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THE BREEDING OF THE SCALLOP, *PECTEN MAXIMUS* (L.), IN MANX WATERS

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(Plates I and II and Text-figs. 1–5)

MATERIAL AND METHODS

An important fishery for the scallop, *Pecten maximus* (L.), is carried on during the winter months round the Isle of Man. A knowledge of the breeding of this lamellibranch would be useful should legislation become necessary with regard to the fishery.

Regular samples of scallops were dredged, whenever possible, at roughly weekly or fortnightly intervals throughout the period October 1950–October 1952, from a depth of 13–16 fm. off Bradda Head and Bay Fine, near Port Erin. Approximately 8000 scallops of all ages up to 13 years were examined, though very few young ones were caught. Scallops were aged by means of the growth-rings on the shell, of which one is laid down each spring (Mason, 1957).

The gonad of every scallop was examined macroscopically and classified as regards degree of development (see p. 656). *Pecten maximus* is a hermaphrodite, the gonad consisting of separate male and female parts.

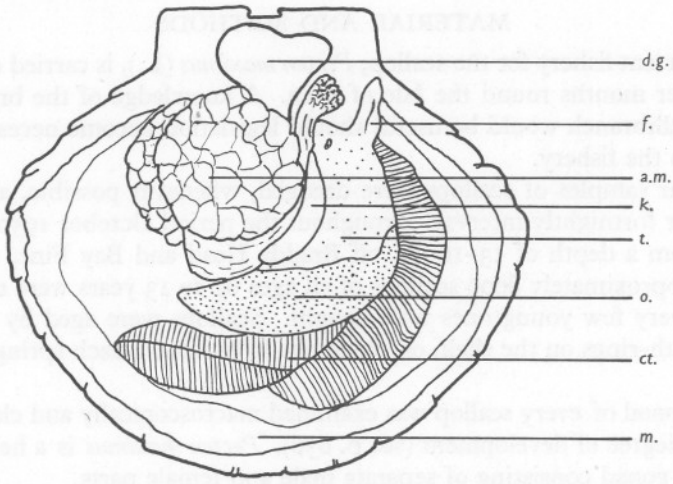
Several gonads in each stage of development were examined histologically by means of transverse sections, and serial sections were prepared of the whole of some small gonads. The material was always taken so as to include both ovarian and spermatic tissue. Three fixatives were used, Bouin, Heidenhain's Susa, and Zenker, of which Bouin proved the most satisfactory.

There is always some loss of reproductive cells from the cut surface of the gonad, and so all pieces to be fixed were cut large enough to allow for this loss. Penetration of the fixative was facilitated by making needle-holes in the material, which was then placed in the fixative and left for several days. The material was then cut into halves, each half containing both ovary and testis, and replaced in the fixative. This second cutting involved no loss of reproductive cells. After dehydration with ethyl and *n*-butyl alcohols, clearing in cedarwood oil and embedding in paraffin wax, sections were cut parallel to the newly-cut face. Sections were cut between 5 and 8 μ thick, and stained with Ehrlich's acid haematoxylin and eosin.

Fixation always resulted in a slight contraction of the gonad, and so did handling.

THE STRUCTURE OF THE GONAD

The mature gonad of *Pecten maximus* was described, but not in detail, by Dakin (1909). The single gonad is posterior and ventral to the rudimentary foot, forming a tongue-shaped mass attached to the adductor muscle (Text-fig. 1). The proximal part is white and forms the testis; the ovary is orange-red and lies distal to the testis. A loop of the alimentary canal passes through the gonad, penetrating into the ovary. This loop cannot be seen in the mature gonad unless, as occasionally happens, it passes close to the free, ventral edge of the ovary.



Text-fig. 1. The gonad of *Pecten maximus in situ*, seen from the right side. *a.m.*, adductor muscle; *ct.*, ctenidium; *d.g.*, digestive gland; *f.*, foot; *k.*, kidney; *m.*, mantle; *o.*, ovary; *t.*, testis.

The boundary between testis and ovary is usually quite sharp, though irregular, but sometimes islets of tissue of one kind occur within the tissue of the other kind. This irregularity in the distribution of the spermatic and ovarian tissue occasionally reaches a state in which the gonad is almost exclusively either male or female. I found two gonads composed entirely of female tissue.

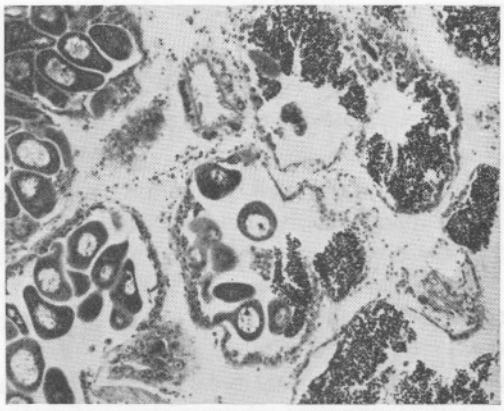
The gonad is made up of many branched, ciliated tubules or ducts, which bear many sacs, the alveoli or follicles. The ducts are round in cross-section, 70 μ or more in diameter. The lumen may be as small as 20–25 μ, and is lined with ciliated epithelium. In serial sections the ducts may be traced and are seen to join and rejoin. They eventually join one of the two main ducts, one on each side, which are much wider, up to 1000 μ in section, and open dorsally, one into each kidney.

The sexual products arise by proliferation of the germinal cells which line the follicle walls. The follicle wall is usually less than 1 μ thick. A few scat-

tered nuclei, 4–7 μ long, which are elongated and sometimes spindle-shaped, may be seen in the follicle wall, though they may be difficult to find in a full gonad.

The follicles become filled with sexual products, and those near the surface of the gonad appear to the naked eye as small, rounded, red or white bodies; the full follicles range in size from 300 to 700 μ.

In each follicle all the contents are normally of one sex, though in one gonad follicles were found containing both male and female elements, spermatozoa, spermatocytes and large oocytes being found side by side (Text-fig. 2).



Text-fig. 2. Transverse section of an abnormal gonad, showing ambisexual follicles. × 100.

The male follicle usually contains a few early stages of spermatogenesis near the follicle wall, but the lumen is filled with spermatozoa. Each spermatozoon has a minute conical head, about 1·4 μ, which stains intensely in haematoxylin, and a tail about 50 μ long. The spermatozoa are arranged radially from the centre of the follicle, or from the point where the follicle opens into the ciliated duct, with their tails pointing towards the centre or towards the duct. The female follicle contains a few young oocytes attached to the wall, while the lumen is full of large oocytes. The large oocytes appear polygonal in sections, and are packed tightly in the follicles; their greatest diameter in sections is about 80–90 μ. The large oval, or spherical, vesicular nucleus has a diameter roughly two-thirds that of the cell. A delicate network of chromatin fibres extends through the nucleus, and one conspicuous acentrally-placed nucleolus is present. The nucleus is surrounded by granular cytoplasm, which often contains bodies which stain purple in haematoxylin. The whole cell is surrounded by a membrane some 1·5 μ thick, which is not stained by either haematoxylin or eosin, but which stains blue in Azan.

