

How do coral reef Gastropods feel about nuclear blasts?

A long-term study of the effects of man-made perturbations

Atmospheric nuclear tests
Clustering
Coral reefs
Gastropods
Perturbation

Essais nucléaires atmosphériques
Groupement
Récifs coralliens
Gastéropodes
Perturbation

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ABSTRACT

The resistance to perturbations of reef-dwelling gastropod assemblages was studied on the seaward reefs of Fangataufa atoll (French Polynesia) after their exposure to atmospheric nuclear tests, a major man-made perturbation. We focused on two important aspects: (1) the temporal evolution of the densities of the most important species before and after the tests, and (2) the temporal evolution of the spatial structure of the assemblages. Three transects, crossing several geomorphological zones, were established on the seaward reefs of the atoll. Each transect was sampled at irregular time intervals during a twenty-year period. Several univariate and multivariate methods were used to study (1) the temporal fluctuations in species abundances and ranks, and (2) the spatial structure of the assemblages and its temporal evolution. Results suggest that, even if the densities of several species dropped immediately after the nuclear tests, most species were able to quickly recolonise the perturbed reefs. The spatial distributions of several species are not greatly influenced by abiotic conditions, thus creating an unstable spatial structure for the assemblages through time (except in the supralittoral zones).

RÉSUMÉ

Comment les gastéropodes des récifs coralliens réagissent-ils aux essais nucléaires? Une étude à long terme des effets d'une perturbation d'origine anthropique

La résistance aux perturbations de peuplements de gastéropodes a été étudiée sur les récifs extérieurs de l'atoll de Fangataufa (Polynésie française) après que ce dernier ait été soumis à des essais nucléaires atmosphériques. Nous nous sommes concentrés sur deux aspects principaux : (1) l'évolution temporelle de la densité des espèces les plus importantes avant et après les essais et (2) l'évolution

temporelle de la structure spatiale des peuplements. Trois transects furent mis en place sur les récifs extérieurs de l'atoll; ils traversent différentes zones géomorphologiques qui présentent des conditions abiotiques différentes. Ces transects furent échantillonnés à intervalles irréguliers sur une période de vingt ans. Des méthodes d'analyse univariées et multivariées ont été utilisées pour étudier (1) les fluctuations temporelles de l'abondance et du rang de chaque espèce et (2) la structure spatiale des peuplements et son évolution. Les résultats suggèrent que, même si la densité de plusieurs espèces a chuté immédiatement après les tests, la plupart des espèces ont recolonisé rapidement les récifs. De plus, la distribution spatiale de la plupart des espèces ne semble pas être particulièrement affectée par les conditions abiotiques, si bien que la structure spatiale des peuplements varie beaucoup au cours du temps (sauf dans les zones supralittorales).

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INTRODUCTION

The effects of perturbations on coral reefs have been among the major research areas in coral reef ecology during the past two decades (Endean, 1976). Such studies find their justification in the fact that (1) coral reefs are increasingly subject to man-made perturbations like overfishing (Munro *et al.*, 1987), mining (Shepherd *et al.*, 1992) and pollutions of various kinds (Jackson *et al.*, 1989), and that (2) theoretical and empirical studies have shown that perturbations are structuring agents in the benthos of marine ecosystems (Dayton *et al.*, 1984, Sousa, 1984).

Most perturbation-oriented studies to-date have been conducted on sessile organisms (corals, algae, gorgonians). This is mainly because of their structural and trophic importance on coral reefs, the ease with which they can be monitored through time, and the better theoretical understanding we have of the processes involved in their succession and zonation. These studies are usually of relatively short duration, a problem that was noted by Pearson (1981). Short-term studies are useful to describe the effects of a given perturbation on a given environment and may also give insights about the processes involved in the early phase of a potential re-establishment of the perturbed community, but they do not answer the question of whether the previous community re-established itself, or if it was replaced by some other type of community. This kind of long-term study is rarely found in the coral reef literature; the recent papers of Guzman *et al.* (1994) and Kaly and Jones (1994) are notable exceptions.

The response of mobile coral reef organisms to perturbations has also been studied, though to a lesser extent. Fish and sea urchins have been the focus of most research (Lessios, 1988, Walsh, 1983) although some work has also been done on molluscs (Leviton and Kohn, 1980; Miller, 1986), the cryptofauna (Moran and Reaka-Kudla, 1991) and, recently, on a predator-prey interaction (Aronson, 1992). The drawback of these studies, however, is still their relatively short time scale after the perturbation.

The present paper describes the effects of three atmospheric nuclear tests on the reef-dwelling gastropod assemblages of Fangataufa atoll (138° 43' W, 22° 14' S), in the

Tuamotu Archipelago, French Polynesia (Fig. 1a). These tests, conducted by the French *Direction des Centres d'Expérimentations Nucléaires*, were carried out in August 1968 (2 megatons), May 1970 (1 megaton) and August

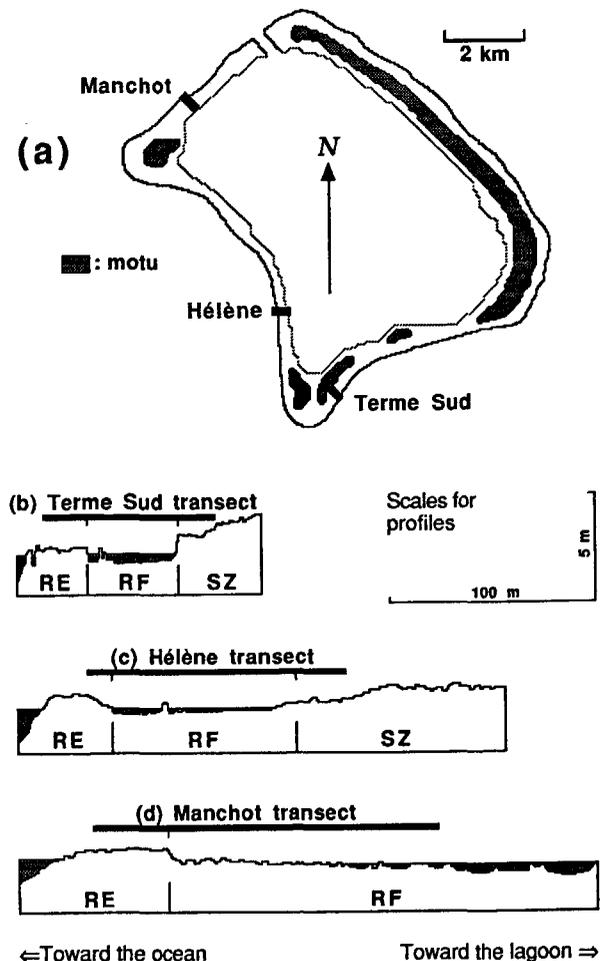


Figure 1

Aerial view of the Fangataufa atoll showing (a) the locations (black rectangles) and (b, c, d) the lateral profiles of the three study sites. Black lines over profiles identify sampled areas (transects), divided into zones: RE: reef edge, RF: reef flat, SZ: supralittoral zone. Motu: reef islet with vegetation.

1970 (less than 0.1 megaton; this is the last atmospheric test to have taken place over Fangataufa). All tests took place at an altitude of a few hundred metres and a distance of 4 to 7 km from the outer reefs that we were monitoring.

