THE FECUNDITY OF *OSTREA EDULIS*

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(Text-figs. 1–4)

Introduction and Review of Previous Work

Galtsoff (1930) has shown that females of the American oyster (*Ostrea virginica*) may discharge from 15 million to 114 million eggs in a single spawning period, while even after such heavy spawning the gonad still contains a large quantity of eggs. A female of *Ostrea gigas* was shown by the same writer to be capable of producing up to 92 million eggs. These oysters both belong to the group of large oviparous species, which Ranson (1938) and Nelson (1938) have proposed should be separated from the so-called flat oysters under the generic name of *Gryphaea*, with the Portuguese oyster *Gryphaea angulata* as the type. Nelson (1938) and Elsey (1935) have shown that in addition to their fundamental difference in process of reproduction the oviparous and viviparous types differ considerably in the relations between the mantle and the visceral mass. The differences between the two types appear to the writer to warrant the adoption of the two generic names as suggested. The viviparous oysters of the genus *Ostrea* are usually much smaller than the oviparous species, and those which have been investigated have been found to produce far fewer eggs, generally discharging the gonad completely in one spawning act. The earliest known estimate of the number of embryos produced by a European oyster is that of Eyton (1858), who arrived at the figure 1,800,000 for very large oysters. Buckland in 1865 (quoted by Philpots, 1890) stated that he had examined several native oysters of average size and weight, and had never found 'the highest number of spat to be more than 829,655 and the lowest 276,555'; his method of estimation is not recorded. Moebius (1883), by weighing separately the total broods of five individuals and also a small fraction of each, and by counting the embryos contained in the small fraction, arrived at the conclusion that adult females of *O. edulis* produced on the average a brood of 1,012,955 embryos. It is probable that Moebius was dealing with what would be considered to-day to be very large oysters. This estimate has been extensively quoted, for no further detailed observations of the production of adult oysters have since been published. Dantan (1913) has, however, published details of a series of counts of the broods of 1-, 2- and 3-year-old oysters from Arcachon and Brittany, in France. Dantan employed a satisfactory method of counting aliquot parts and gives figures for the broods of six 1-year-old, three 2-year-old and eight 3-year-old oysters; his mean values are 95,500, 247,000 and 725,000 respectively. Gaarder & Bjerkan (1934) also give figures for 1-, 2- and 3-year-old oysters and also for older oysters, viz. 100,000, 250,000, 800,000 and about 1,000,000 respectively, but no details are given of the method of arriving at these figures, or of the number of broods counted. It is not clear whether these represent new estimates or are merely a quotation of the work of Dantan and Moebius. Orton (1937) states that a 1-year-old native oyster from Essex was found to be carrying a brood of about 240,000, while a small 3- or 4-year-old oyster, also from Essex, carried 525,000.

The only other species of flat oyster of which the size of brood is known is *O. lurida*, for which Hopkins (1937) has made some careful observations. Hopkins concludes that the average market-size individual of this species, i.e. one about 5 cm. across the shell, produces a brood of from 250,000 to 300,000 larvae. This figure is the result of examining, and estimating by counting aliquot parts of the whole brood, the broods of twenty-five individuals. Hopkins found that the range of variation was considerable, the smallest brood he found being only 69,490 while the largest was 355,500.

In the course of a study of the sexual cycle and breeding in 1- and 2-year-old oysters, the writer found several with broods of embryos, and it was thought worth while to preserve these broods and to make estimates of the numbers present, inasmuch as the age of the parent oysters was known with certainty, for they had been reared from spat setting on limed tiles in the breeding tanks at Conway, N. Wales (see Cole, 1938). As Dantan (1913) points out, it is especially desirable in work of this kind to have oysters other than native oysters from the natural beds, the age of which is always uncertain. The work of estimating the fecundity of oysters in their first few seasons was later extended, as it became necessary to determine the average size of the brood produced by adult oysters kept under tank conditions at Conway, and to compare this figure with the productivity of different types of oysters from the natural beds.

Material and Methods

The material from which our own observations are drawn consists of several distinct categories of oysters.

In the first place there are groups of 1-, 2- and 3-year-old oysters from our relaying ground in the Menai Straits, all of which had settled on tiles in the Conway tanks before being transferred to the Menai Straits.

Secondly, there is a group of young oysters from the Helford River, Cornwall, the age of which could be determined with more or less certainty, comprising both French relaid oysters of 3 and 4 years, and a number of small native brood oysters whose age was believed to be 2 years. It is possible, however, that one or two of the latter may have been 3 years old.

Thirdly, there is a group of large oysters taken from those used as breeding stock in the Conway tanks, and obtained by us from the Yealm River, S. Devon. The majority of these oysters originated in France, being laid down for a year or more in the Yealm River before dispatch to Conway.

Fourthly, there are two groups of large oysters from the Helford River, Cornwall, one consisting of those native to the river, the other comprising Brittany oysters, which are laid down annually in large quantities in the Helford River.

The following method was adopted in determining the number of embryos comprising a brood. The embryos were carefully washed free from the gills, palps and mantle of a gravid oyster, and were killed with formalin. They were then collected by pipette and placed in a round-bottomed flask or a beaker, and the volume made up to a fixed amount, either 250 or 400 c.c. The contents of the flask or beaker were thoroughly agitated and five, or on some occasions ten, exactly determined samples were removed with an automatic pipette. The pipettes used delivered 0·52 and 0·45 c.c. respectively. The embryos contained in each of these aliquot parts were counted under a binocular microscope on a squared counting plate and a mean value determined; multiplied by the appropriate factor, this gave a figure for the total brood. At the same time, the colour, to the naked eye, of the brood as a whole and the stage of development reached by the embryos were noted. Where oysters were dredged from the beds they were opened as quickly as possible, as abortion of embryos may occur through rough handling.

