SOME ASPECTS OF THE BIOLOGY OF

VENERUPIS PULLASTRA (MONTAGU).

by

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Volume I

Text

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Table of Contents.

Introduction.

The original plan in this investigation was to study the general biology of Venerupis pullastra (Montagu). It was soon realised that the work would have to be confined to certain phases of the life history and these were chosen in an effort to cover the sections in which the information on marine Lamellibranchia, such as Venerupis, was felt to be inadequate. As a result, the work viewed as a whole may lack continuity and coherence.

In the main, the investigation centres on the larval and spat stages of the life history; a part which has been largely neglected in Lamellibranchia other than oysters. The efforts of Thorson, culminating in his extensive report (Thorson 1946) on the reproduction and larval development of Danish marine bottom invertebrates, have assisted greatly in correlating and furthering work in this field.

In addition to the larval and spat work, some emphasis has been placed on breeding, and while the results from this work are in no way conclusive, they may be of interest in a comparative way.

According to Winckworth (personal communication 1948), until recent years the genus Venerupis has been grouped with Paphia and Tapes into one genus, sometimes called Tapes and sometimes by the older name Paphia. Winckworth recommends Thiele's (1935) arrangement in which, for the species being studied here, the name Venerupis pullastra (Montagu) is recognised. In addition the species

/species will occasionally be referred to by the name "clam", and D'Arcy Thompson (1947, p.288) is cited as the authority, although the name is used extensively in North America.

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The Identification of the Veliger.

The literature on the identification of the veliger larvae of lamellibranchs is not extensive. Stafford (1912) was one of the first to do important work on the subject. He indicated suitable methods of investigation and figures, and describes eight Canadian Atlantic species. Ohdner (1914) has identified several species from Rovigno and his figures for Saxicava and Lima are good. Kandler (1926) in one of the better papers on the subject, described several North Sea species and his figures are clear and accurate. Lebour (1937, 1938a, 1938b) did extensive work on lamellibranch larvae and has described 17 species from Plymouth. Unfortunately, both the figures and the descriptions are vague and are consequently of limited use. Miyazaki (1935, 1936a, 1936b) has given useful descriptions of 8 species of Japanese lamellibranch veligers. Werner (1939) in an excellent paper, goes into the problem in detail and studies shell structure of the veliger and uses hinge teeth and ligaments as diagnostic features. He also found the erstwhile prodissoconch could be divided into a first and a second prodissoconch on the basis of shell development and structure. The size of the first prodissoconch, designated as Prod. 1, is relatively constant for any given species and is apparently a more reliable diagnostic feature than Prod. 11, the setting size of the larva, which several authors have found to vary between wide limits; although Lebour (1938b) has set up a key for the identification of the various species/

/species of Cardium found at Plymouth, on the basis of such measurements. Jorgensen (1946) describes and figures about 25 species of veligers from Danish waters and on the whole this is a most useful work. The larvae of all commercial species of oysters have been figured many times and these are probably the best known of all marine lamellibranch veligers.

A fact to be taken into consideration when describing lamellibranch veligers is that those who are apt to make most use of the identifications are the oceanographic plankton workers, whose material is usually preserved. The colour goes quickly and all that is left is the outline, its shape and size, and the hinge teeth and ligament. All this is present only if the material has not been too well preserved for even neutral formaling in time becomes acid and dissolves away the fragile shells. Colour, then, often a valuable aid in identification, is lost to the plankton research worker, as are other anatomical details such as the position of the digestive gland, and the presence or absence of eye-spots or flagella.

Therefore in the description to be given for the larva of V. pullastra, attention will be directed to those diagnostic features remaining after fixation. The essential part of a description of a veliger is the illustration. No amount of written description can take its place. Drawings of the complete animal will be given as well as the external view of a single valve. Using the whole veliger, the tilt/

/tilt due to the lift of the umbonal region may vary a good deal, so affecting the outline. The only consistent shape is obtained from an external view of a single valve. Most authors on veliger identification have relied entirely on camera lucida drawings; in addition to these it is believed that photomicrographs of the veliger will in the future be used to a greater extent. No photomicrographic apparatus was available for the present investigation, so the author's own 35 mm. camera was adapted for the purpose, and all the photomicrographs in the thesis have been taken with the adaptation. The results are not as good as they might be, because of the difficulty in obtaining the correct focus. However, the photographs give much better representations of the larvae than the camera lucida drawings; and Mr. C.B. Rees of the Leith Laboratory of the Hull Oceanographic Department, who has been studying lamellibranch larvae from plankton recorder records, has found them to be of more value than drawings.

Method.

There are two main approaches to the study of lamellibranch veligers from the point of view of identification. The first is to study the succession of sizes of various forms as they appear and develop in the plankton and then associate the largest of these larvae with the newly settled spat. In turn, the spat are followed through individuals or groups of gradually increasing size until specific identification is possible. Peculiarly enough,/

/enough, it is the identification of the spat that is often more difficult than the linking up of larva and spat. To obtain the spat, cardboard egg separators dipped in a mexture of tar and pitch, separated by shells of Ostrea, and strung on wire, were used. The cardboard soon became coated with algae, detritus, and the normal sequence of fouling organisms, the whole of which provides an ideal settling surface for many species of lamellibranchs. In addition, sand and mud from the habitats of likely species may be sieved and ellutriated.

The second approach to the identification problem is to culture the larvae, either from the fertilised eggs or by picking out numbers of any one species, and attempting to culture these through to the spat stage. Both these methods were used, but the latter one was more successful and easier. Culture from the fertilized egg after natural spawning by the female may be carried out, but this was not always possible. The veligers picked out of the plankton were kept in 2 litre jars stirred by the plunger system. They were fed with cultures of naked flagellates, but it was found that unfed veligers grew and metamorphosed as well as those which were fed. Groups with sand or mud in the plunger jar were no more successful than those without. There was no consistency about any of the culture results. Some species, among which V. pullastra was fortunately included, were more easily cultured than others.

Plankton tows with fine mesh nets were taken at frequent intervals throughout the summer, from Keppel Pier. The ebb tide runs southward at a rate of 3-4 knots past the pier, so that on normal tides the plankton nets fish well from the pier and the use of a boat is unnecessary. The tows were purely qualitative in nature. The lamellibranch larvae from the tow-netting were settled out by gravity, taken by pipette to a watch glass, and by gentle hand centrifuging, separated from the remainder of the plankton. The material was always examined in the fresh condition for useful identification characteristics are lost on preservation. At first, camera lucida drawings were made of each stage of each new species as it entered the plankton. Later, the camera lucida was replaced by the camera, and now a library of several hundred negatives is available for reference purposes. At first it was necessary to study the whole plankton in order to isolate V. pullastra, but after this was identified, interest was maintained in other species, a final total of 17 being identified of which five are new. Three of these are specific, the other two still generic.

There are a number of standard features which may be used in identification of lamellibranch veligers, but often in the last analysis, due no doubt to the fact that many species vary so little from one another, the general impression, a composite picture of all details, is probably the most important. Some of these characteristics are :-

1. General outline or shape: The wedge shape of Lima hians illustrates this well. Its shape is unique amongst larvae hitherto described.

2. Colour: Usually only useful in fresh material, although the deep yellow of the ventral shell area of V. pullastra may persist for some time after being preserved. The colour of the digestive gland is often a useful characteristic, that of Tellina tenuis is green, while Hiatella arctica is brown.

3. Shape, prominence and position of umbones: The shape and prominence of the umbones is best illustrated in the oysters. The incubatory (larviparous) species have large, broad, round umbones, while the "oviparous" species have long narrow, pointed and slightly hooked umbones. Of an equivalve species the relatively short, small and centrally placed umbones of Teredo are most characteristic.

4. Equivalve or inequivalve: Readily distinguishable. The larva is similar to the larva in this respect. Ostrea larvae are inequivalve and V. pullastra is equivalve.

5. Presence or absence of eye spots: The Anisomyaria nearly all have black eyespots. Lima is an exception. Monia has a brilliant red spot under the posterior adductor muscle.

6. Special features: Few have been found. The cleft in the ventral area of the right valve (anlage of the byssal notch) of Heteranomia is an example.

7. Dimension and shape of Prod.1 and Prod.11: These are guides, but within limits, because they tend to be somewhat variable.

8. Number, shape and position of hinge teeth: Most species of the Anisomyaria have larvae with taxodont teeth, although they may occur in other groups. The large teeth of Zirphaea, two on one valve and three onthe other are characteristic.

Of all these points, the most important appear to be the general outline or shape and the hinge differences, especially with preserved material. The other characteristics are useful for original identification work.

The larva of V. pullastra.

Throughout the summer of 1946 samples of sand from various beaches were sieved and ellutriated and the spat picked out. At the same time, cardboard collectors from strings of cultch that had been hung from a raft near the Marine Station, were removed at intervals. From these, samples of the settled spat were picked off, and these collectors proved a better source of material than the sand. An examination on June 12th produced about 30 spat from a square foot of surface, indicating that spawning had occurred some time before and that larvae should be present in plankton. Fortunately, previous experience with spat of various species enabled immediate identification of the earliest spat of V. pullastra. From the shape of/

/of Prod. 11 on the very young spat, in addition to its mean length of 260 u., association was made with a veliger of similar shape and size in the plankton. Further study of large veligers and young spat strengthened the opinion that this was the veliger of V. pullastra. Attempts were immediately made to culture the larvae by picking them out of the plankton and placing them in plunger jars. They were fed with a mixture of Chlamydomonas and an unknown u-flagellate from the stock cultures of the Millport Station. These food species were cultured both in Miquel's solution and in Erdschreiber's mixture. A small number of the larvae survived and metamorphosed into easily recognised spat, thus proving the correctness of the identification. Many cultures of these larvae were started, both in 1946 and in the summer of 1947, with very variable success. From one culture, 357 larvae metamorphosed into spat, of which 43 or 12% were of abnormal shape. Other attempts were made to culture them in plankton cages made of bolting silk and suspended from a raft. No spat were ever found in these despite repeated attempts.

Description of the Larva.

The earliest larval stage definitely recognised as V. pullastra was in the late straight hinge condition, 168 u. longe and 144 u. high (Pl.1, fig.1). The ventral shell area is light yellow but becomes much deeper in older larvae. The ends are well rounded and the straight hinge is placed somewhat to the posterior, thus causing the/

/the anterior margin to fall away more rapidly than the anterior. Pl.1, fig.2 shows an early umbo stage, 204 u. long and 180 u. high. Here the veliger is beginning to assume the typical shape, generally rounded, slightly more pointed to the anterior and deep in relation to the length. The anterior and posterior dorsal margins are slightly convex. The ventral margin is yellow and the colour extends further to the anterior than the posterior. The digestive gland is apparent at this stage and is also yellowish. The remainder of the animal is colourless.

In Pl.1, fig.3 is shown a mature larva, 260 u. long and 240 u. high. The ventral margin and the centrally placed digestive gland have the characteristic yellow colour. There are three to four gill plates and the statocyst is plainly visible through them. The umbones in most positions in which the larvae are seen, merge with the general outline of the shell. In Pl.1, fig.4 is shown the interior view of the left valve of a larva 256 u. by 238 u. The length of Prod.1 in this specimen was 108 u. In Pl.1, figs. 5 and 6 are shown the hinge areas (internal view) of a larva 227 u. by 209 u. Fig.5 shows the right and fig.6 the left, valve. The ligament (L) is at the posterior end of the hinge. In Pl.2, fig.7 is shown a photomicrograph of a setting veliger, and fig.8 is a photograph of external views of single valves. Pl.2, fig.9, shows an internal view of the hinge of a setting veliger and the teeth and the ligament are evident. Pl.2, fig.10, shows a newly settled spat with/

/with just a trace of the dissoconch showing. The older spat in Pl.2, fig.10 is 0.4 mm. in length, in which the shape, especially the anterior end, has changed from that of the larva. In a number of species it has been observed that the outline of the larval shell changes with the growth of the spat. The prodissoconch becomes nearly surrounded by the solid spat shell, and doubtless the pressures set up on all sides of the fragile larval shell causes the distortion. Care must be taken in using the outline of the larval shell on spat for making the link-up between them, and only newly settled specimens should be used.

Fluctuations in Abundance and Vertical Distribution of the Veliger.

The only lamellibranch veliger upon which any quantitative work has been done is the oyster, partly no doubt because of its economic importance and partly because it is one of the veligers that has been long identified and is easily recognisable, even in the young stages. In some ways the oyster veliger presents a special problem in that it is most often found in sheltered and enclosed waters; at any rate it is in this type of water that it has been most thoroughly studied quantitatively. The summer of 1946 was occupied in identifying the veliger of *V. pullastra* and in becoming familiar with it. In the summer of 1947 a pump that could be adapted for the quantitative studies of plankton became available. The work was essentially preliminary but it has revealed some of the problems.

Method.

The pump used was a centrifugal ex-N.F.S. machine powered by an 8 H.P. Standard Gwynne engine that had been used by the Marine Station plankton team for plankton work in Loch Striven. The apparatus was light enough to be loaded and unloaded from a forty foot boat without undue difficulty. The pump was initially placed on Keppel Pier and the sampling done by pumping water from 2 feet below the surface through a No.120 bolting silk plankton net into measuring tanks of 333 litres capacity. At first, one cubic/

/cubic metre was used but later increased to two. The contents of the net were washed into a large jar and the volume reduced by siphoning off excess water with a thistle funnel covered with bolting silk. The whole sample was then examined in a counting cell, in the fresh condition whenever possible, for identification is then easier and more certain.

For sampling from depths greater than 15 metres, a 1½" diameter, instead of the usual 4", intake hose was used. This thinner hose had the disadvantage that with its use it required 15 minutes to pump a cubic metre, due to the friction.

Sampling began on June 26th, the day after the first veligers were observed in the plankton. On August 6th, owing to the pump being required for other purposes, the sampling station was moved from Keppel Pier to a point in a small bay to the north-east of Keppel Point. The pump was located on the shore above high water mark and the intake pipe was led down over the rocks and the intake end, two feet below the surface, was floated on a buoy. (Pl.23, fig.2). At high tide the intake was 12 to 15 yards off shore, but at low tide, only about 2 yards. This was not the most suitable position, but under the circumstances, there was no alternative. Some information was certainly obtained of the larval movements in a bay which is typical of the Island of Cumbrae, and in no way unnatural.

Currents.

The currents are known to exert a great influence on the movements of larvae, and Tait (1937) has found an eddy which nearly overlies the area on the Dogger Bank of the North Sea, where Davis (1923) found and carefully mapped out areas of bottom containing huge populations of *Spisula* and *Mactra*. These areas appear like islands with definite borders and are indicative that some agency like a current must have been responsible for thus concentrating the larvae. Orton (1937) in a study of the spatfalls of *Cardium edule* in Morecambe Bay, found that the heaviest spatfalls occur where (a) tidal streams meet, and (b) where banks shelter a stretch of ground from prevailing winds. The current configurations in the region of the Cumbrae are not well known and the work of Mill (1892, 1894) gives little information on small local areas. However, observations during the sampling period, as well as at other times, gave some indications of the surface picture. On the early part of a flood tide the flow of water comes in across the mouth of Kames Bay (see Plate 3, Map) from between the Cumbraes; it strikes Farland Point and is deflected to the southward across to Hunterston Perch. As flooding proceeds, the direction of the current backs and flows more directly up Fairlie Channel and in time swings far enough to be deflected by Keppel Point. First to the East, and later to the North of this stream, there occurs a reverse eddy or swirl. Early/

/Early in the tide it affects the whole shore between the Lion Rock and Keppel Point; later it is confined to the small bay between Keppel Pier and Keppel Point. This is a rough picture of the average surface current conditions on the flood tide in this area, but many variations occur. The ebb stream is more straightforward and for a period during each ebb, the tide will flow strongly southward past Keppel Pier where it is often used for fishing plankton nets. At no time, however, in spite of the rate at which it strikes Keppel Pier, does it hit the north-east shore of Keppel Point with any force and the surface current past the intake of the plankton pump, was not observed to exceed an estimated ½ to ¾ knots.

Seasonal Fluctuations in Abundance of Larvae.

To determine fluctuations in abundance of larvae throughout the summer, samples were taken as nearly as possible every four days during the period when veligers were present in the plankton. The results from June 26th when the first larvae appeared, to September 30th when they disappeared, are shown in the graph Plate 4. Included are the average weekly temperatures taken at the surface from Keppel Pier. These temperatures were kindly supplied by Mr. K.A. Pyefinch, B.I.S.R.A., Millport. Practically all larvae represented in the graph range from 180 to 260 u. in length. For some unknown reason the younger stages did not appear to be represented in either the qualitative or quantitative samples in adequate numbers comparable to the/

/the frequency of the older stages. This precluded the possibility of obtaining size-frequency distributions from which it may have been possible to make an estimate of the length of larval life.

The first larvae noted on June 24th were at least 160 u. in length, showing they were about half grown. If the drop in the frequency curve on July 12th indicates the disappearance of this initial population due to settlement, the duration of larval life is approximately 30 days. This is not improbable, especially when the temperatures are considered. Thorson (1946) gives figures of 4 weeks for Mytilus edulis and 2 weeks for Mya arenaria. Nelson (1928) considers the larval life of Mytilus edulis to be three weeks and the same time for Mya arenaria at temperatures under 20° C. Weymouth, McMillan and Holmes (1925) believe the larval life of the razor clam, Siliqua, is about two months, but that it is not free swimming during all this time. Field (1922) estimated a larval period of two months for Mytilus edulis by comparing reared larvae with those found in nature. The duration of larval life indicated by laboratory cultures fluctuate greatly according to the author's experience with V. pullastra. Ostrea gigas (Elsey, 1933) requires about 3 weeks at temperatures between 18 and 20° C. Schaeffer (1938), found that the larvae of O. gigas took 3 to 6 weeks depending on temperature, to reach setting size in Quilcene Bay. Surface temperatures varied between 16 and 23° C. Hopkins (1937) states that/

/that the larvae of O. lurida have a free swimming period of a month after being released from the brood chamber. Orton (1937) estimates the free swimming period of O. edulis to be 10 to 14 days, and various other authors, Cole (1936, 1939), Mazzarelli (1922), Hagmeier (1916) and Erdman (1934), find the times to vary between 9 and 17 days depending on the temperature within the range 15.0 to 22.0° C.

Assuming a larval life of 30 days for V. pullastra the date of the first spawning would be about June 10th and the mean weekly temperature at this time (Keppel Pier) was 9.7° C. One female has been observed to spawn in the laboratory at 10° C. but that is the exception rather than the rule; the majority require a minimum temperature of about 16° C. June 23rd-28th was the first 5-day period in 1947 that the surface temperature at Keppel Pier rose above 10° C. It must be remembered that animals on the beaches may be subject to higher temperatures, and on a sunny day during the time of spring tides, the temperature of the incoming tide over the beach may be at least 5° higher than the temperature recorded at Keppel Pier.

The group forming the peak number on August 23rd would have spawned approximately 2 weeks earlier, which would coincide with the increase in temperature beginning about August 10th. This is largely conjectural, and a more satisfactory sampling station, with an extensive study/

/study of the length-frequency of the larvae, would verify these assumptions.

One point that is elicited from the data is the exact period of the breeding season. In 1946 spawning began before June 1st, for the larvae were first identified in the first week of that month. On June 12th a number of newly settled spat were found and this indicated, assuming a free swimming period of a month, that spawning had occurred about the middle of May. The temperature in mid-May, 1946 was only 8.5° C. at Keppel Pier, not rising above 10° C. until the first week in June. In 1946 the larvae disappeared from the plankton in the middle of August. Thus in 1946 the spawning season lasted from mid-May to mid-July, assuming a larval period of a month. In 1947 the season was from mid-June to the end of August. Spawning in two successive years lasted for about the same length of time, but it commenced a full month later in 1947. This lag may have been due to the retardation in gonad development subsequent to the exceptionally low winter temperatures in 1946-47. It is usually in the pre-spawning period that the intense proliferation and ripening of the molluscan gonad takes place.

Vertical Distribution.

Thorson (1946) and Barker Jorgensen (1946) have provided the only information on the vertical distribution of lamellibranch veligers, other than oysters. In the Sound, however, the distribution is markedly influenced by/

/by the layering of the so-called Kattegat and Baltic waters, and the data from those works have only limited application.

It was hoped to determine the normal vertical distribution of the larvae of V. pullastra and to correlate this with the vertical distribution of the settled spat. To collect information about spatfall, a number of strings of cultch were suspended from surface to bottom, in various depths, down to 40 metres, in several localities. Extreme care was used in the preparation of this experiment; only new rope, with new galvanised thimbles and shackles, and special anchors and buoys were used: however, every string was lost and in the opinion of the Station boatmen, vandalism was the cause.

To obtain a general picture of the distribution of larvae, surface samples were taken on July 29th at 4 stations - Balloch Bay, Hunterston Perch, Trail Island and Keppel Point. Larvae of V. pullastra were found only from Keppel Point, where 20 were counted. This trip coincided with a period when the population was low, as indicated by the counts from the regular series of samples (Graph, Plate 4). It is significant that this evidence corroborated the information from the regular series. A station was later set up in Fairlie Channel (Plate 3, F), and samples of one cubic metre were taken from depths of 3, 9, 15, 25 and 30 metres. A period of 90 minutes elapsed between the first and last sample of this series. The results are summarised below.

Table 1.

Venerupis pullastra.

Vertical Distribution of Larvae in Fairlie Channel
1 cubic metre samples. 29.7.47.

Time	Depth in metres	No. of Larvae	Remarks.
13.25	3	0	Few lamellibranch veligers.
13.10	9	1	Normal surface larvae present.
13.00	15	6	Considerable number of normal surface forms.
12.35	25	0	Small no. of Mytilus edulis.
12.15	30	1	A no. of M. edulis. 1 Modiolus modiolus. No other lamellibranchs.
Weather : Calm during the surface samples. Slight chop during the vertical series.			

These numbers are too small for much significance to be attached to them. Nevertheless, they indicate that the larvae of V. pullastra do penetrate below the surface layers and the small numbers found agree with the results of the regular surface series.

A second vertical series was taken at a station placed as nearly as possible to the position of the July 29th station, (Plate 3, F). Sampling was done in the same manner but from the depths of 0, 5, 10, 15, 20, 25, 30, 40 and metres. A volume of 2 cubic metres was used for each sample and a period of 7 hours elapsed between the first and the/

/the last sample. The results are summarised below and graphed on Plate 5.

Table 2.

Venerupis pullastra.

Vertical Distribution of Larvae in Fairlie Channel
2 cubic metre samples. 22.8.47.

Time	Depth in metres	No. of Larvae.	Remarks.
10.10	0	26	Few other veligers.
10.30	3	30	Normal complement of surface forms.
10.55	5	32	Fair no. of other veligers.
11.20	10	97	50% of veligers were V. pullastra.
11.50	15	87	Normal complement of veligers.
12.30	20	54	Normal complement of veligers.
15.20	25	15	Normal complement of veligers.
16.00	30	26	Normal complement of veligers.
16.50	40	0	Few veligers. Mytilus edulis and Modiolus modiolus.
17.10	0	91	Veligers mainly V. pullastra.
Weather : Calm and sunny.			

Owing to the long period of time between samples, comparisons between numbers at different depths have little significance. The information does indicate that V. pullastra and other veliger larvae may be found over a/

/a considerable range of depth. It is not known whether the behaviour of the larvae is responsible for this or whether the observed distribution is the result of a fairly complex tidal system at this station. Thorson (1946), found that larvae were confined to their 'native' water, characterised by a certain salinity and temperature; and Nelson (1928) found that the larvae of O. virginica congregate at the halicline in Barnegat Bay. No hydrographic estimations were made, but there is little evidence for the existence of a definite halicline in a tideway such as Fairlie Channel. Perkins (1931), also working in Barnegat Bay, found a possible correlation between the vertical distribution of the larvae O. virginica and the and the strength of the current, although at low current velocities and marked salinity variations, this latter factor appeared to effect the distribution as found by Nelson. The interpretation (Korringa 1940) of Perkin's data is that the effect of salinity changes is greater than that of current velocities. Working in the Oosterschelde, Korringa found the larvae of O. edulis were uniformly distributed in a vertical plane at any time of the day or night, in all kinds of weather, and at all stages of the tide. It may be pointed out that the water in the Oosterschelde is shallow.

Diurnal Movements.

On August 14th, 15th and 16th, 1947, samples of 2 cubic metres were pumped at each low, half and high tide period from the Keppel Point shore station (Pl.3, Map C), giving a series of 16 samples over 48 hours. Results of the larval counts for these samples are tabulated in Table 3, and shown graphically on Plate 6. This shows that the number of larvae is closely correlated with the stage of the tide and also, to some extent, with the periods of darkness.

In order to check this data and, if possible, to eliminate the possible effect of local conditions such as the eddy factor and the proximity of the intake to the shore, a series of samples were taken from the 'Nautilus' during the period 26th-28th August 1947, at a station (Pl.3, D) 200 yards south of Keppel Pier in 40 metres. These samples of 2 cubic metres volume were taken, as before, approximately every three hours, coinciding with the times of high and low water and the half tides. In addition to the surface sample, one was taken near the bottom at 12 metres. It required 15 minutes to take each sample. The results of this series are tabulated in Table 4 and graphed in Plate 7.

The direction of the surface current during the times of sampling was interesting. It appeared to occur at random and no direct correlation with the rise and fall of the tide existed. This may be true only for this area/

Table 3.

Venerupis pullastra.

Number of Larvae from 2 Cubic Metres Pumped from the Keppel 1 Point Shore Station at 3 Hour Intervals. August 14-16.1947.

Time	Number of Larvae	Light	Tide
11.30	35	Day	H
14.15	14	Day	Half
17.15	2	Day	LL
20.17	2	Day	Half
23.25	30	Night	HH
02.25	89	Night	Half
05.10	4	Day	L
09.15	25	Day	Half
12.15	70	Day	H
15.10	11	Day	Half
18.15	8	Day	LL
21.20	120	Day	Half
00.20	92	Night	HH
03.30	155	Night	Half
06.20	25	Day	L
09.55	88	Day	Half

H = High. HH = Higher High.
L = Low. LL = Lower Low.
Weather : Bright and sunny. No wind or sea.

Table 4.

Venerupis pullastra.

Diurnal Distribution of Larvae, Fairlie Channel, from Surface and from 12 Metre Samples of 2 Cubic Metres, August 26-28.1947.

Time	Depth in Metres	No. of Larvae.	Light	Tide	Remarks
12.05	0.6	12	Day	Half	Ebb stream.
12.20	12.0	21	Day	Half	Ebb stream. More of other species of veligers than in surface sample.
15.16	12.0	34	Day	Low	Flood stream. Normal veligers complement.
15.30	0.6	11	Day	Low	Almost pure culture of tintinnid Favella striatus. Only veligers, V. pullastra and Cardium edule.
18.20	0.6	45	Day	Half	Ebb stream - flood stream 50 yards south. Relatively few tintinnids. Veliger content normal.
18.36	12.0	29	Day	Half	Ebb steam - flood stream 50 yards south. Relatively few tintinnids. Veliger content normal.
21.40	12.0	3	Night	High	Easterly chop. Few veligers Some crustacea and some Ceratium.
22.00	0.6	70	Night	High	Normal complement of veligers. Ebb steam.
00.51	0.6	107	Night	Half	Flood stream. Fair number of Favella. Normal veligers species.
01.09	12.0	1	Night	Half	Few veligers - mainly Histella and Heteranomia.
03.50	12.0	11	Night	Low	Flood stream. Normal complement.
04.10	0.6	77	Night	Low	Flood stream. Normal complement.

/Over

Table 4. (contd.)

Time	Depth in Metres	No. of Larvae.	Light	Tide	Remarks
07.04	0.6	16	Day	Half	Ebb stream. No deep sample - pump trouble.
10.33	0.6	2	Day	High	Flood stream. Few planktors of any sort.
10.48	12.0	25	Day	High	Normal plankton.
13.30	0.6	5	Day	Half	Ebb stream. Little plankton Few Mytilus.
13.45	12.0	50	Day	Half	Normal veliger complement.
16.30	0.6	7	Day	Low	Changing from Ebb to Flood stream. Little plankton of any sort.
16.50	12.0	15	Day	Low	Normal complement.
19.50	0.6	47	Day	Half	Flood stream. Few other veliger species.
20.05	12.0	56	Day	Half	Normal complement.
22.45	0.6	105	Night	High	Flood stream. Veligers normal.
23.00	12.0	20	Night	High	Changing to Ebb stream. Veligers normal.
01.53	0.6	206	Night	Half	Ebb stream. Veligers normal.
02.13	12.0	0	Night	Half	Few veligers.
05.00	0.6	20	Day	Low	Slack water.
05.20	12.0	34	Day	Low	Beginning of flood stream.
08.25	0.6	34	Day	Half	Ebb stream. Normal veligers
08.40	12.0	33	Day	Half	Slight ebb. Many crustacean Veligers of larger size groups. Mytilus dominant.
11.27	0.6	69	Day	High	Light flood.
11.45	12.0	14	Day	High	Slight ebb. Few veligers.

/area as the station was close to the outer edge of the Keppel Point-Lion Rock swirl. Some of the samples were no doubt taken from the 'swirl' water, while others were from the main current. The complexity of the surface current has been emphasized.

The maximum numbers in the surface samples coincide with the periods of darkness. In the 12 metre samples the numbers rise to a peak during the hours of daylight, but are always much lower than those in the surface samples. The explanation probably is that the larvae are widely distributed in depth during the day but concentrated near the surface at night, as with many plankton organisms. In this series there appears to be no correlation between number of larvae and the stage of the tide.

Another series of samples was taken, again from the shore station at Keppel Point, but at less frequent intervals. The samples were most often taken at high tide with smaller numbers at low tide. Sampling was continued for five days and six nights, from August 29th to September 4th, 1947, and the counts are presented in Table 5 and graphed on Plate 8.

In five out of the six night samples the numbers of larvae are significantly higher than those taken at comparable stages of the tide during the day. This corroborates the evidence from the two previous series/

Table 5.

Venerupis pullastra.

Day - Night Distribution of Larvae at the Keppel Point Shore Station, August 29th to September 4th, 1947.

Time	Number of Larvae	Light	Tide	Remarks
12.15	9	Day	High	Calm. Few veligers.
24.00	96	Night	High	Calm. Fair number of veligers.
12.55	24	Day	High	Calm. Few veligers.
19.00	31	Day	Low	Calm. Large number of small veligers.
01.00	311	Night	High	Calm. Many thousands of veligers.
07.15	-	Day	Low	Too much weed - impossible to count.
13.25	29	Day	High	Calm. Few veligers.
19.15	1	Day	Low	Calm. Few veligers.
01.30	378	Night	High	Calm. Moonlight. Numerous veligers.
08.30	42	Day	Low	Calm. Fair number of veligers.
13.50	10	Day	High	Calm. Few veligers, mainly Modiolaria marmorata.
19.30	9	Day	Low	Calm. Few veligers.
02.00	151	Night	High	Calm. Fair number of veligers.
14.30	108	Day	High	Calm. Fair number of veligers.
02.30	17	Night	High	Slight westerly. Few veligers.
15.15	19	Day	High	Cloudy. Extremely few veligers.
03.30	137	Night	High	Southerly breeze, rain. Numerous veligers.

/series, that these larvae undergo diurnal vertical migrations. In the shore samples it is possible that there may be a diurnal horizontal movement, but this is hardly likely in view of the information from the 12.0 metre samples in the August 26th-28th series and from the vertical series of August 22nd in Fairlie Channel. Further evidence is needed on this point, and the present work has only pointed out a strong possibility that some sort of a diurnal rhythm exists. Further sampling is needed at more and other stations in addition to laboratory experiments and observations on the larvae.

If a vertical migration does exist, even within the comparatively narrow limits of the surface and 15 metres, a mechanism for bringing about this movement is required. Several of the samples indicated that the migration may take place within a period of three hours. This requires a velocity of 3 metres per hour, or roughly 10.0 cm. per minute. No data is available on the rate of swimming of these larvae.

Diurnal movements have been observed in a number of animals and Welch (1935) states, "Diatoms, flagellates and other organisms with weak locomotion have been observed to manifest diurnal movements, but are restricted to narrow limits." Fox (1925), found that Paramecium and echinoid larvae under certain conditions swim down in light and up in darkness, and so concludes that diurnal movements occur in organisms moving by ciliary action. Kikuchi (1930),/

/Kikuchi (1930), reviews the literature on diurnal movements of planktonic Crustacea and mentions that limited diurnal migration of diatoms, flagellates, Protozoa, Rotatoria and other organisms with weak locomotor activity have been observed, but that Ceratium and Anuraea make more extensive movements. He does not give his authority for the information on Ceratium and Anuraea, and this has not been found elsewhere. Rose (1925), discusses in detail the possible causes of diurnal movements. Holmes (1902), discusses phototaxis in Volvox which he finds is phototactic in normal light, negatively so in intense light, and with no reaction in weak light. Thus the literature throws little light on the possible mechanism other than ciliary activity for carrying out diurnal movements by Y. pallastra.

Metamorphosis of the Larva.

The change from the free living larval stage into the more or less fixed or sedentary form in lamellibranchs is recognised as perhaps the most critical stage in their life history. The anatomical changes that occur in the fixed forms like the Ostreidae are more drastic than those which take place in, for instance, the active burrowing forms like the Veneridae. As well as the loss of the typically larval organs there is also the loss of the foot, of all or part of one adductor muscle, and a general shift in the symmetry of most of the organs of the attached forms.

It is on these attached forms, especially the oysters, that the major part of the work on metamorphosis of larval lamellibranchs has been carried out. Ryder (1882, 1884), Jackson (1888, 1890), Stafford (1913) and Prytherch (1934) have given accounts of the process in the American oyster, Ostrea virginica. On the European oyster, O. edulis, until the work of Cole (1937, 1938a, 1938b), there had been no adequate description of the transition stages. Yonge (1926), gave a description of the early spat, and Erdman (1934), gave a complete description of the fully developed "ansatzreifen" larva.

Most of the remaining studies on metamorphosis have been done on freshwater mussels. Because of the parasitic stage in their life history, comparisons with marine species are not easy to make. Ziegler (1885) on/

/on Cyclas cornea, Harms (1909) on the Unionidae generally and Hebers (1913) on Anodonta gallensis, have gone into detail on the metamorphosis of these forms. In addition, Sigerfoos (1904) on the Teredinidae and Drew (1897, 1898, 1904) on the Protobranchia, have contributed to an understanding of the change from the pelagic to the benthic life.

The purpose of this study of the metamorphosis of larvae into the spat of V. pullastra is to examine, in a general way, the major changes that take place during this critical period, and to see whether they throw light on the activities and reactions of the young animals. It is not proposed to go into the changes in much detail, for the embryological and developmental studies that would be involved are beyond the scope of the present research. It is also necessary to limit the size of the spat examined and this has been placed at a length of 1.0 mm.

Materials and Methods.

Plankton was taken in the ordinary way by tow netting or by pump and the larvae separated out and fixed in Bouin, which decalcified at the same time. The spat, also fixed in Bouin, were obtained from plunger jars in which they had been reared from the larvae, or were taken from plates of various materials which had been exposed as cultch. Fixation was good though considerable shrinkage occurred (Orton, 1937). Sections were cut at 7 u. in Ester/

/Ester wax and stained with methylene blue and erythrosin. Whole mounts and dissections were stained in various ways but methylene blue was found to be satisfactory.

To form a basis for following the process of metamorphosis, a description of the larval anatomy is deemed necessary. Development will not be discussed as that is another problem, and the organs to be described here are those of the mature larva ready to metamorphose. Pl.9, fig.14 is a semi-diagrammatic illustration of a larva reconstructed from examination of living specimens, whole mounts and sections. The individual organs will be discussed separately.

The Anatomy of the Larva.

The Shell.

The larval shell, according to Werner (1939), is a calcified structure with a conchyolin base, and at this stage of development, it completely encloses the body of the larva. It has the characteristic shape with the deep yellow colour, especially in the ventral region toward the edge of the shell. There are two main parts to the larval shell, an earlier formed area designated by Werner (1939) as the first prodissoconch or Prod.1, and the part formed later, the second prodissoconch, Prod.11. Prod.1 is of uniform surface structure with an anterior-posterior length of between 95 and 105 u. in different individuals. Prod.11, the large outer part of the larval shell, is concentrically/

/concentrically striated with fine lines. Werner's explanation is that Prod.1 is laid down uniformly by the shell gland, whereas Prod.11 is laid down by the mantle edge as in the manner of the adult, and the striae are actually growth lines. The length of Prod.11 at the end of larval life is between 250 and 260 u. As far as can be ascertained, there is little variation in shape at this time. The hinge of the larva is roughly 80 u. in length and is in the form of a solid bridge studded with 15 small teeth (Pl.2, fig.9), the centre one being bifid. At the posterior end of the row of teeth is a ligament (L) 10 u. wide and 15 u. long. When the valves are separated by dissection the ligament splits into two parts, one remaining with each valve.

The Mantle.

The mantle, one cell layer thick, is well developed and the edges are already functioning as a region of shell deposition (Werner, 1939). The lobes are separated except for a short distance near the origin of the gills and dorsally between the adductor muscles where fusion with the visceral mass occurs.

The mantle edges carry two lobes instead of the three normally found in the adult (Yonge, 1948). There are three cell layers in this region, one of which continues into each of these two lobes, while there is a third central one with nuclei which stain bright green with methylene blue, (Pl.13, fig.26). Presumably the two lobes present are the/

/the inner muscular and the outer secretory. No nerve was observed in the mantle lobes of the larva.

On the inner side of each muscular lobe posteriorly below the gill origin is a line of cilia (Pl.13, fig.26C). The cilia from the two lobes may interlock and may thus form an effective barrier to the flow of water into and out of the mantle cavity. The velum is the organ of feeding and the gills are not concerned with this in any way. The cilia of the gills are very active indicating that they may be functioning as a respiratory organ, so doubtless there are currents in and out of the mantle cavity. It is therefore likely there is a mechanism for controlling the force and direction of these currents and for preventing the entry of particles. It is suggested that the rows of interlocking cilia in conjunction with the muscular lobe of the mantle may function as the controlling mechanisms.

Gills.

The gills of the mature larva consist of four filaments. In the larva of this and most other siphonate forms, the gills appear to be formed considerably in advance of those of Ostrea edulis according to the description given by Cole (1938). Erdman (1934), in his figure of an "ansatzreifen" larva of O. edulis, shows only a row of six short processes representing the gills.

The gills lie in the vertical plane between the /

/the posterior part of the digestive gland and the mantle edge (Pl.9, fig. 14, i.g.). They are attached anteriorly in the region of the anterior foot root; dorsally by strands of muscle to the visceral mass and posteriorly to the region of mantle fusion. At this point filaments originate by vertical splits in the block of tissue lying in that region. In a mature larva the longest (oldest) filament is 50 u. long and the shortest (youngest) 25 u. in the fixed condition (Plate 11, fig.17, i.g. 1-4). The arrangement of the cilia is difficult to determine at this stage, but living material shows working cilia between the filaments.

Foot and Byssal Gland.

The foot of the larva occupies the postero-ventral part of the mantle cavity, adjacent to the velum which lies directly in front of it (Pl.9, fig.14f). In the natural resting condition the sole of the foot lies parallel to the ventral margin of the mantle edge with the tip pointing forward.

The posterior pedal retractor (Pl.10, fig.16, p.r.) runs along the heel of the foot, continues dorsal past the anterior margin of the visceral ganglion, then posteriorly over the top of the posterior adductor. At the level of the visceral ganglion it bifurcates and the branches extend on each side of the rectum to be finally inserted into the shell just above the adductor muscle. The anterior pedal retractor runs along the anterior edge of the foot and/

/and above the cerebral ganglion to be inserted, one branch on each valve, above the anterior adductor.

The musculature of the foot is not well developed at this stage, for it is unlikely that it is used to any extent in the pelagic period. However, planktonic larvae, resting on the ventral shell edges, may move along the bottom of a watch glass by the ciliary activity of the foot which is extended forward in the direction of the movement. Newly metamorphosed larvae do not use this method of locomotion, but exhibit feverish pedal activity in the form of the typical sequences of digging movements of the adult. The larvae of Mytilus edulis also move by means of the ciliary activity of the extended foot, and this method of locomotion is retained in the young spat. It is remarkable that the nerve patterns of the adult are outlined so early.

According to various authorities, the byssal gland is originally paired, but whatever its previous history, in the mature larvae of Y. pullastra it consists of a relatively large single sac occupying the major part of the foot (Pl.9, fig.14, b.g.). It extends from near the tip of the foot to the edge of the pedal ganglion. At this time there is no duct connecting the gland to the deep byssal groove (b.gr.). The contents of the byssal gland in the larva stain a light blue with methylene blue, quite different from the darkly staining mass characteristic of the byssal secretion in the adult.

Musculature.

The musculature of the foot has already been dealt with and the velar muscles will be described along with the velum, thus leaving only the adductor muscles. These occupy the same relative position they do in the adult. In some sections they appear to be divided into two parts, which may represent the "quick" and the "catch" sections, but it is not too definite. Erdman (1934), also mentions that some of his sections of Ostrea edulis larvae seem to show this division, but he does not commit himself further.

Digestive System.

The digestive system consists of a mouth situated on the posterior lip of the velum and is guarded by an oral flap (Pl.9, fig.7 o.f.). From the mouth proceeds a long oval oesophagus, 25 u. wide and 10 u. deep in a fixed condition, lined with long cilia. The oesophagus extends along the posterior edge of the velum to the point where this joins the visceral mass, and then continues into the base of the stomach. This is a sac-like body on the roof of which lies the gastric shield. At the posterior end is a constricted portion with heavily ciliated walls, the style sac. The posterior extremity of this (Pl.9, fig.14, k.s.), lies close to the posterior adductor and the visceral ganglion. From the posterior part of the stomach, close to its junction with the style sac, emerges the slender intestine which rises dorsally/

/dorsally and runs in an anterior direction over the top of the stomach. It loops to the left at the front of that organ and returns in a posterior direction high within the left umbone. Along this course it takes several short vertical loops until it begins to descend, still close to the dorsal edge, passing between the fork of the posterior retractor muscle, with the anus just below the base of the posterior adductor.

Two digestive diverticula, one on each side, are connected to the stomach. In frontal section they are pear-shaped bodies whose pointed extremities extend to the anterior limit of the stomach and whose single ducts open into it about the level of the visceral ganglion.

Nervous System and Sense Organs.

The nervous system of the mature larva is comparatively well developed. All the ganglia found in the adult are present as singularly large bodies of nerve tissue. The ganglia, which are paired, are complete with commissures, but the connectives, if they exist at this time, are not readily evident.

The visceral ganglia are adjacent and anterior to the posterior adductor muscle. The cerebral ganglia are intimately connected with the apical area of the velum, one ganglion lying on each side of the apical groove (Pl.10, fig.15). The pleural ganglia lie close to the mantle against the thin roof of the velum and ventral to/

/to the cerebral ganglia, to which they are linked by connectives. The pedal ganglia are situated in the root of the foot (Pl. 9 and 10, fig. 14, 15, 16). Connected with the pedal ganglia are the paired statocysts, which lie one on each side of, and above, the ganglia. Each statocyst contains a single statolith.

Neither the abdominal sense organ or the osphradium has been observed in the larva of V. pullastra.

Heart, Pericardium and Kidney.

Various authors place the anlage of these organs as a group of cells close to the rectum, between the posterior part of the stomach and posterior retractor muscles. In these sections of adult larva, it is impossible to point with any certainty to any group of cells as being the anlage of these organs. In the mature larva no heart or kidney exists as such, and the essential development takes place after metamorphosis.

Velum.

The velum is one organ characteristic of pelagic lamellibranch larva. In the fully developed veliger it is the largest single organ and occupies at least 2/5ths of the volume of the shell cavity. When extruded, it is circular and about 180 u. in diameter and appears to be ciliated along its whole margin. The long peripheral cilia are roughly 50 u. in length and the shorter about 10 u.

The margin of the velum is a thick heavy structure of cuboidal epithelium, which folds and creases when the velum is retracted (Pl.9, fig.14, v.l.). In the centre of the roof of the velum is located the cone-shaped apical plate, which stains deeply with methylene blue. In its centre is a groove (Pl.10, fig.15, a.p, a.g.) in the plane of the dorso-ventral axis of the body.

There are anterior and posterior pairs of velar retractor muscles, the latter are inserted in the arch of the shell anterior to the hinge ligament, and the former on the bulge of the valves posterior to the anterior adductor. The single strands of the velar muscles branch at the ends to give multiple insertions on the valves and on the velum.

The Spat.

The spatting or settling act in non-sedentary forms like V. pullastra is not so defined as it is in cementing forms. Three of the most important and readily evident changes that may be taken as indications of metamorphosis are : 1. The loss of the velum; 2. The functioning of the byssal gland; and 3. The formation of the spat shell or dissoconch.

The immediate loss of the velum in V. pullastra corresponds with a similar state found in other marine lamellibranchs. Its larval function in feeding has to be taken over by some other organs, ultimately the gills.

This will be discussed further in the section on gill development.

The functioning of the byssus gland at spatting is apparently common to all lamellibranchs, even though in some cases, the byssus gland is lost in the adult. Especially in littoral species, the spat would be liable to be shifted unless it was firmly attached or in a sheltered spot. In the Teredinidae (Sigerfoos, 1907), the byssus gland is functional for only a short period after settlement.

The immediate development of the dissoconch is important in providing additional protection, for the larval shell is extremely fragile.

Further consideration of the spatting process will be dealt with in another section, and now the changes that take place in the various organs of the newly settled spat will be discussed.

The Anatomy of the Spat.

Shell.

The development of the dissoconch follows rapidly the transition from pelagic life. The shape and proportions of the spat shell are somewhat different from those of the adult, but this will be dealt with in the section on growth. Development of the molluscan shell is treated in detail by Ehrenbaum (1885), Biederman (1902), Bernard (1896), Weymouth (1923), Boggild (1930), Trueman (1942) and many others.

Mantle.

In the young spat the mantle changes little from the single layer of epithelium, with sparse, elongated nuclei. The mantle edge still consists of the muscular and secretory lobes only. The third or sensory lobe does not appear until after the animal has reached a length of 1.0 mm. when it is formed by a longitudinal splitting of the outer secretory lobe, and the groove so formed becomes the periostracal groove (Pl.13, fig.27), (Yonge, 1948). Previous to the formation of the groove the periostracum originated from the tip of the secretory lobe or from a point on its external surface (Pl.13, fig. 26 pl.).

The lines of cilia found on the inner mantle edge of the larva are retained (Pl.16, fig.35c) in the spat for some time as a row in the region of the future inhalent siphon. By the time a length of 1.0 mm. is reached, however, these cilia are confined to a depression (Pl.19 fig. 46. c. gr.) below the inhalent opening. The further history of this area requires to be followed. Both Harms (1909) and Hebers (1913) for the Unionidae and Anodonta cellensis respectively, figure and describe the ciliation of the inner mantle edge but do not discuss the possible function.

In the literature there is little reference to the formation of the lobes of the mantle edge. Stafford (1913), gives a short description of the mantle of the/

/the young spat of Ostrea virginica. It is interesting that the figures in his plate 7. show only two lobes in the 1.0 mm. spat, but three for the spat 1.5 mm. in length. Jackson (1890), mentions the mantle but gives no details on its development in O. virginica. Hebers (1913) considers the order of appearance of the three mantle folds in Anodonta cellensis, to be first the external, then the middle, and finally the inner.

Siphons.

In the fully grown larva there already exists the tissue bridge sometimes called the siphonal septum, connecting the two inner lobes of the mantle. Through metamorphosis, this bridge retains its identity and becomes a more definite structure (Pl. 14, fig.28, s.s.), (Pl.14, fig.31), (Pl.15, fig.34).

Soon after metamorphosis, the primary exhalent siphon develops from the inner lobes of the mantle edge as a thin walled membranous sac, open at the free end (Pl. 15, fig.33 e. si.). A similar structure has been personally observed in Mya arenaria less than 0.5 mm. in length, though it has not been observed in life in M. pullastra. In M. arenaria, it is a very active organ and is rapidly extruded and retracted, much like a proboscis. It would seem essential that some such structure should be developed early in the sedentary stage in order to keep the mantle chamber and gills free of faeces.

At a length of about 0.4 mm. the first indication of the inhalent siphon takes the form of tentacular development in the region of the siphonal septum. Grooves form in the inner (muscular) lobe of the mantle edge ventral to the septum, penetrating inward from the free edge of the lobe. The tissues between these grooves thicken and elongate into definitive tentacles (Pl.14, fig. 29, si.t.). The tentacles nearest the septum are formed first and are consequently the largest, while new tentacles are formed by further grooving down the lobe. This process takes place on each mantle edge and stages are developed similar to those shown in Pl.14, fig.30; Pl.15, fig.34. Soon after a length of 1.0 mm. has been reached, although considerable variations may occur, the upper and lower ends of these two groups of tentacles fuse to form the margin of the inhalent siphon. At first this consists of 8 or 9 short tentacles which form the inner row of the adult siphon (Yonge, 1948). Approximately at the same time, the sensory lobe of the mantle edge is formed and, no doubt, as the siphon grows and elongates, it takes with it a covering of tissue from the sensory lobe, from which the outer rim of tentacles of the adult will be formed (Yonge, 1948). In Pl.15, fig.34, se.t., the first indication of the formation of this outer ring of tentacles around the exhalent siphon is shown.

On the development of siphons little information may be found in the literature. Harms (1909) indicates/

/indicates that the respiratory siphon of the Unionidae is formed from the contact of two cone-shaped proliferations on each side of the posterior mantle edge. On this opening appear small papilla-like elevations which become the "fimbriae" of the siphon. Meissenheimer (1901), leaves the siphons out of his extensive work on Dreissensia polymorpha as being of secondary importance. Hebers (1913) briefly describes the formation of the siphons in Anodonta cellensis. A bridge is formed by the fusion of the two sides of the inner lobe of the mantle and under this appears the first sign of the anlage of the respiratory siphon ('Atemsipho').

Wasserloos (1911) describes the formation of the siphons in Cyclas cornea and shows it to be a double fusion of the posterior part of the 'Mantelfalte', the exhalent siphon being formed first and then the inhalent. There are no details as to whether a particular part of the 'Mantelfalte' is involved or whether it is an overall fusion which, from the figures, it appears to be. Sigerfoos (1911) shows the larval Xylotrya gouldi to have siphons and they are also found in the larva of Zirphaea crispata (Werner, 1939).

In connection with the development of the siphons is the local enlargement of the pallial muscles to form the siphonal retractors. They originate from the muscular lobe of the mantle near the siphonal septum. They begin/

/begin as short muscle fibres which extend posteriorly into the mantle (Pl.14, fig.30, p.r.m.). As the animal grows they extend and radiate out until they cover an arc of nearly 180°. Pl.13, fig.27, p.r.m. and Pl.15, fig.32, p.l.m., show cross and horizontal sections respectively through these retractor muscles.

Gills.

The significant change that occurs in the gills of the newly settled spat of Y. pullastra is the development of the adult type of ciliation, which has been described many times, Peck (1877), Pelseneer (1889, 1892), Ridewood (1903), Orton (1912, 1913), Yonge (1923, 1926), Atkins (1936, 1937 a-c, 1938 a-c, 1943) and others. In addition, there is a continuous increase in the number of filaments, from the larval number of four, to approximately twelve in a spat 1.0 mm. long.

With the loss of the velum, the gills must be assumed to become the food collecting organs of the spat. However, as pointed out by Yonge (1947), the filaments cannot function as food collectors until the food groove is present. In Y. pullastra, as in most of the other species that have been studied, the food groove does not appear until after the "reflection" of these first formed filaments has occurred, not until the spat is nearly 1.0 mm. or more in length. It is therefore necessary to postulate a method of feeding other than that involving the food groove. Details of the exact method must await the examination of/

/of living material. It is doubtful if the palps are as yet functioning as sorting mechanisms. They are funnel-shaped, ciliated on the inside and directed with the opening toward the ventral margin of the row of filaments. This ventral margin may act as a temporary food tract. The palps are relatively large structures, and it would not be necessary for the food directing mechanism to be finely adjusted for the food particles to strike the palp area. No doubt the rapid development of the adult type of ctenidial ciliation is associated with the gill becoming functional as a feeding organ.

The method of increase in the number of filaments is most easily observed in the spat, although it is evidently a continuation of the same process in the larva. Attached to the siphonal septum are two blocks of tissue, one on each side of the median line, which are the the gill anlagen. From each of these are "budded" off (to use Lankaster's term for the process in Pisidium (1875) sections which elongate into ciliated gill filaments. These form the outer lamella of the inner demibranch. The process is shown in lateral view in Pl.14, fig.29, and in frontal view in Pl.16, fig.35. Lacaze-Duthier's (1856) lucid description of the process in Mytilus edulis can hardly be improved.

Thus the lamella is added to from the posterior, the oldest and longest filaments being the most anterior. The first filament, which is never reflected, is attached/

/attached to the visceral mass, with the ventral end lying between the upper and lower palps. The free ventral tips of the filaments which are enlarged longitudinally are rather loosely united, probably by cilia alone. At a length of 1.0 mm. two well defined rows of inter-filamentary junctions are present and the free ventral edge of this lamella begins to fold inward and upward. This is the beginning of the reflected (indirect or ascending) inner lamella of the inner demibranch. The further development of the gills is beyond the scope of the present research, but parts of it have been observed and they may be of interest.

Soon after the reflection of the outer lamella of the inner demibranch, the outer demibranch begins to form along the axis by an upward growth of newly formed filaments. The process differs from that in Mytilus edulis (Lacaze-Duthier's 1856, Rice 1907) in which the corresponding growth is downward, but it is similar to that described for Cyclas cornea by Wasserloos (1911). In Y. pallastra, the formation of the outer lamella of the outer demibranch cannot take place by outward and upward reflection of the inner lamella. The terms 'reflected' or 'ascending' which are appropriate for the inner demibranch, are hardly applicable to the outer. The formation of the double lamella must take place as shown by Wasserloos (1911) for Cyclas cornea by a bending or doubling downward of the single, first formed lamella.

This approaches more closely the method of gill formation suggested by Yonge (1947) based on functional and theoretical considerations. However, there still remains the question of the formation of the food groove, of which there is no evidence before the bending or doubling has taken place. In addition, there is the formation and disposition of the ctenidial blood vessels to be considered.

