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21-year Changes of Backreef Coral Distribution: Causes and Significance

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ABSTRACT

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The distribution of corals and their decadal change were observed in Kabira Reef, Ishigaki Island, Southwest Japan. Kabira Reef has distinct topographical and ecological zonation from the shore to the ocean and in addition, ecological zonation along the shore. Coral communities on hard substratum correspond to the current gradient. By analyzing aerial photographs taken in 1973, 1977, 1983, 1986, and 1994, together with the field observations of the change of communities in 1 m^2 quadrats, an area with marked changes was detected in the moat. The area is composed of fragile branching *Montipora digitata* on thick bioclastic sediments. Supply of fragments from the upstream zone, the reef pavement, maintains the communities in this zone. Accretion and removal of coral fragments are attributed to the wind direction of typhoons: northern and eastern winds from the ocean to the shore enhance the fragmentation and the expansion of *Montipora digitata* habitats, whereas southern winds remove the fragments in the moat.

ADDITIONAL INDEX WORDS: *Coral reef, decadal change, aerial photograph, typhoon, Ryukyu Islands.*

INTRODUCTION

A zonal distribution of the topography and communities in a coral reef has been recognized parallel to the shoreline, and the correlations between the ecological zonation and environmental factors have been discussed (DONE, 1983). The water movement and light intensity have been regarded as important factors (ADEY and BURKE, 1977; GEISTER, 1977).

The correlations between the distribution of corals and environmental factors are discussed on an assumption that all the communities are in the same state. However, coral communities are not stable at a decadal scale in contrast to the stability at a millennium scale (JACKSON, 1992, but see also KAN *et al.*, 1997). In the Caribbean, coral communities are disturbed by overfishing, mass mortality of *Diadema*, or bleaching events (*e.g.* HUGHES, 1994), and as a result, coral communities there have been degraded. In the Ryukyu Islands, *Acanthaster planci* predation played a significant role during the 1970's to 1980's (YAMAGUCHI, 1986), and recently, inflow of red soil into the moat (shallow backreef lagoon) due to land development is increasingly becoming a major factor causing the degradation of coral communities (NISHIHIRA, 1987).

Typhoons or hurricanes also cause a significant decline of coral abundance (*e.g.* WOODLEY *et al.*, 1981; HUGHES, 1994). However, at the same time, they enhance the fragmentation of corals (HIGHSMITH, 1982) and thus contribute to the expansion of coral habitats in the sand substratum on which coral larvae cannot settle. GEISTER (1977) suggested that the difference in substratum substantially plays an important role in the zonation, and coral communities in the moat established on bioclastic sands have different characteristics from other coral communities on hard substratum. In a series of studies on Caribbean reefs, LIRMAN and FONG (1996) showed the zone specific damage induced by a hurricane and storms in a Caribbean reef. They also showed that backreef coral communities were supplied from the reef crest by fragmentation induced by one hurricane. However, they were carried away by another hurricane (LIRMAN and FONG, 1997a, b). The condition of hurricanes whether they enhance the fragmentation or remove the fragments was not discussed.

As stated above, we should understand the present distribution of corals in a coral reef as a result of reef environment and disturbances. Recently, to understand the dynamics of coral communities in response to disturbances or environmental changes, observations based on a decadal time scale have been conducted (SHULMAN and ROBERTSON, 1996; CONNELL *et al.*, 1997, see review by CONNELL, 1997). However, these studies mainly depend on the data from small quadrats or transects, which do not necessarily represent the habitat as JACKSON (1991) suggested. Although CONNELL *et al.*, (1997) showed that coral cover in small quadrats was similar to that found on a larger scale within the same habitat, they also agreed on the necessity of large-scale observation and

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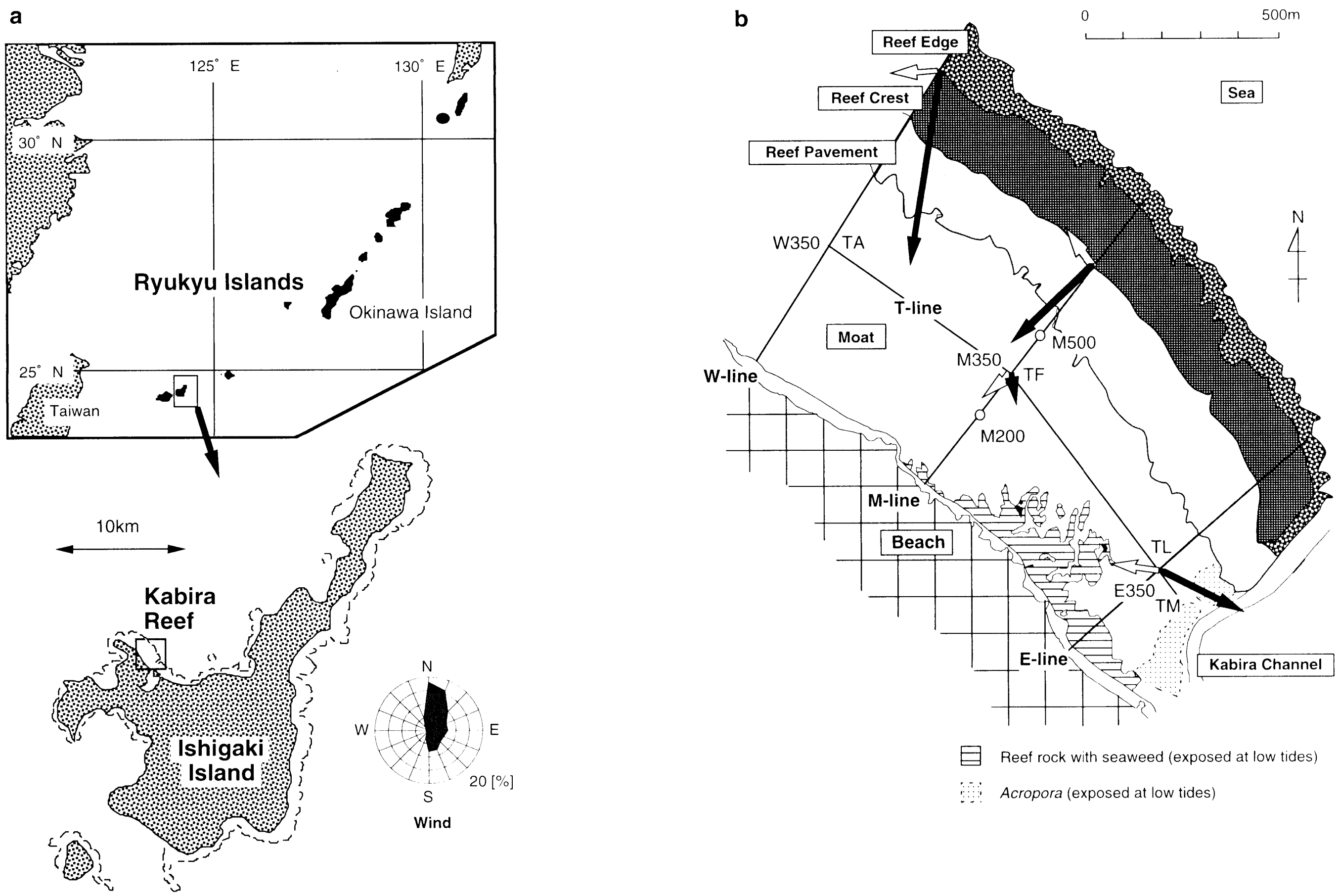


