THE POPULATION DYNAMICS AND ECOLOGICAL ENERGETICS OF *Parechinus angulosus* AT ROBBEN ISLAND AND IN FALSE BAY SOUTH AFRICA

BY

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TO MY PARENTS

for more than encouragement

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POPULATION STRUCTURE, DYNAMICS AND PRODUCTION

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INTRODUCTION

GENERAL

The need for a quantitative approach to ecology, and the importance of the sea urchin Parechinus angulosus (Leske) in the sublittoral of Cape waters, are the underlying themes to the research which has led to this thesis.

The Cape Peninsula (South Africa) is a land mass 6,5-11,5 Km wide which separates two marine systems with different temperature conditions, the cold west coast and the warmer False Bay area. This afforded a unique opportunity to investigate the effect of temperature difference on Parechinus angulosus around the Peninsula. In this work, some aspects of the dynamic ecology of a population of P. angulosus at Robben Island (west coast) and one at Oatland Point (False Bay), have been investigated in order to asses their rôle in the kelp bed community quantitatively.

The methods of ecological energetics developed by the International Biological program (IBP) to quantify the energy budget of a population have been used. The balanced energy equation given by Ricker (1968) is as follows:

$$C = P + R + F + U$$

where $P = Pg + Pr$

C = Consumption - the energy content of food consumed by the population.

P = Production - the total energy produced by the population as body growth and gonad growth

Pg = the energy content added to the population due to body growth or recruitment (settlement of young or immigration)

Pr = energy content of gametes which are discharged during spawning.

R = Respiration - the energy lost as heat through metabolism.

F = Egestion - energy lost as faeces.

U = Excreta - energy lost as dissolved organic matter.

Assimilation can be calculated by manipulation of the terms in the balanced energy equation :

$$P + R + U = C - F = A$$

A = Assimilation - the energy absorbed through the alimentary canel, also called physiologically useful energy.

Each component of the equation may be expressed as Kilocalories per unit area per annum.

The volume of work has precluded the determination of the whole energy budget. Work has therefore been concentrated on two terms in the balanced equation, production (P = Pg (body growth) + Pr (gonad growth) (see Fricke, 1974) and Respiration (R)). A short section on consumption (C) has also been included.

The summation of Production and Respiration gives a measure of assimilation or energy flow through the population, if one ignores the energy lost as excreta (U), as has often been done in the past (Hughes, 1970; Miller and Mann 1973).

This thesis is presented in three main sections. Each section is treated as a separate entity. The first deals with population structure, dynamics and production. The second reports on population respiration and the third section touches briefly on consumption. Conclusions are drawn in each section and a resumé of the work concludes the thesis.

This work is being followed up by other researchers tackling other populations in the system to build up a model of structure and functioning of the kelp bed community and ultimately to trace the fate of the primary production of the kelp plants.

The close association of sea urchins with kelp in temperate seas appears to be a world wide one of substantial ecological importance (Swan, 1961; Leighton, Jones and North, 1966; Ebert, 1968; Miller and Mann, 1973). This is certainly true of the urchin-kelp bed relationship in the seaweed zone on the west and south-western coasts of Southern Africa

The abundance and obvious importance of regular echinoids in the sublittoral of the Northern Hemisphere has resulted in intensive study into the dynamic ecology of several species (Fuji, 1962, 1967; Ebert, 1968; Miller and Mann, 1973). That echinoids can destroy large areas of vegetation in the sublittoral has been well documented (Kitching and Ebling, 1961; Leighton <u>et al</u>, 1966; Kain and Jones, 1966; Jones and Kain, 1967; Pearse, pers.comm.). The importance of urchins as a food source of economically important species has been reported by Miller, Mann and Scarratt, 1971; Himmelman and Steele, 1971; and Newman and Pollock, 1974; while Fuji (1962, 1967) reports on their importance as a food of man.

Parechinus angulosus (Leske) is the most widespread Southern African echinoid (Day, 1969) and is believed to be the dominant herbivore in the kelp zone of the western Cape. Despite its wide distribution and obvious importance in the sublittoral of the Cape Peninsula, little is known of its biology. Apart from the larval studies of Cram (1971) and the work of Fricke (1974) on the reproductive biology, done concurrently with the present work, no other ecological studies have been done on *P. angulosus*.

THE STUDY AREAS AND THEIR HYDROLOGY

Robben Island

Robben Island (33° 48' S, 18° 22' E) lies 7 km from Cape Town opposite Table Bay. (fig. 1.1.) The Island was chosen as the study site on the west coast largely because it is a restricted area and its inaccessibility allows little disturbance from the general public.

The temperature conditions along the west coast of Southern Africa are largely influenced by the cold Benguela Current System flowing northwards (Andrews and Cram, 1969; Bang, 1973 b).

The waters in the region of the Cape Peninsula and Robben Island are therefore affected by the cold nutrient rich Antarctic Central Water (about 9°C) brought to the surface by upwelling which is characteristic of the Benguela System, (Day 1961, Darbyshire 1964, Shannon 1966, Andrews and Cram 1969, Bang 1973). The upwelling phenomenon is a seasonal one and usually predominates during the summer - autumn period (November - April) when South-easterly winds of high velocity are prevalent (Andrews and Cram 1969, Bang 1973, Bang 1973 b). Temperatures in this area vary between 9°C and 15,5°C. (fig. 1.3.). The cold nutrient-rich upwelled waters have a marked effect on density of the fauna and flora around Robben Island and along the west coast.

The density of <u>Ecklonia maxima</u>, <u>Laminaria pallida</u> and <u>Marcrocystis pyrifera</u> appears to be greater at Robben Island than is <u>Ecklonia maxima</u> in False Bay. The commonest Rhodophytes (red algae), which are also denser at Robben Island, are represented by <u>Gigartina radula</u>, <u>G. scabiosa</u>, <u>G. striata</u>, <u>Plocamium rigidum</u>,

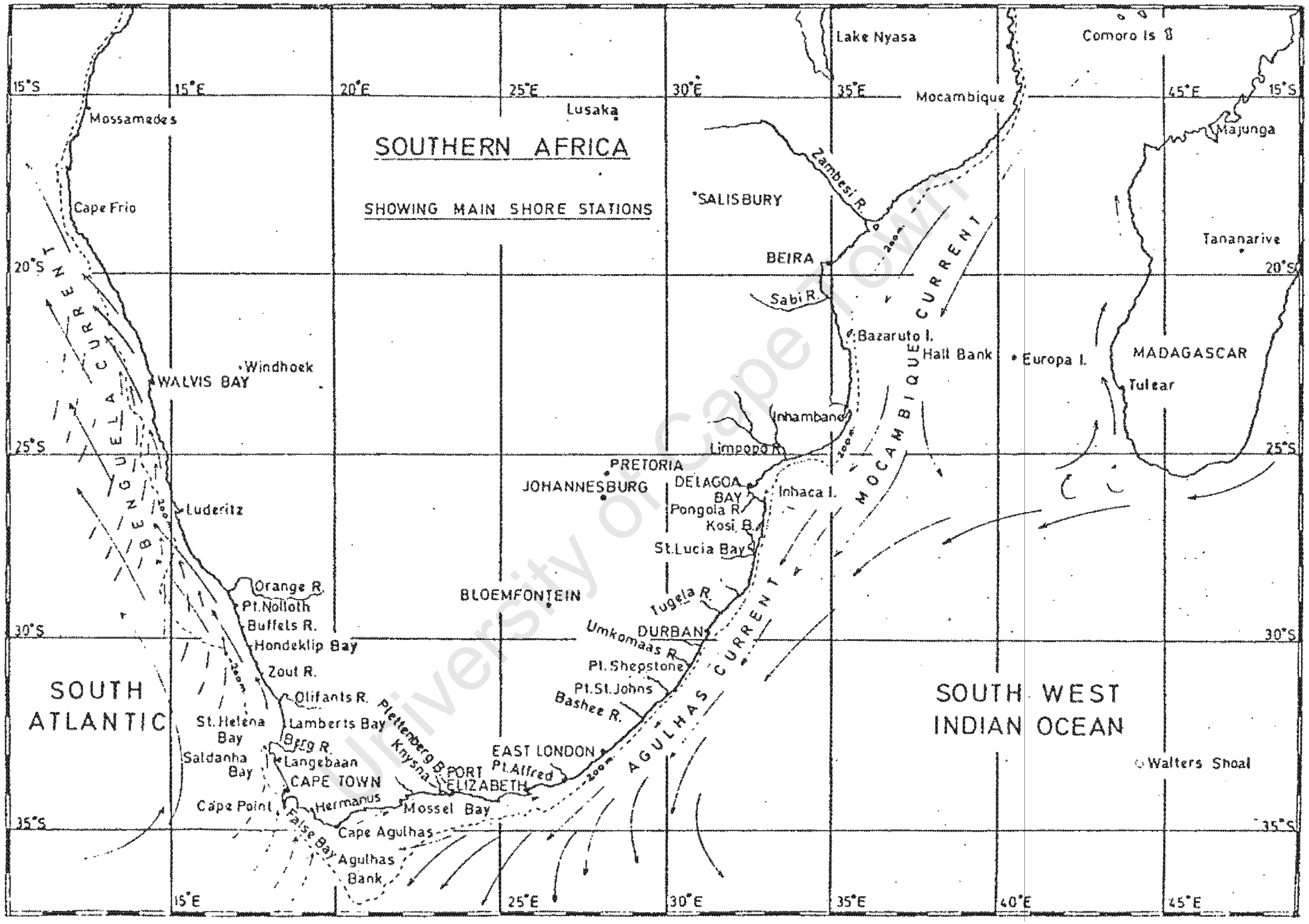


Fig. 1.1 Map of Southern Africa showing the Benguela and Agulhas Currents. (After Day 1969)

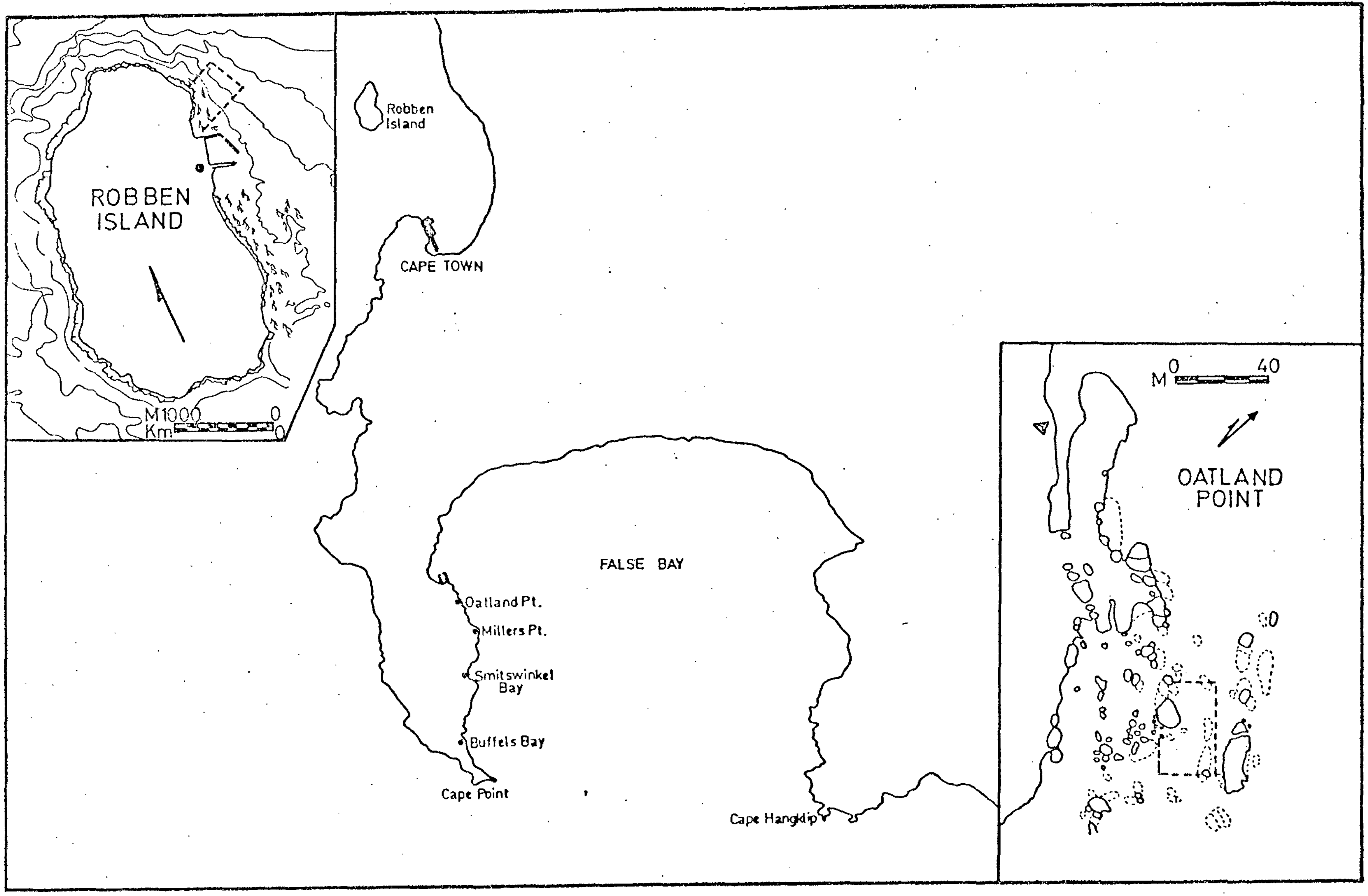
P. maxillosum, Pachymenia carnosa and P. cornea and the Chlorophytes (green algae) by Codium fragile and Cladophora mirabilis.

The major animal species inhabiting this area are the filter feeders represented by the ribbed mussels Aulacomya ater and the holothurian Pentacta doliolum. Swarms of mysids are also found. Parechinus angulosus is the predominant grazer in the kelp bed, but evidence in this thesis will show that it would be better termed a debris feeder, as it feeds largely on seaweed fragments which are caught floating in the water. It is important to note that P. angulosus on the west coast is found seaward of the Ecklonia maxima "belt" and not amongst the E. maxima as is the case in False Bay.

The major predator on P. angulosus is the rock lobster Jasus lalandii (Newman and Pollock, 1973). The asteroid Marthasterias glacialis is also known to feed on P. angulosus (Branch, pers. comm.) but the predatory pressure exerted is unknown.

At the study area along the northern end of the island (fig 1.2.) the sea bed slopes off to the north east in a series of reefs which run parallel to the shore and are occasionally interspersed by patches of sand. At approximately 15 m. depth, the reef structure gives way to isolated rocky outcrops surrounded by sand. The predominant rock type is Malmsbury shale which forms a very craggy substrate of large surface area which affords newly settled animals ideal protection and attachment surfaces. The prevailing wave direction in the area is south-westerly. However, this site is well exposed to refracted south-westerly waves. Waves of more than 7 m have been recorded at a more exposed site 7 km north of Robben Island (Shillington, 1974) and as energy is lost when refracted

Fig. 1.2 Location of study areas with insets showing details of the Robben Island and Oatland Point study sites. Broken lines enclose sampling area.



maximum waves at the Robben Island study area would be expected to be of the order of 3-5 m in height.

Oatland Point (False Bay)

Oatland Point is situated 40 km. from Cape Town and 17 km from Cape Point (fig. 1.2.). This area is not a popular diving spot and is therefore relatively undisturbed by the public.

The east and southeastern seaboard of Southern Africa is influenced by the warm (21 - 26°C) southward-flowing Agulhas Current (Bang, 1970, 1973). In the region between Cape Agulhas and False Bay the water is cooler due to a region of mixing where the Agulhas and Benguela systems converge (Bang, 1973). The resultant mixed water influences the temperature conditions of False Bay. The configuration of False Bay is such that it is not markedly affected by deep sea conditions (Atkins, 1970). The northerly region of False Bay (eg. Oatland Point) is unaffected by the plumes of cold upwelled water that occasionally appear off Cape Hangklip (Cram, 1970) in the summer months, or by the insurgence of cooler water into the mouth of the bay during the winter season (Atkins, 1970).

Generally therefore the area experiences temperature conditions ranging from 12-20°C, some 4-5°C higher than Robben Island on the west coast. Cooler conditions occur in late winter (August), with temperatures reaching a maximum in mid-summer (fig. 1.3.), contrasting with the situation at Robben Island where minimum temperatures occur in summer.

The biotic density and diversity is lower than at Robben Island with *Ecklonia maxima* being the only large phaeophyte

represented in the kelp bed. The other common brown algae are Bifurcaria capensis and Zonaria subarticulata. Rhodophyta are represented by Pachymenia cornosa and P. cornea and the green algae by Caulerpa filiformis. For a more detailed list of algal species see Morgans (1959). Algal density has not been determined quantitatively but appears to be lower in False Bay than at Robben Island (Dieckmann, pers. comm.). The holothurian Pentacta doliolum is found only in small numbers while the ophiuroid Ophioderma leonis and the crinoids Annametra occidentalis and Comanthus walhbergi are abundent.

This area also supports a large population of the sea urchin Parechinus angulosus. Predators of the urchin are scarce. Few rock lobster have been seen in the study area, so it appears that predation is minimal and the only predators on Parechinus are possibly some of the rock fish such as the Roman Chrysoblephys laticeps (Penrith, pers. comm) and the mollusc Phalium labiatum iredalei.

The rocky substrate is one of large granite boulders and smaller rounded cobbles on a sandy bed. A sandy bottom largely devoid of rocks occurs at a depth of 12 m. and deeper. The Oatland Point site is sheltered from wave action by the presence of large boulders. (fig. 1.2.)

Smitswinkel Bay (False Bay)

The growth rate and the structure of a population of urchins was studied at a third site to corroborate data obtained at Oatland Point. The site was an artificial reef created by the sinking of the diamond barge "Rockeater". It was scuttled in 35 metres of water on the 15th December 1972. The urchins that were collected were therefore of known maximum age and determination of their growth rate was not complicated by the presence of older age groups.

POPULATION STRUCTURE AND RECRUITMENT

Field Methods

Samples were collected from January and February 1973 to April and May 1974 at Robben Island and Oatland Point respectively. Weather permitting, between 7 and 15 random samples were taken at monthly intervals using S.C.U.B.A. This method is slightly biased in that animals less than 2,5mm in diameter are overlooked when sampling in turbid conditions.

The sampling procedure adopted at Robben Island and Oatland Point was as follows:

The diver reads two numbers in the range 1 - 20 from a table of random numbers. The first number gives the number of fin kicks he swims perpendicularly away from the shore using a compass, while the second gives the number of fin kicks he swims parallel to the shore and to the left. The two random numbers then give co-ordinates from a fixed reference point on the inshore part of the sampling area in terms of fin kicks. The quadrat is dropped and the urchins are cleared from the ¼ m^2 area inside the quadrat. The procedure is then repeated for subsequent sampling sites using the previous site as the starting point in each case. This method of sampling allows one to note the changes in animal distribution along the shore and the changes with depth. Samples from each quadrat are collected in separate plastic bags and returned to the laboratory where the animals are measured (major axis - interambulacrum to opposite ambulacrum) to the nearest 0,1 mm. with knife edge vernier calipers. They are then sorted into 2 mm. size classes for size - frequency analysis.

At Smitswinkel Bay samples were collected by S.C.U.B.A. diving at irregular intervals owing to the difficulty of getting to the site and locating the wreck. A maximum of two ¼ m^2 quadrats were sampled on each occasion, as a diver's working time at 35 metres is limited to 15 minutes if decompression is to be avoided. As samples were taken from flat horizontal surfaces of the wreck, the quadrat could be cleared with a metal paint scraper, so that animals of 2 mm. were sampled quantitatively. Collected material was returned to the laboratory for sorting.

Density and Distribution

The average density of urchins over the sampling period at Robben Island, Oatland Point and Smitswinkel Bay was 220,0 ± 12,56, 145,4 ± 9,44 and 303,75 ± 16,75 animals /m^2 respectively.

On the west coast urchins are found down to a depth of 10 m though the rocky substrate extends to 15 m at Robben Island and as deep as 20 m at Oudekraal. (Zoutendyk, 1974)

In False Bay the numbers decrease with depth to 12 m after which there is a sandy substrate unsuitable for urchin attachment.

Data Processing

For the construction of size/frequency histograms, all the individual sampling units of one quadrat taken at a particular time were lumped together. Size/frequency histograms with a size class interval of 2 mm. were drawn for each of the monthly samples. From the histograms, cumulative percentage curves were plotted on probability paper. Following the method of Harding (1949) and Cassie (1954 the mean, and standard deviation and the theoretical limits of each cohort in the population were determined. Knowing these statistics one is able to determine the growth and mortality of the individual cohorts making up the population.

A running-average plot was constructed to smooth the data and reduce sampling errors. The component normal distributions were then generated from the smoothed polymodal curve on a Hewlett-Packard (model 9100 B) desk top calculator using Taylor's (1965) method. In essence, the method is based on the assumption that each cohort in the population will be represented by a normally distributed size-frequency curve. From the probability plots, an estimate of the size of the first mode is made. The shape and breadth of the left half of the first curve are calculated from the running average plot, while the right hand half is plotted by assuming symmetry. Subsequent curves are plotted sequentially by subtracting the calculated values of the preceeding curve from the observed values of the polymodal curve. (For details of the technique see Appendix 1.).

Age determination using the growth ring method of Jensen (1969) was attempted but was abandoned as the reliability of ring counts in P. angulosus was dubious as has been found in some other species (Jensen, 1969; Dix, 1972).

Cram (1971) reports that development from fertilization to metamorphosis takes about 56 days at a temperature of 15°C, but metamorphosis can be delayed up to 11 days in the absence of a suitable substrate. He points out that larval development is temperature dependant but gives no indication of developmental times at different temperatures. The newly metamorphosed individual is approximately 0,8 - 1,0 mm. in diameter.

Fricke (1974) has shown that there is a definite biannual spawing cycle. Though there may be some shift in time from year to year, the west coast population can be said to spawn in autumn and spring. The Oatland Point population spawns in spring-early summer and again later in summer.

The works of Cram (1971) and Fricke (1974) and the continuous termperature records at Robben Island and at Millers Point (False Bay) (Fricke, 1974) are important in predicting developmental and settling time of P. angulosus in the field.

Robben Island

Fig. 1.4. shows the size-frequency distribution of the west coast population studied. The population shows a polymodal distribution which is typical of populations having a number of distinct age groups (Hughes, 1970; Sameoto, 1971, 1973). The running average of the total size-frequency distribution is given together with calculated normal distribution curves for each of the assumed cohorts present at the time of sampling. The persistance of modes throughout the sampling period was taken as an indication of their reality (Sameoto, 1971).

