

**POPULATION DYNAMICS OF THE GIANT CLAM, Tridacna maxima, AT
ROSE ATOLL**

1985



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ABSTRACT

There is a paucity of knowledge on the population dynamics of the giant clams of the family Tridacnidae. Such information on population dynamics is necessary for responsible management and conservation of giant clam resources. In the present study data were analyzed to provide ecological information on the giant clam (*Tridacna maxima*) community in the undisturbed reef ecosystem of the Rose Atoll National Wildlife Refuge. Data from field surveys, marking experiments and age determination studies were coupled to provide a model of population dynamics of an unperturbed giant clam community. This study includes information on growth, mortality and potential yield. The resultant information provides significant knowledge of giant clam ecology and will have a profound effect upon critical conservation decisions at local and world levels.

INTRODUCTION

The family Tridacnidae is comprised of only six living species and includes the largest bivalves known to have existed. Hence the title "giant clams." Of the six existent species, five belong to the genus *Tridacna* while one species belongs to the genus *Hippopus*. Due to their algal symbiont lifestyle, these bivalves are restricted to the coral reef shoals of the Indo-Pacific.

A great deal of research has been done on the Tridacnidae in general. Among the most important of these are the work done by Yonge (1975) on nutritional problems, those by Wada (1954) on reproductive modality and that on systematic revision by Rosewater (1965; 1974). In recent research, the larvae and post larval development have been studied by Labarbera (1974; 1975). In addition, haemolymph in tridacnid clams have been studied by numerous researchers. The haemolymphs appear to differ between different species of clams (Uhlembruck et al., 1979).

The subject of the present study is the middle-sized giant clam, *Tridacna maxima*, which can reach a length of 36 cm. This a respectable size for a clam and definitely constitutes being a "giant". In the bivalve world. However, *Tridacna maxima* is dwarfed by the grandfather of giant clams, *Tridacna gigas*, which reach weights of almost 270 kilograms. *Tridacna maxima* is found from the Red Sea to American Samoa.

Like most other bivalves, *Tridacna maxima* begins its life as a planktonic veliger larvae. After a period of time in the plankton, the length of which may account for its wide distribution, the larvae settle onto shallow coral reef areas. After setting the

veligers lose their cilia and acquire clam characteristics. *Tridacna maxima*, like the other members of the Family Tridacnidae, then spends the rest of its life as an upside-down clam with its valve edges pointed toward the sun so that their colorful, undulate mantle lobes can absorb sunlight for food production.

Like all bivalves, *Tridacna maxima* has three mantle segments. The outside mantle component secretes one of the largest and strongest shells of the bivalve domain. The center fold is greatly enlarged and is the most conspicuous mantle segment. The interior mantle portion forms the siphon and controls water flow. It is these adaptations in mantle morphology which have helped make the large size of giant clams attainable.

Giant clams inhabit tropical waters that are notoriously poor in nutrients and plankton. Consequently, the large size achieved by the Tridacnidae would appear to be incongruous with filter feeding of plankton. However, they compensate for habitation of nutrient poor waters by having a morphology and living in an environment which makes it possible for them to "farm" their own food. Giant clams are not man eaters as has been contended by Hollywood, but gentle giants. They are able to cultivate much of their own nourishment in the enormously extended middle mantle lobe due to the presence of large numbers of unicellular, symbiotic algae called zooxanthellae (Goreau and Yonge, 1973). Numerous studies have concentrated on these zooxanthellae (Dean et al., 1979).

The symbiotic relationship between the giant clam and the algae zooxanthellae restricts the clam to the photic zone, and indeed they thrive there. Weight analyses of *Tridacna maxima* show that 80% of the flesh is within the mantle and that the mantle contains most of the zooxanthellae. These mantle tissues extend over the outer dorsal margin with cells concentrating solar radiation and utilizing it in photosynthesis. The bivalves receive nutritional supplement from the algae. Although the exact means of this energy transfer is not known. It may be a direct consumption of the algae or organic compounds or by-products of photosynthesis (Mansour, 1946; Muscatine, 1967; Goreau et al., 1973; Galbert, 1977; Shard and Saldut, 1977).

Zooxanthellae have a nutritional symbiotic relationship with many tropical marine organisms, the most notable among these being reef corals. In corals zooxanthellae obtain waste products from the coral polyps for growth and supply nutrition to their hosts. The same nutritional exchange appears to be true of the zooxanthellae-giant clam alliance. The zooxanthellae algae may also assist in giant clam

calcification as they do in corals, but no documented studies have yet been accomplished. Tridacnidae are almost alone in the bivalve world in maintaining zooxanthellae for nourishment. The only other bivalve known to keep zooxanthellae is the heart cockle, Corculum candida (Kawaguti, 1950). It is likely that the farming of food resources by giant clams is responsible for the body size Tridacnidae reach and the increase in mantle size and coloration. In addition, stable isotopes have been studied in giant clams (Aharon, 1983 and Jones *et al.*, 1985). This information shows that the zooxanthellae may cause a fractionation of the stable isotopes. The stable isotopes can also be utilized as environmental markers or environmental records of what the clam has experienced throughout its life.

The problems encountered in managing a natural resource are a major concern for the continued viability of that resource. Such concerns surround the giant clam, Tridacna maxima, resource at Rose Atoll, American Samoa. To tackle these concerns, information is needed to provide a population dynamics model for this natural resource. The need for objectiveness in dealing with these resource problems precedes a necessity for deriving quantitative assessments.

Giant clams have been depleted in virtually every area in which they exist. Much of this over exploitation is the result of a lack of knowledge about giant clam population dynamics. Moreover, such knowledge of giant clam ecology would result in better conservation decisions and a consequent increase in population size with benefits extending to the surrounding ecosystems.

In the present study, demographic parameters for a population of giant clams, Tridacna maxima, at Rose Atoll, American Samoa are established in order to provide information for responsible management and resource utilization. Population surveys and age determination data are analyzed to provide population dynamics parameters. The information obtained will have widespread application to giant clam populations worldwide.

A giant clam population can be considered a biological entity and as such has characteristics of size, density, mortality, longevity, growth rates, sex ratios, etc. The aforementioned population features can be analyzed from data readily collected. These data are in need of experimental inquiries or statistical calculations which can then be applied to the entire population. In this regard it is not feasible to examine the entire population. Hence fractions of the population are observed and then inferences concerning the whole population can be constructed.

Many areas of the Indo-Pacific have been heavily fished for giant clams and this has resulted in few "natural" populations. Investigations of pristine clam populations would provide unbiased knowledge of the age, growth rates and population dynamics and demonstrate how a clam community performs in an undisturbed state. Giant clams have been utilized as organisms which can provide a benchmark for environmental perturbations (Hignette, 1979). In particular, arsenic has been found to accumulate in the kidneys of giant clams in extremely high concentrations Benson and Summons (1981). Thus consumption of the entire kidney may have some detrimental effects on human populations. Other heavy metals have also been found in giant clams such as Iron, magnesium, copper, zinc, and lead (Khristophorova, 1980). In this regard the giant clams at Rose Atoll may be of unequalled value because of the unperturbed environment and thus the lack of contamination of the clams at Rose Atoll by pollution.

STUDY SITE

The site of study is Rose Atoll, American Samoa. Rose Atoll is an isolated atoll located approximately 180 miles east of Pago Pago, American Samoa at 14°33' S 168°09' W. Within the Rose Atoll National Wildlife Refuge is a large area of submerged reefs which are still in a pristine state. (Figure 1). Discovered in 1819, Rose Atoll is one of the only square atolls known to occur in the world. The atoll exhibits a rose color due to calcareous algae, but was named after the discoverer's wife whose name was Rose. Rose Atoll has two islands, Rose Island which is about 10 acres in area and smaller Sand Island, located near the inlet to the lagoon.

Rose Atoll is an unperturbed, pristine atoll. Rose Island is densely covered with vegetation composed mostly of the tree Pisonia grandis. The Pisonia trees provide nesting habitat and refuge for thousands of birds, mainly boobies, noddies and frigate birds. The steady rain of guano greatly contributes to the island's luxuriant growth. The lagoon within Rose Atoll is approximately 100 acres in size, making Rose one of the smallest atolls in the world. The maximum depth of the lagoon is 16 meters and visibility in the water column is over 30 meters. Water washes over the atoll rim during tidal changes and outgoing currents reach speeds in excess of 6 knots in the inlet. Water temperature ranges from 31° to 34°C in the lagoon proper and is as high as 36°C in shoal areas at slack tide. This is an ideal environment for giant clams and Tridacna maxima are notably abundant in such areas where hard substrate exists.

