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Na afsluiten van het bovenstaande kreeg ik in handen het werkje van Dr. J. H. Schuurmans-Stekhoven Jr.: „Wormen" uit de serie „Wat leeft en groeit", deel 37. Het boekje is niet afzonderlijk in den handel, wat ten zeerste betreurd moet worden, daar nu velen, dit zoo vlot geschreven, interessante werkje nooit zullen aanschaffen.

Opmerkelijk is dat *Lymnaea ovata* hier als tusschengastheer in een adem genoemd wordt met *truncatula*. Tevens wordt een teekening geplaatst van een „Posthoornslak met ontwikkelingscyclus van *Fasciola*", terwijl in de tekst *Planorbis* niet wordt genoemd. Als tusschengastheer van *Opisthorchis felineus* wordt *Bithynia Leachi* gesignaleerd; *Planorbis corneus* biedt de larven van *Bilharziella polonica* een gastvrij onderkomen.

Crepidula fornicata's invasion in Europe

by
Dr. P. KORRINGA.

Man's intensive intercontinental traffic is frequently the cause of the accidental transportation of living animals. They are either transported as stow-aways in cargoes and ballast-tanks or attached to the immersed parts of a ship's plating. In most cases the invading strangers do not succeed in settling in the new country[1]), but on the other hand intruders may find

[1]) Thus *Anomia ephippium* and *Gryphaea angulata* were brought to Holland with French oysters, but soon disappeared again. Only once did I find a young *Anomia* born in the Zeeland waters (Dec. 1937).

a very congenial home far from their native country, either owing to the absence of natural enemies or very propitious external conditions, so that they not only succeed in maintaining themselves, but often even extend so rapidly that they become a serious menace to many of the native species. *Petricola pholadiformis*, *Eriocheir sinensis* and *Crepidula fornicata* represent some of the species that have successfully invaded Europe.

About the invasion of *Crepidula* many particularities are known. *Crepidula* used to live quietly on the East coast of North-America, from Canada of the Gulf of Mexico and was by no means a menace to any of the animals in which man has an interest. *Crepidula* can be found regularly on American oyster-beds, where possibly natural enemies or diseases keep them within bounds. The slipper-limpet takes the same nourishment as oysters do by filtering off the seawater and retaining the plankton. As, generally speaking, the slipper and the oyster thrive in similar conditions, American oyster farmers consider the presence of thriving slippers as an indication of the health of oyster-beds (W i n s l o w). Generally the common mussel is a far greater menace to oyster-culture there, as a competitor for space and food. Regular mussel-cleaning keeps the slipper within bounds there. (N e e d l e r, 1932). I found but one description of the occurrence of *Crepidula* in large masses in its native country, viz. on the shore of Nantucket isle near the mouth of Long Island Sound (J o h n s o n, 1926). How different would be the behaviour of *Crepidula* in Europe!

About 1870 the English oysterbanks, at one time so prosperous, declined more and more. No efficacious measures were taken to compensate for overfishing. Exportation of oysters for relaying was replaced by importation from other countries. In about 1880 the importation of American oysters *(Ostrea virginica)* for relaying purposes was begun with, at first on a small scale. The Great International Fisheries Exhibition held in London in 1883 gave a great stimulus to

the importation of American oysters (M u r i e, 1911). Most probably American oysters had *Crepidula* attached to them from the first moment they were imported in England, but it was not till 1887 that English conchologists (A. S m i t h and B. S. D o d d) noticed their presence on oysters arriving for relaying purposes at Cleethorpe (mouth of the Humber). In 1891 C r o u c h found the first shell of *Crepidula* on the shore near St. Osyth (Essex) and in 1893 the first living slippers were found on oyster-banks in the river Crouch. Soon living slippers were detected in several places on the Kent and Essex coast, in most cases near the places where American oysters had been relayed. *Crepidula* extended its range repidly in the coastal waters of these counties and became by its abundance a menace to oyster culture there, especially in the estuary of the Thames.

