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# THE IMPORTANCE OF LARVAL MOLLUSCA IN THE PLANKTON

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# The Importance of Larval Mollusca in the Plankton.

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LITTLE was known about the biology of larval marine molluscs until quite recently, although a fair amount of scattered information may be found in the works of various authors, most of whom dealt with the eggs or newly hatched forms[1]). Their importance in the economy of the sea is very great. During the last few years the present writer has undertaken researches in the Plymouth Marine Laboratory with the object of investigating the planktonic molluscan larvae, the work so far dealing with the gastropods only. The results are astonishingly interesting, for not only have many elaborately formed and beautiful free-swimming larvae, hitherto unknown or undetermined, been identified with their adults, but many of them are found to occur in such numbers that they must influence considerably the general life of the plankton. They may do this in two ways.

(1) They are wholly planktonic feeders and, in the veliger stage, with every movement they are taking into their bodies the nanno-plankton, chiefly diatoms, but also other minute organisms both animal and vegetable, thus competing to a large extent with the other plankton feeders.

[1]) References to these works are not given. The sign × after a name indicates that the observation is new but still unpublished, O indicating that the observation is not new but has been confirmed by the present writer. The dates after species refer to the present writer's works, a list of which may be found at the end of the paper.

The nomenclature followed is that of Mr. R. Winckworth's new list of British Marine Mollusca (Journal of Conchology, Vol. 19, No. 7, 1932.) If different from that used in the revised Plymouth Marine Fauna 1931 (Marine Biological Association) the equivalent names are inserted in brackets.

(2) They are themselves food for many planktonic animals and in some cases are so important in this way that they may form the chief food of our plankton-eating fishes (Herring, Pilchard and Sprat) especially in their young stages. At certain times of their lives many invertebrates also feed on them, thus indirectly helping in food chains, the green plant being eaten by the larval mollusc, the mollusc by some invertebrate which is itself eaten by a fish and the fish eaten by man.

Both bivalves and univalves usually have free-swimming larvae which are members of the plankton for a short or long period (from a few hours to probably several months) although this is not universally the case and in gastropods some species are viviparous and others hatch out in the crawling stage, in both cases a veliger stage being observed within the egg.

In most lamellibranchs there is a short free-swimming stage, the eggs being sent out in clouds into the sea, there to be fertilised and develop quickly into veligers with a simple round velum: the British oyster, however, keeps the young in its gills until both velum and shell are well developed and the young swim away from this shelter soon to settle down as spat. The primitive gastropods *(Archaeogastropoda)* mostly have a similar simple velum. Patella (O) and its relatives send out their eggs into the sea and these hatch as small shell-less veligers, the shell forming in a few hours. Some of the *Trochidae* do the same. This is the case in the species of *Gibbula* whose eggs are known *(G. magus, G. cineraria)* but *Cantharidus*[1]) and *Calliostoma* lay their eggs in gelatinous masses or ribbons. *Cantharidus striatus* and *C. exasperatus* attach these masses to some substratum, in *Calliostoma papillosum* they float. *Calliostoma ziziphinum* (O) lays gelatinous chains on the glass sides of the aquarium. In *Cantharidus* and *Calliostoma* the larvae are hatched without a velum, having passed the veliger stage within the egg.

In the *Mesogastropoda* the velum is bilobed, and multilobed in some of the later stages of the larger veligers. In the *Lacunidae* (including *Littorina)* we have several very common littoral gastropods, some of which live above the region of ordinary spring tides and are only watered by the spray. Typical of this region is the common *Littorina saxatilis (= rudis)* (O) which is well known to be viviparous in all its many varieties. *Littorina littoralis* (O) and *Lacuna* (O) deposit their eggs on *Fucus* in small gelatinous masses, the former hatching in the crawling stage, the various species of the latter, which may also be found beyond the low water limit, hatching out as veligers with a fairly large bilobed velum and remaining in the plankton for some time. *Littorina littorea* (O) the common periwinkle, living between tide-marks and just below the low water limit has planktonic egg-capsules shaped like the British infantryman's shrapnel helmet and containing usually two to five eggs. The young hatch

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[1]) In the Plymouth Marine Fauna the genus *Cantharidus* is by an error spelt *Cantharus* (p. 254).

