THE BIOLOGY AND TREMATODE PARASITES OF THE GASTROPOD *LITTORINA NERITOIDES* (L.) ON THE PLYMOUTH BREAKWATER

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(Text-figs. 1–11)

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Introduction

Crevices in rocks about high-water mark are usually regarded as the typical habitat of *Littorina neritoides* (L.). The species was thought to be viviparous until in 1935 Linke and Lebour showed that its egg capsules were pelagic, and the investigation described here was begun primarily to ascertain how these egg capsules reached the sea. The first part of the paper deals with the type of habitat occupied by the adults, and their distribution at different levels. The second part deals with spawning and comprises three sets of observations; first, the state of the gonads was determined by dissections through the year; secondly, field experiments were carried out to find whether there was any downwards migration for spawning; and thirdly, the egg capsules were collected from the plankton for a part of one winter and the following spring, and an attempt is made to show that their occurrence is related to meteorological conditions. The third part of the paper deals briefly with the distribution of size groups in the population, growth rate, and the sex ratio. The fourth part is an account of the occurrence of larval trematodes in the species. Dissections showed that the snails were heavily infected with cercariae, and records were kept of their incidence in order to find out whether they caused sterility, influenced the growth rate, or produced sex reversal.

The Plymouth Breakwater was selected as a starting-point for this investigation, as it is a long stretch where conditions are much more uniform than on the same length of shore. It was originally intended to extend the observations to other localities, but this has been impossible save to a very limited extent; all the work described below was carried out on material collected from the Breakwater except where other places are specifically mentioned.

I am greatly indebted to Dr E. J. Allen, F.R.S., through whose kindness I was able to begin this work; to Dr Kemp, F.R.S., Director of the Plymouth Marine Laboratory, who has given me every facility and encouragement for continuing it; and to the Zoological Society for the use of its table at the Plymouth Laboratory for a month in 1939. Amongst the many people who have helped me I wish particularly to thank Dr Lebour for her constant interest, Dr H. B. Moore for much assistance with field work, Mr G. M. Spooner for his help with statistical data, and Mr G. I. Crawford for reading part of the manuscript. Mr William Searle, of the M.B. *Gammarus*, collected all the samples for me, from May 1937 to June 1938, and I am most grateful to him for much help with field work, particularly in August 1939.

The Plymouth Breakwater Habitat

The building of the Breakwater was begun in 1812 and completed in 1851; four million tons of native limestone and two and a half million tons of granite facings were used in its construction. It is approximately 1600 m. long, and consists of a central part and two arms of about 330 and 360 m. (see map in *Plymouth Marine Fauna*, 1931). The central part faces 2° west of south, the eastern arm about 15° east of south, and the western arm about 17° west of south. Levels were kindly given to me by the Civil Engineer in Chief at the Admiralty. The top is approximately 13·7 m. wide, and its mean level is 0·76 m. above high-water ordinary spring tides. The northern and southern sides are at slopes of 2 to 1 and 5 to 1, respectively. Numerous small cylindrical holes, which were probably used in hoisting the blocks into position, occur on the surface. They vary in size, but are generally 7–9 cm. across, and 8–15 cm. deep.

Very heavy seas sometimes sweep over the Breakwater during the winter. Twenty-four merchantment were wrecked in the Sound in one storm early in the nineteenth century, and about 30 years ago two 80-ton blocks of concrete lying on the southern face of the Breakwater were skidded across the top near the lighthouse at the west end. The degree of exposure is therefore very considerable and fucoids are sparse on both slopes. The factor for the wave exposure of certain localities may be calculated, according to Moore's formula (1935, p. 80; 1936, p. 66), as "the number of days per 100 days in which any wind blows into the exposed aperture of the locality in question, this opening being the seawards aperture measured at a distance of half a mile". This formula does not seem applicable to the Breakwater. If the aperture is measured at a distance of half a mile it is 180°, and the modifying effect of the land-masses to the east and west is not taken into account. It seems better then that the aperture should be taken from the angle between two lines drawn from the middle of the Breakwater to Reny Rocks and Penlee Point, that is approximately a quadrant facing south-east to south-west. According to unpublished wind roses at the Meteorological Office at South Kensington (observations from 1893 to 1922, Fig. 1), the percentage number of winds blowing through this aperture throughout the year is 33. The mean for

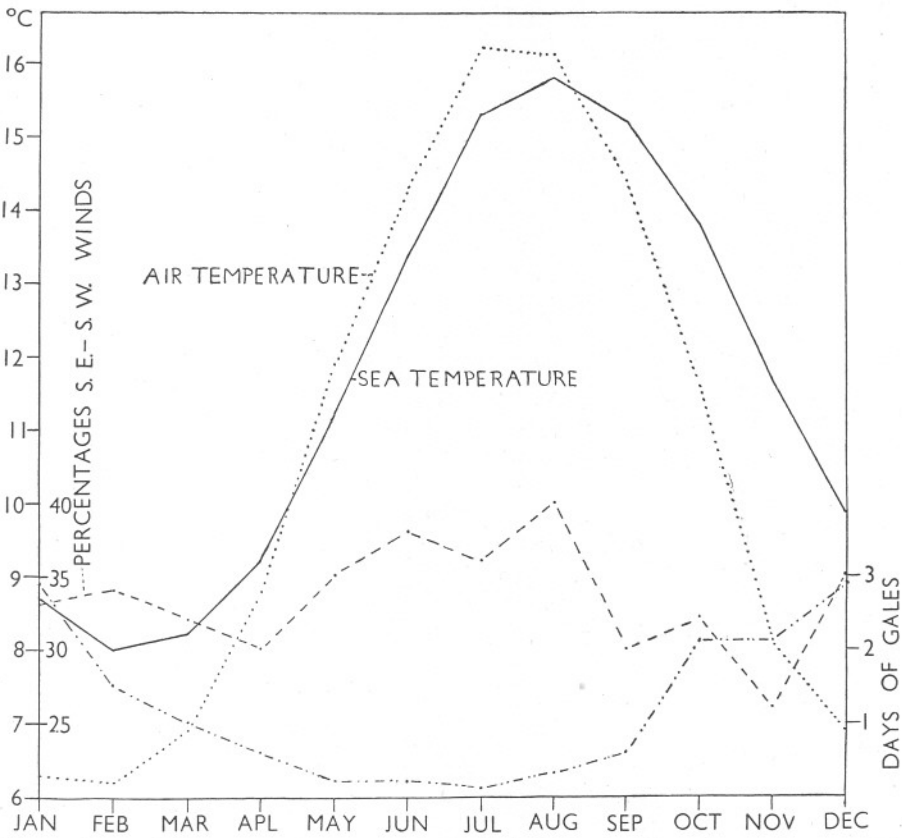

Fig. 1. Sea and air temperatures, percentages of winds blowing from the south east-south west quadrant, and the numbers of days of gales per month in Plymouth Sound.

