Aspects of population structure of *Parechinus angulosus* Leske, around the Cape Peninsula

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Aspects of the community structure of *Parechinus angulosus*, a locally dominant echinoid, were studied in two inshore temperature environments on the Cape Peninsula for a year. Stratified, random transects of 10 stations were run seasonally across the areas of maximum density at each locality and urchins were counted, measured and sexed. Percentage substrate cover was calculated, and variation in urchin size with distance from shore was investigated. Individual and combined effects of locality, season, distance (and depth) and sex were tested. Results indicate that urchins found at the cold-water locality, were on the average smaller, more numerous and included more size classes than the other. Urchin density did not vary with distance from shore at either locality, but was dependent on kelp, the occurrence of which is controlled by the nature of the substrate and by light penetration. A test of sex ratios was significant, males being more numerous. No seasonal effect on urchin distribution could be shown. There was no interaction of factors, except a small one between locality and season.

S. Afr. J. Zool. 1980, 15: 177 – 185

Aspekte van die gemeenskapstruktuur van *Parechinus angulosus*, 'n echinoïed wat plaaslik dominant is, is 'n jaar lank in twee verskillende kus-temperatuuromgewings aan weerskante van die Kaapse Skiereiland bestudeer. Gestratifiseerde ewekansige transekte van 10 stasies is seisoenaal by albei lokaliteite uitgevoer waar die maksimum digtheid voorgekom het, en die seekastaiings is getel, gemeet en hul geslag bepaal. Persentasie bodemdekking is bereken, en verandering in die grootte van seekastaiings met afstand van die kus, is ondersoek. Individuele en gesamentlike effekte van lokaliteit, seisoen, afstand (en diepte) en geslag is getoets. Resultate toon dat seekastaiings in 'n kouewateromgewing gemiddeld kleiner en meer talkryk was met meer grootteklasse as in 'n warmwateromgewing. Bevolkingsdigtheid was by geen omgewing afhanklik van strandafstand nie, maar wel van die voorkoms van seebamboes, wat deur bodemgeaardheid en ligindringing beheer word. 'n Toets vir geslagsverhouding het bevestig dat daar 'n groter aantal mannetjies was, maar seisoenale verskille in verspreiding kon nie aangetoon word nie. Daar was geen wisselwerking tussen faktore nie behalwe in 'n geringe mate tussen lokaliteit en seisoen.

S.-Afr. Tydskr. Dierk. 1980, 15: 177 – 185

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Parechinus angulosus has a geographical range from Lüderitz to Umhlali (Zululand) (Day 1969). The dense concentrations around the Cape Peninsula, closely associated with luxuriant stands of *Ecklonia maxima* and *Laminaria pallida*, form a conspicuous feature of the benthos to a depth of some 20 m (Fig. 8). The urchin *Parechinus* is the most common echinoid around the Peninsula and its numbers are high when compared with figures given for species elsewhere, such as *Echinus esculentus* (Nichols 1979), *Strongylocentrotus franciscanus* and *S. purpuratus* (Mattison, Trent, Shanks, Akin & Pearse 1977), *S. droebachiensis* (Breen & Mann 1976 a & b; Mann 1977), *Strongylocentrotus* spp. (Lowry & Pearse 1973), *Lytechinus anamesus* (Leighton, Jones & North 1966). The feeding pattern of some species such as *S. intermedius* (Fuji & Kawamura 1970; Leighton 1966) and *S. pulcherrimus* (Nagai & Kaneko 1975) led to numerous field studies, particularly in view of the severe impact on kelp beds in California and on the east coast of Canada by *Strongylocentrotus* sp. (Breen & Mann 1976 a & b; Mann 1977; Lang & Mann 1976; North & Pearse 1970; Sinenstad, Estes & Kenyon 1978). Personal observations in the field and measurements in the laboratory (Buxton 1977; Anderson in prep.), indicate that *P. angulosus* possesses a similar appetite but merely reduces the climax situation rather than causing visible damage (Fricke 1979). The impetus for this study was given by the need to discover whether differences found in the reproductive rhythm of *Parechinus* in two different aquatic temperature environments (Fricke & Thum 1975; Fricke in prep.) are also reflected in differences in population structure.

