THE ECOLOGY OF FANGA'UTA LAGOON, TONGATAPU, TONGA

Sponsored by

Institute of Marine Resources
University of the South Pacific
Suva, Fiji

International Sea Grant Program
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by

Leon P. Zann
William J. Kimmerer
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Sea Grant Cooperative Report
UNIHI-SEAGRANT-CR-84-04

This Cooperative Report was prepared under the auspices of the University of Hawaii Sea Grant College Program for the University of the South Pacific/University of Hawaii project under the International Sea Grant Program Grant No. NA79AA-D-00112 from NOAA Office of Sea Grant, Department of Commerce.

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PREFACE

In the fall of 1981, the Institute of Marine Resources of the University of the South Pacific and the Hawaii Institute of Marine Biology conducted a joint survey of the ecology of Fanga'uta Lagoon, Tongatapu, Tonga, under the auspices of the International Sea Grant Program. This survey was the result of requests made by the Tonga Fisheries Division and Ministry of Lands and Surveys following two decades of declining fish catches and reported environmental changes in Fanga'uta Lagoon. In a combined effort, specialists from these institutions aided by support staff from Tonga Fisheries Division spent 2 weeks in September and 1 week in November 1981, studying the ecology, hydrography, and fisheries as well as assessing the pressures on the lagoon from commercial fisheries, land reclamation, and sand mining for construction purposes.

This report is presented in two parts. The first part is a nontechnical summary of the scientific findings and recommendations. This is followed by seven technical sections that serve as the basis for the summary.

ACKNOWLEDGMENTS

The authors wish to acknowledge the help of members of the Tonga Fisheries Division, especially the scientific officer, Mr. T. Hopson, and the support staff, notably Mr. Jack Lee (Peace Corps), Mr. Akio Kuramatsu (Japanese aide) and Mr. Vainga Teu (Tonga Fisheries). Mr. Sione Tongilava of the Ministry of Lands, Surveys and Natural Resources, Mr. Lloyd Belz and Ms. Rene Godfrey of the World Health Organization, and Mr. Setivani Halapua of the Institute of Marine Resources provided helpful background information. The project was initiated by Dr. Uday Raj, Director of the Institute of Marine Resources at the University of the South Pacific, and Dr. Philip Helfrich, Director of the Hawaii Institute of Marine Biology at the University of Hawaii, and funded by the International Sea Grant Program under grant number NA79AA-D-00112 from NOAA, Office of Sea Grant, Department of Commerce.

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NONTECHNICAL SUMMARY
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INTRODUCTION AND SUMMARY

Fanga'uta Lagoon is a shallow, almost enclosed embayment (Figure 1) located on the northern coastline of Tongatapu, the largest island in the kingdom of Tonga. For many centuries the lagoon supported an important mullet fishery but catches have declined during the past two decades causing widespread concern. The lagoon was therefore closed to commercial fishing in 1975 but was reopened in 1981. Other reported recent environmental changes in Fanga'uta Lagoon include shoaling, mangrove encroachment, and a decline in the number of formerly prolific edible mussels. Also, human population increases are putting greater pressures on the lagoon resources. These pressures include anticipated dredging for building aggregate and increased land reclamation.

Tongan planners needed information on Fanga'uta Lagoon for its management. A survey was conducted jointly by the University of Hawaii and the University of the South Pacific under the auspices of the International Sea Grant Program to fill this need. Specifically, the objectives were: (1) to characterize the circulation, hydrology, water chemistry, and productivity of the lagoon as well as describe its biota; (2) to evaluate the decline in fisheries; and (3) to recommend management procedures.

Fanga'uta Lagoon is composed of two branches separated from each other and from the ocean by a complex system of reefs and channels. The westernmost part, here referred to as the Nuku'alofa branch, is made up of a wide, sinuous channel -- the Folaha sector; and a broad, shallow basin surrounding Kanatea Island -- the Pe'a sector. The Mu'a branch can be subdivided into the Vaini sector, a shallow basin with dense seagrass cover, and the deeper Mu'a sector.

Within the channel areas are two distinct passes: one from the ocean into the lagoon (the entrance channel) and the other connecting the two branches. The main pass consists of a deep channel and a second wider, shallower channel through a broad expanse of reef flat. The side pass has a few channels that are less than 1 m deep at low tide as well as reef flats that are exposed at low tide. This pass is further restricted by a pair of small islands.

The history of the lagoon is sketchy. The only document showing water depths is an old admiralty chart which proved to be of limited use for comparison of soundings with this study because of positioning difficulties. Evidence derived from examination of the reefs in the main pass suggests that this area was uplifted 20 to 40 cm in recent geological history, perhaps 40 to 200 years ago. Because of the influence of channel topography on water level and circulation, the character of Fanga'uta Lagoon today must differ markedly from that before the uplifting.

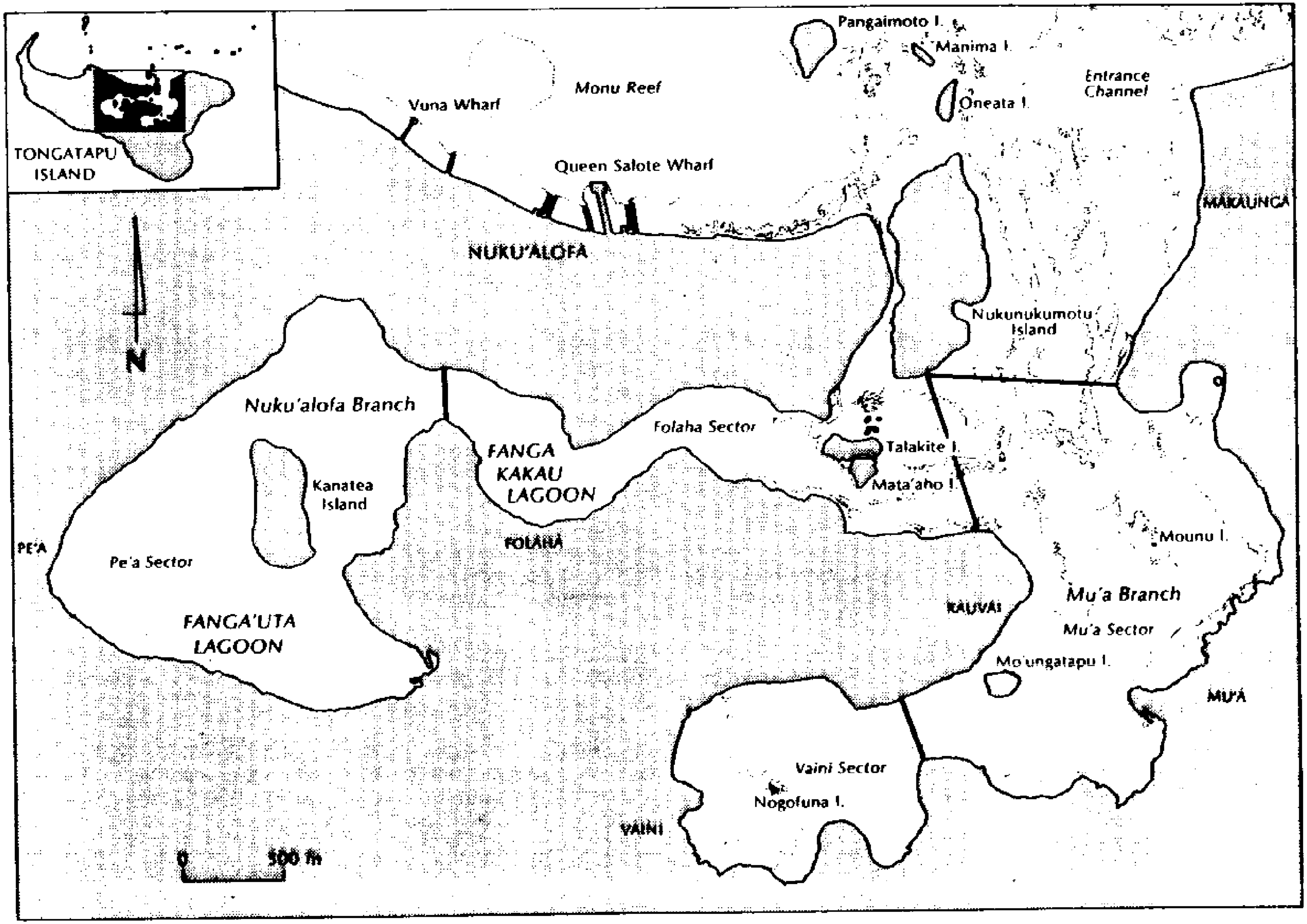

Figure 1. Fanga'uta Lagoon, Tongatapu

Circulation in Fanga'uta Lagoon is driven predominantly by tides. The ocean tidal range of about 1 m drives a current of up to 2.6 knots in the main channel, producing a tide within the Mu'a branch that is smaller than and which lags behind the ocean tide. This tide causes the current to flow through the side pass to and from the Nuku'alofa sector, producing a tidal range at Nuku'alofa of only 0.13 m. This tide lags behind the ocean tide by 3 to 4 hours. Thus, the small cross-section of the passes allows relatively little tidal exchange between ocean and lagoon.

Computer model studies were combined with measurements of freshwater content and current velocities in the channels to produce a freshwater budget for the lagoon. This enabled an estimate to be made of the residence time of about 23 days. This means that a particle of water entering the lagoon from the ocean will spend, on the average, 23 days inside the lagoon. It also means that tidal mixing of ocean and lagoon waters results in exchanges of 1/23 or about 4 percent of the lagoon's volume each day. Since this is less than the actual amount of water flowing in and out with the tides, it also shows that mixing of water on each tidal excursion is only about 12 percent complete; that is, most of the water coming in on the flood tide leaves on the following ebb tide without mixing.

Freshwater input to the lagoon occurs entirely from the groundwater lens except during heavy rains. Average input is about 26,000 m^3 per day, of which 85 percent enters through diffuse subsurface springs and 15 percent from solution channels on the shore. The groundwater is rich in nutrients and provides essentially the entire nutrient supply to the lagoon.

Because of the long residence time of water in the lagoon, most of the nutrients are incorporated into living organisms and ultimately remain in the lagoon sediments. This continuous accumulation of organic matter normally would cause an infilling of only a few millimeters in a century. It is highly likely that much more rapid infilling occurs through erosion and runoft during infrequent heavy storms. Thus, the uplift in the lagoon entrance area created a damming effect, allowing sediments to accumulate more rapidly than before the uplift.

Biological processes within the lagoon are controlled by nutrient input, tidal exchange, water depth, and wind. Where the wind influence is strong and the water is shallow, as in the Pe'a sector, the water is turbid and the bottom has only slight seagrass cover. The Vaini sector is also shallow but is more protected from wind; a dense mat of seagrass has developed there, further stabilizing the sediments on the bottom. Thus, while the Pe'a sector is plankton-dominated, the Vaini sector is dominated by benthic processes. The Folaha and Mu'a sectors are both deeper, so seagrass cover is restricted to the margins. Plankton growth is more rapid in the Pe'a sector than in the Mu'a sector, probably because of the high concentration of particulate matter, and therefore, higher availability of recyled nutrients.

Corals, normally a conspicuous feature of tropical marine benthos, are virtually absent within the lagoon. The combination of low salinity, soft substrate, and high turbidity prevents significant coral growth beyond the lagoon side of the main pass. The benthos of the pass area is a rather diverse assemblage of hard- and soft-bottom components. Further into the lagoon the benthos consists of typical estuarine soft-bottom infauna and a seagrass community.

There are conflicting opinions in Tongatapu on the decline of the lagoon's mullet fishery; however, no catch and effort data are available. Most fishermen claim that the lagoon fishery has greatly declined, but the Tonga Fisheries Division believes that there has been an increase in fishing effort (number of fishermen) and that actual catch has not declined. This 1981 survey results suggest that both have occurred.

The net survey results indicate that the finfish resources are low despite the (6-year) ban on commercial activities within Fanga'uta Lagoon. Although the lagoon is open to subsistence activities, it appears that the present level of exploitation is great enough to keep the standing crop of finfish resources low.

This survey of Fanga'uta Lagoon indicates that benthic (macroalgal) production is about 1,492 metric tons of carbon per year which is available to the higher trophic categories (such as mullet). Rough calculations suggest that this algal production could easily sustain a virgin (unfished or managed) mullet population that yields 187 metric tons per year. These figures are in the range of managed mullet fisheries in other parts of the world.

An increase in demand for fresh fish resulting from Tonga's population increase and Nuku'alofa's urbanization, together with the introduction of highly effective fish fences and gillnets, may have resulted in the overfishing of mullet. Other lagoon species have also been subjected to heavy exploitation. Prawns were commercially fished by trawling in 1974 but the negative impacts associated with this method wisely led to the banning of its use. Clearing of sediment-trapping mangroves, reclamation of swamps, and large-scale clearing and changes in land use have all probably had an impact on most species inhabiting the lagoon.

RECOMMENDATIONS

Fanga'uta is an extremely productive shallow estuarine lagoon having limited water exchange with the ocean. It has been subjected to considerable overfishing and localized disturbances as a result of the removal of mangroves and reclamation of land. No evidence of pollution or other human impact was found during the short survey period.

The proposed reintroduction of commercial fishing and large-scale dredging for fill and building aggregate will place heavy pressures on the lagoon. It is unlikely that fishing pressure could be effectively reduced for a sufficient period of time to allow fish stocks to recover. Thus, the reopening of the lagoon to commercial fishing is regarded as an unwise decision. If continued, it is suggested that the Fisheries Division carefully monitor catch and effort in the lagoon and adjoining waters. Such data would provide the basis for any future management decisions regarding the fisheries.

A small but potentially valuable prawn resource exists in Fanga'uta Lagoon. With appropriate management it would be possible to sustain a modest fishery supplying the luxury food to the restaurant and hotel industries in Tonga. However, establishing a fishery for prawns or other species that involve trawling is not recommended. The disruption of the sensitive seagrass habitat and the negative impact to juvenile fish would ultimately eliminate any short-term advantage of establishing such a fishery. For a prawn fishery, the use of baited trap techniques or monofilament "pocket" nets for harvesting such as are used in Japan is suggested.

Dredging in the lagoon, particularly the cutting of channels in the passes, is not recommended. Besides the disruption to the benthic communities, the effect on tidal heights in the lagoon could be severe.

Fanga'uta Lagoon's high productivity could best be utilized through the development of aquaculture. While it is noted that the Tonga Fisheries Division's attempt to culture mussels in the lagoon several years ago was a failure, that program was unsuccessful because of equipment losses, lack of supervision, and thefts and not because the lagoon was unsuitable. The shallow and productive waters may be appropriate for the aquaculture of filter-feeding bivalves such as oysters, clams, and mussels. Other species with aquaculture potential include mullet, milkfish, and baitfish for use in a pole-and-line tuna fishery.

TECHNICAL SUPPLEMENTS

CIRCULATION AND HYDROLOGY

W.J. Kimmerer

The study of circulation in a lagoon such as Fanga'uta can provide useful information for predicting lagoon tides, estimating water exchange with the ocean, and understanding lagoon ecology.

Circulation in Fanga'uta Lagoon is predominantly tidally driven. The ocean tide forces a current to flow through several restricted passes into the lagoon (Figure 2), resulting in a lagoon tide smaller and lagging behind the ocean tide. Although wind may play an important role in internally mixing lagoon basins, destratification, and resuspension of sediments, tides appear to drive most of the circulation between different parts of the lagoon. Thus, an understanding of tidal circulation can provide insight to the flow of materials between the lagoon and the ocean and among parts of the lagoon.

One difficulty often encountered in studies of lagoon circulation is that mixing during a tidal cycle is never complete. An outgoing tidal current may contain a substantial fraction of ocean water from the previous incoming tide. The effective volume flux, which is the amount of water actually exchanged daily, is always less than the tidal flux. The effective volume flux is an important variable because it can be used to determine residence times of water and other materials in the lagoon and to calculate mass fluxes of various materials between lagoon sectors.

Several alternative methods of estimating the effective volume flux are available, most involving the measurement of salinity differences. If the rates of evaporation and input of freshwater to the lagoon are known, then the effective volume flux can be calculated from the salinity difference between the lagoon and ocean waters. Most of the freshwater enters Fanga'uta Lagoon as groundwater, making the supply rate difficult to estimate.

An alternative way of determining effective volume flux is to measure salinity changes and volume flow rates in channels. This method works only if the salinity changes are large and reasonably regular. This method was used to calculate groundwater input into each part of the lagoon, and then used for several calculations of effective volume flux. The approach used in this study was to construct a computer model of tidal flow in the lagoon and to use model output and salinity data for the effective volume flux calculations.

Most of the data on lagoon bathymetry, freshwater inflow, salinities, and currents were gathered during September through October 1981. Model development revealed a need for more data, specifically on reef flat bathymetry, currents, and salinity

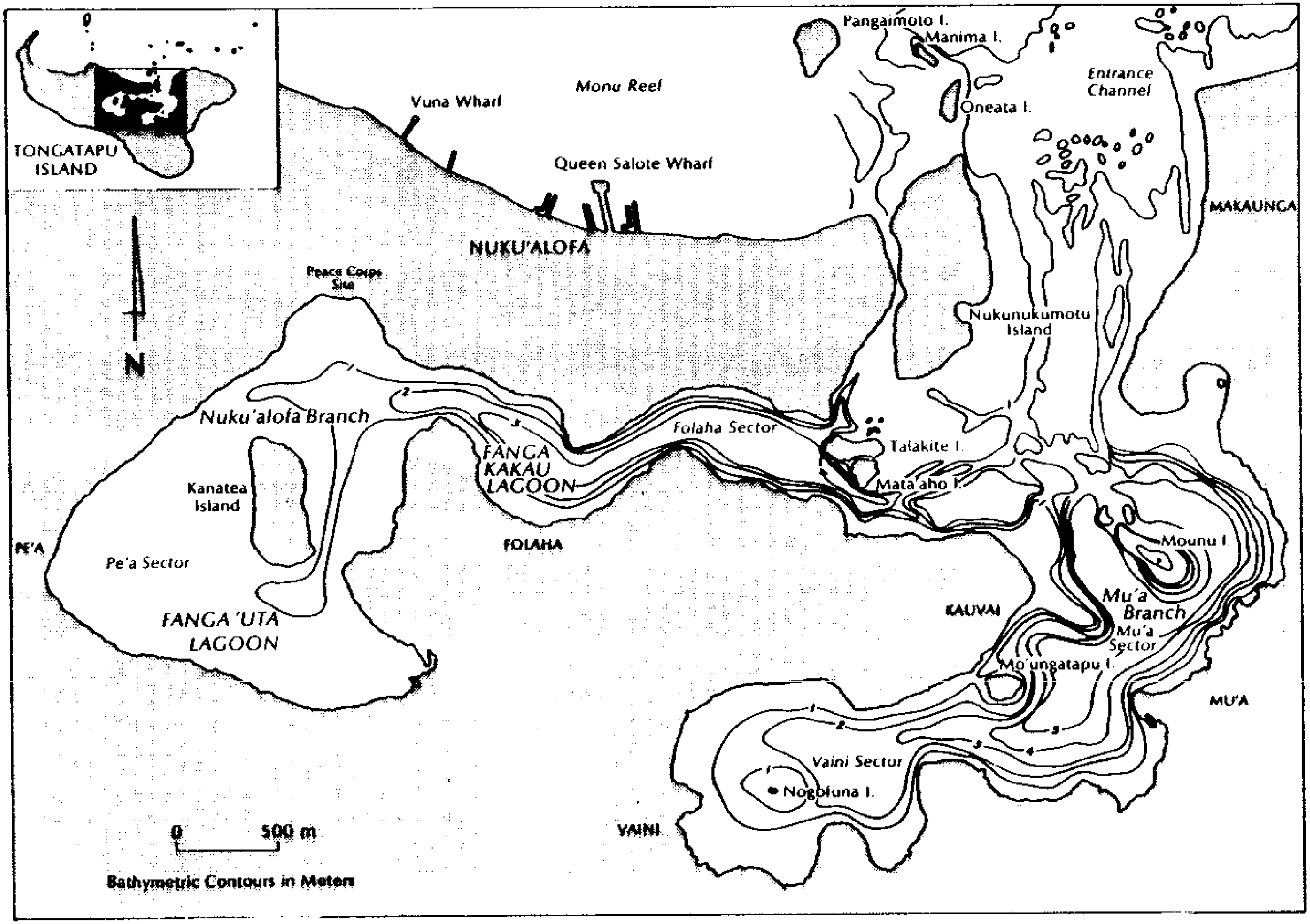

Figure 2. Bathymetric map of Fanga'uta

changes in the channel. A brief return trip in November 1981 provided the data needed to refine the model and the freshwater flux estimates.

Another point of interest in circulation arose during the first visit, when it was suggested that a dredge be brought into Fanga'uta Lagoon for sand mining. Since dredging would alter the channel configuration, several runs of the model were used to predict the effects of channel alterations on circulation.

METHODS

Positioning within the lagoon was based on an excellent series of topographic maps available at the Ministry of Lands, Surveys, and Natural Resources. Positions were estimated visually using prominent landmarks or, when precise positioning was needed, by the use of a sextant held horizontally to measure angles between landmarks. Lagoon bathymetry was determined by numerous soundings with a lead or stick. These were used to construct a depth contour chart (Figure 2) from which areas within contours were measured by planimetry.

All sampling and measurement were done from small outboard-motor boats. Current velocities in the channels were measured with ducted impeller current meters and tethered drogues. Salinity and temperature were measured with a Bendix RS5-3 field salinometer, and unfiltered water samples were collected in polyethylene bottles for salinity measurement in the laboratory. These measurements were made in Hawaii with a Plessey 6230N laboratory salinometer.

Tidal heights were taken from an ocean gauge at Nuku'alofa and a lagoon gauge located near the Peace Corps office (Figure 2). Weather data were transcribed from hourly records at Fua'amota Airport.

The hydrodynamic model was based on that used by Gallagher (1973) for Pala Lagoon, American Samoa. The model is based on a balance of forces and water volume. The former is represented by:

$$F = ma$$

where

F = the sum of the forces acting on the water
m = the mass of water
a = the acceleration

The forces expected to be important in flow in the channels are friction and the pressure gradient due to differences in sea surface elevation along the channels. The acceleration term consists of a steady spatial acceleration from an assumed state of nel, and velocity changes of the entire flow field over the tidal cycle. Preliminary estimates revealed that the latter term was much smaller than the former, so the latter was dropped from the model. The first acceleration term was also negligible for the reef flats when compared with the pressure gradient and friction.

Friction was calculated using the method of Goncharov (1964) which is based on water depth, bottom area, and a roughness factor. The latter is difficult to estimate but is related to the size of obstructions within the channel.

The mass balance portion of the model is a simple relationship among volume flow into the lagoon, lagoon area, and tidal height. This volume flow is calculated from the currents over the reef flats and through the deep channels. One assumption of the model is that no flow occurs between the channels and the adjoining reef flats.

The model considered flow into the entrance and into the Nuku'alofa branch of the lagoon separately. Thus, there were a total of six equations, three for each pass: one specified the velocity in the channel, another the velocity over the adjoining reef flats, and the third the rate of change of lagoon tidal height. See Appendix A for the equations and the method of solution.

The equations were solved numerically on a computer. Initial parameter values were best estimates from field measurement of dimensions of the passes. Various parameters, notably the roughness factor, were adjusted until the model gave results close to several criterion variables. Further model runs then revealed the effects of the presence of additional channels, such as would be created by dredging.

