

INTERTIDAL MIGRATION AND FORMATION OF BREEDING CLUSTERS
OF LABIAL-SPINE MORPHS OF THE THAID GASTROPOD,
ACANTHINA ANGELICA

by

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The work which follows is a reflection of every life--person, animal and plant--that I have known, as much as I am a reflection of them. I sincerely hope this work is an accurate reflection of the life patterns of *Acanthina angelica*.

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ABSTRACT

Acanthina angelica populations at Playa Estación, Puerto Peñasco, Mexico begin to migrate down the intertidal zones in November, the month of steepest drop in mean sea surface temperature. This is followed in January and February, the months of lowest sea surface temperature, by the formation of clusters of snails and the deposition of large masses of egg capsules under boulders and in crevices.

Long- and short-spined morphs of *Acanthina* are found in the same breeding clusters in proportions comparable to the proportions of each morph found in the adult population before breeding. After breeding in March and April, when sea surface temperatures begin to increase again, adults of the long- and short-spined morphs move into the upper intertidal areas, while juvenile snails do not.

By the following October the number and proportion of short-spined snails is reduced in the *Tetraclita* area, possibly due to their movement to a habitat with more appropriately-sized prey. Such habitat selection based prey availability is suggested to maintain the spine polymorphism in the population. Evidence which shows inter-

breeding between spine morphs suggests, however, that the spine polymorphism will not be evolutionarily stabilized, despite strong selective forces.

CHAPTER I

INTRODUCTION

The prosobranch gastropod *Acanthina angelica* Oldroyd (Family Thaididae) is an abundant, endemic carnivorous snail of the northern Gulf of California rocky intertidal zone. Like many other members of the families Thaididae, Muricidae and Fasciolaridae it bears a spine on the outer lip of its shell aperture. Though contrary to Paine (1966), the labial spine in *Acanthina* is generally considered to be used as a wedge to pry open the opercular plates of its barnacle prey (MacGinitie and MacGinitie 1968; Yensen 1979; Houston 1980). Two spine-size morphs have been distinguished in *Acanthina* and their intertidal distributions have been correlated with two species of different-sized barnacle prey (Paine 1966; Yensen 1979). Snails with long spines are generally found in the high intertidal zone amongst the large barnacle *Tetraclita stalactifera* (base diameter of 25-50 mm) (Fig. 1), whereas short-spined snails generally occur in the lower intertidal zone where the small barnacle, *Chthamalus anisopoma* (6-9 mm base diameter), is abundant (Fig. 2). The correlation of spine length with prey size and species has been further substantiated by



Figure 1. The long-spined morph of *Acanthina angelica* with its large barnacle prey, *Tetraclita stalactifera*. Scale mark = 1 cm.



Figure 2. The short-spined morph of *Acanthina angelica* with its small barnacle prey *Chthamalus anisopoma*. Scale mark = 1 cm.

laboratory feeding experiments which have shown that individual *Acanthina* have the ability to alter their spine length to accommodate the available prey (Yensen 1979).

The formation of breeding aggregations have been reported for *Acanthina angelica* (Houston 1976; Yensen 1979), as well as for other thaid gastropods (see review by Underwood 1979). From November to March *Acanthina angelica* aggregate in crevices or under boulders where copulation between the separate sexes is assumed to take place (Houston 1976). Individual egg cases reach up to 250 μ in diameter and contain 200 to 500 eggs (Wolfson 1970; Houston 1976). The egg cases are attached to the substrate adjacent to one another in large masses of up to 3,000 egg capsules. Within a few weeks tiny snails emerge from the demersal egg cases (Yensen 1979) having passed through larval stages within the egg case (i.e. they are non-planktotrophic). Most dispersal occurs through the juvenile and adult phases and eventually results in the distribution of long-spined snails in the upper *Tetraclita* areas and short-spined snails in the lower *Chthamalus* zones (Paine 1966; Yensen 1979).

This study follows the intertidal movements of the two spine morphs of adult *Acanthina angelica* with respect to their breeding season and barnacle prey distributions.

The data are presented in the following general format:

- 1) pre- and post-mating intertidal migrations and distributions,
- 2) formation of breeding aggregations.

In light of the breeding behavior and the seasonal variation in spine morph distributions I consider mechanisms potentially maintaining or stabilizing the spine-size morphs in the *Acanthina* populations at Puerto Peñasco, Sonora, Mexico.

CHAPTER II

MATERIALS AND METHODS

All observations and data were taken in the vicinity of Puerto Peñasco, Sonora, Mexico in the northern Gulf of California. The primary study site, Playa Estación (Station Beach), is located directly east of the town (Fig. 3) in front of the eastern edge of the Universidad de Sonora and the former University of Arizona research facility, UEP (Unidad Experimental Peñasco). At the high tide line this site is a coarse sand and shell beach, running east and west from the mouth of Estero Morua to Punta Peñasco. At low tide two-thirds of a 170 meter wide coquina limestone platform reef is exposed (Fig. 4). (The most extreme tides have an amplitude of 7.5 meters at this site.)

Additional observations were made at Punta Pelicano (Pelican Point), about 10 km northwest of Puerto Peñasco (Fig. 3). This point is an exposed granitic headland, characterized by large rounded boulders of various sizes and orientations (Fig. 5). Sharply demarcated ecological zones, not generally observed at Playa Estación, are characteristic of the relatively steep slopes of this intertidal region.

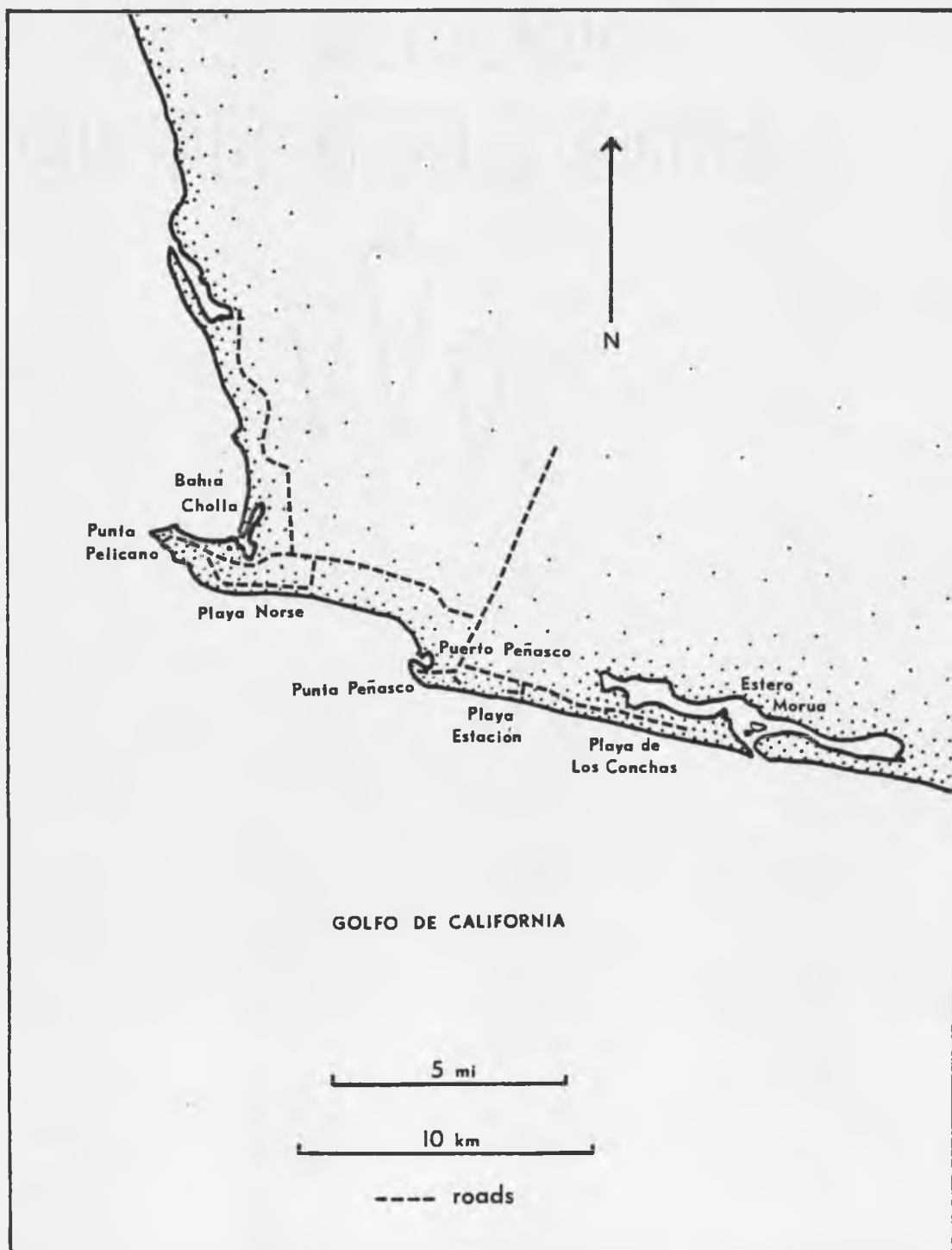


Figure 3. Map of the study sites in the vicinity of Puerto Peñasco, Sonora, Mexico in the northern Gulf of California.



Figure 4. The Playa Estación study site at low tide.



Figure 5. The Punta Pelicano study site at low tide.

Pre- and Post-Mating Intertidal Migration

To monitor the intertidal movements of *Acanthina angelica* at Playa Estación, I delineated a quadrat typical of *Acanthina* habitat 10.7 by 27.9 m (Fig. 6). Within this area three zones were distinguished based on the barnacle cover and the substrate. The highest rocky intertidal zone, T-I, is an isolated terrace of shell-hash beachrock bearing the large barnacle *Tetraclita stalactifera*. It borders the beach and extends a length of nine meters from the +2.2 m (7.3 ft) tidal level to the +1.2 m (3.8 ft) level. Another *Tetraclita* outcrop (T-II) is located about 12 m east of the T-I zone and is 5.5 by 6.6 m. Since the T-I and T-II zones are similar in elevation and in physical and biological compositions, data from the two areas (termed T zone) are combined. Moving seaward from the T-I zone there is an expanse of platform reef strewn with basalt boulders. For a distance of 3.6 m below the T-I zone to the +1.0 m (3.1 ft) tidal level the boulders are virtually devoid of barnacles. Nonetheless, *Acanthina* abound in this region. This zone is referred to as the bare boulder or B zone. Below this zone is the C zone where the boulders are covered with the small barnacle *Chthamalus anisopoma*. This zone extends 15.3 m from the lower border of the B zone down to the +.7 m (2.3 ft) tidal level.