Little connective tissue is present between the follicles of the full gonad, although some is present round the loop of the alimentary canal and the ducts, and sometimes near the outer wall of the gonad. The connective tissue

consists mainly of a network of fibres in which are seen various nuclei, spindle-shaped, oval and spherical, whose functional relationships are not known. Among the fibres are a few vacuolated cells. Also present are some small cells, 6–7 μ in diameter, each with a nucleus 2 μ in diameter, surrounded by a clear cytoplasm which stains pink in eosin; similar cells are seen in the lumina of the thick-walled blood vessels which are sometimes seen in sections of the gonad. Also between the follicles are transverse muscle fibres.

The outer wall of the gonad consists of two layers, an outer epithelial and an inner muscular layer. The muscles of the wall, together with the transverse muscles, probably assist the ciliated lining of the ducts in ejecting the genital products.

THE BREEDING OF THE SCALLOP

THE BREEDING CYCLE

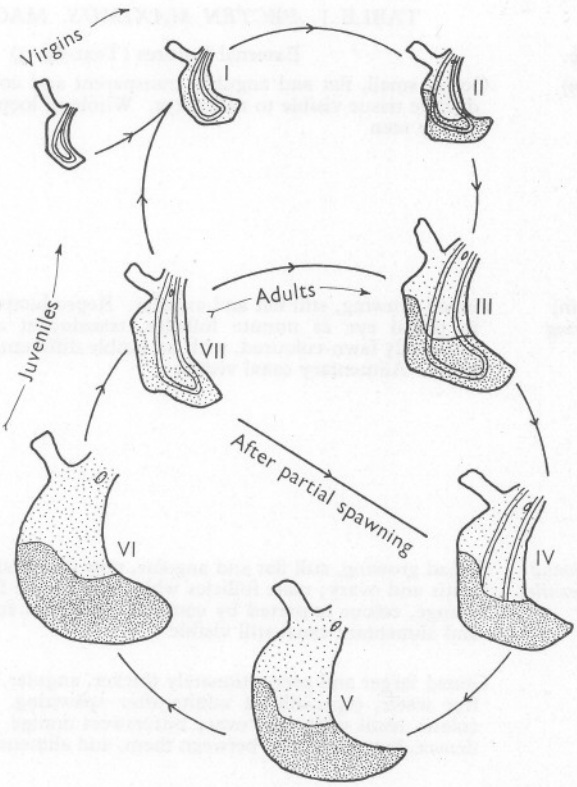
In Manx waters, scallops first spawn in the autumn following the deposition of the second growth-ring on the shell, when most of them are just 2 years old (Mason, 1957). In the following year they have one main spawning, in autumn, and thereafter they have two main spawnings each year, one in spring and one in autumn. In this paper scallops which have never spawned are called virgins, between the first and second spawnings they are called juveniles, and after the second spawning adults.

In order to determine the breeding cycle, gonads from the regular samples of scallops were classified into eight arbitrary stages of maturity, stages 0–VII, which are described in Table 1, the colour nomenclature being that of Ridgway (1912). The external features of the various gonad stages are shown in Text-fig. 3, and their microscopic structure in Text-fig. 4 and Pls. I and II.

Tang (1941) and Gibson (1956), who made similar studies of scallops, used a classification of only five stages, but their material consisted largely of commercial samples of adult scallops, and no account was taken of the differences between virgins, juveniles and adults. The classification shown in Table 1 assigns three stages (0, I and II) to young scallops, virgins and juveniles, which were not, therefore, represented in the material studied by Tang and Gibson. The 'spawning' stage of Tang and Gibson was not used in the present study, since the duration of the act of spawning was found to be so short as to make it most unlikely that many scallops in the spawning condition would be observed in nature.

The virgin scallop

Table 2 shows the monthly percentages of gonads of virgin scallops in each stage of maturity during the first 2 years or so of the scallop's life. So few young scallops were caught that data for corresponding months in the period considered (e.g. March 1951 and March 1952) were combined, and all the scallops were treated as if they were spawned in the same year.



Text-fig. 3. Macroscopic changes in the gonad of *Pecten maximus*.

Text-fig. 4. Transverse section of stage 0 gonad, 2–3 months old (December). × 100.

TABLE 1. *PECTEN MAXIMUS*. MACROSCOPIC AND

Gonad stage	External features (Text-fig. 3)
0. *Immature (virgin)*	Gonad small, flat and angular, transparent and colourless. No reproductive tissue visible to naked eye. Whole of loop of alimentary canal clearly seen
I. *Developing (virgin) or spent-recovering (juvenile)*	Gonad growing, still flat and angular. Reproductive tissue now visible to naked eye as minute follicles, translucent and sparse. Gonad uniformly fawn-coloured, with no visible differentiation into testis and ovary. Alimentary canal visible
II. *Differentiated gonad (virgin and juvenile)*	Gonad growing, still flat and angular, now obviously differentiated into testis and ovary; male follicles white and female fawn or light salmon orange, colour imparted by contents. Follicles still small and sparse, and alimentary canal still visible
III. *Recovering*	Gonad larger and proportionately thicker, angular. Flabby, containing free water, especially in adults after spawning. Assuming brighter colour, testis white and ovary bittersweet orange. Follicles larger and denser, but still spaces between them, and alimentary canal still visible
IV. *Filling*	Gonad still larger and thicker (thickness about $\frac{1}{3}$ width); still somewhat flabby, containing a little free water. Outline less angular, but not completely smooth. Colouring brighter due to denser colouring of follicles, testis white, ovary bittersweet orange or grenadine pink. Follicles larger and closer together, the latter especially in ovary. Alimentary canal still visible between follicles in testis, but not in ovary, but its outline still discernible owing to thinness of gonad
V. *Half-full*	Gonad again larger and thicker, firmer, and containing very little free water. Rounded, with tapering tip. Brighter, testis creamy-white, ovary grenadine pink or grenadine. Follicles larger, becoming packed together. Loop of alimentary canal invisible, but still causes wall of gonad to bulge
VI. *Full*	Gonad is now at its largest, thickest (thickness about $\frac{1}{2}$ width) and firmest, containing no free water. Rounded to tip. Bright, with follicles highly coloured and closely packed; testis cream coloured, ovary usually grenadine. Loop of alimentary canal indiscernible
VII. *Spent and partially spent*	Spawning may be partial or complete. Gonad dull, angular, thin and collapsed; flabby, containing much free water *Spent gonad* fawn-coloured and loses visible differentiation into testis and ovary after spawning for first time. Older scallops usually retain differentiation, testis yellowish-brown, ovary dull orange pink. Follicles appear empty *Partially spent gonad* always retains differentiation; testis yellowish white, ovary dull, bittersweet orange or orange chrome. Follicles appear hollow, with a coloured ring round periphery indicating retention of some genital products

