ATOLL RESEARCH BULLETIN

NO. 488

VARIABLE RECRUITMENT AND CHANGING ENVIRONMENTS CREATE A FLUCTUATING RESOURCE: THE BIOLOGY OF *ANADARA UROPIGIMELANA* (BIVALVIA: ARCIDAE) ON TARAWA ATOLL

BY

TEMAKEI TEBANO AND GUSTAV PAULAY

ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D.C., U.S.A.
JUNE 2000

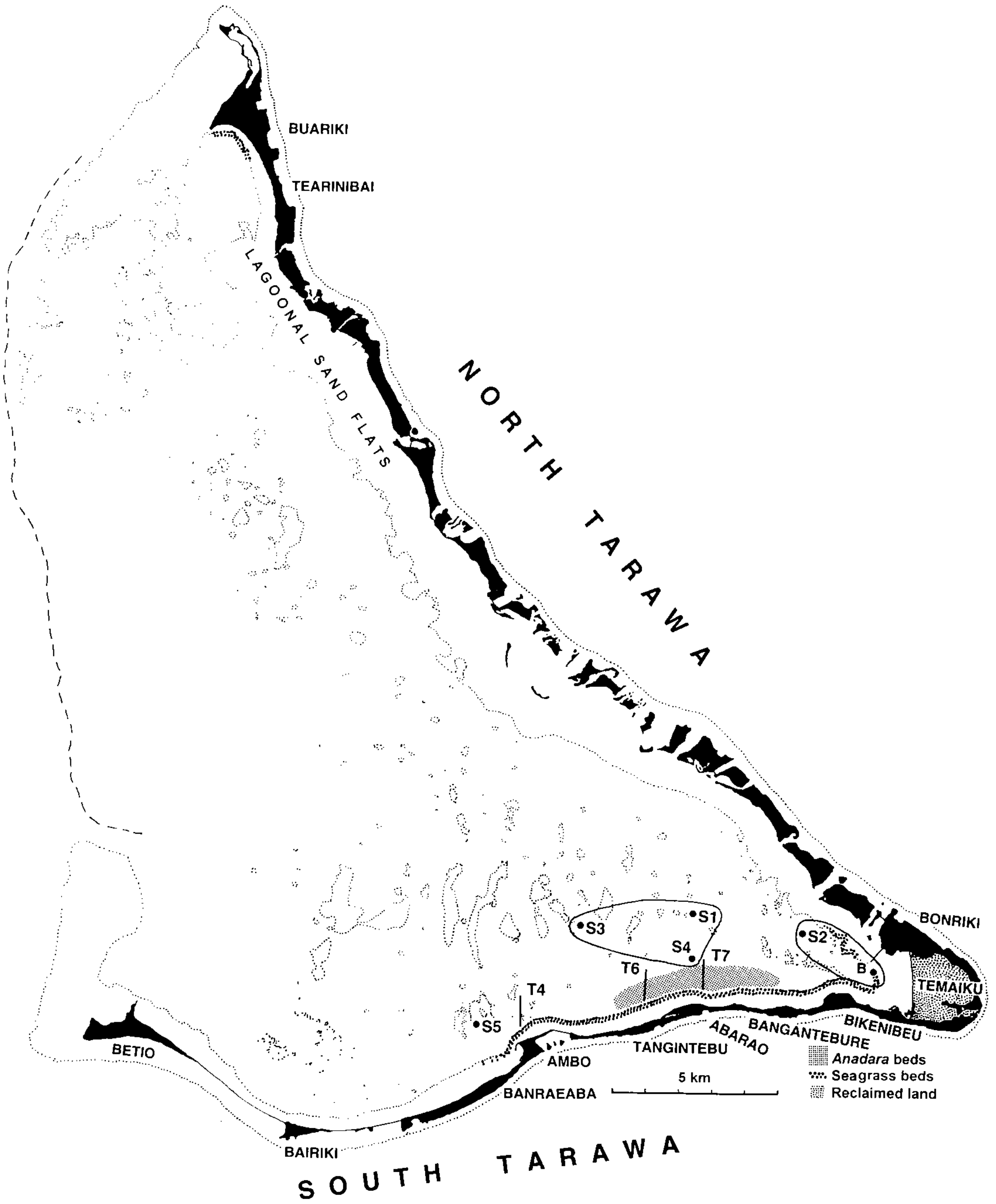

Figure 1. Map of Tarawa showing location of lagoon slope *Anadara* bed, major seagrass beds (including B = Bonriki seagrass bed), five shoals sampled (S1 – S5), and lagoon slope transects (T4, 6, 7) mentioned in text. The centers of the two most recent recruitment events are encircled. These are the areas that were dominated (>50% of individuals / sample) by the 10-20 mm and 20-30 mm-size classes.

VARIABLE RECRUITMENT AND CHANGING ENVIRONMENTS CREATE A FLUCTUATING RESOURCE: THE BIOLOGY OF *ANADARA UROPIGIMELANA* (BIVALVIA: ARCIDAE) ON TARAWA ATOLL

BY

TEMAKEI TEBANO[1]

AND

GUSTAV PAULAY[2,3]

ABSTRACT

The arcid bivalve *Anadara uropigimelana* (*te bun*) is the most important shellfish resource in the central atolls of Tungaru (former Gilbert Islands), with a yearly catch of ca. 1400 tons on South Tarawa alone. Species of *Anadara s.s.* are also important in artisanal shellfisheries on several central Pacific islands. Tungaru atolls lying in the highly productive zone of equatorial upwelling harbor dense *te bun* beds, while those occurring outside this zone have fewer *Anadara*. *Te bun* are abundant in seagrass beds, lagoonal shoals, and shallow-lagoon bottoms. They reproduce year round with a lunar spawning periodicity. Size frequency data and observations on the occurrence of small juveniles indicate that, despite frequent reproduction, there is high spatio-temporal variation in recruitment within the Tarawa lagoon. One massive recruitment event in 1993 opened a novel fishery in Bonriki village, where no *te bun* were available for two decades previously. Highly variable recruitment, as well as changes in the extent of seagrass habitats, may explain marked historical fluctuations in the abundance of this important resource.

INTRODUCTION

Human populations on atolls, more than on any other type of island, have traditionally relied on the ocean for much of their nourishment. Although a great diversity of marine species is exploited, fishes constitute the most important resource. Molluscs are widely exploited on atolls, but perhaps nowhere as heavily as on the equatorial atolls of the Tungaru (former Gilbert) Islands in the Republic of Kiribati.

