

Observations and Experiments on Sex-Change in the European Oyster (*O. edulis*.)

Part I. The Change from Female to Male.

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With 4 Figures in the Text.

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SECTION A. INTRODUCTION.

OBSERVATIONS indicating a change of sex in the European oyster (*O. edulis*) from female to male have been made by many naturalists in the past, and especially by Davaine, Möbius, and Hoek. The latter states (1883, p. 235) that individuals after spawning as females begin to produce sperm. Later Hoek (1902, Table 7, p. 175) gave details of the microscopic examination of the gonad of eight individuals which were carrying larvæ in the mantle cavity, and although in some of these cases Hoek found only scattered clumps of germ-cells, while in others abundant sperm, he confirmed his previous opinion that sperm-production begins after an individual has spawned as a female. Möbius (1877, p. 11, and 1883, p. 693) also found ripe sperm in blacksick oysters, but no sperm in whitesick ones. As both Hoek and Möbius held the view that individual oysters (*O. edulis*) function after the manner of one sex or the other at the moment of spawning, they concluded that a change of sex occurred from female to male at some time after the act of spawning as a female.

Other naturalists, of whom Lacaze-Dathiers may be cited, had observed hermaphrodite individuals, and disagreed with those who contended the general unisexuality of individuals, while Hoek himself, in a later work (1902, p. 174), records fairly high percentages of hermaphrodites; thus considerable confusion occurred in the literature as to what are the actual sex-phenomena in this species. This confusion persisted down to recent years, and is well brought out by Spärck in a recent review of the literature (1924).

The present writer was attracted to this problem by noticing the rapidity with which an oyster which had recently spawned as a female attained a condition—with the gonoducts full of ripe sperm—ready to spawn again as a male (1921), and from a review of the conflicting views found in the literature arrived at the conclusion that nothing less than a collection of facts and definite experimental results would offer critical evidence of the sex-conditions existing in *O. edulis*. A change of sex from male to female was inferred by many workers, and Hoek (1883, p. 235) states that in his opinion a class of individuals function as males, and afterwards—but only in the following year—function as females, and at once remarks, “toutefois nous n'avons point la preuve que cela doive nécessairement arriver.” In 1921 (*loc. cit.*), the present writer began experiments to obtain the proof which Hoek saw was necessary, and later (1924) was able to give a preliminary report of experiments which proved the change of sex from male to female in a small proportion of cases. At about the same time Spärck (1924), who had been

experimenting on similar lines, was also able to report the observation of a change of sex from male to female in three individuals.

A change of sex from male to female in all young individuals, i.e. protandry, has also been a popular conception for many years, but the writer has shown (1922) that the evidence for this view is not satisfactory, and will be difficult to obtain, nor has the matter been advanced critically by Spärck's recent work in the Limfjord (1924). These subjects may be discussed later, when the data accumulated have been presented.

In order to obtain definite information on the problems of sex-change in the oyster it was decided :—

(a) To examine the living tissues, or if necessary in some cases microscopic sections also, of 1000 female-functioning oysters, at about the time of spawning and at various periods afterwards, from as many different localities as possible, and to note the condition of the gonad with regard to the production of sex-elements.

During the years 1920–26 more than 1000 such individuals have been examined, and the results are given and discussed herein, but an extended discussion of various aspects of the work is necessary before the results obtained can be approached in a logical manner.

(b) To isolate in cages in the sea individuals proved to be males at the instant of examination—by tapping the gonad through a boring in the shell—and to re-examine the same oysters at successive periods for female spawning and ripe female individuals, which must therefore have undergone sex-change from male to female.

A number of experiments on these lines have been carried out, and will be discussed later in Part II of this work.

(c) To isolate in cages in the sea female-functioning individuals carrying spawn with a view to their examination at later dates, for

- (1) individuals which might again be found carrying eggs, embryos, or larvæ, and
- (2) the state of the gonad at a definite epoch in the (presumed) sex-cycle.

Experiments in this category are noted in Table IV, but will be discussed later in Part II.

MATERIAL AND METHODS.

Oysters in spawn have been obtained from most of the beds in the South of England (see below) through the courtesy of the owners and managers of the beds. The opportunity of thanking the owners and their assistants given in the following list is here gladly taken.

Owners of Beds.	Assistants.
Tollesbury and Mersea Native Oyster Co., R. Blackwater	Mr. Louis French.
Corporation Oyster Committee, Truro Beds, Fal River and Estuary	Mr. E. Searle.
Corporation Oyster Committee, Falmouth Beds, Fal Estuary	Mr. C. May.
Seasalter and Ham Oyster Co., Whitstable, Thames Estuary	Mr. E. Luckhurst.
Duchy Oyster Farm, Helford River, Cornwall	Mr. S. Hodges.
Oyster Beds, Burnham River, by courtesy of	Mr. E. Luckhurst.
Yealm Oyster Fisheries, River Yealm, near Plymouth	Mr. J. Kingcome.
*Saltash Oyster Beds, River Tamar, near Plymouth	—
*Public Beds off Swansea, S. Wales	—
*Public Beds, Isle of Wight	—

A good deal of the valuable material examined on the beds at West Mersea was obtained when carrying out experiments subsidised by a Government grant from the Royal Society. Without this grant the earlier experiments on sex-change herein recorded could not have been carried out.

Oysters in spawn were obtained in various ways: from samples sent by post; individuals found "sick" on the beds and forwarded to Plymouth; from the examination of thousands of individuals in the Tollesbury and Mersea Company's stores; from the examination of samples on the shore adjacent to the working oyster-dredgermen, especially at Falmouth, in order to open the oysters with the least possible delay after their capture. In this way were obtained oysters carrying embryos from the unsegmented—but mitotically dividing—egg, through a great variety of stages of development to the fully formed shelled larva ready for independent life in the sea. The age of embryos and larvæ in various stages has been determined approximately by observation and experiment. Since a series of individuals was obtained carrying a graded series of spawn with regard to age, so also was obtained from the parent a series of gonads with regard to age, reckoned from the time of the act of spawning as a female. In such a series of gonads of approximately known age (as defined) the condition of the sex-elements, and especially the male elements, was carefully noted in each individual and recorded in tabular form, as shown in Tables IV and IX, pp. 999 and 1025. In this way the age of the gonad—reckoned from the time of the last female-spawning

* I am indebted to Mr. F. S. Wright as the representative of the Ministry of Agriculture and Fisheries, London, for samples from these beds.

act—is determined from the (approximately) known age of the embryos or larvæ carried by an individual, and can be correlated with the state of development of the male sex-elements. It will be seen from the results discussed later that there is a general progressive development of sperm from the first day of the female-spawning act.

SPERMATOGENESIS.

In order to determine the condition of the gonad with regard to the development of male-elements, sperm, it is necessary to know the major details of spermatogenesis. The complete details of spermatogenesis in the oyster are badly needed and not yet known, and would well repay study. Hoek, however, as long ago as 1883, followed the main divisions of the sperm-mother cell to the production of a sperm-ball or sperm-morula. In an abstract of Hoek's paper, Bourne (1890) translates that "the minute mother-cells of the spermatozoa have a diameter of scarcely 8μ , they stain deeply with alum carmine and have dark granular contents and a small nucleus. The spermatozoa are developed from them as follows. In each cell after the division of the nucleus, the cell-body divides into two portions. Of these one is destined to give rise to numerous spermatozoa, the other seems to serve only as a provisional connexion between the developing spermatozoa and the wall of the follicle. The former cell grows rapidly, and the nucleus subdivides rapidly and repeatedly until a large cell is formed $25-30\mu$, containing 40 to 50 nuclei. Each nucleus is about 4μ in length. At this stage the whole structure looks like a club of which the swollen part is formed by the other derivative of the primitive cell. At this stage the multi-nuclear cell becomes separated from its peduncle. Its nuclei continue to subdivide, and become darker and more opaque. Finally, the mother-cell becomes entirely developed into spermatozoa derived from the subdivided nucleus, but one cannot explain precisely the steps by which the smallest nuclei are transformed into spermatozoa."

In contradistinction to the characters of the sperm-mother cell, Bourne, in the same abstract, shows that "in the youngest stage observed the ovum of the oyster is a little cell $20-24\mu$ in diameter, flattened on the side of the canal wall and rounded on its free surface. The protoplasm of the cell-body is feebly granular; the nucleus is large, spherical, and has a highly refringent single nucleolus of moderate size. The youngest ovules pass by insensible gradations into the more advanced, and those again into the mature ova."

Hoek therefore shows that from a very early stage developing spermatogonial aggregates can easily be distinguished from a young ovum, since even the youngest ovum seen by Hoek at $20-24\mu$ had a well-marked nucleus and nucleolus, while a sperm mother-cell begins to divide when

only about 8μ , and contains 40 to 80 nuclei when $25-30\mu$ at a size a little bigger than the smallest ovum seen by Hoek.

It will be noted that Hoek does not give any final limit to the size of the ripe sperm-morula, that is, the stage at which all the spermatozoa in one subspherical mass are fully developed and have tails. The reason is simple; there is great variation in size of the ripe sperm-morula from subspherical masses 50 or 60 to 80μ in diameter to irregular cylindrical masses up to 110μ long by 40μ or more in diameter. It is not improbable that the masses developed from different mother-cells may fuse in groups of two or more.

In the fresh condition it is easy to distinguish young spermatogonial aggregates when about 20μ in diameter and containing about 10 cells, and identification is only difficult when there are only about 4 to 8 daughter-nuclei at sizes of about 10μ to 14μ . In these latter cases microscopic sections are necessary to confirm observations on the freshly teased gonad. There is, however, an outstanding appearance of living developing sperm-morulae, which makes it a very simple matter to distinguish them under the microscope from ripe sperm-morulae, namely, the clear translucent appearance of the former up to the stage in which the tails of the spermatozoa may occasionally appear, and the dark granular appearance of the sperm-morula with fully developed spermatozoa with active tails. There is a very sharp differentiation into clear translucent, unripe, and opaque ripe sperm-masses. It would seem that the granular appearance arises at about the time when the spermatids are transformed into spermatozoa, and that this phase occurs in a very short space of time.

In practice developing sperm-masses from 20 to about 60μ are easily distinguished by their general appearance and translucency, and there are no other tissues in the oyster with which these can be confused; the ripe sperm-masses are opaque, of characteristic appearance with actively vibrating tails radiating outwards from the surface of the mass; moreover, it was found that sperm develop so rapidly that only in relatively few cases were they so little developed that identification in the fresh material required to be supplemented by prepared microscopical sections.

It may be observed that in Hoek's account of the early development of the sperm-mass he describes that one of the cells derived from the first division "seems to serve as a provisional connexion between the developing spermatozoa and the wall of the follicle." There can be little doubt that this provisional connexion forms the channel of nourishment for the developing spermatozoa, and also develops into the protoplasmic strands visible in the freshly teased ripe sperm-morula (see Orton, 1924, Plate IX). When living ripe sperm-morulae are obtained on a slide, and when a little sea-water has been added to the body fluid, the sperm become more and more active until first a few and, finally, all wriggle away from the

residual matrix, a tenuous reticular mass, which is probably also partly the remains of the original provisional connexion noted by Hoek.

It is an interesting observation that sea-water needs to be added to ripe sperm-morulæ, in order to induce the sperm to segregate; in the first place separate sperm are not found normally in the gonoducts, as they are, for example, in the Portuguese oyster, or in sea-urchins and numerous similar cases. In case of doubt, therefore, the condition of the ripe sperm serves as a character to distinguish the Portuguese from the European oyster. Among the thousands of male European oysters examined by the writer, only one or two cases of the occurrence of separate sperm in the gonoducts have been met with, and in these cases the oysters were either dead or dying, and doubtless sea-water had entered the relaxed ducts and induced segregation of the sperm. As ripe sperm-morulæ do not disintegrate in the ducts, they must either pass into sea-water or some medium, which probably needs to be—like sea-water—slightly alkaline, before the sperm are set free to effect fertilisation of the ova, a fact which indicates—but does not prove—an adaptation to cross-fertilisation in the species. As ripe sperm-morulæ disintegrate in sea-water, it is suggested that sperm are normally distributed through the water where the sperm-morulæ are spawned, and it may therefore be inferred that sperm are collected by female-functioning oysters (as Hoek and Mobius believed) in the region of the reproductive apertures for the purpose of effecting cross-fertilisation. Further investigations are required on these matters, and are being carried out.

ON SPAWNING.

Sperm-spawning.

In *O. edulis* a class of individuals with a well-developed gonad containing millions of ripe sperm-morulæ undoubtedly occurs, but there are few—if any—records of the observation of spawning males. In the writer's experience probably not more than six individual males have been under observation during the spawning act. In one well-marked case, a male spawned millions of ripe sperm-morulæ into a petrie dish, the spawn having a greyish white appearance which might easily have been mistaken by the unwary for embryos or larvæ in the mass. Similar less complete spawnings have been seen, and in a very large number of cases ripe sperm-morulæ are found in the liquor obtained when the oyster is opened; but as in these latter cases the frail gonoducts on the surface of the body are generally broken, it is more probable that these sperm-morulæ have escaped from the broken ducts than that they have been naturally spawned.

Although sperm-spawning individuals have rarely been met with, it is quite possible for the inexperienced observer to mistake a spawning

male for a spawning female, especially when the spawn is extruded from the edge of the shell in an oyster out of water, but a glance at the spawn rinsed into water is sufficient to discriminate between them. The spawning of the males is an important phase in the general course of reproduction in the oyster, and as yet little attention has been given to the subject. The writer will be able to give figures later which prove that there is a big spawning of males at the beginning of the breeding season at about the time the earliest females are found in spawn, and probably the oyster is seasonally protandrous; at the same time observations (see pp. 1025 to 1034) made in summer on individuals at various times after these have spawned as females—earlier in the same year—show that there must also occur a considerable amount of sperm-spawning in summer also. It is highly probable that the spawning of the males is correlated in some way with that of the females, but the manner of this correlation (if any) is not known. It is possible, for instance, that a female with ripe ova may retain its ova until a sufficiency of sperm has been accumulated (assuming for the time that self-fertilisation does not occur), for it is rare to find unfertilised eggs in the mantle cavity of a female which has spawned naturally.

It will be convenient at times to refer to sperm-spawning as andro-spawning when the term is used in the sense of spawning as a male, and in the same manner ovum-spawning may be referred to as gynes-spawning to imply the act of spawning as a female.

Egg-spawning and the Fate of Unspawned Eggs.

It is normal in *O. edulis* for the whole of the eggs to ripen at the same time, and for the ripe female to extrude the whole of the ova contained in the gonad and gonoducts in one act. The ova are fertilised normally at some instant of their passage from the gonoducts to the exterior. In many cases, however, a portion—which may be small or great—of the ova may remain behind in the gonad after the spawning act has taken place. A glance at the column reserved in Table IV, pp. 999 to 1021, for remarks on such ova left in the gonad after the spawning act, will show that it is quite common for isolated small or large patches of ova to remain unspawned. Such ova may either be retained in the gonad and degenerate and become absorbed, or they may be included in egg-cysts and extruded in masses and excreted *en bloc* on to the internal face of the shell and covered over with nacreous or horny matter in the form of an excretion blister. From a study of the records of the gonad condition given in Table IX, pp. 1025 to 1034, it seems probable that relict ova may also be extruded later through the reproductive aperture, and in a small percentage of cases, where a large part of the gonad retained its eggs, it would certainly seem possible that a second spawning act of one set of

eggs may occur. If such a second batch of eggs is fertilised then the individual will appear to have spawned twice as a female within a very short time, although the two spawnings are made from one batch of eggs. This possibility is believed to have been a probability *in a few cases* out of the large number observed; it is a serious handicap to some experiments on sex-change, and necessitates the demonstration of sex-change in a significant number of individuals to render the results free from doubt. Thus *isolated* experimental cases of change of sex from male to female or from female to female again must always be regarded with a reasonable amount of suspicion, and the factor of the proportion of individuals showing sex-change in any experiment is an important one. From examination of weekly samples of oysters from the Falmouth Oyster Beds in 1925 (Orton, 1926)—confirmed in 1926—the writer was able to show that the largest proportion of ripe females occurs in a population at the beginning of the summer and gradually diminishes throughout the summer until at the end of the breeding season, only a few ripe females remain. The proportion of ripe females remaining unspent at the end of the summer was found to be from 0 to 5% in 1925 and 1926 in the Fal Estuary and in 1926 in the Blackwater Beds. The proportion of females ripe at the beginning of the breeding season is a variable factor, not yet sufficiently known; it undoubtedly varies with age, and for samples of mixed ages, which were *estimated* at mainly 4 to 5 years, the proportion on the Truro Beds in the Fal Estuary at the beginning of the breeding season in 1925 was about 50% (Orton, 1926, p. 205). (See also Table I, p. 979). On other beds in other years it is probable that smaller percentages of ripe females occur, but fresh observations in the light of recent work are required to obtain comparable figures extending over a number of years.

HERMAPHRODITE INDIVIDUALS AND OTHER SEX-CATEGORIES.

The examination of the gonad of a large number of individuals carrying embryos or larvæ—detailed in Table IV, pp. 999 to 1021—has shown that a fair proportion of individuals do not spawn all their eggs at the gyne-spawning act, and as it will be shown later that the gonad becomes actively sperm-producing at about the time of the egg-spawning, the appearance of such a gonad with ripe eggs and developing, or later, fully developed sperm may be essentially that of a hermaphrodite individual. Nevertheless such individuals are not hermaphrodite (in a strict sense which will be defined later). In spite of the occurrence of such incompletely spawned females, it is certain that true hermaphrodite individuals also occur in fair proportion. True hermaphrodites are defined as individuals with ripe ova and ripe sperm developed generally evenly throughout the

gonad. These hermaphrodite individuals resemble females in the appearance of the body to the naked eye when the sex-elements are ripe, and statistical observations indicate that such individuals do actually spawn as females and extrude normally the whole of their genital products at the same time, and further that such individuals hatch a batch of larvæ. Direct proof of this should be obtained, however, by the examination of the whole of the sex-elements of a number of individuals—apparently female—caught in the act of spawning, but it is a very difficult matter to catch individuals in this phase. One such case is, however, recorded in Table IV, individual No. 614, p. 1016. (See note 15, p. 1021.)

In the case of hermaphrodite individuals as defined above, the occurrence of *developing* sperm-morulæ with ripe ova has very rarely been observed, and in only a very small percentage of the hermaphrodites examined. This observation may probably be important.

It was noticed during the course of the investigations that hermaphrodite individuals have varying proportions of *ripe* spermatozoa in relation to the number of ova in the gonad, so that in an effort to compare individuals of one population with those of another, it became necessary to adopt arbitrary categories for oysters with abundant ripe eggs, but with a varying amount of ripe sperm-morulæ. The conditions are not dissimilar to those described in *Crepidula* (Orton, 1909), but there the gradation occurs in relation to both primary and secondary sexual characters, whereas in the European oyster, as is well known, there are no morphological secondary sexual characters visible to the naked eye.

In the oyster the arbitrary categories adopted are:—

1. Hermaphrodite, ♂, individuals with a large quantity of ripe spermatozoa and abundant ripe ova.
2. Hermaphrodite female, ♂(♀), individuals with fewer ripe sperm-morulæ than the foregoing category and abundant ripe ova.
3. Female with a trace of maleness, ♀(♂), with a gonad filled with ripe ova, but where a few ripe sperm-morulæ may also be found.

All these three categories are regarded, however, as essentially functional females. In addition to these, two other categories of mixed sexes are recognised.

4. Male with a trace of femaleness, ♂(♀), (A), individuals in which ripe and occasionally also developing sperm-morulæ occur in predominant proportion in a well-developed gonad along with numerous though relatively few large ova.

This category, which may consist of two or three different kinds of individuals, is not properly understood, and has been marked down for a separate research. Successive weekly statistical examinations of

samples at the beginning of the breeding season indicate that this category may consist of hermaphrodite forms in which maleness is well advanced or fully developed, while femaleness is not quite fully developed. This view is supported to some extent by an examination of the fresh gonad; the eggs, although large, have not the resilience of ripe ova and burst with the slightest pressure, but the contents of the egg have not the same appearance as obviously degenerating ova left behind in the gonad of an incompletely spawned female. It is, however, possible that some individuals in this category may be either well-fished (i.e. with large stores of reserve products) males which have retained and are absorbing unspent ova, or may even be abortive females.

Male with a trace of female, ♂(♀) B, individuals in which the gonad is not usually well developed and contains ripe or ripe and developing sperm-morulae and also a small or fair number of degenerating and obviously relict ova; these individuals are obviously and undoubtedly in a functional male stage.

5. Female-like ♂'s, individuals which in the living condition have the appearance of and are indistinguishable with certainty by the naked eye from pure females, but whose sex-elements consist entirely of sperm-morulae, ripe or ripening in a matrix of granular reserve products. It is difficult to resist the impression that this category is derived from individuals in which ova have been absorbed, and in which the resultant nutriment of the ova is being transformed into viable metabolic products, but there is no other sex-designation of the category possible than simply males. It is not impossible, however, that the reserve products in these individuals may be an expression of imminent female potentialities coexisting with well-developed maleness.

To complete the sex-categories of individuals it is necessary to add:—

6. Pure ♂'s, individuals with a well-developed ramifying gonad full of ripe or in addition ripening sperm-morulae and in the spawning condition with the gonoducts on the surface of the body crammed full of ripe sperm-morulae ready to be shot out.

This kind of male is quite a different individual—or perhaps phase—from the male phase, into which the ripe female passes after spawning. Indeed, it is not impossible that there are two kinds of male in the oyster—and perhaps other molluscs—but this subject may be discussed more fully later.

7. Pure ♀'s, individuals whose gonad, when ripe, contains entirely and only ripe ova. The appearance of ripe ♀'s to the naked eye is similar to that of the ♀(♀), ♀(♂), and ♂ like ♀'s, all of which can easily be distinguished from the great variety of male and neuter phases which occur—at a glance.

In the ripe ♀ and ripe ♀-like forms the body has an opaque somewhat yellowish chalky and creamy appearance, in contrast with the white to grey creamy and more translucent appearance of the pure males and the post-sick male phases.

8. Other categories. In addition to the categories mentioned above, all of which have ripe or ripening sex-elements of some kind in the gonad, a number of definable phases in the sperm-producing gonad of the post-sick oyster have been recognised, as well as certain neuter phases, but so far the effort to discriminate the post-spawning phases of the *pure* male has failed. A discussion of these matters is reserved for a later communication, when it is hoped to describe the microscopical character of the gonads of the different kinds of male categories recognised herein, and the neuter and young female stages which follow the male phase attained after a previous spawning as a female.

EXAMPLES OF THE CONSTITUTION OF AN OYSTER POPULATION AT THE BEGINNING OF THE BREEDING SEASON.

The proportion in which the individuals of the foregoing sex-conditions occur in an oyster population is a matter of importance in the problem under investigation, and in order to give some indication of their relative frequency the following analyses in Table I of several samples may be given :—

The first six samples given in Table I, p. 979, were examined at the beginning of the breeding season (in 1926), when the proportion of the different kinds of egg-bearing individuals can best be determined, for it has been shown (Orton, 1926) that the proportion of females—and it may be added egg-bearing individuals—gradually diminishes during the breeding season.

The last two examples in Table I were examined after the breeding season had begun in 1922 and 1923, when some of each kind of egg-bearing category might already have spawned; it may be noticed that there is a reduced percentage of the mixed sexes as compared with the samples examined at the beginning of the breeding season in 1926.

PRELIMINARY DISCUSSION ON THE SIGNIFICANCE OF MIXED SEXES.

It has been mentioned above that both Hoek and Möbius considered the oyster as essentially a bisexual species with regard to spawning. The figures given in Table I, p. 979, lend support to this view, but the relatively high proportion of mixed sexes (hermaphrodites of various categories) justifies the view maintained by Lacaze-Duthiers that the gonad of this oyster appears to be “sometimes male, sometimes female, and sometimes hermaphrodite.

TABLE I.

FREQUENCIES OF DIFFERENT SEX-TYPES IN DIFFERENT POPULATIONS OF OYSTERS AT THE BEGINNING OF THE BREEDING SEASON, 1926.

Date.	Locality.	Total examined.	Pure Male.			Im-pure ♂'s with eggs un-spawned.	Neuter. ♀	Mixed sexes.			Female		Total. Functional ♀ and ripe ♀	Total. With eggs.	Total. Pure ♂'s	Total. Mixed sexes.
			Ripe ♂'s	Fair* ♂'s	Indif-ferent ♂'s			♂	♀ (♀)	♀ (♂)	Pure ripe ♀	With embryos and larvæ.				
1926. FAL ESTUARY BEDS.																
June 9	Turnaware Bar	174	53 (30.5)	23 (13.2)	21 (12.1)	22 (12.7)	6 (3.4)	9 (5.2)	4 (2.3)	6 (3.4)	28+1† (16.1)	1 (0.5)	48 (27.6)	71 (40.8)	97 (55.8)	19 (10.9)
„ 22	East Bank	151	41 (27.2)	30 (20)	17 (11.3)	15 (10)	3 (2)	13 (8.6)	2 (1.3)	4 (2.6)	24 (15.9)	2‡ (1.3)	45 (29.8)	60 (39.8)	88 (58.3)	19 (12.6)
„ 23	Turnaware Bar	100	30	5	5	12	4	6	4	6	28	0	44	56	40	16
	Totals	425	124 (29.2)	58 (13.6)	43 (10.1)	49 (11.5)	13 (3)	28 (6.6)	10 (2.3)	16 (3.7)	80+1 (18.8)	3 (0.7)	137 (32.2)	187 (44)	225 (53)	54 (12.7)
	Percentages															
1926. WEST MERSEA BEDS.																
June 10	Thornfleet	107	45	6	10	19	3	6	3	2	9	4	24	43	61	11
„ 16	do.	103	24	15	14	5	1	4	3	5	17	15	44	49	53	12
„ 23	do.	100	3	45§	4	4	1	2	3	3	8	27	43	47	52	8
	Totals	310	72 (23.3)	66 (21.4)	28 (9)	28 (9)	5 (1.6)	12 (3.9)	9 (2.9)	10 (3.2)	34 (11.1)	46 (14.9)	111 (36)	139 (45)	166 (53.8)	31 (10)
	Percentages															
June 28-29, 1922		105	—	—	—	15	4	5	0	3	18	7	33	48	53	8
July 24, 1923		156	—	—	—	19	12	5	1	0	16	10	32	51	93	6

NOTES TO TABLE I.—Percentages where necessary are given in brackets, all other figures give the number of each sex-type found.

* Includes individuals which may be partly spent and others probably completing development of maleness.

