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DEPARTMENT OF AGRICULTURE AND TECHNICAL INSTRUCTION FOR IRELAND.

FISHERIES BRANCH.

SCIENTIFIC INVESTIGATIONS, 1920.

No. I.

Notes on the breeding habits and life history of the Periwinkle.

BY

W. M. TATTERSALL, D.Sc.
Keeper of the Manchester Museum.

PLATE I.

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VIII.—HOLT, E. W. L.,—The Freshwater Eel. A Review of Recent Contributions to Knowledge and its Life-History, pp. 27. [1909].

IX.—HOLT, E. W. L.,—Report on the Artificial Propagation of Salmonidae during the Season of 1907-1908, pp. 11, and

Substance of Reports received from Clerks of Conservators relative to Salmon Fisheries, pp. 22, and

HOLT, E. W. L.,—Summary of Reports relative to Eel Fry, 1907-1908, pp. 6. [1909].

X.—Title-page, Table of Contents and Index for 1907.

NOTES ON THE BREEDING HABITS AND LIFE HISTORY OF THE PERIWINKLE.

BY

W. M. Tattersall, D.Sc.

Keeper of the Manchester Museum.

Plate I.

Some years ago I commenced a series of observations on the periwinkle, *Littorina littorea*, with the object of finding out, if possible, its breeding habits and life history. I succeeded in inducing these molluscs to breed in aquaria, and traced out roughly the general life history. Brief abstracts of my results were read at the meeting of the British Association, at Dublin, in September, 1908 (see *Nature*, Oct. 22nd, 1908, p. 649), and at the Challenger Society, in January, 1909 (see *Athenaeum*, February 13th, 1909, pp. 203–204). Reference to these abstracts was made by Mr. B. B. Woodward in his presidential address to the Malacological Society of London in February, 1909 (*Proc. Malacol. Soc. London*, vol. viii, No. 5, July, 1909, p. 282), and by Simroth (*Nordisches Plankton, Gastropoden*, p. 35, 1911). Beyond these brief notes no account of my observations has yet been published, because I hoped to work out the development in greater detail before doing so. Circumstances have prevented me from accomplishing this work, and as I now see no immediate possibility of taking up the work again, I am induced to publish my incomplete notes, more especially in view of a paper, which appeared in 1911, by MM. les Professeurs M. Caullery and P. Pelseneer, "Sur la ponte et le développement du vignot, (*Littorina littorea*)." *Bull. Sci. France et Belgique*, 7th sér. t. xliv, fasc. 4, pp. 357-360, pl. ix. In this paper the authors described a pelagic Gastropod egg, found in abundance at Wimereux, France, which, by a process of elimination and inference, they refer, and correctly, as my observations show, to the periwinkle. They were not able to induce the adults to breed in the laboratory and thereby confirm their deductions. So it has seemed well to publish my own results, because they are based on direct observation which confirms in detail the work of the French authors.

It is a commonplace, which almost amounts to a scientific axiom, that the most abundant and familiar forms in Nature are those which are least known from a morphological, anatomical or embryological point of view. *Littorina littorea*, Linn., the common periwinkle, offers a case in point. It is, perhaps, the most abundant and characteristic mollusc of our shores, yet an exhaustive search through the literature of molluscan embryology has revealed the fact that practically nothing is known of its breeding habits and life history.

It seems to have been assumed generally that the periwinkle is oviparous, but one writer, at least, Bouchard-Chantereux, according to Jeffreys (*British Conchology*, vol. iii, p. 372), believed it to be viviparous, and gave an interesting account of its life history. Jeffreys rightly points out that Bouchard-Chantereux was probably dealing with one of the many varieties of *Littorina rudis* and not *Littorina littorea*.

The supposed eggs of *Littorina littorea* figured in Bronn's *Tierreich*, both the first and second editions, are, as Caullery and Pelseneer point out, and as my own observations prove, referable to *L. obtusata*, and not to the periwinkle at all. This figure, the authority for which I have been unable to trace, also appeared in the *Introduction to Conchology* by Johnstone and was copied by Step, *Shell Life*, London, 1901, p. 225, and by Newbigin, M., *Life on the Seashore*. These are the only references to the life history of *Littorina littorea* which I have been able to trace in the literature dealing with mollusca.