Crepidula, unlike the large majority of his fellow-Gastropodes leads a sedentary life. Though free-swimming during the first weeks of its existence and capable of crawling about in the first weeks of its sedentary life, *Crepidula* soon attaches to some solid piece of substratum to stay there. The gills produce a strong current through the mantle chambers and sieve off the plankton content, which is conducted to the mouth, where the radula grasps the food (O r t o n, 1913). The capacity of the filtering mechanism is considerable; faeces and pseudo-faeces bring about the sedimentation of a soft mud. Its rapid propagation and powerful feeding mechanism made the slipper a serious competitor for food and space to the oyster. Oyster-beds on the South-East coast of England were soon covered with enormous masses of slippers, which were a terrible nuisance to English oyster-farmers. Profits (manufacture of manure and chicken-food) were quite insignificant compared with the enormous disadvantages.

Crepidula did not confine its range to the mouth of the Humber, Kent and Essex, but gradually extended its range to Sussex, Hampshire and Dorset, so in South-Westerly direction and to Suffolk (R o b s o n, 1929; B u r t o n, 1930).

How are such a rapid extension and increase to be accounted for? Leaving aside O r t o n's unexplained "invigorating effects of the new environment", the absence of natural enemies and diseases (although according to O r t o n (1924), *Asterias rubens, Purpura lapillus, Murex erinaceus* and *Pleuronectes limanda* occasionnally feed on slippers, they are by no means able to keep them within bounds) in co-operation with a very efficacious propagation, may well be regarded as the principal causes of these.

Unlike the large majority of sessile animals *Crepidula* does not spawn freely into the water, which procedure requires an abundance of eggs and sperm. From its free-living ancestors *Crepidula* has retained copulation as an efficient method for fertilization. For this purpose the individuals form chains, which are permanent associations. The young slipper- limpet, while still able to move about, tries to find fellow-Crepidula's for its future substratum. It attaches itself with the aid of the muscular suckerfoot preferably on the shell of another slipper. In doing so, the right anterior edge of the shell is placed as close as possible to the right anterior edge of the underlying slipper, since copulation-organs are to be found in the right anterior part of the animals. This peculiar position brings about spiral-shaped slipper-chains. In this position the slipper can copulate without changing place; only a slight raising of the shells is necessary, which is also the way to reach the normal feeding and breathing attidude. Young individuals are male; they become hermaphroditic later on and turn female at a more advanced age, to remain so, so that the undermost slippers in the chains will be found to be female. After copulation (in which process intermediate individuals may be passed over) the eggs are deposited in peculiar membraneous bags under the shell of the mother- slipper, where they are sheltered till the larvae are ready to swim off. As big losses are thus prevented, propagation is very efficacious. In this way "Crepidula appears to have become adapted to a sedentary life without losing any of the procreative advantages of a free-living habit" (O r t o n, 1909).

Without doubt *Crepidula* has been introduced several times and in several places on the English coast and in some cases it has succeeded in extending its range along the shore. Many authors, especially Orton (1912, 1915) lay stress on the free-swimming larvae as efficacious agent in extending the domain of the slipper-limpet. I do not doubt that it is the free-swimming larvae that are responsible for the extension over short distances, by which dense populations are brought about. Robson (1915, 1929) doubted, however, if it was the larvae that could be held responsible for the entire distribution along the English coast. According to him the occurrence of secundary areas of distribution, quite disconnected with the original ones, pleaded against a gradual coastwise penetration. *Crepidula* was noticed e.g. at Emsworth before its arrival at Brighton.

It is my belief, that the peculiar method of propagation discussed above hinders an unlimited extension of the species by means of free-swimming larvae, for we must remember, that successful settlement is only possible, if two or more slippers settle in exactly the same place, so that the formation of a chain is possible, in order that copulation may take place. The more the larvae are scattered by the currents, the smaller the chance that the young slipper will sooner or later find a life-mate and if he does not find one, he is doomed to remain sterile. If some part of the coast happens to be unfavourable to *Crepidula*, for lack of suitable substratum (e.g. an extensive sandy estuary without shells or gravel), this will form an almost unsurmountable obstacle. Only if a couple of adult animals, attached on wreckage or drifting seaweed, succeed in passing this region together, the formation of a new centre of distribution can be started. The peculiar way of reproduction requires a pushing on in dense masses since a few scattered pioneers are unable to extend the range of *Crepidula* efficiently. Therefore *Crepidula fornicata* will show a less gradual and less extensive distribution than sessile animals without copulation as, for instance, *Petricola pholadiformis*, which was introduced on the English coast at about the same time with

American oysters and is now very common in many parts of the North Sea.

