

GROWTH RATES OF, AND PREDATION ON, DIFFERENT SIZE
CLASSES OF QUIDNIPAGUS PALATUM (BIVALVIA)
ON TWO REEF-FLATS OF GUAM

by

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Title: Growth Rates of, and Predation on, Different Size Classes of Quidnipagus Palatum (Bivalvia) on Two Reef-Flats of Guam.

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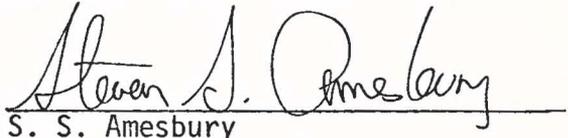
Six hundred individuals of the bivalve Quidnipagus palatum Iredale were notched and placed into cages or fences on two reef-flats on Guam. After three months the growth increments were measured. Smaller size classes showed the most growth as well as the most variation in growth. The number of new growth rings formed during the three-month period varied from one to nine rings. Clams inside the cages did not grow as rapidly as clams inside fences. Predation rates were significantly higher on smaller individuals of Q. palatum. Predation rates, bivalve diversity and predator diversity increased in a seaward direction along the transect. Low predation rates on mature Q. palatum suggest that commercial harvesting would have minimal effects on the reef-flat food web.

TO THE GRADUATE SCHOOL:

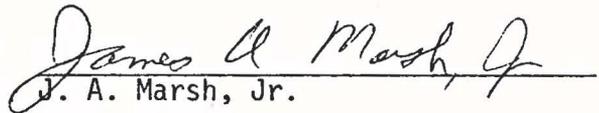
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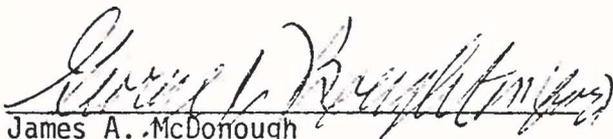


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INTRODUCTION

Factors influencing growth rates of bivalves are of economic importance to fisheries biologists. Molluscan growth rates characteristically vary with regard to developmental stage, age, and environmental conditions (Wilber and Owen, 1964). For example, a variety of laboratory-reared bivalve larvae showed considerable variation in their growth rates even though all larvae were reared under the same conditions (Loosanoff and Davis, 1963). Age differences also influence growth rates. Johannesson (1973) found that seasonal growth in length of the bivalve Venerupis pullastra depends on the length and age of the clams at the beginning of the growing season. In addition, Johannesson noted that clams of the same age may not be the same length since environmental conditions can delay larval settlement and hence shorten the time period in which young bivalves have to grow after settlement. That the proper salinity and substrate must be present to initiate larval settlement was noted by Loosanoff and Davis (1963). Other environmental conditions such as waves may retard shell growth (Stromgren, 1976). Growth rates of bivalves are also affected by tidal exposure (Newcombe, 1936) and food availability (Fox and Coe, 1943). In addition temperature, salinity, dissolved oxygen, and population density influence the rate of molluscan growth according to an extensive review by Dehnel (1955). In this paper I will examine the growth rates of different size classes of the bivalve mollusc Quidnipagus palatum Iredale at varying water depths and distances from shore on two reef-flats of Guam.

Bivalve growth rings may be useful in determining a clam's age and growth rate. According to Wilbur (1964), rings indicate changes in mantle secretory activity and alternations in the ratio of matrix (conchiolin) to crystalline deposition. Coe (1945) used growth rings to measure the growth rates of individual mussels of the species Mytilus californianus on a monthly basis. Distinct annual rings enabled him to follow growth rates of mussels of different ages. In temperate regions many organisms, including bivalves, have periods of rapid growth associated with favorable growing conditions of spring and summer months followed by periods when virtually no growth occurs during winter months. Growth alternations like these often leave distinct concentric bands upon the shell. Molluscan growth is more difficult to study in the tropics where growth rings still occur, but seasonal variation is slight and presumably growth occurs throughout the year (Frank, 1969).

Wells' (1963) paper on coral growth and geochronometry has stirred interest in growth increments. Wells submitted that the small ridges and annulations on the epitheca of corals represent daily and yearly variations in skeletal growth. Pannella and MacClintock (1968) have also observed periods of shell deposition in bivalves. They saw clear 14-day cycles in the shells of Tridacna squamosa. Using shell growth as a paleoclock, Pannella and MacClintock (1968) suggested that the length of the lunar month is decreasing. In this paper I will test the validity of using shell growth increments of Q. palatum as indices of time.

Predation data as well as growth data are needed by fisheries biologists in order to estimate yields. Such data would enable the

biologists to determine the species, size, and reef locations which might be least susceptible to predation. Although Jackson (1972) did not find a prey preference among bivalve predators, he did find that smaller sized valves were more frequently drilled, and that the percentage of drilled valves increased with distance from shore in a Jamaican Thalassia community. Bivalves transplanted to a site where they do not normally occur suffered increased decapod predation (Kitching and Ebling, 1967), indicating that predation may restrict the range of some bivalve species on rocky shores. This is clearly shown on rocky shores by the well-defined lower limit of the vertical zonation of mussels caused by sea star predation (Paine, 1969). Not all sizes of prey species are attacked at the same rate. Johannesson (1973) found that oystercatchers fed only on clams larger than 10 mm, whereas Thorson (1966) lists scores of meiobenthic invertebrates preying on newly settled benthic organisms, including juvenile bivalves. In this paper I will discuss the bivalve prey preferences and size preferences of two reef-flat predators and discuss the relationship of predation to water depth and distance from shore.

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METHODS AND MATERIALS

Sampling was begun during the summer of 1976 to determine which reef-flat areas contained large enough populations of Q. palatum for study. Many of Guam's beaches could not be considered for study since large quantities of sediments were removed when Typhoon Pamela swept directly over Guam in May, 1976. On the basis of the preliminary samplings, two areas of study were selected: Pago Bay on the southeast coast of Guam, and Alupang Cove on the northwest coast of Guam (Figs. 1, 2, 3, 4a, and 4b).

The Pago Bay study area is on the windward side of Guam and is characterized by an extensive seagrass bed composed primarily of the marine angiosperm Enhalus acoroides. The seagrass is anchored so firmly to the reef that these plants suffered little damage from the typhoon, and they prevented the substrate from being washed away. Beneath the mat of the rhizoid-like roots of Enhalus the substrate is composed mostly of cobbles and rubble that have been tossed onto the reef-flat by storm waves. Relief of the Pago Bay seagrass bed is slight (Fig. 4b) except for the portion near the Pago River channel where the depth increases rapidly.

The second study site is at Alupang Cove, which is a sheltered portion of East Agana Bay situated behind Alupat Island on the leeward side of Guam. Because land surrounds this pocket of East Agana Bay, the infauna of Alupang Cove was not disturbed by the typhoon. The fine sediments composing these extensive mud flats would have easily been washed away had they been exposed to the storm. There is a very

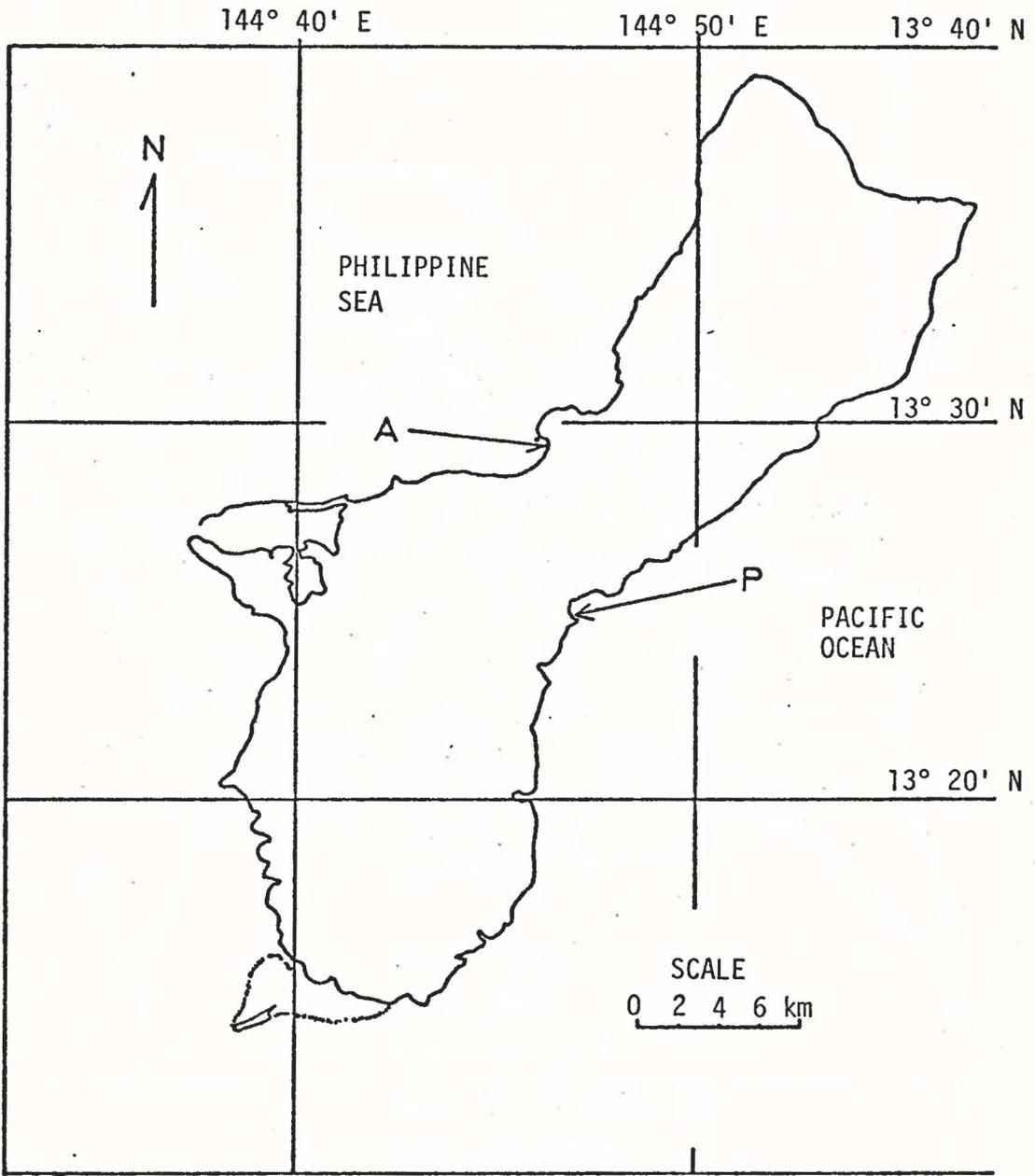


Fig. 1. General locator map of Guam showing the study sites at A (Alupang Cove) and P (Pago Bay).