Figure 1. Map of Ishigaki Island, and location of Kabira Reef (a). The wind rose depicts the annual distribution. Geomorphological map of Kabira Reef and transects (b). Three transects (W, M, and E-line) are set perpendicular to the shoreline, and one transect (T-line) is set parallel to the shoreline for conducting observations and measurements. Circles show the points where we set 1 m² quadrats. Black and white vectors represent the current pattern under northern and southern wind conditions, respectively (Adapted from YAMANO *et al.*, 1998).

argued that observational and experimental studies at as many scales as possible were needed.

As a large-scale observation, aerial photographs are an effective tool for mapping marine habitats (SHEPPARD *et al.*, 1995; LEHMANN *et al.*, 1997) because of their high resolution, and together with satellite data and maps, they are increasingly utilized to estimate the decadal change of sand cays (KUCHLER, 1978; HASEGAWA, 1990) or marine plant communities (CUBIT, 1985; FERGUSON *et al.*, 1993; LUGO-FERNANDEZ *et al.*, 1994). In coral reefs, there have been many studies utilizing aerial photographs for mapping habitats (*e.g.* HOPLEY and STEVENINCK, 1977; HOPLEY and CATT, 1988; THAMRONGNAWASAWAT and HOPLEY, 1994). However, there have been few studies that utilize them to detect decadal changes of a coral reef (see review by GREEN *et al.*, 1996). Infrared aerial photographs are very effective for discriminating corals from other biota (HOPLEY and CATT, 1988), but it is hard to obtain historical infrared photographs. Satellite data seems to be now inferior to aerial photographs in coral reefs because their resolution is lower (GREEN *et al.*, 1996). Recently, MUMBY *et al.* (1998) showed the effectiveness of an airborne multi-spectral sensor (CASI) for mapping coral reefs, but it is impossible to obtain the historical images. Thus, we must rely on the true color or B/W historical aerial photographs for detecting decadal changes in the past based on a large spatial scale.

Coral reefs fringing the land often appears in historical aerial photographs. ARMSTRONG (1981) visually detected the changes in Puerto Rican reef from 1936 to 1979. In this case, the distribution of corals did not change significantly, whereas the increase of mangrove area and the formation of boulder-rampart due to hurricane event were detected. In fringing reefs of Ryukyu Islands, we can obtain aerial photographs from the 1970's to the present at intervals of about five years. In addition, it is easy to detect the change of backreef coral distribution because of its shallow depth and clear water quality. Moreover, it is possible to cover one coral reef by several aerial photographs obtained at different times. So, it is possible to detect decadal changes of backreef coral distribution.

MATSUNAGA and KAYANNE (1997) showed the effectivity of satellite data and aerial photographs in the change of dark patches on Kabira Reef. They visually detected the areas showing significant changes from satellite images and colored aerial photographs. They mainly focused their attention on the changes of patches in the moat of Kabira Reef, and the correlation between the patches and the environment they establish or the cause of the changes were not discussed.

In this study, first, we describe the ecological zonation on Kabira Reef in association with the topographical zonation and environmental setting including the results from shallow borings at ten points, and show the characteristics of backreef communities. Next, by analyzing aerial photographs together with the field observation of 1 m^2 quadrats, we show the decadal change of communities in the moat established on bioclastic sands at a spatial scale of one whole coral reef. Finally, we discuss the possible cause of these changes in association with typhoons and their significance in the expansion and removal of backreef corals.

METHODS

Study Area

Kabira Reef is a well-developed fringing reef located on the northwestern coast of Ishigaki Island, southwest Japan (Figure 1a), with a distinct topographical zonation: moat, reef pavement, reef crest, and reef edge distributed from the shore to the ocean (Figure 1b). Kabira Reef stretches about 3 km in length along the shore, and it is about 800 m from the shoreline to the reef crest. The southeast side of Kabira Reef is bounded by the narrow and deep Kabira Channel. Ishigaki Island is situated in a monsoon area, and the dominant wind blows from south in summer and north in winter. Water circulation in Kabira Reef shows a marked wind influence. The circulation pattern under calm conditions is characterized by an inflow of ocean waters into the moat over the reef crest and an outflow through Kabira Channel. Current vectors change according to wind conditions, and this pattern is weakened and strengthened under southern and northern wind conditions, respectively. Northern wind is dominant here throughout the year, and the dominant circulation pattern shows the pattern under a northern wind condition (Figure 1b, YAMANO *et al.*, 1998). The tidal range here is about 1.8 m.

The topographical zonation is apparent in the eastern part of Kabira Reef, so, our observation was mainly conducted there. We set three transects labeled W, M, and E, from the beach to the reef crest perpendicular to the shoreline (Figure 2). The transects are located in the east side of Kabira Reef. We also set observation points on these transects. Each point is named by its transect name and the distance (m) from the shoreline. For example, M700 is located 700 m from the shore along the M-line. We set an additional transect named T-line parallel to the shoreline. T-line starts from W350 and ends on the side of Kabira Channel by way of M350 and E350.

Reef Environment and Distribution of Corals

Water depths were measured by a staff with scales along W, M, and E-line at intervals of 5 m. They were corrected, based on the calculated tide values at Ishigaki Port, and described by the depths below the mean sea level (MSL). Ten cores were obtained from M-line using a portable core sampler (Geoact, Kitami, Japan): 5 from the moat (M200, M250, M300, M400, and M500), 2 from the reef pavement (M600 and M650), 2 from the reef crest (M700 and M800), and 1 from the reef edge (M880). Then the substratum on which coral communities establish themselves was analyzed.

Hermatypic corals were classified mainly by genus and growth forms and partly by the species which represents the ecological zone. Abundances of corals were measured by the quadrat method and they were described as coverage. This procedure was conducted at intervals of 50 m along W, M, E-line and at 13 observation points (TA-TM) along T-line at intervals of about 100 m. TA, TF, and TL are corresponding to W350, M350, and E350, respectively. These observations were conducted in March 1995.

