

Mollusk Habitats and Fisheries in Kiribati: An Assessment from the Gilbert Islands¹

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Abstract: Biological and ecological attributes of 24 species of edible bivalves and gastropods from the Gilbert Islands Group, Kiribati, Micronesia, were assessed for their resilience by examining size at maturity, intertidal burying, adjacent subtidal populations, benthic mobility, and larval type. Foraging for mollusks is largely confined to the intertidal and shallow subtidal regions, although modern diving gear and outboard motors now provide human foragers access to offshore resources. Changes brought about by human demographic pressures have resulted in overexploitation of a number of molluscan resources. It is suggested that the sustainable use of invertebrates and other marine species for food and nonfood purposes in Kiribati rests on a remodeled form of marine tenure.

ATOLLS PRESENT A variety of marine environments and molluscan resources that have provided subsistence living to generations of Pacific islanders (Tebano et al. 1993, Taniera 1994). Kiribati (Figure 1) is but one of more than 20 nations in the Pacific, each of which possessed a rich inshore fisheries tradition and lore. In recent years, however, traditional ecological knowledge (TEK) has suffered the inevitable decline that characterizes similar bodies of knowledge throughout most of Oceania. High human population density, urban drift, more efficient extractive technologies, and expanding market opportunities all have inevitably affected the ocean resources of these islands. In this study, I examined the prey biology and ecology of mollusk fisheries in Kiribati, Gilbert Islands, looking at factors distinguishing vulnerable

from resilient resources, and their effect on subsistence.

Can traditional ecological knowledge be wedded with modern technology to revive the fisheries? Because the thrust of this paper is limited to prey biology and ecology in the context of mollusk fisheries, details of analytic methodology related to foraging efficiency are not discussed here, but can be found in Thomas (1999).

Data on molluscan resources of the Gilbert Islands date back to the 1950s when Banner and Randall (1952) described the invertebrates of Onotoa Atoll, but identifications were poor and there were few detailed descriptions of exploitive strategies. A major interdisciplinary environmental survey on the main atoll of Tarawa, Republic of Kiribati (Abbott and Garcia 1995), expanded species identification and habitat description, and provided an assessment of the impact of human activities (Figure 2). The Tarawa Lagoon Project of 1992–1994 (Paulay 1995) is a major study of the lagoon, and data from that project are included in this study.

MATERIALS AND METHODS

Several communities engaged in subsistence and commercial exploitation of mollusks were investigated intermittently between 1993 and 1998. Research focused on four atolls in the central Gilberts: Abaiang, Tarawa (both urbanized and rural sectors), Maiana, and Abe-

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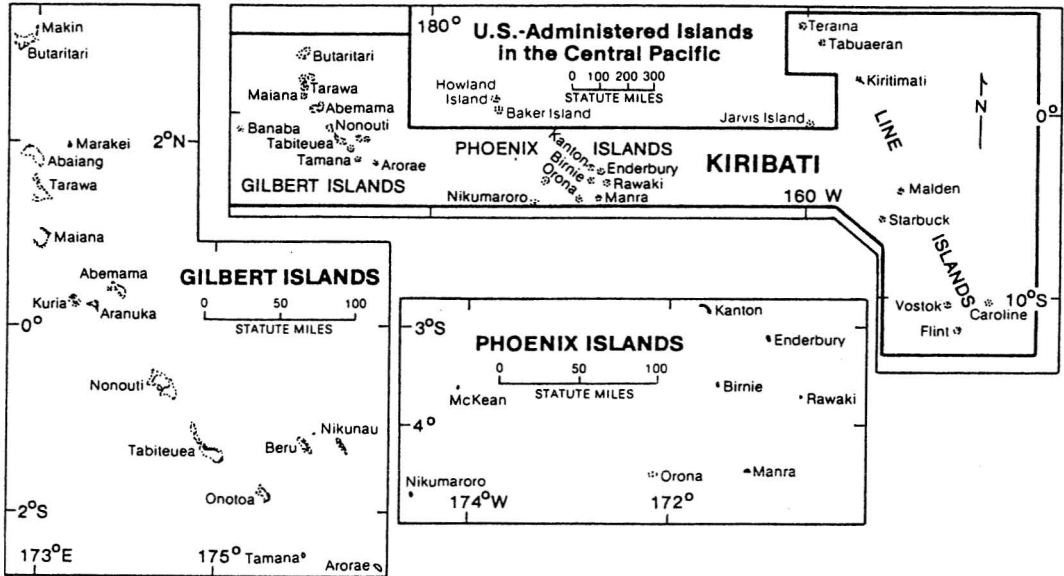


FIGURE 1. The Republic of Kiribati (modified from Motteler 1986:16; reprinted with permission from Bishop Museum Press, Honolulu, Hawai'i).

mama, and one atoll in the Southern Group, Tabiteuea North (Thomas 1999). Data on various aspects of mollusk gathering were obtained by participant observation, interviews, and from the Shellfish Gatherer Survey (SGS) of the Tarawa Lagoon Project (TLP), in cooperation with BioSystems, Inc., of Santa Cruz, California.

I accompanied foragers, both individuals and groups, on 73 foraging trips covering 69 days, for a total of 139.63 hr of direct observation (286.92 forager-hours). Mean group size was 2.6 foragers ($SD = 0.9$, $n = 146$). Fifty-nine different individuals took part in these activities. When it was not possible to record foraging activities directly, the relevant information was elicited via interviews. A total of 65 foraging trips was recorded over a period of 51 days, for an estimated total of 88.5 hr of foraging effort (161 forager-hours). Mean group size was 3.1 foragers ($SD = 0.7$, $n = 148$). A total of 19 different individuals was interviewed.

Information was also derived from data sheets made available by personnel of the TLP. These data originated from landings

along the southern portion of Tarawa Atoll, with samples taken between December 1992 and February 1994. This information greatly expanded the sample size of foraging events, with 83 foraging trips covering 26 days and approximately 191 hr of foraging time (257 forager-hours). Mean group size was 1.3 foragers ($SD = 0.7$, $n = 112$).

Prey type identifications and basic habitat information are based on Cernohorsky (1971, 1972), Eisenberg (1981), Abbott and Dance (1982), Paulay (1995), and personal observations. For each prey type, five factors were examined to assist in distinguishing vulnerable from resilient resources: (1) size at maturity; (2) intertidal burying; (3) adjacent subtidal populations; (4) benthic mobility; and (5) larval type (see Catterall and Poiner 1987). In a number of cases, the description of relevant properties was limited, reflecting gaps in the data.