Freshwater flow estimates were based on salinity measurements over two complete tidal cycles in each channel. The freshwater flux was calculated as:

$$\Phi_{FW} = \sum P_{FW} \cdot V$$

where

Φ_{FW} = freshwater flux
P_{FW} = proportion freshwater in each channel
V = the volume flow rate in each channel

V for the side channel was estimated from the rate of change of tidal height at the Peace Corps tide gauge. For the main channel, V was calculated from the flow velocity at the 3-m depth and the ratio of total volume flow rate to flow velocity taken from the model. The sums were taken across a complete tidal cycle to balance total inward and outward water flow.

Effective volume fluxes and residence times were then calculated for the two passes and for the boundaries between two sectors in each lagoon branch. The effective volume fluxes were calculated from a freshwater balance and the salinity differences between sectors.

RESULTS

Bathymetry and Dimensions

Not including the entrance channel, the lagoon encompasses an area of 27 km^2, with about half the area in each of the two branches (Figure 2). The lagoon is shallow, with a mean depth of 1.4 m and a maximum of 6 m. On the basis of apparent flow restrictions and consistency of water depth, each branch can be further divided into two sectors whose dimensions are given in Table 1. The Mu'a sector is deepest and the Pe'a sector shallowest.

TABLE 1. FANGA'UTA LAGOON DIMENSIONS BY SECTOR

Sector	Area ($10^6 m^2$)	Volume ($10^6 m^3$)	Mean depth (m)	Maximum depth (m)	Watershed Area ($10^6 m^2$)
Nuku'alofa branch					
Pe'a	8.8	6.8	0.8	2.5	34
Folaha	4.9	7.3	1.5	3.2	07
Total	13.7	14.1	1.0	3.2	41
Mu'a branch					
Vaini	3.8	4.5	1.6	2.8	23
Mu'a	9.7	19.4	2.0	6.0	16
Total	13.5	23.9	1.8	6.0	39
TOTAL	27.2	38.0	1.4	6.0	80

The lagoon entrance is a complex area. The main channel consists of extensive reef flats with depths between 0.2 m above and 1 m below chart datum, as well as a single deep (5.6 m) channel through which strong currents flow. On the seaward side the reef flat breaks up into numerous patch reefs. The lagoonward margin of the reef system is complex, with many channels leading either to the Mu'a sector or into a pair of channels across another reef into the Folaha sector. These channels are wide and as shallow as 0.4 m below chart datum. The reef flats surrounding the side channels and the lagoonward end of the main channel become exposed at low tide.

Tidal Circulation

Ocean tides during the study were semidiurnal with a slight diurnal inequality. Low tide occurred at 0.05 to 0.29 m above chart datum (mean 0.13) and high tide at 1.06 to 1.27 m (mean 1.19), for a range of 1.06 m.

Tidal circulation in the lagoon is constrained by the geometry of the reef flats and channels. Therefore, tides inside the lagoon can be expected to have a smaller range than outside and also to lag the ocean tide. Measured tides at the Peace Corps gauge had a mean range of only 0.13 m. A comparison of ocean and lagoon tides (Figure 3A and 3B) illustrates the differences in heights as well as the lag of 3 to 4 hours. The difference in rate of rise and fall of the lagoon tide is caused by the changing channel cross section (Gallagher, 1973). Note that the absolute heights of the lagoon tide are in error, apparently because of incorrect leveling of the tide gauge relative to the ocean gauge.

The main channel current (Figure 3C) follows the rise and fall of ocean tides. Peak currents are around 1.5 m/sec or 3 kt. Irregularity of the channel walls results in considerable turbulence which manifests itself as eddies, standing waves, and current velocity fluctuations.

Circulation Model

The best set of model parameters, selected by iterative model runs, is listed in Table 2. A comparison of numerically generated data with mean observed data (Table 3) shows good agreement for most values. In particular, the tidal height and timing of highs and lows within the Nuku'alofa branch showed very good agreement. Current velocities in the main channel and reef flat were also well simulated in the model. Simulated currents in the side channel did not agree with the observed data for two reasons. First, the complex physiography of the reefs in that area made straightforward simulation of current in the channel and reef flats difficult. Second, the observed currents were highly variable and difficult to measure with current meters because of the shallow depth. The timing and height of the inner lagoon tide depend on the accuracy of simulation of both volume flow in the channel and changes in channel cross-section with time. Thus, the discrepancy between observed and predicted side channel currents is not a serious flaw in the model.

As a further check of model response, rainfall input was simulated for the Nuku'alofa branch as a 0.15-m step increase in lagoon water level. The increase decayed with a half life of about 28 hours. A heavy rainfall on September 19-20 increased tidal elevations by about 0.15 m, according to the Peace Corps gauge; the tidal elevations returned to normal in about 3 days. Stratification caused by heavy rainfall could be expected to alter the circulation patterns within the lagoon, but also

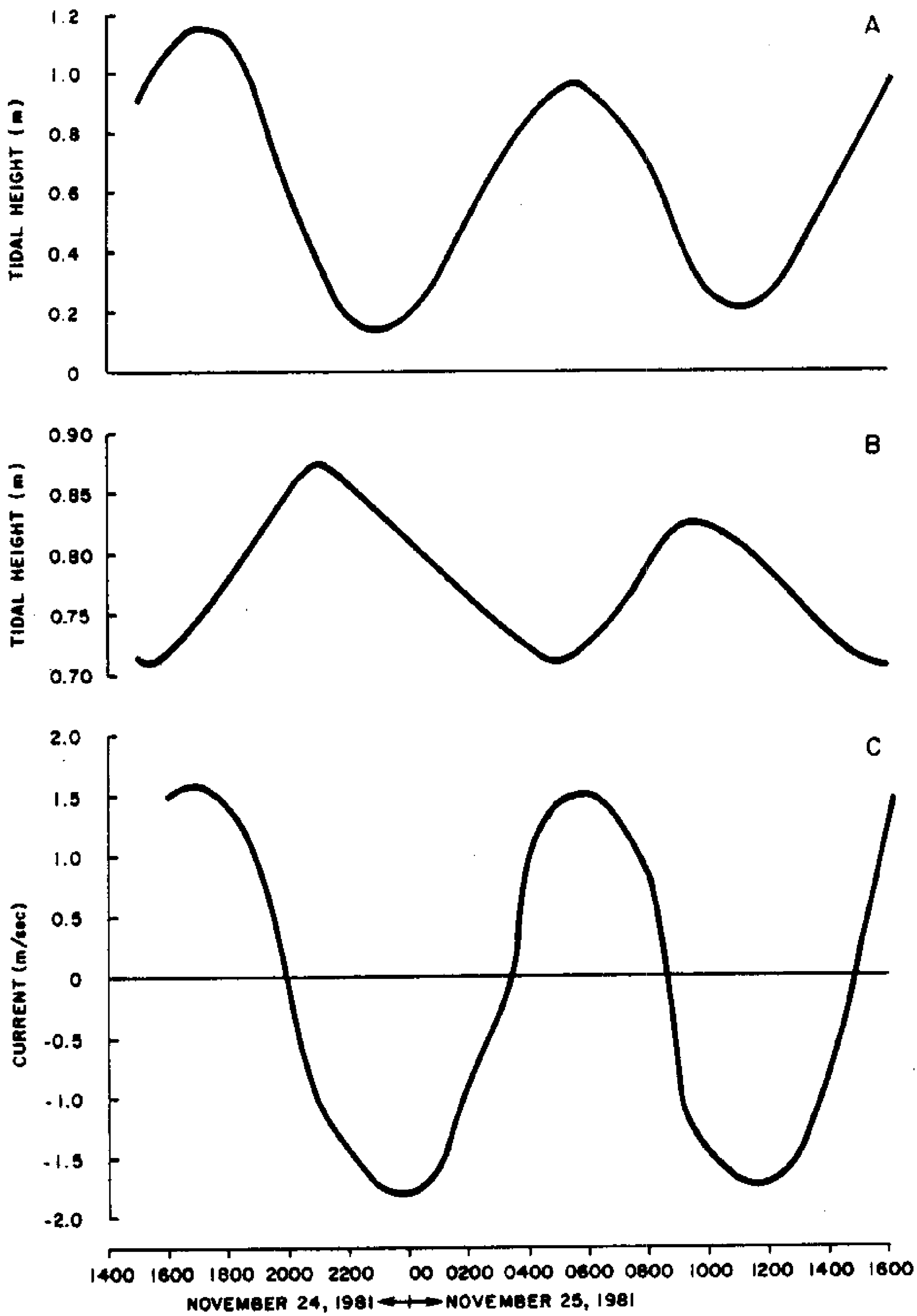

Figure 3. Tide cycles, a comparison of tides: (A) ocean tide; (B) lagoon tide; (C) main channel current

TABLE 2. PARAMETER VALUES FOR MODEL RUN GIVING BEST FIT OF CRITERION VARIABLE

Parameter	Main passage		Side passage	
	Channel	Flat	Channel	Flat
Length (m)	1,800	1,800	1,500	1,500
Maximum depth (m below datum)	5.6	0.25	0.4	-0.6
Width at maximum depth (m)	50	440	50	200
Roughness (m)	3.0	1.5	0.5	0.75
Increase in width per meter of water depth	3.7	625	154	1,600

TABLE 3. CRITERION VARIABLES FOR FANGA'UTA LAGOON TIDAL MODEL

Variable	Expected Value	Model Value
Time lag between ocean tide and tide in Nuku'alofa sector (hours:minutes)		
High	3.13	3.10
Low	4.49	4.56
Range of tide in Nuku'alofa sector (m)	0.13	0.13
Peak currents in main channel (m/sec)		
In	1.2	1.20
Out	1.3	1.27
Peak current on main reef flat (m/sec), out only	0.2	0.22
Peak currents in side channel (m/sec)		
In	0.9	0.65
Out	0.6	0.56

Note: Expected values based on measurement; model values based on the best choice of parameters. Variables are listed in approximate order of precision.

expected to break down within the channels because of turbulence. A 28-hour half-life would result in an excess tidal elevation of only 0.02 m after 3 days; thus, the model agrees reasonably well with the observed data.

The model was then used to simulate additional channels, such as would be produced by dredging. The design channels were asssumed to be 50 m wide, with depths of 5 m through the main passage and 3 m through the side passage, and to have a roughness of 1 m. The latter is an arbitrary figure based on the assumption that the new channels would be straight with relatively smooth walls. Variations in roughness had little effect on model results.

The effects of the additional channels on tidal heights are illustrated in Table 4. The effect is small but could be significant in some parts of the lagoon. In particular, a lowering of the low tides by 10 to 22 cm would expose large areas of reef and shallow mangrove flats to dessication. An increase of the high tide by 11 cm in the Nuku'alofa branch could, under conditions of heavy rainfall, inundate some of the lower-lying fill areas around the northern margin of that branch.

TABLE 4. EFFECTS OF ADDING CHANNELS OF 50-M WIDTH, 5- OR 3-M DEPTH, AND 1 M ROUGHNESS TO THE MAIN AND SIDE PASSAGES

	Resulting Tidal Heights (m)			
	Mu'a Branch		Nuku'alofa Branch	
	High	Low	High	Low
Original Model	1.12	0.33	0.84	0.71
5-m channel in main passage	1.18	0.16	0.91	0.76
5-m channel in main passage and 3-m channel in side passage	1.15	0.23	0.95	0.49

Freshwater Flux

Daily evaporation rates needed to compute the freshwater budget are shown in Table 5 for the sampling dates. The mean evaporation rate in the Pe'a sector is significantly higher than those for the other sectors (paired-sample t-test, $p < 0.05$). This high evaporation rate is due to higher temperatures in this shallowest part of the lagoon.

TABLE 5. EVAPORATION RATES BY SECTOR AND RAINFALL FOR EACH SAMPLING DATE

Date	Evaporation Rate (mm d^{-1})				Rainfall (mm d^{-1})
	Pe'a	Folaha	Vaini	Mu'a	
Sep 21	2.3	0.9	1.6	1.5	1.4
Sep 22	7.7	5.5	6.2	5.5	0.1
Sep 23	5.0	4.0	3.6	3.9	7.4
Sep 25	6.4	4.0	4.6	4.8	0
Sep 28	10.0	8.3	9.1	7.9	0
Sep 29	4.1	1.6	2.2	2.4	7.0
Nov 25	6.7	6.3	5.3	5.4	0.3
Nov 26	7.5	7.6	7.2	7.2	0.2
Sector means	6.2	4.9	5.0	4.8	
95% confidence interval of the mean	1.7	1.8	1.8	1.6	

Mean open ocean salinity during the two visits was 35.43 $^{o}/oo$. The mean salinity over two tidal cycles in the main channel was 33.95 $^{o}/oo$, or 4.2 percent freshwater. Salinity variations over two tidal cycles gave estimated freshwater fluxes of 4 and 5 x 10^4 m^3 per tidal cycle, or 8 and 10 x 10^4 m^3 d^{-1} (mean = 9 x 10^4). The side channel had an average salinity of 33.73 $^{o}/oo$ or 4.8 percent freshwater. Current and salinity variations were irregular, with calculated fluxes of 0.6 x 10^4 and 2.2 x 10^4 m^3 d^{-1} during each of two tidal cycles (mean = 3 x 10^4 m^3 d^{-1}).

The above fluxes and the evaporation and rainfall data were used to calculate groundwater input for the November sampling period. The inputs required to balance the freshwater budgets are 14.4 x 10^4 m^3 d^{-1} and 12.2 x 10^4 m^3 d^{-1} in the Mu'a and Nuku'alofa branches, respectively.

Groundwater input to the lagoon can be expected to be roughly proportional to watershed area. The watershed areas are listed in Table 1. The Nuku'alofa branch comprises 52 percent of the watershed area and receives 46 percent of the estimated groundwater input; the difference between these figures is well within the limits of accuracy imposed by the freshwater flux measurements.

Solution channels may supply a significant proportion of the freshwater input to the lagoon (Lao, 1979). To estimate this source of freshwater, salinity and flow were measured in all solution channels found by inspection of the lagoon perimeter at low tide. The total freshwater input from these sources was about 15 percent of the estimated total for the lagoon, entering the various sectors in rough proportion to the calculated groundwater input. Thus, most of the freshwater enters the lagoon by diffuse percolation up through lagoon sediments.

To calculate effective volume fluxes between sectors several assumptions were made. First, it was assumed that each sector was internally well mixed and could be represented by at most two stations. Second, it was assumed that the Folaha sector exchanges water directly with the ocean through both channels and not with the Mu'a sector. The third assumption was that groundwater inputs to each sector are proportional to watershed area, and the fourth that groundwater input was the same on all sampling days. The latter assumption is based on the long residence time (ca. 20 years; Lao 1979) in the groundwater lens.

The model for freshwater and volume flux calculations is:

$$Ri + Gi - Ei = \sum \Phi_{ij} \ (f_i - f_j)$$

where

Ri = rainfall in sector i ($m^3 \ d^{-1}$)
Gi = groundwater in sector i ($m^3 \ d^{-1}$)
Ei = evaporation in sector i ($m^3 \ d^{-1}$)
Φ_{ij} = effective volume flux between sectors i and j
f_i and f_j = proportion of freshwater in sectors i and j

Four Φ values were calculated from four equations to represent flux between Pe'a and Folaha, Folaha and the ocean, Vaini and Mu'a, and Mu'a and the ocean.

Table 6 lists the means of data used in the calculations and the resulting flux estimates. Calculations were made separately for the high and low measured values of freshwater flux in the channels for each of three dates. The September 28 data gave negative fluxes and thus were dropped from the analysis.

Exchange efficiency is the ratio of effective volume flux to tidal flux expressed as a percentage. Tidal exchanges were about 10 percent efficient, meaning that mixing of the water passing across the boundaries on each tidal cycle was only 10 percent complete. This is to be expected because the sectors are elonga-

TABLE 6. EFFECTIVE VOLUME FLUX ESTIMATES

	Sector			
	Pe'a	Folaha	Vaini	Mu'a
Sector area (km^2)	8.8	4.9	3.8	9.7
Sector volume ($10^6 m^3$)	6.8	7.3	4.5	19.4
Rainfall (mm d^{-1})	1.4	1.4	1.4	1.4
Evaporation (mm d^{-1})	6.7	6.2	5.4	5.5
Groundwater ($10^4 m^3 d^{-1}$)	10.1	2.1	8.4	6.0
Net freshwater m, $10^4 m^3 d^{-1}$	5.7	−0.6	7.1	2.0
Salinity (^{o}/oo)	25.67	31.35	26.70	32.85
Effective volume fluxes, $10^5 m^3 d^{-1}$ (mean ± 95% confidence limits of the mean)				
Between sectors	3.6 ± 1.1 (Pe'a–Folaha)		4.8 ± 2.5 (Vaini–Mu'a)	
Between sectors and ocean	4.5 ± 2 (Pe'a–Folaha)		12 ± 4 (Vaini–Mu'a)	
Residence times (days), with 95% confidence intervals				
By sector	19(15–25)	9(7–15)	9(6–20)	12(9–16)
By branch	31(17–76) (Pe'a–Folaha)		20(15–30) (Vaini–Mu'a)	
Entire lagoon	23(19–38) (all sectors)			
Exchange efficiency (%)				
Between sectors	18 ± 5 (Pe'a–Folaha)		8 ± 4 (Vaini–Mu'a)	
Between sector and ocean	12 ± 7 (Pe'a–Folaha)		11 ± 4 (Vaini–Mu'a)	

Note: Values given are means for September 23 and November 25–26, 1982 ted. The higher exchange efficiency between the Pe'a and Folaha sectors may be due to wind-driven circulation in the wide, shallow basin of the Pe'a sector.

The mean residence time for the entire lagoon is 23 days. The mean residence time for the Pe'a sector is higher than that for the other sectors but the difference is statistically significant only for the Folaha sector. The rather large confidence intervals are a result of the small number of sampling dates and the large difference between the two measurements of freshwater flux in the side channel. To get a better estimate of the residence times of the sectors, more samples would be required.

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Appendix A. Details of the Circulation Model

Terms used in model development are as follows:

Fixed terms:

- l = Length of channel (m)
- z = Depth of channel below chart datum (m)
- g = Gravitational constant ($m\ s^{-2}$)
- ρ = Density ($gmcm^{-3}$)
- Δ = Roughness factor (m)
- P = Plan area of lagoon branches (m^2)

Time-varying terms:

- u = Velocity ($m\ s^{-1}$)
- w = Width of channel (m)
- H = Height of channel above datum (m)
- h = Mean channel water column height (m)
- V = Volume flow rate ($m^3\ s^{-1}$)

Subscripts:

- c = channel
- f = reef flat
- o = ocean
- 1 = Mu'a branch
- 2 = Nuku'alofa branch

The model is based on a single balance of forces and conservation of mass. The balance of forces can be expressed as:

$$F = ma$$

or

$$\text{Pressure} - \text{Friction} = \text{Inertia}$$

Expressions for the forces are:

$$\text{Pressure} = \rho\, g\, (H_o - H_1)\, wh \qquad \text{(A1)}$$

$$\text{Inertia} = ma \approx \frac{\rho u^2}{2}\, wh \qquad \text{(A2)}$$

$$\text{Friction} = \frac{\rho u^2 lw}{32\left(\ln \dfrac{6.15\ h}{\Delta}\right)^2} \qquad \text{(A3)}$$

where

$$h = \bar{H} + Z$$

Expression A3 comes from equation 1.21 in Goncharov (1964) which gives an estimate of frictional forces in a channel.

Several assumptions are implicit in the above formulation. First, the temporal acceleration is neglected; i.e., that occurring as the mean stream velocity changes. Rough calculations reveal that this is a significant component only around slack water. Second, the flow is assumed to be a plane flow in which wall friction is neglected. This assumption is obviously valid for the reef flats and obviously not for the channels. The result is an underestimate of friction in the channels which is corrected for by the use of a large value for Δ. Third, the channels and reef flats are assumed to have sloping sides, but the effect of these is to change the width only; the depth used in the calculations is the average depth. Finally, water is assumed not to flow between reef flats and channels.

The equation for force balance is solved for U, which is:

$$U_{c_{ol}} = \left[\frac{g h_{ol} w_{ol} |H_o - Hi|}{\dfrac{h_{ol} w_{ol}}{2} + \dfrac{lw}{32 \left(\ln \dfrac{6.15\, h_{ol}}{\Delta} \right)^2}} \right]^{1/2} \operatorname{Sgn}(H_o - Hi)$$

for the main channel. The expression for the reef flats is the same except that the first term in the denominator, the inertial term, is omitted. Tidal heights are calculated from two differential equations

$$\frac{dH_2}{dt} = \frac{1}{P_1} \left[V_{c_{ol}} + V_{f_{ol}} - \left(V_{c_{12}} + V_{f_{12}} \right) \right]$$

$$\frac{dH_2}{dt} = \frac{1}{P_2} \left[V_{c_{12}} + V_{f_{12}} \right]$$

where

$$V_{ij} = u_{ij}\, w_{ij}\, h_{ij}$$

The equations were solved by a fourth order Runge-Kutta numerical integration method with a time step of 0.1 hr. The solution was started with assumed heights in the two lagoon branches and with a sinusoidal ocean tide forcing function. The tidal heights were used to calculate velocities, which were then used to calculate the differentials. The Runge-Kutta predictive procedure was then used to calculate the heights at the end of the time step.

WATER CHEMISTRY, PLANKTON ABUNDANCE, AND PRIMARY PRODUCTION

W.J. Kimmerer

The nutrient supply rate can affect the structure, species composition, diversity, and biomass of a marine ecosystem. Nutrients can enter shallow marine ecosystems via groundwater, runoff, sewage, and ocean water. Because the nutrient levels in the surrounding ocean are low and runoff is infrequent, most of the natural nutrient input to Fanga'uta Lagoon occurs through groundwater discharge. An additional source is sewage outfall from the hospital at the western end of the Nuku'alofa branch.

Typically, nutrients entering a shallow tropical marine ecosystem are rapidly taken up and converted to biomass by planktonic or benthic plants. This is particularly true for the limiting nutrient; i.e., the nutrient which, if added to the system, would stimulate further growth. Thus, to investigate nutrient supply, one cannot examine limiting nutrient concentration but must look either at the products of nutrient uptake or at other nutrients. In most marine ecosystems nitrogen is the limiting nutrient; it enters the water as nitrate or ammonium and is rapidly converted to dissolved and particulate organic nitrogen.

The effects of nutrient enrichment are increased plant production and biomass. Water clarity is often reduced because of the production of particles associated with plant growth -- phytoplankton, zooplankton, and detritus. This increase is modified by wind-driven stirring which resuspends detrital particles. Thus, a shallow, wind-stressed system is likely to be turbid regardless of the nutrient input.

Another modifying influence is the water residence time. If the residence time is long, then both the ambient levels of nutrients and organic matter and the rate of loss of nutrients to the benthos should be high.

Measurements of water chemistry and productivity made during the September-October and November visits are given below. Information is also provided on the flow of nutrients into and out of the lagoon and on nutrient utilization within the lagoon.

