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# Variations in population structure in the genus *Tetraclita* (Crustacea: Cirripedia) between temperate and tropical populations. I. Fecundity, recruitment, mortality and growth in *T. rubescens*

by

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**Abstract:** Studies in a population of *Tetraclita rubescens* in Ellwood and Arroyo Hondo, California indicate that individuals of this species reach sexual maturity at the end of the second year of life but reproduction occurs in the third year. Recruitment seems to be lower when compared with other barnacle species. The results suggest that successful recruitment occurs every two years.

As expected, the mortality is extremely high in the Zero and one year old classes. Predation appears to be important as a factor controlling differential mortality rates.

When the two study sites are compared no significant differences are found on the growth rate of barnacles. The younger age classes exhibit a period of rapid growth during the winter and early spring. Growth then tends to be fairly constant.

Most of the information available on the characteristics of single species populations refers to a particular latitude. However, for many years, it has been observed that there are differences in the rate of growth between populations latitudinally separated, presumably due to temperature differences. These differences may affect not only the growth rate but also such characteristics as life expectancies, fecundity, age at first maturity, etc.

Generally, the assumption has been made that species of marine organisms which inhabit the colder waters of the higher latitudes grow slower, attain a larger size and have a greater longevity than individuals of the same or closely related species from warmer waters.

Thus, Weymouth *et al.* (1931), demonstrated that growth in clams from southern localities is more rapid but less sustained than in northern populations. This should produce smaller size and shorter life span. No single explanation, however, was proposed to account for these differences, although temperature was suggested as a major factor. P.W. Frank (personal communication) in comparing populations of *Tegula funebralis* from California and Washington, found that individuals of this species along the coast of California were no older than 10 years, while those from Washington live up to 30 years.

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Newcombe (1936) Swan (1952) and Thorson (1936) have also considered latitude as an important factor contributing to differential growth rates.

It is thus the objective of this study to compare the structure of latitudinally separated populations of species of the genus *Tetraclita* (e.g. *T. rubescens* in California and *T. stalactifera* in Costa Rica).

## RESULTS AND DISCUSSION

**Areas of study and notes on distribution of** *Tetraclita:* Two localities near Santa Barbara on the California coast were chosen for detailed work. The first was on intertidal area of boulders and sand about 15 miles west of Santa Barbara on the Burman Oil and Gas property at Ellwood ($34^{o}$ 25'N). This area has a gently sloping shoreline of shallow sand overlying Monterey shale, with small to large boulders scattered on the beach. These boulders are densely covered by the barnacles *Chthamalus fissus* and *Balanus glandula* and to a less extent by patches of the mussel *Mytilus californianus* and the clonal budding phase of the anemone *Anthopleura elegantissima.*

The second is an area located in Arroyo Hondo, some 14 miles west of Ellwood. In this area, continuous reefs of Monterey shale project approximately 1 m high, parallel to the shoreline. Stimpson (1970) indicated that these reefs lie between the minus one foot and plus five feet tide level. The mussels *M. californianus* and *M. edulis* grow in clumps on exposed surfaces. Tight colonies of the cirriped *Pollicipes polymerus* often interrupt the otherwise continuous beds of the mussels.

The thatched barnacle, *T. rubescens* (Fig. 1) appears to be a relatively rare component of the intertidal fauna of the west coast of temperate North America. Although small groups occur in both exposed and semi-exposed surfaces of boulders and reefs, its relative density is fairly low when compared with such abundant barnacle species as *Chthamalus* and *Balanus.* Densities of up to 49 individuals of these species per square centmeter have been recorded by Connell (1961), which contrasts highly with the observed densities of *Tetraclita* at any of the study sites (Table 1).

**Fecundity:** Table 2 summarizes the proportion of individuals of different ages that contained eggs, from monthly collections of *Tetraclita* during 1975 at both Ellwood and Arroyo Hondo. Individuals of *Tetraclita* seem to reach sexual maturity at the end of the second year, which contrasts highly with the pattern observed in other barnacles. Thus, Crisp and Bhupendra (1960) noted that the barnacle *Elminius modestus* reaches maturity within a few weeks of settlement. In *Tetraclita,* sexual maturity seems to be primarily dependent on age and to a less extent on size. For example, incipient egg masses were first noted in barnacles two years old, independently of individual size.

