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THE ECOLOGY OF LAGOS LAGOON
III. THE LIFE HISTORY OF *BRANCHIOSTOMA NIGERIENSE* WEBB

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A study has been made of the distribution of the lancelet *Branchiostoma nigeriense* in the neighbourhood of Lagos.

From observations on the development of fertilized ova in the laboratory, an estimate of the duration of the embryonic period in this species has been made.

Systematic collections of both larvae and adults were made during the years 1953 to 1955, and from these the duration of the life cycle and the rate of growth of both the larva and the adult have been assessed.

It has been established that lancelets in the brackish lagoons at Lagos are derived annually from marine populations outside the harbour. The larvae enter brackish water when the salinity is not lower than 13 parts per thousand in the autumn, metamorphose at the end of December and give rise to adults which colonize the sand deposits of the lagoons. The adults reach maturity and spawn in the spring, but die shortly afterward when the salinity of the water falls below the threshold value for survival. The marine populations have an annual cycle, spawning from August to October or November each year.

Introduction

Considering the attention the lancelet has received from morphologists and the interest this animal has aroused as a chordate of comparatively simple if not primitive form (Medawar 1951), it is surprising how little is known with certainty of its life history, ecology and behaviour. At one time considered rare, it now appears that lancelets are not only extremely common in some localities, but are of world distribution in tropical and temperate zones. In the principle genus, *Branchiostoma*, twenty-two species have so far been described. These are closely similar in structure and, in many cases, can only be separated with the aid of a statistical analysis of the numbers of the repetitive parts and by minor differences in general form. The uniformity of this genus and its very wide distribution suggests, first, that it is monotypic and, second, that it is of considerable antiquity. Thus Medawar's (1951) hypothesis, that lancelets may have originated comparatively recently from ascidian stock and that some such form as the lancelet may have arisen on more than one occasion, should be viewed against the background of systematics and distribution. The lancelet may or may not be near the ancestor of higher chordates, but it would, nevertheless, appear to be an ancient form not unlike the primitive chordate. The life histories of lancelets and the reaction of these animals to different environments, therefore, are of interest, if only as an indication of the way in which an animal at this grade of organization might have lived and behaved under the changing conditions which evidently led to selection and to the evolution of higher forms.

In no single species of the genus *Branchiostoma* has the life history been worked out in detail. The embryology and larval development of *B. lanceolatum* was first described by

Willey (1890, 1891) from material taken at Faro near Messina, and his account of the later larval development is still the major work on the subject. He noted that spawning took place between April and September and occurred 1 h after sunset. Development reached the first gill pouch stage 36 h after cleavage, the second gill pouch appearing 2 weeks later. The period of larval life was believed to be about 3 months, metamorphosis taking place at the 14 to 15 gill pouch stage. In 1932, Conklin described lancelet embryology and development up to the 8th day, also in *B. lanceolatum* from Naples, and provided the account which is well known to students of zoology. Beyond this early stage, however, there is very little information on the rate of growth and duration of life in either the larva or the adult, while such observations on the mode of life of the animal as have been recorded often differ in detail. The reason for this probably lies in the difficulty of obtaining material and in the fact that the observations relate to more than one species.

The only species in which the rate of growth is known is *B. belcheri*. Chin (1941), in a paper on the biology of this lancelet at Amoy on the Chinese coast, states that *B. belcheri* normally lives for 2 to 3 years, first spawns when 1 year old and thence twice yearly in May to July and again in December. He found that the adult grew to a length of 30 mm in 1 year, 40 mm in 2 years and reached a length of 60 mm at the end of the 3rd year. As the maximum recorded length for this species is 70 mm (Webb 1955), it may be presumed that *B. belcheri* does occasionally live as long as 3 to 4 years. On the other hand, Bigelow & Farfante (1948) report that sexual maturity in *B. belcheri* is reached in the 2nd to 3rd year, but give no information on longevity. There is also a difference of opinion with regard to the mode of life of the larva. Van Wijhe (1926) suggests that the larva of *B. lanceolatum* is a bottom-living form, whereas Chin (1941) mentions that, in *B. belcheri* the larvae appear, in surface waters at low light intensity. It is unlikely that the behaviour of the larva in these two species is different and more probable that the observations were made on different stages in the larval life. There also seems to be some doubt as to the stage at which metamorphosis takes place, since Van Wijhe (1926) found that metamorphosis in *B. lanceolatum* occurred at the 18 to 19 gill stage and not at the 14 to 15 gill stage as reported by Willey (1890, 1891). As Van Wijhe's material was probably obtained from the North Sea, this may indicate a difference between the North Sea population and that in the Mediterranean. There is little else of value in the literature relating to the life history of lancelets and the general picture, therefore, is incomplete and confused.

The species considered here, *B. nigeriense*, occurs along the western half of the Nigerian coast and enters brackish lagoons and estuaries (Webb 1955, 1956). In the lagoons this animal is easy to collect in large quantities, and the various conditions under which it lives can be studied in a way that would be difficult if not impossible in the sea. In this paper an account is given of the life history of *B. nigeriense*. The reactions of this species to its environment will be considered in part IV.

The distribution of *Branchiostoma nigeriense* at Lagos

Branchiostoma nigeriense has been found in large numbers at Lagos and also at Port Harcourt in the Niger Delta (Webb 1955, 1956) and presumably occurs at suitable localities between these points. This lancelet tolerates water of low salinity and occurs in two morphologically distinct forms, the marine form from the open sea and the lagoon form from brackish water. The distribution of the adult lancelet in the Lagos area is given in figure 1 which shows the position of the localities sampled, together with the presence or absence of lancelets.

In the vicinity of Lagos, the marine form has been found in sand deposits immediately to the east of Lagos Harbour and, further afield, 12 miles E.S.E. of the harbour (see part II), but, from the very large numbers of larvae in the plankton at certain times of the year, it is evident that there must be extensive populations of this animal in the sea nearby.

