# ASPECTS OF THE COMMUNITY STRUCTURE AND REPRODUCTIVE ECOLOGY OF THE COMMON SEA-URCHIN *PARECHINUS ANGULOSUS* LESKE AROUND THE CAPE PENINSULA, SOUTH AFRICA

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TO SHIRLEY

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# SYNTHESIS OF RESULTS AND DISCUSSION

The geographic distribution of *Parechinus angulosus* according to present records extends from Umhlali (Zululand) to Lüderitz Bay (Day, 1974). The urchins are therefore adapted to a fairly wide range of temperatures. Maximum fluctuations probably occur along the stretches of coastline affected by upwelling, the south-west and west coasts, with differentials of twelve degrees Centigrade and more. Furthermore, these fluctuations may take place within a matter of a few hours or even less, i.e. almost capriciously like temperature changes encountered on land but, unlike, the latter, by virtue of movement of different water masses, rather than cooling rate.

The importance of temperature as a regulator of reproductive cycles in marine organisms, specifically invertebrates, is discussed in Giese and Pearse's (1974) detailed review on the subject. A local study by Newman (1969) considers the effect of temperature on the spawning behaviour of abalone *(Haliotis midae)*. This study was commenced in the light of this information and subjective preliminary observations underwater, which revealed striking density and relative size differences between urchins on the Atlantic side of the Peninsula and in the warmer False Bay. A detailed *in situ* record of sea temperatures at two study sites, Röbbeneiland and Millers Point was obtained by installing temperature measuring devices. This monitoring covered a period of one year, while coupled with monthly collections of urchins in the mature size range. The variations of male and female gonad indices were found to be essentially in agreement, though lagging behind sea temperature changes. The spawning periods of urchins at both study sites was similar, occurring in spring and autumn, despite the significantly different water temperature averages. A clear pattern was observed at Millers Point, while being poorly defined at Robbeneiland. This is in agreement with the findings of Newman (1967, 1969), whose observations included data from St. Helena Bay to beyond Port Elizabeth. Newman found higher spawning intensities at localities having a clear seasonal pattern of sea temperature variations, compared to those of low seasonality, in other words, better synchrony of gamete release. A possible mechanism was mentioned by Giese & Pearse (1974), suggesting that the ripest individuals may be induced to spawn by a sharp temperature change, thereby stimulating other less mature individuals to follow suit. The degree of perturbation necessary to initiate such a sequence can very widely. Many species are known to have breeding seasons in areas where temperature fluctuations are slight, such as parts of the polar, tropical and abyssal ocean.

My observations indicate that a confused temperature regime, involving rapid changes, such as occur during periodic upwelling cycles, results in repeated, incomplete spawn-outs. Consequently, gonad indices are always lower at Robbeneiland than at Millers Point. Urchins at both localities show a low reproductive status during winter. Stained histological thin sections were prepared of gonad portions of selected urchins of both sexes covering all maturity (gonad index) stages and compared with lipid values obtained for the same respective animals. It was found that during maturation, there is a gradual build up of gametes passing through the well known developmental stages, rather than a snap conversion of accumulated storage material (I only tested for lipid for practical reasons) into sperms or eggs. Even relatively regressed (low gonad index) urchins could be induced to release fertilizable spawn, by injection of potassium chloride solution. Lipid values form a surprisingly small portion of the total dry mass of the urchin, when it is realised that it is the gonads which function as the major storage organ in addition to the intestine (Boolotian, 1966). Except for a few high, possibly spurious, values, male lipid levels were on the whole lower than those found for females. It would have been interesting to have values for glycogen as well for comparison, particularly since calorific values obtained for representative male and female *Parechinus* by micro-bomb calorimetry were found to be in very close agreement, in fact practically identical.

The significant mean size differences between urchins of the 2 study sites could be shown to be very likely due to the availability of food. This was shown by a comparison of gut states of urchins collected during the period of study. Although it is true that suspended food material is more plentiful in an upwelling locality, like Robbeneiland and unlike Millers Point, this situation is only important to the planktonic and recently settled juvenile stages of *Parechinus*. Once the animal has reached a test diameter of 10 mm (Greenwood, 1980), macroscopic and attached food sources are required. In this respect Robbeneiland is clearly limiting. Hence urchins of a smaller mean size relative to Millers Point enter the reproductive life cycle, since only that fraction over and above the animal's metabolic requirements is available for growth and reproduction. The significantly lower (one quarter) gamete output of urchins from Robbeneiland is evidence of this fact.

Recruitment of *Parechinus* into the benthonic stage appears to be strongly dependent on substrate, in that the eroded, slaty structure of the reefs at Robbeneiland afford many suitable microhabitats to juveniles at this particularly vulnerable stage, while the rounded granite boulder terrain at Millers Point does not offer a comparable number and choice of such sites. Tegner and Dayton (1977) showed that substrate type may play an important role in the recruitment of a Californian species, *Strongylocentrotus purpuratus*, which like *Parechinus* is flexible in its recruitment behaviour, which means that the urchins select suitable sites from a range of choices, while *S. franciscanus* juveniles shelter under the spine canopy of adults. The size class study sites must be seen in this light. In effect then we have a situation, where substrate type and availability jointly select against the smaller size classes at Millers Point.

The strongly contagious distribution of *Parechinus* is very likely a response to the proximity of food. Since debris tends to accumulate on horizontal surfaces, urchins can be expected to be more numerous there than on inclined substrate. This was found to be true in a study by Velimirov *et al.* (1977), who made the dividing line between horizontal and vertical at 45° inclination. In addition minor adjustments according to sea strate take place. It was found that under turbulent conditions urchins shelter on rockfaces away from the sea and under overhangs to avoid strong swell action and contact with loose material such as torn off kelp plants.

Predation was not studied and therefore only tentative impressions gained per chance in the field are at hand. Robbeneiland lying in a security area is largely undisturbed and harbours many rock lobsters (*Jasus lalandii*), which prey on *Parechinus* in addition to their main food, the ribbed mussel (*Aulacomya ater*). Indeed lobsters were seen to feed on urchins on a number of occasions, apparently selecting the smaller individuals. At Millers Point *Jasus* has been rare for many years through overexploitation.

There appears to be no significant departure from the 1:1 sex ratio at either site according to Chi-square analysis. However, a more powerful analysis of variance and co-variance indicated a higher number of males at Robbeneiland. The discrepancy may be due to the fact that while Chi-square analysis was done on small (30 batches of urchins collected on a monthly basis and comprising mainly sexually matureindividuals at various stages of gonadal development, the Anova involved material obtained during seasonal transects including a wide range of size classes, particularly at Robbeneiland. Indeterminate urchins were excluded from the analysis, but nevertheless, misidentifications favouring males did occur. It would therefore appear that there is little reason to assume that the sex ratio of *Parechinus* is significantly unsymmetrical.

This would also be in conflict with the findings on other marine invertebrates.

In conclusion it can be said that Robbeneiland represents a good example of over-population, which fact could have significance in terms of a possible luxury fishery by controlled cropping. The favourable conditions for newly settled larvae and early juveniles seem to represent a stable situation.

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Frontispiece. Dense colony of *P. angulosus* on the western side of the Cape Peninsula showing some associated animals. (Starfish, sea-cucumbers, mussels and whelks. A stand of kelp *(Laminaria* and *Ecklonia)* is visible in the background.

# SUMMARY

The work presented in the following covers a natural experiment involving measurements, collections and observations for a year and a half. In addition, some apparatus had to be specially constructed, which is described in two separate publications, giving a biological example. More than 80 diving excursions were performed during which a number of ecological aspects of *Parechinus angulosus* Leske, and its interaction with local kelps were studied.

*Parechinus* is a very common echinoid around the Peninsula, inhabiting rocky substrate on the west coast and False Bay sides of the Cape Peninsula and sometimes forming dense, patchy populations exceeding 100 urchins $m^{-2}$. Interest in the ecology of this species stems from numerous reports of the great impact another form (*Strongylocentrotus purpuratus)* is causing to kelp stands in Canada and on the West Coast of the United States. Like its counter-part, *Parechinus* is associated with major kelp species. In a local, well advanced study (Velimirov et al., 1977; Field et al., 1977) *Parechinus* was considered to be mainly an important detritus feeder, but was subsequently also found to graze on young kelp sporophytes. Tentative commercial interest in its exploitation as a luxury fishery has added to the pertinence of this work.

The existence of two different marine temperature regimes around the peninsula provided an opportunity for the synoptic study of the role of water temperature on the reproductive rhythm of *Parechinus*. Records of daily surf measurements by local authorities proved to be unrepresentative of *in situ* conditions at the study sites at Robben Eiland and Millers Point. This discrepancy was not unexpected, considering the complex hydrography of inshore waters (Harris, 1978).

It became necessary therefore to instal sensing instruments capable of recording temperature variations over extended periods. A simple bi-metal helix clockwork-drive system in a watertight enclosure was found satisfactory and robust to withstand the rough sea for which the Cape is known. (The method has been also adopted by the Sea Fisheries Branch). The time resolution of the instruments was unfortunately insufficient to yield more than one daily maximum and minimum reading. For this reason temperature persistence graphs (Ainslie, 1971), which are very informative in seasonal studies could not be constructed.

The reproductive rhythm of *Parechinus* was monitored by monthly collections of mature urchins at selected points on the study sites. The seasonal variations in gonad index, suggested a bi-annual spawning cycle at both sites in spring and autumn. This evidence was supported by lipid assays of subsamples of the same urchins and selected histological sections of gonad material. It appears that temperature is probably not the only physical factor regulating spawning (although most likely acting as proximate trigger), but that light may be involved as well, since gamete release at both sites occurs during seasons of similar photoperiod, by urchins experiencing significantly different water temperature regimes. A gonad output calculation showed a four times higher value for Millers Point than for Robben Eiland.

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# PART I

# ASPECTS OF THE POPULATION STRUCTURE OF *PARECHINUS ANGULOSUS* LESKE, A COMMON ECHINOID AROUND THE CAPE PENINSULA (R.S.A.)

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# ASPECTS OF POPULATION STRUCTURE OF *PARECHINUS ANGULOSUS* LESKE

# A COMMON ECHINOID AROUND THE CAPE PENINSULA (RSA)

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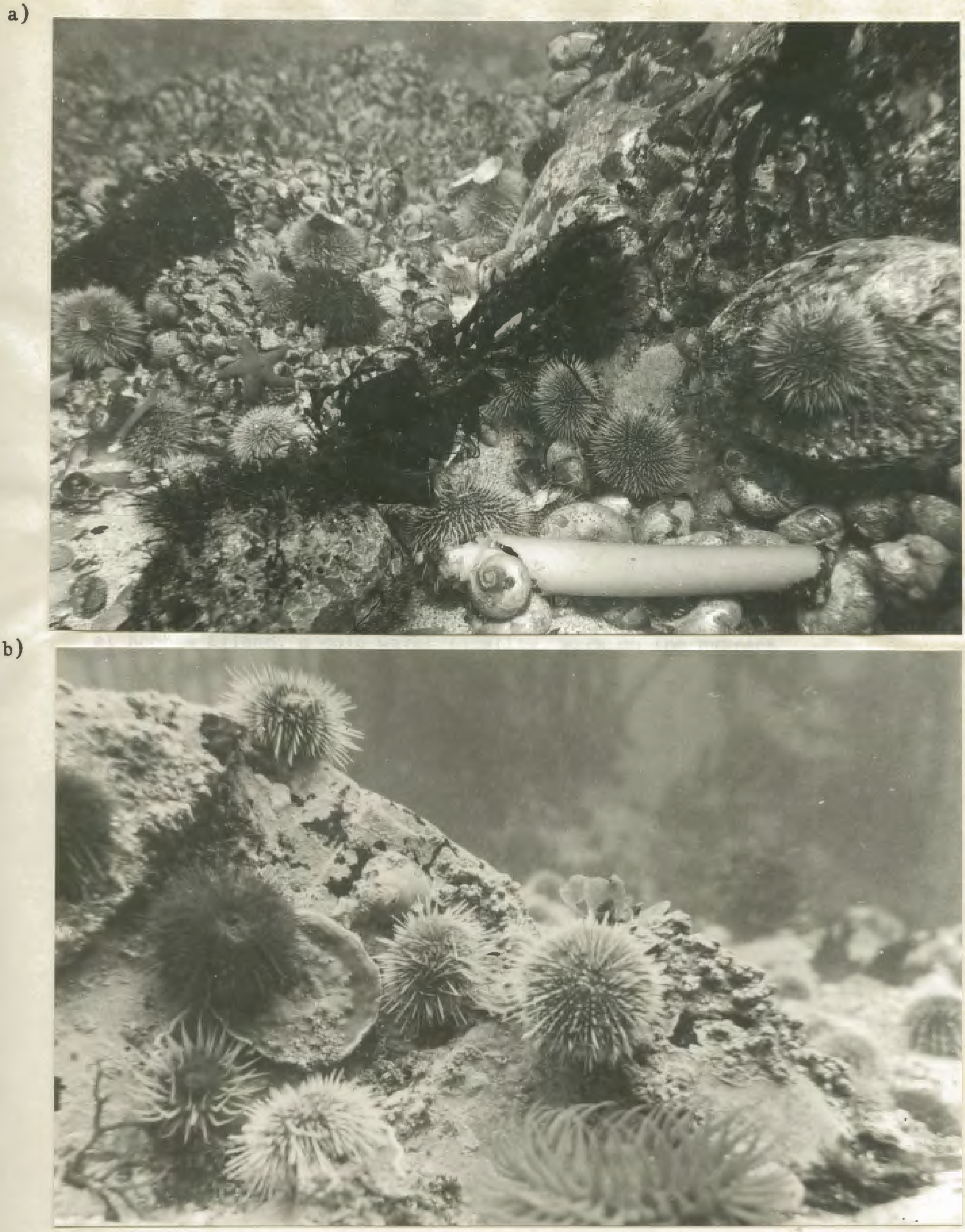

<u>Plate 1</u>. *P. angulosus* in its natural habitat at Robben Eiland(a)and at Millers Point(b)showing substrate and some associations. A kelp bed is visible in the background (1b)

# ABSTRACT

Aspects of the community structure of *Parechinus angulosus* Leske, a locally dominant echinoid were studied in two inshore temperature environments on the Cape Peninsula for a year. Stratified, random transects of ten to twelve stations were run seasonally across the areas of maximum density at each locality and urchins counted, measured and sexed. Percentage substrate cover was calculated from projected test surface areas as a measure of substrate occupation. Variations in urchin size with distance from shore were investigated. Individual and combined effects of locality, season, distance (and depth) and sex were tested by three way factorial analysis of variance, using an expanded BMDP 2V programme. Results indicate that urchins found at Robben Eiland, a cold water locality, were on the average smaller, more numerous and included more size classes than was the case at Millers Point. Urchin density could not be shown to vary with distance from shore at either Robben Eiland or Millers Point, but was dependent on the occurence of kelp, itself substrate and depth controlled 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 interaction between locality and season.

# BEKNOPTE OORSIG

Aspekte van die gemeenskapstruktuur van *Parechinus angulosus* Leske, 'n echinoïed wat plaaslik dominant is, is 'n jaar lank in twee verskillende aanlandige temperatuuromgewings aan weerskante van die Kaapse Skiereiland bestudeer. Gestratifiseerde ewekansige transekte van tien tot twaalf stasies is seisoenaal by albei lokaliteite uitgevoer daar waar die maksimum digtheid voorgekom het en die seekastaiings getel, gemeet en hul geslag bepaal. Persentuele bodembedekking is vanaf geprojekteerde toetsoppervlaktes as 'n maatstaf van bodembesetting bereken. Verandering in die grootte van seekastaiings met afstand van die strand is ondersoek. Individuele en gesamentlike effekte van lokaliteit, seisoen, afstand (en diepte) en geslag is getoets deur drierigting faktoriaal-analise met behulp van 'n uitgebreide BMDP 2V program. Resultate dui daarop dat seekastaiings te Robbeneiland, 'n kouewaterlokaliteit, gemiddeld kleiner en meer talryk was met meer grootteklasse as by Millerspunt. Bevolkingsdigtheid van seekastaiings was nog by Robbeneiland nog by Millerspunt afhanklik van afstand van die strand, maar was wel afhanklik van die voorkoms van kelp, wat self ten opsigte van substraat en diepte deur ligindringing beheer word. 'n Toets vir geslagsverhouding het bevestig dat daar 'n groter aantal mannetjies was. Geen seisoenale verskille in seekastaaing-verspreiding kon aangetoon word nie. Daar was geen wisselwerking tussen faktore nie behalwe 'n kleine tussen lokaliteit en seisoen.

# INTRODUCTION

The dense concentrations of *P. angulosus* 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. *Parechinus* is easily 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 et al. 1977), *S. droebachiensis* (Breen and Mann 1976 a & b, Mann 1977), *Strongylocentrotus spp.* (Lowry and Pearse 1973), *Lytechinus anamesus* (Leighton et al. 1966). The feeding pattern of some species such as *S. intermedius* (Fuji and Kawamura 1970; Leighton 1966) and *S. pulcherrimus* (Nagai and 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 and Mann 1976; Mann 1977; Lang and Mann 1976; North and Pearse 1970, Sinenstad et al. 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 their study was given by the need to discover whether differences found in the reproductive rhythm of *Parechinus* in two different aquatic temperature environments around the peninsula (Fricke 1975; Fricke, in prep) also extended to contrasts in the population structure of this echinoid.

## Study sites:

Plate 1a & b)

Two distinct marine temperature regimes existing around the peninsula (Fricke, 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 1975) and showed significant differences. Typicality of faunal and floral assemblage and absence of pollution inputs ranked high in the choice of the study sites. The False Bay site, at Millers Point, tends to be more exposed to south-easterly winds and waves during spring and summer. The site on the west coast (Robben Eiland) receives heavy refracted turbulence during the southern winter.

Robben Eiland lies in a security area and is therefore largely undisturbed. The sea bottom can be compared to the mediate assemblages described by Field et al. (1977), Velimirov et al. (1977) at Oudekraal, except that the substrate at Robben Eiland consists of laminated Malmesbury slates and phyllites, rather than massive Cape granite. The kelp bed is composed of clumped stands of *Ecklonia maxima* in shallower water and of *Laminaria pallida* and *Macrocytis* s/ *angustifolia* further offshore. The steeply dipping substrate is covered by multitiered invertebrate communities in which *Aulacomya ater*, *Pentacta doliolum*, *Thione aureum* and *P. angulosus* dominate with numerous sponges, ascidians, bryozoa 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 consists of rounded granite boulders with small intervening patches of quartz sand yielding to featureless sand bottom about 120 m offshore. The kelpbed is an almost pure stand of *E. maxima* with *Bifurcariopsis capensis* and *Pachymenia carnosa* forming the larger species of the understorey. Much of the rock surface is covered by the coralline alga *Lithothamnion*. Few bivalves and echinoderms other than *Marthasterias glacialis* and *Ophioderma* *leonis* are seen. The benthic community is not structured in a series of layers as at Robben Eiland, neither is water depth anywhere near the site greater than 5 m.

## METHODS:

### Sampling pattern:

Four seasonally spaced stratified random transects were laid perpendicular to shore across each study site from surveyed bench marks ashore. A weighted line marked at 1 m intervals was used for this purpose. Every 10 meter sector was sampled randomly by means of a 0,25 $m^2$ quadrat with one movable side to facilitate operation among kelp stipes. The quadrat method of sampling used here can be regarded as a meaningful method given the densities found, while a plotless approach is more suitable for low densities (Ebert, 1971). Surfaces steeper than $45^{\circ}$ were not sampled, since observations by Field et al. (1978) showed that *Parechinus* densities differ significantly on such surfaces.