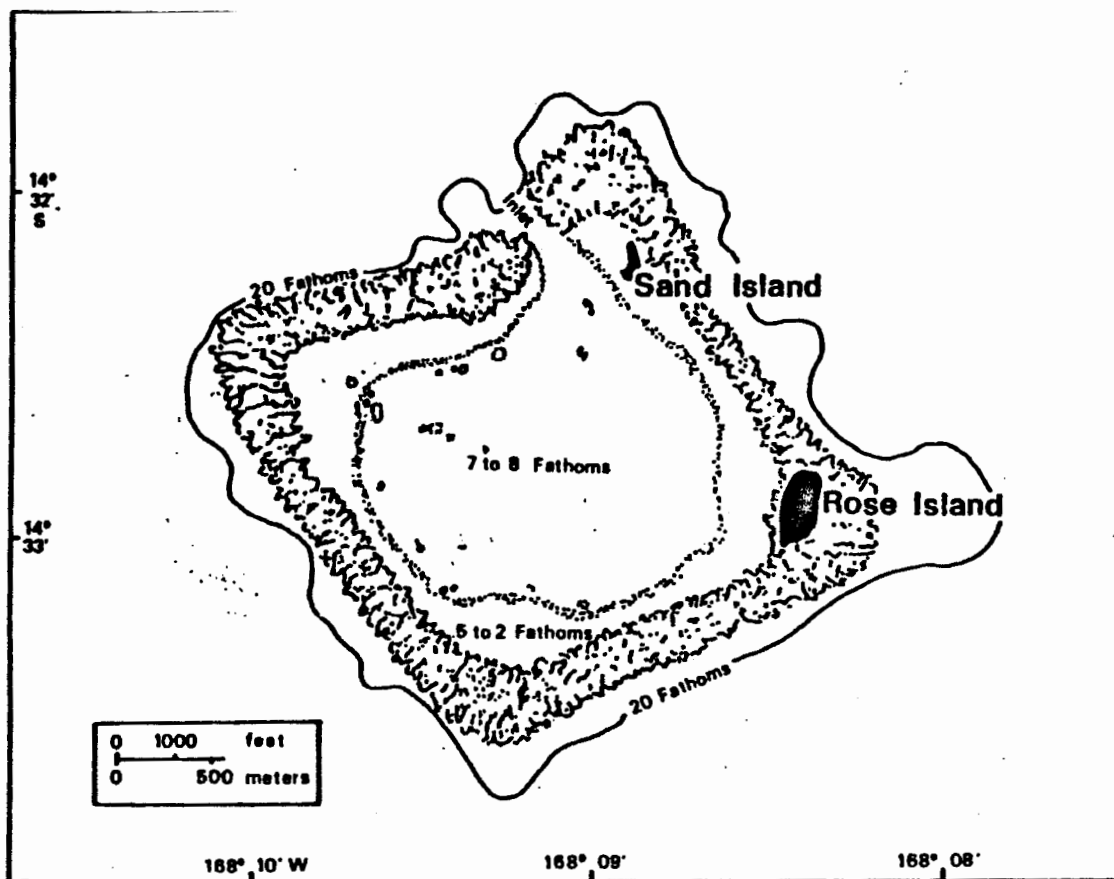


Figure 1. Map of Rose Atoll.

POPULATION SIZE

Any endeavor to assess the status or potential of a giant clam resource requires determination of the size of the population. As a consequence biological inventories are basic to resource management. Population size is the direct result of the processes of recruitment, growth and mortality. Comprehension of the dynamics of giant clam populations has to date been hampered by a lack of data on these parameters. Determination of population abundance is necessary to understand population number and composition, for estimating population yield, and as a basis for sound management.

The most accurate method in the determination of population size would be by direct enumeration. However, this is often not feasible even with a small population such as is resident on Rose Atoll. In this regard, the "Area Density Method" would be more appropriate (Everhard and Young, 1981). The "Area Density Method" consists of counting the number of giant clams along a series of transects. Such transect counts have been accomplished for Rose Atoll and have been analyzed. In these analyses the sample counts were expanded to provide an estimate of the total population by multiplying the aggregate sample

counts by the fraction where the total area is divided by the sum of the sample areas.

These analyses are represented by the model:

$$\hat{e} = \frac{A}{a} \sum_{i=1}^n N_i$$

where $\hat{e}$ is the estimated population, A is the total area of the total population, a is the number of units sampled and N_i is the number counted in the i th sample area. Through computer manipulation an estimate was obtained for the giant clam population at Rose Atoll.

In order to obtain information on the distribution and numbers of *Tridacna maxima*, transects were accomplished through the use of SCUBA, which maximized counts in the studied area. All clams within 2 meters of a 30 meter transect line were counted. Clam counts were done on a minimum of 10 transects within all habitat areas and all clams of all sizes including juveniles were counted. The survey sites and their associated transects are shown in Figure 2.

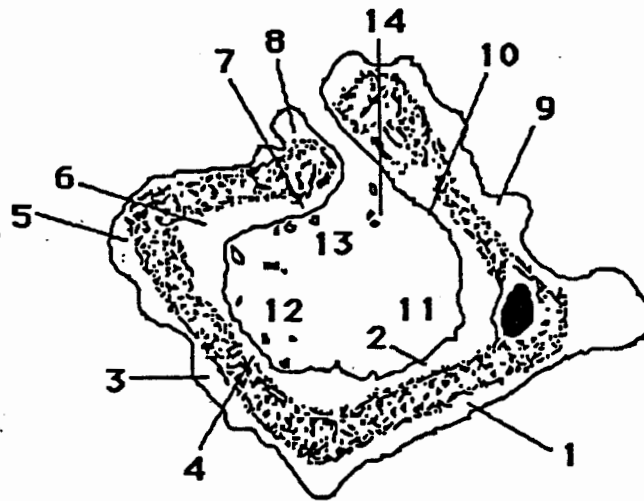


Figure 2. Location of transect areas on Rose Atoll.

Sites 2, 4, 6 and 10 are located between the inner edge of the reef flat and the drop off to the floor of the lagoon at a depth of one to five meters. Sites 11, 12 and 13 are located at the base of the drop off at 10 to 13 meters. Sites 7 and 14 are located on coral pinnacles rising from the floor of the lagoon to about 15 meters from the surface. Sites 1, 3, 5, 8 and 9 are located on the reef terrace outside the lagoon at a depth of 3 to 10 meters.

Distribution surveys indicate that *Tridacna maxima* are found throughout the shallow areas of the lagoon and at the present time it appears that only *Tridacna maxima* is found at Rose Atoll. The clams are imbedded within the hard carbonate substrate and prefer a horizontal position to provide maximum solar radiation for mantle tissues. Areas along the reef flat edge are dry at low tides and *Tridacna maxima* is not distributed within these areas. Large numbers of juvenile clams are found within the shallow areas of the lagoon. Most often juveniles are found in areas that are susceptible to storm perturbation and it appears that these may be more recently recruited animals. Deeper locations with more stable conditions show an increase in average clam size with community succession resulting in a climax population of middle sized clams, most of them sexually mature.

Coral patches and patch reefs were pinpointed from aerial photographs. The accuracy of the resultant maps was checked by means of field

measurements. The coral patches and patch reefs were grouped according to size, and transects were established over numerous patches within sandy areas in order to determine the number of clams inhabiting the bottom of the lagoon. A multiplication gives an evaluation of the number of *Tridacna maxima* for a given type of habitat. These data, although approximate, are satisfactory for calculating the homogeneity of population densities in the lagoon. A summary of these analyses are presented in Table 1. The distribution and abundance of *Tridacna maxima* at Rose Atoll was studied by means of a large number of transects (<100 transects per year). At the stations the individuals were sized in order to establish the population structure and samples were taken for age and sexual determination.

At Rose Atoll the total number of *Tridacna maxima* estimated to be 1,338,700 individuals $\pm$ 423,000 with a 95% confidence interval. This may appear to be a large number of clams, but this total would include the smallest settled clams. Distributions of size classes can be utilized to provide estimated numbers of each size.

SIZE DISTRIBUTION

In order to study size distribution of giant clams at Rose Atoll, clams were measured at the same time enumeration was accomplished. Measurements of shells were performed as shown in Figure 3.

Table 1. Summary of transect data (Length of transects = 100 ft.) of Tridacna maxima, associated with different habitat types. Patch Reefs are defined as large columnar limestone aggregations which rise more than 2 meters above the atoll floor; Coral Patches are defined as separate coral areas surrounded by sand and less than 2 meters in height above the atoll floor; and Lagoon Substrate includes reef flats and the remaining atoll floor.

Patch Reefs

Percent area colonization = 40-50%
 Maximum density = 6 individuals per m²
 Estimated habitat area = 82 hectares
 Estimated number of clams = 723,400

Coral Patches

Percent area colonization = 17-20%
 Maximum density = 3 individuals per m²
 Estimated habitat area = 119 hectares
 Estimated number of clams = 214,200

Lagoon Substrate

Percent area colonization = 19-22 %
 Maximum density = 5 individuals per m²
 Estimated habitat area = 191 hectares
 Estimated number of clams = 401,100

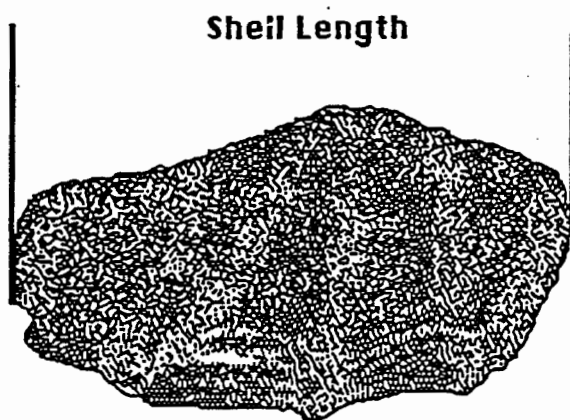


Figure 3. Length measurement of shells of the giant clam, Tridacna maxima, taken for analyses.

The clams at Rose Atoll had a wide size distribution, with the highest number of clams being small. Transect data for all habitats were combined in order to provide a size frequency for the entire population of giant clams at Rose Atoll. Size frequency data were analyzed for two sampling periods. The size frequency data for the year 1982 are demonstrated in Figure 4. The size frequency data for the year 1984 are demonstrated in Figure 5 and show a subtle shift in size frequency towards

larger individuals.

