AN ABSTRACT OF THE THESIS OF Thomas L. Smalley for the Master of Science in Biology presented August 12, 1981.

Title: The distribution and abundance of *Nerita plicata* in a tropical, rocky intertidal habitat.

Approved: Lucius G. Eldredge

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On Guam, the herbivorous gastropod *Nerita plicata* is one of the most common and widely distributed organisms of the high rocky intertidal habitat. This species is commonly found on windward and leeward shores and occurs in the greatest abundance on semiprotected horizontal shores. Distribution patterns within and between shores, however, are patchy.

Although *N. plicata* exhibited a clumped dispersion pattern at Ylig Bay, daily distribution patterns are constantly in a state of flux in relation to the tidal cycle. At high tide individuals aggregate immediately above the water line, in the littoral fringe, whereas at low tide they occupy a relatively narrow zone above the water line in the high intertidal zone.

Furthermore, distribution and abundance of *N. plicata* varied significantly along the shore in relation to structural complexity as well as over time in relation to daily and seasonal variation in meteorological and sea conditions.

Reproductive aspects such as structure of the egg capsule and position of capsule deposition on the shore in relation to substrate topography and physical factors are similar to those described for other members of the family. Sex ratios did not deviate from the expected 1:1 ratio for the four smallest size classes (≤5.0, 5.1-10.0, 10.1-15.0, 15.1-20.0 mm). The largest size class (≥20.1 mm), however, differed significantly from the expected ratio in favor of males (3.1:1).

Growth rate of *N. plicata* varied considerably among individuals as well as within an individual over a number of months. A significant negative correlation existed, however, between growth rate and initial shell diameter.

The results of field observations and experiments (transplanting with and without predator-exclusion cages) suggest that predation may play a less significant role in setting the lower limit of high intertidal gastropods than has been previously suspected.

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Chuck –
Thanks for everything.
Your comments, suggestions and
interest are greatly appreciated.
You really turned me on to ecology.
Again, Thanks.
Tom

THE DISTRIBUTION AND ABUNDANCE OF *NERITA PLICATA* IN A TROPICAL, ROCKY INTERTIDAL HABITAT

by

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INTRODUCTION

The purpose of this study was to determine the effects of predation in structuring a tropical rocky intertidal population of the motile herbivorous gastropod *Nerita plicata* Linnaeus, 1758.

Among the eight families of gastropods occurring in tropical rocky high intertidal assemblages, the Neritidae are the most diversified, widespread, and numerous in relative number of species, in the Indo-Malaysian region (Vermeij, 1974). In a review of the literature, it was therefore surprising to find little work on the autecology of the neritids. Shore level distribution of intertidal gastropods, including the neritids, has been described on tropical rocky shores in the Capricorn and Bunker Island Groups of the Great Barrier Reef (Endean et al., 1956), in the British Solomon Islands (Morton and Challis, 1969; and Morton, 1973), at Aldabra Atoll, Indian Ocean (Taylor, 1971), at Ceylon (Atapattu, 1972), at Cocos Island off Central America (Bakus, 1975), and at Dar es Salaam on the East African coast (Hartnoll, 1975).

Some aspects of the biology, general ecology and population biology of neritids have been presented. Adegoke et al. (1969) discussed aspects of the biology and population dynamics of *Neritina glabrata* and *Neritina* n. sp., and the effects of the environment on the shell shape of N. violacea were presented by Murty and Balaparameswara (1978). Behavioral studies comprise much of the ecological literature available for the family. Much of this has dealt with maintaining shore level position and orientation (Warburton, 1973; Chelazzi and Vannini, 1976, 1980; and Vannini and Chelazzi, 1978). In addition Suzuki (1935) discussed tropisms of Nerita japonica and Hoffman et al. (1978) reported on the flight response of three species of nerites to predatory gastropods.

Studies specifically addressing the ecology of N. plicata are limited. Zann (1973) discussed the "circatidal" rhythmicity of four species of Neritidae, including N. plicata, in relation to vertical zonation. Hughes (1971) presented patterns of zonation, population size-frequency structure, and biomass of five species, including N. plicata, at Aldabra Atoll, Indian Ocean.

Life history aspects of an animal are critical to understanding the animal's role in nature as well as its distribution and abundance. The following life history aspects were therefore investigated: reproduction, growth, and behavior. This study contributes to the knowledge of one of the major component species of tropical rocky intertidal shores.

METHODS

The distribution and abundance of a dense population of Nerita plicata was studied from March 1980 through June 1981. Although the population was atypical in density and uninterrupted spread on the shore, it fulfilled the two most important criteria for choosing a natural population for study--ease of measurement and ease of experimental manipulation (Connell, 1970). In addition to the major study area, qualitative observations of the distribution and abundance of N. plicata were conducted at a number of other sites on the windward and leeward coasts of Guam to obtain information on island-wide (between habitat) patterns of distribution and abundance.

Study Area

The major portion of this study was conducted in Ylig Bay south of Tagachan Point on the windward coast of Guam. Randall and Eldredge (1976) have characterized this coastline (between the Ylig River and Tagachan Point) as one having steep slopes and cliffs composed of reef facies of the Mariana limestone and Agana argillaceous member.

A 100-m permanent transect area was established parallel to the shore (running NE to SW) in the littoral fringe, approximately 400 m south of Tagachan Point, within the limits of a dense population of N. plicata. The local physiography of the transect area is low lying pitted and pinnacled limestone gently sloping up to a vertical height of approximately 0.3 to 0.6 m above the reef pavement. A gradient in structural complexity of the habitat exists along the transect, increasing towards the NE end.

Field Methods

The within-habitat distribution and abundance of *N. plicata* were determined from analysis of 1/16 m^2 quadrats placed at 0.5 meter intervals along permanent transects perpendicular to the shore. A total of nine permanent-perpendicular transects were positioned in a stratified-random fashion at 10-m intervals along the 100-m transect area running parallel to the shore. Abundance was recorded as the absolute number of individuals sampled.

The upper limit of each transect was placed at the seaward margin of a zone of *Pemphis acidula*, whereas the lower limit was determined by the water line at the time of the counts. The length of the transects ranged from approximately 2.8 m, during the highest high water, to 10.0 m, at the lowest low water.

Transects were run twice monthly for one year, at high and low tides, in order to determine short-term (daily and weekly) and long-term (one year) patterns of distribution and abundance. Meteorological conditions as well as qualitative observations (e.g., sea conditions, extent of splash above the water line, occurrence of egg capsules, etc.) were recorded on each sample date.

