

## PATTERNS OF CORAL REEF DEVELOPMENT ON TARAWA ATOLL (KIRIBATI)

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### ABSTRACT

Tarawa Atoll lies in the equatorial upwelling region, has the largest human population of any Pacific atoll, and has an unusual, asymmetrical form: the triangular lagoon is largely enclosed along the east and south, but communicates with the ocean through a submerged barrier reef along its entire western border. How do these unusual characteristics affect reefs? After characterizing lagoonal reefs, the interactions and influence of various physical and biotic factors are examined. Coral cover and diversity increase from northwest to southeast as a consequence of polarized exchange with the surrounding ocean. Macroalgae are abundant in the central lagoon, probably as a result of high productivity and low levels of herbivory, the latter a likely consequence of overfishing. Coral communities of these central reefs are dominated by clonal, fragmenting species of encrusting *Montipora* and branching *Acropora*. A substantial loss of coral cover and diversity occurred in the southeastern lagoon apparently a few hundred years ago. As a consequence of this mortality, much of the reef habitat and associated communities of the southeastern lagoon were lost, and patch reefs in the area developed into sand-dominated shoals by intense bioerosion and burial. The high productivity of the region has also resulted in high rates of mobile sediment production through bioerosion and the accumulation of skeletal remains of a rich suspension and deposit feeding lagoonal biota. The productivity and sediment production in turn had major geomorphological consequences, creating an atoll with an unusually wide, sand-dominated rim and shallow, sediment-choked lagoon, and may have been partly responsible for the submergent nature of the western barrier reef through the impact of inimical lagoonal backwaters.

Reef systems around islands vary greatly in extent, geomorphology, and the range and types of habitats encompassed. Most of the variation among island reefs is attributable to differences among inner reefs: backreef and lagoonal environments lying landward or lagoonward of the reef crest. In contrast outer reef habitats, lying seaward of the reef crest, show considerably less inter-island variation (Salvat, 1969; Chevalier, 1981; Paulay, 1990). Variation in inner reef systems is especially striking among atolls, as they differ substantially in the characteristics of their lagoons (size, shape, bathymetry, connectedness with the ocean, abundance of patch reefs, types of soft bottoms, etc.) and barrier reef rims (width, depth, proportion covered by islets, occurrence of passages, etc.) (Wiens, 1962; Stoddart, 1965). The geomorphology of and variation among reef systems is a function not only of the tectonic, climatic, oceanographic, and sea level setting and history, but also depends on the biotic communities that are ultimately responsible for their construction. Conversely the nature of habitats and biotic communities are strongly dependent on the geomorphology of the reef system. Thus there is a dynamic interaction between the physical setting and the biota of reefs, that shapes the development of both. Here we describe physical and biological features of the reefs and reef communities of Tarawa atoll (Tungaru (former Gilbert) Islands, Kiribati). We consider how some of the unusual features of this atoll—location in the equatorial upwelling region, asymmetrical shape, and high human population density—may have influenced reef communities.

Conversely we explore how patterns of carbonate production by the reef community may have contributed to the geomorphology of the atoll.

Tarawa, the metropolitan center of Kiribati, has a larger human population than any other Pacific atoll (28,800 people in 1990; Kiribati Statistics Office, 1991), and the population is rapidly growing. While most central Pacific atolls lie in the northern and southern oligotrophic gyres, Tarawa's location in the nutrient-rich waters of the equatorial upwelling zone provides for much higher levels of productivity than typical of Oceania (Kimmerer and Walsh, 1981; Kimmerer, 1995; Paulay, 1997). The geomorphology of the atoll rim (Fig. 1), with shallow eastern and southern sides capped almost entirely by islets and a western margin submerged several meters below the surface, creates a polarized connection between the lagoon and surrounding ocean. This polarization has been further exacerbated by the closure of many reef flat spillways (hoas), which have in the past provided a limited connection between the ocean and lagoon along the eastern and southern rims, by causeways constructed in the past 50 yrs. Causeway construction has obliterated all hoas along the metropolitan southern rim known locally as 'South Tarawa', and a few of the hoas along the eastern rim known as 'North Tarawa'. The polarized exchange of water has created a lagoon with marked northwest to southeast gradients in water characteristics (inorganic nutrients, salinity, turbidity, etc.), planktonic productivity, composition and biomass, benthic sediment composition, and so on (Weber and Woodhead, 1972; Kimmerer and Walsh, 1981; Kimmerer, 1995). These in turn have led to marked gradients in the distribution of benthic habitats and in the composition of both soft and hard bottom communities (Paulay, 1997).

#### INSULAR SETTING

Tarawa is roughly triangular, with a relatively shallow lagoon largely enclosed by the eastern and southern rims, but with a submerged western rim providing extensive communication with the surrounding ocean (Fig. 1). Inner reef habitats can be divided into the atoll rim, lagoon floor, and patch reefs-shoals.

The southern and eastern atoll rim is comprised of a relatively narrow outer reef flat, a series of low islets (motus), and a wide, lagoonal sand flat. The outer reef flat was briefly investigated along the southern rim, where it consists of a largely intertidal reef pavement, devoid of living coral, that breaks gradually into the fore reef slope without a reef crest. The intertidal to shallow subtidal lagoonal sand flats are unusually wide (to ~2.5 km), are dominated by soft sediments, and are largely devoid of living corals; their physiography and biota are discussed by Paulay (2001). Extensive beds of the sea grass *Thalassia hemprichii* line the lagoonal margin of these sand flats along the eastern half of the southern rim and the northern end of the eastern rim of the atoll (Paulay, 1997). Coral communities and loosely-constructed fringing reefs occur locally on the lagoon slope just off the sand flats: comprised mainly of occasional large *Porites* heads along the southern rim, while dominated by staghorn *Acropora* thickets along the eastern rim.