---

[1] Atoll Research Programme, University of the South Pacific, Tarawa, Kiribati

[2] Marine Laboratory, University of Guam, Mangilao, Guam 96923 USA

[3] Present address: Florida Museum of Natural History, University of Florida, Gainesville FL 32611-7800; email: paulay@flmnh.ufl.edu

Manuscript received 1 October 1995; revised 26 March 2001

These atolls lie in the equatorial upwelling zone, and the high productivity of the region influences many aspects of their form and biota (Paulay, 1997). Tarawa is typical of these atolls in its productivity but unusual in that, as the metropolitan center of Kiribati, it has the largest human population of any atoll in the Pacific. One manifestation of the high productivity is the large populations of several bivalve and gastropod species on lagoonal sand flats, slopes, and shoals (Paulay, 2001). Much of the population on Tarawa still relies on the ocean for their protein need and the abundant molluscan resources of the atoll are heavily exploited.

Tarawa is a triangular atoll with islet-studded eastern and southern rims and a submerged western flank (Fig. 1). Much of the human population lives along the southern rim ("South Tarawa"), where islets have been connected entirely by causeways. In contrast, North Tarawa remains rural and has considerably lower population density. The lagoon has striking physical, chemical, and biological gradients north-to-south and west-to-east, as a result of the largely unidirectional flushing of the lagoon across the submerged western barrier reef. The largest shellfish populations are found near the southeastern lagoon where they occur on the intertidal sand flats lying lagoonward of the islands, on the numerous shoals that dot the lagoon, as well as on the shallower parts of the lagoon bottom (Paulay, 2001).

The arcid bivalve *Anadara uropigimelana* is the most important shellfish resource on Tarawa, as well as throughout central Kiribati. Its importance stems in part from its abundance, large size and accessibility. It is the largest (to 7+cm) of the commonly harvested shellfish species (giant clams are now a rare resource in the area) and also one of the most common; the largest *Anadara* bed in South Tarawa has a mean population density of 14 m^{-2} clams. In South Tarawa alone, ca. 1400 tons of *te bun* are harvested annually. Mean daily *Anadara* catches average 9 kg each for several hundred subsistence gatherers that collect daily on the sand flat and 112 kg each for the ca. 35 commercial divers working from canoes on an offshore bed (Paulay, 2001). No other island group in Polynesia and Micronesia supports similarly extensive molluscan fisheries. Even among the large and productive islands of Melanesia, molluscan fisheries are less significant. Thus Squires et al. (1973) found that near Suva, Fiji, where *Anadara* is the most important marine shellfish harvested, the average daily catch of gatherers was 2 kg. Being abundant in near-shore seagrass beds accessible by wading, as well as in deeper beds requiring canoes and diving gear, *te bun* are accessible to all members of the population. Consequently, most households partake in shellfish gathering (Phillips, 1995).

Reflecting the importance of this shellfish is the significant role it plays in traditional Kiribati society. On Abemama, if fish are not available, *te bun* are presented at traditional gatherings in a meeting house (*maneaba*). *Te bun* shells are worn around the waist on dancing costumes by women and girls. *Anadara* shells are still in use, especially by older men and women for grating mature coconut meat and babai (giant swamp taro, *Cyrtosperma chamissonis* (Schott) Merrill).

Here we summarize what is known about the biology of *Anadara uropigimelana* on Tarawa, considering its identity, distribution, ecology, reproductive biology, and population dynamics.

METHODS

The size structure of *Anadara* in several areas was surveyed during a general benthic lagoon survey, as outlined in Paulay (2001). In addition to samples obtained in that survey, we sampled five shoals in the southeastern lagoon of Tarawa Atoll (Fig. 1). At these shoals, ten 0.25 m^2 quadrats were haphazardly tossed on the top of the shoal and all *Anadara* encountered within counted and measured. When fewer than 100 *Anadara* were so encountered, additional areas in the same area were systematically searched until at least 100 clams were found. All clams were measured with dial calipers to the nearest mm. Shellfish gatherers were surveyed as described in Paulay (2001).

The present distribution and qualitative abundance of *Anadara* was evaluated on several atolls from site visits by Tebano. Historical changes in the abundance of the species were recorded from the recollection of older informants on Abemama, Maiana, and Abaiang Atolls.

RESULTS AND DISCUSSION

Identity of *te bun*

Identification of species of *Anadara* is difficult at present, because the genus includes numerous closely related forms whose phenotypic variability and nomenclatural identity have not been fully worked out. As a result, identifications of Indo-West Pacific *Anadara* species in the nontaxonomic literature are often unreliable.

While several *Anadara* species occur in the western Pacific (e.g. at least six species in Fiji; Paulay, pers. obs.), only two, *A. antiquata* (Linné, 1758) and *A. uropigimelana* (Bory de St Vincent, 1824), are known from islands of the Pacific tectonic plate (Paulay, 1996). They both belong to *Anadara s.s.*, are illustrated by Kilburn (1983), and although they exhibit considerable intraspecific variation, can be readily distinguished as follows (Fig. 2):

1. The ribs of *A. antiquata* become gradually grooved with age, starting with a single central groove and often followed by the development of smaller grooves on either side. This grooving is best developed on the anterior half of the shell and makes it appear as if the ribs were bifurcating (which, however, they are not). The ribs (as well as the interstices) of *A. uropigimelana* are finely grooved by several, inconspicuous, minute grooves that do not increase in number as the animal grows.
2. The periostracum of *A. antiquata* is coarsely bristled with large, flattened setae arising from the interstices as well as from the grooves that develop on the ribs as the animal grows. In contrast, the periostracum of *A. uropigimelana* is velvety, with series of minute bristles arising from the numerous fine grooves on both ribs and interstices.

3. The shell of *A. antiquata* is less inflated, more posteriorly produced (umbo lying relatively more anteriorly), and has the posterior slope gently demarcated. In contrast, the posterior slope of *A. uropigimelana* is offset by a strong break in slope from the rest of the shell.
4. *Anadara antiquata* has 35-39 ribs among the samples we examined compared with 31-35 in *A. uropigimelana.*