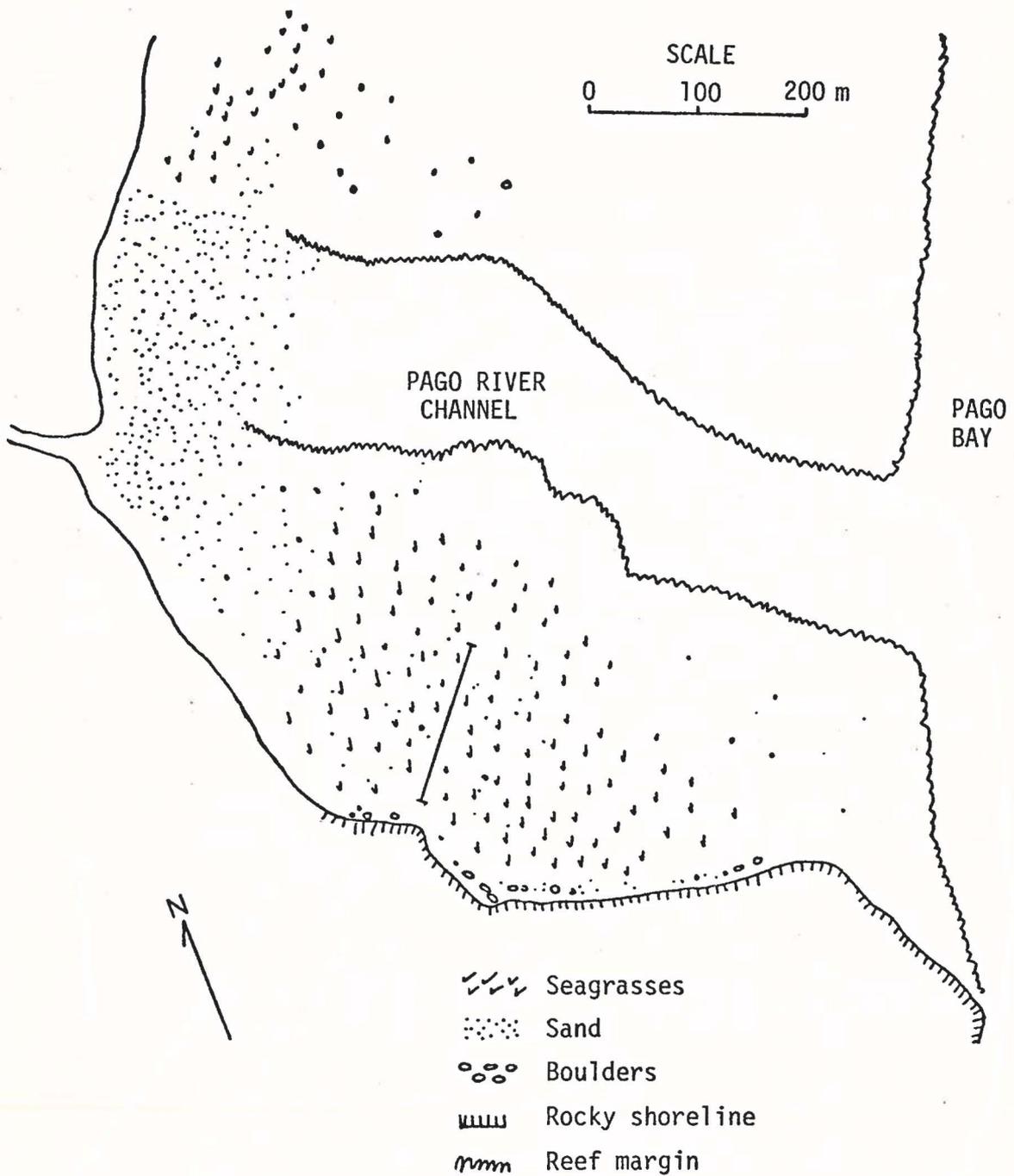


Fig. 2. Map showing southern portion of Pago Bay, including the study transect. Figure taken from Randall and Eldredge (1976).

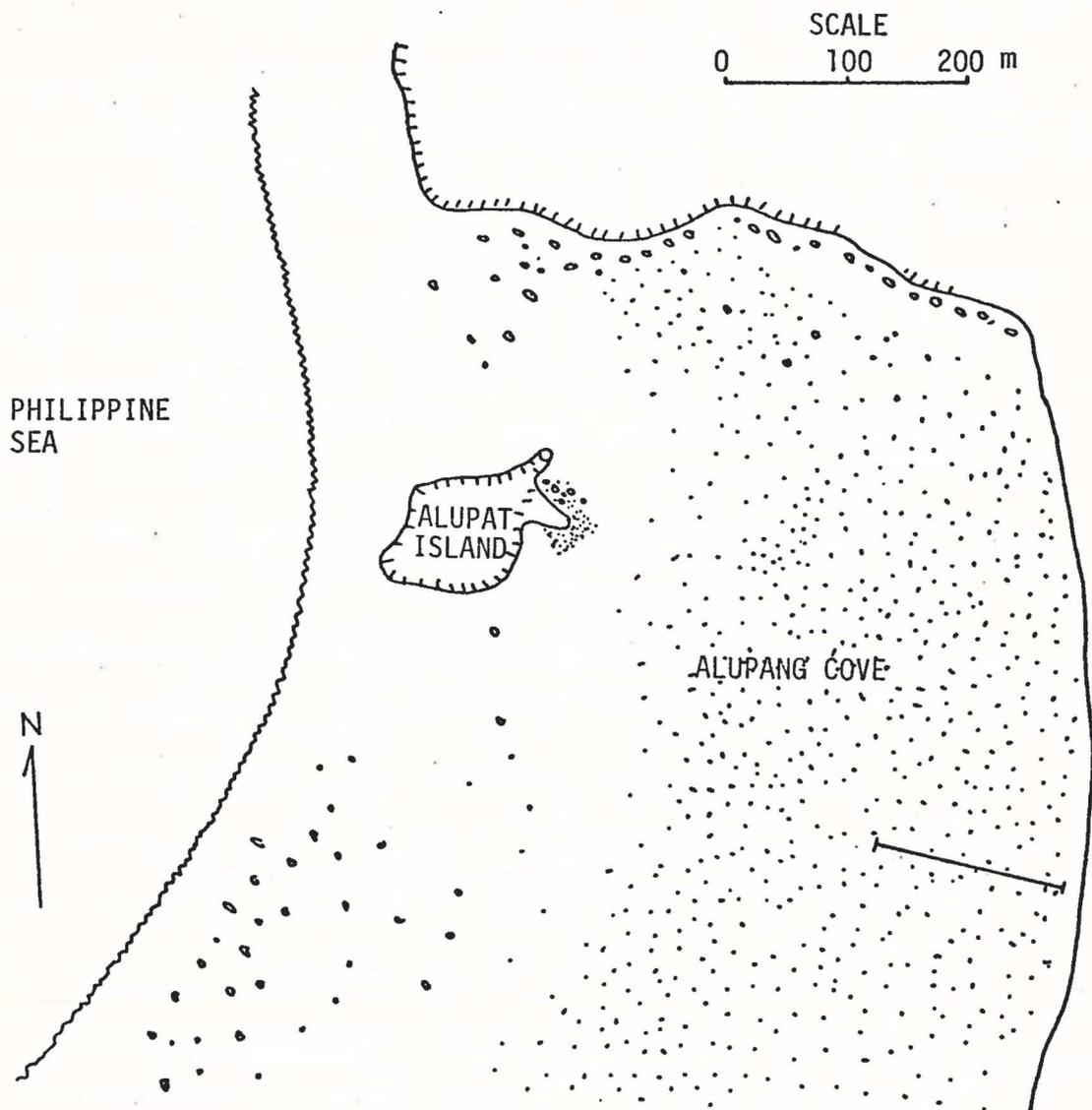


Fig. 3. Map showing Alupang Cove, Alupat Island, and Alupang Cove transect. Symbols explained on Fig. 2. Figure taken from Randall and Eldredge (1976).

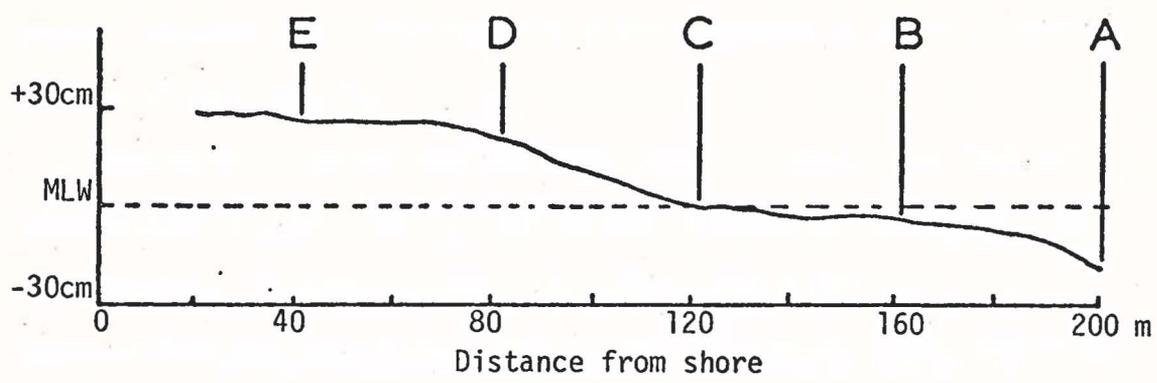


Fig. 4a. Vertical profile of Alupang Cove transect. Distances are in meters; elevations in centimeters and relative to mean low water (MLW).

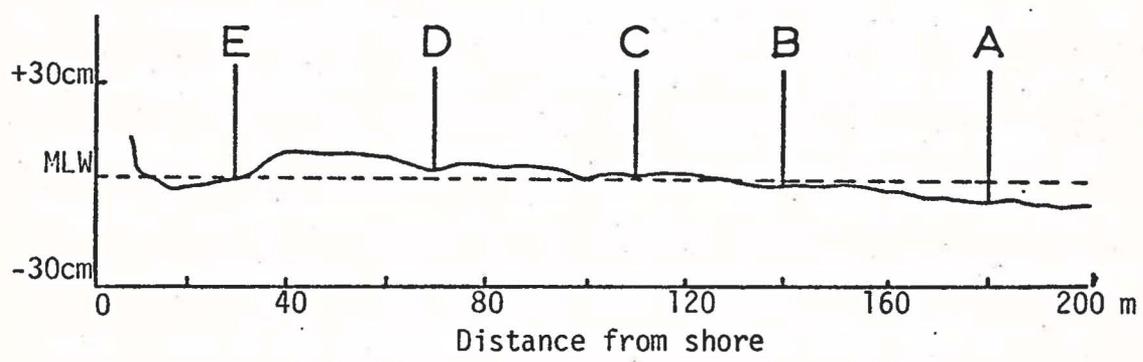


Fig. 4b. Vertical profile of Pago Bay transect. Distances are in meters; elevations are in centimeters and relative to mean low water (MLW).

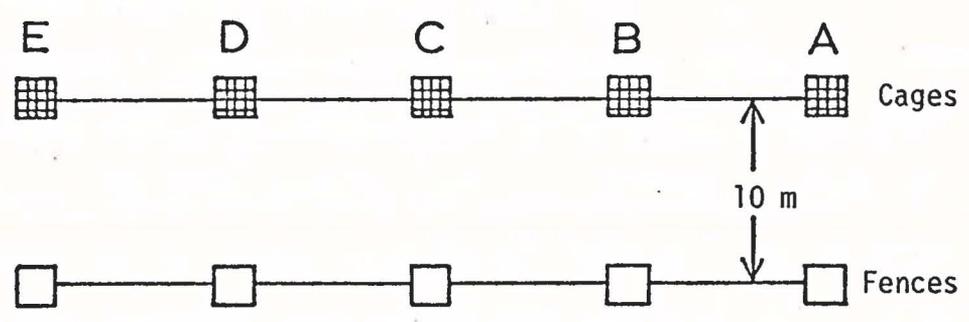


Fig. 4c. Parallel transects of cages and fences in Pago Bay and Alupang Cove. Distances are not shown to scale.

gradual seaward slope resulting in a 45 cm change in beach elevation along a 200 m transect.

Each study area was divided into five stations. The shoreward station marked approximately the innermost limit of the Quidnipagus distribution. Succeeding stations were placed 40 m apart along a transect leading toward the reef margin. A cage with the dimensions 50 cm by 50 cm by 15 cm made of heavy gage galvanized steel mesh with 4 mm by 4 mm openings was placed at each station along the transect. Fences were made by cutting four sections of the steel mesh into 50 cm by 15 cm lengths. These lengths were joined at right angles forming the enclosures (fences) which I placed on a line to one side of the cages so that two parallel transects for each beach were formed (Fig. 4c). (For constructing heavy duty marine cages see Sadykhova, 1969.) The cages and fences were driven or dug into the substrata so that the top of the wire mesh was just below the water-sediment interface. When the experiment was set up each beach had received a total of five cages and five fences evenly spaced along two parallel transects extending 200 m in a seaward direction.

Three hundred individuals of the species Q. palatum were collected, coded with epoxy paint, and notched on the anterior and ventral shell surfaces with a high speed jeweler's drill. On October 23, 1976, 30 clams were measured and numbered and placed within each cage or fence at Alupang Cove. Two weeks later an additional 300 individuals of the species Q. palatum were similarly collected, coded, and notched, then set out in five cages and five fences in Pago Bay. The shell length of the clams in each fence and cage ranged from 1.0 cm to 3.5 cm.

After three months I retrieved the marked clams from the field. Sediments were removed from the enclosures and sieved. The number of dead and missing clams from fences and cages was noted. An optical micrometer on a Wild dissecting microscope was used to measure the increase in shell length and shell height of the notched clams to the nearest 80 microns. The number of new growth rings formed during the three-month period was also recorded.

Population data for Q. palatum in areas near the cages were collected from each station on the Alupang Cove and Pago Bay transects. At each station a 10 m by 10 m grid was marked off. Using a table of random numbers I selected ten 0.1 m² quadrats, each of which was dug to a depth of approximately 15 cm and sieved through nesting screens retaining materials larger than 8 mm. All live bivalve specimens and empty bivalve shells retained by the sieves were returned to the lab for identification and measurement. Live specimens of Q. palatum were counted and measured so that population densities could be calculated for each station and size-frequency histograms could be drawn for each study site. The variances and means from population data are used in the formula $C.D. = \frac{s^2}{\bar{x}}$ to obtain the coefficient of dispersion (Sokal and Rohlf, 1969). Coefficient of dispersion values less than one indicate somewhat uniform distribution; C.D. values greater than one indicate clumped distribution; and values not significantly different from one indicate random distribution. The shell length of all dead valves of Q. palatum were measured, and the percent of drilled valves in each size class was noted. Dead valves of other clam species were also examined for drill holes to determine the extent of naticid predation.

