## The Breeding of Littorina neritoides.

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With 11 Figures in the Text.

Littorina (Melarhaphe) neritoides (Montagu) is stated by Tattersall to be viviparous. Living usually above high-water mark, often with Littorina saxatilis (L. rudis in Plymouth Marine Fauna 1931, Marine Biological Association), it would seem at first sight that free-swimming larvæ would be useless. L. saxatilis is truly viviparous and provided with a special pouch for its young which crawl out as small individuals similar to the parent. Tattersall (1908, 1909, 1920) when he discovered the planktonic egg-capsules of L. littorea (Caullery and Pelseneer (1910) having described them at almost exactly the same time) then regarded L. neritoides as viviparous. He has, however, kindly sent me the statement given below.\* Following him many workers have also declared that this species is viviparous (Flatteley and Walton, 1922, Colman 1933 Russell, 1934 and others). It is now possible to show that, not only is it not viviparous but it lays planktonic capsules very similar to those of L. littorea.

It was with surprise that I could never find any young inside L. neritoides although they were always to be found in L. saxatilis. Moreover, although their usual habitat is in crevices of dry rock where only spray on rare occasions can reach them (Figs. 10 and 11),† I also found them at times in small shallow pools a few inches deep in the rocks. At Wembury, below the cliffs and sometimes covered at high tides, they are to be found with Monodonta lineata (Osilinus lineatus of the Plymouth Fauna, 1931) which sends its eggs out singly into the water in a similar way to Gibbula. Robert (1902) states that it is probable that Monodonta should do this and I have found in this species ripe eggs which are surrounded by a gelatinous layer swelling up in the water in exactly the same way as in Gibbula. On the other hand Colman (op. cit.) states that L. neritoides at

† Mr. D. P. Wilson has kindly supplied me with two photographs of L. neritoides in their natural habitat.

<sup>\*</sup> The statement in my paper on the breeding of *Littorina littorea*, that *L. neritoides* is viviparous was based on similar statements which I thought I had read in the literature of the subject. I cannot now trace the source of this information. I have never observed viviparity in this species myself nor indeed investigated the problem at all.

Wembury "extend up the rocks several feet above high-water mark where for weeks during a calm summer their sole source of moisture is dew, rain, if any, and perhaps the dampness caused by the salt on the rocks. They congregate not only in cracks and crannies where it is damp, but also in hollows which are quite dry and bare and also directly facing the sun. It is possible that this search for hollows and cracks is more an avoidance of the mechanical force of the wind than of the dessication caused by it." Below the Plymouth Laboratory they are to be found in numbers high up in the cliffs, but sometimes in small pools in the crannies.

I studied this species for many months to see if it laid eggs, but was unsuccessful. At the same time I was finding the eggs and young of many shore prosobranchs, amongst them Rissoa sarsii whose larvæ are so common in the plankton in winter and serve as food for the very young herring (Lebour, 1933, 1934). I then attributed to R. sarsii a planktonic egg capsule, somewhat similar to that of Littorina littorea but much smaller, of a different form, and containing only one egg. I never succeeded in obtaining this capsule from the Rissoa itself but the identification was in accord with the fact that the shell of the veliger inside the capsule was sculptured in the same way as those very young larvæ from the plankton eaten by the herring and certainly belonging to Rissoa sarsii (later larvæ of the same species having been reared to the adult stage), the planktonic capsules occurring at the same time. This identification of the planktonic capsule is now found to be erroneous for the Rissoa sarsii reared from the late larvæ which were certainly the same species as the young eaten by the herring, laid eggs in the aquarium and there were in typical sessile rissoid capsules, lens-shaped, containing several eggs and attached by the flattened base to weeds. All known rissoids therefore have a similar type of egg capsule and the planktonic capsule must belong to some other mollusc.

At the same time that I was making these observations Dr. Otto Linke of Leipzig was carrying on researches on the reproductive organs of the Littorinidæ (1933). During a correspondence in which I suggested that L. neritoides was not viviparous he agreed, indeed he said he was sure it was not, and, later, he told me that he thought he had obtained pelagic egg capsules from it, somewhat similar to those of L. littorea. His sketch of the capsule was very similar to the capsule which I had attributed to Rissoa sarsii. This observation made me redouble my efforts to obtain eggs from L. neritoides and quite recently I found inside some of them eggs surrounded by true capsules, which, although much softer than those in the plankton, were of the same form and size. On writing to Dr. Linke on this matter he told me that he had recently obtained the capsules actually laid by the mollusc. He kindly allows me to refer to his discoveries and he is certainly the first to find that Littorina neritoides undoubtedly

lays planktonic egg capsules. His specimens came from Rovigno and breed in late winter and spring. In Plymouth the capsules are found in the inshore plankton through the winter and early spring, and they were found inside the female, ready to be laid, in April.