At the start of the sampling program in January 1973 the population consisted of seven subpopulations (cohorts) labelled G to A in Fig 1.4. Their modal sizes were 7,0; 11,0; (17,0; 20,0); 29,0; 33,0; 39,0; and 45,0 mm respectively. An eighth cohort a, with a modal size of 53,0 mm only persisted in the population for 3 months. As it showed no appreciable growth during this period it has been excluded from the growth analysis. The modal sizes in parentheses correspond to the cohorts labelled E' and E" in Fig. 1.4. The origin of E" is uncertain and since E' and E" could not be distinquished after 5 months, they have been considered to be parts of a single cohort E.

Knowing spawning times (Fricke, 1974) and assuming a larval developmental time of about 2 months (Cram, 1971), time of settling was estimated by back extrapolation.

Three new cohorts were recognised during the sampling period, labelled 1, 2 and 3 (fig. 1.4) in order of settlement. Cohort 1 first sampled in June 1973 was probably the result of 1972 spring spawning. That cohort 1 was a new group entering the population was indicated by the fact that the mode of cohort G had moved from 7,0 mm. to 13,0 mm. in the space of 5 months, and the new cohort had a modal size of 7,0 mm. Cohort 2 which was first detected in September 1973 appears to be the result of the 1973 autumn spawning, while cohort 3 first sampled in January 1974 probably originated from the spring spawning of 1973.

From back extrapolation to the estimated time of metamorphosis, the numbers of individuals that settled was estimated at between 600 and 700 per square metre at this site, though settling success is dependant on spawning and on larval development which are prone to annual fluctuations, as is indicated by the relative size of cohorts of similar modal size from year to year. The exceptionally high mortality of the newly settled individuals indicated by steep mortality regressions (see section on mortality), quickly reduced their numbers.

The lag period between estimated settling time and recruitment is due to two factors which make detection difficult: Firstly cryptic colouration and secondly the habit of the young of settling between densely packed mussels. Only when they attain a size of 4-6 mm are they sampled quantitatively.

Oatland Point

The polymodal plots of the size-frequency distribution curves are shown in Fig 1.5. The running average of the total size-frequency distribution is given as well as calculated normal distribution curves for each of the assumed cohorts present. Seven subpopulations, labelled S-M were evident when sampling began early in February 1973. The smallest cohort S had a mode at 13,0 mm. Subsequent modes were at 21,0; 29,0; 35,0; 41,0; 45,0; and 51,0 mm respectively.

Four new cohorts labelled 10, 20, 30, and 40 in Fig 1.5 were detected in March, May and September 1973 and February 1974 respectively.

From the work of Cram (1971) and Fricke (1974) the newly recruited cohorts probably settled about January-February 1972, May-June 1972, January-February 1973 and May-June 1973 respectively. This implies that they are the progeny of spawning in October 1971, February 1972, October 1972 and February 1973. The lag period of a year between spawning and detection of new cohorts is due to the

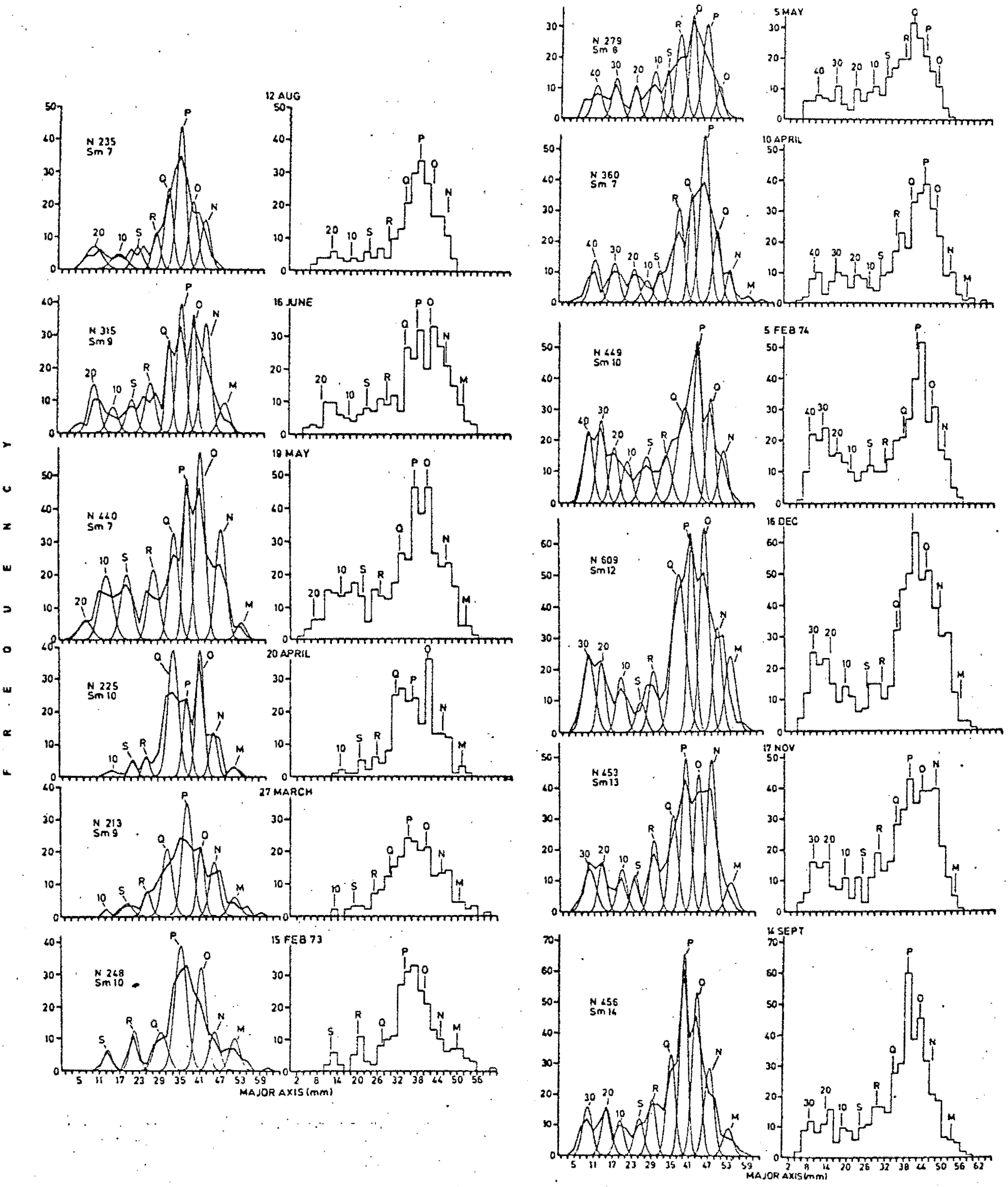


Fig. 1.5 Oatland Point - legend as in Fig. 1.4

difficulty experienced in finding animals smaller than 10 mm in diameter at Oatland Point. This problem has not been resolved in spite of extensive sampling in shallower water, including, the intertidal, under rocks and in holdfasts.

Rockeater (Smitswinkel Bay)

When the first sample was collected in June 1973, only a single cohort was evident, labelled X in Fig. 1.6. A second settlement (Y) was detected in August. The third cohort (Z) was only detected in June 1974 because no samples were collected between mid-November 1973 and June 1974.

By back extrapolation to the expected settling time, cohort X appeared to settle in numbers in excess of $1000/m^2$, while cohort Y which settled in April 1973 did so in numbers of approximately $700/m^2$.

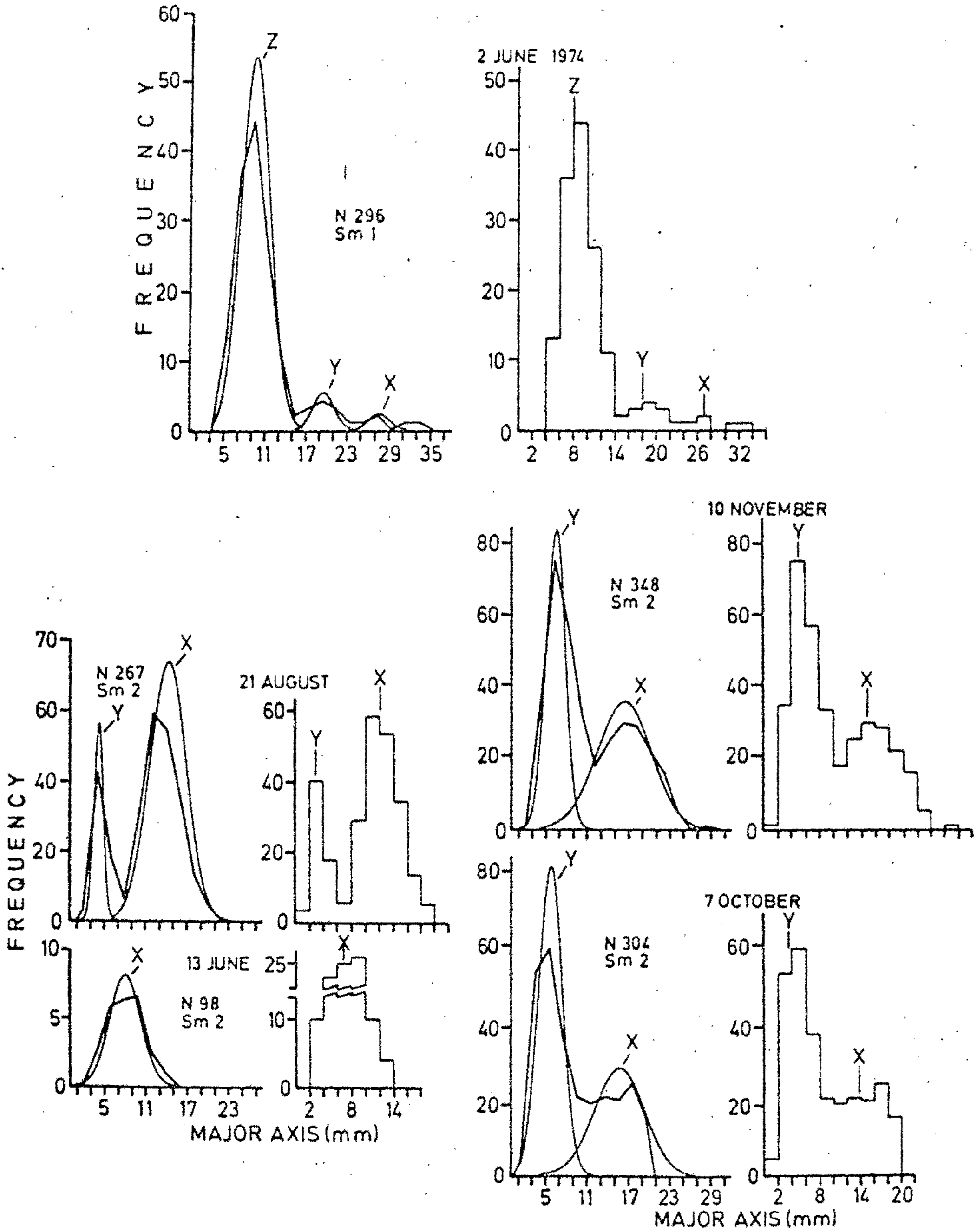


Fig. 1.6 Rockeater - legend as in Fig. 1.4

GROWTH.

The tagging technique used by Ebert (1965) to monitor growth was discontinued owing to high mortality which resulted after tagging. Monitoring the growth of captive animals (Swan, 1960) was also unsuccessful as the cages were destroyed during a storm.

Growth estimates were made by plotting the size-frequency distributions of successive months, and following the movement of cohort means along the abscissa for the full sampling period. The true mean of each cohort was obtained from size-frequency cumulative curves (Cassie, 1954). An estimate of the true mean was considered to be more accurate than the mode and these data were used to plot the composite growth curves. Where necessary individual cohorts in the population were dealt with independantly in order to analyse factors which influenced their growth rates.

Robben Island.

Composite growth curves obtained from the size-frequency curves of fig. 1.4 for each cohort in the population are shown in fig. 1.7. Growth of individuals from metamorphosis to 20mm in diameter takes a sigmoid form. Growth to 10mm is slow (1,0 ± 0,4mm per month). The rate then increases to about 2,0mm per month up to a size of 18-20mm, after which it slows to 1,0mm per month.

Cohorts 2 and 3 were in the slow growth phase over the period of sampling. They had average monthly increments of

1,40 and 0,66mm respectively. Cohort 1 showed the complete sigmoid growth pattern, slow to 9,0mm, fast to 18,0mm and slow between 18,0 and 20,0mm. Cohort G showed a similar pattern up to a size of 18,6mm. Growth then increased between November 1973 and March 1974 after which it slowed once more.

The growth rate of cohort F was sigmoid to 19,0mm. Between July and September the growth rate rose from 0,70mm per month to 2,80mm per month. The rate slowed to 1,10mm between September 1973 and mid-January 1974 and then rose slightly between mid-January and March when sampling stopped.

Cohort E had a similar growth curve to F. Cohorts D-B had similar growth patterns. Growth was fast between January and April 1973, slow between April and September, fast between September and January 1974 and slow from then until sampling was terminated in March 1974. The growth curve of cohort A differed only in the short fast growth phase between June and September.

The average monthly growth increments of each cohort in the population are listed in table 1.1. The tendency is towards an increase in growth rate (3-F) with age, after which the growth rate decreased with age.

Table 1.1 Average monthly increments in test size of the ten cohorts in the Robben Island population over the full sampling period.

Cohort	Average increment (mm)
3	0,66
2	1,14
1	1,36
G	1,066
F	1,253
E	1,00
D	0,66
C	0,61
B	0,41
A	0,38

The mean growth rate of the population (excluding cohorts 1-3) was quantified in two ways. Firstly a plot of initial length (l_t) against the annual increment ($l_{t+1} - l_t$) was made. The resulting negative linear regression is described by the von Bertalanffy growth equation,

$$l_{t+1} - l_t = (1 - e^{-k})(L_\infty - l_t) \quad \text{(Ricker, 1968)}$$

$$= -l_t(e^{-k} - 1) + L_\infty (1 - e^{-k})$$

where,

e = base of natural logarithms

L = maximum size towards which the animal is tending

k = a measure of the rate at which length approaches L_∞

l_t = length at time t

l_{t+1} = length one year later

The theoretical maximum size is given by the intercept on the abscissa (fig. 1.8). The equation of the regression line was calculated as,

$$l_{t+1} - l_t = 0,3271\ l_t + 19,6919$$

which gave a theoretical maximum size ($L\ $) of 60,19mm. This figure is very close to the observed maximum of 60,50mm.

The same data was used to construct a Ford-Walford growth curve, by plotting initial length (l_t) against the length one year later (l_{t+1}). A positive linear correlation was produced and is described by:

$$l_{t+1} = l_t\ (1 - e^{-k}) + L_{\infty} e^{-k}$$

Here the theoretical maximum size to which the animal can grow is represented by the intercept of the linear plot with the 45° line. The regression gave the following equation:

$$l_{t+1} = 20,7965 + 0,6278\ l_t$$

The theoretical maximum length of 58,5mm (fig. 1.9) given by the equation is slightly lower than the observed absolute maximum value of 60,50mm, but this figure is closer to the average maximum size (the mean size of 10 largest animals) of 56,6mm than that given by the von Bertalanffy growth equation.

Oatland Point.

The seasonal variation of the gonad index is reflected in the growth patterns of the subpopulations shown in Fig. 1.10.

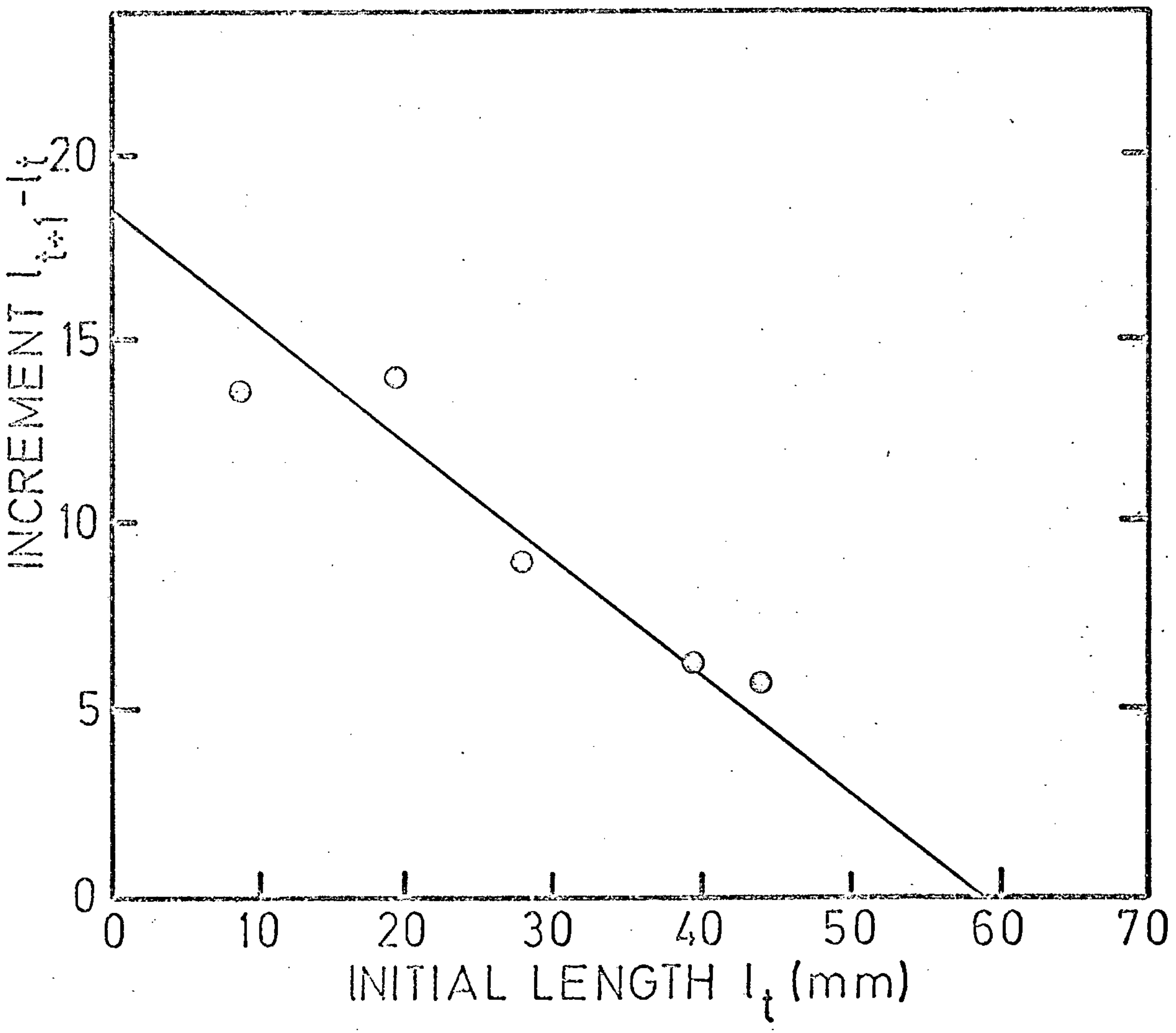


Fig. 1.8 Von Bertalanffy plot of test diameter in January 1973 (l_t) on the abscissa, and test increment ($l_{t+1}-l_t$) one year later, on the ordinate, for the Robben Island population.

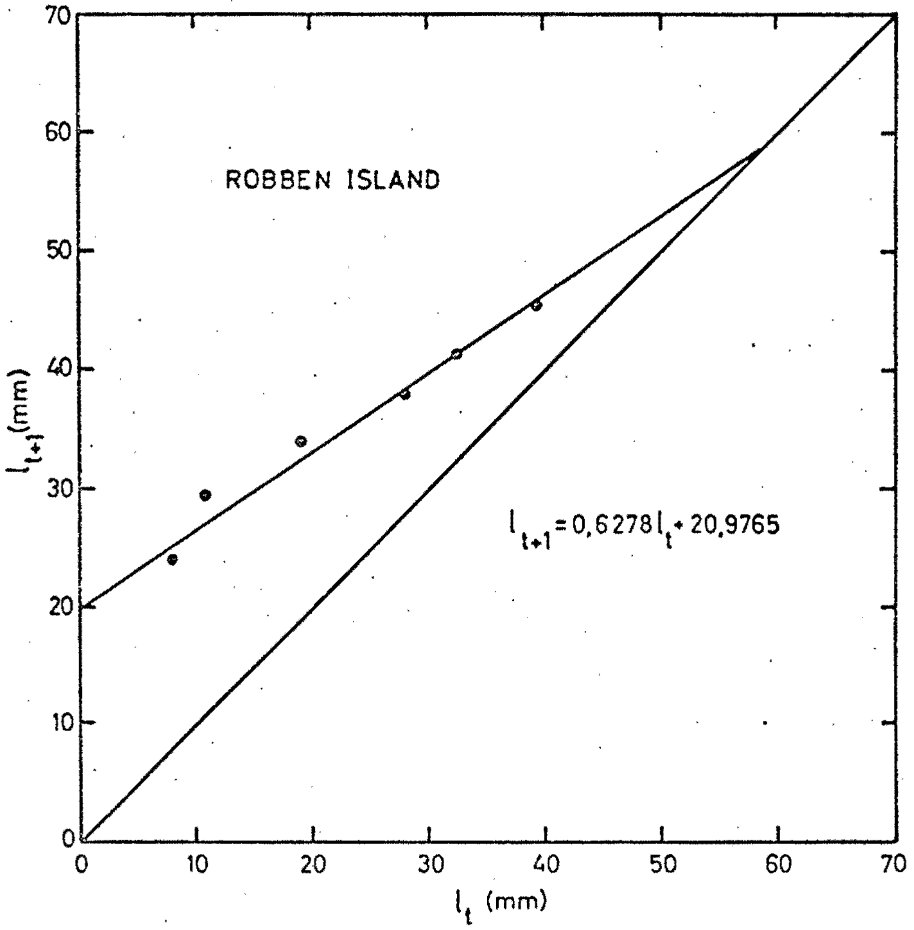


Fig. 1.9 Ford-Walford plot of test diameter in January 1973 (l_t) on the abscissa, and test diameter one year later (l_{t+1}) on the ordinate, for the Robben Island population.

Mean monthly size increments of all the cohorts in the population at Oatland Point are listed in table 1.2.

Table 1.2 Average monthly increments in test size of the 11 cohorts in the population at Oatland Point.

Cohort	One monthly increment (mm)
40	0,622
30	1,171
20	1,160
10	0,857
S	1,316
R	1,096
Q	0,825
P	0,761
O	0,658
N	0,438
M	0,438

Diet and gonad development appear to be the two major factors influencing somatic growth. At sizes less than 20mm in diameter, diet influences growth, and above 20mm in size, gonad development affects body growth. The sexually mature cohorts R, Q, P, O, N and M have very similar growth patterns. They differ only in the magnitude of size increase during the post-spawning fast growth phase, there being a general decline in growth rate with age.

