NOTES ON THE BIOLOGY OF SOME ESTUARINE BIVALVES

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ABSTRACT

Studies on bivalves in the Swartkops estuary have indicated that spatfall occurs during late summer. After adult populations had been decimated by floods in 1971 spat made up a large proportion of the bivalve population in 1973. Growth rates vary at different intertidal levels and in different parts of the estuary and growth has been shown to vary seasonally. In two species age determinations from growth rings corresponded well with age determinations from size frequency histograms.

INTRODUCTION

The growth rates and population dynamics of bivalves in estuaries and shallow seas in the Northern Hemisphere have been extensively studied. In these regions bivalves occur in densities up to 7 000/m^2 (Stephen 1928) and densities of 1 000/m^2 are common. Further, growth studies on these animals have been facilitated by the usually distinct growth rings, which are laid down in bivalve shells as a result of the cold winter conditions (Green 1957, Holme & McIntyre 1971). In South Africa, bivalves are relatively uncommon and the winters mild in comparison with those experienced for example in Northern Europe. Because of this, no South African bivalves, except *Donax serra* Röding (de Villiers, personal communication), have had their growth rates studied.

The burrowing bivalve populations of the Swartkops estuary (described by McLachlan and Grindley, in press), though considerably smaller than those of estuaries in the Northern Hemisphere, are sufficiently large to enable a study of their growth rates and related factors to be made. In this article the following parameters will be discussed: spat fall, vertical and horizontal size variations in bivalve populations and the growth rates of some common species.

This work formed part of an M.Sc. thesis on burrowing bivalves in the Swartkops estuary. It is being published in several parts in this journal as well as in the form of some short notes in the *Strandloper*, the publication of the Conchological Society of South Africa.

MATERIALS AND METHODS

Spat sampling in 1972

During May 1972, nine stations (Figure 1, stations 1–10 except 7) in the estuary were sampled for spat (newly settled, postlarval bivalves). At each station, four areas, each 0,25 m^2 in extent, were sampled to a depth of approximately 50 mm. The substrate sampled was passed through a sieve of area 0,25 m^2, and mesh aperture 1 mm. Specimens longer than 4 mm were measured to the nearest 0,1 mm with sliding callipers. Those smaller than 4 mm were measured to the nearest mm on a measuring board. Length in all cases has been taken as the longest antero-posterior diameter of the shell.

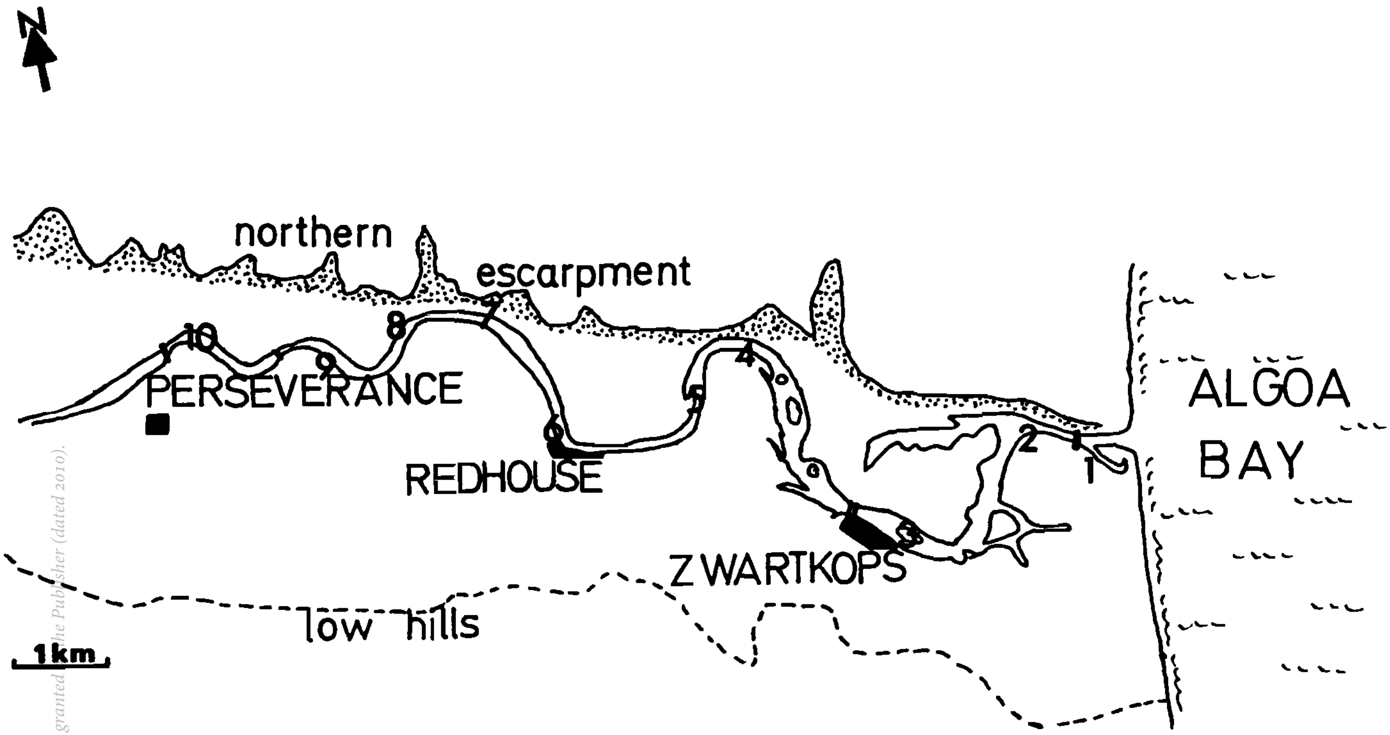

Figure 1
Map of the Swartkops estuary showing sampling stations mentioned in the article.

As workers have generally found spat-fall to occur in summer and/or spring (Stephen 1928, 1931, 1932, Green 1957, Ansell 1961), it was thought that by May (early winter) the spat would have attained sufficient size to make this sampling accurate. Some small spat may nevertheless have been lost by passing through the sieve. Upper limits on sizes accepted as spat were based on studies to be mentioned later in this publication, and were as follows:

Species	*Upper size limit*
Dosinia hepatica (Lamy)	7,0 mm
Macoma litoralis Krauss	7,5 mm
Solen corneus Lamy	27,0 mm
Solen capensis Fischer	27,0 mm
Psammotellina capensis Sowerby	7,0 mm
Eumarcia paupercula (Holten) (*Pitaria kochii*)	9,0 mm

Size distribution as related to depth in the substratum

During February 1971 and September 1972 stations 7, 8 and 9 were sampled in order to obtain an idea of the vertical positions different species occupied in the mud. This was done by removing and sieving different depths of mud with sieves 0,25 m^2 in area and with mesh apertures of 4 mm and 1 mm. The method was as follows. First the top 3 cm of mud would be removed and sieved. Bivalves so obtained would be placed in a bottle labelled 0–3 cm. Then the next 3 cm of mud would be removed and treated similarly and the bivalves obtained placed in a bottle marked 3–6 cm. In this manner an area of 500 × 500 mm would be excavated to a required depth. Six such areas were excavated at LWN, but using different depth intervals, and the results pooled. This method is, however, not very accurate for species which can move rapidly up and down their burrows such as *Solen* spp. In such cases this method gives an indication of the depth of the burrow but not of the normal position an animal occupies within it.

