Physical factors of differentiation in macrobenthic communities between atoll lagoons in the Central Tuamotu Archipelago (French Polynesia)

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ABSTRACT: Nine atolls were characterized in order to understand how physical factors control the species composition, diversity, and abundance of macrobenthic (coral, mollusc, echinoderm, and algal) communities inside the lagoons. Only one region, the central part of Tuamotu Archipelago, French Polynesia, was considered, in order to minimise the variation due to regional factors between regions. The lagoons investigated showed a gradient of physical factors, providing various landscape configurations. The physical factors were surface area, abundance of pinnacles, degree of hydrodynamic aperture, and relative importance of passes in this degree of aperture. Macrobenthic communities were characterized by low diversity and strong dominance of a few mollusc or echinoderm species that generally occurred in lagoons without passes. Correlation analyses indicated that species richness increases with the surface area of the lagoon. Species richness of corals, echinoderms, and macroalgae was also higher in lagoons having numerous pinnacles. Canonical correspondence analyses revealed that the distribution and the relative abundance of coral, echinoderm, and macroalgae species were correlated to the relative importance of passes, whereas degree of aperture of the lagoon was also relevant for corals and molluscs. The physical factors that control the processes of water exchange between ocean and lagoon, including passes, submerged reef flats, and spillways, influence the identity and the abundance of most macrobenthic species inside the lagoons.

KEY WORDS: Coral reefs · Tuamotu Archipelago · Canonical correspondence analysis · Correlations · Species composition · Diversity · Abundance

INTRODUCTION

Ecologists have abandoned the notion that a single monolithic process governs community organisation (Dunson & Travis 1991). Most recent studies have recognized the relative contribution of biotic and abiotic factors to, and the importance of both local and regional

processes on, local diversity and spatial heterogeneity (Quinn & Dunham 1983, Cornell & Lawton 1992, Karlson & Hurd 1993, Cornell & Karlson 1996, Caley & Schluter 1997, Karlson & Cornell 1998). In coral reef ecosystems, equilibrium theories invoked competitive interactions as an important factor in the control of species assemblages and diversity, and consequently in the dissimilarities among ecosystems (Smith & Tyler 1972). Patterns of local species richness and assemblages have

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also been associated with local factors such as extent of adequate substrate, habitat diversity, sedimentation, and water motion (Roy & Smith 1971, Jokiel & Tyler 1992). Then, more recently, it was demonstrated that non-equilibrium processes have profound effects on the spatio-temporal structure of reef communities, both at local and regional scales. These processes include major disturbances (cyclones, *Acanthaster planci* starfish outbreaks, coral bleaching, dystrophic event, climate change), recruitment and extinction, and may be related to large-scale historical and geographical factors (Sousa 1984, Hughes 1989, Ricklefs & Schluter 1993, Hughes 1994, Karlson & Cornell 1998, Hughes & Connell 1999, Porter et al. 1999).

As pointed out by Karlson & Cornell (1998), an interesting strategy to assess the influence of local and regional factors on community structure is the comparison of pristine similar ecosystems, geographically close enough to be bathed by a homogeneous oceanic environment but significantly different according to several environmental factors. This is especially true in the Indo-Pacific regions, where coral richness is significantly dependent on regional factors such as geographic remoteness (Karlson & Cornell 1998). As a consequence, to assess the influence of landscape configuration (surface, degree of aperture of the lagoon, connectivity, patchiness, etc.) on community structure in Indo-Pacific reefs, it is more suitable to consider separately regions where reefs have a similar history, are of similar distance from the mainland and have a similar oceanic environment (i.e. current patterns). Within such a homogeneous region, it can be assumed that it is possible to separate the influence of landscape configuration or local factors in community structure. Consistent with this strategy, the multidisciplinary program 'Typatoll' aimed to compare and understand the functioning of the remote, almost uninhabited, atoll lagoons of the central part of the Tuamotu Archipelago (Dufour & Harmelin-Vivien 1997).

In this study, in agreement with the objectives of Typatoll, our goal was to explore among 9 atolls which could be the physical factors of differentiation in species composition, diversity, and abundance of macrobenthic communities. We considered the 4 major taxa of the macrobenthic communities of Polynesian reefs: corals, molluscs, echinoderms, and algae. We also paid attention to the identity, abundance and assemblages of species, following the recommendations given by Hubbell (1997), and we did not limit the description to overall variation in species richness when comparing different systems. The atoll lagoons were selected in order to provide a gradient of 4 lagoonal physical factors: surface, abundance of pinnacles, degree of hydrodynamic aperture, and relative importance of passes in this degree of aperture. These factors discriminate dif-

ferent landscape configurations. The choice of these 4 factors results from general considerations in the context of biogeography, but is also in good agreement with conclusions of previous studies conducted in the Tuamotus Archipelago. Indeed, it is generally considered that large islands near mainlands have more species than small or remote islands (MacArthur & Wilson 1963, 1967, Heatwole 1991). Surface area is probably not the primary factor affecting species diversity in most situations. However, it was linked to fish diversity in atoll lagoons of French Polynesia (Galzin et al. 1994) because it presumably increases the variety of available habitats (Martin et al. 1995) and the opportunity for new recruitment (Ault & Johnson 1998). We included pinnacles because they represent a particular habitat in atoll lagoons with a high structural complexity (Guilcher 1988). For Tuamotu Archipelago lagoons, Salvat (1967, 1969, 1971b) assumed that the species richness and the abundance of molluscs and echinoderms in atoll lagoons were primarily influenced by the presence or absence of passes. The pass was supposed to be the major factor controlling the exchange between oceanic and lagoonal waters (Salvat 1971b). The degree of hydrodynamic aperture of the lagoon definitely depends on passes, but also on the width of submerged reef flats and spillways. Therefore, we had to account for an overall degree of hydrodynamic aperture, a factor generally strongly emphasised in the classification of coral reef ecosystems (Hatcher 1997).

