

**Variations in population structure in the genus  
*Tetraclita* (Crustacea: Cirripedia) between  
temperate and tropical populations. IV. The  
age structure of *T. stalactifera* and  
concluding remarks**

by

Carlos R. Villalobos\*

(Received for publication May 7, 1980)

**Abstract:** Studies of a population of *Tetraclita stalactifera* from Bahía Ballena, Costa Rica, indicate that, as expected, the Zero year class exhibits the fastest growth rate. For any age, net increments per year are higher here than those observed in northern populations. Growth seems to be very consistent during the year. It slightly declines during the period August through October, just before the release of the nauplii. These and other differences, such as longevity and reproduction, may be influenced by the variation and constancy of the prevailing temperature.

As early as 1920, Pütter theoretically inferred that animals from areas of high temperatures should exhibit a more rapid growth rate but a smaller final size and a shorter life expectancy. Since then, several authors have presented evidence concerning the assumption that species of marine organisms which inhabit the colder waters of the higher latitudes grow slower, attain a larger size and live longer than individuals of the same or closely related species from warmer waters.

Thus, P. Frank (personal communication) compared populations of *Tegula funebris* from California and Washington and found that individuals of this species along the coast of California were no older than 10 years, compared with those from Washington which live up to 30 years. From this he concluded that the individuals of this species live longer, grow more slowly, but attain a larger size than those further south.

Frank's (1969) results on the growth rate and longevity of gastropods at Heron Island, Queensland, are inconclusive because he had no data from the same species from different geographical areas. In addition, the growth of mature animals proved to be much along the lines experienced on the coast of Oregon by similar gastropods. Similar results were observed by Ansell (1968) and Thorson (1936). In

---

\* Escuela de Biología and Centro de Ciencias del Mar y Limnología. Universidad de Costa Rica.

most instances, temperature has been suggested as the major factor responsible for the observed differences. Thus, Newcombe (1936) in discussing the factors responsible for the more rapid growth of *Mya arenaria* in the Gulf of St. Lawrence, suggested that the higher mean temperature of the water there in the fall, was the important factor. A similar suggestion was made by Weymouth, *et al.* (1931).

A somewhat different approach was presented by Dehnel (1955) who studied the growth rate of larval stages of several species of intertidal molluscs from areas in two different latitudes. He found that embryos and larvae from northern latitudes grow faster than southern ones of the same species at a given temperature. He proposed that intrinsic as well as extrinsic factors were responsible for such differences, the former being represented by compensatory mechanisms and the latter by a growth factor in more northern Pacific waters that was not detected at that time.

A similar growth factor was also suggested by Wilson (1952) to explain differences in the development of *Echinus* and *Obelia* larvae, based on samples from the Atlantic and the North Sea. It is the contention of these authors that Atlantic waters contain traces of accelerating elements not found in North Sea waters.

This work presents the results on the growth and age structure of *Tetraclita stalactifera* and a comparison of the differences and similarities between this and the northern *T. rubescens*. Consideration is also given to the possible role of temperature.

## MATERIAL AND METHODS

Growth studies were initiated in March, 1976. In an area consisting of a series of pilings at Bahía Ballena, Nicoya Península, Costa Rica (Villalobos, 1980), 260 barnacles were tagged using the same procedure as previously described (Villalobos, 1979). Measurements were taken at monthly intervals during low tides, by means of a Mitutoyo dial caliper (0.05 mm graduation).

## RESULTS

From growth data and size distributions, the age structure was established. The results are presented in Table 1.

The size distribution observed in March 1976 (Villalobos, 1980 a) showed that the population comprised mainly individuals one and two years of age. That is, barnacles of the 1974 and 1973 generations. Assuming that settlement occurs in late December and early January, all individuals less than 10 mm in diameter should represent the generation of 1975. As previously indicated the small fraction (less than 3%) of individuals with a size between 30 and 40 mm represent the survivors of the settlement that occurred in late December 1971 or early January 1972.