All bivalves were measured to the nearest 0,5 mm on a measuring board.

In order to see if the depths at which different individuals of each species occurred in the mud were related to their sizes, animals from different levels were compared using t-tests wherever possible.

Horizontal and intertidal size distribution

All bivalves obtained during the surveys mentioned by McLachlan & Grindley (in press) and during three transects carried out in the middle reaches of the estuary were measured to the nearest 0,5 mm. Populations of different species at different places and tidal levels were compared by means of t-tests. This was done in order to determine whether sizes (*i.e.* growth rates) varied in different parts of the estuary.

Growth Rates

Only the following species could be obtained in sufficient numbers for growth studies: *Solen corneus*, *Macoma litoralis* and *Dosinia hepatica*. All specimens were collected near the LWS level at Stations 5 and 6. As no significant differences between the sizes of the above-

TABLE 1

RESULTS OF A SPAT SURVEY, SHOWING TOTAL NUMBERS PER m^2, THE PERCENTAGE OF THE POPULATION MADE UP BY SPAT AND THE MEAN SIZES OF SPAT (IN mm) OF EACH SPECIES AT EACH STATION.

	PSAMMOTELLINA			*DOSINIA*			*MACOMA*		
Station	*No.*	*% Spat*	*Spat Mean*	*No.*	*% Spat*	*Spat Mean*	*No.*	*% Spat*	*Spat Mean*
1	—	—	—	—	—	—	—	—	—
2	47	68	4,88	—	—	—	—	—	—
3	16	100	4,44	1	100	3,00	—	—	—
4	—	—	—	6	84	3,90	2	100	3,50
5	—	—	—	50	80	3,35	40	70	4,99
6	—	—	—	23	91	3,90	77	86	3,67
8	—	—	—	52	100	3,81	12	94	4,64
9	—	—	—	11	100	3,33	1	100	3,00
10	—	—	—	—	—	—	—	—	—

	S. CORNEUS			*EUMARCIA*			*S. CAPENSIS*		
Station	*No.*	*% Spat*	*Spat Mean*	*No.*	*% Spat*	*Spat Mean*	*No.*	*% Spat*	*Spat Mean*
1	—	—	—	—	—	—	—	—	—
2	—	—	—	—	—	—	1	100	19,5
3	5	100	14,4	—	—	—	—	—	—
4	33	90	12,33	—	—	—	—	—	—
5	49	97	14,30	—	—	—	—	—	—
6	26	100	13,16	5	80	6,60	—	—	—
8	6	100	12,80	—	—	—	—	—	—
9	—	—	—	—	—	—	—	—	—
10	—	—	—	—	—	—	—	—	—

mentioned species at these stations had been found, pooling of the results was considered permissible. Shell lengths and growth-ring lengths were both measured to the nearest 0,1 mm with sliding callipers in *Dosinia hepatica* and *Macoma litoralis*. In *Solen corneus* measurements were taken to the nearest 1 mm.

RESULTS

Spat fall

The results of the sampling for spat of the following species are shown in Table 1: *Psammotellina capensis, Dosinia hepatica, Macoma litoralis, Solen corneus, Pitaria kochii* and *Solen capensis*. This shows the number of spat recorded per square metre, the percentage of the individuals of each species that fell in the spat size-range and the mean lengths of the spat at each station.

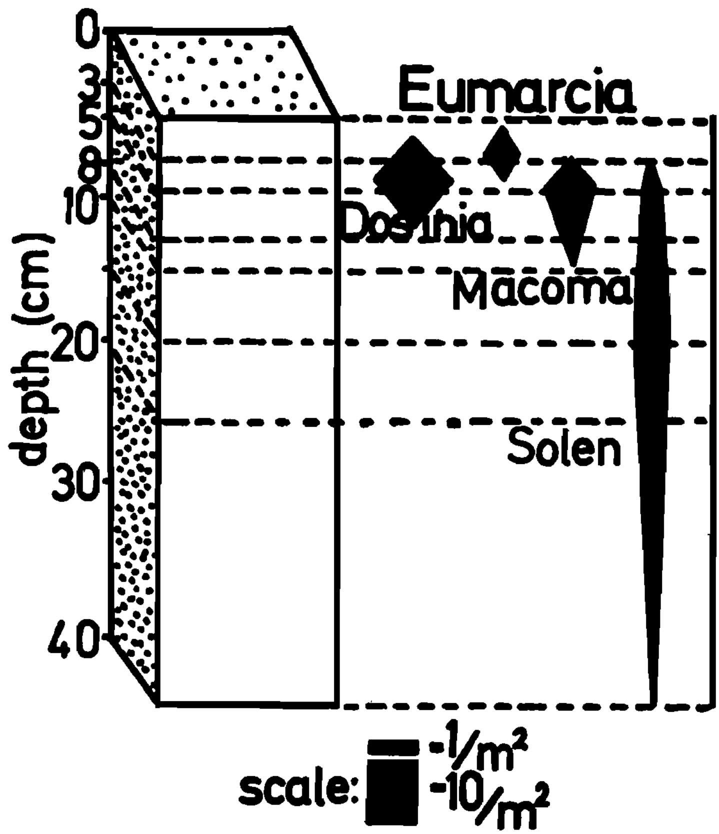

FIGURE 2
Diagram of vertical sections at Stations 7 and 9 showing the vertical distribution of four bivalve species in the substrate.

If any small spat did pass through the sieve the mean spat sizes recorded would be higher than the actual mean sizes. Adult populations were small after the floods of 1971 and there should thus have been adequate settling area for the spat but the results in Table 1 indicate a moderate spat fall. The spat numbers and sizes recorded indicate that the spat fall probably occurred during February and March as anticipated.

Vertical size distribution

The distribution patterns found from the vertical sections are shown in Figure 2. This illustrates the depths at which different species lie in the mud at LWN. Figures 3 and 4 show the results of size analyses of these vertical sections for *Dosina hepatica* and *Macoma litoralis* respectively. Figure 2 illustrates adult distribution only (*i.e.* specimens being retained by a 4 mm sieve) while Figures 3 and 4 include all sizes. Figures 3 and 4 show the means, standard deviations and ranges of sizes of specimens from different depth ranges. For both *Dosinia* and *Macoma*, shallow-lying specimens were found to be significantly smaller ($p = 0,01$) than deeper-lying ones.