Study sites
Two distinct marine temperature regimes existing around the peninsula (Fricke & Thum 1975) resulted in the choice of one study site on the west coast and one in False Bay (Fig. 1). Continuous records of water temperature on the sea bottom are available for both localities (Fricke & Thum 1975) and showed significant differences (Fig. 9). Typicality of faunal and floral assemblage and absence of pollution ranked high in the choice of the study sites. The False Bay (warm-water) site, at Millers Point, tends to be more exposed to south-easterly winds and waves during spring and summer. The cold-water site on the west coast (Robbeneiland) receives heavy refracted turbulence during the southern winter.
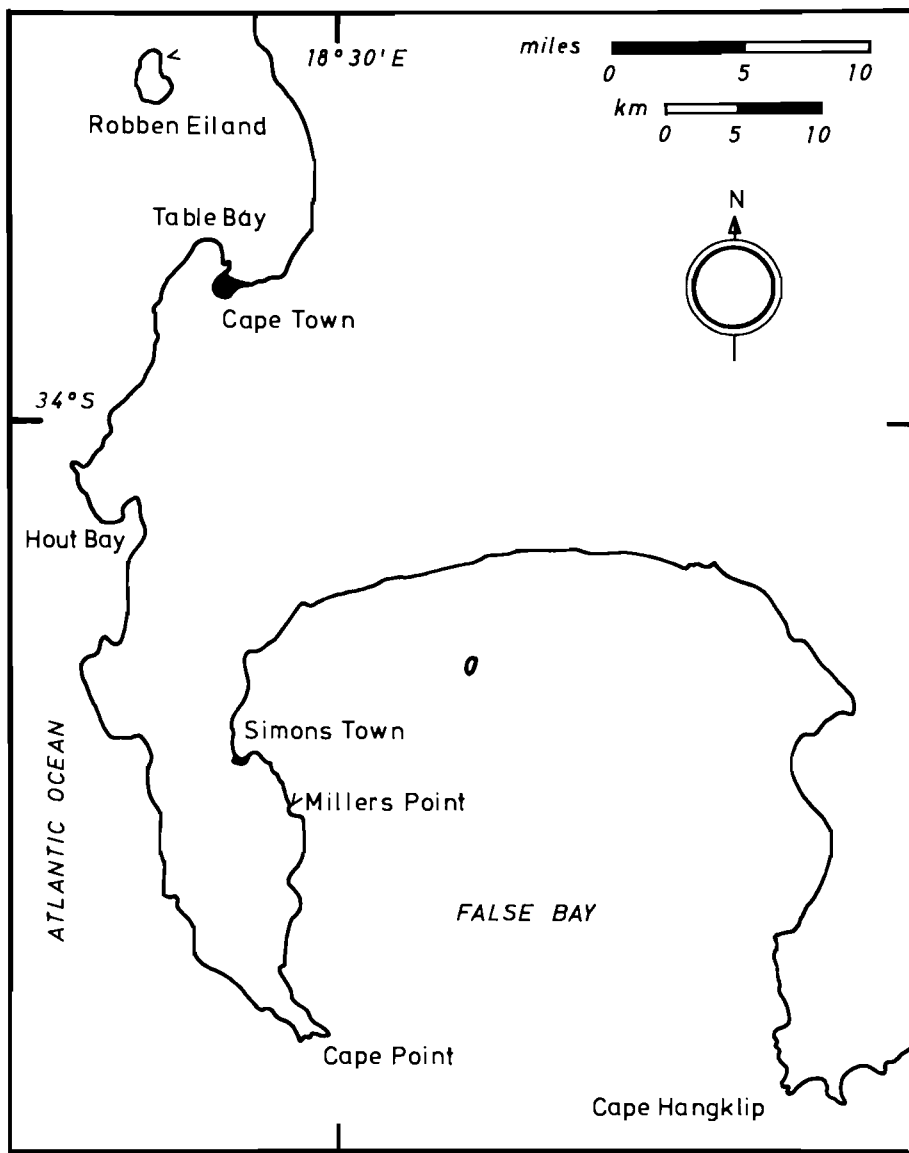
Fig. 1 Map of the Cape Peninsula, showing the location of study sites in two different marine environments.

Robbeneiland lies in a security area and is therefore largely undisturbed. The sea bottom can be compared to the mediate assemblages described by Field, Jarman, Dieckmann, Griffiths, Velimirov & Zoutendyk (1977) at Oudekraal, except that the substrate at Robbeneiland consists of laminated Malmesbury slates and phyllites, rather than Cape granite. The kelp bed is composed of clumped stands of *Ecklonia maxima* in shallower water and of *Laminaria pallida* and *Macrocystis angustifolia* further offshore. The steeply dipping substrate is covered by multi-tiered invertebrate communities in which *Aulacomya ater*, *Pentacta doliolum*, *Thione aureum* and *Parechinus angulosus* dominate. There are also numerous sponges, ascidians, bryozoans and soft corals. Practically no bare rock surface exists except on reefs of low profile which are exposed to sweeping sand under turbulent conditions. Reefs become patchy from 250 m offshore giving way to a sandy bottom.

The site at Millers Point is typical of western False Bay. The inshore region consists of rounded granite boulders with intervening patches of quartz sand yielding to feature-less sand about 120 m offshore. The kelp bed is an almost pure stand of *E. maxima* with *Bifurcariopsis capensis*, *Pachymenia carnosa* and *Codium stephensiae* forming the

larger species of the understorey. Much of the rock surface is covered by the coralline alga *Lithothamnion*. Few bivalves are seen and echinoderms are represented by *Marthasterias glacialis*, *Patiria granifera* and *Ophioderma leonis*. The benthic community is not structured in a series of layers as at Robbeneiland, neither is water depth greater than 5 m anywhere near the site.

Methods

Sampling pattern

Stratified random transects were laid seasonally for one year perpendicular to the shore across each study site from surveyed bench marks ashore. A weighted tunny line marked at 1 m intervals was used for this purpose. Every 10 m sector was sampled randomly by means of a 0,25 m² quadrat with one movable side to facilitate operation among kelp stipes. The quadrat method of sampling used here can be regarded as a reliable method for urchin densities as were found at the research sites, while a plotless approach (Ebert 1971) is more suitable for low densities. Rock surfaces steeper than 45° were regarded as vertical and not sampled, since it was shown by Velimirov et al. (1977), that urchin numbers were significantly higher on horizontal sur-

faces (t = 4,29, df = 6, P < 0,01) in the depth range of the study sites.

Urchins were collected in numbered, perforated plastic bags and processed alive in the laboratory. Their maximum test diameter was measured with calipers to the nearest mm. Total drained wet mass was measured to 0,01 g. The animals were opened along their equator and their sex established wherever possible.

Mass determinations were made on an analytical balance using aluminium dishes. Perivisceral fluid was included in the weighings. The material was dried to constant mass in a ventilated oven at 60 °C.

Temperature measurements

Two mechanical temperature recorders (Thermoscript by Goerz) operating on a bimetal helix principle, were enclosed in closefitting stainless steel (marine specification A1S1 316) housings and firmly bolted to concrete anchors placed on the sea bottom at the study sites. The recorders were replaced monthly by a spare instrument and the charts evaluated under magnification. Continuous temperature recordings were made (Fig. 9), since a comparison with daily spot measurements showed that these do not meaningfully reflect the environmental temperature perturbations (Fricke & Thum 1975).