Ridewood (1903), Rice (1907) and especially Wasserloos (1911) have reviewed the literature on gill development and since that time there has been little or no work on the development of that organ in lamellibranchs.

The mode of gill formation in Y. pullastra throws little new light on the subject. The inner demibranchs of both Mytilus edulis and Y. pullastra are formed in essentially the same manner, but different from that of Cyclas cornea. The outer demibranchs of Y. pullastra and C. cornea appear to be formed in a similar manner, but different from that of M. edulis. In addition, Rice (1907) found the formation of the later filaments to be different from that of the earlier filaments. This brings to mind the often used quotation from Rice (1896) regarding the extreme plasticity of the lamellibranch gill. It is becoming increasingly evident that functional interpretation is required to go hand in hand with morphology in the study of development.

Foot and Byssus Gland.

The byssus gland becomes functional the time of metamorphosis when the gland becomes connected with the byssal groove. The foot becomes shorter and broader, but the ciliation is retained (Pl.19, fig.46). The byssus gland moves further back into the foot and becomes relatively smaller.

Nervous System

The nervous sytem changes slightly at metamorphosis with the alteration in the position of the cerebral ganglia and their fusion with the pleural ganglia. The connectives now become evident. The statocysts and statoliths increase in size. Immediately below the visceral ganglion, a part of the epithelium becomes specialised into the sense organ described as the osphradium (Pl.16, fig.36, o.s.) which is evident when the animal reaches a length of 1.0 mm.

Digestive System

The major change in the digestive system is the alteration in the position of the mouth and oesophagus. On the disappearance of the velum they move dorsally and to the anterior until the mouth lies immediately in front of, and on a level with, the anterior adductor muscle (Pl. 11, figs. 18, 19, 21). In the earliest spat stages it is close to the adductor, but later moves a short/

/short distance back from it. Up to a length of 1.0 mm., the mouth opens directly downward, while the oesophagus, now relatively shorter than in the larva, bends round to enter the stomach (Pl.19, fig.46 o.e.s.) The stomach enlarges rapidly and the posterior end is tilted downward, bringing the style sac into a more vertical position (Cf. Pl.9, fig.14 and Pl.19, fig.46).

The intestine extends back parallel to the base of the stomach, behind which it bends sharply upward (Pl.19, fig.46, i.n.t.). It makes a short loop in the vertical plane to the right and proceeds almost to the dorsal limit of the body where it bends to the left in a horizontal plane, with the loop partly overlying the stomach. It now passes directly backward along the dorsal body wall and as the rectum, passes through the heart and pericardium (Pl.19, fig.46, r,p,h.). It then circles behind the posterior adductor to which it is closely applied, and bends far back on itself to end in an anal bush just below the visceral ganglion.

The digestive diverticula (Pl.16, fig.38 d.d.) undergo no important change other than increasing in size with the formation of numerous branched ducts. They cover the visceral mass in the anterior dorsal region and the ducts enter the anterior part of the stomach at the upper limit of the style sac.

Heart and Pericardium.

The heart and pericardium, together with the kidney, are generally assumed to originate from a common anlage, which takes the form of bands of cells just anterior to, and above, the visceral ganglion and posterior pedal retractor muscles (Meissenheimer 1901, Hebers 1913, Fernando 1931, Erdman 1934). The anlage could not be identified with certainty in the larva of *V. pullastra*, but the appearance of the three organs in the spat was unmistakable. In a spat of 0.28 mm. the thin walled pericardium appeared as a comparatively long shallow cavity surrounding the rectum, extending from the posterior end of the hing ligament to the posterior retractor muscles. The heart showed as a double membrane tightly enclosing the rectum but as yet there is no cavity.

At a length of 0.35 mm. (Pl.17, fig.44), the development from the preceding stage is considerable. The external heart membrane has now separated from the internal to form a cavity surrounding the rectum. The heart is surrounded by the pericardium which is bounded to the posterior by the kidney. A sagittal section through the heart, pericardium and kidney of an animal 1.0 mm. in length (Pl.17, fig.43), shows the muscle fibres in the heart wall just beginning to appear.

The larval kidney could not be identified with certainty. Very soon after spatting, in animals 0.28 mm. long, the beginnings of the kidney were identified at the/

/the posterior end of the pericardial cavity, against the posterior retractor muscles. The organ consists of a paired vesicle with occasional groups of cells which resemble the excretory cells of the mature kidney. In an animal 0.5 mm. in length it is a shallow body with a central lumen, lying anterior to, and vertical against, the posterior retractor muscle (Pl.17, fig.40, k.). A diagrammatic reconstruction of a kidney in an animal 0.5 mm. in length is shown in Pl.17, fig.39. The frontal view is shown with the upper part of the figure corresponding to the dorsal part of the organ. A. and B. are cross sections in the regions indicated by the two lines. In Pl.17, figs.41 and 42, are shown reconstructions of the right half of a kidney in an animal 1.0 mm. long; and Pl.17, fig.43, k. shows a sagittal section of the kidney in an animal of the same size. The gland consists of two tubes, one within the other. The inner, thinner tube is the reno-pericardial duct which leads from the postero-ventral part of the pericardium into the dorsal part of the excretory section of the kidney. The direction of the current is shown by the disposition of the cilia in the reno-pericardial duct. The excretory pore discharges near the reno-pericardial opening into which will later be the suprabranchial chamber. No ducts are evident in animals 0.5 mm. in length.

The two lobes, right and left, of the kidney are united by a communicating tube below the rectum.

Later the walls of the kidney become greatly folded in order to increase the surface area.

Hebers (1913) considers that in Anodonta cellensis the kidney is so well developed that the reno-pericardial duct functions shortly before the beginning of the free living period. Comparisons are difficult but there is certainly no evidence of the kidney being able to function in V. pullastra until a length of at least 0.5 mm. has been reached. Ohdner (1912) in his extensive work on the morphology and phylogeny of the lamellibranch kidney describes that of Venus gallina as a representative of the Veneridae. The structure of the kidney of the adult V. pullastra is similar to that of Venus gallina, but both are different from the organ found in the spat less than four or five mm. in length.

Gonad.

In animals 1.0 mm. in length the gonad appears as a small cluster of cells attached to the outer side of the wall of the ventral pericardium (Pl.19, fig.46, g.).

The fate of the Velum.

The most drastic anatomical change that occurs at metamorphosis is the loss of the velum. From sections of a number of newly spatted specimens, in only two was found any evidence of what might have been remains of the velum. This consisted of cellular debris in the mantle cavity in the region of the mouth, which did not exhibit/

/exhibit the normal clear-cut outline. It appears from this that the bulk of the velum is sloughed off and that the operation is a rapid and effective one which occurs soon after the larva ceases to be pelagic.

With the loss of the velum the mouth and oesophagus are free to dorsally and to the anterior, taking with them the cerebral ganglion and the apical plate. As shown in Pl.9, fig.14, these organs were closely associated in the larva. The pleural ganglia have now become fused, or nearly so, with the cerebral ganglia which take up a position adjacent to the anterior adductor muscle (Pl.11, fig.21, c.p.g.). The apical plate maintains approximately the same relative position that it did in the larva, and so comes to lie directly above the mouth. It is presumed by various authorities to form the beginning of the upper palps. This also appears to be the case in Y. pallastra, for in the earliest spat the tissue of the palp region is identical to that of the apical plate (Pl.11, fig.18, a.p.). In Pl.12, fig.22 is shown the mouth region in frontal section in a newly settled spat. From this origin the upper palp grows rapidly and at a shell length of 1.0 mm. they are 0.1 mm. long. The 1.2 mm. spat of Ostrea edulis described by Yonge (1926) also had relatively huge palps.

Up to a length of at least 1.0 mm. the upper palp forms a hood above and around the mouth (Pl.12, fig.25 u.p., fig.24 u.p.). In Pl.12, fig.25 is shown a semi-diagrammatic/

/semi-diagrammatic drawing of the palps dissected from an animal 0.75 mm. long. After severing the oesophagus the whole was dissected out as a unit, which may indicate the close tissue relationship between the upper and lower palps. The origin of the lower palpsis, however, debatable and there is the suggestion that they originate as outgrowths of the upper. The definite break in epithelial structure between the lower lip of the mouth and the lower palp is shown in Pl.11, fig.20 j.m.p. The mouth and oesophagus are lined with tall columnar cells with lightly staining nuclei and the palp with more cuboidal cells with heavily staining nuclei. It would therefore appear more likely that the lower palps are outgrowths of the upper.

Loven, as early as 1848, associated the development of the palps with the apical area of the velum, and Gerbe (1875) suggested the velum was transformed into the palps. Davaine (1852) believed in the shedding of the velum toward the end of larval life. Ryder (1884) working on the metamorphosis of Ostrea virginica, agreed with none of this. Sigerfoos (1908) believed that the velum of the Tenedinidae is suddenly cast off and eaten soon after the attachment of the larva and that, as a consequence of this loss, the formation of the palps has no connection with the velum. Stafford (1913) discusses at some length the theories of palp formation and questions whether the velum has anything to do with the palps in Ostrea virginica.

Jackson (1890) speaks about the palps and the velum existing at the same time in O. virginica. Field (1922) studied the formation of palps in Mytilus edulis from whole mounts only, and came to the conclusion that the development in M. edulis is similar to that worked out for Dreissensia polymorpha by Meisenheimer (1901).

While much research has been done on the development of freshwater lamellibranchs, most of the species studied have no veliger larvae and the palps are described as originating either from papillae as in Anodonta (Hebers 1913, Harms 1909), or as outgrowths from the upper and lower lips of the mouth as in Cyclas (Ziegler 1885, Wasserloos 1911). Meisenheimer (1901 in his very detailed paper on Dreissensia describes the upper palps as originating from the apical area. He also described the formation of the inner or lower palps as "outgrowths of the posterior and inner side of the outer palps." Cole (1938) again took up the question of palp development in Ostrea edulis and he agrees with Meisenheimer as to the mode of formation.

The Spatting of Venerupis pullastra on Plane Surfaces.

It is known that oyster larvae tend to set more readily on under surfaces of various cultch materials. Schaeffer (1937) has demonstrated a functional relationship between the angle of surface and the frequency of attachment of the larvae of Ostrea gigas in Quilcene Bay. Essentially the same relationship was found by Hopkins (1935) for O. lurida. They attempt to ascribe this setting behaviour to a "negative geotropism or to the purely mechanical factor of the swimming position of the larva where the foot and velum are uppermost, and would therefore most often, fortuitously, come into contact with under surfaces." (Schaeffer 1937). The swimming position of the larvae of V. pullastra and most lamellibranch veligers is not different from that of the oyster. It is not impossible for byssus attaching forms to settle on under surfaces, and in a few instances, this has been found to occur. Experience has shown most non-cementing species prefer to settle on the upper surface of cultch material. On beaches, the spat of V. pullastra are most often found attached to the under edge of overhanging ledges on pebbles and small stones. To gain some information on the setting behaviour of V. pullastra the following experiment was carried out.

Nine 4" x 4" ground glass plates were held at various angles in frames of ½" mesh galvanized wire. These were duplicated with plates of Tufnol (trade name for plastic sheeting). Four sets of nine plates were hung 18" /

/18" below the surface, from a raft moored off the station slip, previous experience having shown this to be an excellent settling area. The frames were hung free to swing at random relative to the direction of the current, which in the region of the raft does not conform to a discernable pattern. It is probable that the frames would swing so as to offer minimum resistance to the prevailing current, i.e. parallel to its direction. In this case similar amounts of water would flow over all surfaces regardless of the angle at which the plates were held. Partial clogging of the meshes of the wire frames with algae may have altered this. The frames were placed close together to insure equality of exposure and remained in the sea from July 25th to September 2nd, 1947, during which time no storms occurred. The detritus from the upper sides of the plates was examined in a counting cell. In addition, both sides of the plates were examined under a binocular microscope. Both spat and settled larvae were counted, the latter being assumed to be undergoing metamorphosis.

Results.

No spat were found on the under surfaces of plates. This corroborates many other observations on flat horizontal collectors, and this behaviour appears to be typical of most veligers which do not become permanently attached like those of the oyster. Even in the Anomiidae a slightly higher proportion of larvae settle on the upper surface of cultch material.

The counts given in Table 6. indicate a good correlation between the frequency of spatting and the angle of the settling surface; the greatest settlement occurs on the upper surfaces which are nearest to the horizontal. As shown clearly in Table 6, and in the graph Pl.21, there is little difference in the amount of settlement on glass and on Tufnol; and the application of a test of significance proved no difference statistically. The original intention in using glass was to determine whether light exercised any influence on the setting behaviour. However, the upper surfaces of the plates, even those inclined at a steep angle, were soon fouled by a coating of detritus which prevented the transmission of light.

Some spatting took place on the inclined plates. The areas of these were projected on to the horizontal, and the number of spat per square inch calculated. The following results were obtained and plotted on the graph Pl.20.

Angle	Areas in Square Inches.		No. of Spat per Square Inch.	
	Total	Projected	Total Area	Projected Area
0	16	16	5.0	5.0
30	16	12	4.6	6.2
45	16	8	4.0	7.0
60	16	4	3.0	12.0
90	16	0	0.0	0.0

Table 6.

Venerupis pullastra.

The Number of spat found on ground glass and Tufnol plates (4" x 4") held at various angles and exposed from July 25th to September 2nd, 1947, near Keppel Point, Millport. (0 or 360 is vertical).

Angle	Tufnol	Ground glass
	Number of spat	Number of spat
270	96	45
300	95	62
315	99	71
330	89	40
360	0	0
30	86	74
45	71	54
60	95	71
90	87	97
120	49	112
135	45	67
150	44	39
180	0	0
210	62	54
225	58	75
240	50	62

When the total exposed area is considered, the efficiency of the plates as spat collectors decreases as the angle of the plate increases; but when the areas are projected on to the horizontal, the efficiency increases with the angle. Theoretically the curve for the projected areas would continue to rise after the 60 degree point, but since no spat were caught on the vertical plates, a zero value is graphed for the efficiency of the plate held at that angle.

If the setting was the result solely of gravity, there would have been an equal catch per unit of area on projected surfaces. But this was not found to be so, for the plates held at an angle proved to be most efficient. Therefore, it appears that the setting act is due to a horizontal movement of the larvae, and this is doubtless brought about by currents striking the faces of the plates. On the other hand, upper and under sides of all plates, regardless of angle, were theoretically exposed to equal amounts of flow. The non-settling on the under and vertical surfaces may be explained by the lack of fouling. If equal amounts of water did pass all plates, then all of them, if equally fouled, should have caught equal numbers of spat, regardless of angle, total exposed, area, or of projected area. It may be concluded that the supposition that all plates were equally available for settlement does not hold good, possibly because, owing to the fouling of the meshes, the frames did not swing as anticipated. The/

/The conclusion that the setting act is due to a horizontal carriage of the mature larvae in currents which strike the plates more or less at right angles, coupled with initial fouling of the setting surface, seems to be valid under the conditions of this experiment.

Nelson (1926, 1927), Prytherch (1934), Cole and Knight Jones (1939), Korringa (1940) and others, have investigated the relationship between the number of oyster spat and the angle of the setting surface. Korringa (1940) is the only investigator to find that more oyster larvae (O. edulis) settle on upper than on under surfaces. No adequate explanation has been given. Korringa (1940) gives the guarded explanation that it is the result of the efforts of the mature larvae to attain their ecological norm.

Mortality of the Spat.

The large spatfall of Y. pullastra in Balloch Bay from the breeding in summer of 1946 suggested the possibility of following this brood so as to obtain information on its distribution relative to tidal levels, its mortality and its rate of growth. The beach as a whole does not conform to a habitat for Y. pullastra, so this spatfall also presented the opportunity of determining whether the small population of adults was due to unfavourable habitat or to normal lack of spatfall.

After larvae had disappeared from the plankton, three one-square foot samples of beach surface, to a depth of two inches, were taken from each of 7 stations in a line running from high water mark to low water mark, on a spit in the centre of the Bay. The stations were placed at thirty yard intervals down the beach, and their tide levels determined by taking the times at which the tide reached them on a calm day, and finding the corresponding heights from methods given in the Admiralty Tide Tables for 1947, Supplementary Tables, page 249. The stations were found to be at the following tide levels: 8.0, 7.0, 5.0, 4.5, 4.0, 3.0 and 1.0 feet. The beach along the line of stations is composed mainly of a fine layer of sand to a depth of 3 to 12inches, overlying a bed of clay. The whole area is scattered with fairly large boulders (Pl.22, figs. 1 and 2). Various dispersed areas are studded with small pebbles 1.0 /

/1.0 to 10.0 cm. in diameter, and it is in these regions that the maximum spatting of Y. pullastra occurs. Flattely and Walton (1922) Appendix 111, give a description of Balloch Bay.

The tidal streams in this area have not been studied in detail, but there appears to be a current parallel to the shore, especially on the ebb, with a strong likelihood of an eddy on the flood tide, caused by the projection of Clashfarland Point (Pl.3, Map), which marks the southern extremity of the bay. The beach supports a small population of Mya arenaria and of M. truncata especially at the lower levels, with Cardium edule and comparatively small numbers of Venerupis pullastra.

Sampling.

Sampling was done with a one foot square iron frame which could be pressed down into the beach, and the sand and gravel taken from within with a small shovel. The samples were placed in cloth sacks as they were collected and taken to the laboratory where the spat were separated out. This was done first by sieving the whole sample through a 1.75 mm. mesh sieve. The residue was carefully picked over and all the pebbles and rocks examined, some under the binocular microscope. In this way the larger spat were removed. The finer sand which passed through the first coarse sieve, was then put through another 0.75 mm. mesh. The residue was examined in a counting cell under the binocular microscope. A number of animals less/

/less than 0.75 mm. were obtained, indicating the possibility that part of these smaller size groups was lost. A more refined method would have been prohibitive in time.

All shells or parts of shells, as well as the living animals, were taken and counts made of the animals living at the time of sampling, of the complete single valves, and the number of single shells drilled by gastropod, which was taken as the number of animals bored. To arrive at an estimation of the number of dead animals, the number of unbored single valves was multiplied by the factor 2/3. This is a more suitable conversion factor than 1/2 because the chances are greater that more single than both valves representing a pair, will be found. In estimating the number of valves from fragments, any part that could not be duplicated, such as the hinge, was considered to be a single valve. The complete data is tabulated in Table 7.

The first sampling was done in September, 1946, and further samples were taken in December, 1946, February, April, June and October of 1947. The sample from the 1.0 foot level in the October samples was not obtained until a month later because of the unsuitable tides.

Results.

In Pl.24 is shown the distribution of the spat over the beach for the 1946 and the 1947 spatfalls. A striking feature of the graph is the similarity in density/

TABLE 7.

Tables A and B showing the number of living Venerupis spat, the dead (single valves converted), the number of shells bored and the combined alive and dead animals, from the one square foot mortality study samples at the different stations from Balloch Bay in September and December, 1946., February, April, June and October, 1947.

* November, 1947. x Sample not taken.

	A. Alive						B. Dead					
Station	Sep	Dec	Feb	Apl	Jun	Oct	Sep	Dec	Feb	Apl	Jun	Oct
1 - 1	0	X	X	5	X	X	0	X	X	7	X	X
2	0	X	X	5	X	X	0	X	X	13	X	X
3	X	X	X	8	X	X	X	X	X	3	X	X
Total	0	X	X	18	X	X	0	X	X	23	X	X
Av/sq.ft	0	X	X	6	X	X	0	X	X	8	X	X
2 - 1	2	5	2	14	7	22	1	17	15	50	10	6
2	1	7	4	8	X	17	0	7	33	9	X	4
3	X	11	10	7	X	27	X	19	33	5	X	4
Total	3	23	16	29	7	66	1	43	81	64	10	14
Av/sq.ft	1	8	5	10	7	22	1	14	27	21	10	5
3 - 1	43	113	5	27	1	47	5	16	10	57	3	9
2	1	89	25	17	X	32	0	11	7	54	X	3
3	70	192	18	21	X	26	5	31	9	13	X	1
Total	114	394	48	65	1	105	10	58	26	124	3	12
Av/sq.ft	38	131	16	22	1	35	3	19	9	41	3	4
4 - 1	141	79	31	2	0	129	23	25	26	3	6	8
2	249	247	44	59	X	243	17	73	8	8	X	22
3	188	25	39	42	X	207	9	4	5	5	X	14
Total	578	351	114	103	0	579	49	102	39	16	6	44
Av/sq.ft	193	117	38	34	0	193	16	34	13	5	6	15
5 - 1	77	11	7	4	0	243	14	95	22	9	0	71
2	324	6	13	13	X	254	83	65	26	3	X	188
3	262	2	1	13	X	284	84	63	15	9	X	94
Total	663	19	21	30	0	781	181	223	63	21	0	353
Av/sq.ft	221	6	7	10	0	263	60	74	21	7	0	118
6 - 1	17	7	2	1	0	60	4	105	1	3	14	33
2	48	19	9	14	X	142	31	90	4	1	X	27
3	16	21	53	2	X	41	9	121	15	5	X	26
Total	81	47	64	17	0	243	44	316	20	9	14	86
Av/sq.ft	27	16	21	6	0	81	15	105	7	3	14	29
7 - 1	698	160	68	4	5	120*	160	89	19	10	13	127
2	346	92	15	21	X	247	94	101	3	31	X	112
3	30	84	16	21	X	185	0	75	7	11	X	123
Total	1274	336	99	46	5	552	254	265	29	52	13	362
Av/sq.ft	425	112	33	15	5	184	85	88	10	17	13	121

Tables B and C showing the number of living Venerupis spat, the dead (single valves converted), the number of shells bored and the combined alive and dead animals, from the one square foot mortality study samples at the different stations from Balloch Bay in September and December, 1946., February, April, June and October, 1947.

X Sample not taken

	C. Bored						D. Alive and Dead					
Station	Sep	Dec	Feb	Apl	Jun	Oct	Sep	Dec	Feb	Apl	Jun	Oct
1 - 1	0	X	X	1	X	X	0	X	X	12	X	X
2	0	X	X	0	X	X	0	X	X	18	X	X
3	X	X	X	0	X	X	0	X	X	11		X
Total	0	X	X	1	0	X	0	X	X	41	X	X
Av/sq.ft	0	X	X	1	0	X	0	X	X	14	X	X
2 - 1	0	1	1	5	0	0	3	22	17	64	17	28
2	0	1	0	0	X	0	1	14	37	17	X	21
3	X	0	0	0	X	0	X	10	43	12	X	31
Total	0	2	1	5	0	0	4	66	97	93	51	80
Av/sq.ft	0	1	1	2	0	0	1	22	32	31	17	27
3 - 1	1	0	0	1	0	1	48	129	15	84	4	56
2	0	1	0	0	X	0	1	100	32	71	X	34
3	0	1	0	0	X	0	75	223	27	34	X	27
Total	1	2	0	1	0	1	124	452	74	189	12	117
Av/sq.ft	1	1	0	1	0	1	41	151	25	63	4	39
4 - 1	2	2	1	0	0	0	164	104	57	5	6	137
2	0	2	0	1	X	0	266	320	52	67	X	265
3	0	0	0	0	X	2	197	29	44	47	X	221
Total	2	4	1	1	0	2	627	453	153	119	18	623
Av/sq.ft	1	1	1	1	0	1	209	151	51	40	6	208
5 - 1	4	2	0	0	0	4	91	106	29	13	8	314
2	7	3	5	2	X	5	407	71	39	16	X	242
3	6	0	0	1	X	2	346	65	16	22	X	328
Total	17	5	5	3	0	11	844	142	84	51	8	884
Av/sq.ft	6	2	2	1	0	4	281	47	28	17	3	294
6 - 1	0	5	0	0	1	0	21	112	3	4	14	93
2	5	2	0	0	X	2	79	109	13	15	X	169
3	1	3	0	0	X	1	25	142	68	7	X	67
Total	6	10	0	0		3	125	363	84	26	42	329
Av/sq.ft	2	3	0	0	1	1	42	121	28	9	14	110
7 - 1	15	3	1	0	2	5	858	249	87	14	18	247
2	1	4	0	3	X	3	740	193	18	32	X	339
3	0	2	0	0	X	4	30	159	23	32	X	328
Total	16	9	1	3	4	12	1628	601	128	98	54	914
Av/sq.ft	5	3	1	1	2	4	543	200	43	33	18	305

TABLE 8.

Statistics of the mortality samples of spat from various stations in Belloch Bay. September, 1946. All measurements are those of length and are given in mm.

Station	Sample size	Range	Mean	Variance	Standard Deviation	Standard Error
2	-					
	-					
	1	1.87 - 2.18				
3 - 1	41	0.75 - 4.81	2.47	0.600	0.802	0.131
2	1	0.37 - 4.37	3.75			
3	65	0.75 - 5.56	2.22	1.002	1.044	0.016
4 - 1	125	0.75 - 5.18	2.03	0.889	0.929	0.083
2	211	0.75 - 7.94	2.64	1.911	1.450	0.099
3	166	0.75 - 5.56	2.14	0.920	0.957	0.123
5 - 1	71	1.12 - 4.43	2.66	0.706	0.853	0.101
2	255	0.93 - 5.18	1.52	0.748	0.908	0.058
3	241	0.37 - 5.18	1.41	0.397	0.656	0.042
6 - 1	17	0.75 - 2.18	1.37	0.110	0.340	0.085
2	43	0.75 - 2.56	1.51	0.209	0.485	0.074
3	20	0.75 - 3.68	1.64	0.437	0.685	1.564
7 - 1	642	0.37 - 5.56	1.54	0.459	0.709	0.027
2	518	0.37 - 5.18	1.58	0.418	0.683	0.029

/density and distribution between the two years. This would appear to indicate that the physical nature of the beach is the essential factor, for this is relatively constant. Similarity in density did not occur in the case of Mya arenaria and Cardium edule, for the former species spatted lightly in 1946 and heavily in 1947, while the latter spatted heavily in 1946 and lightly in 1947. It is believed the low value for V. pullastra at the tide level of 3 feet is due to the unsuitability of the ground for setting, as it is composed of nearly pure sand, and thus provides no attachment for the byssus. Stations at the 5.0, 7.0 and 8.0 foot tidal levels are much of the same nature, although, doubtless, the high level on the beach may account in large measure for the small spatfall there.

Returning to the low value at the 3.0 foot level, it seems unlikely that in the short distance between this and the 4.0 and the 1.0 foot stations, there should be any factor such as tidal swirl to prevent initial spatting, when this was heavy above and below. The absence of natural cultch either prevents setting; or, if there is setting, survival beyond the earliest stages after metamorphosis. A sample taken below the zero tide mark at the outer edge of the Laminaria zone failed to yield any spat, and here again the bottom is of pure sand.

Mortality.

The reduction in the number of spat per square foot throughout the year is shown in Table 7, and the mortality rate on Plate 27. By June 1947, the mortality had reached nearly 100%. The causes may be tentatively attributed to three factors:

1. The unusually sever winter of 1946-47.
2. Predators.
3. General unsuitability of the habitat.

It is true the winter of 1946-47 was unusually severe, but no drastic effects were noticed on other invertebrates in Balloch Bay. Sampling at Cross Houses Beach disclosed no heavy mortality of V. pullastra there, though the original numbers were not large. It is doubtful if the severe winter played a significant part in causing the excessive mortality in this brood of V. pullastra.

Probably three types of predators have to be considered. Balloch Bay is the feeding ground for large flocks of several species of shore and sea birds, such as gulls, curlews, oyster catchers, red legs, eider and mallard ducks. It is known that these types of birds do feed on small mollusks, and even a small number of birds feeding regularly over a period of nearly a year, could make a considerable inroad in a population of littoral molluscs, especially in such a favoured feeding ground. Fish are well known to feed on small mollusks (Davis 1923, Blegvad 1928, Peterson 1915). Flatfish are known to/

/to frequent the intertidal zones of Balloch Bay during high tide as evinced by their traces in the sand. A third type of predator is the drill or gastropod borer. Approximately 5% of the dead spat had been drilled. This is a minimum figure for it is likely that a drilled shell will break up more readily than an undrilled one. Hunt (1925) considers that Natica is responsible for the numerous drilled shells of bivalves in the Plymouth area.

It is believed that the main cause of mortality in Balloch Bay is the unsuitability of the ground for older spat. The surface layers of the beach in which the young spat must at first maintain themselves is not a stable environment and the surface layers of sand shift about considerably. This was observed: one instance was the appearance, over the winter, of a bed of fossil Lutraria and Pecten shells to one side of the station at the 4.0 foot level. Thus the young spat, along with the holdfast, may be buried by shifting sand. At this stage the siphons are not more than 4 - 5 mm. long in the larger specimens, so it does not require a deep layer of sand to smother them. On the other hand, they may be more exposed by the shifting of the sand to predators or to wave action. The theory of the instability of the environment is further supported by the fact that the small adult population on the beach is found between the 0. and the 2.0 foot tide levels; an area where boulders and pebbles provide good protection for both the young and old.

The Cross Houses Beach at Millport, which supports the densest population of V. pullastra on the island is nearly a solid mass of large flat rocks providing plenty of attachment and protection; an extremely stable environment as far as movement of the substratum is concerned. From the small adult population on Balloch Bay it seems that a high mortality is not unusual.

Two similar species are found in British Columbia, the indigenous Paphia staminea and the imported Japanese Paphia philippinarum; but their habitat is different from that of Venerupis pullastra. They prefer a protected beach of mixed gravel, shell and mud. It is not known whether V. pullastra is found in such an environment, for the writer has seen nothing comparable in Scotland. All beaches on the Isle of Cumbrae are exposed to wave action that at times may become considerable.

Discussion.

It is striking that the rate of mortality of a large population such as that of young V. pullastra in Balloch Bay should be so high as practically to destroy the whole population within a year. Such occurrences are not unknown in other species, for Weymouth, McMillin and Holmes (1925) record a mortality of approximately 66% for the spat of Siliqua patula on Copalis Beach, Washington, between August, when they settled, and the/

/the beginning of December. A storm in that month reduced the numbers still further from 494 per square foot (the 33 % survival level), to 18 per square foot, and by February these had been reduced to 16 per square foot. Few, if any, were reported in the following summer. Thus it is seen that a heavy set of clams, originally 1450 per square foot, may be completely destroyed, even when they have settled in the type of habitat which is optimal for the species. Therefore, in comparison, one might expect considerable mortality in Balloch Bay, for it does not represent a habitat in which the adult V. pullastra is found in greatest abundance.

This raises once again the problem of metamorphosis, choice of substratum, delay and mortality. Thorson (1946, pp. 460-467) has discussed this at some length and concludes that the "either, or " hypothesis of settlement of marine invertebrate larvae is not tenable. Belding (1912) was among the first to point out that the survival of lamellibranch larvae depends on the character of the bottom in which they settle. Nelson (1928) puts the matter succinctly when he said, "When the time for settling arrives, the larvae must attach or die." Yonge (1937) assumed that the survival of the two species of Aporrhais in Herdla fjiord depends on whether or not they settle in the habitat for which the adult is adapted,/

/adapted, but that in an intermediate region both species are able to exist. Thorson (1946) cites Mortensen's (1921) experiment in which he was able to induce metamorphosis in the larva of the echinoid Mellita sexies-perforata by adding sand to the dish in which they were living. Day and Wilson (1934), and Wilson (1937), have shown that the larvae of various polychaetes are able to postpone metamorphosis until a substratum suitable for adult life is encountered. It is significant that Thorson's most convincing data comes from laboratory experiments. Larvae of Branchioma vesiculosum kept by Wilson (1936) had a fairly suitable substratum available, but there was considerable variation in the time of settling. Lamellibranch larvae are very difficult to rear in the laboratory and the results, in relation to time, of such experiments must be treated with caution. Russell (1934) says, "It is possible that the settling down of pelagic larvae is a much more precise and complex affair than we imagine, involving specific behaviour acts or trains of behaviour."

It is not unlikely that the larvae of marine invertebrates have a certain power of selection of their environment for settling in; witness the search of the larval oyster for a clean surface; but the larva's horizon is limited because of its size. A larva of V. pullastra may settle in the thin film of detritus and sand particles on a glass plate and this is suitable/

/suitable enough for the spat, because the thickness of the film is adequate relative to the size of the spat. But it very soon outgrows this environment. What must be considered is the comparative size of the cosmos of the larva or small spat and the cosmos of the adult. Suitable setting grounds for the larvae and spat of V. pullastra are common, but there are few habitats suitable for adults. Balloch Bay provides environments suitable for the spat, yet few adults are found there, and all the mortality cannot be attributed to predators.

Many more examples might be given but one will suffice. Both types of ground inhabited by Aporrhais (Yonge 1937) are no doubt suitable for the newly settled larva of both A. pes-pelicani and A. serresiana. The mortality may well take place after the young have outgrown the larval environment and need the more restricted environment for which the adult is adapted. No amount of delay in metamorphosis or occasional "touching down" to test the substratum as they are carried along by the current, as suggested by Thorson (1946, page 465), can overcome the difference in the needs of the metamorphosed larva and of the adult.

Careful examination of a variety of surfaces in the littoral and sub-littoral zones reveals the spat of many different species, often in considerable numbers, in areas totally unlike the adult habitat. Not always is the settling area even suitable for the young spat.

This period after setting, possibly up to a year after this, is the stage in the life history of many sessile marine invertebrates at which considerable mortality occurs and this is certainly the case with Y. pullastra. Contrary to the new school of thought on the subject, it is still believed that survival of the spat and final success of any spatfall is largely a matter of chance. It is agreed that the larvae, or at any rate the larvae of certain species or groups, may exercise a certain amount of choice in the selection of a suitable substratum, but it is a choice that in the main fulfils only the immediate needs of the spat. It also appears that in most cases the high mortalities suffered by many species after metamorphosis (formerly attributed to the period immediately after metamorphosis) may be spread over a considerable period. This would certainly explain the mortality of the 1946 brood of Y. pullastra in Balloch Bay.

Rate of Water Propulsion.

Considerable interest is being shown in the rate of water propulsion, or filtration rate, in various marine invertebrates, initially because of the economic and hygienic importance in oysters, but more recently in other filter feeding organisms in connection with food intake and metabolism. Similar studies on *Y. pullastra* were undertaken partly for the latter reasons, but mainly to ascertain whether, and if so how, the filtration currents and consequent pressures are involved in the spawning act.

Direct methods of study have been used where the siphons of the animals concerned have been tapped by tubes or rubber aprons and the actual quantity of water passed through these tubes has been measured. Indirect methods have also been used by measuring the rate at which animals were able to clear suspensions of various types of particles.

A direct method was used by Parker (1914) who measured the strength and volume of water currents produced in sponges by attaching a tube to the osculum. Placing the tube in a vertical position and observing the increase in height of the water in the tube in relation to that in the tank in which the sponges were living, he obtained a measure of the pressure produced by the exhalent current. By measurement of the velocity of/

/of the floating particles in the tube, he estimated the volume of water pumped and concluded that the current produced by sponges consists of relatively large volumes of water flowing at low pressure. For the sponge Spinosella he obtained a water flow of 3.2 litres per hour at a pressure of 2.9 mm. of sea water. The volume estimations are criticised on the grounds of failure to realise that the speed of flow through a tube varies along its radius, the maximum velocity being at the centre.

Allen (1914) using a similar method for fresh water mussels made the same error. He had difficulty in introducing the tube because of the sensitivity of the siphons and obtained only a single reading which gave a rate of 1.4 litres per hour. Hecht (1916) measured the current pressure and volume of water pumped in the ascidian, Ascidia atra and pointed out the differences in the current velocities of the atrial and oral siphons, together with the angle at which they work, as being factors in preventing the mixing of two streams of water. He also measured the velocity of particles in a tube inserted in the oral siphon. The pressure was found to vary between 1.7 and 2.1 mm. of sea water and the filtered volume to be 7.2 litres per hour for animals of 100 grams weight. The temperature was not given. Hecht considers the energy distribution in developing the water current in A. atra to be quite efficient: the pressure being just sufficient to overcome the inertia of the water. He also concluded that the volume of water/

/water moved per unit of body weight varies inversely with the size of the animal, a conclusion which is in general supported by the work of Jorgensen (1943) on lamellibranchs.

Nelson (1921) modified the method of Moore (1908) using a rubber apron over the exhalent area and obtained for Ostrea virginica a value of 5.7 litres of water filtered per hour. Later he obtained a value of 26 litres per hour from a 4 inch oyster at 30° C.

Galtsoff (1926, 1928b) in a broad study on the oyster gill in relation to sanitation and culture, describes two direct methods of measuring the flow through the gill of Ostrea virginica. In both methods a tube is introduced into the cloacal chamber and made fast and water tight with cotton packing. In the "tank" method, the oyster pumps water from a tank in which it rests into a measuring vessel which is connected to the oyster by the tube inserted in the cloacal chamber. The level of the two vessels is kept constant and equal by overflow siphons. This equality is most necessary, for a differential level in one direction, would cause a siphoning effect through the gills, while in the other direction the gill would be pumping against a pressure caused by the head of water.

In the "carmine-cone" method the tube inserted in the cloaca is connected to a further system of tubing which allows measurement of the velocity of a cone of carmine/

/carmine carried by the exhalent stream; then using a modification of Poiseuille's formula for stream line flow, the rate may be calculated. Galtsoff obtained slightly higher values with the latter method and considers them more valid as a measure of rate of flow. He secured values of 2.5 to 2.9 litres per hour at 26.9° C. Nelson (1935) criticised the use of a tube in the cloacal chamber on the grounds of interference with the operation of the branchial hearts and visceral ganglion, as well as Galtsoff's neglect of the water flow through the "promyal" chamber. Dodgson (1928) attempted to measure the volume of water circulating through the mantle cavity of Mytilus edulis, initially and unsuccessfully by means of tubes and rubber aprons. He then turned to the indirect method of determining the rate of clearing of suspended material in known volumes of water. Using chiefly fine clay suspensions the rate was taken to be the time required for a number of animals to clear a known volume. While he recognised that the water, in which the mussels are placed, may be filtered several times in order to clear it completely, no quantitative adjustment was made. The rate was found to be 2 litres per hour at 17° C. Hopkins (1933) studying the relative rate of flow of water over the gills of Ostrea gigas used a method in which the normal functions of the animal are not interfered with. He found the relation temperature and optimum gill activity similar to that obtained by Galtsoff for O. virginica, lying between 25 and/

/and 30° C. at which point the maximum rate of flow is 3.9 litres per hour. Hopkins, however, believes the optimum temperature for feeding, considering the animal as a whole, to be about 20° C., for above this temperature the valves begin to close and so act as brakes to the water current.

Sparck (1933) in a preliminary investigation on the power of filtration in O. edulis resolved the problem into how large a bulk of water is at the disposal of the animal if the surrounding water is almost completely calm. To solve this problem he placed an oyster in a vessel containing water of a salinity of 30‰. Above this was a layer of water coloured with methylic blue with a salinity of 27‰, and on top of this a layer of fresh water to prevent evaporation, cooling, and the formation of vertical currents in the salt water, other than those produced by the oyster. At a distance of 30 cm. an adult oyster was able to produce a disturbance in the coloured layer by clapping the valves, but no mixing was effected.

Fuller and Clarke (1936) in a study of setous feeding of Calanus investigated the rate of filtration by the speed of removal of carmine particles from a suspension in which the animals were living. They calculated a figure of 5.61 cc. per day, but made it clear that these experiments were preliminary, and calculations based on nutritional requirements by Marshall, Nicholls and Orr (1935) indicated that the values obtained were far below the volume sufficient/

/sufficient to supply the nutritional needs of the animal. Later Fuller (1937) again attempted to estimate the feeding rate of Calanus finmarchicus. He did this by determining the rate at which a group of animals depleted cultures of the diatom, Nitzschia. The formula developed by him was:- $Wx = V \ln \frac{C1}{C2}$ where Wx is the amount of water swept free of diatoms by each copepod in x hours; V is the volume of water per copepod; C1 and C2 are concentrations of the diatoms at the beginning and end of time x. This formula is identical to the one here derived in another way. By this method he found the amount of water filtered per day was 1.09 cc. which, in relation to the amount of available food, would provide only one tenth of the necessary nutriment estimated on the basis of oxygen consumption.

In a comprehensive paper, Fox, Sverdrup and Cunningham (1937) give a survey of the literature and estimate the rate of water propulsion in the large California mussel, Mytilus californianus. Groups of mussels were placed in stirred suspensions of marine clay or calcium carbonate. The rate at which the animals removed the suspension by filtration was measured by chemical estimation of the calcium content of successive samples taken at equal intervals of time. They made the assumption, "in unit time each mussel pumps M litres of water through its system and removes all suspended calcium from this quantity of water," and on this basis they develop an equation for the filtration rate. This equation is essentially the same/

/same as those derived by Fuller and by the present author. Fox et al (1937) concluded that the mussel removes virtually all suspended matter from the water passed over the mucous surface of the gills and mantle, and that the water is propelled rhythmically and at a rate which is on the average constant. Medium sized mussels, between 95 and 130 mm. in length, gave propulsion rates between the values of 2.2 and 2.9 litres per hour, with an average of 2.6 litres per hour.

Jorgensen (1943) studied the rate of water transport through the gills of young Mytilus edulis by means of photometric determinations of the percentage amounts of the unicellular alga Synechococcus from a known quantity of the suspension of the algae. He obtained filtration rates of between 45 and 186 ml. of water per hour for a group of 5 animals, each 0.2 grams in weight, at temperatures between 11 and 22° C. From the literature Jorgensen also calculated filtration rates per hour per gram for stages from the pelagic larvae (oysters) to the adult (various species). These varied from 6.7 litres for larvae to 0.19 litres for young bottom stages, and 0.01 - 0.04 litres for adults.

In a study of the feeding of O. virginica, Loosanoff and Nomejko (1946) used the "tank" method of Galtsoff (1928) modified by the rubber apron of Moore (1908) and Nelson (1921) over the exhalent aperture. Pumping rates for 4 inch oysters within the temperature/

/temperature range of 17.0 to 28.0° C. averaged 25 to 27 litres of water per hour with a maximum of 34 litres. The rates found on the ebb tide were equal to or greater than those found on the flood, thus refuting the generalisation by Nelson (1923)? that relatively little food is taken on the ebb. They conclude also that there is no correlation between periods of shell closure and darkness and that the pumping rate is the same for both daylight and darkness. It is pointed out that O. virginica is able to pump in one hour a volume of water 1500 times the volume of its own body.

The Problem.

The direct method of determining the rate of flow is exceedingly difficult in the case of siphonate lamellibranchs due to the great sensitivity of the siphons in most species. When tubes are inserted in the siphons, and this can only be done during anaesthesia, they are later either forced out of the siphons or are cut by the pressure of the shells against the tube. The use of blocks to prop open the valves was unsuccessfully tried. In a few cases the inserted tubes were retained in the siphons, but the animals did not exhibit normal reactions, and soon died.

The alternative was the indirect suspension clearing method of Viallanes (1892), Dodgson (1928), Damas (1935) and Fox, Sverdrup and Cunningham (1937). The latter authors are the only ones who have developed and used the method with any degree of accuracy, and it is/

/is their method, further modified, that was used.

The fundamental basis of this method rests on the assumption that the gills completely filter out all particles in the suspension. Kellog (1915) considered that a lamellibranch was able to feed only when the water was comparatively clear, so that food particles would be brought to the surfaces of the gills a few at a time. He maintained that in muddy water all suspended particles, whatever their nature, are led to the outgoing tracts. He also describes the mucous production of ciliated surfaces and the large amounts of mucous that may be produced by continued stimulation. Damas (1935) describes the formation of mud deposits in the Zeebrugge roadstead by worms and mollusks, and indicates that colloidal particles as well as detritus are filtered out of the water and deposited. Ranson (1926) describes the filtering and depositing action of lamellibranchs, especially oysters and mussels, and describes the quantitative work of Viallanes who measured filtration rates by weighing dry the amounts of faeces and pseudofaeces deposited in a given time. Zobell and Landon (1937) found that 99.9% of added bacteria are retained by the gills of Mytilus californianus, though Galtsoff (1928) states that only 20 - 50% of the bacteria added are retained by Ostrea virginica. Jorgensen (1943) assumed that a large majority of Synechococcus cells which are only 2 - 3 microns long, are retained by young Mytilus edulis. Y. pullastra was found to be able to clear suspensions of graphite and of/

/of monolite fast scarlet, whose particle size ranges are between 1 and 5 microns. It appears that most lamellibranchs are able effectively to filter small particles out of water. McGinitie (1941) investigated the method of feeding in four Pacific species by observing the process through a glass window placed over an opening cut in the shell. He came to the conclusion that feeding can only take place when a sheet of mucus entirely covers the gill. He also maintained that because a bivalve is pumping it is not necessarily feeding, and the straining of the particles from the water currents by mucus is emphasised. It is interesting to note in this connection, that Hopkins (1933) in discussing the marked changes in pumping rates observed in O. gigas, says (page 488), "It may be also, as suggested by Galtsoff (1928a), that mucus forms a layer over the gills, clogging the pores and impeding or stopping the current."

In order to check McGinitie's observations, similar windows were made in a number of specimens of V. pullastra. Observations failed to disclose evidence of a continuous sheet of mucus over the gill, though it must be admitted that, due to the transparency of the mucus, it was frequently difficult to decide as to its presence or absence. The introduction of particles of a variety of sizes into the inhalent stream always resulted in those particles being conveyed over the gill entangled in strings of mucus and not in a sheet. Furthermore, the introduction/

/introduction of a coloured suspension during pumping invariably resulted in the production of coloured faeces, indicating that, with these suspensions, pumping was always accompanied by feeding.

The modification of Fox, Sverdrup and Cunningham's method used here was the replacement of the estimation of concentrations of suspended material by chemical means with one based on the principle of light absorption, which was later found to have been used by Jorgensen (1943), with a Rehberg electrophotometer. The instrument used here was the Spekker Absorptiometer which is a sensitive instrument recording quantitatively minute changes in intensity of colour.

The normal procedure in using the absorptiometer is to develop a calibration curve by taking readings at various known dilutions of a solution or suspension of known concentration. However, since in the case of the suspension (jeweller's rouge) used in these experiments, a linear relationship exists between concentration and absorptiometer or "Spekker" readings, as they are called, there was no necessity for knowing the absolute concentrations of the suspensions used in terms of weight per unit volume. Thus the need for a large number of chemical analyses was obviated. The original "Spekker" reading, that is, the one at the start of each experiment, represents a concentration of 100% of the suspension in use, and the concentration at any given time is the ratio/

/ratio of the "Spekker" reading at that time to the "Spekker" reading at the beginning of the experiment.

The major difficulty was to obtain a suspension material that would meet the demands of the conditions imposed by the experiment. The following criteria of an ideal suspension material was set up:-

1. Coloured.
2. Non-toxic and Non-irritable.
3. Low settling rate.
4. Non-flocculating when stirred in sea water.
5. Low surface tension.
6. Small particle size.

In an effort to obtain a material that would meet most or all of these requirements, a large number of substances were tested. The requirement in which most substances failed was that of non-flocculation. Many gave good suspensions in fresh water, and were satisfactory in unstirred sea water, but flocculated into aggregations when agitated. Jeweller's rouge, a red oxide of iron, gave the best consistent results, and a suspension of this was used in most of the recorded experiments.

Monolite Fast Scarlet, an I.C.I. pigment, was most promising,for the particles are uniformly small in size, non-flocculating, and the settling rate is negligible. However, though non-toxic, the dispersal medium in which it/

/it is made up appeared to have, at times, an inhibitory effect on pumping activity and further experiments are necessary to overcome this difficulty. Aquadag, a colloidal graphite, with small particle size, kindly supplied by E.G. Acheson Ltd., gives a fine dispersion with a low settling rate, but it flocculates badly when stirred in sea water.

Experimental Method.

With minor variations, the following technique was used in conducting the experiments.

One gram of iron oxide was added to two litres of filtered sea water and stirred with a high speed electric stirrer for 5 minutes. This suspension was allowed to settle for 30 minutes to allow the larger aggregations of particles unbroken by the stirring to settle out. 1.5 litres of the supernatant fluid was then decanted off and made up to 3.0 litres. A dead clam, equal in size to the experimental animals, was used in the settling controls to make them and the experiments as comparable as possible, for it was found that, in stirring, some of the suspended particles adhered to the shells. Each of the experimental animals and the dead control had previously been placed in a litre beaker containing 500 cc. of pure filtered sea water, and to each of these was added 500 cc. of the oxide suspension to make up the experimental volume of one litre. The final concentration of oxide was not greater than/

/than 0.1 grams per litre, equivalent to 0.02 cc. of solid material per litre. The stirring apparatus was set in motion as the suspension was added to the beakers. This apparatus consisted of a 1" by # $\frac{3}{16}$" perspex plate inserted in each beaker to a distance of 2 inches from the bottom. The plates were rotated on their own axis by electric motor and pulley, geared down to approximately 90 R.P.M., a speed sufficient to keep the main body of particles in suspension, but not sufficient to lift from the bottom of the beakers the heavier aggregations that had settled out, or the strings of faeces and pseudofaeces. The purpose of the stirring is two-fold. First, to attempt to reduce the settling out effect to a minimum, and second, to keep the concentration of particles homogeneous throughout the suspension. If the suspension were not stirred the animal would, due to its own feeding activity, soon find itself in an area devoid of particles, and this is a criticism that may be levelled against Jorgensen's method in which no stirring was done. Three experimental animals, and one control, were used in each trial, and all four beakers were stirred and treated in the same manner. Results from 26 individual experiments given in Appendix 1, were obtained using iron oxide, 9 experiments were conducted with Monolite and 3 with Aquadag, as well as many test experiments and others that were abandoned for various reasons. Samples for "spekkering" were taken with a pipette, always from the/

/the same point at mid-depth and an inch from the wall. The initial sample was taken immediately after the stock rouge suspension had been added, and from then on, usually at half hourly periods for intervals of 3 to 5 hours. For experiments 1-15, 30 cc. samples were taken for use in the 30 cc. "spekker" cell. A water setting of 1.000 was used with neutral filters. For experiments 16-40, 8 cc. samples were taken to use in 8 cc. "spekker" cell with a water setting of 0.400. A standard procedure was adopted for sampling and "spekkering" and this was rigidly adhered to throughout the experiments, so that the technique was standardised.

* Mathematical Treatment.

Dodgson (1928) used the time required to clear completely a known volume of suspension for determining the rate of filtration of Mytilus edulis. No account was taken of the fact that the suspension was becoming progressively diluted, and with the progress of time, greater amounts of water had to be filtered to obtain equivalent diminution in the concentration of particles. However, he pointed out that the values so determined were minimum ones.

* Dr. H. Barnes, Millport, assisted with the mathematical treatment which was further checked by Dr. R.A. Robb, Mathematics Department, University of Glasgow.

It would appear that the process might be interpreted by the mathematical concept of compound interest with a negative sign, using the following assumptions:-

1. The filtration rate is constant.

2. All suspended material in the water passing through the inhalent siphon is removed by the gills.

3. The amount of suspended material filtered out is proportional to the concentration of the suspension present.

On this basis, there should be a linear relationship between time and the rate of removal.

Thus if :

V- equals ------ original volume in litres.

a equals ------ original weight of suspended material.

y equals ------ final weight of suspended material at time t.

t equals ------ time.

r equals ------ rate of filtration.

P equals ------ "spekker" reading.

Each time r/v of the amount present is filtered, the amount $\left\{ \frac{r}{v} \times \text{amount present} \right\}$ is removed.

$$y = a \cdot e^{-\frac{r}{v} t} \qquad 1.$$

$$\frac{y}{a} = e^{-\frac{r}{v} \cdot t}.$$

$$\log_e \frac{y}{a} = -\frac{r}{v} t \qquad 2.$$

But the concentration of suspended material is K x "spekker" reading.

So that :

$$s = K.\ P\ 1$$

$$y = K.\ P\ 2$$

$$\text{and } \log_e \left(\frac{K\ P2}{K\ P1}\right) = -\frac{x}{v}\ t. \qquad 3.$$

$$\text{or } \log_e \left(\frac{P2}{P1}\right) = -\frac{x}{v}\ t.$$

$$r = \frac{y}{t}\ \log_e \left(\frac{P2}{P1}\right)$$

The natural logarithm of the ratio, successive "spekker" to the original "spekker" reading at time zero, is plotted against time to give the filtration rate at which the suspended material is removed. Since the rate of removal of suspended material in the experiments with live animals is due to a combination of the amount actually filtered out by the animals plus the amount that is settled out by gravitational effect, it is necessary to estimate that latter amount. This was obtained from the control settling experiments, one of which was run in conjunction with three live experimental animals as described above. From the type of curve derived by plotting the amounts settled out against time, it would appear that the amount precipitated in unit time is proportional to the total amount which is suspended, and equation 3 above can be used to describe that rate of settling.

Thus the actual rate of filtration by the animals can be expressed by :

$$\text{Rate} = \frac{V}{t} \left[\log_e \left(\frac{P2^a}{P1^a}\right) - \log_e \left(\frac{P2^c}{P1^c}\right) \right]$$

when $\log_e \left(\frac{P2^a}{P1^a}\right)$ is the tangent of the curve describing the rate of filtration by the animals, in which is included the settling rate, and $\log_e \left(\frac{P2^c}{P1^c}\right)$ is the tangent of the curve describing the rate of settling to gravitation.

The data is first plotted as $\ln\left(\frac{P2^a}{P1^a}\right)$ against time, and as $\ln \left(\frac{P2^c}{P1^c}\right)$ against time. These curves are shown in Plates 28 and 29. In Table 9 are listed the logarithmic decrements for the first hour of the experiment both in the animal and the control experiments, and the rates are calculated from the difference between these two values and reduced to a unit of time of one hour.

On Plate 30 is plotted the filtration curve (lower line of long dashes), for Experiment 35, data in Appendix 1. The line of short dashes is a straight line fitted by the method of Least squares. The upper line of long dashes is the curve representing the rate of settling of the suspension, also plotted from the data of Experiment 35, Appendix 1. The filtration rate is obtained by taking the difference of the tangents of the 2 curves and modifying this by the time and volume ratio as indicated in the equation, page 88.

TABLE 2.