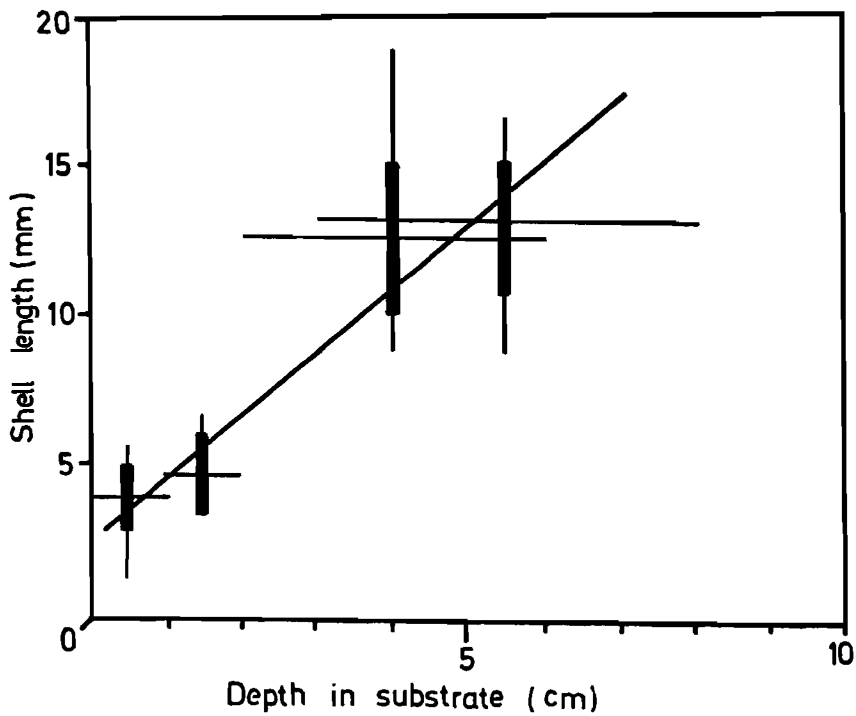

FIGURE 3
Plot of shell lengths of *Dosinia hepatica* from different depths in the substrate. The means, S.D.'s and ranges of shell lengths at each depth range are shown.

Horizontal and intertidal size distribution

Only the populations of *Dosinia hepatica*, *Macoma litoralis* and *Solen corneus* were large enough to allow statistical analysis. All three species occur along more than 12 km of the estuary and all occupy the intertidal areas between the low tide mark and the lower edge of the *Spartina capensis* Nees zone. Because of the great range of sizes encountered in *Solen corneus* no significant comparison could be made. In both *D. hepatica* and *M. litoralis* the following tendencies were found significant:

From the surveys:

1. Specimens of *Dosinia* collected at LWS at Station 5 (X = 14,5 mm) were significantly larger (p = 0,01) than those collected at LWS at Station 9 ($\bar{X}$ = 12,8 mm) ($\bar{X}$ = mean).
2. Specimens of *Macoma* collected at LWS at Station 6 ($\bar{X}$ = 16,1 mm) were significantly (p = 0,01) larger than those from LWS at Station 8 ($\bar{X}$ = 15,0 mm).

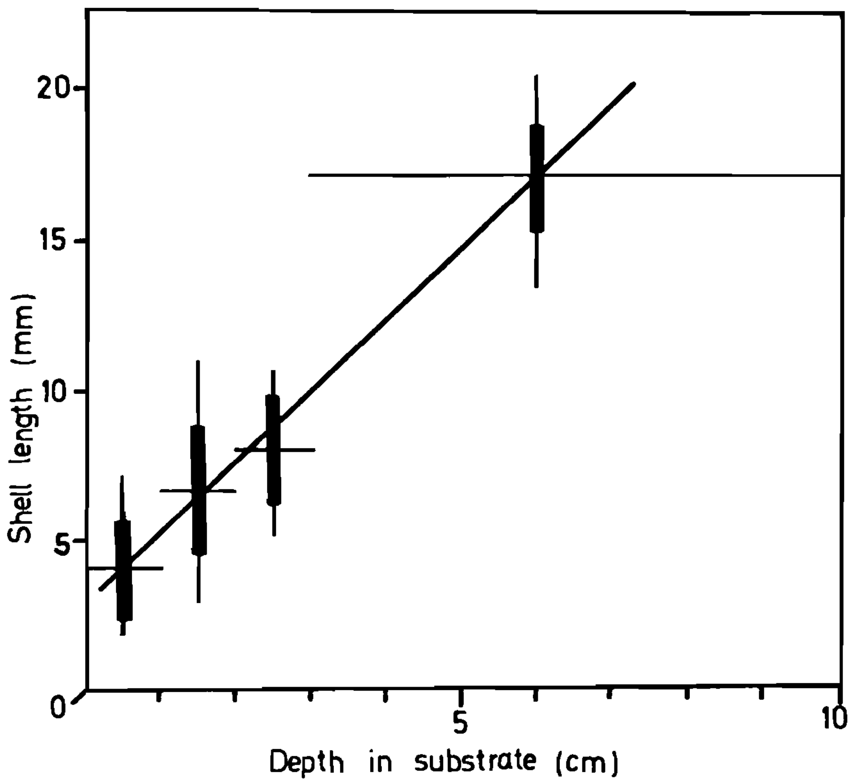

FIGURE 4

Plot of shell lengths of *Macoma litoralis* from different depths in the substrate. The means, S.D.'s and ranges of shell lengths at each depth range are shown.

From the transects:

3. Specimens of *Dosinia* at LWS at Station 5 (X = 14,2 mm) were significantly larger (p = 0,01) than those 30% up the intertidal zone at the same station (X = 13,25 mm).
4. Again at Station 9, *Dosinia* at LWS (X = 12,6 mm) were significantly larger (p = 0,01) than those 30% up the intertidal zone (X = 11,8 mm).
5. At Station 9, *Macoma* at LWS ($\bar{X}$ = 17,7 mm) were significantly larger (p = 0,01) than those 30% up the intertidal zone ($\bar{X}$ = 14,9 mm).

Growth rates

In *Solen corneus* growth-rings were too indistinct and irregular to be of any aid in studying growth. Only size-frequency histograms have therefore been used for growth studies in this species.

Figure 5 is a size frequency histogram for 164 *Solen corneus* obtained between Stations 5 and 6 during January 1972. Class intervals of 5 mm have been used here. Figure 6 is a similar

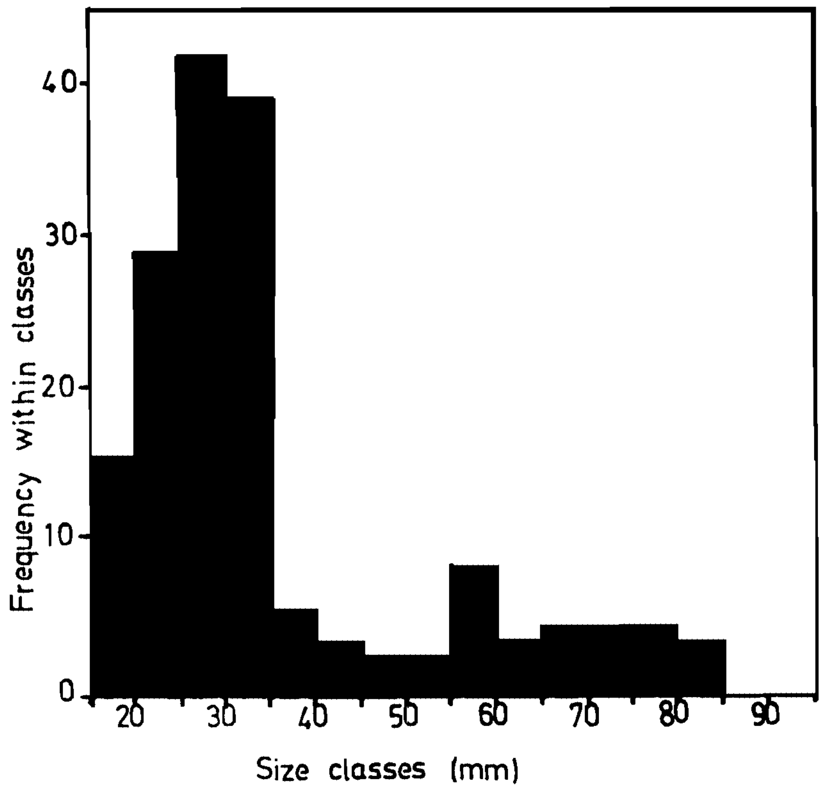

FIGURE 5
Size-frequency histogram for 164 *Solen corneus* from Stations 5 to 6 during January 1972.