MICROSCOPIC CHANGES IN THE GONAD

Histological details (Text-fig. 4; Pls. I and II)

Youngest scallops caught (2–3 months old) showed beginning of development, which then continues. Gonad at first almost completely occupied by loop of alimentary canal, but later connective tissue develops. Narrow tubules, bearing primary germ cells on walls, ramify and give rise to follicles and ciliated ducts, rounded in section. Primary germ cells irregular, 8–14 μ, with oval, vesicular nucleus and scattered chromatin, lightly stained in haematoxylin. Follicular cells also present. Primary germ cells give rise to gonia, each with a spherical, vesicular nucleus, 3·5–7 μ; chromatin scattered, but stains more densely than primary germ cell; well-defined nucleolus; usually a little cytoplasm. Formation of gametocytes, shown by synapsis, occurs first in distal (female) part of gonad (synapsis shows as clumping together of chromatin into an irregular, densely-staining mass). Gonad increases in size with formation of follicles and connective tissue. (Text-fig. 4; Pl. I A)

Developing (*virgin*). Follicles growing. Synapsis now occurs in proximal (male) part of gonad. Male follicles lined by several layers of spermatogonia, and lumina filled with synaptic and post-synaptic spermatocytes, with occasionally a few spermatids. Spermatocyte has a little cytoplasm, and appears polygonal in sections; nucleus roughly spherical 2·5–3·5 μ, unevenly distributed chromatin, fairly densely stained, no visible nucleolus. Spermatid 2 μ, spherical nucleus, chromatin evenly or somewhat unevenly distributed. Female follicles have oogonia and synaptic oocytes near walls, and young oocytes up to 30 μ, growing rapidly, in lumina. Young oocytes have somewhat fibrillar cytoplasm; nucleus spherical, vesicular, with a delicate chromatin network and spherical nucleolus. Spaces in female follicles. Much connective tissue between follicles. (Pl. I B, C)

Spent-recovering (*juvenile*) is similar, but has larger spaces in follicles. Before recovery becomes obvious to naked eye many gonia are produced from residual gonia and primary germ cells, and synapsis occurs as above

Spermatozoa appear at centre of male follicles; many synaptic and post-synaptic spermatocytes and some spermatids; several layers of spermatogonia near walls. A few oogonia and synaptic oocytes on wall of female follicles; many half-grown (30–60 μ) oocytes, appearing stalked, with granular cytoplasm, and a few young oocytes. Less connective tissue, but still continuous between follicles. (Pl. I D)

Male follicles contain more spermatozoa, not yet closely packed, arranged radially; still many spermatogonia and spermatocytes near walls, and some spermatids. Few oogonia and synaptic oocytes in female follicles, and lumina almost filled with growing oocytes, mostly half-grown, a few larger and smaller. Few spaces left in follicles, rather more in adults (in which stage III is the first recognizable stage of recovery after spawning) than in virgins and juveniles. Connective tissue still present, but disappearing. Main genital ducts becoming flattened. (Pl. I E)

Spermatogonia still form a continuous layer on walls of male follicles, and inside them a band of spermatocytes and a few spermatids; lumina contain many spermatozoa arranged radially. Few oogonia and synaptic oocytes in female follicle; fewer young oocytes; lumen contains more half-grown and a few almost fully grown (60–80 μ) oocytes. Little connective tissue except round alimentary canal and ducts. Main ducts larger and more flattened. (Pl. I F, G)

A few spermatogonia and spermatocytes remain near walls of male follicles, lumina full of spermatozoa which are becoming closely packed. Walls of female follicle lined with a few young and half-grown oocytes; lumina filled with almost fully grown oocytes, each with germinal vesicle still intact; very few oogonia and synaptic oocytes, indicating that production of oocytes has now almost ceased. Very little connective tissue

Follicles maximum size. Male follicles packed with spermatozoa, still arranged radially; few scattered spermatogonia and spermatocytes persist near walls. Female follicles packed with fully-grown (80–90 μ) polygonal or pear-shaped oocytes, whose germinal vesicles show signs of breaking down; very few scattered oogonia and young oocytes persist near walls. No connective tissue except round alimentary canal and ducts. Main ducts flattened. (Pl. II H, J)

Follicles smaller and collapsed, containing large spaces. Main ducts wide. Some connective tissue visible

Spent gonad after spawning for first time contains a few residual primary germ cells, spermatogonia and spermatocytes on walls of male follicles, but few or no spermatozoa; female follicles have a few primary germ cells, oogonia and young oocytes on walls. Older scallops retain more spermatocytes and a few spermatozoa, and more young and some half-grown oocytes. (Pl. II N)

Partially spent gonad retains more genital products. Many residual spermatocytes and spermatozoa, and half-grown and almost fully grown oocytes. (Pl. II M)

TABLE 2. MONTHLY PERCENTAGES OF VIRGIN SCALLOPS AT EACH STAGE OF MATURITY DURING THE FIRST 2–2½ YEARS OF LIFE

[Owing to the small numbers caught, data for scallops caught in corresponding months of the period of the investigation (e.g. March, 1951 and March, 1952) are combined, and all the scallops are treated as if they were spawned in the same year.]

Month	Gonad stages: o	I	II	III	IV	V	VI	VII	No. of gonads
Apr.	—	—	—	—	—	—	—	—	—
May	—	—	—	—	—	—	—	—	—
June	—	—	—	—	—	—	—	—	—
July	—	—	—	—	—	—	—	—	—
Aug.	—	—	—	—	—	—	—	—	—
Sept.	—	—	—	—	—	—	—	—	—
Oct.	100·0	—	—	—	—	—	—	—	2*
Nov.	—	—	—	—	—	—	—	—	—
Dec.	100·0	—	—	—	—	—	—	—	1
Jan.	100·0	—	—	—	—	—	—	—	2
Feb.	100·0	—	—	—	—	—	—	—	12
Mar.	100·0	—	—	—	—	—	—	—	17
Apr.	100·0	—	—	—	—	—	—	—	3†
May	100·0	—	—	—	—	—	—	—	9†
June	100·0	—	—	—	—	—	—	—	5
July	100·0	—	—	—	—	—	—	—	2
Aug.	100·0	—	—	—	—	—	—	—	5
Sept.	100·0	—	—	—	—	—	—	—	6
Oct.	100·0	—	—	—	—	—	—	—	12
Nov.	100·0	—	—	—	—	—	—	—	23
Dec.	100·0	—	—	—	—	—	—	—	18
Jan.	100·0	—	—	—	—	—	—	—	15
Feb.	97·7	1·2	1·2	—	—	—	—	—	85
Mar.	92·3	5·5	2·2	—	—	—	—	—	91
Apr.	40·2	27·8	8·2	12·4	11·3	—	—	—	97‡
May	22·7	14·7	28·0	20·0	10·7	4·0	—	—	75‡
June	10·2	28·6	16·3	10·2	16·3	6·1	12·2	—	49
July	—	17·4	21·7	17·4	30·4	8·7	4·3	—	23
Aug.	—	8·3	13·9	8·3	8·3	5·6	5·6	50·0	36
Sept.	—	—	—	8·1	13·5	5·4	9·5	63·5	37

* Millport scallops. † 1st growth ring. ‡ 2nd growth ring.