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

## RESULTS

The distribution pattern (aggregation) of *P. angulosus* was tested by considering the counts per quadrat of four seasonal transects as replicates. The coefficient of dispersion $CD = S^2/\bar{Y}$ was used to test for aggregation (Spiegel 1961). A summary of the values obtained for both sexes is given in Table 1. Dispersion of urchins at both localities is very clumped (see also Ebert 1971) confirming field impressions. Males and females were treated separately to test for sexual aggregation related to the reproductive rhythm.

TABLE 1 Summary of dispersion patterns of male and female *Parechinus angulosus* collected in stratified, random quadrats of 0,25 $m^2$ during four seasonal transects at two localities.

ROBBEN EILAND

| | C.D. ♂ urchins | dispersion | C.D. ♀ urchins |
|---|---|---|---|
| Transect 1 summer | 8,01 | clumped | 10,34 |
| 2 autumn | 8,44 | " | 5,08 |
| 3 winter | 10,46 | " | 11,30 |
| 4 spring | 8,56 | " | 8,26 |

MILLERS POINT

| | | | |
|---|---|---|---|
| Transect 1 summer | 6,00 | clumped | 5,37 |
| 2 autumn | 4,76 | " | 5,26 |
| 3 winter | 5,12 | " | 2,26 |
| 4 spring | 5,59 | " | 3,09 |

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

Urchins increased in numbers to a maximum, rapidly declining thereafter as the bottom changed from rock to mainly sand. No correlation of urchins abundance with distance and depth from shore could be shown by linear regression analysis. The larger average number of urchins at Millers Point relative to Robben Eiland is shown in Figs. 2 and 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 $m^2$) was covered by closely packed, partly over-lapping urchins. Substrate cover (S.C.) was calculated thus:

$$\text{S.C.} = 100 \cdot \sum_{n} \pi (\tfrac{d}{2})^2 / 250\ 000\ \%$$

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

Although spines contribute significantly to substrate cover by urchins (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 between spine length and test diameter (Fig. 4). The values given in Figs. 2 and 3 are therefore approximate.

TABLE 2 Seasonal comparison of mean maximum test diameter (mm) and standard error of *P. angulosus* collected along transects at two localities.

| | | | |
|---|---|---|---|
| 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 |

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 established and the results plotted as histograms (Figs 5 and 6). Since successive transects (no data shown) did not vary significantly, the values for the whole period of observation were combined.

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

*Parechinus* biomasses were calculated and the results for the two sites compared (Table 3). The comparisons were made from weighings and are expressed as afdm.m$^{-2}$ (ash free dry mass and kJ. m$^{-2}$). Conversions were obtained from listed values given by Field et al. (in press).

TABLE 3 Comparison of biomass of *P. angulosus* collected at two localities during four seasonal transects.

ROBBEN EILAND

| Transect | Total wet mass g.m$^{-2}$ | $\bar{X}$ wet mass· urchin$^{-1}$ (g) | S.D. | n | Dry mass .m$^{-2}$ (g) | afdm .m$^{-2}$ | kJ.m$^{-2}$ |
|---|---|---|---|---|---|---|---|
| 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 |

As many urchins as possible were sexed and the male-female ratio of the study sites compared by Chi-square analysis, (Zar 1974) see: Table 4.

TABLE 4 Chi-square analysis of male-female sex ratios of *P. angulosus* collected during period of study at Robben Eiland and at Millers Point. Undetermined urchins are excluded.

| | Male | Female | $\chi^2$ |
|---|---|---|---|
| Robben Eiland | 446 | 401 | 2,3908 |
| Millers Point | 351 | 287 | 3,8410 * |

* significant at 95% level

The density of *P. angulosus* (per $m^2$) collected during four seasonal transects was calculated for both localities. A summary of basic statistics is given in Table 5. The high degree of variability of counts is shown by the large standard deviations.

TABLE 5 Summary of basic statistics of urchin density $m^{-2}$ along transects at two study sites.

| | | ROBBEN EILAND | | | 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 |

Consistent size contrast between urchins of the two study sites may be a reflection of differences in the availability of food for unknown environmental reasons. Gut states of urchins freshly opened for sexing were used to help explain such a possibility. 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 $\chi^2$ = 255,965 for df2. The value of $\chi^2$ 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 at Millers Point have a full gut than at Robben Eiland.

Urchin frequencies, locations and sex differences including undertermined 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:

$$Y_{ijke} - \mu + \alpha_i^L + \alpha_i^Q + \alpha_k^s + \alpha_{ij}^{LQ} + \alpha_{ie}^{LS} + \alpha_{jk}^{QS} + \alpha_{ijk}^{LQS} + e_{ijke}$$

Side conditions:

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

Any SS with a T was pooled in the error and the degrees of freedom added to find the error d.f.

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

TABLE 6 Anova Table

| Source | d.f. | F | 5% crit. F. |
|---|---|---|---|
| Mean ( ) | 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 | | |

The analysis shows frequency differences between the two study sites; furthermore 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.

## DISCUSSION

Temperature differences between marine environments have long been known to exert a considerable influence on the distributional and reproductive pattern of organisms. This study of *P. angulosus* which is so very common around the peninsula was stimulated by preliminary observations of the echinoids underwater, which suggested that populations in the cold and warm water regime differed. This was shown for the reproductive rhythm of *P. angulosus* (Fricke and Thum 1975) and forms the subject of a further, more detailed paper (Fricke, in prep). The ideal experimental situation of finding study sites differing only with respect to water temperature was not achieved, indeed seems difficult. Leaving alone effects on reproduction, temperature *per se* can certainly not be singled out as the main physical factor producing the observed differences in urchin distribution at the two study sites, except indirectly by keeping out *Laminaria* (Dieckmann 1978) which is known to affect urchin distribution by the sweeping action of adult plants (Velimirov & Griffiths, 1979). Turbulence, substrate, food and predators on the other hand play key roles. The near-shore absence of *Parechinus* at the Robben Eiland site is without doubt the result of wave energy. The Millers Point site on the other hand is only moderately exposed, which together with the bouldery substrate, permits urchin attachment very close inshore, indeed in water too shallow for kelp growth. Substrate dominated as an environmental factor throughout. The eroded, sheetlike structure of bedrock at Robben Eiland evidently provides abundant opportunities for shelter for juvenile urchins which were abundant and can be collected with some effort (Greenwood, 1975). The rounded, massive granite boulders at Millers Point do not offer such shelter. As the results show, few juveniles were collected there, these animals being found at the boulder-sand interface, partly buried by sand. Although *P. angulosus* will settle on a variety of substrates including metal sheets (ship hulks) and concrete pilings, it most likely has substrate preferences, which differ for adult and juvenile animals. Ebert (1971) discusses this behaviour for Hawaaian echinoids. The considerable heterogeneity of the study sites was reflected in the strongly clumped distribution of urchins (Table 1), which did not seem to change diurnally (only one night observation was made). Urchins were often tightly packed together with their spines meshing, occasionally crowded on top of one another and thus complicating calculations. No mass movements of urchins were ever recorded, but rather responses to sea conditions and individual reactions to the proximity of food. Repeated counts of urchins within a 1 $m^2$ quadrat placed on the sea bottom showed remarkable constancy (no data shown). These were also essentially the observations of Mattison *et al*. (1977) working on *Strongylocentrotus franciscanus*.

The striking difference in size frequency distribution and mean test diameter between Robben Eiland and Millers Point (Figs. 2 & 3) appears to be due to two factors, namely food availability, competition and to a lesser extent predation. The significantly lower percentage fullness of urchin intestines sampled under a variety of sea conditions over extended time at the cold water site favours this argument. Furthermore urchins at Robben Eiland were not seen to penetrate the kelp stands to the same degree as at Millers Point. Mattison *et al*. (1977) found that the feeding activity of sea urchins depending on drift material decreased at increasing distances from kelp forests. It appears that a similar situation may apply here and urchins at Robben Eiland do not enjoy the same level of food abundance as their counterparts at Millers Point. Competition possibly plays a role judging by the very dense multitiered substrate occupation seen at Robben Eiland and contrasting this situation with Millers Point, where much bare rock is in evidence, although at both sites *P. angulosus* is the dominant debris feeder. *Parechinus*, by virtue of its large size and dominance at Millers Point compared with Robben Eiland, makes a high contribution to invertebrate biomass. Male female ratios were found to be significantly if slightly skewed (Table 4) as shown by statistical analysis, with males being more numerous in all cases. Examination of batches of *Parechinus* from several localities close by, revealed even larger deviations from a 1:1 ratio. At present this cannot be explained.

Predation on *Parechinus* at the False Bay site appears to be low judging by the greater average age reached by urchins (Greenwood, in press). The rock lobster (*Jasus lalandii)* although not feeding preferentially on urchins but rather on mussels as reported by Griffiths & Seiderer (in prep.) has been greatly decimated here but remains abundant at Robben Eiland.

## CONCLUSIONS

From the information presented, it appears that *P. angulosus* is an echinoid tolerant of widely fluctuating water temperature and a range of substrates adjusting its population structure mainly in response to substrate quality, turbulence and food availability. Competitition and predation although not specifically tested here seem to play a role in affecting longevity, hence size. Distance and depth from shore did not appear to influence urchin distribution in this study, except in so far as distance correlates with turbulence and depth with the growth limits of macrophytes. Movements of urchins occur 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 <u>et</u> <u>al</u>. in press). Seasonality played no role in affecting population structure.

## ACKNOWLEDGMENTS

Encouragement to undertake this study came from Dr. Alan B. Thum (presently at the Lockheed Ocean Laboratory, San Diego, California). Through the cooperation of Sea Fisheries Branch regular visits by ship to Robben Eiland were made possible. I am grateful for help with underwater work by their divers G. Dieckmann, R. Harding and Peter Sims. Dr. June Juritz of the Department of Mathematical statistics and Ms. Jane Hall went to much trouble in the computer analysis of data.

My thanks are finally due to Dr. C. Griffiths for critical perusal of the manuscript.

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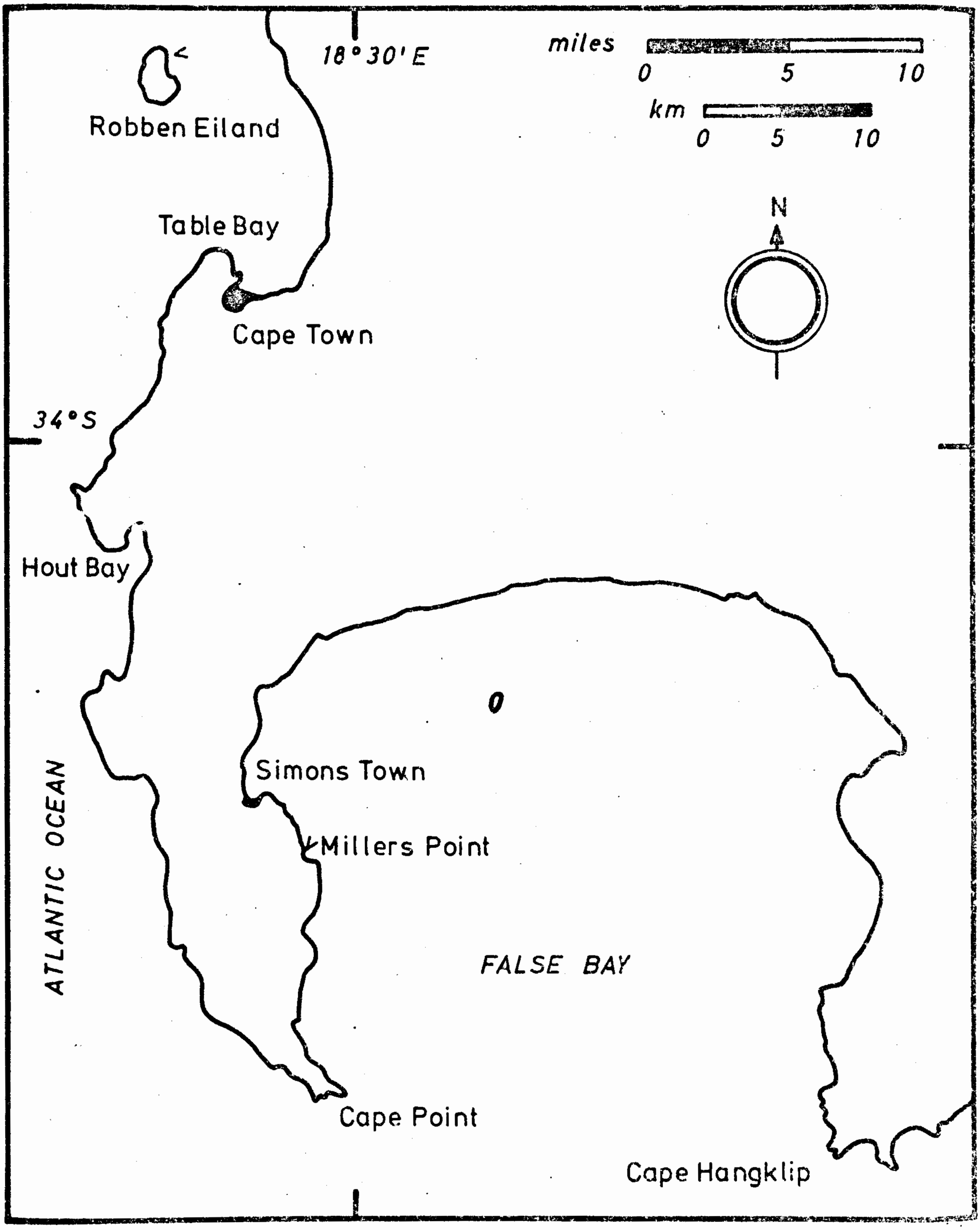

Fig. 1. Map of the Cape Peninsula showing location of study sites at Millers Point and Robben Eiland.

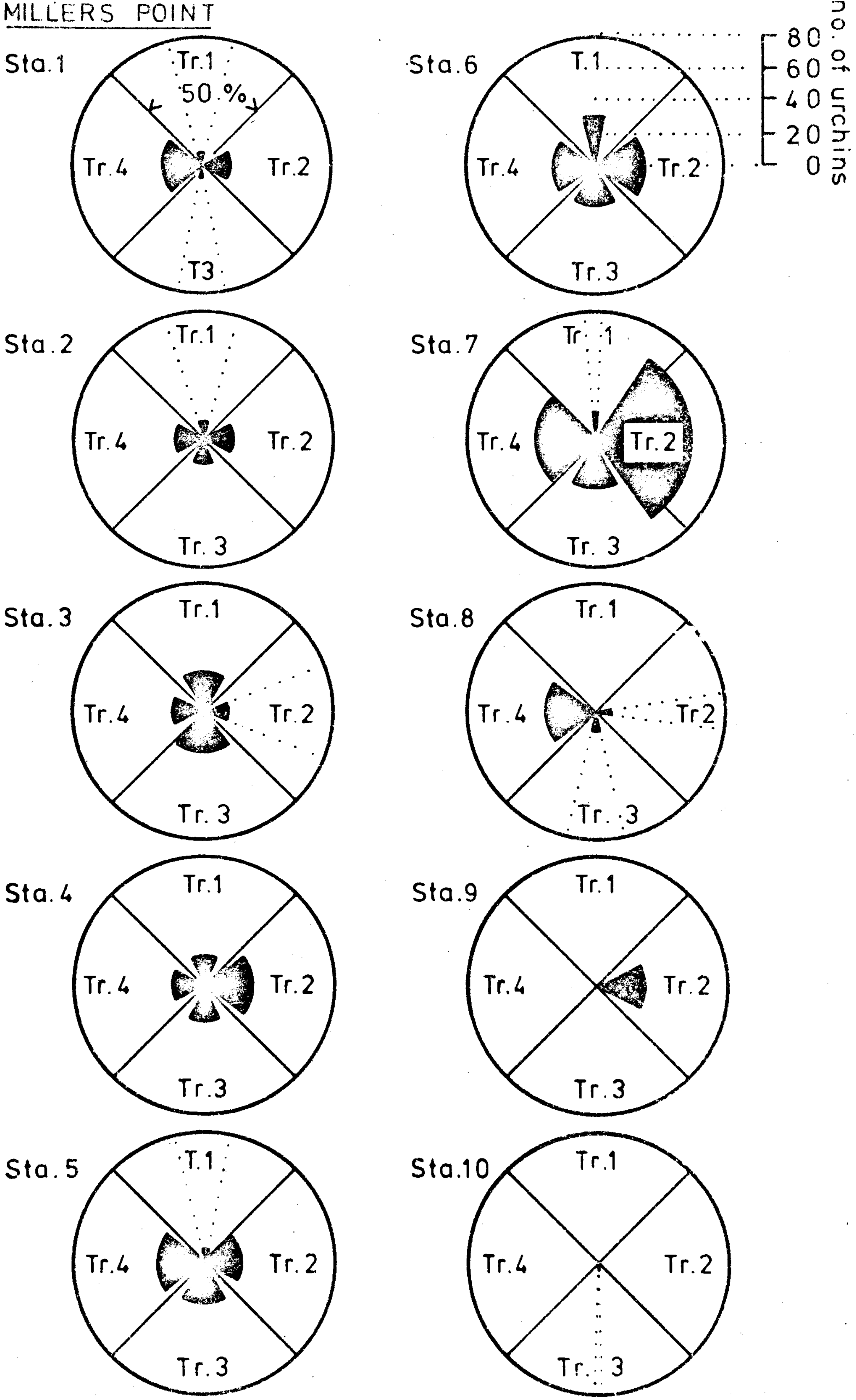

Fig. 2. Density and percentage substrate cover of *Parechinus* for seasonal transects at Millers Point. The radii of the sectors indicate animal numbers, while arc width shows percentage substrate cover of unit area (1 $m^2$). A value of >50% was found in one instance. (M.P. station F, transect 2).

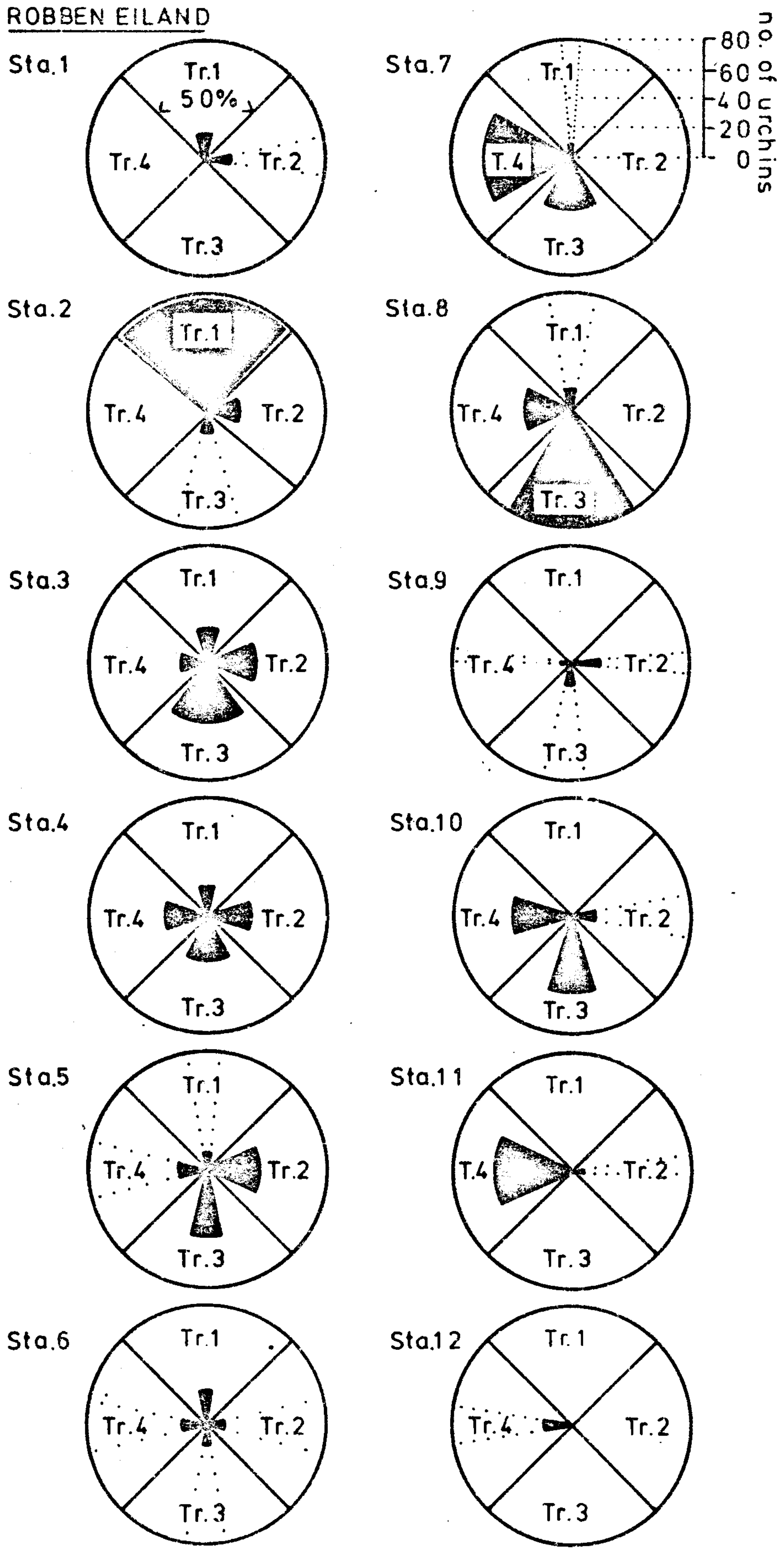

Fig. 3. Density and percentage substrate cover of *Parechinus* for seasonal transects at Robben Eiland. The radii of the sectors indicate animal numbers, while arc width shows percentage substrate cover of unit area (1 m$^2$).

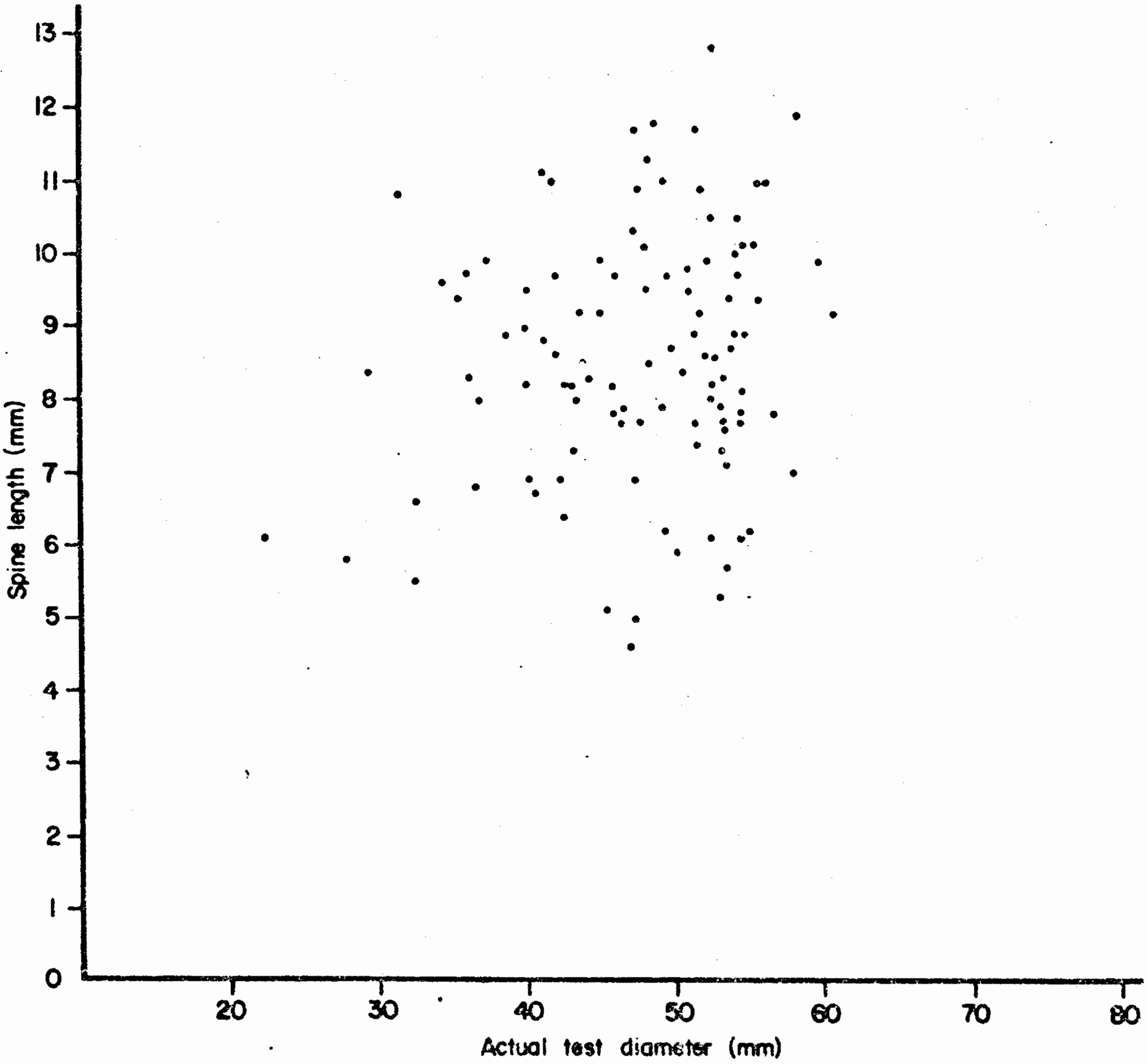

Fig. 4. Scatter diagram of test diameter of *Parechinus* against spine length showing poor correlation. An unbiassed sample of 107 urchins was measured.

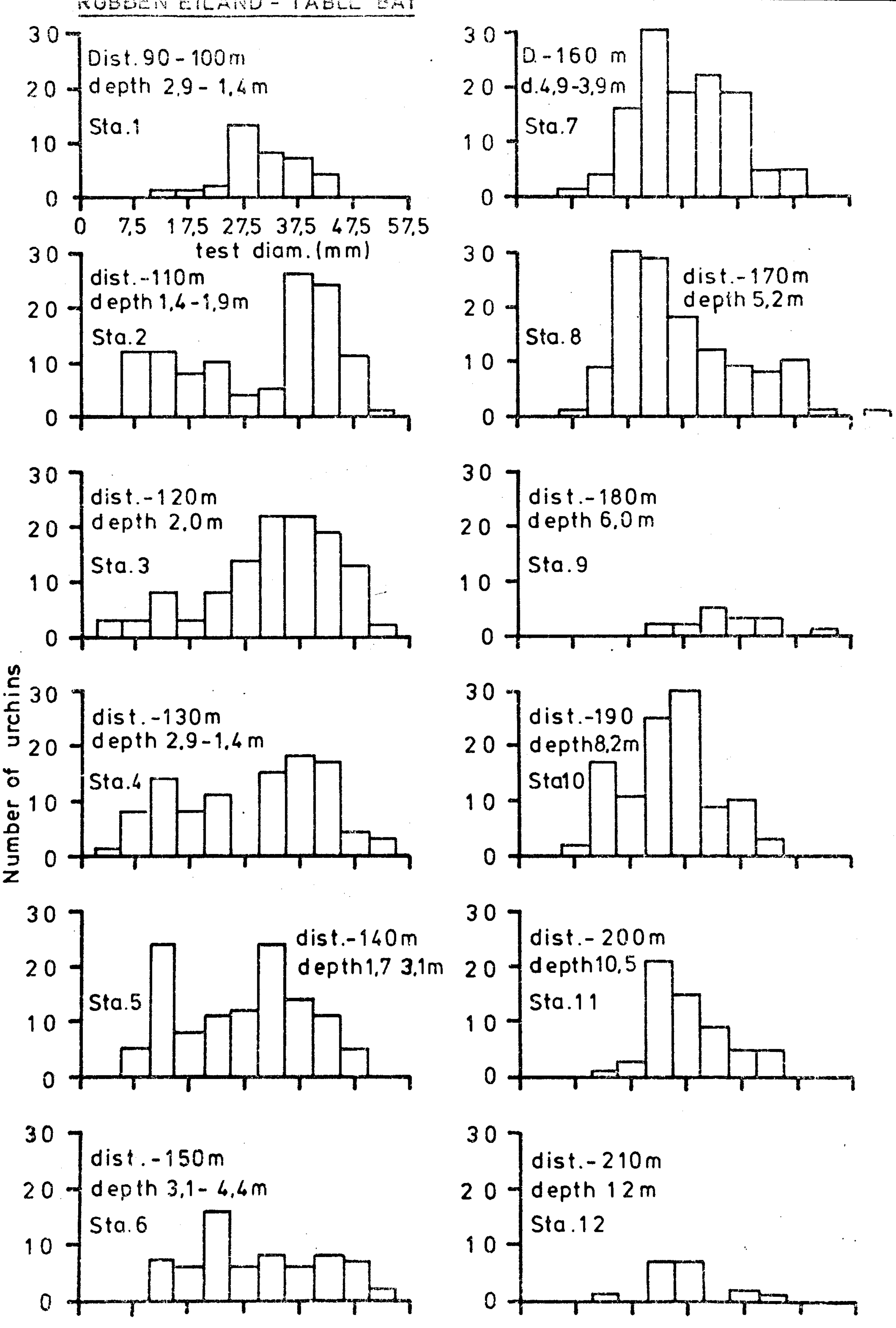

Fig. 5. Combined size frequency histogrammes showing change of size (test diameter in mm) of *P. angulosus* with distance (and depth) from shore for Robben Eiland.

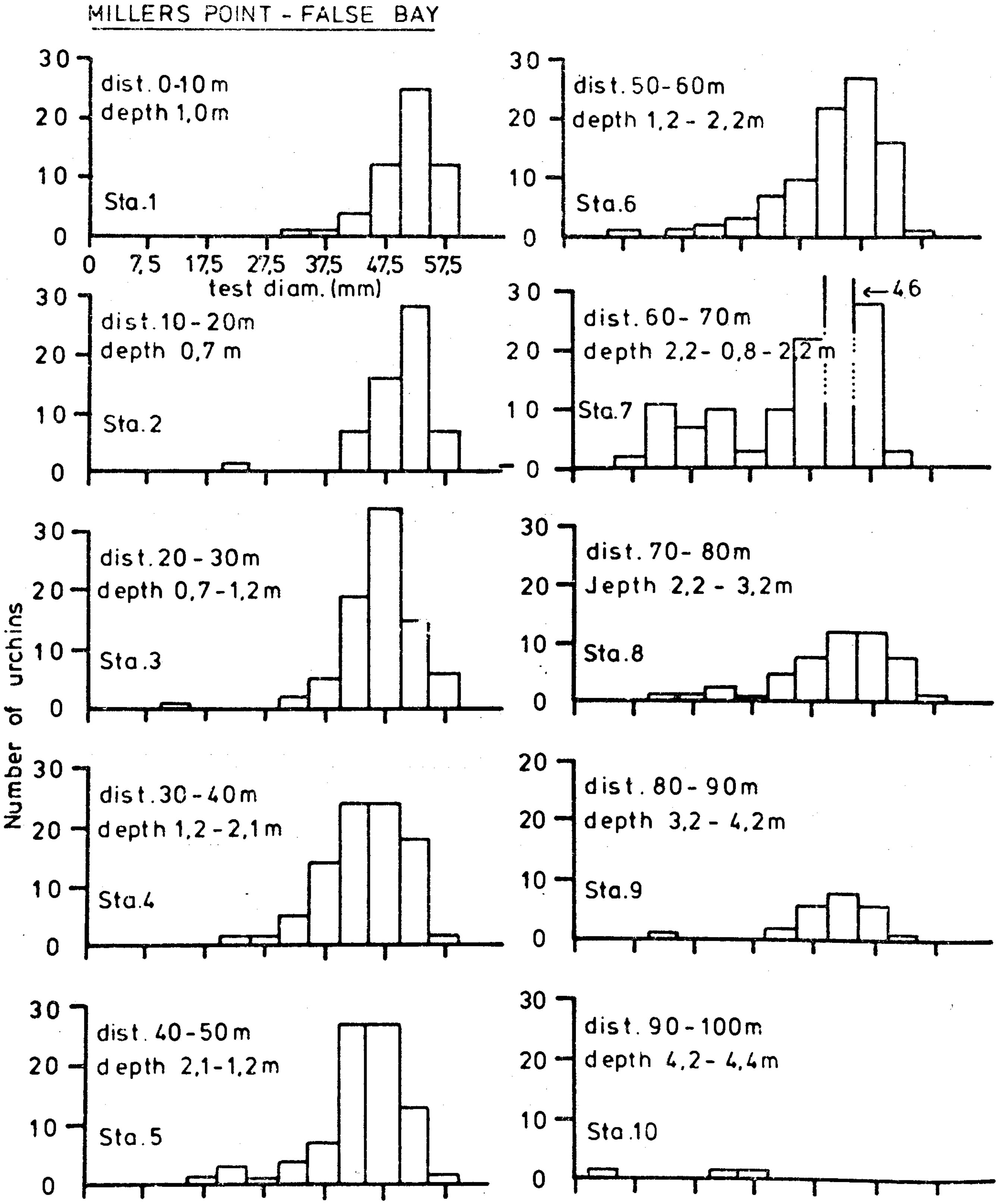

Fig. 6. Combined size frequency histogrammes showing change of size (test diameter in mm) of *P. angulosus* with distance (and depth) from shore for Millers Point.

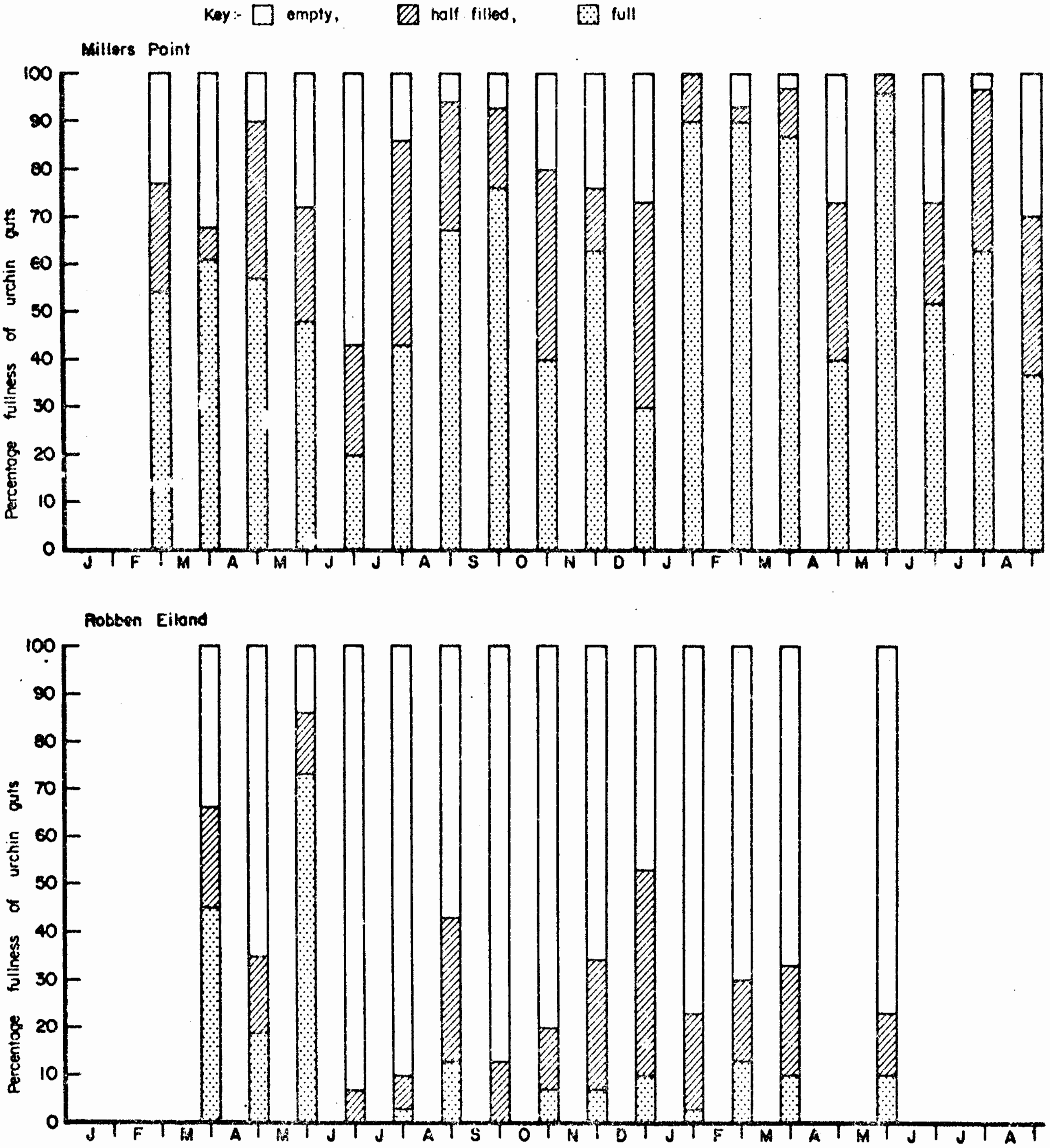

Fig. 7. Gut states of urchins collected on study sites at Millers Point and Robben Eiland. The urchins were processed soon after collection.

# PART II

## KELP GRAZING BY THE COMMON SEA-URCHIN *PARECHINUS ANGULOSUS* LESKE IN FALSE BAY, CAPE.

# Kelp grazing by the common sea urchin *Parechinus angulosus* Leske in False Bay, Cape

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The effect of grazing by the common sea urchin on a local kelp bed was studied. The need for this investigation was felt in view of the importance of kelp beds to the near-shore ecosystem and reports describing the extent of damage to some Californian and eastern Canadian kelp beds by the grazing activity of certain urchin species. Experimental sites typical of the area were permanently marked. A study site was protected from urchins, while the control was not. Urchins were regularly removed from the study site. Kelps growing on the experimental plots were harvested seasonally, counted and their biomass calculated. Results over one year suggest that although the grazing potential of sea urchins is considerable, little impact was made on kelp beds in the study area. The grazing potential of *Parechinus* seems to be directed principally at the early sporophytes of *Ecklonia maxima* rather than at adult plants.

*S. Afr. J. Zool.* 14: 000-000 (1979)

Die gevolg van beweiding op 'n plaaslike seewierbedding bestaande uit *Ecklonia maxima* deur die gewone seekastaiing is ondersoek. Daar was 'n behoefte vir 'n soortgelyke studie, in die lig van die belangrikheid van seewierbeddings vir die nabye kus ekosisteem. Daar bestaan menige berigte in die literatuur met betrekking tot die omvang van skade aangerig in sommige Kaliforniese en Kanadese ooskus kelpbeddings deur beweiding van sekere soorte seekastaiings. Ons het proefpersele wat tipies vir die gebied is, gekies en blywend gemerk. Die proefperseel is herhaalde kere gedurende die studie-tydperk van seekastaiings bevry, maar nie die kontroleperseel nie. Kelpe wat op die persele gegroei het, is elke seisoen ge-oes, getel, en die droë massa bepaal. Resultate gedurende een jaar dui aan dat, ofskoon die beweidingspotensiaal van *Parechinus* aansienlik is, daar nietemin uitwerking op die kelpbeddings van die area blyk te wees. Beweidingsdruk van *Parechinus* blyk tot 'n hoë mate teen die spoorkiemplante van *Ecklonia maxima* gerig te wees, in plaas van 'n uitdunningseffek op volwasse plante te hê.

*S.-Afr. Tydskr. Dierk.* 14: 000-000 (1979)

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*Parechinus angulosus* Leske is the most widespread of South African echinoids, forming very dense, sometimes continuous populations of up to 90 animals per m$^2$ in some inshore localities around the Cape Peninsula. Their high population density and voracious feeding pattern (Greenwood 1975; Buxton 1977) imply that these echinoderms play a major role in the kelp ecosystem. Kelp beds have recently been shown to have considerable importance not only as nursery grounds for numerous invertebrates and fish species (Mann 1972a, b; Miller & Mann 1973; Field *et al.* 1977), but also to be of great potential commercial importance as a source of valuable extracts (Simons 1977).

The destructive effect of intense grazing by Californian urchins *Strongylocentrotus* spp. on beds of *Macrocystis pyrifera* has been described by North (1965), North and Pearse (1970), Leighton *et al.* (1966), Mattison *et al.* (1977), Breen and Mann (1976) and Lang and Mann (1976). Along the eastern coast of Canada evidence for advancing destruction of beds of *Laminaria longicruris* and *L. digitata* by *Strongylocentrotus* spp. has been the subject of detailed study by workers in Nova Scotia. Interest in our study was stimulated by similarities between the situation in the vicinity of the Cape Peninsula and parts of the Californian and Canadian coast. In all these areas kelp productivity is high because environmental conditions are favourable, while over-exploitation of the controlling predators of the herbivorous urchins appears to have affected the balance of the kelp ecosystem. The destruction wrought by increased numbers of urchins in Californian and Canadian kelp beds does not seem apparent in the vicinity of the Cape Peninsula. A map of the area is shown in Fig. 1.

The pronounced upwelling conditions along the Cape west coast, with their high productivity (Field *et al.* 1977) and generally turbulent sea conditions, may prevent urchins from grazing on attached kelps, while generating an abundant supply of organic matter as food for the echinoids. Observations on a plot near the study area at Millers Point, False Bay suggested however, that protection from sea urchins for a matter of months resulted in a dramatic increase in the density of a stand of *Ecklonia maxima* within little more than a year. Following upon these preliminary findings, an experiment was started which

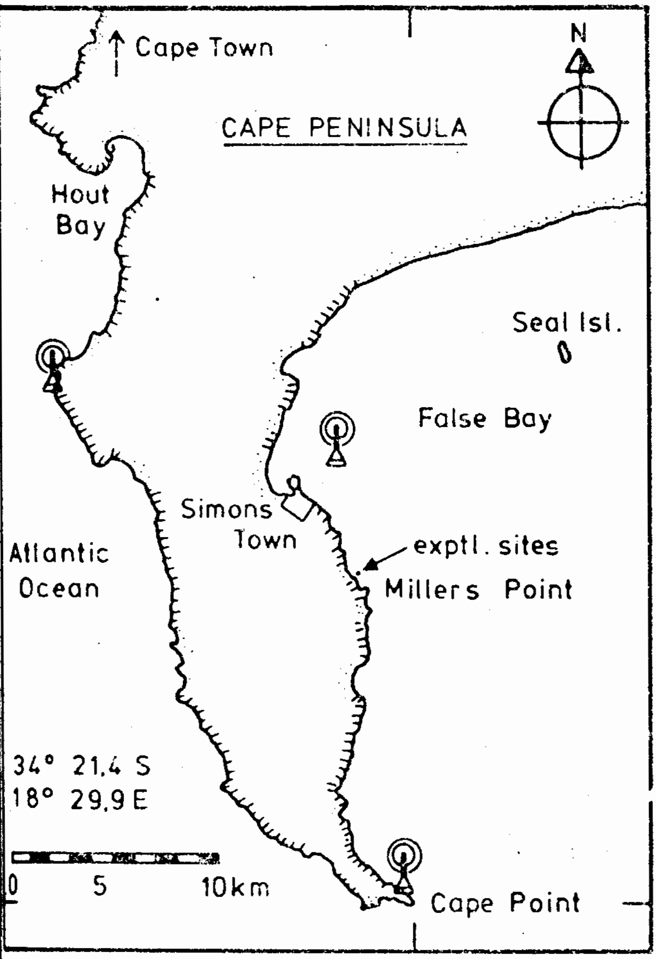

Fig. 1 Map of Cape Peninsula showing the location of experimental stations.

consisted of a series of seasonal kelp harvests over a study site and control.

## Methods

### Permanent stations

These were established at Miller's Point, False Bay, by placing circular concrete anchors of low relief, weighing 70 kg in air, on level positions on the sea-bed (Fig. 2). The anchors were fitted with small sub-surface buoys to facilitate relocation. It was essential that the arrangement should withstand turbulent sea conditions and possible tampering. Under no account was the anchor to move or else the study would be affected. For the sake of clarity, the terms *cropping* and *harvesting* will be used for plant material, while urchins are *cleared* or *removed.*

Two experimental stations in a kelp bed (the study site and the control) were selected so that they were as similar as possible with respect to substrate topography and aspect. The stations consisted of circular areas of 10 m². Such an area was swept by a radial line 1,78 m in length. For purposes of harvesting, the stations were divided into four quadrants by means of weighted lines laid out in the compass directions.

The experiment was started by clearing all urchins from the study site and also from a ring-shaped outer zone 1,22 m wide. The entire cleared area thus had a radius of 3 m (area = 20 m²). Experience suggested that the buffer zone was wide enough to effectively protect the study site, provided urchins were cleared away at roughly monthly intervals. Both sites were initially cropped free of all but adult kelps, which were left *in situ* to provide canopy cover. Holdfasts of harvested *Ecklonia* were removed since recolonization is favoured by the protective shelter offered by the meshwork of the haptera.

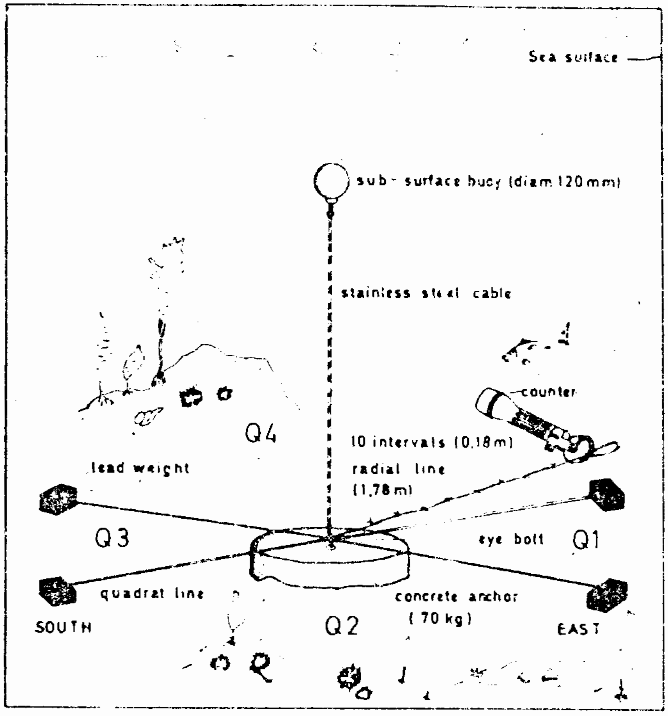

Fig. 2 Layout of quadrant lines on experimental stations.

The kelps harvested were counted and their dry mass (at 105 °C) determined from a wet/dry mass regression given by Buxton (1977) (dm = − 0,11 + 0,15 wm; N = 20; r² = 0,84). Adult canopy plants were counted to check on losses in the course of time.

After this initial preparation, a three-month period was allowed to elapse before the first quadrants (Fig. 2) on the study site (Qs) and control (Qc) were cropped of newly grown kelps. After successive three-month periods of quadrants 2, 3 and 4 on both stations were similarly harvested. Finally, the entire algal cover on both stations was cropped. This was done in order to determine the total amount of kelp produced during the period of study.

### Correction for substrate surface irregularities

Available solid substrate surface seems to be of importance in the density distribution of sea urchins at high population densities (Dahl 1973; Laxton & Stablum 1974; Greenwood 1975; Fricke 1976) since the echinoids avoid unconsolidated sediment. Measurement of substrate surface within the 10 m² of both experimental plots was done after the last kelp harvest had left the two plots barren. A counting wheel, described in an earlier paper (Fricke 1976) was employed for this task.

Four weighted quadrant lines, 1,78 m long were laid out as equally-spaced radii from the central anchor. Each quadrant was treated individually. A moving radial line of the same length and marked in ten equal intervals, each representing a step in the measurement, was used in conjunction with the counting wheel (Fig. 2). The device was carefully pushed over the irregularities encountered in the arc delimiting a quadrant at each of the ten marks. Sand patches were ignored. Initial and final readings were noted on each arc, giving the number of revolutions of the wheel and hence linear distance travelled.

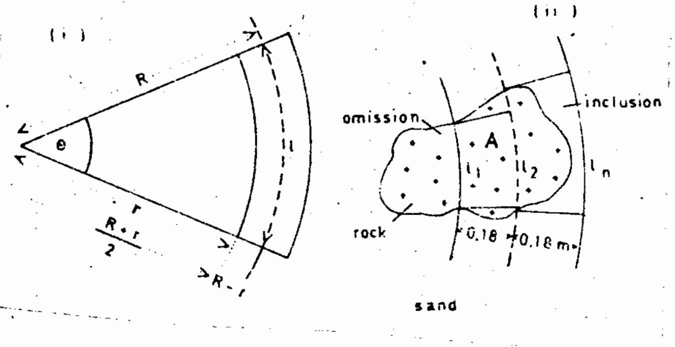

Fig. 3 Geometrical construction to determine area of partial annulus A.

## Calculation of surface area

Each block of solid substrate was considered to approximate a parallel-sided slab (strictly speaking a segment of a partial annulus, as in Fig. 3(i). This assumption results in omissions of area, but these are cancelled out on the average by compensating over-estimates (Fig. 3(ii)).

For the sector in Fig. 3(i)

Area of sector = $\frac{1}{2}L^2 \times \theta$ radians
Therefore area A required = $\frac{1}{2}(R^2 - R^2) \times \theta$
and $l = (R + R)/2\theta$
Eliminating the area term:

$$\frac{\text{area}}{\text{length}} = \frac{R^2 - R^2}{R + R} = R - R;$$

Thus required area = $(R - R) \times$ length of medial l
= spacing of block $\times$ l
Therefore $\Sigma$ area of blocks = spacing $\times$ $\Sigma$ length of blocks

The precision of the above approximation was tested by three replicate measurements of a circle of 10 $m^2$ on firm terrain. The replicates fell within 4% of the theoretical value.

## Results and Discussion

### Urchin density, immigration and removal

When initially cleared, the study site had a *Parechinus* density of 61 individuals $m^{-2}$ (76 $m^{-2}$ when corrected to actual surface area). At the conclusion of the experiment, the urchins living on the control site were also counted and their numbers corrected (Table 1). There was no significant difference between the two sites. This supports the well-known fact that substrate surface availability is of importance to many sessile and slow-moving marine organisms (Marsh 1970; Dahl 1973; Laxton & Stablum 1974).

**Table 1** Number of *Parechinus* cleared from experimental stations, corrected for actual benthic area

| | Study Site | Control |
|---|---|---|
| Project area ($m^2$) | 10 | 10 |
| Actual area ($m^2$) | 8,0 | 11,5 |
| Percentage difference | −20 | +15 |
| Number of urchins | 609[a] | 831[b] |
| Urchins $m^{-2}$ | 61 | 83 |
| Urchins $m^{-2}$ (corrected) | 76 | 72 |

[a] Urchins cleared from the study site at the beginning of the experiment.
[b] Urchins cleared from the control at the end of the experiment.

The total number of *Parechinus* removed during the study (excepting the control) was 785 animals.

The schedule of maintenance clearings of urchins is summarized in Fig. 4. Data from a pilot study are also shown and support the evidence for a fluctuating seasonal immigration rate. The two studies were performed on different scales, hence the difference in urchin numbers. Immigration of *Parechinus* shows highest values between September and November, while those for the period from November to April are low. This appears to be related to the reproductive cycle of the urchin (Fricke 1974). Near spawning, *Parechinus* appears to remain relatively stationary (*pers. obs.*), while the feeding rate of gravid urchins is much reduced (Greenwood 1975; A.H. Fricke *unpubl.*).

### Kelp harvests

Table 2 summarizes the harvesting data for the entire study. Although the actual surface area between the sites differs by 35%, the adult population of *Ecklonia* found initially was similar (14 kelps were found on the study site and 11 on the control). Surface area appears to be of no importance to kelp density (K.H. Mann *pers. comm.* 1976, A. Chapman *pers. comm.* 1977) unless the water column is underutilized. This would be the case if sand patches larger than a mature kelp plant intervened between solid substrate.

### *Initial cropping*

This operation served the purpose of determining standing stock at the start of the experiment. The number of individuals harvested on the study site was almost twice that obtained from the control, while the ratio of biomass was 1,8:1 (Table 3). Adult canopy kelps were counted during successive field trips to follow their fate (Table 4). Such information is valuable because sudden breaks in the canopy (e.g. as a result of a storm) may significantly change light

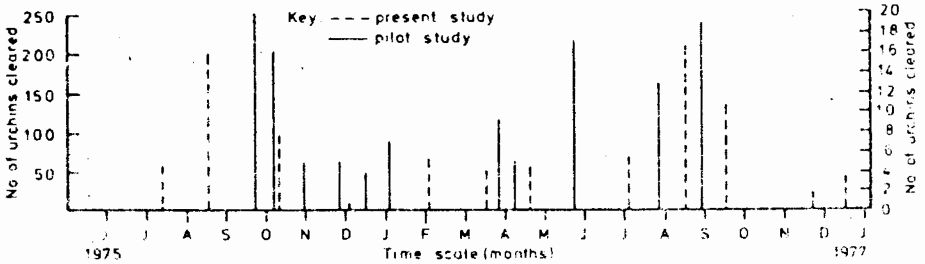

Fig. 4 Immigration of *Parechinus angulosus* into cleared sites. The solid line denotes data of the present study (scale on left). Dashed lines refer to data of a pilot study (scale on right).

**ble 2** Initial, seasonal and final harvests of *Ecklonia axima* on experimental stations at Millers Point, False y

| | Quadrants of study site | | | |
|---|---|---|---|---|
| | Qs1 | Qs2 | Qs3 | Qs4 |
| ial harvest | | | | |
| Date | 7.9.76 | 7.9.76 | 7.9.76 | 7.9.76 |
| Numbers | 57 | 74 | 80 | 13 |
| Mass (g) | 1575 | 2217 | 1792 | 645 |
| sonal harvest | | | | |
| Date | 3.12.76 | 10.3.77 | 7.6.77 | 10.9.77 |
| Numbers | 68 | 175 | 60 | 29 |
| Mass (g) | 5 | 58 | 102 | 110 |
| al harvest | | | | |
| Date | 25.12.77 | 25.12.77 | 25.12.77 | 25.12.77 |
| Numbers | 24 | 24 | 45 | 2 |
| Mass (g) | 27 | 16 | 43 | 3 |

| | Quadrants of control | | | |
|---|---|---|---|---|
| | Qc1 | Qc2 | Qc3 | Qc4 |
| tial harvest | | | | |
| Numbers | 34 | 38 | 27 | 17 |
| Mass (g) | 1912 | 742 | 422 | 485 |
| asonal harvest | | | | |
| Date | 3.12.76 | 10.3.77 | 7.6.77 | 10.9.77 |
| Numbers | 45 | 11 | 55 | 1 |
| Mass (g) | 28 | 4,5 | 121 | 0,1 |
| nal harvest | | | | |
| Numbers | 13 | 8 | — | — |
| Mass (g) | 16 | 26 | — | — |

vailability to sub-canopy kelps, resulting in an unexpected rowth response (Kain 1977). In the shallow-water environment of this locality (4–6 m) this consideration was particularly relevant.

The two sites being relatively small (10 m²), individual omparisons of plants could not be made. Therefore the rop for a site was considered as a whole. The cropping of ub-canopy kelps served the purpose firstly of determining he standing stock of immature *Ecklonia* and secondly of evealing any seasonality in recruitment. Differences etween the two sites would suggest an effect of urchins razing on young sporophytes.

**able 3** Comparison of kelp yield between study site nd control (excluding adult kelps)

| | Study site (Qs1 — 4) | Ratio (Qs/Qc) | Control (Qc1 — 4) |
|---|---|---|---|
| Initial harvest | | | |
| No. of individuals | 224 | 1,9:1 | 116 |
| Biomass (g dry mass) | 6228 | 1,8:1 | 3562 |
| Final harvest | | | |
| No. of individuals | 95 | 4,5:1 | 21 |
| Biomass (g dry mass) | 88 | 2,1:1 | 42 |
| Combined seasonal harvest | | | |
| No. of individuals | 332 | 3,0:1 | 112 |
| Biomass (g dry mass) | 274 | 1,8:1 | 154 |

**Table 4** Fate of canopy kelps on experimental stations (numbers of plants)

| Date of count | Study site | Control |
|---|---|---|
| 2 December 1976 | 14 | 11 |
| 1 February 1977 | 12 | 10 |
| 7 March 1977 | 8 | 10 |
| 26 April 1977 | 7 | 9 |
| 3 November 1977 | 6 | 6 |

### *Seasonal cropping*

Three months after initial cropping of sub-canopy kelps on both sites the respective first quadrants (Qs1 and Qc1) were harvested. A response to protection from urchin grazing emerged clearly (Table 2), in that 34% more plants survived on the study site. The figures obtained for the biomass were however, puzzling. The plants which grew on the study site, although much higher, had a combined biomass of roughly one-sixth of those obtained on the control. A depth difference found between the two plots was probably the cause.

Kain (1977) came to the tentative conclusion that protection due to depth may be the cause of thinness of small (young) fronds. *Ecklonia* which grew on the shallower site (control) possessed thicker fronds, also being larger on the average (50% of plants from the control exceeded 90 mm in length, but only 13% from the study site reached that value).

The second harvest (Qs2 and Qc2) showed the response to protection even more clearly (Table 2). Once again the juvenile kelps are both smaller and filmier on the study site.

The third harvest (Qs3 and Qc3), which took place in winter, showed a drop in numbers by two-thirds relative to the previous crop, while the control showed an increase. In the course of the nine months which had elapsed since the original cropping, a number of *Ecklonia* had developed secondary fronds. The low winter yields were unlikely to result from storm damage, since young kelps were never found washed up on the shore. Observations during winter showed few juveniles, while adult kelps had much front-tip erosion and appeared flaccid and blanched. A few canopy kelps were seen to be dying off.

The fourth harvest (Qs4 and Qc4) was small, in fact the control was almost devoid of *Ecklonia*.

The variations of these seasonal harvests tie in well with results obtained in the pilot study carried out in a similar manner (Fig. 5). The peak number of kelps harvested was found between January and March, while the lowest values were recorded during the period from June to September. It therefore appears that young sporophytes of *Ecklonia* commence active growth in early summer and continue on into autumn. In other words, the southern winter represents a period of dormancy for *E. maxima*. This agrees with the findings of G.S. Dieckmann & N.G. Jarman (*pers. comm.* 1978).

### *Final site cropping*

At the end of the one-year study, both plots were cropped clear of all kelps in order to assess the overall change in numbers of plants and biomass ratios (Tables 2 and 3).

Since harvest intervals could for unavoidable reasons not be kept exactly to three months, it was considered more meaningful to compare respectively the yields of the initial, the combined seasonal and the final site harvest.

rey algal community, especially *Pterosiphonia iophylla* which then covers much of the available solid bstrate.

Most active visible growth of *E. maxima* appears to take ce from December to April. The highest invasion rates of *echinus* into cleared plots were observed during spring, sibly in anticipation of an increased food supply. Protion from urchin grazing results in an increased survival young *E. maxima* in False Bay kelp beds.

## knowledgements

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# PART III

# REPRODUCTIVE RHYTHMS AND THE ROLE OF TEMPERATURE IN THE REGULAR ECHINOID *PARECHINUS ANGULOSUS* LESKE IN TWO DIFFERENT MARINE ENVIRONMENTS AROUND THE CAPE PENINSULA

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ABSTRACT

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## ABSTRACT

Temperature is considered to be an important factor regulating reproductive behaviour in many echinoderms. The unusual hydrographic structure around the Cape Peninsula made it possible to test this hypothesis by monitoring the reproductive activites of two natural populations of *P. angulosus* living in different temperature regimes. Monthly samples of 30 urchins were collected for over a year near Robben Eiland and Millers Point in False Bay. Gonad indices were calculated to determine the reproductive state. Variations of lipid content relative to dry body mass were determined. Histological sections of corresponding gonad subsamples were prepared for individual urchins. Lipid levels agree well with gonad indices, the Robben Eiland values being consistently lower than those of Millers Point. Six developmental stages could be distinguished, supporting the gonad index evidence. It does not appear that temperature alone influences the reproductive cycles of *Parechinus*, but that light is also involved. Annual gonad output of Millers Point urchins is four times greater than the Robben Eiland value.

# INTRODUCTION

Echinoderms have long been a convenient source of material for developmental and biochemical studies by virtue of their abundance, ease of maintenance and simple body plan. Most early information on reproduction in echinoderms originates from studies initiated for embryological information (Boolotian, 1966). The whole subject was thoroughly reviewed by Giese and Pearse (1974), who pointed out the difficulty of separating extrinsic and intrinsic triggers in reproductive rhythms. Endogenous factors, for example nutritional state may affect gametogenic cycles in individuals, while extrinsic influences like temperature, light and others serve to synchronize gamete release. The whole complex is still far from being fully understood.

The present study was conducted as a natural experiment in view of the difficulty with which aquarium results can be translated to processes in the field. Laboratory studies furthermore tend to overemphasize isolated clues - temperature in this case - normally part of an interacting, multifacetted situation.

Seasonally changing sea temperatures seem to be a reliable environmental influence, closely followed by light. Since reproduction is of such cardinal importance in nature, it is probably controlled by such basic principles. Apelöf (1912) and Orton (1920) were among the first workers to investigate the connection between temperature and reproduction.

It appears from evidence obtained in this study that a convincing correlation exists between temperature and breeding-cycles in *Parechinus*. The relatively modest seasonal fluctuations in sea temperature around the Cape Peninsula (Clowes, 1950; Atkins, 1970; Harris, 1978) seem of sufficient magnitude as a regulator when compared with the insignificent changes of 0,5°C experienced in the Antarctic (McMurdo Sound) and reported by Pearse (1965). A similar situation may exist in the tropics (Yonge, 1940); Pearse, 1968). Conditions in the sea around the Peninsula show definite seasonality but no extremes; for example, detrital and attached plant food for *Parechinus* is available throughout the year, probably only changing in quality (kelp beds are dormant during the winter months). It was therefore of interest to find whether *Parechinus* follows a seasonal or continuous breeding pattern, thereby falling into one of Fenaux' (1968) thermal categories. Like other west-facing continental margins, the peninsula experiences pronounced, periodic upwelling particularly during summer. A confused thermal regime is produced and partly masks the seasonal fluctuations (Fricke & Thum, 1974). False Bay, which is partly sheltered by aspect shows a much clearer pattern of change. If temperature alone were to act as gonadal regulator in west coast urchins, additional clues from temperature variations would have to be obtained, such as persistence or exceedence beyond a critical range. The existance of two distinct marine temperature environments close by, populated by large numbers of *Parechinus* acted as impetus to this study. Previous work by Greenwood (in press) and Fricke (in prep.) showed that significant differences with regard to body size and density exist between urchins at the two localities. Establishing their reproductive pattern would help explain the extent to which water temperature is used as trigger in spawning behaviour. The evidence from gonad changes over the seasons was supported by lipid assays and histological preparations.

## STUDY SITES

The Cape peninsula, having different temperature regimes on its western and eastern shore offered a convenient locality for this synoptic study (Fig. 1.). The west coast site was chosen near the north eastern side of Robben Eiland in Table Bay and is periodically exposed to upwelled intermediate water particularly in summer when temperatures may change by 6°C and more within a few hours.

An inshore site typical of western False Bay was chosen at Millers Point, which is generally warmer. South easterly winds drive warm surface water and tongues of the Agulhas current into the bay. The differing temperature regimes were clearly demonstrated by continuous *in situ* records of instruments installed on the sea bottom (Fricke & Thum, 1974).

Considerations of accessibility even during poor weather and absence of pollution inputs ranked high in the site selection. Robben Eiland is exposed to refracted north-westerly swells during winter, while Millers Point is fairly sheltered.

*Parechinus* is the dominant invertebrate (Plate 1 a and b) frequently showing high substrate coverage, but there is also much bare rock, colonized by encrusting algae (Lithothamnia). The substrate at Robben Eiland on the other hand, along with many westcoast sites shows dense multitiered animal communities of mussels, holothurians, sponges and ascidians in addition to urchins. *Parechinus* is closely associated with dominant macrophytes *Ecklonia maxima* and *Laminaria pallida*, the latter being uncommon at Millers Point; presumably intolerent of the warmer water (Dieckmann, 1978).

# METHODS

## Sample size and location

Practical considerations demanded that sample size be kept to a minimum (30 animals month $^{-1}$ site$^{-1}$) while remaining statistically meaningful. Males and females were processed separately throughout. A suitable site inhabited by urchins of uniform size was found in a previous study (Fricke & Thum, 1975) by running a random, stratified transect across a typical area of high urchin density. The site selection was made from a plot of urchin size against distance (and depth) from shore.

## Permanent stations

Circular concrete anchors of low profile and divided into ten equal sectors on the periphery with embedded plastic strips were placed on even bottom at the selected spots. Monthly collections were by a plotless method of random choice along a roving radial line 2 m long. A different random angle with respect to north was sampled monthly.

## Treatment of urchins

Urchins were processed live. The tests were opened sub-peripherally and the gonads excised whole. The animals were sexed and checked microscopically when in doubt. One instance of hermaphroditism was seen but not followed up. A subsample of gonad tissue was fixed in Bouin's fluid for sectioning,another larger one stored at $-20^{o}C$ for lipid assay. Weighing was done to the nearest mg.

## Estimation of total lipids

The large sample number required a simple, rapid method. A gravimetric procedure described by Bligh and Dyer (1959) was used in a modified form. The method is reputedly superior to standard Soxhlet extraction, by removing more lipid, i.e.also the structural fraction (Martin, 1963). Histochemical tests would refine the evidence, since storage materials are often highly localized (Pearse, 1960; Nimitz, 1964). Extraction was effected by blending a mixture of methanol, water and chloroform, centrifugation and phase separation. Lipid extracts were blown dry and freed of residual solvents in a vacuum desiccator containing silica-gel and wax chips.

## Histology

Fixed specimens slected from peaks and troughs in the gonad cycle were wax embedded and sectioned at 9 nm transverse to the long axis of the gonad lobe. The specimens were stained in Harris haematoxylin-eosin and mounted in Canada balsam. In order to reduce effort, only 3 specimens (male and female) were selected from a median ranking (in 6 steps) of gonad indices. These were then considered representative of the gonad state of urchins in the field at that time. This manipulation was necessary since maturity stages were nearly always skewed. Six stages were distinguished: (See also Plate 1 and 2).

1) inactive, 2) early recovery, 3) active recovery, 4) ripe, 5) spawning, 6) spent (terminology by G. v.d. Horst, pers. comm.)

## Determination of gonad index

The gonad lobes were removed from freshly opened urchins and dried at 60°C, while the test was dried with the pooled perivisceral fluid after washing out gut contents. Gonad index was expressed as dry gonad weight ÷ total test weight x 100 (Gonor, 1972).

## RESULTS

A plot of monthly variations of gonad indices of male and female *Parechinus* for the period of study is shown in Fig. 2 a & c. The graph shows mean (bar), 95 percent confidence limits and the number of animals per sample for both locations.

Fluctuations of *in situ* sea temperature were drawn in as a running average of 5 items and given to the nearest 0,5°C. The watertight units were not ready at the start of the experiment, hence the lack of data at the beginning. A graph of exceedence (see also Ainslie, 1971) of water temperature for two months bracketting a spawn out is given in Fig. 3 a & b. The graph shows cumulative percentage of occasions when water tmeperature was below a given value. Daily maxima and minima of continuous recordings were used.

Variations in percentage lipid, relative to total dry body weight of males and females for a one year period are shown in Fig 2b. The data for both sexes show a similar trend. The lipid values for males from the Robben Eiland sample were consistently lower than for females, while the pattern at Millers Point was more variable, and the sexes less well synchronized.

A calorific value for male and female gonad tissue was obtained by microbomb technique. (The tissue sample was pooled from 4 animals each) Two replicate analyses gave very close values (Table 1).

TABLE 1

| | Replicate 1 kJ.g$^{-1}$ dry weight. | Replicate 2 kJ.g$^{-1}$ dry weight. |
|---|---|---|
| Male gonad: | 19,05 | 19,09 |
| Female gonad: | 19,03 | 19,29 |

Furthermore, the value for males and females were almost identical.

Annual gonad production per $m^2$ was calculated, using the above calorific values. Greenwood (in press) found a minimum mature size for *Parechinus* by evaluation of Allen production curves. The smallest "mature" urchin from False Bay sites has a diamter of 30 mm and 20 mm at Robben Eiland.

Gonad output for Millers Point urchins is 3463 $kJ.m.^{-2}$ $yr.^{-1}$
and for Robben Eiland " " 822 $kJ.m.^{-2}$ $yr.^{-1}$
- a four fold output despite the higher urchin density at Robben Eiland.

## DISCUSSION

The duration of this study was rather too brief to produce a final picture of the reproductive pattern, but all the same, informative trends emerged.

Millers Point shows a marked temperature seasonality (see also Fricke & Thum, 1974). The gonad index plot follows the temperature curve with a lag, which is to be expected. Monitoring a natural spawning in the field is difficult, but personal observations suggest that the process may take several days, i.e. occurs in pulses. Two spawnings are apparent, one in autumn, and a second, less intense one in spring. The values obtained in a lipid assay on subsamples of the same urchins were plotted in register with gonad index variations (Fig 2b). Although these data once again essentially follow the trend of gonad indices, agreement is only partial; there is an unusually high peak for males at the end of July which seems out of context. Lipid values for respective sets of males and females show inconsistent correlation. The evidence of histological sections closely supports the gonad index trends in terms of state of maturity. Although only 3 male and female specimens were selected for this purpose for practical reasons, it was possible to differentiate by microscopy between a small difference in gonad index of urchins collected in March (2nd pair of blocks). The females (higher index of the two) showed early recovery (in terms of the ranking seen on Plate 1 a & b) while corresponding males were still spent.

Robben Eiland. The temperature data obtained at this site is without clear seasonality. Winter temperatures may be uniform for prolonged periods, with changes of less than 1°C (Fricke & Thum, 1974). Generally, temperatures are lower than those at Millers Point but periodic upwelling may reverse this situation. Furthermore tongues of warm Agulhas water occasionally reach the site producing an erratic temperature regime, characteristic of this area. Two spawnings take place at similar periods to those of Millers Point. Incomplete additional gamete releases occur, probably as a result of sudden, temperature drops. This may be one reason why gonad indices, which should be size independent for mature urchins (Gonor, 1972) are consistently lower. Essentially the same type of diet is available, but difference in the availability may exist. This was not followed up. Competition seems to be more intense, judging by dense substrate colonization. Lipid values for both sexes show good agreement and essentially follow the trend of gonad variations. Male values are consistently lower than female ones. Examination of sectioned gonad samples supports the evidence of gonad indices.

From the evidence presented in this synoptic study, some doubt arises concerning the exclusive role of temperature as a regulator in the reproductive rhythm of *P. angulosus*. Certainly, the close agreement of sea temperature variations in False Bay with gonad index changes, suggests temperature control. This cannot be said for the situation at Robben Eiland. These urchins, while showing similar reproductive timing as those in False Bay, are exposed to a colder (Fig. 3a & b) and moreover erratic temperature regime. The possibility that light may act as a second clue can therefore not be ruled out especially since the spring and autumn photoperiods are similar, in fact light could be more important than originally expected. Boolotian (1963) reports such a combined response for *S. purpuratus* in an eight year study in California. The findings for *P. angulosus* are interesting in the light of the well known fact (Crisp, 1957) that the breeding season of an organism may vary over the different parts of its range, according to annual temperature variations. Gonad output for *Parechinus* appears to be significantly affected by location. Despite a higher density at the cold water site, the kiloJoule value is only a quarter that of False Bay. Mature animals only were considered in the calculation. The identical calorific valuesfound for male and female gonad tissue question the long held ideas about the so-called "cheap male phase".

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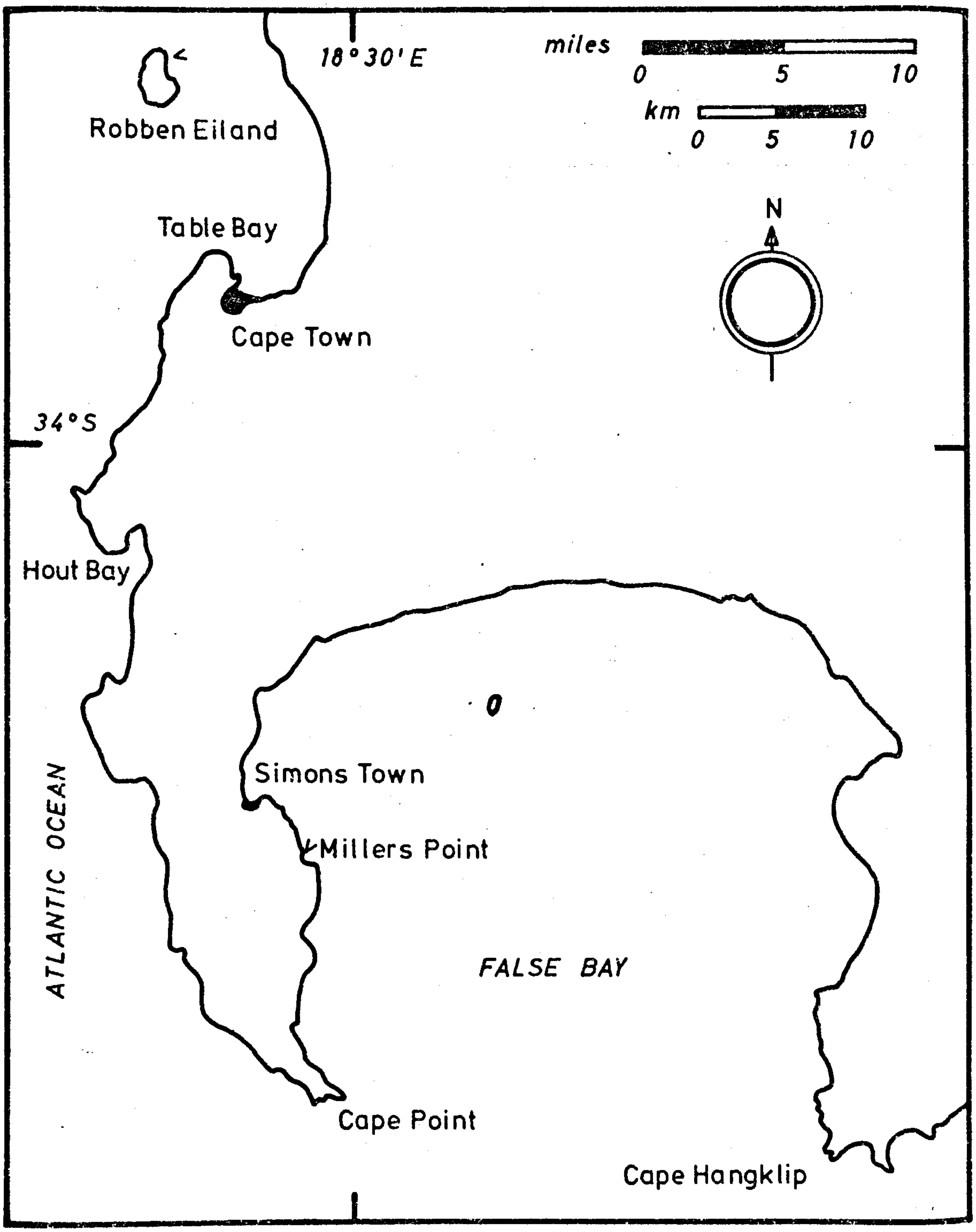


Fig. 1. Map of the Cape Peninsula, showing the location of study sites in two different marine environments.

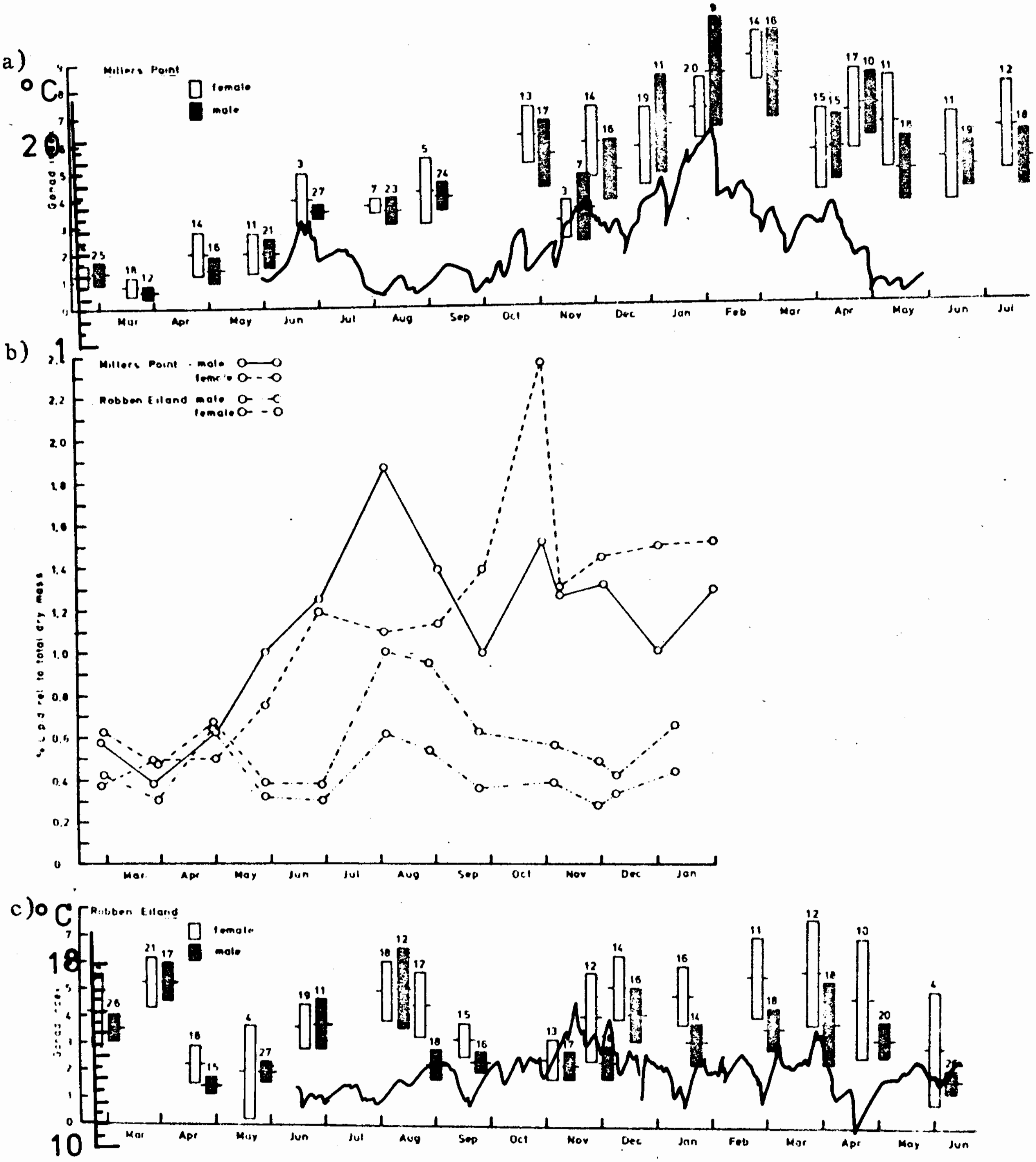
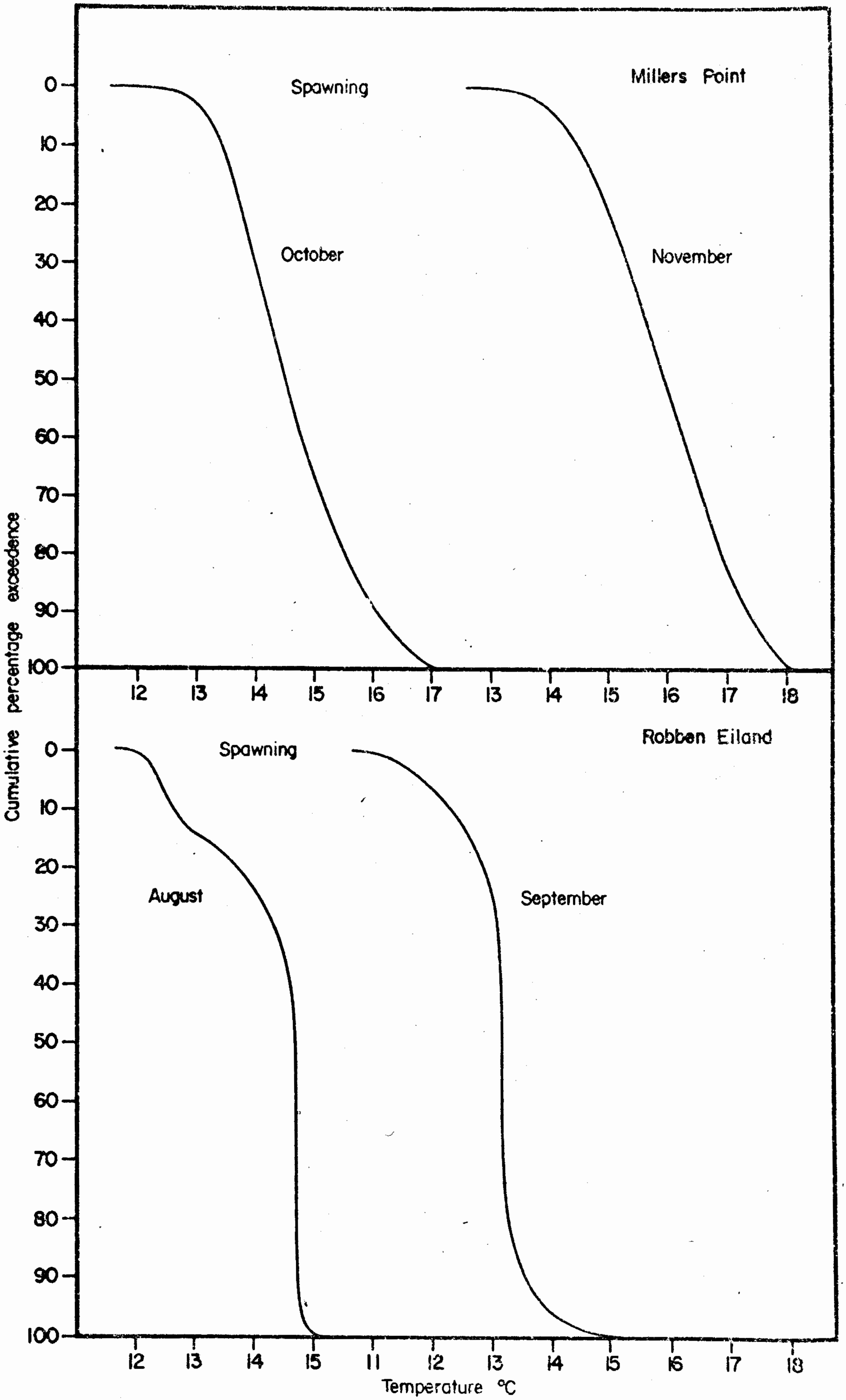


Fig. 2a, b, c. Combined graph of change in Gonad Index of *Parechinus angulosus* in time, showing mean (bar), 95% confidence limits (rectangles) and number of animals collected per sample for both sexes.

Fluctuations of sea temperature (drawn as running average of 5 items) for Millers Point and Robben Eiland.



3a & b. Graph of cumulative percentage exceedences of temperature at Millers Point, bracketting a spawning. The left hand curve in each case describes the temperature regime under which gamete release occurred. The data covers two months.

## PLATE 1.

Thin sections of *P. angulosus* male gonads, stained with Harris haematoxylin-eosin and cut transverse to the long axis of the lobe. The photomicrographs are arranged in order of maturation.

a) Inactive gonad (no evidence of spermatids or spermatozoa, interstitial tissue regressed.

b) Early recovery (some spermatozoa visible in centre of sections).

c) Late recovery. Microtubular spaces nearly filled with spermatozoa .

d) Ripe gonad crammed with spermatozoa.

e) Spawning (tubules partly emptied, showing large interstitial spaces).

f) Spent. (No spermatozoa left. Interstitial tissue not yet regressed).

## Plate 1

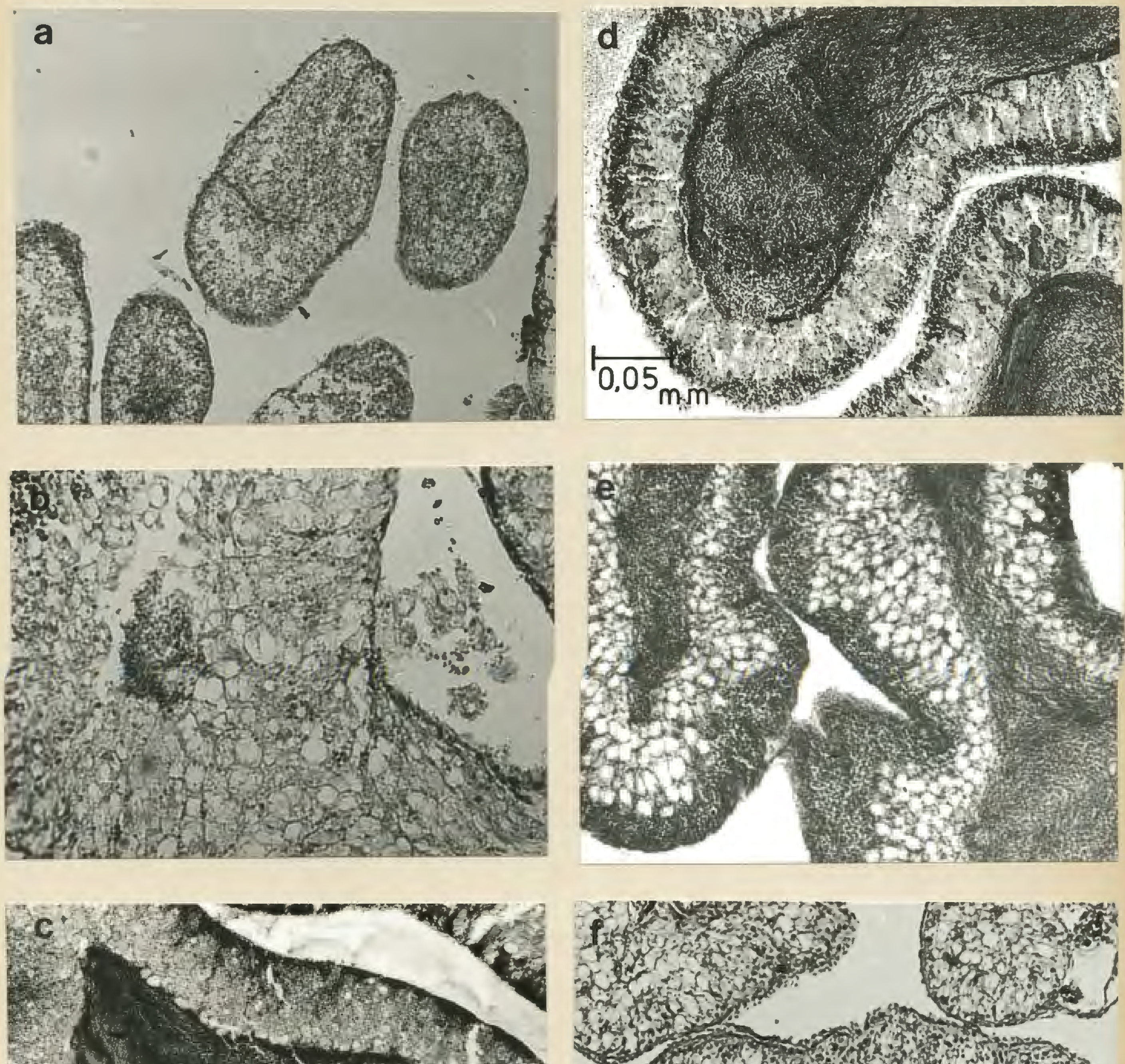


PLATE 2.

Thin sections of *P. angulosus* female gonads, showing stages of maturation.

*a) Inactive. A few oogonia are visible near gonad wall.*

b) Early recovery. Numerous oocytes near gonad wall, few eggs in centre.

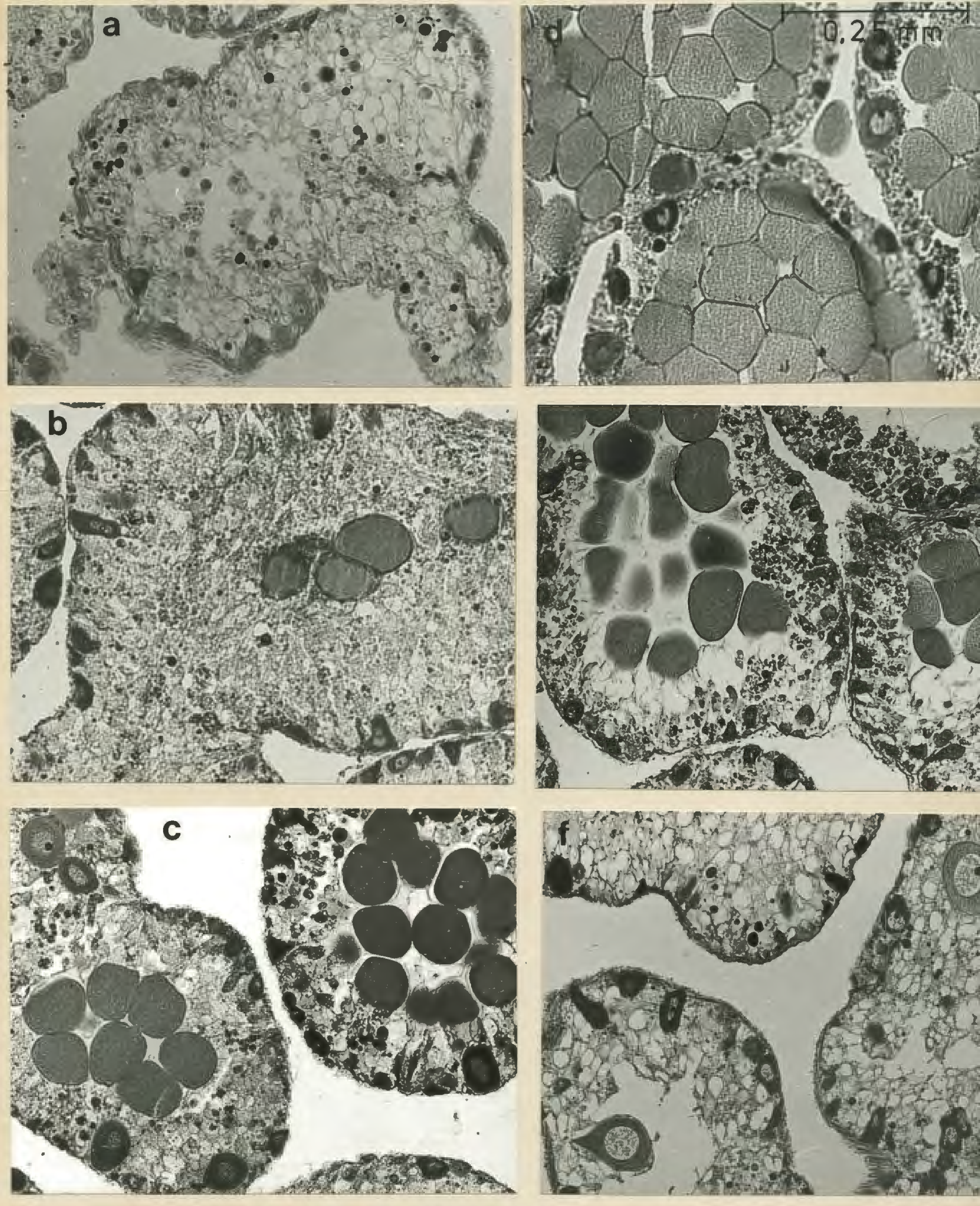
c) Late recovery. Lumen of tubule partly filled with mature eggs.

d) Ripe. Eggs pushed out of shape by tight packing.

e) Spawning. Empty sites of shed ova can be seen.

f) Spent. No ova left. Large gaps in interstitial tissue.

Plate 2



# PART IV

## TEMPERATURE RECORDING IN SHALLOW MARINE ENVIRONMENTS

# TEMPERATURE RECORDING IN SHALLOW MARINE ENVIRONMENTS

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(With 3 text-figures and 1 plate)

(Read November 20, 1974)

## Summary

The shallow inshore water masses around the Cape coast are mixed with regard to temperature and frequently experience marked fluctuations. We needed a device giving a continuous record of *in situ* temperature to investigate its effect on the reproductive behaviour of *Parechinus angulosus* Leske, a common local sea urchin. Commercial temperature recorders were enclosed in watertight housings designed for the purpose and installed on the sea-bed at the study sites.

## Introduction

Two different thermal regimes are found in the region of the Cape Peninsula. The predominantly upwelled cold-water regime of the west coast differs markedly in magnitude and season from the warmer water of False Bay on the east coast. The difference might be even greater were it not for the fact that False Bay is a mixture of warm south coast and cold Atlantic water. This situation has been attributed by Clowes (1950) and Day (1970) to the movement of variably mixed warm Agulhas Current water and cold West Wind Drift water into False Bay, to local upwelling along the western shores of False Bay and to the movement of cold Benguela Current water into the Bay by rounding Cape Point (fig. 1). Despite this, certain animal and plant species survive on both sides of the Peninsula with varying degrees of success. One such species, *Parechinus angulosus* Leske, is found abundantly, though discontinuously, on both coasts and is associated with kelp beds from low water of springs to a depth of about 25 m, the outer margin of the kelp beds, and more where clarity of water permits sufficient light penetration for kelp growth. The broad distribution of the animal provides an opportunity to explore the role of environmental factors in the reproductive ecology of this sea urchin.

The aforementioned temperature regimes, although studied in False Bay by Day (1970), Atkins (1970) and Cram (1970), and on the west coast by Andrews & Cram (1969), Andrews (in press), Andrews & Hutchings (in press) and Andrews & Visser (in press), have never been monitored in detail. Such data as have been available are inadequate for assessing short-term temperature changes. We required a local continuous *in situ* record of inshore perturbations. This sort of information has proved invaluable in assessing and comparing the reproductive cycles of *P. angulosus*, on both coasts. Economic considerations dictated the choice of a relatively inexpensive, simple instrument. Since sea conditions in the southern Cape are frequently turbulent, the device had to be robust and capable of recording for extended periods.

## Instrumental Design

The temperature recorder employed is manufactured by Goerz of Vienna under the trade name 'Thermoscript' (plate 11a). The recorder was originally designed as a general purpose temperature monitor for use in factories and mines.

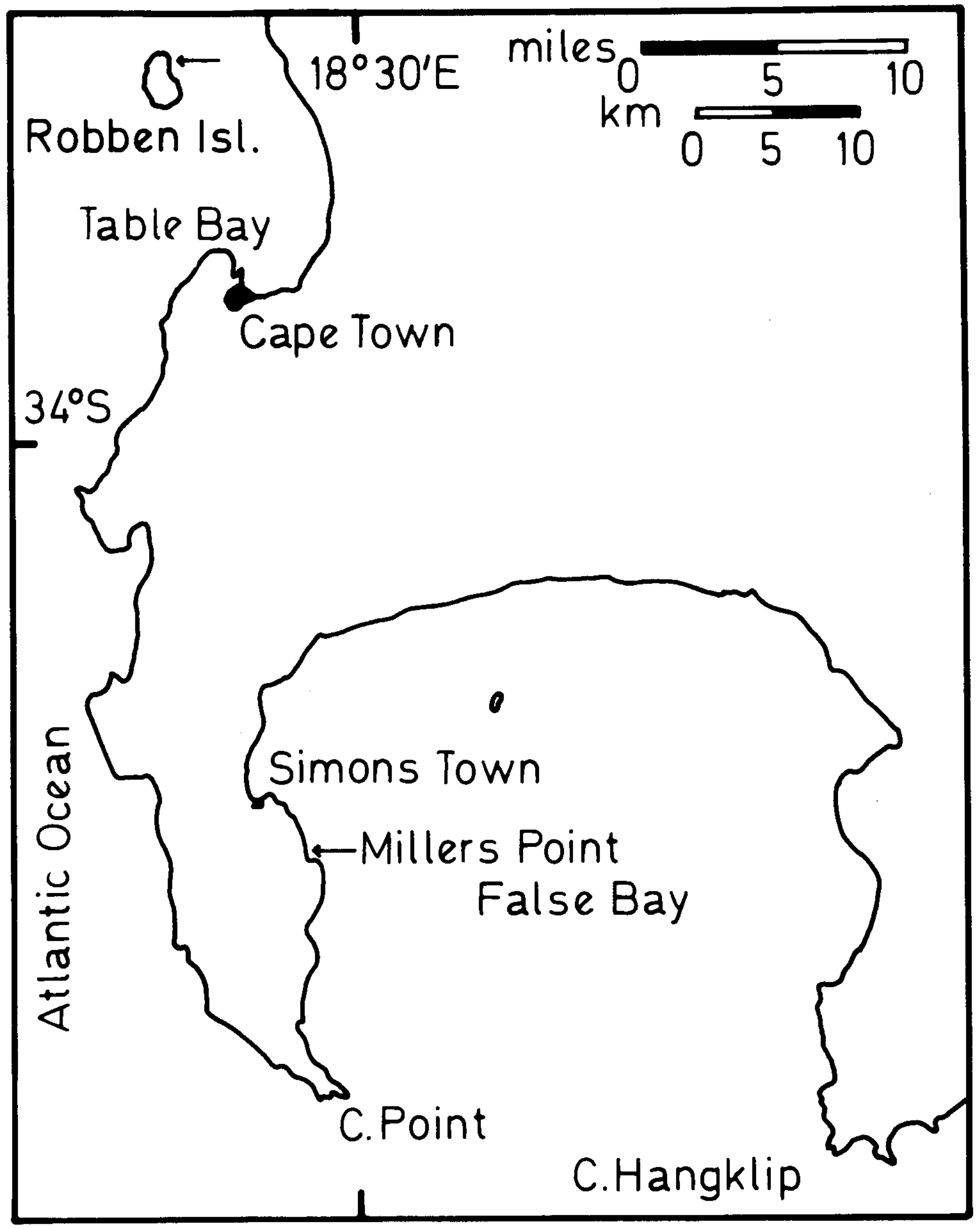

Fig. 1. Map of Cape Peninsula and False Bay, showing location of study sites.

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The instrument is ruggedly made. It is essentially a die-cast metal box (165 mm × 92 mm × 46 mm) containing a Swiss 40-day movement. This mechanism drives a plastic take-up cylinder via interchangeable gears, thereby pulling a pressure-sensitive chart rolled over a polished pressure plate. A fine metal stylus attached to the free arm of a stout bimetal helix produces the temperature record. The gear ratios can be adapted to give recording periods of 7, 15 or 30 days. A visual indication of temperature can be gleaned from an engraved scale on top of the instrument.

An underwater housing for the recorder was manufactured to our design by an engineering firm from stainless steel (specification AISI 316) (plate 11b). The air space between the instrument and the housing was minimized (4 mm), thereby reducing equilibration time. The housing is essentially a matchbox-shaped container fitted with a welded flange on to the open end. The opening is closed by means of a flat stainless steel lid (3,2 mm thick) which possesses 10 equally spaced holes, corresponding to a matching set in the flange. Both flange and lid were machine-ground to ensure flatness, since welding almost invariably introduces some distortion, and fitted with a gasket of smooth neoprene rubber sheeting. The unit is sealed by uniformly tightening ten bolts and nuts (length 29 mm, diameter 6 mm). A sachet of silica gel is enclosed to absorb any condensate which may form under low temperature conditions in the sea. The enclosure was tested for watertightness to a depth of 25 m. A concrete anchor system of low relief was made from two 500 × 500 mm slabs, sandwiched and held by heavy galvanized steel bolts. The upper slab is provided with two stainless steel bolts which fit through registering holes in the lid of the recorder housing. A thin plank of teak (5 mm) cushions the unit against the concrete. The housing bolt heads serve to keep the instrument proud of the wooden plank, thereby ensuring free circulation of the water, which is essential to avoid electrolytic corrosion of the steel. Likewise, dead water must not be trapped between the gasket and the lid. This happened once during the study and led to severe pitting within a month (plate 11b). Care must also be exercised in the selection of sites for installation. We found a flat terrain, reasonably free from boulders, ideal. The slab must in any case lie in direct contact with the sea-bed to prevent eddy currents from upending it during heavy weather. Surface buoys should be avoided, because they attract the attention of the public. In order to maintain data continuity a complete spare instrument is recommended, since servicing in the field is difficult.

## Results

The thermoscript units were installed in two different temperature regimes (Robben Island and Millers Point) and have functioned well for over twelve months. Before installation, the instruments were checked for accuracy and response time. Accuracy of indication was tested with the aid of a pair of certificated mercury thermometers calibrated to 0,1 °C. The recorders departed from 'true' indication by ± 0,15°C, which exceeded the readability of the analogue record of ± 0,1°C. The chart must be read under magnification.

A test to determine the effect of the housing in slowing down the temperature

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response time of the thermorecorder was conducted by us under controlled conditions. Two recorders were allowed to cool in air to a constant temperature (9,0°C) and, after equilibration, warmed up again to 18,0°C (fig. 2). The instruments were transferred quickly.

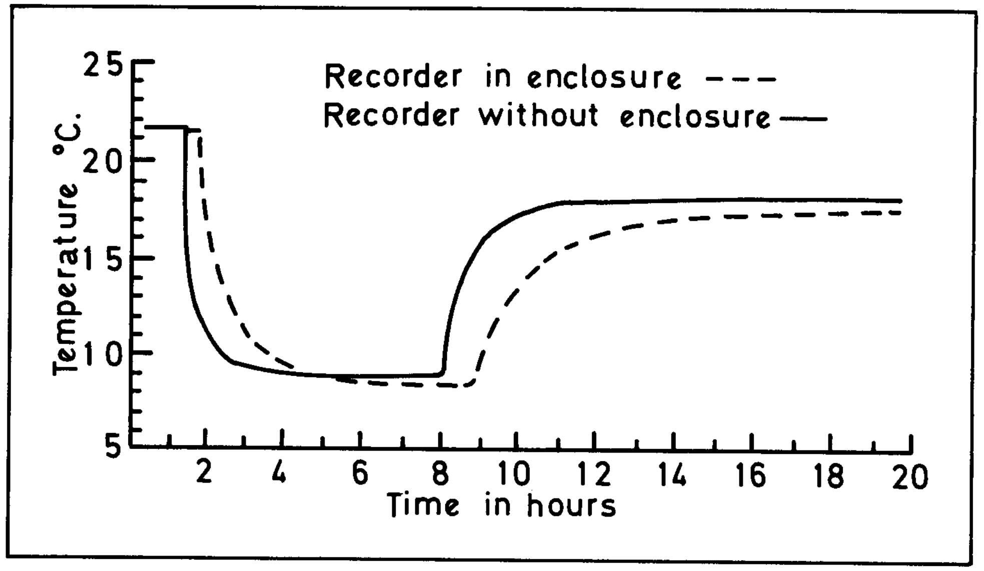

Fig. 2. Comparison of temperature response in time between recorder in watertight enclosure and without enclosure.

The 'open' unit equilibrates to an instantaneous temperature change of 9,0°C within about 15 minutes, which is the period given by the manufacturers for a temperature change of 50% of the total change (Table 1). Placing the instrument in an underwater enclosure extends this equilibration period by a factor of one, despite efforts made to minimize the effect by keeping the enclosed air volume to a minimum and omitting paint finishes on the metal housing. Immersion in the sea undoubtedly reduces this effect through better heat conductance to the recorder. Differences in the end point indication of the two units compared are due to inherent mechanical differences. A further point to note is the asymmetry of the cooling and warming curves. This is due to differences in the thermal conductivity of the environmental media, notably humidity, which was not controlled.

Daily median sea temperatures were extracted from the continuous analogue recording and compared to daily sea surface bucket thermometer readings taken by the municipality. Tests of significance of difference of monthly means indicated that approximately 40% of the values differed at the 0,10 level of significance, demonstrating that single daily measurements are not representative. An example of one use of such continuous data is shown in figure 3 where variation in the temperature regime is readily compared with the cycle of change in gonad mass of the sea urchin *P. angulosus*. The False Bay temperature regime shows marked seasonality, with high summer and low winter temperatures. The curve of the gonad indices follows the one for sea temperatures, although gonad indices lag behind. The pattern of reproduction of male and female gonad indices agrees closely throughout the year; not so, however, the variance. There appear to be two spawnings, one in the autumn and another, less intense, in spring. The temperature data on the Atlantic side, i.e. at Robben Island, possess no clear seasonal pattern. Winter temperatures are rather uniform, with changes less than 1°C for periods of several weeks (fig. 3b). Temperatures are generally lower than in False Bay (compare figs. 3a, b). Rapid perturbations during the summer months are caused by upwelling of cold (9–10°C) water on the one hand and occasional tongues of warm Agulhas water (20–21°C) sweeping into Table Bay. However, the latter probably lacks a sufficiently pronounced regime of temperature changes, persisting for some time, to cause complete spawning. This is very evident in the variance of the female urchins. The marked inequality of the sex ratios is also noteworthy. This difference was found to be significant, but remains unexplained (Millers Point: $\chi^2 = 51{,}733$; $p = 0{,}5\%$; d.f. $= 17$. Robben Island: $\chi^2 = 39{,}915$; $p < 0{,}5\%$; d.f. $= 15$).

Table 1

Comparison of temperature response between enclosed and open recorder.

| *Instrument* | *Total change* °C | | 50% *of total* °C | *Time taken* (*minutes*) | *Mean* (*minutes*) |
|---|---|---|---|---|---|
| Recorder in enclosure . . . | Drop | 12,5 | 6,25 | 40 | 55 |
| | Rise | 8,7 | 4,35 | 70 | |
| Recorder without enclosure . . | Drop | 12,4 | 6,20 | 10 | 15 |
| | Rise | 9,0 | 4,50 | 20 | |

*Continuous temperature recording*

## Discussion

Comparison of temperature information obtained by spot measurements, in contrast to data gained by continuous monitoring, clearly shows that the use of such singular information does not meaningfully reflect the environmental temperature perturbations. The water masses around the Cape coast are thermally heterogeneous, caused largely by strong prevalent winds (Atkins 1970*a*, 1970*b*; Cram 1970) Dietrich (1935) and Clowes (1950) demonstrated that the region between Cape Agulhas and Cape Point receives a mixture of warm water from the Agulhas Current and the cold West Wind Drift. This produces within a few hours changes in water

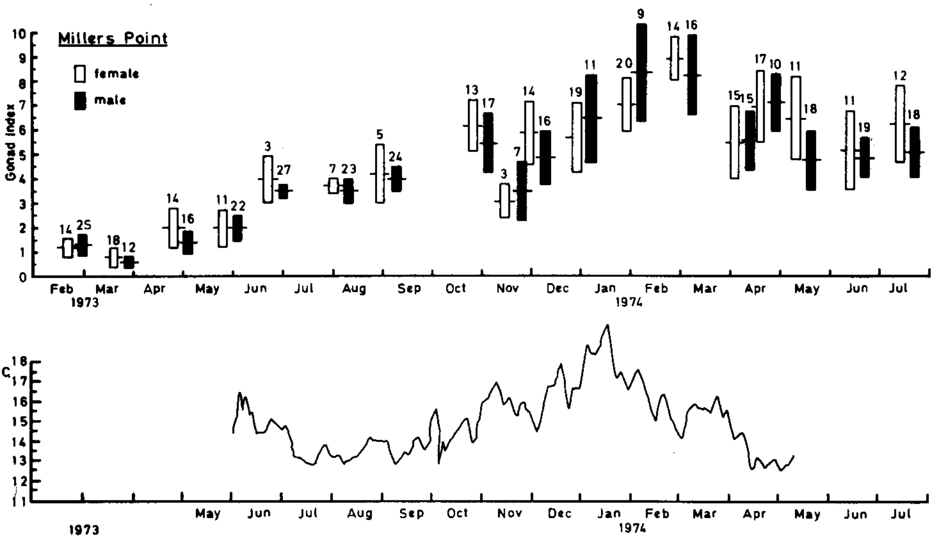

Fig. 3*a*.

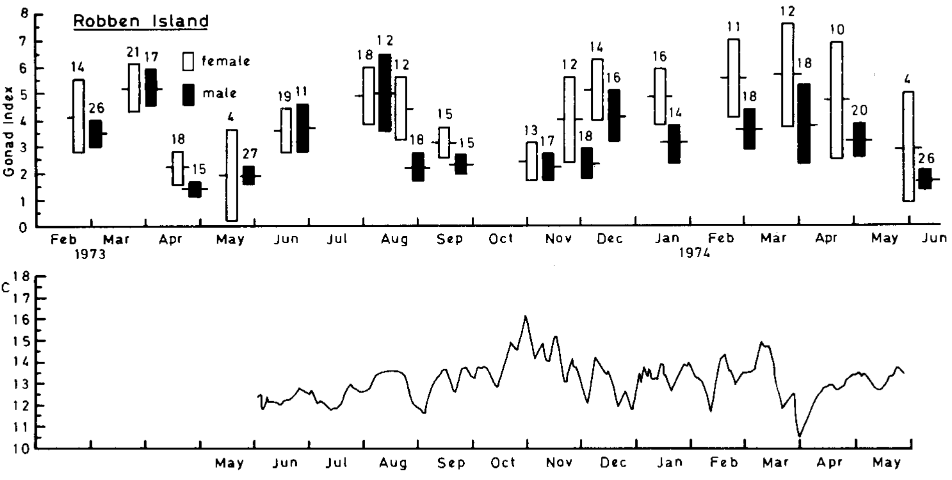

Fig. 3*b*.

Fig. 3a and b. Combined graph of change in Gonad Index of *Parechinus angulosus* in time, showing mean (bar) 95% confidence limits (rectangle) and number of animals collected per sample for both sexes. Fluctuations in sea temperature are drawn as running average of 5 items for both Millers Point and Robben Island.

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temperature, which cannot be detected by manual spot checks. Upwelling on the Atlantic coast has been mentioned; False Bay likewise receives incursions of cold Benguela water as well as streams of warm Agulhas water depending on wind direction, strength and persistence. This justifies the installation and maintenance of recording instruments at points of interest. The instruments, although slow in their response, nevertheless yielded a useful indication of the temperature regime for the period of study. Work currently in progress attempts to elucidate the relationship between sea temperature and spawning behaviour by using the recorded data in other ways as well, by drawing curves of exceedance frequency and persistence of chosen temperature ranges in time (Ainslie 1971).

## Suggested Improvements

With little alteration of the basic design by the manufacturer, the thermoscript could be made more useful. The outer casing of the instrument could be made waterproof and of a non-corrosive material such as stainless steel (AISI 316). The inspection window serves no purpose in the present application and could be eliminated. The most significant improvement would lie in a reduction of the temperature range to which the recorder responds. A full scale range from 5 to 30°C would make the instrument practical for most aquatic environments. Narrowing of response range would increase the trace amplitude and thus make digital evaluation feasible.

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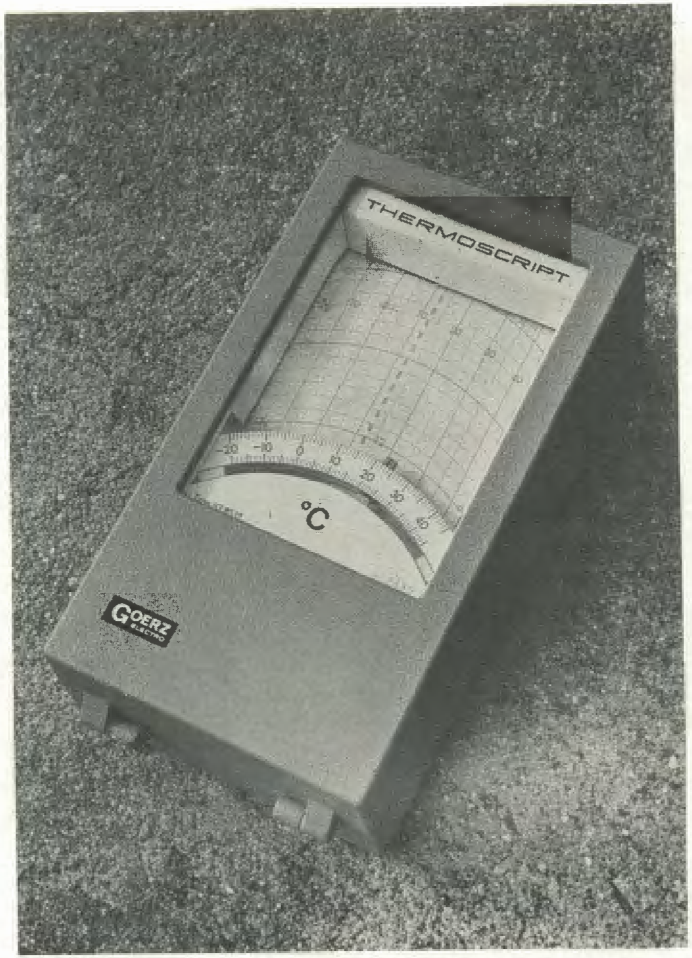

Plate 11a. View of temperature recorder used in experiment.

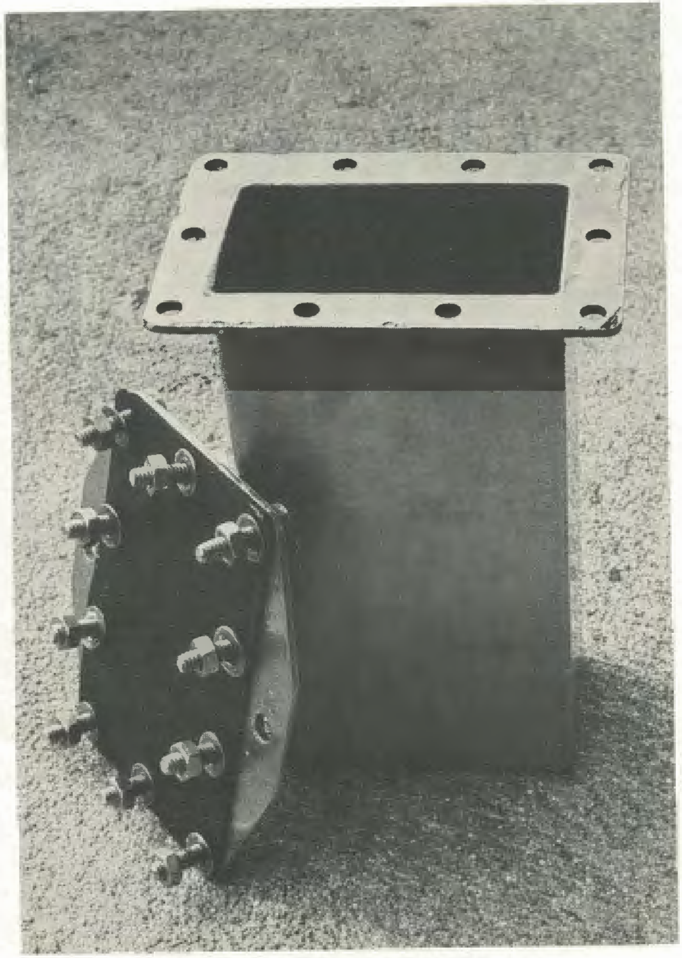

Plate 11b. View of stainless steel housing and lid for 'Thermoscript'.

# PART V

## A DISTANCE MEASURING WHEEL FOR ESTIMATING SUBSTRATE SURFACE AREA

## (WITH A BIOLOGICAL EXAMPLE)

SUMMARY

INTRODUCTION

CONSTRUCTION OF INSTRUMENT

OPERATION IN THE FIELD

CALCULATION OF SURFACE AREA OF SUBSTRATE

RESULTS

DISCUSSION

ACKNOWLEDGEMENTS

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# A DISTANCE-MEASURING WHEEL FOR ESTIMATING SUBSTRATE SURFACE AREA

(With a biological example)

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(With 2 figures)

(Read October 15, 1975)

Summary

A submersible distance-measuring wheel for determining surface area enclosed by benthic survey quadrats is described. The instrument permits the accurate determination of actual substrate surface area on an uneven sea bottom. The device is inexpensive, hand held and battery operated. An example to demonstrate its use is included in the text.

## INTRODUCTION

In order to explore the change in size and the density distribution of the echinoderm *Parechinus angulosus* at two sites near Cape Town, along a gradient of increasing depth, it was necessary to estimate the actual substrate surface area sampled. Observations during preliminary collections using a 0,25 $m^2$ quadrat suggested that such a frame enclosing a flat surface is not strictly comparable to a quadrat lying over a very rocky surface. This situation applies in the areas of study. Since *P. angulosus* avoids sand, unconsolidated substrate is not included in area determinations. In consequence, the surface area enclosed by a particular quadrat may measure less than the minimal plane surface area of 0,25 $m^2$ for a uniform flat surface. Subtidal sampling is further complicated by poor visibility (especially during the summer months) and prevailing turbulent sea conditions, which are particularly obstructive at the shallow depths in which this work is being carried out. This precluded more sophisticated methods. Laxton (1974), for example, used vertical photography to obtain estimates of percentage cover of sedentary organisms along a transect over a coral reef. Marsh (1970), on the other hand, fitted aluminium foil to selected algal crusts and weighed the foil to get surface area values. Both methods were developed for relatively quiet, clear water, such as found over coral reefs, and are thus generally unsuitable for local conditions of poor visibility. Therefore a simple, submersible device to estimate surface area of consolidated substrates was required.

## CONSTRUCTION OF INSTRUMENT

Since the housing for the electrical counter had to be water-tight, a commercial underwater flashlight barrel proved ideal for the basic body of the instrument and

*Trans. roy. Soc. S. Afr.*, 42, Part 2, August, 1976.

required only minor mechanical modifications. The housing employed was the French-made Espadon-Tarzan Aquaflash which is made of an impact-resistant plastic material (Fig. 1). This unit normally accepts three type D 1,5 V dry cells. Only two cells were used in the instrument described, the remaining space being occupied by the electrical digital counter (4-digit electromagnetic type POC-2). The counter is advanced by the closing of a reed switch triggered by a short bar magnet radially cemented into a perspex wheel, which moves over the surface under investigation. A single count records one rotation of the wheel, the circumference of which (200 mm) reflects the distance travelled. Greater precision can be achieved by reducing the wheel radius or by the incorporation of further magnets.

A commercially available magnetic reed switch (30 mm long), sealed in a thin glass tube, was mounted in a suitably machined groove in a perspex disc (dia. 31 mm; thickness 8,5 mm) in such a way that the contacts closed along the axis of the instrument. The switch must be mounted firmly and accurately for reliable operation. For easy removal the perspex disc was provided with a central threaded hole. The equally threaded withdrawal rod does not quite reach the level of the reed switch when screwed home, thus avoiding possible damage. A helical spring, part of the original flashlight, bears against the top of the switch assembly and in turn makes contact with the dry cells. The digital counter was installed last. A good fit of the counter was guaranteed by attaching a perspex disc, slightly smaller than the internal diameter of the housing, to the end of the counter opposite the display, by means of two small countersunk brass screws. A central hole drilled into this disc locates the positive pole of the dry cell in contact with the counter. The wire connections are shown in Fig. 1. The display end is covered by a thin foil of Teflon. This prevents scratching of the perspex lens of the housing during assembly. The original O-ring is retained to make the instrument waterproof. The counter wheel (Fig. 1.4) is provided with a gripping surface on its periphery to prevent slipping during use. A suitable length of nylon reinforced rubber tooth-belt was glued on to the roughened circumference with contact adhesive. The profile height of the rubber belt was taken into consideration in the final dimension of the wheel (dia. 63,9 mm). A nickel-plated brass sleeve, which slips over the barrel of the housing, was secured by means of a knurled nut (Fig. 1.3*a*) and supports the counter wheel on an axle running in bushes. Teflon washers were punched out of sheeting and fitted between the ends of the axle and the supporting bushes. These washers resist the free rotation of the counting wheel. The sleeve assembly was attached to the housing so that the wheel just clears the bottom end of the barrel. Available bar magnets of the dimensions required in the above application are not strong enough to close the reed switch contacts if the intervening gap is in excess of 15 mm, including the thickness of the material.

## OPERATION IN THE FIELD

After a quadrat (0,25 m$^2$) was dropped on to the sea bottom under study, ten regularly spaced traverses of the wheel were run—five each in both co-ordinate directions—over the surface enclosed by the quadrat. The initial and final readings of the digital counter were noted on an underwater slate. Before commencing a set of traverses, the magnet should be in a position just past a contact. The instrument should be operated in a steady fashion, since misses of the counter occur if the wheel rotates too fast. The instrument should be stored with the reed switch contacts open, or else the batteries become drained.

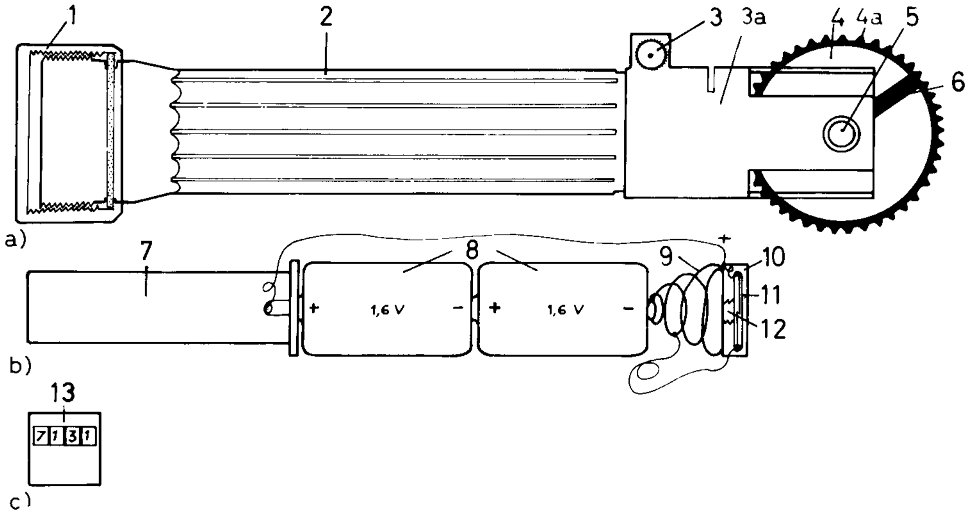

Fig. 1. Distance measuring wheel (and components) for estimating benthic surface area.

*Key to Fig. 1*

(*a*) Lateral view of Distance Measuring Wheel.
(*b*) Electrical components.
(*c*) Frontal aspect of digital counter.
1—perspex lens (threaded); 2—housing of Aquaflash; 3—knurled nut to tighten sleeve; 3(*a*)—nickel-plated sleeve body; 4—perspex counting wheel; 4(*a*)—nylon reinforced tooth belt; 5—axle of wheel; 6—bar magnet cemented into wheel; 7—digital counter; 8—dry cells (D type); 9—helical spring; 10—perspex disc supporting reed switch; 11—reed switch; 12—threaded hole for withdrawing switch assembly; 13—frontal view of digital counter.

## CALCULATION OF SURFACE AREA OF SUBSTRATE

The number of co-ordinate traverses run over the quadrat determines the accuracy of the final result. For our purpose, five traverses each in the x- and y-directions were found to be practical. The total linear distance covered is:

(final reading—initial reading) × circumference of the wheel

(in this instance the circumference of the wheel is 0,20 m). This is divided by ten to obtain the mean size of the quadrat. The result is squared to obtain the area:

$$\text{i.e.}\quad \text{Area} = \left[\frac{(\text{Final reading} - \text{initial reading}) \times 0{,}20}{10}\right]^2 \text{m}^2$$

## RESULTS

During a study on the reproductive ecology of *P. angulosus*, two populations were sampled randomly along replicated subtidal transects, stratified according to depth and distance from shore. A sample of the results is shown in Fig. 2. These data reveal that the size (mean major axis) of urchins generally decreases with depth at both sites (Fig. 2). Furthermore, the urchins at Millers Point are consistently larger than those at Robben Island by 31 % (table not shown). Measurement of surface index according to Dahl (1973), a ratio statistic obtained by dividing the actual surface area by the theoretical area enclosed by a quadrat, yields a significantly higher value (by variance analysis) for the Millers Point site compared with that of Robben Island.

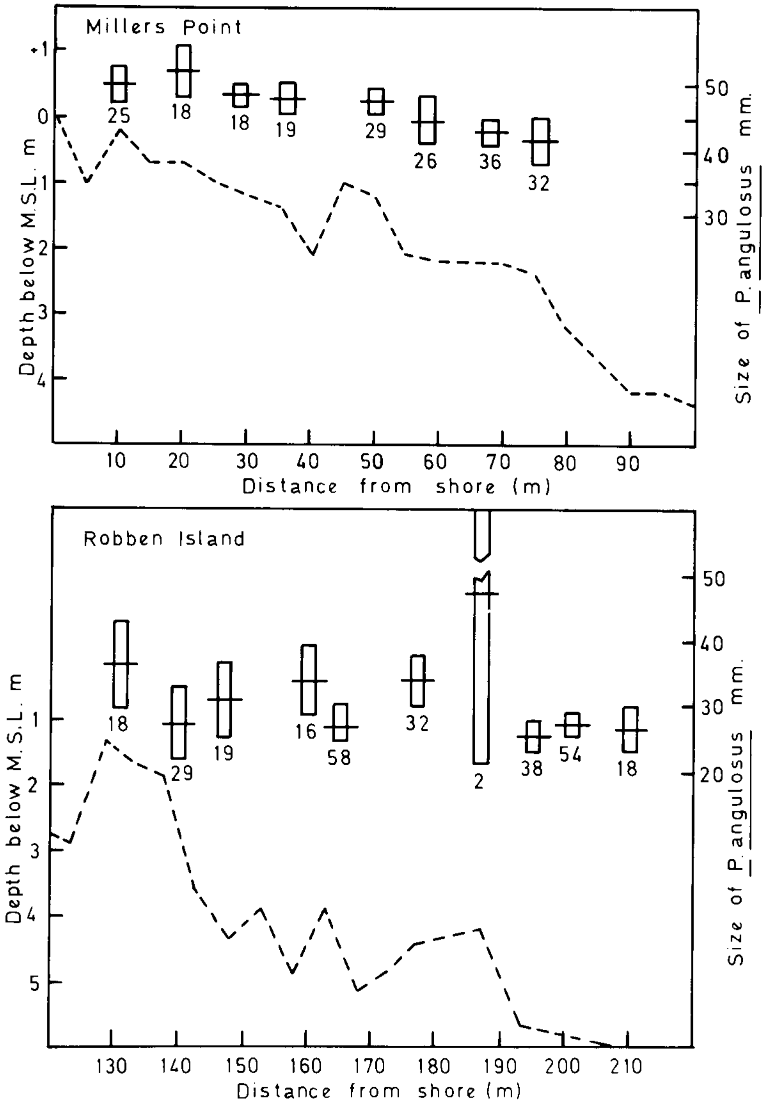

Fig. 2. Variation in mean size (bar) of the sea urchin *Parechinus angulosus* with increasing depth (dashed line) and distance from shore at two localities. The sample size (n) and 95% confidence limits of the mean (rectangle) are also given.

The elucidation of population density of *P. angulosus* entails an estimation of the surface area inhabited by the echinoderm. The actual surface area measurements obtained by the use of the wheel measuring apparatus are shown in Table 1 for the identical sites and stations given in Fig. 2. The actual surface area is shown to deviate from the plane area enclosed within a 0,25 $m^2$ quadrat (minimal theoretical area). The observed population density was corrected on this basis to density per 0,25 $m^2$ plane with one modification. Since the measuring wheel for technical reasons (e.g. skidding) underestimates surface area and in order to avoid the scaling up of densities, which is not permissible, the lowest actual surface value obtained (see Table 1) was made equivalent to the minimum theoretical figure minus the error due to the edge effect (16%), thus 0,21 $m^2$. The uncorrected densities are therefore over-

Table 1

Comparison of actual benthic area and density determination of *Parechinus angulosus* at two localities: Robben Island (*a*) and Millers Point (*b*)

(*a*)

| *Station No.* | *Depth (m) corrected to MSL* | *Actual area surveyed (mm²)* | *Density per quadrat (uncorrected)* | *Density per 0,25m² surface (corrected)* | *SI* | *% Base cover* |
|---|---|---|---|---|---|---|
| 1 | 5,8 | 186 800 | 18 | 18 | 0,75 | 11,2 |
| 2 | 6,1 | 186 720 | 29 | 29 | 0,75 | 11,8 |
| 3 | 7,7 | 291 750 | 19 | 16 | 1,17 | 5,5 |
| 4 | 7,7 | 105 031 | 16 | 16 | 0,42 | 14,9 |
| 5 | 7,0 | 186 720 | 59 | 59 | 0,75 | 20,4 |
| 6 | 5,8 | 205 430 | 32 | 32 | 0,82 | 15,2 |
| 7 | 5,5 | 205 392 | 2 | 2 | 0,82 | 1,7 |
| 8 | 8,5 | 119 034 | 41 | 41 | 0,48 | 18,2 |
| 9 | 8,5 | 134 205 | 54 | 54 | 0,54 | 24,3 |
| 10 | 8,9 | 168 048 | 18 | 18 | 0,67 | 6,2 |

(*b*)

| *Station No.* | *Depth (m) corrected to MSL* | *Actual area surveyed (mm²)* | *Density per quadrat (uncorrected)* | *Density per 0,25 m² surface (corrected)* | *SI* | *% Base cover* |
|---|---|---|---|---|---|---|
| 1 | 1,6 | 91 493 | 25 | 25 | 0,37 | 54,5 |
| 2 | 2,5 | 291 750 | 18 | 15 | 1,17 | 12,5 |
| 3 | 2,5 | 392 579 | 18 | 11 | 1,57 | 8,6 |
| 4 | 4,1 | 392 615 | 20 | 13 | 1,57 | 8,8 |
| 5 | 4,7 | 291 570 | 29 | 25 | 1,17 | 16,4 |
| 6 | 5,8 | 315 557 | 26 | 21 | 1,26 | 13,4 |
| 7 | 6,2 | 315 473 | 36 | 29 | 1,26 | 16,9 |
| 8 | 6,5 | 153 790 | 32 | 32 | 0,62 | 29,8 |

estimates. The area difference can now be used to correct densities. Such information permits a further estimate, namely, the true percentage cover of substrate by urchins:

$$(\% \text{ base cover} = \frac{\text{Total projected surface area of urchins}}{\text{Actual surface area surveyed}} \times 100)$$

which is a measure of occupational intensity of surface area. Percentage base cover by urchins is a little higher at Millers Point than at Robben Island. The corrected population density of both localities does not differ significantly at the 95% confidence limit when subjected to a variance analysis (ANOVA).

## DISCUSSION

Dahl (1973) pointed out that the quantification of surfaces has recently been recognized as a further important parameter in addition to the classical ones of volume and mass in the study of ecosystems. The presence or absence of suitable rocky substrate profoundly influences the extent of kelp beds, with which *P. angulosus* is closely associated, since these plants cannot attach themselves on an unconsolidated sea bottom. Suitability of substrate is of cardinal importance to many sessile and grazing animals. Absence of colonization is usually indicative of disturbing factors such as excessive turbulence or mechanical abrasion by transported material. Personal observations (see also Greenwood 1974) led us to believe that competition for surfaces for attachment is keen.

In approaching the quantification of a complex surface, Dahl (1973) resorts to a mathematical approximation of basic reef forms, which he reduces to simple geometric shapes. The actual surface is then calculated in terms of these three-dimensional elements. The highly irregular nature of the sea bottom at the study sites does not permit application of his approach. The substrate at the sites under investigation consists of eroded granite, scattered variously sized boulders and pockets of sand and pulpy detritus near Millers Point, while the situation near Robben Island presents itself as steeply dipping reefs of slates and shales running roughly parallel to the western island shore. These reefs are eroded on a small scale on their exposed edges, with gullies and channels criss-crossing the general topography. Owing to this fact, the instrument used by us, which is similar to that of Fager *et al.* (1966), who made use of a plastic tracking odometer and a Veeder-Root direct drive revolution counter, seemed the only convenient means of obtaining an estimate of actual benthic surface area. However, while the device of Fager had the estimation of extensive sandy sea bottoms as its underlying idea, our measuring wheel was specially constructed to resolve dissected irregular rocky bottom: hence the small size of the measuring wheel and the need for overall compactness. The two devices are thus clearly different, though similar in principle. Use of a wheel method for determining such surfaces underestimates the real surface area, since it is impossible to move the wheel right up to the edge of the quadrat frame. Hence a narrow band of unmeasured surface remains along the inner margin. This is a constant error, however, amounting to 16,6% in the present study. The final surface area obtained was corrected for this error (Table 1).

This difficulty could be solved by increasing the frame size by the amount in question. Such a modification would, however, result in erroneous information with respect to the number of animals collected within the quadrat.

Several interesting results have been found by the application of the measuring wheel. The apparent population density of a location may differ significantly from the actual one, obtained by correcting for the irregularity of the substrate. A student's t-test was applied to uncorrected and corrected densities at Millers Point and Robben Island and found to show significance at the 95% confidence level for the Millers Point site, but not for Robben Island. We believe that the latter is due to the peculiar rock structure there, leading to considerable underestimations of surface area.

It is thus important to exercise care when attempting to compare benthic environments differing in their structural make-up, since the surface variations may locally be of a scale below the power of resolution of the counting wheel, while being of a scale significant for the organism studied. No single instrument can be ideal for all terrains. Our measurements of surface index (SI) for Millers Point compare interestingly with the theoretical value found by Dahl (1973) for massive and crustose corals about 0,25 m in diameter. Likewise, the average value found by Dahl (1973) for rubble and pavement during a barrier reef transect is of the same order of magnitude. More complete resolution of surface irregularities at Robben Island would raise the percentage base cover difference between the former and Millers Point to the 95% confidence limit, showing up the smaller contribution to base cover made by numerous small animals when compared to that of fewer larger ones.

## ACKNOWLEDGEMENTS

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