In each quadrat all N. plicata were counted and assigned to one of five size classes (≤5.0 mm, 5.1-10.0 mm, 10.1-15.0 mm, 15.1-20.0 mm and ≥20.1 mm) by a measure of shell length (from the apex to the farthest point away on the anterior outer lip). This measurement led to some error for large individuals, particularly for those greater than 17 mm, because the apex was often worn. This resulted in a greater number of individuals being assigned to the 15.1-20.0 mm size class and fewer to the ≥20.1 mm size class.

Size frequency distributions were constructed from the transect data. Evidence of recruitment from settlement was inferred from the resulting size frequency distributions, whereas sex ratio was determined by collecting individuals at random from a number of quadrats. Unlike some other nerites, N. plicata cannot be sexed externally by the observation of the penis in the mantle cavity. Animals were therefore returned to the laboratory and the shell broken so that the gonads could be examined. For each individual shell length and diameter were measured.

Individual growth rates and migratory patterns were obtained from a tagging study. A total of 115 individuals, with representatives from each size class, was tagged on four occasions over a period of 3.5 months. The initial size and position on the shore were recorded for each individual and subsequent size and position recorded upon recapture. Tagging involved filing smooth a small area of the body whorl at the anterior edge of the columellar pad. A number was then inscribed on the shell with black, waterproof India ink. The ink was allowed to dry (about 3 min.) and was then covered with a drop of cyanoacrylate adhesive. This hardened within 3-5 min. at which time the snail was returned to its original position on the shore. This method was adequate, at least for the duration of the study, as only a few individuals lost their tags and a total recovery of 59.1 percent was obtained.

Predation upon *N. plicata* was studied in the field by both day and night observations and experimental methods. The incidence of shell repair was calculated on a number of occasions to obtain an indication of the intensity of predation on the population. Experimental field evaluation of the significance of predation in determining the lower limit of the distribution of *N. plicata* was carried out by transplanting snails without predator-exclusion cages and transplanting with exclusion cages.

Replicate predator exclusion cages were placed at three levels on the shore--littoral fringe (control, for a cage effect), mid-intertidal (experimental), and subtidal (experimental)--in order to determine the role of predation in limiting the distribution of *N. plicata* as well as resource availability at these levels. Experimental cages, 25 x 25 x 10 cm, were constructed of black plastic 1/4" mesh with a 10 to 15 cm apron. Control cages were form fitted to the substrate to enclose an area of approximately 625 cm^2 on the raised pitted, pinnacled limestone of the littoral fringe. All cages were attached by sinking lead lag shields into the substrate and screwing down with 1/4" x 1 1/2" zinc coated lag bolts. Gaps between the substrate and cage were filled in with a quick setting marine epoxy (Sea Goin' Poxy Putty). Twelve N. plicata of approximately 11.0 mm in length were placed in each cage. Growth and mortality were assessed every 2-3 weeks for 4 months. Density was maintained at 12 individuals per cage throughout the study by replacing dead individuals with live individuals of approximately the same shell length. Replacements were not included in the statistical analysis of growth increments of the caged animals.

To obtain information on predation intensity along the gradient from the mid-intertidal to the littoral fringe, a transplant experiment was conducted in replicate. On each occasion one hundred N. plicata, 25 individuals from each of the four largest size classes, were transplanted to an area of raised pitted limestone within 30 m of the reef margin. This limestone patch is almost completely exposed on the lowest tides and completely submerged on the highest tides. It thus falls within the zone typically considered the mid-intertidal. The transplant area was searched each day and the experiment terminated when no live individuals could be found. All dead individuals and shell fragments that could be found were collected and returned to the laboratory whereas live individuals that had moved away from the release point were returned to this point.

Laboratory Methods

In order to evaluate the predation potential and mode of attack, laboratory observations and experiments were conducted on a number of known predators (from field observations) and suspected predators. In addition the response of *N. plicata* to these predators was noted.

The predatory gastropods *Muricodrupa fenestrata* (5 specimens ranging from 30.2 to 37.2 mm in length) and *Thais aculeata* (1 specimen, 51.7 mm in length) as well as the xanthid crab, *Lydia annulipes* (4 specimens, 2 male and 2 female, ranging from 28.5 to 36.7 mm in carapace width), were collected from the field site. These individuals were returned to the laboratory and isolated in 25-gallon aquarium compartments, separated by a fine vinyl mesh. All predators were initially starved for one week. Compartments were provided with a limestone rock, a water depth of approximately 3 to 4 cm, aeration, and were given a cleaning and water change every seven to ten days.

One measured *N. plicata* was introduced into each compartment and was checked daily. Predators which fed were starved for two to four days. If *N. plicata* had crawled off the bottom, out of reach of the predator, it was returned to the bottom. Prey that were not successfully attacked within four days were removed and replaced by a new individual.

An attempt was made to obtain information on the reproductive biology and development of *N. plicata* but this met with little success. In August 1980 egg capsules were brought to the laboratory for examination of eggs and larvae. Subsequently laboratory experiments were set up to determine the relationship between adult size and number and size of egg capsules produced, number of eggs per capsule, and larvae per capsule as well as to follow development of eggs and larvae to hatching. Although the success of the laboratory investigations was less than adequate for statistical analysis, some descriptive information on eggs and larvae were obtained.

Individuals of *N. plicata*, measured to the nearest mm in length and diameter, were isolated in aquaria provided with limestone as a substrate, water at a depth of approximately 4 cm, and aeration. The number and size of egg capsules were recorded if present. Each individual was allowed 4 days to produce capsules at which time the sex of each individual was determined and the experiment terminated. Several egg capsules were examined every 2-3 days after deposition to gain information on development. Artificially hatched larvae were maintained in petri dishes with filtered seawater and approximately 100 μg/l penicillin.

RESULTS

Distribution and Abundance

Nerita plicata is widely distributed on Guam, being found on most rocky shores. It occurs in greatest abundance on horizontal shores of wide, windward reef flats (semi-protected shorelines), such as Ylig Bay. Lowest densities were seen on highly protected shores (e.g., wide leeward reef flats), or extremely exposed shores (e.g., vertical cliffs along windward and leeward benches), as well as on shores having low structural complexity. Distribution patterns, both within (local) and between (island-wide) habitats, are patchy.

At the study site, distribution and abundance varied significantly within the habitat, both among transects and among months (Table 1). Among the transects differences are attributed to variability in structural complexity of the shore (Figure 1), whereas monthly differences are attributed to seasonal as well as daily variability in weather and sea conditions. Variance to mean ratios for high and low water abundance were significantly greater than 1.0 ($p<0.005$) indicating a clumped dispersion pattern. N. plicata aggregate immediately above the water line, in the littoral fringe, during high tide. In contrast during low tide they occupy a relatively narrow zone above the water line, in the

Table 1. Results of two-way analysis of variance (Model I) without replication for the effects of position along the shore and time of year on abundance of *Nerita plicata* at Ylig Bay. The analysis was performed on the common logarithmic transformation of the raw data.