The population within Rose Atoll consists of a large number of young individuals with a small older population. However, recruitment appears to be stable. A mean adult giant clam in the lagoon would be approximately 37 grams with a shell size of 108 mm.

The habitat preference of the giant clam population at Rose Atoll is presented in Figures 6 and 7. These data suggest that smaller clams are more often

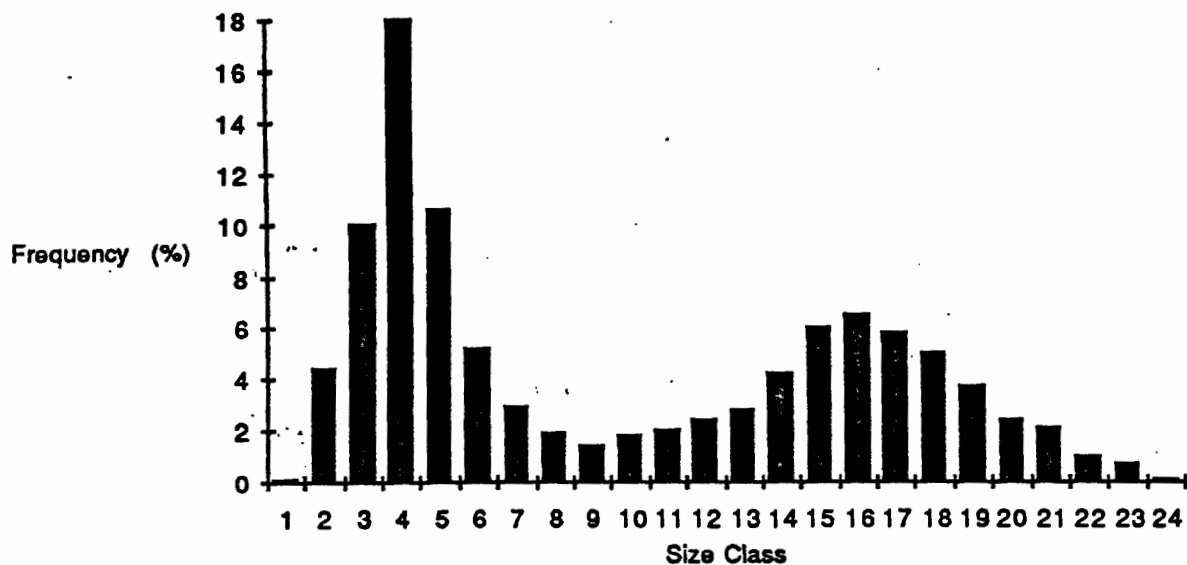


Figure 4. Size frequency distribution of the giant clam, *Tridacna maxima*, at Rose Atoll for 1982. Data utilized were the result of transects demonstrated in Figure 2. Size classes are presented in 10 mm increments. N = 1634.

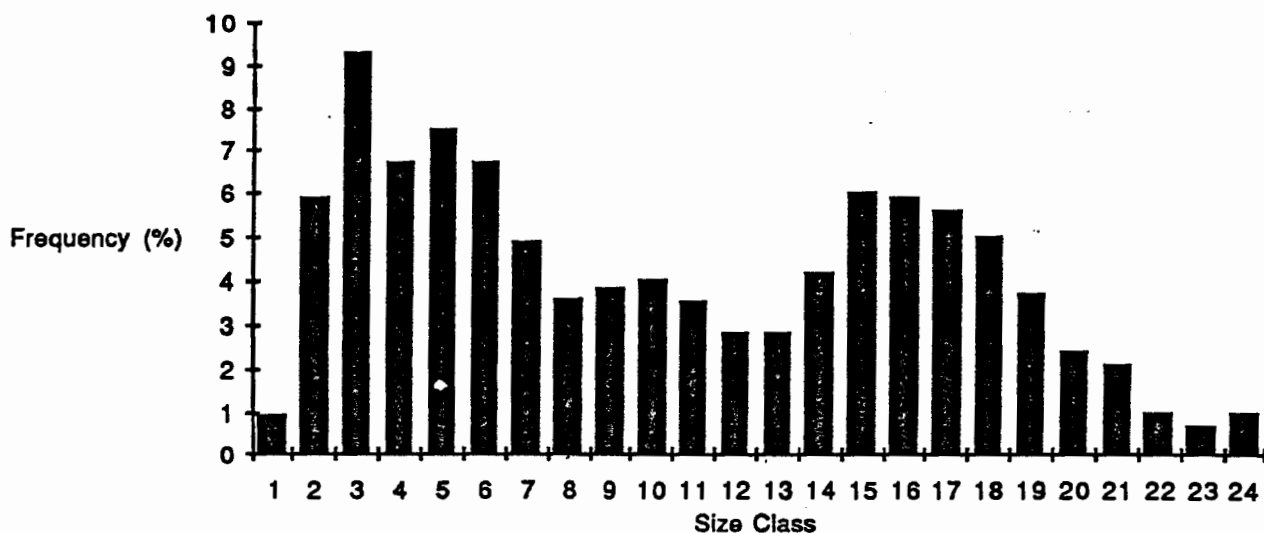


Figure 5. Size frequency distribution of the giant clam, *Tridacna maxima*, at Rose Atoll for 1984. Data utilized were the result of transects demonstrated in Figure 2. Size classes are presented in 10 mm increments. N = 2051.

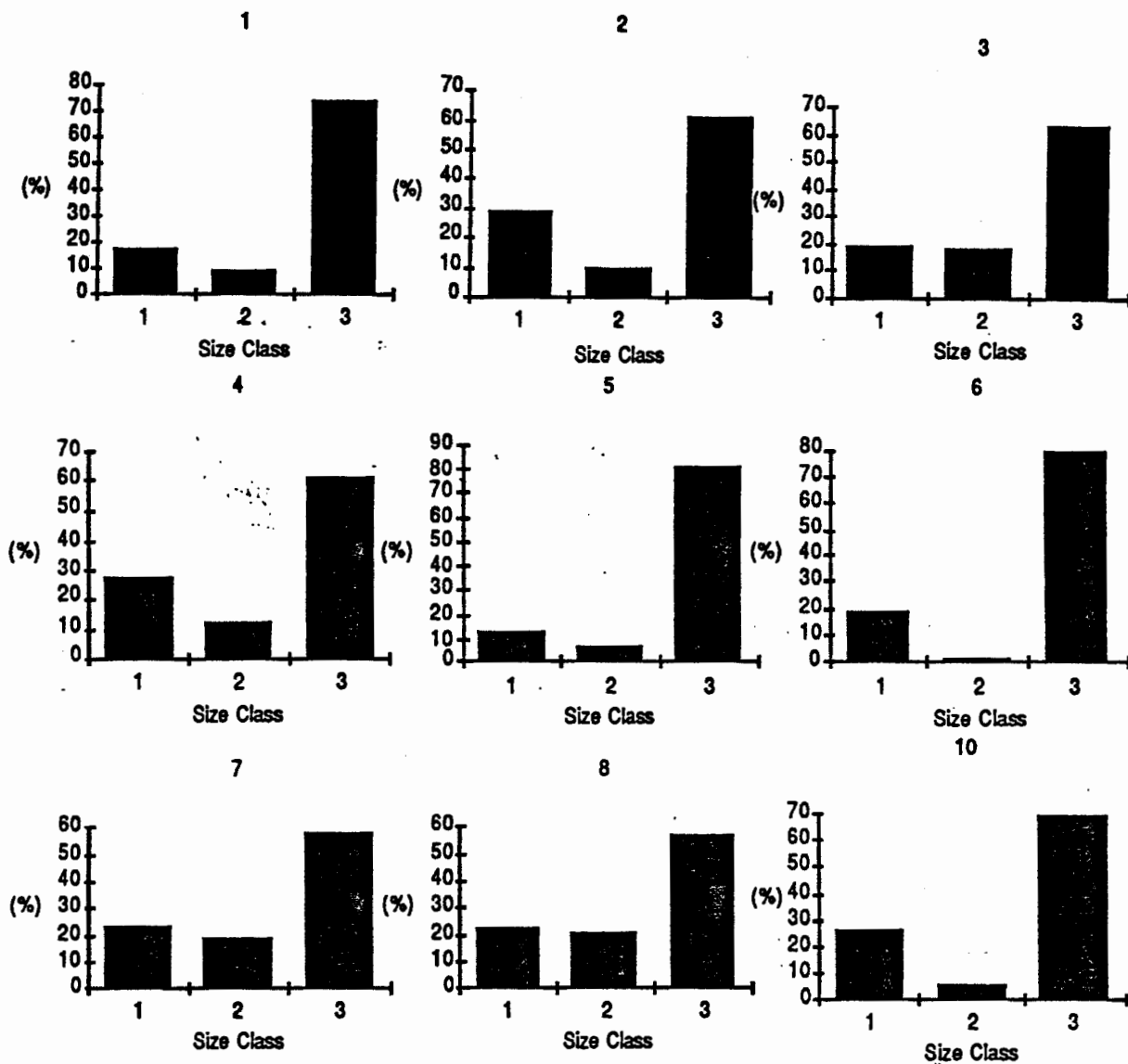


Figure 6. Length frequency (%) distribution of *Tridacna maxima* from Rose Atoll from the transect locations shown in Figure 2. Values presented are the summation of all transect data. Size classes are: 1 < 50 mm, 2 = 50 - 140 mm, 3 > 140 mm.

distributed in deeper waters with larger clams predominating in shallower waters. It appears that depth of water is the major factor affecting size distribution.

