OBSERVATIONS ON GROWTH IN CERTAIN MOLLUSCS AND ON CHANGES CORRELATED WITH GROWTH IN THE RADULA OF *PYRAZUS PALUSTRIS*.

By R. B. SEYMOUR SEWELL, *M.A., F.A.S.B., F.Z.S., Surgeon-Naturalist to the Marine Survey of India and Superintendent, Zoological Survey of India.*

During the past four years I have from time to time made notes on the rates of growth and other correlated changes in the structure and life-history of certain Indian molluscs, and in view of the little that is at present known regarding the bionomics of this group it has been thought advisable to publish the results that I have obtained, imperfect though they are. I have divided the paper into two portions, dealing respectively with (A) inhabitants of freshwater and (B) marine or brackish-water forms.

A. INHABITANTS OF FRESHWATER.

I have already (Annandale and Sewell, 1921) published the results of my researches on the life-history of *Vivipara bengalensis*, but during my investigations in 1919 and 1920 regarding the possibility of the more common species of freshwater molluscs in this country acting as hosts for the development of the cercariae of human-infecting schistosomes, I had occasion to keep a large number of examples of several other species in my experimental tanks, and during the progress of my work a number of young were born and continued to live. In several cases the dates on which the parent molluscs were introduced into and removed from these tanks is known, and also the date on which these young forms were subsequently examined and measured. In this way I have obtained a record of the rate of growth in early life and have been able to compare these young examples with adults of the same species obtained from other sources. It must be remembered that these young forms were living under somewhat artificial conditions, though I attempted to reproduce in my tanks a habitat as nearly as possible identical with their natural surroundings. Consequently the rates of growth observed may differ somewhat from those that pertain in the same species in the ' wild ' state but at any rate they serve as a rough indication of the progress attained under normal conditions.

1. **Acrostoma variabile** (Benson).

The parent molluscs were introduced into my tanks between the 29th April and the 23rd May, 1919 : a number of young were produced and were subsequently examined and measured. The measurement taken was the maximum height of the shell, from the extreme apex to the furthest point on the margin of the peristome. The first batch of 33 examples were measured on 29th July, 1919, on which date they were between 68 and 92 days old. Their height measurements range from

6·0 mm. to 13·0 mm., the average for the group being 9·3 mm. On the same day a batch of 46 adults were taken from the tank in the Indian Museum and their measurement ranged from 27 mm. to 43 mm. On the 19th September, 1919, a further series of 42 young specimens from my experimental tanks were examined and measured, and it was found that the height measurement now ranged from 9·0 mm. to 16·0 mm., the average being 12·0 mm. These examples were between 110 and 144 days old.

The results of these measurements are plotted out in the accompanying text-figure (text-fig. 1).

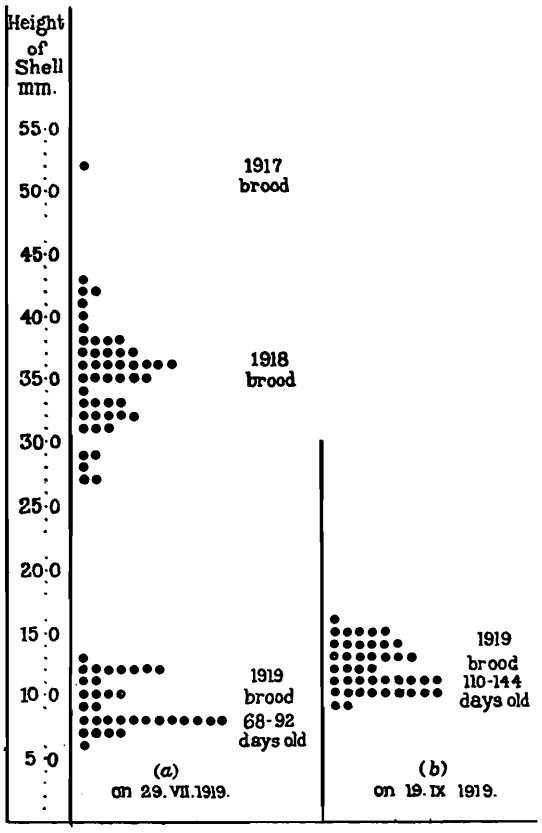

FIG. 1.—Growth stages of *Acrostoma variabile* (Benson).

The average rate of growth of the young of this species is thus seen to be to a height of 9·3 mm. in 92 days or less and to one of 12·0 mm. in 153 days or less.

The group of 46 adult examples taken from the Museum tank I believe to be composed of individuals who had completed a full year's growth and belonged to the 1918 brood. Larger specemens than this are rare, but a single example measuring 52 mm. in height was obtained at the same time and this I believe to be a survivor from the 1917 brood. If this be so then it would appear that the usual length of life of this species is but a little more than one year, and in only very exceptional cases does an individual survive for a second year.

2. **Melanoides lineatus** (Gray).

In the case of this species two series of examples were bred and examined. In series (1) the parents were introduced into my experi-

mental tanks between the 6th and 20th of May, 1919 (both dates inclusive), and they were removed from the tanks between the 22nd and 27th of July, 1919; all the young in this series must, therefore, have been born between these two dates, *viz.*, the 6th May and the 27th July. In series (2) the parents were introduced into tanks [different from those containing series (1)] on the 12th and 13th June, 1919, and were removed between the 1st and 6th of August, 1919. All the young examples in this series had therefore been born between the 12th of June and the 6th of August.

The young of both series were examined and measured on the 19th September, 1919, and the results are given in text-fig. 2.