METHODS

Water samples were collected from outboard-motor skiffs at several stations in the lagoon (Figure 4) and in the ocean, as well as from wells, ponds, and springs along the shoreline. Water was collected by dipping brown polyethylene bottles just below the surface. Samples to be tested for salinity were put into clear polyethylene bottles for storage at ambient temperature. Nutrient samples were filtered immediately through precombusted GF/C glass fiber filters and frozen. Surface zooplankton samples were taken with a 200-μm mesh, 0.5-m diameter

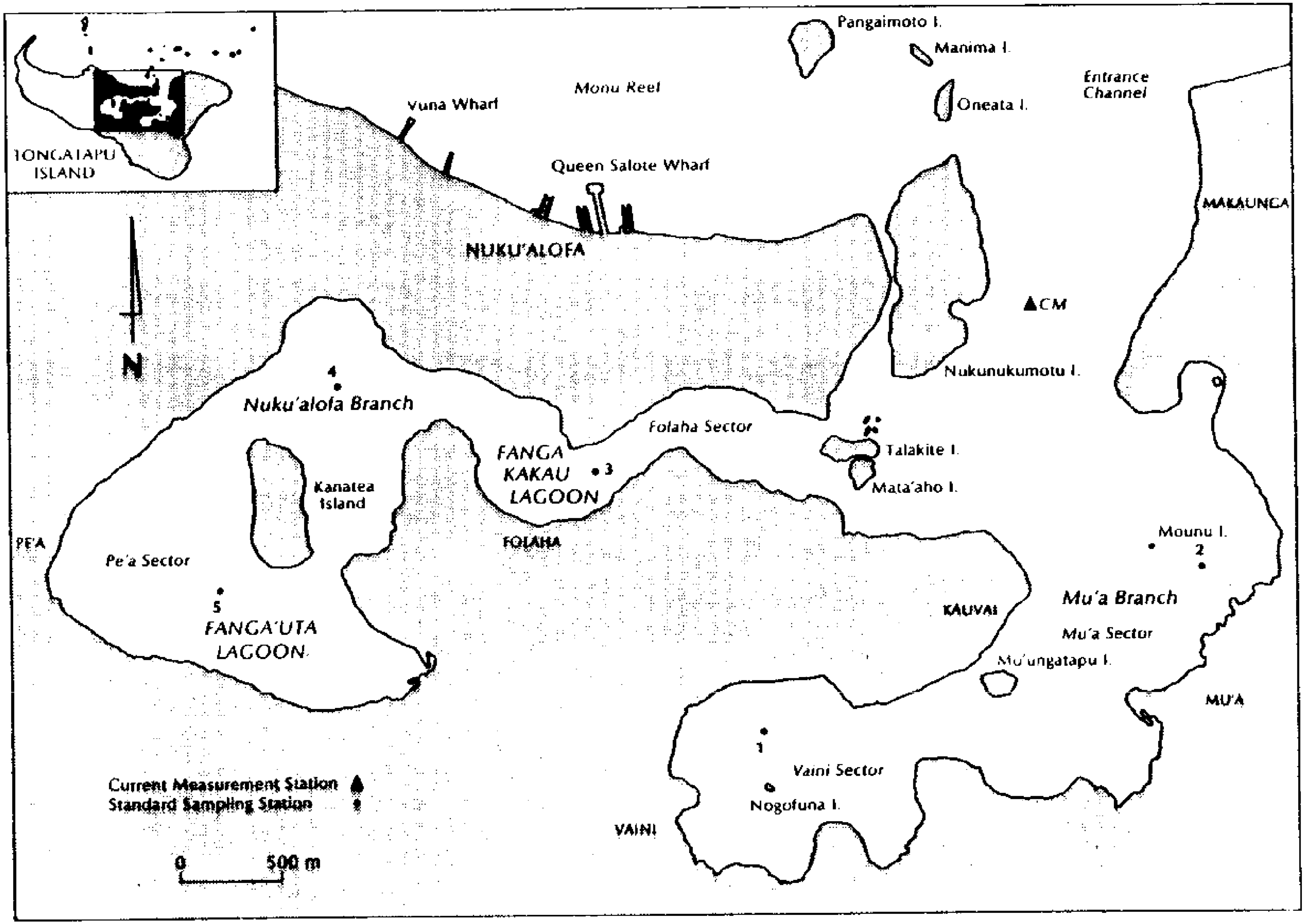

Figure 4. Locations of sampling stations in Fanga'uta Lagoon

net and then preserved in formaldehyde for later subsampling and counting.

All other water samples were held at ambient temperature in a bucket or cooler for transport to the laboratory. *In situ* temperature and salinity were measured with a Bendix RS5-3 field salinometer.

In the laboratory pH of the water samples was measured with a digital pH meter. Aliquots of 150 to 300 ml were then filtered onto GF/C filters which were precombusted for particulate carbon and nitrogen but not for chlorophyll. The filters for carbon and nitrogen determination were dried at 60 degrees C; those for chlorophyll were placed in 90 percent acetone and stored frozen in the dark. All frozen samples were transported on ice to Hawaii for analysis.

Samples for productivity were collected at dawn at stations 2 and 4 (Figure 4). Samples were inoculated with ^{14}C bicarbonate and incubated *in situ* in two light and one dark 125-ml glass-stoppered bottles, each at depths of 25 and 75 cm. Aliquots of the inoculum were put into a CO_2 trap for calibration. Water samples for alkalinity were filtered and stored unfrozen. Just before sunset, bottles were retrieved, and then transported in the dark to the laboratory for filtration on GF/C filters. The filters were then dried in a dessicator.

All analyses were done using standard methods (Strickland and Parsons, 1972). Nutrients were analyzed on a Technicon AutoAnalyzer II and total nitrogen and phosphorus by UV oxidation followed by nutrient analysis. Chlorophyll was measured fluorometrically. Carbon and nitrogen were measured using a Hewlett-Packard Model 185 B CHN analyzer. Samples for primary productivity were counted using a Beckman liquid scintillation counter.

RESULTS AND DISCUSSION

Water Chemistry

Nutrients in groundwater were high, as expected (Table 7). In particular, nitrate and silica were extremely high, but phosphate was proportionately low. The N:P ratio was 130, higher than the ratio required by plants. This high ratio suggests that phosphorus, not nitrogen, may limit plant growth in the lagoon.

Light penetration, as measured with a Secchi disk, was 1.5 to 2 m in the Folaha and Mu'a sectors and only 0.3 to 1.1 m in the Pe'a sector. In the Vaini sector the bottom was always visible at 1.5 to 1.8 m so the Secchi disk depth could not be measured. Only the Pe'a sector had noticeably more turbid water, especially during windy periods. This is the shallowest and widest sector, so wind influence on the bottom is greatest.

TABLE 7. NUTRIENT CONCENTRATIONS IN GROUNDWATER

Nutrient	Concentration, μg-at l^{-1}	
	Mean	95% C.L.
Nitrate	78	57-99
Ammonium	<0.5	--
Phosphate	0.6	0.25-0.95
Silica	310	240-380

Note: Means and 95% confidence limits of the mean (N=16)

Variation in water chemistry within a single sector was examined on September 22, 1981. Samples were taken at six stations in the Pe'a sector. Differences in a particular measurement among samples from the six stations reflect sampling and analytic variability as well as spatial differences and give an idea of the confidence to be placed in samples from a single station within a sector.

Coefficients of variation (CV) indicate the degree of uniformity in each variable. The CV for percentage of freshwater (determined from salinity) indicates that Pe'a sector was fairly well mixed internally (Table 8). A salinity gradient from north to south in the lagoon is a result of mixing processes with the Folaha sector and of freshwater entry along the lagoon margin. Sampling with the salinometer revealed little small-scale variability in salinity, suggesting that mixing was thorough and confirming the conclusion that groundwater inputs were diffuse (see "Circulation and Hydrology" section).

Of the other variables, only nitrate and ammonium had CVs over 35, and these were caused by a single, possibly contaminated, sample. Other than that sample, nitrate was near the limit of detection. Clearly, even near the groundwater sources, uptake is rapid enough to effectively strip the incoming water of nutrients. There was no evidence that either nitrogen or phosphorus was first to limit production, so the limiting nutrient remains unidentified.

TABLE 8. SPATIAL VARIABILITY IN PE'A SECTOR WATER CHEMISTRY, SEPTEMBER 22, 1981

Variables	Mean	Standard Deviation	Coefficient of Variation (%)
Freshwater (%)	28.1	3.0	11
Nitrate	0.14	0.19	135
Ammonium	0.57	0.24	42
Phosphate	0.08	0.03	35
Silica	96	10	10
Dissolved organic nitrogen	27.1	4.4	16
Particulate nitrogen	9.4	1.9	20
Total nitrogen	37.9	4.3	11
Particulate organic carbon	120	24	20
Particulate inorganic carbon	5.9	1.9	32
Organic C:N ratio	12.8	1.9	15
Chlorophyll (g m^{-3})	3.0	0.5	17
Secchi depth (cm)	47	15	32

Note: All values in μg-at l^{-1} unless otherwise noted (N=6).

Summary statistics for several water chemistry variables measured or calculated for all lagoon sectors are listed in Table 9. These values are based on means for each day so as to prevent bias toward days when numerous samples were taken. More samples were taken in the Mu'a and Pe'a sectors than elsewhere. Still, significant differences can be noted among the sectors. Phosphate and nitrate were generally near the limits of detection except for nitrate in the Vaini sector. The high values there were not accompanied by elevated values of phosphate and silica so these high values are enigmatic. Ammonium showed high variability and no consistent differences among the sectors. Silica was highest in the Pe'a sector and lowest in the Mu'a sector; the differences among sectors were significant (analysis of variance [ANOVA], $p < 0.0001$).

Dissolved organic nitrogen, a product of nitrogen uptake and subsequent release of organic matter, was also highest in the Pe'a sector. Differences among sectors were smaller than those for silica but still significant (ANOVA, $p < 0.0005$).

The various measures of particulate matter in the lagoon showed several patterns. Chlorophyll values were highly variable, possibly because of degradation during the long period between collection, filtration, and ultimate analysis. This variability masks any difference among lagoon sectors. Particulate organic carbon was about threefold higher in the Pe'a sector than in the other three sectors, and the difference was significant (ANOVA, $p < 0.002$). This is consistent with the Secchi disk

TABLE 9. SUMMARY STATISTICS FOR WATER CHEMISTRY VARIABLES IN FANGA'UTA LAGOON SECTORS

Variable	Sector			
	Pe'a	Folaha	Vaini	Mu'a
Nitrate	0.11 ± 0.06(6)	0.11 ± 0.08(3)	0.97 ± 0.5(3)	0.4 ± 0.3(5)
Ammonium	0.7 ± 0.4(6)	0.5 ± 0.01(3)	0.05 ± 0.07(3)	0.7 ± 0.3(5)
Phosphate	0.08 ± 0.04(6)	0.5 ± 0.004(3)	0.04 ± 0.01(3)	0.09 ± 0.08(5)
Silica	91 ± 19(6)	48 ± 3(3)	39 ± 11(3)	17 ± 4(5)
Dissolved organic nitrogen	23 ± 3(5)	16 ± 0.5(3)	11 ± 3(3)	10 ± 2(5)
Particulate nitrogen	10 ± 1(3)	6 ± 1(2)	4 ± 3(3)	3.0 ± 0.2(3)
Total nitrogen	34 ± 4(3)	21 ± 4(2)	17 ± 4(3)	13 ± 2(3)
Particulate organic carbon	116 ± 10(3)	40 ± 8(2)	41 ± 27(3)	39 ± 3(3)
Particulate inorganic carbon	3.3 ± 1.7(3)	6.5 ± 2(2)	5 ± 2.5(3)	4.5 ± 1.3(3)
Organic C:N ratio	12 ± 1(3)	7 ± 0.3(2)	9.2 ± 0.8(3)	13 ± 2(3)
Chlorophyll mg m^{-3}	1.8 ± 0.9(6)	1.7 ± 0.3(2)	1.9 ± 1.6(3)	1.2 ± 0.6(5)
% plant carbon	11 ± 6(3)	17 + (1)	26 ± 5(3)	18 ± 5(3)

Note: Mean ± standard deviation (N). All values in μg-at l^{-1} unless otherwise noted.

visibilities, which were about 33 percent as much in the Pe'a sector as elsewhere. The reduction in visibility is evidently caused by particulate organic matter unrelated to phytoplankton abundance, namely detritus stirred off the bottom by wind.

The approximate carbon content of particulate matter containing chlorophyll and degradation products was calculated by multiplying total pigment values by 4.2 (carbon:chlorophyll weight ratio assumed to be 50). This fraction includes phytoplankton and detritus recently derived from phytoplankton or benthic plants. This fraction comprised between 3 and 30 percent of the particulate organic carbon; as could be expected from the chlorophyll and carbon results, this proportion differed significantly among sectors, being lowest in the Pe'a sector (ANOVA, $p < 0.025$). Particulate inorganic carbon represented only a small fraction (0 to 8 percent) of total carbon. No differences among sectors were observed in the concentration or proportion of inorganic carbon. This carbon fraction includes small carbonate-containing organisms and detritus derived from the predominantly carbonate rock of the island. The low proportion occurs because of a near absence of physical erosion in this low-energy lagoon.

Particulate nitrogen is related to particulate organic carbon by the C:N ratio. This ratio varied between 9 and 15 and was generally higher in the Pe'a and Mu'a sectors. The C:N ratio of living zooplankton is around four and that of phytoplankton around six; a higher ratio indicates the presence of detritus. Thus, the contribution of detritus to organic carbon was evidently highest in the Pe'a and Mu'a sectors.

Total nitrogen (i.e., the sum of particulate and dissolved organic nitrogen, ammonium, and nitrate) varied significantly among sectors (ANOVA, $p < 0.002$). Again, the highest values were in the Pe'a sector and lowest in the Mu'a sector.

The patterns of dissolved and particulate matter described above can be summarized by a consideration of the three important forcing functions in the lagoon: nutrient input, washout, and wind mixing. The nutrients entering the lagoon in the groundwater are almost immediately taken up by plants. Much of the uptake occurs in the plankton, which in effect converts inorganic nutrients to dissolved and particulate organic matter. This material is then diluted out of the lagoon by tidal mixing. If there were no wind effect, one would expect concentrations of organic matter to be highest in the sectors with the longest residence times. Superimposed on this effect is the influence of wind mixing. It is most apparent in the Pe'a sector which is shallow and wide, has a muddy bottom with little seagrass (see "Fish and Benthic Communities" section), and is surrounded by land having little vertical relief. The Folaha sector, in addition to greater dilution from the sea, has a short fetch for wind mixing and is surrounded by low bluffs that help to shield it from wind. The Vaini sector is also well protected and small. Although shallow, this sector has a thick carpet of seagrass on the bottom that stabilizes the sediment, further reducing the effect of wind. The Mu'a sector has a muddy bottom and is large and poorly sheltered, but it is also deep. The combination of depth and short residence time keeps the total concentration of materials low here, but some resuspension of detritus is taking place, as suggested by the high C:N ratio.

Mass Balance

The effective mass fluxes determined in the previous section were used to construct a crude model of nitrogen and silica flow between lagoon sectors. To complete this model the mean concentrations shown in Tables 7 and 9 and concentrations in the open ocean samples of 8 μg-at l^{-1} for total nitrogen and 2 for dissolved silica were used. Total nitrogen was used in the model because the difference between input and output in a sector is the uptake or release by the benthos in that sector. Nitrogen is of particular interest because it is potentially the limiting nutrient and the concentrations of all forms are known. Phosphorus was not used because there were no data on particulate phosphorus. Dissolved silica was used as a tracer of excess nutrient since it is plentiful throughout the lagoon.

The mass balance model shows the fluxes of total nitrogen and dissolved silica into each sector, between sectors, and between the lagoon and the ocean (Table 10). Overall, the input of nitrogen in groundwater to the lagoon is 21 Kmoles d^{-1} and the output is 12; the difference is uptake or sedimentation, which occurs in all sectors. For silica the input is 81 Kmoles d^{-1} and the output 41, so 40 Kmoles d^{-1} remains in the lagoon.

Some concern was expressed over sewage input to the Pe'a sector from the hospital sewage outfall. Strictly in terms of nutrients, using reasonable estimates of the number of people at the hospital and daily per capita nutrient production, this input is insignificant compared with that from the groundwater. However, the addition of more lagoon sewage outfalls should be discouraged.

Based on the calculated uptake rates in each sector, the uptake per unit of lagoon area was determined (Table 10). These figures are presented without confidence limits because of the complications involved in their calculations. The confidence bands around these values are necessarily large because of the errors associated with the flux estimates and the variability in measurement of concentrations. Thus, only crude comparisons are realistic.

TABLE 10. MATERIAL FLUX MODEL FOR TOTAL NITROGEN AND DISSOLVED SILICA

	Pe'a Sector	Folaha Sector	Vaini Sector	Mu'a Sector
	Total Nitrogen			
Input in groundwater	8.0	1.3	6.6	4.7
Flux with adjacent sector	-6.0	6.0	-1.9	1.9
Flux to ocean	0	-6.2	0	-5.9
Uptake (net loss to benthos)	-2.0	-1.1	-4.7	-0.4
Sector area (km^2)	8.8	4.9	3.8	9.7
Uptake per unit area (mmoles $m^{-2}d^{-1}$)	0.2	0.2	1.2	0.1
	Dissolved Silica			
Input in groundwater	31.0	6.0	26.0	18.0
Flux with adjacent sector	-20.0	20.0	-11.0	11.0
Flux to ocean	0.0	-22.0	0.0	-18.0
Uptake (net loss to benthos)	-11.0	-4.0	-15.0	-11.0
Sector area (km^2)	8.8	4.9	3.8	9.7
Uptake per unit area (mmoles $m^{-2}d^{-1}$)	1.3	0.8	3.9	1.1

Note: Fluxes are in Kmoles d^{-1} and are positive for flux into the sector.

The results of these calculations show that the Vaini sector apparently incorporates much more of the incoming nitrogen and silica than do the other sectors on an areal basis. The other sectors all incorporate these materials at about the same rate. This is consistent with the observed difference in bottom types: the Vaini sector is the only one with nearly complete seagrass cover. In this sector the seagrasses and associated algae are probably actively taking up nutrients and sequestering them and not releasing much back to the water.

Two facts can be combined to support the above hypothesis. One is that the mean seagrass biomass per unit area in the Vaini sector is two- to fourfold higher than that in the other sectors (see "Fish and Benthic Communities" section). The second is that seagrass specific productivity, which was not measured, is likely to be highest in the Vaini sector because the water is shallow and clear. High specific production and high biomass are likely to be accompanied by high nutrient uptake.

The picture that emerges from these calculations and from the discussion of material concentration is that nutrient fluxes in the Vaini sector are dominated by benthic processes and those in the Pe'a sector by plankton and detritus. The Mu'a and Folaha sectors, having shorter residence times and greater depths, tend to be dominated more by planktonic processes and fluxes of materials from the Pe'a and Vaini sectors.

The approximate rate of infilling of the lagoon can be inferred from the data on nutrient uptake if it is assumed that terrigenous inputs are insignificant. If it is then assumed that the composition of sediments is similar to that of suspended matter in the Pe'a sector, that the dry matter in these sediments is 50 percent carbon by weight, and that the dry weight density in the sediments is 1 g/cc, then the rate of infilling is about 3 mm per century. This rate could be increased several orders of magnitude by just a few storms causing runoff into the lagoon; thus, the above estimate may be far too low, and data on sediment composition will be needed to assess the importance of terrigenous material.

Plankton Productivity

Plankton productivities were measured on September 25 and 29, 1981. On both dates the daily productivity (Table 11) was significantly higher at station 4 in the Pe'a sector than at station 2 in the Mu'a sector ($p < 0.05$, Fisher exact probability test). In addition, plankton productivities were higher on September 25 than on September 29 ($p < 0.05$). Part of this difference was due to chlorophyll concentration.

TABLE 11. PRIMARY PRODUCTION AND RELATED VARIABLES IN FANGA'UTA LAGOON

Date	Sector	Primary Production				
		Raw ($mgC\ m^{-3}d^{-1}$)	Corrected for Respiration ($mgC\ m^{-3}d^{-1}$)	Chlorophyll ($mg\ m^{-3}$)	Productivity Index ($mgC\ (mg\ Chl)^{-1}\ d^{-1}$)	Growth Rate (d^{-1})
Sep 25 81	Pe'a	149 ± 42	127	1.34	95	1.9
	Mu'a	88 ± 16	75	1.24	60	1.2
Sep 29 81	Pe'a	69 ± 28	59	0.85	69	1.4
	Mu'a	21 ± 2	18	0.96	19	0.4

Note: Mean ± 95% confidence limits (N=4)

The net daily production was calculated assuming a dark respiration loss of 15 percent. Productivity index, the ratio of daily production to chlorophyll, was also determined. Finally, the daily growth rate was calculated assuming a carbon:chlorophyll ratio of 50:1. The results of this calculation (Table 11) give a range of growth rates between 0.4 and 1.9 d^{-1}, with the higher growth rates in the Pe'a sector.

The higher values of growth rate are near the maximum for some orders of phytoplankton. The cause of the lower values on September 29 is probably related to light levels; there were 10.7 hours of sunshine on September 25 vs 0.6 hours on September 29, as recorded by the local weather station. The higher growth rates in the Pe'a sector are probably related to higher nutrient availability through recycling from the larger pool of dissolved and particulate organic matter.

Zooplankton

Zooplankton samples were dominated numerically by a species of the copepod Bestiola (formerly Acrocalanus). Other common taxa included the neustonic copepod Labidocera pavo, the chaetognath Sagitta bipunctata, and crab and shrimp larvae. An unidentified large lobate ctenophore was present in all samples taken in the Nuku'alofa branch but only found once in the Mu'a branch; however, numerous dead individuals were seen in shallow waters. The highest copepod abundances (over 10 per liter) were found in the Mu'a branch, but no other patterns were apparent. Thus, little can be said except that Bestiola appears to be more abundant in the clearer waters of the Mu'a branch.

THE CORALS: A CLUE TO FANGA'UTA'S PAST

L.P. Zann

Well-developed fringing and coral patch reefs surround the northern shores of Tongatapu, an uplifted coral reef from Pliocene to Quaternary times. Coral reefs, among the most productive of all ecosystems, provide food and habitats for many important edible species in the South Pacific. In addition, they are a source of sand and rock fill for construction purposes.

The coral reefs of Fanga'uta Lagoon were briefly examined to ascertain their ecological importance and to look for recent mortalities or changes. Corals, having low tolerances to environmental changes and especially to high silt levels, are good indicators of environmental disturbances (e.g., Johannes, 1975). Their skeletons remain long after their death to indicate past changes.

METHODS

Two reefs off the lagoon entrance, eight small patch reefs along the main passage, three transects along the minor channel, and each of the 106 lagoon stations were examined for corals (see "Fish and Benthic Communities" section). Dominant genera were noted, percentage of cover was estimated visually, and specimens were collected for later identification.

Reefs were examined by skin and scuba diving in the clear entrance waters, but in the more turbid parts of the lagoon transects were made at low tide and grabs were used in deeper parts. Aerial photography was useful in identifying large coral heads. For consistency, dive surveys were confined to reef edges and limited to 10-minute duration at each station.

RESULTS

The coverage of living corals and the number of coral genera present declined rapidly as one progressed into Fanga'uta Lagoon through the entrance channel. The reef edge of Pangaimotu Island had at least 12 genera of stony corals but this number declined to four to ten at the lagoon mouth, to three to six by the southern end of Nukunukumotu Island, and to only two at the southern end of the passage (see Table 12 and Figure 5).

Only one genus, _Porites_, extended into the Mu'a branch of Fanga'uta Lagoon. Living coral coverage declined from 70 percent outside the entrance, to 15 to 30 percent at the entrance, to much less than 0.1 percent in the lagoon. However, as one progressed into the lagoon the proportion of dead coral rapidly increased (Table 13).