From Table 1 it should be noted that, as expected, the Zero year class exhibits the fastest growth rate, the mean net increment per year being considerably higher when compared with that observed in individuals of similar age in northern population. In other words, while individuals of *T. rubescens* in California required two years to reach a diameter of 20 mm, this size is reached in just one year by individuals of *T. stalactifera* in Costa Rica. Furthermore, individuals of *T. stalactifera* reach sexual maturity at the above size, which means they begin reproduction at the age of two years, while, barnacles from northern populations do not reproduce until they are three years old.

In Costa Rica, growth of barnacles seems to be very consistent during the year, which highly contrasts with the pattern observed in northern *Tetraclita* populations. In the latter, individuals older than four years, while bearing well developed eggs, did not exhibit any significant growth. In Costa Rica, the growth rate declines slightly during the months of August, September and October, the period previous to the appearance of the nauplii, but does not completely stop.

TABLE 1

*Mean growth increments for March, 1976 through March, 1977 and mean size for each age class of individuals of T. stalactifera from Bahía Ballena, Costa Rica*

Age at start of the year	N	Mean size (mm)				Mean net increment per year (mm)	
		March 1976 $\bar{X}$	range	N	March 1977 $\bar{X}$		range
0				23	19.2	16.9 – 21.2	19.2
1	88	19.0	18.4 – 21.5	58	27.1	25.8 – 28.0	7.9
2	83	26.9	25.4 – 28.1	68	33.2	31.7 – 34.8	6.1
3	41	33.1	30.9 – 24.9	36	36.7	35.0 – 38.3	3.5
4	8	36.4	35.2 – 38.4	16	38.8	36.6 – 39.9	2.1

TABLE 2

*A comparison of several population characteristics between temperate and tropical populations of the genus Tetraclita*

	Temperate regions	Tropical regions
Growth	Slow	Fast
Size	Large	Small
Longevity	Great	Short
Sexual maturation	At the end of second year	At the end of first year
Reproduction	Every two years	Every year
Mortality by predation	High for all classes	High for small individuals. Low for large individuals.

### CONCLUDING REMARKS

Table 2 is a comparison between individuals of *T. rubescens* in California and *T. stalactifera* in Costa Rica with regards to several population parameters which

show that *T. stalactifera* exhibit a faster growth rate for all the age classes. However, they seem to stop growing earlier. In fact, individuals of 60-70 mm in diameter were frequently observed in samples taken in northern populations. In Costa Rica, on the contrary, in spite of a fairly complete survey along the Pacific coast, no barnacles larger than 55 mm were noted. Observations in several intertidal areas showed the populations being primarily composed by individuals of 25 to 30 mm in diameter, larger animals being extremely rare.

Considering that mortality by predation in large barnacles is very low due to the absence of large predators, one may expect longevity to be greater in tropical barnacles. However, since large individuals are quite uncommon, it may suggest that, once large barnacles stop growing they die as a consequence of physiological processes (Medawar, 1957). Second and more feasible: longevity is as great as in temperate populations; but the fact that individuals stop growing early does not mean that longevity is in any sense shorter. Barnacles simply reach a maximum size and remain there until death occurs.

Sexual maturity occurs in both temperate and tropical populations when individuals reach a test diameter around 20 mm. Barnacles in Costa Rica reach that size at the end of the first year of life, while in California it takes them two years. Although individuals in tropical populations mature at a rate that seems to be twice that of northern populations, reproduction is in some aspects similar in both groups. For instance, the release of larvae occurs a year after maturation takes place. However, the frequency is different, *T. stalactifera* reproduce every year while in *T. rubescens* it occurs every two years.

This pattern seems to agree with the idea that organisms in tropical rocky intertidal communities are subject to extremely severe physical hazards that result in high mortality rates, primarily in the youngest size classes, that therefore require annual reproductive cycles. Evidence to support this contention has been presented by Villalobos (1980 b) for algal communities on the Pacific coast of Costa Rica.