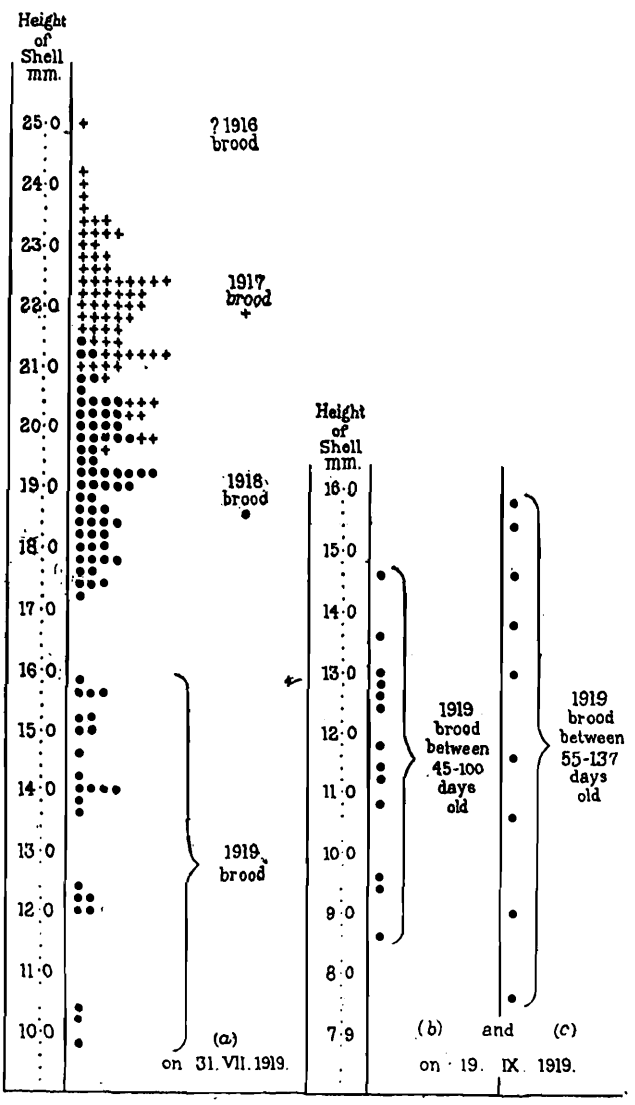

FIG. 2.—Growth stages of *Melanoides lineatus* (Gray).

In series (1), containing examples whose length of life is known from the above dates to have been between 55 and 137 days, the height measurements range from 7·6 mm. to 16·8 mm., and we have an average rate of growth of 12·6 mm. in 96 days. In series (2) the height measurement ranges from 8·6 mm. to 14·6 mm. and the length of life of all these specimens must from the above dates have been between 45 and 100 days, or an average of 11·7 in 73 days.

A number of examples, 160 in all, of this species were obtained on 31st July, 1919, from a tank in the Zoological Gardens, Alipore; these were examined and the results of their measurements are given in text-fig. 2 (*a*). The smaller examples form a scattered group whose height measurement ranges from 9·8 to 15·8 mm., and a comparison with the examples reared in my tanks shows conclusively that these were members of the 1919 brood and were, if the height attained by individuals bred in captivity is any guide, from 2 to 4 months old. It would appear then that the breeding-season in this year began early in April and was still in full swing as late as August: this agrees very well with my observations on *Vivipara bengalensis* (*vide* Annandale and Sewell, 1921, p. 279), in which species I found that the breeding-season "commences early in the year and seems to extend throughout the whole of the hot-weather and monsoon periods up to and probably beyond September; but the period of most intense reproduction is from April to July." The larger examples of *Melanoides lineatus* were all adults and form, if we consider size alone, a somewhat scattered group whose height measurements range from 17·2 mm. to 25·0 mm. From this one might conclude that they were all examples of the 1918 brood. The shells, however, of certain individuals showed a marked difference from those of others; in some the shell was perfectly clean, whereas in others it was rough and thickly overgrown with algae. Examples with clean shells are represented in the figure by a circle O, and those with algae-incrusted shells by a cross +, and it is clear that they fall into two groups, the first having a height measurement ranging from 17·2 mm. to 21·4 mm. and having an average of 19·1 mm., and the second from 19·6 to 25·0 mm. with an average of 22·0 mm. These two groups, I believe, to be composed of individuals of the 1918 and 1917 broods respectively. Possibly the single example that had a length measurement of 25 mm. is a representative of the 1916 brood that has managed to survive.

It would seem probable that in this species the average period of life is as long as two years, and that occasionally an individual may survive even for a third year.

3. **Melanoides tuberculatus** (Müller).

In the case of this species my results are based on two series of observations. In series (1) the parent adults were introduced into my experimental tanks between the 14th and 18th May, 1919, and were removed between the 22nd and 27th July, 1919; while in series (2) the parents were introduced into different tanks on the 14th and 15th of June, 1919, and were removed between the 1st and 6th of August, 1919. All the young examples from both series were collected and measured on the 19th of September, 1919.

In the case of series (1) unfortunately only two examples survived. These measured respectively 15·8 mm. and 16·4 mm. in length. From the dates on which the parents were introduced and removed we know that the period of life of these two specimens was between 55 and 129 days. Series (2) was more successful and 33 examples were obtained and measured. The length measurement ranges from 6·2 mm. to

13·8 mm. the average length of the whole series being 10·8, while the length of life of these individuals lay between 44 and 98 days or an average of 71 days.

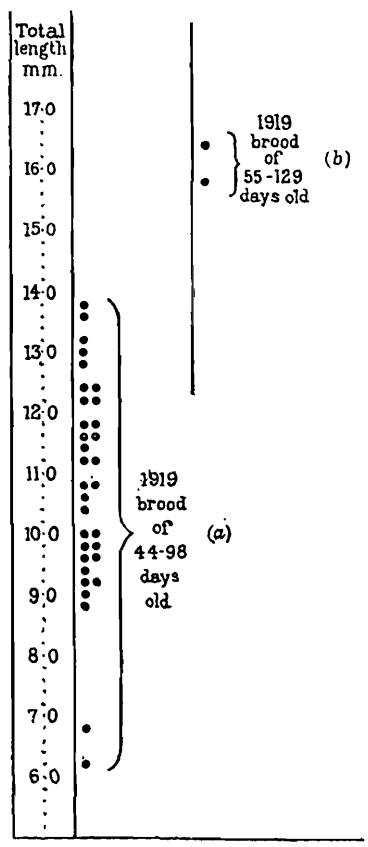

FIG. 3.—Growth stages of *Melanoides tuberculatus* (Müller).

It is interesting to note that this rate of growth corresponds very closely with that found in *Melanoides lineatus* and it is possible that a particular rate of growth under similar conditions may be characteristic of a genus, rather than merely of a species. On the other hand the height of the shell in these two species at the end of the first year of life is so little different—16·5 mm. in the case of *M. tuberculatus* (*vide* Sewell, 1922, p. 14) and 19·1 mm. in *M. lineatus*—that one would expect to find a very similar rate of growth.