TABLE 12. CORAL SPECIES OF FANGA'UTA LAGOON AND ADJACENT REEFS, TONGATAPU

Species	Location	Species	Location
SCLERACTINIA			
Stylophora pistillata	D	Montipora cf. ramosa	A,B,D,G
Seriatopora hystrix	C		I
Pocillopora damicornis	A,B,C,F	Montipora sp. (ramosa group)	E
	G,I	Astreopora cf. myriophthalma	D
Pavona cactus	D	Goniastrea pectinata	D
Fungia fungites	A,B,C,D	Favia cf. pallida	C
Cycloceris cf. vaughani	D	Favites abdita	G
Porites cf.murrayensis	J,M	Platygyra cf. daedalea	E
Porites andrewsi	G	Leptoria phrygia	D
Porites cf. lobata	D	Lopophyllia hemprichi	D
Acropora cf. kenti	D	Echinophyllia cf. echinata	B
Acropora cf. formosa	C,D	Acrhelia horrescens	A
Acropora cf. pulchra	B,C	Echinopora lamellosa	A
Acropora species 1	F	Dendrophyllia sp.	A
Acropora species 2	C	Turbinaria cf. reniformis	F
HYDROZOA			
Millepora platyphyllia	A-1		
ALCYONARIA			
Sinularia sp.	A,B	Lobophyton sp.	A,B
Sarcophyton sp.	A,B,C	Dendronephthya sp.	C

Note: Locations are shown in Figure 5. Identifications from Veron and Pichon (1976); Veron, et al., (1977), and University of the South Pacific Reference Collection (ident. Pichon; Cardin Wallace).

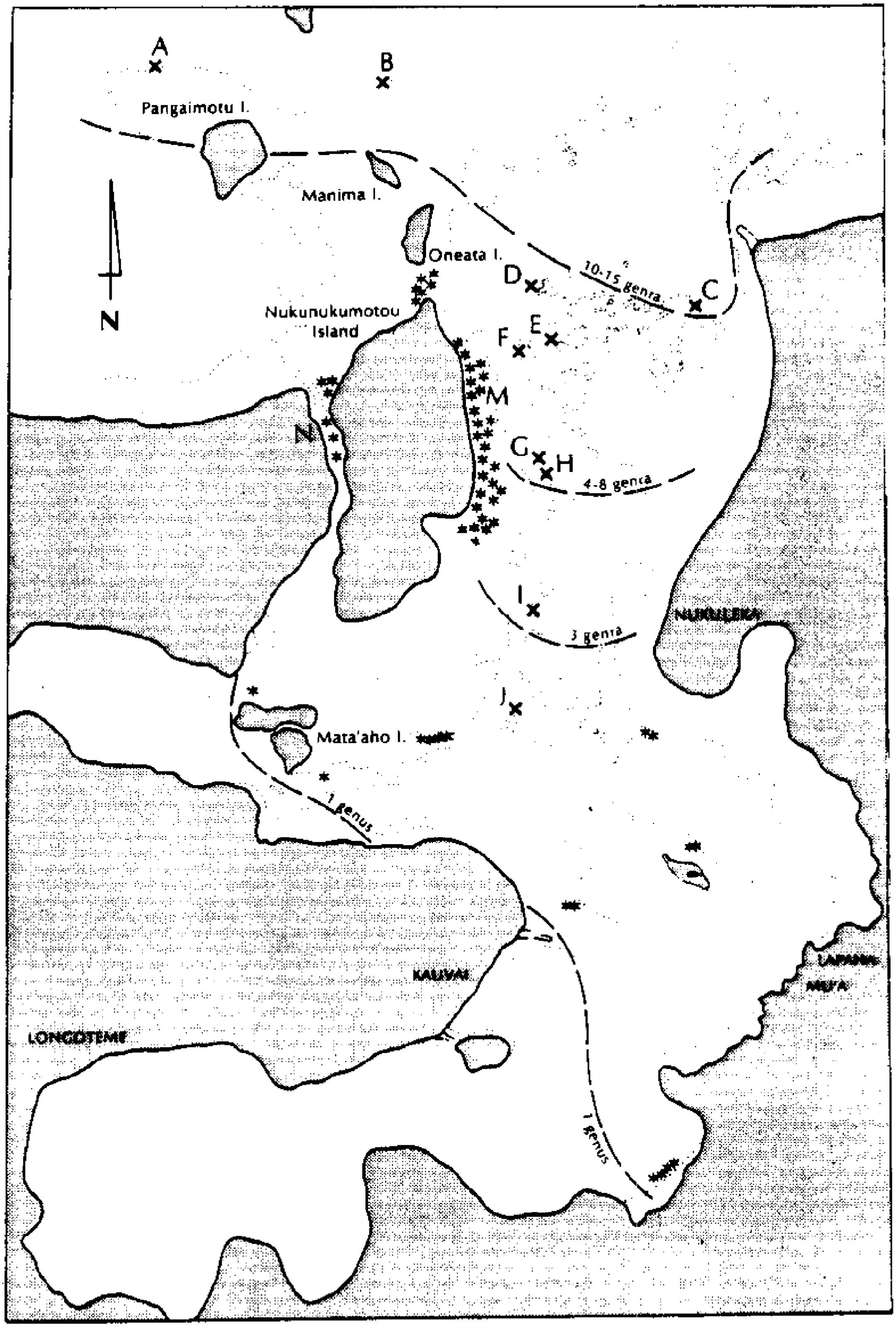

Figure 5. Genera of stony coral at dive sites, Fanga'uta Lagoon

TABLE 13. NUMBER OF GENERA OF STONY AND SOFT CORALS FOUND AT FANGAU'TA LAGOON STATIONS

GENERA	A	B	C	D	E	F	G	H	I	J
STONY CORALS										
Porites	X		X	X	X	X	X			X
Millepora	X	X	X	X	X	X	X	X	X	
Acropora	X	X	X	X	X	X	X	X		
Pocillopora	X	X	X			X	X		X	
Favia	X	X	X		X		X	X		
Montipora	X	X		X			X		X	
Fungia	X	X	X	X						
Stylophora		X		X		X				
Favites	X	X		X						
Goniastrea	X			X						
Lobophyllia		X		X						
Seriatopora			X							
Acrhelia	X									
Echinophyllia			X							
Cycloceris				X						
Platygyra								X		
Echinopora	X									
Leptoria				X						
Astreopora										
Pavona				X						
Turbinaria						X				
Dendrophyllia	X									
TOTAL	12	9	8	12	4	6	6	4	3	1
SOFT CORALS										
Sarcophyton	X	X	X							
Sinularia	X	X								
Lobophyton	X	X								
Dendronephthya			X							
TOTAL	15	12	10	12	4	6	6	4	3	1
% LIVING CORAL COVER	60	70	30	20	1	15	<0.5	<0.5	<0.5	+

The reefs outside the lagoon (stations A and B in Figure 5) were typical of sheltered oceanic environments, having a high species diversity and living coral cover. Those patch reefs at the entrance (stations C, D, E, and F in Figure 5) were more typical of inshore estuarine areas, with low diversity, low coverage of living coral, and a large amount of dead coral and rubble. The tops of these reefs were entirely dead and dominated by coralline algae, mainly Halimeda. The sides of the reefs consisted mainly of coral rubble (Acropora), with some living coral present. The surrounding sea floor was covered by very fine silt or mud.

The sides of the patch reefs at the southern or lagoon end of the channel (station I and J in Figure 5) consisted of dead coral rubble largely infilled with fine sediment, whereas the tops were of fine calcareous sand and mud, bound by seagrasses and Halimeda.

Porites (Plate 1), found in parts of the Mu'a branch, is a massive coral forming large heads or "bommies" (pupu'a), or flattopped "microatolls" in intertidal areas. Individual heads are shown in Figure 5.

Plate 1. Small Porites head off Nukunukumotu I., site M. This was found 0.3 m to 0.4 m below the level of the dead microatolls nearby.

Many dead "microatolls" were seen on the sandflats on both sides of Nukunukumotu Island (stations M and N in Figure 5) (Plate 2). Porites heads were present but these were small (5 cm) unattached "pebbles," some cup-shaped, or slightly larger (to 30 cm) rounded heads attached to dead coral. Significantly, all living coral were found 20 to 40 cm below the upper level of the dead microatolls. This difference in levels indicates either a sudden change in sea level or an elevation of the land. The latter most likely occurred for Tonga is situated in a geologically active zone and earthquakes are frequent.

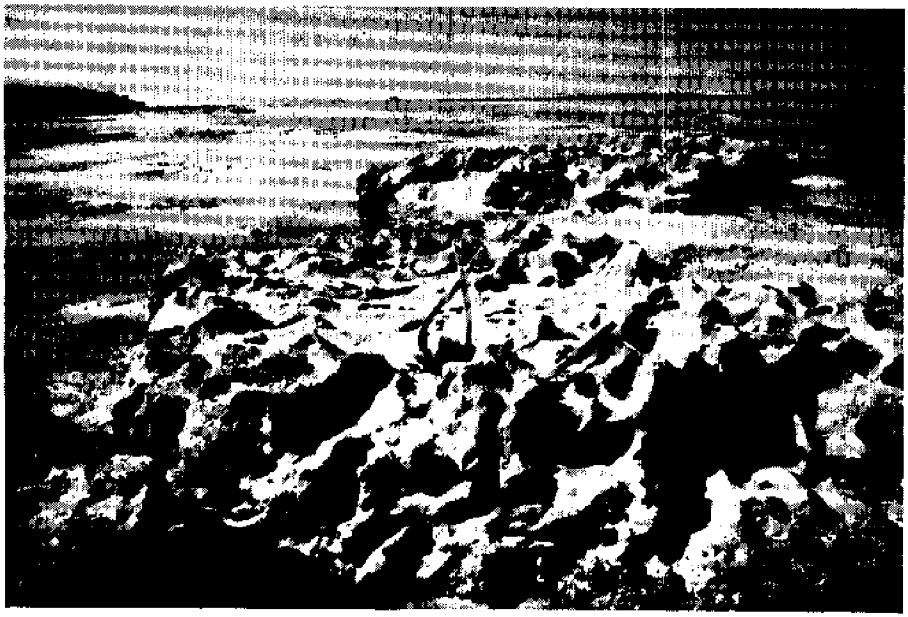

Plate 2. Dead, elevated, and eroded Porites microatolls off Nukunukumotu I, site M

The time of death of the elevated microatolls is unknown. Some were considerably eroded or weathered, others were better preserved (Plates 2 and 3). In some, the corallites were still discernible and the dead corals could be identified as Porites. One Favia was identified at station N (Plate 3). Several dead heads were broken up and some coral borers (Lithophaga bivalves and sipunculid worms) were found. Little chemical alteration of the heads was evident; the inner parts were still white and crumbly. It is the author's opinion that the heads were killed in very recent times geologically, perhaps between 40 and 200 years ago.

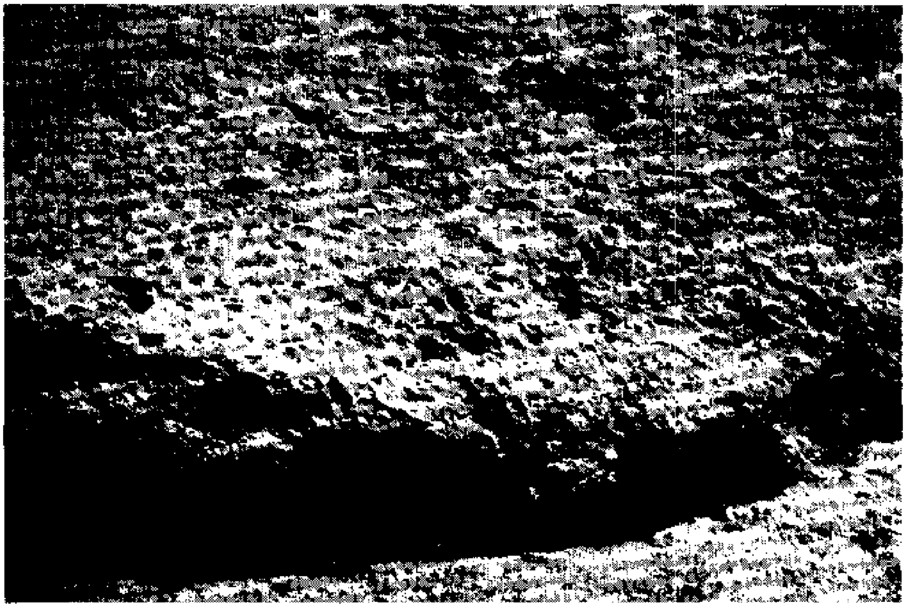

Plate 3. Dead, elevated, favid microatoll off Nukunukumotu I, site N. (Note: calyces still evident)

DISCUSSION

Corals comprise an insignificant part of Fanga'uta Lagoon. Even where present on the entrance patch reefs, living coral cover constitutes generally less than 1 percent of the reef area.

The rapid reduction in the amount of coral genera as one moves from the sea into the lagoon reflects the low tolerance of most corals to reduced salinities and high suspended silt loads in the lagoonal waters (see "Circulation and Hydrology" section). Porites had the widest distribution (and highest tolerances), followed by Millepora (a hydrocoralline). Acropora (several species present), Pocillopora, and Montipora also extended some distance into the lagoon.

The large amount of dead coral on the patch reefs at the entrance is not unusual in an inshore estuarine location. However, the large amount of Acropora rubble on the inner patch reefs and a complete absence of living Acropora suggest that conditions which were once favorable to its growth have now changed. The causes are not known, but elsewhere similar mortalities of Acropora have been attributed to high siltation resulting from changes in land use such as dredging, or to natural phenomena such as unusually heavy rainfall and cyclones (Johannes, 1975).

The presence of elevated, dead Porites "microatolls" around Nukunukumotu Island indicates a large scale disturbance in the vicinity of the entrance channel in recent times. It appears that an uplift occurred in this region between 40 and 200 years ago. An uplift apparently occurred during earthquake activity about 1914 (S. Tongilava: personal communication). This corresponds to the state of degradation of the corals.

An uplift of 20 to 40 cm would be responsible for large-scale mortality in the Acropora-dominated patch reefs in the channels and subsequent alteration to the water budget of Fanga'uta Lagoon, especially of the Nuku'alofa branch which is particularly isolated from the sea by shallow sand banks in the vicinity of Mata'uho Island.

The local belief that the lagoon is rapidly shoaling and that mangroves are encroaching the lagoon may be correct in light of an uplift in the region of the sea entrance.

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FISH AND BENTHIC COMMUNITIES

R.E. Brock

Benthic communities and their productivity are important in that they provide much of the sustenance for the fish and crustacean components exploited by human beings. Thus, a knowledge of these communities is a key to understanding the forcing functions that regulate fish and crustacean abundance and hence their fisheries. The objectives of this study were to describe the benthic communities, determine their productivity, and relate the production to the fisheries of Fanga'uta Lagoon.

Fanga'uta Lagoon is dominated by extremely productive soft substratum communities which are characteristic of estuarine waters. These productive communities are usually of great importance to humans as a source of protein due to their proximity and ease of exploitation. Because of this proximity and easy access, pollution and overfishing frequently occur. The latter has been a problem in Fanga'uta Lagoon for some time. Thus, an additional objective of this study was to elucidate these problems and provide guidelines for their improvement.

MATERIALS AND METHODS

Initial inspection of the lagoon's benthic communities dictated that a number of methodolgies be used in sampling the benthos due to a wide range in organism sizes, life history modes, substratum differences, and generally poor water clarity. Thus, in the inner and midsections of the lagoon, dredge and grab sampling methods were used extensively; towards the lagoon entrance, a number of visual census techniques were utilized.

Sampling was carried out at discrete stations generally along imaginary "transect lines" between prominent points in the lagoon. Stations were numbered consecutively; their approximate locations are shown in Figure 6. Within the lagoon, sampling was primarily by dredge and grab at deeper stations (greater than 50-cm depth). At shallower stations, the grab was used and a visual appraisal made of the surrounding macrobenthic components.

Seagrasses and macroalgae were quantitatively assessed by use of the grab representing a random 150 cm^2 sample. In the laboratory, algae and seagrasses were sorted to species, patted with towels to damp dryness, and weighed. Benthic algal and seagrass standing crops were calculated on a square meter basis for each of the two branches and connecting channels of Fanga'uta Lagoon. These values were averaged over 1 m depth intervals for the entire lagoon. In the field, water depth measurements were taken at all stations. Through the use of aerial photographs and these water depth measurements at known points, a bathymetric map of Fanga'uta Lagoon was constructed (Figure 2). Areas in each bathymetric division (1 m) were calculated and used in determining benthic algal and seagrass standing crop.

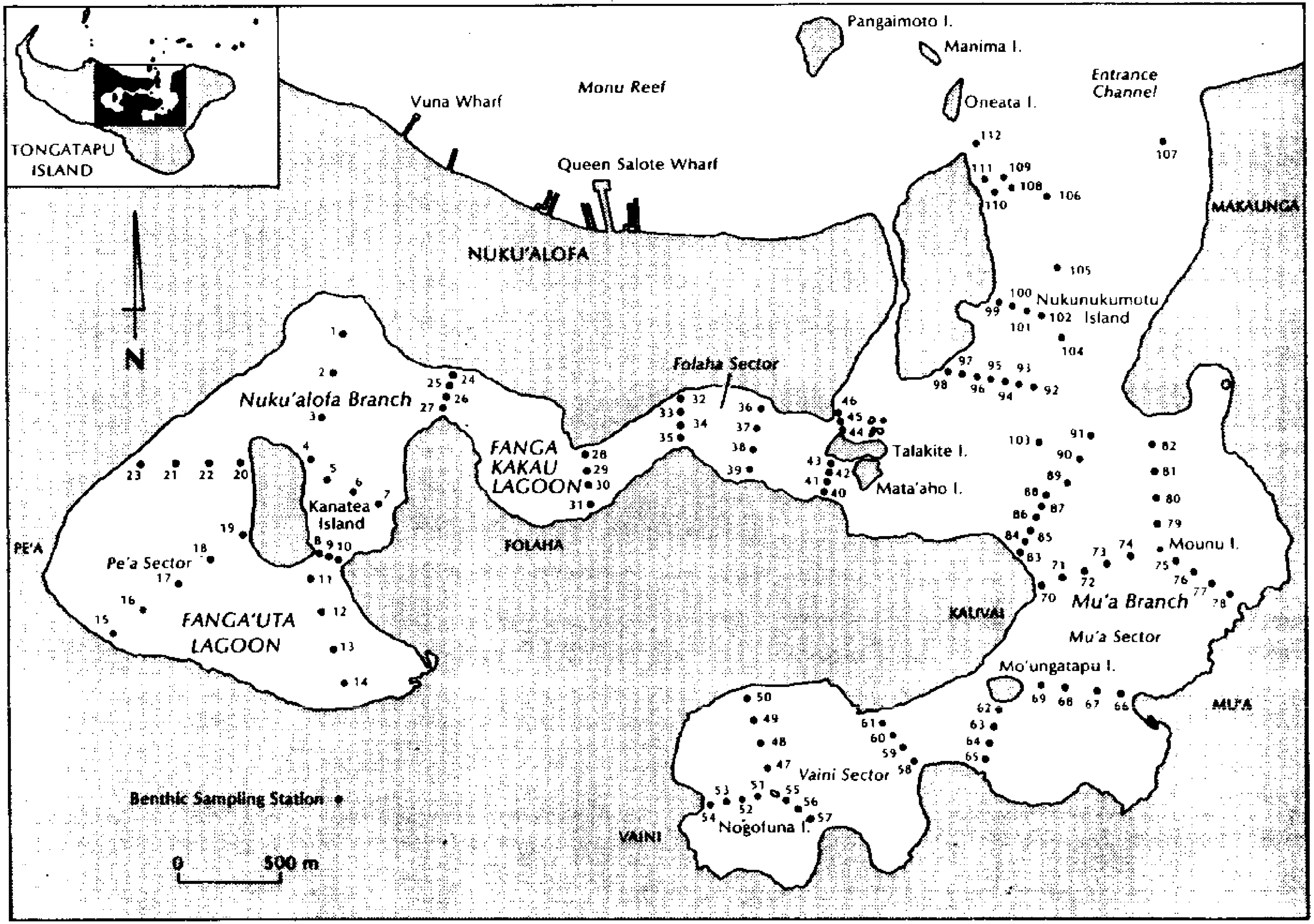

Figure 6. Approximate locations of benthic sampling stations in Fanga'uta Lagoon, Tongatapu

In the field macroinvertebrates were counted on a per unit area basis depending on their size. Only the most common of the smaller invertebrates and infaunal forms were collected and identified. Fish and larger motile invertebrates were sampled by use of trammel nets (33 m x 1.2 m, mesh openings of 16 and 5 cm) and a 1 m x 0.5 m trawl or dredge. In the vicinity of the lagoon entrance where water clarity permitted, observations on these larger forms were made by snorkeling. The results from net sampling and underwater observations are given as the catch per unit of soak time or species encountered per unit of observation time.

Trammel nets were set in the afternoon and retrieved on the following morning. The locations of these sets are given in Figure 7. Lengths were estimated for all fishes and crustaceans taken in the nets; these data were later used to estimate the wet weights of fish using the relation: Weight = K $(\text{Length})^3$. The values of the constant K differ for each species and were obtained from Hawaii Division of Aquatic Resources data as well as from personal unpublished data.

RESULTS

In general the lagoon benthic communities display an increase in diversity and complexity in a seaward direction (see "Corals" section). This increasing community complexity is related to the presence of a greater amount of hard substratum and normal marine conditions appearing in the vicinity of the entrance channel.

Benthic station data (station number, algal and seagrass species and invertebrate species present) are given in Appendix B. Tables 14 through 17 summarize those data. Table 14 presents the wet weights (standardized to a 1 m^2 area) of the most common algae and seagrasses found in the three major sectors of the lagoon. The average weights of seagrasses and algae (on a square meter basis) are given in 1 m bathymetric intervals for these three sectors in Table 15. Table 16 takes these data one step further and presents the total benthic algal and seagrass standing crop calculated for the entire lagoon. More than 70 percent of the total benthic plant standing crop is found in the 0 to 1 m bathymetric isobath of the lagoon. Below 5 m in depth benthic biomass is negligible (Table 16). This decrease is graphically depicted in Figure 8 as a regression of macrothalloid algal and seagrass standing crop against depth.