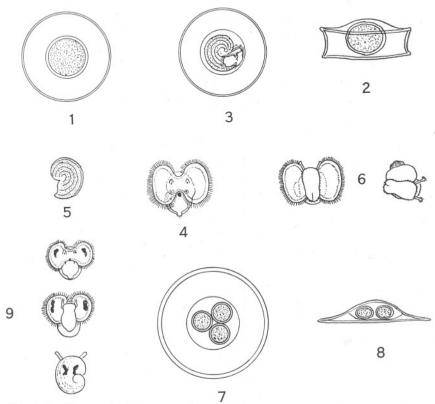


Fig. 1, 2.—Egg capsule of *Littorina neritoides* from plankton, newly laid, 0·18 mm. across. Fig. 3.—Egg capsule from plankton with veliger nearly ready to hatch.

Fig. 4.—Veliger from plankton, presumably belonging to L. neritoides, shell 0.06 mm. across.

Fig. 5.—Shell of same.

Fig. 6.—Late veliger of Littorina sp., possibly L. neritoides, shell 0.54 mm. high.

Fig. 7, 8.—Egg capsule of Littorina littorea 0.96 mm. across.

Fig. 9.—Veligers of L. littorea, swimming and crawling, shell 0.48 mm. to 0.5 mm. across.

This exceedingly interesting find shows that the capsules must somehow get into the water and the fact that the molluses have been found in shallow pools in the rock crannies probably shows their method of reaching the sea. It may be that those very high up in the dry rock crevices move towards water in the breeding season. It is certain that the capsules occur fairly commonly in the coastal plankton in winter and spring. It

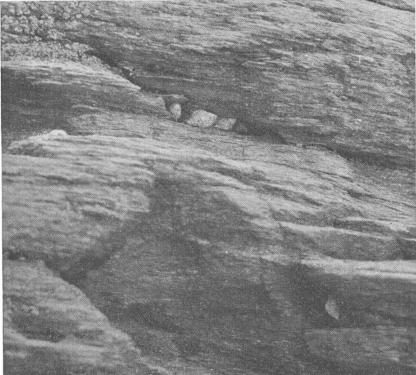
is more difficult to conceive how the crawling young reach the dry rocks. Possibly the spray deposits them near, or very high tides.

A figure of the capsule is repeated here (Figs. 1–3) together with one of L. littorea for comparison (Figs. 7–8). The capsule of L. neritoides measures 0·16 to 0·18 mm. across, 0·09 mm. high, the newly laid egg 0·08 mm. across. The capsule of L. littorea measures 0·96 mm. across.

The egg is covered by a thin membrane and bathed in a fluid surrounded by an egg covering (=egg capsule of Linke). Surrounding this is the capsule (=laich of Linke) which is circular in outline, rounded in the centre on both surfaces, one surface more rounded than the other (Fig. 2). Eggs in all stages can be found in the plankton, finally a shelled veliger is seen, the velum with long cilia, the shell being sculptured with spiral lines and dots in between in a similar way to that of Rissoa sarsii. Early free-swimming veligers in the plankton have probably been mistaken for those of R. sarsii being, however, rather smaller when newly hatched (Fig. 3). There is sometimes found in the coastal plankton round Plymouth a late veliger (Fig. 6) which is apparently a species of Littorina and which does not belong to L. littorea, the latter species being recognisable by the two distinct dark purple marks one on each side of the velar lobes. Also L. littorea metamorphoses at a smaller size (Fig. 9). This unknown veliger has a perfectly colourless velum and a dark brown shell of about 21 whorls with faint striation. In shape the shell is much like a late rissoid larva, metamorphosing at much the same size and with 2½ whorls being able either to swim or crawl. The animal, however, shows it to be a Littorina. It occurs in spring and summer coastal plankton and may possibly belong to L. neritoides. If this be a correct identification then the fact that it remains long in the plankton and metamorphoses at a comparatively large size may account for its being able to migrate to some extent in order to reach the dry rocks.

All this emphasises the fact that it is not a fixed rule for those molluscs inhabiting regions beyond or near high water mark to be viviparous or have the veliger stage suppressed.





Figs. 10 and 11.— $Littorina\ neritoides$  in its natural habitat in the rock crevices (photographs by Mr. D. P. Wilson).

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