Undeveloped egg masses first appeared during February, 1975. At that time, no eggs were observed in individuals of the Zero and one year old classes. Those observed in individuals of the second year class seemed to be smaller, thinner and showed a paler yellow coloration than those of older year classes. In the latter, the egg masses completely fill the ovary, located at the base of the mantle cavity. The egg masses were thicker and showed a deep yellow coloration.

Most *Tetraclita* individuals were observed bearing unfertilized eggs even by late fall, 1975. Fertilization occured in 1976 and larvae were released by mid-fall.

TABLE 1

*Comparison of physical and population characteristics at Ellwood and Arroyo Hondo, California*

| | Ellwood | Arroyo Hondo |
|---|---|---|
| Habitat characteristics | Isolated boulders | Reefs |
| Percent bare rock | 11 | 27 |
| Mean number of predatory snails/$m^2$ | 72 | 26 |
| Mean number of *Pisaster ochraceus*/100 $m^2$ | 1 | 10 |
| Mean number of *Tetraclita* /$m^2$ | 19 | 24 |
| Mean number of *Lottia*/$m^2$ | $<$20 individuals on the entire boulder field | 3 |

**Recruitment:** Recruitment seems to be extremely low in *Tetraclita* and restricted to a very short period (October through December). This markedly contrasts with the pattern observed in other barnacle species. In *Chthamalus fissus,* for example, at least three settlements per year were observed at both Ellwood and Arroyo Hondo, each showing very high densities. Similarly, Crisp and Davies (1955) found *E. modestus* able to produce several broods in one season.

Differences in the recruitment of *Tetraclita* were observed at Ellwood in 1974 and 1975. Tiny individuals were first noted in January, 1975. These comprised approximately 6% of the population (Fig. 2). In contrast, in spite of careful observations in December, 1975 and early January, 1976, no evidence was found of the 1976 year class as being present on the boulders (Fig. 3), even though larvae may have been released by a small fraction of the population as indicated in Table 2.

Recruitment appears to be slightly higher at Arroyo Hondo, but still seems to be fairly low when compared with other species. As in Ellwood, similar differences in the recruitment of *Tetraclita* were also found in Arroyo Hondo in 1974 and 1975. Observations made in January, 1975 showed tiny *Tetraclita* as being abundant on the reef surfaces. In fact, 10% of the population sample taken in February belonged to the Zero year class (Fig. 2). In contrast, the Zero year class comprised only 4% of the population sample taken in late December, 1975 (Fig. 3). This drop in the recruitment of *Tetraclita* in both localities is correlated with the observation that in 1975 most of the barnacles did not release any larvae, but kept unfertilized eggs during the entire year. From these results, it is suggested that successful recruitment in *Tetraclita* occurs every two years, and that the whole population is synchronized, regardless of age. In fact, the settlement that occurred in late fall of 1976 was a dense one, as in 1974.

TABLE 2

*Proportion of individuals of different ages that contained undeveloped eggs or developing larvae from monthly collections of* Tetraclita *during 1975 at both Ellwood and Arroyo Hondo*

| Date | Age | Number of individuals in sample | %With undeveloped eggs | %With developing larvae |
|---|---|---|---|---|
| | 0.2 | 5 | 0 | 0 |
| | 1.2 | 8 | 0 | 0 |
| FEBRUARY | 2.2 | 7 | 72 | 0 |
| 1975 | 3.2 | 5 | 100 | 0 |
| | ≥4.2 | 3 | 100 | 0 |
| | 0.5 | 6 | 0 | 0 |
| | 1.5 | 5 | 0 | 0 |
| MAY | 2.5 | 4 | 100 | 0 |
| 1975 | 3.5 | 7 | 100 | 0 |
| | ≥4.5 | 4 | 100 | 0 |
| | 0.8 | 3 | 0 | 0 |
| | 1.8 | 7 | 0 | 0 |
| AUGUST | 2.8 | 6 | 100 | 0 |
| 1975 | 3.8 | 5 | 100 | 0 |
| | ≥4.8 | 4 | 100 | 0 |
| | 0 | 3 | 0 | 0 |
| | 1 | 6 | 0 | 0 |
| NOVEMBER | 2 | 8 | 100 | 0 |
| 1975 | 3 | 6 | 100 | 0 |
| | ≥4 | 7 | 86 | 14 |