FILTRATION RATES

Number of Experiment.	Logarithmic decrement		Difference.	Time (minutes)	Rate Litres per hour.	Experimental Animal.
	Animal	Control				
1.	0.7636	0.3427	0.3209	53	0.344	X1
3.	0.2860	0.1054	0.1806	60	0.181	X2
4.	1.3262	0.1301	1.1961	77	0.932	1
5.	1.4024	0.1301	1.2723	77	0.992	2
6.	1.3280	0.1301	1.1979	80	0.934	3
7.	0.5863	0.2319	0.3544	60	0.354	1
8.	0.4231	0.2319	0.1912	60	0.191	2
9.	0.6832	0.2319	0.4513	60	0.451	3
10.	0.5888	0.2263	0.3625	60	0.363	1
11.	1.0024	0.2263	0.7761	60	0.776	2
12.	0.7864	0.2263	0.5611	60	0.561	3
13.	1.1744	0.5159	0.6585	60	0.659	1
14.	1.1394	0.5159	0.6235	60	0.623	2
15.	1.4784	0.5159	0.9625	60	0.964	3
16.	0.5846	0.3774	0.2072	60	0.207	1
17.	0.7550	0.3774	0.3776	60	0.378	2
18.	0.5226	0.3774	0.1452	60	0.145	3
32 (2)	0.7036	0.1143	0.5893	60	0.295	2, 3
33 (2)	1.4077	0.1143	1.2934	60	0.647	1, 11
34 (2)	0.9574	0.1143	0.8431	60	0.422	6, 7
35.	0.3302	0.1278	0.2024	60	0.202	4
36.	0.5260	0.1278	0.3982	60	0.398	7
37.	0.4216	0.1278	0.2938	60	0.294	1
38.	0.7326	0.1878	0.5448	60	0.545	8
39.	0.9972	0.1878	0.8094	60	0.809	9
40	0.6520	0.1878	0.4642	60	0.464	10

1 - 15 : 30 cc. sample removed.
16 - 18 : 30 cc. sample removed and returned.
32 - 40 : 8 cc. sample removed and returned.

(2) : 2 animals used in the one experiment.

Results.

The graphs on Plates 28 and 29 show the relationship between the rate of removal of the suspension and time, and the tangents of these lines are the filtration rates. For the first 90 minutes this is a straight line relationship: thereafter in a number of cases the slope of the line alters. This may be attributed to the fact that the rate of filtration has changed, if the original assumptions given on page 88 are correct. On the other hand the change in the slope may be due to these assumptions being incorrect, and the filtration rate has remained constant. It would appear that the former conclusion is the more likely because in at least 50 % of the experiments the straight line relationship holds over the whole period, and in nearly all cases for the first third. Also it is not unreasonable to assume that the filtration rate may be subject to change, especially when the animals are in such an abnormal environment.

Nelson (1921) found that O. virginica continued to feed under conditions of high turbidity, when the solid matter in the water reached 0.4 grams per litre. As stated above, the maximum concentration of solid in the suspensions used in these experiments was only 0.1 grams per litre. No check was made on the possible changes in pH, oxygen concentration, or carbon dioxide tension which influence ciliary activity (Gray 1928). In the relatively small volume of water, any one or a combination of these may/

/may have caused an alteration in the filtration rate.

The rates found for V. pullastra given in Table 9, vary between a minimum of 0.145 litres to a maximum of 0.992 litres per hour, with a mean of approximately 0.5 litres at temperatures between 15 and 16° C.

In Table 10 are given the measurements of the experimental animals with the average weight of 22.1 grams the filtration rate is found to be 0.0226 litres per gram per hour. In comparison with Jorgensen's figure for M. edulis and M. californianus, this value is low, although too much emphasis cannot be placed on comparisons of this sort; first because of the difference in gill structure, and second because of the temperature differences at which the experiments were conducted. As pointed out by Galtsoff (1926, 1928) and Hopkins (1933), the rate at which gills pump water depends on the temperature which, in turn, affects other mechanisms such as the adductor muscles which control the size of the apertures and so influence the amount of water that can be moved, regardless of ciliary action.

In Table 11 are given the filtration rates obtained by a number of investigators for various species. Part of Table 11 is taken from Fox, Sverdrup and Cunningham (1937), with the addition of the results of more recent work.

Mucus Production.

The reduced filtration rate after the first 90 minutes in some of the experiments was thought possible due/

TABLE 10.

No.	Length in 0.1 mm.	Height in 0.1 mm.	Weight in 0.1 mm.	Weight in Grams.	Total Volume in cc.	Volume of Meat	Volume of Shell	Volume of Mantle Cavity	Gill Area in sq.cm.
1.	445	306	214	19.84	13.20	4.60	3.80	4.80	43.56
2.	441	307	207	19.32	12.70	3.85	3.55	5.30	30.00
3.	473	316	230	24.95	15.90	4.00	4.85	7.85	33.52
4.	422	310	210	19.07	12.00	3.70	3.75	4.55	34.60
5.	430	294	215	19.72	12.60	4.40	4.00	4.20	34.88
6.	453	307	222	22.00	14.70	4.00	4.40	6.30	44.00
7.	470	317	220	22.71	15.00	5.10	4.40	5.50	42.44
8.	433	290	220	20.30	12.80	4.25	3.90	4.65	42.00
9.	445	387	220	18.37	12.50	4.40	3.30	4.80	42.76
10.	487	328	230	25.87	17.30	5.50	4.85	6.95	51.08
0.	450	307	216	24.28	15.20	3.60	4.80	6.80	36.72

TABLE 11.

Filtration of Water by Plankton Feeders

Investigator	Animal	Method	Average rate of filtr. per hour per animal
Grave (1905)	Oyster	Plankton counts in water and stomach	0.167
Moore (1913)	Oyster	Plankton counts in water and stomach	1.25
Allen (1914)	Freshwater Mussel	Rubber tube in exhalent chamber	1.4
Wells (1916)	Oyster	Plankton counts in water and stomach	7.5
Hecht (1916)	Ascidian	Tube in atrialsiphon	7.2
Nelson (1921)	Oyster	Rubber apron over exhalent area	5.7 & 26
Galtsoff (1928)	Oyster	Rubber tube in exhalent chamber	2.5-2.9 24-26.9° C.
Dodgson (1928)	Mussel (*Mytilus*)	Clearing of suspensions	2.0 - 17° C.
Parker (1914)	Sponge	Tube in osculum	3.2
Damas (1935)	*Cardium*	Clearing mud suspensions	0.1
Fox et al (1937)	Mussel *M. californianus*	Clearing $CaCO_3$ suspension Chemical analysis	1.4-6.4 18-20° C.
Jorgensen (1943)	Mussel *M. edulis*	Clearing algal suspension Electrophotometric analysis	0.15 11-22° C.
Loosanof & Nomejko	Oyster	Rubber apron over exhalent area	25-27 19-26° C.
Coe (1947)	Clam *Tivella stultorum*	Not stated	2.5

/due to exhaustion of supplies of mucus from the gills. To test this, several experiments were arranged in which the animals had been placed in a concentrated suspension of iron oxide for periods of from two to three hours previous to the experiment. During this time they had all pumped actively, as indicated by the clearing of the suspension. Experiment No. 34 is one of these in which two animals were used in the single experiment, the controls were Nos. 32 and 33. By examination of the graph on Pl. 29, it is seen there is no significant difference in the rates between experiments 33 and 34. In experiment 32, one of the two animals was inactive.

The animal in experiment 35 had previously been in pure water. The animals in experiments 36 and 37 were together in 2.5 litres of a concentrated suspension for three hours before the experiments and had nearly cleared this. There is no appreciable difference in the filtration rates of the three animals. In experiments 28, 29, 30, 31, (Pl. 29A), where the suspension was Aquadag "S", the animals in the last two had been placed in a concentrated suspension of rouge for three hours previously. The controls (28, 29) show a slightly higher filtration rate. No settling control was used for this group, but previous tests had shown that the initial settling rate of Aquadag "S" is negligible. The sharp drop in the curves after the 90 minute period is doubtless due to the/

/the flocculation of the graphite particles. In general, it would appear from the experiments described above, and from other tests, that V. pullastra is able to secrete mucus steadily for periods up to six hours while filtering water containing large amounts of suspended material.

In Table 12 is given the rates obtained from three animals which were used in five groups of three experiments. The mean rates of 0.54, 0.59, and 0.54 litres per hour show little difference, although over the five experiments there is a considerable range of rates for any one animal.

Gill Area.

It is difficult to obtain accurate measurements of gill area owing to the extent to which the lamellae distend and contract, and from the difficulty of removing all the gill tissue from the body mass. The experimental animals were anaesthetised and the gills dissected out with all possible care. They were then placed on a slide and the outline projected and enlarged on squared paper. Attempts were made to measure the areas with a planimeter, but the method was discarded owing to wide variability in results. Counting squares gave reasonable accuracy and the average gill area of the experimental animals was approximately 40 square centimetres. With a filtration rate of 500 cc. per hour, one square centimetre of gill is capable of filtering 12.5 cc. per hour. It would be interesting to/

TABLE 12.

Rates by Individual Animals

Animal	1.	2.	3.
Rates in Litres per hour	0.93	0.99	0.93
	0.35	0.19	0.45
	0.36	0.78	0.56
	0.66	0.62	0.96
	0.21	0.38	0.15
	0.54	-	-
Average Rate	0.51	0.59	0.51

/to know whether all parts of the gills are equally concerned in filtering or whether the "ascending" lamella of the outer demibranch bears the brunt, for in observing the gills through a window, the demibranchs seem to approximate very closely to each other and to the visceral mass. Careful comparison of the histological structure of the various areas of the gills may reveal a differential development, for Ridewood (1903) has pointed out variations implication in different areas of the gills, for example, in the number of filaments in the plicae. No mention is made of function in relation to these variations.

Current Speed.

Considering the siphons as tubes, the mean velocity, Sm, of the whole sectional area of the siphon is half the velocity at the axis and the rate of discharge, V., in cc. per second is :

$$V = \frac{\pi D^2 S}{8}$$ (Gibson, 1925, page 63; after Galtsoff, 1928).

The mean diameter of the exhalent siphon of the experimental animal is 0.3 cm. and substituting in the above formula, the velocity of the stream at the axis, using the discharge rate of 1,000 cc. per hour (the maximum value), is found to be approximately 8 cm. per second. The mean inhalent aperture is 0.5 cm. when pumping, and substituting again the axis current speed is found to be approximately 3.0 cm. per second, which is only $\frac{1}{3}$ the speed of the exhalent current. This represents an adaptation for/

/for discharging the excreta and de-oxygenated water as far as possible away from the inhalent aperture. Coupled with this, is the pronounced divarication of the siphonal tips, the minimum angle between them when active is 90° . The inhalent siphon is usually directed vertically, while the exhalent is directed backwards in the direction of the animal itself and approximately parallel to the surface of the substratum. This bifurcation must be a great aid in separating the inhalent and the exhalent currents.

Discussion.

The results of this section of the work are in some ways preliminary, for while clear information about the rates of filtration of adult animals has been obtained, this applies only within a limited range of temperatures and of size. Further experiments enlarging these ranges would be of value and would contribute much to an assessment of the reliability of the results. An examination of Table 11 shows the wide range in filtration rates that have been obtained by various investigators. The range is so great that one is at a loss to decide even within broad limits what values may consitute reasonable estimates. Comparisons are made difficult because of differences in sizes of the animals used, as well as in the variety of species, and in the wide range of temperature. Galtsoff (1928) used two methods for comparison, but the basis principle underlying both methods is open to criticism.

The results of Fox, Sverdrup and Cunningham (1937) appear to be sound on a comparative basis. The main criticism of their method is the high concentration of the suspension, about 3 grams of calcium carbonate per litre, which is much above normal. Nelson states that very turbid water, natural in Barnegat Bay, contains only 0.4 grams of dry material. Estimates of normal water at La Jolla, California, place the dry material at 0.05 grams per litre.

Jorgensen's use of the electrophotometer is an advance, but the use of algae has its disadvantages. The cultures must be fresh and since large quantities are necessary, a proper supply would be difficult to maintain. It is also possible that numbers, and therefore the colour, may vary during the course of an experiment.

The work of Loosanoff and Nomejko (1946) appears to be sound, but mean values of 25 to 27 litres per hour seem extremely high. Coe (1947), on what evidence he does not state, estimated that a Pismo clam (Tivella stultorum), 70 mm. long, filtered 2.5 litres per hour at La Jolla. At this rate it is capable of obtaining about about 0.3 grams of suspended material per day, though only a small part of this may be swallowed and digested. On the other hand Coe believes that the daily requirements of the clam are very small except during gametogenesis, because the dry organic matter in a clam 70 mm. long, and about three years old, is only 1.5 to 2.9 grams. On this basis, a specimen of Ostrea virginica, four inches high, is/

/is claimed to filter at least 25 litres per hour (Loosanoff and Nomejko, 1946) and should be able to obtain 3 grams of potential nutriment daily, which is roughly equivalent to its own dry body weight. If previous estimates of the filtering efficiency in marine invertebrates have been too low, this would explain the disparity between the nutritional needs indicated by oxygen consumption and the supply of food based on estimates of filtration.

Comparative filtration rates per unit of weight of other species, such as Mytilus californianus, indicate that the rate found for V. pullastra is somewhat low. The rate is comparable to that given by Coe (1947) for the related Pismo clam. Also the temperatures of the experiments here described were rather lower than most of those quoted. What is needed is a comparative study of a number of species and it is believed that the method developed here provides a relatively rapid and accurate means of determining filtration rates. But owing to the limitations of this type of experiment, the results will not be more than good estimates of the true values.

The pressures set up in V. pullastra by the water currents are difficult to assess because of the complex route taken from the inhalent siphon into the pallial cavity, through the gills into the suprabranchial cavity and out through the exhalent siphon. However, because of the low filtration rate, it may be assumed that/

/that the pressures are low and it is doubtful if they play any part in the spawning act.

The speed of 8 cm. per second agrees quite well with direct observations on the speed of particles such as clumps of eggs leaving the exhalent siphon. The gametes are carried as much as 15 cm. from the siphon in undisturbed water, although this distance varies a good deal and spawning animals have been observed in which the ova merely trickled out of the siphon, and sank immediately to the bottom. This is another possible indication that the rate of water propulsion is not constant even under identical physical and chemical conditions.

Shell Movements.

A considerable amount of data on the shell movements and their significance in the physiological activities of various species of oysters now exist. See Galtsoff (1928), Nelson (1921, 1924, 1938), and Loosanoff and Nomejko (1946) on Ostrea virginica; Hopkins (1931) on O. lurida; and Webb (1930) on O. edulis. On other lamellibranchs the research of Loosanoff (1939, 1942) on Mytilus edulis and on Venus mercenaria are the only papers known.

The primary purpose of this brief examination of the shell movements of V. pullastra was to determine these for comparison with movements occurring during spawning. However, when the spawning season arrived, it was soon observed that shell movements played no significant part in the spawning act of either sex, as is the case with the female of several species of oysters. Nevertheless, one or two points of interest have arisen from an-alysis of the kymograph recordings of the shell movements.

To make the conditions as natural as possible the recording apparatus was set up so that the animal was buried in the sand in a natural position. The apparatus is shown in Pl.31. A block of sealing wax 'B' is attached by two metal pins to a lead weight 'A'. The clam 'C' is attached to the sealing wax by one of the valves and a perforated perspex pin is connected to/

/to the posterior end of the other valve. This part of the apparatus is buried in the sand of the aquarium, with the posterior end of the clam just below the surface of the sand. A solid perspex lever with no whip in it is swung from a hinge at point 'F'. The hinge arrangement is attached to a heavy adjustable weight 'G'. A length of stiff brass wire 'D' connects the bottom of the vertical lever at 'I' to the clam through the perforation in the perspex pin. The recording pen 'JK' is connected solidly with the vertical lever 'I J', and the whole hinged at point 'J'. 'I H' is a light connecting rod joined to 'IJ' and 'EH' by hinge connections. When the clam opens its valves, it will be seen by following the lever system, that the recording pen rises. The temperature in the aquarium was thermostatically controlled. A series of experiments at low temperatures would have been desirable to round out the investigation, but no equipment was available to maintain them for an extended period.

A criticism that may be levelled at this experimental procedure is the fact that the animal is in an aquarium and subject to the composition and variations of stored sea water. On the other hand the animal was in a perfectly normal position. Loosanoff (1942) was able to keep his specimens of Venus mercenaria in large tanks which were connected with outside sea water and in which the natural tidal fluctuations occurred. However, his clams were cemented to a block by one valve and were/

/were consequently lying on their sides; an unnatural position. It is difficult to estimate how much a lateral position may interfere with the disposition of material accumulated in the mantle chamber. A combination of Loosanoff's method and the one used for V. pullastra would have been ideal.

Results.

Approximately 300 hours of recordings were made over the temperature range whose lower limit was governed by the temperature of the laboratory circulation system and the upper limit at what was considered the maximum the animals may be subject to in nature. Photographs of some of the recordings are given in Plates 32, 33 and 34. In Table 13 is given the analysis of each recording and below is given a summary of that analysis.

Summary of Results from the Analysis of Recordings.

1. The shells of V. pullastra remain open nearly 100 % of the time at temperature between 15.0 and 22.0° C.

2. Shell movements are frequent; and they have a mean amplitude equal to half the maximum distance to which the valves are opened.

3. The closing movement is rapid and the following opening movement is almost instantaneous, although in the final phases of opening the movement slows down.

Summary of Analysis of Kymograph Recordings of Shell Movements

Date	No. of animal	No. of experiment	Temp. Range degrees C.	Duration (Hrs)	%. of time open	Av. degree of shell expansion %	Rhythm	Day and night effect	Temp. effect
30.6.46	A	1	15.0	19	100		yes	nil	nil
30.6.46	B	2	15.0	19	100		nil	nil	nil
2.7.46	C	3	16.2	8	100	80	yes	nil	nil
2.7.46	D	4	16.5	5	100	60	yes	nil	nil
2.7.46	E	5	16.5	5	100	80	yes	nil	nil
4.7.46	F	10A	21.0 - 22.5	4	100	90	yes	nil	nil
4.7.46	G	10B	19.0 - 21.0	4	100	95	yes	nil	nil
4/5.7.46	F	11A	19.0 - 20.8	9	100	95	nil	nil	nil
4/5.7.46	G	11B	19.0 - 22.0	9	100	75	yes	nil	nil
5.7.46	F	12A	18.7 - 20.5	8	100	80	nil	nil	nil
5.7.46	G	12B	22.8 - 20.6	8	100	90	yes	nil	nil
5.7.46	F	13A	18.0 - 16.6	3½	100	75	nil	nil	nil
5.7.46	G	13B	20.4 - 18.5	3½	100	90	yes	nil	nil
5/6.7.46	F	14A	16.5 - 15.1	8	100	50	yes	nil	nil
5/6.7.46	G	14B	18.3 - 16.0	8	100	75	yes	nil	nil
6.7.46	F	15A	15.3 - 16.0	8					
6.7.46	G	15B	16.0 - 16.5	8	100	80	yes	nil	nil
8.7.46	H	16A	17.0 - 17.4	7½	100	60	nil	nil	nil
8.7.46	J	16B	17.4 - 18.0	7½	80	45	yes	nil	nil
8.7.46	H	17A	19.0 - 21.4	7	100		nil	nil	nil
8.7.46	J	17B	18.7 - 21.2	7	100		nil	nil	nil

TABLE 13.

Summary of Analysis of Kymograph Recordings of Shell Movements

Date	No. of animal	No. of experiment	Temp. Range degrees C.	Duration (Hrs)	%. of time open	Av. degree of shell expansion %.	Rhythm	Day and night effect	Temp. effect
8/9.7.46	H	18A	29.0 - 23.0	8	nil	nil	nil	nil	nil
8/9.7.46	J	18B	28.0 - 24.8	8	nil	nil	nil	nil	nil
10.7.46	K	19A	21.3 - 20.3	13	100	85	yes	nil	nil
10.7.46	L	19B	19.5 - 21.5	13	100		?	nil	nil
11.7.46	M	20A	18.5	7½	100		yes	nil	nil
11.7.46	N	20B	18.5	7½	100		nil	nil	nil
11/12.7.46	M	21A	18.0	8	100	90	yes	nil	nil
11/12/7.46	N	21B	18.0	8	100	60	yes	nil	nil
12.7.46	M	22A	18.5 - 13.5	7½	100	85	yes	nil	nil
12.7.46	N	22B	18.5 - 19.5	7½	100	90	yes	nil	nil
12/13.7.46	M	23A	19.3	8	90	90	yes	nil	nil
12/13.7.46	N	23B	19.3	8	100	90	yes	nil	nil

4. The degree of separation of the valves over the period is nearly maximal.

5. There appears to be no correlation between type and amount of shell activity and temperature over the range investigated.

6. Changes in temperature, positive or negative, over the range investigated, had no apparent effect on shell movements.

7. Presence or absence of light have no effect on the period or degree of separation of the valves or on general activity.

8. Shell movements may be classified as being associated with digging, cleansing or random activities, but none of these is associated with any characteristic kymograph tracing.

9. Some animals show a definite rhythm in their shell movements at one time and not at others. Individual animals may have a rhythm peculiar to themselves.

10. There may be considerable siphonal activity; opening, closing, extension or retraction, without any correlated shell movements.

Discussion.

In Pl.32, fig.1, is shown a tracing of the shell movements of *V. pullastra* at a temperature range of 16 to 18° C. On the bottom of the tracing may be seen the base line which marks the position of the recording pen when/

/when the valves are closed. Over the period of 4 hours and 50 minutes covered by the photograph, the shell is never more than half closed. Opening movements are very rapid. Approximately every half hour there is a period of no shell activity (indicated by the horizontal unbroken line) with intervening half-hourly periods of activity. A certain rhythm of shell movements is evident although it is difficult to determine the borderline between rhythmic and non-rhythmic movements. While the closure baseline is not shown in every case, most of the tracings indicate that the valves are open practically all the time. An exception to this may be seen in Pl.32, fig.3, where, for a period, the tracing touches the closure baseline. Loosanoff (1939) found that Venus mercenaria remained open 69 to 90 % of the time over a twenty four-hour period at a temperature range of 11 to 27.9° C, while between 21 and 22° C they remained open 90 % of the time. Nelson (1921) found Ostrea virginica to be active 20 hours out of 24, while Galtsoff (1928) found the same species was active for only slightly over 17 hours out of the 24. Hopkins (1931) found a diurnal variation in the amount of time O. lurida remained open, but that this could be directly correlated with the fluctuation in temperature, even though the mean variation was only 2.1° C. He found the animals opened for 50 % of/

/of the time at the lower end of this temperature range, and for 95 % at the upper end. Loosanoff and Nomejko (1946), working with O. virginica found that it remained open for 94.3 % of a 24 hour period within a temperature range of 17 to 28° C. Thus it appears that over a temperature range of 15.0 to 22.5° C., V. pullastra remains open longer than either Ostrea virginica or Venus mercenaria; also comparison of the tracings for this species with those published by the authors cited above indicates that V. pullastra is considerably more active on the basis of frequency of shell movements.

There appeared to be no correlation between temperature and the amount or type of shell activity in V. pullastra, nor did changes in temperature have any effect. Hopkins (1931) believed that it is the rate of change of temperature rather than the amount of change that is significant in causing variation in the amount of shell opening in Ostrea lurida. Galtsoff (1928) believed that O. virginica tended to keep its shells open as long as possible and could find no correlation between temperature and opening and closing within the temperature range of 13 to 22° C.

Nelson (1921) concluded that O. virginica tended to be less active during the night than during the day, and that this species feeds less actively during the ebb tide. Both Loosanoff and Nomejko (1946) and Galtsoff (1928) for O. virginica appear to have disproved both of/

/of these contentions and, in addition, Webb (1930) found that there was no difference in the activity of the adductor muscle of Q. edulis between day and night. Loosanoff (1939) found that Venus mercenaria was closed for somewhat longer periods in daytime than at night. No such effect was found for V. pullastra which showed a tendency to stay open as much as possible, regardless of the time of day or night or of temperature. Galtsoff (1928) pointed out that partial closures of the shells of Q. virginica may occur without rejection; also periodic contractions of the adductor muscle. This also occurs in V. pullastra. The periodic nature of some of the contractions has been indicated on the photographs of the tracings. Repeated observations showed that only at infrequent intervals did shell closures or partial shell closure coincide with rejection.

Hopkins (1936) was able to analyse into three groups the movements shown on kymograph recordings of the shell activity of Q. gigas; those involving discharge from the branchial chamber, others concerned entirely with the cloacal chamber, usually resulting in the discharge of faeces, and a third type which he terms non-specific, which may be due to a variety of causes. In V. pullastra the adductor activities have been classified as being associated with digging movements, cleansing, or random movements. A comparison between Pl.34, fig.3 showing a/

/a tracing of digging movements (this should be viewed upside down for comparison) and of any shell closure tracing, shows little fundamental difference. It has been pointed out that the tracings resulting from the rejection of solid material are identical with those in which no discharge occurs. No doubt many of the partial closures are the results of attempts to carry out digging movements. Hopkins (1936) in analysing the random contractions in *O. nigra* finds no correlation between their frequency and temperature over a range of between 2 to 30° C. and believes they may be traceable to some external stimulation such as light, vibration, suspended material in the water, or to an accumulation of secreted mucus. It would appear that this explanation is hardly satisfactory, especially for *Y. pullastra*, when so many of these movements are periodic.

Spawning.

The object of this section of the work was to determine whether there exists in V. pullastra a stimulus which initiates spawning, as there is in other marine invertebrates.

Galtsoff (1938a, 1938b, 1940) in extensive work on the physiology of spawning of Ostrea virginica and on O. gigas found that there may be several "critical" temperatures for spawning, different for male and female. These temperatures are partly determined by the physiological conditions of the animal. Galtsoff also showed the importance of chemical stimulation in the initiation of the spawning act and that this lowered the "critical" temperature. Greve (1927) made the statement, "Spawning is caused at particular times in nature by various specific stimuli and is not determined by temperature alone." He believed that shock or the mere removal of Cumingia tellinoides into the laboratory was sufficient to stimulate spawning and that spermatozoa did not stimulate the female to spawn. Morgan (1910) believed that the presence of sperm in the water incites female C. tellinoides to spawn more readily. Chemical stimulation has been described for several species of chitons (Heath 1905), for Nereis limbata (Lillie and Just 1913) and for Strongylocentrotus lividus (Fox 1924). Elsey (1936) was able to bring about artificial stimulation of spawning of Ostrea gigas on a larger scale in Ladysmith Harbour.

Methods.

During part of the time no thermostat control was vailable so the temperature was regulated manually. These experiments were carried out in breffit jars and the temperatures were adjusted by the addition of water. When a thermostat became available battery jars were used. The lowest temperature that could be controlled was governed by the temperature of the stored sea water used in the circulation system of the Marine Station; therefore most of the experiments were carried out at temperatures considerably higher than the animals would experience in nature. However, the temperatures appeared to have no harmful effects.

The aquarium water used in the experiments varied between 12.0 and 16.0° C. and was filtered to avoid contamination by sexual products which may have been present in the normal supply. Egg and sperm suspensions of approximate concentration 1.0%, from the gonads of V. pullastra, were used.

Animals were prepared for connection to the kymograph by securing one valve to a glass slide with a mixture of bitumen and pitch. With the same material a wire hook was attached to the other valve. The glass slide was held to the bottom of the tank by a weight, and the hook was attached to a vetical lever, which in turn moved the hinged writing pen. Opening of the valves, caused a downward tracing.

The animals were stimulated in the following ways :

1. A gradual rise in temperature with and without chemical stimulation (egg and sperm suspensions).

2. An initially high temperature with and without chemical stimulation.

3. Normal water temperatures with and without chemical stimulation, the latter serving as a control in every experiment.

Spawning of the Male.

In spawning a fine stream of sperm, not more than 1.0 mm. in diameter issues from the centre of the exhalent siphon. The stream maintains its identity for a distance of about 3 or 4 cm. and then begins to spread. The sperm may reach a maximum vertical distance of 15.0 cm. from the siphon. Spawning is not necessarily continuous, the longest time a male was observed to spawn was three hours. A small number of observations indicated a refractory period of between two and three days. Galtsoff (1940) found no refractory period in male Ostrea virginica, which could be stimulated repeatedly until the animal became spent or fatigued. The adductor muscles play no part in the spawning act of the male Y. pallastra, but during the period of spawning the adductor muscles appear to be less active than normal.

Spawning of the Female.

The spawning of the female is not unlike that of the male and a steady stream of eggs issues from the centre of the exhalent siphon. The stream does not extend as far as that of the male due to the difference in density between sperm and eggs. One female was observed to spawn the eggs in clumps of approximately 1,000 each. These trickled out of the siphon and sank immediately to the bottom. Sampling and counting disclosed that this female spawned a million eggs in 30 minutes. Smear examination of the gonad immediately after showed no evidence that the animal had spawned and this indicates the care that must be taken in using the condition of the gonad, other than by examination of prepared slides, as evidence of the breeding condition. As with the male there appears to be a refractory period of two to three days after spawning, during which the female cannot be stimulated. Galtsoff (1940) found the refractory period of the female Ostrea virginica to last from two to five days.

Summary of Experiments with Positive Results.

In the summer of both 1946 and 1947 a series of experiments were carried out using temperature and egg and sperm suspensions, individually and combined. In not more than 20 % of the experiments were positive results obtained. Attempts have been made to summarise/

/summarise these in table form, but no satisfactory method could be devised, so some of the pertinent data is listed below.

May 18th: At a temperature of 18.5° C., 50 minutes after the addition of a sperm suspension, a male spawned. The temperature had been raised from 13.3° C. during the period of 1 hour.

June 19th: At a temperature of 20.5° C., 270 minutes after the addition of an egg suspension, a male spawned for 40 minutes. The temperature had been raised from 15.1° C. during the period of 7 hours.

June 19th: At a temperature of 18.0° C., a male and a female spawned with no stimulation other than a rise in temperature from 15.0° C. during the period of 1 hour.

June 19th: At a temperature of 20.0° C., a female spawned 85 minutes after the addition of a sperm suspension. The temperature had been maintained at 20.0° C. during the period.

June 19th: At a temperature of 20.0° C., a male spawned 115 minutes after the addition of a sperm suspension and 30 minutes after a female had spawned in the same vessel. The temperature had been maintained at 20.0° C. during the period.

June 19th: At a temperature of 20.0° C., a female spawned 4 hours after the addition of a sperm suspension and 150 minutes after a male had spawned in/

/in the same container. The temperature had been maintained at 20.0° C. during the period.

June 19th: A male and a female spawned 6 hours after being placed in water maintained at a temperature of 20.0° C.

June 20th: Two females and a male spawned 40 minutes after the addition of a sperm suspension. Within a few minutes of these, approximately 15 animals of both sexes began to spawn. The temperature was maintained at 20.0° C. from the beginning.

June 22nd: At a temperature of 23.0° C., a male spawned 20 minutes after a mixed suspension of egg and sperm had been added. 10 minutes later 2 males and 2 females spawned. The temperature had been maintained at 23.0° C. from the beginning.

June 23rd: 5 males spawned 4 hours after the addition of a sperm suspension. The temperature over the period was 20.0° C.

June 25th: At a temperature of 20.0° C., a male spawned 47 minutes after the addition of an egg suspension. The temperature had been maintained at 20.0° C. during the period.

July 1st: At a temperature of 22.0° C., 2 males spawned after periods of 16 and 35 minutes respectively. The first spawned for 41 minutes and the second for 90 minutes.

July 1st: At a temperature of 22.5° C., two previously spawned females spawned 40 minutes after the addition of a sperm suspension.

July 1st: A male spawned 90 minutes after the addition of an egg suspension. The temperature had been maintained at 22.0° C. for 5 hours.

July 2nd: At least half the animals in a group of 100 kept in an aquarium at a temperature of 16.0° C. spawned together, without any applied stimulation. The smallest female found spawning was in its fourth summer with a length of 2.3 cm. The smallest male found spawning was in its third summer with a length of 1.9 cm.

On July 7th, a female was induced to spawn and attached to the kymograph. While this was being done the animal was out of water for about 15 minutes, yet it continued to spawn as soon as it was replaced. The kymograph tracing of the valve movements of this spawning female is shown in Pl.35, fig.3. At first there was considerable pedal activity which appeared to be quite independent of either the spawning act or of valve movements. At 14.44 hours the shells were caused to close by stimulating the siphons in order to test the working of the kymograph pen.

On July 9th, a female was found spawning in the aquarium at a temperature of 16.0° C., and it was/

/was immediately connected to the kymograph. The recording is shown in Pl.35, fig.5. At 18.52 hours the animal was spawning vigorously.

On July 11th, after a latent period of 3 hours, at 20.0° C., a male began to spawn. After a further period of 15 minutes a female began spawning and this animal was connected to the kymograph, the recording of which is shown in Pl.35, fig.1. AT 19.32 hours, point x, spawning was under way. At 21.10 the temperature was 21.0° C. and spawning was completed at 21.30 hours.

On July 12th, the activities of another spawning female were recorded and this is shown in Pl. 35, fig.4. The main spawning period occurred between 21.10 and 22.25 hours, and this animal showed more activity than the average during the spawning act.

From these few recordings, however, in addition to numerous direct observations of spawning females, activity of the adductor muscle has been shown to play no significant part in the spawning act.

Discussion.

No definite quantitative conclusions may be drawn from the above experimental data. However, it does appear that *Y. pullastra* is susceptible to both chemical and thermal stimulation, although the latent period is often long. The mass spawnings in the aquarium also indicates the presence of a common spawning/

/spawning stimulus, and points to the sex products as being the most likely cause. It has been suggested by Thorson (1946, page 424), based on the fact that there appears to be a correlation between the breeding season of various invertebrates and the amount of phytoplankton present, that this may be the spawning stimulus. He supports this conjecture by citing the works of Miyazaki (1938) on the use of algal extracts, such as from Ulva, for stimulating spawning in the males of Ostrea gigas. Orton (1936, 1937) points out that gravid individuals are sensitive to variations in oxygen tension and that this may be a spawning stimulus. Galtsoff's (1938, 1939, 1940) work, stimulation by means of sex products and other chemicals combined with temperature, has already been quoted. That some means is required to induce simultaneous spawning in lamellibranchs such as Y. pullastra is unquestioned, and it remains to find the exact nature of the stimulus. The above simple experiments have indicated that chemical stimuli, especially in combination with temperature, are effective within limits.

Compared with the ease and certainty with which Galtsoff (1940) and others were able to stimulate spawning in Ostrea virginica, as well as the author's own experience with O. gigas, Y. pullastra is not very susceptible. Whether this is a reflection of the reaction of this species to life in aquaria, or whether it indicates more exacting requirements for stimulation, is not known.

Seasonal Gonad Changes.

In connection with the determination of the breeding season and its relation to temperature and other physical factors, it is of interest to follow the development of the gametes which involves the study of the seasonal changes in the gonad. For oysters such as O. gigas, after spawning, a period of fattening ensues when the glycogen content of the body mass greatly increases. This "fat" condition exists throughout the winter until the late spring, when the increase, presumably of temperature, causes proliferation of the dormant gonad tissues and gradual replacement of the "fat" by the sex cells, until the largest part of its mass is occupied by the gonad. If, for some reason, spawning does not take place or is incomplete, the residual sex cells are usually resorbed and converted into glycogen.

This cycle is not followed by other species so far studied; such as Teredo navalis (Coe 1936), Venus mercenaria (Loosanoff 1937), Mya arenaria (Coe and Turner 1938) and Paphia staminea (Quayle 1943). A comparison of the sexual conditions in V. pullastra with those of other animals which have been studied may be of interest.

Methods.

Samples of 50 adults from the same area were taken each month throughout the year. The series was started in May 1946 and carried on until October 1947/

/October 1947, during which a total of 923 animals were examined. In this way, a complete annual cycle, with an additional breeding period, was followed. A sample of 50 animals monthly is not many for a study of this nature, and represents the minimum that should be used, but larger samples could not have been dealt with because of the time required in the preparation of slides.

A sample of gonad tissue approximately 0.5 cm. square, was removed from the mid-region of one of the sides of the visceral mass and fixed in Bouin for 24 hours. The ester wax embedding technique (Steedman 1945, 1947) was used exclusively and found to be most satisfactory. All sections were at first ribbon stained with methylene blue and mounted immediately without counter-staining. The only operations after the sections had dried on the slide, was the removal of wax and mounting in balsam. This gave all the details necessary for an accurate determination of the state of maturity of the gonad. As the slides were being assessed, those required for detailed study, drawing or photography, were noted. The ester blocks having been numbered, further sections were cut and stained with other methods such as Heidenhain. This latter stain alone gives a clear picture of the gonad tissue and even the thin walls of the follicle cells show up clearly.

In a description of the seasonal changes in the gonad, the immediate post-spawning period is the most/

/most suitable starting point because then the female begins to develop. Since most of the spawning is completed by the end of September, that month may be chosen as a suitable starting point.

Female.

In normal years most of the animals are completely spawned out by the middle of September, though isolated individuals may show evidence of having only partly spawned as indicated by the relatively large number of residual mature ovocytes, whereas those animals which may be described as "spent" contain only a few ovocytes in the otherwise empty and collapsed follicles, (Pl.37, fig.1). By this time, however, animals which have spawned earlier in the summer have their alveoli filled or partly filled with follicle cells (Pl.37, fig. 1) which are relatively large cells, most often with a thin layer of peripheral cytoplasm enclosing a vacuole. From the description of Coe and Turner (1938), the follicle cells of Mya arenaria and Y. pullastra are very similar, except that the inclusions found by Coe and Turner in M. arenaria have not been observed in Y. pullastra. They ascribe a nutritive function in the follicle cells and this explanation appears to be likely in the case of Y. pullastra, for in both sexes the first development after spawning is the formation of the follicle cells, and their later disappearance coincides with the development and ripening of the gametes. Thus the period of follicle cell formation may be described as/

/as a recuperative period. During this period there appears to be some development of ovogenia and by the middle of October many of them have become ovocytes with a diameter of 35 u. (Pl.37, fig.4). By the middle of November, nearly all the alveoli are filled with follicle cells and the ovocytes vary between 20 and 40 u. in diameter. Residual ova are still present and do not appear to be undergoing cytolysis (Pl.37, fig.3). Development continues slowly during the winter, as shown by the increased size of the ovocytes which average between 40 and 45 u. by the middle of February (Pl.36, fig.2). Development now seems to be accelerated for, by the middle of April most of the animals sampled are ripe or nearly so, although a few are still developing. By June practically all are fully ripe with the tubules extended with ovocytes approximately 55 u. in diameter. The follicle cells have disappeared, initially in the centre of the lumens, as the ovocytes increased in size and number, until in the ripe animal there are only single peripheral layers, or in some cases only single isolated follicle cells. The ovocytes, at first flat against the germinal epithelium of the tubules, assume a pear-shaped form with the thin stalk attachment on the follicle wall as they grow and develop. On becoming ripe they are detached and occupy the centre of the lumen (Pl.36, figs. 3, 4.). Externally, the ripe animals appear plump and creamy white in colour. A fully ripe animal is easy to/

/to identify, but the intermediate stages are more difficult, even with smear examination, the sections are necessary for an accurate determination of the condition of the gonad.

The June 1946 sample contained a number of animals which were spawned or partly spawned, but no spent animals were found in the June 1947 sample, corroborating the evidence from the plankton hauls that initial spawning in the latter year was about one month later than in 1946. In this connection, it must be remembered that populations from different areas may spawn at different times and it is this point which, no doubt, partly accounts for the long breeding season. The July samples showed that the bulk of the population from the Cross Houses Beach had spawned and were in the recuperative stage. Varying amounts of residual ovocytes were found in most animals, the amounts varying even between different follicles in the same animal.

Briefly then, the cycle for the female is one of recuperation followed by proliferation of follicle cell tissued immediately after spawning. Almost simultaneous with the proliferation of the follicle cells is the development of the ovogonia into ovocytes and their slow growth during the winter months. The higher spring temperatures seem to bring on, or are at least coincident with, an acceleration in the development of the gonad, culminating in maturity in May or June. The spawning process has been described elsewhere, but it may be noted/

/noted here that in common with the finding of Belding (1916) and Coe and Turner (1938) for Mya arenaria, the ova of V. pullastra cannot be artificially inseminated unless spawned naturally through the oviducts. The fate of the unspawned or residual ovocytes of V. pullastra is uncertain. No evidence of cytolysis has been observed which, according to Coe and Turner (1938), is what happens in Mya arenaria. Loosanoff (1937) is inclined to think that the residual ova in Venus mercenaria are also spawned out by the end of November, such spawning being carried on at intervals after the main summer spawning has been finished. Orton (1933) found a similar process in Ostrea edulis. Since in V. pullastra no evidence of cytolysis or resorbtion has been observed, and from the fact that morphologically mature ova may be found in some gonads throughout the winter up to the time when the new crop becomes mature, it may well be that these relict ova are spawned along with the new ones; though whether or not they may be fertilised is problematical. Another argument, too, is that these mature appearing ova usually form only a small percentage of the ovocytes present until March or April. However, with the present evidence, the fate of the unspawned ova remains in doubt.

Males.

The male cycle is not unlike that of the female. The bulk of the males are also spawned or partly spawned/

/spawned out by the middle of September and some are in the recuperative stage in which the follicle cells proliferate rapidly. In only a small percentage of the males is spawning complete with the lumina left devoid of sperms (Pl.39, figs. 3 and 4). There is much variation, but on the average, about 10 to 20 % of the sperms are retained (Pl.39, fig.2). When the pressure exerted by a full complement of sperms is reduced by spawning, the remaining cells in the follicles are arranged in columnar and circular patterns, as shown in Pl.38, fig.2.

Development of the male sex cells after spawning is apparently rapid and by November most of the sections show the testis to contain a considerable number of sperms, arranged in the characteristic columnar manner (Pl.38, fig.1). By this time, the follicle cells have disappeared from the centre of the lumina which are now filled with sperms (Pl.38, fig.3). A few spermatogonia and spermatocytes are present in the peripheral region of the follicles, but the bulk of the cells are spermatozoa. There is little change until April, when proliferation begins again, and by the middle of May, the lumina are full of cells, the central ones being sperms, and from there to the germinal epithelium there exists a progression of spermatids, spermatocytes and spermatogonia of both orders (Pl.38, fig.3). There is now no definite pattern except in the arrangement noted above. During June males are still/

/still ripening, although some may have spawned in late May. As with the ova, the fate of the retained sperms is doubtful, but the occurrence of many of these at all times of the year, in addition to the fact that only a small percentage of the males spawn out completely, suggests that they, too, are discharged normally during the next spawning season. Follicle cells are not as apparent in the males as they are in the females. This may be because they are not as easily observed owing to the presence of residual sperms in such a high proportion of spawned animals. However, in the animals which are completely spawned out leaving the centres of the lumina empty, the alveoli become filled with follicle cells as in the ovary (Pl.39, fig.1). Spermatogenesis appears to be normal, the details of which need not be repeated.

The male breeding season then, consists of a period of recuperation during which there is proliferation of follicle cells. In conjunction with this, there is a certain amount of spermatogenesis between September and November, when lower temperatures apparently curbs activity. The animals go through the winter with the testis containing roughly a quarter of the possible sperm content. Spermatogenesis is renewed with the advent of higher temperatures in April, and by the middle of June most gonads are extended with ripe gametes.

Sex Ratio.

Of the 923 animals sectioned, 432 were females/

/females and 487 were males; the sex of the remaining four was not determined. Thus the sex ratio is approximately equal. Only one hermaphrodite was found (Pl.36, fig.1), comprising 0.1% of the population sampled, indicating that the species is normally unisexual.

Approximately 1% of the population was parasitised by a trematode of an unidentified species.

Discussion.

A study of the seasonal gonad changes in Y. pullastra shows that after spawning there is a period of recuperation followed by a short period of gametogenesis. Development during most of the winter is at a standstill or proceeds very slowly. The advent of higher temperature in early spring initiates, or accelerates, production of gametes, and most animals are fully ripe by May or June. Spawning occurs between the middle of May and the middle of September. Spawning may not be completed at one operation, but it appears doubtful if a second crop of gametes are formed and released during the one spawning season. Completely spent animals, especially males, are seldom found, as residual ova and sperms in varying quantities are usually present. This cycle is similar to that found by Loosanoff (1937) for Venus mercenaria of the Atlantic coast of America, although the gonad type of Y. pullastra resembles that of Mya arenaria (Coe and Turner, 1938) more than it does Y. mercenaria. The structure of the gonad and the seasonal gonad changes,/

/changes, closely resemble that of the Pacific Coast Parhia staminea (Quayle, 1943).

In common with V. mercenaria, part of the gonad development takes place, as pointed out by Loosanoff (1937) during periods of rather low temperatures. In other species, notably the oysters, the time of gamete production is confined to periods of higher water temperatures, as in late spring and summer. No gamete formation takes place in Ostrea gigas until the following spring. Amemiya (1929) and Coe (1932) found that in O. lurida also, the main period of gametogenesis after the last summer spawning, is in the following spring when water temperatures begin to rise, and the same is true for O. commercialis (Roughley, 1933). However, in V. pullastra, too, the increase of temperature in spring brings on the final ripening of the gametes. Unfortunately, the sampling did not go back into the early spring of 1946, so the condition of the gonads then cannot be compared with their condition at the same time in the spring of 1947, when the water temperatures lagged a full month behind. However, the effect was operative in that spawning in 1947 occurred a month later than it did in 1946, and no doubt, part of this may be attributed to retarded gonad development as well as to the late incidence of the so-called "critical" spawning temperature.

On the question of the fate of residual gametes, Loosanoff (1937) agrees with Orton (1933), that they are/

/are finally discharged before the winter. It is certain that this is not the case with *V. pallastra* and it is tentatively suggested that they may be retained and spawned in the next season. Kisey (1953) states that the sexual products of *O. kisutch* may be carried into or throughout the winter and mature eggs have been found in April. Normally the unspawned sexual products are resorbed during the fall and early winter.

Growth.

A large part of the information on growth in lamellibranchs other than oysters, is based on observations of North American species such as, Tivella stultorum (Weymouth 1923); Siliqua patula (McMillin 1923; Weymouth, McMillin and Holmes 1925); Venus mercenaria (Kellog 1905); Dosinia discus (Crozier 1914); Mytilus edulis (Moosop 1921, 1922) and Mya arenaria (Newcombe 1935a,b,c; 1936a,b). For British species there are the observations of Orton (1926) on Cardium edule; Stephen (1928, 1929, 1931, 1932) on Tellina tenuis and several other species; Ford (1925) on a number of sublittoral species; and Davis (1923) on Spisula subtruncata and Mactra stultorum from the Dogger Bank. There is need for further growth studies on lamellibranchs, especially of a comparative nature.

Growth in lamellibranchs may be studied by any one of, or a combination of, three main methods. 1. Measurements of individuals from random samples of a population. 2. Successive measurements of marked individuals. 3. Measurement of annual growth rings, if their validity as indications of seasonal growth has been established.

Adequate data can be obtained from random samples only when the breeding season is short, so that each new brood enters the population as a well defined group with a limited size range. If the species has this characteristic, each year class will appear as an isolated or nearly isolated mode in a size frequency/

/frequency distribution. This is well illustrated by Winckworth (1934) who was able to separate two well defined groups in Raphia undulata, and determine their age and rate of growth. If, however, the breeding season is extended, there will be a large range in size, and the large animals of one year class may be confused with the smaller animals of the succeeding year class. This, combined with individual differences in rate of growth and differential mortalities, limits the usefulness of this method.

The successive measurements of marked individuals is the most direct method of measuring growth, and marking lamellibranchs is not difficult. One disadvantage is that each time the animals are removed from their habitat, growth stops and a disturbance ring is formed. Orton (1926) discusses the formation of disturbance rings in Cardium edule, as does Weymouth (1923) for Tivella stultorum, and as there is no essential difference in V. pullastra further discussion is unnecessary. The amount of growth lost by disturbances may be calculated and adjustments made, but frequent disturbances may have a significant effect.

The measurement of annual growth rings provides an accurate method of estimating rates of growth. In this case the animal is unmolested, other than by natural disturbances. The method hinges on whether the rings which appear as surface sculpture on the shells of most/

/most lamellibranchs are annual or seasonal in nature. Weymouth (1923) has reviewed the literature on annual rings of molluscs and he sums up in these words: "Of fourteen papers by thirteen different authors, one flatly denies that age can be told from the shell, two are unwilling to commit themselves, five feel that there is some sort of connection between age and the lines, but that they are of no practical use even if their annual occurrence could be established, and six go on record as believing that the rings are annual, though only one of these actually makes use of the method in constructing a growth curve. In only two can the case be considered as firmly established on adequate data." Weymouth himself goes on to establish beyond doubt that the rings in Tivella stultorum are annual and can be used as a means of measuring age and rate of growth. He considers in detail how the shell is laid down and how the rings are formed. Since then a number of authors have proved the validity of the rings as measures of annual growth for a number of species. Among these are McMillin (1923), Orton (1923), Ford (1925), Fraser and Smith (1928) and Newcombe (1936). It has been shown, however, that in certain species such as Dosinia discus (Crozier 1914), the annual ring method is not applicable, and its validity must be proved for every species. With Y. pullastra, all three of the above mentioned methods have been used, one serving as a check/

/check against the other.

A large number of animals were sexed as the shells were opened prior to fixation of the gonad for the work on seasonal gonad change, but no striking differences between the sizes of males and females was observed. Such differences would have been even more apparent when observing spawning animals. Fraser and Smith (1928) investigated this point with Panhia stamina and Saxidomus giganteus but found no difference between the sizes of the males and females of similar ages, nor did Weymouth, McMillin and Rich (1931) with the razor clam Siliqua patula, though they refer to Chamberlain (1927) as having established that, "In some molluscs there is sufficient sexual dimorphism to permit the recognition of the sex of an individual by the shell." It is possible there may be a difference in the growth rate of the sexes of M. pullastra, but it would be detected only by careful statistical study, and for the present work the equal sex ratio gives equal weight to any possible differences and no distortion should ensue.

In this study, length is the measure of growth that will be used most extensively, for this factor appears to be as good or better than any other such as weight, height or thickness. Height (dorso-ventral measurement) and thickness (greatest lateral measurement) are used only to establish their relationships to length. Weight is not used because it is too variable. Ring/

/Ring number and not age is used throughout in the discussion, table and graphs. Age may be determined approximately by subtracting one half from the ring number, i.e. an animal with two rings is roughly one and a half years old, the first ring being formed between four and seven months, and the second ring one year after the first. Only absolute growth will be treated.

Samples were measured with a dial caliper reading to 0.1 mm. This instrument is accurate, sensitive, easy to handle, rapid, and so ideal for measuring shells. The length of V. pullastra is taken to be the greatest distance between the anterior and posterior ends of the shells; the ring length is the greatest distance along its longitudinal axis; the height is the distance between a line along the hinge margin of the shell and a line parallel to it which is tangent to the most ventral part of the shell, briefly the dorso-ventral measurement; the thickness is taken to be the greatest lateral distance. The spat up to 10.0 mm. long were measured either with a micrometer eye-piece or by projecting the outline on a scale by means of a 35 mm. photographic enlarger.

Growth in the Young.

The normal breeding season of V. pullastra is from May-June to September, so a considerable variation in size will exist between the animals spatted early in the season and those spatted toward the end. This has/

/has been pointed out by Orton (1926) for Cardium edule, and it is partly for this reason that Elsey (1936) advocates the artificial stimulation of spawning in Ostrea gigas. By inducing spawning early in the summer, advantage is taken of the longer growing season, and as a result the oyster spat are 2 to 3 cm. greater in diameter than they would be if spawned late in the summer.

In connection with the investigation of the mortality of the 1946 spatfall in Balloch Bay, the September series of samples were measured and these data are given in Table 8, and plotted in the graphs, Plates 25 and 26. The highest mean values for length occur at the stations at the higher tide levels. Stephen (1928) found the rate of growth of Tellina tenuis to be greater at higher levels on the beach than at lower levels. The means of lengths of the spat of V. pullastra at the 4.0, 4.5 and 5.0 feet tide levels differ from each other and from the means at the 1.0 and 3.0 feet levels at the 5% level of significance. Means at the 1.0 and 3.0 feet levels do not differ significantly. Whether these differences are the result of single brood settling at different levels on the beach and the observed differences are a reflection of variable growth rates, or they are the result of several broods settling at different times and at different levels, cannot be determined. It is unlikely that four successive spatfalls in one summer should be distributed in the latter way.

An examination of Table 8, page 63-64, shows that these spat vary between 0.375 and 6.53 mm. There is the possibility that some growth occurred after this sampling was done. However, measurement of the winter ring in the following spring and summer, while showing a higher mean than the September samples, have no greater ranges and the increases in the mean are probably due to differential mortality. This appears to be so from the higher value for the lower end of the range in the spring and summer samples. In Plates 40 and 41 are shown photographs of spat of nearly comparable size. In Plate 40 the left hand series is from September 1946 samples, and show no marked ring. The right hand series is from June 1947 samples, and the winter rings (R1) are evident. In Plate 41 the left hand series is from June 1947 samples, and show the winter ring (R1). R2 is the outside edge of the shell and is the approximate location of the future ring 2. The right hand series is from September 1946 samples, and no winter ring has yet been formed. R1 shows the position of the winter ring when it is formed.

In Table 14 are shown the mean lengths of new growth put on in the period from the beginning of new growth early in April and the time of sampling in late April and in early June. The mean increment for the first month of growth is 0.89 mm. and that for the first two months 1.96 mm., with a mean monthly increment of/

TABLE 14.

Mean Length in mm. of Winter Ring (Ring 1) and of total measurement of samples of Balloch Bay Venerupis spat at

April 30th. 1947.

Ring	Sample size	Range	Mean	Variance	Standard Deviation	Standard Error
R1	171	1.10 - 5.89	3.01	0.213	0.924	0.710
Total Length	143	1.10 - 6.89	3.89	0.523	1.129	0.946

June 3rd. 1947.

Ring	Sample size	Range	Mean	Variance	Standard Deviation	Standard Error
R1	201	0.70 - 5.89	2.63	0.270	1.039	0.073
Total Length	194	1.10 - 7.24	4.51	0.709	1.512	0.108

/of 1.0 mm. The increment between the first and the second rings in large samples of adults from the Cross Houses Beach in Millport, is 7.7 mm., with a mean monthly increment of 1.3 mm. for a growing season of six months. More information would have been desirable from further samples of animals in their second summer, but the mean monthly increments derived in the two ways indicated above, are close enough to provide a reasonable check.