At the same time I am convinced that the eggs of the periwinkle have been seen by previous observers without being recognised. As far back as 1887, Hensen described a pelagic egg, which he called "Barbierbecken-statoblast" (Ueber die Bestimmung des Plankton, 5. *Bericht Komm. Wiss. Unters. Meere*, p. 67, Taf. 4, figs. 25 and 26). Bergh (6. *Bericht Komm. Wiss. Unters. Meere*, p. 116, 1890) suggested that this egg belonged to one of the species of Gastropoda, but was unable to say to which one it should be referred. This egg shows many points of resemblance to the egg which is here identified as that of *Littorina littorea*, but differs rather markedly in size. Hensen gives the overall measurement of his egg capsule as ·352 mm., and that of the contained egg as ·11 mm. The egg capsules of *Littorina littorea*, as described below, measure ·8 to ·9 mm. overall, and the contained eggs ·15 mm. While, therefore, the actual eggs are very much the same size, there is some discrepancy in the size of the capsules which cannot be explained, if Hensen's statoblast is really referable to *L. littorea*.

Ramsay Wright ("The Plankton of Eastern Nova Scotia Waters," p. 15, pl. vii, figs. 1-3. *Further contributions to Canadian Biology, 39th Ann. Rep. Dept. Mar. Fish., Fisheries Branch*, 1907) also describes and figures a pelagic Gastropod egg which he is unable to identify, but which I am convinced belongs to *L. littorea*, whose distribution extends to North American waters. Wright also noticed the resemblance between his eggs and Hensen's "Barbierbeckenstatoblast."

To complete the references to the life history of *L. littorea* in literature, I may be allowed to quote from J. T. Marshall (*Journal Conchology* vol. ix, No. 4, 1898) a passage from a letter written by a correspondent to *Science Gossip* in May, 1890 :— "Periwinkles thrive remarkably well in my vases. I have had the same individuals for ten years and they breed freely. They must be long-lived creatures, for they seem to grow very slowly. The young ones are at first quite unlike their parents, and it is three years before they begin to assume anything like the form of a winkle." No more detailed observations on the breeding habits of the periwinkle appear to have been published by this observer.

It will be seen, therefore, that, previous to the appearance of the paper quoted above by Caullery and Pelseneer, nothing worth speaking of was known of the life history of *L. littorea*.

When my own observations were commenced in 1906, careful search was made along the shores and rocks, in the hopes that adults would be found in the act of depositing their spawn, or, at any rate, in such association with spawn as would lead one to suspect that it belonged to this species. Nothing, however, came of this search, and it was then decided to keep periwinkles under observation in aquaria. This proved most successful, as they were found to breed quite readily there, and the explanation of my failure to find their spawn on the shores soon became apparent.

The sexes in *L. littorea* are separate, and, in the breeding season, the males are readily distinguished from the females by the possession of a long, rather stout penis on the right side of the body. The penis appears to exhibit seasonal variations in size, and only attains its full development when the testis is completely ripe. At the close of the breeding season the penis becomes reduced in size externally, and against the darkly pigmented epidermis of the body, is almost invisible. The separation of the sexes becomes difficult except the animals are removed from their shells. When the next breeding season is approaching and the generative cells are once more active, the penis again increases in size, and, keeping pace with the maturation of the sperm cells, reaches full size with the appearance in the vas deferens of ripe spermatozoa. The testis is a diffuse organ, ramifying through the hepatic coil, and giving to it a pale yellow-brown colour in the breeding season.

The ovary is likewise diffuse, but pink in colour.

The breeding season is a long one, lasting from the middle of January to June, with a maximum in April and the early part of May.

The males become mature early in January, but I have not found females with the ovary ripe till the middle of February. Spent males may be found after the beginning of April, and the penis begins to develop again at the beginning of November.