† One individual was a young female.

‡ Two individuals which probably spawned prematurely as a result of being dredged.

§ Includes an unknown proportion of indifferent males.

|| Percentages are not given for these samples, because some spawning females may have been taken from them before they were examined microscopically; and the pure males are not classified into ripe, fair and indifferent groups. These samples are given merely to show the reduced proportion of mixed sexes at a period after the beginning of the breeding season.

Hoek also held that cross-fertilisation always or mostly occurred in this species inasmuch as (1) the eggs are extruded in a fertilised condition (Hoek quotes and infers that the eggs are always extruded in a segmenting condition, but this incorrect view is only a minor point), and (2) Hoek found and figured discrete spermatozoa aggregated in the region of the external opening of the oviduct (gonoduct). The views of Hoek and Möbius may be accepted with regard to pure females and pure males without at present admitting that cross-fertilisation necessarily occurs in all cases. There is, however, at present no information about the mode of fertilisation in the mixed sexes, and the mode of spawning of these can only at present be inferred from (1) statistical studies of the seasonal variation in the proportion of the various sex-categories in an oyster population, and (2) the condition of the gonad immediately after a gyne-spawning. It is important at this point to recall the observation that hermaphrodite forms with ripe ova have in only an insignificant number of cases developing sperm in the gonad in addition to ripe sperm. Thus if a hermaphrodite form did not spawn completely, some eggs and some ripe sperm-morulae would remain behind in the gonad, but very rarely would *developing* sperm from the pre-spawning period be left. Proof will be given later that sex-change does occur from female to male and from male to female and from female back to female again: such changes indicate the control of sex by some kind of factor. These facts are probably sufficient for the moment to explain a proportion of mixed sexes in an oyster population, since a slight deviation from a presumed normal sequence of sex-changes may be sufficient to cause an overlapping in the manifestations of the sex-causative factors—whatever these may be—and result in a mixed sex. Further discussion on sex in this species may be deferred until the data herein presented have been examined.

SECTION B. RESULTS OF EXAMINING THE GONAD IN 702 (♀) "SICK" OYSTERS.

It has already been noted that many observers (especially Hoek, 1883) have in the past recorded the occurrence of ripe or developing sperm in the gonads of oysters carrying embryos or larvae in the mantle cavity, but no systematic examination has been made to determine whether such a condition is always the case, or whether only a certain proportion of individuals show ripe sperm in the gonad after spawning as females. For the establishment of a specific rhythmic sex-change it is not sufficient to know that sex-change occurs in some cases, hence the need for a systematic examination of the gonad of individuals carrying embryos or larvae in as great a variety of conditions of development as can be obtained.

The condition of the sex-cells in the gonad of individuals which have recently or within a known time spawned as females may be represented in most cases by one of the following ten categories. A gonad which does not fall into one of these categories will be noted specially.

TABLE II.
CATEGORIES OF GONAD CONDITION IN ♀ "SICK" AND
♀ "POST-SICK" INDIVIDUALS.

Category	SEX-CELLS PRESENT IN THE GONAD.		
	Ripe sperm-morulae.	Developing sperm-morulae.	Ripe unspawned ova.
I	none	none	none or a variable no.
II	none	some doubtful	do.
III	none	a few to ∞ young up to 40μ	do.
IV	none	$f \infty$ or ∞ over 40μ	do.
V	few or occasional	∞	do.
VI	$f \infty$ or ∞	$f \infty$ or ∞	do.
VII	∞	few to fair no.	do.
VIII	$f \infty$ or ∞	none	do.
IX	few to fair no.	none	do.
X	none	none	none or a variable no.

NOTES ON TABLE II.

The abbreviations used in Table II have the following meanings:—

∞ = numerous.

$f \infty$ = fairly numerous.

The final stage or category, X, is indistinguishable from the first stage, but in view of the results obtained there is justification for using the figure X in the case of individuals which have long ago evacuated their young.

Ripe sperm-morulae have a dark granular appearance in the fresh condition, and when transferred to sea-water at ordinary room-temperature break up into active sperm; they may vary in size and shape from about 50μ spherical to 80μ or more elongate cylindrical (see Plate V, Hoek, 1883; and Plate IX, Orton, 1924).

Developing sperm-morulae are translucent agglomerations of cells arising from spermatogonia, and vary in size in the fresh condition from about 10μ in the 4-celled stage, 14μ in the 7- or 8-celled stage, 19μ in the 10-celled stage to as much as 80μ in the penultimate stage, when the tails of the sperm may just be beginning to be developed, but even at this last stage the cytoplasm of the mass remains translucent.

Normally all ova are extruded in the spawning act, but in a not inconsiderable number of cases tiny or large isolated patches of ripe—and occasionally some unripe—eggs may remain in the gonad after the spawning act; in a smaller proportion of cases considerable irregular areas may remain undischarged. Rare cases have been observed where one gonad—the right—was spent, and the other remained full of ripe ova.

Young ova become recognisable in the fresh tissues at a size of about 40 to 50μ , but only a few gonads with young ova were encountered and recorded; it was not, therefore, necessary to retain a column in this Table for developing ova.

THE AGE OF ARBITRARY PROGRESSIVE PERIODS IN THE DEVELOPMENT
OF THE OYSTER EMBRYO AND LARVA.

As the condition of the gonad of individuals carrying embryos or larvæ may vary directly with the period which has elapsed since the instant of spawning, it is important to know what this period is approximately in hours or days in the case of each gonad examined. Although no direct observation of this period is possible a close approximation can be made from the stage of development of the embryos or larvæ, since the rate of development has been observed in sufficient cases to give such an approximation. The rate of development of embryos and larvæ will undoubtedly vary with the conditions and especially with temperature, but conditions which retard or hasten embryonic development may not unreasonably be regarded as having generally a similar effect on sperm-development. Therefore the stage of development of embryos or larvæ may be more closely related to sperm-development in the gonad of the adult carrying them than to the actual time which has elapsed after the spawning act, if it is a fact that sperm-development does begin normally after the spawning act. In Table IV, p. 999, are given details of the stages of development of the embryos and larvæ, but the variety of these stages renders it necessary to group them into successive time-periods in order to obtain a perspective view of the successive changes in the sex-condition of the adults as their eggs develop into larvæ.

Accordingly the whole range of development from the time the egg is fertilised to the time the larvæ is set free from the parent has been divided up into six periods as shown in Table III on page 983,

CORRELATION BETWEEN THE AGE OF THE GONAD—RECKONED FROM
THE INSTANT OF EGG-SPAWNING—AND THE DEVELOPMENT OF MALE-
NESS IN THE SAME GONAD.

By the use of Tables II and III it will now be possible to summarise the whole of the observations made on embryos and larvæ and gonad condition; for with the categories of gonad-condition—which are arranged in successive stages of development of maleness—in Table II, and the periods of development of embryos and larvæ—which give the age of the post-spawned gonad of individuals carrying the young—it is possible to show in a correlation table and in graphs the results of examining hundreds of individuals for both these sets of characters.

The detailed results of the examination of 702 oysters carrying embryos or larvæ are set out in Table IV, pp. 999 to 1021. It will be observed that "sick" oysters have been obtained from a good number of different beds in the southern part of England during the years 1920–1926, while

the results obtained show that there is an essential similarity in behaviour of all oysters from all the beds examined throughout at least the main part of the breeding season. Remarks on various anomalies and other points of interest are made in the notes and discussion on the Table on p. 1019 onwards.

TABLE III.

DEFINITIONS OF SUCCESSIVE ARBITRARY PERIODS OF DEVELOPMENT OF THE EMBRYO AND LARVA OF *O. EDULIS*.

Age.	State of development.
Period A. 0 to about $4\frac{1}{2}$ hours.	0 to mainly 4-celled stages.
Fertilised unsegmented eggs have on several occasions been found in the mantle cavity, evidence of fertilisation existing in the occurrence of mitotic spindles in the egg, and in subsequent segmentation.	
Period B. About $8\frac{1}{2}$ to about 20 hours.	8 to about 32-celled stage.
Some caution must be exercised in dealing with embryos in this group in which arrested development may have occurred. Many samples of oysters have necessarily had to be examined the day after they were dredged, and also after being out of water for about a day. Under these conditions—in summer—the liquid in the mantle cavity becomes more or less fouled. In such samples embryos in the 16- to 32-celled condition have so often been met with, that it is highly probable that development may have been arrested at these stages owing to the unfavourable conditions. In some cases therefore the embryos may be a little older than this state of development indicates, and it follows that in such cases the age of the gonad—reckoned from the gyne-spawning—would also be a little older than is indicated by the stage of development of the embryos.	
Period C. About 30 hours to $2\frac{1}{2}$ days.	More than 32 blastomeres to the elongate heart-shaped but unciliated embryo.
Period D. 3 to 4 days.	Elongate heart-shaped but now ciliated embryo, with or without a mere rudiment of the larval shell.
Period E. 4 to 5 days.	White to grey ciliated embryos with a growing larval shell ranging in length from 50 to about 150μ .
Period F. 6 to 10 (or 12 days) normally, but may be older at the end of the breeding season, or under cold conditions.	Coloured fully-shelled larvæ, that is, lilac, slate or blue, black or purplish-black larvæ, with shells ranging in length from 150 to 200μ usually — and rarely 210 to 220μ .

Table IV is summarised in Table V, which faces p. 984, in order to show the *frequencies* of occurrence of the different sex-conditions of the post-spawned gonad correlated with the different periods of development of the embryos or larvæ. Table V is in turn again summarised to give the

correlation table, shown on p. 985 as Table VI. From Table VI, with its accompanying graphs, Fig. 1, p. 991, it is possible to see at a glance the relation between the condition of the sex-elements in the gonad of individuals and the age of the gonad—reckoned from the recent gyn spawning—as inferred from the age of the embryos or larvæ carried by the same individuals.

A glance at the correlation table, Table VI, on p. 985, shows that :—

1. The youngest gonad (reckoned from the instant of the recent spawning) has the youngest male sex-elements—or none at all—and has no ripe male elements.

2. As the gonad increases in age (as defined above), so the ripe male-elements increase and the unripe ones decrease. Exception to these statements occurs but so rarely as to be non-significant.

3. There is a clear correlation between increasing ripeness of male products and increasing age of gonad (as defined).

4. As the period of age of the gonad increases so also advances the progressive development of maleness in the gonad.

5. The occurrence of eight gonads with no maleness in the F period is contrary to the general trend of the table (see below).

6. The mean stage of development of maleness shows a progressive increase in correlation with the progressive ages of gonads, and this fact along with the progressive distribution of the categories with 50% of individuals or more in each period, is proof of a positive correlation.

The frequencies of the different kinds of sex-condition in the gonad of individuals carrying embryos or larvæ in each of the periods A to F are plotted (as percentages) to give the series of graphs shown in Fig. 1, p. 991. These graphs show clearly the points noted above, and bring out the fact that about 50% of the individuals contain few or a great number of ripe sperm in the gonad already at the D period, that is, at an age of three or four days. For the periods earlier than D, the stage of development of maleness is retrogressively less advanced, and beyond D the development of maleness is successively greater. In stages E and F the percentage of individuals with *only* developing sperm dwindles to about 22% in the E stage (four to five days), and 3 to 6% in the F stage (six to twelve days). In the F period eight individuals (3 to 13%) had no sex-elements at all in the gonad; it is highly probable that these eight individuals are abnormal, and some possibly pathological; but it is certainly significant that six of these individuals occurred amongst the

last spawners at the end of the breeding season : one in September and three in October, 1925, and two on September 29, 1926.

EXPERIMENTS ON THE RATE OF DEVELOPMENT OF SPERM-MORULÆ.

When the examination of the gonad of a large number of "sick" oysters had shown that maleness is developed at once in nearly all individuals at or soon after egg-spawning, an experiment was carried out in order to obtain additional information and data.

On July 14, 1925, a sample of 3,700 oysters of various ages, from three years upwards, was examined, and nine blacksick and eleven whitesick individuals picked out of the pile by simple inspection of the whole individuals; the sample was dredged on the previous day, and had lain in a pile in the store overnight. Amongst the eleven whitesick individuals were nine in which the embryos were found to be in very early segmentation stages, ranging from 0 to the 8-celled condition. Particulars of the eleven individuals are as follows :—

	Length in mms.	Depth in mms.	1925 shoot in mms.	State of embryos.
1	61	69	4	2 to 4-celled.
2	64	66	11	2 to 8 "
3	52	57	?	Unsegmented eggs only.
4	57	62	9	2 to 6-celled.
5	53	56	2	0 to 2 "
6	56	56	12	0 to 2 "
7	66	60	19	0 to 8 "
8	63	59	17	0 to 2 "
9	52	57	4	4 to 8 "
10	53	59	11	ca. 16 "
11	65	61	15	Morulæ.

Ten of the whitesick individuals (excluding No. 11) were chosen for the experiment; one was opened and examined microscopically on July 14th and the others at successive intervals of one or two days, after being put back in the sea at a depth of about one fathom, in a stramin bag attached to the stern of an old store-vessel, which was moored in midstream in $2\frac{1}{2}$ fathoms of water at low water, in Thornfleet, West Mersea. The results of the several examinations appear in Table VII, p. 987.

TABLE VI.

CORRELATION BETWEEN THE PROGRESSIVE DEVELOPMENT OF MALENESS AND THE PROGRESSIVE AGE OF THE GONAD—RECKONED FROM THE INSTANT OF EGG-SPAWNING—
IN 702 OYSTERS CARRYING EMBRYOS OR LARVÆ

Mean age of gonads in each period.	A to F, progressive periods of age of gonads inferred from age of embryos or larvæ.	Numbers and percentages (in brackets) of Categories I to X, progressive stages in the development of maleness observed in gonads at each period.										Total No. of individuals examined in each period.	Mean stage of development of maleness.
		I	II	III	IV	V	VI	VII	VIII	IX	X		
2¼ hours	A period	5 (20.9)	2 (16.6)	12 (50)	5 (20.9)	0	0	0	0	0	0	24	2.71
14 hours	B do.	1 (1.97)	4 (7.85)	25 (49.1)	19 (37.3)	1 (1.97)	1 (1.97)	0	0	0	0	51	3.26
45 hours	C do.	1 (0.77)	1 (0.77)	26 (20.1)	83 (63.9)	14 (10.8)	5 (3.85)	0	0	0	0	130	3.95
3½ days	D do.	0	1 (0.9)	12 (10.9)	39 (35.2)	33 (29.8)	26 (23.5)	0	0	0	0	111	4.65
4½ days	E do.	1 (0.77)	0	3 (2.31)	25 (19.3)	27 (20.8)	74 (57.1)	0	0	0	0	130	5.31
8½ days	F do.	8 (3.12)	0	0	6 (2.34)	31 (12.1)	197 (76.9)	11 (4.29)	3 (1.17)	0	0	256	5.73
Total no. in each category of maleness		16	8	78	177	106	303	11	3	0	0	702	
Total per cent in each category of maleness		(2.28)	(1.14)	(11.1)	(25.2)	(15.1)	(43.1)	(1.56)	(0.4)				

NOTES ON TABLE VI.

In the A category only 24 individuals were examined and recorded, owing partly to the relative scarcity of this type, but also to the reluctance and inability to spare the time for the long examination often necessary in these cases to prove a negative. In a number of additional cases a partial examination was made, but the results not recorded as it was felt that a longer period of examination than could be afforded on the beds would be necessary before a correct description of the gonad could be recorded with certainty. In these unrecorded cases the gonad would fall in one of the first two categories of sex-condition, that is, either no maleness, or doubtfully developing very young spermatogonia. For these reasons it is probable that the mean state of development of maleness in the gonad of this category, namely, 2.69, is slightly too high. Although the total number of individuals recorded in this category is small, it is sufficient for the purposes of the present problem, and a special investigation of this particular period of the gonad will be worth while later to determine more nearly the limits of the beginning of the development of maleness. It is interesting that the largest number of individuals in this category should just show definite signs of early developing maleness.

In the B category 88 per cent of the individuals show early signs of the acquisition of maleness, and two individuals show well advanced maleness. In view of the general character of the correlation table these latter individuals cannot be regarded as having developed their maleness wholly since the last gyne-spawning.

In the C category the highest percentage of individuals has maleness obviously developing, while in the D group more than 50 per cent have now few or abundant ripe male-elements.

In the E group all individuals are definitely male in some stage of development except one neuter individual, with a maximum percentage, 57, with abundant ripe sperm-morulae.

In the F group there is a still bigger percentage with abundant ripe sperm-morulae, 77, and a few individuals show a waning in the development of maleness, or absence of developing sperm. The waning of the production of sperm in this group is confirmed by the examination of the gonad of individuals which have extruded their larvæ (see p. 1025). It has already been noted that of the eight neuter individuals in this group six were found at the tail-end of the breeding season, and demand special consideration.

The end columns in this table give respectively the mean age of the arbitrary progressive periods of development of embryos or larvæ in hours or days, and the mean stage of development of maleness in the gonads of the adults carrying the young of the corresponding periods. The stage of development of maleness is obtained by dividing the total number of individuals in each category into the sum of the products of the number at each stage and the number denoting that stage. These two means can be used to plot a graph depicting the average rate of development of maleness (see Fig. 2, p. 993).

TABLE VII.
EXPERIMENT ON THE RATE OF DEVELOPMENT OF SPERM-MORULÆ
IN SITU IN THE GONAD.

Approximate age of post-sick gonad.	Date.	Serial number of oyster.	Elements in gonad.			Stage* of development of maleness.	
			Ripe sperm-morulae.	Unripe sperm-morulae.	Ripe ova left in gonad.	A	B
6 hours	July 14	1	none	few about 30 μ	fair no.	3	3.0
2 $\frac{1}{4}$ days	„ 16	2	none	f ∞ up to 40 μ	few; rounded off	3	3.5
do.	„ 16	3	∞	∞	few	6	6.0
3 $\frac{1}{4}$ days	„ 17	4	none	∞ large up to 60 μ some nearly ripe	do.	4	4.0
do.	„ 17	5	few	f ∞	do.	5	5.0
5 $\frac{1}{4}$ days	„ 19	6	fair no.	∞ up to 70 μ and 60 μ spherical	do.	6	5.5
do.	„ 19	7	do.	∞ up to 80 μ	few patches	6	5.5
6 $\frac{1}{4}$ days	„ 20	8	few	∞ full size and nearly ripe	rare	5	5.0
8 $\frac{1}{4}$ days	„ 22	9	f ∞	∞	few	6	5.75
—	„ 22	10	dead	—	—	—	—

* In column A are given numerical figures corresponding to those given in Tables IV, V, and VI; in column B are given figures to show smaller differences in the stages of development of sperm-morulae.

The variation in the temperature conditions on the site of the experiment on the rate of development of sperm-morulæ in the oyster is very nearly shown by the following readings, taken at a depth of 1 foot with a certificated Calderara thermometer. Where only one observation was made on one day on the site of the experiment—S.V. Frolic, in mid-Channel, Thornfleet, West Mersea—additional observations from other similar thermal situations are given for comparison. These readings were generally taken at about the time of high and low water as indicated.

1925.	Time.	Approx. state of tide.	Tempera- ture, °F.	Position.
July 13	7 a.m.	H.W.	65	Thornfleet.
„ 13	1 p.m.	L.W.	67	do.
„ 14	8 a.m.	H.W.	65	do.
„ 14	2 p.m.	L.W.	67	do.
„ 14	8 p.m.	ca. H.W.	66	do.
„ 15	9 a.m.	H.W.	67	do.
„ 15	3 p.m.	L.W.	69	Dan's Moorings.*
„ 15	6 p.m.	—	67	Thornfleet.
„ 16	6 a.m.	2 hrs. after L.W.	69	Dan's Moorings.
„ 16	10 a.m.	H.W.	69	Off Mell Pier.
„ 16	8 p.m.	—	69	Thornfleet.
„ 17	6 a.m.	1 hr. after L.W.	70	Dan's Moorings.
„ 17	11 a.m.	H.W.	67	Mell Pier.
„ 17	8 p.m.	—	71	Thornfleet.
„ 18	6 a.m.	ca. L.W.	68	Dan's Moorings.
„ 18	12 noon	ca. H.W.	67	Thornfleet.
„ 18	8 p.m.	—	70	do.
„ 20	6 a.m.	ca. L.W.	67	Dan's Moorings.
„ 20	12 noon	ca. H.W.	67	South Shore.
„ 21	7 a.m.	L.W.	68	Thornfleet.
„ 21	1 p.m.	H.W.	67	Mell Pier.
„ 22	8 a.m.	L.W.	68	Thornfleet.
„ 22	2 p.m.	H.W.	69	Mell Pier.

An inspection of Table VII shows that—excepting No. 3 oyster—there was a gradual increase in size of the developing sperm-morulæ, and a gradual production of ripe tailed sperm-morulæ in the series of oysters examined: indeed, except for numbers 3 and 8, the individuals form a surprisingly good graded series, considering that individual variation does occur in the rate of development of maleness (see Table VI).

* m. b. Dan's moorings are in $1\frac{1}{2}$ fathoms of water at L.W. in Salcot Creek. All readings are in mid-Channel except off Mell Pier and South Shore.

Since all these individuals spawned on July 13th or a few hours later, the following deductions can now be drawn. Within one day after spawning, a few sperm-morulæ developed and attained a size of 30μ , and within three days after spawning numerous sperm-morulæ were developed to a size of 40μ . (No. 3 oyster is omitted for the moment.) Within four days after spawning, numerous sperm-morulæ were now developed to a size of 60μ in one individual, and in another the first ripe sperm-morulæ are now fully developed.

In the sixth day the number of ripe sperm-morulæ is increasing, and ripening morulæ have a size now of 70 to 80μ . The individual examined on the seventh day is lagging, and is no further advanced than the more advanced one examined on the fourth day. On the ninth day ripe sperm are now found in greater quantity than in any of the ones previously examined—excepting No. 3. The latter individual is an aberrant one, and it may be seen from Table VI that similar individuals occurred very rarely even in Periods A to C. In Periods A and B only 2 such individuals occurred among 75 examined, and in Period C only 5 occurred in 130 examined, so that in Periods A to C only 7 such individuals occurred in 205 examined.

It is not possible to state whether No. 3 had developed maleness unusually quickly, or, as is possible, was previously hermaphrodite and did not extrude all its gonadial products at the last spawning. It may be noted from Table VII that a few ova were left behind in this gonad after spawning, but at the time of the examination no observation was made as to whether ripe sperm-morulæ were confined to the portion of the gonad where the eggs occurred. Although No. 3 oyster in the experiment breaks the graded series of results obtained, it draws attention to the fact that individuals—in small proportion—may have ripe sperm-morulæ in their gonad on the third day after gyne-spawning.

Although the number of individuals made use of in this experiment is small, it may be noted that they were picked out of a sample 3,700. A similar experiment carried out with a larger number of individuals should be repeated, and with our increased knowledge of spawning epochs in this species, such an experiment may be possible in the near future.

The following additional observations have also been made. An oyster proved to be male in July, 1923, and kept afterwards in a cage in the sea, extruded ciliated larvæ on July 1, 1924, after the cage was hauled. The gonad was examined by tapping the gonad with a fine pipette through the reperforated shell on July 2, 1924. The oyster was then replaced in the sea—in an oyster pit—and opened and examined on July 8, 1924, with the following results, which show a rather slower than average rate of development of ripe sperm. Temperatures were

not taken on this occasion. The rather slow rate of development of ripe sperm in this case was probably partly due to an injury, as the rectum was perforated when tapping the gonad on July 2nd.

July 2, 1924.	No ripe sperm-morulae.	Fair no. of young sperm-morulae.	Fair no. of unspawned ova.	Male category = No. III.
July 8, 1924.	A few ripe sperm.	f ∞ large developing sperm-morulae.	Fair no. of ova in spots.	do. = No. V.

GENERAL REMARKS ON THE SEX-CONDITION FOLLOWING EGG-SPAWNING.

The results of the examination of the sex-condition of oysters at various periods after egg-spawning given in Table VI, p. 985, and shown in the series of graphs in Fig. 1, p. 991, may now be reviewed along with the information obtained from the experiments on the rate of development of sperm. The correlation between increase of age of gonad after egg-spawning and increase in maleness is clear, in spite of the slight weakness in the evidence due to the small numbers of individuals examined in Periods A and B. It is therefore a fact that the gonad of an oyster changes at once to sperm-producing at some very early period after the egg-spawning act, and very quickly develops fair quantities of freshly formed ripe sperm-morulae. The change of the gonad to a purely sperm-producing phase occurs generally, but not always, within at least a few hours after the spawning act has taken place. In a small percentage of cases observed, this change did not occur apparently up to twelve days or more after the egg-spawning, but it has been noted that a good proportion of these abnormal gonads occurred amongst individuals which spawned late in the season. Although the sperm-producing phase usually begins within a few hours after spawning and continues at a quick average rate a small proportion of individuals show lagging on this general rate. The average rate of development of maleness can be obtained by plotting the mean age of the gonads—after egg-spawning—in each period, against the mean stage of development of maleness in the same gonads, the figures for which are given in Table VI, p. 985. The graph obtained from these data is given in Fig. 2 on p. 993. It will be seen that Fig. 2 is a common form of growth curve, showing a very rapid growth on the average during the first three days and thereafter slowing down considerably; growth indeed would appear to be approaching a maximum even in the period under consideration, that is, on the average $8\frac{1}{2}$ days, but covering a period up to 10 to 12 days. Thus the development of maleness is very rapid, and serves as an example of the difficulties which have to be overcome in observing sex-changes. It is necessary at this point to draw attention to the fact that the growth curve in Fig. 2 is more qualitative than quantitative; it is probable that a quantitative curve—such as

might be obtainable by a possible modification of Manoiloff's sex-reaction—would show a similar sharp rise, but a continuance of the rise over a longer period. Further, there is no doubt whatever that an imaginary

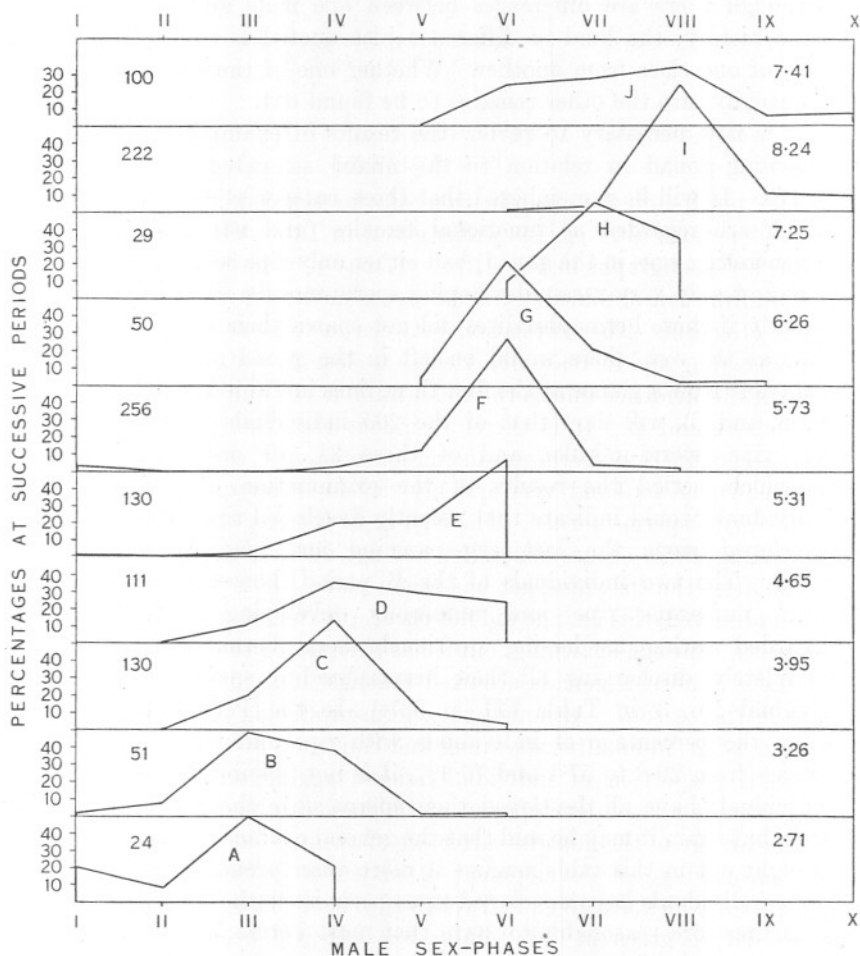


FIG. 1.—The series of graphs A to J show the percentage frequencies of different male sex-phases of *O. edulis*, in relation to the progressive ages A to J of the gonad—reckoned from the instant of the last egg-spawning.

