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DEPARTMENT OF INDUSTRIES

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No. 64

REPRODUCTION OF THE SOUTH AFRICAN ABALONE

Haliotis midae

by

G. G. NEWMAN

THE BIOLOGY OF THE ABALONE HALIOTIS MIDAE

by

G.G. NEWMAN

Submitted in fulfilment of the regulations governing the Degree of Master of Science at the University of Cape Town, December 1969.

C O N T E N T S

INTRODUCTION

The abalone Haliotis midae is commercially exploited in South Africa. A maximum production of canned abalone was attained in 1965, when about one point five million lbs. were produced. Subsequently the catch has declined, due to overfishing, and in 1968 canned production fell to about seven hundred thousand lbs.

The Division of Sea Fisheries is responsible for managing the exploitation of marine stocks in South Africa. To do this effectively, data are required on the general biology and population dynamics of the stocks concerned. Apart from some notes on distribution (Stephenson 1944) no information was available on Haliotis midae. In 1962 the Division therefore started research on the biology of Haliotis midae, to provide an essential basis for later stock assessment.

This thesis deals with three aspects of the above programme, that is reproduction, growth and movement. The first two topics are presented in the form of Investigational Reports published by the Division of Sea Fisheries. The section on movement is based on the findings of a more detailed paper by the candidate which was also published as an Investigational Report.

Included in the thesis is a review of mathematical growth functions. A growth model was required for abalone, and perusal of the literature revealed a range of growth equations which were widespread throughout the literature. The candidate therefore reviewed the more important papers dealing with growth functions. This was done to facilitate an appreciation of the differences between growth curves, and thus ensure that the most suitable curve was selected to represent abalone growth.

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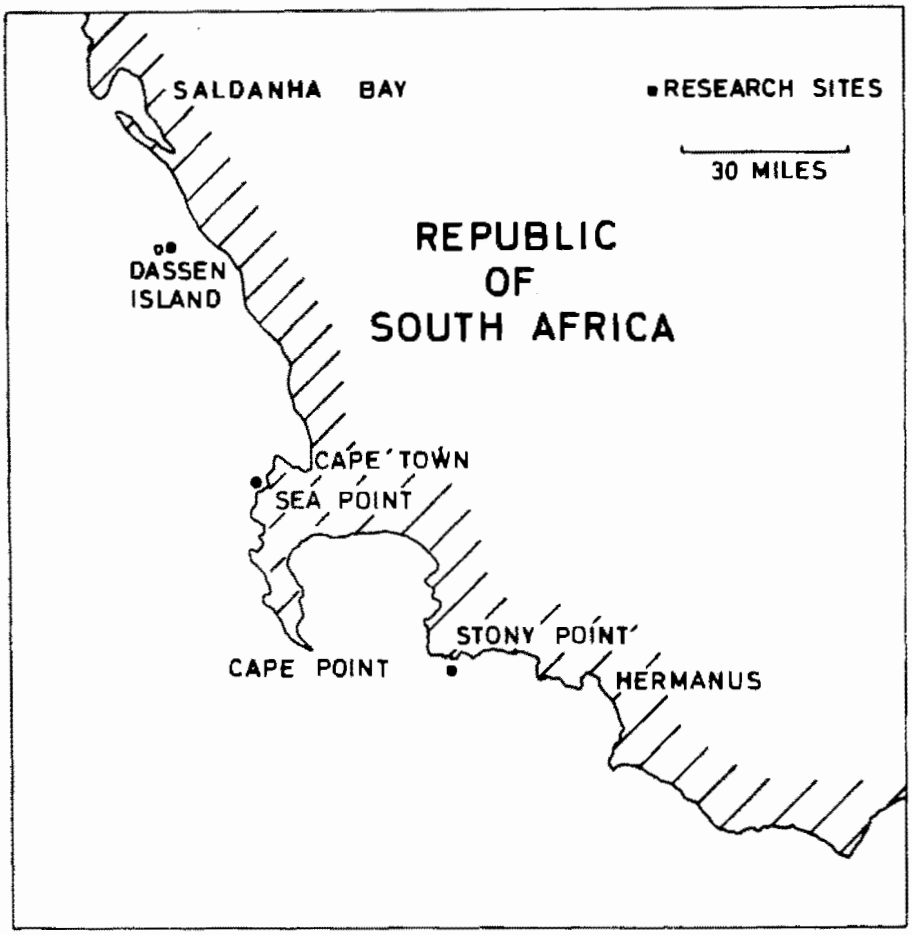


FIG. 1. Abalone research sites

ABSTRACT

The structure of the testis and ovary of the South African abalone is described and the mechanism of spawning is discussed. Male and female abalone are represented equally in the population and at Stony Point one hundred per cent sexual maturity can be expected at a shell breadth of 10.5 cm. Spawning occurs twice per year in certain areas, namely during spring and autumn. There are, however, variations due to locality. At Stony Point spawning is associated with a well-defined increase in water temperature but in areas with less marked seasonal temperature fluctuations spawning was found to be less intense.

A linear relationship between fecundity and animal weight has been established. Within a ripe ovary two discrete groups of eggs are found and these are released on consecutive spawnings. Egg production is of the order of several million per individual and is a function of ovary volume due to the arrangement of the germinal surfaces.

1. INTRODUCTION

This paper describes the reproductive biology of the South African abalone *Haliotis midae*. The gonad structure, sex ratio, sexual maturity, spawning cycle and fecundity are discussed and conclusions are drawn about the stimulus and mechanism of spawning. The investigation was conducted at three localities within the Republic's abalone fishing grounds. These are shown on Fig. 1.

The gonad structure of abalone, especially that of the male, has not received much attention from research workers. Crofts (1929) described and illustrated a young female *Haliotis tuberculata* while Ino & Harada (1961) presented photomicrographs of female *Haliotis discus* at various stages of the spawning cycle. Reproductive cycles for abalone have been described with varying degrees of confidence and are all summarized by Boolootian *et al.* (1962). These authors conclude that haliotids are generally summer breeders. Laboratory experiments have been done to investigate spawning stimuli, and temperature changes as well as shed gametes have been shown to be important (Ino, 1952; Carlisle, 1962; Oba, 1964). In addition Ino observed in the field that a temperature of 20° C. is required to promote the spawning of Japanese abalone. The onset of sexual maturity of *Haliotis tuberculata* is briefly dealt with by Stephenson (1924) and Crofts (1929) and apart from one fecundity estimate for the above species (Fretter & Graham, 1964), no fecundity studies are reported in the literature.

2. GONAD STRUCTURE

Methods:

Male and female abalone in various stages of sexual maturity were collected at three research stations by S.C.U.B.A. divers. The structure of the gonads was then examined by means of histological sections stained with eosin and Mayer's haemulum.

Results:

Haliotis midae is dioecious and has an extensive superficial gonad. This lies around the digestive gland which forms the bulk of the visceral mass. Basically the gonad consists simply of a large lumen which is bounded by germinal epithelium with a connective tissue base.

The lumen of the testis is traversed by tubes of connective tissue which are normally vertical in well-developed organs. A vertical section through a fairly mature testis is illustrated by Fig. 2. The connective tissue tubes are clearly evident and one in particular bifurcates in three places. Within the tubes lacunae or blood sinuses are present and these are often connected to branches of the visceral arteries or veins. In this respect Crofts (1929) has fully described the circulatory system of *Haliotis tuberculata* and has shown that the connective tissue between the gonad and the digestive gland is relatively well supplied with blood vessels. In some lacunae amoebocytes are found. These are large cells (8—10μ) which stain lightly and have a fairly regular form. A well-defined nucleus is also present. Amoebocytes are typically found in molluscan haemolymph and their presence would confirm the circulatory function of the tube canals or lacunae.

The *outer* surfaces of the connective tissue tubes are lined with a germinal epithelium, similar to that of the walls of the testis. The arrangement of these tubes, which run vertically between the inner and outer testis walls, is shown by Fig. 3, a photomicrograph of a well-developed testis sectioned horizontally. The lacunae within the tubes are also clearly shown.

The germinal cells of the epithelium of the testis are approximately 4 μ in diameter and give rise to spermatocytes of about the same size. Within the latter, chromosomes can clearly be seen under high magnification (x 1,860). From the spermatocytes smaller spermatids (about 2 μ in diameter) develop and these have darkly staining nuclei. The sper-

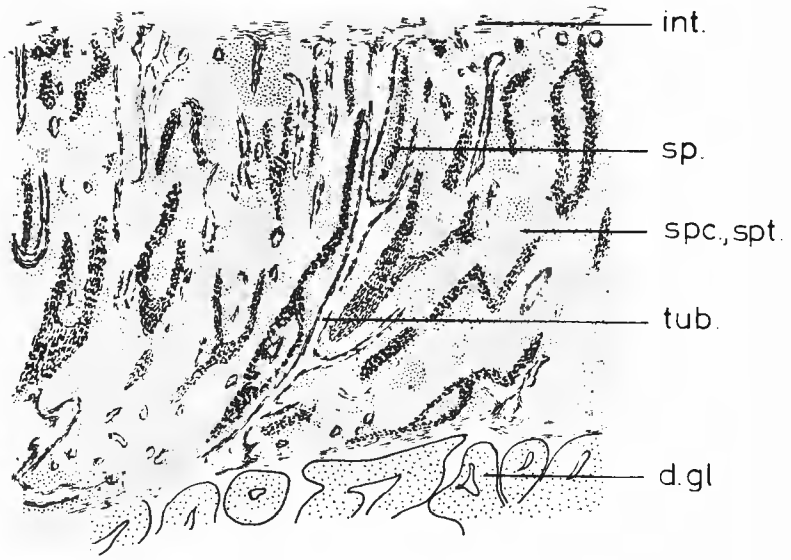


FIG. 2. Vertical section of a testis recovering after spawning
(int. integument; sp.=sperm; spc., spt.=spermatocytes, spermatids; tub. tubule; d.gl.=digestive gland)

matids in turn produce sperm which are about 6 μ long, excluding the tail. The cell content is very clearly defined, with an anterior acidophilic section and a posterior basiophilic part. In addition, the tail is strongly vibratile in fresh smears.

Fig. 2 illustrates a testis in the process of recovering after spawning. Sperm occupy a relatively small part of the lumen in the section but spermatocytes and spermatids are abundant. When fully mature, however, the whole testis lumen is packed with sperm.

A spawned testis in vertical section is illustrated by Fig. 4. The whole organ is considerably reduced in size and within the lumen relatively few darkly staining sperm occur, presumably a residue from the previous spawning. The connective tissue tubes are more convoluted due to the collapsed testis and are sectioned both along and across their length. A connection between a tubule and a visceral blood vessel can also very clearly be seen in the figure. Germinal cells are apparent in the epithelium but little spermatogenesis is taking place.

The ovary is similar to the testis in that it is a simple organ lying around the digestive gland.

A fully developed ovary is illustrated by Fig. 5. The lumen is filled with large eggs, which have a maximum diameter of about 200 μ. These eggs are imbedded in a gelatinous matrix, the form of which is clearly seen when separating eggs from an ovary hardened in formalin. Within the ovary trabeculae occur. These are sheets of connective tissue which support a germinal epithelium. The trabeculae appear to run parallel to one another except near the digestive gland where this pattern is not so well defined. Here the eggs are less closely packed than those near the integument and their shape is less distorted. Horizontal sections through the ovaries reveal that near the integument the trabeculae are in fact arranged as a series of well-defined polyhedral columns within which the eggs occur (Fig. 6). Nearer the digestive gland the pattern changes and the intervening walls break down so that the eggs can move relatively unhampered

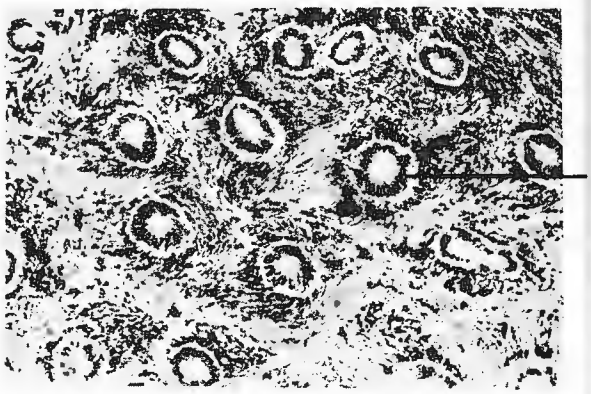


FIG. 3: Photomicrograph of a horizontal section of a well-developed testis (tub=tubule)

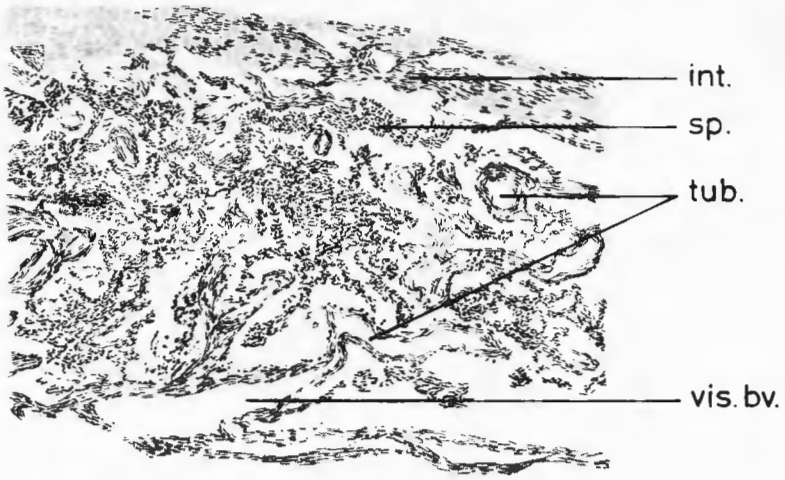


FIG. 4. Vertical section of a spawned testis (int. = intergument; sp. = sperm; tub. = tubule; vis. bv. = visceral blood vessel)

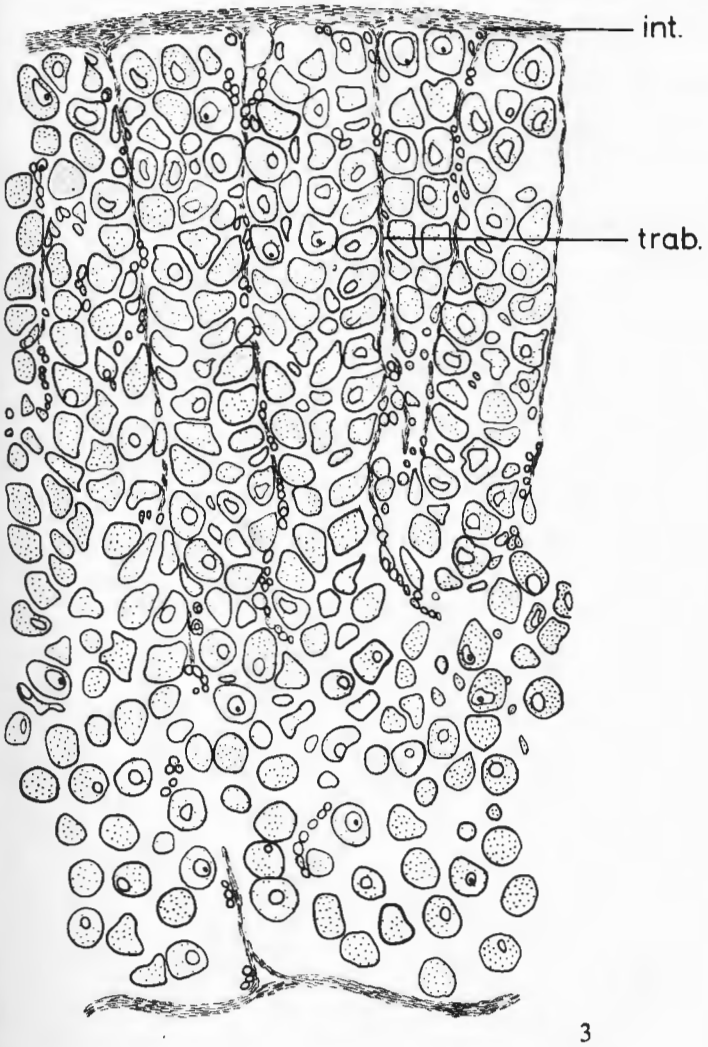
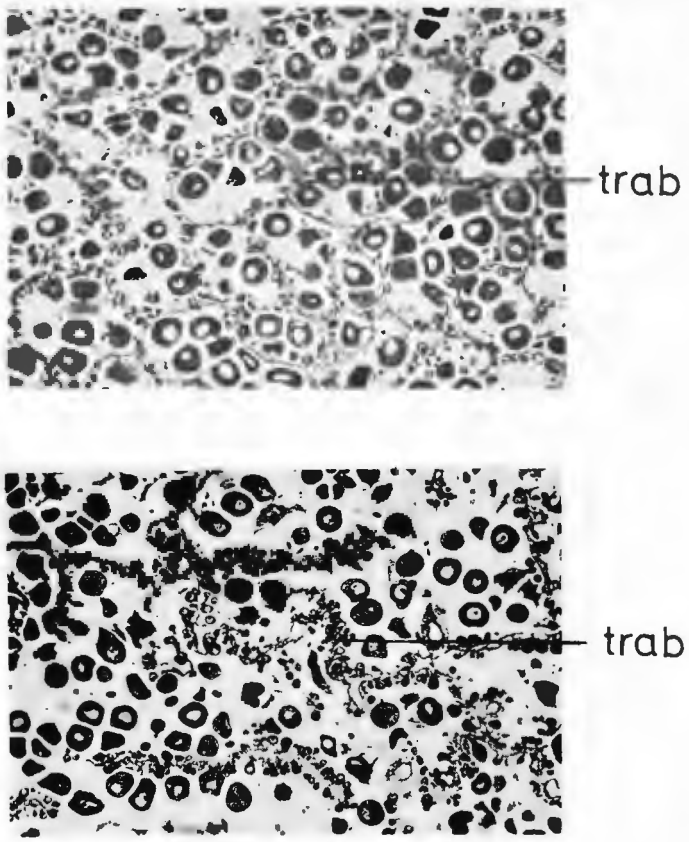


FIG. 5. Vertical section of a fully developed ovary (int. = intergument; trab. = trabecula)



FIGS. 6 AND 7: Photomicrographs of a fully developed ovary sectioned horizontally near the integument and near the digesti
gland (trab.=trabecula)

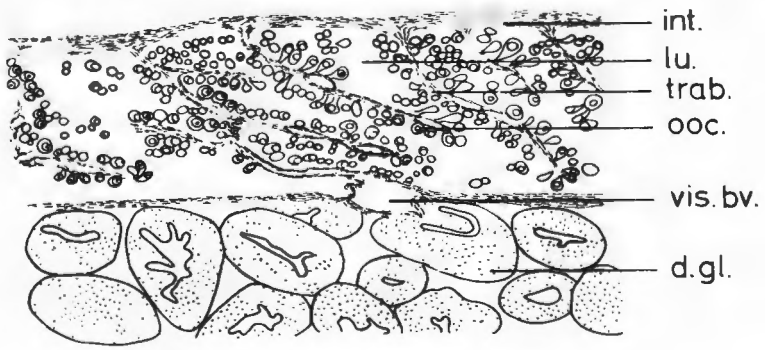


FIG. 8. Vertical section of a spawned ovary (int.=integument; lu.=lumen; trab.=trabecula; ooc.=oocyte;
vis. bv.=visceral blood vessel; d.gl.=digestive gland)

during spawning. This arrangement is shown by Fig. 7.

Apart from the fully developed eggs, smaller eggs seem to be relatively common in the ripe ovary and are attached to the trabeculae. There is evidence to suggest that this group of smaller eggs will form the basis of the next but one spawning, and this will be fully discussed in Section 6.

A spent ovary is illustrated by Fig. 8. The organ is considerably reduced in size and the trabeculae are inclined due to the collapsed state of the lumen. The germinal cells of the germinal epithelium are easily seen and are about 10 μ in diameter. Attached to the trabeculae by means of delicate stalks are numbers of small eggs with diameters of approximately 50 μ. These have well-defined vitelline membranes and prominent nuclei, for the egg is not yet filled with yolk. A spherical nucleolus can also be seen. Lacunae are present in the trabeculae and their junction with blood vessels in the connective tissue wall of the digestive gland is apparent from the section. Within the lacunae amoebocytes are often found.

An ovary stage intermediate between spent and fully recovered is illustrated by Fig. 9. Here eggs of various sizes are attached to the trabeculae within which lacunae are still found. In fully recovered ovaries no lacunae are, however, apparent (Fig. 5) and it is assumed that these have been compressed by the egg mass.

3. SEX RATIO

Fretter & Graham (1964) note that in dioecious molluscs females tend to be more numerous than males and this is especially evident in older populations. Such a tendency was not found in *H. midae*. In fact, from Table I it appears that males are in the majority. The difference between the observed sex ratio and that expected under the hypothesis of equal representation was therefore tested. As large samples were available the normal approximation to the binomial distribution was used. In this manner the observations at each station as well as the overall ratio was tested. With the exception of Sea Point (P ·05) no significant differences could be shown and it would seem that generally the sexes are equally represented.

TABLE I: FREQUENCY OF MALE AND FEMALE ABALONE AT THREE RESEARCH STATIONS

Station	Number males of	Number of females	Total
Stony Point	233	238	471
Sea Point	295	255	550
Dassen Is.	331	302	633

The sex ratios of two other haliotids have been reported. Stephenson (1924) examined 121 *H. tuberculata* and found 50 males. The probability of obtaining this result under the hypothesis of equal representation is less than 5 per cent. A larger sample of 280 *H. tuberculata* was examined by Crofts (1937) who found that the sexes were almost equally distributed. Sinclair (1963) examined 598 *H. iris* (the New Zealand paua) and found 352 males. The probability of obtaining such a result under conditions of equal representation amounts to less than 1 per cent and this is convincing evidence of a disparity in the sex ratio of *H. iris*.

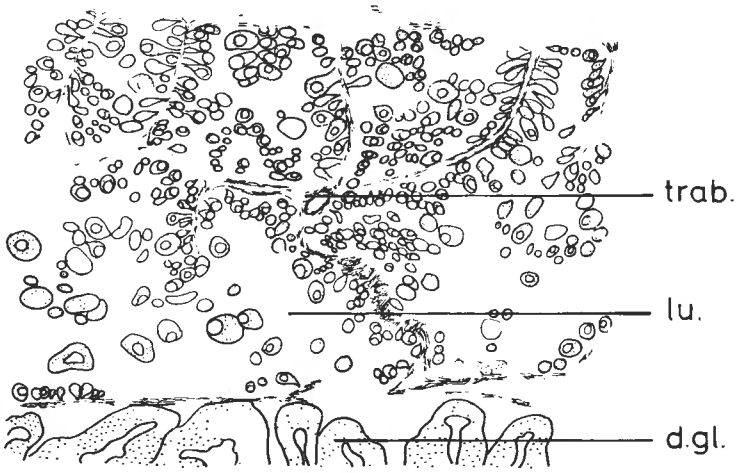


FIG. 9. Vertical section of an ovary recovering after spawning (trab. trabecula; lu. lumen; d.gl. digestive gland)

4. THE ONSET OF SEXUAL MATURITY

The size at which abalone first spawn has not been determined, but some idea of sexual maturity may be obtained by noting the size at which gametes are first produced. The results of such observations are shown in Table II. This collection was made at Stony Point in July, when adult abalone had recovered completely from the last season's spawning. As males and females developed their first gametes at similar sizes, the sexes have been combined in the table. On plotting the data it is apparent that 50 per cent of the population can be expected to have gametes at a body weight of 140 g. At 275 g all members of the population have gametes.

TABLE II: BODY WEIGHT AT SEXUAL MATURITY AS INDICATED BY THE PRESENCE OF RECOGNISABLE MALE OR FEMALE GONADS

Body Weight (g)	Total examined	Percentage mature
1– 50	45	0
51–100	45	20
101–150	33	42
151–200	20	85
201–250	15	87
251–300	16	100
301–350	9	100
351–400	11	100

Similarly, by establishing 1 cm shell breadth intervals, the data on Table III were obtained. When plotted these data showed that at a shell breadth of 8·0 cm and 10·5 cm respectively, gametes were found in 50 and 100 per cent of the abalone examined.

TABLE III: SHELL BREADTH AT SEXUAL MATURITY AS INDICATED BY THE PRESENCE OF RECOGNIZABLE MALE OR FEMALE GONADS

Shell breadth (cm)	Total examined	Percentage mature
3·0–3·9	10	0
4·0–4·9	10	0
5·0–5·9	11	1
6·0–6·9	23	26
7·0–7·9	18	23
8·0–8·9	23	61
9·0–9·9	14	79
10·0–10·9	25	100
11·0–11·9	30	100

The sexual maturity of the populations at Sea Point and Dassen Island could not be determined, as it was difficult to obtain sufficiently large samples of small abalone in these areas.

5. SPAWNING

Methods:

The annual spawning cycle was investigated at three research sites, namely, Stony Point, Sea Point and Dassen Island, where monthly sampling was carried out by S.C.U.B.A. divers. At Dassen Island and Stony Point abalone were obtained from dense populations within relatively small areas of about 30 sq. yards. The Sea Point population was less extensive and abalone were found in smaller groups of up to a few dozen. During the period April 1962 to May 1963 at least 20 abalone per month were examined from Dassen Island and Sea Point, but these sample sizes were increased during the period June 1963 to June 1964. Sampling at Stony Point commenced in August 1963 and continued until October 1964. All abalone were randomly selected above 11 cm shell breadth to ensure that only sexually mature specimens were considered. Each animal was removed from its shell, weighed and the shell dimensions were recorded. The abalone were sexed by noting the colour of the gonad, which is cream in males and green in females. The conical portion of the visceral mass was then removed by sectioning immediately behind the shell apex. During the first twelve months of the investigation the appearance of each section was recorded by means of accurate scale drawings. This method proved slow if accuracy was to be maintained and thus for the second part of the study photographic methods were used. In this case the dissected cone of the visceral mass was hardened in 5 per cent formalin or Bouin's fluid. It was then sectioned again about 3 mm from the original cut. The freshly cut surface, which consisted of areas of digestive gland and gonad, was then photographed at a constant reduction.

From the negatives enlarged (x 4) pencil outlines of the surface areas were made. In both the hand-drawn and the photographic records the total area as well as the gonad area was measured planimetrically and a gonad bulk index was calculated as follows:

$$\text{Gonad bulk index} = \frac{\text{gonad area x 100}}{\text{total area}}$$

The period of spawning was then determined from changes in the distribution of the indices in the monthly samples.

The above approach is essentially similar to that used by Ino & Harada (1961) and Boolootian *et al.* (1962), who described the spawning cycle of Japanese and Californian abalone. Ino in particular

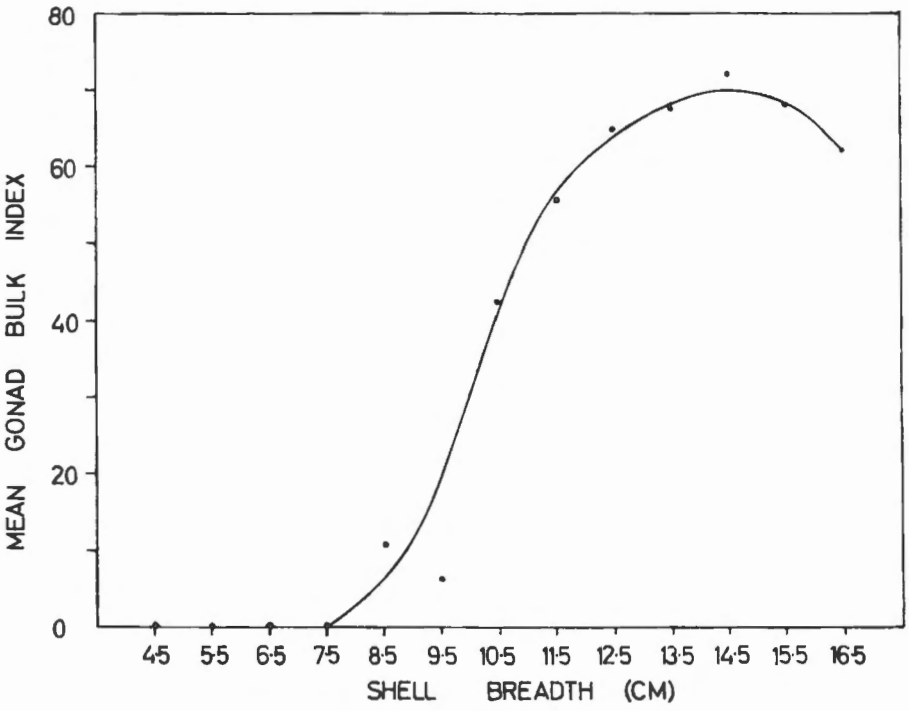


FIG. 10. Mean gonad bulk indices of females July 1964

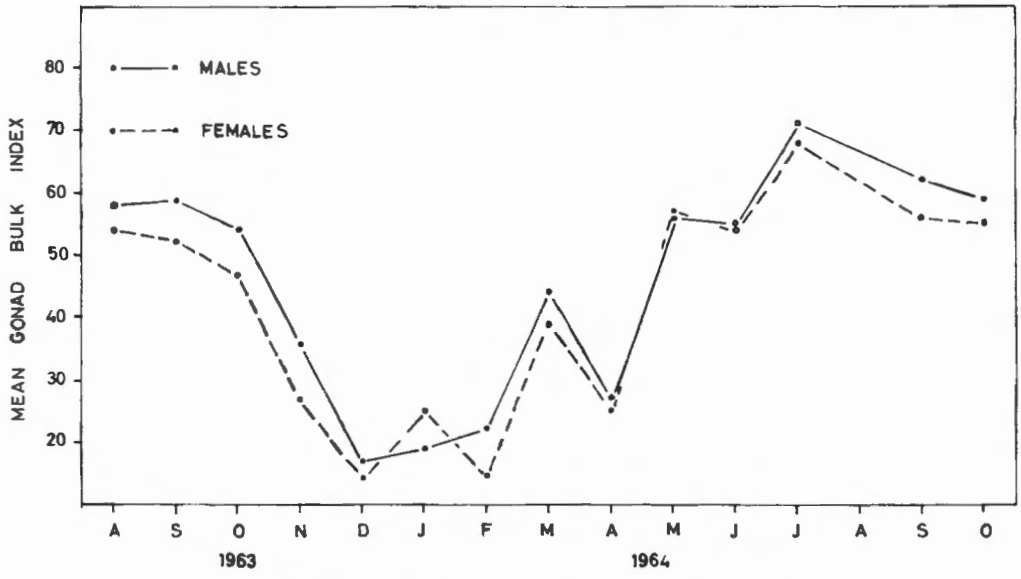


FIG. 11. Mean monthly gonad bulk indices at Stony Point

illustrates the method of sectioning the visceral mass.

To qualify the above quantitative observations, notes were made on the colour and consistency of the gonads but these characteristics were not found to vary in a manner which facilitated description of the reproductive cycle.

Results:

The gonad bulk index incorporates a factor "total section area" to standardize the gonad size with respect to animal size. To assess the standardizations' effectiveness, the relationship between gonad bulk index and size was drawn up for a large collection of females made at Stony Point in July 1964. During this month gonads were fully recovered after spawning. The mean indices were established for 1 cm shell breadth size classes throughout the whole size range and are plotted against their class marks on Fig. 10. It is apparent that the indices are independent of animal size above about 11 cm shell breadth. As abalone within the monthly samples were generally larger than the above minimum, no account need be taken of fluctuations in the size composition of the samples. This independence was applied to males as well, for fluctuations of male indices generally followed those for females.

The spawning cycle at Stony Point was most clearly defined and this will be dealt with first.

For the period August 1963 to October 1964 mean indices were calculated separately each month for males and females (Fig. 11). It is clear that the two variables are closely associated and that both undergo marked fluctuations. After a constant high phase (August—October 1963) indices fell abruptly, indicating that spawning took place between October and December. The gonads remained reduced in December, January and February but showed a rapid recovery by March. Another rapid decline in April suggests that spawning again took place. After this there is a fairly rapid recovery to the previous year's high level. Except for the mean value for July 1964, the level during the period May 1964 to October 1964 was similar to that during the same period of the previous year.

The above interpretation was further examined by determining the statistical significance of changes in the index distributions of certain consecutive months. Non-parametric median tests were used, the method being that of Siegel (1956). The tests were conducted with pairs of samples consisting of males and females combined. Equal representation of both sexes was assured in these samples by discarding excess male or female abalone by means of a table of random digits.

The actual distributions are shown on Fig. 12 and the results of the relevant tests are listed in Table IV.

TABLE IV: RESULTS OF MEDIAN TESTS, STONY POINT

Test	Samples	N	χ^2	P
1	Oct. '63–Nov. '63	68	3·79	·100
2	Oct. '63–Dec. '63	64	43·80	·001
3	Nov. '63–Dec. '63	68	17·00	·001
4	Feb. '64–Mar. '64	66	37·90	·001
5	Mar. '64–Apr. '64	54	9·28	·002
6	Apr. '64–May '64	48	24·30	·001
7	June '64–July '64	56	12·10	·001
8	July '64–Sept. '64	58	8·35	·004

In each case the null hypothesis that no difference exists between the medians of two samples was tested. The median test was therefore used as a two-way test. The tests show that the decline between October and December 1963 was significant. The upward fluctuation of the index during February and March 1964 was also significant. Likewise the decline in March and April 1964 was significant and spawning must have taken place during this period. (This second spawning will be confirmed by the results for Dassen Island.) The very obvious increase during April and May 1964 can also be shown to be significant. The unexpectedly high value for July 1964 was examined and differed significantly from those for June and September of the same year. No explanation of this can be offered.