	Source of Variation		Sum of Squares	Mean Square	F_s	p
Total Population	Between transects	8	10.8863	1.3608	28.953	<0.001
	Between months	10	1.2094	0.1209	2.572	<0.05
	Within groups (error)	80	3.7602	0.047		
	Total	98				
Individuals ≤ 5.0 mm	Between transects	8	1.5788	0.1974	2.449	<0.05
	Between months	10	3.7673	0.3767	4.674	<0.001
	Within groups (error)	80	6.4497	0.0806		
	Total	98				

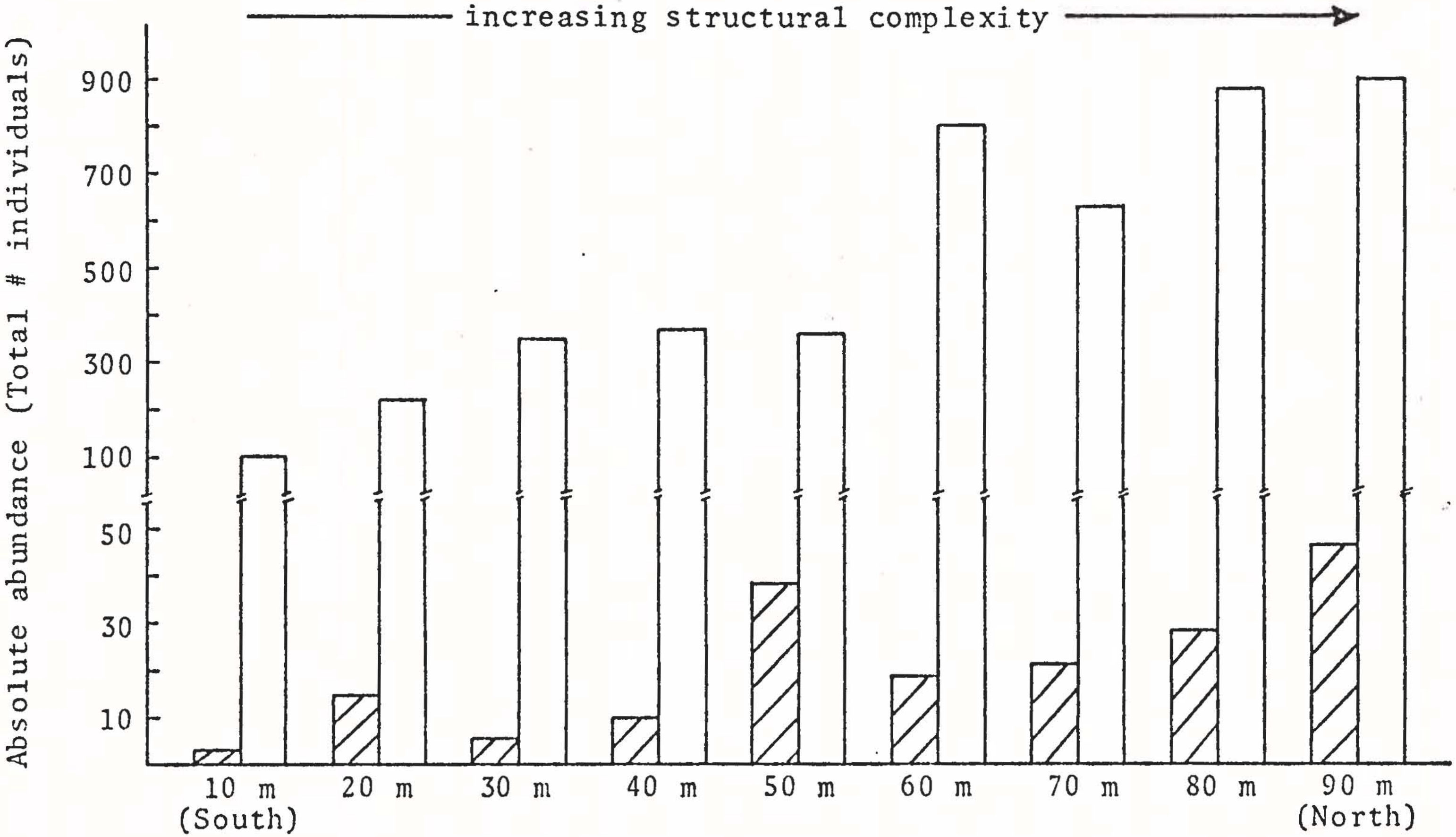

Figure 1. Relationship between absolute abundance of *Nerita plicata* and structural complexity of the shore. Number of individuals on each transect are pooled abundances for the transect for one year. Hatched bar represents ≤5.0 mm size class and unhatched bar represents all size classes pooled (≤5.0 mm to ≥20.1 mm).

high intertidal zone. Although vertical distribution on the shore is constantly in a state of flux, no significant difference ($t_s = 0.311$, d.f. = 9, $p<0.05$) was noted between abundance at mean high water and at mean low water within months (high water: $\bar{Y} = 437$, sd = 47.5, n = 10; low water: $\bar{Y} = 432$, sd = 57.8, n = 10).

The daily distribution patterns (as height on the shore) are related to the tidal cycle. Observations reveal that *N. plicata* migrate daily, moving down the shore on ebb tides. Although daily mass migrations of the population occurred, juveniles (<12.0 mm) and newly settled individuals (<5.0 mm) were not observed to migrate. Instead they commonly aggregated in crevices and pits, that provide shade and moisture, at the limestone-reef flat interface (high intertidal).

Individual daily vertical excursions (feeding migrations) varied in distance and reached a maximum of 15 to 20 m for some individuals. No homing behavior was observed. The lateral component of vertical migrations however was significantly larger ($t_s = 2.771$, d.f. = 109, $p<0.01$) for long term (>30 days) movements ($\bar{Y} = 9.5$, sd = 14.3, n = 65) versus short term (≤30 days) movements ($\bar{Y} = 3.1$, sd = 6.4, n = 46).

Reproduction

The sex ratio of *N. plicata* at the study site was determined from examination of 319 individuals. The male to female ratio of 1.3:1 did not differ significantly from the expected 1:1 ratio ($X^2 = 2.429$, $p<0.05$). Further analysis of mature specimens (≥ 10.1 mm), revealed no deviation from the expected 1:1 ratio in the 10.1-15.0 mm and 15.1-20.0 mm size classes (Table 2). The 3.1:1 sex ratio in favor of males among individuals ≥ 20.1 mm however was significantly different from the expected 1:1 ratio ($X^2 = 6.821$, $p<0.01$) (Table 2).