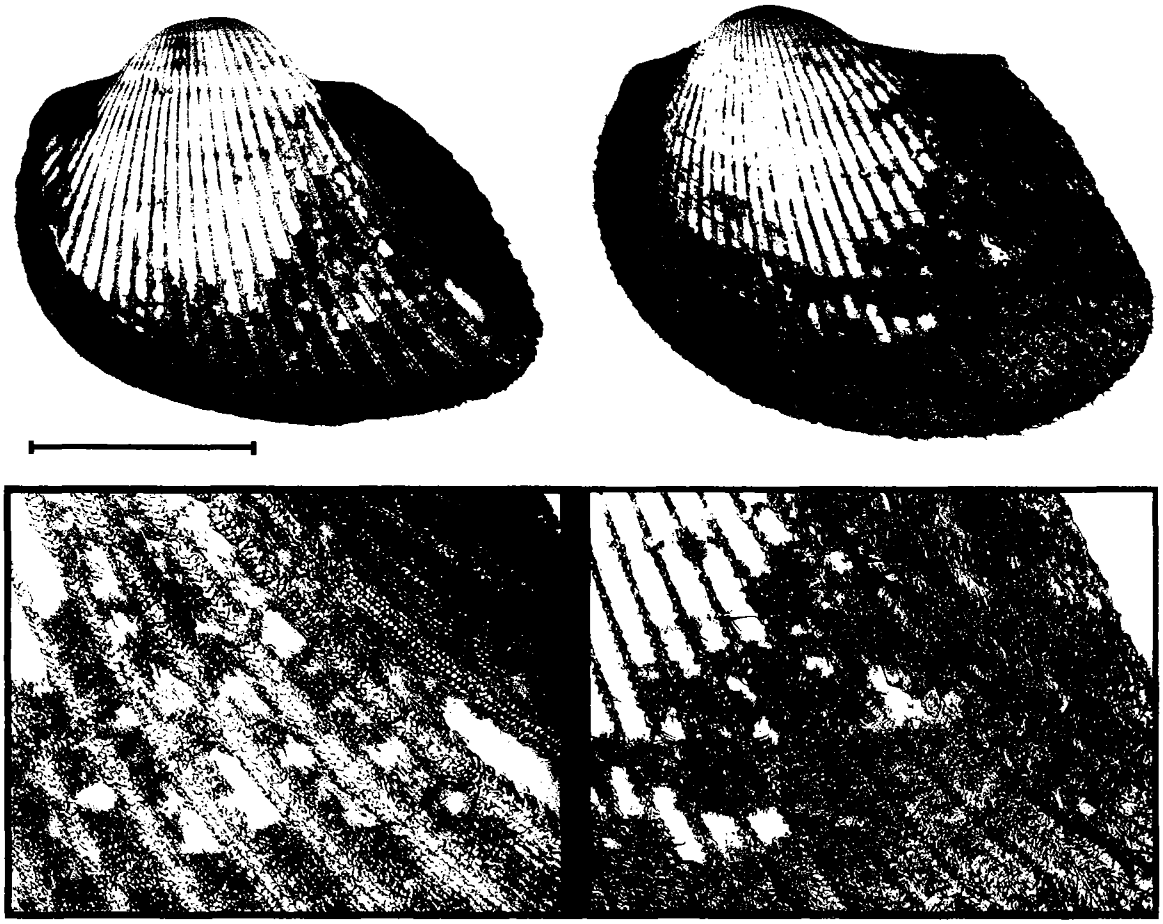

Figure 2. *Anadara uropigimelana* (left, Tarawa, UF 282607; Tarawa) and *Anadara antiquata* (right, UF 282606, Tonga). Scalebar: 2 cm.

Both *Anadara antiquata* and *Anadara uropigimelana* are widely distributed from East Africa to the Central Pacific. The occurrence of both species appears to be patchy in Oceania (Paulay, 1996). *Anadara antiquata* is known in Oceania from the Mariana Islands (Guam, Saipan), Tonga (Tongatapu), Cook Islands (Aitutaki, ?Holocene fossil), and Hawaii (Oahu, Pleistocene fossil). *Anadara uropigimelana* is known from the Federated States of Micronesia (Chuuk), and the Marshall, Tungaru, Tonga (Tongatapu and Haapai), and Society (Tahiti) Islands (Paulay, 1996 and pers. obs.). This patchy distribution is likely attributable in part to the relatively recent colonization of the Central Pacific by *Anadara.* Both species are restricted to lagoonal habitats in Oceania, and all lagoons are stranded in this area during glacial low sea stands (Paulay, 1990; 1996).

Thus the present occurrence of these species in the region must postdate the Holocene sea-level rise, unless they survived in unexpected refugia.

The patchy distribution of *Anadara* species likely is also related to the patchy distribution of their preferred habitats. Both species have a tendency to be associated with marine angiosperms: *Anadara antiquata* with mangroves; and *A. uropigimelana* with seagrass beds. On Guam, *A. antiquata* is restricted to muddy sands adjacent to mangroves and is also very common in such habitats in Fiji. *Anadara uropigimelana* appears to be absent near mangrove habitats, but is common in seagrass beds. We have collected this species in seagrass beds in Kiribati, Tonga, and the Marshall Islands. Although *A. uropigimelana* does occur outside of seagrass beds, including deeper lagoonal habitats (Paulay, 2001), its abundance in seagrass meadows is generally higher than in adjacent sand-flat habitats (Tebano, 1990).

These two species of *Anadara*, which form the basis of local fisheries on many Pacific islands where they occur, including New Caledonia (Baron and Clavier, 1992), Fiji (Squires et al., 1973), Tonga (Spennemann, 1987), Chuuk (Federated States of Micronesia, A. Davis, pers. comm.), and prehistorically in the Mariana Islands (Amesbury, 1999; see below) as well as in Kiribati (Tebano, 1990), although they are recorded in the literature under a variety of names.

Abundance within Kiribati

Anadara uropigimelana is widely distributed in the Tungaru Islands of Kiribati, but shows marked differences in abundance among atolls. It is uncommon on the northernmost atoll of Butaritari, abundant on all the north-central atolls (Marakei, Abaiang, Tarawa, Maiana and Abemama), rare on Nonouti, and unknown on other southern atolls, although it may occur there in low population densities (Table 1). The species is also rare on Majuro Atoll of the neighboring Marshall Islands just to the north. Although other atolls in the Marshalls were not searched for *Anadara*, the lack of a local fishery and importation of *te bun* from Kiribati suggests that they are generally rare there. Attempts to establish shell beds by transplanting *Anadara* to atolls in southern Kiribati (Tabiteuea North in 1981 and 1984; Onotoa in 1984), although not recently evaluated, appear to have failed. Bolton (1981), in one of her evaluations of Tabiteuea Atoll for *te bun* transplant, noted the general scarcity of shellfish there and speculated that this may be due to unfavorable environmental conditions.

The location of the belt of atolls with dense *Anadara* corresponds to the zone of equatorial upwelling, both centered at 0-3°N latitude. This correlation strongly suggests that large *Anadara* beds develop only where abundant food supplies are available, as a result of high planktonic productivity resulting from upwelling-derived nutrient enrichment (Kimmerer and Walsh, 1981; Kimmerer, 1995).

Ecology

Anadara is most common on Tarawa in: 1) seagrass beds of the lagoonal sand flat; 2) a large shell bed on the lagoon slope at 1-8 m depths in the southeastern lagoon; and 3) several shallow (0-2 m) sandy shoals in the southeastern lagoon (Fig. 1).

Occasional *Anadara* are also encountered on deeper lagoon bottoms; however, these likely represent stragglers and appear not to constitute a significant resource. Abundance data and stock estimates of this and other shellfish on the sand flat and lagoon slope are presented in Paulay (2001).