The above results thus qualify the original interpretation of monthly means and it appears that spawning at Stony Point takes place twice during a twelve-month period, namely during late spring and early summer and during autumn.

Spawning at Sea Point was observed over a two-year period. From May 1962 to May 1963 gonad bulk indices were calculated from scale drawings as described under "methods". Mean monthly male and female indices are plotted on Fig. 13.

TABLE V: RESULTS OF MEDIAN TESTS, SEA POINT

Test	Samples	N	χ^2	P
1	Sept. '62–Oct. '62	34	5·78	·020
2	Oct. '62–Nov. '62	34	2.95	·080
3	Sept. '62–Nov. '62	36	18·78	·001
4	July '63–Sept. '63	54	13·00	·001
5	Jan. '64–Feb. '64	48	10·37	·002
6	Apr. '64–May '64	56	8·64	·003

It is apparent that during May to September

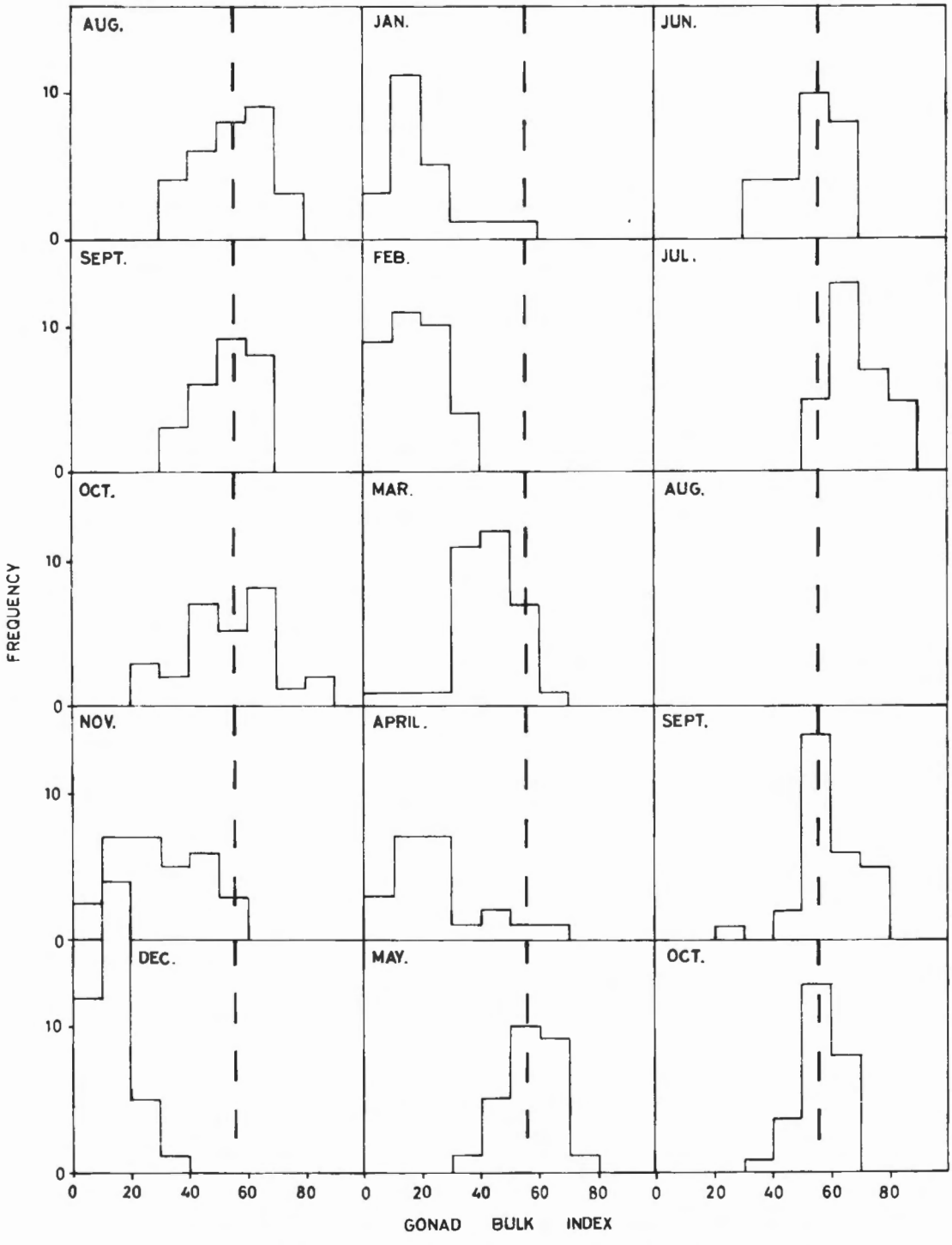


FIG. 12. Gonad bulk index distributions at Stony Point, August 1963 to October 1964

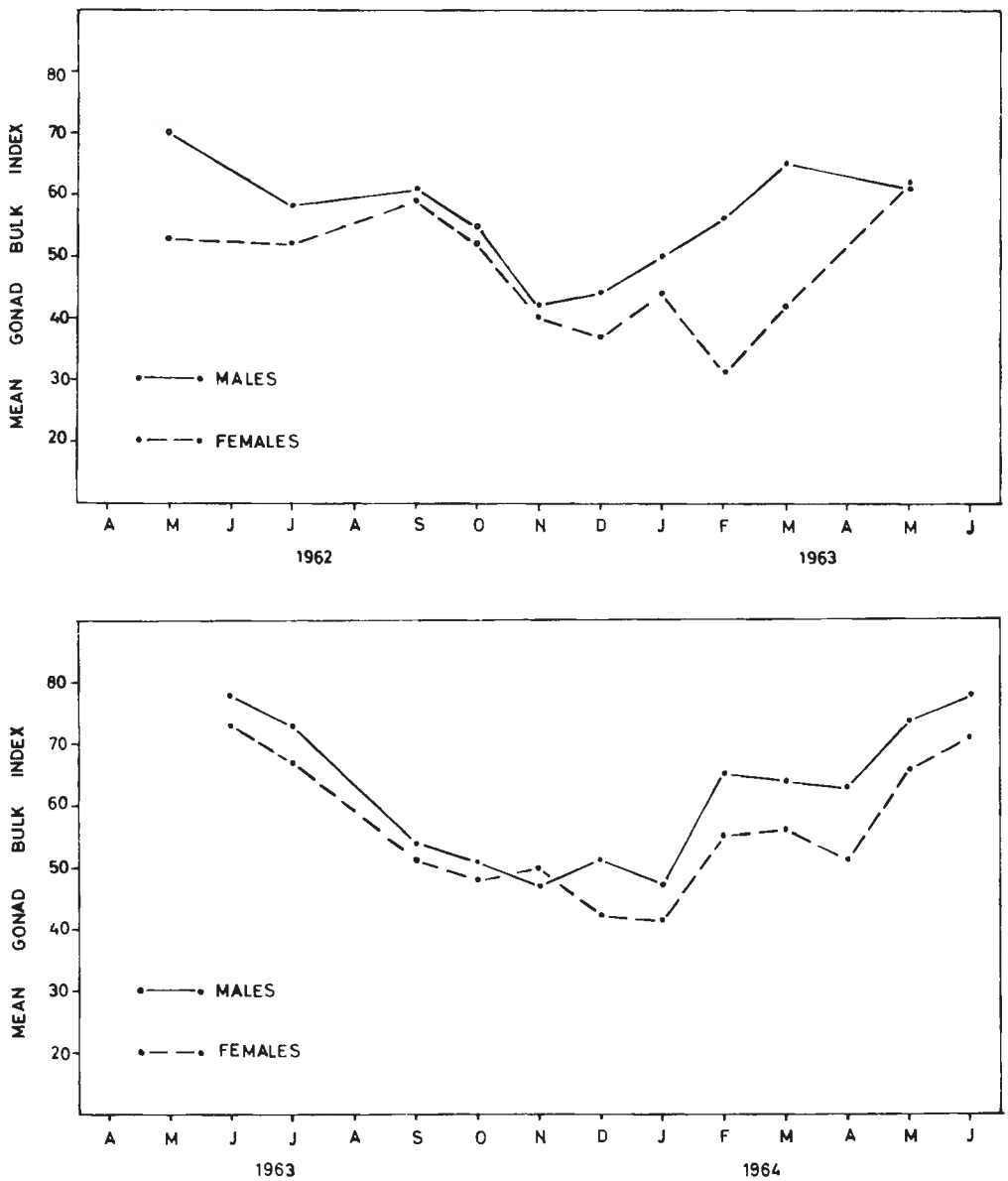


FIG. 13. Mean monthly gonad bulk indices at Sea Point

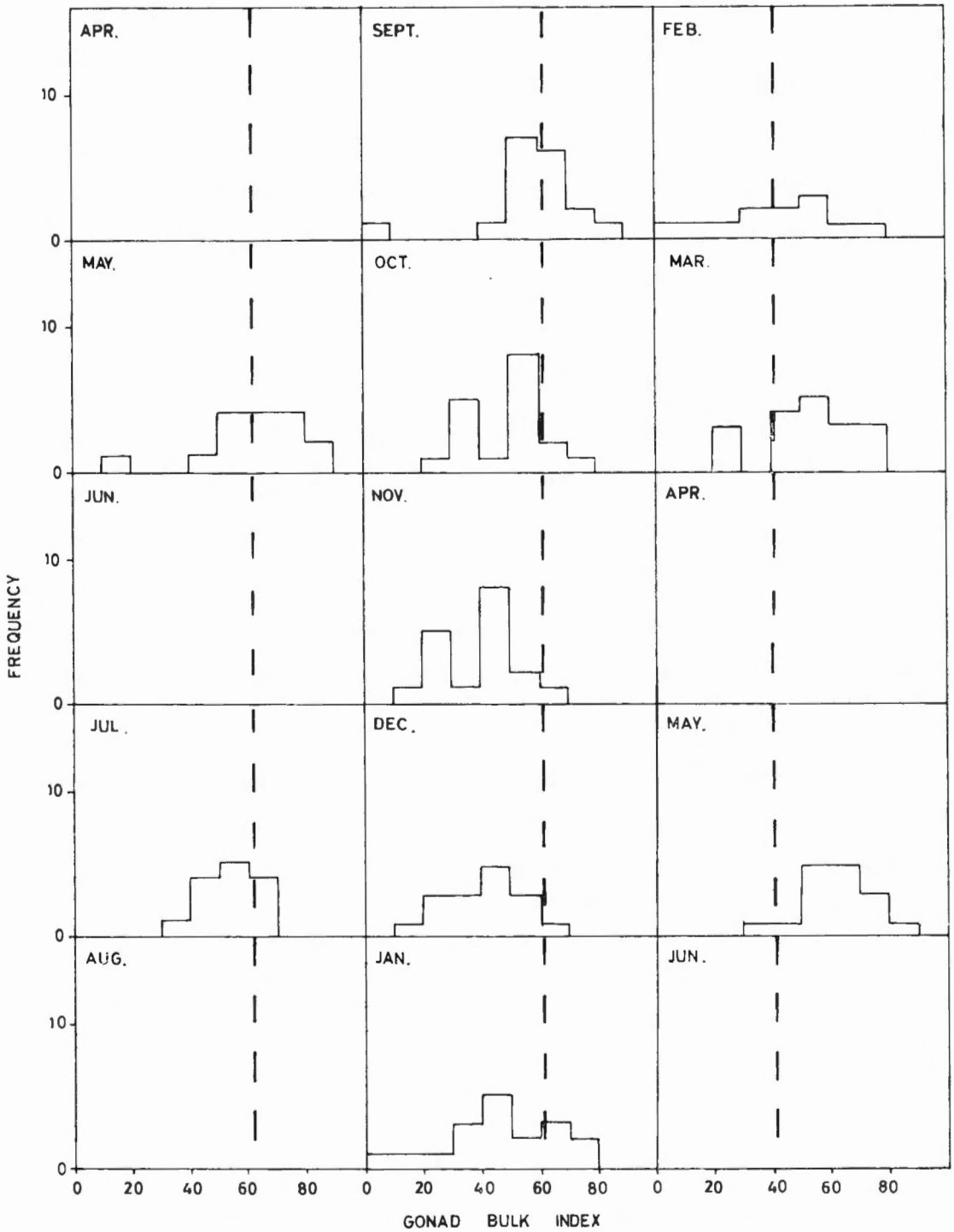


FIG. 14. Gonad bulk index distributions at Sea Point, April 1962 to May 1963

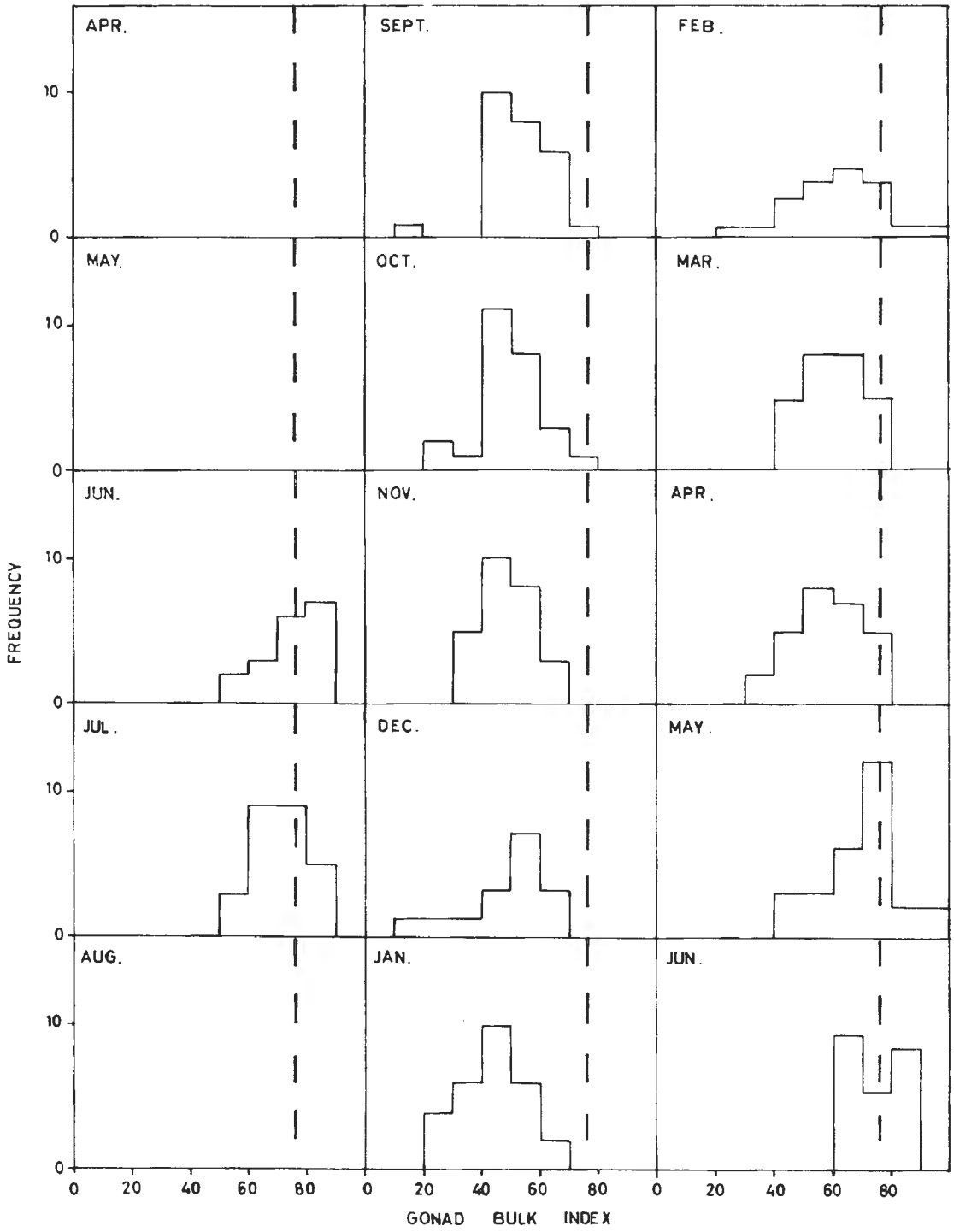


FIG. 15. Gonad bulk index distributions at Sea Point, June 1963 to June 1964

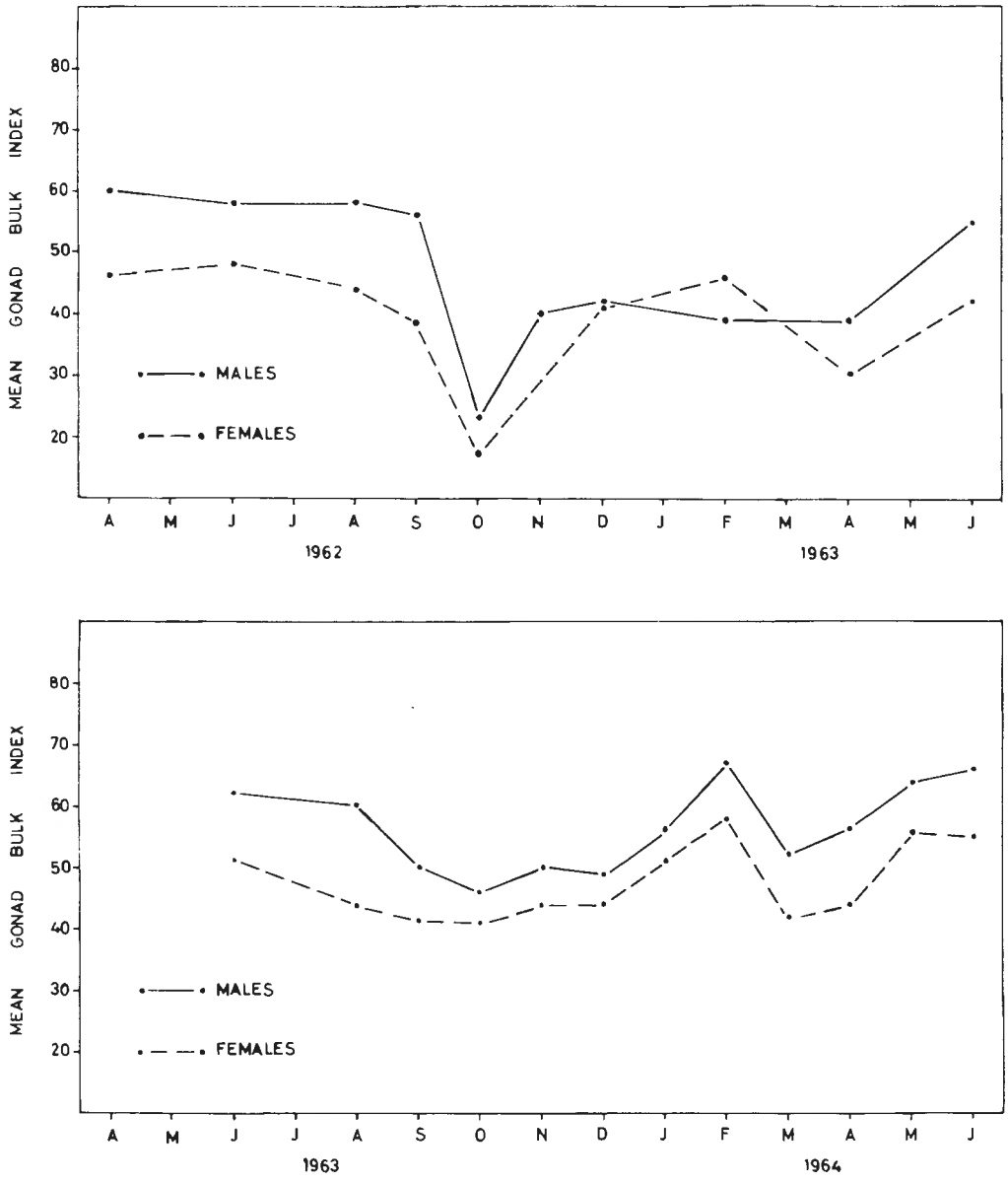


FIG. 16. Mean monthly gonad bulk indices at Dassen Island

1962 gonad bulk indices were relatively constant at a high level. Between September and November 1962 a fairly well-defined decrease occurred indicating some spawning activity. The female values remained at a low level until an abrupt increase took place in April/May 1963. The male indices increased gradually after December 1962 and in March 1963 they attained a high level comparable to that of the previous year.

The median test results for this station appear in Table V and the distributions are illustrated by Fig. 14. The decline during September/November can be shown to be significant. There are, however, no signs of a second spawning within the period.

During June 1963 to June 1964 the size of the monthly samples was increased and indices were calculated from photographic records. The mean monthly values appear in Fig. 13 which shows that male and female indices are closely associated and that fluctuations are apparent in the cycle.

Between July and September 1963 the mean indices declined and this decline is statistically significant. The indices then remained fairly constant until January 1964 after which an abrupt recovery took place to a level which was maintained during February, March and April. In April/May a further increase took place and in June 1964 the level found in June 1963 was regained. The statistical significance of these two increases may be confirmed from Table V. As in the previous cycle, there was no evidence of a second spawning at this station. Both cycles indicate, however, that spawning at Sea Point takes place in late winter/early spring.

The reproductive cycle at Dassen Island was investigated over 27 months, from May 1962 to July 1964. Fluctuations of indices during the period May 1962 to June 1963 were calculated from scale drawings and will be considered first.

TABLE VI: RESULTS OF MEDIAN TESTS, DASSEN ISLAND

Test	Samples	N	χ^2	P
1	Sept. '62–Oct. '62	32	21·12	·001
2	Oct. '62–Nov. '62	34	5·78	·020
3	Feb. '63–Apr. '63	30	6·56	·010
4	Apr. '63–Jun. '63	42	8·18	·004
5	Jun. '63–Sept. '63	52	1·90	·170
6	Dec. '63–Jan. '64	62	5·20	·020
7	Jan. '64–Feb. '64	62	5·23	·020
8	Feb. '64–Mar. '64	66	7·34	·006
9	Apr. '64–May '64	76	6·72	·009

During the period May to September 1962 the mean monthly indices remained relatively constant, although male indices were appreciably higher (Fig. 16). During September/October a marked decrease in the indices for both sexes took place and this is shown to be significant by Table VI. Recovery after spawning was immediate and significant, and after remaining relatively constant during December 1962 and February 1963 female indices again declined. This decline was sufficient to cause a significant difference between the samples for February and April 1963. Spawning may well have occurred during this period suggesting that the Dassen Island population spawns twice in twelve months.

In the second year of the investigation the June 1963 sample serves as the start of the new series at Dassen Island.

In August/October 1963 the male indices fell markedly but the decline in females was more gradual (Fig. 16). The decline of the sexes combined during June/September 1963 could not be shown to be significant (Table VI). From October 1963 male and female indices fluctuated in unison until December 1963 when they increased gradually reaching a high level in February 1964. This increase was statistically significant. A well-defined and significant decrease then occurred followed by a constant period during March and April 1964. Both indices then increased abruptly and significantly and the level of the previous year's June index was attained.

Although a statistically significant change cannot be shown to have taken place during August/September 1963 two spawning periods are suggested by the Dassen Island data. These are in early spring and early autumn.

6. FECUNDITY

Spawning in abalone occurs simply as the release of gametes into the surrounding water and fertilization takes place externally. The larval development of European and Japanese species has been described (Murayama, 1935; Crofts, 1937; Ino 1952 and Oba, 1964) and it is apparent that the planktonic larval stage in *Haliotis* is fairly short. This has been reported to last for three to eleven days for different species. Abalone can be expected to produce large numbers of eggs, and Fretter & Graham (1964) recorded that *Haliotis tuberculata* carries 10^4 eggs but no animal size is associated with this value. Crofts (1937) also notes that large numbers of eggs are spawned by the same species. The fecundity of *Haliotis midae* was investigated at Stony Point and a relationship between the number of eggs carried and animal size has been established.

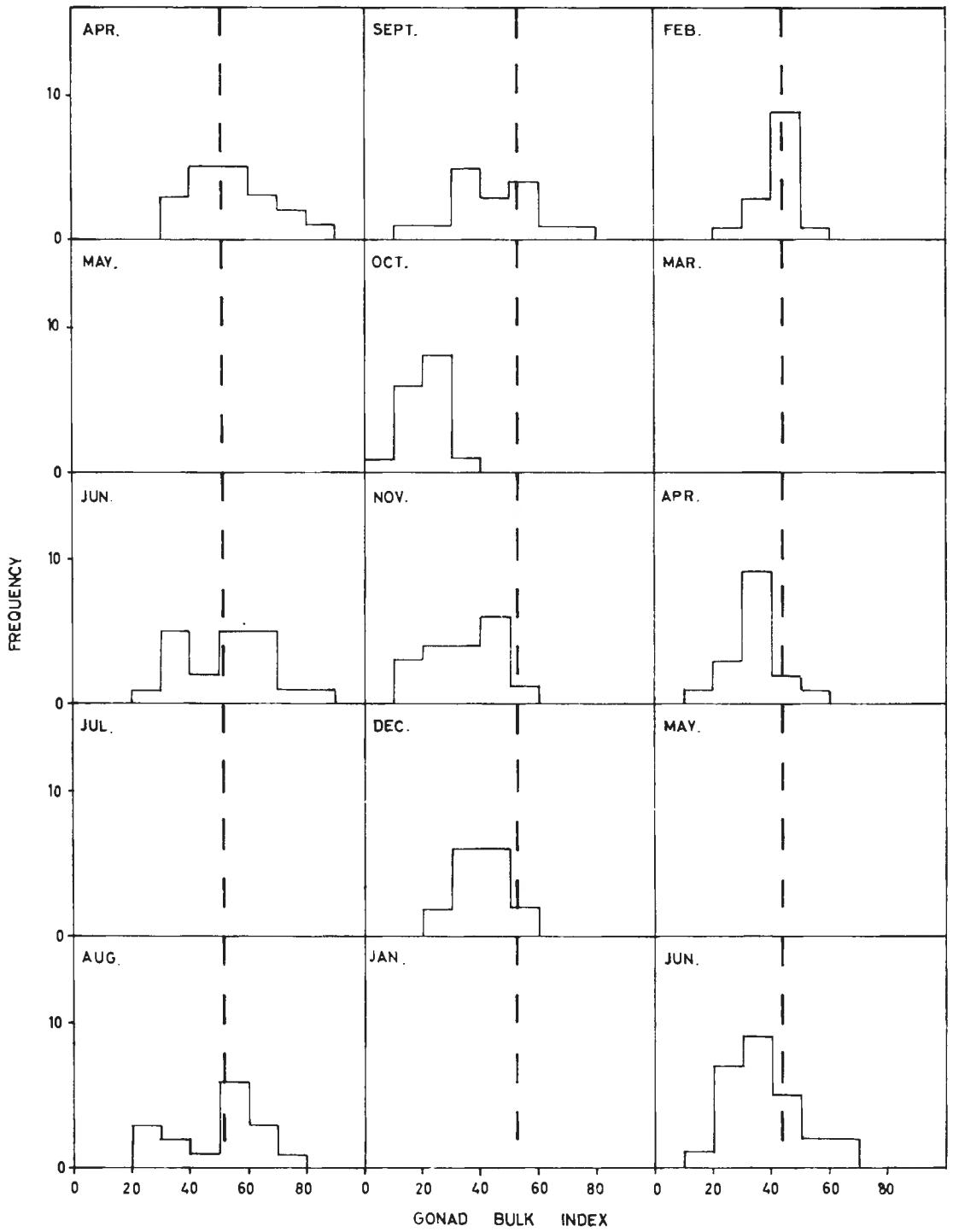


FIG. 17. Gonad bulk index distribution at Dassen Island, April 1962 to June, 1963

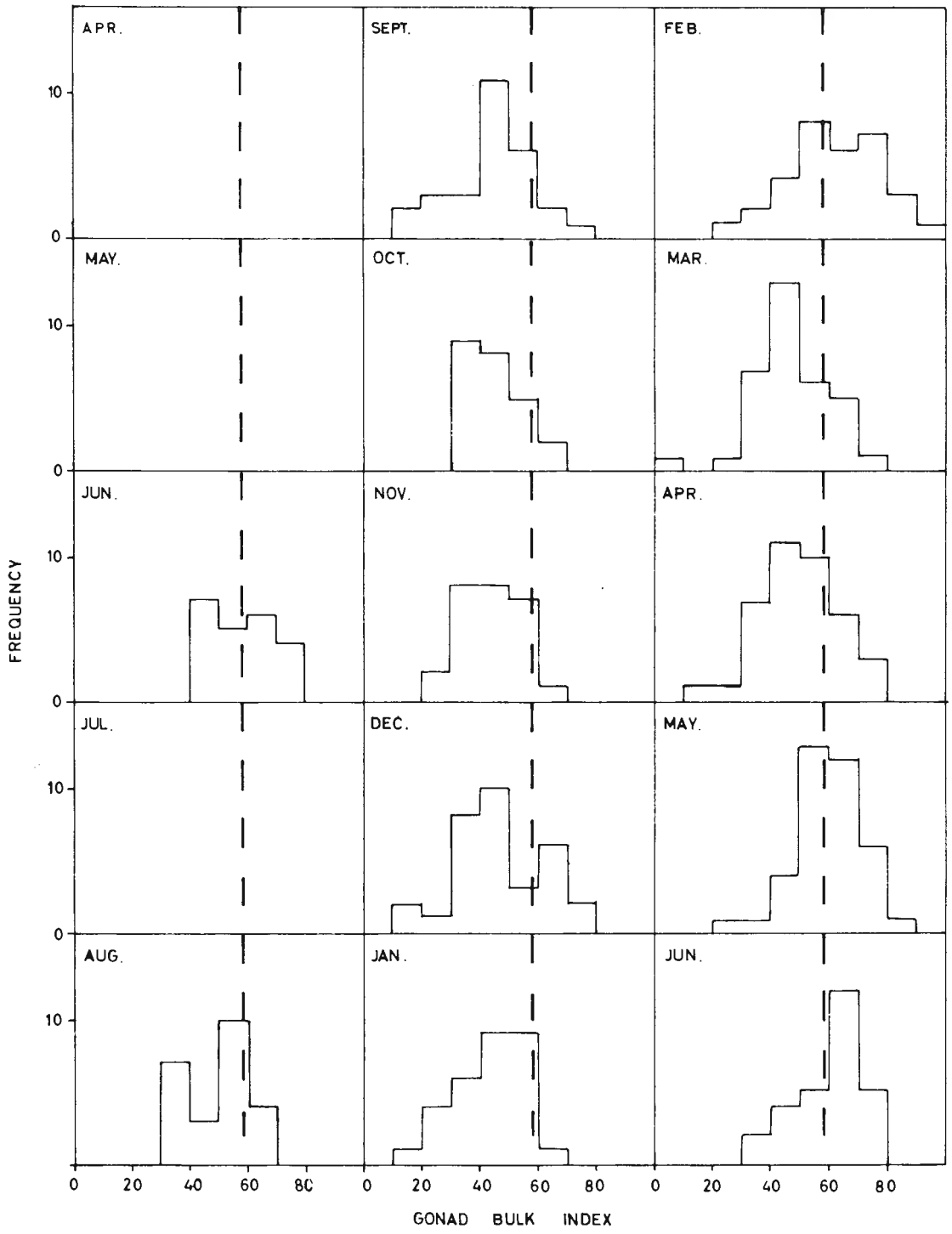


FIG. 18. Gonad bulk index distribution at Dassen Island, June 1963 to June 1964

Methods:

Abalone within the size range 200 g to 1,100 g were collected by S.C.U.B.A. divers in July 1964 when the population had recovered fully from spawning. After recording shell dimensions and body weights, the abalone were preserved in ten per cent formalin to harden the ovaries which were then separated from the visceral mass and weighed. A small piece (about .04 g) was removed from the anterior, middle and posterior part of the gonad for egg counting. After being accurately weighed, this material was stored in five per cent formalin.

Before counting, the eggs were easily separated from the ovary trabeculae by means of dissecting needles and a stiff paint brush. Counts were done under fifty times magnification and a grid system was used to ensure accuracy. From the egg count and the proportion of ovary weight to subsample weight the total number of eggs was calculated.

Results:

Examination of eggs prior to counting suggested that these fell into two broad size categories. The maximum diameters of random samples of eggs from a few abalone were therefore measured and size frequency diagrams were drawn. Two such diagrams are shown in Fig. 19 and the bimodal nature of the two samples can clearly be seen. As no increase in gonad size took place between collection of the material and spawning (the collection was made in July when gonads were fully developed) it is assumed that only the larger eggs will be released at the next spawning. This is confirmed by the histological sections discussed earlier where it was seen that in recently spawned ovaries (Fig. 8) a large number of small eggs, with diameters of about 50 μ remained attached to the trabeculae and these were also found in ripe ovaries. Accordingly, only eggs within the large size range were counted. Counts of the smaller size ranges would have confirmed the numbers of eggs to be released at the next but one spawning. These counts were extremely difficult as the small eggs were still firmly attached to the trabeculae and difficult to separate without damage. Under the circumstances it is unlikely that accurate counts could have been made.

Sample code number	Number of large eggs per g (diam. 170-310 μ)	Number of small eggs per g (diam. 30-110 μ)
2	16×10^3	12×10^4
91	20×10^3	12×10^4

An attempt was made, however, to count small eggs and the results, which are listed, indicate that small eggs are well represented. It must be borne in mind that due to their fragile nature their numbers are probably underestimated.

The ovary is an extensive organ with a fairly uniform structure. It was, however, necessary to test the variation in egg density in different parts of the gonad, to determine whether representative egg counts could be made from any one place. This was done by analysis of variance.