Laboratory predation experiments were run to test the bivalve species preference and bivalve size preference of Natica gualtieriana Recluz, which was the most common naticid drill found during the field sampling. In each of a series of prey preference experiments one member of the species N. gualtieriana was introduced to a 40 l aquarium containing one individual each of the following common reef-flat bivalves, all of which were approximately the same size: Q. palatum, Ctena divergens, Ctena sp., Gafrarium pectinatum, and Jactellina clathrata. A similar set of experiments was run using different size classes of Q. palatum as the prey species. In addition to this, general notes were made as to whether suspected reef-flat predators would kill Quidnipagus.

Regression analyses were used to determine which method of recording shell size and shell growth would give the best fit for a growth curve. The possible combinations that I tested included: $Y=a + bX$; $Y=a + b(\ln X)$; $\ln Y=bX$; $\ln Y=a + b(\ln X)$. Y is the increase in shell length, and X is the shell size at time t_0 .

Analysis of covariance was used to determine if a single regression line would describe the growth rates of the clams on both reef-flats at varying distances from shore and at different depths. Similarly, analysis of covariance was used for each beach separately to compare growth rates at varying depths and distances from shore.

RESULTS

Field Survey Data

In Alupang Cove the bivalve species diversity estimate increased seaward from station E (Fig. 5a). At station A the following bivalve species were found in order of their abundance: Jactellina clathrata, Arcopagia (Pinguitellina) robusta, Quidnipagus palatum, Ctena sp., and Ctena divergens. At station E only two bivalve species were found: Quidnipagus palatum and Ctena divergens. In Pago Bay the bivalve species diversity estimate was found to be greatest at station D where the following clam species were collected in order of abundance: Quidnipagus palatum, Ctena divergens, Pinna muricata, and Anodontia edentula. Individuals of the species Q. palatum and C. divergens were the only bivalve species found at station B.

The population density of Q. palatum is greater in Pago Bay than in Alupang Cove (Figs. 6 and 7). The mean density of Q. palatum ranged from 15.6 clams per m² at station E to 25.0 clams per m² at station A in Pago Bay. In Alupang Cove the mean densities ranged from 0.4 clams per m² at station A to 7.3 clams per m² at station C. Compared to other bivalve species, Quidnipagus is the most abundant in-faunal bivalve on Guam. This is shown by counts of all live bivalve species (Fig. 5b), and by counts of all dead bivalve shells (Table 1).

Valve lengths of Q. palatum individuals showed more variation between stations in Alupang Cove (\bar{x} =3.08 cm; s=1.0) than in Pago Bay (\bar{x} =2.91 cm; s=0.55). No pattern was seen between the valve length and distance from shore (Figs. 6 and 7).

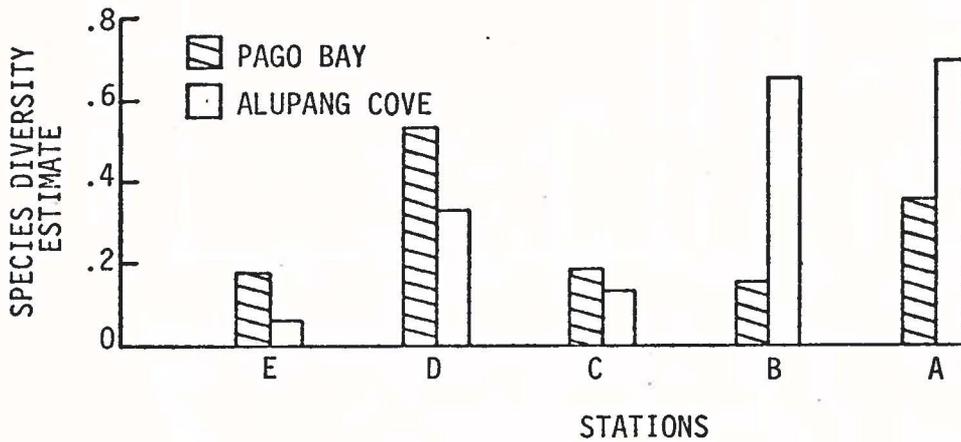


Fig. 5a. Bivalve species diversity estimate for each station at Alupang Cove and Pago Bay. Diversity estimate $\alpha = \frac{s-1}{\log_e N}$ where s =the number of species, and N =the total number of individuals of all species.

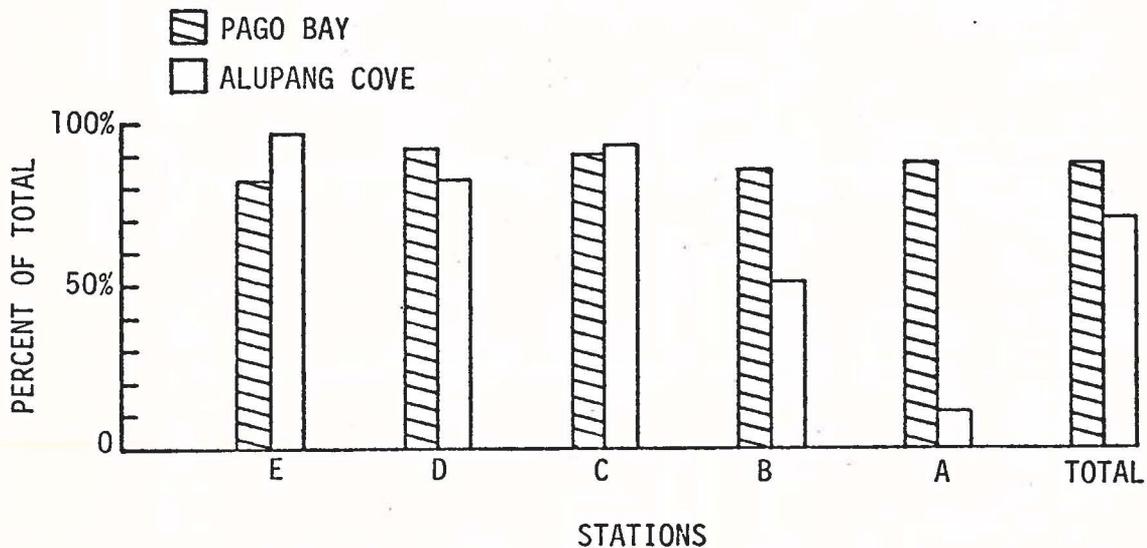


Fig. 5b. The percent of the total number of clams collected at each station in Alupang Cove and Pago Bay that are of the species Quidnipagus palatum.

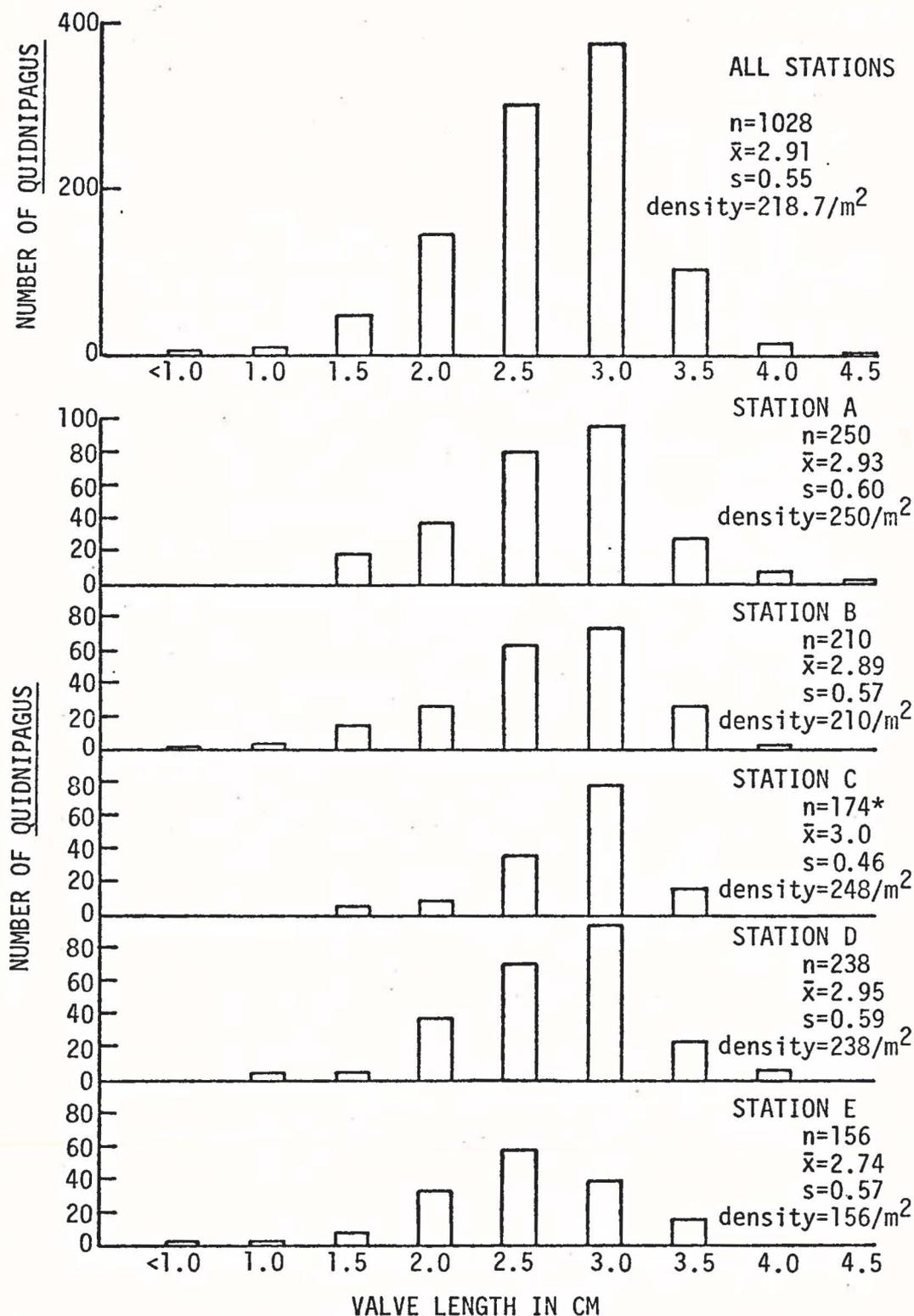


Fig. 6. Length-frequency histograms of *Quidnipagus* from ten $0.1\ m^2$ random samples collected at each station along the Pago Bay transect. (*Denotes seven samples collected at station C.)

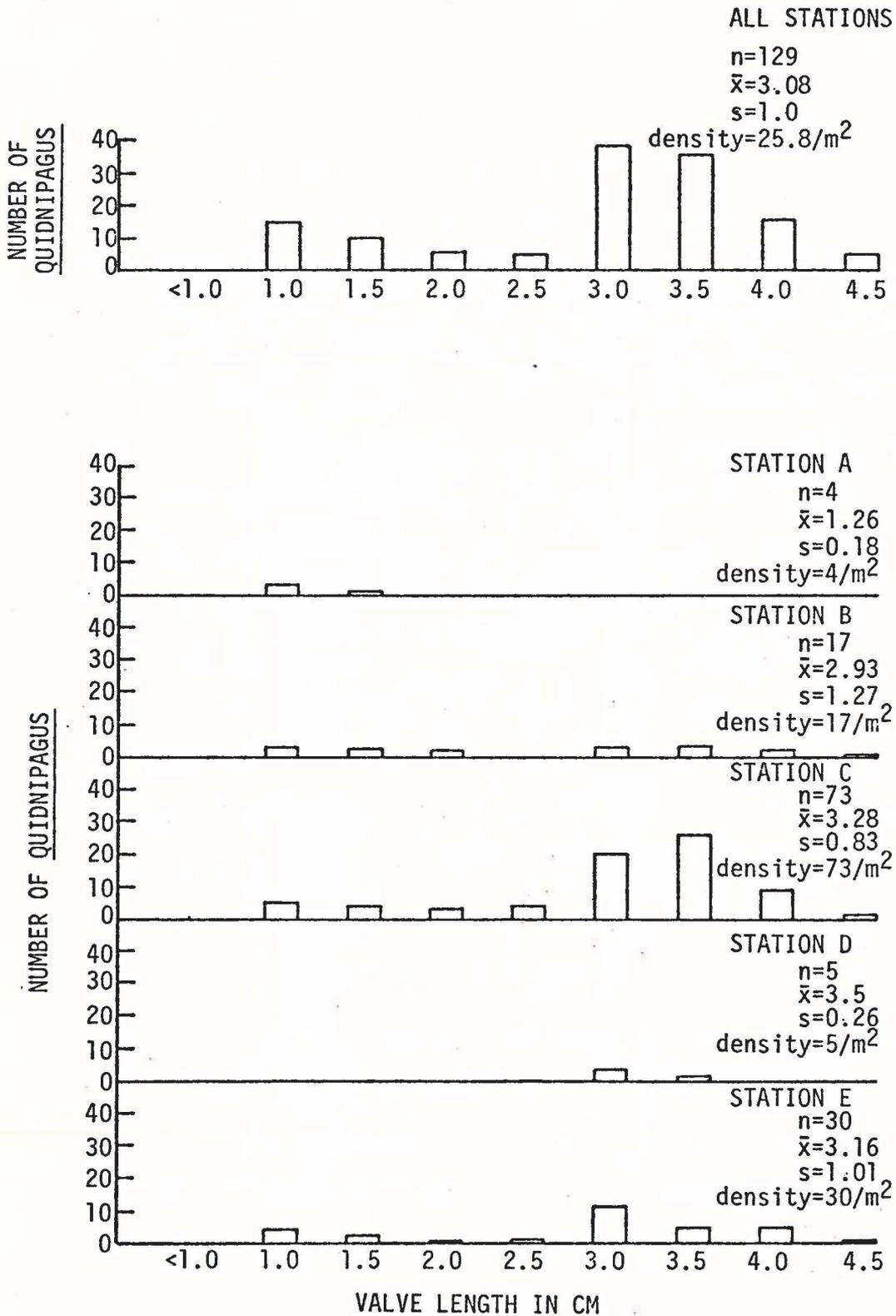


Fig. 7. Length-frequency histograms of *Quidnipagus* from ten $0.1 m^2$ random samples collected at each station along the Alupang Cove transect.

