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INITIAL RECOLONIZATION OF FUNAFUTI ATOLL CORAL REEFS DEVASTATED BY HURRICANE "BEBE"

By

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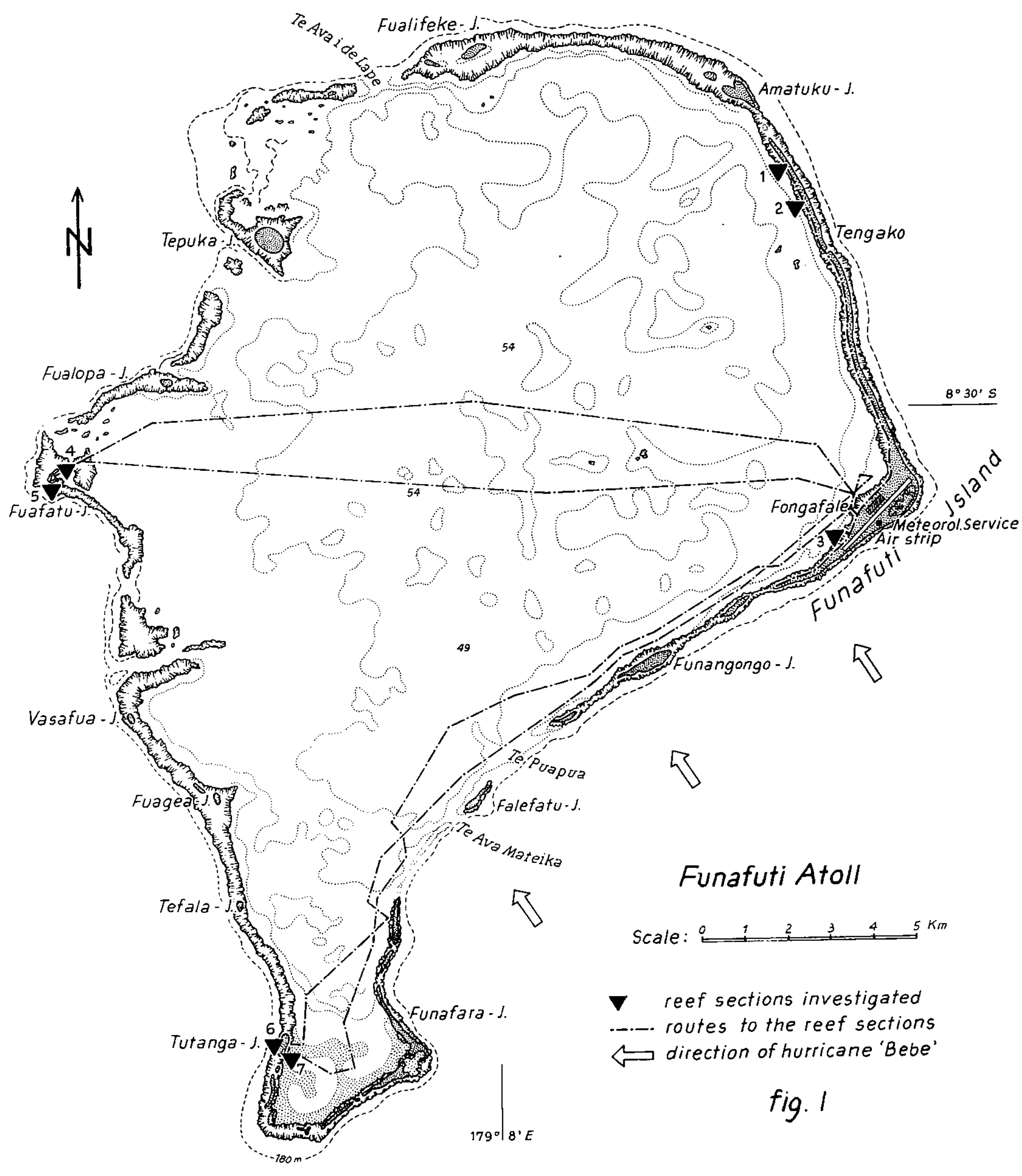
Te Ava i de Lape
Fualifeke - J.
Amatuku - J.
Tengako
Tepuka - J.
Fualopa - J.
54
8° 30' S
Fuafatu - J.
Fongafale
Meteorol. Service
Air strip
Funafuti Jsland
Funangongo - J.
49
Vasafua - J.
Te Puapua
Falefatu - J.
Fuagea - J.
Te Ava Mateika
Tefala - J.
Funafara - J.
Tutanga - J.
180 m
179° 8' E
Funafuti Atoll
Scale: 0 1 2 3 4 5 Km
reef sections investigated
routes to the reef sections
direction of hurricane 'Bebe'
fig. 1

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INITIAL RECOLONIZATION OF FUNAFUTI ATOLL CORAL REEFS DEVASTATED BY HURRICANE "BEBE"

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HANS MERGNER

Abstract

On the 21st of October, 1972, hurricane "Bebe" devastated a large part of Funafuti atoll in the Ellice Islands. Among the most spectacular geomorphological alterations caused by the hurricane was a storm beach 19 km long, 4 m high and 37 m wide. The amount of coral debris washed up from the offshore coral reefs onto the reef flat was estimated at 2.8×10^6 tons of material (Baines, Beveridge and Maragos, 1974). The oceanside reef communities of the SE and E rim of the atoll had been totally destroyed, and those of the inner reefs of the lagoon side had been heavily damaged. Eight months after the storm a quantitative analysis of the resettlement and recruitment of coral species on 7 reef sections was carried out: the destruction of the biophysiographic zones could be described as increasing from the northern border and also to the W rim of the atoll. Near the centre at Fongafale the lagoon reef flat was covered by thick carpets of the brown alga *Dictyota bartaysii*, possibly brought about by eutrophication effects. The resettlement of the reef flat by corals began with the recolonization of branching corals as well as regeneration of the very few surviving massive corals: about 80% of the number of new colonies belong to *Acropora* (mainly *A. humilis* and *A. hyacinthus*), and about 20% to *Pocillopora eydouxi*, *Porites lutea* (?) and some Faviidae. The percentage of the area settled by the massive coral species is, however, greater than that settled by the branching species. Nevertheless, in the long-term, branching corals are expected to have a decisive influence on the future structural and biophysiographic zonation of the reef edge and reef flat, due to their more numerous young colonies, which are evenly scattered over the reef area, and due to their rapid growth rate. Consequently, an *Acropora humilis - hyacinthus*-community or an *Acropora - Pocillopora eydouxi*-assemblage can be predicted as the future biophysiographic zone.

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Introduction

On the 21st of October, 1972, hurricane "Bebe" devastated a large part of Funafuti atoll, Ellice Islands (now Tuvalu) in the Southwestern Pacific. Six weeks later, December 10-24, 1972, Maragos, Baines and Beveridge (1973) investigated the geomorphological alterations caused by the cyclone especially on the SE side of the Atoll. A storm beach 19 km long, nearly 4 m high and 37 m wide was the most conspicuous geomorphological change. The amount of coral debris washed up from depths down to 20 m and onto the reef flat was estimated at 2.8×10^6 tons of material and was derived from the outer reefs of this side which had been totally destroyed. In addition, the inner reefs of the lagoon side had also been heavily damaged. The authors gave a detailed report and some personal comments on the alterations which they found and the condition of the reefs at the Second International Coral Reef Symposium in Brisbane, 1973 (Baines, Beveridge and Maragos, 1974). These were used as a basis for the planned investigation on the recolonization of the destroyed reefs.

Observations on the effects of tropical cyclones have been published by Blumenstock (1958, 1961) and Blumenstock et al. (1961), McKee (1959), Stoddart (1963, 1965, 1974), Tunnicliffe (1981), Woodley et al. (1981) and others. New growth and recolonization of corals have been described among others by Fishelson (1973), Loya (1976a, 1976b), Mergner (1979, 1981), Pearson (1981) and Schumacher (1977). Scientific descriptions of Funafuti atoll and its geology have been given by David and Sweet (1904), and as to the biology of the reef-forming organisms by Finckh (1904).

