Rev. Biol. Trop., 27(2): 293-300, 1979

Variations in population structure in the genus *Tetraclita* (Crustacea: Cirripedia) between temperate and tropical populations. II. The age structure of *T. rubescens*

by

Carlos R. Villalobos *

(Received for publication May 22, 1979)

Abstract: Observation of *Tetraclita rubescens* in Ellwood, Arroyo Hondo and Carmel, California, showed significant differences in size distribution and age structure. At Ellwood, the age structure seemed to be characterized by a dominance of the older age classes. At Arroyo Hondo, most of the barnacles belonged to the younger age classes. In Carmel, 99% of the population was under three years of age. Competition and predation seem to be the main factors responsible for such differences.

Differences in the age structure of latitudinally separated populations have been observed in several marine organisms (Frank, 1969; Dehnel, 1956). In most cases, attention has been focussed on the role of physical factors (e.g. temperature) as critically responsible for such differences. Little attention has been paid to the possible role of biological interactions in producing these differences. The role of biological interactions (e.g. competition, predation) has been more often recognized with regard to local populations. Thus, Connell (1972) observed that the selective feeding behavior of predatory snails in Scotland accounted for the differences in age structure exhibited by barnacles at different shore levels.

MATERIAL AND METHODS

As explained in a previous paper (Villalobos, 1979) the age structure of the barnacles was determined from growth rates and size distributions at both Ellwood and Arroyo Hondo.

RESULTS AND DISCUSSION

Preliminary observations on the size distribution of *Tetraclita* in Ellwood and Arroyo Hondo suggested that biological interactions might be involved in producing the observed differences (Fig. 1). At Ellwood, a high proportion of the barnacles were large, that is, the age structure seemed to be characterized by a dominance of the older age classes. At Arroyo Hondo, on the contrary, large barnacles were fairly

* Escuela de Biología, Universidad de Costa Rica.