We will focus on describing the variations in abundance and spatial distribution of the assemblages. This will allow us to find out (1) whether these assemblages are able to rapidly recolonise a disturbed environment, and (2) whether the spatial structure of these assemblages remains constant through time even after major perturbations. These observations will serve as a basis for examining hypotheses concerning some of the mechanisms possibly involved in the control of both the spatial structure and the densities of these assemblages and, thereafter, to discuss the contribution of these processes to their stability (resistance to perturbations). The definition of stability given in Pimm (1984) will be used throughout this work.

A "BACI" (Before/After, Control/Impact; Stewart-Oaten *et al.*, 1986) or "Beyond BACI" (Underwood, 1991) design has not been used in the present study. For one thing, the theory of BACI was only developed years after the present study was initiated. Then, and besides Mururoa (located 45 km away, but where nuclear tests were also conducted), the nearest atolls in the Tuamotu are located 170 to

200 km away from Fangataufa; because of microclimatic condition variations, they would hardly provide suitable control sites; differences between the control and impacted sites could be attributed to differences in locations as much as to treatment. The sampling design of the present study provides at least for Before/After comparison (with a single pre-test observation). Despite the well-known limitations of such designs for interpretation (Underwood and Peterson, 1988; Underwood, 1991), authors of perturbation studies are usually happy when they have at least that (e.g. Jackson *et al.*, 1989). Although the data do not allow one to describe the natural variability of species assemblages before the nuclear tests, they provide a reference point against which to judge the immediate effects of perturbations, and the after-impact data series allow one to follow the long-term succession in gastropod assemblages.

STUDY SITE AND MATERIALS

Transects, established on the seaward side of the atoll at three different sites, called Hélène, Manchot and Terme Sud, have been studied by one of us (BS). A description of their geomorphology can be found in Salvat (1970);

Table 1

Total abundance of the gastropod species counted on Terme Sud each year, and retained for the analysis. A: along the reef edge and the reef flat stations: 21 species. B: along the supralittoral zone: 3 species. The last column is a qualitative appreciation of the effect of the nuclear tests: + increasing, - decreasing, ? uncertain.

A.	1968	1969	1972	1974	1977	1987	Effect of nuclear tests (1968 vs. following years)
<i>Patella flexuosa</i>	127	0	0	6	0	3	-
<i>Turbo argyrostomus</i>	0	2	0	0	0	0	?
<i>Turbo setosus</i>	60	7	37	26	24	13	-
<i>Nerita plicata</i>	0	4	6	5	3	38	+
<i>Cerithium mutatum</i>	0	5	0	14	3	12	+
<i>Cerithium nesioticum</i>	0	0	15	0	0	0	?
<i>Cerithium sp.</i>	0	0	17	0	0	0	?
<i>Cypraea moneta</i>	0	0	4	1	1	1	+
<i>Tectarius grandinatus</i>	0	0	0	0	1	4	?
<i>Strombus maculatus</i>	0	5	0	2	1	2	+
<i>Conus ebraeus</i>	3	0	5	9	4	7	?
<i>Conus miliaris</i>	19	11	6	24	31	25	?
<i>Conus nanus</i>	5	3	4	7	11	9	?
<i>Conus sponsalis</i>	3	1	1	1	10	18	?
<i>Conus vermiculatus</i>	8	0	0	0	0	0	-
<i>Drupa grossularia</i>	0	0	2	8	1	9	+
<i>Drupa ricinus</i>	104	12	71	96	21	42	-
<i>Morula granulata</i>	37	7	26	32	29	31	?
<i>Morula uva</i>	45	27	83	108	109	81	?
<i>Imbricaria conovula</i>	0	0	5	1	7	2	+
<i>Mitra litterata</i>	43	79	60	149	105	38	?
B.	1968	1972	1974	1977	1987	Effect of nuclear tests (1968 vs. following years)	
<i>Nerita plicata</i>	13	7	28	17	54	?	
<i>Tectarius grandinatus</i>	253	47	57	69	45	-	
<i>Morula granulata</i>	0	0	0	1	0	?	

see also Figure 1*b*, *c* and *d*. These sites are characterised by different hydrodynamic regimes; we tried to maximise the diversity of habitats inhabited by reef gastropods. The transects are two metres wide and extend from the supralittoral zone, through the reef flat, and up to the middle of the reef edge where ocean waves are breaking. According to hydrodynamic conditions (reef locations around the island and dominant swell), this reef edge zone is either an elevated algal crest (covered by more than 80% calcified red algae), or a much less elevated zone (mainly coral, covered by less than 20% red algae). Terme Sud and Hélène present elevated algal crests but Manchot has a low reef edge. The supralittoral zone is above mean high sea level; it is a spray zone only covered by seawater at periods of rough weather and large swell. The reef flat is always covered by a few centimetres to a few decimetres of water at low tide on Terme Sud and Hélène, while a large section is exposed at low tide on Manchot. The reef edge emerges at low tide. In the remainder of this paper, we will often refer to the supralittoral zone, reef flat and reef edge as "zones". The transects were divided into segments three metres long, thus creating strings of contiguous stations with 6 m² surface area each.

The three transects were visited at irregular time intervals over a twenty-year period. Replicate transects could not be sampled because of time and logistic constraints during the campaigns. Manchot was sampled in 1968, 1972, 1974, 1977 and 1987; Terme Sud, in 1968, 1969, 1972, 1974, 1977 and 1987 (the supralittoral zone could not be sampled in 1969); Hélène, in 1967, 1969, 1972, 1974, 1977 and 1987 (in 1972 the supralittoral zone could not be sampled, and in 1969 only the supralittoral zone was visited). The 1967 sampling campaign on Hélène, and

the 1968 campaigns on Manchot and Terme Sud, were completed before the 1968 atmospheric nuclear test.

All gastropods present at each station were collected, identified to species and counted. Vermetids, Hipponicids and rare species were excluded from the study because accurate quantitative assessment of these groups could not be insured. The species (with abundances) retained for the analysis of each transect are presented in Tables 1, 2 and 3.

NUMERICAL METHODS

Spatial structure of the transects

The question addressed in this analysis concerns differences in density, diversity and species composition among zones, along each transect and for each sampling period; this is the background against which the effect of the perturbations will be evaluated. Mean densities (number of gastropods per m²) were calculated for each zone and year and were tested for statistical differences among the zones described above. Kruskal-Wallis (for three zones) or Wilcoxon-Mann-Whitney tests (for two zones) were used, because the conditions of homoscedasticity and normality required by parametric tests could not be met by the gastropod density data. Species richness (number of different species) and diversity (Shannon's H' , using natural logarithms) per zone were also calculated. Finally, for each transect and each sampling campaign, a (stations \times species) data matrix was constructed and a correspondence analysis was conducted to check for differences in faunal composition among zones. Canonical correspondence analyses (ter Braak, 1986) were also carried out for the (stations \times species) data

Table 2

Total abundance of the gastropod species counted on Hélène each year, and retained for the analysis. A: along the reef edge and the reef flat stations: 14 species. B: along the supralittoral zone: 2 species. The last column is a qualitative appreciation of the effect of the nuclear tests: + increasing, - decreasing, ? uncertain.