AGE

At the the present time there is a paucity of knowledge on giant clam life history, biology and ecology. In particular there is a lack of information on age, growth rate and maximum age. The ability to discern the age of any organism is a prominent problem in ecological research. Age data can provide growth estimates as well as make it possible to incorporate age specific parameters such as mortality and age related fecundity into population

dynamics models. Age determination can also provide basic life history information such as maximum age, population structure, changes in population growth due to environmental perturbations, recruitment success, trophic relationships and a host of other values which increase our understanding of population biology.

The rhythmic deposition of calcium in the shells of giant clams holds much promise for age determination. Giant clams have been estimated to range in age from eight years (Pelseneer, 1984) to several hundred years (Comfort, 1957) based on shell laminations. A reasonable estimate is probably situated somewhere between these two estimates. Growth assessments have been determined for

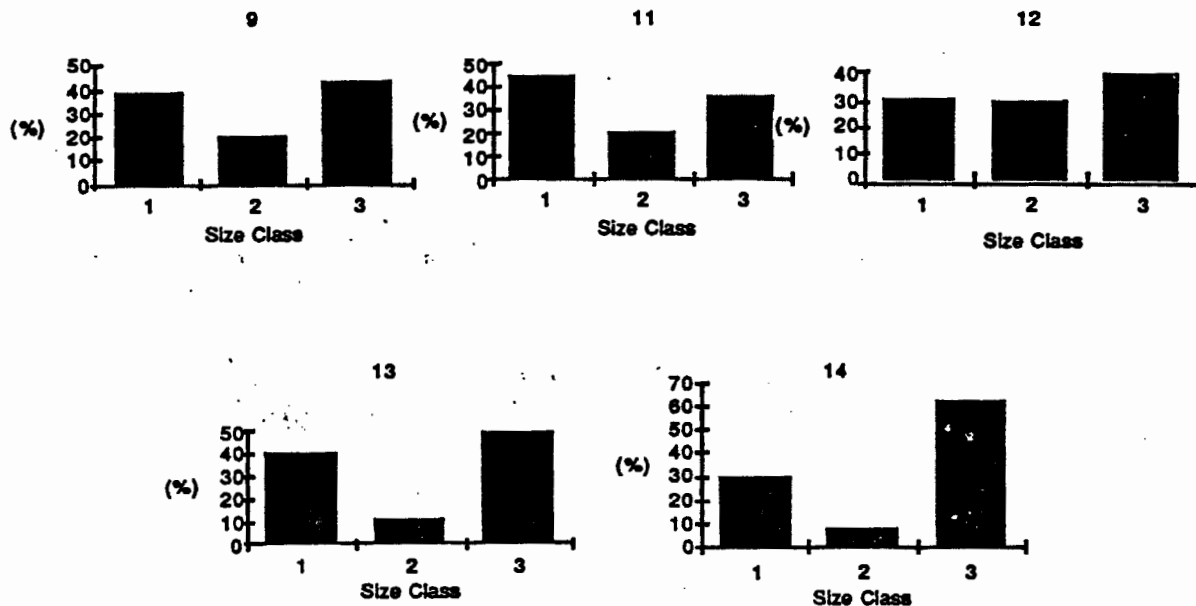


Figure 7. Length frequency (%) distribution of *Tridacna maxima* from Rose Atoll from the transect locations shown in Figure 2. Values presented are the summation of all transect data. Size classes are: 1 < 50 mm, 2 = 50 - 140 mm, 3 > 140 mm.

Tridacna gigas by Rosewater (1965) and Bonham (1965) and for *Tridacna maxima* by McMichael (1974). Moreover, these growth estimates call for further study to improve the accuracy of the methodology used. These studies apply to specific areas, and there is reason to believe that there are large differences in individual growth between clams which appear to be of the same cohort. It becomes necessary to expand upon previous growth investigations in order to increase the accuracy of age assessment and to analyze a range of individuals.

Discernment of growth of a population is essential in the determination of potential yield and reliable management schemes. In order to discern growth, longevity, and, age at maturity and to learn which life history periods represent critical stages, individual age must be determined. Hence age determination is a major part of population analyses.

Two methods can be employed to assess age. They are length frequency distribution and enumeration of internal shell laminations. Length-frequency distributions are achieved graphically and numerically on data collected from giant clam surveys. Modes in length-frequency are analyzed to determine if they are representative of age classes. These analyses also provide insights into the numbers of giant clams in representative size groups. A compilation of the data available for *Tridacna maxima* from Rose Atoll is presented in

Figure 8.

The data on length-frequency do not demonstrate any rhythmic patterns which could be interpreted to denote age. These data do suggest a slight shift in length frequency from 1982 to 1984 and this shift may be indicative of mortality in these organisms as they become older.

Length-frequency distributions can be compared to age estimates obtained from enumeration of internal shell laminations. The rhythmic deposition of calcium carbonate in the shell of *Tridacna maxima* can be utilized as a time indicator. Data obtained from examination of internal shell laminations can be analyzed to examine individual ages of clams of different shell sizes and those of the same cohort. Comparisons of these two ageing methods increases the accuracy of age determinations and is helpful in the determination of important population dynamics parameters.

In the clams which were sampled for age determination, both valves from each specimen were cleaned, weighed and measured. Length measurements of the right valve were obtained from the greatest distance between parallel points (Figure 3). The right valve, which is the valve on the right when both shells are held with the umbo downward and the byssal opening farthest away, was then prepared for thin section and Scanning Electron Microscope (SEM) investigations.

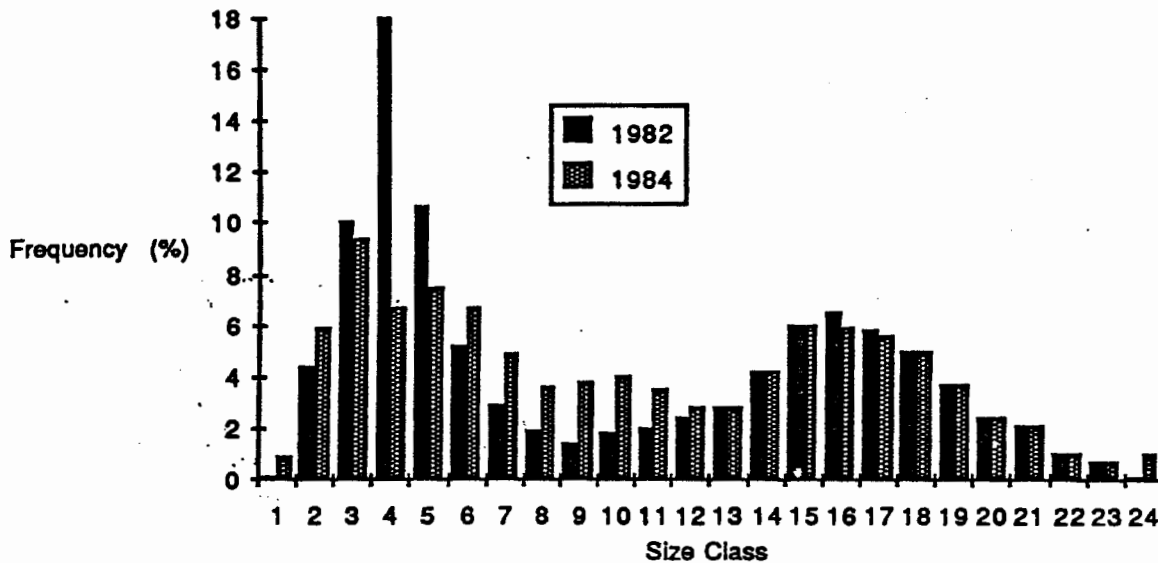


Figure 8 . Compiled length-frequency data for *Tridacna maxima* at Rose Atoll.

For SEM study, thin sections were cut from across the hinge area. The hinge sections were affixed to SEM viewing stubs with five minute epoxy and extensively polished with 0.3 micron alumina paste. The polished sections were then etched for five to fifteen minutes with 7% EDTA (disodium ethylene diamine tetraacetate), pH adjusted to 8 by NaOH, to reveal incremental patterns in the surface relief. The etched hinge sections were washed in water, dried, coated with gold and viewed in a SEM. Structures revealed from SEM analyses were photographed with Polaroid Type 55 positive-negative film for later study and comparisons. Thin shell sections, ground until they were translucent, displayed rhythmic stratifications which were interpreted to be annual and increasing in number with shell size. Corresponding interpretable rhythmic patterns were seen in SEM preparations of hinge areas. These major incremental laminations were also interpreted to be annual and were analogous to incremental layers evident in translucent thin sections. Enumeration of these incremental patterns and their interpretation as being yearly provided an age estimation and growth model of length and weight of shells of giant clams, *Tridacna maxima*, from Rose Atoll. There was a direct linear relationship between shell length and age and a direct exponential correlation between shell weight and age. It appears that calcification (shell weight deposition) increases as the animal grows and increases more rapidly as age increases. These data contribute a small amount of support to the judgement that rhythmic stratifications in giant

clam, *Tridacna maxima*, shell hinges are annual in occurrence. These investigations are some of the first verification analyses performed on giant clams. Results of these analyses are demonstrated in Figure 9.