Changes in Distribution of Corals

We used aerial photographs taken on 19 March, 1973 (B/W), on 1 December, 1977 (colored), on 21 September, 1983 (colored), on 24 December, 1986 (B/W) and on 7 September, 1994 (colored). Table 1 shows the attributes of the photographs. These photographs were converted into a digital form using a scanner at a 300 DPI resolution and georeferenced using PCI EASI/PACE software. All the images were converted in a grayscale form, and the irradiance along the two transects (W and T) was extracted using NIH Image software. As a result of these procedures, we can ascertain the extent of dark patches along the transects, and as for an image in 1994, we can compare them with the actual coral distribution observed in March 1995. In the field experiments, we set 1 m^2 quadrats on M500 and M200 from 20 July 1995 to 6 October 1995 and recorded the distribution of corals at each time.

RESULTS

Reef Environment and Distribution of Corals

Figure 2a–c shows the classification of topography, the topographic profiles, and the coverage of corals and substratum along W, M, and E-lines. As for M-line (Figure 2b), substratum is also shown from the analysis of the drilling cores. Figure 2d shows the coverage of corals and substratum along T-line.

In Figure 2a–c, the upper line shows the mean sea level at Ishigaki Port, the solid line shows the topographic profile of each transect. The elevations in the moat are constructed by dead and living corals. The hatched area represents the bioclastic sediments, and the broken line shows the estimated profile of hard substratum in the moat. The water depth is around 2 m in the moat, 0.3–1.0 m in the area where reef rocks are exposed, 0.6–1.0 m at the reef pavement and the reef crest. The areas where water depth is less than 1.0 m are exposed during spring low tides.

The reef crest and the reef edge are composed of reef rock derived mainly from hermatypic corals. The reef pavement is composed of branching *Montipora digitata* and is established on bioclastic sands. The moat is composed of bioclastic sediments and corals are distributed in patches except for E50 to E100 which are exposed during low tides. The thickness of bioclastic sediments in the moat is more than 365 cm at M400 and 514 cm at M500.

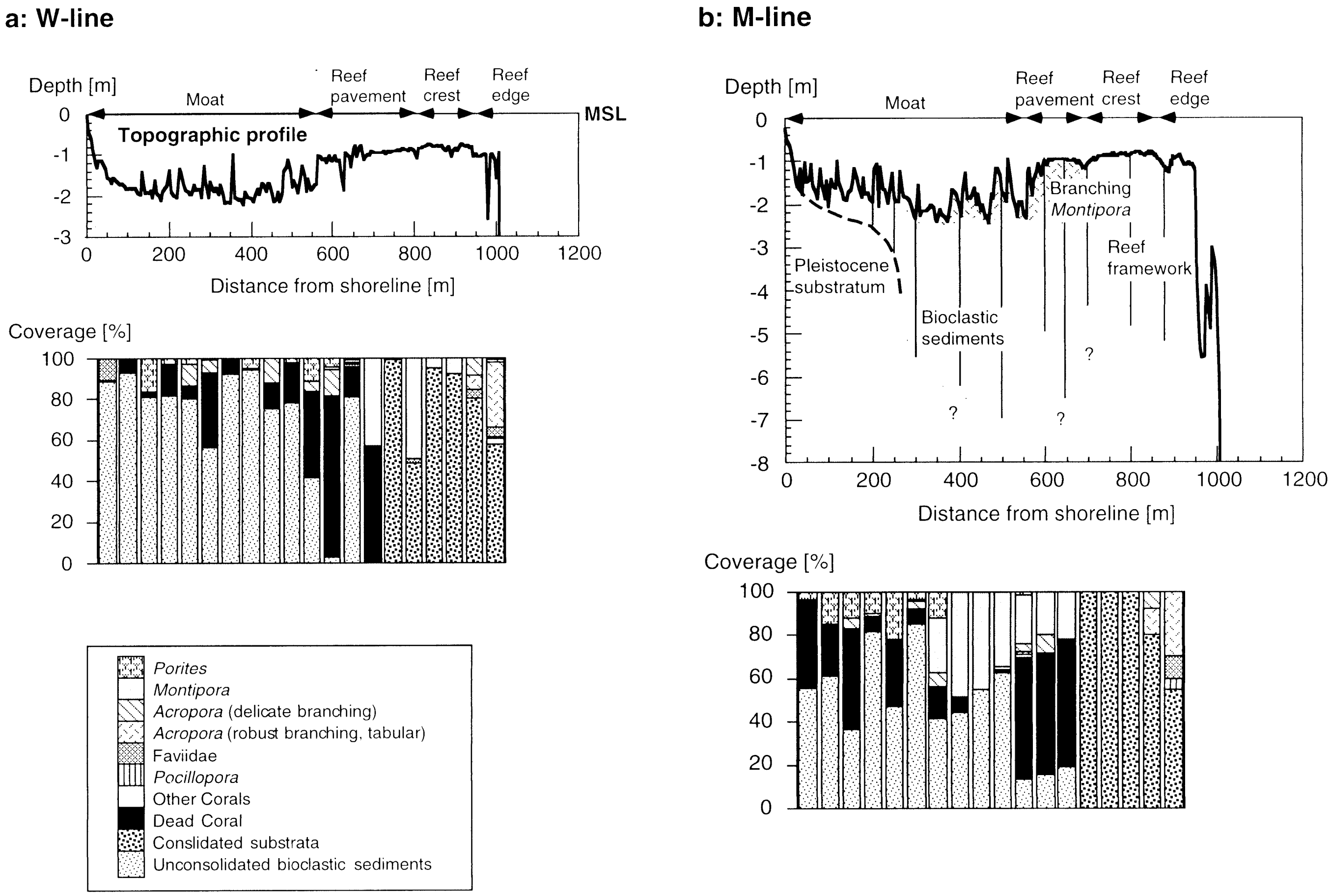


Figure 2. The classification of topography, the topographic profiles, and the coverage of corals and substratum along W, M, and E-lines (a–c). The upper line shows the mean sea level at Ishigaki Port, the solid line shows the topographic profile. The coverage of corals and substratum along T-line (d). In Figure 2b, vertical lines indicate the drill holes, and the hatched area represents the bioclastic sediment facies.