Ten abalone with approximately the same body weight (i.e. 500 g) were selected and three egg counts were made with each individual from the anterior, posterior and middle gonad. Each count was converted to an estimate of the number of eggs per gram of ovary weight and these details are listed in the Appendix together with other relevant details of the sample. The two-way analysis of variance is shown on Table VII. The F value for the variance between ovary locations amounts to 1·98 which with 2 and 18 degrees of freedom is not significant at the ten per cent level. There is therefore no significant difference in the number of eggs per gram in different parts of the ovary and thus with the remaining material only one count per specimen was made. This was usually done with a sample from the middle of the ovary.

For the investigation a further 29 counts were made with abalone selected so as to ensure equal representation throughout the size range. These data are also listed in the Appendix and, on a scattergram, the total number of eggs was plotted against body weight (Fig. 20). Also shown is the least squares estimate of the relationship between fecundity and size which was calculated as:

$F = \cdot 0198\ W - 2 \cdot 196$

where F = fecundity in millions of eggs

W = body weight in g.

It is evident that large but variable numbers of eggs are produced by *H. midae*. In addition the linear relationship between eggs and body weight means that the growth of the ovary in mature

TABLE VII: ANALYSIS OF VARIANCE OF EGGS PER GRAM FROM DIFFERENT PARTS OF THE OVARY

Source of variation	Sum of squares	Degrees of freedom	Estimated variance
Between ovary location	2,392,618,281	2	1,196,309,140
Between ovaries	6,565,278,251	9	729,475,360
Residual	10,850,832,898	18	602,824,050
	19,808,729,430	29	

TABLE VIII: MEAN MONTHLY TEMPERATURES AT RESEARCH SITES (THE VALUES IN BRACKETS INDICATE THE NUMBER OF RECORDS)

	Jan.	Feb.	March	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Stony Point	—	16·7 (2)	—	15·5 (2)	13·0 (2)	14·0 (1)	13·9 (1)	14·5 (2)	15·7 (2)	15·0 (1)	15·8 (2)	18·1 (2)
Sea Point	13·7 (26)	14·6 (14)	12·1 (12)	13·8 (15)	14·3 (19)	13·8 (17)	13·7 (12)	13·9 (12)	13·9 (11)	14·1 (18)	13·7 (12)	13·8 (18)
Dassen Island	15·1 (3)	15·6 (3)	15·9 (1)	14·7 (3)	16·0 (1)	14·3 (4)	14·1 (2)	14·9 (3)	15·0 (2)	15·3 (2)	12·9 (4)	10·6 (1)

abalone is isometric. The ratio of the number of eggs to body weight remains constant and is in fact the slope coefficient of the linear model.

The relationship between fecundity and shell breadth is exponential and was calculated as:

$F = \cdot 0004257\ B^{3 \cdot 787}$

where F = fecundity in millions of eggs

B = shell breadth in cm.

The above is illustrated by Fig. 21.

7. DISCUSSION

Comparison of the cycles at the three research stations reveals that at Stony Point spawning tends to occur later than at the stations west of Cape Point, i.e. during late spring and early summer as opposed to the late winter spawning at Dassen Island and Sea Point. In addition spawning at Stony Point seems to be more complete. The gonad bulk index here decreases to a much lower level than at Sea Point and Dassen Island although the October 1962 spawning at Dassen Island is a possible exception.

The difference in the intensity of spawning was confirmed by comparing the structure of "spent" gonads at Stony Point and at Sea Point and Dassen Island. At Stony Point reduced gonads were almost completely devoid of large mature eggs as is shown by Fig. 8. This was not the case at the other two stations where, after spawning, many mature eggs remained in the gonad, thus accounting for the relatively small fluctuations in the gonad bulk index. The eggs were also understandably less densely packed than in the ripe gonad. Smaller eggs, as found in the Stony Point sections, were also present. Examination of a series of gonads collected after spawning showed no signs of resorption of unspawned eggs, and it must be assumed that these will be emitted at the next spawning.

It is apparent that individual abalone spawn twice a year at Stony Point and Dassen Island and that staggered spawning does not take place within the population. This may be confirmed from Figs. 12, 17 and 18. To provide a reference point for each set of histograms a dashed line is drawn. This represents the median of a combination of all samples in the series which were judged as having fully developed gonads. From the figures it will be seen that fluctuations in the indices are generally due to shifts of the whole sample distribution and not to changes in the indices of only certain sections of the population. Spawning therefore involves most of the abalone at a particular site and if two spawnings per year occur this implies that most individuals in the area spawn twice.

It is well known that the reproductive cycle of molluscs is to a large extent governed by environmental factors and that temperature is especially important. Apart from acting as a stimulus for spawning, changes in temperature may also play a part in gonad maturation (Fretter & Graham, 1964).

Temperature changes have been shown to cause spawning in captive *H. discus hannai* and *H. diversicolor supertexta* (Ino, 1952; Oba, 1964) but these observations have not been confirmed in the field. The relationship between environmental temperature and spawning of *H. midae* was therefore examined.

Temperature records at Stony Point and Dassen Island were collected over a two-year period during which monthly abalone tagging and sampling was conducted. In addition a large number of temperature records were available for the Sea Point area, which has been intensively investigated by the Division for a number of years. From all the above data mean monthly temperatures were calculated and these are illustrated by Fig. 22 and listed in Table VIII.

Seasonal fluctuations of temperature are apparent at Stony Point. Temperatures tend to be high in summer and low in winter and it is significant that this pattern is similar to that described by Stephenson *et al.* (1937) for False Bay, which is a few miles from Stony Point. For comparison, Stephenson's

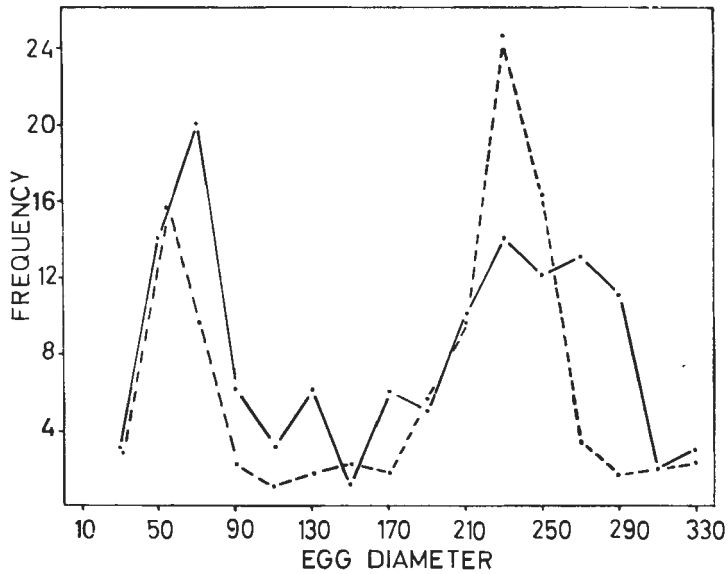


FIG. 19. Egg size frequency of two fully developed ovaries

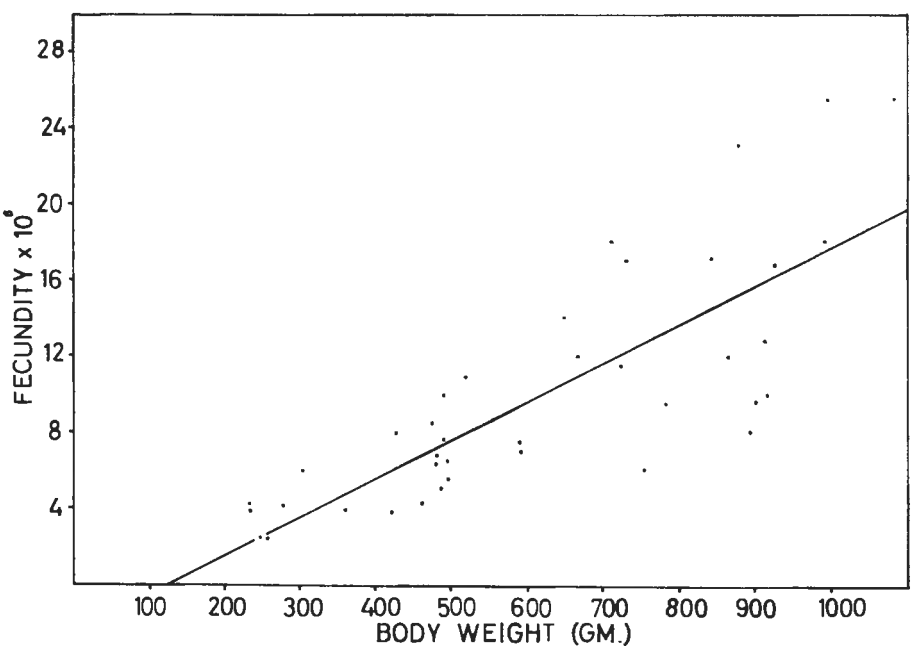


FIG. 20. The relationship between fecundity and body weight

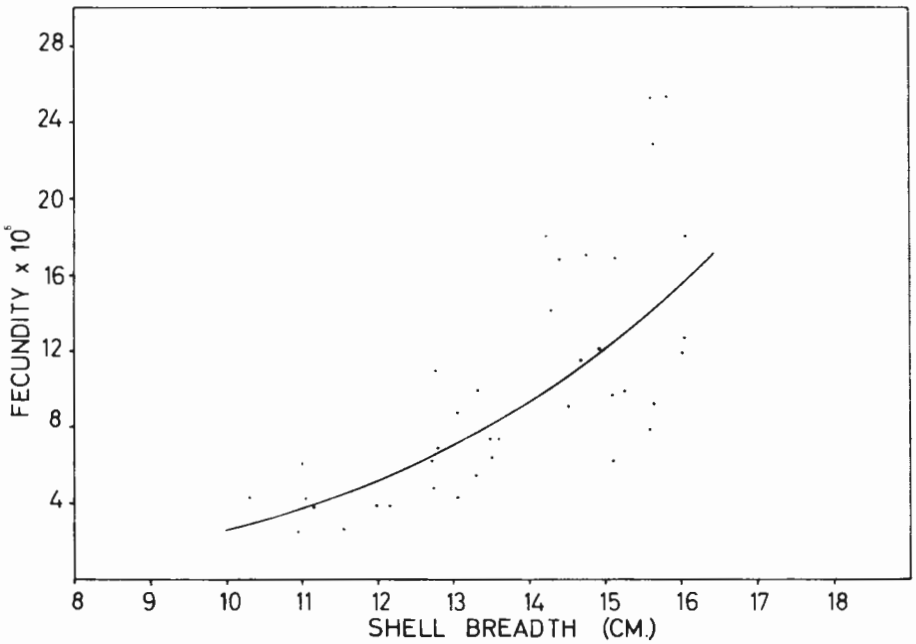


FIG. 21. The relationship between fecundity and shell breadth

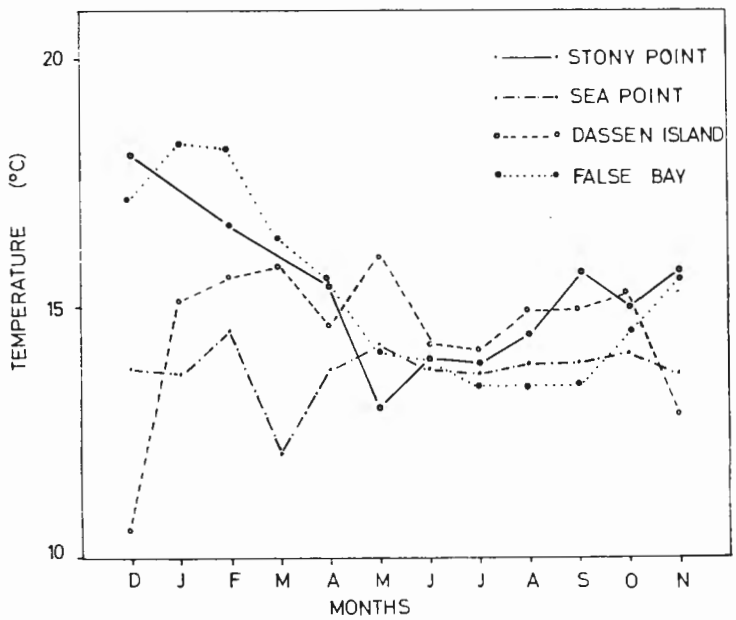


FIG. 22. Mean monthly temperature curves

temperature curve is also included on the figure. It would appear therefore that the November/December spawning at Stony Point is associated with a rise in water temperature. Spawning in March/April coincides with an apparent decline in temperature. This observation must, however, be interpreted with caution as during this period the winds are variable at Stony Point. This in turn causes fluctuating temperatures due to upwelling of cold water or, alternately, inflowing of warm surface water. Thus although Oba (1964) has shown experimentally that a decrease in temperature may stimulate *H. diversicolor supertexta* to spawn, the field evidence of this effect of temperature for *H. midae* is not reliable.

It is revealing to compare the temperature and spawning patterns at Stony Point with those at Sea Point and Dassen Island. At Sea Point very representative temperatures are available and these show little seasonal variation. In addition the mean monthly temperatures are lower than those at Stony Point especially in the summer months. In Section 5 it was shown that spawning at Stony Point was more intense than at Sea Point and from Fig. 22 it would seem that the temperature at the latter site remains constant at too low a level to promote really effective spawning. The temperatures at Dassen Island are generally higher than at Sea Point but show no well-defined seasonal trends. With the exception of October 1962 no intense spawning was recorded at this station.

Boolootian *et al.* (1962) have summarised all the haliotid spawning cycle results in the literature. They found that *H. cracherodii*, *H. lamellosa*, *H. tuberculata*, *H. kamtschatkana*, *H. gigantea*, *H. sieboldii* and *H. discus* spawn between late spring and early autumn with slight modifications due to local conditions. The above species occur in the northern hemisphere. Comparing these results to *H. midae* it appears that at least a spring/summer spawning is common to *H. midae* and haliotids in the northern hemisphere. In this respect Fretter & Graham (1964) make the following general observation about molluscs: "More frequent summer and spring breeders may be reacting to heating of the water or salinity or food changes". The fact that *H. midae* spawns twice a year in certain South African localities is interesting, for two spawnings per year have only been previously reported in one species, namely, *H. discus hannai* from Japan. These occured in spring and winter (Ino & Harada, 1961).

From the structure of the gonads certain conclusions can be drawn about the mechanics of spawning. In Section 6 it was shown that eggs for the next but one spawning are present in the ripe ovary. These smaller eggs have to be maintained during spawning and damage to the ovary by rupturing of the trabeculae must therefore be kept to a minimum. To achieve this the trabeculae and eggs are arranged as follows. The eggs occur within polyhedral columns formed by the trabeculae which "hang" from the integument. Near the digestive gland, however, the intervening trabeculae walls disappear and thereby provide a free passage for the mature eggs during spawning. In the male the lumen is not partitioned by trabeculae and sperm develop simply on the outer surface of tubes within the lumen. The flow of sperm in the testes is therefore unobstructed.

The gametes in both sexes are discharged from the right nephropore via the right nephrocoel, which is extensive and lies adjacent to the anterior end of the gonad. Crofts (1929) reports a longitudinal slit through which the gametes pass into the kidney of *H. tuberculata*. The wall of the kidney has many invaginations and this opening is not easily found in *H. midae*, but by opening the nephrocoel of a fresh specimen and gently massaging the well-developed gonad, the passage of gonad material into the kidney can be seen.

The walls of the gonad consist of connective tissue lined with epithelium and are not contractile. Extrusion of eggs is, however, caused by contractions of the large aductor muscle which compresses the visceral mass between the muscular foot and the shell. Spawning has not been observed in the field but on one occasion at Sea Point a male and a female were collected in ripe and running condition, with eggs and sperm in the mantle cavity. This was a rare occurrence and both were transferred to an aquarium. The abalone were in poor condition but the female released eggs by means of contractions of the aductor muscle. The male released no sperm of its own accord but when the author raised and lowered the shell firmly and quickly, seminal fluid was emitted.

The relationship between fecundity and body weight is linear and ovary growth is isometric. This is confirmed by the exponential relationship between shell breadth and fecundity which has a power coefficient close to three. The production of eggs is a surface phenomenon and should strictly be proportional to a length dimension squared. Beverton & Holt (1957) suggest that if the germinal epithelium is very convoluted, the power coefficient of the relationship may be higher, until ultimately egg production becomes a function of ovary volume and hence weight if the gonad is homogeneous. With the uniform arrangement of the trabeculae in

numerous columns, this is certainly the case with *H. midae*.

8. ACKNOWLEDGEMENTS

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9. LITERATURE CITED

BEVERTON, R. J. H. and S. J. HOLT 1957—On the dynamics of exploited fish populations. *Fishery Invest., Lond.* 29: 1-533.

BOOLOOTIAN, R. A., A. FARMANFAMAIAN and A. C. GIESE 1962—On the reproductive cycle and breeding habits of two western species of *Haliotis*. *Biol. Bull.* 122 (2): 183-193.

CARLISLE, J. G. 1962 -Spawning and early life history of *Haliotis rufescens* Swainson. *Nautilus* 76 (2): 44-48.

CROFTS, D. R. 1929—*Haliotis*. *L.M.B.C. Mem. typ. Br. mar. Pl. Anim.* 29: 1—174.

CROFTS, D. R. 1937—The development of *Haliotis tuberculata* with special reference to organogenesis during torsion. *Phil. Trans. R. Soc.* (B) 228: 219—268.

FRETTER, V. and A. GRAHAM 1964—Reproduction. In *Physiology of mollusca* ed. Wilbur, K. M. and C. M. Yonge, New York, Academic Press. 473 pp.

INO, T 1952—Biological studies on the propagation of the Japanese abalone (genus *Haliotis*). *Bull. Tokai reg. Fish. Res. Lab.* 5: 102 pp.

INO, T. and K. HARADA 1961—On the spawning of abalone in the vicinity of Ibaragi Prefecture. *Bull. Tokai reg. Fish. Res. Lab.* 31: 275—281.

OBA, T. 1964—Studies on the propagation of an abalone, *Haliotis diversicolor supertexta* Lishke II. On development. *Bull. Jap. Soc. scient. Fish.* 30 (10): 809—820.

SIEGEL, S. 1956—*Non-parametric statistics for the behavioural sciences*. New York, McGraw-Hill. 312 pp.

SINCLAIR, M. 1963—Studies on the Paua, *Haliotis iris* Martyn in the Wellington district, 1945-1946. *Zoology Publs Vict. Univ. Coll.* 35: 16 pp.

STEPHENSON, T. A. 1924—Notes on *Haliotis tuberculata* *J. mar. biol. Ass. U.K.* 13 (2): 480—495.

STEPHENSON, T. A., A. STEPHENSON and C. A. DU TOIT 1937—The South African intertidal zone and its relation to ocean currents. I. A temperate Indian Ocean shore. *Trans. R. Soc. S. Afr.* 24: 341—382.

STEPHENSON, T. A. 1944—The constitution of the intertidal fauna and flora of South Africa. Part II. *Ann. Natal Mus.* 10 (3): 261—358.

APPENDIX

Sample no.	Body weight g	Gonad weight g	Shell breadth cm	Gonad sample location	Gonad sample weight g	Egg count	Number of eggs per gram	Fecundity x 10^6
2	463	26·2	13·05	M	·0276	4,530	164,130	4·3
5	249	13·6	11·55	M	·0411	7,772	189,099	2·6
6	423	25·4	12·00	M	·0316	4,775	151,018	3·8
7	498	35·6	13·30	A	·0410	8,604	209,853	
				M	·0495	7,640	154,343	5·5
				P	·0383	7,709	201,279	
9	427	50·0	12·10	M	·0613	9,813	160,082	8·0
11	480	48·1	12·70	A	·0666	15,760	236,636	
				M	·0449	5,822	181,893	6·3
				P	·0453	9,374	206,931	
12	277	22·7	11·05	M	·0428	7,991	186,705	4·2
15	234	21·7	11·15	M	·0319	5,707	178,903	3·9
16	482	31·0	12·80	A	·0291	7,129	244,983	
				M	·0405	8,816	217,679	6·7
				P	·0439	7,969	181,526	
17	302	28·1	11·00	M	·0441	9,509	215,623	6·1
28	232	22·6	10·30	M	·0469	9,020	192,324	4·3
36	256	10·2	10·95	M	·0318	7,438	249,623	2·5
60	996	108·9	15·60	M	·0482	11,198	232,324	25·3
61	361	18·1	12·15	M	·0266	5,707	214,549	3·9
77	489	45·6	13·30	A	·0524	10,974	209,427	
				M	·0334	7,280	217,964	9·9
				P	·0294	7,069	240,442	
78	876	100·3	15·65	M	·0328	7,494	228,476	22·9
89	592	36·4	14·50	A	·0403	7,148	177,370	
				M	·0427	8,350	195,550	7·1
				P	·0584	11,839	202,723	
91	519	53·1	12·75	A	·0542	13,953	257,435	
				M	·0619	12,779	206,446	11·0
				P	·0677	16,358	241,625	
99	843	95·1	14·75	M	·0453	8,134	179,558	17·1
141	495	27·6	13·50	A	·0463	9,684	209,157	
				M	·0444	10,337	232,815	6·4
				P	·0444	8,356	188,198	

Sample no.	Body weight g	Gonad weight g	Shell breadth cm	Gonad sample location	Gonad sample weight g	Egg count	Number of eggs per gram	Fecundity x 10^6
142	588	40·8	13·50	M	·0273	4,988	182,711	7·4
143	488	25·5	12·75	A	·0454	9,407	206,747	
				M	·0217	4,063	187,189	4·8
				P	·0312	6,100	195,513	
147	895	48·0	15·60	M	·0657	10,784	164,140	7·9
150	475	43·4	13·05	A	·0350	7,039	201,114	
				M	·0534	10,757	201,442	8·7
				P	·0322	6,948	215,776	
157	721	95·9	14·70	M	·0555	6,667	120,126	11·5
165	1,086	150·5	15·80	M	·0497	8,391	168,833	25·4
180	916	72·3	16·05	M	·0671	11,832	176,334	12·7
181	867	77·7	16·00	M	·0516	7,935	153,779	11·9
189	993	84·1	16·05	M	·0522	11,190	214,368	18·0
192	916	51·9	15·25	M	·0452	8,605	190,376	9·9
221	755	32·0	15·10	M	·0509	9,874	193,988	6·2
223	489	39·7	13·60	A	·0518	10,098	194,942	
				M	·0514	9,583	186,440	7·4
				P	·0745	14,615	196,174	
224	782	57·0	15·00	M	·0576	9,828	170,625	9·7
225	648	68·2	14·30	M	·0270	5,577	206,556	14·1
226	710	95·2	14·25	M	·0512	9,686	189,179	18·0
227	728	79·8	15·10	M	·0421	8,938	212,304	16·9
232	666	68·5	14·95	M	·0679	11,880	174,963	12·0
235	901	52·7	15·65	M	·0241	4,254	176,514	9·3
237	925	112·6	14·40	M	·0474	7,076	149,283	16·8

A anterior gonad

M = middle gonad

D posterior gonad

REPUBLIC OF SOUTH AFRICA

DEPARTMENT OF INDUSTRIES

DIVISION OF SEA FISHERIES INVESTIGATIONAL REPORT

No 67

GROWTH OF THE SOUTH AFRICAN ABALONE

Haliotis midae

by

G. G. NEWMAN

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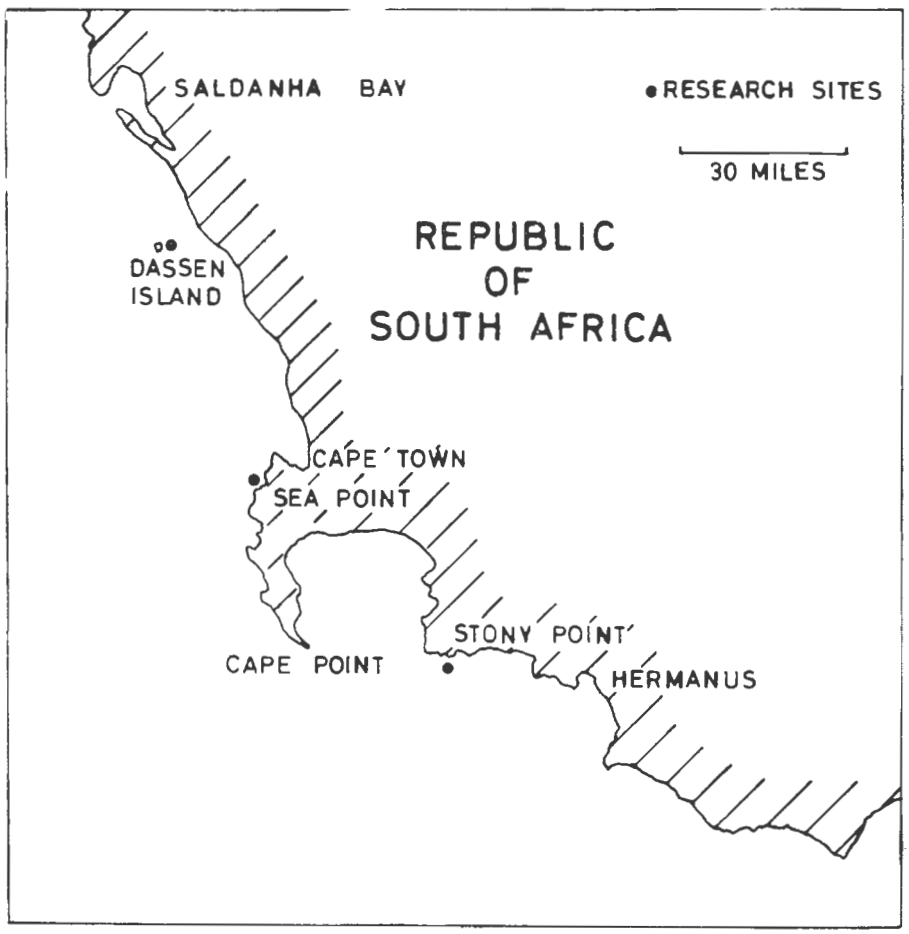

FIG. 1. Abalone research sites

ABSTRACT

The growth of *Haliotis midae* was investigated by means of tagging and population sampling. Multiple regression analysis of tagging results showed a seasonal variation in growth rate, which appears to be associated with spawning. This pattern was recorded in both mature and immature abalone. The following von Bertalanffy equation was found to represent the growth of *H. midae* in terms of shell breadth:

$$L_t = 19{\cdot}33\,(1-e^{0{\cdot}0593(t\ 1{\cdot}8820)})$$

Shell shape and shell length/body weight relationships were examined at four localities. Differences in shell length/depth and shell length/body weight relationships were noted in populations east and west of Cape Point. Inflection points were found in the otherwise linear shell length/breadth and shell length/depth relationships and the significance of these is discussed.

1. INTRODUCTION

The growth of molluscs is most conveniently described in terms of shell increments. The deposition of shell material, which is fully discussed by Wilbur (1964), is briefly as follows:
Crystals of calcium carbonate are deposited on an organic matrix called conchiolin. The tissue responsible is the mantle and the rate of increase in shell area is therefore a function of mantle area. The rate of increase in shell thickness and weight is, however, a function of the rate of secretion of the calcium carbonate and the organic matrix. This rate is of lesser importance as it does not directly reflect the increase in size of the abalone. In addition it is difficult to measure and is therefore seldom described in growth studies.

There are various methods of determining the growth rate of molluscs.

Annual rings provide a convenient method of age determination and have been applied to *Haliotis discus hannai* (Sakai, 1962), but in *Haliotis midae* these rings are not evident and tagging techniques had to be used to investigate growth.

Population sampling and the plotting of length frequency diagrams (Petersen's method) provide further means of assessing the growth rates of species which spawn over a restricted season. The method is especially effective in animals with a short larval life followed by fairly rapid growth. Using this technique Williams (1964 a, 1964 b) was able to describe the growth of the gastropods *Littorina littorea* and *Gibbula umbilicalis* over certain size ranges. This method was also applied in this investigation to determine the growth of young *H. midae*.

The annual rings shown by some abalone indicate seasonal variations in growth. It is uncertain whether such variations also occur in *H. midae*, where no rings are apparent. Tagging results were therefore examined to establish possible seasonal patterns.

Having determined growth in terms of a particular shell dimension, this rate of increase may be transformed to increments in body weight or other shell dimensions if the relationship between the shell dimensions concerned is known. In the literature the representation of such relationships varies from a simple statement of the mean ratio of two dimensions within a specified size range (Yamamoto, 1949; Crofts, 1929) to the use of linear and exponential regression equations (Sakai, 1962). In addition, a logarithmic or equiangular spiral equation was suggested as a means of representing shell shape by Thompson in 1917 and was used by Moore (1936) to describe variations in the shell shape of the gastropod *Purpura lapillus*. In this report on *H. midae* variations in length/weight relationships and shell shape due to size and locality were studied by means of regression equations.

2. GROWTH ESTIMATES FROM TAGGING

2.1 Methods

The tagging programme was conducted at Stony Point (Fig. 1) over a two-year period, from January 1962 to December 1963. A total of 2645 abalone were tagged and the overall rate of recovery for the experiment was ten per cent. During the programme tagging activities were concentrated over a fairly wide size range, i.e. from 5·0 to 12·0 cm shell breadth. In addition, all tagging took place in a fairly restricted area which was intensively searched periodically by SCUBA divers from the Division of Sea Fisheries. This assured the recovery of sufficient tagged animals to allow a meaningful growth equation to be determined for the species.

Petersen tags were used to mark abalone. One disc, on which was printed a message requesting the finder to return the animal to the Division of Sea Fisheries, was placed inside the shell and fixed to an external, numbered disc by means of a non-corrosive nickel pin passing through a respiratory pore. So as not to interfere with normal growth, tags were attached at the fourth anterior pore, well away from the growing edge of the shell. The shell length and breadth were then measured to the nearest 0·05 cm by means

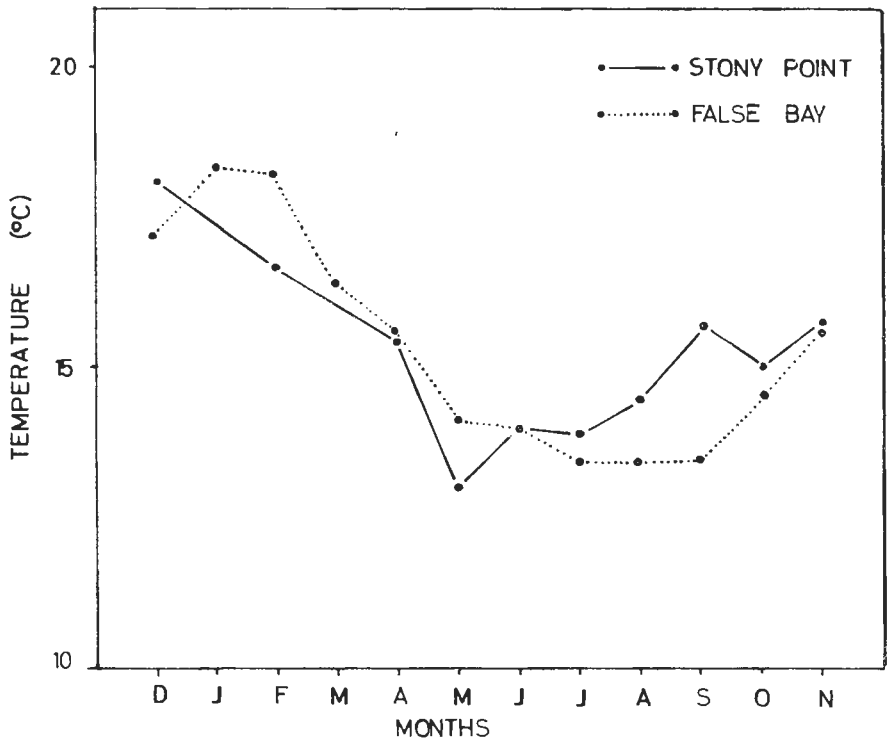

FIG. 2. Mean monthly temperature curves

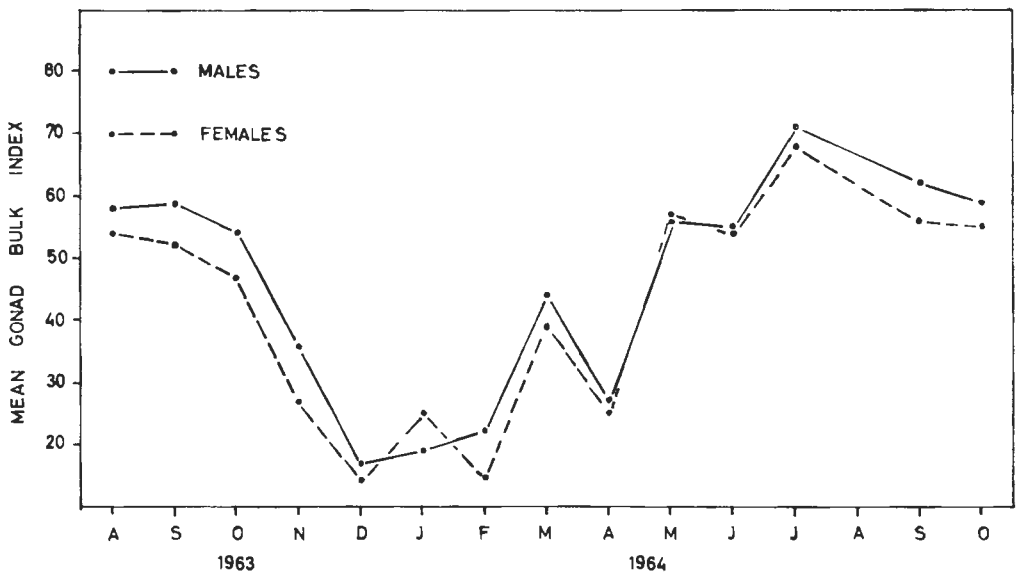

FIG. 3. Mean monthly gonad bulk indices at Stony Point

of vernier calipers and recorded against the relevant tag number. In order to reduce mortality or physiological disruption due to exposure to the air, abalone were kept submerged in rock pools between collection and tagging, except for a period of two to three minutes during which tagging and measuring took place. No abalone damaged during collection were used for tagging, and to reduce damage by predation or wave action, tagged animals were individually replaced by divers who held them against the substratum until they adhered firmly to the rock. Recoveries were made during systematic searches (Newman, 1966) as well as during subsequent tagging operations in the area.