These data and analyses show that *Tridacna maxima* can be as old as 18 years old at a shell length of over 200 mm and probably reach older ages. Additional SEM inspection of the internal microstructure of giant clam, *Tridacna maxima*, shells revealed minute increments demonstrative of rhythmic formation. Each increment was composed of a protein ridge and valley. Crystals of calcium are interdispersed in the protein matrix and it is the increase or decrease in protein which is seen as an increment. These rhythmic structures deviate as the shell increases in size. Transition areas were visualized which were indicative of a change in direction and velocity in shell growth. Deposition appeared always to be associated in a rhythmic pattern which could be discerned to possibly be daily. It is not feasible at the present time to determine the exact periodicity of these microstructural events. However, the symbiotic zooxanthellae algae are thought to participate in calcification, and since they grow in a daily rhythm of sunlight it can be suggested that these microstructural episodes are daily. Giant clams inhabit the shallow reef areas of the tropical Indo-Pacific where the lack of seasonality can cause difficulties in the interpretation of growth laminations. As a result, age determinations may warrant application of new techniques. It was the impression from the present study that the proper

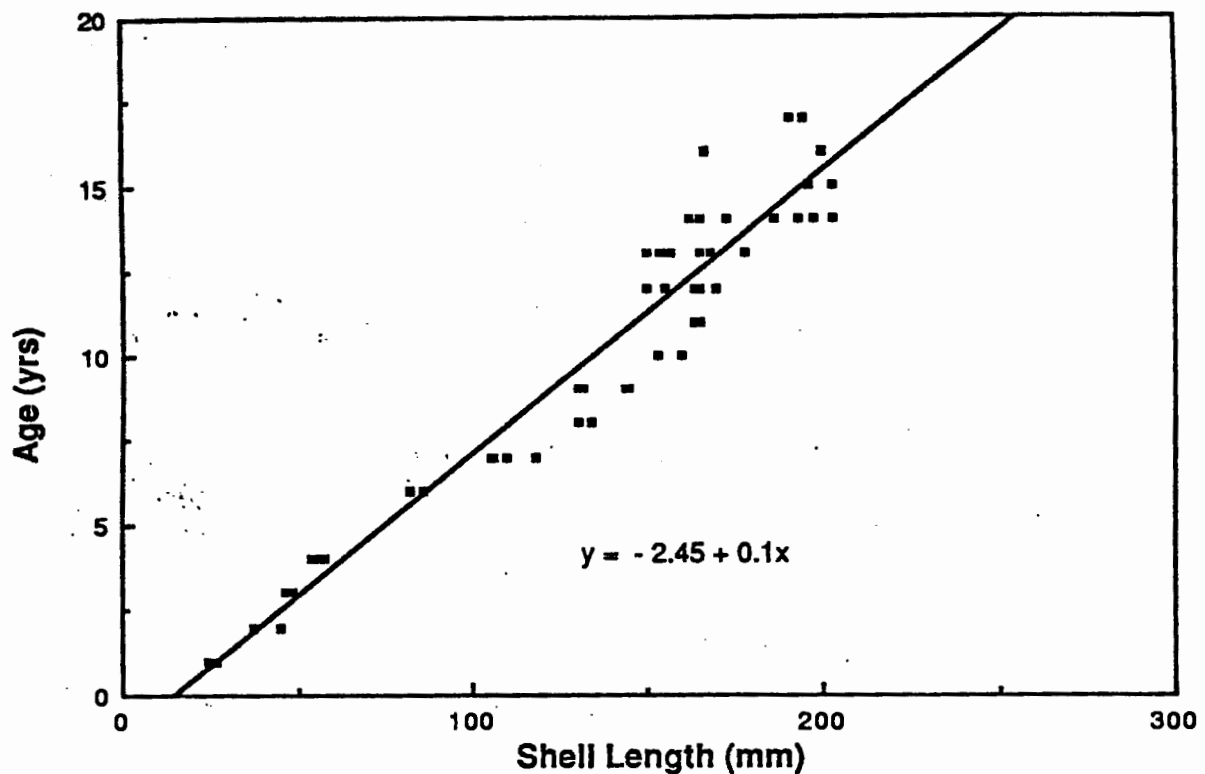


Figure 9. Age estimates for *Tridacna maxima* determined from internal laminations found in shells compared to shell lengths. These estimates are in close agreement with values obtained from marked clams.

use of SEM techniques to study microincrements would provide the ability to define growth increments.

There is a small amount of evidence which supports the contention that major increments in shell structure are annual. Shell formation is a result of secretions by the outermost mantle fold. Shell growth takes place by accretion of calcium carbonate crystals of the aragonite polymorph into a protein matrix. These processes are metabolically controlled and the zooxanthellae probably assist in calcification. Hence, the calcification process would be regulated by the 24 hr cycle of light which does change its duration enough even in the tropics so that the annual layers would be deposited. There is also a slight (2-4°C) temperature change with the seasons which could augment the light changes. These environmental changes could account for a seasonal depositional pattern in giant clam shells.

The internal microstructure of mollusc shells has been applied to age estimation in northern oceanic clams (*Antarctica islandica*). Murawski *et al.* (1982) marked clams and investigated rhythmic patterns in the hinge areas which were demonstrated to be annual in occurrence. The accomplishment of verification analyses substantiated the methodology of viewing hinge rhythmic stratifications for age

estimation. The present research appears to be the first application of similar techniques to giant clams. This methodology provided interpretable results which provided a credible growth model for giant clams, *Tridacna maxima*, at Rose Atoll. In addition, literature values available on *Tridacna maxima* ages by McMichael (1974) and McKay (1980) are in close agreement with those values established by the present research. This conformity of the present data with literature values lends a small supplementary amount of creditability to the techniques utilized. It is the impression from the present studies that analogous marking (Murawski *et al.*, 1982) research will validate shell formation in giant clams and will demonstrate the applicability of internal shell structure as an indicator of age and life history events.

Furthermore, the number of shell increments in *Tridacna maxima* from Rose Atoll increased with the size of the shell. While this evidence alone does not document the nature of the increments, when these data are joined with preceding data they strongly suggest that a rhythmic event, conceivably annual, occurred and resulted in the incremental patterns displayed in shell microstructure. Additional research and validation investigations should provide other essential documentation of age estimates.

Microincrements were also discovered in shell structure and are very likely daily rhythmic patterns. Daily increments are present in a host of plants and animals (Neville, 1967) and have been utilized to age invertebrates (Radtko, 1983) and vertebrates (e.g. Radtko and Dean, 1982). Most organisms are influenced by a 24 hour light cycle and there is no reason to believe that *Tridacna maxima* would be an exception. Instead, due to the presence of symbiotic algae which presumably enhance calcification, a 24 hour light cycle would have a more pronounced effect on shell growth. This light effect could manifest itself as a microincremental stratification. Structures analogous to those discovered in *Tridacna maxima* shell sections have been used to determine age in fish (Radtko and Targett, 1984). The similarities are striking. Both fish otoliths and giant clam shells are composed of calcium carbonate in the aragonite crystal form and have aragonite crystals deposited in a protein matrix and microincrement patterns. The microincremental patterns in giant clam shells also showed transition areas which may represent life history changes. It is our interpretation that giant clam shells contain a tremendous amount of information when the proper analyses are performed. Microincrements hold much promise as indicators of daily events.

Originating from a microscopic fertilized egg, giant clams undergo growth periods to become the largest bivalve known to exist. To accomplish this feat giant clams pass through a series of growth stanzas delineated by settlement, nutritional changes, maturation and death. Growth of individuals contributes to population growth. To obtain this information the growth rates for individual giant clams can be determined from internal structural patterns in shells. This information can then be utilized to compute the production of a species related to specific habitats.

In the present research, progress has been achieved in the determination of age in giant clams and in particular growth in the pristine *Tridacna maxima* population at Rose Atoll, American Samoa. New techniques and information have been revealed. However, many questions remain unanswered and like many scientific studies new information begets new questions. The present investigations have revealed numerous discoveries which will function as a foundation for future studies.

GROWTH

Once age has been assessed, growth of a population can be determined. To perform these analyses it is necessary to have a model which describes the

processes of growth on giant clams sufficiently. The growth rate of giant clams can be described by a number of different mathematical expressions. The following models were tested:

Linear model $Y = a + bx$

Logarithmic model $Y = a + b \ln x$

Power model $Y = ax^b$

Exponential model $Y = ae^{bx}$

von Bertalanffy growth model

$$L_t = L_{\infty} (1 - e^{-k(t-t_0)})$$

Through utilization of these models it was feasible to calculate relative growth (gain in size for a time period) and absolute growth (increase in average size at each age). From these calculations, comparisons of growth of *Tridacna maxima* with other populations were accomplished (i.e. McMichael, 1974; Munro and Heslinga, 1983). The resultant analyses can be readily incorporated into models of population assessment (Ricker, 1975; Gulland, 1983).

For the giant clams sampled at Rose Atoll it was determined from the length-weight measurements that, within any stage of a giant clam's life, the weight of the shell varies as a power of shell length. This relationship is represented by the equation $W = .001 L^{3.17}$ and is demonstrated in Figure 10.

It is believed that the equation, $W = .001 L^{3.17}$, is an excellent approximation of the length weight analogy for *Tridacna maxima* at Rose Atoll, and this equation has an r^2 value of .98. From these data it can generally be resolved that valve weight increases geometrically in comparison to shell length. These results do not deviate from the normal expected relationship. The present length-weight association is specific for the population at Rose Atoll. Comparisons of length-weight relationships within the Indo-Pacific provide limited insights into population dynamics of giant clam communities.

Growth in shell length is best represented by the equation $y = -2.45 + 0.1 x$, where y = age in years and x = shell length in mm, and has an r^2 of .98 (Figure 9) while growth in shell weight is best presented by the equation $y = 0.97 x^{0.38}$ (Figure 11), where y = age in years and x = weight in grams, and has an r^2 of .94.

