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IS THE GEOGRAPHIC PATTERN IN THE ABUNDANCE OF SOUTH AFRICAN BARNACLES DUE TO PRE-RECRUITMENT OR POST-RECRUITMENT FACTORS?

*J. M. BOLAND**

Intertidal barnacles are significantly more abundant on the south than on the west coast of South Africa. Abundances measured at 11 sites, covering 740 km of coastline, showed that South Coast and West Coast sites averaged 1 323 and 67 individuals·m^{-2} respectively. Barnacles were not replaced by other sessile organisms on the West Coast; instead the amount of bare space increased proportionately. Two general, alternative hypotheses can explain the abundance pattern: either pre-recruitment factors, those affecting the abundance of larvae, settlers and juveniles (<5 mm in basal diameter), or post-recruitment factors, those affecting the abundance of larger individuals (>5 mm in basal diameter), are significantly different on the two coasts. Measurements conducted on adults of the two most common barnacle species, *Tetraclita serrata* and *Octomeris angulosa*, over a three-year period at a West and a South Coast site did not support the post-recruitment hypothesis. Measurements showed that adult growth and survival were not inferior on the West Coast. First, the average sizes and maximum sizes of adults of the two species were greater at the West Coast site. Second, the growth rate of *Octomeris angulosa* was significantly higher at the West Coast site. Third, the survival rates of adults of both species were higher at the West Coast site. Additional support for the pre-recruitment factors hypothesis was provided by the number of recruits that were present in clearings that had been left for three years; these being 70 times more abundant in the clearings at the South Coast site. The results suggest that the geographic pattern in barnacle abundance along the South African coast is produced by differences in pre-recruitment factors rather than post-recruitment factors.

Intertidal barnacles are not uniformly abundant around the coast of South Africa. Along the South Coast, barnacles are abundant and can dominate the mid-shore, whereas on the West Coast, they are rare and most of the mid-shore is bare space (Branch and Branch 1981, this study). The same species of barnacles occur on both coasts, predominantly *Tetraclita serrata* and *Octomeris angulosa*, and one of the main structural differences between the South and West coast communities is the population sizes of these species.

There are many possible reasons for this South Coast/West Coast abundance pattern, but they fall into two general hypotheses. Either pre-recruitment factors or post-recruitment factors are significantly different on the two coasts. In this study, recruitment is considered to take place when juveniles reach approximately 5 mm basal diameter. Prior to recruitment an individual would have passed through a planktonic larval stage, settled on the substratum, metamorphosed and survived as a juvenile. After recruitment the juvenile would grow into a reproducing adult and possibly survive for many years (Keough and Downes 1982). Therefore, the pre-recruitment factors hypothesis includes factors affecting the abundance of larvae, settlers and juveniles (<5 mm in basal diameter), whereas the post-recruitment factors hypothesis includes factors affecting the abundance of larger individuals (>5 mm in basal diameter).

Either of these hypotheses could be correct, because the offshore and intertidal conditions are different along the two coasts. Offshore, the South Coast is influenced by the warm Agulhas Current, whereas the West Coast is affected by the Benguela Current, a cold, wind-driven upwelling system (Branch and Branch 1981, Boyd *et al*. 1992). Onshore, the South Coast is characterized by a Mediterranean-type climate, whereas the West Coast is more arid and backed by semi-desert (Schulze 1974).

Pre-recruitment factors that could result in a lower recruitment on the West Coast are current direction, abundance of predators in the water column and abundance of predators on the shore (e.g. Connell 1985, Roughgarden *et al*. 1988). Larvae may tend to be carried nearshore on the South Coast, but be swept far offshore on the West Coast as a result of the prevailing upwelling winds and currents. Predators of planktonic larvae, such as fish, may be

* California Coastal Commission, 3111 Camino del Rio North, Suite 200, San Diego, California 92108, U.S.A. E-mail: jboland@well.com; formerly Zoology Department, University of Cape Town, Rondebosch 7701, South Africa

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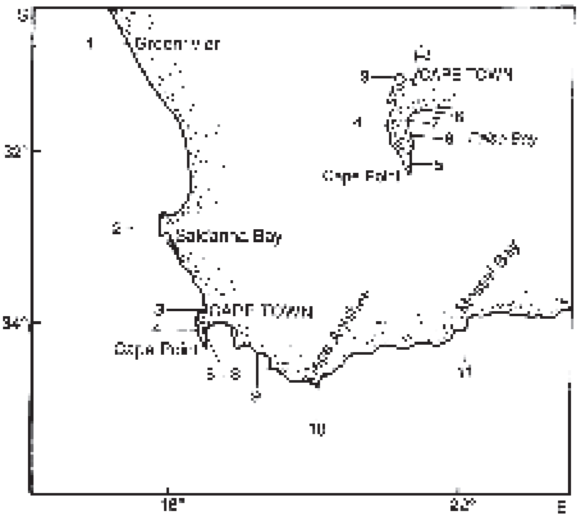

Fig. 1: Map of southern South Africa showing the location of the 11 study sites

more abundant along the West Coast because fish that feed on barnacle larvae live predominantly in offshore kelp beds (Gaines and Roughgarden 1987), and kelp beds are more common along the West Coast (Velimirov *et al*. 1977). Also, limpets that consume and bulldoze newly settled larvae are more common on the West Coast (Branch 1981).