Observations

One-year-old oysters. Gerbe (1876) was the first to observe that oysters may produce eggs even in the first year of their life, i.e. in the summer following that in which they attached themselves. He found thirty-five with embryos out of a total of 435 1-year-old oysters from Arcachon. This observation was followed by the work of de Lacaze-Duthiers (1893), who, after several years' experience of oysters held in the aquaria of the biological station at Roscoff, concluded that only a very few oysters bred during their second and third years, and then only to a slight extent, and that reproduction was not fully assured until their fourth year. Gerbe's work has, however, since been supported by Dantan (1913), who found that of 133 1-year-old oysters from Arcachon, opened on 8 August, six contained broods of embryos. There is good reason for believing that Dantan was able to determine exactly the age of the material with which he was dealing, always a difficult matter unless the oysters have been reared on tiles or have been under observation since settlement. Orton (1922) has recently recorded also that of oysters settling in 1920 in English waters, certain of the larger individuals liberated larvae in the summer of 1921, but the same author later states (Orton, 1937) that in his opinion this state of affairs is not usual in England 'where young oysters may not usually produce the first batch of eggs until their third or even fourth summer'. Work which I have at present in hand shows that the proportion of young oysters functioning as females in the summer following attachment may in some years be larger than was formerly suspected.

Dantan was fortunate in obtaining six 1-year-old oysters with broods of embryos, the mean number in a brood being 95,500 with a range of from 69,000 to 144,000. The average length of the shell of these oysters was 3·4 cm. I have unfortunately only opened one such oyster which was actually carrying a brood of embryos, although ripe females have been of fairly frequent occurrence. This one oyster measured 3·8 cm., and carried a brood of 91,628 when opened on 25 October 1938. The embryos were in the late gastrula stage.

TABLE I. BROODS OF EMBRYOS OBTAINED FROM 2-YEAR-OLD OYSTERS FROM THE MENAI STRAITS, NORTH WALES

Date	No. of embryos	Stage of development of embryos	Colour
29. vi. 38	432,200	Trochophores	White
29. vi. 38	320,900	Trochophores	White
29. vi. 38	272,400	Shelled veligers: 0·15–0·165 mm.	White
29. vi. 38	259,100	Gastrulae	White
29. vii. 38	270,900	Trochophores	White
29. vii. 38	189,300	Shelled veligers: 0·15–0·165 mm.	Light grey
Average	290,800		

TABLE II. BROODS OF EMBRYOS OBTAINED FROM SUPPOSED 2-YEAR-OLD OYSTERS FROM THE HELFORD RIVER, CORNWALL

Date	Length of shell cm.	No. of embryos	Stage of development of embryos	Colour
2. viii. 39	5·0	257,800	Shelled veligers: 6 % 0·14 mm., 76 % 0·15 mm., 18 % 0·16 mm.	Light grey
16. viii. 39	4·5	108,800	Shelled veligers: shell not completely enclosing body, *ca.* 0·14 mm. in length	White
16. viii. 39	5·3	161,300	Trochophores	White
21. viii. 39	4·7	41,900	Shelled veligers: 18 % 0·14 mm., 38 % 0·15 mm., 36 % 0·16 mm., 8 % 0·17 mm.	Light grey
1. ix. 39	4·1	84,400	Shelled veligers: 20 % 0·16 mm., 66 % 0·17 mm., 14 % 0·18 mm.	Medium grey
Average	4·72	130,800		

Two-year-old oysters. During 1938 small samples of 2-year-old oysters from our relaying ground in the Menai Straits were opened at monthly intervals from June to September, and from twenty-six oysters opened on 29 June four were found carrying broods, while a further lot of twelve oysters opened on 29 July yielded two more with broods of embryos; the details of these broods are set out in Table I. Those lots of thirty-one and thirteen oysters opened in August and September respectively gave none with broods. All these oysters formed part of the crop obtained on tiles during 1936 in the breeding tanks at Conway. They were transferred to the Menai Straits about a month or so after settlement and were detached from the tiles when about 12 months old.

In Table II are shown details of the broods of embryos obtained from a number of small native oysters from the Helford River, Cornwall. From a knowledge of the normal growth rate in this river, it was possible to say with fair certainty that practically all of these oysters were 2 years old, but it is possible that one or two were unusually small 3-year-old oysters.

TABLE III. BROODS OF EMBRYOS OBTAINED FROM 3-YEAR-OLD OYSTERS FROM THE MENAI STRAITS, NORTH WALES

Date	Length of shell cm.	No. of embryos	Stage of development of embryos	Colour
19. vii. 39	6·0	374,600	Shelled veligers: shell not completely enclosing body, *ca.* 0·14 mm. in length	White
19. vii. 39	6·2	601,600	Shelled veligers: shell not completely enclosing body, *ca.* 0·13 mm. in length	White
19. vii. 39	6·3	519,800	Shelled veligers: shell not completely enclosing body, *ca.* 0·13 mm. in length	White
22. vii. 39	5·0	440,000	Trochophores	White
22. vii. 39	5·5	416,300	Trochophores	White
22. vii. 39	6·0	349,400	Trochophores	White
22. vii. 39	6·0	562,800	Shelled veligers: 84 % 0·17 mm., 16 % 0·18 mm.	Dark grey
22. vii. 39	6·5	496,100	Shelled veligers: 48 % 0·17 mm., 52 % 0·18 mm.	Dark grey
22. vii. 39	6·5	693,700	Gastrulae	White
22. vii. 39	7·0	555,400	Gastrulae	White
Average	6·1	501,000		