**Growth:** Growth studies were initiated in August, 1974 for the Ellwood sample and in January, 1975 for the Arroyo Hondo sample. Barnacles were marked by placing a drop of "Loctite" a quick-set adhesive, on the surface of test along with a self-adhesive numbered tag. A coat of the same adhesive dried as a transparent film within 10 minutes. Test diameter was recorded by means of a Mitutoyo dial caliper (0.05 mm graduation). Measurements were taken at monthly intervals during low tides. The results are presented in Table 3 and Figure 4.

No significant differences were found in the growth rates between barnacles at Ellwood and those at Arroyo Hondo (Fig. 5). By following for one year the growth increments of the very small individuals that had settled in late autumn of 1974 (the Zero age class), it was possible to obtain the growth rate during the first year of life (Table 4). Using the upper limit of the range of sizes of these known one year-olds, the one year class was identified in November, 1974 and their annual

TABLE 3

*Monthly net growth increments in diameter of individuals of* Tetraclita rubescens *from Ellwood and Arroyo Hondo. Each value represents the mean increment of a population sample from the two areas*

Monthly average net growth increment in Cm

| YEAR CLASS | N | 1974 S | O | N | D | 1975 J | F | M | A | M | J | J | A | S | O | N |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 74 | 16 | | | | | 1.17 | 1.48 | 1.31 | 1.04 | 1.06 | 1.02 | .98 | .76 | .62 | .55 | |
| O | | | | | | | | | | | | | | | | |
| 73 | | .90 | .48 | .68 | | | | | | | | | | | | |
| 73 | 36 | | | | .64 | .85 | .91 | .90 | .65 | .68 | .54 | .60 | .54 | .61 | .57 | .74 |
| 1 | | | | | | | | | | | | | | | | |
| 72 | 12 | .80 | .65 | .30 | | | | | | | | | | | | |
| 72 | 21 | | | | .29 | .43 | .76 | .72 | .63 | .54 | .32 | .36 | .38 | .40 | .39 | |
| 2 | | | | | | | | | | | | | | | | |
| 71 | 11 | .61 | .72 | .58 | | | | | | | | | | | | |
| 71 | 22 | | | | .40 | .42 | .36 | .23 | .25 | .30 | .15 | .15 | .18 | .23 | .18 | |
| 3 | | | | | | | | | | | | | | | | |
| 70 | 20 | .56 | .46 | .29 | | | | | | | | | | | | |
| 70 | 10 | | | | .39 | .11 | .10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 4 | | | | | | | | | | | | | | | | |
| 69 | 14 | .60 | .42 | .46 | | | | | | | | | | | | |
| >69 | 15 | | | | .39 | .26 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| >4 | | | | | | | | | | | | | | | | |

growth followed, and so on for older age class. Although the samples studied also contained barnacles older than five years, it was practically impossible to ascertain their age, due to their very slow and variable growth rates. A conservative estimate, however, is that barnacles 40 mm across are probably around 20 to 25 years old.

As shown in Figure 4, there is a definite trend of the younger age classes to exhibit a period of rapid growth during the winter and early spring. The growth then tends to be fairly constant. As expected, the Zero year class exhibited the fastest growth rate. As the maturing barnacles start to allocate more energy into reproduction, their growth slows down (Fig. 6). Similar growth patterns have been observed by Barnes and Powell (1953) in *Balanus crenatus* and Connell (1961) in *B. balanoides.* As seen in Figure 6, in 2 to 4 year old barnacles, there is a gradually reducing trend when the growth in September and October, 1974 is compared with that in the corresponding months of 1975. Barnacles less than 2 years old showed similar growth during 1974 and 1975. This finding seems to be correlated with the observed absence in these barnacles of egg masses during the same periods. That is, the growth rate in barnacles less than 2 years old appears to be relatively independent of reproduction, mainly because these barnacles seem to reach sexual maturity at the end of the second year.