Gonadal development occurs in individuals between 12.0 and 14.0 mm in shell length. Within this range only 27.7 percent of examined individuals were immature. In addition predator-exclusion cage residents, ranging from 12.0 to 14.0 mm in shell length, deposited egg capsules within the cages. These observations, in conjunction with the results of the von Bertalanffy growth equation (see Figure 3), suggest that sexual maturity is attained at an age of 10 to 12 months.

Laboratory experiments to determine whether there exists a relationship between adult size, and number and size of egg capsules, as well as number of eggs or larvae per capsule were inconclusive. Of the 36 individuals examined (during May-June 1981) only 16 were female, of which 7 deposited egg capsules. The total number of egg capsules deposited per individual ranged from 1 to 22 during the four days each individual was observed.

Table 2. Results of chi-square analysis of sex ratio by size class.

Size Class (Length in mm)	Sex Ratio	Observed M	Observed F	Expected	df	X_2	p
10.1 - 15.0	1.1:1	30	28	29	1	0.34	>0.05
15.1 - 20.0	1.1:1	85	76	81	1	0.252	>0.05
≥20.1	3.1:1	37	12	25	1	6.821	<0.01

In the field, egg capsules of N. plicata were most abundant from May to July but were present, in very low abundance, during the remainder of the year. Laboratory-maintained individuals were also observed to produce egg capsules throughout the year. Field observations on the distribution of egg capsules revealed a wide range in the location of deposition on the shore. Capsules were observed on the substrate between the highest high water and the lowest low water. The greatest numbers of capsules, however, occurred in a relatively narrow band between approximate mean high water spring and mean high water neap. The majority of capsules were deposited at the water line, on the sides of small pools formed in the raised pitted and pinnacled limestone. Many of these pools provided shade and contained water between tides.

Freshly deposited egg capsules were easily recognizable in the field by their ivory-white color which gradually became a straw color within 48-56 hours (from laboratory observations). The capsule was slightly domed and ellipsoid in shape with dimensions ranging from 1.2 by 1.4 mm to 1.5 to 2.2 mm. A mean number of 76 eggs or live larvae (sd = 19, range = 30 to 113) was found in the egg capsules.

Trochophore and veliger larvae were examined from artificially hatched egg capsules. Two groups of trochophore larvae, the first developing for 7 days, the second for 9 days, in the egg capsule were indistinguishable in development. These individuals were composed of two unequal lobes.

The larger lobe was translucent yellow and contained an aggregation of 3 to 5 large oil globules and numerous oil droplets whereas the smaller lobe was unpigmented. On the larger lobe, opposite the position of the small lobe, occurs a constriction surrounded by a circlet of beating cilia. The veliger larvae examined belonged to two stages of development. Within any given capsule all larvae were at the same stage. In the first of these two stages, the velum is bi-lobed and colorless, with cilia which became actively beating within 5 minutes of removal of the larvae from the egg capsule. A prominent black eyespot was present on each lobe of the velum. The larval shell was well formed, contained considerable yolk material, and was operculate. In the following stage the larvae had not changed in any noticeable way except for the development of a red patch, in a lateral position, on each side of the larval foot. Further larval development was not examined as no other stages were found in artificially hatched capsules, and due to the difficulty in maintaining these live veligers for more than 3 or 4 days in the laboratory.

From March 1980 to June 1981 only 11 copulating pairs of N. plicata were observed in the field, all during daylight in June 1981.

Monthly variations in size frequency distributions reflected periods of settlement and subsequent recruitment to larger size classes. Although settlement occurred year round it had a strong seasonal component, peaking in July and August.

Growth

Results indicate a considerable variation in growth rate among individuals of the same size. Furthermore, growth rate varied considerably within individuals over a number of months. In spite of this variability, a significant negative correlation ($r = -0.72$, $p<0.01$) existed between growth rate and initial shell diameter (Figure 2).

The theoretical maximum shell size was estimated to be 22.4 mm in diameter (from Figure 2). This size compares favorably with the observed maximum size of 23.8 mm.

Since sex ratio analysis showed an excess of males for individuals $\geq$20.1 mm, growth rate information was partitioned for males and females to examine differences in their growth rates as well as their predicted maximum sizes. Unfortunately, not enough information was obtained from the tagging study to predict maximum size or to generate a reliable regression and correlation coefficient for growth rate on initial shell size for males. As a result, sexual dimorphism in growth rate and maximum size could not be ascertained. Females showed a significant negative correlation ($r = -0.88$, $p<0.01$), as expected, between growth rate