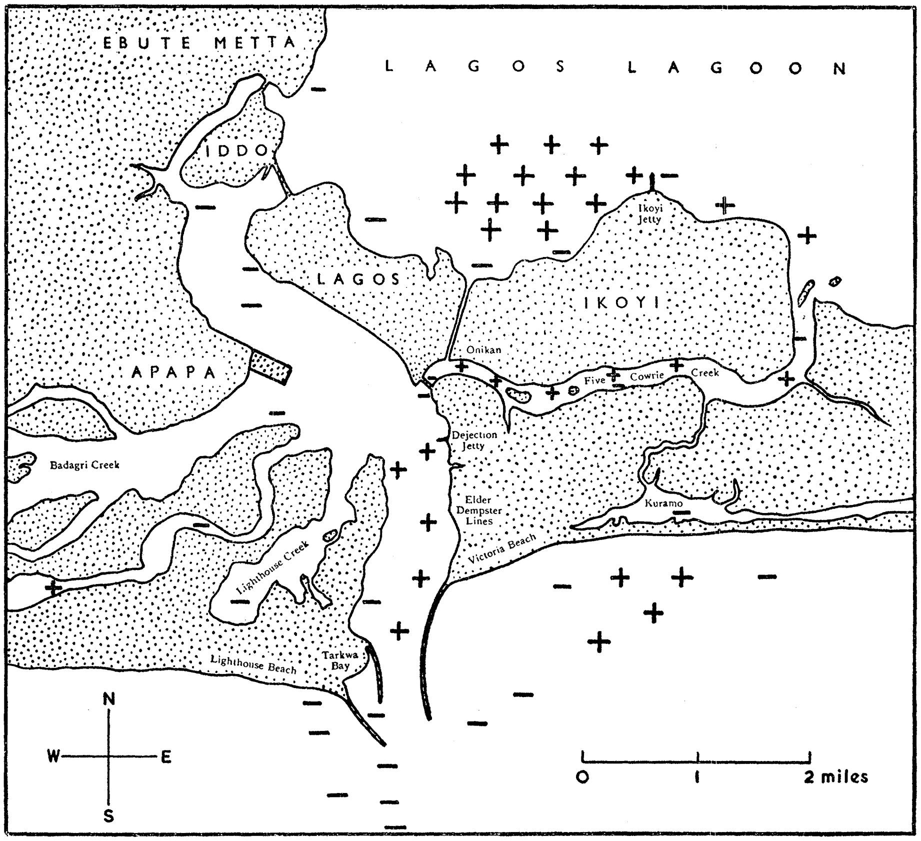

Figure 1. The distribution of *Branchiostoma nigeriense*

The lagoon form occurs in a number of restricted localities in the harbour and lagoon during the months of January to June when the salinity of the water is high (see part II). At this time, adult lancelets are present in the sand deposits of the southern reaches of the harbour, the north bank of Five Cowrie Creek, Lagos Lagoon north of Ikoyi Island and the southern arm of Badagri Creek (see figure 1). Lancelets are not found, however, in the deposits immediately seaward of the harbour mouth or, inside the harbour, on the west side of the southern region, or in the northern part opposite Lagos Island. They do not occur on the southern side of Five Cowrie Creek, nor in the south-west corner of Lagos Lagoon. They are also absent from the deposits immediately to the east of Ikoyi Jetty and from Lighthouse Creek and the greater part of Badagri Creek on the west side of the harbour (see figure 1).

In most of the areas where they occur, the lancelets are offshore in deposits permanently covered by water, but, on the north bank of Five Cowrie Creek and particularly at Onikan, they are numerous in the sand of the intertidal region.

The distribution of larvae in the plankton of the harbour is also seasonal. Larvae are present in salt water in the harbour from mid-September to mid-June, the salinity during the remainder of the year being too low for their survival (see part II). The number of larvae present at any one time, however, varies enormously and likewise their degree of development. Surveys of the incidence of larval lancelets in the harbour plankton carried out in 1953–54 and 1954–55 showed that, in September, larvae with from 6 to 8 gill pouches appeared in the plankton in the deeper water where the salinity was highest (see figure 2). At first they were few, but they increased in number until, by mid-December,

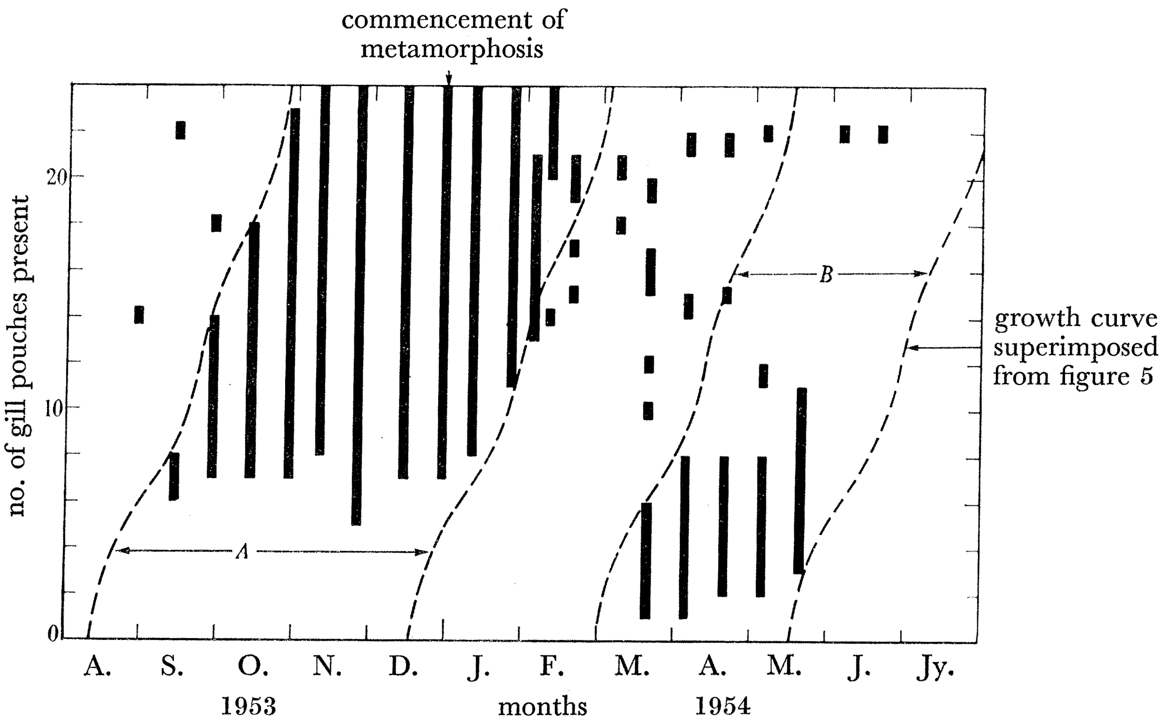

Figure 2. The distribution of larvae in the harbour plankton in the year 1953–54. *A*, autumn brood from the spawning of marine adults; *B*, spring brood from the spawning of Lagoon adults.

they were by far the most prominent organism in the plankton. The larvae grew rapidly and reached a length of 5 to 6 mm at the 20 to 25 gill pouch stage. At the end of December metamorphosis occurred in all individuals with more than 20 gill pouches, resulting in a sudden fall in the number of larvae in the plankton. During January and February the range in size of larvae decreased as those remaining in the harbour plankton approached metamorphosis while none of smaller size entered from the sea.

At the end of December young adults appeared at several localities in the harbour and Five Cowrie Creek and, about 2 to 3 weeks later, in Lagos Lagoon (see figure 1). These lancelets reached maturity by March and, in the latter half of that month, large numbers of very small larvae ranging from the 1 to 6 gill pouch stage appeared in the harbour plankton (see figure 2). There is little doubt that these larvae were the product of spawning of adults in the harbour, creeks and lagoon, as at this time of the year fertile ova were obtained from lagoon adults. The larvae were present until mid-May, growing to the 12 gill pouch stage, but then disappeared when the fall in salinity destroyed the adults and brought spawning to an end (see part II). After this date larvae were virtually absent from the plankton until mid-September except for an occasional specimen taken near the harbour mouth. Two broods of larvae, therefore, appeared in the harbour during 1953–54, as shown in figure 2, but neither completed there the entire period of growth from egg to metamorphosis.