In July (6-11), 1973, 8 1/2 months after the hurricane, and just after the Symposium, I carried out the first quantitative analysis of the recolonization of some reef sections of the atoll. For the purposes of comparison, several regions of the reef both flourishing and partly damaged, were investigated. The following is a report of these investigations.

Seven sections examined on Funafuti reefs

Funafuti atoll (Fig. 1) is located on the undersea ridge of the Ellice Islands about 1000 km north of the Fiji-Archipelago arising from a depth of more than 4000 m. It consists of 29 coral islands differing greatly in size, sometimes oblong in shape, sometimes round and very small, and covered with forest (Cocos nucifera, Pandanus tectorius, Pisonia grandis and others). The islands are connected by reef barriers and form a rectangle with one elongated corner (Fig. 2). Aside from numerous shoals, nine outlets (locally called "Te Ava") connect the open sea with the lagoon, which reaches a depth of 54 m at two positions and flattens to a few meters especially in the south. Some of the passages are navigable: in 1899 Agassiz (1903) had entered two of them on board the research vessel "Albatross".

The Centre of hurricane "Bebe" struck the SE side of the atoll in October, 1972, and thus caused the greatest damage to the reefs located there (see Baines, Beveridge and Maragos, 1974). But the reefs of the NE side and of the S tip also suffered conspicuous damage in contrast to those of the SW and NW sides, which showed only few or nearly no effects of the storm because they had been better protected by the sheltering eastern reefs and the atoll lagoon. According to these criteria, the test areas and the reefs for comparison purposes had to be selected (Figs. 1, 12).

Two sections were selected for the N rim of the destruction zone close to the N end of the isle of Tengako (sections 1 and 2), two for the S rim of this zone near the isle of Tutanga at the S end of the atoll (sections 6 and 7), two for the W side of the atoll lagoon near the isle of Faufatu at the W end of the atoll (sections 4 and 5) and one for the centre of the destruction zone near the E end of the main island Funafuti (section 3). Because of the high swell from the east and correspondingly high breakers, the exposed outer reef section could not be investigated.

In all sections, the biophysiographic zonation was studied in a strip 20 to 100 m wide from the sea-shore across the reef flat to the fore reef or the lagoon floor. The distances from the mean water level to the reef edge were between 120 and 250m; greater distances could not be reached by snorkeling.

In contrast to reef sections 4-7, which showed no or only little damage, nearly the whole reef flat of sections 1-3 had been destroyed. Here, in each case, a test area of 20 x 20 m or 20 x 10 m was marked with plastic lines extending from the lagoon floor or reef slope over the reef edge onto the outer reef flat. Within the borders of each area all living remains of former coral colonies (without exception,e.g. massive or crustose species) and newly settled colonies were marked on a map and their sizes were calculated by taking the average between the longest and shortest diameters. All drawings, measurements and underwater photographs were made by snorkeling down to a depth of 5 m.

Results of zonation studies of reef sctions 1-7

First, the structure, the flora and fauna and the biophysiographic zonation of all reef sections investigated will be briefly characterized. Then, the recolonization of the reef platforms will be analyzed using reef sections 2 and 3 as examples.

Reef section 1

Reef section 1 is situated at the N rim of the central destruction zone of hurricane "Bebe", and 300 m south of the N end of the isle of Tengako. It extends SW from the shore of the lagoon for 160-180 m with a minimum breadth of 20 m, and its zonation is shown in Table 1, Fig. 12.

Reef section 1 shows serious damage to the reef platform and reef edge. Its biophysiographic zonation is characterized by sparse growth of different algae species on the abraded reef flat. Within more than 500 m^2 of the reef front, only 17 massive faviid colonies had survived, but no scleractinian colony had resettled. Aside from a few Pagurids and fishes no mobile fauna is visible.

Reef section 2

Section 2 (Fig. 3) runs parallel to and about 1200 m from section 1 and is located nearer the centre of the hurricane "Bebe" zone. It runs in a SW direction, is 140 m long and has a minimum breadth of 20 m. In many respects, its structure, settlement and zonation are similar to those of section 1. It does, however, differ from section 1 in that there is--aside from some remainders of dead coral colonies--a total lack of surviving living colonies. There are many species of fish in this area and, above all, there is a recolonization of numerous young scleractinian colonies (Table 2, Fig. 12).

Reef section 2 had been damaged to a greater extent by the hurricane than section 1: the old reef flat was largely eroded, the reef edge destroyed and its Acropora-zone totally demolished. No coral colony survived, but within 136 m^2 of the reef front 84 young coral colonies had resettled. The fish fauna is much more plentiful than in section 1, both in numbers and in species.

Reef section 3

Reef section 3 is situated in the middle of the central destruction zone of hurricane "Bebe", 120 m SW of the small jetty of Fongafale on Funafuti Island. It covers the inner reef of the lagoon side with a length of 120 m and a breadth of 20 m westward. Possibly due to the eutrophication by sewage of the surface water, which is only slightly agitated, a thick layer of the brown alga Dictyota bartaysii (Fig. 4) loosely covering the reef flat has developed. It largely conceals the serious damage due to the storm and allows only fragmentary insights into the settlement structures of this section. However, on alga-free coral rock areas along the reef edge large numbers of young stony coral colonies have resettled (Table 3, Fig. 12).

Of all the reef sections investigated, section 3 was hit the hardest by the hurricane. Aside from damage caused by hurricane "Bebe", much of this area has been changed during World War II. In addition, large areas of the reef edge and the reef slope are covered with dense algal carpets that have probably resulted from eutrophication effects of sewage. Nowhere can uninjured surviving stony corals be found; living faviid colonies can only be found in limited areas. However, 67 coral colonies, mostly species of Acropora, have resettled on the alga-free areas along the reef edge, covering an area of nearly 50 m^2. The occurrence of numerous herbivorous and detritophagous fish species like Acanthuridae, Chaetodontidae, Mullidae and Pomacentridae probably should be attributed to the mass population explosion of the algal stocks.

Reef section 4

Reef section 4 (Figs. 5-7) extends eastward from the NE end of the horseshoe-like island of Faufatu in the middle of the W side of the atoll. It runs for a length of 120 m and a maximum breadth of 100 m through the inner reef but does not reach the reef edge. In spite of its location facing the path of hurricane "Bebe", the storm damage--apart from some overthrown colonies of Acropora hyacinthus--is minimal, because the section is protected by an extensive reef platform located on its E side. This section is therefore suitable for comparison with the greatly damaged reef sections 1-3. Quantitative investigations of surviving and resettled young coral colonies were not necessary. Because of the breadth of section 4, it is differentiated into a northern (N), a middle (M), and a southern (S) strip in Table 4 when necessary (Table 4, Fig. 12).

Generally speaking, reef section 4 is a suitable example of an undamaged inner reef with characteristic coral assemblages and biophysiographic zones. The reef edge with its coral communities at a distance of more than 800 m could not be reached by swimming because of the strong currents. However, a strong current of 25 cm/s also occurred within the shore channel, and here similar assemblages, among others a well-developed Acropora hyacinthus (Pocillopora eydouxi)-zone, have settled. Their species composition should be comparable with those of the former zones of reef sections 2 and 3 before their destruction by the hurricane. Fishelson (1973), Loya (1976a) and Mergner (1981) have shown that damage caused by man-made perturbations and natural catastrophes will be gradually erased by regeneration and recolonization of the coral colonies if no further perturbation is added. Therefore, the expectation that the destroyed zones will gradually regain their former structure and species composition is also justified in this case.

Reef section 5

Reef section 5 begins at the curved south side of the isle of Faufatu, 250 m south of reef section 4. It covers the outer reef with a length of 120-180 m and a maximum breadth of 80 m to the SSW up to the surf zone (Table 5; Figs. 7, 12).

This reef section shows the typical zonation of the southwest Pacific outer reef. Because of the strong surf, reef slope and fore-reef could not be inspected. The storm damage seems to be relatively small. Thus, reef section 5 is a good comparison for the destroyed outer reefs of the E side of the atoll.