In general, the evidence accumulated on the behavior of latitudinally separated populations of *Tetraclita*, tends to support the idea that organisms in temperate regions grow slower, attain a larger size and have greater longevities than closely related species from tropical areas.

What does not seem to be clear is the actual role of temperature. Fig. 1 shows water temperature records for the two main study sites (Villalobos, 1979). As expected, in California surface temperature varies considerably during the year. Extreme values ranged from 19.7 C during the summer of 1974 to 10.1 C during the winter of 1975. Mean values ranged from 18.3 C to 12.1 C for the same period. Net variations were respectively 9.6 and 6.2 C.

In Bahía Ballena, Costa Rica, on the contrary, surface temperature varied little during the period of study. The maximum value observed (26 C) was recorded during several months. Minimum temperature seems to be 21 C and was also registered during several months. Mean values ranged from 24.1 C. to 22.8 C. Net variations were respectively 5 C and 1.3 C.

From these data it is obvious that in tropical regions, surface water temperature is highly constant during the year. In temperate waters, on the contrary, it fluctuates considerably.

What this constancy or variability of temperatures actually mean to the growth of the organisms is not yet well understood. Ansell (1968) in discussing relationship between temperature and growth in *Mercenaria mercenaria* indicated that throughout the continuous range of the species, approximately the same annual

increments are recorded. The seasonal distributions of growth, however, show marked differences. Ansell also observed that in northern areas growth is restricted to the summer months, while in the southernmost parts of the range, some growth occurs in all months of the year. This pattern, in some way, is similar to the one observed in latitudinally separated populations of *Tetraclita*. The high temperatures of the water in tropical areas resemble the summer temperatures where maximum growth has been observed.

It should be pointed out however, that in the case of *T. rubescens* growth seems to be relatively independent of seasonal changes. Rather, growth alternates with reproduction for full years. Other factors then might have induced northern populations to develop a different strategy. For instance, competition for space is very intensive in rocky substrates where opportunistic algae and communities such as *Polycipes-Mitillus*, may become extremely dominant. A full year of egg maturation may result in greater and stronger broods that will have a much better possibility to survive and become established.