Post-recruitment factors that could reduce the growth and survival of barnacles on the West Coast relative to the South Coast are low food abundances, smothering by intertidal algae, disturbance by kelp wrack and thermal stress. Food for intertidal barnacles may be in short supply on the West Coast, because frequent upwelling carries detritus-poor water into the intertidal (Seiderer and Newell 1985), whereas on the South Coast, bacteria-laden detritus is abundant nearshore (Cliff 1982a,b). The only large alga that is common in the Balanoid Zone on the coasts of South Africa and which is capable of overgrowing and smothering barnacles is the annual *Porphyra capensis*, and it is more abundant on the West than on the South Coast (unpublished data). Kelp wrack dragged by large waves can dislodge adult barnacles (pers. obs.) and kelp grows almost exclusively on the West Coast (Velimirov *et al*. 1977). Finally, barnacles are susceptible to thermal stress (Foster 1987) and air temperatures are higher along the West than along the South Coast (Schulze 1974).

It is not possible to determine from existing information whether pre- or post-recruitment factors are more likely to be affecting numbers of barnacles in the intertidal communities along the West and South coasts. The major aims of this paper are therefore:

(i) to describe the geographic patterns in the abundances of barnacles, and
(ii) to test the post-recruitment hypothesis by monitoring the growth and survival of adult barnacles at a South and a West Coast site. In addition, the pre-recruitment hypothesis is addressed by monitoring recruitment rates at those sites.

MATERIAL AND METHODS

Geographic pattern

For the purpose of definition, the South and West coasts of South Africa are considered in this study to converge at Cape Point (34°22′S, 18°31′E). Barnacle abundances were censused at 11 sites (Fig. 1) during January and February 1989. The sites were: 1 – Groenrivier (approximately 400 km north of Cape Point), 2 – Jacobs Bay, 3 – Sea Point, 4 – Kommetjie, 5 – Buffels Bay, 6 – Simonstown, 7 – Glencairn, 8 – Muizenberg, 9 – Hermanus, 10 – Cape Agulhas, and 11 – Mossel Bay (approximately 340 km east of Cape Point). Several sites were chosen close to Cape Point in order to identify where the transition from West to South coast occurred.

At each site, an exposed rocky shore with no sand was censused in a stratified, random manner. The shore was divided into three adjacent sections 50 m wide and one randomly placed belt transect was run from the high intertidal to the low intertidal in each section. Each transect was 25 cm wide and ran from the highest elevation where there was a barnacle within 5 m of the transect to the lowest elevation where there was a barnacle within 5 m of the transect. A 25 × 25 cm flexible quadrat (625 cm^2) was moved down the length of the transect so that every barnacle within the belt was counted. As barnacles are not found in large tidal pools, such areas were bypassed. If fewer than 100 quadrats were censused in the three transects, more complete transects were used until that number of quadrats was achieved. The 11 sites were each represented on average by 3.9 ($SE = \pm 0.5$) transects and 114 ($SE = \pm 5$) quadrats.

In each quadrat, the following information was collected: the number of individuals of each barnacle species; an estimate of the percentage cover of all barnacles; and an estimate of the percentage cover of bare space, i.e. space not occupied by sessile or mobile organisms. The percentage cover of barnacles or bare space was estimated for each quadrat by tallying the number of whole quadrat squares and fractions of quadrat squares occupied by barnacles or bare space and dividing by 25, i.e. the total number of quadrat squares.

Comparison of population processes on the South and West coasts

Two of the sites used in the geographic pattern analysis were chosen to represent the two coasts: Kommetjie (Site 4, West Coast) and Glencairn (Site 7, South Coast). These sites are only 12 km apart and are at the same latitude on opposite sides of the Cape Peninsula (Fig. 1). The sites are similar in structure; their intertidal areas are composed of the same rock type, i.e. Table Mountain sandstone (McQuaid *et al.* 1985), they have similar slopes, tidal ranges and exposure to waves.

The most abundant barnacle species on both the South and West coasts were *Tetraclita serrata* and *Octomeris angulosa* (hereafter referred to as *Tetraclita* and *Octomeris*). These species have similar vertical ranges, from approximately MLWS (Mean Low Water Spring), to MHWS (Mean High Water Spring), but they tend to be segregated by wave exposure, with *Octomeris* being more wave-tolerant (Boland 1997). For example, when both species occur on an isolated boulder, *Octomeris* is most abundant on the seaward side of the boulder, whereas *Tetraclita* is most abundant, at the same elevation, on the landward side. Comparisons of the population processes of barnacles on the South and West coasts were made by comparing the size frequencies and rates of growth, survival and recruitment of these two species at the two sites. The intertidal ranges of the barnacles were slightly different at the two sites. At Glencairn they were from -0.01 to 1.78 m above LAT (Lowest Astronomical Tide = chart datum), whereas at Kommetjie they occurred from 0.37 to 1.32 m above LAT. Therefore, care was taken to take measurements at all tidal heights at both sites.

SIZE FREQUENCIES

Basal shell diameters of *Tetraclita* and *Octomeris* were measured at Kommetjie and Glencairn during August 1989. So that individuals from all elevations were included, measurements were made along the same transects described above. Because of the large differences in barnacle numbers at the two sites, the widths of the belt transects differed. At Glencairn all the barnacles within 1 cm of one side of the transect line were measured, whereas at Kommetjie all the barnacles within 20 cm of the transect line were measured. A total of 841 individuals was measured at the two sites.