How did *Crepidula* reach the continental coast of Europe? I do not agree with T e s c h (1924), O r t o n (1915), A d a m and L e l o u p (1934), A n k e l (1935) and S p ä r c k (1935), who assume that the freeswimming larvae were the first to reach the continental coast. I explained above why *Crepidula* is checked in its expansion by areas without suitable substratum for attachment. The bottom of the North Sea has vast areas without shells and gravel. These "deserts" make a gradual penetration along the sea-bottom impossible. Granting the possibility of the larvae being carried with the currents from England to the coast of Holland (which possibility remains to be proved) there is little chance of the larvae succeeding in finding a suitable substratum for attachment on this sandy shore, while the idea that two slipper-larvae will find each other on the same piece of substratum after so long a journey is inconceivable.

Still *Crepidula* did reach the Dutch coast! The facts show, however, that the slippers came over in couples or chains of adult specimen. The first shell was found on the beach at Bergen N.H. (O o r t h u y s, 1924), traces of seaweed indicating how the transportation took place. The first living slippers in Holland were detected by me, attached on a large piece of wreckage at the beach near Zandvoort (N.H.) in October 1926. More than a dozen living slippers, arranged in small chains, were found on it. If such a piece of wreckage is washed ashore in a favourable place, where larval development is possible and where many shells cover the bottom, this may lead to successful invasion. The most favourable place on the Dutch coast is the Oosterschelde. Unlike the estuaries of the great rivers the Oosterschelde discharges no water into the sea and contains water of a high salinity. Moreover its bottom is covered by extensive mussel-beds and by shells sown out as cultch for oyster-culture. So we need not be surprised that the first successful invasion took place in the Oosterschelde.

In May 1929 two living slippers, large specimens attached to each other, one of them sheltering egg-capsules, were found in this centre of oyster-culture, where American oysters had never been relayed[1]). It was in that same year (1929) that about a dozen more slippers were found in the Oosterschelde. The shell-covered bottom offered very suitable setting-conditions. In 1930 hundreds of slippers were found and already in 1932 and 1933 the situation grew alarming. Dense masses of slippers soon covered vast areas of the bottom of the Oosterschelde. Clean bottoms from which the shells have been removed cannot be invaded. Severe winters (1939—1940) killed the slippers in shallow water, but they survived in deeper water. Dutch oyster farmers had a lot of trouble and went to great expense in keeping the slippers within bounds and in cleaning the oyster-banks. In 1941 war-circumstances made the use of slippers for human food profitable (they are used in the manufacture of food-products, but raw their taste is also excellent, while unlike the raw mussel they do not irritate the throat; cooked slippers are tough), which has already led to the working up of more than 4.000.000 kg (K o r r i n g a, 1941).

Though wreckage is a probable disseminating agent, it is not the only possible one. The possibility of transportation by seaweed is not excluded. Though solitary slippers on which seaweed grows will only go adrift after the death of the animal, the drifting away of entire slipper-chains is conceivable if large bunches of seaweed grow on them and the undermost slipper dies or the piece of substratum is very small. Oyster-farmers know but too well how even the largest oysters may go adrift, when seaweed is growing on them abundantly and when the currents are strong. It remains to be seen, however, if in this way it is possible for the slipper to cross the North Sea alive.