October to March, inclusive, is 32, for the summer months 35, and the highest average for a single month 40 for August. But gales are most frequent during the winter months (Fig. 1), and, as Johnson points out (1919, p. 72), the prevailing wind may not be the dominant wind. The foreman of the repairing gang on the Breakwater tells me that the most destructive wind there comes from the south-east. The factors that affect the degree of exposure there are thus very complex and cannot be expressed by a single figure. Direct measurement of the dynamic force of the waves by some type of dynamometer

(Gaillard, 1904) will probably prove to be the most satisfactory method of comparing the exposure of different localities.

The figures for the sea temperatures were kindly supplied by the Plymouth City Meteorologists, Messrs Prigg, Lynden and Ivory. The monthly means are compiled from observations from 1897 to 1932, the temperatures being taken three times weekly at a depth of 6 ft. off the end of Promenade Pier. The air temperatures, for Plymouth Hoe, were supplied by the Meteorological Office at South Kensington. They are compiled from daily means from 1906 to 1935.

Zonation on the Breakwater

Two traverses were made across the Breakwater in August 1939, the first, A (Fig. 2), 345 m. west of the midpoint, and the second, B (Fig. 3), 184 m. east of the midpoint. Two surface samples were taken at each level at A, but, owing to limitations of time, only one at each level at B, where there were also fewer stations. Each sample consisted of the total number of snails collected in 100 sq. cm. The population in the pools on the top was estimated from two pools at each of four stations in both traverses; the first station being situated at the north edge, and the others 4·5, 9 and 13·5 m. south of it. The depth of each pool and the volume of water in it were measured and the approximate area of the sides and bottom calculated from the formula $2\pi\,(\sqrt{v/\pi H})\,H$. The results are shown in Table I and Figs. 2 and 3.

TABLE I

Levels of "dry" stations in relation to mean sea-level m.	Traverse A No. per 100 sq. cm.	Traverse A Height of shell Range mm.	Traverse A Height of shell Mean mm.	Traverse B No. per 100 sq. cm.	Traverse B Height of shell Range mm.	Traverse B Height of shell Mean mm.
North slope 0·8	0	—	—	0	—	—
1·7	0	—	—	—	—	—
2·2	6	2·0–3·2	2·6	—	—	—
2·6	11·5	2·0–3·2	2·4	61	2·0–4·7	2·7
[E.H.W.S. 2·72]						
Top 3·0 *A*	6·5	2·0–5·9	3·3	27	2·0–4·4	2·6
B	23	2·3–6·2	3·7	37	2·6–6·5	4·3
C	83	2·0–5·9	3·0	14	2·6–7·1	5·0
D	109	2·0–3·8	2·5	56	2·3–4·4	3·1
[E.H.W.S. 2·72]						
South slope 2·6	134	2·0–4·5	2·7	70	2·0–5·0	3·0
2·2	59·9	2·0–3·8	2·4	—	—	—
1·7	27	2·0–3·2	2·3	—	—	—
1·3	6	2·0–2·6	2·3	17·5	2·0–2·9	2·4
0·8	6	2·0–2·6	2·2	—	—	—
[M.S.L. 0]						
−0·1	2	2·0–2·6	2·3	—	—	—
−0·6	0	—	—	—	—	—
"Wet" stations						
Top 3·0 *A*	13·2	2·0–7·7	4·5	8·6	2·0–7·1	3·5
B	54	2·0–6·8	4·6	19·2	2·3–8·0	5·1
C	33·1	2·0–7·4	4·5	33·85	2·9–7·7	5·3
D	20·8	2·0–6·8	3·8	44·2	2·3–6·8	4·1

E.H.W.S. = extreme high-water springs; M.S.L. = mean sea-level.

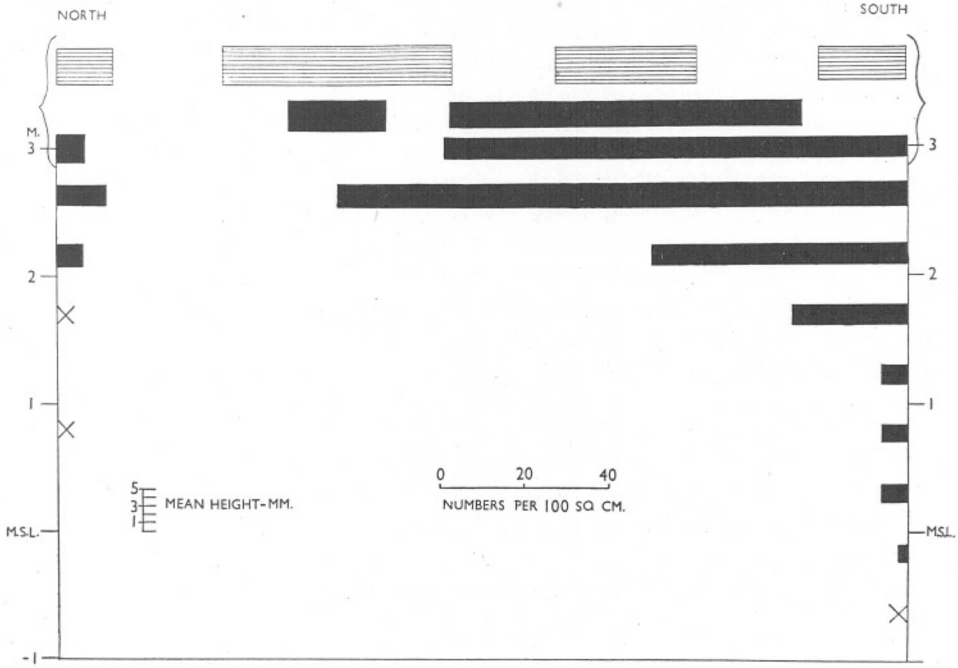

Fig. 2. Numbers of snails per 100 sq. cm. at different levels on the Breakwater in traverse A. Those collected from "dry" stations are shown in solid blocks, and those from the pools in horizontally ruled blocks. The height of the blocks shows the average height of the snails at each station. The eight bracketed samples were all taken across the top of the Breakwater, 3 m. above mean sea-level (M.S.L.).