As for coral distribution along W, M, and E-lines perpendicular to the shore, robust branching and tabular *Acropora* (*A. digitifera* and *A. gemmifera,* and *A. palifera*) is dominant on the reef edge, delicate branching *Acropora* (*A. aspera* ?) occurs on the reef crest just behind the reef edge, branching *Montipora* (*M. digitata*) is dominant on the reef pavement, and massive and branching *Porites* (*P. lutea* and *P. cylindrica*) are distributed in the moat near the shore. On the other hand, in the moat near the reef crest, *Porites,* branching *Montipora digitata,* and delicate branching *Acropora* are dominant at W, M, and E-lines, respectively. This change of distribution is shown along T-line (Figure 2d). Massive and branching *Porites* and branching *Montipora digitata* are dominant from TA to TF, and branching *Montipora digitata* is dominant from TG to TK. Delicate branching *Acropora* occurs from TJ and is dominant at TM near Kabira Channel, and its coverage at TM is 26%. Branching *Montipora digitata* in the moat near the reef pavement on M-line are established on thick loose bioclastic sediments (Figure 2b), whereas other communities are established on hard substratum such as the reef rock and dead corals (Figures 2a and c). The patches are smaller than those on the reef pavement (Figure 2b).

Seagrasses were rare. As for macroalgae, we found *Sargassum* sp. at M700 whose coverage was about 2%, and other

Table 1. *Attributes of photographs used in this study.*

Year	Date	Scale (c.a.)	Color	Water Level (cm, from MSL)	Authority Photographed
1973	3/19	1:20000	B/W	−16	Geographical Survey Institute, Japan
1977	12/1	1:10000	Colored	+14	Geographical Survey Institute, Japan
1983	9/21	1:10000	Colored	+30	Okinawa Prefecture, Japan
1986	12/24	1:20000	B/W	+8	Ishigaki City, Okinawa, Japan
1994	9/7	1:10000	Colored	−15	Okinawa Prefecture, Japan

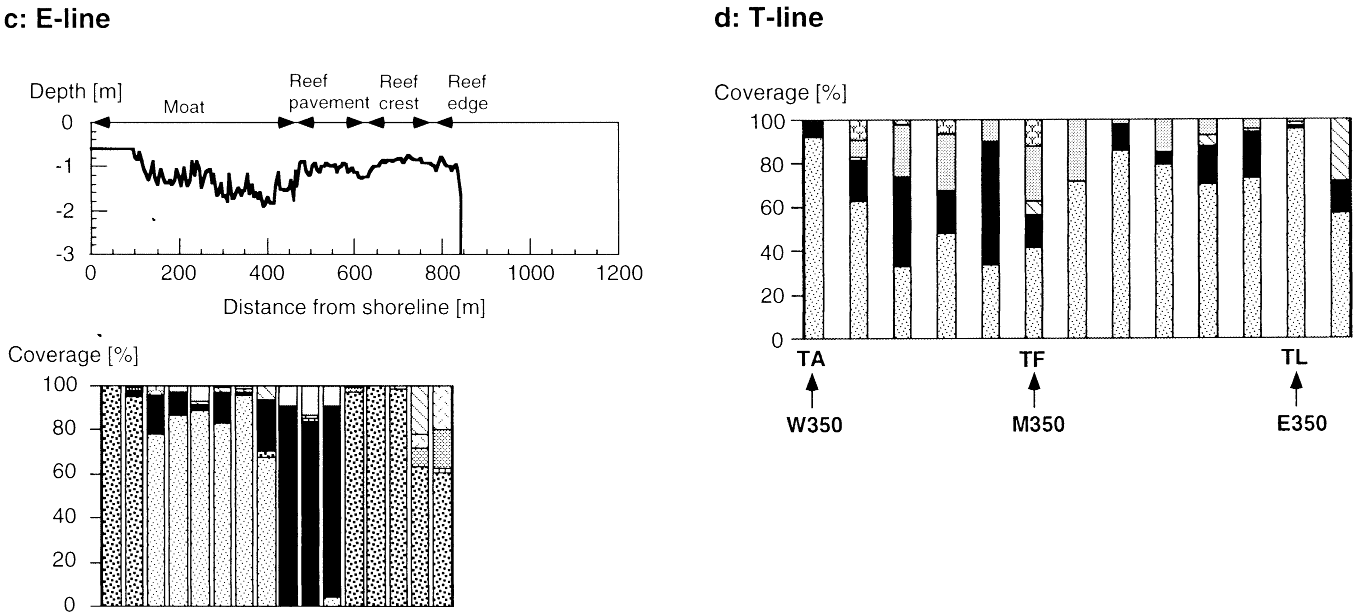


Figure 2. *Continued.*

macroalgae in the moat near the shore (W200, W300, M150 and M250) whose coverage was about 10%. Turf algae occur on the reef crest, and their coverage is about 40%.

Changes in Distribution of Corals

Figure 3a–e shows the georeferenced photographs taken in 1973, 1977, 1983, 1986, and 1994. Figure 4a, b shows the irradiance along M and T-lines at each image. Although the contrast, color, and the water depth were different in each photograph, the dark patches were detected from the difference of the irradiance. In the field observation, branching *Montipora digitata* communities were dominant from M350 to M500 and from TB to TG in March 1995 (Figure 2b, d) in the moat, and their coverage was about 40%. They correspond to the dark patches shown in Figure 4a, b. Seagrasses and macroalgae may be detected as dark patches in aerial photographs. However, seagrasses are rare in this reef, and macroalgae are also rare from M350 to M500. The dark patches in the western part of Kabira Reef were also mainly composed of branching *Montipora digitata* (YAMANO, unpublished data). Furthermore, as for other images, in 19[illegible], NAKAMORI (1986) showed that *Montipora digitata* were distributed in the western part of the moat, which corresponds well to the dark patches in Figure 3c. For these reasons, we consider the dark patches in the moat to be mainly composed of *Montipora digitata*. As for TM, delicate branching *Acropora* comprised dark patches (Figure 2d and Figure 4b). Sands and dead corals covered more than 80% from M0 to M300 in March 1995, thus, the area with lower irradiance values in Figure 4 represents sand substratum and dead corals.

In the moat, in 1973, there were *Montipora digitata* patches of large extent in the moat from M-line to E-line, stretching themselves from M150 to M500 and from TI to TM. In 1977, the patches slightly increased and covered more than half the area of the eastern part of the moat. However, in 1983, almost all the patches disappeared. Neither were these patches seen in 1986. In 1994, the patches returned, stretching themselves from M350 to M550, but their area is smaller than that in 1973 and 1977. These figures clearly show that there was some increase of *Montipora digitata* patches during 1973 and 1977, apparent disappearance of patches during 1977 and 1983, and some increase in patches during 1986 and 1994. In the reef pavement, *Montipora digitata* are densely distributed, and there were relatively small changes among the photographs (Figure 4a). At the end of T-line, situated near Kabira Channel, delicate branching *Acropora* lives, and the patches showed little change from 1973 to 1994 (Figure 4b).