EXPLANATION OF PLATES I AND II

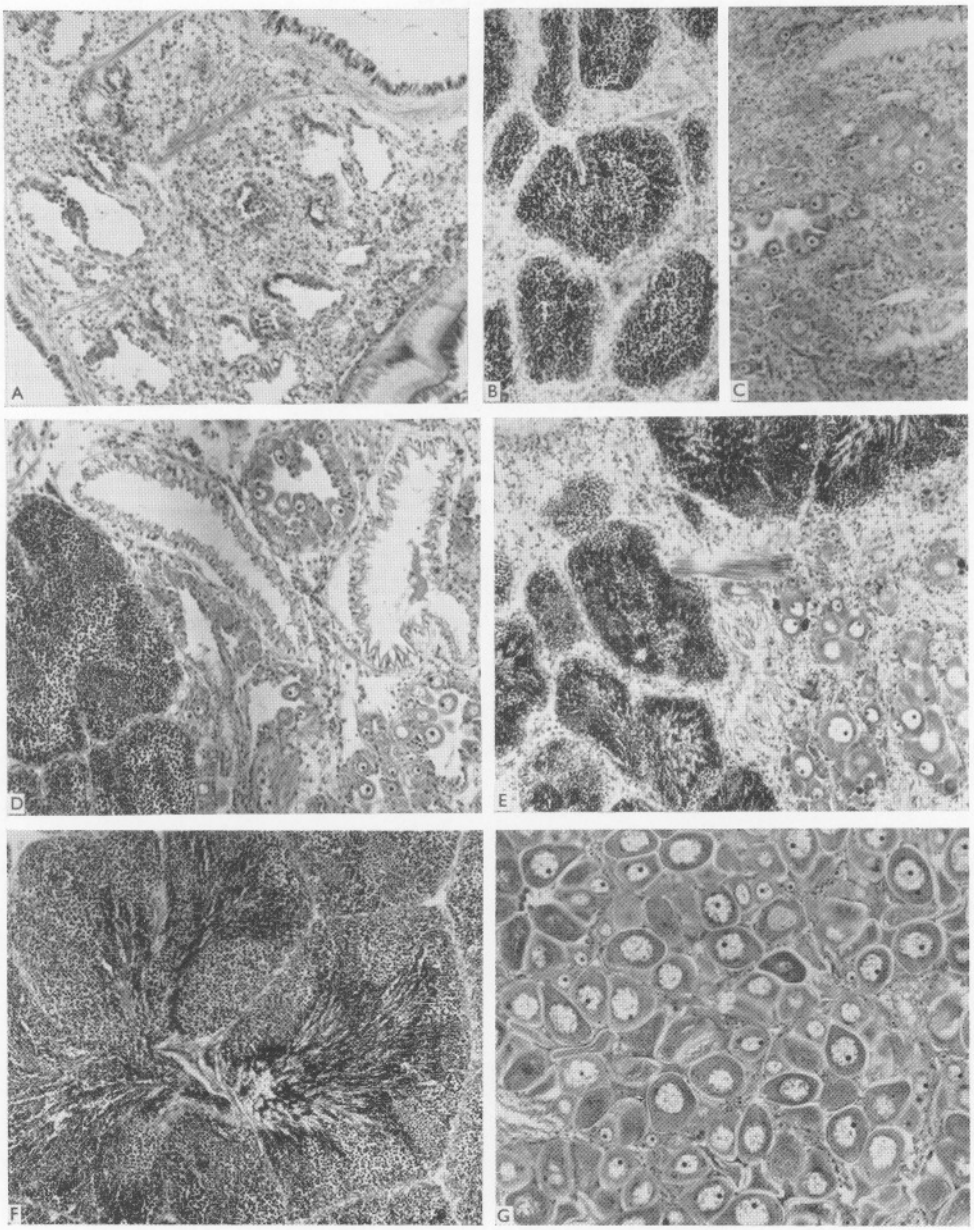
Pecten maximus. Photomicrographs of transverse sections through gonads in the various stages of maturity.

PLATE I

A. Stage o gonad, at time of deposition of second growth ring (April). Gonia showing as thickenings on edge of follicles. × 96.
B. Stage I testis. × 96.
C. Stage I ovary (cells with enlarged nuclei are young oocytes). × 96.
D. Stage II testis and ovary. × 96.
E. Stage III testis and ovary (spermatozoa have appeared in the former). × 96.
F. Stage IV testis. × 96.
G. Stage IV ovary. × 96.

PLATE II

H. Stage VI testis. × 93.
J. Stage VI ovary, showing fully-grown oocytes. × 93.
K. Running testis, showing sperm in genital ducts. × 93.
L. Running ovary, showing mature ova. × 93.
M. Stage VII testis and ovary (partially spent). × 93.
N. Stage VII testis and ovary (spent). × 93.