The present study focussed on the inter-lagoon analysis. Typatoll atolls were sampled only once, during 2 to 4 d spent on each of them. So, it was necessary to understand the links between community structure and physical factors using only a snapshot vision of an ecosystem, and not a long-term data set. Methodologically, multivariate techniques are more suitable to identify patterns using such data. We explored the links between community data and physical factors using correlation analysis and canonical correspondence analysis (CCA) (ter Braak 1986, 1987).

METHODS

Study area and atoll configuration. Among the 425 atolls of the world, 77 are in the Tuamotu Archipelago, which is one of the 5 archipelagoes in French Polynesia (Fig. 1). French Polynesia covers a vast region of the eastern Indo-Pacific province. It comprises 34 high volcanic islands and 84 atolls, representing a surface area of 4000 km² of emergent land (Payri & Bourdelin 1997). The lagoonal waters cover 12000 km². The tides are semi-diurnal, with an amplitude rarely exceeding 40 cm. Tropical cyclones occurred in 1906 and during 3 El Niño events: 1982–1983, 1991, and 1997–1998.

Additionally, bleaching events have been reported in 1983, 1984, 1987, 1991, 1994 and 1998.

We consider atolls to be composed of 3 ecological systems: (1) the outer oceanic slope; (2) the lagoon, including water column and bottom; and (3) the rim which is the boundary between these two. Nine atolls, presented in Table 1, were selected to provide a gradient of the physical factors that we aimed to test. The factors were quantified consistently using SPOT satellite images (spatial resolution of 20 m), and specific image-processing programs (Andréfouët 1998). It was possible to quantify: (1) the lagoon surface area; (2) the degree of hydrodynamic aperture of the lagoon; (3) the relative contribution of passes, spillways, and submerged reef flats to the degree of aperture; and (4) bathymetric information. The surface area of the lagoon is strongly correlated with the mean depth ($r = 0.962$, $p < 0.0001$) and with the surface area of the atoll ($r = 0.992$, $p < 0.0001$). The degree of hydrodynamic aperture of the lagoon depends on the presence and the extent of 3 geomorphological units that were not always present in each atoll. These units are: (1) The submerged reef flats, which are shallow and large sections of the rim without any emergent land. Only the algal ridge on the oceanic side or sandbanks at the lagoon side can emerge during low tide and quiet weather. (2) The

spillways, which are narrow transversal shallow channels between emergent deposits of coral rubble. Their mean depth is less than 0.5 m. They may be non-functional if coral rubble and other debris obstruct them. (3) The passes, which are interruptions of the algal ridge on the oceanic side. Passes may be shallow and narrow (1 to 2 m depth, 30 m wide in Marokau) or deep and large (15 m depth, 300 m wide in Kauehi).

The degree of hydrodynamic aperture is quantitatively defined as the ratio between (1) the sum of the width of the passes, spillways and submerged reef flats and (2) the perimeter of the atoll (Andréfouët 1998).

Sampling strategy. The most conspicuous macrobenthic species were considered. Four taxa were examined: (1) cnidarians (including hard and soft corals and *Millepora*, herein classified as corals); (2) molluscs; (3) echinoderms; and (4) macroalgae (Chlorophyta, Phaeophyta, and Rhodophyta except coralline algae).

This study focuses on inter-lagoonal differences. Lagoons were sampled using a stratified sampling strategy based on geomorphological strata. Indeed, a preliminary survey on 3 lagoons recognized geomorphology as a useful stratifying factor (Dufour & Harmelin-Vivien 1997). Despite that the study of intra-lagoon differences (i.e. inter-strata) is out of the scope of this study, we describe here how the sampling was

Fig. 1. Map of French Polynesia showing the location of the 9 atolls surveyed

Table 1. Overview of the 9 atolls surveyed during this study. *Physical factors included in correlation and canonical correspondence analyses

	Haraiki	Hiti	Kauehi	Marokau	Nihiru	Reka Reka	Taiaro	Tekokota	Tepoto Sud
Geographical coordinates	17° 28' S 143° 26' W	16° 43' S 144° 06' W	15° 50' S 145° 09' W	18° 03' S 142° 16' W	16° 41' S 142° 50' W	16° 50' S 141° 55' W	15° 45' S 144° 38' W	17° 19' S 142° 34' W	16° 49' S 144° 17' W
Surface area of the atoll (km ²)	24.6	25	343	256	100	52	17.3	7.3	6.2
• Surface area of the lagoon (km ²)	10.4	15	315	217	80	0.7	11.8	5.1	1.6
Average depth in the lagoon (m)	10	10	50	30	20	1	15	3	5
• Degree of aperture of the lagoon ^a	0.189	0.194	0.216	0.174	0.245	0.017	0.009	0.595	0.152
Contribution (%) to the degree of aperture:									
Submerged reef flat	0	100	58.7	71.4	80.6	0	0	0	0
Spillways	85.7	0	37.9	28.0	19.4	100	100	59.4	93.7
Pass	14.3	0	3.4	0.6	0	0	0	40.6	6.3
• Relative importance of the pass ^b	3	0	2	1	0	0	03	2	Small, shallow
• Relative abundance of pinnacles ^c	1	0	2	3	2	0	0	3	1
Population (no. of inhabitants)	0	0	302	65	30	0	7	0	0
No. of sampling stations surveyed	10	8	12	10	10	8	8	8	8

^aSum of the widths of the passes, spillways, and submerged reef flats divided by the total length of the atoll rim

^bBased on the contribution of passes to the degree of aperture: between 0 (no pass) and 3 (contribution > 10%)

^c3 = abundant, 2 = common, 1 = rare, 0 = no pinnacles

actually performed in the field to give a picture of what the sites look like. In each lagoon, and for each species of the 4 taxa examined, the mean abundance or biomass obtained at each stratum were weighted by the relative extent of the stratum and added in order to get values representative of the entire lagoon. These weighted abundances were more appropriate for inter-lagoonal comparisons.