Atoll Zonation and Molluscan Patch Types

From windward to leeward (Figure 3), the basic zones and molluscan patch types char-

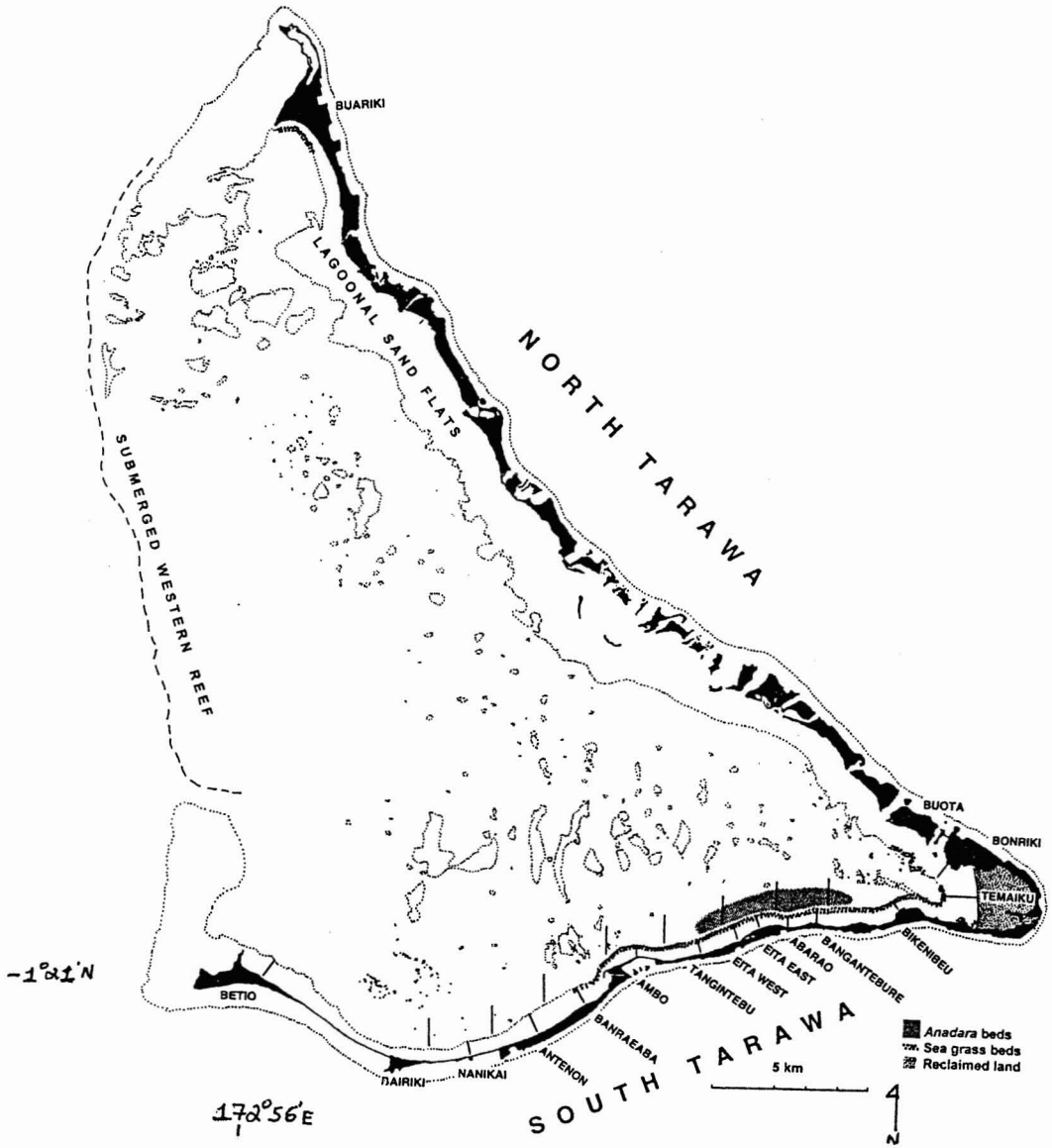


FIGURE 2. Tarawa Atoll (modified from Paulay 1997: fig. 1; reprinted with permission from Gustav Paulay).

acteristic of the open atolls of the Gilbert Islands are the: (1) reef slope; (2) submarine terrace; (3) reef front; (4) reef margin; (5) moat; (6) reef crest; (7) reef flat; (8) shoreline; (9) lagoon reef flat including mangrove, sand flats, and sea grass beds; (10) lagoon slope and floor; and (11) leeward reef.

THE SEAWARD REEF: The seaward reef slope descends steeply from the upper limit of vigorous hermatypic corals at a depth of about 18 m to the deepest seaward portion of the reef between 4000 and 6000 m. In the Gilberts, little is known of the biota below 40 m, but mollusks commonly found in the

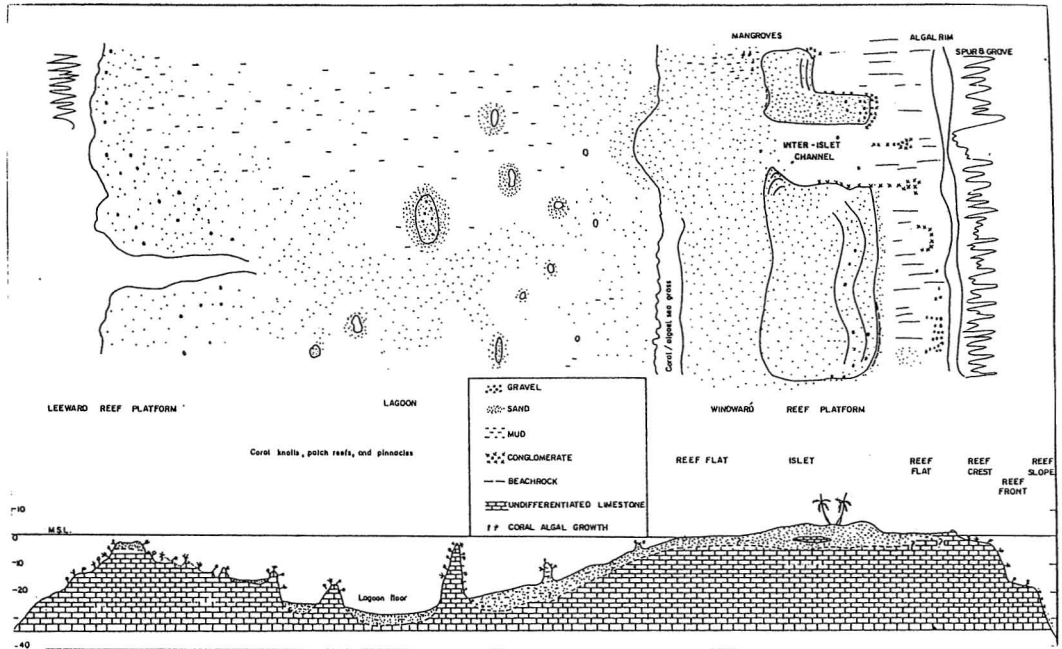


FIGURE 3. Schematic diagram of atoll features of the Gilbert Islands (modified from Richmond 1993:17, fig. 5; reprinted with permission from the South Pacific Applied Geoscience Commission [SOPAC]).

