THE REPRODUCTION AND DEVELOPMENT OF PECTEN MAXIMUS (L.)

by

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C O N T E N T S.

THE REPRODUCTION AND DEVELOPMENT OF THE ESCALLOP, PECTEN MAXIMUS (L).

I. INTRODUCTION.

A fishery for escallops (*Pecten maximus*) was started in the Isle of Man in 1937; thirteen boats were employed in the dredging off Port Erin Bay, and the nett proceeds for that season amounted to nearly six thousand pounds sterling.

The fishing ground was situated to the south-west of the island, and landings were made at Port Erin, so that it was possible to obtain large numbers of escallops for study at the Biological Station.

Comparatively little is known about the breeding time or the life-history of the escallop (see e.g.Ministry of Agriculture and Fisheries Publication F.G. 14034). The escallop, in fact, has attracted much less attention than certain other bivalves. Fullarton (1889) worked upon the development of *Pecten opercularis* which were obtained from the Firth of Forth. He dealt intensively with the cell-division stages, but left the later stages obscure. Drew (1906) investigated the habits, anatomy and embryology of the American Giant escallop, *Pecten tenuicostatus*. Nevertheless the embryology was only a small part of his paper and did not give complete knowledge.

Dakin (1909) produced a Memoir upon Pecten in the L.M.B.C. series. He worked mainly upon Pecten maximus which was obtained from the beds at Port Erin, and naturally dealt most fully with the anatomy of the adult, although he made some reference to the embryology. A rather complete life history of Pecten irradians, the bay or shallow water escallop, was produced by Belding (1910) and later Gutsell (1930) worked on the same species. Certain important points, however, were not included in these papers, especially the metamorphosis of the animal during the formation of the intestine.

The present paper is intended to fill up such gaps in our general knowledge and to give an account of the spawning time, which may be of use should any legislation be necessary to protect the beds in Manx waters from overfishing.

Experimental work was started in November 1937, and finished in December 1938. Of this, the artificial fertilisation experiments were carried out at Port Erin, Isle of Man, during the period from November 1937 to July 1938, and observations upon the gonads of the adult were also made at Port Erin and finished in the Department of Oceanography, Liverpool University. The total number of escallops examined during the period was 1,024.

The work was carried out at the suggestion of Dr. R. J.

Daniel; and I wish to thank Mr. W. C. Smith, the Curator of Port Erin Biological Station for his kindness in obtaining the samples of escallops used in these investigations.

II. MATERIAL AND METHOD.

II) Material.

The escallops (Pecten maximus) used in the investigations were dredged by a fisherman from Port Erin who was working the ground off Port Erin Bay. The dredging was carried on inside an area 12 miles long and 5 miles wide. It lies along the south-west coast of the Isle of Man, and stretches from the Calf past Bradda Head and Fleshwick Bay to Niarbyl. (Map). The depth of water over the beds is from 14 to 17 fathoms. Once a week, or once a fortnight, a fisherman supplied four dozen live escallops for use in these experiments and this continued for fourteen months from November 1937 to December 1938.

Owing to the fact that the net mesh of the escallop dredge is limited to a certain size by the fishery authority, for preserving the seed escallops on the beds, the samples which were obtained from the fisherman and examined for these investigations were mostly confined to the market size. Occasionally, however, some seed escallops were contained in the net, but only a small number were landed.

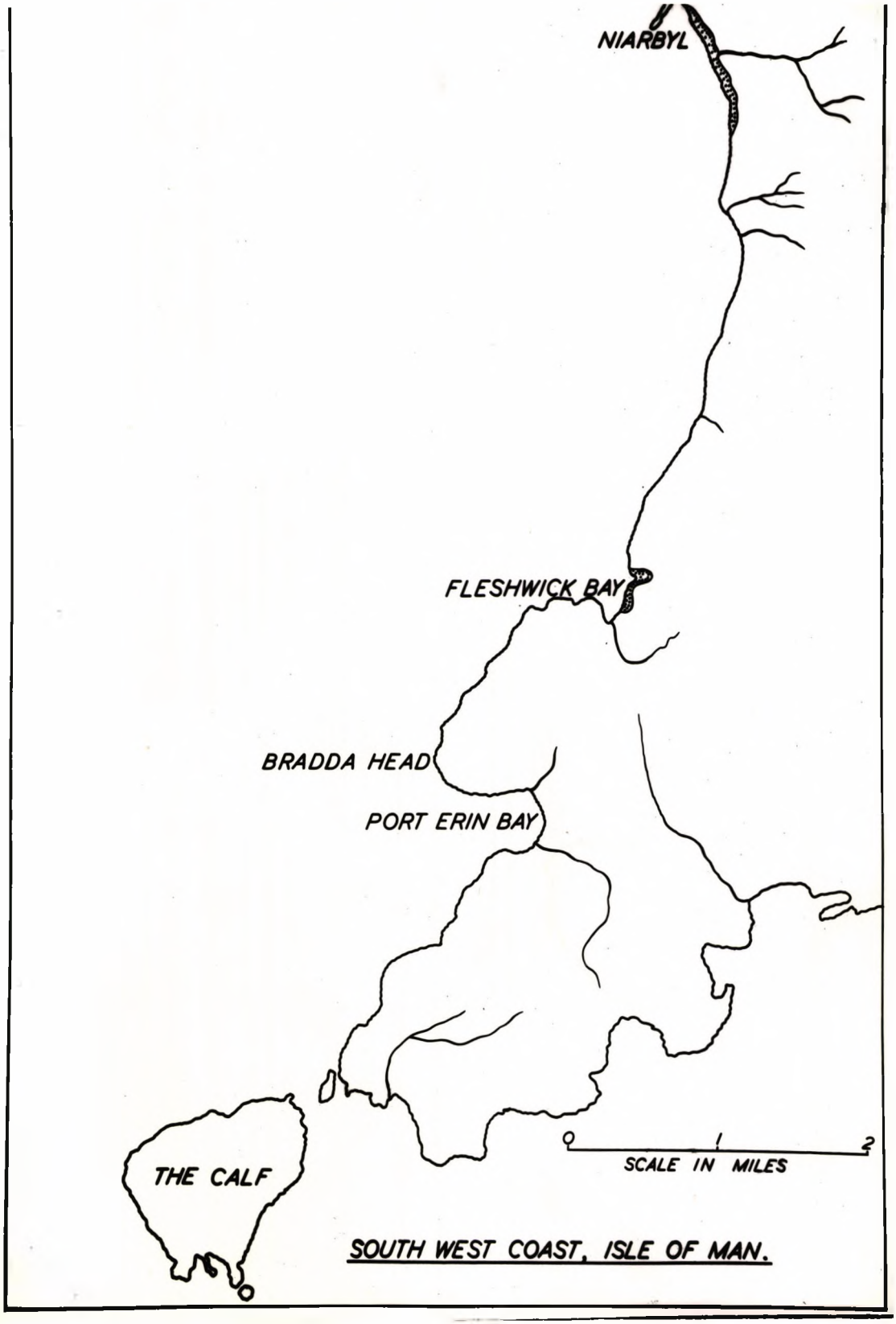
When the escallop season was over in April 1938, special arrangements were made for a fisherman to continue supplying samples throughout the close season, using the same type of boat, and dredge, and working on the same ground.

A description of the Escallop Dredge. The implement which was used for dredging escallops at Port Erin by the fishermen was an ordinary dredge, "The Scraper." It is made of two parts, the frame and the net. The frame is a triangular iron framework, except that the two sided curve is at nearly 90° towards the base; these curved parts form the sides of the net entrance. On the upper side, an iron cross piece connects the two arms; while at the bottom an iron blade extends across the dredge. This blade has 11 teeth which dig into the ground. The dimensions of the dredge frame are:- arms 110 cm. long, thickness of the iron 2 cm; cross bar, 17 mm. in thickness. Height from this bar to the blade, i.e. height of the net mouth, 33 cm.; blade, 144 cm. long, 4 cm. wide; teeth, 10 cm. high, 26 mm. wide at the base.

The net is made of two different pieces, the upper side is a twine net which is fastened to the iron bar; on the lower side, it is a network of iron rings attached, at the forward end, to the blade. The iron rings are connected to one another by ringlets. The upper part is 12 rows by 16 rows, and made of twine 4 mm. in diameter; the distance between knots is 65 mm. The lower part has 9 rows of rings by 10 rows; the ring itself is 6 mm. in thick-

ness, and 96 mm. in diameter. The ringlet is 6 mm. in thickness, and 20 mm. in diameter.

At the bag end of the net, a rectangular wooden bar, 48 mm. thick and 126 cm. long, is attached for buoying and extending the net when working in the sea.



SOUTH WEST COAST, ISLE OF MAN.

II) Method.

This investigation was carried out in three different ways. First, observations were made upon the state of the gonad throughout the year; secondly, artificial fertilisation of the ripe ova was carried out and subsequent rearing of the larvae in plunger jars; and thirdly, there was examination of water samples for the presence of escallop larvae. These samples were obtained from two sources, namely a pond at the Port Erin Biological Station containing four dozen adult escallops, and the area of sea over the escallop beds outside Port Erin Bay.

(a) Observations were made on gonad conditions in escallop samples for fourteen consecutive months from November 1937 to December 1938. A total number of 1,024 were examined. Comparisons were made in the colour of the gonad contents, the size and shape of the whole gonad, the condition of the gonaducts, and microscopical examination of the ova and sperms, obtained from the gonad or from the kidney duct through which the reproductive elements are extruded.

As a result of such comparisons it was possible to divide the annual reproductive cycle of the escallop into five well-defined stages. These were as follows:
a) Recovering stage, b) Filling stage, c) Full stage, d) Spawning stage, e) Spent stage. The percentages of the different stages in each sample were obtained. Measure-

ments of the gonad were made with a caliper scale, and the colour standards are those given in the plates of the international work "Colour Standards and Colour Nomenclatures" by Robert Ridgeway, Washington 1912. The gonads representing each stage in each sample were fixed in Bouin's fluid and then sectioned and stained in Ehrlich haematoxylin and eosin.

(b) Artificial fertilization. Before starting an experiment all the finger bowls and other apparatus which were to be used for the experiments were sterilised by boiling for 10 minutes and then kept as clean as possible. Sea-water for use in the bowls and jars was collected from outside the Bay, and then run through fine silk in order to remove the macroplankton. The water was brought from the escallop beds in four dozen clean glass jars. During stormy weather the water was turbid, and in such cases it was allowed to settle before being siphoned out of the jars.

Ripe escallops were selected for the fertilisation experiments. Twenty-four bowls each of 500 c.c. capacity were then taken and each one filled up to two-thirds of its volume with clean sea water; one of these bowls was used for collecting sperms, the others for the ova.

The female part of the gonad was opened by means of scissors, but the ripe ova ran out easily into the bowls. Usually the ova in each bowl was obtained from one escallop.

Sperms were also obtained by cutting the gonad epithelium. The cutting had to be done carefully because the loop of the intestine inside the gonad is quite near the posterior end of the female part. If any part of this intestine is injured, the contents will soil the reproductive products and the experiment will fail.

Before adding sperms to the ova it was necessary to allow the latter to stand a few minutes in the bowls, and then decant the surface layer of water, which carried away any burst ova and epithelial tissue which had run from the gonad during the operation. The sound, orange-coloured ova lay on the bottom of the bowl and were retained. The bowl was filled up with a fresh supply of sea water and then one or two drops from the bowl containing sperms were added.

Fertilization was possible in a few minutes and certainly took place within half an hour if the water temperature was above 10°C. Every ten minutes the contents of the bowl were stirred gently in order to assist in the mixing of sperms and ova. After several stirs, the ova were allowed to settle, and then the super-natant water was decanted and the bowl filled up again with sea water. This was done every half hour during the first three hours, then once an hour for the next three hours. At the end of this time the water in the bowls was clean and needed only to be changed every three hours.

On the second day of the experiment when the gastrula stage was reached, the brood had to be transferred into the plunger jars. In spite of the plunger mechanism it was necessary to change the water three times a day.

In order to avoid changes of temperature when changing the sea water in the jars, the newly collected water, always obtained from over the escallop beds three miles outside the bay, was allowed to stand in the experimental room for at least one day before being transferred to the jars.

In order to change water in the experimental jars, one third of the volume was siphoned away, and for this purpose a funnel with fine silk stretched across it was used to keep back the larvae. Silk was also used in a similar way in order to filter out organisms when the new sea-water was used to replenish the plunger jars. In this way larvae as small as 68 μ x 61 μ were kept back and any plankton organisms bigger than the larvae had no chance to intrude into the plunger jars.

In order to keep the experimental bowls and jars clean, flat glass plates or "Windolite" covers were used. In all twenty-seven experiments of this type were set up during the period of time from February 1st 1938 to the end of July of the same year.

c) Planktonic examination. Four dozen adult escallops

were placed in one of the Station large outdoor ponds. At given intervals a fine plankton net was drawn through the pond water at different depths, and the collected plankton was examined for the presence of escallop larvae.

Samples of outside sea water were also obtained during the same period, at intervals of approximately one week. The plankton filtered from this water was also examined.

Larvae to be kept for examination were plunged into hot Bouin's fixative, and left to cool in it for six hours. They were then washed and stained in a saturated solution of cochineal for five days. This was found to be a superior stain to Para-carmine or Borax-carmine. In order to retain the larvae through the various processes in staining they were confined in a small tube closed at the lower end with fine silk.

The sperms were fixed by Osmic acid vapour, and then stained with one drop of N/10 Potassium Iodide. This stain gave a yellowish brown colouration, and showed distinctly the head, nucleus, and tail under the microscope.