We considered 6 strata: (1) the inner reef flat in front of submerged reef flats; (2) the inner reef flat in front of the emergent rim; (3) the inner reef flat in front of spillways; (4) passes; (5) pinnacles or knolls (defined here as hard substrate rising from the lagoon floor to near the water surface); and (6) the lagoon floor. The surface of the strata in the 0 to 12 m range were quantified using SPOT satellite images (Andréfouët 1998). Within each of the 6 strata, 2 stations were established. The number of sampling stations varied between atolls according to the existence of the geomorphological strata (Table 1). A station is made of 8 or 16 quadrats of 5 m² (2 × 2.5 m). Each quadrat was sampled for corals, molluscs and echinoderms. For macroalgae, for each of the 5 m² quadrats, only 2 subquadrats of 0.25 m² (0.5 × 0.5 m), placed on the upper right and the lower left corners of the 5 m² quadrats, were sampled. For the first 4 strata (i.e. submerged reef flats, emergent rim, spillways, and passes), stations consisted of 16 quadrats of 5 m² (and 32 subquadrats of 0.25 m²) arranged contiguously along a transect perpendicular to the shore, between 0.5 and 5 m depth. The pass and spillway stations were located approximately 50 m to the right or left at the edge of the channels. The lagoon floor stations were located at depths below 20 m; each station consisted of 8 contiguous 5 m² quadrats (and 16 subquadrats of 0.25 m²). The pinnacle stations were made of 4 quadrats of 5 m² (and 8 subquadrats of 0.25 m²) placed contiguously on the top of the pinnacle, and by 4 quadrats of 5 m² (and 8 subquadrats of 0.25 m²) placed at approximately 3 m depth. The location of stations was chosen to cover the greater surface of the lagoon.

Observations were carried out by SCUBA diving or snorkelling. For corals, molluscs, and echinoderms, all individuals or colonies of more than 1 cm in length and visible without the need to move rocks were identified and counted in each quadrat of 5 m². Corals were identified to the generic level, while molluscs and echinoderms were identified to the species level. For macroalgae, species richness and biomass were estimated using photographs and samples collected in each quadrat of 0.25 m². Macroalgae were determined to the species level, and biomasses of the more conspicuous species were estimated using values of dry weight matter (dried at 80°C for 36 h).

Data analysis. Two types of analyses were performed. First, correlation coefficients were calculated between physical factors and synthetic descriptors such as species richness and total weighted abundance or biomass per lagoon. The Pearson coefficient was calculated for quantitative factors (lagoon surface area and degree of aperture), whereas the Spearman coefficient was calculated for non-quantitative factors (relative abundance of pinnacles and relative contribution of passes to the degree of aperture). The significance of the correlation coefficients was then tested using an analysis of variance (Zar 1984). Second, physical factors influencing the distribution and relative abundance of macrobenthic species within lagoons were determined by CCA, a recent method developed by ter Braak (1986, 1987). CCA is an increasingly popular method for multivariate analysis of ecological community data (Palmer 1993, McCune 1997, Legendre & Legendre 1998). This method constrains the axes in classical correspondence analysis (CA) to be linear functions of measured variables associated with species records. As CCA uses data on environment to structure the community analysis, it has been called a method for 'direct gradient analysis' (ter Braak 1986).

The overall contrast in species composition and abundance between stations is measured by an inertia obtained as the sum of the eigenvalues of the species matrix. Comparing the inertia associated with CCA to the inertia of CA indicates the extent to which the measured variables explain the variation in the species matrix. Analyses were undertaken with the weighted abundance or biomass per lagoon and the physical factors indicated in Table 1. CCA classified the different factors, beginning with the one that extracted the greatest amount of the variance in the species data matrix. Significant factors entering the final analysis were selected by a permutation test, a stepwise procedure analogous to backward elimination in multiple regression analysis (Draper & Smith 1981). Surface area of the atoll and mean depth of the lagoon, which are highly correlated with the surface area of the lagoon, were not included in CCA in order to avoid problems of colinearity (ter Braak 1987). In the ordination diagram, significant factors are represented by arrows, along with species and atolls. The robustness of the final analysis was determined using a Monte-Carlo permutation test (ter Braak 1988). Additional details of how to interpret CCA results are given in ter Braak (1986), Palmer (1993) and Legendre & Legendre (1998).

A further and very interesting development of this analysis allows partial CCA, where the computations are made after removing, by multiple linear regression, the effects of undesired covariables (ter Braak 1988). The partial CCA was used to separate the environmental variation from the spatial variation, as suggested by

ter Braak (1987) and demonstrated by Legendre (1990). The spatial variation corresponds to the fraction of the variability in the species data matrix that is explained by the spatial structure of the species data alone (for details see Borcard et al. 1992, Borcard & Legendre 1994). In the present study, the spatial structure is actually the geographic coordinates of the atolls. Subsequently, the total variation of the species matrix was partitioned into: (1) the fraction of the species variation that can be explained by environmental factors independently of any spatial structure ('pure' environment); (2) the spatial structuring that is shared by the environmental data (environment + space); (3) the spatial patterns that are not shared by the environmental data ('pure' space); and (4) the fraction of species variation explained neither by spatial coordinates nor by environmental data ('undetermined') (Borcard et al. 1992).