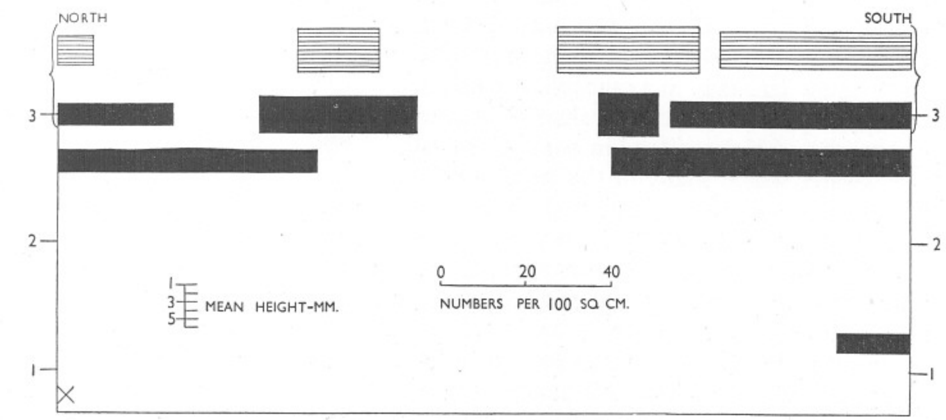

Fig. 3. Numbers of snails per 100 sq. cm. in traverse B. Explanation of blocks as in Fig. 2.

The height of the shell was measured with a pair of sliding callipers with a 0·1 mm. Vernier scale. Snails less than 2 mm. in height are included in the 2 mm. groups owing to the difficulty of measuring them with any degree of accuracy. They rarely occurred except at the lowest levels.

The traverses showed that the snails were most abundant towards the top of the southern slope just below extreme high-water springs, i.e. 2·6 m. above mean sea-level (Fig. 2, Table I). Small snails were found 0·15 m. below mean sea-level, and also occurred at the top of shelter blocks (not included in the traverses) 5 m. above mean sea-level. Colman (1933) found that at Wembury they occupied a zone of only 2·72 m., extending vertically from about 1·25 m. above extreme high-water springs down to mean high-water neaps. The zone occupied on the Breakwater is therefore of considerably greater vertical extent than at Wembury, but it is possible that the small snails at the bottom of the zone were overlooked in the latter locality as they usually shelter amongst the barnacles and are difficult to find. Owing to the high degree of exposure on the Breakwater all the snails are within the splash zone at least during the winter months, when, owing to the heavy swell, the sea washes over the top twice a day at high tide.

Relation to Ecological Factors

Light

The habitats selected are very variable with respect to light. It has already been noted that on the Breakwater the population is most dense almost at the top of the southern slope where the maximum amount of sunlight falls. During the winter the top of the Breakwater is covered with a fairly dense layer of algae, which retains moisture and gives a certain amount of shelter. During the summer, however, algal growth is negligible, and the snails have to endure prolonged exposure to the sunshine. At Tinside, Plymouth, they are common in crevices on the southern slopes, but also underneath overhanging rocks at the entrance to a cave where there is no direct sunlight. They occur in equally exposed and equally shaded situations on Drake's Island, and also at Crantock and Kelsey Head in north Cornwall. Furthermore, on the top of the Breakwater where many of the larger snails live in water in small cylindrical pits, they are equally distributed on all sides of these pits, and at all depths.

Flattely & Walton (1922), discussing the distribution of this species in Cardigan Bay, say that it occurs there in crevices just above high-water mark, which are not exposed to the midday sun, and that the same type of distribution occurs on the Devon coast. Colman (1933), however, found that at Wembury the snails "congregate not only in cracks or crannies where it is damp, but also in hollows which are quite dry and also directly face the sun". He goes on to remark that "they are always very loosely attached to the rock so that one can easily blow them off" and suggests that "the search for hollows and cracks is more an avoidance of the mechanical force of the wind than of the desiccation caused by it". He refers to Fränkel's (1927) work on taxes in this species, which was found to be negatively geotactic, negatively phototactic when above a horizontal substratum, but positively phototactic when hanging from a horizontal ceiling. Colman concludes by saying that the resultant of these reactions would make the animals congregate round the entrance to fissures and in hollows, where, in fact, they are found in nature. Actually, Fränkel qualifies his remarks. He says (free translation): "However, this change in phototactic response occurs only in water. In air *Littorina* is negatively phototactic even when hanging from horizontal ceilings."

That these responses are highly modified under certain conditions in the field is obvious from the distribution of the snails on the Breakwater, and it seems likely that the concentration on the exposed sunlit slopes there may prove indicative of the general distribution of the species. The following observation by Fischer-Piette (1936, p. 248) is of considerable interest in this respect: "Il est curieux de voir cette espèce mieux réprésentée sur la côte anglaise que sur la côte française de la manche, étant donné que, par ailleurs, elle est particulièrement bien développée dans les régions plus méridionales telles que la Loire Inférieure, la côte basque, la Méditerranée."

Gravity

The distribution of the snails at different levels is set out in Figs. 2 and 3 and in Table I, and shows clearly that the smallest individuals are commonest at the lower levels and the larger ones at the upper levels.

The average size of the snails in the samples on the northern and southern slopes varied from 2·2 to 3·0 mm.; at the surface stations across the top from 2·5 to 5·0 mm.; and in the pools across the top (the "wet" stations) from 3·8 to 5·3 mm. The largest snail found on the slopes was 5·0 mm. high, and on the top 7·7 mm. Large snails occur in the deep crevices between the blocks where the water drains away as the tide goes down, but no estimate was made of their size or of the density of the population in such situations.

The distribution of the size groups suggests that the metamorphosing larvae settle in the *Chthamalus-Balanus* zone and that there is a gradual migration towards the higher and drier levels generally recognized as their typical habitat. Further evidence of upward migration in the field is given in the section dealing with spawning (p. 53, Table II).

In the laboratory when the snails are placed in water in a finger bowl they immediately crawl to the top; this reaction is sufficiently constant to be an efficient method of separating them from *Littorina saxatilis*, which is common in the lower part of the zone occupied by *L. neritoides*.