**Mortality:** Annual rates of mortality were estimated by determining the percentage of individual tagged barnacles lost in a year period. As seen in Figure 7, mortality appears to be extremely high in the Zero and one year old classes and diminishes with age. This pattern also applies to the Arroyo Hondo population, but the mortality was lower except for the oldest classes. These differences, as will be discussed in a later paper, may be the result of greater predation intensities upon different age classes, as well as the result of competition being stronger in Ellwood than in Arroyo Hondo.

TABLE 4

*Mean growth increments for November, 1974 through November, 1975, and mean size for each age class of individuals of* T. rubescens *from Ellwood and Arroyo Hondo*

| Age at Start of the year | Meam size (mm) | | | | | | Mean net increment/ year (mm) |
|---|---|---|---|---|---|---|---|
| | November 1974 | | | November 1975 | | | |
| | N | $\overline{X}$ | RANGE | N | $\overline{X}$ | RANGE | |
| 0 | | | | 16 | 12.7 | 10.5 - 14 | 12.7 |
| 1 | 46 | 12.1 | 11.2 - 14.5 | 36 | 20.5 | 17.5 -21.5 | 7.8 |
| 2 | 28 | 21 | 16.5 - 22 | 21 | 26.3 | 23 - 27.5 | 5.8 |
| 3 | 25 | 25.8 | 24 - 27 | 22 | 29.4 | 27.5 - 31.5 | 3.1 |
| 4 | 13 | 29.1 | 27.5 - 32 | 10 | 30.5 | 28.5 - 33 | 1.06 |

Fig. 1. Typical isolated *Tetraclita rubescens* at Ellwood, California.

## ACKNOWLEDGMENTS

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## RESUMEN

Estudios realizados en poblaciones del cirripedio *Tetraclita rubescens* en Ellwood y Arroyo Hondo, California indican que los individuos de esta especie alcanzan la madurez sexual al final del segundo año de vida aunque la reproducción no ocurre hasta el próximo año. El reclutamiento observado es relativamente bajo cuando se compara con otras especies de cirripedios. Los resultados sugieren que un reclutamiento exitoso ocurre cada dos años.

Como es de esperar, la mortalidad es extremadamente alta en la clase zero y en la de un año. La depredación parece ser importante como un factor que controla la mortalidad en diferentes clases de edades. Cuando se comparan los dos sitios de estudio, no se observan diferencias significativas en la tasa de crecimiento de los cirripedios. Las clases de edad más jóvenes exhiben un período de rápido crecimiento durante el invierno y principios de primavera. Posteriormente, el crecimiento tiende a ser más o menos constante.

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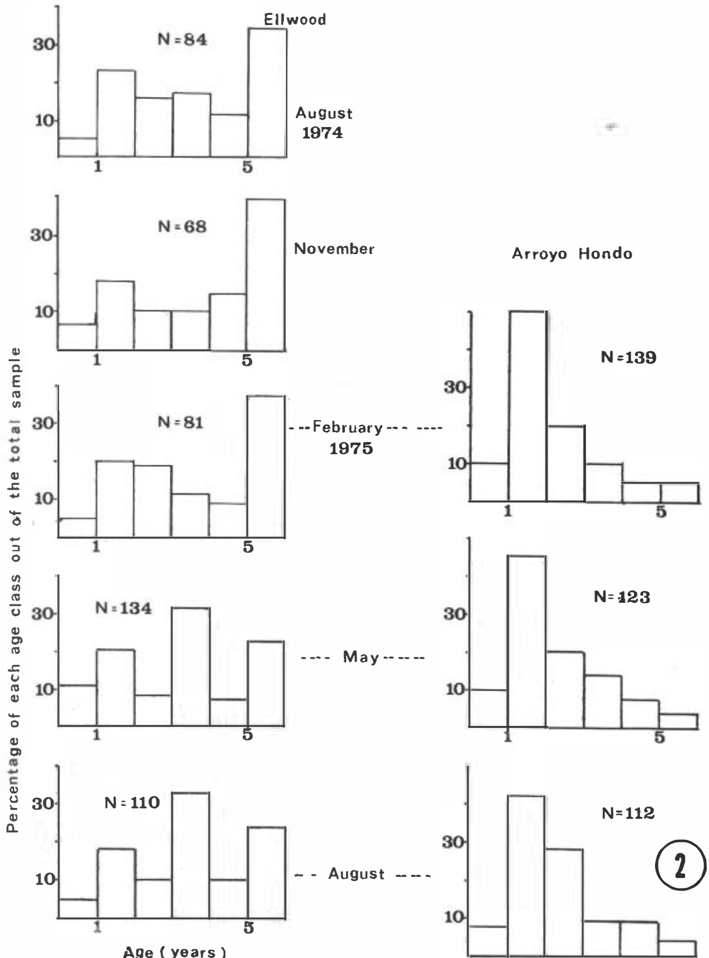
Fig. 2. A comparison of the age structure of *Tetraclita rubescens* between Ellwood and Arroyo Hondo.

