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Variations in population structure in the genus *Tetraclita* (Crustacea: Cirripedia) between temperate and tropical populations. III. *T. stalactifera* in Costa Rica

by

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Abstract: Studies on the population structure of the cirriped *Tetraclita stalactifera* were conducted at two localities in Bahía Ballena, Nicoya Península, Costa Rica.

The results indicate that reproduction occurs every year. Well-developed gonads are present from April through August, the nauplii being clearly defined in October and November. Release of larvae takes place in late November and early December. As in California, the individuals reproduce the year after they reach sexual maturity.

The relative density is fairly constant through the year showing values slightly higher than those observed in northern populations. Mortality is heavy in the youngest size classes. It appears to be extemely low in individuals with a test diameter over 25 mm, in particular because of the lack of large predators.

As discussed in previous papers (Villalobos, 1979a, 1979b), there is a lack of information on the population characteristics of closely related species which are widely separated latitudinally.

Most of the work that has been done refers to a particular latitude (Swan, 1952; Dehnel, 1956; Harger, 1970). The work by Newcombe (1936), on the growth rate of *Mya arenaria* is one of the first studies in which a comparison was made between populations occuring in areas of significant ecological differences.

The first comprehensive study to recognize latitude as a factor influencing some population characteristics did not appear until 1931 with Weymouth, McMillin and Rich's work on the razor clam *Siligua patula*.

The present work presents the results of two years of observations on a population of the cirriped *Tetraclita stalactifera* in Costa Rica and the results are presented in such a way as to be comparable with those expressed in a previous paper (Villalobos, 1979a).

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RESULTS AND DISCUSSION

Areas of study and notes on distribution of Tetraclita: Two localities in Bahía Ballena, Nicoya Península (9°45') Costa Rica were chosen for the study. Both areas are located approximately 1 km southwest of the town of Tambor, Puntarenas Province (Fig. 1).

Area A is an intertidal zone of boulders and sand, some 400 m long and 100 m wide. Within this zone, an area of 1,000 m^2 with a gently sloping shoreline and with small to large boulders scattered throughout, was chosen for detailed work.

Individuals of *Tetraclita stalactifera* are primarily found on the exposed and semi-exposed surface of the boulders. The upper part of these boulders is almost bare rock, except for a few patches of the barnacles *Chthamalus panamensis* and *Balanus amphidrite.* On the vertical surfaces, *Tetraclita* alternates with the bivalves *Chama echinata* and *Ostrea palmula.* Another bivalve, *Brachidontes semilaevis* occurs in dense aggregations in the spaces between individuals.

In the lower parts of the mid-littoral region the gastropod *Siphonaria gigas* occurs scattered on top of boulders. The limpets, *Collisella pediculus* and *Notoacmea fascicularis* are also found on these boulders, but density of both species appears to be extremely low. The lower surfaces of the boulders are partially covered by the polychaete *Sabellaria* sp., but at a lower density than the northern *Sabellaria cementarium.* Scattered also in the lower surfaces and inside crevices, the predators *Acanthina brevidentata, Thais melones* and *Anachis rugosa* might be observed.

Area B is located about 500 m SW of Area A and consists of a series of concrete pilings that support a restaurant. These pilings are of two types: rectangular, with a mean surface area of approximately 0.85 m^2, or shaped like a truncate pyramid.

In this area, *Tetraclita* individuals occur mainly on the exposed surfaces alternating with *Chthamalus panamensis, Balanus amphidrite* and *Balanus* sp. Barnacles other than *Tetraclita* seem to be more abundant here than in Area A. *Ostrea palmula* is only occasionally found while *Chama echinata* is absent. As in Area A, *B. semilaevis* occurs in dense groups in the spaces between individuals of *Tetraclita.* The limpets *C. pediculus* and *N. fascicularis* are uncommon while *S. gigas* is absent.