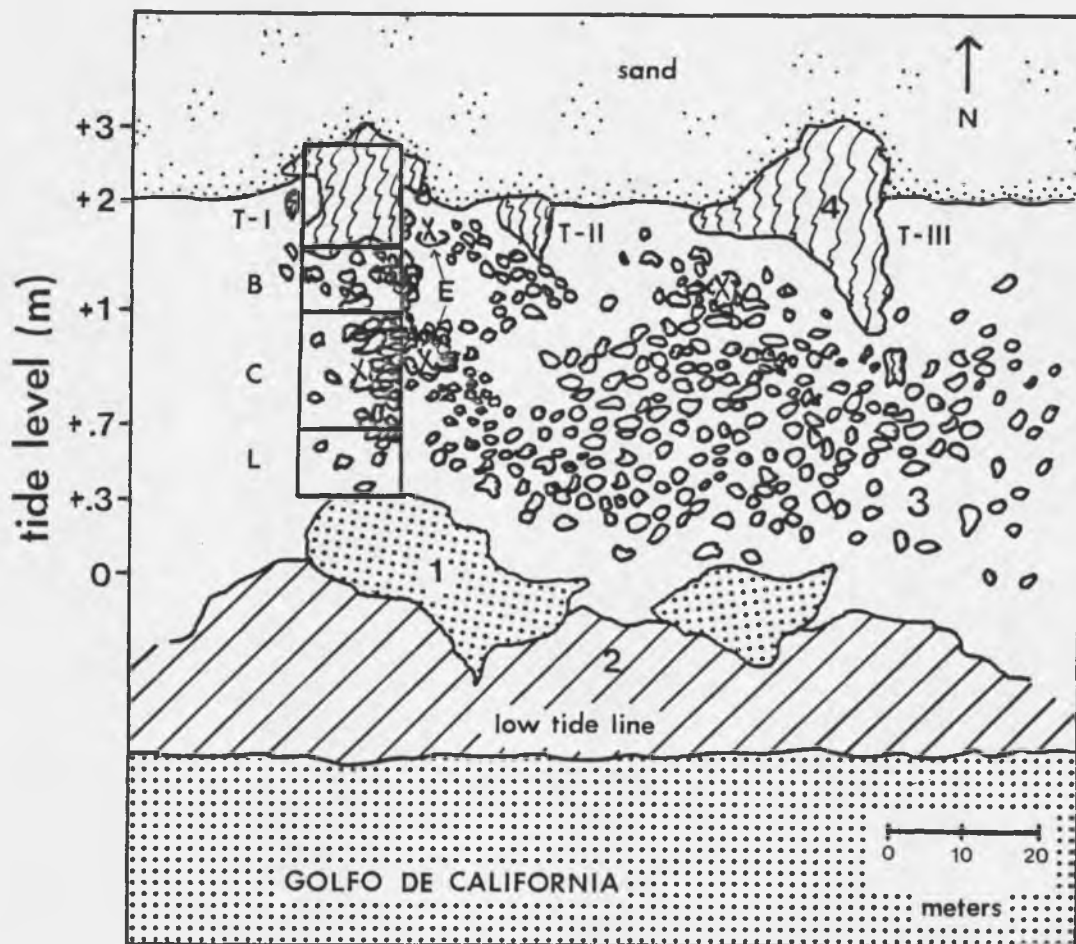


Figure 6. Map of the Playa Estación study area at low tide. -- 1) tide pools, 2) elevated beachrock terrace covered with algal turf, 3) beachrock platform covered with basalt boulders, 4) upper beachrock terrace where *Tetraclita* is found. Tide levels are given in meters from mean low water. The study zone is delineated: The T-I, T-II, T-III areas represent *Tetraclita*-covered beachrock; The B zone is an area of bare basalt boulders; The C zone is an area of *Chthamalus*-covered basalt boulders; The L zone is a lower area of *Chthamalus*-covered boulders; The E zone represents two boulders in the area to the east and adjacent to the other study zones, where two breeding clusters were observed. X's mark the location of breeding clusters of *Acanthina angelica*.

On October 21 and 22, 1979 I marked 54, 107 and 248 *Acanthina angelica* of the T, B and C zones, respectively. Since only 54 snails were originally found in the T zone, 11 more snails found there on 2 November 1979 were marked to increase the sample size to 65. I removed the snails from crevices or from under boulders at low tide and placed them "face" down on a piece of cardboard to air dry. The shells were then sprayed with Krylon fluorescent paint while most of the snails had their bodies retracted. After allowing the paint to dry the snails were returned to the base of their original boulder or crevice.

The *Acanthina angelica* from each of the T, B and C zones were visually examined and categorized according to spine-size morphs. At Playa Estación snails over 25 mm long diverge with respect to spine length such that snails from the *Tetracelita*-covered terraces have longer spines than snails from *Chthamalus*-covered regions (Yensen 1979). Snails from the *Chthamalus* area with spines exceeding 3.3 mm in length are rare (7%) (after Yensen 1979), regardless of the shell length. Snails with spines less than 3.3 mm, however, also comprise 28% of the T zone populations measured in February 1977 (after Yensen 1979). For the purpose of this study spines greater than or equal to 3.3 mm are considered long spines (after Yensen, pers. commun.).

The long-spined snails of the T zone (ls_T) were sprayed with lime-green fluorescent paint. The short-spined snails of the B zone (ss_B) were painted two colors; the apex lime-green and the spine-bearing end bright orange. The short-spined snails of the C zone (ss_C) were painted bright orange.

The T, B and C zones were censused monthly during the spring tides from October 1979 through April 1980 (Table 1). In each zone the number, color and size class of snails were noted. Two size classes of snails were arbitrarily distinguished. Any snail with a shell length greater than approximately 20 mm was considered an adult and any snail whose shell was less than approximately 20 mm in length was considered a juvenile.

After October the censusing was extended 7.7 m into a lower area, the L zone (Fig. 6). The snails from the L zone were not marked. Two breeding clusters were observed in the area to the east and adjacent to the study zones. These breeding clusters were censused monthly following their discovery and are collectively referred to as the E zone, after Ed Boyer, a graduate student who has a study site there.

The *Tetraclita* zone was censused in April 1980 after the breeding event and again in October 1980, before the next year's breeding event. In April 1980 the shell and

Table 1. Numbers of marked and unmarked (U) *Acanthina angelica* found in all the study zones from October 1979 through April 1980, and in the *Tetraclita* zones in October 1980. -- Marked snails include long-spined morphs originally from the T zones (ls_T), short-spined morphs originally from the B zone (ss_B) and short-spined morphs originally from the C zone (See Fig. 6).

<u>Date</u>	<u>ls_T</u>	<u>ss_B</u>	<u>ss_C</u>	<u>Total Marked</u>	<u>U</u>	<u>Total</u>
Oct. (21,22)	54	107	248	409	0	409
Nov. (2,3)	34 (11)*	73	156	289	161	367
Dec. (Nov. 30,) (Dec. 3)	9	110	180	299	-	-
Jan. (Dec. 31,) (Jan. 2,3)	5	89	137	231	323	554
Feb. (2,14)	8	50	123	181	333	514
Mar. (13,15)	13	62	85	159	404	563
Apr. (27,29,30)	6	46	99	141	486	594
Oct. (19)	2	1	-	3	16	19

*This represents 11 unmarked snails found in the T zones which were subsequently marked.

spine lengths of all the *Acanthina angelica* found in the T-I and T-II zones were measured using a plastic ruler with mm divisions and in October 1980 using vernier calipers.

Breeding Aggregations

The techniques presented above for observing snail migration are not fine grained enough to detect aggregations in a crevice or under a boulder. Clustering under boulders, however, is easily identified once the egg cases are laid down. Since only two clusters were found within the study area I made observations on two clusters in the adjacent E zone and another cluster closer to a third beachrock outcrop (T-III), for a total of five cluster observations at Playa Estación. Each cluster was examined for the number and color of snails present. All marked snails and approximately 20 additional unmarked snails selected from the cluster without design were measured for shell and spine length using vernier calipers. Number of egg cases was estimated for each cluster. Color, number, and in some cases, spine size of the clustered snails were recorded monthly. The individuals of two clusters (#3 and #5) were marked with a dot of red and purple fingernail polish, respectively, thus enabling me to track daily movement in and out of the cluster.

Spine and shell length data were also obtained from various clusters at the Punta Pelicano study site. Breeding

clusters were abundant in the *Tetraclita* zones as well as in the lower *Chthamalus* zones. I measured samples of 22 and 23 snails, drawn without design from each of two breeding clusters (P_3 and P_4 , respectively) in the *Tetraclita* zone, at the +2.4 m (8 ft) tidal level. This was also done for two breeding clusters (P_1 and P_2) in the *Chthamalus* zone, at about +1.2 m (4 ft) tidal level, with sample sizes of 18 and 17 snails, respectively, and for a single *Acanthina* cluster in an intermediate zone at about +1.8 m (6 ft) tidal level, with a sample size of 43 snails (P_5).

CHAPTER III

RESULTS

Pre- and Post-Mating Intertidal Migration

The data regarding the migratory movements of snails are presented in two general ways. First, I present the relative change in total snail density for each of the ecological zones over time, then I present the changes in snail frequency in each zone over time for each of the three spine-zone categories (ls_T , ss_B , ss_C) and for unmarked snails. The former method of presentation elucidates the migration pattern of the experimental population, while the latter allows comparison of the distinct movements of long- and short-spined *Acanthina* morphs.

Migration of the Study Populations of *Acanthina angelica*

The study zones were not of equal sizes; hence, the densities were standardized and are presented as the number of snails/m² (Fig. 7). The data show a continuous decrease in the density of both *A. angelica* morphs in the *Tetraclita* zone and the lower *Chthamalus* zone beginning in November and continuing through February. In March and April the densities increased again, to the point of equaling the original density in the *Chthamalus* zone and surpassing by

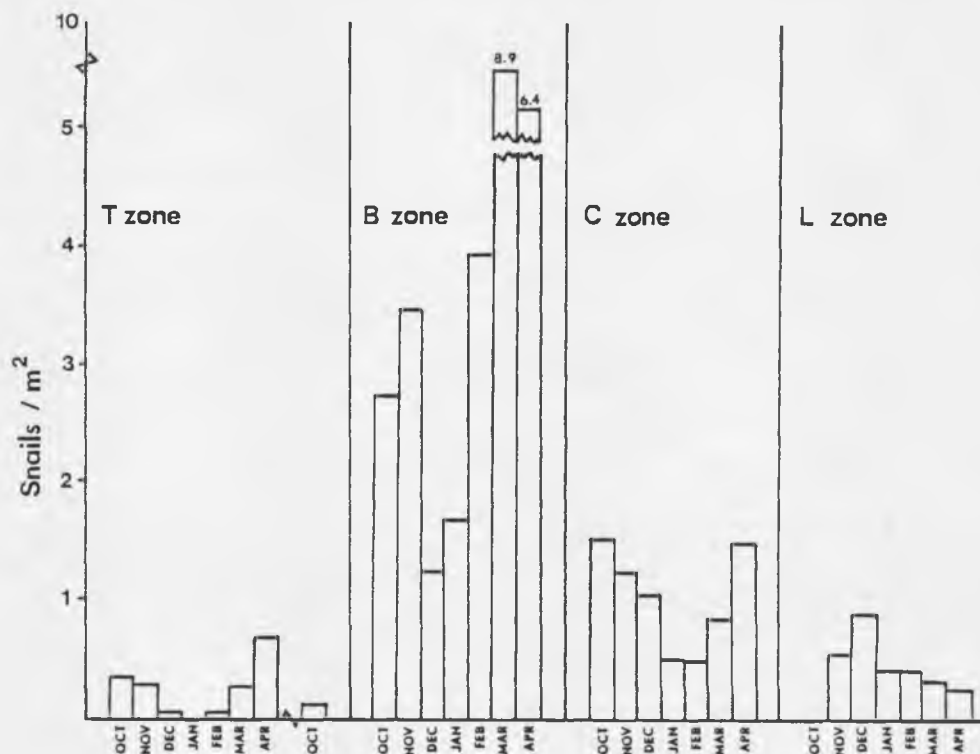


Figure 7. Density of *Acanthina angelica* at Playa Estación. -- Each of the study zones, T, B, C and L, as described in Fig. 6, are presented over the study period (October 1979 - October 1980).

almost 100 percent the original density in the *Tetraclita* zone. Snail density of the bare boulder zone, intertidally between the *Tetraclita* and *Chthamalus* zones, showed an increase from October to November, but then from November to December it decreased and remained low with only a slight increase from December to January. From January to February and again from February to March the density of snails in the B zone increased until it was about three times the original density. In April there was a slight drop, but the density was still two times the original density at 6.4 snails/m². The L zone had a slight increase in snail density from November to December, but a decrease in density from December to January. In February the density did not change, but from then until the end of April the density of snails in the low zone drops steadily, though slightly.