The western atoll rim is a drowned barrier reef, interrupted by a deep and wide channel ca 7 km north of its southern end. Most of the western reef lies at a depth of several meters (max. ~9 m; Weber and Woodhead, 1972), but reaches into the intertidal at its northern end and south of the channel (Fig. 1). The submerged rim is several hundred meters wide and exhibits considerable topographic variation with a local relief of typi-

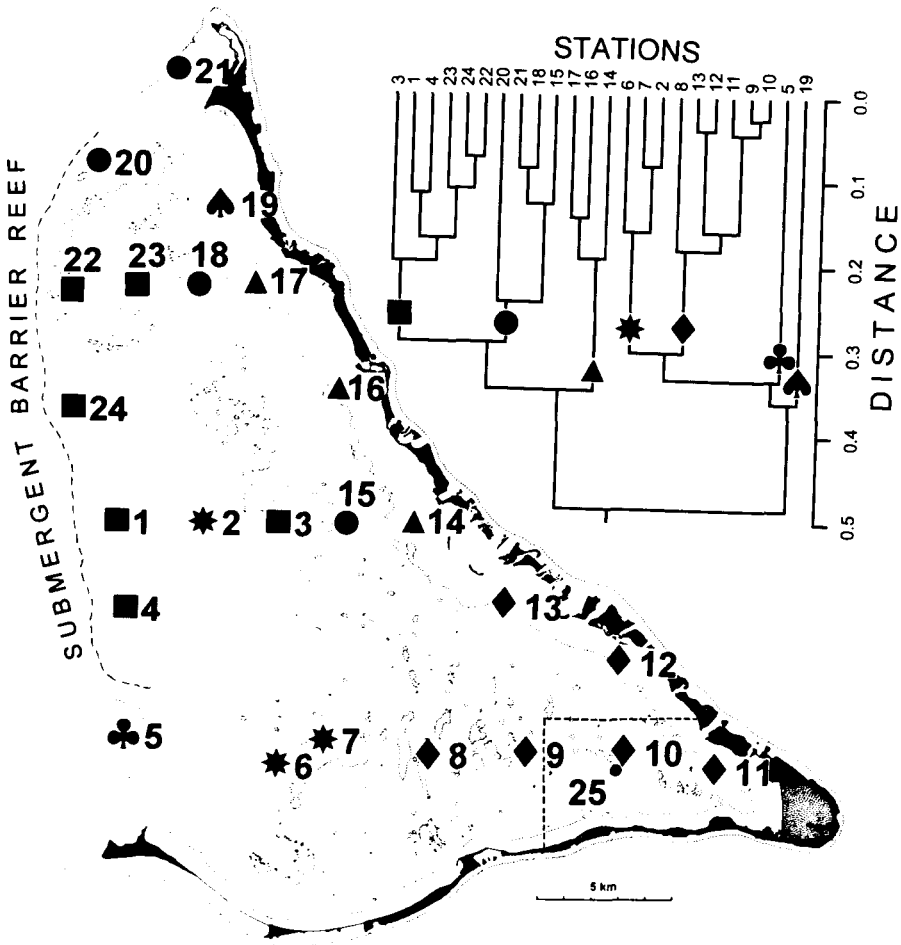


Figure 1. Map of Tarawa Atoll and result of cluster analysis on bottom cover. Map is based on UK Ordnance Survey for the Government of Kiribati, edition 1-OSD 1985, and shows location of quantitative survey stations (C1-C24) and station C25. The main area of coral mortality in the southeastern lagoon was south of  $1^{\circ}24'N$  and east of  $173^{\circ}4'E$ , as indicated by dashed lines. Thin lines connecting islets represent causeways. Dendrogram depicts cluster analysis of Jaccard similarity coefficients of bottom cover between each site using the single linkage algorithm and average euclidean distance.

cally 1–5 m. Short sand channels and pockets of coarse sand are interspersed among reef promontories. This drowned barrier reef grades imperceptibly into a fore reef slope of similar physiography. The dissected nature and gentle slope of the fore reef along the western rim contrasts with the relatively smooth, almost pavement-like topography and steep slope of the fore reef along the southern rim.

The lagoon bottom slopes gently from the sand flats and barrier reef to a relatively level lagoon floor, that lies mostly at a depth of 5–20 m (max. 25 m; Bolton, 1982). Patch reefs and shoals rising from the lagoon bottom, like the narrow fringing reefs that locally flank marginal sand flats, often harbor rich coral communities. The lagoon slope and

floor, however, are largely devoid of corals; only occasional colonies, mostly of *Pocillopora damicornis* and *Porites* spp., were encountered there.

Numerous patch reefs and shoals rise from the lagoon floor. Topographic rises dominated by hard bottoms are defined as patch reefs, while those covered largely by soft sediments are defined as shoals, although the two clearly intergrade. A striking series of large shoals, many elongated north-to-south, lie ca 2–7 km north of, and parallel to, the southern atoll rim margin (Fig. 1). These shoals partially divide the lagoon into a larger northern and a smaller southern section (cf Kimmerer and Walsh, 1981). Patch reefs are prevalent in the northern lagoon, while shoals characterize the southeastern lagoon. Patch reefs and shoals range from submerged mounds rising just above the lagoon floor, to structures that extend above sea level. Several shoals in the southern lagoon extend well into the intertidal, and one, capped by Bikemaan Islet, was high enough to harbor lush vegetation until it disintegrated through erosion during the 1980s.

In this study we consider the reef habitats of Tarawa lagoon: the fringing reefs bordering the sand flats, the patch reefs and shoals in the lagoon, and the western barrier reef. The biota and ecology of soft bottom habitats is reviewed elsewhere (Paulay, 2001).

## METHODS

Bottom cover and coral diversity were measured at 24 stations in June 1993. Numerous additional sites were examined qualitatively on several occasions between 1992–1994. Reef stations were situated along five transects: three crossing the lagoon west to east, one along the western barrier reef, and one along fringing reefs / patch reefs bordering the sand flats of the eastern rim (Fig. 1). All stations were situated on fringing, barrier or patch reefs/shoals, as the lagoon floor and nearshore sand flats are dominated by mobile sediments and have minimal coral cover. We attempted to place stations evenly along each transect; however scarcity of reefs in some areas necessitated adjustments. We chose shallow (0–5 m depth at low tide) sites for most stations, but only deeper reefs (to 11 m) were available at a few sites. Site locations were determined by GPS.

Bottom cover (live coral, macroalgae, reef pavement, rubble, sand, and other) was measured under 0.25 m<sup>2</sup>, stringed quadrats, placed in pairs at 5 m intervals along a 30 m transect line. Cover was recorded at each of 16 points defined by string intersections in each quadrat. Coral cover, identified to genus, was measured by the line-intercept method under the same 30 m transect. Coral diversity was measured in 10-min timed searches, in which all coral taxa encountered were recorded.

