACT

From the lagoon at Fangataufa Atoll, French Polynesia, forty-two species of harpacticoid copepods belonging to 21 genera were identified; over a third of them are new. The assemblages were largely dominated by epipsammic forms of the family Diosaccidae. Some endopsammic harpacticoids were found in deep water silty-sands, but mesopsammic forms were very rare. The harpacticoid community structure of the lagoon appears to be determined primarily by sediment granulometry as controlled by reef hydrodynamics. The harpacticoid copepod assemblages permit the identification of two major zones within the lagoon, namely the muddy deep central zone, and the inner sandy fringe at the periphery.

RÉSUMÉ

Structure de la communauté des copépodes harpacticoïdes dans un lagon récifal tropical (Atoll de Fangataufa - Polynésie française).

La composition des peuplements de copépodes harpacticoïdes a été étudiée dans le lagon de l'atoll de Fangataufa, Polynésie française. Quarante-deux espèces se répartissant dans 21 genres ont été identifiées, plus du tiers sont nouvelles. Les peuplements sont largement dominés par des formes épipsammiques de la famille des Diosaccidae. Quelques harpacticoïdes endopsammiques ont été trouvés dans les sables envasés profonds, alors que les formes mésopsammiques sont très rares. La structure de la communauté des harpacticoïdes dépend en grande partie de la granulométrie du sédiment, elle-même contrôlée par les conditions hydrodynamiques. Les peuplements de copépodes harpacticoïdes permettent d'identifier deux zones majeures à l'intérieur du lagon, à savoir : la zone centrale profonde envasée et la frange interne sableuse à la périphérie du lagon.

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INTRODUCTION

The ecology of harpacticoid copepod communities has been studied in a wide range of habitats, mostly in temperate and subtropical seas (Hicks and Coull, 1983). In contrast, little is known of harpacticoid copepods inhabiting carbonate sands in coral reefs. Previous studies of harpacticoids have focused on taxonomy (Sewell, 1940; Vervoort, 1964). The first attempts to analyse the composition and structure of harpacticoid communities in coral reefs were made by Coull (1970) on the Bermuda Platform and by Hartzband and Hummon (1974) in the U.S. Virgin Islands. More recently, Villiers *et al.* (1987) and Villiers (1988) published a study of the diversity of harpacticoids in a detailed account of Mururoa meiobenthos (French Polynesia).

This study focuses on the distribution of the benthic copepod assemblages in the lagoon of the Fangataufa atoll. We have attempted to determine the criteria governing the distribution of species in the studied area which differs from the lagoon of Mururoa by a very narrow pass linking it with the open sea. Harpacticoid copepod assemblages have a large number of species, high densities, no planktonic phases, a small size and morphological adaptations which allow them to take advantage of the microhabitats of the bottom.

Harpacticoids play an important trophic role in coral sands along the Australian Great Barrier Reef because of their numerical dominance, capacity to recycle nitrogen and high bacterial ingestion rates (Gray, 1985; Moriarty *et al.*, 1985). Furthermore, the meiofauna communities correspond well with macrobenthos communities (Govaere *et al.*, 1980) and can be a potential source of food for higher trophic levels, particularly the harpacticoid copepods for numerous larval, juvenile and small fishes (Bodiou and Villiers, 1979; Hicks and Coull, 1983; Morais and Bodiou, 1985; Alongi, 1989; Gee, 1989; Coull, 1990).

This work provides further information on the functioning of coral reef habitats in the Central Pacific and adds to our knowledge of reef lagoon ecology.

MATERIALS AND METHODS

Study area

The Fangataufa atoll is located south of the Tuamotu Archipelago (138° 43' W; 22° 14' S), about 1200 km south-east of Tahiti (French Polynesia). Prevailing winds in the area are from the east and the prevailing swells come from the south-west (Anonymous, 1985). The reef-crown is roughly rectangular in shape, with a perimeter of 28 km, maximum lagoon depth is about 45 m. The leeward rim of the atoll is continuously emerged. The windward rim is composed of a series of small islets («motu»), separated by shallow channels («hoa») bringing oceanic waters into the lagoon (Fig. 1).