The graphs A to F are constructed from data derived from oysters actually carrying embryos or larvæ at the time of examination; graphs G to J from individuals which, after being found with young, had been isolated in tanks or in experimental cages in the sea.

I to X are sex-phases defined on p. 981; the figures on the right-hand side of each graph give the mean sex-condition in each period.

A to J are periods defined on pp. 983 and 1022; the numbers on the left-hand side of each graph give the total number of individuals examined in each period.

quantitative determination of maleness in the well-fished pure males, which one finds especially at the beginning of the breeding season, would give numerical results estimated fiftyfold of those obtainable from the males which develop immediately from the recently spawned females. Although there are differences between one male and another of the same history, the kind of difference just quoted is regarded rather as that of one class from another. Whether one of these classes develops eventually into the other remains to be found out.

It is now necessary to review the results of examining the post-egg-spawning gonad in relation to the mixed sex-categories recorded on p. 976. It will be remembered that those categories of hermaphrodites, which are regarded as functional females (and not individuals with degenerating eggs in the gonad) had either only ripe sperm-morulae in the gonad or only very rarely developing sperm-morulae in addition. Consequently if these hermaphrodites did not spawn their sperm at the same time as the ova, there would be left in the gonad mainly *ripe* sperm-morulae. Now a glance at the first three lines in Table VI, p. 985 (Periods A, B, and C), will show that of the 205 individuals examined only 21 had ripe sperm-morulae, and of these 21, 19 occur in Period C, in which period the results of the examination of the B and D individuals would indicate that recently developed ripe sperm-morulae—developed since the last egg-spawning act—may be expected to occur. The two individuals of the B period, however, which showed both numerous ripe and numerous developing sperm, must be regarded rather as having previously been hermaphrodite without completely discharging all their hermaphroditic sperm. (Compare individual No. 3 in Table VII, p. 987.) In the Periods D, E, and F, when the percentage of individuals with ripe and ripening sperm increases from 29.8 to 57.1 and 76.9%, it is not possible to say that these individuals have all developed their sperm since the last egg-spawning act; but again it may be said that the general character of the correlation brought out in this table renders it more than probable that nearly all these individuals have developed ripe sperm since the last egg-spawning. It is therefore reasonable to state that most hermaphrodite individuals spawn completely—or rather as completely as the pure females—and that only in those cases where an incomplete spawning occurs will ripe sperm-morulae be left behind in the gonad after the spawning act. Therefore the views of Hoek and Möbius—that individuals of *O. edulis* spawn essentially as males or females—are justified by the results described above.

When the results obtained in this work are looked at as a whole—after making allowance for the non-development of maleness in some individuals, and for other small deviations, which may be pathological or abnormal—it is clear that the instant an oyster spawns as a female a

distinct point is reached in the sexual rhythm in the species. It will therefore now be possible to work towards this fixed point and forward from it in order to unravel systematically the sex-phenomena in the species. It is possible, therefore, to state categorically that—excepting a small percentage of abnormal or pathological individuals, among which are included the spawners at the end of the season—all female

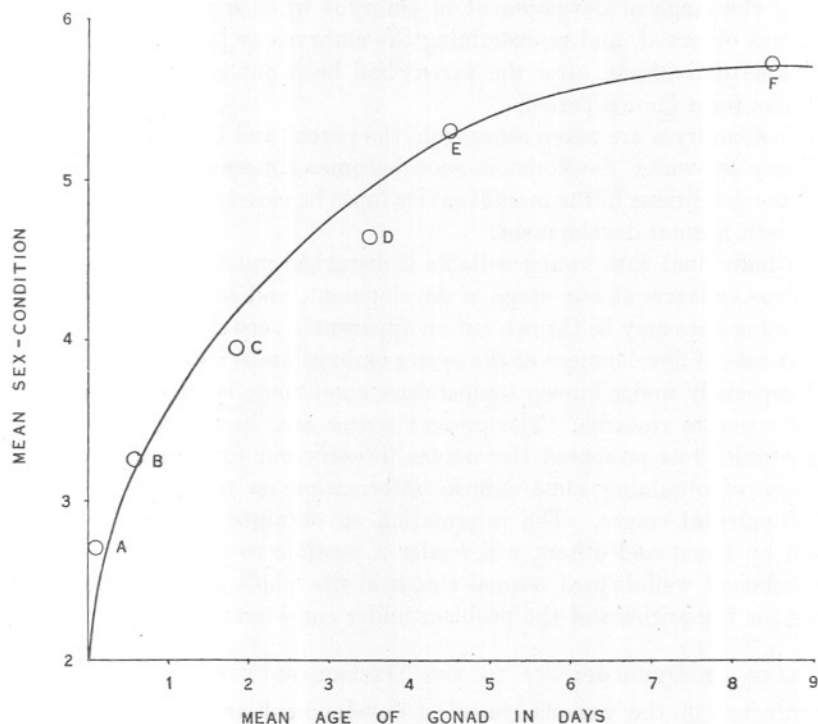


FIG. 2.—Graph showing rate of development of maleness in 702 oysters which were carrying young at the time of examination.

A to F are mean periods of age of the post egg-spawning gonad in groups of individuals with gonads of progressively increasing age as defined on p. 983.

oysters (*O. edulis*) normally change their sex at, or within, a few hours after spawning, and develop ripe sperm, generally in abundance, before their larvæ are normally set free in the water.

EXPERIMENTS AND OBSERVATIONS ON THE RATE OF DEVELOPMENT OF THE OYSTER EMBRYO AND LARVA.

A good general account of the development of the oyster larva (*O. edulis*) is given by Horst (1883), who, like preceding workers, found it impossible to rear the larvæ outside the body of the oyster from the segmentation stages, or, indeed, from later stages. The course of the development

was therefore determined by observing overlapping sectional periods of differentiation. Artificial fertilisation cannot be performed at present in the case of *O. edulis* with much chance of obtaining a normal rate of development, therefore Horst's method of finding the age of embryos and larvæ at different stages of development has been used mainly by the present writer, but some stages have in addition been followed by noting the stage of development of embryos when a gravid individual was first observed, and re-examining the embryos or larvæ given off by the same individuals, after the parent had been put back in the sea or in tanks for a known period.

When embryos are taken away from the parent and kept in unchanged ordinary sea-water, development soon becomes abnormal, and it is clear that the conditions in the mantle cavity must be closely imitated in order to obtain normal development.

An individual with young is liable if disturbed much to throw out its embryos or larvæ at any stage of development, and sometimes in tanks the young ones may be thrown out on apparently very slight provocation.

The rate of development of the oyster embryo under known conditions, and especially under known temperature conditions, is still a fit subject for a separate research. The present writer has, however, taken such opportunities as presented themselves to carry out experiments for the purpose of obtaining some definite information on the age of various developmental stages. The information so obtained, along with that given by Horst and others, will render it possible to fix an average age for sufficient well-defined normal stages in the whole course of development for the purpose of the problem under consideration.

OUTLINE OF DEVELOPMENT IN THE OYSTER TO THE LARVAL STAGE.

Drawings of the various stages of development are given by Horst (loc. cit. Plate VI). In the mantle cavity of an oyster all stages in development may be found from the unsegmented—but generally fertilised egg as is denoted by the presence of two nuclei with or without a spindle—to the fully formed pigmented and fully shelled larvæ.

In the early segmentation stages embryos with any number from one to eight blastomeres may be found, but regular division at least into two and afterwards into four blastomeres is more common. In stages later than eight to sixteen blastomeres it becomes difficult to see at a glance how many blastomeres occur, and it is safer to count the nuclei by compressing the embryo, in order to obtain information from the fresh object. From the 16-celled to the 32-celled stage the embryo often takes on the appearance of a morula, that is, a sphere made up of small spheres, whose outlines stand out on the periphery of the larger sphere. In the 32-celled stage, and a little later, the embryo attains a good

spherical shape, and with a slight depression at one place marking the beginning of the blastoporal invagination. At about the 64-celled stage the blastopore is well developed, and the depression noted above is well-marked. At about the 100 nucleated condition the embryo lengthens, and a new depression (the shell anlage) appears to give an elongated heart-shaped embryo. At this stage the embryo becomes ciliated, and a shell rudiment appears in the new depression noted and gradually extends over the embryo, while at the same time the original band of cilia develops into the velum. Finally, the shell completely covers the embryo, and the velum can be retracted entirely within the larval shell. At this stage the larva leaves the parent.

The colour of the embryos from the early stages to the ciliated heart-shaped larva is white, and an individual carrying such embryos is said to be whitesick. From the early stage of development of the shell to the stage when the shell is about 150μ long, the colour of the larvæ is white in bulk, but appears more and more grey as the shell develops when the larvæ are seen dispersed in a little water. When the shell is about 160μ long the larvæ have first a grey appearance in bulk, and then with very slight increase in length of the shell begin to acquire colour, due to pigment appearing in the digestive gland. The grey larvæ pass successively through shades of lavender-grey, heliotrope, light slate, dark slate, to a purplish black, and in some cases to quite a good black colour when seen in bulk as the pigment increases in the digestive gland. Individuals found with grey-coloured larvæ are called greysick, and others black-sick when carrying any of the definitely coloured larvæ. The length of the shell in the coloured larvæ increases with the pigmentation from about 170μ to about 190 to 200μ . Occasionally larvæ are found in the mantle cavity with shells 210μ long and rarely 220μ , but the purplish black larva generally has a shell ranging from 180 to about 200μ , and undoubtedly varies in size at equivalent stages of differentiation. Indications have been obtained that the shell is developed more rapidly at high temperatures (e.g. over 70° F.) and retarded in growth at low temperatures (e.g. about 60° F.). It is probable that larvæ develop somewhat differently, and are emitted in slightly different conditions at different seasons, and places.

Generally all the embryos or larvæ of an individual are developed to the same stage, but occasional instances have been noted of slightly different early stages in one mantle cavity, and rather more frequently, but not commonly, two sizes of coloured larvæ; the latter cases have seemed to be more common in dumpy oysters.

Experiment 1.

On June 23, 1926, a sample of oysters was dredged at Turnaware Bar, Fal Estuary, and brought at once to the beach for examination. The

oysters were opened rapidly, and at 11.55 a.m. an individual which had just spawned was discovered. The history of the development of this batch of eggs is as follows:—

		Approximate age of embryos.
June 23	11.55 a.m. Eggs just extruded, entire, with 2 nuclei, transferred to sea-water: estimated that egg-extrusion occurred at about 11.30 a.m.	
	2.40 p.m. Practically all in 2-celled stage, one 3-celled stage seen	3 hours.
	2.50 p.m. 4 nuclei showing clearly	
	4.30 p.m. 4-celled stages now distinct	5 hours.
	8.45 p.m. Small proportion 8-celled and a few with 16 nuclei	9 $\frac{1}{4}$ hours.
	midnight 16-celled stages common; no 32-celled stages seen	12 $\frac{1}{2}$ hours.
June 24	1.30 a.m. do.	
	2.30 a.m. 16-celled beginning to pass to 32-celled stage; a few 20 to 21 nucleated stages seen	15 hours.
	9.30 a.m. 32-celled stages common, good spherical embryos in morula and early blastopore stages; one 50-nucleated stage seen	22 hours.
	3 p.m. 32 to 64 nuclei present, but embryos mostly still in 32-celled stage and of good spherical shape	27 $\frac{1}{2}$ hours.
	6.25 p.m. Mostly 40 to 50 nuclei; 64 nuclei rare .	
June 25	10.25 a.m. Beginning of heart-shaped stage, but 50 to 64 nuclei only (cold overnight). The embryos could not be examined afterwards	47 hours.

The temperature conditions could not be determined accurately in this—partly a field—experiment; the water in the vessel used was, however, probably 65° to 70° F. from June 23 to 2.30 a.m. June 24, and thereafter colder, and falling to below 60° F. in the night of June 24–25.

When the individual used for Experiment 1 was obtained, the dredging was continued at the same place as before, from 11.30 a.m. to 2 p.m., and a sample of oysters obtained which was not opened until 10.40 to 11 a.m. on

June 25th. One individual in this sample was found with young embryos, which may not unreasonably (see Table I, p. 979) be regarded as a control on Experiment 1. At about 11 a.m. on June 25 the embryos of this oyster were found to be mainly 32-celled in good morula stages with a fair number of 50-to 64-celled stages. These embryos were therefore in almost exactly the same stage at the same time as the experimental embryos, and since natural spawning had not begun on the beds on June 23, it is reasonable to suppose that spawning had been precipitated in both these cases by the act of dredging, and that therefore the embryos were about the same age.

Experiment 2.

A sample of oysters were dredged, June 30, 11.30 a.m. to about noon (East Bank, Fal Estuary), and when examined later the following sick oysters were found:—

1926.		No. 1.	No. 2.	Approximate age* of embryos.	
				1.	2.
June 30	3.50 p.m.	Embryos in 2- and 3-celled stages			4 hrs.
	4.15 p.m.		Embryos in 2-celled stages		4 $\frac{1}{4}$ hrs.
		transferred samples of embryos to water.			
July 1	1.15 a.m.	Embryos in 7-celled stages			13 $\frac{1}{2}$ hrs.
	1.25 a.m.		Embryos in 16-celled stages		13 $\frac{1}{2}$ hrs.
	10.15 a.m.	16 passing to 32-celled stages, 20 nuclei seen			22 $\frac{1}{2}$ hrs.
	10.20 a.m.		16 passing to 32-celled stages, 24 nuclei seen		22 $\frac{1}{2}$ hrs.
			Embryos of good spherical shape, odd ones showing beginning of blastopore invagination.		

In this experiment the room temperature remained fairly constant between 65.5° F. and 66.5° F.

* Assuming that spawning occurred about 11.45 a.m.

Experiments 1 and 2, confirmed by other similar observations, suffice to enable the approximate times of the attainment of definite early segmentation stages to be fixed as follows :—

No. of blastomeres.	2	4	8	16	32, morula and early blastopore stage.
Age	2-2½ hrs.	4½ hrs.	8½-9 hrs.	11-12 hrs.	about 20 hrs.
	64, early heart-shaped not ciliated embryo, about 46 hours.				

From this information can safely be extracted the data required for the purposes of determining the early periods of development, namely,

(A) that the 0 to 4-celled stage is attained in 0 to about 4½ hours, and

(B) that the 8 to 32-celled stages is attained in about 8½ to 20 hours.

A number of experiments designed to obtain information on the succeeding stages of development can be summarised as follows :—

Expt.	Date.	Approximate age.			
		12 to 20 hrs.	1½ to 2 days.	2½ to 3 days.	3½ to 4 days.
III.	July 6-7, 1924.	Morulae at 7 p.m.	Heart-shaped, not ciliated.	—	—
IV.	July 6-8, 1924.	do.	—	Heart-shaped, not ciliated.	—
V.	June 4-5, 1926.	Early blastopore.	Heart-shaped, not ciliated.	—	—
VI.	June 3-7, 1926.	Morula at 7.30 p.m.	Early heart-shape.	Good heart-shaped, not ciliated.	Ciliated at 11 a.m., 7th, trace of shell.
VII.	June 3-5, 1926.	Morula at 7.20 p.m.	—	Heart-shaped and just ciliated.	—

The experiments just recorded, confirmed by many similar ones, enable us to fix the next period of development required for the purposes of the present paper, namely, that

(C) the 40-nucleated stage to the elongated heart-shaped, but not ciliated, stage is reached in from 30 hours to 2½ days.

(D) The elongate heart-shaped and ciliated stage with or without a trace of the larval shell is attained in from 3 to 4 days.

Some experiments on the rate of development to the coloured and fully-shelled larva have already been recorded (Orton, 1926, p. 217), showing that this stage was attained in temperatures mainly 62.5° to 64.0° F. in 6 to 7 days. Spärck (1924, pp. 31 and 46) has made similar observations. It is now possible, therefore, to complete the definition of periods of development as follows :—

(E) The incompletely shelled larva with a shell varying in length from about 40 to 150μ—or rarely to 170μ—is normally developed in from 4 to 5 days.

(F) The coloured and fully-shelled larva is developed normally in 6 and retained normally to 10 or 12 days (see Orton, 1926, p. 216), and has an average length of shell ranging from 170μ to 200μ.

It has been found, however, that at temperatures of about 60° F., the grey-shelled period may be prolonged to as long as 12 days, and in a similar way coloured larvæ may be retained in isolated cases for a long period in cold weather, and especially towards the end of the breeding season.

TABLE IV.

DETAILED RESULTS OF THE EXAMINATION OF THE EMBRYOS AND LARVÆ, THE GONAD, AND OTHER CHARACTERS OF 702 OYSTERS IN SPAWN.

1 Serial Numbers.	Gonad of adult.			Embryos and larvæ.		7 Period of develop- ment of embryos and category of gonad.	8 Remarks.
	2 Ripe sperm- morulæ.	3 Unripe sperm- morulæ.	4 Ripe unspawned. ova.	5 Colour.	6 Stage of develop- ment.		
1. 1920. DREDGED YEALM, JULY 17; KEPT IN PLYMOUTH TANKS, EXAMINED JULY 30.							
1	none	∞	some	White	heart shaped	C4	
2. 1921. A WHITSTABLE OYSTER KEPT IN THE TANKS AT PLYMOUTH, JUNE 15.							
2	∞	∞	—	Black	Not Observed.	F6	
3. A COWES OYSTER KEPT IN TANKS AT PLYMOUTH, JULY 6.							
3	few	∞	—	Bl.	N.O.	F5	
4	∞	∞	—	do.		F6	
4. YEALM OYSTERS KEPT IN TANKS AT PLYMOUTH, NUMBER 5, WHITESICK, JULY 4; ALL EXAMINED JULY 7.							
5	some	some	—	Wh.	N.O.	—	
6	none	∞	—	Wh.	N.O.	—	
7	some	∞	—	Grey	N.O.	E5	
5. HAND-COLLECTED, GREAT WESTERN WHARF, PLYMOUTH, JULY 12; EXAMINED JULY 13.							
8	none	some	a few	Wh.	early segm. stages	B3-4	
6. WHITSTABLE OYSTER, DREDGED JULY 26; EXAMINED AUGUST 4.							
9	—	∞ young	∞	Wh.	heart shaped ciliated	D3	
7. SWANSEA OYSTER KEPT IN TANKS AT PLYMOUTH; EXAMINED SEPTEMBER 12, 1921.							
10	none	∞	—	Wh.	heart shaped ciliated	D4	
8. 1922. DREDGED WEST MERSEA, JUNE 15; EXAMINED JUNE 19.							
11	∞	∞	—	Bl.		F6	
12	none	a few	some	Wh.	N.O.	—	
13	fair no.	fair no.	some	Bl.		F6	
14	none	a few	∞	Wh.	N.O.	—	

1	2 6 4			5 6		7	8
9. DREDGED YEALM, JUNE 21; EXAMINED JUNE 22.							
15	a few	∞	occ.	Wh.	ciliated	D5	
16	none	fair no.	none	do.	do.	D4	
17	none	a few	∞	do.	do.	D4	
10. DREDGED IN DEEPS, WEST MERSEA, JUNE 28; EXAMINED JUNE 28 AND 29.							
18	none	a few	—	Wh.	ciliated	D4	
19	a few	∞	none	do.	do.	D5	
20	none	a few	do.	do.	do.	D4	
21	none	fair no.	∞ relict	do.	morula	B4	
11. DREDGED THORNFLEET, WEST MERSEA, JUNE 29; EXAMINED 29 AND 30.							
22	fair no.	∞	none	Bl.		F6	
23	none	fair no.	∞	Wh.	1-4 celled	A4	inc. sp.
24	fair no.	∞	none	Bl.		F6	
25	none	a few	—	Wh.	1-5 celled	A4	
12. DREDGED VARIOUS GROUNDS, WEST MERSEA, JULY 3; EXAMINED JULY 4							
26	∞	∞	none	Bl.		F6	
27	∞	∞	none	do.		F6	
28	∞	∞	none	do.		F6	
13. DREDGED VARIOUS GROUNDS, WEST MERSEA, JULY 4; EXAMINED JULY 5.							
29	f ∞	∞	none	Bl.		F6	
30	∞	∞	do.	do.		F6	
31	f ∞	∞	do.	do.		F6	
14. DREDGED JULY 8 VARIOUS GROUNDS, WEST MERSEA; EXAMINED JULY 9.							
32	none	fair no. young	fair no.	Wh.	N.O.	—	
33	do.	do.	do.	do.	segn. stages	B3	
34	do.	few very young	do.	do.	heart shaped	C3	
35	do.	f ∞ young	a few	do.	late segn. stages	C3	
36	do.	∞	none	do.	do.	C4	
37	do.	∞	fair no.	do.	do.	C4	
38	a few	∞	a few	Wh.-gr.	small shells	E5	
39	none	few young	some	Wh.	1-3 celled	A3	
		large number very young?					
40	none	∞ young	a few	do.	late segn. stages	C3	
41	do.	do.	do.	do.	N.O.	—	
42	do.	∞	some	do.	late segn. stages	C4	
15. DREDGED HELFORD RIVER, JULY 12/22; EXAMINED JULY 13.							
43	rare	∞	none	Bl.		F5	
44	∞	∞	none	do.		F6	V, 162
16. DREDGED WHITSTABLE 21.7.22; EXAMINED 23.7.22.							
45	a few	∞	a few	Bl.		F5	
17. DREDGED WHITSTABLE, 27.7.22; EXAMINED 31.7.22.							
46	fair no.	∞	N.O.	Wh.	early shelled stage	E6	V, 178
47	fair no.	∞	∞ relict	Wh.	ciliated	D6	
48	do.	do.	few	Bl.		F6	
49	f ∞	f ∞	a few	do.		F6	
50	fair no.	∞	none	Bl.		F6	

1	2	3	4	5	6	7	8
18. DREDGED PORT NAVAS 31.7.22; EXAMINED 1.8.22.							
51	few	∞	few	Wh.	ciliated	D5	
52	f ∞	∞	few	Wh.	early shelled	E6	
53	rare	∞	none	Bl.		F5	
54	f ∞	∞	N.O.	Wh.	‡ shelled	E6	
55	few	v. ∞	few	Bl.		F5	
56	few	few only	few	Bl.		F5	
57	f. no.	∞	none	do.		F6	
58	few	∞	few	do.		F5	
59	f ∞	∞	few	do.		F6	
19. DREDGED WHITSTABLE, 1.8.22; EXAMINED 2.8.22.							
60	f no	∞	none	W.	late segn. stages	C6	
61	few	∞	few	do.	just ciliated	D5	
62	none	∞	none	do	heart shaped	C4	
63	rare	∞	fair no.	do.	late segn. stages	C5	
64	none	∞ young	few	do.	late segn. stages	C3	
65	do.	∞ young	fair no.	do.	middle segn. stages	B3	
20. DREDGED WHITSTABLE, 3.8.22; EXAMINED 4.8.22.							
66	none	few to fair no.	good no.	Wh.	∞ unseg- mented to late segn. stages	C4	
67	∞	∞	none	Bl.		F6	
68	none	fair no.	few	Wh.	∞ unseg- mented to late segn. stages	C4	spotty
69	none	none	∞	do.	do.	C1	Note 1
70	none	fair no.	few	do.	do.	C4	
71	none	few	few	do.	do.	C4	
21. DREDGED WEST MERSEA, 3.8.22, EXAMINED 4.8.22 (BROOD OYSTERS, 33 TO 40 MMS. LONG).							
72	none	few young	few	Wh.	morula stage	B3	
73	few	few	N.O.	Bl.		F5	
74	— none	few	∞	Wh.	late segn. stages	C4	
75	none	∞ v. young	few	do.	do.	C3	
76	few	∞	few	do.	just ciliated	D5	
22. DREDGED, HELFORD RIVER, 16.8.22; EXAMINED 17.8.22.							
77	f ∞	f ∞	some	Bl.		F6	
23. DREDGED, RIVER YEALM, 23.8.22; EXAMINED 24.8.22.							
78	few	∞	none	Wh.	early shelled stage	E5	
79	do.	f ∞	do.	do.	do.	E5	
24. DREDGED, RIVER YEALM, 30.8.22; EXAMINED 31.8.22 AND 1.9.22.							
80	f ∞	f ∞	none	Bl.		F6	
81	f ∞	f ∞	none	do.		F6	
82	v ∞	v ∞	none	do.		F6	