The duration of embryonic development

Mature adults of *B. nigeriense* were collected from Lagos Lagoon in early April 1952, and placed in jars of lagoon water. They were taken by road to Ibadan, a distance of over 100 miles, and spawned shortly after arrival, thus providing fertilized ova from which embryos were obtained and the embryonic stages of development observed. Larvae were reared in the laboratory up to the 1st gill pouch stage, but attempts to keep them alive for a longer period proved unsuccessful. Other attempts to induce artificial spawning in Lagos were also unsuccessful, indicating that vibration during the journey to Ibadan may have led to the discharge of ova and sperm from lancelets in which the gonads happened to be ripe at that time. The duration of the various stages in the development of embryos at 30 °C and in water of salinity 20 parts per thousand, the temperature and salinity of the natural habitat, is given in the following list:

Embryonic development of Branchiostoma nigeriense

	hours
Fertilization to early gastrula	*ca.* 12
Early gastrula to late gastrula	2
Late gastrula to neural plate	1
Neural plate to neural groove and 3 somites	1
3 somites to 10 somites	4
10 somites to escape from vitelline membrane	2
Larva moving freely by cilia	4
Elongation of notochord	10
Commencement of muscular movement. Gill rudiments formed (length 0·5 mm)	2
Active and co-ordinated muscular movement	2
Appearance of 1st gill pouch (length 0·75 mm)	2
Time of development from fertilization to the appearance of the 1st gill pouch	42

Thus, under tropical brackish conditions, an actively swimming young larva at the 1 gill pouch stage developed in $1\frac{1}{2}$ to 2 days from fertilization. The times given are approximate, particularly for the period up to gastrulation, as the precise time of fertilization was not determined beyond the fact that it occurred subsequent to arrival at Ibadan at 7.0 p.m. Early the following morning all stages up to the early gastrula were found. The remaining times were based on the rate of development of a number of embryos.

These observations confirm the times for embryonic development given by Willey (1890, 1891) and Conklin (1932). It was noticed that the ova and developing embryos were heavier than water and sank to the bottom of their container. Thus Willey's (1890) statement that the embryos float on the surface of the water does not apply to *B. nigeriense* under lagoon conditions. However, as the material Willey used was collected from a small pantano or lake connected with the Straits of Messina, it is probable that the salinity of the water there was considerably higher than that from Lagos Lagoon, in which the embryos were reared in the present case, and this may have caused flotation. Although the precise time of spawning of *B. nigeriense* was not taken, it was certainly after sunset and therefore was not at variance with Willey's observation that spawning in *B. lanceolatum* occurs 1 h after sunset.

An assessment of the duration of larval life

The duration of the post-embryonic stages of development up to metamorphosis has been determined from both living and fixed larval material collected from the harbour plankton at intervals of 2 weeks throughout the years 1953 to 1955. During 1953–54 the collections made were purely qualitative, but, in 1954–55, steps were taken to assess not only the different larval stages present in the plankton but also their relative abundance.

Table 1. Body lengths of larvae of *B. nigeriense* at each stage in development as determined by the number of gill pouches present

number of larval gill pouches	body length of the larva (mm): range in length	average length
1	0·75	0·75
3	0·8 –1·25	1·0
4	1·0 –1·5	1·25
5	1·5 –2·0	1·75
6	2·0 –2·25	2·15
7	2·25–2·5	2·4
8	2·5 –2·75	2·7
9	2·75–3·0	2·9
10	3·0 –3·25	3·1
11	3·0 –3·25	3·2
12	3·25–3·5	3·3
13	3·25–3·5	3·4
14	3·25–3·75	3·5
15	3·25–3·75	3·55
16	3·5 –4·0	3·7
17	3·75–4·0	3·85
18	4·0 –4·25	4·1
19	4·25–4·5	4·35
20	4·5 –4·75	4·6
21	4·75–5·0	4·9
22	5·0 –5·5	5·4
23	5·25–6·5	5·9
24	5·75–6·75	6·4
25	6·0 –7·0	6·7

Larvae collected from plankton were measured either by length or by the number of gill pouches present. In fixed material it was difficult to count the gill pouches, particularly when these were numerous, without first clearing and mounting the specimens. Thus, when large numbers of fixed larvae were examined, measurement of length was found to be preferable in view of the great saving in time and labour. In the transparent living larva, however, it was frequently easier to count the gill pouches than to obtain an accurate measurement of length. In order to relate the number of gill pouches to the length of the larva, counts of gill pouches and measurements of length in a number of specimens at each stage of development have been made and are given in table 1.

Although some variation in body length at each stage, as determined by the number of gill pouches, was found, there was no overlap in the range of variation in length between successive stages except in larvae with from 10 to 17 pouches and again from 22 to 25 pouches (see table 1). When the average length at each stage was calculated, however, it was seen that there was a progressive increase in length of body with increase in number of gills. Nevertheless, the relationship between body length and gill number was not regular as is shown in figure 3 where the number of gill pouches is plotted against average body length. In the young larva and again in the late larva, the number of gill pouches increased slowly relative to the length of the body, but, in the mid-larva, the number of pouches increased from about 10 to 16 with very little increase in body length. The graph given in figure 3 is of value in calculating the approximate body length equivalent to a given number of gill pouches and vice versa, particularly for small and for large larvae, and enables measurements made by either method to be correlated.

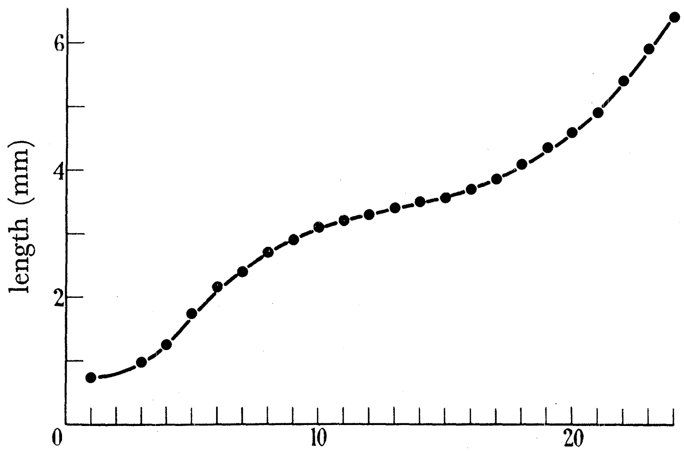

FIGURE 3. The number of gill pouches in relation to length in larvae of *Branchiostoma nigeriense*

The large number of gill pouches in the late larva of *B. nigeriense*, as compared with that in the corresponding stage of *B. lanceolatum*, appears to constitute a major difference between the species. Willey (1890, 1891) has shown that, in *B. lanceolatum*, only 14 or 15 gill pouches are formed prior to metamorphosis, while Van Wijhe (1926) found 18 or 19 gills in that species. In the Nigerian lancelet 21 or 22 larval gill pouches are usual, but the number may reach 25 in exceptional cases. As there is variation in the number of gill pouches formed before metamorphosis in *B. nigeriense*, it is possible that similar variation in *B. lanceolatum* may be responsible for the difference in the gill numbers given by Willey and by Van Wijhe.