TABLE IV. BROODS OF EMBRYOS OBTAINED FROM 3-YEAR-OLD RELAID BRITTANY OYSTERS FROM THE HELFORD RIVER, CORNWALL

Date	Length of shell cm.	No. of embryos	Stage of development of embryos	Colour
1. viii. 39	5·5	482,800	Shelled veligers: 0·15–0·16 mm.	Light grey
1. viii. 39	6·2	275,900	Shelled veligers: 8 % 0·17 mm., 28 % 0·18 mm., 52 % 0·19 mm., 12 % 0·20 mm.	Dark grey
16. viii. 39	5·7	216,200	Shelled veligers: shell not completely enclosing body, *ca.* 0·13 mm. in length	White
16. viii. 39	6·4	492,200	Shelled veligers: shell not completely enclosing body, *ca.* 0·13 mm. in length	White
Average	5·95	366,800		

Three-year-old oysters. During 1939 a number of 3-year-old oysters from our relaying ground in the Menai Straits were opened and any broods found were preserved. The details of these broods are shown in Table III. These oysters formed part of the crop obtained in 1936 in the tanks at Conway. Unfortunately it was not possible to collect gravid oysters at different times during the season, as the writer was away from Conway during the greater part of the summer.

A small number of individuals carrying embryos were found among samples of 3-year-old relaid Brittany oysters, opened on the Helford River, Cornwall, during the summer of 1939. The details of these broods are shown in Table IV. These oysters had been obtained in April 1939 from Locmariaquer in the Gulf of Morbihan and were stated to be '2-year olds', i.e. 1936 crop, when bought. There is no reason to doubt that they were correctly described, since they were originally caught on tiles, so that the time of settlement would be known. When opened they were of course in their fourth summer, i.e. they were a month or so over 3 years old.

TABLE V. BROODS OF EMBRYOS OBTAINED FROM RELAID BRITTANY OYSTERS, 4 YEARS OR MORE OF AGE, FROM THE HELFORD RIVER, CORNWALL

Date	Length of shell cm.	No. of embryos	Stage of development of embryos	Colour
18. vii. 38	7·5	1,163,700	Shelled veligers: 25 % 0·17 mm., 65 % 0·18 mm., 10 % 0·19 mm.	Light grey
19. vii. 38	8·0	567,400	Shelled veligers: 16 % 0·16 mm., 32 % 0·17 mm., 48 % 0·18 mm., 4 % 0·19 mm.	Medium grey
5. viii. 38	6·5	1,393,300	Trochophores	White
5. viii. 38	7·0	181,800	Gastrulae	White
5. viii. 38	9·5	1,730,200	Trochophores	White
8. viii. 38	6·5	1,189,400	Shelled veligers: 30 % 0·16 mm., 70 % 0·165 mm.	Light grey
*5. viii. 39	6·4	1,239,100	Shelled veligers: 26 % 0·16 mm., 74 % 0·17 mm.	Medium grey
Average	7·34	1,066,400		

* 4 years old.

Oysters 4 years old, or older. An oyster when 4 years old has frequently reached marketable size and, for practical purposes, may be regarded as adult. The only oyster actually known to be 4 years old from which I have obtained a brood of embryos was a single relaid Brittany oyster from the Helford River. This individual measured 6·4 cm. across the shell and carried a brood estimated at 1,239,100. This oyster is included in Table V, which also gives details of the broods of a number of relaid Brittany oysters, 4 years or more of age, from the Helford River, Cornwall. It is probable that most of the oysters whose broods are detailed in this table were actually 4 or 5 years old when opened, as Brittany oysters are usually sold from the Helford River at this age.

In addition to those from relaid Brittany oysters, broods of embryos were also obtained from a number of oysters native to the Helford River, and the details of these are shown in Table VI. It is possible that one or two of the smallest of these native oysters may have been only 3 years old, but the majority would be 4 or 5 years of age.

From time to time broods of embryos have been collected from adult oysters used as breeding stock in the Conway tanks. Such oysters are brought into the tanks early in May of each year and are taken out again in September and relaid on our own grounds in the Menai Straits, where they remain until taken up again early in the following May. All were originally obtained from

TABLE VI. BROODS OF EMBRYOS OBTAINED FROM ADULT OYSTERS NATIVE TO THE HELFORD RIVER, CORNWALL

Date	Length of shell cm.	No. of embryos	Stage of development of embryos	Colour
19. vii. 38	6·0	571,600	Shelled veligers: 20 % 0·165 mm., 10 % 0·17 mm., 60 % 0·18 mm., 10 % 0·19 mm.	Medium grey
27. vii. 38	5·75	944,200	Segmenting eggs and morulae	White
27. vii. 38	6·0	353,100	Trochophores	White
27. vii. 38	7·0	1,075,900	Trochophores	White
27. vii. 38	8·5	1,401,500	Shelled veligers: shell not completely enclosing body, *ca.* 0·15 mm. in length	White
5. viii. 38	8·0	322,200	Gastrulae	White
Average	6·88	778,100		