III. ANNUAL REPRODUCTIVE CYCLE OF THE ESCALLOP.

Pecten maximus is hermaphrodite and there is one bisexual reproductive organ, the tongue-like gonad, which only becomes apparent when the escallop approaches maturity at 2 - 3 years of age.

Although Pecten maximus is fished commercially in the British Isles, no clear views have yet been expressed as to the extent of the breeding season. An examination of gonad condition throughout 1938 showed that on the Port Erin beds, spawning escallops were present for eight months, from January to August, and from the observations, it is possible to state the time of breeding for this locality.

As a preliminary to this part of the work, however, it will be well to describe the gonad itself and the age at which the escallop reaches maturity.

1. AGE OF MATURITY.

Because the samples obtained from fishermen for this investigation were confined to market size of escallops, younger ones, under five years of age, were not obtained in large numbers, but sufficient of them were examined to determine the age of maturity.

Escallops as young as two and a half years were brought in by fishermen during March 1938, and in these the gonads

were just beginning to develop. The gonads were whitish in colour and semi-transparent and the largest ones measured about 3 cm. x 8 mm.

There was the beginning of sexual differentiation in these gonads; the whitish male portion seemed to occupy a larger volume than the semi-transparent female portion, although at such an early stage of maturity it was not easy to distinguish the two parts. The whitish area extended to the point where the gonad was attached to the adductor muscle; the seat of this extension is female in older escallops.

Sections of such gonads reveal that they had reached a stage of spermatogenesis and oogenesis, midway between the virgin and maturing stages.

Therefore Pecten maximus is probably at least two years and a half old before it reaches maturity.

In two younger stages, the male contents of the gonad had begun to develop a little earlier than the female.

It may be seen in sections that when female follicles are only just beginning to produce a few mother cells, the male follicles already contain quantities of spermatogonia. In more advanced cases, when there are plenty of oogonia in the female portion of the gonad, together with a few mother cells in each follicle, the male follicles are entirely filled

with spermatogonia. These observations agree with statements made by Petersen and Spärck about Ostrea edulis. Petersen (1907) says that oysters with spawn are at least two years old, and usually three years; and Spärck (1924) states that in the oyster spermatogenesis always precedes egg-development.

2. DESCRIPTION OF THE GONADS.

a) Position of the Gonad.

The gonad lies postero-ventral to the rudimentary foot and to the adductor muscle, and is also attached to the latter. (Fig.31).

When the escallops are maturing or have recovered from spawning, the gonad generally consists of two different parts, one a white-coloured male portion and the other an orange-coloured female portion. The male part is adjacent to the foot and extends to the middle of the gonad; the female part runs from the middle part to the posterior end of the gonad.

The gonad is comparatively broad and thick in the middle position, flattened at the male end, and assumes a conical shape at the female end. The free ventral keel is convex in outline and sharp; while the dorsal boundary, attached to the adductor muscle, is concave and thickened.

b) Distribution of Sexual Products.

The male elements occupy the anterior and most of the

dorsal part of the gonad; the female, the posterior and ventral part. These parts interlock, and the curved line of junction is made very irregular by the presence of a series of depressions and prominences. If cross sections of the gonad are taken, the main male part is shown to be triangular in shape; the middle, ellipsoid, and the main female part, circular.

A transverse section in the vicinity of the junction shows that the male tissue is partly surrounded by the female tissue.

A loop of the intestine runs through the gonad from one end to the other end.

When the male products multiply, the anterior portion of the gonad swells up and then extends forward until it envelops part of the digestive gland.

c) Ducts of the Gonad.

The gonad has two main ducts which open into the kidney respectively from both sides. Ova and sperms from the ducts pass through the passage of the kidney out into water by the way of the posterior opening of the kidney.

When the escallop is spawning the orange-coloured ova can be seen inside the main gonoducts and the kidney passage. They show up more clearly on the right side, because this duct is much bigger than the one on the left side.

The ramified branches of the gonoducts can be seen with the naked eye when the colour of the ripe ova makes a background for them.

d) Gonad Volume.

The average volume of a ripe gonad of an escallop of market size is 12 cubic centimetres, and the average surface area is 27 square centimetres. With regard to the surface area only, the female portion covers a larger area than the male, because the former spreads superficially on the right side of the gonad and envelops the latter to some extent. On the right side of the gonad, the male surface area is comparatively about six-sevenths that of the female; while on the left side, the ratio is eight-elevenths.

e) Male Outgrowth.

On the male part of the gonad there are two similar outgrowths each situated on a lateral side and lying in a position between the antero-dorsal corner of the gonad and the extremity of the kidney.

Each outgrowth is oblong, semi-lunar in shape, lying vertical or parallel to the kidney, and measures approximately 7.0 mm. in length and 4.0 mm. in width.

Sections reveal that it lies within the boundary of the main part of the gonad and the ducts distributed in it are

directly connected with those of the main part.

It is found that the condition of the outgrowths is changeable in accordance with the general state of the main gonad. The outgrowth, therefore, is a reflection of the condition of the gonad.

It is,however, not present on gonads of escallops which are less than three years old.

It is also found that in specimens where the gonads are in a partly-spent condition, the male outgrowth may be empty of contents or partly full. In the latter condition the reproductive products are confined to the outgrowth on the right side. This may be due to the fact that there is an earlier discharge of the male products on the left side.

f) Encroachment of Male and Female Reproductive Products.

Under normal conditions male and female products do not intermix with one another in the gonad. Abnormal cases, however, did occur in certain specimens examined during this investigation.

Islets of male tissue were found embedded in the female part of the gonad in five cases out of a thousand; female islets in the male part were also found in five cases out of a thousand.

In only one case was the whole of the gonad female.

Such encroachment of sexual products may also happen

in the male outgrowth on the male part of the gonad. In three out of a thousand specimens examined, the male outgrowth contained also a certain amount of ovigerous tissue; this was found only to the right side of the outgrowth, since the female tissue always tends toward the right side in the escallop.

3. Variations in Gonad Condition.

As mentioned briefly in the section on Method, observations on the gonad conditions of each sample were made macroscopically and microscopically.

In order to facilitate comparison of gonad condition the following convenient types of stages were chosen.

a) Recovering spents.

b) Gonad Filling.

c) Gonad Full.

d) Gonad Running. (Spawning).

e) Spents.

These five stages make up the annual reproductive cycle, and may be easily separated one from another. In particular this is due to the characteristic colours of the gonad found in each stage. These colour differences in the female tissue depend on the proportion of red and orange pigments that are present.

As the animal proceeds to the ripening stage during its

annual cycle, a quantity of nutritive matter or deutoplasm is gradually stored in the ova. As a result of this deposition, the colour of the female varies considerably with the stages.

It has been convenient to refer to these colours to the Colour Standards adopted by Ridgway (1912). Under this system the female part of the organ ranges from Bittersweet Pink to Orange Chrome.

In the year's record under review the five stages were distinguished as follows:-

a) Recovering spents. - Bittersweet Pink or Bittersweet orange.

b) Gonad filling. - Safrano Pink or Grenadine Pink

c) Gonad Full. - Grenadine or Shrimp Pink.

d) Gonad Running. - Strawberry Pink or Peach Pink.

e) Spents. - partly spents - orange chrome.
- completely spents - transparent.

The amount and kind of pigment laid down as the gonad develops may be measured according to Ridgeway's scale. The following table reveals that the percentage of the red hue gradually increases with gonad maturity.

Names	Red %	Orange %	Gonad Stages
Bittersweet Pink	18	72	Recovering spents
Bittersweet Orange	20	80	
Safrano Pink	31	47	Gonad filling
Grenadine Pink	36	54	
Grenadine	40	60	Gonad full
Shrimp Pink	47	31	
Strawberry Pink	52	36	Running
Peach Pink	60	40	
Orange Chrome	0	55	Partly spent

The testicular part also shows differences in colour, but these are less marked. As spermatogenesis starts in the stage of recovering, the organ becomes opaque; during the filling stage, it is whitish and opalescent, and at the full stage it is creamy. At the time of extrusion of the male elements, this part of the gonad is grey or brownish in colour. When it is completely spent, the male part of the gonad is colourless and transparent. These changes are a sure indication of increase in the male products before ripening.

It is also possible to distinguish more vital changes in the gonad from stage to stage and the characteristics for each stage are given below.

a) The Recovering Stage - (Gonad less than half-filled).

During this stage, the whole gonad has a tongue-like shape, with the free end rather flattened. (Fig.1). When the tissues become partly recovered the gonad takes on a different appearance; it is filled with new elements, and in colour some of the female side has a bright Bittersweet Pink or Bittersweet Orange Tint which is due to the newly deposited pigments in the ovigerous tissue. While on the male part it is still dark grey and dull.

A transverse section of the male part at this stage shows a concave-acute triangular outline. The contents mostly are spermatocytes with a small number of spermatogonia at the periphery of the follicle.

The spermatocytes are smaller in size than the spermatogonia and the chromatin in the nucleus is not clearly shown by haematoxylin staining. Spermatocytes themselves take this stain heavily, while the spermatogonia are bigger, more lightly stained, and the chromatin in the nucleus is very distinct.

A transverse section at the junction between the two sexes shows an ellipsoid shape, of which the minor axis is about half of the major axis.

In transverse section of the female part the minor axis is proportionally less than half of the major axis, and the

contents are mostly oocytes, with young ova as big as 56 μ x 45 μ. These are irregular, triangular or polyhedral in shape. The nucleus of the ovum is transparent, vesicular and no chromatin is apparent in it. The egg membrane is obscure and the intercellular spaces in each follicle are wide, measuring approximately 8 μ; this is because the gonad increases in size before the reproductive elements have been laid down to any extent.

The ducts of the gonad are very fine; the male outgrowths on the male part of the gonad have begun to fill and the intestine is visible from the surface of the hinder part of the gonad.

This condition was observed in specimens which were obtained in the months of September, October, November and December. In 1938 the percentage of this stage in the catches of escallops reached its highest point (48%) in November. (Table I).

b) The Filling Stage - (Gonad half-full).

In this intermediate stage, as the new tissues are growing quickly, the walls of the gonad become stretched in all directions, especially the hinder part which elongates posteriorly very much beyond the attached point to the adductor muscle. The free end is pointed. The gonad becomes

more curved in outline. (Fig.1).

Since the contents are increasing, the whole gonad swells and becomes rounded in appearance. At the same time the surface becomes smooth and bright in appearance owing to the turgidity of the contents.

In colour the female part is Safrano-Pink or Grenadine Pink and the male is of a whitish hue.

A transverse section from the male part shows a triangular outline which indicates that the concave-acute state of the preceding stage is being filled up. The anterior extremity of this part, however, does not extend forward to the region of the digestive gland. The sections mostly contain the spermatids at the centre with a number of spermatocytes at the periphery in the follicles. The spermatids are arranged in clusters and take a reddish stain in haematoxylin.

At the junction between both sexes the transverse sections show an elliptical outline, of which the minor axis is about half of the major axis.

The hinder part of the gonad is now circular in section and pointed. This point is always transparent (Fig.1), because it has not yet been filled up with the newly growing elements. The clear point to the gonad is characteristic

of this stage. The contents are mostly young ova, which may have flattened sides and measure approximately 57 μ x 48 μ. The nucleus is clearly seen and is transparent. The outer membranes of the ova are thin. Deutoplasm has just been deposited towards the centre of the ova giving them a light yellowish colour under the microscope. The inter-cellular spaces in the follicle measure approximately 4 μ.

Ducts on the surface of the gonad appear fine and dendriform. Male outgrowths on the male part are now more than half-filled and the part of the intestine inside the gonad becomes invisible, because the underlying area has been completely filled with newly growing elements.

This condition was observed in specimens which were obtained in November, December, January, February, March and April. During these six months the percentage (63%) in December 1938 was the maximum record for the year.(Table 1). There was no such stage observed from May to October in 1938.

c) <u>The Full Stage - Gonad full</u>).

The whole gonad at this stage has been filled with the ripening or ripe elements and its capacity has reached the maximum for the year's reproductive cycle. Since the con-

tents are packed and pressed against the walls, the gonad becomes solid in constitution, firm in consistency, and highly curved at the posterior part. The free end is round and conical.(Fig.1).

Owing to the high turgidity of the contents, the surface of the gonad has a brilliant, shining appearance, although it is granular and uneven in texture.

In colour, the female part has a Shrimp Pink or Grenadine Pink tint; while the male is a greyish cream.

The male part has now extended forward and impinges on the digestive gland. A transverse section of the male part reveals a phase in which the outline is an obtuse triangle. The testicular follicles are packed with spermatids which are arranged so that they radiate from the centre to the periphery of the follicle. Mature spermatozoa are found in numbers at the centre of the follicle and also in the sperm ducts, and stained a deep purple in haematoxylin.

Transverse sections at the junction between both sexes show the gonad to be circular in outline at this point.

The posterior part of the gonad is conical. The point has become solid. Ova in the follicles are packed, so that they are square, or pentagonal in shape; the average dimensions are 64 μ x 65 μ. The nucleus is still distinct; and

chromatin has begun to appear at its centre. The membrane of the ovum has thickened, and the deutoplasm is abundant so that under the microscope the ova appear brownish and somewhat opaque.

Ducts become wide and prominent; among these prominent ducts the ovigerous tissue looks like millions of islets of red coral barely separated from one another in the sea. The inter-cellular spaces are very small, measuring approximately 1.8 μ.

The male outgrowths are stretched with contents and therefore very prominent.