upper reaches of this zone include *Pinctada* and *Trochus* (Wells 1957), which also occur on the submarine terraces between depths of 15 and 18 m. The dominant mollusks on the reef front, the shoreward face of the seaward reef slope where coral growth is sparse and heavy surf dominates, are gastropods such as *Patella* and *Trochus* (Demond 1957). The seaward reef margin, distinguished by spur-and-groove formations, which disperse and channel ocean water, supports compact and encrusting corals and coralline algae such as *Porolithon*. Mollusks found in this zone include *Trochus*, *Turbo*, *Cypraea*, and *Drupa* (Wells 1957, Zann 1982). Shoreward of the seaward reef margin are moats, areas of shallow water normally awash even at extreme low tide. In many respects, moats resemble lagoon habitats, except for the hard bottom of coralline rock or gravel. Thick-branching *Acropora* and *Heliopora* are the dominant corals, and the mollusks include *Cypraea*, *Conus*, *Lambis*, *Hippopus hippopus*, and *Tridacna gigas* in the deeper sections (Wells 1957). The reef crest, a high-energy environment,

demarcates the seaward limit of the reef flat; it supports the gastropod *Turbo setosus*. The reef flat itself is commonly exposed or barely awash at lowest tide. It consists of a truncated floor zoned by the tides, which effect varying degrees of exposure and temperature between seaward edge and inshore margin. The surface of the reef flat supports *Cypraea*, *Thais*, *Trochus*, *Turbo*, and other species of gastropods adapted primarily as crab predators and to the force of waves (Banner and Randall 1952).

The shoreline of islets (motus) on both lagoon and ocean sides consists of both cemented and uncemented topographic features. Beachrock, lithified beach sand and coral debris, and conglomerates, cemented storm deposits between 1 and 2 m above low-tide level, are occupied by dense concentrations of the gastropod *Nerita plicata*, adapted to withstand heat and desiccation, as well as rain (Cloud 1952). Moderately to poorly sorted medium sand, gravel, and cobbles that rise with a relatively sharp change in slope above the reef flat harbor the bivalves

Asaphis violascens and the small beach clam *Atactodea striata*. The latter is also locally abundant in other intertidal sandy areas.

THE LAGOON: Lagoon beaches tend to be well to moderately sorted, from fine sand to gravel; highest elevation is generally less than 1 m above the highest tide; and sand spits are a common feature, especially near interislet channels and as lagoon-directed seaward-produced growth at the ends of the atolls. *Asaphis violascens* and *Atactodea striata* are common in this zone (Paulay 1995).

The lagoon reef flat is typically a depositional surface built up by ocean-to-lagoon sediment transport. Sediments tend to be poorly sorted with some silt. The reef flats are generally better developed along the sections facing the prevailing winds than elsewhere and are zoned as are the windward reef flats. The reef flat is primarily intertidal, grading into subtidal zones toward the center of the lagoon. Except during periods of westerly storms, waters are generally calm. Mangroves, mainly *Rhizophora mucronata*, may rim the shoreline. The sediments associated with mangroves are characteristically soft, of sand mixed with rich organic matter. Fiddler crabs, *Uca* sp., and stomatopod burrows occur in transitional areas between the mangrove sediments and the sand flats. The bivalve *Gafrarium pectinatum* is occasionally found in the mangroves.

Sand flats are the most extensive habitat on the lagoon reef flat. The fauna varies with depth of the water, size of sand particles, amount of wave action, and depth of the sand. This habitat supports the economically important *Anadara uropygmelana*, *Strombus lubuanus*, and *Gafrarium pectinatum* (Paulay 1995). The low intertidal and subtidal regions of the lagoon border may support extensive beds of *Thalassia hemprichii* that stabilize and bind fine sand and silt rich in organic matter. The sea grass beds are productive grounds for *Anadara uropygmelana*, *Trachycardium angulatum*, *Gafrarium pectinatum*, *Timoclea marica*, *Strombus lubuanus*, and other mollusks (Paulay 1995).

Atoll lagoons in the Gilberts encompass a much larger area than the landmass. They vary from an almost enclosed lagoon at Marakei to poorly defined shallow expanses

at Nonouti and Tabiteuea. The deepest lagoon, at Butaritari, at 33 m is shallower than atoll lagoons in the Marshalls and Tuvalu. Deep reef passes are restricted to leeward lagoon margins. There is an increase in live coral coverage and decrease in sediment coverage toward the leeward margin. The lagoon slope, predominantly covered with sand or coral rubble, begins at the deepest edge of the sea grass bed, approximately 0.5 m deep at low tide. It slopes gently to depths of 8–10 m at 1 km from the sea grass margin, if present. This area supports scattered colonies or clumps of primarily *Porites* spp. and *Pocillopora damicornis* in South Tarawa. Mollusks such as *Anadara uropygmelana* and psammophilic crustaceans and echinoids predominate (Wells 1957, Paulay 1995) on fringing or patch reefs often dominated by *Acropora* on the lagoonal slope in North Tarawa.

The lagoon floor is the more or less level bottom of a lagoon. Sandbars, pinnacles, coral knolls, and patch reefs (dead and living) present sharp irregularities in the bottom. Lagoon depth, sedimentation rates, and other physical factors affect the growth of coral and thus species density and diversity. Mollusks are uncommon and constitute only a small fraction of the biomass on Tarawa. The leeward reef platform is characterized by irregular outer reefs and few or no islets. Leeward reefs are commonly submerged over most of their area, even at low tide, and show relatively vigorous coral growth. This zone supports *Lambis* and *Tridacna*. The seaward slope is generally much steeper than on windward reefs. As with the seaward (windward) reef slope and submarine terrace, *Trochus* and *Pinctada* may be abundant (Wells 1957).

TIDES AND CURRENTS: The greatest tidal fluctuations (spring tides) occur on the days of full and new moons; the smallest fluctuations (neap tides) are about halfway between spring tides, during the first and last quarters. In Tarawa Lagoon, semidiurnal tides have a mean amplitude of 1.5 m (neap range, 1.2 m; spring range, 1.8 m) (Gillie 1993). Fluctuations in sea level (on the order of 10–20 cm) follow seasonal changes in the location and strength of the trade winds. During the El Niño event in 1982–1983, the monthly mean

sea level was 28 cm above the long-term mean in 1982, but 21 cm below mean in late 1983. Repeated cycles of submergence and exposure and variation along these lines as a result of lunar periodicity make the intertidal a zone of high environmental stress.

Foraging

The indigenous Micronesian population considers many species of mollusks edible, but only a handful appear to be specifically targeted. Only 24 of the perhaps 1000 or more species that may occur in the Gilbert Islands (see Kay and Johnson [1987] for the numbers estimated from the Marshall Islands) composed the major "crop" in this study.

A foraging bout usually takes place within a single patch type, for example, a sand flat, sea grass bed, or nearshore biotope. Most households on Tarawa and other atolls are concentrated on the lagoon side of the motu and harvest mollusks and other resources from this habitat. Where sea grass beds occur, they are the focus of the most intensive gathering pressure (Paulay 1995). Women and children concentrate on resources in the intertidal and shallow subtidal areas where they can easily located telltale marks of their prey. Offshore diving is an activity carried out by male divers only. Limited ocean-side gathering does take place, however.

