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BENTHIC ECOLOGY AND BIOTA OF TARAWA ATOLL LAGOON: INFLUENCE OF EQUATORIAL UPWELLING, CIRCULATION, AND HUMAN HARVEST

BY

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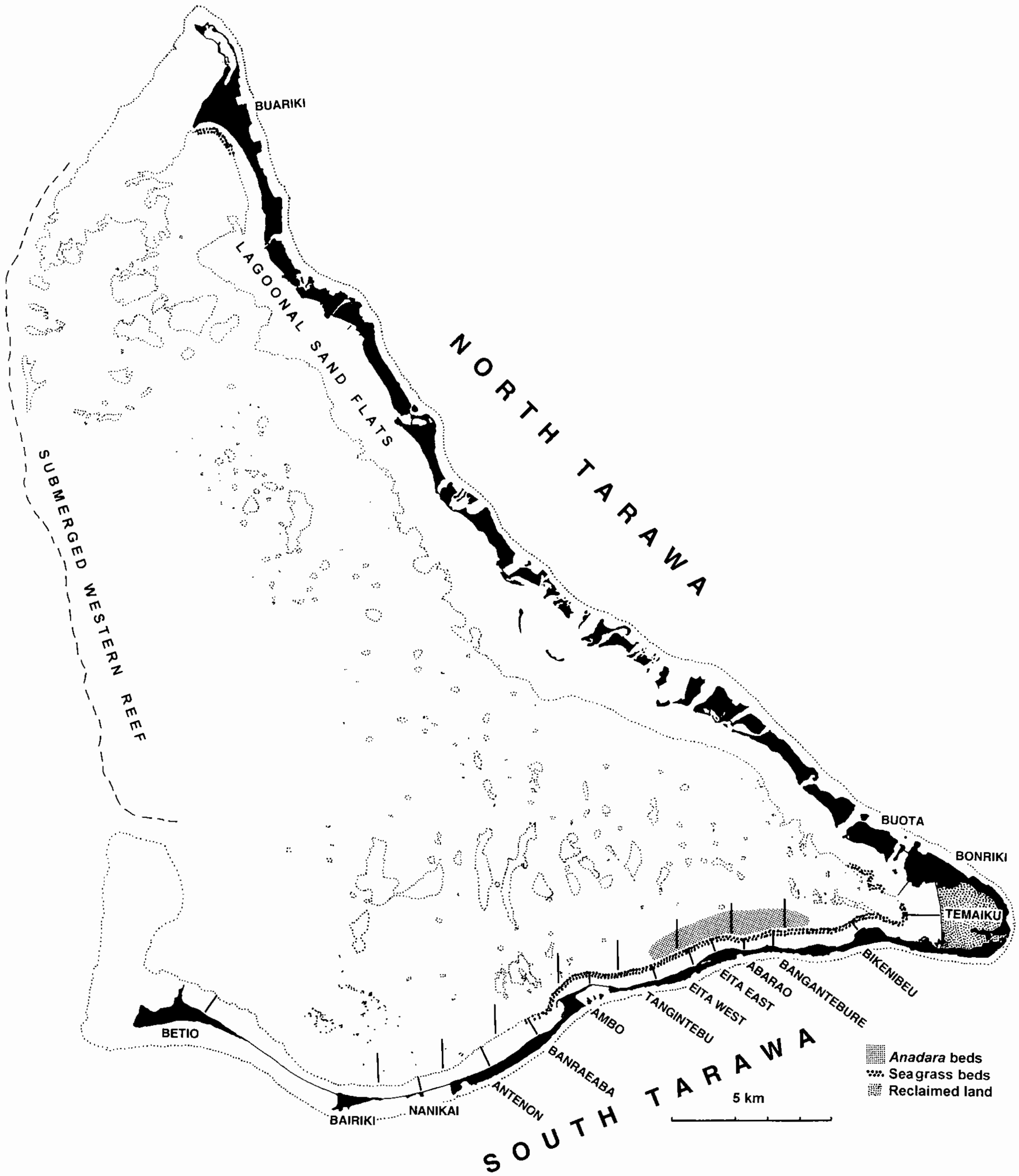

Figure 1. Map of Tarawa Atoll, with main habitat types, offshore Anadara bed, and locations of sand-flat and lagoon-slope transects (short lines) indicated. The 12 sand-flat transects are referred to by the adjacent islet name; lagoon-slope transects are numbered 1-9 west to east (see Appendix I for coordinates of all). Thin lines connecting islets represent causeways. Not all patch reefs and shoals have been charted. True North toward top of page.

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ABSTRACT

The lagoon of Tarawa harbors the richest benthos documented for any Pacific atoll. The biota is strongly influenced by its setting in the equatorial upwelling zone and the unusual geomorphology of the atoll, with a submerged western rim, but largely closed and islet-strewn eastern and southern sides. As the metropolitan center of the Republic of Kiribati, Tarawa also has the largest human population of any Pacific atoll. These three attributes impose a strong influence on all aspects of the lagoon. The high regional productivity supports unusually high population densities of heterotrophic mollusks and irregular echinoids for an "open" atoll. The dense human population on the atoll relies largely on marine resources for its protein needs. The lagoonal sand flat harbors dense and diverse mollusk communities, particularly in seagrass beds. These communities support an intensive subsistence fishery with an annual harvest of ca. 1,000 tons in South Tarawa. Much of the available biomass of the two preferred species, the blood cockle *Anadara uropigimelana* (*te bun*) and the small conch *Strombus luhuanus* (*te nouo*), is taken. Both the seagrass and shellfish beds appear to have expanded considerably in the past 50 years, likely as a result of nutrient enrichment from the rapidly growing human population. Dense mollusk communities along the southeastern lagoon slope at 2-8 m depth support an intensive commercial fishery that harvests approximately 1,000 tons of *Anadara* per year, again representing much of the available production. Three species of irregular echinoids are conspicuously abundant on the floor of the eastern lagoon, with combined densities >100 m^{-2} in the muddy facies of the inner lagoon. All aspects of the benthos follow a marked west-to-east and north-to-south zonation, reflecting the one-sided exchange of oceanic waters along the western atoll rim. While mollusk and echinoid biomass increases southeastward, coral diversity and cover decreases in that direction.

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INTRODUCTION

Among the many islands that dot the central Pacific, atolls are the most prevalent because the subsidence of the Pacific plate leads to the geologically rapid submergence of high islands, usually with their conversion into atolls. Although roughly similar in origin and structure, atolls nevertheless vary considerably in geomorphology, habitats, and biota. Atoll lagoons show the greatest variation and often differ substantially even from neighboring atolls, while outer reef habitats and biotas tend to be much more similar (e.g., Salvat, 1967; Chevalier, 1976, 1979). Much of this variation is the result of diversity in atoll geomorphology, and attendant diversity of oceanographic and ecological conditions. The nature of the atoll rim (depth, portion covered by islets, number and location of deep passages traversing it) is perhaps the most important variable as it determines the nature of water exchange between the lagoon and surrounding ocean. The degree of water exchange in turn affects many environmental parameters such as water quality, nutrient cycling, productivity, the nature of bottom sediments, sediment production rates, rates of reef growth and erosion, etc. In addition to differences arising from atoll geomorphology, atoll biotas are affected by a variety of other factors. Variation in productivity, both in the surrounding ocean and lagoon waters, can lead to substantial differences among reefs (e.g. Highsmith, 1980). The impact of humans, rapidly accelerated by growing populations, improved technologies, and the resulting increased utilization of limited resources, also exerts strong influences on reef communities in many areas of the tropics (Wilkinson, 2000).

The purpose of this paper is to describe aspects of the benthic ecology and biota of Tarawa Atoll (Tungaru [former Gilbert] Islands, Republic of Kiribati) and to consider how the unusual setting of the atoll has affected the benthos. This study was part of multi-disciplinary efforts to develop a management plan for the Tarawa lagoon. The benthic surveys carried out were aimed at evaluating the benthic invertebrate resources of the lagoon, their production, and harvest levels. Thus the focus of this paper is on habitats that have important benthic resources and on species that are fished.

Three aspects of Tarawa's environment appear to have especially noticeable consequences on the benthos: 1) The atoll lies in the nutrient-rich waters of the equatorial upwelling area, in an area of high planktonic productivity and biomass (Kimmerer and Walsh, 1981; Kimmerer, 1995). This enrichment has widespread consequences on the atoll, enhancing benthic productivity and biomass, and even affecting the geomorphology of the atoll (see below; Paulay, 1997). 2) Water exchange between the lagoon and surrounding ocean is extensive but largely confined to the submerged west side of the atoll (Fig. 1) (Chen et al., 1995). The directionality of this limited exchange has created marked west-to-east and north-to-south gradients in nutrients, phytoplankton, sediment composition, coral diversity and abundance, bioerosion, etc. across the atoll lagoon (Kimmerer and Walsh, 1981; Kimmerer, 1995; Paulay and Kerr, 2001). 3) As the metropolitan center of Kiribati, Tarawa has one of the densest populations among Pacific atolls. This has lead to varied impacts including heavy fishing pressure on marine organisms, sewage-derived microbial pollution, and localized nutrient enrichments along the nearshore sand flat (Kelly, 1993).

Previous work on the benthic marine biota of Tarawa and neighboring atolls is limited. Zann and Bolton (1985) described the ecology of *Heliopora* and quantitatively described the reefs around Betio on Tarawa. Zann (1982) described the marine ecology of the Betio area and provided a checklist of reef corals there prior to the construction of the large Betio-Bairiki causeway. Bolton (1982a) described the epifauna and infauna of the intertidal lagoonal sand flat fronting the islets of South Tarawa. Numerous other shorter technical reports describe aspects of economically important shellfish (including giant clams and pearl oysters), bêche-de-mer, and fishes on Tarawa (see Gillett et al., 1991).

Randall (1955) reviewed the fishes of the Tungaru Archipelago, and Banner and Randall (1952) described the marine biology of Onotoa Atoll, south of Tarawa. Lobel (1978) (as well as Banner and Randall) reviewed the indigenous names of marine organisms in Kiribati. Among the island groups surrounding Tungaru, the marine biota of the Marshall Islands to the north have been extensively studied (e.g., Devaney et al., 1987), while the marine biota of Nauru to the west and Tuvalu to the south are poorly known. Canton Atoll (Phoenix Islands) and Fanning Atoll (Line Islands) (both now part of the Republic of Kiribati) to the east have been the subjects of multidisciplinary studies by teams from the University of Hawaii, summarized in issues of Atoll Research Bulletin (1978 [No. 221]) and Pacific Science (1971 [25:2] and 1974 [28:3]), respectively. These atolls have special relevance to Tarawa because they also lie in waters influenced by equatorial upwelling.

Tarawa is a triangular atoll, with a wide reef rim on the eastern (called North Tarawa locally and hereafter) and southern (called South Tarawa locally and hereafter) sides bearing a near-continuous chain of islets, and a largely submerged barrier reef forming the west side (Fig. 1). The submerged barrier reef lies at a depth of several meters, shallowing northward, and is traversed by a deep channel near its southern end. The benthic habitats of Tarawa Lagoon can be divided into four major categories: 1) the intertidal to shallow subtidal sand flat that fronts the lagoonal sides of islets and passages along the southern and eastern sides of the atoll; 2) the lagoon slope and floor that cover much of the lagoon interior; 3) the patch reefs and shoals that rise from the lagoon bottom; and 4) the submerged barrier reef that forms the western atoll rim (Fig. 1). An extensive, largely intertidal, outer reef flat is also developed along the ocean side of the islets lining the southern and eastern rim. These outer reef habitats were not surveyed and are not considered further here. Here I deal mostly with the soft-bottom habitats of Tarawa lagoon; reef habitats, including fringing reefs, patch reefs and shoals, and the western barrier reef, are discussed in Paulay and Kerr (2001). The major habitat types of the lagoon are first reviewed below, followed by an analysis of the impact of human gathering pressures on invertebrate populations.

METHODS

Sand Flat

The sand flat was studied through quantitative surveys, qualitative examination of the fauna, and mapping of seagrass beds from aerial photographs. Because the primary purpose of our surveys was to evaluate the shellfish resources of this habitat in South Tarawa, quantitative surveys focused on mollusks.

Fifteen transects with nine stations each were set perpendicular to shore at regular intervals along the length of South Tarawa (Fig. 1; Appendix I). Nine stations were selected on each transect as follows. Stations 1-3 were on the beach slope. Station 1 was halfway between the upper strand line and the lower end of the slope (where it abruptly meets the plain of the sand flat), Station 3 was at the lower end of the slope, and Station 2 was halfway between Stations 1 and 3. Stations 4-6 were spaced equidistantly along the sand flat between Station 3 and the landward end of the seagrass bed, if present. Stations 7-9 were in the seagrass bed, if present. Station 7 was set 5 m lagoonward from the landward margin of the seagrass bed, Station 8 was in the middle of the bed, and Station 9 was 5 m shoreward from the lagoonward margin of the seagrass bed. At locations lacking seagrass beds, Stations 4-9 were evenly spaced along the sand flat, from one-sixth lagoonward of Station 3 to the edge of the sand flat. The field work for the sand-flat survey was carried out mostly by Andy Teem and Nabuaka Tekinano of the USAID project.

Two 0.25 m^{-2} quadrats were placed haphazardly within 5 m of each other at each station. The sediment at each quadrat was excavated to 20 cm deep or until bedrock was reached and the depth of the excavation noted. Sediment was passed through a 2 mm-mesh screen, and all live mollusks and echinoids collected. This process, carried out in the field, was not entirely effective because the abundant lag (large sediment grains retained by the screen) made noticing and picking all of the numerous smaller (<1 cm) mollusks difficult. Thus the data presented here represent minimum estimates only, and actual population densities of especially the smaller species were likely higher. All specimens were identified to species in the laboratory and their maximum length measured.

At many quadrats, including most of those at Stations 1-3, the technicians recorded no shellfish. These quadrats may represent areas devoid of shellfish (for example because of hard bottom), or samples may have been collected but subsequently lost. Most of the missing data are from samples at Stations 1-3 (where lag was excessive and the fauna is poor) and at three of the 15 transects (located at Teaoraereke, Dainippon causeway, and Temakin-Betio; these three transects are not mapped on Figure 1). These stations and transects are not considered further. Because most of the stations and transects that lack data are in areas (i.e., beach slope and western sand flat) characterized by gravelly sediments or hard substrata, the lack of data probably reflects a lack of shellfish, rather than lost collections. The few (5% of the total, $N = 144$) quadrats with missing data at Stations 4-9 in the other 12 transects are therefore assumed to not contain shellfish; an error in this assumption would increase shellfish abundance slightly.