Information on the duration of larval life up to the 8 gill pouch stage was available from the spring brood of larvae resulting from spawnings in the lagoon. The earliest date at which this spawning could have taken place in 1954, judging from the development of the gonads in lagoon adults, was very early in March. Collections of plankton in the harbour made on 5 March yielded no young larvae, but those on 19 March and 4 April contained larvae up to the 6 and 8 gill pouch stages respectively (see figure 2). These larvae, being the largest present, were likely to have been the products of the first spawnings. Allowing that the embryonic period occupied not more than 2 days and that embryos were unlikely to have been recovered from the plankton, it seems probable that the 2-day larva at the

1 gill pouch stage could have been reached by about 4 or 5 March at the latest. If this was so, then development to the 6 gill pouch stage would have occupied a period of the order of 16 to 20 days and development to the 8 gill stage about 30 days. These figures, however, do not agree with those of Willey (1890) who states that the appearance of the 2nd gill pouch in *B. lanceolatum* occurs 15 to 16 days after fertilization. In collections of harbour plankton made after 4 April, although larvae at the 6 to 8 gill pouch stage were numerous, larvae either smaller or larger than this were rare or absent. It is unlikely that the larvae in this spring brood ceased to grow beyond the 8 gill stage, and it is perhaps more probable that they migrated out to sea or were carried out of the harbour on the ebb tide. Information on the rate of development to be obtained from the spring brood, therefore, is limited to the early period up to the 8 gill stage and, in view of the difficulty of establishing the precise time of spawning, is to some extent conjectural.

An estimate of the duration of larval life beyond the 8 gill stage was made from the autumn brood. The autumn larvae first appeared in September in the harbour at the 6 to 8 gill pouch stage. These larvae, then, were either the product of a spawning of marine adults in the first half of August, as no adults are present in the harbour during the summer, or else they were the spring larvae returning on the rise in salinity without an increase in size. There is good circumstantial evidence that the first view is correct. It is known that larvae from the lagoon spawning disappeared from the harbour by the beginning of June, either being killed by the fall in salinity or being swept, or migrating, out to sea. Here the set of the current is predominantly from west to east across the harbour mouth. Thus, although the spring larvae were produced in immense numbers, it is difficult to see how they could have become widely distributed in the sea and, in the face of a current tending to carry them away from the harbour, have returned in September in even greater numbers. Moreover, plankton samples taken in November and December 1954 as far as 10 miles out to sea revealed large numbers of larvae in the surface waters. This suggests that, in the autumn, larvae were present in the waters around Lagos in numbers far in excess of those which could have been expected to have arisen from the limited populations of lagoon adults in the spring. In addition, the occurrence of small larvae with about 8 gill pouches in the harbour plankton during the entire period from September to December suggests that more or less continuous spawning was taking place in breeding populations outside the harbour during the months of August to November. This view is supported by the fact that the number of larvae in the harbour plankton increased to a maximum at the end of December prior to metamorphosis. To assume that the small larvae in the harbour in the autumn were the spring brood returned from the sea supposes that some at least of the spring larvae remained 4 to 6 months outside the harbour and, during this time, had grown scarcely at all. The evidence, therefore, clearly suggests that the autumn larvae were the product of extensive marine populations.

The absence of very small larvae from plankton samples collected in the autumn, even outside the harbour, may have been due either to the samples having been taken at some distance from the spawning grounds, or to the very young larvae remaining at the sea bottom until they had reached the 6 gill stage. However, even in samples from the more turbulent waters of the harbour in the spring, which might be expected to contain some bottom-living forms, larvae younger than the 6 gill stage were very rare, whereas those at the 6 and 8 gill stages were numerous, and these samples were taken above grounds in which adults were known to occur. It seems highly probable, therefore, that the larva up to the 6 gill stage is normally a bottom-living rather than a planktonic form. If at this stage the larva becomes planktonic preparatory to entering a migratory phase, the predominance of 6 to 8 gill larvae and the rarity of earlier or later forms in the harbour plankton in the spring would be explained.

From the collections of larvae made in the autumn of 1953 and shown in figure 2, it is seen that the most advanced larvae taken in mid-September were at the 8 gill pouch stage and 15 days later had grown to the 14 gill stage. Similarly, later collections showed that development from the 14 to the 18 gill stage also occupied 15 days, while that from the 18 to the 23 gill stage, a size at which metamorphosis could have occurred, took a further 14 days. The period of development from 8 to 23 gills, therefore, was 44 days which, with the 30 days suggested for the period from fertilization to the 8 gill stage, gives a total period of larval development of 74 days. However, it is also evident from figure 2 that this period was not necessarily the same as the larval life, for, although many larvae reached maximum size in November, metamorphosis did not take place until the end of December and then involved all larvae of the requisite size irrespective of the time they had been at that stage of development.

To corroborate these findings, further samples were taken a year later in the autumn and winter of 1954–55 using a method which would give, in addition to a qualitative indication of the size range present at any one time, some estimate of the relative abundance of larvae at different stages of development. Accordingly, standard samples of plankton were collected near the harbour mouth at each high spring tide. In each case five vertical hauls were made from a depth of about 5 fathoms. The samples were fixed in Bouin's fluid and all lancelet larvae contained therein were measured and counted. The larvae were divided into three groups (small, medium and large) corresponding approximately to the sizes 2·5 to 4·0 mm, 4·0 to 5·0 mm and over 5·0 mm in length, and to the gill pouch numbers of 8 to 16 gills, 17 to 21 gills and 22 to 25 gills respectively. These sizes were chosen as they were the most easily recognized in sorting. The results obtained are given in figure 4, where the number of larvae of each size per haul is plotted against time.

Two methods of analyzing this data seemed appropriate. As in the treatment of the 1953 samples, it was possible to compare the times of first appearance of larvae in each of the arbitrary size groups and thus trace the development of larvae presumed to be from the first spawning. Alternatively, a comparison could be made of the times at which an equivalent density of larvae was reached in each group. In each case it was considered that, as the youngest larvae collected in the first sample early in September had already reached the 8 gill pouch stage, they must be about 30 days old. In applying the first method, it was found that the first medium size larvae were collected 30 days after the first appearance of small larvae, but it was evident from their numbers and from the backward projection of the graph in figure 4 that larvae in this group had probably been present in the plankton 5 days earlier. It may, therefore, be assumed that growth from the 8 gill stage to the 16 to 18 gill stage, at which the average length of the larva was about 4·0 mm, took approximately 25 days. Similarly, the first large larvae were collected after a further 19 days and this can be assumed to be the time of development from the 16 to 18 gill to the 22 gill stage at which metamorphosis could occur. The total period of development estimated in this way, therefore, was 74 days, which agrees precisely with the estimate made from samples taken the previous year.