Table 1. Analysis of dead bivalve shells collected from ten 0.1 m² randomly placed quadrats near each station in Alupang Cove. The total number of dead half shells for each species appears in the right column. The percentages of the valves that had drill holes appears in the center column. (The symbol* indicates 20 quadrats sampled at station B, instead of ten.)

STATION	SPECIES	% DRILLED	NUMBER OF SHELL HALVES
A	<u>Ctena divergens</u>	32.0	25
	<u>Ctena sp.</u>	22.2	18
	<u>Jactellina clathrata</u>	5.5	54
	<u>Arcopagia (Pinguicellina) robusta</u>	3.0	33
	<u>Fragrum fragrum</u>	0.0	38
	<u>Quidnipagus palatum</u>	0.0	7
B	<u>C. divergens</u>	54.5	11*
	<u>Gafrarium pectinatum</u>	40.0	5*
	<u>C. sp.</u>	20.0	10*
	<u>J. clathrata</u>	12.2	41*
	<u>A. robusta</u>	10.9	64*
	<u>F. fragrum</u>	6.8	44*
C	<u>Q. palatum</u>	4.0	25*
	<u>C. divergens</u>	26.7	15
	<u>C. sp.</u>	15.4	13
	<u>J. clathrata</u>	5.4	37
	<u>F. fragrum</u>	2.9	34
	<u>Q. palatum</u>	1.6	123
D	<u>A. robusta</u>	0.0	30
	<u>C. sp.</u>	46.7	15
	<u>C. divergens</u>	41.6	77
	<u>Q. palatum</u>	0.5	222
	<u>A. robusta</u>	0.0	11
	<u>F. fragrum</u>	0.0	19
E	<u>J. clathrata</u>	0.0	14
	<u>G. pectinatum</u>	33.3	3
	<u>C. divergens</u>	31.8	22
	<u>C. sp.</u>	20.0	15
	<u>J. clathrata</u>	18.2	11
	<u>Q. palatum</u>	7.4	81
TOTAL	<u>A. robusta</u>	0.0	6
	<u>C. divergens</u>	38.00	150
	<u>G. pectinatum</u>	37.50	8
	<u>C. sp.</u>	25.40	71
	<u>J. clathrata</u>	7.64	157
	<u>A. robusta</u>	5.56	144
<u>F. fragrum</u>	2.96	135	
<u>Q. palatum</u>	2.18	458	

Growth

During a three-month interval, the amount of shell growth (length) of Quidnipagus varied (Fig. 8). Smaller clams grew as much as 6.8 mm, while clams larger than 2.0 cm grew considerably less. A negative relationship was found between the initial shell length and the growth rate of Quidnipagus (Fig. 9).

Individuals of the species Q. palatum of the same size class grew at varying rates along the Alupang Cove transect (Fig. 8). Regression analysis of growth data from the stations in Alupang Cove was subjected to an ANCOVA test to determine if a single growth equation could describe Quidnipagus growth. This hypothesis was rejected ($F_{.01}[8,80] = 5.768$). Therefore a consistent pattern of growth throughout all stations could not be expressed in a single regression line.

If we assume that all members of the species Q. palatum attain a similar maximum size, then the slope of the regression equation may be used as an expression of the change in growth rate for Quidnipagus. The different regression slopes calculated for each station show that clams grew significantly faster at some stations than at others (Table 2a and 2b). The results of F-tests to compare the differences between regression coefficients of stations at Alupang Cove appear in Table 3a. At Alupang Cove the clams at station A grew significantly faster than clams at stations B, C, or E. The results of F-tests to compare the difference of growth rates between stations in Alupang Cove and Pago Bay appear in Table 4. From Fig. 8, we can see that the mean instantaneous relative growth rate for each size class of clams in Alupang Cove was greater than in Pago Bay. The rate of Quidnipagus growth was found not to be significantly influenced by water depth or

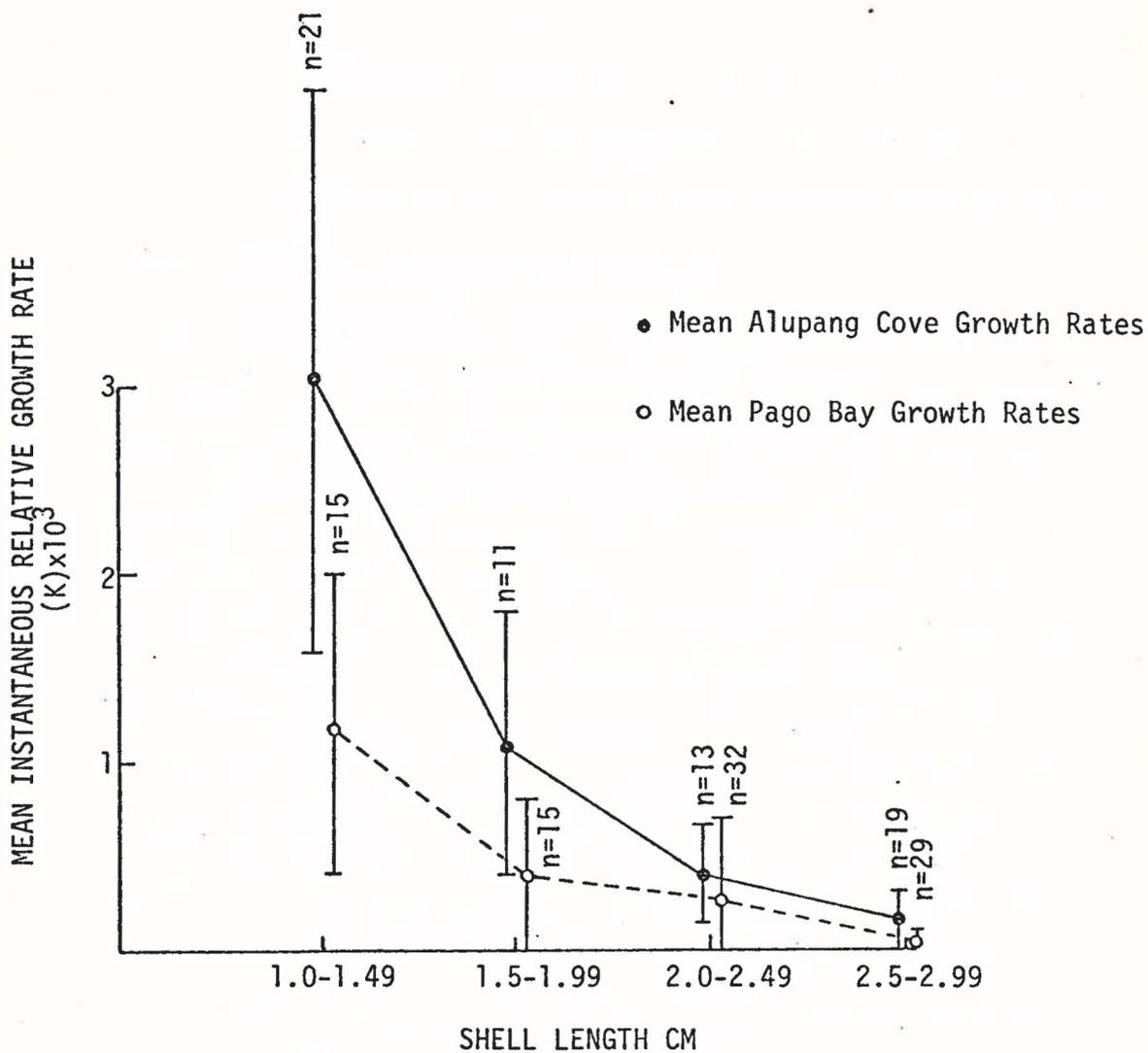


Fig. 8. A comparison of the mean instantaneous relative growth rates (K) of length of shell of Quidnipagus at Alupang Cove and Pago Bay as a function of shell size. Each point represents the mean growth rate (K) of a group of bivalves \pm standard deviations.

distance from shore. A product-moment correlation coefficient of $r_{12}=0.0779$ ($n=97$) for clams growing inside fences at Alupang Cove at different depths indicates no significant correlation between water depth and rate of Quidnipagus growth within the depth range tested. The fact that growth rates of Quidnipagus are not a function of water depth is further exemplified by Tables 2a and 2b, which compare growth rates between stations, hence between depths.

Distance from shore had no significant effect upon the growth rate of Quidnipagus. This was determined by calculating a regression coefficient for the growth rates of the clams at each station located at n , $n+40$ m, $n+80$ m, etc. from shore. A t-test of the regression coefficient showed that the regression coefficient was not significantly different from zero $t_{[97]}=2.57582$. It appears that increasing distance from shore does not affect the growth rate of individuals of Q. palatum. That distance from shore is not a growth rate determining factor may be seen in Table 2a. The slope of the regression equation at station A (farthest from shore) is not significantly different from the slope of the regression equation for station D (second closest to shore) ($F_{.01}[1,28]=2.9612$). Since there is no progression in growth rates from stations A to E in Alupang Cove it is unlikely that a direct relationship exists between growth rate and distance from shore.

Population density is another variable that may affect growth rates of individuals. Figures 6 and 7 show the density per 0.1 m^2 of the Quidnipagus population at each station. Because no clams were removed from the field population when the fences were anchored in the substrate, the density of the Quidnipagus population inside each fence was assumed to be representative of the field population outside the

Table 2a. Quidnipagus palatum: Relationships between \ln length at t_0 and increase in shell length during a three-month period at five stations in Alupang Cove.

STATION	$b_{y.x}$	s_b	n	Y-int.	95% Confidence Limits for $b_{y.x}$	
A	-.5333	.0541	15	.6236	-.6502	-.4164
B	-.2818	.0355	19	.3426	-.3568	-.2068
C	-.2534	.0334	24	.3172	-.3226	-.1841
D	-.3855	.0635	14	.4339	-.5238	-.2472
E	-.3333	.0302	25	.4101	-.3958	-.2708

Table 2b. Quidnipagus palatum: Relationships between \ln length at t_0 and increase in shell length during a three-month period at five stations in Pago Bay.

STATION	$b_{y.x}$	s_b	n	Y-int.	95% Confidence Limits for $b_{y.x}$	
A	-.1648	.0283	25	.1814	-.2232	-.1063
B	-.1130	.0169	24	.1195	-.1480	-.0780
C	-.1687	.0275	22	.1799	-.2261	-.1112
D	-.2237	.0361	18	.2366	-.3003	-.1470
E	-.0502	.0138	26	.0504	-.0786	-.0218

Table 3a. The results are shown of F-tests for differences between regression coefficients of growth rates for Quidnipagus within fences in Alupang Cove. (N.S. denotes Not Significant; *= $p < .05$; **= $p < .01$; ***= $p < .001$.)

Fences from which Regression Coefficients are Compared	Fs	Results
A and B	15.757	***
A and C	22.147	***
A and D	2.961	N.S.
A and E	12.46	**
B and C	0.335	N.S.
B and D	2.312	N.S.
B and E	1.206	N.S.
C and D	3.969	N.S.
C and E	3.157	N.S.
D and E	0.668	N.S.