In addition to surveying the infauna, the cover formed by an abundant zoanthid (probably *Zoanthus* sp.) was measured on seven transects (at Betio, Nanikai, Antenon, Ambo, Eita west, Eita east, and Abarao: Fig. 1) in the same quadrats. Zoanthid cover was measured by the line-intercept quadrat method, i.e. by counting what proportion of the 16 string intersection points, set in 0.25-m^2 stringed quadrats, had zoanthids lying under them.

The extent of seagrass beds was evaluated from site visits throughout North and South Tarawa and from aerial photographs (from 1943: housed at the Bishop Museum; from

1984: housed at the Survey Department, Tarawa) for South Tarawa. Most aerial photographs available for North Tarawa did not include the seagrass zone.

Lagoon Slope

The gently sloping lagoon bottom bordering the lagoon sand flat in South Tarawa supports a dense community of *Anadara* clams that forms the basis of a substantial, canoe-based, diving fishery (see below). The lagoon slope, defined as the area within 1 km of the lagoonward edge of the seagrass beds that form the sand flat margin, was surveyed to evaluate the geographic spread of these beds and to identify the macrobiota associated with them.

Two surveys were run to characterize the benthos of the South Tarawa lagoon slope. The first ran along the length of the southern rim, while the second focused on the major known *Anadara* beds. The first was carried out mostly by Andy Teem and Nabuaka Tekinano of the USAID project, and the second jointly by them and the author. In the first survey, nine transects, oriented north to south, were run on the lagoon slope at evenly spaced locations between Nanikai and Bikenibeu (Fig. 1; Appendix I). On each transect, paired 0.25 m^2 quadrats were haphazardly placed on the bottom at five stations located by Global Positioning System (GPS) at 0.05' (minutes of latitude, which represents 90 m), 0.15', 0.25', 0.35', and 0.55' north of the lagoonward end of the seagrass beds. Depth and GPS location were recorded for each station (see Appendix I). Within each quadrat, divers searched for large (>2 cm) mollusks and echinoids, visually and by hand, to a sediment depth of approximately 10 cm. This method is faster and just as effective as sieving for large mollusks and echinoids. Collected specimens were identified and measured in the laboratory.

The second survey focused on the *Anadara* bed offshore of Tangintebu-Bangantebure (Fig. 1). A series of rapid spot dives were conducted from east to west across this bed to establish its length followed by four north-south passes to establish its width. Finally, the population density of larger mollusks and echinoids was surveyed at 10 haphazardly selected stations within the bed, with four replicate 0.25 m^2 quadrats at each, using the method described above.

Lagoon Floor

The lagoon floor was surveyed at 14 stations set up to lie in three east-west lines across the atoll (Figure 9; Appendix I). At each station, two divers swam for five minutes and recorded or collected the conspicuous macrofauna. Two 0.25 m^2 quadrats were then haphazardly placed for quantitative enumeration of smaller macrofauna, and the larger epibenthic species (mostly irregular echinoids) in each collected. The bottom sediment within each quadrat was then excavated to a depth of ca.10 cm, taken on board in a large bag, and sieved through a 2 mm-mesh screen. This survey was carried out by Alex Kerr, Nabuaka Tekinano, Andy Teem and the author.

Mollusks and echinoids were the dominant fauna retained by the 2 mm-mesh screen, although small polychaetes were visibly abundant on the bottom. Species were identified, and shell and test lengths were measured for all mollusks and echinoids to the nearest mm.

Gatherer Surveys

Shellfish are an important part of the diet on Tarawa and the productive lagoon provides abundant stocks that are easily accessible even to people with no fishing equipment. Landing surveys were conducted to evaluate the type and intensity of gathering pressure on shellfish.

Surveys were implemented to count the number of people collecting shellfish and to measure the weight and species composition of their catches. Both types of surveys were implemented for gatherers on the South Tarawa sand flat and for divers on the offshore Tangintebu-Bangantebure *Anadara* bed. Qualitative observations and brief interviews with gatherers also were conducted whenever possible.

To measure the catch of people collecting on the sand flat, technical personnel of the USAID project intercepted gatherers at 13 locations along the shore of South Tarawa as they arrived from collecting trips to the sand flat. The number of gatherers who contributed to each catch, the time spent gathering, the habitat (nearshore-sand flat, mid-sand flat, seagrass bed, or deep lagoon) where they gathered, and the time of arrival were recorded based on information provided by the gatherers. Each catch was weighed as a whole, and the weight and number of individuals of each species were determined from either the whole catch or a subsample. The maximum shell length of a haphazard subsample of 20 (or the number available, whichever was greater) shells of each species in each catch was measured with calipers to the nearest mm. Because not all samples were processed with equal thoroughness, not all this information is available for every catch. Where the number of individuals of a single species was recorded within a catch, but the total weight of that species within the catch was not determined, the latter figure was estimated from the average weight per shell for the given species, as determined from other samples.

We counted the number of gatherers working the Tangintebu-Bangantebure *Anadara* bed from a boat on six occasions by skirting all vessels seen in the area and counting the number of divers associated with each. The harvest of divers working the Tangintebu-Bangantebure *Anadara* bed was largely determined by interviewing divers on-site. This method was more effective than a landing survey because, with only a few vessels working the area, their catches would have been difficult to intercept on shore. In addition, the standard-sized rice bags (holding 34 ± 1.5kg per bag; $N = 5$) that divers use to hold shellfish allow for a fairly accurate assessment of catch size.

To estimate the number of people gathering on the sand flat, I counted gatherers from the western tip of Betio to the tip of the Bonriki jetty from a series of vantage points that allowed observations throughout the entire sand flat. These counts were made around low tide by driving from one end of South Tarawa to the other, and were probably >90% accurate for that time. Six such counts were made.

Unless otherwise noted, data are given as mean ± 1 standard error (SE). Coordinates of quantitative stations and transects are given in Appendix I. Author and year of species discussed in text are given in Appendix II, together with a listing of invertebrates for which I was able to get I-Kiribati names.

RESULTS AND DISCUSSION

Sand Flat

Physiography and habitats

The extensive intertidal to shallow subtidal sand flat that borders the lagoon ranges from approximately 300 m to 2.5 km wide and harbors dense communities of infaunal invertebrates (Bolton, 1982a; below). The sand flat fronting the lagoonal sides of islets in South Tarawa differs from that in North Tarawa. The former averages about half the width of the latter (< 1 km vs. typically 1-2 km), has a more extensive marginal seagrass bed, and has poorer fringing-reef development off its lagoonal margin. The two areas must also have differences in the benthos; however, as our surveys were limited largely to South Tarawa, these remain to be documented.

The sand flat is dominated by poorly sorted coarse sands with abundant gravel comprised of shells and coral fragments (Weber and Woodhead, 1972; Richmond, 1990). The sand flat in South Tarawa can be demarcated into three zones: 1) a relatively steep beach slope; 2) a wide, gently sloping plain constituting the bulk of the sand flat; and 3) seagrass beds developed along the lagoonal margin of the sand flat in many, but not all, areas. Some nearshore areas of the sand flat (especially in the southeastern "elbow" of the atoll and along sections of North Tarawa) support stands of shrub-sized mangroves (*Rhizophora mucronata*) with dense fiddler-crab populations.

The gentle slope of the sand flat abruptly gives way to the steeper lagoonal slope at approximately 0.5-1 m below lowest low water, at the lagoonward edge of the seagrass bed, if present. Although no living corals were seen on the sand flat, the adjacent lagoonal slope supports scattered colonies or clumps of colonies of corals, mostly *Porites* spp. and *Pocillopora damicornis*, in South Tarawa. In North Tarawa this zone often has contiguous fringing and patch reefs that are generally more diverse and tend to be dominated by *Acropora*.

Seagrass Beds

Extensive beds of the seagrass *Thalassia hemprichii* are developed along the lagoonal margin of the sand flat in southeastern Tarawa Lagoon and are the focus of much of the shellfish harvesting effort there (see below). The abundance of bivalves in the seagrass beds is striking, and many of the best shellfish grounds are clearly in areas of seagrass abundance. Seagrasses are well known to host a greater abundance of benthos than surrounding soft bottoms because: they serve as refuges from predation; provide greater habitat complexity, increased food supplies, and more stable substrata; and create hydrodynamic conditions that are especially favorable for larval settlement (Peterson, 1986; Orth, 1992). Bivalve populations have been found to have greater growth rates within seagrass beds, probably because of increased food supplies (Peterson et al., 1984). Tebano (1990) showed that the density of *Anadara* clams in Kiribati is significantly correlated with seagrass density; several other shellfish species also appear to show a preference for seagrass habitats.

Seagrass beds extend in a largely unbroken band along the eastern half of South Tarawa (Banraeaba to Bikenibeu), are somewhat discontinuous along the atoll's southeastern "elbow" (Bikenibeu to Buota), and are widespread again at the north end of the lagoon (around Buariki) (Fig.1). These areas correspond to the locations of the longest islets on Tarawa. Seagrass beds are rare along the western half of South Tarawa (Betio to Antenon) and along most of North Tarawa. The only seagrass encountered along the central section of the latter was a single small (a few square meters) patch off Abatao Islet. Aerial photographs from 1943 indicate additional small patches of seagrass lagoonward of the passage between Tabangaroi and Tabonimata islets, but whether these patches survive today is unknown.

Aerial photographs from 1984 show that the average widths of South Tarawa seagrass beds were 100-150 m, reaching a maximum of 250 m. The geographic spread of seagrass beds does not appear to have changed much between 1943 and 1984 in South Tarawa; however, the width of these beds has more than doubled. In 1943, a narrow seagrass bed extended virtually continuously from Banraeaba to Bikenibeu as it does today; however, most of it was <100 m wide. The width of these beds was measured by evenly spaced transects for two stretches that were clearly discernible in photographs from both 1943 and 1984. In the Abarao-Eita stretch, the seagrass bed had increased significantly, from 46 ± 37 m (s.d.) wide in 1943 to 100 ± 52 m (s.d.) wide in 1984 ($N = 2 \times 11$, $P < 0.05$, t test). In the Eita-Taborio stretch, the seagrass bed increased from 43 ± 16 m (s.d.) to 136 ● 47 m (s.d.) wide in 1984 ($N = 2 \times 11$, $P < 0.0001$, t test).

Biota - Mollusks

The South Tarawa sand flat hosts a dense and diverse assemblage of mollusks. Twenty-six mollusk and five echinoderm species were noted in the quantitative surveys, and numerous additional species were noted outside these surveys. Bivalves dominated the fauna both in species richness (20 bivalves versus 6 gastropods) and numerically (93% of mollusk individuals encountered).

The mean population density of 10 species exceeded 1 m^{-2}, averaged over the sand flat (12 transects, Stations 4-9) (Fig. 2). The most abundant species encountered were three small (<2 cm) clams: *Codakia bella*, *Wallucina haddoni*, and *Timoclea marica.* Of these, *C. bella* and *T. marica* are harvested in small quantities. The three most important species for local consumption, *Gafrarium pectinatum* (*te koumara*), *Anadara uropigimelana* (*te bun*), and *Strombus luhuanus* (*te nouo*), were also among the 10 most abundant species.

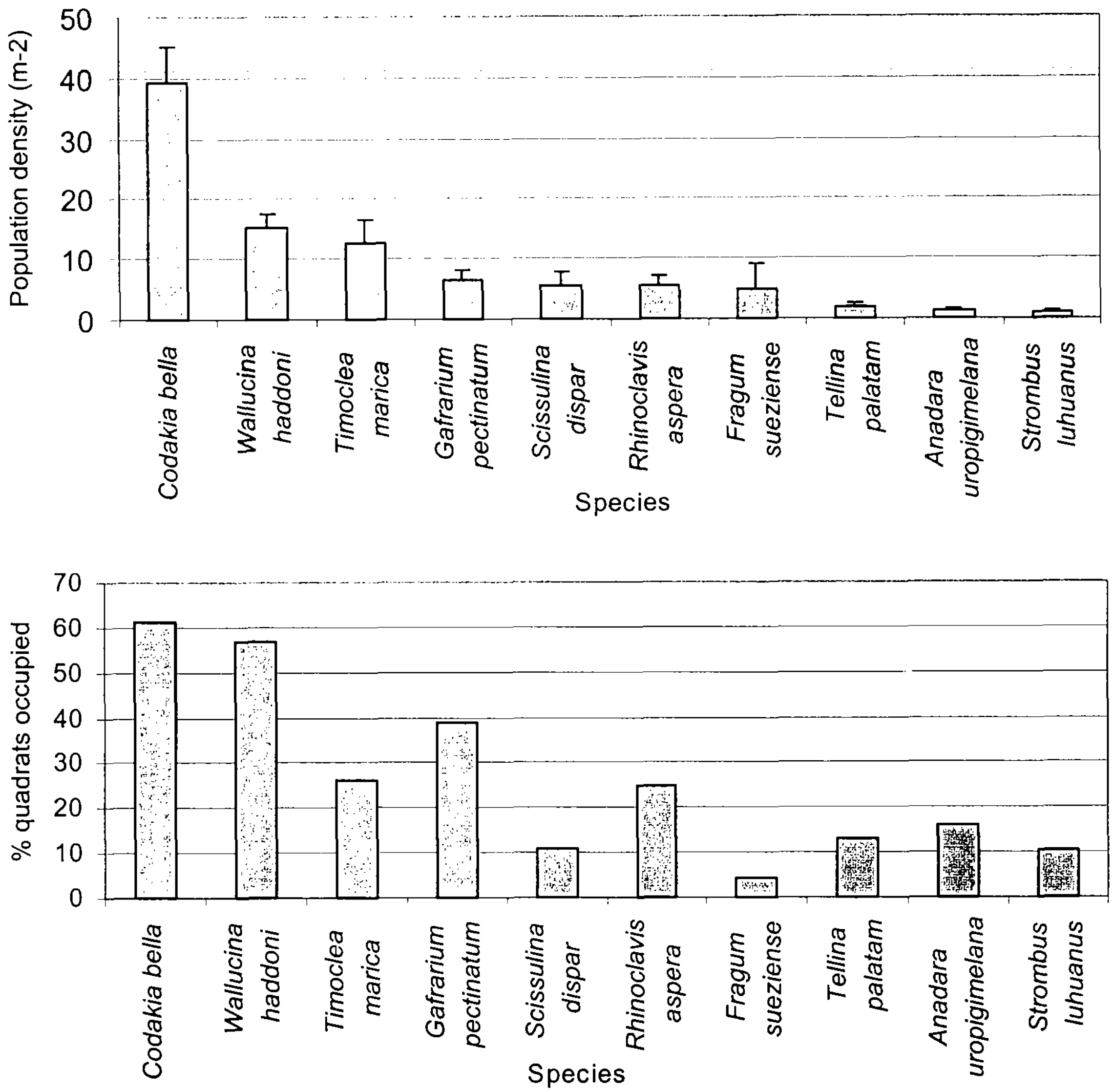

Figure 2. (Top) Mean (± SE) population density of the 10 most common mollusks on South Tarawa sand flat averaged over 12 transects and Stations 4-9 (N = 144 quadrats). Note that the abundance of smaller species here indicated is underestimated (see Methods). (Bottom) Percentage of quadrats in which the numerically most common species were found.