In the field this negatively geotactic response is sometimes reversed. Throughout most of the year the snails are evenly distributed on the vertical sides of the pits on top of the Breakwater. During the winter there is usually a swell sufficiently heavy to sweep over the top at high water, so that the water in the holes is constantly renewed. Under hot and dry conditions when tides are low this does not happen, and evaporation causes a considerable increase in salinity. The snails then crawl up the sides and congregate in dense masses between the water level and the lip of the holes. When the water has been renewed they crawl down again. If these snails are collected and placed in water in glass finger bowls they give a negatively geotactic response and immediately crawl to the top of the bowls.

Moisture

A certain amount of moisture is essential for the survival of *L. neritoides*. First, the snails feed on minute algae that grow on the rocks, and they move about and feed only when the surface is moist; they are as active during rain as when they are submerged in sea water. Secondly, it is most unlikely that spawning occurs except when the snails are submerged; evidence supporting this is given later on.

That they live in very dry situations has long been known (Jeffreys, 1865; Forbes & Hanley, 1853). They are able to survive in situations at the top of their zone where they may not be reached by spray for months at a time. Patanè (1933) found that they were able to survive absence of moisture for at least 5 months, and that they regained their activity within a few minutes of being placed in sea water.

On the other hand, observations in recent years have shown that not only do they sometimes occur in shallow pools (Lebour, 1935), but that they are able to live in places where they are permanently submerged. When they are placed with small pieces of rock in sea water in finger bowls most of the snails remain on the projecting pieces, but a few of them crawl beneath the water and remain there. Dr H. B. Moore kindly gave me a few living specimens that he collected from old piles lying beside the pier at Plymouth, which had been submerged for at least a year, and ripe sex cells were present in both a male and a female that I dissected. Mr G. M. Spooner first drew my attention to the fact that on the Breakwater many of the snails live in water. When individuals collected from the pools there were marked with paint and replaced, 95 of 103 recovered a year later were still in the pools. The density of the population in water in the holes is very similar to that on the exposed rock surfaces (Figs. 2, 3, Table I); the most noticeable difference between the snails in the two situations is that the largest ones are more numerous in the holes. This is significant in view of the fact that no snails live in water in the holes on the slopes save just at the upper edge, so that none occurs in pools at levels where the smaller sizes predominate. Yet under laboratory conditions small snails are much less able to withstand emersion than are the large ones.

It is probable that the holes on top are inhabited mainly on account of the shelter from heavy seas that they afford and that the need for moisture plays little part in their selection. No other locality has been found in the Plymouth area where many snails live permanently in water. Fischer-Piette (1932) states that at Cap Martin the species is abundant in holes above high-water mark. He notes particularly that there they are always to be found in the water despite great variation in the salinity.

One final point of interest with reference to moisture may be mentioned here. Fischer *et al.* (1933) have shown that the consumption of oxygen by *L. neritoides* is 5–6 times higher in water than in air.

Shelter

A suitable settling ground for the metamorphosing larvae of *L. neritoides* is afforded by populations of *Chthamalus stellatus* and *Balanus balanoides*. The presence of abundant fucoids appears to be inimical to the larvae. Hatton & Fischer-Piette (1932) state that on rocky shores the absence of these algae indicates high wave exposure, and that their abundance is proportionate to the degree of shelter available.

At the head of Crantock Bay, north Cornwall, cliffs rise from a sandy beach which is exposed for several hours at low tide. *Littorina neritoides* is not abundant there except on rocks where barnacles are present. Fucoids are absent. The mollusc is scarce on the west side of the bay where there are slopes of broken rock and these algae are fairly abundant. At the end of June 1939, a similar type of distribution was found in Northern Ireland. East of Whitepark Bay in County Antrim there is a limestone cliff at the foot of which the snails are so scarce that in 5 min. search only six were collected. A shelf of low boulders extends seawards for 20–30 yards from the foot of the cliff, and is covered with a mat of fucoids so dense that it is extremely difficult to walk across it. At the edge of the shelf there are larger limestone boulders, 2–4 ft. high, which are bare of *Fucus*, and beyond them the water deepens and *Himanthalia* and *Laminaria* are abundant. On these larger boulders there is a dense population of the snails, and *Balanus balanoides* (kindly identified by Dr H. B. Moore) is fairly common. *Littorina neritoides* was also abundant and very conspicuous on finely pitted white limestone boulders in a very wave-beaten bay, Larry Ban, west of Carrick-a-rede, where there was no appreciable algal growth above the *Laminaria* zone. It was, however, scarce on smooth-surfaced limestone rocks in a very exposed position east of Ballintoy Harbour. Barnacles are common and fucoids very sparse on the Plymouth Breakwater where the snails are very abundant.

Dr H. B. Moore has very kindly supplied me with notes (Appendix) on some localities in Scotland where he has searched for *Littorina neritoides*; these notes support my conclusions that the presence of the species is positively correlated with a high wave exposure and the presence of barnacles, and negatively correlated with abundant fucoids.

Kitching (1935) says "the absence of *Balanus balanoides* from the immediate neighbourhood of fucoids is almost certainly due to the rubbing of the fronds, which might either prevent the larvae from settling, or damage the young barnacles", and Moore & Kitching (1939, p. 525) consider that the distribution of *Chthamalus* is affected in the same way.

It has already been observed that the small snails are able to survive emersion for a much shorter period than are the large ones. They are negatively geotactic and gradually migrate towards the top of the zone, apparently in their search for shelter. The large snails are able to withstand very dry conditions. Where, on the Breakwater, the highest and driest level available does not afford the maximum amount of protection some snails have become positively geotactic, and live permanently in water.

Spawning

The Spawning Season and its Duration

Samples of *Littorina nerotoides* were dissected at different times of the year and the state of the gonads determined. Males are defined as *unripe* when the spermatozoa were present only in bundles, *ripe* when active spermatozoa were present either alone or with bundles, and *spent* when no spermatozoa, either alone or in bundles, could be distinguished. Females are defined as *unripe* when oocytes alone or with all stages of developing eggs except ripe ones were present, as *ripe* when ripe eggs were present perhaps in addition to large numbers of unripe ones and oocytes, and as *spent* when there were no eggs, or very few, either ripe or unripe. It appears that infection with some trematode parasites produces sterility, so that individuals in which unencysted cercariae occurred are not considered here although they formed a considerable part of some samples. The snails examined were all collected from the top of the Breakwater, and most of them were taken from the pools or their immediate vicinity.