Movements of Long- and Short-spined Snails

The movements of snails of the various spine-location categories (ls_T , ss_B , ss_C) throughout the study area from October 1979 through April 1980 are depicted in Figures 9, 10 and 11. The number of snails of a given spine category found on a given date in a specific zone is presented as a percentage of the total number of snails of that category recaptured in all the zones during that census period. The data within a spine category are thus standardized,

enabling comparisons to be made from zone to zone within a time period, and within a zone from one time period to the next. In this way problems in analysis due to loss in numbers of recaptured snails and thus changes in sample size with time are eliminated.

As few as five of the ls_T snails were recaptured during the January census, while the numbers of recaptured ss_B and ss_C snails remain relatively large throughout the study period (Table 1). The ls_T snails were first marked on an overcast day and consequently the shells did not dry quickly, nor thoroughly, prior to painting, probably resulting in an early loss of marking. This, in combination with the small initial sample size of ls_T snails, helps explain the lower recapture of ls_T snails relative to ss_B and ss_C snails. Figure 8 compares the percentage of recaptured snails in each spine-location category for each month of the census. The lowest recapture of ss_C snails at 34.3% was in March and for the ss_B snails at 43.0% was in April. This compares with the lowest recapture of ls_T snails at 7.7% in January. By March the percent of recaptured long-spined snails increased to 18.5 but then decreased again in April. This secondary increase in recaptured snails could be significant and will be discussed later.

Figure 9 shows that 100% of the ls_T snails found in October were in the T zone, as defined by the marking

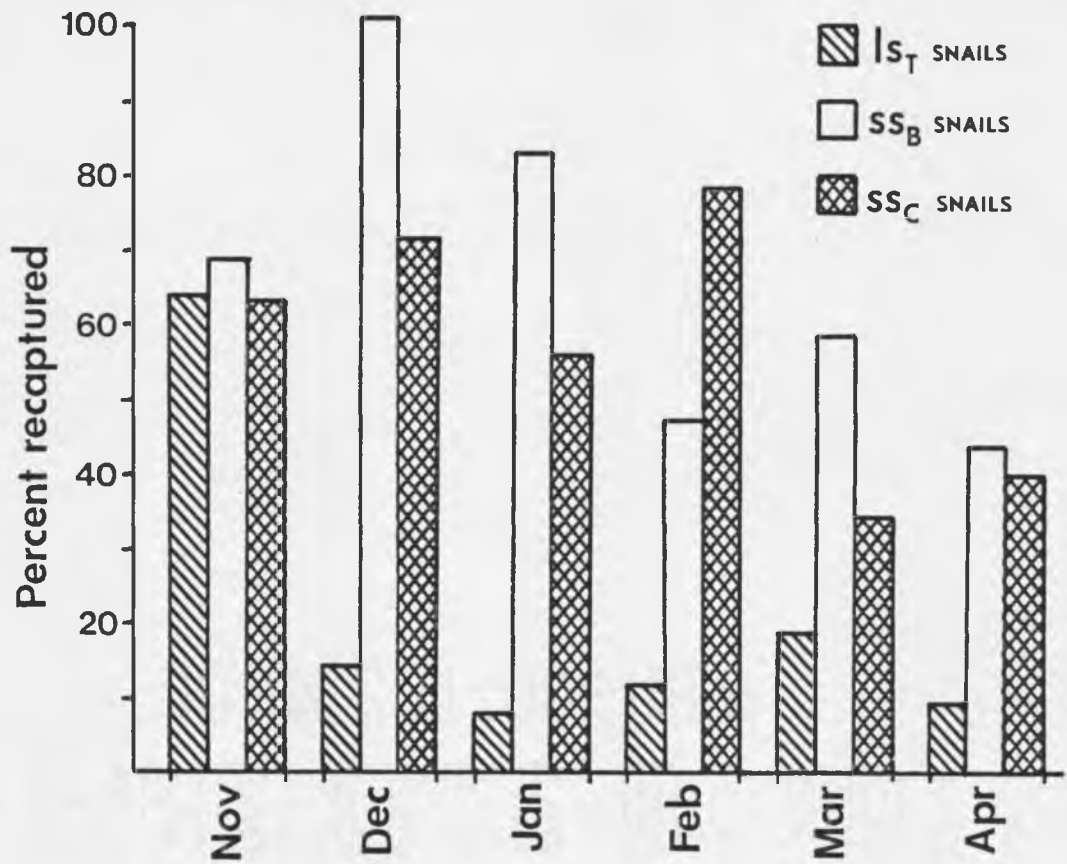


Figure 8. Monthly percent of recaptured *Acanthina angelica* at Playa Estación. -- In October 1979, 54 long-spined snails from the T zone (ls_T), 107 short-spined snails from the B zone (ss_B), and 248 short-spined snails from the C zone (ss_C) were marked and censused through April 1980.

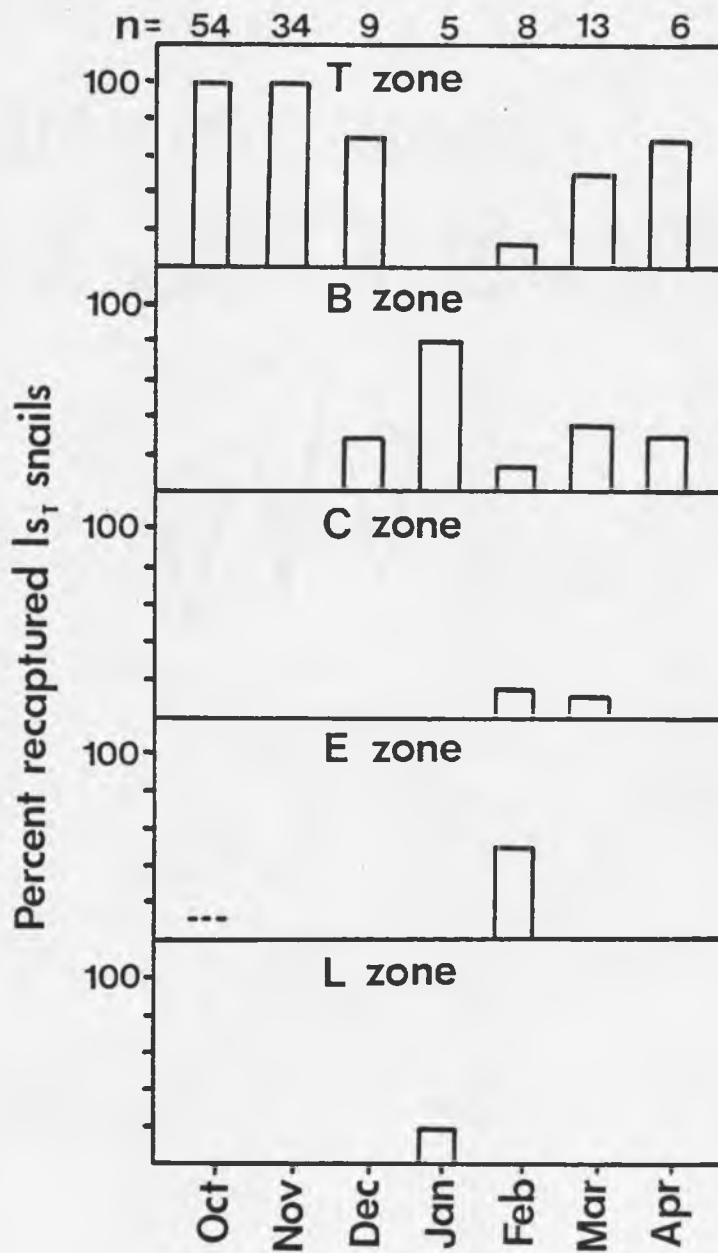


Figure 9. Monthly distribution of recaptured long-spined *Acanthina angelica* (ls_T). -- Each of the study zones (T, B, C, E and L) is presented from Oct. 1979 through April 1980. The total number of recaptured ls_T snails per month (N) is given at the top of the figure.

technique. By January the small number of recaptured ls_T snails were spread out between all zones with the greatest number in the E zone in clusters. The ls_T snails began to reappear in the upper intertidal zones, especially the T zone, by March and April.

Figure 10 shows that initially the ss_B snails tended to decrease in the B zone and increase in the lower *Chthamalus* region in November. In January and February there was a great increase in ss_B snails in the E zone clusters. By March ss_B snails increased again in the B zone and by April they also moved into the T and C zones.

A decrease in numbers of ss_C snails in the *Chthamalus* zone also began in November (Fig. 11). This decrease was associated with an increase in snails in the L zone. By January there was considerable movement into the cluster zone (E) and out of the B, C and L zones. In February the ss_C snails increased in the B zone and by April the *Tetraclita* zone was also colonized by these snails.