The mean growth rate of the entire population computed by the von Bertalanffy and Ford-Walford methods yielded the following

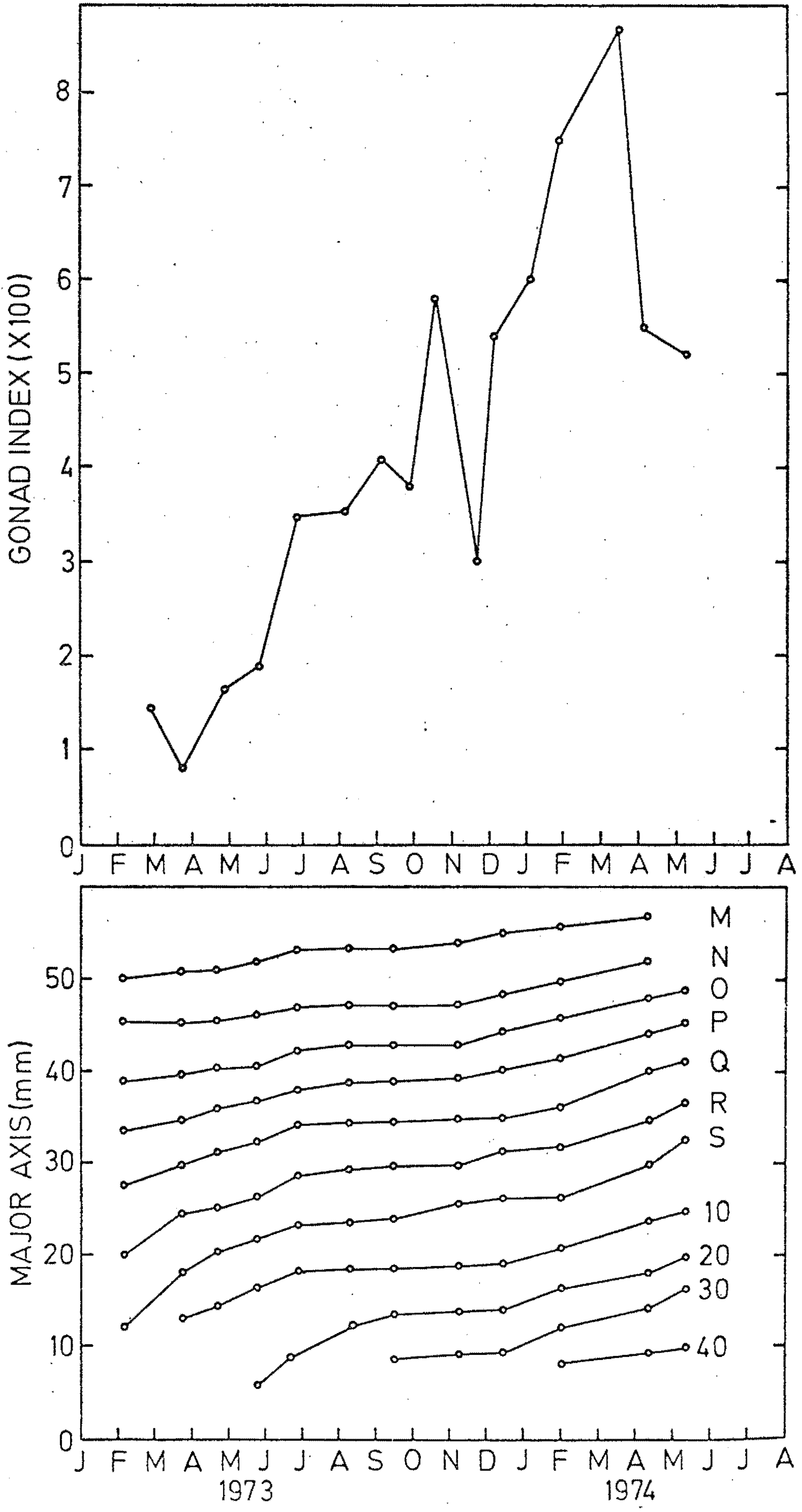


Fig. 1.10 Composite growth curves for the Oatland Point population.

equations respectively.

$$l_{t+1} - l_t = -2420\ l_t + 16{,}1692 \qquad r = -0.98$$

$$l_{t+1} = 16{,}1692 + 0{,}7579\ l_t \qquad r = -0.99$$

The theoretical maximum size limit given by the von Bertalanffy growth equation is 66,80mm as opposed to the observed maximum size of 62,8mm. This overestimate is due to the unusually high growth rate estimate of cohort M which is possibly due to an error induced by cohort overlap. Excluding this cohort from the analysis gives the growth curve as:

$$l_{t+1} - l_t = -2673\ l_t + 16{,}7646 \qquad r = -0.98$$

and a theoretical maximum size of 62,71mm (fig. 1.11). The Ford-Walford growth equation gives L as 64,2mm. If cohort M is excluded the growth equation becomes,

$$l_{t+1} = 16{,}7646 + 0{,}7326\ l_t \qquad r = 0{,}99$$

and L is reduced to 61,30mm (fig. 1.12) which is closer to the average maximum size (average size of ten largest animals sampled) of 59,20mm than the figure computed by the von Bertalanffy growth equation, though the von Bertalanffy equation gives a more accurate estimate of the observed maximum.

Rockeater.

The first cohort to settle was probably the result of the 1972 spring spawning, as larval development would have been complete by mid December. If settlement occurred almost immediately then growth rate proceeded at a rate of 1,39mm/month up to the time cohort X was first sampled in June 1973 (fig.1.13.). Between

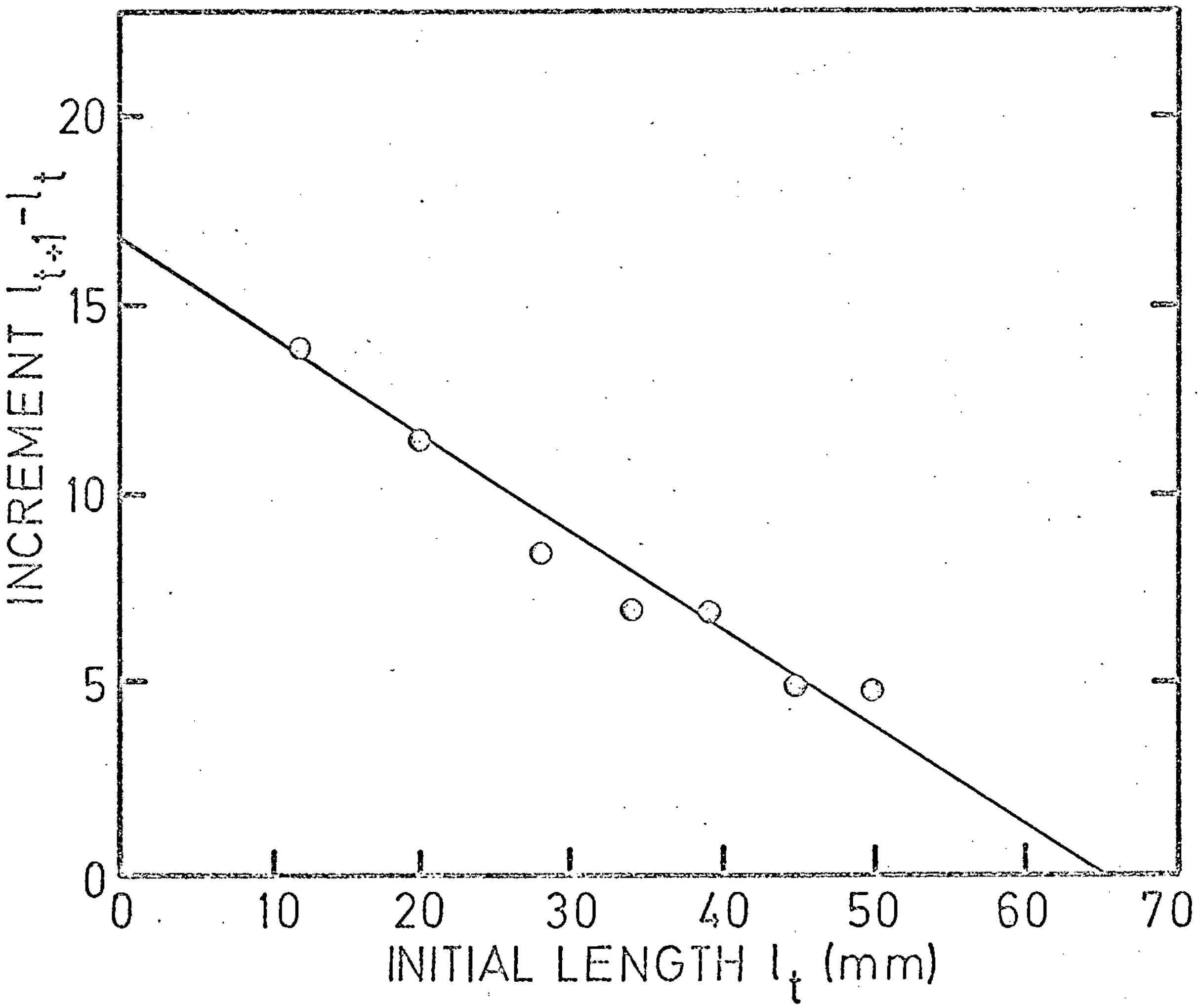


Fig. 1.11 Von Bertalanffy plot for the Oatland Point population.

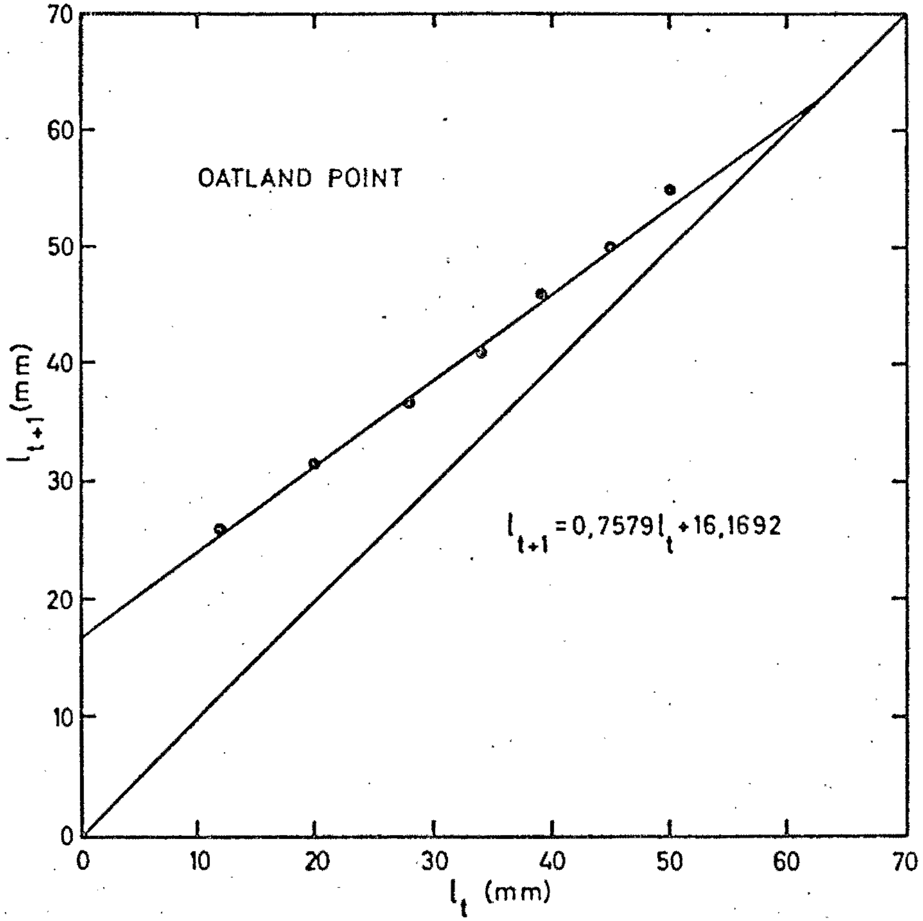


Fig. 1.12 Ford-Walford plot for the Oatland Point population.

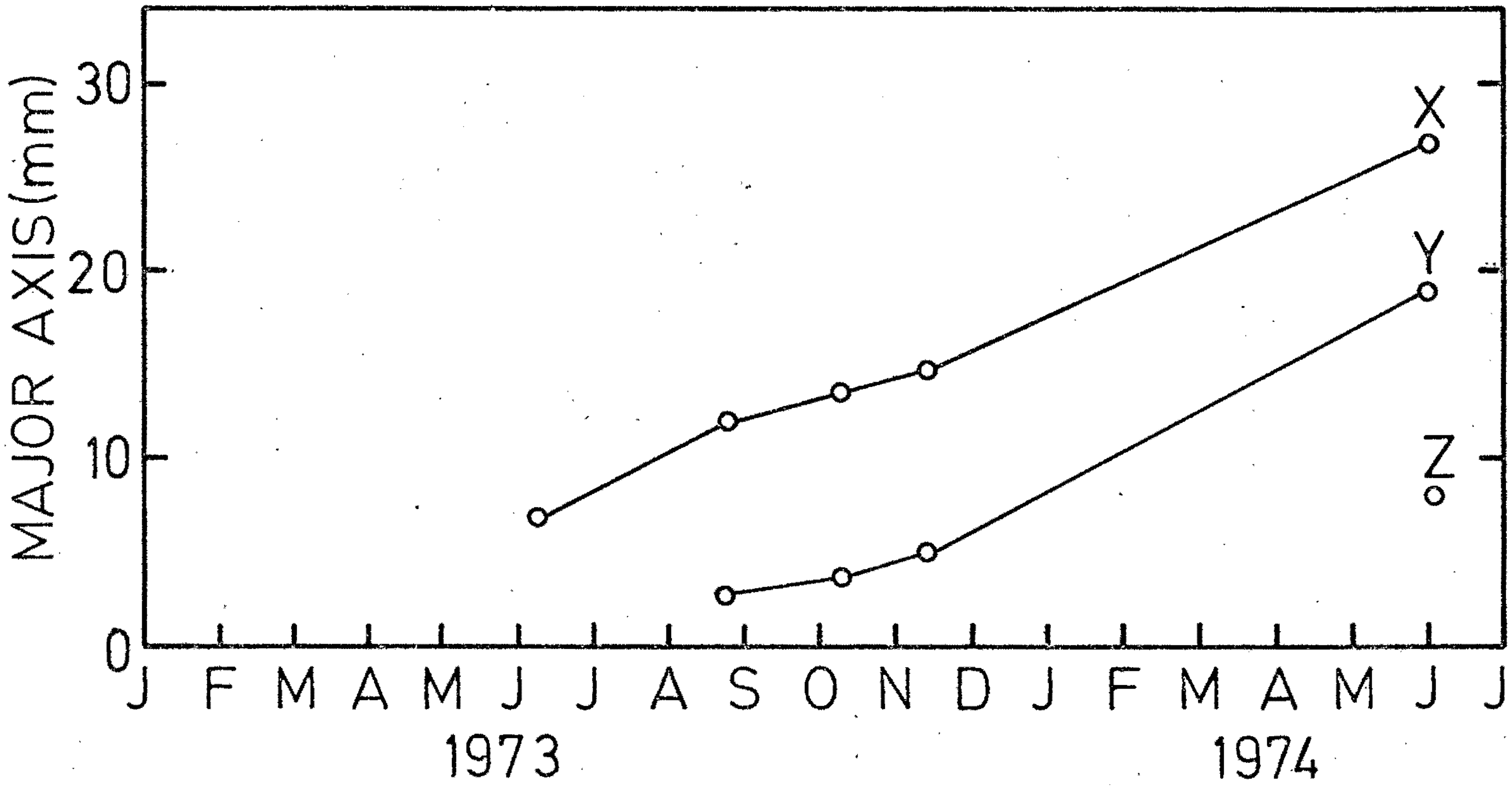


Fig. 1.13 Composite growth curves for the Rockeater population.

first and second sampling, the growth rate increased slightly to 1,50mm per month. Between late August and mid September growth rate dropped to 0,972mm per month after which time it increased to an average of 1,89mm per month. The average growth rate over the whole period was 1,702mm per month. If settling occurred in mid December immediately after the vessel was scuttled, then the inclusion of this initial period reduces the mean growth rate to 1,48mm per month. Cohort Y was probably produced by the mid-summer spawning and settled in early April. Initial growth was very slow, 0,42mm per month. Between August and November the rate increased to 0,73mm per month. Between November and the final sample in June 1974 the growth rate rose to 2,102mm per month. The mean growth rate from settling to June 1974 was 1,285mm per month.

Growth Patterns

By drawing on results of other workers some explanation can be offered regarding the growth patterns shown by P. angulosus. Swan (1961), Ebert (1968) and Dix (1972) have shown that food type and availability influence echinoid growth rates. Fuji (1967) reports that 70% of the gut contents of individuals of Strongylocentrotus intermedius smaller than 8mm in diameter is detrital material, the remainder being algal pellets. The ratio of detritus to algal pellets decreased with increasing size until animals 10mm and larger were feeding almost exclusively on seaweed. If one assumes that the same transition in food preference occurs in P. angulosus, the slow growth rate at sizes below 10mm can be attributed to the detrital feeding phase and presumably a lower calorific intake, since the food probably has a lower calorific content and is more diffusely scattered on the substrate. Increased growth rate at sizes greater than 10mm can be attributed to a change to feeding on attached algae and whole fragments, which are a more concentrated form of food than detritus and may have a higher calorific content.

Gonad development is the second factor which affects the somatic growth rate. Individuals of _Strongylocentrotus intermedius_ and _Parechinus angulosus_ which are smaller than 20mm in diameter show some gonad development, though sex differentiation is impossible at this stage (Fuji, 1967, Fricke pers. comm.). It is possible to distinguish the sexes in animals ranging in size from 20-30mm but they remain virgin until the following season when they become sexually mature, at which time they are between 32 and 35mm in size (Fuji, 1967). Similar gonad development appears to be true of _P. angulosus_ (Fricke, pers. comm.). Thus it seems reasonable to infer that in those animals less than 20mm in size, all assimilated "growth energy" (ie. assimilated energy excluding that lost as heat during respiration) is directed towards test growth. However, as test size approaches 20mm some "growth energy" is diverted into gonad development and test growth decreases. The probable effect of gonad development on test growth becomes more apparent in older age groups.

The four older age groups of the Robben Island population A, B, C and D, which are considered to be sexually mature (Fricke, 1974) exhibit growth curves which appear to be closely associated with the gonad cycle. Test growth is slow when the gonad index is rising, May-September and November-January, and increases when spawning occurs and the gonad index drops (fig. 1.7). The same association between the gonad cycle and somatic growth is evident in the Oatland Point population (fig. 1.10).

Thus it appears that there is a cyclic alternation between test growth and gonad growth.

The effect of temperature alone could not be determined, though it appears to be insignificant.

AGEING

Robben Island

A knowledge of larval development and the reproductive biology as well as information on post-larval growth of P. angulosus allowed estimation of their ages at various sizes. Assuming a larval developmental time of 56-67 days (Cram, 1971), post-larval growth rate of about 1,0mm per month (see section on growth) and detection size of 4,0-5,0mm, the young resulting from the autumn spawning (Fricke, 1974) would be sampled in October-November. Those from the spring spawning would be detected in March-April of the following year.

On these asumptions cohort G is likely to be the result of the autumn spawning of 1972. This group designated 0 + age group was therefore nearing the end of its first year of post-larval growth when first sampled in January 1973. Assuming that all spawnings were successful and resulted in recruitment, cohorts E and F would be the remaining animals of the 1971 autumn and spring spawning respectively, while cohorts C and D are the progeny of the 1970 spawnings. Cohorts A and B would therefore be the survivors of the 1969 spawnings.

By the middle of 1974 when sampling was stopped, cohorts A, B, C, D, E, F, G, I and 2 would be approximately 5,0+; 4,5+;4,0+; 3,5+; 3,0+; 2,5+; 2,0+; 1,5+ and 1,0+ years respectively. Cohort a was almost 6,0 years old in April 1973 when it could no longer be distinguished.

Oatland Point

Drawing on the work of Cram (1971) and Fricke (1974) and compensating for the effect of temperature on larval development, the ages of the cohorts 40 to M are estimated to be 1; 1,5; 2; 2,5; 3; 3,5; 4; 4,5; 5; 5,5 and 6 years old respectively.

MORTALITY

An estimate of the proportion contributed by each cohort to the population was made from each of the polymodal plots. From these statistics and the overall density of the population, the numbers of each cohort at each sampling period could be estimated. In this way a knowledge of the decrease in numbers of each cohort could be gained. Regressions lines were constructed by plotting $\log_{10}$ numbers against time.

Robben Island

Table 1.3 gives the regression equations of lines representing the mortality of each cohort. The two youngest cohorts were excluded because they were too small to be sampled reliably.

Table 1.3 Regression equations for $\log_{10}$ of numbers versus time in months for eight of the cohorts in the population

Cohort	Equation	Correlation coefficient
A	$\log_{10} N = 0{,}0107t + 0{,}928$	-0,49
B	$\log_{10} N = 0{,}0068t + 1{,}614$	-0,42
C	$\log_{10} N = 0{,}0253t + 1{,}700$	-0,49
D	$\log_{10} N = 0{,}0099t + 1{,}549$	-0,44
E	$\log_{10} N = 0{,}0189t + 1{,}376$	-0,95
F	$\log_{10} N = 0{,}0169t + 1{,}614$	-0,64
G	$\log_{10} N = 0{,}0340t + 2{,}086$	-0,89
I	$\log_{10} N = 0{,}0377t + 2{,}453$	-0,79

The low correlation coefficient values of the older age groups indicate a large scatter of the data points around the computed regression. The scatter could be due to seasonal variations in mortality in the older cohorts while mortality appears to be more constant in smaller animals. However, seasonal variations in mortality are impossible to determine with the present data. Though mortality is assumed to be constant throughout the year in all age groups, the differences in slopes of the computed regressions indicate that mortality rate is very high in early post-larval life, and decreases markedly with age. Larval settlement appears to very dense and by back extrapolation of the calculated mortality regression lines, the numbers in cohorts G and 1 at the beginning of the sampling program were estimated as $100/m^2$ and $250/m^2$ respectively. The numbers in these cohorts dropped to $15/^2$ (87,5% decrease) and $25/m^2$ (90% decrease) respectively, during a year. Cohort A (starting size 44mm) showed a drop in numbers from $10/m^2$ to $4/m^2$ (60% decrease) in the same period of time.