Table 1 Abundance of *Anadara* from Majuro to South Tungaru

Atoll	***Anadara* abundance**	**Latitude**
Majuro	+	7°10'N
Butaritari	++	3°10'N
Marakei	+++	2°00'N
Abaiang	+++	1°50'N
Tarawa	+++	1°30'N
Maiana	+++	1°00'N
Abemama	+++	0°20'N
Aranuka	?	0°10'N
Nonouti	++	0°40'S
N Tabiteuea	-/+	1°10'S
Beru	?	1°20'S
S Tabiteuea	-/+	1°30'S
Onotoa	-/+	1°50'S

All islands in Tungaru except Makin, Kuria, Nikunau, Tamana, and Arorae (which all lack functional lagoons and thus appropriate habitats for *Anadara*) are listed together with Majuro of the neighboring Marshall Islands. Abundance is depicted as absent or very rare (-/+), rare (+), occasional (++), abundant (+++), or unknown (?).

Unlike some anadarine bivalves (e.g. *Anadara granosa* - Broom, 1985), *Anadara uropigimelana* remains byssate throughout life. All juveniles <15 mm in size we encountered were attached to rubble or adult shells (Fig. 3; see below). This habit likely limits the distribution of *Anadara* to sediments with a rubble component such as coral gravel or shell hash. All the large *te bun* beds on Tarawa occur in gravely sand. Similarly, the two best *te bun* beds on Maiana Atoll are uniquely characterized by the presence of both hard and soft substrata (Tebano, 1990).

Although humans are undoubtedly the most important predator on *te bun* today, removing much of the production of this species from South Tarawan waters (Paulay, 2001), several marine predators also take their toll. The presence of numerous freshly crunched *te bun* shells, especially on shoals, appears to be evidence of ray predation. Rays were commonly seen in the southeastern lagoon and were the only species observed in the lagoon that is known to produce such damage. *Anadara* of all sizes were seen crushed, as were shells of the much larger (up to 13+ cm) bivalve *Periglypta sowerbyi* (Deshayes, 1853). *Te bun* clearly do not have a size refuge from these predators.

Large piles of *Anadara* shells frequently are found adjacent to patch reefs along the outer margin of the sand flat and lagoon slope. Most of these shells are intact or have only small nicks taken out of them. No potential predators that could be responsible for these piles were seen near these patch reefs. These piles may be the result of the activities of potentially night-active octopus or fish.

Bonefish (*Albula glossodonta* (Forsskål, 1775)) are probably the most abundant molluscivorous fish in the lagoon (Beets, 2001). A study of bonefish gut contents revealed that *te bun* were a minor component of their diet, with only 4 shells seen in 111 (91 with contents) stomachs surveyed. All *te bun*, as well as other bivalve shells in bonefish stomachs, were small (<30 mm), indicating that only juveniles are vulnerable to bonefish predation (Beets, 2001).

Several species of naticid gastropods and the ranellid gastropod *Cymatium muricinum* (Röding, 1798) are important predators on bivalves in Tarawa. Both appear to prefer other bivalves than *Anadara*, although the *C. muricinum* has been observed feeding on *te bun* (Yamaguchi et al., n.d.). Both occur in moderate abundance on sand flats and are taken by shellfish gatherers. These gastropods are fairly small relative to *Anadara*, and the clam attains a refuge in size from them.

Reproductive biology

Tebano (1990, pers. obs.) found that *Anadara* on Tarawa reproduces year-round, spawning monthly around the full moon. A similar cycle of year-round spawning and one two-month-long gametogenic cycles were reported for *A. antiquata* in the Philippines (Toral-Barza and Gomez, 1985). In contrast, Baron (1992) found that "*A. scapha* (Linné)" (the identity of this species is dubious as Linné did not describe an *A. scapha*; it may represent *A. uropigimelana*) spawns only during the southern summer in New Caledonia. This difference could be attributable to the greater seasonality of New Caledonia (ca. 21°S) and/or to potential interspecific differences.

Tebano (1990) showed that gonadal development is first seen in *te bun* of a length of 27 mm, and mature gonads are first found in females of 38 mm length and in males of 42 mm length. In southwest New Caledonia, *A. "scapha"* was found with developing gonads of a length of 22 mm and first spawned at 30 mm. While we found *te bun* to reach a size of at least 73 mm, the New Caledonian form reaches a predicted maximum size (based on a von Bertalanffy equation) of 52 mm (Baron, 1994).

Tebano (1990) found that while the overall sex ratio of *te bun* among all samples was near 1:1, significantly biased sex ratios, ranging between 0.4-2.1, were observed in individual samples. No evidence for simultaneous hermaphroditism was found, and the males and females showed completely overlapping size distributions. Tebano (1990) suggested that *te bun* may exhibit some type of sequential hermaphroditism. Baron (1992) similarly found no evidence for simultaneous hermaphrodites in *A. "scapha"* in New Caledonia, but observed a male-biased sex ratio of 1.47. He also showed that small size classes were significantly male dominated while large size classes were female dominated, and proposed that the species may be a protandric hermaphrodite. Toral-Borza and Gomez (1985) also showed minor departures toward a male-biased sex ratio in *A. antiquata* in the Philippines.

Little is known about the larval biology of *Anadara s.s.* Yamaguchi et al. (n.d.) found some arcid larvae in lagoonal plankton samples on Tarawa. The life span of *Anadara uropigimelana* veligers is not known, but likely exceeds the lagoonal residence time of about one week (Chen et al., 1995), as a considerable pelagic period would be necessary to colonize Kiribati, especially since colonization must have occurred within the past 8000 years (see below).

Population dynamics - recruitment

Although *te bun* appear to spawn monthly, recruitment is episodic, and sizable recruitment events are uncommon. Juveniles are usually rare but can be locally abundant at certain times, indicating high spatio-temporal variability in recruitment. The majority of sites we sampled were dominated by one or a few striking size classes, presumably reflecting one or a few major past recruitment events that were responsible for each clam bed. Size-frequency distribution of *Anadara* samples differed among different sites within the lagoon, indicating that recruitment events were localized.

The rarity of new recruits was noted by Yamaguchi et al. (n.d.), who was unable to find any in the field but obtained some on spat collectors made of coconut husk. Our initial attempts to find juveniles also failed. These attempts included a survey of the sand-flat molluscan fauna that included sieving sediment from 72, 0.25 m^{-2} quadrats in *Anadara* habitat, and visual searches of rubble in many areas on the sand flat and on shoals. Later we observed small (9 mm mean, range of 5-25 mm) *Anadara* occasionally attached to the posterior third of the shells of adults in the dense lagoon slope *Anadara* bed (Fig. 3). In three samples, the average adult had 0.15 ± 0.08 juveniles attached (N=223 adults; s.d. among three samples). Although we examined numerous other potential substrata (dead *Anadara* and other shells, reef rubble) in the area and searched through large areas of sand (see Paulay, 2001), all juveniles encountered in the lagoon slope bed were attached to living adults. These beds have an abundance of adults and little rubble. The smallest juveniles were attached near the posterior margin of adults, with progressively larger ones found further down toward mid shell. At around 20 mm, size, juveniles took up a free-living existence (Fig. 3).

In contrast to the general rarity of juveniles and to their close association with adults only in the lagoon-slope *te bun* bed, we found abundant juveniles attached to reef rubble at Shoal 2 in June 1993 (Fig. 4). Adult clams were uncommon at this location and hosted only a few juveniles. No quantitative measures of population density were made, but juveniles occurred at estimated densities of tens to hundreds m^{-2}. These juveniles appear to represent a large recruitment event in the area (see below).