Table 3b. The results are shown of F-tests for differences between regression coefficients of growth rate for Quidnipagus within fences in Pago Bay. (N.S. denotes Not Significant; *= $p < .05$; **= $p < .01$; ***= $p < .001$.)

Fences from which Regression Coefficients are Compares	Fs	Results
A and B	2.547	N.S.
A and C	0.010	N.S.
A and D	1.728	N.S.
A and E	12.746	***
B and C	3.003	N.S.
B and D	9.132	**
B and E	7.889	**
C and D	1.505	N.S.
C and E	13.48	***
D and E	23.287	***

Table 4. Results of an F-test to compare the regression coefficients of growth rates from stations in Alupang Cove and Pago Bay. (N.S. denotes Not Significant; *=p<.05; **=p<.01; ***=p<.001.)

ALUPANG COVE STATION	PAGO BAY STATION	F _s	RESULTS
A	A	F _{.001} [1,30]=38.77	***
B	A	F _{.05} [1,40]=6.612	*
B	B	F _{.001} [1,30]=19.24	***
C	B	F _{.01} [1,44]=12.22	**
C	C	F _{.05} [1,42]=3.58	N.S.
E	E	F _{.001} [1,40]=47.81	***

fence. No significant correlation was observed between Quidnipagus density and the growth rate of Quidnipagus ($r_{12} = -.0466$; $n=55$).

An artifact of this experiment which influenced Quidnipagus growth rates was the cage. Clams inside the cages grew significantly slower than the clams placed inside fences ($F_{.01}[2,150] = 16.625$).

Growth Rings

Growth rings are often convenient for assessing the age structures of populations and growth rates of individual organisms from counts made at a given point in time. The number of rings on the valves of Quidnipagus is correlated with the length of the valve (Fig. 10), but not with an interval of time (Fig. 11). I found that the number of new growth rings added to individuals of the species Q. palatum during a three-month interval varied (Fig. 11). During the same period of time, the number of new growth rings formed ranged from nine to less than one. In Alupang Cove clams smaller than 2.0 cm had more variation in the number of rings formed ($CV=0.4252$; $s_{CV}=0.053$; $n=32$) than did the clams larger than 2.0 cm ($CV=1.8448$; $s_{CV}=.1477$; $n=78$). A highly significant difference exists between these two coefficient of variation values ($t_{[108]}=52.86$; $p<.001$). In Pago Bay, clams smaller than 2.0 cm had more variation in the number of rings formed ($CV=0.7127$; $s_{CV}=0.0735$; $n=49$) than did the clams larger than 2.0 cm ($CV=2.1473$; $s_{CV}=0.1165$; $n=170$). A highly significant difference exists between these two coefficient of variation values ($t_{[219]}=80.658$; $p<.001$), indicating that the valve length of an individual of the species Q. palatum is inversely proportional to the number of growth rings that will be formed in a given time period.

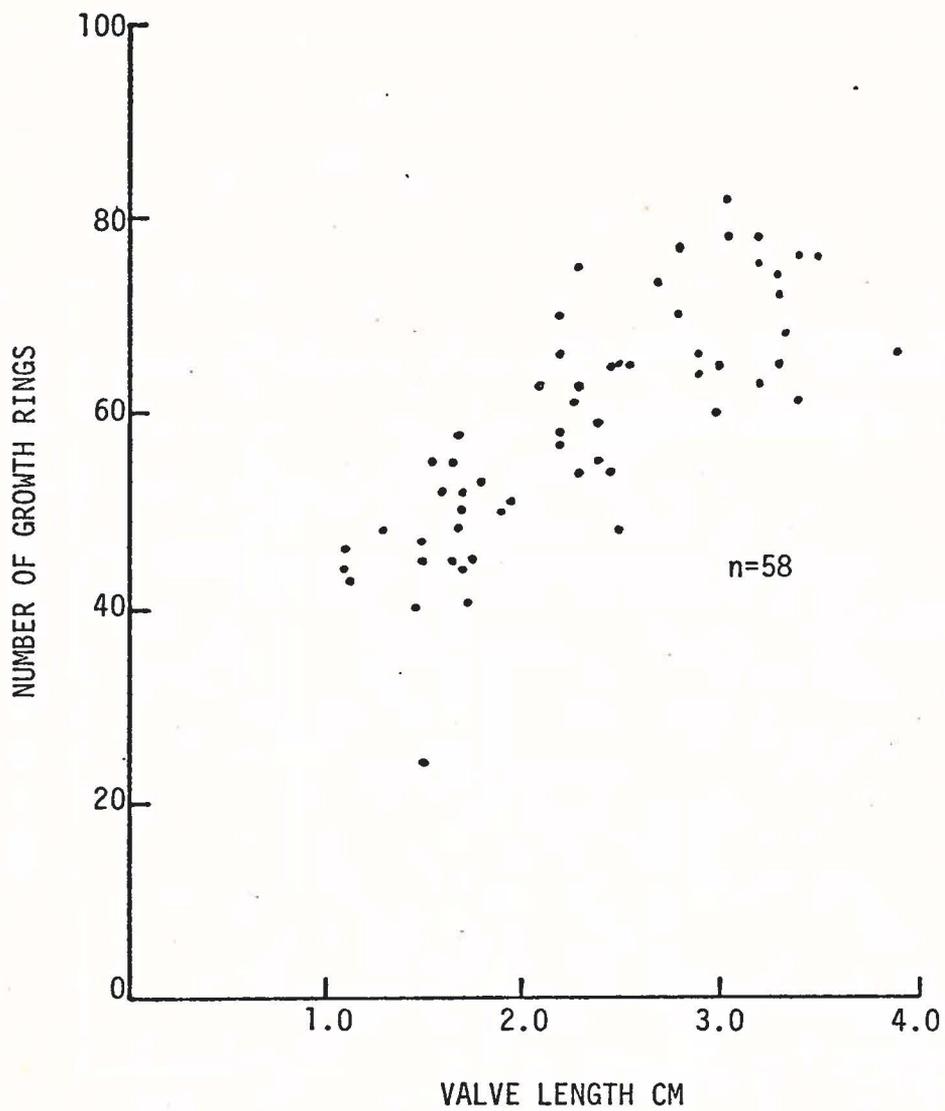


Fig. 10. A scattergram showing the relationship between the growth rings and valve length on Quidnipagus.

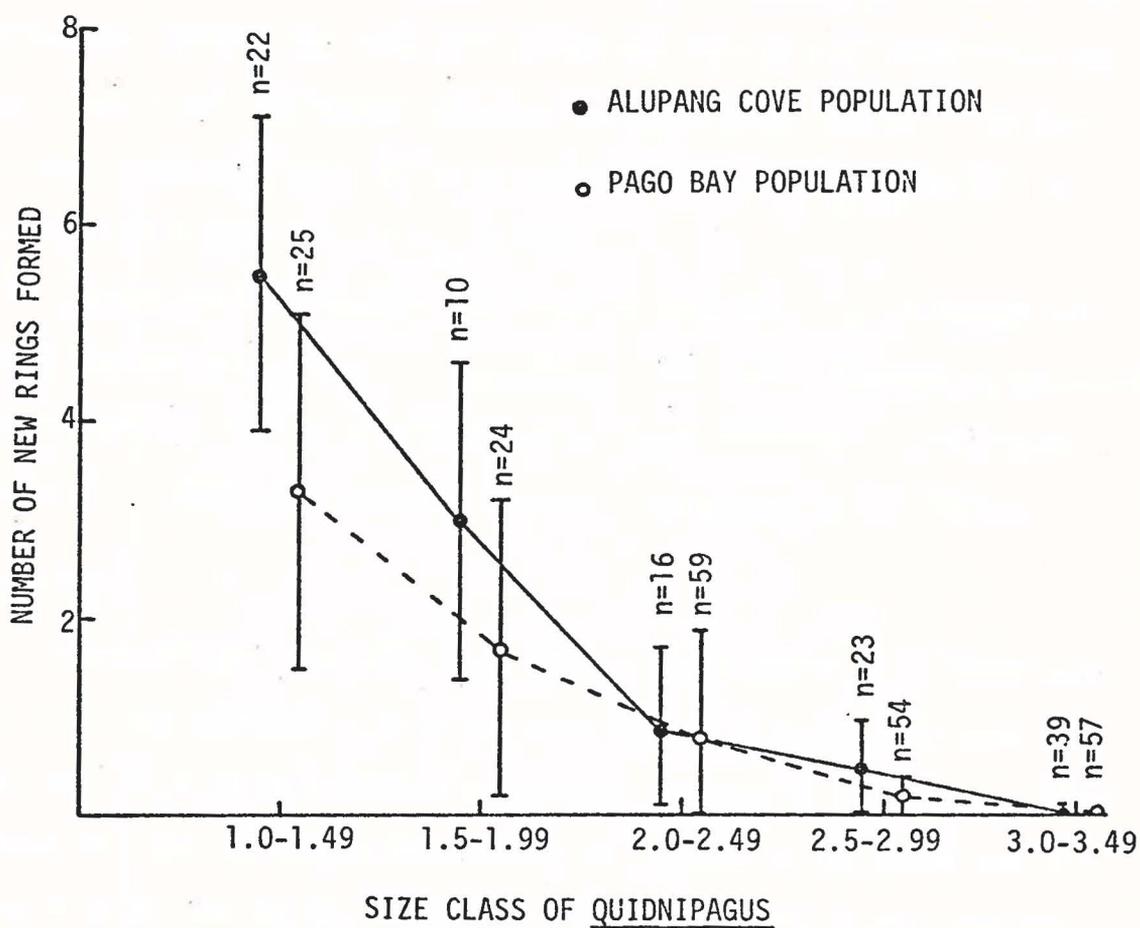


Fig. 11. A comparison of the mean number of new rings formed by different size classes of Quidnipagus at Alupang Cove and Pago Bay as a function of shell size. Each point represents the mean number of rings of a group of bivalves \pm standard deviations.

The number of rings formed on the shell also differed according to locality. Q. palatum in Alupang Cove added significantly more growth rings during a three-month period than did members of the same species in Pago Bay ($t_{[342]}=2.868$; $p<.01$).

Distance from shore does not appear to influence the rate of ring formation. Within the same size class the rate of ring deposition was not significantly different between the seaward two stations and the shoreward two stations. This was true for Pago Bay $t_{[17]}=0.5619$ as well as for Alupang Cove $t_{[16]}=0.8257$.

A negative relationship was found between the initial number of rings and the growth rate in Quidnipagus (Fig. 12). Regression analysis showed that initial valve length has a closer relation to the growth rate ($r^2 = .7529$) than does the initial ring number ($r^2 = .6421$).

Predation

Predation upon the 150 clams placed inside fences at Alupang Cove was less than expected. Only one clam (length 1.31 cm) was found to have been drilled by a naticid gastropod. However not all of the clams placed in cages or fences were recovered (Table 5). Recovery work was done at night during the winter low tides; therefore, some clams may have been overlooked inside the cages and fences. The number of clams missing from cages was significantly less than the number of clams missing from fences ($t_{[298]}=14.5064$; $p<.01$). Ten percent of the 150 clams placed inside the cages were not recovered, whereas 24.8 percent of the 150 clams inside fences were not recovered. I cannot be certain that the clams missing from fences were taken by predators.