No abalone were used for growth studies if they showed signs of any tag interference in the growth pattern or had obviously damaged shells (and negative increments). Furthermore, no returns obtained within less than 95 days were used, because the growth increment during this period was small and it was difficult to maintain relative accuracy of the measurements. Of the 260 returns during the experiment, 135 proved suitable for growth estimates. About 90 per cent of the total rejections were due to short tag-return periods.

Recoveries were placed in size classes according to their initial shell breadth at tagging. The intervals in this case were 1 cm, the range of returns being from 5·00 to 11·95 cm shell breadth. The frequencies of returns within the tag-return classes are shown in Table I.

TABLE I: SIZE FREQUENCY OF TAGGED ABALONE USED FOR GROWTH STUDIES AT STONY POINT

Shell breadth (cm)	Frequency
5 — 6	20
6 — 7	38
7 — 8	38
8 — 9	17
9 — 10	13
10 — 11	4
11 — 12	5

Estimates of the growth per annum within these size classes were made by regression equations. In order to determine and adjust for possible seasonal variations in growth rates, regression models with five and then three variables (dependent and independent) were fitted to the data. As the calculations involved were considerable, an I.C.T. 1500 computer was used. A suitable programme for this type of analysis was the standard multiple regression analysis programme supplied by International Computers and Tabulators (Pty) Ltd.

2.2 Seasonal growth

The seasonal representation of tagging data was examined by calculating the total number of autumn, winter, spring and summer days in the tag-return periods within particular size classes. These totals appear in Table II and it will be seen that the seasons are not typically represented in the tag-return periods.

In fact, the number of winter days, and to a lesser extent spring days, exceed those of the other seasons. Under the circumstances seasonal variation of growth would invalidate the assumption that representative growth per annum can be calculated directly from the tagging data. Thus, although the establishment of seasonal growth variations is in itself interesting, it is important that these variations be defined and accounted for before calculating growth parameters. Accordingly the following model was first fitted separately to the data in each of the classes listed in Table II:

$$G = b_1 x_1 + b_2 x_2 + b_3 x_3 - b_4 x_4 + b_0 \quad \ldots (1)$$

Where G = growth increment

x_1 = number of summer days — b_1 = summer growth coefficient

x_2 = number of autumn days — b_2 = autumn growth coefficient

x_3 = number of winter days — b_3 = winter growth coefficient

x_4 = number of spring days — b_4 = spring growth coefficient

b_0 = error term

The generally accepted combination of months,

summer = December, January and February;
autumn = March, April and May;
winter = June, July and August;
spring = September, October and November,

was applied to the model. The coefficients of the five equations, i.e. one for each size class, are listed in Table III. The coefficients of each equation are also ranked, the rank being indicated by the bracketed figure below the particular coefficient.

It appears that a pattern of growth is present, and, with one exception, that growth is most rapid in winter. The second season of faster growth is possibly spring but this is less certain.

Among poikilotherms seasonal changes in the growth rate may be due to temperature (Ursin,

TABLE II: THE PRESENTATION OF THE SEASONS WITHIN TAG-RETURN PERIODS

Shell breadth (cm)	Spring days	Summer days	Autumn days	Winter days
5 - 6	1,000	808	1,137	1,446
6 — 7	2,338	1,070	2,003	3,017
7 8	2,307	1,276	2,255	2,878
8 — 9	1,192	557	773	1,246
9 10	799	642	652	909
Total	7,636	4,353	6,820	9,496

1965; Rounsefell & Everhart, 1953), food supply (Pantulu, 1962; Cox, 1962) or the reproductive cycle (Sakai, 1960). With *H. midae* the reproductive cycle seems to influence seasonal growth, while fluctuations in temperature and food supply would seem to have little effect. The latter two factors will, however, be dealt with first.

A mean monthly temperature curve for Stony Point is illustrated in Fig. 2. Also appearing on the figure are more complete monthly mean temperatures for False Bay, which is a few miles from Stony Point. The values for False Bay are from Stephenson *et al.* (1937) while the Stony Point figures were collected by the Division of Sea Fisheries (Newman, 1967). Both curves show that temperatures are high in summer, when growth appears to be slow and that faster winter growth is in fact accompanied by low temperatures. This is unexpected as temperature and growth rate are generally positively related within reasonable temperature ranges (Taylor, 1958, 1959). It is therefore unlikely that temperature has any real effect at Stony Point.

Examination of stomach contents has revealed that the kelp, *Ecklonia maxima*, is by far the most important food of the Stony Point population. Abalone have been observed actively feeding on kelp fronds and, in the vicinity of groups of abalone, these usually show characteristic signs of feeding activity. The above alga is found in prolific beds along the whole Stony Point coastline, and its occurrence does not vary seasonally. Variations in food supply cannot therefore explain the seasonal growth patterns obtained.

Spawning in *Haliotis midae* involves the loss of large quantities of gonad material within a short period. The replacement of this material, which in mature females represents between five and ten per cent of the total body weight, occurs rapidly and may well interrupt growth processes.

Changes in gonad size due to spawning are reflected by the mean gonad bulk indices appearing in Fig. 3. These are fully discussed by Newman (1967) and show that individuals spawn twice per year at Stony Point, i.e. in late spring/early summer and in autumn. In summer and autumn abalone are therefore recovering from spawning and growth can be expected to be slow. There does in fact seem to be a tendency for growth coefficients to be lower during these seasons and likewise high coefficients tend to be associated with winter and spring when little gonad recovery is taking place.

By varying the regression model this effect could be shown more clearly.

TABLE III: COEFFICIENTS OF FIVE-VARIABLE REGRESSIONS FITTED TO TAGGING DATA

Coefficient / Size Class	b_1 Summer	b_2 Autumn	b_3 Winter	b_4 Spring	b_5
5 — 6	0·00359 (2)	—0·00071 (4)	0·00511 (1)	0·00161 (3)	—0·01975
6 — 7	—0·00085 (4)	0·00328 (2)	0·00474 (1)	0·00290 (3)	—0·21480
7 — 8	—0·00011 (4)	0·00058 (3)	0·00328 (1)	0·00302 (2)	0·03469
8 — 9	0·00118 (4)	0·00118 (3)	0·00309 (1)	0·00211 (2)	—0·13472
9 10	0·00061 (3)	0·00002 (4)	0·00214 (2)	0·00439 (1)	—0·11165

A three-variable model was used, with two six-month periods being selected in such a way as to separate as far as possible the gonad recovery phase from the rest of the cycle. During the period June to November the gonads are either fully recovered or starting to spawn and growth can be expected to be fast. In December to May, however, the gonads are recovering after two spawnings and slow growth is likely.

The following model was therefore fitted to the data:

$$G = b_1 x_1 + b_2 x_2 \quad b_0 \quad . \quad . \quad . \quad . \quad . \quad (2)$$

Where G = growth increment

x_1 = number of days within period 1 December to 31 May

b_1 = growth coefficient December-May period

x_2 = number of days within period 1 June to 30 November

b_2 = growth coefficient June-November period

b_0 = error term

From the coefficients which are listed in Table IV it is quite clear that faster growth always occurs during periods of low gonad activity.

Having established a pattern of seasonal variations in growth rate on the basis of ranks, the significance of the differences between coefficients was examined by means of t-tests. As there are theoretical grounds for assuming that coefficients associated with low gonad activity are higher than those representing growth rates during spawning and recovery periods, one-tailed tests could be used. The required standard errors of the differences between coefficients were calculated from the following equation (from Fisher, 1932):

$$SE_{b_r - b_s} = S^2 (C_{rr} - 2C_{rs} + C_{ss}) \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (3)$$

Where S^2 = estimated residual variance

and C_{rr}, C_{rs}, C_{ss} = appropriate elements of the inverse matrix

As the computer programme used in this investigation makes provision for the printing out of the requirements of (3) the standard error could conveniently be calculated by hand. In addition, the degrees of freedom for the tests were estimated as $n = \acute{n} - p - 1$ where $\acute{n}$ — number of sets of observations and p = the number of independent variables in the model.

Test results with the five-variable models are listed in Table V. It appears that in two size classes the winter growth coefficients (b_3) are significantly higher than those for summer (b_1) ($P < 0{\cdot}05$).

Similarly from Table VI it will be seen that in the 7-8 cm class the probability that $b_2 > b_1$ amounted to 0·001 which clearly indicates that growth in June to November was significantly higher than that in December to May. A similar difference is apparent in the case of the 8-9 cm size class ($P < 0{\cdot}05$) and with less certainty in the 5-6 cm class ($P < 0{\cdot}10$).

From the patterns of coefficient ranks, as well as tests of significance, it would appear that seasonal variations of growth rate occur throughout the size range investigated, and that these are associated with the reproductive cycle. This is especially interesting when the onset of sexual maturity is considered. Newman (1967) has found that at a shell breadth of 8 cm only 50 per cent of the population are sexually mature. One hundred per cent maturity can only be expected at a shell breadth of 10·5 cm while at 6 cm only one per cent are mature. It would seem therefore that immature abalone react in sympathy with larger mature individuals with respect to seasonal growth patterns.

TABLE IV: COEFFICIENTS OF THREE-VARIABLE REGRESSIONS FITTED TO TAGGING DATA

Coefficient / Size Class	b_1 (Dec.—May)	b_2 (June—Nov.)	b_0
5 — 6	0·00153 (2)	0·00346 (1)	—0·03644
6 — 7	0·00150 (2)	0·00279 (1)	—0·02605
7 — 8	0·00026 (2)	0·00310 (1)	0·05075
8 — 9	0·00107 (2)	0·00255 (1)	—0·11730
9 — 10	0·00109 (2)	0·00344 (1)	—0·22141

TABLE V: RESULTS OF ONE-TAILED *t* TESTS TO DETERMINE THE SIGNIFICANCE OF DIFFERENCES BETWEEN COEFFICIENTS OF FIVE-VARIABLE MODELS

Size class	Degrees of freedom	Probability			
		b_3 b_1	$b_3 > b_2$	$b_1 > b_1$	b_4 b_2
5 — 6	15	0·30	0·10	—	0.25
6 — 7	33	0·05	0·30	0·15	
7 - 8	33	0·05	0·20	0·15	0·20
8 9	12	0·20	0·25	0·50	0·35
9 — 10	8	0·30	0·35	0·30	0·15

TABLE VI: RESULTS OF ONE-TAILED *t* TESTS TO DETERMINE THE SIGNIFICANCE OF DIFFERENCES BETWEEN COEFFICIENTS OF THREE-VARIABLE MODELS

Size class	Degrees of freedom	Probability b_2 b_1
5 — 6	17	0·10
6 — 7	35	0·20
7 — 8	35	0·001
8 — 9	14	0·05
9 — 10	10	0·15

Seasonal variations in the growth rate of other species of *Haliotis* have been reported. Ino (1952) confined *H. discus* and found that food consumption fluctuated in phase with changes in the growth rate, which was at minimum in the breeding season. He concluded that food consumption and growth variations are due to internal physiological conditions rather than environmental effects. Sakai (1960) reared *H. discus hannai* and found that the growth rate fell and a shell ring was formed during the breeding season. No ring was, however, formed by immature abalone. In a subsequent publication (Sakai, 1962) low temperatures were also found to cause ring formation but during these experiments the temperature range was large and not comparable to that at Stony Point. The determination of seasonal growth fluctuations with tagging data was also attempted by Leighton & Booloottian (1963) who concluded that *H. cracherodii* grows faster in summer.

It is apparent that seasonal fluctuations in growth can be shown to occur in *H. discus*, *H. discus hannai* as well as in *H. midae*. They may well also occur in *H. cracherodii*. In the case of the Japanese abalone, seasonal effects are associated with the reproductive cycle and are not manifested by immature individuals. This was not found to be the case with *H. midae* where regression analysis with individuals which were predominantly immature produced the same seasonal patterns as those observed in mature abalone.

2.3 Annual growth

For the determination of the growth rate per annum within each size class, two alternative regressions are available. To obtain the best estimate of the annual growth rate within each size class, the standard errors of estimate of the respective regressions were considered. These appear in Table VII. The standard errors of each of the regressions of the five size classes have been ranked. With the exception of size class 6-7 cm, the standard errors of estimate of the three-variable regressions were the lowest in the series. The best estimates of the annual growth increments were therefore obtained by substitution in these equations. The resultant values are listed in Table VIII together with the frequencies within the classes.

TABLE VII: STANDARD ERRORS OF ESTIMATE OF REGRESSION MODELS

Shell breadth cm / Regression series	STANDARD ERROR OF ESTIMATE				
	5—6	6—7	7—8	8—9	9—10
5 variables	0·10010 (1)	0·08714 (2)	0·08570 (1)	0·03917 (1)	0·08274 (1)
3 variables	0·09428 (2)	0·08991 (1)	0·08104 (2)	0·03380 (2)	0·06952 (2)

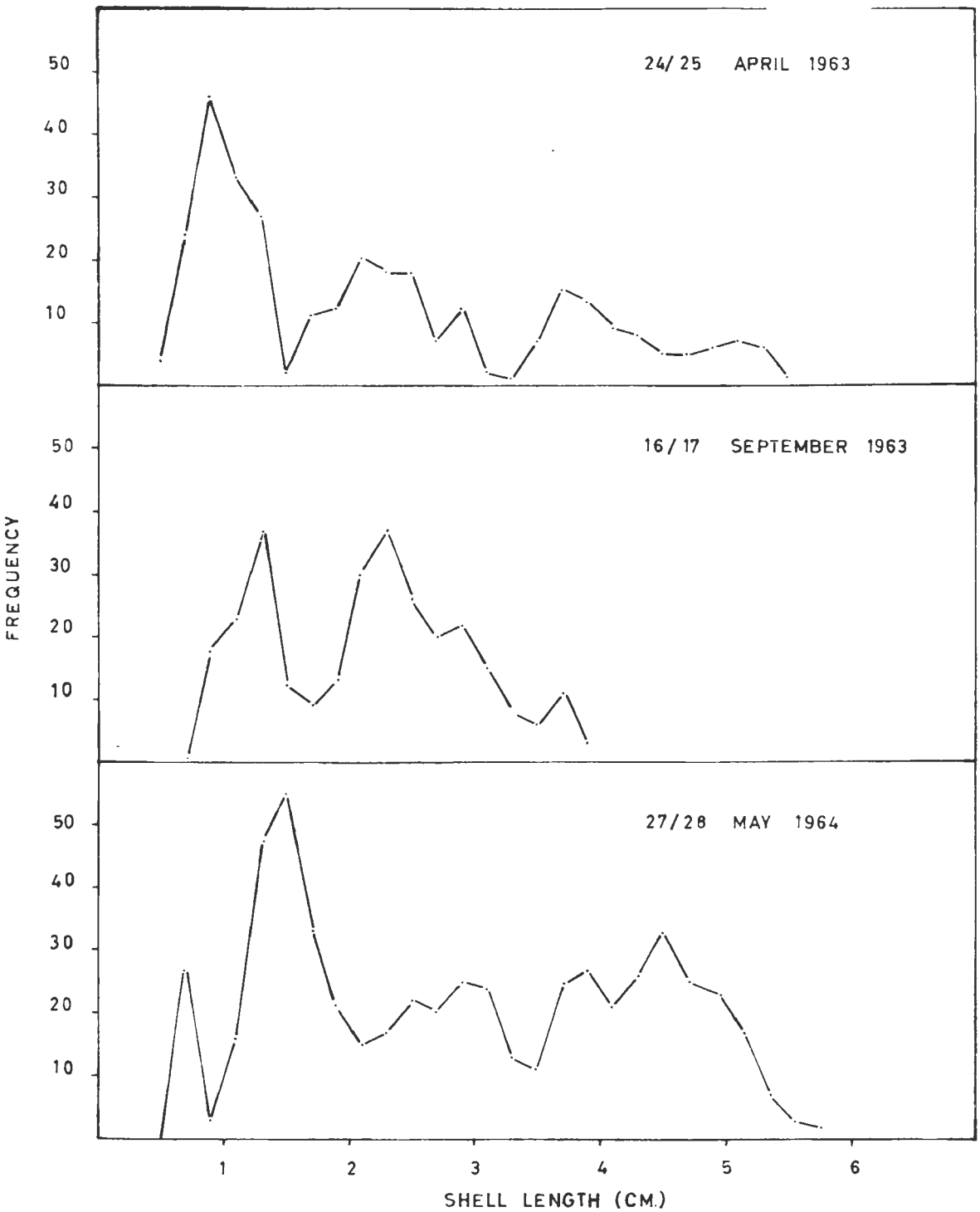

FIG. 4. Size frequency of abalone under rocks at Stony Point

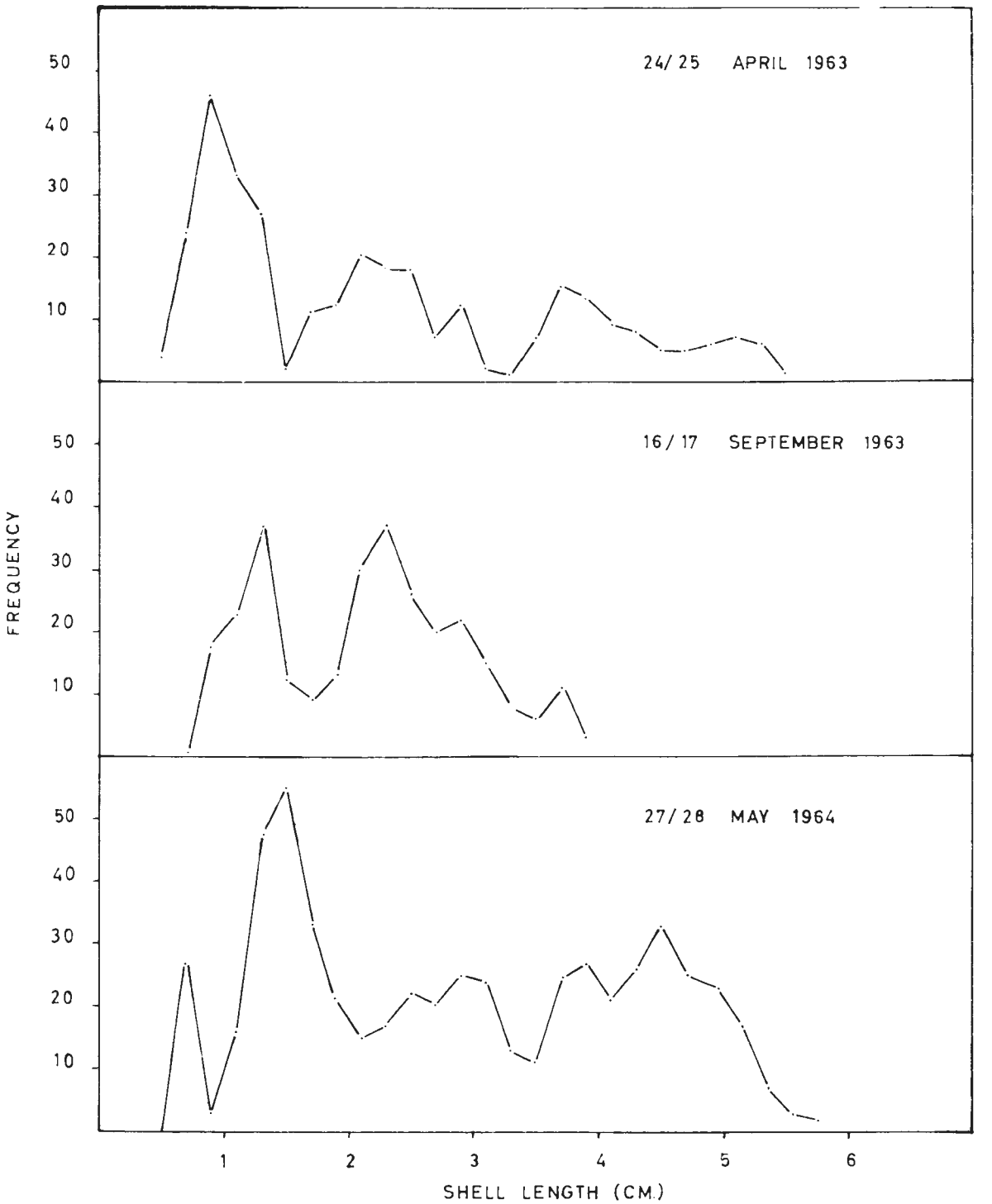

FIG. 4. Size frequency of abalone under rocks at Stony Point

In addition to the above results some tag-returns were available for size classes within the range 10-12 cm. The frequencies in these cases were low, all being below six returns. Under the circumstances the fitting of a multiple regression model was not justified. The best estimate of the annual increment was therefore obtained from the linear model:

$$G = b_1 x_1 + b_0 \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (4)$$

Where G = growth increment
x_1 = tag return period
b_1 growth coefficient
and b_0 = error term

TABLE VIII: ESTIMATES OF THE MEAN ANNUAL GROWTH INCREMENT

Shell breadth (cm)	Frequency	Estimated annual shell breadth increment (cm)
5 — 6	20	0·88
6 — 7	38	0·76
7 — 8	38	0·67
8 9	17	0·54
9 10	13	0·61
10 — 11	4	(0·52)*
11 — 12	5	(0·51)*

* Values in brackets are estimates from model $G = b_1 x_1 + b_0$

3. GROWTH ESTIMATES FROM POPULATION SAMPLING

Tagging methods cannot be used to estimate the growth rate of *Haliotis midae* below about 5 cm shell breadth for the delicate shell and body structure within this size range renders tagging unpractical. In addition, juveniles are found under boulders and stones, which complicates both the collection and recovery of tagged animals.

The growth rate of small abalone was therefore determined from size frequency polygons of large random collections made beneath stones and boulders at the Stony Point research site. In the course of this analysis probability paper was used to define distributions resulting from specific spawnings. These plots also enabled the mean and variance of the distributions to be estimated with fair accuracy.

3.1 Methods

Three large collections were made at Stony Point on 24/25 April 1963, 16/17 September 1963 and 27/28 May 1964 in depths ranging from one to six feet below mean low spring tide. Divers overturned likely boulders and all abalone beneath them were collected. As a bottom surge tended to wash away smaller individuals, collections could only be made during dead calm seas. These conditions prevailed on the three occasions mentioned above and it may be assumed that the samples are unbiased and representative of the populations below boulders and stones in the Stony Point area.

The shell length and breadth of all the material was measured by means of vernier calipers to the nearest 0·05 cm. From these data, shell length size frequency tables with 0·2 cm intervals were drawn up and represented by the frequency polygons appearing in Fig. 4. The data were also plotted on probability paper according to the method of Harding (1949). For this purpose frequency tables with intervals of 0·1 cm were used. Probability plots of the three collections made appear in Figs. 5, 6 and 7.

The unimodal distributions in Fig. 4 could be identified by referring to the spawning cycle for Stony Point illustrated by Fig. 3. (Reproduction at Stony Point is fully discussed by Newman, 1967.) From this it was assumed that spawning took place on 1 April and 1 December in any one year. Defined unimodal distributions in the frequency polygons were accordingly identified by considering the date of collection as well as the position of the particular distribution in the sequence of modes.

3.2 Analysis of population samples

24/25 April 1963:

A total of 333 individuals were collected on this occasion. The size frequency diagram of the sample is illustrated by Fig. 4 and it is apparent that three well-defined distributions occur with modes at 0·9, 2·1 and 3·7 cm respectively. A less distinct distribution occurs with a mode at 5·1 cm. The data plotted on probability paper appear in Fig. 5. Four well-defined straight lines occur, with obvious inflection points between them, and the pattern confirms the existence of four normally distributed groups within the whole collection. The expanded form of each of the above distributions is also shown on Fig. 5. These lines were fitted by eye to points calculated according to the method of Harding (1949). From the expanded straight lines the distribution means were graphically estimated as being 1·0, 2·2, 4·0 and 5·1 cm respectively, values which agree with modal interpretation discussed earlier. The distributions may be identified as follows. Collection took place on 24/25 April 1963, thus unless growth was partic-

ularly fast it is unlikely that the results of the April spawning would be available for collection. The first distribution, with a mean of 1·0 cm was regarded as the result of spawning activity during October-December 1962. Assuming a hypothetical spawning date of 1 December, this distribution represents abalone which are approximately five months old. Similarly it may be assumed that the next distribution is the result of April 1962 spawning activity and that individuals within this group are approximately 13 months old, with a mean shell length of 2·2 cm. The subsequent distributions would then be the results of December 1961 and April 1961 spawning, being therefore 17 and 25 months old respectively, with mean lengths of 4·0 and 5·1 cm.

27/28 May 1964:

During May 1964 a large collection was made in the vicinity of Stony Point. The size frequency curve of the 594 abalone collected appears in Fig. 4 and five fairly discrete distributions occur with modes at 0·7, 1·5, 3·0, 4·1 and 4·7 cm. The data plotted on probability paper appear in Fig. 7, where five distributions may again be discerned, with inflection points at 5·2, 35·0, 60·0, 79·3 and 98·0 per cent. Mean values for the distributions, estimated graphically from the expanded straight lines appearing in the figure, amounted to 0·8, 1·5, 2·9, 4·1 and 5·0 cm respectively. These values agree fairly closely with the modal values on Fig. 4. The first distribution of the series was identified as the result of April 1964 spawning, i.e. it may be assumed to be 2 months old, with a mean shell length of 0·8 cm. The age of the next distribution is estimated as 6 months, with a mean length of 1·5 cm. This is the result of December 1963 spawning activity. Similarly subsequent distributions are identified as the results of April 1963 spawning (14 months; 2·9 cm) December 1962 spawning (18 months; 4·1 cm) and April 1962 spawning (26 months; 5·0 cm).

TABLE IX: IDENTIFICATION AND DESCRIPTION OF UNIMODAL DISTRIBUTION WITHIN A SAMPLE OF *Haliotis midae*, 24/25 APRIL 1963

Distribution	Frequency	Mode (cm)	Mean (cm)	Age in months	Standard deviation (cm)
December '62	125	0·9	1·0	5	0·19
April '62	105	2·1	2·2	13	0·41
December '61	62	3·7	4·0	17	0·38
April '61	20	5·1	5·1	25	0·09

16/17 September 1963:

The size frequency polygon of 344 abalone collected on the above dates appears in Fig. 4, and two well-defined unimodal distributions occur, with modes at 1·30 and 2·30 cm. The probability plot of this data appears in Fig. 6. Two straight lines occur in the figure with inflection points at 26·5 and 73·0 per cent. These were expanded and found to have means at 1·3 and 2·5 cm respectively, which coincide closely with the modal values quoted above. As the collection was made halfway through September it may be assumed that the first distribution is the result of spawning activity in April 1963, and therefore that abalone within this group attained a mean shell length of 1·3 cm in four and a half months. Similarly the next distribution, spawned during December 1962, has a mean shell length of 2·5 cm after a period of 10·5 months.

The validity of the interpretations of all the above samples seems to be borne out by the similarity and regularity of the distributions isolated on the three different collection dates. Referring to Fig. 4, the modal value of the December 1962 spawning group is identifiable in all three collections and its regular movement along the shell length axis with time can clearly be seen. Similarly the movement of the April 1962

TABLE X: IDENTIFICATION AND DESCRIPTION OF UNIMODAL DISTRIBUTIONS WITHIN A SAMPLE OF *Haliotis midae*, 16/17 SEPTEMBER 1963

Distribution	Frequency	Mode (cm)	Mean (cm)	Age in Months	Standard deviation
April '63	91	1·3	1·3	4·5	0·21
December '62	160	2·3	2·5	10·5	0·35

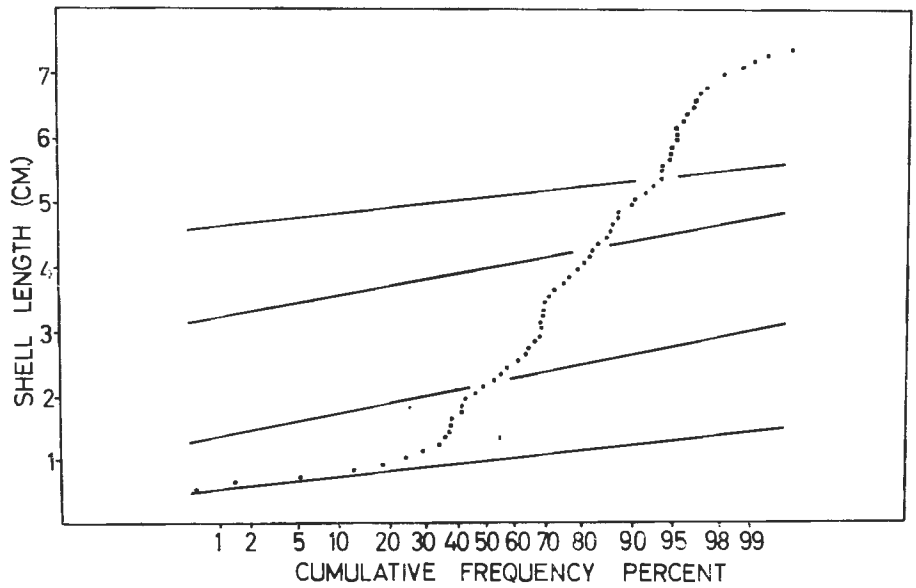

FIG. 5. Probability paper plot of April 1963 sample

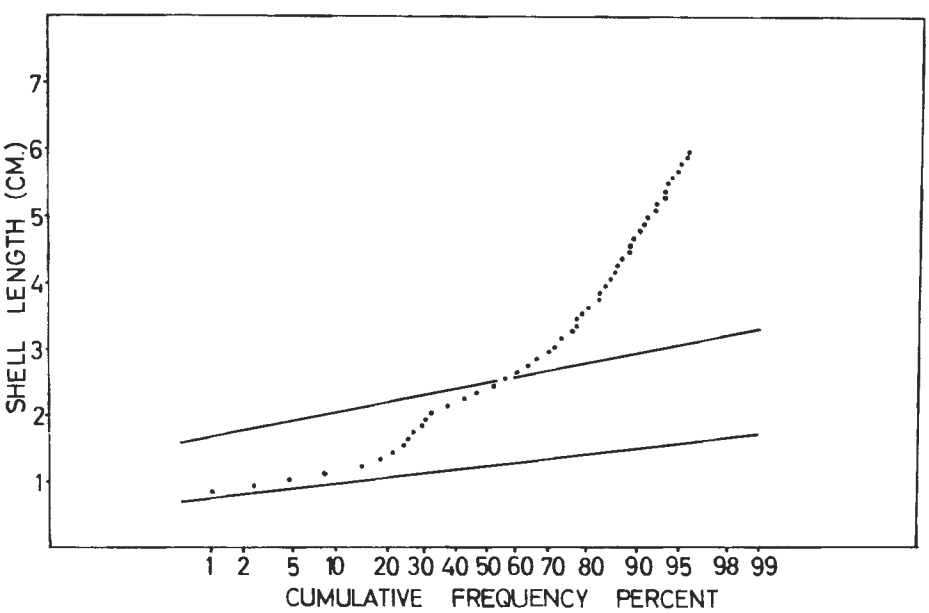

FIG. 6. Probability paper plot of September 1963 sample

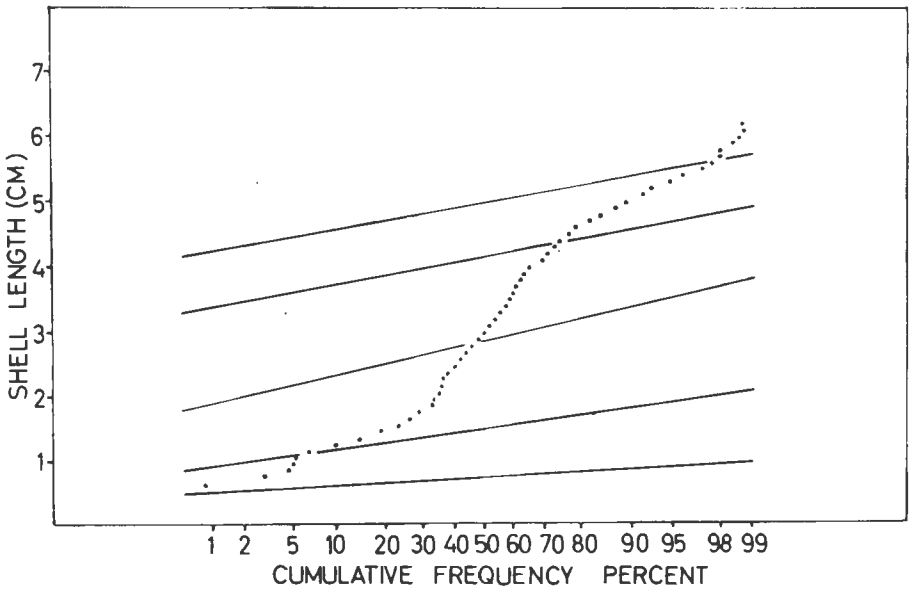

FIG. 7. Probability paper plot of May 1964 sample

TABLE XI: IDENTIFICATION AND DESCRIPTION OF UNIMODAL DISTRIBUTIONS WITHIN A SAMPLE OF *Haliotis midae*, 27/28 MAY 1964

Distribution	Frequency	Mode (cm)	Mean (cm)	Age in months	Standard deviation (cm)
April '64	31	0·7	0·8	2	0.11
December '63	177	1.5	1.5	6	0.26
April '63	148	3.0	2.9	14	0.44
December '62	115	4.1	4.1	18	0.34
April '62	111	4.7	5.0	26	0.33

and April 1963 components can be traced in the figure.