In Table 15 are given the length-increment frequencies for the various length groups of spat (length of ring 1) and it is important to note that over this particular size range, the larger increments are gained by the larger animals. In comparison, Table 18A shows that for the adult size groups the converse is true; the larger increments are gained by the smaller animals. Whether this is true for other species is not known, for this early period of growth has been little studied in this way. In Table 16 are given the absolute increments in length for the various size groups of spat, and the percentage increase in length, which also increases directly. For complete analysis more data is needed on animals ranging from 0.6 to 2.0 cm. In the marking experiments, discussed later, the highest mortality occurred among the smaller animals, and only a single animal with less than three rings survived.

TABLE 15.

Length - increment frequency table. To show the frequency at various sizes (length in mm. at the formation of the Winter Ring) of Spat from Salloch Bay. The increment is from the start of growth in April to June 3rd, 1947.

Mid Point Winter Ring	Increment						
	0.25	0.75	1.25	1.75	2.50	3.25	4.00
1.29	4	6					
2.08		13	5				
2.87		1	11	3			
3.66		1	3	27	4		
4.45			1	13	22		
5.24				5	14	16	
6.03					8	9	6
6.82				1	3	7	6

Table 16.

Length-increment Table. Increase at Various Lengths of Shoot from the Formation of the Winter Ring to June 3rd.1947.

Length of Winter Ring	Sample Size	Mean Increment	% increase in Length.
.9 - 1.69	10	.55	42.0
1.7 - 2.49	18	.88	42.0
2.5 - 3.29	15	1.31	45.0
3.3 - 4.09	35	1.76	47.0
4.10 - 4.89	36	2.19	48.0
4.90 - 5.69	35	2.73	51.0
5.70 - 6.49	23	3.18	52.0
6.50 - 7.24	17	3.29	49.0

Growth in the Adult.

Monthly Samples.

A series of monthly random samples varying in size from 100 to 200 animals, were taken from a limited area on the Cross Houses Beach. This beach has been described in another section and as far as could be ascertained, carried a larger population of *Y. pullastra* than any other on the island. Even then it required at least an hour to collect a sample of 100 animals. The sampling technique consisted merely of turning over the flat rocks, taking the specimens showing above the surface of the sand, and then digging over the area with a small trowel. A more efficient method of sampling would have been desirable, because of the difficulty in finding the well camouflaged smaller specimens the samples are somewhat biased toward the larger size groups. Owing to the rocky nature of the habitat, and the comparatively small amount of loose sand, sieving was impossible.

The information from this series of samples is summarised in Tables 17A, B and C. A typical length-frequency distribution is shown in Pl.42, where the dominance of the larger animals may be noted, as well as the absence of a definite series of modes indicating the various size and age groups. This is no doubt a reflection of the considerable range in length of each year class resulting from the comparatively long breeding season and the overlapping of sizes in the older year classes./

Length - Frequency Distributions of Mid-Monthly samples of Venerupis from Cross Houses Beach 1946 - 1947. Length in mm.

Mid Point	1946 May	June	July	Aug	Sept	Oct	Nov	Dec	1947 Feb	Mar	Aprl	Total
6.95	2											2
8.95		1	1				1					3
10.95	3	6	2	4	1	3	3	1		1	1	25
12.95	3	7	1	5	5	5	1	1		2	1	31
14.95	3	12		4	13	11	4	5		3	6	61
16.95	6	17		4	17	28	2	11		13	7	105
18.95	5	15	5	7	10	20	8	9	7	9	7	102
20.95	7	22	10	2	9	10	12	8	2	9	6	97
22.95	7	21	5	1	12	15	6	4	3	2	1	80
24.95	8	20	7	6	17	21	10	8	6	11	8	122
26.95	5	19	3	6	28	23	7	14	3	10	6	124
28.95	11	23	5	6	18	32	3	11	5	7	3	124
30.95	14	32	11	8	17	29	13	5	9	7	9	154
32.95	11	36	11	4	11	28	10	12	6	6	7	142
34.95	11	45	8	13	13	36	14	16	3	9	14	182
36.95	11	29	7	8	9	30	12	22	7	6	10	151
38.95	7	24	5	6	10	18	10	13	11	1	5	110
40.95	2	16	8	7	8	11	8	2	5	7	8	82
42.95	1	6	3	3	3	9	1	8	9	3		46
44.95	1	2	1	4	1	3	3	3	1			19
46.95				2		1			3			6
48.95				1			1					2

TABLE 17 B.

LENGTH - FREQUENCY Table of mid-monthly samples of Venerupis to show length frequencies at various ages (ring numbers). Length in mm.

Mid. Pt.	R. 1.	2.	3.	4.	5.	6.	7.	8.	9.
6.95		2							
8.95		4							
10.95		21	4						
12.95		21	10						
14.95		22	36	3					
16.95		24	76	2					
18.95		7	87	8					
20.95			79	16	2				
22.95			36	40	4				
24.95			36	75	10		1		
26.95			17	36	19	2			
28.95			6	60	55	2	1		
30.95				41	82	20			
32.95				21	74	41	4		
34.95				9	58	94	20	1	
36.95				1	29	74	40	7	
38.95					7	45	45	11	2
40.95					2	17	37	18	8
42.95						8	18	15	5
44.95						1	2	9	5
46.95							3	2	1
48.95								1	1
Total		101	387	362	342	304	171	64	22

TABLE 17 C.

Statistics of Mid-Monthly Samples of Venerupis from the Cross Houses Beach. The Measurement is total length in mm.

Date	Sample size	Range	Mean	Variance	Standard Deviation	Standard error
May 46	121	6.0 - 45.9	28.27	1.837	8.586	0.780
June 46	120	8.0 - 45.9	28.41	2.027	8.988	0.822
June 46	118	8.0 - 45.9	31.39	1.742	7.980	0.732
July 46	101	8.0 - 45.9	29.76	1.496	7.680	0.768
Aug. 46	103	10.0 - 49.9	24.11	3.114	10.056	0.966
Sept. 46	98	12.0 - 45.9	29.01	1.552	7.878	0.800
Sept. 46	112	10.0 - 35.9	28.25	1.053	6.452	0.612
Oct. 46	157	10.0 - 47.9	30.69	1.713	8.088	0.648
Oct. 46	119	10.0 - 43.9	28.76	1.550	7.860	0.724
Oct. 46	179	10.0 - 47.9	28.90	1.784	8.320	0.624
Nov. 46	128	10.0 - 49.9	27.49	1.989	8.802	0.761
Dec. 46	154	10.0 - 45.9	29.07	1.803	8.202	0.664
Feb. 47	95	16.0 - 47.9	31.66	2.242	9.442	0.974
Mar. 47	132	10.0 - 45.9	27.30	1.967	8.088	0.706
Apr. 47	99	10.0 - 41.9	28.81	1.762	8.278	0.836

Orton (1926) describes the growth of young Cardium edule as overtaking that of older animals. Weymouth, McMillin and Holmes (1925) found difficulty in identifying age groups in their length-frequency distributions of Siliqua patula.

A striking feature of this series of samples is the extreme variability, as may be seen by comparing in Table 17C the means of samples taken in consecutive months, as well as in different samples taken on the same day (those for October). The adequacy of the samples could not have been improved without difficulty. Each time a sample was taken a new section of ground was used, so the fact that samples were not returned, should not have influenced further sampling. The whole beach is a comparatively small one and all the V. pullastra ground is within the tidal range of one foot or less, so that the growth rates from one part to another should not vary significantly. In addition, there is no real evidence of the presence of dominant year classes. Therefore, other than providing animals for the measurement of growth rings, a series of random samples is of little use in determining the rate of growth in V. pullastra in this area.

Marking Experiments.

The main object of the marking experiments was to provide a check on the information derived from the measurement of individual winter rings, and to test the/

/the validity of the rings as measures of annual growth.

The animals were marked in several ways; the most satisfactory one was to number them with India ink and cover this with a layer of distrene dissolved in Xylol. This method gave the clearest mark, was easily applied and caused little disturbance to the animal. Its use is limited to animals having comparatively smooth shells. Marking numbers on the shells by means of a dentist's drill was also used, and notching the shell edges with a file gave a permanent reference mark.

After being marked, measured and the age estimated by the annual ring method, the specimens were replanted in half inch mesh galvanized wire cages. These were buried in the beach until the flat top was flush with the surface of the sand, after which they were filled with sand and gravel. The animals were planted just below the surface of the sand and the top of the cage closed up. The cages were deep enough to allow burrowing to the maximum depth of which this species is capable. The beach on which the cages were planted was a gently sloping one composed of sand and gravel, and carried a small population of Y. pullastra. It was located on the northern side of the island and chosen because of its comparative isolation and the suitability of the substratum for this type of experiment.

The main experimental group of animals were planted on September 17th, 1946 and first examined on/

/on April 26th, 1947. The mortality over this period was about 25%. Only a few young animals showed a fine sliver of new growth on the ventral shell margin, and measurement indicated no change in length. This showed clearly the winter cessation of growth as far as the external dimensions of the shell are concerned, and that new growth was just beginning. The temperature at this time was 6.0° C. as measured at the surface at Keppel Pier.

The animals were next examined on July 16th and finally taken up on October 20th, 1947. The mortality had increased by this time to 60% and was centred, as mentioned in another section, on the younger animals. New growth had occurred in practically all and was easily distinguished by the white new shell, in contrast to the dun colour of the old. At the margin of the shell where the new growth began, a groove had been formed, separating the new growth from the old. In addition, the file mark on what was formerly the edge of the shell coincided with the position of the groove. The mean increments for the summer period of growth are shown in Table 18 and graphed on Plate 43. These data are taken from 109 animals, the survivors of a total of 298 originally marked, and gave an annual mortality of 62%. The high mortality is a decided weakness in this type of experiment, especially when the mortality is selective.

In Table 18A is shown the ring-increment frequency, demonstrating in another way how the larger increments are gained by the smaller animals in this wide/

Table 18.

Mean Increments in length in mm. for the period September 17th. 1946 to October 20th. 1947 in marked and planted animals of various ages.

Ring	Sample size	Range	Mean	Variance	Standard Deviation	Standard error.
1						
2			6.60			
3	24	2.1 - 10.0	6.46	1.391	1.857	0.387
4	30	2.1 - 8.5	4.55	1.050	1.414	0.262
5	25	0.1 - 6.5	2.72	0.964	1.494	0.305
6	17	0.6 - 4.5	2.18	0.447	1.050	0.262
7	8	0.1 - 4.0	1.82			
8	4	1.1 - 1.75				

TABLE 18 A.

INCREMENT - Age Frequency Table to show the amount and frequency of the annual increment in mm. at various ages. Taken from 109 marked and planted animals for the period September 17th. 1945 to October 20th. 1947.

Increment	Ring Number						
	2	3	4	5	6	7	8
0.1 - 0.5				1		1	
0.6 - 1.0				1	4	1	
1.1 - 1.5				2	1	2	3
1.6 - 2.0				9	3	2	
2.1 - 2.5		1	3	1	2		
2.6 - 3.0			2	1	4	1	
3.1 - 3.5		1	4	4	1	-	1
3.6 - 4.0			4	-	1	1	
4.1 - 4.5		1	4	2	1		
4.6 - 5.0		2	1	2			
5.1 - 5.5		2	4	1			
5.6 - 6.0		3	3				
6.1 - 6.5		2	2	1			
6.6 - 7.0	1	5	1				
7.1 - 7.5		1					
7.6 - 8.0		1					
8.1 - 8.5			2				
8.6 - 9.0		2					
9.1 - 9.5		2					
9.6 - 10.0		1					

/wide range of lengths. Ring 1 is, unfortunately, not included, for animals of this size are difficult to mark satisfactorily, and even then there arises the problem of keeping them in a natural environment. It was hoped to gain this information indirectly by the measurement of spat, but the mortality was so great, as described in another section, that a representative sample could not be obtained after June, 1947. However, much of the required information has been obtained from the measurement of the appropriate rings in adults, as will be described in the next section.

Measurement of Age from Annual Growth Rings.

Based on the above conclusions that the ring markings (Pl.44), or at least some of them, represent annual growth rings, or more accurately, winter checks; these were assessed and measured. After some experience and basing judgement on the nature of the various rings and their position relative to one another, reasonable estimations were made in the majority of cases as to which were true checks. Many animals showing numerous or ill-defined checks were discarded; others were measured, but when inspection showed they did not conform to the sigmoid curve of growth, they were put aside. A number of animals were not used because the ring markings were worn away by abrasion. A typical example and one of distortion, are shown in Pl.45. Whether the abrasions are/

/are the result of movements of the animal against the rock on which it was lying; or of the movement of the rock against the animal, is not known: possibly it is a combination of both.

From a series of 12 random samples from the Cross Houses Beach, about 8,000 ring measurements were made, of which 6300 were used in the compilation of length-frequency distributions from the individual rings. During the growing season the measurements of new growth were segregated from the other measurements, so that only rings formed during the 'hibernation' period were used. All the measurements of each ring number were grouped together to obtain a mean length for that ring. This compilation is shown for each sample in Appendix 2. The information was further condensed by averaging and the final result is given in Table 19 and this forms the basis for the growth curve in Pl.46. In addition to the arithmetic means, the median values were calculated and they are also listed in Table 19 for comparison. It will be noted that with each ring the two measures of central tendency are nearly identical and indicates that the distributions conform very closely to the normal curve.

Examination of the tables shows the large variation in the lengths of any given ring, but this is to be expected, for in these measurements are included not only lengths of comparative rings of animals of the/

Table 19.

Mean Lengths and Median Values (in mm.) of Winter Rings Calculated from 6300 Ring Measurements, from Mid-Monthly Samples from the Cross Houses Beach, 1946-47.

Ring No.	No. of samples	Range	Mean	Median	Increment	% increment. increment / (length of previous ring)
1	12	0.7 - 8.2	3.65	3.35	3.65	-
2	12	6.7 - 17.2	11.32	11.34	7.67	200
3	12	14.2 - 27.7	19.91	19.27	8.58	80
4	12	23.7 - 36.7	28.45	28.30	8.54	40
5	12	28.7 - 41.2	33.81	33.90	5.36	20
6	12	33.7 - 44.2	37.35	37.40	3.54	10
7	12	38.1 - 47.2	39.58	39.25	2.23	6
8	8	35.2 - 46.3	41.75	41.70	2.17	5

/the same year class but also those of a number of year classes. For example, ring 8 of the 1938 year class was formed in the winter of 1945-46, while ring 8 of the 1939 year class was formed in the winter of 1946-47. Thus the final mean length of any ring is derived from the growth rates of animals of like ages in a number of different years. Growth rates are known to vary from year to year (Orton, 1926) depending on temperature, food supply, and possibly to factors not yet understood. Coe and Fox (1944) found that the average monthly growth increment in the California sea mussel (Mytilus californianus) showed an annual variation of more than 50 %. Thus the growth rate of Y. pullastra determined in the above manner, possibly gives a better general mean value than the information derived from one or more years by marking experiments. There is the limitation that the higher ring numbers are not so well represented as the smaller ones because of the normal increase of mortality with age.

In Table 20 are shown the annual growth increments between the formation of the various rings derived in several ways:-

A. The mean length of rings from a large sample of animals (6300 measurements) of various ages from the Cross Houses Beach.

B. The mean amount of new growth during the 1947 growing season at the Cross Houses Beach, calculated partly by summation of monthly growth/

TABLE 20.

Comparison of amount (annual) of growth between formation of various rings. Data derived from :

A. Average lengths of rings from large sample (6300 measurements) of animals of various ages from Cross Houses Beach.

B. Average amount of new growth during the 1947 growth season from Cross Houses samples (445 animals).

C. Average amount of growth during the 1947 growth season from marked animals on a beach - the north side of Great Cumbrae (109 animals).

Annual increment in mm.

Between Rings	A	B	C
0 - 1	3.65		
1 - 2	7.67	4.80	
2 - 3	8.58	7.28	6.60
3 - 4	8.54	8.81	6.46
4 - 5	5.36	6.16	4.55
5 - 6	3.53	4.66	2.72
6 - 7	2.22	2.51	2.18
7 - 8	2.17	2.06	1.82

/growth increments (Table 24), and partly by the measurement of the total summer's growth (Table 24, 20.10.47) from 445 animals.

C. The mean amount of growth during the 1947 growing season obtained from 109 marked individuals (Table 18) grown on the north side of the Island.

Increments in A and B are quite close and indicate that from the point of view of growth, 1947 approached what might be considered the norm of recent years, in spite of the delayed rise in temperature after the sever winter and early spring. In C. the increments are lower and this may be accounted for by the fact that they were replants in a not entirely typical environment. But in the main, the increments as derived in the three ways, tally closely and indicate in another manner that the annual ring method is valid for estimating the rate of growth in V. pullastra.

In addition, a total of 1500 ring measurements from the Cross Houses Beach samples of October 15th and 16th, 1946 were plotted to show the length frequency distribution (Pl.47). Theoretically this distribution should give a multi-modal curve, with the modes representing the lengths of the various rings. However, only the first two modes are definitely significant of the first and the second ring. The modes thereafter are not distinct enough, that is, there is little difference in frequency between the minimum values occurring between two/

TABLE 21.

Increment and Mean Increment in length in mm. for the stated periods for the various Rings from monthly samples taken from the Cross Houses Beach.
April to September. 1947.

Ring	Apl - May	May - June	June - July	July - Aug	Aug - Sept	Total Increment	Mean Increment
1			3.21	1.49	0.09	4.80	1.60
2	1.30	3.01	1.54	0.93	1.06	7.86	1.57
3	0.48	2.33	1.38	4.13	1.38	9.71	1.94
4	0.79	1.11	0.58	3.91	0.40	6.80	1.36
5	0.92		1.08	1.59	1.40	5.00	1.25
6			1.01 Total to date	0.60	0.72	2.34	0.78
7			1.45 Total to date	0.16	0.58	2.20	0.73
Total Increment for All ages	3.50	6.46	10.27	12.33	5.64		
Mean Increment for All ages	0.87	2.15	1.46	1.76	0.80		

TABLE 21 A.

Monthly Increments in mm. from measurements of new growth at various ages from Cross Houses samples

Date	Ring	Sample size	Range	Mean
18-5-47	1			
	2	2	1.2 - 1.4	1.30
	3	19	0.2 - 1.3	0.48
	4	17	0.3 - 2.1	0.79
	5	4	0.3 - 1.8	0.92
	6	2	0.3 - 0.9	0.60
	7			
18-6-47	1	3	2.9 - 4.2	3.46
	2	11	2.1 - 8.5	4.31
	3	26	0.5 - 4.4	2.81
	4	36	0.6 - 6.6	1.91
	5	25	0.4 - 2.1	0.92
	6	12	0.2 - 2.6	1.01
	7	2	0.4 - 1.4	0.90
17-7-47	1	7	4.6 - 8.1	6.68
	2	3	5.3 - 6.4	5.86
	3	37	1.1 - 6.4	4.19
	4	23	0.6 - 4.9	2.49
	5	17	0.6 - 3.9	2.09
	6	6	0.5 - 1.6	1.01
	7	2	1.1 - 1.8	1.45

TABLE 21 A.

Date	Ring	Sample size	Range	Mean
21-8-47	1	12	7.3 - 11.4	8.13
	2	5	3.0 - 10.8	6.80
	3	27	4.4 - 12.2	8.32
	4	12	3.1 - 9.5	6.40
	5	13	1.3 - 5.4	3.39
	6	6	1.0 - 4.3	2.56
	7	6	0.9 - 2.2	1.66
21-9-47	1	4	6.2 - 9.7	8.27
	2	25	3.4 - 2.2	7.86
	3	29	6.1 - 13.6	9.71
	4	11	1.9 - 10.2	6.80
	5	23	1.8 - 8.2	4.99
	6	10	1.3 - 6.4	3.29
	7	7	1.6 - 3.0	2.20
	8	5	0.3 - 3.0	1.72
20-10-47	1			
	2	31	1.3 - 13.9	6.74
	3	33	2.6 - 13.1	7.92
	4	18	1.7 - 10.7	5.51
	5	15	1.2 - 8.0	4.32
	6	14	1.4 - 6.0	2.68
	7	6	0.5 - 3.6	1.93
	8			
	9	2	1.5 - 1.7	1.60

/two peaks and the peaks themselves. This obscuring is no doubt due to the overlapping sizes in the older year classes. However, the first and second rings are definite enough, and the modal lengths correspond well with the mean values in Table 19.

During the growing season the new growth on the animals of various ages was noted in the monthly random samples and this information has already been utilised (Table 20). It is also arranged separately in Table 21 from which the mean monthly increment is obtained, and this is plotted on the graph, Pl.48, along with the mean weekly temperature for the period. The growth increment curve follows the temperature curve very closely until the time of the first spawning (sp.) when the increment curve drops. This would be more pronounced if the immature animals had not been included. A similar condition exists in the Pismo clam (Coe 1947) where there is an increase in the rate of growth with the spring increase in temperature up to an optimum when growth falls off to a minimum in August, although the water temperatures are then highest. Coe considers the decline in the growth rate as due to "the requirements of the reproductive system and the successive acts of spawning." The same trend in growth takes place in both species of Mytilus found in California and in other invertebrates there (Coe and Fox 1944). They consider that food supply has more influence on rates/

/rates of growth than have small increases in temperature. Orton (1928) has shown there is a spring and an autumn period of shell growth in Ostea edulis with little or none during the breeding period when the temperatures are highest. He concludes that shell growth is a function of temperature and feeding and suggests a physiological antagonism between shell growth and breeding.

With V. pullastra, at least in 1947, the summer decline in growth rate coincided closely with the onset of spawning and the decrease persists for some time. According to Marshall and Orr (1927) there is the usual spring increase in diatoms in the Millport region, but the autumn increase does not appear until growth has almost ceased, although the temperatures at this time are still high. It would seem that there must be a source of food in addition to diatoms to permit growth during the period when the diatom population is low. A small mid-summer bloom of diatoms is normal and in 1947 it appeared to be greater than usual. The Millport plankton is rich in larval forms and other small organisms throughout most of the summer. Coe and Fox (1944) consider the bulk of the food of Mytilus californianus to be detritus. Coe (1947) believes that the eggs and sperms of algae and invertebrates form the food of the Pismo clam as well as detritus and living phytoplankton and zooplankton. No attempt was made to investigate the food of V. pullastra, for there is no reason to doubt that/

/that it is unlike any other suspension feeding lamellibranch. A correlation between the amount of food available throughout the growing season and the rate of growth in various animals would be of interest.

Height-length and Thickness-length Relationships.

In Table 22 is shown the height-length relationships for spat between the lengths of 0.5 and 5.0 mm., and in Table 23 is given the height-length and the thickness-length ratios for animals between 10.0 and 45.0 mm. In the early part of the range in the spat, height tends to approximate to length, but very soon, at a length of 2.0 mm. the ratio changes to that found in the adult. The height-length ratio in the setting larva is 0.92, and there is a gradual change from a nearly spherical shape in the larva to an oval shape in the older spat. The oval shape adopted quickly by the spat has its advantages for burrowing. It will be observed from the tables how relatively constant the height-length ratio is maintained in comparison to the more variable thickness-length ratio. This variability may well be a reflection of the variable consistency of the substratum. If this is hard and unyielding, it may prevent the shell from assuming its normal shape. Certainly some of the burrows have had walls of nearly rock-like consistency. The thickness-length ratios for Tivella stultorum (Weymouth 1923), a pure sand dwelling form, appear to be more consistent than those of T. pullastra. These ratios for/

TABLE 22.

Height - Length Ratio of Venerupis spat of various sizes.
Samples from Ballough Bay, September, 1946.
Measurement in mm.

Mid Point	Sample size	Length	Height	Height Length
0.531	31	0.578	0.523	0.906
0.906	161	0.901	0.713	0.797
1.281	120	1.235	0.941	0.764
1.656	75	1.630	1.182	0.725
2.031	56	1.970	1.341	0.670
2.406	31	2.350	1.630	0.693
2.781	23	2.712	1.758	0.646
3.156	12	3.114	2.023	0.649
3.531	11	3.487	2.278	0.653
3.906	10	3.862	2.500	0.647
4.281	7	4.290	2.759	0.647
4.656	3	4.667	2.958	0.633
5.031	4	5.062	3.394	0.670

TABLE 23.

Height-length, Thickness-length Ratios of Adults of Various Sizes. Cross Houses Beach Samples, 1945. Measurements in mm.

Mid.Pt.	No. of Specimen	Length	Height	Thickness	Height Length	Thickness Length.
109.5	1	110	67	40	.609	.363
129.5	5	125.4	79.8	50.2	.636	.629
149.5	13	151.9	96.69	63.84	.640	.422
169.5	17	162.64	108.11	71.82	.664	.441
189.5	9	185.66	127.22	71.66	.684	.385
209.5	7	212.55	141.55	96.14	.665	.452
229.5	11	228.36	151.18	102.09	.662	.447
249.5	18	250.44	165.61	113.11	.661	.451
269.5	28	270.46	179.89	125.32	.665	.463
289.5	18	289.00	192.77	132.33	.667	.458
309.5	17	306.72	209.70	142.05	.683	.463
329.5	18	328.27	225.5	156.05	.686	.475
349.5	14	348.57	234.42	183.64	.672	.526
369.5	9	369.55	245.66	171.00	.664	.462
389.5	11	391.00	269.00	196.72	.687	.503
409.5	8	407.50	276.90	199.75	.678	.490
429.5	2	428.50	289.50	221.00	.675	.515
449.5	1	450.00	316.00	230.00	.702	.511

/for *Y. pullastra* are plotted in Pl.49 and the graphs represent the average relationship which is simple and direct with no radical change in shape with age. Crozier (1914) in his study of *Dosinia discors* also found a simple tangential relationship. The ratios for the size groups above 40.0 mm. in Table 23 indicates that growth in length may be slowing down slightly in relation to growth in height. This point has been observed directly in older animals where no new shell growth is evident on the ends of the shells, although there may be a small amount of new growth on the ventral edge. It may also be noted that new growth in young animals first occurs on the ventral margin of the shell.

Discussion.

The mean monthly growth rate of *Y. pullastra* has already been compared with that of other lamellibranchs. Direct comparison of growth is difficult when dealing with different species from several localities. From examination of the modes of his length-frequency curves for *Tellina tenuis*, Stephen (1929) found that the annual increment of any one year class decreases at a rate of 50% annually, which is in agreement with the data for *Cardium edule* (Orton 1926). Stephen points out that if this rule holds good for all lamellibranchs, a means is at hand for estimating the age of numerous small but economical species, when only the first full year's increment is known. But, as pointed out by Blegvad (1930)/

/Blegvad (1930) the matter is not quite so simple, for the growth rates of several Danish species do not conform to this rule, nor does the growth rate of Y. pullastra. It is interesting to note, however, as shown in the last column of Table 19, the regularity in the decrease of the percentage increment from year to year.

Walford (1946) in an interesting paper describes a method for transforming absolute growth curves into straight lines by plotting the lengths at age N years against the length at age N + 1 years. Such lines may be used for studying growth variation within and between populations, and the limiting length of the species estimated. When the two sets of data for Cardium edule from Orton (1926) (River Yealm), and from Stephen (1931) (Hunterston Sands), are plotted according to Walford's method, the two straight lines so produced, although there are few points, have the same slope of 0.84. This indicates that the yearly growth increments decrease at the same rate, although the absolute values are different. The data for Y. pullastra plotted in this way, also give a straight line with the same slope, but until more information is available on growth rates from other localities the full significance of this slope cannot be determined.

Summary.

1. The problem and methods of identifying lamellibranch veligers are discussed, as well as the characters most useful in identification.

2. The veliger larva is described and figured.

3. The fluctuations in abundance of larvae throughout the summer of 1947 have been determined by quantitative plankton methods which have been described. From this information, an estimate of the length of larval life has been made.

4. The exact limits of the beginning and end of the breeding season in 1947 have been determined.

5. Preliminary information on the vertical distribution of larvae in Fairlie Channel has been obtained.

6. A diurnal movement of larvae, being most abundant at the surface in hours of darkness, has been observed for the area near the Millport Marine Station.

7. The organs of the fully developed larva have been described.

8. The organs and their development in newly settled spat up to a length of 1.0 mm. have been described.

9. The changes that occur during metamorphosis are discussed and the three most important changes are considered to be :

   A. The loss of the velum.

   B. The active functioning of the byssal gland.

   C. The formation of the spat shell or dissoconch./

The functional significance of these events are considered.

10. Y. pullastra is found to settle almost entirely on the upper surface of spat collectors.

11. There is a relationship between the angle of the surface of the collectors relative to the horizontal and the number of spat caught per unit of area.

12. On the basis of projected areas, the efficiency of the collectors increases with the increase in angle. From this it is concluded that spatting is not a purely gravitational effect.

13. The distribution of the 1946 and 1947 spatfalls in the littoral zone of Balloch Bay, Isle of Cumbrae, has been studied by sampling at various tidal levels on the beach. The distribution and the numbers in the two years has been found to be almost identical.

14. The factors causing the type of distribution found have been discussed.

15. The rate of mortality of the spat of the 1946 brood year was found to be nearly 100% within one year. The possible factors contributing to this high mortality have been discussed.

16. The problem of spatting and the selection of a suitable substratum by the larva have been discussed. It has been shown that the needs of the spat and of the adult are different, and whatever power of selection the spat may have is exerted in the selection of an environment/

/environment suitable for its immediate needs. If that environment is not suitable for the adult, then mortality occurs.

17. The rate of water propulsion by adults 4.5 cm. long was found to range between 0.14 and 0.99 with a mean of 0.5 litres per hour in a temperature range of 15.0° to 16.0° C.

18. The animal filters approximately 100 times its own volume in one hour.

19. If all parts of the gill are equally concerned in filtering, 1 square centimetre of gill filters 12.5 cc. of water per hour.

20. The current speeds of water through the two siphons are different and this prevents mixing of the two currents.

21. The gills are shown to be efficient in filtering particles down to the size of 1 u.

22. The secretion of mucus by the gills does not appear to be a limiting factor in its ability to filter suspended material in considerable concentration for periods up to 6 hours.

23. Kymograph recordings of shell movements have been analysed and the results compared with those found by other investigators for other species.

24. Shell (Adductor muscle) movements have been found to play no part in the spawning act.

25. The method of spawning in both sexes is described./

26. Y. pullastra has been stimulated to spawn both by temperature stimulus and by a chemical stimulus in the form of a suspension of eggs or of sperms of the species.

27. A long latent period and a refractory period during which spawning cannot be induced, have been observed.

28. Y. pullastra is not as susceptible to stimulation as the "oviparous" oysters.

29. Seasonal changes in the gonads of both sexes was followed by examination and study of sections of over 900 mature animals.

30. The sex ratio was found to be approximately equal.

31. Only 0.1% of the population studied were hermaphrodites.

32. Approximately 0.1% of the population studied were parasitised by an unidentified species of trematode.

33. The length of spat at the formation of the first winter ring varies between 0.4 and 7.0 mm.

34. The mean lengths of samples of spat from Balloch Bay appear to indicate that a slightly higher rate of growth may occur at the higher tidal levels on this beach.

35. In the early spat up to the formation of Ring 2 the largest growth increments are gained by the larger spat, but thereafter the growth increments decrease with increase in size and age.

36. The method of modal groups from length-frequency distributions of random samples is shown to be not/

/not applicable to Y. pullastra as a means of determining age groups.

37. Marking experiments have indicated that certain of the rings appearing as surface sculpture on the shells of Y. pullastra are valid as measures of annual growth.

38. From the marking experiments the annual growth increment of animals of various ages was determined and checked against similar measurements determined in other ways.

39. From 6300 measurements of the length of growth rings on animals from a confined area, a length-on-age curve has been drawn. This curve follows the typical sigmoid form.

40. The mean monthly increment of growth for the 1947 growing season are shown to follow the temperature curve until the onset of spawning, when there is a decrease in the growth rate. Later in the summer there is an increase which cannot be definitely correlated with a particular factor on the basis of available information on food, etc.

41. The height-length and the thickness-length ratios for various sizes have been calculated and they have been found to follow a simple and direct tangent relationship.

References

The abbreviations are according to the World List of Scientific Periodicals.

The arrangement is according to the instructions for publication given by the Zoological Society of London.

* Refers to those papers not seen in the original.

Allen, W.R.(1914). The food and feeding habits of freshwater mussels. Biol. Bull. Wood's Hole. 27, (3), 127-146.

Amemiya, I.(1928). Ecological studies of the Japanese oyster, with special reference to the salinity of their habitats. J. Coll. Agric. Tokyo, 9, (5), 333-382.

Amemiya, I.(1929). On the sex-change in the Japanese oyster, Ostrea gigas Thunberg. Proc. imp. Acad. Japan, 5, 284.

Ashworth, J.(1904-5). Notes on Tapes pullastra. Proc. Lpool. biol. Soc. 19, 15.

Atkins, D.(1936). On the ciliary mechanism and inter-relationships of lamellibranchs. Part 1. Quart. J. micr. Sci. 79, 181-308.

Atkins, D.(1937a). Part II. Quart. J. micr. Sci. 79, 339-373.

Atkins, D.(1937b). Part III. Quart. J. micr. Sci. 79, 375-421.

Atkins, D.(1937c). Part IV. Quart. J. micr. Sci. 79, 423-445.

Atkins, D.(1938a). Part V. Quart. J. micr. Sci. 80, 321-329.

Atkins, D.(1938b). Part VI. Quart. J. micr. Sci. 80, 331-344.

Atkins, D.(1938c). Part VII. Quart. J. micr. Sci. 80, 345-436./

Atkins, D.(1943). Part VIII. Quart. J. micr. Sci. 84, 187-256.

Belding, D.L.(1912). Report on the quahaug and oyster fisheries of Massachusetts. Commonwealth of Mass. State printers, Boston, 1-134.

Belding, D.L.(1916). Report on the Clam Fishery. Fiftieth Annual Rep. Comm. Fish. and Game (Mass). Public Doc. 25, 93-234.

Bernard, F.(1896). Sur le developpement et la morphologie de la coquille chez les lamellibranches III. Anisomyaires. Bull. Soc. geol. Fr. (3), 24, 412-449, Paris.

Biedermann, W.(1901). Untersuchungen uber Bau und Entstehung der Mollusken-Schaler. Jena. Zeitschr.m, 36, 1-164.

Blegvad, H.(1928). Quantitative investigations of the bottom invertebrates in the Limfjord 1910-1927 with special reference to the plaice - food. Rep. Danish biol. sta. 34, 33-52.

Blegvad, H.(1930). Review of Stephen's 1929 paper on Tellina tenuis Cons. int. Explor. Mer. V.

Boggild, O.B.(1930). The shell structure of the Molluscs. Danske Selskabs Skrifter. 2, 235-326.

Burkenroad, M.D.(1934). Sex in the Louisiana oyster. Ostrea virginica. Science, 79, 71-72.

Chamberlain, T.K.(1927). Thesis. Stanford Library.

Coe, W.R.(1932). Development of the gonads and the/

/the sequence of the sexual phases in the California oyster (Ostrea lurida). Bull. Scripps. Instn. Oceanogr. tech. Series 3, 119.

Coe, W.R.(1936). Sex ratios and sex changes in molluscs. Pelseneer Jubilee Memorial Volume. Mem. Mus. Hist. nat. Belg. (2) Fasc. 3. 69.

Coe, W.R. & H.J. Turner Jr.(1938). Development of the gonads and gametes in the soft shell clam (Mya arenaria). 23 figs. J. Morph. 62, no.1.

Coe, W.R. & Denis L. Fox.(1944). Biology of the California sea mussel (Mytilus californianus) III. Environmental conditions and rate of growth. Biol. Bull. Wood's Hole, 87, 59-72.

Coe, W.R.(1947). Nutrition, Growth and Sexuality of the Pismo clam (Tivella stultorum). J. exp. Zool., 104, no.1.

Cole, H.A.(1936). Experiments in the breeding of oysters (Ostrea edulis) in tanks with special reference to the food of the larva and spat. Fish. Invest. (2), 15, no.4.

Cole, H.A.(1937). Metamorphosis of the larva of Ostrea edulis. Nature, 139, 413-414.

Cole, H.A.(1938a). The fate of the larval organs in the metamorphosis of Ostrea edulis. J. Mar. biol. Ass. U.K., 22, no.2, 469-485.

Cole, H.A.(1938b). A system of oyster culture. Comm. int. Explor. Mer. 13, no.2, 221-235./

Cole, H.A.(1939). Further experiments in the breeding of oysters in tanks. Fish. Invest. (2), 16, no.4.

Crozier, W.J.(1914). The growth of the shell in the lamellibranch Dosinia discus (Reeve). Zool. Jb. Abt. f. Anat. 38, 577-584.

Damas, D.(1935). Le role des organismes dans la formation des vases marines. Ann. Soc. geol. Belg., 58, 143.

Davaine, C.(1852). Recherches sur la generation des huitres. Compt. Rend. et Mem. Soc. Biol., 4, 297.

Davis, F.M.(1923). Quantitative studies on the fauna of the sea bottom, no.1. Preliminary investigation of the Dogger Bank. Fish. Invest. (London 2), 6, no.2, 1-54.

Day, J.H. & D.P. Wilson (1934). On the relation of the substratum to the metamorphosis of Scolecolepis fuliginosa (Claparede). J. Mar. biol. Ass. U.K., 19, 655-662.

Dodgson, R.W.(1928). Report on Mussel Purification. Fish. Invest. (2), 10, no.1.

Drew, G.A.(1899a). Yoldia limulata. Mem. biol. Lab. Johns Hopk. Univ. 4, (3) 1-37.

Drew, G.A.(1899b). Some observations on the habits, anatomy and embryology of members of the Protobranchs. Anat. Anz., 15.

Drew, G.A.(1901). The history of Nucula delphinodonta. Quart. J. micr. Sci., 44./

Drew, G.A.(1907). The habits and movements of the Razor-shell clam, Ensis directus Con. Biol. Bull. Wood's Hole, 12, 127-140.

Ehrenbaum, E.(1884). Untersuchungen uber struktur der schale in der Kieler Bucht hsufig vorkommenden Bivalven. Zeitschr. f.wiss. zool., 41, 1-47.

Elsey, C.R.(1933a). The japanese oyster in Canadian Pacific waters. Fifth Pac. Sci. Congr. Section B. 8, 4121-4127.

Elsey, C.R.(1933b). Oysters in British Columbia. Biol. Bd. Canada. Bull. 34, 1-34.

Elsey, C.R.(1936). Artificial stimulation of spawning in the Pacific oyster. Progress Report, Pacific, no.29.

Erdman, W.(1934). Untersuchungen uber die lebensgeschichte der Auster. Nr. 5. Uber die entwicklung und die Anatomie der "ansatzr eifen" Larve von Ostrea edulis, mit Bemerkungen uber die Lebensgeschichte der Auster. Wiss. Meeresuntersuch, Helgo., 19, nr.6, 1-25.

Fernando, W.(1931). Origin and development of the pericardium and kidney in Ostrea. Proc. roy. Soc., 107.

Field, I.A.(1922). Biology and economic value of the sea mussel, Mytilus edulis. Bull. U.S. Bur. Fish., 38, 127.

Flattely, F.W. & C.L. Walton.(1922). The Biology of the Sea Shore. Sidgwick and Jackson Ltd., London./

Ford, E.(1923). On the growth of some lamellibranchs in relation to the food supply of the fishes. J. Mar. biol. Ass. U.K., (n.s.) (3). 13, 531.

Fox, H.M.(1923). Lunar periodicity in reproduction. Proc. Linn. Soc. Lond., B, 95, 523-550.

Fox, H.M.(1925). The effect of light on the vertical movement of aquatic organisms. Proc. Camb. phil. Soc. biol. Sci., 1, 49-55.

Fox, Sverdrup & Cunningham (1937). The rate of water propulsion by the California mussel. Biol. Bull. Wood's Hole., 72, (3), 417-438, 4 fig.

Fraenkel, G.V.(1927). Die Grabbewegung der Solemiden. Z. vergl. Physiol., 6B, 1 Hett.

Fraser, C. McLean, & G.M. Smith.(1928a). Notes on the ecology of the little neck clam, Panhia staminea. Conrad. Trans. roy. Soc. Can., (3), 22, Section V, 249-269.

Fraser, C. McLean, & G.M. Smith.(1928b). Notes on the ecology of the butter clam Saxidomus gigenteus. Deshayes. Trans. roy. Soc. Can., (3) 22, Section V, 271-284.

Fuller, J.L. & G.L. Clarke,(1936). Further experiments on the feeding of Calanus finmarchicus. Biol. Bull. Wood's Hole., 70.

Fuller, J.L.(1937). Feeding rate of Calanus finmarchicus in relation to environmental conditions. Biol. Bull. Wood's Hole, 72./

Galtsoff, P.S.(1926). New methods to measure the rate of flow produced by the gills of oysters and other molluscs. Science, 63, 233.

Galtsoff, P.S.(1928a). Experimental study of the function of oyster gills. Bull. U.S. Bur. Fish., 44.

Galtsoff, P.S.(1928b). Experimental study of the function of the oyster gills and its bearing on the problems of oyster culture and sanitary control of the oyster industry. U.S. Bull. Bur. Fish., 44, 1.

Galtsoff, P.S.(1938a). Physiology of reproduction of Ostrea virginea. 1. Spawning reactions of the female and male. Biol. Bull. Wood's Hole, 74, no.3, 461-486.

Galtsoff, P.S.(1938b). Physiology of reproduction of Ostrea virginea. II. Stimulation of spawning in the female oyster. Biol. Bull. Wood's Hole, 75, no.2, 286.

Galtsoff, P.S.(1940). Physiology of reproduction of Ostrea virginea. III. Stimulation of spawning in male oyster. Biol. Bull. Wood's Hole, 78, no.1, 117-135.

Gerbe, Z.(1875). Zool. Rec. 1876.

Gibson, A.H.(1925). Hydraulics and its Applications. D. Van Nostrand Co., New York.

Grave, B.H.(1927). The natural history of Cumingia tellinoides. Biol. Bull. Wood's Hole, 53, 208-219.

Gray, J.(1928). Ciliary Movement. Cambridge Univ. Press./

Hagmeier, H.(1916). Über die Fortpflanzung der Auster und die fiskalischen Austernbanke. Wiss. Meeresunt. Abt. Helge., 18.

Harms, W.(1909). Postembryonale Entwicklungsgeschichte der Unioniden. Zool. Jb., Anat. u. ontog. Bd. 28, Hft. 2.

Heath, H.(1905). The breeding habits of chitons of the California coast. Zool. Anz., 29, 390-393.

Hecht, S.(1916). The water current produced by Ascidia atra. J. exp. Zool. 20.

Herbers, K.(1914). Entwicklungsgeschichte von Anodonta cellensis, Schrot. Z. wiss. Zool. 108.

Holmes, S.J.(1902-3). Phototaxis in Volvox. Biol. Bull. Wood's Hole, 4, 319-326.

Hopkins, A.E.(1931). Temperature and the shell movements of oysters. U.S. Bull. Bur. Fish., 47, 1-14.

Hopkins, A.E.(1933). Experiments on the feeding behaviour of the oyster, Ostrea gigas. J. exp. Zool., 64, no.3, 469-494.

Hopkins, A.E.(1935). Attachment of the Olympia oyster, Ostrea lurida to plane surfaces. Ecology, 16 (1), 82-87.

Hopkins, A.E.(1936). Activity of the adductor muscle in oysters. Physiol. Zool., 9, (4), 498-507.

Hopkins, A.E.(1937). Experimental observations on spawning, larval development and setting in the Olympia oyster, Ostrea lurida. U.S. Bull. Bur. Fish., 48, no.23./

Hori, J.(1933). On the development of the Olympia oyster, Ostrea lurida, Carpenter, transplanted from United States to Japan. Bull. Jap. Soc. sci. Fish., 1, (6), 269-276.

Hunt, O.D.(1925). The food of the bottom fauna of the Plymouth fishing grounds. J. Mar. Biol. Ass. U.K., 13, 560-599.

Jackson, R.T.(1888). Development of the oyster. Proc. Boston Soc. nat. Hist., 23.

Jackson, R.T.(1890). Phylogeny of the Pelecypoda. The Aviculidae and their Allies. Mem. Boston Soc. nat. Hist., 4.

Jordan, H.(1915). Uber die Art; wie Mactra inflata sich in den Sand einwuhlt. Zool. Jb., Abt.f.allg. Zool. u. Physiol., 35.

Jorgensen, C. Barker.(1943). On the water transport through the gills of bivalves. Acta Physiol. Scand., 5, fasc.4, 297-304.

Jorgensen, C. Barker.(1946). Lamellibranch veligers from Danish waters. Reprint from: G. Thorson: Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the sound (oresund). Medd. Komm. Danmarks Fisk. og Havunders., Serie: Plankton, Bd. 4. /

Kandler, R.(1926). Muschellarven aus dem Helgolander Plankton. Bestimmung ihrer artzugehorigkeit durch Aufzucht. Wiss. Meeresunters., Abt. Helgo., 16, no.5, 1-8.

Kellog, J.L.(1903). Feeding habits and growth of Venus mercenaria. Bull. N.Y. St. Mus. 71.

Kellog, J.L.(1915). Ciliary mechanisms of lamellibranchs, with descriptions of anatomy. J. Morph., 26, no.4, 625-701.

Kikuchi, K.(1930). Diurnal migration of Plankton crustacea. Quart. Rev. Biol., 5.

Korringa, P.(1940). Experiments and observations on swarming pelagic life and setting in the European flat oyster, Ostrea edulis L. Arch. Neerl. Zool., 5, 1-249.

Lacaze-Duthiers.(1856). Memoire sur le developpement des branchies des mollusques acephales lamellibranches. Ann. Sci. nat., 4, Ser. Tome 5.

Lebour, M.V.(1937). Larval and post larval Lima from Plymouth. J. Mar. Biol. Ass. U.K., 21, no.2. 703-710.

Lebour, M.V.(1938a). Notes on the breeding of some lamellibranchs from Plymouth and their larvae. J. Mar. biol. Ass. U.K., 23 no.1, 119-145.

Lebour, M.V.(1938b). The life history of Kellia suborbicularis. J. Mar. biol. Ass. U.K., 22, 447-452. /

Lillie, F.R. & E.E. Just.(1913). Breeding habits of the heteronereis form of Nereis limbata at Wood's Hole, Mass. Biol. Bull. Wood's Hole, 24, 147-168.

Loosanoff, V.L.(1937). Seasonal gonadal changes of the adult clam Venus mercenaria (L). Biol. Bull. Wood's Hole, 72, 406-416.

Loosanoff, V.L.(1939). Effects of temperature upon the shell movements of clams, V. mercenaria. Biol. Bull. Wood's Hole, 86, 171-182.

Loosanoff, V.L.(1942). Shell movements of the edible mussel Mytilus edulis (L) in relation to temperature. Ecology, 23, 231-234.

Loosanoff, V.L. & C.A. Nomejko,(1946). Feeding of oysters in relation to tidal stages and to periods of light and darkness. Biol. Bull. Wood's Hole, 90, no.3.

Loven, S.(1848). Bidrag till Kannedomen om utvecklingen of Mollusca Acephala Lamellibranchiata. Stockholm Vetensk. Acad. Handl. for 1848. German translation without figures by Creplin in : Arch. Naturgesch., 15. 1849.

MacGinitie, G.E.(1941). On the method of feeding of four Pelecypods. Biol. Bull. Wood's Hole, 80, no.1.

Marshall, S.M. & A.P. Orr.(1927). The relation of the plankton to some chemical and physical factors in the Clyde sea area. J. Mar. biol. Ass. U.K., 15,

837.

Marshall, S.M., Nicholls, & A.P. Orr.(1935). On the biology of Calanus finmarchicus.V. Seasonal distribution, size, weight and chemical composition in Loch Striven in 1933 and their relation to the phytoplankton. J. Mar. biol. Ass. U.K., 19, 793-828.

Mazzarelli, G.(1922). Note sulla biologia dell ostrica (Ostrea edulis L.) 1. Nascita delle larvee durata periodo larvale. Boll. Soc. Nat. Napoli, 34, 151-159.

McMillin, H.C.(1924). The life history and growth of the Razor clam. State of Washington, Department of Fisheries, 52.

Meisenheimer, J.(1901). Entwicklungsgeschichte von Dreissensia polymorpha Pall. Z. wiss. Zool., 69, 1-137. Taf. 1-13, 18 Abb.

Mill, H.R.(1892). The Clyde Sea Area. Part 1. Physical Geography XXXV, (1892), 641-663. Part 2. Salinity and chemical composition of the water. XXXVI, (1892), 664-729. Part 3. Distribution of temperatures XXXVIII, (1894), 1-161. Trans. roy. Soc. Edin.

Miyazaki, I.(1935). On the development of some marine bivalves with special reference to the shelled larvae. J. Fish. Inst. Tokyo, 31, no.1. 1-10.

Miyazaki, I.(1936a). On the development of some marine bivalves with special reference to the shelled larvae, II. J. Fish. Inst. Tokyo, 31, 35-41./

Miyazaki, I.(1938b). On the development of bivalves belonging to the genus, Corbicula. Bull. Jap. Soc. sci. Fish. 5, 249-254.

Miyazaki, I.(1938a). On the development of Tellina juvenalis. Bull. Jap. Soc. sci. Fish., 7, 179-182.

Miyazaki, I.(1938b). On the development of Mistella orientalis, Bull. Jap. Soc. sci. Fish., 7, 183-185.

Miyazaki, I.(1938c). On a substance which is contained in green algae and induces spawning setion of the male oyster. (Preliminary note). Bull. Jap. Soc. sci. Fish., 7, 137-138.

Moore, H.F.(1908). Volumetric studies of the food and feeding of oysters. U.S. Bull. Bur. Fish., 28, 1297-1308.

Morgan, T.H.(1910). Cytological studies of centrifuged eggs. J. exp. Zool., 9, 593.

Morse, E.S.(1913). Observations on living Solenomya (velum and borealis). Biol. Bull. Wood's Hole, 25, 261-281.

Mortensen, Th.(1921). Studies of the development and larval forms of Echinoderms. G.E.C. Gad, Kobenhavn, 266.

Mossop, B.K.(1921). The rate of growth of the sea mussel (Mytilus edulis L) at St. Andrews, N.B: Digby, N.S; and in Hudson Bay. Trans. Roy. Ca. Inst., 15, Toronto.

Moesop, B.K.(1922). The rate of growth of the sea mussel (Mytilus edulis) at St. Andrews, N.B; Digby, N.S; and in Hudson Bay. Studies from the Biological Stations, Biological Board of Canada, 15, 22, Toronto.

Needler, Alfreda, B.(1932). Sex reversal in Ostrea virginica. Contrs. Canad. Biol. (series A), 7, 285.

Nelson, T.C.(1921). Report of the Dept. of Biol. of the N.J. Agric. Coll. Exp. Stat. for the year ending June 30th, 1920 (1921), 317.

Nelson, T.C.(1924). Report of the Dept. of Biol. of the N.J. Agric. Coll. Exp. Stat. for the year ending 30th June, 1923.

Nelson, T.C.(1928a). Pelagic dissoconchs of the common mussel, Mytilus edulis, with observations on the behaviour of the larvae of allied genera. Biol. Bull. Wood's Hole, 55, 180-182.

Nelson, T.C.(1928b). Relation of spawning of the oyster to temperature. Ecology, 9, 145.

Nelson, T.C.(1935). Water filtration by the oyster and a new hormone effect thereon. Anat. Rec. 64, (suppl.1), 68.

Newcombe, C.L.(1935a). A study of the community relationships of the sea mussel, Mytilus edulis. Ecology, 16 (2), 234-243.

Newcombe, C.L.(1935b). Certain environmental factors of a sand beach in the St. Andrews region, N.B., with a preliminary designation of the intertidal communities. J. Ecol., 23, 334-355.

Newcombe, C.L.(1935c). Growth of Mya arenaria L. in the Bay of Fundy region. Canad. J. Res. 13 (sec.D), 97-137.

Newcombe, C.L.(1936a). Validity of concentric rings of Mya arenaria L. for determining age. Nature, 137 (3457) 191-192.

Newcombe, C.L.(1936b). A comparative study of the abundance and the rate of growth of Mya arenaria L. in the Gulf of St. Lawrence and Bay of Fundy regions. Ecology, 17, no.3, July 1936.

Odhner, N. Hj.(1912). Morphologie und phylogentische Untersuchungen uber die Nephridien der Lamellibranchien. Zeitschr. f. wiss. Zool., 100, 287-391, 40 Abb.

Ohdner, N.Hj.(1914). Notizen u ber die Fauna der Adria bei Rovigno. Beitrage zur Kenntnis der marinen Mollusken fauna von Rovigno in Istrien. Zool. Anz., 44, no.4, 156-170.

Orton, J.H.(1912). The mode of feeding of Crepidula with an account of the current producing mechanism in the mantle cavity, and some remarks on the mode of feeding in Gastropods and Lamellibranchs. J. Mar. biol. Ass. U.K., N.S., 9, 444-478.

Orton, J.H.(1913). The ciliary mechanisms on the gill and the mode of feeding in Amphioxus, Ascidians and Solenomya togata. J. Mar. biol. Ass. U.K., N.S., 10, 19-49.

Orton, J.H.(1923). On the significance of rings on the shells of Cardium and other molluscs. Nature, July 7th, 1923.

Orton, J.H.(1926). On the rate of growth of Cardium edule. Part 1. Experimental observations. J. Mar. biol. Ass., U.K. 14, no.2, Aug. 1926.

Orton, J.H.(1927c). A note on the physiology of sex, and sex-determination. J. Mar. biol. Ass. U.K., 14, 1047-1055.

Orton, J.H.(1928). Observations on Patella vulgata. Pt.II. Rate of growth of shell. J. Mar. biol. Ass. U.K.(n.s.), 15, no.3, 868-874.

Orton, J.H.(1933). Observations and exper. on the sex-changes in the European oyster. Pt.III. On the fate of the unspawned ova. Pt. IV. On the change from male to female. J. Mar. biol. Ass. U.K. 19, 1-55.

Orton, J.H.(1936). On Sex-change in the oyster, Ostrea edulis L. Part 5. A simultaneous study of spawning in 1927 in two distinct localities. Mem. Mus. roy. Hist. Nat. Belg.(2) Fasc. 3, 997-1056.