The part of the intestine inside the gonad is now absolutely invisible.

Escallops at this stage may be found in samples obtained during the nine months of the year from November to the middle of the following July.

During 1938 the maximum percentage of the full stage escallops (71%) occurred in March. (Table 1.)

d). The Spawning Stage. - (Gonad running).

When the escallops are spawning, their gonads lose some of their turgidity. (Fig.1).

In colour the female part is Strawberry pink or Peach Pink; and the male, brownish or greyish.

A transverse section through the male part shows an acute triangular outline; the sides are somewhat concave and indicate a small quantity of the male elements which remain inside. In each follicle, there are no spermatids, but mature spermatozoa, which stain darkly in haematoxylin. Free individuals are found at the centre of the follicle. But the majority of the mature spermatozoa still retain their original positions in such a way that their heads all point towards the centre of the follicle. Their tails are gathered together like the ropes of a parachute.

Under the high power of the microscope it is seen that the long tails, bound together in this way, form spoke-like axes which run from the periphery of a follicle toward the centre.

A transverse section cut at the junction between the sexual products shows an ellipsoid outline, of which the minor axis is about half of the major axis.

The posteior part of the gonad is much more flattened than the other parts, and the curvature at the hinder portion has been much reduced. (Fig.1).

Besides there is always a very distinct depression at the region just underneath the base of the intestinal loop.

The ripe ova are rounded, measuring approximately 70 μ - 80 μ. The nucleus is hardly visible under the microscope,

because the deutoplasm is so abundant that it obscures the outline of the nucleus and gives to the ova a deep brown colour. Sections of the ova show deep deposits of chromatin. The membranes of the ova are thick and opaque.

Ducts are transparent and wide. On the right side of the gonad the gonoduct is always full of ripe ova which imparts to the duct a characteristic orange colour. If a gentle pressure is applied to this duct, ova may be passed out through the opening of the kidney.

Moreover, in the kidney the presence of ripe ova is also a usual thing so that the organ may be turned to an orange colour.

The depression in the gonad underneath the intestinal loop and the presence of coloured ova in the duct on the right side of the gonad are two main characteristics of the spawning condition.

The male outgrowth becomes half-discharged; the intestine is semi-visible, and intercellular spaces in the female follicles are absent.

This stage was observed during the period from January to August. No escallops with spawning gonads were obtained in September, October, November and December.

According to the curve (Fig.2) the maximum percentage of the stage (79%) in 1938 occurred in June. (Table 1).

e) The Spent Stage. - (half spawned or empty gonad).

The escallop may spawn in one of two different ways. A few empty the gonad contents completely, whereas others do not shed the whole of the reproductive products at one time.

Gonads which remain in this half-shed condition are very similar in appearance to those that are in the running stage. There are the following differences, however, between partly spawned gonads and those that are actually running.

First the actual running gonads have ripe ova in the ova duct on the right side of the gonad and also possibly in the passage of the kidney as mentioned before; but this is not the case in the partly spent fish, and even if a gentle pressure is applied to the gonad, no ova can be forced out. Secondly, the appearance of the actual running gonad is always bright and shining, but the gonad of a partly spent fish is always dull and wrinkled. Thirdly, although the whole gonad when partly spent is not empty, yet some parts of the gonad are . (Fig.1). In the male part, there is always a transparent area which lies along the free edge or keel of the part; in the female part the intestine is always visible and the narrow end is usually empty. (Fig.1).

There is a high mortality among completely spent/escallops both under experimental conditions and under natural conditions. Judging by actual evidence from the beds, this fact needs to

be taken into consideration when interpreting the percentage curves in Fig.2.

After the discharge of the generative products the whole gonad loses its consistency and becomes smaller and flattened, being in a somewhat collapsed condition. The female portion of the gonad, in particular, contracts in a remarkable manner. As a result of such contraction, the curvature of the gonad diminishes to a minimum. (Fig.1).

The completely spent gonad is entirely transparent, and there is no differentiation between the male and female portions. In case of the partly spent escallops, the remaining elements may give a dull orange-chrome colour in the female part, and dark brown in the male.

A transverse section at the junction of ovary and testis has the outline of an elongated ellipse.

The tissue changes are also different in the two kinds of spent escallops. In the case of the completely spent, all the follicles of both sexes are empty and vesicular. There remain only a small number of mother cells budding off from the follicular epithelium. When an escallop is partly spent, the male part sustains the spermatozoa as in the running condition, but the female part undergoes a remarkable change. The remaining ova become irregular and cytolysis begins.

Stained sections at cytolysis show that the ova lose their membranes and massive dark-stained naked nuclei lie in the brown-yellowish matrix. Besides, there are a great number of oocytes measuring approximately 38 μ x 44 μ. It is possible that the naked nuclei may be re-absorbed during the formation of new oocytes.

Ducts on the partly spent gonad form a semi-transparent network, but those on the completely spent gonads are clear.

The male outgrowths on the gonad of a completely spent escallop are either empty or have disappeared. In the case of a partly spent escallop the male outgrowth on the right side may still have a residue of contents remaining in it. Owing to the collapsed condition of the gonad, there are no inter-cellular spaces in the follicles.

Specimens at this stage were observed throughout the year. The maximum part of the curve (Fig.2) stretches from July to November with an apex of 100% in September, when there was no other sexual condition found. (Table 1). However the spent fish which were observed during the period from September to December were at a resting stage before recovering.

Partly and completely spent stages occur at the same time in the samples, but the partly spent stages are always

in the majority and are most evident during the intense breeding season.

Fig.1.

Gonad viewed from the left side showing the differences in size and shape of the different stages.

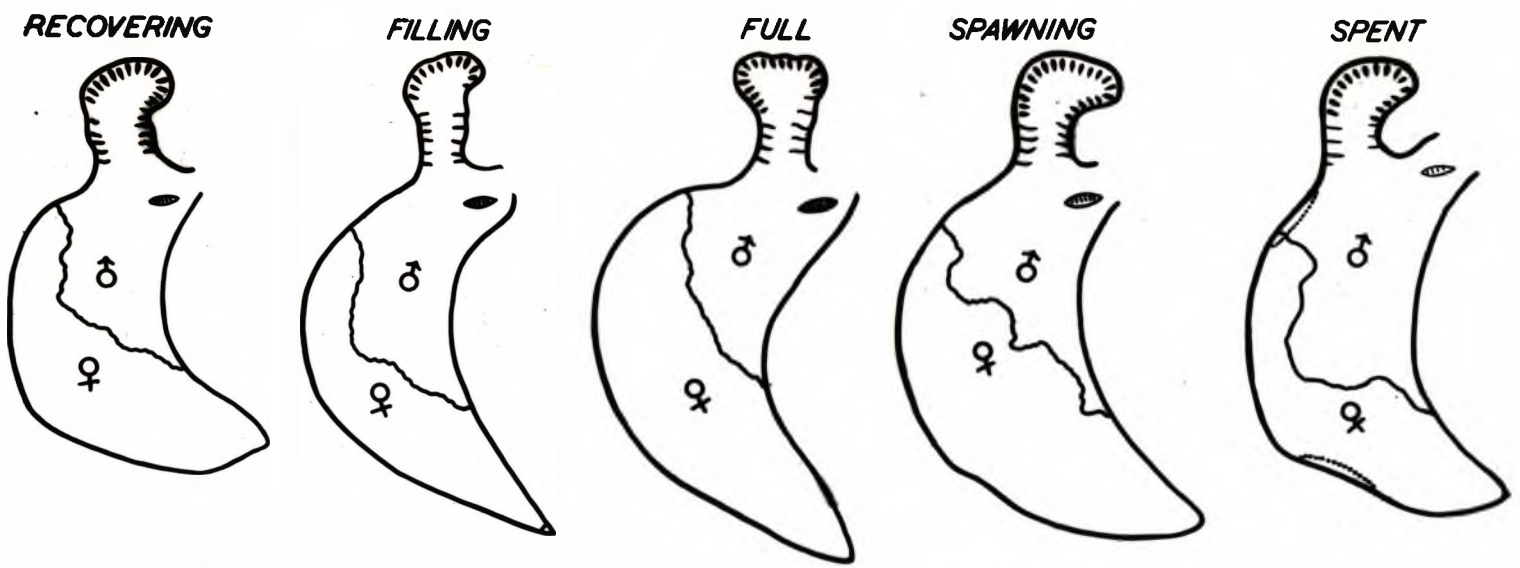


FIG. I.

Table 1.

Percentages of the different gonad conditions for samples examined through the whole year 1938.

Date	Total Number in sample	Recovering %	Filling %	Full %	Running %	Spent %
Jan. 8	38	-	42	24	24	10
Jan. 16	62	-	34	30	31	5
Jan. 31	23	-	43	35	18	4
Feb. 7	48	-	29	46	21	4
Feb. 15	24	-	17	46	33	4
Feb. 22	24	-	17	46	33	4
Mar. 8	25	-	25	42	25	8
Mar. 15	24	-	4	71	21	4
Mar. 24	30	-	10	53	34	3
Mar. 30	37	-	-	51	38	11
April 8	36	-	3	66	28	3
April 29	36	-	-	25	69	6
May 19	48	-	-	15	68	17
May 28	38	-	-	13	79	8
June 14	36	-	-	19	78	3
June 22	46	-	-	8	79	13
July 7	48	-	-	19	65	16
July 13	48	-	-	6	63	31
Aug. 24	18	-	-	-	30	70
Sept. 8	29	-	-	-	-	100
Sept. 22	15	7	-	-	-	93
Oct. 14	23	9	-	-	-	91
Nov. 8	27	48	-	-	-	52
Nov. 17	48	42	18	9	-	31
Dec. 8	48	21	35	4	-	40
Dec. 14	48	23	63	2	-	12

Fig.2

Showing the frequencies of the different stages of the gonad-conditions of the escallops and also its correlation with the lunar periodicity and the water temperature change at Port Erin Bay during the year 1938. Full moon is shown by circles and the new moon by the filled-in circles. The monthly temperature curve is in degrees Centigrade.

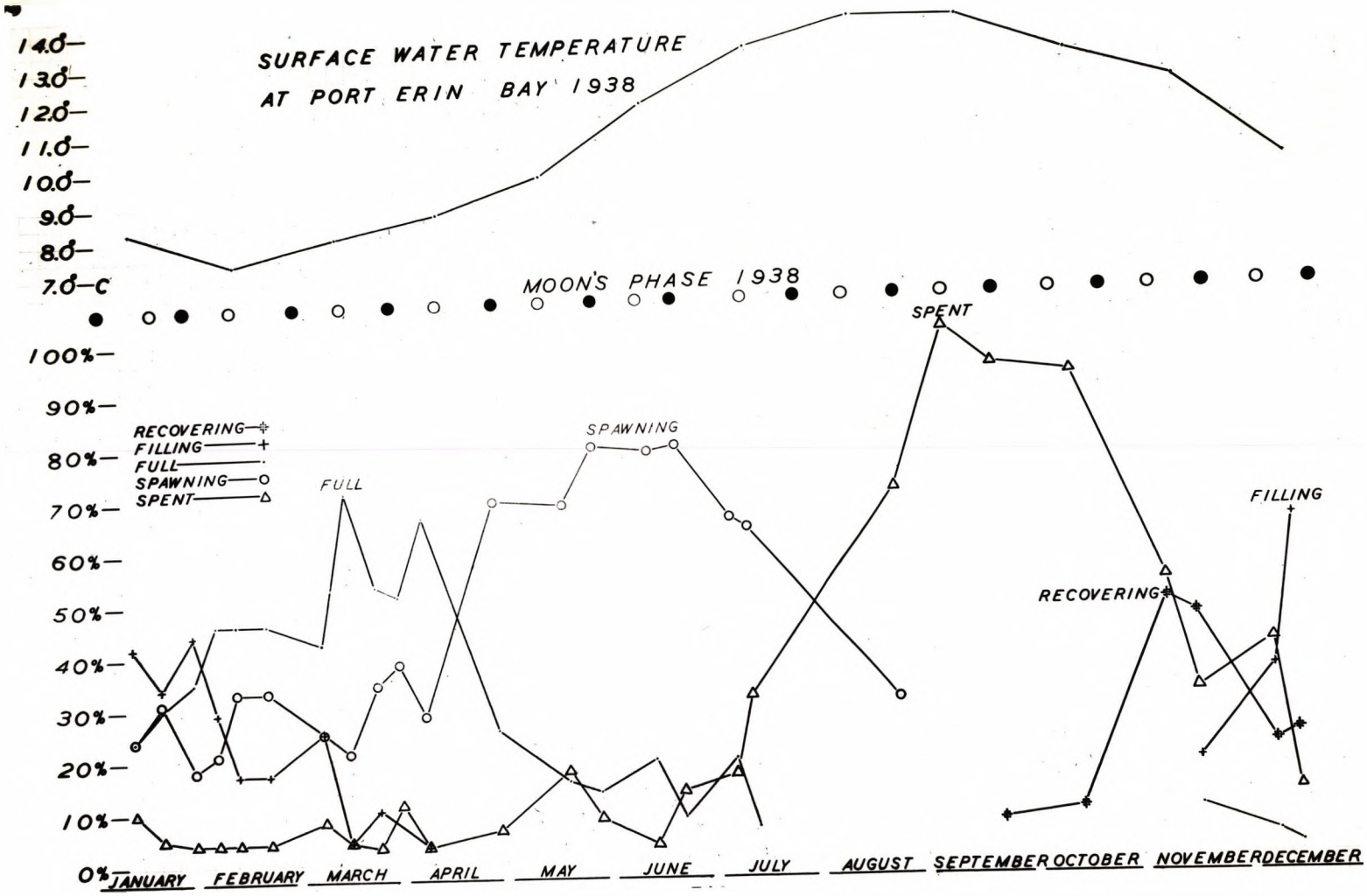

SURFACE WATER TEMPERATURE
AT PORT ERIN BAY 1938
14.0
13.0
12.0
11.0
10.0
9.0
8.0
7.0 C
MOON'S PHASE 1938
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
RECOVERING
FILLING
FULL
SPAWNING
SPENT
FULL
SPAWNING
SPENT
RECOVERING
FILLING
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER

Fig. 2.