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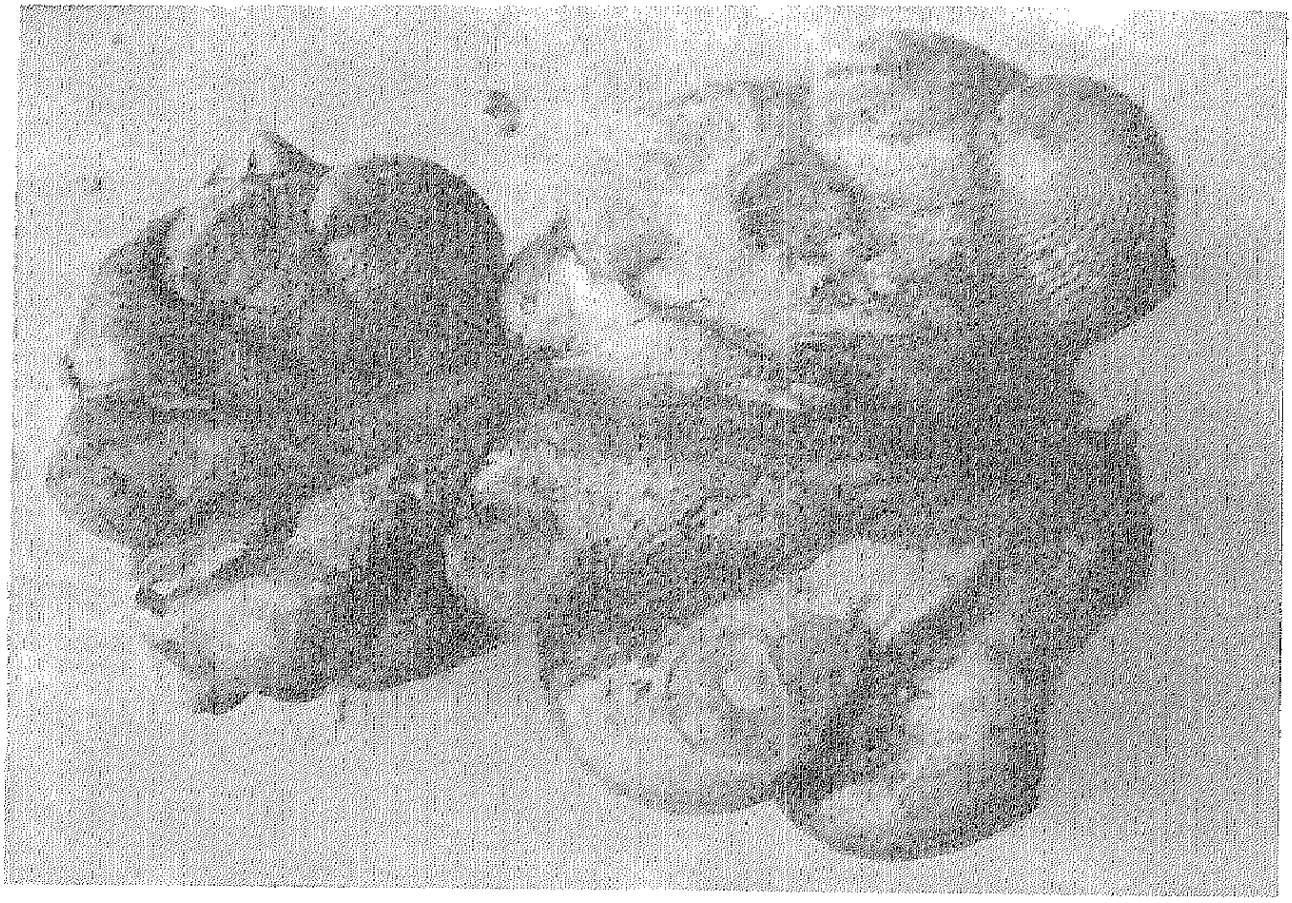
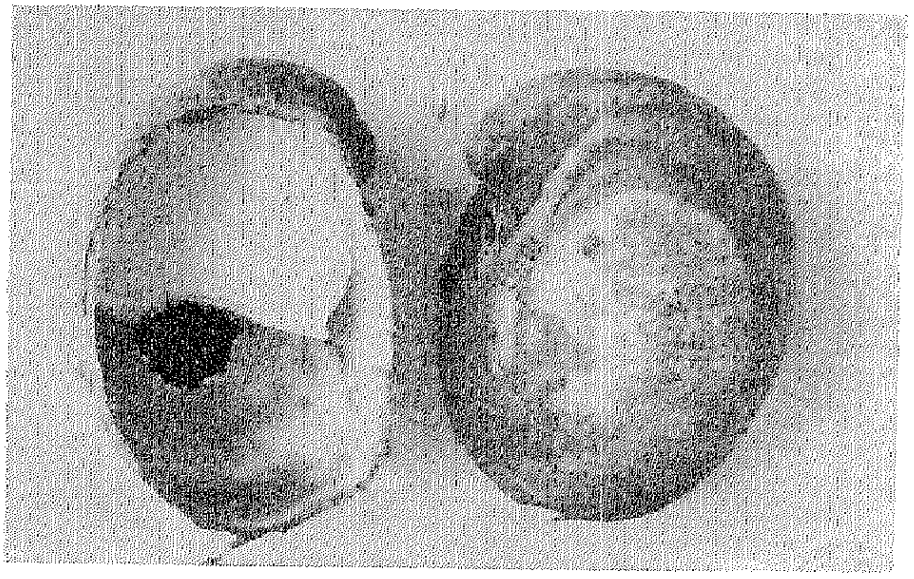
[1]) A living slipper is reported to have been found in the nearlying Grevelingen already in 1927. This specimen has not been preserved, however.