Fangataufa was a closed atoll but in 1966 an artificial pass (80 m wide and 8 m deep) was cut in the north rim allowing ships to enter the lagoon. The opened «hoa» and drowned reefs, west and north rim, permit an inflow of oceanic water when there is a heavy swell, whereas, in the pass, the current is alternately incoming and outgoing according to the tidal cycle, though the outflow is greater than the inflow (Fig. 1). The alternating current in the pass gives a generally circular movement of the lagoonal bottom water on the inner platform and slope (Bablet, pers. comm.). Residence time of lagoon water is about 16 days (Ricard and Delesalle, pers. comm.).

Twelve sublittoral stations were established in different areas of the lagoon during February and March 1987 (Fig. 1). Seven stations (1, 3, 5, 7, 8, 9, and 12) were located on the inner slope (depths 8-26 m). Stations 3 and 7-8 along the windward side were subjected to oceanic incoming waters from drowned reef flat and «hoa», respectively (Fig. 1). These oceanic incoming waters, eroding the outer reef flat, carried detritus and sand particles into the lagoon. Stations along the leeward side (1, 5 and 9) with the exception of station 12 were located in a calmer zone. Station 12, close to the pass, was affected by the inflowing-outflowing currents. Five stations (2, 4, 6, 10 and 11) were situated in the deep central zone (depths ≥ 30 m) where the calmest water is found.

Sediment sampling

All of the sampling was carried out using SCUBA-operated corers. Four replicate cores were taken at each station for fauna studies (10 cm deep, 2.7 cm internal diameter). The faunal samples were washed through two superposed sieves of 1 mm and 40 µm mesh. The fauna retained on the finer sieve was extracted from sediment by the Ludox centrifugal technique (Jonge and Bouwman, 1977). On average, 170 adult harpacticoids taken at random were

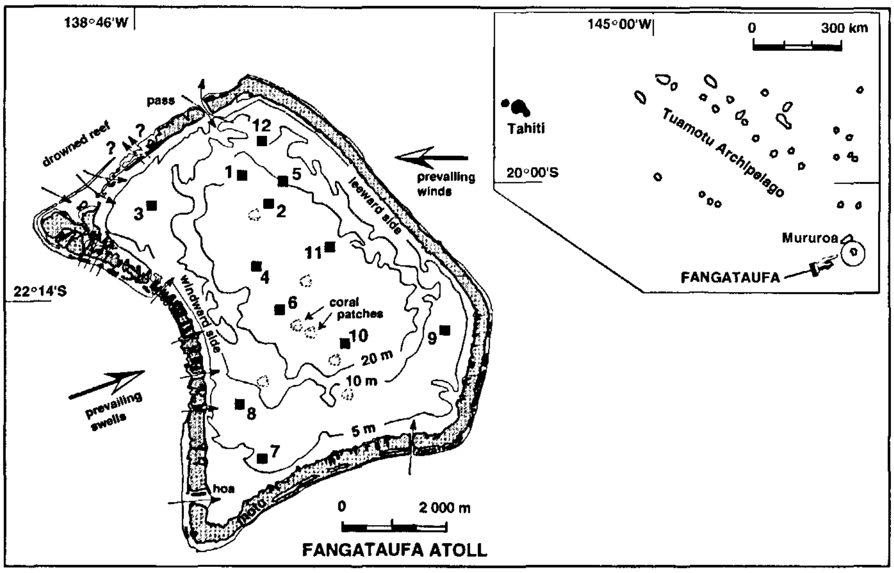

Figure 1

Map of the investigated area and location of sampling stations in lagoon of Fangataufa atoll. Stations are black squares numbered 1 to 12, arrows indicate the oceanic inflows and lagoon outflows and the scale of arrows the possible comparative rate.

identified to species level at each station. This number was sufficient to ensure a reliable estimation of the composition and diversity of a particular biotope, for it is situated far above the stabilization level of Sanders rarefaction curves (Sanders, 1968) established for each site.

Separate cores were collected at each station for grain-size analysis (10 cm deep, inner diameter 6.3 cm). The sediments were dried and sieved through a series of standard sieves (from 40 µm to 4000 µm). The weight of sediment retained by each sieve was used to calculate the mean grain size (Mz) and standard deviation (Sd_{Φ}) by the statistical moments method (*see* Rivière, 1977). The percentages of silt (< 63 µm) and gravel (≥ 2 mm) were recorded.

Data analysis

The diversity was calculated for each station using Shannon-Wiener (H'; with $\log_2$) and Pielou equitability (J) indices (*see* Daget, 1976). The relationships between diversity indices with sedimentary data were examined using Spearman's coefficient of rank correlation.