To investigate a major loss of coral diversity evident in the southeastern lagoon, all coral species encountered alive, as well as those encountered dead were enumerated on several shoals in this area. Samples of coral species commonly encountered dead but never alive were collected at stations C10, C11 and C25, and radiocarbon dated by Beta Analytic, Inc. (Miami, Florida). Ages determined by radiocarbon dating depend on the reservoir effect of the ocean, which could be particularly large in areas of upwelling like Tarawa. The reservoir effect at Enewetak (Marshall Islands), to the north of Tarawa and outside the equatorial upwelling region, is ca 140 yrs (Beta Analytic, Inc., 23 May 1994). To evaluate the potential local reservoir effect, we dated samples from two specimens (Museum of Comparative Zoology catalog numbers: MCZ 5939 and MCZ 5954) of *Porites cylindrica* collected on Abaiang Atoll ca 1860 by Andrew Garrett. Abaiang lies immediately north of Tarawa. These were the only samples we were able to locate in this area that predated radiocarbon contamination created by the atomic age. Although exact locality data from Garrett's collection is lacking, *P. cylindrica* is a predominantly lagoon-inhabiting coral.

To examine trends in coral cover we analyzed the relationship between coral cover and distance from the northernmost station (C21) with simple linear regressions. Data were log transformed

when necessary, then rechecked with Bartlett's tests to insure homoscedasticity and with Rankit plots to confirm normality (Sokal and Rohlf, 1995). We also performed a cluster analysis of Jaccard similarity coefficients of bottom cover between each site using the single linkage algorithm and euclidean distance. Regressions were performed on Statistix 4.0 (Analytical Software, St Paul, Minnesota) and the cluster analysis on BMDP 5.0 (BMDP Statistical Software, Inc., Los Angeles, California).

## RESULTS

Coral cover in the lagoon generally decreased from northwest to southeast (Fig. 2). This is clearly shown by a regression between log coral cover and distance from the northernmost station (C21) on the western barrier reef (Fig. 3, adjusted  $r^2 = 0.74$ ,  $P < 0.001$ ). While coral cover was consistently moderately high at northern stations (20–40%) and always very low in the southern lagoon (0–3%), it fluctuated considerably among patch reefs around the middle of the lagoon (5–50%) (Fig. 2). Much of this fluctuation is likely attributable to variation in minimum depth, reef size and shape, and relative abundance of soft vs. hard substrata among patch reefs in the central lagoon. In contrast, coral cover decreased rather uniformly north to south along the physiographically less variable barrier reef. Coral cover also decreased north to south along the fringing reefs bordering the eastern sand flats. Coral cover was lowest on the shoals in the southeastern lagoon.

Mobile substrata (sand and rubble) generally increased in abundance on lagoon shoals/patch reefs from northwest to southeast (Fig. 2). This may be partly responsible for the low coral cover of the southeastern lagoon, as the paucity of hard substrata may limit coral recruitment. Shoals, i.e., mounds covered largely by soft sediment and coral rubble, characterize the southeastern lagoon. In contrast the northern lagoon has abundant patch reefs, which have a more limited cover of mobile sediments.

The paucity of hard bottoms is not in itself sufficient to explain the paucity of corals in the southeastern lagoon, as dense thickets, comprised of several species of arborescent *Acropora*, grow over large areas of sandy bottom in the northern lagoon. For example a freestanding *Acropora* thicket over sand at station C19 had 35% coral cover. On all southern shoals dead *Acropora* sticks litter the bottom, indicating that similar thickets likely existed there in the past. Moreover many if not all southern shoals largely covered by sand today are underlain by extensively bioeroded reef framework or by a jumble of branching-coral rubble just a few centimeters under the surface, indicating that they recently evolved from typical patch reefs by reef death and burial.

Fleshy benthic algae are unimportant as cover on the submerged western barrier reef (0–7%), but often dominate on patch reefs in the central lagoon (5–54%) (Fig. 2). They are also uncommon in the southeastern lagoon (5–13% at the southeastern-most stations C9–12), an area dominated by soft bottoms and hence providing poor opportunities for algal attachment. The southernmost station (C5) on the western barrier reef is an exception to this trend; however the 54% algal cover there was due entirely to *Halimeda*, an alga that was rare at the other stations surveyed.

*Montipora*, *Acropora*, *Porites*, *Heliopora* and *Pocillopora* dominate coral cover, comprising over 80% of the coral cover at the stations surveyed. There is considerable variation among areas in the relative abundance of these genera, however. Patch reefs in the mid and northern lagoon are dominated by a diversity of *Montipora* and *Acropora* spe-