GROWTH RATES

In order to follow the growth of known individuals, photographs were taken of barnacleinhabited areas (approximately 12 × 20 cm) at sites randomly chosen along vertical transects at both sites. Each area photographed was marked with a small piece of marine epoxy. In all, 47 photographs were taken at Kommetjie and 76 at Glencairn. A few days later, *Tetraclita* and *Octomeris* individuals were chosen for measuring and were numbered on the photographs. These naturally occurring adults are referred to as "naturals". Between one and nine naturals were chosen per photograph. The naturals included some individuals that were completely isolated from others, but most were in contact with others and therefore their shells were distorted by their neighbours.

Because there were only a few small (< 10 mm basal shell diameter) barnacles occurring naturally at Kommetjie, small individuals of both species were transplanted from a South Coast site to both Glencairn and Kommetjie. These "transplants" were collected by hammering off pieces of rock with barnacles and then attaching them to the new site.

A total of 472 natural and transplanted barnacles was measured during June/July 1989. They were measured again 16 weeks later but, because they showed no measurable growth, these data are not presented. Three years later, during July/August 1992, all remaining individuals were measured again and these data are presented herein. The shell height, basal shell diameter (along the rostro-carinal axis) and the diameter of the opercular opening (along the rostro-carinal axis) were measured on each barnacle with calipers. A precision test, in which the same barnacles were measured on two consecutive days, showed an average difference of <5% between measurements. Barnacle volume 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 the opercular opening, R the radius of the shell base and h the shell height (Merritt 1962). Volume is a more accurate measure of size

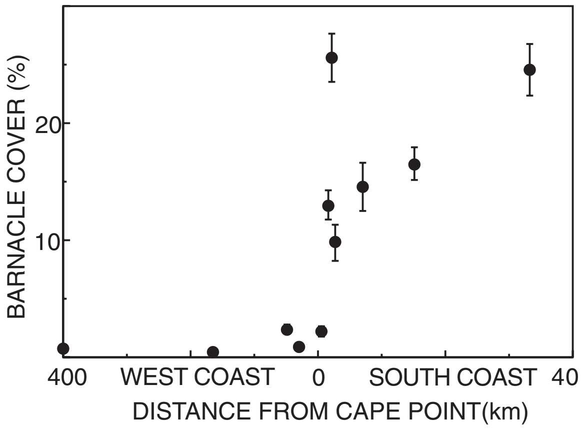

Fig. 2: Mean percentage cover of barnacles at the 11 sites. Error bars denote ± 1 standard error

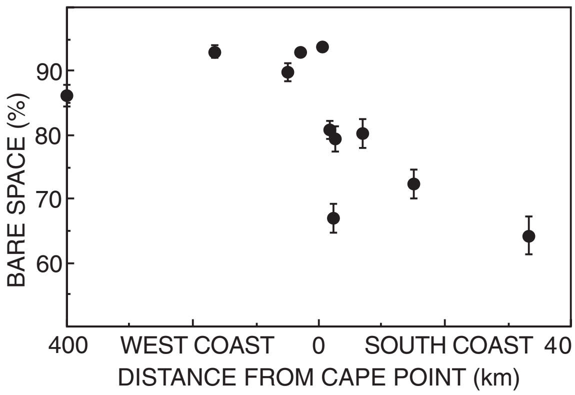

Fig. 3: Mean percentage cover of bare space at the 11 sites. Error bars denote ± 1 standard error

than basal diameter of the shell, because the basal spread of many of the individuals was distorted by neighbours. Mass was more strongly correlated with volume in both species (*Tetraclita,* r^2 = 0.992, n = 20, p < 0.01; *Octomeris,* r^2 = 0.922, n = 20, p <0.01) than with basal diameter (*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* were estimated by comparing the number alive in July 1992 with the number in the photographs taken during May/June 1989. Numbered barnacles (those used for growth measurements) and unnumbered barnacles were used, but transplants were not.

RECRUITMENT RATES

The recruitment of barnacles at Kommetjie and Glencairn was compared by making randomly placed clearings (10 × 5 cm) along vertical transects at both sites during May 1989. Clearings were made by scraping barnacles and any other organisms off the rocks using a paint scraper and hammer. No chemicals were used. A total of 27 clearings was made at Kommetjie and 40 at Glencairn. From June to November 1989, the clearings were examined monthly and new recruits searched for using a hand lens. The clearings were inspected again in July 1992. The clearings were then searched by the naked eye and all barnacles were identified and counted. The clearings in July 1992 contained "recruits" that could have been up to 2 years of age.

RESULTS

Geographic pattern

Barnacles were more abundant on the South than on the West Coast (Fig. 2). The transition in numbers of barnacles between the two coasts was not at Cape Point, but approximately 10 km east of it, between Buffels Bay (Site 5) and Simonstown (Site 6). Barnacles occupied up to 26% of the intertidal area on the South Coast, but <4% of the area on the West Coast. On average, the South Coast sites had 1 323 barnacles·m^{-2} (SE = 370, n = 6 sites), whereas the West Coast sites had only 67 barnacles·m^{-2} (SE = 31, n = 5 sites), a significant (t-test, p < 0.05), 20-fold difference in density.

Barnacles were not replaced by other sessile organisms on the West Coast; instead the amount of bare space increased (Fig. 3). Bare space accounted for up to 90% of the intertidal area on the West Coast and approximately 75% of the area on the South Coast. The percentage cover of barnacles and the percentage cover of bare space were significantly, negatively correlated (r^2 = 0.924, p < 0.001).