In comparing the times at which an equivalent density of larvae was reached in each group, the means of the curves for the numbers of each of the three sizes were taken from figure 4. In the cases of the curves for the small and medium size groups, the mean is also approximately the mode, but in the curve for the large larvae this is not the case. This curve is asymmetrical since metamorphosis intervenes at a definite time and appears to involve almost all larvae in the group. If this curve is extended, however, to give the expected number of large larvae which would have been present had metamorphosis not

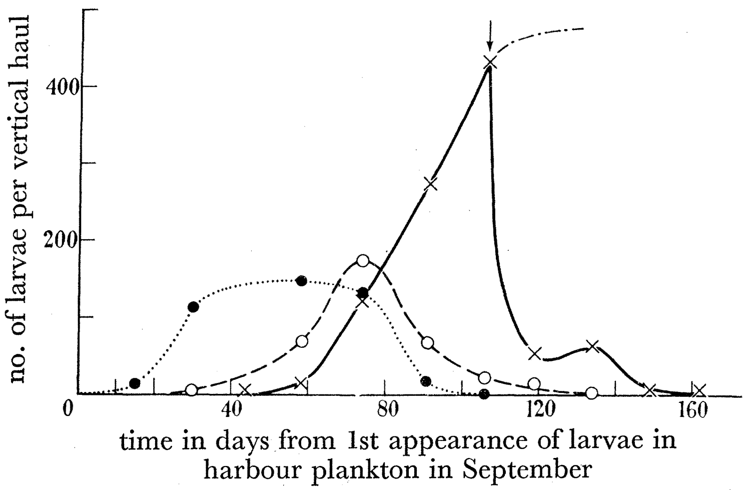

FIGURE 4. The relative proportions of small (●) medium (○) and large larvae (×) in the harbour plankton in the autumn and winter of 1954–55. ·—·—, hypothetical extension of curve. ↓, metamorphosis.

taken place, it then becomes symmetrical with the mean at 84 days from the time of commencement of sampling. As the means of the curves for the small and medium-sized larvae fall on the 55th and 75th days of sampling respectively, it can be assumed that the time of development of larvae from the mean size of the small group to that of the medium group was 20 days and from the mean size of the medium group to that of the large group was 9 days. In other words, development from the 12 gill to the 19 gill pouch stage occupied 20 days and to the 23 gill stage a further 9 days. These figures are in agreement with an estimate of between 70 and 75 days for the total larval development. Similar calculations choosing different densities of larvae can also be made on the assumption that the differences between the times at which a definite density in each of the three groups is first reached in the plankton will be approximately equal to the times taken for the larvae of one size to grow to the next, assuming no mortality. If a density of larvae giving 100 specimens per haul within one range of size is taken as the point for comparison, it is seen from figure 4 that this density occurred in larvae of small size 28 days after their first appearance in the harbour plankton. These larvae grew to medium size and were equally numerous 34 days later, and to larvae of large size, also at the same density, 8 days later still. Thus development from a little beyond the 8 gill stage to the 22 gill stage occupied 42 days, giving a total period of development a little in excess of 72 days.

As these estimates of the duration of the later larval life have been made using different points on the distribution curves, they assess the rates of growth of the larva at slightly different periods of the year. The difference in time between the first appearance of larvae in a size group and the point at which a density of 100 per haul was reached varied from 26 to 37 days according to the group, while the difference between time of first appearance and that of peak density or the mean of each curve varied from 40 to 55 days. The close agreement of the estimates both from one year to the next and at different times within the one year suggests that the larval development is not subject to great variation. A list showing the duration of the successive stages in the larval life computed from these figures is given below:

The larval development of Branchiostoma nigeriense *at* 26 *to* 28 °C

	days
Fertilization to appearance of 1st gill pouch	2
1st to 6th gill pouch	16
6th to 8th gill pouch	12
8th to 12th gill pouch	12
12th to 14th gill pouch	5
14th to 17th gill pouch	10
17th to 18th gill pouch	5
18th to 19th gill pouch	4
19th to 23rd gill pouch	9
Duration of larval development	75

When the computed developmental periods taken from the spring and autumn data and given in the above list are plotted against the number of gill pouches (see figure 5, broken line), the graph thus obtained is an irregular curve. If, however, the number of gill pouches is converted into the average length of the larva in millimetres by reference to the graph in figure 3 and the length of the larva is then plotted against time as in figure 5 (full line), it is seen that a regular curve is obtained. This curve rises steeply for the first period of 12 to 15 days, less so for the next 50 days and again steeply for the last 8 to 10 days when the 23 gill pouch stage is reached. The regularity of this growth curve suggests that the determinations of the duration of the larval stages based on the rate of increase in the number of gill pouches are reliable.

It has already been mentioned that metamorphosis in the autumn brood did not take place until the end of December, although young larvae estimated to be about 30 days old were present in the harbour plankton by mid-September. It is evident, therefore, that some of these lancelets remained in the larval state for as long as 140 days, although they had reached a size when metamorphosis could have occurred in 75 days. This is demonstrated when the growth curve given in figure 5 is superimposed on the chart showing the distribution of larvae of different sizes at different times of the year at appropriate points to separate the broods (see figure 2). It then becomes clear that the young larvae spawned at sea in August, grew to full size by early November and remained at this stage for about 2 months before metamorphosis occurred. In samples taken in November and early December there were no signs of metamorphosis in any of the larvae examined, such as was found in almost all cases of fully grown larvae taken at the end of December and early in January. The late December larvae metamorphosed in the laboratory, whereas others equally large taken earlier did not. The reason for the delay in metamorphosis in certain cases is not understood. The fact that larvae of ages ranging from 75 to 140 days metamorphosed within a few days of one another suggests that the stimulus was environmental and connected with changes that took place in the harbour at that time of the year. Changes in salinity are unlikely to have been directly responsible, for the larvae remained in the deep water of high salinity. The onset of metamorphosis, however, may have been in response to a change in light intensity. Until the latter part of November, the surface waters of the harbour were of low salinity and the larvae were restricted to the deeper

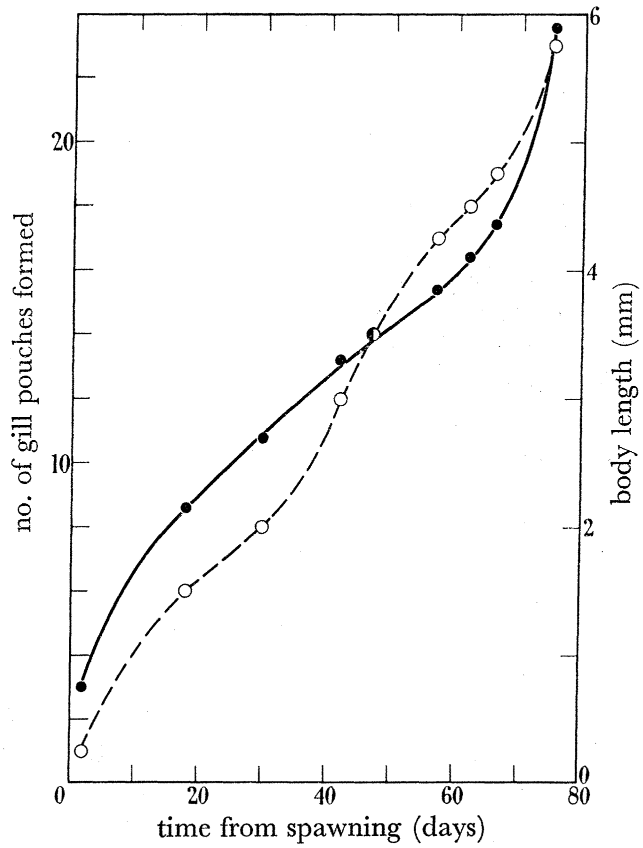

Figure 5. Computed rate of growth of larva of *B. nigeriense*. ○, development of gill pouches; ●, increase in body length.

levels where salinity was high and, in view of turbidity, light intensity must have been low. In late November and in December the salinity of the surface water rose, turbidity decreased and the larvae appeared near the surface. In these surface waters the larvae were subject to light of high intensity and it may have been this change which was responsible for initiating the physiological processes which led to metamorphosis. Whether this was in fact the case requires to be proved by further investigation.