The densities of several species (e.g. the clams *Codakia bella, Gafrarium pectinatum,* and *Anadara uropigimelana*) increased lagoonward across the sand flat and were highest in the marginal seagrass beds. Other species (e.g. the clams *Wallucina haddoni* and *Timoclea marica*) showed less clear trends or were most common at mid-sand flat (Fig. 3). In contrast, a few species, most notably the clams *Atactodea striata* and *Asaphis violascens*, were restricted to the higher reaches of the sand flat and to the beach slope (pers. obs.). The overall abundance of mollusks showed some variation across the sand flat with a moderate increase lagoonward (Fig. 4).

The increased abundance of many mollusks lagoonward could be natural, or it could be the result of greater human harvesting pressures in the higher intertidal zone, which is exposed more frequently to gatherers, than in the lower zone. For abundant and little harvested species such as *C. bella* (Fig. 3), the former explanation is more likely, particularly because lucinid bivalves are known often to prefer seagrass habitats (Jackson 1970). In contrast, for economically important shellfish such as *Anadara*, human harvest is highly likely to contribute at least to zonation. Rough calculations (see below) indicate that a large portion of the standing crop of this and a few other species are taken by humans, supporting the above hypothesis.

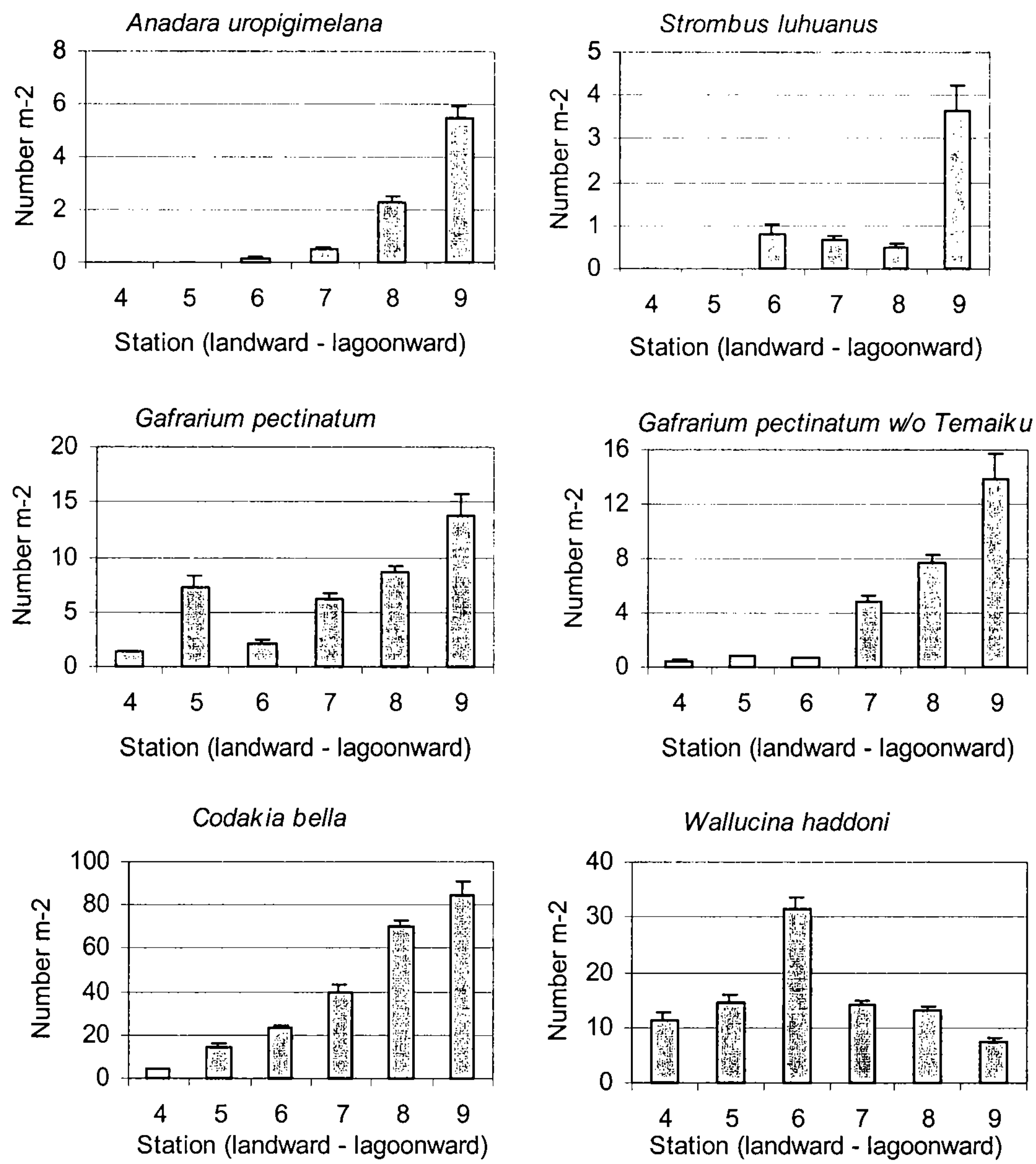

Figure 3. Mean (± SE) population density of selected species across the South Tarawa sand flat from nearshore to lagoon slope margin (Stations 4-9) averaged over 12 transects. *Gafrarium pectinatum* data is shown both in its entirety and without the data from the Temaiku transect (see text for discussion).

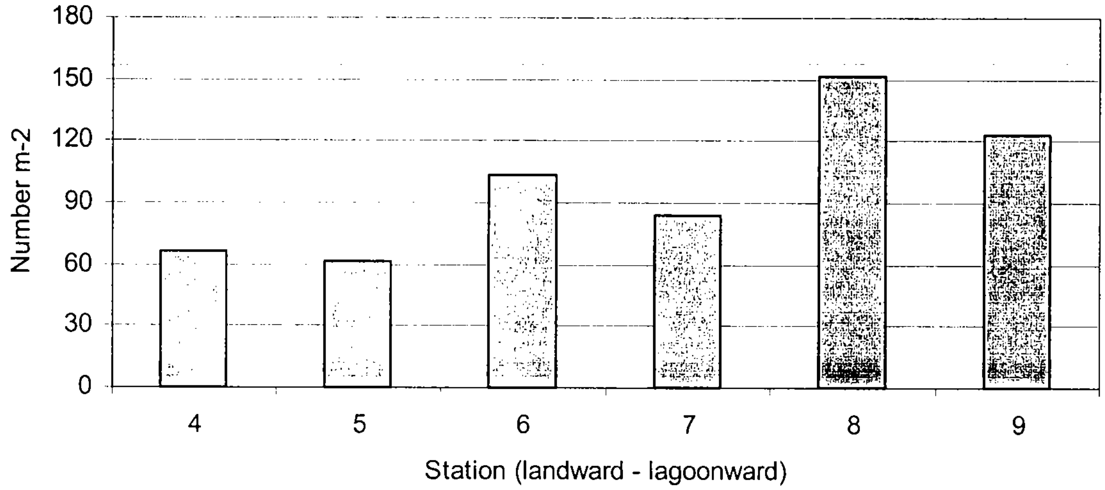

Figure 4. Mean population density of mollusks encountered across South Tarawa sand flat from nearshore to lagoon slope margin (Stations 4-9) averaged over 12 transects.

Economically Important Shellfish Species

Anadara uropigimelana (*te bun*). The shallow-burrowing, endobyssate arcid bivalve, *Anadara uropigimelana* (erroneously identified as *Anadara maculosa* in several past reports from Tarawa), is the most important shellfish resource in South Tarawa (see below; also Tebano and Paulay, 2001). The distribution of *Anadara* (Fig. 5) closely parallels that of seagrass beds (Fig. 1; see below) along South Tarawa. Both are best developed along the eastern half of the South Tarawa shoreline continuously between Banraeaba and Bikenibeu.

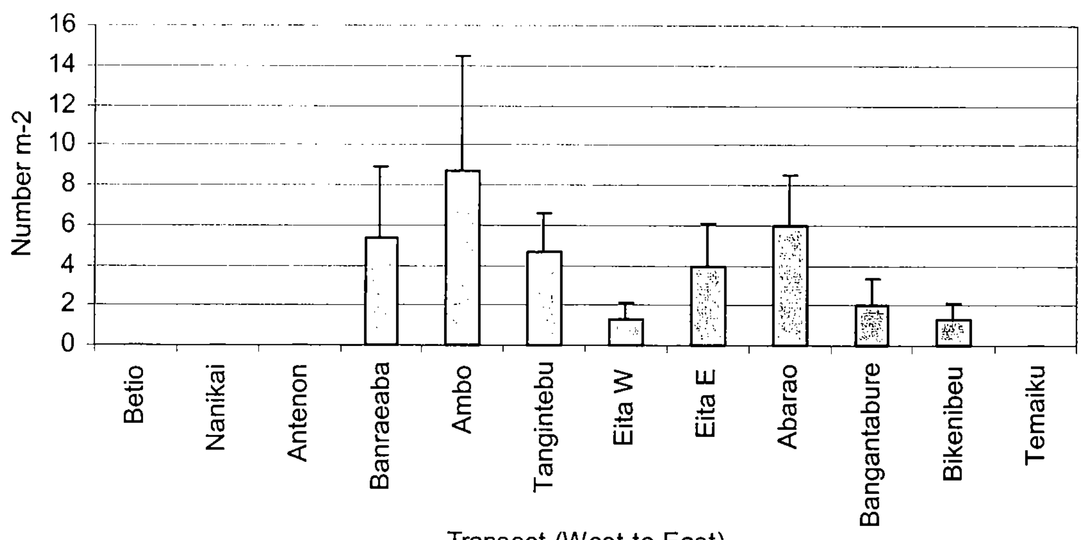

Figure 5. Mean (± SE) population density of *Anadara uropigimelana* among Stations 7-9 along the South Tarawa sand flat, per transect location.

Anadara was found almost exclusively at Stations 7-9, i.e. in the seagrass bed. Its density increased steadily lagoonward within the seagrass bed from 0.75 ± 0.40 m^{-2}

(Station 7; s.d.=1.6)) to 3.5 ± 1.3 m^{-2} (Station 8; s.d.=5.0) and 8.3 ± 2.3 m^{-2} (Station 9; s.d.=9.3). These density values are based only on transects between Banraeaba and Bikenibeu, i.e. in the area corresponding to the main habitat of *Anadara* along the South Tarawa shoreline in the Banraeaba-Bikenibeu seagrass bed. Therefore, these values are larger than those plotted across the entire sand flat in Figure 3. Overall, *Anadara* density averaged 4.2 ± 1.7 m^{-2} (s.d.=6.8) throughout the seagrass bed in this region. Yamaguchi et al. (no date) found comparable densities (means of 0.9-7 m^{-2} at four sites) in 1991. Assuming a seagrass bed approximately 10 km long and 150 m wide, this population density translates to an abundance of approximately 6.3 ± 2.6 x 10^6 shellfish. Because the population extends lagoonward onto the shallow lagoon slope, the total number accessible by wading is considerably larger, however (see Lagoon Slope section below).

Strombus luhuanus (*te nouo*). The epibenthic conch *Strombus luhuanus* was the second most important shellfish in South Tarawa and dominated catches in many areas of the coastline (see below). This conch was restricted largely to the lagoonward half of the sand flat (Stations 6 through 9; see Fig. 3). The distribution of *S. luhuanus* was highly variable among transects and stations surveyed, with an average density of 1.4 ± 0.6 m^{-2} (for Stations 6 through 9; s.d.=5.9). Taken at face value, this density corresponds to an abundance of approximately 7 ± 3 x 10^6 animals along the 20 km long sand flat of South Tarawa, given an approximate habitat width of 250 m. The observed population densities are considerably below those (means of 4.0-30.5 m^{-2} at four sites) encountered by Yamaguchi et al. (no date) in 1991, and also appear low given the tremendous gathering pressure that this species experiences (see below). The high variability in the data, as well as qualitative observations, indicate that the distribution of *S. luhuanus* is patchy on the sand flat, perhaps as a result of the conch's mobility (see below). The presented estimates are based on only 34 specimens encountered in quadrats, and may considerably underestimate the actual abundance of this species.

Gafrarium pectinatum (*te koumara*). Although numerically more abundant than the other two species, the venerid clam *Gafrarium pectinatum* is harvested less frequently, probably because of its burrowing habit and smaller size. Nevertheless, *G. pectinatum* is an important local bycatch and can dominate catches in some areas. The distribution of *G. pectinatum* varied greatly among transects with the Temaiku and Banraeaba transects traversing particularly dense beds (Fig. 6). The Temaiku *Gafrarium* bed, extending across the wide sand flat of the "elbow" of the atoll, is well known and the focus of much gathering activity. *Gafrarium pectinatum* was found at all stations lagoonward of the beach slope and its overall abundance increased offshore (Fig. 3). This species was strikingly more abundant in the seagrass zone than further inshore, except at the unusual Temaiku sand flat (Fig. 3). The mean abundance of *G. pectinatum* across the sand flat (Stations 4-9) was 6.6 ± 1.6 m^{-2} (s.d. = 18.9). Yamaguchi et al. (no date) found comparable densities (means of 0-19.1 m^{-2} at four sites) in 1991. Given the 20 km long and approximately 500 m wide South Tarawa sand flat, the projected abundance of this species is approximately 6.6 ± 1.6 x 10^7 animals.