Hierarchical clustering and factorial correspondence (reciprocal averaging) analyses were used on harpacticoid data to detect similarities between the stations and the interspecies liaisons. These analyses were performed only on species whose relative contribution sums were ≥1 %. The basic data matrix was a 36 species × 12 stations table; relative contributions of species were $\log_{10}(x+1)$ transformed. Further details are given on these analyses, among others, by Lance and Williams (1966), Chardy *et al.* (1976) and Lebart *et al.* (1982).

RESULTS

Sediment characteristics

The lagoonal soft-sediments are carbonate sands consisting of coral, mollusc and crustacean shells, coralline algae and *Halimeda* debris as well as foraminiferan and radiolarian tests. The ranges of sediment organic carbon and nitrogen were, respectively, 0.22-0.50 % (mean 0.33 %) and 0.24-0.58 ‰ (mean 0.38 ‰). Highest values occurred at the periphery of the lagoon (Bablet, pers. comm.). In lagoonal water near the bottom: chlorophyll *a* pigment concentrations ranged from 0.10 to 0.73 mg/l, the highest values being found in the eastern sites subjected to waves and oceanic inflows; oxygen concentrations varied between 3.75 and 6.35 mg/l, the lowest concentrations occurring in the deepest stations (central zone: depth ≥ 30 m); salinity was 35.4 and average temperature ranged from 27 °C in the deepest parts to 27.9 °C on the leeward border stations (Ricard and Delesalle, pers. comm.).

Sediments at stations 1, 2 and 4 to 11 were ordered according to the Wentworth scale as fine sands (125 < Mz < 250 µm). The fine sands with the highest silt contents (stations 2 and 4) and the moderately silty fine sands (stations 6, 10 and 11) were located in the deep central zone. Sediments at stations 3 and 12 were classified as medium sand (250 < Mz < 500 µm). The fine and medium sands with lower silt contents (stations 1, 5, 7, 8, 9 and 3, 12) were situated in the shallow stations on the periphery of the lagoon (Tab. 1 and Fig. 1). According to the Weydert scale (1971) carried out on the coral sediments, the sands at stations 2, 3, 4, 6, 7, 8, 10, 11 and 12 were poorly sorted ($1.5 \leq Sd_{\Phi} < 2$), whereas stations 1, 5 and 9 were well sorted ($1.1 \leq Sd_{\Phi} < 1.5$).

Table 1

Sedimentary data at the study stations. Mz = mean grain size; Sd_{Φ} = standard deviation; silt and gravel contents.

Station	Depth (m)	Mz (µm)	Sd_{Φ}	% Silt (< 63 µm)	% Gravel (≥ 2 mm)
1	26	219	1.16	3.6	1.5
2	30	133	1.59	21.3	1.5
3	22	348	1.63	1.5	12.4
4	36	134	1.63	24.3	1.2
5	20	225	1.03	5.9	1.6
6	35	224	1.69	13.7	4.8
7	9	230	1.59	4.1	6.8
8	8	225	1.40	3.8	4.7
9	10	243	1.26	3.6	4.5
10	35	252	1.76	10.4	6.0
11	36	223	1.59	11.1	4.1
12	9	396	1.66	6.9	7.8

Species composition

The specimens examined (2050) were divided into ten different families, 31 genera and 42 species with a third of the species being new (Tab. 2). Diosaccidae constituted the dominant family (69.1 %) with the greatest diversity, followed by Ameiridae (15.9 %), Canthocamptidae (5.5 %), Cletodidae (4.4 %) and Laophontidae (2.6 %). The other families were represented by few individuals.

Using literature data on sandy bottoms (Hicks and Coull, 1983; Bodin, 1988) and our own observations, each harpacticoid species has been placed in one of three ethologic categories, epi-, meso- or endopsammic forms. 78.6 % of the species, representing 91.4 % of the observed individuals were epipsammic. The endopsammic (five species) and mesopsammic (four species) forms comprised much lower dominances, 7.7 % and 1 % respectively (Tab. 2).

Half of the species together accounted for 93.8 % of the assemblage (Tab. 3). Thirteen species (Tab. 3, ranks 1-11, 13 and 21) occurred in over half of the stations. Among these, three common species, namely Diosaccidae gen. and sp.1, *Stenhelia (D.)* sp.1 and *Ameira parvula* s. lato represented a cumulative dominance around 50 %. Eight species (Tab. 3, ranks 12-13 and 15-20) occurred in 50 % and less of the stations (cumulative dominance = 11.6 %). The other 21 species formed a set of minor and rare species (dominance/species < 1 %).