The majority of the barnacles on both coasts were *Tetraclita* and *Octomeris* (Fig. 4). Their relative abundances did not show a geographic pattern, but local conditions appeared to influence the proportions of the species present at a given site. *Octomeris*, the species that is most wave-tolerant (Boland 1997), was the most abundant species on

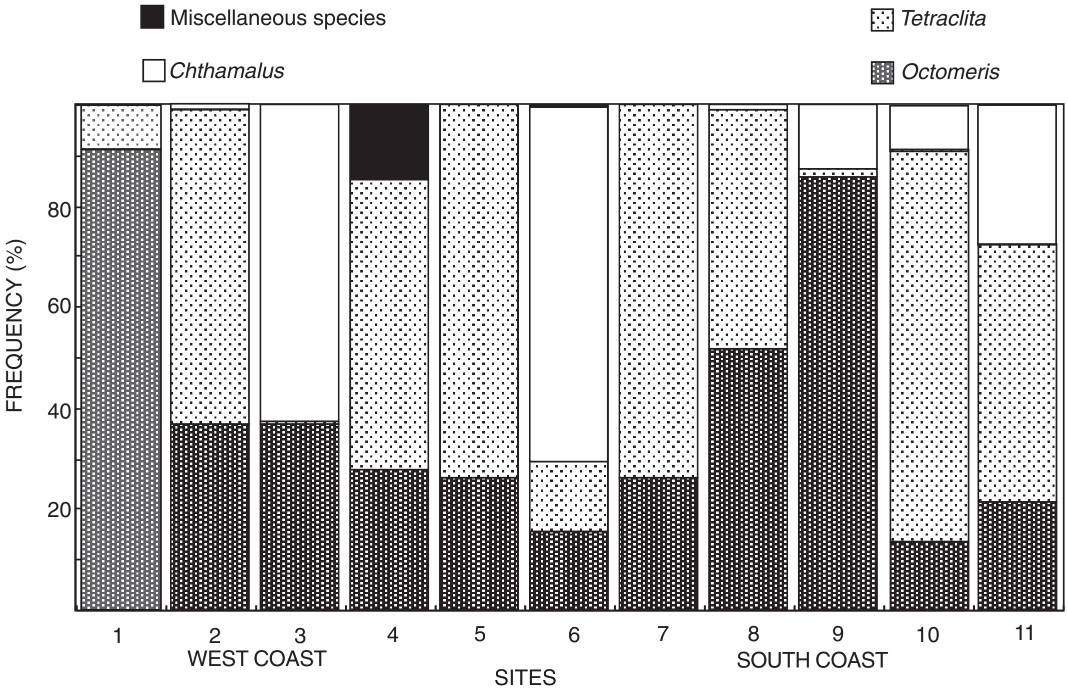

Fig. 4: Species composition at the 11 sites (see Fig. 1 for site numbers)

shores where strong waves can hit at all tidal heights, i.e. the steepest shores (Site 1 – Groenrivier, and Site 9 – Hermanus). By contrast, *Tetraclita* was more common on more gently sloping shores. It is noteworthy that *Tetraclita* and *Octomeris* had similar relative abundances at Site 4 (Kommetjie) and Site 7 (Glencairn), the two sites used for the comparisons of population processes.

Three other species were present at the study sites. The high intertidal species *Chthamalus dentatus* was most abundant on granite shores (Site 3 – Sea Point and Site 6 – Simonstown), possibly because granite stays cooler than other rock types (Raimondi 1988). *Notomegabalanus algicola* and *Chthamalus stellatus*, the "miscellaneous species" in Figure 3, were also present at some sites, but were generally very rare.

Comparison of population processes on the South and West coasts

SIZE FREQUENCIES

Adults of *Tetraclita* and *Octomeris* were significantly larger at Kommetjie than at Glencairn (Kolmogorov-Smirnov Two-sample test, $p < 0.01$; Fig. 5). Both the average and the maximum size of *Tetraclita* and *Octomeris* were greater at Kommetjie. This is the first indication that conditions along the West Coast, and at Kommetjie in particular, were not detrimental to the persistence of adult barnacles. All distributions were approximately normal, with no obvious peak of recent recruits among the small sizes.

GROWTH RATES

Tetraclita growth rates were not significantly different between the two coasts, but *Octomeris* growth rates were significantly different. *Octomeris* grew faster at Kommetjie than at Glencairn (Table I). This contrasts with the outcome predicted by the post-recruitment hypothesis. These data therefore do not support it.

Tetraclita and *Octomeris* are relatively slow growing barnacles; virtually no growth could be detected in six months, and measurable growth took place only after three years. Based on those growth rates and the growth of barnacles that settled on the epoxy, the largest individuals measured (approximately 30-mm shell diameter) were at least five years old