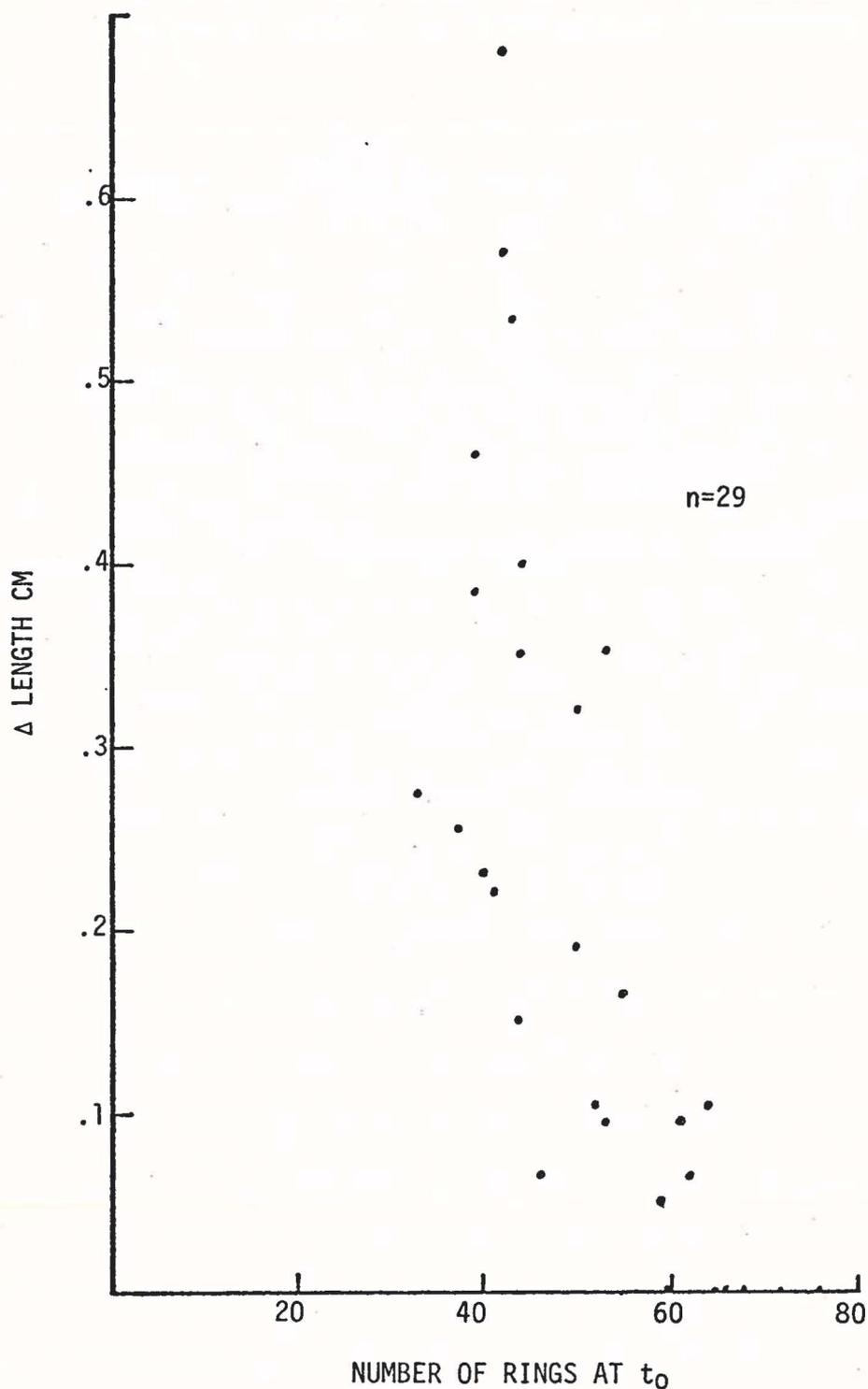


Fig. 12. Scattergram showing the growth rate of *Quidnipagus* individuals as a function of the initial number of rings during a three-month period in Alupang Cove.

Table 5. Survivorship of clams placed inside cages and fences for three months in Alupang Cove. All cages and fences contained 30 individuals of the species Quidnipagus palatum at t_0 .

STATION	CAGES				FENCES			
	LIVE	DEAD	MISSING	TOTAL	LIVE	DEAD	MISSING	TOTAL
A	17	9	4	30	15	3	12	30
B	18	12	0	30	20	1	9	30
C	20	7	3	30	25	1	4	30
D	13	12	5	30	15	8	7	30
E	2	25	3	30	25	0	5	30

Field observations indicated that several suspected bivalve predators occur in the study area. Drilled valves of Quidnipagus indicate naticid gastropod predators. Broken shells suggest the presence of decapod crustaceans. Two large decapods (5 cm) were noted in the study area of Alupang Cove: Thalamita crenata and Calappa gallus. T. crenata was found in densities of five individuals per m^2 near station B. Clams missing from inside the fences may have been carried away by fish. Numerous species of fish including a flounder were seen in the study area at high tide. An octopod was also seen in the area. At low tides flocks of 30-40 shore-birds including Numenius phaeopies were noted. Quidnipagus shells along with bird excrement were found on top of boulders adjoining the study area. I did not observe any Quidnipagus shell fragments in the feces. Instead appendages of the common decapod Ocypoda sp. were found. Although none of the suspected predators were actually seen attacking Quidnipagus in the field, drilled clam shells unmistakably indicate naticid gastropod predation.

That naticids prey on smaller size classes of Q. palatum is illustrated by the size-frequency histogram of all dead and drilled valves of Quidnipagus collected in Pago Bay (Figs. 13a and 13b). Since the mean sizes of drilled valves and non-drilled valves do not clearly indicate a prey size preference by the naticids, I tested the null hypothesis that there is no difference in the frequency of predation upon succeeding size classes of Q. palatum. This null hypothesis was rejected ($\chi^2_{[6]}=12.93$; $p<.05$). A significant difference was found between the percent of drilled Q. palatum valves of the size class 1.5 cm and the percent of drilled valves of Q. palatum in larger size classes ($\chi^2_{[1]}=4.15$; $p<.05$).

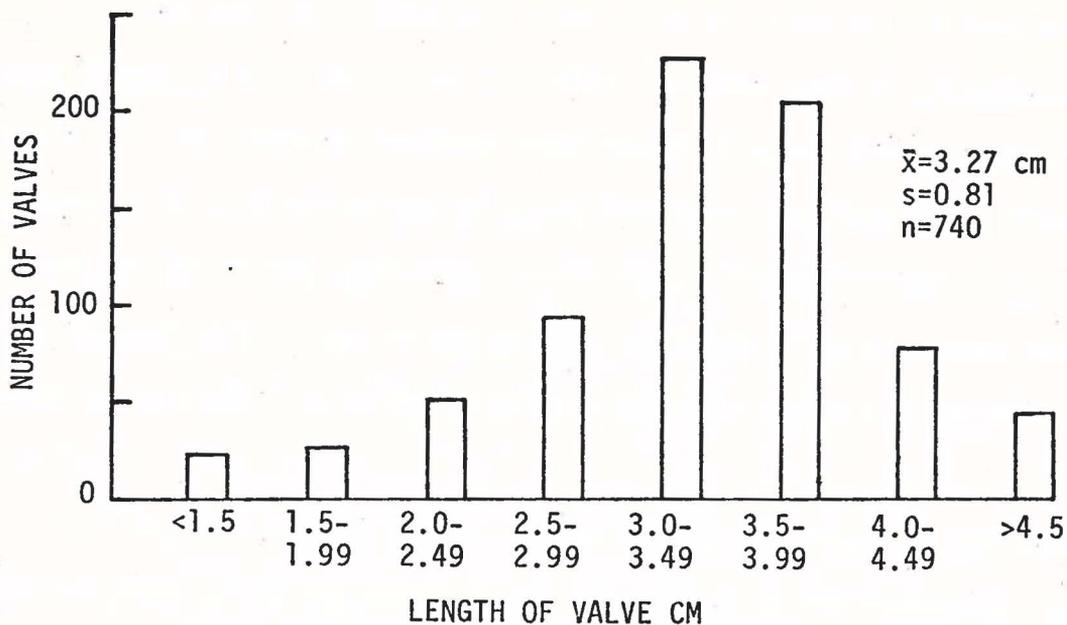


Fig. 13a. Histogram of dead Quidnipagus palatum valves collected at Pago Bay.

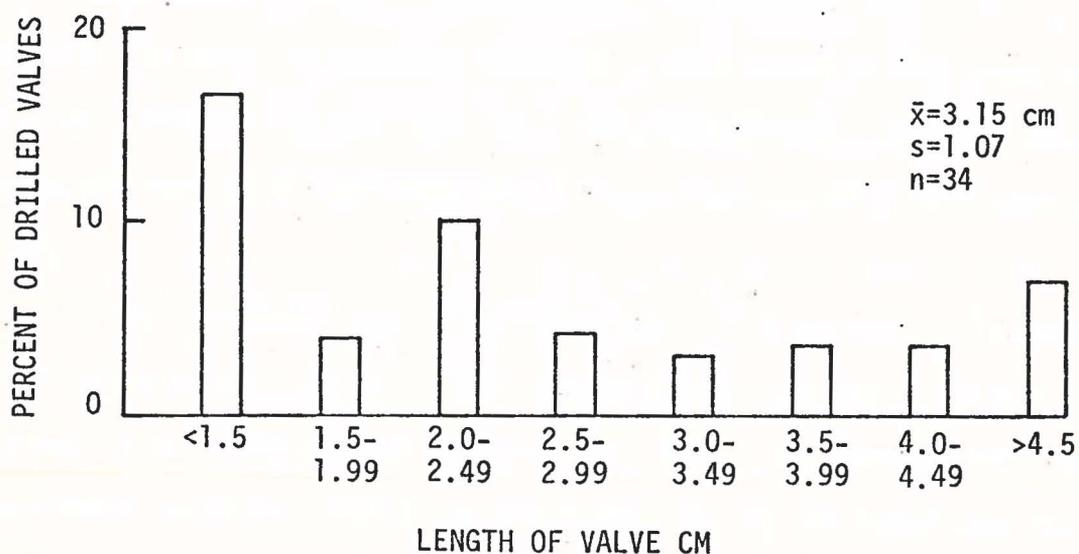


Fig. 13b. Histogram of drilled valves of Quidnipagus palatum from Pago Bay.

Naticids prey significantly more often on clams of the species Ctena divergens than on other reef-flat bivalves such as Quidnipagus (Table 1). At three of the five stations in Alupang Cove, a higher percentage of drilled valves of Ctena divergens was found than Ctena sp., Jactellina clathrata, Gafrarium pectinatum, Fragrum fragrum, Arcopagia (Pinguitellina) robusta, or Quidnipagus palatum. Ctena sp. was the second most commonly drilled bivalve along the transect ($\chi^2_{[5]}=47.16$; $p<.005$).

The largest density of naticid gastropods was found at the same station where the highest percentage of drilled valves occurred. In Alupang Cove, the area of greatest naticid activity was in the vicinity of station B. At this station 18 percent of all dead shells found had been drilled (Fig. 14), while the density of live naticid drills was (0.2 naticids/m² (s=0.42)). In addition, the greatest density of naticid egg cases lay between stations C and B where 40 egg cases were counted per 120 m² (1 egg case per 3 m²), and between station B and A where the density of egg cases was 20 cases per 120 m² (1 egg case per 6 m²).

In the laboratory Natica gualtieriana preyed significantly more on the 1.4-1.5 cm size class of the species Q. palatum than on larger size classes of the same species ($\chi^2_{[2]}=8.0$ $p<.025$). In aquaria where the experiment could continue after the first kill it was noted that the next larger Q. palatum was killed second. The largest prey specimen was chosen last.

Additional laboratory experiments were set up to test the prey preference of suspected bivalve predators. N. gualtieriana killed significantly more Jactellina clathrata or Q. palatum than

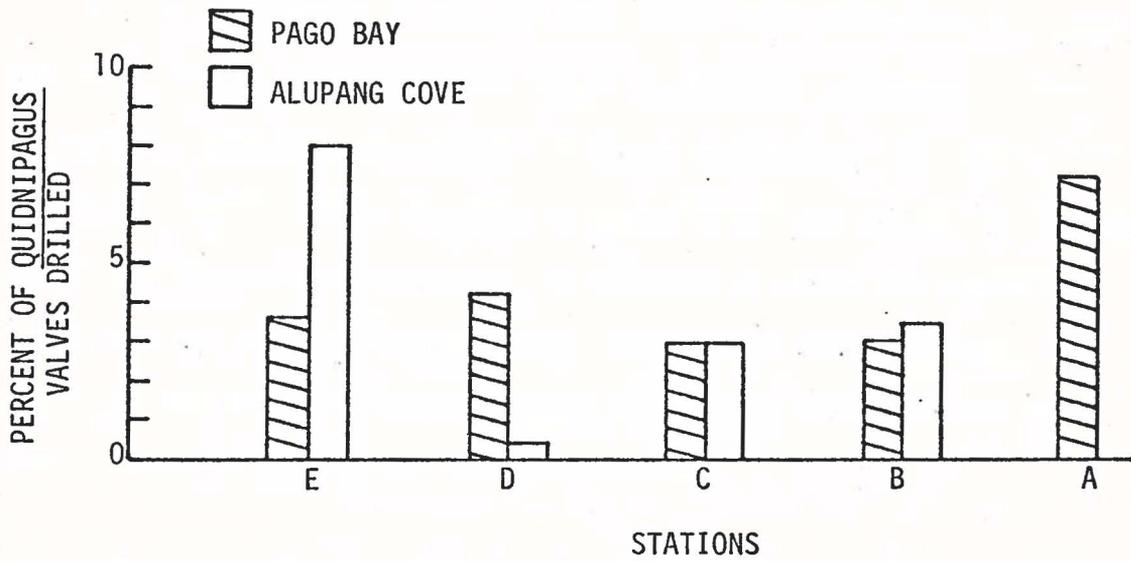


Fig. 14. Percentage of drilled *Quidnipagus* shells found at each station at Alupang Cove and Pago Bay.