4. **Limnaea acuminata** (Lamarck) var. **gracilior** (v. Martens).

In the case of this species, the parent adults were introduced into my experimental tanks between the 4th and 14th of May, 1919, and were removed between the 22nd and 27th of July, 1919. The resulting progeny were collected and measured on the 19th of September, 1919; they were therefore between 54 and 139 days old.

The height of the shell exhibits a very considerable range of variation, the smallest measuring only 11·3 mm., while the largest measured as much as 27·3 mm., the average being 18·8. This rate of growth is obviously much more rapid than in the case of the different species we have so far been considering. Semper (1874) has, however, shown that though the rate of growth is affected by the amount of water in which the young are living, in *Limnaea stagnalis* individuals may attain

to a height of from 7·8 mm. to 26·0 mm. in 56—64 days or from 4·6 mm. to 21·0 mm. in 59—63 days. This agrees very closely with the results

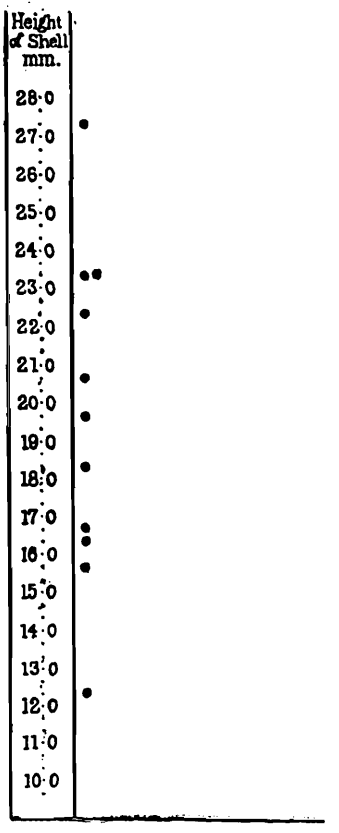

Fig. 4.—Height of shell in *Limnaea acuminata* var. *gracilior*, after 54 to 139 days growth.

given above, and it is possible that this rapid rate of growth may be characteristic of the genus.

5. **Indoplanorbis exustu** (Deshayes).

In the accompanying text-figure (Fig. 5) I have given the maximum breadth of the shell in a number of specimens of the above species that were collected in two tanks in Calcutta during the months June and July, 1919. The measurement taken was across the breadth of the spiral in the diameter at right angles to the mouth, as in this way one avoided any slight difference that might arise owing to damage or breakage of peristome.

At one end of the series are a few specimens measuring from 4·0 to 5·8 mm., these I believe to be individuals that had been born during the 1919 breeding-season, and the fact that not a single one was infected by Cercariae certainly indicates that they were less than three months old (*vide* Sewell, 1922, p. 14). Extending from 6·0 mm. to 8·8 mm. is a well-defined compact group that almost certainly belong to the 1918 brood and were therefore just over one year old. A number of individuals of considerably larger size, ranging from 9·2 mm. to 13·2 mm. form a less well-defined group that I believe represents the 1917 brood, and they were, therefore, just over two years of age. These larger specimens all came from the tank in the Indian Museum compound

and were collected during the month of June. During the early part of July, 1919 there was a very heavy mortality among the snails in this

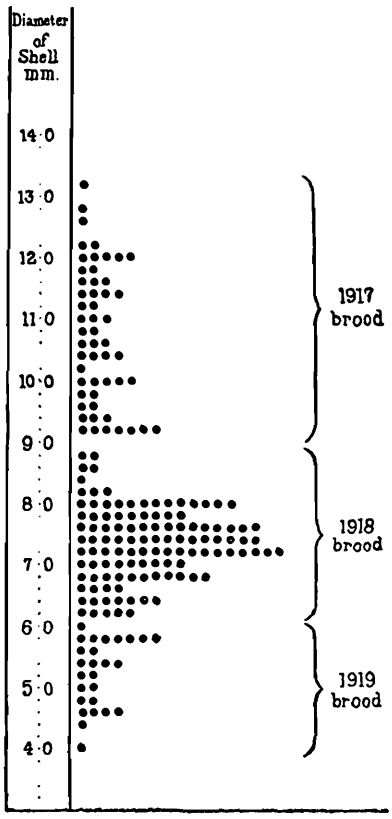

FIG. 5.—Growth stages of *Indoplanorbis exustus* (Deshayes).

tank and as I have already pointed out (Sewell, 1922, p. 13) this appears to be of universal occurrence and is due to the snails having reached their extreme limit of age. This mortality affected the examples of *Indoplanorbis exustus* equally with the other species, and during July only examples belonging to the middle group could be found—all those of the largest group having presumably died off.

This seems to us to indicate that the length of life of this species is two years, at the end of which period they die off.

B. MARINE AND BRACKISH-WATER FORMS.

During several survey seasons, from 1913-14 onwards, and at other times as the opportunity has occurred, I have made collections of certain marine molluscs and have examined and measured them with a view to determining, if possible, the rate of growth and average length of life attained by these species. Although much work has been done on these lines in temperate waters, particularly in connection with fishery work and regarding certain species that are of economic importance, little or nothing has, so far as I am aware, been done in tropical seas.

6. **Littorina scabra** (Linn.).

Large numbers of this species of *Littorina* were found in Nankauri Harbour, Nicobar Islands, living on the trunks and branches of trees

that had fallen along the beach or on an old wooden hulk that lies at the edge of the water in Spiteful Bay.