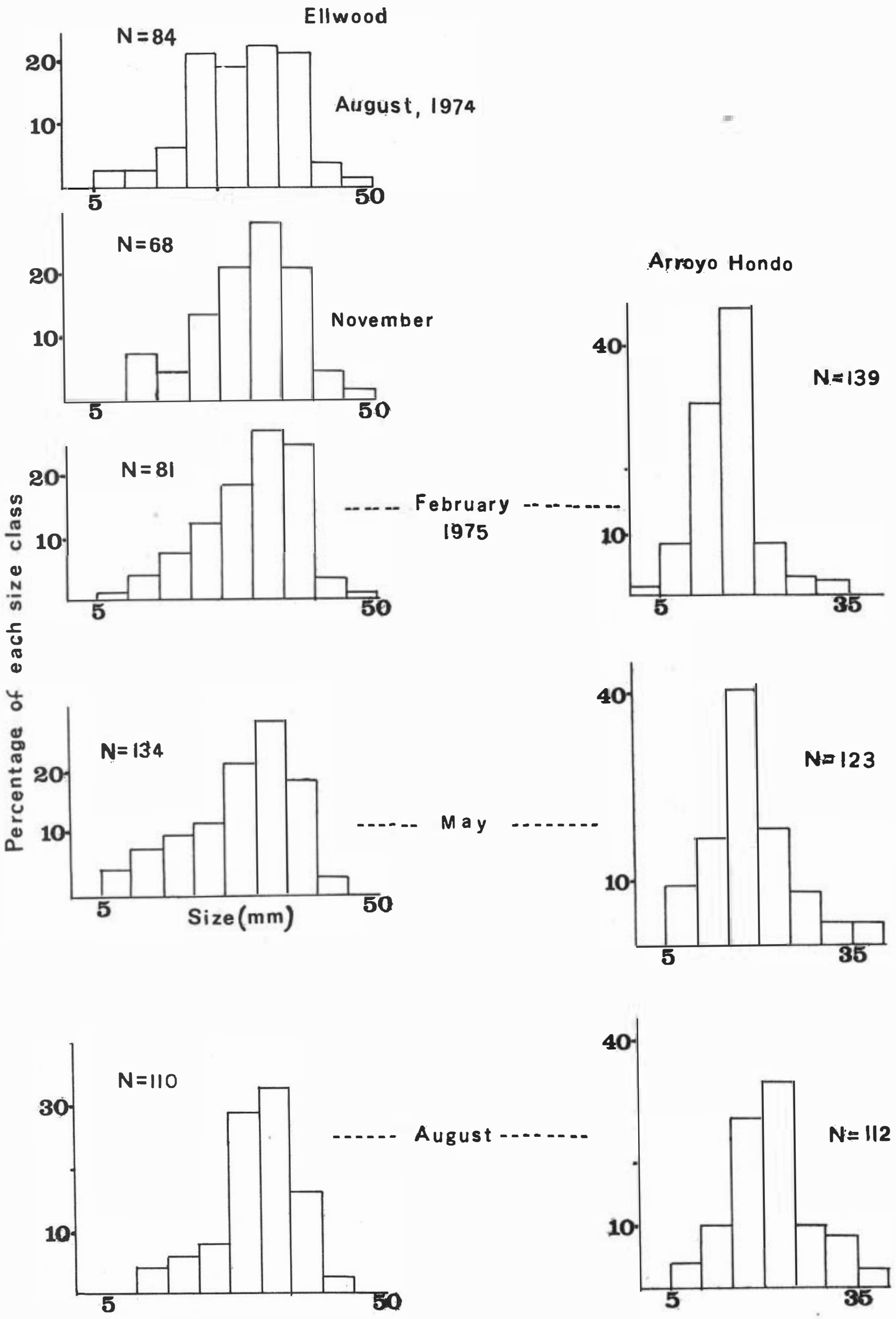

Fig. 1. Size distribution of *Tetraclita rubescens* at Ellwood and Arroyo Hondo, California.

rare and the age structure appeared to be characterized by predominantly younger classes. At least three mechanisms could explain such differences: mortality during the planktonic larval stages; competition for space; and predation by snails and starfishes.

Planktonic mortality: Evidence concerning planktonic mortality is lacking. Mortality on the free-swimming larval stages has been well demonstrated for several other intertidal invertebrates (Pyefinch, 1950). However, this factor does not appear to be significant in the case of *Tetraclita* because mortality in the larval stages should be about the same for both localities, since they are only a few miles apart. Also, several heavy settlements of *Chthamalus* were observed at both areas during the year, providing evidence that recruitment is possible in both areas. Therefore, although planktonic mortality may eliminate a fraction of the larval population, this cannot account for the differences between the two places.

Competition for space: To get estimates of the amount of open space, counts of *Lottia gigantea* and line transects were used. Density estimates for *Lottia* were made in Arroyo Hondo in November, 1975, by using quadrats 0.5m x 0.5m along transects of various lengths. This method proved to be impractical at Ellwood, due to the patchy distribution of boulders. Hence, a relative density estimate was obtained by counting the number of individuals in the entire boulder field. The results are shown in Table 1. A comparison, in terms of percentage of clear space, between the three localities is also presented in Table 1. These data were obtained by estimating the amount of bare rock observed directly underneath a transect 23 m long. There is twice as much open space at Arroyo Hondo as at Ellwood. This is presumably due to the presence in Arroyo Hondo of many *Lottia* territories and to physical disturbances by local fishermen. Although different methods were used to estimate the relative density of *Lottia* between the two areas, the difference is nevertheless highly significant. No more than 20 *Lottia* were observed on the entire boulder field. At the main study reef in Arroyo Hondo, on the contrary, a mean density of 3 *Lottia* per square meter was noted. Densities of up to 5 *Lottia*/m^2 were observed on some other reefs at Arroyo Hondo on which no *Tetraclita* individuals occur. These reefs are located a few meters shoreward above what seems to be the upper limit for the vertical distribution of these barnacles. Several areas 0.5m x 0.5m were scraped clean and sterilized with 10% formalin at Ellwood in May, 1975 in order to provide cleared space on which *Tetraclita* could settle. However, several heavy settlements of the fast-growing barnacle *Chthamalus* and the opportunistic alga *Ulva* occured in August and October, previous to the annual *Tetraclita* settlement in November. The *Chthamalus* and algae were removed from some of the cleared areas in October but again, additional settlements of *Chthamalus* in November and early December probably prevented *Tetraclita* from setting on the available surfaces. In the census of the population at Ellwood in early December, 1975, there were no Zero year class individuals present (Fig. 1). It is important to point out that this absence of the Zero year class appears not to be exclusively due to competition. Observations on adult barnacles collected at monthly intervals during 1975 showed unfertilized egg masses even by late fall. In other words, most of the local barnacles did not produce larvae during 1975. A similar pattern has been observed in some other barnacle species. Thus, adult barnacles of *Balanus balanoides* seem to brood the nauplii for several months before releasing them. As pointed out by Barnes (1956), in some instances this delay in releasing the larvae appears to be correlated with the plankton blooms. With regard