1	2	3	4	5	6	7	8
	25. 1923. DREDGED WEST MERSEA, AUGUST 3; EXAMINED AUGUST 6/23 (1921 SPAT).						
83	few	∞	none	Wh.	shelled	E5	
	26. YEALM OYSTER, KEPT IN PLYMOUTH TANKS; EXAMINED AUGUST 31/23.						
84	∞	∞	none	Bl.		F6	
	27. YEALM CAGE OYSTER ♂, JULY 9/23; EXAMINED FOR EMBRYOS 31.8.23, FOR SEX-CONDITION 4.9.23.						
85	a few	∞	none	Bl.	mainly 170μ	F5	
	28. DREDGED THORNFLEET, WEST MERSEA, 18.7.23; EXAMINED 18.7.23.						
86	∞	∞	—	Sl.	180μ	F6	
	29. DREDGED THORNFLEET, WEST MERSEA, 25.7.23; EXAMINED 26.7.23.						
87	none	f ∞	∞	Wh.	early shelled	E4	patchy
	30. DREDGED NOSS END, WEST MERSEA, 26.7.23; EXAMINED 27.7.23						
88	fair no.	∞	none	Bl.	170μ	F6	
89	none	a few very young	—	Wh.	early shelled	E3	
	31. DREDGED NOSS END, WEST MERSEA, 27.7.23; EXAMINED 28.7.23.						
90	none	fair no. v. young, a few nearly ripe	few	Wh.	early shelled	D4	
		70μ					
91	a few	fair no.	none	Gr.		E5	
	32. DREDGED THORNFLEET, WEST MERSEA, 30.7.23; EXAMINED 31.7.23 (ESTIMATED 1921 SPAT).						
92	∞	∞	none	Bl.		F6	
93	∞	∞	none	Wh.	early shelled	E6	
	33. SAME, 2.8.23; EXAMINED 3.8.23.						
94	none	f ∞ young	some	do.	late segn. stages	C3	
	34. 1924. DREDGED JUNE 3, 1924, VARIOUS GROUNDS, WEST MERSEA EXAMINED 7-8.6.24.						
95	none	f ∞ young	some	Wh.	unseg- mented	A3	
96	—	some very young	few	Wh.	N.O.	—	
97	—	∞ young	none	do.	N.O.	—	
98	—	∞ large with 500 subdivisions	none	do.	just ciliated	D4	
99	none	few young 8-30 cells; a few bigger	few	do.	late segn. stages	C3	
	35. DREDGED BURNHAM RIVER BEDS, 3.6.24; EXAMINED 7.6.24.						
100	none	∞ young	—	Gr.-Wh.	shell young	E3	
101	∞	∞	—	Wh.	N.O.	—	
102	some	fair no.	—	do.	N.O.	—	

1	2			3	4	5		6	7	8
36. DREDGED THURSLEET AND NOSS END, WEST MERSEA, 12.6.24; EXAMINED 13.6.24.										
103	∞	∞	none	Bl.	N.O.	F6				
104	∞	∞	none	do.	N.O.	F6				
37. DREDGED BACK OF NOSS, WEST MERSEA, 30.6.24; EXAMINED 1.7.24.										
										Colour of digestive organ.
105	f ∞	a few	none	Lilac Grey		F7				— Note 2
106	∞	a few	do.	Bl.		F7				fawny brown
107	∞	∞	do.	do.		F6				do.
108	∞	∞	few spots	Bl.		F6				do.
109	fair no.	fair no.	fair no.	Wh.	trace of shell	D6				—
110	∞	∞	few spots	Bl.		F6				fawny brown
111	none	fair no. v. young	few spots	Wh.	early segn. stages	B3				brown
112	none	do.	do.	do.	do.	B3				do.
113	∞	∞	do.	do.	ciliated with shell rudiment	D6				yellow
114	none	∞	few	do.	late segn. stages	C4				fawny brown
115	f ∞	∞	one spot	do.	‡ shelled	E6				yellow-brown
116	none	∞	few	do.	late segn. stages	C4				choc. brown
117	fair no.	∞	few	do.	just ciliated	D6				yellow-brown
118	none	f ∞	few	do.	late segn. stages	C4				light choc. brown
119	few	∞	few	do.	ciliated	D5				yellow
120	none	∞	few	do.	late segn. stages	C4				choc. brown
121	∞	∞	do.	Gr.	shelled	E6				yellow-brown
122	one seen	∞	fair no.	Wh.	late segn. stages	C5				choc. brown
123	none	f ∞ v. young	few	do.	do.	C3				do.
124	few	∞	few	do.	shell rudiment	D5				yellow-brown
125	none	fair no.	few	do.	late segn. stages	C4				light choc. brown
38. DREDGED VARIOUS GROUNDS, WEST MERSEA, 1.7.24; EXAMINED 2.7.24.										
126	∞	fair no. large	none	Bl.		F6				N.O.
127	∞	do.	do.	do.		F6				N.O.
128	∞	do.	do.	do.		F6				yellow-brown
129	rare	∞	do.	Wh.	late segn. stages	C5				choc. brown
130	none	f ∞ young	do.	do.	do.	C3				N.O.
131	few	v ∞	few spots	do.	do.	C5				light choc. brown
39. DREDGED SOUTH SHORE, WEST MERSEA, 2.7.24; EXAMINED 3.7.24.										
132	few	∞	few spots	Wh.	heartshaped	C5				choc. brown
133	∞	few	none	Bl.		F7				yellow-brown
134	f ∞	∞	few	Gr.	‡ shelled	E6				fawny colour
40. DREDGED VARIOUS GROUNDS, WEST MERSEA, 4-6-7.24; EXAMINED 5-7-7.24.										
135	f ∞	∞	few	Bl.		F6				brown
136	∞	∞	none	do.		F6				good chocolate

1	2	3	4	5	6	7	8
41. YEALM CAGE EXPERIMENT OYSTERS "SICK," 1923, AND "SICK" AGAIN 16.7.24; EXAMINED FOR SEX 18.7.24.							
137	none	f ∞ to 40μ	none	Wh.	ciliated	D3	
138	none	a few to 40μ	fair no.	Wh.	do.	D3	
42. YEALM CAGE EXPERIMENT OYSTERS ♂ 1923, AND "SICK," 8.8.24.							
139	f ∞	∞	a few	Sl.	160-175μ	F6	
140	∞	∞	none	Bl.	170-180μ	F6	
YEALM CAGE EXPERIMENT OYSTER "SICK," 1923, AND "SICK" AGAIN 8.8.24.							
141	fair no.	∞	none	Sl.	180-190μ	F6	
43. DREDGED PERCUL RIVER, FAL ESTUARY, 15.8.24; EXAMINED 18.8.24 FOR EMBRYOS, 23.8.24 FOR SEX.							
142	∞	fair no.	none	Gr.	170μ	E6	
143	∞	f ∞	none	Wh.	ciliated	D6	Note 3
144	fair no.	∞	none	Sl.		F6	
44. YEALM CAGE 3 OYSTERS, MALE 1923; SPAWNED 27/28-8.24; EXAMINED 28.8.24.							
145	f ∞	f ∞	none	Sl.	170μ	F6	
146	f ∞	a few	none	do.	170μ	F7	
147	f ∞	f ∞	few	do.	N.O.	F6	
45. EXPERIMENTAL OYSTERS FROM CAGE KEPT IN THE SEA AT WEST MERSEA, CAGE HAULED JUNE 30, OYSTERS EXAMINED JULY 1ST TO 8TH 1924.							
148	N.O.	N.O.	N.O.	Wh.	ciliated	—	♂ in July, 1923,* (July 1, 1924.)
149	none	fair no. young	fair no.	N.O.		D3	♂ in July, 1923, (July 2, 1924.)
150	few	f ∞ large	do.	N.O.		F5	♂ in July, 1923, (July 8, 1924.)
151	none	∞110 × 30.μ	few spots	Wh.	heart shaped	C4	♂ in July, 1923, (July 7, 1924.)
152	none	∞ tailed and nearly ripe	fair no.	do.	do.	C4	♀ in July, 1923, (July 8, 1924.)
153	none	∞	few	do.	morula stages on the 6th	C4	♀ in July, 1923, (July 8, 1924.)
154	f ∞	∞	none	Sl.		F6	♂ in July, 1922 (July 1, 1924.)
155	none	f ∞ young	f. ∞ relict	Wh.	morula stages on 6th	C3	♂ in July, 1922, (July 8 1924.)
156	none	a few very young ?	v. ∞ relict	do.	segmenta- tion stages	B2	♀ in July, 1922, (July 6, 1924.) ‡ spent.
46. DREDGED EAST BANK (WATERING), FAL ESTUARY, 1.7.25; EXAMINED 2.7.25.							
157	none	f ∞ to 60μ	few groups	Wh.	heart shaped	C4	
158	a few	do.	do.	do.	do.	C4	
159	f ∞	f ∞	none	do.	trace of shell	D6	
160	none	f ∞ to ca 60μ	∞ patches	do.	heart shaped	C4	
161	none	few full size	f ∞	do.	ciliated	D4	d
162	do.	do.	∞	do.	stage doubtful	—	d
163	f ∞	∞	none	do.	‡ shelled	E6	d
164	rare	f ∞	few	do.	do.	E5	d
165	none	few young	few	do.	morula	B3	d
166	rare	fair no.	few patches	do.	do.	B5	d

* The dates of examination of individuals in lot 45 are given in brackets.

1	2	3	4	5	6	7	8
THE SAME LOT EXAMINED 4.7.25.							
167	rare	f ∞	none	do.	ciliated	D5	
168	none	few small	fair no.	do.	heart shaped	C3	
169	fair no.	f ∞	few patches	Gr.	early shelled	E6	
170	none	f ∞	do.	do.	do.	E4	
171	do.	fair no.	do.	do.	do.	E4	d
172	do.	fair no.	none	do.	do.	E4	d
		medium size					

47. DREDGED TURNAWARE BAR, FAL ESTUARY, 8.7.24; EXAMINED 11.7.25.

173	none	∞ to 50μ	few patches	Wh.	ciliated	D4	11.7.25
174	few	∞	do.	do.	do.	D5	do.
175	none	few very young	do.	do.	late segn. stages	C3	do.
176	do.	∞ to 80μ	—	do.	just shelled	C4	12.7.25
177	do.	f ∞	few	do.	ciliated	C4	do.
		nearly ripe					
178	f ∞	∞	—	do.	early shelled	D6	do.
179	rare	∞	few	do.	ciliated	D5	do.
180	∞	∞	few patches	Bl.		F6	do.
181	∞	some	none	do.		F7	do. d
182	none	few	—	Wh.	ciliated	D4	do. d

48. DREDGED EAST BANK, 15.7.25; EXAMINED 18.7.25.

183	none	few very young	few	Wh.	spherical	C3	
184	do.	∞ to 30μ	do.	do.	do.	C3	
185	few	f ∞ to 70μ	f ∞	Bl.		F5	
186	none	∞ to 70μ	none	do.		F4	
187	f ∞	f ∞	few	do.		F6	
188	fair no.	f ∞	few	do.		F6	
189	none	∞ v. young?	some	Wh.	just shelled	D2	
190	do.	∞ to 30μ	few	do.	spherical	C3	
191	do.	∞ v. young?	fair no.	do.	do.	C2	

49. DREDGED EAST BANK (WATERING) AND MYLOR BANK, 22.7.25; EXAMINED 24.7.25.

192	none	∞	few patches	Gr.	little shell	D4	
193	∞	∞	—	Bl.		F6	
194	∞	f ∞	∞	do.		F6	
195	few	f ∞	few patches	Gr.	some shell	E5	
196	∞	∞	none	Bl.		F6	
197	∞	f ∞	do.	Wh.	trace of shell	D6	
198	none	f ∞ to 30μ	do.	Wh.	do.	D3	
199	f ∞	∞	few patches	do.	ciliated	D6	
200	none	∞ to 70μ	do.	do.	trace of shell	D4	
201	f ∞	∞	do.	do.	½ shelled	E6	
202	few	∞	none	Bl.		F5	
203	none	f ∞ small	few patches	Wh.	trace of shell	D3	d
204	do.	f ∞	∞ patches	do.	ciliated	D4	d
205	do.	∞	few patches	do.	do.	D4	d
206	do.	few	do.	do.	trace of shell	D4	d
207	∞	∞	few patches	Wh.	½ shelled	E6	d
208	fair no.	f ∞	one patch	do.	nearly fully shelled	E6	d
209	rare	∞	few patches	Gr.	½ shelled	E5	d
210	none	few	∞ patches	Wh.	late segn. stages	C4	d
211	do.	∞	few patches	do.	trace of shell	D4	sl. d
212	rare	very rare	none	do.	½ shelled	E5	d
213	fair no.	∞	∞ patches	do.	½ shelled	E6	d

1	2	3	4	5	6	7	8
214	v ∞	v ∞	few patches	Gr.	170μ	E6	sl. d
215	v ∞	fair no.	none	Bl.		F6	d
216	none	rare	few patches	Wh.	trace of shell	D4	d
217	do.	f ∞ small	—	do.	heart shaped	C3	d
50. DREDGED 30.7.25, TURNAWARE BAR; EXAMINED 31.7.25.							
218	none	v ∞ to 60μ	one patch	Wh.	late segn. stages	C4	d Note 4.
219	fair no.	∞	occ. patches	Gr.	fully shelled	E6	d
220	f ∞	∞	—	do.	do.	E6	
221	f ∞	v ∞	—	Bl.	190μ	F6	d
222	v ∞	f ∞	—	Gr.	fully shelled	E6	
223	f ∞	∞	—	Bl.		F6	sl. d.
224	none	∞	∞ patches	Wh.	late segn. stages	C4	Examined 2.8.25
225	∞	∞	few patches	Gr.	150μ	E6	
226	∞	∞	one patch	Gr.	150μ	E6	
227	none	f ∞ to 50μ	several patches	Wh.	late segn. stages	C4	
228	do.	∞ nearly ripe	few patches	Gr.	150μ	E4	
229	do.	∞ do.	occ.	do.	do.	E4	sl. d
230	v ∞	v ∞	do.	do.	do.	E6	d
231	few	∞	∞ patches	do.	do.	E5	d
232	none	∞	occ.	Wh.	ciliated trace of shell	D4	sl. d
233	∞	∞	none	do.	‡ shelled	E6	sl. d
234	none	∞	occ. patches	do.	heart shaped	C4	d
235	fair no.	v. ∞	do.	Lilac-grey		F6	sl. d.
51. DREDGED TURNAWARE POINT AND EAST EDGE, 5.8.25; EXAMINED 6.8.25.							
236	f ∞	∞	none	Grey-white	150μ	E6	sl. d
237	∞	f ∞	do.	Bl.	200μ	F6	d
238	none	∞ nearly ripe	rare patches	Wh.	ciliated trace of shell	D4	d
239	none	none	none	Bl.	180μ	F1 or 10	Note 5. d
240	few	f ∞	fair no. of patches	Gr.	‡ shelled	E5	
241	none	∞	none	Grey-white	ciliated trace of shell	D4	
242	∞	∞	none	Bl.	180μ	F6	
243	v ∞	f ∞ large	do.	do.		F6	
244	∞	∞	do.	do.	180μ	F6	
245	fair no.	f ∞	do.	Wh.	ciliated trace of shell	D6	d
246	none	f ∞ to 50μ	few	do.	do.	D4	d
247	few	∞ full size	—	White-grey	‡ shelled	E5	d
248	∞	∞	few patches	Bl.	200μ	F6	sl. d
52. DREDGED FALMOUTH NORTH BANK 10.8.25; EXAMINED 12.8.25.							
249	none	∞ up to 50μ	few patches	Wh.	spherical	C4	d
250	∞	∞	none	Bl.	200μ	F6	d
251	rare	∞	few	Wh.	heart shaped	C5	
252	∞	∞	none	White-grey	‡ shelled	E6	d
253	f ∞	∞	do.	Bl.	180-190μ	F6	
254	none	∞	few	Wh.	late segn. stages	C4	
255	∞	∞	few patches	Grey-white	‡ shelled	E6	Examined 13.8.25
256	fair no.	v ∞	none	Bl.	190μ	F6	
257	none	∞	occ.	Wh.	late segn. stages	C4	
258	few	∞	few	Bl.	180μ	F5	sl. d

SEX-CHANGE IN THE OYSTER.

1007

1	2	3	4	5	6	7	8
259	f ∞	∞	few patches	Purplish-grey	170μ	F6	
260	∞	∞	∞ patches	Bl.	200μ	F6	d
261	∞	∞	none	do.	190μ	F6	d
262	∞	f ∞	—	Bl.	200μ	F6	N
263	few	few	few patches	Gr.	170μ	E5	N
264	none	v ∞	2 do.	Wh.	late segn. stages	C4	d
265	f ∞	v ∞	2 do.	Gr.	150μ	E6	sl. d
266	f ∞	∞	—	Bl.	180μ	F6	d
267	fair no.	∞	—	Gr.	170μ	E6	d
268	f ∞	f ∞	few patches	Bl.		F6	sl. d
269	none	rare	few patches	Wh.	4-32-celled	B3	
		probably ∞ v. small					
270	none	probably some v. small	∞	do.	heart shaped	B2	‡ spent
271	do.	a few young	few	do.	early segn. stages	B3	
272	fair no.	∞	fair no. in patches	do.	heart shaped	C5	
273	none	few to 50μ	few patches	do.	late segn. stages	C4	
274	f ∞	∞	occ. patches	Purplish-grey	180μ	F6	
275	v ∞	v ∞	none	do.	160μ	F6	
276	none	few	few patches	Wh.	late segn. stages	C4	
277	∞	∞	none	Bl.		F6	
278	f ∞	∞	none	Purplish-grey	170μ	F6	

53. DREDGED EAST EDGE, FAL ESTUARY, 11.8.25; EXAMINED 13.8.25.

279	none	none	∞ small patches	Wh.	4-16-celled	B1	d
280	∞	∞	none	Bl.	170μ	F6	d
281	none	∞ small	do.	Wh.	0-4-celled	A3	N
282	do.	probably ∞ v. young	few patches	do.	0-4-celled	A2	N
283	f ∞	∞	occ. patches	do.	ciliated	D6	Sl. d
284	few	∞	—	do.	do.	D5	N
285	none	∞ large	few patches	do.	do.	D4	N
286	few	∞	one patch	Grey-white	ciliated trace of shell	D5	N
287	none	few small	∞ patches	Wh.	0-4-celled	A3	sl. d
288	∞	∞	one patch	Bl.	200μ	F6	N
289	f ∞	∞	none	do.	180μ	F6	sl. d
290	none	none	3 or 4 patches	Wh.	0-4-celled	A1	N
291	none	∞	fair no. of patches	White-grey	ciliated trace of shell	D4	N
292	do.	occ. young	∞	Wh.	0-4-celled	A3	N
293	do.	∞ 50μ	2 patches	do.	heart shaped	C4	N
294	do.	∞	∞ patches	do.	ciliated	D4	N
295	f ∞	∞	few patches	Bl.	190μ	F6	N
296	f ∞	∞	none	do.		F6	N
297	∞	∞	none	Bl.	160-180μ	F6	N
298	∞	∞	do.	do.	200μ	F6	N
299	∞	f ∞	—	do.	160-180μ	F6	N
300	f ∞	f ∞	1 patch	do.	180μ	F6	N
301	f ∞	∞	none	do.	180μ	F6	N
302	∞	∞	—	do.	180μ	F6	sl. d

Examined 14.8.25

1	2	3	4	5	6	7	8
54. DREDGED EAST END MYLOR BANK, FAL ESTUARY, 18.8.25; EXAMINED 20.8.25.							
303	∞	f ∞	few patches	Bl.	200μ	F6	sl. d
304	few	∞	many do.	Grey-white	ciliated	D5	d
305	few	∞	none	Gr.	‡ shelled	E6	d
306	none	f ∞ small	one patch	Wh.	to 16-celled	B3	N
307	none	∞ to 80μ	1 big patch	do.	heart shaped	C4	N
308	few	∞ full size	∞ scattered	do.	ciliated	D5	d
309	none	v ∞ full size	few	do.	do.	D4	sl. d
310	fair no.	∞	few	do.	do.	D6	N
311	do.	∞	few spots	White-grey	‡ shelled	E6	N
312	none	∞	fair no. of patches	Wh.	ciliated	D4	d
313	∞	∞	none	Grey-white shells	150μ	E6	d
314	f ∞	∞	occ. patches	Gr.	150μ	E6	N
315	few	∞	do.	Wh.	ciliated	D5	N
316	f ∞	∞	do.	Grey-white	‡ shelled	E6	N
317	∞	∞	none	Bl.	200μ	F6	N
318	∞	v ∞	few patches	Gr.	150μ	E6	sl. d
319	none	∞	fair no.	Wh.	‡ shelled	E4	d
320	do.	∞	occ. patches	Wh.	heart shaped	C4	d
321	do.	f ∞	many patches	do.	do.	C4	sl. d
322	do.	∞	occ. patches	do.	ciliated	D4	sl. d
323	do.	f ∞	fair no.	do.	heart shaped	C4	sl. d
324	do.	∞	∞ patches	do.	ciliated	D4	sl. d

55. DREDGED MYLOR BANK, FAL ESTUARY, 26.8.25; EXAMINED 28.8.25.

325	∞	fair no.	none	Bl.	180-190μ	F6	d
326	∞	f ∞	do.	do.	do.	F6	d
327	∞	do.	do.	do.	170-190μ	F6	d
328	∞	do.	do.	do.	190μ	F6	d
329	∞	do.	do.	do.	180-200μ	F6	d
330	f ∞	∞	do.	Grey-white	‡ shelled	E6	d
331	f ∞	∞	do.	Bl.	180-190μ	F6	N
332	none	∞	do.	Bl.	mainly 180μ range 170-190μ	F4	N
333	none	∞ small	do.	Wh.	heart shaped	D3	d
334	few	∞	do.	Bl.	180μ	F5	N
335	∞	few only	none	Bl.	190-200μ	F7	N
336	rare	∞	none	do.	full size	F5	N
337	none	∞	∞ small patches	Wh.	heart shaped	C4	N
338	few	∞	none	Bl.	full size	F5	N
339	∞	∞	do.	do.	do.	F6	N
340	∞	∞	1 or 2 patches	do.	do.	F6	N
341	f ∞	∞	none	do.	180-200μ	F6	N
342	none	f ∞	few	do.	180μ	F4	N
343	v ∞	v ∞	few patches	Grey-white	‡ shelled	E6	d
344	∞	∞	—	Bl.	180-190μ	F6	d
345	none	fair no.	none	Wh.	late segn. stages	C4	d
346	∞	∞	do.	Bl.	200μ	F6	d
347	∞	few	do.	do.	180μ	F7	d
348	few	∞	none	Purple-grey	160μ	F5	sl. d
349	f ∞	∞	do.	Bl.	180μ	F6	sl. d
350	∞	∞	—	do.	180μ	F6	sl. d

1	2	3	4	5	6	7	8
56. DREDGED TURNAWARE BAR, FAL ESTUARY, 3.9.25; EXAMINED 5-6.9.25							
351	rare	∞	few patches	Gr.	ciliated trace of shell	D5	d
352	∞	fair no.	none	Bl.		F6	d
353	none	∞	∞ small patches	Wh.	heart shaped	C4	N
354	∞	∞	none	Grey-white	‡ shelled	E6	d
355	∞	∞	2 or 3 patches	Grey-wh.	trace of shell	D6	d
EXAMINED 6.9.25.							
356	∞	fair no.	none	Bl.	160-170μ	F6	d
357	none	few	few patches	Wh.	heart shaped	C4	d
358	do.	∞	none	do.	do.	C4	d
359	fair no.	∞	few patches	do.	‡ shelled	E6	sl. d
360	few	f ∞	none	Bl.	180μ	F5	d
361	∞	∞	1 or 2 patches	do.	full size	F6	d
362	rare	∞	none	Wh.	ciliated	D5	d
363	none	∞	1 or 2 patches	do.	heart shaped	C4	d
364	do.	fair no. young	few patches	do.	ciliated	C3	sl. d
365	do.	v ∞	none	Purplish- grey	150-160μ	F4	d
366	few	v ∞	few patches	Wh.	heart shaped	C5	sl. d
367	none	few	none	do.	do.	C4	sl. d
368	do.	∞ young	∞	do.	do.	C3	N
369	do.	do.	do.	do.	ciliated	D3	N
370	fair no.	v ∞	1 or 2 patches	do.	heart shaped	C6	N
371	none	∞	few patches	do.	late segn. stages	C4	N
372	few	∞	1 or 2 patches	Wh.	heart shaped	C5	N
373	fair no.	∞	1 patch	do.	ciliated	C6	N
374	none	∞	several patches	do.	heart shaped	C4	N
375	do.	∞	many	do.	ciliated	C4	N
376	do.	∞ nearly ripe	∞ patches	do.	heart shaped	C4	N
377	do.	fair no. young	some	do.	do.	C3	N
378	∞	∞	none	Bl.	170-180μ	F6	N
379	few	v ∞	few patches	Wh.	ciliated	C5	N
57. DREDGED EAST EDGE, FAL ESTUARY, 9.9.25, EXAMINED 11-12.9.25.							
380	f ∞	f ∞	several big patches	Purplish grey	160μ	F6	d
381	none	v ∞	few patches	Wh.	late segn. stages	B4	d
382	fair no.	∞	none	Gr.	150μ	E6	d
383	∞	∞	none	Purplish grey	160μ	F6	d
384	f ∞	f ∞	fair no. in patches	Gr.	160μ	E6	d
385	∞	∞	few patches	Bl.	170μ	F6	d
386	∞	f ∞	none	do.	170μ	F6	d
387	∞	∞	occ. patches	do.	160-170μ	F6	d
388	∞	∞	none	Purplish grey	160μ	F6	d
389	none	∞ young a few to 60μ	few patches	Wh.	heart shaped	C4	d
390	∞	∞	fair no. of patches	Gr.	150μ	E6	d
391	∞	∞	—	Gr.	155μ	E6	sl. d
392	∞	∞	none	Bl.	—	F6	N
393	∞	f ∞	do.	Gr.	160μ	E6	N
394	∞	∞	few patches	Bl.	160μ	F6	N
395	f. no.	∞	∞ scattered	Gr.	160μ	E6	N

1	2	3	4	5	6	7	8
EXAMINED 12.9.25.							
396	few	∞	1 or 2 patches	do.	160μ	E5	N
397	∞	none	none	Bl.		F8	N
398	∞	rare	do.	do.		F7 Note 6	N
399	?	some	∞	Purplish-grey	poor condition	—	N
400	∞	f ∞	∞	Bl.		F6	N
401	few	some	few	Gr.		E5	N
402	∞	none	several patches	Bl.		F8	N
403	∞	∞	none	do.		F6	N
404	none	few small	several large patches	Wh.	morula stage	B3	N
405	few	∞	none	Purplish grey	150μ	F5	sl. d
406	do.	∞	rare	do.	150μ	F5	N
407	∞	∞	none	do.	160μ	F6	N
408	∞	∞	do.	do.	160μ	F6	N
409	f ∞	f ∞	none	Purplish grey	160μ	F6	N
410	none	∞	few patches	do	do.	F4	N
411	∞	∞	none	do.	do.	F6	N
412	f ∞	f ∞	do.	Bl.	170μ	F6	N
413	∞	∞	rare patches	do.	180μ	F6	N
414	∞	∞	none	Gr.	150μ	E6	d
415	∞	f ∞	few patches	do.	160μ	E6	N

58. DREDGED TURNAWARE POINT, 16.9.25; EXAMINED 18-19.9.25.

416	∞	∞	none	Bl.	170-180μ	F6	N
417	∞	f ∞	rare patches	do	190-200μ	F6	N
418	none	∞	small and 1 large patch	Wh.	ciliated	D4	N
419	do.	f ∞	young few patches	Wh.	½ to ⅓ shelled	E3	N Note 7

EXAMINED 19.9.25.