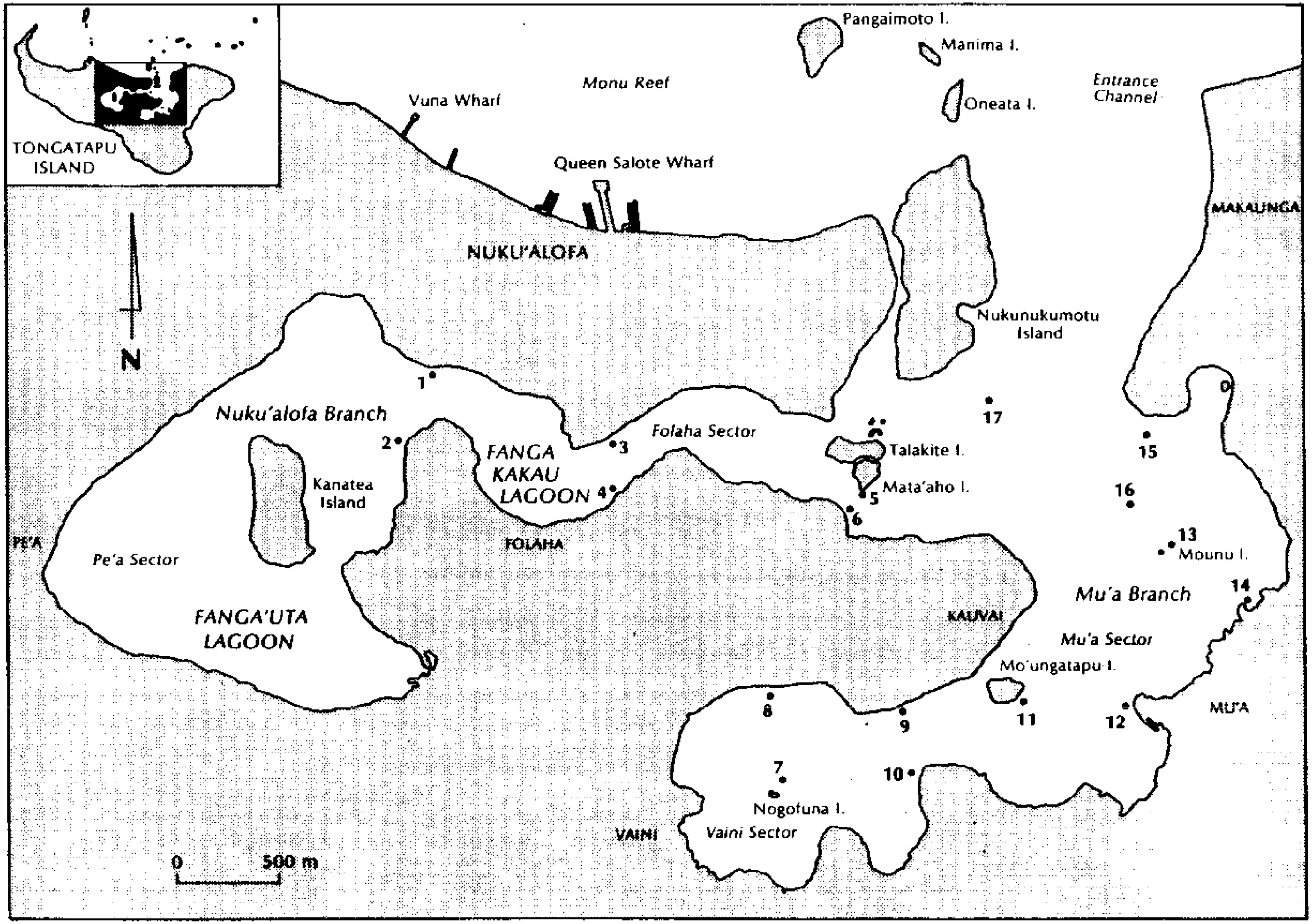

Figure 7. Approximate locations of 33 m x 1.2 m overnight trammel net sets in Panga'uta Lagoon, Tongatapu (shown by numbered dots)

TABLE 14. WET WEIGHT IN GRAMS OF THE MOST COMMON SEAGRASS AND ALGAL SPECIES COLLECTED FROM 150-CM^2 RANDOM GRAB SAMPLES FROM EACH OF THE THREE MAJOR SECTORS OF FANGA'UTA LAGOON (ALL DEPTHS COMBINED)

Species	Wet Weight (g/m^2)		
	Nuku'alofa Sector	Folaha Sector	Mu'a Sector
Seagrasses			
Halophilia ovalis	113	33	13
Halodule pinifoliosa	113	140	193
Algae			
Caulerpa serrulata		293	
C. ramosa	80		240
C. ashmeadii	0.7		320
Cladophora sp.			53
Chlorodesmis spp.	93		
Halimeda discoidea		207	147
Gracilaria sp.			7

TABLE 15. AVERAGE WET WEIGHT OF ALGAE AND SEAGRASSES BY 1 M BATHYMETRIC INTERVALS

Area	Depth Interval (m)	N	Average Wet Weight (g/m^2)
Nuku'alofa Sector	0-1	26	1,052
	1-2	10	784
	2-3	4	39
	3-4	6	37
Folaha Sector	0-1	15	1,055
Mu'a Sector	0-1	10	2,389
	1-2	10	3,139
	2-3	7	610
	3-4	9	21
	4 & greater	11	17

Note: Data summarized from Appendix B

TABLE 16. AREAS WITHIN 1 M BATHYMETRIC INTERVALS, MEAN MACRO-ALGAE AND SEAGRASS STANDING CROPS FOR FANGA'UTA LAGOON, TONGATAPU

Depth Interval (m)	Area (ha)	Average Macroalgae and Seagrass Standing Crop	
		(g/m^2)	Total (metric tons)
0-1	1,937	1,232	23,864
1-2	374	2,159	8,075
2-3	284	402	1,142
3-4	239	29	69
4-5	371	8	30
5 or more	217	0	0
TOTAL	3,423		33,180

TABLE 17. LIST OF ALL FISH SPECIES KNOWN TO OCCUR IN FANGA'UTA LAGOON, TONGATAPU

Species	Net Survey	Trawl	Visual Census					Fisheries Staff Survey	Other Visual Sightings
			103	104	105	106	107		
Abudefduf coelestinus			10						
Acanthurus nigrofuscus	x			1	1				
A. nigroris						1			
A. xanthopterus	x			27	3			x	
Alectis sp.	x								
Archamia bureonsis (?)			1						
Arothron hispidus	x								
A. immaculatus	x								
A. stellatus	x								
Asterropteryx semipunctatus				97	106	81	42		
Bothidae sp. (juv)	x								
Canthigaster janthinopterus									
Caranx ignobilis								x	
C. melampygus	x								
C. sexfasciatus								x	
Chaetodon auriga				1	2	1			
C. facula			1						
Chanos chanos								x	
Cheilinus sp.						1			
Chromis acares						3			
C. caerulea					41	42			
C. cyanea			6		7				
C. lepidolepis (?)					3				
Conger marginatus	x								
Conger sp.	x								
Dascyllus aruanus				98	58	215	149		
Equula fasciata								x	
Eupomacentrus nigricans			3		3	9			
Flammeo sammara					1				
Foa brachygamma		x							
Gaterin sp. (juv)	x								
Gerres oyaena								x	
G. poeti	x								
Gnathodentex aureolineatus			4			4	1		
Gnathodon specicusus	x								
Gobidae sp.				1			1		
Gymnothorax pictus	x								
G. thyrsoidea	x								
Gymnothorax sp.								x	
Haliochoeres trimaculatus				1	1	2	1		
Haliochoeres sp.				1		1			
Hemirhamphidae sp.									x
Heniochus sp.						1			
Labroides dimidiatus						1			
Lepidozygus tapeinosoma (?)						1			
Leiognathus brevirostris		x							
Leiognathus sp.								x	
Leptoscarus vaigiensis	x							x	
Lethrinus fletus	x								
L. rhodopterus				1				x	
L. obsoletus								x	
L. nebulosus			1					x	
Liza macrolepis								x	
Loyamia novemfasciata (?)			3	3	8				
Lutjanus argentimaculatus (?)	x								
L. fulviflamma		x							
L. fulvus								x	

TABLE 17. LIST OF ALL FISH SPECIES KNOWN TO OCCUR IN FANGA'UTA LAGOON, TONGATAPU (continued)

Species	Net Survey	Trawl	Visual Census					Fisheries Staff Survey	Other Visual Sightings
			103	104	105	106	107		
L. gibbus			4				1		
L. rufolineatus	x								
L. sebae						2			
L. vaigiensis					3				
Lutjanus sp. (juv)		x				1			
Macropharyngodon sp.						2			
Megalops cyprinoides								x	
Mugil cephalus								x	
Oxyurichthys sp.		x							
Parapercis cylindrica					1	1	4		
Parupeneus barberinus	x								
P. cuvieri									
P. cyclostromus	x								
P. indicus	x								
P. porphyreus	x								
Periophthalmus sp.									x
Plectorhynchus cuvieri						2			
Pomacentridae sp.						4			
Pomacentrus pavo				4	8		37		
Psilogobius sp. (?)					$\sim 1/m^2$	$\sim 1/2m^2$			x
Pterois volitans						1			
Saurida gracilis	x					1			
Scarus oviceps									
S. ghobban	x				1			x	
S. sordidus			5	6	12	4			
S. taeniurus	x								
Scarus sp.	x								
Scarus sp. (juv)			31	21	3	22			
Siganus chrysospilos	x							x	
S. spinus								x	
S. vermiculatas			4						
Sphyraenidae sp.								x	
Stethojulis sp.			4						
Synodontus variegatus	x				1				
Therapon jarbua								x	
Thrissina baelama	x								
Trichiurus lepturus								x	
T. blochii								x	
Zebrasoma veliferum					1	1			
No. of species seen by method	30	5			46			23	3

Note: Data were collected by a variety of methods as given in separate columns. The "Net Survey" was carried out by overnight sets of 1.2 x 33 m trammel nets (locations in Figure 7), the "Trawl" method used a small 1 x 0.5 m trawl for approximately 5 minutes on the bottom in a number of localities, and the "Visual Censuses" utilized a 15-minute swim tallying all fishes seen (locations given in Figure 6). Fishes that had previously been collected by the fisheries department staff are noted under the "Fisheries Staff Survey" column and miscellaneous sightings made during this survey are given under the "Other Visual Sightings" column.

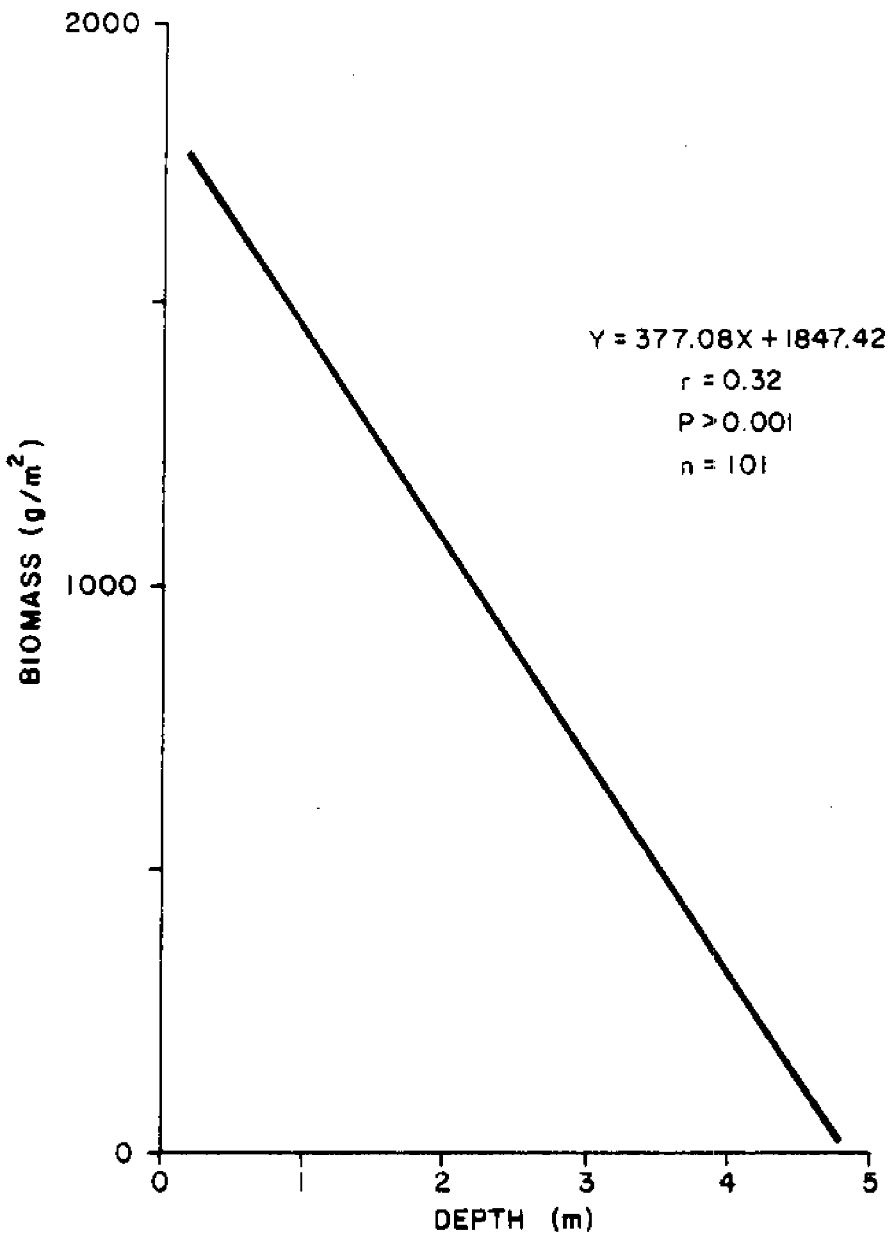

Figure 8. Regression line of best fit for algal and seagrass biomass against depth

The calculated annual production of seagrasses, *Halimeda* and macrothalloid algae, are given in Appendix C. The total benthic production amounts to 2,723 metric tons of carbon fixed per year. *Halimeda* production (1,231 metric tons C/year) is assumed to be of no direct use to organisms utilized by human beings. Thus 1,492 metric tons of carbon per year is available to organisms of higher trophic levels. Mullet, penaeids, and the mud crab (*Scylla serrata*) all utilize algal and seagrass detritus to varying degrees. The calculated mullet production in Fanga'uta Lagoon is 187 metric tons per year. These figures are based on the assumptions that (1) 25 percent of the detritus resulting from macroalgal and seagrass breakdown is used by mullet, (2) it makes up 50 percent of their total diet, and (3) this production is based on an unfished population.

A number of small and usually cryptic invertebrates were encountered throughout the lagoon. Low mounds ranging from 20 cm to over 1 m in diameter and heights to 15 cm were seen in soft sediment habitats. These mounds were made by bioturbators (probably callianassid shrimps, holothurians, or polychaetes). Likewise holes dug in the sediments by the alpheid shrimp (*Alpheus mackayi* -- collected) and shared with a goby (*Psilogobius* sp.? -- not collected) were equally common. Other crustaceans that appear to have lagoonwide distribution include crabs (*Scylla serrata*, *Thalamita prymna*, *Calappa hepatica*, several species of the family Xanthidae), mantis shrimps (*Squilla* sp., *Lysiosquilla* sp.) and the commercially important prawns (*Metapenaeus ensis* and *Penaeus semisulcatus*).

The holothurian *Holothuria atra* is common in parts of the lagoon; *H. edulis*, *H. leucospilota*, *H. impatiens*, *Stichopus variegatus*, and *S. chloronotus* are all found on the patch reefs near the entrance to the lagoon. The starfishes *Archaster* sp. and *Astropecten* sp. are common on the intertidal flats and deeper soft-bottom areas of the Vaini, Mu'a, and entrance channel regions. The blue starfish, *Linckia laevigata*, and the sea urchins, *Diadema setosum*, *Tripnuestes gratilla*, and *Toxopneustes pileolus*, are frequently seen on the entrance channel patch and fringing reefs.

A number of small polychaete species (family Capitellidae) were found in the the sediments of the lagoon. On the patch and fringing reefs of the lagoon entrance, sand trapping chaetopterids were commonly seen (forming mounds with diameters of up to 2 m and heights to 10 cm) as well as several species of calcareous tube-dwellers under loose rocks (spirorbids, *Hyroides* sp., *Vermiliopsis* sp.). A more complete account of the polychaete fauna of Fanga'uta Lagoon is in preparation (J. Brock: personal communication).

Several species of sponges were seen on the shallow fringing reefs around the lagoon. They were most common in the entrance channel sector. Among those frequently encountered was a large (to 50 cm) globose brown-yellow sponge that occurred on shallow subtidal flats. Other sponges that were seen (as noted in Appendix B) were usually differentiated only by color.

A number of bivalve species was found throughout Fanga'uta Lagoon. Small tellinids and Gafrarium tunidum were common in the sediments of all sectors; towards the lagoon entrance Anadara maculata, Fragum unedo, Tellina sp., Periglypta sp., Lucina sp., and Pecten sp. were found along with the pinna (Atrina sp.) and the pearl oyster (Pinctado marginatifera). Many of the larger and conspicuous gastropods were found in the vicinity of the lagoon entrance. Among these were cowries (Cypraea annulus, C. moneta, C. vitellus, and C. tigris), lambid (Lambis lambis), strombid (Strombus gibbrulus), cone (Conus pulicarius), as well as two unidentified vermetid species on rocky outcrops.

The jellyfish Cassiopea sp. is harvested for consumption and is very common in the Nuku'alofa branch of the lagoon, locally reaching densities exceeding $4/m^2$ over areas of 50 m^2 or more. In the Mu'a branch two species of anemones believed to be Boloceroides sp. and Aiptasia sp. were seen. The corals of the lagoon are discussed in a separate section.

As with the invertebrates, the fish communities of Fanga'uta Lagoon became increasingly more diverse towards the entrance channel. The list of fish species present in the lagoon is given in Table 17. Stations 103 through 107 (Figure 6 and Table 17) were conducted as 15-minute underwater visual surveys, and the results given are the number of individuals of each species encountered during that period at each site. These tallies were all carried out in areas preferred by many species, i.e., along the edges of patch reefs or channels where considerable hard substratum and structural relief was present. In all, 96 species of fishes are known to occur in the lagoon. All identifications must be considered tentative because many were made by rapid visual sightings only. By far the most effective method of species enumeration was the visual census technique, albeit it was used only in the entrance channel region.

The results of the trammel net survey are given in Table 18. Figure 7 gives the locations of all net settings. In total, 36.2 kg of fish and crustaceans were caught in 18 sets or about 2 kg/net/night or 0.11 kg/hr of soak time. The catch per unit of effort (catch in kg/hr of soak time) was best in the Folaha sector and, as expected, out in the entrance channel area. The herbivorous scarid, Leptoscarus vaigiensis, contributed substantially to the weight of fish caught. Analysis of the stomachs of several L. vaigiensis showed that this species feeds primarily on the seagrass Halodule pinifoliosa. Several goatfish species were quite common in the catches made in the channels of the lagoon entrance. A number of large (to 1.8 kg) mud or Samoan crabs (Scylla serrata) were caught in nets made near mangrove stands. This crab was the most common crustacean (by weight) to be caught in our trammel net survey; in contrast, few prawns were caught.

TABLE 18. LIST OF FISHES AND CRUSTACEANS AND THEIR APPROXIMATE WEIGHTS CAUGHT IN 1.2 X 33 M TRAMMEL NETS SET OVERNIGHT IN FANGA'UTA LAGOON

Net No.	Species	No. Caught	Approx. Weight (kg)	Total Weight (kg)	Catch kg/hr Soak time
1	FINFISH				
	Lutjanus argentimaculatus	1	0.09	0.09	
	CRUSTACEANS				
	Penaeid sp.	1	0.2		
	Thalamita sp.	1	0.01	0.21	0.01
2	FINFISH				
	Leptoscarus vaigiensis	1	0.04		
	Arothron hispidus	1	0.2	0.24	
	CRUSTACEANS				
	Thalamita prymna	13	0.14	0.14	0.01
3	FINFISH				
	Conger marginatus	1	2.6		
	Leptoscarus vaigiensis	9	3.5		
	Synodontus varigeatus	2	0.04		
	Acanthurus nigrofuscus	1	0.01		
	Lethrinus fletus	1	0.05		
	Bothidae sp.	1	0.01		
	CRUSTACEANS				
	Scylla serrata	2	0.4	0.4	0.28
4	FINFISH				
	Leptoscarus vaigiensis	10	5.5		
	Scarus taeniurus	2	0.4	5.9	
	CRUSTACEANS				
	Thalamita prymna	2	0.02	0.02	0.25
5	FINFISH				
	Saurida gracilis	1	0.02		
	Leptoscarus vaigiensis	3	2.5		
	Lethrinus fletus	1	0.05		
	Parupeneus porphyreus	1	0.1		
	Gymnothorax thyrsoidea	1	2.3		
	*Arothron immaculatus**	1	0.1	5.07	0.17

TABLE 18. LIST OF FISHES AND CRUSTACEANS AND THEIR APPROXIMATE WEIGHTS CAUGHT IN 1.2 X 33 M TRAMMEL NETS SET OVERNIGHT IN FANGA'UTA LAGOON (continued)

Net No.	Species	No. Caught	Approx. Weight (kg)	Total Weight (kg)	Catch kg/hr Soak time
6	FINFISH				
	Leptoscarus vaigiensis	1	0.3		
	Scarus sp.	3	0.6		
	Scarus taeniurus	1	0.3		
	Caranx melampygus	1	0.09		
	Lethrinus fletus	1	0.09		
	Siganus chrysospilos	1	0.02		
	Gymnothorax pictus	1	0.2	1.60	
	CRUSTACEANS				
	Scylla serrata	2	3.5		0.20
7	FINFISH				
	Leptoscarus vaigiensis	1	0.2	0.2	
	CRUSTACEANS				
	Scylla serrata	1	1.5	1.5	0.08
8	FINFISH				
	Siganus chrysospilos	1	0.03	0.03	0.001
9	FINFISH				
	Conger sp.	1	1.3	1.3	0.06
10	No fish caught				
11	FINFISH				
	Gerres poeti	1	0.04		
	Saurida gracilis	2	0.04	0.08	
	CRUSTACEANS				
	Scylla serrata	1	0.1		
	Thalamita sp.	1	0.01	0.11	0.01

TABLE 18. LIST OF FISHES AND CRUSTACEANS AND THEIR APPROXIMATE WEIGHTS CAUGHT IN 1.2 X 33 M TRAMMEL NETS SET OVER-NIGHT IN FANGA'UTA LAGOON (continued)

Net No.	Species	No. Caught	Approx. Weight (kg)	Total Weight (kg)	Catch kg/hr Soak time
12	FINFISH				
	Siganus chrysospilos	1	0.04		
	Paraupeneus cyclostomus	1	0.05		
	Alectis sp.	1	0.09		
	Scarus sp.	3	0.5	0.68	
	CRUSTACEANS				
	Penaeid sp.	1	0.2		
	Thalamita prymna	2	0.01	0.21	0.04
13	FINFISH				
	Parupeneus porphyreus	1	0.1		
	Gnathodon speciosus	1	0.05		
	Lutjanus rufolineatus	1	0.04		
	Arothron immaculatus*	2	0.7	0.89	
	CRUSTACEANS				
	Scylla serrata	1	1.0		0.08
14	FINFISH				
	Leptoscarus vaigiensis	1	0.7		
	Lethrinus fletus	1	0.09	0.79	
	CRUSTACEANS				
	Thalamita sp.	1	0.01		
	Scylla serrata	1	0.1		
	Scallop sp.	1	0.02	0.13	0.04
15	FINFISH				
	Siganus chrysospilos	1	0.04		
	Parupeneus porphyreus	2	0.4		
	Caranx melampygus	1	0.05		
	Thrissina baelama	1	0.01		
	Leptoscarus vaigiensis	2	1.0		
	Scarus ghobban	1	0.7	2.2	
	CRUSTACEANS				
	Xanthidae sp.*	1	0.01	0.01	0.09

TABLE 18. LIST OF FISHES AND CRUSTACEANS AND THEIR APPROXIMATE WEIGHTS CAUGHT IN 1.2 X 33 M TRAMMEL NETS SET OVERNIGHT IN FANGA'UTA LAGOON (continued)

Net No.	Species	No. Caught	Approx. Weight (kg)	Total Weight (kg)	Catch kg/hr Soak time
16	FINFISH				
	Parupeneus barberinus	4	1.5		
	Acanthurus xanthopterus	3	0.1		
	Parupeneus porphyreus	3	0.6		
	Scarus ghobban	2	2.2		
	Gaterin sp.	1	0.05	4.36	0.18
17	FINFISH				
	Leptoscarus vaigiensis	6	3.8		
	Saurida gracilis	1	0.02	3.82	0.16
18	FINFISH				
	Parupeneus barberinus	4	3.0		
	Parupeneus indicus	2	2.2		
	Siganus chrysospilos	3	0.08		
	Scarus ghobban	1	1.8		0.30
	Grand Mean				0.11

Note: Given are the total weight of finfish and crustaceans collected in a set and the calculated catch per unit of effort (catch in kg/hour of soak time). Species considered to be inedible are marked with an asterisk.