TABLE 1

Comparison of several characteristics of the three study sites in California

	Ellwood	Arroyo Hondo	Carmel
Habitat characteristics	Isolated boulders	Reefs	Continuous rocky areas
Percent bare rock	11	27	10
Mean number of predatory snails/m^2	72	26	6
Mean number of *Pisaster ochraceus*/100 m^2	1	10	2
Mean number of *Tetraclita*/m^2	19	24	210
Mean number of *Lottia*/m^2	$<$20 individuals on the entire boulder field	3	–

to *Tetraclita,* however, this seems unlikely. Censuses of the population at Ellwood in August and November of 1974, showed traces of the 1973 year class (Fig. 2). In addition, barnacles were observed still to be growing during the same period, even those older than 4 years in which the largest unfertilized egg masses were found. In 1975, however, these barnacles completely stopped growing. Hence, based on the available information, it is suggested that *Tetraclita* alternate their reproductive and growing seasons, once they reach maturity (at the end of the second year). The fact that barnacles of this species completely stopped growing during a full year may be an adaptation to increase the output of offspring. A higher proportion of energy during a longer period of time (one year) can be allocated to the development of eggs and larvae instead of to growth.

It is quite possible that a small fraction of the *Tetraclita* population did actually release larvae at Ellwood in 1975 but due to the lack of suitable space and the abundance of competing species, they did not survive to be individually recognized. This contention is supported by the fact that at Arroyo Hondo a small Zero year class was detected (9% of sample) by mid. December (Fig. 1).

