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Thirty-year recovery of mollusc communities after nuclear experimentations on Fangataufa atoll (Tuamotu, French Polynesia)

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A 30-year study of temporal changes in gastropod community structure on the reefs of a Pacific Ocean atoll (Fangataufa, Tuamotu Archipelago) subjected to atmospheric nuclear tests during the 1960s offered the opportunity for an otherwise impossible field experiment that could help ecologists understand mollusc primary succession. Reef molluscs were partly or entirely wiped out by the heat of the nuclear tests and the reefs were recolonized by ocean larvae. On all reefs, community composition before the tests was very different from what it evolved to afterwards. A new method of analysis was developed to study the temporal variation in community composition before versus after the tests (temporal beta diversity). Analyses showed that community compositions diverged through time among the reefs. Only some species can survive the harsh conditions of supralittoral zones, so the same species recolonized them; environmental filtering controlled the development of the new communities. In the reef flat and edge zones, differences in community composition seem to be the result of neutral stochastic colonization by larvae coming from the open ocean. All reefs developed a community composition quite different from that before the nuclear tests.

1. Introduction

Are ecological communities structured by internal or external forces, or by random processes? Internal forces include species interactions (e.g. competition and predation); external forces refer to environmental factors filtering species according to their niches; among random processes, random dispersal is most important in ecology.

To answer the question above, one ideally has to compare communities before and after a major catastrophic event that wipes out communities and restarts primary succession. In nature, this happens after landslides, earthquakes or volcanic eruptions, for example. In this paper, we will take advantage of atmospheric nuclear tests conducted on an atoll in the Pacific Ocean for which we were invited to conduct ecological monitoring; the tests offered the occasion for an otherwise impossible field experiment. The nuclear tests annihilated previous reef communities. The new communities that developed on the exposed reefs were compared with the communities surveyed before the tests to assess hypotheses about recolonization mechanisms of the reefs.

A long-debated question is whether species assemble into communities following describable rules, or if the assemblages are formed by random ecological processes. Much theoretical work has been published during the last quarter of the twentieth century. Studying birds, Diamond [1] provided rules describing mechanisms through which competition and niche overlap

determined species assemblages. Connor & Simberloff [2] criticized this approach by showing that many of Diamond's rules were tautological and did not lead to predictions that can be tested against empirical evidence. Some of the rules led to predictions that could be tested, though. The proposed mechanisms behind assembly rules are now usually tested using null models [3,4]. In opposition to assembly rules, Hubbell [5] proposed in his neutral theory that the diversity of species in a community is determined mostly by random dispersal (e.g. of larvae in animals, or propagules in plants), speciation and extinction.

Fangataufa atoll (22°14' S, 138°43' W; figure 1a), located in the Tuamotu Archipelago in south-central Pacific (French Polynesia), has been used as a nuclear testing site. Four atmospheric nuclear tests were conducted between 1966 and 1970, followed by underground tests until 1996. The French Direction des Centres d'Expérimentations Nucléaires asked ecologists to survey the evolution of the mollusc communities on reefs impacted by the nuclear tests. Monitoring the ecological impact of this experiment will hopefully help marine ecologists understand the primary succession and the following structuring of mollusc communities on reefs after they were partly or entirely wiped out by the nuclear tests.

This paper compares the observations across surveys over 30 years and makes comparisons between reefs to assess hypotheses about the mechanisms that determined recolonization. We will determine whether the mollusc assemblages found on three reefs after the tests were the same or different from those found before. Recurrence of similar assemblages before and after the tests would support environmental control (species sorting), whereas different assemblages would indicate random (neutral) processes, which may include replacement by ecologically equivalent or different species.

2. Surveys on Fangataufa atoll

Surveys were done on the supralittoral zones, reef flats and reef edges of two outer reefs and one inner reef of the atoll (figure 1).

Transect Terme Sud (35 quadrats; see §4), located on the outer reef on the southern side of the atoll, is highly exposed to the swell. The original transect that was surveyed from 1968 to 1987 was located at 22°16'30" S, 138°44'48" W (position of a steel peg cemented on the conglomerate in 1987, quadrat 23). In July 1996, a storm with strong southerly winds (25 knots) hit Fangataufa, causing strong swell and 8 m waves on the southern side of the atoll, including the Terme Sud site. The swell broke coral colonies from the outer slope and transported coral blocks that covered the Terme Sud transect that had been surveyed from 1968 to 1987. Considering the geomorphologic homogeneity of the zone, a new transect was established 30 m to the east, at 22°16'30–31" S and 138°44'48–50" W, and used for the 8 May 1997 survey.

Transect Hélène (42 quadrats), located on the outer reef on the western side of the atoll, is moderately exposed to the swell. The position of a steel peg located between the reef flat and the supralittoral zone is 22°15'28" S, 138°45'42" W.

Transect Manchot (60 quadrats), located on the inner reef on the northwestern side of the atoll, is sheltered from the swell. At high tide, waves breaking on the outer reef supply it with ocean water. The position of a steel peg cemented on the reef flat in 1987 at quadrat 40 is 22°12'45" S, 138°46'99" W.

Eight field surveys were conducted on the three reefs from 1967 to 1997. Reef Hélène was sampled in October 1967 and the other two (Terme Sud and Manchot) in March 1968. During the 1969 expedition, there was only time for the survey of two reefs, Hélène and Terme Sud. In 1972, 1974, 1977, 1987 and 1997, all three reefs were surveyed.

