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OBSERVATIONS ON THE BREEDING AND SETTLEMENT OF *MYTILUS EDULIS* (L.) IN BRITISH WATERS

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(Text-figs. 1–8)

The literature on *Mytilus edulis* is particularly extensive. The most comprehensive account yet published is that of Field (1922), who gives excellent descriptions of the anatomy, physiology and embryology, as well as the bionomics, of this species. White (1939) adds little additional information upon the breeding and growth of *Mytilus*. Pelseneer (1935) gives an extensive bibliography covering both breeding and growth, whilst of the more recent work upon the breeding behaviour, the contributions of Battle (1932), Whedon (1936) and Young (1942) are most important. The occurrence of larvae in the plankton has been described in detail by Thorson (1946) and others; Visscher (1927), Orton (1933), Kändler (1926) and many others have given much information upon the spat-fall and settlement in several localities.

In spite of this wealth of published data there still remains considerable doubt over the time of onset and the duration of the breeding period of *M. edulis*, especially in relation to environmental factors. In particular, few recent investigations on *Mytilus* from beds in the sheltered and estuarine areas of the British coasts have been published, whilst the conclusions to be drawn from the older work (Herdman & Scott, 1895; Johnstone, 1898; Scott, 1900, etc.) are conflicting and lacking in precision. Finally, no attempt has previously been made to investigate the breeding, settlement and growth of this species simultaneously in a number of distinct geographical localities. This was the aim of the investigation, described below, which was commenced in 1946 as part of a general investigation of the breeding, settlement and growth of a number of common sessile littoral animals, and which is still in progress.

The author is indebted to Mr J. Baird of the Mussel Purification Station, Conway, to Mr J. Porteous of Portree, and to Mr R. Chestney of Brancaster for their invaluable assistance in supplying material regularly throughout the investigation. In particular, the author is indebted to the late Prof. J. H. Orton, F.R.S., for generously given advice and criticism, and to the Directors of Imperial Chemical Industries, Paints Division, under whose auspices the investigation was conducted.

Materials and Methods

The major part of the investigation was completed in 1946 and 1947. In the former year, samples of at least fifty specimens of adult *M. edulis* were obtained every two weeks from Liverpool (Prince's Landing Stage pontoons); Plymouth (Marine pier); the Blyth Estuary, Northumberland; Ramsey, Isle of Man, and also from one of the outdoor sea-water tanks at the Marine Biological Station, Port Erin, Isle of Man, where a supply of *Mytilus* taken originally from Ramsey was kept. In 1947, weekly (and sometimes more frequent) samples of at least 100 individuals were examined during the spring and early summer. Some of these were obtained from Liverpool, Port Erin and Ramsey as before, but the bulk of the material was obtained from Loch Portree, Isle of Skye; Conway, from the beds below the Benarth Road; and Brancaster Staithe (north Norfolk), from the Creek. Only one sample was received from Plymouth in 1947. Owing to the poor physiological condition of the *Mytilus* obtained from the Blyth Estuary during 1946, samples from this source were discontinued in the following year.

In subsequent years, the spawning of *Mytilus* was investigated at Brixham, South Devon, whilst the settlement and growth was followed closely at Liverpool in 1946 and 1947, and at Brixham in 1948, 1949 and 1950 under intertidal and continuously submerged conditions. Some observations on settlement were also made at Ramsey, Conway, Blyth, Portree, and Brancaster in 1946 and 1947, and at the River Dart in 1950.

Wherever possible, records of air and sea temperature were kept, and in a few localities salinity samples or records of salinities were also obtained.

The stages of gonad development were assessed from the colour and thickness of the mantle, and the degree of development of ova and sperm ascertained from the microscopic examination of smears. In some cases, sections of the mantle were prepared in order to establish the criteria of each of the five stages of development, described below.

Settlement of the spat and its subsequent growth were followed by observations upon the density and size of young *Mytilus* clustered upon the byssus threads of adults, or from the examination of non-toxic panels exposed for the purpose at Liverpool (1946–7) and Brixham (1948–50). Further information was obtained by the examination of submerged and intertidal substrata where and when opportunity arose.

Anatomy and Development of the Gonads

In *M. edulis* the sexes are separate, although in the early stages of development it is difficult to distinguish between them. In both sexes, the reproductive system consists of many branching ducts, which ramify throughout the mesosoma or 'abdomen' (see White, 1939, p. 33) and the mantle, and which, in a well-developed specimen, frequently spread into the connective tissue between the other internal organs, and over the digestive gland. In the mantle, the gonads extend as far as the pallial muscle.

Outgrowths from the ducts terminate in follicles, in which ova and sperm are produced. In males, the follicles are more uniform in size than those in the female. In both they are extremely numerous.

There are five principal gonoducts in the mantle and these converge on each side below the pericardium. From this point, the main genital canal, on either side, runs to the corresponding genital papilla, which is situated immediately anterior to the posterior adductor muscle. Field (1922, pp. 182 *et seq.*) gives a full description of the morphology and histology of the gonads.

Stages of Gonad Development

The development of the gonads was referred to five arbitrary, but readily distinguished, stages, including a 'resting-spent' stage in which no trace of sexuality is apparent, as follows:

Stage O. Neuter or resting spent stage. No follicles in mantle tissue.

Stage I. Onset of gametogenesis and appearance of follicles in the mantle.

Stage II. Follicles well developed and filled with unripe ova and sperm.

Stage III. Ova ripe and capable of fertilization, sperm activated by sea water.

Recently spent stage. Most of follicles empty; a few relict ova and sperm present only.

Stage O. The mantle characteristics vary according to the amount of reserve food material stored therein. When 'fat' the mantle is thick, yellow-cream or buff in colour, and of a very smooth appearance. It contains abundant glycogen and considerable fat. No ova or sperm can be seen and the genital ducts are usually obliterated by the great growth of connective tissue containing the reserve food products.

In starved specimens, or those in poor 'fattening' areas, where little accumulation of glycogen occurs, the neuter mantles are thin and semi-transparent, and in these the onset of gametogenesis is more easily distinguished.

Stage I. This stage includes all specimens showing the first signs of gametogenesis. In this stage, the ovarian and testicular follicles can be distinguished in the mantle tissue. Regeneration of the follicles commences at the outer face of the mantle, forming a single layer.

In the male follicles, only sperm mother cells and spermatids are present, whilst in the female, the oocytes are small and few have budded from the germinal epithelium.

In this early stage of the development, the colour of the mantle in each sex varies considerably, depending on the degree of development of the follicles and the amount and distribution of residual glycogen in the connective tissue. The female mantle is usually a red-brown or orange, and the male a light orange upon which background the small, but opaque follicles are readily apparent.

Stage II. In this stage well formed but unripe spermatozoa and ova are present in the follicles, which are well developed and prominent. Owing to wide variations in the nutritional condition of *Mytilus* from different localities, the thickness of the mantle (i.e. the number of layers of follicles) cannot be taken as a criterion of development. At this stage, however, the colours of the male and female mantles are distinct, owing to the mass of sperm or ova in the follicles. The male mantle has a brownish ground colour, which is almost obscured by the opaque white follicles. The female mantle is reddish orange or amber in colour, although the presence of ova bestows upon it a distinct apricot hue. Owing to the smaller size and more irregular distribution of the follicles, the female mantle appears to have a much smoother texture than the male mantle.

Stage III. Morphologically stage III is similar to stage II, except that the mass of the gonad is greater, and the connective tissue lying between the follicles in the mantle is even more occluded, although great variability occurs in material from the several localities, presumably owing to differences in nutrition. The general colour of the stage III female mantle is a very definite apricot, due entirely to the colour of the ova. The stage III male mantle is usually a full cream, or a yellowish cream in colour. The colour changes at maturity occur in individuals with mantles of any thickness. Thus within certain limits maturity appears to be independent of nutritional conditions, and ripe gametes can be obtained from poorly nourished individuals with thin mantles, whilst individuals with very thick mantle walls may yet contain unripe ova and sperm (see Young, 1945).

The ripeness of the ova and sperm in these mature individuals was determined from observations of their behaviour in sea water, and whether artificial fertilizations could be induced. The spermatozoa, when ripe, appear to be activated by sea water, whilst unripe sperm remains immotile. In no case has motile sperm been observed within the testicular follicles, and motility is induced solely by contact with sea water. Artificial fertilizations can be made with motile sperm only. Smears of the follicles of stage III males show few spermatids; thus it is clear that in *Mytilus*, as in *Pecten maximus* (Tang, 1941), a decline in spermatogenesis takes place as the gametes become mature. Occasionally individuals are found in which the gonoducts are filled with sperm; in smears of the follicles of these, no spermatids are found. The ripe sperm are arranged in lamellae converging towards the centre of the follicle.

In the stage III female, owing to the great development of the ovaries, the oocytes are of irregular shape. Within each oocyte is a large germinal vesicle containing a prominent nucleolus. The extreme growth of the follicles and the reduction in reserve food materials almost obliterates the interfollicular connective tissue. The ovarian egg possesses a distinct vitelline membrane about 1 μ in thickness, which readily bursts under slight pressure. The cytoplasm is very granular.

On being shed into sea water, the ripe oocytes rapidly assume a more or less spherical form (*c.* 0·068 mm. in diameter). During this process, maturation occurs, the germinal vesicle breaking down and the first polar body being budded off, the entire process occurring spontaneously in less than 20 min. at 12° C. Field (1922), however, states that fertilization is necessary before the first polar body can be budded off. Unripe oocytes do not round off in sea water, nor does the germinal vesicle break down.

The breakdown of the germinal vesicle in sea water was regarded as a criterion of the physiological maturity of the oocyte, and was used as such throughout this investigation.

