

THE HORIZONTAL ZONATION OF TWO SPECIES OF INTERTIDAL BARNACLE IN SOUTH AFRICA

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Along the west and south coasts of South Africa, the two most abundant intertidal barnacles *Octomeris angulosa* Sowerby and *Tetraclita serrata* Darwin have similar vertical ranges, but tend to be segregated along a horizontal gradient of wave exposure. This horizontal pattern is described and the mechanisms producing the pattern at Glencairn in False Bay are examined. Survival rates of *Tetraclita* were significantly higher in *Tetraclita*-dominated areas than in *Octomeris*-dominated areas, whereas survival rates of *Octomeris* were higher in *Octomeris*-dominated areas. Five hypotheses to explain differences in survival were examined. There was no support for three of the hypotheses, i.e. the Structure of Cirri, Competition and Predation hypotheses. There was support for the Wave Tolerance and Temperature Stress hypotheses. The results suggest that: (1) physical factors vary along the horizontal gradient: wave height and wave strength are greatest at the exposed end, whereas temperatures and desiccation rates are highest at the calm end; (2) *Octomeris* is better adapted to withstand strong wave forces because it forms a strong, single-layered matrix; and (3) *Tetraclita* is better adapted to hot and dry conditions because its shell appears to have many characteristics that reduce heat-loading. *Tetraclita* and *Octomeris* therefore occur alone at either end of the gradient and overlap in the middle, where conditions are intermediate.

In contrast to the extensive literature on vertical zonation of rocky shores, there is little published information on horizontal zonation patterns (but see Harger 1972, Menge 1976, Underwood *et al.* 1983, Bushek 1988). This is unfortunate, because understanding mechanisms producing horizontal zonation may yield new insights into mechanisms that regulate species distributions in marine systems in general. For example, Bushek (1988) described a horizontal zonation pattern that occurs on pier pilings along the Texas coast. The American oyster *Crassostrea virginica* is more abundant on nearshore pilings, whereas the ivory barnacle *Balanus eburneus* is more abundant on pilings farther from shore. That author found that the barnacle is better adapted to growing where water motion is more pronounced and that the horizontal pattern is produced by differential settlement of larvae.

Along the west and south coasts of South Africa, the two most abundant barnacle species in the intertidal zone, *Octomeris angulosa* and *Tetraclita serrata*, have similar vertical ranges, but they appear to be segregated along a horizontal gradient of wave exposure (Field 1963, Branch and Branch 1981, Delafontaine and Flemming 1989). Their horizontal zonation is most obvious on gently sloping rocky shores, where *Octomeris* is most abundant on the rocks at the seaward end and *Tetraclita* is most abundant at the landward end of the intertidal zone.

In this paper, the horizontal zonation patterns of

the two species are described, their growth and survival rates in *Tetraclita*-dominated and *Octomeris*-dominated areas are estimated, and five hypotheses concerning the mechanisms producing the pattern are addressed. First the hypotheses are described and their logical predictions listed (Table I).

THE HYPOTHESES

Field (1963) found in laboratory experiments that *Octomeris* and *Tetraclita* fed, i.e. protruded their cirri, at different current speeds; *Octomeris* fed at high current speeds and *Tetraclita* at low speeds. These results have led to the hypothesis that *Tetraclita* has more fragile cirri and therefore cannot survive in areas of strong currents and wave action (Branch and Branch 1981). This Structure of the Cirri Hypothesis predicts that: the growth of *Tetraclita* is lower in areas dominated by *Octomeris*; that the survival of *Tetraclita* is slower in areas dominated by *Octomeris*; and that the cirri of *Octomeris* and *Tetraclita* are significantly different. Henceforth, *Octomeris*-dominated areas (i.e. areas that are exposed to wave action where *Octomeris* was the more abundant species) and *Tetraclita*-dominated areas (i.e. calmer areas where *Tetraclita* was the more abundant species) will be referred to in the text as O-areas and T-areas respectively.

The vertical distribution of barnacles can be influ-

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Table I: The predictions of the five hypotheses. O-areas denote where *Octomeris* is more abundant than *Tetraclita* and T-areas denote where *Tetraclita* is more abundant than *Octomeris*

Hypothesis	Growth	Survival	Other
Structure of Cirri Hypothesis	Of T: O-areas < T-areas	Of T: O-areas < T-areas	O and T cirri different
Competition Hypothesis	Of T: O-areas > T-areas Of O: O-areas > T-areas In O-areas: O > T;	Of T: O-areas < T-areas	Undercutting or smothering; competitive release in site where space is not limiting
Predation Hypothesis	None	Of T: O-areas < T-areas Of O: O-areas > T-areas	Predators that prefer T in O-areas and/or O in T-areas
Temperature Stress Hypothesis	None	Of O: O-areas > T-areas	Temperature regimes different in O- and T-areas; O and T different shell structures
Wave Tolerance Hypothesis	None	Of T: O-areas < T-areas	Wave regimes different in O- and T-areas O and T different responses to simulated waves O and T different shell and/or matrix structures

T = *Tetraclita*
O = *Octomeris*

enced by competition (e.g. Connell 1961) and predation (e.g. Paine 1974). Because it is possible that these factors also play a role in the horizontal zonation of these two species, the Competition and Predation hypotheses are addressed. Competition is likely to be for space. Space is limiting at the exposed, seaward end of the gradient, where *Octomeris* is the more abundant species and frequently occupies 100% of the primary space. The Competition Hypothesis explains the horizontal pattern by holding that *Octomeris* is the competitive dominant and is able to exclude *Tetraclita* from the most preferred seaward sites. Therefore, the predictions of the Competition Hypothesis are that: both species grow faster in O-areas than in T-areas but, in O-areas, *Octomeris* growth is significantly greater than *Tetraclita* growth; *Tetraclita* survival is lower in O-areas than in T-areas; and *Octomeris* can be observed to undercut and/or smother *Tetraclita*. Finally, *Tetraclita* should experience competitive release, i.e. become abundant in O-areas, at sites where *Octomeris* is rare and space is not limiting.

The Predation Hypothesis explains the horizontal pattern by holding that a predator is present that prefers *Tetraclita* in O-areas and/or *Octomeris* in T-areas. The predictions of the Predation Hypothesis are that: *Tetraclita* survival is lower in O-areas than in T-areas; *Octomeris* survival is higher in O-areas than in T-areas; and that a predator (or predators) is present that prefers *Tetraclita* in O-areas and/or *Octomeris* in T-areas.