The estimated ages of *Tridacna maxima* were modeled through the utilization of the von-Bertalanffy growth model which is the most often used growth model in fisheries science. The data conformed well to the von-Bertalanffy growth model (Table 2) and the parameters presented should be representative of the giant clam population at Rose Atoll. A graphic comparison of growth models for giant clams is presented in Figure 12.

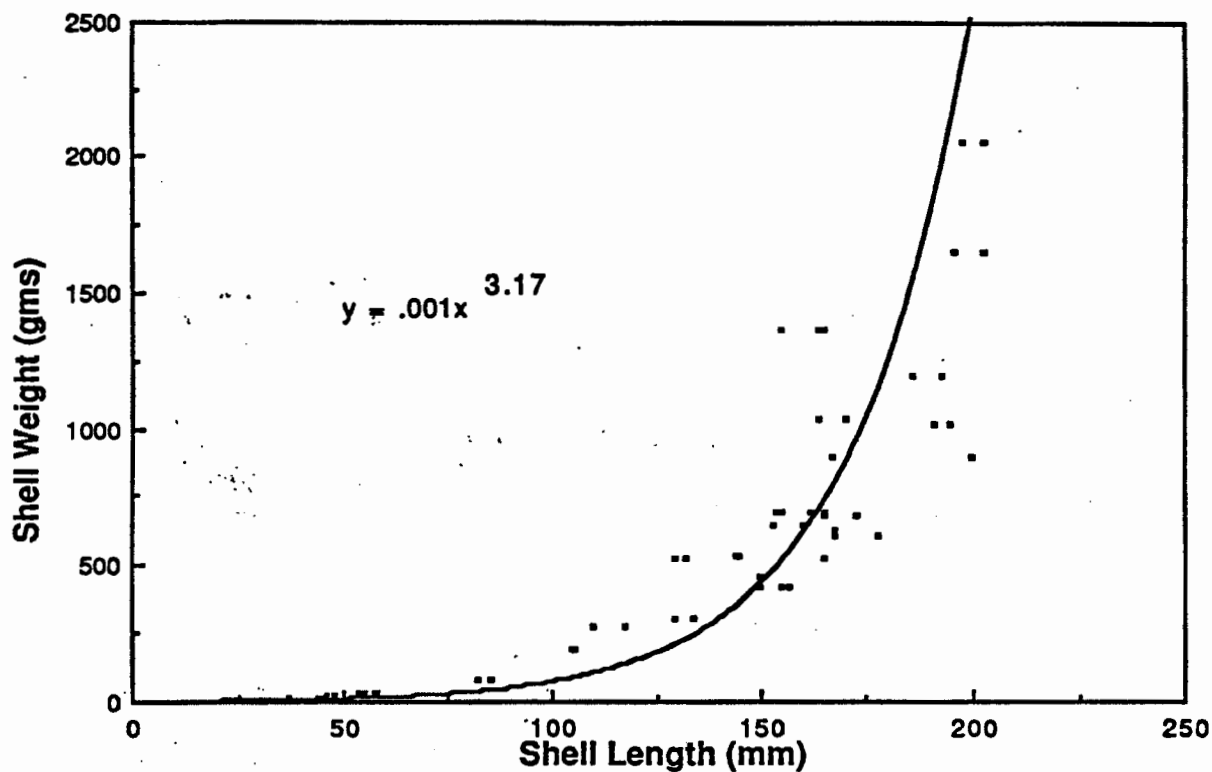


Figure 10. Shell length - weight relationship for *Tridacna maxima* at Rose Atoll which demonstrate the increase in shell mass as a result in shell length.

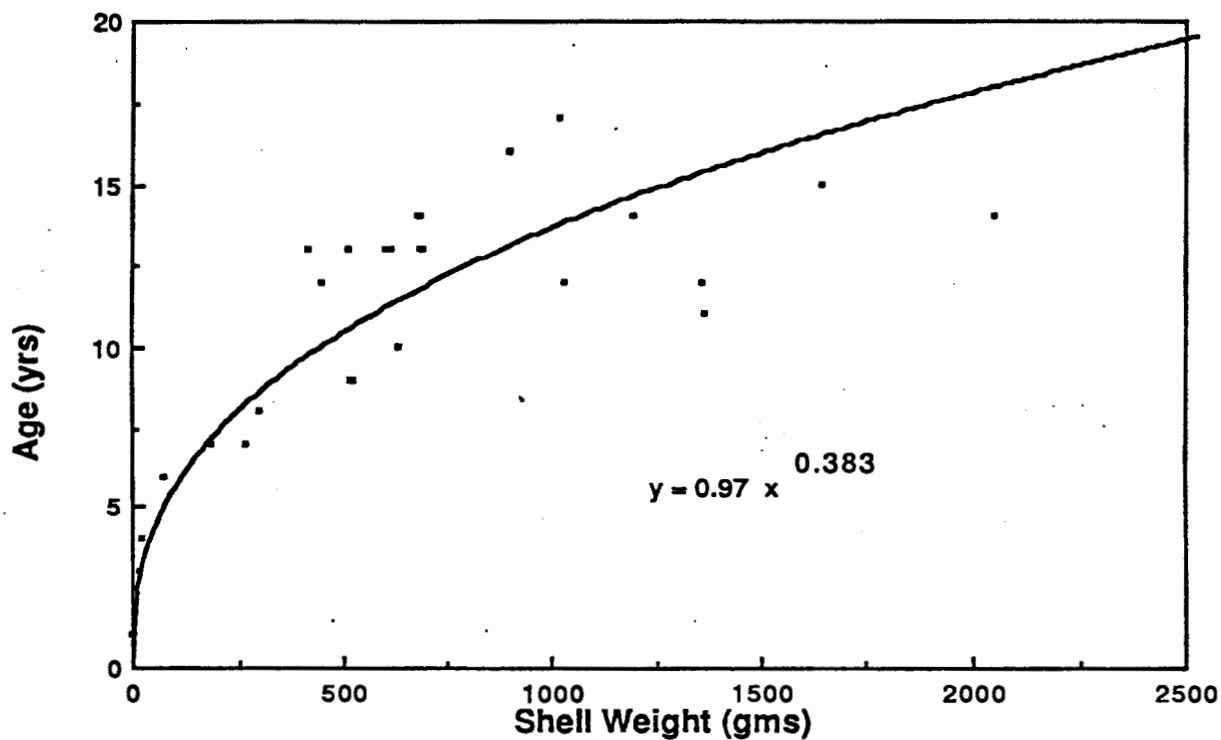


Figure 11. Growth in shell weight for *Tridacna maxima* at Rose Atoll.

TABLE 2. Parameter estimates, with 95% confidence intervals, derived from the von-Bertalanffy growth equation for giant clam shell length. K is the defined growth coefficient, t_0 is the time at the initiation of growth, and L_{∞} is the hypothetical maximum size attained.

Population total		95% confidence intervals	
		Lower	Upper
K	0.065	0.014	0.094
t_0	-0.062	-0.676	0.553
L_{∞}	294.242	218.947	369.536

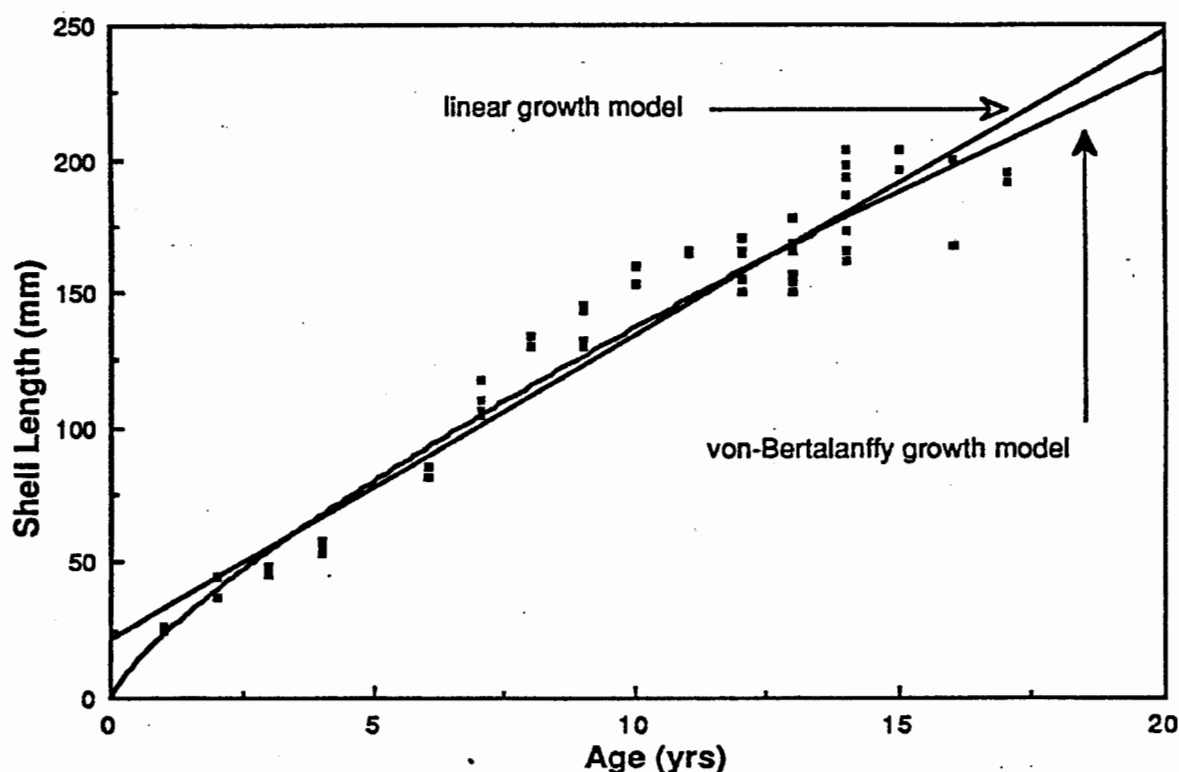


Figure 12. Comparison of shell growth in *Tridacna maxima* utilizing linear and von-Bertalanffy growth models.