out as veligers with a conspicuous bilobed velum having dark purple marks on each lobe, the larvae remaining in the plankton for some time (×). In the *Hydrobiidae (= Assimineidae)* which prefer estuarine waters, *Hydrobia jenkensi* is viviparous and *H. ulvae* (O), living on mud, lays its lens-shaped egg-capsules on the shells of its companions, the larva hatching out as a free-swimming veliger with a bilobed velum. Most of the *Rissoidae* so far known have lens-shaped egg-capsules laid on weed, hydroid or bryozoon, containing several eggs, but *Rissoa sarsii* (×), which is being investigated at the present moment, has minute planktonic egg-capsules, each containing one egg, the free-swimming larva coming from it serving as an important food for the newly-hatched Herring (see below, page 000). *Cingula (Cingula) semistriata* (×) has the typical rissoid capsules with several eggs but *Cingula (Onoba) semicostata* (×) lays its eggs singly in a thick oval capsule, the young emerging without any velum. *Rissoa parva* (O),and *R. membranacea* (O) have typical rissoid egg-capsules but whereas only a few larvae hatch from the capsules of *R. membranacea* (×), some of them devouring the others ("nurse eggs"), in those of *R. parva* (×) and *R. guerini* (×) and also *Cingula semistriata* the complete number of eggs develop. In all a bilobed veliger results, usually (except in *R. membranacea,* whose larva is large and soon crawls) remaining for some time in the plankton. All these are littoral forms living between tide-marks or near low water. In the *Tornidae, Tornus subcarinatus* (×) has a beautiful little bilobed veliger and much ornamented shell, remaining for some time in the plankton, the adult living on the rocks between tide-marks, and in the *Skeneopsidae, Skeneopsis planorbis* (O) lives in rock pools high up, the young having no free veliger stage.

In the *Turritellidae, Turritella communis* (1933 d), abundant locally on mud from about 15 to 40 fathoms, lays its eggs in grapelike masses of capsules, each capsule containing several eggs which hatch as veligers with a bilobed velum, the larva only remaining in the plankton for a short time. In the *Cœcidae,* the larvae of two species of *Cœcum* are to be found in the coastal plankton, swimming about with a planorbis-shaped shell and bilobed velum (×).

The adult, living either in the shallow water or rather further out, loses the whole of this coiled shell and remains sausage-shaped with the tip filled in by a shelly plate. The *Cerithiopsidae* are mainly associated with sponges, *Cerithiopsis tubercularis* (1933 c) usually living in the crevices of *Hymeniacidon sanguinea* or, more rarely, *Halichondria,* on which it lays its eggs, and *C. barleei* (1933 c) living in or on *Ficulina ficus,* biting holes in it and laying eggs in the holes. Both species hatch out as bilobed veligers remaining in the plankton until they have several whorls. The closely related *Triphora perversa* (1933 c) also has a bilobed velum and a long larval stage. These three species may occur as larvae in the plankton from the coastal waters to far out over a depth of 30 to 40 fathoms. In the *Eulimidae* the species of *Eulima* have several whorls before settling down, the larva

with a bilobed velum. The eggs of *Eulima polita* (×) are laid in oval, opaque, white capsules on some substratum and contain many eggs. The closely related *Pelseneeria stylifera* (= *Stylifer stilifer*) (1932 b) lives on echinoids, laying its eggs in triangular bags on the test, the larvae emerging as veligers with a bilobed velum. In the *Pyramidellidae*, all of which have sinistral embryonic shells but are dextral animals, those whose eggs are known lay them in small capsules on some substratum, the young hatching with a bilobed velum and metamorphosing when the shell becomes dextral and not staying long in the plankton. Those whose eggs have been seen are *Chrysallida (Parthenia) decussata* (= *Pyrgulina decussata*) (×), *Odostomia (Brachystomia) eulimoides* (1933 b), living on *Chlamys opercularis* and laying its eggs there, and *Turbonilla (Tragula) fenestrata* (= *Tragula fenestrata*) (×). In the *Calyptraeidae*, *Calyptraea chinensis* (O) covers its eggs, which are in triangular capsules, with its shell until the young emerge in the crawling stage having lost the velum, the adult living in shallow water beyond the low tide level. In the *Aporrhaidae*, *Aporrhais pespelicani* (1933 d) living in shallow or deeper water deposits its eggs singly in shell gravel, the larva emerging as a veliger with a bilobed velum soon changing to four and then to six lobes, each lobe having a mass of almost black pigment at the end. The larva of *Aporrhais* remains for a long time in the plankton and reaches a large size (1.25 mm.) before metamorphosis. In the *Naticidae*, *Natica (Lunatia) catena* (O) and *N. (Lunatia) poliana* (= *N. alderi*) (O) form spirals or semi-spirals of agglutinated sand with the eggs in capsules embedded in them. Both species live in sandy gravel, *N. catena* having "nurse eggs" but not *N. poliana* (O). Both have brown pigment on the velum which at first is bilobed in both species, one of them (probably *N. catena*) having four long lobes later. Both larvae remain for some time in the plankton.