As Tattersall (1920, pp. 6, 7) has pointed out there is in the different species of *Littorina* a marked correlation between the habitat and the life-history; thus *Littorina littorea* lives in the *Laminaria* and *Fucus* zones and is therefore only exposed at extreme low water spring tides and lays egg-capsules singly and unattached to weeds, while *L. obtusata* in its habitat is practically exposed at every low water and lays its egg-

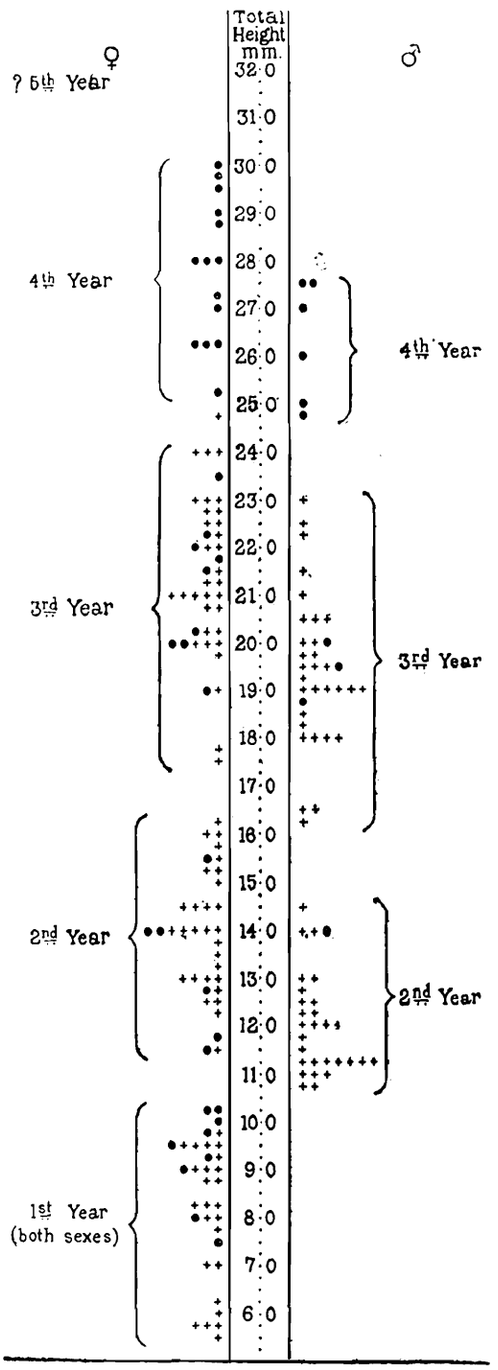

Fig. 6.—Growth stages of *Littorina scabra* (Linn.).

+ Specimens obtained in 1921.
O Specimens obtained in 1922.

capsules in masses attached to weeds. Finally *L. rudis* and *L. neritoides* live for the most part out of water and are viviparous. *L. scabra* also

has this latter type of existence, and appears to be exposed for days at a time, and have too we find the viviparous habit. The developing ova are small and are produced in enormous numbers : they form a brownish mass which partially fills the branchial chamber, occupying the dorsal and left hand portions of the cavity.

In all, I collected 192 examples. These were not all collected at one time, the dates and the numbers collected thereon being as follows :—

	Examples.
On October 27th and 28th, 1921	111
On November 5th, 1921	48
On October 19th, 1922	33

Each of these examples was carefully measured, the measurement taken being the maximum height from the apex of the shell to the margin of the peristome, and the results obtained are shown in the accompanying figure.

The specimens fall into a series of groups according to their size and, owing to the presence in this genus of a penis in the male, it was possible to determine the sex of a specimen in all but the very smallest examples.

The smallest examples form a somewhat scattered group whose height ranges from 5·50 mm. to 10·25 mm.

In the accompanying figure I have indicated the examples obtained in 1921 by a cross, and those taken in 1922 by a circle. It is interesting to note that examples of this group taken in 1922 were on the average somewhat larger than those of the previous year, although they were obtained at a slightly earlier date. The average length attained by this group in each year is as follows :—

In 1921	8·05 mm.
In 1922	9·28 mm.

The examples comprising this group I take to be individuals that had been born during the present breeding-season. Many of the individuals of the larger groups were taken in the act of copulation and still more adult females were ovigerous, so that there can be no doubt that a breeding-season was in progress. Tattersal (1920, p. 3) gives the breeding-season of *Littorina littorea* in English waters as " lasting from the middle of January to June, with a maximum in April and the early part of May." A comparison of the size of the individuals in the smallest group with the rate of growth of young examples in other species seems to me to indicate that these could not have been much older than two to three months, that is to say, they probably belong to a brood produced about August and September just after the close of the South-West monsoon season. I have already shown (Annandale and Sewell 1921, p. 279 and *vide supra*) that the breeding-season for fresh-water gastropods in India occurs during the hot weather and the early part of the South-West monsoon, from about March to September, with the most intense reproduction in April to July, and it is possible that *Littorina scabra* has a double breeding-season each year, namely, just before and

just after the South-West monsoon, but, if so, any distinction in size between the two broods appear to become obliterated by subsequent growth before the completion of the first year of growth.

In the next larger group, comprising 64 individuals, a study of anatomy showed that 35 examples were females and 29 were males. There is a marked disparity in the size of the two sexes : the females range in height from 11·50 mm. to 16·25 mm., and have an average of 13·9 mm., while the corresponding males measure only from 10·75 mm. to 14·50 mm., and have an average of only 12·04 mm. Although I cannot be certain on this point, I believe this group to be composed of individuals belonging to the 1920 brood in the case of specimens taken in 1921, and of the 1921 brood in those examples taken in 1922, *i.e.*, they are individuals who have commenced their second year of growth. Each succeeding group represents individuals of an additional year's growth.

The third group includes 73 examples, of which 42 are females and 34 males. Here again one finds the same disparity in size between the two sexes and I was inclined to think that both in this and the succeeding group I could detect a slight difference in the sexes in the breadth of the body-whorl, the female shell appearing to be slightly broader than the male, but I could not be certain of this. The females in the group have a height measurement varying from 17·50 mm. to 24·75 mm. and an average of 21·85 mm., while the males vary from 16·25 mm. to 23·0 mm. and have an average of 19·42 mm. In 1921 I obtained only one example larger than this, but in 1922 I succeeded in obtaining evidence of the existence of yet another group.

This additional group, that I believe is composed of individuals who have survived to a fourth year of life, includes 15 females and 6 males. At this age the height of the females varies from 25·25 mm. to 31·75 mm. and gives an average of 28·10 mm., while the males vary from 24·75 mm. to 27·50 mm. and have an average of 26·29 mm.