Individuals of *Tetraclita* are also observed on the basal areas of the pilings where they alternate with *Sabellaria* sp. The predators *A. brevidentata, T. melones* and *A. rugosa* are restricted to the basal areas of the pilings but they also occur under stones scattered in between the lines of pilings.

Fecundity: Collections of *Tetraclita* were made at zones outside Areas A and B, from April, 1976 through December, 1977, in order to observe changes in the development and maturation of the gonads and eggs. The results are presented in Table 1. Although well-developed eggs were found in the larger individuals, both in April, 1976 and April, 1977, most nauplii appeared in October and November. Well-developed gonads bearing no eggs were observed in the samples taken in December, January, and February, thus indicating that release of larvae occurs mainly in late November and early December. This pattern is fairly similar to the one previously observed in populations of *Tetraclita* in California (Villalobos, 1979a). The results also indicate that in Costa Rica, as in California, individuals of *Tetraclita* reach sexual maturity at a size approximately 20 mm in diameter. In addition, it was found that most individuals in the size category 20.00–29.00 mm, bearing well-developed eggs, belong to the upper part of this range. This suggests that, as in California, individuals do not reproduce the year they reach sexual maturity, but the following year.

Recruitment: Larvae of *Tetraclita* begin to settle on the rocky surfaces around the middle of October. Observations on the size distribution appear to indicate that recruitment is slightly higher at Area B. In fact, 18% of the population sample taken at Area B in March 1976, belongs to what is probably the 1975 Zero year class. In contrast, the Zero year class comprised only 6% of the sample taken in the same month at Area A (Fig. 2) A similar pattern was observed for the 1976 Zero year class when both areas were compared in late December, 1976. However, in January when censuses were made, a high mortality was noted at Area B, particularly in the small individuals. This explains the lower percentage shown in Fig. 2 in January 1977 for Area B.

Recruitment occurs every year, which highly contrasts with the pattern observed in California. As will be discussed later, a combined effect of high temperature and strong predation intensity on the smallest size classes results in high mortality rates that requires an annual reproductive cycle.

The absence of large barnacles in Area B can be explained by the fact that the pilings were built in 1971. Hence, the small fraction (< 3%) of barnacles with a test size between 30 mm and 40 mm probably represents the survivors of the first settlement that occurred at that time.

Density: Estimates on the relative density of *Tetraclita* were made at three-month intervals beginning in April, 1975, for areas A and B by using quadrats 0.5 x 0.5 m randomly distributed. The results are shown in Table 2.

The relative density is fairly constant and seems to be higher at Area A. This is due to a greater availability of substrate as a consequence of large boulders being fairly common. At Area B, it is only the lower half of the pilings that is suitable for colonization.

The overall density of *Tetraclita* at both study sites is significantly higher than that exhibited by northern populations (Villalobos, 1979b). Again, a greater availability of substrates as well as an annual reproductive season may result in larger populations in Costa Rica.

Mortality: Mortality rates were estimated by determining the percentage of individual tagged barnacles lost in a year. The results indicate that mortality is fairly high in individuals less than 20 mm in diameter at both study sites. At area A, a combined effect of predation by snails and high environmental temperatures that result in rapid evaporation rates, may explain the mortality in the youngest individuals. In fact, temperatures up to 46 C were recorded at midday, during low tides on the surface of the boulders. This contention is also supported by the fact that mortality in the smallest size classes is about 20% lower on the surfaces of the pilings which are not directly exposed to the sun. At area B, therefore, mortality in these groups is primarily due to predation by snails. Predator exclusion experiments significantly increased the survival of young *Tetraclita.*

Figures 3 and 4 show the vertical distribution of the main predators as well as values on the relative density of each species for both areas. At area B *Acanthina brevidentata, Planaxis planicostatus* and *Thais melones* seem to be the most important predators. As seen in Figure 3, the vertical distribution of these three species matches the corresponding distribution of *Tetraclita* (broken line). The vertical distribution of *Anachis rugosa* has little overlap with the distribution of *Tetraclita.*