Results

The distribution pattern (aggregation) of *P. angulosus* was tested by considering the combined counts per quadrat of four seasonal transects. The coëfficient of dispersion CD = $S^2/\overline{Y}$ (where S^2 = the variance and $\overline{Y}$ the average number of events/sample). If CD $\gg$ 1, then $S^2 \gg \overline{Y}$ and dispersion is clumped (contagious). This relationship was used to test for aggregation (Sokal & Rohlf 1969) assuming that the urchins follow a Poisson distribution. A summary of the values obtained for both sexes is given in Table 1. Dispersion of urchins at both localities is very clumped (Ebert 1971) confirming field impressions. Males and females were treated separately to test for sexual aggregation related to the reproductive rhythm.

Variations in urchin numbers between stations along successive transects are shown in Figs 2 & 3. A patchy distribution is suggested by the lack of correlation between transects. The impossibility of superimposing transect lines exactly and the rugged nature of the substrate no doubt contributed to this effect.

Urchins seemed to be most dense on hard substrate close to kelps, but thinned rapidly as the bottom changed from rock to mainly sand. This was especially evident at Millers Point. Kelp density and distribution was not measured in this study. No correlation of urchin abundance with distance from shore and depth could be shown by linear regression analysis. The larger average number of urchins at Robbeneiland relative to Millers Point is also shown in Figs 2 & 3 by the length of the respective radii in the sector diagrams, while percentage substrate cover is indicated by arc width. In one case (Millers Point, Station 7, Transect 2) more than 50% of the quadrat area (0,25 m²) was covered by closely packed, partly overlapping urchins. Substrate cover (S.C.) was calculated thus:

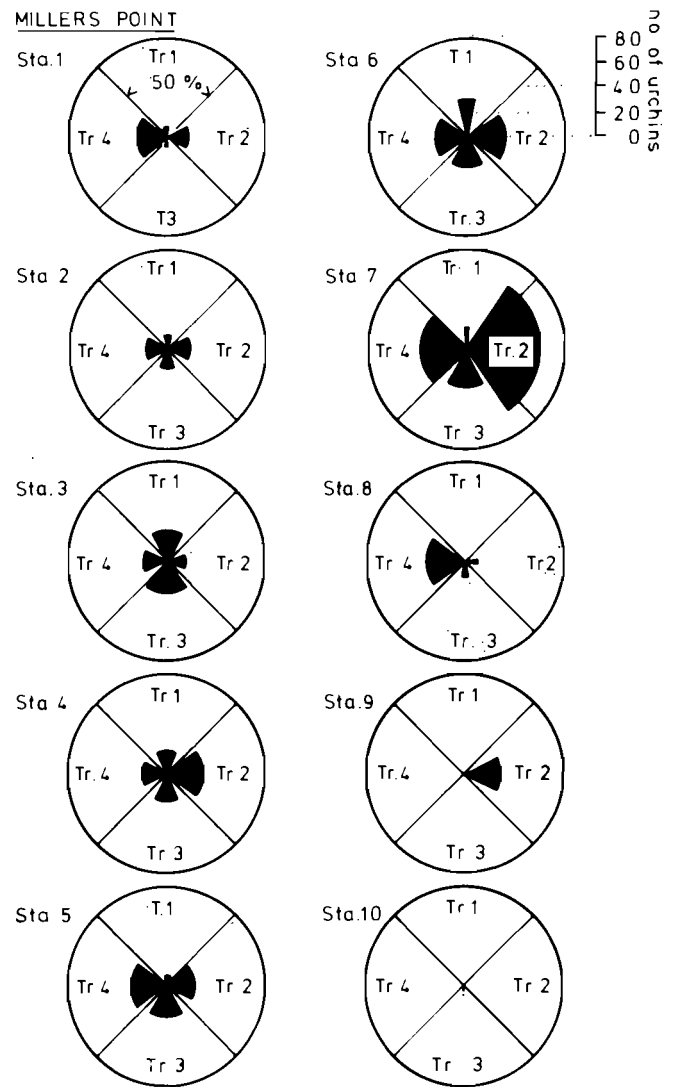$$S.C. = 100. \Sigma \pi \frac{(d)^2}{2} / 250\ 000\ \%$$

Fig. 2 Density and percentage substrate cover of *Parechinus* for seasonal transects at Millers Point. The radii of the sectors indicate animal numbers, while arc width shows percentage substrate cover of unit area (1 m²). A value of >50% was found in one instance, namely Transect 2, Station 7.

Table 1 Summary of dispersion pattern of male and female *Parechinus angulosus* collected in stratified, random quadrats of 0,25 m² during the period of study. The results represent combined data of four transects since no seasonal variation could be shown

	Coëfficient of dispersion (CD)		
	Male	Female	Dispersion
Robbeneiland	5,57	5,83	Clumped
Millers Point	3,50	3,23	Clumped

where n = number of urchins and $\pi \frac{(d)^2}{2}$ the projected surface of an urchin.