Figure 5a, b shows the distribution of corals in 1 m^2 quadrats set at M200 and M500, respectively. Branching *Porites cylindrica* is dominant on M200, and branching *Montipora digitata* is dominant on M500. The distribution of *Montipora digitata* in the quadrat at M500 on the sand substratum significantly changed from 20 July 1995 to 6 October 1995, whereas no change in live *Porites cylindrica* at M200 occurred on the dead corals.

DISCUSSION

Coral Distribution in Kabira Reef

We observed the spatial distribution of the topography, the substratum, and the distribution of corals in Kabira Reef, and it is clearly shown that Kabira Reef has topographical and ecological zonation from the shore to the ocean (Figure 1b and Figure 2a–c) which fact is in agreement with previous studies described in DONE (1983). The zonation is also shown in NAKAMORI (1986) where the topography and coral distribution in

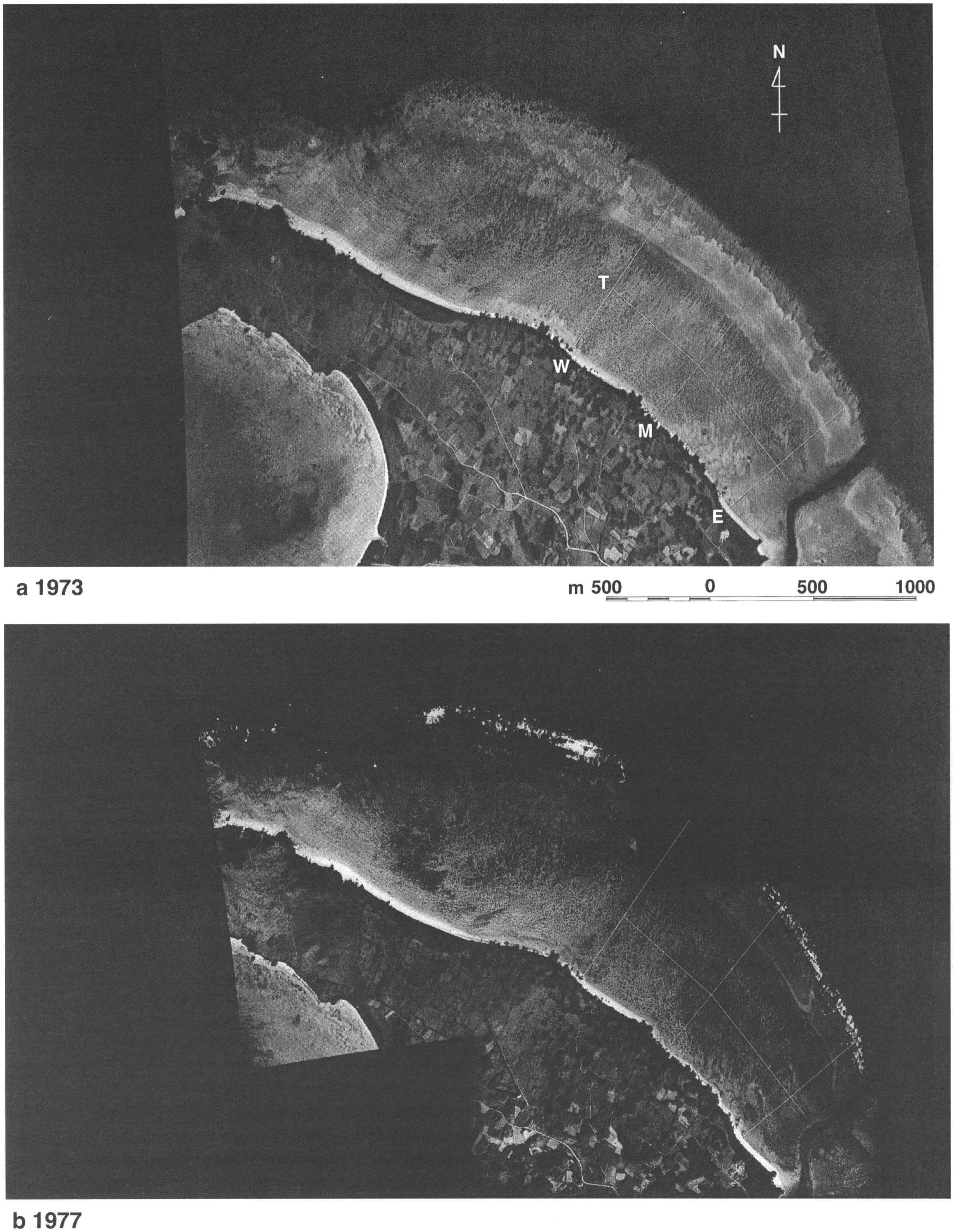
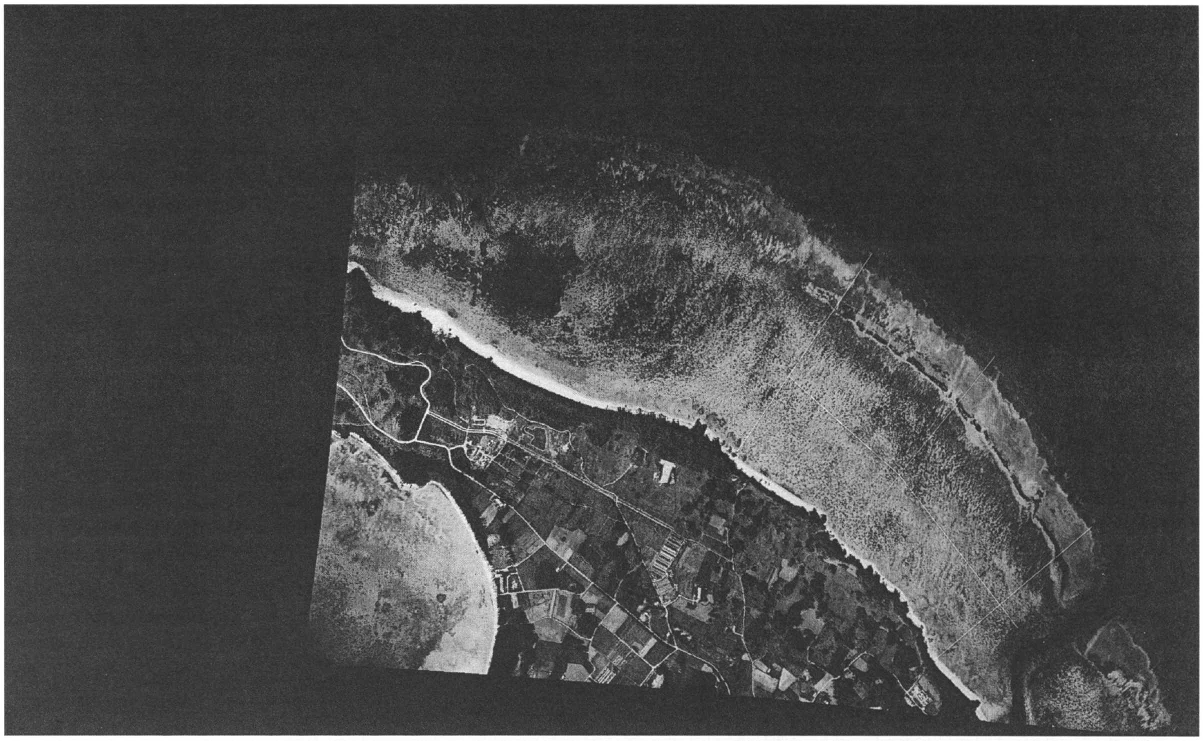