Species diversity

The lowest values of diversity (H' = 2.20) and equitability (J = 0.60) were recorded at station 9; it was also a station with a small number of species (13) and the greatest degree of dominance (58.8 %) by a single species, namely Diosaccidae gen. and sp.1. H' and J values for other stations ranged upward to maxima in station 2 (H' = 3.80, J = 0.89). The highest values resulted from a community where several species were practically equal in abundance (Tab. 2). Diversity and equitability in the deep central

Table 2

Relative contributions (%) of harpacticoid copepods collected at each station. Code = abbreviations of species; Ethological groups using literature data and the authors' observations: epi. = episammic form; meso. = mesopsammic form; endo. = endopsammic form.

Species	Code species	Ethological group	N° Station											
			1	2	3	4	5	6	7	8	9	10	11	12
Longipediidae														
Longipedia scotti	Lsc	epi.		1.4		0.5							0.8	
Ectinosomatidae														
Ectinosoma sp.	Ect	epi.		2.8				0.5	0.4	4.4				
Diosaccidae														
Stenhelia (D.) sp.1	St1	epi.	39.9	8.5	16.1	8.6	35.1	15.1	1.8		6.2	20.5	15.5	8.1
Stenhelia (D.) sp.2	St2	epi.		5.6	0.6	2.5		2.7		2.9				
Stenhelia (D.) sp.3	St3	epi.						0.5						
Stenhelia (D.) sp.4	St4	epi.		10.6			2.0	0.5	7.5	0.7				0.6
Stenhelia (D.) sp.5	St5	epi.		8.5	8.0	8.1	5.7	0.5	2.2	2.9	3.4	3.8	10.9	
Stenhelia (D.) sp.6	St6	epi.			6.9				0.7				0.8	
Robertsonia knoxi	Rkn	epi.			1.1		0.5				0.6			1.7
Amphiascus sp.1	Asp	epi.		0.7		0.5			1.1					
Amphiascus propinqvus	Apr	epi.	1.2	1.4	5.1		1.4	1.6	1.4		7.3		2.3	1.2
Amphiascopsis cinctus	Aci	epi.					1.9		1.1					1.7
Paramphiascopsis sp.	Par	epi.												1.7
Bulbamphiascus imus	Bim	epi.	6.0	1.4	9.1		7.1		14.1	20.4	2.8			37.6
Typhlamphiascus lamellifer	Tlm	epi.		2.8		5.6	8.5	1.6		30.7		2.6	1.6	
Amphiascoides aff. *subdebilis*	Asu	epi.			4.6	0.5			4.0				1.6	
Paramphiascella aff. *robinsoni*	Pro	epi.	1.8		0.6									2.3
Paramphiascella aff. *calcarifer*	Pca	epi.		3.5		1.0	3.3	1.6	1.8		7.3		0.8	
Haloschizopera aff. *pygmaea*	Hpy	epi.	3.6		0.6	3.5		1.6	6.5	1.5	1.7		7.0	2.3
Haloschizopera aegyptica	Hae	epi.		1.4		1.0		9.7		1.5			4.7	4.0
Melima sp.	Mel	epi.	3.0		3.4	1.0		12.9	8.7		0.6	5.1	8.5	2.3
Diosaccidae gen. and sp.1	Dio	epi.	20.2	17.6	4.6	33.8	7.6	15.6	8.7	22.6	58.8	20.5	14.0	11.6
Metidae														
Metis holothuriae	Mho	epi.					3.8		0.4			1.3		
Ameiridae														
Ameira parvula s. lato	Apa	epi.	13.7	7.7	24.6	2.5	8.1	11.3	40.9		9.3	6.4	9.3	5.8
Nitocra affinis	Naf	epi.												4.0
Psyllocamptus (P.) sp.	Psy	epi.			5.1		4.3		1.8	6.6				
Ameiropsyllus arianus	Aar	epi.					0.9							
Praeleptomesochra aff. *similis*	Psi	meso.												5.2
Paramesochridae														
Apodopsyllus sp.	Apd	meso.									0.6			
Scottopsyllus (Sc.) aff. *robertsoni*	Sro	meso.	0.6		0.6		0.5							2.9
Kliopsyllus sp.	Kli	meso.							0.7					
Tetragonicipitidae														
Phyllopodopsyllus sp.1 (*furciger* gr.)	Ph1	epi.												0.6
Phyllopodopsyllus sp.2 (*furciger* gr.)	Ph2	epi.							0.4					5.8
Phyllopodopsyllus sp.3 (*pauli* gr.)	Ph3	epi.			0.6									
Canthocamptidae														
Mesochra pygmaea	Mpy	epi.	3.0	9.9	5.7	4.0	6.2	7.0	2.9	1.5	0.6	1.3	5.4	
Psammocamptus sp.1	Psm	endo.		4.9		9.1		2.2					1.6	
Cletodidae														
Enhydromosa aff. *latipes*	Enl	endo.		3.5		3.0	1.4	0.5		4.4		16.7	12.4	
Enhydrosoma sp.	Ens	endo.				5.6		2.2				3.8	2.3	
Enhydrosomella sp.	Ems	endo.	3.0	0.7		1.5	0.5				1.1	9.0	0.8	
Laophontidae														
Laophonte inornata	Lin	epi.						0.5	0.4					0.6
Cletopsyllus tertius	Cte	epi.	4.2		2.9		1.9							
Sarsocletodes sp.	Sar	endo.		7.0		3.5	0.9	4.8				9.0		
Sample size														
Total size: 2050 individuals			168	142	175	198	211	186	276	137	177	78	129	173