In samples containing 39, 74 and 62 normal males, collected on April 30, June 10 and July 30 1937, respectively, 85, 100 and 79% were spent, but by mid-September active spermatozoa were present in 90% of those examined (Fig. 4). Nearly 100% were ripe in samples examined in October, December and January. In early March a few spent males were found, and by May and June their numbers had risen to 67 and 93%, respectively.

Egg production is at a minimum during June, July and August (Fig. 5). In mid-September 1937, more than half the females examined contained oocytes or unripe eggs. Ripe eggs were found in 60% of those examined in December, and in 50–60% in January, March and May 1938. Although the percentage of ripe females did not exceed 63 in any sample examined in 1937–8, it rose to 73 and 76 in February and March 1936.

The spawning period thus lasts altogether for about 8 months, that is, from September to April. The sea temperature (Fig. 1) drops from 15·2 to 8·0° C. and rises again to 9·2° C. during this period; the corresponding figures for the air being 14·4, 6·2 and 8·8° C.

Linke (1935), working on material from Rovigno and Majorca, says that the maximum development of the whole genital apparatus in this species is

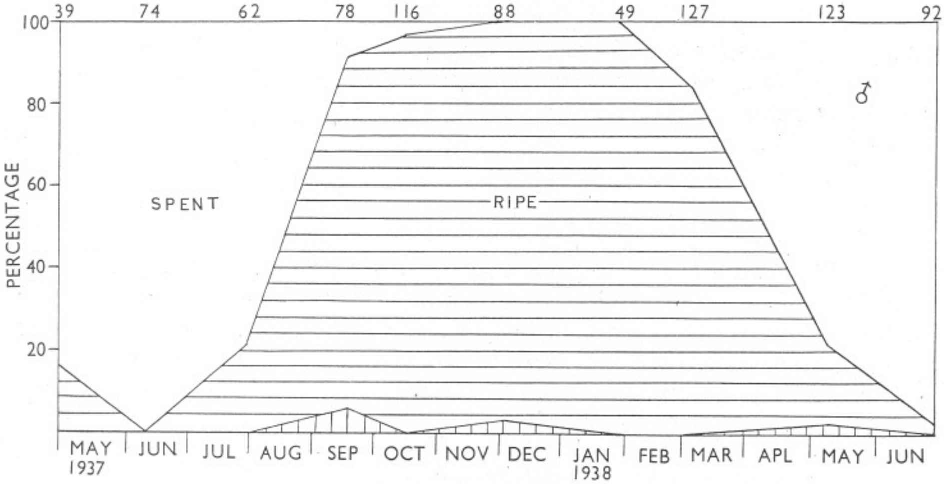

Fig. 4. Percentages of unripe, ripe, and spent males in samples examined every 4–8 weeks from May 1937 to June 1938. The upper figures show the numbers of snails in each sample.

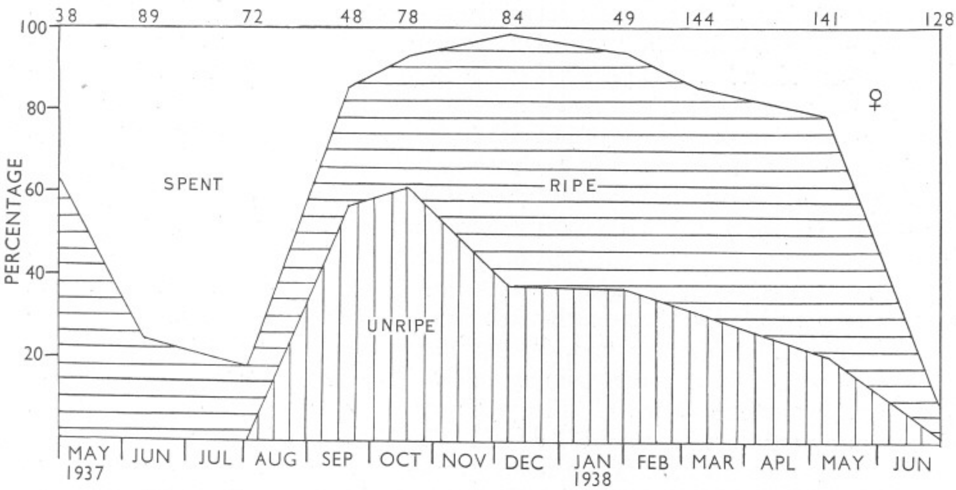

Fig. 5. Percentages of unripe, ripe, and spent females as in Fig. 4.

attained in the spring, but he does not give the size of the samples with which he worked.

An interesting point that emerged from the above dissections is the difference of more than two months in the maximum production of ripe sperms and ova. Moore (1937, p. 733) found that in *L. littorea* the males were ripe about a month earlier than the females, and that the breeding season of this species in the Plymouth area lasted from November to June. *L. saxatilis* breeds all the year round (Lebour, 1937, p. 127). In other localities *L. littoralis* usually breeds from the spring to the autumn (Pelseneer, 1935, p. 452; Linke, 1933), but there is a considerable fluctuation, depending on the temperature, in the breeding period of this species.

Experiments on possible Spawning Migration

Field experiments on migration were carried out by marking the snails with a cellulose paint. If conditions permit the paint should be renewed after 6 months, but this was not actually done. Although a certain amount of wear occurred, some marked snails were conspicuous even after 12 months on the Breakwater: on other snails so little paint was left that they were very difficult to find. This applies particularly to the smaller sizes. Sometimes the snails were painted in situ; at other times they were brought into the laboratory, painted and replaced on the rocks the following day, or sometimes later.

On December 13 1935, two lots of 50 and 200 snails on the rocks at Tinside, Plymouth, were marked in situ with red paint. They occupied zones the lower limits of which were (A) 0·14 and (B) 0·16 m. below M.H.W.S. A month later 44 and 192 individuals respectively were recovered, and only one of these was found below the original zone. On January 24, 222 of these marked snails were placed in a horizontal cleft about 1 m. below the levels A and B. A fortnight later none could be found below these levels. The snails had crawled at least a metre up the rock face, and although they were not counted the marked population was approximately as dense as previously.