420	few	few	none	Bl.	170-180μ	F5	N
421	∞	∞	do.	do.	180-190μ	F6	N
422	none	none	none	do.	170-180μ	F1-10	d
423	∞	∞	none	do.	180-190μ	F6	d
424	v ∞	v ∞	do.	do.	180μ	F6	d
425	∞	∞	do.	do.	190-200μ	F6	sl. d
426	∞	∞	do.	do.	180μ	F6	sl. d

59. DREDGED TURNAWARE POINT, 23.9.25; EXAMINED 24.9.25.

427	f ∞	∞	few patches	Slate-grey	150-155μ	F6	
428	fair no.	∞	none	do.	160-170μ	F6	

60. VARIOUS GROUNDS, FAL ESTUARY, OCTOBER, 1925.

429	none	few v. young	few	Wh.	heart shaped	C3	Dredged and examined 30.9.25, Mylor Pool.
430	∞	none	none	Bl.	180-190μ	F8	do. 2.10.25, Turnaware Point. Note 8
431	few	few	do.	do.	170μ	F5	do. 7.10.25, Mylor Pool.
432	none	few young	none	Wh.	heart shaped	C3	do. 8.10.25, Mylor Pool.
433	do.	none	none	Bl.	190μ	F1-10	do. do.
434	none	none	none	do.	195-200μ	F1-10	do. 14.10.25, 15.10.25, Turnaware Point.

1	2 3 4			5 6		5	8
435	none	few to 50 μ	none	Gr.	1 to 2 shelled	E4	Turnaware Point.
436	none	fair no. up to 50 μ	none	Sl.	180 μ	F4	Hand collected, Turnaware Point, 19.10.25.
437	none	a few large	few	Bl.	180 μ	F4	Dredged 27th; examined 29.10.25; Mylor Bank.
438	none	none	none	do.	190-200 μ	F1-10	do. 3rd, do. 5.11.25, Turnaware Bar.

61. DREDGED VARIOUS GROUNDS, WEST MERSEA, 10.7.25; EXAMINED 11.7.25.

439	none	∞	few	Wh.	4 to 8-celled stages	B4	
440	do.	∞	—	do.	heart shaped	C4	
441	do.	few young	—	do.	do.	C3	
442	few	∞ full size	few	do.	do.	C5	
443	none	some probably ∞ very young	few	do.	2-3-celled stages	A3	
444	none	f ∞ to 50 μ	patches	do.	0-4-celled stages	A4	
445	none	∞ v young few to 50 μ	few	do.	0-2-celled stages	A4	
446	none	few to 30 μ	fair no.	do.	4-8-celled stages	B3	Dredged 13th, examined 14.7.25

62. SAMPLE OF BROOD ESTIMATED IN SECOND AND THIRD SUMMER; DREDGED SOUTH SHORE AND EXAMINED 21.7.25.

447	∞	∞	none	Wh.	1 shelled	E6	37	36	8
448	few	∞	few	do.	ciliated	D5	35	42	10-25
449	∞	∞	few	do.	do.	D6	39	43	4
450	none	∞ 40 μ	—	do.	spherical	C3	37	38	6
451	do.	do.	—	do.	ciliated	D3	43	42	12
452	do.	∞	few patches	do.	spherical	C4	48	50	4
453	do.	∞	∞ patches	do.	partly shelled	E4	45	49	10

OYSTERS FROM EXPERIMENTAL CAGE SUNK IN DEEPS, WEST MERSEA; CAGE HAULED 2.7.25.

63a. A. INDIVIDUALS WHITESICK 10.6.24 TO 9.7.24, NOW "SICK" AGAIN; EXAMINED 3-13.7.25.

454	∞	∞	none	Bl.		F6	
455	rare	f ∞ to 60 μ	few patches	Wh.	ciliated	D5	
456	none	∞	do.	do.	do.	D4	

63b. B. INDIVIDUALS BLACKSICK 1-9.7.24, NOW "SICK" AGAIN; EXAMINED 13-14.7.25.

457	few	few large fair no. very young	few	Wh.	ciliated	D5	
458	f ∞	∞	none	Bl.		F6	
459	none	f ∞	none	Wh.	ciliated	D4	
460	none	a few nearly ripe f ∞ to 35 μ	few	do.	do.	D3	

1926.

64. DREDGED TURNAWARE BAR, FAL ESTUARY, JUNE 2, 11.30 A.M. TO 3 P.M.; EXAMINED JUNE 3, 1926.

461	none	f ∞ 30 μ a few 70 μ of small patches	fair no.	Wh.	32 celled	B4	
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1	2	3	4	5	6	7	8
EXAMINED JUNE 5, 11.0 A.M.							
462	none	∞ to 40-50 μ	∞ in small patches	Wh.	heart shaped only	C4	
EXAMINED JUNE 14.							
463	a few	f ∞	fair no. in patches	Grey-white	150-160 μ	E5	
464	f ∞	∞	few patches	Gr.	160 μ	E6	
65. DREDGED TURNAWARE BAR, FAL ESTUARY, JUNE 9, ABOUT LOW-WATER MARK, 10 A.M.-1.15 P.M.; EXAMINED JUNE 9, 4.30 P.M.							
465	rare	v ∞	a few relict	Wh.	$\frac{1}{2}$ shelled	E5	
65a. DREDGED TURNAWARE BAR, FAL ESTUARY, JUNE 16, 9.30-12 NOON; EXAMINED JUNE 17, 11.30 A.M.; TWO DUMPS EXAMINED JUNE 18 AT NOON.							
466	none	f ∞ 50 μ	occ. patch	Wh.	morula stage 70% unsegmented	B4	
467	f ∞	∞ large to 70 μ	occ. spots	Wh.	$\frac{1}{2}$ to $\frac{3}{4}$ shelled	E6	
468	none	∞ 50 μ	few patches	Wh.	to morula stages 10% unsegmented	B4	sl. d
469	none	∞ fo 50 μ	one fair patch	Wh.	to 32-celled stages 15% unsegmented	B4	sl. d
66. DREDGED BROWN ROSE BAR, EAST BANK, FALMOUTH, JUNE 22, 9 A.M. ONWARDS, EXAMINED JUNE 22, 6.10-6.45 P.M.							
470	none	few to 30 μ	few patches relict	Wh.	32 or a few more cells	B3	58 62 3
DREDGED BELOW LOW-WATER MARK, TURNAWARE BAR, JUNE 23, 9-11.25 A.M.; EXAMINED JUNE 24, 6.20 P.M.							
471	none	∞	few	Wh.	40-50 nuclei, 64 rare	C4	
DREDGED TURNAWARE BAR, JUNE 23, 11.30 A.M. TO 2 P.M.; EXAMINED JUNE 25, 10.40 TO 11.0 A.M.							
472	none	∞	none	Wh.	ciliated	D4	58 62 nil trs.
473	none	∞	∞	do.	up to 64 celled	C4	ca. $\frac{1}{2}$ spent
67. DREDGED THORNFLEET, WEST MERSEA, JUNE 23, 7-8 A.M.; EXAMINED JUNE 24, NOON TO 3.45 P.M.							
474	f ∞	∞ large	small patches	Bl.	200 μ	F6	Liver a little black, i.e. nearly choc-brown; sl. curd.
475	∞	∞	few	Sl.	180 μ	F6	Liver a little black, i.e. nearly choc-brown
476	∞	∞	none	Slate-purple	190-200 μ	F6	do.
477	f ∞	∞	do.	Sl.	200	F6	do.
478	f ∞	∞	f ∞ in spots	Sl.	200	F6	do. spotted
479	f ∞	∞	none	Purple-slate	190	F6	Liver a little black, i.e. nearly choc-brown
480	f ∞	∞	none	Sl.	200	F6	do.

1	2	3	4	5	6	7	8
481	f ∞	∞	few spots	Sl.	200 × 160-170μ	F6	do. sq.
482	∞	∞	none	do.	do.	F6	do. trs.
483	f ∞	f ∞	do.	do.	do.	F6	do. trs. & sq.
484	f ∞	∞	few spots	Light slate	180-190	F6	do. Note 9. trs.
485	none	∞	fair no. of patches	Wh.	ca 64-celled	C4	trs. spotty
486	none	none	∞ patches	do.	unsegmented	A1	unspent
487	f ∞	∞	few patches	do.	just ciliated	D6	trs.
488	f ∞	∞	fair no. of patches	do.	do.	D6	trs.
489	none	∞	do.	do.	64-celled	C4	sq. and † trs.
490	do.	f ∞ large	few patches	do.	do.	C4	trs.
491	none	few	very ∞ patches	do.	ciliated trace of shell	D4	Note 10 sl. curdled
492	do.	f ∞	few big patches	do.	ca 64-celled	C4	trs.
493	do.	∞	fair no. small patches	do.	do.	C4	trs.
494	do.	∞	few	do.	32-64-celled	C4	trs.
495	do.	∞	few	do.	do.	C4	trs.
496	∞	∞	none	do.	ca †-shelled	E6	trs.
497	rare	few	∞ incom- pletely spawned	do.	just ciliated	D5	Note 10 † spent
498	rare	∞	few	do.	ciliated trace of shell	D5	
499	rare	∞	none	do.	64 nuclei	C5	trs.
500	none	few young	few	do.	32-64 nuclei	C3	trs.

68a. A. COLLECTED AT L.W., TURNAWARE BAR, F. E. JUNE 28, 1.40-3 P.M.
AND B. DREDGED BEFORE AND AFTER L.W. JUNE 28; EXAMINED
JUNE 28, 6-10 P.M.

A.							
501	rare	∞ 60μ	occ.	Wh.	just ciliated	D5	
502	few	∞ 80μ	few patches	do.	do.	D5	
503	rare	∞ 80μ	none	do.	heart shaped	C5	
504	none	∞ 80μ	∞	do.	do.	C4	‡ spent
505	none	∞ 80μ	fair no. of patches	do.	do.	C4	
506	none	∞ young 30μ	occ.	do.	50 % just ciliated 50 % unsegmented	D3	Note 11
507	none	∞ young	few patches	do.	32-celled	B3	
508	rare	∞	rare	do.	ciliated	D5	d Dumps
509	none	∞	occ.	do.	16-32 nuclei	B4	d
510	do.	few	∞	do.	64-celled	C4	Note 12 d $\frac{5}{8}$ spent
511	f ∞	∞	few	do.	heart shaped	C6	d
512	f ∞	f ∞	few	do.	$\frac{1}{2}$ shelled	E6	d
513	none	∞	∞	do.	heart shaped	C4	d
B.							
514	none	∞ 60μ	few patches	do.	heart shaped	C4	
515	none	∞ young	none	do.	16-20 nuclei	B3	
516	∞	∞	none	Bl.	200μ, shells purplish	F6	
517	none	∞ 40-50μ	none	Wh.	16-32 nuclei 20 % unsegmented	B4	d
518	∞	∞	none	Wh.	$\frac{1}{2}$ shelled	E5	d

1	2	3	4	5	6	7	8
68b. DREDGED TURNAWARE BAR, F, 9.50-11 A.M. ON THE FLOOD TIDE, JUNE 28 ; EXAMINED JUNE 29, 9.45 A.M. (TWO DUMPS AT 8 P.M.).							
519	none	∞	fair no.	Wh.	32 nuclei	B4	
520	fair no.	∞	none	Sl.	150μ	E6	
521	none	∞	very ∞	Wh.	64-celled	C4	‡ spent
522	none	∞ young	∞	Wh.	16-32-celled 50 % unsegmented	B3	‡ spent
523	none	∞ young	∞	Wh.	64 nuclei 20 % unsegmented	B3	‡ spent
524	f ∞	∞	rare	Sl.	160μ	F6	
525	none	∞	∞	Wh.	‡ shelled	E4	‡ spent
526	∞	∞	none	Bl.	200μ	F6	d trs.
527	none	∞ young	none	Wh.	32 nuclei	B3	d
69. DREDGED MYLOR BANK, F, 11.30 A.M.-3.15 P.M., JUNE 29 ; EXAMINED 10 P.M. JUNE 29.							
528	a few	∞	∞	Wh.	ciliated trace of shell	D5	Note 13. ‡ spent
529	∞	∞	few	Wh.	do.	D6	
530	rare	∞	few patches	Wh.	do.	D5	d
531	none	∞	f ∞	Wh.	shells 100μ	E4	d spotty
70a. DREDGED EAST BANK, F, 11.30 TO ABOUT NOON ; EXAMINED JULY 1, 1.0 A.M.							
532	none	∞	none	Wh.	16-32-celled	B4	d
533	do.	∞	none	do.	32-64-celled	C4	d
534	do.	few	∞	do.	heart shaped	C4	d patchy
535	do.	∞	none	do.	32-celled	B4	d
70b. DREDGED EAST BANK, F, ABOUT NOON TO 2.40 P.M., JUNE 30 ; EXAMINED 5.20 TO 8 P.M., JUNE 30.							
536	few	∞	none	Wh.	ciliated trace of shell	D5	60 63 3
537	none	f ∞	∞ patches	do.	heart shaped	C4	65 58 5
538	fair no.	∞	few	Wh.	do.	C6	60 61 7
539	none	f ∞	few	do.	32-celled	B4	55 55 5
540	do.	∞	none	do.	ciliated	D4	64 61 8
541	do.	∞	∞ relict	do.	do.	D4	64 73 3 ‡ spent
542	f ∞	∞	few patches	do.	do.	D6	60 60 5
543	∞	∞	f ∞ relict	do.	trace of shell	D6	61 62 0
544	none	∞	f ∞ relict	do.	4-celled stages	A4	61 67 8
545	do.	∞	do.	do.	heart shaped	C4	60 67 5
546	do.	∞	do.	do.	do.	C4	51 50 0
547	f ∞	∞	few	Sl.		F6	51 63 5 d
548	f ∞	∞	none	Bl.		F6	57 67 0 d
549	none	some	∞ relict	Wh.	heart shaped	C4	55 56 2 d
550	do.	some	∞ relict	do.	do.	C4	47 53 6 d
551	f ∞	∞	none	do.	‡ shelled	E6	55 66 0 d
71. DREDGED TURNAWARE BAR, BELOW L.W. MARK ON FLOOD TIDE JUNE 30, 3.15 TO 5.30 P.M. ; EXAMINED JUNE 30, 8.42 P.M. TO 1.4 A.M. JULY 1.							
552	few	∞	f ∞	Wh.	heart shaped	C5	71 78 5-13
553	none	∞	none	do.	do. and ciliated	D4	57 58 4
554	f ∞	∞	few patches	do.	do.	D6	57 67 0-5
555	f ∞	∞	∞ relict	do.	heart shaped only	C6	53 53 4 ‡ spent

1	2	3	4	5	6	7	8
556	none	few v. young	∞ Wh.	heart shaped only	1-5-celled	A3	52 60 3
557	none	∞	fair no.	do.	heart shaped	C4	53 60 6
558	none	∞	v ∞	do.	do.	C4	64 60 10 ‡ spent
559	f ∞	∞	none	Bl.	180-190μ	F6	58 62 5
560	f ∞	∞	rare patches	do.	200μ	F6	55 60 4
561	f ∞	∞	none	do.	190-200μ	F6	56 61 7
562	f ∞	∞	none	do.	200μ	F6	60 57 10
563	∞	∞	none	do.	190-200μ	F6	68 68 5
564	none	∞	∞ patches	Wh.	heart shaped only	C4	65 74 7 spotty
565	f ∞	∞	f ∞ relict	do.	140μ ‡ shelled	E6	62 61 4 do.
566	none	∞ young	few patches	do.	heart shaped only	C3	66 65 3
567	none	few young	rare	do.	do.	C3	57 65 5
568	none	∞	∞ in one large patch	do.	do.	C4	64 75 11
569	none	v ∞	none	do.	do.	C4	58 67 4-8
570	a few	∞	few patches	do.	do. and ciliated	D5	62 77 0
571	none	∞ young	∞ in patches	do.	8-celled stages	B3	58 67 5
572	none	∞ 50μ	few	do.	do.	B4	50 60 7 d
573	none	∞	rare	do.	64-celled	C4	57 63 2 d
574	none	∞	∞	do.	heart shaped only	C4	48 60 2 d ‡ spent
575	none	∞ v. young	none	do.	4-celled stages	A3	54 63 5 d
576	few	∞	none	Sl.	170μ	F5	45 57 4 d

72. DREDGED SOUTH SHORE, WEST MERSEA, JULY 5, 7 A.M. TO 2 P.M.,
EXAMINED JULY 7, 11.30 A.M. TO 1.40 P.M.

577	∞	∞	none	Sl.	180μ	F6	
578	f ∞	∞	occ. small patches	Gr.	140-150μ	E6	48 48 5

73. DREDGED THORNFLEET, 7-8 A.M.; EXAMINED 12.30 P.M. JULY 7,

579	∞	∞	none	Bl.		F6	trs.
580	∞	∞	do.	do.		F6	trs.
581	∞	∞	few in ducts?	do.		F6	trs. and sq.
582	none	∞	few	Wh.	trace of shell 60μ	E4	trs.
583	∞	∞	none	Bl.		F6	trs.
584	∞	∞	none	Sl.	180μ	F6	trs. and sq.
585	∞	∞	none	Gr.	150-160μ	E6	trs. and sq.
586	few	∞	few	Wh.	trace of shell	D5	sq. and trs.
587	f ∞	∞	none	do.	shell 50μ	E6	trs.
588	rare	∞	occ.	do.	ciliated	D5	trs.
589	few	∞	∞ in patches	do.	do.	D5	sq. and trs.
590	rare	∞	∞ in patches	do.	shell ca 30μ	D5	‡ spent
591	f. no.	∞	f ∞ in small spots	do.	do.	D6	trs.

74. DREDGED SOUTH SHORE, WEST MERSEA, JULY 7, 7.30-2.0 P.M.
EXAMINED JULY 8, NOON TO 1 P.M.

592	∞	∞	none	Sl.	180μ	F6	trs.
593	∞	∞	few small patches	Wh.	shells 100-120μ	E6	trs.

1	2	3	4	5	6	7	8
594	f ∞	∞	none	Slate-grey	150-160μ	F6	trs.
595	f ∞	∞	do.	Gr.	150μ	E6	trs.
596	f ∞	∞	do.	do.	do.	E6	trs.
597	rare	∞	few patches	Wh.	trace of shell 60μ	E5	trs.
598	f ∞	f ∞	none	Bl.		F6	trs.
599	∞	∞	do.	Bl.	190μ	F6	trs.
600	∞	∞	do.	Sl.	180μ	F6	trs.
601	few	fair no.	none	Gr.	140-150μ	E5	trs.
602	f ∞	∞	few patches	do.	do.	E6	Note 14 sq. and trs.
603	none	f ∞	none	Wh.	trace of shell 60μ	E4	trs.

75. DREDGED TURNAWARE BAR, FALMOUTH, JULY 6, 6 TO 7 A.M.
EXAMINED JULY 9, 11 TO 11.40 A.M.

604	∞	∞	fair no. of small patches	Wh.	ciliated only	D6	trs.
605	none	f ∞ young	few	Wh.	16-32-celled	B3	trs.
606	do.	f ∞	few	do.	32-celled	B4	trs.
607	do.	some young?	∞ in small patches	do.	1-6, occ. 8-celled	B2	trs. and spotty
608	none	∞ young	few small patches	do.	1-8-celled	B3	trs. and sq.
609	none	f ∞ young	few small patches	do.	1-6 or 8	B3	trs.
610	none	?	∞ small patches	do.	4-celled	A2	$\frac{5}{8}$ spent
611	∞	∞	several patches	Gr.	170-180μ	E6	trs. spotty
612	f no.	∞	none	Slate-black	190μ	F6	sq. and trs.
613	none	f no. young	fair no. in small patches	Wh.	1-4-celled	A3	trs. spotty
614	f ∞ in ducts	f ∞ young	∞ ova in ducts	Wh.	heart shaped ciliated	D6	A spawning ♂ (♂). Note 15 $\frac{1}{2}$ spent
615	none	∞ young	∞ large patches	do.	1-16-32- celled	B3	trs. patchy
616	none	do.	do.	do.	16-32-celled	B3	$\frac{5}{8}$ spent
617	∞	∞	none	Sl.	170μ	F6	sq.
618	none	∞	occ. patches	Wh.	ciliated shells 120-130μ	E4	trs.
619	none	∞	occ.	Wh.	do.	E4	sq.
620	∞	∞	occ. patches	Bl.	200μ	F6	trs.
621	f ∞		one big patch	White-grey	120μ	E6	trs.
622	none	∞	occ. small patches	do.	110μ	E4	trs.
623	none	?	∞	Wh.	4-celled.	A1	ducts $\frac{1}{2}$ full of ova
624	∞	∞	none	Sl.	190μ	F6	trs.
625	none	f no. v. young	none	Wh.	1-5-celled	A3	trs.
626	none	few	∞ in small patches	Wh.	ciliated, shells 80-100μ	E4	trs. and sq.
627	none	f no. some nearly ripe	none	Wh.	do.	E4	sq.
628	f no.	∞	one patch	Slate Grey	180μ	F6	sq. and trs.
629	f no.	∞	several small patches	Sl.	180μ	F6	trs.
630	f no.	f ∞	f no.	Sl.	170μ	F6	sq.
631	none	∞ young	none	Wh.	1-4-celled	A3	trs.
632	a few	∞	f no.	White-grey	shells 120μ	E5	sq. and trs.

1	2	3	4	5	6	7	8
76. DREDGED NOSS END, WEST MERSEA, JULY 10, EARLY MORNING; EXAMINED JULY 10, 1 TO 2.30 P.M.							
633	∞	∞	none	Bl.	200μ	F6	trs.
634	∞	f ∞	none	do.	200μ	F6	sq. and trs.
635	few	∞	fair no. of spots	Wh.	ciliated shell 50μ	E5	trs. spotty
636	f ∞	∞	occ.	Wh.	do.	E6	trs.
637	f ∞	∞	one patch	Wh.	do.	E6	trs.
638	none	∞	∞	Wh.	do.	E4	trs. and sq. and curdly
639	∞	∞	none	Bl.	210 × 200μ	F6	trs.
640	∞	f ∞	none	do.	210μ	F6	sq.
641	∞	∞	none	Black-slate	190μ	F6	trs.
642	f ∞	∞	none	Sl.	180 × 160μ and 190 × 170μ	F6	trs.
643	f ∞	∞	none	Slate-grey	180 × 150μ	F6	sq. and trs.
644	f ∞	∞	few spots	White-grey	130-140μ	E6	trs.
645	f no.	∞	occ. patches	Wh.	ciliated trace of shell	D6	trs. and sl. spotty
77. DREDGED NOSS END, WEST MERSEA, JULY 12, 7.30-2 P.M.; EXAMINED JULY 12, 4 TO 7.30 P.M.							
646	f ∞	∞	none	Wh.	shells 150-150μ	E6	trs.
647	none	f no.	one spot	Wh.	32-celled	B4	trs.
648	none	f no. young	none	Wh.	7-8-celled	B3	trs.
649	none	few v. young	none	do.	16-20-celled	B3	trs.
650	f no.	∞	one spot	Gr.	160-170μ	E6	trs.
651	none	none	none	Sl.	180μ rela- tively few	F1or10	sq.
652	f no.	few only	none	Bl.	185μ	F7	sq.
653	v ∞	∞	none	Bl.	220 × 200μ	F6	sq. and trs. Note 16.
654	f ∞	v ∞	none	Wh.	16-celled	B6	trs. Note 17.
655	none	few	one patch	do.	do.	B4	trs.
656	do.	f no.	∞ scattered	do.	do.	B4	trs. spotty
657	∞	f ∞	none	Gr.	160μ	E6	trs. and sq.
658	∞	∞	none	Bl.	205μ	F6	sq.
659	∞	∞	none	do.	200μ	F6	sq.
660	∞	∞	none	do.	195μ	F6	sq. and trs.
661	a few	∞	a few	Sl.	180-190μ	F5	sq.
78. DREDGED THORNFLEET, WEST MERSEA, AUGUST 4, 7-7.30 A.M.; EXAMINED AUGUST 5, 4 P.M.							
662	∞	∞	none	Sl.		F6	sq. and trs.
663	f no.	f ∞	∞	Slate-grey	160-170μ	F6	sq. and trs. spotty Note 18.
664	f no.	∞	none	Grey-slate	170μ	F6	sq. and trs.
665	∞	∞	none	Wh.	shells 130μ	E6	trs.
79. DREDGED MYLOR BANK, FALMOUTH, AUGUST 10, 11 A.M. TO 2 P.M.; EXAMINED FOR SEX, 10.40 P.M., FOR DEVELOPMENT 7 P.M. AUGUST 10.							
666	f ∞	∞	none	Slate-black	190μ	F6	sq. and trs.
667	f ∞	∞	do.	Slate-grey	170-180μ	F6	do.
668	none	f ∞	none	Gr.	170-180μ	E4	do.

1	2	3	4	5	6	7	8
669	few	∞	none	Gr.	170μ	E5	sq. and trs.
670	few	few	none	Slate-grey	180μ	F5	do.
671	few	∞	none	do.	180μ	F5	trs.
672	f no.	∞	none	do.	170μ	F6	sq. and trs.
673	rare	∞	none	do.	160-170μ	F5	trs.
674	none	none	none	Wh.	4, a few 5-celled	A1	sq. and trs. inc. spent
675	none	occ. young	none	Wh.	4-celled	A3	sq. and trs.
676	rare	∞	none	Grey-white	ca 140μ	E5	sq. and trs.
677	none	∞	none	do.	ca 140μ	E4	d do.
678	none	few young?	∞ relict	Wh.	mainly un- segmented ca 10% 32-celled	B2	d do. and spotty
679	∞	∞	none	Gr.	ca 140μ	E6	d sq. and trs.