A.	1967	1972	1974	1977	1987	Effect of nuclear tests (1967 vs. following years)
<i>Patella flexuosa</i>	29	2	1	5	32	?
<i>Turbo setosus</i>	8	7	6	0	37	?
<i>Nerita plicata</i>	0	4	11	22	12	+
<i>Tectarius grandinatus</i>	0	0	0	0	1	?
<i>Conus chaldeus</i>	6	6	5	3	3	?
<i>Conus miliaris</i>	14	2	13	1	5	?
<i>Conus nanus</i>	68	28	80	27	38	?
<i>Conus sponsalis</i>	7	3	8	20	10	?
<i>Drupa grossularia</i>	6	1	4	0	4	?
<i>Drupa ricinus</i>	19	57	103	117	72	+
<i>Morula granulata</i>	1	27	23	30	47	+
<i>Morula uva</i>	64	95	436	945	551	+
<i>Imbricaria conovula</i>	0	3	3	1	1	+
<i>Mitra litterata</i>	2	41	82	29	120	+
B.	1967	1969	1974	1977	1987	Effect of nuclear tests (1967 vs. following years)
<i>Nerita plicata</i>	12	30	9	9	19	?
<i>Tectarius grandinatus</i>	393	12	112	149	111	-

Table 3

Total abundance of the gastropod species counted along the reef edge and the reef flat of Manchot each year, and retained for the analysis: 16 species. The last column is a qualitative appreciation of the effect of the nuclear tests: + increasing, - decreasing, ? uncertain.

A.	1968	1972	1974	1977	1987	Effect of nuclear tests (1968 vs. following years)
<i>Cerithium mutatum</i>	649	12	17	6	0	-
<i>Cerithium torulosum</i>	25	0	4	0	0	-
<i>Cypraea caputserpentis</i>	1	0	3	0	23	?
<i>Engina alveolata</i>	14	1	0	0	0	-
<i>Conus chaldeus</i>	3	7	17	9	18	+
<i>Conus ebraeus</i>	24	17	18	34	52	?
<i>Conus miliaris</i>	29	17	13	16	18	-
<i>Conus nanus</i>	67	42	69	112	74	?
<i>Conus sponsalis</i>	10	4	2	18	41	?
<i>Drupa grossularia</i>	15	35	3	19	6	?
<i>Drupa morum</i>	7	4	1	5	3	?
<i>Drupa ricinus</i>	19	57	103	117	72	+
<i>Morula granulata</i>	2	17	92	78	79	+
<i>Morula uva</i>	168	126	35	130	211	?
<i>Imbricaria conovula</i>	3	7	17	10	6	+
<i>Mitra litterata</i>	19	86	486	122	397	+

matrices against a matrix of dummy variables representing the two (1 dummy variable) or three zones (2 dummy variables); this is the equivalent of multivariate analysis of variance for species abundance data. Since the canonical axes can be tested for significance using a permutation test, these analyses allowed to determine whether there existed faunal differences among zones. Each permutation test involved 999 permutations. Sokal and Rohlf (1995) as well as Legendre and Legendre (1997) give a brief description of what permutation tests are. More details are found in Edgington (1987). The permutation tests used in canonical correspondence analysis are described in ter Braak (1990).

Temporal evolution of the assemblages

The second part of the analysis focuses on the evolution of the gastropod assemblages over time. We are interested in the ecological hypothesis that nuclear tests had some measurable effect on the assemblages of the reef under study. Species richness and diversity per zone, as well as mean densities of prosobranchs for each zone, were compared qualitatively, through time, in order to relate the changes to the perturbation events.

Changes in species composition of the assemblages have been studied through Kendall's coefficient of concordance (Rahel, 1990). For each zone of each transect, sampling years were compared using this coefficient; the variable was the (ranked) numbers of individuals of the various species in the given transect, zone and year. Values of this coefficient range from zero (no concordance in species ranks through time) to one (complete concordance). The null hypothesis was that species ranks were not correlated through time in a given assemblage, which would mean that an assemblage is unstable.

Finally, a cluster analysis was computed, for each transect, to get an overall view of the evolution of the spatial

structure of the gastropod assemblages over time. Three Steinhaus similarity matrices were constructed, each one containing the data for all the sampled stations of a given transect for the whole study period. These matrices were first subjected to an unconstrained proportional-link linkage agglomerative clustering with 50% connectedness (Sneath, 1966; Legendre and Legendre, 1983) in order to obtain a first approximation of the number and nature of the groups. The final grouping was obtained by *k*-means clustering (MacQueen, 1967; Anderberg, 1973). This is a non-hierarchical partitioning method that tries to minimise the multivariate sum of within-group variances or, which is the same thing, the sum of within-group distances to the group centroids, thus producing compact groups in descriptor space. In principle, *k*-means clustering can be computed either from raw data (metric variables), or from a distance matrix. The program available, however, allowed to compute the solution only from raw data. Species abundance data collected along a spatial gradient, like our transect data, pose the problem of containing many zeros without ecological significance, because the absence of a species from two stations does not indicate that these stations are similar (they may be from the opposite ends of tolerance for that species); this problem has been discussed at length in the ecological literature (Legendre and Legendre, 1983, 1997). Such data should not be subjected to methods of analysis, such as the *k*-means partitioning method, that consider double zeros as an indication of resemblance. So, we used the Steinhaus similarity matrices computed above and subjected them to principal coordinate analyses in order to obtain new sets of Euclidean coordinates (we kept the first 25 principal coordinates), to be used as input for *k*-means clustering. The Steinhaus similarity coefficient is appropriate for species abundance data, as it discards double zeros from the assessment of similarity; it is widely used by ecologists.

Table 4

Mean gastropod density (counts per m²) within each zone. The values in parentheses are the standard deviations; *n* is the number of stations within each zone. The last column gives the results of the Kruskal-Wallis or Wilcoxon-Mann-Whitney tests (N.S.: non significant, *: *p* < 0.05, **: *p* < 0.01).

Terme Sud	Reef edge <i>n</i> = 7	Reef flat <i>n</i> = 15	Suprallitoral zone <i>n</i> = 6	Significance of test of difference among zones
1968	6.62 (7.47)	1.96 (1.17)	7.39 (3.90)	**
1969	1.31 (0.35)	1.20 (0.79)		N.S.
1972	4.19 (3.16)	1.84 (1.14)	1.50 (1.57)	N.S.
1974	4.71 (2.74)	3.39 (1.06)	2.36 (1.70)	N.S.
1977	3.62 (1.73)	2.32 (1.60)	2.42 (1.06)	N.S.
1987	2.24 (0.83)	2.81 (1.33)	2.75 (1.13)	N.S.
Hélène	Reef edge <i>n</i> = 4	Reef flat <i>n</i> = 31	Suprallitoral zone <i>n</i> = 7	Significance of test of difference among zones
1967	2.33 (0.87)	0.90 (0.62)	9.64 (8.40)	**
1969			1.00 (0.84)	
1972	3.42 (2.16)	1.04 (0.84)		**
1974	13.79 (6.25)	2.39 (1.84)	2.88 (2.47)	**
1977	19.13 (21.02)	3.98 (5.44)	3.76 (2.22)	*
1987	5.71 (2.64)	4.27 (5.09)	3.10 (1.25)	N.S.
Manchot	Reef edge <i>n</i> = 12	Reef flat <i>n</i> = 44		Significance of test of difference among zones
1968	1.64 (1.03)	3.52 (2.09)		**
1972	2.47 (0.82)	0.79 (0.49)		**
1974	6.25 (4.27)	1.30 (1.11)		**
1977	4.00 (2.39)	1.10 (0.64)		**
1987	5.65 (3.09)	2.07 (1.61)		**

Table 5

Species richness (*R*) and species diversity (*H'*) in each zone.