Reef section 6

Reef section 6 (Fig. 9) also belongs to the outer reefs of the W side of the atoll. It begins near its southern end on the SW edge of the isle of Tutanga and runs westwards for 150 m with a breadth of 50 m to the upper reef slope. Because of its location on the lee-side of the path of hurricane "Bebe" and at the most extreme S edge of its destruction zone, the damage is minimal. The surface current was very rapid (40 cm/s), but the surf of this reef site was weak during the investigation period. Therefore, a short study of the coral assemblages in the region between reef edge and fore reef was possible (Table 6, Fig. 12).

Reef section 6 shows a characteristic boulder zone: the large coral blocks were apparently thrown up by storm waves of former cyclones coming from westerly directions. They are even cited in David and Sweet (1904). The coral assemblages of the greatly cleft reef edge and the steep reef slope with its deep spurs and grooves are very diversified. Both zones characterize this reef section, which combined with the zonation of the reef flat in section 5, gives an approximate impression of the original appearance of the outer reefs destroyed on the eastern atoll side.

Reef section 7

Reef section 7 (Figs. 9, 11) covers 160-200 m of the inner reef, is 50-70 m wide and runs from the SE corner of the isle of Tutanga towards the SE. Just as outer reef section 6, section 7 is influenced by a strong surface current of at least 25 cm/s flowing from the lagoon outwards to the open sea. In spite of its location at the S edge of the destruction zone of hurrricane "Bebe", no serious storm damage can be observed along this section. Possibly, the narrow south tip of the atoll lagoon did not provide a long enough fetch (only 1.5 km) with enough water (it is very shallow here) for the hurricane to build up large enough waves to cause extensive damage. Section 7 thus gives the impression, just as section 4, that it is an intact inner reef. Its biophysiographic zonation, however, differs in many respects from that of section 4 and all other inner reef sections by the prevalence of microatolls, especially of *Porites lutea*, and by the lack of a characteristic reef slope (Table 7, Fig. 12).

Seen as a whole, section 7 is of less interest for a comparison between undestroyed and destroyed inner reefs.

Results of the quantitative analysis of reef sections 2 and 3

All the inner and outer reef sections investigated on the W and SW side of Funafuti atoll (4-7) proved to be relatively undamaged and generally suitable models for comparison with the seriously damaged reefs of the E side. This is especially true for section 4 as an inner reef and a combination of sections 5 and 6 as model of an outer reef (Fig. 12).

Thus, the reef flat of outer reef section 5, within the area of the abrasion zone, the shingle zone and the algal ridge, shows typical features of the zonation of SW Pacific atolls. In addition, its remaining coral zone in the region bordering on the algal ridge indicates the former existence of large stocks of the *Halimeda*-*Montipora foliosa*-community. However, the boulder zone on the reef flat, which is almost always present, is lacking in section 5, but well developed in outer reef section 6. The reef edge and upper reef slope of this section show the characteristic species composition of their coral assemblages. Therefore, a combination of the zonation of both sections probably offers a true representation of the sequence of zones on a W outer reef on Funafuti atoll. Unfortunately, this view could not be compared with the present aspect of the destroyed outer reefs on the E side. For details of their former aspect see the contributions of "The Atoll of Funafuti" (1904) and for the situation immediately after the hurricane see Baines, Beveridge and Maragos (1974).

An impression of the later result of the recolonization of the eastern inner reefs can be formed much more easily by examining the coral zones of western inner reef section 4: these zones are characterized by Acropora humilis-hyacinthus and Pocillopora eydouxi-communities, but not by massively growing faviids and poritids, which, in spite of early regeneration of the surviving colonies, are less important as predominant species compared with Acropora and Pocillopora. In contrast to that of section 4, the zoning of section 7 is less helpful for comparison with damaged inner reef sections 2 and 3, because it is characterized by microatoll formations especially of Porites lutea. Only isolated areas of the immediate reef edge are settled by typical Acropora-Pocillopora-communities. Conspicuous in both inner reef sections of the western side (4 and 7) is the almost complete lack of macroalgae on the reef flat, whereas on the inner reefs of the eastern side luxuriant algal stocks have developed.

All three reef sections investigated on the E side of Funafuti atoll must be considered as largely damaged by storm, with the extent of damage increasing from the northern border (reef sections 1 and 2) to the central destruction zone (section 3). An initial comparison of the three sections shows that, in the northernmost section a number of massively growing Plesiastrea colonies had indeed survived, but no new colonization was observed. On the other hand, in the more southerly sections 2 and 3, no colonies survived without damage and only smaller regenerating areas have arisen, but, at the same time, numerous young colonies of different size have initiated the first phase of recolonization (Figs. 13, 14). Almost all of these pioneer species belong to Acropora, a few to Pocillopora and Porites, and some to the faviids.

In order to verify results on species composition, species diversity, and settling density during the first phase of the recolonization, a careful quantitative analysis within the area of the reef edge and the close reef flat of both sections is necessary.

Reef section 2

Quantitative study of recolonization in reef section 2 (Fig. 13) consisted solely of enumerations and measurements of the resettled and regenerated areas of the scleractinians within a strip 8 to 15 m wide behind the reef edge. In this area of about 136 m^2, for reasons of simplification, all holes and channels with sandy bottom or debris were included, although these are usually not colonized. Thus, the area actually colonized should be reduced by about 25%.

Within the area studied, 84 stony coral colonies were counted belonging to the following genera and species:

Acropora (*corymbosa*, *humilis*, *hyacinthus*)	67 colonies = 79.7%
Goniastrea (*retiformis*)	12 colonies = 14.3%
Platygyra (*lamellina*)	1 colony = 1.2%
Pocillopora (*damicornis*, *eydouxi*)	2 colonies = 2.4%
Porites (*lutea*)	2 colonies = 2.4%
Scleractinia	84 colonies =100.0%

It is possible that some growth areas of *Goniastrea* originate from several regenerating segments of a formerly uniform larger colony, but this is not likely in the case of an *Acropora humilis* colony 30 cm in diameter. All remaining coral heads with smaller diameters may be considered as young colonies that settled during the 8 1/2 months after the passage of hurricane "Bebe" and since then have continued to develop, to reach varying and often considerable sizes. According to the time of settling the following diameters (Ø) and base areas of *Acropora* were determined:

6 colonies	with up to 2 cm Ø	and 3.1 cm^2,	altogether 18.6 cm^2
14 colonies	with 2.5- 3 cm Ø	and 7.1 cm^2,	alogether 99.4 cm^2
27 colonies	with 3.5- 5 cm Ø	and 19.6 cm^2,	altogether 529.2 cm^2
10 colonies	with 5.5- 8 cm Ø	and 50.2 cm^2,	altogether 502.0 cm^2
8 colonies	with 8.5-10 cm Ø	and 78.5 cm^2,	altogether 628.0 cm^2
1 colony	with 10.5-15 cm Ø	and 176.6 cm^2,	altogether 176.6 cm^2
1 colony	with 15.5-30 cm Ø	and 706.5 cm^2,	altogether 705.5 cm^2
67 colonies	with a settling area of altogether		2660.3 cm^2

By contrast, only 12 young colonies or regenerating segments of the massively growing *Goniastrea* inhabit 4979 cm^2, an area twice as large as that occupied by *Acropora*. The other 5 newly settled colonies, covering 528 cm^2 (*Platygyra* with 314 cm^2, *Pocillopora* with 157 cm^2 and *Porites* with 57 cm^2) are less significant for the recolonization of the reef area analyzed, which totals ca. 8168 cm^2. Of 136 m^2 of the area concerned, the 84 young colonies occupy only about 0.6%, which can be divided up as follows:

Acropora	with	67	colonies	and	2660	cm^2	area	amounts to	0.20 %
Goniastrea	with	12	colonies	and	4979	cm^2	area	amounts to	0.37 %
Platygyra	with	1	colony	and	314	cm^2	area	amounts to	0.02 %
Pocillopora	with	2	colonies	and	157	cm^2	area	amounts to	0.01 %
Porites	with	2	colonies	and	57	cm^2	area	amounts to	0.004%
Scleractinia	with	84	colonies	and	8168	cm^2	area	amount to	0.60 %

Goniastrea retiformis dominates all other coral species regarding its share of the settling area, but is not dominant in its significance for the future structural and biophysiographic zonation. The Acropora species, with their 67 young colonies equally distributed over this reef segment, are much more important and will influence the later appearance of the reef edge and the neighboring reef platform. There are two reasons for this: first, Acropora species grow much more rapidly than the massive colonies of Goniastrea, and are also able, because of their favorable distribution, to roof over the area of settlement within a relatively short period. Therefore, they are at an advantage over all the others in the competition for space and light. Second, they form a varied landscape with their diversified structures providing numerous hiding places and a good food source as the biocenosis for many different species of reef fauna.