Delafontaine and Flemming (1989) suggested that the pattern was a result of the emergence/submergence regime and exposure to wave impact. These two separate hypotheses are termed the Temperature

Stress Hypothesis and the Wave Tolerance Hypothesis. The Temperature Stress Hypothesis explains the pattern by holding that, in T-areas, temperature stress is higher because temperatures are higher and/or exposure to air is longer, and for some reason *Tetraclita* is best able to persist there. The predictions of the Temperature Stress Hypothesis are that: *Octomeris* survival is greater in O-areas than in T-areas; the temperature regimes are different in O- and T-areas; and *Tetraclita* shows adaptations to high temperatures that *Octomeris* does not show, e.g. their shell structures are significantly different.

The Wave Tolerance Hypothesis explains the pattern by holding that in O-areas wave forces are higher and for some reason *Tetraclita* is unable to persist there. The predictions of the Wave Tolerance Hypothesis are that: *Tetraclita* survival is greater in T-areas than in O-areas; that the wave regimes are different in O- and T-areas; *Octomeris* survives the effects of simulated waves better than *Tetraclita*; and *Octomeris* shows adaptations to high wave forces that *Tetraclita* does not show, e.g. their shell structures, or shell matrix structures, are significantly different.

MATERIAL AND METHODS

Except where indicated, this work was conducted at Glencairn (34°10'S, 18°27'E) in False Bay, near Cape Town, South Africa. The rocky shore is composed of gently sloping Table Mountain sandstone. Occasionally, the basement forms gullies with vertical walls and in other places it is covered by rocks

and boulders. The site is typical of the South Coast, where *Octomeris* and *Tetraclita* are abundant in the intertidal zone (Boland 1997). Both species have similar vertical ranges, from approximately MLWS (Mean Low Water Springs) to MHWS (Mean High Water Springs), and at Glencairn they occurred from -0.01 m to 1.78 m above LAT (Lowest Astronomical Tide = chart datum).

The horizontal zonation pattern

The horizontal zonation pattern was documented at two sites: along a prominent vertical gully wall (1 m high and 25 m long), perpendicular to the shore, and on large boulders in a boulder field. On the wall, barnacle abundances were measured at four equal-elevation sites 1, 8, 15 and 22 m from the seaward edge. At each site, three 25 × 25 cm quadrats were placed at the same elevation and next to each other. The percentage cover of all barnacles was determined and the number of individuals of each barnacle species counted in each quadrat. In the boulder field, barnacle abundances were counted on all of the large boulders (>1 m³, *n* = 10). At equal-elevation sites on the seaward face and the landward face, one quadrat (25 × 25 cm) was placed over the barnacles, the percentage cover of all barnacles determined and the number of individuals of each barnacle species counted in each quadrat.

Comparison of population processes in the *Tetraclita*-dominated and *Octomeris*-dominated areas

Known *Octomeris* and *Tetraclita* individuals were monitored to calculate growth and survival rates. Care was taken to follow individuals at all tidal heights and in many O-areas and T-areas. Recruitment of *Octomeris* and *Tetraclita* into O- and T-areas was also monitored by conducting monthly searches for recruits in 73 randomly placed clearings (10 × 5 cm). However, because no recruits were observed between May and November 1989, recruitment rates are not used in this comparison.

GROWTH RATES

The growth rates of *Octomeris* and *Tetraclita* were obtained by monitoring the individuals over a three-year period. In both areas, barnacle-inhabited portions of the rocky intertidal (approximately 12 × 20 cm) were randomly chosen, marked with a small piece of marine putty and photographed. A few days later, *Octo-*

meris and *Tetraclita* individuals were chosen for measuring and these were numbered on the appropriate photograph. Between one and nine barnacles were chosen per photograph. Many of the barnacles measured were touching other individuals, because in many of the photographs the barnacles were so close together that there were no completely separated individuals.

Because *Octomeris* were rare in T-areas and *Tetraclita* were rare in O-areas, *Octomeris* and *Tetraclita* adults were transplanted into both areas. Transplants were collected from friable rocks near Glencairn Station by hammering off pieces of rock with barnacles on them. The rocks containing the transplants were glued to several cleared sites in the middle of the O- and T-areas using a marine epoxy. Transplants were used in the calculation of growth rates, but not in the calculation of survival rates.

A total of 291 barnacles (154 naturals and 137 transplants) was measured during May/June 1989 and those remaining (89 naturals and 32 transplants) were re-measured during July/August 1992. The height, the basal diameter of the shell (along the rostro-carinal axis) and the diameter of the opercular opening (along the rostro-carinal axis) were measured on each barnacle by means of dial calipers. A precision test, in which the same barnacles were measured two days in a row, showed an average difference of <5% between measurements.

Barnacle volume (*V*) was calculated using the formula for the volume of a frustum of a cone of revolution:

$$V = \pi h/3 (R^2 + r^2 + Rr) \quad ,$$

where *r* is the radius of opercular opening, *R* the radius of shell base and *h* the shell height (Merritt 1962). Volume is a more accurate measure of size than basal diameter of the shell, because the basal spread of many of the individuals was distorted by neighbours. Volume was strongly correlated with wet mass in both species (*Tetraclita*, *r*² = 0.992, *n* = 20, *p* < 0.01; *Octomeris* *r*² = 0.922, *n* = 20, *p* < 0.01), whereas basal diameter was not as strongly correlated with wet mass (*Tetraclita*, *r*² = 0.815, *n* = 20, *p* < 0.01; *Octomeris* *r*² = 0.668, *n* = 20, *p* < 0.01).

SURVIVAL RATES

The survival rates of *Tetraclita* and *Octomeris* at the two study sites were estimated by examining the photographs taken during May/June 1989 for growth measurements and counting the number of barnacles still alive during July/August 1992. Numbered barna-

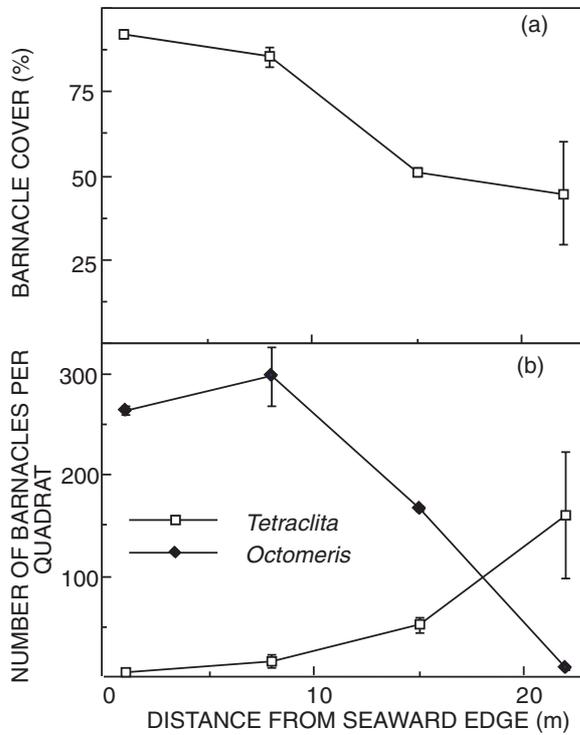


Fig. 1: Barnacle abundances along the Glencairn wall – (a) total percentage cover, (b) mean number of individuals per quadrat (625 cm²) of the two species ($n = 3$ quadrats per site). Error bars denote ± 1 standard error

cles, i.e. those used for growth measurements, and unnumbered barnacles were used in the calculations of survival rates. Transplants were not used in the calculations of survival rates because some of their deaths were a result of transplantation problems, such as weak attachment of the epoxy.