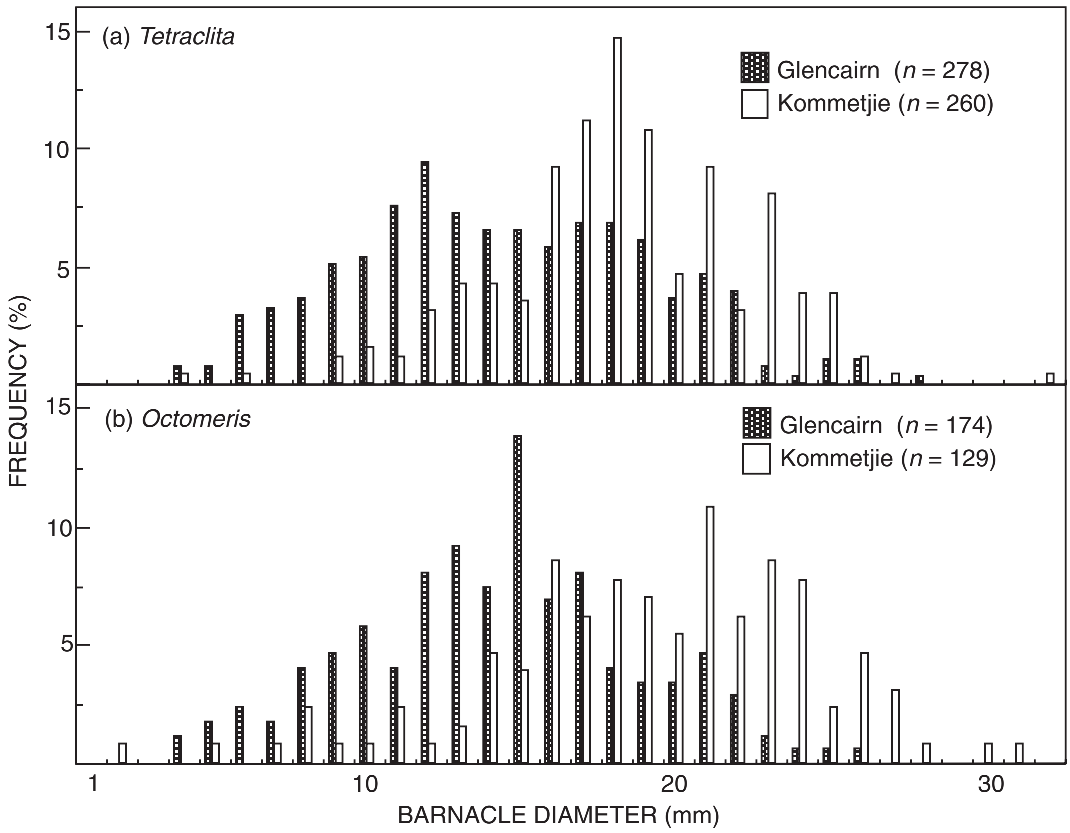

Fig. 5: Size frequency distributions of (a) *Tetraclita* and (b) *Octomeris* at Glencairn and Kommetjie. The number of individuals measured are indicated

but, because they grow little once they are near maximum size, their ages could not be estimated accurately.

SURVIVAL RATES

The survival rates of both species were high and ranged between 55 and 93% for the three-year period, or up to 97% survival per year (Table II). These rates show that both of these species are long-lived. In contrast, *Chthamalus* is a relatively short-lived species; of the 54 individuals photographed in 1989, none survived to 1992.

Survival rates for both *Tetraclita* and *Octomeris* differed between the two coasts; survival was significantly higher at Kommetjie than at Glencairn (Table II, χ^2 test, $p < 0.005$). These results provide further evidence that conditions at Kommetjie are not detrimental to the growth and survival of barnacle adults. Therefore, the post-recruitment hypothesis, that holds that the geographic pattern in barnacle abundance is attributable to the significantly lower growth and/or survival of adult barnacles on the West Coast, should be rejected.

RECRUITMENT RATES

There was no recruitment during the first six months after clearing on either coast. However, on inspection of the clearings in June 1992, after 2 years had elapsed, some "recruits" were found in the clearings. At that time, the majority of the cleared space was still unoccupied, no other sessile organisms had become established in the clearings and, although some barnacles had recruited, none of the clearings had reached the initial density of barnacles when the clearings were created. For example, 551 individuals were removed at Glencairn when creating the clearings in 1989 and only 104 barnacles were present in

Table I: Growth rates of *Tetraclita* and *Octomeris* on the west and south coasts of South Africa. 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 K>G indicates that Kommetjie growth rate was significantly greater than Glencairn growth rate

Parameter	Kommetjie (West Coast)			Glencairn (South Coast)			ANCOVA
	Intercept	Slope	Coefficient of determination (r^2)	Intercept	Slope	Coefficient of determination (r^2)	
		($n = 48$)	*Tetraclita*		($n = 60$)		
Shell height (mm)	6.308	0.549	0.602	5.265	0.573	0.401	*NS*
Shell diameter (mm)	11.59	0.515	0.524	10.640	0.534	0.498	*NS*
Opercular-opening diameter (mm)	2.498	0.781	0.845	3.281	0.616	0.480	*NS*
Shell volume (mm^3)	815.1	0.839	0.771	596.8	0.964	0.706	*NS*
		($n = 42$)	*Octomeris*		($n = 60$)		
Shell height (mm)	3.020	0.775	0.745	3.491	0.523	0.407	K > G**
Shell diameter (mm)	7.517	0.688	0.674	6.443	0.647	0.780	K > G **
Opercular-opening diameter (mm)	3.833	0.722	0.895	4.200	0.650	0.774	*NS*
Shell volume (mm^3)	500.2	0.943	0.872	235.3	1.905	0.789	K > G**

** $p < 0.005$
NS = not significant ($p > 0.05$)

the clearings in 1992.

The 1992 observations provide some information on the relative recruitment rates on the two coasts. At Kommetjie, only one recruit occurred in one clearing (i.e. in only 1/27 or 4% of the clearings, Table III). By contrast, at Glencairn 24/40, or 60%, of the clearings had recruits and recruitment rates were significantly higher than at Kommetjie (χ^2 test, $p < 0.005$). On average, the number of recruits was 7.4·m^{-2} at Kommetjie and 520·m^{-2} at Glencairn – a 70-fold difference. Even when these results are expressed as mean number of recruits per adult, there were more at Glencairn (0.355·adult^{-1}) than at Kommetjie (0.271·adult^{-1}). Although these 1992 recruitment observations are problematic, because the data include some post-recruitment mortality, they support the pre-recruitment hypothesis.