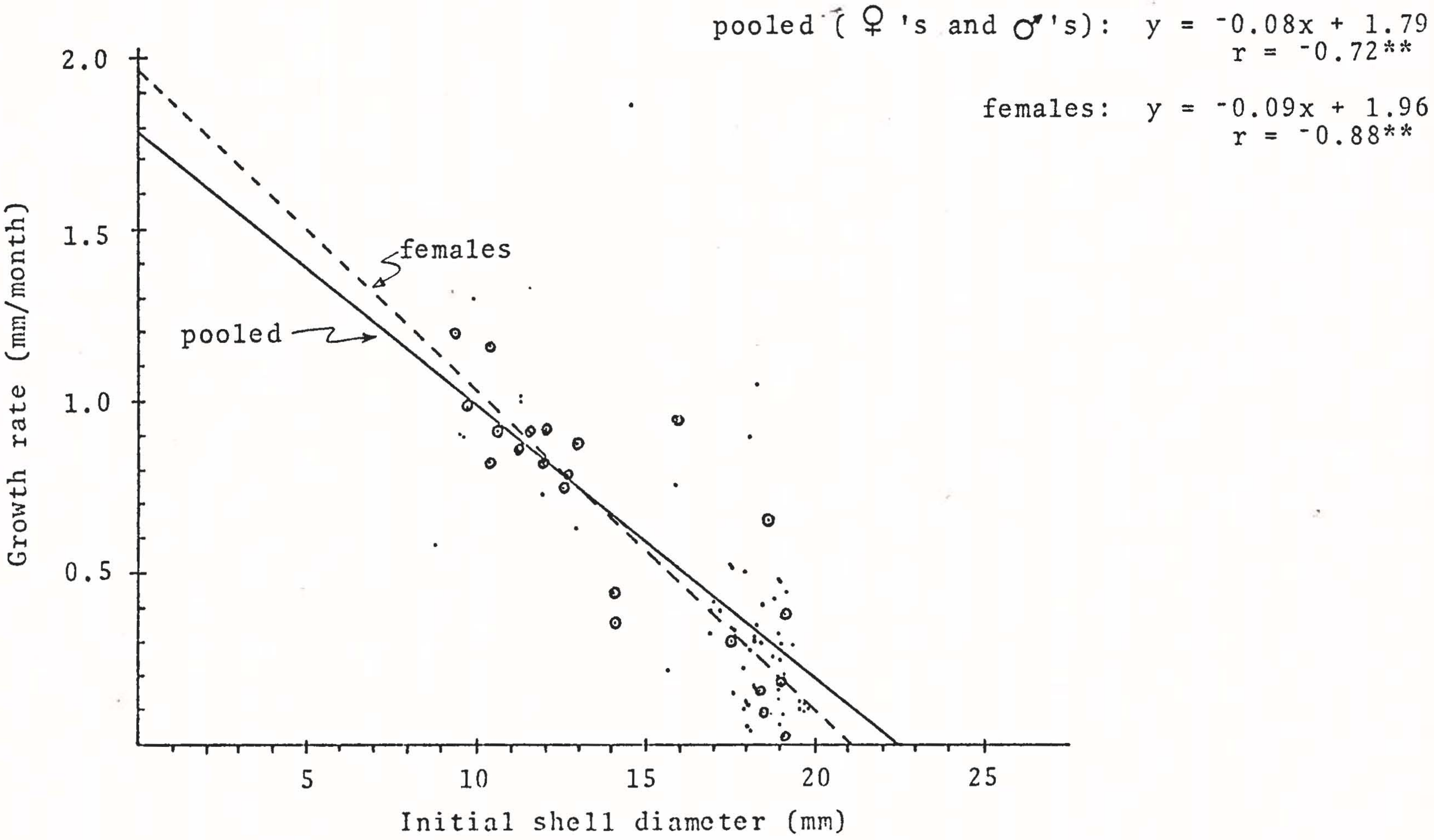

Figure 2. Growth rate of *Nerita plicata* in relation to shell diameter and maximum size. Note: ** significant at $p<0.01$.

and initial size. Their predicted maximum size (21.1 mm, from Figure 2) also compared favorably with the observed maximum female size of 22.4 mm.

An estimated maximum age of almost 4 years was obtained for *N. plicata* at 95% of its theoretical maximum size from a fit of the von Bertalanffy equation (Figure 3) to the growth data. The von Bertalanffy growth model, which expresses growth on the basis of theoretical physiological relationships, presumes that the animal exhibits isometric growth and maintains a constant specific gravity. The mathematical representation of the von Bertalanffy growth equation is $L_t = L_\infty[1-e^{-k(t-t_o)}]$ where L_t is length at time t, t is time, L_∞ is a theoretical maximum length, k is the Brody growth coefficient, and t_o is the theoretical time at which length is zero. In this study it was assumed that t_o equals zero.

Predation

Predation upon *N. plicata* was never observed in the littoral fringe. Two xanthid crabs, however, were observed in this zone on a number of occasions. The larger species, *Eriphia sebana*, is a known predator upon intertidal gastropods and has been observed in the field manipulating *N. plicata* in its claws (L. G. Eldredge, personal communication).

The smaller species, *Lydia annulipes*, was observed only once in the littoral fringe, among rubble on sand, in a damp depression. *L. annulipes*, ranging in size from <20.0

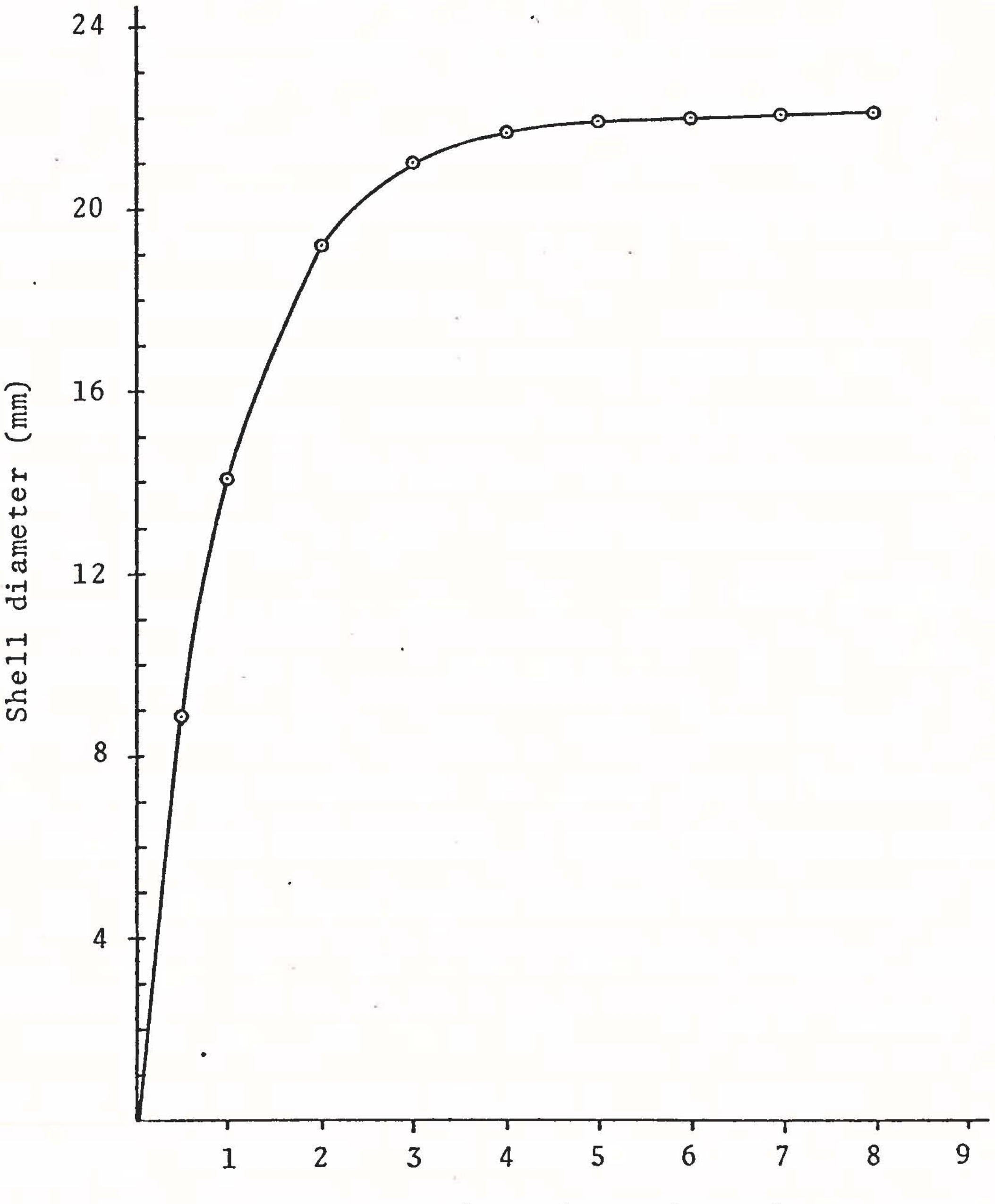

Figure 3. Growth of Nerita plicata represented by the von Bertalanffy growth curve. The growth equation for N. plicata at Ylig Bay had the following form: $L_t = 22.4[1-e^{-1.015(t)}]$.