TABLE VII. BROODS OF EMBRYOS OBTAINED FROM OYSTERS, 4 YEARS OR MORE OF AGE, FROM THE CONWAY BREEDING TANKS

Date	Length of shell cm.	No. of embryos	Stage of development of embryos	Colour
17. viii. 38	6·35	1,172,800	Shelled veligers: shell not completely enclosing body, *ca.* 0·14 mm. in length	White
17. viii. 38	6·5	559,100	Shelled veligers: shell not completely enclosing body, *ca.* 0·14 mm. in length	White
19. viii. 38	8·0	1,115,800	Shelled veligers: 10 % 0·15 mm., 20 % 0·16 mm., 70 % 0·165 mm.	Black
20. viii. 38	7·0	1,245,800	Shelled veligers: 15 % 0·165 mm., 65 % 0·17 mm., 20 % 0·18 mm.	Black
31. viii. 38	6·7	544,000	Morulae	White
31. viii. 38	7·3	663,600	Early gastrulae	White
8. ix. 38	7·0	588,700	Shelled veligers: 5 % 0·165 mm., 90 % 0·17 mm., 5 % 0·18 mm.	Dark grey
8. ix. 38	7·0	749,000	Shelled veligers: 5 % 0·16 mm., 95 % 0·165 mm.	Dark grey
3. vii. 39	No record	1,091,400	Shelled veligers: 40 % 0·16 mm., 60 % 0·17 mm.	Medium grey
Average	*6·98	858,900		

* Average of eight only.

the Yealm River, S. Devon, from which a new consignment is added each year. The majority of these oysters are French oysters from the Gulf of Morbihan, and were laid down in the Yealm River for at least 12 months before being sent to Conway. Details of the broods of embryos obtained are shown in Table VII. The majority of these oysters were probably 5 or 6 years old when opened.

The data derived from all the above year-groups of oysters are summarized in Table VIII.

TABLE VIII. SUMMARY OF THE DATA FROM ALL BROODS OF EMBRYOS

Age	No.	Mean length of shell cm.	Range of variation in number of embryos	Average number of embryos per brood	Origin of parent oysters
1 year	1	3·8	—	**91,600**	Conway oyster from Menai Straits
2 years	6	No record	189,300–432,200	290,800	Conway oysters from Mena Straits
*2 years	5	4·72	41,900–257,800	130,800	Helford River natives
All 2-year-old oysters	**11**			**218,100**	
3 years	10	6·1	349,400–693,700	501,000	Conway oysters from Menai Straits
3 years	4	5·95	216,200–492,200	366,800	Brittany oysters, relaid Helford River
All 3-year-old oysters	**14**	6·06	—	**462,600**	
4 years	1	6·4	—	1,239,100	Brittany oyster, relaid Helford River
4 years and over	6	7·5	567,400–1,730,200	1,066,400	Brittany oysters, relaid Helford River
4 years and over	6	6·88	181,800–1,401,500	778,100	Helford River natives
4 years and over	9	†6·98	544,000–1,245,800	858,900	Oysters from Conway tanks, mainly relaid Brittanys from Yealm River, S. Devon
All oysters 4 years old and over	**22**	‡7·07		**902,900**	

* Probable age, may have been 3 years old in few cases.
† Average of eight only (see Table VII).
‡ Average of twenty-one only (see Table VII).

DISCUSSION

In Fig. 1 length of shell is correlated with brood strength. It will be seen that the number of embryos produced varies rather widely in oysters of similar age and length of shell. A comparable variation has also been recorded in *Ostrea lurida* by Hopkins (1937). Such a variation may in part be due to the fact that length of shell alone is not a completely satisfactory criterion of reproductive capacity, as in oysters with shells of similar length the volume of the meat and the degree of fatness, upon which the reproductive capacity presumably depends, may vary rather considerably. In recent work on the sexual cycle of young oysters I have adopted the weight of the soft parts as giving a better measure of the reproductive capacity.

This variation in brood size among oysters of similar age is well brought out in Fig. 2, in which the observations have been grouped in year-classes, those observations appertaining to adult oysters being grouped arbitrarily opposite the 5-year mark. This method of treating the data shows that the 2- and 3-year-old oysters apparently belong to more or less homogeneous groups, but the observations of brood size among adult oysters appear to group themselves about two points, and this suggests that we are dealing with two distinct classes of adult oysters varying considerably in brood strength. The reason for this peculiar grouping is not clear, but it may perhaps be due to a considerable reduction in the number of embryos produced by oysters