RESULTS

Variation in the macrobenthic communities among lagoons

There were 24 coral genera in the 9 lagoons (Table 2). As shown in Fig. 2, a relatively high percentage of coral genera was frequent (found in 4, 5, or 6 lagoons), common (found in 7 or 8 lagoons), or ubiquitous (found in all 9 lagoons). Except for Taiaro and Reka Reka, which were characterized by a low diversity, the lagoons shared a large number of genera. The variation in spe-

Fig. 2. Percentage of rare (observed in 1 lagoon), occasional (observed in 2 or 3 lagoons), frequent (observed in 4, 5, or 6 lagoons), common (observed in 7 or 8 lagoons), and ubiquitous (observed in all 9 lagoons) species among the 4 taxa examined in this study

Table 2. Weighted abundance of coral, mollusc, and echinoderm species or genera, and biomass of macroalgae species in the 9 lagoons surveyed. Abundance is expressed as no. of individuals (or colonies for corals) per 5 m² quadrat, and biomass is given in g m⁻². The mean abundances or biomass calculated for each stratum (submerged reef flat, emergent rim, spillways, passes, pin-nacles, and lagoon floor) were weighted by the relative extent of the stratum, and added in order to give values representative of the entire lagoon. +: macroalgae species observed, but not abundant enough to calculate their biomasses

	Haraiki	Hiti	Kaeuhi	Marokau	Nihiru	Reka Reka	Taiaro	Tekokota	Tepoto Sud
Corals									
<i>Acanthastrea</i>	0.6505	0.5900	0.0040	0.0736	0.6686				
<i>Acropora</i>	0.7467	2.5240	0.9508	1.1414	4.2874			0.2963	1.2089
<i>Astreopora</i>	0.2084	1.0587	1.9123		3.9031			2.4162	0.2831
<i>Cyphastrea</i>	1.1159	1.2717	0.9211	0.9696	7.9807			0.4897	
<i>Dendrophyllia</i>			0.0010	0.0055					
<i>Echinopora</i>			0.0533		0.1457				
<i>Favia</i>	0.2870	0.7864	0.0644	0.6700	3.9784			0.0158	0.0122
<i>Fungia</i>	0.0201		0.0003	0.1198	0.0014				
<i>Herpolitha</i>				0.0616					
<i>Leptastrea</i>	0.2447	0.1882	0.2940	0.7309	0.6092			0.9816	1.5710
<i>Leptoseris</i>	0.0001								0.0814
<i>Lobophyllia</i>	0.1256	0.9188	0.0038	0.0577	3.5839				
<i>Millepora</i>			0.0087	0.0103					
<i>Montastraea</i>			0.0042		0.2291			0.0153	
<i>Montipora</i>	0.5329	2.4668	0.8389	3.8180	1.1589			10.6128	0.1546
<i>Palythoa</i>			0.0097						
<i>Pavona</i>	0.0065	0.0962	0.0063	0.4056	0.0286			0.0266	0.0233
<i>Platygyra</i>	0.5945	2.4620	0.9057	0.1684	2.7625				
<i>Plesiastrea</i>			0.0001		0.0500				
<i>Pocillopora</i>	0.0025		0.1522	0.0134	0.0939			0.0291	0.1440
<i>Porites</i>	0.0440	0.2273	0.4847	0.7741	0.8340	0.0472	0.0399	2.6926	0.4201
<i>Psammocora</i>	0.1280		0.6290	0.1848	0.0309			0.0134	0.1073
<i>Stylocoeniella</i>			0.4794	0.2938	0.4504				
<i>Tubastraea</i>			0.0001						
Generic richness	15	11	22	17	18	1	1	11	10
Total abundance	4.7074	12.5901	7.7240	9.4985	30.7967	0.0472	0.0399	17.5894	4.0059
Molluscs									
<i>Arca ventricosa</i>	0.1668		0.0961	0.1550	0.1412		6.1695		0.1586
<i>Cerithium echinatum</i>	0.0001		0.0006	0.0016	0.2428			0.0319	0.0465
<i>Chama imbricata</i>	0.0619	0.2420	0.6427	0.1666	0.5453		3.8536		0.1198
<i>Chama pacifica</i>		0.0459		0.1956					
<i>Conus ebraeus</i>			0.0011		0.0074				0.0145
<i>Conus lividus</i>			0.0004						0.0007
<i>Conus miliaris</i>			0.0042						
<i>Conus pulicarius</i>			0.0004						
<i>Conus rattus</i>			0.0004						
<i>Crassostrea cuculata</i>							0.0299		
<i>Cypraea moneta</i>				0.0042		0.1046			
<i>Drupa grossularia</i>			0.0001						
<i>Drupa ricinus</i>			0.0001						
<i>Drupa rubusidaeus</i>									0.0007
<i>Lambis truncata</i>			0.0533						
<i>Mancinella tuberosa</i>					0.0002				
<i>Mitra ferruginea</i>	0.0115								
<i>Morula granulata</i>									0.1122
<i>Morula uva</i>			0.0004		0.0097				
<i>Pedum spondyloideum</i>			0.0038	0.0006	0.0001				
<i>Peristernia nassatula</i>				0.0006					
<i>Pinctada maculata</i>				0.1561			17.6629		
<i>Pinctada margaritifera</i>			0.0571						
<i>Pycnodonta hyotis</i>	0.0211		0.0001	0.0406					0.0116
<i>Spondylus varians</i>			0.0004	0.0193	0.0014				
<i>Strombus gibberulus</i>					0.0002				0.0052
<i>Thais aculeatus</i>					0.0019				
<i>Tridacna maxima</i>	0.0011	0.0175	0.3116	0.0386	0.4171		0.8087	0.4288	0.5293
Species richness	6	3	17	11	11	1	5	2	10
Total abundance	0.2625	0.3054	1.1728	0.7788	1.3673	0.1046	28.5246	0.4607	0.9991