Terme Sud	Reef edge		Reef flat		Suprallitoral zone	
	<i>R</i>	<i>H'</i>	<i>R</i>	<i>H'</i>	<i>R</i>	<i>H'</i>
1968	3	1.0	9	1.8	2	0.2
1969	9	1.8	9	1.4		
1972	7	1.5	14	2.1	2	0.4
1974	10	1.6	13	1.6	2	0.6
1977	11	1.9	12	1.8	3	0.5
1987	9	1.8	15	2.2	2	0.6
Terme Sud	Reef edge		Reef flat		Suprallitoral zone	
	<i>R</i>	<i>H'</i>	<i>R</i>	<i>H'</i>	<i>R</i>	<i>H'</i>
1967	6	1.2	8	1.5	2	0.1
1969					2	0.5
1972	7	1.0	12	1.7		
1974	6	0.8	13	1.6	2	0.3
1977	6	0.7	10	0.8	2	0.3
1987	5	1.4	13	1.2	2	0.4
Terme Sud	Reef edge		Reef flat			
	<i>R</i>	<i>H'</i>	<i>R</i>	<i>H'</i>		
1968	14	2.1	15	1.2		
1972	11	1.9	14	2.0		
1974	10	1.0	14	1.6		
1977	7	1.6	13	2.0		
1987	11	1.0	13	2.0		

There is a second problem with the k -means method: the algorithms are not guaranteed to find the optimal solution, *i.e.* the one for which the sum of within-group variances is minimum. A well-known solution around this problem is to provide the algorithm with an initial partition of the objects which is expected to be close to the final solution one is looking for. The k -means program was asked to produce the same number of groups, k , as identified in the approximate solutions obtained by hierarchical clustering runs; these approximate solutions were given to the k -means program as starting configurations.

Simple and canonical correspondence analyses were computed with the help of the CANOCO package, version 3.01 (ter Braak, 1988, 1990). Similarities, principal coordinate analyses as well as hierarchical and k -means cluster analyses were computed using "The R package" (Legendre and Vaudor, 1991). Nonparametric tests of significance were computed with StatView™.

RESULTS

Spatial structure of each transect

The mean densities of prosobranchs are significantly different among zones on Manchot and H el ene but this

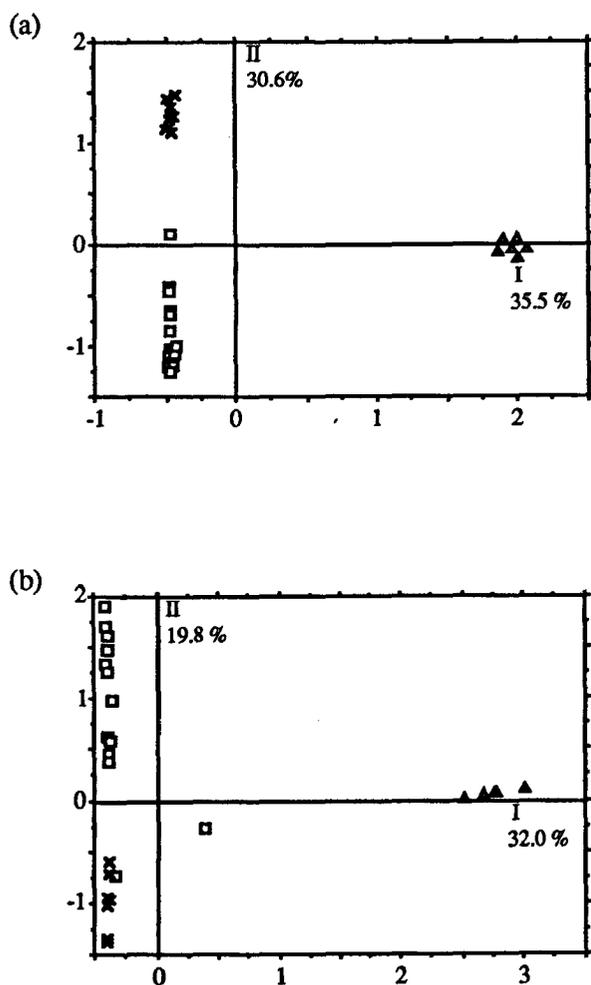


Figure 2

Correspondence analysis of Terme Sud. a: 1968, b: 1972. x, reef edge; squares, reef flat; triangles, supralittoral zone.

is not the case on Terme Sud, except for 1968 (Table 4). One interesting fact is that, in two out of three cases, prosobranch densities were higher after the nuclear tests on the reef edge of each transect; on the contrary, they were highest in the supralittoral zone before the tests.

While the reef edge is the zone with the highest prosobranch density (Table 4), the reef flat is the zone with the highest species richness, both before and after the tests (Table 5). The species diversity data do not display any clear pattern other than the fact that the supralittoral zone always has the lowest diversity; it also has the lowest richness.

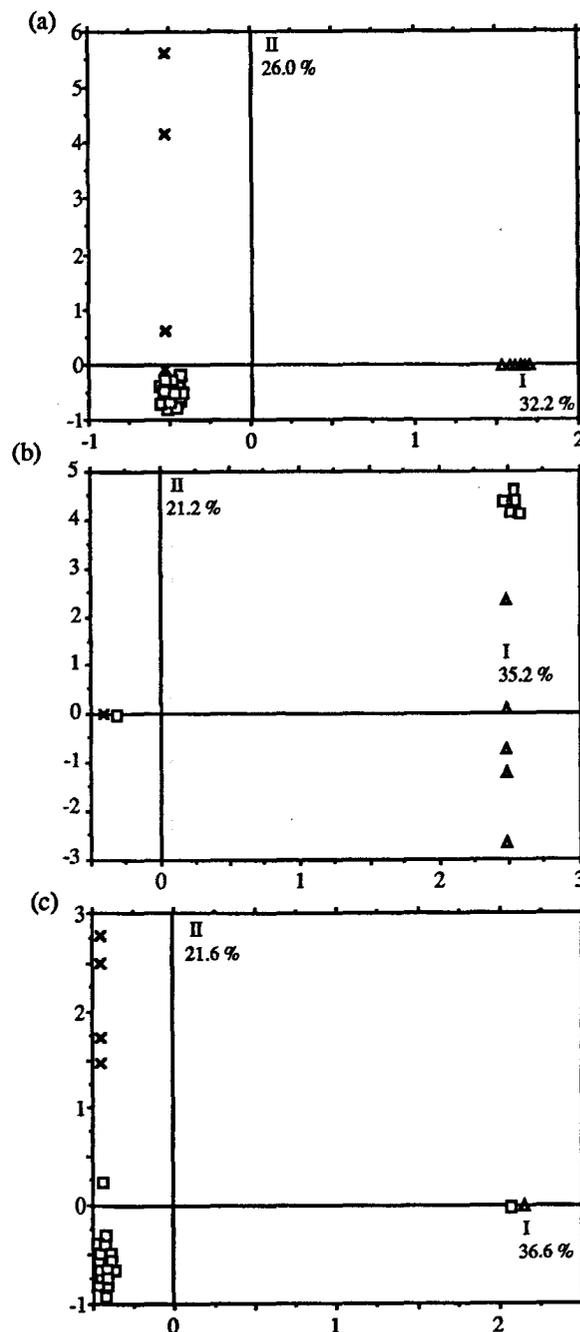


Figure 3

Correspondence analysis of H el ene. a: 1967, b: 1974, c: 1987. x, reef edge; squares, reef flat; triangles, supralittoral zone.