Recently spent. Recently spawned individuals of both sexes are readily distinguished by the semi-transparent mantle and mesosoma (see Field, 1922), usually of a reddish brown colour, in which a few relict ova or sperm can usually be found. It is only the presence of these residual gametes which enables the sex of the spawned individual to be determined. When the gametes are absorbed—probably by phagocytosis—all trace of sexuality is lost, and in *Mytilus* from most localities glycogen is rapidly accumulated in the connective tissue. It is unusual for less completely spawned individuals to be found, except at such times when spawning is slow.

The process of spawning has been observed *in vitro*. In both sexes the gametes are passed between the valves of the shell to the exterior, via the exhalant aperture. Sperm is emitted in a continuous stream, whilst ova are aggregated into short rods, which break up as they reach the exterior. No flapping movements of the shell have been observed. Emission of the eggs and sperm normally continues for 30–60 min., after which time spawning is virtually complete, only a few residual gametes remaining in the follicles.

Spawning Behaviour in Relation to Environmental Conditions

Data obtained from samples examined during the spawning investigations carried out from 1946 to 1950 are given in Tables I–VII for Liverpool (1946, 1947), Plymouth (1946), Conway (1947), Portree (1947), Brancaster (1947), Ramsey (1947), and Brixham (1948, 1949), respectively. In order to assess clearly the state of sexual maturity in each sample, an 'index' or 'mean stage' of gonad development was calculated from the data, the number of individuals falling into each of the four developing stages (i.e. 'O' to 'III') being multiplied by a numerical factor equal to the arbitrary rating of the stage and the sum of these products divided by the number of individuals in the sample. Thus, a weighted mean stage of development is obtained, which has a minimum

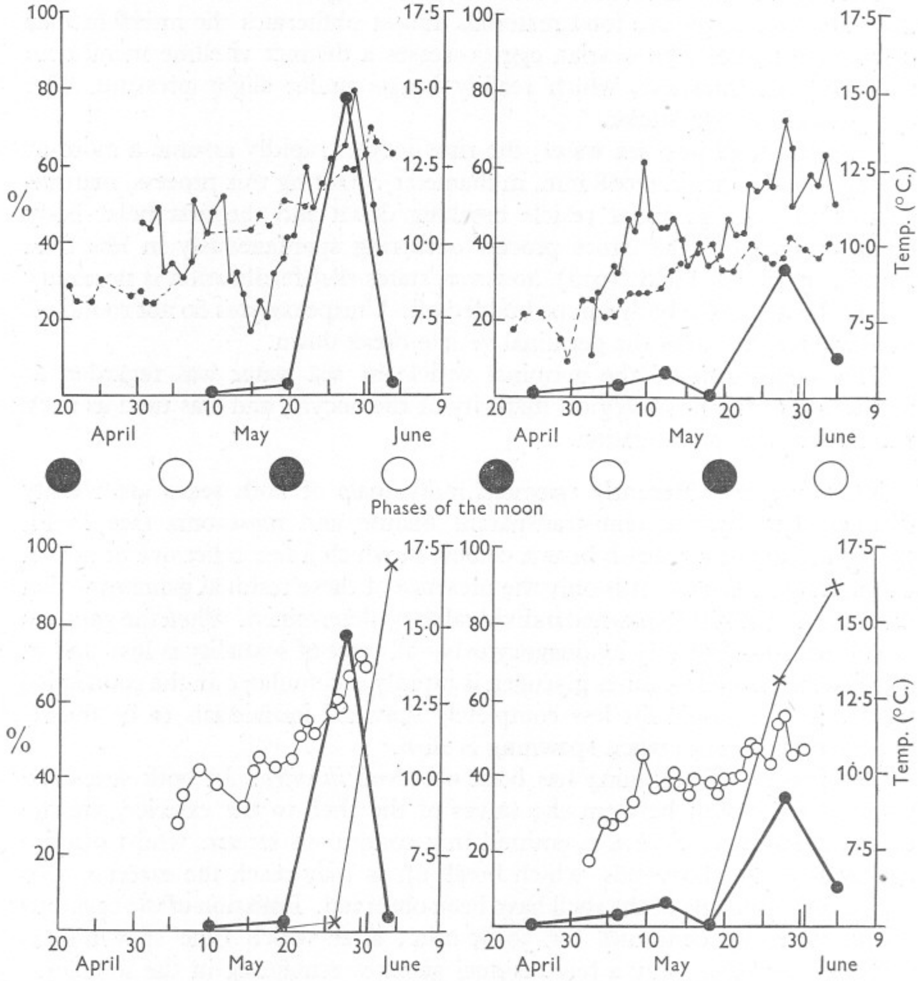

Fig. 1. Spawning of *M. edulis* at Conway in 1947, in relation to the lunar period and the sea and air temperatures, and the mean temperature to which the intertidal mussels were exposed during the spawning period.

Fig. 2. Spawning of *M. edulis* from the intertidal zone at Portree, Isle of Skye, in 1947.

●——●, % in sample recently spawned; ×——×, % resting spent; •- - -•, sea temperature (daily mean); •——•, air temperature (daily mean to which mussels exposed); ○——○, mean of sea and air temperatures.

value of zero, and a maximum value of 3·0 when the entire sample is sexually mature and ready to spawn. The weighted mean stage of gonad development for each sample is given in the tables.

The proportions of spawned males and females and of 'resting spent' individuals in each sample are plotted against time in Figs. 1–4 for Conway, Portree, Liverpool, Brancaster, together with the lunar phases, and daily sea temperatures. Where intertidal material was employed, mean air temperatures are also plotted.

TABLE I. BREEDING OF *MYTILUS EDULIS* AT LIVERPOOL

Date of collection	No. in sample	% of sample: Female Total	Female Ripe	Female Spawned	Male Total	Male Ripe	Male Spawned	Total % spawned	% Neuter	Total spawned and neuter	Index of gonad development
1946											
7. v.	75	48·0	25·3	1·3	49·3	26·7	2·7	4·0	2·7	6·7	2·39
17. v.	43	51·2	27·9	11·6	39·6	23·2	7·0	18·6	9·3	27·9	1·95
29. v.	50	52·0	6·0	46·0	22·0	4·0	18·0	64·0	26·0	90·0	0·30
13. vi.	45	2·2	0·0	2·2	4·5	0·0	4·5	6·7	93·3	100·0	0·0
27. vi.	31	0	0	0	0	0	0	0	100	100·0	0·0
16. vii.	43	0	0	0	2·3	0	0	0	97·7	97·7	0·023
28. viii.	29	0	0	0	0	0	0	0	100	100·0	0·0
16. ix.	33	16·1	0	0	21·4	0	0	0	63·6	63·6	0·36
22. x.	41	46·5	0	0	26·8	0	0	0	26·8	26·8	1·00
5. xi.	33	45·5	0	0	45·5	0	0	0	9·1	9·1	1·50
11. xii.	35	51·4	0	0	34·4	0	0	0	14·2	14·2	1·20
1947											
20. i.	19	36·8	0	0	63·2	0	0	0	0	0	1·31
27. ii.	25	40·0	0	0	48·0	0	0	0	12·0	12·0	1·08

TABLE II. BREEDING OF *MYTILUS EDULIS* AT PLYMOUTH

Date of collection	No. in sample	% of sample: Female Total	Female Ripe	Female Spawned	Male Total	Male Ripe	Male Spawned	Total % spawned	% Neuter	Total spawned and neuter	Index of gonad development
1946											
16. v.	42	57·0	42·8	4·7	43·0	43·0	0	4·7	0	4·7	2·76
3. vi.	45	48·9	11·1	37·8	51·1	8·8	42·3	80·1	0	80·1	0·60
17. vii.	49	22·4	0	8·2	10·1	0	4·0	12·2	67·5	79·7	0·36
29. vii.	58	8·6	0	1·7	6·9	0	3·4	5·1	84·5	89·6	0·19
13. viii.	69	23·2	0	5·0	11·6	0	2·2	7·2	65·2	72·4	0·46
28. x.	54	9·3	0	0	9·3	0	0	0	81·4	81·4	0·26
1947											
7. v.	69	45·0	1·5	0	43·5	1·5	0	0	11·6	11·6	1·25

From Fig. 4 it will be noted that, for a short period before spawning commenced, material from Brancaster was obtained from two sources, viz. the Creek, and a mussel pond, filled at high water, in which mussels are stored for marketing. The *Mytilus* obtained from this latter source were collected from the Creek and placed in the pond when the gonads were beginning to mature, two weeks before spawning took place. Daily temperatures of the water in this pond were taken, and from Fig. 4 it is clear that a considerably more rapid increase occurred here than in the Creek.