Table 2. (continued)

	Haraiki	Hiti	Kaeuhi	Marokau	Nihiru	Reka Reka	Taiaro	Tekokota	Tepoto Sud
Echinoderms									
<i>Actynopyga mauritiana</i>					0.0049				
<i>Bohadschia argus</i>	0.0001			0.0007	0.5527	0.0116			0.0007
<i>Culcita novaeguineae</i>	0.0001		0.0001	0.0035	0.0046				
<i>Echinometra mathaei</i>			0.0049	0.0021	0.0304			0.0319	0.0861
<i>Echinothrix calamaris</i>			0.0002	0.0002				0.0082	0.0015
<i>Echinothrix diadema</i>			0.0004						0.0015
<i>Holothuria atra</i>		13.2153	0.0041	2.6391	3.7331		1.5275		0.0238
<i>Linckia multifora</i>				0.0021					
Species richness	2	1	5	6	5	1	1	2	5
Total abundance	0.0002	13.2153	0.0097	2.6477	4.3257	0.0116	1.5275	0.0401	0.1136
Macroalgae									
<i>Amphiroa</i> sp.								+	
<i>Antithamnion breviramosus</i>									+
<i>Avrainvillea lacerata</i>				+		+			
<i>Caulerpa bikinensis</i>	0.0019		+	0.9801	+		0.2014	+	
<i>Caulerpa pickeringii</i>					0.0174	+			0.082
<i>Caulerpa racemosa</i>				+					
<i>Caulerpa serrulata</i>	0.3611								
<i>Caulerpa seuratii</i>		+	0.1171	0.0048	0.0313				
<i>Caulerpa</i> sp.				+					
<i>Caulerpa urvilliana</i>	3.1169	9.5235	0.8673	9.0504	25.0756		8.9306	0.9401	
<i>Caulerpa webbiana</i>								+	
<i>Ceramium</i> sp.	+								
<i>Ceramium gracillimum</i>			+						
<i>Chondria simpliciuscula</i>			+	+					
<i>Chondria</i> sp. 1					+				
<i>Chondria</i> sp. 2		+							
<i>Chondria</i> sp. 3		+							
<i>Cladophora</i> sp.									+
<i>Cladophoropsis luxurians</i>	+			+					
<i>Codium geppiorum</i>	+								
<i>Coelothrix irregularis</i>	+								+
<i>Dasya baillouviana</i>			+						
<i>Dasya iyengarii</i>	+		+						
<i>Dasya mollis</i>			+						
<i>Dictyosphaeria cavernosa</i>	+					+		+	+
<i>Enteromorpha</i> sp.									+
<i>Galaxaura filamentosa</i>				+					+
<i>Griffithsia ovalis</i>			+						
<i>Griffithsia</i> sp.	+			+					
<i>Griffithsia subcylindrica</i>			+						
<i>Halimeda lacunalis</i>				0.1882					
<i>Halimeda micronesica</i>			0.2856						
<i>Halimeda opuntia</i>			0.6385						
<i>Halimeda taenicola</i>			0.5146		0.0017				
<i>Herposiphonia crispella</i>			+						
<i>Herposiphonia secunda</i>									+
<i>Herposiphonia</i> sp. 1					+				
<i>Herposiphonia</i> sp. 2						+			
<i>Hypnea</i> sp.	+								
<i>Jania adhaerens</i>			+		+				
<i>Liagora ceranoides</i>	1.2673		+	+	0.0216			+	
<i>Liagora</i> sp.	+	+						+	
<i>Lobophora variegata</i>			+		+			0.0133	
<i>Microdictyon aghardianum</i>				+		+			
<i>Microdictyon okamurae</i>	7.4103	2.4637	11.0808	1.007	27.2214	2.89	+	0.3778	10.5695
<i>Microdiction umbilicatum</i>		+	+		+		+	+	
<i>Neomeris vanbossea</i>		+	+	0.0001				0.0088	
<i>Palmogloea protuberans</i>		+		+					
<i>Polysiphonia Scopulorum</i>	+					+	+		+
<i>Polysiphonia</i> sp.									+
<i>Vaolnia aegagropila</i>	+								
Species richness	16	9	20	16	12	7	5	11	11
Total biomass	12.1575	11.9872	13.5039	11.2306	52.3690	2.8900	9.1320	1.3400	10.6515

cies composition and species richness among these lagoons was mainly caused by the addition of rare (found in only 1 lagoon) or occasional (2 or 3 lagoons) genera. A high abundance of colonies of several genera was found in Nihiru, while Tekokota was characterized by the high abundance of colonies of *Montipora*.

The overall diversity of molluscs consisted of 28 species, among which more than 80% were rare or occasional. Consequently, a high variation in species composition and richness among lagoons was found. Kauehi and Nihiru were characterized by several species not found in other lagoons. *Pinctada maculata*, *Arca ventricosa*, and *Chama imbricata* were particularly abundant in Taiaro.

The diversity of echinoderms was relatively low (8 species), with no common or ubiquitous species found. Half of the species were frequent, and half were rare or occasional. This resulted in a moderate variation in the species richness among the 9 lagoons. Hiti, and to a lesser degree, Nihiru, were characterized by the high abundance of *Holothuria atra*.

A total of 51 species of macroalgae was recorded in the 9 lagoons. Species were growing exclusively on hard substratum. The vegetation is typically dominated by the large Chlorophyta, including a wide range of *Caulerpa* and *Microdictyon* species, while the Rhodophyta were more numerous and were chiefly small species often epiphytic on larger algae. The single species of Pheophyta confirms the low diversity of this division on atolls. As for molluscs, more than 80% of the species were rare or occasional, and *Microdictyon okamurae* was the only species found in all 9 lagoons. Therefore, a high variation in species composition and species richness among lagoons was found. Nihiru was characterized by the high biomass of *Caulerpa urvilliana* and *M. okamurae*.