Support for the hypotheses

To address the five hypotheses, the growth rates, survival rates, and the results of the determinations listed below were used.

STRUCTURE OF CIRRI HYPOTHESIS

Octomeris and *Tetraclita* cirri were compared by measuring the length and cross-sectional area of the second pair of cirri on different-sized animals of each species. In all, 13 *Octomeris* and 19 *Tetraclita* were

carefully scraped off rocks, blotted dry, weighed and dissected under a dissecting microscope. The second cirrus was removed from each individual and measured using an ocular micrometer.

COMPETITION HYPOTHESIS

Intertidal barnacle abundances are significantly lower on the west than on the south coast of South Africa (Branch and Branch 1981, Boland 1997). On the West Coast, much of the intertidal is bare space and space is therefore unlikely to be a limiting resource for barnacles. To determine whether the horizontal zonation pattern is the result of competitive exclusion and whether *Tetraclita* exhibits competitive release when *Octomeris* is rare, the distributions of *Octomeris* and *Tetraclita* were measured at a West Coast site, Kommetjie (34°09'S, 18°19'E). A gully wall similar in structure to the Glencairn wall was chosen and the abundances of the barnacles on the wall were counted using the methods described above.

PREDATION HYPOTHESIS

The whelk *Nucella dubia* is the most important barnacle predator in the intertidal zone (Day 1969, McQuaid 1985, Boland personal observation). During six low tides between June and October 1989, extensive searches were conducted throughout the intertidal zone for *N. dubia*, and a total of 528 individuals was found. If an individual was feeding, its prey was identified and, if it was feeding on a barnacle, the local relative abundances of *Octomeris* and *Tetraclita* were determined by placing a 25 × 25 cm quadrat over the *N. dubia* and counting the number of *Octomeris* and *Tetraclita* in the quadrat.

TEMPERATURE STRESS HYPOTHESIS

In order to examine the Temperature Stress Hypothesis, it was first determined whether the temperature regimes were significantly different in the O- and T-areas, and whether *Octomeris* and *Tetraclita* had different tolerances of high temperatures.

Because barnacles become heat stressed and/or desiccated when they are exposed during low tides (Southward 1987), it was investigated whether barnacles in the O- and T-areas were exposed for significantly different lengths of time during a neap-tide day (5 November 1989) and during a spring-tide day (14 November 1989). On both days, waves were small (<1.5 m). At the Glencairn wall, obvious horizontal lines were painted on the rock face at the same tidal heights in the middle of the O-area (10 m from the seaward edge) and in the middle of the T-area (20 m

from the seaward edge). These lines were observed from a position opposite the gully wall and every half-hour, from maximum low tide to 6 hours after maximum low, the number of seconds per minute that the lines were underwater was recorded. The lines were monitored alternately for three one-minute "samples" each, every half-hour.

The aspect of a slope, i.e. whether it faces towards or away from the direct rays of the sun, determines how hot and dry it becomes (Lewis 1964). A 4 km stretch of rocky shore, near Glencairn, was searched for sites (e.g. large boulders) that had two aspects and fitted the following criteria: (1) one aspect was sunny and one was shaded, i.e. they faced generally east (within 25° of E) v. generally south (within 25° of S) respectively; (2) they were within 1 m of each other; (3) they had similar slopes; (4) they received similar wave forces, i.e. they faced the waves and had similar obstructions in front of them; and (5) barnacle percentage cover was >25% on at least one aspect. In all, 12 areas fitted the criteria; all were at intermediate positions along the exposure gradient. The abundances of *Octomeris* and *Tetraclita* on the sunny and shaded aspects were then measured by counting the number of barnacles within a 25 × 25 cm quadrat placed at the same elevation and centrally on each face.

WAVE TOLERANCE HYPOTHESIS

In order to examine the Wave Tolerance Hypothesis, it was determined whether the heights of the waves were significantly different in O- and T-areas, and whether *Octomeris* and *Tetraclita* had different tolerances to strong wave action.

At the Glencairn wall, on 16 November 1989, two vertical metre scales were painted on the rock face, one in the O-area (10 m from the seaward edge) and one in the T-area (20 m from the seaward edge). Then, from one hour before high tide until high tide, from a relatively dry position opposite the gully wall, the heights of the breaking waves as they passed over the scales were estimated. Because breaker heights are proportional to wave energy (Brown and McLachlan 1990), the measured heights estimate the wave forces that the areas experience.

In the same area, strong waves and the effects of boulders tossed by wave action were simulated by striking barnacle-covered rocks three times with a mallet. The number of barnacles that were dislodged were collected and counted. The simulated waves were struck in 10 randomly chosen T-areas and 10 randomly chosen O-areas where percentage cover of barnacles was >40%. It was clear that many of the barnacles dislodged by the simulated waves were indi-

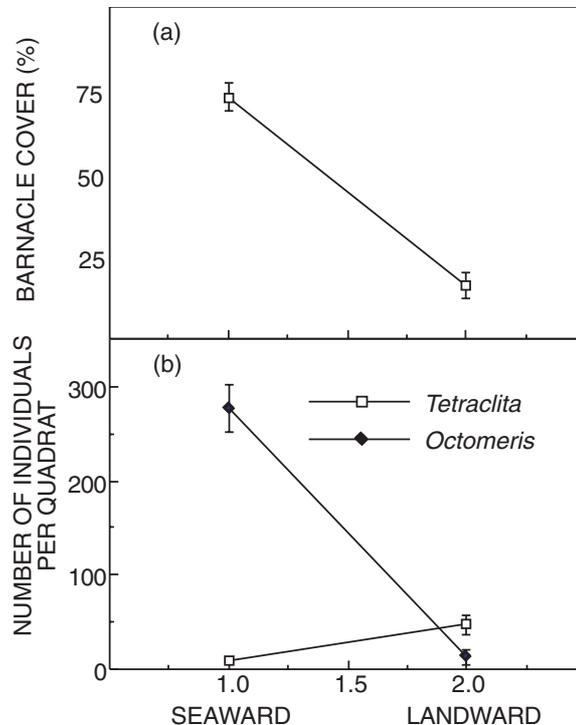


Fig. 2: Barnacle abundances on the Glencairn boulders – (a) total percentage cover, (b) mean number of individuals per quadrat (625 cm²) of the two species ($n = 10$ boulders). Error bars denote ± 1 standard error

viduals that were not attached to bare rock (i.e. primary space), but rather to other barnacles (i.e. secondary space). Therefore, before striking the area with the simulated waves, the number of barnacles growing on primary space and on secondary space within a 25 × 25 cm quadrat was determined.