TABLE III. BREEDING OF *MYTILUS EDULIS* AT CONWAY

		% of sample									
		Female			Male						
Date of collection	No. in sample	Total	Ripe	Spawned	Total	Ripe	Spawned	Total % recently spawned	% Neuter	Total spawned and neuter	Index of gonad development
1946											
5. x.	99	36·3	0	0	51·5	0	0	0	12·1	12·1	0·95
23. xi.	102	52·8	0	0	46·1	0	0	0	1·2	1·2	1·16
10. xii.	48	45·9	0	0	43·8	0	0	0	10·3	10·3	1·83
1947											
27. i.	51	—	0	0	—	0	0	0	8·0	8·0	1·35
19. ii.	138	—	0	0	—	0	0	0	5·9	5·9	1·20
29. iii.	73	49·3	1·4	0	39·7	0	0	0	10·9	10·9	1·18
19. iv.	85	54·0	3·5	0	40·0	3·5	1·2	1·2	5·9	7·1	1·36
28. iv.	78	44·9	0	0	55·0	0	0	0	0	0	1·45
10. v.	107	51·4	5·6	0	48·6	1·9	0	0	0	0	1·59
20. v.	87	55·1	37·9	1·1	44·8	23·0	1·1	2·7	0	2·2	2·48
27. v.	84	41·7	0	33·3	55·9	0	46·4	79·9	2·4	82·1	0·35
3. vi.	110	0·9	0	0·9	1·8	0	1·8	3·6	97·2	99·9	0·0
16. vi.	97	0	0	0	0	0	0	0	100	100·0	0·0
1. vii.	165	0	0	0	0	0	0	0	100	100·0	0·0
15 vii.	83	0	0	0	0	0	0	0	100	100·0	0·0
28. vii.	57	—	0	0	—	0	0	0	91·5	91·5	0·9
14. viii.	40	12·5	0	0	7·5	0	0	0	80·0	80·0	0·20
24. ix.	57	26·3	0	0	22·8	0	0	0	51·0	51·0	0·65
1. x.	38	36·8	0	0	23·6	0	0	0	39·5	39·5	0·92
10 x.	50	38·0	0	0	48·0	0	0	0	14·0	14·0	1·13
31. x.	42	45·2	0	0	40·4	0	0	0	14·3	14·3	1·07
21. xi.	53	43·6	0	0	38·0	0	0	0	17·4	17·4	1·15

TABLE IV. BREEDING OF *MYTILUS EDULIS* AT PORTREE

		% of sample									
		Female			Male						
Date of collection	No. in sample	Total	Ripe	Spawned	Total	Ripe	Spawned	Total % recently spawned	% Neuter	Total spawned and neuter	Index of gonad development
1946											
16. ix.	32	9·4	0	0	6·6	0	0	0	84·0	84·0	0·16
22. x.	54	13·0	0	0	16·7	0	0	0	70·3	70·3	0·36
27. xi.	46	50·0	0	0	47·8	0	0	0	2·2	2·2	1·23
1947											
8. ii.	21	52·4	0	0	38·1	0	0	0	9·5	9·5	1·19
19. iv.	66	42·4	27·3	0	57·5	30·3	0	0	0	0	2·57
25. iv.	121	49·6	31·4	0	49·6	38·0	0	0	0·8	0·8	2·58
7. v.	85	43·5	37·6	1·2	54·0	41·2	1·2	2·4	2·4	4·8	2·69
12. v.	109	48·6	27·5	4·6	51·4	25·7	1·8	6·4	0	6·4	2·46
19. v.	177	39·6	31·7	0	60·4	44·6	0	0	0·5	0·5	2·76
28. v.	96	17·7	2·2	15·6	17·7	1·1	16·7	32·3	64·5	96·8	0·94
4. vi.	90	5·5	0	5·5	5·5	0	5·5	11·0	89·0	100·0	0·0
25. vi.	201	0	0	0	0	0	0	0	100	100·0	0·0

Table V. Breeding of *Mytilus edulis* at Brancaster

Date of collection	No. in sample	% of sample: Female Total	Female Ripe	Female Spawned	Male Total	Male Ripe	Male Spawned	Total % recently spawned	% Neuter	Total spawned and neuter	Index of gonad development
28. iv.	144	53·5	12·5	0	43·0	6·25	0	0	3·5	3·5	1·70
5. v.	157	42·0	14·7	1·9	58·0	21·6	2·5	4·4	0	4·4	2·17
10. v.*	131	45·0	27·5	3·8	55·0	25·2	1·6	5·4	0	5·4	
14. v.*	119	53·0	5·0	44·7	39·5	6·7	30·9	75·6	7·5	83·1	
14. v.	128	51·8	28·1	0	46·8	26·6	0	0	1·6	1·6	2·55
19. v.	133	54·1	25·6	3·0	41·4	18·1	2·3	5·3	4·5	9·8	2·24
26. v.	124	39·6	8·2	31·4	43·6	6·5	37·1	68·5	17·0	85·5	0·28
4. vi.	216	42·6	0	42·6	41·6	0	41·6	84·2	15·7	99·9	0·0
14. vi.	210	16·4	0·9	15·5	8·6	0	8·6	24·1	75·3	99·4	0·03
30. vi.	150	0	0	0	0	0	0	0	100	100·0	0·0
15. vii.	119	1·5	0	0·5	3·0	0	1·5	2·0	95·5	97·5	0·04
6. viii.	43	14·0	0	0	9·3	0	0	0	76·7	76·7	0·23
26. ix.	127	19·7	0	0·8	15·0	0	0	0·8	65·4	66·2	0·34
28. x.	46	41·4	0	0	43·4	0	0	0	15·2	15·2	1·00
19. xi.	37	59·4	0	0	35·1	0	0	0	5·4	5·4	1·24

* From Mussel Pond.

Table VI. Breeding of *Mytilus edulis* at Ramsey (Isle of Man)

Date of collection	No. in sample	% of sample: Female Total	Female Ripe	Female Spawned	Male Total	Male Ripe	Male Spawned	Total % recently spawned	% Neuter	Total spawned and neuter	Index of gonad development
1946											
18. vii.	40	15·0	0	15·0	12·5	0	12·5	17·5	72·5	100·0	0·0
30. viii.	49	0	0	0	0	0	0	0	100	100·0	0·0
12. ix.	100	14·0	0	0	7·0	0	0	0	79·0	79·0	0·26
6. xi.	48	6·2	0	0	20·8	0	0	0	73·0	—	0·33
2. xii.	40	15·0	0	0	15·0	0	0	0	70·0	—	0·53
1947											
3. v.	69	47·8	4·6	0	40·6	0	0	0	11·6	11·6	1·29
30. v.	48	20·8	0	20·8	12·5	0	12·5	33·3	66·6	99·9	0·0

Table VII. Breeding of *Mytilus edulis* at Brixham

Date	No. in sample	% of sample: Female Total	Female Ripe	Female Spawned	Male Total	Male Ripe	Male Spawned	% Neuter	Total % spawned	% standard error of spawned individuals	Total % ripe
1948											
20. iv.	40	45	25	0	53	35	0	2	0	0	60
28. vi.	45	53	44	2	47	35	0	0	2	6·7	79
5. v.	58	47	35	4	50	41	5	3	7	3·3	76
12. v.	57	44	14	25	49	9	30	7	55	6·7	23
20. v.	58	36	9	22	41	5	29	22	51	6·6	14
1. vi.	42	14	2	10	17	2	10	69	20	6·2	4
16. vi.	40	25	0	0	5	0	0	93	0	0	0
1949											
7. iv.	25	44	28	0	56	44	0	0	0	0	84
14. iv.	51	47	39	0	53	41	0	0	0	0	80
21. iv.	36	56	39	3	44	30	3	0	6	4·0	69
29. iv.	75	43	27	11	52	33	16	5	26	5·1	50
3. v.	86	36	15	14	40	21	17	24	31	4·8	35
20. v.	41	29	2·5	22	37	5	24	34	46	7·8	7·5
25. v.	60	25	0	25	35	7	15	40	40	7·5	7·0
3. vi.	35	6	0	0	14	0	6	80	6	4·0	0

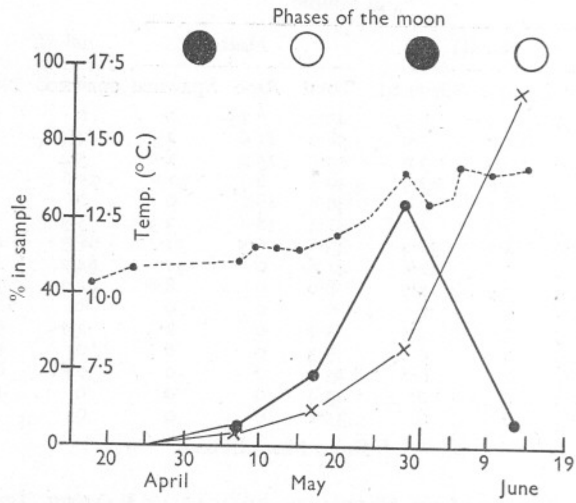

Fig. 3. Spawning of *M. edulis* at Liverpool in 1946. ●——●, % recently spawned; ×——×, % resting spent; •- - - -•, sea temperature.

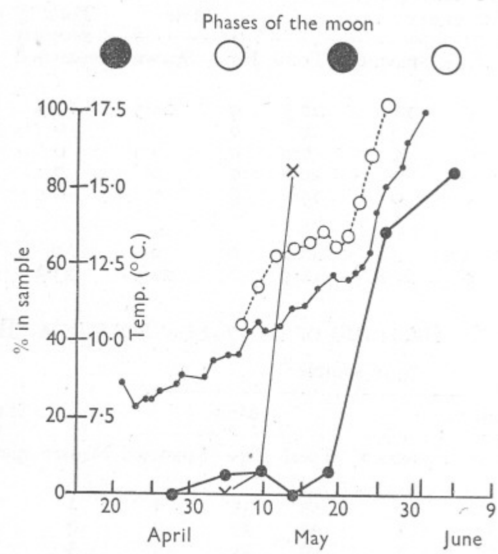

Fig. 4. Spawning of *M. edulis* at Brancaster Staithe, Norfolk, in 1947. ●——●, % recently spawned in creek; •——•, temperature in creek; ×——×, % recently spawned in pond; ○ - - - ○, temperature in pond.