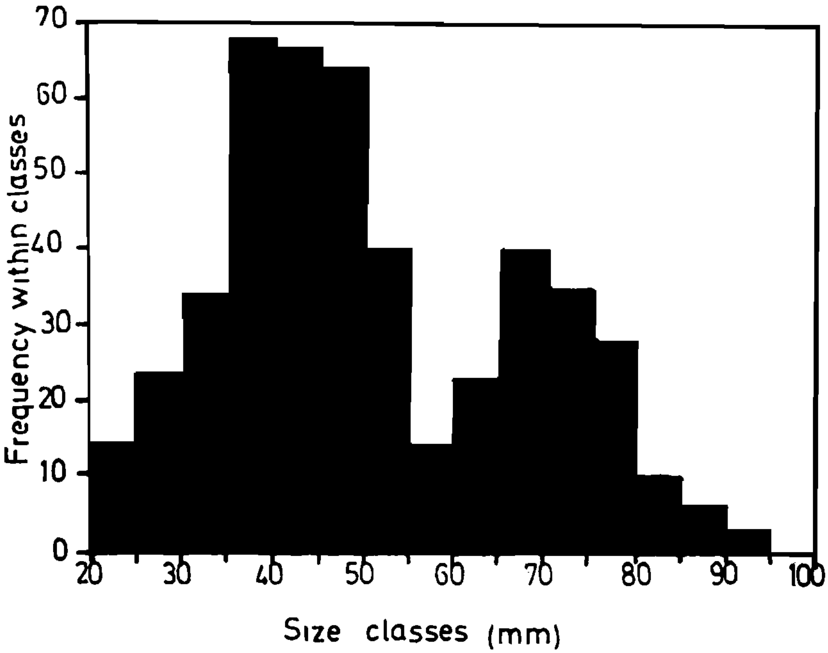

FIGURE 6
Size-frequency histogram for 470 *Solen corneus* from Station 5 during April 1972.

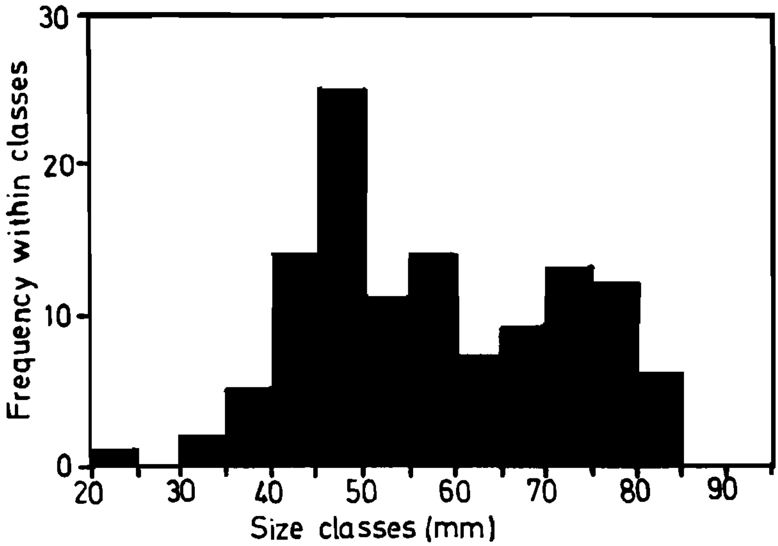

FIGURE 7
Size-frequency histogram for 119 *Solen corneus* from Station 5 during September 1972.

histogram of 470 animals collected during April; Figure 7 is based on 119 animals collected during September 1972; and Figure 8 is based on 165 animals collected during January 1973. It can clearly be seen in these figures how the first year peak shifts from 28,5 mm during January to 44,0 mm during April, to 48,0 mm during September and finally to 56 mm during the following January. Similarly the second year peak shifted as follows: 58,0–69,0–75,0–83 mm. This seasonal change in growth rate of the 1st year class is shown in Figure 9.

Assuming that spat fall occurs on March 1 each year, Figure 10 has been constructed by plotting the estimated age against the shell lengths of the above-mentioned peaks. The values obtained from Figure 10 have been used in Table 2, which is a list of estimated shell lengths at a series of ages in *Solen corneus*.

From Figures 5–8 it can be seen that the 1971 year class of *Solen corneus* was a relatively good year class and this indicates a relatively heavy spat fall in 1971. The 1970 year class (second

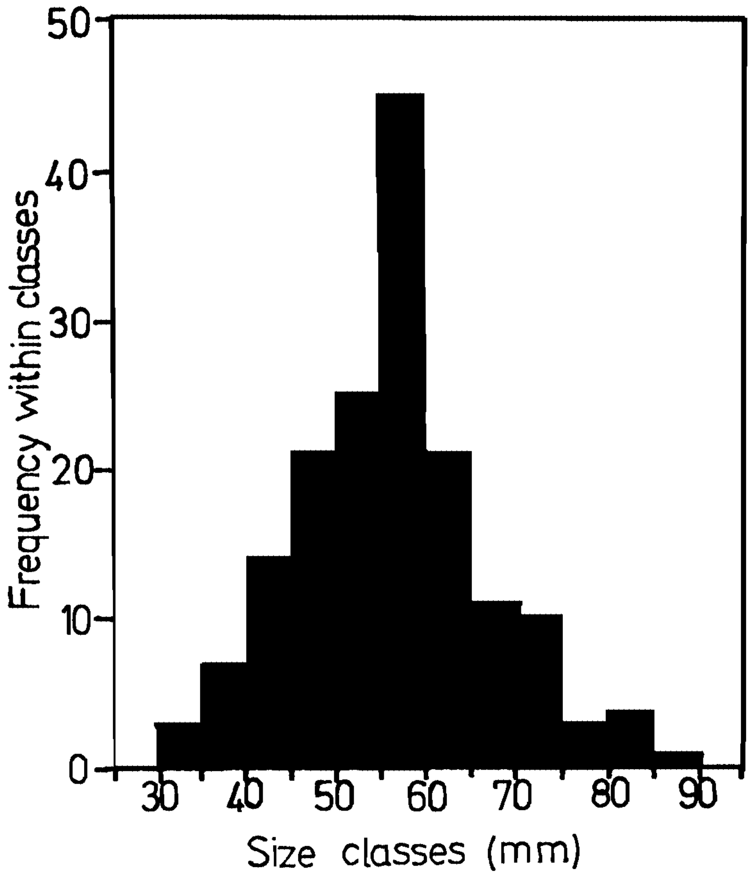

FIGURE 8
Size-frequency histograms for 165 *Solen corneus* from Station 5 during January 1973.

peak in Figure 5) also appears to have been good. Without a knowledge of mortality rates it can, however, not be compared with the 1971 year class. The largest living specimens of this species found in the estuary were 90–93 mm long and would have been four to five years old.