A single example, a female, was obtained in 1921, that had a height measurement as long as 40·00 mm. I have on account of its disparity in size excluded it from the group that I believe is composed of individuals in their fourth year of life, and it seems probable that it is an example of a survivor who has managed to exceed the usual span of life and has attained to the age of a fifth year. It is interesting to note that this individual was ovigerous and that the larger size was therefore not due to parasitisation.

A study of the proportions of the sexes in each of these groups reveals several interesting features. In the group corresponding to the first year of growth, sexual maturity has not yet been attained, and it appears probable that sexual maturity is not usually attained much before the end of the first year of life.

In the group corresponding to the second year of growth, the proportions of the sexes are very similar : in every 100 examples we should, judging from the figures I have given above, find 45 males and 55 females, but my examination of the individuals captured in 1921 and 1922 seems to indicate that these figures are liable to very considerable variation,

and in the Table below I give the percentages as calculated from my examination :—

	1921		1922	
	♂	♀	♂	♀
	Per cent	Per cent	Per cent	Per cent
2nd year	48	52	14	85
3rd year	46	54	33	67
4th year	...	...	29	71
5th year	...	100	...	...

Examples that were in their second year in 1921 were in their third year in 1922 and it is extremely interesting to note the way in which the number of males becomes reduced in proportion to the females. I have shown that an exactly similar state of affairs is found in *Vivipara bengalensis* and it is probably of universal occurrence among Mollusca in tropical regions. During the period of life between the third and fourth year this disparity in the proportion of the sexes becomes even more marked, and the sole example in what I believe to have been the fifth year of life was a female.

A further indication of the greater susceptibility of the males to adverse conditions is to be found in the proportions of the two sexes that exhibit a ' varix ' across the shell. This ' varix ' I consider is produced by a period of arrested growth followed by a subsequent recovery and growth in size of the individual, and I think one is justified in assuming that the arrest of growth is caused by some adverse condition that has affected the snail in a greater or less degree. The subsequent growth shows that, whatever the cause, the individual has survived. Out of a total of 10 examples that possessed a ' varix ' 8 were in their second year and of these five were females and three males, or a proportion of 71 : 29 ; and in the case of the two examples in the third year of life that showed a ' varix ' both were females, which indicates that far fewer males than females survive after being affected by adverse conditions.

It is possible that this increased susceptibility of the male to adverse conditions is correlated with the time of life at which sexual maturity is attained. I have no evidence of its being the case, but in view of what occurs in other molluscs it seems reasonable to conclude that the males become mature at the end of the first year of life. A study of the numbers of females that were found to be producing ova seems to indicate that in this sex the onset of sexual maturity may be delayed, and I give the actual figures below :—

Out of	24	females in the	2nd	year of life	7	were ovigerous	= 29	per cent
,,	40	,,	3rd	,,	23	,,	= 57	,,
,,	11	,,	4th	,,	9	,,	= 82	,,
,,	1	,,	5th	,,	1	,,	=100	,,

This certainly seems to indicate that in the female the onset of sexual maturity may be delayed even as late as the 4th year of life.

In certain individuals, belonging respectively to the third and fourth year groups, I carefully examined the radula to see it I could detect any changes in the structure of the teeth, similar to that which, as I shall describe below, occurs in *Pyrazus palustris* but I could detect no difference.

7. **Littorina obesa** Say.

A number of examples of this species were collected from the same locality as the specimens of *L. scabra*. This species is distinctly smaller in size but appears, as one might reasonably expect, to have a very similar life-history.

The smallest examples that I obtained, and which I believe to belong to the 1921 brood, were in their natural condition of a dark chocolate colour with white markings. No attempt was made in this group to differentiate between the members of the two sexes nor do I believe that it would without a microscopical examination of the developing gonad be possible to do so. In size these individuals range in height from 6·0 mm. to 8·25 mm., the average being 7·1 mm.

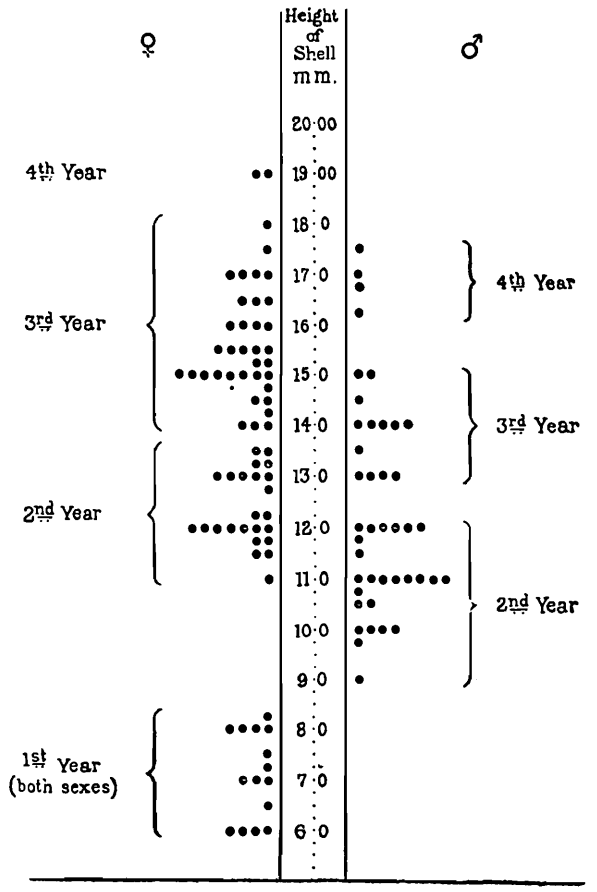

Fig. 7.—Growth stages of *Littorina obesa* Say.

In the second group, whose members could now easily be separated into their respective sexes owing to the presence of the penis in the male, there were 24 females and 26 males. Here again one finds a well-marked difference in the size of the females and males, the females being much the larger.

The height of the shell in the females varies from 11·0 mm. to 13·5 mm. and the average is 12·38 mm., whereas in the males the height is from 9·0 mm. to 12·0 mm., the average being 10·95 mm. The members of this group I believe to be in the second year of life, and it is interesting to note that eight individuals, seven females and one male, possessed a well marked 'varix' close to the margin of the peristome.