The results for the material obtained from Blyth (1946) and for the material from the plaice tanks at Port Erin (1946) are not tabulated, as spawning had occurred before the first samples were obtained. In 1947 only two samples were obtained from Ramsey (Isle of Man), spawning having taken place

TABLE VIII. SUMMARY OF THE SPAWNING BEHAVIOUR OF *MYTILUS EDULIS*

Locality	Date of commencement of spawning	Date of completion of spawning	Duration of spawning period (days)	Sea temp. range between spawning commencement dates (° C.)	Phase of moon at spawning and date	Approx. date of commencement of gonad ripening	Approx. temp. at commencement of ripening (° C.)
1946							
Liverpool	7. v.	13. vi	31	11·5–14·0	F.M. 17. v.	Mid April	8·5
Plymouth	16. v.–3. vi	3. vi	18	11·5–13·0	F.M. 17. v.		
Blyth Estuary	—	6. vi†					
Ramsay (I. of Man)	—	10. vi†					
1947							
Liverpool	19–27. v	6. vi	18	12·5–15·0	N.M. 20. v.	Early May	8·0
Ramsey	3–30. v	30. v	27	?	F.M. to N.M. 20. v.	Early May	
Brancaster (pond)	10–14. v	19. v	9	12·0–14·5	L.Q. 12. v.	Late April	8·0
Brancaster Creek	19–26. v	14. vi	26	12·0–15·5	N.M. 20. v.	Late April	8·0
Portree	19–28. v	4. vi	16	10·0–10·5 (9·5–12·0)*	N.M. 20. v.	Late March	6·5
Conway	10–14. v	19. v	9	11·5–13·0	N.M.	Late April	8·5
1948							
Brixham	5–12. v	1. vi	27		N.M.	March	9·0
1949							
Brixham	21–29. iv	3. vi	51	8·5–12·0	F.M. 13. iv. N.M. 28. iv.	March	6·5
1950							
Brixham	29. iv.–11. v	5. vi	37	10·5–13·0	F.M. 2. v.		
River Dart (Greenway)	28. iv.–18. v	18. v	21	10·5–13·5	F.M. 2. v.		

* Means of sea and air temperatures.
† Completed before this date.

between the dates of collection (see Table VI). Only small numbers of adult *Mytilus* could be found upon the pontoons of the floating landing stage at Liverpool in 1947, owing to severe storms during April, when the bulk of the population had been washed away. Observations were, however, made upon those which remained.

In Table VIII the spawning behaviour of *Mytilus* in the several localities is summarized, together with sea temperatures, etc.

In every case spawning commenced during the period late April–May and was completed within 3–4 weeks except at Brixham where a few (5%) ripe individuals were found a week or two later. Emission of ova and sperm during the first 7 days was always intensive, at least 70–80% of the population releasing its genital products (see Figs. 1–4). The remaining proportion of the population spawns during the ensuing fortnight or 3 weeks. No evidence of periodic spawning, nor of more than one discrete spawning period, was obtained in any locality during the 4 years of investigation.

Spawning, in each locality except Portree, commenced when the sea temperature had risen to 11·0–13·0° C. At Portree, however, the sea temperature (taken at high water) at the commencement of spawning was 10·0–10·5° C. If, however, the daily mean temperature to which the intertidal mussel bed was exposed during this period is computed from the maximum and minimum air temperatures, and the sea temperature, in relation to the times of high and low water, using a linear interpolation in estimating the air temperatures at the times of low water (where these do not correspond with the times of minimum and maximum air temperatures), it is shown that spawning commenced during a period when the daily mean temperature rose from 9·5 to 12·0° C. Similarly, spawning took place in the intertidal bed at Conway at the period when the daily mean temperature to which the bed was exposed rose from 10·5 to 13·0° C.

In the majority of the fourteen series of observations spawning was initiated during a period of spring tides, e.g. at Liverpool in 1946 and 1947, and Brixham in 1948 and 1949 after a new moon, and at Plymouth in 1946, and Brixham in 1949 and 1950, after a full moon. The mussels in the storage pond at Brancaster, however, spawned at a last quarter period, although those on the Creek beds commenced to spawn a week later, i.e. at new moon. Further, in each locality and in each year, spawning of *Mytilus* coincided with a period of predominantly bright sunny weather with little or no rainfall.

Period of Spawning

Of the many published accounts of the spawning period of *M. edulis*, two only refer to localities in which the present investigations were made, viz. Plymouth and the Isle of Man.

Matthews (1913) states that the spawning period of *M. edulis* at Plymouth in 1911 lasted from January until March, although samples which she took between May and August suggested that spawning took place in early spring. However, Matthews found that artificial fertilizations could be made only in late May, which suggests that natural spawning, in that year, took place at this period. The results of the investigations in 1946 (see Table II) are in conformity with this suggestion, for few ripe individuals were observed later than May. Additional evidence of a spring spawning at Plymouth is given by Lebour (1938) who states that the veliger of *Mytilus* is a principal constituent of the plankton in late spring and early summer.

Bruce (1926) obtained mussels from Ramsey, Isle of Man, and kept them for experimental purposes in a shallow concrete tank of running sea water at Port Erin. He states that spawning occurred at the end of May, eggs and sperm 'running freely on May 27th, 1925'. The results for Port Erin tank material in 1946 and for Ramsey material in 1947 point to a May spawning (see Table VI).

The majority of the published records of the spawning of *M. edulis* in British waters are based upon observations of the presence of larvae in the plankton or of settlement, although a few are based upon observations of gonad development. These records, in the main, suggest April and May as the spawning months (cf. Table VIII). In the Barrow and Morecambe Bay area, Herdman & Scott (1895) found mature *Mytilus* in May. Working in the same area and employing microscopic examination of the gonads as well as observations upon the plankton and upon settlement, Johnstone (1898) describes rapid emission of genital products in July 1898, but suggests that spawning may begin in April, and concludes that spawning occurs throughout May, June, July and August. Scott (1900) reports spawning of females only in tanks at Piel, and upon the Barrow beds, in May 1899, the emission of ova continuing until 13 June, when the males also spawned. In more recent years, Daniel (1921) gives April and May as the spawning period in 1921, but as late March in the following year (a warm year). The heavy spat-fall in Morecambe Bay in June 1933, reported by Orton (1933), suggests a May spawning (cf. spawning at Liverpool in 1946 and 1947).

McIntosh (1891) gives March–May as the spawning period of *Mytilus* in the Tees, Esk and Humber, whilst Williamson (1907) concludes that March and April are the months during which maturity occurs on the Scottish beds. At Millport, Elmhirst (1923) describes the spawning period of *Mytilus* as April to June, although Pyefinch (see Harris, 1946) finds that the heaviest settlement takes place during August and September. In a more recent paper (Pyefinch, 1950), however, he modifies this view extensively, suggesting that the heaviest settlement occurs in June–July. It would thus seem that spawning at Millport normally takes place in late May or early June.

There are a number of references to the spawning of *Mytilus* upon the western sea-board of Europe. Spärck (1920) states that spawning occurs in the Limfjord in May and June, and Thorson (1946) describes the sudden appearance of the veligers of *Mytilus* in late May or early June in the Øresund and the Isefjord. Kändler (1926), however, describes the occurrence of larvae of *Mytilus* at Heligoland over a very long period, although he states that a maximum occurs from April to June. Werner (1939), in reviewing the literature upon the spawning of North Sea lamellibranchs, suggests that *M. edulis* spawns from spring to autumn, and quotes in support the work of Havinga (1929) based upon the state of maturity of the gonads. On the other hand, Berner (1935), as the result of observations upon the gonads of *Mytilus* at Calais, states that the spawning period is February and March. The season of sexual maturity of *M. edulis* in the Gulf of Naples is stated by Lo Bianco (1899) to be March and April.

The spawning of *M. edulis* in the western hemisphere has been described by Stafford (1912), Field (1922), and Battle (1932). The former states that spawning takes place on the west coast of Canada in June, whilst Battle (1932) gives the spawning period as July to September in Passamoquoddy Bay. Field (1922) states that spawning commences on the Atlantic coast in April and continues until September. The work of Engle & Loosanoff (1944) suggests a principal spawning in late May in Milford Harbour, Long Island.

The past records of the period of spawning of *Mytilus* thus, in general, show considerable variation in the time of onset and duration, although a number agree with the observations described in this paper.

The Duration of the Spawning Period

In the present investigation the duration of the spawning period of *Mytilus* was followed on fourteen occasions. In eight of these, spawning was completed in 3–4 weeks (see Table VIII), in two in 9 days, whilst in two others (at Blyth and Ramsey in 1946) it was not possible to make an estimate of the duration of the spawning period. On the remaining occasions (at Brixham in 1949 and 1950) a few unspawned but ripe *Mytilus* (both males and females) were observed until 3 June in 1949, and 5 June in 1950, giving spawning periods of 51 and 37 days respectively. Observations at Brixham were too limited to enable the incidence of spawning to be followed during the spawning period in 1950, but in 1949 55% of the population had spawned during the first 14 days, whilst over 90% had completed spawning within 28 days from the commencement. It is possibly significant that, in both years, the sea temperature rose rapidly immediately prior to spawning, and then fell again, to rise slowly towards the maximum previously recorded. Further, the mean sea temperature at Liverpool in 1946 rose more slowly than in 1947, whilst the duration of spawning in the previous year was greater than in 1947 (31 days and 18 days respectively). The rapid spawning-out of the population at Conway and in the pond at Brancaster in 1947 may be associated with the rapid rise in temperature in those localities at the onset and throughout the period of spawning. It, therefore, seems possible that not only is the onset of spawning determined directly or indirectly by a rapid rise in temperature, but that the rate of increase of temperature subsequently influences the rate of spawning of *M. edulis*, a rapid increase of temperature producing a higher spawning intensity.

Once spawning was completed, in no locality or year was any evidence obtained of rapid re-development of the gonads, leading to a later spawning. The later maturation of the gonads of smaller and younger individuals, described by Jensen & Spärck (1934) was not observed in the present investigation.

Thus, in the localities investigated, spawning is limited to a period of 3–4 weeks in the late spring, during which time the entire adult population releases its genital products. This appears to be true even of semi-starved individuals with thin poorly developed mantles (e.g. those from Blyth).