Figure 3. Georeferenced aerial photographs taken in 1973 (a), 1977 (b), 1983 (c), 1986 (d), and 1994 (e). All colored images were converted in a grayscale form. Note the significant decrease of dark patches in the eastern part of the moat between 1977 and 1983 and the slight increase of them between 1986 and 1994.

c 1983

d 1986

Figure 3. *Continued*.



e 1994

Figure 3. *Continued.*

the western part of Kabira Reef were detected. Therefore, Kabira Reef can be regarded as a typical fringing reef. In addition, it has an ecological zonation along the shore in the moat near the reef pavement as shown in T-line (Figure 2d).

Corals on hard substratum (reef rocks and dead corals): *Montipora digitata* on the reef pavement, delicate branching *Acropora* near Kabira Channel, and *Porites cylindrica* on dead corals have been relatively stable in the recent 21 years (Figure 4a, b and Figure 5b), thus, we consider that coral zones on hard substratum can be regarded as corresponding to the gradient in currents as GEISTER (1977) indicated. The light intensity proposed by ADEY and BURKE (1977) was neglected because of the shallow depth. YAMANO *et al.* (1998) showed that the dominant water circulation throughout the year shows a pattern under northern wind conditions as shown in Figure 1b. Ocean waters come inshore over the reef crest and flow out through Kabira Channel. The wave action is severe on the reef edge facing the ocean, and the current is stationary in the moat because of energy loss caused by wave breaking on the reef crest. The current velocity near Kabira Channel (E350) is greater than that of the middle part of the moat (M350). This shows that Kabira Reef has a gradient in water motion not only from the shore to the ocean but also in the moat parallel to the shore. The zonal distribution of corals and currents are as follows: massive and branching *Porites* zone in the moat where water motion is stationary, large-patched branching *Montipora digitata* zone on the reef pavement and delicate branching *Acropora* zone, situated just behind the reef edge where wave actions were attenuated by wave breaking on the reef edge. Robust branching and tabular *Acropora* zone is on the reef edge where wave actions are severe. Delicate branching *Acropora* zone is situated near Kabira Channel where currents are amplified.

On the other hand, *Montipora digitata* in the moat are established on bioclastic sands (Figure 2) and susceptible to distribution changes at intervals ranging from a decade (Figure 4a, b) to a month (Figure 5a). These changes are also shown by MATSUNAGA and KAYANNE (1997) describing the disappearance of the patches in the eastern part and the appearance of the patches in the western part during 1977 and 1984.

Possible Cause of the Change of Patches

Montipora digitata communities in the moat are established on bioclastic sands on which coral larvae cannot settle, and the larger patch exists upstream of this zone (the reef pavement, Figure 2a–c). For these reasons, we consider that this community originates from the reef pavement. It is well documented that corals can expand their habitat by fragmentation (*e.g.* TUNNICLIFFE, 1981; HIGHSMITH, 1982). Dominant water circulation in this reef (Figure 1b) shows that, under normal conditions, *Montipora digitata* in the moat are supplied from the reef pavement, and this indicates that there is a continuous increase of dark patches in the moat. However, coral patches significantly decreased during 1977 and 1983 in the eastern part of the moat (Figure 3b, c and Figure 4).

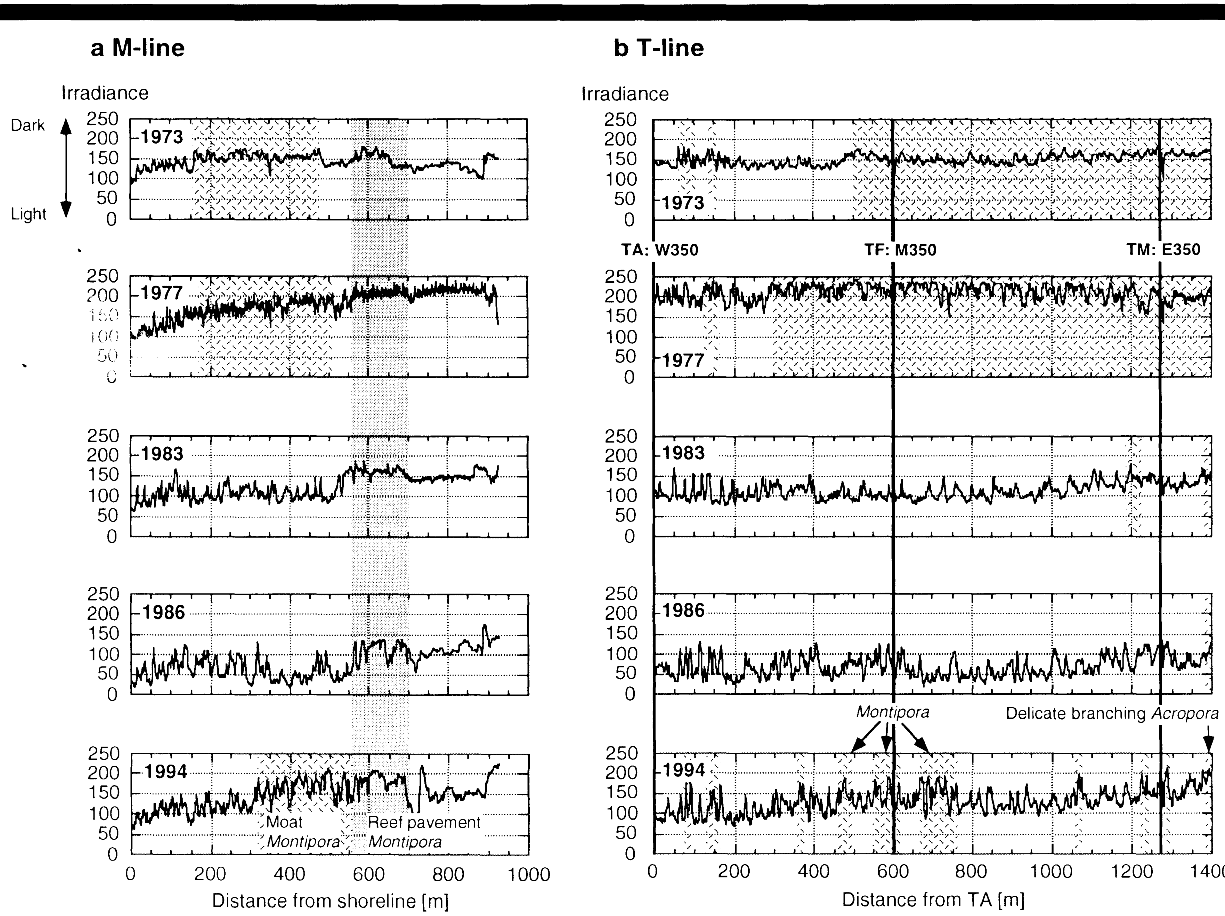


Figure 4. Irradiance along M-line (a) and T-line (b) in each image. The hatched areas represent dark patches of *Montipora digitata* and delicate branching *Acropora*.