From the data listed in Tables IX, X and XI a composite picture may be built up of the growth of *Haliotis midae* during the first two years of life. The mean shell length values obtained have been plotted against their respective ages in Fig. 8. A curve has been fitted by eye to the points which seem to be positioned fairly consistently about this line. An exception is the mean value for individuals spawned in April 1962 and collected in April 1963. The two means in the region of 5·0 cm were not taken into account, for at this size abalone move out from below the boulders. These distributions, therefore, may be biased as the samples were only collected underneath boulders.

From the growth curve presented in Fig. 8 it is apparent that mean shell lengths of 2·7 and 3·9 cm are attained at ages of one and one and a half years respectively. Comparison of these means with data presented by Sakai (1962) shows a similarity between the growth rate of *H. midae* and *H. discus hannai* for the first two years of life. Sakai's data, obtained from observations of the well-defined annual rings which occur in *H. discus hannai*, showed that after one and two years mean shell lengths of approximately 27·0 and 48·0 mm were attained.

4. GROWTH CURVES FOR *Haliotis midae*

The growth rates of small and medium sized

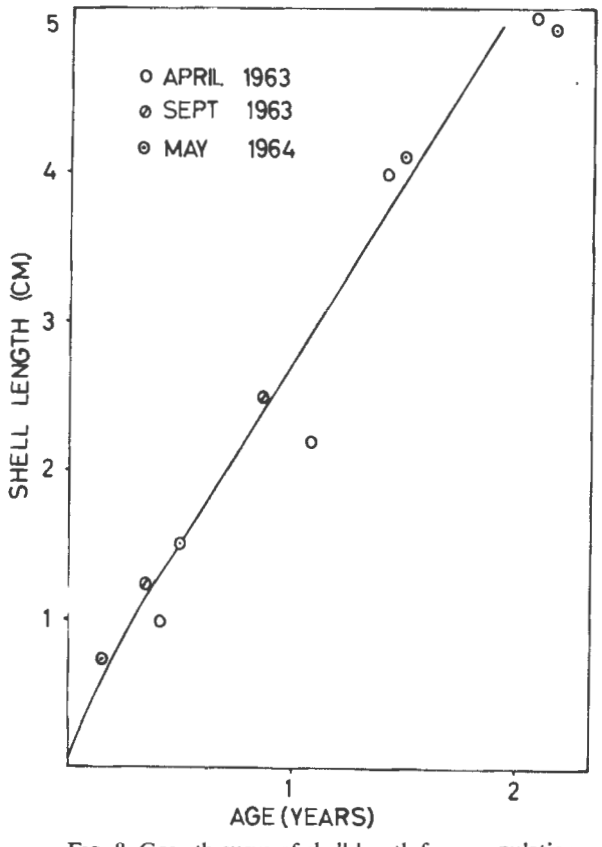

FIG. 8. Growth curve of shell length from population sampling at Stony Point

H. midae have been determined by two different techniques. The results will now be combined to build up a composite picture of growth.

4.1 Shell breadth

As a first step towards estimating growth parameters a curve relating growth rate and shell breadth was drawn. Within the size range 5·5 to 11·5 cm, points on this curve were easily obtained from tagging results. These growth rate values are listed in Table VIII and are plotted on Fig. 9. In all but the two largest size classes the rates are adjusted for seasonal effects. Annual increments of the smaller size ranges were obtained by transforming the shell length/age curve of Fig. 8 to a shell breadth/age curve. This was done by means of the relationship:

$$B \quad 0{\cdot}6812\,L - 0{\cdot}0071$$

where B shell breadth in cm
L shell length in cm.

which will be fully discussed in Section 5. The curve thus obtained (Fig. 10) is linear over most of its range. The slope at particular sizes provides an estimate of the growth rate, and at shell breadths 0·5, 1·5 and 2·5 cm this was a constant 1·7 cm per annum. This information is also plotted on Fig. 9 and a freehand curve has been drawn.

Taylor (1962) has described a versatile and generalized growth rate function, that is:

$$\frac{dL}{dt} \quad EL^{(a-b+1)} - KL \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (5)$$

where L length
E — a coefficient supposedly related to anabolism
K a coefficient supposedly related to catabolism
a the exponent relating length to the surface involved in anabolic processes
b = the exponent relating length to effective metabolic weight

if $a \neq b$ the solution of the above rate equation is

$$L_t^{(b-a)} - L_\infty^{(b-a)} \left(1 - e^{-K(b-a)(t-t_0)}\right) \quad . \quad . \quad . \quad . \quad . \quad (6)$$

This is the generalized von Bertalanffy equation.

A Walford plot provides a convenient first step in the estimation of the parameters of the above curve. With *H. midae* the required values of L_t and L_{t+1} are not directly available. These values, or good approximations thereof, could be obtained from the growth rate data appearing in Table VIII. The growth rate per annum values of this table represent a mean estimate of $L_{t+1} - L_t$ within each of seven size classes. The size associated with these mean rates may be assumed to be the class mark in each case. Under the circumstances the best estimates of L_{t+1} and L_t (the values of t are unknown) are

$$L_{t+1} \quad V + \tfrac{1}{2}g$$
$$\text{and } L_t \quad V - \tfrac{1}{2}g$$

where V class mark
g mean annual growth increment of a particular class.

TABLE XII: L_t AND L_{t+1} VALUES

Shell breadth (cm)	Increment (cm)	L_t (cm)	L_{t+1} (cm)
5·50	0·88	5·060	5·940
6·50	0·76	6·120	6·880
7·50	0·67	7·165	7·835
8·50	0·54	8·230	8·770
9·50	0·61	9·195	9·805
10·50	0·52	10·240	10·760
11·50	0·51	11·245	11·755

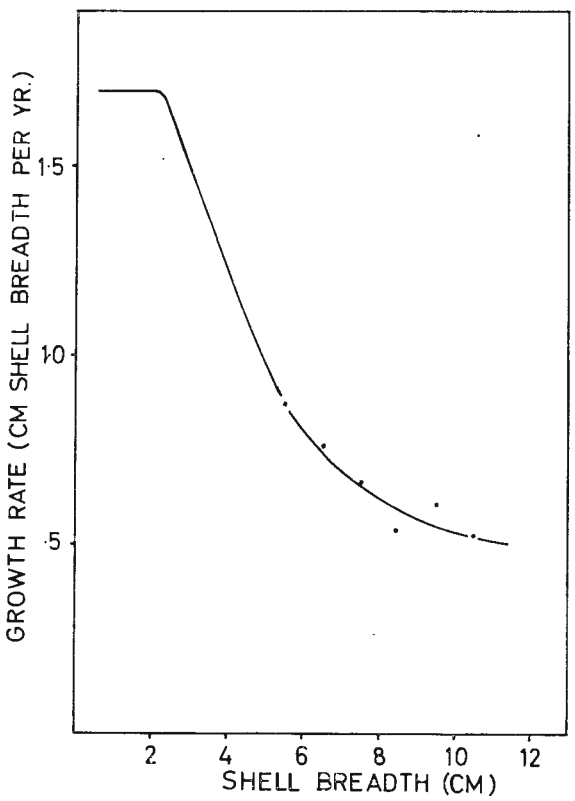

FIG. 9. Relationship between shell breadth growth rate and size of abalone

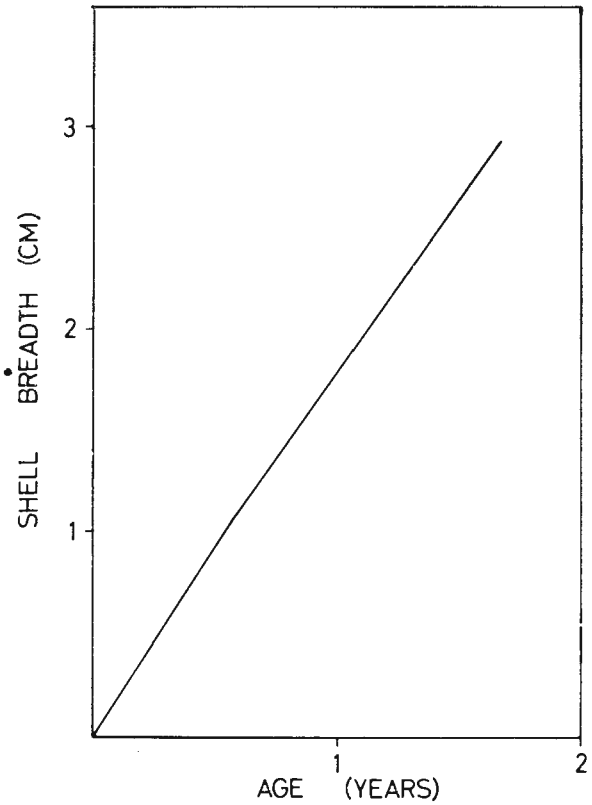

FIG. 10. Growth curve of shell breadth from population sampling at Stony Point

Values for L_{t+1} and L_t derived in this manner are shown in Table XII. A plot of L_{t+1} on L_t is illustrated by Fig. 11. It is apparent that the relationship between L_{t+1} and L_t is linear, and that the line describing this relationship intercepts the 45° diagonal on the figure at an L_t value in the region 19·5 cm. This value is an estimate of the maximum theoretical size which *H. midae* can attain and it coincides fairly closely with field observations in the area. The largest animal recorded by the Division's divers was 18·5 cm in breadth, although larger individuals have been collected by commercial divers. In view of the fact that a plot of L_{t+1} on L_t is linear and provides a reasonable estimate of the value of L_∞, the coefficient $(b-a)$ of the generalized von Bertalanffy equation may be assumed to be equal to one (Taylor, 1962). The generalized equation is therefor reduced to the familiar form

$$L_t = L_\infty\ (1-e^{-K(t-t_o)}) \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (7)$$

derived originally by von Bertalanffy in 1938.

From equation (7) it can be shown that

$$L_{t+1} \quad L_\infty(1-e^{-K}) + L_t\, e^{-K} \quad . \quad . \quad . \quad . \quad . \quad . \quad (8)$$

is a linear function of L_{t+1} on L_t and is essentially the Walford plot of Fig. 11 (Ricker, 1958). This expression may therefore be used to estimate the parameters of (7). A linear equation was accordingly fitted to the data from Table XII by the method of least squares. This was found to be:

$$L_{t+1} = 0{\cdot}9425\ L_t + 1{\cdot}1120 \quad . \quad . \quad . \quad . \quad . \quad . \quad (9)$$

From the above equation the parameters K and L_∞ were calculated as 0·0593 and 19·33 cm respectively.

The remaining parameter to be calculated is t_o and it may be obtained from the value of the intercept of

$$Log_e\,(L_\infty - L_t) = Log_e\, L_\infty + Kt_o - Kt \quad . \quad . \quad (10)$$

which is a linear expression of $Log_e\,(L_\infty - L_t)$ on t.

The estimation of the coefficients of the above

expression requires that lengths at time t be known and this information is not directly available for tagged *H. midae*. If, however, the age of any one point L_t on the Walford plot can be determined, then the size at successive ages can easily be calculated from equation (9). From Fig. 10 it is apparent that the mean size at the age of one year (L_1) is 1·8 cm. Unfortunately the shell breadth at the age of two years does not fall within the range of the above curve and this is required if L_1 is to be used to determine the age of successive sizes on the Walford plot. The shell breadth L_2, and for that matter subsequent values of L_t, may be obtained indirectly from Fig. 9. Considering that portion of the curve between the shell breadth values 2·5 cm and 6·0 cm the following growth rate values may be interpolated.

Shell breadth (cm)	Growth rate (cm per annum)
2·5	1·70
3·0	1·54
3·5	1·39
4·0	1·26
4·5	1·13
5·0	1·00
5·5	0·88
6·0	0·81

From the above the approximate values of L_t and L_{t+1} were derived as follows: At the size 2·50 cm at age 17 months (Fig. 10) the shell breadth/age curve was extrapolated by calculating and accumulating the time required to fulfil successive growth increments at the growth rates listed above. This technique requires that the growth rate quoted for a particular shell breadth be representative of a mean rate throughout the increment. Under these circumstances the smaller the shell breadth increment used the better, the ideal being the integration of infinitely small increments. In this case intervals of 0·5 cm were used and the ages of abalone of various sizes within the range 2·50—6·00 cm shell breadth were obtained. These sizes, together with the time required to fulfil the 0·5 cm increment immediately preceding them and the cumulative time, are listed in Table XIII.

TABLE XIII: EXTRAPOLATION OF THE SHELL BREADTH/AGE CURVE

Shell breadth (cm)	Period for 0·5 cm increment (years)	Cumulative period (years)
2·50		1·42
2·75	0·15	1·57
3·25	0·32	1·89
3·75	0·36	2·25
4·25	0·40	2·65
4·75	0·44	3·09
5·25	0·50	3·59
5·75	0·57	4·16
6·25	0·62	4·78

The data of Table XIII were plotted and the following mean sizes at particular ages were graphically estimated:

Age (years)	*Mean shell breadth* (cm)
1	1·8 (From Fig. 10).
2	3·4
3	4·7
4	5·7

These values were in turn plotted on Fig. 11 and, except for the values 4·7 and 5·7 cm, they do not appear to coincide with the straight line describing the data for the larger sizes. This phenomenon has been noted by other authors using Walford plots and is attributed to the fact that the growth of smaller individuals of a species does not necessarily conform to the pattern found in later life (Ricker, 1958).

From Fig. 11 it will be seen that the point of the plot of L_4 (5·7 cm) on L_3 (4·7 cm) is located almost exactly on the extrapolated Walford line. The sizes at two ages which conform to the Walford pattern are therefore known.

The shell breadth at 5 years (L_5) could therefore be calculated by substituting 5·7 cm in equation (9) and the resultant value was in turn used to calculate L_6.

By repeating this operation it was possible to calculate the mean shell breadths at particular ages within the size range for which tagging data were available, i.e. between 5 and 12 cm. These values, which appear in Table XIV, could then be used to calculate t_o from the intercept of the regression of $\text{Log}_e (L_\infty - L_t)$ on t.

This relationship is perfectly linear as the original L_t values are calculated from the linear Walford equation. In this case t_o was — 1·8820 and the von Bertalanffy equation describing the growth of *H. midae* becomes:

$$L_t \quad 19{\cdot}33\,(1 - e^{-0{\cdot}0593\,(t\,+\,1{\cdot}8820)}) \quad . \quad . \quad . \quad (11)$$

This function is illustrated by Fig. 12. As the Walford plot of Fig. 11 has shown that, below 4·0 cm, growth does not conform to the pattern for larger animals, this section of the curve is reproduced from Fig. 10. Also illustrated is the *hypothetical* growth of individuals larger than 12 cm, and the theoretically determined maximum size L_∞. These are represented by interrupted lines in the figure.

TABLE XIV: ESTIMATED GROWTH IN TERMS OF SHELL BREADTH, SHELL LENGTH AND BODY WEIGHT

Age (years)	Shell breadth (cm)	Shell length (cm)	Body weight (g)
3	4·7	6·4	26
4	5·7	7·5	45
5	6·5	8·4	65
6	7·2	9·2	86
7	7·9	9·9	111
8	8·6	10·7	141
9	9·2	11·4	170
10	9·8	12·0	202
11	10·3	12·6	232
12	10·8	13·1	265
13	11·3	13·7	301
14	11·8	14·2	339

4.2 Shell length

Growth in terms of shell length may easily be obtained by transforming the shell breadths of Table XIV to shell lengths by means of the relationship:

$$L = 1{\cdot}0925\ B^{1{\cdot}2995}$$

where L shell length in cm
B shell breadth in cm.

This function will be fully discussed in Section 5.

The mean shell length values are also listed in Table XIV.

Sakai (1962) has presented mean shell lengths for *Haliotis discus hannai* for the first six years of life. This species has well-defined annual rings on the shell surface and the growth history could conveniently be traced in individuals from different localities within Onagawa Bay, northern Japan. Growth was found to vary considerably with locality and the results from three sites have been extracted from Sakai's Table III. These are presented in Table XV together with some results from Stony Point. From the table it appears that the growth of *H. midae* is essentially similar to that recorded at Maeami and Tzushima. Sakai's results for Hazaka indicate that growth here is faster than that noted for *H. midae* or *H. discus hannai* at the two abovementioned localities.

4.3 Body weight

Using the expression

$$W = 0.3608\ B^{2{\cdot}7736}$$

where W body weight in g
B — shell breadth in cm,

the mean shell breadth values of Table XIV were converted to body weights. These are also listed in the table.

It is interesting to note that over the size range investigated the relationship between age and body weight is exponential. The point of inflection of the normally sigmoid curve of weight on age has not been attained at an age of 14 years and a body weight of 339 g. This weight is just over 30 per cent of the maximum recorded at Stony Point, which was 1126 g.

5. GROWTH RELATIONSHIPS

Growth in molluscs is most conveniently expressed in terms of increases in a particular shell dimension with time. These increments are, however, manifestations of a more complex overall increase which can be better appreciated if the relationships between selected shell dimensions as well as that between shell dimensions and body weight are known. Such relationships have been studied intensively and marked variations in shell shape have been recorded within the same species. These variations have been attributed to size and environmental factors (Wilbur & Owen, 1964).

Two methods of representing growth relationships are available. Thompson (1942) has shown that in many molluscs the pattern of growth in the horizontal plane may be represented by a logarithmic or equiangular spiral and Moore (1936, 1937) used this method for an investigation of variations in shell shape of the gastropods *Purpura lapillus* and *Littorina littorea*. In addition Sinclair (1963) calculated the parameters of this equation for *Haliotis iris* and *Haliotis australis*.

Alternatively, and more directly, the change in shell shape throughout the size range can be expressed by means of exponential or linear

TABLE XV: GROWTH IN SHELL LENGTH (CM) OF *H. midae* FROM STONY POINT AND *H. discus hannai* FROM THREE LOCALITIES IN NORTHERN JAPAN

Species	Age (years) 1	2	3	4	5	6
H. midae, Stony Point	2·7	4·7	6·5	7·5	8·4	9·2
H. discus hannai, Maeami	2·7	4·1	6·0	7·5	—	—
H. discus hannai, Tzushima	2·9	4·7	6·7	8·4	9·5	10·1
H. discus hannai, Hazaka	2·8	5·0	7·5	9·7	11·1	—

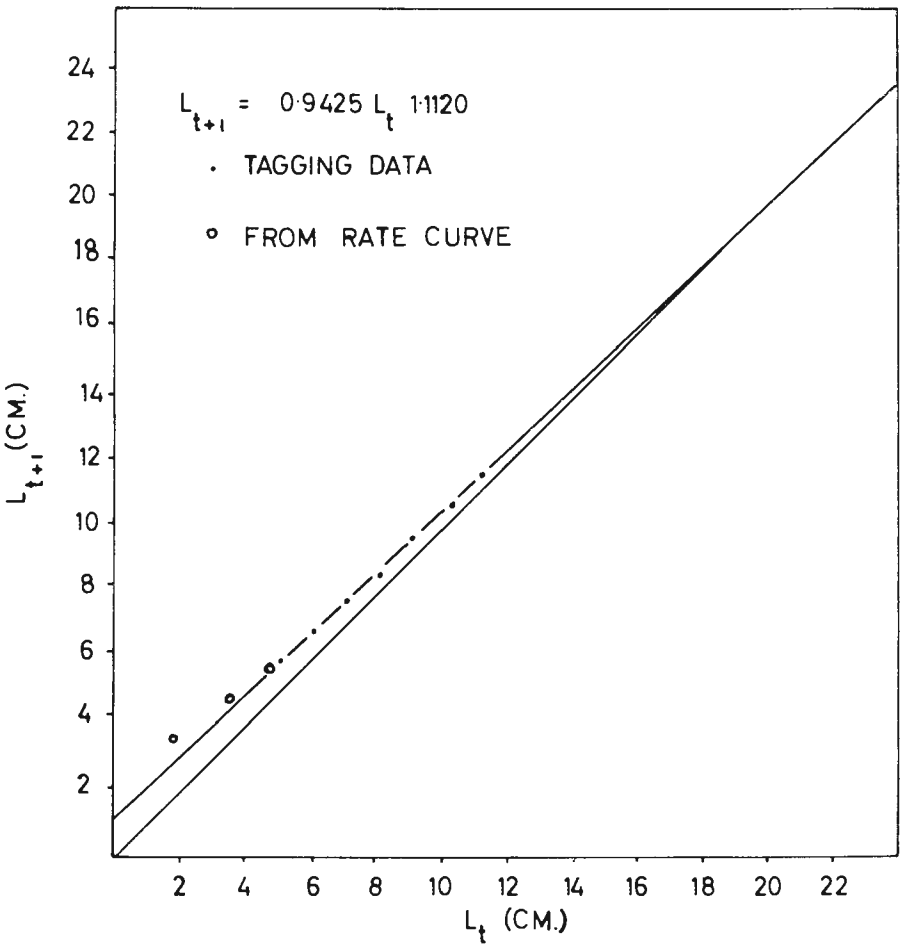

FIG. 11. Walford plot of shell breadth

regression equations. This method has proved to be more popular than that advocated by Thompson (1942) and has been used to describe the shell shape of many gastropods and bivalves, including haliotids (Wilbur & Owen, 1964). Regression methods are advantageous because of the ease with which the dimensions can be recorded and later represented by equations.

As a large amount of data were available for *H. midae* of both sexes in different localities, a fair number of regression equations could be fitted. Pairs of equations had to be tested to locate statistically significant differences between them. The calculations involved were considerable, so use was made of an I.B.M. 1620 computer.

Data for the above analyses were available from the four research stations, three of which are indicated on Fig. 1. These were at Stony Point, Dawidskraal (about one mile from Stony Point), Sea Point and Dassen Island. The relationships which will be described are:

shell length/body weight;
shell length/shell breadth;
shell length/shell depth;
shell breadth/body weight.

5.1 Methods

Data were collected in the course of monthly sampling for reproductive cycle studies, special sampling collections, year class investigations, and tagging operations. Shell lengths and breadths were measured by means of vernier calipers and, except in the case of tagging operations, abalone were

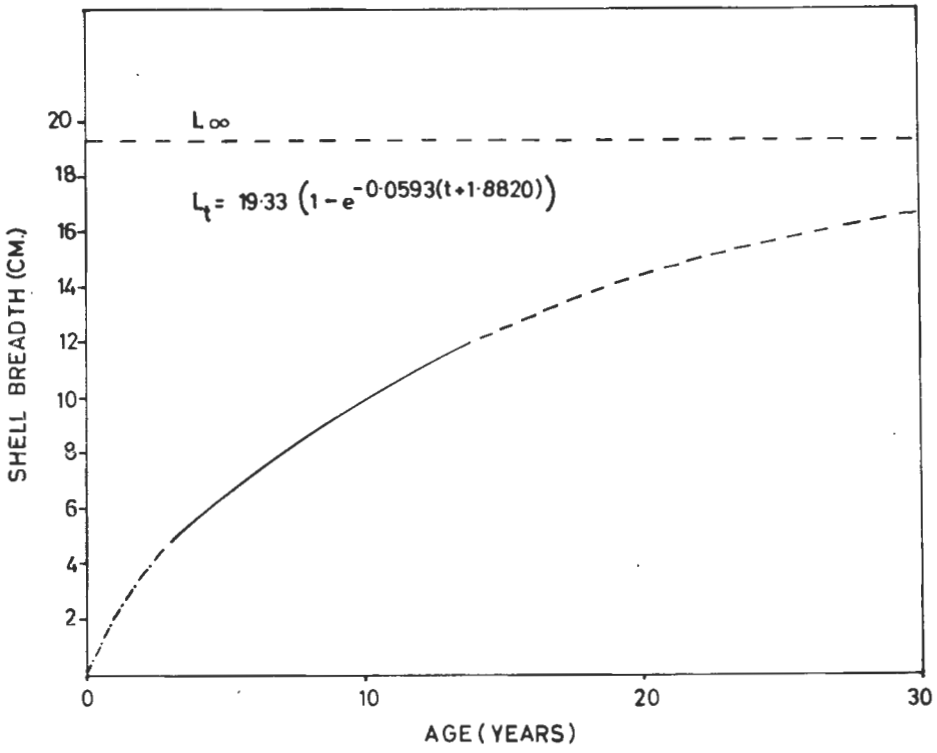

FIG. 12. Growth curve of shell breadth for abalone at Stony Point

removed undamaged from their shells and weighed to the nearest g. Length/weight curves were only calculated from animals collected during the period June to October in any one year, to ensure that these curves were based on abalone with fully developed gonads.

After weighing, the shell depth was measured by means of an apparatus designed at the Division and illustrated in Fig. 13. The functioning of this apparatus may best be described with reference to the figure. Shells were placed with the ventral side uppermost beneath the perspex stage which was lowered to make contact with the edge of the shell. The internal shell depth was then determined as the difference between the horizontal plane in contact with the shell edges and the level of the shell apex. This distance was measured by means of the depth gauge illustrated, which could be positioned correctly within one of three slots in the perspex stage.

The shell length/body weight relationship, as judged from preliminary scattergrams, was obviously exponential but there was some doubt as to the form of the shell length/breadth and shell length/depth curves. To establish these, the mean shell breadths and depths within shell length size classes of one cm were computed. Both mean shell breadths and depths were then plotted on shell length and on this basis the form of the relationship was obtained.

For each relationship males and females were treated separately to locate possible sexual dimorphism and differences between the coefficients were tested to determine their significance. As the relationships examined were either linear or exponential, tests of slopes and intercepts were used, the method being that of Bennett & Franklin (1954). This test could be used because the scattergrams showed that the variance around the log-transformed or linear least squares estimates was more or less constant over the size range of mature abalone. No sexual dimorphism, significant at the five per cent level, could be shown in any of the relationships considered and separate curves for males and females are therefore not presented.

5.2 Results

Stony Point

The shell length/body weight relationship through-

FIG. 13. Apparatus for measuring shell depth

out the whole size range was calculated as:

$W = 0{\cdot}0859\ L^{3{\cdot}1276}$

where L = shell length in cm
W = body weight in g.

The standard error was 1·229 and the equation is based on 1049 abalone.

On Fig. 14, mean shell breadths are plotted against mean shell lengths throughout the size range 0·4 to 19·8 cm shell length. These means include male, female and immature abalone. It is interesting to note that two linear equations are required to describe the data throughout the whole size range, for a well-defined change in direction occurs at about 4·5 cm shell length.

For shell length $\leqslant$ 4·5 cm,
$B = 0{\cdot}6812\ L - 0{\cdot}0071$
standard error = 0·07780 cm.

For shell length $\geqslant$ 4·5 cm,
$B = 0{\cdot}9066\ L - 1{\cdot}0843$
standard error = 0·3649 cm.

Where B = shell breadth in cm
L = shell length in cm.

Both length and breadth are expressed in cm and the equations are based respectively on 770 and 1461 abalone. The above functions are also plotted on Fig. 14.

Similarly to shell length/breadth relationships, plots of mean shell depth on mean shell length revealed that two linear regressions provided the best fit for these data over the size range 1·75 to 19·25 cm shell length. The change in slope in this case occurs in the region of 11 cm shell length and the equations are as follows:

For shell length $\leqslant$ 11 cm, $D = 0{\cdot}2306L - 0{\cdot}1577$
standard error = 0·7164 cm.

For shell length $\geqslant$ 11 cm, $D = 0{\cdot}3810L - 1{\cdot}9429$
standard error = 0·5240 cm.

Where D = shell depth in cm
L = shell length in cm.

The above are based on 287 and 600 individuals respectively and are plotted on Fig. 15.

An exponential function was required to convert the shell breadth growth curve to units of body weight. It was calculated from 1366 male

and female abalone as:

$$W = 0{\cdot}3608\ B^{2{\cdot}7736}$$

where W = body weight in g
B = shell breadth in cm.

Similarly, to convert the shell breadth growth curve to shell length units, a function was required. This was calculated from 1461 individuals with shell lengths of more than 4·5 cm as:

$L = 1{\cdot}0925B + 1{\cdot}2995.$

Having described the important shell dimension and body weight relationships for the intensively sampled Stony Point research station, it was possible to use the somewhat limited data from the three other research sites for intraspecific comparison. The three other sites were situated at Dassen Island and Sea Point, both on the Atlantic side of Cape Point, and at Dawidskraal, near Stony Point. At the former two localities the size range of the population was fairly restricted, and small abalone (below approximately 13 cm) were extremely rare. At Dawidskraal, however, smaller individuals were available from certain inshore reefs but sampling was concentrated on the population occurring further off shore, with the result that few animals below 13 cm were collected. Because of the absence of smaller size ranges at these stations, single linear equations were used to describe length/breadth and length/depth relationships. The relationship between shell length and body weight is an exponential one.

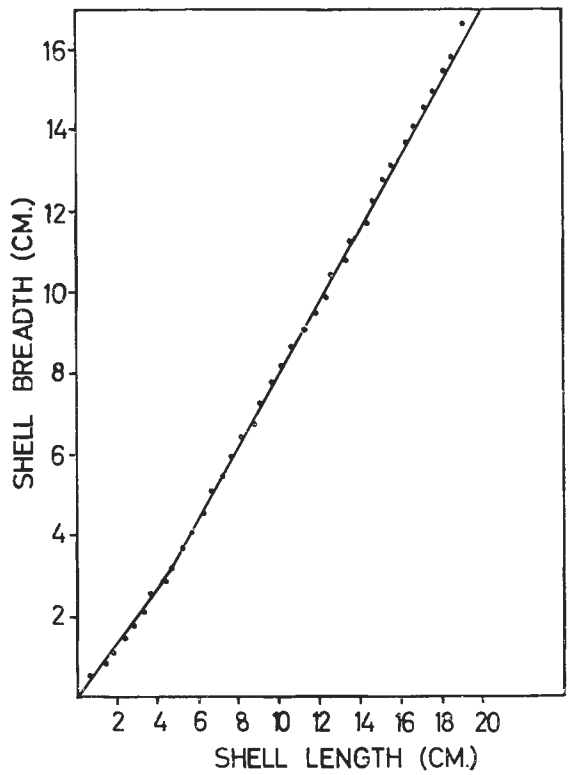

FIG. 14. Shell length/shell breadth relationship at Stony Point

Dassen Island

All samples were collected from a shallow reef in the middle of House Bay, a large protected bay on the east side of the island. A luxuriant kelp growth covers the reef, and a large dense population of *H. midae* occurs on the rocky substratum between 10 and 25 feet.

The following relationships were calculated for this site.

$W = 0{\cdot}1223L^{3{\cdot}0819}$	N = 170, standard error = 1·146
$B \quad 0{\cdot}9017L - 1{\cdot}2050$	N 643, standard error = 0·4248 cm
$D \quad -0{\cdot}4658L - 2{\cdot}1476$	N = 395, standard error = 0·6901 cm

where N = sample size.

The second research site west of Cape Point was at Sea Point, Cape Town. Collections were made in depths ranging from 10 to 25 feet on a rocky substratum well covered by kelp. This particular research site was fairly thinly populated and exposed to severe wave action during rough weather.

Relationships here were:

$W = 0{\cdot}2718L^{2{\cdot}8227}$	N 108, standard error = 1·167
$B = 0{\cdot}8910L - 0{\cdot}8017$	N 436, standard error = 0·5247 cm
$D = 0{\cdot}4166L - 1{\cdot}6284$	N 227, standard error = 0·7612 cm

Dawidskraal

The Dawidskraal station lies within a mile of Stony Point. Collection at this site took place in a dense and extensive bed of kelp. The depth at this station varies between 10 and 30 feet and the area is reasonably exposed to southerly swells.

Relationships here were:

$W = 0{\cdot}0297L^{3{\cdot}5039}$	N 169, standard error = 1·247
$B = 0{\cdot}9206L - 1{\cdot}1320$	N 234, standard error = 0·4354 cm
$D = 0{\cdot}4216L - 2{\cdot}3306$	N = 209, standard error 0·7028 cm

5.3 Discussion

Small abalone were not freely available at sites other than Stony Point and collections were mostly limited to mature specimens at these stations. For comparison with other stations therefore, linear and exponential regressions were calculated for Stony Point mature males and females combined as follows:

$W = 0{\cdot}0474\ L^{3{\cdot}3385}$
$B \quad 0{\cdot}9124\ L \quad 1{\cdot}1555$
$D = 0{\cdot}3558\ L - 1{\cdot}5330$

different stations were therefore tested for significance. The results of tests on the slopes and intercepts of paired stations are shown by Table XVI. It is apparent that except for the intercepts of the Dassen Island and Dawidskraal expressions, no two parameters could be shown to differ at the 5 per cent level. The above results are not unexpected in view of the relatively large standard errors of the functions concerned.