4. THE BREEDING PERIOD OF THE ESCALLOP.

It is important to know the actual time of breeding under natural conditions and attempts have been made to fix this period for Pecten maximus in Manx waters.

It may be seen from Fig.2 that spawning escallops were obtained from the beds from January to August, and that a second phase in the annual cycle was the absence of spawners from September to December.

The period during which the spawning condition is represented in more than fifty per cent of the escallops, however, is confined to the four months from April to July, and certain evidence will be examined which suggests that these months cover the period during which there is successful production of larvae.

a) First appearance of Larvae over the Beds.

Samples of 150 litres of sea water were taken over the beds from November 1937 onwards, at intervals of three days a week. No escallop larvae were found in these samples until July 24th, 1938. Judging by the time of development in experimental jars, these larvae would be about a month old. That is, they were spawned towards the end of May, when the surface temperature in Port Erin Bay was 10°.0 C. (Fig.2).

The water over the beds has a similar temperature at

this time of the year, and there is a mixing of water from top to bottom owing to the strong tidal flow.

It may be concluded that escallop larvae were produced in quantity when the temperature of the water in the area of the beds reached 10.0°C., and this time coincided with a sudden rise in the percentage of spawning escallops (69%) on the beds in May. (Table 1).

The annual changes of temperature in Port Erin Bay for 1938 are given in the following Table.

Month	Jan.	Feb	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Water Temp. in C.	8.3	7.3	8.0	8.6	9.6	11.6	13.1	13.9	13.8	12.7	11.8	9.5

The supply of larvae over the beds did not start to fall off until July, when the number of spawning adults is rapidly decreasing.

If the escallops in spawning condition before May produced larvae, it can be taken from the evidence that this was not done in great quantity.

b) Appearance of Larvae in Pond at Port Erin Biological Station.

Forty-eight escallops were taken from the beds and placed in one of the sea-water ponds at the station. The pond was netted for larvae at regular intervals, but none were obtained

until May 24th,1938, when a quantity of veligers occurred near the surface.

These would be spawned about May 10th,1938, and there is no evidence from the pond, which has a slightly higher temperature than the open sea after March, that larvae were produced before this date in May, which is included in the natural maximum spawning period.

c. Artificial Fertilization.

Attempts at cross-fertilization, using spawning escallops taken from the beds, were not successful until February 26th, 1938, and larvae were not produced in the experiment until March 10th, 1938, and on these dates the temperature of the water in the experimental vessels had reached 10.3°C, which is near the sea temperature in May 1938. (Fig.2), that is the month during 1938 in which larvae were first obtained from the pond, and were apparently first produced in quantity on the beds.

From the evidence available, therefore, it may be deduced that for the successful production of larvae the temperature of the water requires to be at least 10.0°C, and it may be further deduced that the months from January to April contribute little to the larval stock of escallops although during this period the spawning adults on the beds vary from 18% to

38% of the total population. In short, the spawning and breeding seasons of the escallop do not necessarily coincide.

It may be suggested that escallops spawning so early in the year do so before maximum physical conditions necessary for the development of larvae have been reached.

Certainly under some conditions abnormal spawning may happen from either ripe or unripe gonads. For instance, certain escallops kept in tanks under low temperature conditions died from the effects of such exposure. Before they died, however, gonad contents, both ripe and unripe, were discharged. A sudden rise in temperature may have the same effect without killing the escallops. The same thing may occur if escallops are kept out of water for a day. It is possible that in all such cases as these mentioned a sudden change in temperature is the stimulus for the premature ejaculation and abnormal spawning.

The condition of the adductor muscle certainly indicates that during the period from the end of March to the end of September the adults in the spawning stage are in a physiological condition very different from that at other times of the year.

The adductor muscle before the end of March, even in the spawning escallops, is white and shining in appearance, and

is in excellent tone. From April to the end of September the muscle is yellow and dull in appearance and very flabby in consistency. This is a reflection of the general debility brought about by the more intensive reproductive effort during the period April to July, and the adductor muscle does not begin to recover its sound condition until October.

In connection with this discussion upon the breeding period of Pecten maximus, it is necessary to refer to similar investigations on the relative species Pecten operculatis.

Amirthalingam (1928) states that at Plymouth in Southern England the breeding season for Pecten operculatis is from January to June. In connection with the same species from the Firth of Forth, Scotland, Fullarton (1889) remarks that the reproductive organ had the colour characteristic of maturity from the end of February to September with a maximum in July and August.

These differences in period may be due to the water temperatures which differ from south to north.

The period of maturity for Pecten maximus in Manx water is similar to that found in Pecten operculatis by Fullarton; but the maximum spawning of the species in question is in May and June and not in July and August as found in Pecten operculatis in the Firth of Forth.

5. LUNAR PERIODICITY AND THE GONAD OF THE ESCALLOP.

Escallops, besides an annual reproductive cycle, are known to have a secondary rhythm, which is termed "lunar periodicity."

Observations of this rhythm were made by Amirthalingam (1928) in connection with Pecten opercularis at Plymouth in 1927-28.

Although samples in the present investigation were concerned with the annual cycle and were, therefore, not so intensive in their nature as Amirthalingam's work, yet there is enough data to give results on lunar periodicity similar to those found by Amirthalingam for Pecten opercularis.

In Manx water, from January to April and from November to December, the gonads of Pecten maximus are filling up with reproductive elements. During these six months the percentage at the filling stage in each sample falls at the time of the full moon.(Fig.2).

The period for the full stage during a year is from January to July and from November to December. During those nine months the apices of the percentage curve for the full stage occur before the time of the full moon.(Fig.2).

During the period of spawning escallops from January to August, the apices of the spawning frequency happen during the time of the full moon or a few days after it. (Fig.2). The spawning stage is not considered as a separate stage by Amirthalingam.

IV. THE DEVELOPMENT OF THE ESCALLOP.

1. Sperm and Egg.

a) Sperm. The spermatozoa of Pecten maximus is very much like that of Pecten opercularis figured by Fullarton (1889), except that the former is shorter than the latter. The head of a ripe sperm is ovoid, rounded posteriorly and tapered anteriorly to an apex which, under the microscope, appears almost transparent. The nucleus has the appearance of two petal-shaped objects. The length of the tail, 0.064 mm., is a little more than ten times that of the head, 0.006 mm. x 0.004 mm. (Fig.3). These measurements are very nearly those given by Belding (1910). (Length 0.07 mm., head 0.006 mm.) for the Giant Escallop.

Spermatoblasts in different stages measured show the following variations, 32 μ, 40 μ, 72 μ, 102 μ, and 120 μ. A number of sperms may attach themselves to an ovum or other body floating in the water. The tails are pointed outwards, and these sperms give to the ovum or body a rotary motion.

b) Ovum. The ova in the gonad from the filling to running stage are packed together, and, before maturity, may be polyhedral, pear-shaped, or kidney-like bodies. They

become ellipsoid when ripening, and spherical after fertilisation. The unripe ova is flattened like a water melon seed, so that the measurements of length and breadth (136 μ x 85 μ) are greater than those of later stages. Mature ova measure approximately 108μ x 54μ, and when fertilised they are about 72 μ in diameter. The last measurement is greater than that given by Dakin (1909) for the same species (0.05 mm.) and also greater than Fullarton's figure of 0.06 mm. for Pecten opercularis.

Under a microscope the unripe ova is semi-transparent and yellowish; the ripe ova is brownish, and the fertilised egg is dark brown. When the unripe ova are liberated into water they always adhere to one another at first, but separate quickly; then some burst and the contents run out, others can absorb water and round off within a few minutes, but eventually they break down, and in each case the nucleus becomes extruded. Even the ripe ova may have the same fate if the weather is too cold for development. This is what happened in the artificial fertilization experiments carried out before March. The brown colour of the ripe ovum is due to the contents of the nutritive vitelline which is evenly distributed in the cytoplasm of the ova. Thus the cytoplasm is more darkly coloured than the nucleus or the peripheral part of the ovum.

The nucleus is saddle-shaped or sub-rounded, and it is a big proportion of the whole egg cell. In an unripe ovum, 136μ x 85μ, the length of the nucleus is about 54μ, i.e. about two-thirds of the short axis. In the ripe ovum the ratio is one-third, due to the ovum becoming more rounded; while in the fertilized egg the ratio is two-thirds again owing to actual growth of the nucleus (Fig.4).

2. Fertilization.

a. Artificial cross-fertilization. A small number of eggs in experiments were first successfully fertilised in the later part of February 1938. After the middle of March the number of broods in the experimental bowls were increased to a remarkable degree. Now air temperature at Port Erin for the year began to rise in the last part of February, and the upward trend was reflected in the temperature of the sea-water in the various experimental bowls and jars. On the 26th of February the water of the bowls containing the fertilised eggs was 10.3°C, so it would seem from the records that successful artificial fertilization can only take place at or above this temperature.

From this point of view, the progress of the fertilisation experiment was very significant. During the first part of February there was no fertilisation at all. The ripe ova

which were liberated artificially into the experimental bowls with sea-water, began to swell and finally the egg envelopes were left empty with extruded nuclei floating in the surface water. Towards the middle of February a few fertilized eggs, each with two nuclei inside, were first seen, but these did not develop further. The first successful experiment, which reached the veliger stage, was No.6, carried out on February 24th, 1938, when fertilization took place three hours after the experiment began. The ovum underwent profound changes, both internally and externally. In a ripe ovum, the nucleus is transparent and the cytoplasm brown in colour. When fertilisation had taken place, the whole ovum became dark brown and the nucleus was obscured. A few minutes later, there was another alteration in colour due to redistribution of the vitelline material. The ovum darkened considerably at one pole where the yolk was concentrated. The opposite pole became transparent, showed active cell division, and elongated (Fig.5). Owing to the packing of ova in the ovigerous alveoli, even the ripe ova was ellipsoid in shape, and somewhat flattened; that is, the three axes of the ripe ovum under such conditions are never equal. After fertilization the ova rounded off and became spherical bodies, which no longer floated near the surface of the water

until the swimming gastrula stage had been reached.

b. Discharge of Reproductive Products. Although Pecten maximus is hermaphrodite, the male and the female parts do not ripen at the same time in one animal. In order to ascertain the interval of time between the discharge of ova and sperms, attempts have been made to watch certain escallops when they were in spawning condition. In general the ova were discharged a day or two before the male elements, but occasionally the procedure was reversed. In one case, for instance, an escallop began the discharge of its male products at 9 a.m. and continued until 3 p.m. An hour later the female portion of the gonad began to extrude ova. The chances of self-fertilization were much restricted by these natural differences in the times of extrusion.

c. Self-fertilisation. The possibility of self-fertilisation, however, cannot be ruled out, and so attempts were made to bring about self-fertilisation in certain escallops and to compare results with those of cross-fertilisation. Two artificial fertilisation experiments were commenced on March 28th, and carried through under exactly the same conditions, except that in one case fertilisation was brought about by fully ripe ova and sperms

from the same escallop, while in the other case, ripe ova were obtained from one escallop, and sperms from another. The result showed that self-fertilisation is possible in Pecten maximus. Furthermore, embryos passed through the segmentation stages, and reached the gastrula stage at the same time as the developing embryos from cross-fertilisation. Only some of them, however, reached the gastrula stage, and none went beyond it. On the contrary, the cross-fertilisation experiment produced innumerable successful embryos and a proportion of these became advanced larvae, twenty-eight days old.

3. Polar Bodies.

Three hours or more after mixing the ova and sperms polar bodies are budded off. One ovum usually bears a single polar body which is about one-tenth of the whole ovum in diameter. Sometimes there are two polar bodies, rarely three. In cases where two appear, the second is formed half an hour later and is usually smaller. As to their relative positions, the second polar body lies on top or to one side of the first body. If the water temperature is too cold, then the fertilised ovum may disintegrate even in the polar body stage. This happened on February 25th in an outside tank in which experimental

fertilised eggs were put when the water temperature was 7.0°C.

Usually the polar body disappears before the gastrula stage, but in some cases it may persist in this stage and indeed for three or four days. The polar body of a gastrula has cilia which are much finer than those covering the embryos. When the latter want to settle upon some object they may do so by using the fine cilia of the polar body and become so fixed that a gentle current of water from a pipette can not detach them. As the relative position of the polar body to other organs must be important for the orientation of the embryos, reference may be made to sketches such as Figs.15 and 16. If we take the position of the shell gland as dorsal, and the velum as ventral in the late veliger stage, then the polar body is posterior.

4. Segmentation.

The first segmentation of the embryo is unequal so that at the two-celled stage one macromere and one micromere have been formed. The former is about 54u in diameter, and the latter 27μ - 36μ (Fig.6). At the four-celled stage, the micromeres are much smaller than at the two-celled stage, but the dimensions of the whole embryo remain the same. It was found impossible to watch one embryo

throughout its whole life in order to trace, as far as possible, all the successive stages. It was necessary, therefore, to start on one set of experiments in the early morning, for the first twelve hours' observations, and another set at midnight, so that the second twelve hours' observations could be made on the following day. In this way it was possible to sort out and connect all the observations in their proper time sequence.