TABLE 1

Proportion of individuals of different sizes that contained undeveloped eggs, well-developed or nauplii from collections of Tetraclita *at monthly intervals during 1976 and 1977*

Date	Size category (mm)	Individuals in each category	Percentage undeveloped eggs	Percentage well-developed eggs	Nauplii
April 1976	0 – 9.99	0	0	0	0
	10.00 – 19.99	27	100	0	0
	20.00 – 29.99	27	14.8	29.65	0
	30.00 – 39.99	23	0	100	0
May	0 – 9.99	0	0	0	0
	10.00 – 19.99	77	100	0	0
	20.00 – 29.99	55	12.73	20	0
	30.00 – 39.99	3	0	100	0
June	0 – 9.99	00	0	0	0
	10.00 – 19.99	96	100	0	0
	20.00 – 29.99	130	57.69	23.08	0
	30.00 – 39.99	7	0	100	0
July	0 – 9.99	0	0	0	0
	10.00 – 19.99	81	100	0	0
	20.00 – 29.99	55	54.55	7.27	0
	30.00 – 39.99	7	0	100	0
August	0 – 9.99	0	0	0	0
	10.00 – 19.99	85	100	0	0
	20.00 – 29.99	49	42.86	14.28	0
	30.00 – 39.99	6	0	100	0
September	0 – 9.99	0	0	0	0
	10.00 – 19.99	98	79.59	0	0
	20.00 – 29.99	38	60.53	0	0
	30.00 – 39.99	4	0	100	0
October	0 – 9.99	0	0	0	0
	10.00 – 19.99	33	96.97	0	0
	20.00 – 29.99	85	15.29	47.06	1.18
	30.00 – 39.99	19	0	84.21	5.26
November	0 – 9.99	0	0	0	0
	10.00 – 19.99	15	86.66	0	0
	20.00 – 29.99	96	2.08	9.38	7.29
	30.00 – 39.99	47	0	36.18	31 91
December	0 – 9.99	0	0	0	0
	10.00 – 19.99	13	100	0	0
	20.00 – 29.99	99	4.04	33.33	0
	30.00 – 39.99	30	0	100	0
January 1977	0 – 9.99	0	0	0	0
	10.00 – 19.99	41	100	0	0
	20.00 – 29.99	69	34.78	0	0
	30.00 – 39.99	25	0	40	0
February	0 – 9.99	0	0	0	0
	10.00 – 19.99	30	100	0	0
	20.00 – 29.99	85	9.41	21.18	0
	30.00 – 39.99	24	0	100	0
March	0 – 9.99	0	0	0	0
	10.00 – 19.99	74	100	0	0
	20.00 – 29.99	86	45.35	5.81	0
	30.00 – 39.99	15	0	40	0
April	0 – 9.99	0	0	0	0
	10.00 – 19.99	31	80	0	0
	20.00 – 29.99	40	11	31.6	0
	30.00 – 39.99	21	0	98.5	0
May	0 – 9.99	0	0	0	0
	10.00 – 19.99	56	91	0	0
	20.00 – 29.99	72	13.4	25	0
	30.00 – 39.99	15	0	100	0

Date	Size category (mm)	Individuals in each category	Percentage undeveloped eggs	Percentage well-developed eggs	Nauplii
June	0 – 9.99	0	0	0	0
	10.00 – 19.99	82	100	0	0
	20.00 – 29.99	94	46	28	0
	30.00 – 39.99	12	0	100	0
July	0 – 9.99	0	0	0	0
	10.00 – 19.99	74	100	0	0
	20.00 – 29.99	43	51.5	18.4	0
	30.00 – 39.99	13	0	100	0
August	0 – 9.99	0	0	0	0
	10.00 – 19.99	83	100	0	0
	20.00 – 29.99	45	50.84	21.62	0
	30.00 – 39.99	7	0	100	0
September	0 – 9.99	0	0	0	0
	10.00 – 19.99	90	89	0	0
	20.00 – 29.99	24	59.5	0	00
	30.00 – 39.99	8	0	100	0
October	0 – 9.99	0	0	0	0
	10.00 – 19.99	54	98.32	0	0
	20.00 – 29.99	66	17.15	36	6.14
	30.00 – 39.99	13	0	93.5	23.8
November	0 – 9.99	0	0	0	0
	10.00 – 19.99	21	93.2	0	0
	20.00 – 29.99	82	6.5	11.5	13.8
	30.00 – 39.99	8	0	40	42.5
December	0 – 9.99	0	0	0	0
	10.00 – 19.99	19	100	0	0
	20.00 – 29.99	72	7.6	2.4	0
	30.00 – 39.99	17	0	100	0