HASEGAWA (1993, 1998) suggested the change in Shiraho Reef, situated at the opposite side of Kabira Reef, was caused by anthropogenic factors: inflow of red soil through rivers into the moat due to land development. *Acanthaster planci* attacked Ishigaki Island during 1981 and 1983 (YAMAGUCHI, 1986). These disturbances can cause significant decline of corals in the moat. However, Kabira Reef has no rivers, and there also occurred an increase of coral patches in the western part of Kabira Reef during this period (Figure 3b, c, see also MATSUNAGA and KAYANNE, 1997). Therefore, the change of patches cannot be explained by these two causes only.

LUGO-FERNANDEZ *et al.* (1994) interpreted the changes in the photograph of a Caribbean reef as products of sediments transported by a hurricane. HASEGAWA (1990) also attributed the shoreline change of the cays in Kume Island, the Ryukyu Islands to typhoons. Table 2 shows the main typhoons and tropical storms (Max. wind > 17 m/sec) struck Ishigaki Island, and Figure 6 shows the wind vectors of the typhoons and the resultant wind vectors during the times the photographs were taken. The number of severe typhoons (Max. wind > 25 m/sec) which struck Ishigaki Island in the recent century is about 65 (YAEYAMA METEOROLOGICAL STATION, 1968; JAPAN METEOROLOGICAL AGENCY, 1968–1996), and this value is far greater than that found in Caribbean seas (19 as a maximum value, TREML *et al.,* 1997). From 1965 to the present, 13 severe typhoons have struck Ishigaki Island, whereas only 4 cyclones have struck Heron Island on the Great Barrier Reef (CONNELL *et al.,* 1997). Table 2 also records severe hurricanes and tropical storms on the Caribbean Elkhorn Reef according to LIRMAN and FONG (1997b), indicating that severe typhoons have an effect similar to that of severe hurricanes in the Caribbean.

We experienced one severe typhoon during the observation of quadrats (Table 2), resulting in significant change in the distribution of *Montipora digitata* (Figure 5a). This also indicates the importance of typhoons as a factor influencing the change of patches in the moat. Circulation in Kabira Reef shows a marked wind influence shown in Figure 1b. Between 1977 and 1983, we had one severe typhoon with strong southern winds in 1982 (Table 2), and other eight small typhoons with southern winds, which can explain the distinction of the patches in the east as a result of the migration to the west. The wind vectors (Figure 6) indicate Kabira Reef suffered strong southeast and southern winds in this period. Between 1986 and 1994, of all four severe typhoons, three typhoons were with predominating northern winds. Eight small ty-

Table 2. *List of dates, maximum values of wind speed, gusts, wind directions, and names of hurricanes and typhoons. Data on Elkhorn Reef (Carribean) are from* LIRMAN *and* FONG *(1997b). Data on Ishigaki Island are from the Monthly Report of the Japan Meteorological Agency from 1968 to 1996, and partly from web page http://wxp.atms.purdue.edu/. Shaded typhoons show severe typhoons with winds greater than 25 m/sec. ND: No description.*

Area	Date	Max. Sustained Winds (m/sec)	Gusts (m/sec)	Wind Direction	Name	
Elkhorn Reef	8/24/92	63.0	79.2	ND	Hurricane ANDREW	
	3/12–13/93	20.8	27.8	ND	Storm of the CENTURY	
	11/14–17/94	23.3	36.7	ND	Tropical Storm GORDON	
Ishigaki Island	9/22/68	18.8	ND	NNW		
	8/7–8/69	18.7	ND	E		
	9/26–27/69	32.8	ND	SE	Super Typhoon ELSIE	
	10/5/69	19.7	ND	NNW		
	7/3/70	18.0	ND	NW		
	7/25/71	21.3	ND	ESE		
	9/18/71	18.7	ND	ESE		
	9/22/71	38.6	ND	SSE	Super Typhoon BESS	
	7/23–24/72	20.0	ND	WNW–NW		
	8/15–17/72	22.5	ND	NNE–W–SSE		
						1973 Photo
	7/16–18/73	21.3	ND	WNW–WSW–SSW		
	8/2–3/75	19.5	ND	NE–E		
	9/21–22/75	18.1	ND	NNE–E		
	8/9–10/76	39.2	ND	S–SSE	Super Typhoon BILLIE	
	7/25/77	17.8	ND	SSW		
	7/30–31/77	53.0	ND	NE–SE	Typhoon VERA	
	8/22–23/77	18.8	ND	SSW		
						1977 Photo
	7/31/78	18.0	ND	SW		
	9/11–13/78	19.5	ND	SSE–S–SSW		
	8/14–16/79	24.1	ND	W–SW–SSW		
	10/17–18/79	18.2	ND	N–NNW		
	8/27/80	24.1	ND	SE		
	10/12/80	19.2	ND	NW		
	6/20–21/81	19.2	ND	S		
	7/22–23/81	17.1	ND	SSW–S		
	8/31–9/1/81	19.6	ND	W–WSW–SSW		
	7/28–29/82	21.0	ND	SE		
	8/9–10/82	36.7	ND	ESE–SSW	Super Typhoon CECIL	
						1983 Photo
	9/25–26/83	19.6	ND	NW		
	8/22–23/85	31.8	ND	SSW	Typhoon NELSON	
	10/4/85	28.5	ND	SSE	Typhoon BRENDA	
	8/22–24/86	19.4	ND	WSW–N–ENE		
	9/18–19/86	20.0	ND	ESE–SSE		
						1986 Photo
	7/27/87	19.2	ND	SSE		
	8/29–30/87	21.0	ND	NNW		
	6/2/88	18.8	ND	N		
	9/9–13/89	17.4	25.8	ENE–E–SE–S–S		
	6/23/90	18.9	33.0	ESE		
	7/10/90	17.7	24.9	SSW		
	8/18–20/90	26.4	43.4	NE–ENE–SE	Typhoon YANCY	
	8/29–30/90	26.0	42.1	NNW–WSW	Typhoon ABE	
	9/6–8/90	17.9	29.8	NNE–E–ESE		
	9/25–26/91	19.9	35.5	NNE–N		
	6/28/92	22.3	42.5	NE		
	8/29–31/92	18.7	29.8	ESE–SSE–S		
	9/3–4/92	17.8	28.7	NE–E		
	9/22/92	17.8	29.4	SE		
	9/1–2/93	18.7	34.0	N–NW		
	7/10/94	17.7	29.5	ESE		
	8/7–8/94	28.8	46.5	ESE–SE	Typhoon 9413	
	8/19–21/94	27.4	47.1	NNE–NNW–SW	Typhoon 9416	
						1994 Photo
	10/8–10/94	32.5	56.5	NE–ESE–SSE	Typhoon 9429	
						1995 Observation
	9/22–23/95	32.1	63.5	E–WNW	Typhoon 9514	Observation of quadrats
	7/30–8/1/96	36.1	57.2	NNE–SE–SSE	Typhoon 9609	
	9/28–30/96	17.3	34.5	N–NNW–NNW		