It was necessary first to obtain copulating pairs of adults, and to isolate them in separate small aquaria. It was found to be quite easy to induce copulation by the simple expedient of changing the sea water in the aquarium. It should be explained that a circulating supply of fresh sea water was not available, and the periwinkles were kept in shallow open aquaria, in which the sea water was changed daily at least, sometimes twice a day. From twenty minutes to two hours after the fresh sea water had been added, copulation between males and females went on readily, and any number of pairs required could be obtained and isolated. After about two hours copulation practically ceased. It appears probable that the fresh sea-water was the stimulus which induced copulation, because it contained a greater amount of dissolved oxygen than the water which had been in the aquarium for any length of time. It may, of course, be a question of temperature. The water in the aquarium was generally at a higher temperature than the sea, especially after being in for any length of time, and sometimes the difference was as much as 5° C. But I have observed the winkles inactive in stale water at 12·7° C. and stimulated into action by fresh sea water at 12·4° C., not a very great difference in temperature. The female commenced to deposit her eggs from two to twelve hours after copulation was completed, and it is rather a curious fact that most of the eggs were deposited during the hours of darkness.

The eggs, which are pink in colour, are enclosed, usually singly or in pairs, in small curiously shaped transparent capsules resembling a soldier's tin hat with the eggs lying in the crown of the hat. I have not infrequently found three eggs in the same capsule and on one occasion four. The first egg capsules deposited by a female usually contain but one egg, the latter capsules two or more. The capsules vary in size from ·6 mm. to ·9 mm. in total diameter, and the eggs themselves are generally ·15 mm. to ·16 mm. in size.

The following measurements of two capsules and their contained eggs give a very general idea of the average size :—

Diameter of the entire capsules	·875 mm.	·775 mm.
Width of the brim	·16 mm.	·15 mm.
Diameter of the egg membrane	·175 mm.	·175 mm.
Size of the egg	·15 mm.	·15 mm.

The capsules are not aggregated together in a common gelatinous matrix as a mass of spawn, such as is familiar among Nudibranchs and most Gastropods, and this fact explains the failure to find their eggs on the shore and weeds. The eggs are laid freely on the sea-shores and after inducing winkles to breed in aquaria, I examined some of the fine deposit on the shore at low water mark and found numerous eggs of the periwinkle there. The eggs are pelagic to a certain extent. Caullery and Pelseneer found them comparatively numerous in the inshore plankton at Wimereux. At Ardfry, near to Galway, they were not nearly so abundant in the plankton as the numbers of winkles on the shore would justify, and I never obtained them except in a net hauled near to the bottom. It should, however, be explained that the specific gravity of the sea water at Ardfry was low compared with more oceanic water, since Ardfry is situated at the head of Galway Bay, and the water is considerably influenced by the River Corrib.

The same female may go on depositing eggs intermittently for a month or more, the original act of copulation sufficing for the whole of the eggs laid. One female in my aquarium began depositing eggs on the 20th March. It laid further batches on the 21st, 22nd, and 30th of March, and on the 4th, 7th, 11th, and 24th of April, after which none were laid. The total number of egg capsules a single female may deposit is estimated at about 5,000, but this estimation is not based on any careful calculation.

Having obtained the eggs, considerable difficulty was at first experienced in rearing them through the various stages of their development. I have already explained that a circulating supply of sea water was not at my command, and I was at first compelled to adopt the crude method of keeping the eggs in shallow glass dishes and changing the sea water frequently. This method was not successful, since it encouraged the rapid multiplication of numerous species of Infusoria which attacked the eggs, and either devoured them or so weakened them as to retard their development and cause their ultimate death.

Finally I hit on a simple method which proved successful. A large glass jam jar was filled with fresh sea water which had been strained through the finest bolting silk. The eggs were transferred to the jar, and the mouth of the jar was covered by a piece of the same bolting silk tied on with string or thread. The jar was then submerged in the sea. By this means the temperature of the water in the jar was kept the same as the surrounding sea, and all extraneous matter likely to harbour infusoria was excluded by the silk covering of the jar mouth. Under these conditions development proceeded smoothly.

Segmentation is completed during the first day and appears to be very complete. The first two segmentation planes divide the egg into four equal cells, but at the third stage the embryo divides into four macromeres and four micromeres, the latter alternating with the former. This is a familiar stage in most gastropods.