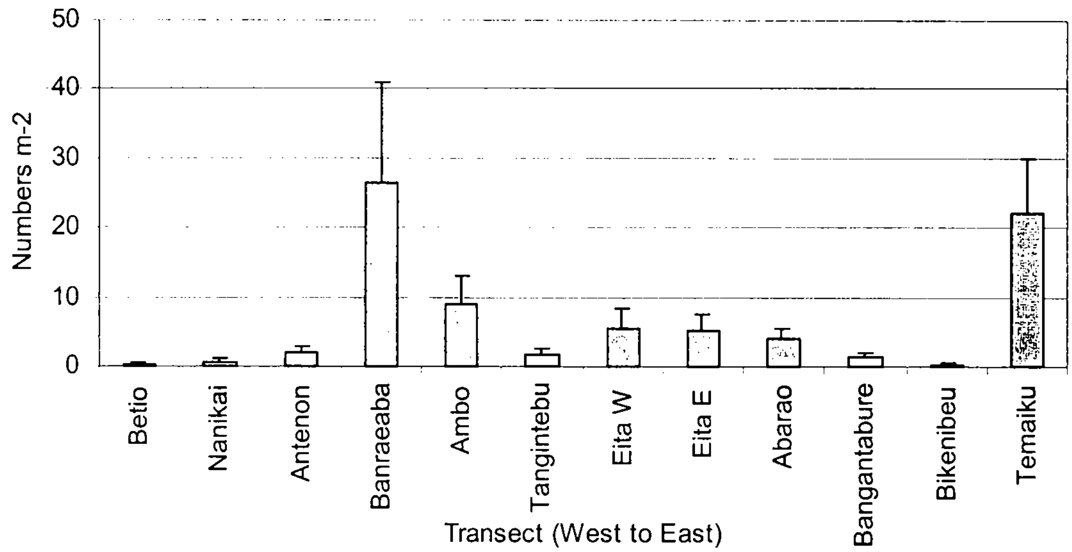

Figure 6. Mean population density (among Stations 4-9) of *Gafrarium pectinatum* along South Tarawa sand flat, per transect location.

Asaphis violascens (te koikoi). This species is restricted to the mid-high intertidal beach slope, an area that was not effectively sampled by our surveys. On Tarawa, *Asaphis* is common in a narrow zone on beaches on the lagoon side and in similar habitats on the ocean sides of islets. It is the dominant, and often the only, bivalve in this habitat. On many islands, *Asaphis* are harvested as single clams, with people searching for the siphonal openings and then extracting the shellfish (pers. obs.). On Tarawa, however, gatherers dig up large areas of suitable habitat, usually with spoons, to uncover all the clams in the area. This difference in method implies that these clams are more abundant on Tarawa (as are many other shellfish) than on many other central Pacific islands, thus making wholesale digging productive. Although we did not observe the abundance of *Asaphis*, the species appears to occur in densities of tens-per-square meter in its habitat, based on observing people digging for it.

Atactodea striata (te katura). This small surf clam is abundant on high intertidal lagoon beaches around Tarawa and is the focus of a minor fishery, mostly as a favored baby food or as a side catch with *Asaphis*. *Atactodea striata* has separate sexes and an extended breeding period in New Caledonia (Baron 1992).

Biota - Other Organisms

In addition to supporting a rich molluscan community, the sand flat harbors a diversity of other invertebrates; however, these species were not studied quantitatively. Bolton (1982a) provides abundance data on a variety of other groups, especially polychaetes and crustaceans; however, many of her identifications appear to be erroneous. A few conspicuous organisms and some species that dominate other habitats on the atoll are discussed here.

Holothurians and irregular echinoids were the only echinoderms encountered on the sand flat during the surveys. Only a single specimen each of three larger irregular echinoids, *Maretia planulata*, *Laganum depressum,* and *Metalia sternalis*, were encountered in the quantitative surveys. These species may be more common locally near the lagoonward end of the sand flat and they dominate deeper lagoon waters (see below). Three holothurian species, *Holothuria atra*, *Bohadschia vitiensis*, and *Holothuria pardalis*, were encountered on the sand flat. *Holothuria atra* was fairly common, with a population density of 0.83 ± 0.34 (s.d. = 2.92) across stations 7-9 (to where it was limited to) on the sand flat. *Bohadschia vitiensis* is common at the lagoonward margin of the sand flat at low intertidal to shallow subtidal depths where it partially burrows in the sand bottom. Bolton (1982a) recorded eight species of holothurians from the sand flat, four at densities of up to several hundred per square meter; reconciling her data with the present findings is difficult.

An unidentified zoanthid (probably a *Zoanthus* species; cf. Muirhead & Ryland, 1993) covers large patches of the sand flat in some areas but is rare or absent in others. Zoanthids were encountered in four of the seven transects in which they were consistently sampled, and were limited to Stations 5-9 on these transects (mid-sand flat to lagoon-slope margin) (Fig. 7). Bolton (1982a) found them in two of her six transects, and again found them limited to the lagoonward two-thirds of the sand flat. Zoanthid cover was consistently high (25 ± 5.6 %; across stations 5-9) in the three transects situated in the Abarao-Eita area, but low (0.47 ± 0.47 %) in the four transects situated west of there. Zoanthids dominated Bolton's (1982a) Bairiki and Teaoraereke transects in this western area.

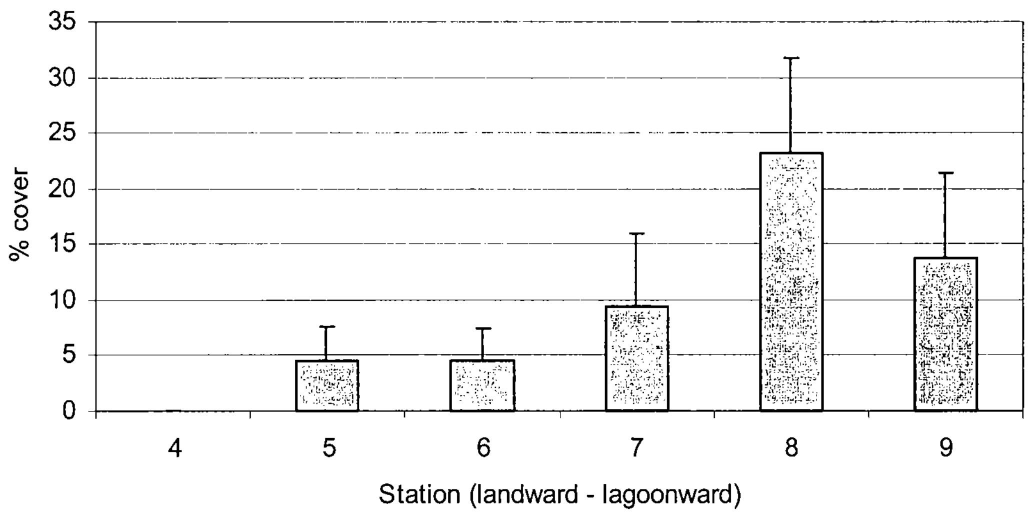

Figure 7. Mean percent cover (± SE; among seven transects with zoanthid data) of zoanthids across South Tarawa sand flat from nearshore to lagoonal slope margin (Stations 4-9)

Overall, zoanthids covered 11 ± 3% of the sand flat averaged across all transects where they were measured in South Tarawa (Stations 5-9). Cover was highest in the Abarao-Eita seagrass beds (Station 7-9 in 3 transects) where 36 ± 8% of the bottom was covered by zoanthids. At such a high abundance, zoanthids must have an important effect on the benthos, especially in combination with high seagrass cover. They may limit access to the sediment or water column, may affect recruitment by feeding on larvae of infaunal organisms, and stabilize the sediment. Nevertheless, abundant shellfish occur in such dense zoanthid beds.

Lysiosquilla maculata (*te varo*), the world's largest stomatopod (to 38.5cm; Manning, 1978), is common along the lagoonward margin of the sand flat, and is the focus of a specialized local fishery. The abundance of this species was not measured, but burrows are spaced a few meters apart on the outer sand flat around lowest low water. *Te varo* fishing is a skill practiced by few families (B. Yeeting, pers. comm.). I observed one fishing party harvesting this spectacular animal. Each fisher inserted a bait (a small pufferfish, used because its tough skin makes it reusable), tied by a length of coconut senit to half a coconut shell (serving as anchor), into a *te varo* burrow. The bait was then left for a couple of minutes after which the line was felt for the activity of the stomatopod. If the animal was feeding, it was slowly teased out of its burrow by pulling the bait back up, and swiftly grabbed at the burrow entrance. This teasing-out process apparently requires much skill and there was considerable variation in success among the fishers. The animal is grabbed with one hand when it is still mostly in its burrow, then grabbed at the abdomen with the other hand as it is slowly pulled out of the burrow. The notorious armature of the uropods is then bitten off, making the animal safer to handle. According to Being Yeeting (pers. comm., based on Yeeting's discussion with *te varo* fishers) these stomatopods live in pairs with the males doing all the prey capture; thus males are readily caught. After catching a male, the fisher marks the burrow and comes back in a couple of days to catch the by-then-famished female, using the same method.

Lagoon Slope

The lagoon slope, as here defined, begins at the outer edge of the seagrass bed at approximately 0.5 m depth at lowest low water. It slopes gently to a depth of about 8-10 m, about 1 km from the sand-flat margin in South Tarawa. *Anadara* beds on the lagoon bottom were encountered only on this marginal slope along the eastern section of South Tarawa (Fig. 1), within 1 km of the sand-flat margin, lying largely at depths of <8 m. The bottom of this area is composed of silty sand and usually has a pronounced crater and mound topography created by the infauna with 10-20 cm vertical relief.

The most abundant species encountered in both surveys of the lagoon slope were the heart urchins *Maretia planulata* and *Metalia sternalis,* the sand dollar *Laganum depressum*, and the mollusks *Anadara uropigimelana* and *Strombus luhuanus* (Table 1). Among smaller species, the gastropods *Turritella cingulifera* and *Strombus erythrinus* were abundant and the minute irregular echinoid *Fibularia* sp. common, although these species were not consistently sampled.

The distribution of these five species is patchy, with one or a few often dominating in patches of tens of meters or more across. The domination of the epibenthic *Laganum* and *Strombus* are especially conspicuous, although the infaunal species are also patchy. *Anadara* is largely confined to a few well-defined beds (see below).

Table 1. Population density (m^{-2}) of dominant macrofauna in quantitative surveys of lagoon slope in South Tarawa.

Survey	*Anadara*	*Strombus*	*Laganum*	*Maretia*	*Metalia*	All echinoids
Transect	4.8 ± 1.7	5.3 ± 1.9	11 ± 3.0	23 ± 4.3	8.5 ± 1.1	43 ± 6.0
Bed	15 ± 2.6	10 ± 3.2	19 ± 4.4	12 ± 1.9	7.2 ± 1.1	38 ± 5.1
Combined	7.8 ± 1.2	6.7 ±1.7	13.5 ± 2.5	20 ± 3.1	8.1 ± 0.9	42 ± 4.2

Transect = data from transect survey along length of South Tarawa lagoon slope (N = 90 quadrats)
Bed = data from survey of Tangintebu-Bangantebure *Anadara* bed (N = 40 quadrats)
Combined = combined data from the above two surveys.
Echinoids = combined data for three irregular echinoids. *Strombus* is *S. luhuanus* only.

Anadara uropigimelana

The survey along the length of the South Tarawa lagoon slope showed that offshore *Anadara* populations were localized to one large and a couple of small beds. *Anadara* was absent from most stations and some entire transects, but was abundant at a couple of sites, thus showing great overall variation in population density (4.8 ± 11.1 m^{-2} s.d.; N = 90 quadrats). No *Anadara* were found on two transects, and mean density was >2 m^{-2} on only four of the nine transects. The well-known Tangintebu-Bangantebure *Anadara* bed was traversed by two transects (#6 and #7), and these encountered *Anadara* at all stations except the one closest to land. In contrast the other five transects that encountered *Anadara* found the clams only at one of the four stations sampled, implying that the patches encountered were small. Two of these transects (#3 and #4) encountered *Anadara* at high (26-42 m^{-2}), and three (#5, #8 and #9) at low (2-10 m^{-2}) densities. Furthermore, in three of these transects (#3, #8, and #9), *Anadara* were encountered only at the nearshore station located only 90 m from the margin of the sand flat. These may represent extensions of the sand-flat beds rather than be independent slope *Anadara* beds. The results thus support the hypothesis that the only large *Anadara* bed on the lagoon slope is in the Tangintebu-Bangantebure area, although a few small beds exist elsewhere.

Spot surveys of the Tangintebu-Bangantebure *Anadara* bed showed that it extends for ca. 4.6 km (ca. 173°03.2'E to ca. 173°05.7'E) and is 640 ± 210 m wide (s.d.; N = 4 transects, range: 420-900 m wide), encompassing a total area of 2.9 ± 0.5 km^2. Within this area, spot checking revealed that *Anadara* was sufficiently abundant at 87% of the sites (N = 30) to be visually apparent within one to three free dives. It was also present at all 10 stations haphazardly selected for sampling within the bed and occurred in 90% of the 40 quadrats surveyed at these stations (Fig. 8). The few sites in the survey where no *Anadara* was seen appeared to be off the bed; adjacent landward or lagoonward sites always supported the shellfish. Thus, *Anadara* appears to form a single, largely contiguous bed in this region.