Expressions representing the shell length/shell breadth relationships for data from the four stations are illustrated by Fig. 17. The four linear

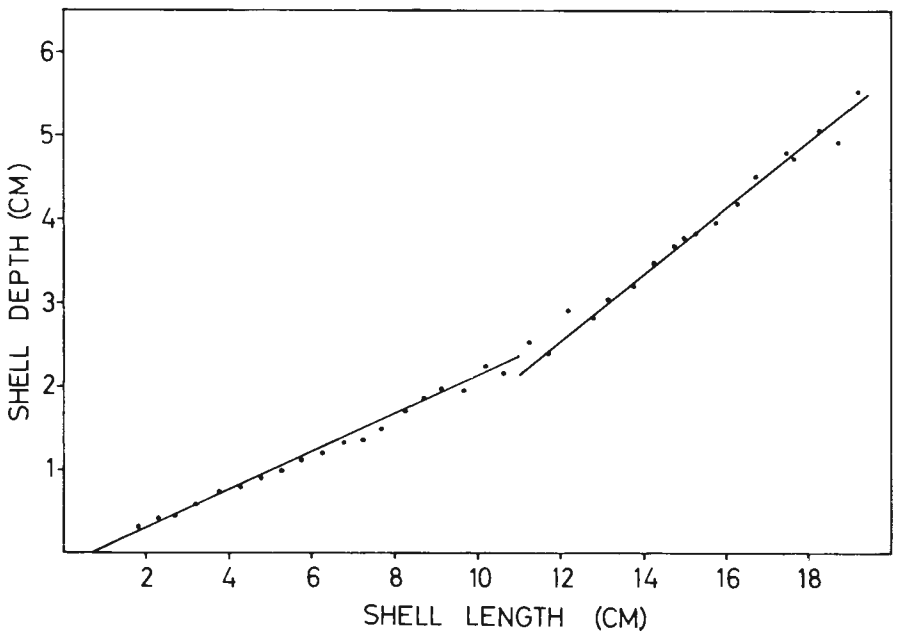

FIG. 15. Shell length/shell depth relationship at Stony Point

These functions have been plotted on Figs. 16, 17 and 18 together with data from the other research sites.

Fig. 16 suggests an interesting difference between length/weight relationships of different localities. The Stony Point and Dawidskraal curves are similar for much of their length, as could be expected with data from adjacent localities. The curves for Dassen Island and Sea Point are located above those calculated for the stations east of Cape Point. For example, the best estimates of body weight associated with shells 15 cm long are 400 g and 570 g at Stony Point and Sea Point respectively. The differences between the models representing the length/weight relationships at the graphs are essentially very similar and, unlike the length/weight curves, do not suggest a pattern which is associated with the site of collection. The differences between the parameters of pairs of expressions were tested and the probability levels, which are listed in Table XVII, are such as to indicate no real difference between shell length/shell breadth relationships from different stations.

Finally, the shell length/shell depth relationships may be considered. As in the case of the length/weight relationships a pattern is suggested by Fig. 18. Shell depths at Stony Point (and to a lesser extent at Dawidskraal) seem to be less at equivalent shell lengths than at Dassen Island and Sea Point.

TABLE XVI: RESULTS OF TESTS OF THE SIGNIFICANCE OF DIFFERENCES IN SHELL LENGTH/BODY WEIGHT RELATIONSHIPS DUE TO LOCALITY

Locality	Parameter tested	Degrees of freedom	*t*	Probability
Stony Point — Dawidskraal	Slopes Intercepts	577	1·12 0·03	·30 ·90
Stony Point — Sea Point	Slopes Intercepts	517	0·08 0·02	·90 ·90
Stony Point — Dassen Island	Slopes Intercepts	579	1·30 0·45	·20 ·70
Dawidskraal — Sea Point	Slopes Intercepts	274	0·07 0·01	·90 ·90
Dawidskraal — Dassen Island	Slopes Intercepts	336	1·81 2·21	·10 ·10
Sea Point — Dassen Island	Slopes Intercepts	276	0·02 0·002	>·90 >·90

TABLE XVII: RESULTS OF TESTS OF THE SIGNIFICANCE OF DIFFERENCES IN SHELL LENGTH/SHELL BREADTH RELATIONSHIPS AT DIFFERENT LOCALITIES

Locality	Parameter tested	Degrees of freedom	*t*	Probability
Stony Point — Dawidskraal	Slopes Intercepts	903	0·38 0·42	·80 ·70
Stony Point Sea Point	Slopes Intercepts	1105	1·10 0·01	·30 ·90
Stony Point — Dassen Island	Slopes Intercepts	1212	0·58 0·57	·60 ·50
Dawidskraal Sea Point	Slopes Intercepts	666	0·99 0·31	·40 ·80
Dawidskraal — Dassen Island	Slopes Intercepts	773	0·72 0·89	·50 ·40
Sea Point — Dassen Island	Slopes Intercepts	975	0·43 0·56	·70 ·60

The results of significance tests are shown on Table XVIII. The tests reveal a very significant difference between the slope coefficients of the Stony Point and Dassen Island data, but the difference was less significant between Sea Point and Stony Point ($P = 0 \cdot 10$). In addition there was also a significant difference between the slopes at Stony Point and Dawidskraal. This latter result is not unexpected as a marked difference in the slopes of the two sets of data is apparent from the figure. In all other comparisons no significant differences could be shown.

It is interesting that Barnard (1963—page 304), when discussing the taxonomy of South African *Haliotidae*, remarks as follows on *Haliotis midae:* "The name *elatior* was given to unusually high individuals; such forms are reported to be of more frequent occurrence at Saldanha Bay than elsewhere".

Saldanha Bay is on the Atlantic coastline, near Dassen Island. The subspecies *H. midae elatior* is not, however, recognized by Barnard.

Although it cannot be proved statistically, it appears that abalone from the Atlantic stations weigh more per unit length than those collected at stations east of Cape Point. Comparisons of

TABLE XVIII: RESULTS OF TESTS TO DETERMINE THE SIGNIFICANCE OF DIFFERENCES IN SHELL LENGTH/SHELL DEPTH RELATIONSHIPS AT DIFFERENT LOCALITIES

Locality		Parameter tested	Degrees of freedom	*t*	Probability
Stony Point	Dawidskraal	Slopes	800	2·04	·05
		Intercepts		0·51	·70
Stony Point	Sea Point	Slopes	818	1·87	·10
		Intercepts		0·17	·80
Stony Point	Dassen Island	Slopes	986	3·53	·001
		Intercepts		2·22	·05
Dawidskraal	Sea Point	Slopes	432	0·09	·90
		Intercepts		0·70	·50
Dawidskraal	Dassen Island	Slopes	600	0·90	·40
		Intercepts		1·13	·30
Sea Point	— Dassen Island	Slopes	618	0·99	·40
		Intercepts		0·35	·80

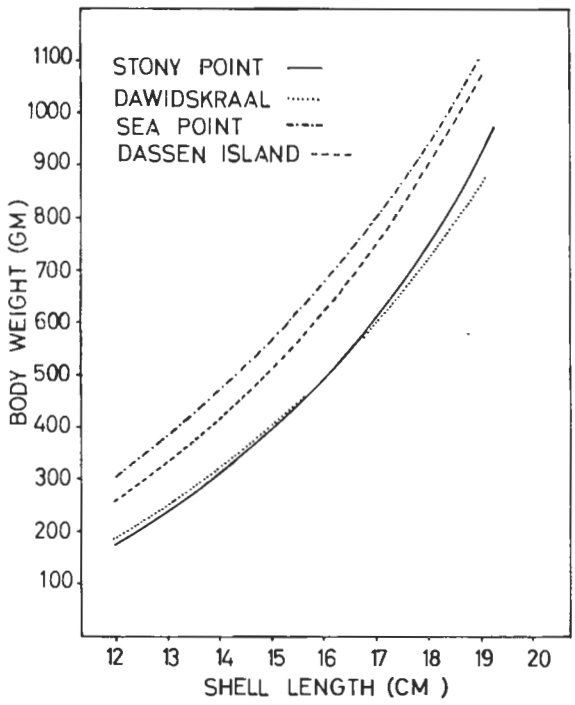

FIG. 16. Shell length/body weight relationships at four research sites

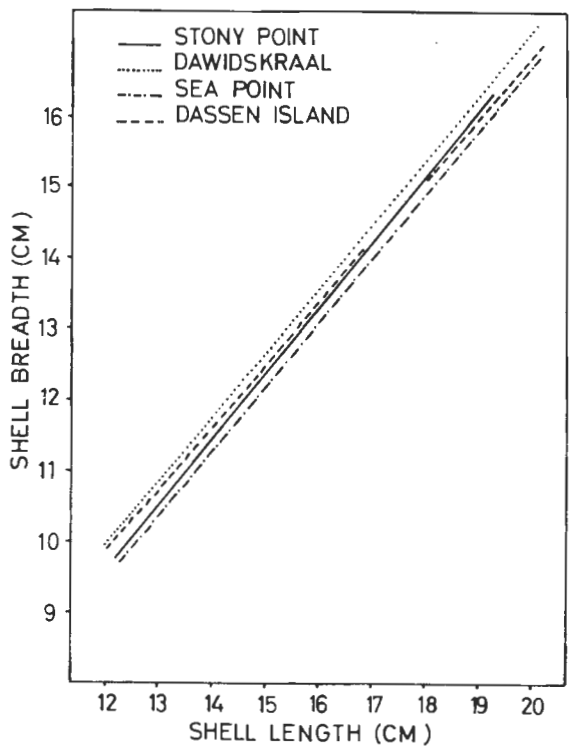

FIG. 17. Shell length/shell breadth relationships at four research stations

shell relationships indicate that this increased weight is due rather to greater shell depth per unit length than to greater shell breadth.

An interesting aspect of the shell dimension relationships for *H. midae* is the inflection point occurring in both shell length/shell breadth and shell length/shell depth relationships. Considering the former, the constant slope below 4·5 cm shell length means that the ratio of the absolute growth rates of the two dimensions remains constant over

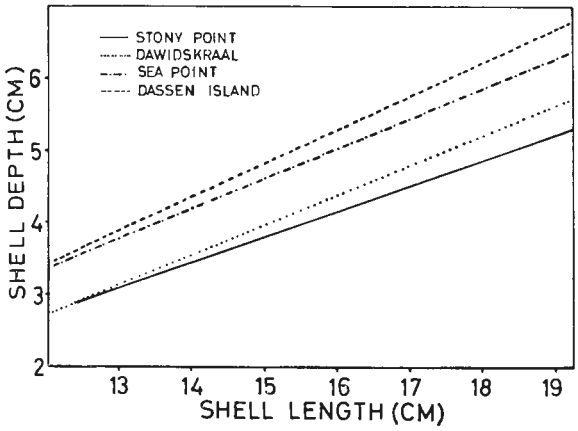

FIG. 18. Shell length/shell depth relationships at four research stations

this size range. Above 4·5 cm, a fairly abrupt change in this ratio occurs, but thereafter the new absolute ratio remains constant. The ratio of the relative growth rates remains constant only if the relationship is linear and passes through the origin of both the shell length and breadth axes. In the case of *H. midae* smaller than 4·5 cm, the intercept coefficient is low (—0·0071) and the ratio of relative growth rates may be assumed to be constant. This is not true for individuals above 4·5 cm in length, for, in this case, the intercept coefficient is — 1·0843. The results for the shell length/shell depth relationship are essentially similar except that the inflection point occurs at about 11 cm.

The significance of the well-defined inflection points of the above curves is doubtful. *Haliotis midae* with shell lengths below 5 cm occur very commonly beneath loose rocks and boulders. Above this size they move to cover shallow reefs, for, by virtue of their size, they are relatively safe from predation by fish. This change in their immediate environment may be associated with the abrupt change in the growth pattern, but this is only a tentative suggestion.

No explanation can, however, be offered for the inflection point of the shell length/shell depth relationship.

6. ACKNOWLEDGEMENTS

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7. LITERATURE CITED

BARNARD, K. H. 1963—Contributions to the knowledge of South African marine mollusca. Part IV. Gastropoda: Prosobranchiata: Rhipidoglossa, Docoglossa. Tectibranchiata. Polyplacophora. Solenogastres. Scaphopoda. *Ann. S. Afr. Mus.* 47: 201-360.

BENNETT, C. A. AND N. L. FRANKLIN 1954—Statistical analysis in chemistry and the chemical industry. New York, John Wiley and Sons, Inc. 724 pp.

COX, K. W. 1962—California Abalones, Family Haliotidae. *Bull. Dep. Fish Game St. Calif.* 112: 142 pp.

CROFTS, D. R. 1929—*Haliotis. L.M.B.C. Mem. typ. Br. Mar. Pl. Anim.* 29: 1-174.

FISHER, R. A. 1932—Statistical methods for research workers. Edinburgh. Oliver and Boyd, 307 pp.

HARDING, J. P. 1949—The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. mar. biol. Ass. U.K.* 25: 141-153.

INO, T. 1952—Biological studies on the propagation of the Japanese abalone (genus *Haliotis*). *Bull. Tokai reg. Fish. Res. Lab.* 5: 102 pp.

LEIGHTON, D. AND R. A. BOOLOOTIAN 1963—Diet and growth in the black abalone *Haliotis cracherodii*. *Ecology* 44(2): 227-238.

MOORE, H. B. 1936- The biology of *Purpura lapillus*. I. Shell variation in relation to environment. *J. mar. biol. Ass. U.K.* 21(1): 61-89.

MOORE, H. B. 1937—The biology of *Littorina littorea*. Part I. Growth of the shell and tissues, spawning, length of life and mortality. *J. mar. biol. Ass. U.K.* 21(2): 721-743.

NEWMAN, G. G. 1966—Movements of the South African Abalone *Haliotis midae*. *Investl Rep. Div. Sea Fish. S. Afr.* 56: 1-20.

NEWMAN, G. G. 1967—Reproduction of the South African abalone *Haliotis midae*. *Investl Rep. Div. Sea Fish. S. Afr.* 64: 1-24.

PANTULU, V. R. 1962—On the use of pectoral spines for the determination of age and growth of *Pangasius pangasius* (Hamilton Buch). *J. Cons. perm. int. Explor. Mer* 27(2): 192-216.

PANTULU, V. R. 1963—Studies on the age and growth, fecundity and spawning of *Osteogeneiosus militaris* L. *J. Cons. perm. int. Explor. Mer* 28(2): 295-320.

RICKER, W. E. 1958—Handbook of computation for biological statistics of fish populations. *Bull. Fish. Res. Bd Can.* 119, 300 pp.

ROUNSFELL, G. A. AND W. A. EVERHART 1953—Fishery Science, its methods and applications. New York. John Wiley and Sons, Inc. 444 pp.

SAKAI, S. 1960—The formation of the annual ring in the shell of the abalone *Haliotis discus* var. *hannai* Ino. *Tohoku J. agric. Res.* 11(3): 239-244.

SAKAI, S. 1962—Ecological studies on abalone, *Haliotis discus hannai* Ino IV. Studies on growth. *Bull. Jap. Soc. scient. Fish.* 28(9): 899-904.

SINCLAIR, M. 1963—Studies on the Paua, *Haliotis iris* Martyn in the Welligton district, 1945-1946. *Zoology Publs Vict. Univ. Wellington* 35: 16 pp.

STEPHENSON, T. A., A. STEPHENSON AND C. A. DU TOIT 1937—The South African intertidal zone and its relation to ocean currents. I: A temperate Indian Ocean shore. *Trans. R. Soc. S. Afr.* 24: 341-382.

TAYLOR, C. C. 1958 Cod growth and temperature. *J. Cons. perm. int. Explor. Mer* 23: 366-370.

TAYLOR, C. C. 1959—Temperature and Growth—The Pacific razor clam. *J. Cons. perm. int. Explor. Mer* 25(1): 93-101.

TAYLOR, C. C. 1962—Growth equations with metabolic parameters. *J. Cons. perm. int. Explor. Mer* 27(3): 270-286.

THOMPSON, D'ARCY W. 1942—Growth and form. Cambridge Univ. Press.

URSIN, E. 1965—On the seasonal variation of growth rate and growth parameters in Norway Pout (*Gadus esmarki*) in the Skagerrak. *Medd. Damm. Fisheri og Havunders N.S.* 4: 17-29.

WILBUR, K. M. 1964 Shell formation and regeneration. In Physiology of Mollusca. ed. Wilbur, K. M. and C. M. Yonge. New York Academic Press.

WILLIAMS, E. E. 1964 a—The growth and distribution of *Littorina littorea* (L) on a rocky shore in Wales. *J. Anim. Ecol.* 33(3): 413-431.

WILLIAMS, E. E. 1964 b—The growth and distribution of *Gibbula umbilicatis* (da Costa) on a rocky shore in Wales. *J. Anim. Ecol.* 33(3): 433-442.

YAMAMOTO, T. 1949—Biometrical studies of *Haliotis* shell. *Bull. Jap. Soc. scient. Fish.* 15(5): 209-215.

A B S T R A C T

The South African abalone, Haliotis midae can move over 300 yards in periods of 104 to 558 days. Within just over one month one, three and four individuals covered distances of 132, 176 and 220 yards. The mean rate of movement of a sample of 23 individuals within the size range 5.60 to 12.30 cm shell breadth was about 1000 yds. per annum. The incidence of movement was found to be high. Of 59 returns found during one search, 38 or 64 per cent had moved away from the tagging area in periods of 27-112 days.

The movement of H. midae is such that dense groups of smaller abalone are capable of replenishing stocks of larger animals in their vicinity by movements to favourable but exploited reefs.

INTRODUCTION

This paper is part of a series which describe the results of an abalone (Haliotis midae) research programme conducted at the Division of Sea Fisheries. It deals with movement as shown by a tagging experiment. The experiment was run for a period of two years, from January 1962 to December 1963, at Stony Point, a peninsula near Hermanus, Cape. This area is the centre of the South African abalone industry.

The kinematics of the locomotion of Haliotis tuberculata were investigated by LISSMAN (1945) by means of a series of laboratory experiments. His results

showed that locomotion is by means of ditaxic waves of characteristic form and frequency. Haliotis tuberculata is described by the above author as being "a very active creeper with agile turning movements".

Although literature dealing with the movement of Haliotis in the field is somewhat limited, there is evidence that members of this genus actively move about within their habitat.

STEPHENSON (1924) reports that H. tuberculata is extremely active and moves suprisingly fast. A homing habit for this species is not suggested, because no scar is apparent on the rocks from which these animals were removed. Further evidence of the mobility of this European species is cited by CROFTS (1929) who tagged an undisclosed number of H. tuberculata. In only two instances were these marked abalone recovered where they had been re= placed after tagging. In addition, this author observed individuals moving at between 8-20 inches per minute. In the case of Japanese abalones, changes in the size composition of commercial catches are offered as evidence of a seasonal influx of large abalone into shallow exploited waters during the breeding season (INO 1952). Comments on the movements of Californian abalones are available from various publications by K.W. COX. The Californian red abalone, Haliotis rufescens, is reported to have moved over a 100 yds. in a horizontal direction but has never been observed to move from deep to shallow water. Transplanted red abalone have moved from the top of a shallow reef to deeper water, while a tagged black abalone (Haliotis cracherodii) is reported to have

remained in the same place for two years (COX 1960). In a later publication COX (1962) describes how after 1 to 4 years, tagged H. rufescens were recovered in the same general area in which they were replaced.

SINCLAIR (1963) reports that occasional large specimens of the New Zealand paua, Haliotis iris, have been seen moving during the day. In a subsequent section of her paper she states that at no time during the day was a specimen seen moving unless it had been disturbed. From these statements it would appear that movement of this species rarely occurs during the day. SINCLAIR surmises that nocturnal foraging movements must take place, for there is often a scarcity of algal food in the vicinity of this species. In addition, it is highly probable that these animals exhibit a homing instinct.

In the case of the commercially important South African abalone, Haliotis midae, no published observations on movement are available. Many commercial divers have reported that reefs "cleaned out" during fishing operations are often repopulated within periods ranging from six months to a few years. As the growth rate of H. midae is not sufficiently fast to account for larval repopulation within these periods, this must be due to movement of the animals from adjacent areas to favourable but exploited reefs. It thus becomes important from the conservation viewpoint to confirm whether or not movement amongst the population commonly occurs, and, if so, what distances can be covered by H. midae during specified time intervals.

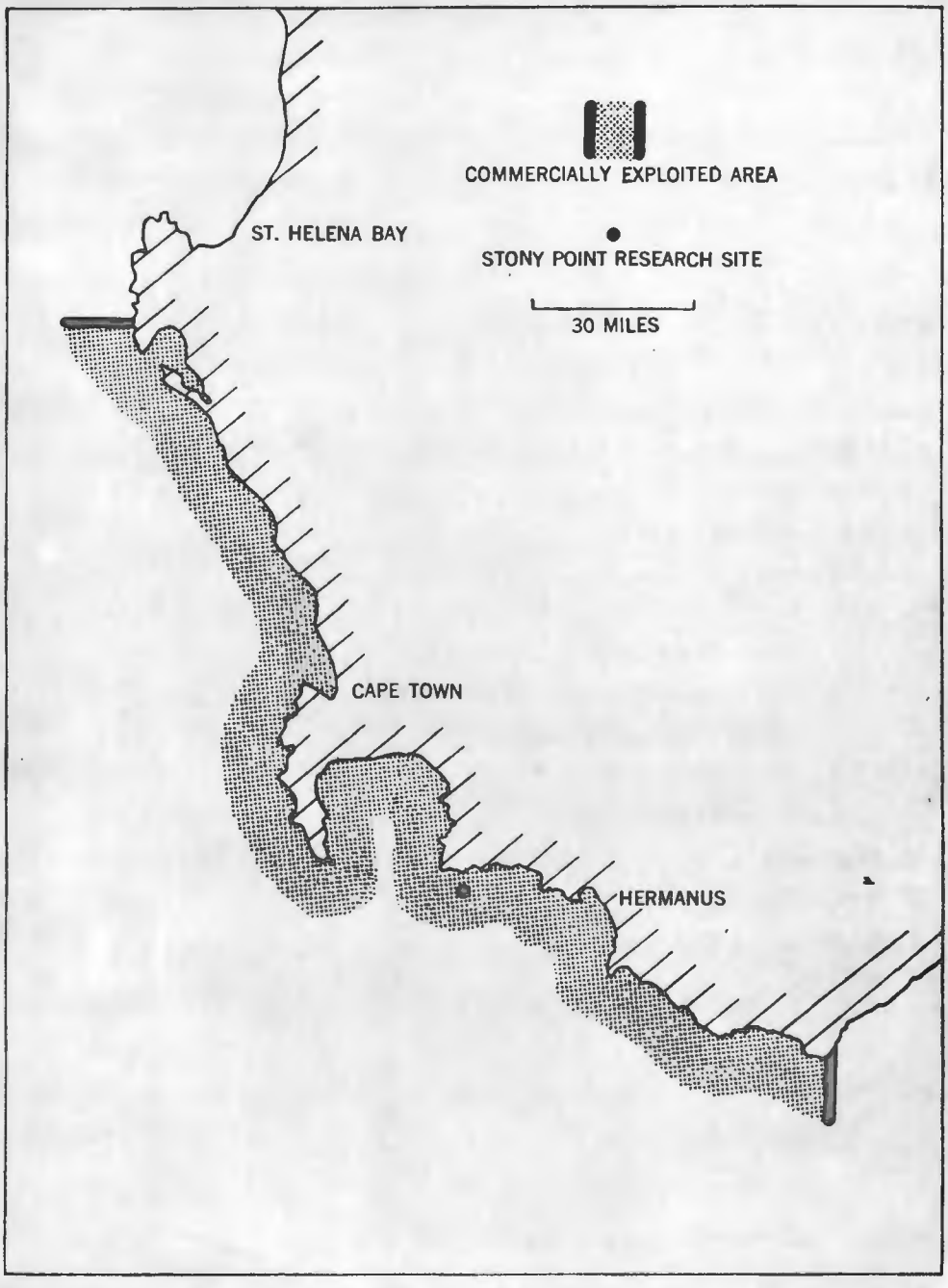

FIG. 1 THE SOUTH AFRICAN ABALONE FISHING GROUNDS AND THE STONY POINT RESEARCH SITE

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The tagging experiment was conducted on the eastern side of the Stony Point peninsula, along approximately 400 yds. of coastline. The location of Stony Point, together with the limits of the commercially exploited abalone area, appear in Figure 1. A detailed map of the experimental area is illustrated in Figure 2.

From the eastern shoreline of the peninsula a rocky bottom extends seawards for a distance of about 50 yds. forming a band along the whole length of Stony Point. Beyond this, at depths of 15-20 feet, a sandy bottom occurs and this effectively bars abalone from moving off-shore, except at the seaward end of the point where the rocky bottom extends over a large area and into deep water. The shoreline of this peninsula is comparatively sheltered from wave action and supports a dense population of small abalone which occur on fairly shallow reefs. At the seaward end of the peninsula, exposed to a fair amount of wave action, a very dense population of larger individuals occurs. This area is fairly typical of many similar environments in the vicinity of Hermanus which seem to be particularly suitable for the maintenance and growth of large populations of small abalone. An additional advantage of this site, from the point of view of a movement study, was that the rocky bottom was long (400 yds) but narrow (50 yds) with good landmarks on the shore. This enabled the movement of recoveries to be accurately recorded.

METHODS

During the period January 1962 to June 1963, 2,645 H. midae were tagged at Stony Point by divers from the Division of Sea Fisheries using SCUBA. Weather permitting, 200 to 300 animals were tagged during two to three days

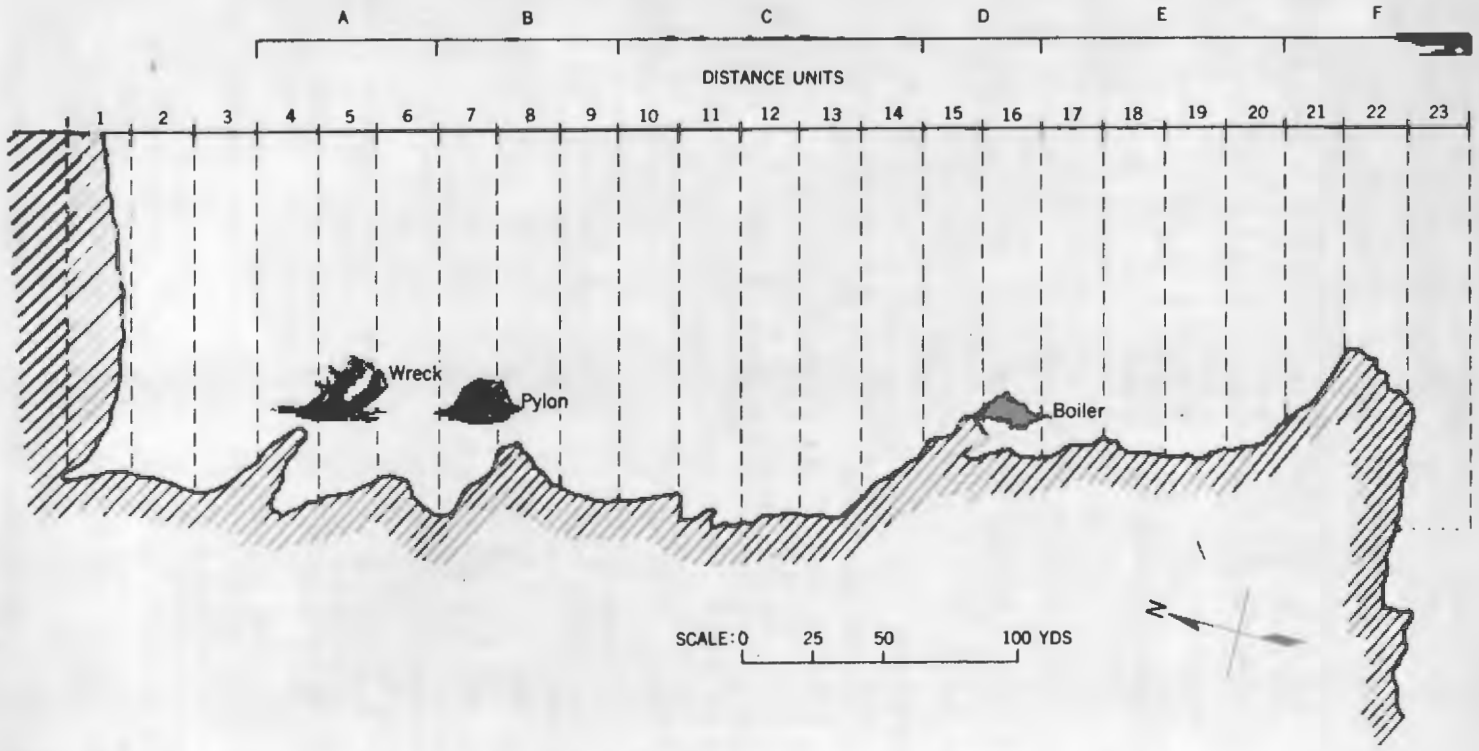

FIG. 2 THE EXPERIMENTAL AREA AT STONY POINT, SHOWING HOW THE COASTLINE WAS DIVIDED INTO DISTANCE UNITS AND SECTIONS TO FACILITATE THE LOCATION OF RECOVERIES

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each month. The abalone were carefully removed from the rocks with levers and placed in collecting bags carried by divers. After the collection of sufficient animals, usually about 60, tagging on the shore commenced. Abalone were marked by means of Petersen discs. A message disc was placed inside the shell and fixed to an external numbered tag by means of a nickel pin passing through a respiratory pore. So as not to interfere with normal growth, tags were placed in position opposite the fourth anterior respiratory pore, well away from the growing edge of shell. A specimen tagged in this manner is illustrated in Figure 3. The shell length and breadth of each animal was measured by means of vernier calipers. After a batch of abalone had been tagged they were returned to the seabed by divers to within a few yards of the site of collection, the position of return being noted in the case of each batch. In order to reduce mortality due to exposure to the air abalone were kept submerged in rockpools between collection and tagging except for a period of two to three minutes during which tagging and measuring took place. Although no estimate is possible, tagging mortality is believed to be low, because:

No damaged abalone were used for tagging;

Divers replaced abalone on the seabed, holding them against the substratum until such time as they adhered firmly to the rock and were comparatively safe from predation or damage by wave action.

Few tagged but empty shells were found in the experimental area on subsequent dives.

FIGURE 3. A TAGGED HALIOTIS MIDAE SHELL

The loss of a few tags is known to have occurred. Occasional toothmarks and bent Petersen discs indicated that the bright, yellow, plastic tags used in the investigation were subject to attack, presumably by fish. No such attacks were however witnessed. A few tags were so severely bent that cracks were apparent and on occasions animals without outer tagging discs were found.

Recoveries were made during systematic searches by divers from the Division. Two divers swam abreast down transects from the shore to the rock bottom boundary (a distance of about 50 yds.) and collected or noted all tagged animals. To fix recovery positions prominent points on the shore were selected and the areas between these were referred to as sections. These were denoted A, B, C, D, E and F (see Table 1 and Figure 2). Each section was searched by means of a series of transects which covered strips of the sea bed about 22 yds. in width. To locate th transects the whole peninsula was divided into 22 yd lengths, called distance units for convenience. This system is shown on Figure 2, from which it can be seen that a search of section A would consist of three transects located approximately at distance units 4, 5 and 6.

On one occasion abalone found on each transect were recorded separately, and this gave a fairly accurate record of movement. This method proved very time consuming and limited the area which could be searched, so generally, although searching was by means of transects located at distance units, the recoveries were allocated to sections i.e. A, B etc. on Figure 2. The midpoint of each section was then regarded as the recovery position of all tagged abalone found within it. These mid-points, together with the

limits of the sections, appear in Table 1. The length of each section in yds. is also shown by the table.

Similarly the position of tagging was regarded as the mid-point of the section in which abalone were replaced after marking. The difference between the two mid-points was therefore an estimate of the distance travelled.

TABLE 1: THE SIZE AND LOCATION OF COASTLINE SECTIONS SEARCHED DURING THE PERIOD 17/6/62 - 26/11/63.

Section	Limits (dist. units)	Mid-point (dist. units)	Length of section (yards)
A	4 - 6	5.5	66
B	7 - 9	8.5	66
C	10 - 14	12.5	110
D	15 - 16	16.0	44
E	17 - 20	19.0	88
F	21 - 23	22.5	66

Abalone movements were therefore measured in a direction parallel to the straight line approximating the eastern coastline of Stony Point. The change in distance from the shore of tagging and recovery positions has been ignored but this omission is not regarded as serious because abalone were confined to the relatively narrow (approximately 50 yds. wide) band of rock running the length of the peninsula. Consequently large on and off-shore movements, relative to movements parallel to the coastline, could not take place.