The rate of growth of the adult

The rate of growth of the adult has been measured from lancelets collected at regular intervals from the sand at Onikan and also less frequently from the deposits in Lagos Lagoon north of Ikoyi Island and from locations in the sea to the east of Lagos Harbour (see figure 1). The advantage of the brackish lagoons as a site at which the rate of growth of the adult can be studied lies in the fact that, as all adults in the lagoons are killed by falling salinity in the summer, recolonization by newly metamorphosed lancelets in December can be observed without complications arising from the presence of lancelets of previous generations.

At Onikan during the months of January to May 1953, sand in which the animal was known to occur was taken from the same area of a few square yards just below the low spring tide level at intervals of about 2 weeks. The sand was treated with formalin and sieved to recover all lancelets. The catch varied in numbers from time to time, but was never less than 80 and on one occasion exceeded 500 specimens. The length of each lancelet was measured and the number of each size expressed as a percentage of the total obtained from each sample. A series of curves showing the distribution of animals of each size at monthly or half monthly intervals is given in figure 6.

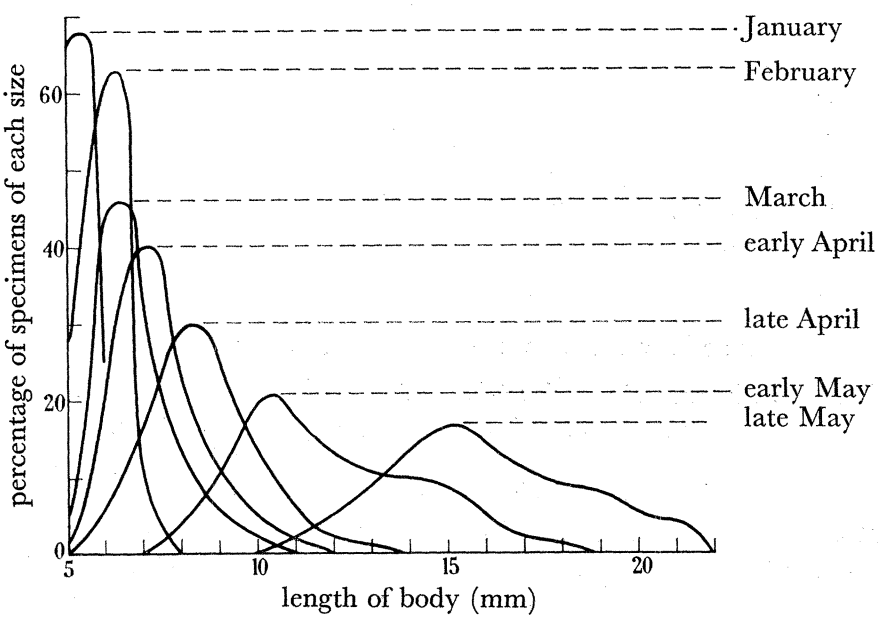

FIGURE 6. The range of size of adults collected at Onikan in 1953.

Young adults on settlement were found to vary in length from 5 to 6 mm and the 1st sample taken on 15 January contained specimens within this range. The series showed an approximately normal distribution with the mode at 5·3 mm. As the presence of post-metamorphic lancelets was first observed at Onikan on 31 December, it may be assumed that the sample taken on 15 January was composed of newly metamorphosed individuals and all ages up to 2 to 3 weeks after metamorphosis. It is evident, therefore, that not more than 1 mm of growth had occurred in the oldest lancelets during this period. Specimens 5 mm in length were present in all succeeding samples taken up to the latter half of April, although in decreasing numbers. This indicates that settlement of newly metamorphosed individuals took place continuously until April, which is in accordance with the presence of larvae in the plankton samples from the harbour during that period (see figures 2 and 6). As a result of continued settlement, the range in length in samples of adults from Onikan gradually increased. The rate of growth of the lancelets can be calculated from these samples by comparing either the largest specimens in each, or the smallest specimens, or the modes of the distribution curves. A comparison of the length of the largest specimens in each sample gives a measure of the maximum rate of growth throughout the period of 18 weeks from early January to early May, while that of the smallest, in view of the continued settlement of larvae until April, gives the minimum rate of growth during the period late April to early May of newly metamorphosed lancelets. Thus it is possible to compare the early stages of adult growth at different times (in January and in April) and also the early stages with the later stages at the same time (in April and May). The modes of the distribution curves of the separate samples give an approximately average figure for the rate of growth during the entire period of sampling. The growth curves obtained in

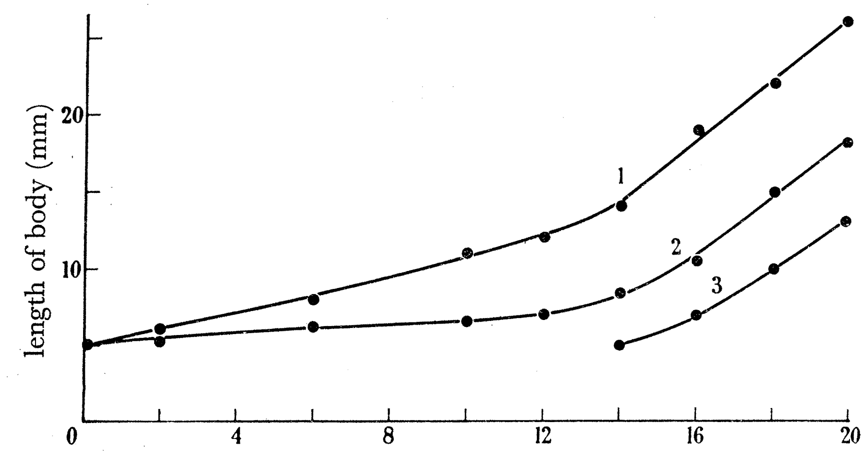

FIGURE 7. The rate of growth of the adult at Onikan in 1953. 1, largest adults; 2, modes of distribution curves; 3, smallest adults.

these three ways are given in figure 7. From these graphs it can be seen that there was a steady increase in the length of the largest specimens until the middle of April (14 weeks' growth) followed by a much more rapid increase from the end of April onward. This greater rate of growth might be held to have been due to the increased feeding capacity of the larger animals except that the rate of growth of the smallest lancelets was nearly as rapid as that of the largest during the same period and considerably more rapid than that of the largest lancelets at a comparable stage of growth 14 weeks earlier. It is evident, therefore, that the rate of growth of all stages was more rapid in April and May than during the period January to March. This can be attributed to an increase in food supply following the influx of fresh water into Lagos Lagoon with the onset of the rains at the end of March (see part II). The rivers bringing down mineral salts and organic debris presumably increased the fertility of the lagoon and thus caused a spectacular growth of phytoplankton in the lagoon and harbour which was observed at that time.