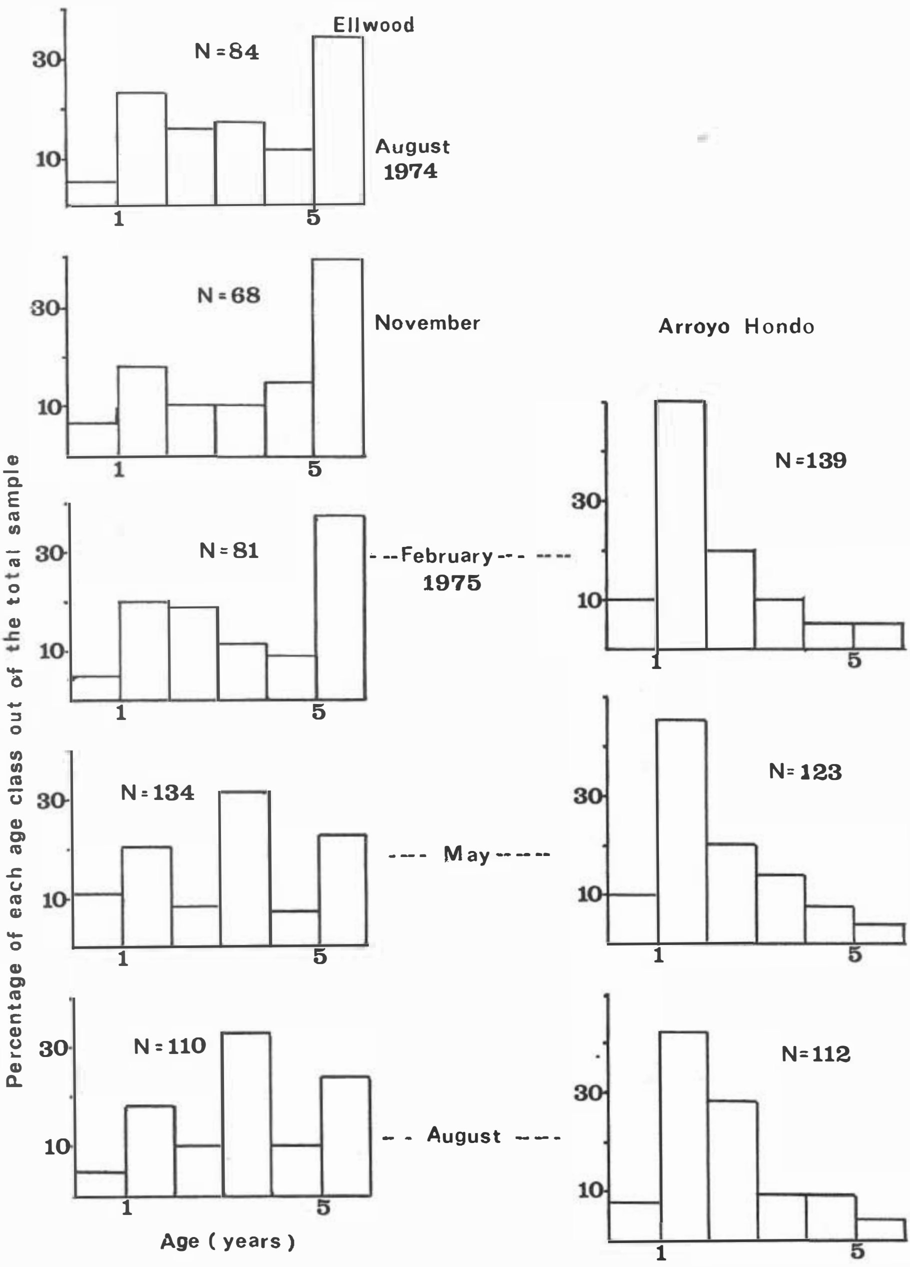

Fig. 2. A comparison of the age structure of *Tetraclita rubescens* between Ellwood and Arroyo Hondo.

Predation: Another mechanism proposed is that predation may be more severe at Ellwood than at Arroyo Hondo. Evidence to support this contention was obtained by comparing the relative densities of the snail predators, *Acanthina spirata* and *Thais emarginata,* in three different localities. This was done by using quadrats 0.5m x 0.5m along transects of various lengths. Similar data were also obtained from a population sample in Carmel, near the Monterey Peninsula. In addition, the relative density of the starfish, *Pisaster ochraceus,* was estimated in Ellwood and Arroyo Hondo. This starfish is known to feed occassionally on large barnacles (R. Landerberger, personal communication). In Arroyo Hondo, density was estimated by first measuring three reef areas and then counting the number of starfish in each area. A total of 80 starfish were counted in an area of 835 m^2. At Ellwood, due to the patchy distribution of boulders, it was necessary to search the whole area. Although one or two individuals were occasionally observed, none was found at that particular observation. The results are shown in Table 1, together with the mean number of small snail predators per square meter, which decreases from Ellwood to Arroyo Hondo and Carmel.

An inverse relationship between prey and predators is found when the mean number of barnacles per square meter is compared between the three areas. In other words, in addition to the discussed negative effects that competition for space may have on *Tetraclita* at Ellwood, the high density of the snail predators there lowers the survival rate of *Tetraclita.* This should explain the overall lower *Tetraclita* densities found at Ellwood. At Carmel, on the contrary, the number of predators is extremely low, and densities of *Tetraclita* are high.

A combined effect of predation by snails and starfish, on the other hand, could explain the observed differences in the age structure of *Tetraclita,* between Ellwood and Arroyo Hondo. As seen in Figure 1, the barnacle population of Ellwood seems to be characterized by a dominance of the older classes. In fact, 58% of the population is over 4 years old. At Arroyo Hondo, on the contrary, 73% of the population sample falls between 1 and 3 years of age, with only 19% being over 4 years. Similar results have been obtained by Dayton *et al.* (1974) who observed that when a prey has size-frequency distributions skewed toward the larger sizes, it suggests heavy mortality on the settled larvae or juveniles caused by predators.

The data obtained at Carmel are even more striking. Even if we assume that the growth rate of the barnacles at this locality is only one half of that exhibited by barnacles in either Ellwood or Arroyo Hondo, a trend that has been demonstrated for some other intertidal organisms (Frank, 1969), still the results show a very young population: at Carmel, 99% of the population sample was under 3 years of age. One possible explanation for these differences lies in the fact that at Ellwood there is a much higher density of predatory snails, which kill most of the young barnacles before they reach the age of one year, at which size, they are no longer eaten by snails. Because starfish are rare, older barnacles are almost free from predation. Thus, once the barnacles grow large enough to escape predation by snails, mortality is very reduced.