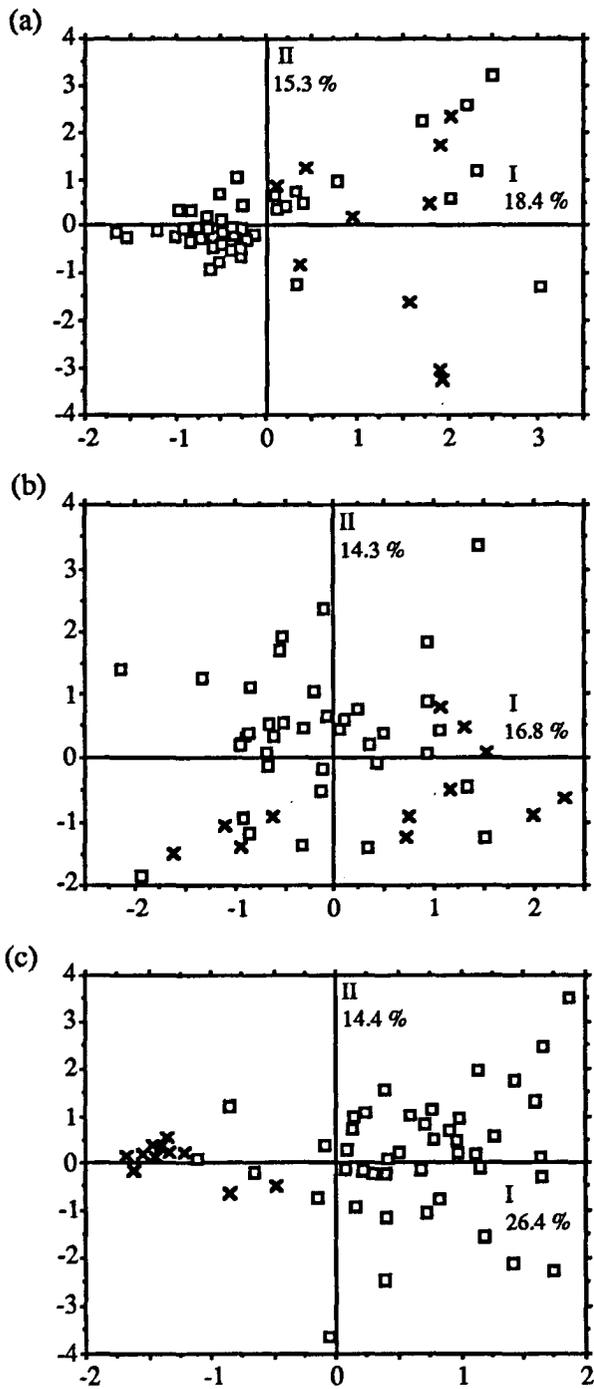


Figure 4

Correspondence analysis of Manchoy. a: 1968, b: 1972, c: 1987. x, reef edge; squares, reef flat.

For Terme Sud, the correspondence analysis ordinations for the various sampling years, based on species composition, yielded comparable results. The first axis, which accounts for the largest fraction of variability, always isolates the supralittoral zone from the other zones (except, of course, in 1969, where the supralittoral zone was not sampled). A few examples are given in Figure 2; other years yield comparable results. Axis II discriminates between the reef edge and the reef flat: perfectly before the nuclear tests (in 1968, Fig. 2a) and imperfectly thereafter (in 1972 for example: Fig. 2b); after the tests, there is some overlap in

species composition between the reef flat and the reef edge. In summary, the supralittoral zone is the most different of all three zones in species composition.

Ordination results on H el ene are very similar. In 1967 (that is, before the nuclear tests), the first axis separates the supralittoral zone stations from all the others, while axis II discriminates the reef edge from the reef flat stations

Table 6

Results of the permutation tests of significance (1000 permutations) of the differences in faunal composition among zones, performed on the canonical axes for each of the three transects (*: $p < 0.05$, **: $p < 0.01$). NT: not tested due to the fact that it is impossible to reach the 5% level, because the number of observations is too low.

	Axis I	Axis II
Terme Sud:		
1968	**	**
1969	**	NT
1972	**	*
1974	**	**
1977	**	**
1987	**	**
H�el�ene		
1967	**	**
1972	**	NT
1974	**	*
1977	**	**
1987	**	**
Manchoy		
1968	**	
1972	**	
1974	**	
1977	**	
1987	**	

Table 7

Kendall's coefficient of concordance (W) of species assemblages through time, for each zone of each transect, computed for species composition. The last column gives the results of the statistical tests (*: $p < 0.05$, **: $p < 0.01$, NT: not tested due to the fact that it is impossible to reach the 5% level, because the number of observations is too low).

Terme Sud	W	Significance of test
Reef edge	0.952	**
Reef flat	0.641	**
Supralittoral zone	0.840	NT
H�el�ene	W	Significance of test
Reef edge	0.486	*
Reef flat	0.791	**
Supralittoral zone	0.360	NT
Manchoy	W	Significance of test
Reef edge	0.752	**
Reef flat	0.659	**

(Fig. 3a). After the nuclear tests (Fig. 3b, 3c), the first axis of variability serves either to discriminate the reef edge (1974, 1977) or the supralittoral zone (1987). In summary, before the nuclear tests, the supralittoral zone is the most different of all three zones in species composition, while after the tests the most different zone was either the reef edge or the supralittoral zone.

There is no supralittoral zone on Manchot. Before the nuclear tests, there is no clear differentiation of the reef edge and reef flat stations, similar assemblages being found on both sides of the dividing line (Fig. 4a, 1968). After the tests, the situation is even more mixed-up than before (Fig. 4b, 1972), but a clearer differentiation establishes itself with time; the results for 1987 are presented as an example (Fig. 4c).

The permutation tests performed on the canonical correspondence analyses axes clearly show that there are significant differences in faunal composition among zones for each of the three transects (Table 6). But, as will

be established more clearly with the *k*-means clustering results, several gastropod species are able to live in more than one zone.

Temporal evolution of the assemblages

On Terme Sud, the mean density of gastropods on the reef edge, the reef flat and the supralittoral zone were lower during the sampling periods (1969 and 1972) immediately following the 1968 nuclear test (Table 4). While reef flat pre-perturbation densities were re-established and even exceeded in the following years, the same cannot be said of the supralittoral zone and the reef edge; their gastropod densities always remained below their pre-perturbation level. A few species are responsible for that: species like *T. grandinatus* in the supralittoral zone, or *P. flexuosa* and *T. setosus* on the reef edge/reef flat, which were very abundant in 1968, had much reduced abundances following the perturbations (Table 1). Other species were more