At the third day the circumoral ring of cilia is complete, and the embryo begins to rotate within its membrane. When two or more eggs are contained in the same capsule, the oral poles of all the embryos are found to be turned towards the centre of the capsule, and the rotation of the embryo on its longitudinal axis always proceeds in one direction.

At the sixth day the embryo breaks out from the capsule, and swims freely about in the water. Caullery and Pelseneer have noticed that the larvae break through the flat side of the capsule when escaping.

The newly hatched larva is in the early veliger stage, and the figure which I reproduce here from Ramsay Wright's paper gives a very good idea of the general external appearance. It possesses no very distinctive features except an irregular development of purple pigment in two patches, one at the oral pole and one about the centre of the body. The development of the veliger is completed by the fourteenth day, and when fully formed, the shell has the dorsal edge of the mouth produced into a prominent beak, resembling in this respect the veliger of *Natica.* The veliger stage of *Littorina littorea* is a prominent feature of the pelagic life of inshore waters in May, June and July.

The length of time required for the change from a veliger larva to the adult is not certain.

The chief features of this life history are :—

(1) The deposition of the egg capsules singly, and the fact that they are unattached to weeds and stones.

(2) The hatching of the egg as an early veliger larva which passes through a late veliger stage before the adult is reached.

(3) The prolonged larval life in the free-swimming stages.

All these points indicate a generalised type of life history.

If we compare the life history of *Littorina littorea* as here set forth, with those of the other three British species of the genus, some interesting facts are brought out.

The life history of *Littorina obtusata* is characterised by the following points :—

(1) The egg capsules are aggregated together in masses and attached to weeds.

(2) The earlier veliger stage is suppressed, and the egg hatches as a fully formed veliger larva.

(3) Free-swimming larval life is thus much abbreviated.

This is a much more specialised type of life history than that of *L. littorea,* and the specialisation is completed in *L. rudis* and *L. neritoides,* which are both viviparous and in which free-swimming larval life is entirely suppressed.

The four species of *Littorina*, in the order in which they are dealt with above, exhibit four stages in the specialisation of habitat.

L. littorea lives in that zone of the seashore characterised by the growth of *Laminaria* and *Fucus serratus*, and partially exposed only at extreme low water spring tides.

L. obtusata lives in the zone of *Fucus vesiculosus* and *Ascophyllum nodosum*, and is exposed at practically every low water.

L. rudis inhabits the zone of *Pelvetia canaliculata* and *Fucus platycarpus*, that is, near the high water mark of neap tides, and is, therefore, exposed for the greater part of every day.

L. neritoides inhabits the zone between high water mark spring tides and high water neap tides, and is thus often exposed for days at a time, during which it is only moistened by the spray from the waves.

I have not followed the bewildering changes which have been, and are still being made, in the nomenclature of the mollusca, but I think conchologists are still agreed that these four species should be retained in the one genus. If this is so, we have, within the limits of a single genus, four stages in the evolution of land mollusca from marine forms, showing four stages in the passage from a generalised to a specialised habitat, correlated with four stages in the specialisation of reproduction, and the gradual abbreviation and final suppression of free-swimming larval life.

In the illustrations which accompany these notes I have added to my own figures of the egg capsules and early segmentation stages copies of the figures of the larvae as given by Ramsay Wright and Caullery and Pelseneer, so that the account of its life history may be completed, as far as at present known. I append a few notes on the habits of *Littorina littorea.*

The climbing habits of the periwinkle have attracted considerable attention from time to time, and the researches of Pelseneer (*Arch. de Biologie*, t. xiv, p. 351, 1895) have demonstrated that this habit has resulted in certain modifications and specialisation in the respiratory organs. The wall of the pallial cavity, between the gills and the hypobranchial glands is vascular, like that of the pulmonary chamber of the true Pulmonata. It would appear, therefore, that the habit is normal and characteristic of the species. This is all the more remarkable in an animal whose life history is of the generalised type noted above.