The decrease in mortality of older animals is probably related to the animals' size, which makes them available to fewer species as prey. Himmelman and Steele (1971) report that the american lobster Homarus americanus feeding on Strongylocentrotus droebachiensis, is only able to eat individuals which are small enough to be dislodged from the substrate, as initial penetration of the test is through the soft tissue surrounding the lantern. Consequently vulnerability to predation is inversely proportional to size. If the same is true of Jasus lalandii feeding on P. angulosus then this could be one explanation for the decrease in mortality with size. This together with the fact that Jasus lalandii does not feed at a constant rate throughout the year (Pollock, pers, comm.) may cause seasonal variation in mortality and a consequent scatter indicated by the low correlation coefficients of the regressions describing mortality in the older cohorts.

Oatland Point

Mortality at Oatland Point is more difficult to estimate than at the west coast site due to the apparently poor recruitment and resulting scarcity of juveniles. Mortality was estimated as before and the resultant regression equations are presented in table 1.4.

Table 1.4. Regression equations of $\log_{10}$ numbers per m^2 against time in months for nine cohorts in the population.

Cohort	Equation	Correlation Coefficient
M	$\log_{10} N = -0{,}0102t + 0{,}7918$	$r = -0{,}69$
N	$\log_{10} N = -0{,}0120t + 1{,}3659$	$r = -0{,}64$
O	$\log_{10} N = -0{,}0104t + 1{,}4427$	$r = -0.56$
P	$\log_{10} N = -0{,}0036t + 1{,}5539$	$r = -0{,}46$
Q	$\log_{10} N = -0{,}0148t + 1{,}4942$	$r = -0{,}58$
R	$\log_{10} N = -0{,}0127t + 1{,}3278$	$r = -0{,}48$
S	$\log_{10} N = -0{,}01780t + 1{,}1249$	$r = -0{,}98$
10	$\log_{10} N = -0{,}0081t + 1{,}1491$	$r = -0{,}28$
20	$\log_{10} N = -0{,}0038t + 0{,}9869$	$r = -0{,}27$

The very low correlation coefficients of the regressions representing mortality of cohorts 10 and 20 indicate a large scatter and reflect the limited reliability of the calculated mortality lines for the younger groups, contrasting with the results at Robben Island. This is due to the lower numbers of animals in the smaller size classes sampled. Table 1.5. gives the numbers of animals/m^2 in February 1973 and February 1974.

Table 1.5. Numbers of animals per square metre in February 1973 and February 1974.

Cohort	Numbers at time t	Numbers at time t + 1	Percentage mortality
M	6	4	33,4
N	24	12	50,0
O	27	17	37,1
P	35	27	22,9
Q	31	16	48,4
R	18	8	55,6
S	13	6	53,9
10	19	8	57,9
20	12	8	33,4

The relatively poor inverse correlation between mortality and size may be due to migration which is thought to occur in this eara, in the absence of any other explanation of the lack of juveniles. The fact that the high numbers of large animals bears no relation to the low recruitment figures strengthens this supposition.

Rockeater

Mortality was extremely high as indicated by steep gradients of the mortality versus time regressions (table 1.6.)

Table 1.6. $\log_{10}$ numbers versus time regressions for P. angulosus on the "Rockeater".

Cohort	Regression equation	Correlation Coefficient
X	$\log_{10} N = -0{,}1407t + 3{,}1000$	$r = -0{,}99$
Y	$\log_{10} N = -0{,}1239t + 3{,}1068$	$r = -0{,}99$

Mortality occured at a very high rate in both cohorts and by June 1974 the numbers had dropped to $21/m^2$ and $41/m^2$ in cohorts X and Y respectively. The high mortality in the older animals adds support to the supposition that individuals above 10mm in size feed on debris. As there was no macroscopic algae evident on the "Rockeater" (probably due to inadequate light at a depth of 35m), the high mortality is probably attributable to insufficient food supply, and possibly due to insufficient protection from fish predators on the flat deck.

PRODUCTION.

Wet weight was used in the determination of production (Pg) as changes in gonad size are offset by inverse changes in coelomic fluid volume which has the same specific gravity as the gonad (Fuji, 1967; Miller and Mann, 1973). Therefore any change in total body weight could only be due to a change in test size. Because change in gonad weight has no effect on the size-weight relationship, only a single graph was necessary.

Fig. 1.14 shows the least squares fit of the exponential relationship between test size (major axis) and the live wet weight of the Robben Island population. The curve described by:

$$w = al^b$$

where, w = wet weight

a = intercept on the ordinate

l = test size (major axis)

b = exponent

gave the following equation:

$$w = 0{,}000592\ l^{2{,}898} \qquad r = 0{,}99$$

or $$\log_e w = \log_e 0{,}000592 + 2{,}898 \log_e l$$

The exponential size-weight relationship of the Oatland Point population (fig 1.15) is represented by the equation

$$w = 0{,}000751\ l^{2{,}846}$$

or $$\log_e w = \log_e 0{,}000751 + 2{,}846 \log_e l$$

Production was calculated by the Allen curve method using the slight modification introduced by Peer (1970), who fitted separate

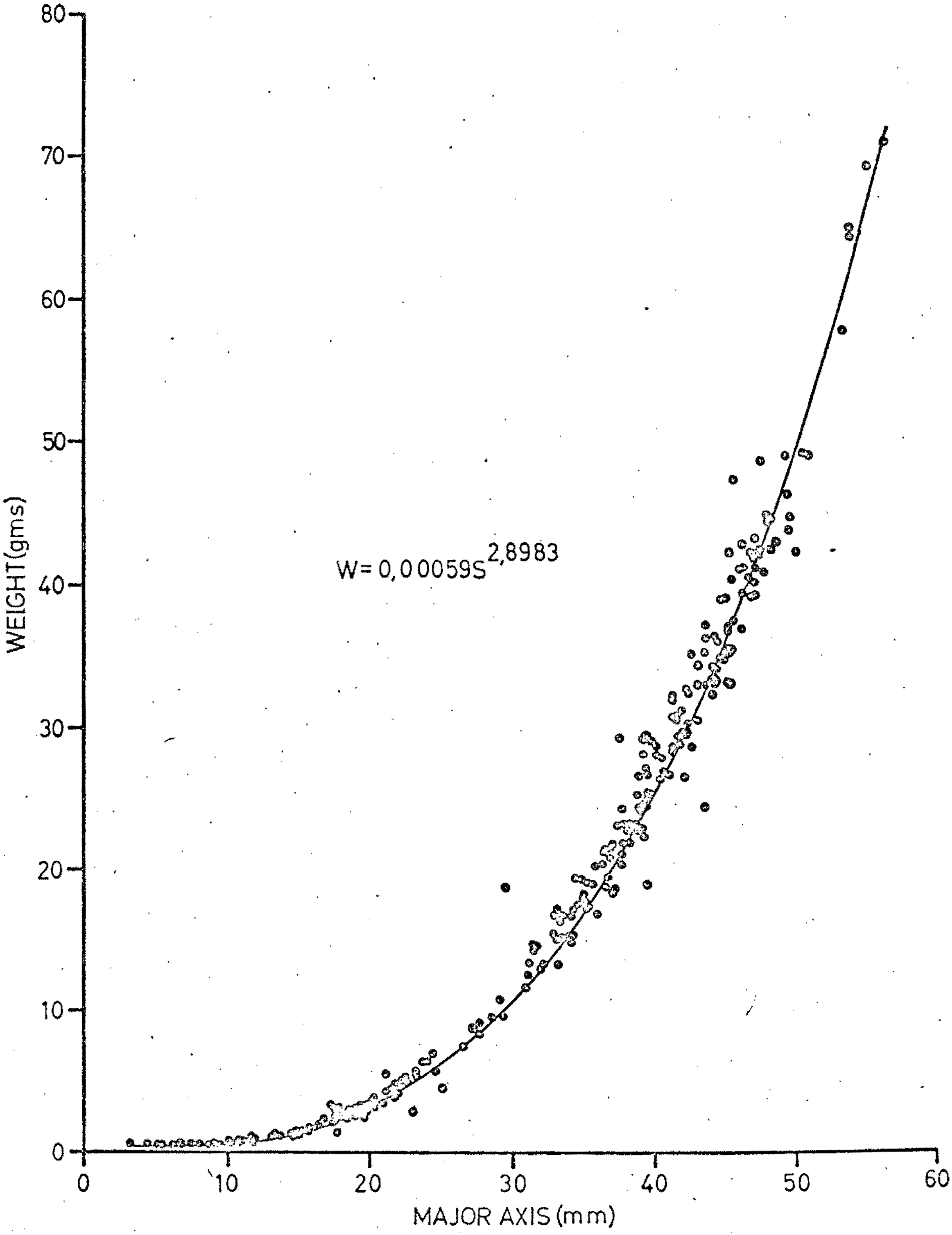


Fig. 1.14 Size-wet weight relationship for P. angulosus at Robben Island.

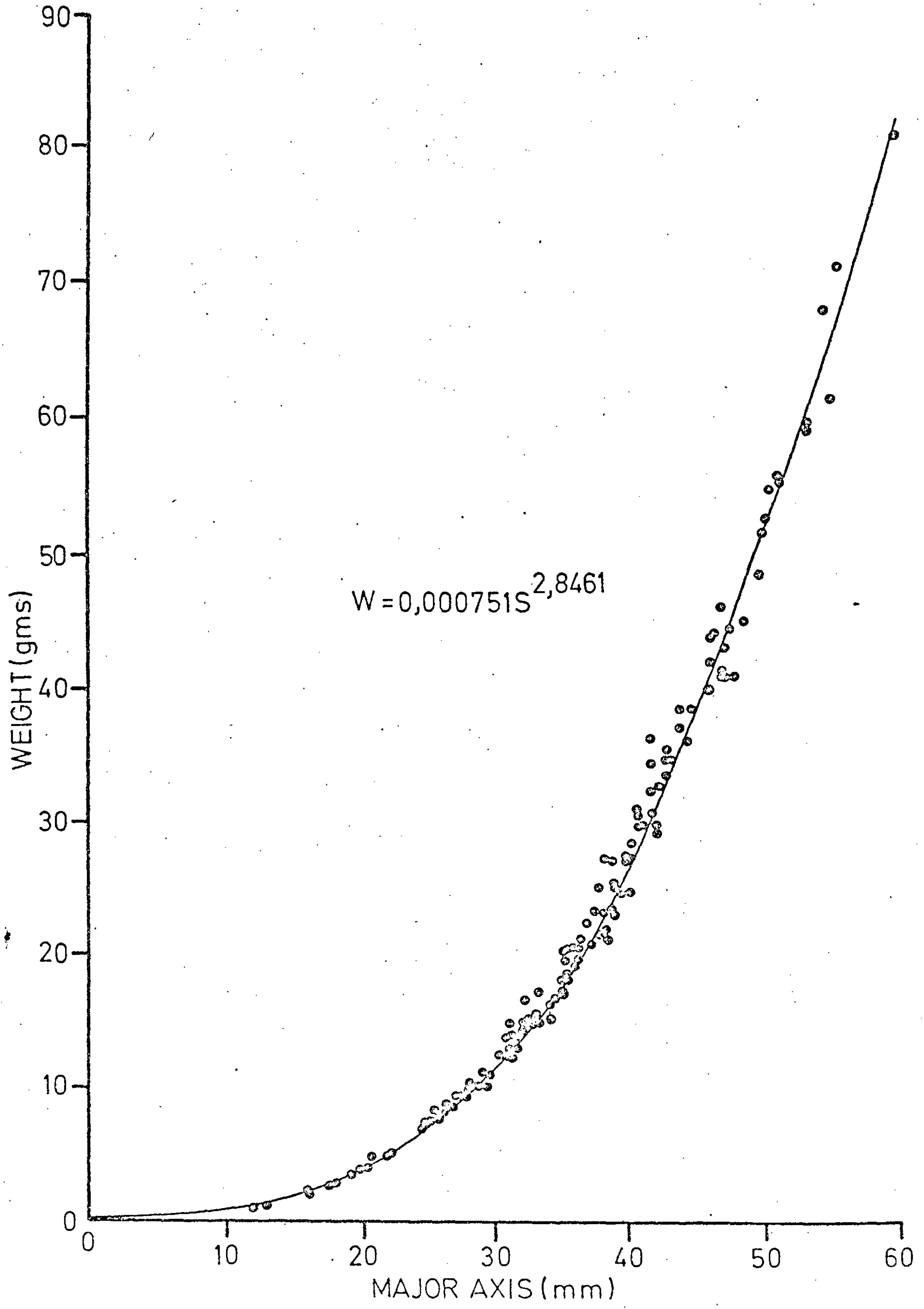


Fig. 1.15 Size-wet weight relationship for the Oatland Point population.

regressions to data on numbers and mean weight against time and constructed a smoothed Allen curve by transferring points at regular time intervals. The mean weight curves have been derived from the composite growth curves and the Allen curves were constructed by plotting the decrease in numbers (mortality regressions) against weight on the first day of every month. Production is given by the area under the Allen curve.

Robben Island.

Fig. 1.16 shows the method of constructing the smoothed Allen curves used in estimating the production of each cohort. The resultant production curves for each cohort are shown in fig. 1.17.

The changes in biomass, mortality losses and production of each cohort determined from the Allen curves are listed in Table 1.7.

Table 1.7 Production parameters for P. angulosus calculated from the smoothed Allen curves.

Cohort	Annual production (Pg) gm/m^2	Mortality losses (E) gm/m^2	Biomass (B) Kg/m^2
A	87,2	26,4	3,12
B	179,2	35,2	5,89
C	532	185,6	5,74
D	411	104,8	4,38
E	163,8	61,8	1,11
F	220,8	90,4	1,28
G	151	91,57	0,750
1	112	31,28	0,264
Population	1,857 Kg	0,627 kg	22,62 Kg
			$\bar{B}$ = 1,786

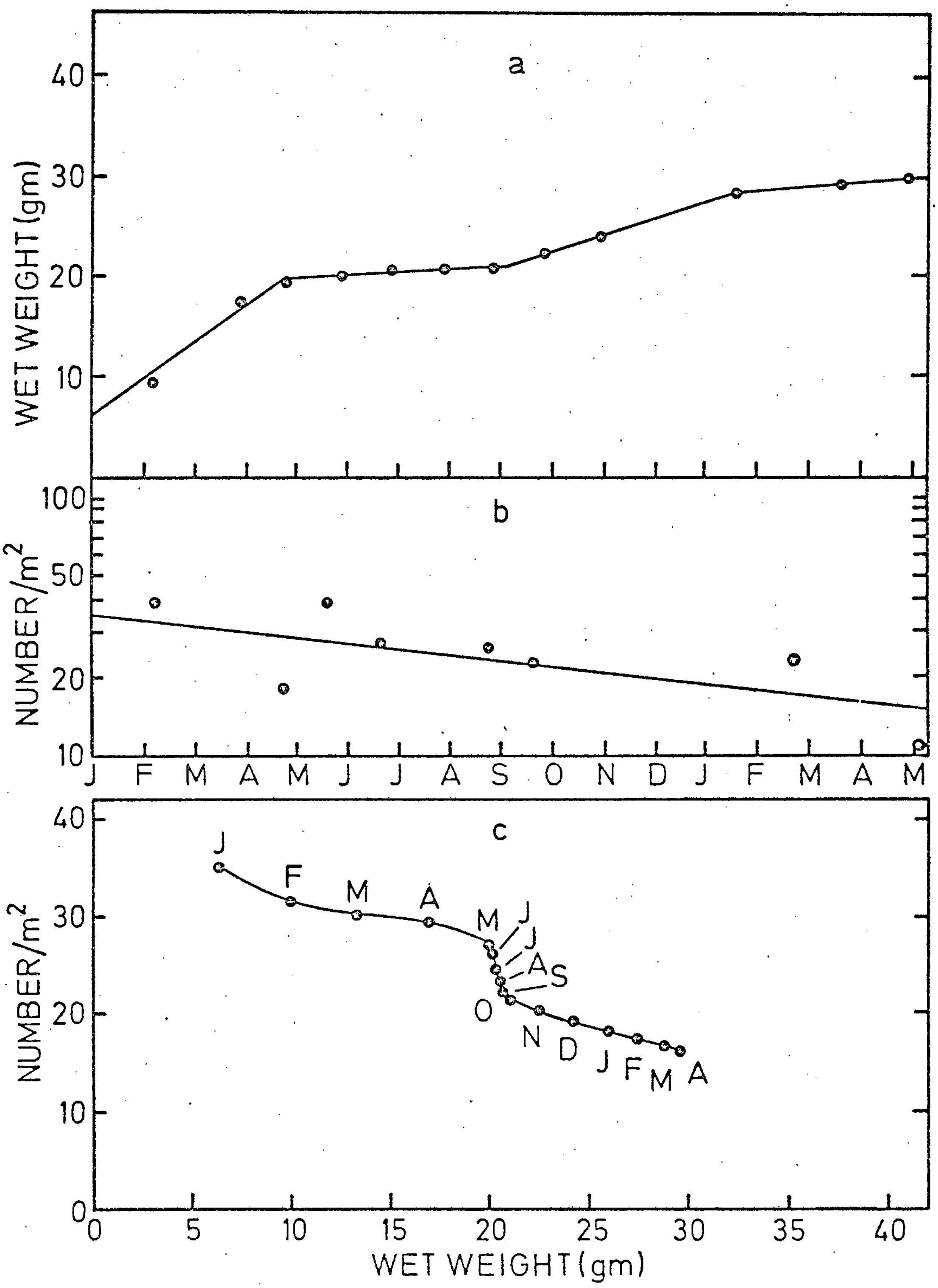


Fig. 1.16 Method used for deriving smoothed Allen curves from growth and mortality data.

(a) Increase in wet weight against time

(b) Decrease in numbers against time

(c) Resultant Allen Curve

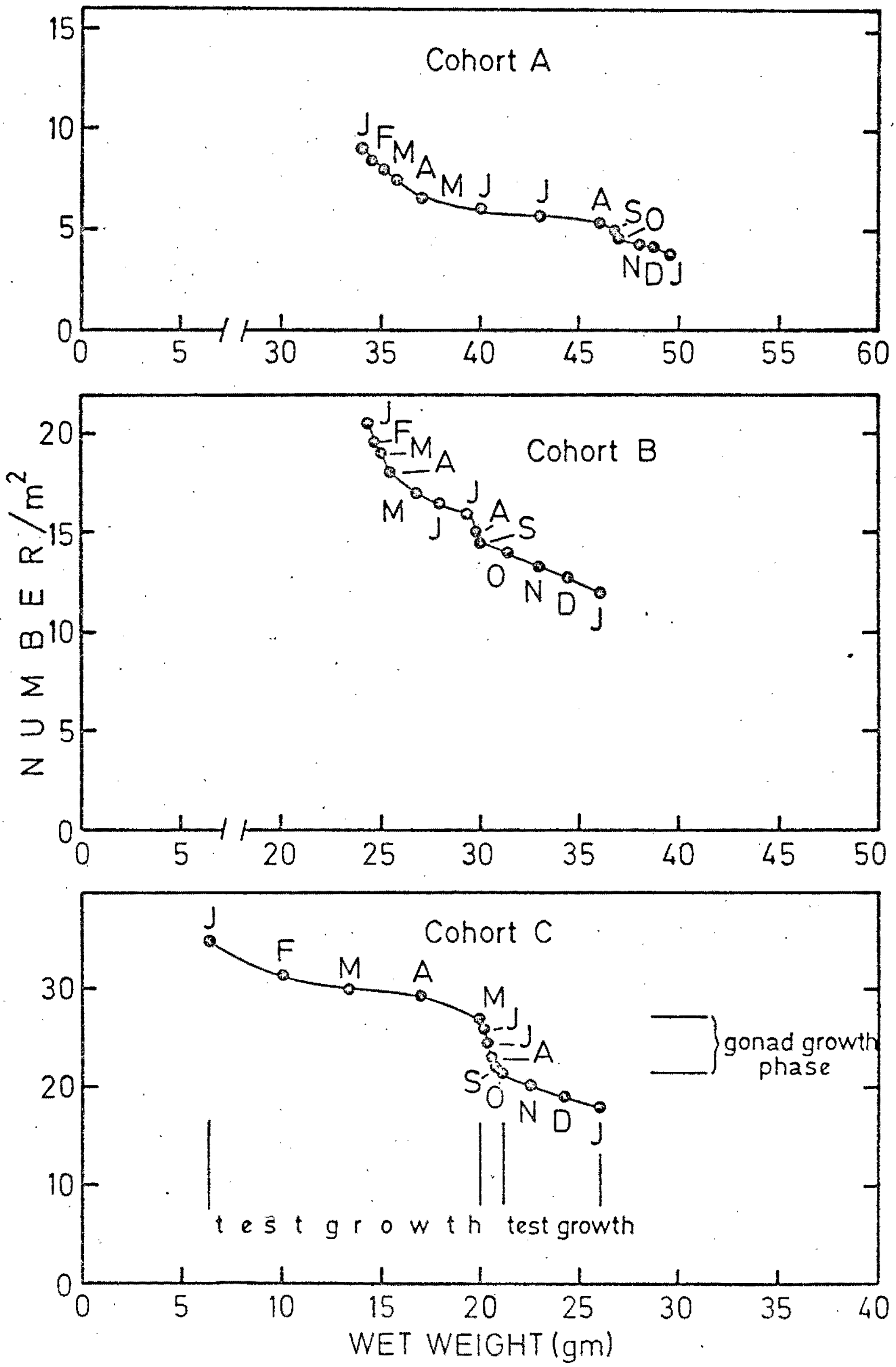


Fig. 1.17 Production curves for each cohort in the Robben Island population derived by the method used in Fig. 1.16.