Orton, J.H.(1937a). Oyster biology and oyster culture. The Buckland Lectures for 1935. London. Edward Arnold and Co.

Orton, J.H.(1937b). Some inter-relations between bivalve spat-falls, hydrography and fisheries. Nature, 140, 503-506.

Parker, G.H.(1914). On the strength and the volume of the water currents produced by sponges. J. exp. Zool., 16, 443./

Peck, R.H.(1877). The minute structure of the gills of lamellibranch molluscs. J. micr. Sci.(n.s.), 17.

Pelseneer, P.(1892). Introduction a l'Etude des Mollusques. Ann. Soc. zool. Belg. 27, Bruxelles.

Perkins, E.B.(1931). A study of oyster problems in Barnegat Bay during 1930. Report of the Dept. of Biol. N.J. Agric. Exp. Stat. July 1st 1929-June 30th 1930.

Petersen, C.G.Joh.(1915). On the animal communities of the sea bottom in the Skagerrak, the Christiana Fjord and the Danish waters. Rep. Danish Biol. Sta., 23.

Prytherch, H.F.(1934). Role of copper in the setting, metamorphosis and distribution of the American oyster, Ostrea virginica. Ecol. Monogr., 4, no.1.

Quayle, D.B.(1943). Sex, gonad development and seasonal gonad changes in Paphia staminea, Conrad. J. Fish. Res. Board of Canada, 6, no.2.

Ranson, G.(1926). Le Filtration de l'eau par les lamellibranches et ses consequences. Bull. Inst. oceanogr. Monaco, no.469, 1.

Rice, E.L.(1897). Die systematische Verwert barkeit der Kiemen bei den Lamellibranchiaten. Jena. Z. Naturw., 31, 29-89.

Rice, E.L.(1905). Notes on the development of the gill in Mytilus. Science, (n.s.), 21, no.532, 377-378.

Rice, E.L.(1908). Gill development in Mytilus. Biol. Bull. Wood's Hole, 14, no.2, 61-77./

Ries, E.L.(1930). Fusion of filaments in the lamellibranch gill. Biol. Bull. Wood's Hole, 2.

Ridewood, W.G.(1903). On the structure of the gills of the Lamellibranchia. Philos. Trans. (B), 195, 147-284.

Rose, M.(1925). Contribution a l'etude de la biologie du plankton. Le probleme des migrations verticales journalieres. Arch. zool. Univ. Coimbra., 64, 387-524.

Roughley, T.C.(1933). The life history of the Australian oyster, O. commercialis. Proc. Linn. Soc., 58 (3/4), 279-333.

Ryder, J.A.(1884). The metamorphosis and post larval stages of development of the oyster, Rep. U.S. Comm. Fish., 10, 779-791.

Schaefer, M.B.(1937). Attachment of the larvae of Ostrea gigas, the Japanese oyster to plain surfaces. Ecology, 18 (4), 523-527.

Schaefer, M.B.(1938) Preliminary observations on the reproduction of the Japanese common oyster, Ostrea gigas, in Quilicene Bay, Washington. Biol. Rep. No. 36, F. Dept. of Fish., State of Washington.

Sigerfoos, C.P.(1895). The Pholadidae I. Note on the early stages of development. Johns Hopk. Univ. Circ., 78-79.

Sigerfoos, C.P.(1896). The Pholadidae II. Note on the organisation of the larva and the post larval development of shipworms. Johns Hopk. Univ. Circ., 15, 87-89./

Sigerfoos, C.P.(1907). Natural History, organisation and late development of the Teredinidae or shipworms. U.S. Bull. Bur. Fish., 27, 191-234.

Sparck, R.(1933). Preliminary investigation on the power of filtration, Ostrea edulis. Rep. Danish Biol. Sta. 38.

Stafford, J.(1912). On the recognition of bivalve larvae in plankton collections. Contr. Canad. Biol., 1906-10. 221-242.

Stafford, J.(1913). The Canadian oyster: its development, environment and culture. Ottawa, 1913. The Mortimer Co.

Steedman, H.F.(1945). Ester Wax: a new embedding medium. Nature, 156, 121.

Steedman, H.F.(1947). Ester Wax: A new embedding medium. Quart. J. micr. Sci., 88, 123-133.

Stephen, A.C.(1928). Notes on the Biology of Tellina tenuis da Costa. J. Mar. biol. Ass. U.K., 15, no.2.

Stephen, A.C.(1929). Notes on the rate of growth of Tellina tenuis da Costa, in the Firth of Clyde. J. Mar. biol. Ass. (n.s.), 16, no.1. 117-129.

Stephen, A.C.(1931). Notes on the Biology of certain lamellibranchs on the Scottish Coast. J. Mar. biol. Ass. U.K., 17, no.2.

Stephen, A. C.(1932). Notes on the Biology of some lamellibranchs in the Clyde area. J. Mar. biol. Ass. U.K. (n.s.), 18 (1), 51-68./

Stoll, E.(1937). Beobachtungen über die Fortbewegung bei einigen grabenden Muscheln. Rev. suisse. Zool., 44. 383-390.

Stoll, E.(1938). Sur le mode de locomotion de quelques mollusques marins. Trav. Sta. biol. Roscoff., 15. 5-29.

Tait, J.B.(1937). Fish. Scotland, Sci. Invest. (No.1).

Thiele, J.(1935). Handbuch der Systematischen Weichtiere Kunde. Fischen, Jena. 3.

Thompson, Sir, D'Arcy W.(1947). A Glossary of Greek Fishes. Oxford University Press.

Thorson, G.(1946). Reproduction and Larval development of Danish Marine Bottom Invertebrates, with special reference to the Planktonic Larvae in the Sound. Medd. Komm. Danmarks Fisk.-og Havunders, Serie: Plankton, Bd. 4, Kobenhavn, 1946.

Trueman, E.R.(1942). The structure and deposition of the shell of Tellina tenuis. J. R. micr. Soc., 72, 69-92.

Viallanes, H.(1892). Recherches sur la filtration de l'eau par les mollusques et applications a l'Ostreiculture et a l'Oceanographie. Compt. Rend. et Mem. Soc. Biol. 114 (2), 1386.

Vles, F.(1904). Locomotion de la Nucule. Bull. Soc. zool. Fr. T. 29./

Walford, L.A.(1946). A new graphic method of describing the growth of animals. Biol. Bull. Wood's Hole, 90.

Wasserlocs, E.(1911). Die Entwicklung der kiemen bei Cyclas cornea und andern Acephalen des Suseen Wassers. Zool. Jb. Bd. 31, Hft., 2.

Webb, M.H.(1930). An apparatus for recording the valve movements and the extrusion of dejects of oysters. J. Cons. int. Explor., % 5, (3), 361-382.

Welch, P.S.(1935). Limnology. McGraw Hill, N.Y. 1935.

Werner, B. (1939). Uber die Entwicklung und Artun terscheidung von Muschellarven des Nordsee planktons, unter besonderer Berucksichtigung der Schalentwicklung. Zool. Jb., Abt. Anat., 66, Heft. 1., 1-54, Jena.

Weymouth, F.W.(1923). The life history and growth of the Pismo clam (Tivella stultorum). Calif. Fish Game Bull. No.7, 120.

Weymouth, F.W., H.C. McMillin, H.B. Holmes.(1925). Growth and age at maturity of the Pacific razor clam, Siliqua patula (dixon). U.S. Bur. Fish. Doc. no.984, 41, 201-236.

Weymouth, F.W., H.C. McMillin, W.H. Rich.(1931). Latitude and relative growth in the razor clam, Siliqua patula. J. exp. Biol., 8.

Winckworth, R.(1931). On the growth of Panhia undulata (Veneridae). Proc. Malacol. Soc. Lond., 19, 115-116.

Wilson, D.P.(1936). The development of the Sabellid, Branchiomma vesiculosum. Quart, J. micr. Sci., 78, 543-603.

Wilson, D.P.(1937). The influence of the substratum on the metamorphosis of Notomastus larvae. J. Mar. biol. Ass. (n.s.), 22, 227-243.

Wright, F.S.(1927). A report on the Cockle beds and Cockle industry of England andWales. Fish. Invest. Series II, 9, no.5.

Yonge, C.M.(1923). The mechanism of feeding, digestion and assimilation in Mya. Brit. J. exp. Biol., 1, 15-64.

Yonge, C.M.(1926). Structure and function of the organs of feeding and digestion in Ostrea edulis. J. Mar. biol. Ass. U.K. 14, 295-386.

Yonge, C.M.(1937). The biology of Aporrhais pes-pelicani(L), and A. serresiana (Mich). J. Mar. biol. Ass.(n.s.), 21, no.2, 687-704.

Yonge, C.M.(1947). The pallial organs in the Aspidobranch Gastropoda and their evolution throughout the Mollusca. Philos. Trans. Series B, no.591, 232, 443-518.

Yonge, C.M.(1948). Formation of siphons in Lamellibranchia. Nature, 161 no.4084.

Ziegler, H.E.(1885). Die Entwickelung von Cyclas cornea Lam. (Sphaerium corneum L.). Z. wiss. Zool. Bd. 41, 525-569.

Zobell, C.E. & W.H. Landon.(1937). The bacterial nutrition of the California mussel. Proc. Soc. exp. Biol. and Med.

Appendix 4.

APPENDIX I. (FILTRATION)

The original "Spekker" drum readings and the logarithmic ratios of the converted readings

Time	Control		Experiment 1.		Time	Control		Experiment 2.	
	Drum Reading.	ln $\frac{P2}{P1}$	Drum Reading.	ln $\frac{P2}{P1}$		Drum Reading.	ln $\frac{P2}{P1}$	Drum Reading.	ln $\frac{P2}{P1}$
0	340	0	354	0	0	522	0	532	0
19	310	$\bar{1}$.8854	262	$\bar{1}$.6989	30	494	$\bar{1}$.9455	470	$\bar{1}$.8767
35	290	$\bar{1}$.8185	202	$\bar{1}$.4379	60	470	$\bar{1}$.8946	400	$\bar{1}$.7140
53	247	$\bar{1}$.6573	165	$\bar{1}$.2364	90	440	$\bar{1}$.8292	327	$\bar{1}$.5139
67	230	$\bar{1}$.5859	130	$\bar{2}$.9976	120	425	$\bar{1}$.7842	285	$\bar{1}$.3745
81	210	$\bar{1}$.4962	105	$\bar{2}$.7860	150	392	$\bar{1}$.7136	300	$\bar{1}$.4273
99	187	$\bar{1}$.3796	100	$\bar{2}$.7341	180	357	$\bar{1}$.6202	207	$\bar{1}$.0558
116	178	$\bar{1}$.3388	80	$\bar{2}$.5128	210	342	$\bar{1}$.5769	185	$\bar{2}$.9444
134	150	$\bar{1}$.1584	68	$\bar{2}$.3487	240	328	$\bar{1}$.5348	165	$\bar{2}$.8208
159			60	2.2280	270	320	1.5106	157	2.7792

Time	Control		Experiment 4.		Experiment 5.		Experiment 6.	
	Drum Reading.	ln P2/P1	Drum Reading.	ln P2/P1	Drum Reading.	ln P2/P1	Drum Reading.	ln P2/P1
0	0	0	031	0	025	0	050	0
47	060	$\bar{1}$.9381	565	$\bar{2}$.9381	583	$\bar{1}$.1514	479	$\bar{1}$.4166
77	122	$\bar{1}$.8699	743	$\bar{2}$.6731	760	$\bar{2}$.5976	748	$\bar{2}$.6720
107	177	$\bar{1}$.8052	819	$\bar{2}$.3223	810	$\bar{2}$.3652	832	$\bar{2}$.2684
137	223	$\bar{1}$.7477	858	$\bar{2}$.0799	855	$\bar{2}$.0962	868	$\bar{2}$.0267
167	271	$\bar{1}$.6839	883	$\bar{3}$.9443	853	$\bar{2}$.1095	888	$\bar{3}$.8629
197	300	$\bar{1}$.6433	900	$\bar{3}$.7899	863	$\bar{2}$.0339	900	$\bar{3}$.7462
227	343	$\bar{1}$.5332	913	$\bar{3}$.5876	878	$\bar{3}$.9205	903	$\bar{3}$.7172
257	363	$\bar{1}$.5490	910	$\bar{3}$.6237	885	$\bar{3}$.8629	895	$\bar{3}$.7927
287	387	1.5106	916	$\bar{3}$.5547	893	$\bar{3}$.7927	895	$\bar{3}$.7927

Time	Control		Experiment 7.		Experiment 8.		Experiment 9.	
	Drum Reading.	ln P2/P1	Drum Reading.	ln P2/P1	Drum Reading.	ln P2/P1	Drum Reading.	ln P2/P1
0	487	0	518	0	550	0	545	0
30	548	$\bar{1}$.8733	645	$\bar{1}$.6948	655	$\bar{1}$.7347	670	$\bar{1}$.6784
60	593	$\bar{1}$.7681	732	$\bar{1}$.4137	705	$\bar{1}$.5769	770	$\bar{1}$.3168
90	627	$\bar{1}$.6812	783	$\bar{1}$.2026	755	$\bar{1}$.3912	833	$\bar{2}$.9976
120	657	$\bar{1}$.5913	820	$\bar{1}$.0151	760	$\bar{1}$.3708	841	$\bar{2}$.9212
150	691	$\bar{1}$.4925	853	$\bar{2}$.8125	822	$\bar{1}$.0711	863	$\bar{2}$.7993
189	720	$\bar{1}$.3948	878	$\bar{2}$.6236	900	$\bar{2}$.4949	880	$\bar{2}$.6682
240	748	$\bar{1}$.2887	900	$\bar{2}$.4273	933	$\bar{2}$.0862	895	$\bar{2}$.5346
270	760	$\bar{1}$.2397	914	$\bar{2}$.2763	942	$\bar{3}$.9519	906	$\bar{2}$.4201
300	775	$\bar{1}$.1755	923	$\bar{2}$.1663	948	$\bar{3}$.8458	915	$\bar{2}$.3233
338	787	$\bar{1}$.1205	935	$\bar{3}$.9975	945	$\bar{3}$.8863	913	$\bar{2}$.3445

Time	Control		Experiment 10		Experiment 11		Experiment 12	
	Drum Reading.	ln $\frac{P_2}{P_1}$	Drum Reading.	ln $\frac{P_2}{P_1}$	Drum Reading.	ln $\frac{P_2}{P_1}$	Drum Reading.	ln $\frac{P_2}{P_1}$
0	373	0	400	0	415	0	407	0
30	450	$\bar{1}.8693$	563	$\bar{1}.6825$	633	$\bar{1}.5332$	610	$\bar{1}.5857$
60	500	$\bar{1}.7737$	667	$\bar{1}.4112$	785	$\bar{2}.9976$	730	$\bar{1}.2136$
90	581	$\bar{1}.5965$	800	$\bar{2}.9004$	840	$\bar{2}.7017$	804	$\bar{2}.8928$
120	630	$\bar{1}.4732$	846	$\bar{2}.6413$	863	$\bar{2}.5476$	843	$\bar{2}.6708$
150	667	$\bar{1}.3677$	870	$\bar{2}.4721$	880	$\bar{2}.4152$	862	$\bar{2}.5420$
180	700	$\bar{1}.2639$	895	$\bar{2}.2570$	890	$\bar{2}.3287$	880	$\bar{2}.4020$
210	723	$\bar{1}.1835$	910	$\bar{2}.1029$	890	$\bar{2}.3307$	890	$\bar{2}.3148$
240	739	$\bar{1}.1234$	919	$\bar{3}.9975$	898	$\bar{2}.2513$	900	$\bar{2}.2198$
270	759	$\bar{1}.0442$	930	$\bar{3}.7544$	905	$\bar{2}.1798$	910	$\bar{2}.1140$
300	762	$\bar{1}.0311$	930	$\bar{3}.8544$	911	$\bar{2}.1161$	918	$\bar{2}.0210$
330	781	$\bar{2}.9488$	940	$\bar{3}.6974$	922	$\bar{3}.9826$	922	$\bar{3}.9711$

Time	Control		Experiment 13		Experiment 14		Experiment 15	
	Drum Reading.	ln $\frac{P_2}{P_1}$	Drum Reading.	ln $\frac{P_2}{P_1}$	Drum Reading.	ln $\frac{P_2}{P_1}$	Drum Reading.	ln $\frac{P_2}{P_1}$
0	183	0	255	0	243	0	262	0
30	332	$\bar{1}.7985$	631	$\bar{1}.2988$	508	$\bar{1}.3930$	690	$\bar{1}.2534$
60	512	$\bar{1}.4841$	770	$\bar{2}.8256$	758	$\bar{2}.8606$	834	$\bar{2}.5216$
90	660	$\bar{1}.1229$	833	$\bar{2}.5039$	830	$\bar{2}.5039$	845	$\bar{2}.4393$
120	721	$\bar{2}.9256$	855	$\bar{2}.3632$	855	$\bar{2}.3448$	910	$\bar{3}.8963$
150	759	$\bar{2}.7792$	881	$\bar{2}.1656$	885	$\bar{2}.1161$	910	$\bar{3}.8963$
180	781	$\bar{2}.6832$	900	$\bar{3}.9916$	905	$\bar{3}.9805$	925	$\bar{3}.7172$
210	801	$\bar{2}.5877$	910	$\bar{3}.8861$	910	$\bar{3}.8714$	935	$\bar{3}.5696$
255	820	$\bar{2}.4859$	915	$\bar{3}.8284$	935	$\bar{3}.5454$	935	$\bar{3}.5696$
300	825	$\bar{2}.4582$	921	$\bar{3}.7557$	945	$\bar{3}.3786$	950	$\bar{3}.3077$

Time	Control		Experiment 16		Experiment 17		Experiment 18	
	Drum Reading.	ln $\frac{P2}{P1}$	Drum Reading.	ln $\frac{P2}{P1}$	Drum Reading.	ln $\frac{P2}{P1}$	Drum Reading.	ln $\frac{P2}{P1}$
0	292	0	211	0	245	0	203	0
20	276	$\bar{1}.9027$	327	$\bar{1}.8410$	383	$\bar{1}.7979$	315	$\bar{1}.8492$
40	364	$\bar{1}.7731$	515	$\bar{1}.5137$	557	$\bar{1}.4673$	420	$\bar{1}.6825$
60	453	$\bar{1}.6226$	640	$\bar{1}.2154$	645	$\bar{1}.2450$	527	$\bar{1}.4774$
90	542	$\bar{1}.4431$	675	$\bar{1}.1133$	695	$\bar{1}.0936$	618	$\bar{1}.2805$
120	600	$\bar{1}.3088$	795	$\bar{2}.8708$	730	$\bar{2}.9728$	666	$\bar{1}.1301$
150	636	$\bar{1}.2178$	787	$\bar{2}.6907$	750	$\bar{2}.8943$	720	$\bar{2}.9539$
180	660	$\bar{1}.1467$	822	$\bar{2}.5110$	765	$\bar{2}.8320$	760	$\bar{2}.7993$
210	673	$\bar{1}.1079$	842	$\bar{2}.3915$	780	$\bar{2}.7656$	759	$\bar{2}.7993$
240	690	$\bar{1}.0545$	860	$\bar{2}.2713$	795	$\bar{2}.6943$	785	$\bar{2}.6907$
270	294	$\bar{1}.0008$	880	$\bar{2}.1179$	808	$\bar{2}.6296$	808	$\bar{2}.5770$

Time	Control		Experiment 32		Experiment 33		Experiment 34	
	Drum Reading.	ln $\frac{P2}{P1}$	Drum Reading.	ln $\frac{P2}{P1}$	Drum Reading.	ln $\frac{P2}{P1}$	Drum Reading.	ln $\frac{P2}{P1}$
0	178	0	202	0	212	0	215	0
30	187	$\bar{1}.9586$	267	$\bar{1}.6333$	306	$\bar{1}.3878$	273	$\bar{1}.6238$
60	202	$\bar{1}.8857$	305	$\bar{1}.2964$	354	$\bar{2}.5923$	329	$\bar{1}.9426$
90	210	$\bar{1}.8445$	320	$\bar{1}.1248$	373	$\bar{2}.0592$	355	$\bar{2}.5865$
120	222	$\bar{1}.7793$	335	$\bar{2}.9165$	384	$\bar{2}.5364$	379	$\bar{2}.8248$
150	230	$\bar{1}.7355$	350	$\bar{2}.6540$	395	$\bar{2}.3724$	392	$\bar{2}.8593$

Time	Control		Experiment 35		Experiment 36		Experiment 37	
	Drum Reading.	ln $\frac{P2}{P1}$	Drum Reading.	ln $\frac{P2}{P1}$	Drum Reading.	ln $\frac{P2}{P1}$	Drum Reading.	ln $\frac{P2}{P1}$
0	175	0	180	0	180	0	182	0
30	192	$\bar{1}.9812$	202	$\bar{1}.8948$	232	$\bar{1}.7321$	216	$\bar{1}.8304$
60	202	$\bar{1}.8722$	242	$\bar{1}.6698$	270	$\bar{1}.4740$	257	$\bar{1}.5784$
90	219	$\bar{1}.7624$	288	$\bar{1}.3249$	303	$\bar{1}.1813$	303	$\bar{1}.1903$
120	230	$\bar{1}.7198$	340	$\bar{2}.7005$	333	$\bar{2}.8125$	333	$\bar{2}.8191$
150	247	$\bar{1}.6143$	360	$\bar{2}.2950$	351	$\bar{2}.4904$	355	$\bar{2}.4151$
180	265	$\bar{1}.4892$	374	$\bar{3}.8646$	363	$\bar{2}.1862$	367	$\bar{2}.1095$
210	272	$\bar{1}.4361$	377	$\bar{3}.7423$	366	$\bar{2}.1292$	370	$\bar{2}.1095$
240	287	$\bar{1}.3461$	380	$\bar{3}.6012$	371	$\bar{3}.9759$	371	$\bar{3}.9826$

Time	Control		Experiment 38		Experiment 39		Experiment 40	
	Drum Reading.	ln $\frac{P2}{P1}$	Drum Reading.	ln $\frac{P2}{P1}$	Drum Reading.	ln $\frac{P2}{P1}$	Drum Reading.	ln $\frac{P2}{P1}$
0	149	0	167	0	167	0	160	0
30	171	$\bar{1}.9084$	244	$\bar{1}.5980$	264	$\bar{1}.4618$	246	$\bar{1}.5568$
60	192	$\bar{1}.8122$	288	$\bar{1}.2674$	314	$\bar{1}.0028$	275	$\bar{1}.3480$
90	205	$\bar{1}.7486$	323	$\bar{2}.8922$	334	$\bar{2}.7384$	305	$\bar{1}.0736$
120	235	$\bar{1}.5801$	351	$\bar{2}.4407$	361	$\bar{2}.2120$	328	$\bar{2}.7960$
150	250	$\bar{1}.4848$	359	$\bar{2}.2627$	375	$\bar{3}.7680$	334	$\bar{2}.7020$
210	284	$\bar{1}.2278$	389	$\bar{3}.5042$	389	$\bar{3}.9466$	356	$\bar{2}.3017$
240	294	$\bar{1}.1377$	384	$\bar{3}.3220$	395	$\bar{3}.1579$	360	$\bar{2}.2102$
270	307	$\bar{1}.0084$	389	$\bar{3}.9466$	395	$\bar{3}.1579$	365	$\bar{2}.0339$

Appendix 2.

Frequency Distributions of Ring Lengths from Random Samples from Cross Houses Beach 1946 - 47.

Class Interval R. 1.	Frequency.	Class Interval R. 2.	Frequency.	Class Interval R. 3.	Frequency.	Class Interval R. 4.	Frequency.
5 - 9	9	65 - 69	16	140 - 144	7	235 - 239	7
10 - 14	53	70 - 74	49	145 - 149	41	240 - 244	35
15 - 19	48	75 - 79	57	150 - 154	51	245 - 249	42
20 - 24	66	80 - 84	64	155 - 159	46	250 - 254	53
25 - 29	100	85 - 89	74	160 - 164	67	255 - 259	66
30 - 34	97	90 - 94	79	165 - 169	69	260 - 264	65
35 - 39	93	95 - 99	90	170 - 174	76	265 - 269	50
40 - 44	70	100 - 104	100	175 - 179	83	270 - 274	72
45 - 49	57	105 - 109	115	180 - 184	89	275 - 279	51
50 - 54	57	110 - 114	114	185 - 189	69	280 - 284	80
55 - 59	28	115 - 119	126	190 - 194	98	285 - 289	65
60 - 64	19	120 - 124	93	195 - 199	80	290 - 294	57
65 - 69	10	125 - 129	98	200 - 204	73	295 - 299	59
70 - 74	5	130 - 134	87	205 - 209	82	300 - 304	60
75 - 79	2	135 - 139	68	210 - 214	79	305 - 309	51
80 - 84	2	140 - 144	58	215 - 219	78	310 - 314	46
		145 - 149	54	220 - 224	67	315 - 319	49
		150 - 154	52	225 - 229	49	320 - 324	38
		155 - 159	32	230 - 234	35	325 - 329	26
		160 - 164	24	235 - 239	41	330 - 334	31
		165 - 169	15	240 - 244	47	335 - 339	24
		170 - 174	13	245 - 249	39	340 - 344	12
		175 - 179	2	250 - 254	37	345 - 349	17
				255 - 259	28	350 - 354	11
				260 - 264	22	355 - 359	9
				265 - 269	16	360 - 364	5
				270 - 274	9	365 - 369	2
				275 - 279	7		

Appendix B.

Frequency Distributions of Ring Lengths from Random Samples from Cross Houses Beach 1946 - 47.

Class Interval R. 5.	Frequency.	Class Interval R. 6.	Frequency.	Class Interval R. 7.	Frequency.	Class Interval R. 8.	Frequency.
285 - 289	2	335 - 339	3			350 - 354	1
290 - 294	7	340 - 344	20	340 - 344	7	355 - 359	
295 - 299	18	345 - 349	30	345 - 349	3	360 - 364	
300 - 304	40	350 - 354	32	350 - 354	8	365 - 369	1
305 - 309	37	355 - 359	38	355 - 359	8	370 - 374	1
310 - 314	32	360 - 364	32	360 - 364	9	375 - 379	1
315 - 319	55	365 - 369	37	365 - 369	19	380 - 384	2
320 - 324	55	370 - 374	39	370 - 374	15	385 - 389	2
325 - 329	41	375 - 379	32	375 - 379	18	390 - 394	1
330 - 334	68	380 - 384	35	380 - 384	23	395 - 399	6
335 - 339	43	385 - 389	14	385 - 389	14	400 - 404	6
340 - 344	57	390 - 394	20	390 - 394	21	405 - 409	4
345 - 349	54	395 - 399	19	395 - 399	8	410 - 414	4
350 - 354	44	400 - 404	15	400 - 404	23	415 - 419	4
355 - 359	40	405 - 409	16	405 - 409	17	420 - 424	6
360 - 364	38	410 - 414	11	410 - 414	24	425 - 429	6
365 - 369	32	415 - 419	17	415 - 419	17	430 - 434	8
370 - 374	18	420 - 424	5	420 - 424	6	435 - 439	2
375 - 379	22	425 - 429	6	425 - 429	9	440 - 444	4
380 - 384	16	430 - 434	2	430 - 434	14	445 - 449	2
385 - 389	12	435 - 439		435 - 439	7	450 - 454	2
390 - 394	13	440 - 444	2	440 - 444	3	455 - 459	3
395 - 399	3			445 - 449	3	460 - 464	2
400 - 404	3			450 - 454	3		
405 - 409	1						
410 - 414	2						

Appendix 2 - C

Statistics of length distributions of Ring 1 measurements (in mm.) from bi-monthly samples of Vaporepis from Cross Houses March 1956 - 57.

Date	Sample size	Range	Mean	Variance	Standard Deviation	Standard Error
Sept.56	121	0.7 - 7.7	3.37	0.667	1.067	0.097
Oct. 56	45	0.7 - 5.2	3.02	0.353	0.593	0.132
Oct. 56	116	0.7 - 6.2	2.92	0.772	1.364	0.127
Dec. 56	19	1.7 - 5.7	3.41	0.521	1.104	0.260
Feb. 57	19	1.7 - 6.7	4.38	0.896	1.425	0.335
Mar. 57	30	1.2 - 6.7	3.93	0.690	1.294	0.184
Apr. 57	64	1.7 - 8.2	4.58	1.112	1.635	0.206
May 57	55	1.2 - 6.7	4.38	0.636	1.248	0.169
June 57	115	0.7 - 5.7	3.04	0.782	1.353	0.126
July 57	55	1.2 - 6.7	3.52	0.718	1.338	0.180
Aug. 57	64	0.7 - 6.7	3.09	1.162	1.525	0.190
Sept.57	68	1.2 - 6.2	3.25	0.705	1.349	0.161

D

Statistics of length distributions of Ring 2 measurements (in mm.) from mid-monthly samples of Venerupis from Cross Roads Beach 1946 - 47.

Date	Sample size	Range	Mean	Variance	Standard Deviation	Standard Error
Sept.46	241	6.7 - 17.2	11.68	2.829	2.615	0.168
Oct. 46	88	6.7 - 17.2	11.28	2.360	2.393	0.256
Oct. 46	245	6.7 - 17.2	11.77	2.390	2.331	0.155
Dec. 46	78	7.7 - 15.2	11.87	1.338	1.799	0.205
Feb. 47	69	6.7 - 16.7	11.33	3.134	2.704	0.334
Mar. 47	124	6.7 - 17.2	11.72	2.976	2.676	0.242
Apr. 47	142	6.7 - 16.2	12.15	2.043	2.216	0.186
May 47	145	7.2 - 17.2	11.93	2.411	2.336	0.194
June 47	115	7.2 - 15.7	10.75	2.046	2.217	0.208
July 47	83	6.7 - 14.7	11.06	1.344	1.828	0.201
Aug. 47	76	6.7 - 15.2	10.29	2.257	2.125	0.233
Sept.47	99	6.7 - 14.7	10.03	1.811	2.020	0.214

Statistics of length distributions of Ring 3 measurements (in mm.) from mid-monthly samples of Venerupis from Cross Houses Beach 1946 - 47.

Date	Sample size	Range	Mean	Variance	Standard Deviation	Standard Error
Sept.46	232	15.2 - 27.7	21.08	3.634	2.491	0.196
Oct. 46	90	14.7 - 27.7	19.55	4.303	3.166	0.335
Oct. 46	263	14.2 - 27.7	19.76	4.590	3.359	0.207
Dec. 46	96	15.2 - 26.2	21.17	3.368	2.362	0.293
Feb. 47	78	15.2 - 26.2	21.42	2.980	2.632	0.298
Mar. 47	120	14.7 - 27.7	20.33	4.090	3.134	0.237
Apr. 47	134	14.7 - 27.2	20.40	4.402	3.242	0.281
May 47	139	14.7 - 26.7	20.76	3.518	2.465	0.252
June 47	110	14.7 - 25.7	19.73	3.280	2.363	0.274
July 47	110	14.2 - 25.7	18.74	3.659	2.368	0.274
Aug. 47	73	14.7 - 24.2	18.48	2.510	2.409	0.282
Sept.47	76	14.7 - 24.2	18.59	2.372	2.335	0.269

F

Statistics of length distributions of Ring 4 measurements (in mm.) from mid-monthly samples of Venerupis from Cross Houses Beach 1946 - 47.

Date	Sample size	Range	Mean	Variance	Standard Deviation	Standard Error
Sept.46	176	23.7 - 26.7	29.88	4.315	3.284	0.248
Oct. 46	62	24.2 - 35.7	28.70	4.009	3.001	0.384
Oct. 46	177	24.2 - 36.2	29.27	3.895	3.119	0.235
Dec. 46	86	24.2 - 35.7	29.64	3.066	2.768	0.300
Feb. 47	64	24.2 - 33.2	27.48	2.654	2.539	0.319
Mar. 47	17	24.2 - 32.2	27.91	1.761	2.078	0.266
Apr. 47	115	24.7 - 35.7	29.19	3.400	2.910	0.272
May 47	105	24.2 - 33.7	28.74	2.291	2.349	0.230
June 47	75	24.2 - 35.7	28.30	3.597	2.996	0.348
July 47	54	24.2 - 34.2	28.23	3.159	2.640	0.362
Aug. 47	49	24.2 - 34.2	27.66	2.697	2.383	0.344
Sept.47	47	24.2 - 32.7	27.19	2.309	2.322	0.342

Statistics of length distributions of Ring 5 measurements (in mm.) from mid-monthly samples of Venerupis from Cross Houses Beach 1946 - 47.

Date	Sample size	Range	Mean	Variance	Standard Deviation	Standard Error
Sept.46	125	28.7 - 41.2	33.78	3.387	2.908	0.261
Oct. 46	39	29.2 - 37.7	32.71	1.979	2.165	0.351
Oct. 46	116	29.7 - 39.2	34.40	2.447	2.445	0.228
Dec. 46	62	30.2 - 38.2	34.62	1.535	1.957	0.250
Feb. 47	42	30.2 - 41.2	35.58	3.402	2.798	0.437
Mar. 47	39	29.7 - 37.7	33.17	1.820	2.133	0.346
Apr. 47	85	29.7 - 40.2	34.58	1.240	1.721	0.188
May 47	74	29.7 - 39.2	34.01	1.790	2.091	0.245
June 47	45	29.7 - 38.2	33.92	2.014	2.249	0.339
July 47	45	30.2 - 39.2	33.44	2.328	2.409	0.361
Aug. 47	42	29.7 - 38.2	32.81	1.535	1.692	0.264
Sept.47	43	29.7 - 38.2	33.43	2.084	2.202	0.339

Statistics of length distributions of Ring 6 measurements (in mm) from mid-monthly samples of Venerupis from Cross Houses Beach 1946 - 47.

Date	Sample size	Range	Mean	Variance	Standard Deviation	Standard Error
Sept.46	80	33.7 - 43.2	37.71	2.556	2.481	0.279
Oct. 46	20	34.7 - 40.2	36.92	1.645	1.699	0.389
Oct. 46	61	34.2 - 42.7	37.60	0.781	1.263	0.163
Dec. 46	32	35.7 - 42.2	38.73	1.400	1.793	0.322
Feb. 47	31	33.7 - 43.2	38.79	2.796	2.613	0.477
Mar. 47	20	34.7 - 38.7	36.27	1.245	1.710	0.391
Apr. 47	55	34.2 - 44.2	38.17	2.013	2.233	0.305
May 47	56	34.2 - 39.2	37.02	0.950	1.383	0.186
June 47	25	34.2 - 41.7	38.64	2.072	2.233	0.455
July 47	25	34.2 - 41.7	33.70	2.042	2.258	0.451
Aug. 47	32	34.2 - 40.2	36.52	0.834	1.278	0.232
Sept.47	25	34.2 - 42.7	38.16	2.176	2.269	0.453

Statistics of length distributions of Ring 7 measurements (in mm.) from mid-monthly samples of Venerupis from Cross Houses Beach 1946 - 47.

Date	Sample size	Range	Mean	Variance	Standard Deviation	Standard Error
Sept. 46	54	34.2 - 45.2	39.19	4.309	2.966	0.407
Oct. 46	10	35.2 - 41.2	39.11			
Oct. 46	43	34.2 - 45.2	39.26	3.204	2.829	0.436
Dec. 46	16	37.7 - 44.7	41.10	2.131	2.123	0.545
Feb. 47	21	34.7 - 44.2	39.41	3.200	2.813	0.625
Mar. 47	19	34.2 - 43.2	38.64	2.736	2.615	0.615
Apr. 47	26	36.2 - 43.7	40.23	1.292	1.797	0.359
May 47	34	35.7 - 41.7	38.72	1.005	1.514	0.263
June 47	13	34.1 - 45.0	40.36			
July 47	14	35.2 - 47.2	39.55			
Aug. 47	20	35.2 - 41.7	38.87	1.265	1.753	0.39[illegible]
Sept. 47	17	36.7 - 43.2	40.52	2.058	2.113	0.5[illegible]

Statistics of length distributions of Ring 8 measurements (in mm.) from mid-monthly samples of Venerupis from Cross Rousea Beach 1946 - 47.

Date	Sample size	Range	Mean	Variance	Standard Deviation	Standard Error
Sept.46	23	37.2 - 44.2	40.32	1.865	2.134	0.455
Oct. 46	14	35.2 - 46.3	42.37			
Oct. 46						
Dec. 46	5	41.6 - 44.5	42.65			
Feb. 47	7	37.0 - 46.3	40.71			
Mar. 47						
Apr. 47	7	39.7 - 45.7	42.05			
May 47	12	36.9 - 44.7	40.87			
June 47	6	39.4 - 45.3	42.50			
July 47	6	38.9 - 45.6	42.38			
Aug. 47						
Sept.47						

Appendix 3.

Digging Movements.

The literature on digging movements of lamellibranchs is not extensive and other than the work of Drew (1906) on Ensis directus and Jordan (1915) on Mactra inflata, there is little of significance until the extensive investigations of Fraenkel (1927) on the Solenidae. Later, Stoll (1938), gave brief descriptions of methods of locomotion in various species. Drew (1898), Morse (1913), Vles (1904) and Stoll (1938) have described locomotion in various protobranchs. Of all lamellibranchs, the Solenidae lend themselves best to a study of locomotion because they are probably the most active and rapidly burrowing, and it is possible to induce movement of the foot by stimulation (Fraenkel, 1927). This is impossible in species such as V. pullastra in which almost any type of stimulation causes immediate contraction, generally accompanied by closure of the shells. While the nerve-muscle physiology of movement in V. pullastra was not studied, the general pattern of digging movements was observed and the results may be of some interest.

When V. pullastra is removed from its burrow and is allowed to remain undisturbed for some time on any surface, the shells open and efforts are made to burrow. If the substratum is too hard for the foot or the shell to penetrate, horizontal movements result; but if the substratum is soft enough for penetration, then the same/

/some sequence of movements allows the animal to burrow. Unless the animal is moved from its burrow, it appears that the amount of movement in nature is relatively little. The typical habitat is under rather flattish angular stones (see Pl.23, fig.1) covering shallow pockets of sand and gravel. Nearly all animals are attached to some solid object, a stone or a shell, by a byssus. This thread is single proximally where it leaves the foot; distally where it is attached to the holdfast, it is divided into several strands. There is an affinity for crevices, or against overhanging rocks whose base is buried deeply enough. Most animals are buried an inch or two below the surface, but a number may be found with at least part of the shell showing and some may have Pomatoceros triqueter growing on them.

In nature the orientation is variable. The animals lie with the transverse andlongitudinal axes in various planes. When they are allowed to burrow into pure sand they assume a position with the dorsal margin of the shell nearly parallel with the surface.

The digging movements have been observed many times in all sizes of animals from the youngest spat to the largest adult in sand, mud, gravel, powdered glass and on flat surfaces. In every case, regardless of the position and the environment, there was an inevitable sequence of movements.

Using the medium of sand, in which the movements are best executed, assuming the animal to be imbedded just deeply enough to prevent it falling over, and with the long axis parallel to the surface of the sand; the sequence of movements is as follows:

1. The valves are opened.

2. The foot is protruded, pointed with a probing motion. This back and forth searching motion is continued until the foot is fully extended. The tip of the foot may extend to a length equal to that of the animal. The degree of vertical penetration in this phase may vary considerably and is partly dependent on the type of substratum. (Pl.50, fig.a).

3. The heel of the foot is protruded ventrally. (Pl.50, fig.b).

4. The heel expands both laterally and posteriorly, so that, coupled with the anterior extension of the foot, an anchor is formed. If the substratum is firm enough, the foot maintains this position and the shell moves.

5. The valves open slightly.

6. The two siphonal apertures close, and the adductor muscles contract reducing the volume of the mantle cavity forcing out the excess water in a stream from the anterior end just below the adductor muscle. Presumably the pallial curtain maintains a seal around the foot and the remainder of the mantle edge during this operation./

Almost immediately the anterior pedal retractors contract and the posterior retractors relax, causing the anterior end of the shell to dip down and the posterior to rise upward. It is probable, and this description of the play of the muscles is only conjectural, that contraction of the anterior retractors is confined to that part near its insertion into the shell. (Pl.50, fig.c).

7. The final movement now takes place as the shell moves forward and down. The foot remains in its position of anchorage and the more distal portion of the anterior retractors now comes into action and the body is drawn forward. At the same time elements of the posterior retractors running downward and forward to the base of the foot contract, so assisting in the movement. (Pl.50, fig.d).

In Plate 50 the lines 'XX' and 'YY' are vertical and horizontal reference lines respectively. In figs. b, c and d, the foot is in relatively the same position and the shell and body have moved in relation to this. The figures are diagrammatic.

This sequence of movements is repeated until the animal reaches the required depth. Kymograph recordings, an example of which is shown in Pl.34 fig.3, substantiate the analysis given above. The recording reads from left to right and the kymograph arrangement was such that a downward movement of the animal is shown in an /

/an upward movement of the tracing pen. The attachment of the shell was on its anterior lateral area, so the maximum downward movement is recorded. It is difficult to compare the kymograph tracings of digging movements in Y. pullastra and in Solen (Fraenkel, 1927), for the latter was held in a clamp and vertical movements of the foot recorded.

In the tracing Pl.34, fig.3, will be noticed a slight dip of the pen just prior to the long upstroke. This is interpreted as a slight relaxation of the adductor muscles, allowing the valves to gape slightly and in this way loosening the sand around the shells. Then follows the sharp upsweep of the pen showing the downward movement of the "nose" of the animal (Movement 6), (Pl.30, fig.e). The "nose" very rapidly tips up again allowing the pen to drop. This upward movement slows down in its later stages, and the beginning of the next sequence may be under way before the animal has come to rest, as shown by the horizontal lines in the first few sequences of Pl.34, fig.3. One vertical sweep of the pen up and down, plus the following horizontal line, constitutes a sequence. This term is analogous to the "Grabstufe" of Fraenkel (1927). The initial probing of the foot he terms, "Grabschritt", and a number of "Grabschritt" form a "Grabstufe." In turn, a number of "Grabstufe" form a "Grabperiode", which presumably ends when the animal reaches the required depth in the sand./

In the description of Movement 6 is mentioned the stream of water that is forced out of an anterior separation of the pallial curtains. The valve closure responsible for this is not represented on the tracing because it appears to be coincident with the downward movement of the "nose", and as closure of the valves would result in an upward movement of the pen, the two movements are no doubt incorporated. The purpose of this current has been interpreted, first by Drew (1906) for Ensis directus, and later by Jordan (1915) for Mactra inflata, Fraenkel (1927) for the Solenidae, and Stoll (1937, 1938) for several lamellibranchs, as serving to loosen the sand in front of the animal to allow easier penetration. Certainly in V. pullastra the jet is powerful, for a considerable disturbance is created in the sand even when the animal is at some depth. There appears to be no good reason to doubt the interpretation of the above authors.

An analysis of six kymograph recordings of digging movements, given in Table 23, shows that once digging has begun, the average time for each sequence is 2.42 minutes. The average number of consecutive sequences is 17, and the mean extent of the initial downward movement is 1.8 mm. The effective downward movement is appreciably less than this due to the lift of the anterior end in the second phase of the sequence, but the extent is variable depending on the type of substratum.

Horizontal Movement./

TABLE 1.

Experiment	Length of animal in m.m.	Date	Av. time between sequence (in minutes)	No. of consecutive movement sequences	Average Extent of downward movement in 1st phase in (m.m.)	Maximum downward movement in 1st phase in (m.m.)	Temp. ^{o} C.
2	41.3	10.9.46	3.00	16 - 33	1.2	2.6	15.2
3	41.3	10.9.46	2.44	15	1.5	2.4	15.2
4	41.3	10.9.46	2.60	11	3.0	3.7	15.2
5	40.0	14.9.46	1.90	18	1.2	2.7	13.5
6	40.0	14.9.46	2.00	18	2.3	4.0	14.8
8	44.7	17.9.46	2.60	6	1.7	3.0	14.0

Horizontal Movement.

When V. pullastra is first placed in an aquarium tank with suitable substratum, the first reaction is to burrow which it does rapidly. During the first period of darkness, however, many of the smaller animals return to the surface and move about considerably, as shown by the long furrows cut on the surface of the sand. Whether there is an actual 'darkness' effect is debatable for the animals may have returned to the surface in any event, but this point was not investigated. The travel movement is accomplished by the same sequence used in digging, except that the initial dip of the anterior end is not so extensive. If the sand is very loose many of the larger animals have difficulty in obtaining the initial anchorage for the anterior end of the shell. That is, once the "nose" of the clam is buried, the rather flattened lunule region forms a pressure plate, and the weight of the sand on it holds it steady as the posterior end is pulled down. If the initial anchorage is not obtained the animal will plough along the surface for some distance before the "nose" gets a grip.

Discussion.

It has been shown that the digging movements consist of strict and undeviating sequence of movements, which involve fine synchronisation of the adductor muscles, the retractor muscles and the muscles of the foot. The role of the blood system in contributing to the pedal/

/pedal activities has not been investigated. Drew (1906) and Fraenkel (1927) have shown that the blood assists in pedal movements, but the latter author has shown that blood pressure plays only a minor role in comparison to the musculature in inducing changes in the form of the foot. However, in Y. pullastra, there is not the rapid and extensive changes such as occurs in Solen, and the extension of the tip and heel of the foot forms an anchor, rather than the exclusive swelling of the tip as in Solen.

The stimulation which causes burrowing has not been determined, other than that it occurs whenever the animal is not buried. \ Also, what is the stimulus which causes the animal to stop burrowing? Fraenkel believes it is not necessary to assume a nervous inhibition, but that the cessation of digging movements occurs as a result of fatigue, but this is hardly likely with Y. pullastra, which will burrow repeatedly, though the period of shell closure caused by the removal from the sand may serve for recuperation. However, the amount of muscular activity in the two species is hardly comparable, nor is the time required for burrowing. Fraenkel (1927) found that Solen orientates itself in a direction which corresponds approximately to the direction of the resultant of the centrifugal force and the force of gravity. Y. pullastra may be found orientated in nature in nearly every conceivable manner./

The same applies to their orientation in an aquarium with a homogeneous substratum such as sand. No experiments with centrifugal force were tried.

Stimulations of the siphons and mantle in Y. pallastra invariably cause shell closure. Similar stimulation in Solen, according to Fraenkel (1927), nearly always initiates digging movements, and he determined by elimination experiments that the visceral ganglion plays an important role in the release of digging movements, but the cerebral ganglion was ascertained to be the actual nerve centre for the movements. With the different effect of mantle and siphonal stimulation, it would be interesting to investigate nervous control of the movements in Y. pallastra.

SOME ASPECTS OF THE BIOLOGY OF *VENERUPIS PULLASTRA* (MONTAGU).

By

D.B. Quayle

Volume II

Plates

A thesis presented to the University of Glasgow for the degree of Ph.D. May, 1948.

Plate 1.

Figure 1. Larva just out of the straight hinge stage. 168 u. x 144 u.

Figure 2. Larva. Early umbo. 204 u. x 180 u.

Figure 3. Larva just before metamorphosis 260 u. x 240 u.

Figure 4. Internal view of right valve of a veliger showing the hinge area and teeth. 256 u. x 238 u.

Figure 5. Hinge area of right valve of larva. 227 u. x 209 u. Internal view.

Figure 6. Hinge area of left valve of larva. 227 u. x 209 u. Internal view.

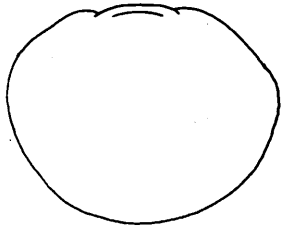


FIG. 1

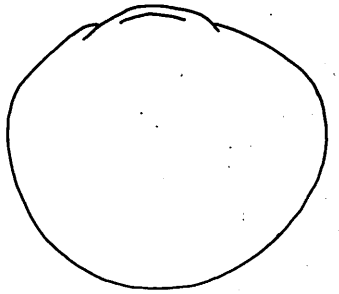


FIG. 2

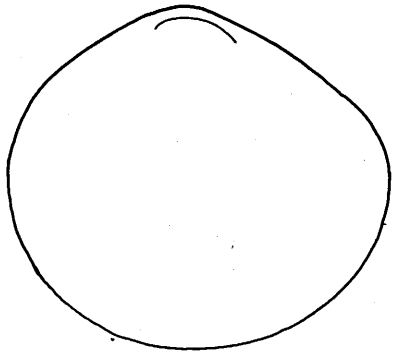


FIG. 3

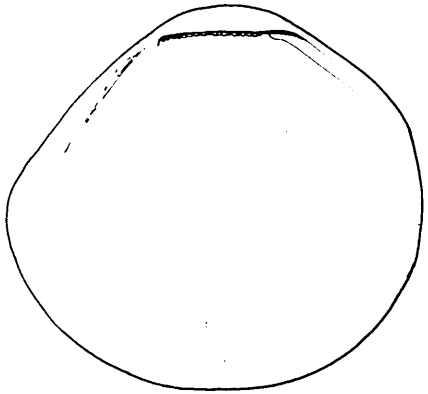


FIG. 4

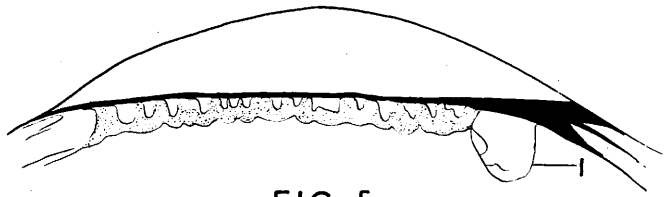


FIG. 5

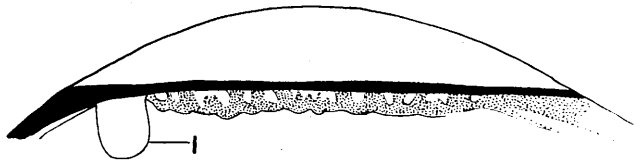


FIG. 6

PLATE I

Plate 2.

Figure 7. Photomicrograph of complete veliger from the left side. Length 240 u.

Figure 8. Photomicrograph of the external view of both valves of a veliger, 225 u. in length. Prod. 1 is the light unringed area inside the hinge and umbo.

Figure 9. Photomicrograph of the internal view of hinge area of the right valve of a veliger, showing the hinge teeth and ligament. x 400.

Figure 10. Photomicrograph of the external view of the left valve of a spat 0.4 mm. long by 0.35 mm. high.

Figure 11. Photomicrograph of the external view of the right valve of a spat 0.3 mm. in length. Note the difference in density between Prod. 11 and the dissoconch.

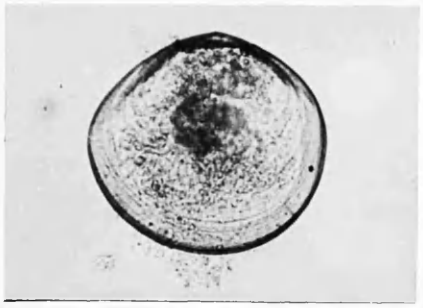


FIG. 7

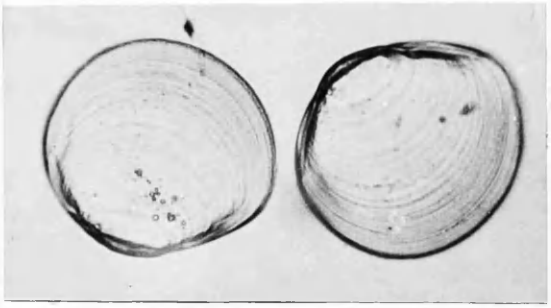


FIG. 8

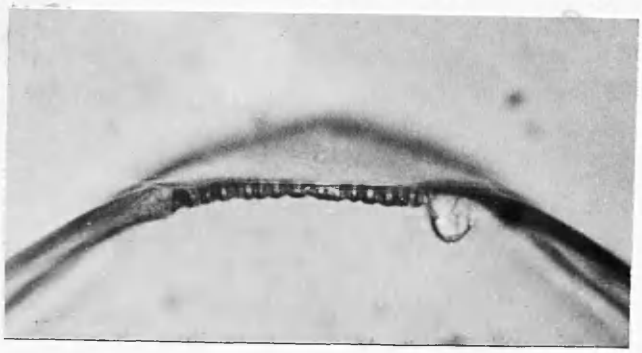


FIG. 9

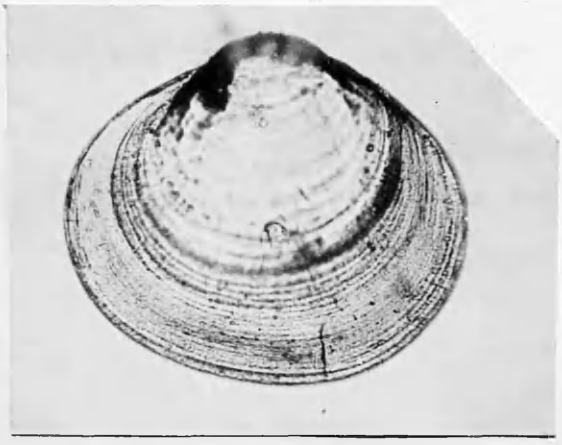


FIG. 10

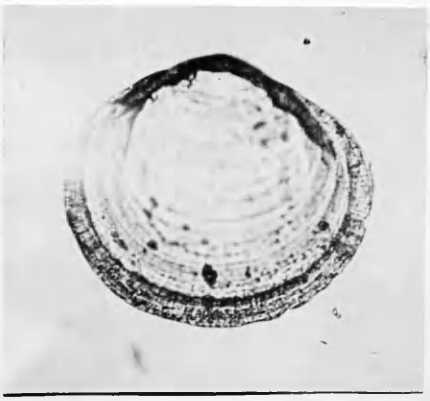


FIG. 11

Plate 3.

Map showing Little Cumbrae Island and Great Cumbrae Island, with some of the landmarks and Stations mentioned in the text. The 10 and 20 fathom depth contours are shown.

Legend.

A - Location of spat sampling stations.
B - Keppel Pier.
C - Shore pumping Station on Keppel Point.
D - Plankton Station off Keppel Pier, August 26th-28th, 1947.
E - Approximate location of the Lion Rock.
F - Sampling Station for Vertical Series, August 22nd, 1947.
G - Hunterston Perch.
H - Location of Cross Houses Beach.