In connection with the periwinkle industry so important on the South and West coasts of Ireland, it was suggested that advantage might be taken of the climbing habits of the molluscs to facilitate their gathering for market, by putting in stakes on those parts of the shore which they frequent. In order to test this possibility, an experimental "periwinkle farm" was laid down in Ardfry Harbour, Co. Galway. The "farm" consisted of four rows of sixty stakes, $3' \times 3'' \times 2''$ extending from about the level of low water neap tides to that of low water spring tides, on a shore made up of small stones and rocks, on which *Fucus serratus* and *Fucus vesiculosus* grew in abundance. The original intention was to make observations on this "farm," as frequently as possible, noting the relative abundance of winkles on the stakes and on the ground bounded by the stakes, and to note specially whether those winkles found on the stakes were relatively larger than those found on the ground. It is manifest that if the climbing habit in periwinkles is sufficiently strong to cause them to take advantage of stakes and piles driven into the ground they naturally frequent, the gathering of periwinkles for marketing purposes would be greatly facilitated by the provision of "periwinkle farms," for it is much easier and quicker to collect the molluscs from stakes than to search for them on the ground under stones and weed. If the habit is more strongly developed in the larger winkles, the advantage of "periwinkle farms" would be enhanced. Unfortunately the observations which I was able to make on the experimental "farm" are by no means conclusive, but, nevertheless, the results seem to me to be worth recording, more especially as their deficiency in certain directions is the result of factors which seem to militate against the practical utility of "periwinkle farms."

The normal home of the periwinkle is in that zone of the shore characterised by the growth of *Laminaria* and *Fucus serratus*. This part of the shore is only exposed at low water during the best spring tides of the year, those which occur in winter. The "farm" had naturally to be put up in that zone of the shore. Hence it happened that I was only able to make observations on the "farm" during the winter months, and that for six months in the year the stakes were completely covered by the tide. My observations are, therefore, deficient, in so far as they concern the habits of the winkle during the Summer months. Practically, this is not of much moment, for during the Summer months the winkles are breeding, and, moreover, they are not marketed during that season.

The number of winkles on a given area of the foreshore varies very much, according to the relative abundance of drift weed, such a characteristic feature of the shores on the West coast of Ireland during the winter months. The more drift weed there is on the shore the more abundant are periwinkles found to be. The quantity of drift weed on a particular foreshore varies rapidly from day to day according as the wind is onshore or offshore. A shore thickly strewn with drift weed by an onshore wind is frequently cleaned completely in the course of a tide, if the wind should change to an offshore direction and carry the weed with it to another part of the coast. My observations, therefore, show no correlation between the relative abundance of periwinkles and the season of the year. The number of winkles found on the "farm" depended entirely upon the character of the weather during the two or three days immediately preceding the census. Further, no relation could be traced between the number of winkles found climbing the stakes and the number on the ground bounded by the stakes, or between the "frequency" of the climbing habit and the season of the year. The number of climbing winkles was found to vary between 15 per cent. and 35 per cent. of the total number on the area investigated. But both the higher and lower percentages were found to occur at the same seasons and times of the year without any suggestion of rhythm or periodicity. The possible explanation of this erratic behaviour occurred to me during the taking of a census of the "farm" at Easter, 1907. It may be remembered that this Easter was characterised by particularly warm and calm sunny weather, and I found that the percentage of climbing winkles was high, 35 per cent. A month earlier it had been low, only 15 per cent., and a month later it was equally low. Reflecting on the weather conditions prevailing at the time of these observations I came to the conclusion that *calm* weather was a necessary condition for a successful indulgence of the climbing habit. Observations readily demonstrate that the purchase which a winkle is able to obtain, even on a comparatively rough climbing surface, is but slight. One has only to agitate slightly the water round a stake on which winkles are climbing to realise that a very small amount of wave action is detrimental to a successful ascent, and is sufficient to prevent the mollusc from retaining its hold. Consequently, it follows that the relative number of winkles found climbing at a given observation depends entirely upon the nature of the weather conditions prevailing at the time.