Ctena divergens, Gafrarium pectinatum, or Ctena sp. ($\chi^2_{[1]}=10$; $p<.005$). A first choice of J. clathrata in these trials was significant ($\chi^2_{[2]}=6.5$; $p<.05$). Under laboratory conditions N. gualtieriana shows a highly significant prey preference for either J. clathrata or Q. palatum. That C. divergens was not a preferred food of N. gualtieriana may indicate other reef-flat naticid species such as Mammilla opaca Recluz are feeding within the same community. Both these species occur in the study area.

In another series of bivalve prey-preference experiments Calappa gallus killed Q. palatum before attacking Asaphis violascens, Ctena divergens, Gafrarium pectinatum, or Pitar pellucidus. At least under laboratory conditions Q. palatum is a preferred food choice by Calappa gallus and Natica gualtieriana. In addition to these two predators, the portunid crab Thalamita crenata, the xanthid crab Atergatis floridus, and the gastropod Cymatium nicobaricum have been observed feeding upon Q. palatum in the laboratory.

DISCUSSION

The rate of growth ring deposition is highly variable for Quidnipagus. Smaller individuals produced more rings than larger individuals. Kusakabe (1959) found similar results with larvae of bivalves such as Anadara subcrenata which formed several rings within a few days, whereas ring formation was not as rapid in older individuals. Yoshida (1953) related the high rate of juvenile ring formation to specific physiological events. He showed that in nine species of marine bivalves, a ring was laid down between the prodissoconch and spat stages, and that another ring was formed at the time the spat detaches from the substratum. For Quidnipagus, variability in the rate of ring formation exists between stations along the transects (Table 6a, 6b) as well as between transects on different beaches (Fig. 11). To account for such variation within the same size class, we need to examine the process of shell growth and ring formation more closely.

The mantle, a soft outer tissue of molluscs, is the site of shell formation. The rate of shell growth is thus a function of mantle growth. The outer fold of the mantle edge is responsible for secreting the periostricum and prismatic shell layers. The entire mantle surface secretes the remaining calcareous portion (Barnes, 1974).

Since the outer two layers of the shell are secreted only by the edge of the mantle, these portions of the valves therefore show the concentric markings of discontinuous growth. The inner or nacreous layer of shell is smooth because the entire surface of the mantle is continuously forming new inner crystalline layers. As a result, the

Table 6a. Mean number of rings formed during a three-month period by each size class of Quidnipagus inside fences at different stations at Alupang Cove.

SIZE CLASS CM	STATIONS					TOTALS
	E	D	C	B	A	
1-1.49	$\bar{x}=6$ $s=1.3$ $n=7$	$\bar{x}=1$ $n=1$	$\bar{x}=2$ $n=1$	$\bar{x}=3.7$ $s=2.1$ $n=3$	$\bar{x}=6.1$ $s=1.6$ $n=7$	$\bar{x}=5.53$ $s=1.87$ $n=19$
1.5-1.99	$\bar{x}=5$ $n=1$			$\bar{x}=4$ $n=1$		$\bar{x}=4.5$ $s=0.71$ $n=2$
2.0-2.49	$\bar{x}=1.33$ $s=0.577$ $n=3$	$\bar{x}=1$ $n=1$	$\bar{x}=0.33$ $s=0.577$ $n=3$			$\bar{x}=0.857$ $s=0.69$ $n=7$
2.5-2.99	$\bar{x}=0.9375$ $s=0.678$ $n=8$			$\bar{x}=0.25$ $s=0.5$ $n=4$	$\bar{x}=0.33$ $s=0.58$ $n=3$	$\bar{x}=0.663$ $s=0.67$ $n=15$
3.0-3.49	$\bar{x}=0$ $n=4$	$\bar{x}=0$ $n=1$	$\bar{x}=0$ $n=5$	$\bar{x}=0.125$ $s=0.354$ $n=8$	$\bar{x}=0$ $n=4$	$\bar{x}=0.045$ $s=0.21$ $n=22$

Table 6b. Mean number of rings formed during a three-month period by each size class of Quidnipagus inside fences at different stations at Pago Bay.

SIZE CLASS CM	STATIONS					TOTALS
	E	D	C	B	A	
1.1-1.49	$\bar{x}=2$ $n=1$	$\bar{x}=4$ $n=1$	$\bar{x}=3.7$ $s=0.58$ $n=3$	$\bar{x}=2.3$ $n=3$	$\bar{x}=2$ $n=1$	$\bar{x}=2.89$ $s=1.05$ $n=9$
1.5-1.99	$\bar{x}=0$ $n=3$	$\bar{x}=2$ $s=1.7$ $n=3$	$\bar{x}=1$ $n=1$	$\bar{x}=0.4$ $s=0.55$ $n=5$	$\bar{x}=2.33$ $s=0.58$ $n=3$	$\bar{x}=1.07$ $s=1.22$ $n=15$
2.0-2.49	$\bar{x}=0.2$ $s=0.4$ $n=10$	$\bar{x}=0.33$ $s=0.58$ $n=3$	$\bar{x}=0.33$ $s=0.82$ $n=6$	$\bar{x}=0.2$ $s=0.45$ $n=5$	$\bar{x}=0.17$ $s=0.41$ $n=6$	$\bar{x}=0.23$ $s=0.5$ $n=30$
2.5-2.99	$\bar{x}=0$ $n=8$	$\bar{x}=0$ $n=7$	$\bar{x}=0.4$ $s=0.89$ $n=5$	$\bar{x}=0$ $n=4$	$\bar{x}=0.2$ $s=0.45$ $n=5$	$\bar{x}=0.103$ $s=0.41$ $n=29$
3.0-3.49	$\bar{x}=0$ $n=4$	$\bar{x}=0$ $n=4$	$\bar{x}=0$ $n=7$	$\bar{x}=0$ $n=7$	$\bar{x}=0$ $n=9$	$\bar{x}=0$ $n=31$

macroscopic growth rings reflect changes in mantle secretory activity, while the microscopic layers of the nacre record daily patterns of deposition seen in a vertical section of a shell.

By microscopically examining the fine increments in vertical, radial sections of Mercenaria mercenaria valves, Pannella and MacClintock (1968) described the periodic occurrence of annual, monthly, tidal (fortnightly), bidaily, daily, and subdaily growth patterns. Although all of the taxa examined by Pannella and MacClintock showed continuous growth in the sense that some growth occurs each day, they did find that breeding, increased water depth, and cooler water temperatures interrupted the rate of shell formation in M. mercenaria growing under varying tidal conditions.

Macroscopic variations on the outer shell surface of valves have been successfully used to analyse growth rates and year class frequencies in Venerupis pullastra (Johannesson, 1973), Ostrea edulis (Wilbur and Owen, 1964), Macoma balthica (Gilbert, 1973), Mya arenaria (Newcombe, 1936), Mytilus edulis diegensis (Coe, 1945), and Tivela stultorum (Coe, 1947). The advantage of using macroscopic observations of shell growth patterns is that it lends itself to fast analysis of age class data. However, before growth rings can be used as an indicator of age it must be shown that a temporal pattern of ring deposition exists. This is not the case for Quidnipagus.

Although growth rings apparently indicate periods of growth cessation, the clams which exhibited the greatest amount of shell growth also produced the greatest number of shell rings (Fig. 15). This may indicate that smaller clams are growing at a faster rate than larger clams. However, these periods of rapid growth are frequently interrupted.

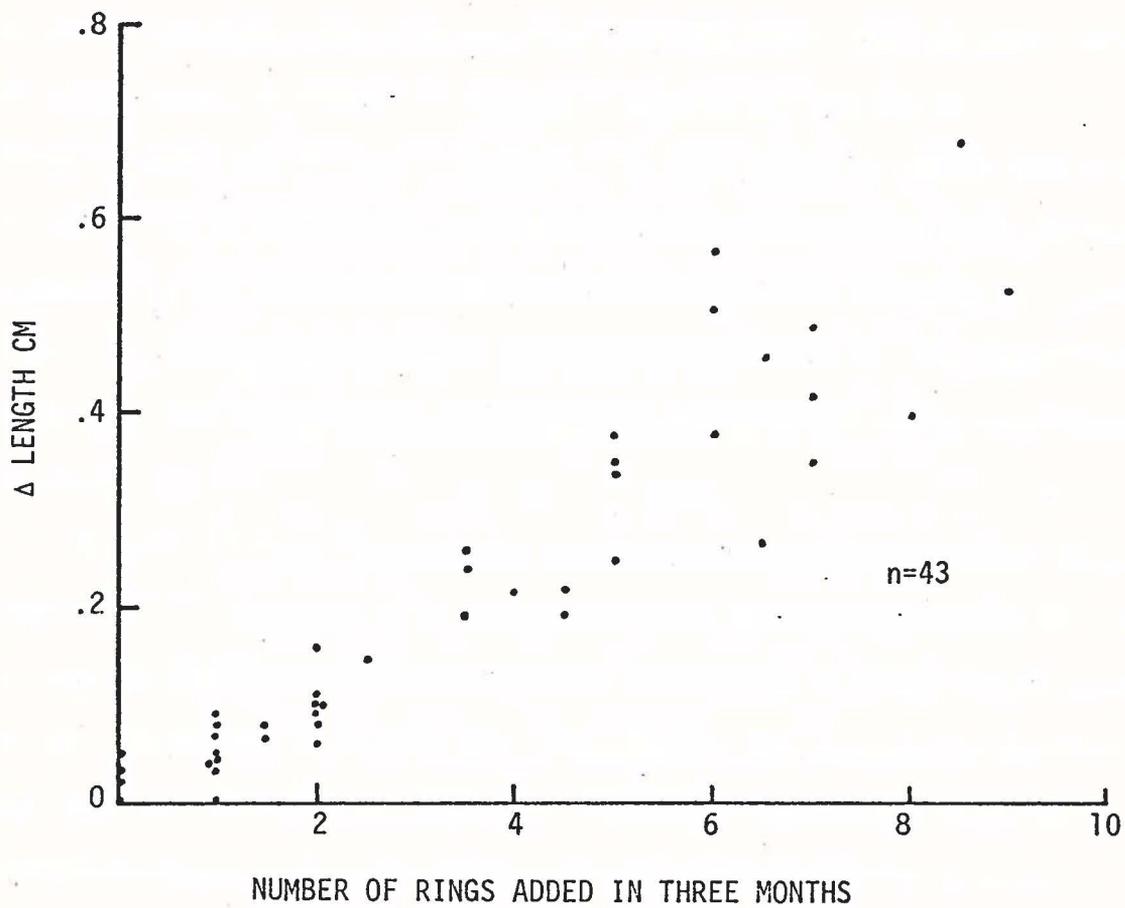


Fig. 15. A scattergram showing the relationships of the increase of shell length to the increase of ring number for Quidnipagus.

Several parameters were examined in an attempt to determine a correlation between ring deposition and a particular event.

No consistent pattern in the rate of growth ring deposition was noted at any station in Alupang Cove or Pago Bay (Table 6a, 6b). For example, the mean number of rings formed by the 1.0-1.49 cm size class of Quidnipagus at station B was significantly lower than the mean number of rings added by clams at the other stations of the same size class at Alupang Cove ($t_{[2]}=4.326$). However, the mean number of rings added by the 3.0-3.49 cm size class is not significantly different from the mean number of rings formed by clams of the same size at different stations. Therefore, Quidnipagus shows a highly variable rate of ring deposition that does not appear to be attributed to microhabitat variations between stations.

Rings in larger bivalves may be caused by breeding periods. Quidnipagus individuals larger than 2.3 cm were found to be sexually mature during the months of June through April (Day, University of Guam, unpublished data). Therefore it is possible that growth interruptions on the valves may indicate breeding periodicity. Synchrony in breeding activity of organisms helps maximize the probability of fertilization. Day (unpublished data) found Modiolus auriculatus often spawned during late spring when being transported in a bucket to the laboratory. Such spawning behavior may be initiated by elevated water temperature or lack of water in the containers. Therefore the spawning M. auriculatus may be initiated by the tidal and or temperature conditions associated with afternoon spring tides of late spring or early summer. Quidnipagus however, does not spawn when subjected to the stimuli of elevated water temperature, desiccation, or even rough handling as M. auriculatus

received when transported in buckets to the laboratory. The exact nature of stimuli needed to release spawning behavior in Quidnipagus is not known. I attempted unsuccessfully to induce spawning in sexually mature Quidnipagus individuals using procedures outlined by Loosanoff and Davis (1963). It may be that Quidnipagus, once sexually mature, breeds asynchronously throughout the year. That elevated temperatures and desiccation do not release spawning activity suggests that the periodic stimuli of low spring tides of early summer and the accompanied elevated reef-flat temperatures do not trigger spawning in Quidnipagus. Hence, the shell growth cessation corresponding to spawning activity will not reflect the same lunar periodicity as the tides.