80. DREDGED EAST BANK, FALMOUTH, AUGUST 10, 9 TO 11 A.M.; EXAMINED FOR DEVELOPMENT 8.30 TO 9.5 P.M., AND FOR SEX 10.50 TO 11.45 P.M. AUGUST 10.

680	∞	f no.	none	Bl.	190μ	F6	sq. and trs.
681	∞	∞	do.	do.	do.	F6	trs.
682	few	few	few	do.	180-190μ	F6	sq. and trs. and spotty
683	∞	∞	none	Wh.	ciliated shell ca 40μ	E6	sq. and trs.
684	few	∞	few spots	do.	ciliated	D5	trs.
685	∞	∞	none	do.	ciliated trace of shell	D6	trs.
686	f ∞	∞	none	do.	ciliated no shell	D6	sq. and trs.
687	rare	f no.	none	do.	do.	D5	do.
688	∞	∞	do.	do.	ciliated shell ca 40μ	E6	trs.
689	none	none	∞ relict	do.	do. 60μ	E1	sq. and trs. Note 19.
690	none	none	few	Wh.	2-4-celled	A1	d sq. and trs. and spotty
691	f. no.	∞	none	Wh.	ciliated trace of shell	D6	d sq. and trs.
692	∞	rare	do.	Bl.	190μ	F7	d do. Note 19.
693	∞	f ∞	do.	do.	190-200μ	F6	d do.
694	f no.	∞	do.	do.	190μ	F6	d do.
695	∞	∞	do.	Sl.	170-180μ	F6	d do.

81. DREDGED THORNFLEET, WEST MERSEA, SEPTEMBER 1; EXAMINED SEPTEMBER 2, 12.30 P.M.

696	f no.	∞	none	White-grey shell	80-90μ	E6	sq.
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82a. DREDGED TURNAWARE BAR, FALMOUTH, SEPTEMBER 7, IN THE MORNING; EXAMINED SEPTEMBER 7, 7 P.M.

697	a few	∞	none	Gr.	shells ca 130μ	E5	sq. and trs.
698	none	∞	∞	do.	do. ca 60-70μ	E4	sq. and trs. and spotty

82b. DREDGED EAST BANK, FAL ESTUARY, SEPTEMBER 8, 12.30-3 P.M.; EXAMINED SEPTEMBER 8, 7-7.40 P.M.

699	none	v ∞	none	Gr.	150μ	E4	trs.
700	a few	∞	do.	Bl.	170-180μ	F5	trs.
701	none	a few	none	Gr.	150-160μ	E4	d sq. and trs. Note 20.

1	2			3			4			5			6			7	8
82c. DREDGED TURNAWARE BAR, FAL ESTUARY, SEPTEMBER 9, 7-8.30 A.M.; EXAMINED SEPTEMBER 9, 6.15 P.M.																	
702	f ∞	few	none	Purple-black	190-200μ	F7	sq. and trs.										
703	f ∞	fair no.	do.	Bl.	180μ	F6	trs.										
704	f ∞	fair no.	do.	Lilac-grey	160-170μ	F6	sq. and trs.										
705	f ∞	∞	do.	Sl.	170-180μ	F6	sq. and trs.										
82d. DREDGED TURNAWARE BAR, FAL ESTUARY, SEPTEMBER 15; EXAMINED SEPTEMBER 16, 7.20 P.M.																	
706	∞	a few	none	Bl.	190μ	F7	trs.										
707	none	few small	none	Wh.	ciliated no shell	D3	sq. and trs.										
82e. DREDGED TURNAWARE BAR, FAL ESTUARY, SEPTEMBER 21, 9.30-11.0 A.M.; EXAMINED 7.17 P.M.																	
708	few	f ∞	none	Gr.	170μ	E5	trs.										
709	none	one large, one small seen	none	Gr.	160-170μ	E4?	trs.										
82f. HAND-PICKED AT L.W., TURNAWARE BAR, FAL ESTUARY, SEPTEMBER 22, 12.30-1.30 P.M.; EXAMINED 7.30 P.M.																	
710	∞	∞	none	Bl.	180-200μ	F6	sq. and trs.										
82g. DREDGED TURNAWARE BAR, FAL ESTUARY, 1.30-3 P.M.; EXAMINED 4.45 P.M. OCTOBER 1.																	
711	f no.	f ∞	none	Gr.	160-170μ	E6	trs.										
82h. DREDGED FALMOUTH NORTH BANK, FAL ESTUARY, OCTOBER 7; EXAMINED OCTOBER 7, 1926.																	
712	f no.	∞	none	Bl.	180-190μ	F6	sq. and trs.										
83. HAULED IN CAGES, FAL ESTUARY, SEPTEMBER 29/26; EXAMINED SEPT. 29/26.																	
713	none	none	none	Bl.	190 × 170μ	F1-10?	trs.										
714	none	occ.?	none	Bl.	180-190μ	F1-10?	sq.										
715	∞	∞	∞ young?	Bl.		F6	sq. and trs.										

NOTES ON TABLE IV.

The same abbreviations are used as in Tables II and III. Abbreviations used specially in describing sperm and eggs are as follows:—

∞ = numerous; f ∞ = fairly numerous; f. no. or fair no. = fair number; occ. = occasional; N.O. = not observed macro- or microscopically; v. = very.

The figures 1, 2, 3, 4, 5, 6 = sex-categories given in Table II, p. 981.

Abbreviations used in describing the colour of embryos and larvae are:—

Wh. = white; Gr. = grey; Sl. = slate; Bl. = black.

The letters A, B, C, D, E, F denote the periods of development defined in Table III, p. 983.

Abbreviations used in describing the appearance of the gonad or tissues to the naked eye are:—
inc. sp. = incompletely spent, sl. curd. = slightly curdled in appearance with groups of unspawned ova.
spotty = gonad spotty in appearance, with patches of unspawned ova.

trs.=tissues soft with a general translucent appearance.

sq.=tissues opaque with a consistency approaching—but not quite so firm as—that of the mantle wall of a squid; hence the term "squiddy" or squid-like tissues.

sq. and trs.=tissues partly translucent and partly opaque as defined.

Abbreviations referring to the form of shell-growth are:—

N=normally- to well-grown shells.

d=dumpy or generally biconvex shells of stunted growth (see Orton, 1926).

sl. d.=slightly dumpy shells, or shells intermediate in growth characters between N and d.

L=length of shell in an antero-posterior direction.

D=depth of shell in a dorso-ventral direction.

sh=shoot, that is, the recent increment in growth in depth of the shell in the year of examination, measured in the median dorso-ventral line on the left valve.

REMARKS ON SPECIAL INDIVIDUAL RECORDS AND OTHER MATTERS IN TABLE IV.

Note 1. No. 69 is an example of the delay in sperm-production not infrequently associated with the retention of numbers of eggs in the gonad.

Note 2. In Groups 37 to 40, Nos. 105 to 136, and at other times, the relation of the colour of the digestive gland to the state of development of the embryos and the state of development of sperm-morulae was noted. It was found that in oysters carrying white embryos the frequency and occurrence of ripe-tailed sperm-morulae could be predicted with good accuracy from the colour of the digestive gland. See also records of the colour of this gland in numbers 765 to 795, Table IX, p. 1026.

The series of stages observed are as follows:—

	Digestive gland.	Embryos.	ripe sperm mor.	unripe sperm mor.
a. Ripe ♀.	chocolate-brown.	—	—	—
b. Just spawned ♀.	light do.	segn. to early blasto- pore stages.	none	a few
c. Do. later.	yellow-brown.	heart shaped embryos.	a few	∞
d. Still later.	yellow tinged with brown.	early shelled stage.	∞	∞
e. Late blacksick stage.	brown.	fully developed larvæ.	∞	∞
f. A few days after ex- truding larvæ.	choc.-brown.	—	∞	∞

This loss of colour in the digestive gland after spawning is probably due to a break in the active feeding habits of the animal. As "sick" oysters, especially whitesick ones, are well known to be weak, this weakness and the loss of colour in the liver are probably due to the same cause. The normal colour, chocolate-brown, is also lost at the approach of winter and may then become brick-red; in this case also the change in colour may be due solely to absence of active feeding (see Savage, 1925).

Note 3. Nos. 142 to 144 were examined for sex five days after the condition of the embryos were noted, therefore the gonad may be expected to show, as in No. 142, a state of development in advance of the average state associated with D embryos.

Note 4. In lots 47 and 50, one, two or three days elapsed between dredging and examining the samples. In such cases as these embryos and spent gonad may develop at slightly different rates, and the occurrence of low categories in period D in these samples might be due to a greater effect of exposure out of water on the adult than on the embryos.

Note 5. No. 239 is a rare case of absence of male elements in an oyster blacksick in the summer-time, namely, August 6.

Note 6. Lot 57, Nos. 397, 398, 399, 402, 410 are interesting in all showing unusual features with regard to sperm development in the month of September.

Note 7. Nos. 419, 420 and 422 show similar phenomena to those in Note 6.

Note 8. Nos. 431 to 438, found with spawn in October, 1925, are all peculiar and show a slowing down in sperm-production at this season of the year. This observation was confirmed in 1926 and may be important in its bearing on the conditions necessary for the proper development of maleness.

Note 9. No. 483 had very few larvæ which were obviously not fully developed. It was estimated that about 50,000 only were present in the mantle cavity: although it is probable that a large number may have been extruded, it is also possible that only a few eggs were spawned. As some ♂'s may function as females and extrude relatively few eggs, cases like this are worth recording.

- Note 10. Nos. 490 and 496 are additional cases of arrest of sperm-development correlated with incomplete egg-spawning.
- Note 11. No. 506 is interesting in carrying about 50% embryos advanced to the ciliated stage and 50% of unsegmented, and in this case almost certainly unfertilised eggs. Unfortunately no record was made of the nuclear condition of the eggs.
- Note 12. No. 510 was only $\frac{5}{8}$ spent, and again there is the correlation of few—or delay in production of—developing sperm. See also the following numbers 521, 522, 523 and 525, 626, 638.
- Note 13. No. 528 is a case where although the gonad was only $\frac{1}{2}$ spent yet sperm development is about normal.
- Note 14. No. 601 is an example of a gonad with relatively few developing sperm, but the sequence, few ripe—fair no. developing, is normal. See also Nos. 670 and 682.
- Note 15. No. 614 is interesting in proving that a heramphrodite-female individual can spawn as a female. In this case ripe sperm and ripe ova were found in the ducts and developing young sperm-morulae in the gonad.
- Note 16. No. 653 had remarkably large-shelled larvæ with shells 220μ long by 200μ deep.
- Note 17. No. 654 is strikingly an abnormal case where ripe sperm are developed to a fairly numerous condition with embryos only in the 16-celled stage, and with a gonad emptied of eggs. The simplest explanation of this case is that prior to spawning it was hermaphrodite, but left behind fully developed sperm, but no eggs on egg-spawning.
- Note 18. In No. 663 the sperm were found in a "squiddy" part of the gonad where there were no relict ova.
- Note 19. Nos. 689 and 692 are unusual and occurred, it is noteworthy, in August, 1926.
- Note 20. In Lot 82, samples dredged in September, 1926, again occur abnormal forms, namely: (1) blacksick individuals with ripe but few developing sperm, (2) blacksick individuals with no developing sperm, and (3) generally relatively little development of sperm in other late spawning individuals.
Two more blacksick individuals with no recognisable developing or developed sperm occur also in Lot 83 (September 29).

SECTION C. RESULTS OF EXAMINING THE GONAD IN 444 OYSTERS WHICH HAVE REARED AND EMITTED THEIR LARVÆ.

In addition to investigating the gonad of oysters which were actually carrying embryos or larvæ at the time of examination (see Table IV, pp. 999 to 1021), a large number of individuals have also been examined at various periods *after* they had extruded their young. In the latter cases the material was obtained experimentally by isolating in cages groups of individuals which had previously been found with embryos or larvæ in the mantle cavity. The detailed records of the examination of the material are given in Table IX, pp. 1025 to 1034, in a form exactly comparable with that of the "sick" individuals given in Table IV, p. 999. Table IX is summarised in Table X, which in turn provides the figures for the correlation table, Table XI, p. 1023, and for the graphs G, H, I, and J in Fig. 1, p. 991. In Table X, facing p. 1022, are given also the mean stage of development (now including waning) of the male phase, and the mean age of the gonad reckoned from the last egg-spawning. In defining the age of the post-"sick" gonad, the four periods given in the following table, Table VIII, are

recognised, and the notation is continued onwards from F, the final stage dealt with in Table VI, p. 985.

TABLE VIII.

DEFINITIONS OF PROGRESSIVE PERIODS OF AGE RECOGNISED IN THE EXAMINATION OF OYSTERS WHICH HAVE EXTRUDED LARVÆ.

Mean age of gonad* at each period.	Notation of progressive periods.	Range of period.
24 days	G	All individuals examined within 28 days after being observed "sick."
45.7 days	H	All individuals examined within 29 to 56 days after being observed "sick."
77.5 days	I	All individuals examined within 57 to 84 days after being observed "sick."
About 12 months	J	All individuals examined about 12 months after being observed "sick."

The results of the examination of these gonads can be discussed from a consideration of the summary given in Table X, opposite. From this table it is at once seen that the 50 per cent or more category of gonad lies in period G in VI; in H in VII; in I in VIII; and in J is contained in VII and VIII categories. There is thus a regular progression in the categories of the male phase in the periods G to I, which now include both waxing and waning phases of maleness. This progression is again reflected in the mean stage of development of maleness which from periods G to H increases through 6.39 to 8.2, but again falls to 7.43 in the J period. Table VI, p. 985, shows that the corresponding mean in the F period was 5.73. The increase in maleness developed in the gonad of oysters after spawning is therefore seen to be continued into our G period, that is, for about one month after spawning (mean age of gyn-spawned gonad=24 days); but thereafter the development of maleness wanes, since in the H period (one to two months after spawning) the categories VII and VIII become predominant. In these categories *developing* sperm become scarce in the former and are completely developed in the latter, which therefore marks the completion of the development of maleness. Category IX, which includes gonads with only a few ripe sperm, constitutes a definite stage in the decline of maleness which is completed in category X, in which the sex elements are in the primitive quiescent stage, that is, not developing. It may be remarked again that category X is the same as category I, but it is permissible in

* Reckoned from the average day when egg-spawning occurred.

TABLE X.
SUMMARY OF SEX-CATEGORIES 4 TO 10 (SEE TABLE II, P. 981), FOUND IN GONADS OF OYSTERS AT VARIOUS SUCCESSIVE PERIODS
AFTER THE EMISSION OF LARVÆ.

Group No. and No. examined in each group.	Date found with embryos or larvæ.	Date gonad examined.	Post-"sick" period in days unless stated in months.	Locality of origin of oysters.	Period J About 12 months after wintering after "sickness" in previous summer. Categories of gonad.																														Ripe ♀'s or ♀ functioning.
					Period G 0 to 28 days. Categories of gonad.						Period H 29 to 56 days. Categories of gonad.						Period I 57 to 84 days. Categories of gonad.																		
					4	5	6	7	8	9	10	5	6	7	8	9	10	5	6	7	8	9	10	4	5	6	7	8	9	10					
84. 1	1921, May 6	1921, July 7	62	Mylor Bank, Fal Estuary	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-					
85. 8	1922, June 8	1922, July 15	37	West Mersea	-	-	-	-	-	-	-	1	5	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
86. 4	" 23	" 15	22	Whitstable	-	-	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
87. 2	" 15	" 15	30	West Mersea	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
88. 4	" 16	" 15	29	Whitstable	-	-	-	-	-	-	-	1	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
89. 2	" 12	" 15	33	"	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
90. 2	" 8	" 15	37	"	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
91. 5	" 26	" 15	19	Falmouth	-	-	4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
92. 2	" 17	" 28	41	Helford	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
93. 6	" 20-2	" 28	36	Whitstable	-	-	-	-	-	-	-	3	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
94. 3	July 5	" 18	13	"	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
95. 3	" 11	" 18	7	"	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
96. 1	" 3	" 28	25	No. 19, West Mersea	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
97. 1	1923, June 19	1923, July 3	14	Helford	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
98. 1	July 18	Sept. 3	50	Whitstable	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
99. 2	" 25	" 3	42	"	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
100. 1	Aug. 7	Aug. 20	13	Yealm Cage	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
101. 13	1924, June end	July 3	ca. 7	West Mersea	-	-	12	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
102. 18	" end	" 4	ca. 7	"	-	-	14	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
103. 1	" 24	" 16	22	Yealm Cage	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
104. 26	" —	Aug. 25	> 56	West Mersea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	26	0	0	-	-	-	-	-						
105. 100	" —	" 28-9	> 59	"	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-						
106. 6	1922, June 28- July 7	1923, July 14	12 months	Cage Oysters, W. M.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	93	3	4	-	-	-	-	-			
107. 2	1923, July end	Oct. 20	> 81	" "	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	1	-	-	-	-	-			
108. 2	" "	1924, June 8	10½ months	" "	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-			
109. 1	June	" 24	12 "	" Yealm	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-			
110. 18	" "	July 1-8	11½ "	" W.M.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	4	3	0	1	4					
111. 38	1924, July 1-9	1925, July 13-15	12 "	" "	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	10	9	3	0	5					
112. 48	June 10- July 9	" 3-16	12-13 "	" "	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	13	21	3	5	3					
113. 25	1925, July 21	1926, July 3-7	12 "	" *	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11					
114. 58	1926, July 29	Sept. 29	63 days.	" (River), F. E.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	4	23	11	12	2					
115. 40	July 21	Sept. 30	72 "	" Pole Rocks, F. E.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	4	16	12	4	3					
444				Totals	0	2	36	10	1	1	0	0	3	16	10	0	0	0	3	8	164	26	21	0	1	24	28	34	6	7	29				
				Totals in each period	50						29						222 + 5♀ = 227						100 + 13♀ = 113												

* Fifty-seven oysters in this experiment, were not examined microscopically, therefore 14 ♂ individuals of this sample, which were examined microscopically, are not included in the totals for the J period.

TABLE XI

CORRELATION BETWEEN WAXING AND WANING OF MALENESS AND THE AGE OF THE POST-"SICK"
GONAD IN INDIVIDUALS WHICH HAVE EMITTED THEIR LARVÆ.

Mean age of gonad* at each period.	Progressive periods of age of post-"sick" gonad.	Numbers and percentages (in concave brackets) of progressive stages (I to X) of maleness in post-"sick" oysters.										Ripe ♀ or ♀ functioning.	Not observed.	Totals examined in each period.	Mean stage of development of maleness.
		I	II	III	IV	V	VI	VII	VIII	IX	X				
24 days	G	0	0	0	0	2 (4)	36 (72)	10 (20)	1 (2)	1 (2)	0	0	0	50	6.26
45.7 days	H	0	0	0	0	0	3 (10.4)	16 (55.2)	10 (34.5)	0	0	0	0	29	7.25
77.5 days	I	0	0	0	0	0	3 (1.35)	8 (3.61)	164 (73.9)	26 (11.7)	21 (9.46)	5	0	222+5	8.24†
ca. 12 months	J	0	0	0	0	1 (1)	24 (7) (24)	28 (4) (28)	34 (3) (34)	6 (0) (6)	7 (0) (7)	13 (11)‡	0 (57)‡	100+13 (82)‡	7.41§
Totals in each category		0	0	0	0	3	66	62	209	33	28	18+[11]		401+18	
Percentages	do.					(0.75)	(16.5)	(15.5)	(52.1)	(8.2)	(7)			[82]	

* Reckoned from the average date of the last act of spawning as a female.

† The mean stage of development of maleness in Period I gonads is calculated for the total number, male or neuter, that is, 222. If the five individuals found in a female condition or with larvæ be considered to have passed through stage X, the mean sex-condition for the whole sample becomes 8.28.

‡ Fourteen well-fished individuals in this sample were examined microscopically and are recorded in their categories in right-angled brackets, fifty-seven obviously indifferent males or neuter were not so examined, and eleven individuals were either ripe females or female-functioning forms, i.e. carrying embryos or larvæ at the time of examination.

§ In the J period the mean stage of development of maleness is calculated as in the I period. If the thirteen female-functioning individuals be considered to have passed through stage X, the mean stage works out at 7.71.

periods I and J to denote this stage by the figure X, rather than I, as a deduction from the general progression observed of the 50 or more per cent category throughout the series of periods A to J.

In period I it is interesting to note that ripe females begin to appear (see Table XI), and this reappearance of the female stage coincides with the attainment of category X (no sex elements developed) in a fair percentage of cases (9.46). It is therefore clear that from 2 to 3 months in the same summer, after spawning as a female, an oyster has completed, or is nearing completion of, its post-gyne-spawning male phase, and may have begun to change, or, indeed, may have completely changed its sex back again to female. In period J, 12 months after the previous female-spawning act, the results obtained are peculiar, but it may first be noted that the number of functioning females has increased on the period I, from 5 out of 227 to 24 out of 180 examined in their respective periods. Now the individuals in period J were mostly examined in the month of July (see Table IX, p. 1025), and since some of these individuals had already changed sex from male back again to female, it is fairly certain that—not only had some individuals changed back to female from male, but that—some had gone still further and changed back again to male. There is every probability that *some* of the individuals in period J with gonad categories V and VI had extruded a batch of larvæ within a few weeks or days prior to the examination, but there is also a strong probability that others of these categories, and particularly those individuals with gonad in category VII, have carried their male phase over the previous winter period into the following summer. At this point of the discussion it must be emphasised that the J period oysters on the whole were found in the first observed female-functioning stage (i.e. the first female-functioning stage, on which observations were made during the course of these experiments; but this female stage is not necessarily the first egg-bearing stage in the life-history of the individuals under observation) later on in the breeding season on the average than those in periods G to I. Since the records of the G to I individuals show that waning of maleness occurs on the average from 2 to 3 months after the onset of this sex-phase it is quite probable that individuals which spawn as females late in the season do not, or may not, complete the post-gyne-spawning male phase in the same summer, and may carry over to the next breeding season the completion of that male phase. The writer has little doubt that this does, in fact, occur.

TABLE IX

RECORDS OF THE INVESTIGATION OF THE GONAD, ETC., OF 444
OYSTERS EXAMINED AT VARIOUS PERIODS (see p. 1022) AFTER
EXTRUSION OF THE LARVÆ.

1 Serial No. of oyster.	Gonad.			Condition of		7 Period and category of gonad.	8 Remarks.
	2 Ripe sperm- morulæ.	3 Unripe sperm- morulæ.	4 Ripe ova left in gonad.	5 Gonoducts.	6 Fish.		
84. 1921. MYLOR BANK, WHITESICK, MAY 6/21; EXAMINED JULY 7/21.							
716	∞	f ∞	some	—	—	I6	
85. 1922. EXAMINATION OF OYSTERS, JULY 15-17/22; "SICK," JUNE-EARLY JULY /22; WEST MERSEA, "SICK," 8.6.22.							
717	∞	a few	none	full	f good	H7	
718	∞	none	do.	fairly full	poor	H8	
719	∞	few	do.	full	do.	H7	
720	∞	do.	do.	do.	do.	H7	
721	∞	none	do.	f full	do.	H8	
722	f ∞	f ∞	do.	empty ?	very poor	H6	
723	∞	rare	do.	a little sperm	fair	H7	
724	∞	fair no.	do.	full	fair	H7	
86. WHITSTABLE, "SICK," 23.6.22.							
725	∞	f ∞	none	f full	good	G6	
726	∞	none	do.	full	f good	G8	
727	∞	f ∞	do.	do.	do.	G6	
728	∞	rare	do.	do.	do.	G7	
87. 2 WEST MERSEA, "SICK," 15.6.22.							
729	∞	a few	do.	f full	poor	H7	
730	∞	rare	do.	do.	good	H7	
88. 4 WHITSTABLE "SICK," 16.6.22.							
731	∞	fair no.	none	full	poor	H7	
732	∞	∞	do.	full in parts	do.	H6	
733	∞	a few	do.	full on left side	f good	H7	
734	∞	none	do.	full milky	do.	H8	
89. 2 WHITSTABLE, "SICK," 12.6.22.							
735	f ∞	none	none	little on left	poor and watery	H8	
736	∞	occ.	do.	full	f good	H7	
90. 2 WHITSTABLE, "SICK," 8.6.22.							
737	∞	f ∞	none	full	poor, watery	H6	
738	∞	a few	do.	full	do.	H7	
91. 5 FALMOUTH, "WHITESICK," 26.6.22.							
739	∞	f ∞	none	nearly empty	poor, watery	G6	
740	f ∞	f ∞	do.	do.	fair	G6	
741	f ∞	f ∞	do.	a little	good	G6	
742	∞	fair no.	do.	ca. full	do.	G7	
743	∞	∞	do.	empty ?	f good	G6	
92. HELFORD OYSTERS "SICK," 17-22.6.22, EXAMINED 28.7.22.							
744	∞	rare	none	full	little, watery	H7	
745	∞	rare	do.	do.	do.	H7	