DISCUSSION

The marine communities of Fanga'uta Lagoon form a complex series of communities displaying varying zonation that is largely dependent on a number of physical parameters. These forcing functions include the amount of soft substratum, hard substratum, the tidal exposure (related to water depth), freshwater and nutrient input, and wind stress which directly affects water clarity.

Soft sediments dominate the benthic communities of Fanga'uta Lagoon, dictating that forms adapted to such habitats are the most important community components; the invertebrate species lists reflect this. Hard substratum is more common in the vicinity of the entrance channel. The presence of hard substratum and more normal marine conditions in the entrance channel area are factors responsible for the greater diversity of fishes and invertebrates seen in this sector (Table 17, Appendix B).

The Nuku'alofa branch is composed of soft sedimentary materials as are the other areas, but is shallow and is directly exposed to the prevailing winds. As a consequence, this section is extremely turbid (see "Circulation and Hydrology" section). These soft-bottom and turbid conditions are not favorable for most marine organisms. The catches from the two trammel net sets (Figure 7 and Table 18) made in this area were particularly low. Other than seagrasses and some algal species, the scyphozoan _Cassiopea_ sp. is one of the dominant macroinvertebrates present in this basin. The substratum of the Vaini sector is also composed of soft sedimentary materials but, in contrast, is somewhat deeper and protected from wind mixing due to surrounding bluffs. Hence, it has good water clarity and well-developed seagrass communities.

It is the seagrass and algal communities that are of particular interest here due to their high standing crops and productivity. Water clarity directly affects benthic productivity through inhibition of light transmission with increasing turbidity or water depth. In Fanga'uta Lagoon the standing crop of macrothalloid algae and seagrasses disappears at 4.9 m in depth (Figure 8), showing that benthic production is restricted to shallower waters. In these areas the total primary production is 7.5 metric tons of carbon fixed daily or 2,723 metric tons per year (Appendix C).

Few organisms of consequence to human beings found in Fanga'uta Lagoon can directly utilize this production. The parrotfish (_Leptoscarus vaigiensis_) and rabbitfishes (_Siganus chrysospilos_, _S. spinus_, and _S. vermiculatus_) do feed directly on seagrass (_Halodule pinifoliosa_). In the unfished situation the green sea turtle (_Chelonia mydas_) would probably be present and use the seagrass resource. Many other species such as the mullet (_Mugil cephalus_), the penaeids (_Penaeus semisulcatus_ and _Metapenaeus ensis_), and the mud crab (_Scylla serrata_) probably feed, in part, on detritus derived from this benthic production. Detritus may range in size from a few microns to an entire leaf attacked by fungi and bacteria. These organisms begin oxidation, hydrolysis, and assimilation of the basic carbon structure of the substrate and at the same time they remove dissolved nutrients from the water. Protozoa graze the bacteria and create a rich bacteria-fungi-protozoa-detritus complex of great potential food value (Odum, 1970).

Knowledge of the benthic production in the lagoon allows one to make an estimate of its fishery potential. The mullet fishery of Fanga'uta Lagoon once sustained much of Tongatapu's population (see "Fisheries" section). The old capital at Mu'a on Fanga'uta's shores suggests that the fishery and fishing in the lagoon must have had more importance than they do today.

When data are insufficient for normal fisheries assessment, approximate methods must be used to obtain estimates on potential yield. This has been done for a hypothetical virgin or unfished mullet (Mugil cephalus) population in Fanga'uta Lagoon (Appendix C). Mullet are singled out for this exercise because of their reported former importance in the fisheries of Fanga'uta Lagoon (see "Fisheries" section). Based on present estimates of primary productivity, the annual mullet production would be 187 metric tons, while the virgin stock size is estimated to be 480 metric tons. There are 3,423 ha in Fanga'uta Lagoon which translates to 140 kg of mullet per hectare. This standing crop value is comparable to natural populations found in coastal ponds and embayments from Nigeria (Sivalingam, 1975) to Hawaii (Cobb, 1903).

The results of the trammel net survey suggest that the finfish resources of Fanga'uta Lagoon are low despite the previous ban on commercial activities. The lagoon is open to subsistence activities. It, however, appears that the present level of exploitation is enough to keep the standing crop of finfish resources low. Thus, a large proportion of the benthic production of the lagoon is now lost to the sediments. The long water residence times (see "Circulation and Hydrology" section), coupled with high benthic production (especially by carbonate producers such as Halimeda), result in rapid lagoon infilling. Halimeda fragments are a common element of the sediments. There is evidence that uplift (see "Corals" section) has probably accelerated the infilling by reducing circulation and washout of sedimentary materials.

Sand mining or any attempt to improve the circulation of the lagoon by dredging would have a negative impact on extant benthic communities. The high natural productivity has probably been an attribute of the lagoon from the time of humankind's first exploitation of its resources; dredging or any other physical disruption will negatively affect benthic production. Seagrasses are notoriously slow in their recovery from natural or induced disturbance (Ogden and Zieman, 1977). Thus, any resumption of a penaeid fishery based on trawling methods (Braley, 1979) should not be allowed.

To capture more of the lagoon's high primary production for human use, either the fishery resources must be improved by decreasing fishing activities or the aquaculture of appropriate species must be undertaken. It probably is not realistic to assume that fishing in the lagoon and its environs could be curtailed for any period of time needed to build up the stocks. Thus, the development of aquaculture should be strongly considered as a viable alternative for the future.

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Appendix B. List of Stations, Methods Used, Water Depth, and Species Present in 112 Stations Throughout Fanga'uta Lagoon, Tongatapu

Station No.*	Sample Type	Water Depth (m)	Species Present
a	Grab	0.75	*Halophila ovalis*, *Caulerpa racemosa*, *Cerithium* sp., several small penaeids, *Leiognathus brevirostris*
b	Grab/Trawl	1.1	*Leiognathus brevirostris*, penaeids, *Halodule pinifoliosa*, *Cerithium* sp., juvenile Tellindae
c	Grab/Trawl	1.1	*Lutjanus fulviflamma*, *Leiognathus breveirostris*, Sponge sp. (yellow), Sponge sp. (orange), *Cassiopea* sp. *Alpheus mackayi*, *Isognomum* sp. (?), juvenile Tellinidae, Amphinomidae, *Halophila ovalis*
d	Grab/Trawl	0.6	*Foa brachygamma*, *Cassiopea* sp., Sponge sp. (Green), *Lutjanus fluviflamma*, penaeid, *Caulerpa racemosa*, *Caulerpa taxifolia*
1	Grab	0.75	*Halophila ovalis*, juvenile Tellinidae, *Caulerpa racemosa* (1,848 g/m^2)
2	Grab	1.1	*Halodule pinifoliosa* (528 g/m^2)
3	Grab	1.1	*Halophila ovalis* (594 g/m^2)
4	Grab	0.6	*Caulerpa racemosa*, *Caulerpa taxifolia* (4,158 g/m^2)
5	Grab	1.1	*Halophila ovalis*, juvenile Tellinidae (528 g/m^2)
6	Grab	0.9	*Halophila ovalis*, juvenile Tellinidae (33 g/m^2)

*Station numbers correspond to those given in Figure 6; those listed by letter were made in the Nuku'alofa branch and do not appear in Figure 6.

Station No.*	Sample Type	Water Depth (m)	Species Present
7	Grab	0.6	Halophila ovalis, Halodule pinifoliosa, Alpheus mackayi, juvenile Tellinidae (1,320 g/m^2)
8	Grab	0.9	Halodule pinifoliosa, Halophila ovalis, Chlorodesmis sp., juvenile Tellinidae (297 g/m^2)
9	Grab	1.0	Halodule pinifoliosa, Halophila ovalis (1,914 g/m^2)
10	Grab	0.5	Halodule pinifoliosa (2,310 g/m^2)
11	Grab	0.7	Halodule pinifoliosa, Halophila ovalis (814 g/m^2)
12	Grab	0.75	Halodule pinifoliosa, Halophila ovalis, Chlorodesmis sp. (145 g/m^2)
13	Grab	0.75	Halophila ovalis, Chlorodesmis sp. juvenile Tellinidae (242 g/m^2)
14	Grab	0.75	Halophila ovalis, Halodule pinifoliosa, Chlorodesmis sp., juvenile Tellinidae (158 g/m^2)
15	Grab	0.7	Halodule pinifoliosa, Halophila ovalis, juvenile Tellinidae (356 g/m^2)
16	Grab	0.8	Chlorodesmis sp., Halodule pinifoliosa, Halophila ovalis (83 g/m^2)
17	Grab	0.75	Chlorodesmis sp., Halodule pinifoliosa, juvenile Tellinidae (284 g/m^2)
18	Grab	0.75	Chlorodesmis sp. (308 g/m^2)
19	Grab	0.6	Halophila ovalis, Halodule pinifoliosa (220 g/m^2)
20	Grab	0.4	Halophila ovalis (594 g/m^2)
21	Grab	0.6	Halophila ovalis, Halodule pinifoliosa, Chlorodesmis sp., juvenile Tellinidae (308 g/m^2)

Station No.*	Sample Type	Water Depth (m)	Species Present
22	Grab	0.6	Halophila ovalis, Chlorodesmis sp., juvenile Tellinidae (660 g/m^2)
23	Grab	0.6	Halophila ovalis, Chlorodesmis sp., juvenile Tellinidae (858 g/m^2)
e	Trawl	2.0	Halimeda discoidea, Halodule pinifoliosa, Serpulidae, Foa brachygamma, Cassiopea sp., Ulva sp., Caulerpa taxifolia
f	Trawl	2.8	Penaeid, stomatopod, Halophila ovalis, juv. portunid, Astropecten polyacanthus
g	Trawl	4.0	Halophila ovalis, errant polychaetes, Halimeda discoidea, Holothuria atra
24	Grab	0.9	Halodule pinifoliosa, Halophila ovalis (634 g/m^2)
25	Grab	1.7	Caulerpa serrata (7,459 g/m^2)
26	Grab	2.3	No macrobiota
27	Grab	1.5	Halophila ovalis, Halodule pinifoliosa (482 g/m^2)
28	Grab	2.8	Halophila ovalis (12 g/m^2)
29	Grab	3.0	No macrobiota
30	Grab	2.0	Halodule pinifoliosa, juvenile Tellinidae (1,980 g/m^2)
31	Grab	0.7	Halodule pinifoliosa, Caulerpa serrata (1,475 g/m^2)
32	Grab	0.75	Caulerpa serrata, Halimeda discoidea (4,376 g/m^2)
33	Grab	3.1	No macrobiota
34	Grab	3.5	No macrobiota
35	Grab	0.9	Halodule pinifoliosa, Caulerpa serrata (1,914 g/m^2)

Station No.*	Sample Type	Water Depth (m)	Species Present
36	Grab	1.25	Halimeda discoidea (924 g/m^2)
37	Grab	3.2	Halophila ovalis (51 g/m^2)
38	Grab	3.2	Halophila ovalis (66 g/m^2)
39	Grab	2.5	Caulerpa serrata (143 g/m^2)
40	Grab	0.6	Caulerpa serrata, Halimeda discoidea (1,879 g/m^2)
41	Grab	3.2	Caulerpa serrata (17 g/m^2)
42	Grab	4.0	Halophila ovalis (86 g/m^2)
43	Grab	2.0	Caulerpa serrata, Halimeda discoidea (1,212 g/m^2)
44	Grab	1.2	No macrobiota
45	Grab	1.3	Halimeda discoidea (845 g/m^2)
46	Grab	0.9	Caulerpa serrata (172 g/m^2)
47	Grab	1.2	Halodule pinifoliosa, Caulerpa serrata (2,079 g/m^2)
48	Grab	1.6	Halophila ovalis, Halodule pinifoliosa, Caulerpa serrata (4,951 g/m^2)
49	Grab	1.2	Halodule pinifoliosa, Caulerpa taxifolia (4,224 g/m^2)
50	Grab	1.0	Halodule pinifoliosa, Caulerpa serrata (5,545 g/m^2)
51	Grab	1.0	Cladphora sp., Halodule pinifoliosa (4,092 g/m^2)
52	Grab	1.0	Halodule pinifoliosa, Caulerpa serrata (4,158 g/m^2)
53	Grab	0.7	Halodule pinifoliosa (3,630 g/m^2)
54	Grab	0.5	Halodule pinifoliosa, Caulerpa serrata (1,386 g/m^2)
55	Grab	1.1	Halodule pinifoliosa, Caulerpa serrata (1,848 g/m^2)

Station No.*	Sample Type	Water Depth (m)	Species Present
56	Grab	1.6	*Halodule pinifoliosa* (990 g/m^2)
57	Grab	1.1	*Caulerpa taxifolia* (3,432 g/m^2)
58	Grab	1.1	*Caulerpa taxifolia* (7,789 g/m^2)
59	Grab	2.5	*Halophila ovalis* (33 g/m^2)
60	Grab	2.8	*Halophila ovalis* (66 g/m^2)
61	Grab	1.7	*Caulerpa racemosa* (2,574 g/m^2)
62	Grab	2.0	*Caulerpa serrata*, *Halimeda discoidea* (3,234 g/m^2)
63	Grab	3.0	No macrobiota
64	Grab	3.0	No macrobiota
65	Grab	2.3	*Halophila ovalis*, *Caulerpa taxifolia* (376 g/m^2)
66	Grab	2.5	*Caulerpa serrata* (99 g/m^2)
67	Grab	4.2	No macrobiota
68	Grab	4.0	No macrobiota
69	Grab	4.0	No macrobiota
70	Grab	0.5	*Caulerpa racemosa*, *Halimeda discoidea*, *Udotea glaucescens* (1,342 g/m^2)
71	Grab	2.0	*Halimeda discoidea* (1,848 g/m^2)
72	Grab	4.0	No macrobiota
73	Grab	6.0	No macrobiota
74	Grab	2.0	*Halimeda discoidea* (1,650 g/m^2)
75	Grab	0.7	*Halimeda opuntia* (1,056 g/m^2)
76	Grab	3.9	No macrobiota
77	Grab	4.0	No macrobiota
78	Grab	2.3	*Caulerpa racemosa* (3,696 g/m^2)

Station No.*	Sample Type	Water Depth (m)	Species Present
79	Grab	0.7	Caulerpa racemosa, Halimeda opuntia (1,168 g/m^2)
80	Grab	5.0	No macrobiota
81	Grab	4.0	Halophila ovalis (26 g/m^2)
82	Grab	0.4	Halimeda discoidea, Gracilaria sp. (264 g/m^2)
83	Visual	0	Halimeda discoidea patch, Chaetopterus sp. in abundance ~50/100 cm^2
84	Visual	0.1	Periopthalmus sp., Palaemon sp., Littorina scabra, Caulerpa taxifolia, Halimeda opuntia, Cladosphora sp., Halodule pinifoliosa, Hypnea sp., Holothuria atra ~1/2 m^2, Archaster sp. ~1/2m^2; Porifera sp. (brown) ~1/5m^2: bioturbation 1 mound/m^2
85	Visual	0.1	Halodule pinifoliosa dominant, Holothuria atra ~4/m^2, bioturbation 1 mound/3m^2
86	Visual	0.1	Halodule pinifoliosa (coverage ~40%), Caulerpa racemosa (~10%), Halimeda opuntia (~1%), Holothuria atra ~1/m^2, Archaster sp. ~1/3m^2, occasional Chaetopterus sp. mounds, bioturbation 1 mound/m^2, occasional large Squilla sp. holes
87	Visual	0.1	Caulerpa racemosa (~8%), Halodule pinifoliosa (~30%), Halimeda opuntia-patchy, Holothuria atra ~1/m^2, Archaster sp. ~1/2m^2, occasional Porifera sp. (brown), bioturbation 1 mound/10 m^2 (to 50 cm diameter)
88	Grab	0.5	Caulerpa racemosa, Halimeda discoidea (1,254 g/m^2)
89	Grab	4.0	No macrobiota
90	Grab	5.0	Halophila ovalis (33 g/m^2)

Station No.*	Sample Type	Water Depth (m)	Species Present
91	Grab	4.0	Halodule pinifoliosa, Caulerpa taxifolia (165 g/m^2)
92	Visual/Grab	0.3	Halodule pinifoliosa, Caulerpa serrata, Halimeda opuntia, Holothuria atra, Stichopus chloronotus, Psilogobius sp./Alpheus mackayi holes 1/m^2, bioturbation 2 mounds/3m^2 (495 g/m^2)
93	Visual/Grab	0.1	Porites lobata pieces, biologically similiar to #92, Caulerpa serrata, Caulerpa racemosa (396 g/m^2)
94	Visual/Grab	0.1	Halodule pinifoliosa (~50%), Holothuria atra ~1/3m^2, bioturbation 1 mound/2m^2 (diameter ~50 cm), Calappa sp. (726 g/m^2)
95	Visual/Grab	0	Halodule pinifoliosa (~60%), Caulerpa racemosa, Cypraea annulata, Archaster sp., Porites sp. (~10 cm), Calappa sp., Udotea glaucescens, Linkia sp., Holothuria atra 2/m^2, Porifera sp. (black), (330 g/m^2)
96	Visual/Grab	0	Halodule pinifoliosa (~70%), Halimeda opuntia (<1%), Caulerpa taxifolia (~3%), Holothuria atra ~1/m^2, Porifera sp. (brown to 50 cm dia.), bioturbation mounds 1/5m^2, Psilgobius sp. and Alpheus mackayi holes ~1/3m^2, occasional Stichopus chloronotus, (1,320 g/m^2)
97	Visual/Grab	0	Halodule pinifoliosa (~80%), Holothuria atra ~1/5m^2, bioturbation mounds ~1/10m^2 (25-35 cm dia.) (1,716 g/m^2)
98	Visual/Grab	0	Chlorodesmis sp. (~50%), Uca sp. burrows, Porites sp. (small balls), Astropecten sp. ~1/m^2, mangroves (4,554 g/m^2)

Station No.*	Sample Type	Water Depth (m)	Species Present
99	Visual/Grab	0	Halodule pinifoliosa (~70%), Halimeda opuntia (10%), Holothuria atra ~1/2m^2, Psilogobius sp., Alpheus mackayi holes ~1/5m^2, bioturbation mounds ~1/3m^2 (20-80 cm dia.), Porifera sp. , purple-occasional, few scattered Porites lutea lumps (1,155 g/m^2)
100	Visual/Grab	0	Halodule pinifoliosa (~50%), Halimeda discoidea (~5%), Caulerpa racemosa (~5%), Stichopus chloronotus ~1/30m^2, Dictyosphaeria versluysii, Psilogobius sp. -Alpheus mackayi holes ~1/4m^2, bioturbation mounds ~1/2m^2 (20-100 cm dia.), Vermetids (2 sp.) on old uplifted Porites, Porifera sp. (black), (1,386 g/m^2)
101	Visual/Grab	0.1	Hard bottom-patches of emergent limestone 2-5 m across once every 40 m, small Porites lutea (5-15 cm dia.) Pocillopora damicornis-occasional, Stichopus chloronotus ~1/m^2, soft bottom-Halodule pinifoliosa (~30%), Caulerpa racemosa (~10%), Halimeda discoidea (~1%), Holothuria atra ~1/5m^2, bioturbation mounds ~1/m^2 (20-40 cm dia.) (858 g/m^2)
102	Visual/Grab	0.4	Caulerpa racemosa (~30%), Halodule pinifoliosa (~40%), Halimeda opuntia ~10%, Holothuria atra ~1/m^2, bioturbation mounds ~1/10m^2 (20-40 cm dia.) (3,168 g/m^2)
103	Fish Transect	1-4	See Table 17
104	Fish Transect	0.5-4	See Table 17
105	Fish Transect	1-6	See Table 17
106	Fish Transect	1-5	See Table 17

Station No.*	Sample Type	Water Depth (m)	Species Present
107	Fish Transect	0.5-5	See Table 17
108	Visual/Grab	0.4	Halimeda sp. mounds 30-50 cm dia. ~3 to 5 m apart, Holothuria atra ~1/m^2, Holothuria edulis ~1/m^2 (0 g/m^2)
109	Visual	0.2	Halodule pinifoliosa (~60%), Halimeda discoidea (~10%), Linkia sp. small Porites sp., Calappa sp., Holothuria atra ~2/m^2 (1,320 g/m^2)
110	Visual/Grab	0.1	Halodule pinifoliosa (~30%), Halimeda discoidea (~10%), Archaster sp. ~5/m^2, Atrina sp., Holothuria atra ~1/3m^2, bioturbation mounds 1-3 m dia. about 1 m apart, (330 g/m^2)
111	Visual/Grab	0	Halodule pinifoliosa (~60%), Chlorodesmis sp. (~70%), Halimeda discoidea (~5%), Marginopora sp. common in pools (1-5 m dia) ~2 m apart; between are bioturbation mounds ~1 m dia., (2,574 g/m^2)
112	Visual	0.2	Strombus gibberulus ~12/m^2, Astropecten sp. Conus pulicarius, collected bivalves for identification

Appendix C. **Calculated Production of Seagrasses (*Halophila ovalis* and *Halodule pinifoliosa*), the Calcareous *Halimeda* (*Halimeda opuntia* and *Halimeda discoidea*) and Other Macrophyte Algae for the 0 to 3-m Isobath and Mullet of Fanga'uta Lagoon.** (Assumptions used in making these calculations are given below.)

I. SEAGRASS

1. Zieman (1975) found that in a average tropical seagrass community (2,800 g/m^2)dry weight has a production of ~2 $gC/m^2/day$.

2. Average dry weight of seagrasses over the 0 to 3 m isobath of Fanga'uta Lagoon is 52 g/m^2.

3. Assume production is proportional to standing crop:

   52/2,800 : X/2

   X = 0.05 $gC/m^2/day$

   or 18.25 $gC/m^2/year$

4. There are 2,595 ha in the 0 to 3 m isobath in Fanga'uta Lagoon.
   Thus:

   18.25 X 2,595 X 100 = 474 metric tons C/year

II. HALIMEDA

1. Hillis-Colinvaux (1974) found a net *Halimeda* productivity of 2.3 $gC/m^2/day$ in *Halimeda* communities of ~2,500 g/m^2 (dry weight).