One or a few size classes tend to dominate among *Anadara* at any given location (Fig. 4, Table 2). Dominant size classes appear to represent particularly successful, localized, recruitment events. For example, two size classes, 10-20 mm and 20-30 mm, were particularly abundant during June-August, 1993. The distribution of these attests to the geographically patchy nature of each recruitment event: the first dominated the southeastern corner of the lagoon (sites S2, B) and the second was abundant off of Tangintebu (S1, S3, S4) (Fig. 1). The first event was particularly striking because of the great abundance of *te bun* it represented (see below). The growth rate of *Anadara* from this event was rapid, with clams nearly doubling in length between June, 1993 and February, 1994 (Fig. 5).

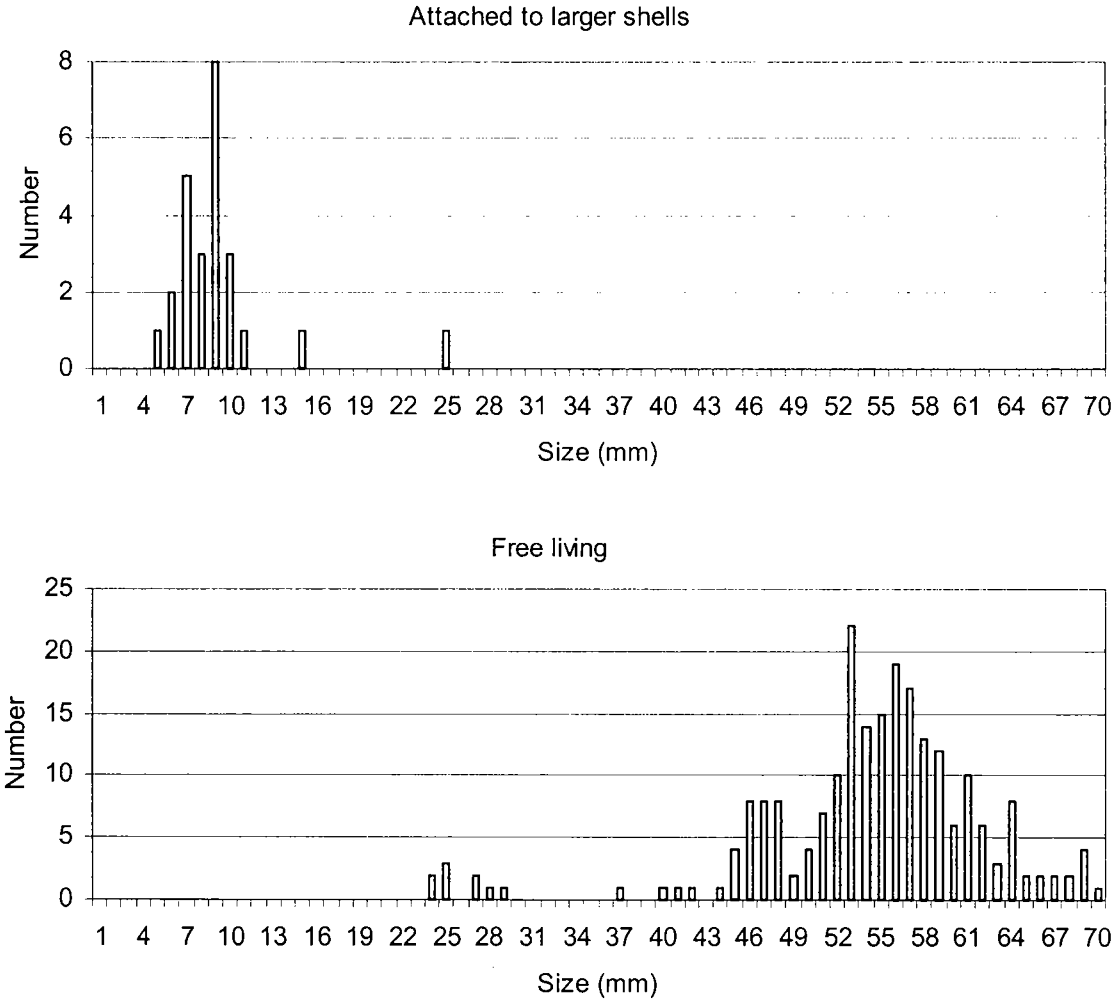

Figure 3. Size frequency distribution of free-living and attached (to larger conspecifics) *Anadara uropigimelana* in the Tangintebu-Bangantabure lagoon slope *te bun* bed (173°05.3'E; 1°22.2'N) in June 1993.

This recruitment event created a novel fishery in adjacent Bonriki. Until June 1993 the venerid clam *Gafrarium pectinatum* (Linné, 1758) was the main targeted species in the Bonriki-Temaiku area where, on the wide sand flat, it is particularly abundant (Paulay, 2001). *Anadara* did not occur in catches from this area at that time. Interviews with resident gatherers established that *te bun* were unknown in the Bonriki-Temaiku area during the past 20 years even though there is a well developed seagrass bed on the lagoonal margin of the sand flat that appeared to be reasonable *Anadara* habitat. By February 1994, when the new recruits increased to a harvestable size (Fig. 5), gathering activity shifted almost completely from *Gafrarium* to *Anadara,* a preferred food because of its larger size as well as its great abundance at the time. This shift also involved a move by gatherers from mid-sand flat *Gafrarium* habitat to the