RESULTS

The horizontal pattern

Along the transect of constant elevation on the Glencairn gully wall, total barnacle percentage cover was high at the seaward edge and declined at increasing distance from the seaward edge (Fig. 1a). The horizontal pattern in the distribution of the species was obvious: *Octomeris* was numerically dominant at the seaward end of the wall, whereas *Tetraclita* was nu-

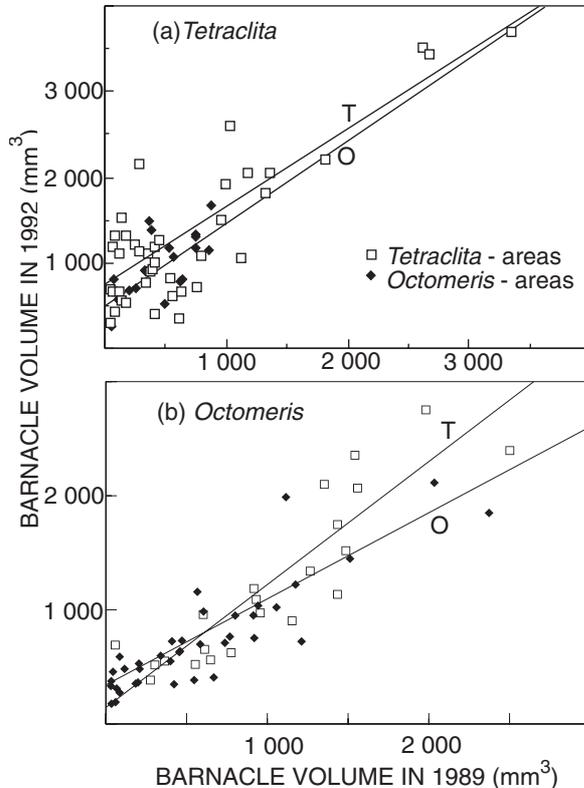


Fig. 3: The growth of (a) *Tetraclita* and (b) *Octomeris*, expressed by the change in shell volumes between 1989 and 1992, for *Tetraclita*-areas (T) and *Octomeris* areas (O)

merically dominant at the landward end of the wall (Fig. 1b). The same horizontal pattern was found at other elevations on the Glencairn wall and on other gully walls. The pattern was also obvious on the large boulders: barnacles were more abundant on the seaward side of the boulders (Fig. 2a), *Octomeris* was numerically dominant on the seaward faces, and *Tetraclita* was numerically dominant on the landward faces of the boulders (Fig. 2b).

Population processes

GROWTH RATES

To determine the cause of the horizontal zonation pattern, growth and survival of barnacles in O-areas and T-areas were monitored. *Tetraclita* and *Octomeris* are relatively slow-growing barnacles; virtually no

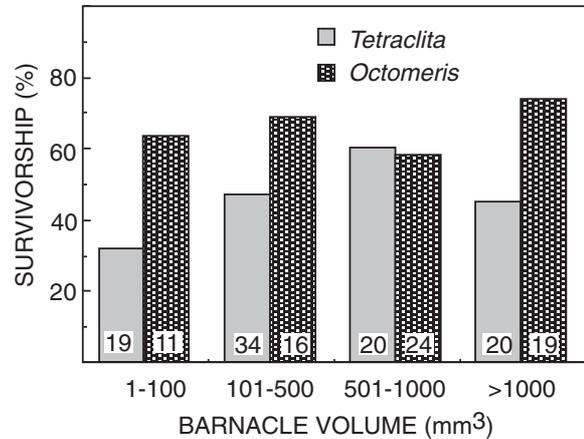


Fig. 4: Percentage survival over three years (1989–1992) of *Tetraclita* and *Octomeris*, by shell volume. The numbers of individuals in each size category are shown

growth could be detected in six months and the organisms had to be left for three years in order to obtain measurable growth. Smaller individuals grew faster than larger individuals (Fig. 3). For example, an average *Tetraclita* of 500 mm³ more than doubled in size during three years, whereas an average *Tetraclita* of 2 000 mm³ added only approximately 300 mm³ during that period. The largest adults measured were estimated to be at least five years old but, because they grow little once they are near maximum size, their age cannot be estimated accurately.

The growth rates of *Tetraclita* and *Octomeris* were not significantly different between the T-areas and O-areas (Table II). Also, there was no significant difference between the growth rates of the two species in O-areas. However, *Tetraclita* growth rates were significantly greater in T-areas than those of *Octomeris*, using measurements of shell diameter and volume (ANCOVA, $p < 0.05$). In T-areas, small *Tetraclita* grew faster than small *Octomeris*.

SURVIVAL RATES

The survival rates of both species were high and ranged between 41 and 80% over the three-year period (Table III), or approximately 80–93% survival per year. Survival rates did not vary significantly with size for either species (χ^2 test, $p > 0.05$, Fig. 4). However, small *Tetraclita* (<100 mm³) did experience the lowest survival rate of 32% over three years, or 68% per year.