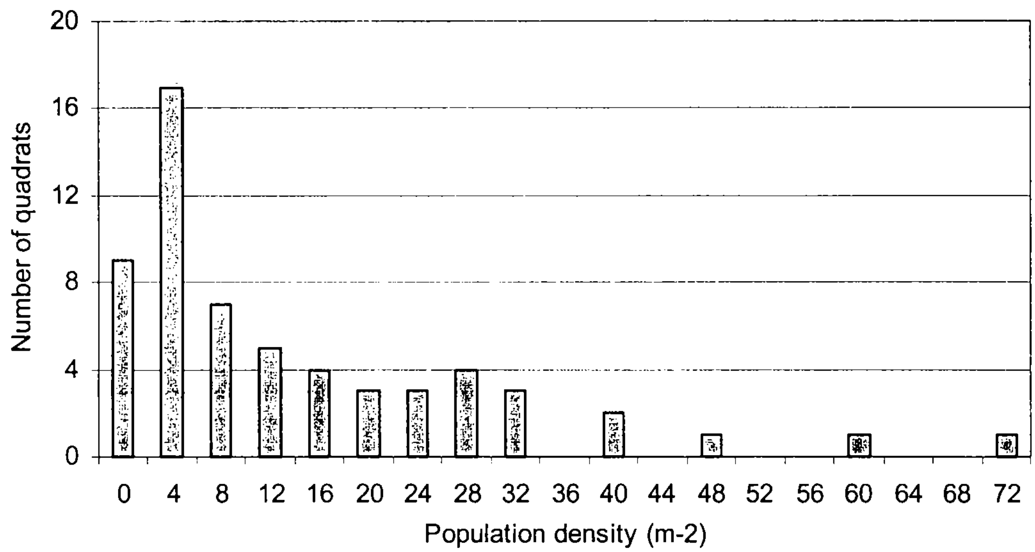

Figure 8. Frequency distribution of per-quadrat population density of *Anadara uropigimelana* within Tangintebu-Bangantebure bed in Tarawa Lagoon. Based on combined data from *Anadara* bed survey and transects six and seven (which traversed the bed) of the transect survey (n=60).

There is considerable variation in population density within this *Anadara* bed (Fig. 8). Part of this variation is likely due to human harvest. Free divers focus their attention on the densest beds and probably find that moving on, before an area is completely exhausted, is economically advantageous (see below).

The two surveys yielded similar estimates of population size for offshore *Anadara.* The transect survey along the 15 km long, 1 km-wide-lagoon slope yielded an estimated abundance of $7.2 \pm 2.6 \times 10^7$ clams. The survey of the Tangintebu-Bangantabure *Anadara* bed yielded an estimated abundance of 4.4 ● 1.6×10^7 animals in this bed. Note that both surveys focused only on large (>2cm) *Anadara.*

Strombus spp.

The patchy distribution of the two abundant *Strombus* species, *S. luhuanus* and *S. erythrinus*, is strikingly apparent on dives over the lagoon slope; a third species, *S. variabilis*, is less common. Mature and juvenile *S. luhuanus* and *S. erythrinus* tend to aggregate and segregate by species, and *S. luhuanus* also by maturity. Thus, in any given area, either *S. erythrinus* or mature or juvenile *S. luhuanus* dominate. *Strombus luhuanus* tends to be most common where exposed rubble is present, probably because it feeds on benthic macroalgae that attach to rubble. In contrast, *S. erythrinus* feeds on the red alga *Grateloupia* that lies on the sand in large (typically 10-50 cm), loose, or poorly attached, fluffy masses.

Strombus luhuanus had a mean density of ca. 7 m^{-2} (combined surveys, with comparable densities in both) (Table 1). Like *Anadara*, *S. luhuanus* is restricted to the marginal ca. 1 km-wide portion of the lagoon bottom. Along the 15 km-stretch survey the abundance of this conch was $8 \pm 1.7 \times 10^7$, while an estimated $2.9 \pm 1.0 \times 10^7$ occurred within the Tangintebu-Bangantabure *Anadara* bed. *Strombus erythrinus* and *S. variabilis* were counted regularly only in the *Anadara* bed surveys, where densities were 8.5 ± 2.2 m^{-2} and 1.1 ± 0.4 m^{-2}, respectively.

The occurrences of *Anadara* and *S. luhuanus* were significantly associated (P <0.0001, G test, combined data from both surveys) and although *S. luhuanus* occurred in only 28% of the quadrats, it co-occurred with *Anadara* in 89% of them. The mean density of irregular echinoids was somewhat, but not significantly, lower (32 versus 50 m^{-2}) in quadrats where *Anadara* occurred, compared with those where the clam was absent.

Two hypotheses could explain this association between a benthic algal grazer and a suspension feeder:

1) *Anadara* needs hard substrata (rubble or adult shells) for attachment when young, whereas *S. luhuanus* feeds on benthic algae, which also need hard substrata for attachment. Thus, the correlated abundance of these shellfish may be a function of the availability of exposed hard substrata. *Anadara* beds may themselves create such a habitat by littering the bottom with their abundant dead shells, which are suitable for algal attachment as well as for the attachment of young clams.

2) The abundance of both species may correlate negatively with that of irregular echinoids and thus they may congregate at the few sites where irregular echinoids are uncommon. Irregular echinoids bulldoze soft bottoms and can greatly influence small infaunal organisms (Highsmith, 1982). Even if such disturbance does not affect adults of these two mollusks, it may negatively influence recruitment. The relatively weak correlation between the density of irregular echinoids and mollusks, however, speaks against this hypothesis.

Other Species

Fishes were uncommon on the open sandy expanse of the lagoon slope, although stingrays were occasionally seen. However, small acanthurids, lutjanids, serranids, occasional balistids, and other reef fish hovered around the scattered bits of reef. Patch reefs on the lagoon slope were mostly <2 m across and were comprised largely of *Porites*. *Pocillopora damicornis* was the only other coral seen in the fringing patch reefs of the southeastern lagoon, although off Betio *Montipora* and *Acropora* were also common (Zann and Bolton, 1985). Areas around these small patch reefs were densely strewn with shells, especially of *Anadara*, apparently gathered by predators. Some of the shells had been crushed near their posterior end, indicating possible attack by triggerfishes; others were intact.

Lagoon Floor

The lagoon floor is a relatively flat plain, mostly 5-20 m deep (25 m max.; Bolton, 1982a), that stretches between the intertidal sand flat and the submerged western barrier reef and includes the lagoon slope just considered. Numerous patch reefs and shoals rise above the plain of the lagoon floor (Fig. 1). Although no significant invertebrate resources are taken from the lagoon floor, a limited survey was conducted to characterize its biota.

The lagoon floor exhibits marked west-to-east and north-to-south gradients in most variables, including the nature of benthic habitat, species composition, and abundance of mollusks and echinoids. Sediment grain size (Weber and Woodhead, 1972; Richmond, 1990) and coral cover and diversity decreased markedly from north to south and west to east. While only occasional *Porites* and *Pocillopora damicornis* colonies were noted on the southern transects, diverse coral communities were encountered on the much coarser, gravelly sand bottoms of the northwestern and west-central stations. This trend in northwesterly increasing coral diversity and abundance was also observed and quantitatively documented on the patch reefs and shoals (Paulay and Kerr, 2001).

Three species of medium-sized (ca. 5 cm max. test length) irregular echinoids (*Laganum depressum*, *Maretia planulata*, and *Metalia sternalis*) dominate large areas of the inner (i.e. southeastern) lagoon floor, while mollusks, except for a few small species (see below), are uncommon and constitute only a small fraction of the biomass in this area. The minute irregular echinoid *Fibularia* sp. also appears to be very abundant. The distribution of these three echinoids is closely related to the distribution of sedimentary facies (Fig. 9).

Maretia planulata is the most abundant, and also the most striking, species in the deeper inner lagoon. While this echinoid is infaunal on sandy bottoms, it becomes strictly epifaunal on muddy bottoms, apparently unwilling to burrow into such fine sediments. On muddy bottoms this species tends to occur in huge "herds", often with population densities well in excess of 100 m^{-2}, providing a striking sight as they move around on top of the mud with the aid of their elongated spines. This species was encountered at all seven stations (in 12 of 14 quadrats) in the southeastern lagoon, at a mean density of $55 \pm 18\ m^{-2}$ (Fig. 9). Within this area, the abundance of *M. planulata* was correlated with sedimentary facies. Densities were much higher at the four stations in the sandy mud facies ($88 \pm 27\ m^{-2}$) than at the three stations in the silty sand facies occupied by these echinoids ($10.7 \pm 3.2\ m^{-2}$) (Fig. 9). *Maretia* was absent from all seven stations in the northwestern lagoon.

Laganum depressum was also limited to the southeastern lagoon where it was encountered at the nine southeasternmost stations (Fig. 9) at a mean density of $3.6 \pm 1.7\ m^{-2}$. In contrast, it was absent from the five stations to the northwest. *Metalia sternalis* was the most widespread species; it was ubiquitous (encountered in 19 of 20 quadrats) through the mid- and eastern-lagoon at a mean density of $13.5 \pm 2.2\ m^{-2}$, but was absent at the four western stations (Fig. 9).

Thus, the distribution of all three echinoid species is limited largely to lagoonal bottoms with a high silt fraction. The combined density of these three species is significantly higher among stations located within the sandy-mud facies ($116 \pm 27\ m^{-2}$, 4 stations) than in the silty-sand facies ($4 \pm 1.8\ m^{-2}$, 8 stations) (ANOVA, $p < 0.001$).

We found only a few species of mollusks on the silty and muddy bottoms of the southeastern lagoon. A small (ca. 5 mm), unidentified, transparent tellinid bivalve was the only abundant infaunal species living even in the finest lime mud. The turritellid gastropod *Turritella cingulifera* occurred in large epibenthic aggregations while the skeneid gastropod

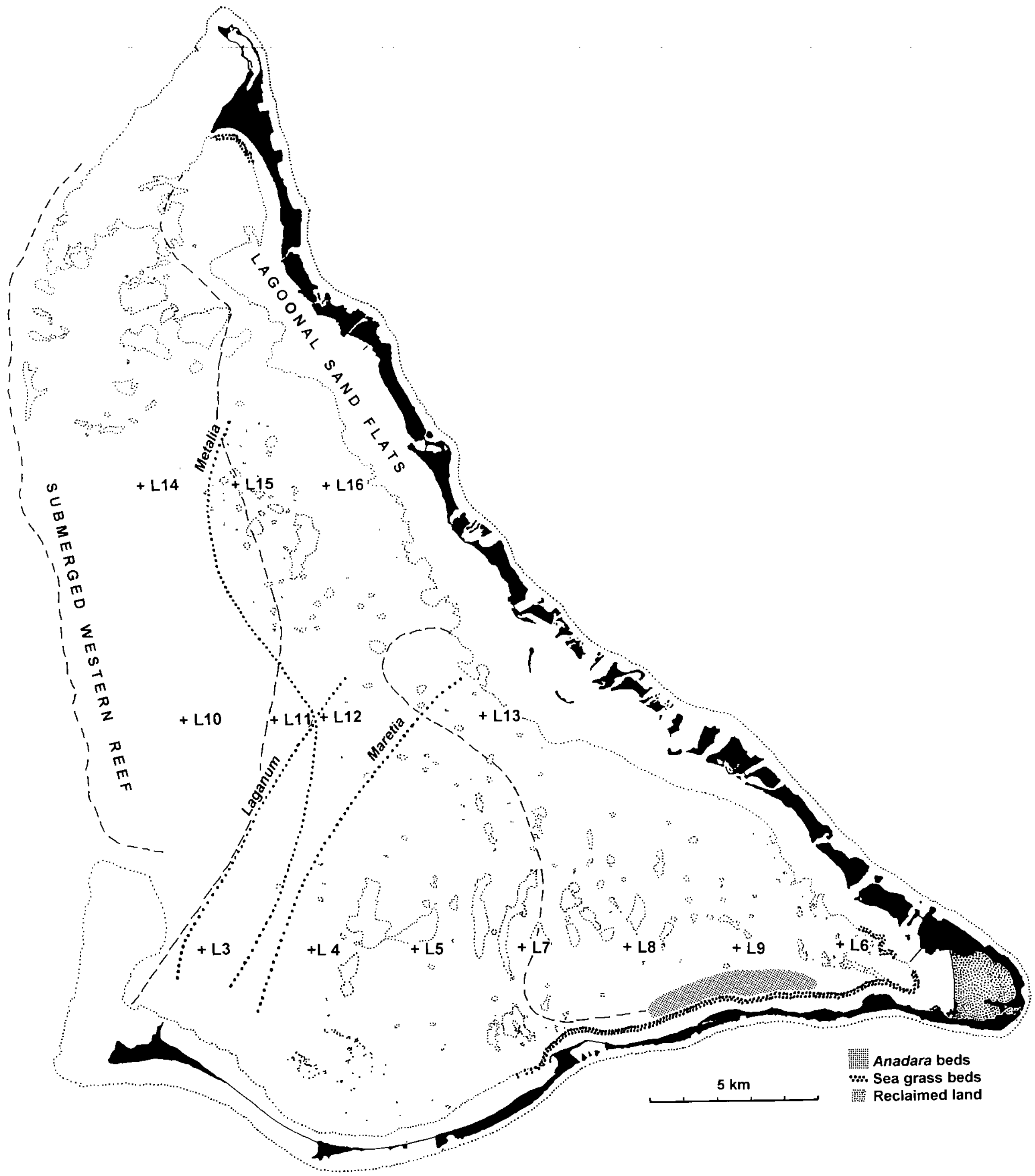

Figure 9. Lagoon bottom of Tarawa. Dashed lines traversing lagoon delineate three major sediment facies: gravelly sand, silty sand and sandy mud (west to east) (after Richmond, 1990). Dotted lines mark western distributional boundary of three irregular echinoids (*Maretia planulata, Metalia sternalis, Laganum depressum*) within the lagoon; each species was encountered at all lagoonal stations southeast of, and at none northwest of, lines. Locations of 14 lagoon-bottom stations indicated by L3 - L16 (see Appendix I for coordinates). True north toward top of page.

Cyclostremiscus cingulifera was fairly common cruising on top of the mud. The naticid gastropod *Tectonatica robillardi* was also fairly common. Dead mollusk shells occurred in much higher diversity then living mollusks. Although this in part may be the result of a sampling artifact caused by the relative rarity of larger species together with the durability of their shells, it may also reflect temporal changes in lagoon-floor mollusk assemblages. The presence of vast quantities of empty shells but no living individuals of several small, fragile species (e.g., *Musculus* sp., perhaps the most common mollusk shell on the lagoon floor) indicates that these species were much more abundant at some time in the past than today. This trend may reflect periodic, short-lived blooms of certain species or the gradual, long-term turnover of bottom communities (cf. Holocene turnover in lagoon-bottom mollusks in Enewetak Atoll, Kay and Johnson, 1987; Paulay, 1991).