The unmarked snails observed in the study area probably came from a variety of indistinguishable sources: 1) they entered as immigrants from surrounding areas and from the low zone where snails were never marked, 2) they were previously marked snails that had lost their marking and 3) they showed up as offspring of the original or

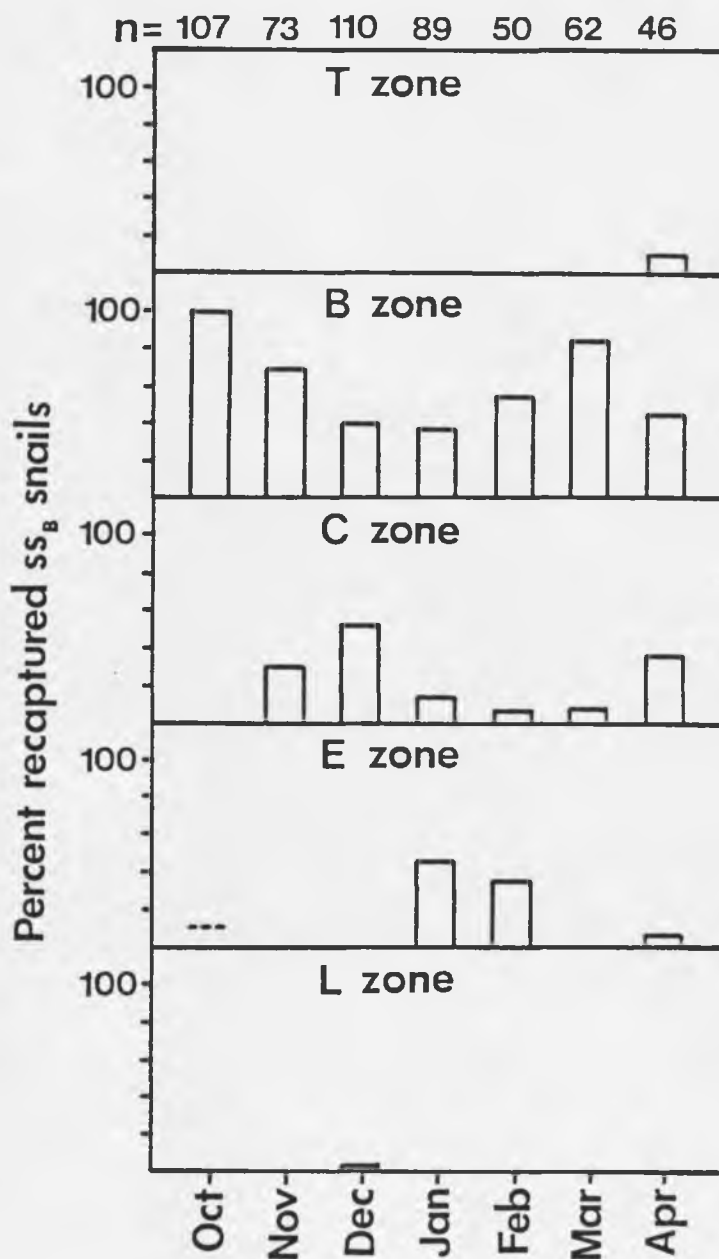


Figure 10. Monthly distribution of recaptured short-spined *Acanthina angelica* (originally from the B zone, ssB). -- Each of the study zones (T, B, C, E, and L) is presented from Oct. 1979 through April 1980. The total number of recaptured ssB snails per month (N) is given at the top of the figure.

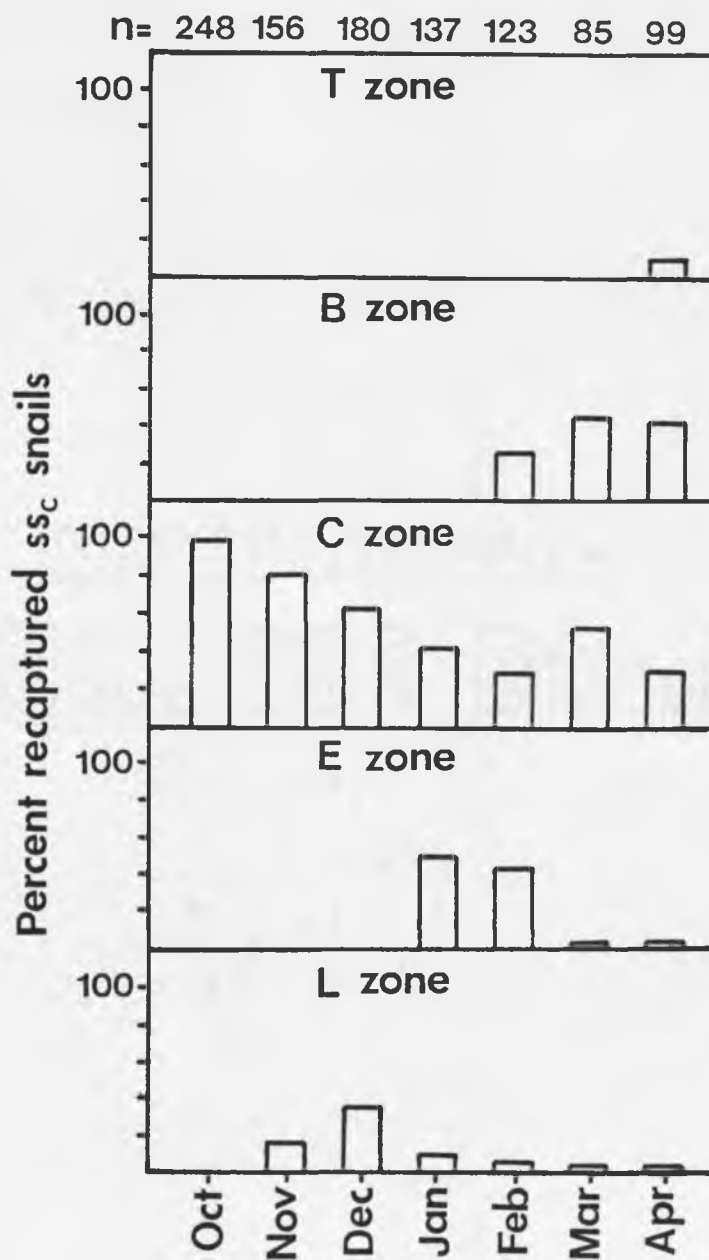


Figure 11. Monthly distribution of recaptured short-spined *Acanthina angelica* (originally from the C zone, ssC). -- Each of the study zones (T, B, C, E and L) is presented from Oct. 1979 through April 1980. The total number of recaptured ssC snails per month (N) is given at the top of the figure.

surrounding adult populations. Care must therefore be taken in the interpretation of any observed movement patterns when unmarked snail numbers are lumped in the following manner (Fig. 12). In November unmarked snails began to appear in the B, C and L zones, but it was followed in January by a decrease in these snails in the B and C zones and strong clustering activity in the E zone. This trend continued in February but by March, there was a reappearance of unmarked snails in the B zone, which corresponded to a decrease in the clusters. Like the ss_B snails, the unmarked snails increased in the T and C zones in April.

The data for unmarked *Acanthina* can be subdivided into size classes, thus separating the dispersal of the juveniles from the dispersal of the adult population. Figure 13 presents percentages of the total unmarked adult population for a given month and shows their distribution throughout the zones. The percentages of the total unmarked juvenile snails for a given month are similarly presented for each zone, adjacent to the adult data to allow for easy comparison. There are no immediately obvious patterns that arise from this comparison. Juvenile snails first appeared in the largest numbers in the L zone in January. Comparable numbers, however, were also found in the B and C zones by February. By March and April the number of juvenile snails as well as the number of adults

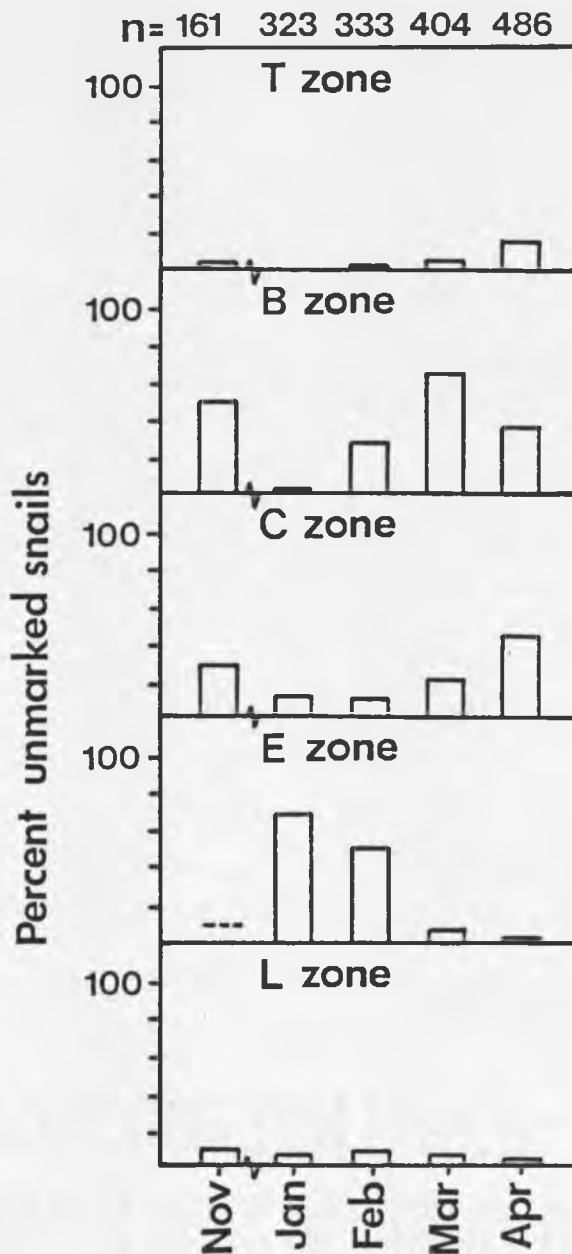


Figure 12. Monthly distribution of unmarked *Acanthina angelica* (U). -- Each of the study zones (T, B, C, E and L) is presented from Oct. 1979 through April 1980. The total number of unmarked snails per month (N) is given at the top of the figure.

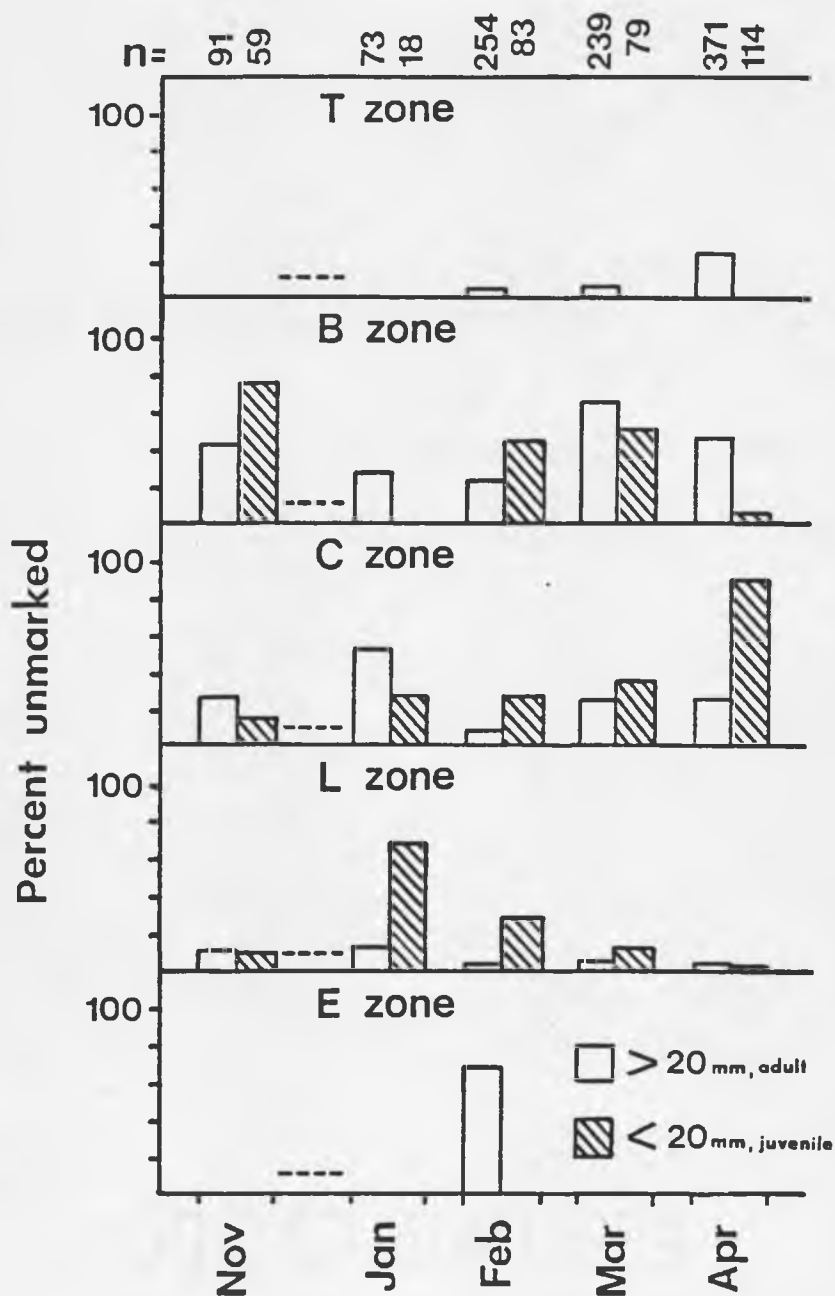


Figure 13. Monthly distribution of unmarked adult and juvenile *Acanthina angelica*. -- Each of the study zones (T, B, C, L, E) are presented from Nov. 1979, Jan. 1979 through April 1980. The total (N) for each month is presented at the top of the figure for adults and juveniles.

decreased in the L zone. By April the juveniles appear to be concentrated in the C zone, while adults were in the greatest concentration in the B zone but the adults were also abundant in the C and T zones.