In *Macoma litoralis* growth-rings are distinct enough to be useful in growth studies. Growth studies on this species have therefore been based on growth rings and size-frequency histograms. Figure 11 is a size-frequency histogram for 196 specimens of *Macoma litoralis* taken from Stations 5 and 6 during April 1972. Here 1 mm class intervals have been used. Figure 12 is a similar histogram except that growth-ring lengths and not shell lengths have been used. These rings were measured on approximately 80% of the 196 specimens which had distinct growth-rings. It has been assumed that these growth-rings are laid down on July 1 each year. Figure 13 is a plot of the modal values from Figures 11 and 12 against the estimated ages of the specimens making up these modes. The broken line in Figure 13 is a growth curve taking into account the seasonal variation in growth rates. Based on Figure 13, Table 2 gives the estimated shell lengths of *Macoma litoralis* at a series of ages. From Figure 11 it appears that the 1971 year class of *Macoma litoralis* (peak at 9,0 mm) was small. This is partly due to many of the smaller of these specimens being lost by passing through the collecting sieve. The 1970 year class (peak at 13,5 mm) was poor, while the 1969 (peak at 17,2 mm) and 1968 (peak at 19,5 mm) year classes seem to have been very good. The largest specimens of *Macoma litoralis* recorded alive at Stations 5 and 6 were 24,0–24,6 mm long and were probably five to six years old.

In *Dosinia hepatica* growth-rings are also sufficiently distinct to be used in growth studies.

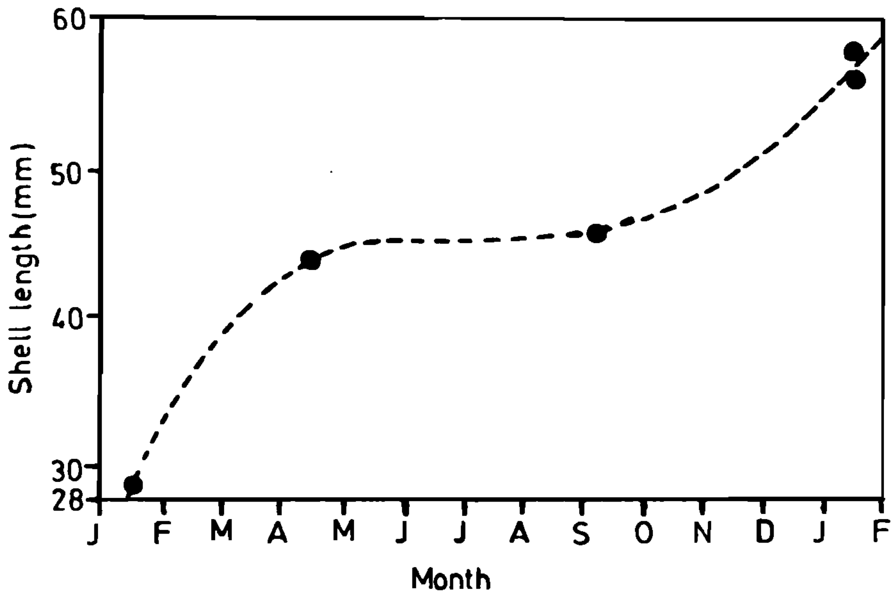

FIGURE 9
Mean shell lengths of the first year class of *Solen corneus* at different times over a period of a year. Based on peak values from Figures 5, 6, 7 and 8.

Figure 14 is a size-frequency histogram for 204 specimens collected at Stations 5 and 6 during April 1972. Class intervals of 1 mm have been used here. Figure 15 is a similar histogram but with growth-ring lengths plotted instead of shell lengths. These growth-rings were measured on those of the above-mentioned 204 specimens which had distinct rings. The modal values in Figures 14 and 15, obtained by means of cumulative curves, have been plotted against estimated ages in Figure 16, and the values in Table 2 have been taken from this figure.

In Figure 14 the 1971 year class (mode at 10,0 mm) of *Dosinia* appears to have been poor although this was probably due to some extent to small specimens passing through the sieve. The 1970 (mode at 13,5 mm) and 1969 (mode at 17,5 mm) year classes were both good, especially the 1969 class. The largest living specimens of *Dosinia hepatica* recorded at Stations 5 and 6 were 21,0–21,6 mm long and were probably five to six years old.

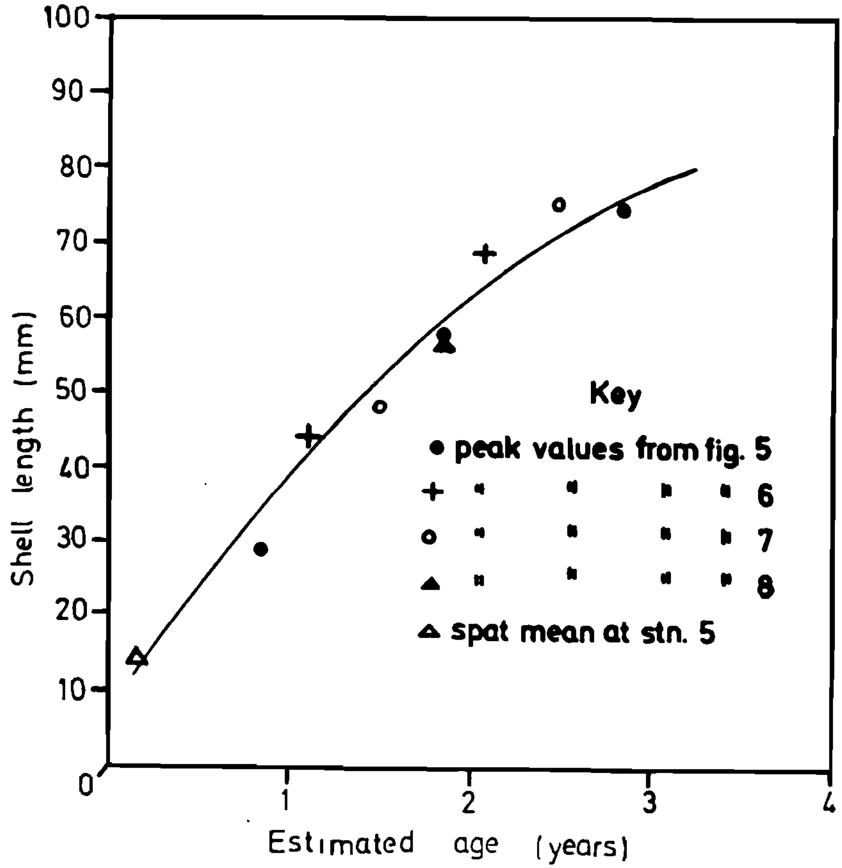

FIGURE 10
Curve of shell length against estimated age in *Solen corneus*. Based on results of spat samples of 1972 and Figures 5, 6, 7 and 8.

TABLE 2

ESTIMATED SHELL LENGTHS (IN mm) OF THREE BIVALVE SPECIES AT A SERIES OF AGES. THE RANGE OF SIZE AT EACH AGE HAS NOT BEEN CALCULATED. SEASONAL VARIATION HAS NOT BEEN ALLOWED FOR.

Age	*Solen corneus*	*Macoma litoralis*	*Dosinia hepatica*
4 months (1st winter)	20	5,5	5,5
1 year	40	8,5	9,5
16 months (2nd winter)	49	10,0	11,0
2 years	63	12,5	13,5
28 months (3rd winter)	69	14,0	14,5
3 years	76	16,3	16,5
40 months (4th winter)	79	17,2	17,5
4 years	—	19,0	19,0
52 months (5th winter)	—	20,0	19,5

DISCUSSION

Spat Fall

Spawning in bivalves generally takes place over a period ranging from a few weeks to a few months (Battle 1932, Ansell 1961) and spat sizes at any one time would thus be expected to be very variable. This has been found in the Swartkops estuary where spat generally ranged between 1 and 7 mm, except in *Solen* spp., where it varied between 8 and 27 mm, about two months after spat fall (Table 1).