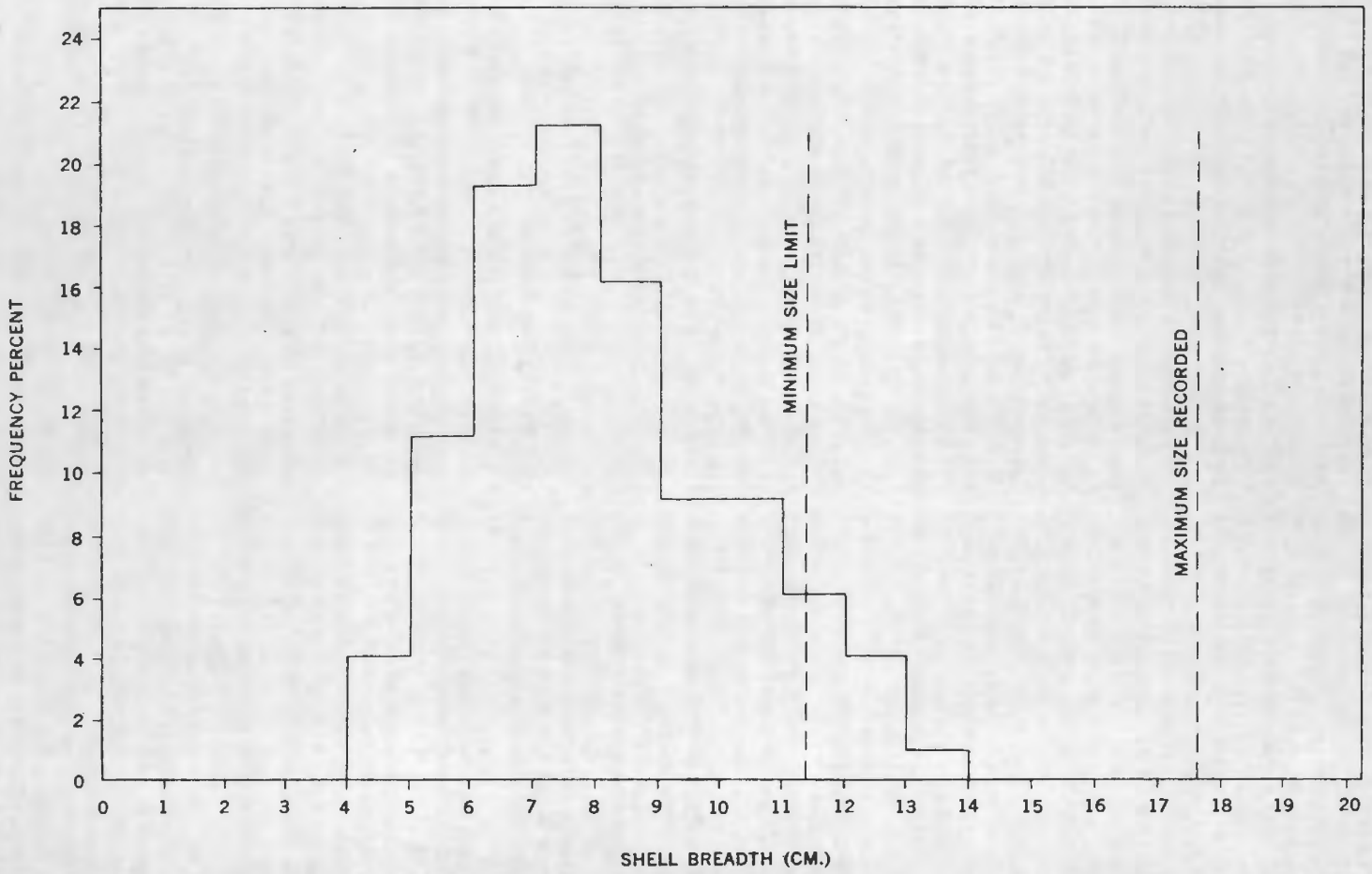

FIG. 4 SIZE COMPOSITION OF TAGGED ABALONE RECOVERED DURING THE INVESTIGATION

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Estimates of movement were made in all cases where recoveries could be associated with one of the sections listed in Table 1. These estimates, together with details of each recovery's tag number, initial shell breadth, date tagged and recovered, tag-recovery period as well as position tagged and recovered are listed in Appendix 1.

The bulk of tag recoveries were made by the Division's divers during the searches described above. As the majority of the animals concerned in the experiment were below the legal minimum size limit, tag-returns by commercial divers were negligible. This is illustrated by the recovery size frequency histogram of Figure 4 on which the minimum legal size limit and the maximum size recorded by the Division are also shown.

Searching was only practical during calm clear sea conditions. On only two occasions was it possible to search an extensive length of coastline in a short time period. During August and September 1962 the coast between units 3 and 17 was searched within seven days. In November 1963 the area between units 4 to 24 was covered in two days. In the course of this latter search the method of searching within the sections listed in Table 1 could not be strictly adhered to and some of these recoveries could not be used to estimate movement.

In addition to the above, abalone were recovered during tagging as well as during searches of individual sections at different times.

RESULTS

A total of 2,645 *H. midae* were tagged in the area and 373 (14 per cent) were recovered within 558 days.

Twenty-eight of these were recovered or noted twice within the area and one abalone was recovered three times during the experiment.

The recovery position of 232 tagged abalone was known, so these could provide data on movement. Their recovery information is summarised in Table II, from which it appears that fairly large distances can be covered by this species. There are no less than 15 records of abalone which have travelled at least 308 yds. along the Stony Point peninsula in periods ranging from 104 to 558 days. Within just over one month, one, three and four individuals covered distances of 132, 176 and 220 yards respectively. Conversely, many abalone were found not to have moved significant dis= tances. The first row of Table II, which includes movements of 0 to 43 yards, contains periods ranging from 21 to 556 days. This indicates that some abalone remain in the same small area for comparatively long periods, although the possibility that abalone leave and then return to the area in which they were tagged cannot be discounted.

The range of abalone movement rates could only be fully described from data recovered during searches which covered an extensive continuous area within a reasonably short period. On occasions when only one or two isolated sections were searched the rates of movement recorded are of

TABLE 2: FREQUENCY OF MOVEMENTS OF TAGGED ABALONE AT STONY POINT DURING 17 MAY 1962 TO 26 NOVEMBER 1963.

Movement yds.	Tag-recovery Period in days*	Freq.
0- 43	21 (7) 23 (6) 28 (21) 34 (3) 35 (6) 55 (2) 56 (2) 57 (3) 78 (4) 79 (3) 84 (3) 91 (2) 96 (5) 104 (1) 110 (5) 111 (2) 112 (1) 119 (1) 120 (1) 145 (8) 174 (1) 175 (1) 180 (2) 207 (1) 215 (2) 271 (2) 277 (1) 311 (2) 322 (1) 453 (1) 556 (1)	101
44- 87	10 (16) 27 (2) 28 (1) 34 (2) 49 (1) 57 (1) 71 (2) 141 (1) 145 (1) 161 (3) 208 (4) 215 (4) 277 (1) 340 (1) 381 (1) 431 (2) 432 (1)	44
88- 131	50 (4) 54 (1) 55 (2) 103 (1) 116 (3) 180 (2) 220 (2)	15
132- 175	33 (1) 77 (2) 117 (6) 118 (1) 166 (4) 167 (1) 200 (1) 363 (1) 368 (1)	18
176- 219	34 (3) 55 (2) 77 (1) 110 (1) 111 (4) 116 (1) 117 (3) 118 (1) 271 (1) 363 (1) 364 (1) 396 (1)	20
220- 263	33 (3) 34 (2) 55 (2) 110 (1) 117 (1) 139 (2) 318 (1) 319 (1) 361 (1)	14
264- 307	118 (1) 319 (1) 363 (1) 364 (1) 397 (1)	5
308- 351	104 (1) 165 (1) 181 (1) 216 (2) 278 (1)	6
352- 395	166 (1) 167 (1) 208 (1) 274 (4) 390 (1) 558 (1)	9
		232

* The figures in brackets indicate that number of recoveries within each category.

little significance for these are too dependent on the location of the search area.

Data from only one recovery season proved suitable for the examination of movement rates. This was during August/September 1962 when the area between distance units 3 and 17 was covered and many recoveries with short tag-return periods were noted.

The rate of movement was expressed as the distance moved per annum and could easily be calculated from the recorded movement and the tag-return period. Such estimates were made for all abalone recovered in the abovementioned search and these have been classified in Table 3.

From the table it is evident that the maximum rate of movement, as shown by 7 recoveries, lies between 2,000 and 2,499 yards per annum, The rate does, however, seem to vary considerably. Recoveries with short tag-return periods, that is 27-35 days, occur throughout the range of rate intervals listed in Table 3 but abalone at large for longer periods tend to be confined to the slower intervals of the table. This is probably due to the fact that the faster moving individuals of the latter group travelled beyond the area searched in the time between tagging and searching. In spite of this, movement rates between 500 and 999 yards per annum are fairly common. In addition a large proportion of all recoveries made during this search had a low rate of movement viz. 0 to 249 yards per annum. Tag-return periods in this case ranged from 34 to 112 days.

The above data inidicate that the rate of movement of this species is extremely variable. For practical purposes it was necessary to obtain some estimate of the mean rate of movement. For this 23 recoveries with short, tag-return periods (27 to 35 days) were selected from the above sample. The short tag-return periods ensured as far as possible that even fast moving individuals would be recovered before they moved beyond the search area.

These recoveries appear in Table 4, which also lists details of the tag number, shell breadth, tag-recovery period, distance moved and rate of movement. The mean rate of movement of these abalone, which occur within the size-range 5.60 to 12.35 cms., amounts to 1083 yds. per annum. The range about this mean is 229 to 2433 yards per annum.

The above figures are based on data measured against a fairly crude scale. As such the calculated mean rate of movement can only indicate the order of the movement per year which can be expected from individuals within the size range investigated. In addition the observations used were all at large during the winter months only. No allowance has therefore been made for possible seasonal variations in the rate of movement.

The arrangement of values for shell breadth and rate of movement in Table 4 suggest that there may well be some association between these variables. Smaller abalone within the sample tend to exhibit lower rates of movement than their larger counterparts. The significance of this association was examined by calculating the Spearman Rank Correlation coefficient, r_s as described by SIEGEL (1956).

TABLE 3: FREQUENCY OF RATES OF MOVEMENT FOR ALL ABALONE RECOVERED ON THE 30 AUGUST 1962 AND 5-6 SEPTEMBER 1962.

Rate of movement (yds. per annum)	Tag-return periods * in days	Freq.
0- 249	34 (3) 35 (6) 56 (2) 57 (3) 71 (2) 78 (4) 79 (3) 104 (1) 111 (2) 112 (1)	27
250- 449	34 (2) 49 (1) 57 (1) 200 (1)	5
500- 749	28 (1) 50 (1) 77 (2) 110 (2) 111 (4) 139 (2)	12
750- 999	27 (2) 50 (3) 77 (1)	6
1000-1249		-
1250-1499	33 (1) 55 (3)	4
1500-1749		-
1750-1999	34 (1)	1
2000-2249	34 (2)	2
2250-2499	33 (3) 34 (2)	5
		62

* Numbers in brackets indicate the number of recoveries within each tag-return period.

This non-parametric measure of correlation was selected because the distribution of the rates of movement within the sample was obviously not normal. The value for s, which incorporates the correction required for the high proportion of tied ranks in the sample, amounted to 0.4694. For a sample of 23 individuals this value is significant at the 5% level only. The result suggests that although there is a significant association between size and rate of movement, the nature of s is such that the relationship cannot be considered to be very marked. Further conclusions about this are beyond the scope of the investigation.

The extent and rate of movement have been discussed. From these results it is apparent that the proportion of abalone which move must be fairly high. Reference to the frequencies listed in Tables 2, 3 and 4 will confirm this. These proportions can be defined more exactly for specific time periods if the results of the extensive search conducted during August/September 1962 be considered. During this search 59 abalone were recovered between distance units 3 to 17. These had been at large for 27-112 days. Of the recoveries, 38 or 64 per cent had moved beyond the area in which they were replaced after tagging.

Because the coastline beyond the 16th distance unit was not covered during this search the actual percentage of tagged abalone which moved could be higher, depending on the extent of movements within the time limit 27 to 112 days. Movements of more than 10 units (220 yards) would carry abalone from tagging site beyond the area searched on this occasion. The mean rate of movement is such that movements of this magnitude are possible within the time

TABLE 4: RATES OF MOVEMENT OF 23 ABALONE RECOVERED WITHIN 27-35 DAYS AFTER TAGGING.

Tag Number	Initial shell breadth (cms)	Tag recovery period (days)	Distance moved (yds)	Rate of movement (yds. per annum)
C 405	12.35	27	66	892
C 368	12.10	33	220	2433
C 302	11.90	34	198	2126
C 240	11.65	35	22	229
C 285	11.15	34	176	1889
C 424	11.05	27	66	892
C 392	10.95	34	44	472
C 410	10.80	34	44	472
C 225	10.75	34	220	2362
C 396	10.40	34	22	236
C 365	10.10	33	132	1460
C 353	10.00	33	220	2433
C 230	9.60	28	44	574
C 260	9.15	34	198	2126
C 397	9.00	33	220	2433
C 197	8.55	35	22	229
C 219	8.45	34	220	2362
C 356	7.60	34	22	236
C 345	7.20	34	22	236
C 218	6.95	35	22	229
C 202	6.90	35	22	229
C 182	6.20	35	22	229
C 261	5.60	35	22	229

limit and the percentage quoted, that is 64, must be regarded as a minimum estimated.

In deriving this percentage, only movements parallel to the peninsula coastline have been considered. Movements parallel to the mainland, that is at approximately right angles to the peninsula, have been excluded from these estimates. Although the sandy bottom extending along most of the length of the peninsula effectively prevents movements in this direction, the bottom near the mainland shore consists of loose boulders over which tagged abalone could travel to settle on a group of densely populated reefs occurring about 120 yards to the east. These reefs were searched on one occasion (8 November 1962) but no marked animals were found. Movement of tagged abalone in this direction would result in still further underestimation of the true percentage of abalone which moved. It is not however possible to estimate the importance of this effect.

DISCUSSION

Laboratory experiments by LISSMAN (1945) and field observations by STEPHENSON (1924), CROFTS (1929) and SINCLAIR (1963) have shown that Haliotis tuberculata and Haliotis iris are capable of active movement. CROFTS (1929) and COX (1960, 1962) have respectively reported on tagging experiments with H. tuberculata, Haliotis cracheradii and Haliotis rufescens, but the movement results described have been confined to remarks about isolated recoveries. In the course of the Division's Haliotis midae tagging programme an attempt was made to evaluate aspects of movement on a more quantitative basis. This

proved difficult from the practical point of view as thorough searching of the seabed by means of SCUBA divers proved to be time-consuming and could only be done on rare occasions when calm, clear water conditions prevailed. A compromise therefore had to be made between accurate location of recoveries and adequate coverage of a large enough area to ensure significant results. Movement has accordingly been described in terms of distances parallel to the straight line approximating the eastern shoreline of the Stony Point peninsula, and the limitations of these estimates have been discussed.

During the investigation no attempt was made to associate movement with any environmental or physiological factors. In the course of tagging divers returned abalone to the seabed close to the site of collection so there is no reason why abnormal movements should occur in order to resettle in a favourable environment. The physical stimulus of tagging, which included exposure to the air for a short time, may initiate movement but it is unlikely that this stimulus would be prolonged sufficiently to cause the comparatively large scale movements recorded. It is therefore felt that experimental techniques did not interfere with the normal behaviour of this species and that the conclusions which may be drawn reflect the state of affairs occuring naturally in the environment.

Haliotis midae within the size range tagged have shown that they can move up to 350 yards in periods ranging from 167 to 558 days. In addition, records show that in some cases no appreciable movement took place even after fairly long tag-return periods.

The calculation of the rates of movement of a sample of recoveries has shown that these values, expressed in yards per annum, are extremely variable. The mean rate of movement of the particular sample examined amounts to 1083 yards per annum. The sample range was 229 to 2433 yards per annum.

Data on the extent and rate of movements suggest that a large proportion of tagged abalone moved. This is substantiated by the fact that of a sample of 59 recoveries 38 or 64 per cent had moved away from the original tagging area.

The general picture which emerges from this field study is that, within the size range investigated, Haliotis midae is by no means a sedentary species. Movement commonly occurs and relatively large distances can be covered.

These movement characteristics are in accordance with those required to explain the distribution of abalone in the Hermanus area. Juvenile specimens, with shell breadths below 5 cm, are found under stones where they are protected from predators. They occur very commonly in calm shallow bays on substrata composed of loose boulders. Larger abalone are not usually found in these areas. Abalone of intermediate sizes that is above 5 cm. but below 10 cm shell breadth, tend to occur more frequently on fairly shallow inshore reefs (1 to 6 ft. below the low watermark) which are protected from severe wave action. Larger abalone are found within a wide range of depths, the maximum depth record for the species being 75 feet. In all three cases that is juvenile, intermediate and large sizes, there is a tendency for

individuals to occur in dense concentrations or "beds". Commercial divers report the removal of up to 20,000 abalone from such beds of large animals, where the density may be from 15 to 20 abalone per square yard.

The fact that differences associated with size occur in the distribution of the species implies that at least the juvenile and intermediate sizes must move about in order to eventually change their depth or situation, as well as to congregate on favourable reefs. This indirect evidence of movement is confirmed by the experimental findings of this paper.' Under the circumstances claims made by certain commercial divers that favourable but exploited reefs were often repopulated after a few years are substantiated. Such repopulation within the period of a few years could not be the result of larval settlement for growth is not sufficiently fast. Restocking of these reefs must therefore be due mainly to recruitment of intermediate sizes from densely populated shallow reefs in the vicinity.

LITERATURE CITED

BARNARD, K.H., 1963 - Contributions to the knowledge of South African marine mollusca Part IV. Gastropoda: Prosobranchiata: Rhipidoglossa, Docoglossa. Tectibranchiata. Polyplacophora. Solenogastres. Scaphopoda. Ann. S. Afr. Mus. 48 (2): 201-360.

COX, K.W. 1960 - Review of the abalone in California. Dept. Fish Game St. Calif. 46 (4): 381-406.

COX, K.W. 1962 - California Abalones, Family Haliotidae. Bull. Dept. Fish Game St. Calif. 112, 122 p.

CROFTS, D.R. 1929 - Haliotis. L.M.B.C. Mem. typ. Br. Mar. Pl. Anim. 29: 1-174

INO, T., 1952 - Biological studies on the propagation of the Japanese abalone (genus Haliotis). Bull Tokai reg. Fish Res. Lab. 5, 102 p.

LISSMANN, H.W. 1945 - The mechanism of locomotion in gastropod molluscs. I. Kinematics. J. Exp. Biol. 21, 58-69

SIEGEL, S., 1956 - Non-parametric statistics for the behavioral sciences. McGraw-Hill, New York.

SINCLAIR, M. 1963 - Studies on the Paua, Haliotis iris Martyn in the Wellington district, 1945-1946. Zool. Publ. Vict. Univ. N.Z. 35, 16 p.

STEPHENSEN, T.A., 1924 - Notes on Haliotis tuberculata. Mar. biol. Ass. U.K. 13 (2): 480-495.

INTRODUCTION

Various mathematical models are available for describing the growth of organisms. These were originally independently derived by different workers and as such will be first discussed separately. More recent research has however shown that these supposedly different models can all be derived from a common, more generalized growth rate function. (RICHARDS 1959, TAYLOR 1962). This development will be dealt with in the second part of the review, against the background presented initially.

Ideally a growth model should not only provide a good empirical representation of the growth of an organism, but its parameters should have a physiological interpretation relevant to growth. It will be apparent from the review that this latter requirement is satisfied to a varying degree in present day models.

The description of growth by means of mathematical expressions has very definite advantages, which may be summarized as follows:-

1. They facilitate the comparison and testing of differences in the growth of allied species or of the same species in different localities.

2. They allow interpolation or extrapolation to size ranges within which it may be difficult, from the practical point of view, to measure growth.

3. Such expressions can conveniently be incorporated in production computations for exploited stocks.

4. The nature of changes of the parameters of growth equations may shed light on the physiology of growth.

Under the circumstances appreciation of the range, and selection of the optimum mathematical model would seem to be a prerequisite of any growth study.

MODELS

The Von Bertalanffy Equation.

This equation was derived by VON BERTALANFFY (1934, 1938) from physiological considerations. BEVERTON and HOLT (1957) have presented a concise account of von Bertalanffy's treatment and the following is essentially a summary of their description utilizing the same mathematical notation.

If an organism be regarded as analogous to a reacting chemical system, which obeys the law of mass action, the resultant of two groups of processes, that is anabolism (synthesis) and catabolism (breakdown), will be reflected by changes in the total weight of the organism. Mathematically this may be expressed as follows:-

$$\frac{dW}{dt} = HW^n - kW^m \qquad (1)$$

where H and k are coefficients of anabolism and catabolism respectively and n and m are some powers of the body weight (W). Following general physiological concepts von Bertalanffy suggests that the rate of anabolism is pro= portional to the absorbtion rate of nutritive material, which is in turn dependent on the size of the absorbtion surfaces. Catabolism however, could be proportional to the total mass being broken down. Thus

(1) becomes

$$\frac{dW}{dt} = Hs - kW \qquad (2)$$

where s = the effective physiological surface of the organism.
and H = rate of synthesis of mass per unit "physiological surface"
k = rate of destruction of mass per unit mass.

Equation (2) may be expressed in terms of length (L) if it can be assumed that the organism grows isometrically and has a constant specific gravity for, under these circumstances,

$$s = pL^2$$
$$W = qL^3$$

p and q being constants.

This being the case

$$\frac{dW}{dt} = \frac{d(qL^3)}{dt} = 3qL^2 \frac{dL}{dt}$$

Substitution of the above in (2) gives

$$3qL^2 \frac{dL}{dt} = HpL^2 - kqL^3$$

therefore

$$\frac{dL}{dt} = \frac{HpL^2}{3qL^2} - \frac{kqL^3}{3qL^2}$$

$$= \frac{Hp}{3q} - \frac{kL}{3}$$

if $\frac{Hp}{3q} = E$ and $\frac{k}{3} = K$

then $\frac{dL}{dt} = E - KL$ (3)

Intergrating (3) as follows:

$$\int \frac{dL}{E - KL} = \int dt$$

$$\frac{1}{-K} \text{Log}_e (E-KL_t) = t + c$$

The intergration constant c may be evaluated as follows:

let $t = o$, then $L_t = L_o$

and $c = \frac{1}{-K} \text{Log}_e (E-KL_o)$

thus $t = \frac{1}{-K} \text{Log}_e (E-KL_t) + \frac{1}{K} \text{Log}_e (E-KL_o)$

$$-Kt = \text{Log}_e \frac{E-KL_t}{E-KL_o}$$

$$e^{-Kt} = \frac{E-KL_t}{E-KL_o}$$

$$KL_t = E-(E-KL_o)e^{-Kt}$$

$$L_t = \left(\frac{E}{K} - \frac{E}{K} + L_o\right) e^{-Kt}$$

but $\lim_{t \to \infty} \left(\frac{E}{K} - L_o\right) e^{-Kt} = o$

$$L_\infty = \frac{E}{K}$$

$$L_t = L_\infty - (L_\infty - L_o) e^{-Kt} \quad (4)$$

which is an expression of length at time t. Parameters of this equation which have to be estimated are therefore

L_∞ = the maximum size attained by the organism

L_0 = the length at zero time

and **K** = one third of the rate of destruction of mass per unit mass.

Equation (4) is more commonly presented in the form:

$$L_t = L_\infty(1-e^{-K(t-t_0)}) \qquad (5)$$

which may be derived as follows:

$$L_t = L_\infty - (L_\infty - L_0)\, e^{-Kt} \qquad (4)$$

if $L_t = 0$ when $t = t_0$ then the constant L_0 may be evaluated as:

$$0 = L_\infty - (L_\infty - L_0)\, e^{-Kt_0}$$

$$= L_\infty (1-e^{-Kt_0}) + L_0 e^{-Kt_0}$$

$$L_0 = L_\infty (1-e^{Kt})$$

substituting in (4)

$$L_t = L_\infty - \left\{ L_\infty - L_\infty (1-e^{Kt_0}) \right\} e^{-Kt}$$

$$= L_\infty (1-e^{-K(t-t_0)}) \qquad (5)$$

The constant t_o may be interpreted as the age at which an organism, with the same pattern of growth as that in later life, would have had zero weight.

Equation (5) does not therefore describe growth over the whole size range unless t_o is very near or equal to zero.

Assuming a cube relationship between length and weight equation (4) may also be expressed in terms of weight as follows:

$$W_t = \left[W_\infty^{\frac{1}{3}} - (W_\infty^{\frac{1}{3}} - W_o^{\frac{1}{3}}) e^{-Kt} \right]^3 \qquad (6)$$

and similarly to equation (5), (6) may be expressed as:

$$W_t = W_\infty \left(1 - e^{-K(t-t_o)}\right)^3 \qquad (7)$$

Estimation of the parameters of equation (5) is described by RICKER (1958). If length at age t + 1 be considered then:

$$L_{t+1} = L_\infty \left(1 - e^{-K(t+1-t_o)}\right)$$

$$= L_\infty \left(1 - e^{-K(t-t_o)} e^{-K}\right)$$

but from (5) it can be shown that:

$$e^{-K(t-t_o)} = 1 - \frac{L_t}{L_\infty}$$

By substitution:

$$L_{t+1} = L_\infty \left[1 - \left(1 - \frac{L_t}{L_\infty}\right) e^{-K}\right]$$

$$= L_\infty (1 - e^{-K}) + e^{-K} L_t$$

Putting $e^{-K} = k$ (It should be noted that k in this case is not equivalent to that of (2)),

$$L_{t+1} = L_\infty (1-k) + kL_t \qquad (8)$$

This expression describes the linear relationship between the variables L_{t+1} and L_t, Plotting L_{t+1} on L_t and/or fitting a regression equation therefore provides a convenient way of estimating K and L_∞

RICKER (1958) mentions that fitting expression (8) directly may not be satisfactory because both variables are subject to sampling error and points may be erratically distributed with respect to the line fitted. For a better fit RICKER suggests the following:

Writing equation (5) as:

$$L_t = L_\infty - L_\infty e^{-K(t-t_o)}$$

then $L_\infty - L_t = L_\infty e^{-K(t-t_o)}$

Log transforming the above gives

$$\text{Log}_e (L_\infty - L_t) = \text{Log}_e L_\infty - Kt + Kt_o$$

Thus $\log_e (L_\infty - L_t)$ plotted on t is linear, and this linearity is sensitive to values of L_∞. Using an initial L_∞ value selected from a freehand plot of (8), a few trial plots will quickly yield the L_∞ value which gives the straightest line, and this can usually be judged by eye. The coefficient K, which is the slope of (9), can then easily be ascertained and, from the intercept value the coefficient t_o is derived.

The growth equation discussed above was derived by VON BERTALANFFY (1934, 1938) from physiological considerations. A more empirical drivation of essentially the same expression occurs in the literature. RICKER (1958) states that growth in fishes commonly follows a pattern of an initial rapid absolute increase in length followed by a progressive decrease in growth rate, that is the growth curve is an asymmetrical sigmoid. Furthermore the initial period of increasing absolute growth rate is usually comparatively short so that the point of inflection lies so near the zero line axis that it may not even appear in a graph of yearly increments.

Considering only the part of the sigmoid having a decreasing slope, the function

$$L_t = B - Ce^{-Kt} \qquad (10)$$

may be used to describe the length (L_t) at time t where B and C are constants having dimensions of length and K is a constant determining of rate of change in the length increment.

Following RICKER (1958) (10) can be written as

$$L_t + C = B + C - Ce^{-Kt}$$

$$\text{and } L_t - (B-C) = C\,(1-e^{-Kt}) \qquad (11)$$

also from (10) when $t \rightarrow \infty$

$$L_\infty = B$$

and from (11)

when $t = o$

$$L_t = B-C$$

The constant quantity B-C is therefore an adjustment which shifts the time axis of the graph to ensure the adjusted length is zero when the age is zero. As in the von Bertalanffy derivation the same effect can be achieved by shifting the length axis and introducing the constant t_o, that is:

$$\text{If } t = t_o,\ L_t = o$$

and from (11)

$$B = Ce^{-Kt_o}$$

$$C = Be^{Kt_o}$$

Substituting the above in (11)

$$L_t - B = -Be^{-K(t-t_o)}$$

$$L_t = B\,(1-e^{-K(t-t_o)}) \qquad (12)$$

As $B = L_\infty$

$$L_t = L_\infty\,(1-e^{-K(t-t_o)})$$

which is (5).

The above empirical derivation is advantageous in that it does not specify conformation to the surface and cube laws of anabolism and catabolism respectively.

- As for length, graphs of weight on age are asymmetrical sigmoid, but the point of inflection is at a greater age in the latter curve. The empirical curve of (10) can therefore only be applied to ages above the point of inflection. Similarly to (12), it can be shown that

$$W_t = W_\infty \left(1-e^{-K(t-t'_o)}\right) \qquad (13)$$

where t'_o is the age at which weight would have been zero if growth had always conformed to expression (13).

It will be noted that (13) differs from the similar expression (7) derived in the initial discussion of (5) in that t' is used in place of t_o and the term equivalent to $(1-e^{-K(t-t_o)})$ in (7) is not cubed as in (13). These differences are due to the fact that whereas (7) applies over most of the life span of an organism (13) describes only that section above the point of inflection of the weight/age curve.

As discussed, the parameters of equation (5) may conveniently be estimated from a plot of L_{t+1} on L_t. It frequently occurs in the course of tagging experiments that specimens cannot be recovered at yearly intervals after tagging, that is values of L_t and L_{t+1} may not be available. Instead sizes at intervals of less than a year or a year plus may have been noted. If sufficient specimens are available with the same tag-return interval (not necessarily one year) the parameters of (5) may be estimated by the following method which is due to GULLAND and HOLT (1959).

Assuming growth is according to equation (5), L_t will increase to L_{t+a} after an interval of a, as follows:

$$L_{t+a} = L_\infty \left(1-e^{-K(t-t_o+a)}\right)$$

The growth increment ${}_aY$ during time a, will be

$${}_aY = L_{t+a} - L_t = L_\infty \left[e^{-K(t-t_o)} - e^{-K(t-t_o+a)}\right]$$

$$= L_\infty e^{-K(t-t_o)} (1-e^{-Ka})$$

and growth per unit time, that is Y,

$$\text{is } Y = L_\infty e^{-K(t-t_o)} \left(\frac{1-e^{-Ka}}{a}\right) \qquad (14)$$

The mid-point of the length interval is $\frac{1}{2}(L_t + L_{t+a})$ and will be denoted by x

then

$$x = \tfrac{1}{2} L_\infty \left(2-e^{-K(t-t_o)} - e^{-K(t-t_o+a)}\right)$$

$$= L_\infty - L_\infty \frac{e^{-K(t-t_o)}}{2} (1+e^{-Ka})$$

$$L_\infty e^{-K(t-t_o)} = \frac{2(L_\infty - x)}{(1+e^{-Ka})} \qquad (15)$$

Substituting (15) in (14)

$$Y = (L_\infty - x) \frac{2(1-e^{-Ka})}{a(1+e^{-Ka})}$$

let $b = \frac{1}{2} Ka$

then

$$Y = \frac{(L_\infty - x)\ K\ (1-e^{-2b})}{b\ (1+e^{-2b})}$$

$$= K (L_\infty - x) \frac{\tanh b}{b} \qquad (16)$$

Thus for a group of data reflecting growth over a fi[illegible] time duration a plot of Y, the increment per unit time, against x, the mid-point of the corresponding length interval will be linear with a slope $-K\frac{1}{b} \tanh b$ and intercept KL_∞ on the x axis.

If separate plots of Y on x are made for groups of data with different time intervals, the slopes of the lines will differ but the intercepts should be similar. If the time intervals are short then, as $\frac{1}{2}Ka = b$ b will be small. For small values of b, tanh $b \approx b$ and the term $\frac{\tanh b}{b}$ becomes equal to one. Thus for a small time interval the relationship between Y and x will be linear with slope -K and intercept KL_∞. The authors provide a table of values of $\frac{x}{\tanh x}$ from which the error in assuming $\frac{x}{\tanh x}$ equal to one can be judged for various values of x.

For data for which time intervals are long, but some groups with short intervals are available, the following method may be used.

Equation (16) may be expressed as

$$\frac{b}{\tanh b} Y = K (L_\infty - x)$$

thus plotting $\frac{b}{\tanh b} Y$ and x

will result in a straight line with slope -K. From the data with relatively short time intervals an estimate of K can be obtained. From this first approximation to K and the known time interval, the values of $\frac{b}{\tanh b} Y$ may be calculated utilizing a table presented by Gulland and Holt. These points, plotted on x, may then be added to the original plots for data with short time intervals. The parameters L_∞ and K can then be estimated from the slope and intercept of the combined plots.

The Walford growth curve.

WALFORD (1946) independently developed an empirical growth curve which is in fact a derivation of the von Bertalanffy curve discussed in the previous section. Walford recognised that in most cases growth over the major part of life can be represented by that section of a sigmoid curve occuring above the inflection point, that is, the "self inhibiting" phase of the curve. WALFORD found that this type of curve could be transformed to a straight line by plotting the length at age t+1 on the length at age t that is L_{t+1} and L_t. This plot is essentially the same as (8) which was derived by mathematical manipulation of (5). The author mentions that for several species for which published data are available, plots of L_{t+1} on L_t proved to be linear. In addition, some interesting characteristics of this type of growth representation are described. If the relationship between L_{t+1} and L_t is linear then

$$\frac{L_3-L_2}{L_2-L_1} = \frac{L_4-L_3}{L_3-L_2} = \frac{L_n-L_{n-1}}{L_{n-1}-L_{n-2}} = K$$

or more simply

$$L_n-L_{n-1} = K\,(L_{n-1}-L_{n-2}) \qquad (17)$$

also if $L_o = o$ then

$$L_2-L_1 = K(L_1-L_o) = K\,L_1$$

$$L_3-L_2 = K\,(L_2-L_1) \qquad = K^2L_1$$

$$L_n-L_{n-1} = K\,(L_{n-1}-L_{n-2}) = K\,K^{n-2}L_1 = K^{n-1}L_1 \qquad (18)$$

$\frac{L_n - L_{n-1}}{L_{n-1} - L_{n-2}}$. This may be extended to

$$\frac{L_\infty - L_{n+1}}{L_\infty - L_n} = K$$

This leads to an interesting interpretation of the characteristic growth represented by (20) and (5). From the above equation it appears that the growth remaining unfulfilled at the beginning of any time interval i.e. n+1, is a constant proportion of that which remained at the beginning of the previous interval i.e. n. Walford notes that the higher the K value the more slowly the limiting length is approached.