In the third group, corresponding to individuals in their third year of life, the disproportion between the two sexes has become much more marked; out of a total of 48 examples, 35 were females and only 13 were males. The height of the shell in the females varies from 14·00 mm. to 18·00 mm., the average being 15·57 mm., whereas in the males, which are much smaller, the height ranges from 13·00 mm. to 15·00 mm., with an average of only 13·85 mm. In this group 19 individuals exhibited a well-marked varix of which 14 were females and only 5 were males. In seven females and 3 males the 'varix' was situated close to the margin of the peristome and had only recently been formed, probably during the preceding South-West monsoon season (1921). In the remaining seven females and two males the varix was at some distance from the peristome and had probably been produced at the end of the first year of life, that is to say during the South-West monsoon of 1920.

The fourth group, which I believe to consist of individuals in their fourth year of life, is only very poorly represented in my collection, and contains two females, both of 19·00 mm. in height, and four males, whose height ranges from 16·25 mm. to 17·50 mm., with an average of 16·87 mm.

It appears then the maximum length of life in *Littorina obesa* is about four years, but that the majority of specimens perish after three years. We again find, as in *Vivipara bengalensis* and *Littorina scabra*, a tendency for the proportions between the two sexes to vary as age progresses; thus—

	♂	♀
In the 2nd year of life the proportion is	52	48
In the 3rd year of life the proportion is	27	73

In this species, however, there seems to be a tendency towards an equalisation of the proportions again in the fourth year. The proportion between the sexes in my collection in examples of this length of life was 67 ♂ to 33 ♀, but as I only obtained seven specimens in all one cannot place much reliance on these figures. As in *Littorina scabra* we get an indication of the greater susceptibility of the male to adverse conditions in the comparatively few males in proportion to females, *viz.*, 6 : 21, that survive a period of adverse condition and so live to form a varix in the shell, and in view of the possible tendency to equalisation of the sexes in the later years of life it is interesting to note that the proportion of males to females with a varix in the second year of life is only 21·4 : 78·6, whereas in the third year of life it has risen to 42·9 to 57·1, so that at the end of their second year a much greater number of males are able to survive the ill-effects of a period of adverse circumstances and so live to form a varix in their shells than do so in examples that are affected at the end of their first year.

8. **Pyrazus palustr** (Linn.).

On the western side of Mayo Point in Nankauri Harbour, Nicobar Islands and close to the village of Innanga is a small low-lying area separated from the beach by a thin fringe of trees. The southern portion of this area is swampy and is connected by a narrow channel with the waters of the bay which flow in and out with the rise and fall of the tide. At high water most of the area is submerged but as the tide recedes a large part becomes exposed while only here and there isolated pools of water are left behind.

Living in this swamp were enormous numbers of the mollusc *Pyrazus palustris* and associated with them were also a few examples of *Telescopium telescopium*. The examples of *Pyrazus palustris* varied enormously in size and a number of examples, 212 in all, were collected between the 27th November and 10th December, 1921.

These were subsequently measured, the measurement taken being the extreme height of the shell from the apex to the margin of the peristome. In Fig. 8 I give the results of this measurement and it is seen that individuals fall into four quite distinct groups, of which the two of smaller size are compact, while the other two groups comprising the larger specimens are somewhat scattered and tend to be subdivided.

The first group, comprising examples having a maximum height of shell that varies from 9·0 mm. to 19·0 mm., I believe to include those individuals that were in the first year of life.

The second group includes those individulas whose height ranges from 24·0 mm. to 38·0 mm. and in my opinion corresponds to the second year of life.

The third group is a somewhat scattered one and includes specimens whose height of shell varies from 58·0 mm. to 91·0 mm. In this group we appear to get a quite distinct tendency towards a sub-division into (*a*) examples that are grouped round an average of about 72 mm. in length and (*b*) those that tend to have an average of about 95 mm. This tendency towards sub-division, which would, I think, become clearer if more specimens had been obtained and measured I attribute to a dimorphism between the two sexes. I have already shown that males appear in all species examined to be smaller than females of the same age, and although none of the examples examined by me appeared to be sexually mature, and I was unable to determine their sex, I believe that the smaller sub-group includes the males and the larger the females in the third year of life. If this be so then the proportion of males to females appears to be 57·7 : 42·3.

The fourth group is again a scattered one with a tendency towards sub-division into a smaller sub-group having an average length of about 109 mm. and a larger sub-group having an average of about 120 mm., which I again attribute to sexual dimorphism. In this case, if my assumption is correct, the proportion of males to females has now dropped to 36·6 : 63·2, which agrees very well with the tendency that we have seen in other species for the proportions of males to females to diminish as age advances.

Associated with this gradual increase in size is a very remarkable change in the character of the radula. So marked is the difference

between the smallest and the largest specimens that one might reasonably doubt whether they were individuals of the same species. I have, therefore, submitted all my examples to Dr. N. Annandale who agrees with me that they are specifically identical and, moreover, a study of their internal anatomy reveals no difference other than that noted above in the character of the radula.