Many writers in the past have ascribed a longer breeding season to *M. edulis* than the above. Care must be taken in comparing their findings with the present ones as many of the former are based upon the results of systematic plankton observations (e.g. Stafford, 1912, on the west coast of Canada; Kändler, 1926, at Heligoland; Borisiak, 1909, in the Black Sea; Thorson, 1946, in the Øresund; and Lebour, 1938, at Plymouth) or upon observations of intensity of settlement (Harris, 1946). In these instances there is no assurance of a homogeneous larval population (i.e. larvae spawned in one hydrographical area), and the long season of larval abundance or settlement may be due entirely to the incursion of larvae from other localities or from deeper beds in which the local hydrographical conditions cause a later, or earlier spawning. In this connexion, it should be noted that Thorson (1946) observed the presence of the larvae of *M. edulis* in the plankton over a considerably longer period in Øresund than in the relatively enclosed body of shallow water in the Isefjord.

Field (1922), although making observations in many localities on the eastern sea board of America, does not give details of the variation in the spawning period, and in America only Battle (1932) investigated the length of the breeding period of *Mytilus* by gonad examinations as well as plankton observations; she concluded that, in Passamoquoddy Bay, the spawning period lasts for 3 months.

Bruce (1926) and Daniel (1921) ascribe a short breeding period to *Mytilus*. The former states that spawning in laboratory tanks at Port Erin, which commenced in 1925 on 27 May, was completed by 5 June, whilst the latter observed a short spawning period on the Morecambe beds in 1921 and 1922 which were both warm years. He quotes Mr F. Gardner, the bailiff, as saying spawning occurs in April, the actual date varying according to the weather, and that some beds ripen before others. Berner (1935), too, finds that *M. edulis* at Calais spawns for a brief period only. Similarly, the fishermen at Brancaster Staithe, Norfolk, give the spawning period of the mussels in the creeks as April or May and state that the water becomes milky with milt suddenly, this condition lasting for a few days only, after which the mussels are thin and watery.

Thus, of those workers whose conclusions were based upon gonad examinations, only Battle (1932) and Havinga (1929, quoted by Werner, 1939), have found evidence of a lengthy period of spawning.

The intense initial spawning so strongly in evidence in most localities in 1947 has been noted by several workers, e.g. Field (1922), Daniel (1921), and Bruce (1926) and suggested by Thorson (1946), who observed a very sudden rapid increase in the number of larvae in the Limfjord, this high density lasting for a short time only.

It would thus appear that from observations upon the gonad condition, *M. edulis* may spawn during a period of 3–4 weeks, with the major release of ova and sperm occurring during the first 7 days, as was recorded in most localities in the present investigations, or that this species may spawn over a considerably longer period, the gonads possibly regenerating and discharging several times during the period (e.g. Battle, 1932; Havinga, 1929). At Plymouth and Brixham in 1946 and in 1949 and 1950 respectively the period during which a small number of ripe individuals could be found was greater than in other localities. Such observations suggest that where the initial rate of increase in temperature is small, the spawning period of *Mytilus* becomes protracted. In this respect it is significant that the rate of increase of sea temperature in the two localities in which Battle made her investigations (St Croix and Birch Cove, Passamoquoddy Bay) was low, the maximum temperature being slightly less than 14° C. in each instance, and the mean rate of increase 0·05° C./day during the spawning period. It appears probable that an upper limiting temperature to the regeneration of the gonads is achieved in those localities where spawning takes place during a short period, or that the temperature coefficient for laying down reserve materials is greater than that controlling the regeneration of the gonads; either or both would limit the spawning period in those localities where the sea temperature rises rapidly.

Ripening of the Gonads

In all localities, ripening of the ova and sperm commenced during a period of up to 6 weeks before the onset of spawning. This is shown clearly in Tables I–VII by the increase in the proportion of ripe individuals and the index of gonad development. Ripening of the gonads took place rapidly within 3 weeks of spawning at Conway and Brancaster in 1947, whilst at Portree in the same year a fair proportion of ripe individuals were found 5 weeks before the commencement of spawning (see Figs. 1, 2 and 4 for Conway, Portree and Brancaster respectively). Similarly, at Brixham in 1948 and 1949 some ripe individuals were present in samples taken during March, 5 or 6 weeks before the beginning of the spawning period. It is possibly significant that the minimum sea temperature at Brixham and Portree is considerably higher than at Conway and Brancaster (see Table IX), where the rate of increase in sea temperature from the annual minimum is greater, this greater rate of increase in temperature leading to a later but more rapid development of the gonads and a more rapid increase in the proportion of ripe individuals immediately before the occurrence of spawning.

TABLE IX. RATE OF INCREASE OF SEA TEMPERATURE

Locality	Seasonal minimum temperature (mean of 7 days)	Rate of increase in temperature from minimum to time of spawning
Portree (1947)	4·5° C.	0·066°/day
Conway (1947)	1·0° C.	0·151°/day
Brancaster (1947)	0° C.	0·142°/day
Brixham (1949)	7·5° C.	0·102°/day

A possible relation between sea temperature and rate of development of the gonads of *M. edulis* is further emphasized by the observation that the sea temperature at the commencement of the period of ripening is 7–8·5° C. in most localities where such estimates could be made (see Table VIII). It would thus seem that the gonads of *M. edulis* mature when the sea temperature is above *c.* 7·0° C., and that the rate of ripening is roughly proportional to the rate of increase in temperature.

There appears to be no direct relationship between nutrition and ripening of the gonads of *Mytilus*. Loosanoff (1942) has shown that *Mytilus* can ingest food at any time at temperatures above 0° C., whilst the observation that many *Mytilus* with very poorly developed mantles from Portree contained ripe ova and sperm, and spawned normally, suggests that maturity is not dependent upon good nutritional condition. Young (1942 and 1946) has also reached this conclusion in the case of *M. californianus*. In this connexion it is possibly significant that the glycogen content of *M. edulis*, as in *Echinus* and *Ostrea*, is reduced to a minimum value immediately prior to spawning (Daniel, 1921; Stott, 1931), suggesting that the development of the gonads occurs at the expense of reserve nutrient and is not dependent upon food ingested at this period, (see Fig. 8, p. 469).

During the period of ripening of the gonads in 1947, estimates were made of the proportion of mature ova obtained from the mantles of ripe individuals. As the spawning period approached, the proportion of ova rounding off in sea water, with the loss of the germinal vesicle, increased from a small value to over 90%. Artificial fertilizations made at these latter times were very successful, 80–90% of the fertilized ova segmenting normally. Further, as the gonads develop, an increasing proportion of the ova ripen at the same time in each individual.

Spawning Inducements

The rapidity of onset and the magnitude of the initial spawning phase of *Mytilus* strongly suggests that spawning is induced by a stimulus affecting the bulk of the population. That this stimulus is external is indicated by the variation in the length of the period during which a high proportion of mature individuals is found in the several localities before the onset of spawning.

The information derived from the present investigation strongly suggests that it is a rapid rise in the mean temperature to which the mussels are exposed to 11·5–13·0° C. which induces spawning (see Table VIII). It is also possible that the coincidence of the onset of spawning with a period of spring tides, in twelve of the fourteen instances summarized in Table VIII, is significant. Inshore temperatures, however, have been shown to rise in many localities during periods of spring tides in late spring and early summer, so that the apparent positive correlation between spawning and spring tides may in fact be due to the rise in sea temperature at new and full moon at this time of year.

Berner (1935) has described the spawning of *M. edulis* at Calais after a rapid change of sea temperature from 5 to 10° C., and a sudden decrease in salinity, whilst Nelson (1928) and Runnström (1929) give 10–12° C. and 14–16° C. respectively as the temperatures at which spawning takes place. Hutchins (1947) lends further support to the conclusion that *Mytilus* spawns at *c.* 11·5° C. in observing that the northern limit of distribution of the species is coincident with the 10° C. summer isotherm. Battle (1932), however, discovered no correlation between spawning and temperature in Passamaquoddy Bay. Whedon (1936), Coe & Fox (1942) and Young (1942, 1946) all state that there is no definite evidence that spawning in *M. californianus* is induced by temperature, or by temperature changes.

However, Battle (1932) found that the gonads of *M. edulis* at Passamaquoddy Bay matured at new moon during the summer months and that spawning followed immediately. Korringa (1947) implicitly suggests that the full moon spring tides were almost obliterated in this area in 1930, when the observations were made, and therefore ripening in normal years might occur at both new and full moon tides. Lunar periodicity in spawning is well known in many species (see Korringa, 1947, for an extensive bibliography), but the mechanism is extremely obscure. In *M. edulis* the effect of the greater variations in hydrostatic pressure at spring tides upon individuals with mature gonads may be of importance in inducing spawning. However, personal observations of spawning *in vitro*, and the observation of Bruce (1926) of rapid spawning in static tanks at Port Erin suggest that pressure is not a principal factor in stimulating mussels to spawn.

During 1947 attempts were made to induce *Mytilus* to spawn in the laboratory as the result of changes in environmental conditions. The results were extremely conflicting. It was found that mechanical shock (by pulling the byssus threads, or agitating vigorously) almost invariably produced a positive response from a number of the ripe mussels employed in the experiments. Young (1945) suggests that mechanical shock is the stimulus inducing spawning in *M. californianus* under natural conditions. Similarly, Field (1922) states that rough handling induces spawning in *M. edulis*, whilst Orton (1924) has shown that dredging operations during the breeding season can cause oysters to spawn. On the other hand, instances of spawning of *M. edulis* have been observed frequently under completely static conditions *in vitro*.

