# Respiration and ecological energetics of the sea urchin *Parechinus angulosus*

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Respiration rates of *Parechinus angulosus* collected from intertidal pools at Dalebrook, False Bay, were measured in the laboratory at 16 °C using the sealed-vessel method. No respiratory rhythms were detected over three 26-hour runs each involving eight animals of different sizes. Respiration rates, expressed for an animal of standard diameter, increased proportionally to gonad index. Annual production of the intertidal *P. angulosus* population was calculated from the respiration and population data using the P/R regression of Miller, Mann and Scarratt (1971), and was estimated to be about 1200 kJ $m^{-2}$ $year^{-1}$.

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Respirasietempo van *Parechinus angulosus*, versamel van tussengetypoele te Dalebrook, Falsbaai, is in die laboratorium teen 16 °C in 'n geslote sisteem gemeet. Geen respirasieritmes is ontdek nie, toe agt diere van verskillende groottes oor 'n tydperk van 26 uur drie keer getoets is. Respirasietempo vir 'n dier van standaarddeursnit, het eweredig met gonade-indeks toegeneem. Die produksie van die tussengety-populasie van *P. angulosus* is op grond van die gegewens vir respirasie en populasie bereken. Volgens die P/R regressie van Miller, Mann en Scarratt (1971) word die jaarlikse produksie op ongeveer 1200 kJ $m^{-2}$ $jaar^{-1}$ geskat.

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The sea urchin, *Parechinus angulosus* is an important component of kelp bed communities of the west coast of southern Africa, where it feeds on detached kelp and other seaweed debris (Greenwood 1980, Field, Jarman, Dieckman, Griffiths, Velimirov & Zoutendyk 1977). It is also predominant along the east coast to Zululand where it occurs subtidally as well as densely in intertidal pools.

Because of its ecological importance, a study of the population dynamics and energetics of *P. angulosus* was undertaken by Greenwood (1980). The present paper aims to solve two problems concerning respiration which were raised by Greenwood's work. The first is that *P. angulosus* respired slightly faster at night than by day, but the differences were not statistically significant and it is possible that the experiments may not have been performed at the time of maximum nocturnal respiration. If large differences exist, these would affect population energy budget calculations. Lewis (1964), working on the tropical sea urchin *Diadema antillarum philippi*, discovered that its feeding activity was most intense in the early evening, and Dix (1970) observed that the urchin *Evechinus chloroticus* moved more at night than during the day. Both these phenomena could lead to increased metabolic rates at night.

The second problem involves the relationship between respiration rate and maturity of the gonads. During the reproductive cycles of sea urchins, the gonads may increase greatly in mass within a few months, while the test and other organs show little change.

## Materials and Methods

Experimental animals were collected from intertidal pools and gullies at Dalebrook, False Bay (34°7,6′S, 18°27,2′E), and were transported to the laboratory where they were acclimatized in running sea water for four to five hours. Fronds of the kelp *Ecklonia maxima* were always available as food.

All experiments were performed at 16 °C to eliminate temperature as a source of variation. This temperature was chosen as it is midway between the mean winter surface temperature of 14 °C and the mean summer surface temperature of 18 °C in False Bay (Atkins 1970). The sealed-vessel method was employed to measure respiration rates. Each urchin was gently placed in a wide-mouth bottle which was sealed under water and left for two hours. The size of the container was appropriate for the oxygen concentration to fall 10 – 20% during an experiment. A variety of bottle sizes was used to accommodate urchins 5 – 53 mm in diameter and more than one individual was used per jar for animals less than 15 mm in diameter. Two containers without urchins served as controls for each experimental run. After two hours a 250-ml water sample was siphoned from each container and the oxygen concentration measured by the Winkler method (Strickland & Parsons 1972). Oxygen consumption per animal was calculated from the difference between experimental and control vessels.

When investigating diurnal respiratory rhythms, the rate of oxygen consumption was measured for two hours every four hours from 12h00 until 14h00 the following day. Between each reading the animals were returned to the tanks where kelp fronds were provided as food. The entire experiment was repeated three times with eight urchins of different sizes in each run. Large windows on the north side of the aquarium provided natural illumination.

After each experiment the maximum oral test diameter, wet mass and dry mass of each urchin was recorded, while in the second (gonad state) experiment, the gonad index (ratio of gonad dry mass to urchin dry mass × 100) was also noted.

To calculate the relationship between dry mass and ash-free dry mass, eight urchins were ashed in a muffle furnace for 10 h at 480 °C, the temperature being chosen to prevent loss of $CaCo_3$ and consequent underestimation of the ash content (Paine 1964). All regression equations were calculated on a programmable calculator (H.P. 65) using the least squares method. Statistical tests follow Zar (1974).

The response surface technique (Box & Wilson 1951) was used to analyse the interrelationships between respiration rate, body size and gonad index. A multiple regression equation was derived using the computer program 'STEPREG 1' (STATJOB, Madison Academic Computing Center, USA). The independent variables were diameter and gonad index, with quadratic and cubic terms being introduced to describe the curvi-linear relationship. Interaction terms between the two independent variables were necessary to obtain a good fit to the data. A 3rd-order response surface was generated from the multiple regression equation using the computer program 'GRAPHUNCTION' written for this purpose.

## Results

### Respiratory rhythms

The following regression equations were obtained from data on the diameter (in mm), wet mass (WM), dry mass (DM), and ash-free dry mass (AFDM) of the experimental urchins, all expressed in grams:

$$\log(\mathrm{DM}) = -0{,}3864 + 0{,}9410.\log(\mathrm{WM}) \quad (r^2 = 0{,}9989;\ n = 66) \qquad \ldots(1)$$

$$\log(\mathrm{AFDM}) = -0{,}7228 + 0{,}9068.\log(\mathrm{DM}) \quad (r^2 = 0{,}9940;\ n = 8) \qquad \ldots(2)$$

$$\log(\mathrm{DM}) = -3{,}5229 + 2{,}8048.\log(\mathrm{Diam}) \quad (r^2 = 0{,}9930;\ n = 66) \qquad \ldots(3)$$

In view of the close correlation between dry mass and ash-free dry mass (equation 2) respiration results were expressed in terms of dry mass or diameter, thus simplifying the procedure in each experiment.

Figure 1 presents respiration rate results for animals of different sizes. Table 1 shows that there were no significant differences in slopes or intercepts of the regressions comparing day and night respiration.

**Table 1** Relationship between respiration rate, $V_{O_2}$ (µl $O_2h^{-1}$) and dry mass (g), for corresponding two-hour periods of day and night. Each regression combines the results of all three runs, and $t_s$-values comparing the slopes and intercepts are given (Zar 1974). The regressions have the form: log ($V_{O_2}$) = log a + b.log (DM). The coefficient of variation, $r^2$, is given; $n$ = 20; $t_{(0,05)}$ = 2,028

| Time | log a | b | $r^2$ | $t_s$-value for slope | $t_s$-value for intercept |
|---|---|---|---|---|---|
| 12h00 – 14h00 | 1,7789 | 0,7725 | 0,9075 | 0,5333 (ns) | 0,1959 (ns) |
| 00h00 – 02h00 | 1,8222 | 0,7241 | 0,9154 | | |
| 16h00 – 18h00 | 2,000 | 0,6133 | 0,9450 | 0,4250 (ns) | 0,4575 (ns) |
| 04h00 – 06h00 | 2,0605 | 0,5448 | 0,8543 | | |
| 20h00 – 22h00 | 1,9543 | 0,6115 | 0,9039 | 0,3125 (ns) | 0,1466 (ns) |
| 08h00 – 10h00 | 1,9777 | 0,5936 | 0,8724 | | |

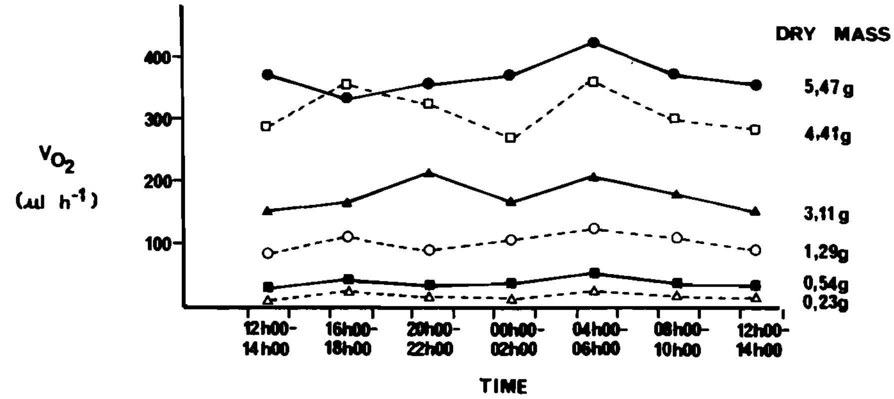

**Fig 1** Respiration rate of urchins of different sizes measured for two hours every four hours over a 26-hour period at 16 °C. Results of two other runs were similar.

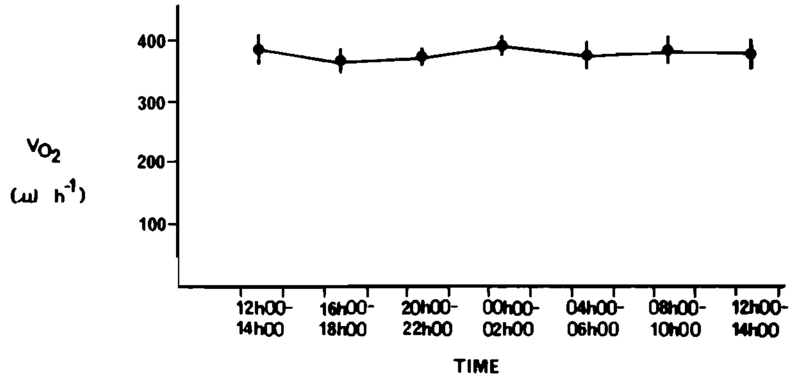

**Fig 2** Mean respiration rates of all experimental animals over 26 hours (±1 SE). Rates are for standard 9,91 g (DM) animals and were measured over two-hour periods.

To improve use of the data, all respiration results were also transformed to that of a standard animal of mean size in the experiments (9,91 g dry mass), using the relationship:

$$V_{O_2}(9{,}91\text{g}) = \frac{(9{,}91)^b}{(\text{DM})} V_{O_2}(\text{exp}) \qquad \ldots (4)$$

(Newell *et al.* 1977)

where b = slope of regression comparing log $V_{O_2}$ with log dry mass for each 2-h period

DM = dry mass (g) of experimental animal

$V_{O_2}$(exp) = respiration rate (µl $O_2h^{-1}$) of each experimental animal.

The results of transforming all data in this way are shown in Figure 2, demonstrating again that the slight fluctuations between day and night respiratory rate lie well within the bounds of experimental error.

## Effect of gonad size

Figure 3 shows the relationship between respiration rate and body mass separately for sexually mature and immature urchins, the arbitrary division being taken at 17 mm diameter. The regression equations fitted to the lines are given in Table 2. In all cases respiration rates increase faster with mass in immature urchins.

To ascertain whether the differences were purely due to size or to the state of gonad development, 20 urchins in the size-class 43 – 48 mm diameter were selected for another respiration experiment, because the gonad index of this class had been found to display a wide range of values. To eliminate the effect of size in investigating the influence of gonad state, respiration rates of the 20 urchins were expressed in terms of the mean diameter of

**Table 2** Regression equations relating log $V_{O_2}$ (µl $O_2h^{-1}$) to log dry mass for sexually mature and immature animals (<17mm diameter). Equations have the form: log ($V_{O_2}$) = log a + b.log (DM)

| | Sexually mature | | | | Sexually immature | | | |
|---|---|---|---|---|---|---|---|---|
| Date | log a | b | $r^2$ | *n* | log a | b | $r^2$ | *n* |
| 1978.5.23 | 2,1438 | 0,5107 | 0,9663 | 6 | 1,9297 | 0,9333 | 0,9699 | 7 |
| 1978.5.29 | 1,9121 | 0,6454 | 0,9559 | 5 | 1,8860 | 0,7421 | 0,9609 | 5 |
| 1978.6.5 | 2,0324 | 0,6632 | 0,9719 | 7 | 2,0121 | 1,0077 | 0,9990 | 3 |

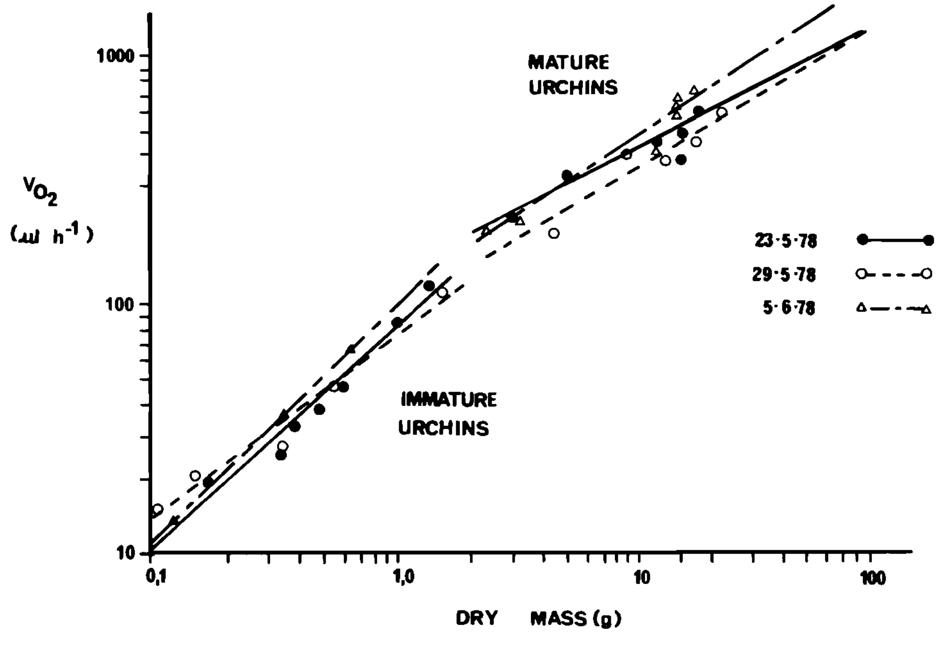

**Fig 3** Respiration rates of sexually mature (>17 mm diameter) and immature urchins plotted against dry mass on logarithmic scales. Equations for the regression lines are given in Table 2.

this size-class (45,25 mm) using equation 5.

$$V_{O_2}(45{,}25\text{mm}) = \frac{(45{,}25)^b}{(\text{Diam.})} V_{O_2}(\text{exp}) \qquad \ldots (5)$$

where b = slope of regression comparing log $V_{O_2}$ with log diameter for animals over the whole size range (b = 2,0914)

Diam. = diameter (mm) of experimental animal.

$V_{O_2}$(exp) = respiration rate (μl $O_2h^{-1}$) of each experimental animal.

These results, plotted against increasing gonad index, are displayed in Figure 4. Although only 45% of the variation in the data is accounted for by this regression against gonad index ($r^2 = 0{,}45$) there is nevertheless a clear increase in respiration rate with gonad index.

Respiration rates have also been tabulated after dividing the urchins arbitrarily into two groups, one of low gonad index (0 – 3,9) and the other of high gonad index (4,0 – 7,9). The results have been expressed in three different ways in Table 3. All columns show statistically significant differences ($p < 0{,}01$) between the respiration rates of low and high gonad index groups, but the results expressed in μl $O_2$ animal$^{-1}$h$^{-1}$ give the lowest *t*-value.

## Combined effects

The following equation was obtained by stepwise multiple regression of the experimental data:

$$\text{Resp.} = -4{,}908 + 0{,}368\ \text{Diam.}^2 - 0{,}004\ \text{Diam.}^3 - 2{,}299\ \text{GI}^2 + 0{,}466\ (\text{Diam.x GI}^2) \qquad \ldots (6)$$

($n = 52$, $r^2 = 0{,}925$)

where Diam. = Diameter (mm)

GI = Gonad Index

Resp. = Respiration rate (μl $O_2h^{-1}$)

This equation accounts for 92,5% of the variation in the data, the remainder being ascribed to other variables not considered, experimental error, or natural variability.

Figure 5 presents the curved response surface generated using equation (6) in three dimensions, showing the relationships of respiration rate to diameter and gonad index simultaneously. The response surface is a ridge rising to show fastest respiration rates in the region of greatest diameter and gonad index. The shaded area indicates the region where no data were obtained and where extrapolation of the surface is therefore invalid (i.e. no small urchins <30-mm diameter were found with gonad index greater than 3,5). Extrapolations into this area were excluded from the response surface by using a 'cut-off' command. This example emphasizes the need for caution in not using regression equations to extrapolate beyond the limits of the data. By following section lines on the response surface, it can be seen that respiration rate varies with gonad index in a different manner for animals of medium diameter than those of large diameter which show a very steep increase in respiration rate with gonad index.

**Table 3** The rate of oxygen consumption of urchins between 43 and 48 mm diameter, expressed in three different ways. The t-test statistic ($t_s$) for comparing the respiration rates of urchins of low gonad index with those of a high gonad index are indicated below each column (Zar 1974)

| Diameter | Gonad Index | $V_{O_2}$(μl h$^{-1}$) | $Q_{O_2}$(μl(g WM)$^{-1}$h$^{-1}$) | $Q_{O_2}$(μl(g DM)$^{-1}$h$^{-1}$) |
|---|---|---|---|---|
| 43 | 1,71 | 413,80 | 9,79 | 28,89 |
| 46 | 1,78 | 365,50 | 8,30 | 24,49 |
| 46 | 1,86 | 405,95 | 8,62 | 27,43 |
| 45 | 2,20 | 337,15 | 6,82 | 21,54 |
| 48 | 2,72 | 524,25 | 9,87 | 30,22 |
| 48 | 3,18 | 471,35 | 9,28 | 29,13 |
| 43 | 3,41 | 627,85 | 17,90 | 53,82 |
| 44 | 3,53 | 424,65 | 10,12 | 27,47 |
| 44 | 3,58 | 465,10 | 10,10 | 30,21 |
| 45 | 3,69 | 466,35 | 12,30 | 37,71 |
| 45 | 4,31 | 398,65 | 11,33 | 31,82 |
| 43 | 4,34 | 506,70 | 14,18 | 40,44 |
| 45 | 4,35 | 472,35 | 12,83 | 40,01 |
| 47 | 4,49 | 661,80 | 13,86 | 44,87 |
| 45 | 4,88 | 694,00 | 15,45 | 46,92 |
| 45 | 5,39 | 604,95 | 14,49 | 42,73 |
| 48 | 5,48 | 733,35 | 14,28 | 44,01 |
| 48 | 5,81 | 756,65 | 16,40 | 48,90 |
| 43 | 7,16 | 460,25 | 13,62 | 40,30 |
| 44 | 7,23 | 611,65 | 15,05 | 42,91 |
| $t_{0,01} = 2{,}878$ | | $t_s = 2{,}96$ | $t_s = 3{,}64$ | $t_s = 3{,}47$ |

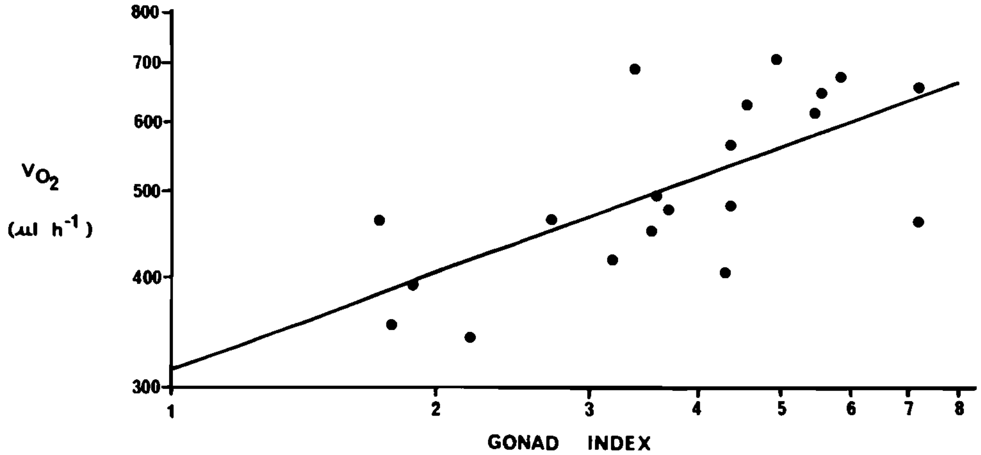

**Fig 4** Log-log regression of respiration rate against gonad index for animals of 43 – 48 mm diameter. Data are for a standard animal (45,25 mm diameter). The regression line has the equation: log ($V_{O_2}$) = 2,5014 + 0,3526. log(GI) ($r^2 = 0{,}45$; $n = 20$)

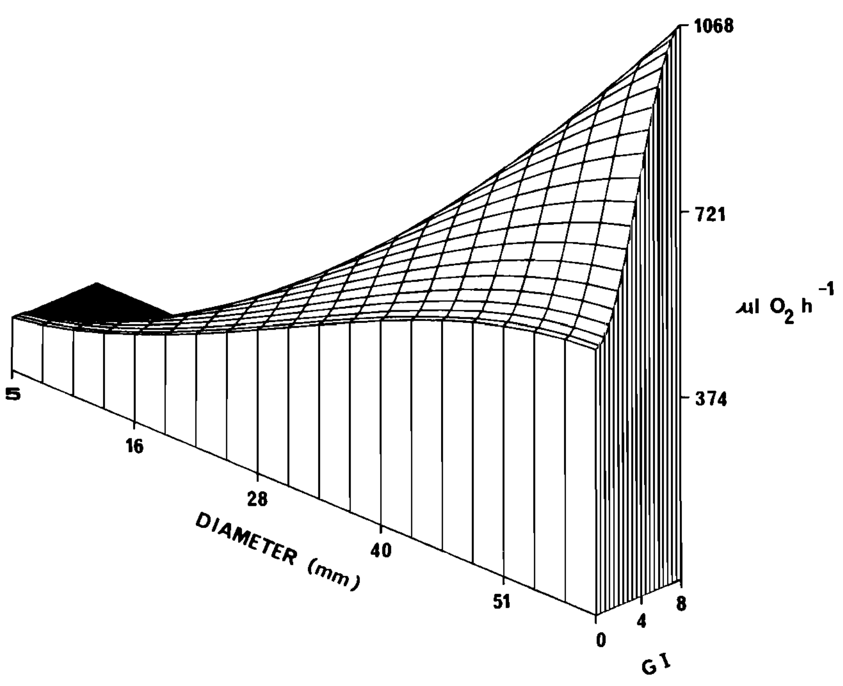

**Fig 5** Three-dimensional response surface showing simultaneously the relationship between respiration rate, diameter and gonad index. The shaded area indicates a region of no data, into which the model is not extrapolated (see text).

## Discussion

Our results show no statistically significant differences between day time and night time respiration rates and Figure 1 gives little indication of any diurnal respiratory rhythm. These laboratory results therefore refute the suggestion of higher nocturnal respiration rates in *Parechinus angulosus* given by the *in situ* experiments of Greenwood (1974, 1980). It is possible that nocturnal activity was inhibited in the laboratory, but the experimental containers were very similar to those used in the field by Greenwood and the delay in transport to the laboratory and amount of handling were kept to a minimum. Lewis (1968), Ulbricht & Pritchard (1972) and Miller & Mann (1973), working on various urchin species, also found no significant difference between day and night respiration rates. Thus it appears that population energy budgets based on daytime respiration measurements need not be disputed on these grounds.

It has been shown that the state of *P. angulosus* gonad development influences the respiration rate measured. The effect of gonad index is least clear when oxygen uptake is expressed as $V_{O_2}$ ($\mu$l $O_2$ animal$^{-1}$h$^{-1}$) and most marked when expressed as $Q_{O_2}$ in terms of $\mu$l $O_2$g$^{-1}$h$^{-1}$. McPherson (1968) reported that there was no significant correlation between oxygen uptake and gonad index in *Eucidaris tribuloides*. His conclusion might have been different if he had expressed respiration rates as $Q_{O_2}$ rather than $V_{O_2}$.

Giese, Farmanfarmaian, Hilden & Doezema (1966), Bellman & Giese (1974), and Webster & Giese (1975) studied several species of sea urchin and found no relationship between oxygen consumption and reproductive condition. All their results were expressed in terms of wet mass of urchin which does not change during the reproductive cycle because spent gonads are replaced by perivisceral fluid of similar density (Giese 1967). This may account for the lack of correlation between respiration rate and reproductive condition in their results, but our results show significant differences even when expressed in terms of wet mass (Table 3).

McNeill & Lawton (1970) and Miller, Mann & Scarrat (1971) have shown that it is possible to estimate population production from population respiration, although the confidence limits of such estimates are wide. To this end the annual population respiration of intertidal *P. angulosus* at Dalebrook was estimated.

The area covered by pools was calculated from a series of intersecting transects on the shore, and twelve 0,0625-m$^2$ quadrats placed randomly in intertidal pools were used to estimate the density and size-frequency distribution of the *P. angulosus* population. The total intertidal study area of 3400 m$^2$ included 723 m$^2$ covered by rock pools. Table 4 shows the results of the population estimates. Standing stock was converted to energy units using a conversion factor of 6,06 kJ g$^{-1}$ (dry mass) for *P. angulosus* (Field, Griffiths, Griffiths, Jarman, Zoutendyk, Velimirov & Bowes 1980). Respiration rates were converted to metabolic heat loss assuming an oxycalorific coefficient of 20,15 J (ml $O_2$)$^{-1}$ (Grodzinski, Klekowski & Duncan 1975) and using the mean respiration rate for each size-class calculated from all the data. These calculations are based on a temperature of 16 °C.

The annual population production ($P_{\text{ann}}$) of *P. angulosus* was estimated using the general relationship:

$$P_{\text{ann}} = 0{,}6440 \times R_{\text{ann}}^{0{,}8517}$$

(Miller, Mann & Scarratt 1971)

where $R_{\text{ann}}$ is the total annual population respiration in kJ m$^{-2}$year$^{-1}$. By substituting the annual population respiration estimate from Table 4 (6812 kJ m$^{-2}$year$^{-1}$), annual population production is estimated to be 1185 kJ m$^{-2}$year$^{-1}$.

**Table 4** Population data for *Parechinus angulosus* in intertidal pools at Dalebrook

| Size class Diameter (mm) | Mean no. urchins $m^{-2}$ | Standing stock (biomass) g $m^{-2}$ (DM) | Standing stock kJ $m^{-2}$ | Population respiration kJ $m^{-2}$ $year^{-1}$ |
|---|---|---|---|---|
| 4,50 – 17,49 | 18,3 | 4,39 | 26,60 | 93,71 |
| 17,50 – 30,49 | 11,6 | 30,62 | 185,56 | 423,85 |
| 30,50 – 43,49 | 47,1 | 379,15 | 2 297,65 | 3 601,15 |
| 43,50 – 56,49 | 27,2 | 392,22 | 2 376,85 | 2 693,96 |
| Total | 104,2 | 806,38 | 4 886,66 | 6 812,67 |

Table 5 shows that the annual $P/\overline{B}$ ratio calculated for the intertidal population is only 0,24, suggesting a very slow turnover rate of intertidal urchins. From Table 5 it can be seen that the standing stock of intertidal urchins is twice that of the subtidal population in False Bay studied by Greenwood (1980), while the density of numbers is comparable. Thus it appears that the mean size of intertidal urchins is much larger than that of subtidal ones, a suggestion borne out by the size-frequency distribution (Table 4) which shows very few small individuals. The Robben Island population, in contrast, has far more small urchins, fewer large ones and a higher $P/\overline{B}$ ratio (Table 5, Greenwood 1980). The slow turnover rate therefore appears to be the result of the population being dominated by large, old and slow-growing individuals.

**Table 5** Comparison of measurements of subtidal populations (Robben Island and Oatlands Point, False Bay — Greenwood 1980) with the intertidal population at Dalebrook. Asterisks indicate estimates calculated from population respiration

| | Numbers (Nos. $m^{-2}$) | Standing stock (kJ $m^{-2}$) | Production (kJ $m^{-2}$ $year^{-1}$) | P/B (annual) |
|---|---|---|---|---|
| Robben Island | 138 | 1 810 | 1 880 | 1,04 |
| False Bay | 145 | 2 490 | 1 470 | 0,59 |
| Dalebrook pools | 104 | 4 890 | 1 190* | 0,24* |

Recruitment is probably reduced by the grazing activity of the dense adult population which keeps intertidal pools noticeably stripped of algae but, like limpets (Branch 1975), probably also removes newly-settled young. Mortality rates of intertidal urchins are likely to be very low due to the lack of predation by the rock lobster *Jasus lalandii* which is common at Robben Island, rare at Oatland Point (False Bay) and absent intertidally. In addition, rock fish such as Roman (*Chrysoblephus laticeps*) which feed on urchins subtidally in False Bay, probably have little opportunity to feed in intertidal pools. Therefore we suggest that the productivity of sea urchins is linked to predatory pressure on the population and its age-structure, heavy predation being associated with a young, fast-growing and productive population and vice versa.

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