Table 3

Ranks = rank of species with a dominance ≥ 1 % of total harpacticoid counts; Nb. individuals = total number of each species; % = dominance of each species; Nb. sites = number of stations where present.

Species	Rank	Nb. Individuals	%	Nb. Sites
Diosaccidae gen. et sp.1	1	392	19,4	12
Stenhelia (D.) sp.1	2	292	14,2	11
Ameira parvula s.lato	3	276	13,5	11
Bulbamphiascus imus	4	180	8,8	8
Stenhelia (D.) sp.5	5	88	4,3	10
Typhlamphiascus lamellifer	6	86	4,2	7
Mesochra pygmaea	7	82	4,0	11
Melima sp.	8	81	4,0	9
Haloschizopera aff. *pygmaea*	9	53	2,6	9
Enhydrosoma aff. *latipes*	10	50	2,4	7
Amphiascus propinqvus	11	41	2,0	9
Haloschizopera aegyptica	12	37	1,8	6
Paramphiascella aff. *calcarifer*	13	36	1,8	7
Stenhelia (D.) sp.4	14	36	1,8	6
Sarsocletodes sp.	15	35	1,7	5
Psyllocamptus (P.) sp.	16	32	1,6	4
Psammocamptus sp.1	17	31	1,5	4
Stenhelia (D.) sp.2	18	23	1,1	5
Amphiascoides aff. *subdebilis*	19	22	1,1	4
Enhydrosoma sp.	20	21	1,0	4
Enhydrosomella sp.	21	20	1,0	7

zone (stations 2, 4, 6, 10, and 11) were significantly higher than in shallow waters of the lagoon periphery (stations 1, 3, 5, 7, 8, 9 and 12) ($P \leq 0.05$ and $P \leq 0.01$, respectively, t-tests).

Spearman's test showed that species diversity and equitability were positively correlated only to the silt content of the sands ($P \leq 0.05$, respectively), and not to the mean grain size or gravel content.

Interpretation of lagoon sites and species assemblages

Ascending hierarchical clustering

Classification of the lagoon stations by 36 species permits the identification of two distinct faunal sites and two major faunal clusters (Fig. 2). Station 12 is the most specific, followed by station 8 and two other groupings. Station 12, situated in the north-east littoral fringe (leeward side) is moderately affected by the inflowing-outflowing currents in the pass. Station 8 located on the windward side of the lagoon and at the front of the low-energy «hoa» is subject to waves and to intermittent oceanic incoming waters. The first cluster consists of the deepest confined stations located in the central zone with richest silt and calmest sediments (2, 4, 6, 10, and 11). The second cluster consists of shallow stations on the periphery of the lagoon where the sediment contains a smaller silt fraction (1, 3, 5, 7 and 9). Among these sites, stations 3 and 7 are distinctive for being exposed to constant low oceanic incoming flows over the submerged reef flat and through a large opened «hoa», respectively. The other stations (1, 5 and 9) are located in the eastern lagoon, where lagoon waters are certainly calmer.