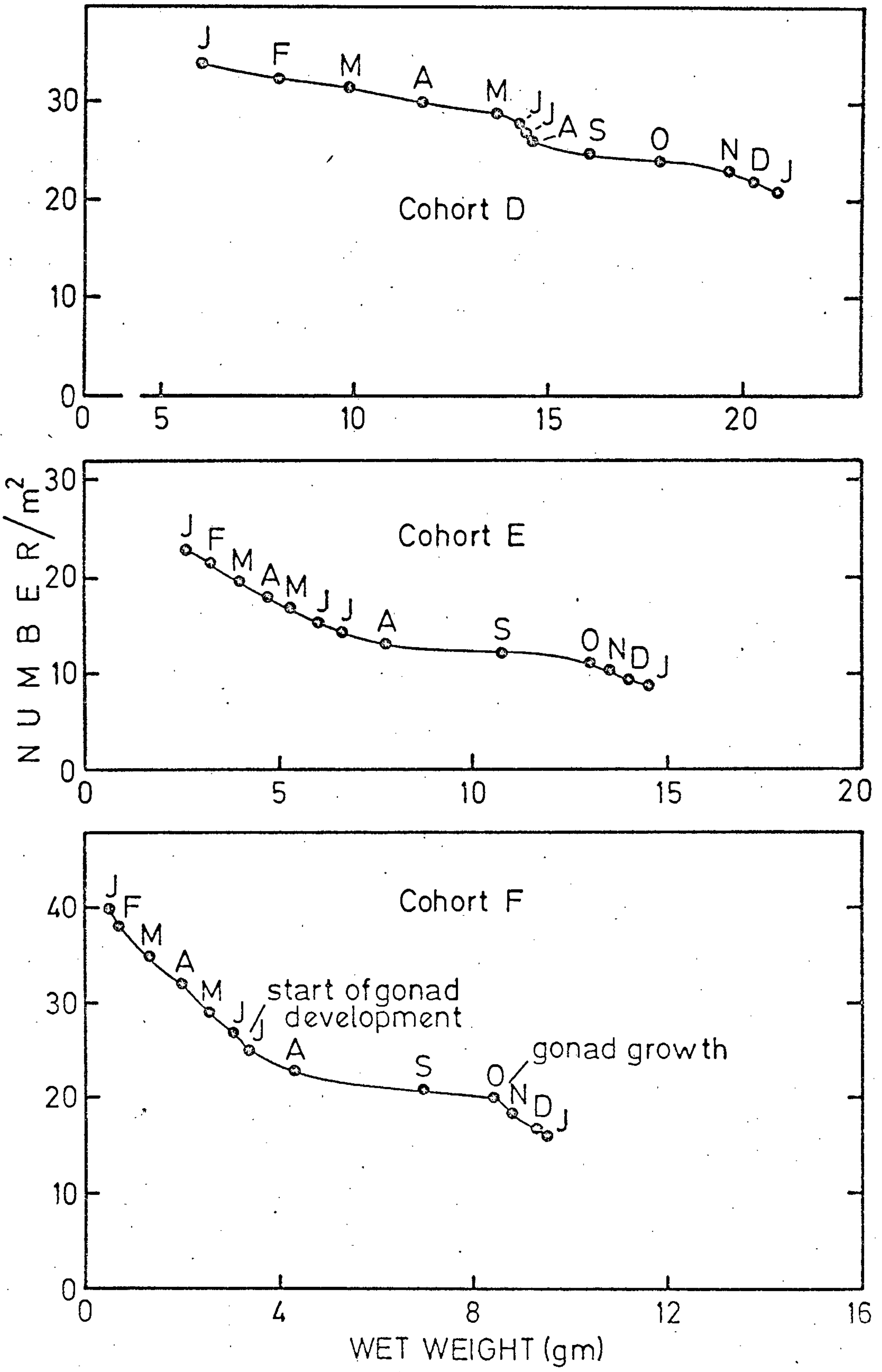


Fig. 1.17 (Contd)

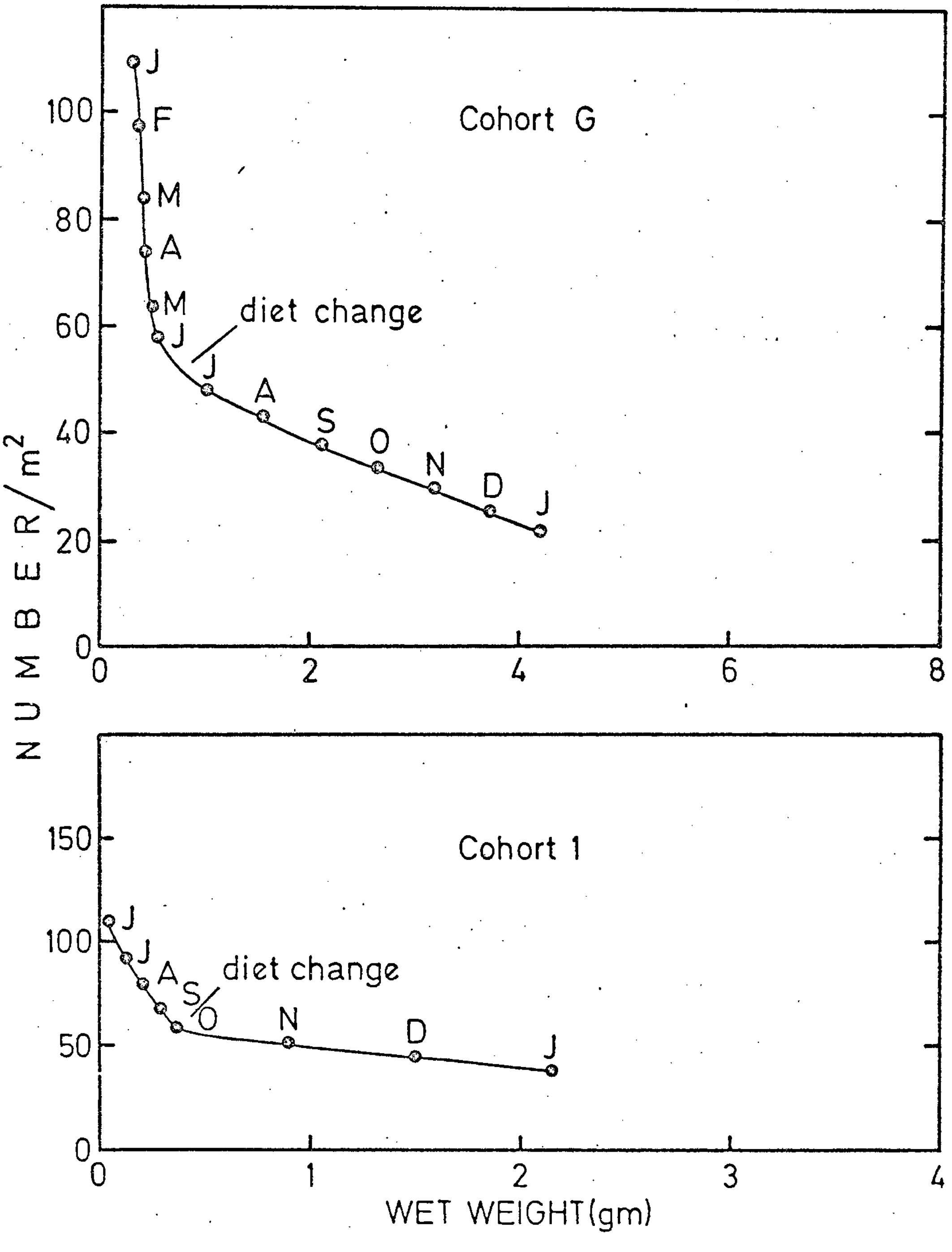


Fig. 1.17 (contd)

Both cohorts G and 1 (minimal gonad development) exhibit typical Allen curves. Any production that occured before June 1973 in Cohort 1 was considered negligible and has been ignored. The steep left hand tail of the G and 1 curves indicate high mortality and low production of individuals below 10mm in size. The marked increase in weight (ie. production) exhibited by cohort G in July, and by Cohort 1 in October corresponds with the presumed change in diet from detritus to debris at 10mm diameter.

In the sexually mature age groups, somatic production alternates with gonad production, with high production at low gonad index and vice versa. The production curves of Cohorts A and B only show a single period of fast growth rate which indicates that they only spawned once during 1973. This may indicate a tendency toward reproductive senility after about 5 years, a phenomenon also exhibited by Evechinus chloroticus (Dix, 1970c).

Oatland Point.

The production curves calculated by the Allen method are shown in fig. 1.18 and the production parameters estimated from the curves are listed in table 1.8.

Animals in the Oatland Point population show a similar increase in growth rate from 10mm to 20mm due to diet change. After 20mm in size gonad development again alternates with somatic growth. The two populations studied differ only in the duration of gonad development and somatic growth.

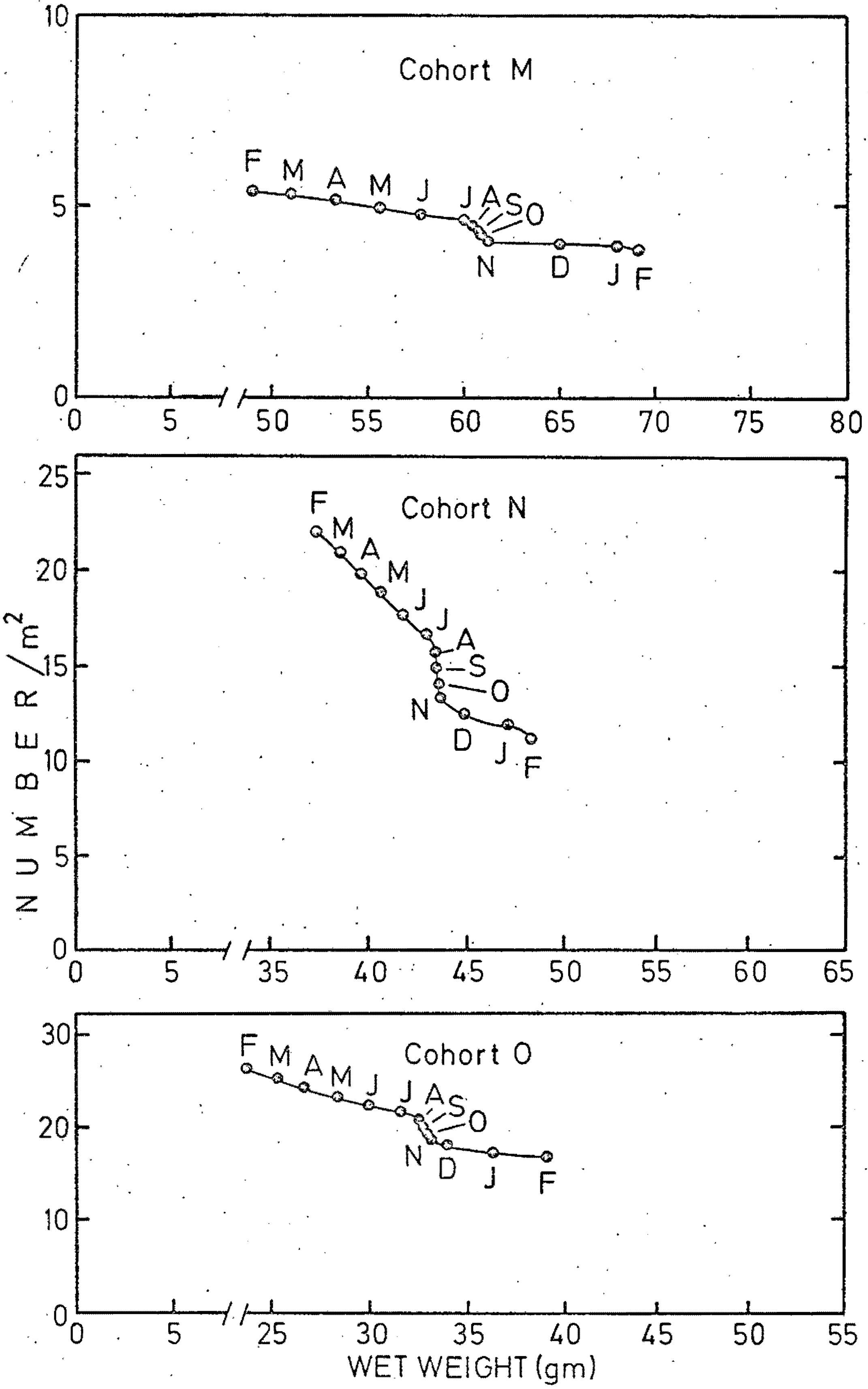


Fig. 1.18 Oatland Point production curves-legend as in Fig. 1.17.

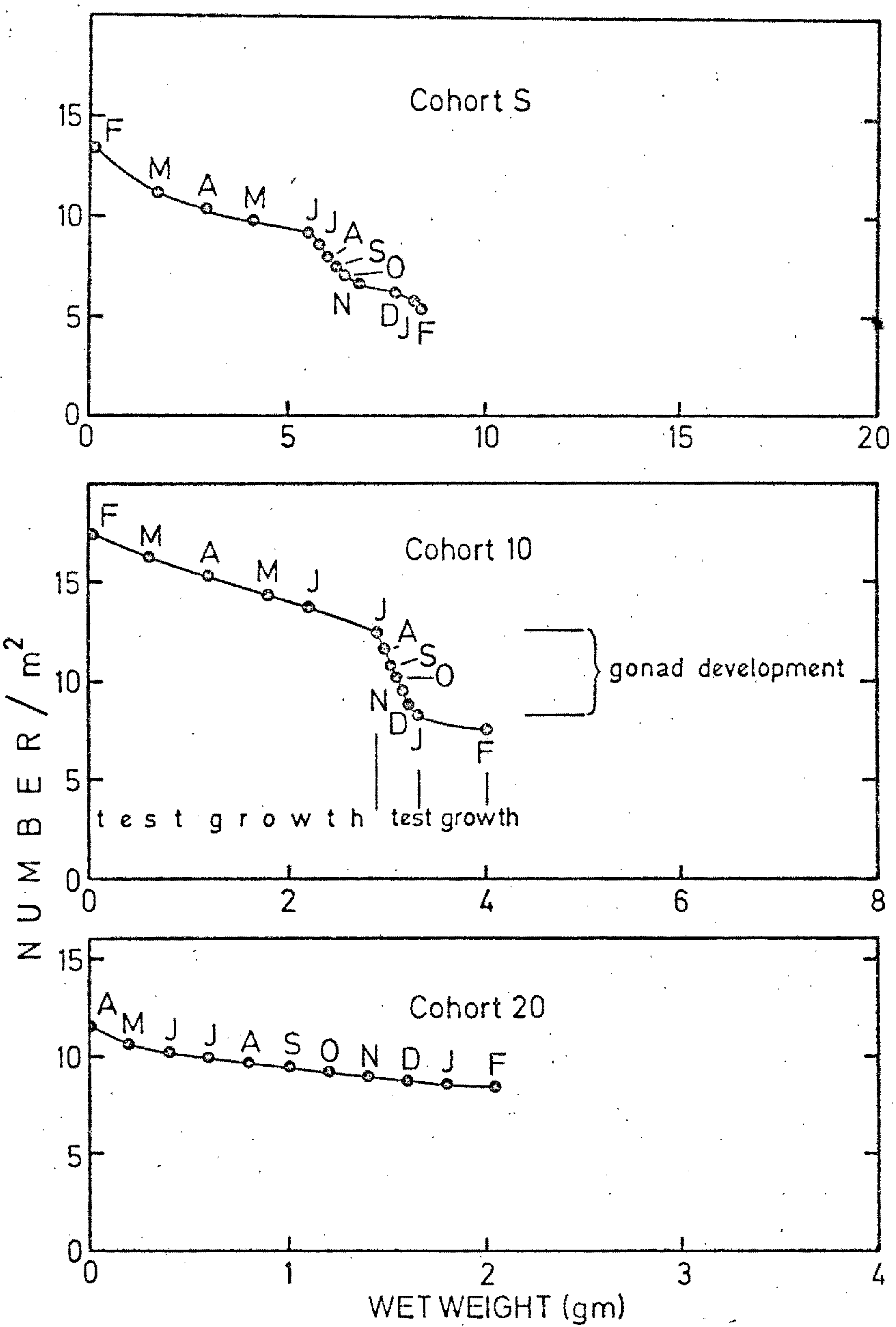


Fig. 1.18 (contd)

Table 1.8 Production parameters of the Oatland Point population of *Parechinus angulosus* calculated from the smoothed Allen curves.

Cohort	Annual production (Pg) gm/m^2	Mortality losses (E) gm/m^2	Biomass (B) Kg/m^2
M	92,7	11,5	3,48
N	176,2	50,1	9,03
O	320,0	65,6	8,31
P	458,2	64	8,60
Q	292,6	113,2	4,14
R	128,2	56,3	1,11
S	75,12	29,77	0,471
10	52,0	21,84	0,304
20	18,20	2,16	0,082
Population	1,613 Kg	0,414 Kg	35,526 Kg
			$\bar{B}$ =2,729 Kg

BIOMASS

Robben Island

The biomass curve shown in fig. 1.19. was calculated from the Allen production curves shown in fig. 1.17. The fact that change in wet weight is due only to test growth is reflected in the biomass curve. The rapid production (Pg) rate of the population between January and May, coupled with an assumed constant mortality rate, is shown by a rise in biomass from 1,33kg/m^2 to 1,82kg/m^2 over this period. The tail off in (Pg) body growth between April and August coincides with an increase in gonad index. Thus although gonad production (Pr) increased between April and August it was not reflected by an increase in wet weight biomass. The second rise in biomass between August and November coincided with the post-spawning period of rapid growth, followed by a tail off to January 1974 as gonad development progressed. Population biomass was higher by 0,57kg/m^2 at the start of 1974 than it was a year earlier. Biomass did however start to drop from January to April when sampling was terminated. The mean biomass for the January 1973 - January 1974 period was 1,786kg/m^2 and the P/$\bar{B}$ and E/$\bar{B}$ (elimination/biomass) ratios were 1,039 and 0,351 respectively.

Oatland Point

Fluctuations in biomass calculated from the Oatland Point production curves are shown in fig. 1.20. A steady rise between February and June indicates that growth (Pg) was greater than mortality. The sharp drop in biomass from 3,0kg/m^2 in July to 2,5kg/m^2 in December indicates that elimination is greater than growth. This phase coincides with the extended period during

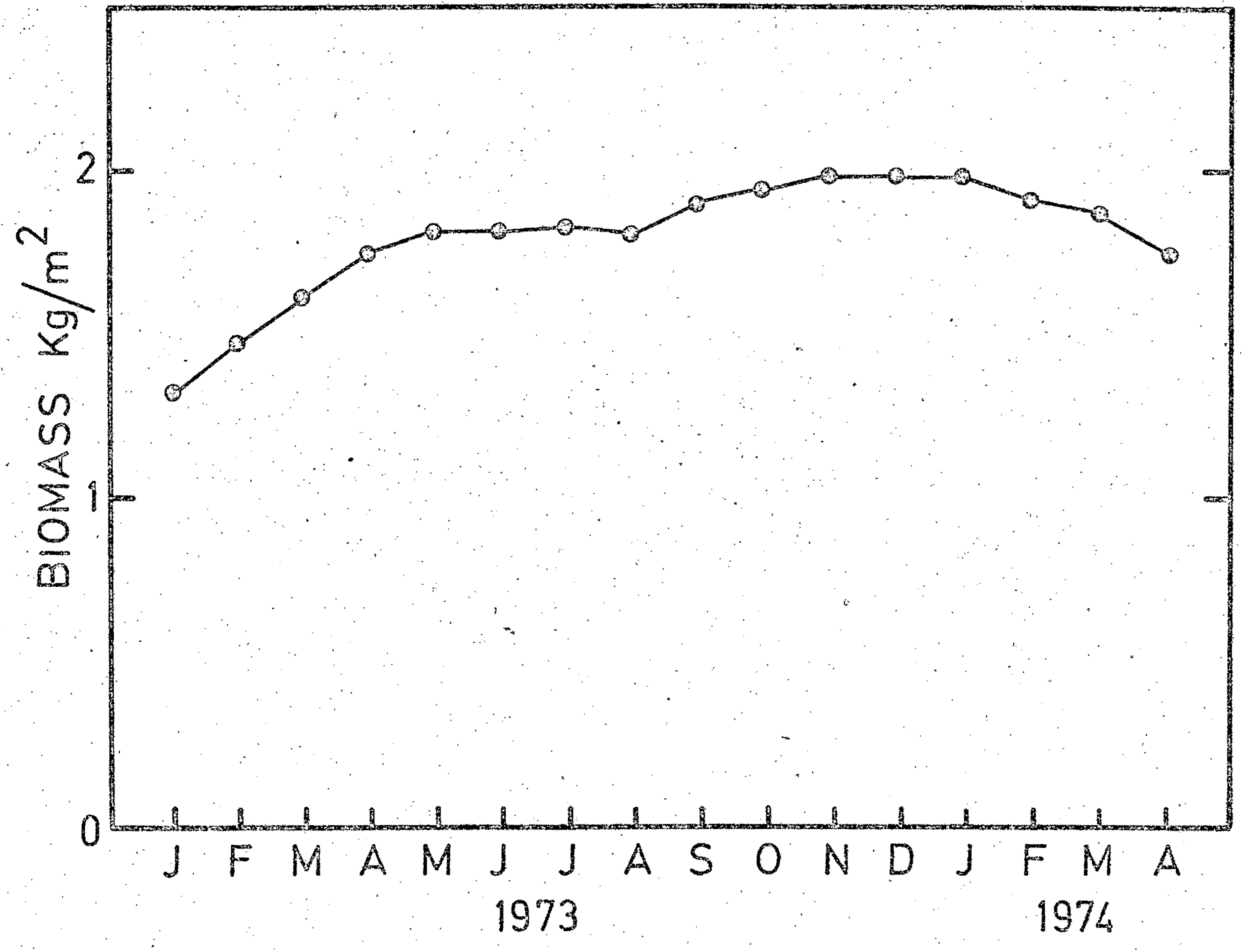


Fig. 1.19 Mean biomass fluctuation of the Robben Island population between January 1973 and April 1974.

which the gonad index increased. Biomass then began to increase with test growth after the October spawning. The Oatland Point population had a residual biomass of 2,45kg/m^2, while the average biomass over the study period was 2,73kg/m^2. The P/$\bar{B}$ ratio of the population was 0,591 and the E/$\bar{B}$ ratio was 0,151.

DISCUSSION

Population Structure

The structure of the populations at Robben Island and at Oatland Point (False Bay) differ very little. The Oatland Point population may live slightly longer.

Recruitment appears to be very much lower in the False Bay population as reflected by the low numbers of small animals sampled at Oatland Point. However, this may be due to the cobble-like substrate at the study site being unsuitable for larval settlement as apposed to the craggy substrate at Robben Island which appears to provide protected habitats for small animals and to be ideal for larval settling. Resolution of this problem requires samples to be taken over a much greater area than was done in this study.

Growth

The growth patterns were essentially the same in the three populations studied. Initially growth appeared to be governed by the nature of the food consumed and later by the development of gonads.

Up to 10mm in diameter, detritus is assumed to be the major food source and the growth is slow. From 10 - 20 mm in diameter the ingested material is predominantly debris and the average growth rate is almost double the rate of growth during the early phase. At 20 mm growth rate decreases as gonad development becomes more prominant. Once gonad development has started, there is an alternation between gonad growth and test growth. The populations studied differ in the duration of the test growth and gonad growth phases in that the duration of the gonad growth to test growth is shorter in the Robben Island population than in the Oatland Point group. A comparison of the regressions of mean growth rates described by the von Bertalanffy growth equations, shows that statistically the difference in slopes is not significant, while the intercepts are significantly different $(P < 0,01)$. This implies that the average growth rate of the younger animals in the Robben Island population is slightly higher than those in the Oatland Point population, while the growth of the older animals at Robben Island is slightly lower than those at Oatland Point. The differences in growth rate of the small animals could be attributed to a difference in food supply as there is a far greater volume of detrital material on the west coast than False Bay.