In summary, short-spined snails began a movement down the intertidal zone from their respective areas (B and C zones) in November and December. In January and February their movement was generally out of these areas into clusters and in March and April the clusters broke up and the ss_B , ss_C and unmarked snails increased in the upper areas, including a marked dispersal into the terraces of the *Tetraclita* zone. After breeding, unmarked juvenile snails appeared first in the L zone in January but in general were concentrated in the B and C zones until April.

The long-spined snails began to disappear from the T zone in December and January. In January they appeared in small numbers in the B zone and in February they were in clusters in the E zone. In March and April the ls_T snails inhabited the B zone and also increased in the *Tetraclita* zones. The peak of long-spined snails appearing in the clusters seemed to lag behind the peak of clustering in the short-spined snails.

Dispersal into the *Tetraclita* Zone

As can be seen from Figure 8 the densities of *Acanthina angelica* were remarkably higher in the T zone in April 1980 than in either October 1979 or October 1980. The study began in October 1979 with 54 *Acanthina* in the *Tetraclita* zones; the number rose to 102 snails by the following April and then dropped to 19 snails by October 1980.

At the onset of the study quantitative measurements of the shell and spine lengths of *Acanthina* in the T zone were not made, but all the snails inhabiting the T zone, with one exception, appeared to be long-spined. However, measurements made on snails in the T zone at the end of the study period, April 1980, after breeding, were compared with measurements made on snails found in the T zone the following October 1980, before the next breeding period. Using a Student's t-test for comparing the slopes of spine length vs. shell length regressions for the two dates, the slopes were shown to be significantly different ($t = 4.9$, d.f. = 115, $p < .001$) (Fig. 14). In April only 12/102 (.12) snails were long-spined with a mean spine length of 2.3 ± 1.4 mm, as compared to 11/19 (.57) long-spined snails in October 1980 with a mean spine length of 3.9 ± 1.8 mm. Three of the short-spined snails found in the T-II area in October 1980 were close to the lower edge of the T-II zone which, unlike the T-I zone, has *Chthamalus*-covered rather than

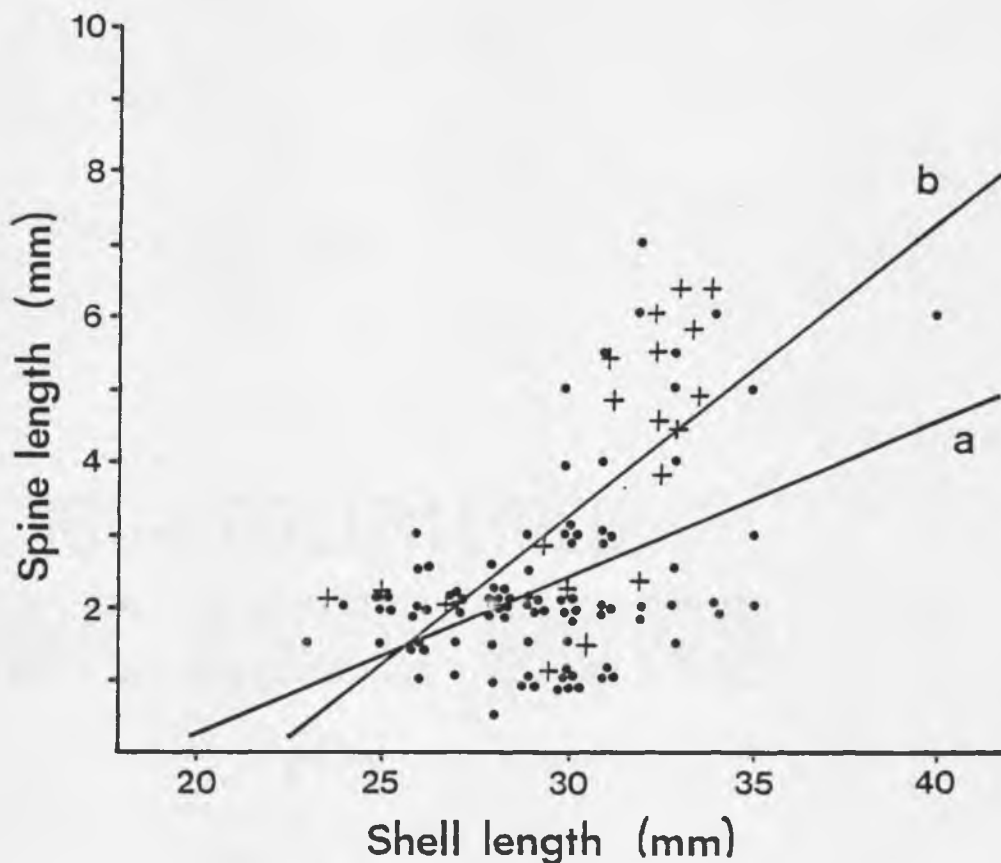


Figure 14. Scatter graph of spine lengths on shell lengths of *Acanthina angelica* found in the *Tetraclita* zones in April and October 1980. -- a) April 1980 (dots), $y = .22x - 4.03$, $n = 99$ and b) October 1980 (+), $y = .43x - 9.26$, $n = 19$. A comparison of the slopes of linear regressions using a Student's t-test shows the slopes to be significantly different ($p < .001$).

bare boulders. Snails at the boundary between these two zones were exposed to two different sizes and species of barnacle prey. Of the five short-spined snails in the T-I area, two had spines which had been broken and two were small snails below the size of divergence in spine length.

These data, in general, show a post-breeding influx of *Acanthina angelica* into the *Tetraclita* zone. Among these *Acanthina* both long- and short-spined snails occur, but by the following October, just before breeding, the number of short-spined snails was greatly reduced and the proportion of long-spined snails was greater.

Formation of Breeding Aggregations

Playa Estación Breeding Clusters

The first breeding aggregation and egg cluster was observed in the study area at Playa Estación on December 31, 1979. A year later, however, egg cases were found at the Punta Pelicano area as early as 22 November 1980 (Curt Lively, pers. commun.). Observations by Houston (1976) suggest mid-December is the onset of the *Acanthina angelica* breeding season. From this it is inferred that the formation of aggregations, copulation, and egg-laying begin from mid-November to December.

Immediately following this first observation, egg clusters #2 and #3 were found in the E zone adjacent to the

study area on January 2 and 3. Other clusters were observed outside the study area but data were taken for only one other cluster (#5) beginning February 20.

All clusters were observed in the +0.8 to +1.0 m (2.5 ft to 3.3 ft) region of the intertidal zone at the level of the C zone and into the B zone under medium to large flat-bottomed basalt or coquina boulders, except cluster #2 which was found in a crevice of a small patch of coquina terrace, similar to the *Tetraclita* outcrops, but without living *Tetraclita*. This terrace was at the +1.5 m (5 ft) level of the intertidal zone to the east of and separated from T-I by a narrow (less than two feet in width) spit of sand, and surrounded on all other sides by sand. The egg cases hung from the ceiling of a deep crevice, which was open at both ends and the 171 various colored snails were packed inside. This location proved to be a sub-optimal place to breed. During the following census period on February 2, the crevice was found buried under sand with no trace of any snails.

Cluster #1 at the lower extreme of the observed breeding range, +0.8 m (2.5 ft), for less obvious reasons, was also found dispersed on February 2. The original cluster of 68 snails was reduced to two snails. I observed most of the approximately 500 egg cases with tiny holes on their sides, less than .5 mm in diameter, possibly drilled

by *Mitrella guttata*, a small carnivorous gastropod which was found aggregated under this boulder. It is possible that predation pressure on the egg cases drove the snails of cluster #1 to disperse at this time, perhaps to lay eggs in a habitat more conducive to their survival.

Egg cluster #4 was seen only on February 2 and consisted of only one snail and two associated egg cases.

Cluster #5 was at a distance from the other clusters, close to a third large *Tetracelita* outcrop (T-III) to the east of T-I at about +1.0 m (3.3 ft). This cluster was unique in that it harbored no painted snails when discovered on February 20. The 44 snails found under the large coquina boulder were measured, marked with a purple dot and returned. Additional snails found there the following day were similarly marked. From the first to the second day of observation this cluster showed a 100 percent increase in size and within two days it dropped to only one snail. Perhaps two days in a row of painting and measuring was too much to be tolerated.

Cluster #3 was also checked daily in February to detect movement in and out of the cluster. Cluster #3, unlike #5, was originally composed of unmarked, ls_T , ss_B , and ss_C snails, as it was located adjacent to the study area at +0.9 m (3.0 ft) at the same level as the upper C zone, about eight meters from the low edge of the T-I zone. The

234 snails clustered there on February 20, regardless of their color, were painted with a red dot of fingernail polish. In an attempt to control for the disturbance done on cluster #5, cluster #3 was not checked quantitatively on February 21 and no painting or measuring was done. The cluster, however, qualitatively appeared intact, i.e. approximately the same size as before with most snails having the red mark. Two days later the cluster appeared more or less the same. By March 13 there was significant dispersal out of the cluster and some snails without a red mark had moved in.

The dispersal of cluster #3 into the surrounding study areas in March and April can be seen in Figure 15. Of the 234 *Acanthina* marked in cluster #3 in February, 105 were recaptured in March in the surrounding zones. This 45% recapture for March was further reduced to 31% in April. These *Acanthina*, like the population in general, first dispersed predominantly into the B zone, but also dispersed substantially into the C zone in March. By April the dispersal reached into the terraces of the T zone.

Clustering in Each of the Spine-Location Categories

As discussed previously, Figures 9-12 show January and February to be the months of strong clustering for the ss_B , ss_C and unmarked snails, and only in February was there strong clustering in the recaptured ls_T snails.