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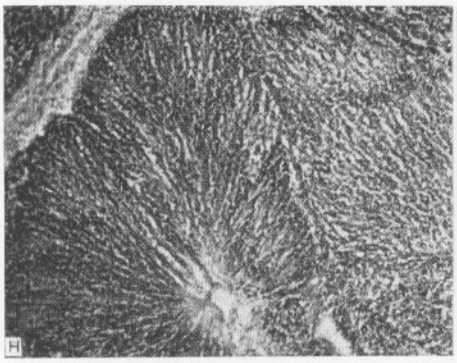
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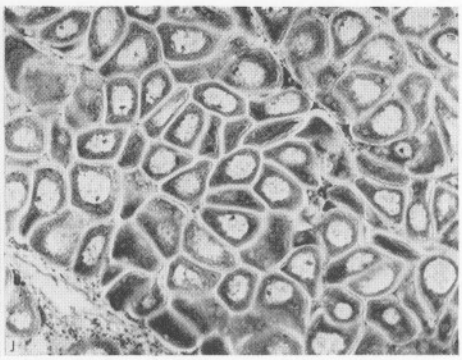
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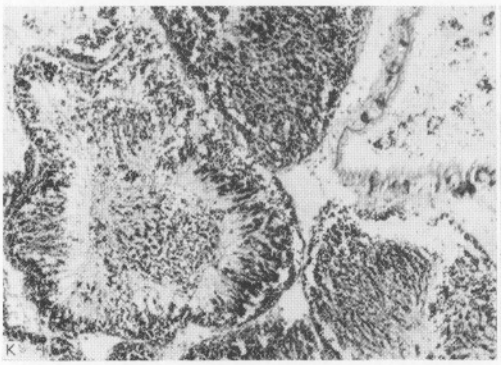
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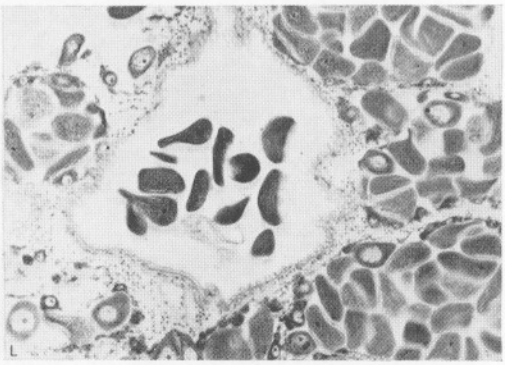
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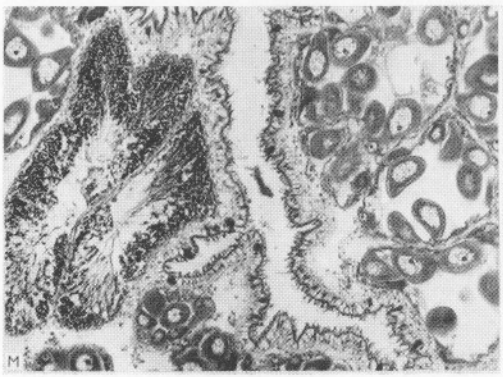
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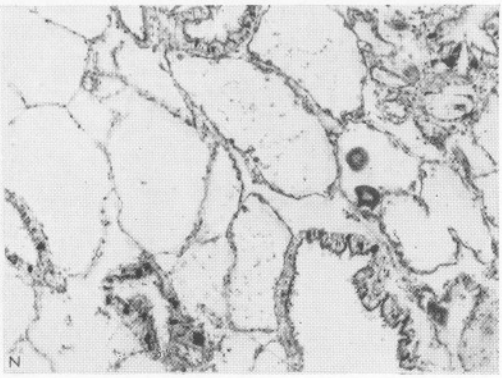
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All scallops with no growth-rings and almost all with one ring possessed stage 0 (immature) gonads, and the first sign of development obvious to the naked eye appeared in the late winter or early spring about the time of deposition of the second growth-ring, although development of tubules and germ cells had been going on continuously since a very early age (Table 1). Development continued throughout the spring and summer, through stages I to VI, and culminated in the act of spawning in the August or September after the deposition of the second growth-ring. Spawning was complete in most individuals, and involved the complete loss of differentiation into testis and ovary. The macroscopic and histological details of the various stages of gonad development are given in full in Table 1.

The juvenile scallop

The breeding cycle of the juvenile scallop begins with those scallops which have just spawned for the first time in August or September. Since the juveniles themselves spawn in the following August or September, the period of the investigation, October 1950–October 1952, almost covers two complete breeding cycles.

The gonads began to show signs of recovery externally in October or November (Table 3), although production of gonia had occurred before this. Since most gonads had spawned completely and lost their differentiation into testis and ovary, it was possible to distinguish stages I (spent-recovering) and II (differentiated), which cannot be distinguished in adult gonads owing to their retention of more genital products, and, therefore, of their differentiation. Recovery continued throughout the winter, stages III and IV predominating from January to March. The third growth-ring was laid down on the shell in the spring. Stage V gonads were commonest in April and May, and by June or July most juvenile scallops had full (stage VI) gonads. The main spawning occurred in the second half of August in 1951 and between 5 and 11 September in 1952 (Table 3B), and most scallops of this age took part. Spawning was almost complete in most individuals, but more sexual products were retained than in the first (virgin) spawning, and the gonads usually retained their differentiation. In addition, some juvenile scallops released a very small proportion of their gametes between 9 and 17 July 1952 (Table 3B).

The adult scallop

The principal spawning of adult scallops, like that of juveniles, was found to occur in August or September, so that two annual breeding cycles are again almost covered by the period October 1950–October 1952. At the beginning of each cycle were found mostly spent and a few partially spent gonads resulting from the spawning of juvenile and adult scallops (Table 4). Recovery soon began, and, owing to the larger numbers of reproductive cells

TABLE 3. PERCENTAGE OF JUVENILE SCALLOPS AT EACH STAGE OF MATURITY

(A) MONTHLY PERCENTAGE

(All samples in each month combined.)

Month	October 1950–September 1951 Gonad stages I	II	III	IV	V	VI	VII	No. of gonads
Oct.	—	—	—	—	—	—	100·0	6
Nov.	25·0	8·3	16·7	8·3	—	—	41·7	12
Dec.	—	25·0	—	50·0	—	—	25·0	4
Jan.	17·6	19·6	5·9	33·3	7·8	—	15·7	51
Feb.	17·0	5·4	19·7	39·5	4·8	—	13·6	147
Mar.	11·9	6·8	13·7	36·3	15·9	7·9	7·9	278
Apr.	2·3	4·7	7·0	30·2	14·0	41·9	—	43
May	—	0·8	2·5	27·5	34·2	27·9	7·1	120
June	—	—	—	0·8	27·7	68·1	3·4	177
July	—	—	—	—	10·3	88·5	1·3	39
Aug.	—	—	—	—	21·2	51·5	27·3	33
Sept.	—	—	12·3	36·3	0·9	12·3	38·2	106

Month	September 1951–October 1952 Gonad stages I	II	III	IV	V	VI	VII	No. of gonads
Sept.	—	—	16·7	22·2	—	—	61·1	18
Oct.	—	14·3	21·4	14·3	—	—	50·0	14
Nov.	2·3	4·5	25·0	13·6	2·3	—	52·3	44
Dec.	—	—	—	37·5	—	—	62·5	8
Jan.	2·4	11·9	19·0	33·3	13·1	1·2	19·0	42
Feb.	6·0	1·2	20·2	46·4	16·7	7·1	2·4	84
Mar.	—	—	11·1	50·0	22·2	16·7	—	18
Apr.	1·1	1·4	2·8	37·9	43·3	13·2	0·3	178
May	—	—	1·3	10·2	51·6	36·8	—	152
June	—	—	—	1·4	56·4	40·0	2·1	70
July	—	—	—	6·7	15·6	62·2	15·6	90
Aug.	—	—	—	6·8	12·8	65·5	14·9	74
Sept.	—	—	—	4·1	8·2	58·2	29·6	49
Oct.	—	—	34·4	37·5	—	9·4	18·8	32

(B) SPAWNING MONTHS

(Samples arranged to show dates between which spawning occurred.)