Although spines contribute significantly to substrate cover by urchins ($\overline{X}$ = 54,0; SD = 6,9; n = 108), they are known to be temporary structures (Ebert 1967) and difficult to measure accurately. Much evidence of repair and replacement was seen in the field. There is poor correlation
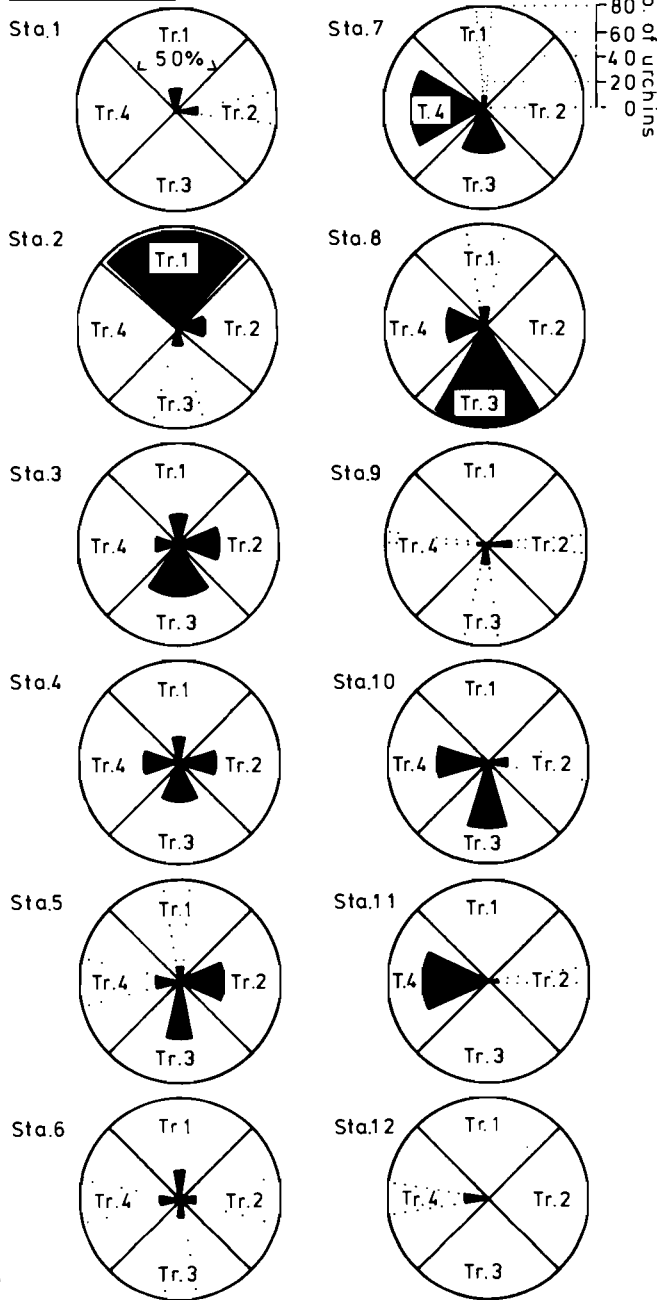
ROBBEN EILAND

Fig. 3 Density and percentage substrate cover of *Parechinus* for seasonal transects at Robbeneiland. The radii of the sectors indicate animal numbers, while arc width shows percentage substrate cover of unit area (1 m²). A value of >50% was found in one instance.

Fig. 4 Scatter diagram showing poor correlation of test diameter with spine length in *P. angulosus*. The plot represents an unbiassed sample of 108 urchins.

Table 2 Urchin counts in a 1 m² quadrat placed on the sea bottom in a typical area at Millers Point

Date	Urchins counted	
27.7.76	58	
3.8.76	63	
5.8.76	65	$\bar{X} = 74$
2.11.76	81	SD = 13,2
11.3.77	88	
8.4.77	87	

Table 3 Summary of basic statistics of urchin density m⁻² along transects at two study sites. A high degree of variability of counts is shown by the large standard deviations

	Robbeneiland			Millers Point		
Transect	$\bar{X}.m^{-2}$	SD	n	$\bar{X}.m^{-2}$	SD	n
Summer 1	80	90	10	38	33	10
Autumn 2	79	58	10	90	64	10
Winter 3	124	84	10	64	43	10
Spring 4	95	77	12	81	49	10

between spine length and test diameter (Fig. 4). The values given in Figs 2 & 3 are therefore approximate.

Observations indicated that urchin mobility was generally low. Table 2 shows successive counts of urchin density in a 1 m² quadrat. Urchins were not manipulated during this experiment, nor was plant matter removed which had become wedged under the steel frame. This did occur and may account for the rise in the number of animals attracted by this extra food source.

Size changes (maximum test diameter) of *P. angulosus* with distance and depth from shore were calculated for all urchins collected during the study. Twelve size-classes at five mm intervals were selected and the results plotted as histograms (Figs 5 & 6). Since successive transects did not show systematic variations (Tables 3 & 4) the values for the
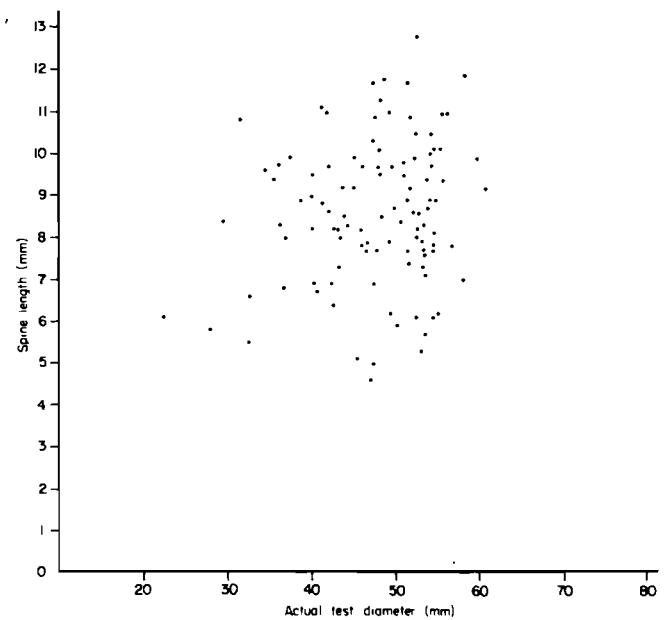
Table 4 Seasonal comparison of mean maximum test diameter (mm) and standard error of *P. angulosus* collected on transects at two localities. No seasonal change in animal size could be found