The field surveying methods were the same during all surveys. The transects, marked by metal posts, were the same except for a small change in the position of Terme Sud in 1997, described above. Descriptions of the geomorphology of the transects can be found in papers by Salvat [6] and Lanctôt *et al.* [7]. The transect profiles are shown in figure 1b–d. The Terme Sud and Hélène transects present a high reef edge forming an algal crest beaten by strong waves and swell from the ocean, followed by a reef flat and a supralittoral zone of grey coral blocks cemented together, called conglomerate. The Manchot reef is located inside the lagoon. Its edge is low, mostly consisting of coral instead of massive red calcareous algae, followed by the reef flat, without a supralittoral zone. Preliminary results of the 1967–1977 observations were published in the scientific literature by Lanctôt *et al.* [7].

3. Nuclear tests and other anthropogenic impacts on the reefs

The following atmospheric nuclear tests were conducted by the French Direction des Centres d'Expérimentations Nucléaires between 1966 and 1970:

- On 24 September 1966, the *Rigel* test (125 kt) was conducted on a barge anchored in the lagoon. It had little impact on the outer reefs of the atoll.
- On 24 August 1968, *Canopus* (2.6 Mt, on a platform held by a moored balloon) was the most powerful test in French Polynesia. The blast, conducted at low tide, burned all vegetation on the atoll and caused important damage to the supralittoral zone, reef flat and reef edge (algal crest) mollusc communities, which were mostly eliminated.
- 30 May 1970, *Dragon* (945 kt, on a platform held by a moored balloon) also had major effects on communities.
- 2 August 1970, *Orion* (72 kt) had more limited effects.

Another man-made perturbation affected the inner reefs in 1965. See electronic supplementary material, appendix S3.

4. Surveying method

Molluscs were selected as the target taxonomic group to survey the effects of atmospheric nuclear tests on reefs because they are unmoving or slowly moving organisms. After disturbance or annihilation, populations can be replenished by larvae living in the ocean and the lagoon, which settle in suitable locations. Another interesting aspect of mollusc communities is that they can be sampled on outer reefs without recourse to boats and other heavy equipment.

Molluscs that were emerged at low tide were unprotected against the heat of nuclear blasts. On the reef flat, molluscs living in puddles where water remained at low tide were protected by seawater. On the reef edge (algal crest) and in the supralittoral zone, the heat flash was also very destructive.

In this study, a sampling unit is a portion of a transect: either the supralittoral zone, or the reef flat and reef edge together. A rope ladder was positioned on the reefs forming

a transect perpendicular to the shoreline, with three parts on Terme Sud and Hélène (reef edge, reef flat and supralittoral zone) and two parts on Manchot (reef edge and reef flat). The ladder delimited 6 m² quadrats (3 m long × 2 m wide). All gastropods present in each quadrat were collected, identified to species and counted, except for vermetids (tube worms) and hipponicids (gastropods), which could not be accurately counted.

Bivalves were only found on the Manchot reef flat (*Chama croceata* and *Tridacna maxima*; electronic supplementary material table S1.5, appendix S1), except for a few *Isognomon isognomum* (*Isognomonidae* family) found on the reef flat bordering the conglomerate on Terme Sud and Hélène. The *Isognomon* were not counted because they were attached under decimetre-length erratic blocs transported across the flat by waves when the swell is important at high tide. In addition to molluscs, a sea cucumber (echinoderm) species was found in fair abundance on Manchot (electronic supplementary material, table S1.5). Manchot is an inner reef where sea cucumbers are not washed away by the surf and can maintain a population. The counts of that species were kept in the data subjected to the analyses because they were part of the sedentary reef fauna.

5. Statistical methods

The following methods were used in the analyses.

(a) Alpha diversity

Alpha diversity for the various transects and years was estimated by the species richness, the Shannon diversity index H and the exponential of H , which is Hill's [8] diversity number N_1 . N_1 is a more easily interpretable estimator of alpha diversity than H [9].

(b) Redundancy analysis

Redundancy analysis (RDA) [10] (see also [11]) is an extension of multiple regression that allows one to explain (in the same sense as in regression analysis) the variation of a multivariate response data table (here, mollusc community composition data) using explanatory variables (here, a second-degree polynomial function of time). A linear function of time would only have allowed us to model the variation in community composition among years as a straight line, whereas a second-degree polynomial function allowed the community time series to double back upon itself, as will be seen in the results. In the analyses made separately for the three transects, the linear and quadratic functions of time were both significant explanatory variables of the community variation among years. RDA produces the same sort of test of significance as linear regression analysis. It also produces ordination plots that allow one to visualize the relationships between the observations (sampling years in our study) and the species. RDA were computed on log-transformed data, $y' = \log(y + 1)$.