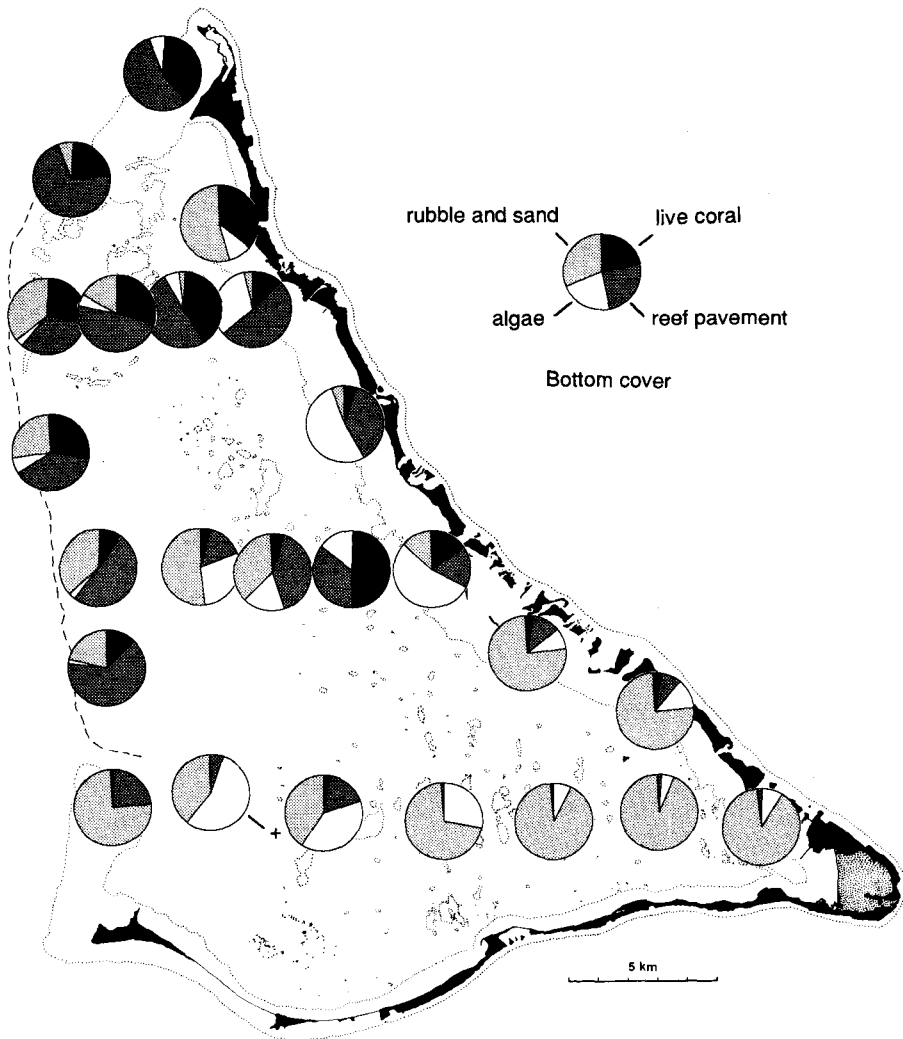


Figure 2. Bottom cover based on quadrat data (see methods). Miscellaneous includes mostly sedentary invertebrates other than hard corals. Algal cover is of red and brown macroalgae, except at station 5, where it is entirely of *Halimeda*. *Halimeda* was not encountered in quantitative survey at other stations.

cies, while reefs in the southern lagoon (stations C6–C12) largely lack these genera and have a low cover of mostly *Porites* and *Pocillopora damicornis*. In contrast the western barrier reef hosts a much more heterogeneous coral assemblage, with *Acropora*, *Montipora* and *Pocillopora* all unimportant, and *Porites*, *Heliopora*, and a variety of faviid and other genera dominating (Fig. 4). Changes in coral community composition follow a similar northwest to southeast gradient as noted for coral cover above, as illustrated by cluster analysis (Fig. 1).

Coral generic richness, as measured by 10 min, timed searches, shows a similar pattern to coral cover, increasing from south to north and from east to west (Fig. 5, Table 1).

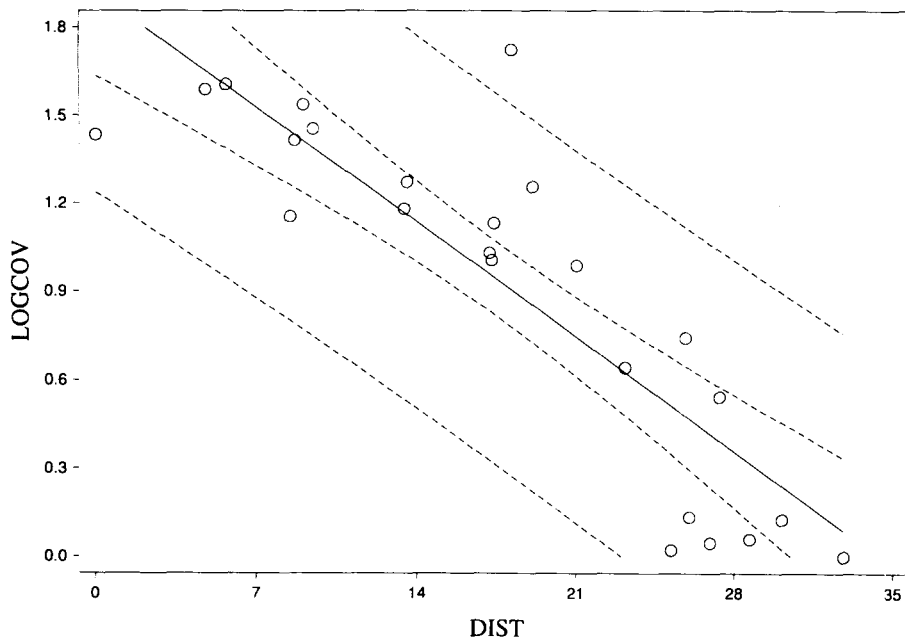


Figure 3. Regression between log coral cover (LOGCOV) and distance from the northernmost station (DIST, in km).  $LOGCOV = 1.9203 - 0.0558 * DIST$ . 1 and 2  $\sigma$  confidence intervals indicated.

Generic diversity is clearly highest on the western reef, moderately high throughout the central patch reefs, and lowest on the southern shoals and the fringing reefs bordering the eastern sand flats. Generic richness decreases strikingly from west to east along the southern transect, so that in the southeastern corner, only a single genus, *Porites*, was found alive.

Generic richness appears to show less variability through the central lagoon than coral cover. The great variation in coral cover in the central lagoon appears to be the result of the dominance of a few genera (especially *Montipora* and *Acropora*; Fig. 3). Several stations, especially in areas of the eastern lagoon, have low coral diversity combined with high coral cover, as a result of large mono- or pauci-specific coral stands. The western barrier reef has a fairly uniform generic richness through most of its extent, with 18–21 genera per 10-min search. Ten minute searches were reasonably comprehensive: about two thirds of the genera encountered in the entire quantitative survey were found within 10 min on a typical barrier reef station.

In contrast to the low present diversity of corals in the inner southeastern lagoon, dead skeletons indicate considerably greater species richness in the past. Only *P. damicornis*, *Porites* spp. and a single *Montipora* colony were found alive south of  $1^{\circ}24'N$  and east of  $173^{\circ}04'E$  (Fig. 1). In contrast, we encountered dead skeletons of *Millepora*, *Acropora*, *Montipora*, *Astreopora*, *Fungia*, *Stylophora*, *Goniastrea*, *Platygyra*, *Favia*, and *Cyphastrea* on the surface of shoals in this area (Table 2). *Acropora* skeletal debris predominates on these shoals, indicating that it was likely important if not dominant cover in the past. The calibrated radiocarbon dates of two specimens of *P. cylindrica* collected in the 1860s by Andrew Garrett were 1800–1950 AD. This indicates that contrary to expectations the