DISCUSSION

The difference in the abundance of barnacles along the West and South coasts of South Africa is striking; barnacle densities being 20 times greater on the South Coast. This pattern has been noted previously (e.g. Stephenson and Stephenson 1972, Branch and Branch 1981), but its cause has, until now, not been investigated. Two general, alternative hypotheses are proposed here to explain the pattern: the pre- and post-recruitment factors hypotheses.

The comparisons of population processes at two study sites do not support the post-recruitment factors hypothesis. First, the average and maximum sizes of adult *Tetraclita* and *Octomeris* were greater at the West Coast site. Second, the growth rates of

Table II: Survival of *Tetraclita* and *Octomeris* on the west and south coasts of South Africa over the three-year period 1989–1992. The results of the χ^2 tests are given, where K > G indicates that Kommetjie survival rate was significantly greater than Glencairn survival rate

Species	Kommetjie (West Coast)			Glencairn (South Coast)			χ^2 test
	Survived	Died	Survival (%)	Survived	Died	Survival (%)	
Tetraclita	77	41	65	363	292	55	K > G*
Octomeris	151	12	93	617	164	79	K > G**
Total	228	53	79	980	456	67	K > G**

* $p < 0.05$
** $p < 0.005$

Table III: Recruitment of *Tetraclita* and *Octomeris* on the west and south coasts of South Africa over the three-year period 1989 –1992. The results of the χ^2 tests are presented, where K < G indicates that Kommetjie recruitment rate was significantly less than the Glencairn recruitment rate

Species	Kommetjie (West Coast, n = 27)			Glencairn (West Coast, n = 40)			χ^2 test
	Number of recruits	Number of clearings with recruits	Clearings with recruits (%)	Number of recruits	Number of clearings with recruits	Clearings with recruits (%)	
Tetraclita	0	0	0	21	8	20	K < G*
Octomeris	1	1	4	83	17	43	K < G**
Total	1	1	4	104	24†	60	K < G**

* $p < 0.05$
** $p < 0.005$
n = Total number of clearings per site
† = One clearing contained both species

adult *Octomeris* were higher at the West Coast site. Third, the survival rates of adult *Tetraclita* and *Octomeris* were greater at the West Coast site. Therefore, it is suggested that the post-recruitment factors that are likely to affect adult growth and survival, such as predation, competition, physical disturbance and thermal stress, are relatively unimportant in producing the differences in barnacle abundances observed on the West and South coasts. Instead, these results support the pre-recruitment factors hypothesis.

The recruitment data also support the pre-recruitment factors hypothesis. A significantly greater number of recruits of both species occurred in the clearings at Glencairn. However, because these data were collected after 2 years, it cannot be determined whether the pattern in recruitment of young barnacles to the population is attributable to patterns in settlement or post-settlement mortality (Keough and Downes 1982). Therefore, these data do not help identify where the pattern is produced, but provide further evidence that the pattern is produced before the adult stage.

It appears that the greater abundance of barnacles on the South Coast is the result of moderate recruitment of young barnacles (>5 mm basal diameter) to the community, whereas the lower abundance of barnacles on the West Coast is because of relatively poor recruitment of young barnacles to the community. It is noteworthy that, because both recruitment and mortality rates were relatively low at Kommetjie and both those rates were relatively high at Glencairn, both population sizes remained relatively stable, despite the fact that the population processes at each site differed.

This study points to the factors that influence recruitment rates as being a fruitful area of further study. Recruitment is the result of several steps, including reproduction, larval dispersal, settlement and early post-settlement survival (Keough and Downes 1982, Connell 1985). Of these steps, only reproduction by *Tetraclita* and *Octomeris* has been documented, and it appears to be similar between South Africa's south and west coasts (Griffiths 1979).

Larval supply has been shown to control the abundance of barnacles on shores elsewhere (e.g. Raimondi 1990, Gaines and Bertness 1992), and it may control the abundance of barnacles on the rocky shores around South Africa as well. *Tetraclita* and *Octomeris* larvae are planktonic during the austral spring and summer (Lazarus 1974, Griffiths 1979). During that period, the prevailing, strong southerly and south-easterly winds tend to blow onshore on the South Coast and offshore on the West Coast (Shannon 1985). Those offshore winds on the West Coast produce one of the strongest upwelling systems in the world – the Benguela system. The near-surface currents of that system can be fast, and plankton may be advected offshore at rates of 10–15 km·day^{-1} (Hutchings 1981). A causal relationship can therefore be inferred from differences in nearshore currents, leading to differences in larval availability along the two coasts.

Early post-settlement mortality may also be important. Limpets may influence barnacle abundances by consuming newly settled larvae or by bulldozing them off the rocks (Branch 1981). Limpets are larger and more abundant on the West Coast (Branch 1981) and they have been hypothesized to be an important factor in the scarcity of barnacles on that coast (Branch and Griffiths 1988). However, recent limpet experiments on removal on the West Coast have not led to any increase in *Tetraclita* and *Octomeris* recruitment (unpublished data), and a limpet-removal experiment conducted on the East Coast produced ambiguous results (Dye 1995). Therefore, of these pre-recruitment factors, the dispersal and supply of larvae may be the most likely ones influencing the abundance of adult barnacles.