The higher in-patch returns offered by present-day lagoons compared with ocean patches in general seem to provide a likely explanation for the overwhelming importance of lagoonal gathering. Although foragers are quite willing to walk relatively long distances on the exposed intertidal lagoon flat (often in excess of overland distances to the ocean side), they also have more opportunities to increase their net energy acquisition rate across the various lagoon patches as the tide comes in and they are compelled to move closer to shore to the less-productive patches (but still more productive relative to the intertidal ocean patches).

RESULTS

The Mollusk Harvest

Twenty-four species of mollusks are the principal objects of foraging in the Gilbert Islands, with three species composing the bulk of the harvests. The relative dietary contributions of lagoonal shellfish from the intertidal beach to the lagoon slope on South Tarawa, derived from the SGS, are listed in Table 1. Thomas (1999) converted gross weights into edible meat weights using ratios presented. Protein and energy were calculated by multiplying the values per 100 g, illustrated in Thomas (1999) by the total weight of the harvested mollusks (Table 1).

TABLE 1

Relative Dietary Contribution of Mollusks during 83 Lagoonal Gathering Trips on South Tarawa (in Rank Order According to Edible Meat)

Species	No. of trips	Edible meat (kg)	Protein (kg)	Kcal
<i>Strombus l.</i>	59	93.89	18.31	79,807
<i>Anadara</i>	51	61.73	7.35	34,569
<i>Gafrarium</i>	42	5.13	0.68	3,748
<i>Asaphis</i>	5	1.00	0.08	393
<i>Atactodea</i>	3	0.66	0.10	498
<i>Quidnipagus</i>	2	0.62	0.04	255
<i>Trachycardium</i>	11	0.40	0.04	186
<i>Strombus v.</i>	5	0.07	0.01	48
<i>Cymatium</i>	15	0.06	0.01	56
Other	12	0.05	—	—
<i>Spondylus</i>	2	0.03	0.003	15
<i>Timoclea</i>	1	0.004	0.001	3
<i>Pitar</i>	2	0.004	0.001	3

Strombus lubuanus Linnaeus, 1758. The strombid, te nouo, is common throughout much of the low intertidal and shallow subtidal areas of Tarawa Lagoon. It also occurs on sandbars with mixed sand and coral rubble that rise to within 0–2 m below the surface. Like other strombids, te nouo is an herbivore and feeds on algae attached to hard substrata (Abbott 1960). It often occurs in large colonies. Maturity is reached within 2 yr after settlement, at which time shell length stabilizes at 40–60 mm, and the shell lip thickens. Adults are distinguished from juveniles by a distinct stromboid (anterior) and posterior notch (Poiner and Catterall 1988). Average edible weight is estimated at 2 g.

Adults are usually epibenthic; juveniles tend to be buried in sediment. However, up to 30% of adults at Heron Island, Great Barrier Reef, were also buried, with an increase in this behavior during periods of inclement weather (Catterall and Poiner 1987, Poiner and Catterall 1988). Large numbers of mature individuals occur in deep water, with migration to shallower depths related to breeding. Like other strombids, te nouo can rapidly migrate from subtidal to intertidal areas by means of its powerful foot. In southern Papua New Guinea and eastern Australia, this strombid breeds from August to March and deposits up to 200,000 eggs. The planktonic larval stage may last between 2 and 3 weeks (Poiner and Catterall 1988).

Commercial exploitation occurs on Tarawa, but at a smaller scale than that of the arcid te bun, *Anadara uropygmelana*. Te nouo is gathered by visually searching for exposed individuals, making no distinction between large and small shells or thin- and thick-lipped shells. The annual harvest is estimated at 400 t (Paulay 1995). Total edible weight stands at 85.2 t, with 16.61 t of protein, and over 72 million kcal. Like most gastropods, te nouo are boiled in large metal pots over an open fire to facilitate meat extraction. The large, pointed operculum allows for relatively easy extraction with the fingers, whereas other gastropods usually require the use of a twig or metal pin. In the absence of stone, empty shells are occasionally utilized in earth ovens to heat up certain foods.

Anadara uropygmelana (Bory de Saint-Vincent, 1824). This arcid, te bun, is the most often-targeted mollusk in the central Gilberts, notably on South Tarawa where it occurs in low intertidal and subtidal regions of the lagoon (Figure 4). Unlike other anadarine bivalves, *A. uropygmelana* is attached to both hard and soft substrata by a slender byssus, even in its adult stage, although byssal threads were often lacking among te bun examined by Tebano (1990). Byssal attachment may be crucial in the early stages of its life history, with the root system of *Thalassia hemprichii* appearing to provide suitable surface. Individuals from depths of 2 to 8 m tend to be larger than those in the intertidal and are abundant in habitats with fine, soft substratum. Te bun reaches maturity at 38 mm in females and 42 mm in males (Tebano and Paulay 1995). Reports on traditional gathering practices from various geographical areas describe minimum shellfish length collected as 20–30 mm (Catterall and Poiner 1987). For South Tarawa the value is closer to 10 mm (Paulay 1995). Te bun yields about 4 g of edible meat in the lagoon reef flat, with a mean length of 45 mm, and 8 g offshore for an average length of about 55 mm.

These bivalves live half buried in sea grass beds where young individuals may escape detection in thick undergrowth. Like most bivalves, te bun is sedentary in its adult stage; consequently, replenishment of heavily exploited intertidal areas by reproductive individuals from the subtidal regions cannot take place. Little is known about larval biology or recruitment in this species. Tebano (1990) suggested that spawning may be continuous, with peaks during full moon. However, there is high spatiotemporal variability in recruitment. *Thalassia* may be important in larval settlement and development by providing a refuge from predation and acting as a buffer against wave action and currents, preventing settled recruits from being swept away.

The bivalves are located in the intertidal zone by a telltale slit in the sand marking their presence. Offshore diving for te bun is confined to Tarawa. There are reports from South Tarawa of te bun artificially buried in



FIGURE 4. *Anadara* midden, Tebanga Village, Maiana (photo by F. Thomas).

sand and surrounded by large rectangular coral enclosures near the lagoon shore, similar to those of the tridacnid gardens (Zann 1985).

Yearly harvest of te bun gathered offshore from Tarawa Lagoon, including export to Majuro and Nauru, has been estimated at 1000 t, with an additional 370 t taken from sand flats and sea grass beds (Paulay 1995). The figures translate into 217.83 t of edible meat, 25.92 t of protein, and more than 121 million kcal. It should be noted that these figures are not consistent with the rank order in Table 1, where *Strombus lubuanus*, te nouo, exceeds te bun in all categories. Diver counts, average weight of the daily catch, and the estimated number of days when diving is possible (about 275 days per year excluding the traditional day of rest, Sunday, and the average duration of stormy weather), however, indicate that te bun is harvested in greater

numbers than those reported in the SGS, where sampling error is suspected. Paulay (1995) noted an increase in te bun densities from sea grass (42,000 specimens per ha, SD = 68,000) to lagoon slope (78,000 specimens per ha, SD = 136,000). For the highly mobile te nouo, mean densities of 14,000 specimens per ha, SD = 59,000, and 67,000 specimens per ha, SD = 191,000, were reported for sea grass and lagoon slope, respectively.