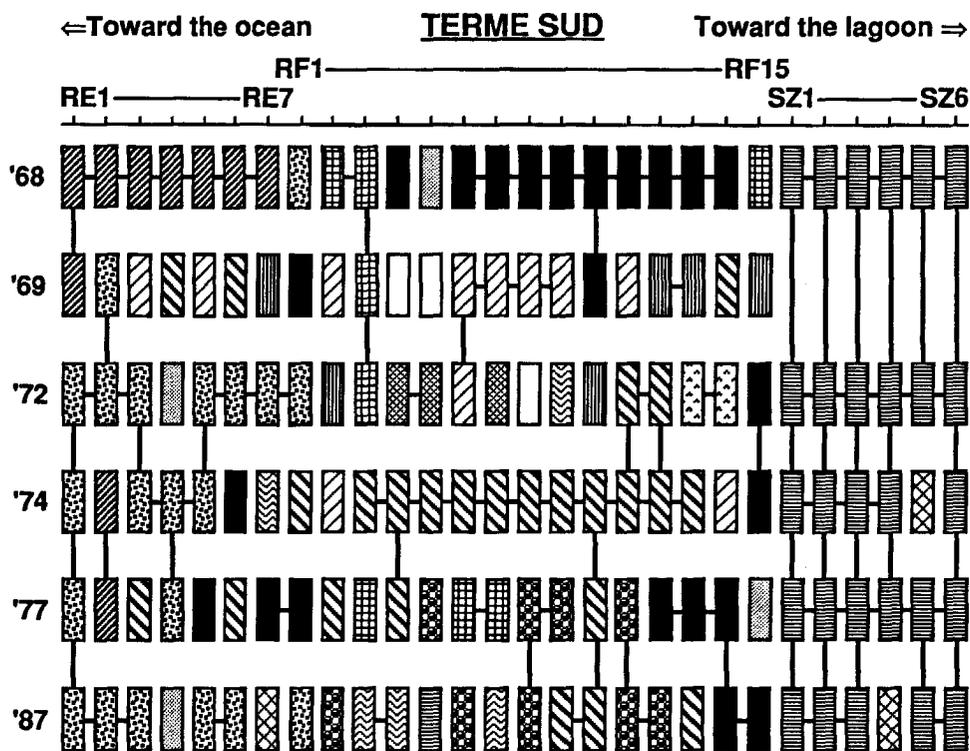


Figure 5

K-means cluster analysis across space and time on Terme Sud. RE: reef edge, RF: reef flat, SZ: supralittoral zone. Horizontal black lines link spatially contiguous stations clustered on the basis of their faunal composition; similarly for vertical black lines, that link similar stations through time. White boxes are empty stations (no gastropod found). Groups of quadrats are characterised by the following dominant species assemblages:

Morula uva; *Mitra litterata*, *Morula uva* and *Cerithium nesioticum*; *Morula uva* and *Conus sponsalis*; *Tectarius grandinatus* and *Nerita plicata*; *Mitra litterata*, *Morula granulata* and *Morula uva*; *Mitra litterata* and *Morula uva*; *Mitra litterata* with species of genus *Cerithium*; *Drupa ricinus*, *Morula granulata*, *Morula uva* and *Turbo setosus*; *Drupa grossularia*; *Drupa ricinus* and *Morula granulata*; *Nerita plicata* and *Tectarius grandinatus*; *Mitra litterata*; *Patella flexuosa*, *Turbo setosus* and *Drupa ricinus*; *Mitra litterata* with several other species.

abundant after the perturbations (*M. uva* and *M. litterata* on the reef edge/reef flat, *N. plicata* in the supralittoral zone), while a few others remained fairly constant through time (*M. granulata*, *C. miliaris*, *C. nanus*).

On H el ene, data collected immediately after the test are available only for the supralittoral zone; gastropod density dropped considerably, and then came back to an intermediate level. On the contrary, as of 1972, densities on the reef flat and reef edge were always higher than before the nuclear tests (Table 4). Table 2 shows that in the supralittoral zone, *T. grandinatus* had reduced abundances for the entire period following the perturbations, much like on Terme Sud. *P. flexuosa* had reduced abundances on the reef edge/reef flat following the perturbations but its abundance was back to its pre-perturbation level in 1987. On the reef edge/reef flat, *M. litterata*, *M. uva*, *M. granulata* and *D. ricinus* grew to much higher abundances following the perturbations.

On the Manchot transect, gastropod densities grew higher on the reef edge following the tests, while they remained lower on the reef flat (Table 4). A few species only are responsible for the situation on the reef flat (Table 3); the most important species in 1968 was *C. mutatum*

which never recovered from the perturbations. Several other species were more abundant after the perturbations (*D. ricinus*, *M. litterata*, *M. granulata*, *C. chaldeus*) while others showed abundance fluctuations with no clear pattern (*M. uva*, *C. nanus*).

Altogether, these results indicate that while the nuclear tests immediately reduced gastropod densities, they grew higher than the pre-perturbation levels in half the zones, and remained lower in the other half. The same applies to the species richness and diversity data (Table 5). Some pre-test dominant species became inconspicuous and were replaced by others, while other species seemed less affected by the perturbations.

The results of Kendall's coefficient of concordance for the reef edge, reef flat and supralittoral zone all indicate that species ranks remained fairly constant through time in each zone (Table 7). A notable exception is the low value for the supralittoral zone of H el ene. This is due to the 1969 change in ranks between *N. plicata* and *T. grandinatus*. Since there are only five sampling years and two species present, this single change greatly influenced the value of the coefficient of concordance. Overall, since Kendall's coefficient *W* is based on species ranks and not on the numerical values

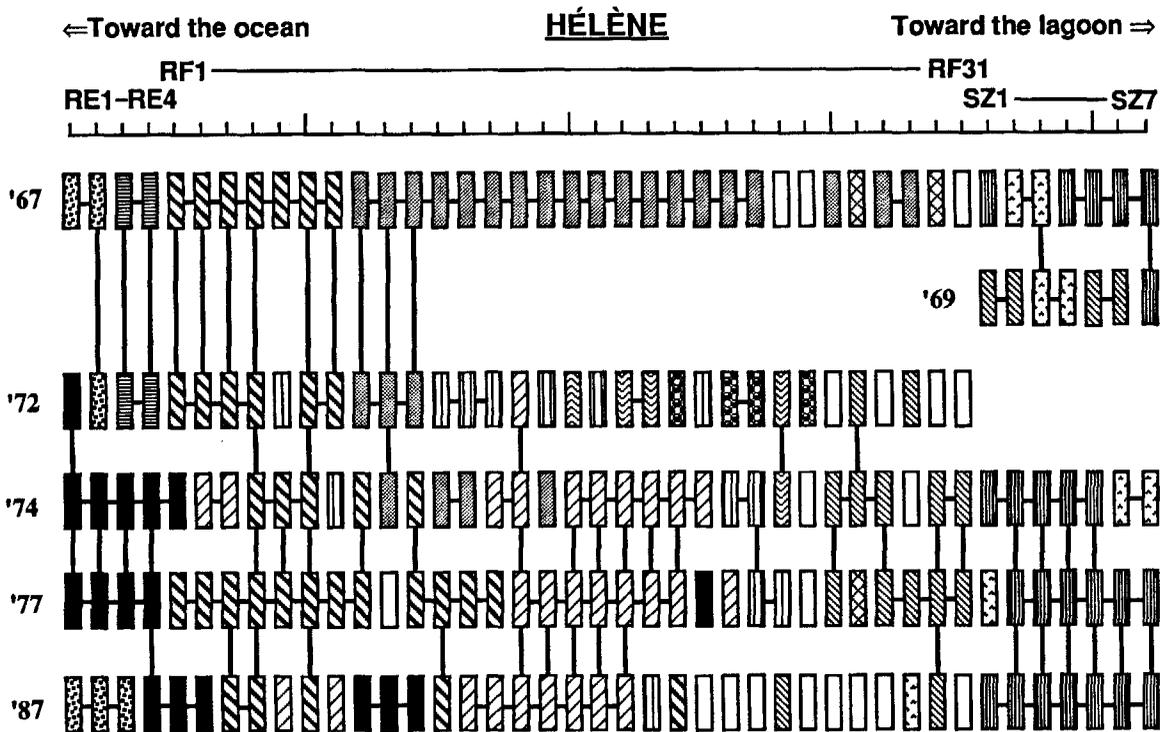


Figure 6

K-means cluster analysis across space and time on H el ene. Groups of quadrats are characterised by the following dominant species assemblages:

- Patella flexuosa*, *Turbo setosus* and *Drupa ricinus*; *Drupa ricinus* and *Morula uva*; *Tectarius grandinatus* and *Nerita plicata*;
- Morula uva*, *Morula granulata*, *Mitra litterata* and *Conus nanus*; *Mitra litterata* with several other species; *Nerita plicata*;
- Morula uva* and *Drupa ricinus*, both at high densities; *Nerita plicata* and *Tectarius grandinatus*; *Morula uva* and *Mitra litterata*;
- Morula uva* and species of the superfamily *Conacea*; *Morula granulata*; *Morula uva*; *Conus nanus*.