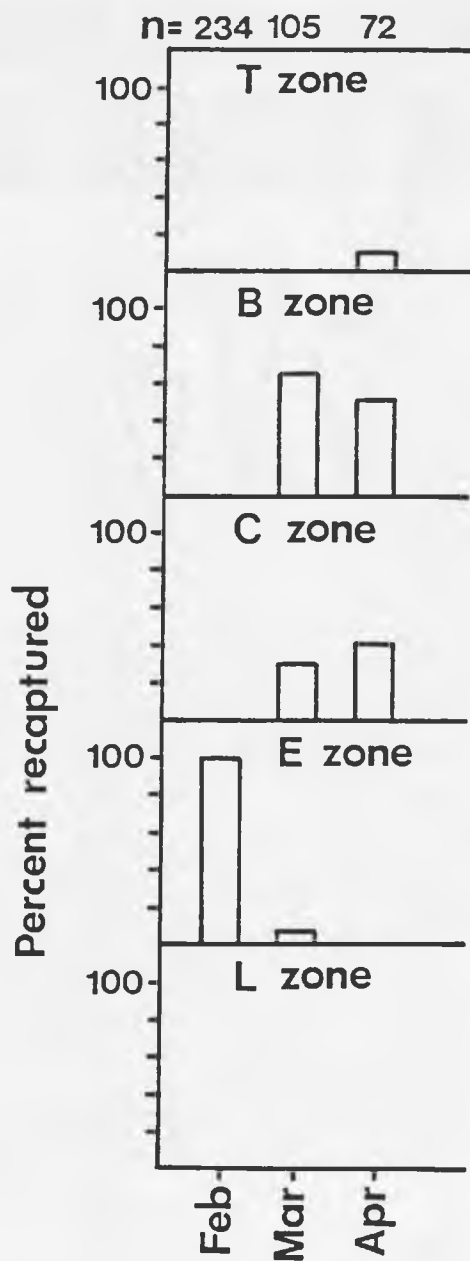


Figure 15. Dispersal of *Acanthina angelica* from cluster #3. -- The dispersal from cluster #3 of the E zone is presented from Feb. through April 1980. The total number of recaptured cluster #3 snails (N) is presented at the top of the figure.

Figure 16 (a-d) gives another perspective on the clustering activity of each spine category of snail over time. In January only 20% of the recaptured ls_T snails were clustered, but the percentage increased to 50% clustered in February and decreased to 12.5% in March. All other spine categories, however, showed a peak in the percentage of clustered recaptures in January with a decline in this percentage through March. In January 62% of the recaptured ss_C snails were in a cluster while 54% of the ss_B snails were clustered and 81% of all the unmarked snails censused in January were in these breeding aggregations. In each case, except that of the ls_T snails, over half of the censused snails were found in breeding groups in January.

It is especially noteworthy that 50% of the recaptured ls_T snails were clustered in cluster #3 with short-spined (ss_B and ss_C) snails in February. Though it amounts to only four snails, it is significant that these long-spined snails were found in breeding aggregations with 51 short-spined_C, 19 short-spined_B and 171 long- and short-spined unmarked snails.

Shell and Spine Size Within the Clusters

Playa Estación. The spine and shell lengths of marked *Acanthina* and a sample of unmarked *Acanthina* from each of the three breeding clusters at Playa Estación are

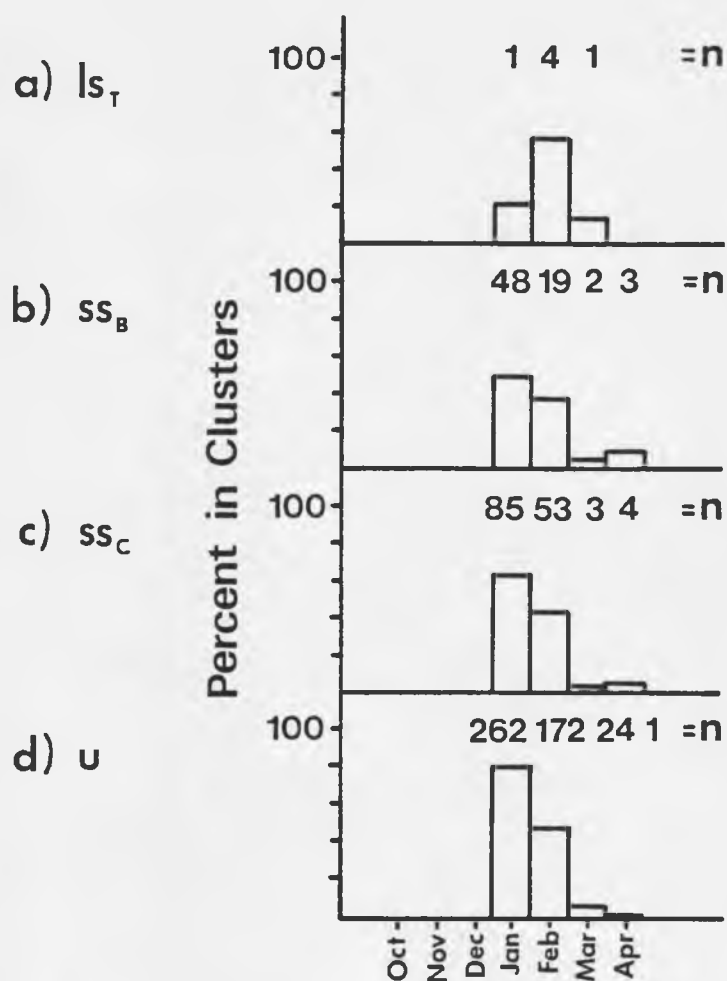


Figure 16. Monthly distribution of marked *Acanthina angelica* found in breeding clusters. -- Data are presented from Oct. 1979 through April 1980. a) long-spined snails (ls_T), b) short-spined snails from the B zone (ss_B), c) short-spined snails from the C zone (ss_C) and d) unmarked snails. N values are presented above each X-axis.

presented in Figure 17. The fraction of measured snails which had long spines in each cluster, using 3.3 mm minimum length as the criterion for a long spine, is presented in order from the highest intertidal cluster to the lowest (Table 2). In the highest clusters 4.4% of the *Acanthina* were long-spined while 8.9% were long-spined in the intermediate cluster and 12.2% in the lower cluster. The percentage of long-spined snails in each cluster increased slightly as the tide height of the cluster decreased. The range of tide heights of the observed clusters, however, is only 1.9 ft and any real intertidal pattern would not necessarily be observed in this limited range. These data, however, show that small numbers of long-spined snails were breeding in clusters with predominantly short-spined *Acanthina* at Playa Estación.

Punta Pelicano. The spine and shell lengths of the *Acanthina* breeding cluster samples measured at Punta Pelicano are presented according to tidal height (Fig. 18). The fraction and percentages of long-spined snails in the observed clusters are also recorded in order of decreasing tidal level (Table 2). The percentage of long-spined snails appears to be greatest in the clusters at the highest tidal level, intermediate at the intermediate level and lowest in the lower clusters. As the clusters go from *Tetraclita*-covered boulders to an intermediate area where the *Tetraclita*

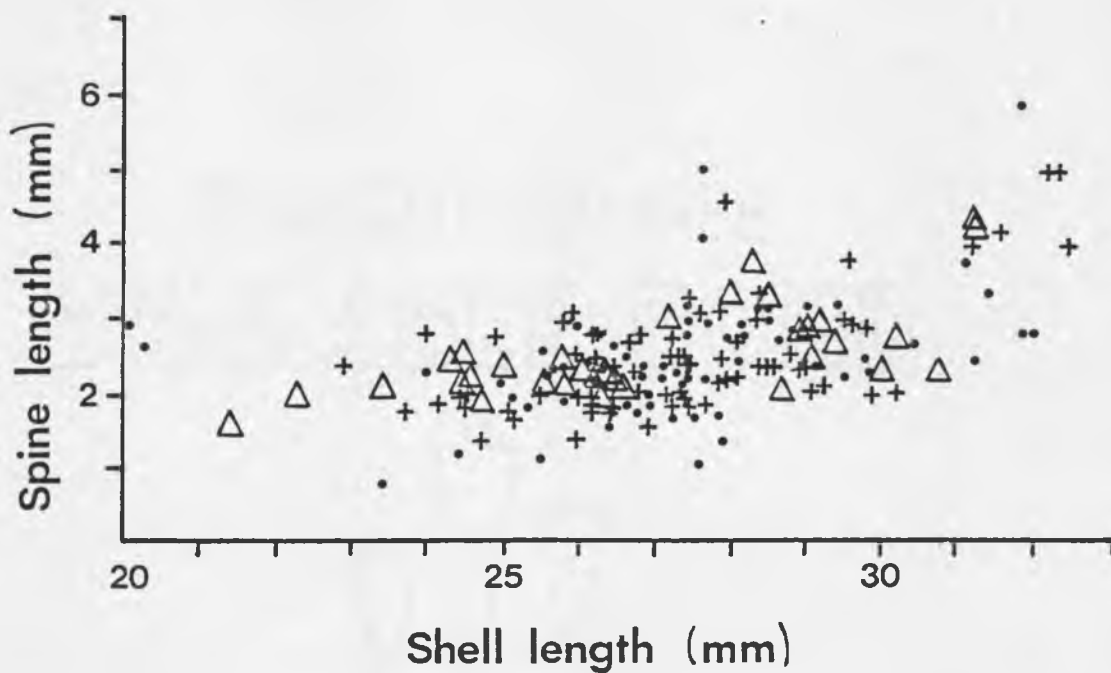


Figure 17. Scatter graph of spine lengths on shell lengths of *Acanthina angelica* in breeding clusters at Playa Estación. -- Cluster #2 is presented as dots (.), cluster #3 as crosses (+) and cluster #5 as triangles (Δ).

Table 2. Fraction and percentages of long-spined *Acanthina angelica* morphs in breeding clusters at Playa Estación and Punta Pelicano in Jan. and Feb. 1980.

<u>Location</u>	<u>Cluster #</u>	<u>Tidal Level</u> <u>m</u> <u>ft</u>	<u>Fraction Long-Spined</u>	<u>Combined Fraction Long-Spined</u>	<u>% of Long-Spined</u>	<u>\bar{X} % of Long-spined</u>
Playa Estación	2	+1.5 +5.0	3/68		4.4	
	5	+1.0 +3.5	4/45		8.9	8.6
	3	+0.9 +3.1	9/74		12.2	
Punta Pelicano	P ₃	+2.4 +8.0	6/22			
	P ₄	+2.4 +8.0	4/23	10/45	22.2	
	P ₅	+1.8 +6.0	6/43	6/43	14.0	15.4
	P ₁	+1.2 +4.0	2/18	3/35	8.6	
	P ₂	+1.2 +4.0	1/17			