It can be assumed, and comparable observations from Red Sea coral reefs (Fishelson 1973, Loya 1976a, Mergner 1981) substantiate this assumption, that further undisturbed development will result in the establishment of an Acropora humilis-hyacinthus-zone as the biophysiographic zone of the reef edge and neighboring reef flat, such as found in other reef regions of Funafuti atoll, as in reef section 4 for example (Fig. 7).

Reef section 3

In reef section 3 (Fig. 14), all newly-settled and regenerating stony corals were also enumerated, measured and exactly marked on underwater maps. However, here only a narrow strip, 2.5 m wide on the average along the reef edge, could be mapped, because large reef areas were covered by carpets of the brown alga Dictyota bartaysii (Fig. 4), and all new-settled stony coral colonies were found only on algal-free coral rock. In the test area of about 50 m^2, 67 young colonies were found belonging to the following genera (with species names):

Acropora (humilis, hyacinthus, pulchra etc.)	50 colonies = 74.6%
Faviidae (Favia, Goniastrea etc.)	7 colonies = 10.5%
Pocillopora (damicornis, eydouxi)	7 colonies = 10.5%
Porites (lutea)	3 colonies = 4.4%
Scleractinia	67 colonies =100.0%

Only one faviid colony can be assumed to be newly settled, the other 6 are regenerating parts of a former larger colony. Such an origin can also be assumed for one Porites lutea colony and possibly one for Acropora colony with a diameter of 20 cm. All the other coral heads are young colonies that have settled since the passing of hurricane "Bebe". The following diameters (Ø) and base areas corresponding to the time of settling have been ascertained for Acropora:

3 colonies	with up to 1 cm Ø	and 0.8 cm^2	altogether	2.4 cm^2
9 colonies	with 1.5- 2 cm Ø	and 3.1 cm^2	altogether	27.9 cm^2
16 colonies	with 2.5- 3 cm Ø	and 7.1 cm^2	altogether	113.6 cm^2
14 colonies	with 3.5- 5 cm Ø	and 19.6 cm^2	altogether	274.4 cm^2
2 colonies	with 5.5- 8 cm Ø	and 50.2 cm^2	altogether	100.4 cm^2
4 colonies	with 8.5- 10 cm Ø	and 78.5 cm^2	altogether	314.0 cm^2
1 colony	with 10.5- 15 cm Ø	and 176.6 cm^2	altogether	176.6 cm^2
1 colony	with 15.5- 20 cm Ø	and 314.0 cm^2	altogether	314.0 cm^2
50 colonies with a settling area of altogether				1323.2 cm^2

By contrast, only 6 regenerating and one young faviid colony cover an area of 7870 cm^2, which is nearly 6 times more than Acropora; Porites, which also grows massively, with only one regenerating and 2 young colonies, covers 648 cm^2, which is half that occupied by Acropora. The branched coral Pocillopora claims 563 cm^2 for 7 young colonies. Thus, the total area recolonized by corals amounts to 10403 cm^2. Based on 50 m^2 of the reef area analyzed along the reef edge, the recolonization involves about 2%, which can be divided up as follows:

Acropora	with 50 colonies and	1323 cm^2	area amounts to	0.26%
Faviidae	with 8 colonies and	7870 cm^2	area amounts to	1.57%
Pocillopora	with 7 colonies and	563 cm^2	area amounts to	0.11%
Porites	with 3 colonies and	648 cm^2	area amounts to	0.13%

In reef section 3 it is much more evident than in reef section 2 that the area covered by the massive stony corals (Favia, Goniastrea, Porites) is much larger than that covered by the branched corals (Acropora, Pocillopora). But regardless of this fact, the latter corals will definitely influence the future structural and biophysiographic zonation of the reef edge. The rapidly growing Acropora species will soon predominate in this reef area both numerically and physionomically and together with Pocillopora will build up a varied biocenosis for a reef fauna rich in species and numbers. A condition favoring this is the high initial settling density along the reef edge in section 3: on each square meter of free coral rock 1.14 young colonies of branched corals settle, compared to only 0.5 colonies in reef section 2. It cannot be proved that this is due to the reduced amount of free settling area resulting from the unusual proliferation of algae. With further undisturbed development, an Acropora humilis-hyacinthus-zone or a mixed Acropora-Pocillopora-zone, will also develop in section 3 as the biophysiographic zone of the reef edge and neighboring reef platform. Estimates differ as to the time required for this development. However, further damage caused by new storms and/or by man's influence may change or delay or even prevent this evolution.

Conclusions

1. The geomorphological alterations of large parts of Funafuti atoll caused by hurricane "Bebe" have been described by Baines, Beveridge & Maragos (1974). Here some reef sections destroyed on the E side are compared with undestroyed sections on the W and SW side, and the first phase of the recolonization of two reef areas by stony corals is analyzed.

2. The extent of the damage to the reef sections studied can be ascertained by the alterations of their structure and biophysiographic zonation: it increases from the northern border zone of the cyclone (reef sections 1 and 2) to the central destruction zone where section 3, close to Fongafale, had been most intensively struck. Wide areas of its devastated reef flat are covered by thick carpets of the brown alga Dictyota bartaysii possibly because of eutrophication.

3. Quantitative analyses in destroyed reef regions 2 and 3, show that recolonization by scleractinians is a result of regenerating segments of the few surviving massive coral colonies and of newly settling branched corals. Among them Acropora humilis and A. hyacinthus (and with reservations also A. corymbosa, formosa and pulchra) and Pocillopora eydouxi are especially prominent: Acropora comprises 79.7% (sect. 2) to 74.6% (sect. 3) of the number of all young colonies, Pocillopora 2.4% (sect. 2) to 10.5% (sect. 3). However, the massive growth species outweigh the branched corals with respect to percentage of area settled; the massive growth species occupy 0.4% to 1.7% of the entire area, while the branched corals occupy only 0.2% to 0.4%.

4. In spite of this, the branched corals will have a decisive influence on the future structural and biophysiographic zonation of the reef edge and the neighboring reef flat. This is indicated by the fact that their young colonies are much more numerous and evenly distributed over the area to be settled and by their large initial settling density (0.5 to 1.14 young colonies for each square meter of free coral rock area). This initial advantage and their more rapid growth rate causes them to form a varied coral landscape within a reltively short period of time with diversified

hiding places and food sources providing niches for a reef biocenosis rich in species and numbers.

Thus, it is predicted (as in comparable structures in Red Sea coral reefs) by the indicator species present, that with further undisturbed development, an Acropora humilis-hyacinthus-assemblage or an Acropora-Pocillopora eydouxi-community will develop into the future biophysiographic zone of the reef edge and the neighboring reef flat.

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Fig. 2. Approach flight to Funafuti atoll. Aerial photograph from south. Location of sections 6 and 7 below top of propeller.