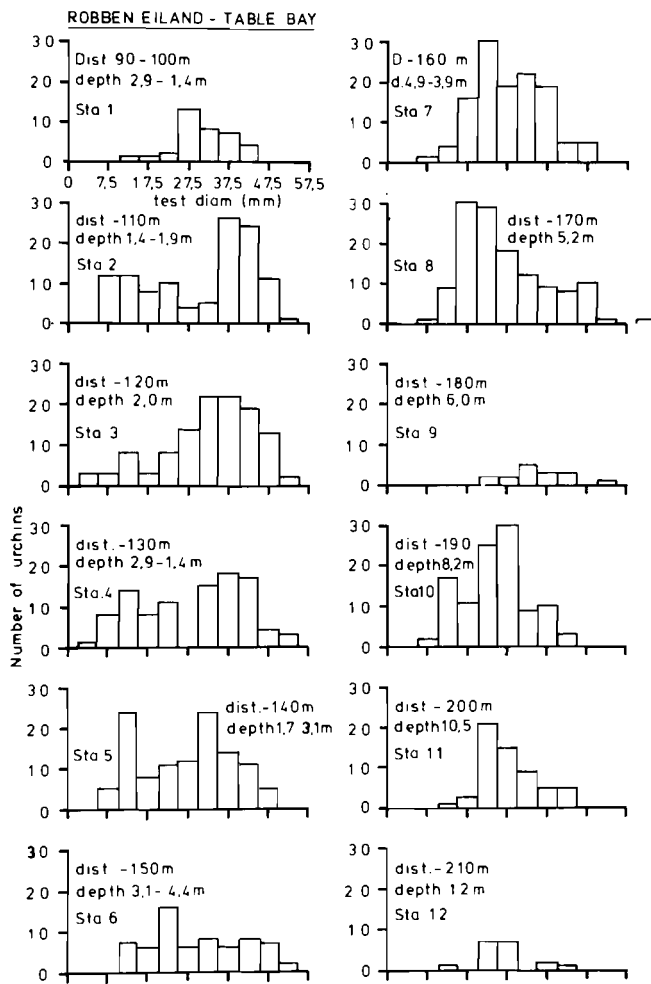|	Robbeneiland	Millers Point
	Mean max. diam. (mm) SE	Mean max. diam. (mm) SE
Summer 1	30,03 ± 1,79	46,66 ± 1,26
Autumn 2	31,20 ± 2,21	43,05 ± 1,71
Winter 3	29,70 ± 1,55	42,67 ± 2,37
Spring 4	31,51 ± 2,16	46,47 ± 1,27

Fig. 5 Size frequency histograms showing change of size (test diameter in mm) of *P. angulosus* with distance (and depth) from shore for Robbeneiland.
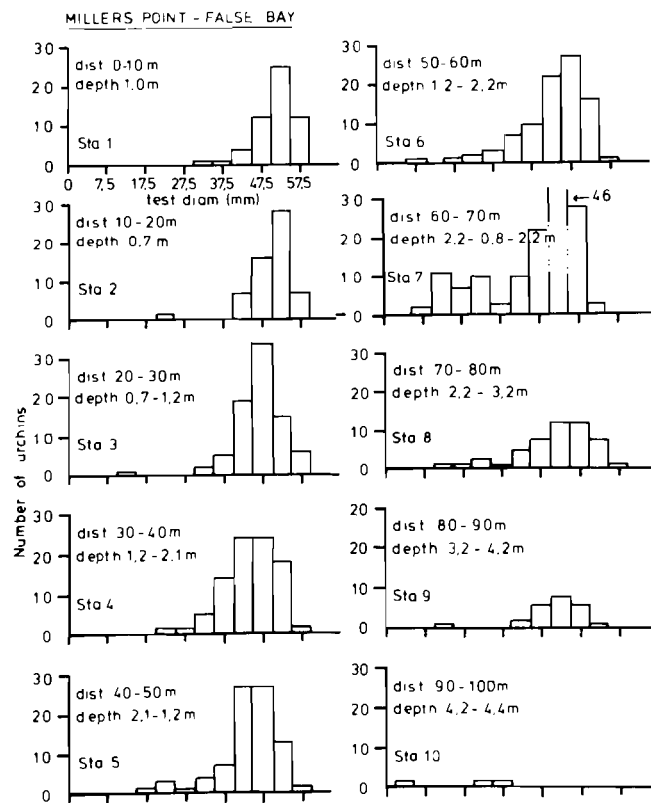

Fig. 6 Size frequency histograms showing change of size (test diameter in mm) of *P. angulosus* with distance (and depth) from shore for Millers Point.

whole period of observation were combined. Table 4 shows a significant size difference between urchins from the two localities, those at Millers Point being consistently larger than those at Robbeneiland.

The relative paucity of small-sized urchins at Millers Point was puzzling. Also at neither locality were the largest urchins found near the extremes of their range of occurrence, i.e. close inshore or furthest out. This can be explained by substrate topography and kelp distribution but was not measured in this study.

No urchins were found closer inshore than 90 m at Robbeneiland. The 100 m mark (Fig. 5) is therefore considered equivalent to the 0 m mark at Millers Point (Fig. 6).

Parechinus biomass was calculated and the results for the two sites compared (Table 5). The comparisons were made from weighing and are expressed as afdm.m^{-2} (ash-free dry mass) and kJ.m^{-2}. Conversions were obtained from listed values given by Field, Griffiths, Griffiths, Jarman, Zoutendyk, Velimirov & Bowes (in press).