On Drake's Island, in Plymouth Sound, in an exposed position above some rocks on the shore, there is a rectangular concrete block approximately 77 cm. high, and 45 by 46 cm. broad; the top of the block is 2·74 m. above mean sea-level. The aspect is roughly south-south-east by north-north-west. On February 4 1936 the west-south-west face was divided into four equal horizontal zones. In the top one, A, 100 snails were painted red, and in the bottom one, D, 100 were painted yellow. No snails were painted in the intermediate zones, B and C. The positions of the snails recovered after 1, 2 and 12 months are shown in Table II. These recoveries show that there is a pronounced tendency for the snails to move upwards, and that only a very small proportion of them move more than a few centimetres in the opposite direction.

In a more sheltered area on Drake's Island where, on January 27 1936, 100 snails were marked with red paint, 67, 48, 49, 47 and 22, respectively, were recovered at their original level when recounts were made on February 4, March 5, April 27 and August 5 1936, and in February 1937. Whenever recounts were made the surrounding rock surfaces were carefully examined, but although the red paint made the snails very conspicuous they were found only once or twice at more than a few centimetres from their original situation.

TABLE II. RECOVERIES OF MARKED SNAILS ON CONCRETE BLOCK, DRAKE'S ISLAND

Date	Colour	No. recovered	Percentage in zones A	B and C	D
4. ii. 36	Red	—	100	0	0
5. iii. 36	,,	77	92·2	7·8	0
5. iv. 36	,,	51	78·5	19·6	1·9
– ii. 37	,,	5	100	0	0
4. ii. 36	Yellow	—	0	0	100
5. iii. 36	,,	69	0	79·8	20·2
5. iv. 36	,,	44	25·0	52·3	22·7
– ii. 37	,,	13	100	0	0

The results of these experiments make it unlikely that there is any downwards migration for spawning as suggested by Lebour (1935, p. 375); and Jeffreys (1863, p. 354) says of the snails, "they have never been observed to go to the sea when the tide comes in".

Occurrence of Egg Capsules

In order to determine when the egg capsules were present in the plankton tow-nettings were examined daily, as far as possible, from November 29 1935 to May 1 1936. The capsules were fairly common at times during the winter and spring in tow-nettings taken by the M.B. *Gammarus* in the Sound, but occurred so rarely in those taken by the S.S. *Salpa* beyond the Sound that the latter were not examined after February 4 1936. The internal diameter of the hoop supporting the mouth of the tow-nets was 45 cm. The capsules, which vary at the height of the breeding season from 0·162 to 0·225 mm. in diameter with an average of 0·205 mm., were not taken in the coarse tow-nets, with a mesh of 26 strands of silk to the inch (25·4 mm.), and very rarely in the medium, 50 strands to the inch, but were commonest in the fine and very fine nets with 100 and 180 strands to the inch, respectively. At first the "*Gammarus*" nets were arranged so that the very fine net was at the surface, the fine at a depth of 2 fathoms, and the medium at 6–8 fathoms. Most of the capsules were then taken at 2 fathoms. The medium net was replaced in March by the very fine net, and capsules were then taken at 6–8 as well as at 2 fathoms. It is obvious that the numbers of capsules collected from the tow-nettings, which were taken in several different places in the Sound and independently of the state of the tide, are not strictly comparable amongst themselves and have no direct relation with samples which were collected from the Breakwater. (In the latter situation water was pipetted from the bottom of seventy holes and about two breffits were filled at each sampling.)

The capsules were found to sink at the rate of 150 mm. in 109–203 and 271–514 sec. at temperatures of 15·5 and 10·0° C. Linke (1935) observed that they sink in still water but tend to remain suspended when it is agitated. This property was useful in separating them from the tow-nettings, which were strained through coarse muslin into a cylinder and left to settle for about half an hour. Most of the water was then gently siphoned off, and the capsules collected from the residue.

The total number of capsules collected, together with some of the factors that may influence spawning, are shown in Fig. 6. If no downwards migration takes place the possible immersion of the snails living above extreme high-water springs would depend on the phase of the moon and the corresponding tides, the direction and force of the wind, and the state of the sea. In Fig. 6 full and new moons are shown by white and black circles, respectively; the predicted tidal heights are given, and those more than 15 ft. above Admiralty Datum are blacked in; the state of the sea is scaled according to the meteorological charts issued by the Air Ministry; onshore and offshore winds tending to raise and depress the predicted tidal levels are shown by arrows pointing upwards and downwards respectively, and where the force of the wind exceeded 3 on the Beaufort scale double barbs have been used. The solid columns show the numbers of egg capsules collected from the tow-nettings in the Sound, and those which are cross-hatched the numbers from the Breakwater samples. The blanks in the base-line show the days when no samples were taken.

Notes on the stage of development of the capsules in some of the samples are given in Table III.

TABLE III. NOTES ON THE STAGES OF DEVELOPMENT OF SOME OF THE EGGS COLLECTED FROM THE TOW-NETTINGS AND BREAKWATER SAMPLES

Date	Locality	No. capsules	Remarks
9. iii. 36	Jennycliff Bay	62	All were undergoing the first or second cleavage
10. iii. 36	Breakwater	75	Most of these had not completed the first cleavage
19. iii. 36	"	5	All were in different stages of development
23. iii. 36	Jennycliff Bay	52	Embryos with 2–32 cells were present
24. iv. 36	Breakwater	800	Many had not begun to segment and none had passed the first cleavage
31. iv. 36	Jennycliff Bay	46	At a depth of 6–8 fathoms there were 31 embryos of 32–64 cells, and at 2 fathoms 15 with 2–4 cells. Some of the eggs were abnormally small, 0·126–0·144 mm. in diameter, and were segmenting irregularly
1. v. 36	Breakwater	38	There were 2 embryos with 4 cells, 23 with 2 cells, and 14 in which segmentation had not begun

In the five months during which samples were taken there were five periods when more than 50 egg capsules per set of samples were obtained, and four of these coincided with sets of high tides. The apparently exceptional sample,