A problem with the population processes comparisons in this study is that each coast is represented by only one site, and therefore the observed differences may be a result of differences between the sites rather than between the coasts. The likelihood of this was reduced by choosing two sites that were similar in many respects, i.e. latitude, intertidal slope, tidal range, rock type and exposure to waves. In addition, observations of average and maximum shell basal diameters at the other West and South coast sites support the conclusions presented here.

Recruitment rates were low during this study and there was no recruitment between May and November 1989, when monthly observations were made. However, Griffiths (1979) found high recruitment (on average 155 recruits·m^{-2}·$month^{-1}$, $SE = 50$, $n = 6$) of *Tetraclita* and *Octomeris* during the same months in 1974 at a site on the South Coast only 4 km from Glencairn. The 1992 recruitment observations show that the addition of juveniles to the population is slow. At Glencairn, only one-fifth of the original number of barnacles had colonized the clearings in three years. At that rate, it may take 15 years for the clearings to regain their original density. However, it is more likely that recruitment is erratic, as has been found for these species elsewhere (Dye 1988, 1992), and that the period 1989–1992 was characterized by poor recruitment at the study sites. Another good recruitment year similar to 1974 could quickly return the clearings to their previous density. This type of episodic recruitment has been documented for many marine species (Reed *et al*. 1988).

Many of the current paradigms in intertidal ecology are based on research conducted in only three regions: western Scotland (e.g. Connell 1961), the north-west coast of the U.S.A. (e.g. Dayton 1971, Paine and Levin 1981), and New England (e.g. Menge 1976, Lubchenco 1978). Recently, it has been realized that these regions are areas of strong recruitment and consequently are not representative of all coasts (Underwood *et al*. 1983, Connell 1985, Menge 1991). Interest has therefore shifted to poor-recruitment coasts and the existing paradigms are being evaluated on those shores. Poor-recruitment coasts include central California (Roughgarden *et al*. 1987), Panama (Menge 1991) and the eastern shores of Australia (Underwood *et al*. 1983). The present data suggest that, at least for barnacles, the South African west coast is another poor-recruitment coast and the South Coast can be considered one of strong recruitment.

At least two intertidal species recruit regularly to the West Coast in high numbers – the alga *Porphyra* and the barnacle *Chthamalus*. But the question arises as to how they manage to recruit to the West Coast if the prevailing spring/summer offshore winds and currents advect planktonic larvae offshore? For *Porphyra*, the answer lies in the fact that they recruit during winter (personal observation), when the winds and currents along the West Coast are predominantly onshore (Shannon 1985). For *Chthamalus*, it is hypothesized that this short-lived species has larvae in the water column most of the year and that, although its larvae may be carried offshore during spring and summer, it is able to recruit to the West Coast during the other seasons, when onshore winds prevail (Shannon 1985).

The faunas of the West and South coasts of South Africa have been thoroughly described and the coasts are dominated by different species (Stephenson and Stephenson 1972, Brown and Jarman 1978). The distributions of these faunas are correlated with sea temperature, which has been presumed to be the major factor controlling which species inhabit the West and South coasts (McQuaid and Branch 1984). However, what is the mechanism determining their abundance and distribution? As pre-recruitment factors appear to determine the abundance of barnacles on the two coasts, these factors may also determine the abundance of other taxa. The characteristics of *Tetraclita* and *Octomeris* that appear to make them susceptible to pre-recruitment sources of mortality or loss are their planktonic larval stages, which are released during spring and summer, when offshore winds prevail on the West Coast, and their intertidal recruitment, which makes them susceptible to predation or disturbance by limpets. Other species with these life history characteristics may show a South Coast/West Coast abundance pattern similar to barnacles, because of factors influencing their pre-recruitment stages.

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LITERATURE CITED

BOLAND, J. M. 1997 — The horizontal zonation of two species of intertidal barnacle in South Africa. *S. Afr. J. mar. Sci*. **18**: 49–61.

BOYD, A. J., TAUNTON-CLARK, J. and G. P. J. OBERHOLSTER 1992 — Spatial features of the near-surface and midwater circulation patterns off western and southern South Africa and their role in the life histories of various commercially fished species. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci*. **12**: 189–206.

BRANCH, G. M. 1981 — The biology of limpets: physical factors, energy flow, and ecological interactions. In *Oceanography and Marine Biology. An Annual Review* **19**. Barnes, M. (Ed.). Aberdeen; University Press: 235–379.

BRANCH, G. [M.] and M. [L.] BRANCH 1981 — *The Living Shores of Southern Africa*. Cape Town; Struik: 272 pp. + 60 pp. Plates.

BRANCH, G. M. and C. L. GRIFFITHS 1988 — The Benguela ecosystem. 5. The coastal zone. In *Oceanography and Marine Biology. An Annual Review* **26**. Barnes, M. (Ed.). Aberdeen; University Press: 395–486.

BROWN, A. C. and N. [G.] JARMAN 1978 — Coastal marine habitats. In *Biogeography and Ecology of Southern Africa* **2**. Werger, M. J. A. (Ed.). The Hague; W. Junk: 1241–1277.

CLIFF, G. 1982a — Seasonal variation in the contribution of phytoplankton, bacteria, detritus and inorganic nutrients to a rocky shore ecosystem. *Trans. R. Soc. S. Afr*. **44**: 523–538.

CLIFF, G. 1982b — Dissolved and particulate matter in the surface waters of False Bay and its influence on a rocky shore ecosystem. *Trans. R. Soc. S. Afr*. **44**: 539–545.