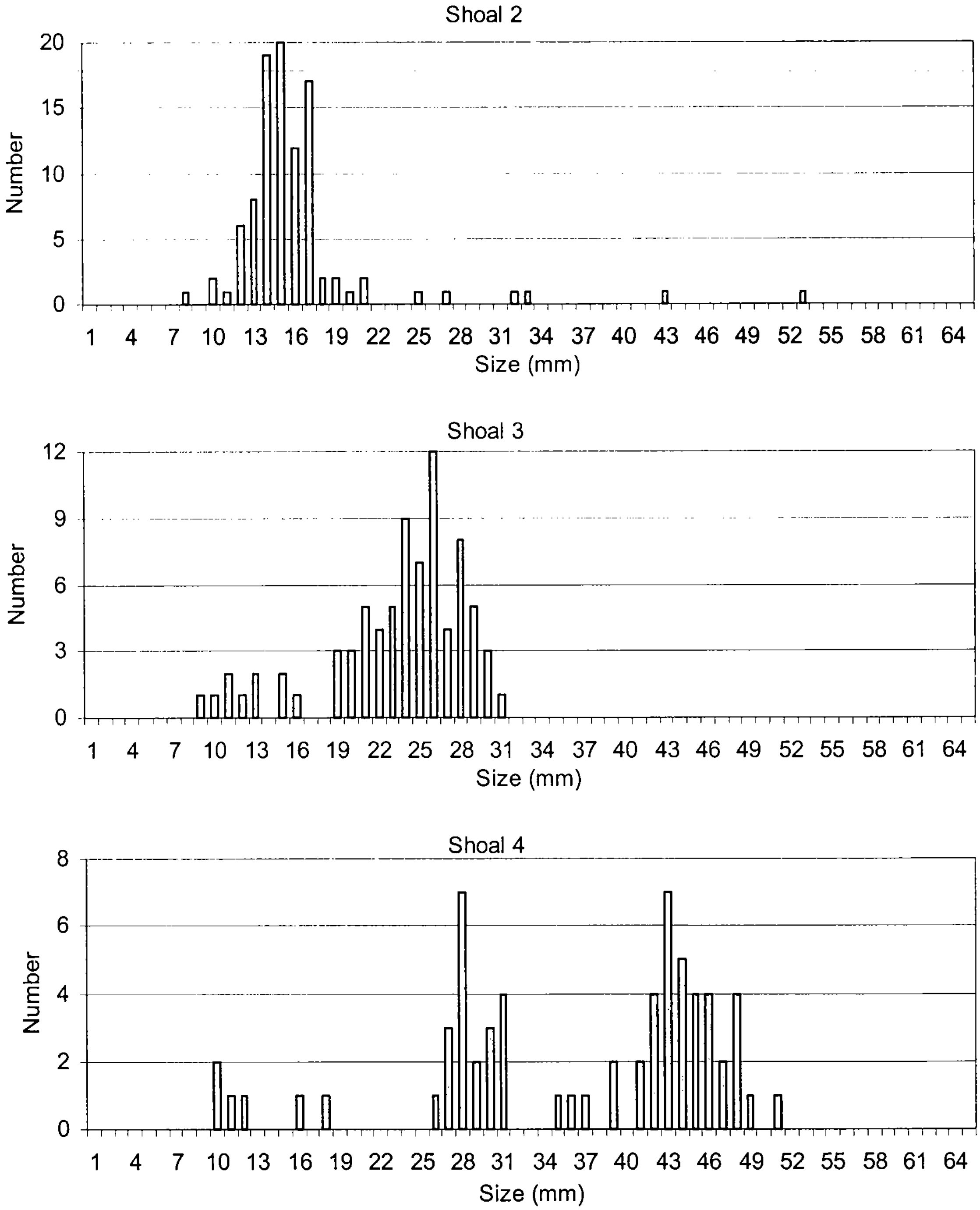

Figure 4. Examples of size frequency distribution of *Anadara* at different sites. Based on quadrat samples at shoals 2, 3, 4 (see Figure 1 for locations).

seagrass beds lying on the lagoonal edge of the sand flat adjacent to Bonriki village where the *Anadara* recruitment was localized (Fig. 1). Interviews established that this shift in harvesting focus took place in the second half of 1993. An average of 30-40 people harvested *Anadara* in the Bonriki bed during good low tides in February 1994 (data from gatherer study outlined by Paulay, 2001) with mean catch weight of 13 kg compared to overall South Tarawa-wide mean shellfish catch weight of 8 kg (Paulay, 2001). The harvested *te bun* were 26+/-5 mm (N=100) (Fig. 6), in the same size range as on Shoal 2 (29+/-6 mm) at that time. In contrast, *te bun* caught at the same time west of Bikenibeu were considerably larger (44+/-8 mm; N=80) with <30 mm shells virtually absent (Fig. 6).

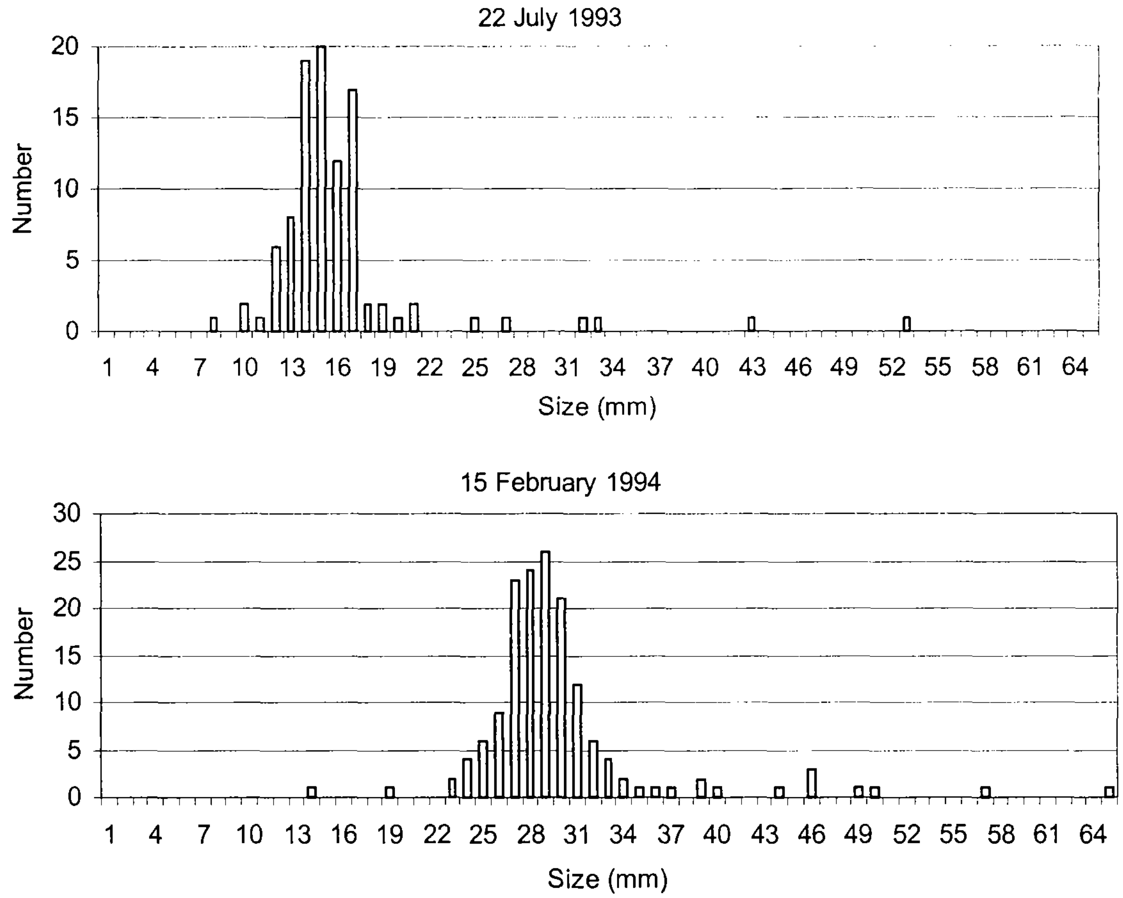

Figure 5. Growth of *Anadara* at Shoal 2 between 22 July 1993 and 15 February 1994.