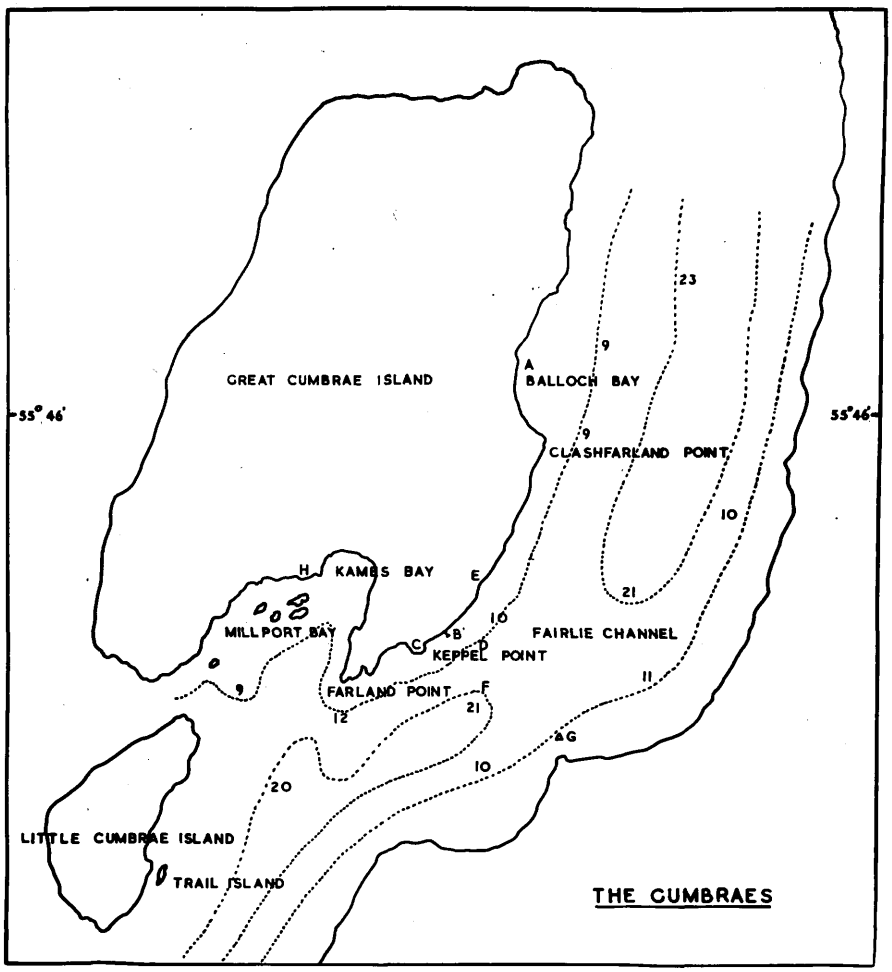

GREAT CUMBRAE ISLAND
A
BALLOCH BAY
CLASHFARLAND POINT
55° 46'
55° 46'
23
9
9
10
21
H
KAMES BAY
E
MILLPORT BAY
C
B
D
KEPPEL POINT
FAIRLIE CHANNEL
16
9
FARLAND POINT
F
12
21
11
G
10
20
LITTLE CUMBRAE ISLAND
TRAIL ISLAND
THE CUMBRAES

Plate 4.

Graph showing the seasonal variation in the number of larvae as shown by pump samples from Keppel Pier and Keppel Point during the breeding season of 1947. The mean weekly temperatures at the surface at Keppel Pier, and the tidal series for the period, are shown. The temperature data was supplied by the B.I.S.R.A., and the Tidal data is from the Admiralty Tide Tables, 1947.

PLATE 4

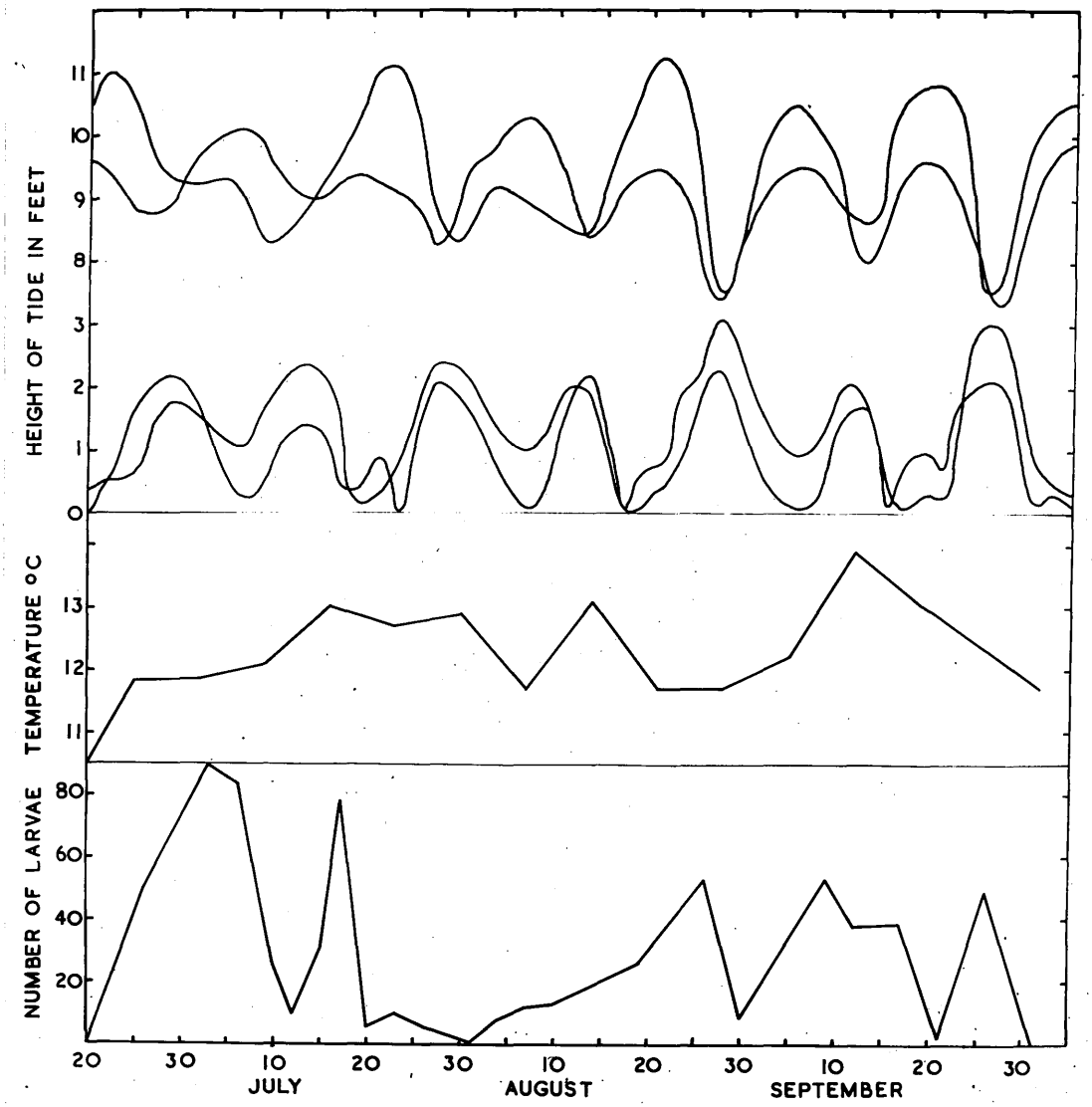

HEIGHT OF TIDE IN FEET
11
10
9
8
3
2
1
0
TEMPERATURE °C
13
12
11
NUMBER OF LARVAE
80
60
40
20
20
30
10
20
30
10
20
30
10
20
30
JULY
AUGUST
SEPTEMBER

Plate 5.

Graph showing the number of larvae in pump samples of 2 cubic metres, taken at various depths down to 40 metres, from a Station in Fairlie Channel, August 22nd, 1947. Data from Table 2.

PLATE 5

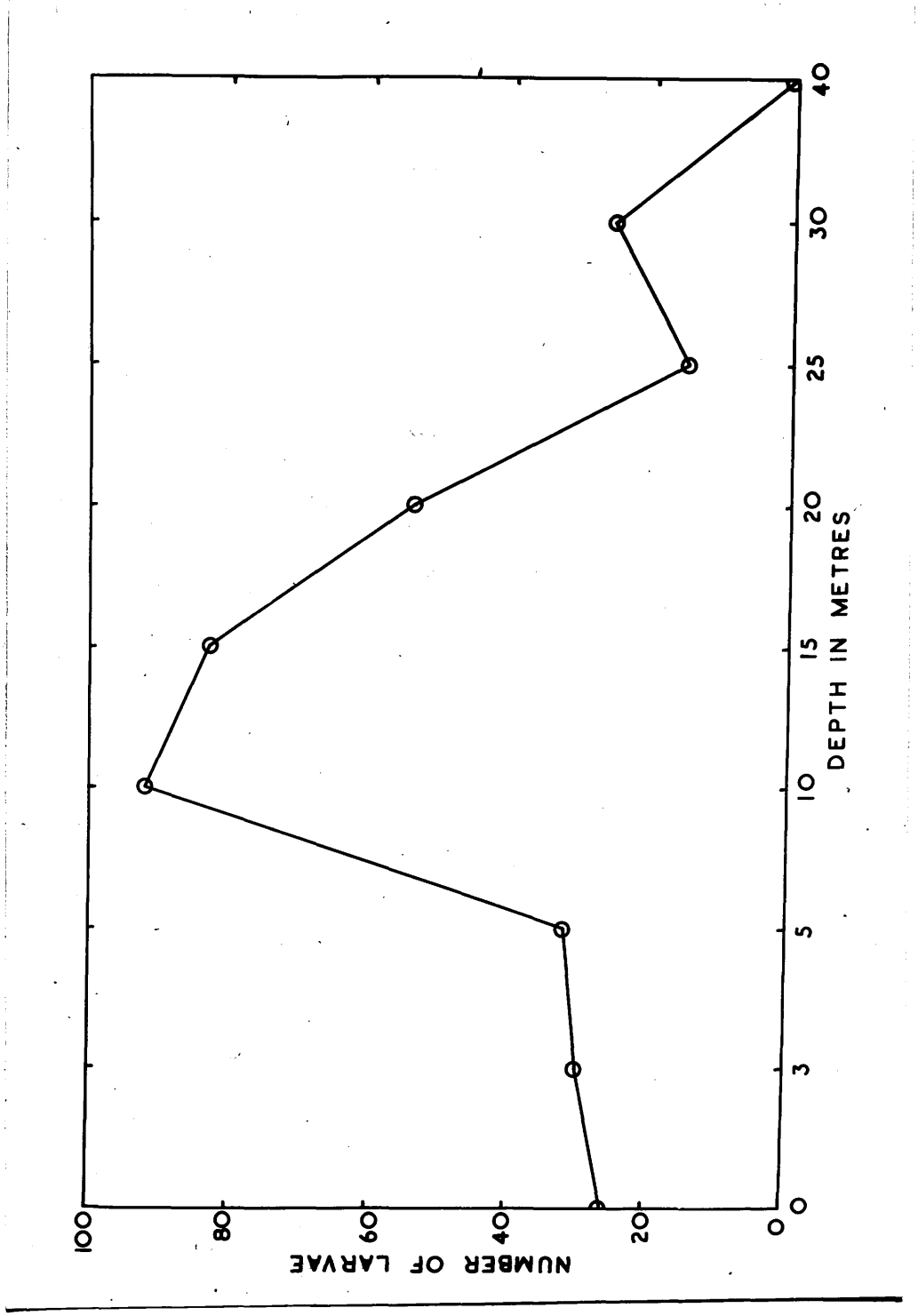

NUMBER OF LARVAE
100
80
60
40
20
0
0
3
5
10
15
20
25
30
40
DEPTH IN METRES

Plate 6.

Graph showing the number of larvae per 2 cubic metres of pumped water from the Keppel Point Shore Station, 14th-16th August, 1947. The periods of darkness and the rise and fall of the tide are shown. Data from Table 3.

PLATE 6

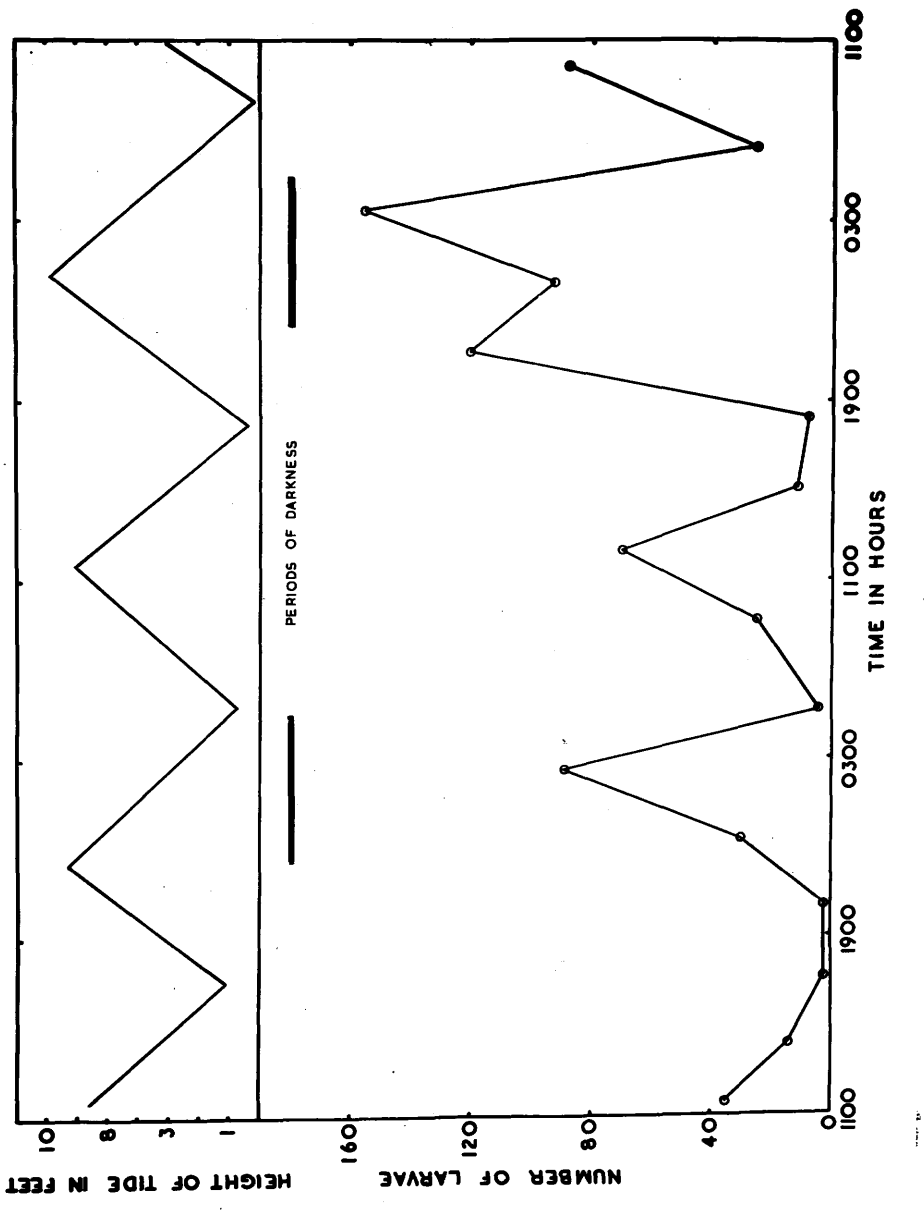

HEIGHT OF TIDE IN FEET
10
8
3
1
NUMBER OF LARVAE
160
120
80
40
0
PERIODS OF DARKNESS
1100
1900
0300
1100
1900
0300
1100
TIME IN HOURS

Plate 7.

Graph showing the number of larvae from 2 cubic metres of pumped water from a Station off Keppel Pier in Fairlie Channel, August 26th-28th, 1947. In addition are shown the rise and fall of the tide and the periods of darkness. The broken line represents the 12 metre samples, and the solid line the surface samples. Data from Table 4.

PLATE 7

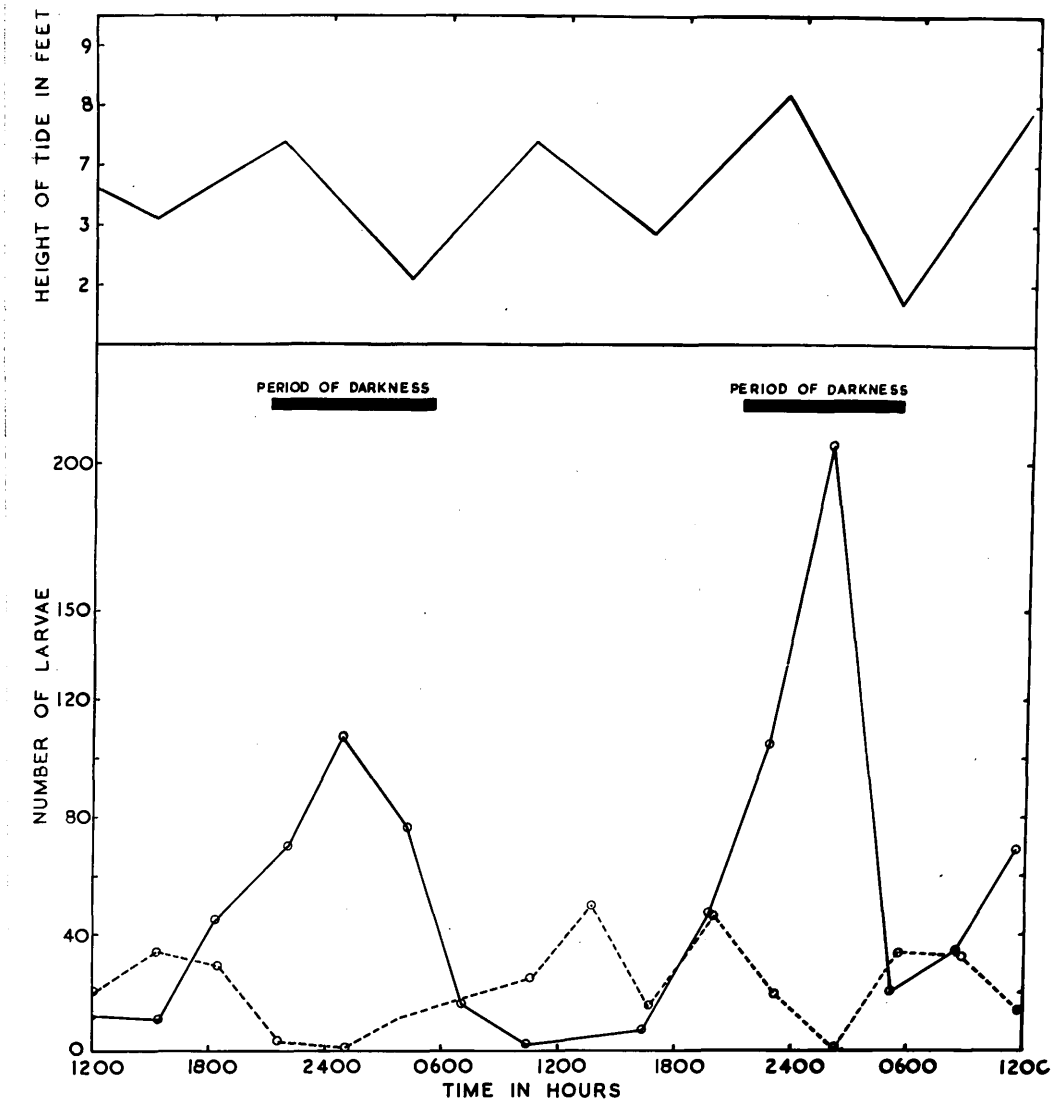

HEIGHT OF TIDE IN FEET
9
8
7
3
2
PERIOD OF DARKNESS
PERIOD OF DARKNESS
NUMBER OF LARVAE
200
150
120
80
40
0
1200
1800
2400
0600
1200
1800
2400
0600
1200
TIME IN HOURS

Plate 8.

Graph showing the number of larvae per 2 cubic metres of pumped water from the Keppel Point Station, August 29th to September 6th, 1947. The periods of darkness, and the rise and fall of the tide, are shown. Data from Table 5.

PLATE 8

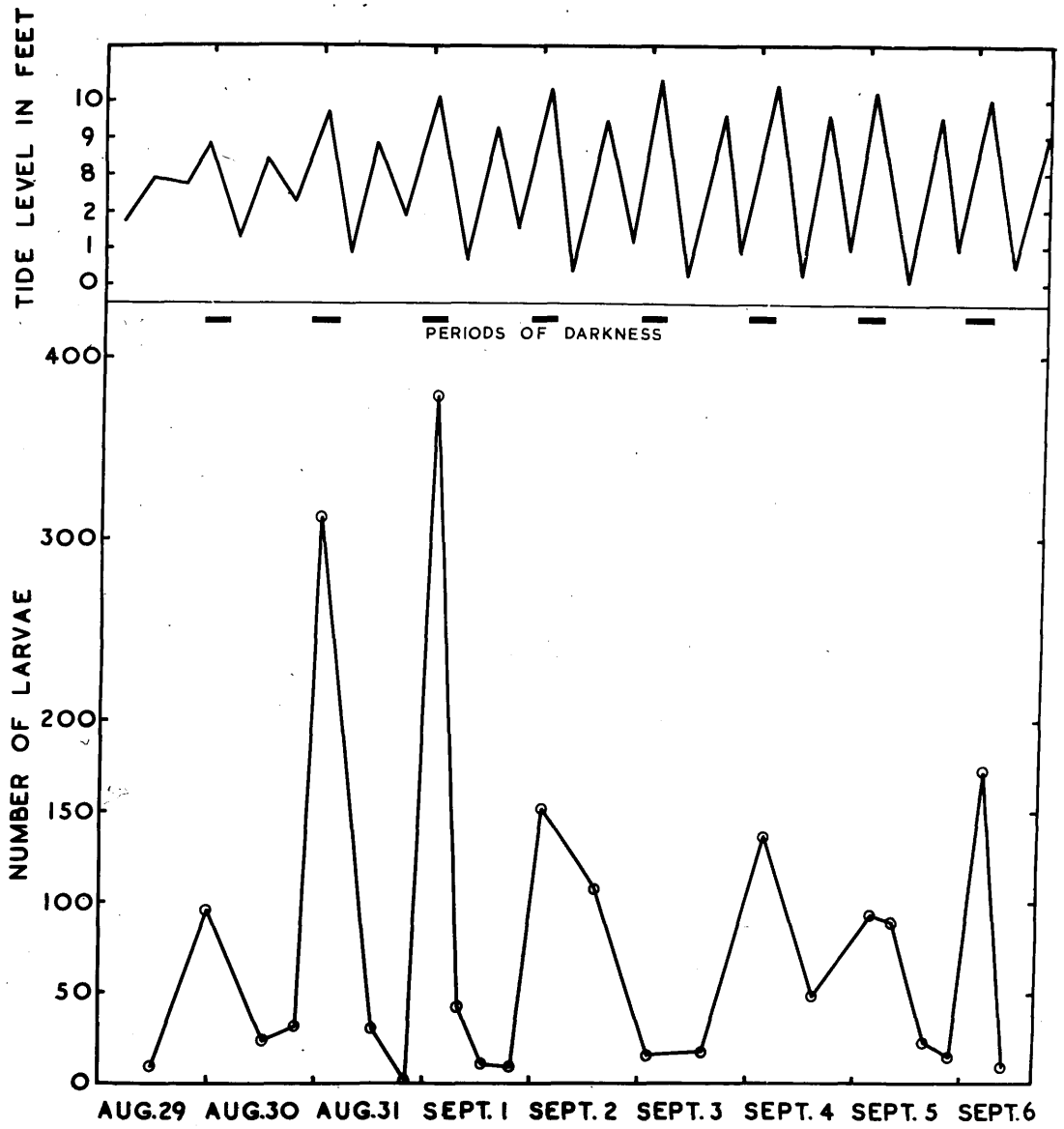

TIDE LEVEL IN FEET
10
9
8
2
1
0
PERIODS OF DARKNESS
NUMBER OF LARVAE
400
300
200
150
100
50
0
AUG.29
AUG.30
AUG.31
SEPT. 1
SEPT. 2
SEPT. 3
SEPT. 4
SEPT. 5
SEPT. 6

Plate 9.

Key to lettering.

a.a. - anterior adductor muscle.
a.p. - apical plate.
b.g. - byssal gland.
b.gr. - byssal groove.
c.g. - cerebral ganglion.
d.d. - digestive diverticula.
f. - foot.
g.s. - gastric shield.
i.g. - inner gill.
i.l. - intestinal loop.
k.s. - crystalline style sac.
mo. - mouth.
oes. - oesophagus.
o.f. - oral flap.
p.a. - posterior adductor muscle.
p.g. - pedal ganglion.
r. - rectum.
s. - stomach.
st. - statocyst.
u. - umbo.
v.g. - Visceral ganglion.
v.l. - lobe of velum.

Figure 14. Semi-diagrammatic reconstruction of a full grown larva from sections, whole mounts and from the living animals. x 400.

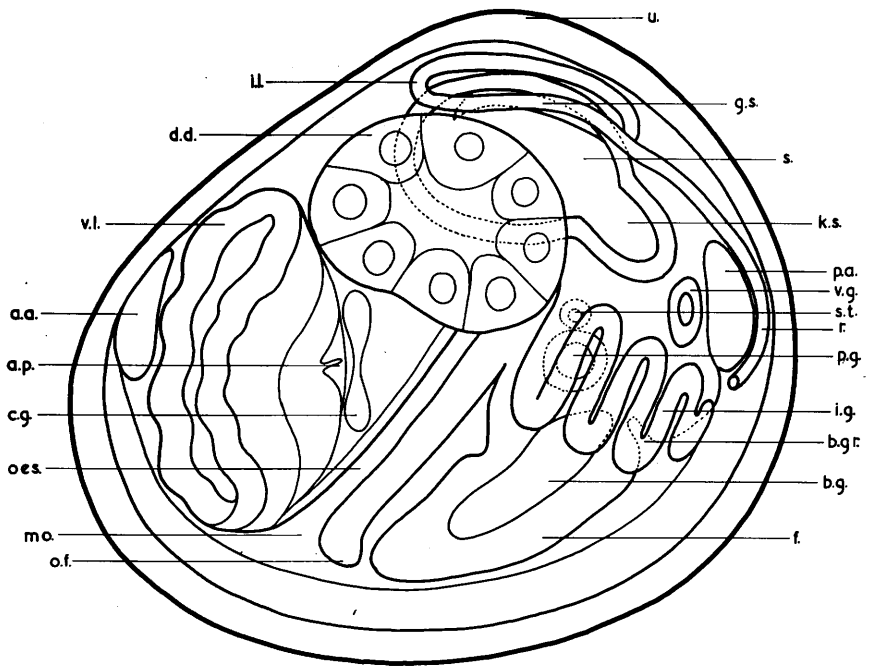


FIG. 14

Plate 10.

Key to Lettering.

a.a.	-	anterior adductor muscle.
a.g.	-	apical groove.
a.p.	-	apical plate.
c.g.	-	cerebral ganglion.
e.p.	-	mantle epithelium.
f.	-	foot.
i.g.	-	inner gill.
m.l.	-	muscular lobe of the mantle.
oes.	-	oesophagus.
p.e.	-	periostracum.
p.g.	-	pedal ganglion.
p.l.	-	secretory lobe of the mantle.
p.r.	-	posterior retractor muscles.
r.	-	rectum.
st.	-	statocyst.
st.l.	-	statolith.
v.c.	-	velar cilia.
v.g.	-	visceral ganglion.
v.l.	-	velar lobe.
v.r.m.	-	velar retractor muscles.

Figure 15. Frontal section of a larva to show the relationship between the various organs x 400.

Figure 16. Slightly oblique cross section of a larva to show the relationship of the various organs x 300.

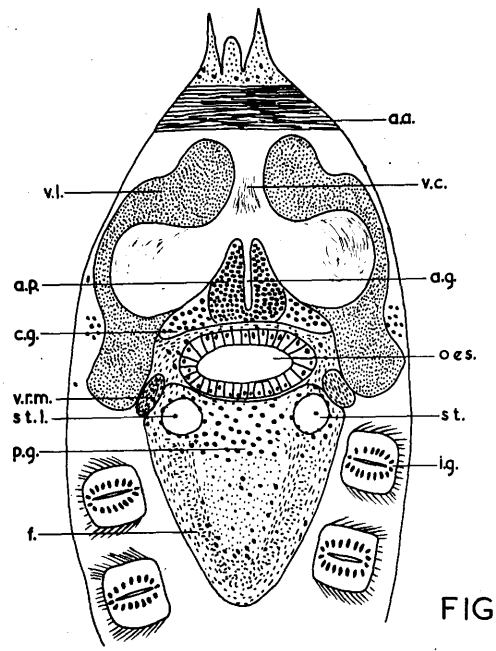

a.a.
v.l.
v.c.
a.p.
a.g.
c.g.
oes.
v.r.m.
s t. l.
s t.
p.g.
i.g.
f.

FIG.15

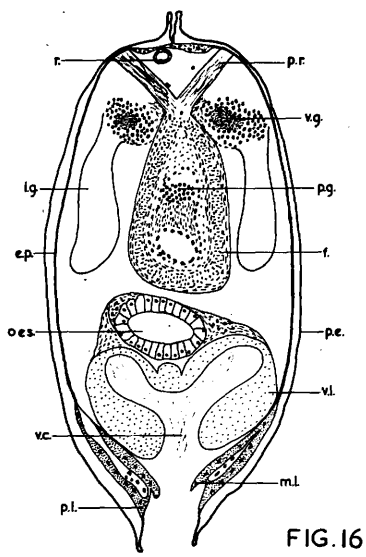

r.
p.r.
v.g.
l.g.
p.g.
e.p.
f.
oes.
p.e.
v.l.
v.c.
m.l.
p.l.

FIG.16

Plate 11.

Key to lettering.

a.a.	-	anterior adductor muscle.
a.p.	-	apical plate area.
a.r.	-	anterior retractor muscle.
c.p.g.	-	cerebro-pleural ganglion.
c.g.	-	cerebral ganglion.
d.d.	-	digestive diverticula.
e.p.	-	mantle epithelium.
g. 1-4	-	larval gill filaments.
i.g.	-	inner gill.
j.m.p.	-	mouth - palp junction area.
l.p.	-	lower palp.
m.e.	-	mantle edge.
mo.	-	mouth.
oes.	-	oesophagus.
oes. ep.	-	oesophagea epithelium.
p.a.	-	posterior adductor muscle.
u.p.	-	upper palp.

Figure 17. Sagittal section through the right side of a larva showing the gill filaments x 475.

Figure 18. Sagittal section through an 0.35 mm. spat, to show the deeply staining multinucleate tissue of the apical plate area in relation to the cerebral ganglion, mouth and anterior adductor muscle. x 1000.

Figure 19. Sagittal section through the mouth region of a 1.0 mm. spat, to show the lower palp and its relationship to the mouth region x 600.

Figure 20. Sagittal section through the mouth region of a 1.0 mm. spat, to show the division, and the attachment between, the lower palp and the lip of the mouth. x 600.

Figure 21. Sagittal section through the mouth region of a 1.0 mm. spat to show the upper palp and mouth and the proximity of the gills x 500.

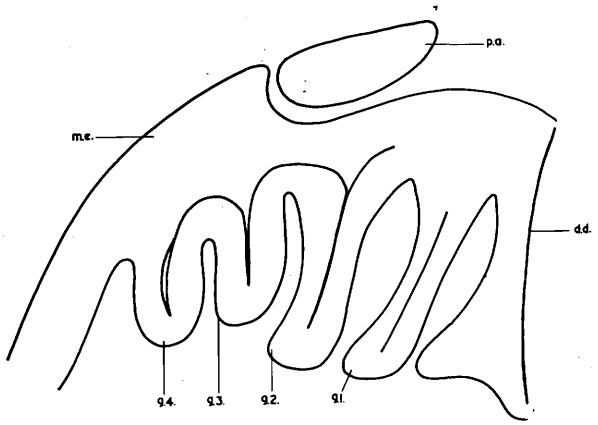


FIG.17

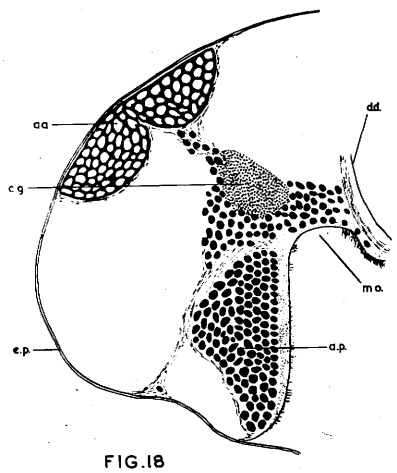


FIG.18

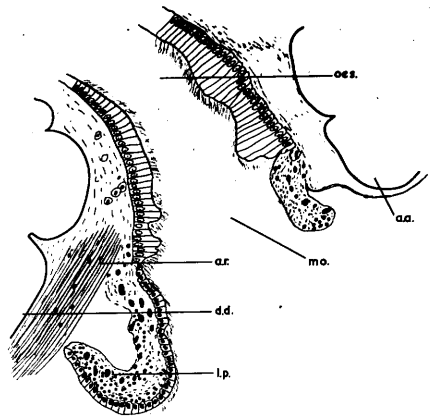


FIG.19

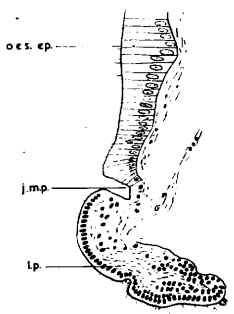


FIG. 20

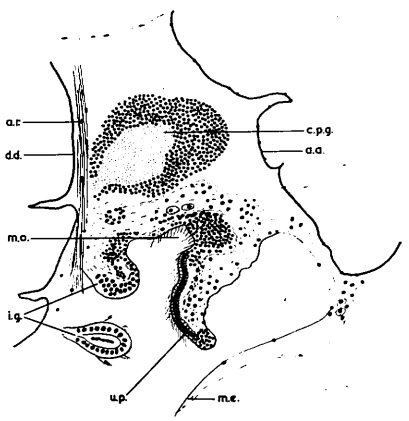


FIG. 21

Plate 12.

Key to lettering.

a.r.	-	anterior retractor muscles.
c.p.g.	-	cerebro-pleural ganglion.
c.tr.	-	ciliated tract.
d.d.	-	digestive diverticula.
e.p.	-	mantle epithelium.
i.g.	-	inner gill.
l.p.	-	lower palp.
m.c.	-	mucus cells.
m.e.	-	mantle edge.
mo.	-	mouth.
oes.	-	oesophagus.
u.p.	-	upper palp.
v.m.	-	visceral mass.

Figure 22. Frontal section through the mouth region of an 0.35 mm. spat, showing the mouth and the upper palps. x 320.

Figure 23. Cross section through the mouth region of an 0.4 mm. spat, to show the lower palps x 300.

Figure 24. Cross section through the mouth region of an 0.4 mm. spat, to show the upper palps x 300.

Figure 25. Drawing of a whole mount of the upper and lower palps of a 1.0 mm. spat. The view given is frontal, looking directly into the mouth. x 400.

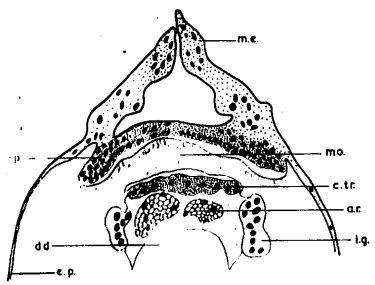


FIG.22

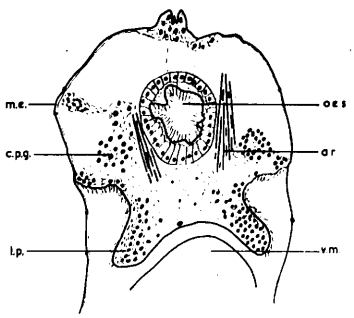
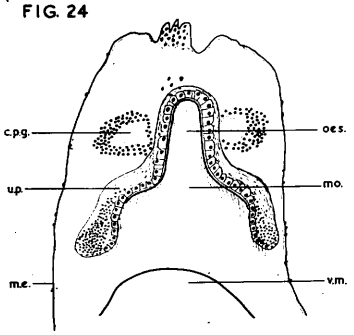


FIG.23

FIG. 24



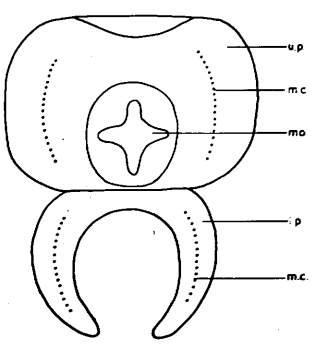


FIG.25

Plate 13.

Key to lettering.

c.	-	cilia.
e.p.	-	mantle epithelium.
m.l.	-	muscular lobe of mantle.
m.s.	-	muscle strand.
n.	-	nerve.
p.c.	-	periostracum.
p.l.	-	secretory lobe of mantle.
p.l.m.	-	pallial line muscles.
p.r.m.	-	pallial retractor muscles.
sh.	-	shell.
s.l.	-	sensory lobe of mantle.

Figure 26. Cross section of the mantle edge of a larva to show the two mantle lobes present at this time. x 1500.

Figure 27. Cross section of the mantle edge of a 1.2 mm. spat, to show the three mantle lobes and the siphonal retractor muscles. x 450.

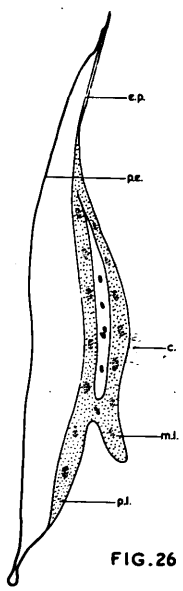


FIG.26

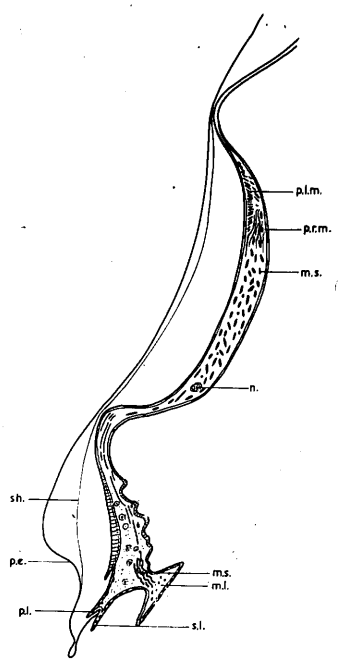


FIG.27

Plate 14.

Key to the lettering.

i.g.	-	inner gill.
m.	-	mantle.
m.e.	-	mantle edge.
m.f.	-	mantle fusion.
m.l.	-	muscular lobe of mantle.
m.s.	-	muscle strand.
p.a.	-	posterior adductor muscle.
p.e.	-	periostracum.
p.l.	-	secretory lobe of mantle.
p.r.m.	-	pallial retractor muscles.
s.s.	-	siphonal septum.
si.t.	-	siphonal tentacles.

Figure 28. Frontal section of an 0.4 mm. long spat, to show the formation of the siphonal tentacles. Section is through the mid-line. x 700.

Figure 29. Drawing of a whole mount of the right posterior ventral mantle region, to show the formation of the siphonal tentacles and the gills, from a spat 0.50 mm. x 400.

Figure 30. Internal view of a whole mount of the right posterior mantle edge of a spat 0.75 mm. in length, to show the siphonal tentacles. Stained with methylene blue. x 250.

Figure 31. Frontal section of an 0.3 mm. spat, to show the fusion of the mantle x 350.

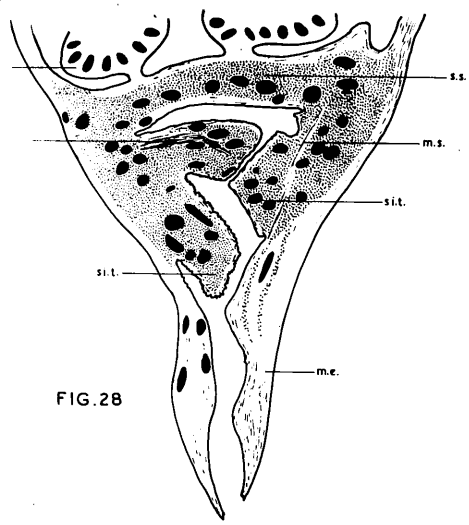


FIG.28

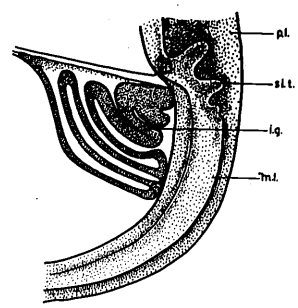


FIG. 29

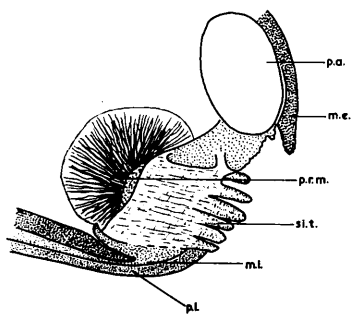


FIG.30

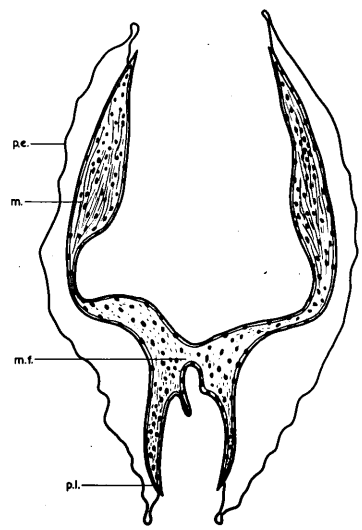


FIG.31

Plate 15.

Key to lettering.

a.	-	anus.
e.p.	-	mantle epithelium.
e.si.	-	exhalent siphon.
f.	-	foot.
i.g.	-	inner gill.
m.e.	-	mantle edge.
m.s.	-	muscle strands.
m.t.	-	mantle thickening.
p.a.	-	posterior adductor muscle.
p.e.	-	periostracum.
p.l.m.	-	pallial line muscles.
r.	-	rectum.
s.l.	-	secretory lobe of mantle.
ss.	-	siphonal septum.
s.t.	-	sensory tentacles.
si.t.	-	siphonal tentacles.
v.g.	-	visceral ganglion.

Figure 32. Frontal section of an 0.35 mm. spat at the approximate level of the anus, to show the siphonal tentacles, the exhalent siphon and the siphonal retractor muscles x 400.

Figure 33. Frontal section of an 0.45 mm. spat, cut at the approximate level of the mouth, to show the exhalent siphon x 300.

Figure 34. Drawing of a whole mount of the posterior region of a 1.0 mm. long spat, to show the siphonal septum and the siphonal tentacles. Stained with methylene blue x 170.

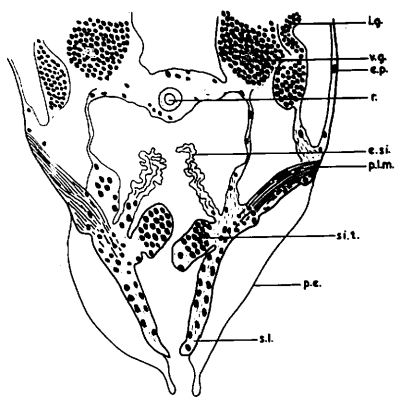


FIG.32

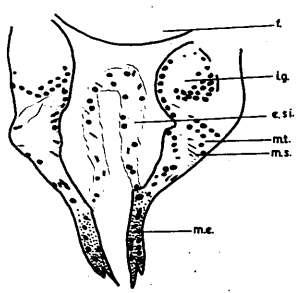


FIG.33

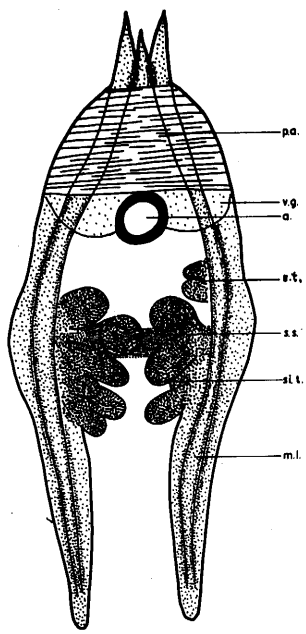


FIG. 34

Plate 16.

Key to lettering.

c.	-	cilia.
d.d.	-	digestive diverticula.
d.d.d.	-	duct of digestive diverticula.
e.p.	-	mantle epithelium.
f.	-	foot.
i.g.	-	inner gill.
i.g.o.	-	origin of inner gill.
k.	-	kidney.
k.s.	-	crystalline style sac.
m.	-	mantle.
m.e.	-	mantle edge.
m.l.	-	muscular lobe.
m.t.	-	thickening of mantle.
os.	-	osphradium.
oes.	-	oesophagus.
p.e.	-	periostracum.
p.l.	-	secretory lobe.
p.r.	-	posterior retractor muscles.
r.	-	rectum.
s.	-	stomach.
v.g.	-	visceral ganglion.

Figure 35. Frontal section through the posterior region of an 0.4 mm. spat, showing the gill origin x 400.

Figure 36. Frontal section through the posterior dorsal region of a 1.0 mm. long spat, to show the specialised epithelium which is described as the osphradium x 450.

Figure 37. Frontal section through a 1.0 mm. long spat, to show the relationship between the gills, mantle and siphonal retractor muscles x 50.

Figure 38. Frontal section through an 0.35 mm. long spat, to show the ducts of the digestive diverticula leading into the stomach x 200.

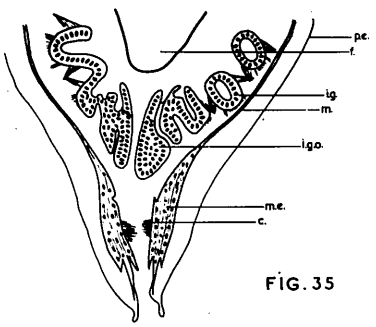


FIG. 35

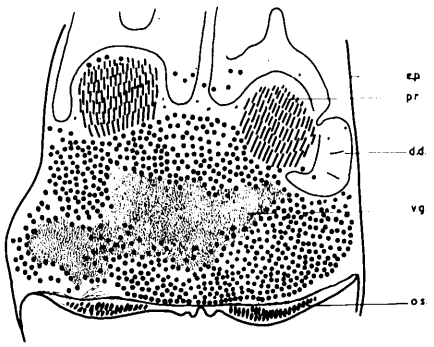


FIG. 36

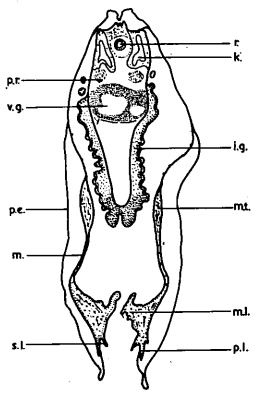


FIG. 37

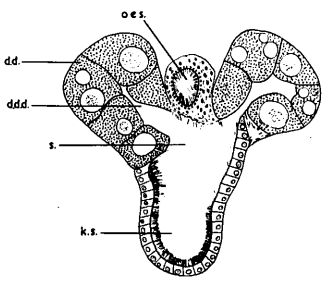


FIG. 38

Plate 17.

Key to the lettering.

au. - auricle.
a.v.o.- atrio-ventricular opening.
d.d. - digestive diverticula.
d.p. - dorsal pericardium.
e.p. - mantle epithelium.
h. - heart.
h.m. - heart muscle.
int. - intenstine.
ky. - kidney.
i.g. - inner gill.
m. - mantle.
p. - pericardium.
p.a. - posterior adductor muscle.
p.r. - posterior retractor muscle.
r. - rectum.
r.p. - reno-pericardial duct.
v. - ventrical.
v.g. - visceral ganglion.
v.p. - ventral pericardium.

Figure 39. Diagrammatic reconstruction of the kidney of an 0.5 mm. long spat. The figure on the left is in frontal view, and the dotted line marks the outline of the lumen. Figure 39A. is a cross section at point A. Figure 39B. is a cross section at point B. x 900.

Figure 40. Frontal section of the posterior dorsal region of an 0.5 mm. spat showing the heart, kidney and pericardium x 1000.

Figure 41. Lateral view of a reconstructed half kidney of a 1.0 mm. long spat. Dotted line indicates the reno-pericardial duct. Top of the diagram is dorsal and the left is anterior x 400.

Figure 42. Frontal view of a reconstructed right half of a kidney in a spat 1.0 mm. in length x 400.

Figure 43. Sagittal section through the posterior dorsal region of a 1.0 mm. long spat, to show the heart, kidney and pericardium x 600.

Figure 44. Frontal section through the posterior dorsal region of an 0.35 mm. long spat, to show the heart x 350.

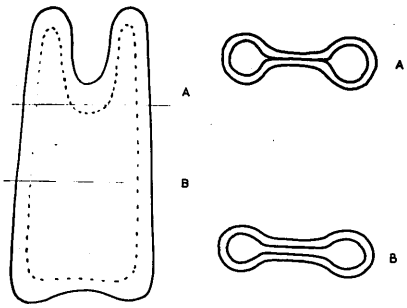


FIG.39

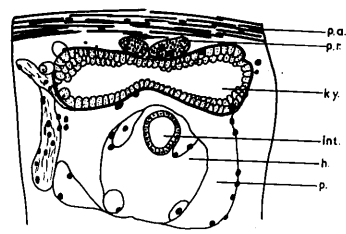


FIG.40

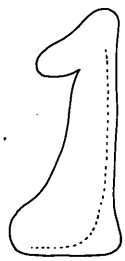


FIG.41

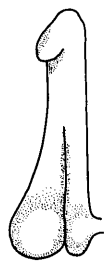


FIG.42

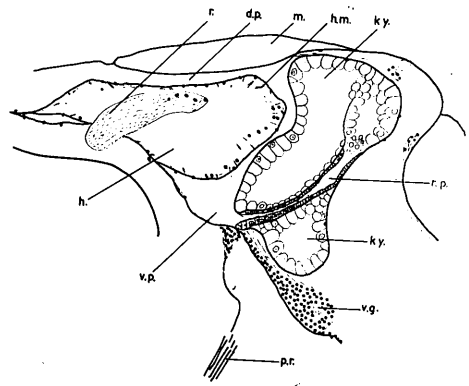


FIG.43

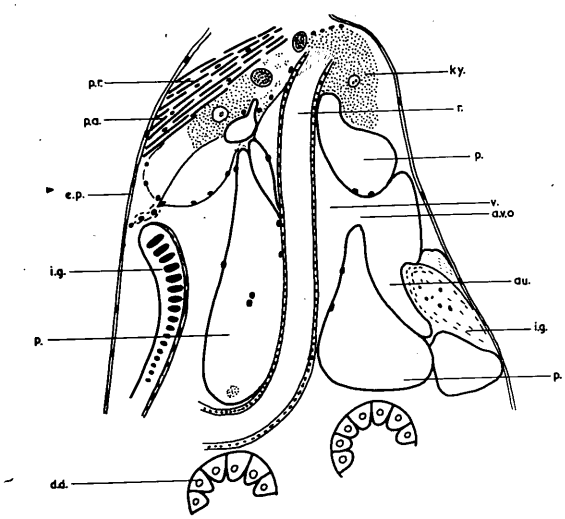


FIG.44

Plate 18.

Key to the lettering.

a. - anus.
a.a. - anterior adductor muscle.
c.pg.- cerebro-pleural ganglion.
f. - foot.
i.g. - inner gill.
l. - ligament.
m. - mantle.
oes. - oesophagus.
p.a. - posterior adductor muscle.
p.r. - posterior retractor muscle.
r. - rectum.
u.p. - upper palp.

Figure 45. Drawing of a whole amount of a 1.0 mm. spat from the right side x 100.

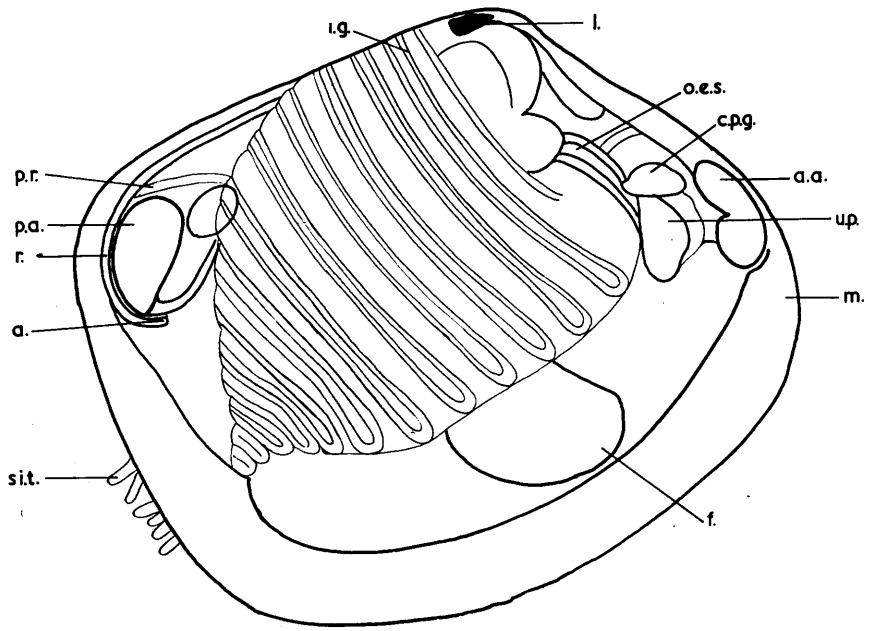


FIG. 45

Plate 19.

Key to the lettering.

a.a. - anterior adductor muscle.
a.b. - anal bush.
a.r. - anterior retractor muscle.
b.g. - byssal gland.
b.gr. - byssal groove.
c.gr. - ciliated groove.
d.d. - digestive diverticula.
f. - foot.
g.s. - gastric shield.
g. - gonad.
h. - heart.
i.g. - inner gill.
int. - intestine.
k.s. - crystalline style sac.
m. - mantle.
m.c. - mucous cells.
m.o. - mouth.
oes. - oesophagus.
p.a. - posterior adductor muscle.
p.g. - pedal ganglion.
p.r. - posterior retractor muscle.
p.c. - pericardium.
s. - stomach.
st. - statocyst.
v.g. - Visceral ganglion.