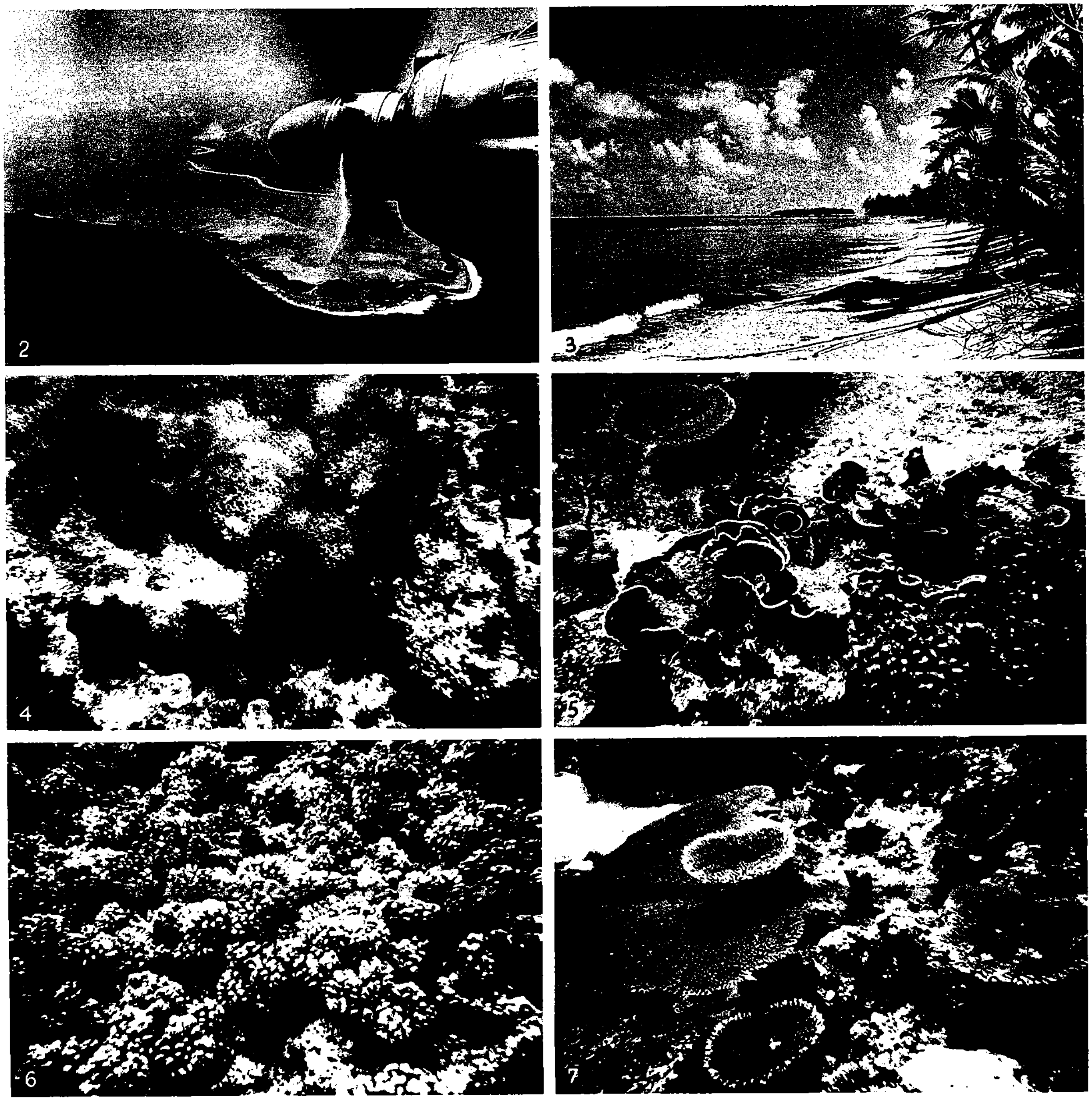
Fig. 3. Tengako Island, lagoon-side. View from SSE to Amatuku Isle (middle background) and the location of reef section 2 (middle foreground).

Fig. 4. Funafuti Island, lagoon-side. The destroyed reef edge of reef section 3, 120 m south from the jetty of Fongafale, covered by thick layers of Dictyota bartaysii.

Fig. 5. Fuafatu Island, lagoon-side. Inner reef at the NE-end with reef section 4. Parts of the Montipora foliosa-zone (middle) with Acropora hyacinthus (above left), Goniastrea sp.? (left) and Pocillopora eydouxi (below right).

Fig. 6. Fuafatu Island, reef section 4. Reef flat with the well-developed Pocillopora eydouxi-zone.

Fig. 7. Fuafatu Island, reef section 4. Crevasses in the reef flat with the Acropora hyacinthus - Pocillopora eydouxi-zone.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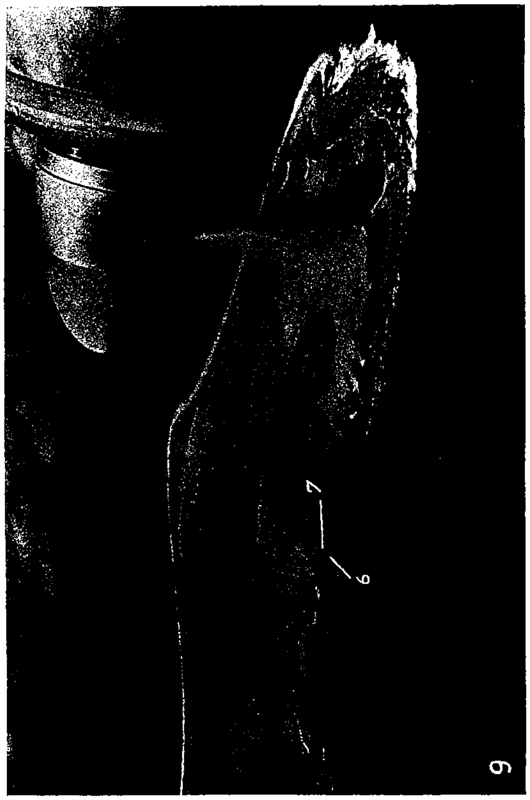
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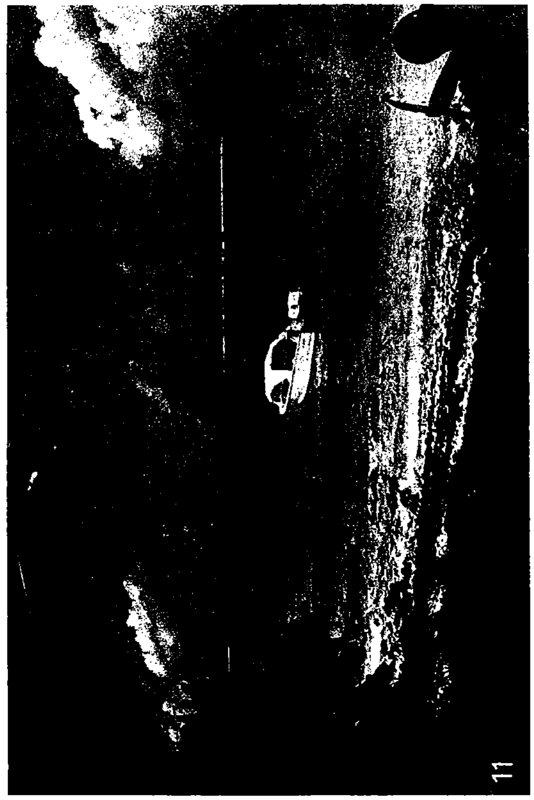
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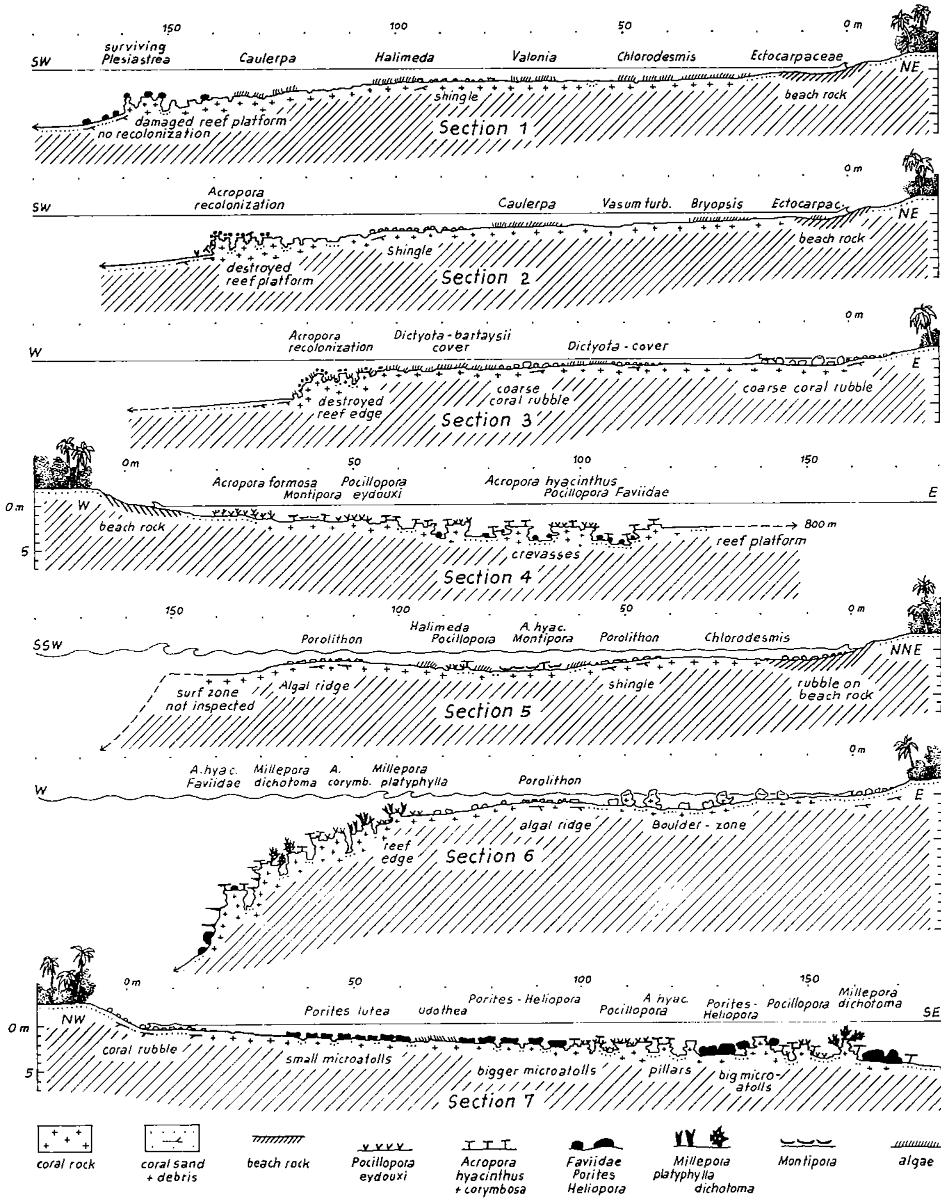
Fig. 8. Fuafatu Island, SE-side. Outer reef with reef section 5. Former living reef platform with extended *Montipora foliosa*-crusts (middle) and dense *Halimeda*-stocks (above, right).