By extending this method it was possible to complete observations during the first 72 hours of the larval development, and in this way the various stages were examined several times. Experiment No.19, which was started on 2nd June 1938, may be taken to illustrate results obtained by this method of working.

A few minutes after mixing up the ova with sperms, fertilisation takes place. Each ovum becomes spherical and turns dark. After four hours one or more polar bodies begin to bud off. At six hours cell-division starts and the two-celled stage is reached. (Fig.6). Half an hour later the four-celled stage follows, one macromere with three micromeres (Fig.7). At the seventh hour, two of the three micromeres divide again and the macromere begins to be surrounded by the five micromeres (Fig.8). After

eight and a half hours two of the five micromeres begin to divide again so that the embryo now consists of one macromere in a central position and seven micromeres (Fig. 9). At the tenth hour, the macromere begins to divide, and evidently does this rapidly because the two macromere stage has not been observed; the first obvious result of the division is represented by Fig.10 in which the embryo already has four macromeres as well as nine micromeres which envelop them. At the fifteenth hour the four macromeres are more clearly marked from one another, and the micromeres have become numerous; twelve of them show clearly at the margins (Fig.11). During this time the embryo changes from a spherical to a symmetrical ovoid shape. By the seventeenth hour two big changes have taken place, there are eight macromeres which have arranged themselves into three rows. Further the micromeres have formed a sac, so that they enclose the macromeres, except for one small opening which constitutes the blastopore. Along the middle line of the embryo a transparent streak shows the beginning of the formation of the primitive gastrula cavity. (Fig.12).

5. Gastrulation.

In the embryonic stage of Pecten maximus, like oysters and mussels, no distinct cleavage cavity can be seen before the gastrula stage is reached. During the time

from seventeen to twenty hours after fertilisation, gastrulation has taken place and cilia also come into existence (Fig.13). The gastrula cavity is formed by two parts, the archenteron and stomodaeum. The archenteron is entirely built up by the macromeres in such a way that when they have become numerous, they arrange themselves to form a sac-like body within the cleavage cavity (Fig.14). The stomodaeum is formed at the junction of the inner sac of macromeres and the outer cup of micromeres. This opening lies in a gastrula groove formed by an invagination in the micromeres. During this time, morphologically, the macromeres are endoderm, the micromeres are ectoderm, and the cells between them are mesoderm. The mesoderm cells are more transparent and a little smaller than those macromeres from which they are derived (Fig.13). During gastrulation the endoderm cells are not of the same size; those forming the more convex side of the cavity are comparatively large in size and few in number; while others in the more concave side are smaller and packed together. (Fig.14). The embryo has now become pear-shaped, with a bilateral symmetry.

6. <u>The Swimming Gastrula Stage</u>.

During the year 1938 the swimming gastrula stage was first seen in experiments on the 26th of February, when the

water temperature in the plunger jars was 10.3°C. In order to establish this time as closely as possible the records of observations from twenty-seven experiments, carried on from February to July 1938, have been summarized. The records show that the length of time from the mixing of the ova and sperms to the occurrence of the swimming gastrula stages varies with the water temperature which, in the case of the experiments, was affected by room temperature. In general, the higher the temperature the shorter is the time for development. This may be as short as twenty-four hours, or as long as three days. In March, the gastrula stage was reached on the third day when the water temperature in the experimental jars was 10.7°C. In April the period was shortened to two days and even twenty-nine hours, when the water temperature in the jars was 11.3°C. From May until July the stage was always reached in twenty-four hours or even less in very warm weather, when the water temperature was above 13.0°C. The conclusion may be drawn that if the water temperature in experiments during the breeding season is above 13.0°C, the usual time for bringing forth the swimming gastrula is always twenty-four hours. This is very near to Gustsell's (1930) statement (1 to 2 days), but much longer than Belding's (1910) statement (12-14 hours) in the case of the Bay

escallop, Pecten irradians.

The behaviour of the early gastrula is of interest. When the cilia are well developed the gastrula begins to move about with a rotary motion in a counter-clockwise direction on an axis that runs through the polar body; it moves in a definite direction near the surface water. The speed of rotation is variable and may be from one to three rotations per second. After a period of activity the gastrula will then attach itself to some object by means of the cilia on the polar body, and remain in that position. This attachment by means of the polar body was observed several times and always with great care, because, so far as is known, such a phenomenon has not been recorded before. When the embryo is more than forty hours old it can move either backwards or forwards, and may also alter its vertical position in the water. At this period the position of the gastrula opening or the blastopore is nearly opposite the polar body (Figs.15 & 16).

7. The Trochophore Stage.

The trochophore stage is always reached by the third day after fertilisation. It is dark brownish in colour, more active and able to swim quicker than before, because of the developed swimming organ or velum. The velum is formed from specialised cells which, at this stage in embryonic development, are situated immediately dorsal to the

gastrula opening, or the blastopore; this area extends until a disc-like plate is formed. The centre of the disc is thin and depressed, whereas the margin thickens and grows upwards like an almost complete circular band which is broken only in the position of the gastrula groove. At the same time elongated cilia appear on the outer margin of the disc and these increase in length. The disc is now provided with long cilia which become longer than those on the other parts of the body and the latter degenerates and disappears in the later veliger stages (Figs.17,18 and 19).

8. Veliger Stage.

The veliger stage is usually reached four days after fertilization, when the shell gland appears (Fig.20); on that day larvae from one brood may have produced the shell gland and others may not have done so. The trochophore stage, therefore, may last for one day or longer.

The complete veliger stage has a longer existence and may last for a month or more under experimental conditions, owing to such factors as insufficient food and changes in temperature which may even prevent the veligers from developing further.

a. Size of Veliger. From the time of fertilization to the last veliger stage, under experimental conditions,

the escallop larvae do not grow much beyond 200 μ. The fertilized egg has been described as 72 μ in diameter. After one week, that is, in the early veliger stage, it is found that the average measurements of seven specimens gave 126 μ x 90 μ. On the tenth day the larvae may have increased to 160 μ x 108 μ. Even the late veliger, or prodissoconch stage, is still about the size of two hundred microns.

b. Shell. The shell of the veliger is secreted by the shell gland. At first, on the dorsal side of the gastrula opening and at a dorso-posterior position to the velum, there is a deep-coloured shell gland. This gland secretes the primitive valves lying side by side in the mid-dorsal line. (Figs.20 and 21).

These shell valves grow downwards from the mid-dorsal line and spread until they cover the soft parts of the larvae. The shell valve is transparent, and appears to be homogeneous except for fine lines of growth that run parallel to the free edge. (Fig.29).

c. Muscles. Two adductor muscles appear in the developing Pecten maximus, the anterior and posterior adductor muscles. The anterior forms earlier, and the posterior

later. When the posterior one begins to develop the anterior begins to degenerate. The anterior adductor muscle does not come into existence until the veliger is nearly covered by a complete shell, when it is about six days or one week old. It is situated in the dorso-anterior part of thelarvae (Figs.26 & 27).

When the larvae is eleven days old the anterior adductor muscle begins to degenerate and a new adductor muscle, the posterior adductor, appears and is completely formed when the veliger is about one month old. The posterior adductor muscle is situated in the dorso-posterior part of the veliger. The rectum passes along the dorsal side of this adductor muscle, and then comes down to the anus opening (Fig.28).

Retractor Fibres. Meanwhile the velum is also provided with a few retractor fibres which run between the shell and the velum. On the shell they are fastened to the dorsal side beneath the hinge line, one anterior and two posterior. The anterior one comes down to join the anterior end of the velum. One set of fibres, posteriorly placed, runs to the centre of the velum; and the other posterior set, to the posterior end of the velum, with an attachment also to the space between the mouth and anus. (Fig.28).

d. Swimming Behaviour. The escallop larvae has three different ways of moving through the water during the development of the early stages. First the gastrula which rotates by means of its uniform cilia; second the trochophore which depends for propulsion mainly upon specialised long cilia on the velum. In the veliger stage the long cilia are still retained and in addition several long cilia go to make a flagellum, which vibrates and guides the larvae. In addition, the veliger has two shell valves, and by clapping these together, it is able to project itself backwards with a quick jerky movement.

As a result of watching a veliger of two weeks old, it was found to swim by taking up a position with the hinged position of the shell turned away from the surface of the water. The valves open and the velum is extruded and then the larvae commences its swimming motion, moving backwards or downwards upon occasion by flapping the valves.

The flagellum, which appears when the veliger is three weeks old, moves so rapidly, both when the larvae is at rest and in motion, that it is not easy to follow the movements under the microscope. (Fig.28).

9. Mesoderm and Digestive Tract.

When the macromeres and micromeres are joined together and form the gastrula cavity, the mesoderm cells which ap-

pear between them are developed from the macromeres.(Fig.13). As stated before, these mesoderm cells are different from the others in size, position and appearance, but they do not become active until the trochophore stage has been reached. When the velum begins to form, the mesoderm cells darken in appearance and show considerable increase in size. (Fig.17). At first, there are two big cells of dark colour within the cleavage cavity of the trochophore larva. Then these divide again into six, then into eight, and so on (Figs.19,20 & 21), until they reach a large number and arrange themselves on the outer side of the endoderm lining the gastrula cavity. It is at this stage that the digestive tract begins to be laid down.(Figs.20 & 21).

a. Stomach. The stomach is made from endoderm cells in the gastrula cavity. Its first appearance is like a large sac, lined with very long cilia which are concentric towards the centre of the sac; they are able to set up a strong water circulation within it as part of the feeding process. (Figs.21 & 22).

Stomach Contraction. The veliger of two to three weeks old possesses a strong muscular stomach which is capable of contracting and expanding. It is possible that these movements, together with the forwards and backward beating of the cilia, create a water circulation which

brings food to the tract. The stomach movements are very rhythmical and take place when the cilia and flagellum are most active. The rate of movement seems to increase with hunger. There are alternatively large and small contractions. In a veliger eleven days old, measuring 116μ x 85μ, it was found that the small contractions occurred at intervals of ten minutes and the big ones at intervals of twenty minutes.

b. Mouth and Oesophagus. It was shown by careful examination of numbers of larvae that the mouth in the veliger stage occupies the same position as the earlier gastrula opening. In the veliger stage, however, the opening becomes highly ciliated and funnel-shaped, with the wide end situated on the right side of the larvae, in a position postero-ventral to the velum. (Figs.22 & 23). In the escallop larvae, therefore, the gastrula opening becomes the mouth opening which is different from what occurs in the oyster larvae; in the latter a new opening is formed when the stomach develops.

Oesophagus. When the larvae is four days old and the mouth has become newly ciliated, the stomach makes a forward extension to meet the mouth; thus a curved oesophageal tube is produced. This tube between the mouth and the stomach does not show a well-defined wall even when exam-

ined under a microscope, but is marked by differentiation of tissues. (Fig.22).

c. Intestine and Anus. During the fifth day of the larva, the stomach extends backwards and by joining up with an anal invagination forms the intestine. Owing to these extensions both ways, forward and backward, the stomach itself becomes smaller and tube-like. At this juncture a complete digestive tract or tube has been built up, and it is entirely homogeneous in nature, and its dimension seems similar throughout its whole course, although morphologically it is made up of three parts, oesophagus, stomach and intestine.(Fig.23).

The anus is made up of two parts, one is the invagination of the posterior end of the veliger; another part is the backward extension of the intestine toward the posterior extremity. When these meet each other, the rectum and the opening of the anus are formed. Then a digestive tract, which has a well-defined wall with an opening at each end, is completed.

The Coil of the Intestine. The intestine at first is a simple tube.(Fig.23). When the veliger is six days old the intestine assumes a zig-zag course (Fig.24), and finally in the adult it passes through the gonad, making an

ascending and descending loop of the same length.

d. Digestive Gland. The digestive gland, referred to also as the "liver," is stated by Dakin (1909) to be composed of the hepato-pancreas and the gastric gland. When the veliger is six days old, as mentioned above, it has a double-coiled intestine. The middle part of the digestive tube forms a sac-like bag, the stomach. From the stomach there grows a dark coloured gland which consists of two lobes. (Fig.26). The lobes enlarge and eventually enclose the stomach (Fig.31). Owing to the dark pigment of the gland the inner organs of a late veliger stage are obscured. The connection between the gland and the stomach is by means of two distinct ducts.(Fig.25).

e. Changes in the position of mouth and velum in development.

Owing to the formation of new organs in the larva from time to time, and to the growth of organs within the body cavity, the relative position of the various parts of the larva are changed. This leads in particular to a change in the position of such movable parts as the mouth and velum. This is the reason why the mouth and velum become shifted from an antero-dorsal to postero-ventral position during development. This change begins in the early veliger stage when the mouth and velum begin to move

downwards due to the appearance and lengthening of the intestine. (Fig.23). Later, when the stomach and the digestive gland appear, the mouth and velum are compelled to move further down to the ventral position (Figs.25 & 26). The final postero-ventral position is reached in the post-veliger stage (Figs.27 & 28).

10. Foot.

The foot appears as an ectodermal evagination into which the mesoderm grows. As the larvae passes into the late veliger stage, the velum becomes smaller and its swimming power deteriorates. At the same time the ventral surface between the mouth and the anus forms a massive projection of ectoderm. When the veliger is about six days old, this particular part (Fig.25) begins to broaden out and becomes wedge-shaped, highly contractile and covered with more and longer cilia. It elongates as its development continues. Later a long ciliated foot is formed and serves as a swimming organ instead of the velum. A more important function than this in the prodissoconch stage is the secretory work of the byssal gland. By means of the threads secreted from this gland the animal can fix itself to the substratum or crawl about on it. It was not possible to observe further development of the foot,

because the larvae did not advance beyond the dissoconch stage under experimental conditions.