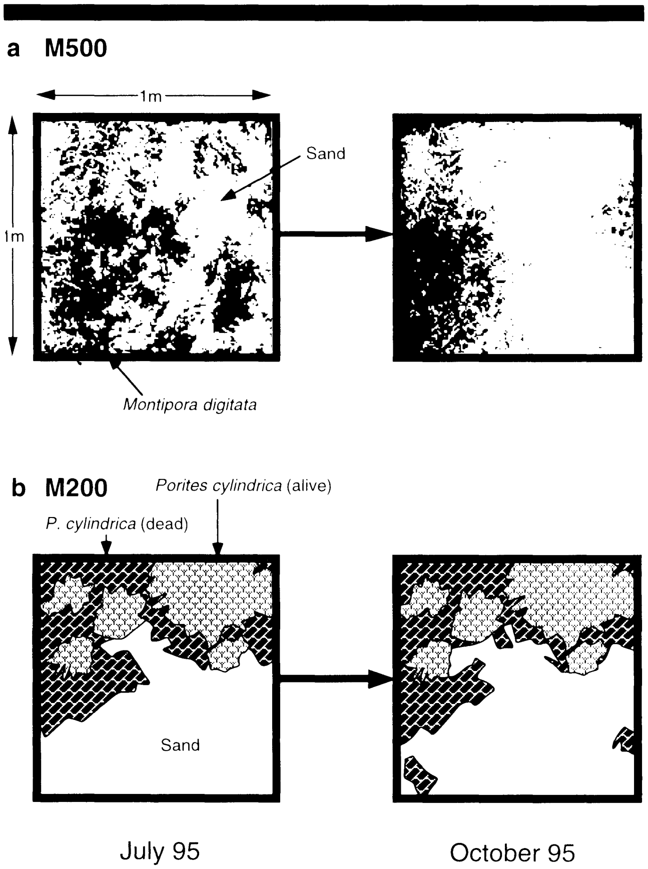


Figure 5. Change of coral distribution in a 1 m^2 quadrat set at M500 (a) and M200 (b). The coral distribution was described on 20 July 1995 and 6 October 1995.

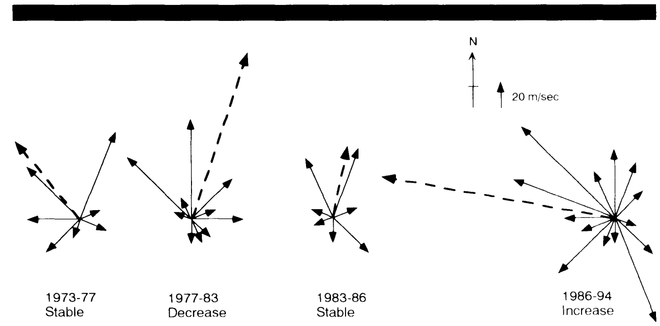


Figure 6. Wind vectors of typhoons during the intervals between the times the photographs were taken. Broken line vectors indicate the resultant vectors of typhoon winds. Notes describing the decrease and increase are on patches in the eastern part of Kabira Reef moat.

phoons out of fourteen had northern winds, whose gust values are generally greater than those of typhoons with southern winds (Table 2). These typhoons can enhance the fragmentation on the reef pavement and the accumulation of the fragments in the moat. The resultant wind vector (Figure 6) is westward. It also indicates the enhancement of the fragmentation on the reef pavement. Little increase in coral patches in the eastern part of Kabira Reef was observed between 1973 and 1977, although four typhoons out of six had southerly winds (Table 2) and the resultant wind vector was northwestward (Figure 6). This may be explained by the effect of fragmentation under the normal condition of northern winds that supply coral fragments from the reef pavement into the moat. This normal fragmentation can also explain the expansion of *Montipora digitata* patches from 1986 to 1994. Typhoon 29 in October 1994 had both northern and southern winds and seems to have caused no significant change of *Montipora digitata* communities at least around M500, because the extent of patches in Figure 4a corresponds well with the actual *Montipora digitata* distribution shown in Figure 2b. The direction of typhoon winds may influence the accretion and removal of coral fragments in the moat.

CONCLUSIONS

We present the spatial structure of coral zonation in Kabira Reef. In the previous studies, coral zonation has been discussed as it is found along the transect perpendicular to the shoreline (DONE, 1983). We show here that backreef environmental gradient along the shore influences the distribution of corals. Compared to other zones which are established on hard substratum and correspond to the environmental gradient, *Montipora digitata* zone in the moat, established on thick bioclastic sands, shows significant decadal and temporal changes.

Aerial photographs are a very effective tool for detecting the change of coral communities on the spatial scale of an ecological zone or a whole coral reef. It is hard to represent distribution of corals in the moat of Kabira Reef by small quadrats or transects, because the ecological zone itself is dynamic: patch formation and extinction occur at a decadal time scale. Our results clearly show that large-scale observations are also useful to detect and understand the dynamics of coral communities as JACKSON (1991) and CONNELL *et al.* (1997) suggested.

Furthermore, our results indicate that the wind direction of typhoons plays a significant role in the accumulation and removal of coral fragments, which may cause the zone specific characteristics as LIRMAN and FONG (1996, 1997a, b) have shown. In the eastern part of Kabira Reef moat, north and east winds may enhance the fragmentation from the reef pavement, a source area of *Montipora digitata* fragments, and induce the expansion of *Montipora digitata* habitats in the moat, whereas south winds will remove the fragments in the moat.

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