Fig. 9. Funafuti atoll, south-end with the location of reef sections 6 and 7 (see arrows) near Tutanga Island. Aerial photograph from west.

Fig. 10. Tutanga Island, outer reef at the SW-side. Boulder zone of reef section 6 with large boulders thrown by cyclones from western directions onto the reef flat. View from WNW.

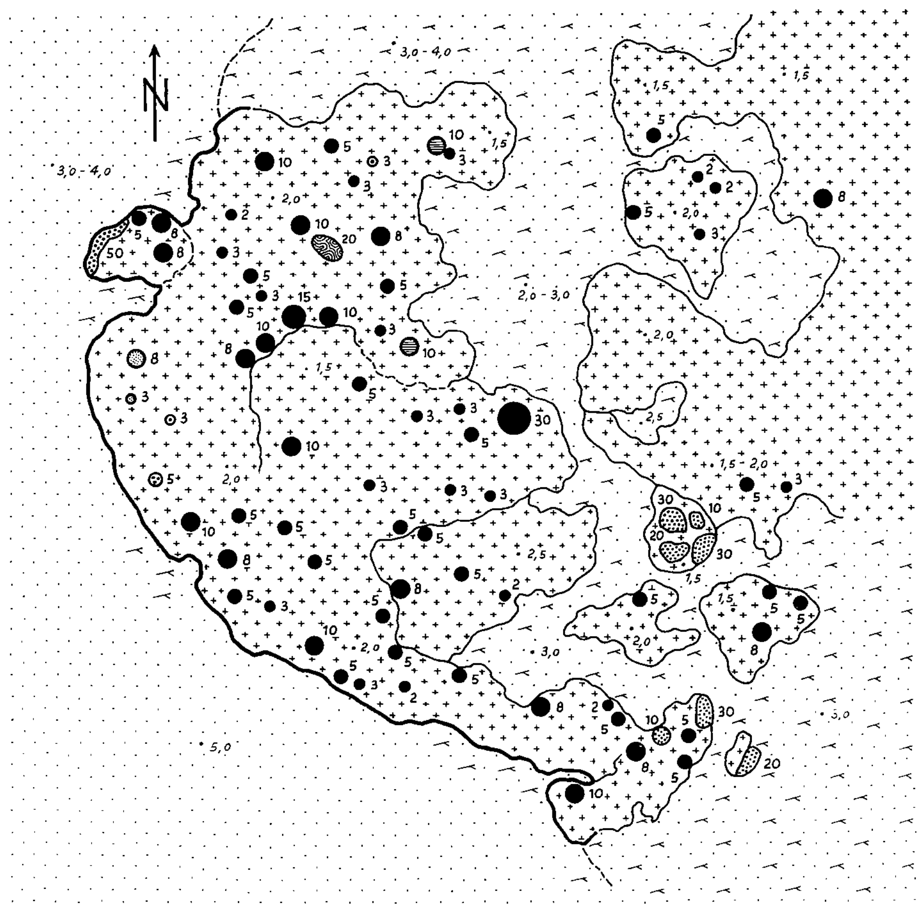
Fig. 11. Tutanga Island, inner reef at the SE-side with location of reef section 7 (middle right). View from NW.