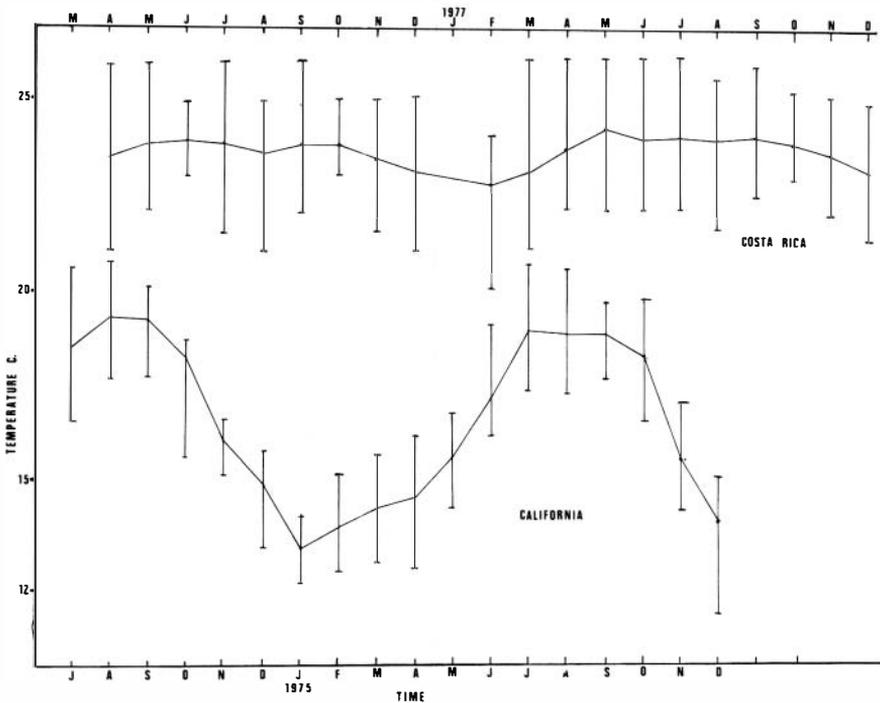


Fig. 1. Surface temperature records for Bahía Ballena (1976-1977) and Santa Barbara, California (1974-1975).

#### ACKNOWLEDGEMENTS

Thanks are given to the University of Costa Rica for providing logistic support. The following students, Enrique Lahmann, Jorge Jiménez, Luis Cruz,

Marta F. Valdéz and Jesús Rojas, helped in the collection of data. Mr. Hermán Pérez from Tambor collected most of the temperature records at Bahía Ballena.

Temperature records for Santa Barbara were kindly provided by the Authority of the Port of Santa Barbara.

### RESUMEN

Estudios en una población del cirripedio *Tetraclita stalactifera* en Bahía Ballena, Costa Rica, indicarán que la clase de edad cero exhibe la tasa más alta de crecimiento. Los incrementos netos por año para cualquiera de las edades son mayores si se les compara con aquellos encontrados en poblaciones del norte.

El crecimiento es bastante consistente durante todo el año, aunque se observa una pequeña reducción en los meses de agosto, setiembre y octubre, que corresponden al período previo de la liberación de las larvas.

Se incluye en el presente trabajo además, una discusión en torno a las diferencias y similitudes observadas entre *T. rubescens* de California, EUA, y *T. stalactifera* de Costa Rica. De manera similar se analiza el posible papel de la temperatura como factor importante en las diferencias observadas.

### LITERATURE CITED

- Ansell, A.D.**  
1968. The rate of growth of the hard clam, *Mercenaria mercenaria* throughout the geographical range. J. Cons. perm. int. Explor. Mer., 31: 364-409.
- Dehnel, P.A.**  
1955. Rates of growth of gastropods as a function of latitude. Physiol. Zool., 28: 115-144.
- Frank, P.W.**  
1969. Growth rates and longevity of some gastropod mollusks on the coral reef of Heron Island. Oecologia, 2: 232-250.
- Medawar, P.B.**  
1957. Old age and natural death. In "Uniqueness of the Individual", Methuen, London. pp. 17-43.
- Newcombe, C.L.**  
1936. A comparative study of the abundance and the rate of growth of *Mya arenaria* (L) in the Gulf of St. Lawrence and Bay of Fundy Regions. Ecology, 17: 418-428.
- Pütter, A.**  
1920. Lebensdauer und Altersfaktor. Z. Allg. Physiol., 19: 9-36.
- Thorson, G.**  
1936. The larval development, growth and metabolism of arctic marine bottom invertebrates. Medd. om. Gronland. Vol. 100. N° 6.
- 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: 279-291.

**Villalobos, C.R.**

- 1980 a. Variations in population structure in the genus *Tetraclita* (Crustacea: Cirripedia) between temperate and tropical populations. III. *T. stalactifera* in Costa Rica. *Rev. Biol. Trop.*, 28: 193-201.

**Villalobos, C.R.**

- 1980 b. Algunas consideraciones sobre el efecto de los factores físicos y biológicos en la estructura de una comunidad de algas en el Pacífico de Costa Rica. *Brenesia* (en prensa).

**Weymouth, F.W., H. McMillin, & W. Rich**

1931. Latitude and relative growth in the razor clam *Siliqua patula*. *J. Exp. Biol.*, 8: 228-249.

**Wilson, D.P.**

1952. The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially the larvae of *Ophelia bicornis* (S). *Ann. Inst. Oceanogr. Monaco*, 27: 40-156.