Factorial correspondence analysis

The simultaneous projection of stations and species in the same ordination space clarifies the underlying faunal compositional causes of the trends exhibited in the ascending hierarchical clustering of stations. The first three factorial axes extract 73.1 % of the total variance (35.6 %, 21.5 % and 16.0 % respectively).

Axis I (plane I-II) isolates, in negative scores, station 12 and nine species (*i.e. Praeleptomesochra* aff. *similis*, *Nitocra affinis*, *Paramphiascopsis* sp. *Phyllopodopsyllus* sp.2, *Scottopsyllus (Sc.)* aff. *robertsoni*, *Paramphiascella* aff. *robinsoni*, *Robertsonia knoxi*, *Amphiascopsis cinctus*, *Laophonte inornata*). Together they form the group G_1 (Fig. 3). The deeper stations (2, 4, 6, 10 and 11) with a set of muddy sand and muddy species including typical burrowers (*i.e. Sarsocletodes* sp., *Enhydrosoma latipes*, *Enhydrosoma* sp., *Enhydrosomella* sp., *Psammocamptus* sp.) constitute the G_2 group in the positive scores of axis I (Fig. 3). The G_3 group, close to the intersection of the axes, is formed by the shallow stations of the lagoon periphery 1, 5, 7, 9 and the muddy sand species found at most stations (*i.e. A. parvula* s. lato, *Melima* sp., *Amphiascus propinqvus* and *Haloschizopera pygmaea*). Axis II isolates in negative scores, the station 3 and three species (*i.e. Stenhelia (D.)* sp.6, *Cletopsyllus tertius* and *Amphias-*

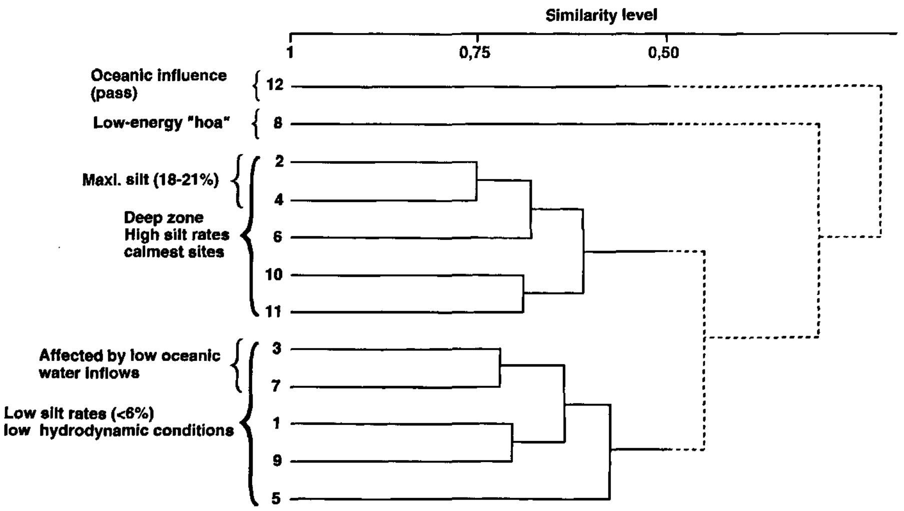

Figure 2

Ascending hierarchical clustering (AHC) of stations. The metric adopted is the Bravais-Pearson's correlation coefficient. The aggregation strategy is the unweighted mean sorting. The upper scale measures the degree of homogeneity of the assemblages.