The rate of Quidnipagus growth decreases with initial shell size. Similarly, Gilbert (1973) noted that the growth rate of Macoma balthica had a negative linear relationship between the initial length and the total annual increment. Age and size are positively correlated in organisms having indeterminate growth patterns. The amount of growth decreases with age. Walford (1946) noted that "the amount of growth that remains unfilled at the beginning of any time interval, is a constant percentage of the amount of it which had remained at the beginning of the preceding time interval." Thus the larger the organism, the more slowly growth proceeds. Analyzing the growth rings of Venerupis pullastra, Johannesson (1973) concluded that younger members of a size class grew faster than older members even though the clams were of the same size at the beginning of a growing season. The scattergram in Figure 12 indicates that the growth rate of Quidnipagus is negatively correlated to initial ring size. Comparing the results of a regression analysis of growth rates on initial size and growth rates

on initial number of rings, I found that the initial size of the valve gives the best fit to the regression equation. As a result I cannot determine to what extent initial age has an effect on the variability of growth rates within a size class of Quidnipagus.

The rate of growth of Q. palatum is not significantly influenced by water depth or distance from shore. This is in contrast to previously reported results in the literature. Water depth was found by Fox and Coe (1943) to be an important growth determining factor for suspension-feeding mussels since organisms exposed at low tide are unable to feed. Similarly, Newcombe (1936) reported that individuals of the species Mya arenaria grew at a faster rate in deeper water, and Mercenaria mercenaria added more CaCO_3 in a subtidal habitat than in an intertidal region of the same beach (Pannella and MacClintock, 1968).

If the rate of growth is controlled by a density dependent variable such as food, then the growth rate should be inversely proportional to the population density. Holme (1950) found individuals of the tellinid deposit feeder Tellina tenuis uniformly distributed. When feeding, the tellin's long siphon describes a circular area on the sea floor in which only that Tellina individual may live. In this study I found no regularity of the Quidnipagus distribution and no significant relationship between the growth rate of Quidnipagus and the population density of Quidnipagus. I do not see any evidence to believe that Quidnipagus is food-limited.

Growth rates of Quidnipagus were, however, significantly influenced by the cage. Deposit feeding bivalves such as Quidnipagus depend upon detrital matter settling within reach of their extended flexible inhalent siphons. A mesh cage restricting the amount of detritus available

for the bivalves to eat could explain decreased growth rates inside the cage. This is unfortunate, because caging is an otherwise useful method of experimentation in the field. Sadykhova (1969) used experimental cages to study the growth rates of Mytilus grayanus Dunker. Because the large mesh (4 cm x 4 cm) of the cage did not become fouled, it was assumed that the cage did not affect the growth rate of the mussels inside. This should have been tested. Although the larger mesh size of Sadykhova's cage would be less likely to interfere with feeding, it would not serve its purpose as a barrier to the small predators such as Natica which I wanted to exclude,

The fact that all clams placed inside cages and fences were obtained in the vicinity of station D in Alupang Cove may have influenced some of the growth data. It may have been that clams grew faster in Alupang Cove than in Pago Bay because the Alupang population is better adapted to living in Alupang Cove. The station with the second greatest growth rate of Quidnipagus is at station D (Table 2a), where the growth rate is significantly different from growth rates at stations B, C, or E (Table 3a). Hence, we must be cautious when comparing growth data from Alupang Cove with growth data from Pago Bay, since all clams were originally obtained from Alupang Cove. Finally, handling and marking the clams may have disrupted their growth rates (Wilber and Owens, 1964; Loosanoff and Nomejko, 1955). A clear disturbance ring adjacent to the notched shell margin could be seen on many valves (Fig. 16). Since a disturbance is formed as a result of growth cessation, the growth rates given in this paper are not maximum values. All clams were subjected to the same disturbances so the effects of growth checks should have similar effects on the clams of the same size class, and the results

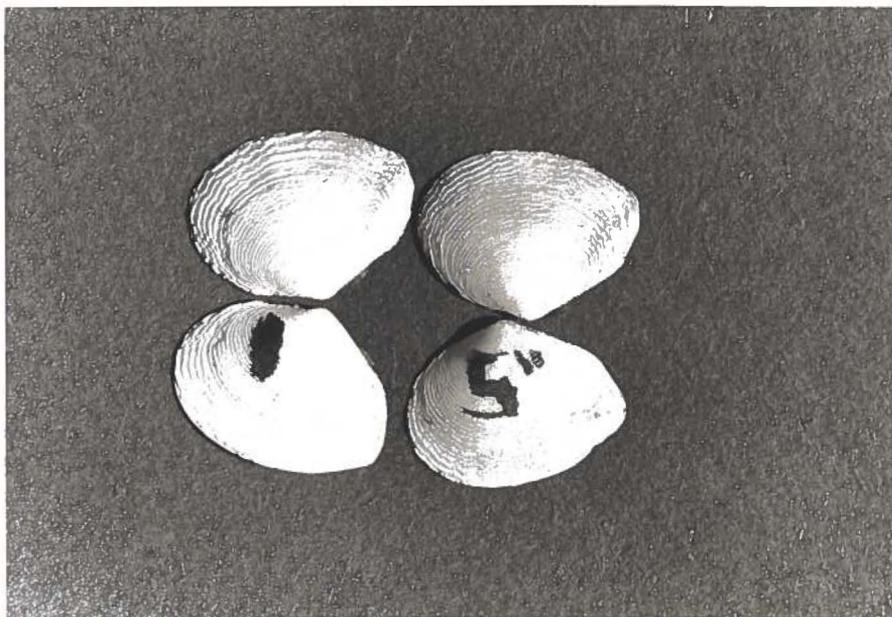


Fig. 16. Photograph showing disturbance ring near notch in shell.

therefore should be valid for comparing growth rates of Q. palatum in this experiment.

The seagrass bed in Pago Bay is the most productive area for Quidnipagus that I found on Guam. Analysis of the structure of the established population of Quidnipagus in Pago Bay (Fig. 6) suggests that there are no distinct age groups. This may indicate that breeding occurs continuously throughout the year, and that recruitment from year to year is relatively constant. This is in contrast to the Alupang Cove population where the age groups shown within the size frequency histogram suggest fluctuations in recruitment.

It is unlikely that food availability is responsible for the larger standing crop of Quidnipagus in Pago Bay. If more detrital food were present in Pago Bay, then experimental clams growing in Pago Bay should have grown faster. However, in this study experimental clams of the same size class grew significantly faster in Alupang Cove.

Thorson (1966) listed the types of substrate as one of the factors necessary for benthic larval settlement. The substrate in Pago Bay is considerably more coarse than in Alupang Cove. Working 600 m north of the Alupang Cove transect, Day (unpublished data) found that the population density of Quidnipagus did not vary significantly even though the median grain size of the sediments varied from 0.258 mm to 0.613 mm. Therefore it is unlikely that the population differences between Alupang Cove and Pago Bay can be attributed to the grain size of the sediments.

Naticid drill holes in the empty valves of Quidnipagus indicate a higher rate of predation by Natica sp. in Pago Bay (4.6%) than in Alupang Cove (2.25%). This suggests that naticid predators may not be responsible for the smaller standing crop of Quidnipagus in Alupang Cove.

However, it is difficult to ascertain the effects that predator species other than naticids have on Quidnipagus populations. It is possible that the cobbles covered by the network of Enhalus roots in Pago Bay make a formidable barrier to predators such as crustaceans and fish.

Rates of naticid predation on Quidnipagus individuals inside fences was also low. The fences may have prevented naticids from entering and attacking the prey species. The predator Natica gualtieriana moves in a burrow approximately 1 cm below the surface of the sediments. When the fences were put into place, the fence top was driven below the surface so that it could not be seen. Although it is possible that some deeper burrowing gastropods may have been excluded by the fence, I doubt that N. gualtieriana would be excluded by the fence.

Since predation rates are greater on smaller size classes, the larger sized individuals of Q. palatum inside the fences may not have been prey choices for the naticids. Furthermore both laboratory results and field results indicate that smaller bivalves are killed by naticids before larger individuals are killed. Jackson (1972) found similar results in Jamaica, where greater drill predation on smaller individuals than on adults of larger species was noted.

Young stages of invertebrate predators are extremely voracious, often consuming about 25% of their living body weight per day (Thorson, 1960). These juvenile invertebrates are not only more numerous than their parents, but they also prey on smaller size classes of the bivalve population. Large clams offered as prey species may have attained a refuge in size from naticid predators.

Predation on Quidnipagus may be low because naticid drills prefer other bivalves. Although Jackson did not notice any bivalve species

preference by Caribbean naticids, the field data from the present study indicate a different situation. A greater percentage of Ctena divergens valves was found drilled than the valves of any other species. Preliminary laboratory results also reveal that Natica gualtieriana shows a significant preference in prey selection. Interestingly, Ctena divergens was not the first or second prey choice of N. gualtieriana. This may indicate that a different species of the genus Natica was selectively preying upon C. divergens. This also implies that Quidnipagus may not have been the proper food choice for predators other than N. gualtieriana.

Finally predators other than gastropods may have removed clams from inside fences. Jackson (1972) found increased predation and greater predator diversity in deeper water. Similarly, I noted that more clams were missing from fences in deeper water, and that fish and decapods more frequently inhabit portions of the transect in deeper water. The presence of Quidnipagus in the stomach of a ray caught in the Maldives (J. Taylor, British Museum, London, personal communication) suggests that other predator species are capable of removing Quidnipagus from the fences.

Low recruitment rates or periodic catastrophes may have more bearing on the present population than predation. Although numerous tropical organisms such as Quidnipagus breed throughout the year, very few juveniles of Quidnipagus were collected in Pago Bay or Alupang Cove. This may be due to the fact that pelagic larvae produced by bottom invertebrates have a very hazardous existence. Proper food, temperature, salinity, and substrate conditions must be met before settlement will take place (Thorson, 1966). Accordingly, Yamaguchi (1973) found it

difficult to explain how larvae of coastal animals can maintain positions close to shore until the time of settlement.

In a short span of time, a natural catastrophe can devastate entire populations of reef animals. Reef-flat populations can also be depleted by several years of continuously poor recruitment. Typhoons are the most common type of local catastrophes affecting Guam. Excessively high tides and strong beach erosion caused by typhoons may remove considerable portions of the sediment habitat (Randall and Eldredge, in press). A second, less frequent, type of natural catastrophe affecting reef-flat organisms is the phenomenon of sea-level depression. The latest occurrence of such a sea-level fluctuation on Guam was in 1972 when a massive reef kill was associated with the extreme low tides occurring over a two-week period (Yamaguchi, in press).

The results of this study may lead to the following conclusions for fisheries. Q. palatum is the most abundant infaunal reef-flat bivalve on Guam. Because Q. palatum grows well on Guam and it is edible, it should be considered as a species with fisheries potential. Larger individuals of the species Q. palatum do not appear to be heavily preyed upon. Perhaps smaller members of the species Q. palatum should be reared in a predator free environment until such a size is reached that the effects of predation will be minimal. If few predators are eating Q. palatum, then harvesting mature members of the species of Q. palatum should not be altering the natural environment by taking food away from predators.

The method of growing bivalves in submerged cages did affect bivalve growth. The purpose of the cage was to maintain the clams in one spot, and to keep predators out. For these tasks the cage was

satisfactory. However, the rate of bivalve growth in cages was significantly less than the rate of bivalve growth in fences. Therefore, one should be cautious when interpreting growth data derived from caged marine populations.

As a result of this study I have found that the growth rates of Quidnipagus individuals varied considerably with regards to initial size and beach location. Growth rates of smaller size classes of Quidnipagus varied more than larger size classes. Growth rates of clams inside experimental cages were significantly lower than growth rates of clams inside fences. In addition, the smaller sized clams added more shell rings than larger clams. I found that the growth rings of Quidnipagus are not correlated with periodic phenomena such as spring tides or lunar cycles. Consequently, growth rings cannot be used to determine the clam's age.

Predation is greatest on Quidnipagus individuals smaller than 1.5 cm. However, it does not appear that adults of the species are predator limited. The remains of drilled valves suggest that bivalve predators show a preference for clams other than Quidnipagus. Because of the apparent minimal rate of predation on larger Quidnipagus individuals, the number of mature Quidnipagus in a population may be more strongly influenced by natural catastrophes than by predators. Therefore, commercially harvesting adult Quidnipagus should not greatly alter the reef-flat food web.

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