Te bun with perforated umbo were recovered archaeologically and may have functioned as paring knives (Takayama et al. 1990). I was informed that shells with holes knocked through the top of the valve are currently used as supports for the alga *Eucheuma*. Perforations may also result from predators, such as the gastropod *Cymatium muricinum* (Tebano and Paulay 1995). The opportunistic use of discarded valves to scale



FIGURE 5. Digging for *Asaphis*, Kariatebike, Abemama (photo by F. Thomas).

fish and for grating coconut meat was also noted. Like te nouo, the shells of te bun are used as heating surfaces in earth ovens.

Gafrarium pectinatum Linnaeus, 1758. This venerid, te koumara, is found in a variety of settings, from shallow, silty environments of the intertidal to sea grass beds and sandbars. These gastropods mature at a shell length of between 16 and 20 mm, reaching a maximum length of just over 35 mm (Morton 1990). It yields just under 1 g of edible meat at about 27 mm in length (Yamaguchi et al. 1993). Te koumara is found buried up to 15 cm deep in the sand, has sedentary subtidal populations, and reproduces at a low level throughout the year, with seasonal peaks during spring and fall in Hong Kong mangroves (Morton 1990). The planktonic larval stage probably lasts 3 to 4 weeks (see Catterall and Poiner 1987). Except in the Bonriki-Temaiku area, this species is rarely the focus

of gathering on South Tarawa. Nevertheless, it remains an important secondary catch, with an annual harvest estimated at 45 t (Paulay 1995), representing 3.92 t of edible meat, 0.52 t of protein, and close to 3 million kcal. Te koumara was at the time of my investigations the prominent mollusk gathered by the people of Tebanga Village on Maiana, where systematic digging took place.

Asaphis violascens (Forskål, 1775). The psammobiid, te koikoi, is mainly an upper intertidal species, particularly common in gravely sands on both lagoon and ocean sides. The closely related or conspecific *Asaphis deflorata*, found in the western Atlantic, provides a model for the biology of te koikoi. The bivalve matures at a length of 25 mm or greater and may attain a length of 77 mm (Berg and Alatalo 1985). Average edible weight is estimated at 9 g. This psammobiid burrows in sand to a depth of 30 cm. Mass

spawning occurs in late summer and the larval stage is about 2 weeks (Berg and Alatalo 1985). Where te koikoi is abundant, harvesting involves systematic digging (usually with spoons) (Figure 5). They are also harvested by visually searching the sand for the siphonal openings. Te koikoi, and the tellinid *Quidnipagus palatam*, te nikatona, must be carefully processed before consumption: the valves are individually opened with a knife, the sandy stomach extracted, and the meat is washed in fresh water. Discarded valves are still occasionally used as scrapers for removing coconut meat. Te koikoi occurs in areas of the lagoon used for defecation (Paulay 1995) and may be somewhat protected for that reason. Nevertheless, on South Tarawa, te koikoi appears to be below the maximum length that may be attained by the species, perhaps as a result of overharvesting (mean = 53.3 mm, SD = 9.3, $n = 101$).

Atactodea striata (Gmelin, 1791). The mesodesmatid, te katura, is abundant in sand on both leeward and windward beaches. The shell reaches maturity at about 20 mm and may grow to about 30 mm in length (Eisenberg 1981). Te katura is easily accessible, often buried at depths of less than 5 cm. The species has an extended breeding period, with peaks during the summer months in New Caledonia (Baron 1992). Te katura is among the smallest edible mollusk gathered in Kiribati, with a meat weight of less than 1 g. Because of high densities, however, large quantities can be collected in a narrow strip of sand.

Quidnipagus palatam (Iredale, 1929). The tellinid, te nikatona, appears restricted to the upper intertidal, both in gravely and silty sands. Mature individuals typically range in length between 44 and 70 mm (Eisenberg 1981). Mean length of specimens measured on Tarawa and Abemama is 45.5 mm (SD = 7.4, $n = 85$), with an average edible weight of about 3 g. Individuals burrow in 20–30 cm of sand. Harvesting involves searching for the siphonal openings, systematically digging when densities are high, and excavating water-covered sand with sweeping hand motions. The presence of water reportedly facilitates digging.

Trachycardium angulatum (Lamarck, 1822). The cardiid, te koikointari, is found mainly in areas of *Thalassia* growth and on sandbars. Adults average 60 mm (Abbott and Dance 1982). Mean length recorded in the field is 60.4 mm (SD = 10.1, $n = 22$). This species yields about 16 g of edible meat. A linear groove in the sand, similar to that of te bun, indicates the presence of buried cockles. However, they may be capable of moving about with short leaps engendered by their long foot, as do other Cardiidae (see Kay 1979). Informants say te koikointari used to be more abundant at Kariatebike, Abemama, than it is now, and it is considered rare. It is not known whether overharvesting caused this change or an environmental factor such as reduction in *Thalassia* cover.

Strombus variabilis athenius Duclos, 1844. The strombid, te newenewe, is reported from sandy lagoon flats, but was most often noted on the seaward reef flat where sand occurs, and in mangrove-covered passages just below the low-water mark. The species ranges in length between 27 and 43 mm (Abbott 1960). Specimens measured on Tarawa average 41.9 mm (SD = 7.9, $n = 40$). Edible meat weight is about 2 g. Many of the attributes described for *Strombus lubuanus* such as rapid maturity, high mobility, a long planktonic stage, and great capacity for dispersal may also be applicable in this species. Numerous shells from my archaeological excavations on Abemama display a broken-off spire, presumably to extract the meat. The identified pattern may indicate uses other than for human consumption, however. According to local sources, te newenewe damaged in this way may reflect meat extraction for use as fish bait, notably for bonefish, te ikari, *Albula glossodonta*. A similar explanation may account for the missing spires among other gastropods, such as te wiaau, *Cymatium muricinum*.

Cymatium muricinum (Röding, 1798). The ranellid, te wiaau, is found in sandy lagoons at both low intertidal and subtidal depths. It is also reported from the deeper portions of seaward reef flats (Demond 1957). Maturity is reached when the shell attains a length of about 25 mm (Eisenberg 1981). Average edible weight is estimated at 1 g. The larval

stage may last up to 4 weeks (Clench and Turner 1957). As with most gastropods, this prey type is boiled in the shell and the meat pulled from the aperture. However, among the archaeological remains found on Abemama, there is a consistent pattern of shell breakage with the spire missing. This pattern may indicate that the animal was eaten raw or that part of the shell was broken off after it was cooked (Thomas 1999).

Spondylus squamosus Schreibers, 1793. The spondylid, te koikoinanti, lives firmly attached to dead coral in intertidal and shallow subtidal regions on the ocean side of the motu and in the lagoon where it is found on sandbars. Average adult length is 100 mm (Abbott and Dance 1982); mean length of local specimens is 75.2 mm (SD = 10.3, $n = 6$) with an average of 10 g of edible meat. Although sedentary, large te koikoinanti are often difficult to locate because of the heavy deposition of marine growth on the valves that blends with the environment. The shell was the preferred species for pendants, which were kept as heirlooms (Koch 1986).