CONNELL, J. H. 1961 — The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus. Ecology* **42**(4): 710–723.

CONNELL, J. H. 1985 — The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J. expl mar. Biol. Ecol*. **93**(1&2): 11–45.

DAYTON, P. K. 1971 — Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* **41**(4): 351–389.

DYE, A. H. 1988 — Rocky shore surveillance on the Transkei coast, southern Africa: temporal and spatial variability in the balanoid zone at Dwesa. *S. Afr. J. mar. Sci.* **7**: 87–99.

DYE, A. H. 1992 — Recruitment dynamics and growth of the barnacle *Tetraclita serrata* on the east coast of southern Africa. *Estuar. coast. Shelf Sci*. **35**(2): 167–177.

DYE, A. H. 1995 — The effects of excluding limpets from the lower balanoid zone of rocky shores in Transkei, South Africa. *S. Afr. J. mar. Sci*. **15**: 9–15.

FOSTER, B. A. 1987 — Barnacle ecology and adaptation. In *Barnacle Biology*. Southward, A. J. (Ed.). Rotterdam; Balkema: 113–133.

GAINES, S. D. and M. D. BERTNESS 1992 — Dispersal of juveniles and variable recruitment in sessile marine species. *Nature., Lond.* **360**: 579–580.

GAINES, S. D. and J. ROUGHGARDEN 1987 — Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. *Science*, *N. Y.* **235**: 479–481.

GRIFFITHS, R. J. 1979 — The reproductive season and larval development of the barnacle *Tetraclita serrata* Darwin. *Trans. R. Soc. S. Afr*. **44**: 97–111.

HUTCHINGS, L. 1981 — The formation of plankton patches in the southern Benguela Current. In *Coastal and Estuarine Sciences*. **1**. *Coastal Upwelling*. Richards, F. A. (Ed.). Washington, D.C.; American Geophysical Union: 496–506.

KEOUGH, M. J. and B. J. DOWNES 1982 — Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia* **54**: 348–352.

LAZARUS, B. I. 1974 — The inshore zooplankton of the Western Cape. Ph.D. thesis, University of Stellenbosch: 300 pp. + 76 pp. of Figures and Tables.

LUBCHENCO, J. 1978 — Plant species diversity in a marine intertidal community: importance of herbivore food preferences and algal competitive abilities. *Am. Nat.* **112**: 23–39.

McQUAID, C. D. and G. M. BRANCH 1984 — Influence of sea temperature, substratum and wave exposure on rocky intertidal communities: an analysis of faunal and floral biomass. *Mar. Ecol. Prog. Ser.* **19**(1+2): 145–151.

McQUAID, C. D., BRANCH, G. M. and A. A. CROWE 1985 — Biotic and abiotic influences on rocky intertidal biomass and richness in the southern Benguela region. *S. Afr. J. Zool.* **20**(3): 115–122.

MENGE, B. A. 1976 — Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecol. Monogr.* **46**: 355–393.

MENGE, B. A. 1991 — Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *J. expl mar. Biol. Ecol*. **146**: 69–100.

MERRITT, F. S. 1962 — *Mathematics Manual*. New York; McGraw-Hill: 378 pp.

PAINE, R. T. and S. A. LEVIN 1981 — Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.* **51**(2): 145–178.

RAIMONDI, P. T. 1988 — Rock type affects settlement, recruitment, and zonation of the barnacle *Chthalamus anisopoma* Pilsbury. *J. expl mar. Biol. Ecol*. **123**(3): 253–267.

RAIMONDI, P. T. 1990 — Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecol. Monogr*. **60**: 283–309.

REED, D. C., LAUR, D. R. and A. W. EBELING 1988 — Variation in algal dispersal and recruitment: the importance of episodic events. *Ecol. Monogr*. **58**(4): 321–335.

ROUGHGARDEN, J., GAINES, S. D. and S. W. PACALA 1987 — Supply side ecology: the role of physical transport processes. In *Organization of Communities.* Gee, J and P. Giller (Eds). Oxford; Blackwell: 491–518.

ROUGHGARDEN, J., GAINES, S. D. and H. POSSINGHAM 1988 — Recruitment dynamics in complex life cycles. *Science*, *N. Y.* **241**: 1460–1466.

SCHULZE, B. R. 1974 — *Climate of South Africa*. **8**. *General Survey*. Pretoria; South African Weather Bureau: 330 pp.

SEIDERER, L. J. and R. C. NEWELL 1985 — Relative significance of phytoplankton, bacteria and plant detritus as carbon and nitrogen resources for the kelp bed filter-feeder *Choromytilus meridionalis. Mar. Ecol. Prog. Ser.* **22**: 127–139.

SHANNON, L. V. 1985 — The Benguela ecosystem. 1. Evolution of the Benguela, physical features and processes. In *Oceanography and Marine Biology. An Annual Review* **23**. Barnes, M. (Ed.). Aberdeen; University Press: 105–182.

STEPHENSON, T. A. and A. STEPHENSON 1972 — *Life between Tidemarks on Rocky Shores*. San Francisco; Freeman: 425 pp.

UNDERWOOD, A. J., DENLEY, E. J. and M. J. MORAN 1983 —

Experimental analyses of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. *Oecologia* **56**(2+3): 202–219.
VELIMIROV, B., FIELD, J. G., GRIFFITHS, C. L. and P. ZOUTENDYK 1977 — The ecology of kelp bed communities in the Benguela upwelling system. Analysis of biomass and spatial distribution. *Helgoländer wiss. Meeresunters.* **30**: 495–518.