Shucking of the cooked slippers, Arnemuiden (Zeeland) 1941. *(Foto De Soomer)*



Chains of *Crepidula fornicata* (L.)



Crepidula fornicata (L.)

(Foto's Dr. B. Havinga)

I believe with R o b s o n (1915) that it is difficult to explain the slippers importation attached on immersed parts of vessels. Usually the ships are cleaned regularly so that entire chains of slippers capable of invasion will seldom or never be found on them. Even in the Oosterschelde we seldom find slippers attached to vessels. It was found that ships arriving from London at Bergen op Zoom never had slippers attached to them. Even if young slippers should fall off from a ships plating (e.g. in one of the muddy harbours of the Oosterschelde, at low tide) their chance of survival is small and that of propagation is smaller still.

From the Oosterschelde the slipper-limpet reached the neighbouring Grevelingen. To the oystergrounds near the isle of Texel it was brought with oysters for relaying from the Oosterschelde. *Crepidula* also reached other places on the continental coast of Europe, but none of them by means of the free-swimming larvae. *Crepidula* was introduced with Dutch oysters to the German Wattenmeer (A n k e l, 1935), where the free-swimming larvae saw to a further distribution over short distances, which has already led to the slipper's occurrence in large masses near the isle of Sylt (H a g m e i e r, 1941). The Limfjord in Denmark was reached with oysters from Holland (S p ä r c k, 1935), just as the oyster-bassins of Oostende and Blankenberghe in Belgium (A d a m and L e l o u p, 1934). It seems that in the Bassin de Chasse at Oostende propagation takes place (L el o u p, 1940). The French oyster regions have till now been spared the invasion of this oyster pest. Prevalent sea-currents safeguard this part of the French coast against direct invasions and rigid prescriptions prohibit the relaying of Dutch oysters and mussels. Still invasion is for ever threatening, for sometimes those prescriptions are infringed (P e r c e v a u l t, 1938).

Finally I want to mention the noteworthy fact, that *Crepidula* not only extended its range to the East of its native country, but also in a Westerly direction, to the West coast of North America. It reached the Puget Sound attached on

oysters for relaying purposes originating from the East coast. In the Puget Sound, just as in Europe, it became a terrible nuisance to oyster culture (Hopkins, 1937), many expenses being necessary to keep it within bounds!

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Samenvatting.

Crepidula fornicata bereikte omstreeks 1880 de Engelsche kust met zendingen oesters, afkomstig van de Oostkust van Noord-Amerika, welke op de Engelsche oesterbanken werden uitgezaaid. *Crepidula* breidde zich daar sterk uit en werd tot een ware plaag voor de Engelsche oestercultuur. Verspreiding over korten afstand vindt plaats met behulp van vrijzwemmende larven. De bijzondere wijze van voortplanting maakt verspreiding over grootere afstanden met behulp van de larven vrijwel onmogelijk. De Nederlandsche kust werd dan ook naar alle waarschijnlijkheid niet door de larven het eerst bereikt, maar door groepen volwassen dieren. In de Zeeuwsche wateren vond de eerste geslaagde invasie plaats. De slipper werd in de Oosterschelde tot een ernstigen overlast voor de oestercultuur. Veel kosten en moeite moesten worden besteed om de slipper binnen de perken te houden. Eerst gedurende den oorlog kon hieruit geldelijk voordeel worden getrokken. De slipper bereikte eenige andere landen in Europa met Hollandsche zaaioesters.

Beiträge zur Ökologie der niederländischen Pisidien

von

J. G. J. KUIPER.

Über die niederländischen Pisidien wurde bis jetzt wenig publiziert. In spärlichen Abhandlungen geben einige Autoren Fundortberichte bekannt, ohne jedoch eingehender die ökologische Seite der Verbreitung zu berühren.

Die Absicht dieses Aufsatzes ist, zu versuchen, jede Pisidienpopulation in ihrer Gesamtheit in ein Schema einzuordnen, um