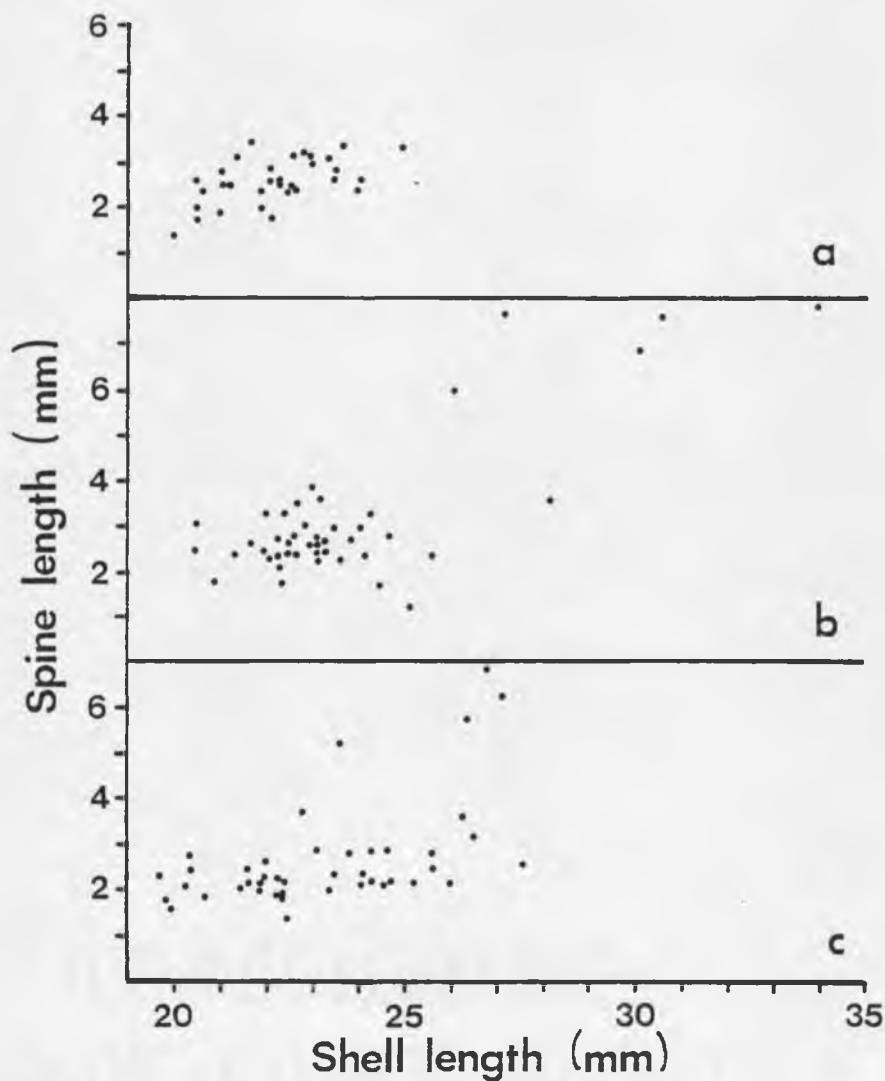


Figure 18. Scatter graph of spine lengths on shell lengths of *Acanthina angelica* in breeding clusters at Punta Pelicano. -- a) Clusters P_1 and P_2 amongst the *Chthamalus* prey, b) Clusters P_3 and P_4 amongst the *Tetraclita* prey and c) Cluster P_5 in an intermediate area with both prey species.

and *Chthamalus* barnacles meet, to the lower zones of strictly *Chthamalus*, spanning a tidal range of 4 ft, the percentages of long-spined snails in these clusters goes from 22.2% to 14.0% to 8.6%, respectively. Considering that long-spined *Acanthina* are best adapted to eat *Tetraclita*, one would predict that in the *Tetraclita* area the proportion of long-spined snails in breeding clusters would be large, but most assuredly that it should be larger than the proportion of long-spined snails in the clusters of the lower zones, where the small barnacle prey dominate the surface of the boulders. This is indeed the case.

The five Punta Pelicano samples were compared by using an analysis of covariance, testing the null hypothesis that the slopes of the regressions of spine size on shell size were equal. The F statistics for both pooled and non-pooled data ($F_{0.05(1), 2, 117} = 1.93$ and $F_{0.05(1), 4, 117} = .97$, respectively) show the slopes are essentially equal ($p < .05$). Though the proportion of long-spined snails differs at the three tidal levels observed, there appears to be no significant difference in the spine/shell length ratios of *Acanthina* in the two *Tetraclita*-area clusters, the intermediate cluster and the two *Chthamalus*-area clusters. The breeding clusters at Punta Pelicano, like those at Playa Estación appear to be composed of small

numbers of long-spined, but predominantly short-spined snails, at all the observed intertidal levels.

CHAPTER IV

DISCUSSION

Pre-Mating Intertidal Migration

Migratory behavior in intertidal gastropods during the breeding season is not an uncommon phenomenon. Downward migration by the high intertidal *Littorina neritoides* during the spawning season presumably increases its opportunities for shedding eggs into the sea (Fretter and Graham 1962). Other lower-shore trochids have been observed to migrate upshore coincidentally with the spawning season (Desai 1966; Underwood 1973, 1979). The study by Desai (1966) correlates changes in geotactical responses of the snail *Monodonta lineata* with temperature changes indicating temperature could be an important environmental cue in stimulating this intertidal migration.

The exact nature of the stimulus for movement of *Acanthina angelica* is beyond the scope of this study, but temperature is probably an important component of it. The annual range of sea surface temperature at Puerto Peñasco is extreme, sometimes reaching an amplitude of 23.0°C (Thomson and Lehner 1976). It can be seen from curves of the mean annual cycle of sea surface temperature in the

Puerto Peñasco vicinity (Maluf in press) that November is the month of steepest drop in temperature, January and February are the months of lowest sea surface temperature and the greatest temperature increase occurs in April, reaching a maximum in August.

From Figure 7 showing monthly changes in total population density in each zone and Figures 9 through 11 showing long- and short-spined snail movements it is clear that November, the month of the most drastic drop in sea temperature, is the onset of a general migration of the *Acanthina* population at Playa Estación. The data imply the initial movements in all zones are seaward. By January the movement of all but the long-spined *Tetraclita* zone snails is strongly into clusters and 50% of these ls_T snails join the clusters by February. January and February, the months of peak clustering activity are also the months of the lowest sea surface temperatures.

The initial downward migration of *Acanthina* could function to: 1) gather the population together for the formation of breeding clusters, 2) minimize desiccation and cold temperature stresses for both eggs and hatching juveniles, 3) provide optimal egg laying sites and 4) provide food for hatching juveniles, which are frequently found inside the tests of the low intertidal barnacle (Dungan, pers. commun.).

Though the stimulus for formation of these aggregations is unknown, it seems likely that it could be a response to a chemical signal released into the water (Kohn 1961). The tendency for *Acanthina* to move toward boulders harboring egg masses but devoid of snails (Yensen, pers. commun.) suggests that the egg cases could be the source of such a chemical cue. If chemotaxis is involved, a downward gathering of the population seems a better alternative than up-shore gathering in terms of delivering the chemical message to the population as lower individuals spend more time immersed in sea water, the proposed medium of chemical transfer.

The low intertidal regions probably provide the best boulder habitat for aggregating with minimal exposure to desiccation and temperature stresses for both eggs and hatching juveniles. The data from Playa Estación, however, show more clustering in the mid and high intertidal zones. It is possible that the flat-bottomed boulders selected for laying down egg masses were limiting in the L zone studied and snails were secondarily forced toward shore in search of suitable habitat (see Fig. 6). Though no clusters were observed in the L zone, I have observed clusters in the adjacent low intertidal areas where boulders are abundant. It should be noted also that *Acanthina* clustering and egg laying at Punta Pelicano is for the most part done in the

deep crevices of huge granitic boulders. These crevices are abundant at Punta Pelicano and offer excellent protection against exposure. Here I found clusters abundant throughout the intertidal range of *Acanthina*.

Another strategy, however, would be to gather at the center of the intertidal range of the population. At the onset of the study snails from the low zone were not marked due to the scarcity of boulders in this area. The movement of these snails is lumped in with movement of all unmarked snails from various other sources, and consequently any up or downward movement of these low snails is indistinguishable. Snails from all the upper regions, however, show an initial tendency to move down the shore.

Breeding Aggregations

Gregarious behavior as observed in *Acanthina angelica* during the breeding season could be adaptive in several ways. First, it is inferred from the structure of the reproductive systems (Houston 1976) that *Acanthina* has internal fertilization and from this it is assumed that the formation of aggregations would facilitate bringing the separate sexes together for copulation. Secondly, large masses of egg capsules as described by Wolfson (1970) and Houston (1976) are likely to be more capable of retaining moisture than individual egg capsules. Gregarious behavior

would also serve to protect the egg capsules from predation, since there is hardly room for even the tiniest predator to enter an egg capsule mass when hundreds of adult *Acanthina* are clustered together so as to form a cohesive mound above the eggs. One egg mass which was found in February at Playa Estación without any *Acanthina* clustered about it had mostly empty egg cases which bore tiny gastropod drill holes on their sides.

Observations made on cluster #3 over a four-day period suggest that individual *Acanthina* remain with the egg masses for a while. Nothing conclusive can be said, however, about the length of time an individual stays with a cluster, nor can anything be said about the possibility of short feeding bouts taken while in these breeding aggregations. If *Acanthina* remain in clusters beyond the time period necessary for copulation and egg laying, this behavior could be construed as a form of parental care. Yensen (1979) has observed as few as 10 to 15 snails emerge from egg capsules which contained up to 500 eggs in an aquarium. The clustering of *Acanthina* over the egg masses could serve to increase the probability of survival of this limited number of offspring.

Post-Mating Dispersal and Intertidal Distribution

There is a clear tendency for adult long- and short-spined *Acanthina angelica* to disperse after breeding into

the C zone and especially into the upper B and T zones (Fig. 9-12). Juvenile *Acanthina*, however, disperse first into the low zone and then concentrate in the C and B zones, but do not disperse into the upper *Tetraclita* areas at Playa Estación (Fig. 13). Intraspecific shore-level size gradients showing both increases and decreases in size with intertidal tide height are well known among gastropods (see review Vermeij 1972). In other thaid gastropods such as *Thais lapillus* of the British Isles (Feare 1970) and *Thais lamellosa* and *T. emarginata* of the Pacific Puget Sound intertidal (Bertness 1977), unlike *Acanthina angelica* at Playa Estación, the juveniles inhabit higher regions of the intertidal. Vermeij (1972) considers such gradients where shell size decreases in an upshore direction to be characteristic of lower shore species in which pre-reproductive, post-larval mortality is due to predation or biotic interactions, usually most intense in the lower intertidal regions. Bertness (1977) considers predator-prey size selection which acts on all members of the population, rather than merely the pre-reproductive members, to be responsible for the intraspecific and interspecific size gradients observed for *T. lamellosa* and *T. emarginata*. The Pacific coast barnacles, the major prey of these thaid, show a size gradient with the larger barnacle species lower

in the intertidal zone corresponding to the size class distribution and species size distribution observed in *Thais* spp.

In the northern Gulf of California the observed interspecific barnacle size gradient increases with elevation. This is opposite the pattern observed in Pacific coast barnacles. It does, however, roughly correspond to the size distribution of the Gulf predator, *Acanthina angelica*. After breeding only adult snails are found amongst the high, large barnacle *Tetracelita stalactifera*, while both juvenile and adult snails are found in the mid and lower end of the species intertidal range amongst the small barnacle prey *Chthamalus anisopoma*. It is possible that small individuals are eliminated from the high intertidal regions because of the harshness of the physical environment, especially in terms of the stresses of exposure which would be most effective against small individuals (Vermeij 1972). The northern Gulf of California with its extreme tidal range is known to be physically extreme and other intertidal communities there are also considered to be physically controlled (Thomson and Lehner 1976).