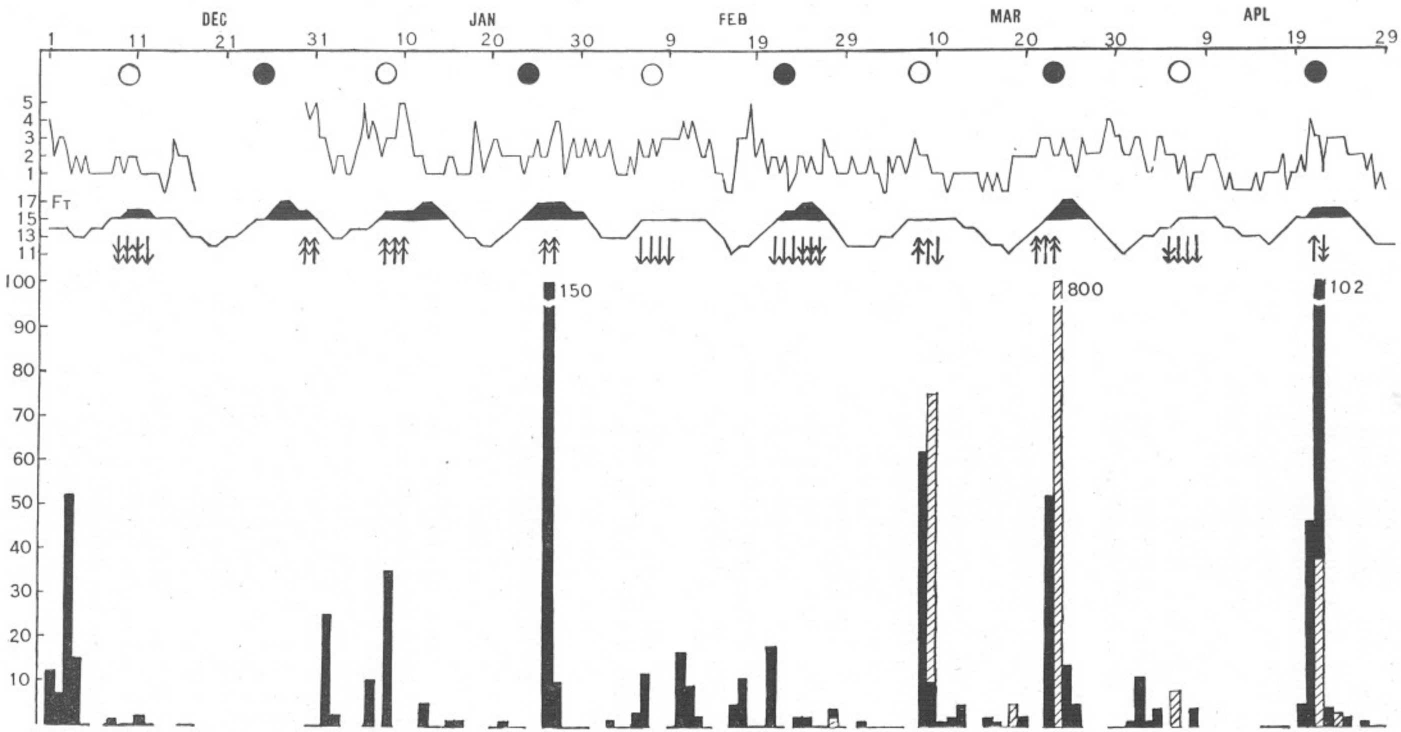

Fig. 6. Abundance of egg capsules of *Littorina neritoides* together with factors affecting the height of the tides and the moisture of the splash zone. The state of the moon is indicated by open and black circles. The upper continuous line shows the state of the sea. The lower continuous line shows the predicted height above Admiralty Datum of high tide, the highest for each day being plotted; heights above 15 ft. are blocked in. The arrows indicate onshore (upwards) and offshore (downwards) winds. For details see text, p. 54. The solid columns show the numbers of egg capsules collected from tow-nettings in the Sound; the cross-hatched columns show numbers collected from Plymouth Breakwater. Blanks in the base line indicate days when no observations were made.

taken in Cawsand Bay at the beginning of December, contained a large proportion of capsules that were sufficiently old to have been spawned during the previous high tides. The eggs hatch in 7–8 days in the laboratory. During five other sets of high tides the capsules were not found in any quantity, but it is probable that the prevailing meteorological conditions lowered the predicted tidal levels, and prevented spawning except in those adults living in the lower part of their zone. When the water in the Sound is calm, as often happens when there is a light wind from the north, even if the tide were sufficiently high to submerge those in the upper part of the zone it is probable that the capsules are not readily dispersed and are therefore less likely to be collected in the tow-nettings.

The strongest indication of the presence of a fortnightly rhythm in the spawning habits of this species is shown by the Breakwater samples. Although many of the snails there live permanently in water, egg capsules were abundant in only three out of seven sets of samples that were examined, and these three were taken when the moon was new or full. This is of particular interest, as during the winter and spring, when breeding takes place, the sea usually sweeps over the Breakwater twice a day. In these samples, as well as in the tow-nettings, when the capsules were plentiful they were usually at the same stage of development. Full notes on the incidence of these stages were not kept, but a few are given in Table III. They suggest that the onset of major spawning periods is determined by some stimulus in addition to immersion. Lunar periodicity has been shown to occur in many other species of Molluscs (Pelseneer, 1935).

Linke (1935) observes that in the spring the egg capsules of *Littorina neritoides* were fairly abundant in the neritic plankton in the Mediterranean, but he does not refer to the presence of any spawning rhythm there.

Composition of the Population

Incidence of the Size Groups

The material for this part of the investigation was all collected from the Breakwater. The 1936 samples included snails from the southern slope, so that there is a larger proportion of small snails in these than in the 1938 samples, which were all taken from the top and mostly from the pools or their immediate vicinity. The snails were measured with sliding callipers with a 0·1 mm. Vernier scale, and are grouped in 0·3 mm. series (Fig. 7).