This species is probably more significant as a predator for other species of barnacles such as *Chthamalus panamensis.*

At area A *P. planicostatus, T. melones* and *A. brevidentata* also appear to be the acting predators (Fig. 4) *A. rugosa* shows a greater overlap with the distribution of *Tetraclita* and is probably more significant as a predator of young *Tetraclita,* since barnacles other than *Tetraclita* are quite scarce in this area.

In comparing the community structure of predators between temperate and tropical zones, it should be noted that at the latter, top predators such as starfishes, are absent. This results in barnacles being relatively free of predation once they reach a certain size. In fact, at both study sites in Costa Rica, barnacles with a test diameter over 25 mm are almost free of predation, since large predators such as *Leucozonia cerata* are quite uncommon.

TABLE 2

Relative density of T. stalactifera *from samples taken at three-month intervals at Areas A and B*

	Relative density (N°. Ind/m²)						
	1976			1977			
Area	A	J	O	J	A	J	O
A	88	156	159.4	134.4	142.2	148.4	160
B	66	45	69.4	36.8	29.6	32.2	46.4

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RESUMEN

Estudios sobre la estructura de población del cirripedio *Tetraclita stalactifera* en dos áreas de Bahía Ballena en la Península de Nicoya, Costa Rica, indican que los individuos se reproducen una vez al año. Las gónadas se muestran en su máximo desarrollo entre abril y agosto. Los nauplios son visibles en octubre y noviembre y la liberación de las larvas ocurre a finales de noviembre y principios de diciembre. Al igual que en California, los individuos no se reproducen en el año que alcanzan la madurez sexual sino en el siguiente.

La densidad relativa de *T. stalactifera* es más o menos constante durante el año pero sus valores son superiores a los observados para *T. rubescens* en California. La mortalidad es intensa en las clases de tamaños menores. Es relativamente baja en aquellos individuos con un diámetro mayor de 25 mm, en particular debido a la ausencia de depredadores grandes.

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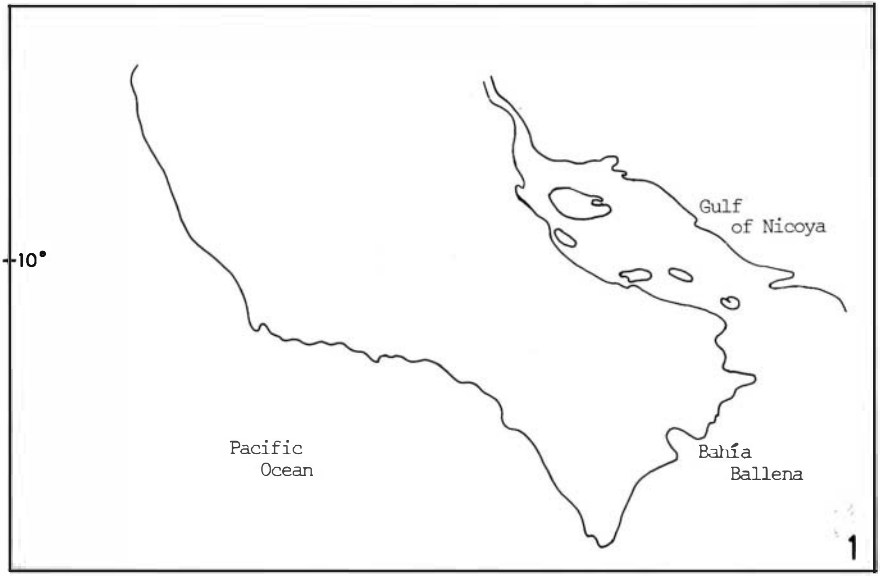