Fig. 3. A comparison of the age structure of *Tetraclita rubescens* in December, 1975.
A. Ellwood
B. Arroyo Hondo
C. Carmel


Ellwood
Arroyo Hondo
August
1974
November
--- February --- ----
1975
---- May -----
-- August ---
N = 84
N = 68
N = 81
N = 134
N = 110
N = 139
N = 123
N = 112
30
10
1
5
Percentage of each age class out of the total sample
Age ( years )

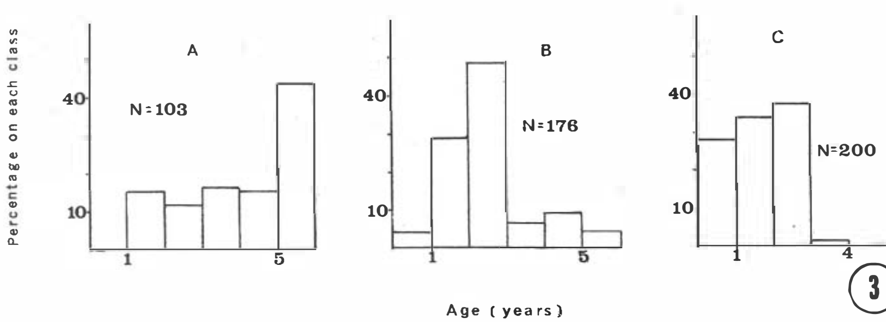

A
B
C
N = 103
N = 176
N = 200
40
10
1
5
4
Percentage on each class
Age ( years )
3

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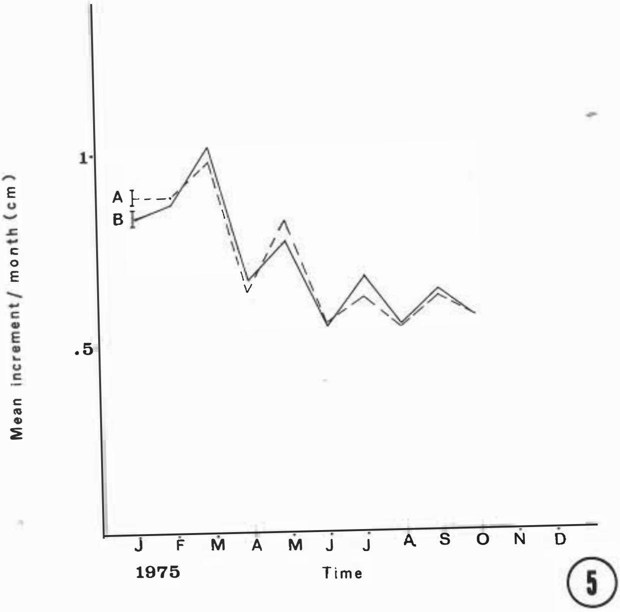
Fig. 4. Monthly mean increments of individuals of *T. rubescens* from Ellwood and Arroyo Hondo. Vertical lines denote standard erros for each sample. Standard errors are highly consistent for each year class.

Fig. 5. A comparison of the growth rates of the first year class of *T. rubescens* between a sample from Ellwood (A) and Arroyo Hondo (B). Vertical lines denote standard errors in January, 1975. These were similar in other monthly samples.