Survival rates differed for each species in each

Table II: The growth of *Tetraclita* and *Octomeris* in *Tetraclita*-areas and *Octomeris*-areas over a three-year period. Results of regression analyses of the linear relationship between 1989 sizes (abscissa) and 1992 sizes (ordinate) for shell height, shell diameter, opercular-opening diameter and shell volume. The results of the ANCOVA tests are given, where T > O indicates that *Tetraclita* growth was significantly greater than *Octomeris* growth

Parameter	Value in <i>Octomeris</i> -area			Value in <i>Tetraclita</i> -area			ANCOVA
	Intercept	Slope	Coefficient of determination (r^2)	Intercept	Slope	Coefficient of determination (r^2)	Within sp., across areas
	(n = 21)			<i>Tetraclita</i>			(n = 40)
Height (mm)	4.486	0.572	0.383	5.894	0.543	0.401	NS
Shell diameter (mm)	9.805	0.604	0.483	10.81	0.525	0.514	NS
Opercular-opening diameter (mm)	3.564	0.583	0.311	3.142	0.632	0.575	NS
Volume (mm ³)	570.0	0.858	0.391	664.0	0.942	0.718	NS
	(n = 38)			<i>Octomeris</i>			(n = 22)
Height (mm)	3.848	0.446	0.381	2.701	0.656	0.388	NS
Shell diameter (mm)	7.021	0.580	0.724	5.935	0.703	0.787	NS
Opercular-opening diameter (mm)	4.294	0.629	0.748	4.086	0.673	0.760	NS
Volume (mm ³)	292.0	0.753	0.764	143.2	1.051	0.792	NS
	ANCOVA (between spp., within areas)						
Height (mm)		NS				NS	
Shell diameter (mm)		NS				T > O	
Opercular-opening diameter (mm)		NS				NS	
Volume (mm ³)		NS				T > O	

NS = not significant ($p > 0.05$)

area. *Tetraclita* survival was significantly greater in T-areas (χ^2 test, $p < 0.005$). *Octomeris* survival was greater in O-areas, but not significantly greater (χ^2 test, $p = 0.06$).

Support for the hypotheses

STRUCTURE OF CIRRI HYPOTHESIS

Little support was found for this hypothesis to explain the horizontal zonation pattern of the two species. The survival rate results were as predicted, but the other measurements did not support this hypothesis. A prediction of this hypothesis is that

Tetraclita growth rates would be lower in O-areas. However, this was not the case; there was no significant difference between the growth rates of *Tetraclita* in the two areas (Table II). Furthermore, although the colours of the cirri were different (*Octomeris* cirri are dark and appear robust, whereas *Tetraclita* cirri are light and appear fragile), there were no structural differences between the cirri of the two species. The species had cirri of similar lengths and similar cross-sectional areas (ANCOVA, $p > 0.05$, Fig. 5).

COMPETITION HYPOTHESIS

Little support was found for this hypothesis to ex-

Table III: The survival of *Tetraclita* and *Octomeris* in *Tetraclita*-areas and *Octomeris*-areas over a three-year period. The results of the χ^2 tests are given, where T > O indicates that survival in the *Tetraclita*-areas was significantly greater than in the *Octomeris*-areas

Species	<i>Octomeris</i> -areas			<i>Tetraclita</i> -areas			χ^2 test
	Survived	Died	Survival (%)	Survived	Died	Survival (%)	
<i>Tetraclita</i>	94	134	41	529	383	58	T > O**
<i>Octomeris</i>	707	175	80	279	92	75	O > T*

* $p = 0.06$

** $p < 0.005$

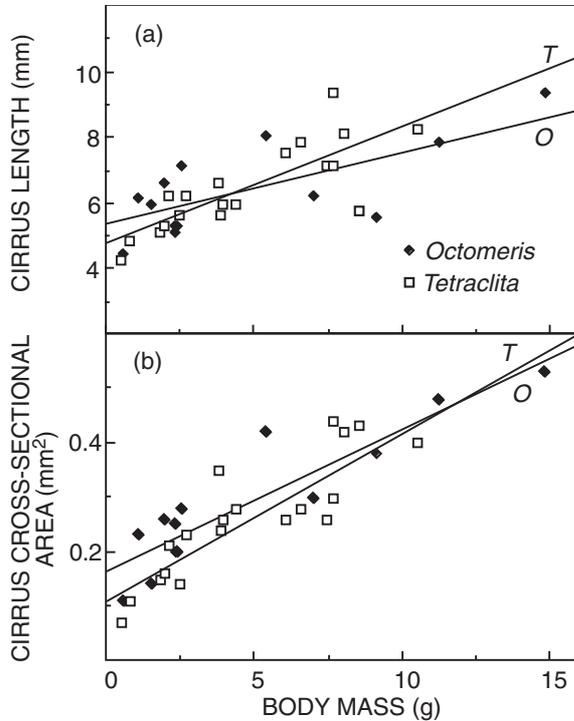


Fig. 5: Relationship between (a) second cirrus length and body mass and (b) second cirrus cross-sectional area and body mass for *Tetraclita* (T) and *Octomeris* (O)

plain the horizontal zonation pattern of the two species. The survival rates were as predicted, but the other four predictions did not hold. First, there was no significant difference between the growth rates of the two species in O-areas (Table II). Second, *Octomeris* did not grow significantly faster than *Tetraclita* (Table II) in O-areas. Third, *Octomeris* was not observed to undercut or smother *Tetraclita* frequently. None of the deaths observed during this study could be attributed to this type of competition. Finally, at Kommetjie, where barnacles are relatively rare and space is not limiting, there was no indication that *Tetraclita* experienced competitive release and overlapped more with *Octomeris* (Fig. 6). Instead, the Kommetjie horizontal zonation pattern was similar to the Glencairn pattern.

PREDATION HYPOTHESIS

Little support was found for this hypothesis. Although the survival pattern was as predicted (Table

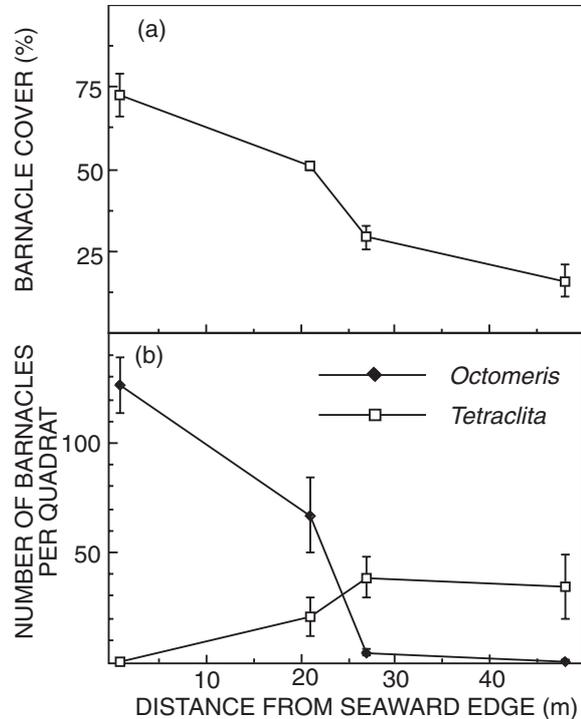


Fig. 6: Barnacle abundances along the Kommetjie wall – (a) total percentage cover, (b) mean number of individuals per quadrat (625 cm²) of the two species ($n = 3$ quadrats per site). Error bars denote ± 1 standard error

III), there was no evidence of a barnacle predator that preferred *Tetraclita* in O-areas and *Octomeris* in T-areas. The whelk *N. dubia* was common in the intertidal zone but, of the individuals that were found feeding, only 27% (9 out of 33 individuals) were feeding on barnacles. The rest were feeding on molluscs: *Littorina africana* (45%), *Patella granularis* (15%), *Siphonaria capensis* (6%), *Kellya rubra* (6%) and *Perna perna* (1%). Of the nine whelks feeding on barnacles, four were feeding on *Chthamalus dentatus*, five on *Tetraclita*, and none on *Octomeris*. The *Tetraclita* were being eaten in both the O-areas (three) and the T-areas (two). It is concluded that, although *N. dubia* did eat barnacles, there was no indication that it influenced the horizontal distribution of *Tetraclita* and *Octomeris*.