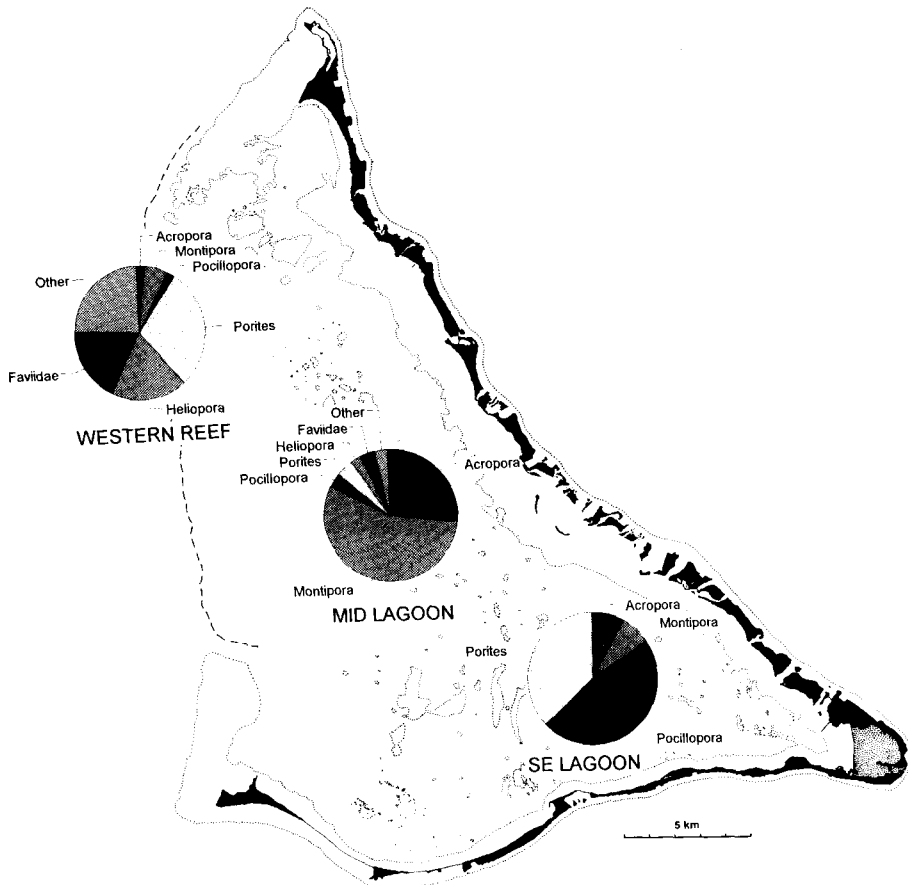


Figure 4. Coral cover based on line-intercept transect data, summed for three distinct habitat regions in the lagoon. A) W reef: all stations (C1,4,5,20,21,22,24) along the western barrier reef. B) Mid-N lagoon: all patch reef stations (C2,3,14-19,23) in mid and northern lagoon. C) SE lagoon: all shoal/patch reef stations (C6-12) in southeastern lagoon.

local reservoir effect is inconsequential. Calibrated radiocarbon dates of eight samples of locally extinct corals collected in this area range from 330–605 AD to 1445–1665 AD (Table 3).

#### DISCUSSION

How does the nature and historical development of the marine environment of Tarawa influence the atoll's lagoonal reefs and biota? Important variables to consider include (1) the asymmetrical form of the atoll, (2) the location of the atoll in the equatorial upwelling zone, and (3) potential natural and anthropogenic disturbances.

CONSEQUENCES OF GEOMORPHOLOGY.—The diversity and abundance of corals and other benthos in the lagoon follows conspicuous north to south and west to east gradients. Marked gradients have also been documented in nitrate, phosphate, sediment grain size (all decreasing west to east), phytoplankton biomass, and turbidity (increasing west to

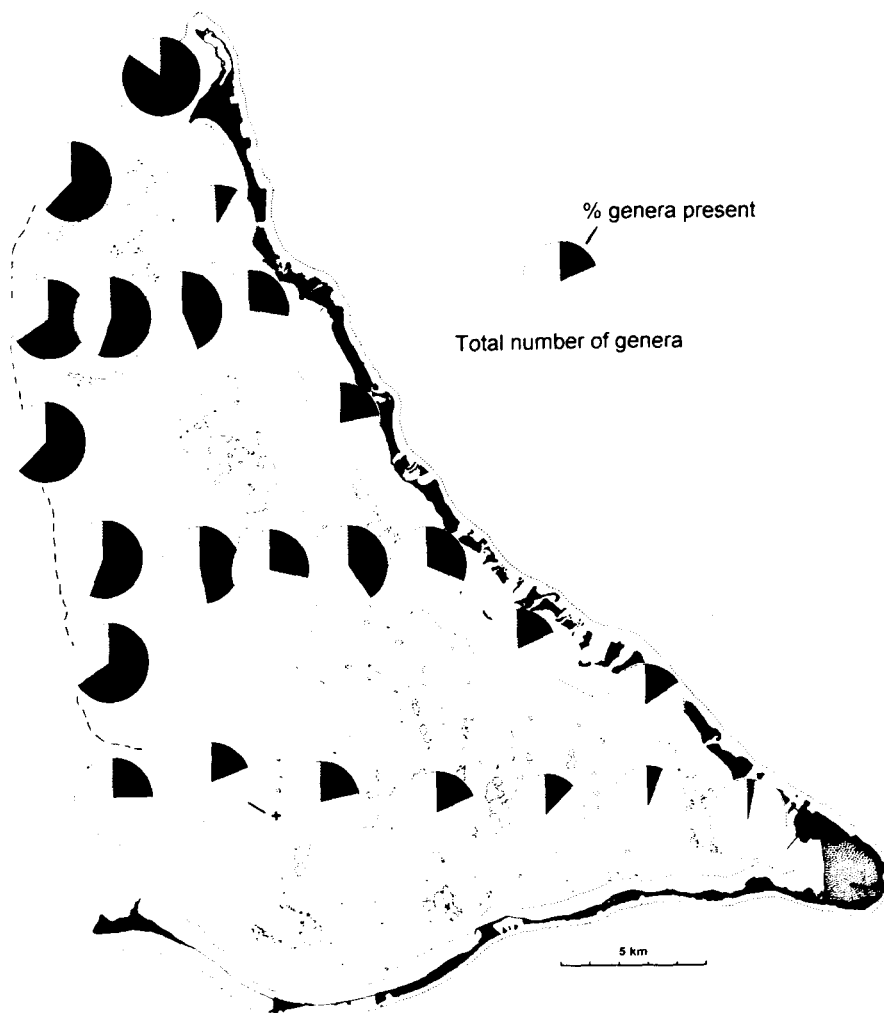


Figure 5. Relative generic richness of corals. Shows fraction of total generic diversity encountered during 10 min search at station. Total generic diversity (32) is the number of genera encountered during all such searches at all 24 stations. Based on data in Table 1.

east), for example (Weber and Woodhead, 1972; Kimmerer and Walsh, 1981). These gradients appear to be ultimately related to the form of the atoll. As most of the water exchange with the surrounding ocean is through the western, submerged barrier reef, oceanic conditions dominate toward the west, while inshore, lagoonal conditions prevail toward the east. The southeastern lagoon is the most distant and restricted from this oceanic interchange.