The slower growth of the larger animals and the lower maximum size attained at Robben Island may be a function of exposure. Ebert (1968) reports on an inverse relationship between growth rate, "optimum size" and exposure, which he attributes to spine abrasion and breakage, and the channeling of energy into spine repair as opposed to test growth. The number of animals at the exposed Robben Island site that have broken spines is far higher than the relatively sheltered Oatland Point community. Growth rates of the Rockeater population compare closely with the Oatland Point group which implies that the estimated growth rates were representative of the animals in the warmer False Bay region.

Mortality

From the regressions of log numbers against time it appears that mortality is higher in the west coast population. However, the biomass lost through mortality is $0,627kg/m^2$ and $0,414kg/m^2$ per year and the $E/\bar{B}$ ratios are 0,351 and 0,151 at Robben Island and Oatland Point respectively. Assuming a calorific value of 287 cal/g live weight (found for *Strongylocentrotus droebachiensus* (Brawn *et al*, 1968), then the Robben Island population passes on 179,94 Kcal/m^2 per annum through mortality and the Oatland Point population 118,81 Kcal/m^2 per annum.

Production

The west coast population produces (Pg) 447,72 Kcal/m^2/yr while the False Bay animals produce 350,95 Kcal/m^2/yr. The $P/\bar{B}$ ratios of 1,039 and 0,591 for the west and False Bay communities respectively, show that the annual (Pg) production per unit biomass on the west coast is twice that in False Bay. The fact that the rate of production (Pg) depends on the rate of body growth which in turn is dependant on size, could explain the higher production rate on the west coast. The Oatland Point population is made up of a high proportion of large (slow growing) animals, reflected by the low density (145/m^2) with high biomass (2,729kg/m^2) while the Robben Island population has a higher proportion of smaller (faster growing) animals shown by the high density of 220/m^2 and low biomass (1,786kg/m^2). Thus the low Pg at Oatland Point coupled with a high biomass reduces the $P/\bar{B}$ ratio and vice versa.

PART II

CONSUMPTION, EGESTION AND ASSIMILATION

INTRODUCTION

A number of sea urchin species including Strongylocentrotus fransicanus, S. purpuratus and Lytechinus anamesus have been seen actively attacking the holdfast of established kelp plants (Leighton etal, 1966). The Southern African echinoderm Parechinus angulosus has only on rare occasions been seen to actively feed on attached plants, It appears to be a fortuitous feeder and feeds mainly on detached pieces of seaweed. It would therefore be better termed a debris-feeder rather than an active grazer as debris feeding is the rule rather than the exception. These terms are not mutually exclusive because P. angulosus does prevent the establishment of new plants (Fricke, pers. comm.) by removing any new sporelings and will also feed on the ends of attached fronds which touch the substrate and can be trapped by the urchins.

Generally Parechinus angulosus capture floating algal fragments on the aboral surface where they are held before being passed to the jaws. The delay between capture and passing to the mouth may allow "skin digestion" to occur (Pequignat, 1966), though this aspect of digestion has not been investigated.

Feeding experiments in the laboratory on sea urchins are of limited value due to the change in consumption rate with variation in food availability. (Lasker and Boolootian, 1960). Therefore under laboratory conditions with a plentiful food supply feeding and defaecation rate would be maximal. Farmanfarmaian and Phillips (1962) mention a transition of algal fragments from a "bite form" without bacterial enrichment to a semidigested "bag form" enriched with bacteria, in the stomach of urchins ingesting a limited amount of food. Under these conditions faecal pellets are egested in the bag form. However, when food is plentiful the stomach contents do not attain the bag form and faecal pellets are egested in the bite form. Here digestion is incomplete, and assimilation per unit weight of ingested alga is minimal.

METHODS AND MATERIALS

A single six day feeding experiment was conducted in a recirculating seawater aquarium system. The experiments had to be discontinued due to recurring failure of the system.

From 3 - 6 animals of three size classes from Robben Island and Oatland Point were placed in separate tanks. The animals were allowed to acclimate to the water temperature of 13,1°C for one week. Temperature was kept constant throughout the experiment as temperature variations alter the feeding rate (Fuji 1962, 1963). During the acclimation period the animals were fed on *Ecklonia maxima* fronds. *E. maxima* was used as the food source because it is common to both study areas. This also rules out food preference as a factor which appears to operate in a number of benthic invertebrates (Paine and Vadas, 1969) Feeding during the holding period prior to the start of the experiment allowed the gut to reach a fullness equilibrium (Fuji, 1967; Miller and Mann, 1973). 20 gm of *Ecklonia* frond cut into pieces, was supplied to each group of urchins at the start of the experiment. After three days any remaining food was removed and replaced by a further 20 gm. The removed kelp was weighed wet, after blotting off excess water, and was then dried at 60°C for 48 hours before reweighing. A linear regression of wet weight against dry weight was calculated in order to estimate dry weight of kelp eaten from the wet weight measurements before and after the experiment. Every 24 hours egested material in the form of faecal pellets was siphoned off the bottom of each holding tank and collected. Each collected sample was filtered through Whatman's No. 1. filter paper and then dried at 60°C for 48 hours to determine the dry weight of the faeces egested.

RESULTS

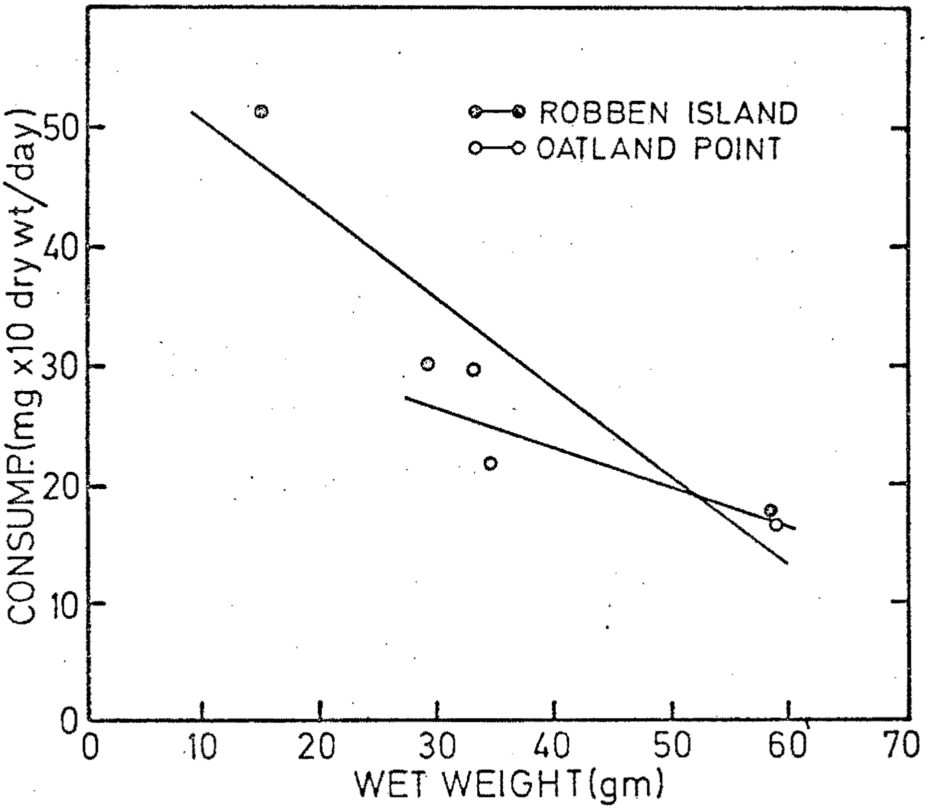
The daily rate of feeding, defined as the ratio of ingested food over a 24-hour period against the total body weight of the sea urchin (Fuji, 1967) was calculated for each population. The results are very crude as they are based on a single feeding experiment.

In both cases the regressions of daily rate of feeding per gram animal expressed as mg. dry weight of E. maxima, versus live body weight, showed negative linear correlations (fig. 2.1). There is a statistically significant difference in both the slope and intercept of the linear regressions of the daily rate of feeding versus size in the Robben Island and Oatland Point populations. (table 2.1).

Table 2.1. Regression equations of the daily rate of feeding per gm animal (dry wt. of *Ecklonia maxima*) versus live weight of *Parechinus angulosus* from Robben Island and Oatland Point. Y = daily rate of feeding (mg) X = animal live weight (gm)

Study Area	Regression equation Y = mX + C	Probability of difference between regressions	
		Slope	Intercept
Robben Island	Y=-0,7280X + 58,26	0,02	0,001
Oatland Point	Y=-0,0371X + 38,54		

Fig. 2.1 Daily rate of feeding per gm animal (dry wt. of *Ecklonia maxima*) (ordinate) and live weight of *P. angulosus* (abscissa) from Robben Island and Oatland Point.



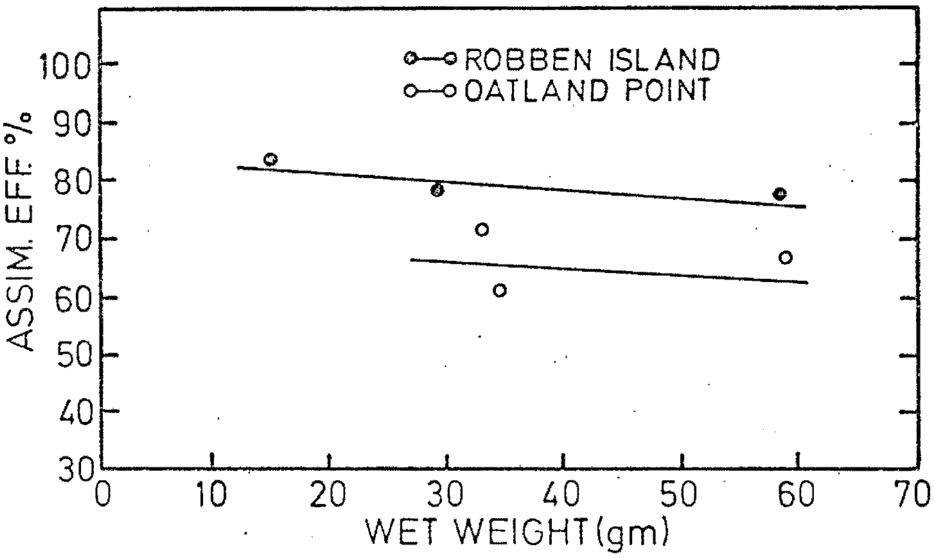


Fig. 2.2 Assimilation efficiency against live weight of *P. angulosus* from Robben Island and Oatland Point.

The mean size of the animals above 10mm in diameter (as 10mm and above are assumed to eat debris) were 30,06 (11,31gm) and 36,50mm (20,84gm) for the Robben Island and Oatland Point populations respectively. The consumption rate of an animal of mean size was 50mg dry weight of E. maxima/day for the Robben Island population and 49mg dry weight/day for the Oatland Point group. Thus with a mean population density of $220/m^2$, the population consumption of the Robben Island population is 11,00gm dry weight of kelp/day which is equivalent to 77,44gm wet weight of Ecklonia maxima per day.

The Oatland Point group has a density of $145/m^2$ and a consumption rate of 7,11gm dry weight or 50,019gm wet weight of E. maxima per day. Assuming a calorific value of 2,7 Kcal/gm dry weight for kelp and 2,6 Kcal/gm dry weight for faeces (Miller and Mann, 1973), the annual consumption is 10840,5 Kcal and 7001,97 Kcal for the west coast and False Bay populations. 13mg and 21mg dry weight/day are egested by an animal of average size in the Robben Island and Oatland Point populations respectively. This is equivalent to the egestion of 2714,14 Kcal/year and 2889,7 Kcal/year respectively.

Assimilation efficiencies were calculated for both populations following the assimilation notation given by Fuji (1967):

$$\text{Assimilation efficiency in } \% = \frac{\text{dry weight of food assimilated}}{\text{dry weight of food eaten}} \times 100$$

when,

$$\text{dry weight of food assimilated} = \text{Dry weight of food eaten} - \text{dry weight of faeces}$$

Assimilation efficiency plotted against size on a linear scale gave negative correlations (fig 2.2). There was no statistically significant difference between slopes of the regressions but a strongly significant difference in intercepts (table 2.2).

Table 2.2. Regression equations of the assimilation efficiency versus live weight of P. angulosus from Robben Island and Oatland Point.
Y = assimilation efficiency (%) X = wet weight (gm).

Study Area	Regression equation Y = mX + C	Probability of difference between regressions	
		Slope	Intercept
Robben Island	-0,0791X + 74,09	-	0,001
Oatland Point	-0,1705X + 54,11		

Discussion

The decrease in feeding rate with age shown in fig. 2.1., appears to be correlated with a decrease in metabolic rate with age and also with gonad development (Fuji 1962, 1967). Fuji (1963, 1967) also reports that Strongylocentrotus intermedius shows a decrease in feeding rate with temperature rise. However, as temperature was kept constant for the duration of the experiment, the lower feeding rate exhibited by the Oatland Point population implies a fundamental difference in metabolic rate possibly associated with the generally higher temperature regime of False Bay.

The assimilation results are similar to those found by Fuji 1962) working with <u>Strongylocentrotus intermedius</u>. He mentioned that there was no statistically significant difference in the assimilation efficiency of juveniles and adults. A significant difference in slope from the horizontal would imply a difference in assimilation efficiency between juveniles and adults. In the case of <u>Parechinus angulosus</u>, the assimilation efficiency versus size regressions of the Robben Island and False Bay populations show significant differences from the horizontal. The assimilation efficiency of the Oatland Point population is significantly lower than that of the Robben Island urchin community although the temperatures in False Bay are generally higher. This is contrary to the findings of Fuji)1962, 1967) who found that the assimilation effieiency of <u>S. intermedius</u> increase with rising water temperature.

These results must be veiwed with caution due to the limited data on which the results were based. Nevertheless they do give some indication of the feeding rates and the assimilation efficiencies of <u>Parechinus angulosus</u> from regions of differeing temperature conditions.

PART III

RESPIRATION

RESPIRATION.

INTRODUCTION

The sea urchin *Parechinus angulosus* forms one of the major prey species of the commercially important rock lobster *Jasus lalandii* and is also the major herbivore in the Southern African kelp beds. A knowledge of its productivity would be beneficial in manipulation of the kelp zone ecosystem to increase the yield of rock lobster. However, determination of population production by conventional means is time consuming and laborious and requires data on population dynamics and ecological energetics of the species. A short cut method would therefore be advantageous. McNeill and Lawton (1970) have shown that there is a correlation between respiration and production. Though their population respiration-population production regression has rather wide confidence limits it does not affect the major conclusions (Miller, Mann and Scarratt, 1971).

This approach to the determination of population production has been applied to two populations, one off Robben Island which comes under the influence of the cold Benguela Current System, and the other at Oatland Point in False Bay where the water is generally 4-5°C warmer.

METHODS AND MATERIALS

The execution of respiration experiments in the field was dependant on weather and sea conditions. When possible experiments were carried out at bimonthly intervals for twelve months. Animals of various sizes were removed from rocks with minimum disturbance and individuals of approximately equal size were assembled into groups and placed in 900 ml. wide mouthed jars. Their numbers were appropriate to the use of 10-20% of the oxygen in the water during a 2 hour experiment. Two jars were left empty as controls. The bottles were sealed and suspended on a bar by floats just off the sea bed (fig. 3.1). After two hours, samples were taken from each jar and their oxygen concentration determined by the Winkler method (Strickland and Parsons, 1972). The volume of the oxygen used by the different sized animals was obtained by difference between experimental and control jars. The live animals were returned to the laboratory where they were weighed wet. Before weighing they were allowed to drain on absorbant towelling for 5 minutes (Giese, 1966, Belman and Giese, 1974).

On two occasions the experiments were repeated at night at Oatland Point, in an attempt to determine whether a diurnal fluctuation in respiration rate resulted from increased nocturnal activity. The margin of error was decreased on the second occasion (11-2-74) as the animals were placed in a compartmented cage (Appendix 2) on the sea bottom, and fed with fronds of Ecklonia maxima for four days prior to the experiment. In this way it was hoped that any difference in respiration rate that may result from previous feeding variations (Newell, 1970) would be ruled out. On completion of the experiment the animals were returned

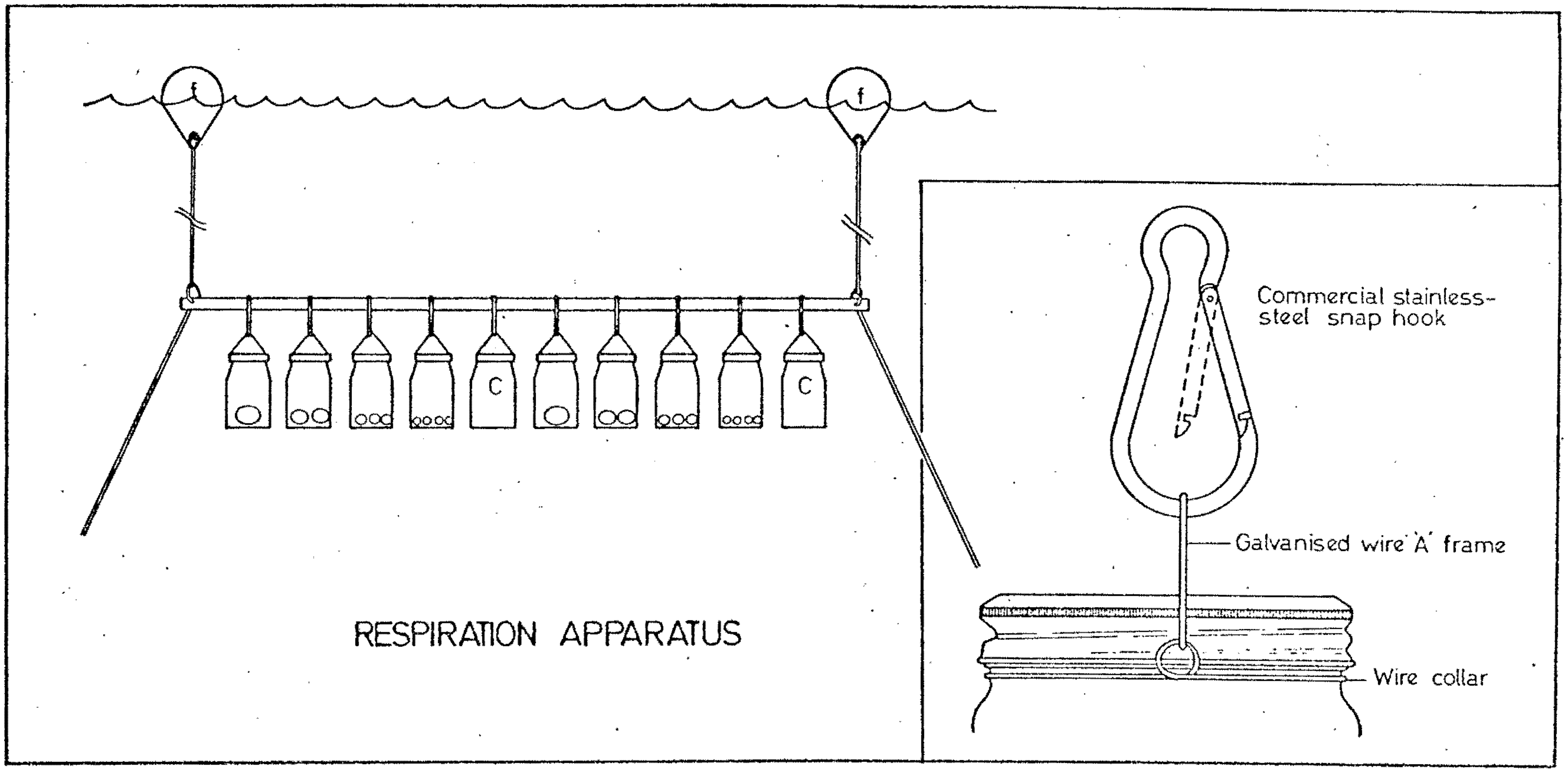


Fig. 3.1 Respiration apparatus.

to their respective compartments in the cage where they were left for a further four days with an abundant food supply. The temperature difference between the two experimental runs was only 0,2°C and could therefore be ignored. The animals were then weighed as previously described.

All results were corrected to a 24 hour time scale. Log/log regressions of the Oxygen consumption/weight relationship were calculated by the least squares method on a Univac 1106 computer. These calculated regressions were used to construct annual respiration curves.

RESULTS

Robben Island

Fig. 3.2. shows the oxygen consumption per animal per day plotted against live weight on logarithmic scales, for eight occasions between June 1973 and March 1974 when respiration was measured in the field. The regression equations are listed in table 3.1., for equations of the form:

$$R = aW^b$$

where R = respiration rate (ml 0_2/24hrs)

a = intercept on the ordinate

W = wet weight

b = exponent.

Table 3.1. Regression terms for the equation relating $\log_e$ Oxygen consumption (ml 0_2 per animal/24hrs) to Log_e live weight of all the size classes between June 1973 and March 1974.