Next come the *Lamellariidae* including *Velutina* and *Lamellaria*, and the *Cypraeidae* including *Erato*, *Trivia* and *Simnia*. There seems to be a close relation between the larvae of *Lamellaria* and *Velutina* on the one hand and *Erato* and *Trivia* on the other, *Simnia* being quite different and more like the true Cypraeas. *Lamellaria perspicua* (O) is well known for making its nests in compound ascidians, the larvae hatching out with a beautiful little nautiloid *Echinospira* shell, this *Echinospira* surrounding the true shell and serving as a float. The larva hatches with a bilobed, but slightly indented, velum, the later stages having six lobes. An allied form from deeper water at Plymouth also has six lobes. These *Echinospira* larva remain for a long time in the plankton. *Velutina* (×) has a gelatinous covering over the true shell, serving the same purpose and occupying the same position as the *Echinospira* of *Lamellaria* but without perceptible whorls. *Trivia* bites holes in compound ascidians and deposits its eggs in these enveloped in their vase-shaped capsules, the lips of which protrude. The two species *Trivia monacha* (1931 c, 1933 a) and *Trivia arctica* (1933 a) have *Echinospira* shells slightly different from those of *Lamellaria*, the

late veligers differing in the shape of the velum, that of *T. monacha* being only slightly indented at the sides, of *T. arctica* being four lobed. *Erato voluta (= laevis)* (1933 b) has a helicoid *Echinospira* shell with a velum similar to that of *T. monacha*. All these which have an accessory float in the form of an *Echinospira* shell or gelatinous covering are so specially modified that they may stay some time in the plankton and reach a large size *(Lamellaria* 2 mm., *Erato* 2 mm., *Trivia* 1.25, 1.6 mm.). *Simnia patula* (1932 a) which lives and feeds on the soft corals *Eunicella* and *Alcyonium* lays its eggs in a layer of capsules on these, the young hatching with a dark brown reticulated shell and colourless bilobed velum, the velum later growing out into four long lobes and the larvae staying for a long time in the plankton.

Coming now to the *Stenoglossa*, many of these lay vase-shaped capsules attached to some substratum and in several cases the young are hatched in the crawling stage having passed the veliger stage within the egg. Here we have *Trophonopsis muricatus* (O) with lens-shaped capsules containing very few eggs, the young crawling when newly hatched, *Nucella lapillus* (O) with vase-shaped capsules laid on the rocks, most of the eggs being devoured within the capsules by the few which hatch out in the crawling stage, *Ocinebra erinacea* (O) with angular vase-shaped capsules, *Buccinum undatum* (O) with its large masses of capsules containing many eggs most of which are devoured within the capsule. Most of the other species of the Buccinidae known hatch in the crawling stage. In the *Nassariidae*, *Nassarius reticulatus* (1931 a) and *N. incrassatus* (1931 a) both lay flattened flask-shaped egg-capsules attached to weed, bryozoon or hydroid, all the eggs hatching and the veligers remaining for a long time in the plankton. *N. reticulatus* has the velum bilobed and but slightly indented in the later stages, but in the older veliger *N. incrassatus* has four long lobes each with brown pigment at the end and this larva extends much further out to sea than *N. reticulatus*. In all the *Turridae* known, lens-shaped capsules are laid on some substratum. The Philbertias have beautifully sculptured larval shells, *P. leufroyi* (×) and *P. linearis* (×) with colourless four-lobed velum, *P. (Comarmondia) gracilis* (1933 e) with four long lobes decorated with orange and brown spots, *Mangelia nebula* with an enormous velum covering the shell like a real veil. All these have horny shells, which attain a large size before settling down, and remain for a long time in the plankton *(P. gracilis* = 1.76 mm.).