(c) Beta diversity for surveys along time

Beta diversity is the variation in community composition among sites in a study area, or among survey times for a survey across years. The total variance of the community composition data is a convenient and flexible measure of that variation if the community composition data have been

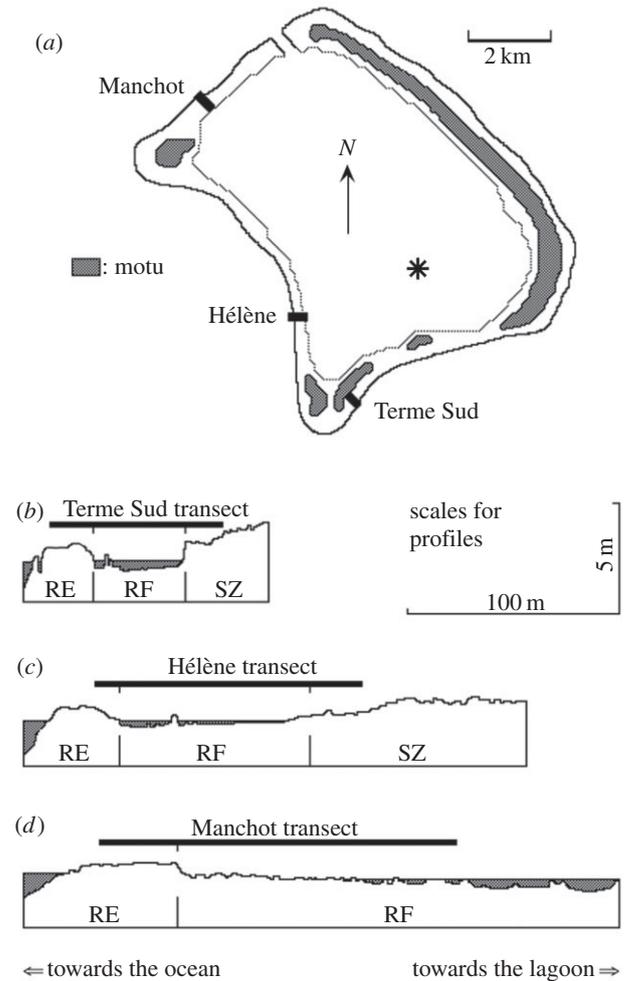


Figure 1. Map of the Fangataufa atoll showing (a) the transects perpendicular to the shoreline (black rectangles) and (b–d) their profiles at low tide. The horizontal lines above the profiles identify the sampled transects, divided into zones: RE, reef edge; RF, reef flat; SZ, supralittoral zone; motu, reef islet with vegetation. Asterisk represents the approximate position of the nuclear firing platform for all atmospheric nuclear tests.

transformed in an appropriate way [12]. The Hellinger transformation [13] is a widely used and suitable transformation; it consists of dividing all abundances by the sampling unit (row) sum and taking the square root of the result. After that transformation, the Euclidean distance among the rows of transformed data is the Hellinger distance among the original data, and that is one of the distances suitable for beta diversity studies [12]. The total variance, or total beta diversity (BD_{Total}), computed on Hellinger-transformed data is a value between 0 and 1, which is comparable among study sites provided that the sampling units are of the same size; that is the case in this study.

(d) Local contributions to beta diversity for surveys along time

BD_{Total} can be partitioned into contributions of individual sampling units, called local contributions to beta diversity (LCBD) indices [12]. These indices, which sum to 1 for a given data matrix and can be tested for significance, indicate how exceptional each sampling unit is, compared with a synthetic unit with mean species composition. Legendre & Gauthier [14] have shown that BD_{Total} and LCBD indices can also be computed for repeated surveys forming a time series. In this study,

these indices will be computed separately for each transect (Terme Sud, Hélène and Manchot) across the surveys that took place between 1967 and 1997. The tests of significance of the LCBD indices will indicate which years were significant, and thus exceptional in community composition, compared with the other survey years on each transect.

(e) Before–after analyses

We analysed the survey data (electronic supplementary material, appendix S1) to answer the following question: after the nuclear tests, were the assemblages generated during primary succession similar to those found before the tests? Strong similarity (i.e. small dissimilarity) would support the hypothesis of environmental control (species sorting by environmental conditions). Or were the assemblages different, and if so, were some (or many) species replaced by functionally similar or different species? A mixture would be in agreement with the hypothesis of random (neutral) processes, partly or entirely independent of the environmental conditions. Neutral primary succession can produce species replacement by functionally equivalent or non-equivalent species.

We examined the data of the reef flat and edge zones of the three transects (electronic supplementary material, tables S1.1, S1.3 and S1.5). We compared the pre-test data (1967 or 1968) with the 1972 to 1998 post-test data in turn. We did not use the 1969 data from Terme Sud because additional nuclear tests took place in 1970 (see §3); we used only the pre-*Canopus* and post-test surveys in these analyses.

For each comparison of two survey vectors, y_1 and y_2 , we computed the following indices for the herbivore and carnivore feeding categories (electronic supplementary material, appendix S1). Results for the detritivores and filter feeders are not reported because there were too few species.

- a_j is the part of the abundance of species j that is common to the two survey vectors: $a_j = \min(y_{1j}, y_{2j})$. A is the sum of the a_j values for all species in the functional group under study. It represents the unscaled similarity between two surveys.
- b_j is the part of the abundance of species j that is higher in survey 1 than in survey 2: $b_j = y_{1j} - y_{2j}$. B is the sum of the b_j values for all species in the functional group under study. It is the unscaled sum of species losses between time 1 and time 2.
- c_j is the part of the abundance of species j that is higher in survey 2 than in survey 1: $c_j = y_{2j} - y_{1j}$. C is the sum of the c_j values for all species in the functional group under study. It is the unscaled sum of species gains between time 1 and time 2.