The byssal notch, however, through which the foot protrudes is clearly shown in the prodissoconch shell (Fig.29).

11. Prodissoconch Stage.

On account of the darkness of the digestive gland the inner organs of the veliger during this stage are almost obscured. The only thing to be seen through the shell is the constant ciliary movement of the digestive tract. The velum is quite degenerated and there is no flagellum or any long cilia moving on the ventral side as before. One particular feature of the shell is the deep byssal notch at the left side of the umbo. It is possible to assume that the foot is well developed at this stage and protrudes through this notch. Along the edge of the shell the lines are much thicker and darker; according to Belding (1910), probably this is a well-defined growth line between the prodissoconch veliger stage and dissoconch stage.

The prodissoconch shell is asymmetrical, because the left valve is larger and more convex than the right. This condition is similar to that found in adult shells of Pecten opercularis (Dakin 1909) and Pecten tenuicostatus (Drew 1906), but the opposite to that found in its own adult Pecten maximus (Fig.29).

12. Length of life of developing larvae in the Experimental Jars and Bowls.

It is interesting here to discuss the length of time that escallop larvae were able to live under the conditions of these particular experiments. They never lived longer than five days in small bowls and thirty-three days in the plunger jars.

It was always necessary, therefore, to transfer larvae from the bowls to the plunger jars by the second day, that is, as soon as they have reached the swimming gastrula stage. The plunger jars themselves were of 24 litres capacity and the automatic plunger worked fifteen times per hour.

The sea water was changed in each jar three times a day, with its contained microplankton, and as an additional source of food, 25 c.c. of a culture of small flagellata of 1.5μ - 2.0μ (designed F, used for rearing oyster larvae at Port Erin Biological Station) were added.

The larvae, therefore, were given the opportunity of obtaining food material, both from the microplankton and from the added flagellates. Under these conditions, so far as is known, the larvae never lived beyond thirty-three days. Numbers of dead shells were found in the jars as late as two months, but none of these exceeded 200μ.

If the marks on the shell of the thirty-three days old veliger and its size (200μ) are taken into account, then it would seem from comparison with Belding's data (1/140 inch) for Pecten tenuicostatus, that this veliger of thirty-three days old has reached the end of the prodissoconch stage (Fig.29).

13. The Mortality of Developing Larvae in Plunger Jars.

If steps are taken to stefilise all the implements and vessels used in dealing with the larvae, there is no mortality for the first three days; it becomes serious, however, at the end of a week and reaches a maximum in a fortnight. A sudden change of weather, bringing about consequent fluctuations of temperature, affects the mortality rate. For instance on June 2nd, 1938, the air temperature changed from 13 .0° C to 8 ,8° C overnight, and, as a reflection of this, all the larvae in the plunger jars were killed off. Three experiments were ended in this abrupt fashion, and each one at a different stage of progress, that is after 6, 14 and 33 days from fertilisation respectively. There is no doubt that the successful rearing of escallop larvae, like those of the oyster, depends upon equable temperature, but during the present experiments there were no facilities for controlling the water temperature in the plunger jars.

14. Veligers obtained from a Hatchery Pond at Port Erin Biological Station.

As mentioned before, under Method and Material, four dozen adult escallops were placed in one of the hatchery ponds at Port Erin. During the time from February to July 1938 fine tow-net drags were taken at set intervals and the net contents examined. Escallop larvae were first found on 24th May, and they were numerous and much bigger than those at corresponding stages in the experimental jars. There is no doubt that copepods in the pond were enemies of the escallop larvae. Left with copepods in a bowl, the larvae soon disappeared.

V. THE GROWTH OF THE ESCALLOP.

Measurements of the shells of the adult escallops which were examined in the course of these investigations were made by a special measuring apparatus which was devised by the writer, and calipers. The following measurements were taken for each specimen; the length (antero-posterior axis), the breadth (dorso-ventral axis), and the depth (lateral axis). Distance between the ring formations on the shells was also measured in order to obtain a general idea of the rate of growth in the escallop.

The first ring - The first ring is more distinct than the later rings, and this is partly due to the fact that the shell between the first ring line and the umbo has more colour than the rest of the shell. On the right valve, it is greenish yellow, or entirely purple. On the left valve, it is very shining, yellowish or entirely purple in colour, sometimes with a few purple markings.

1. Period and Cause of the Cessation of Growth.

During the breeding season the escallop undergoes considerable changes as mentioned before, in the section on "Breeding Period." The adductor muscle undergoes a physiological change and is in very poor condition when spawning

has reached its maximum.

Now it is also found that a shell ring, marking the time of cessation of growth, is also formed during this period.

During examinations carried on from October 1937 to December 1938 these rings on the shell were observed to be laid down only during the month of June 1938.

The period for this cessation of growth covered only about a week, and then the animals began to grow and show new shell formation. The first signs of the cessation of shell growth in the spawning or spent escallops were obtained in the sample for 9th June 1938. In the sample for 17th June new growths were already from 0.5 - 1.0 mm. beyond the last laid down rings.

Since ring formatiom occurs only at a time when the escallops, except for a few that have reached the full stage, are actually spawning or in the spent condition (see Table 1), the cause of this cessation of growth may be correlated with the general poor condition of those animals which are exhausted after the formation and extrusion of reproductive products.

Risser (1901) and Gutsell (1930) both found the same connection between ring formation and spawning in Pecten

irradians. Gutsell suggested that some metabolic activities, indirectly connected with the development of eggs and sperms, must be responsible for ring formation. This is not the case in Pecten maximus, because growth outside a ring starts about the middle of June, whereas the gonads do not recover until toward the end of September (Fig.2 and Table 1).

With regard to the formation of rings in the shells of the young escallops before maturity is reached, the annual sexual cycle does not explain their appearance, and it can only be suggested that it is due to a physiological rhythm inherited from the parents.

2. Annual Growth Rates.

It is interesting to know the annual growths of the escallop throughout its life.It is found that when the escallops reach ten years of age they grow very little, usually less than one millimetre for each year. Therefore, the annual growths from year to year can be shown distinctly only on the shells up to ten years old.

For this reason, the age group of eleven years old escallops which had grown under the same environmental condition from year to year was chosen, and the annual growths on each shell of the total number, 128 escallops,

were carefully measured with a view to showing the average annual growths from the first year to the tenth year.

It can be seen, from Table 2, that on the average the escallops grew about 19.0 mm. in the first year; the maximum annual growth occurred when the animals were three years of age; after then the rate of growth of the escallops decreased from year to year, and it was little more than one millimetre after the eighth year.

Table 2.

Average growth for each year in eleven years old Escallops.

Year	Ranges in mm.	Averages in mm.
1st.	12.0 - 29.0	19.0
2nd.	15.0 - 42.5	26.3
3rd.	15.5 - 41.5	31.2
4th.	10.5 - 34.5	21.6
5th.	5.0 - 22.5	12.1
6th.	4.0 - 12.5	6.7
7th.	3.0 - 8.5	4.0
8th.	2.0 - 6.5	2.6
9th.	1.5 - 4.0	1.4
10th.	1.0 - 3.0	0.5

Fig.32.

Showing the average annual growths from the first year to the tenth year in the eleven years old escallops.

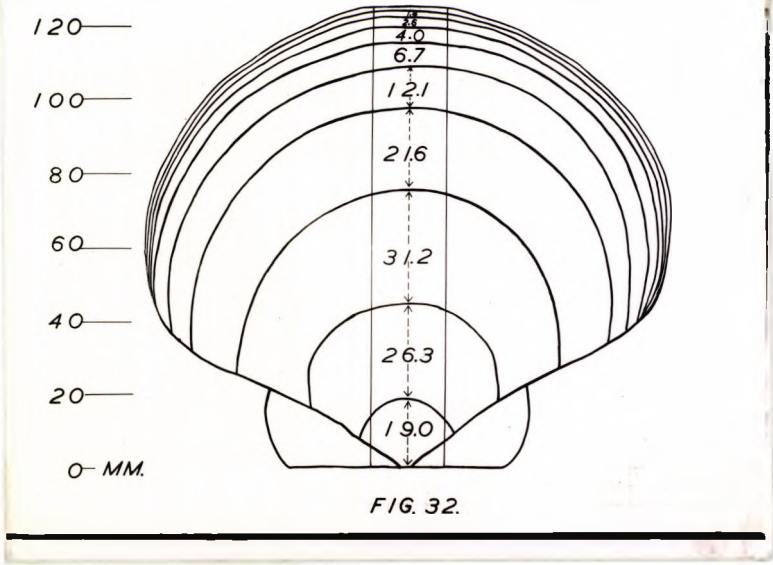


FIG. 32.

3. Size of the Escallop.

As it is shown in Table 3 the age groups on the whole range from two to twenty-two years old. The majority of the market escallops which were dredged from the Port Erin beds during 1937-1938 belonged to age groups from four to twelve. However, only those specimens obtained during the months from April to June were selected for taking measurements in length (antero-posterior axis), breadth (dorso-ventral axis), and depth (lateral axis). In this way measurements are restricted to specimens that have practically completed the annual growth and this avoids the complications that would arise if shells in the fractional year growths at the edges were included.

The average dimensions for each age-group are tabulated in Table 3.

The growth of the escallop shows a regular increase in all dimensions of the shell until six years of age is reached (Table 3).

All round growth is most rapid in the first three years, and then growth in length and breadth falls off fairly rapidly up to fourteen to fifteen years of age. The two measurements are, on the whole, proportional to each other.

The increase in depth also slows down at three years

of age; this measurement shows a slight but steady increase throughtthe subsequent years.

It may be true that there is no growth in length and breadth in the escallops older than seventeen years old, although there may be a slight increase in depth.

The increase in the three dimensions, of course, is not absolutely proportional, even in age groups seven to twelve where the numbers involved would tend to smooth out sample errors. There is, for instance, increase in length and depth but not in the breadth in age groups seven, thirteen and fifteen; an increase in length and breadth but not in depth in age groups nine, eleven, fourteen, and seventeen; and an increase in depth only in age groups ten, nineteen, twenty and twenty-two.

There are, also,age groups which show no annual increase over those of the previous year in the three measurements, as for instance in age groups sixteen, eighteen, and twenty-one.

It is true that,no matter what the age,the length of the shells is always ~~bigger~~ greater than the breadth.

As the figures in Table 3 and the curves in Fig.33 show, the maximum length, 154.5 mm., and the maximum breadth, 142.0 mm., were both found in the age group of seventeen years old, In depth, the maximum, 44.0 mm. was found in the oldest age group, i.e.twenty-two years old.

Table 3.

Average sizes in mm. of the escallops in different age-groups.

Number in brackets denotes the total number of the age-group.

Age	No. of escallops	Length	Breadth	Depth
2	2 (3)	78.0	70.0	21.0
3	2 (25)	107.0	100.0	31.0
4	4 (88)	115.8	104.8	31.3
5	17 (150)	125.6	113.4	33.4
6	18 (71)	133.7	118.4	35.1
7	20 (82)	134.3	117.5	37.0
8	43 (96)	139.4	123.6	37.5
9	26 (83)	141.0	125.1	37.2
10	33 (108)	138.5	123.9	38.4
11	58 (128)	143.1	126.7	38.2
12	33 (70)	144.1	128.5	39.0
13	13 (48)	146.5	127.8	40.3
14	7 (20)	149.3	132.6	39.7
15	7 (21)	149.9	130.9	41.3
16	4 (12)	145.3	128.3	38.3
17	2 (6)	154.5	142.0	40.0
18	2 (4)	140.5	122.5	38.5
19	2 (5)	136.0	124.2	42.0
20	1 (2)	145.0	125.0	42.0
21	1 (1)	140.0	123.0	41.0
22	1 (1)	147.0	131.0	44.0

Fig.33.

Showing the average lengths, breadths and depths of the escallops from two years old to twenty-two years old group.