Besides all these planktonic forms mentioned above there are innumerable larval Opisthobranchs (including the *Pleurocœla, Pteropoda* (1931 c, 1932 c) and *Ascoglossa)* most of which are free-swimming for part or the whole *(Pteropoda)* of their life. If we add to these all the larval lamellibranchs we have a host of molluscs in the plankton which must be of enormous importance in the sea.

The coastal waters differ slightly from the more open waters (15—40 fathoms) in the kind of larvae present in the plankton,

although in many cases there is overlapping. In the shallow-water plankton near the coast are the larvae of *Patella*, the *Trochidae*, *Littorinidae*, most of the *Rissoidae*, *Cæcum*, *Tornus*, many of the *Pyramidellidae*, the two species of *Nassarius*, the two species of *Trivia*, some turrids, *Cerithiopsis*, *Triphora*, *Lamellaria*, *Aporrhais*, and *Eulima*. The first three are almost confined to the shallower waters but all the others may be found further out. In the deeper waters, however, we find the larvae of *Trivia arctica* and not *T. monacha*, *Philbertia leufroyi* and not *P. linearis*, *Nassarius incrassatus* and not *N. reticulatus*, *Erato*, *Simnia*, and the second species of *Lamellaria*.

The velum of the larval mollusc is large or small according to the length of time the larvae stay in the plankton, those with the largest shells usually possessing the most elaborate velum (*Aporrhais*, *Philbertia gracilis*, *Trivia*, *Lamellaria*, *Erato*, *Nassarius*, *Mangelia nebula* etc.). The velum is a powerful swimming organ and is bordered at the edge by a groove having an upper layer of long cilia and an under layer of shorter cilia, the groove leading to the mouth on the ventral surface in front of the foot in the early stages, the foot usually growing beyond it later. These cilia constantly moving create a current in the groove which continually wafts food, nannoplankton, into the mouth. This food consists chiefly of diatoms and minute flagellates, but dinoflagellates and even tintinnids (*Infusoria*) have been observed inside the larger veligers and also such diatoms as *Thalassiosira*, *Skeletonema* and *Lauderia* — even the needle-shaped *Rhizosolenia* and stiff chains of *Paralia* are sometimes taken.

In the plunger jars where the mollusc larvae were reared (either from the egg or from the planktonic larva) a pure culture of *Nitzschia closterium* was given and on this diatom together with others which appeared in the water *Nassarius reticulatus* was reared from the egg to the crawling stage, the process taking two months. The chief forms found inside these larvae in the plunger jar were *Nitzschia closterium*, *Thalassiosira gravida* and *Skeletonema costatum* the two last often still in chains in the stomach. In the same species from the plankton *Thalassiosira* and *Skeletonema* were very frequently found. In smaller veligers very small diatoms and small green cells were seen (probably flagellates). *Nitzschia closterium* is too large for the smallest forms which in the plunger jar appear to feed on some much smaller unidentifiable organisms, the stomach usually being full of greenish substance.

In one specimen of a late larva of *Nassarius reticulatus* from the plankton, the following food was identified:—

*Thalassiosira gravida* many, some in chains, some separate.
*Skeletonema costatum* many.
*Paralia sulcata* one
parts of *Rhizosolenia* sp.
*Tintinnopsis heroidea* 2.

The natural position of the larva when swimming in the plankton is with the shell below and the foot and velum above, but the velum, especially when long lobes are present, may alter its position in many ways, the lobes flapping slowly, completely covering the shell or remaining outspread. As the cilia move the whole time, the food is being wafted into the mouth continually and there is no cessation of feeding. It is clear that mollusc veligers must compete with other planktonic feeders to an enormous extent.