The values A , B and C are the building blocks of well-known quantitative dissimilarity coefficients used in community analysis to estimate beta diversity, in particular, the Ružička (D_R) index $(B + C)/(A + B + C)$ and the percentage difference ($D_{\%diff}$) index $(B + C)/(2A + B + C)$, described, for example, by Legendre [15]. B and C express the directionality of the process of losses and gains of individuals between two surveys. The graphs in the Results section show B and C scaled by division by $(A + B + C)$, as well as the D_R dissimilarity, which measures temporal beta diversity. Values of these three indices are in the $[0, 1]$ range. When applied to presence–absence data, D_R becomes the Jaccard dissimilarity index and $D_{\%diff}$ becomes the Sørensen index.

We carried out the before–after analysis of the supralittoral zone data of the two outer reefs by visual inspection. That was sufficient to draw conclusions because only a few species were capable of surviving in the harsh conditions of water shortage found therein. Analysis did not require computation of the indices described in the previous paragraph.

(f) Software

The calculations were performed in the R language [16]. Alpha diversity indices were computed using the *diversity()* function of the *vegan* package [17]. Redundancy analyses were computed with the *rdaTest* package available on <http://adn.biol.umontreal.ca/~numeralecology/Rcode>. BD_{Total} and LCBD indices were computed with function *beta.div()* [12] (electronic supplementary material, appendix S4). A simple ad hoc R function was written to compute indices for the before–after comparison.

6. Results

Gastropod counts along the sampling years on the three transects are presented in electronic supplementary material, appendix S1. Electronic supplementary material, table S1.6 reports the scientific names of species collected on the transects following current nomenclature, the synonyms used in [7], as well as the species feeding categories.

(a) Reef flats and edges of the outer reefs (Terme Sud and Hélène)

Alpha diversity values and total numbers of animals are reported in table 1. On Terme Sud, fewer animals were found after the *Canopus* test (August 1968) than before; numbers increased again during the following surveys. On both reefs, species richness was higher after *Canopus* than before, indicating that the reefs were again suitable habitats for the fauna and that primary colonization by larvae brought in a good diversity of molluscs. On both reefs, the N_1 diversity number was higher (or about equal) in 1972 than in 1967 or 1968.

After Hellinger transformation of the data, BD_{Total} among years was 0.162 on Terme Sud (7 data years) and 0.107 on Hélène (6 data years). For both transects, yearly LCBD indices were high and significant for the first year only, which is, before the *Canopus* nuclear test in August 1968 (table 2).

The RDA biplots show the among-year variation (figure 2a,b). Different species displayed different patterns of variation along the years:

- *Scutellastra flexuosa* was a characteristic species on Terme Sud in 1968, where it was found exclusively on the reef edge. It had completely disappeared during the 1969 to 1977 surveys, to reappear in 1987 and 1997. On the reef flat, a group of species increased in abundance from 1969 to 1977 and a few species, not seen or rarely seen previously, appeared in 1987 (*Nerita plicata*) and 1997 (e.g. *Mancinella armigera*, *Drupa morum*) (figure 2a; electronic supplementary material, table S1.1).
- On Hélène, *S. flexuosa* was also a characteristic species of the reef edge in 1967. It had nearly disappeared at the time of the 1972 to 1977 surveys, to reappear in 1987 and 1997. On the reef flat, a group of species increased in abundance from 1972 to 1987 (*Mitra litterata*, *Tenguella granulata*, *Morula*

Table 1. Alpha diversity indices and total numbers of animals per year for the three transects.

	1967 October	1968 March	1969 March	1972 January	1974 October	1977 September	1987 January	1997 May
Terme Sud transect								
<i>reef flat and reef edge</i>								
richness	—	10	12	15	16	16	17	18
Shannon H	—	1.88	1.76	2.11	1.96	1.96	2.36	2.29
$N_1 = \exp(H)$	—	6.57	5.79	8.29	7.12	7.08	10.62	9.87
total animals	—	446	163	342	489	361	335	332
<i>supralittoral zone</i>								
richness	—	2	—	2	2	3	2	5
Shannon H	—	0.20	—	0.39	0.63	0.55	0.69	0.69
$N_1 = \exp(H)$	—	1.22	—	1.47	1.88	1.74	1.99	2.00
total animals	—	266	—	54	85	87	99	193
Hélène transect								
<i>reef flat and reef edge</i>								
richness	12	—	—	14	14	12	15	14
Shannon H	1.99	—	—	1.98	1.61	1.02	1.63	1.90
$N_1 = \exp(H)$	7.32	—	—	7.28	5.02	2.78	5.13	6.70
total animals	246	—	—	356	821	1259	1008	765
<i>supralittoral zone</i>								
richness	3	—	2	2	2	3	3	3
Shannon H	0.58	—	0.68	0.58	0.44	0.31	0.91	0.74
$N_1 = \exp(H)$	1.78	—	1.97	1.78	1.55	1.36	2.48	2.10
total animals	567	—	58	19	133	174	253	262
Manchot transect								
<i>reef flat and reef edge</i>								
richness	—	21	—	17	23	20	19	19
Shannon H	—	1.76	—	2.15	1.61	2.25	2.03	2.00
$N_1 = \exp(H)$	—	5.80	—	8.56	5.02	9.50	7.60	7.40
total animals ^a	—	995	—	382	776	616	964	1631

^a*Cerithium punctatum* not counted. See electronic supplementary material, table S1.5.