mm to >40.00 mm carapace width, was observed on a number of occasions in small depressions containing rubble as well as fresh shell fragments of *N. plicata*, at the interface between the reef flat pavement and the raised limestone (= high intertidal). Despite the relatively small size of this crab, the master claw (crusher claw) is similar in structure to the master claw of other xanthid crabs known to feed upon shelled prey, except that a large lateral tooth projects away from the midline toward the outer face of the movable finger. A number of other crustaceans were commonly observed in this habitat, although no evidence of predatory activity was noted. These included three, or four species of grapsoid crab, the largest being *Grapsus tenuicrustatus*, as well as four species of terrestrial hermit crab belonging to the family Coenobitidae (*Birgus latro*, *Coenobita brevimanus*, *C. rugosa*, and *C. perlatus*).

Actual field observations of predation upon *N. plicata* were restricted to intertidal predatory shell drilling gastropods of the family Muricidae. The most commonly observed member of this family, as well as the most commonly observed species actively feeding upon *N. plicata*, was *Muricodrupa fenestrata*. The distribution of *M. fenestrata*, which occurs in shaded areas, is restricted to the transition between the reef flat pavement and raised limestone (high intertidal). Although *M. fenestrata* is believed to drill its prey, evidence of this mode of attack was only observed once in the field. In all other cases the mode of attack was through the aperture. Individual M. fenestrata, actively feeding upon N. plicata in the field, ranged in size from approximately 30.0 mm to 38.0 mm in shell length, whereas prey items ranged from approximately 14.0 mm to 20.0 mm in shell length.

The large predatory gastropod Thais aculeata was observed only once above mean low water during the study. This individual, found under a large boulder at the interface between reef pavement and raised limestone (high intertidal), did not show any evidence of feeding activity. Another predatory gastropods observed was Morula anaxeres, a relatively small predator, generally observed to occur among rubble, in small depressions at the pavement-raised limestone interface. On one occasion M. anaxeres was observed feeding upon egg capsules of N. plicata by drilling through the top of the capsule. In the cluster of capsules observed, 28 to 63 capsules had needle-like holes drilled through them. These contained no fluid or eggs as was found in undrilled capsules in the cluster.

The incidence of shell repair, as a rough estimate of the intensity of predation upon the study population, was relatively low and exhibited little variation over time. Between March 1980 and May 1981 five estimates of the incidence of shell repair yielded a range of 3.5 to 6.7 percent.

Under field conditions no successful escape from a predator by N. plicata was observed. The only response

N. plicata exhibited was apertural closing by the operculum during feeding attempts of M. fenestrata.

Under laboratory conditions, four Lydia annulipes, 2 males (28.5 and 32.0 mm in carapace width) and 2 females (32.7 and 36.7 mm in carapace width), successfully attacked and fed upon N. plicata. Nerita plicata from 5.0 to 15.0 mm in length were offered to male L. annulipes, whereas female L. annulipes were offered prey to about 22.0 mm in length. The small and large male were successful to a size of 6.5 and 8.5 mm respectively. The larger male, however, was capable of damaging the outer lip of N. plicata to a length of 10.9 mm. Females had higher success rates and were able to take larger prey. The smaller female was successful to a prey size of 10.0 mm, whereas the larger female was successful with a 19.3 mm N. plicata. Male L. annulipes completely crushed the shells of prey upon which they were successful, leaving fragments of the body whorl and spire as well as the entire, cresent shaped, outer lip. Lethal damage inflicted by the larger females, however, was of two distinct types. Among smaller prey (<15.0 mm in shell length) the body whorl was crushed as was observed for males, whereas among larger prey (>15.0 mm) damage was similar except that in some cases the entire apertural area (outer lip and columellar region) was still intact. The second type of damage, seen only among the largest prey items, was a large gash on the dorsal side of the body whorl. This portion of the shell appears to be the weakest part and might possibly have been punctured by the large lateral tooth projecting from the crusher claw of L. annulipes. With subsequent enlargement of the puncture hole by the tooth, the soft parts may be extracted through the hole. These types of damage were observed in the field, although the puncture method is uncommon.

Under laboratory conditions, Muricodrupa fenestrata generally fed upon N. plicata in the same manner as noted in the field. Five isolated individuals, tested over a period of five weeks in the laboratory, showed very low feeding rates and fed exclusively in the typically observed manner (Table 3).

Evidence of drilling was noted in two N. plicata in a large holding tank containing approximately 100 nerites and 5 M. fenestrata. In one case M. fenestrata successfully fed, whereas in the other, N. plicata survived the attack. In addition, mortality in this laboratory population increased dramatically after introducing the five M. fenestrata. Before the addition of these five individuals to the holding tank, mortality had been relatively low (approximately 2 individuals/month). Within four days of introducing M. fenestrata however, 9 dead N. plicata were observed.

Nerita plicata introduced into compartments with predators (L. annulipes, M. fenestrata, and T. aculeata) consistently exhibited the same behavior in response to the predator. Within 5 to 15 minutes of being introduced,

Table 3. Summary of the results of laboratory predation upon *Nerita plicata* by *Muricodrupa fenestrata*.

M. fenestrata length (mm)	Size range of *N. plicata* width (mm)	Total No. prey offered	No. successful attacks	Feeding mode
30.2	14.5 - 20.5	8	1	through aperture
31.1	9.3 - 21.1	8	0	--
34.4	14.0 - 22.8	8	0	--
34.6	17.0 - 19.3	8	2	through aperture
37.2	13.9 - 20.5	8	0	--
Total		40	3	

N. plicata invariably moved up the wall of the tank. At no time during the study did any of the predatory gastropods move up the wall above the water level in the tank. Results of these laboratory observations are presented in Table 4. In control tanks under similar conditions, however, only 5 of 36 *N. plicata* were observed to move well above the water level in the tank (Table 4).

The results of replicate transplant experiments are presented in Table 5. In the two trials, of 8 and 12 days, mortalities were 42 and 63 percent respectively. Most of the dead individuals had been crushed.