Another possible barnacle predator, the seastar *Marthasterias glacialis*, is rare in the intertidal zone at Glencairn with, on average, only one individual per

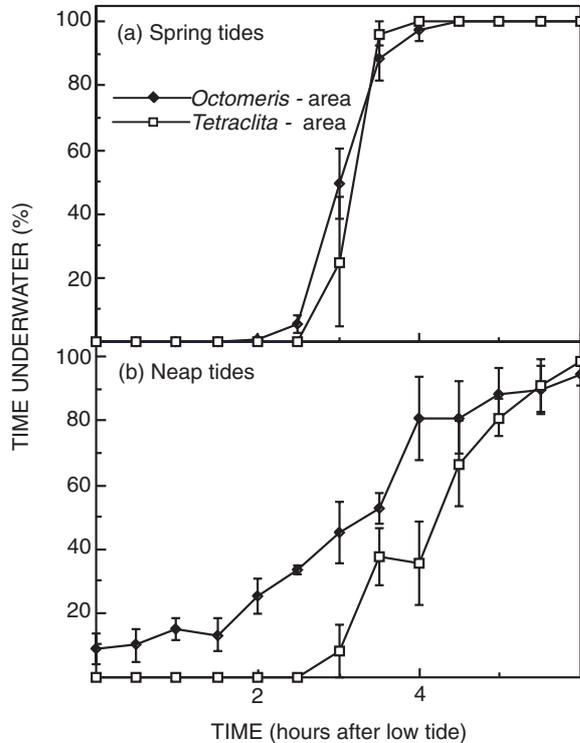


Fig. 7: Percentage of time *Octomeris*-areas and *Tetraclita*-areas spend underwater during (a) spring tides and (b) neap tides. Error bars denote ± 1 standard error

100 m of shoreline. These individuals were always in the extreme low intertidal zone and were unlikely to influence the *Tetraclita* and *Octomeris* horizontal pattern in the balanoid zone, although they may have influenced the vertical distribution of barnacles.

TEMPERATURE STRESS HYPOTHESIS

Support was found for this hypothesis. First, the survival pattern of *Octomeris* was as predicted, with higher survival in O-areas than in T-areas (Table III). Second, the times the O- and T-areas spent inundated were different, particularly during neap tides (Fig. 7). The period of inundation was almost identical in T- and O-areas during the spring-tide day, but T-areas spent significantly less time inundated during the neap-tide day. The reason for this difference was that, during the neap low tide, O-areas were frequently splashed or covered by waves, whereas T-areas were not, because of rapid wave attenuation. This resulted

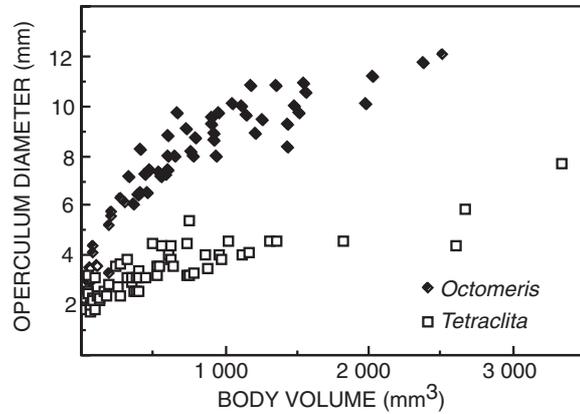


Fig. 8: Relationships between the operculum diameter and body volume of *Tetraclita* and *Octomeris*

in T-areas being exposed for approximately 4.5 h every day, whereas O-areas were completely exposed only on spring tide days. Third, rock surface temperatures taken during the neap-tide series showed that T-areas were significantly hotter than O-areas (O-area = $16.1 \pm 0.4^\circ\text{C}$, T-area = $20.7 \pm 0.4^\circ\text{C}$; *t*-test, $p < 0.05$). The temperature regimes in O- and T-areas are therefore likely to be significantly different, with T-areas being hotter and drier because they are exposed more.

Finally, there were structural differences between the species that could lead to differences in their tolerance of high temperatures. *Tetraclita* have significantly smaller opercular openings than *Octomeris* (ANCOVA, $p < 0.0001$, Figs 8, 9a), indicating that *Tetraclita* may tend to be shaded by their own shells. In addition, the shell wall of *Tetraclita* is thick and composed of numerous tubes, whereas the shell wall of *Octomeris* is relatively thin and solid (Fig. 9b).

In examining whether temperature determines the relative abundance of *Tetraclita* and *Octomeris*, it was found that, in areas that were otherwise similar in elevation and current speed, the aspect of the rock face played an important role in determining the relative abundances of the two species. *Octomeris* were significantly more abundant on shaded slopes, whereas *Tetraclita* were significantly more abundant on sunny slopes (*t*-test, $p < 0.01$, $n = 12$, Fig. 10).

These results support the hypothesis that the *Tetraclita* and *Octomeris* zonation pattern is, at least in part, because of differences in their tolerances to temperature stress. *Octomeris* cannot survive in areas that are frequently hot and dry, whereas *Tetraclita*