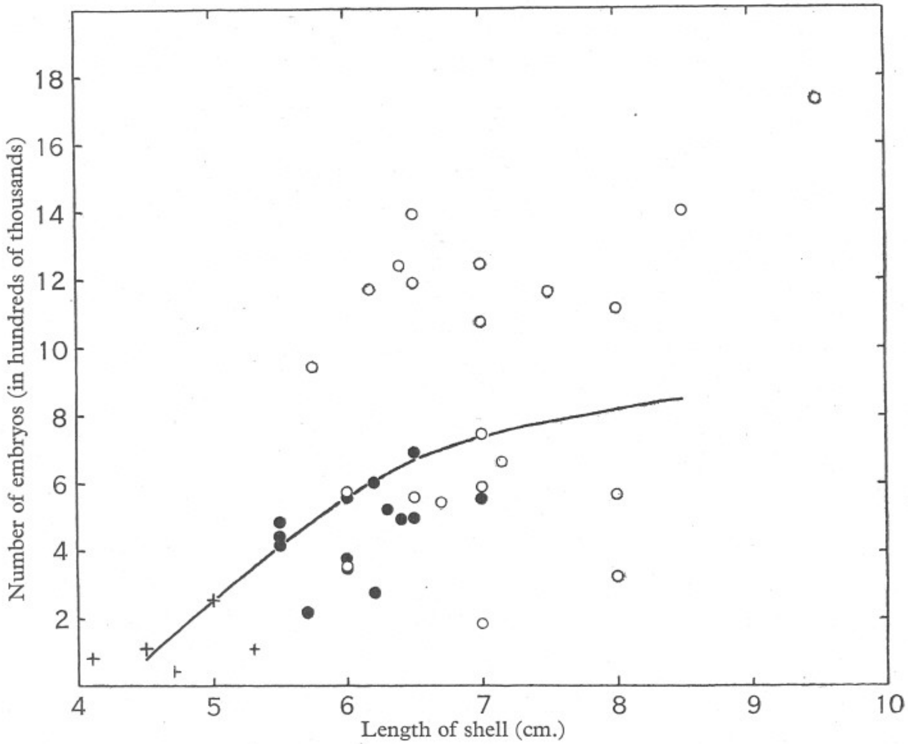

Fig. 1. The relation between length of shell and the number of embryos produced. The curve showing the general trend of the relationship has been drawn through points representing the mean number of embryos per brood in groups of oysters of all ages in the size categories 4·0–4·9, 5·0–5·9, 6·0–6·9 cm., etc. The single observation in the group 9·0–9·9 cm. has been ignored. + = 2-year-old. ● = 3-year-old. ○ = 4-year-old and over.

maturing as females in the second half of the season after an early male phase, when compared with individuals which enter on the female phase as soon as the season begins. This possibility is further discussed later in this paper (p. 255).

The curve showing the general relationship between shell length and the number of embryos produced (Fig. 1) has been drawn through points representing the mean brood size of groups of oysters of shell length 4·0–4·9, 5·0–5·9, 6·0–6·9 cm., etc.; the single oyster in the size-group 9·0–9·9 cm. has been omitted. The trend of this curve appears to indicate that it is unlikely that an average brood of more than 1,000,000 will be produced throughout the whole season, even by a population of very large oysters.

The colour to the naked eye of a brood of embryos as it lies in the mantle cavity of the parent oyster is not a very reliable guide to its state of development, for, as can be seen from the tables, certain broods recorded as being light or medium grey in colour contained larger larvae than those which

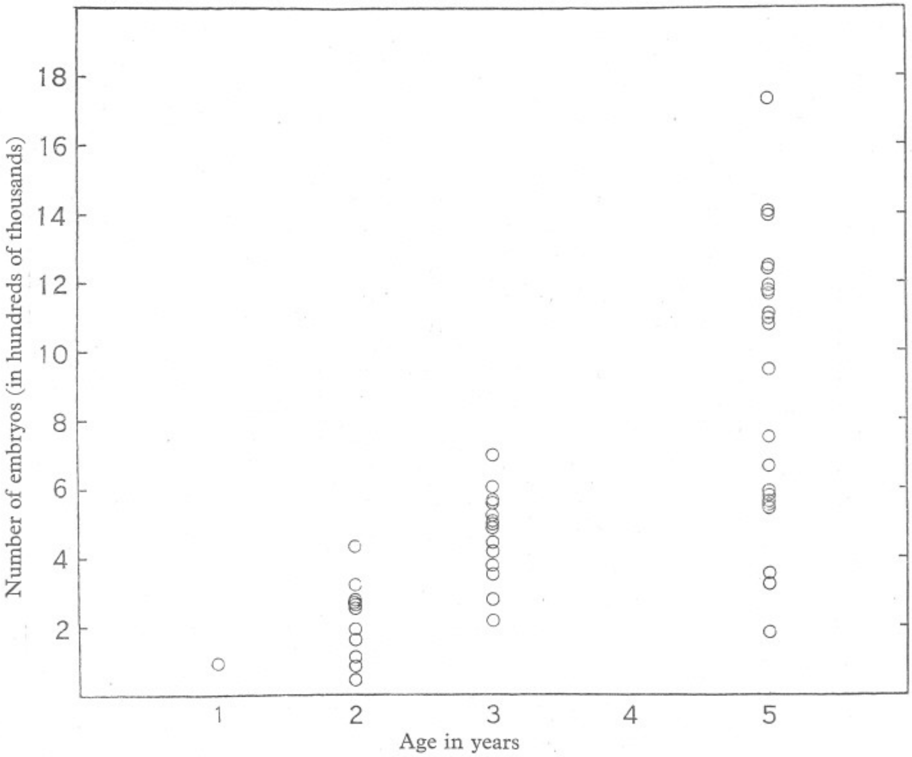

Fig. 2. The relation between the number of embryos produced and the age of the parent oyster. All oysters over 3 years of age have been grouped arbitrarily at 5 years.

appeared almost black to the naked eye. As anyone who has an extensive experience of oyster larvae will confirm, the degree of pigmentation of individual larvae after liberation is very variable.

The figures given in this paper tend to show that as regards the production of larvae an oyster practically doubles its capacity each year during the first 4 years of its life and that it is only when 4 years old that an oyster may be looked upon as adult, and playing its full rôle in the reproduction of the species. This is in close agreement with the opinion of most practical oystermen who are agreed that a 3-year-old oyster is readily distinguishable as a juvenile, while one 4 years old is not.

The data obtained from 1- and 2-year-old oysters do not differ markedly from those of Dantan (1913) and Gaarder & Bjerkan (1934), if the latter represent separate estimates, but the figure for 3-year old oysters given by these authors seems rather high and approximates to that of many adult oysters.