From measurements made on the climbing winkles and those found on the ground at the same time, there appears to be no evidence that the former were in any way larger than the latter. In other words, the climbing habit is just as strongly developed in young winkles as in older ones, as indeed may have been expected from the internal structure of the animal. It must, therefore, be considered that the climbing habit is characteristic of the periwinkle at all ages and at all times of the year, but is dependent on the calmness of the sea for its manifestation.

The chief food of *Littorina littorea* appears to be the hyphal hairs of *Fucus serratus* and allied seaweeds. I have found them grazing readily on these hairs on the *Fucus* in the aquarium in which I kept them under observation. They swallow indiscriminately diatoms and other microscopic organisms found clinging to the hyphal hairs of the seaweed or deposited on its fronds. Consequently their faecal pellets are found to be rich in the skeleton parts of such micro-organisms. Blevgad, however (*XXII. Rep. Danish Biol. Station*, 1915, p. 66), says that *Littorina littorea* is both an herbivorous and carnivorous detritus eater, able to bite off the tips of large fresh algae, and also to devour small bivalves, gastropods, ostracods, etc.

The climbing habit of winkles appears to be in no way related to their search for food, for I have found them climbing readily on stakes thickly encrusted with barnacles, an operation which must have resulted in a minimum of food with a maximum amount of discomfort in the obtaining of it. It seems to me, therefore, that "periwinkle farms" would not be found to be worth the initial expense of putting down, because (1) the number of climatic winkles is so absolutely dependent on the climatic conditions, which are so seldom favourable during the winter in Ireland; (2) the percentage of climbing winkles never exceeded 35 per cent. even when the conditions were as favourable as could be expected; and (3) the average size of the climbing winkles does not appear to be any greater than that of non-climbers.

Another point, which may have a bearing on the commercial aspect of the winkle industry may be briefly touched on here. I refer to the desirability of grading the winkles collected into sizes before dispatching to market. All the winkles collected on the "farm" were graded by being passed through two sieves of perforated zinc, one with holes of $\frac{5}{8}''$ diameter, and the other with holes of $\frac{3}{4}''$ diameter. The two grades thus obtained were then measured in a standard pint measure and the numbers per pint noted. The average number of $\frac{3}{4}''$ winkles to a pint was found to be 84, of $\frac{5}{8}''$ winkles 114. Selecting the largest of the $\frac{3}{4}''$ winkles the average number per pint was 78, while selecting in the same way the smallest of the $\frac{5}{8}''$ winkles, the average number per pint was 145. The winkles which passed through the $\frac{5}{8}''$ sieve were rejected as unmarketable, though it is certain that in practice many of these are actually sent to the markets. Of the winkles considered to be marketable, the $\frac{3}{4}''$ winkles averaged 35 per cent. of the total, or roughly one $\frac{3}{4}''$ winkle to every two $\frac{5}{8}''$ winkles. In a bag of mixed marketable winkles, therefore, the range of size is seen from the above particulars to be considerable, and the value of a consignment of winkles is probably calculated on the assumption that the whole consignment is made up of shellfish uniform in size with the smallest of a sample. If this is so, the fisherman is getting no benefit from any large winkles his consignment may contain. It follows, therefore, that one bag of large winkles and two bags of small winkles are worth together more than three bags of mixed winkles, and that the fisherman would gain considerably if he could be induced to grade his produce. The experience gained in grading other shellfish, such as oysters and mussels, leaves little doubt in my mind that such would be the case, the fact that a fish salesman may rely on a graded consignment alone being worth a considerable amount to the fisherman. From a consideration of the above statistics as to the relative sizes and the proportion of sizes of the winkles in a given lot, I think it can be safely recommended that winkles for the markets should be graded by being passed through two sieves of $\frac{3}{4}''$ and $\frac{5}{8}''$ mesh respectively, and that all winkles which pass through the smaller sieve should be rejected as unmarketable.