The majority of reef corals in the central Pacific prefer oceanic over lagoonal conditions (Maragos, 1974; Chevalier, 1979; Paulay, 1988); thus it is not surprising that both coral diversity and abundance increase in the lagoon northwestward. There is a clear zonation in the occurrence of corals across the lagoon (cf Fig. 4). Several genera, e.g., *Stylocoeniella*, *Pavona*, *Mycedium*, *Hydnophora*, *Oulophyllia*, appear to be limited to

Table 1. Corals encountered in timed searches.

Genus/Station #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
<i>Millepora</i>				X						D	D									X			X	X
<i>Heliopora</i>				X	D		X		X				X	X			X	X		X	X		X	X
<i>Sylocoeniella</i>	X	X		X																X				X
<i>Pocillopora</i>	X		X	X	X		X	X	X	X	D	X		X	X	X	X	X		X	X	X	X	X
<i>Seriatopora</i>														X						X	X	X	X	X
<i>Stylophora</i>				X			X	X	D	D	D		X	X	X	X	X	X	X	X	X	X	X	X
<i>Acropora</i>	X	X	X	X	X		X	X	X	D	D		X	X	X	X	X	X	X	X	X	X	X	X
<i>Montipora</i>	X	X	X	X	X	X	X	X	X	D		X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Astreopora</i>	X	X	X	X	X	X	X	X	X	D	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Porites</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Fungia</i>	X	X		X	X			D		D	D		X	X	X	X	X	X	X	X	X	X	X	X
<i>Herpolitha</i>																					X			
<i>Halomitra</i>					D	D							X							X	X			X
<i>Psammocora</i>	X	X		X	X	X		X			X		X	X	X	X	X	X		X	X	X	X	X
<i>Coscinaræa</i>														X	X	X	X	X		X	X	X	X	X
<i>Pavona</i>	X			X	X										X	X	X	X		X	X	X	X	X
<i>Acanthastrea</i>																					X			X
<i>Lobophyllia</i>	X																							X
<i>Symphyllia</i>					X																			X
<i>Mycodium</i>															X						X	X		X
<i>Merulina</i>	X								X												X	X	X	
<i>Hydnophora</i>	X	X		X											X					X	X	X	X	X
<i>Favia</i>	X	X	X	X											X					X	X	X	X	X
<i>Favites</i>	X	X	X	X		X									X					X	X	X	X	X
<i>Goniastrea</i>	X	X	X	X											X	X	X	X	X	X	X	X	X	X
<i>Platygyra</i>	X	X	X	X						D					X		X	X	X	X	X	X	X	X
<i>Oulophyllia</i>					X										X		X	X	X	X	X	X	X	X
<i>Plesiastrea</i>						X									X		X	X	X	X	X	X	X	X
<i>Cyphastrea</i>	X	X	X	X			X							X	X		X	X	X	X	X	X	X	X
<i>Echinopora</i>	X	X		X	X	X									X		X	X	X	X	X	X	X	X
<i>Leptastrea</i>	X	X		X	X	X									X		X	X	X	X	X	X	X	X
<i>Turbinaria</i>	X			X											X		X	X	X	X	X	X	X	X
TOTAL	18	15	9	21	8	6	7	6	4	2	1	5	6	10	13	7	9	14	3	20	27	21	18	20

X = encountered in 10-min search. D = not encountered at station alive, but found as dead skeleton. See Figure 1 for station locations.

Table 2. Living and dead corals encountered in the southeastern lagoon.

Genus/Station	C10	C25	C11
<i>Porites</i>	L	L	L
<i>Pocillopora</i>	L	L	D
<i>Montipora</i>	D	L	
<i>Millepora</i>	D	D	D
<i>Acropora</i>	D	D	D
<i>Fungia</i>	D	D	D
<i>Astreopora</i>	D	D	
<i>Platygyra</i>	D		
<i>Cyphastrea</i>		D	
<i>Favia</i>		D	
<i>Goniastrea</i>		D	
<i>Stylophora</i>		D	

L: found alive during thorough search; D: found dead only. See Figure 1 for station locations.

areas under considerable oceanic influence on or near the western reef (Table 1). Others, notably several species of *Montipora* and *Acropora*, thrive in the central lagoon, but do not survive today in the most restricted, southeastern area. Finally *Porites* and *P. damicornis* reach the silt-laden, turbid, plankton-rich waters of the southeastern lagoon.

Such striking gradients in water chemistry, sediment composition, coral community composition, etc., are characteristic of atolls where interchange with the surrounding ocean is restricted along the atoll perimeter. Few atolls have such a large portion of their rim submerged as Tarawa, however. In most atolls where water exchange is limited, it occurs through one or a few narrow but deep passes. Chevalier (1979) showed that in Tuamotu atolls with only one or two passes, several coral genera are restricted to the vicinity of passes, where coral diversity is highest. At Canton Atoll (Phoenix Ids., Kiribati), both coral cover and species richness decrease in a striking and significant gradient away from the single, deep passage (Jokiel and Maragos, 1978), as they do at Fanning Atoll

Table 3. Radiocarbon age of extirpated corals from southeastern lagoon.