Adult bivalves populations in the estuary were reduced after the floods of 1971 and as a result of this, spat made up a high proportion of the bivalve populations in the estuary in 1972 (Table 1). The spat densities were, however, very low in comparison with those recorded by Stephen (1931, 1932) in Scotland although spat sizes correspond well with those recorded in the Northern Hemisphere (*i.e.* South African and European bivalves which grow to the same sizes as adults, have spat of similar sizes).

It is interesting that *Psammotellina capensis* spat was recorded at Station 3 although adults have not been found there (McLachlan & Grindley in press). The substrate at Station 3 must be favourable for larval settlement but other factors must prevent this species from remaining and growing there. Competition with *Upogebia africana* (Ortmann) might be the factor responsible for this (McLachlan & Grindley in press). *Solen corneus* spat was also recorded at Stations 3 and 4, although adults have not been found at either of these stations. Some form of competition with *Upogebia africana* might again prevent their surviving at these stations. The same probably holds for *Macoma litoralis* whose spat was recorded at Station 4 where adults were absent. The possibility of this competition is discussed by McLachlan & Grindley (in press).

The upstream distribution of spat was in the same order as that of the adults (McLachlan & Grindley in press), with *Dosinia hepatica* penetrating the furthest up the estuary, followed by *Macoma litoralis* and *Solen corneus*. Although this distribution of spat corresponded with that of the adults, it was not quite as extensive. This is most probably due to conditions for settlement varying slightly from year to year. It would therefore appear that in the upper reaches of the

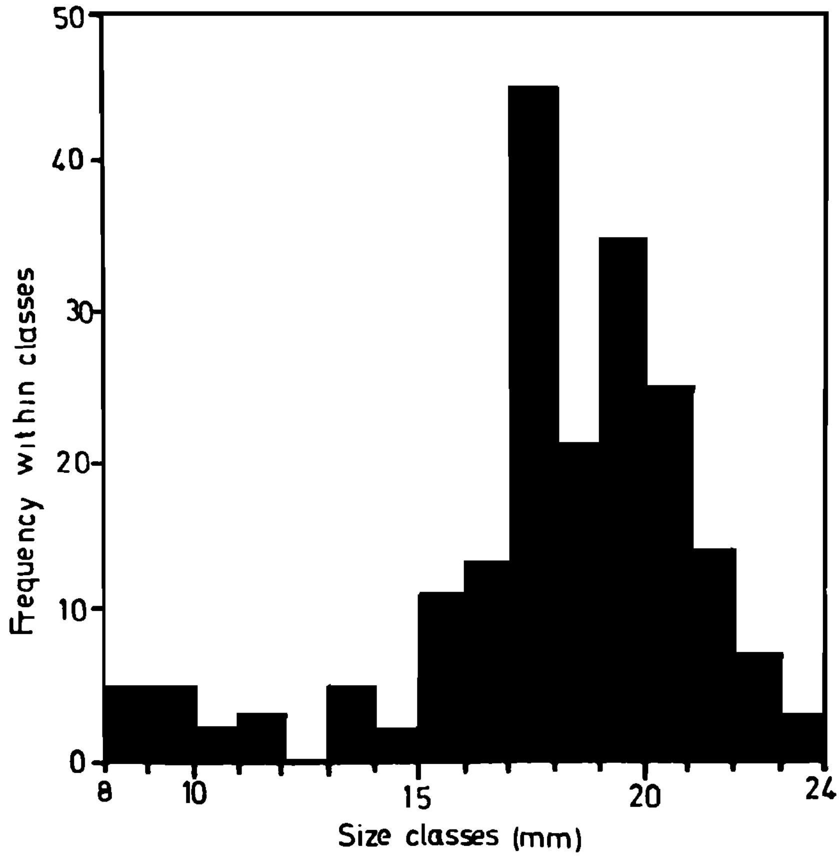

FIGURE 11
Size-frequency histogram for 196 *Macoma litoralis* from Stations 5 and 6 during April 1972.

estuary the growth and development of adults and the settling of spat are limited to the same degree. There does not appear to be any competition between the above-mentioned bivalves and *Callianassa kraussi* (Stebbing), which occupies the upper reaches. No spat of *Dosinia hepatica, Macoma litoralis* or *Solen corneus* was found at Stations 1, 2 or 10 (Table 1), indicating that either substrate or other factors at these stations are unfavourable for larval settlement.

The downstream distribution of spat of the latter three species in the lower reaches is more extensive than that of the adults of the same species. This suggests that the factor limiting the downstream distribution of adults of these species is not substrate but may be competition with *Upogebia africana*, which dominates the lower reaches (McLachlan & Grindley in press). As mentioned above, the upstream distribution appears to be limited by salinity and substrate.

Size distribution as related to depth in the substratum

As bivalves grow older and larger their siphons naturally lengthen. Larger specimens would therefore tend to lie deeper in the substrate than smaller specimens, where they would then benefit from greater protection, but still be able to extend their siphons to reach the surface. Figures 3 and 4 illustrate this tendency very clearly in *Dosinia hepatica* and *Macoma litoralis*. This tendency is probably universal in all bivalves.

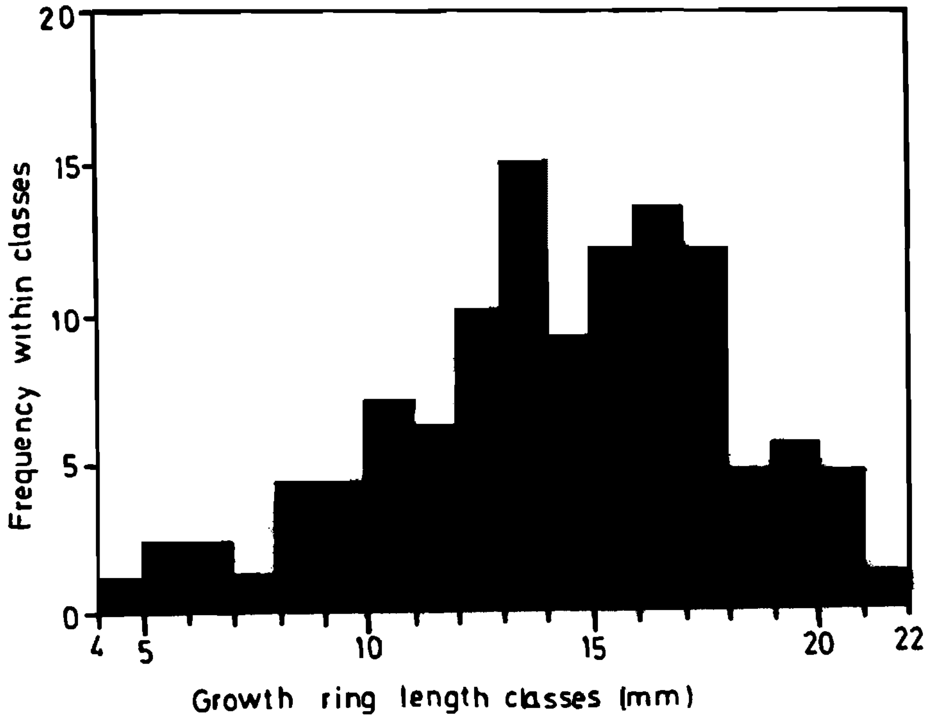

FIGURE 12
Histogram of growth ring length on some of the specimens of *Macoma litoralis* used in Figure 11.