The Gompertz curve.

The above equation was originally developed by Gompertz in 1825 and has been used to describe the growth of organisms such as the razor clam Siliqua patula WEYMOUTH, McMILLIN and RICH (1930), the Pacific cockle Cardium corbis WEYMOUTH and THOMPSON (1930), the catfish Osteogeneicosus militaris PANTULU (1963) and the yellow fin tuna Neothunnus macropterus RIFFENBURGH (1960).

The development of the equation is as follows:

WEYMOUTH, MCMILLIN and RICH (1931) and WEYMOUTH and MCMILLIN (1930) showed that the decline in relative growth rate with age of the razor clam is exponential. When log transformed the relationship therefore becomes linear that is

$$\text{Log}_e \frac{1}{L}\frac{dL}{dt} = a - Kt$$

$$\frac{1}{L}\frac{dL}{dt} = e^{(a-Kt)}$$

$$\frac{dL}{L} = e^{(a-Kt)}dt$$

Integrating the above

$$\text{Log}_e L_t = -\frac{e^{a-Kt}}{K} + b$$

putting $c = \frac{e^a}{K}$

$$\text{Log}_e L_t = -ce^{-Kt} + b$$

$$L_t = e^{-ce^{-Kt}+b}$$

putting $e^b = B$ the above becomes

$$L_t = Be^{-ce^{-Kt}} \qquad (21)$$

which is the Gompertz function.
Expression (21) is an asymmetrical sigmoid which may be used to provide an empirical description of growth curves having this form.

Methods of estimating the parameters of the Gompertz equation are complicated and will not be dealt with. The techniques have however been fully described by RIFFENBURGH 1960.

The Autocatalytic or Logistic equation.

BEVERTON and HOLT (1957) describe the above equation which has limited application as an empirical means of representing growth. Assuming the relationship between growth rate (in terms of weight) and size can be expressed as

$$\frac{dW}{dt} = KW\,(A-W) \qquad (22)$$

a growth curve may be obtained by solving (22) as follows:

$$\frac{dW}{W(A-W)} = Kdt$$

By partial factorization the above becomes

$$\frac{dW}{W} + \frac{dW}{A-W} = AKdt,$$

the solution of which is

$$\mathrm{Log}_e W - \mathrm{Log}_e (A-W) = AKt$$

$$\mathrm{Log}_e \left(\frac{W}{A-W}\right) = AKt$$

$$\frac{W}{A-W} = e^{AKt}$$

$$W = e^{AKt}(A-W)$$

$$= Ae^{AKt} - We^{AKt}$$

$$W\,(1+e^{AKt}) = Ae^{AKt}$$

$$W = \frac{Ae^{AKt}}{1+e^{AKt}}$$

$$= \frac{A}{1+e^{-AKt}}$$

The above equation has a symmetrical sigmoid form and as such has limited application in growth problems. Attempts have been made to introduce asymmetry into it by modification of the parameters, but these have only resulted in empirical expressions with parameters difficult to estimate. (BEVERTON and HOLT 1957).

Parabolic growth curve.

One of the most recent growth functions to be developed is the parabolic expression of PARKER and LARKIN (1959). The concepts from which this expression was derived are interesting and are briefly as follows.

The first observation which the authors make is that the growth rate of fishes is greatly influenced by environmental factors such as abundance of food and population density. Thus, unless the environment remains relatively constant, age and size need not be related in a fixed manner In addition, even under constant physical conditions, growth of fish may not be related to age. To illustrate this point the authors quote the findings of various workers, who found size hierarchies in age groups of fishes which influenced their growth rates. Additional evidence that growth is size and not age dependent in certain fish is cited by PARKER and LARKIN. In this respect they mention that many species change their ecological niche as they grow older, thus revising the "ultimate size" to which they are growing. (LARKIN, TERPENNING and PARKER, 1957). In addition many salmonoids undergo marked

physiological transformations at different periods of their history and these may also be related to a size threshold. (ALM 1959, ELSON 1957, PARRY 1958 in PARKER and LARKIN 1959).

From the above discussion it may be concluded that, due to environmental or physiological changes growth patterns may be revised. This applies especially to Salmonoids which undergo physiological changes at different periods in their life history, and, to quote PARKER and LARKIN (1959) "Growth of fish may thus be visualized as a series of growth stanzas (Brody, 1945) which are entered by ecological and physiological size thresholds and within which size is the basic determined of both ecological and physiological opportunity for growth".

Under these circumstances many mathematical functions describing growth over the whole size range must to a certain extent dampen the discreet stanza effect as it is impractical to incorporate sufficient coefficients to render a model sensitive enough to reflect the effects of the various stanzas. According to Parker and Larkin therefore, a desirable model is one which has a minimum number of constants representing the combined ecological and physiological factors affecting growth throughout life and is based on the view that change in size is a function of size achieved.

To develope their model the authors consider the following expression of growth in mass;

$$\frac{dW}{dt} = EW^x \qquad (24)$$

which has been found to describe empirically the relationship between weight and various physiological processes. (PARKER and LARKIN 1959). The expression (24) therefore

forms a logical basis for the development of a growth function and may be intergrated as follows:

$$W^{-x}dW = E\,dt$$

$$\frac{W_t^{1-x}}{1-x} = Et + c$$

$$W_t^{1-x} = Et(1-x) + c'$$

if $t = o \quad c' = W_o^{1-x}$

$$\text{thus } W_t^{1-x} = (1-x)\,Et + W_o^{1-x} \qquad (25)$$

Considering growth from t to t+1

$$W_{t+1}^{1-x} = (1-x)Et + E(1-x) + W_o^{1-x}$$

$$-W_t^{1-x} = -(1-x)Et - W_o^{1-x}$$

$$W_{t+1}^{1-x} - W_t^{1-x} = E(1-x)$$

$$W_{t+1}^{1-x} = E(1-x) + W_t^{1-x} \qquad (26)$$

Assuming a weight length relationship of

$$W = qL^y \quad \text{and}$$

substituting for W in (26) gives

$$L_{t+1}^{y(1-x)} = \frac{E(1-x)}{q^{(1-x)}} + L_t^{y(1-x)} \qquad (27)$$

The above equation is linear and parallel to a 45^o diagonal passing through the origin oo.

Putting

$$\alpha = \frac{E(1-x)}{q^{(1-x)}}$$

and $z = y(1-x)$

(27) becomes

$$L^{z}_{t+1} = \alpha + L^{z}_{t} \qquad (28)$$

The coefficients of (28) may be interpreted as follows:

If $L^{2}_{t+1} = L^{2}_{t}$ that is $\alpha = 0$ (28) may be represented by a 45° diagonal passing though the origin oo. The value of

therefore determines the distance between the diagonal passing through the origin and that of the diagonal repre= senting through the data. This constant expresses length increments in a manner which is comparable regardless of size or age (PARKER and LARKIN 1959). The value of z has been found by the above authors to be within extremes 0.5 to 1.5. Plotting L_{t+1} against L_{t} reveals the nature of z. A trend diverging from the 45° diagonal indicates that z is likely to be between 0.5 and 1.0. Conversely if the trend approaches the diagonal, z is likely to lie between 1.0 and 1.5. If the data are linear and parallel to the diagonal, z will be close to 1.

Estimation of the coefficients z and α is fully described by the authors, and will not be dealt with in detail here. Briefly two methods are available. Ideally z may be found by assumming trial values for it and determining the value which provides the minimum relative variance of α. Having determined z, α may then easily be calculated. As the calculations required for the above are considerable, computer facilities are required. If such facilities are not available the authors suggest the following approach

The values L_1, L_2, L_3, --- L_n

should be transformed to $L_1^{0.5}$, $L_2^{0.5}$, $L_3^{0.5}$, --- $L_n^{0.5}$

and $L_1^{1.5}$, $L_2^{1.5}$, $L_3^{1.5}$, --- $L_n^{1.5}$

which gives three sets of data with z values 0.5, 1.0 and 1.5

For each set the mean α and its variance should be calculated. The square root of the relative variance $\sqrt{\frac{S_x^2}{\alpha^2}}$ or relative standard deviation Sr can then be calculated for the three sets of data. This statistic has been found to be related to z as the quadratic function

$$Sr \approx a+bz+cz^2 \qquad (29)$$

and therefore provides a means of estimating the latter parameter.

As three sets of values of Sr and z are available (29) can be solved simultaneously. The optimum z value is that which minimizes Sr. Thus differentiating (29) and equating to zero

$$2cz+b = o$$

$$\text{and } z = \frac{-b}{2c} \qquad (30)$$

The authors have used the above techniques to investigate aspects of the growth of steelhead trout (Salmo gairdneri) and chinook salmon (Oncorhynchus tshawytscha). By estimating the value for individual steelhead trout, and subjecting the data to analysis of variance techniques they were able to show significant differences in growth due to sex and life history.

The generalized model.

The more important growth models available to biologists have been described above. It is apparent that each model has been developed relatively independently from physiological or strictly empirical considerations. Fairly recently it has been shown that the curves mentioned above can all in fact be derived from a more general expression with four parameters. RICHARDS (1959) derived empirically the monomolecular (equation (5)) autocatalytic and Gompertz curves from the general equation.

$$W = \left[\frac{N}{K} - \left(\frac{N}{K} - W_o^{1-m}\right)e^{-(1-m)Kt}\right]^{\frac{1}{1-m}} \qquad (31)$$

by considering variations of the parameter m.

Essentially the same function as (31) was independently developed by TAYLOR and published posthumously in 1962. In this case the generalized equation was developed as an extension of von Bertalanffy's original physiological justification of a growth model. The derivation considered here will be that of TAYLOR (1962), as differences between his equation and that of RICHARDS (1959) are due solely to notation.

A limitation of the Bertalanffy equation (5) is that it implies a cube and square relationship between length dimensions and body weight and body surface respectively. Values of the weight exponent of length weight relationships have however been found to range between 1.4 and 4.0 for various species and may thus differ appreciably from 3. In addition data on intestinal lengths has shown that a linear dimension squared is unlikely to provide a reliable

index of surface area (TAYLOR 1962). The data of FRY (1957) also indicate that gill area does not confirm to a linear dimension squared relationship in many fish. In addition RICKER (1958) notes from feeding studies that food is seldom available to fish in excess and therefore absorbtive surface cannot be expected to be a limiting factor with regard to anabolic processes.

From the above it is apparent that the relationships

$$s = pL^2$$

and

$$W = qL^3$$

cannot always be confidently substituted in (2) as required for the derivation of (5). The von Bertalanffy equation can therefore be made more flexible and representative by setting

$$s = pL^a \qquad (32)$$

and $$W = qL^b \qquad (33)$$

and estimating these two power coefficients from the actual data. Using the method and notation of TAYLOR (1962) a generalized equation may be derived as follows:

Differentiating (33) with respect to t

$$\frac{dW}{dt} = bqL^{b-1}\frac{dL}{dt} \qquad (34)$$

Substituting (32), (33) and (34) in equation (2) gives

$$\frac{dL}{dt} = \frac{Hp}{bq} L^{(a-b+1)} - \frac{k}{b}L$$

and setting $E = \frac{Hp}{bq}$

$$K = \frac{k}{b}$$

the above becomes

$$\frac{dL}{dt} = E\,L^{(a-b+1)} - KL \qquad (35)$$

If $a \neq b$ (35) may be integrated as follows:

$$\frac{dL}{EL^{(a-b+1)} - KL} = dt$$

Putting $a-b+1 = m$

$$\frac{dL}{\frac{E}{K}L^{m} - L} = Kdt$$

$$\frac{dL}{L\left(\frac{E}{K}L^{m-1} - 1\right)} = Kdt$$

If $\frac{E}{K}L^{m-1} - 1 = \tan^2\theta$

then $\frac{E}{K}(m-1)L^{(m-2)}dL = 2\tan\theta\sec^2\theta d\theta$

$$dL = \frac{2\tan\theta\sec^2\theta d\theta}{\frac{E}{K}(m-1)L^{(m-2)}}$$

Thus $$Kdt = \frac{2\tan\theta\sec^2\theta d\theta}{\frac{E}{K}(m-1)L^{(m-1)}\left(\frac{E}{K}L^{m-1} - 1\right)}$$

but $\frac{E}{K}L^{m-1} = \tan^2\theta + 1$

so $$Kdt = \frac{2\tan\theta\sec^2\theta d\theta}{(m-1)\,(\tan^2\theta+1)\tan^2\theta}$$

$$= \frac{2}{m-1}\ \mathrm{ctn}\theta d\theta$$

Integrating the above expression gives

$$Kt + c = \frac{2}{m-1} \quad \text{Log}_e \sin \theta$$

Sin θ may be evaluated as follows:

$$\sec^2\theta = \frac{E}{K} L^{m-1}$$

$$\tan^2\theta = \frac{E}{K} L^{m-1} - 1$$

$$\text{Sin } \theta = \sqrt{\frac{\frac{E}{K} L^{m-1} - 1}{\frac{E}{K} L^{m-1}}}$$

Substituting in the above equation

$$Kt + c = \frac{2}{m-1} \frac{1}{2} \text{Log}_e \frac{\frac{E}{K} L_t^{m-1} - 1}{\frac{E}{K} L_t^{m-1}}$$

Putting t = o and L = L_o c may be evaluated as

$$c = \frac{1}{m-1} \text{Log}_e \frac{\frac{E}{K} L_o^{m-1} - 1}{\frac{E}{K} L_o^{m-1}}$$

and thus

$$(m-1)Kt = \text{Log}_e \frac{\frac{E}{K} L_t^{m-1} - 1}{\frac{E}{K} L_t^{m-1}} - \text{Log}_e \frac{\frac{E}{K} L_o^{m-1} - 1}{\frac{E}{K} L_o^{m-1}}$$

Integrating the above expression gives

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Substituting in the above equation

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and thus

$$(m-1)Kt = \text{Log}_e \frac{\frac{E}{K} L_t^{m-1} - 1}{\frac{E}{K} L_t^{m-1}} - \text{Log}_e \frac{\frac{E}{K} L_o^{m-1} - 1}{\frac{E}{K} L_o^{m-1}}$$

$$(m-1)Kt = \text{Log}_e \frac{\left(\frac{EL_t^{m-1}}{K} - 1\right) \frac{EL_o^{m-1}}{K}}{\frac{EL_t^{m-1}}{K}\left(\frac{EL_o^{m-1}}{K} - 1\right)}$$

$$e^{(m-1)Kt} = \frac{\left(\frac{EL_t^{m-1}}{K} - 1\right) \frac{EL_o^{m-1}}{K}}{\frac{EL_t^{m-1}}{K}\left(\frac{EL_o^{m-1}}{K} - 1\right)}$$

$$1 - \frac{KL_t^{(1-m)}}{E} = e^{Kt(m-1)}\left(1 - \frac{KL_o^{(1-m)}}{E}\right)$$

$$L_t^{1-m} = \frac{E}{K} - \left(\frac{E}{K} - L_o^{(1-m)}\right) e^{Kt(m-1)}$$

But $m = a-b+1$, therefore

$$L_t^{b-a} = \frac{E}{K} - \left(\frac{E}{K} - L_o^{(b-a)}\right) e^{-K(b-a)t} \qquad (36)$$

which is essentially the same equation as (31) derived by RICHARDS (1959).

From equation (35) and its integrated form (36) it is possible to derive the growth models discussed earlier by considering variations in the parameter (b-a). These derivations, which will be dealt with in detail, may be summarized as follows.

Equation	Parameter characte-restics	Derived function
(36)	$b > a$	Generalized von Bertalanffy
	$b-a=1$	von Bertalanffy
	$b < a$	Logistic
(35)	$b=a$	Exponential
	$b-a \to 0$	Gompertz
	$b > a, K=0$	Parabolic

Considering equation (36), if b > a than the generalized von Bertalanffy equation may be obtain as follows:

$$\text{Lim } L_t^{(b-a)} = \frac{E}{K} = L_\infty^{b-a}$$

$$t \longrightarrow \infty$$

also if $L_o = o$ when $t = t_o$ then similarly to (5), (36) may be written as

$$L_t^{(b-a)} = L_\infty^{(b-a} \left(1-e^{-K(b-a)\ (t-t_o)}\right) \qquad (37)$$

and as for (8) the equation

$$L_{t+1}^{(b-a)} = mL_t^{(b-a)+i} \qquad (38)$$

may be derived from (37). This indicates a linear relation= ship between $L_{t+1}^{(b-a)}$ and $L_t^{(b-a)}$ with slope $m = e^{-K(b-a)}$ and intercept

$$i = L_\infty^{(b-a)} \left(1-e^{-K(b-a)}\right)$$

Expanding both sides of (37) to the power $\frac{1}{b-a}$ we have an expression relating length to age that is:

$$L_t = L_\infty\left(1-e^{-K(b-a)(t-t_o)}\right)^{\frac{1}{b-a}}$$

The point of inflection of the above equation may be located by differentiating twice and equating the resulting terms to zero.

This gives the following function,

$$t_i = t_o - \frac{\text{Log}_e(b-a)}{K(b-a)} \qquad (39)$$

where t_i is the age at the inflection point.

Thus (37) and (38) may be used to describe growth data showing an inflection point on the curve of L_t on t. If such an inflection occurs, then the parameter (b-a) will be less than one but positive.

Inspection of (37) and (38) will show that when b-a = 1 these expressions will reduce to the more well known von Bertalanffy equations (5) and (8). Whereas the values of a and b demanded by von Bertalanffy's derivation were 2 and 3 respectively (see derivation of (3)) the generalized equation (37) requires only that b-a=1 irrespective of the individual values of a and b. The Bertalanffy equation (5) is everywhere concave with no inflection point. This may be illustrated by equation (39) for, as (b-a) approaches 1, t_i tends to t_o.

The Logistic or Autocataytic equation may also be derived from (36). If b-a is negative, then

$$L_t^{(a-b)} = \frac{1}{\frac{E}{K} - \left[\frac{E}{K} - 1/L_o^{(a-b)}\right] e^{K(a-b)t}}$$

$$= \frac{\frac{K}{E}}{1 - \left[1 - \frac{K}{EL_o^{(a-b)}}\right] e^{K(a-b)t}}$$

$$= \frac{\frac{K}{E}}{1 + \left[\frac{K}{EL_o^{(a-b)}} - 1\right] e^{K(a-b)t}}$$

which is the generalized Logistic equation with an upper asymptote at $\frac{K}{E}$ (when $t = \infty$) and a lower asymptote at zero

(when $t = -\infty$). It should be noted that in this equation both E and K must be minus. Physiologically this does not make sense, and the logistic equation is therefore purely empirical.

When a = b, equation (36) becomes insoluble. However, from integration of the rate equation it can be shown that this condition leads to an exponential growth curve. This is derived as follows:

From (35), when a = b,

$$\frac{dL}{dt} = L\,(E-K)$$

$$\frac{dL}{L} = dt\,(E-K)$$

Integrating the above:

$$\mathrm{Log}_e L_t = t(E-K) + c, \text{ and}$$

c may be evaluated by placing

$$t = o \text{ thus } c = \mathrm{Log}_e L_o \quad .$$

The above becomes

$$\mathrm{Log}_e L_t = t(E-K) + \mathrm{Log}_e L_o$$

or $$L_t = L_o e^{t(E-K)} \qquad (41)$$

Equation (41) has been used to describe growth in weight by RICKER (1944) and BRODY (1945) has used it to represent the accelarating phase of growth i.e. the growth often occurring in extremely young animals.

When b-a→o, a different solution to (35) can be shown, which gives the Gompertz function. This function may therefore be regarded as a limiting form of the generalized von Bertalanffy when b - a→ o. TAYLOR (1962-) does not derive the Gompertz equation but this has been done by RICHARDS (1959) from equation (31). Using Richards approach the Gompertz function was obtained from equation (35) as follows.

$$\frac{dL}{dt} = EL^{(a-b+1)} - KL \qquad (35)$$

$$= KL\left(\frac{E}{K}\ \frac{L^{(a-b+1)}}{L} - 1\right)$$

$$= KL\left(\frac{E}{K\ L^{(b-a)}} - 1\right)$$

but $L_{\infty}^{(b-a)} = \frac{E}{K}$, and letting

$$K = \frac{k}{(b-a)}$$

therefore $\frac{dL}{dt}\ \frac{1}{L} = k\left(\frac{L_{\infty}^{b-a} - 1}{(b-a)}\right)$

$$\underset{(b-a)\to o}{\text{Lim}}\ \frac{dL}{dt}\ \frac{1}{L} = k\text{Log}_e\ \frac{L_{\infty}}{L}$$

$$\frac{dL}{dt} = kL\ \text{Log}_e\ \frac{L_{\infty}}{L} \qquad (43)$$

Considering the Gompertz function

$$L_t = Be^{-ce^{-kt}} \qquad (21)$$

when $t = \infty$,

$$L_{\infty} = B$$

Thus (21) can be expressed as

$$L_t = L_\infty e^{-ce^{-kt}}$$

where c reflects the choice of zero on the time axis. The above may then be differentiated as follows

$$\frac{dL}{dt} = L_\infty e^{-ce^{-kt}} \quad kce^{-kt}$$

$$= kL_t ce^{-kt}$$

but $\frac{L_t}{L_\infty} = e^{-ce^{-kt}}$

therefore

$$\frac{L_\infty}{L_t} = e^{ce^{-kt}}$$

$$\text{Log}_e \frac{L_\infty}{L_t} = ce^{-kt}$$

thus $\frac{dL}{dt} = kL_t \text{Log}_e \frac{L_\infty}{L_t}$

which is (43).

The parabolic growth curve of PARKER AND LARKIN (1959) may also be derived from rate equation (35).

The above authors obtained the parabolic expression by regarding growth as purely additive, that is the effect of catabolism is not considered. In mathematical terms therefore K of (35) is equal to zero. Assuming b>a and K = o (35) becomes

$$\frac{dL}{dt} = EL^{(a-b+1)}$$

which is integrated as follows:

$$L_t^{(b-a)} = (E\ t+c)\ (b-a)$$

if $t = o \quad c = \frac{L_o^{(b-a)}}{b-a}$

thus $L_t^{(b-a)} = (b-a)Et + L_o^{(b-a)}$ (42)

This equation is essentially the same as (25) but is expressed in terms of length not weight.

The estimation of the parameters of the generalized von Bertalanffy growth equation will now be dealt with.

SOUTHWARD And CHAPMAN (1965) recently utilized the generalized Bertalanffy equation in an exhaustive analysis of the growth rate of the Pacific Halibut. Growth parameters were estimated by means of a computer using the method of least squares. The program was so arranged as to vary the four parameters to obtain those values which minimized the term

$$\left[L_t - \left(L_\infty^{(b-a)} - (L_\infty^{(b-a)} - L_o^{(b-a)})\, e^{k(b-a)t}\right)^{\frac{1}{b-a}}\right]^2$$

Should a computer not be available, or the data not be suitable for such analysis the simpler though less precise method of TAYLOR (1962) may be applied. It has been shown that the linear function.

$$L_{t+1}^{(b-a)} = mL_t^{(b-a)} + i \qquad (38)$$

may be derived from the generalized equation (37) when $a < b$. This is directly comparable to the equation

$$L_{t+1} = mL_t + i$$

from which it is possible to estimate the parameters of (5). Thus similarly the parameters of (37) may be derived from (38) as follows.

If an initial plot of L_{t+1} on L_t suggests non-linearity or unrealistic values of L_∞, trail values of (b-a) should be introduced and $L_{t+1}^{(b-a)}$ plotted on $L_t^{(b-a)}$. The trial value of (b-a) providing the most realistic L_∞ dimension, (as judged from field observations) as well as a linear relationship between the two variables may then be accepted as a good estimate of the true parameter value. Estimation of the remaining parameters then easily follows from (38).

CONCLUSION

From the above review it is apparent that there is a fairly wide selection of mathematical models available for describing growth. The models range from the purely empirical to those which might well have parameters reflecting metabolic processes.

The initial development of the von Bertalanffy equation (8) was from physiological concepts, but, because the derivation requires rigid adherence to the square and cube laws of anabolism and catabolism respectively, some doubt is cast on its general applicability in other than an empirical guise. The introduction of a fourth parameter to equation (8) by TAYLOR (1962) has eradicated the restrictive square and cube assumption mentioned above.

This parameter, (b-a) represents the actual difference between the power coefficients of the physiological surface and physiological mass values expressed in terms of a length dimension.

The parameter is estimated from the data and its inclusion means that a metabolic basis may still be incorporated in the derivation of the model, even though biometric observations on the species concerned may not suggest confirmation to the square and cube rules.

Evidence to substantiate the physiological justificat- of von Bertalanffy's equation (8) is available from growth studies on the cod (Gadus callarias), TAYLOR (1958) and Pacific razor clam (Siliqua patula) TAYLOR (1959). The growth of these two species was presumably well represented by (8) and the parameter (b-a) of the more generalized equation developed later by TAYLOR may therefore be assumed to be close to one.

In both the above investigations growth data was available from various localities with different environmental temperatures and the relationship between growth parameters and temperature could thus be described.

TAYLOR (1959) presents the following equation which expresses the speeds of chemical reactions in terms of temperature:

$$S = Ae^{cT}$$

where S = speed of process at temperature T(^{o}C)

A = constant

c = the differential increase in the relative rate of change for $1^{o}C$ change in temperature, (that is tha rate of the rate of change of the chemical reaction).

Log transforming the above expression results in

$$Log_{10}S = Log_{10}A+CT$$

where $C = cLog_{10}e$

This expression is linear.

Thus if growth parameters reflect metabolic rates, and therefore have a physiological meaning, their log transformed relationship with environmental temperature should in turn be linear. This was actually found to be the case with both the rod and the razor clam. In both instances the Log_{10} of K and the Log_{10} of L_{∞} (1-K) (see equation 8) were linearly related to the environmental temperature, the correlation coefficients of all four plots being significant at the one percent level.

It is therefore evident that under certain circumstances the generalized von Bertalanffy equation of TAYLOR (1962) may well have parameters which are physiologically meaningful. Other functions derived from TAYLORS rate equation (34) would seem to be more empirical. The logistic curve as derived by TAYLOR requires that coefficient a, the power coefficient of the length/"physiological surface" relationship, be larger than its counterpart for the length "physiological mass" function. This is unlikely to ever occur and as such this growth expression must be regarded as empirical. In addition the parameters E and K must both

be minus, a condition which in no way has a physiological interpretation. In practice this equation is in any case seldom used.

To derive the parabolic curve, TAYLOR sets $a < b$ and $K = o$, that is growth is regarded as purely additive. PARKER and LARKIN (1959), who originally derived the above function to describe the growth of fish such as salmonoids, which exhibit a growth stanza effect, comment as follows on the parameters of the equation. "Under the circumstances it would seem appropriate to choose a method of depicting growth which (1) summarizes the complex of interacting factors in each stage of growth into a minimum number of constants which reflect the combined effects of both ecological and physiological factors, (2) chooses as a basic premise the widely accepted view that change in size is a function of size achieved". Interpretation of the constants of the parabolic expression is therefore extremely complicated and to a certain extent the curve must be regarded as being empirical.

The remaining growth function, the Gompertz equation has been given a physiological interpretation by WEYMOUTH, MCMILLIN and RICH (1931) who maintain that growth is an additive process which is continually slowing down. BEVERTON and HOLT (1957) acknowledge this, but point out that no attempt is made to interpret the coefficients of the equation on a physiological basis, and as such the equation may be regarded as empirical. In addition they mention that abundant physiological evidence exists to indicate that growth is not merely additive but that a breakdown of body material must also be taken into account.

LITERATURE CITED

BEVERTON, R.J.H. and S.J. HOLT, 1957 - On the dynamics of exploited fish populations. Fish Invest. London, Ser. II 19: 553

BERTALANFFY, L. von 1934 - Untersuchungen über die gesetzlichkeit des wachstums. 1. Treil. Allegemeine grundlagen der theorie; mathematische und physiologische gesetzlichen der wachstums bei wassertieren. Archiv. f. Entwicklungsmech., 131: 613-52

BERTALANFFY, L von, 1938 - A quantitative theory of organic growth (Inquiries on growth lans. 11). Human Biology, 10 (2): 181-213.

BRODY, S 1945 - Bioenergetics and growth Reinhold Publishing Corporation, New York. pp. 98

FRY, F.E.J. 1957 - Aquatic respiration of fish. In The physiology of fishes I. (Ed. M.E. Brown) Academic Press, N.Y. 1-63.

GULLAND, J.A. and S.J. HOLT 1959 - Estimation of growth parameters for data at unequal time interval J. Cons. perm. int. Explor. Mer 25: 47-49

SOUTHWARD, G.M. and D.G. CHAPMAN, 1965 - Utilization of the Pacific halibut: Study of Bertalanffys growth equation. Rept. Int. Habitat Comm. 39: 33pp.

TAYLOR, C.C. 1958 - Cod growth and temperature. J. Cons. int. Explor. Mer. 23: 366-70

TAYLOR, C.C. 1959 - Temperature and growth - the Pacific razor clam. J. Cons. int. Explor. Mer. 25: 93-101

TAYLOR, C.C. 1962 - Growth equations with metabolic parameters J. Cons. int. Explor. Mer. 27: 270-286.

WALFORD, L.A. 1946 - A new graphic method of describing the growth of animals. Biol. Bull. 90(2): 141-147

WEYMOUTH, F.W. and MCMILLIN, H.C. 1930 - Relative growth and mortality of the Pacific razor clam (Liliqua paticla Dixon) and their bearing on commercial fishery. Bull. U.S. Fish. Comm. 46: 543-67

WEYMOUTH, F.W., MCMILLIN H.C. and W.H. RICH, 1931 - Latitude and relative growth in the razor clam Liliqua paticla J. Exp. Biol. 8(3): 228-49.

SUMMARY OF FINDINGS

1. Male and female H. midae are equally represented and become sexually mature at the same size. At Stony Point fifty per cent of the population is sexually mature at a body weight of 140 gm and an age of 7 years (shell breadth 8.0 cm). At 275 gm (age 11 years, shell breadth 10.5 cm) one hundred per cent are mature.

2. Abalone may spawn twice a year, that is during late spring/early summer and in autumn at Stony Point. Spawning west of Cape Point seems to occur earlier in the year in late winter. Only one spawning per annum was recorded at Sea Point.

3. Spawning is more intensive at Stony Point than at Dassen Island or Sea Point and this may contribute to the differences in productivity noted in these areas.

4. Seasonal temperature changes are associated with spawning at Stony Point. Spawning took place when tempera= tures were increasing as well as decreasing. The less intense spawning west of Cape Point is attributed to the lack of marked seasonal temperature changes.

5. The testes simply consist of a lumen through which run vertical connective tissue tubules. Lacuna occur within the tubules. Spermatogenesis takes place on the outer wall of the tubule and sperm fill the lumen in ripe tests.

6. In the lumen of the ovary the connective tissue sheets of the trabeculae are arranged as a series of polyhedral vertical columns. Within these the eggs develop from the germinal epithelium covering the trabeculae.

8. In the ripe ovary two discrete egg sizes occur. These groups are released on successive spawnings. During spawning therefore, disruption of the extensive ovary must be kept to a minimum for the eggs of the next spawning must be maintained. A relatively free passage for the eggs is provided for by the fact that near the digestive gland the intervening walls of the trabeculae columns break down.

9. The walls of the gonads are not contractile. The aductor muscle and the shell are used to exude gametes.

10. Fertilization is external and abalone therefore produce large numbers of eggs. The linear relationship between fecundity and body weight was found to be

$$F = .0198\ W - 2.196$$

where F = fecundity in millions of eggs
W = body weight in gm.

The relationship between fecundity and shell breadth was

$$F = .0004257\ B^{3.787}$$

where F = fecundity in millions of eggs
B = shell breadth

Fecundity is therefore approximately proportional to ovary volume and this is due to the columnar arrangement of the trabeculae. In addition constriction of the lacuna in the trabeculae by egg masses probably limits egg production.

11. A seasonal growth model was estimated for abalone. This showed that faster growth occurred during winter and to a lesser extent spring. These variations coincide with phases of the breeding cycle. Slow growth could be associated with period of gonad recovery while faster growth took place when gonad bulk was high and constant.

17. Two linear equations were also required to describe the relationship between shell length and shell depth. The inflextion point was at 11.0 cm. and the interpretation of the ratios of absolute and relative growth rates is similar to that discussed in 15. No explanation can be offered for this abrupt change in the growth pattern.

18. Abalone from the Atlantic stations weighed more per unit length than those collected east of Cape Point. This was due to increased shell depth rather than to wider shells being found at Dassen Island and Sea Point.

19. The vertical distribution of abalone seems broadly associated with size. Small abalone are found beneath stones in the shallows. Intermediate sizes, that is up to about 10 cm. shell breadth, are more commonly found on shallow reefs but larger abalone are found within a wide depth range down to about 75 feet. The maintenance of this pattern requires that abalone move to ensure recruitment to reefs exploited by the fishery.

20. From a tagging programme movements of over 300 yds. were recorded within 104 to 558 days. The mean rate of movement of abalone between 5.6 and 12.3 cm. shell breadth was about 1,000 yds. per annum during winter. It is not known whether seasonal variations of this rate occur. There are indications that the rate of movement is correlated with size within the above range. The proportion of abalone which move was also found to be high. Of 59 returns found during one search sixty four per cent had moved away from the tagging area.

21. A review of biological growth models is presented in the thesis. It is especially interesting to note that some of the more common models in use can be derived from generalized equations presented by Richards (1959) and Taylor (1962). A second important point dealt with is whether the parameters of mathematical growth functions reflect metabolic rates and therefore have a physiological meaning.

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