Fig. 1. **Map of the study site.**

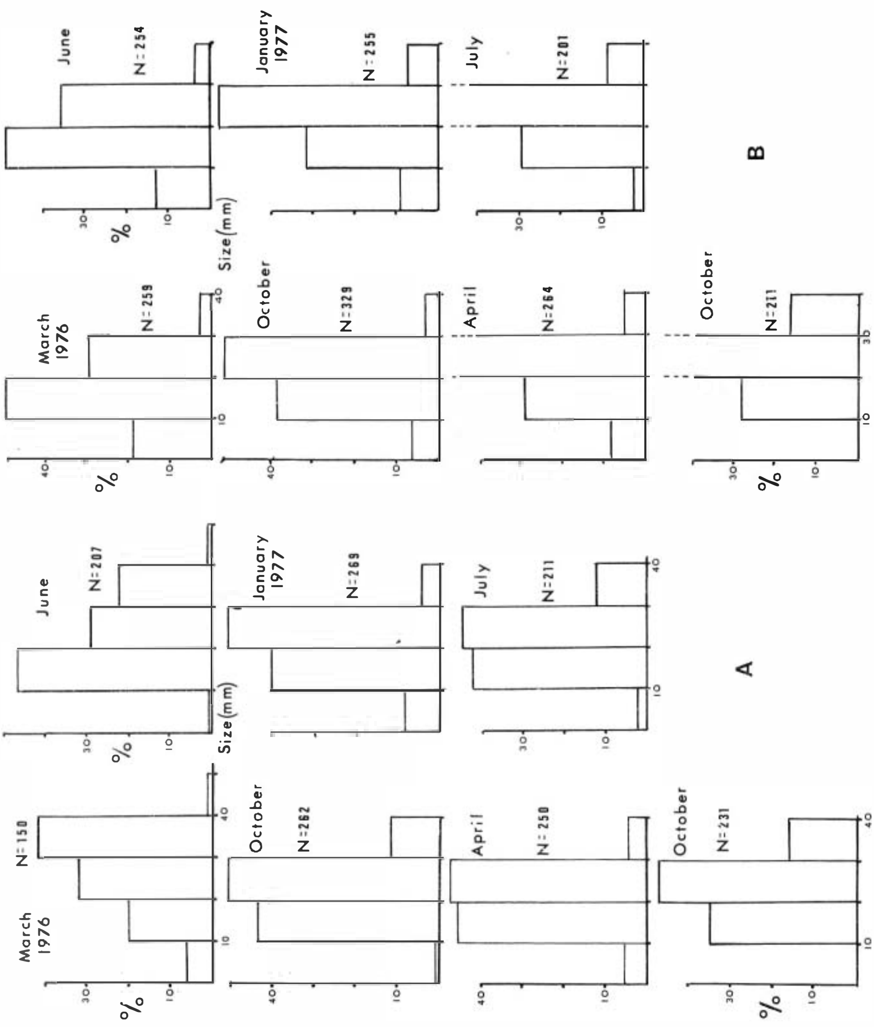
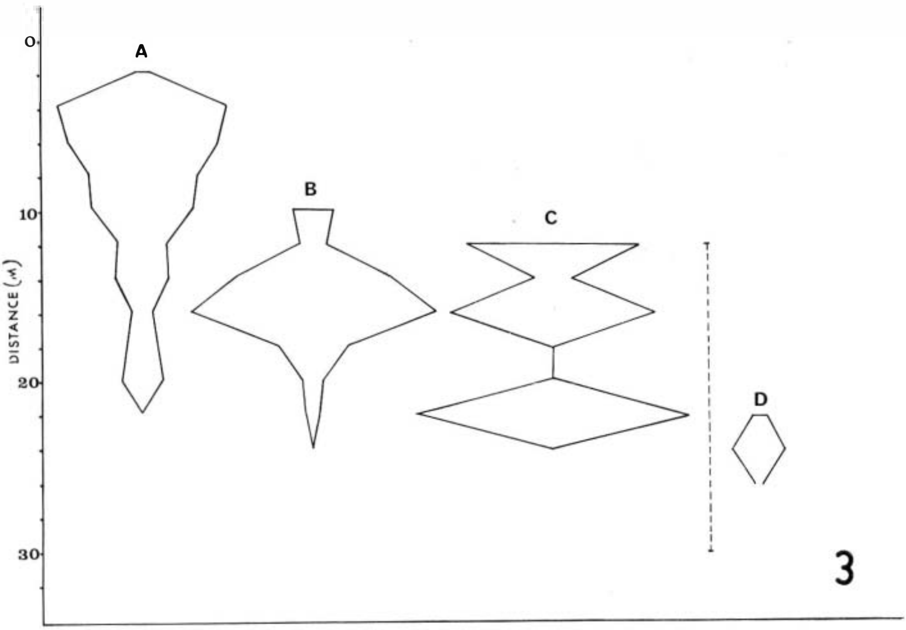