Date	Temperature °C	a	b	r
23-6-73	12	0,7374	0,82	0,99
7-8-73	14	0,5991	0,83	0,98
26-10-73	15	0,9768	0,63	0,94
13-12-73	14	0,4271	0,96	0,95
6-2-74	14,8	0,7381	0,69	0,98
6-3-74	15	0,8999	0,83	0,95
10-5-74	14,6	0,5951	0,79	0,99
27-6-74	15,2	1,0434	0,66	0,98

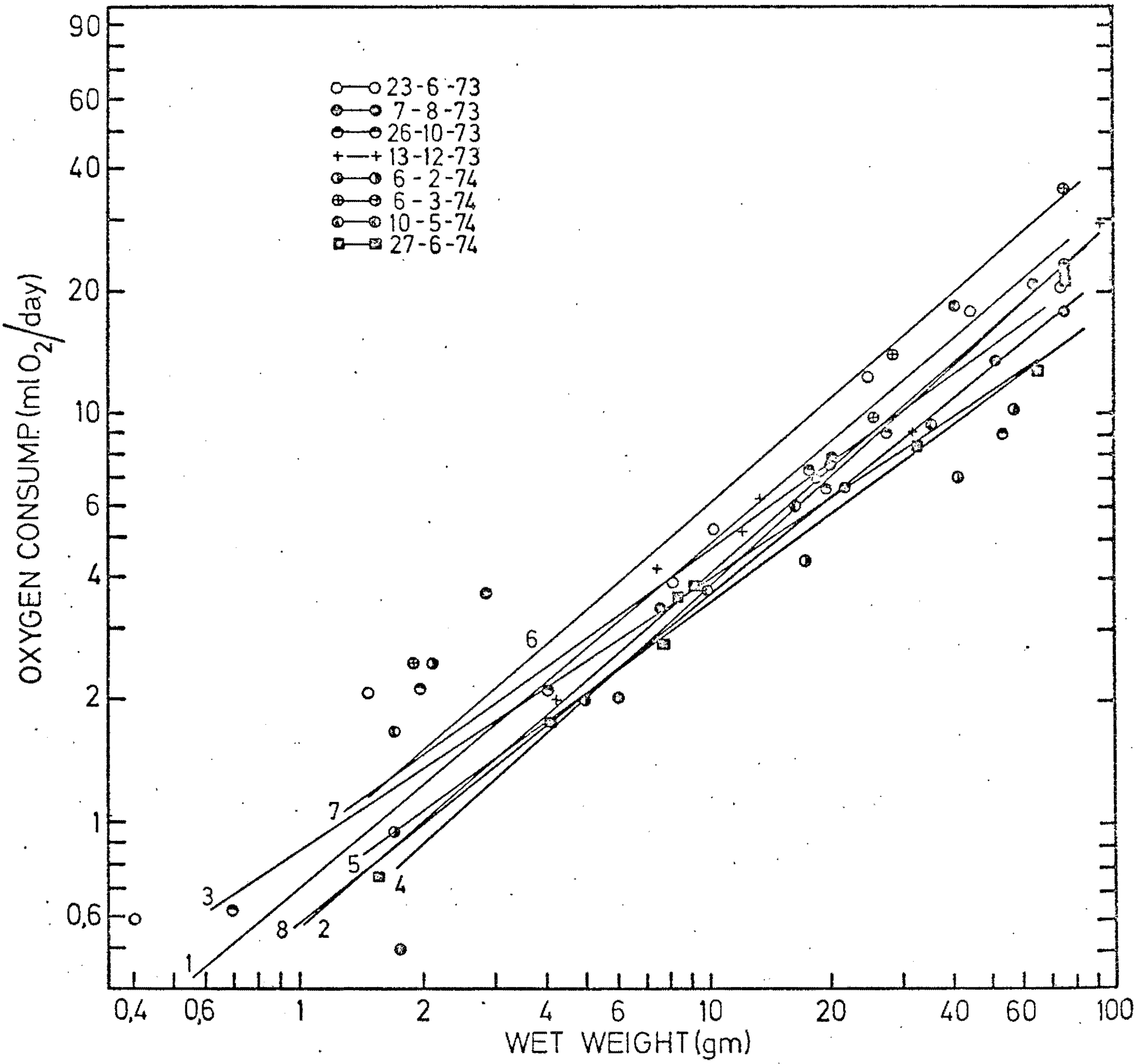


Fig. 3.2 Robben Island. Oxygen consumption of animals spanning the whole size range, plotted against wet weight.

The graphs of oxygen consumption versus weight, show an irregular relationship between respiration rate and temperature. A similar irregularity was found by Miller and Mann (1973) working on <u>Strongylocentrotus droebachiensus</u>.

In <u>Parechinus angulosus</u> seasonal fluctuations of the gonad cycle have a bigger effect on the respiration rate than the small temperature fluctuations experienced both at Robben Island and Oatland Point.

An attempt was made to separate the sexually mature animals from the sexually immature, so as to plot their respiration rates independantly. Unfortunately insufficient numbers of animals of 2gm in weight or less (17 mm or less are immature, Fricke, 1974) were used in the experiments so only a crude picture could be obtained.

Most of the oxygen consumption against log weight regressions (table 3.2.) were calculated from two points only. No regression could be computed for the sexually immature animals in December 1973 or March and May 1974 because only a single point was available in each case. (fig.3.3.) Table 3.2. lists the values for the respiration equations of the form.

$$R = aW^b$$

Similar regressions were plotted for those animals above 11,3 gm in weight (greater than 30mm in diameter) as they were all considered to be sexually mature (fig 3.4.) Table 3.3. lists the regression equations for the lines in fig. 3.4.

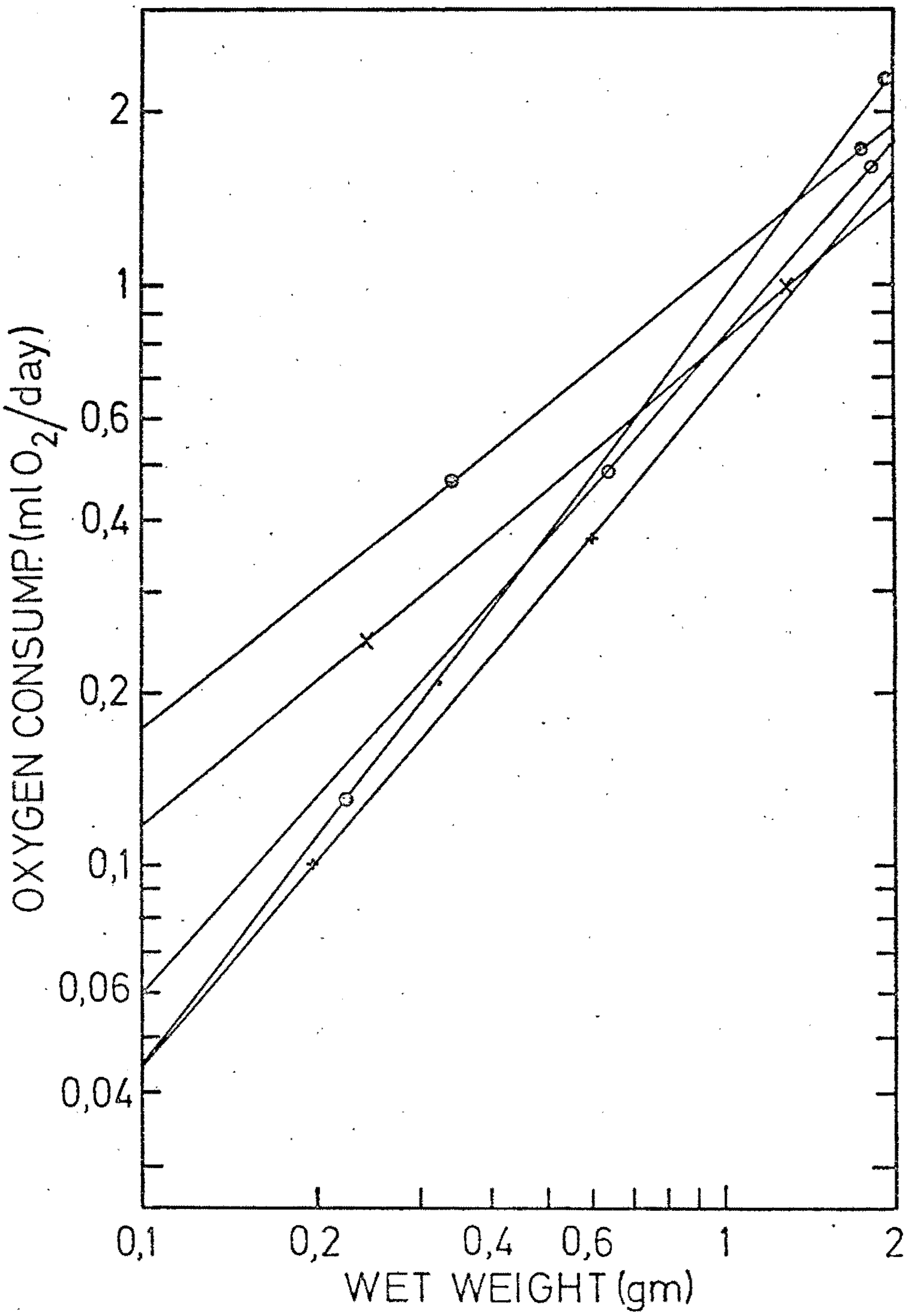


Fig. 3.3 Oxygen consumption of sexually immature animals (less than 2 gm) plotted against wet weight on logarithmic scales.

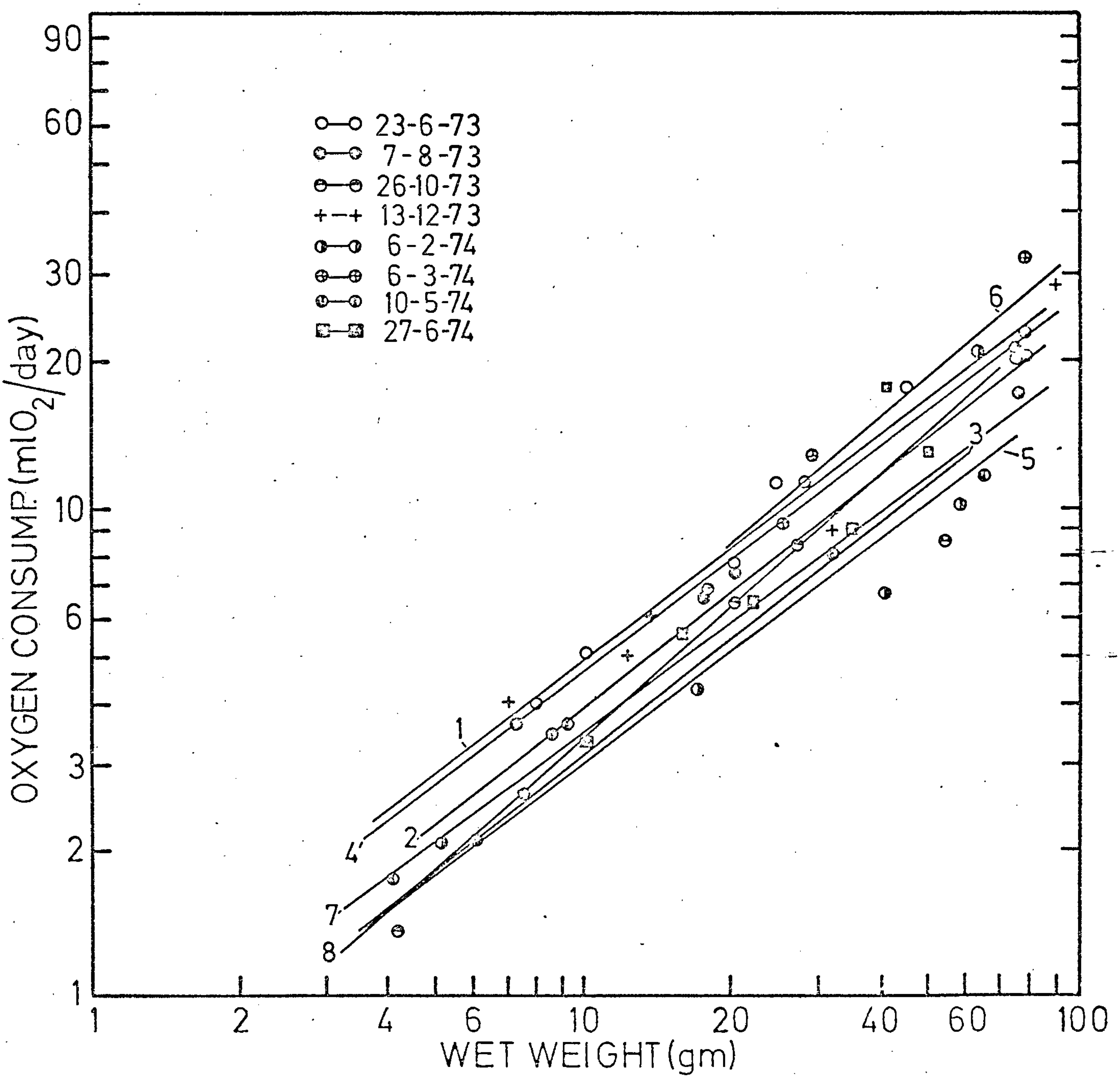


Fig. 3.4 Oxygen consumption of sexually mature animals (above 3gm) plotted againsts wet weight on logarithmic scales.

Table 3.2. Regression equations for $\log_e$ Oxygen consumption during 24hrs. versus $\log_e$ live weight of *Parechinus angulosus* individuals of 2gm or less in weight. (Sexually immature)

Date	Temperature °C	a	b
23-6-73	12	0,00586	1,07
7-8-73	14	0,00663	1,04
26-10-73	15	0,00233	1,31
6-2-74	14,8	0,01858	0,83
27-6-74	15,2	0,02917	0,79

Table 3.3. Regression equations for $\log_e$ Oxygen consumption during 24hrs versus $\log_e$ live weight of *Parechinus* individuals above 11,3gms. (sexually mature)

Date	Temperature °C	a	b	r
23-6-73	12	2,37	0,77	0,99
7-8-73	14	1,64	0.79	0.98
26-10-73	15	1,52	0,78	0,94
13-12-73	14	0.98	0.91	0,56
6-2-74	14,8	1,65	0,76	0,93
6-3-74	15	1,30	0,85	0,92
10-5-74	14,6	1,85	0,76	0,99
27-6-74	15,2	0,07	0,90	0,94

That gonad development has a marked effect on respiration rate is brought out in the composite diagram of oxygen consumption plotted against time together with gonad index against time and temperature fluctuation against time (fig. 3.5.). The immature juveniles

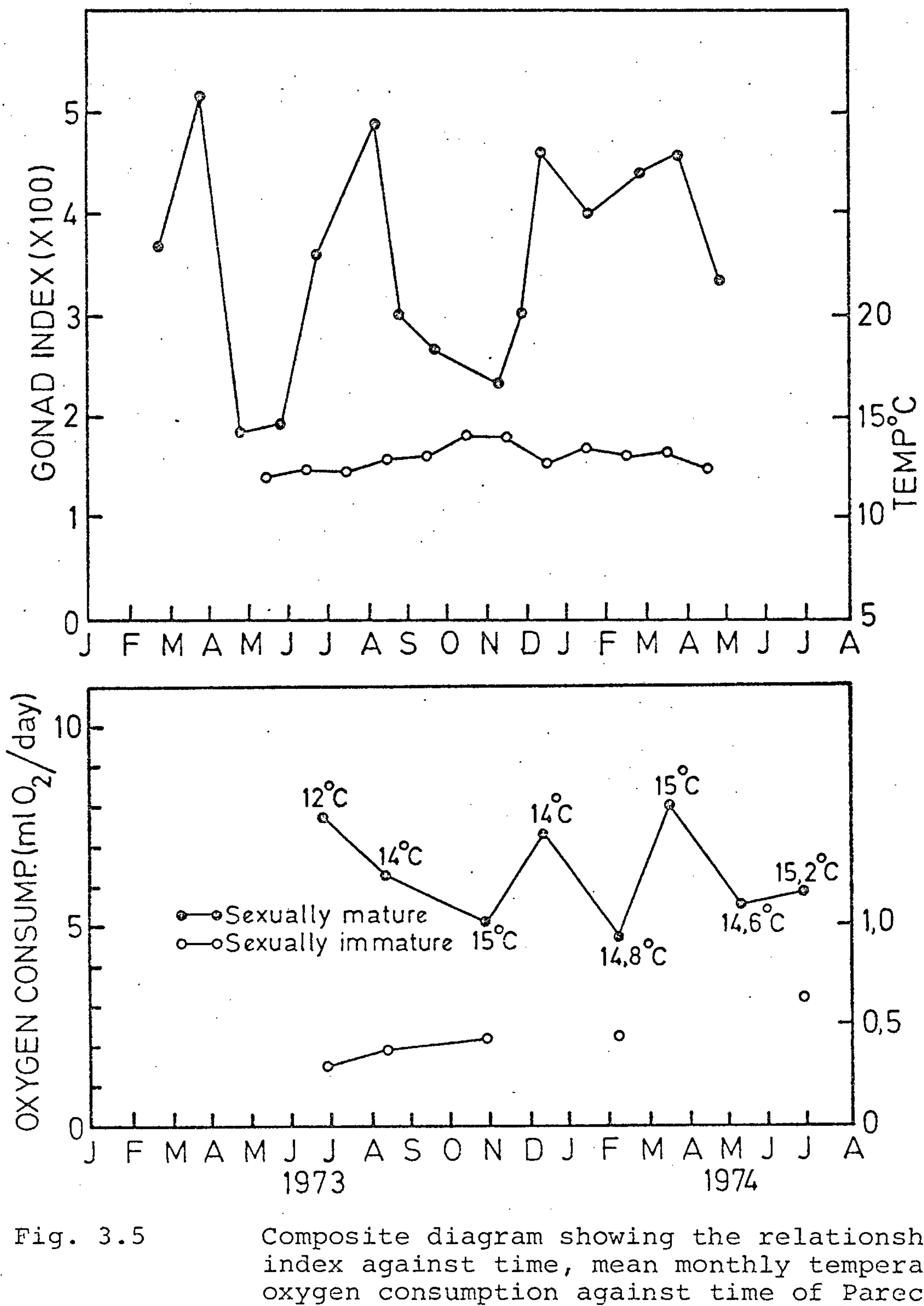


Fig. 3.5 Composite diagram showing the relationship of gonad index against time, mean monthly temperature and oxygen consumption against time of Parechinus angulosus at Robben Island.

have a respiration pattern which follows temperature change as would be expected in poikilotherms, while sexually mature animals show higher respiration rate with an increase in gonad index.

Oatland Point

Six daytime respiration experiments were carried out between June 1973 and June 1974. Owing to strong winds, no data was collected for the December-January period. Graphs showing the relationship between oxygen consumption and weight are shown in fig. 3.6. Their respective regression equations are listed in table

Table 3.4. $\log_e$ (0_2 consumption) versus $\log_e$ (live weight) of Parechinus between June 1973-June 1973 in False Bay.

Date	Temperature °C	a	b	r
13-6-73	14	0,26	0,99	0,99
5-8-73	13,1	2,73	0.76	0.98
18-10-73	14	5,95	0,68	0,97
16-2-74	16,3	3,49	0,76	0,98
8-5-74	13,8	1,37	0,86	0,99
28-6-74	15	1,16	0,89	0,99

The scarcity of animals less than 2gm in weight prevented the plotting of similar graphs for sexually immature animals. Fig 3.7. shows the composite graph of 0_2 Consumption versus time and gonad index versus time. Again fluctuations in oxygen uptake correspond to variations in gonad index. Thus respiration rate in animals showing gonad development appears to be directly related to the state of the gonads, though the magnitude of the respiration rate at a given gonad indexis probably governed by temperature.

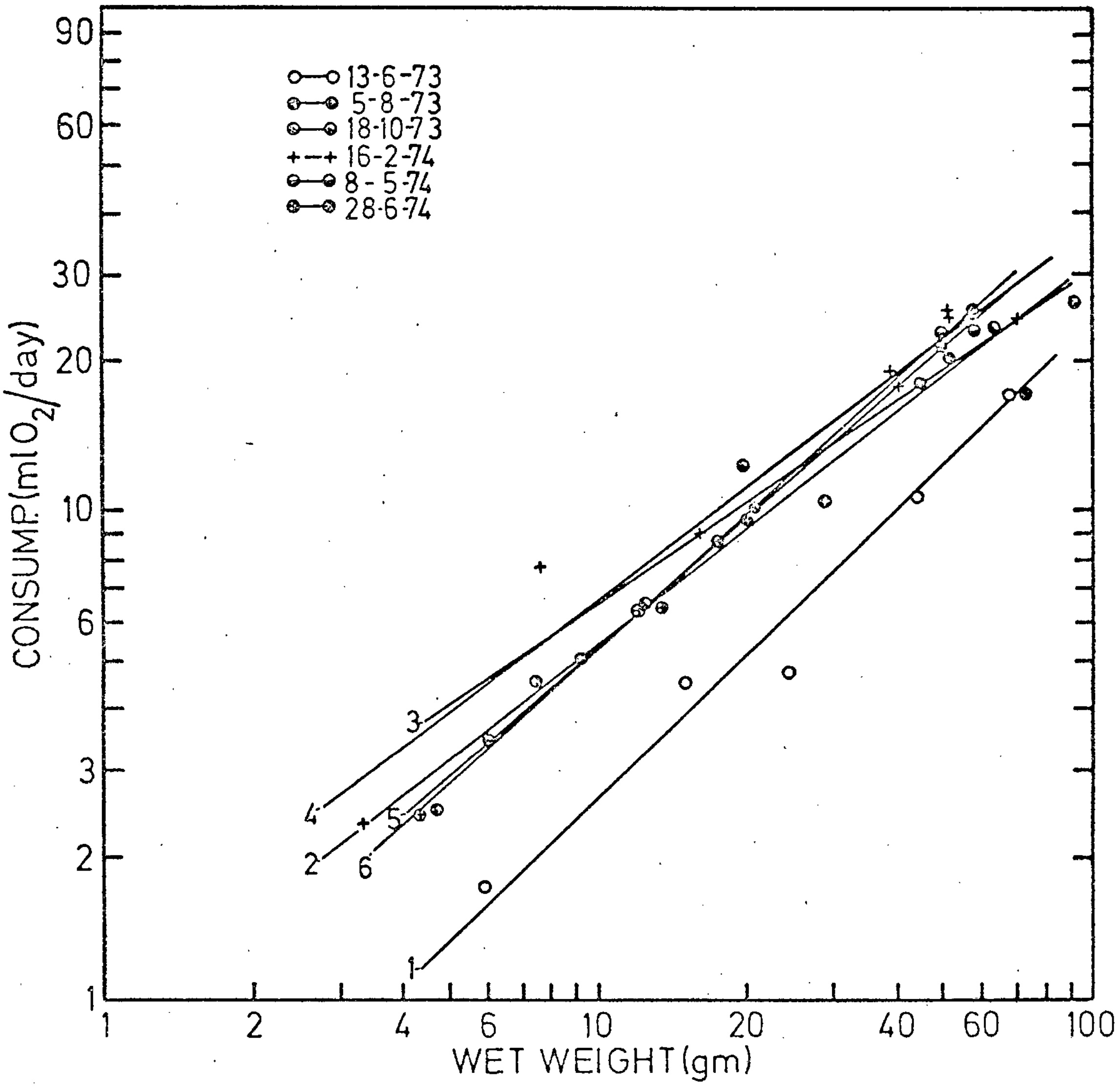


Fig. 3.6 Oxygen consumption of sexually mature and immature animals plotted against wet weight on logarithmic scales.