Table 2. LCBD indices per year and p -values (after 9999 random permutations) for the three reef flat and edge transects. The LCBD indices for each transect are relative values summing to 1; p -values ≤ 0.05 and the corresponding LCBD indices are in bold.

	1967 October	1968 March	1969 March	1972 January	1974 October	1977 September	1987 January	1997 May
Terme Sud transect								
LCBD per year	—	0.28	0.15	0.14	0.04	0.08	0.13	0.18
p -values	—	0.0375	0.3579	0.4382	0.9982	0.8892	0.4603	0.2249
Hélène transect								
LCBD per year	0.40	—	—	0.17	0.07	0.22	0.06	0.09
p -values	0.0022	—	—	0.4551	0.8427	0.2969	0.9014	0.7595
Manchot transect								
LCBD per year	—	0.46	—	0.11	0.16	0.07	0.09	0.11
p -values	—	0.0009	—	0.7593	0.4515	0.9804	0.8734	0.7392

uva) and a few species not seen previously appeared in 1997 (e.g. *Cerithium* sp., *Monetaria caputserpentis*; figure 2b; electronic supplementary material, table S1.3).

Additional canonical analyses (RDA) compared temporal community evolution on the two outer reefs, Terme Sud and Hélène, after the *Canopus* nuclear test. The explanatory variables

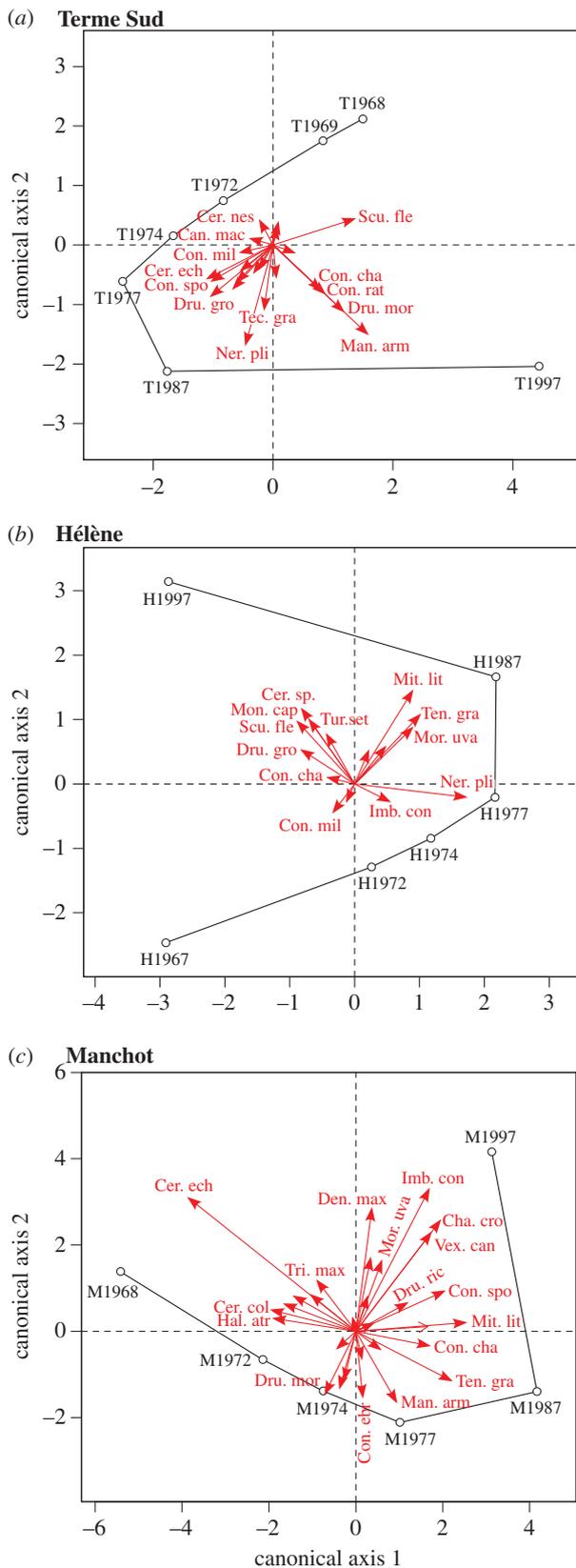


Figure 2. RDA biplots of the reef flat and reef edge data on (a) Terme Sud, (b) Hélène and (c) Manchot transects, showing the species (arrows) and sampling years (points). Name abbreviations of species with small loadings on the canonical axes (short arrows) were removed to improve legibility; see electronic supplementary material, tables in appendix S1 for full species names. The explanatory variables (not shown) formed a second-degree polynomial function of time. (Online version in colour.)

were again a second-degree polynomial function of time, plus a factor identifying the two transects. The differences in community composition between the two reefs were significant in the

supralittoral zone and on the reef flats and edges. The results, detailed in electronic supplementary material, appendix S2, clearly indicate that after the *Canopus* test, community compositions evolved differently on the two reefs. Significant indicator species [18,19] were identified in the reef flat and edge data (electronic supplementary material, figure S2.2); three species were specific to Terme Sud and four to Hélène.

(b) Reef flat and edge of the inner reef (Manchot)

Fewer animals were found after the *Canopus* nuclear test than before; numbers increased during the four following surveys (table 1). Species richness was about the same in all surveys. The N_1 diversity number was higher in 1972 than in 1968.

In the RDA biplot displaying among-year variation (figure 2c), different species had different patterns of variation along the years. *Cerithium echinatum* and the echinoderm *Halodeima atra* were very abundant in 1968; they nearly disappeared from that reef during all following surveys. A group of species increased in abundance from 1968 to 1997 (*Te. granulata*, *Drupa ricinus*, *Imbricaria conovula*, *Mi. litterata*, *Conus sponsalis*). *Mo. uva* was high in 1968, then low, then very abundant in 1997. *Dendropoma maxima* and *Ch. croceata* had medium abundances in 1968, then low, then medium again. Other species remained stable during the six surveys (*Conus ebraeus*, *Conus miliaris*, *Conus nanus*; figure 2c; electronic supplementary material, table S1.5).

The bivalves *Chama* and *Tridacna* completely disappeared from Manchot after the *Canopus* test. *Chama* came back to pre-test levels in 1977 and increased even more in 1997. The gastropod *Ce. echinatum* also nearly disappeared after *Canopus*.

(c) Before–after comparisons for the reef flat and edge data

Carnivores dominated on all three reefs: their proportions were 0.794 on Terme Sud, 0.865 on Hélène and 0.767 on Manchot (over six surveys: one before *Canopus* and five after).

Let us examine the graphs for Terme Sud (figure 3a,b) in detail to understand how to extract information. The left-hand graph concerns the 10 herbivorous species whereas the right-hand graph deals with the 14 carnivores. The abscissa indicates which surveys are being compared: the 1968 pre-*Canopus* survey is compared in turn with the five post-test surveys conducted from 1972 to 1997. The D_R (temporal beta) index computed for all species (grey circles) is shown in both graphs; it is fairly constant over the five comparisons, representing an average change of 62% in community composition. We see that the change among the herbivores (closed circles, left) is more important (86% on average) than among the carnivores (right, 48% on average). Among the herbivores (left), the abundance losses of several species (squares) of the pre-*Canopus* survey are large whereas the gains (triangles) of other species in the second survey are small. The opposite is true for carnivores (right), although the difference is smaller. In each graph, the losses and gains (squares plus triangles) sum to the dissimilarities (filled circles).

On Hélène (figure 3c,d), the overall dissimilarity between surveys (grey circles) is higher than on Terme Sud, representing a change of 77% on average, with a peak for the 1967–1977 comparison. Here, changes in herbivore abundances were higher during the first two comparisons than for carnivores (closed circles), nearly equal in the 1967–1977 comparison, and lower in the last two comparisons (on average, 72% for

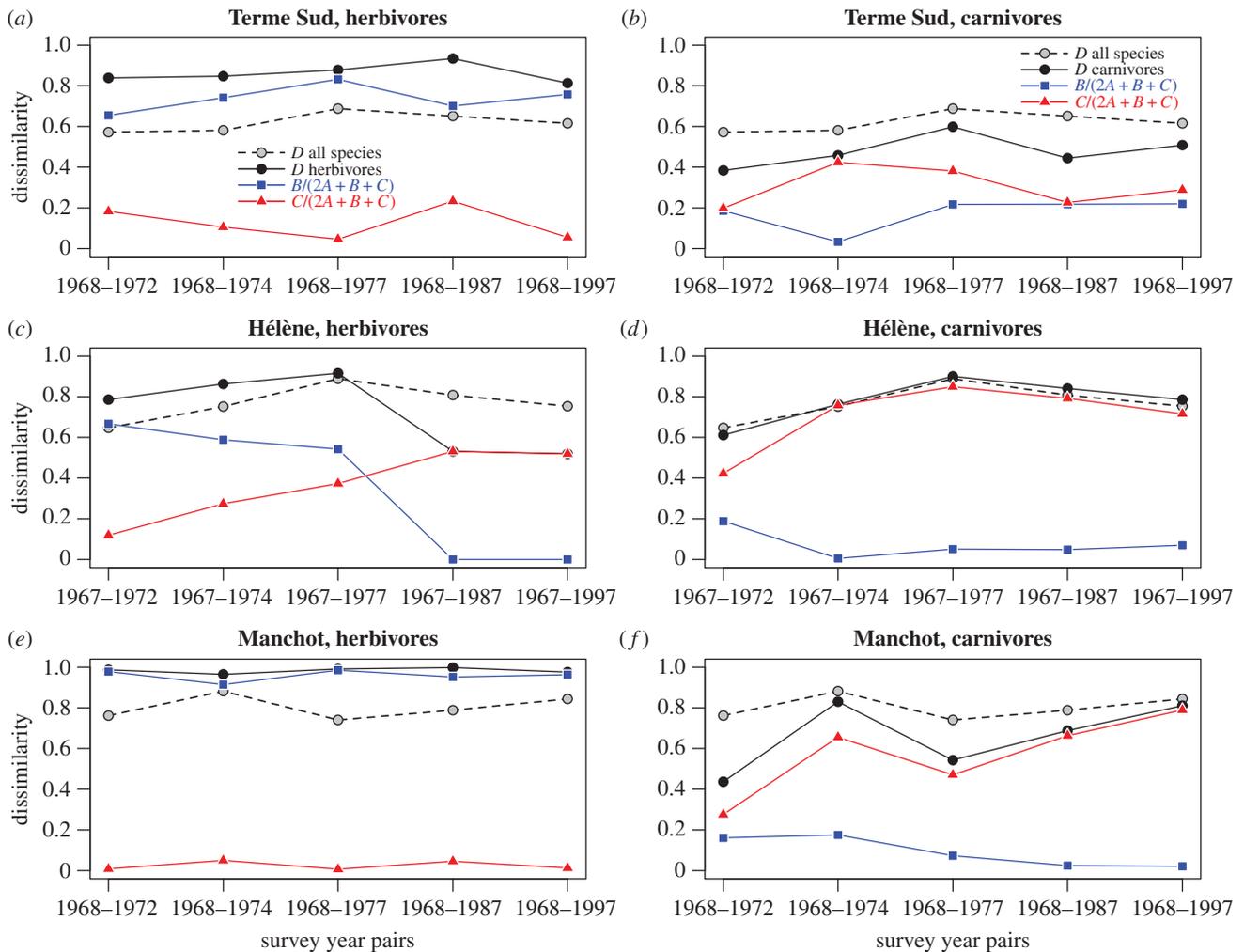


Figure 3. Before–after statistics comparing the pre-test (1967 or 1968) to the post-test surveys. (a,b) Terme Sud, (c,d) Héléne and (e,f) Manchot transects. The indices, represented by points joined by lines, are identified in the upper panel of each column; (a,c,e) herbivores; (b,d,f) carnivores. The indices are described in §5. (Online version in colour.)

herbivores and 78% for carnivores). Among the herbivores, two species found in 1967 were present again in 1972 with reduced abundances; they increased to higher abundances as time went by, and were joined by four other herbivore species (electronic supplementary material, table S1.3). This resulted in a decreasing curve of herbivore losses (squares), and an increasing gain of these and other herbivore species (triangles). Among the carnivores, the abundance losses (squares) of the nine species present in the pre-test survey were small whereas the gains in the post-test surveys (triangles) were large. The gains and losses of the detritivores are not plotted because they involved a single species.

On inner reef Manchot (figure 3e,f), the overall dissimilarity between surveys (grey circles) is the highest of the three surveyed transects, representing a change of 80% on average. The changes in herbivore abundances were higher in all survey pairs (closed circles, 98% on average) and lower for carnivores (66% on average). Among the herbivores, the losses of several species (squares) found in the pre-*Canopus* survey are very high for all survey pairs (91–98%), whereas the gains during the second survey of each pair (triangles) are very small (1–5%). Among the carnivores, the losses of some species found in the pre-*Canopus* survey (squares) are small and decreasing (from 16% to 2%), whereas the gains in the second survey of each pair (triangles) are increasing (from 28% to 79%). The gains and losses of detritivores and

filter feeders are not shown because they only involved two species in each case.

(d) Supralittoral zones of the outer reefs (Terme Sud and Héléne)

Most animals found in the supralittoral zone were killed by the heat flash of the nuclear tests. With time, the surviving individuals were joined on the conglomerate by new ones that settled as larvae (electronic supplementary material, tables S1.2 and S1.4).

On Terme Sud, alpha diversity measured by H and N_1 increased with time (table 1). This is because the dominant gastropod, *Tectarius grandinatus*, decreased notably in abundance after the *Canopus* nuclear test, increasing the evenness of the distribution of the community composition, which was only composed of two to five species. On Héléne, alpha diversity was much more variable through time, with no clear trend (table 1). *T. grandinatus* decreased notably in abundance after *Canopus* and *Littoraria coccinea* disappeared completely from the surveys until 1977.

7. Discussion

Reef molluscs are long-living animals. In the portion of Polynesia south of the equator, most species reproduce during the

austral summer. They can live several years, even decades; they are not necessarily replaced on a yearly basis. New-comers slowly replace animals found on a reef when some die for natural causes, generating temporal autocorrelation in our survey data. Reef carnivorous molluscs do not eat herbivorous molluscs; they eat small prey, including polychaete worms, living in the algal turf.

(a) Temporal variation on the reef flats and edges

On Terme Sud and H el ene, species richness increased during the years following the nuclear tests. On Manchot, it remained at the level it was at before the tests, although species composition was strongly modified.

Total community variation among years (BD_{Total}) was fairly similar on the two outer reefs (0.162 on Terme Sud and 0.107 on H el ene), but it was higher on the Manchot inner reef (0.221); the BD_{Total} values are bounded between 0 and 1, and are comparable among reefs [12]. Species richness was also higher on Manchot than on the outer reefs, especially before the *Canopus* test (table 1). The Manchot inner reef offered more sheltered living conditions than the outer reefs. Furthermore, Manchot was located about 6.5 km from the nuclear firing platform (figure 1a), so that the frying effect of the nuclear tests was probably less important on the Manchot fauna than on Terme Sud (3.5 km) and H el ene (3 km).

Only the LCBD indices corresponding to the first survey years (1967 on H el ene, 1968 on Terme Sud and Manchot), before the main nuclear test (*Canopus*, August 1968) were significant (table 2). This result indicates that community composition before the main test was very different from what it became afterwards on each reef. So the end effect of the nuclear tests was not to reduce species richness, but to allow the establishment of a mollusc community largely different from what it had been before the tests.

The RDA biplots (figure 2) illustrate that process in terms of the changes in species composition. On each reef, the surveys form an ordered sequence starting before *Canopus* and moving on to 1972, 1974, 1977 and 1987, with species (arrows) changing in importance along the years. The 1997 survey is in a position orthogonal to the line joining the 1967–1968 to 1987 surveys, which shows that it is not a simple linear extension of that sequence. The circular (or arched) arrangement of the survey years is due to gradual changes in species composition (electronic supplementary material, tables S1.1, S1.3 and S1.5).

The before–after analyses of the flat and edge portions of the three reefs (figure 3) indicate that after the molluscs were wiped out of the reefs by the *Canopus* and *Dragon* tests, primary succession, which was initiated by larvae coming from the ocean during the following years, caused community composition to vary a lot from transect to transect. Comparing the reefs, we note the following observations.

- On Terme Sud, all carnivorous species found before the tests were also found after, in reduced abundances at first; carnivore losses were replaced by individuals of other carnivorous species that were partly new to the reef (electronic supplementary material, table S1.1). By opposition, two abundant species of herbivores were replaced largely, but not entirely, by other species of herbivores and by carnivores after the tests. The community increased in richness (table 1) along the years after the tests.

- On H el ene, new herbivorous species were found on the reef after the tests; most species (herbivores and carnivores) increased in numbers, forming a community that increased in density (table 1) during the years of surveys after the tests. The species composition changed without significant change in species richness.
- On Manchot, all carnivorous species found before the tests were also found after, some in reduced abundances at first. The herbivores were more strongly affected (losses: squares) as the single dominant species, *Ce. echinatum*, nearly disappeared from all surveys from 1972 to 1997; it was replaced by a sparse representation of other herbivorous species and a strong increase in several carnivorous species, in particular *Mi. litterata* (electronic supplementary material, table S1.5). The community strongly increased in density along the years following the tests (table 1).

Focusing on the two major trophic groups, it is clear that herbivores, which were found in greater abundances before *Canopus*, did not recover their pre-test abundances and were replaced by carnivores (Terme Sud, Manchot) or by other species of herbivores and by carnivores (H el ene) during the post-test surveys.

Larvae coming from the surrounding ocean recolonized the reefs. On the reef flats and edges of the two external reefs (Terme Sud and H el ene) and of the internal reef (Manchot), herbivores were replaced after the nuclear tests either by species of the same (herbivores) or a different feeding group (carnivores). That mixture is consistent with the hypothesis of neutral dynamics, partly or entirely independent of the environmental conditions on the reef flats and edges of Fangataufa atoll.

(b) Supralittoral zones

Few gastropod species can survive the harsh conditions of the supralittoral zone on a tropical atoll; species have different types of shells and different habitats. *Nerita plicata* and *T. grandinatus* have strong, heavy shells. *Nerita* lives in crevices and near water, *Tectarius* is found on conglomerate or coral blocs covered by endolithic *Entophysalis* algae that give the blocs a grey colour. *L. coccinea* has a thin and tiny shell, and lives exposed to the sun. On H el ene transect, populations of *L. coccinea*, directly exposed to the flash of the *Canopus* nuclear explosion (August 1968), were completely eliminated. Some new individuals were found on the supralittoral blocks 10 years later and the population recovered after ten more years (electronic supplementary material, table S1.4, appendix S1). The populations of *N. plicata*, whose individuals are always found in crevices, were not eliminated, and those of *T. grandinatus*, whose individuals are found both in crevices and exposed, were partly eliminated (electronic supplementary material, table S1.4). The picture was almost the same on the Terme Sud supralittoral zone (electronic supplementary material, table S1.2) except for the total absence of *L. coccinea* due to frequent strong currents during strong swell. In summary, community composition did not change much on the supralittoral zones, where only a few species can survive. Strong species filtering by environmental conditions clearly dominated during recolonization of the supralittoral zone on both reefs.

(c) Sampling issues

Eight ecological surveys conducted across three decades represented an important effort to follow the changes in

community composition on a remote atoll of the tropical Pacific Ocean, where transportation and logistics costs are high. In more accessible study sites, more surveys could have been conducted. As a consequence, it is clear that we have only detected the main, long-term trends in the changes of the Fangataufa mollusc communities following the nuclear atmospheric tests. The data we collected do not allow us to say anything about shorter-term variations in community composition, which must also have taken place between our surveys.

8. Conclusion

Our observations of reef recolonization by molluscs after the nuclear tests conducted on Fangataufa allow us to understand the relative roles of neutral processes and environmental filtering that both played a role, but in different portions of the reefs.

Our observations clearly show that environmental filtering played a dominant role on the supralittoral zones. Only a few species were able to tolerate their harsh conditions, where they formed species-poor communities, which greatly differed in composition from the richer communities of the reef flats and edges. Differences observed between the two types of habitat are clearly due to differences in environmental conditions.

In the reef flat and edge zones, however, neutral processes dominated. Quite different communities developed on the three reefs after the tests, as the result of random settlement of larvae from the open ocean. Differences between reefs were cumulative and increased from year to year across 29 years of recolonization. Mollusc assemblages that developed on these

portions of the reefs are likely to be the result of a dynamics governed by stochastic immigration of species that were ecologically equivalent within the herbivore and carnivore trophic groups. This is an interesting case of neutral dynamics, which has been developed to explain diversity patterns in tropical forests and coral reefs [5,20,21].

Data accessibility. The Fangataufa atoll data are available in the electronic supplementary material, appendix S1.

Authors' contributions. B.S. designed the study and carried out the surveys reported in this paper. P.L. participated in the 1997 survey, analysed the data and wrote the manuscript. B.S. participated in the interpretation and discussion of the results. The two authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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