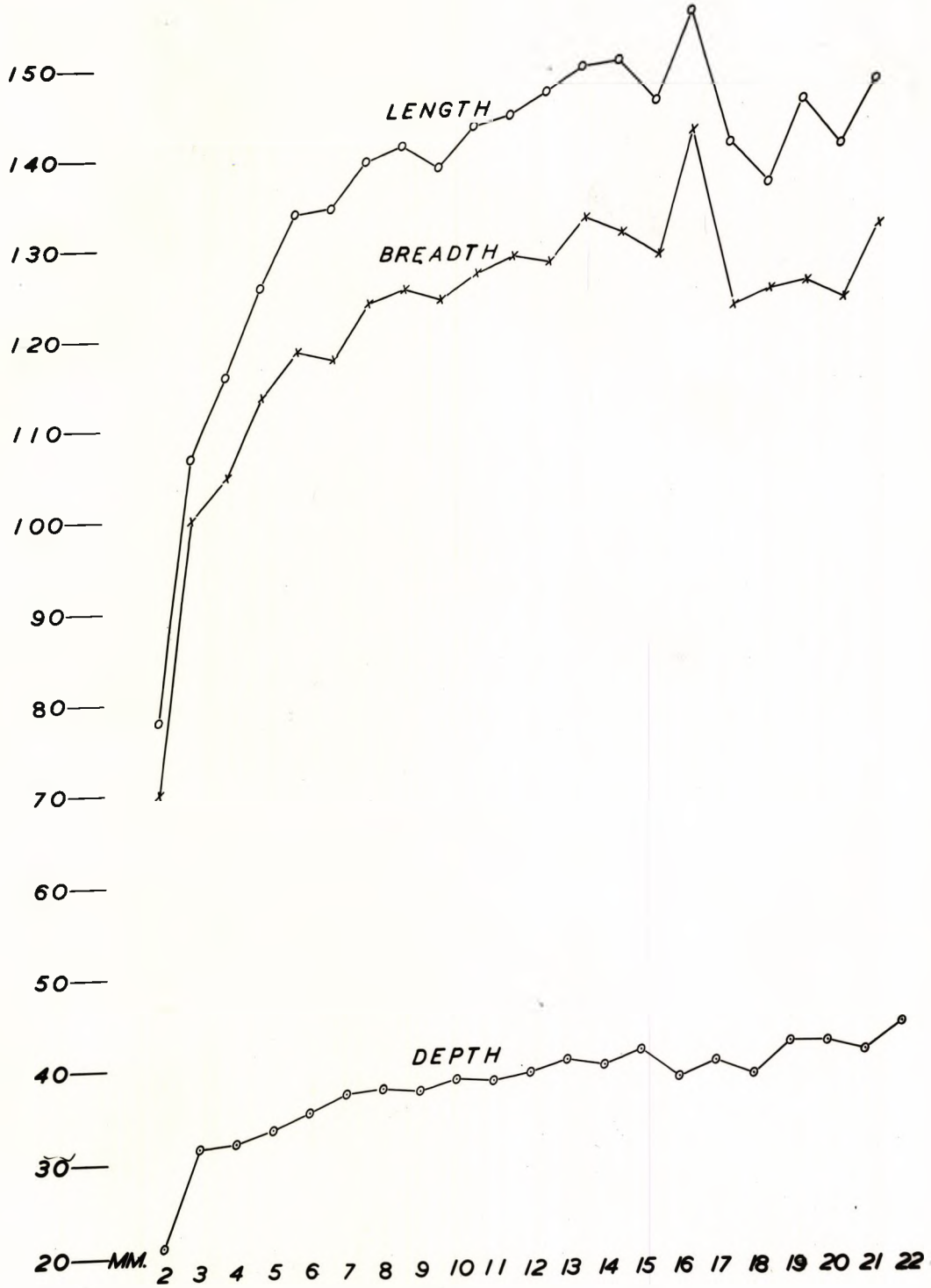

150
140
130
120
110
100
90
80
70
60
50
40
30
20
MM.
LENGTH
BREADTH
DEPTH
2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22
AGE GROUPS

FIG. 33.

VI. GENERAL CONSIDERATIONS ON THE PORT ERIN ESCALLOP FISHERY.

During observations on escallops from the Port Erin beds it was found that although many escallops less than five years old were taken in the dredge, the adductor muscles in these escallops were not fully developed and the gonads were small. Therefore they did not present the most marketable part of the catch, and it would probably be better, from the point of view of fishery preservation, to leave them on the beds.

The sizes of the escallops given in Table 3 show that those under five years of age are less than 120 mm. in length. These could be preserved by increasing the size of the dredge mesh. The mesh of the Port Erin dredge, at present, measures only 60 - 65 mm. from knot to knot, and this does not allow many of the escallops less than five years old to go through. At six years of age the main growth of the escallop has taken place (see Table 3), and little is gained in marketable volume during the subsequent years.

The largest escallop obtained from the beds during the time under review was brought in by a fisherman on the 11th March 1938. It was eleven years old and was in a completely spent condition, measuring 190 mm. in length, 168 mm. in breadth and 48 mm. in depth. The total weight was 734 gms.

The weight of one dozen Port Erin escallops averaged 3827.3 gms., of which the flesh was 1956.2 gms.

For gauging the actual loss in weight during transportation from the beds to the market, one dozen escallops were placed in a bag at the room temperature of 12.8°C; there was a total loss of 198.4 gms. on each of the first two nights and 85.0 gms. on the third night. These escallops were unmarketable on the fourth day.

The escallop beds off Port Erin seem to be moving from south to north. In the experience of the fishermen the escallops from the Calf to Bradda Head were the biggest, those from Bradda Head to Fleshwick Bay, medium size and those from Fleshwick Bay to the Niarbyl the smallest. The writer also found that the samples from the north were always smaller and younger than those from the south.

In Laxey Bay, on the east coast of the Isle of Man, an escallop bed was discovered in the spring of 1938, but the condition of the fish examined was very poor. The average weight for a dozen was 2523.2 gms., of which the flesh was 1091.5 gms. Compared with the weight of Port Erin escallops for a dozen, it was 1304.1 gms. less in total weight and 864.7 gms. less in flesh.

SUMMARY AND CONCLUSIONS.

I. Annual Reproductive Cycle.

1. The escallop, which is hermaphrodite, becomes mature at 2 -3 years of age and the testicular elements develop a little earlier than the ovigerous tissue.

2. The male and female products of the same gonad can encroach upon each other, i.e. male islets may be embedded in the female part and vice-versa.

3. During the year under observation (1937-38) the escallop population on the beds to the south-west of the Isle of Man had finished a prolonged spawning by the month of August, the majority of the gonads began to fill up rapidly with new elements at the end of September, so that by the middle of November some of the escallops were already in the full condition. The greater number, however, did not attain this condition until the middle of the following March. Consequently the maximum breeding season occurred during the months April to July. Certain escallops with full gonads spawned earlier in the year, after January, but no larvae were obtained from the sea, or from the pond at Port Erin Biological Station before the approach of the designated main breeding season. Spent

fish were also observed from September to December, but they were at a resting stage before recovering. It is reasonable to assume, therefore, that from September to December is a non-spawning period and from January to August is a spawning period.

4. If a review is made of the percentages of different stages throughout a calendar year, it is found that, during the spawning season, escallops have a lunar periodicity, the maximum in the percentage curve of escallops with full gonads occurs before the time of full moon, and the spawning maximum occurs at full moon or a few days later.

II. Development.

1. The result of twenty-seven artificial fertilisation experiments shows that successful fertilisation can be made during the time from the end of February to July when the water temperature required in the experimental jars ranges from 10.3°C to 13.0°C.

2. Pecten maximus is hermaphrodite, but both sexual products do not ripen at the same time. The interval of discharge between them may be one or two days, usually the female products are extruded first, but occasionally the reverse is also the case. Self-fertilisation, however, is possible, but larvae thus produced did not develop

beyond the gastrula stage.

3. In segmentation, the first division is unequal so that one macromere and one micromere are formed. During the first ten hours, segmentation only takes place repeatedly on the part of the micromere. At last when the macromere begins to divide, it is already surrounded by numerous micromeres.

4. The gastrula formation is epibolic rather than embolic, since a cleavage cavity is not distinct until gastrulation takes place. The swimming gastrula usually occurs on the day following fertilisation.

5. The trochophore stage may be reached on the third day when the velum comes into existence in the area dorsal to the gastrula opening.

6. The veliger stage may be observed on the fourth day when the shell gland begins to appear and this stage, under experimental conditions, may last three or four weeks.

7. The last larval stage to be reached in the experiments was the thirty-three days'old prodissoconch stage, the shell of which measured little more than 200µ across. This prodissoconch shell is assymmetrical, because the left valve is larger and much more convex than the right. This condition is similar to that found in adult Pecten opercularis and Pecten tenuicostatus, but the opposite to

that found in its own adult.

8. Mesoderm cells seem to originate from endoderm at the time of gastrulation, but they do not become active until the stomach has been laid down in the trochophore stage.

9. During metamorphosis the opening of the gastrula cavity or the blastopore, becomes the mouth opening. This is different from the oyster larva which has a new opening for the mouth.

10. When the larva is four or five days old the stomach extends forward and backward to make up the digestive tract complete, including the mouth, oesophagus, stomach, intestine and anus. On the sixth day, the intestine assumes a zig-zag course and the digestive gland is then added to the stomach.

11. The anterior adductor muscle forms at about a week's time, and it begins to degenerate on the eleventh day when the posterior adductor muscle appears.

12. The foot develops at the postero-ventral region of the larva from an ectodermal origin and it is highly ciliated. The byssal notch through which the foot protrudes is distinctly shown by the shell of the prodissoconch larvae.

III. Growth Rate.

1. The line of cessation of growth between two adjacent annual rings was found to be laid down in June and the period covered only a week; then new growth was immediately laid down.

2. The cause of the cessation of growth in the adult may be correlated with the general poor condition due to exhaustion from spawning.

3. Dealing with one age group, that of eleven years, it was found that the escallops had grown rapidly in the first three years and the maximal annual growth on the shell occurs in the third year. After three years of age growth slows down from year to year and is little more than one millimetre after the eighth year.

4. If the average sizes of escallops taken from the beds are examined according to their ages, it is discovered that, on the whole, the shells grow proportionally in three dimensions, until the age of six years. At the latter age, maximum growth has almost been reached. It is suggested therefore that fishing the beds for escallops under six years of age is not economical, because younger than this age are still growing.

5. The majority of the market escallops dredged from

the Port Erin beds during 1937-38 belonged to age groups from four to twelve. The youngest were two years old, and the oldest one was twenty-two years old.

IV. The Beds.

The escallop beds off Port Erin Bay seem to be moving from south to north; the escallops from the Calf to Bradda Head are the largest and oldest, those from Bradda Head to Fleshwick Bay of medium size and age, and the youngest and smallest escallops are found between Fleshwick Bay and Niarbyl.

EXPLANATION OF THE FIGURES.

The magnification of all the following figures is X1600, except where indicated. The time indicated is the period from the beginning of mixing the sperms and eggs to the first occurrence of the stage concerned. It was not possible to demonstrate the presence of a polar body in the stages represented by Figures 5 - 12 inclusive.

Fig. 3. Mature sperm (Pecten maximus)

Fig. 4. Mature egg.

Fig. 5. At fourth hour, a fertilized egg with the animal pole drawn out showing the fertilization membrane and the disposition of the cell contents during the first segmentation.

Fig. 6. At sixth hour, first stage of segmentation, two-celled stage showing unequal division. The large cell is the macromere, the small one is the micromere. The polar body is seen to the right of the division line.

Fig. 7. At six and a half hours, second stage of segmentation, four-celled stage showing one big macromere and three small micromeres.

Fig. 8. At seven hours time, an oblique side view of the third stage of segmentation showing one macromere at base and five micromeres.

Fig. 9. At eight and a half hours , fourth stage of segmentation, viewed from below. The macromere is seen at the centre of the seven micromeres.

Fig. 10. At tenth hour, macromere has been divided into four cells which are still attached to one another. One of the nine micromeres on the top is more transparent than the others and is larger and more rounded.

Fig. 11. At fifteenth hour, embryo with four separated macromeres and numerous micromeres, of which twelve are seen along the embryo's margin.

Fig. 12. At seventeenth hour, embryo with eight macromeres, showing gastrulation, one micromere (seen at the top of the figure) which is more transparent than the others, marks the position of the primitive opening of invagination; connected with this cell is a transparent streak which runs through the centre of the embryo and finishes in the opposite side. This is the beginning

of the gastrula cavity.

Fig. 13. At seventeen and a half hours, ciliated gastrula with two mesoderm cells, which are more transparent and a little smaller than the macromeres.

Fig. 14. At eighteen and a half hours, ciliated gastrula stage with a complete gastrula cavity.

Fig. 15. One day old, a general view of a swimming gastrula larva showing polar body, cilia on polar body, gastrula groove, and the opening of gastrula cavity.

Fig. 16. Two days old, an optical view of a gastrula from the left side, showing the formation of gastrula cavity, by two layers of endoderm cells.

Fig. 17. Three days old, an optical view of first stage of trochophore, seen from the right side, showing the differentiation of cilia and the anterior-dorsal portion to the gastrula cavity extended to form the velum. Two big mesoderm cells shown.

Fig. 18. Three days old, a late trochophore, showing a frontal view of the velum and a part of the velar cilia.

Fig. 19. Three days old, a late trochophore, seen

as a transparent object from antero-ventral side showing the velar band and part of velar cilia. Six mesoderm cells seen within.

Fig. 20. Four days old, an early veliger seen as a transparent object from the left side showing the formation of digestive sac by endoderm and the appearance of shell gland on dorsal side.

Fig. 21. Four days old, an early veliger seen as a transparent object from the left side showing the cilia in the newly formed digestive sac.

Fig. 22. Four days old, an early veliger seen from the right side tilted away from the observer in order to show the mouth on the mid-ventral line. The ciliated mouth and digestive sac, the beginning of oesophagus and the invagination of anus shown.

Fig. 23. Five and a half days old, a view similar to Fig. 22 of a later veliger showing the strongly ciliated funnel shaped mouth and the slightly coiled digestive tube.

Fig. 24. Six days old, a left side view of a post-veliger showing the coiled digestive tube, mouth and anus partly shown.

Fig.25. Six days old, a right side view of a post-veliger showing the ciliated pharynx, oesophagus, dark coloured digestive gland, two ducts of which are connected with the minute ciliated stomach, intestine extended, velum, primitive foot and anterior adductor muscle.

Fig.26. Seven days old, a left side view of post-veliger, covered by the two of shell valves; velum, digestive gland, anterior adductor muscle and the umbo, which is more prominent on the left side of the animal.

Fig.27. Eleven days old, a right side view of a post-veliger with a more complete shell covering. This stage shows degeneration of the velum and the anterior adductor muscle.

Fig.28. Twenty-seven days old, a right side view of a late veliger with the velum fully extended, showing the appearance of the posterior adductor muscle, velar retractor muscles, flagellum, and mantle.