The data presented above provide a fairly satisfactory answer to the query as to whether breeding oysters held under tank conditions produce larvae as freely as similar oysters living on the natural beds. The oysters from the Conway tanks are themselves mainly relaid oysters from Brittany and are best compared with similar relaid Brittany oysters from the Helford River. The results of such a comparison are slightly in favour of the oysters from the Helford River, with an average brood of 1,066,400, as against 858,900 for those from the Conway tanks, but the average size of the former lot was some 5 mm. greater. Compared with Helford River natives of about the same size, the oysters from the Conway tanks are slightly superior in the production of larvae. We may therefore conclude that the retention of breeding oysters in large tanks such as those at Conway for a period of 4 months does not impair their reproductive capacity, for it has already been shown (Cole, 1939) that the percentage maturing as females under tank conditions may reach or slightly exceed 50 %, the figure arrived at by Orton (1936) working on the natural beds. In making the above estimate (viz. 50 % females) I had assumed that each oyster produced a brood of 1,000,000 embryos; had I employed the average figure of 858,900 arrived at in this paper, the percentage maturing as females would be slightly increased (see Cole, 1939, Table XXI, p. 39).

There is no indication from the figures presented in the tables of any substantial loss or mortality of embryos during the period of development within the mantle cavity, for very large broods of both early embryos and shelled veligers occur in practically all groups. The amount of variation in shell size between the larvae of a brood is itself variable, although in those broods carried by adult oysters the variation rarely exceeds 0·015 mm. In some of the younger oysters the larvae of a brood varied however as much as 0·03 mm., but a marked difference in development between parts of a brood, such as would indicate successive partial spawnings at a few days' interval, was never observed, although Orton (1936), who has examined a great many oysters carrying larvae, records that such a phenomenon is occasionally observed.

Only in one instance were veligers measuring 0·20 mm. across the shell found in the mantle cavity (see Table IV), the maximum size being usually 0·19 mm., although Orton (1927) has recorded larvae up to 0·22 mm. The usual size of larvae when liberated in the Conway tanks is 0·18 or 0·19 mm., but both slightly smaller and slightly larger larvae are not uncommon. Under natural conditions in the Helford River during 1939 I frequently observed larvae as small as 0·15 mm. in the plankton, such larvae appearing very pale.

As can be seen from the tables, those broods which showed most variation in size amongst the veligers occurred principally late in August and more frequently among immature oysters (see Tables III and IV). It has been observed both at Conway and Port Erin (Bruce, Knight & Parke, 1939) that all broods of larvae are not equally viable and that, as a general rule, those broods which show least variation in size amongst the individual larvae show also the best survival under experimental conditions.

A comparison between 2- and 3-year-old oysters bred in the tanks at Conway and oysters of similar age from the Helford River shows the Conway

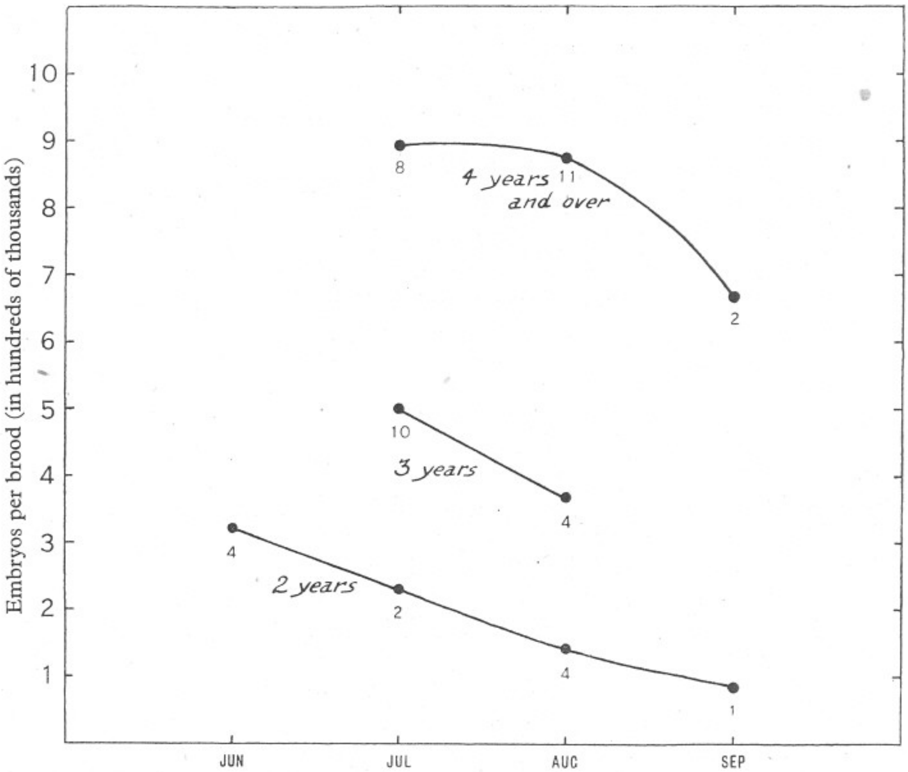

Fig. 3. The variation in the mean number of embryos produced per oyster as the season advances. The observations have been grouped according to the month in which they occur. The figures under the points on the curves indicate the number of observations in each group.

oysters to be distinctly in advance, and is an indication of the viability and general soundness of oysters bred under enclosed conditions. In making this comparison it should not be forgotten, however, that the oysters from the Helford River were collected rather late in the season, during August, and there is a possibility that such late breeding oysters may produce smaller broods than those breeding during June and July. In Fig. 3 the observations have been grouped according to the month in which they occur and curves have been drawn through points representing the mean size of brood for each month in the three year-classes of oysters. The single adult oyster with an unusually large brood has been omitted, as its inclusion produced an abnormal displacement of the mean. All three curves fall more or less sharply in the second half of the season and, although the number of observations is small, it suggests that in oysters of all ages there is a general falling off in the number of embryos in a brood as the season advances.