Table 2 Dominant size classes of *Anadara* at different sites

Site	10-20mm	20-30mm	30-40mm	40-50mm	>50mm
S5	++	++	++	+	+
T4	+	+++	+	-	-
S3	+	+++	+	-	-
T6	+	+	++	+	++
S1	+	+++	-	-	-
S4	+	++	+	+++	+
T7	+	+	+	+	+++
S2	+++	+	+	+	+

Abundance data for major size classes at 9 sites, arranged east to west (Fig. 1). Size class recorded as absent (-), constituting 1-19% (+), 20-49% (++) or 50+% (+++) of individuals. Sites with T numbers correspond to transects on lagoon slope (see Paulay, 2001); sites with S numbers correspond to shoals. All sampled in June-August 1993.

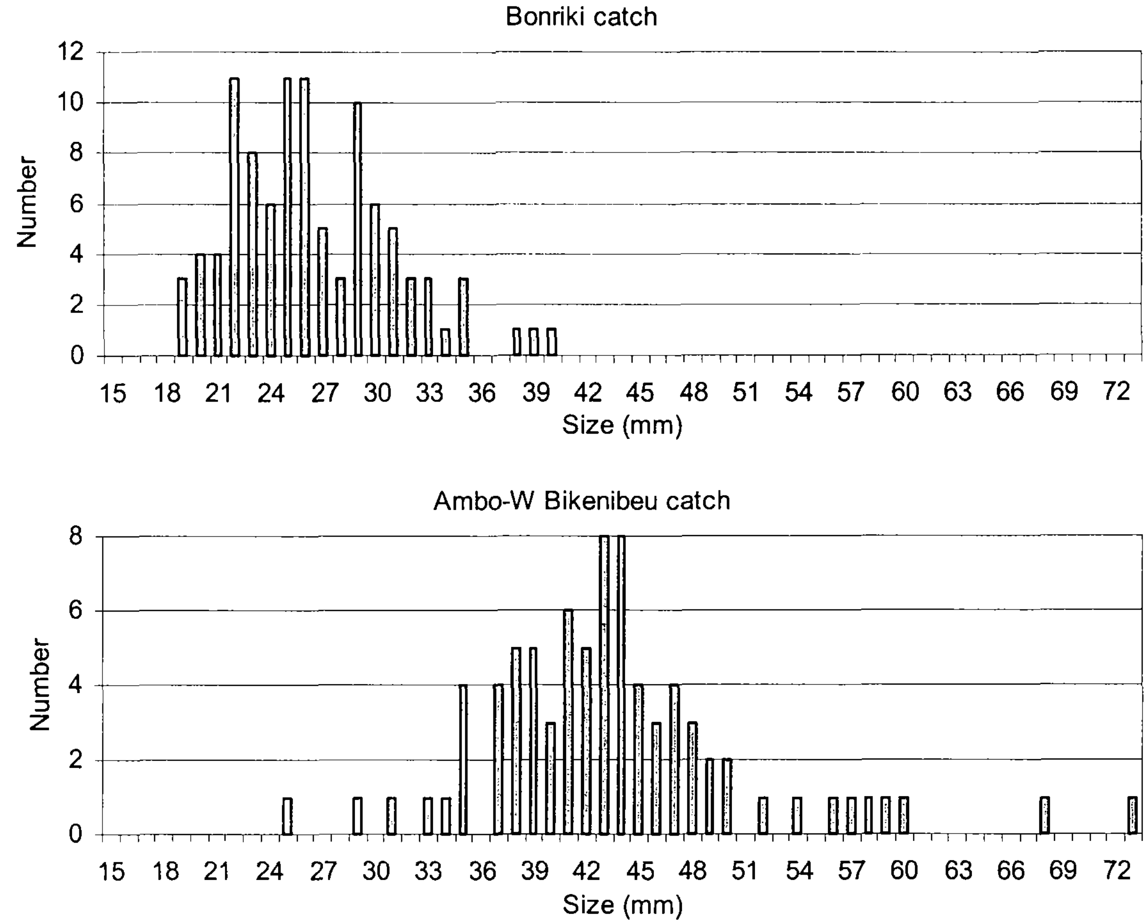

Figure 6. Size frequency distribution of *Anadara* in catches at Bonriki and at localities west of Bikenibeu. Based on N=20 clams sampled per catch in 5 and 4 catches respectively.

Population dynamics - persistence of beds

The observed spatial and temporal variability in recruitment suggests that recruitment limitation is important in structuring *Anadara* populations and could lead to fluctuations in resource abundance through time. The latter is supported by information gathered from older informants who indicate that *te bun* has undergone marked fluctuations in abundance over the past 50 years on several islands. The importance of variation in recruitment in structuring marine populations is increasingly recognized (Doherty and Fowler, 1994; Hughes et al., 1999), and can in extreme cases (as in the crown of thorns sea star, *Acanthaster planci*) lead to outbreak and crash cycles (Birkeland and Lucas, 1990).

The elders on both Abemama and Maiana Atolls recalled that *te bun* fluctuated considerably in abundance over past decades. During the 1920's *Anadara* was claimed to have "disappeared", while during the 1930's and 1940's it came back and was very abundant. On Abemama *te bun* was again scarce during World War II, but became abundant again later. In the 1980's *te bun* was very scarce in most villages of Abemama, and was also rare on Maiana. Today *Anadara* has "disappeared" from Maiana but is still abundant on Abemama. In contrast *te bun* appears to have been fairly stable on Abaiang Atoll through living memory.

Te bun has been known in South Tarawa through living memory, although it is said to have become much more abundant in recent decades. *Te bun* boomed in abundance in South Tarawa after World War II, although it is also reported to have declined slightly in recent years (Johannes, 1992). *Te bun* is reported to be a recent colonist to North Tarawa, however, having appeared there only after World War II in the seagrass beds opposite the villages Buariki and Tearinibai. The massive recruitment of *Anadara* in the Bonriki area in 1993 documented above appears to be a new event because none of the people interviewed had seen the shellfish in abundance in that area in the past. It remains to be seen whether this represents an isolated or recurrent event and thus whether a *te bun* bed will become established in the area.

In addition to the apparently important role of recruitment variation in regulating *Anadara* abundance, environmental changes also can have large-scale effects on settled *Anadara*. Thus, Paulay (2001) found a major increase in the size of seagrass beds off South Tarawa following World War II, perhaps as a result of anthropogenic nutrient input from adjacent islets. This increase in seagrass beds may be partly responsible for the contemporaneous expansion of *te bun* resources in the area noted by Johannes (1992). On Marakei Atoll the formerly abundant *Anadara* is now disappearing. This may be attributable to the general closure of this atoll by the construction of a causeway across the main western passage of its highly enclosed lagoon.