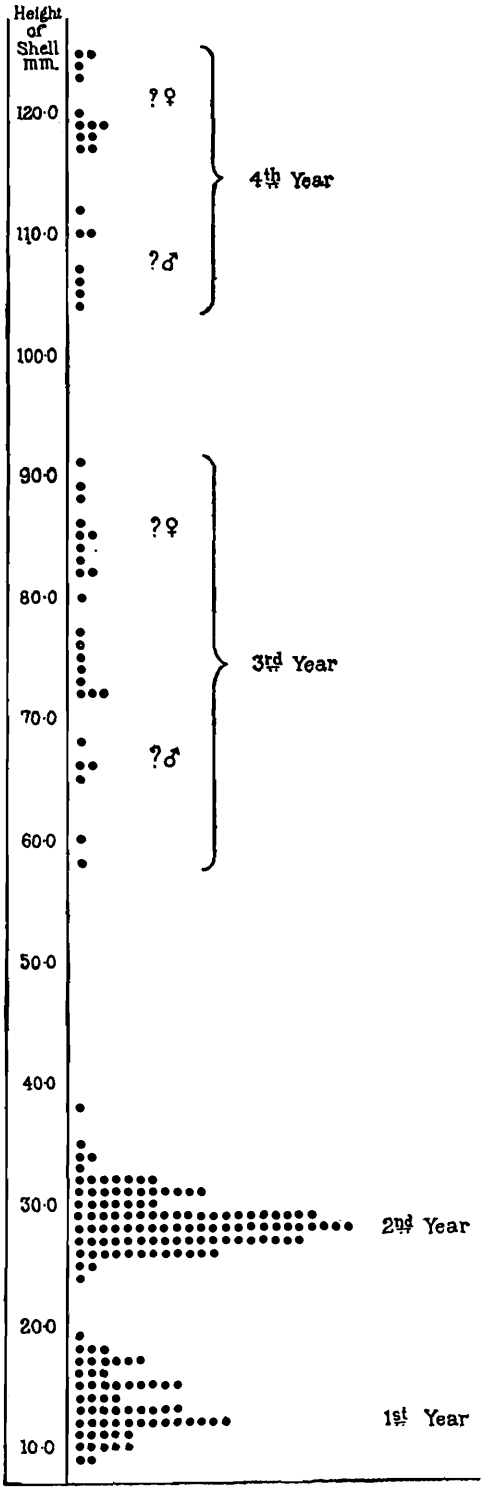

FIG. 8.—Growth stages of *Pyrazus palustris* (Linn.).

In the smallest individuals, having a height of approximately 12 mm., the radula presents the appearance that is characteristic of the genus,

or even of the family. In each row there are in all seven teeth, the dental formula being 2. 1. 1. 1. 2, and each of these teeth are characterised by possessing a number of cusps on their margins. As age progresses and the size of the animal increases a gradual change takes place, the number of individual cusps on the teeth gradually becomes less until in the final largest stage of all the central tooth presents only a single pointed median cusp. The lateral tooth has developed enormously and now consists of a single cusp with a trace of a second one to the outer side, while in the two marginals we find one large cusp with traces of one or two small ones on the mesial side of it.

This change is a very gradual one but even in different parts of the radula of the same individual it is possible to detect slight changes and the gradual reduction in the number of cusps seems to be brought about by a process of fusion rather than by suppession. The accompanying figures (fig. 11, p. 550) show very clearly the way in which this change is carried out.

This extremely interesting change in the character of the radula appears to be confined to this single species. I have already mentioned that I could detect no difference in the radulae of examples of *Littorina scabra* of different ages and I have also examined individulas of different sizes and ages of *Telescopium telescopium* found in the same locality as these examples of *Pyrazus palustris* but here again I was unable to detect any change. Finally examples of *Cerithidea obtusa* obtained from Port Canning, near Calcutta, show that in the aduts of this species the radula is of the usual type and agrees closely with the condition found in the youngest stages of *P. palustris.*

9. **Mytilus variabilis** Krss.

In the shallow water on the shore side of a small coral reef that fringes the coast at Tor in the Gulf of Suez are beds of mussels, *Mytilus variabilis* Krss. At the time when I was stationed at Tor in 1916, these beds appeared to be rapidly disappearing and the mussels becoming killed off owing to an accumulation of sand and mud that was covering the beds, and by a simultaneous deposit of a white chalk-like material.

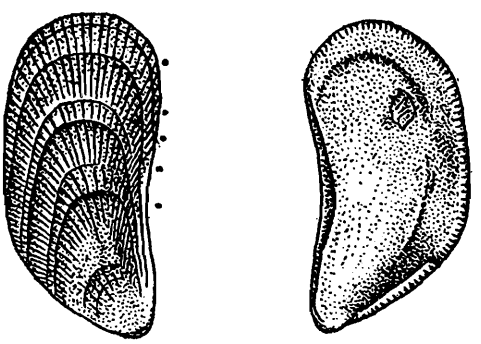

Fig. 9.—*Mytilus variabilis,* showing the rings of growth.

In order to try and determine whether it was possible to ascertain the age of examples of this species a number were collected and examined.

Every shell, that was not encrusted with the above-mentioned chalky-deposit, exhibited a number of rings, more or less distinct, that ran concentrically across the outer surface of the shell, and these rings fall into two categories. The first series of rings are well marked, and are approximately equidistant from each other, while the second series are less marked, though still quite distinct, and are invariably situated much nearer to the ring of the first series on its proximal side than to the ring distal to it.

I do not propose to enter very deeply into a discussion of the varied question whether the age of an oyster can be determined by the number of rings on its shell. Petersen (1908 and 1918) came to the conclusion that "for the practised observer, it is possible to estimate roughly the age from the outer appearance of the shell," and Massy (1913) arrived at exactly the opposite conclusion. In the case of these mussels, however, it seems to me that the above-mentioned rings do in all probability give one a true estimate of the age of the individual.

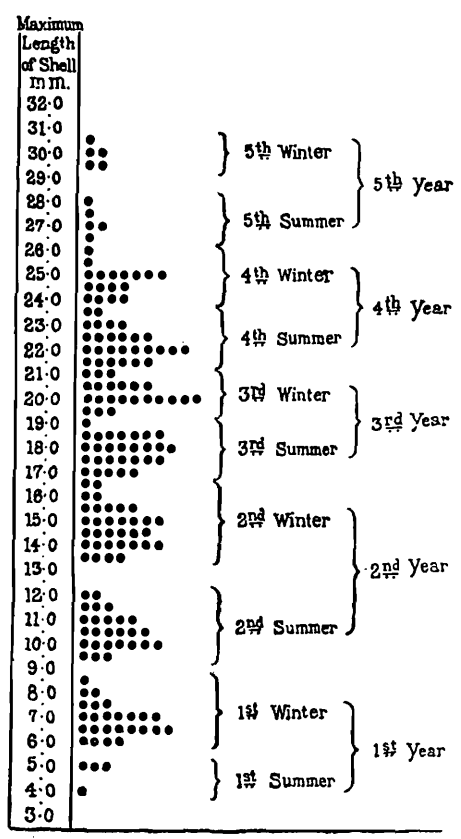

FIG. 10.—Growth stages of *Mytilus variabilis* Krss.