The peculiar grouping of the observations of brood strength in adult oysters, as shown in Fig. 2, strongly suggests that we are dealing with two distinct categories of female spawners differing considerably in brood strength. By taking the mean of each apparent group of observations, the figures obtained for the average number of embryos produced by oysters in the two classes

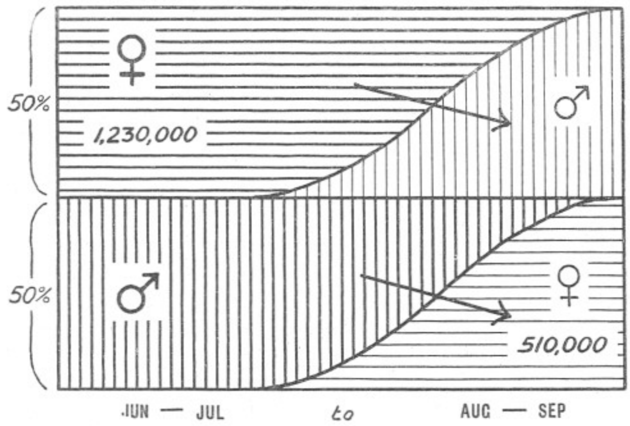

Fig. 4. Diagrammatic representation of the possible effect of sex change during the breeding season on the relative intensities of the male and female phases. The data show the probable mean number of embryos produced by each of the two categories of females.

are 1,230,000 and 510,000 respectively. Taken in conjunction with Fig. 3, which shows a marked decline in brood strength as the season advances, these figures suggest that those oysters spawning as females during the second half of the season produce, on the average, rather less than half as many embryos as those spawning earlier. If this is so, and it is recognized that the observations are few, the most likely explanation appears to be that oysters maturing as females after an early male phase have expended a part of their reserves in maturing a crop of sperm, and consequently are only able to ripen a comparatively small batch of eggs, whereas those oysters maturing as females from the outset of the season, without a preliminary male phase, are able to draw upon the whole of the reserves accumulated during the spring.

As the season advances, the percentage of the population spawning either as males or females, without a preceding phase of the other sex, must clearly decline, thus accounting for the shape of the curves in Fig. 3; but it is not possible to fix a definite date after which, for instance, all oysters spawning as females will have experienced a previous male phase early in the season. In unfavourable circumstances, for example in abnormally cold seasons, it is possible that the ripening of those oysters maturing as females from the outset of the season may be delayed until late July or even August. Experience of breeding oysters held in tanks supports this view, for in 1938, for example, although the Conway tanks contained over a thousand oysters no substantial spawning of females occurred until the third week in July (see Cole, 1939).

We arrive therefore at the conclusion that the majority of adult oysters probably experience a sex-change during favourable seasons, and that the early phase, either male or female, is a strong one, quantitatively speaking, and is followed by a very much weaker phase of the other sex. Fig. 4 represents an attempt to give diagrammatic representation to these possibilities. For the purpose of this diagram it has been assumed that each adult oyster experiences a sex-change every season and functions as both male and female each season. The evidence at present available suggests that this occurs only in favourable circumstances, but further investigation is likely to show that the percentage of female spawners is higher than at present supposed. It should perhaps again be stressed that the observations are few and the conclusions are therefore extremely tentative. They are advanced with the particular desire to call attention to the singular grouping of the observations of brood strength among adult oysters, and the interesting lines of inquiry which these observations suggest.

It is interesting to compare the fecundity of adult *Ostrea lurida*, which rarely exceed 5 cm. in diameter, with that of juvenile *O. edulis* of the same shell size. A 3-year-old Conway oyster of 5 cm. (see Table III) gave a brood of 440,000 embryos, while the 2-year-old Conway oysters averaged 290,800 (Table I). Although the sizes of the oysters composing the latter group were not noted at the time, the usual size of oysters of this age is about 5 cm. The broods produced therefore compare favourably with those of adult *O. lurida*, for which the average figure given by Hopkins (1937) is 250,000–300,000. *O. lurida* has, however, a distinct biological advantage for, due principally to the lengthy breeding season, each individual may be expected to mature as a female during each season, while in favourable years the proportion maturing as females *for the second time* may reach 75 % (see Hopkins, 1937).

Now that the practice of selling four grades of oysters, instead of one or two as in former years, seems well established in this country, it is as well to take stock of the effect of this change on the oyster fisheries. On the majority of British oysterages, except those few which still deal exclusively in the true natives, the stock of marketable oysters is maintained to a very large extent by relaying annually in March or April large quantities of imported French oysters. These oysters may in some instances remain on the beds for two or even three or four breeding seasons before being dispatched to market, but a great many are sold during the winter following that in which they are laid down. Those carried forward to another winter season are usually young oysters 2 years and 8 months old when purchased. The contribution made by such relaid oysters from France towards the natural spatfall on our beds is a matter for dispute among practical oystermen. It is possible that the passage from France, and the disturbance which accompanies taking up and replanting during the spring, may so upset the maturation of the gonads of these oysters that they do not breed effectively during the following summer; this point has not yet been fully investigated. It is, however, probable that during subsequent summers spent on English beds they behave in a very similar manner to native oysters. Evidence collected by the writer appears to indicate that this is so. Protagonists of the view that such Brittany relaid oysters do not give rise to any quantity of spat point to the fact that the natural spatfall obtained in rivers where Brittany oysters are laid down shows little, if any, improvement since the practice of importing these oysters began. This is undoubtedly true, but such poor spatfalls may be the result of the operation of a great many adverse factors the nature of which is not at present understood.