Funafuti Atoll

Diagrams (cross sections) of the 7 reef sites investigated fig. 12

scales: horizontal 1:1000 vertical 1:500



⊙3 Goniastrea (3 = diameter in cm)
Acropora
Pocillopora
Platygyra
Porites

coral rock
coral sand
coral debris

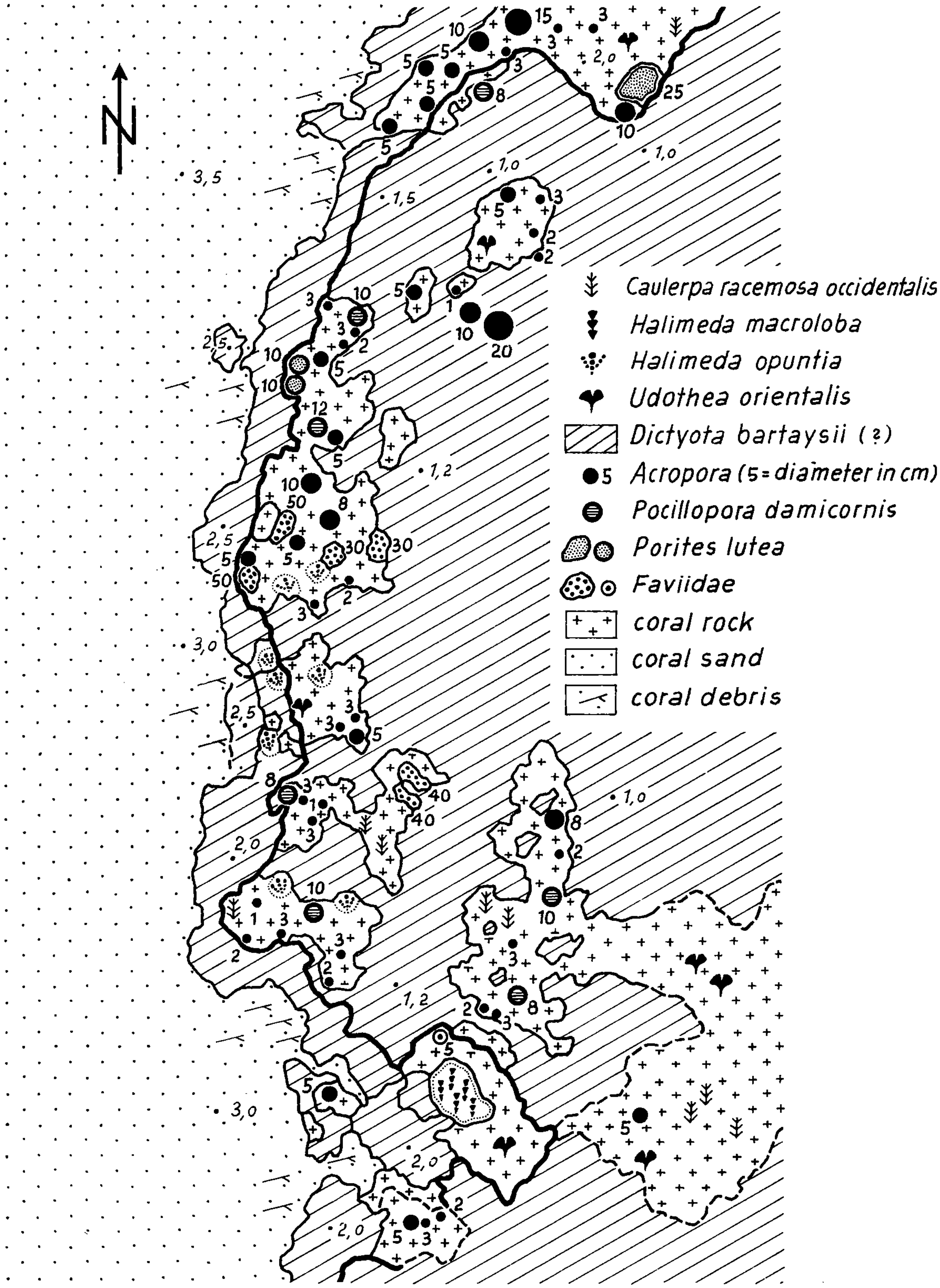
Funafuti Atoll

Recolonization of the reef platform in section 2 on the north end of Tengako,
in July, 1973, 8½ months after hurricane 'Bebe'

Scale: 0 1 2 3 4 5 m

• 1,5 depth in meters

fig. 13



Funafuti Atoll

Recolonization of the reef platform in section 3 near Fongafale,

in July, 1973, 8½ months after hurricane 'Bebe'

Scale: 0 1 2 3 4 5 m

• 1,2 depth in meters

fig. 14

Table 1: Zonation and recolonization of reef section 1

Reef zone; length and depth in m	Structures and biophysiographic zones	Flora and fauna (selection); coral recolonization
Tide zone and shore channel: length 15 - 25 m, at 25 m, depth 1 m	Coral sand and coral debris on greatly cleft beach rock: Ectocarpaceae - zone	Filamentous algal lawn; aside from a few Paguridae no visible fauna
Abraded reef flat: length 110 - 150 m, depth 1 - 2 m;	Sparsely jointed abrasion zone with mud, sand and debris:	Aside from some species of fish no macrobenthic fauna and only poor algal growth in biophysiographic zones:
at 25 - 50 m:	*Chlorodesmis* - zone	25% *Chlorodesmis fastigiata*,
at 70 m:	*Valonia* - zone	single *Valonia ventricosa*,
at 75 - 125 m:	*Halimeda* - zone	1% *Halimeda opuntia*,
at 100 - 150 m:	*Caulerpa* - zone	5% *Caulerpa racemosa occidentalis*
Former living reef platform: length 10 - 25 m, depth 2 - 3 m; at 135 - 160 m:	Dead coral rock flat with coral debris; single living massive corals: *Plesiastrea* - zone	A few surviving massively growing coral colonies in a zone of 25 m along the reef edge: 9 colonies of *Plesiastrea (versipora ?)* and 1 of *Goniastrea retiformis*, each with 0.2 - 0.5 m ∅; no coral recolonization
Reef edge and reef slope: at 160 m, depth 4 m	Roughly cleft coral rock without preserved fine structures: *Caulerpa* - *Plesiastrea* - zone	Aside from a few species of fish no macrobenthic fauna and only 1 - 5% *Caulerpa racemosa occidentalis*; no coral recolonization
Upper fore reef: from 160 - 180 m outwards, depth 4 - 6 m	Coral fine sand with plains of coral rubble	Only 7 surviving colonies of *Plesiastrea* near the reef slope, very few benthic fish species

Table 2: Zonation and recolonization of reef section 2

Reef zone; length and depth in m	Structures and biophysiographic zones	Flora and fauna (selection); coral recolonization
Tide zone and shore channel: length 5 - 10 m, depth 0.5 m	Coral sand and coral debris on greatly cleft beach rock: Ectocarpaceae - zone	Aside from a few Paguridae no visible macrobenthic fauna; filamentous algal lawn: Ectocarpaceae and others
Abraded reef flat: length 100 m, at 20 - 40 m, depth 1-2 m; at 50 - 90 m:	Sparsely jointed, largely eroded and partly muddy abrasion zone with flattened surface and small algal stocks: *Vasum* - *Caulerpa* - zone	Sparse macrobenthic mobile fauna: only 1 living *Conus* species and many *Vasum turbinellum*; algal growth: *Bryopsis pennata* and *Caulerpa racemosa occidentalis*
Former living reef platform: length 15 - 20 m, depth 1.5 - 3 m at 120 - 140 m:	Dead coral rock flat without fine structures and mud, but roughly divided into blocks and channels with debris: *Acropora humilis* - *hyacinthus* - zone	No surviving coral colonies, but numerous resettled young colonies of *Acropora* spp., some of *Pocillopora*, *Porites*, *Goniastrea* and *Platygyra*, altogether 84 young colonies within an area of 136 m^2
Reef edge and reef slope: at 140 m, depth 3 - 4 m	Tabular Acropora - colonies overthrown by storm waves	Rich fish fauna, locally 1 hydroid species along the reef edge
Upper fore reef: from 140 m outwards, depth 3 - 5 m	Coral sand with mud and some coral rubble	More than 50 fish species: many Acanthuridae and Chaetodontidae, but no Scaridae

Table 3: Zonation and recolonization of reef section 3

Reef zone; length and depth in m	Structures and biophysiographic zones	Flora and fauna (selection); coral recolonization
Tide zone, 10 m, shore channel: length 20 m, depth 0.3 m	Coral rock blocks, muddy coral sand with rubble: Paguridae - zone	Aside from a few Paguridae only sparse macrobenthic fauna; almost no macroalgae
Abraded reef flat: length 80 - 100 m, depth 1 - 1.5 m	flattened, muddy abrasion zone, only partly visible due to algal cover, partly with coarse rubble and serious damages: Dictyota bartaysii - zone (Fig. 4)	Flourishing algal stocks: mainly *Dictyota bartaysii*, additionally *Caulerpa racemosa occidentalis*, *Halimeda macroloba*, *Halimeda opuntia* and *Udothea orientalis*; herbivorous macrofauna: *Holothuria leucospilota*, Acanthuridae and others
Former living reef platform: length 15 - 20 m, depth 1 - 1.8 m	Largely eroded and flattened, slightly muddy coral rock area, covered to 75% with *Dictyota*	A few gastropods, some *Holothuria leucospilota*, many herbivorous fishes: Acanthuridae, Chaetodontidae, Pomacentridae (?)
Reef edge and reef slope: at 120 m, depth 3 m	Broken coral rock zone, slightly muddy without fine structures, covered to 50% with *Dictyota*; overthrown *Acropora* spp.: *Acropora - Pocillopora* - zone	Sparse algal stock; no surviving coral colonies, but numerous resettled young colonies, usually *Acropora* spp. + Faviid - regenerates, altogether 67 young colonies within 50 m^2 and 2.5 m breadth along the reef edge
Upper fore reef: from 120 m outwards, depth 3 - 3.5 m	Largely muddy coral sand with coral debris	Very rich fish fauna: especially Acanthuridae and Mullidae, but no Scaridae