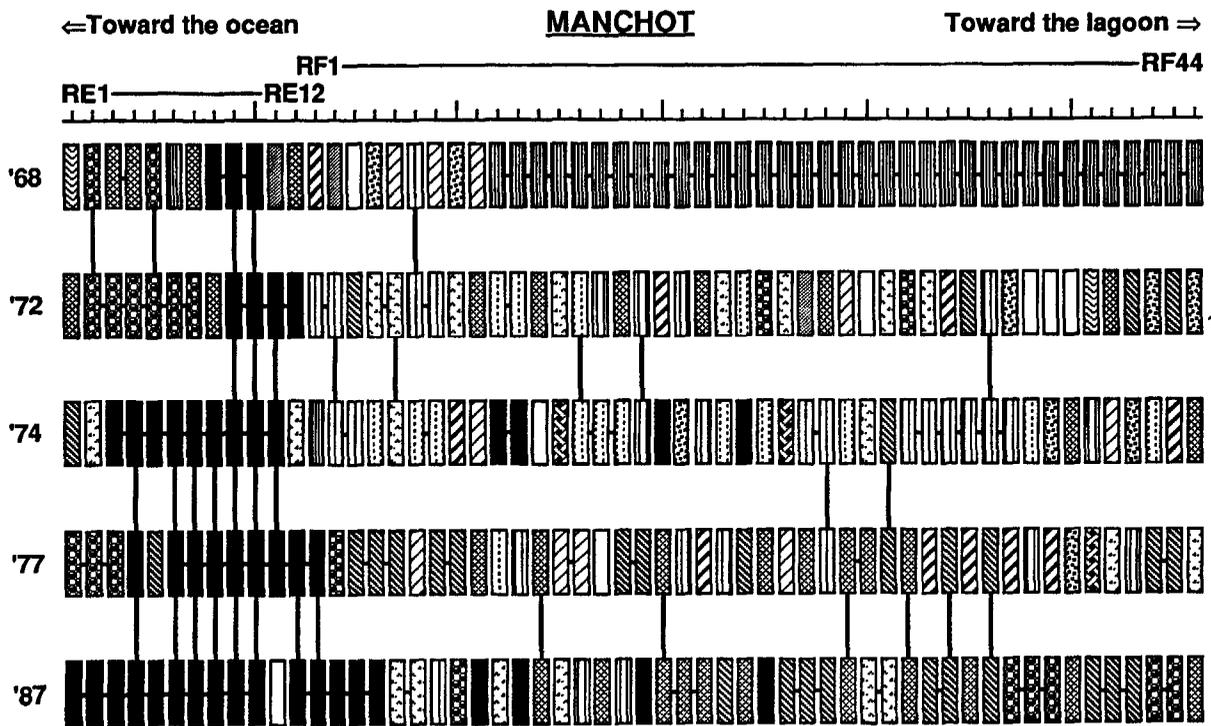


Figure 7

K-means cluster analysis across space and time on Manchot. Groups of quadrats are characterised by the following dominant species assemblages:

- *Mitra litterata*, *Conus nanus* and *Morula granulata*; ■ *Cerithium mutatum*, *Morula uva* and *Conus* spp.; ▨ *Morula uva* and *Imbricaria conovula*; ▩ *Mitra litterata* with several other species; ▧ *Morula uva* and *Mitra litterata*; ▦ *Cerithium mutatum*, *Morula uva* and *Conus nanus*; ▥ *Morula uva* and *Conus nanus*; ▤ *Morula uva* and *Drupa* spp.; ▣ *Drupa grossularia*; ▢ *Conus ebraeus*; □ *Mitra litterata* and *Conus nanus*; ■ *Drupa morum*; ▟ *Conus miliaris* and *Conus nanus*; ▞ *Morula uva* and *Conus ebraeus*.

of species abundances, these results are not incompatible with what was found for species densities. They simply indicate that most numerically important species remained important while most rare species remained rare in each zone of each transect.

The *k*-means clustering results for the spatio-temporal data are presented as arrays of shaded rectangles representing species assemblages, whose codes are explained in Figures 5 to 7. The rows of each array are the sampling years, while the columns are the stations on the reef. Stations that are contiguous horizontally or vertically and have the same species composition (same shading) are linked by lines.

The *k*-means results show that the faunal compositions of the supralittoral zones of Terme Sud and H el ene did not change much through time, except in 1969 on H el ene. The reef edge and reef flat assemblages of each transect, which were fairly homogeneous before the perturbations, differed markedly after. Several stations of the reef edge and reef flat have the same faunal composition on Terme Sud. The same phenomenon can be observed on Manchot, but it is rarely the case on H el ene where the reef edge

is very short. Supralittoral zone assemblages are rarely, if ever, found on the reef edge or reef flat, but *N. plicata*, a common gastropod in the supralittoral zone, has been able to colonise parts of the reef flat on H el ene. Finally, the spatial structure of reef edge or reef flat gastropod assemblages may change through time on any given transect. For example, the gastropod assemblage on the reef flat of Terme Sud (Fig. 5) has a fairly homogeneous structure in 1968 and 1974 (several contiguous stations with the same faunal composition), but this structure is patchy in 1972, 1977 and 1987 (contiguous stations do not have the same faunal composition). Another example is the reef edge of Manchot which had a patchy structure in 1968 but a very homogeneous one in 1974 to 1987.

DISCUSSION

Spatial structure of the transect

Most studies have shown that gastropod densities on coral reefs are higher in the intertidal than in the subtidal zones (Kohn, 1971; Salvat, 1970). On Fangataufa, this difference

has been observed between the reef edge and the reef flat for the past twenty years. One of the reasons invoked to explain this trend is that predation on reef-dwelling gastropods by fish and crabs is more intense in subtidal areas (Leviten, 1978).

If this pattern of higher gastropod densities holds when we compare the reef edge to the reef flat, the situation is different when we compare the reef flat to the supralittoral zone. Here, most of the time, gastropod densities have been higher on the reef flat. Salvat (1970) indicated that gastropods were more abundant in the supralittoral zone. This was the case on Terme Sud in 1968 and on Hélène in 1967 but, after the tests, densities remained higher on the reef flat. Since so little work has been done in this zone on coral reefs, it is difficult to explain such a pattern.

If densities are higher in intertidal zones, species richness and diversity have been found to be higher in the subtidal (Kohn, 1971; Salvat, 1970). This pattern has been found on Fangataufa atoll for species richness, and a similar trend has been found for species diversity. Reef flats have more diverse substrates than what we find on reef edges and in supralittoral zones. This higher diversity of substrates increases the diversity of micro-habitats on reef flats, which in turn is believed to increase the diversity and richness of gastropod assemblages (Kohn and Leviten, 1976).