Unlike the shallow-water habitats in the lagoon, the deeper lagoon floor (but not the lagoon slope, see above) supports few shellfish resources. Lagoon floor communities differ in species composition from shallow (shoal and sand-flat) communities, sharing only a few species. Most of the heavily exploited species of the sand flat are absent or rare on the lagoon floor. Thus, the lagoon floor does not hold important brood stock that could supply overexploited sand-flat populations with recruits.

The only economically important species encountered regularly on the lagoon floor was *Anadara uropigimelana*, apparently a fairly eurytopic animal. Nevertheless, although occasional shells of this species were found at many sites, no living specimens were encountered in the lagoon bottom surveys indicating that this species is not common on the lagoon floor. High population densities of *S. luhuanus* were encountered on the slopes and tops of numerous patch reefs and shoals; however, this species appears to be essentially absent from the plain of the deeper lagoon floor.

Gatherer Surveys

Sand Flat

Tidal height and day of the week strongly influence gathering effort. Time constraints prevented a thorough assessment of how these variables affect the number of gatherers on the sand flat, as only six gatherer counts were made (Table 2). Nevertheless, a rough estimate of gathering pressure can be made. On a Saturday with a relatively low tide (LW 0.2 m, 12 February 1994), 691 people were observed gathering within a 3-hour period centered around low tide. Given that many people collect for only 1-2 hours, many gatherers likely were missed during the drive-through spot checks. An estimated 1,000 people may have been gathering on that day. On a Monday with a moderately low tide (LW 0.5 m, 14 February 1994), 303 people were counted gathering within a 2-hour period centered around low tide and an estimated >400 people likely gathered shellfish that day. Thus, about twice as many people gather shellfish on Saturdays than on weekdays. In contrast, 60 people were counted on the Sunday (LW 0.3 m, 23 February 1994) between these days, indicating that gathering on Sundays is minimal. The height of low water also clearly makes a difference because little gathering activity occurs on days with relatively high low tides (26 people were counted on 19 February 1994, tide 0.9-1.2 m).

Table 2. Number of shellfish gatherers counted on South Tarawa sand flat.

		Low Tide		Survey Time		
Date (1994)	**Day**	**Height**	**Time**	**Start**	**End**	**Count**
2 February	Friday	0.2	10:53	11:50	14:00	148
12 February	Saturday	0.2	11:24	10:40	13:20	691
13 February	Sunday	0.3	11:52	11:20	13:00	60
14 February	Monday	0.5	12:18	11:30	13:15	303
19 February	Saturday	~1.0	17:39	14:25	15:50	26
22 February	Tuesday	0.6	07:45	08:10	09:20	112

The 19 February count was not taken during low tide. Tides changed from 1.2 m at 10:34 to 0.9 m at 17:39 on that day.

Thus the increase in gathering activity on Saturdays roughly cancels out the greatly decreased gathering activity on Sundays. Assuming an average daily gathering population that fluctuates between 500-1,000 during the best low tides and 0-100 during the poorest tides, with a mean of perhaps 200-400 people per day, yields ca. 75,000 - 150,000 person-days on the sand flat of South Tarawa per year. The mean catch of gatherers on the sand flat was 7.6 ± 0.5 kg person^{-1} effort^{-1} (N = 124) (Fig. 10). Thus, about 600-1,200 tons of shellfish are taken per year by people gathering on the sand flat.

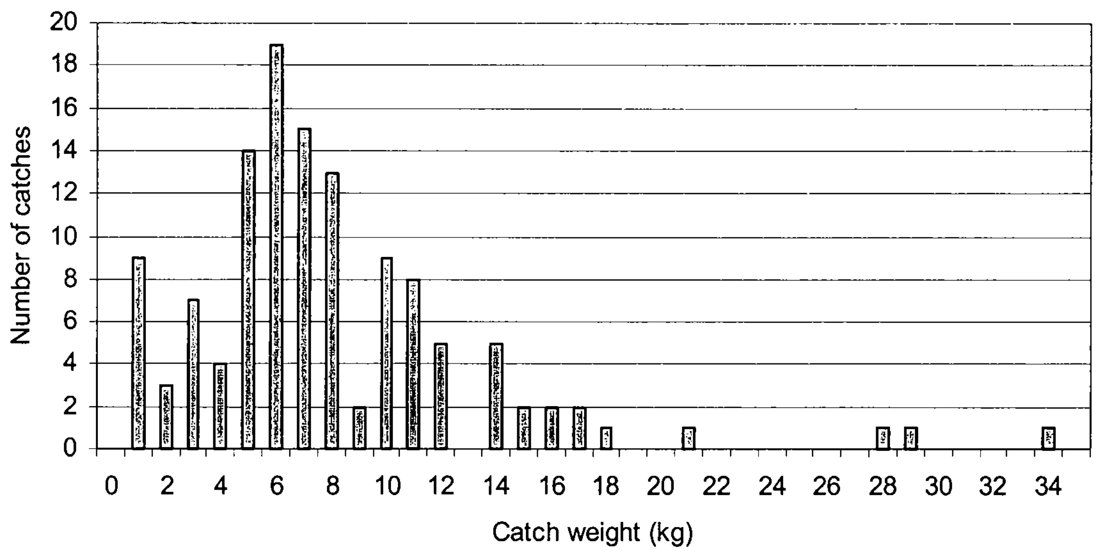

Figure 10. Frequency distribution of catch-per-person effort for shellfish gatherers working South Tarawa sand flat. Mean ± SE: 7.6 ± 0.5 kg. The weight of catches made by parties of >1 gatherers was divided equally among members of the party. N = 124 samples based on N = 96 landing parties.

A total of 19 species was identified in the catches sampled (Fig. 11). Gatherers appear to consume all shellfish species of sufficient size (>ca.1 cm) and many mollusks have common names (Appendix II), suggesting their importance as food.

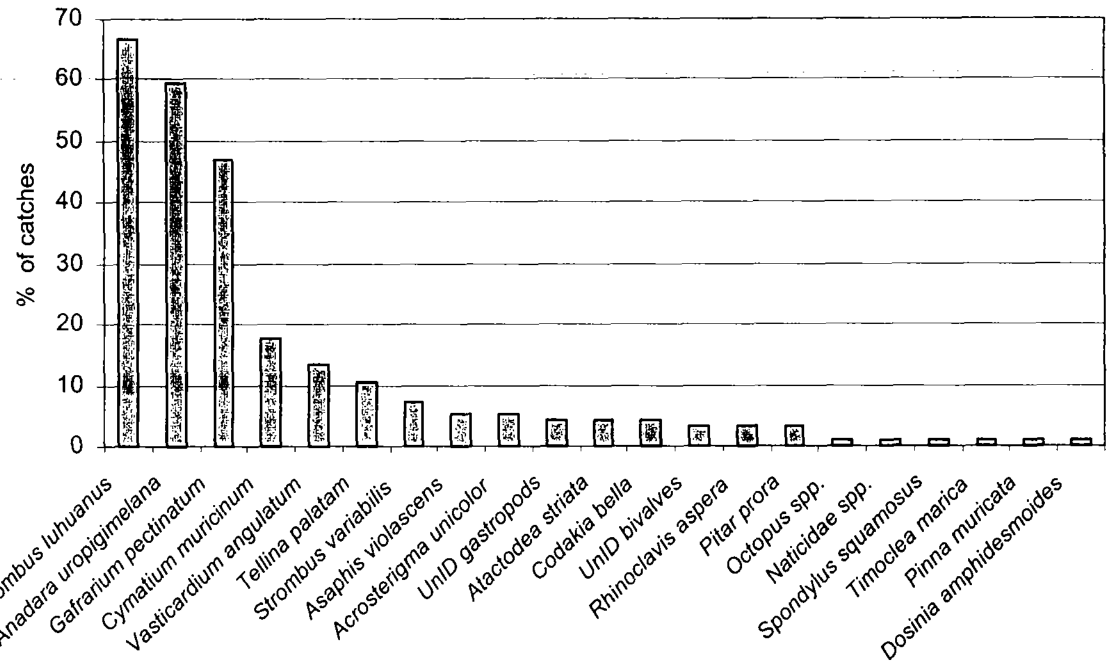

Figure 11. Percentage of catches in which named species were found among all surveyed landings ($N = 96$) from South Tarawa sand flat.

Strombus luhuanus, *Anadara uropigimelana*, and *Gafrarium pectinatum* were by far the most common species in the catches examined, occurring in 67%, 59%, and 47% of the catches ($N = 96$) respectively (Fig. 11). Most (91%) catches were dominated (defined as constituting >75% of catch weight) by one of four species (Fig. 12), most commonly *S. luhuanus* (55% of catches), and *Anadara* (24% of catches). The other catches were not dominated by single species.

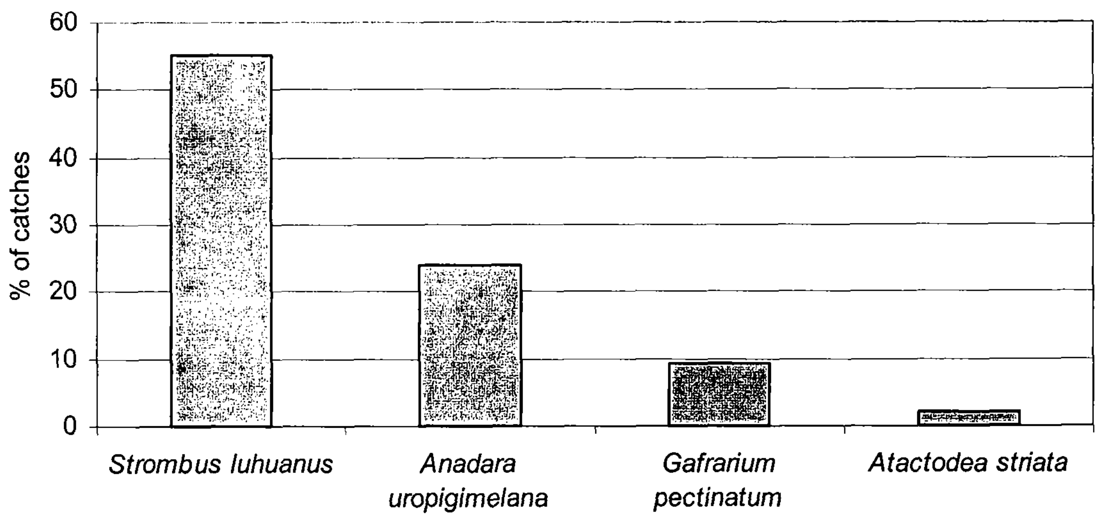

Figure 12. Dominant species in catches from Tarawa lagoon. Percentage of all gathering catches that were dominated (defined as constituting >75% of weight of catch) by single species.

The mean total weight of *S. luhuanus* in each catch in which it occurred was 8.1 ± 1.0 kg, with a value of 8.6 ± 1.2 kg for *Anadara* and 1.2 ± 0.3 kg for *Gafrarium*. These weights are probably slightly overestimated because better species-specific data were available for catches dominated by single species than for catches of mixed species. Nevertheless, they should not be biased against particular species. Multiplying incidence in catch with weight per catch therefore indicates that the three dominant species were taken at a ratio of 5.4 : 5.1 : 0.6 (*S. luhuanus* : *Anadara* : *Gafrarium*). Assuming that these three species constitute about 90% of the total catch, they constituted approximately 44%, 41%, and 5%, respectively, of the South Tarawa-wide sand flat shellfish catch. Given that about 900 tons (see above) of shellfish are harvested, the yearly harvest would be approximately 400 tons of *S. luhuanus*, 370 tons of *Anadara*, and 45 tons of *Gafrarium*. Divers (see below) take an additional 1,000 tons of Anadara. On the basis of a household survey, Bolton (1982b) estimated that about 1,730 tons of *Anadara*, 850 tons of *S. luhuanus* and 280 tons of *Gafrarium* were taken in South Tarawa in 1982. She also noted, however, that the nature of her survey likely leads to an overestimate of the true harvesting pressure.

The mean weight of *S. luhuanus* individuals was 10.5 ● 0.52 g (mean ± SE in $N = 17$ harvests; s.d.= 2.2 g), of *Gafrarium* was 7.5 ± 0.46 g ($N = 15$ harvests; s.d.= 1.8 g), and of *Anadara* was 20 ± 2.5 g ($N = 26$ harvests; s.d.= 13 g). The low variance in *S. luhuanus* weight reflects that only large juveniles and adults of this species with determinate growth are taken. In contrast, the higher variance in *Anadara* weight reflects the great variability in this species' size among beds caused largely by irregular recruitment (see Tebano and Paulay, 2001). Thus, intense recruitment in the southeastern "elbow" started a new *Anadara* fishery in 1993. Those taken in this area in early 1994 averaged 6 ± 0.8 g (mean ± SE in $N =$ 8 harvests) compared with 26 ± 2.6 g ($N = 18$ harvests) for *Anadara* taken elsewhere.

Given these average weights, the yearly harvest tonnage estimated above translates to approximately 4×10^7 *S. luhuanus*, 2×10^7 *Anadara*, and 6×10^6 *Gafrarium* taken from the South Tarawa sand flat. These values are comparable to the rough abundance estimates of these species on the sand flat (see above) of 7×10^6 *S. luhuanus*, 6.3×10^6 *Anadara*, and 6.6×10^7 *Gafrarium*. The disparity between the estimated *Anadara* density and the higher annual harvest is partly a result of the immense recruitment event in the southeastern elbow (see Tebano and Paulay, 2001) that contributed to the harvest of that species in 1994 when much of the harvest data were collected. This event had not yet occurred when the sand flat populations were surveyed in 1992. Nevertheless, these estimates indicate that the harvest of *Anadara* is close to, if not in excess of, its rate of production.

As noted above, the abundance of *S. luhuanus* was probably underestimated but offshore refuges protect *S. luhuanus* populations from overharvesting. This species was abundant in most shallow-water habitats surveyed in the inner lagoon, ranging from the low intertidal zone to ca. 8 m depths. Poiner and Catterall (1988) also found this conch common to a depth of 9 m in Papua New Guinea. The abundance and age structure of this species varies greatly. Although our quantitative surveys encountered it almost exclusively at low densities, *S. luhuanus* is extremely abundant (>50 m^{-2}) in many areas not quantitatively surveyed, especially on the lower slopes of shoals. Juveniles and adults are commonly found in separate aggregations; similar aggregations are well known elsewhere (Poiner and Catterall, 1988). These aggregations probably are behavioral because aggregations of different age classes are often found near each other, well within the crawling range of this highly mobile gastropod.