Figure 46. Sagittal section through the approximate middle of a 1.0 mm. spat, to show the relationship of the various organs at this stage x 100.

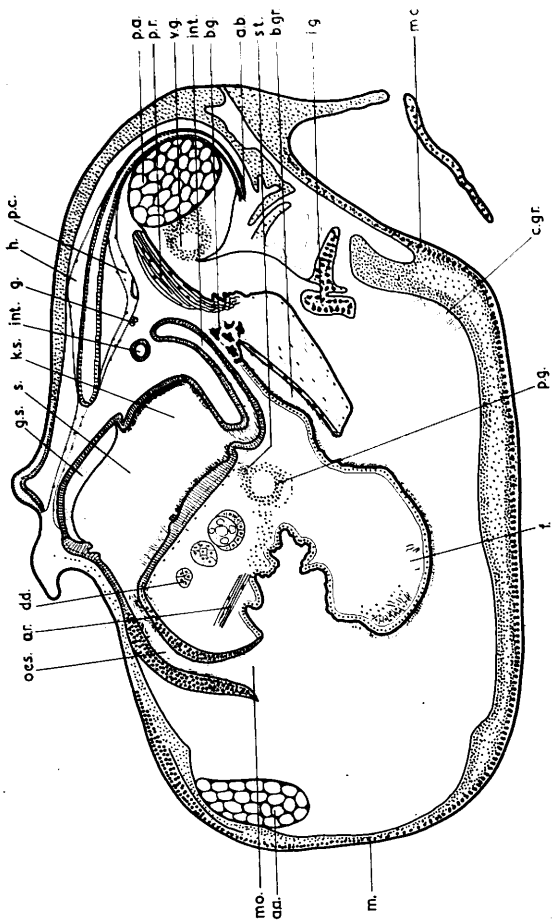

p.a.
p.r.
v.g.
int.
bg
a.b
s.t.
b.gr
l.g
m.c
p.c.
h.
g.
int.
k.s.
s.
g.s.
c.g.r.
p.g.
t.
d.d.
ar.
oes.
m.o.
a.a.
m.

FIG. 46

Plate 20.

Graph showing the efficiency of the plates held at various angles as collectors of spat. The broken line represents the catch per square inch of projected area, and the solid line represents the actual area exposed. The data are taken from Table 6A and are the combined figures for glass and Tufnol.

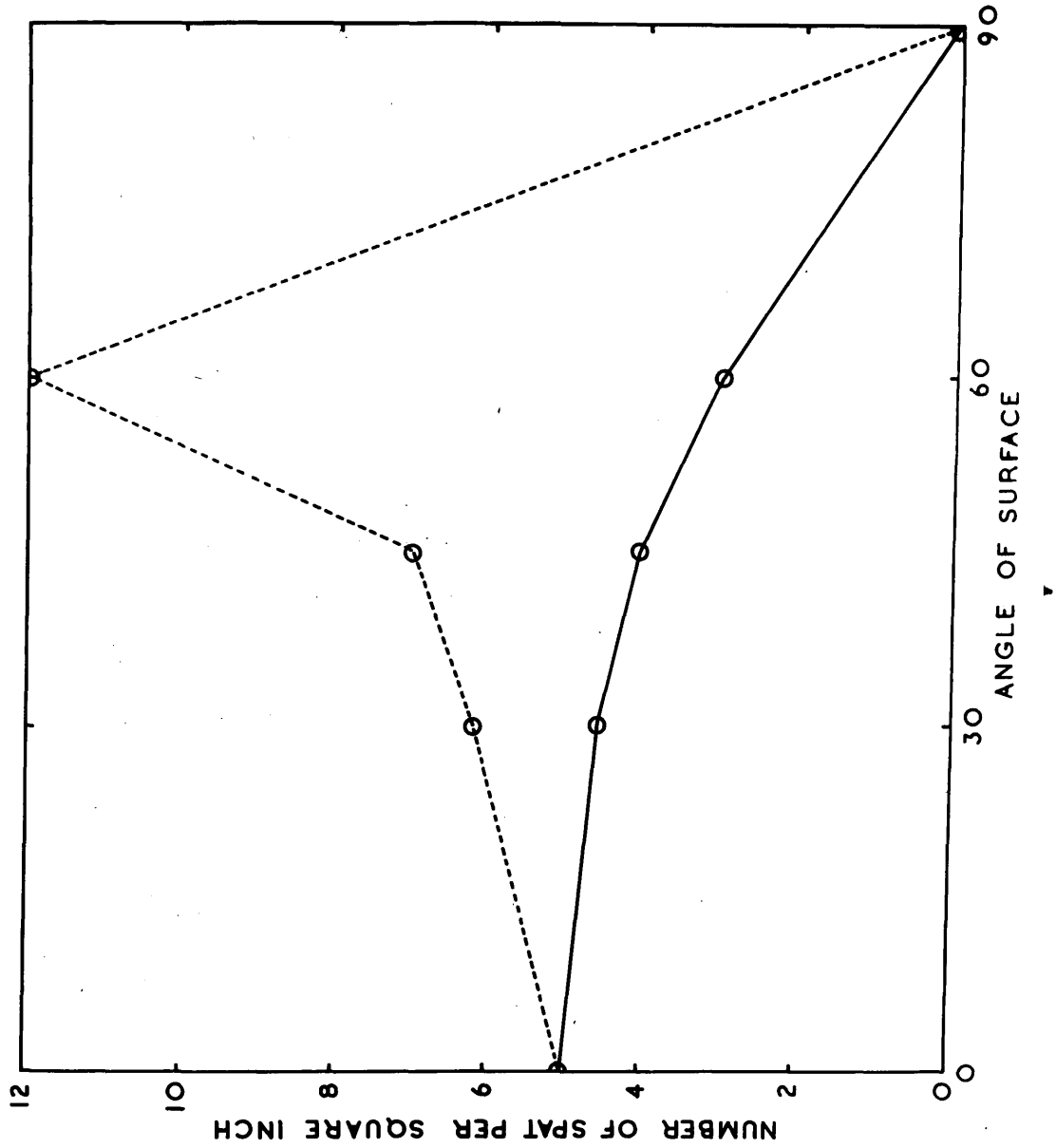

NUMBER OF SPAT PER SQUARE INCH
0
2
4
6
8
10
12
0
30
60
90
ANGLE OF SURFACE

Plate 21.

Graph showing the number of spat on 4 inch square ground glass and Tufnol plates, held at various angles from the perpendicular through 360 degrees. The solid line is Tufnol, and the broken one ground glass. Data from Table 6.

PLATE 21

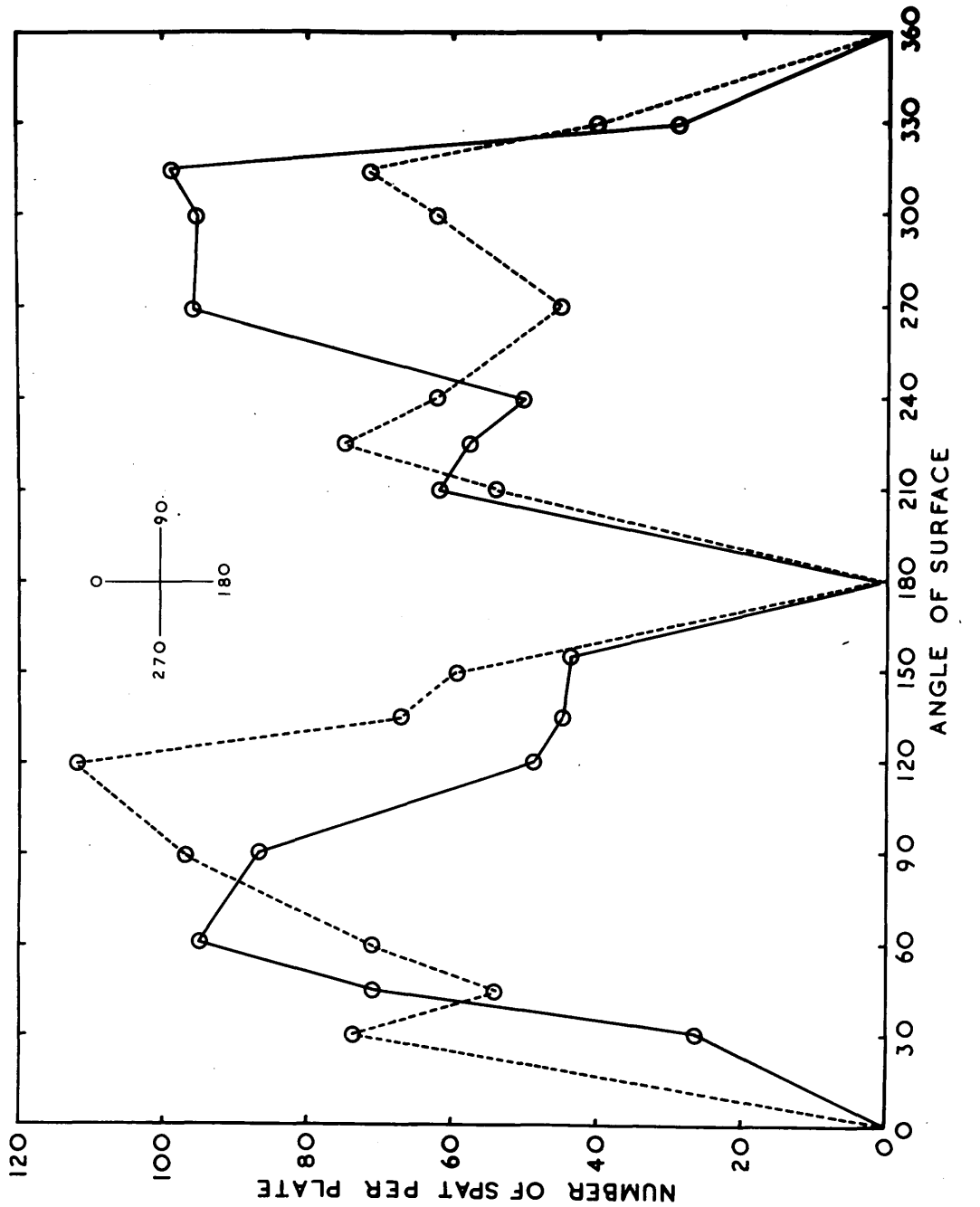

NUMBER OF SPAT PER PLATE
0
20
40
60
80
100
120
ANGLE OF SURFACE
0
30
60
90
120
150
180
210
240
270
300
330
360
90
0
180
270

FIG. 1

FIG. 2

Plate 23.

Figure 1. Photograph of the Cross Houses Beach, Millport, looking south-east across the mouth of Kames Bay. Note the numerous rocks and stones and the attached littorines. The high reef shown in the upper right affords considerable protection from wave action in southerly gales.

Figure 2. Photograph showing the plankton pump apparatus at the shore station on Keppel Point. The intake pipe running up the rocks from the buoy may be seen on the left. The two $\frac{1}{3}$ cubic metre measuring tanks are seen on the right, with the plankton net in the outer one.

FIG. 1

FIG. 2

Table 24.

Graph showing the distribution of spat from the spatfalls for the summers of 1946 and 1947, at various tidal levels in Ballech Bay. The solid line is the September 1946 distribution, and the broken line that of October 1947. Data from Tables 7A, 7B, 7C.

PLATE 24

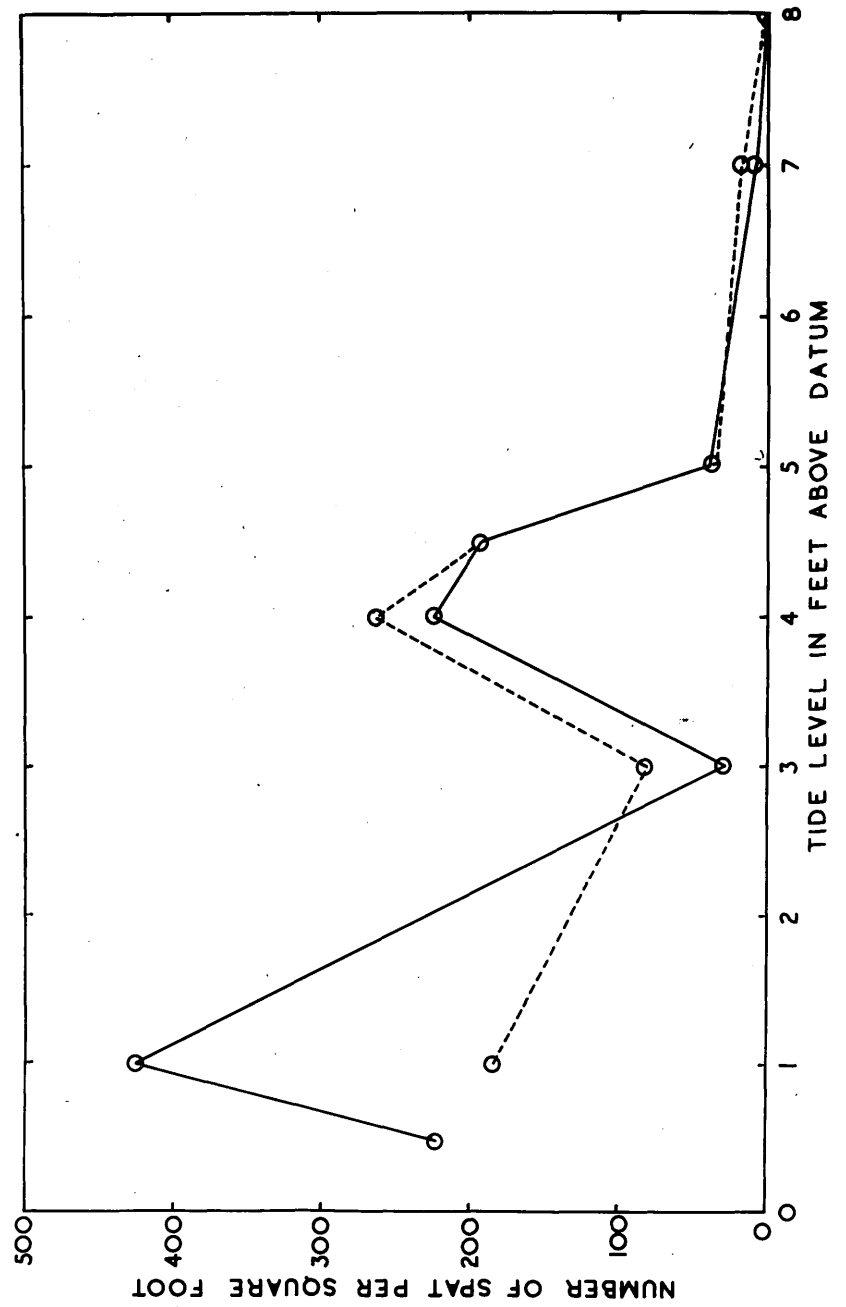

NUMBER OF SPAT PER SQUARE FOOT
0
100
200
300
400
500
TIDE LEVEL IN FEET ABOVE DATUM
0
1
2
3
4
5
6
7
8

Plate 25.

Graph showing the length-frequency distributions of samples of spat from various tidal levels in Balloch Bay, September 1946. The station numbers are marked on each curve, which has its own base line, so the curves are comparative but frequencies must be calculated by estimation and subtraction. Data from Table 26A.

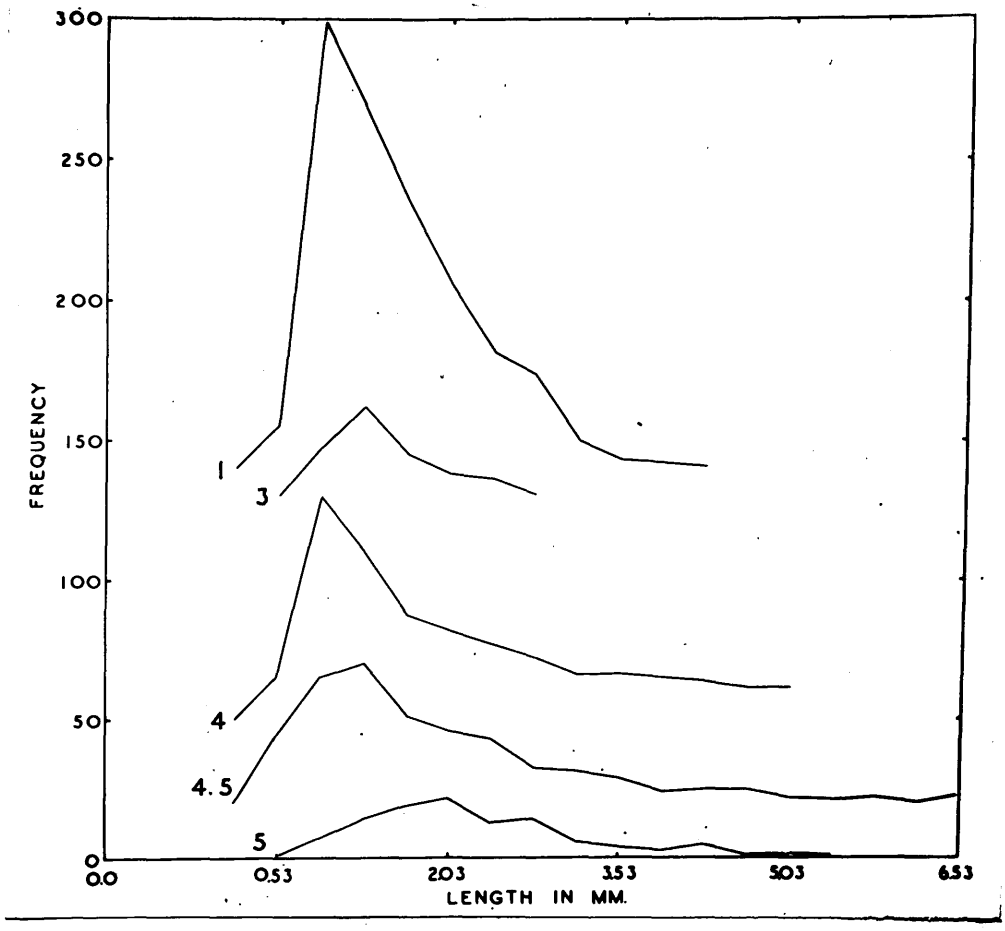

300
250
200
150
100
50
0
FREQUENCY
1
3
4
4.5
5
0.0
0.53
2.03
3.53
5.03
6.53
LENGTH IN MM.

Plate 26.

Graph showing mean lengths of samples of spat from various tidal levels at Balloch Bay, September 1946. Data from Table 8.

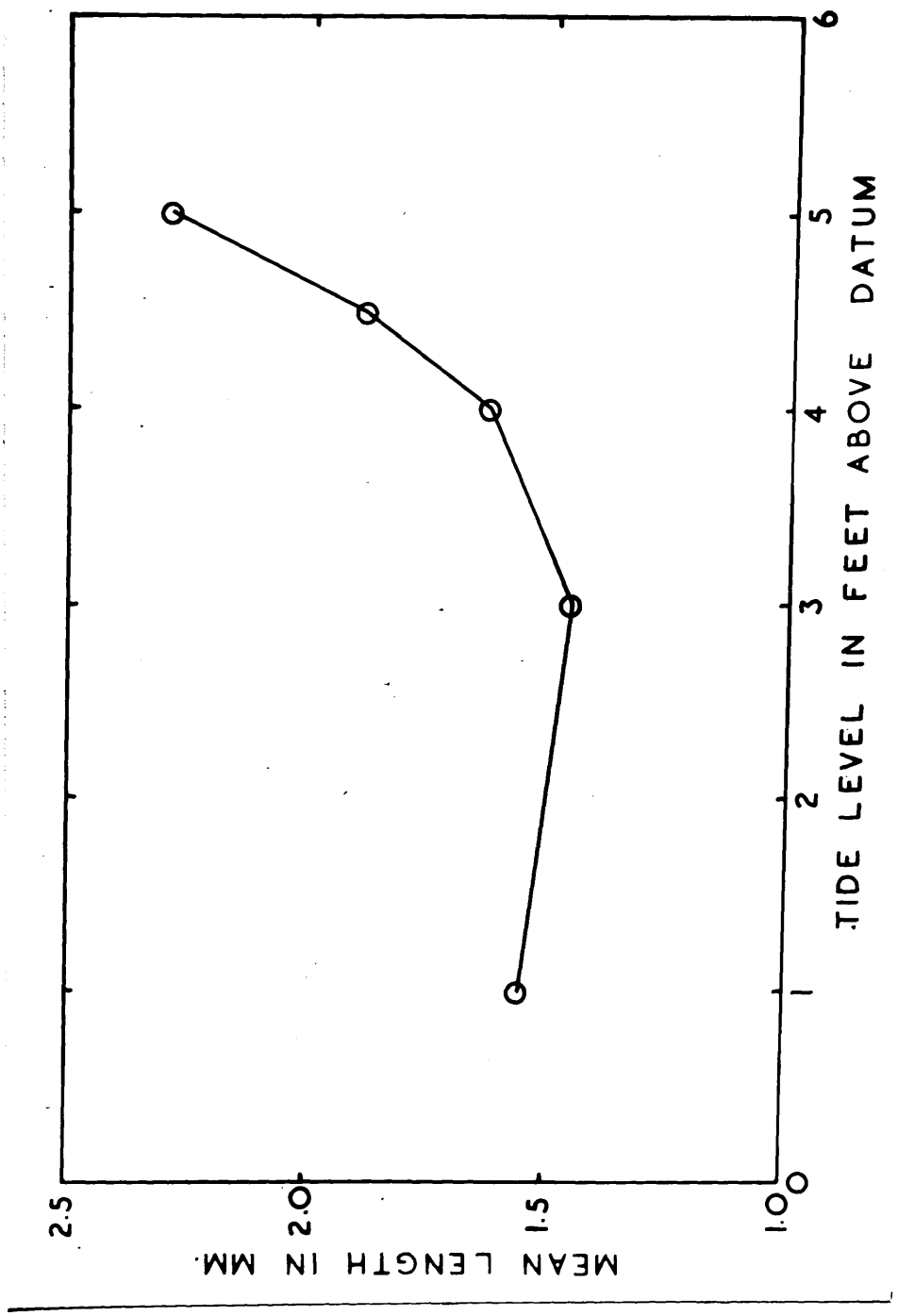

MEAN LENGTH IN MM.
2.5
2.0
1.5
1.0
TIDE LEVEL IN FEET ABOVE DATUM
0
1
2
3
4
5
6

Plate 27.

Graph showing the percentage mortality of spat from Balloch Bay, at various times, from September 1946 to June 1947. Data from Tables 7A, 7B, & 7C.

PLATE 27

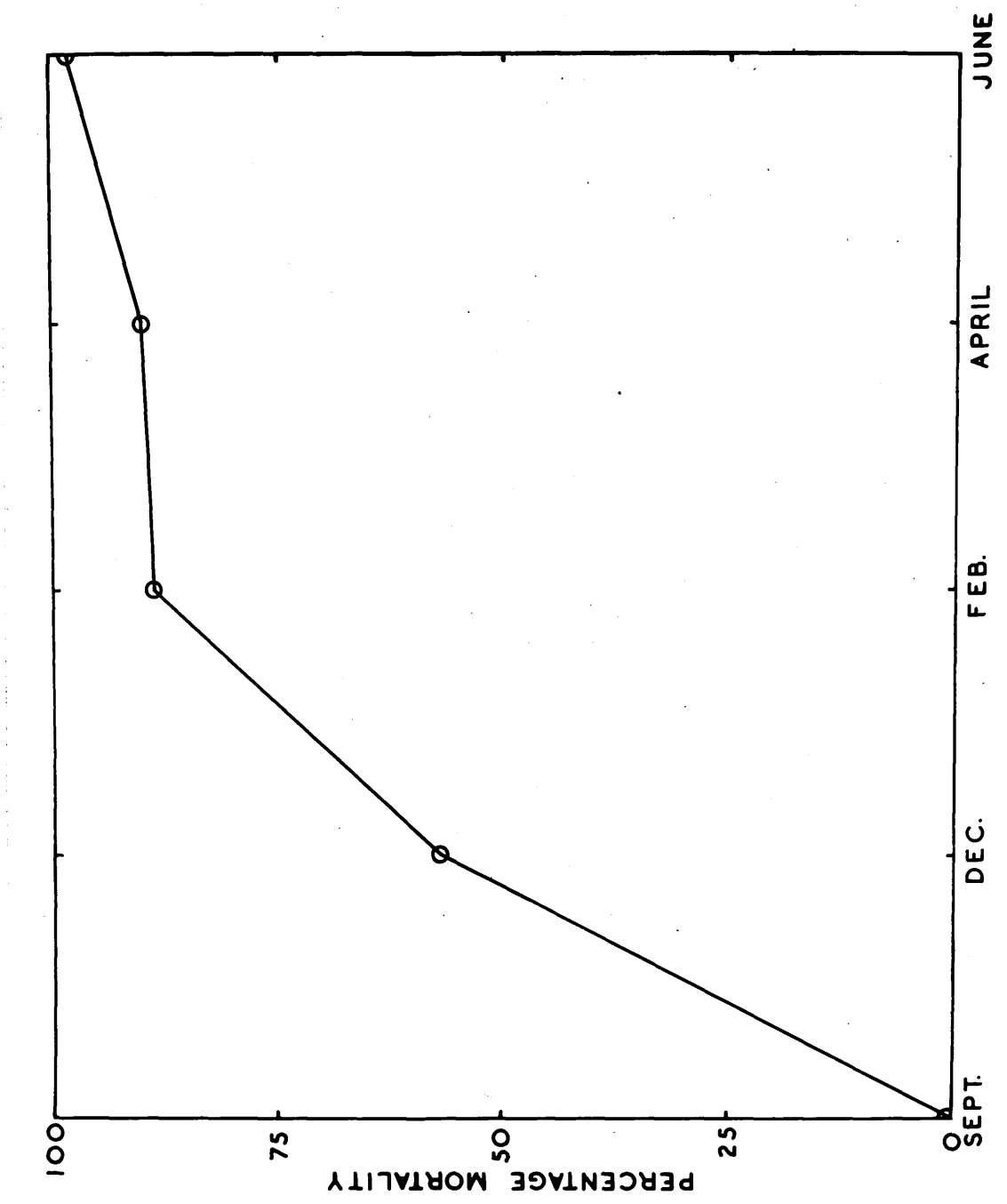


Plate 28.

Graph showing the rate of removal of a coloured suspension. The ordinate is on a sliding scale, in order to accommodate sufficient number of curves, and represents the natural logarithm of the ratio of the "spekker" reading at any given time, to the original "spekker" reading. Data are from Experiments 3 to 14 inclusive, Appendix I.

PLATE 28

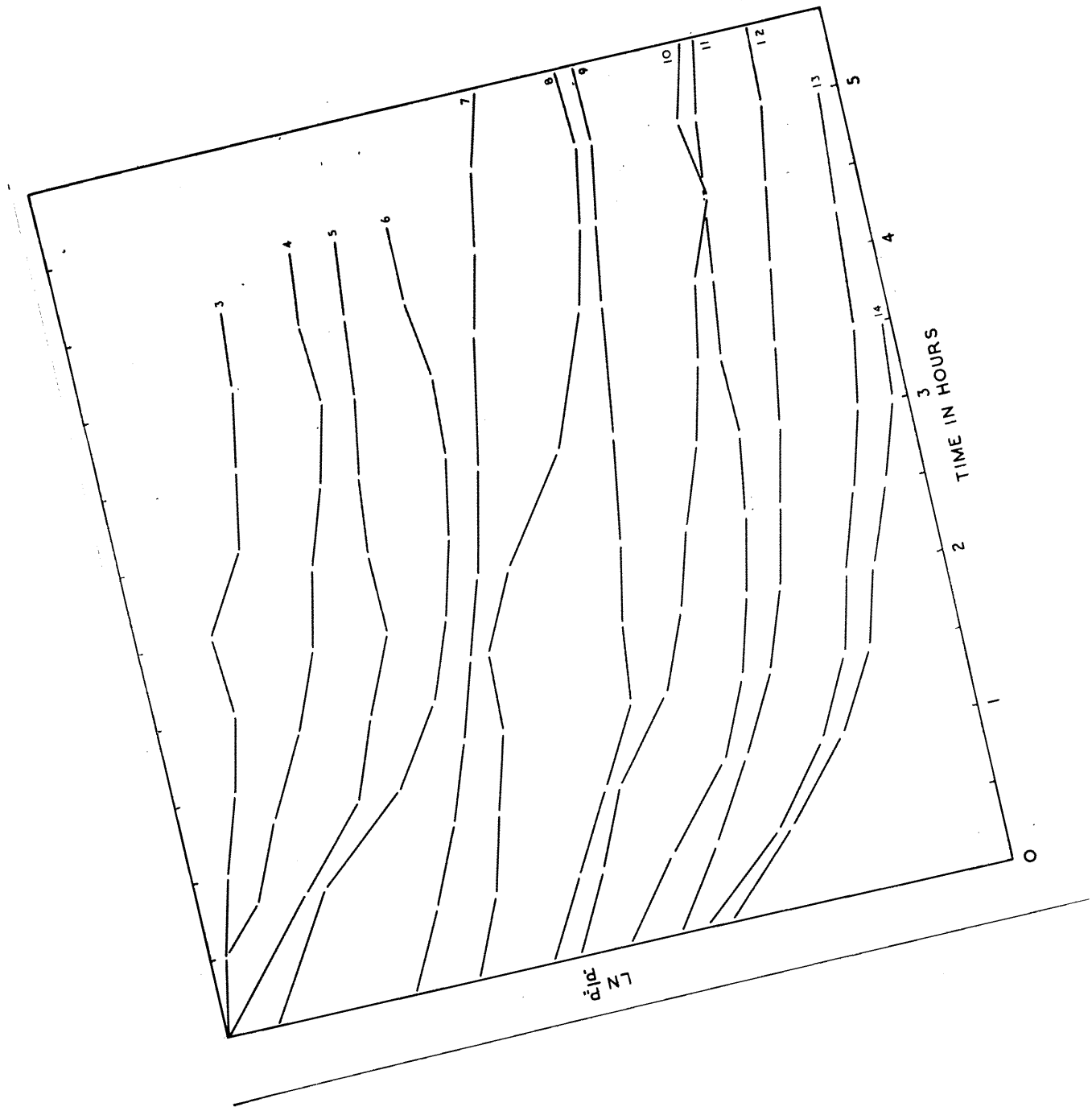


Plate 29.

Graph showing the rate of removal of a coloured suspension. The ordinate is on a sliding scale, in order to accommodate sufficient curves, and represents the natural logarithm of the ratio of the "spekker" reading at any given time, to the original "spekker" reading. The data are taken from Experiments 15 to 38 inclusive, Appendix I.

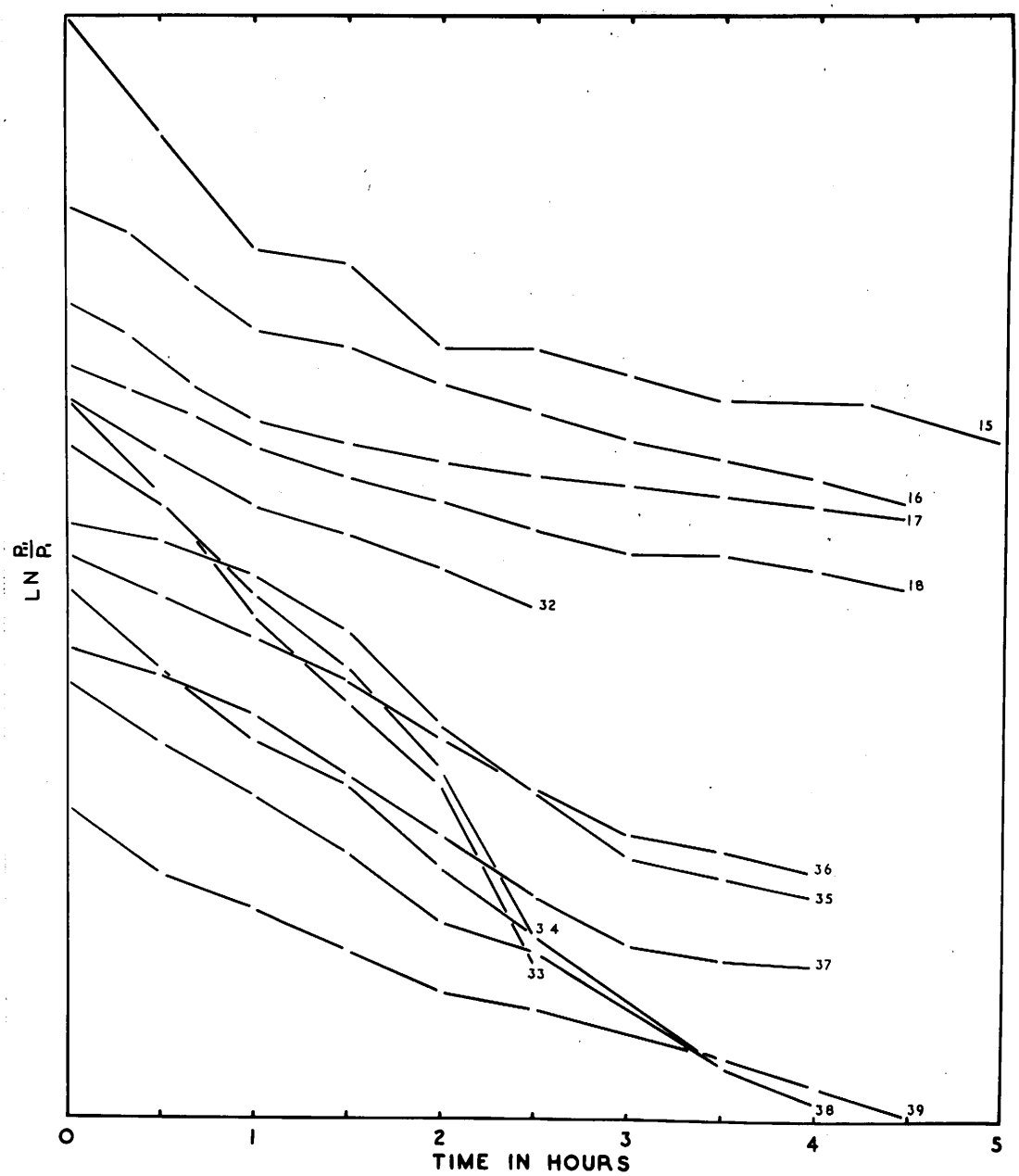

LN Pi/P
15
16
17
18
32
36
35
34
33
37
38
39
0
1
2
3
4
5
TIME IN HOURS

Plate 29A.

Graph showing the rates of filtration in Experiments 28 to 31, in which the suspension medium was colloidal graphite. The animals in Experiments 30 and 31 had been fed for three hours previous to the experiment with a concentrated rouge solution. Description of the experiment, page 92.

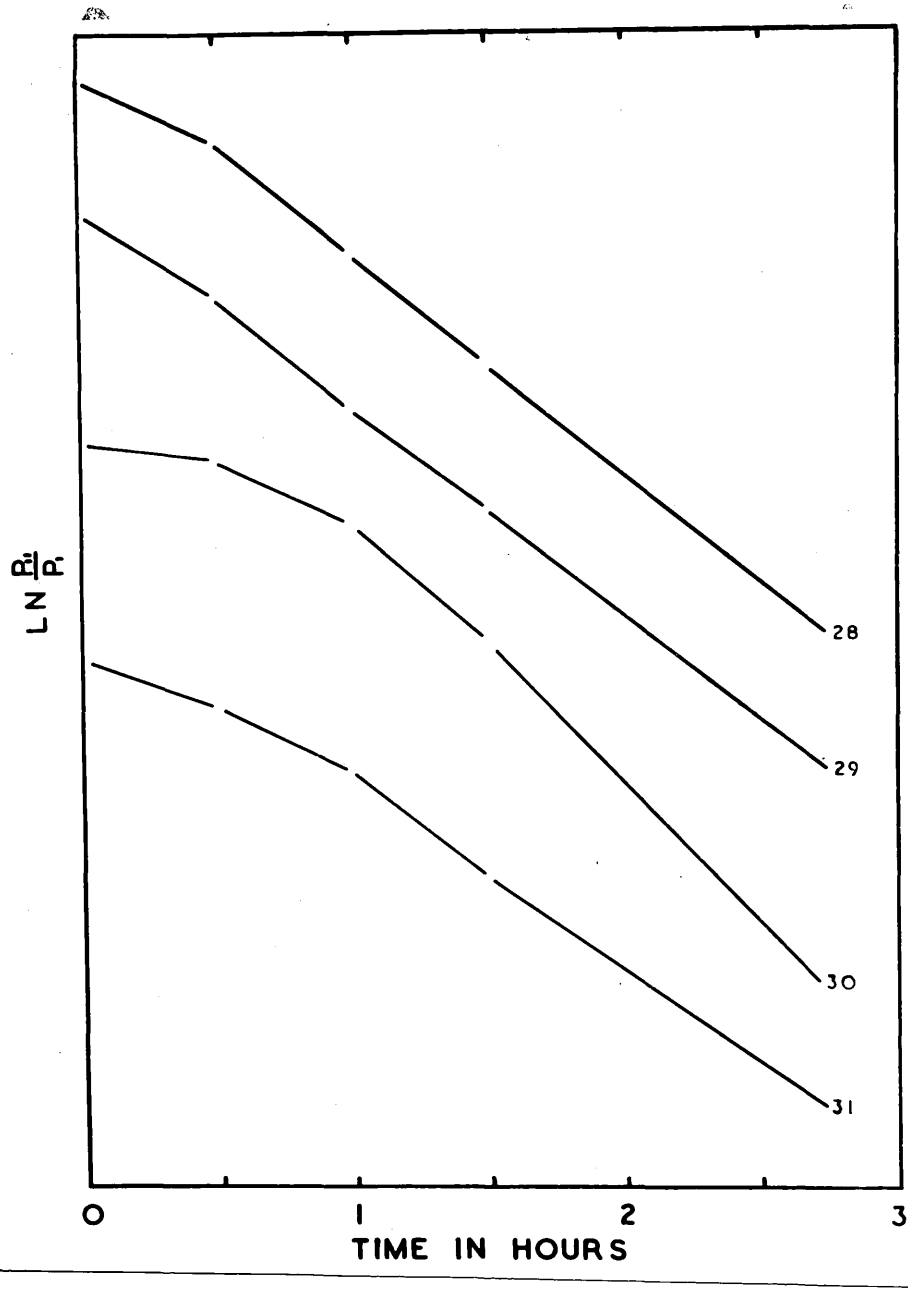

LN P'/P
28
29
30
31
0
1
2
3
TIME IN HOURS

Plate 30.

Graph showing the rate of filtration as shown by the relative changes in concentration ($\ln \frac{P2}{P1}$) of a coloured suspension with time. The lower line of long dashes shows the plotted logarithmic ratios, and the line of short dashes shows a line fitted by the method of Least Squares. The upper line of long dashes is the plotted logarithmic ratios of the control experiment which shows the rate of settling of the suspension. Data from Experiment No. 35, Appendix I.

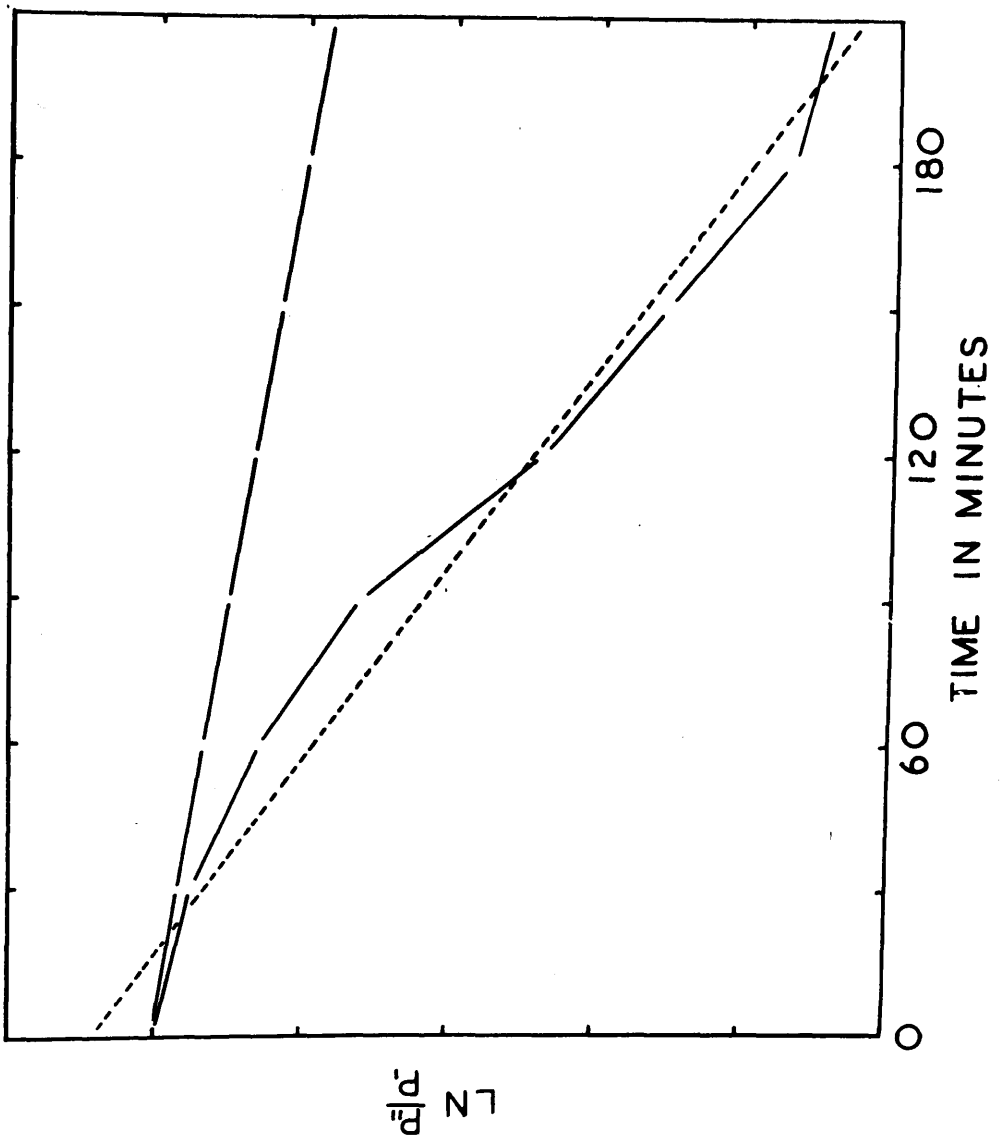
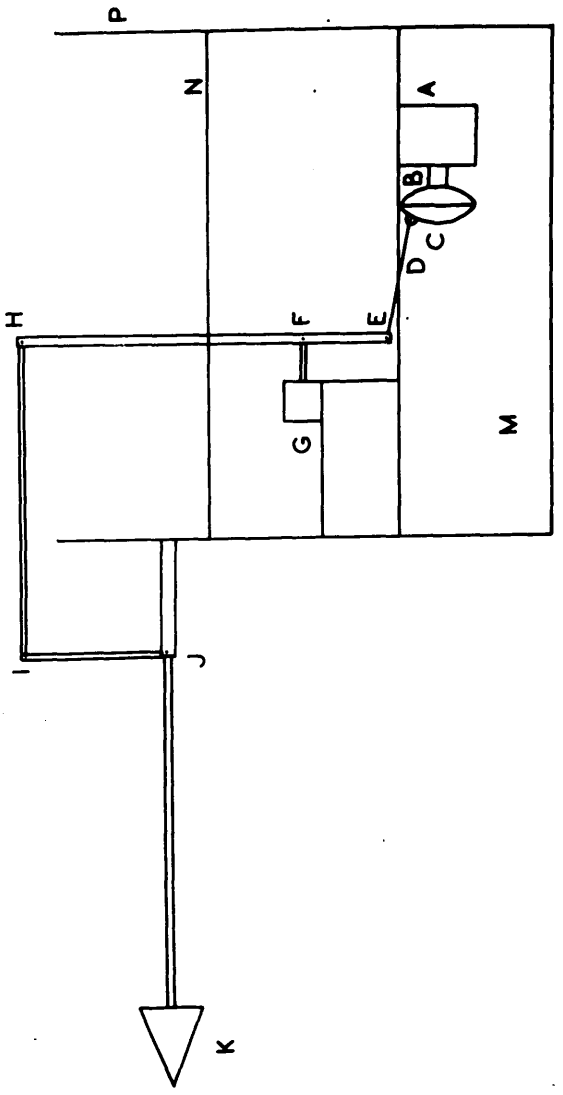

LN P/P°
0
60
120
180
TIME IN MINUTES

Plate 31.

Diagram showing the apparatus used to obtain kymograph recordings of the shell movements.

Legend.

A - Anchor block.
B - Sealing wax.
C - Animal.
D - Wire connecting animal to vertical lever.
EFH - Vertical lever swung at F.
G - Block supporting Hinge F.
IJK - Unit lever combination swung at J.
M - sand.
N - water level.
P - wall of aquarium.

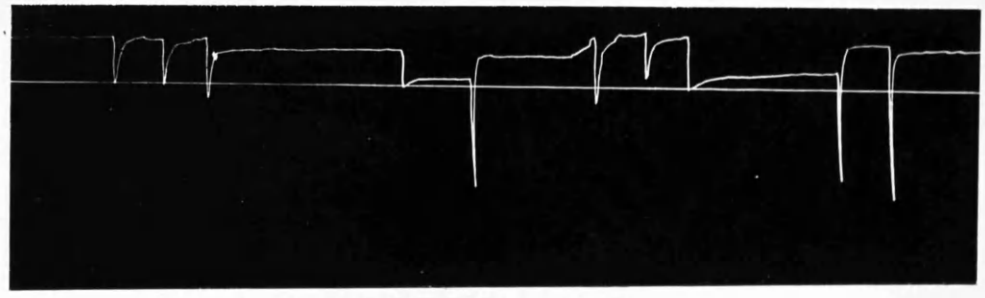

P
N
A
B
C
D
H
F
E
G
M
I
J
K

Tracing 1. Shell Movements 4. 7. 46. 4 hours and 50 mins. recording shown on the tracing. Open 100% of the period. Mean degree of open-ness 75%. A certain rhythm apparent. Temperature 16.6 - 18.0 degrees C.

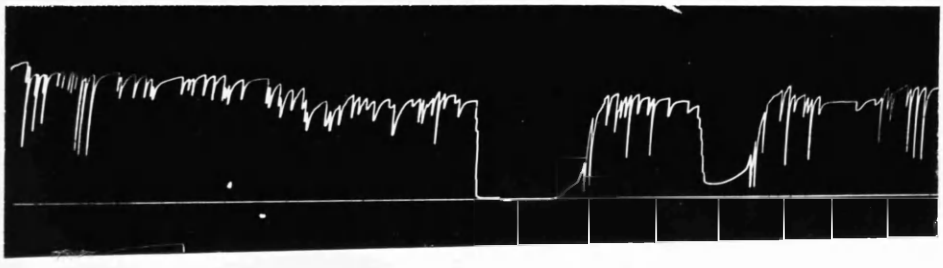
Tracing 2. Shell Movements 4/5. 7. 46. 2 hours and 30 mins. recording shown on the tracing. Open 100% of the period. No definite rhythm apparent. Temperature 19.0 - 20.8 degrees C.

Tracing 3. Shell Movements 12/13. 7. 46. 4 hours recording shown on the tracing. Open 90% of the period. Mean degree of open-ness 90%. Rhythm not apparent. Temperature 19.3 degrees C.

1



2



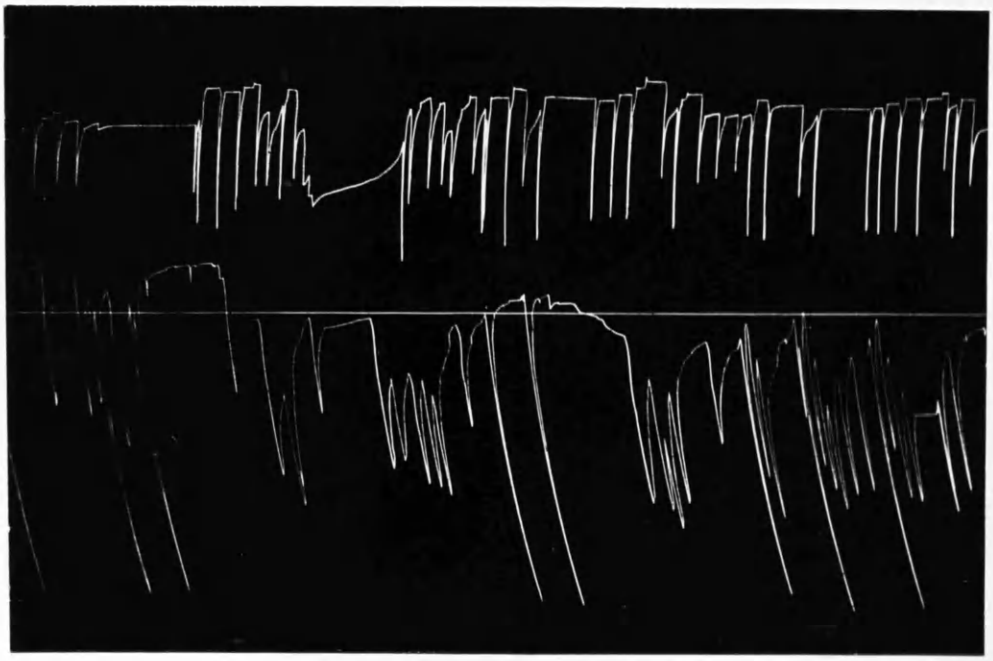
3

Tracing 1. Shell Movements 5. 7. 46. 3 hours recording shown on the tracing. Open 100% of the period. Degree of open-ness 90%. Closure at 4-minute intervals. Some evidence of rhythm. Temperature 18.5 - 20.4 degrees C.

Tracing 2. Shell Movements 5. 7. 46. 3 hours recording shown on the tracing. Open 100% of the period. Mean degree of open-ness 75%. No definite rhythm. Temperature 16.6 - 18.0 degrees C.

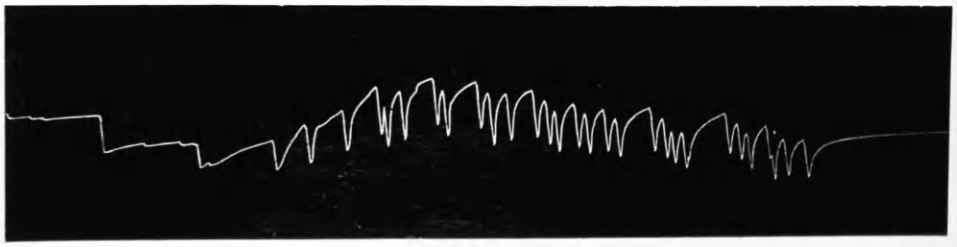
Tracing 3. Shell Movements 12. 7. 46. 2 hours and 25 mins. recording shown on the tracing. Open 100% of the period. Mean degree of open-ness 80%. Definite rhythm. Alternate activity as shown and inactivity at hourly intervals. Temperature 18.0 degrees C.

Tracing 4. Shell Movements 4/5. 7. 46. 2 hours and 30 mins. recording shown on the tracing. Closed shells for several short intervals. Rhythm evident. Temperature 19.0 - 22.0 degrees C.

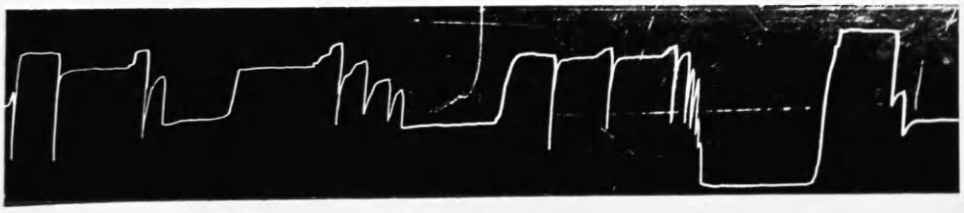


1

2



3

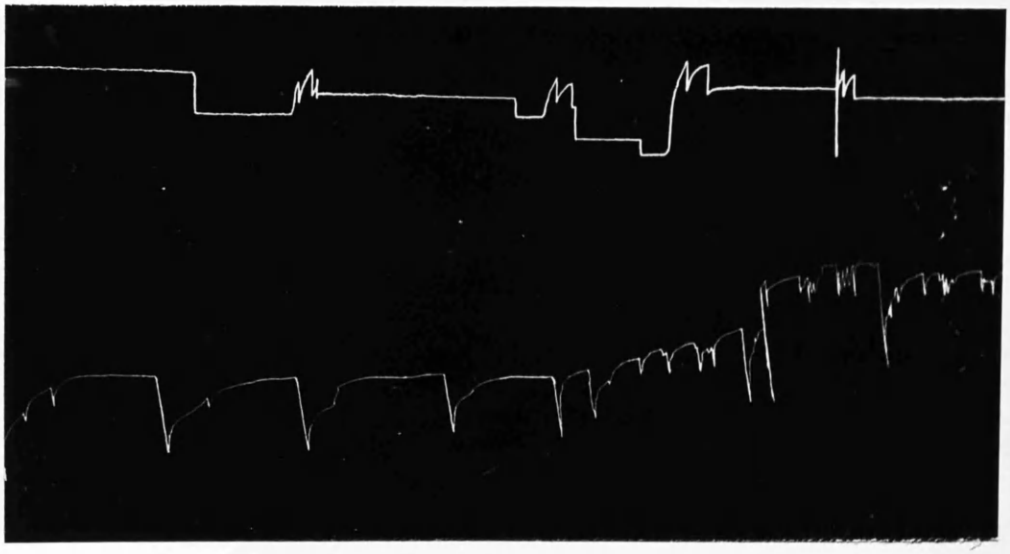


4

Tracing 1. Shell Movements 10. 7. 46. 3 hours and 25 mins. recording shown on the tracing. Open 100% of the period. Rhythm not definite. Temperature 19.5 - 21.5 degrees C.

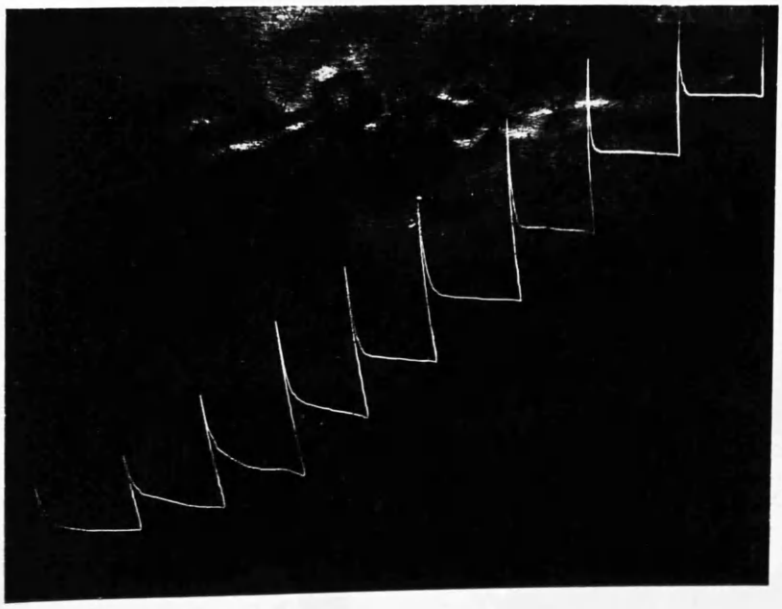
Tracing 2. Shell Movements 10. 7. 46. 3 hours and 25 mins. recording shown on the tracing. Open 100% of the period. Mean degree of open-ness 85%. Some indication of a rhythm. Temperature 20.3 - 21.3 degrees C.

Tracing 3. Digging Movements, soft sand. Number of consecutive sequences is 18, and the mean time between each sequence is 2.0 minutes. The mean extent of the downward movement (upward movement of the kymograph pen) in the first phase is 2.3 mm. with a maximum of 4.0 mm. Mean effective (final result) downward movement for each sequence is 1.3 mm. Note the slight dip before the upstroke of the pen. Movement from left to right.



1

2



3

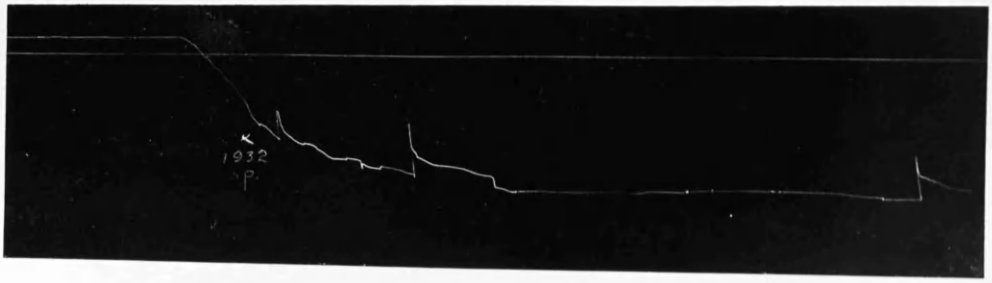
Tracing 1. Spawning Movements 11. 7. 47. Temperature 21 degrees C. Spawning by this female began at a point X at 19.32 hours and continued steadily until 21.33 hours. One hour of recording is shown on the tracing.

Tracing 2. Not significant in relation to spawning. Ordinary shell movements.

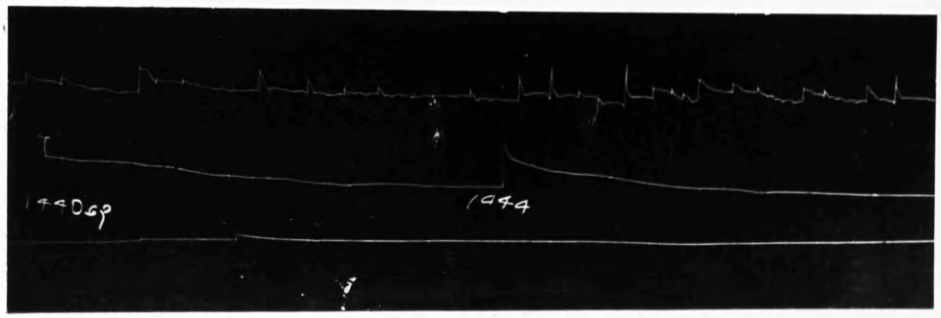
Tracing 3. Spawning Movements 8. 7. 47. began spawning 14.20 hours. Harnessed to the kymograph after several difficulties by 14.38 and restarted spawning at 14.40 hours. There was considerable pedal activity but no associated shell movement as can be seen from the tracing. Shell closure by stimulation was carried out at 14.44 hours. 8 minutes of recording is shown on the tracing. Temperature 18 degrees C.

Tracing 4. Spawning Movements 12. 7. 47. Female spawned between 22.10 and 22.25 hours. One hour and 20 minutes is shown on the tracing. 0.1 mm. 0.8 min. Temperature 16.1 degrees C.

Tracing 5. Spawning Movement 9. 7. 47. Female began spawning vigorously at 18.52 hours. First peak thereafter caused by a stimulated shell closure. One hour of recording is shown on the tracing. Temperature 16.0 degrees C.

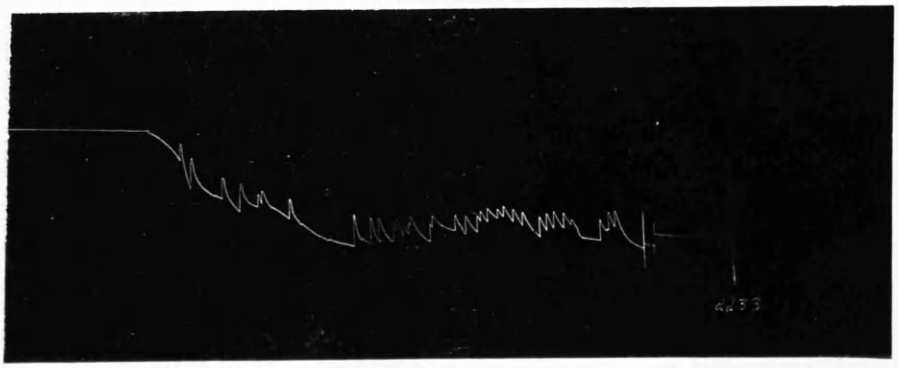


1



2

3



4

5

Plate 36.

Figure 1. Photomicrograph of a gonad section of a hermaphrodite, October 21st, 1947. Residual ova are seen among the follicle cells in the female section (left). Heidenhain. 7 u. x 540.

Figure 2. Photomicrograph of developing female, August 20th, 1946. A considerable number of residual ova are left. The ovocytes and follicle cells are seen against the alveoli walls. Heidenhain. 7 u. x 540.

Figure 3. Photomicrograph of a gonad section of a ripe female, June 23rd, 1946. The large ova are seen, some free in the lumen and some still attached to the follicle wall. Heidenhain. 7 u. x 1200.

Figure 4. Photomicrograph of a gonad section of a ripe female, June 23rd, 1946. Young ovocytes are seen on the follicle walls. Heidenhain. 7 u. x 540.

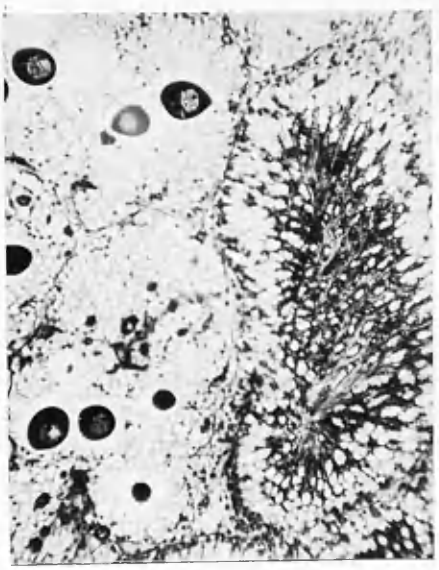


FIG. 1

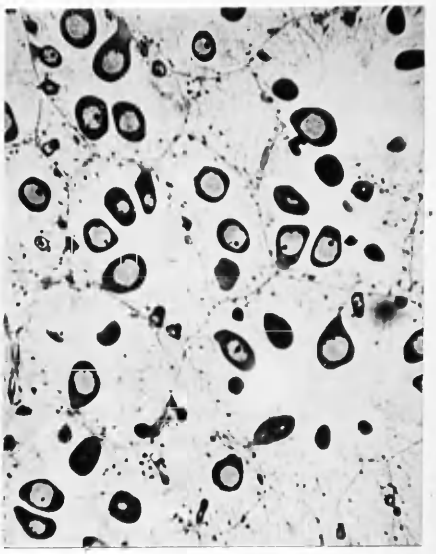


FIG. 2

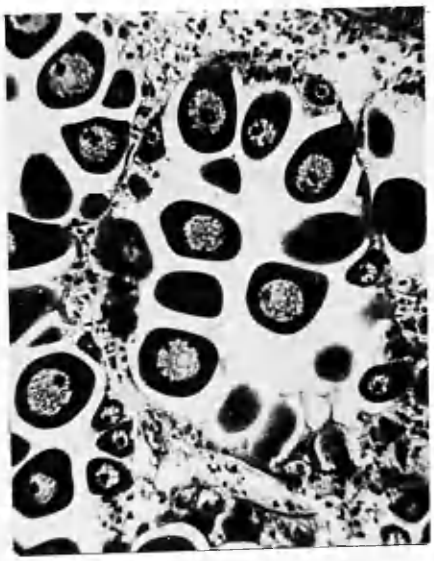


FIG. 3

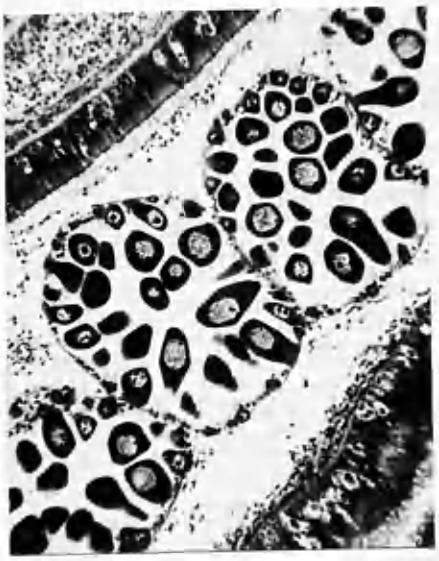


FIG. 4

Plate 37.

Figure 1. Photomicrograph of a gonad section of a spawned out female, July 26th, 1947. A few residual ova are seen, and some of the follicle walls appear to be broken down. Heidenhain. 7 u. x 540.

Figure 2. Photomicrograph of a gonad section of a spawned out female, July 26th, 1947. A few residual ova may be seen. Heidenhain. 7 u. x 1200.

Figure 3. Photomicrograph of a recuperating female, September 21st, 1947. The follicle cells and a few young ovocytes are seen. The residual ova are still present. Heidenhain. 7 u. x 1200.

Figure 4. Photomicrograph of a gonad section of a recuperating female, November 23rd, 1946. The lumens are filled with follicle cells and numerous ovogonia are seen on the follicle walls. Several residual ova are seen. Heidenhain. 7 u. x 540.

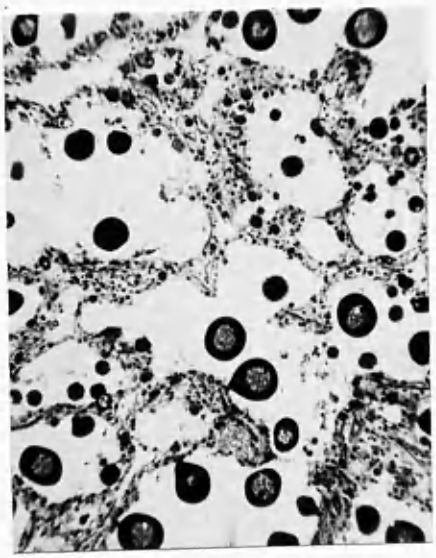


FIG. 1

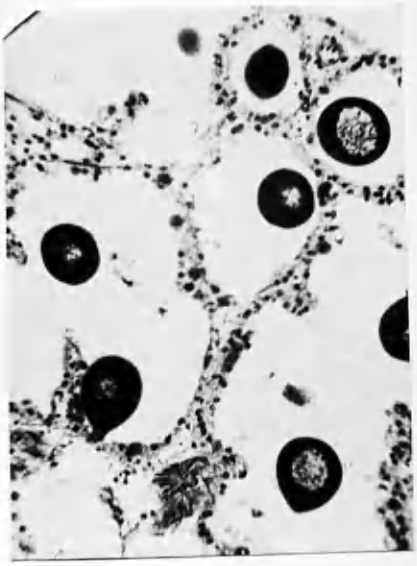


FIG. 2

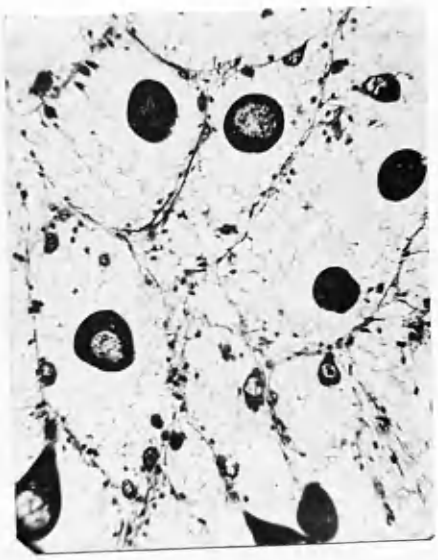


FIG. 3

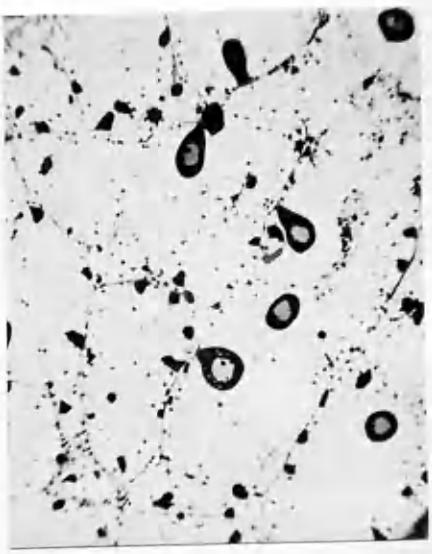


FIG. 4

Plate 38.

Figure 1. Photomicrograph of a gonad section of a male, October 1947. Shows the columnar arrangement of the sex cells, with the primary gonia along the follicle wall, and the sperms and spermatids in the lumen. Heidenhain. 7 u. x 540.

Figure 2. Photomicrograph of a gonad section of recovering male showing a typical "pattern" formation, October 21st, 1947. The sex cells appear to be arranged around the periphery of the follicle cells. Heidenhain. 7 u. x 300.

Figure 3. Photomicrograph of a gonad section of a male, June 23rd, 1946. The lumina of the follicles are nearly full of sperms. A few developing gonia may be seen along the outside edge of the follicle. Heidenhain. 7 u. x 540.

Figure 4. Photomicrograph of a gonad section of a male, May 25th, 1946. The spermatogonia and spermatocytes are scattered loosely throughout the lumina of the follicles. A small nucleus of spermatids and sperms may be seen in the upper right. Heidenhain. 7 u. x 540.

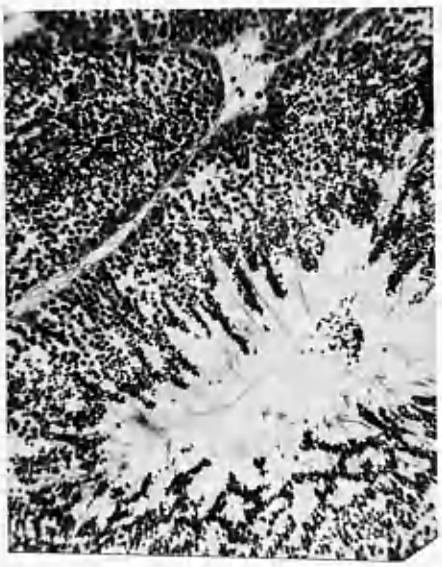


FIG. 1

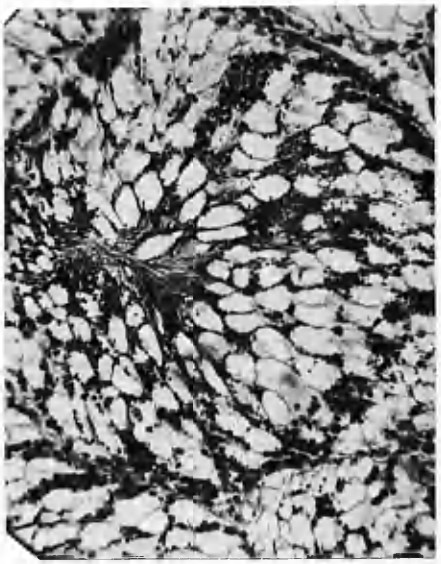


FIG. 2

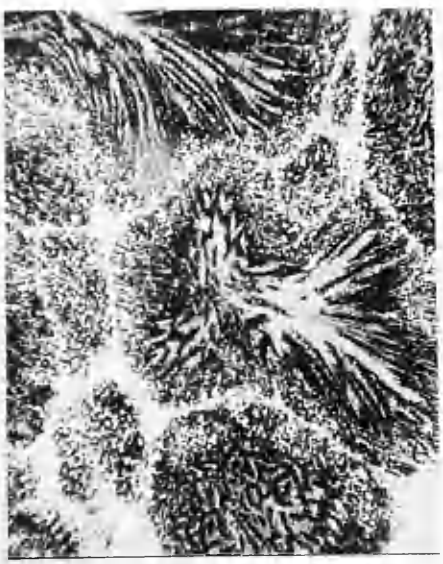


FIG. 3

FIG. 4

Plate 39.

Figure 1. Photomicrograph of gonad section of spawned out and recuperating male, September 18th, 1946. Note the follicle cells andthe thin walls of the tubules. Heidenhain. 7 u. thick x 1200.

Figure 2. Photomicrograph of gonad section of a male almost completely spawned out, August 1st, 1947. The few sperms are lying in the centre of the tubule. Heidenhain. 7 u. x 2160.

Figure 3. Photomicrograph of a gonad section of a spawned out male, August 1st, 1947. A few sperms still lie along the walls of the follicle. Heidenhain 7 u. x 1200.

Figure 4. Photomicrograph of a gonad section of a spawned out male, August 1st, 1947. Note the strands of muscle outside the follicle wall on the right. Heidenhain. 7 u. x 1200.

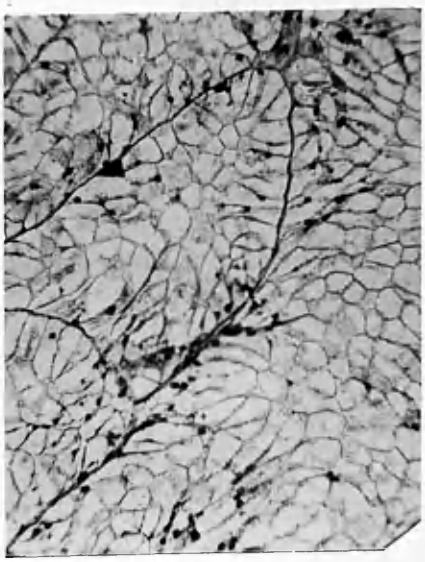


FIG. 1

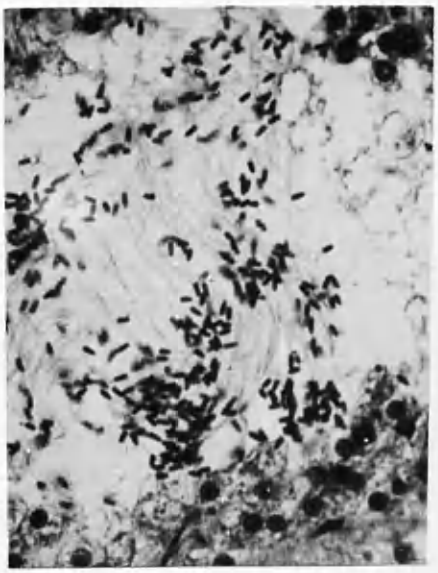


FIG. 2

FIG. 3

FIG. 4

Plate 40.

A series of photographs of spat of various sizes from Balloch Bay. The sizes are given below in the same relative positions. The left hand series do not show a winter ring, as it has not yet been formed, but will be in the position marked R1. These were taken September 3rd, 1946. The right hand series were taken June 2nd, 1947, and the winter rings (R1) are shown. Note the prodissoconch (Prod.) on the small spat in the left hand corner.

Sizes of spat in mm.	
1.63	1.75
3.18	3.70
1.36	1.75

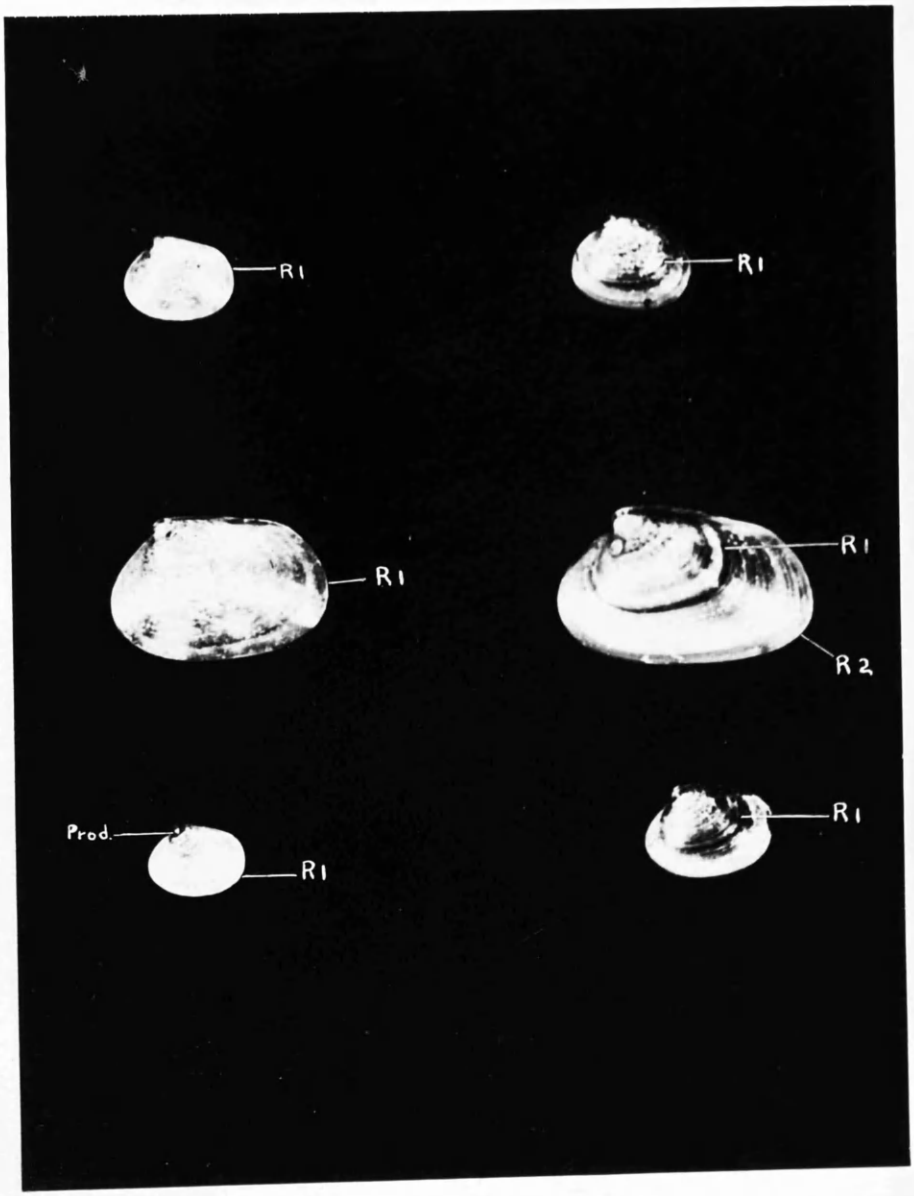

R1
R1
R1
R1
R2
Prod.
R1
R1

Plate 41.

Photographs of spat of the brood year 1946 from Balloch Bay, the sizes of which are given below in the same relative position as they appear in the plate. The left hand pair, taken June 2nd 1947, show the winter ring (R1). R2 shows the position of the second ring which, of course, has not yet been formed. The right hand pair were taken September 3rd 1946, and the winter ring (R1) is still in the process of being formed.

Sizes of spat in mm.	
6.82	5.52
5.46	4.35

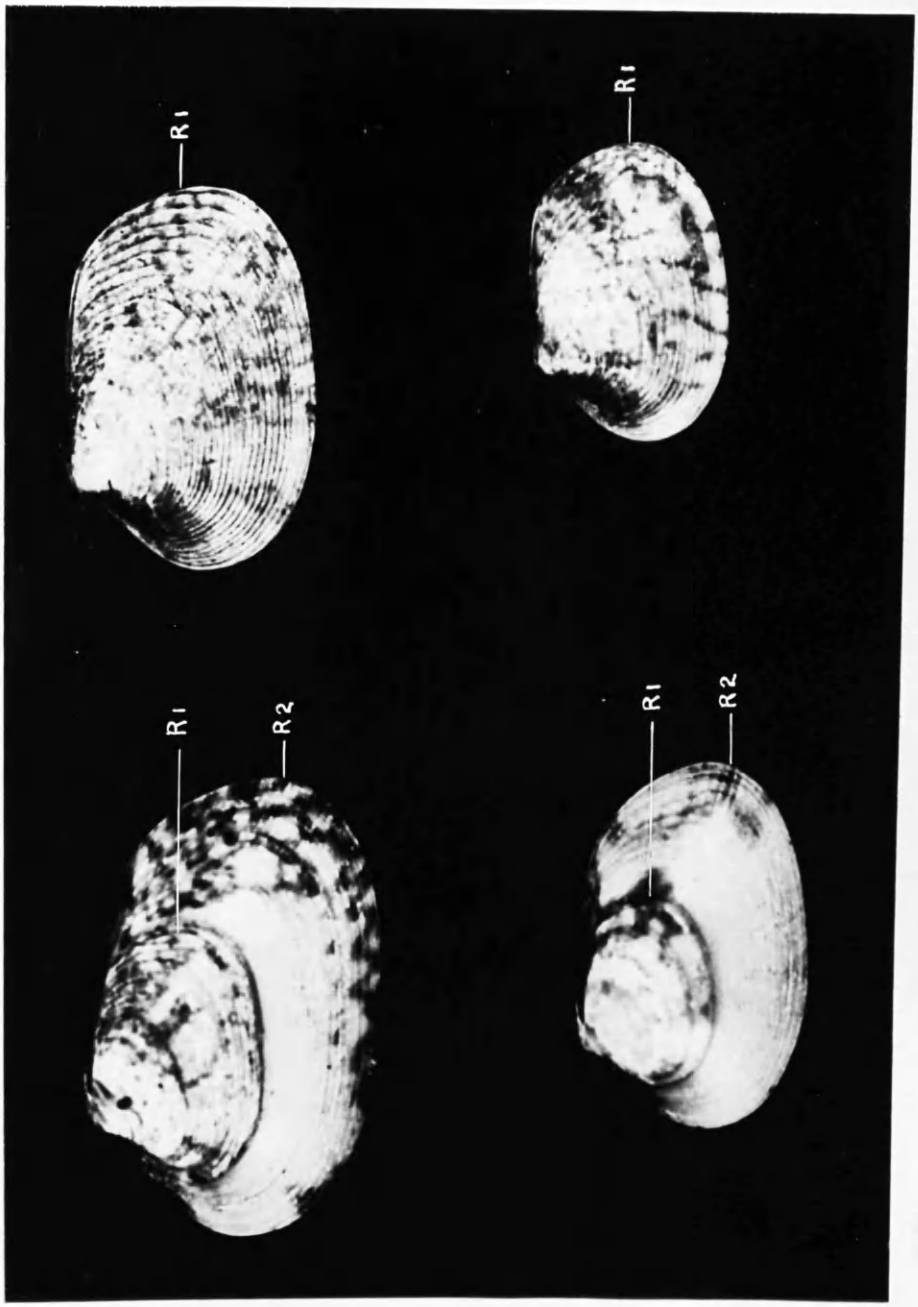

R1
R1
R1
R2
R1
R2

Plate 42.

Graph showing a length-frequency distribution of a June, 1946 random sample from the Cross Houses Beach. Data taken from Table 17a.

PLATE 42

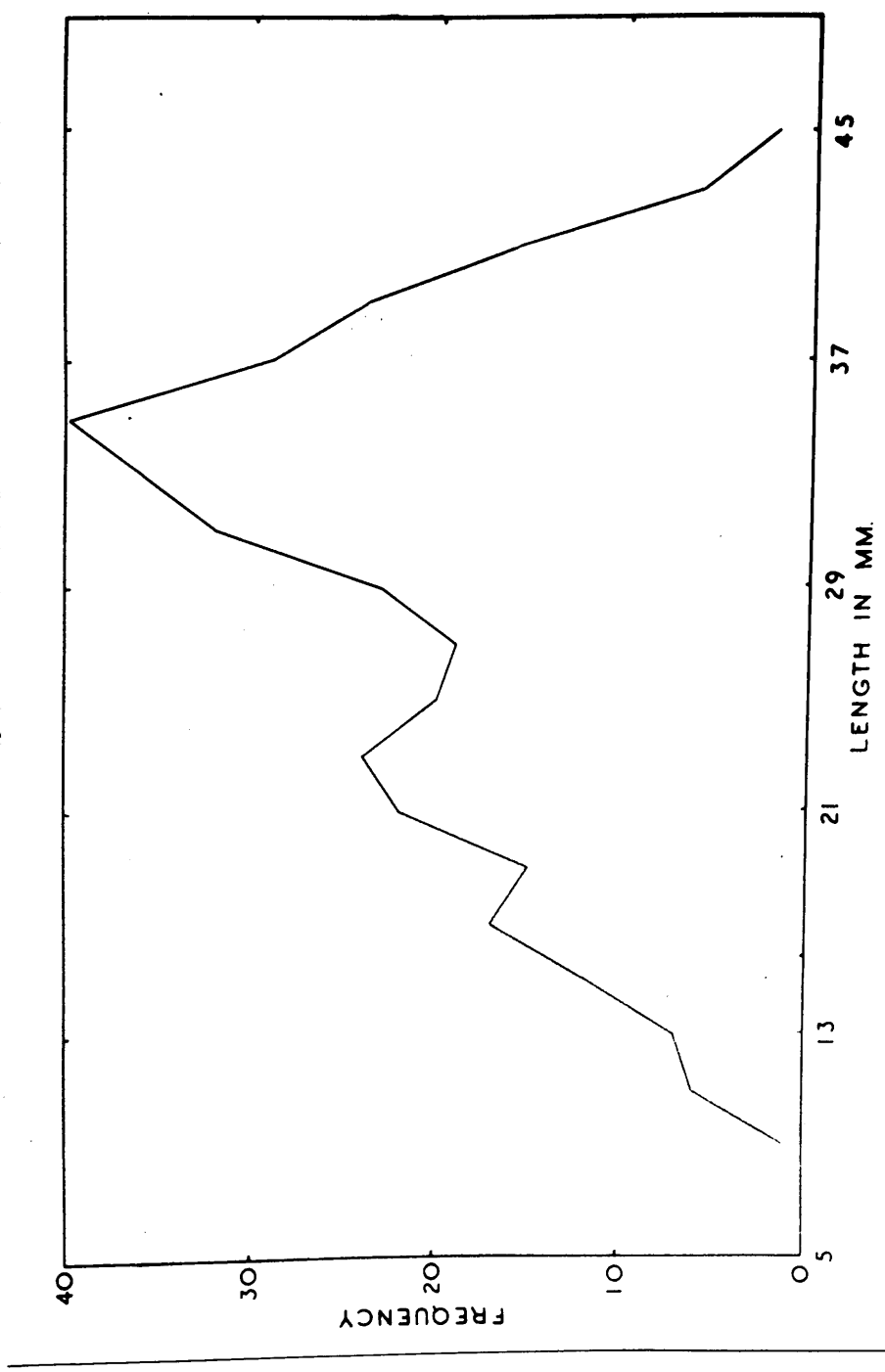


Plate 43.

Graph showing the length increment gained by the various age (Ring number) groups, marked and planted on a beach on North Cumbrae, for the period September 17th, 1946 to October 20th, 1947. Data taken from Table 18.

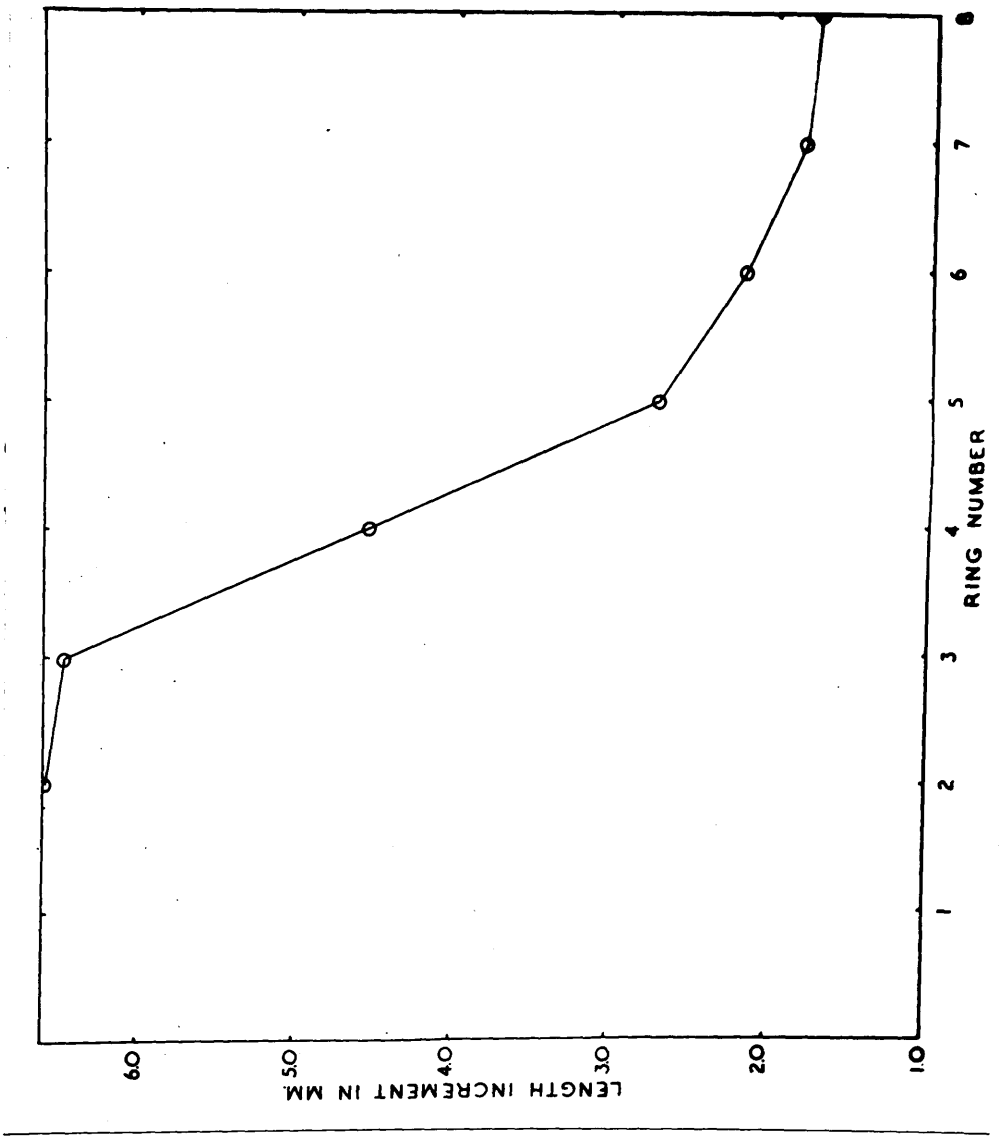

LENGTH INCREMENT IN MM.
1.0
2.0
3.0
4.0
5.0
6.0
RING NUMBER
1
2
3
4
5
6
7
8

Plate 44.

Photographs showing the winter rings on adults. There is an indication of a disturbance ring at the location of the injury in the lower photograph, otherwise the rings appear to be true winter rings. The upper animal is in its seventh year, and the lower one in its fifth.

Plate 45.

Photographs of adults from the Cross Houses Beach. The upper photograph shows the mark of an abrasion caused by the friction against a rock. The abrasion has penetrated to the nacreous layer.

The lower photograph shows the distortion that may be, and quite often is, caused by the cramped position, typical of the Cross Houses Beach habitat.

Plate 46.

Graph showing the length-on-age (Ring number) growth curve. Data taken from Table 19.

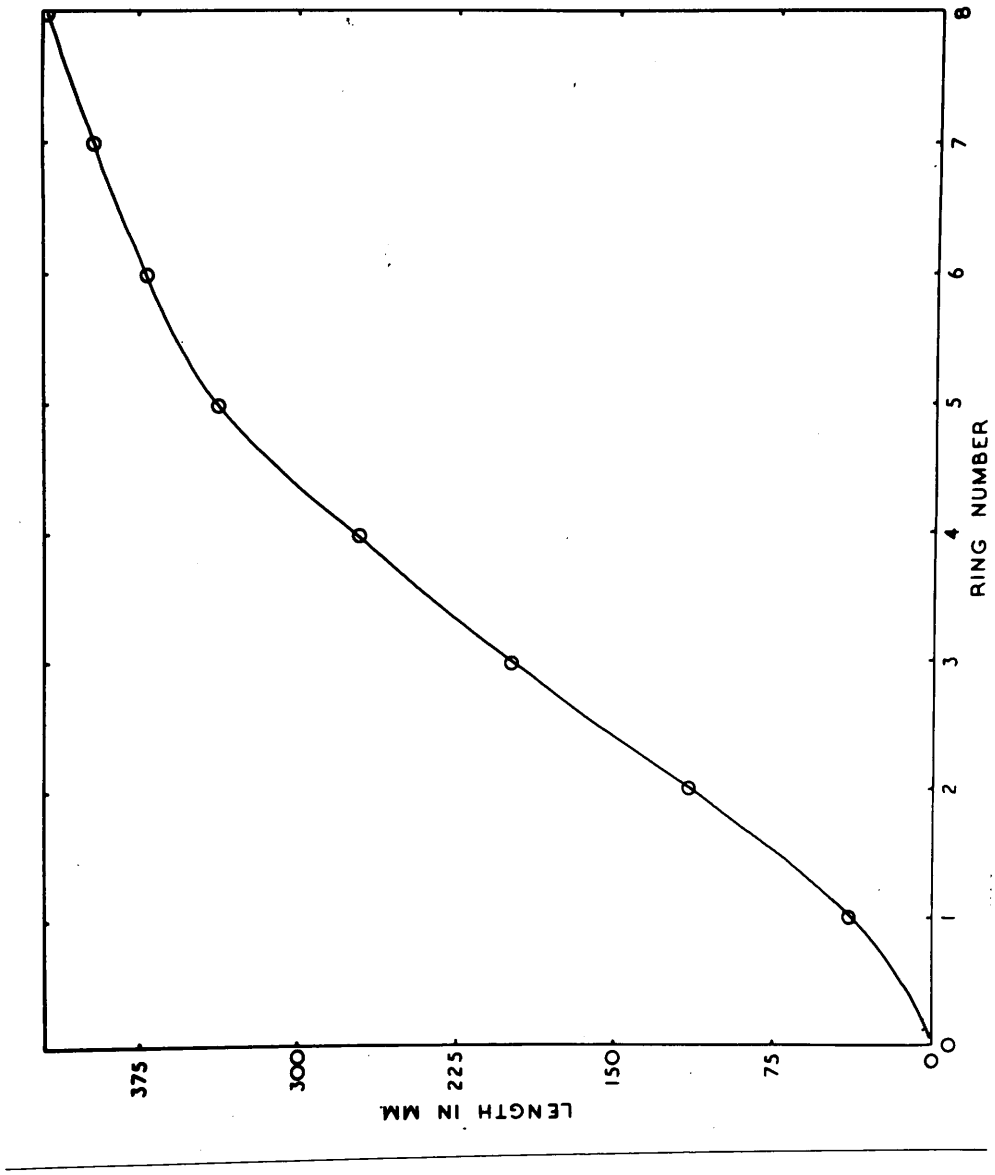

LENGTH IN MM
375
300
225
150
75
0
0
1
2
3
4
5
6
7
8
RING NUMBER

Plate 47.

Graph showing the length-frequency distribution of all the ring length measurements for the October random sample of adults from the Cross Houses Beach. The data is taken from the initial ring measurements and this information is not given as such in any of the Tables.

PLATE 47

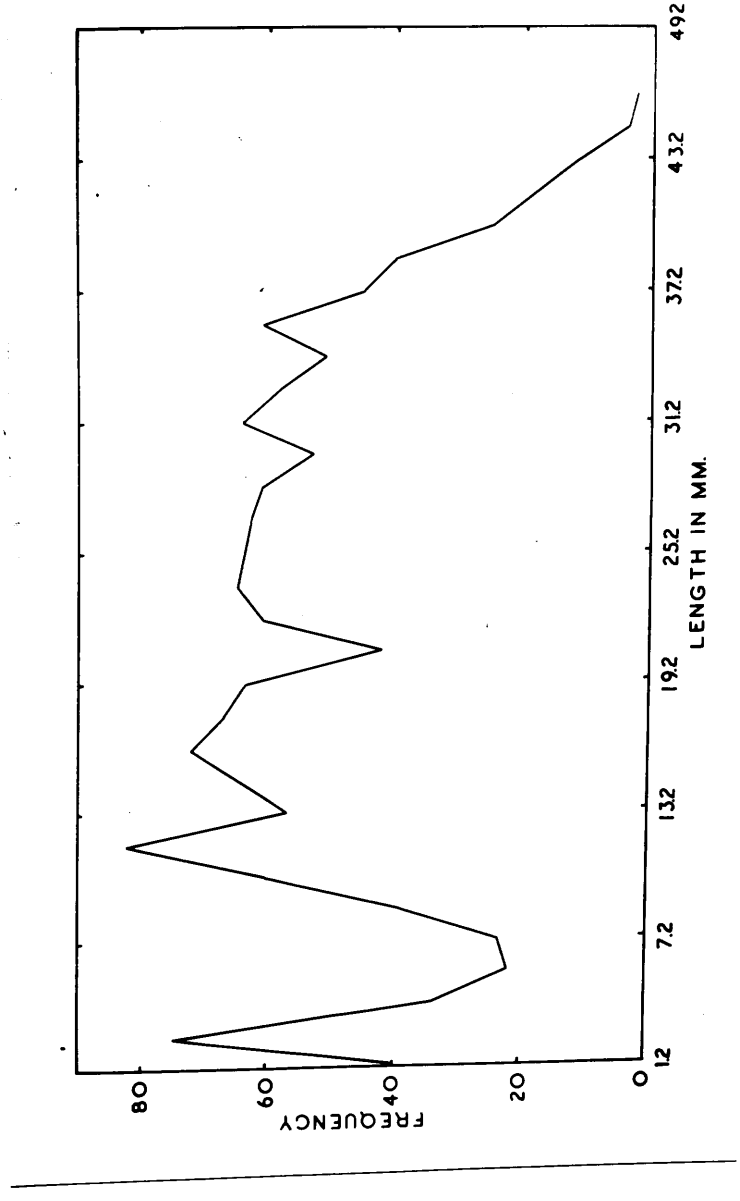

FREQUENCY
0
20
40
60
80
1.2
7.2
13.2
19.2
25.2
31.2
37.2
43.2
49.2
LENGTH IN MM.

Plate 48.

Graph showing the mean monthly increment of all sizes for the period April to September, 1947. The data is taken from Table 21. The broken line is the mean weekly temperature over the period.

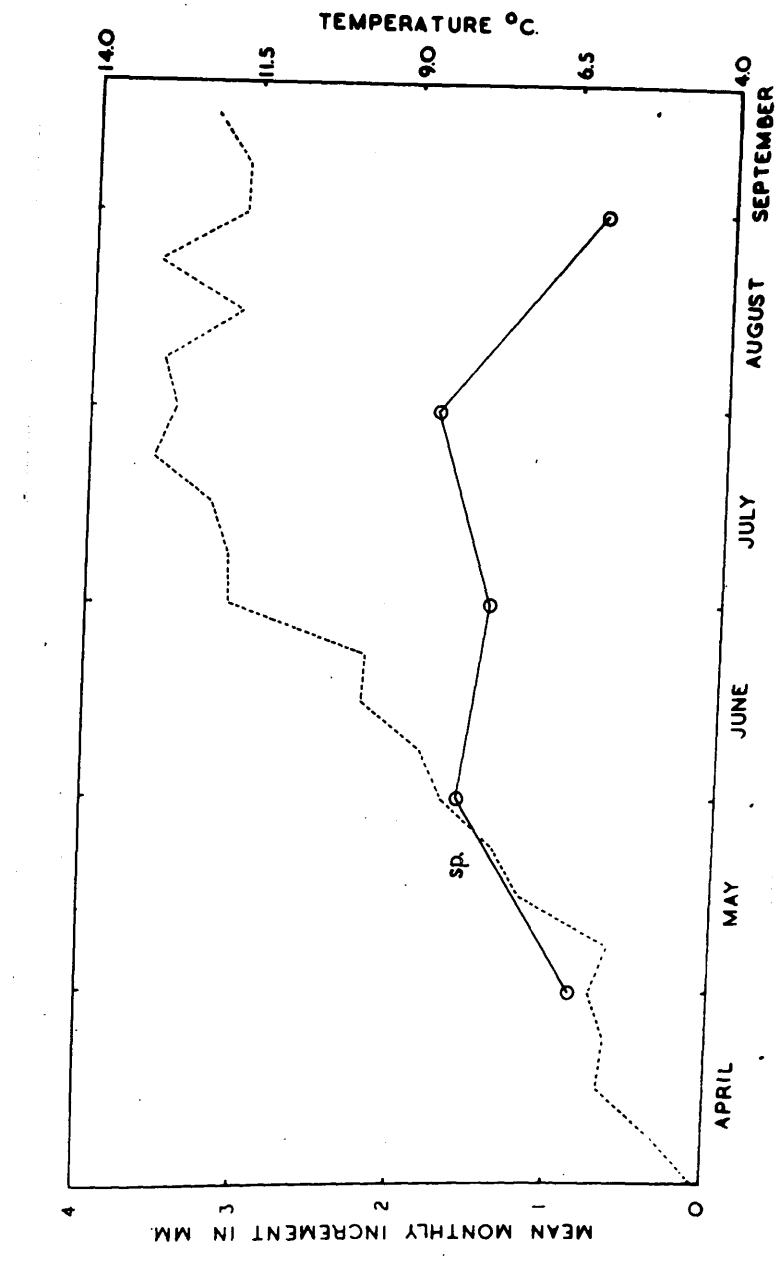

TEMPERATURE °C.
14.0
11.5
9.0
6.5
4.0
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
sp.
MEAN MONTHLY INCREMENT IN MM.
0
1
2
3
4

Plate 49.

Graph showing the height-length (unbroken line) and the thickness-length (broken line) ratios of various sizes of adults from the Cross Houses Beach 1946. The data is taken from Table 23, and the lines are drawn as they best fit by inspection only. The dots represent the plotted data.

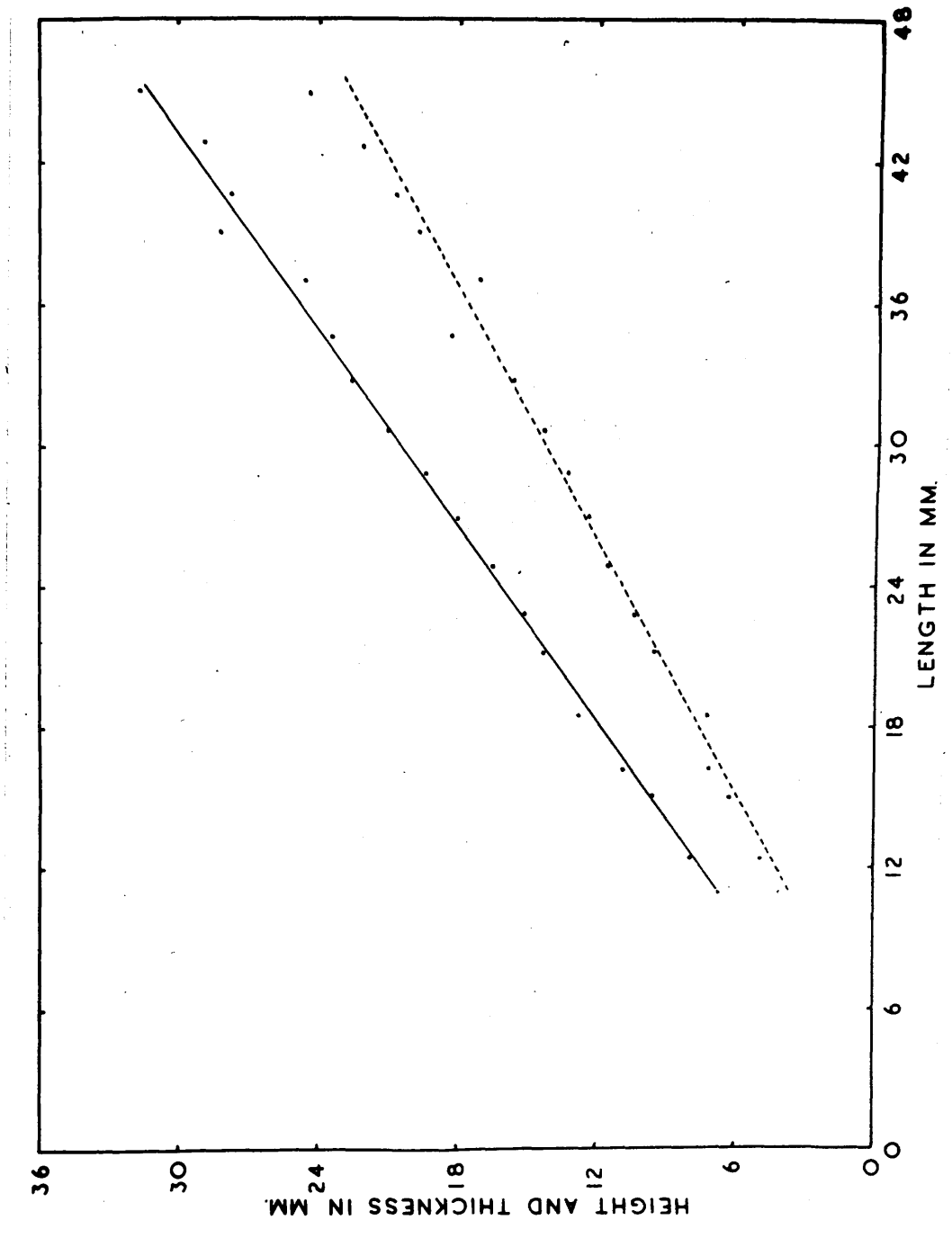
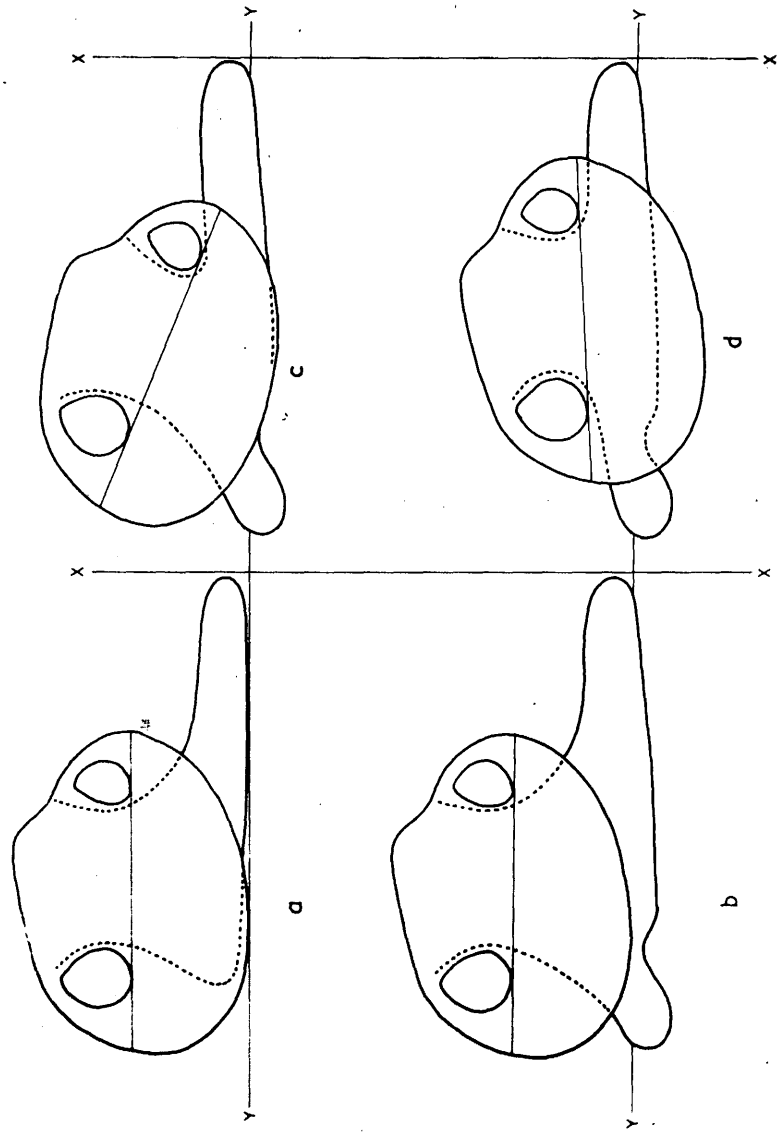

HEIGHT AND THICKNESS IN MM.
0
6
12
18
24
30
36
LENGTH IN MM.
0
6
12
18
24
30
36
42
48

Plate 50.

Diagrammatic representation of the digging movements as described in the text. 'XX' and 'YY' are vertical and horizontal lines of reference.


X
Y
X
Y
c
d
X
Y
X
Y
a
b