Attention is drawn to the low mean wet mass of urchins at Robbeneiland compared to Millers Point. The greater size range (juveniles) of the former is reflected in the large standard deviations. Gravid animals probably have a higher kJ value than spent ones, but this was not tested.

As many urchins as possible were sexed and the male-female ratio of the study sites compared by Chi-square analysis (Zar 1974) in Table 6. There appears to be no significant departure from a 1:1 sex ratio at either locality, which one would expect intuitively. Results of a separate study using 30 urchins per sample on a monthly basis shows a small significant (at the 99% level) imbalance in the 1:1 ratio (n = 20; χ^2 = 40,29*; 0,01 < P < 0,05). This was also seen in a more powerful analysis (Table 7) by variance and co-variance. Microscopic examination of gonads showed that mis-identifications, favouring males, occur especially with spent and immature urchins which were relatively more numerous at Robbeneiland. This also explains the significance seen in the third example in Table 7.

The consistent size difference between urchins of the two study sites as shown in Tables 4 & 5 may be a reflection of differences in the availability of food. Gut states of urchins freshly opened for sexing were used to help explain such differences. The data were ranked in three classes, namely: full, half-full and empty. A histogram plot of this evaluation is given in Fig. 7. A contingency table (not shown) was compiled, followed by Chi-square analysis χ^2 - 255,965 for df2. The value of χ^2 at the 0,10% level is given as 13,816. Hence 255,965 >> 13,816; the null hypothesis can be rejected with confidence and more urchins have a full gut at Millers Point than at Robbeneiland.

Urchin frequencies, locations and sex differences including undetermined echinoids were tested by a three-way complete factorial model (BMDP — 2V analysis of variance and covariance including repeated measures). Transects were treated as replications to obtain a proper error term. The model equation is:

$$Y_{ijke} = \mu + a_i^L + a_j^Q + a_k^S + a_{ij}^{LQ} + a_{ie}^{LS} + a_{jk}^{QS} + a_{ijk}^{LQS} + e_{ijke}$$

Side conditions:

$$a_.^L = a_.^Q = a_.^S = a_{.j}^{LQ} = a_{i.}^{LQ} = a_{i.}^{LS} = a_{.e}^{LS} = a_{.k}^{QS} = a_{j.}^{QS}$$
$$= a_{ij.}^{LQS} = a_{.j.}^{LQS} = a_{..k}^{LQS} = 0$$

Table 5 Comparison of biomass of *P. angulosus* collected at two localities during four seasonal transects

Transect	Total wet mass g.m^{-2}	$\bar{X}$ wet mass urchin^{-1}(g)	SE	n	Dry mass .m^{-2}(g)	afdm .m^{-2}	kJ.m^{-2}
Robbeneiland							
1	1157,90	14,55	12,79	199	364,12	47,34	2 207
2	1217,60	15,14	12,30	202	382,89	49,78	2 320
3	1473,94	12,53	12,46	294	463,50	60,26	2 809
4	1631,40	14,06	13,72	290	513,02	66,69	3 109
Millers Point							
1	3232,00	35,91	17,57	225	1016,35	132,13	6 159
2	1314,39	34,59	18,51	95	413,33	53,73	2 505
3	2646,28	40,59	18,74	163	832,32	108,20	5 044
4	3480,32	42,65	16,18	204	1094,44	142,28	6 632

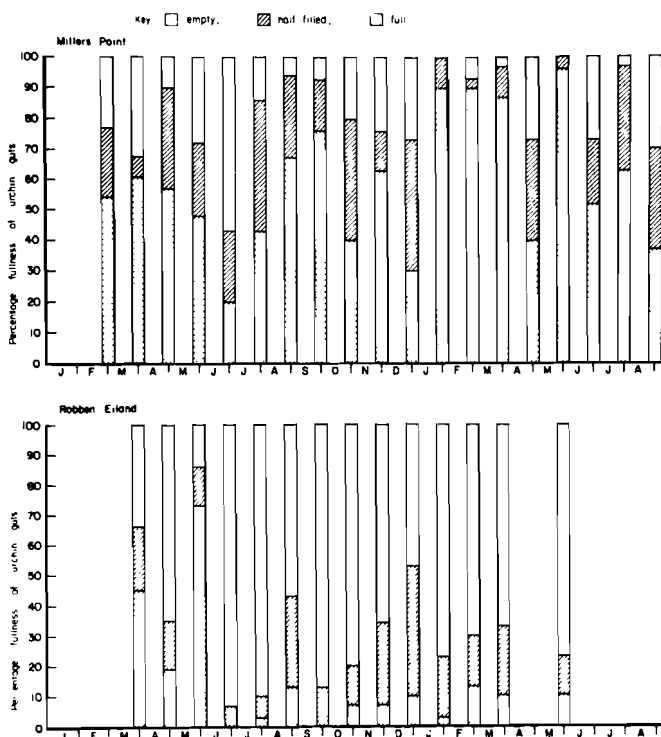**Table 6** Chi-square analysis of male-female ratios of *P. angulosus* at Robbeneiland and at Millers point

Robbeneiland $n = 35; \chi^2 = 33,08; 0,50 < P < 0,75$

Millers Point $n = 31; \chi^2 = 32,92; 0,25 < P < 0,50$

Robbeneiland
v $n = 32; \chi^2 = 73,16;$* $P > 0,001$
Millers Point

Fig. 7 Histograms comparing gut states of urchins collected during period of study at Millers Point and at Robbeneiland.