1951	Gonad stages I	II	III	IV	V	VI	VII	No. of gonads
15, 18 Aug.	—	—	—	—	25·0	75·0	—	4
31 Aug.	—	—	—	—	20·7	48·3	31·0	29
5–12 Sept.	—	—	—	12·0	—	38·0	50·0	25
21, 28 Sept.	—	—	16·0	43·8	1·2	4·3	34·6	81

1952	Gonad stages I	II	III	IV	V	VI	VII	No. of gonads
9 July	—	—	—	—	26·3	73·7	—	38
17 July	—	—	—	9·1	—	45·5	45·5	11
21, 29 July	—	—	—	12·2	9·8	56·1	22·0	41
5 Sept.	—	—	—	5·7	11·4	72·9	10·0	35
11 Sept.	—	—	—	—	—	21·4	78·6	14

TABLE 4. PERCENTAGE OF ADULT SCALLOPS AT EACH STAGE OF MATURITY

(A) MONTHLY PERCENTAGE

(All samples in each month combined)

Month	October 1950–September 1951 Gonad stages III	IV	V	VI	VII	No. of gonads	Month	August 1951–October 1952 Gonad stages III	IV	V	VI	VII	No. of gonads
							Aug.	—	—	12·4	27·0	60·6	113
							Sept.	9·4	30·2	4·0	13·9	42·5	260
Oct.	31·3	34·3	—	—	34·3	67	Oct.	23·0	63·1	3·4	4·9	5·5	293
Nov.	26·3	62·5	6·9	—	4·4	160	Nov.	9·2	53·9	31·4	4·5	1·0	191
Dec.	8·5	74·5	17·0	—	—	47	Dec.	1·8	33·5	40·4	22·0	2·3	109
Jan.	1·2	36·8	54·0	8·0	—	201	Jan.	1·0	15·1	55·4	28·3	0·2	288
Feb.	2·0	14·3	59·2	24·5	—	98	Feb.	—	3·7	49·8	45·7	0·8	246
Mar.	0·3	4·4	32·9	62·2	0·1	343	Mar.	—	1·5	17·6	79·9	1·0	259
Apr.	0·4	2·0	6·5	90·4	0·6	245	Apr.	—	21·0	7·1	59·3	12·5	554
May	—	10·1	4·1	39·0	46·9	318	May	—	5·1	79·6	15·2	0·2	445
June	—	2·9	76·9	10·8	9·4	346	June	—	0·2	52·6	46·5	0·7	227
July	—	—	10·0	85·7	4·3	70	July	—	5·2	10·0	76·2	8·6	296
Aug.	—	0·7	23·4	25·2	50·7	141	Aug.	—	7·1	10·7	71·1	11·1	140
Sept.	5·9	25·8	5·9	14·1	48·3	145	Sept.	—	—	6·8	52·1	41·1	96
							Oct.	43·5	42·7	—	2·4	11·3	62

(B) SPAWNING MONTHS

(Samples arranged to show dates between which spawning occurred)

1951	Gonad stages III	IV	V	VI	VII	No. of gonads	1952	Gonad stages III	IV	V	VI	VII	No. of gonads
4 May	—	—	3·3	93·3	3·3	60	1–12 Apr.	—	0·3	6·6	92·5	0·5	286
11 May	—	5·2	3·4	29·3	62·1	116	15, 17 Apr.	—	—	3·6	41·6	54·8	83
18 May	—	18·3	4·9	23·9	52·8	142	25 Apr.	—	62·4	9·4	15·9	12·2	185
17, 24 July	—	—	10·0	85·7	4·3	70	9 July	—	—	13·2	86·8	—	148
15, 18 Aug.	—	1·8	45·5	34·5	18·2	55	17–29 July	—	10·5	6·8	65·5	17·2	148
23, 31 Aug.	—	—	9·3	19·2	71·5	86	5 Sept.	—	—	11·0	83·1	5·9	59
							11 Sept.	—	—	—	2·7	97·3	37

retained by juveniles and adults after spawning, the first recognizable stage in recovery was stage III (recovering). Recovery continued throughout the winter months, stages III and IV predominating in October and November, and stages IV and V in December. Half-full (stage V) gonads were abundant in the late winter, and by March or April most adult scallops had full (stage VI) gonads. The latter, however, still had considerable numbers of spermatocytes and growing oocytes in the follicles, so that, although a mass-spawning occurred in the spring, it was only partial. In 1951 this spawning occurred between 4 and 11 May, and in 1952 between 12 and 15 April (Table 4B). The spring spawning was followed at once by recovery, and, since only a proportion of the gonad contents had been shed, the resulting partially spent gonad resembled somewhat the stage III gonad, so that the first recognizable stage of recovery was stage IV. Recovery continued throughout the summer, through stages IV and V, so that by July most adult scallops again had full (stage VI) gonads, this time with few spermatocytes and growing oocytes. These then took part in another mass-spawning, which resulted, in most individuals, in the production of almost completely spent gonads. This spawning occurred at approximately the same time as that of the juveniles, i.e. late in August (actually between the 18th and 23rd in the adults) in 1951 and between 5 and 11 September in 1952 (Table 4B). In addition, between 9 and 17 July 1952, again at the same time as the juveniles, a few adult scallops spawned slightly, and recovered quickly to take part in the main September spawning. In 1951, a sample taken on 15 August showed that a similar slight spawning had occurred in a few scallops between 24 July and 15 August, again before the main spawning.

The majority of adult scallops, then, spawn together twice during each annual breeding cycle, partially in April or May ('spring' spawning), and more completely in late August or September ('autumn' spawning). There is also a minor 'summer' spawning in July or early August. Virgin and juvenile scallops differ from adults in having only one major spawning, in autumn, though juveniles show some evidence of a minor summer spawning. The autumn spawning is therefore by far the most important in terms of numbers of gametes released.

SPAWNING

The spawning of *Pecten maximus* was observed on several occasions in the laboratory. The genital products are passed out through the two main ducts, through the kidneys, and into the mantle cavity, whence they are emitted in a cloud through the exhalant opening of the shell. No violent flapping of the shell valves occurs, but they may open and close gently at intervals of 1 or 2 min. The eggs settle and form an orange layer on the bottom of the container, while the sperm become dispersed in the water and make it cloudy.

Both kidneys become filled with either eggs or sperm. Dakin (1909) stated that the smaller left genital duct, which leads into the left kidney, serves only the left-hand side of the testis in the neighbourhood of its opening. In my observations, however, both eggs and sperm were found to pass out through either kidney. Eggs and sperm are not shed at the same time, but usually within a few hours of one another, sometimes the eggs and sometimes the sperm being shed first. This was found to be true in *Pecten maximus* by Dakin (1909) and in *Chlamys opercularis* by Fullarton (1890). In about 4% of cases one or other of the two parts of the gonad remained unspawned.