Table 4: Zonation and recolonization of reef section 4

Reef zone; length and depth in m	Structures and biophysiographic zones	Flora and fauna (selection); coral recolonization
Tide zone: length 10-15 m	(S) Coral rubble on beach rock, (N) eroded beach rock plates	Few visible macrobenthic fauna; no macroalgae
Shore channel: length 20 m, depth 0.5 - 1 m; strong longreef current: 15 m/min.	Coral sand with fine coral debris, (S) areas of living branched corals	No macroalgae, a few fishes; (S) *Acropora formosa* - (group)
Reef flat: length 100 m, depth 1 - 1.5 m	Abraded coral rock flat, on it living coral zones: (S) *Acropora formosa* - zone, (M) *Montipora foliosa* - zone (Fig. 5), (N) *Pocillopora eydouxi* - zone (Fig. 6)	(S) dense barrier of *Acropora formosa* - (group), (M) *Montipora foliosa*, colonies up to 2 m ∅ (Fig. 5), (N) dense stock of *Pocillopora eydouxi* (Fig. 6) with some *P. damicornis*, *Acropora humilis* and *Millepora dichotoma*
depth 1.5 - 2 m, holes up to 4 m deep	In the coral rock flat, crevasses up to 10 - 15 m long, varying in depth, with fine coral sand; along the rims branched corals, on the floor massive stony corals: *Acropora hyacinthus* - (*Pocillopora eydouxi*)-zone (Fig. 7)	(S) dense barrier of *Acropora hyacinthus* (Fig. 7), colonies up to 1.5 m ∅, with less *A. corymbosa* and *A. humilis*, (N) *Pocillopora eydouxi*, in the crevasses *Favia*, *Favites*, *Goniastrea*, *Plesiastrea* (*versipora* ?) and *Porites* (*lutea* ?)
Reef edge: more than 800 m away (impossible to reach)		

Table 5: *Zonation and recolonization of reef section 5*

Reef zone; length and depth in m	Structures and biophysiographic zones	Flora and fauna (selection); coral recolonization
Tide zone: length 10 - 20 m	Coral rubble on beach rock, (SW) beach rock plates	Aside from a few Paguridae no visible macrobenthic fauna
Abraded reef flat: length 50 - 80 m	Abrasion zone: sharp-edged, eroded coral rock	*Chlorodesmis fastigiata* and *Lithothamnion sp.*
at 30 m, depth 0.5 m	*Chlorodesmis* - zone	Very few Pagurids and Gastropods, a few fishes
length 20 - 30 m, depth 0.3 - 0.7 m	Shingle zone: coral debris encrusted with calcareous red algae on largely eroded coral rock, few living corals: *Porolithon* - zone	*Lithothamnion sp.*, *Porolithon sp.*, *Porites lutea* (?), some Gastropods, a few fishes
Former living reef platform: length 20 - 40 m, depth 1 - 1.2 m	Rest of the former coral zone: living coral assemblages largely reduced by storm damages, with overthrown *Acropora* - umbrellas and green algal growth: *Halimeda* - *Montipora* - zone (Fig. 8)	Green algae: 4 *Halimeda* species (*H. cylindracea*, *discoidea*, *macroloba*, *opuntia*) and *Udothea orientalis*; surviving corals: *Acropora humilis* and *hyacinthus*, *Goniastrea*, *Favia*, *Montipora foliosa* - crusts (Fig. 8), *Plesiastrea* (*versipora* ?), *Pocillopora damicornis* + *P. eydouxi*, *Millepora sp.*; recolonization: a few young *Acropora* - colonies
Algal ridge: length 30 m, depth 0.8 - 1 m	Typical algal ridge: minimal damage, coral rubble cemented with calcareous red algae	Aside from *Lithothamnion* and *Porolithon* no macroalgae; no living corals, a few fishes

Reef edge with the surf zone and the reef slope with its spurs and grooves 110 - 200 m away were not possible to reach due to the breakers

Table 6 : Zonation and recolonization of reef section 6

Reef zone; length and depth in m	Structures and biophysiographic zones	Flora and fauna (selection); coral recolonization
Tide zone: length 10 - 15 m	Coral rubble, but no beach rock	Aside from a few Paguridae no visible macrobenthic fauna
Abraded reef flat: length 100 - 150 m, at 20 m, depth 0.5 - 1 m	Abrasion zone: flattened, sharp - edged eroded coral rock plain without fine sediment	No macroalgae; only a few Gastropods, crabs and fishes
at 30 m, depth 0.8 - 1.5 m	Boulder zone (Fig. 10): boulders of up to 2 m ∅ thrown by the storm onto the coral rock	On the coral blocks only blue algae and Gastropods, single fishes beneath the blocks
at 50 - 80 m, depth 1 m rapid surface current (40 cm/s) outwards	Algal ridge: coral debris cemented with calcareous red algae: *Porolithon* - zone	No macroalgae, only *Porolithon sp.* and *Lithothamnion sp.*; aside from fishes no visible macrofauna
Reef edge at 100 m and upper fore reef: length 30 m, depth 3 - 5 m; strong surface current (30 cm/s) outwards at depth 3 - 5 m: at depth 5 - 10 m:	Reef edge largely cleft by surf erosion and settled by branched corals; spurs and grooves lead to deep canyons with plentiful live: *Pocillopora - Millepora platyphylla* - zone, *Acropora corymbosa - A. humilis* - zone, *Millepora dichotoma* - zone	Outwards increasing numbers of coral colonies: 2 species of *Pocillopora* and plenty of *Millepora platyphylla*, then numerous *Acropora humilis* and *A. corymbosa*, single *A. hyacinthus* and dense barriers of *Millepora dichotoma*; fish fauna rich in species + numbers

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Table 7: Zonation and recolonization of reef section 7

Reef zone: length and depth in m	Structures and biophysiographic zones	Flora and fauna (selection); coral recolonization
Tide zone: length 10 m	No beach rock, coarse coral rubble with sand areas	Aside from a few Paguridae nearly no visible macrobenthic fauna
Abraded reef flat: length 100 - 130 m, at 30 m, depth 1 m	Abrasion zone: flattened, sharp-edged, muddy coral rock	No macroalgae; only a few macrobenthic faunal species and fishes
at 40 m, depth 1 - 2 m	Microatoll zone: numerous microatolls cover 10 - 30%: *Porites lutea* - zone	Microatolls of *Porites lutea* (?) up to an heigth of 0.2 m, many of them dead and muddy
at 70 m, depth 2 - 3 m: strong surface current (25 cm/s) outwards	Single plains of coral debris between bigger microatolls: *Porites* - *Udothea* - zone	Aside from *Porites lutea* *Udothea orientalis* and *Lithothamnion*, additionally single *Millepora dichotoma* and *Acropora hyacinthus*; a few fishes
Living reef platform: length 50 - 100 m, depth 3 - 5 m;	Pillar zone: coral rock plain with big microatolls, towards the southeast increasingly divided into	Microatolls of *Heliopora coerulea* with up to 2.5 m ∅ and of *Porites lutea* with up to 5 m ∅
at 100 m, depth 3 m,	pillars densely settled by living corals;	Pillars with *Pocillopora eydouxi* and *Millepora dichotoma*
at 125 m, depth 3 - 4 m,	between them sand floor with mud and fine debris:	
at 150 - 200 m, depth 4 - 5 m	*Heliopora* - *Porites* - zone,	Pillars with *Pocillopora* and some *Acropora* species (*corymbosa*, *formosa*, *humilis* and *hyacinthus*, the latter with umbrellas of up to 3 m ∅)
Reef edge: at 170 - 200 m; only 5 - 8 m of visibility	*Pocillopora* - *Millepora dichotoma* - zone, *Pocillopora* - *Acropora hyacinthus* - zone	Some *Conus* - species and *Tridacna*, only a few fish species