Although the harvesting pressure on the sand flat on *S. luhuanus* is high, large aggregations on the lagoon slope, accessible only by diving, and those on shoals, accessible only by boat, are virtually unfished. The bulk of this conch's stock is in these refuges. Catterall and Poiner (1987) suggested that this species is capable of migrating to shallow water. Migrants from deep water may continually replenish the *S. luhuanus* populations on the sand flat although we have no data to test this hypothesis. Nevertheless, such migration could also explain the discrepancy between sand-flat stock and harvest estimates. In Papua New Guinea, deep-water populations, together with the frequent burial of juvenile stages, offer this species refuge from overexploitation (Poiner and Catterall, 1988). In contrast, *S. luhuanus* populations have been decimated by overharvesting in the Ryukyus (Yamaguchi pers. comm.). The species forms the basis of artisanal fisheries throughout much of its range. *Strombus luhuanus* has separate sexes and determinate growth. Population studies conducted in Papua New Guinea show that this species reaches sexual maturity at about two years of age (Poiner and Catterall, 1988).

On Tarawa, *G. pectinatum* appears to be almost ubiquitous on the intertidal sand flat and many lagoonal shoals but it is rare or absent in reef areas of the western lagoon. Except in Temaiku, this species is rarely the focus of collecting in South Tarawa; it is, however, an important bycatch. Its offshore populations, large population size, and probable rapid growth rate protect this resource. *Gafrarium pectinatum* is harvested in many areas across its wide Indo-West Pacific range, including many Pacific islands. In Hong Kong, Morton (1990) showed that the species has separate sexes, matures at one year of age at a size of 16-20 mm, and lives up to three years, reaching a maximum length of just over 35 mm. It reproduces at a low level throughout the year but has a seasonal peak during spring and fall in that seasonal climate.

Because the survey of gatherers on the sand flat was set up around the lowest tides, it virtually ignored gathering activity focused on the bivalve community of the beach slope, a habitat that is accessible in all but the highest tides. We have frequently observed people gathering in this habitat, collecting the bivalves *Asaphis violascens* (*te koikoi*) and, to a lesser extent, the much smaller *Atactodea striata* (*te katura*). While *Asaphis* is clearly a favored shellfish, *Atactodea* is taken mostly incidentally, or for baby food (so noted by informants), because of its small size. Because *Asaphis* inhabits a zone accessible even on the worst tides, it is a valuable resource for subsistence gatherers. It is generally shunned on beaches adjacent to villages, however, because the population uses *Asaphis* habitat for toilet purposes. All the observed gathering of this species occurred along causeways or in front of the hotel, areas not regularly used for defecation. Although the narrow zonation of *Asaphis* in an accessible habitat makes it vulnerable to overharvesting (Catterall and Poiner, 1987), much of its habitat is in areas shunned by collectors, providing a refuge for the species. The size range of harvested *Asaphis* in South Tarawa, however, appears to be well below the maximum size attained by the species, perhaps as a result of overharvesting. The abundance of the species, however, implies abundant recruitment.

The actual importance of *Asaphis* as a shellfish resource is unclear. No *Asaphis* collectors were encountered in the gatherer surveys, although I have seen people collecting this species on several other occasions. The importance of *Asaphis* relative to *Anadara, S. luhuanus,* and *Gafrarium* appears to be minor. In contrast, on the basis of a household survey, Bolton (1982b) estimated that about 464 tons of *Asaphis* were harvested throughout North and South Tarawa in 1982. She also noted, however, that the nature of her survey probably leads to an overestimate of the true harvesting pressure. Bolton's estimates for *Asaphis* harvesting may also be excessive because the indigenous name for the species, *te koikoi*, is often inappropriately applied to a wide range of shellfish today.

Offshore Anadara Beds

Anadara is frequently harvested by divers on the lagoon slope at depths of 2-8 m. To work in this area, divers need a vessel to hold their catch. A variety of vessels are used, including floats (made from rubber inner tubes fitted to hold bags of *Anadara,* which are the most common vessels), outrigger canoes, and aluminum dinghies; some dinghies are fitted with outboards and some canoes with sails.

Counts of divers on the Tangintebu-Bangantebure *Anadara* bed are much more accurate than counts of gatherers on the sand flat, partly because of the small size of the area, as well as of the gatherer population, and the visibility of harvesters on the water. Counts were made on 6 days: 3 during the early afternoon, when more than 90% of the divers were likely onsite, and three during the late morning, when some divers had not yet arrived. An average of 34 divers worked these beds on the 3 days when counts were made in the afternoon (Table 3).

Table 3. Results of survey of divers collecting *Anadara* from offshore beds.

Date (1994)	Time	Number of Vessels	Number of Divers	Divers per Vessel[1]
15 February	11:00	14	25	1.79
17 February	10:45	9	17	1.89
18 February	11:15	15	27[2]	
21 February	13:00	21	35	1.67
22 February	13:30	17	30	1.76
23 February	13:00	21	38	1.81
Mean ± sd[3]		**16.2 ± 4.6**	**28.6 ± 7.5**	**1.8 ± 0.1**
Mean ± sd[4]		**19.7 ± 2.3**	**34.3 ± 4.0**	**1.8 ± 0.1**

[1]Divers per vessel = calculated mean number of divers per vessel.
[2]Not counted, estimated from divers per vessel ratio
[3]Mean of all values.
[4]Mean of 21, 22, and 23 February, when surveys were conducted during peak gathering times.

Divers pack their *Anadara* catch into standard-sized rice bags that hold 34 ± 1.5 kg per bag (s.d.; $N = 5$). Interviews indicated that the average diver takes 3.3 ± 1.6 bags per day (s.d.; $N = 10$). Thus, the diving fishery lands about 3800 kg of *Anadara* per day. Considering that little gathering occurs on Sundays and that gathering during stormy weather is not possible, divers gather on perhaps 275 days per year, with an estimated yearly harvest of about 1,000 tons. Given that the large offshore *Anadara* have an average weight of ca. 50 g, this annual harvest weight translates to a harvest of 1.6×10^7 *Anadara*. With an estimated population of 4.4×10^7 clams in the Tangintebu-Bangantebure bed, or 7.2×10^7 clams in the entire South Tarawa lagoon slope (see above), this figure represents a harvest of about one-third to one-fifth of the total adult population per year.

The growth rate of *Anadara* in Tarawa Lagoon is not well documented, but preliminary data indicate that the typically harvested 3-6 cm shellfish must be at least 2-3 years old. Recruitment of the species appears to be episodic, being highly variable in both time and space (Tebano and Paulay, 2001). Thus, the harvests in the offshore beds are near to, if not exceeding, sustainable rates.

In contrast to gathering shellfish on the sand flat, a practice primarily motivated by subsistence, diving for *Anadara* is a commercial venture, with 80% of the interviewed divers ($N = 10$) collecting *Anadara* for sale. These divers routinely collect *Anadara* 6 days a week (which is one reason for the low variance in the number of people seen collecting per day). With a bag of *Anadara* selling for A $6 on the roadside (February 1994; A$5 in 1993), they earn ca. A$20 per day, a good wage by Tarawa standards. Although this venture is lucrative, the *Anadara* populations may not be able to support much expansion in harvesting. However, the strenuous nature of harvesting limits over harvesting of offshore *Anadara* beds. Collectors free dive to 3-6 m for many hours each day. Divers search for areas with high *Anadara* densities where they can grab numerous clams on each dive. Divers avoid portions of the bed with lower shellfish density, so once density becomes moderately reduced, harvesting becomes unprofitable, providing a refuge for the shellfish.

SUMMARY AND CONCLUSIONS

The abundance of benthic macroinvertebrates in Tarawa Lagoon is striking and unusual. Oceanic atolls typically support a relatively low abundance and biomass of macrobenthos. The major exceptions to this trend are "closed" atolls where water exchange with the surrounding ocean is limited and the residence time of lagoon waters can be several weeks to months. The lagoons of closed atolls tend to have low-diversity faunas dominated by one or a few extremely abundant species of high biomass (Salvat, 1969). Frequently, the dominant species are photosymbiotic bivalves, which derive much of their nutrition autotrophically. Thus, giant clams (*Tridacna maxima*) are abundant in several closed atolls (e.g., Reao, Takapoto, Vahitahi [Tuamotu], and Caroline [Line]) and the photosymbiotic cockle *Fragum fragum* is extremely abundant on the sand flats of others (e.g., Anaa and Tuamotu) (Salvat, 1969, 1972; Richard, 1977, 1982; Sirenko, 1991). Some closed atolls also host abundant heterotrophic bivalve populations, especially the epibenthic species *Arca ventricosa, Pinctada maculata,* and *Chama iostoma* (Salvat, 1969; Richard, 1978, 1985a, b).

These latter species presumably subsist on the relatively high, indigenous lagoonal productivity of closed atolls (cf. Sournia, 1976; Delesalle, 1982).

In contrast to the macrobenthos of typical closed atolls that are characterized by low diversity and high biomass and the macrobenthos of typical open atolls that are characterized by high diversity and low biomass, Tarawa hosts high diversity and high biomass in an open lagoonal setting. With the entire western side submerged, the residence time of lagoonal waters is about one week (Chen et al., 1995). Three species of large, irregular echinoids and a diversity of mollusks are abundant in a variety of habitats and all the abundant species are heterotrophic.

Because Tarawa lies in the equatorial upwelling region, the concentration of inorganic nutrients, phytoplankton biomass, and productivity is considerably elevated above that of atolls located in the subtropical gyres (Kimmerer and Walsh, 1981). This enhanced planktonic, and probably also benthic, primary production must be largely responsible for the abundance of macrobenthos. Although planktonic secondary production has been estimated to be of insufficient magnitude to directly support the fishery yield of the atoll (Kimmerer, 1995), only an estimated 8-10% of the planktonic primary production is consumed by zooplankton (W. Kimmerer, pers. comm.). This percentage leaves open the possibility that much of the benthos is supported by planktonic primary production. The abundance of suspension and deposit feeders in the benthos is consistent with this hypothesis. Bonefish, as well as many other fish species, rely largely on suspension and deposit feeding invertebrates for their food (personal observation), and therefore could be supported in large part indirectly by planktonic primary production.

Suspension and deposit feeders dominate the macrobenthos. The deep lagoon bottom is dominated by three deposit-feeding echinoids, a suspension-feeding gastropod (*Turritella cingulifera*), a deposit-feeding bivalve (unidentified tellinid), and a variety of suspension- and deposit-feeding polychaetes. The spectacular abundance of irregular echinoids indicates the importance of the detrital food chain. The muddy sediments (indicative of limited horizontal transport) and the absence of macroalgae or photosymbiotic foraminiferans indicate that the deep lagoon bottom community may ultimately be supported largely by planktonic production, although the possible role of benthic microalgae remains to be evaluated.

The shallower lagoon slope is dominated by a similar assemblage of echinoids and polychaetes, and some large suspension-feeding (*Anadara*) and grazing (*Strombus luhuanus, S. erythrinus,* and *S. variabilis*) mollusks. The latter species feed on attached and free-living (*Grateloupia*) benthic algae. The sand-flat community is dominated by bivalves (93% of all individuals encountered), including suspension-feeding, deposit-feeding, and chemo-symbiotic taxa. On the sand flat and shoals, *Strombus* is also abundant.

Seagrasses are locally dominant producers in the benthos and seagrass beds support a greater abundance of shellfish than adjacent areas. Seagrasses are known to facilitate the production of macrobenthos in a variety of ways (see above). The enhancement of particulate food supplies by hydrodynamic baffling and by production of seagrass detritus can be important (Peterson et al., 1984). The importance of benthic plant detritus as a food source for suspension and deposit feeders living under the plants has been demonstrated in temperate kelp beds (Duggins et al., 1989) and probably also applies to seagrass beds. The fact that the most productive *Anadara* beds lie within seagrass beds on the sand flat, or directly lagoonward of such beds on the lagoon slope, may indicate the importance of seagrass primary production for this community.

Both the seagrass beds and associated shellfish resources appear to have increased substantially since World War II, perhaps as a result of increased fertilization by sewage-derived nutrients. The width of seagrass beds has more than doubled off South Tarawa between 1943 and 1984. Since World War II, the population of South Tarawa has increased by 1,700%. Associated with this increase is a large increase in sewage-derived nutrients that enter the lagoon through each tidal cycle. Although sewage-derived nutrients were found by Kimmerer (1995) to be unimportant in the nutrient budget of the southern lagoon as a whole, these nutrients may have considerable influence over the intertidal sand flat that they traverse. This influence is demonstrated by the high bacterial contamination in shellfish taken from the sand flat but not from offshore lagoonal habitats (Danielson et al., 1995).

The effect of causeway construction on seagrass beds is unclear. A correlation seems to exist between the presence of extensive seagrass beds and the lack of passages: the largest seagrass beds lie off the longest islets. Many small seagrass beds, however, including all the seagrass beds in North Tarawa between Bonriki and Buariki, lie immediately on the lagoon side of the passages. Seagrass beds changed markedly, with some portions expanding and other portions contracting, off the Taborio-Ambo passage after causeway construction (based on aerial photographs taken before causeway construction [1943] and after [1968 and 1984]).

Whatever the cause, the observed expansion of seagrass beds was probably partly responsible for the apparent increase in shellfish resources during the past several decades. Older residents of Tarawa recall a considerable increase in the abundance of *Anadara*, and then *Strombus luhuanus*, and modest increases in the abundance of *Gafrarium pectinatum, Asaphis violascens* (*te koikoi*), and *Atactodea striata* (*te katura*) since World War II (Johannes, 1992).

In contrast, Johannes (1992) noted that the edible sipunculan (*te ibo*) has become scarce in South Tarawa within living memory, and most of the worms now are taken in North Tarawa. This worm is generally found on sand flats that lie on the lagoon side of passes between islets (Nabuaka Tekinano pers. comm.). Thus, its disappearance from South Tarawa may be the result of closing the passages with causeways.