On the only occasion on which the act of spawning was observed from the beginning, the ovary spawned in 45 min., and was followed at once by the testis, which became spent in 2 h. On several occasions both parts of the gonad spawned overnight.

The running gonad has a patchy appearance, having dull areas which have shed all their ripe products, and bright areas which still contain them.

Sections of a running testis (Plate II K) show follicles in varying stages of spending; most follicles are partly empty, having spaces in their centres, but, while these spaces contain many free spermatozoa, some spermatozoa are still arranged radially, as in the full gonad, with their tails pointing inwards. The ducts are wide, and their lumina contain spermatozoa. The duct walls contain a secretion which stains purple in haematoxylin, which is thought to facilitate passage of the genital products.

Sections of a running ovary (Pl. II L) show that some follicles are in a spent condition, and contain the remains of oocytes, while others are still full, and in some of these are seen ova which have undergone or are undergoing maturation. In these ova, the germinal vesicle has broken down, the cytoplasm is evenly distributed, and a spindle with chromosomes can sometimes be seen. The ovum is still polygonal, and possesses a conspicuous membrane. Other follicles have shed a few ova, and have a few loose in their lumina. The ducts are wider and contain mature ova, and a purple-staining secretion is sometimes present in their walls.

It was found that ripe oocytes, cut from the full gonad and placed in sea water, quickly become spherical, lose the germinal vesicle, and can then be readily fertilized artificially. Eggs passed naturally from the gonad into the surrounding water behave similarly. These facts suggest that contact with sea water might cause the onset of maturation. It is possible that the eggs are often passed out of the ovary before maturation, since, in an ovary which has commenced to spawn, many fully-grown oocytes still retain their germinal vesicles, and also that contact with sea water in the mantle cavity results in the dissolution of the nuclear membrane. The genital ducts in the running gonad are so wide that water from the mantle cavity and kidneys might conceivably pass along them to the follicles, and cause the onset of maturation

in some oocytes before they leave the follicle. Coe (1933) found such a state of affairs in *Teredo*, with sea water causing the initiation of maturation.

Tang (1941) stated that *Pecten* off Port Erin began to spawn in numbers when the water temperature reached 10° C, but this is contradicted by the present study. Of the six spawnings which occurred in 1951 and 1952 it was possible in five cases to state, to within a few days, when spawning had occurred (the exception was the small summer spawning of 1951, when insufficient samples could be taken). Spawning was not caused by the attainment of a definite temperature, but occurred at several temperatures between 7·2 and 13·7° C, viz. spring 1951—7·2° C, autumn 1951—13·7° C, spring 1952—8·1° C, summer 1952—12·7° C, autumn 1952—13·5° C.

FERTILIZATION

Fertilization is external, and, at the times of the mass spawnings, there are relatively high concentrations of genital products in the sea, greatly increasing the chances of successful fertilization.

In the laboratory, artificial fertilization of eggs cut from the gonad was readily carried out. In nature, where each individual sheds its two types of genital products separately into the sea, cross-fertilization must be the general rule. Experimentally, however, cross- and self-fertilization were obtained with equal facility. On one occasion a rough count showed that about 80% fertilization was obtained, though usually the percentage was much lower than this. Better results were obtained using ripe gametes which had been shed normally by the scallop.

Normally only mature eggs from a full gonad are capable of being fertilized. However, sperm from stage IV, V and VI gonads, as well as residual sperm from partially spent gonads, are capable of fertilizing them.

LARVAE AND SPAT

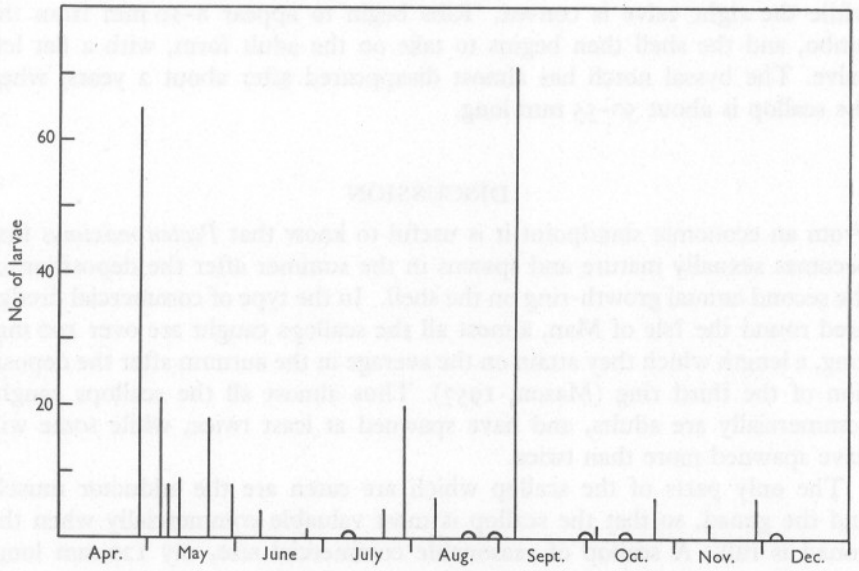
No description of the larva of *P. maximus* as such was found in the literature. Rees (1950) figured and described various pectinid larvae, but was unable to allocate the larvae to particular species.

Plankton samples were taken off Bay Fine, just below the surface, using a fine townet, 129 meshes to the inch, at intervals of 1–2 weeks during the period 28 April–24 December 1952. Dr Rees very kindly examined any pectinid larvae present, together with the prodissoconchs of recently settled spat, and as a result he was able to identify his pectinid E as the larva of *P. maximus* (Rees, 1954).

Text-fig. 5 shows the numbers of larvae in the samples. There are three main peaks, two large ones on 28 April and 5 September, and a smaller one on 29 July. The first large peak would probably be composed of larvae arising from the spring spawning, the small peak of larvae from the small

summer partial spawning, and the second large peak of larvae from the autumn spawning. Since the mass spawning of scallops in the population studied did not occur until between 5 and 11 September, the larvae found on 5 September probably originated from the spawn of a different group of scallops in the vicinity, which had spawned somewhat earlier.

The large numbers of larvae in the plankton haul of 28 April show that the spring spawning resulted in the successful production of larvae. When spawning was recorded, between 12 and 15 April, the temperature was 8·1° C, indicating that a temperature of 10° C is not minimal for the production of larvae, as was thought by Tang (1941).



Text-fig. 5. Numbers of larvae in plankton samples, April-December 1952. Blank hauls are indicated by semicircles.

The sampling was not adequate to show the exact times and compositions of the peaks in Text-fig. 5, this being especially so in the September peak, when there was a gap of 25 days after the sample of 5 September. The September peak would be expected to be much higher than the April peak, owing to the much greater amount of spawn shed in the autumn than in the spring spawning (see above, p. 664).