Timoclea marica (Linnaeus, 1758). The venerid, te koumai, inhabits sand flats and sea grass beds on the lagoon reef flat and the lagoon floor. Te koumai is usually buried under a few centimeters of sand, although some live individuals were found on the sand surface completely exposed at low tide. The species matures at between 15 and 20 mm (Dance 1976). Mean length of Kiribati specimens is 20.6 mm (SD = 1.9, $n = 40$), with a meat weight of less than 1 g. Like te koumara, the planktonic larval stage may be 3 to 4 weeks (Catterall and Poiner 1987).

Pitar prora (Conrad, 1837). The venerid, te nikabibi, occurs in sand flats and sea grass beds and may extend farther offshore. Adults average 40 mm (Abbott and Dance 1982). Mean length for Kiribati is 33.8 mm (SD = 8.8, $n = 16$), with an average meat weight of about 2 g. Attributes of this species' life history and habitat information may be inferred from those of other venerids, te koumara and te koumai.

Nerita plicata (Linnaeus, 1758). The neritid, te kaban, occurs in the high intertidal zone on beachrock and high-level conglom-

erates. The gastropod matures at about 20 mm in 4 yr and may attain 30 mm (Richard 1982). The Kiribati samples have a mean length of 12.2 mm (SD = 1, $n = 20$), with an average weight of less than 1 g. Te kaban is most active at night when it feeds upon surface algae. During the day, it may find refuge in crevices, where it avoids desiccation. As an archaeogastropod, one would expect poor dispersal potential and a restricted range. However, *N. plicata* is very common throughout the Indo-Pacific, from East Africa to as far east as Hawai'i and Clipperton (Demond 1957). The widespread distribution of a species that would otherwise be expected to remain within the relatively narrow confines of the local environment may relate to population dynamics over evolutionary time scales. For both molluscan and fish populations (Leis 1994, Paulay 1996), it seems likely that if species find habitat-related refugia during glacial regressions, their ranges would be fragmented.

Nerita polita Linnaeus, 1758. Despite differences in shell morphology, average size, and habitat preference, all neritids are referred to as te kaban. *N. polita* is a high intertidal species found in sand pockets adjacent to cemented features and in upper layers of gravely sands. Adults are between 20 and 40 mm in length (Eisenberg 1981). The mean for Kiribati is 22.3 mm in length (SD = 2, $n = 23$), with an edible meat weight of just under 1 g. During the day, the gastropod remains buried about 2.5 cm deep in sand. At dusk, it emerges from the sand and feeds on algae occurring on cemented features (Demond 1957). Like *Nerita plicata*, this neritid is widespread in the Indo-Pacific.

Polinices tumidus (Swainson, 1840). The naticid, te tumara, occurs in intertidal sand flats and sandbars. Individuals are typically between 25 and 75 mm in length (Eisenberg 1981). Mean length in field specimens is 31.9 mm (SD = 4.1, $n = 40$), with an average weight of 3 g. As a mesogastropod, it may have a relatively long larval stage with good dispersal potential. Te tumara is usually harvested when the sand is thoroughly exposed at low tide and the gastropod's characteristic track is clearly visible. The animal moves

quickly with the aid of a large foot, plowing up sand as it feeds. The snail marks its presence by a ridge at one end of the track, where it can be dug less than 5 cm below the surface. The naticid is primarily exploited for its shell to make dancing belts (Koch 1986).

Polinices melanostomus (Gmelin, 1791). This naticid, also termed te tumara, occurs in the same habitat as *P. tumidus*, in intertidal sand flats and sandbars. It differs from *P. tumidus* in having a smaller size range and is readily distinguishable by its dark brown columella (the columella is white in *P. tumidus* [Kay 1979]). Adults range between 18 and 46 mm (Eisenberg 1981), and average weight is about 2 g.

Oliva miniacea Röding, 1798. The olivid, te burebangaki, shares the same habitat as te tumara in the sand flats and sandbars. This species is one of the largest of the olive shells, with lengths approaching 100 mm. Maturity is usually reached at 50 mm, but may also occur at a length of less than 40 mm among dwarf populations (Petuch and Sargent 1986). Mean length for Kiribati samples is 53 mm (SD = 4, $n = 24$), with an average edible weight of 4 g. Larvae probably develop rapidly, as would be expected for neogastropods. These sand dwellers also leave well-defined tracks in the sand and lie just beneath the surface at a spot usually marked by a ridge with small cracks. Olives are carnivorous and especially active at night (Eisenberg 1981), although no night foraging activities for this species were documented. The shells of te burebangaki are occasionally strung together as dancing belts.

Barbatia foliata (Forskål, 1775). The arcid, te nikarinei, is found attached to dead coral in shallow areas of the lagoon. There is little information on this species. Adults average 50 mm in length (Abbott and Dance 1982); in Kiribati mean length is 53.1 mm (SD = 16.2, $n = 28$), with an average of just under 4 g of edible meat.

Vasum turbinellum (Linnaeus, 1758). The vasisid, te nimakaka, is gathered from the windward reef flats and is common in tide pools. Populations extend at least as far as the reef margin. Adults are typically between 44 and 85 mm in length (Abbott 1959). Mean

length of individuals gathered on Abemama is 37.9 mm (SD = 3.5, $n = 20$), with an average meat weight of less than 1 g. As with most Neogastropoda, it may be assumed that the free-swimming larval stage is relatively brief.

Turbo setosus Gmelin, 1791. The turbinid, te nimitanin, is mainly found on the reef crest (Richard 1982). Adults are usually between 40 and 60 mm long, occasionally exceeding 90 mm, and yield about 4 g of edible meat (Demond 1957). The free-swimming stage among turbans is short, with larvae remaining for less than a week as plankton (Yamaguchi 1989). Subsequent growth is relatively slow, with individuals attaining 95% of the shell height in 5 yr (Villiers and Sire 1985). These gastropods are more accessible during low spring tides than at neap tides when people can walk greater distances across the seaward reef flat. At full moon, they reportedly migrate from their shelter in coral cracks to the surface. Shells may also be gathered from fish traps, where they find suitable habitats between coral slabs. Freshly caught individuals are boiled in the shell to release the solid, calcareous operculum. Banner and Randall (1952) noted that the shell was also broken and the animal eaten raw. A small portion of the meat was commonly used for fish bait (Cooper 1964). Some of the perforated shells excavated on the northernmost island of Makin may have been used as paring knives or net sinkers (Takayama and Takasugi 1988).

Hermit crabs, te makauro, *Coenobita perlatus*, commonly find refuge in empty te nimitanin shells and are gathered for consumption. The activity is nocturnal, usually occurring along windward beaches in and around strand vegetation. Some hermitted shells can be distinguished by their eroded appearance both inside and out. However, archaeological sites containing operculae suggest that at least some of the shells were gathered for their resident gastropod, rather than for crab meat.