Sample	Species	Station	C13/C12	Adj. age (BP)	Cal. age (AD)
Beta-72240	<i>Acropora ?muricata</i>	C25	+0.5	1950 ± 60	330-605
Beta-72246	<i>Platygyra daedalea</i>	C10	-0.4	1460 ± 70	800-1070
Beta-72247	<i>Cyphastrea serailia</i>	C25	+0.7	1440 ± 60	850-1070
Beta-72242	<i>Millepora dichotoma</i>	C10	+1.9	1330 ± 60	980-1220
Beta-72243	<i>Stylophora mordax</i>	C25	-0.9	1030 ± 60	1275-1440
Beta-72244	<i>Acropora</i> sp.	C11	-0.6	910 ± 60	1345-1515
Beta-72241	<i>Stylophora mordax</i>	C25	+0.4	850 ± 60	1410-1600
Beta-72245	<i>Fungia fungites</i>	C10	+2.2	780 ± 60	1445-1665
Beta-106800	<i>Porites cylindrica</i>	MCZ 5939	-1.0	410 ± 60	1815-1950
Beta-106801	<i>Porites cylindrica</i>	MCZ 5954	-1.1	420 ± 60	1800-1950

Samples are of well-preserved skeletons of extirpated corals taken from the surface of southeastern shoals in Tarawa, except the *P. cylindrica* were collected living by A. Garrett ca 1860 from Abaiang Atoll. See Figure 1 for station locations. C13/C12 in parts per thousand. Adj. Age: Conventional radiocarbon age ± 1σ, reported as RCYBP (radiocarbon years before 1950 A.D.). Cal. Age: Calibrated age, within 2σ (95% probability), is the best actual age estimate, including correction for reservoir effect derived from Abaiang samples. Dating by Beta Analytic Inc., Miami Florida.

(Line Ids., Kiribati) (Maragos, 1974). At Aldabra Atoll (Seychelles), coral communities are entirely restricted to the vicinity of the single pass into the lagoon (Taylor, 1978).

CONSEQUENCES OF UPWELLING.—Although coral cover was <50% at all stations, reefs appeared generally healthy at most. The moderate coral cover, even along the western reef, may in part reflect limitations on reef development imposed by high productivity (Birkeland, 1988) and inimical lagoonal backwaters (Neumann and Macintyre, 1985). The decrease in coral cover along the barrier reef from north to south may be a further reflection of this. Lagoonal waters increase in turbidity, sediment load, phytoplankton content, etc. (cf. Kimmerer and Walsh, 1981; Weber and Woodhead, 1972) southward as a result of the general widening of the lagoon. This change in water quality is clearly evident over the western reef as well. High productivity can impact reefs directly through water quality and indirectly by stimulating the growth of macroalgae, which compete with corals, especially new recruits (Birkeland, 1977, 1988). It can also affect reefs by increasing the abundance of suspension feeders, many of which are reef bioeroders (Highsmith, 1980). The abundance of macroalgae and intensity of bioerosion are both striking in the lagoon.

A striking feature of patch reefs in the middle of the lagoon is the abundance of red and brown macroalgae, which typically account for quarter to half of their surface cover (Fig. 2). Macroalgae frequently occupy more space than corals in this area, typically grow tall, shading and smothering neighboring coral colonies. The abundance of fleshy algae on reefs in the central Pacific upwelling region is not unexpected; it fits Birkeland's (1988) observation that shallow tropical communities shift from coral to algal dominated with increasing productivity. Although high nutrient input may explain the abundance of macroalgae in general, the pattern of algal abundance within the lagoon does not correlate with nutrient gradients. Nutrients decrease inshore (west to east) across the lagoon (Kimmerer and Walsh, 1981), while algal abundance drops at the western reef (Fig. 2). However fish are more abundant on the western reefs than on lagoonal patch reefs, and could be limiting macroalgal populations there by grazing. The lower abundance of fish in the central lagoon is at least in part the result of overfishing in these more accessible areas (Beets, 2001). Thus the overall pattern of macroalgal abundance fits Littler and Littler's (1984) model that reefs exposed to high nutrients and low rates of herbivory are dominated by macroalgae, while those with high nutrients and high rates of herbivory are not.

The dominance of encrusting *Montipora* species on central lagoonal patch reefs (Fig. 4) could be a consequence of the interference of macroalgae with coral recruitment. All reefs where *Montipora* constitutes >40% of the live coral cover have >15% cover of macroalgae. Most of the *Montipora* were encrusting, with irregularly shaped colonies that appear to propagate clonally, by lateral spreading and subsequent mortality separating daughter colonies. The great success of encrusting *Montipora* relative to other corals may be the result of their prolific recruitment via large clonal fragment rather than sexually produced minute propagules.

Asexual fragmentation is likely also an important, potentially a predominant mode of recruitment for the arborescent *Acropora* species that form large mono- or pauci-specific stands in the central lagoon. *Acropora* and *Montipora* together constitute 83% of the coral cover of the central lagoon (Fig. 4). *Montipora* and *Acropora* are also abundant in mid to inner lagoonal reefs at Canton (Jokiel and Maragos, 1978) and Fanning (Roy and

Smith, 1971; Maragos, 1974), other atolls in the equatorial upwelling region that have restricted circulation.

The great planktonic productivity is likely responsible for intense bioerosion in the lagoon. Although rates of bioerosion were not quantified, there is a striking trend in the abundance of bioeroders increasing west to east across the lagoon. This corresponds to the increase in the abundance of phytoplankton from west to east, itself probably a result of the greater residence time of inner lagoonal waters allowing for the accumulation of phytoplankton biomass (Kimmerer and Walsh, 1981; Kimmerer, 1995). Inner lagoonal reefs and corals are riddled with boring mussels (*Lithophaga*, *Botula*), other bivalves, sponges, sipunculans, etc.

**DISTURBANCE.**—Although most reefs in the lagoon appeared healthy, two areas showed evidence of coral mortality: the western barrier reef and nearby patch reefs, and the southeastern lagoon. *Acropora* was uncommon on much of the submerged barrier reef, as well as on several adjacent lagoonal patch reefs (Fig. 4). At several of these sites where living *Acropora* were rare, large, intact, dead *Acropora* colonies were moderately common. There appears to have been recent, selective mortality of *Acropora*, possibly as a result of *Acanthaster* predation or of bleaching, processes that preferentially impact *Acropora* (Birkeland and Lucas, 1990; Fisk and Done, 1985; Paulay and Benayahu, 1999). A major mortality of reef corals was apparent in the southeastern lagoon, where although skeletal remains of 12 coral genera were encountered, only three (one represented by a single colony) were found alive. The main surviving corals, *P. damicornis* and *Porites* species, are renown for their hardiness. This loss of diversity appears to have been accompanied by a major fall in coral abundance and a shift in dominance. The shoals in the southeastern lagoon are largely sand-covered today, but are underlain by heavily-bioeroded reef framework or dense jumbles of *Acropora* sticks just a few centimeters below the surface. Judging from the abundance of skeletal remains, *Acropora* was the dominant coral in the past.