The largest individual within the present study had a shell length of 246 mm, which is well within the 95% confidence interval for the parameters calculated for the *Tridacna maxima* population at Rose Atoll.

Prefactory observations on age and growth of giant clams, *Tridacna maxima*, from various areas of the lagoon at Rose Atoll suggested growth differences. These preliminary data strongly suggest a decrease in growth with an increase in water depth. The giant clams

living at deeper water depths grow slower and have larger shell lengths. Shell morphology seems to change with water depth. Additional data will clarify these discoveries.

Growth in standing stock of giant clams has been studied in numerous locations. In the Philippines, Alcala (1981) looked at growth in four species of Tridacnids, and the growth discovered there for *Tridacna maxima*, was slightly higher than the growth found within the

present study, but not significantly different. Work by Munrow and Gwyther (1981) presented growth rates of Tridacna maxima. Giant clam growth, especially in Tridacna maxima, appears to be variable over the range in which it is found, and the growth of those found at Rose Atoll appears to be within the center of this range. Growth rate shows an important ability of the population to withstand any outside influences, and the growth witnessed at Rose Atoll, with the slower growth of the larger individuals, is common of a stable and climaxed community.

MATURITY

Giant clams are protandric hermaphrodites and as such begin their sexual lives as males and later mature into having both sexes in sequence. The hermaphroditic condition is a common condition and is widespread in the invertebrates. Simultaneous hermaphroditism where the animal functions as both a male and female is not as common as distinct sex changes, but occurs in giant clams (Wada, 1942; 1954). In fully mature clams, gonad follicles containing sperm and eggs can be found throughout the gonad.

Spawning in Tridacna maxima involves the separate release of eggs and sperm and the larval development to settlement is the longest of any of the giant clams (LaBarbera, 1975) which may account

for its widespread distribution. At Rose Atoll gonads were examined from the entire size range of Tridacna maxima, but only 61 animals were examined. In Tridacna maxima the gonads are found at the anterior end of the body between the heart and the hinge, surrounding part of the gut. Smears of the gonads were stained and examined for the presence of eggs and sperm.

The results of the sexual analyses are presented in Figure 13. In small specimens the gonad was very small and sex could not be easily determined. The smallest clam able to be sexed was 37 mm and was a male. There was no sign of eggs in the smaller clams which could be sexed. Tridacna maxima attained full sexual maturity where they also show the female phase by the time they reach a shell length of 89 mm. In the present analyses no non-hermaphroditic females were found. All animals with a shell length greater than 120 mm were fully mature

The data presented are based on small sample sizes and conclusions may be expanded when more data become available.

MORTALITY

Essential to a responsible management of a biological resource is knowledge about mortality. Death is not a repetitive process, and for every death

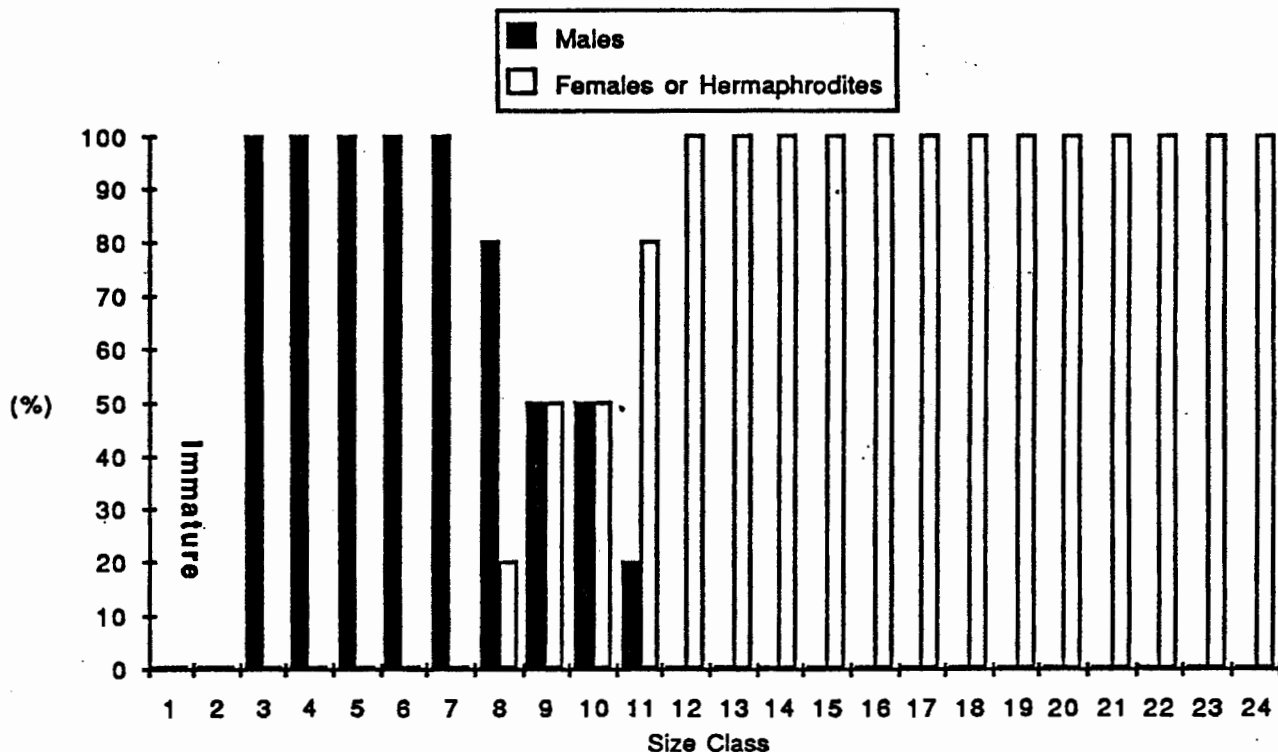


Figure 13. Relationship of sex type and size for Tridacna maxima at Rose Atoll. Size classes are presented in 10 mm intervals.

there is a specific cause. While it is not always possible to determine the exact cause of death, through the utilization of analyses of population size, age distribution and growth rates it is possible to calculate natural mortality. The rate of mortality ascribed to natural causes needs to be determined for a population before harvesting is considered. Empirical observations over time demonstrate that individuals of a particular cohort decline at a rate proportional to the number of clams alive at any particular point in time. This can be expressed as a rate of change of cohort numbers (N) with time as being proportional (Z) to the number present at that time or:

$$N(t) = N_0 e^{-Zt}$$

where $N(t)$ is the number of clams at time t , N_0 is the number of clams at time 0 and Z is the force of mortality. This formula takes into account observed relationships between mortality and oldest clam in samples, mean size in samples, length frequency data and age frequency data. Few estimates of giant clam mortality exist and the present analyses are valuable to resource management.

Utilization of the data presented in Figure 9 would result in an instantaneous mortality rate of 0.154 which represents the percent of the population which will die during the year. Mortality is higher in younger individuals and stabilizes as the clams age. There can be several causes of mortality among the clam population at Rose Atoll. Since Rose Atoll is not harvested, natural mortality must be confined to predation, competition, disease etc. Consequently, such a value for mortality for Tridacna maxima is acceptable.

The sheltered lagoon at Rose Atoll was found to be rich in Tridacna maxima numbers and also corals, as opposed to exposed areas of the reef where coral and giant clam numbers are lower. Where giant clams were found to have died, in most instances it was from an overgrowth of coral which shielded its total radiation and made it impossible for the clams to produce an adequate food supply for themselves and for reproduction. Inter-specific competition for space and solar radiation often occurs between Tridacna maxima and corals on Rose Atoll. Tridacna maxima adults are found burrowed or slightly inlaid into coral substrate and in those places where coral outgrew the giant clams mortality resulted. Because of the lack of numerous corals and low numbers of giant clams per square meter, competition for space and sunlight was limited. However, the major cause of mortality in giant clams appears to be space limitations. Moreover, the clam population at Rose

Atoll appears to be a stable and climaxed population only perturbed by occasional strong storms.

YIELD

The ultimate goal of responsible management is to maximize potential yield while disturbing the population as little as possible. Yield is that portion of a population available for harvest and can be classified as production, which is the total elaboration of new biomass in regard to spatial and temporal units. For giant clams, the yield per unit area model can provide potential yield (P) estimates most readily. In this model:

$$g(P) = k (P_{\infty} - P)$$

where $g(P)$ is a single valued function of the population biomass, k is a constant and P_{∞} is the limiting population biomass.

This approach is not complex and can be used to set a likely boundary to the maximum harvests which could be taken from a given area. This surplus yield model is very applicable to the relatively simple population system at Rose Atoll, American Samoa and can directly relate natural mortality to potential yield. Analyses of giant clam mass combined with numerical and growth data can provide a potential yield. The relationship between calcified biomass and total weight is nearly one-fifth of the total weight from body tissue, while four-fifths of the weight is from shell tissue. This relationship decreases as growth proceeds, meaning that as animals get older more of their weight is within their shells. These data are presented in Figure 14.