Relationships with abiotic factors

The number of coral genera and the number of mollusc, echinoderm, and macroalgae species are strongly and positively correlated with the surface area of the lagoon (Table 3). Coral genera and mollusc and macroalgae species were also positively correlated with the relative abundance of pinnacles. The surface area of the lagoon and the abundance of pinnacles influenced the distribution and the relative abundance of some echinoderm species (Table 4).

The distribution and the relative abundance of coral genera, echinoderms, and macroalgae species among lagoons were influenced by the relative importance of the passes (Table 4). Degree of aperture of the lagoon was also a factor influencing distribution of coral genera and mollusc species. Ordination plots showing spe-

Table 3. Correlation between macrobenthic descriptors (species or generic richness, and weighted abundance or biomass) and physical factors of the 9 lagoons surveyed. For the surface area and the degree of aperture of the lagoon, values represent the Pearson correlation coefficient, whereas, for pinnacles and passes, values represent the Spearman correlation coefficient. Correlation coefficient significance: * $p < 0.05$, ** $p < 0.01$

	Surface area	Degree of aperture	Pinnacles	Passes
Corals				
Generic richness	0.713*	0.415	0.683*	0.283
Total abundance	0.104	0.598	0.627	0.114
Molluscs				
Species richness	0.827**	-0.051	0.492	0.146
Total abundance	-0.174	-0.415	0.189	-0.211
Echinoderms				
Species richness	0.678*	0.114	0.795*	0.365
Total abundance	-0.115	-0.038	-0.170	-0.650
Macroalgae				
Species richness	0.779*	0.332	0.701*	0.571
Total biomass	0.157	-0.003	0.137	-0.070

cies distribution in relation to physical factors selected by CCA are presented in Fig. 3. Each arrow represents a factor and determines a direction that is proportional to the correlation coefficient in Table 4. The projection of a species on this arrow shows its 'preference' for high or low values of this factor (ter Braak 1986). Non-quantitative factors, such as pinnacles and passes, are represented by a point in the ordination plots. For example, the coral genera *Tubastraea*, *Palythoa*, *Leptoseris*, *Psammocora*, *Leptastrea*, and *Pocillopora* were associated with lagoons having a pass, such as Kauehi and Tepoto Sud, whereas *Porites* and *Montipora* were associated with the high degree of aperture of Tekokota (Fig. 3). A high number of mollusc species were exclusively found or were more abundant in Kauehi, Nihiru, and Tekokota, which were characterized by a high degree of aperture. The echinoids *Echinothrix calamaris* and *E. diadema* were exclusively found in lagoons with a pass, whereas the holothurian *Holothuria atra* was more abundant in lagoons without passes. Macroalgae species such as *Caulerpa seuratii*, *C. serrulata*, *Halimeda micronesica*, *H. opuntia*, and *H. taenicola* had higher biomass or were exclusively found in lagoons with a significant pass, such as Kauehi, Tepoto Sud, and Haraiki.

DISCUSSION

Characteristics of macrobenthic communities

An important characteristic of the macrobenthic community structure was the strong dominance of a few

Table 4. Summary of the canonical correspondence analyses performed on the 4 taxa examined. Significant factors were selected by a stepwise procedure analogous to backward elimination in multiple regression analysis. Selected factors are significant at $p < 0.1$

	Axis 1	Axis 2	Axis 3
Corals			
Correlations of environmental variables with ordination axes			
(1) Passes	0.799	0.337	0
(2) Degree of aperture	0.779	-0.379	0
Summary statistics for ordination axes			
Eigenvalues	0.298	0.108	0.169
Cumulative % of variance (species data)	34.8	47.4	67.2
Species-environment correlations	0.870	0.857	0
Sum of all unconstrained eigenvalues			0.856
Sum of all canonical eigenvalues			0.406
Monte Carlo probability for significance of the sum of all eigenvalues			0.04
Molluscs			
Correlations of environmental variables with ordination axes			
(1) Degree of aperture	0.930	0	0
Summary statistics for ordination axes			
Eigenvalues	0.400	0.296	0.166
Cumulative % of variance (species data)	34.0	59.2	73.3
Species-environment correlations	0.930	0	0
Sum of all unconstrained eigenvalues			1.175
Sum of all canonical eigenvalues			0.400
Monte Carlo probability for significance of the sum of all eigenvalues			0.01
Echinoderms			
Correlations of environmental variables with ordination axes			
(1) Passes	0.492	0.158	0.419
(2) Surface area	-0.036	-0.180	0.485
(3) Pinnacles	0.092	-0.488	0.415
Summary statistics for ordination axes			
Eigenvalues	0.654	0.102	0.108
Cumulative % of variance (species data)	71.7	82.9	83.0
Species-environment correlations	0.980	0.910	0.496
Sum of all unconstrained eigenvalues			0.912
Sum of all canonical eigenvalues			0.757
Monte Carlo probability for significance of the sum of all eigenvalues			0.04
Macroalgae			
Correlations of environmental variables with ordination axes			
(1) Passes	0.722	0	0
Summary statistics for ordination axes			
Eigenvalues	0.161	0.305	0.110
Cumulative % of variance (species data)	24.0	69.4	85.9
Species-environment correlations	0.722	0	0
Sum of all unconstrained eigenvalues			0.670
Sum of all canonical eigenvalues			0.161
Monte Carlo probability for significance of the sum of all eigenvalues			0.01

species in some lagoons without passes. The dominant species, which were highly abundant in some lagoons, were only occasionally observed, or even absent, in other lagoons. In addition, the dominant species were different from one lagoon to another. The holothurian *Holothuria atra* was particularly abundant in Hiti, but it was far less abundant in the other lagoons. In Taiaro, the molluscs *Arca ventricosa*, *Chama imbricata*, and *Pinctada maculata* were particularly abundant, but their populations were much lower in the other lagoons.