Elmhirst (1945) stated that the larvae of *P. maximus* settle on *Laminaria saccharina*, while Hertling (1934) found a few young specimens attached to a drifting trunk off Heligoland. On only one occasion, however, did I find the spat of *Pecten maximus*, namely on 29 August 1952, when two specimens, 3·0 and 3·5 mm long respectively, were found on *Desmarestia* on the Bradda

bed. These presumably arose from the small summer spawning. In addition, Mr T. B. Bagenal kindly sent me a few young specimens which he found attached to *Laminaria saccharina* at Millport. My inability to find more young *Pecten maximus* was surprising in view of the large numbers of newly settled *Chlamys opercularis* which I found attached to *Laminaria saccharina*.

The two recently settled individuals of 3·0 and 3·5 mm found off Port Erin were easily recognized, since the shape of the young shell can be deduced from the concentric striae on the adult shell (Mason, 1957). The shell was transparent and almost colourless, with a conspicuous byssal notch, and both shell valves were convex. Larger specimens, some 5–25 mm long, possess a left valve which is concave except for a small convex area near the umbo, while the right valve is convex. Ribs begin to appear 8–10 mm from the umbo, and the shell then begins to take on the adult form, with a flat left valve. The byssal notch has almost disappeared after about 2 years, when the scallop is about 50–55 mm long.

DISCUSSION

From an economic standpoint it is useful to know that *Pecten maximus* first becomes sexually mature and spawns in the summer after the deposition of the second annual growth-ring on the shell. In the type of commercial dredge used round the Isle of Man, almost all the scallops caught are over 100 mm long, a length which they attain on the average in the autumn after the deposition of the third ring (Mason, 1957). Thus almost all the scallops caught commercially are adults, and have spawned at least twice, while some will have spawned more than twice.

The only parts of the scallop which are eaten are the adductor muscle and the gonad, so that the scallop is most valuable commercially when the gonad is full. A scallop of reasonable commercial size, say 120 mm long, with a full gonad, yields on the average approximately 32 g of edible material, of which the muscle accounts for 24 g and the gonad for 8 g. Thus scallops are in the prime of condition in the months immediately prior to spawning, namely March–April and July–August, but they are not normally caught in the summer months owing to the difficulty of keeping them in good condition in hot weather during transport to London, the main market.

The occurrence of two main spawnings yearly among adult scallops has not been noted by previous workers in Manx waters, though recently, since the present work was completed, Gibson (1956) has noted it in *P. maximus* in Irish waters.

With the occurrence of two main spawnings can be correlated the fact that two types of first year's growth can be recognized on the shell, according to the length of time available for growth before the first winter cessation (Mason, 1957). Autumn-spawned scallops are greatly in the majority owing

to the much greater amount of spawn released then as compared with the spring spawning.

In the system of classification used by Coe (1945), *P. maximus* is a 'functional hermaphrodite', in which both types of sexual cells are produced at the same time, but are not usually discharged together. Coe (1945) stated that in the genus *Pecten* there is a strong tendency towards protandry, that in the young gonad spermatogenesis may be in progress long before the ova have begun the deposition of yolk, and that some or all of the sperm is discharged before the eggs are fully ripe. Pelseneer (1935) said that hermaphrodite molluscs in general are protandrous, the sperm being ripe before the eggs, so that self-fertilizing hermaphrodites are rare and cross-fertilization is the general rule. Dalmon (1938) went so far as to say that *P. maximus* is so distinctly protandrous as to render self-fertilization impossible. The results of the present study contradict Dalmon's statement and support one made by Coe (1945) that, experimentally, self-fertilization in fully-ripe functional hermaphrodites seems to take place as readily as cross-fertilization.

The present study has shown that, in the virgin gonad of *P. maximus*, there is an early tendency, not towards protandry, but towards protogyny, in that oocytes are first produced before spermatocytes (Table 1). Later, however, this tendency is reversed, and spermatogenesis so far outstrips oogenesis that the male follicles contain some spermatozoa while the female follicles still contain only half-grown oocytes. Similarly, after spawning, spermatogenesis occurs more rapidly than oogenesis, and many sperm are present long before the oocytes are fully grown. These sperm from the earlier gonad stages are physiologically ripe and capable of fertilizing ripe eggs which, however, occur only in the full (stage VI) gonad. The sperm are stored in the testis until the gonad is full, and the products of the two sexes are discharged separately, but within a few hours of each other, often some weeks after the full stage is reached. The products of either sex may be shed first, so that some individuals are functionally protandrous and others are functionally protogynous.

A retention of morphologically ripe gametes in the gonad for considerable periods of the year was also found in *Venus mercenaria* by Loosanoff (1937). *Pecten maximus* also resembles *Venus mercenaria* in that there is no resting period in the gonad after spawning, and that gametogenesis occurs over most of the year, even in the autumn and winter months when the temperature is falling. Loosanoff considered these phenomena as unusual among lamellibranchs.

This paper is based on parts of a thesis[1] presented to the University of Liverpool in 1953 for the degree of Ph.D. The work was carried out at the Marine Biological Station, Port Erin, while I held a Herdman Studentship

[1] Investigations on the scallop [*Pecten maximus* (L.)] in Manx waters, 1953.

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SUMMARY

Pecten maximus is a functional hermaphrodite, whose gonad consists of separate male and female parts. Its breeding cycle in Manx waters was determined by examination of the macroscopic and microscopic changes in the gonad. The virgin scallops spawn in the autumn after the deposition of the second growth ring on the shell. In the next year, as juveniles, they have one main mass spawning, in autumn, and a very small, partial one earlier in the summer. In all subsequent years, as adults, they have two mass spawnings, a partial one in spring and a more complete one in autumn, while a much smaller, partial one occurs in the summer. Gametogenesis occurs throughout the year, and there is no resting period after spawning.

P. maximus shows an early tendency to protogyny in the development of the virgin gonad, but this is soon reversed, and a tendency to protandry appears, which is also apparent in the recovery after spawning, so that ripe sperm are present long before fully-grown oocytes. These ripe sperm are retained until the gonad is full, and the two parts of the gonad spawn separately within a short time of each other, the whole act of spawning taking a few hours. The products of either sex may be shed first. While cross-fertilization must be the rule in nature, experimentally both cross- and self-fertilization of mature eggs, which had lost their germinal vesicles, were obtained easily.

Spawning does not take place at a definite temperature.

The numbers of larvae in plankton hauls show three peaks, two large and one small, corresponding to the two main and one small spawnings. No reason can be advanced for my inability to find more than a few recently settled individuals.

Almost all scallops caught commercially have spawned at least twice. Scallops are most valuable commercially when their gonads are full prior to spawning.

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