The apparently large population fluctuations, whether due to recruitment dynamics or benthic processes, indicate that *Anadara* may be a somewhat unreliable resource in the long run. This hypothesis is supported by records of Holocene changes in *Anadara* abundance on other Pacific islands. In the Mariana Islands, *Anadara antiquata* was an important component of shell middens in southwest Saipan and northern Guam during the Pre-Latte period (ca. 3500-2000 BP) but disappeared from middens thereafter (Amesbury, 1999). Recent searches in northern Guam have revealed no evidence for the occurrence of *Anadara* in the area today (G. Paulay, pers. obs.). In contrast, in middens from southern Guam, *Anadara* gained prominence only during the past 500 years (Amesbury, 1999). Similarly, *Anadara antiquata* occurs in the Holocene of Aitutaki (Cook Islands), where (as well as elsewhere in the southern Cooks) intensive surveys failed to reveal any living individuals today (Paulay, 1996). *Anadara antiquata* also has undergone local extinction in the Hawaiian Islands since the late Pleistocene, and *Anadara uropigimelana* has disappeared from Niue since the Pliocene, albeit as a result of tectonic uplift at the latter (Paulay, 1996).

ACKNOWLEDGMENTS

This study would not have been possible without the able field assistance of Andy Teem and Nabuaka Tekinano, as well as the general help of Koin Etuati, Kamerea Tekawa and Kabiri Itaaka. We thank Being Yeeting for help with logistics on Tarawa and for their help in both the field and at the station. Wim Kimmerer and Bud Abbott arranged the large-scale logistics of the project and helped with its planning and implementation in numerous ways. We thank Jim Beets and an anonymous reviewer for constructive comments, and Liath Appleton for help with figure preparation. Support by U.S. Agency for International Development (USAID) is gratefully acknowledged. This is contribution #451 of the University of Guam Marine Laboratory.

REFERENCES

Amesbury, J. R. 1999. Changes in species composition of archaeological marine shell assemblages in Guam. *Micronesica* 31:347-366.

Baron, J. 1992. Reproductive cycles of the bivalve molluscs *Atactodea striata* (Gmelin), *Gafrarium tumidum* Röding and *Anadara scapha* (L.) in New Caledonia. *Australian Journal of Marine and Freshwater Research* 43:393-402.

Baron, J. 1994. Growth of *Gafrarium tumidum* Roding and *Anadara scapha* (L.) On the south-west coast of New Caledonia. *Proceedings of the Seventh International Coral Symposium, Guam* 2:816- 820.

Baron, J. and J. Clavier. 1992. Estimation of soft bottom intertidal bivalve stocks on the south-west coast of New limitations of Caledonia. *Aquatic Living Resources* 5:99-105.

Beets, J. 2001. Finfish resources in Tarawa Lagoon: documentation of population declines. *Atoll Research Bulletin*, this volume

Birkeland, C., and J. S. Lucas. 1990. Acanthaster planci: *major management problem of coral reefs*. 257pp. Boca Raton, FL: CRC Press.

Bolton, L. 1981. The introduction of *Anadara maculosa* ('te bun') to Tabiteuea North lagoon. Atoll Research and Development Unit, University of the South Pacific, Tarawa, Report TB/3/81

Broom, M. J. 1985. The biology and culture of marine bivalve molluscs of the genus *Anadara*. In: ICLARM Studies and Reviews. International Center for Living Aquatic Resources Management, Manila, Volume 12

Chen, C. W.; Leva, D.; Kimmerer, W. 1995. Circulation and the value of passage channels to water quality of Tarawa lagoon. In: Abbott, R. R. and Garcia, J. (eds.). Management plan for Tarawa Lagoon, Republic of Kiribati, Volume III. Management Plan. Technical Report of BioSystems Analysis Inc., Tiburon CA

Doherty, P., and T. Fowler. 1994. An empirical test of recruitment limitation in a coral reef fish. *Science* 263: 935-39.

Hughes, T. P., A. H. Baird, E. A. Dinsdale, N. A. Moltschaniwskyj, M. S. Pratchett, J. E. Tanner, and B. L. Willis. 1999. Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397: 59-63.

Johannes, R. E. 1992. Intensive interviews. In: Management strategies for Tarawa lagoon, Kiribati. Trip Report No. 2 BioSystems Analysis, Inc., Tiburon, CA

Kilburn, R. N. 1983. The Recent Arcidae (Mollusca: Bivalvia) of southern Africa and Mozambique. *Annals of the Natal Museum* 25: 511-548.

Kimmerer, W. 1995. Water chemistry and lower trophic levels. In: Abbott, R. R. and Garcia, J. (eds.). Management plan for Tarawa Lagoon, Republic of Kiribati, Volume III. Management Plan. Technical Report of BioSystems Analysis Inc., Tiburon CA

Kimmerer, W. J. and T. W. Walsh. 1981. Tarawa atoll lagoon: circulation, nutrient fluxes, and the impact of human waste. *Micronesica* 17:161-179.

Paulay, G. 1990. Effects of Late Cenozoic sea-level fluctuations on the bivalve faunas of tropical oceanic islands. *Paleobiology* 16:415-434.

Paulay, G. 1996. Dynamic clams: historical changes in the bivalve fauna of Pacific islands as a result of sea level fluctuations. *American Malacological Bulletin* 12:45-57.

Paulay, G. 1997. Productivity plays a major role in determining atoll life and form: Tarawa, Kiribati. *Proceedings of the 8th International Coral Reef Symposium, Panama* 1: 483-88.

Paulay, 2001. Benthic ecology and biota of Tarawa Atoll lagoon: influence of equatorial upwelling, circulation, and human harvest. *Atoll Research Bulletin*, this volume

Phillips, G. 1995. A survey of South Tarawa residents and their perceptions of environmental problems in Tarawa lagoon. In: Abbott, R. R. and Garcia, J. (eds.). Management plan for Tarawa Lagoon, Republic of Kiribati, Volume III. Management Plan. Technical Report of BioSystems Analysis Inc., Tiburon CA

Spennemann, D. H. R. 1987. Availability of shellfish resources on prehistoric Tongatapu: effects of human predation and changing environment. *Archaeology in Oceania* 22:81-96.

Squires, H. J., B. Carlson, T. P. Ritchie and N. Gundermann. 1973. Shellfish on nearshore fishing grounds at Wailoaloa Beach, Nadi, 1973. *Fiji Agricultural Journal* 35:71-74.

Tebano, T. 1990. Some aspects of population biology and ecology of the cockle *Anadara maculosa* in the Gilbert Islands, Republic of Kiribati. M.Sc. Thesis, James Cook University, Townsville.

Toral-Barza, L. and E. D. Gomez. 1985. Reproductive cycle of the cockle *Anadara antiquata* L., in Calatagan, Batangas, Philippines. *Journal of Coastal Research* 1:241-245.

Yamaguchi, M., B. Yeeting, K. Toyama, T. Tekinaiti and T. Beiatau. n.d. Report on a preliminary study on molluscan resources in Tarawa lagoon, with special reference to te bun (*Anadara maculosa*). Unpublished MS on file at Atoll Research Unit, University of South Pacific, Tarawa. 18pp.