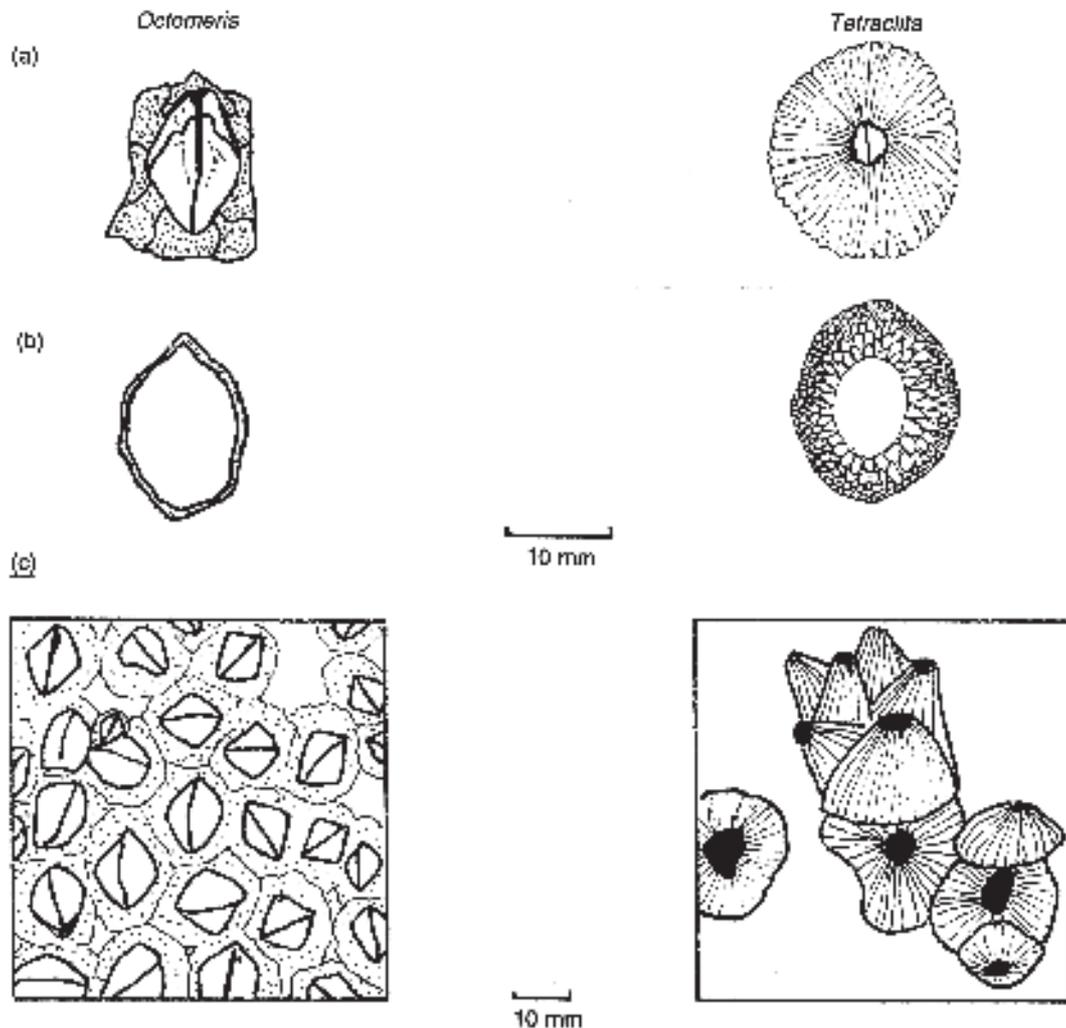


Fig. 9: The structure of *Octomeris* and *Tetraclita* shells from (a) above and (b) below. (c) The matrix that several individuals form (copied from photographs)

appears to be morphologically adapted to these conditions.

WAVE TOLERANCE HYPOTHESIS

Support was found for this hypothesis. First, the survival pattern of *Tetraclita* was as predicted, with lower survival in O-areas than in T-areas (Table III). Second, wave regimes were significantly different between the O- and T-areas. Wave heights were 90 ± 18 cm ($n = 106$) in the O-area and 29 ± 15 cm

($n = 106$) in the T-area. Wave heights therefore declined by more than two-thirds from the O-area to the T-area, resulting in wave heights and wave forces that were significantly lower in T-areas (t -test, $p < 0.001$). Third, *Tetraclita* and *Octomeris* had different tolerances to simulated strong wave action. *Tetraclita* was significantly more susceptible (t -test, $p < 0.01$) and lost, on average, more than 20 times the number of individuals to the simulated waves. On average, *Tetraclita* lost 24.5 ± 19.4 ($n = 10$) individuals to the "waves", whereas *Octomeris* lost only 0.9 ± 1.37

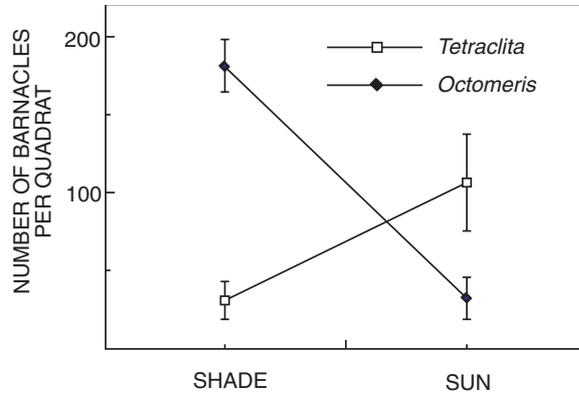


Fig. 10: Mean number of *Tetraclita* and *Octomeris* individuals observed on the sunny and shady aspects of rock faces at 12 sites. Error bars denote ± 1 standard error

($n = 10$) individuals.

Finally, the matrix structures of *Tetraclita* and *Octomeris* were clearly different. These differences appear to lead to differences in their tolerance of strong waves. *Octomeris* tends to form a uniform matrix one individual thick, with very few individuals (<10%) growing on secondary space (Fig. 9c). In 10 high-density areas, only 7.6% of the 1 005 *Octomeris* individuals were growing on other *Octomeris*. *Tetraclita* also forms a uniform matrix when it is rare, but when it is abundant, individuals tend to form clusters in which several younger individuals are attached to two or three individuals that are on primary space (Fig. 9c). In the 10 high density areas, 47.6% of the 639 *Tetraclita* individuals were growing on other *Tetraclita*.

These results support the hypothesis that the *Tetraclita* and *Octomeris* zonation pattern is, at least in part, because of differences in their tolerances to strong wave forces. *Tetraclita* cannot occur in dense stands in exposed areas because its matrix pattern is not strong enough to withstand strong wave forces. However, the matrix structure of *Octomeris* appears adapted to strong wave forces.

DISCUSSION

The horizontal zonation pattern of *Tetraclita* and *Octomeris* is a striking feature of the South African intertidal zone. *Octomeris* is always most abundant in exposed areas and *Tetraclita* in calm areas at the same tidal height. This pattern occurs along gully

walls, where the T- and O-areas may be more than 20 m apart (Figs 1 and 6), and on boulders, where the T- and O-areas may be less than 1 m apart (Fig. 2).

The ultimate process producing the pattern appears to be differential survival: *Tetraclita* adults survived better in T-areas and *Octomeris* adults survived better in O-areas. Each of the five hypotheses attempted to explain this differential survival. No support was found for the Structure of Cirri Hypothesis, the currently popular explanation of the pattern (Branch and Branch 1981). Little support was found for the two biological hypotheses (Competition and Predation), but there was support for the two physical hypotheses (Temperature Stress and Wave Tolerance). Therefore, physical factors appear more important than biological factors in determining the horizontal zonation pattern of the two species.