The high dominance by a few species which are different from one closed lagoon to another has been previously observed in the Tuamotu (Salvat 1967, 1969, 1971a, Renaud-Mornant et al. 1971, Poli & Salvat 1976, Adjeroud 1997b). These authors observed the dominance of the species mentioned above or of the bivalve *Tridacna maxima*. The high dominance in lagoons without passes seems to preferentially affect mollusc and echinoderm species, whereas dominance of coral and macroalgae species was generally less pronoun-

ced. Finally, dominance of one or a few species seems not to persist for a long period of time, since in Taiaro a shift in dominance away from *Crassostrea cucullata* in 1972 to *P. maculata* in 1994 has been observed (Adjer-

oud 1997b). Biotic interactions and relatively low impacts of physical disturbances that occurred in closed lagoons may have failed to prevent dominance by the most resistant species, which has competitively ex-

Fig. 3. Plots of canonical correspondence analysis performed on the weighted abundance (biomass for macroalgae) of species (genera for corals) for the 4 examined taxa. Position of atolls, species, and significant factors along the first 2 axes is given. Quantitative factors are represented by arrows, whereas non-quantitative factors are represented by points. Species or generic names are abbreviated as follow: first 5 letters of the generic names, respectively, for corals, first 2 and 3 letters of the generic and species names for molluscs, echinoderms, and macroalgae (see Table 2 for full generic and species names). The mollusc *Cypraea moneta* was passive in the CA, explaining the absence of Reka Reka in the ordination plot. Passes: relative importance of the passes; aperture: degree of aperture of the lagoon; surface: surface area of the lagoon; pinnacles: relative abundance of pinnacles

cluded all potential invaders (Connell 1978). This is a first possible explanation for the dominance of a few species in closed atolls.

The variation in species composition and diversity among the atoll lagoons showed different patterns among the 4 taxa examined. For corals, a large number of common genera were found, and the variation in composition and diversity was caused by the addition of several occasional or rare genera, and not by a substitution of genera. In contrast, outer reef slope communities are highly similar among atolls (Chevalier 1978, 1979, Bouchon 1983). For molluscs and macroalgae, most of the species recorded were rare or occasional, resulting in a high variation of the species composition and diversity. Only 8 species of echinoderms were identified in the 9 lagoons, and they were all rare, occasional, or moderately frequent, resulting in a low variation of the diversity among lagoons. These patterns are partly explained by our sampling strategy, which was restricted to epibenthic macro-organisms visible without the need to move rocks and therefore ignored endo- and micro-molluscs as well as coralline algae and microalgae (which account for a large part of the overall diversity in French Polynesia). The patterns observed for the 4 taxa were also found in Moorea (Adjeroud 1997a) (i.e. a high proportion of common species for corals, a high proportion of rare species for molluscs and macroalgae, and a low diversity with no common species for echinoderms). Therefore, we suggest that they may be a characteristic of French Polynesian reefs. The high number of rare species for molluscs and macroalgae have important consequences, not only for the sampling strategy in future studies, but also on the temporal variation of these communities. In fact, rare species have the highest ecological turnover (extinction/immigration) and the highest evolutionary turnover (extinction/speciation) (McKinney et al. 1996).

Physical factors influencing species composition, diversity, and abundance

For echinoderms, and to a lesser degree for corals, a high amount of the variation was explained by the physical factors independently of any spatial structure

Fig. 4. Results of partial canonical correspondence analyses indicating the percentage of variation of the species matrix explained by: (a) nonspatial environmental variation (environment), (b) spatial structuring shared by environmental data (env. + space), (c) spatial patterns not shared by environmental data (space), (d) fraction of species variation explained neither by spatial coordinates nor by environmental data (undetermined)

(82.64 and 39.60% respectively; Fig. 4). Whereas for molluscs and macroalgae, these amounts were lower (21.36 and 19.70% respectively) and a relatively large amount of the variation was undetermined. However, with only 1 or 2 factors selected by the CCA, the fraction of the 'explained variation' was still relatively important for molluscs and macroalgae. Adjeroud (1997a) in Moorea (Society Islands), revealed that the fraction of the explained variation was between 24.60 (macroalgae) and 49.20% (corals), but 4 relevant physical and biological factors were selected by the CCA for each of the 4 taxa.

As has been previously found for many organisms regardless of taxon and habitat, we established a positive correlation between surface area and species richness in atoll lagoons of the Tuamotu Archipelago. The diversity of corals, molluscs, echinoderms, and macroalgae in a lagoon greatly increased with its surface area. This has also been observed for fish (Galzin et al. 1994). The increase of richness with surface area is in total agreement with one aspect of the equilibrium theory of island biogeography (MacArthur & Wilson 1967). The theory postulates that the number of species (S) is related to the surface (A) by the equation $S = CA^z$, where C is a constant that varies among taxa and z is an empirical constant. The z values found in this study

for corals (0.35) and molluscs (0.32) are similar to that found for land plants (0.32), ants (0.30), beetles (0.34), and amphibians and reptiles (0.30) (in MacArthur & Wilson 1967). Therefore, it is suggested that the rate at which species richness increases with the surface is of the same order for these taxa. In contrast, the z values found for echinoderms (0.21), and macroalgae (0.12) are not common for island systems and are quite comparable with the one found for continental systems (mainland) (MacArthur & Wilson 1967). The lower z value found for macroalgae and echinoderms indicates that the number of species increases with the area but not as rapidly as that of corals or molluscs.