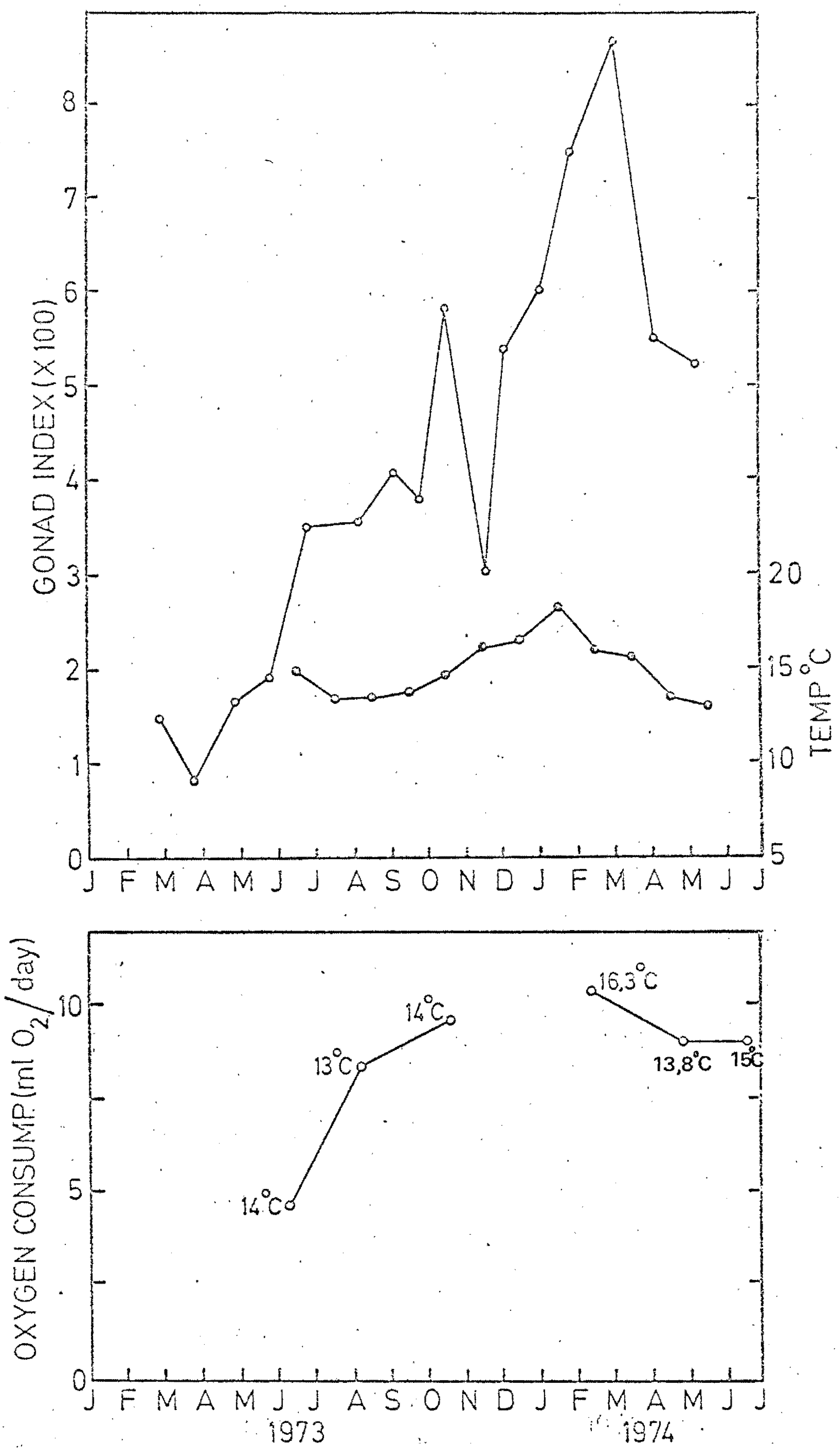


Fig. 3.7 Composite diagram of the Oatland Point population -legend as in Fig. 3.5.

Because the gonad index-respiration rate relationship is not a linear one with time and experiments were not frequent enough to allow partitioning of the data into several linear stages, statistical analysis by stepwise regression is precluded.

The fact that Miller and Mann (1973) based the seasonal respiration changes of S. droebachiensus on the oxygen consumption of sexually mature individuals, could explain the disparity between metabolic rate and water temperature, since gonad state was not taken into account when they plotted respiration rate of the average size animal (live weight) against temperature.

The results of the first night respiration experiment indicated that nocturnal respiration was higher than during the day, when compared with results of a respiration experiment done at the same temperature during the day. (fig.3.8). However, because a number of factors were uncontrolled, limited confidence could be placed in this result. The results of the second day-night respiration experiment, in which food was readily available prior to the run are represented graphically in fig 3.9. There is no significant difference between slopes of the regression lines. However, the intercepts do show some difference though it is only significant at the 10% level. These results are inconclusive, though the difference appears to indicate a tendency towards a higher nocturnal metabolic rate.

The lack of significance between intercepts may be because the experiments may not have been performed at the times of maximum amplitude of the diurnal metabolic cycle. Thus the possibility that nocturnal oxygen consumption is higher than during the day,

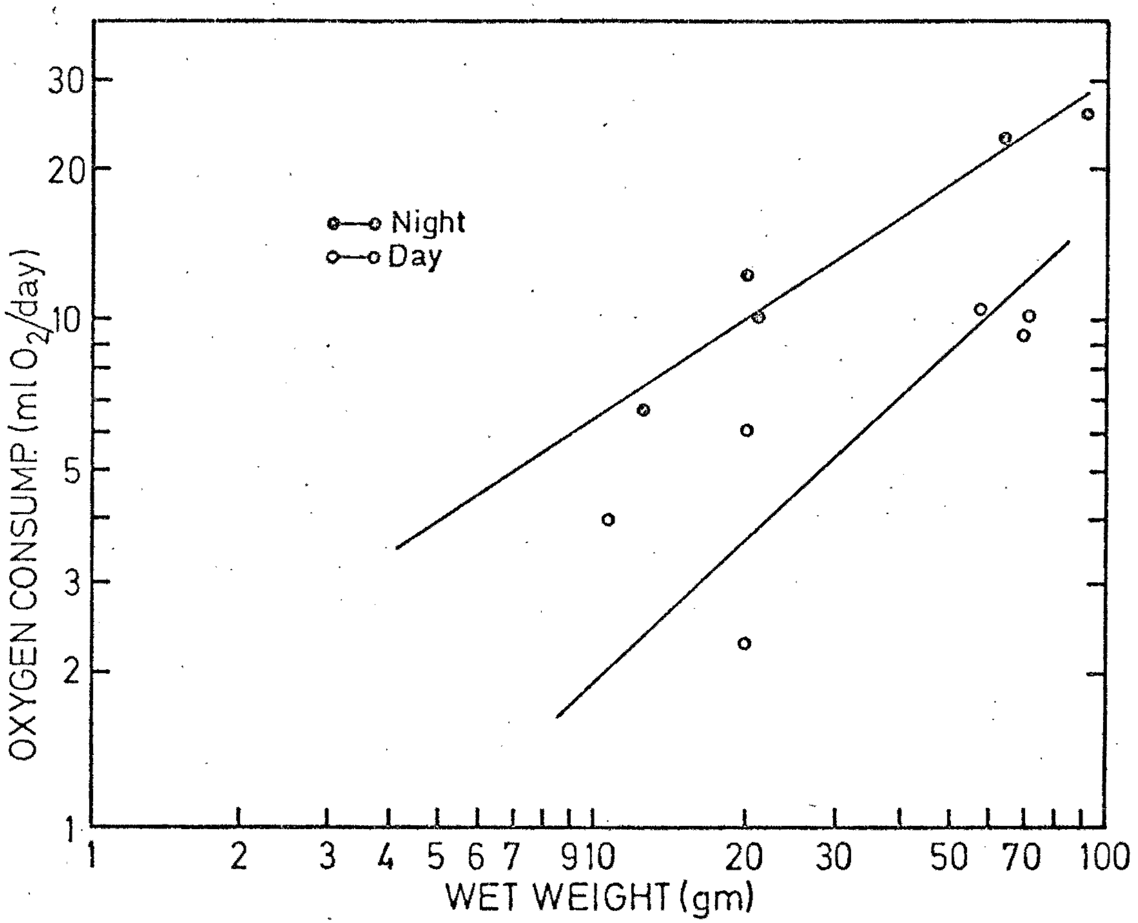


Fig. 3.8 Oxygen consumption of P. angulosus at Oatland Point during the day and night. Data collected in different seasons.

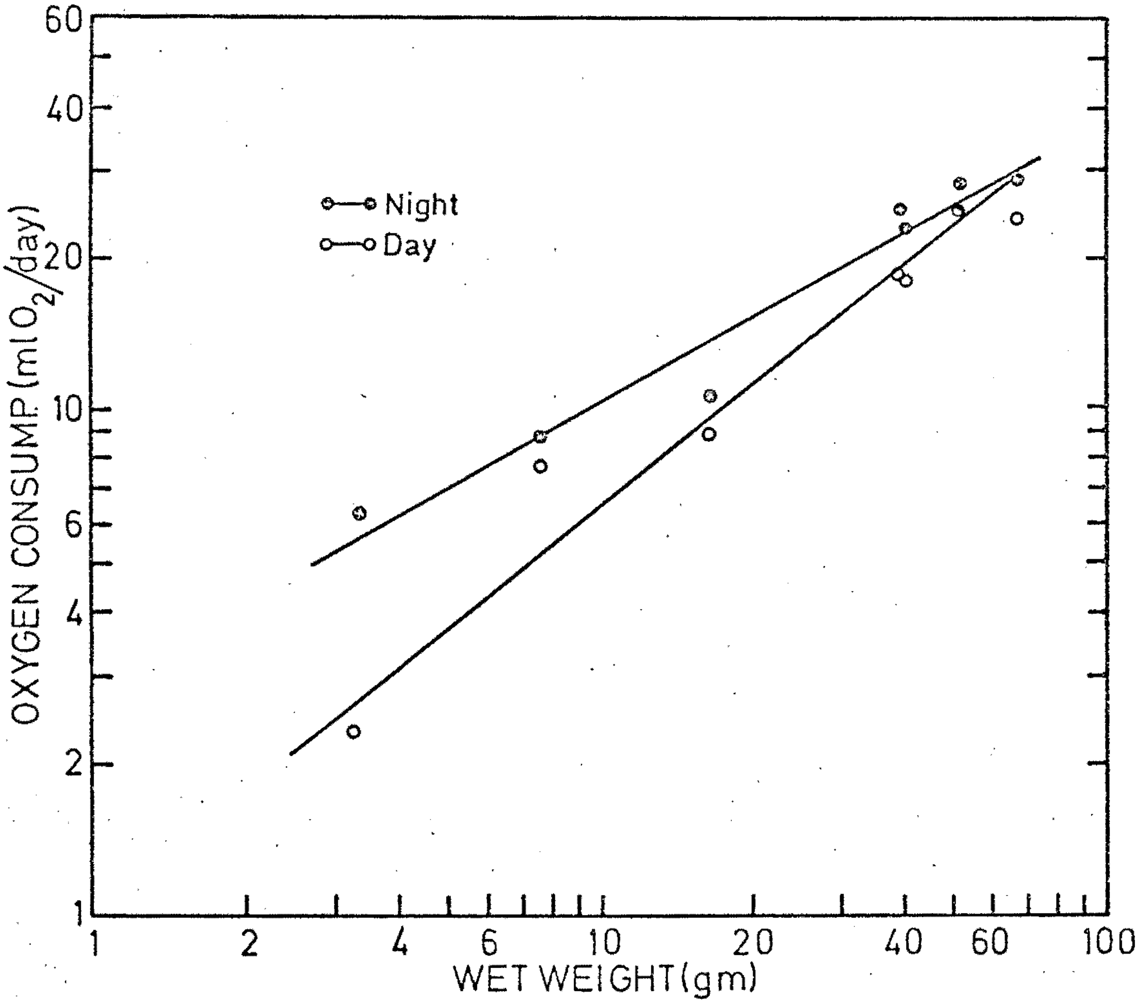


Fig. 3.9 Oxygen consumption of <u>Parethinus angulosus</u> at Oatland Point during the day and night.

places some doubt on the accuracy of annual respiration figures derived from day respiration experiments. This inconclusive result would be best resolved by continuous records of oxygen utilization over a 24 hour period in the field.

POPULATION RESPIRATION

Since a multiple regression analysis could not be applied to the data due to non-linearity, and because there is little difference in slope and intercept of the biomonthly respiration experiment regressions, a mean respiration regression line was used to calculate population respiration. A separate calculation was done for those animals above 20mm (sexually mature) and those below 20mm (sexually immature) for the Robben Island population. Because no regression for the animals in the Oatland Point group below 20mm in diameter could be constructed, a single mean line for the entire population was used to calculate the population production at Oatland Point.

On this basis the annual population respiration of the two study sites was calculated.

Robben Island

The mean density of the animals above 20mm in diameter was 138,6/m^2 and the average size animal in this group utilizes 7,2ml 0_2/day. Using the oxy-calorific constant of 4,83 cal/ml 0_2, the section of the population above 20mm in diameter consume 1759,3 Kcal/yr. The mean-sized animal of the section less than 20mm in diameter utilizes 0,44 ml 0_2/day. Therefore this section of the population uses 62,92 Kcal/yr. Thus by summing these values, the annual population respiration was calculated as 1822,22 Kcal/m^2.

Oatland Point

Here the population respiration was calculated for the population as a whole due to scarcity of animals below 20mm. In this population the average-sized animal consumes 8,0 ml 0_2/day. Thus with a density of 145/m^2, the annual population was calculated as being 2045,02 Kcal/m^2.

Generally the respiration rate of the Oatland Point population is slightly higher than that of the Robben Island group. This is probably due to the larger gonads of the False Bay population together with the higher temperature conditions in False Bay.

POPULATION ENERGY BUDGET

The various terms of the energy budget which have been calculated in the preceeding sections are given in table 3.5.

Table 3.5. Population energy budget in Kcal/m^2/year for the Robben Island and Oatland Point populations of *Parechinus angulosus* (U-calculated by difference)

	C	Pg	Pr	R	F	U
RI	10840,5	447,74	98,28	1822,22	2714,14	5758,12
OP	7001,97	350,95	77,02	2045,02	2889,7	1639,28

Because no figures for the gonad output term (Pr) of the equation were available this was calculated by assuming that the ratio of Pg to Pr was the same as that found by Miller and Mann (1973) working with *S. droebachiensus*.

Assimilation was found from feeding experiments (A = C-F-U) and from the equation wher A = P+R (table 3.6.).

Table 3.6. Assimilation calculated from feeding and by summing respiration and production. (Kcal/m^2/year).

	A = C-F-U	A = P + R
Robben Island	2971,1	2368,2
Oatland Point	1481,9	2472,99

There is close similarity between results obtained from both methods in the Robben Island population, while at Oatland Point A = P+R gives a figure more than twice that obtained from the feeding experiment. This discrepancy lies either in the respiration term, since this was calculated for the population as a whole, or in the consumption and egestion terms derived from the experiment.

If it is assumed that the respiration term is erroneous due to the method of calculation, then 53,19% and 37,5% of the energy consumed by the Robben Island and Oatland Point populations respectively, was unaccounted for in the balanced energy equation. This imbalance could be filled by the U term (dissolved organic carbon). As pointed out by Miller and Mann (1973) a number of benthic grazers also show imbalances in their energy budgets which may be attributed to DOM. The amount of energy lost as DOM varied from 2,3 to 0,75 times the respiration value in S. droebachiensis (Field, 1972). The Robben Island population shows a DOM loss (calculated by difference) of 3,17 times the respiration value while the Oatland Point group has a DOM loss of 0,80 times the respiration value. The low value of DOM for the Oatland Point group may be due to the possibly erroneous respiration value.

The P/R ratios are 0,299 and 0,209 for the Robben Island and Oatland Point populations respectively. The Oatland Point P/R ratio is low due to possibly erroneous respiration figure. If an R value is calculated from R = A-P using the assimilation value obtained from the feeding experiments, then the P/R ratio is 0,335.

The P/R ratios estimated from the log R against log P regression of McNiell and Lawton (1972) are 0,346 and 0,279 (using lower respiration value).

The estimated values are not too different from the experimentally calculated values to preclude the use of the McNiell and Lawton regression for estimating production of P. angulosus.

Therefore in these instances a single respiration experiment at each site could be used for estimating annual population production, saving the long, time-consuming monitoring of population growth and mortality.

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Special thanks are also extended to : Messrs. J.C. Allen, G. Dieckmann, R. Harding, A. Fricke, B. Eyre and many others for their indespensable help in diving operations, Mr. Alex Fricke for allowing me to use his data for constructing the reproduction curves, Mr. Theo van Eck and Mr. Brian Kriederman of the Sea Fisheries Branch for their expert advice and for the use of the Hewlett Packard calculator. Dr. D. Sameoto (Dalhousie University Canada) who kindly supplied the computer program for the polymodal sin analysis.

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Appendix I

Polymodal Analysis after Taylor)1965)

The first assumption is that the component curves of the polymodal distribution are Gaussian (i.e. normally distributed). Secondly in order that sampling "background noise" be reduced, a running average is applied. This process also tends to smoothe the polymodal curve, but in doing so alters the standard deviation (See fig. A1).

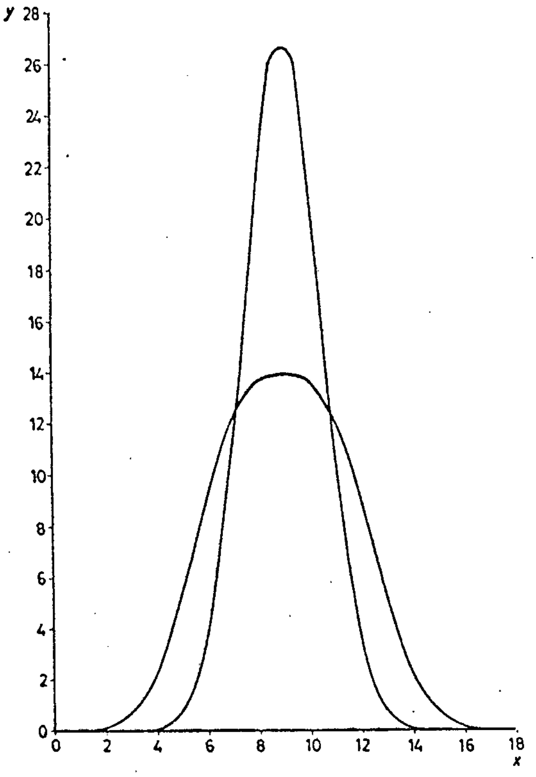


Fig A1. Curves showing the effect of moving averages over seven class intervals upon the standard deviation. The taller curve is Gaussian and the shorter curve results if a moving average is applied to it. Class interval = 1. (after Taylor, 1965).

Having taken these factors into account the curves are plotted as follows:

1) The modal value ($\bar{x}$) for the first range can be determined from probability paper plots (Harding 1949; Cassie 1954).

2) Calculate the sum of squares $\Sigma(\bar{x} - x)^2$ of the deviations of the class mid-mark values negative to the first mode and by assuming symmetry, the observed deviance of the first range is $2 \times \Sigma(\bar{x} - x)^2$.

3) The frequencies of observations in each size class negative to the mode are summed, this figure doubled and the modal frequency added. This value = n = number of individuals forming one normal curve.

4) The standard deviation σ_o (observed standard deviation after applying running average) is calculated from the formula

$$\sqrt{2\ \Sigma\ (\bar{x} - x)^2\ /\ (n-1)}$$

5) σ_t (true standard deviation) is obtained from a correction formula ($\sigma_t \simeq \sigma_o - 0{,}2$).

6) Substitute the value of σ_t in the Gaussian equation:

$$y = \frac{n}{\sigma_t . \sqrt{(2\pi)}} \ . \ \exp \left(- \frac{(x - \bar{x})^2}{2\sigma_t^2} \right) \quad \text{.... eq.1.}$$

for class mark values of x in order that a normal distribution is drawn.

7) The frequencies calculated using equation 1. are adjusted using the running average and are plotted on the moving average curve. If the curves are known to be normal but do not coincide with the original moving average curve, trial and error adjustment of the estimate of the mean ($\bar{x}$) is necessary to obtain the best fit.

8) The calculated moving average frequencies of one mornal curve are subtracted from the remainder of the distribution and the procedure repeated for the next range. Thus by sequential analysis the mean (modal class mark), standard deviation and number of individuals in each component curve can be calculated from the preceeding curve.

Although this technique is somewhat subjective in its approach, it is nevertheless invaluable in that it renders a nearly impossible task relatively simple.

Appendix II

The cage is constructed from hard wood and is covered with 20mm 'Clinton cloth'. The lid is hinged with brass hinges to allow easy removal and replacing of animals. (Fig A2 a).

The inside of the cage is partitioned into nine compartments by a fine mesh covered wire frame (fig. A 2b). The top and insides of the cage are also covered with fine 1mm mesh. The coarse wire mesh on the outside gives strength to the structure while the fine mesh on the inside prevents animals bigger than 1,5mm from escaping, and yet water flow is not restricted, a factor which appeared to be a failing in Swan's (1960) design when small animals were placed in perforated plastic containers.

This is an improvement over Swan's (1960) design as the whole range of animal sizes being studied are subjected to the same conditions as well as the fact that clogging of the holes in the mesh is unlikely.

The cage is clamped to a concrete paving stone with a brass hook at each corner and is attached to a small surface buoy for easy location.

FIG. 2a

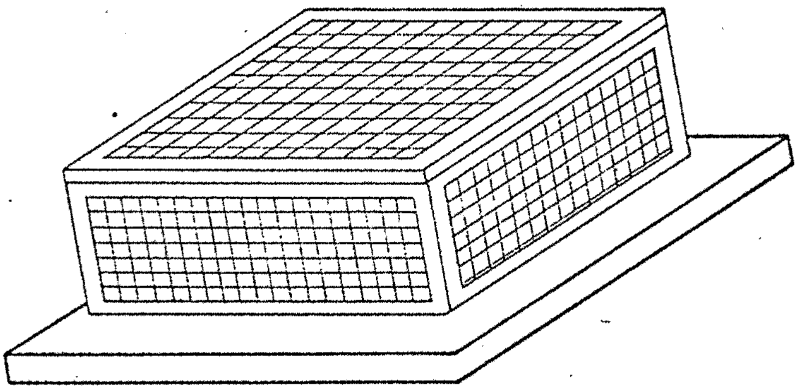
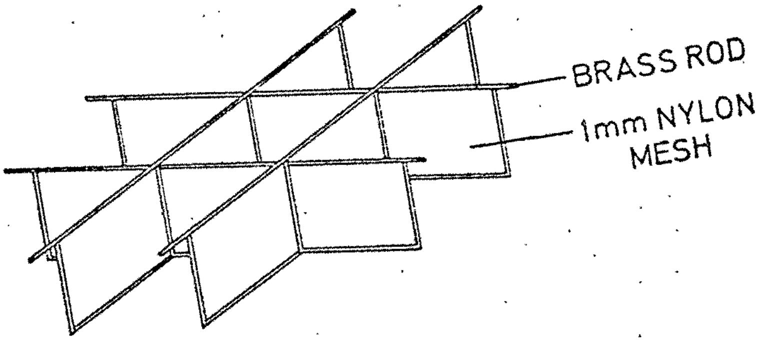


FIG. 2b



CAGE DIVIDER