Since four grades of oysters are now sold almost everywhere, the beds are practically swept clean every winter of large oysters, those remaining in early spring being mainly very small stunted oysters or young oysters which were '2-year-olds' (actually 2 years and 8 months) when laid down. In March or April the grounds are replanted with a fresh consignment of '2- and 3-year-old' oysters from France, but, as indicated above, the rôle played by these oysters is uncertain. Therefore the stock of acclimatized oysters consists in the main of very small rejected adult oysters and beds of oysters 3 years old, together with such native half-grown oysters as the ground carries. It is therefore of some interest to know to what extent these young oysters may be expected to contribute to the stock of larvae in the rivers and hence to the spatfall. As already noted, the observations given in this paper tend to show that a gravid oyster doubles the number of embryos it produces each year during the first 4 years of its life, and that only when it is 4 years old does it play its full part in the reproduction of the species. We may therefore say that as regards the number of embryos which it produces a 4-year-old oyster is equivalent to at least two 3-year-old or four 2-year-old oysters. The balance is probably in fact more heavily weighted in favour of the use of adult oysters for breeding stock, for it is not yet established that among such 2- and 3-year-old oysters the percentage maturing as females is as high as among adults; the evidence at present available suggests quite the reverse. Although work which I have now in hand tends to show that the percentage of oysters maturing as females in their first year (i.e. their second summer) may, in favourable seasons, be larger than hitherto supposed, yet it is not likely that it will be found to exceed 25 %, and it is probable that on investigation the percentage of 2-year-old oysters maturing as females will be found to be less than 50 %; on the other hand, among well-nourished adult oysters it is likely that more than 50 % of the population will spawn as females in favourable seasons and perhaps, in exceptional circumstances, the whole population. If one assumes that the proportions of female spawners among populations of 2-, 3- and 4-year-old oysters are 40, 60 and 80 % respectively, in any given season, then, taking into account the known differences in brood strength, it is clear that as regards its contribution to the stock of larvae one 4-year-old oyster is equivalent to nearly three 3-year-old, or to eight 2-year-old, oysters. Further investigation is therefore likely to lend additional weight to the view that adult oysters are much to be preferred as breeding stock.

Thus it will be seen that the answer to the question whether it is wise to denude a bed of practically all large oysters each winter will depend very much upon whether the newly relaid Brittany oysters breed effectively during their first summer on English beds. If these oysters can be shown to breed early enough and freely enough to give a crop of spat capable of surviving the winter, then there is no reason for supposing that the removal of the major part of the stock of acclimatized adult oysters is likely to lead to any diminution in the natural spatfall. As mentioned earlier, the breeding of these *freshly laid* oysters has not yet been fully investigated, but the general opinion seems to be that they breed very late in the year on our beds during their first summer and that the spat settling is rather too small to survive in any numbers over the winter.

On beds where French oysters are not laid down, and which at the present day generally carry a rather meagre stock of native oysters, it is probable that the selling of several grades of oysters, resulting as it does in practically clearing the beds of all adult oysters, is definitely detrimental to the continuance of the fishery and the proper replenishment of the stock by the natural spatfall. On such beds it seems advisable to establish a reserve of large oysters for breeding purposes, and to replenish this reserve each year, to the extent of about 20 % of the stock, so as to allow for the annual mortality.

Summary

It is shown that the average number of embryos produced by a gravid oyster is approximately doubled each year until the oyster is 4 years old, when it may be regarded as adult. Estimates have been made of the quantities of embryos produced by one 1-year-old, eleven 2-year-old, fourteen 3-year-old and twenty-two adult oysters; the mean values for these year-classes are 91,600, 218,100, 462,600 and 902,900 respectively.

Since it is probable that the proportion of a population of oysters which matures in the female phase increases progressively up to the age of 4 years, it follows that adult oysters are for this reason superior to 2- or 3-year-old oysters as breeding stock, quite apart from the increased number of embryos produced by each oyster.

As the season advances there appears to be a marked decrease in the average

number of embryos produced by oysters of all ages maturing as females. In adult oysters the observations of brood strength appear to be grouped around two points and this suggests the existence of two distinct categories of adult female-spawning oysters differing considerably in the average number of embryos produced. No such separation into two groups can be observed in the observations of brood strength in 2- and 3-year-old oysters. The average brood strengths of the two classes of adult females appear to be about 1,230,000 and 500,000. It is suggested that this great difference is due to the existence of two types of female spawners, the one maturing as females from the outset of the season, and the other functioning as males early in the season and, following a sex-change, spawning again as females towards the second half of the season. In the first class of females all the reserves accumulated during the spring are available and the batch of eggs ripened is consequently very large, whereas in the second class a part of the reserve materials has already been utilized in maturing an early crop of sperms, with a consequent marked reduction in the number of eggs ripened. The tentative nature of these conclusions is stressed.

In the light of the data obtained concerning the relative fecundity of adult and half-grown oysters, the effect is considered of the practice, now general on British beds, of selling several grades of oysters, thereby depleting the beds of large oysters during the breeding season. It is deduced that on beds where French oysters are relaid each spring little diminution in the natural spatfall is likely to result, provided that it can be shown that these relaid French oysters breed satisfactorily during their first summer on British beds. This matter has not yet been fully investigated. On beds where new stocks of oysters are not laid down each year, it is suggested that a breeding reserve of large oysters should be established if the normal winter marketing operations result in serious depletion of the stock of such large oysters, as undoubtedly often happens on some beds.

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