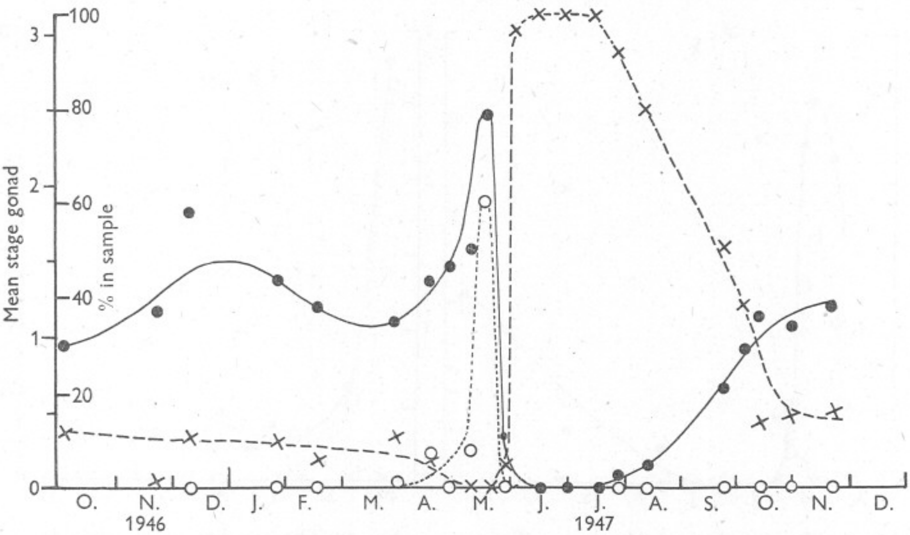

Fig. 5. *M. edulis*. Breeding at Conway, 1946–7. ●—— ●, mean stage of gonad development; × – – – ×, % of resting spent; ○······○, % of ripe adults.

Alternations of high and low temperatures, variations in salinity, and a mixture of mature sperm and ova with the sea water in which the experimental *Mytilus* were immersed produced conflicting results. Few experiments were made, however, and the results therefore are of little significance. A more detailed investigation of spawning inducements is now in progress.

Post-Spawning Changes in the Gonads

Within 10–20 days after spawning, a great regression of the gonads occurs. The decrease in volume on spawning is compensated to some degree by the intake of water (see Daniel, 1921), the mantle tissues becoming soft, spongy and semi-transparent. The residual ova and sperm are probably absorbed by phagocytosis by the cells of the follicle walls, and all trace of sexuality is lost. These individuals are in the 'neuter' or 'resting spent' stage. Growth of the connective tissue of the mantle and mesosoma also takes place immediately, and glycogen and some fat appear. During the latter part of June and throughout July, the amount of glycogen increases at a rate dependent upon the supply of food, until, by the end of July, *Mytilus* from good fattening beds (e.g. Brancaster and Conway), possess thick mantles filled with granules of glycogen. In general, there is no sign of the re-development of the gonads during this period, but at Plymouth in 1946 a small proportion of males and females could be distinguished in July, the proportion remaining constant until the final sample was taken in October 1946 (see Fig. 7).

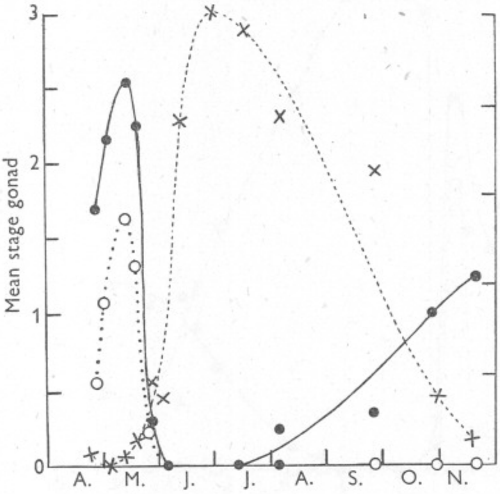

Fig. 6. The breeding of *M. edulis* at Brancaster Staithe, north Norfolk, in 1947.

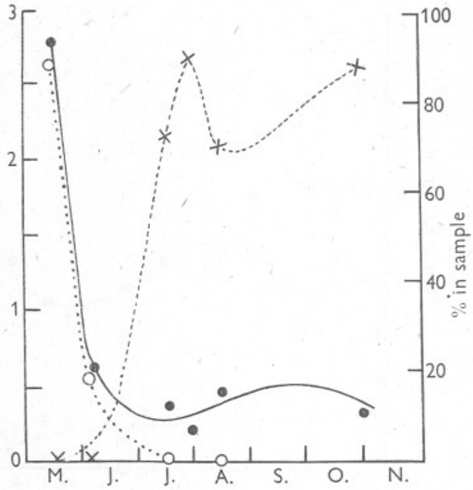

Fig. 7. The breeding of *M. edulis* at Plymouth, in 1946.

●—— ●, mean stage of gonad development; × – – – ×, % resting spent; ○······○, % ripe adults.

In the other localities the first traces of returning sexuality were observed in late July or during August, the gonads beginning to invade the mantle lobes in some specimens (stage I) (Figs. 5, 6 and 8). This process continues throughout September and October, until, by mid-November, the proportion of 'neuter' individuals is small. The connective tissue becomes concentrated as the follicles develop and the glycogen and fat become wedged between them (see Daniel, 1921).

From December 1946 until the end of March 1947, no further development of the gonads took place, but during late March and April a rapid increase in the mass of the gonads occurred, culminating in maturation and spawning in May.

Thus, in *M. edulis*, a non-reproductive period, during which large amounts of reserve food products are accumulated, occurs between successive reproductive phases.

The seasonal variations in the glycogen and fat content of *Mytilus* have been studied by Daniel (1921), who employed material from the Mersey and from Morecambe Bay. If Daniel's figures for the proportion of glycogen and fat per unit weight of the ash-free dry substance are compared with the index of gonad development for the Liverpool material employed in the present investigation (see Fig. 8) it is significant that whilst gonad development was stationary from December to March 1946, the glycogen content of

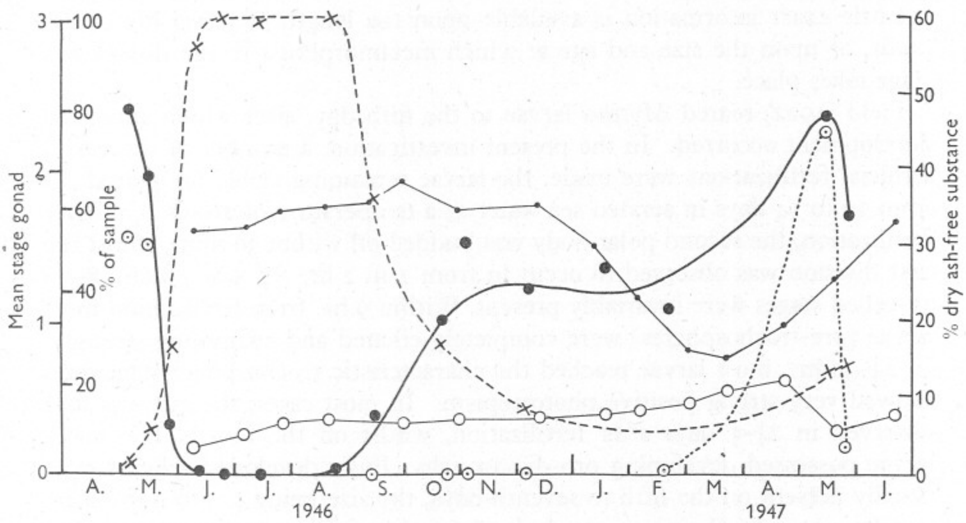

Fig. 8. *M. edulis*. Breeding at Liverpool, 1946–7. •——•, mean stage of gonad development. ×----×, % of resting spent. ●——●, % glycogen; ○——○, % fat; % composition by weight of ash-free substance, from Daniel (1921).

Mytilus declined markedly, suggesting that some was used in the ordinary metabolic processes during a period of low temperatures and possible scarcity of food. This is also suggested by the continuance of the high value of the respiratory quotient after the period of rapid accumulation of glycogen (Bruce, 1926); the decrease in the R.Q. in March and April suggests the conversion of carbohydrates to fats, for storage in the maturing ova. It appears probable that scarcity of food, or the inhibition of assimilation of food by low temperatures, is responsible for the decrease in glycogen content during the early months of the year, as although Dodgson (1928) has reported the opening of the shells and the maintenance of ciliary currents in *Mytilus* even at 0·0° C., he further states that assimilation does not occur at temperatures below 4° C.

Development of the Larvae

Berner (1935) suggests that, in *M. edulis*, the sperm is shed into the sea and drawn into the mantle cavity of the female mussel, where fertilization takes place, the developing embryos being ejected when ciliated. No evidence to substantiate this has been obtained in the course of the present investigation; of the many mussels examined during the spawning period, none has been observed to contain developing larvae in the mantle cavity. Further, sperm from ripe males retains its activity in sea water at a temperature of 15° C. for at least 3 hr., and the ova, once discharged into sea water, are fertilizable for at least the same period.

Little exact information is available upon the length of larval life of *M. edulis*, or upon the size and age at which metamorphosis to the dissoconch stage takes place.

Field (1922) reared *Mytilus* larvae to the fifth day, after which abnormal development occurred. In the present investigation, a number of successful artificial fertilizations were made, the larvae remaining viable for periods of from 10 to 14 days in aerated sea water at a temperature of 16–18° C. After fertilization, the second polar body was budded off within 30 min., whilst the first division was observed to occur in from 1 to 2 hr. In 5 hr., many 8- to 32-celled stages were invariably present. Within 9 hr. from fertilization most larvae (pre-trochospheres) were completely ciliated and swimming strongly. In 24–30 hr., most larvae reached the characteristic trochosphere stage, and showed very strong positive phototropism. In most cases, the gut was first observed in $2\frac{1}{2}$–3 days after fertilization, whilst on the fourth day, many larvae possessed developing pro-dissoconchs. Fully developed veligers were usually present on the fifth to seventh days, the size being *c.* 100–110 μ long and 80 μ broad. Owing to the lack of suitable food organisms no further development occurred, although living larvae persisted for a further 3–7 days. No dissoconch larvae were observed, and no significant increase in size was recorded.