In the transplant area a small population of *Thais aculeata* was observed. In the replicates, one and six dead undamaged *N. plicata* were collected. *T. aculeata* was observed actively feeding upon two of these individuals. As was observed for *M. fenestrata*, the mode of attack appeared to be through the aperture as no evidence of drilling was noted and the two actively feeding individuals were seen employing this method.

In the replicates, 58 and 37 percent of the individuals transplanted were unaccounted for by the end of the experiment.

Within the 5.1 to 10.0 mm size class no evidence of predation was noted, however, they represented the lowest number recovered. The highest observed predation intensity in the replicates occurred upon the 10.1 to 15.0 mm and 15.1 to 20.0 mm size classes (Table 5).

Table 4. Summary of the response of *Nerita plicata* to three predators under laboratory conditions.

			No. of Survivors	
	Total No. of prey offered	Total No. individuals surviving	>20 cm above the water line	≤1.0 cm above the water line
L. annulipes	18	9	8	1
M. fenestrata	40	37	32	5
T. aculeata	4	4	4	0
Total:	62	50	44	6
Controls	36	36	5	31

Table 5. Summary of the results of replicate, uncaged transplant experiments of *Nerita plicata* to the mid-intertidal zone.

Duration (days)	Size Class (mm)	n	Observed Mortality	Fate of Dead Individuals	
				Crushed	Undamaged
8	5.1 - 10.0	25	0	--	--
	10.1 - 15.0	25	10	10	0
	15.1 - 20.0	25	22	21	1
	>20.1	25	10	10	0
	Totals:	100	42	41	1
12	5.1 - 10.0	25	0	--	--
	10.1 - 15.0	25	22	22	0
	15.1 - 20.0	25	25	20	5
	>20.1	25	16	15	1
	Totals:	100	63	57	6

The frequency of escape by N. plicata from intertidal predators appears to be rather low. The combined results of both trials revealed only 2 of 50 individuals (from the ≥ 20.1 mm size class) which escaped initial attacks by crushing predators.

The results of the predator-exclusion cage experiments are presented in Tables 6, 7, and 8. A significantly faster ($F_s = 231.14$, $p<0.001$) growth rate was obtained in control cages (littoral fringe) than in experimental cages (intertidal and subtidal) (Table 6). The analysis of covariance of growth increment on initial size indicates the significant treatment effect is brought about by the shore-level position of the cages, independent of initial shell size. It should be noted however that the treatment effect seen may well have been a caging effect (sedimentation) rather than a shore-level effect. Although animals within control cages grew faster than in experimental cages, they grew significantly slower ($t_s = 7.992$, $p<0.001$) than uncaged animals (tagged) of the same size (Table 7).

Survival of caged individuals was significantly greater in control cages than in experimental cages ($X^2 = 6.70$, $p<0.01$) whereas between experimental treatments the magnitude of mortality was significantly higher ($X^2 = 3.99$, $p<0.05$) in subtidal cages than in intertidal cages (Table 8).

In the predator-exclusion caging experiment some inherent difficulties were encountered. Sedimentation, occurring in experimental cages, was somewhat greater in subtidal cages (25-30 mm/month) than in intertidal cages (10-15 mm/month). In addition, density within cages was high over a more extended period than that which occurs under natural conditions. Finally, cages prevented normal migratory movements.

Table 6. Results of analysis of covariance of growth increment on initial size for *Nerita plicata* in the predator-exclusion cage experiment.

	Source of Variation		Sum of Squares	Mean Square	F_s	p
All cages (controls and experimentals)	Treatments	10	25.708	2.571	51.42	<0.001
	Initial size (error)	40	1.985	0.050		
	Deviations about common line (total)	50	27.693			
All experimental	Treatments	6	0.131	0.022	0.780	>0.05
	Initial size (error)	22	0.611	0.028		
	Deviations about common line (total)	28	0.742			
Controls	Treatments	2	0.453	0.227	2.98	>0.05
	Initial size (error)	18	1.374	0.076		
	Deviations about common line (total)	20	1.827			
Controls (pooled) versus experimentals (pooled)	Treatments	2	24.963	12.482	231.14	<0.001
	Initial size (error)	48	2.569	0.054		
	Deviations about common line (total)	50				

Table 7. Comparison of shell diameter and growth rate of caged and uncaged *Nerita plicata* in the littoral fringe. Values are mean, $\bar{Y}$, ± standard deviation, s, and the number of individuals, (n).

	$\bar{Y} \pm s(n)$	df	t_s	p
Shell diameter (mm)				
Caged (controls)	11.8 ± 0.79(24)	32	0.626	>0.05
Uncaged (tagging study)	11.6 ± 0.82(10)			
Growth rate (mm/month)				
Caged (controls)	0.53 ± 0.11(22)	30	-7.992	<0.001
Uncaged (tagging study)	0.88 ± 0.12(10)			

Table 8. Results of chi-square analysis of mortality within predator exclusion cages. a.) Pooled mortality from control cages versus pooled mortality from all experimental cages. b.) Pooled mortality from intertidal treatment versus pooled mortality from subtidal treatment.

		Observed Mortality	Expected Mortality	df	X^2	p
a.	Controls	1	8	1	6.70	<0.01
	Experimental	23	16			
b.	Intertidal	5	11.5	1	3.99	<0.05
	Subtidal	18	11.5			

DISCUSSION

Although distribution and abundance patterns of Nerita plicata on Guam are patchy, they are widely distributed, being found on most rocky shores.

Horizontal shores of wide windward reef flats, such as Ylig Bay, appear to be the most favorable habitats. Of all shores examined, Ylig Bay had the highest absolute abundance. Lowest abundances were seen on highly protected shores, on extremely exposed shores as well as on shores of low structural complexity. Similarly, Hughes (1971) found N. plicata on very exposed to moderately sheltered shores at Aldabra Atoll.

Nerita plicata exhibited a clumped dispersion pattern as is common among other intertidal gastropods. Moulton (1962) described clumping behavior of intertidal Cerithium moniliferum as a behavioral response to increasing desiccation and temperatures during low tide, whereas Vannini and Chelazzi (1978) described scattering and clustering behavior exhibited by Nerita textilis on vertical surfaces as solutions to the problem of wave action.

At Guam, adult N. plicata (>13.0 mm) participate in daily mass feeding migrations moving out onto the reef flat pavement as the tide recedes and back onto the limestone as the tide comes in. Although similar migratory patterns have been noted for other neritids (Vannini and Chelazzi, 1978) they were not as distinct. In contrast to my observations, Zann (1973) did not mention large scale migratory patterns for N. plicata at Heron Island. Instead, he reported that N. plicata become active with the flooding tide and ceased activity as the substrate dried behind the receding water line. At Guam similar observations were made on semi-exposed vertical surfaces.

Zann (1973) suggested a geographic difference in activity patterns of some species of nerites. It may be more reasonable to attribute these differences to physical features of the habitat such as slope of the shore and degree of exposure. Migratory behavior appears to be of importance to growth and reproductive output in high intertidal populations. Paine (1969) suggested that the relatively reduced growth and reproduction of dense, high intertidal populations have proven conducive to the evolution of migratory behavior. Frank (1965) noted that algal production as well as the opportunity to graze were reduced at the highest shore levels of the Acmaea zone.

Although my results suggest a limited lateral excursion range over short periods (≤30 days), no evidence of homing behavior was seen. Chelazzi and Vannini (1976) presented evidence of intraspecific trail-following for N. textilis, however, they felt that homing behavior was not involved.

The analysis of sex ratio for N. plicata did not reveal any significant deviation from the expected 1:1 ratio. Further analysis, however, by size class showed a significantly greater number of males in the largest size class (≥20.1 mm) (Table 2). In contrast to my results, Kolopinski (1964) reported significantly more females within the largest size class (27.1-32.0 mm) of Nerita fulgurans. It was suggested that female N. fulgurans may live longer or grow at a faster rate than males (Kolopinski, 1964). This may be the case for male N. plicata or possibly growth rate of females is suppressed after sexual maturity because of the energy cost required to produce reproductive products.

Nerita plicata appears to reach sexual maturity in less than one year at a shell length of 12.0 to 14.0 mm (see Figure 3). In contrast, the fluvial Neritina granosa reaches sexual maturity at an age of 1.75 to 2 years and a shell length of 12 to 15 mm (Ford, 1979).

Egg capsules of Nerita plicata are similar to those described for other nerites. Andrews (1935) felt that egg capsule characteristics are species specific. Although capsules are most common on the walls of small pools and pits in the limestone between mean high water spring and mean high water neap, they can be seen from the littoral fringe down to the lowest extent of low water. Hughes (1971) and Kolopinski (1964) found the egg capsules of N. tessellata, N. versicolor, and N. peloronta in shallow water-filled depressions as well as underneath rocks or where irregularities in the rock surface afford some protection from the sun. It was suggested that both surface texture and shade probably influence capsule deposition (Hughes, 1971).

Growth of N. plicata exhibited considerable variation among individuals as well as varying within an individual over a number of months. Wilbur and Owen (1964) suggested this great variation in rate is one of the most notable features of molluscan growth. The actual measured maximum size (23.8 mm) of N. plicata compared favorably to the theoretical maximum shell diameter (22.4 mm). Although the von Bertalanffy equation was used to provide information on growth and age it should be remembered that the equation presumes that the animal exhibits isometric growth. Most gastropods, however, do not conform to the idealized condition of constancy of shape during growth; instead they typically display some degree of allometry (Vermeij, 1980).

The two major distributional patterns exhibited by N. plicata at the study site were vertical zonation and small scale patchiness. The results of this study suggest that surface irregularities of the habitat, daily and seasonal variation in meteorological and sea condition, and possibly predation play a role in maintaining the observed distribution.

My results show significant differences in the distribution and abundance of N. plicata among transects and among months (Table 1). Figure 1 shows an increase in the abundance of N. plicata with an increase in the structural complexity of the shoreline. At the north end of the transect area, individuals of N. plicata were commonly observed in relatively dense localized aggregations, particularly during periods of calm seas and warm weather. Kohn and Leviten (1976) have shown that with increasing habitat complexity (addition of refuges) population densities of predatory gastropods (families Conidae, Muricidae, Mitridae, and Vasidae) increase.

The observed upper limit of N. plicata is probably set by its physiological tolerance to desiccation, temperature, and solar radiation. At high tide during periods of normal wave assault and fair weather (clear, warm days), N. plicata is restricted to a relatively narrow zone, approximately 1 m wide, at the water line. However, during periods of particularly fair weather (clear, hot days) and calm seas (no splash or wash into the littoral fringe), the uppermost limit is lowered relative to the water line. In contrast, with high seas the upper limit is expanded as individuals move farther up the shore. High intertidal sessile populations (e.g., barnacles) are particularly susceptible to physical stress at their upper limits (Connell, 1961; Frank, 1965; Dayton, 1971) and may experience periodic catastrophic mortality. Among motile species, however, this is unlikely because the individuals may move away from the area of stress (Underwood, 1979).

Although daily mass migrations of the population occurred, juveniles (<13.0 mm) are rarely observed above or below their zone of maximum density at the limestone-reef flat interface. Vermeij (1972) suggested that within rocky intertidal gastropod species intraspecific shore-level size gradients may occur because of differences in the causes of mortality, as well as varying intensity of mortality in different parts of the vertical range of a species. The observed distribution of newly settled and small *N. plicata* may therefore result from (1) differential mortality within the vertical range of the population, (2) active migration to the preferred shore level (Vermeij, 1972), as well as (3) preferential settlement (selectivity) at the optimum shore level (Denley and Underwood, 1979).

Predation upon *N. plicata* was never observed in the littoral fringe, although crushing predators occasionally venture into this zone. In addition the predatory gastropod *Muricodrupa fenestrata* could be considered uncommon and observations of it actually feeding were rare. Thus predation in the high intertidal zone and littoral fringe does not appear to have an effect upon the distribution and abundance of *N. plicata* at these levels.

Predation has been shown experimentally to be the major factor responsible for the observed lower limit of most sessile intertidal populations (Connell, 1961; Paine, 1969; Menge, 1976). Underwood (1979) pointed out, however, that the importance of predation in setting the lower limit of intertidal gastropods remains conjectural. Furthermore, Underwood found no evidence that physiological tolerance to physical factors can explain the lower limit to the distribution of any species of intertidal gastropods.

The results of my transplant experiments (Table 5) showed a significantly higher predation intensity at mid-intertidal levels (below the normal vertical range of the population), as expected, that occurs within the normal vertical range of _N. plicata_. Although mortality of _N. plicata_ in the mid-intertidal would be expected to be high, due to predation, the mortality occurring in predator exclusion cages (Table 8) suggests other causes of mortality at lower shore levels. It should be kept in mind, however, that the actual cause of mortality within the experimental cages could have resulted from some caging effect (e.g., sedimentation) and not the treatment effect (i.e., shore-level effect).

Further study is necessary to clearly demonstrate whether the lower limit of _N. plicata_ and other high rocky intertidal gastropods is set by predation, behavioral adaptation, or physiological tolerance to extended periods of submersion. The present study suggests, however, that the significance of predation as a determinant of the lower limit of high intertidal gastropods is not as great as previously suspected.

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