Fig. 2. Size distribution of *Tetraclita stalactifera* from samples measured at three-month intervals, at both Areas A and B.



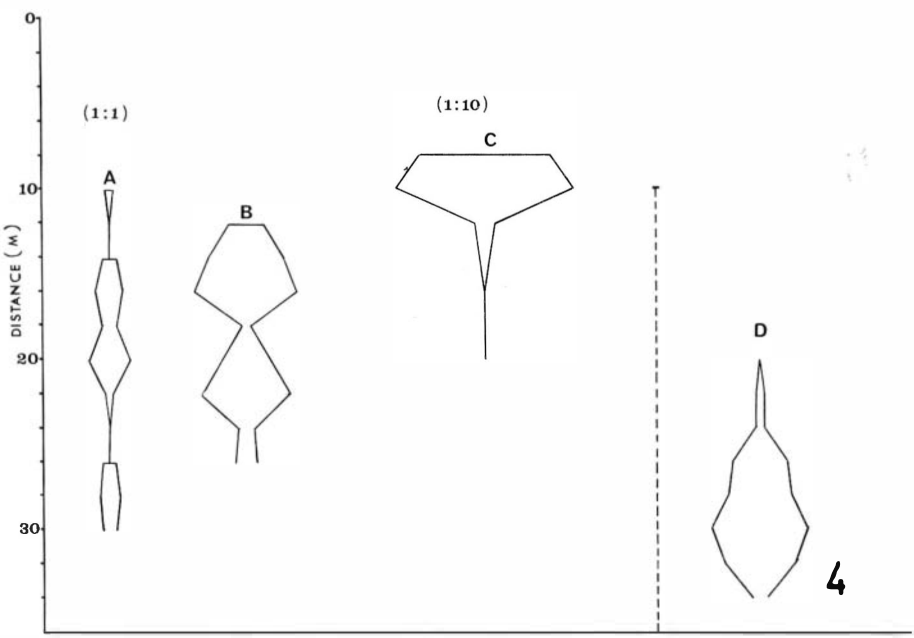


Fig. 3. Vertical distribution of the main predators at Area B: *Anachis rugosa* (A); *Acanthina brevidentata* (B); *Planaxis planicostatus* (C); and *Thais melones* (D). The broken line shows the distribution of *T. stalactifera*.

Fig. 4. Vertical distribution of the main predators at Area A: *Anachis rugosa* (A); *Acanthina brevidentata* (B); *Planaxis planicostatus* (C); and *Thais melones* (D). The broken line indicates the distribution of *T. stalactifera*.