2. Average dry weight of *Halimeda* over the 0 to 3 m isobath of Fanga'uta Lagoon is 145 g/m^2.

3. Assume production is proportional to standing crop:

   145/2,500 : X/2.3

   X = 0.13 $gC/m^2/day$

   or 47.45 $gC/m^2/year$

4. There are 2,595 ha in the 0 to 3 m isobath in Fanga'uta Lagoon.

   Thus:

   47.45 X 2,595 X 100 = 1,231 metric tons C/year

III. OTHER MACROPHYTE ALGAE

1. Assume *Caulerpa* spp. represent the total macrophytic algal standing crop of Fanga'uta Lagoon.

2. Johnston (1969) found a net *Caulerpa* productivity of 0.07 $gC/m^2/day$ in "field populations."

3. Assume "field populations" have a coverage of 20% and an approximate biomass of 500 g/m^2 (wet).

4. Average wet weight of macrophyte algae is 768 g/m^2 in the 0 to 3 m isobath of Fanga'uta Lagoon.

5. Assume production is proportional to standing crop. Thus:

   $$768/500 \quad : \quad X/0.07$$

   $$X = 0.11 \ gC/m^2/day$$

   $$\text{or } 39.24 \ gC/m^2/year$$

6. There are 2,595 ha in the 0 to 3 m isobath in Fanga'uta Lagoon. Thus:

   $$39.24 \times 2{,}595 \times 100 = 1{,}018 \text{ metric tons C/year}$$

IV. MULLET PRODUCTION

1. Total benthic seagrass and macrophytic production is 2,723 metric tons C/year.

2. *Halimeda* is inedible; assume it is lost to the sediments. Thus, 1,492 metric tons C/year is available to other trophic levels.

3. Assume that 25% of this material enters the mullet food web as detritus and comprises 50% of the mullet diet. The remaining 50% comes from benthic diatoms, etc.

4. Assume a 10% efficiency from detritus to mullet:

   $$1{,}492/4 \times 0.10 \times 0.10 = 7.46 \text{ metric ton C/year}$$

5. Converting to dry weight animal biomass (C X 2.5 ≅ animal dry weight):

   $$7.46 \times 2.5 = 18.66 \text{ metric tons of mullet (dry weight)}$$

6. Assume dry weight is 10% of wet weight:

   18.65 X 10 = 187 metric tons of mullet/year in the pristine unfished situation.

7. Ricker (1975) gives the following equation in his derivation of the Schaefer model:

   $$MSY = (K \times B^*)/4$$

   where B* is the carrying capacity for a given stock (hence approximately equal to the unfished biomass) and K is the intrinsic rate of increase of the population.

   Blueweiss et al. (1978) has shown that

   $$K = 0.02 \times W^{-0.26}$$

   where W is the mean weight (in g). Pauly (1980) has combined these two equations to determine annual potential yield:

   $$MSY = 2.3 \times W^{-0.26} B^*$$

   From an estimate on yield (MSY = 187 metric tons/year) and assuming adult mullet weigh 2 lb (900 g), a virgin unfished mullet biomass or standing crop of 480 metric tons obtained.

FRINGING VEGETATION

L.P. Zann

Mangroves are among the most productive of all communities and important resource in the Pacific islands. A nursery ground for many juvenile fish and a feeding (and fishing) ground for important food fish and crustaceans, they are important in stabilizing coastlines. In Tonga they are used for building such things as houses, fish fences, and parts of boats; for dying tapa; and for fuel.

Studies of Tongatapu's mangroves have been conducted by Hurrell and Hassall (in press) and Hassall and Vodonaivalu (in preparation). Both studies include sites on Fanga'uta Lagoon. Observations on the surface area, basic communities and disturbances to mangroves were also made during the 1981 survey.

RESULTS

The coverage of mangroves and extent of their disturbance were ascertained from the 1:50,000 and 1:25,000 D.O.S. (Directorate of Overseas Surveys, British Government) maps, aerial photographs, and boat surveys. Mangroves were represented on the maps, but they were found to be inaccurate and were modified by ground observations.

Figure 9 shows the extent of mangrove cover which dominates the shoreline of the lagoon, covering 90 percent of the Nuku'alofa branch and 55 percent of the Mu'a branch shores.

Of the 58 km of Fanga'uta Lagoon shoreline, 44.5 km are covered by a mangrove tidal forest. The coverage is greater on the Nuku'alofa branch, being about 30 to 35 km, as compared with about 14 km on the Mu'a branch's 24-km circumference. The southern coast of the Mu'a branch is comprised of raised limestone and hence, is less suitable for mangrove growth; where present, the mangrove zone is very narrow.

Detailed botanical descriptions have been made by H.F. Hurrell and D.C. Hassall (in press). In the Pe'a sector Bruguiera gymnorhuza was dominant along the water's edge with Excoecaria agallocha present as a secondary canopy. A rich community of creepers and epiphytes is present. Lumnitzera lottorea and Xylocarpus granatum lie shoreward, with Hibiscus tiliaceus, Pandanus, Acrostichum aureum, and Fiscus obliqua scrubs further inland.

At 'Alaki Rhizophora samoensis and R. stylosa dominate the shoreline community; towards the landward edge the fern Acrostichum aureum is found and taller Xylocarpus range into the coastal or littoral forest behind (Hurrell and Hassall, in press).

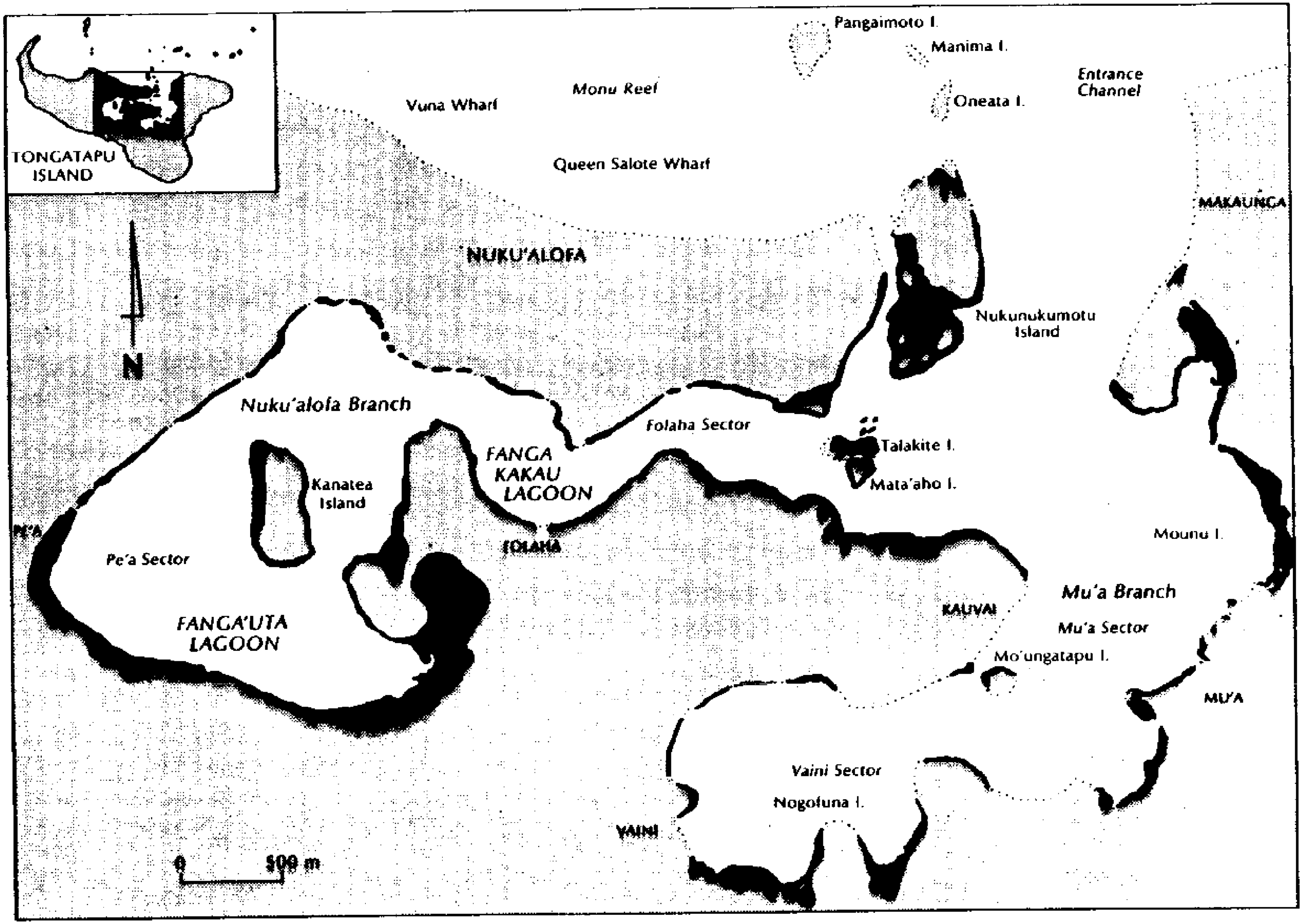

Figure 9. Coverage of mangrove tidal forest, Fanga'uta Lagoon, Tongatapu

The mangrove coasts are similar around the other shores of the lagoon. Brigioera, however, is not widespread around the Nuku'alofa branch and is largely confined to the Pe'a sector visited by Hurrell. Rhizophora samoensis dominates much of the shoreline.

The raised limestone shore from Longoteme to "Kauvai" is distinctly different. Irregular R. samoensis is found in shallower shoreline areas, but elsewhere Hibiscus tiliaceus, Pandances, and Acrostichum dominate the coastline. Shoreward lay remnants of the littoral forest, largely cleared and planted in copra.

Mangroves usually create a habitat suitable for many other organisms: molluscs, crustaceans, fish, etc. However, the associated fauna in the Nuku'alofa branch is impoverished, perhaps because of the low salinities and a lack of tidal movement and currents.

Small crabs (Cardisoma, Helica, Sesarma) were present and large mud crabs (Scylla serrata) were caught near mangroves in the Folaha sector. Many smaller crabs (Thalmita sp.) were netted throughout the lagoon. Absent in the Nuku'alofa branch but present among the mangroves at Longoteme on the Mu'a branch are encrusting barnacles, Chathamalus malayensis, the snail Littorina scabra, and small mussels, Modiolus sp. Small freshwater snails cf. Melampus, and sea anemones are found among the Rhizophora prop roots.

The faunal diversity increases towards the Mu'a branch and the lagoon entrance. Mudshippers (Periophthalmus sp.), fiddler crabs (Uca lactea), nerites (Nerita plicata and N. undata), whelks (Clypeomorus), and other invertebrates are present.

Birds seen in and near the mangroves include Australian grey ducks (Anas superciliosa), grey and white reef herons (Egretta sacra), godwits (Limosa lapponica), and swiftlets (Apus pacificus).

DISCUSSION

The enclosed shores of Fanga'uta Lagoon are dominated by mangroves, mainly Rhizophora samoensis, but R. stylosa and Bruguiera gymnorhiza are also common. Behind this seaward zone lies a community of Lumnitzera littorea and Xylocarpus granatus, with Hibiscus tiliaceus, Rhus taitensis, Pandanus sp., and other coastal vegetation merging into a coastal forest, now almost completely cleared and planted with copra, taro, bananas and other agricultural crops. D.C. Hassall (personal communication) described the Fanga'uta Lagoon mangroves as rich floristically but similar to other Southwest Pacific islands. Undoubtedly they are very productive, important in the Fanga'uta food-web as well as for timber.

The associated biota appears rather impoverished compared with other Southwest Pacific mangroves examined by the author. In the Nuku'alofa branch the biota was confined to several genera of crabs, but in the Mu'a branch typical associates such as the mangrove snail *Littorina scabra*, the small barnacle *Chthamalus malayensis*, mudskippers *Periophthalmus* spp., and a number of other organisms more characteristic of mangrove forests were present.

Restricted circulation, dampened tidal movement, and persistent hyposaline conditions may be responsible for the dearth of associated biota in the Nuku'alofa branch and in the upper-reaches of the Mu'a branch.

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FISHERIES

L.P. Zann

"From the day this country was created until today people have derived sustenance from [Fanga'uta Lagoon]." (Tongatapu's No. 1 Representative Mr. Joe Tu'ilatai Mataele, speaking for repeal of Protection Act, September 1981.)

Fanga'uta Lagoon was once the center of a large commercial and subsistence fishery which supplied much of Nuku'alofa's fresh fish. W.A. Wilkinson (personal communication) estimated that during the 1960s mullet largely caught in the lagoon often comprised 40 percent of the fish marketed at Nuku'alofa. Today mullet is a rarity, and commercial fishing is prohibited [the ban was subsequently lifted] and fish are conspicuously absent in the lagoon's highly productive waters. The lagoon, however, continues to play an important role in the subsistence fisheries of the surrounding villages.

There are many conflicting opinions regarding the lagoon and its fisheries and the nuances are difficult for an outsider to fully understand. However, as there are no data whatsoever on past and present fisheries and catches (despite the operation of a Fisheries Division for many years in Tonga), perhaps only an independent outsider can best evaluate the situation.

History of the Fisheries Decline

For many hundreds of years Mu'a, the capital of Tonga, was situated on the shores of Fanga'uta Lagoon which must have been heavily fished. With Tonga's population explosion -- a fivefold increase in the past century -- and the urbanization of Nuku'alofa, increased pressure has been placed on the lagoon fisheries and a rapid decline in catches was reported during the late 1960s. This decline has been attributed to overfishing, the proliferation of synthetic monofilament gill nets, the introduction of arrowhead fish fences, and environmental pollution. A commercial trawling operation for penaeid prawns began in 1974 but because large numbers of juvenile fish were also caught (Braley, 1976) and the fishery for mullet, milkfish, and bonefish continued to decline, the Fisheries Division submitted protective legislation to the Tongan Parliament which passed on June 26, 1975. The Birds and Fish Preservation Amendment Act prohibited the commercial exploitation of lagoon fish and shellfish by trap, trawl, net, or other means.

The prohibition was never completely observed or enforced. Reports of night fishing and even dynamiting were common, but because of social and political repercussions in a society where family relationships and hereditary rank remain important, there was minimal enforcement of the law.

The legislation was understandably unpopular among commercial fishermen and after continued lobbying the amendment was repealed by parliament in September 1981 by a vote of 9 to 6. At the time of the survey the legislation had not yet been ratified by Tonga's supreme authority, the monarchy.

The repeal of the act was moved by Tongatapu representative Joe Tu'ilatai Mataele who argued that many villagers relied on the lagoon for their livelihood and were finding it increasingly difficult to find or afford enough protein. Also, fish was expensive because of the shortage of fish traps (pa ika T.).[1]

On the Fisheries Division's original moves to protect the lagoon, Mataele said that "this was brought about by a recommendation, made by some foreigners, which stated that Fanga'uta is the spawning ground for fish in Tongatapu." Another Tongatapu representative added that "there were foreigners who procured black coral, pearl shell, and beche-de-mer from Tonga but Europeans ("papalangi") have said nothing of this" (trans., Nuku'alofa: Kalonikali Tonga, September 4, 1981, p. 2).

It was widely believed that the legislation was unnecessary and against God's laws of nature. There exists in Tonga a certain suspicion of Europeans and their motives.

The present European administration of the Fisheries Division has shown little interest in the lagoon issue. On his arrival in 1979 the chief fisheries officer reviewed the fisheries development programs and discontinued a study on the lagoon's mullet by a Peace Corps volunteer. According to the present fisheries officers, there has been no real decline in fish catch but simply a greater increase in fishing effort, although this conflicts with local opinion. Since there is no catch data available, there is no support for either claim.

RESULTS

Mullet

Mullet, because of its oily flesh and strong taste, is the most highly regarded foodfish in Tonga. Despite widespread interest in the declining Fanga'uta mullet fishery there is no information on the species involved and little is known of their biology. J. Martin (personal communication) believes that there may be six species of mullet in Fanga'uta Lagoon although none were caught during this study or seen in the Nuku'alofa market. One specimen seen in 1979 (King and Zann, 1979) was identified as the common grey mullet *Mugil cephalus*.

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[1] T. denotes the common Tongan term

Mullet are very important food fish worldwide (Thompson, 1966) although relatively little is known of the tropical species (Grant, 1976). Mullet are not a strictly catadromous fish, but are associated with fresh or brackish water at some stage of their life cycle. Fanga'uta Lagoon appears to be important in the life cycles of the Tongatapu species. According to Martin (cited in Ludwig, 1979) they enter the lagoon in June-July and leave in August-September when they are ready to spawn. They leave in schools and mostly spawn on the Liku coast. Juvenile mullet also appear to enter the lagoon as fingerlings and are frequently seen on the surface (and were noted in this study).

COMMERCIAL FISHERY

Despite the ban, some illegal commercial fishing was noted during the progress of this survey. On several occasions fishermen fled when they saw the Fisheries Division boat used in the survey. Gillnetting was the main method of fishing observed.

Fish Fences (pa ika T.)

According to some informants the arrowhead fish fences were introduced from Samoa in the early 1960s but others say they were present before then. All agree that the fences, an effective way of catching migratory coastal species such as mullet, proliferated in the mid-1960s and a number were located on the seagrass flats within the entrance to the lagoon.

The arrowhead fences consist of a 15- to 30-m long leader or "shaft" of 5-cm mesh galvanized wire, about 1.5 to 2 m high, suspended by timber stakes driven into the sand or mud. The head is triangular with a base 20 to 30 m long with entrances on either side of the shaft and with circular collectors at both sides and sometimes at the apex of the triangle (Figure 10). Several fences may be arranged, one leading from the other, according to the terrain and pattern of fish movement (Figure 10).

Fences cost about T$1,500 (F$1,500; US$1,700) to erect; about 13 rolls of wire are needed. Although expensive they are often very profitable and catches worth T$200 to T$300 per night are known. Because of corrosion and rust, wire must be replaced every 12 to 18 months or else the fences are simply abandoned.

It is estimated from ground plotting and aerial photos that the existing fish fences cover 50 percent of the entrance and would effectively prevent most fish migration along the western and eastern shores of the entrance. Over a 4-km semicircle at the main lagoon entrance there is a total of 105-km fish fences (Figure 11).

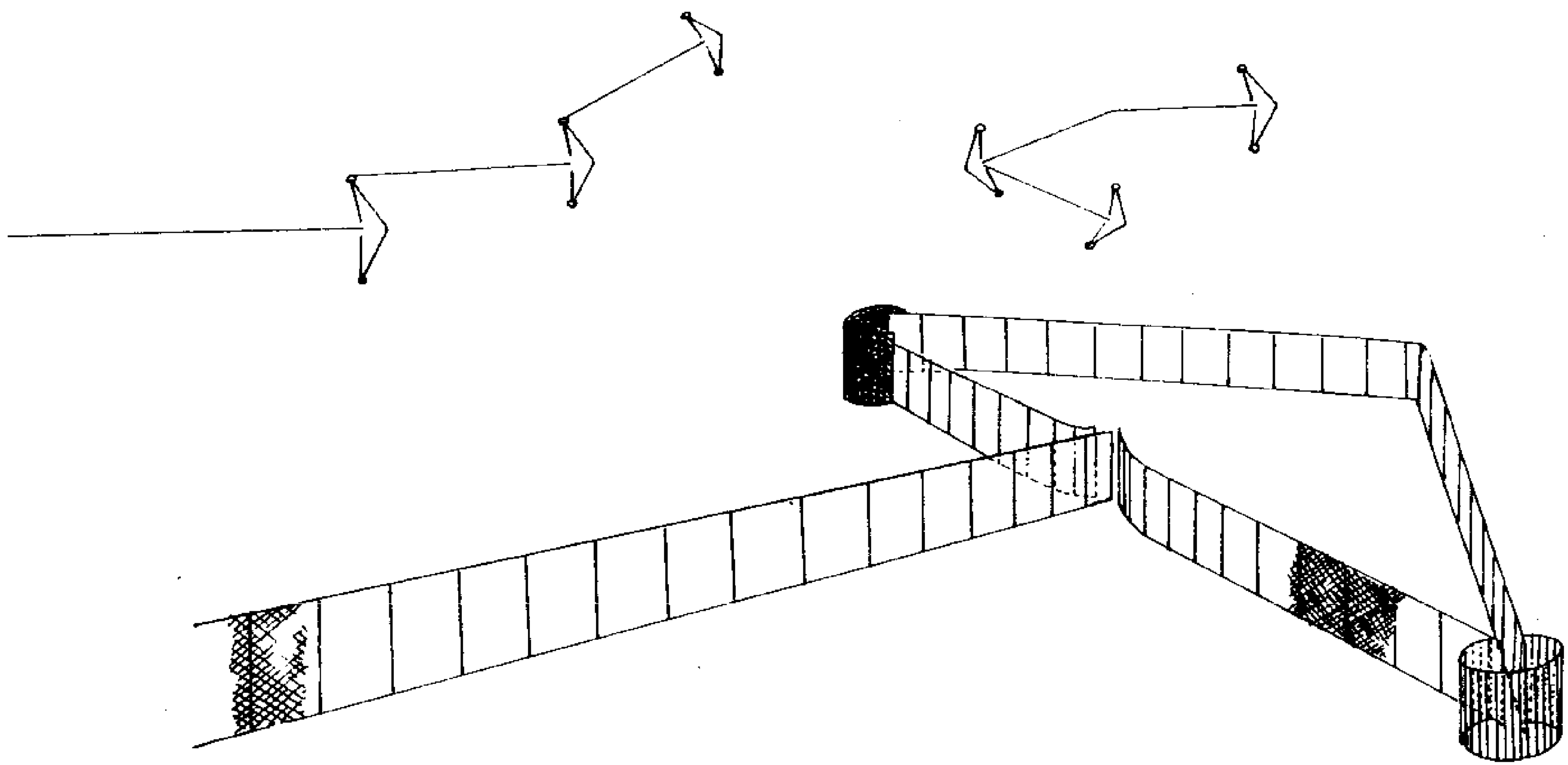

Figure 10. Arrowhead fish fence (T. pa ika), showing design and construction with multiple-trap arrangements (above)

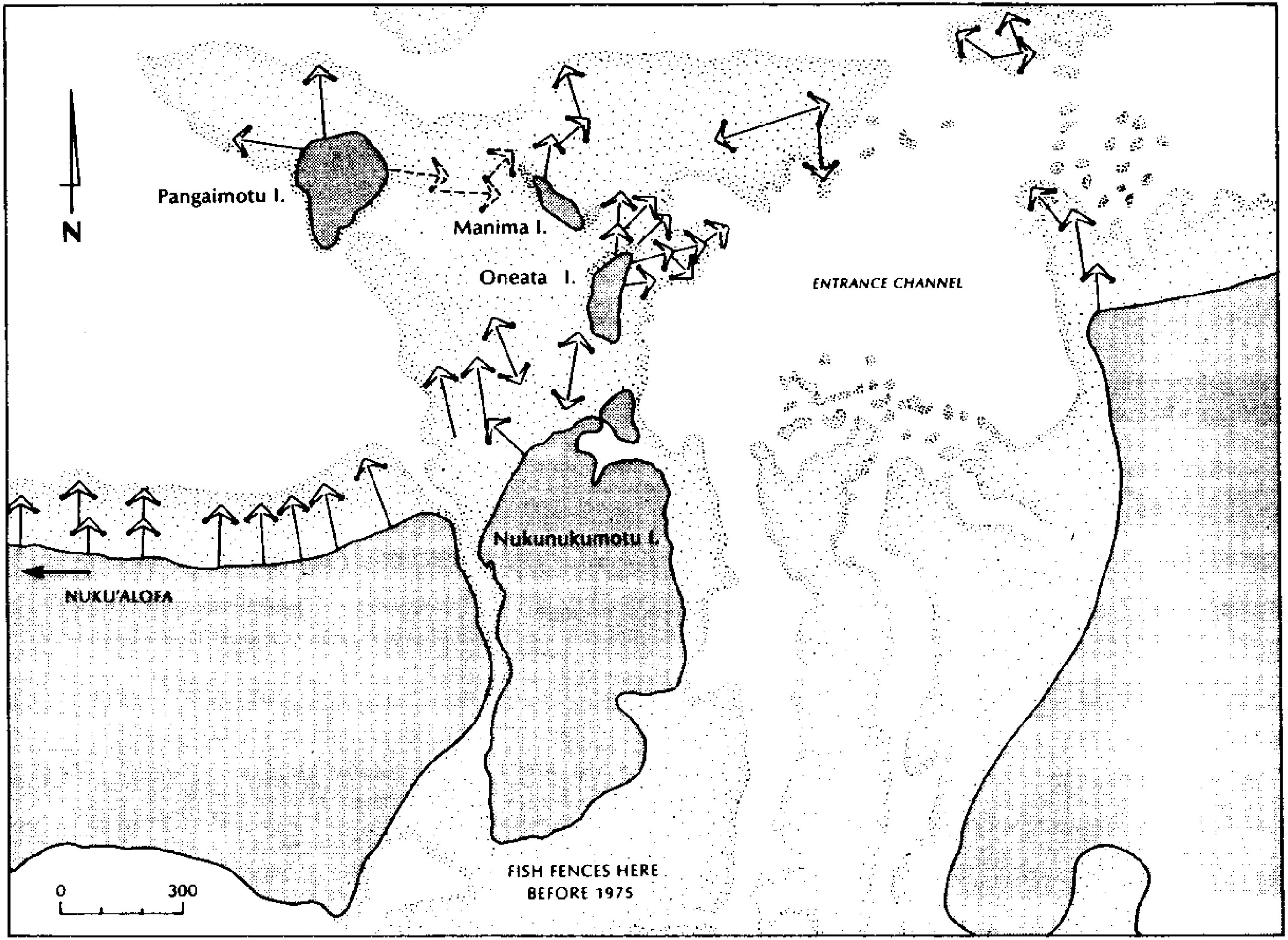

Figure 11. Arrowhead fish fences off entrance to Fanga'uta. Positions and sizes from aerial, land, and sea survey. Dotted lines = mapped in 1979, not confirmed; p.a. = position approximate.

Prawn Fishery

Large numbers of edible prawns, *Penaeus semisulcatus* and *Metapenaeus ensis*, are present in the lagoon (Braley, 1976, 1979).

A small trawl fishery was established by a European businessman in 1974 using otter-board trawls towed by small boats. Catches were reported to have been high and the prawns of excellent table quality, but partially because of high mortalities to juvenile food fish this and other commercial operations were prohibited in 1975.

Because of R.D. Braley's detailed studies (1976, 1979) no attempt was made to assess the prawn resources in this survey although several specimens of each species were captured in sample trawls and gill nets.

SUBSISTENCE FISHERY

Many families supplement their daily food with fish and shellfish collected in Fanga'uta Lagoon. For a few families the lagoon is vital for their survival. Unfortunately, there is no information on subsistence fishery as the authorities do not seem to have been concerned with this aspect of fishery.

Little subsistence fishing was noted in the Nuku'alofa branch although it was accessible to the township. Gillnets were seen daily off the Peace Corps center and off Pe'a Sector but very few fish were caught. Women were occasionally seen in waist-deep water feeling for jellyfish (*kolukolu* T.) and possibly for seaweed (*limu* T.) and bivalves.

Gillnets were seen off Folaha and Talakite Island and at low tide women were frequently seen foraging for shellfish on the seagrass flats from Talakite to Nukunukumotu. Women were collecting bivalves off Vaini on the Mu'a branch and several gillnets were seen around the edges of the lagoon. One fisherman was seen setting crab traps from a canoe.

Most fishing activity was concentrated on the maze of patch reefs at the entrance. Ten to 15 canoes were seen between Nukunukumotu Island and Makaunga on 1 day and 15 to 20 foragers were seen on the tidal flats. Fish drives using surround nets, gillnetting in channels and deeper holes, spearfishing, hooking for octopus, and pole fishing for small fish were the most common techniques used.

FISHING CRAFT

Small dugout outriggers (*popaos*) are the basic craft of the subsistence fishery. The main hull (*katea*) is crudely hewn from a breadfruit or kapok tree by adze, two cross beams (*kiato*) are lashed to one side, and the float (*hama*) is attached to each beam by four to six stanchions, a Y-shaped branch, or U-shaped connectives. The method of attachment varies from village to village. The overall length of each popao is 3 m to 4 m. They can carry one to two adults, are paddled (one gaff-rigged sailing canoe was seen off Oneata), and are used only in sheltered, nearshore waters. Detailed descriptions of the popao and fishing techniques can be found in Zann (1981).

A census of canoes in several villages around Fanga'uta was conducted in 1980 and additional information was taken during this study (Table 19). According to these surveys, approximately 90 canoes and 37 other craft (mainly punts) operate in Fanga'uta Lagoon.

TABLE 19. NUMBER OF CANOES AND OTHER CRAFT, FANGA'UTA LAGOON

Village Place	Canoes	Other Craft	Notes
Nukuleka	9	3	1980
Natutoka	11	*	1980
Talafolou	36	10*	E side entrance (1980)
Nukunukumotu	12	6	W side entrance (1981)
Mu'a	10*	?	Dense mangroves (1981)
Vaini	8	--	1981
Talakite I	--	3	One family (1981)
Folaha	5*	?	Dense mangrove (1981)
Nuku'alofa environs	--	10	1981
TOTAL	91	37	

Note: In certain areas mangroves obscured counting so estimates were made and are shown with an asterisk.

DISCUSSION

Despite some conflicting opinions, it is apparent that there has been a gradual decline in Tongatapu's mullet fishery over the past 20 years. The reason is most likely overfishing by the use of more efficient introduced fish fences and nylon monofilament gillnets, as well as an increase in fishing effort and in the urban demand for fresh fish.

Mullet are linked in some way to inshore or enclosed waters and are therefore vulnerable to overfishing, particularly around small islands with limited suitable waters. Mullet have been overfished both in Laucala Bay (Day: personal communication) and in Fulaga Lagoon (Travers, Botkin: personal communication) in neighboring Fiji.

The prohibition on commercial fishing in the lagoon from 1975 was a sound management procedure but of limited effect. The fish fences were merely moved outside the lagoon where they effectively prevented migration to and from the protected waters.

The arguments for the removal of the prohibition were made on emotional grounds. It was stated that many people depend on the lagoon resources for their food yet subsistence fishing has always been allowed. The reopening of the lagoon for commercial fishing can only be a retrograde step; however, it does represent an important opportunity for the Fisheries Division to gather data upon which any future management policies must be made.

Although the finfish are overexploited, the lagoon has an unfished prawn resource. The 1974 trawl fishery in the lagoon was responsible for high catches of juvenile lutjanids, etc., which used the lagoon as a nursery, and any renewal of the prawn fishery should be carefully regulated. An added risk of large-scale trawling in Fanga'uta Lagoon is the environmental hazard of physically disturbing the benthic seagrasses and algae which are the basis of the lagoon's primary productivity.

R.D. Braley (1979) recommended restrictions on net mesh and size, limiting the number of licenses, limiting the fishing nights to those nights between half to full moon (therefore catching fewer juvenile fish), as well as prohibitions in some areas.

Because of the limited resource the author feels it may be better to prohibit the use of trawl nets and encourage other ways of fishing, e.g., gillnets with pockets along the bottom (Japanese technique) or baited traps (used in South Australia in an area similarly unsuited for trawl fishery).

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SPECIES LISTS

L.P. Zann

LOWER PLANTS

RHODOPHYTA (red algae)

Corallinaceae (coralline)

Lithophyllum sp. Coralline algae.
Found on patch reefs at entrance.

Hydrolithon reinboldii. Coralline algae
Pebble-shaped (as above).

CHLOROPHYTA (green algae)

CAULERPACEAE

Caulerpa ramosa var. *clarifera* (*limu fuofua* T.) Abundant on intertidal and on the lagoon floor. Grape-like. Edible; important in Tongan diet.

C. serrulata. (*limu* T.)
Found on bottom of Fanga'kakau. Common. Zig-zag prostrate branches.

C. ashmeadii. (*limu* T.)
Feathery, mixed with *C. ramosa* in both branches.

CODIACEAE

Chlorodesmis comosa
Present on patch reefs, entrance.

Halimeda discoidea
Abundant. Dominant on intertidal sandflats, on bottom of Mu'a branch, around entrance patch reefs. Calcareous discoid. Important source of lagoon sediment.

H. opuntia
Abundant on intertidal patch reef tops. Similar to above, more calcacified.

Udotea glaucesceus
Present on intertidal sandflats and Mu'a bottom. Fan-shaped, calcareous. Extensive holdfast in soft sediments.

HIGHER PLANTS OF LAGOON SHORES

(Note: List of species of plants recorded from the mangroves in Tongatapu by Yuncker (1959), Thaman (1979), and Hurrell and Hassall (in press). From Hurrell and Hassall.)

PTERIDOPHYTA (Ferns and fern allies)

FILICOPSIDA. ADIANTACEAE.

Acrostichum aureum L. (Hakato)

OPHIOGLASSACEAE.

Ophioglassum pendulum L.

POLYPODIACEAE.
Pyrrosia adnascens (Sw). Ching

MAGNOLIOPHYTA (Flowering plants)
LILIATEAE (Monocotyledons).

ARACEAE
Epipremnum pinnatum (L.) Engelm (Alu T.)

ARECACEAE
Cocos nucifera L. (Niu T.)

ORCHIDACEAE
Oberonia equitans (Forst. F.) Drake
Saccolabium contrictum Reichenb
Taeniophyllum fasciola (J.R. and G. Forst.) Seem (Kumukumu Tahi T.)

PANDANACEAE
Pandanus pyriformis Martelli (Fa T.)

MAGNOLIATEAE (dicotyledons)

COMBRETACEAE
Lumnitzera Littorea (Jack) Voigt (Hangale T.)

EUPHORBIACEAE
Excaecaria agallocha L. (Feta'anu T.)

MELIACEA
Eylocarpus granatum Koenig (Lekileki T.)

RHIZOPHORACEAE
Bruguiera gymnorhiza (L.) Lam (Tongo Ta'ane T.)
Rhizophora samoensis (Hockr) Salvoza (Tongolei T.)
R. stylosa Griff

STERCULIACEAE
Heritiera littoralis Dryander (Mamea T.)

HIGHER PLANTS, FANGA'UTA BENTHOS

POTAMOGETOMACEAE
Halodule pinifoliosa. Seagrass
Abundant on bottom of Fanga'uta Lagoon. Dominant community.

HYDROCHARITACEAE
Halophila ovalis. Seagrass
Abundant on bottom of Fanga'uta Lagoon.

INVERTEBRATES

PROTOZOA

Marginopora sp. Foraminifera
Large discoid foram abundant towards entrance of lagoon. An important sediment former.

CNIDARIA

SCYPHOZOA

Cassiopeia sp. Upside-down jellyfish. (kolukolu T.)
Large bottom-living jellyfish abundant on Nuku'alofa branch of lagoon especially off Kanatea Island.

ACTINARIA

Actinia sp. Sea anemone. (umana T.)
Small grey sea anemones in depressions in limestone rock. Abundant mid-intertidal zone, Mu'a branch.

SCLERACTINIA (hard corals) (fee; punga T.)

Stylophora pistillata. Branching coral
1-2 m, patch reefs, lagoon entrance.
Seriatopora hystrix. Branching coral
2 m (as above)
Pocillopora damicornis. Branching coral
2 m (as above)
Pavona cactus. Foliose, encrusting coral
2.5 m (as above)
Acropora cf. kenti. Staghorn coral
(as above)
Acropora cf. formosa. Staghorn coral
(as above)
Acropora cf. pulchra. Staghorn coral
(as above)
Acropora spp. 1-3. Unidentified species
(as above)
Montipora cf. ramosa. Branching/encrusting
2 m (as above)
Montipora sp. (ramosa group)
2 m off Pangaimotu.
Astreopora cf. myriophthalma. Encrusting coral
2 m, patch reef at entrance to Fanga'uta Lagoon.
Porites cf. murrayensis. "Pebble" growth form Intertidal, seagrass beds at entrance to lagoon.
Porites andrewsi. Massive colony and branching
2-3 m, patch reef off entrance.
Porites cf. lobata. (pupu'a T.)
Massive, forming heads and microatolls. 2 m, entrance to lagoon.
Goniastrea cf. pectenata. "Brain" coral
Rounded heads, 1 m, entrance to lagoon.
Favites abdita. "Brain" coral
(as above)
Favia cf. pallida. "Brain" coral
Rounded head, 2 m, entrance to lagoon.

Platygyra cf. *daedalca*. "Brain" coral
(as above)
Lobophyllia hemprichi. "Brain" coral
(as above)
Leptoria phrygia
(as above)
Turbinaria cf. *reniformis*. Foliose, sheet
(as above)
Acrhelia horrescens
(as above)
Echinophyllia cf. *echinata*
(as above)
Cycloceris cf. *vaughani*. Small "mushroom" coral
(as above)
Fungia fungites. "Mushroom" coral
(as above)

ALCYONARIA (soft coral)
Sinularia sp. Soft coral
1 m, off Nukunukumotu.
Sarcophyton sp. "Cabbage" coral
(as above)
Lobophyton sp. Leathery soft coral
(as above)
Dendronephthya sp. Spiky soft coral
On patch reef at entrance.

HYDROIDEA
Millepora cf. *platyphyllia*. Stinging coral
Branching, encrusting and spatulate forms. Common on patch reefs at entrance.

MOLLUSCA

CEPHALOPODA
Octopodidae. Octopus. (*feke* T.)
Seen in fishermen's catch, lagoon entrance.

AMPHINEURA
Acanthozostera gemmata. Chiton. (*hulihuli; mamatahi* T.)
Large, 8 shells on upper intertidal rocks, lagoon entrance. Edible.

GASTROPODA
Tectis pyramis. Top shell. (*takanike* T.)
Lower intertidal, lagoon entrance. Edible.
Patelloidea cf. *pygmaea*. Capshell
Mid-intertidal on rock, Mu'a.
Littorina scabra. Periwinkle. (*pikitonga* T.)
Upper-intertidal, abundant on mangroves. Note absence of other littorinids in lagoon.
Serpulorbis imbricus. Worm-snail. (*tu'e* T.?)
Subtidal associated with corals, lagoon entrance.
Clypeomorus cf. *traillii*. Creeper
Lower-intertidal, abundant on mud, Mu'a.

Rhinoclavis sp. Creeper
Mid-intertidal, common on sandflats, Nukunukumotu.
Nerita plicata. Nerite
Upper-intertidal, common on rocks, Nukunukumotu.
N. signata and *N. undata*. Nerites
Mid- and upper-intertidal, common on rocks, Vaini, Mu'a.
Strombus gibberulus. Hump-back stromb
Mid-intertidal, abundant on sandy shores of Nukunukumotu. Edible.
Lambis lambis. Spider shell. (*anga ana* T.)
Subtidal, common on patch reefs at entrance. Edible.
Cypraea moneta. Money cowry. (*pule* T.)
Intertidal, abundant on mud and sandflats associated with seagrass. Shells used for decorations.
C. annulus. Ringed money cowry
(as above)
C. vitellus. Milk-spotted cowry
Lower intertidal, subtidal, common on patch reefs at entrance.
C. tigris. Tiger cowry. (*pule makafeke* T.)
Present, subtidal on patch reefs at entrance. Edible, used for decorations.
Polinices pyriformis. White moon snail
Abundant on sandflats off Nukunukumotu. Bivalve predator. Edible.
Natica sp. Moon snail
(as above)
Chicoreus torrefactus. Murex
Subtidal, present on patch reefs at entrance.
Mancinella pica. Murex
Intertidal, present on rocks off Nukunukumotu.
Mitra mitra. Mitre
Intertidal, present on sand flats off Nukunukumotu.
Vasum turbinellus. Vase shell
Intertidal, common on rocks off Nukunukumotu. Edible?
Conus mustilinus. Coneshell. (*fuhu* T.)
Subtidal, present on patch reefs at entrance.
C. eburneus and *C. coronatus*. Cones. (*fuhu* T.)
Mid-intertidal, common off rocks, off Nukunukumotu.
C. ebraeus and *C. omaria*. Cones
Lower intertidal, present in sand and under rocks, off Nukunukumotu.
Dolabella auricularia. Sea hare. (*muli'ene* T.) Subtidal, on muddy bottom, Mu'a. Edible.
Onychidium. Sea slug
Mid-intertidal, common on dead coral and limestone rock, Mu'a and Nukunukumotu. Very well camouflaged.

BIVALVIA
Modiola agripeta. Mussel (*kuku* T.)
Uncommon, lower intertidal among seagrasses. Mu'a, entrance. Formerly an important food source.

Atrina cf. pectenata. Penshell. (fele T.)
Present, lower intertidal in sand-mud towards lagoon entrance. Edible?
Anadara cf. maculata or antiquita. Cockle. (kalea'a T.)
Common, lower intertidal in mud-sand towards lagoon entrances. Important food.
Barbatia sp. Large cockle
Present, lower intertidal in sand, Nukunukumotu.
Fragum unedo. Strawberry cockle
Common, lower intertidal in sand at lagoon entrance. Edible.
Tellina virgata. Tellin. (mehine T.?)
Present, as above.
Periglypta clathrata. Cockle. (tavatava, tava'amanu T.?)
Large. present, as above. Edible.
Codakia tigerina. Bivalve. (te'e T.?)
Large, present, as above.
C. punctada. Bivalve
Smaller, present, as above. Edible.
Gafrarium tunidum. Bivalve
Common, lower intertidal in mud and sand, widespread in lagoon. Important food item.
Pecten sp. Scallop.
Present, subtidal in Mu'a arm. One specimen netted. Many dead shells.
Pinctada marginatifera. Pearl oyster
Present, subtidal on patch reefs, entrance.
Lucina sp., Anodonta sp., Scutarcopagia sp. Miscellaneous small bivalves. Common intertidally on mud-sand flats towards entrance.
Veneridae, Tellinidae, Atactodea?, Lucinacea. ('Chule T.)
Miscellaneous small white bivalves. Abundant subtidally, e.g., in mud off Pe'a.

ARTHROPODA

CRUSTACEA

Squilla/Lysiosquilla.? Mantis shrimp. (vale T.) Common, (as above). Burrows lined. (none collected)
Penaeus semisulcatus and Metapenaeus ensis. Prawn. (uloula'a T.)
Common in Fanga'uta Lagoon. Edible. Formerly fished commercially.
Alpheus/Synalpheus sp. Shrimp. (vale T.)
Burrows in intertidal sandflats on Mu'a arm and entrance. Partnership with goby. Responsible for much bioturbation. (none collected)
Axius sp.? Shrimp
Common burrows (as above).
Scylla serrata. Mud crab. (tolitoli T.)
Common, Fanga'kakau. Several caught in gill nets. Edible, finest table quality.
Thalmita cf. prymna. Crab. (pakatea T.)
Abundant, Fanga'uta Lagoon. Many caught in gill nets. Edible, but small.

Matuta sp. Sand crab
Present, on sand bottom, Mu'a. One specimen in gill net.
Calappa hepatica. Box crab. (_tafola_ T.)
Abundant intertidally on mud/sand flats, Mu'a branch.
Uca lactea. Fiddler crab. (_tulu_ T.)
Abundant upper intertidal mud flats near mangroves, Mu'a and Nukunukumotu passage.
Platylambrus sp. Coral rubble crab
Present, intertidally on patch reefs. Well camouflaged as _Acropora_ rubble.
Pilumnus sp. Weed crab
Present on sand/mud flats, at entrance well camouflaged as seaweed.
Huenia cornigera. Halimeda crab
Present on intertidal Halimeda. Well camouflaged as disc.
Xanthiidae. Miscellaneous small crabs
Common, intertidally under coral rocks and rubble towards entrance.

ECHINODERMATA

ASTEROIDEA

Culcita novaeguineae. Pin-cushion star
Present subtidally on patch reefs off entrance. One specimen seen eating _Acropora_ coral.
Linckia laevigata. Blue starfish. (_mangamanga'atai_ T.)
Present, lower intertidal at entrance. Note small size, paler and green coloration cf. W. Pacific specimens.
Astropecten cf. _polyacanthus_. Spiny starfish
Common, subtidal mud bottoms of Mu'a branch.
Astropecten/Archaster.? Common starfish
Abundant, mid-intertidal sand/mud flats towards entrance of lagoon.

OPHIUROIDEA

Ophiuroidea. Snake star. (_feke tevele_ T.)
Several species common on rocks at entrance to lagoon.

ECHINOIDEA

Diadema setosum. Needle urchin. (_vana_ T.)
Common subtidally on sides of patch reefs at and off entrance.
Tripneustes gratilla. Edible urchin. (_tukumisi_ T.)
(as above). Edible.
Toxopneustes pileolus. Venomous urchin
Present (as above). Venomous pedicellaria. Informants say it is edible!
Echinometra mathaei. Boring urchin
Present in dead coral (as above).
Parasalenia boninensis. Urchin
Resembles above but has longer spines.

HOLOTHUROIDEA

Synapta maculata. Long sea cucumber. (_peva_ T.) Present on sediment adjoining patch reefs at entrance.

Holothuria (Mertensiothuria) leucospilota. Cotton spinner
Long black holothurian, common on sand/rock subtidally at entrance patch reefs. No commercial value. Tongans eat reproductive organs.
Holothuria (Halodeima) atra. "Lollyfish"
Small black beche-de-mer, abundant on sandflats towards entrance. Little commercial value.
H. (H.) edulis. Small, black, pink ventral
Common inter- and subtidally, sand-mud bottom, lagoon entrance. No commercial value.
Holothuria cf. impatiens. Small, brown spiny protuberances
Commonly associated with dead coral at entrance patch reefs.
Stichopus variegatus. "Curryfish"
Large yellow holothurian, present subtidally on sand bottoms off patch reefs at entrance. No commercial value.
S. chloronotus. "Greenfish"
Smaller, green/black holothurian abundant intertidally on entrance sandflats. No commercial value.
Actinopyga mauritania. "Surf-fish"
Larger, tan brown and white spots. One specimen on intertidal rocks, Nukunukumotu. Usually found in exposed conditions.

VERTEBRATES

CHORDATA

REPTILIA

Laticauda colubrina. Banded sea snake
Venomous, amphibious. One specimen seen off outer lagoon patch reef.
Chelonia mydas. Green turtle
Report of turtles once common in lagoon. Tangle net formerly seen across main passage (1979).

AVES

Pluvialis dominica. Golden plover
Seen on adjoining mud and sand flats. Migratory.
Anas superciliosa. Australian grey duck
Common at Pe'a end of Fanga'uta Lagoon.
Fregata cf. ariel. Frigate bird. (hele kosi T.) Several seen over lagoon during rainy weather.
Sterna bergii. Crested tern
Many seen feeding at Mu'a end of lagoon.
S. nereis. Fairy tern
Several seen resting on drift timber in lagoon.
Egretta sacra. Reef heron
White and grey morphs seen on seagrass flats.
Limosa lapponica.? Bar-tailed godwit
Several seen along mangrove shores.
Hirundo tahitica and/or Apus pacificus
Pacific swallow and/or white rumped swiftley. Many seen feeding above lagoon surface.