Plotting the total shell weight (y) vs. body weight (x) presented a linear equation where $y = 7.64x - 73.34$, $r^2 = .98$, while the relationship between tissue weight and shell length is represented by $y = 3.24x^{1.15}$, $r^2 = .98$. These data are shown in Figure 15. Further relationships are demonstrated in Table 3.

From the values taken into consideration for the area inhabited by Tridacna maxima at Rose Atoll, these values are equivalent to a production of 0.1 kg (3-120 mm size clams) per hectare per year. In the entire atoll all clams represent approximately 50 tons of living matter. Theoretically the production of meat per year could be postulated. If the protein percentage 13.6 is taken into account the available production per hectare per year would still be 0.1 kg. Quantitative balance of production of Tridacna maxima at Rose Atoll does not appear to be within the scope of rational exploitation. These data may be conservative while at the same time leaving prospects for improvement.

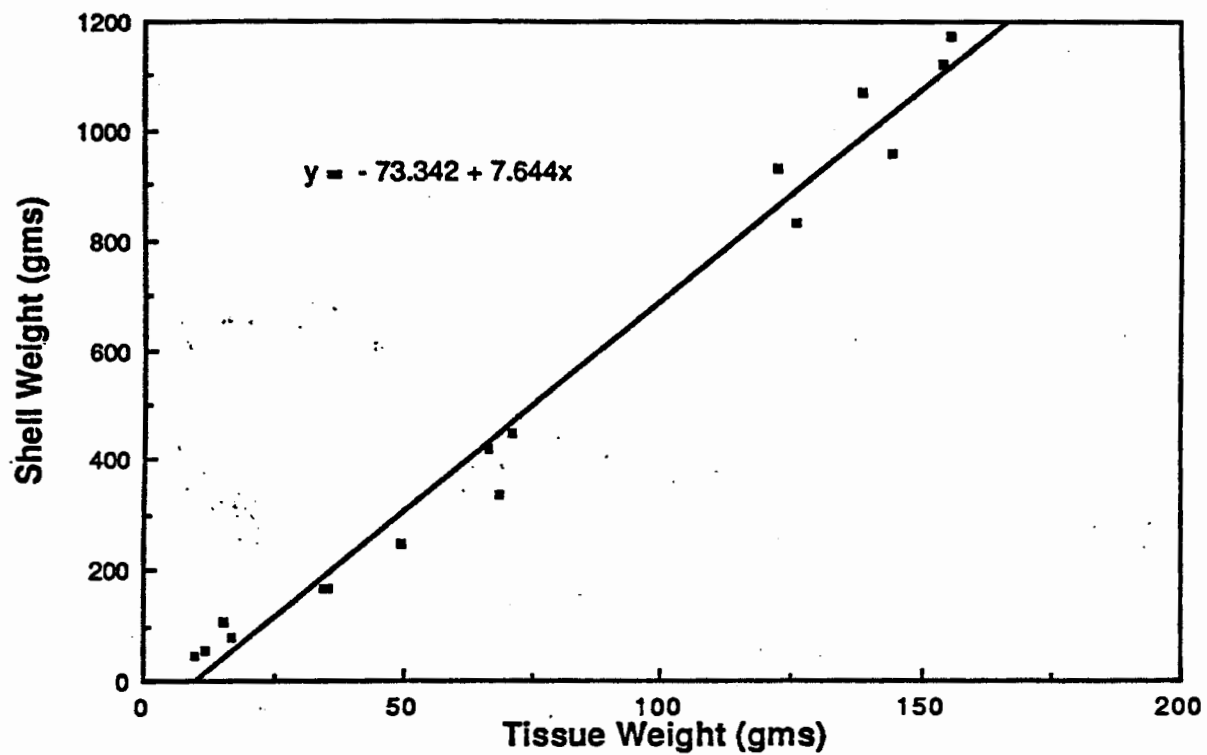


Figure 14. Relationship between shell weight and body tissue weight in *Tridacna maxima* at Rose Atoll.

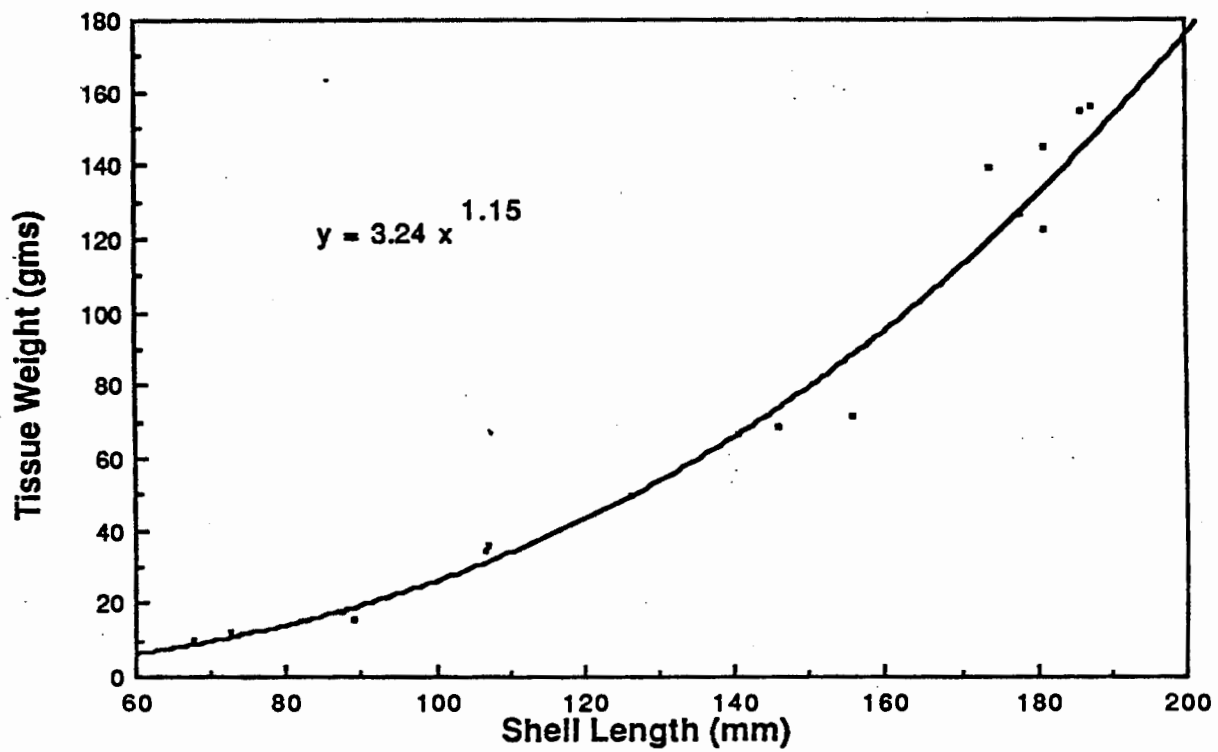


Figure 15. Relationship between shell length and body weight for *Tridacna maxima* at Rose Atoll.

Table 3. Changes in the Relationship of biomass to total weight of Tridacna maxima at Rose Atoll.

Size of class	Relationship of body weight to total weight
20-80 mm	.20
80-100	.19
100-120	.18
120-175	.15
175-220	.13

CONCLUSION

In order to understand how an atoll marine ecosystem functions, the impact of individual components must be understood. Giant clams, Tridacna maxima, are an integral part of the Rose Atoll ecosystem. Consequently, the information presented on this pristine giant clam community will be of unequalled value to population, biological, ecological and evolutionary studies of giant clams, and provides insights into the framework of this unique ecosystem. This information is a basic requirement of many population models and is necessary for accurate production estimates. The reef area of Rose Atoll appears to have the greatest number of individuals, more than the intertidal zone or the channel or the center of the lagoon. In respect to weight excluding shells, wet weight is increased in the internal fringing zone of Rose Atoll. Production estimates can be based on age determination and number of specimens.

Saldat (1977) found concentrations of Tridacna maxima of more than 63 individuals per square meter, with a tissue weight of 4.9 kg per square meter in the atolls surrounding Tahiti while Rose Atoll has a clam tissue weight of 0.1 kg per square meter. The concentrations cited by Saldat (1969) are much higher than those witnessed at Rose Atoll,

and are evidence of the lower productivity of Rose Atoll itself.

It is clear that Tridacna maxima is an important element of the Rose Atoll ecosystem. They have a respectable number of organisms in this ecosystem, but due to their slow growth would have a small sustainable yield. A summary of the population components of Tridacna maxima are presented in Table 4.

Although the present information may be in instances imprecise, quantitative balance of production of Tridacna maxima at Rose Atoll does not appear to be within the scope of rational exploitation and exploitation could endanger the perpetuity of the unique environment.

ACKNOWLEDGEMENTS

This report was done under contract from the U.S. Fish and Wildlife Service. Support for data collections was provided by the National Geographic Society, U.S. Fish and Wildlife Service and Office of Marine Resources, American Samoa. Special thanks are due to Drs. J. Ludwig and R. Wass for data collection.

Table 4. Population dynamic parameters for Tridacna maxima at Rose Atoll. Notation as used in preceding text.

L_{∞}	296 mm	Asymptotic length
K	0.65	Growth coefficient
Z	0.154	Mortality
A	392 hectares	Inhabitable area
P	0.1 kg/hectare	Potential annual yield
$\hat{N}$	1,338,700	Estimated population size

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