Any SS with a T was pooled in the error and the degrees of freedom added to find the error d.f. A summary of the computer analysis is shown in Table 7. This analysis shows frequency differences between the two study sites by comparing individual stations of the transects, thus supporting the evidence given in Table 3. Furthermore it shows that season had no effect on urchin distribution and numbers, and that the sexes were not equally represented, males being a little more numerous. There was no significant interaction of factors.

Table 7 Three-way complete factorial analysis of effects and interactions due to location, season and sex of *P. angulosus* (L = location, Q = season, S = sex)

Source	d.f.	F	5% crit. F.
Mean (μ)	1		
L	1	5,48*	3,84
Q	3	2,28	2,60
S	2	23,21**	3,00
LQ	3	2,52	2,60
LS	2	0,21	3,00
QS	6	0,47	2,01
LQS	6	0,58	2,01
Error	216		

Discussion

Temperature differences between marine environments have long been known to exert a considerable influence on the distributional and reproductive patterns of organisms. This study of *P. angulosus* was stimulated by observations of the echinoids under water. These suggested that the cold and warm water population differed in a number of ways while obviously being tolerant of a wide range of temperatures as indicated by their geographical distribution. Indeed this was shown for the reproductive rhythm of *P. angulosus* (Fricke & Thum 1975). Evidence suggested that the temperature pattern (persistence and rate of change) rather than absolute levels played a role in triggering gamete release. Hence, the markedly seasonal regime of False Bay is reflected in a fairly clear spawning pattern, while incomplete spawn-out is observed in the cold water site, which is characterized by erratic fluctuations of sea temperature. Urchins may be under the influence of a further, more indirect temperature effect in False Bay, in that *Laminaria*, an important member of kelp-stands, is uncommon there, being apparently unsuccessful in the warmer water. Velimirov & Griffiths (1979) showed that the sweeping action of adult *Laminaria* plants restricts urchin distribution. For the present then, temperature does not seem to constitute an important factor influencing the distribution or abundance of *Parechinus*. Turbulence, substrate, food and predation appear to play the key roles in producing the differences observed during the study. The near-shore absence of adult *Parechinus* at the Robbeneiland site is without doubt the result of wave energy reaching the shore under prevailing
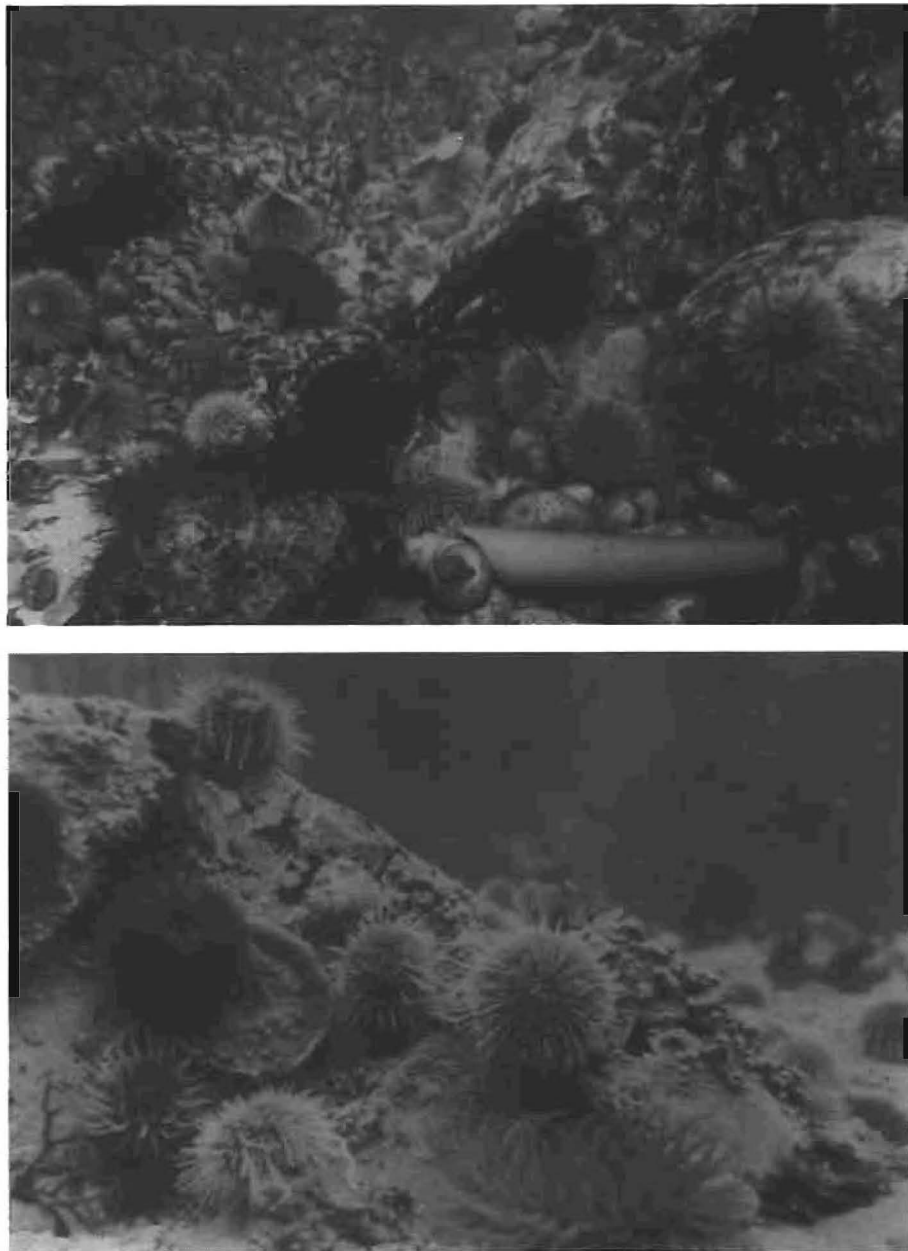
Fig. 8 *P. angulosus* in its natural habitat at Robbeneiland (above) and at Millers Point (below) showing substrate and some associations.
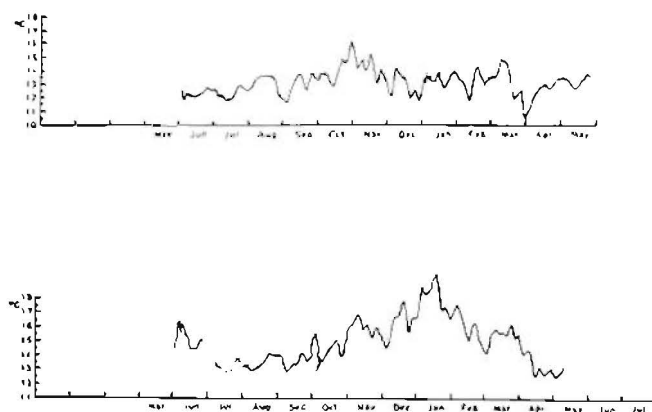

Fig. 9 Fluctuations in sea temperature drawn as running average of five items for Robbeneiland (above) and Millers Point (below).

southeasterly (summer) and northwesterly (winter) conditions. Millers Point on the other hand is only moderately exposed, which, combined with the bouldery substrate, permits adult urchin attachment very close inshore, indeed in water too shallow for kelp growth.

Urchins were often found tightly packed together with their spines meshing, occasionally crowded on top of one another. No mass movements were recorded, but rather responses to sea conditions and reactions to the proximity of food, for example when kelp became lodged under a quadrat at Millers Point. Marking urchins remains a problem and complicates more accurate observations. Substrate dominated as an environmental factor throughout. The eroded, sheetlike structure of Malmesbury formation bedrock at Robbeneiland evidently provides abundant shelter for juvenile urchins which can be collected with some effort (Greenwood in press). The rounded, massive granite boulders at Millers Point do not offer such shelter with the result that few juveniles were collected, these being found at the boulder-sand interface, partly buried by sand. Although *P. angulosus* will settle on a variety of substrates including metal platforms (ship hulls) and concrete pilings, it probably has substrate preferences which differ for adult and juvenile animals. Ebert (1971) discusses this behaviour for Hawaiian echinoids. Distinct substrate preference seems all the more likely since

Parechinus juveniles do not seek shelter among the spines of adult urchins, as was described for a Californian species *Strongglocentrotus franciscanus* by Tegner & Dayton (1977), who believe that newly settled urchins are susceptible to most predators that find them. This means that suitable microhabitats may be of the utmost importance to the recruitment of *Parechinus* analogous to *S. purpuratus* mentioned by the same authors. The present field results indicate that recruitment into the Robbeneiland population is greater relative to that at Millers Point, since the young urchins find more optimal substrate conditions at the former location. This is clearly shown by the presence of a more equitable size-class distribution at Robbeneiland (Fig. 5).

Food resources for the early stages of *Parechinus* are most plentiful in an upwelling area such as Robbeneiland. Hence the larger number of recruits appear to find favourable survival conditions early on in their life history. When a test diameter of approximately 10 mm is reached, the urchins switch over from fine suspended to macroscopic food (mostly debris, but also attached algae) (Greenwood, pers. comm.). It is at this stage that food appears to become limiting, giving rise to a reproductive population of consistently smaller average size compared with urchins from Millers Point. The significantly lower percentage fullness of urchin intestines sampled under a variety of sea conditions at the cold-water site (Robbeneiland) supports this argument. During further observations, *Parechinus* at the latter locality was not seen to penetrate the kelp stands to the same degree as at Millers Point, possibly due to the action of *Laminaria* mentioned earlier and generally rougher sea conditions. Mattison *et al.* (1977) found that the feeding activity of sea urchins depending on drift material decreased at increasing distances from kelp forests. Competition possibly also enters into the picture, judging by the very dense multitiered substrate occupation seen at Robbeneiland. By contrast there is much bare rock in evidence at Millers Point (Fig. 8).

Robbeneiland therefore represents a good example of overpopulation with regard to *Parechinus*. This situation may be significant in view of recent commercial interest in a luxury fishery for sea urchins which are not exploited in South Africa at present. Harvesting small adults at Robbeneiland would probably not be economical since *Parechinus* is not a large urchin by comparison with some other species and the edible gonads comprise a small fraction of the total animal mass.

The greater average age reached by *Parechinus* at Millers Point and localities nearby (Greenwood in press) may be a reflection of lower predation. The rock lobster (*Jasus lalandii*), although not feeding preferentially on urchins (Griffiths & Seiderer in press), has been greatly reduced locally but remains abundant at Robbeneiland where the favourable conditions for settlement and early larval life are likely to perpetuate the present situation.

Conclusions

From the information presented, it appears that *P. angulosus* is an echinoid tolerant of widely fluctuating water temperatures which, however, influence its reproductive pattern. The urchin inhabits a range of substrates, adjusting its population structure mainly in response to substrate

quality, turbulence and food availability. Competition and predation, although not specifically tested here, may play a role in affecting longevity, judged by size. Distance and depth from shore did not appear to influence urchin distribution in these experiments, except in so far as distance correlates with turbulence and depth with the growth limits of macrophytes. Movement of urchins occurs on a small scale in response to sea state and proximity of food. The aggregation suggests an absence of territoriality such as seen in *Echinometra lucunter* (L.) (Grünbaum, Bergmann, Abbott & Ogden). Seasonality played no role in affecting population structure.

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