1	2	3	4	5	6	7	8
93. WHITSTABLE "SICK," 20-2.8.22; EXAMINED 28.7.22.							
746	∞	fair no.	∞ patches.	Little Blacksick, ∞ larvæ	poor	H(F)7	See Note 1, p. 1033, curdled
747	∞	rare	none	full	poor	H7	
748	∞	none	∞ deg.	full	full	H8 Inc. sp.	
749	∞	do.	none	full	N.O.	H8	
750	∞	none	none	full	N.O.	H8	
751	∞	a few	do.	do.	N.O.	H7	
OYSTERS EXAMINED JULY 18/22.							
94. 4 WHITSTABLE WHITESICK, 5.7.22.							
752	none	none	∞ ripe	full	full	ripe ♀	See Note 2
753	∞	f no.	none	nearly full	poor	G7	
754	∞	∞	do.	little	poor, watery	G6	
755	a few	f ∞	do.	empty?	fair	G5	
95. 3 WHITSTABLE WHITESICK, 11.7.22.							
756	∞	f ∞	none	full	poor, watery	G6	
757	∞	∞	do.	partly full	poor	G6	
758	rare	∞	do.	empty?	fair	G5	
96. No. 19 WEST MERSEA OYSTER, SPATTED SINCE JUNE, 1921, WHITESICK, 3.7.22.							
759	∞	fair no.	none	N.O.	N.O.	G7	
97. 1923. HELFORD RIVER OYSTER, WHITESICK, 19.6.23; EXAMINED 3.7.23.							
760	some	∞	N.O.	—	—	G6	
98. WHITSTABLE OYSTER, "SICK," 18.7.23, KEPT IN PLYMOUTH TANKS; EXAMINED 3.9.23.							
761	∞	none	none	—	—	H8	
99. WHITSTABLES "SICK," 25.7.23, KEPT IN TANKS; EXAMINED 3.9.23.							
762	∞	none	none	—	—	H8	
763	∞	do.	do.	—	—	H8	
100. YEALM CAGE OYSTER, SICK, 8.7.23; RE-EXAMINED BY BORING AFTER BEING IN SEA, 30.8.23.							
764	few	—	—	little	poor, watery	G9	
101. WEST MERSEA OYSTERS, BLACKSICK IN JUNE AND EARLY JULY; EXAMINED 3.7.24; THE FIRST 13 INDIVIDUALS WERE THE LAST TO BE ISOLATED, i.e. THEY WERE BLACKSICK AT THE END OF JUNE OR ON JULY 1 AND 2.							
							Colour of Digestive gland.
765	v ∞	f ∞	none	—		G6	chocolate, Note 3
766	∞	∞	do.	larvæ present	200 to 210μ	F6	reddish brown
767	v ∞	v ∞	do.	full ducts		G6	choc.-brown
768	v ∞	f ∞	none	full		G6	good chocolate
769	∞	few	do.	do.		G7	do.
770	∞	f ∞	do.	empty		G6	greeny-brown
771	∞	do.	do.	full		G6	good chocolate
772	∞	∞	do.	empty		G6	brown
773	∞	∞	do.	do.		G6	yellow-brown
774	∞	f ∞	do.	full		G6	greeny-brown
775	∞	∞	do.	do.		G6	choc.-brown
776	∞	f ∞	do.	±-full		G6	greeny-brown
777	∞	do.	do.	empty		G6	good chocolate

1	2	3	4	5	6	7	8
102. SAME SAMPLE, BLACKSICK IN JUNE; EXAMINED 4.7.24.							
778	∞	f ∞	few	little		G6	light brown
779	∞	∞	none	do.		G6	good chocolate
780	∞	∞	do.	fair		G6	do.
781	∞	∞	do.	empty		G6	do.
782	∞	f ∞	do.	full		G6	do.
783	∞	∞	do.	empty		G6	do.
784	∞	∞	do.	full		G6	do.
785	∞	fair no.	do.	fair amount		G7	do.
786	∞	do.	do.	full		G7	do.
787	f ∞	fair no.	do.	little		G7	light brown
788	∞	∞	do.	empty		G6	good chocolate
789	∞	∞	do.	f full		G6	do.
790	f ∞	fair no.	do.	do.		G7	do.
791	∞	f ∞	do.	full		G6	do.
792	∞	do.	do.	empty		G6	do.
793	∞	∞	do.	full		G6	do.
794	∞	f ∞	do.	empty		G6	do.
795	∞	∞	do.	full		G6	do.
103. YEALM CAGE OYSTER, "SICK," 24.6.24; EXAMINED 16.7.24.							
796	∞	few	rare			G7	
104. 26 WEST MERSEA OYSTERS, BLACKSICK JUNE-JULY, 1924; EXAMINED AT PLYMOUTH 21 AND 25.8.24.							
817	∞	none	none	21 full or nearly full		I8	See Note 3
822	∞	do.	do.	5 little to empty		I8	
105. 100 OYSTERS WHITESICK, WEST MERSEA, JUNE-JULY, 1924; EXAMINED AT PLYMOUTH 28-29.8.24.							
832	∞	none	some degenerating	10 individuals		I8	Digestive gland. mostly very light fawny colour*
835	few	none	do.	3 do.		I9	do
918	∞	none	none	83 do.		I8	do.
920	none	none	some degenerating	2 do.		I10	do.
922	none	none	none	2 do.		I10	do.
106. OYSTERS FOUND WITH LARVÆ, JUNE 28-JULY 7, 1922, AT WEST MERSEA; EXAMINED JULY 14, 1923. (KEPT IN EXPERIMENTAL CAGE).							
923	not observed			Grey embryos			hell growth in 1923. 12 Note 4
924	∞	few	none	ducts full		J7	6
925	∞	∞	do.	do.		J6	6
926	fair no.	none	do.			J9	nil
927	do.	rare	do.		poor	J7	8
928	∞	few	do.		good	J7	7-9
107. FOUND WITH LARVÆ OR EMBRYOS, END OF JULY, 1923 (PUT IN EXPERIMENTAL CAGE); EXAMINED OCT. 12, 1923 (2-3 MONTHS AFTER SICKNESS).							
929	none	none	none	gaping		I10	
930	∞	?	none	do.		I8	

* K. and V. 128 D.

1	2	3	4	5	6	7	8
108. SAME SAMPLE, EXAMINED JUNE 8, 1924.							
931	none	none	none	gaping	poor	J10	—
932	∞	∞ nearly ripe	do.	do.	f good	J6	—

109. YEALM CAGE OYSTER, "SICK," JUNE, 1923; PUT IN CAGE IN SEA; EXAMINED 24.6.24.

933	∞	very few rare small relict	—	—	—	J7	—
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110. SAME SAMPLE EXAMINED JULY 1 TO JULY 8, 1924.

							Shell growth in 1924.	
934	∞	none	none		f good	J8	sl. d	
935	—	—	—	Whitesick	—	—	7-12, Note 5	
936	∞	few	none	Blacksick?	—	(J7)	10-11	
937	none	none	∞ripe	ripe ♀			5-10	
938	∞	f ∞	none		good, fat	J6	nil d	
939	∞	∞	do.		good	J6	5-11	
940	∞	none	do.		do.	J8	5-6	
941	∞	∞	do.		f g	J6	1-6	
942	∞	few	do.	ducts full on left	do.	J7	6-12	
943	none	∞	few	Whitesick	fair	B4	10-5	
944	∞	f ∞	none	little in ducts	f g	J6	3-4?	
945	none	none	none	empty do.	f	J10	3-9?	
946	∞	rare	do.	do. do.	f g	J7	?	
947	∞	∞	do.	little in do.	f g	J6		
948	∞	∞	none	ducts empty	good	J6	3-13	
949	∞	few	∞ ripe degenerating?	do. do.	very good	J7	3-10	
950	∞	none	do.	do. a little	do.	J8	3-12	
951	∞	few	∞	empty	do.	J7	5-13	

111. INDIVIDUALS FOUND BLACKSICK, JULY 1 TO 9, 1924, AT WEST MERSEA; PUT IN EXPERIMENTAL CAGE; EXAMINED JULY 13-15, 1925.

JULY 13, 5 WEAK INDIVIDUALS EXAMINED.

952	∞	none	none		fair	J8	8
953	∞	do.	do.		do.	J8	8
954	∞	do.	do.		good	J8	9
955	few	f no. v young	few	Whitesick	poor	C4*	15 Note 6

956	∞	few	none	—	fair	J7	L. 68	Br. 75	Sh. 13
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JULY 14.

957	∞	f ∞	do.	full	do.	J6	68	78	5	sl. d
958	∞	f ∞	do.	f full	do.	J6	60	61	5	sl. d
959	f ∞	∞	do.	Blacksick	do.	F6	65	67	9	
960	∞	none	none	—	poor	J8	55	65	10	
961	∞	fair no.	do.	f full	do.	J7	67	68	16	
962	∞	few	do.	do.	good	J7	67	67	5	sl. d
963	∞	f ∞	do.	—	do.	J6	70	75	7	
964	∞	f ∞	do.	f full	do.	J6	71	73	12	
965	∞	rare	do.	empty	fair	J7	72	73	11	
966	v ∞	rare	do.	—	do.	J7	79	86	5	
967	v ∞	none	do.	f full	poor	J8	65	70	10	
968	∞	rare	do.	little	fair	J7	66	67	15	
969	∞	f ∞	do.	—	good	J6	73	69	8	thin sl. d
970	∞	f ∞	do.	—	fair	J6	64	62	11	

1	2	3	4	5	6	7	8	
971	∞	f ∞	none	full	do.	J6	68	67 13
972	∞	∞	do.	full on left	do.	J6	65	62 10
973	∞	rare	do.	f, do.	poor	J7	72	72 12
974	none	none	∞ ripe	ripe ♀ full	v g	J7	72	78 15
975	∞	few	none	f full	f g	J7	67	71 12
976	none	f ∞	none	Whitesick	f	C4	72	68 11
977	∞	rare	none	f full	g	J7	79	75 13
978	∞	none	∞ relict	— curdley	v g	J8	81	82 10
979	none	∞ to 35μ	few	Whitesick	poor	C3	76	69 15

JULY 15.

980	∞	∞	none	—	poor	J6	80	89 10
981	few	none	none	—	poor	J9	79	82 20
982	f ∞	f ∞	do.	—	f	J6	84	70 11
983	∞	none	do.	—	f g	J8	72	79 11
984	f ∞	none	do.	—	f g	J8	62	65 11
985	∞	rare	do.	—	poor	J7	61	60 11
986	few	none	do.	empty	good	J9	60	61 5 d
987	∞	∞	do.	f full	f	J6	78	82 12
988	rare	none	do.	empty	f	J9	71	66 11
989	∞	none	do.	full	f	J8	68	72 10

112. OYSTERS WHITESICK JUNE 10 TO JULY 9, 1924, PUT IN SEA IN CAGE IN DEEPS, WEST MERSEA, JULY 9, 1924; EXAMINED JULY 3-16, 1925.

JULY 3, 1925, 5 WEAK INDIVIDUALS.

990	∞	none	none		poor, watery	J8		7
991	none	do.	do.		do.	J10		11
992	few	few	do.		poor	J7		14
993	∞	do.	do.		fair	J7		9
994	∞	∞	do.	Blacksick	poor	F6	8	Note 7

JULY 14.

995	occ.	f ∞ to 60μ	few patches	Whitesick	fair	C5	68	71 15
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JULY 15.

996	none	∞	do.	Whitesick	poor	C4	60	65 13
997	∞	none	none		f	J8	60	68 10
998	none	none	∞ patches relict		good	J10	58	66 10
999	∞	none	none		f	J8	62	65 10
1000	f ∞	do.	do.		f	J8	70	66 15
1001	f ∞	none	∞ degen.	curdled	—	J8	70	69 15
1002	∞	f ∞	none		f	J6	57	60 8
1003	∞	none	none	—	f	J8	65	72 10
1004	∞	none	do.	full	f	J8	60	63 8
1005	∞	do.	do.	little	g	J8	55	64 10
1006	∞	do.	do.	do.	poor	J8	60	63 16
1007	∞	few	do.	do.	g	J7	67	70 5
1008	v ∞	none	∞ relict	curdled	v g	J8	59	64 12
1009	few	none	none	empty	f	J9	63	72 9
1010	∞	few	do.		f	J7	68	73 14
1011	∞	none	do.		g	J8	73	74 10
1012	none	none	∞ relict	curdled gonad	f	J10	67	68 9
1013	few	none	big patches relict	do.	g	J9	62	65 6
1014	∞	fair no.	none		g	J7	64	82 18
1015	∞	few	do.		f	J7	65	69 7
1016	fair no.	fair no.	do.		g	J7	70	77 8
1017	few	none	do.		f	J9	94	80 10
1018	∞	few	do.		v g	J7	50	60 8 d

1	2	3	4	5	6	7	8
1019	∞	none	none		g	J8	60 60 5 thin
1020	f ∞	few	do.		f	J7	63 63 4
1021	∞	none	do.		p	J8	60 65 14
1022	∞	rare	do.		g	J7	62 69 6
1023	∞	none	do.		g	J8	60 71 12
1024	f ∞	none	do.		f	J8	68 68 12
1025	∞	none	do.		f	J8	59 68 6
1026	f ∞	f ∞	do.		p	J6	54 60 16 sl. d
1027	∞	none	do.		—	J8	65 68 15

JULY 16.

1028	∞	a few	do.		p	J7	65 67 14
1029	∞	none	do.		p	J8	58 62 7
1030	f ∞	none	do.		p	J8	66 66 9
1031	∞	none	do.		r	J8	59 63 8
1032	∞	f ∞	do.		f	J6	67 68 17
1033	none	none	fair no. relict in big patch	curdley	f	J10	53 63 4-15
1034	none	none	none		p	J10	60 65 11
1035	∞	none	do.		f	J8	61 69 14
1036	∞	few	do.		f	J7	67 65 9
1037	∞	occ.	do.		f	J7	53 66 9

113A. WEST MERSEA, INDIVIDUALS BLACKSICK IN JULY, 1925, PUT IN SEA IN CAGE IN DEEPS, JULY 21, 1925; EXAMINED JULY 3, 1926.

1038	∞	f ∞	none		f g	J6	86 87 10
1039	∞	∞	none		g	J6	69 63 9
1040	∞	∞	do.		g	J6	84 82 9
1041	f ∞	none	∞ ripe	Ripe ♀♀	v g	J6	77 71 0 Note 8
1042	f ∞	f ∞	none		f g	J6	64 65 5
1043	v ∞	f ∞	do.		g	J6	79 85 5
1044	v ∞	few	do.		v g	J7	68 74 5
1045	v ∞	fair no.	few relict?		J7	J7	57 65 8
1046	none	none	∞ ripe	ripe ♀	f g	J7	72 75 10
1047	v ∞	few	none		f	J7	53 54 0
1048	∞	none	none		f g	J8	80 78 3

Seventeen individuals, determined as obviously males by the naked eye, were not examined microscopically.

113B. WEST MERSEA OYSTERS FOUND WHITESICK IN JULY, 1925, PUT IN SEA IN CAGE IN DEEPS, WEST MERSEA, JULY 21, 1925, AND EXAMINED JULY 7, 1926, FOR SIGNS OF FEMALENESS.

1049	none	none	∞ ripe	ripe ♀	f g		68 67 16
1050	none	none	few patches	Whitesick	poor	C1	69 72 10
1051	none	none	∞ ripe	ripe ♀	v g		67 67 12
1052	none	none	∞ nearly ripe	ripening ♀	f g		74 67 10
1053	few	∞	one patch	Greysick	f g	E5	71 69 12
1054	∞	none	none	—	v g	J8	56 57 4
1055	∞	few	none	—	g	J7	67 65 5
1056	∞	f ∞	none		v g	J6	73 71 10
1057	∞	none	fair no. relict?		v g	J8	80 76 14
1058	fair no.	∞	occ. patches	Whitesick	f	C5	68 68 6
1059	fair no.	none	∞ ripe	♂ ♀ ♀	v g		61 67 14

Thirty individuals, obviously male to the naked eye, were not examined microscopically.

13c. FALMOUTH OYSTERS BLACKSICK IN JULY, 1925, PUT IN SEA IN CAGE IN DEEPS,
WEST MERSEA, JULY 21, 1925; EXAMINED JULY 3, 1926.

1	2	3	4	5	6	7	8
1060	∞	f ∞	none		v g	J6	66 66 10
1061	f ∞	none	∞ ripe	♂ ♀ ripe	v g		60 64 13

Five other individuals, obviously male to the naked eye, not examined microscopically.

113b. FALMOUTH OYSTERS WHITESICK IN JULY, 1925, PUT IN SEA IN CAGE IN DEEPS,
WEST MERSEA, JULY 21, 1925; EXAMINED JULY 3, 1926.

1062	none	none	∞ ripe	ripe ♀	v g		68 69 17
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Five other individuals, obviously male to the naked eye, were not examined microscopically.

POST-SPAWNED OYSTERS.

114A. OYSTERS BLACK- OR GREY- "SICK" JULY 29/26 KEPT IN RIVER CAGE,
TRELISSICK REACH, FAL ESTUARY; HAULED AND EXAMINED ON SEPT. 29/26.

						L.	Br.	Sh.
1063	v ∞	none	few relict	GD ram B		I8	72	79 8
1064	f ∞	none	none	GD ram A		I8	82	78 3
1065	∞	do.	do.	ff ♂ A		I8	59	63 7
1066	∞	do.	do.	GD ram B		I8	60	52 8
1067	none	none	none	do.		I10	61	62 4
1068	do.	do.	do.	do.		I10	59	67 8
1069	do.	do.	∞ deg.	do.	gonad spotty	I10	63	62 9
1070	∞	do.	none	GD st. to ram B		I8	61	63 8
1071	few	do.	do.	sq. and trs.		I9	66	61 10
1072	none	none	none	GD ram B to ff ♂ B		I10	60	64 6
1073	f ∞	do.	do.	ram B		I8	69	72 11
1074	∞	do.	do.	st. B—ram B		I8	62	59 8
1075	f ∞	do.	some young?	st. A		I8	63	65 11
1076	v ∞	do.	do.	do.		I8	72	79 6
1077	v ∞	do.	none	ram B—f trs.		I8	59	62 6
1078	∞	do.	do.	st. B—f trs.		I8	75	71 9-22
1079	lost			ram B—st. A		—	62	60 9
1080	none	none	none	ram B—ff ♂ B		I10	65	65 3
1081	do.	do.	do.	ram B—ff ♂ B		I10	74	74 11-25
1082	rare	do.	do.	st. A		I9	67	70 13
1083	do.	do.	do.	st. B—ram B		I9	78	75 14
1084	fair no.	do.	do.	sq. & trs.—st. B		I9	69	78 6
1085	few	do.	do.	ram B		I9	61	66 9
1086	f ∞	do.	do.	ram B—ff ♂ B		I8	75	76 7
1087	∞	do.	do.	do.		I8	65	66 8
1088	v ∞	do.	do.	ram B		I8	61	62 12?
1089	none	none	none	Blacksick ram B & trs. ∞ embryos 190 × 170μ		F1-10	62	63 6
								See note 9.
1090	do.	do.	do.	ram B		I10	59	59 6
1091	do.	do.	do.	ram B—ff ♂ B		I10	72	75 8
1092	do.	do.	do.	do.		I10	57	59 6
1093	∞	do.	do.	st. A. g.w.d.		I8	60	65 5 sl. d
1094	none	none	none	sq. & trs., blood cells v ∞		I10	55	61 3
1095	a few	do.	do.	ram B		I9	65	64 2-10
1096		not observed		poor watery, chambered		—	56	53 nil
1097	f ∞	none	none	ram B		I8	70	72 nil
1098	rare	none	none	ram B (sq. & trs.)		I9	57	61 7

1	2		3	4	5		6	7	8			
1099	v ∞	few	none	none	ff ♂ B			I7	64	65	3-8	
1100	few	none	do.	do.	ram B (sq. & trs.)			I9	68	60	4-11	
1101	∞	do.	do.	do.	blood cells v ∞ sq. & trs. (big green cyst)			I8	68	74	12	
1102	fair no.	do.	do.	do.	ram B—st. B			I9	60	71	6-14	
1103	v ∞	odd ones	do.	do.	st. A			I7	62	65	nil	
1104	v ∞	none	do.	do.	ff ♂—sq. ♂			I8	59	61	6-12	d
1105	v ∞	do.	do.	do.	st. A V.G. fish			I8	54	60	2	d
1106	none	none	do.	do.	do. blood cells v ∞			I10	52	67	7	d
1107	f ∞	do.	do.	do.	do. & sq. & trs. V.G. fish blood cells v ∞			I8	54	65	5	d
1108	few	do.	do.	do.	sq. & trs. to sq. ♂			I9	55	65	8	d
1109	v ∞	do.	do.	do.	ff ♂ B & sq. & trs., blood cells v ∞			I8	60	67	2	d
1110	v ∞	do.	do.	do.	sq. ♂ to sq. & trs.			I8	51	60	nil	d
1111	rare?	do.	do.	do.	sq. & trs. to ram B, big granular cells v ∞			I9	46	55	3	d
1112	∞	none	none	none	ram B to st. A blood cells ∞			I8	54	61	3	d
1113	none	occ. ?	none	none	Blacksick sq. ♂ larvæ 180-190μ f ∞			—	52	64	6	d
1114	v ∞	none	none	none	st. A in parts			I8	59	71	0	d
1115	∞	do.	do.	do.	st. B—ram B			I8	55	58	0	d
1116	∞	fair no.	do.	do.	st. A, B, and sq. & trs., blood cells ∞			I7	55	57	6	d
1117	∞	none	none	none	sq. & trs., blood cells ∞			I8	54	62	4	d
1118	none	none	none	none	ram B, new chamber ∞ big granular cells, blood cells ∞			I10	57	63	2	d
1119	v ∞	do.	do.	do.	ff ♂ B			I8	55	63	3	d
1120	v ∞	do.	do.	do.	ff ♂ B—ram B			I8	56	60	3	d

Two normal and one dump dead.

114b. OYSTERS FROM RIVER FAL, TRELISSICK REACH CAGE, WHITESICK JULY 29/26;
EXAMINED SEPT. 29/26.

1121	∞	fair no.	none	sq. & trs.—ram B			I7	59	66	8	sl. d
1122	∞	∞	none	ram B, V.G. fish			I6	61	68	10	d

115a. OYSTERS FROM THE CAGE MOORED TO POLE'S ROCKS, FAL ESTUARY,
BLACKSICK JULY 21, 1926; EXAMINED SEPT. 30, 1926.

1123	few	none	none	ram B			I9	61	58	?
1124	v ∞	do.	do.	st. A			I8	65	61	2
1125	v ∞	do.	do.	do.			I8	60	65	0-2
1126	∞	fair no.	do.	do.			I7	59	62	nil
1127	∞	none	do.	ram B			I8	70	65	0-3
1128	∞	do.	do.	st. B			I8	62	65	0
1129	v ∞	do.	do.	ff ♂ B			I8	69	70	0
1130	rare	do.	do.	ram B			I9	61	65	0
1131	∞ ducts full	f ∞	do.	ff ♂ B—ram B			I6	60	70	0

1	2 3 4			5 6		7	8		
1132	fair no.	none	∞ young	st. A		I9	57	60	0
									See note 10
1133	∞	do.	none	ram B		I8	63	61	4
1134	∞	do.	few relict	ram A		I8	63	63	0 sl. d
1135	few	none	none	? trs.—st. B		I9	60	55	0
1136	∞	∞	∞ young?	SLATESICK sq. & trs.—st. B embryos f ∞ 170-180μ		F6	86	80	0
									See note 11
1137	none	none	none	st. B		I10	60	57	0
1138	not observed (preserved)			WHITESICK, sl. sq. & trs. embryos only f ∞ heart shaped not ciliated		C?	56	60	0 sl. d
1139	fair no.	none	none	sq. & trs. ∞ big granular cells		I9	58	57	0
1140	v ∞	few	do.	ff ♂ B—sq. & trs.		I7	50	59	0 sl. d
1141	∞	none	do.	st. B—ram B		I8	62	60	0
1142	v ∞	few	do.	ff ♂ B—sq. & trs.		I7	47	62	0 d
1143	few	none	do.	st. A & sq. & trs.		I9	52	58	0 d.
1144	∞	do.	do.	do.		I8	61	66	0 d
1145	fair no.	do.	do.	sq. & trs.		I9	51	59	0 d
1146	do.	do.	fair no. young?	do.		I9	54	59	3? d.
1147	few	do.	some young?	sq. ♂ & st. A		I9	59	77	0 d
									three others dead

115B. OYSTERS FROM CAGE MOORED TO POLE'S ROCKS, FAL ESTUARY,
WHITESICK JULY 21, 1926; EXAMINED SEPT. 30, 1926.

1148	∞	none	none	ram B		I8	63	70	3
1149	v ∞	do.	do.	do.		I8	62	67	0
1150	v ∞	do.	do.	st. B		I8	57	61	0
1151	∞	do.	do.	ram B		I8	53	56	6
1152	none	none	none	st. B		I10	62	59	0-3
1153	few	do.	do.	ram B		I9	70	68	0
1154	none	none	∞ young?	st. B—ram B		I10	67	65	5
1155	few	none	none	ram B		I9	59	58	4
1156	none	none	none	do.		I10	66	62	3
1157	∞	do.	do.	do. V.G. fish		I8	68	73	6
1158	∞ in ducts	do.	do.	ff ♂ B		I8	75	87	0
1159	v ∞	do.	some relict	ram A probably incompletely spent		I8	69	73	0
1160	v ∞	fair no.	none	sq. & trs.		I7	54	73	3 d
1161	v ∞	none	none	do.		I8	47	58	2 d
1162	few	do.	do.	do.		I9	45	48	0 d
									none dead

NOTES ON TABLE IX.

The abbreviations used are the same as those employed in Tables II, IV and VII, those employed in lots 114 and 115 will be described in Part II of the paper when this is published later.

- Note 1. No. 746, found blacksick 36 days after previously being found sick, is best considered as an individual which has retained its larvæ unusually long, although it is possible that an incomplete spawning may have been followed at some later period by a more complete—but as the records show still incomplete—spawning.
- Note 2. No. 752 is an example of an oyster which has spawned only very slightly, and retained most of its ova even a fortnight after its incomplete spawning. Such cases do not occur frequently, but it is possible in some circumstances that they may interfere with experimental results, unless care be taken to choose those individuals which extrude masses of spawn and to record the numbers of individuals dealt with.

- Note 3. Lot 101 of individuals recently found blacksick, were kept for a few days in an oyster pit—covered or freshened at most high tides—until examined. Lots 104 and 105 were portions of the same sample taken to Plymouth from the West Mersea oyster beds and examined at Plymouth. Lot 104, examined at Plymouth, Aug. 21 to 25, had fawny and pale fawny coloured digestive gland (about 137 Klincksieck et Valette, Codes des Couleurs). Lot 105, examined Aug. 28-29, had rather paler digestive glands (ca. 128 D, K. et V.). Both 104 and 105 lots had probably fed little after leaving Mersea at the end of July, and possibly Stage VII of maleness had been hastened for this reason. The gonads of these lots are, however, similar to lots 114 and 115, when one takes into consideration the fact that the Mersea individuals had spawned earlier in the season than the Falmouth samples. It is an interesting fact that very few of these previously blacksick individuals had unspawned eggs left in the gonad at the time of examination; a circumstance which indicates that unspawned ova may normally be extruded later through the gonadial aperture.
- Note 4. No. 923 is an individual which carried larvæ in 1922 and spawned as a female again in 1923.
- Note 5. Nos. 935 to 937 and 943 are individuals found with larvæ in 1923 and again found ♀ or ♀-functioning in 1924.
- Note 6. Nos. 955, 959, 974, 976, 979 were found blacksick in 1924 and again found ♀ or ♀-functioning in 1925.
- Note 7. Nos. 994, 995, 996 were found whitesick in 1924 and again found ♀ or ♀-functioning in 1925.
- Note 8. Nos. 1041, 1059 and 1061 were found respectively black- and whitesick in July, 1925, and again hermaphrodite female in 1926. Other sick individuals in 1925 again found ♀ or ♀-functioning in 1926 are 1046, 1049 to 1053, 1058 and 1062.
- Note 9. No. 1089 and 1113 were found with shelled larvæ on July 29, 1926, and again after being in the sea until Sept. 29, 1926, were found carrying shelled larvæ. Presumably these two individuals had spawned twice in the same season, especially as their larvæ were normal or not quite full-sized. The gonads of these two individuals are characteristic for the time of the year.
- Note 10. No. 1132 is an individual found blacksick, July 21, 1926, and now in male-phase No. IX, but beginning to develop femaleness. If this individual retains its ripe sperm-morulae during the period of egg-development it will become one of the mixed sexes.
- Note 11. Nos. 1136 and 1138 were found with shelled larvæ, July 21, 1926, and again found, respectively, slate- and whitesick on Sept. 30, 1926, and have both, therefore, had two batches of larvæ in the same year. The whitesick individual is especially interesting, as it can only have spawned a few days before being examined.