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APPENDIX I
Site Coordinates

Sand flat transects: all traversing the South Tarawa sand flat (shore to edge of sand flat), perpendicular to shore. Coordinates for origin on shore:

TRANSECT	LAT	LONG
Temaiku	1°22.302'N	173°08.624'E (E-W orientation!)
Bikenibeu	1°21.876'N	173°07.154'E
Banganteburе	1°21.805'N	173°05.686'E
Abarao	1°21.739'N	173°05.218'E
Eita E	1°21.73'N	173°04.75'E
Eita W	1°21.50'N	173°04.25'E
Tangintebu	1°21.339'N	173°03.840'E
Ambo	1°21.350'N	173°02.693'E
Banraeaba	1°20.55'N	173°01.80'E
Antenon	1°20.15'N	173°01.05'E
Nanikai	1°19.872'N	172°59.680'E
Betio	1°21.227'N	172°56.150'E

Lagoon stations:

STATION	LAT	LONG	DEPTH
L3	1°22.839'N	172°56.075'E	11 m
L4	1°22.828'N	172°57.767'E	20 m
L5	1°22.817'N	172°59.465'E	11 m
L6	1°22.889'N	173°06.340'E	6 m
L7	1°22.857'N	173°01.206'E	12 m
L8	1°22.842'N	173°02.899'E	15 m
L9	1°22.781'N	173°04.510'E	12 m
L10	1°26.711'N	172°55.727'E	17 m
L11	1°26.708'N	172°57.322'E	15 m
L12	1°26.703'N	172°58.057'E	17 m
L13	1°26.703'N	173°00.544'E	17 m
L14	1°30.581'N	172°55.186'E	8 m
L15	1°30.462'N	172°56.747'E	17 m
L16	1°30.521'N	172°58.274'E	11 m

Lagoon slope transects: Traversing the South Tarawa lagoon slope, all oriented N-S irrespective of shore-line orientation, and extend from 0.05' N of the sand flat to 0.55' N of the sand flat:

TRANSECT	LAT-Beginning	LAT-Ends	LONG
1	1°19.906'N	1°20.413'N	172°59'E
2	1°20.074'N	1°20.562'N	173°00'E
3	1°20.556'N	1°21.064'N	173°01'E
4	1°21.228'N	1°21.728'N	173°02'E
5	1°21.597'N	1°22.051'N	173°03'E
6	1°21.79'N	1°22.29'N	173°04'E
7	1°22.063'N	1°22.510'N	173°05'E
8	1°22.189'N	1°22.689'N	173°06'E
9	1°22.066'N	1°22.566'N	173°07'E

APPENDIX II
I-Kiribati names of marine invertebrates

Invertebrates for which indigenous names were recorded and those mentioned in this paper are listed with their authorities below. Indigenous names that apply to a group of species are labeled generic and listed under the wider taxonomic category to which they are applied as well as under the species/genus within that category to which I heard the name applied. I-Kiribati names that appear to be utilized inconsistently or otherwise are deemed to need further confirmation, are noted with a '?'. A '?' preceding a scientific name implies that the identity of the organism was difficult to ascertain, generally because no specimens were seen and the name was based on a description. Such species included solely on the basis of informant's descriptions are marked with an '*'. Names specific to southern Kiribati are denoted with an 'S', those to northern Kiribati with a 'N'. The definite article "te" leads species names in I-Kiribati. Names are based on interviews with a small number of people on Tarawa from 1992 to 1994, and do not include compilations from the literature (Banner & Randall, 1952; Lobel, 1978). The latter two papers were disregarded because they include several erroneous names.

Species	I-Kiribati name
CNIDARIA	
Cubozoa	
?*Carybdea alata* Reynaud, 1830*	te baitari
Scyphozoa	
?*Cassiopea* sp.*	te tia
Anthozoa - Scleractinia	
Branching corals (including *Pocillopora, Acropora*)	te enga (generic)
Massive corals, at least *Porites*	te atitaai (generic)
Mushroom corals (Fungiidae)	?te wenei (generic)
MOLLUSCA	
Bivalvia	

Mytilidae	
Modiolus auriculatus Krauss, 1848	
Arcidae	
Barbatia foliata (Forsskål, 1775)	?te nikarinei
Anadara uropigimelana (Bory de St Vincent, 1824)	te bun
Spondylidae	
Spondylus squamosus Schreibers, 1793	te koikoi n anti
Pteriidae	
Pinctada margaritifera (Linné, 1758)	te baeao
Pinnidae	te bwere, te katati (generic)
Atrina vexillum (Born, 1778)	te bwere, te katati (generic)
Pinna sp.	te bwere, te katati (generic)
Lucinidae	
Wallucina haddoni (Melvill & Standen, 1899)	
Codakia bella (Conrad, 1837)	te kairebwe, ?te nikarewerewe
Cardiidae	
Vasticardium angulatum (Lamarck, 1819)	te koikoi n tari
Acrosterigma unicolor (Sowerby, 1834)	incorrectly called te koikoi n tari by some
Fragum sueziense (Issel, 1869)	
Tridacna maxima (Röding, 1798)	te were
Tridacna squamosa Lamarck, 1819	te were matai
Tridacna gigas (Linné, 1758)	te kima
Hippopus hippopus (Linné, 1758)	te neitoro
Mesodesmatidae	
Atactodea striata (Gmelin, 1791)	te katura
Tellinidae	
Tellina (Quidnipagus) palatam (Iredale, 1929)	te nikatona
Tellina (Tellinella) crucigera Lamarck, 1818	?te kabwere
Tellina (Tellinella) virgata Linné, 1758	?te kabwere
Scissulina dispar (Conrad, 1837)	
Psammobiidae	
Asaphis violascens (Forsskål, 1775)	te koikoi[1]
Veneridae	
Gafrarium pectinatum (Linné, 1758)	te koumara
Dosinia amphidesmoides (Reeve, 1850)	
Pitar prora (Conrad, 1837)	
Timoclea marica (Linné, 1758)	te koumai
Gastropoda	
Trochidae	
?*Tectus pyramis* (Born, 1778)*	te baraitoa
Skeneidae	
Cyclostremiscus cingulifera (A. Adams, 1850)	
Turbinidae	
Turbo spp.	te matanin (generic)
Neritidae	

Nerita spp.	te kaban (generic)
<u>Cerithiidae</u>	
Rhinoclavis aspera (Linné, 1758)	
<u>Turritellidae</u>	
Turritella cingulifera Sowerby, 1825	
<u>Naticidae</u>	te tumara (generic)
Mammilla melanostoma (Gmelin, 1791)	te tumara (generic)
Polinices mammilla (Linné, 1758)	te tumara (generic)
Tectonatica robillardi (Sowerby)	
<u>Strombidae</u>	
Strombus erythrinus Dillwyn, 1817	
Strombus luhuanus Linné, 1758	te nouo
Strombus variabilis Swainson, 1820	te newenewe
<u>Cypraeidae</u>	te buro (small), (generic) te bure (large) (generic) te kabaau (some spp.) (generic)
<u>Ranellidae</u>	
Charonia tritonis (Linné, 1758)	?te buu, ?te tau
Cymatium muricinum (Röding, 1798)	te nimakaka, te wiiaau
<u>Cassidae</u>	
Cypraecassis rufa (Linné, 1758)	?te buu, ?te tau
<u>Olividae</u>	
Oliva miniacea (Röding, 1798)	te burebangaki
<u>Terebridae</u>	
Terebra spp.	te buki kakang (generic)
<u>Elobiidae</u>	
Melampus castaneus (Mühlfeldt, 1818)	te ningo ningo (generic)
Melampus flavus (Gmelin, 1791)	te ningo ningo (generic)
<u>Opisthobranchia</u>	
?*Dolabella auricularia* (Lightfoot, 1786)	te ingke (from "ink") not seen
Unidentified slug*	te ubaraniti
Unidentified slug*	te non
Cephalopoda	
Octopus sp. large*	te kika
Octopus sp. small*	te kikao
Octopus sp.*	te kaonako
Octopus sp.*	te riburibunimainuku
?*Sepioteuthis lessoniana* Lesson, 1830*	te riro
ECHINODERMATA	
Holothuroidea	
<u>Holothuriidae</u>	
Bohadschia vitiensis (Semper, 1868)	te kereboki (generic)
Holothuria atra Jaeger, 1833	te n tabanebane (specific)
"	?te nautong (S, specific)
<u>Synaptidae</u>*	te robwe (from 'rope')
Echinoidea	

?Diadematidae	te batinou
Laganidae	
Laganum depressum tonganense Agassiz, 1841	
Spatangidae	
Maretia planulata (Lamarck, 1816)	te katuiaia
Brissidae	
Metalia sternalis (Lamarck, 1816)	te takataka
Ophiuroidea	te kiko n ang (generic)
Asteroidea	
Acanthasteridae	
Acanthaster planci (Linné, 1758)*	te aa (?generic)
ARTHROPODA	
Crustacea	
land crab names from Makin Atoll*	te mama, te bukiroro, te batinana
other crab names*	te n tababa, te kaveana
Palinuridae	te nnewe (generic)
?Panulirus penicillatus (Olivier, 1791)*[2]	te nnewe, te urataake
?Panulirus versicolor (Latreille, 1804)*[2]	te kouratake
Scyllaridae	
?Parribacus sp(p).*	te mnau, te n tabataba
Coenobitidae	
Birgus latro (Linné, 1776)	te ai
Calappidae	
Calappa sp.	te nnon nnon
Carpiliidae	
Carpilius maculatus (Linné, 1758)	te tabanou
Grapsidae	
?Grapsus tenuicrustatus (Herbst, 1783)*	te kamakama
Gecarcinidae[3]	te manaimeri, te manai, te meri
Stomatopoda - Lysiosquillidae	
Lysiosquilla maculata (Fabricius, 1793)	te varo
SIPUNCULA	
?Sipunculus indicus	te ibo
larger sp.*	te ibo raro
ANNELIDA/Polychaeta	
?Amphinomidae*	te karau
HEMICHORDATA	
Ptychodera flava Eschscholtz	te bonubonu
Glossobalanus ?elongatus Spengel, 1904	te bonubonu

NOTES:

[1] The name te koikoi appears to traditionally pertain only to *Asaphis violascens*. However, people not well versed in traditional knowledge apply this name indiscriminately to a variety of bivalve species.

[2] Kouratake and urataake likely represent the same name, with koura and ura being variants of the polynesian "koura" for lobster, and either take or taake being a mispelling of the other.

[3] Tarawa has one or more species of *Cardisoma* as well as *Gecarcoida lalandi*; it is unclear if the indigenous name is specific to one of these or generic.

NOTE OF INSTRUCTIONS THAT WENT WITH MS:

Location of graphs and data in files (on disk): Files .wq1 in QPro for DOS, .wb1 in QPro for Windows. To find data for graphs, look under "series" for graph.

Figure	**File**	**Graph**
Fig. 1	none.......	
Fig. 2A	stransec.wq1	diversity #
Fig. 2B	stransec.wq1	toal by quadrat
Fig. 3	stransec.wq1	density 2
" (more)	"	densit across
Fig. 4	stransec.wq1	sum / m2
Fig. 5	stransec.wq1	te bun by site
Fig. 6	stransec.wq1	nouo transect
Fig. 7	stransec.wq1	koumara transec
Fig. 8	zoanthid.wb1	zo-zonation
Fig. 9	slopesum.wb1	zonation all
Fig. 10	slope-q.wb1	zonation across
Fig. 11	slope-q.wb1	bun in bed
Fig. 12	bunslope.wq1	bun size
Fig. 13	bunslope.wq1	bun tr 4,6,7
Fig. 14	none.......	
Fig. 15	lansum1.wq1	catch per perso
Fig. 16	lansum1.wq1	total catch

Figure 1 is map of Tarawa with major habitats outlined, thus it is the same base map as was requested for our reef ms (also Figure 1 there). In addition, please mark the location of seagrass beds (see sketch) and two sets of transects on this same map, as follows:

Set 1: traversing the S Tarawa sand flat (shore to edge of sand flat), perpendicular to shore. Please print name of each transect (based on locality name), at each location (coordinates given for origin on shore; see sketch for rough location):

TRANSECT	LAT	LONG
Temaiku	$1^{O}22.302$	$173^{O}08.624$ (note E-W orientation!)
Bikenibeu	$1^{O}21.876$	$173^{O}07.154$
Bangantebure	$1^{O}21.805$	$173^{O}05.686$
Abarao	$1^{O}21.739$	$173^{O}05.218$
Eita E	$1^{O}21.73$	$173^{O}04.75$
Eita W	$1^{O}21.50$	$173^{O}04.25$
Tangintebu	$1^{O}21.339$	$173^{O}03.840$
Ambo	$1^{O}21.350$	$173^{O}02.693$
Banraeaba	$1^{O}20.55$	$173^{O}01.80$
Antenon	$1^{O}20.15$	$173^{O}01.05$
Nanikai	$1^{O}19.872$	$172^{O}59.680$
Betio	$1^{O}21.227$	$172^{O}56.150$

Set 2: traversing the S Tarawa lagoon slopes, these transects are oriented N-S, irrespective of shore-line orientation, and extend from 0.05' N of the sand flat to 0.55' N of the sand flat at the following longitudes. Please draw in transect line and label with transect number.

TRANSECT	LONG	LAT-Beginning	LAT-Ends
1	172°59'	1°19.906'	1°20.413'
2	173°00'	1°20.074'	1°20.562'
3	173°01'	1°20.556'	1°21.064'
4	173°02'	1°21.228'	1°21.728'
5	173°03'	1°21.597'	1°22.051'
6	173°04'	1°21.79'	1°22.29'
7	173°05'	1°22.063'	1°22.510'
8	173°06'	1°22.189'	1°22.689'
9	173°07'	1°22.066'	1°22.566'

Figure 14 is another map of Tarawa, copied from Richmond (1990: Fig. 3). Please scan and indicate major sediment types by different shading as they appear on map (a clean copy is enclosed. Then please map the following 14 lagoon bottom stations on this map (below). Finally, please draw in via three lines, the distributional limits of the 3 echinoid species, as shown on sketch.

Lagoon stations:
L3: 1°22.839'N, 172°56.075'E
L4: 1°22.828'N, 172°57.767'E
L5: 1°22.817'N, 172°59.465'E
L6: 1°22.889'N, 173°06.340'E
L7: 1°22.857'N, 173°01.206'E
L8: 1°22.842'N, 173°02.899'E
L9: 1°22.781'N, 173°04.510'E
L10: 1°26.711'N, 172°55.727'E
L11: 1°26.708'N, 172°57.322'E
L12: 1°26.703'N, 172°58.057'E
L13: 1°26.703'N, 173°00.544'E
L14: 1°30.581'N, 172°55.186'E

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