Fig.29. Thirty-three days old, a left side view of a prodissoconch shell from a living larva, showing the byssal notch, a convex umbo, the homogeneous concentric line growth lines and the last thick

growth lines marking the end of the prodissoconch and the beginning of the following dissoconch stage. Size 200μ.

Fig.30. A general sketch of a shell of Pecten opercularis from Port Erin, showing the prodissoconch, dissoconch, and the plicated portions of an escallop shell 3 mm. across. Drawn for comparison with Fig.29.

Fig.31. A general sketch of an adult living escallop, Pecten maximus, showing the position of the gonad. The left valve, the mantle and the gill of the left side have all been removed. Size 12.0 cm x 11.0 cm.

EXPLANATION OF PLATES.

REFERENCE LETTERS.

A. = Anus.

A.A.M. = Anterior adductor muscle.

B.N. = Byssal notch.

C.C. = Cleavage cavity.

C.D. = Cephalic disk.

D.G. = Digestive gland.

D.G.D. = Digestive gland duct.

D.T. = Digestive tube or digestive tract.

D.S. = Dissoconch shell.

E.C. = Ectoderm.

E.D. = Endoderm.

F. = Foot.

F.G. = Flagellum.

F.M. = Fertilisation membrane.

G. = Gill.

G.C. = Gastrula cavity.

GO.O. = Ovigerous part of gonad.

GO.S. = Seminal part of gonad.

H. = Heart.

I. = Intestine.

K. = kidney.

M. = mantle.

MA. = macromere.

ME. = mesoderm.

MI. = micromere.

M.O. = male outgrowth.

MT. = mouth.

N. = nucleus.

NE. = nucleolus.

OE. = oesophagus.

P.A.M. = posterior adductor muscle.

P.A.M.S. = striated part of posterior adductor muscle.

P.A.M.U. = unstriated part of posterior adductor muscle.

P.B. = polar body.

PH. = pharynx.

P.D.S. = prodissoconch shell.

PI.S. = plicated shell.

RE. = rectum.

R.M. = retractor muscle of velum.

S. = shell.

S.G. = shell gland.

ST. = stomach.

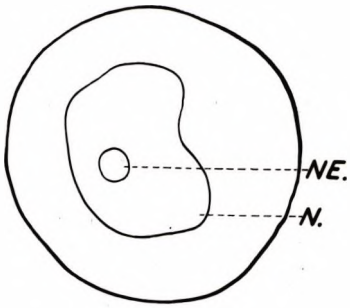
U. = umbo.

V. = velum.

V.B. = band of velum.

V.C. = cilia of velum.

FIG. 3.



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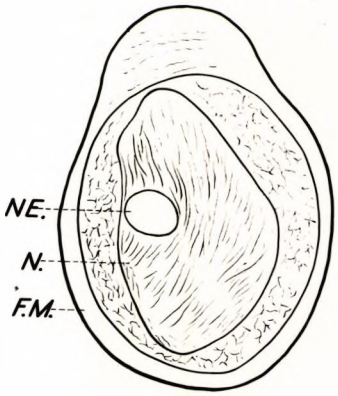

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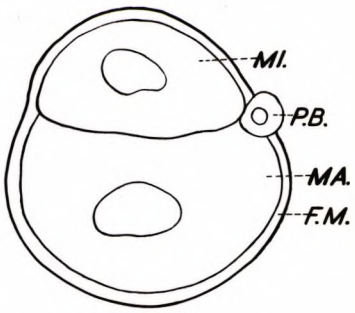

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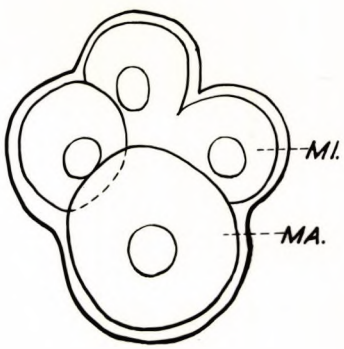

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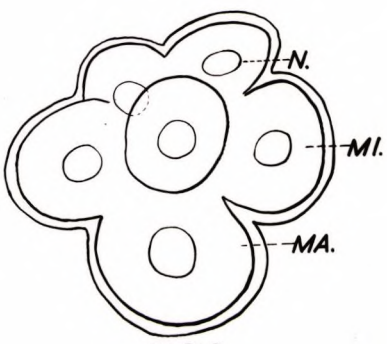

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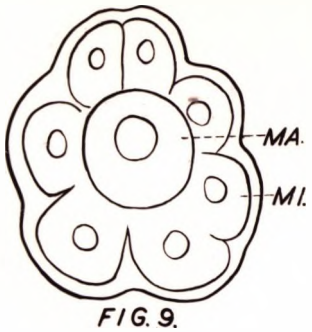

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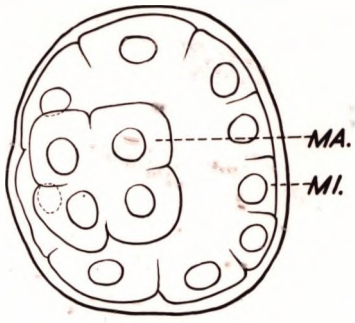

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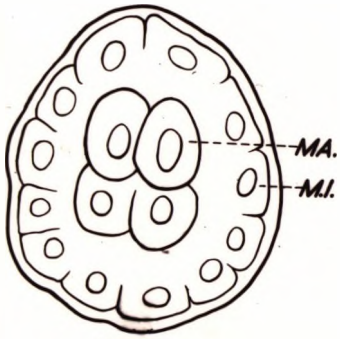

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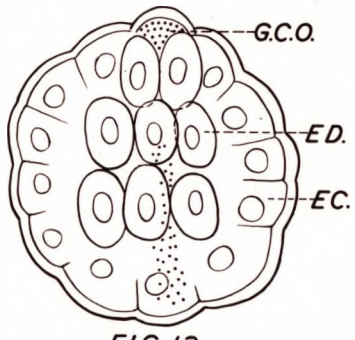

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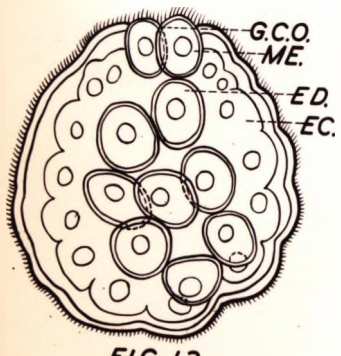

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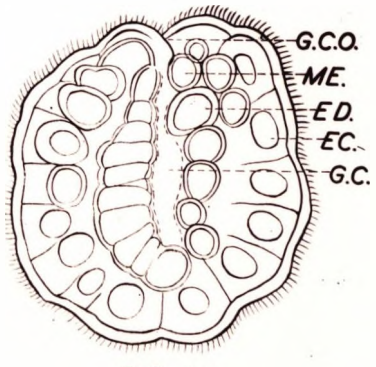

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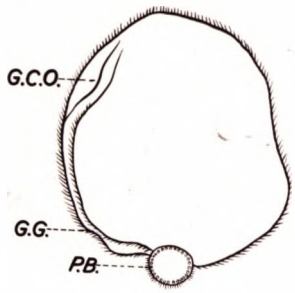

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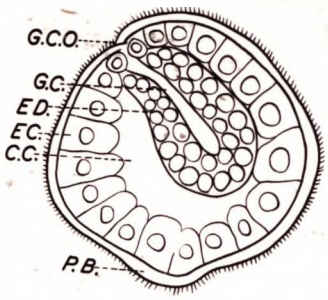

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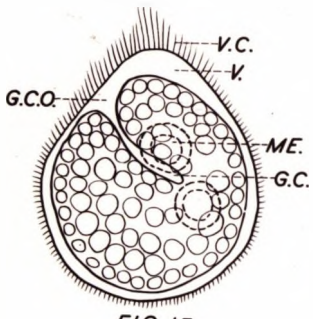

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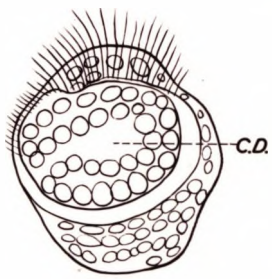

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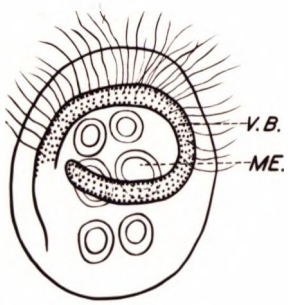

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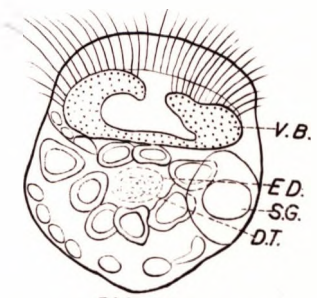

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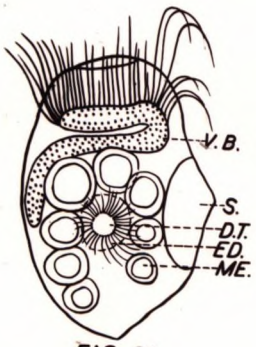

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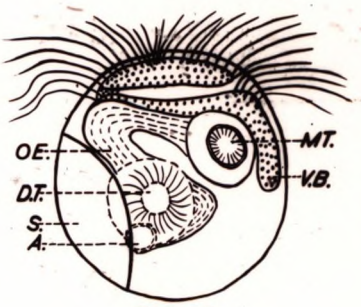

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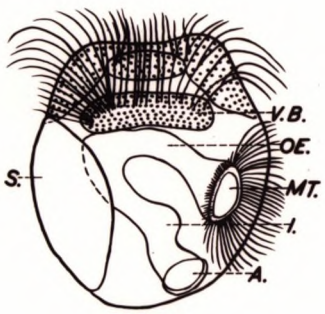

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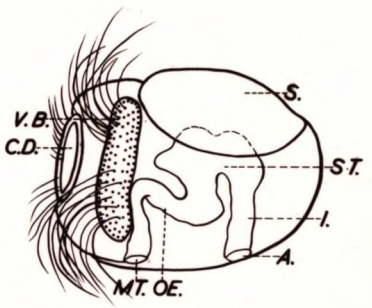

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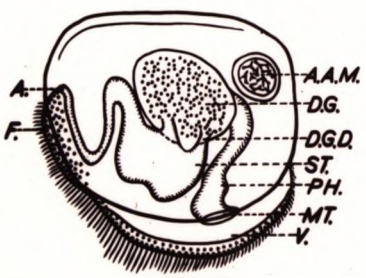

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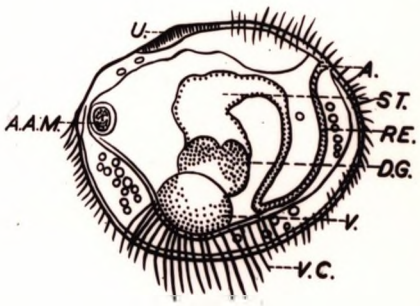

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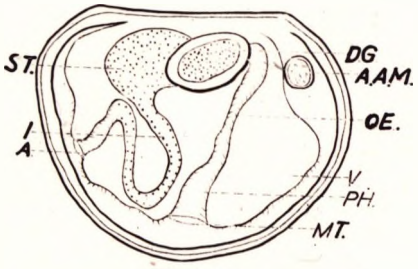

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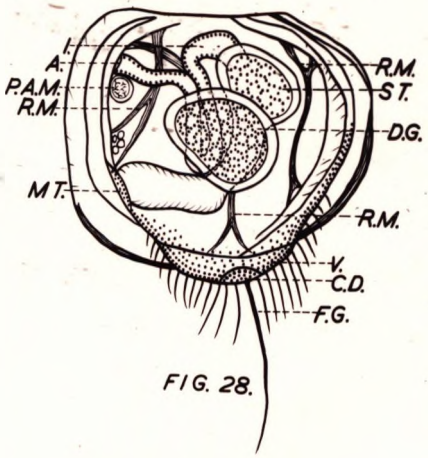

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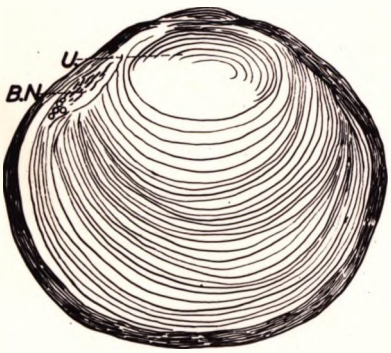

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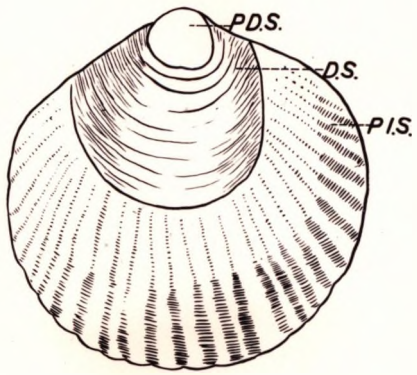

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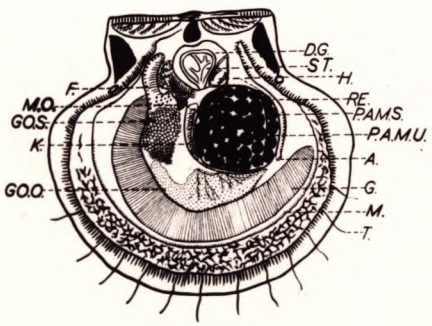

FIG. 31.

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