Similar observations were made by Connell (1970, 1972) when he pointed out that most of the mortality of barnacles at San Juan Island, Washington, was caused by predators. Furthermore, he also observed that if *Balanus cariosus* can survive for two years it is safe from smaller intertidal predators. In fact, only 30% of the 1975 Zero year class barnacles that were tagged at Ellwood in December, 1974, survived to the first year. This markedly contrasts with survivorships of up to 80% in barnacles over 3 years old at the same locality. Death of large barnacles was generally coincident with the occasional presence of an individual *Pisaster* on the same boulder.

In Arroyo Hondo, the number of predatory snails is relatively low (Table 1). This would account for the increased abundance of the younger age classes. However, due to the greater abundance of starfish, compared to Ellwood (one every 10 m^2, on the average), a smaller percentage of barnacles older than three years were observed. Although no data were collected in Carmel with regard to the relative density of starfish, it was found that the snail *Thais emarginata* reaches sizes over 35 mm in length. It is a reasonable assumption that such a big snail should preferentially kill barnacles over three years of age. Since the density of the snail is surprisingly low, younger barnacles should be relatively free from predation. This would explain why more than 90% of the *Tetraclita* population there is found in the younger age classes. In addition, it is also possible that starfishes may be present at higher densities during the summer. In fact, Paine (1974) observed such an increase in the density of *Pisaster ochraceus* during the summer at Mukkaw Bay, Washington.

To test the above expectations, experiments to exclude predators were initiated in October, 1975. At Ellwood snails were removed from two areas and were left undisturbed in a third area. Two additional areas were also cleared in the same boulder field in mid-October and again, predators, mainly *Acanthina spirata,* were experimentally removed from one of the areas. At Arroyo Hondo, in addition to the numerous naturally clear spaces on the reefs, three areas, a few meters apart, also 0.5m x 0.5m, were cleared in an adjacent reef. On all the cleared areas, copper paint was used to keep limpets out. Experimental removal of predators however, did not increase the recruitment of *Tetraclita,* mainly because, as discussed above only a small fraction of the population had developing larvae in 1975 and the experimentally cleared spaces were readily monopolized by *Chthamalus* and *Ulva.*

ACKNOWLEDGMENTS

I wish to express my gratitude to Drs. Joseph H. Connell, William Murdoch and Allan Oaten for reading and correcting the manuscript.

RESUMEN

Observaciones en tres sitios en la costa del Pacífico de California, EE.UU. sobre *Tetraclita rubescens* demostraron la existencia de diferencias significativas en cuanto a la distribución de tamaños y a la estructura de edades.

En Ellwood, la estructura se caracteriza por un marcado predominio de las edades más viejas En Arroyo Hondo, la mayoría de los individuos, por el contrario, pertenecen a las clases de edad más jóvenes. En Carmel, el 99% de la población es menor de 3 años de edad.

La competencia y la depredación parecen ser los factores principales responsables de estas diferencias.

REFERENCES

Barnes, H.
1956. The growth rate of *Chthamalus stellatus.* J. Mar. Biol. Ass. U.K., 35: 355-361.

Connell, J.H.
1970. A predatory prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecol. Monogr., 40: 49-78.

Connell, J.H.
1972. Community interactions on marine rocky intertidal shores. Ann. Rev. Ecol. Syst., 3: 169-192.

Dayton, P., G.A. Robilliard., R.T. Paine, & Linnea B. Dayton
1974. Biological accommodation in the benthic community at McMurdo, Antartica. Ecol. Monogr., 44: 105-128.

Dehnel, P.A.
1956. Growth rates in latitudinally and vertically separated populations of *Mytilus californianus*. Biol. Bull., 110: 43-53.

Frank, P.W.
1969. Growth rates and longevity of some gastropod mollusks on the coral reef at Heron Island. Oecologia, 2: 232-250.

Paine, R.T.
1974. Intertidal community structure: Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia, 15: 93-120.

Pyefinch, K.
1950. Studies on marine fouling organisms. J. Iron Steel Inst. London.

Villalobos, C.R.
1979. Variations in population structure in the genus *Tetraclita* (Crustacea: Cirripedia) between temperate and tropical populations. I. Fecundity, recruitment, mortality and growth in *T. rubescens*. Rev. Biol. Trop., 27: