

An Account of the Natural History of the Slipper-Limpet

(*Crepidula fornicata*),

With some remarks on its occurrence on the Oyster Grounds on
the Essex Coast.*

By

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THE American limpet, or slipper-limpet, known to naturalists as *Crepidula fornicata*, was introduced into England about 1880, being recorded at that time by Mr. B. S. Dodd in the Proceedings of the Malacological Society for 1893. Dodd, it is interesting to note, sounded even at that early time a warning note against the possible spread of this animal, and the probability of its becoming an enemy to the oyster farmer. There is no doubt that this limpet has been, and is probably still being introduced along with American oysters, on which it fixes itself. I have myself seen it unshipped along with oysters, but all the specimens I found had died recently. The spread of the limpet appears to have been very rapid on some grounds, as, for example, at West Mersea, where, since its appearance about eight years ago (from information obtained from local oyster fishermen), it has spread so that it is now more common than oysters.

The rapid spread of *Crepidula* on this coast is probably due chiefly to the abundance of the kind of food which the animal likes, and I am able to show that *Crepidula* feeds on exactly the same food as oysters. Thus the suitability of the Essex coast for the culture of oysters rendered it equally suitable for the spread of *Crepidula*. The mode of feeding of *Crepidula* is the same in principle as that of the oyster. Water is drawn in and expelled at the front end of the shell; the ingoing current entering on the left side, passing over the back of the animal, and out at the right side, as indicated in the accompanying diagrams (see † page 447, Figs. 1 and 2). Between the ingoing and outgoing currents the gill of the animal acts as a strainer, which collects all the food material that occurs floating in the

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† These figures are incorporated in another and fuller account of the mode of feeding of *Crepidula* (see pp. 444-78 of this number) which was written subsequently to the printing of this Report.

water. The collected food material is washed towards the mouth in two main batches, according to whether it is coarse or fine. The coarse particles on being drawn in with the water can be seen to be washed forwards along the left side of the animal towards a pouch which hangs down in front of the mouth. (See Figs. 1 and 2 A.) In this pouch the particles collect, and *Crepidula* can feed when it wants. The greater part of the fine particles, however, are treated differently. These, on being drawn against the gills, are washed towards the tips of the gills, which just roof in a deep groove on the right side of the animal. (See Fig. 1 B and Fig. 2 B.) In this groove the fine particles are collected, and every now and then are shot forward towards the mouth in a cylindrical mass. (See Fig. 1 B.) As the food mass passes forward, the animal seizes it in its mouth and eats it. I have fed *Crepidula* on diatoms, and watched it feeding in this way, and if very fine coloured particles be added to the water, a coloured cylindrical mass may be seen collecting on the right side of the animal just behind the "head," and the action of swallowing easily observed. Examination of the gut contents of *Crepidula* and the oyster shows that the same kinds of diatom are found in both animals, and moreover, that the commonest diatoms are the same in both animals. The faeces of slipper-limpets fed on a culture of diatoms consist wholly of diatom shells embedded in mucus. Thus it will be seen that *Crepidula* can be fed on diatoms. A chain of six individuals lived for nine months in a large-sized jam jar which contained sterilised water, to which supplies of diatoms and other small organisms were added at intervals. At present there are in our tanks a large number of living chains which have already been there nearly a year, and several other chains which I have had about seventeen months. These are all undoubtedly feeding on the floating substances in the tanks. A more detailed account of *Crepidula*'s mode of feeding and of the gut contents of *Crepidulae* and oysters will be published shortly in the *Journal of the Marine Biological Association*.

In accounting for the spread of *Crepidula* in its new environment, some allowance must also be made for the probable absence of some of the enemies which it had in its original home, and also for the probability of an invigorating effect of the new environment. With regard to this latter suggestion may be noted the apparently early spawning of English *Crepidulae*. I am informed by Prof. Conklin that American *Crepidulae* begin to spawn in May and possibly in April, while English *Crepidulae* begin to spawn in early March.*

* Since this Report was written, *Crepidula* spawned in the tanks at Plymouth in early February.

The direct factor in the spread of *Crepidula*, however, lies in connection with the spawning habits, as may be gathered from what follows. *Crepidula* spawns during the period from early March to the beginning of November, but the greater number of individuals appear to spawn about May. This limpet takes special care of its spawn. It constructs about 50 to 60 membranous bags, into each of which it passes about 250 eggs, and as the bags are made and filled with eggs they are closed and fastened together by short cords. These cords are finally all stuck on to the surface on which the slipper-limpet happens to be sitting, so that when by taking away the spawning individual the spawn is uncovered, it looks like a bundle of balloons, each containing a number of eggs. Each spawning individual, therefore, lays about 13,000 eggs, which are carefully protected beneath the shell of the mother until they are hatched. It is unlikely that individuals would spawn more than once a year, but beyond the fact that May seems to be a maximum spawning period, I have as yet no definite information to offer.

* To return to the fate of the eggs of *Crepidula* after they are laid: the eggs are protected by the mother *Crepidula* for about a month, but about the end of the month holes appear in the egg-bags, and the developing *Crepidulae* escape by swimming away from their parent. At this stage the *Crepidulae* resemble tiny shore sea-snails (*Littorina*), having, however, a transparent shell. In this condition they swim about at the surface of the sea, according to Prof. Conklin, for about two weeks. Towards the end of that time the young limpets begin to seek the bottom, and soon afterwards slipper-limpet spat having the typical flat shell may be found on the various objects on the sea-bottom. Thus young *Crepidulae* develop from the egg in about six or seven weeks.†

* The rapid spread of *Crepidula* along the Essex coast is now seen to be easily possible, for young swimming forms could easily have been carried by currents to the various parts of the coast, where they have settled down and formed new centres for a wider distribution. It will be an interesting problem to observe how far this species will spread in the future.

Besides the remarkable rate at which *Crepidula* is over-running the oyster beds, the species presents another feature which the oyster

* These paragraphs were inadvertently omitted from the original Report.

† The information given of the development of *Crepidula* has been drawn largely from Prof. Conklin's work on *Crepidula* (see *Journal of Morphology*, Vol. XIII, pp. 17, 18). By observations similar to his I judge also that the period of development from egg to spat is about six or seven weeks. More definite information, however, is to be desired on this point.

dredgers find very troublesome, namely, the curious habit of sticking together in long chains by one individual sitting on the back of another. These chains are without doubt permanent collections of individuals, as can be seen from the following facts:—

(1) The accurate fitting of the edge of the shell of each animal into the crevices and irregularities of the surface or shell upon which it is seated; hence, only short periods of separation could be possible. Thus the animal has, so to speak, grown in the position.

(2) In cases where a chain is attached to soft rock, the proximal individuals wear in the rock itself a deep impression of the edge of the shell by a lateral movement, probably executed in the search for food. In this way the animal becomes seated on a boss of the rock with a pit all around it.

(3) Experiments on separating the members of chains, and giving the animals an opportunity of re-chaining, indicate that the older animals can only re-attach themselves to anything with difficulty, but attach themselves most easily to a smooth surface. If a number of such animals be left in a dish, they make no attempt to re-chain in their previous order, and indeed large specimens appear unable to move about, or move only with great difficulty.

By supporting dismembered individuals of a chain in the same relative positions which they occupied before being separated, I have succeeded in re-forming a number of chains, but in order to effect this it is necessary to place the animals close together, and to keep a close watch on them, so as to replace them should they fall out of position. In many cases, however, even with such care, the animals are apparently unable to re-attach themselves.

(4) Prof. Conklin states that old individuals sometimes become permanently fixed by a calcareous secretion of the foot, and recently I have observed several old individuals which appeared to be just beginning to form such a calcareous attachment.

(5) I have kept a number of chains of *Crepidula* alive for as long a period as a year without the members of a chain separating, except in one or two cases, which may thus be regarded without doubt as exceptional.

Thus there would appear to be no doubt that the chains are permanent. The chains, however, are composed of almost entirely middle-aged or elderly *Crepidulas*, so to speak. But the very young ones are motile, and move about from place to place. I have shown elsewhere that *Crepidula* is a protandric hermaphrodite, that is to say, that all the individuals are born as males, and, passing through an apparently hermaphrodite stage, change into females. Consequently, chains are formed in the following manner:—

The young male individuals creep about from place to place, and eventually settle down either on shell or some similar surface, or on the end of a chain. Suppose an individual to settle on an oyster shell. The young male grows larger, and at the same time the edge of its shell takes on the contour of the surface to which it is attached, so that they fit accurately together. As the individual increases in age, it begins to change into a female, but meanwhile another young male may creep on to its back and settle down. This latter individual in turn begins to change into a female, another young male in the meantime having crept on to its back. With a repetition of this process, longer and longer chains are formed, until in odd cases as many as thirteen individuals may be found in chain. In this way it will be seen that in any chain the bottom individuals will be females, and the end individuals males, while between these may occur individuals of all intermediate sex forms between male and female.

Regarding, therefore, the fact established that *Crepidula* is protandric, the occurrence of a graded series of sex forms from the outer to the attached ends of the chains is further evidence that the chains are permanent.

With regard to the age of chains, I have not yet finished my investigations, but judging from reports I have received from different stations along the Essex coast, it would seem that the number of individuals in a chain will give also the number of years the chain is old. The longest chains contain about as many individuals as years have elapsed since the first appearance of the species. Thus, at West Mersea, the longest chains are composed of thirteen or fourteen individuals, and I estimate that *Crepidula* would first appear on those grounds about fourteen years ago. Local fishermen will almost certainly underestimate the length of time *Crepidula* has been present in their locality.

With regard to the destruction of *Crepidula* on the oyster grounds, it does not seem at all possible to make any sweeping attack on this pest. However, an attempt might be made to make *Crepidula* saleable by trying various methods of cooking it to make it palatable. In this way *Crepidula* might come to be rather a desirable acquaintance than an enemy. There would appear to be every likelihood of *Crepidula* being equal in value to the common *Whelk* as an article of food. But no doubt the animals should be taken out of their shells before being cooked. After a little practice it is quite easy to take the animal out whole. Fishermen at West Mersea say that *Crepidula* eats rather tough and bitter, but I was told the limpets were cooked in their shells, so that a good result could not be expected.

Another suggested means of combating the spread of *Crepidula* is one which might be put into practice at once, if it has not already been adopted, namely, that of encouraging dredgers to bring in the whole of their catches of *Crepidula* and to destroy them. Possibly, also, something might be done by transplanting enemies of *Crepidula* into the oyster district, but great care should be taken that the enemies of *Crepidula* should not turn out to be also enemies of oysters.

The slipper-limpet, however, is not the only animal on the dredging grounds which is an enemy to the oyster. Sea-squirts, other bivalves than the oyster, many worms, barnacles, and all other animals which feed on the material found on or floating near the sea bottom, are likewise enemies of the oyster, enemies in the sense that they compete for food and space. On the other hand, there may be quite enough food on the sea bottom to support all these animals and many more, but at present we have no definite information as to how much of this kind of food there is, although there would seem to be plenty for all.

In the question of how to treat *Crepidula*, therefore, it would be of great value to have some precise information as to how much oyster food there is on or near the sea bottom, and it is to be hoped that before long the desired information will be obtained.

It has been stated that the presence of *Crepidula* on oyster grounds is evidence that the grounds are healthy, and there can be no doubt now that this is true, since *Crepidula* takes the same food as oysters. An interesting confirmation of this statement lies in the fact that inshore *Crepidulae* at West Mersea are much finer than the specimens obtained on the outer grounds, and it is well known that the inshore oyster grounds are much healthier than those outside.

The substance of this report may now be summed up as follows:—

Crepidula feeds on the same kind of food as oysters, and its presence on oyster grounds may therefore be taken as evidence of the grounds being healthy.

Crepidula takes special care of its spawn. Since all the male *Crepidulae* change into females, every individual produces in its later life at least 13,000 eggs per year.

The eggs develop into free swimming larvae, which may be scattered far and wide.

Whether *Crepidula* is harmful to oysters cannot be determined until some measurements have been made of the actual amount of food on the sea bottom, excepting in cases where it occurs in such quantities as to smother the oysters. *Crepidula* as an enemy to oysters must be put in the same class as the mussel.

There are two main problems to be attended to.

(1) To keep up the food supply of the oysters.

(2) To destroy, besides the oysters' active enemies, as many as possible of those animals which take the same food as oysters, as, for example, the slipper-limpet, mussels, most tube-dwelling worms, other animals similar to the oyster, barnacles, and all the different kinds of sea-squirts.

It should be borne in mind that sea-squirts are nearly as common on some grounds as *Crepidula*, and that they are just as likely to take away the oyster's food as is *Crepidula*.

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I. INTRODUCTION.

The manner in which the slipper-limpet *Crepidula forsteri* feeds has apparently puzzled all the naturalists who have interested themselves in this animal, as may be gathered from what follows. *Crepidula*—like its allies the whelks and other *pedibranchiate* *Gastropoda*—has a well-developed siphon, which leads one to infer that the animal lives a retreating life. But both Conklin and myself have shown that *Crepidula* settles down permanently at an early age to