Nature of the Spine Polymorphism

Adult *Acanthina angelica* at Playa Estación diverge with respect to apertural spine size (Yensen 1979). The

intertidal distribution of the two spine size morphs in the field is more closely correlated with the size distribution of the two barnacle prey species than with shell size alone. Snails with a long spine on their shell aperture are generally found in the high intertidal zone amongst *Tetraclita*, the large barnacle prey. Short-spined *Acanthina angelica* generally occur in the lower intertidal zone of *Chthamalus*, a smaller barnacle prey (Yensen 1979). The labial spine is generally considered to be used as a wedge to pry open the opercular plates of its barnacle prey (MacGinitie and MacGinitie 1968; Yensen 1979; Houston 1980). The direct correlation of *Acanthina* spine size with its prey size in the field is further substantiated by laboratory feeding experiments in which *Acanthina* significantly changed its spine length if the prey species and thus prey size of barnacle was switched. Long-spined *Acanthina* significantly reduced their spine length when fed the small barnacle prey for three months while short-spined snails significantly increased their spine lengths when fed the large barnacle prey for three months. Controls did not alter their spine lengths significantly (Yensen 1979).

The mechanism for regulation of spine length is not known, though Yensen suggests it could be the differential deposition of shell material on the outer lip of

the shell rather than the spine. When shell material is added to the outer lip of the shell the spine length is reduced; when material is deposited on the spine but not on the outer lip, the spine increases in length. It is possible that snails feeding on large barnacles are forced to extend their mantle over the spine further than is necessary when feeding on small barnacles. If deposition of calcium carbonate onto the spine occurs during feeding, this could explain why snails which consistently feed on large barnacles have long spines. Yensen's data (1979) suggests that spine growth in *Acanthina* is somehow stimulated by the size and shape of the available barnacle prey.

Other workers have correlated aspects of diet with intraspecific variation in other morphological parameters of thaid gastropod shells (Moore 1936; Bryans 1969; Spight 1973; Kitching and Lockwood 1974), but without experimental backing. Wave shock (Kitching et.al. 1966; Largen 1971; Wigham 1975), substrate (Gunter 1938) and crowding (Seed 1968) have also been shown to affect molluscan shell form. Such non-morphological parameters of gastropod populations as density, growth rate and survival are also known to vary with local environmental conditions (Spight 1972).

On the other hand the physiological traits which affect shell morphology, growth rate and mortality in

Littorina picta were shown to have a high heritability (Struthsaker 1968). Variations in shell size (Cook 1965, 1967), shape (Staiger 1957) and color (Sheppard 1952; Clarke 1960) are known to have a strong genetic basis in many populations of marine and terrestrial gastropods.

The metabolic rate of a poikilotherm is directly influenced by the environment. Newell (1964) points out that variations in metabolic rate can explain a lot of the morphological variation in gastropod shell form. The metabolic processes themselves, however, are determined by the genetic system and consequently the genetic system imposes certain limits on the general shape and degree of adaptability of an organism to its environment. The relative importance of each factor towards the ultimate production of the observed phenotypes can only be determined conclusively through extensive breeding experiments.

Maintenance of the Spine Polymorphism in the Population

The maintenance of a genetic polymorphism in a population involves the counteraction of gene flow between populations and natural selection by the environment. In the past selection pressures in nature were considered so low that interbreeding between polymorphs would obscure their differences, but selection coefficients as high as .77 have been found (Antonovics 1971). Maynard-Smith (1966)

maintains that in order to first establish a stable polymorphism in a heterogeneous environment a selective advantage of at least 30% is required, and this only in the face of habitat selection resulting in some reproductive separation of polymorphs.

Breeding Clusters and Spine-Size Morphs

Though long- and short-spined snails were noted to form separate breeding aggregations at Playa Estación (Yensen 1979), I did not find this to be the case. The few recaptured long-spined snails were intermixed in the breeding aggregations of predominantly short-spined snails. In the same aggregations with these recaptured long-spined snails, additional long-spined *Acanthina* were also found (Fig. 17, Table 2). In the three breeding clusters measured at Playa Estación 4.4%, 8.9% and 12.2%, a mean value of 8.6% of the *Acanthina angelica* in each cluster were long-spined snails. Of the total 409 snails marked at the beginning of the study 54 were considered long-spined, which estimates the percentage of long-spined snails in the adult population at 13.2%. The percentages of long-spined snails found in the observed breeding clusters does not differ significantly from the estimate of long-spined snails in the adult population ($t_{(2)} = 2.04$, $.10 < P < .05$).

The percentages of long-spined *Acanthina* in the five samples of breeding clusters at Punta Pelicano (Fig. 18, Table 2) have a mean value of 15.4%. The percentages of long-spined snails in the observed clusters at Punta Pelicano are higher than those found at Playa Estación and though I have no estimate of the percentage of long-spined snails in the adult population at large at Punta Pelicano, I suggest that this represents a true difference in the percentages of long-spined *Acanthina* in the two areas.

In the March census there appeared five additional marked long-spined snails in the T-II area which were not accounted for during the peak of clustering activity. Zones below the T-II area, however, were not included in the monthly census and consequently any clustering of these snails in that area would probably go undetected. It is possible that these long-spined snails and some of the other uncaptured long-spined snails were involved in clusters of only long-spined snails. In addition, the possibility that mating within an aggregation is non-random, such that ls snails mate with one another and ss snails mate with one another cannot be excluded since copulation was not observed. The time lag observed for peak clustering in ls snails could force such non-random mating. This seems unlikely, however, since even though short-spined snails peaked in their clustering activities in January at 54 and 62% for ss_B and ss_C

snails, respectively, a large percentage of these short-spined snails were still clustered in February (38 and 43%, respectively) (see Fig. 16). These snails were actively laying down egg cases at this time (pers. obs.).

I have made observations of intermixed breeding aggregations of long- and short-spined snails at Playa Estación and Punta Pelicano in proportions comparable to the proportion of long-spined snails in the adult populations. This in conjunction with my lack of any observations of separate, uni-spine morph aggregations suggests that mating and consequently gene flow between spine morph types can be substantial. This gene flow between morphs would work to mask any genetic polymorphism maintained by selective forces.

Post-Mating Distribution and Selection on Spine-Size Morphs

After breeding there is an influx of both long- and short-spined snails into the *Tetraclita* zone showing no initial selection of habitat based upon spine size or prey size (Fig. 9-11). Before the subsequent breeding season, however, the upper *Tetraclita* areas are once again inhabited by predominantly long-spined snails (Fig. 14). The 45% increase in the proportion of long-spined morphs in the *Tetraclita* area from April to October is largely a result of a decrease in the number of short-spined morphs

rather than an increase in the number of long-spined morphs. In light of the ability of *Acanthina* to change its spine length in the laboratory (Yensen 1979), one might have expected an increase in the number of long-spined morphs to correspond with the decrease in the number of short-spined morphs in the *Tetraclita* areas. Since this was not the pattern observed, the large loss in numbers of short-spined morphs can best be explained by either a strong selection against short-spined snails in the *Tetraclita* areas or the movement of short-spined snails from the *Tetraclita* area to a more suitable habitat, with the smaller barnacle prey.

Yensen (1979) predicted that snails in the field would not switch spine types if the cost of switching was greater than the gain resulting from foraging with a more efficient spine size. Abundance of the available barnacle prey, distance from the other choice of barnacle prey and density of snails in the area are all factors which might affect such a cost-benefit analysis. Paine (1966) found shell/spine length ratios of *Acanthina angelica* near San Felipe, Baja California Norte to decrease from 1959 to 1963 and he attributed this to fluctuations in the barnacle populations. The difference observed in the proportion of long-spined snails in the breeding populations at Playa Estación and Punta Pelicano (Table 2) is also considered

to reflect a difference in the abundance of *Tetraclita* in the two areas.

The selection of optimal habitat after breeding based on barnacle prey abundance and *Acanthina* densities, in conjunction with selection against morphs foraging with an "incorrectly-sized" spine appear to be two strong selective forces working to maintain the spine polymorphism in the populations of *Acanthina* in the vicinity of Puerto Peñasco. These selective forces appear to be incorporated in the term "disruptive switching" used by Yensen (1979) and are probably responsible for the distribution of predominantly long-spined snails in the *Tetraclita* area and short-spined snails in the *Chthamalus* areas. The effects of selection are masked, however, due to the gregarious behavior of *Acanthina angelica* and the intermixing of long- and short-spined morphs during the breeding season. Consequently, the spine polymorphism does not appear to be stabilizing in the population. All the evidence available indicates that *Acanthina* spine size is a plastic character which can vary in response to the availability of the barnacle prey (Yensen 1979) and this in turn determines the proportion of each spine morph in the population.

At Playa Estación sand movement following storms can result in the inundation of large masses of both barnacle

species (Yensen, pers. commun.; Turk, pers. obs.). Sand disturbance is known to have significant effects on the structuring of other intertidal communities at Playa Estación (Mackie, pers. commun.; McCourt, pers. commun.). The extreme temperatures and tides in the northern Gulf of California provide a temporally fluctuating and sometimes unpredictable environment for *Acanthina*. Figures 4, 5 and 6 illustrate the diversity of habitat encountered by *Acanthina angelica* in the vicinity of Puerto Peñasco.

Short-term adaptability with respect to spine length in *Acanthina* enables *Acanthina* populations to successfully exploit the heterogeneous environment they inhabit and in addition it protects them from over-specialization in an environment where there are often extreme and unpredictable temporal fluctuations. The ability of individuals to respond to these fluctuations within a generation would seem to increase their overall fitness. Genetic fixation of spine size, on the other hand, would seem to reduce *Acanthina's* ability to respond to its fluctuating environment and in such an extremely heterogeneous and temporally variable environment as the northern Gulf of California would decrease its overall fitness.

CHAPTER V

CONCLUSIONS

1) The *Acanthina angelica* populations studied at Playa Estación begin a general downshore intertidal migration in November, the month of sharpest drop in monthly mean sea surface temperature.

2) Clustering behavior and the laying of egg masses is strongest in January and February, the months of lowest sea surface temperature at Playa Estación.

3) Both long- and short-spined *Acanthina angelica* were found intermixed in the same breeding aggregations at Playa Estación and at Punta Pelicano. At Playa Estación a mean of 8.6% of the clustered snails were long spined. This is not significantly different from an estimate of the proportion of long-spined snails in the adult population before breeding at Playa Estación, at 13.2%. At Punta Pelicano a mean of 15.4% of the clustered snails were long spined.

4) Juvenile snails disperse into the lower end of the intertidal range of *Acanthina* after hatching; they do not disperse into the upper *Tetraclita* areas.

5) Adult *Acanthina* disperse throughout the intertidal range of *Acanthina* after breeding, but they generally

migrate up the shore and into the *Tetraclita* outcrops at Playa Estación.

6) In April immediately after breeding both long- and short-spined snails were found in the *Tetraclita* areas. The number of short-spined snails in these areas was significantly reduced by the following October.

7) This seasonal change in total number of snails in the *Tetraclita* area, resulting in predominantly long-spined snails there before the breeding season has been attributed to "disruptive switching" (Yensen 1979) resulting in habitat selection. Habitat selection based on the availability of the barnacle prey species could be responsible for maintaining the spine polymorphism in the populations of *Acanthina* at Playa Estación. The force of this selection would tend to be masked by gene flow between long- and short-spined morphs, and consequently the spine polymorphism will probably not be evolutionary stabilized in the population.

8) In conclusion, the ability of *Acanthina angelica* to respond to fluctuation in available prey by changing its spine length enables it to best utilize a heterogeneous environment reducing competition without over-specialization. Such adaptability would tend to increase its fitness in a highly fluctuating, unpredictable heterogeneous environment such as the northern Gulf of California.

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