Species richness of corals, echinoderms, and macroalgae was positively correlated with the relative abundance of pinnacles in the lagoon. With the exception of the shallow, tilted, atoll of Tekokota, pinnacles were more abundant in large and deep lagoons, a fact that confirms previous observations in other atolls by Guilcher (1988). Pinnacles contained several species that were rarely observed elsewhere in the lagoon. Abundance of some species was generally higher than elsewhere. The high species diversity on pinnacles was also observed at Johnston Atoll (Maragos & Jokiel 1986, Jokiel & Tyler 1992). It may be explained by the complexity of these features, where high gradients in depth, light conditions, hydrodynamics and nature of bottom are observed.

The distribution and relative abundance of coral genera and mollusc species were influenced by the degree of aperture of the lagoon, and the pass was a major factor influencing the distribution and the relative abundance of coral, echinoderm, and macroalgae species. Passes, particularly deep and wide ones, and high degree of aperture are both associated with main exchanges between oceanic and lagoonal waters. A high influx of water is likely associated with a high number of colonisers, which increases the probability of introducing 'new' species to the lagoon. The source of coral colonisers of its lagoon is likely to be the oceanic outer reef slope of the same atoll, or nearby islands. In fact, the diversity and abundance of corals are maximal on the outer reef slope, and most of the species found on the lagoonal environments are also found on the outer reef slope (Bouchon 1983, Adjeroud 1997a). As one of the possible explanations for the influence of the pass on the species composition and relative abundance of species, one can argue that passes permit colonisation in a stepping-stone fashion for some species living on the outer reef slope. Passes can also allow the entrance of mobile species, such as some holothurians and molluscs.

Our results partially confirm the assumption of Salvat (1971b), who suggested that the presence or absence of passes was the major factor influencing the

structure of mollusc and echinoderm communities in the lagoon. Our results demonstrated that degree of aperture of the lagoon was also an important factor in the distribution and the relative abundance of coral and mollusc species. Therefore, the distinction between atolls with or without passes suggested by Salvat appears not to be sufficient, and has to be complemented by information on the exchange between oceanic and lagoonal waters. Lagoons without passes, but with a high degree of aperture because of extended reef flats or spillways, may have diversified and abundant macrobenthic communities. Galzin et al. (1994) concluded that the number of fish species is not significantly related to the confinement of the lagoon. However, no analyses were performed on fish communities to examine whether the species composition and relative abundance of species are influenced by the amount of water exchange between the lagoon and the ocean.

The case of Taiaro Atoll needs to be examined with caution since it is not possible to determine exactly whether the low diversity and the high abundance by a few species are caused by the absence of exchange between oceanic and lagoonal waters or by the high salinity (42.88 psu) in the lagoon, which is probably lethal for many organisms, or by both of these factors. Taiaro illustrates the fact that several factors can covary in a manner such that it is difficult to decipher their relative contribution (Jokiel & Tyler 1992, Adjeroud 1997a).

Conducting this study in a unique region was supposed to eliminate interference with regional factors in the interpretation of the patterns. However, regional considerations can be used to explain features observed consistently in the 9 lagoons, such as low diversity. The overall diversity of the 9 lagoons is of the same order of magnitude as that of Moorea, a high volcanic island in the Society Archipelago, where 29 coral genera and 25 mollusc, 12 echinoderm, and 42 macroalgae species were recorded (Adjeroud 1997a). In fact, the low diversity in the atolls can be related to the low diversity of French Polynesia in general. This outcome is in accordance with recent studies (Cornell & Lawton 1992, Caley & Schluter 1997, Cornell & Karlson 1996, Karlson & Cornell 1998) which demonstrated that local diversity is strongly and linearly correlated to regional diversity, particularly in the central Indo-Pacific. Among the large-scale factors (biogeographic, historical) that may explain the low diversity in French Polynesia, remoteness is probably the most relevant one. Despite a lack of consensus about the exact location of the 'colonisation source' in the Western Pacific, it is far westward of French Polynesia and thus not favourably located for the efficient dissemination of larvae and species into that region (Schelltema 1986,

Rosen 1988). Most of the species recorded in French Polynesia are also found in the Western Pacific, and Salvat (1967) observed that a large number of molluscs in French Polynesia have larvae that are adapted to long-distance dispersal.

During the Typatoll campaigns, it was not possible to obtain data relevant to recruitment and settlement processes. The causal relationships between physical factors and community structure could not be thoroughly documented using a multivariate analysis, but in this study the analysis on the differences between lagoons highlights interesting combinations of physical factors and community structure, such as extreme confinement and monospecific dominance. These combinations suggest different patterns and processes of recruitment and settlement according to different landscape configurations. Studies on spatio-temporal patterns of recruitment are available particularly for fish (Dufour & Galzin 1993, Leis et al. 1998) and coral communities (Connell et al. 1997, Hughes et al. 1999). Conversely, few studies address issues on recruitment of molluscs (Dayton et al. 1989), echinoderms (Fisk 1992, Keesing et al. 1993) and algae (Santelices 1990, Stiger & Payri 1999). Our observations are an invitation for experimental research to be conducted on these forgotten taxa and to compare the results for the Tuamotu Archipelago with other regions worldwide. For instance, in closed lagoons such as Taiaro, what are the mechanisms that could explain the community shifts in dominant species of molluscs? In lagoons without human harvesting, are the species that are closely associated with a high degree of aperture, or with a pass, dependent on external supplies of new recruits to maintain their populations in the lagoon? We feel that the various landscape configurations of the Tuamotuan atolls offer suitable sites to conduct hypothesis-driven research, in agreement with the relationships observed in this study.

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