Estimates of the duration of larval life in the sea, based upon observations of the onset of spawning and the commencement of settlement, are accurate only if the larval stock is homogeneous, and if larvae developing from the initial spawning do not suffer a heavy mortality. Thus, the estimates based upon the observations set out in Table X cannot be taken as strictly accurate, but only as an indication of the probable duration of larval life. As a result of these observations, it would seem that the duration of the period between initial spawning and the commencement of settlement is 3–4 weeks. However, the normal larva life may well be 4 or 5 weeks, for in most of the localities in Table X the maximum rate of settlement was attained 2 weeks after the first few spat were observed. Battle (1932) records the occurrence of larvae 310–360 μ in length in 14–21 days, whilst Field's (1922) figures combined with those of Matthews (1913), suggest a considerably lower rate of development, metamorphosis and settlement occurring in *c.* 10 weeks.

From the sizes of spat found upon panels exposed for periods of 7 days during the period of settlement of *M. edulis*, settlement can take place at any time or size after the dissoconch is formed, i.e. from a length of 400μ to 1 mm. Thorson (1946) comments upon the great variation in size at which metamorphosis occurs (250–400μ) and also the great differences in the rates of development, as shown by gill filament differentiation at different sizes.

Nelson (1928) records the ability of the advanced larvae to float near the surface by means of a gas bubble within the valves of the shell, even at a size of 900μ. Attachment is effected initially by the foot, after the larva has become stereotropic. Nelson (1928) states that many surfaces may be explored before attachment by the byssus takes place. The foot is frequently employed as a means of locomotion on the surface film of the water.

Settlement of the Larvae

In general, the period of settlement of *M. edulis* in British waters lasts from May to early July. The observed duration of settlement of the spat of this species in five localities (see Table X) is from 4 to 7 weeks. In each case it is

Table X. Estimated Duration of Larval Life and of the Period of Settlement of *Mytilus edulis*

Locality	Date of commencement of settlement	Estimated larval life (days)	Duration of period of settlement (weeks)
Liverpool	31. v. 46–6. vi. 46	18	6
	13. vi. 47–20. vi. 47	24	5
	8. vi. 48–15. vii. 48		6
Conway	3. vi. 47–16. vi. 47	21	4
Portree	4. vi. 47–25. vi. 47	21	6
Brancaster	4. vi. 47–14. vi. 47	25	5
Brixham	7. vi. 48–11. vi. 48	28	7
	29. v. 49–25. v. 49	26	6
	17. v. 50–31. v. 50	24	6

Mode (of 100) at 0·5 mm.

probable that the extended period is largely due to the incursion of larvae from later-spawning beds in the same general locality. This is exemplified by the occurrence of two distinct maxima separated by about 2 weeks in the number of spat settling at Brixham in 1948. The long periods of settlement described by several workers (e.g. Harris, 1946; Pyefinch, 1950) are possibly due to such an incursion of larvae. Thus a longer period of settlement would be more likely to occur in a deep-water locality, than in a shallow-water locality in which a greater degree of homogeneity in spawning might be expected.

Plankton observations at Brixham in 1949 suggest that although *Mytilus* larvae may be present during July and early August in small numbers, settlement is rarely observed later than mid-July (see also Engle & Loosanoff, 1944).

Mytilus settles most abundantly in areas offering some degree of shelter from water currents and wave action. Settlement is invariably small upon clean smooth non-toxic exposure panels (e.g. glass, bakelite), but can be heavy on panels providing some degree of shelter by reason of the fouling already upon them. Settlement is always heavier upon inset panels than upon panels the surfaces of which are raised 0·5–1·0 cm. above the substratum; in this latter instance, settlement is greater in the depressions between panels, even where the panels are known to be completely non-toxic. Settlement is also greater upon the upper edges of these panels. The heaviest settlements always occur upon hydroid colonies, the rough or frayed surfaces of ropes, and rough shells. In raft exposures, *Mytilus* settles more abundantly in the darker positions, possibly owing to the colonization of the lighter positions by algae, with the consequent reduction in area upon which the spat can attach and grow. Initial settlement can, however, be quite high upon filamentous algae, but the mussels rarely persist, even in small numbers.

When settlement occurs upon a non-toxic panel freely exposed in the sea at a constant depth, it is invariably heavier at the upper edge, becoming rapidly smaller as the distance from the upper edge of the panel increases. In years of good spat-fall an entire panel may be fouled by *Mytilus*, but initially the upper edge and the surfaces bordering it bear more and larger mussels. As settlement declines, greater growth is usually observed where the density of settlement is less. A projection across the centre of the panel will give rise to a heavier settlement of *Mytilus* immediately below it than immediately above. It would thus appear that *Mytilus* spat accumulates where the surface upon which it settles is interrupted by some discontinuity. It is probable that the spat, after initial settlement, migrates vertically upwards upon the surface by means of its ciliated foot until a discontinuity is reached, whereupon it fixes itself by means of its byssus, the discontinuity providing a stimulus for byssus formation. A similar tendency to accumulate at the upper parts of panels, possibly for a similar reason, has been noted in the settlement of *Balanus crenatus* and *B. improvisus* at Liverpool and Burnham-on-Crouch (Chipperfield, 1948).

The spat of *Mytilus edulis* attaches to floating structures most abundantly from just below the surface to a depth of about 2 ft.; below this the density of settlement declines. This is clearly shown by counts of the number of mussels settled on 3 in. long sections of tubular steel panel holders $1\frac{1}{4}$ in. diameter, suspended from a raft at Brixham in 1948 and 1949, made towards the end of the period of settlement. The counts are set out in Table XI. It is apparent that settlement will also occur in the region of the nominal water line, and in that zone above the water line which is subject to constant immersion by wave-action, although the settlement falls off very rapidly in this region.

A similar distribution of settlement is seen in the case of fixed vertical substrata. In 1949 a chain covered with mussels and hanging freely to the bottom from a naval dolphin in Brixham Harbour, was denuded in parts for spawning investigations. Subsequently, the patches cleared of mussels were

TABLE XI. SETTLEMENT OF *MYTILUS EDULIS* IN RELATION TO DEPTH BELOW WATER LINE

Distance from water line (in.)	Numbers/3 in. length of $1\frac{1}{4}$ in. diam. vertical rod: 1. vii. 48			16. vi. 49			
	1	2	Mean	1	2	3	Mean
+6 to +3	0	0	0	5	22	7	11
+3 to 0·0	8	15	11	35	28	58	40
0·0 to 3	33	43	38	101	85	158	115
−6 to −9	284	265	274	412	358	392	387
−12 to −15	221	294	257	329	400	360	363
−24 to −27	236	160	188	266	206	252	241
	Mean size: 4·5 mm.			Mean size: 3·0 mm.			

TABLE XII. INTERTIDAL SETTLEMENT OF *MYTILUS EDULIS* ON CHAIN, BRIXHAM, 14 JULY 1949

(Numbers (approx.) per link of chain. Mean size: 8·0 mm.)

Approx. level	No.	Approx. level	No.
H.W.N.T.	0	L.W.S.T.	50
M.T.L.	0	5 ft. below L.W.S.T.	180
M.T.L.–L.W.N.T.	0	15 ft. below L.W.S.T.	160
L.W.N.T.	8		

extended, and more made at known distances below approximate L.W.S.T. mark. Rough counts of the recently settled and surviving *Mytilus* in these areas were made on 14 July (see Table XII). Below L.W.S.T., settlement was not significantly greater at a depth of 15 ft. than at L.W.S.T. Above L.W.S.T., settlement was considerably smaller, no surviving settlement at all persisting at M.T.L. Similarly, at Liverpool in 1946, although a heavy surviving settlement occurred upon the low-tide floor of the jetty at the Prince's landing stage (see Corlett, 1948), that upon the mid-tide floor and upon the beams immediately beneath was extremely sparse.

Engle & Loosanoff (1944) explain similar results by suggesting that settlement of *M. edulis* larvae occurs only at low-water slack, or at late ebb. It is possible, however, that settlement by adhesion to the substratum by the foot may occur at any state of the tide, but that the time required for secure attachment by the byssus to be completed is of the order of $4\frac{1}{2}$–6 hr. As the byssus is secreted only when the mussel is immersed, spat adhering in positions higher in the intertidal zone would not persist unless they happen to be in a position in which they are constantly wetted, e.g. a small depression in a rock surface. Tidal currents and wave action are obviously complicating factors, but the restricted settlement of mussel spat between L.W.N.T. and M.T.L. on a rocky shore subject to some wave action such as Shoalstone Beach, Brixham, in narrow cracks and small hollows lends support to the suggestion detailed above. The effect of exposure to the air upon the physical and chemical properties of the liquid, or partly solidified, byssus material cannot be ignored in this context.

Summary

During 1946 and 1947, regular samples of *Mytilus edulis* from a number of localities on the British coasts, including Conway, Brancaster and Liverpool, were examined for gonad condition and spawning. For each sample, the mean stage of gonad development was computed. The criteria employed in distinguishing the stages of gonad development are described.

Ripening of the gonads takes place within a few weeks of the onset of spawning, in general commencing when the sea temperature has risen above 7·0° C. There appears to be no correlation between nutritional condition and ripening of the gonads, or subsequent spawning.

In all localities and in each year in which observations were made spawning occurred in late spring (mid-April to the end of May) and in most areas lasted for a short period only (2–4 weeks). At Brixham, in 1949 and 1950, the duration of the spawning period was longer (4–6 weeks). In most cases, 70–80% of the mature population spawned during the first 7–10 days of the breeding period. No evidence of periodic spawning was obtained.