The collection of large numbers of lancelets from a very limited area at frequent intervals at Onikan may be questioned on the grounds that successive reduction in the population may have influenced the rate of growth. There is evidence from observations made in the laboratory, however, that populations of lancelets are not static, a continuous interchange of individuals taking place between adjacent areas. The number of lancelets in one small area of sand may be very high, while in another a few feet away lancelets may be virtually absent. It is evident, however, that the numbers taken in sampling were small in comparison with the size of the populations in the immediate vicinity of the area sampled. Repeated sampling from that area, therefore, was unlikely to have altered the composition of the population sufficiently to have affected the rate of growth of the individuals, and a plentiful supply of lancelets was evidently available for repopulation before the next sample was taken. That this was so was shown by the fact that the variations in the numbers of lancelets taken from time to time showed no trend which might have indicated depletion of the population until the numbers began to be affected by the fall in salinity at the end of May.

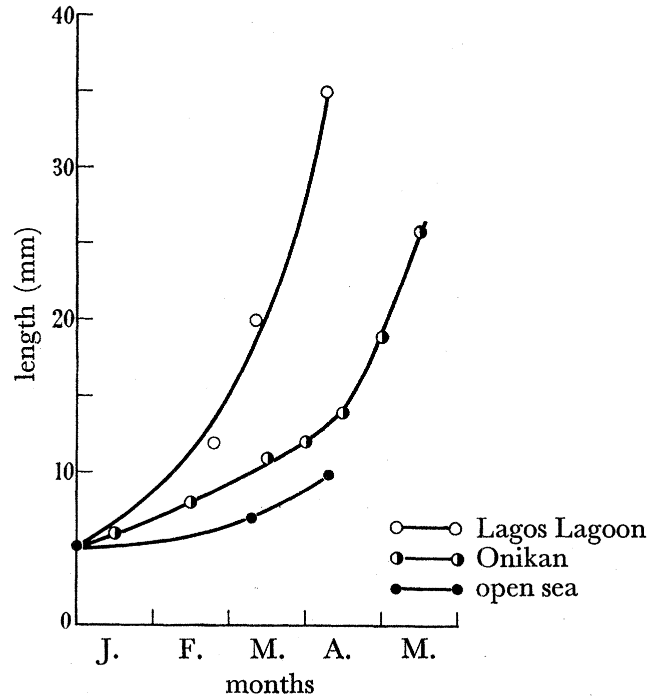

FIGURE 8. Graph showing the difference in rate of growth of adult *B. nigeriense* in Lagos Lagoon, at Onikan and in the open sea.

The samples of lancelets taken from Lagos Lagoon and from the sea east of the harbour mouth were not so comprehensive as those from Onikan. It was found that the lancelets grew considerably larger in the lagoon than in Five Cowrie Creek in spite of a shorter growing period. In the lagoon the rise in salinity in December and January lagged behind that in Five Cowrie Creek and the harbour (see part II), so that the young adults did not appear in the sand deposits north of Ikoyi Island until the end of the third week in January when the salinity had risen above 13 parts per thousand. Similarly, lancelets disappeared from the lagoon early in May, when the salinity fell appreciably below that level, whereas at Onikan they persisted until early June. The period of growth in the lagoon, therefore, was not longer than 16 weeks as compared with 22 weeks at Onikan. In the lagoon, lancelets grew to a maximum length of 35 mm and the majority of specimens were about 30 mm at the end of April. At Onikan, specimens as large as 25 mm were rare. It is evident, therefore, that the increase in length in lagoon lancelets was approximately twice as rapid as in Onikan lancelets, while the increase in weight was between the square and the cube of this figure. A comparison of the rate of growth of lancelets at these localities is given in figure 8. Clearly the great disparity in growth rate in lancelets from the lagoon

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and from Onikan must have been related to the food absorbed by the animal and may have been governed by a number of factors affecting the availability of the food supply which will be discussed elsewhere (see part IV).

Only two samples of the marine population outside the harbour were taken owing to the difficulty of collecting immediately behind the heavy surf. Lancelets from this locality were much smaller than those from either Onikan or Lagos Lagoon. Assuming that they had been derived from larvae metamorphosing at the end of December and of length about 5 mm, the young adults had grown to only 7 mm by the first half of March and to 10 mm 1 month later. A graph showing the rate of growth of these marine lancelets is given in figure 8.

It is quite clear that the food supply in the open sea at Lagos is much inferior to that in the lagoons. At this point on the West African coast the continental shelf is comparatively wide and there is no upwelling of cold water from the Atlantic deeps bringing with it a replenishment of nitrates and phosphates. Moreover, the discharge of rivers into the sea, which would help to maintain the fertility of the coastal waters of Western Nigeria, is effectively prevented by the presence of a barrier beach and lagoon system (see part I). Admittedly there is a discharge of river water from Lagos Harbour, but not at the time at which the lancelet samples were taken. Lancelets of this species do grow to a length of 35 mm in these coastal waters, for a specimen of this size has been taken 12 miles E.S.E. of Lagos Harbour (see Webb 1956). The slow rate of growth of lancelets in the sea provides a clue to the difference in time of spawning in the marine as compared with the lagoon population. It seems probable that, unlike the lagoon lancelet which reaches maturity and spawns in 2 to 3 months after metamorphosis, the marine form takes 7 to 8 months to achieve a similar degree of growth, thus accounting for the appearance of two broods of larvae, a lagoon brood in the spring and a marine brood in the autumn.

The rate of growth in the post-metamorphic stage of *B. nigeriense* can be compared with that in *B. belcheri*. Chin (1941) found that *B. belcheri* in Chinese waters grew to a length of 30 mm in 1 year. The rate of growth of *B. belcheri*, therefore, agrees with that of *B. nigeriense* under marine conditions, but is very much slower than that of the lagoon form of the Nigerian species. However, *B. belcheri* lives for 3 to 4 years and spawns several times during its life, and in this period grows much larger than *B. nigeriense*. The maximum body length the Nigerian species is known to attain suggests that this lancelet lives for one year and spawns only once. From the condition of lancelets which have recently spawned in the lagoon, it seems likely that spawning is followed by death, but this cannot be assumed with certainty as their moribund state may have been due to the low salinity of the water. The relatively small size of the other species of lancelet found in West Africa (see Webb 1955, 1956) indicates that they, too, may possess an annual life cycle.

The relation between the marine and lagoon populations

The relation between the marine and lagoon populations of *B. nigeriense* is illustrated by the diagram in figure 9 showing the growth, distribution and fate of lancelets derived from spawnings of marine adults in August to October. In this diagram the months of the year are given on the horizontal axis of the graph, while the vertical axis is divided into 35 parts representing both the length of the animal in millimetres and the salinity of the water in which it lives in parts per thousand. The curves bounding the stippled area represent the maximum and minimum body length of lancelets to be found at any one time and the stippled area itself the range of size. The symmetrical curve shows the salinity of the surface water of the harbour at different times of the year. Thus, from this diagram it is seen that spawning in the marine population commences in early August and continues until the end of October or early November, although a few larvae may be produced as late as the end of December. During the spawning period the earliest larvae grow to a length of 5 to 6 mm while those from later spawnings are correspondingly smaller. After