Gastropod assemblages found in different reef zones are not always different. There were several instances where stations of the reef flat had a similar faunal composition as stations of the reef edge or the supralittoral zone. Similar observations were made by McClanahan (1990) on coastal reefs in Kenya. Since the reef edge, reef flat and supralittoral zone provide different abiotic conditions (substrate type, wave exposure, desiccation stress, etc.), this strongly suggests that several reef-dwelling gastropods are able to cope with a wide range of abiotic conditions. Spatial segregation of assemblages due to the sensitivity of gastropods to these abiotic conditions, if present, should have been particularly severe on Fangataufa since the geomorphological transition between adjacent zones takes place within just a few metres. This was clearly not the case at some of these transition points (Figs. 6, 7). Of particular importance here is the fact that the nuclear tests did not change the topography of the reefs (BS, personal observations), so that the abiotic conditions did not change much during the twenty year period of the present study.

Temporal evolution of the assemblages

The nuclear atmospheric tests did not reduce the densities of several gastropod species for long. As early as 1972, several species had higher abundances than their pre-perturbation levels. If we consider that our sampling method provides an accurate estimation of gastropod densities, several species were therefore able to recolonise the perturbed reefs rapidly. Since the only possible way to recolonise these reefs is by recruitment of larvae, recruitment limitation does not seem to be a problem for several of the most important species (*M. uva* and *M. litterata* for instance). The same kind of fast recovery by reef-dwelling benthic invertebrates after a perturbation

was noted by Fisk and Harriott (1990), Hunte and Younglao (1988) and Moran and Reaka-Kudla (1991).

Readers may be concerned about the possibility of mutations caused by ionising radiations resulting from nuclear tests. Although this question is academically interesting, it does not apply to the present study, for the following reasons. (a) To our knowledge, no genetic study has been made on gastropods, neither on Fangataufa, nor on Enewetak Atoll (Marshall Islands) where the USA conducted nuclear tests from 1948 to 1958 (Devaney, 1987). However, genetic studies have been carried out on coral reef fish populations in several islands of French Polynesia, including Mururoa where nuclear tests have also been conducted as in Fangataufa (Planes, 1993; Planes *et al.*, 1993). These works have evidenced no genetic differences between Mururoa and the other reef populations. (b) Field observations on Fangataufa reported in this paper, that extended for twenty years after the nuclear tests, have turned up no morphologically detectable mutant gastropods. (c) Reproduction cycles of molluscs are annual, and larvae are recruited from the sea; recruitment is not essentially from locally breeding individuals. Mutants, if any, would be unlikely to come back to the atoll, provided they had managed to survive.

The fact that several gastropod species on Fangataufa do not seem to be recruitment-limited may represent a normal situation for coral reefs of the south tropical Pacific region. At a spatial scale of hundreds to thousands of square kilometres, coral reefs of this region have a patchy spatial distribution. Most gastropod species considered in this study have a pelagic larval stage that can last for several days. Scheltema (1986*a*, 1986*b*) and Scheltema and Williams (1983) have shown that reef-dwelling invertebrate larvae can travel considerable distances in the south tropical Pacific (several hundred to several thousand kilometres). This fact suggests that exchanges of larvae between islands is probably a common phenomenon and it is one of the reasons invoked to explain the very low level of endemism of reef invertebrates in this vast oceanic region. In this area, recruitment limitation would probably occur only if several islands were affected simultaneously by a perturbation, which would therefore reduce the pool of reproducing adults on a regional scale. Lessios (1988) and Karlson and Levitan (1990) made similar comments for the Caribbean Sea. Another way by which recruitment limitation could take place in this area is the isolation of an island by hydrodynamic processes.

It is interesting to note that the few important species that did not rapidly recolonise Fangataufa were all herbivores (*P. flexuosa*, *T. grandinatus* and *C. mutatum*). This is consistent with the destruction of the algal cover that resulted from the nuclear tests (BS, personal observations).

The fact that several species are showing different patterns in the temporal evolution of their abundances could indicate that interactions among these species are weak. This is not a surprise if we consider that studies in the last thirty-five years have shown that most of these species have distinct diets (Kohn, 1959; Kohn, 1970; Taylor, 1976) and that space does not seem to be a limiting resource for reef-dwelling gastropods (Leviten and Kohn, 1980; Reichelt,

1982). Since several species are exhibiting quite different temporal patterns in their abundances (Tables 1-3), this might also indicate that the mechanisms regulating the density of each species is different, or that there are not one but several types of regulating mechanisms in these assemblages. If this is the case, studying this group of benthic invertebrates could prove to be extremely difficult.

Superimposed to these fluctuations in species abundances is the fact that species ranks remained fairly constant through time. Such an observation strongly suggests that there are mechanisms structuring these assemblages but, because of the different patterns in species abundances that we noted earlier, they are probably not acting with the same strength on each species.

The supralittoral zone has always been occupied by *T. grandinatus* and *N. plicata*. This is mainly due to the fact that the abiotic conditions in this zone are particularly severe (strong desiccation stress for instance) and that few species are able to cope with it. The same cannot be said of zones like the reef edge and reef flat where the faunal composition changed through time.

Changes occurred in the spatial structure of these assemblages. The spatial structure within the reef edge or reef flat was patchy in several years and homogeneous in others. To explain such variations is especially difficult because there are several possible mechanisms involved. Predation could affect the spatial distribution of several gastropod species (McClanahan, 1990), as could natural perturbations or stress (Leviten and Kohn, 1980; McClanahan, 1992). No hurricane occurred on Fangataufa, at least since 1975 (information not available before this period); it is then clear that the changes observed between 1977 and 1987 are probably not due to perturbations of that magnitude. Another partial explanation of the changing spatial pattern could be that changes occurred in the spatial distributions of the preys of several of the carnivorous gastropods. Here, we have to keep in mind that most of the carnivorous gastropods under study on Fangataufa have very specialised diets (Kohn, 1959; Kohn, 1970; Taylor, 1976). Therefore, their spatial distributions must be strongly influenced by the distributions of their preys. The influence of the spatial distributions of preys on the spatial distributions of reef-dwelling carnivorous gastropods has never been addressed up to now. Such studies could be particularly useful when we consider that food could be a limiting resource for several carnivorous species in subtidal zones like the reef flats (Leviten, 1978).

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Are reef-dwelling gastropod assemblages stable?

Our observations on Fangataufa give us clues to answer this question. If we compare the pre-perturbation to the post-perturbation assemblages, it is clear that the reef edge and reef flat assemblages are not stable because pre-perturbation abundances and their spatial structures were never re-established. The only time we observed some kind of constancy in these zones was when we considered species ranks. Moreover, stable spatial structures and abundances were never seen during the period following the perturbations (possible exceptions are the spatial structures on the reef edge of Manchot and the reef flat of Hélène; note however that abundances in these two zones changed constantly). If, like we noted earlier, several species are able to cope with a wide range of abiotic conditions, such instability in the spatial structure could be a natural situation. Furthermore, the fact that different gastropod species might have their densities regulated by different mechanisms could imply that the densities of these assemblages are naturally unstable. Reise (1991) showed recently that the concept of stability might not be relevant when one considers the spatial structure and the density of marine benthos through time; his paper covers a wide range of benthic communities (rocky shores, kelp forests, biogenic reefs, mud and sand). In his point of view, mosaic cycles are probably a more realistic way of considering the structure of benthic communities. The assumptions of his model seem to fit well what was observed on the reef edge and reef flat of Fangataufa.

On the contrary, the supralittoral zone assemblage was characterised by a stable spatial structure. This is probably a normal situation since only a few species are able to cope with the severe abiotic conditions that prevail in this zone. Nevertheless, gastropod densities in this zone never came back to pre-perturbation levels but stayed relatively constant through time. The reason why this happened is not understood.

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