Intertidal and horizontal size distribution

From the results of this work the following conclusions may be drawn:

First, in the case of *Dosinia hepatica*, size appears to decrease from LWS up the intertidal zone. This is most probably due to decreased growth rates as a result of decreased feeding time higher in the intertidal zone (Yonge 1949). It is very unlikely to be caused by a predominance of younger individuals above LWS. Stephen (1931, 1932) and Verwey (1952) have found the same tendency in *Cardium edule* populations. In *Tellina tenuis*, however, Stephen (1928, 1932) found that growth rates increased from low to high water levels. This inverse effect in *Tellina tenuis* was probably due to inhibition of growth at low tide levels by very high population densities (Stephen 1928, 1932). However, bivalve densities in the Swartkops estuary are more than an order of

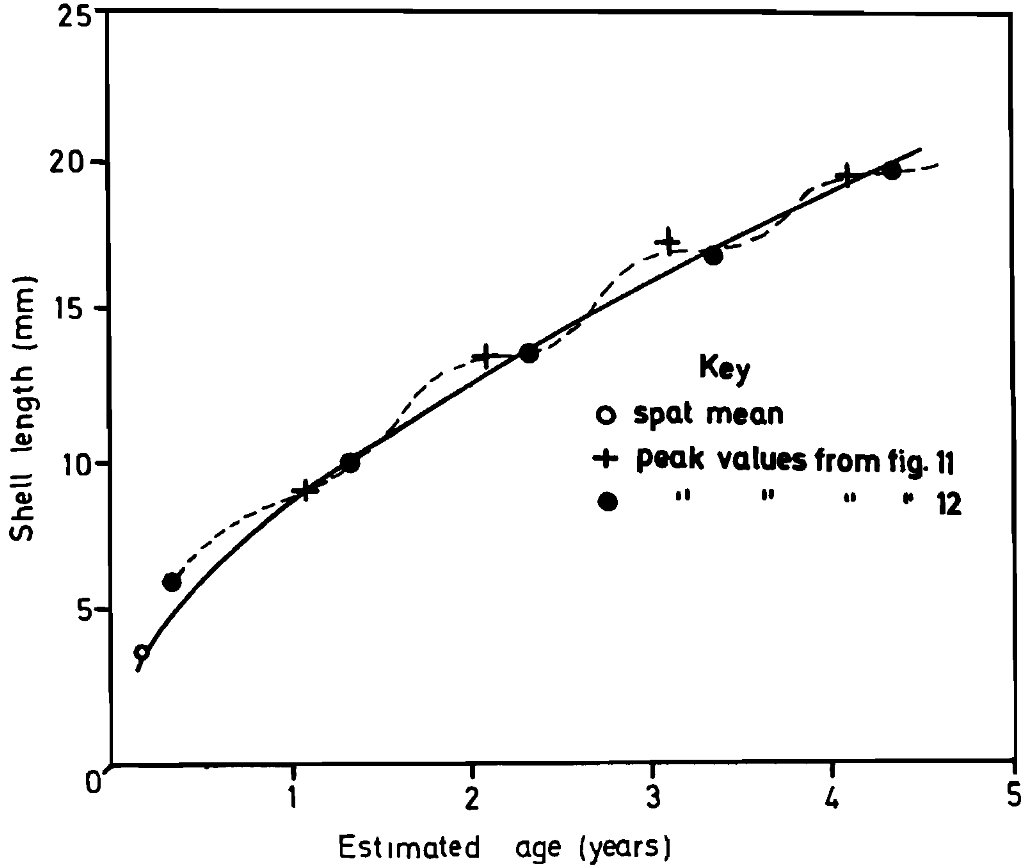

FIGURE 13

Curve of shell length against estimated age in *Macoma litoralis*. Based on the results of the spat samples of 1972 and on Figures 11 and 12. The broken line indicates the actual growth taking into account the seasonal variations in growth rate.

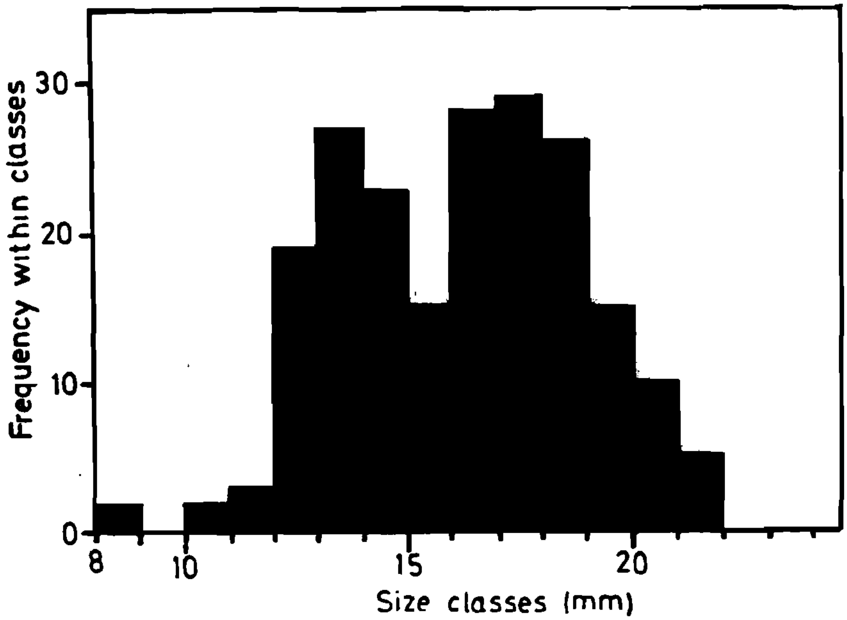

FIGURE 14
Size-frequency histogram for 204 *Dosinia hepatica* from Stations 5 and 6 during April 1972.

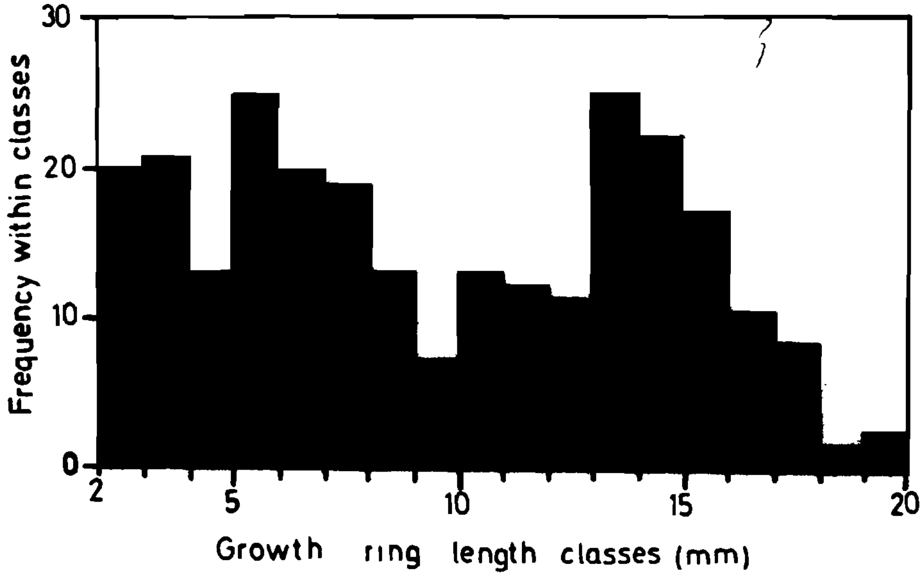

FIGURE 15
Histogram of growth ring lengths on some of the specimens of *Dosinia hepatica* used in Figure 14.

magnitude lower than those recorded in Scotland by Stephen (1931, 1932), and no such inverse effect would therefore be expected in the Swartkops estuary. Size also decreases from LWS upwards in *Macoma litoralis*. This probably holds for all bivalves in the estuary.