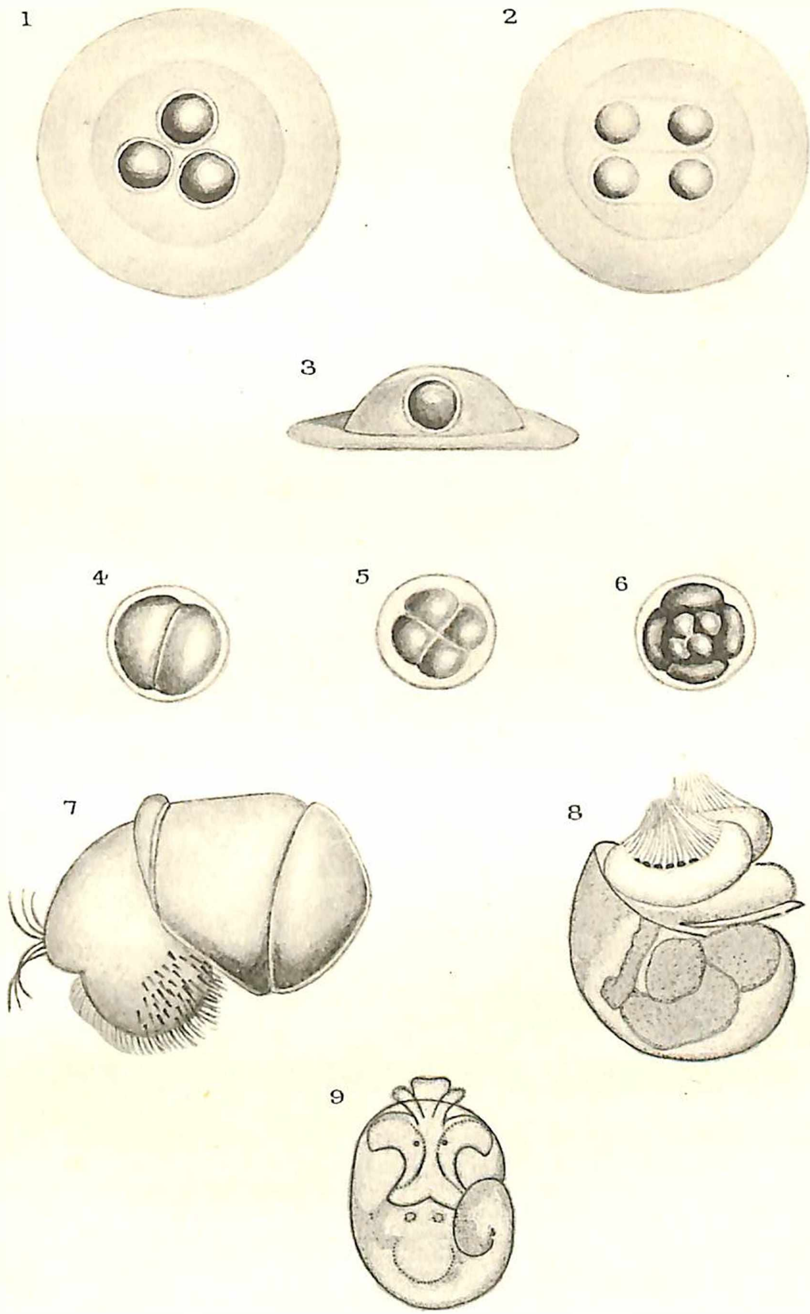
EXPLANATION OF THE PLATE.

Littorina littorea, Linn.

Fig.	1. Egg capsule, with three eggs, from above .	×50
,,	2. ,, ,, four eggs, from above .	×50
,,	3. ,, ,, one egg, from the side .	×50
,,	4. Two celled stage in segmentation . .	×100
,,	5. Four ,, ,, . .	×100
,,	6. Eight ,, ,, . .	×100
,,	7. Newly hatched larva (after Ramsay Wright) .	—
,,	8. ,, ,, (after Caullery and Pelseneer)	×200
,,	9. Later larva (after Caullery and Pelseneer) .	×100

Wt. 7853.—S. 287 750. 1 20. B. & N., Ltd.

Plate I.



Fisheries, Ireland, Sci. Invest., 1908.

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VI.—HILLAS, A. B. E.,—Summary of Reports relative to Eel Fry, 1908–9. pp. 9. [1910].

VII.—Title-page, Table of Contents and Index for 1908.

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