Lambis lambis (Linnaeus, 1758). The strombid, te ang, is the most common and one of the most widely distributed species of *Lambis*, ranging between 92 and 200 mm in length (Abbott 1961). The mean shell length

in the Abemama sample, albeit from a small sample, is 260 mm (SD = 30.3, $n = 4$). Meat weight averages 280 g (SD = 61.5, $n = 43$). Te ang lives in colonies from the low-tide zone to depths of about 3 m on sand adjacent to leeward reefs. Yamaguchi (1989) reported a larval stage of about 3 weeks and juveniles that grow fairly rapidly on small algae. One informant on Abaiang claimed that te ang remains mostly buried during the first and last quarters of the moon phase. Te ang is collected by men, who must dive for it. It is most often roasted in the shell, which is then broken up and the animal removed, but the dorsal section of the shell may also be broken with a hammer and the strombid eaten raw.

Tridacna maxima (Röding, 1798). This bivalve, te were, is one of four species of giant clams found in the Gilberts. It occurs on reef structures, partly embedded in coral or firmly attached to coral heads by byssal threads throughout its adult life. Te were is not fully mature until it attains a shell length of 60–80 mm (Munro 1993). Amount of edible meat is more variable than in some of the other species examined, with an average of 33 g (SD = 27, $n = 30$). Spawning may be continuous near the equator (Munro 1989). Despite very high fecundity, tridacnid larvae suffer considerable losses during their brief 6- to 12-day planktonic period, with populations maintaining themselves primarily through local recruitment (Alcazar and Solis 1986). Te were is often firmly attached and is commonly dislodged by puncturing the adductor muscle and prying the animal free of its byssus before the valves shut. Older individuals tend to grow out of their coral matrix, easing the task of detaching the shells. Like other species of giant clams, they were used traditionally to manufacture adzes, but were quickly replaced by metal tools once they became available. Empty shells are still used for mashing leaves for local medicines. Giant clams are regularly exported from Abaiang to Tarawa. They are also important in the subsistence economy of Tabiteuea.

Tridacna gigas (Linnaeus, 1758). This giant clam, te kima, is the largest living species of bivalve, attaining a shell length of over 1 m and weighing in excess of 200 kg. As with

other tridacnids, amount of meat is highly variable, with a mean of 1050 g (SD = 250, $n = 7$). This species is generally found on sand among corals on shallow reefs to a depth of about 20 m. Compared with other species of giant clams, te kima grows rapidly to maturity, producing eggs at about 500 mm (Munro 1993). Large specimens are capable of releasing hundreds of millions of eggs in a single day, but with reductions in the number of mature individuals, the proportion of eggs that are not fertilized increases dramatically (Tekinaiti 1990). During their week-long free-swimming period, larvae suffer high mortality rates (Heslinga and Fitt 1987).

As with te bun and te ang, diving for te kima is a task accomplished by men. For large specimens, a steel anchor pole may be used to pierce the adductor muscle or an oar prevents the valves from closing before the muscle is cut with a bush knife, releasing the valves. The meat is scraped out of the shell, which may be left in place or carried home.

Small specimens (<40 cm) are occasionally transferred to shallow lagoon reef flats or deposited in passes adjacent to households. In place, they are allowed to grow until ready for consumption. This custom has been observed in other oceanic communities (see Moir 1989, Foster and Poggie 1993, Hviding 1993). Like fish traps, and areas used for *Euchema* farming, giant clam gardens are the property of individual households, whereas the reef flat on both lagoon and ocean sides is now regarded as common property. Giant clam gardens are marked by a circular coral enclosure about 40 cm high, coral rubble, or fish trap. A few are not marked at all. Concentrations in the gardens range from one or two specimens to larger aggregates; they may consist of large individuals, but more commonly small bivalves are used. Because of pilferage in populated areas, giant clam gardens are now confined to relatively isolated locations, such as the motus of the leeward reef. The gardens are disappearing from the Kiribati seascape, however, in large part as a reflection of the erosion of customary marine tenure. Owners are now less inclined to continue to care for giant clams in designated lagoon sections or to invest in maintaining



FIGURE 6. Giant clam "garden" (*Tridacna gigas*, *Hippopus hippopus*), Abatiku, Abemama (photo by F. Thomas).

large fish traps (Figure 6). Informants claim that both the kima and the neitoro, *Hippopus hippopus*, from the gardens are harvested only during periods of inclement weather, when fishing is difficult or when no other meat source is available. Taniera (1988) reported that they were also consumed at feasts.

The kima provided the raw material for adzes, chisels, gouges, and scrapers (Takayama et al. 1990), and the shell was apparently used as a container for cooking (Catala 1957). Contemporary uses of empty te kima valves include troughs for feeding pigs, for crushing certain foods, and as shrine components. Te kima gathering, whether for immediate or delayed consumption, is usually incidental to other activities, such as spearfishing, and may at times become a risky venture, if the fisherman is near a leeward pass where strong currents and large marine predators may be present.

Hippopus hippopus (Linnaeus, 1758). The

giant clam, the neitoro, is found on sandy substrata in intertidal areas to depths of about 10 m. Maturity is attained at a length of about 140 mm or when the shell is no longer attached to coral rubble. Edible meat weight averages 156 g (SD = 316, $n = 26$). Like the kima and the neitoro, the larval stage is short. Settlement of larvae usually occurs within a week after fertilization (Alcala et al. 1986). The neitoro is often found in shallow, nearshore patches, where it may be completely exposed during spring low tides. Under these conditions, the valves are shut tight, and the animal is nearly camouflaged in the midst of dead coral. Neap tides, when the mantle is visible, provide the best opportunities to spot these bivalves. Like the kima, the neitoro gathering is normally incidental to other fishing activities, but it may become a focal prey type, particularly in some sections of the leeward reef platform at low tide where foragers are able to walk on the reef. The shells were used

as ax and adze blades, hammerstones, and containers, the last continuing today (Koch 1986, Takayama and Takasugi 1988). Live specimens were also placed in lagoon gardens with te kima.

DISCUSSION

The degree of lagoon closure plays an important role in determining the number of species that can be found (Salvat 1969, 1972, Kay 1971, 1978, Kay and Switzer 1974). These patterns may not apply in the case of Tarawa and other open atolls influenced by nutrient-rich waters of the equatorial upwelling area, resulting in unusually high molluscan population densities, together with high species diversity (Paulay 1995).

A substantial rise in mollusk consumption has occurred on South Tarawa, a phenomenon linked to changes in water circulation when causeways were built in the 1960s, encouraging the establishment of certain species and increased fertilization by sewage-driven nutrients. Filter feeders exposed to contaminated water may become agents of gastrointestinal diseases, particularly if consumed raw or partially cooked (Danielson et al. 1995). It appears that shellfish contamination resulted in the abandonment of enclosures.