An interesting case well illustrates the above remarks. Recent work on Norwegian oysters (G a a r d e r and S p ä r c k 1933) has shown that the veligers of a species of *Cerithium* is a very important competitor for food with the oyster larvae, hatching at the same time and feeding on the same nannoplankton. The *Cerithium* larvae are in some years many times more numerous than the oyster larvae themselves. If we know the habits of the molluscs which compete for food with those of commercial importance we shall be near the solution of many problems. It has been shown above (page 337) that two species of *Cerithiopsis* (a genus closely related to *Cerithium*) are always found associated with certain sponges and these sponges are probably necessary to them. If a similar association were to be found in the oyster pools we may find a means of ridding them of the competing larvae. Apart from the need of knowing all that is to be known of the biology, including the life history, of all those molluscs which are of commercial importance, it is also necessary to know all we can about their molluscan neighbours which, although neither useful nor harmful from the point of view of human consumption, yet indirectly may be of extreme economic significance.

The breeding season or seasons of each species of mollusc should be carefully ascertained and here there is a wide difference in the various species. Even in winter there are several veligers which are abundant in the plankton. Confining our remarks to the gastropods studied we have *Patella vulgata*, *Littorina littorea*, *Trivia arctica*, *Nassarius incrassatus*, *Lamellaria perspicua* and various members of the *Rissoidae* all spawning in winter, although some of these may continue into the spring or even breed throughout the year. Most of the molluscs, however, breed in spring and summer and after the spring diatom maximum a large influx of veligers is to be seen, continuing throughout the summer and well into the autumn. *Patella vulgata* has practically finished spawning in March, *Littorina littorea* in May, although a few may continue through the summer. *Trivia arctica* gives place to *Trivia monacha*, the latter breeding from late spring throughout the summer, *Nassarius incrassatus* continues through spring and early summer and its larvae are common with those of *N. reticulatus* in spring and summer, the late larvae of *N. incrassatus* usually being a feature of the plankton in late spring and summer. *Lamellaria perspicua* breeds throughout the year but especially in spring and summer. Others beginning in early spring are *Aporrhais*, *Lacuna*, *Cerithiopsis*, *Triphora*, *Odostomia* and its relatives, many rissoids and

turrids. Many of these continue throughout the summer. *Trivia monacha*, *Simnia patula*, *Erato voluta* are almost wholly late spring and summer breeders. Enough has been cited to show that some kind of gastropod veliger is always in the plankton and the various seasons have also their opisthobranchs and lamellibranchs.

The breeding of certain species coinciding with the hatching of others which eat them may be of great significance and this brings us to the second, and perhaps the more weighty, reason for stressing the economic importance of molluscan larvae in the plankton: *they may form the food of commercially important animals.* It is specially the young fishes which illustrate this. To take but one instance, that of the clupeoids; at the whitebait stage the young of herrings, pilchards and sprats occur in enormous numbers round our coasts and have frequently been found to be full of larval lamellibranchs, probably oysters, cockles or mussels. A still more interesting case is now being investigated. The newly hatched herrings from the mouths of the estuaries and just off the coast very frequently are found to contain larval gastropods at the stage when the veliger is just out of the egg. Even when there are remains of the yolk sac still in evidence the baby herring eats this mollusc. In 1921 it was found that out of 140 of these very young herrings examined 91 contained these larval gastropods (I. e b o u r 1921).

This little mollusc has proved to be *Rissoa sarsii*, which is not one of the commonest shore forms. It has been found to hatch from a minute floating egg-capsule, common in the plankton, only 0.16 mm. across, the newly hatched veliger measuring 0.054 mm. across the shell. When still inside the capsule and when newly hatched the shell is marked in a peculiar and characteristic manner with longitudinal striations and small dots in between, and these markings are clearly seen on the shell inside the baby herring. Just at the time the herrings hatch in the coastal waters an enormous number of these veligers also hatch out (December to February). They are some of the commonest if not *the* commonest molluscs in the coastal plankton at that time and occur together with the larvae of other rissoids, *Patella vulgata* and *Littorina littorea*. It was, however, noted that although the baby herrings sometimes contained very young lamellibranchs of about the same size as the gastropod in question, no other gastropod larvae were found inside them, those of *Patella* and *Littorina* probably being too large.

The older larva has been reared in a plunger jar until recognisable as *Rissoa sarsii*. The veliger remains for some time in the plankton, the shell attaining 2½ to 3 whorls when it can either crawl or swim. In this stage the apex of about 1½ whorls is clearly seen to be marked with the characteristic striations and dots. If the adult could be collected in numbers it might be possible to give the baby herrings hatched in the Laboratory that early food which is most natural to them.

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