In all cases, spawning commenced in a period during which the mean temperature to which the mussels were exposed was rising from *c.* 9·5° C. to 11–12·5° C. In most cases, the onset of spawning was coincident with a period of spring tides, and of predominantly bright sunny weather. The initial rate of spawning appears to be directly related to the rate of increase in mean temperature to which the mussels are exposed.

After spawning, mussels enter into a 'neuter' or 'resting spent' stage in which all traces of sexuality are lost. In good 'fattening' areas, the connective tissue of the mantle and 'mesosoma' rapidly becomes packed with glycogen and some fat. Re-development of the gonads usually commences in July or August, 2–3 months after spawning. A rapid increase in the mass of the gonads occurs during early spring.

The period of free swimming larval life is variable and is probably usually *c.* 4 weeks. Settlement can occur at any time after the formation of the dissoconch, corresponding to a length of from 0·4 to 1·0 mm.

Settlement is heaviest on floating structures in the region between the water line and a depth of 2 ft. Below this level the density of settlement declines somewhat. Similarly, upon intertidal structures and upon beds in

estuarine areas, little persistent settlement occurs above M.T.L. and the heaviest settlements take place at and below L.W.S.T. Settlement almost invariably occurs initially at the upper edge of submerged panels, etc.

REFERENCES

BATTLE, H., 1932. Rhythmical sexual maturity and spawning of certain bivalve mollusks. *Contrib. Canadian Biol.*, N.S., Vol. 7, No. 20, pp. 257–76.

BERNER, L., 1935. La Reproduction des Moules comestibles (*Mytiblus edulis* L. et *Mytilus gallo-provincialis* Lmk.) et leur répartition géographique. *Bull. Inst. Ocean., Monaco*, No. 680, 8 pp.

BORISIAK, A., 1909. Pelecypoda du Plankton de la Mer Noire. *Bull. Sci. France Belg.*, T. 42, pp. 149–84.

BRUCE, J. R., 1926. The respiratory exchange of the mussel (*Mytilus edulis*). *Biochem. Journ.*, Vol. 20, pp. 829–46.

COE, W. R. & FOX, D. L., 1942. Biology of the California sea-mussel (*Mytilus californianus*). I. *Journ. Exp. Zool.*, Vol. 90, pp. 1–30.

CORLETT, J., 1948. Rates of settlement and growth of the 'pile' fauna of the Mersey estuary. *Trans. Liverpool Biol. Soc.*, Vol. 56, pp. 2–28.

DANIEL, R. J., 1921. Seasonal changes in the chemical composition of the mussel (*Mytilus edulis*). *Rept. Lancs. Sea Fish. Lab.*, 1920, pp. 74–84.

DODGSON, R. W., 1928. Report on mussel purification. *Min. Agr. Fish., Fish. Invest.*, Ser. 2, Vol. 10, No. 1, 498 pp.

ELMHIRST, R., 1923. Notes on the breeding and growth of marine animals in the Clyde Sea Area. *Ann. Rept. Scot. Mar. Biol.* 1922, pp. 19–43.

ENGLE, J. B. & LOOSANOFF, V. L., 1944. On season of attachment of larvae of *Mytilus edulis* Linn. *Ecology*, Vol. 25, pp. 433–40.

FIELD, I. A., 1922. Biology and economic value of the sea mussel *Mytilus edulis*. *Bull. U.S. Bur. Fish.*, Vol. 38, pp. 127–259.

HARRIS, J. E., 1946. Report on anti-fouling research, 1942–44. *Journ. Iron & Steel Instit.*, Vol. 150, No. 2, pp. 143–56.

HAVINGA, B., 1929. Krebse und Weichteire. *Handb. Seefischerei Nordeuropas*, Bd. 3, H. 2, 147 pp.

HERDMAN, W. A. & SCOTT, A., 1895. Report on the investigations carried on in 1894 in connection with the lancashire Sea-Fisheries Laboratory at University College, Liverpool. *Trans. Liverpool Biol. Soc.*, Vol. 9, pp. 104–62.

HUTCHINS, L. W., 1947. The bases for temperature zonation in geographical distribution. *Ecol. Monogr.*, Vol. 17, pp. 325–35. (*Coll. Reprints Woods Hole*, No. 374.)

JENSEN, A. S. & SPÄRCK, R., 1934. Bløddyr. II. Saltvandsmuslinger. *Danmarks Fauna*, Nr. 40, 208 pp.

JOHNSTONE, J., 1898. The spawning of the mussel (*Mytilus edulis*). *Trans. Liverpool Biol. Soc.*, Vol. 13, pp. 104–21.

KÄNDLER, R., 1926. Muschellarven aus dem Helgoländer Plankton. *Wiss. Meeresunters.*, Abt. Helgoland, N.F., Bd. 16, No. 5, 9 pp.

KORRINGA, P., 1947. Relations between the moon and periodicity in the breeding of marine animals. *Ecol. Monogr.*, Vol. 17, pp. 347–81.

LEBOUR, M. V., 1938. Notes on the breeding of some lamellibranchs from Plymouth and their larvae. *Journ. Mar. Biol. Assoc.*, Vol. 23, pp. 119–44.

LO BIANCO, S., 1899. Notizie biologiche riguardanti specialmente il periodo di maturità sessuale degli animali del golfo di Napoli. *Mitt. Zool. Stat. Neap.*, Vol. 13, pp. 448–573.

LOOSANOFF, V. L., 1942. Shell movements of the edible mussel *Mytilus edulis* (L.) in relation to temperature. *Ecology*, Vol. 23, pp. 231–4.

McINTOSH, W. C., 1891. *Report on the mussel and cockle beds in the estuaries of the Tees, the Esk, and the Humber*. 87 pp.

MATTHEWS, A., 1913. Notes on the development of *Mytilus edulis* and *Alcyonium digitatum* in the Plymouth Laboratory. *Journ. Mar. Biol. Assoc.*, Vol. 9, pp. 557–60.

NELSON, T. C., 1928. Pelagic dissoconchs of the common mussel, *Mytilus edulis*, with observations on the behavior of the larvae of allied genera. *Biol. Bull Woods Hole*, Vol. 55, pp. 180–92.

ORTON, J. H., 1924. An account of investigations into the cause or causes of the unusual mortality among oysters in English oyster beds during 1920 and 1921. *Min. Agr. Fish., Fish. Invest.*, Ser. 2, Vol. 6, No. 3, 199 pp.

—— 1933. Strange spat fall of the common mussel on the common cockle. *Nature, London*, Vol. 131, pp. 513–4.

PELSENEER, P., 1935. *Essai d'Ethologie Zoologique d'après l'étude des Mollusques*. 662 pp. Bruxelles.

PYEFINCH, K. A., 1950. Notes on the ecology of ship-fouling organisms. *Journ. Anim. Ecol.*, Vol. 19, pp. 29–35.

RUNNSTRÖM, S., 1929. Weitere Studien über die Temperaturanpassung der Fortpflanzung und Entwicklung mariner Tiere. *Bergens Mus. Arbok*, Nr 10, 46 pp.

SCOTT, A., 1900. Breeding of *M. edulis*. *Rept. Lancs Sea Fish. Lab.*, 1900, pp. 36–9.

SPÄRCK, R., 1920. Nogle bemaerkninger angående yngleforhold hos *Mytilus edulis* L. *Ved. Medd. Danske Naturh. Foren.*, Bd. 71, pp. 161–64.

STAFFORD, J., 1912. On the recognition of bivalve larvae in plankton collections. *Contrib. Canad. Biol.*, 1906–10, pp. 221–42.

STOTT, F. C., 1931. The spawning of *Echinus esculentus* and some changes in gonad composition. *Journ. Exp. Biol.*, Vol. 8, pp. 133–50.

TANG, SHIH-FENG, 1941. The breeding of the escallop [*Pecten maximus* (L.)] with a note on the growth rate. *Trans. Liverpool Biol. Soc.*, Vol. 54, pp. 9–28.

THORSON, G., 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Øresund). *Medd. Komm. Danmarks Fisk. Havund. København, Ser. Plankton*, Bd. 4, No. 1, 523 pp.

VISSCHER, J. P., 1927. Nature and extent of fouling of ships' bottoms. *Bull. U.S. Bur. Fish.*, Vol. 43, Pt 2, pp. 193–252.

WERNER, B., 1939. Über die Entwicklung und Artunterscheidung von Muschellarven des Nordseeplanktons, unter besonder Berücksichtigung der Schalenentwicklung. *Zool. Jahrb., Abt. Anat.*, Bd. 66, pp. 1–54.

WHEDON, W. F., 1936. Spawning habits of the mussel *Mytilus californianus* Conrad with notes on the possible relation to mussel poison. Mussel poison. I. *Univ. Calif. Pub. Zool.*, Vol. 41, pp. 35–44.

WHITE, K., 1939. *Mytilus*. *L.M.B.C. Memoirs*, Nr 31. 177 pp. Liverpool.

WILLIAMSON, H. C., 1907. The spawning, growth, and movement of the mussel (*Mytilus edulis* L.), horse-mussel (*Modiolus modiolus* L.) and the spoutfish (*Solen siliqua* L.). *25th Ann. Rept. Scot. Fish. Bd*, 1906, *Sci. Invest.*, pp. 221–55.

YOUNG, R. T., 1942. Spawning season of the California mussel *Mytilus californianus*. *Ecology*, Vol. 23, pp. 490–2.

—— 1945. Stimulation of spawning in the mussel (*Mytilus californianus*). *Ecology*, Vol. 26, pp. 58–69.

—— 1946. Spawning and setting season of the mussel *Mytilus californianus*. *Ecology*, Vol. 27, pp. 354–63.