In Kiribati, communities target a limited range of marine invertebrates, although molluscan catches often include several species, which appear as incidental harvests. Paulay (1995) found that *Strombus lubuanus*, *Anadara uropygmelana*, and *Gafrarium pectinatum* occurred in 67, 59, and 47%, respectively, of the South Tarawa sand flat and sea grass catches, but 61% of the catches were dominated (that is constituting greater than 75% of gross catch weight) by *S. lubuanus* and 26% by *A. uropygmelana*. The current observed and interview data confirm the importance of these species, with *A. uropygmelana*, *S. lubuanus*, and *G. pectinatum* occurring in 60, 59, and 33% of sand flat and sea grass catches, respectively. Seventy-eight percent of the catches have dominant species (as defined above, except that weight is for edible meat), with *A. uropygmelana* (19%), *S. lubuanus* (53%), and *G. pectinatum* (28%). The inclu-

sion of other species may give the impression that although foragers are targeting certain prey, they essentially gather all those that they consider edible. In her study of Australian Aboriginal subsistence, Meehan (1982) addressed some of the factors leading to a departure from targeting a single mollusk species. Some of her explanations appear sensible, for example, differences in foraging ability among participants, but her conclusion that among the Anbarra shell gathering is essentially a random process is in sharp contrast to Bird's (1996) demonstration among the Meriam of Torres Strait that shell-gathering activities can be explained in terms of the variable costs and benefits that foragers face while collecting prey.

The significance of size at maturity lies in its relationship with size below which individuals are rejected by foragers. A population will always contain reproducing individuals if size at maturity is less than the rejection size. However, the population is at risk if size at maturity exceeds the rejection size. Some targeted individuals may escape detection if they find refuge by burying themselves. A depleted intertidal population may be replenished through recruitment of individuals from adjacent subtidal areas that are usually inaccessible to traditional gatherers. Reproductive individuals with partially subtidal distributions may migrate into the exploited intertidal zone if they are mobile during their benthic stages. If the duration of the larval stage is sufficiently long, then it is possible for larvae spawned by more distant unexploited populations to settle into the exploited areas.

Prey resilience provides an alternative explanation for the apparent balance between traditional societies and their resources (Catterall and Poiner 1987, Poiner and Catterall 1988). According to the tenets of human behavioral ecology (Cronk 1991, Smith and Winterhalder 1992), if people are behaving to maximize their short-term harvest rate and vulnerable species fall in the optimal diet, a diminished-returns curve, as assumed in the "marginal value theorem" (MVT) (Charnov 1976), could lead to overexploitation and extinction of prey, though this is admittedly less likely than with a step-function curve (where

the expected or marginal harvest rate suddenly drops to zero). However, if a given patch type has a very high return curve relative to other patch types, and some of the prey types in that patch type are not resilient to overexploitation, human foragers following the MVT are quite capable of causing local extinction. With the most vulnerable prey gone or greatly reduced in number, most remaining species presumably possess biological attributes that make them resilient to human predation. Unfortunately, little is known of the response of many tropical mollusk populations to gathering practices, in part at least because of the paucity of detailed information on life history and ecology (Catterall and Poiner 1987, Wells 1989, Munro 1999). Although it has not been possible to compile detailed information for every prey type, certain species are clearly at risk of depletion, even following a regime of traditional gathering.

The influx of human populations from the outer islands to Tarawa, together with a high birth rate, has resulted in the decline (in size and abundance) of easily accessible intertidal resources, particularly te bun, which is often the main source of protein for unemployed and low-income families. During the 1993–1994 field season, the roadside sale of te bun gathered offshore was putting pressure on stocks on Tarawa that were once relatively well protected from harvesting. Divers possessing a floating device (e.g., canoe, rubber inner tube) and goggles could collect large quantities of the bivalve on a daily basis and sell their catch in rice bags holding up to 34 kg of te bun. With approximately 16 million te bun taken annually (before 1995), and an estimated population of 40 million in the heavily fished Taborio-Bangantebure bed, or 70 million from Nanikai to Bikenibeu, the harvest represented about one-third to one-fifth of the total adult te bun population. These figures suggested that harvests were near, if not exceeding, sustainable rates (Paulay 1995).

According to Tebano (1990), reef blasting of Maiana's leeward reef opposite Raweai Village may have contributed to the recent disappearance of te bun in that area. Changes

in water circulation associated with strong currents may have disturbed the nutrient-rich substratum inhabited by these bivalves and larvae washed away. The extent of these disturbances on overall te bun stocks is difficult to assess, but the paucity of small individuals (<20 mm) in other areas surveyed by Tebano suggests a decline in population densities. Informants at Tebanga, about 8 km from Raweai, also stated that te bun were considerably less abundant compared with a few years ago. With less pressure on lagoonal resources, Abemama's te bun stocks are not in apparent danger of reduced recruitment, and densities of more than 20 individuals per meter are said to be fairly common. Tebano (1990) reported that exploitation mainly took place during periods of inclement weather when fishing was hazardous.

Te nouou are conspicuously absent at Maiana and none was located in surface middens. Older informants did not recall a time when this species was present. Because habitats suitable for this gastropod exist, it may be that the absence of the species is linked to chance dispersal or local extinction, resulting in its discontinuous distribution (see Kay 1995). The resilience of te nouou to traditional gathering tends to rule out overexploitation. In contrast to Maiana, the strombid is fast becoming the dominant molluscan species in Tarawa Lagoon, perhaps as a consequence of the demise of many reefs linked to changes in sedimentation (Paulay 1995). The high variability of species density in sea grass beds reported by Yamaguchi et al. (1993) (254,000/ha) and Paulay (1995) (14,000/ha) may reflect increasing gathering pressure, but could also be attributed to patchy distribution, perhaps linked to the species' high mobility. Nevertheless, a small average shell length for Tarawa sand flats (mean = 42.9 mm, SD = 4.9, $n = 206$) may indicate harvesting pressure. On Yap, Kay and Smalley (1989) reported a mean length of 47.9 mm (range, 41–54, $n = 18$). Size range in the Pacific is 32.2–69.5 mm, with an average of 56.5 mm (Abbott 1960).

Current and future leaders will continue to be challenged by the often conflicting goals of implementing policies conducive to economic

development and of assuring sustainable use of the environment. The second goal could be achieved by applying extant TEK for new biological and ecological insights for protected areas and for conservation education, for development planning and environmental assessment, and of course for resource management (see Berkes 1993).

The linkage between TEK and resource management, expressed through various forms of tenurial systems, has received considerable attention in the past few decades (Croccombe 1989, Johannes 1989). Many problems remain, however, in implementing TEK to serve conservation initiatives and related goals. In addition, there is the challenge of how TEK and scientific information can be integrated, and whether such integration is desirable, given unequal power sharing in decision making. The fisheries sector in Kiribati has been described as both a source of essential livelihood at the subsistence level and as a means to achieve greater economic independence by promoting the country's seemingly vast store of marine resources. The impressive number of feasibility studies, with an emphasis on finfish (Gillett et al. 1991), should furnish data for making informed choices.

The sustainability of mollusk fisheries in Kiribati rests in large part on a remodeled form of marine tenure (Johannes and Yeeting 1995). To achieve this goal, local fishers should be encouraged to pursue activities to generate income that could at the same time provide a means to ensure the long-term use of selected high-value resources, such as pearl shell and giant clam farming, using a combination of traditional knowledge and modern technology. Mollusks are especially suited to efforts aimed at establishing limited entry, because they are mostly sedentary and relatively predictable. Therefore, those resources are most economically defensible by various cooperative units already engaged in community projects.

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