This conclusion is supported by the work of others in South Africa. McQuaid (1985) also found low rates of activity in *N. dubia* and low rates of predation on *Tetraclita* and *Octomeris*. Delafontaine (1987) concluded that the distribution of *Tetraclita serrata* was determined by physical factors rather than competition. Finally, Delafontaine and Flemming (1989) believed that physical factors rather than predation and competition were determining the microdistribution of *Tetraclita* and *Octomeris*.

The present results suggest the following scenario. Physical factors vary along a horizontal plane of constant elevation within the intertidal zone on rocky shores: wave height and wave strength are high at the seaward end and decline towards the landward end, whereas temperatures and desiccating rates are high at the landward end and decline towards the seaward end. *Tetraclita* and *Octomeris* are adapted to the conditions experienced at opposite ends of the gradient, and being adapted to one end of the gradient precludes the species from surviving well at the other extreme. *Octomeris* is particularly well adapted to strong wave forces; it is relatively short, and many individuals together form a strong, single-layered matrix. However, the sheet-like nature of the *Octomeris* matrix means that individuals are easily overheated by the sun, and therefore *Octomeris* cannot survive in areas that are exposed too long to direct sunlight. *Tetraclita*, on the other hand, is adapted to hot and dry conditions; it has a tall shell with a small opercular opening, and the shell walls are thick and composed of numerous tubes (Darwin 1854). In addition, *Tetraclita* forms a knobby matrix where many individuals are attached to other individuals rather than to the substratum. All of these characteristics may reduce heat-loading (Newell 1976). However, the tall and relatively poorly attached *Tetraclita* matrix cannot withstand strong waves, precluding its occurrence in

areas exposed to direct wave action. Therefore, *Tetraclita* and *Octomeris* survive alone at either end of the gradient and overlap in the middle, where conditions are intermediate. There are many places in the intertidal zone that are at an intermediate position along the exposure gradient where either *Tetraclita* or *Octomeris* could survive. It appears that the microclimate determines at which site the species is more abundant because, as shown in Figure 10, the aspect of the rock alone can alter the relative abundance of the two species dramatically. Present observations and data support these statements, but each needs to be critically tested.

The temperature regimes in O- and T-areas are different, because T-areas are exposed longer during neap tides. Also the timing of neap low tides suggests that T-areas can become considerably hotter and drier than O-areas. Most spring low tides take place in the early morning, whereas many neap low tides occur during the hotter mid-day. For example, during the summer (December – March) of 1989, there were only five spring maximum lows during the hottest part of the day (12:00 – 15:00), whereas there were 20 neap maximum lows during those hours. By being exposed during neap tides, T-areas are subjected to the strongest heating and desiccating effects of the sun, whereas O-areas are not.

The present results suggest that the relative abundances of *Tetraclita* and *Octomeris* will vary in space and time according to changes in wave action and temperatures during the low tides. If wave action should increase, then *Octomeris* should survive better than *Tetraclita*. However, if wave action should decline and/or temperatures increase, then it is likely that O-areas would become hotter and drier and *Tetraclita* would survive better. These influences of wave action and temperature probably determine the relative abundance of the two species at different sites along the coast, even though recruitment rates appear to determine the absolute abundances of barnacles at the sites (Boland 1997). Also, very intense wave action during 1993 may be part of the reason for the relative decline in adult *Tetraclita* observed at Glencairn between August 1992 and April 1995 (personal observation).

The scenario described above focuses attention on the morphological adaptations of the barnacle species. *Octomeris* forms a single-layered matrix in which individuals are interlocked and cemented together. Each individual is firmly glued to the substratum and to its neighbours, thereby making a matrix structure resistant to wave damage. *Octomeris* individuals are long-lived and holes in the matrix are rare. When a hole is present, larvae recruit to the base of the animals on the perimeter of the hole (per-

sonal observation) and shore-up the exposed adults.

Tetraclita appears to have several characteristics that allow it to withstand severe heat-loading and desiccation stress. The small aperture may increase the amount of extra-visceral water for evaporative cooling (Suzuki and Mori 1963), decrease water loss (Achituv and Borut 1975) and increase shading, and the thick walls, tubules in the walls, ribbing on the shell and knobby matrix may all reduce heat-loading (Newell 1976).

Ecological aspects of the morphology of *Tetraclita* spp. have received some attention. Achituv and Borut (1975) conducted observations on the temperature and water relations of *T. squamosa* in the Red Sea. Those authors found that the shell reflects more incident radiant energy than rock and that the shell serves as an efficient thermal insulator. However, they also found that mantle cavity temperatures of adult barnacles were similar to rock surface temperatures. It must be noted that Achituv and Borut (1975) worked on rocks that were porous and barnacles that were solitary, and they commented (p. 105) that "In the main part of the *Tetraclita* belt . . . the temperatures of the rock and the animals probably do not reach [as high] such as those measured by us."

Vermeij (1978) has noted that many tropical barnacles, including *Tetraclita* spp., are conical and have small apertures, whereas temperate species are more cylindrical and have wide apertures. He hypothesized that the morphological differences are related to gradients in predation by muricid gastropods. He suggested that thick shell walls, produced by the network of tubules and strong ribbing on the shell, and small apertures, inhibit predation by drilling gastropods and allow those barnacles to flourish in the tropics. Vermeij (1978, p. 106) commented that "data to support a possible latitudinal trend in predation intensity by gastropods are unfortunately lacking."

An alternative hypothesis to explain why *Tetraclita* spp. are common in the tropics is that *Tetraclita* are adapted to high thermal stresses and/or high desiccation rates. The morphological characteristics of *Tetraclita* as described by Vermeij (1978) can be interpreted to be adaptations to thermal stress, and there is an obvious latitudinal gradient in temperature. The present study, in which *Tetraclita* survived better in the relatively hot and dry habitat, further supports this hypothesis.

Prior to the 1960s, physical factors were presumed to determine the distribution of rocky intertidal species (e.g. Lewis 1964). Since then, many investigators have shown experimentally that biological interactions can be important (e.g. Connell 1961). More recently, ecologists have emphasized the supply side and have shown that recruitment rates can determine abundances

(e.g. Gaines and Bertness 1992). Since the 1960s, studies have played down the earlier emphasis on physical factors. Despite this fact, it is interesting to note that one of the more obvious patterns in the distribution of two South African intertidal species appears to be the result of their responses to physical factors.

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