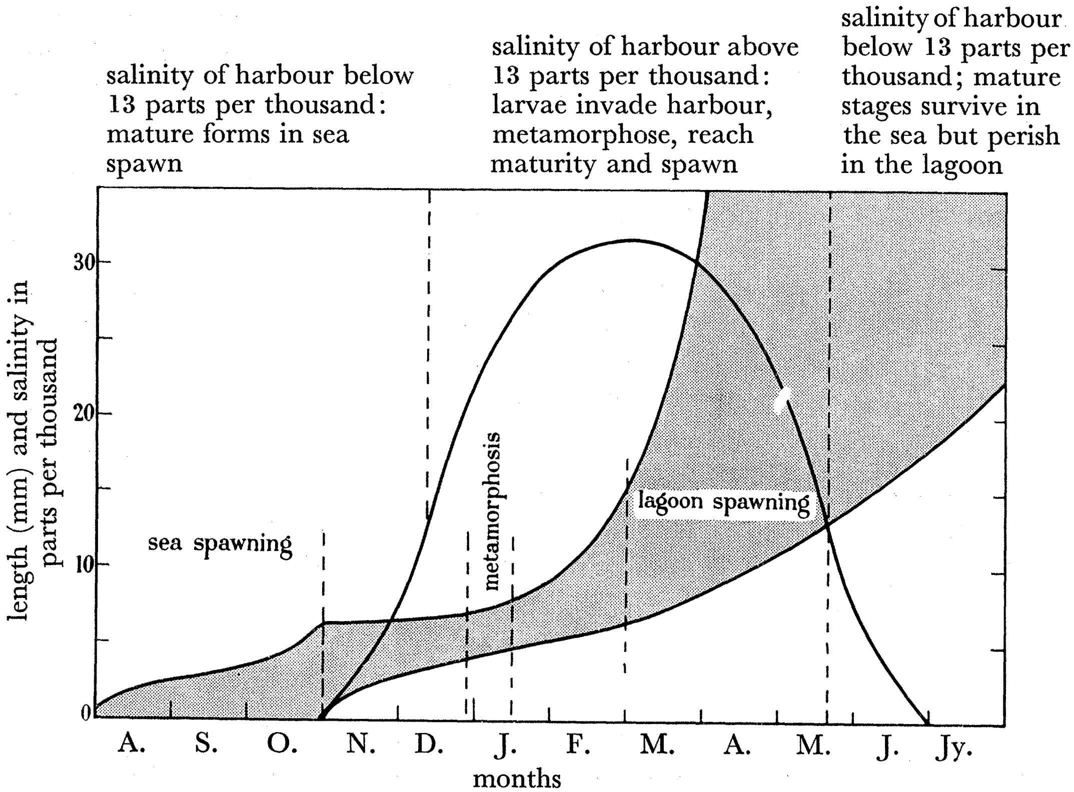

FIGURE 9. Diagram showing the growth, distribution and fate of lancelets derived from spawnings of marine adults during the months August to October.

October, when the main spawnings have ceased, the most advanced larvae remain in a state of almost suspended growth while the younger larvae develop to the stage at which metamorphosis can occur. During this time the salinity of the surface waters of the harbour is rising, as shown by the salinity graph in figure 9, and by about 10 December has reached 13 parts per thousand the limit which can be tolerated by the larvae. About this date, therefore, the larvae first appear in the surface waters of the harbour, although they have been present in the deeper waters near the harbour mouth for some time previous to this. At the end of December, and for 2 weeks following, metamorphosis of 75 % of all larvae in the plankton takes place and young adults appear in the sandy deposits first of the harbour and Five Cowrie Creek and then, toward the end of January when the salinity of the lagoon water is above the threshold value, in the deposits north of Ikoyi Island. The differential rates of growth of the adults in the lagoon, in Five Cowrie Creek and in the sea now give rise to an enormous range in size, as shown by the breadth of the stippled area from March onward in figure 9. The lagoon populations reach maturity in March and spawn, the lagoon spawning continuing until May when the salinity falling below 13 parts per thousand kills the adults (see figure 9). The marine populations, however, persist, reach maturity at the end of July and thus complete the cycle.

The continuity of the species, therefore, is maintained by the marine population and invasion of the brackish water of the harbour and lagoons takes place only when conditions of salinity permit. The fact that these lancelets are able to reach maturity and spawn during the short period of high salinity in the lagoon is entirely fortuitous and appears to play no essential part in the annual life cycle. Some of the larvae from that spawning probably perish and the fate of those that may find their way to sea is not known. As they are out of phase with the life cycle of the marine population, the chance of their eventually producing offspring, if they reach what are evidently densely populated marine sand deposits, would seem to be very small. Adults derived from lagoon larvae would not be expected to mature at the same time as those from marine larvae which have never entered brackish water. Nevertheless, the possibility of some of the lagoon larvae reaching maturity and spawning cannot be ruled out and perhaps the few young larvae which appear in November, December and early January, after the main marine spawning, may have such an origin. Even if this is the case, such late larvae do not give rise to lagoon adults which are sufficiently advanced to spawn and thus there is unlikely to be any direct genetical continuity between the lancelet populations of the lagoon from one year to the next. Thus it becomes quite clear that the morphological differences between the marine and lagoon forms of *B. nigeriense* described by Webb (1956) are environmental in origin and that there is no genetical basis for the distinction between these forms.

Summary

1. The seasonal and regional distribution of both the adult and the larva of the lancelet *Branchiostoma nigeriense* in the neighbourhood of Lagos is given. The adults are found in sandy deposits in Lagos Lagoon and Lagos Harbour during the months of January to June, and also in marine deposits outside the harbour. The larvae are present in the harbour plankton from mid-September to mid-June, but are most numerous in November and December and again in March and April. There are two broods of larvae, the autumn brood being derived from the marine population and the spring brood from the spawning of adults in the lagoon.

2. The duration of the embryonic period of development up to the appearance of the 1st gill pouch in *B. nigeriense* has been estimated to be 42 h at 30 °C and in water of salinity 20 parts per thousand.

3. An assessment of the duration of larval life has been made from the times of appearance of the different larval stages in the harbour plankton. It is estimated that the larvae reach a stage of development when metamorphosis could take place in 75 days from fertilization, but that, for reasons which are not fully understood, metamorphosis may be delayed for a further period of up to 65 days giving a maximum larval life of 140 days.

4. The relation between the number of gill pouches and body length in the larva has been determined, and from this information a growth curve for the larva has been constructed.

5. The rates of growth of adults, both from the lagoons and from the sea, have been measured. It is found that, in the lagoons, growth is more rapid in April and May than during the months January to March. This is correlated with a heavy growth of phytoplankton in the lagoons following the influx of fresh water from the rivers at the onset of the rains. The rate of growth of lancelets is much more rapid in the lagoons than in the sea. The higher fertility of the lagoons as compared with the sea is believed to be due to the presence of a barrier beach which prevents the river water reaching the sea along most of the coast.

6. A diagram has been prepared showing the relation between the marine and lagoon populations. It is demonstrated that the lagoon population is derived annually from the marine lancelets which spawn from August to October. Larvae enter the lagoons from the sea when the salinity rises above 13 parts per thousand and metamorphose to form young adults which colonize the lagoon sand deposits in January. These young adults grow rapidly and reach maturity in March when they spawn giving rise to a spring brood of very young larvae in the harbour plankton. The fall in salinity below the threshold value at the end of May kills the lagoon population and thence no lancelets are found until a fresh brood of larvae enter the harbour in the autumn. There is, therefore, little chance of a direct genetical continuity being maintained between lagoon populations of successive years.

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