The observed coral mortality could be the result of deteriorating conditions resulting from the general enclosure of the inner lagoon. Isolation of the southeastern lagoon started when reefs reached sea level along the southeastern rim of Tarawa ca 5000–6000 yrs ago (Marshall and Jacobson 1985). It continued with subsequent island build-up, and may have been accelerated this century by the closure of shallow passages by causeway construction, although as shown by Chen et al. (1995), the effect of causeways on lagoonal circulation was minor. Nevertheless the closure of passages by natural agencies (e.g., Jokiel and Maragos, 1978) or by causeways (e.g., Dawson, 1959) have been linked to coral mortality on nearby Canton and Palmyra atolls.

The range of dates (330–1665 AD) obtained from extirpated corals indicate that the observed mortality was not a consequence of the mid-Holocene isolation of the lagoon. The dates also do not support a recent demise, as might be expected from the 17-fold increase in the human population in South Tarawa since World War II, and associated environmental impacts such as coastal pollution, overfishing, and causeway construction. Although with a limited sample of eight dates we cannot rule out that reef demise occurred this century, the clustering of the younger half of the dates around the fifteenth century suggests that it occurred several hundred years ago. The four youngest dates are almost statistically indistinguishable ( $2\sigma$  ranges of 1275–1440 to 1445–1665 AD). As the samples are from a time-averaged death assemblage, the youngest dates are most indicative of the date for the demise of these reefs. We chose only exposed, well-preserved

corals for dating to increase our chance of getting samples from the latest survivors. The cause of this mortality thus remains unknown.

Although this coral mortality occurred no more than a few hundred years ago, the area is now dominated by shoals rather than patch reefs. Since that time the relatively diverse reefs of the southeastern lagoon were literally reduced to dust, by the intense bioerosion that prevails in the inner lagoon. The reef framework and coral rubble shallowly underlying these shoals attest to the destruction of these reefs and their conversion to soft bottom-dominated shoals. The buried reef framework and coral skeletons are completely riddled with borings, especially of *Botula* and *Lithophaga*.

The loss of coral likely had repercussions on reef-associated species in general. Several reef-associated bivalves, such as *Tridacna maxima*, *Hippopus hippopus*, *Chama lazarus*, *Chama pacifica*, and an unidentified oyster, all common as dead shells, also appear to have been extirpated in the area. The demise of some of the larger species may have been the result of human harvest or of the same cause that killed the corals. Several of the smaller species (*Chama pacifica*, ostreid sp.) lived cemented to the lower, dead portions of *Acropora* branches and may have disappeared with their 'host'. Finally the paucity of fish on these shoals is striking. The few reef fish (lutjanid, lethrinid juveniles, etc.) seen were invariably associated with, and literally clinging to, the remaining live *Porites* heads. Thus reef death likely impacted fish populations considerably, as has been demonstrated elsewhere (Sano et al., 1987).

Other changes on Tarawa are more closely linked to the expanding impact of humans this century. Sea grass beds along the inner margin of lagoonal sandflats have more than doubled in width since World War II, possibly as a result of nutrient loading from sewage (Paulay, 1997). The expansion of sea grass beds, as well as this nutrient input, may have favored an increase in the populations of several bivalves. Older people have noted an increase in *Anadara* clams over the past 50 yrs in South Tarawa (R. E. Johannes, pers. comm., 1993). In contrast overfishing has decimated lagoonal fish populations, especially near southern Tarawa (Beets, 2001), an effect exacerbated by the gradual loss of reef habitats noted above. The result of these changes has been a gradual shift from fin-fish to shellfish consumption in south Tarawa in recent decades.

**BIOTIC EFFECTS ON GEOMORPHOLOGY.**—Atolls are biogenic structures constructed from the skeletal remains of their biota. Physical forces have a great impact on atoll form, often directly, as by erosion during low sea stands (e.g., Paulay and McEdward, 1990) or islet construction and destruction by catastrophic storms (e.g., Maragos et al., 1973). They also have a major influence on atoll form indirectly, through the biota. Tarawa provides an interesting example of how the interplay between physical and biotic factors can affect atoll geomorphology.

Tarawa and neighboring atolls in Tungaru are characterized by wide rims, including especially wide lagoonal sand flats, and by shallow, sediment-choked, turbid lagoons with numerous large shoals and patch reefs. They contrast strikingly with atolls in the Marshall Islands, their neighbors to the north, which have narrow rims, and deep, clear lagoons with small patch reefs. Schofield (1977) noted that the rims of Tungaru atolls are about twice as wide as those of atolls in neighboring archipelagoes.

The wide, sand-dominated atoll rim and shallow, sediment-choked lagoon of Tarawa reflect high rates of sediment production, which in turn is likely the result of the high productivity of the region. The biomass of both suspension and deposit feeding macrofauna is much higher on Tarawa than on most central Pacific atolls. Irregular echinoids occur at

densities of  $>100 \text{ m}^{-2}$  on the inner lagoon floor, while macromollusks occur at densities of  $>100 \text{ m}^{-2}$  on lagoonal sand flats. Tarawa supports a much larger scale mollusk fishery than exists anywhere else in the central Pacific (Paulay, 1997, 2001). The skeletal remains of this biota, together with the rapid destruction of coral skeletons by intense bioerosion provide a large source of mobile sediments for the atoll.

The abundance of soft sediments, especially the great development of lagoonal sand flats, may have been crucial for islet development on Tarawa. Atolls islets are commonly built by catastrophic storms piling coarse sediment onto the atoll reef, especially from the reef front (Maragos et al., 1973; Richmond, 1994). Tarawa lies near the equator, where typhoons are absent or very rare; thus this mode of islet building is unlikely. Schofield (1977) found that unlike on many atolls, where islets are derived largely from oceanic sources of sediment, the islets of Tarawa are derived from lagoonal sands.

We noted how the uneven development of the atoll rim is responsible for striking patterns of zonation across the lagoon, but what gave rise to this asymmetry? It is not surprising that the windward, eastern rim of the atoll reached sea level first (cf. Hopley, 1982), but the lag of the western reef, given that eastern reefs reached sea level 5000–6000 yrs ago (Marshall and Jacobson, 1985), is striking. Coral cover decreases from north to south along the western barrier reef, and this correlates with the increasing depth, i.e., greater submergence, of the barrier reef from north to south. As noted above these patterns suggest that inimical lagoonal backwaters, likely exacerbated here by the high productivity of the region, may have in part limited the development of the western reef.

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