Second, specimens lower in the middle reaches of the estuary tend to be larger than those higher in the middle reaches. This is probably due to a decrease in growth rate further up the estuary as a result of less available food as well as the less favourable salinity conditions. The latter has been established for *Dosinia hepatica* and *Macoma litoralis* and most probably also holds for other bivalves occurring in the middle reaches of the estuary. It may be argued that the above tendency is due to different proportions of old and young specimens in different parts of the estuary. This has, however, never been noticed and is not supported by the spat/adult ratios from different stations. The salt marshes of the lower reaches appear to be the main source of detritus in the estuary (McLachlan & Grindley in press) and if bivalves in the middle reaches

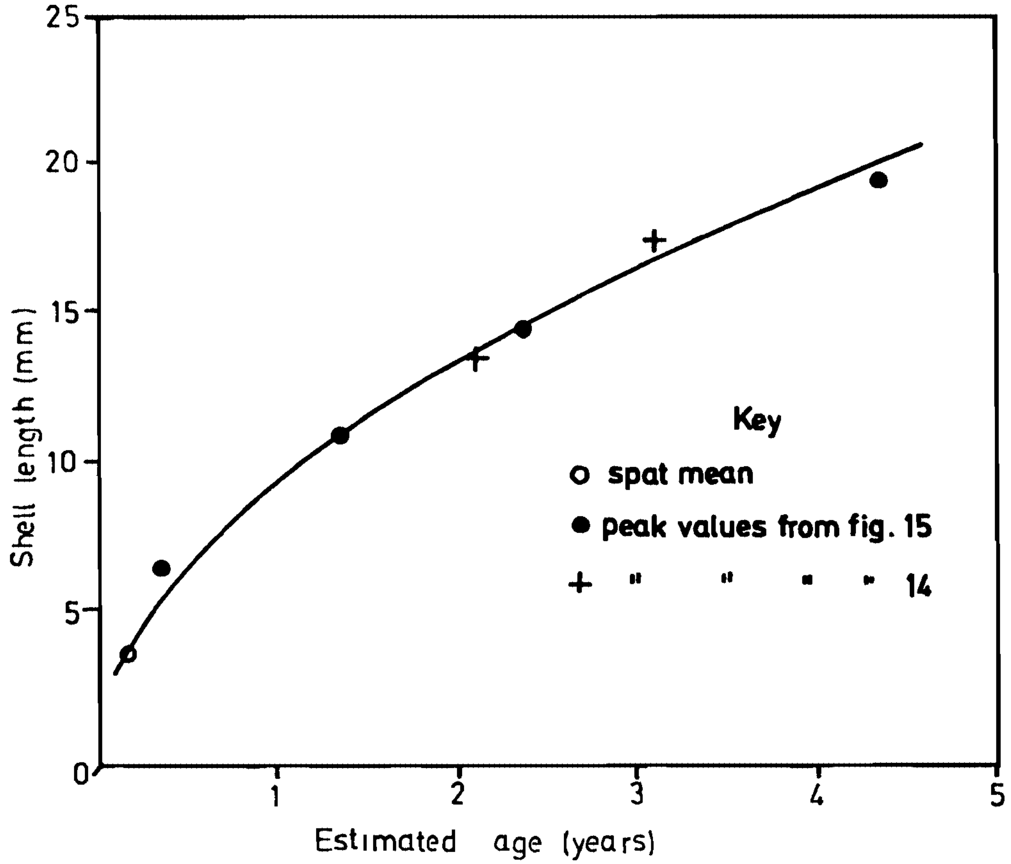

FIGURE 16
Curve of shell length against estimated age in *Dosinia hepatica*. Based on the results of spat samples of 1972 and on Figures 14 and 15.

are dependent on this as their major source of food, then those farthest from the lower reaches would obtain the least food and thus grow the slowest.

Growth Rates

Bivalve growth rates vary seasonally, and it is because of very slow growth during winter that growth-rings are laid down. During summer growth is usually fast. This has been verified in *Venus* by Ansell (1961) and in the mud prawn, *Upogebia africana*, by Hill (personal communication). This variation has been illustrated in *Solen corneus* (Figure 10) and *Macoma litoralis* (Figure 13). Even allowing for slowing of growth with age, Figure 10 indicates a very retarded growth during winter, fast growth during spring and very fast growth during summer. This seasonal variation is probably even more marked in *Dosinia hepatica* and *Macoma litoralis*, which have distinct growth-rings. This growth cycle appears to be related to the seasonal temperature changes in the estuary as the fastest growth in *Solen corneus* occurs in late summer when temperatures are highest and the slowest growth during late winter when they are lowest (McLachlan & Grindley in press).

Growth in *Dosinia hepatica* and *Macoma litoralis* is of the same pattern as that found in Northern Hemisphere bivalves, where growth is rapid in the first year, and slowly decreases during succeeding years. Both of the above species grow to a maximum age of about six years in the Zwartkops estuary while *Solen corneus* lives to about five years. Maximum ages recorded for different northern hemisphere bivalve species vary between about three (*Tellina tenuis*, Stephen 1932) and 18 years (*Scrobicularia plana*, Green 1957). Species that live long generally grow slowly (Green 1957) while those that have short life spans grow rapidly (Stephen 1932). *Dosinia hepatica* and *Macoma litoralis* may be said to grow at moderate rates and to moderate ages, while *Solen corneus* grows rapidly to a slightly younger age.

The growth rate of *Solen corneus* might be exaggerated by the fact that growth occurs mainly in an antero-posterior direction, the animals growing long and narrow. *Dosinia hepatica* and *Macoma litoralis* grow more slowly, but here growth occurs in all directions, their shells being round and oval respectively. The absence of growth rings in *Solen corneus* is probably a result of the very fast growth rate of this species. In such an animal, a single week of very warm or very cold weather might result in rapid growth or the deposition of a small ring. This would tend to blur the winter growth-ring and cause the formation of multiple small rings. This can in fact be seen on *Solen corneus* shells.

Finally, it may be concluded that although the growth-rings in the animals studied here are not as distinct as those recorded in northern hemisphere bivalves (Ansell 1961, Green 1957, Stephen 1931) they have proved useful and have correlated well with age determination from size-frequency histograms.

SUMMARY

1. Spat fall, size distribution and growth of some estuarine bivalves have been investigated.
2. Spat fall appears to occur during late summer and spat sizes are comparable with those recorded in the northern hemisphere.
3. Growth rates have been found to vary at different intertidal levels as well as in different

parts of the estuary.

4. In two species age determinations from growth-rings correlated well with age determinations from size-frequency histograms.
5. Growth rates are comparable with those recorded in the northern hemisphere and vary seasonally.
6. Most species live for five to six years.

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