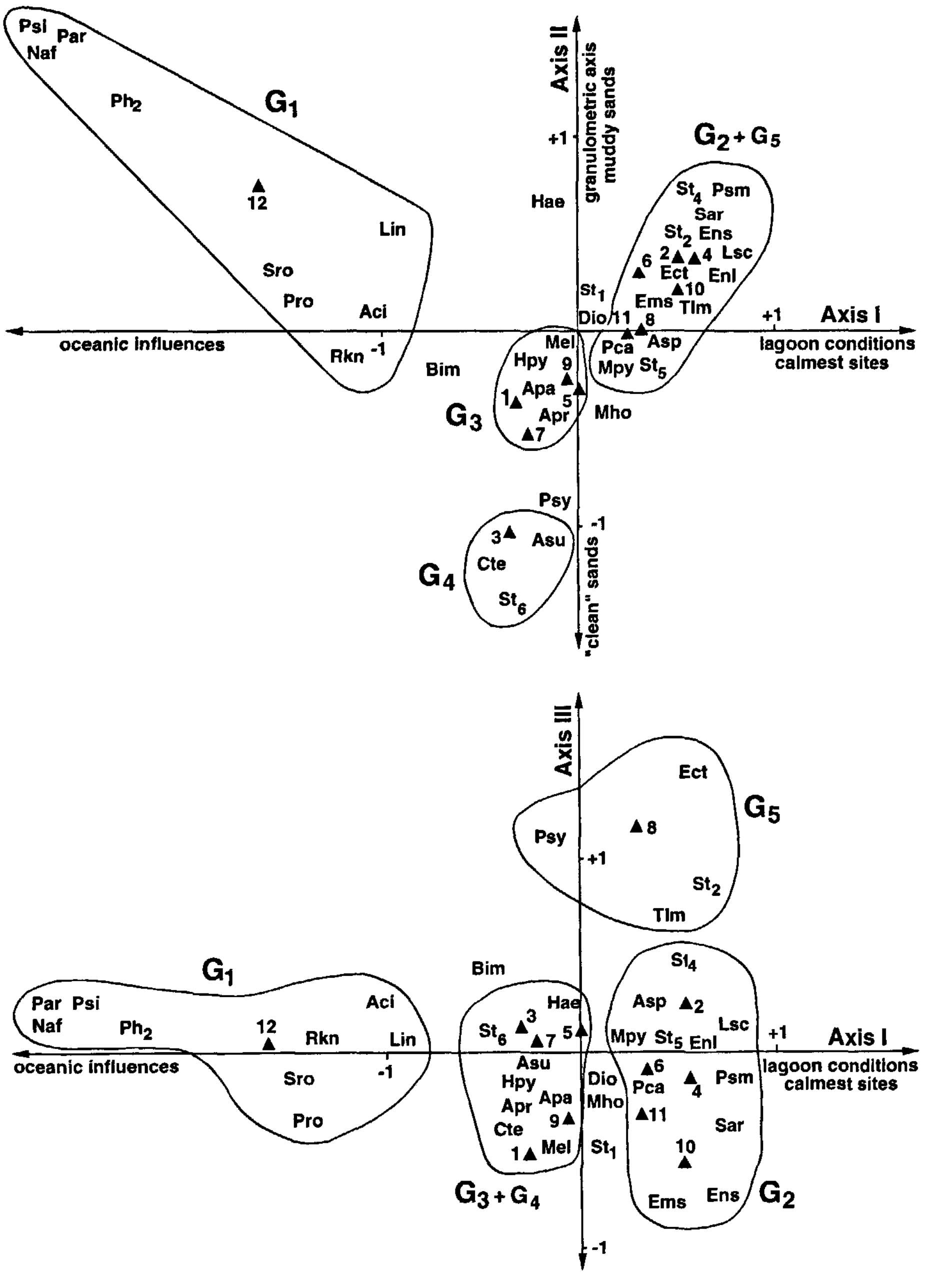

Figure 3

Factorial correspondence analysis with projection of stations and species in the planes of axes I-II and I-III. The species are given three-letter codes (e.g. Ectinosoma *=* Ect*,* Stenhelia (D.) *sp. =* Stl *and* Amphiascus propinqvus *=* Apr*, see Tab. 1); the stations (▲) are numbered from 1 to 12. The 5 groups identified (G_1, G_2, G_3, G_4, and G_5) are represented.*

coides aff. *subdebilis*). The factorial plane of axes I-III (Fig. 3) permits the separation of only station 8 and three species (*i.e. Ectinosoma* sp., *Psyllocamptus* (*P.*) sp. and *Typhlamphiascus lamellifer*). Three important species do not fall within the groups previously defined. *Bulbamphiascus imus* has an intermediate position between G_1 and G_3 groups. It is a very common form (Tab. 3) found almost exclusively in the shallow stations. Diosaccidae gen. and sp.1 and *Stenhelia* (*D.*) sp.1 close to the intersection of the factorial axes are the most ubiquitous sandy mud-dwelling forms. They represent together a high percentage of the entire assemblage (33.6 %).

Axis I represents a complex of ecological factors that are characteristic for the whole lagoon. The position of station 12 on this axis indicates special environmental conditions related to an artificial passage. Considering the homogeneity of all the other lagoon stations, one can surmise that the peculiarity of station 12 is due to the oceanic factors generated by this new junction (Fig. 1).