Mean increment / month (cm)
1
.5
A
B
J F M A M J J A S O N D
1975
Time
5

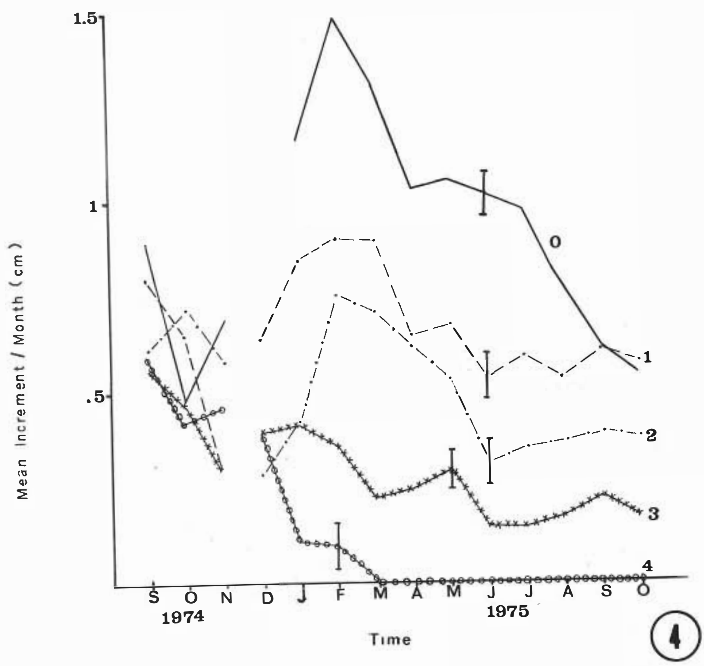
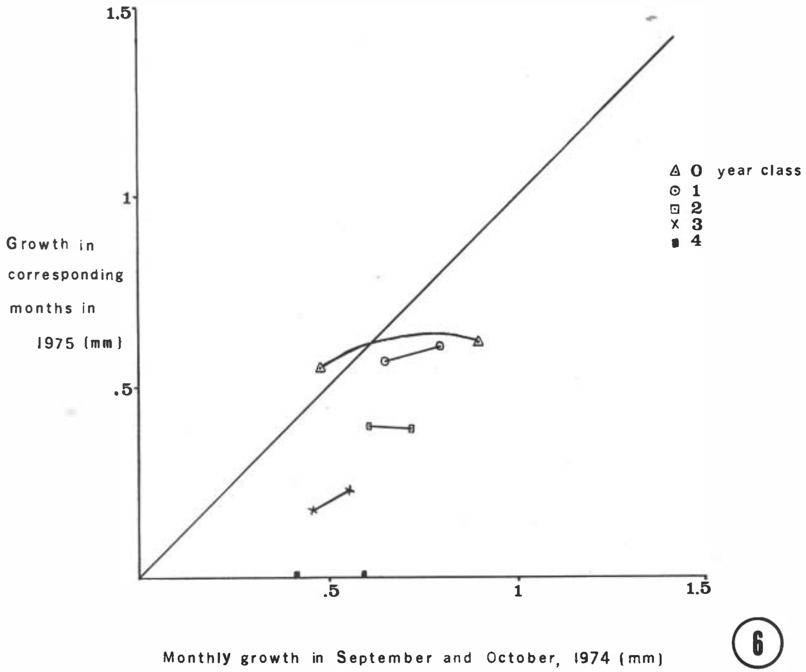

Mean Increment / Month (cm)
1.5
1
.5
0
1
2
3
4
S O N D J F M A M J J A S O
1974
1975
Time
4

Fig. 6. Monthly growth in September and October, 1974 and 1975 of individuals of *T. rubescens* from Ellwood and Arroyo Hondo.

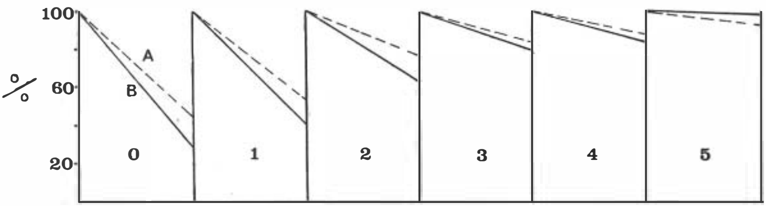
Fig. 7. Percentage survival of each age class during November of 1975.

A. Ellwood

B. Arroyo Hondo


1.5
1
.5
Growth in
corresponding
months in
1975 (mm)
0 year class
1
2
3
4
.5
1
1.5
Monthly growth in September and October, 1974 (mm)

6


100
60
20
%
A
B
0
1
2
3
4
5

7