I selected a number of examples and measured the distance from the extreme apex of the shell to the furthermost points on the various concentric rings and the results are given in the accompanying figure 10. It will be noticed that these measurements fall into very definite groups, that is to say, that allowing for slight individual variations, each example has increased the size of its shell by approximately the same amount between the formation of one ring and the next. I believe that the amount of shell formed between a ring of the primary series and the secondary ring immediately following it represents a winter's growth,

and the much larger amount of shell laid down between the secondary rings and the next following primary ring represents a summer's growth. If this be so then the distance from primary ring to primary ring is one year's growth and the number of primary rings serve as a correct guide to the age. The maximum length of life then of this species would thus appear to be five years though, judging from the number of examples in the two largest groups, most individuals would seem to die off after the fourth year, only a few surviving for the fifth. On the other hand a physiological character of the glands of the mantle margin is that the shell-formation proceeds at different rates at different times—a phase of activity being followed by a period of more or less rest, in which calcium is stored up. A study of the observations made by Miss Massy on the formation of rings in the Oyster, to which I have referred above, brings out an interesting point that seems to me to have a very distinct bearing on this question. Fortunately she gives full details of all her examples, and I have been able to make a careful analysis of her data. She has summed up the results of her observations in the following words : " it is obvious, therefore, that if I have been at all correct in determining the number of rings, it is not of much use to apply the study of growth rings in ascertaining the age of a wild oyster." She, however, does not appear to have noticed that there is a distinct correlation between the size of the oyster and the number of rings present in oysters *of the same age.*

I have taken the data that Miss Massy gives in her paper and in the following Tables I have tabulated the number of rings present in the oysters of different sizes but of $1\frac{1}{2}$, $2\frac{1}{2}$ and $3\frac{1}{2}$ years growth respectively.

Table I.—Oysters of $1\frac{1}{2}$ *years growth.*

Distance from hinge to ventral margin of shell in mm.	No of speci-mens.	No. of individuals exhibiting the following No. of rings.					Average No. of rings present.
		2	3	4	5	6	
11—20	4	4	...	...	...	...	2·00
21—30	16	13	3	...	...	...	2·19
31—40	25	10	13	1	1	...	2·72
41—50	39	16	17	4	2	...	2·79
51—60	18	...	8	10	...	...	3·56
61—70	2	...	...	1	1	...	4·50
TOTAL	104	43	41	16	4	...	

Table II.—Oysters of 2½ years growth.

Distance from hinge to ventral margin of shell in mm.	No. of specimens.	No. of individuals exhibiting the following No. of rings.						Average No. of rings present.
		2	3	4	5	6	7	
21—30	24	5	19	...	...	...	...	2·79
31—40	59	2	38	14	5	...	..	3·37
41—50	103	2	58	26	14	3	...	3·59
51—60	74	...	32	30	10	2	...	3·76
61—70	46	...	16	10	15	4	1	4·22
71—80	10	...	...	7	...	3	...	4·60
TOTAL	316	9	163	87	44	12	1	

Table III.—Oysters of 3½ years growth.

Distance from hinge to ventral margin of shell in mm.	No. of specimens.	No. of individuals exhibiting the following No. of rings.							Average No. of rings present.
		2	3	4	5	6	7	8	
21—30	4	...	4	...	...	...	...	...	3·00
31—40	19	3	12	3	1	...	...	...	3·11
41—50	56	2	30	17	4	3	...	...	3·57
51—60	48	...	12	20	13	3	...	...	4·15
61—70	43	...	3	18	14	6	2	...	4·44
71—80	32	...	3	6	14	6	2	1	4·78
81—90	2	...	...	...	1	...	1	...	6·00
91—100	1	...	...	...	...	...	1	...	7·00
TOTAL	205	5	64	64	47	18	6	1	

A study of these tables shows very clearly that in oysters of the same age there is a marked tendency for the number of rings to increase proportionally to the size to which the individual may attain. In all three series the average numbers of rings present for any given size are very fairly constant, such differences as are present being probably due to insufficient numbers examined and differences in physical conditions in different areas.

No one, I think, will deny that the formation of a ring is due to a period of shell formation followed by a partial or complete arrest of activity in the shell-producing glands of the mantle-margin, and the above tables show that the amount of shell produced during each period of activity increases up to the time when the animal attains to a size of 80 mm. and thereafter begins to diminish. Petersen found that in Danish oysters from the Lim Fjord, this diminution in the rate of growth occurred at 60 to 70 mm. The number of such periods of activity through which a given individual may pass in any given time varies so enormously, *viz.*, from 2 to 5 in 1½ years, from 2 to 7 in 2½ years and from 2 to 8 in 3½ years, that one must agree with Miss Massy that in the case of oysters they are of themselves quite useless as a guide to the probable age.

In the case of *Mytilus variabilis*, however, one is dealing not with individual rings, but pairs of rings, each pair consisting of a narrow part and a wide part, and I cannot help thinking that this difference in the rate of shell deposition corresponds to definite seasons, and is due to the markedly different conditions that exist in the Gulf of Suez in winter and summer respectively, and thus the rings do give a correct estimate of the age of the individual.

BIBLIOGRAPHY.

ANNANDALE, N., and SEWELL, R. B. S., 1921.—"The banded Pond-Snail of India." *Rec. Ind. Mus.*, Vol. XXII, Part III, No. 20. Calcutta.

MASSY, ANNE L., 1914.—"Notes on the evidence of age afforded by the growth rings of oyster shells." *Fisheries Ireland, Sci. Invest.*, 1913, II (1914). London.

PETERSEN, C. G. J., 1908.—First Report on the Oysters and Oyster Fisheries in the Lim Fjord." *Rept. Danish Biol. Sta.*, No. XV Copenhagen.

PETERSEN, C. G. J., 1918.—"The sea-bottom and its production of fish-food." *Rept. Danish Biol. Sta.*, No. XXV. Copenhagen.

SEMPER, 1874.—"Ueber die Wachsthums-Bedingungen des Lymnaeus stagnalis." *Arbeiten Zoologisch-Zootomischen Institut in Wurzburg*, Vol. I, p. 137. Würzburg.

SEWELL, R. B. S., 1922.—"Cercariae Indicae." *Ind. Journal Med. Research*, Vol. X, Supplement. Calcutta.

TATTERSALL, W M., 1920.—"Notes on the breeding habits and life-history of the Periwinkle." *Fisheries Ireland, Sci. Invest.*, 1920, I. London.