DISCUSSION

The harpacticoid copepod assemblages suggest the division of the Fangataufa lagoon into two distinct major sections:

(1) the central deep zone, presenting homogeneous and stable physical and chemical conditions, with characteristic diversification of the assemblages;

(2) the inner fringe, where the assemblages are less diversified due to greater environmental constraints (*e.g.* exposure to wave action, bioturbation, currents between the lagoon and the open ocean). Station 12 differs from the rest of the littoral stations because of its position near of the lagoon/ocean water exchange.

The assemblages in the central zone of the lagoon form a species assemblage associated with silty fine sands. These are epibenthic sand-dwelling and burrowing forms. This association is similar to that found on fine sands in the Mururoa lagoon (Villiers *et al.*, 1987); it presents faunal

Table 4

Diversities (H'), equitabilities (J), sample sizes and number of harpacticoid copepod species at each station.

Station	1	2	3	4	5	6	7	8	9	10	11	12
H'	2,67	3,80	3,44	3,43	3,36	3,62	3,01	2,75	2,22	3,12	3,61	3,29
J	0,74	0,89	0,84	0,79	0,78	0,84	0,70	0,77	0,60	0,87	0,87	0,77
Sample sizes	168	142	175	198	211	186	276	137	177	78	129	173
Nb. species	12	19	18	20	20	20	20	12	13	12	18	19

similarities with the assemblages described from sublittoral muds of the eastern Mediterranean (Por, 1964) and from sandy mud bottoms in a lagoon of Bermuda (Coull, 1970). The wide distribution of this isocommunity suggests a species grouping related to relatively undisturbed muddy sands.

The assemblages at the inner periphery of the lagoon are less homogeneous. They consist of species typical of coarse sands at the littoral fringe, combined with an assemblage of species present on the muddy sands that are also present in the centre of the lagoon.

Gourbault and Renaud-Mornant (1990) also think that the nematofauna in the Fangataufa lagoon is composed of two major faunal groups.

Two stations should be scrutinized in greater detail:
Station 8, where the sediment source can be partly traced to the erosion of the outer reef via the so-called «hoa», shows an atypical assemblage dominated by *T. lamellifer*. This species is known to be abundant on the sandy mud bottom in Bermuda (Coull, 1970) and it has been consistently observed in the muddy fine sands of Mururoa (Villiers, unp. data).

The medium sands close to the passage (station 12) harbour a guild dominated by *B. imus*, together with typically interstitial and meso-endopsammic species of the genus *Phyllopodopsyllus* which are characteristic of gravels and coarse sands. *Bulbamphiascus imus* is a stable component of the fauna inhabiting the inner slope, whereas it is very rare in the central deep zone. This cosmopolitan species is considered as a bio-indicator of organic pollution (Moore and Pearson, 1986; Sandulli and Nicola-Giudici, 1990; Coull and Chandler, 1992).

Fangataufa shows an assemblage of about 30 species that is found also in the neighbouring atoll of Mururoa (Villiers *et al.*, 1987), mainly epibenthic animals living on sand and mud bottoms and some burrowing species. The main faunal difference between the two atolls lies in the high percentage of interstitial copepods at Mururoa; here the medium-grained, well sorted sands of the passage harbour a rich assemblage of mesopsammic and gravel-dwelling species graduated along the axis of the pass. Conversely, the finer grain sizes at the bottom of the Fangataufa lagoon encourage the development of a dominant sandy mud or mud dwelling fauna.

These differences are related to the fact that the Mururoa lagoon communicates with the ocean by a large natural passage (4.5 km) generating currents throughout the lagoon (Buigues *et al.*, 1993), whereas the recently formed passage of the Fangataufa lagoon to the ocean allows only feeble currents to be generated close to the bottom, thus favouring the fine particle deposits (Bablet, pers. comm.) and limiting the establishment of interstitial fauna.

The distribution of harpacticoid copepods permits definition of the major zonation in the Fangataufa lagoon and comparison with those found previously in the Mururoa open lagoon. This faunal group proves to be a reliable tool for the study of lagoon soft bottoms, permitting the identification of the major bionomic areas present. Copepod densities and their diversity, in addition to the easy sampling, are particularly helpful not only for classical studies of bionomy and for ecological long-term surveys, but also for pilot studies in hitherto unprospected areas.

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