GENERAL REVIEW OF THE COURSE OF THE MALE PHASE FOLLOWING EGG-SPAWNING.

It is now possible to review all the changes observed in the gonad of oysters after such individuals have spawned as females. For convenience the records of the whole of the individuals examined are brought together in one comprehensive table, Table XII, given on p. 1035. From this table it is possible to follow easily the rapid development of maleness in periods A to F and its subsequent slowing down in periods G to I, with the recurrence of femaleness in the period I and the greater development of femaleness—some of which, however, may have passed undetected—in period J. Ripe sperm are produced in such oysters commonly within about $3\frac{1}{2}$ days after the female-spawning, and the whole of the sperm becomes ripe within about 2 months from the time of female-spawning, if so long a summer period remains in the same summer in which the female-spawning act occurs. There is a strong probability that if an oyster spawns late in the breeding season, the developmental period

TABLE XII.

CORRELATION BETWEEN PROGRESSIVE MALE PHASES AND AGE OF GONAD OBSERVED AFTER AND RECKONED FROM THE DATE OYSTERS SPAWNED AS FEMALES.

Mean age* of gonad at each period.	Progressive periods of age of gonad.	Numbers and percentages (in brackets) of progressive male phases (categories I to X) in each period.										Ripe ♀s or ♀- functioning individuals.	Total examined in each period.	Mean stage of develop- ment of maleness.
		I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX	X			
2¼ hours	A	5 (20.9)	2 (16.6)	12 (50)	5 (20.9)	0	0	0	0	0	0	—	24	2.71
14 hours	B	1 (1.97)	4 (7.85)	25 (49.1)	19 (37.3)	1 (1.97)	1 (1.97)	0	0	0	0	—	51	3.26
45 hours	C	1 (0.77)	1 (0.77)	26 (20.1)	83 (63.9)	14 (10.8)	5 (3.85)	0	0	0	0	—	130	3.95
3½ days	D	0	1 (0.9)	12 (10.9)	39 (35.2)	33 (29.8)	26 (23.5)	0	0	0	0	—	111	4.65
4½ days	E	1 (0.77)	0	3 (2.31)	25 (19.3)	27 (20.8)	74 (57.1)	0	0	0	0	—	130	5.31
8½ days	F	8 (3.12)	0	0	6 (2.34)	31 (12.1)	197 (76.9)	11 (4.29)	3 (1.17)	0	0	—	256	5.73
24 days	G	0	0	0	0	2 (4)	36 (72)	10 (20)	1 (2)	1 (2)	0	0	50	6.26
45.7 days	H	0	0	0	0	0	3 (10.4)	16 (55.2)	10 (34.5)	0	0	0	29	7.25
77.5 days	I	0	0	0	0	0	3 (1.35)	8 (3.61)	164 (73.9)	26 (11.7)	21 (9.46)	5	222+5	8.24
About 12 months	J	0	0	0	0	1 (1)	24 (24)	28 (28)	34 (34)	6 (6)	7 (7)	13	100+13	7.41
Total no. in each category		16	8	78	177	109	369	73	212	33	28	18	1121	
Total per cent	do.	(1.43)	(0.71)	(6.97)	(15.8)	(9.74)	(32.9)	(6.52)	(18.9)	(2.95)	(2.51)	(1.61)		

* Reckoned from the act of egg-spawning

of maleness will be carried over the ensuing winter period and attain completion only in the following breeding season. After the attainment of a well-defined male phase with fairly abundant ripe sperm some individuals pass into a neuter sex condition in the same season in which the female and male phases have been brought to fruition. In a small number of cases a second female condition in one and the same breeding season appears to have occurred (see period J, Tables XI and XII), but such cases will be examined more closely later. The phases which follow the neuter stage up to the attainment of the ripe female condition have been the subject of a special research, which it is hoped will be completed in the near future. There can be no doubt, however, that a significant number of individuals complete the male phase in the same summer as they have spawned as females, and reattain the state of functioning females at the beginning of the following breeding season, as shown by the results obtained in period J, Tables XI and XII.

THE DURATION OF THE MALE PHASE FOLLOWING EGG-SPAWNING.

The rate of development of maleness in oysters which are still carrying embryos or larvæ has been shown graphically in Fig. 1, p. 991, to be very rapid. With the additional data given in Table XI, p. 1023, it is possible to construct a graph which will show clearly the information obtained on the duration of the male phase, and at the same time be helpful in discussing various aspects of the phase. The graph given in Fig. 3, p. 1037, is constructed from the data given in Table XII on the mean stage of maleness for each age-period, and the mean age of the gonad—reckoned from the date of egg-spawning—in each period. An obvious defect brought out by the graph is the absence of observations intermediate between the points I and J. It will be possible to fill in observations in the gaps in the future, and in the meantime it may be anticipated that, on most oyster beds, there is a general cessation of gonadial metabolism (that is, in so far as oogonia and spermatogonia are concerned) during a large portion of the winter period. Definite facts are required to substantiate statements of this kind, and an effort is being made to obtain them. Although there are indications of a minimum of gonad activity in the mid-winter period, there is unquestionably in a large number of cases a long preparatory period of storage of reserve products and early development of the gonad in the autumn, and no doubt continued in the early spring. Definite data to support the statement with regard to gonad development in the autumn can be given. It may therefore be expected that the curve in Fig. 3 will remain fairly flat from the point I onwards. Under ideal conditions it would

seem that the curve would maintain its general direction and gradually approach the level of sex-stage X until it finally reaches this figure in a period of about 12 months, as is indicated by the light discontinuous line continuing the curve from I. It has already been noted that the apparent regression of the curve between I and J may be accounted for by

(1) the J experimental individuals retaining undeveloped maleness through the winter, owing to being on the whole later spawners than

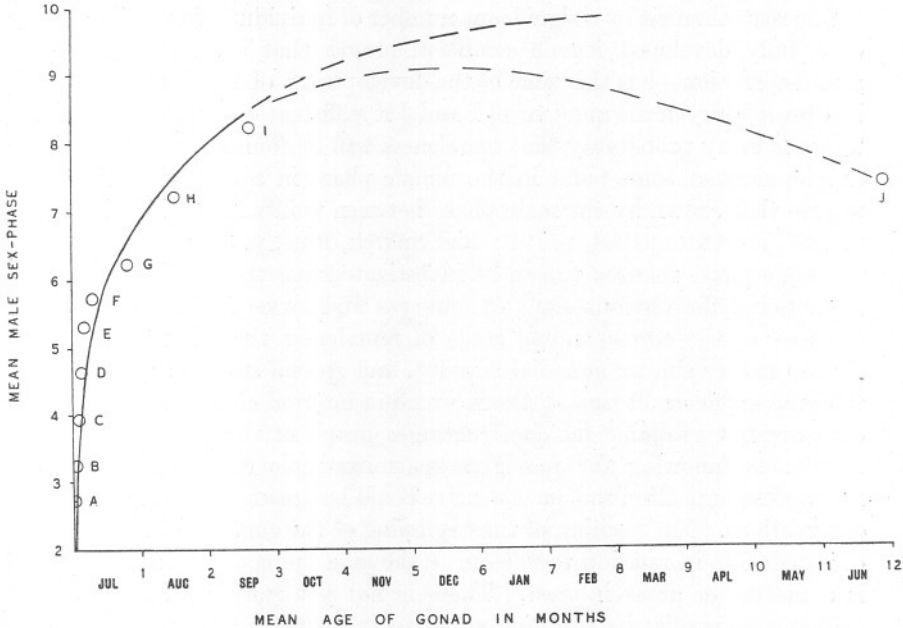


FIG. 3.—Graph showing the rate of development and course of the male sex-phase following egg-spawning in 1,123 individuals of *O. edulis*. (The months of the year apply approximately only, and are inserted to show the general decline of the male-phase towards the approach of winter.)

No observations have yet been made in the period elapsing between I and J; the upper dotted line indicates the continuation of the curve and the probable normal waning of maleness in individuals which spawn early in the preceding breeding season. The lower dotted curve joining I to J gives the mean course of the male sex-phases in a number of individuals which includes some which have already changed back again to the female sex-phase, and probably includes some also which have passed on to a second post-egg-spawning male phase in the period of the observations.

individuals in periods A to H, with a recrudescence of developing maleness occurring in the following summer; and

(2) the occurrence among J of some individuals which have passed the male phase, contemporary with that shown from A to I, and re-attained a spawning female phase which may have occurred early in

the season and escaped notice. In this event a second male phase— younger than anticipated for J individuals—is mixed with the latter, having the effect of reducing the mean male sex-condition of the group. Whether this be the case or not some individuals in this group had passed the male phase, reattained the functioning-female phase, and undoubtedly begun another post gyne-spawning male phase.

THE ONSET OF THE FEMALE PHASE.

The reattainment by a significant number of individuals in the J period of a fully developed female condition proves that a second curve of gonad-condition—but this time of the development of femaleness—could be drawn between the abscissæ of I and J if sufficient data were available. There is every probability that femaleness will be found to accelerate its development at some point in the female phase in a somewhat similar way to that shown by the male phase between points A and F in Fig. 3, p. 1037 (see Orton, 1924, p. 191 ; and Spärck, 1924, p. 31) ; but whereas the male phase referred to can be investigated exactly at this condition by noticing the obvious signs of embryos and larvæ in individuals, in the case of the corresponding stage of femaleness there is no external sign to betray similar gonadial activity, and special studies are required to discover the exact time of the most rapid internal changes. Although data are not available for constructing a graph of the development of femaleness following the post-gyne-spawning male condition, there is now a clear indication that such a curve could be drawn based on practical observations. The position of the beginning of the curve of development of femaleness in relation to the curve showing the complete male phase is a matter of great interest. There is not yet sufficient information available to predict its situation accurately, but there are strong indications that it would *normally* and generally begin at some point after the gonad has become neutral. There are, however, ample reasons—in the occurrence of various kinds of mixed sexes (see p. 976)—for considering it probable that in other cases the curve of development of femaleness may begin at various points in the male phase, but rarely earlier than when the gonad has attained to category VIII in the scheme outlined above, that is, when all the sperm have become ripe.

PRELIMINARY REMARKS ON THE PHYSIOLOGY OF SEX IN THE OYSTER.

The function of sex in the oyster—as in other organisms—is to provide a means for the production of new individuals ; whether the special manifestations of sex in this species are related in any special way to the production of young remains to be shown, and formulates a subject which may be discussed later. The phenomena of sex herein described

however enable at least one fixed point to be determined in the sexual cycle of at least those individuals which produce abundant ripe ova. This fixed point occurs in the sexual cycle or rhythm within a few hours after the individual has spawned as a female, and is signalled by a sudden activity in the gonad in the production of developing sperm. This activity acquires momentum and continues for a period which appears to depend upon external conditions.

In summer—in the warm period—this activity would appear to die down in from one to two months, and is then followed by a quiescent condition of the primordial sex-cells. If the activity of the gonad is maintained until the end of the breeding season, it would appear that that activity may be carried over the winter and continued in the following breeding season. When the male phase being discussed passes during the breeding season there is evidence that it is followed in a significant proportion of individuals by a female phase acquired between the penultimate stages of one breeding season and an early stage in the following one. There is not yet sufficient evidence to show at what period after the male phase the female phase begins, but there is evidence that at some part of this female phase there is an acceleration of egg-development somewhat similar to that found in sperm-development. There exists, therefore, in outline a picture of a male phase as shown in Fig. 3, p. 1037, followed successively by a resting phase, and at some epoch later by a sudden development of eggs (femaleness). There is every reason to believe that an alternation of these male and female phases occurs repeatedly during the lifetime of the individual (probably during each year under normal biological conditions for the species), and it has been shown that although these phases are mostly clear-cut, there is a fair percentage of mixed sexes in nature, a fact which indicates a good deal of overlapping of these phases. The sudden development of both maleness and femaleness suggests the existence of a controlling mechanism, abruptly released, which is most easily visualised as hormonal (as might be effected by a catalytic enzyme), as has already been suggested (Orton, *Nature*, 1924b, p. 191). It is, however, also possible that the phases may be initiated at the culmination of a series of metabolic processes whereby (1) the completion of storage of reserve materials in the eggs (as at egg-spawning) changes the metabolism and the metabolic rhythm towards the production of substances which when absorbed by the gonocytes are suitable for sperm-production, and the male phase follows; and where (2) the accumulation of reserve products assumes such a concentration in the post-male phase that a slight addition to that concentration causes the beginning of egg-development, that is, the laying down of the reserves in all the gonocytes, which then become eggs, or alternatively only in predestined oocytes.

It is unfortunate that no chemical analyses exist of oysters in different definite sex-phases. The remarkable series of analyses by the Government Chemist given in Russell's paper (1923) were carried out on groups of about 50 oysters of unknown sex, but in view of the demonstration that the percentage of female oysters diminishes and the percentage of males increases during the summer (Orton, 1926, also herein, and unpublished), it can be postulated that the analyses detailed (*loc. cit.*) would include an increasingly high percentage of males and a decreasing percentage of females from the beginning to the end of the breeding season.

The graphs of percentage of protein and carbohydrate content in samples of oysters examined monthly from January, 1919, to January, 1920, from four well-known oyster beds in the Thames Estuary given by Russell (*loc. cit.*), show a general inverse variation correlated with the extent of the breeding season. This correlation is especially well marked in the samples from the Whitstable beds, where the breeding season extends normally from about June to September. As the protein percentage composition declines from June to September and the carbohydrate and glycogen content rises from June to September in the Whitstable samples, see Fig. 4, p. 1041, it is clear that with the increasing percentages of males in this period, the metabolism resulting in the storage of carbohydrate (including glycogen) is also increasing, and that resulting in storage of protein decreasing. From the end of the breeding season—about September—in the same series of oysters (Whitstable, *loc. cit.*, Fig. 4 herein), both the carbohydrate—and glycogen—and the protein content increase; now it is just in this period that we have found a high proportion of males beginning to change into females, and the suggestion is strong that carbohydrate metabolism is predominant in males and protein in females. There is therefore some support for an explanation of sex-changes in the oyster based on rhythmical changes in metabolism, whereby, for example, an excess of *unusable* metabolic products characteristic of one sex induce a reversal of the sex-metabolism and sex-manifestation to that of the other sex.

A rhythmic change in the metabolism of an organism controlling its sex-manifestations must be regarded as a property of that organism in the same way as are the metabolic rhythms producing specific organs in the course of ontogenesis. In both cases the change which occurs must depend upon some physico-chemical factor which may either be formed locally or generally and distributed to various parts of the organism as an activator, after the manner of a hormone, while there may exist in the case of the gonad of the oyster and other organisms an ambi-receptor mechanism, i.e. one tending to produce either maleness or femaleness, in *all* the gonocytes.

A theory of the control of sex by rhythmical changes in metabolism may therefore be conceived with or without the intervention of (circulating) hormones.

A theory of the control of sex in the oyster by vague hormones of unknown origin is less simple than that of a metabolic rhythm just outlined,

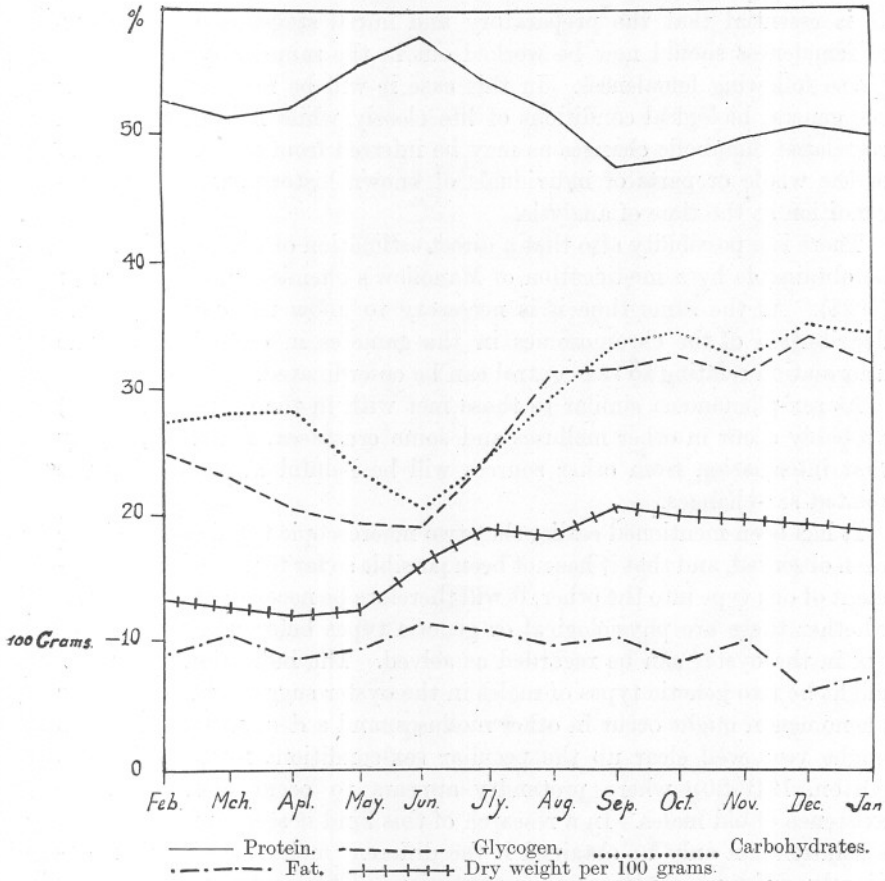


FIG. 4.—Percentage composition in dry weight of oysters* from Whitstable, together with dry weight per 100 oysters, January, 1919–January, 1920. (Reproduced by permission and courtesy of H.M. Stationery Office and Dr. E. S. Russell, from a paper by the latter, 1923.) From analyses by the Government Chemist.

since some stimulus is required in the former theory to activate, or to give greater potentiality to, a male-inducing hormone at one period, and another to activate or give greater potentiality to a female-inducing hormone at another period. A combination of the two views on the

* These analyses were carried out mainly on samples of 50 oysters. (For details see Russell, 1923, p. 16.)

method of sex-control in the oyster is however possible, in that metabolic changes themselves may afford the stimuli for and produce hormonal substances which result in the gonocytes developing alternatively into spermatogonia or oogonia.

A closer insight into the probable controlling factors of sex in the oyster can probably be obtained when more information is available. It is essential that the preparatory and initial stages of development of femaleness should now be worked out in the same way as the male phase following femaleness. In this case it will be necessary to follow the general biological conditions of life closely while investigating such correlated metabolic changes as may be inferred from chemical analyses of the whole or parts of individuals of known history and known sex-condition at the time of analysis.

There is a possibility also that a direct estimation of sex-condition may be obtainable by a modification of Manoilow's chemical reaction for sex (1923). At the same time it is necessary to know the characters and distribution of the chromosomes in the gametes in order that all the information relating to sex-control can be co-ordinated.

As sex-phenomena similar to those met with in the oyster (*O. edulis*) probably occur in other molluscs and some crustacea, it is not unlikely that information from other sources will be helpful in elucidating the related sex-changes.

It has been mentioned earlier that two macroscopic types of male have been observed, and that it has not been possible so far to trace the development of one type into the other, it will therefore be necessary to determine whether these are physiological or genetic types before the problem of sex in the oyster can be regarded as solved. The indication that there might be two genetic types of males in the oyster suggests that a similar phenomenon might occur in other molluscs, and a demonstration of this might very well clear up the peculiar sex-conditions found in *Patella* (Orton, 1919-20), where protandry appears to occur along with the existence of old males. In a research of this kind it seems probable that a solution can only be obtained if the different male types have an obviously different chromosome constitution. The coexistence of males with hermaphrodite forms is well known in other groups, e.g. some Cirripedia, some Nematoda, and possibly also in some Gephyrea, so that the phenomenon may have a general fundamental significance in the true physiology of sex, namely, in its relation to the biology of the species.

SUMMARY.

The gonads of 1,121 oysters have been examined at various periods from a few hours to twelve months after the individuals had spawned as females; the material for the research was obtained by collection and

experiment. In 702 individuals taken with young in the mantle cavity the gonad shows a progressive development of maleness in its primary sexual characters; within a mean period of $2\frac{1}{4}$ hours after spawning eggs, the gonad was found in 50 per cent of cases with only young sperm-masses developing, followed at later periods by a progressive ripening of the sperm-masses, until in individuals carrying shelled and black-coloured larvæ 77 per cent contained abundant ripe sperm-masses as well as advanced developing sperm-masses.

In 444 individuals examined at various periods after extruding their larvæ, the development of sperm was found to continue for about a month after egg-spawning, and to abate in about the second month. In from 2 to 3 months after egg-spawning sperm-development is completed and the male phase begins to wane, and a small percentage of individuals may become female or actively female-functioning again. In 12 months after the last egg-spawning a significant number of individuals become once more functional females.

The varieties of mixed sexes found in *O. edulis* are defined and their frequencies shown by an analysis of samples—from two widely separated beds—examined at the beginning of the breeding season in 1926. Experiments on the rate of growth of sperm-masses and on determining of age at different stages of development in embryos and larvæ are given.

The rapidity and course of development and waning of maleness can be shown graphically by an asymptotic (hormonic) curve.

The general biological conditions accompanying the development of femaleness—following the male phase observed—have not yet been fully worked out.

The cause of sex-control in the oyster is discussed in a preliminary manner.

It is suggested that sex-change in the cases observed is due to a metabolic rhythm in two phases; there is some evidence—as yet, however, incomplete—that in one phase protein metabolism is predominant, and is accompanied by egg-development; while in the other, carbohydrate—and especially glycogen—metabolism is predominant, and is accompanied by development of sperm.

The theory is advanced that the accumulation of *unusable* products of one kind of metabolism above a certain concentration is the stimulus for the change-over to the other phase of metabolism, with its accompanying sex-change. The rhythm is regarded as a specific property of the species. This theory involves a fresh orientation with regard to our ideas of sex-control, in that sex-control is assumed to reside in the general nature of the metabolism.

It follows from this theory that all gonocytes have the potentiality of becoming oogonia or spermatogonia.

The establishment of a sex-change from femaleness to maleness at or within a few hours after the instant of egg-spawning, furnishes a fixed point in the sexual rhythm of the oyster: it will therefore be possible in the future to utilise this fixed point in efforts to unravel all the phenomena associated with the change of sex, and in investigations designed to determine all the sex-changes which may occur during the life of at least those individuals which pass through a number of female phases.

Observations are given pointing to the possibility of the existence of two types of male in the oyster.

REFERENCES.

1877. MÖBIUS, K. Die Auster und die Austernwirthschaft. Berlin, 1877. Translated in U.S.C. of F. and F. Report of Commissioners for 1880. Part VIII, Appendix H, p. 692.
1883. HOEK, P. P. C. Les organes de la génération de l'huître. Contributions à la connaissance de leurs structure et de leurs fonction. Tijdschrift Ned: Dierk: Ver: Supplement Deel I. Leiden, 1883-84.
1883. HORST, R. Embryogénie de l'huître (*Ostrea edulis* L.) Tijdschr: Nederl: Dierk: Ver: Supplement, Deel I. 1883-84.
1889. BOURNE, G. C. The Generative Organs of the Oyster. (Abstract of a paper by Dr. P. P. C. Hoek.) Journ. Mar. Biol. Assoc., Vol. I. 1889-90.
1902. HOEK, P. P. C. Rapport over de oorzaken van den achteruitgang in hoedanigheid van de Zeeuwsche oester. Ministerie van Waterstaat, Handel, en Nijverheid. s'Gravenhage, 1902.
1909. ORTON, J. H. On the occurrence of protandric hermaphroditism in the mollusc, *Crepidula fornicata*. Proc. Roy. Soc. B., Vol. 81, 1909.
1913. SMITH, G. Studies in the experimental Analysis of Sex. The effect of Sacculina on the storage of fat and glycogen, and on the formation of pigment by its host. Q.J.M.Sc., Vol. 59, 1913.
1919. ORTON, J. H. Sex-phenomena in the Common Limpet (*Patella vulgata*). Nature, Vol. 104, 1919-20, p. 373.
1921. —. Sex-change in the Native Oyster (*O. edulis*). Nature, Vol. 107, p. 608, July 7th, 1921.
1922. —. The Phenomena and Conditions of Sex-change in the Oyster (*O. edulis*) and *Crepidula*. Nature, Vol. 110, p. 213, August 12th, 1922.
1923. MANOILOW, E. O. Russian Medical Journal, 15. (Wratchebnaia Gazeta).

1923. GOLDSCHMIDT, R. The Mechanism and Physiology of Sex-determination. Translated by W. J. Dakin, London, 1923.
1923. RUSSELL, E. S. Report on Seasonal Variation in the Chemical Composition of Oysters. Fishery Investigations, London, II, Vol. VI, 1, 1923.
- 1924a. ORTON, J. H. An Account of Investigations into the Cause or Causes of the unusual Mortality among Oysters in English Oyster Beds during 1920 and 1921. Part 1. Report, Fishery Investigations, London. Series II, Vol. 6, No. 3, 1924.
- 1924b. ——. Sex-change and Breeding in the Native Oyster (*O. edulis*). Nature, Vol. 114, p. 191, August 9th, 1924.
1924. SPÄRCK, R. Studies on the Biology of the Oyster (*O. edulis*) in the Limfjord, with special reference to the Influence of Temperature on the Sex-change. Report of the Danish Biological Station, Copenhagen, Vol. XXX, 1924 (1925).
1925. SAVAGE, R. E. The Food of the Oyster. Fishery Investigations, London, Series II, Vol. VIII, No. 1, 1925.
1926. ORTON, J. H. On Lunar Periodicity in Spawning of normally grown Falmouth Oysters (*O. edulis*) in 1925, with a comparison of the spawning capacity of normally grown and dumpy Oysters. Journ. Mar. Biol. Assoc., N.S., Vol. XIV, No. 1, 1926.