The largest sample, measured in July 1938, consisted of 7796 snails; those averaging 4·1, 5·0 and 5·9 mm. in height occurred with the greatest frequency. Snails of 5·0 and 5·9 mm. also predominated in smaller samples collected in March and May 1938, and were conspicuous in the 1936 samples. The 5·9 mm. group is less obvious in the June 1938 sample, where the sizes were more evenly distributed, but predominated in the October sample. Snails in the 4·1 mm. group, so conspicuous in the July sample, are noticeable in only one

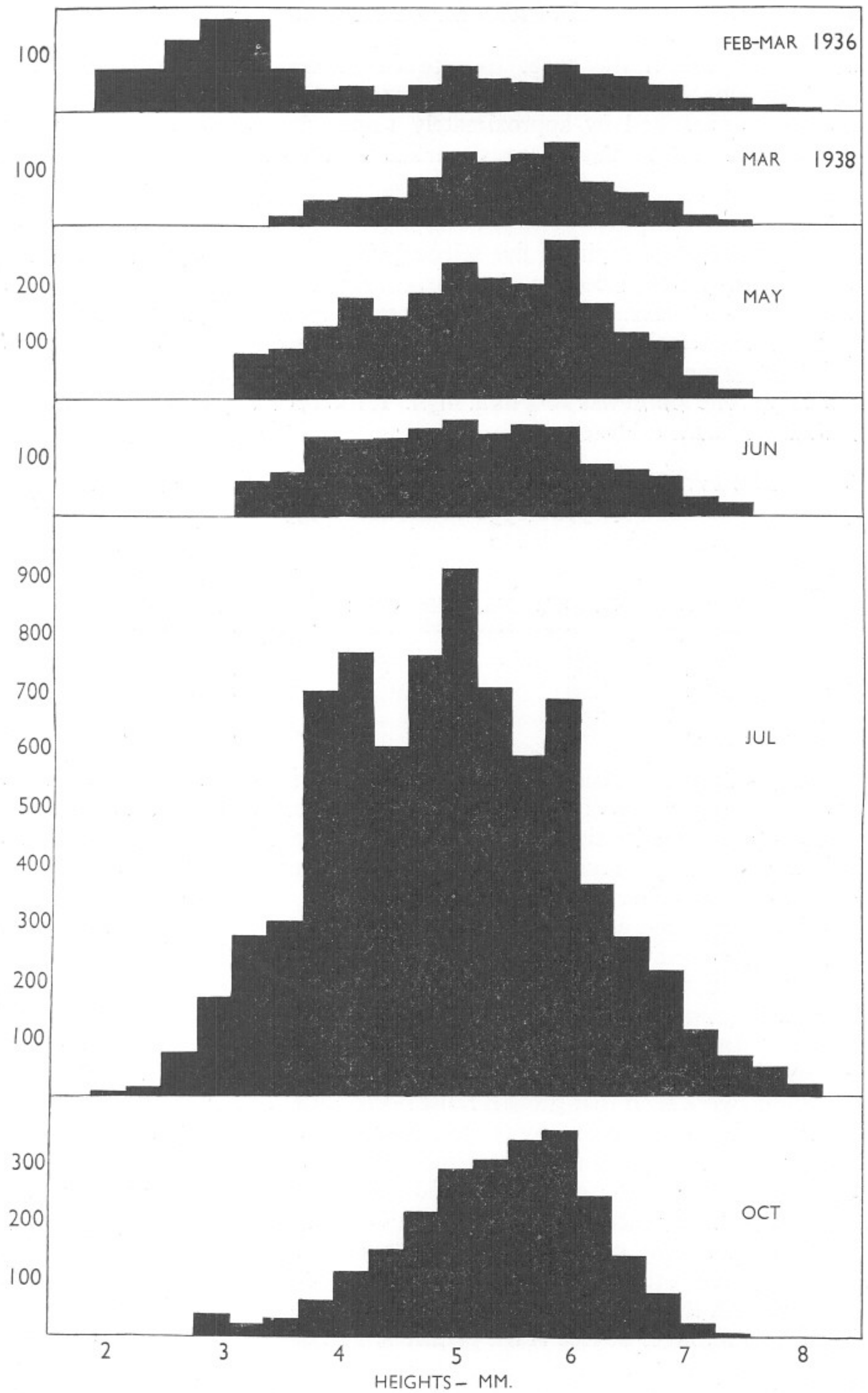

Fig. 7. Numbers of snails in 0·3 mm. size groups in random samples collected from the Breakwater in February–March 1936, and from March to October 1938.

other sample, that of May 1938. In spite of these variations in the incidence of the size groups there appears to be a tendency for the larger snails to fall into size groups separated by approximately 1 mm., but whether these actually represent successive annual broods remains uncertain.

Growth Rate and Sex Ratio

Of 2107 measured snails in five selected size groups, marked with red and yellow paint and replaced on the Breakwater in July 1938, only 102 were recovered a year later. The results of this experiment are shown in Table IV. It will be seen that the growth-rate decreases with age, and is very slow in snails of 6·0 mm. or more. It is probable that those of 8–10 mm. are many years old. The largest one found was 10·4 mm. high. It has been deposited in the British Museum of Natural History.

TABLE IV. GROWTH-RATE AND PARASITES IN MARKED MATERIAL, JULY 1938 TO AUGUST 1939

Height mm.	No. snails marked	No. snails recovered	No. males	Average increase in height mm.	No. infected with Cercaria B and C
3·9–4·0	545	1	0	0·6	0
4·9–5·0	732	38	7	0·48	22
5·8–5·9	448	26	5	0·26	17
6·0	238	9	2	0·14	8
6·8–6·9	144	28	2	0·06	26

The proportion of males is significantly higher in the smaller size groups than in the larger ones (Fig. 8), and the ratio is similar even when only unparasitized ones are considered. This may be due to a differential growth-rate such as Moore (1937) found in *L. littorea*, where the growth-rate is greater in females than in males.

Moore found that on Drake's Island *L. littorea* reached a height of about 14 mm. in the winter of its first year, and 17·4, 22·4, 25·4, and 27·3 mm., respectively, in the second, third, fourth and fifth years. It may grow to a height of 36 mm., that is, about two and a half times the height reached in the first year. In *L. neritoides* the results obtained indicate a comparable steady decrease in the growth-rate. It can also be said that the values of annual increments were such that growth must normally extend over several years.

It has to be noted that many of the snails in this experiment were found to harbour cercarial infections of trematode parasites (dealt with on pp. 59–64). Since Rothschild (1936, 1938 *b*) has found that such infections stimulate growth in *Peringia ulvae*, their presence cannot be ignored when the question of growth-rate is being considered. The number of snails infected is therefore included amongst the data in Table IV. The proportion of infected specimens increases with the size of the snail, until in the largest group only two out of the 28 were found to be free of the parasites. The data as they stand do not, on first inspection, suggest that the parasites stimulate growth; but no conclusion can be drawn, since the real information required, namely comparison of growth-rates of infected and *uninfected specimens of the same initial size*, is not available.

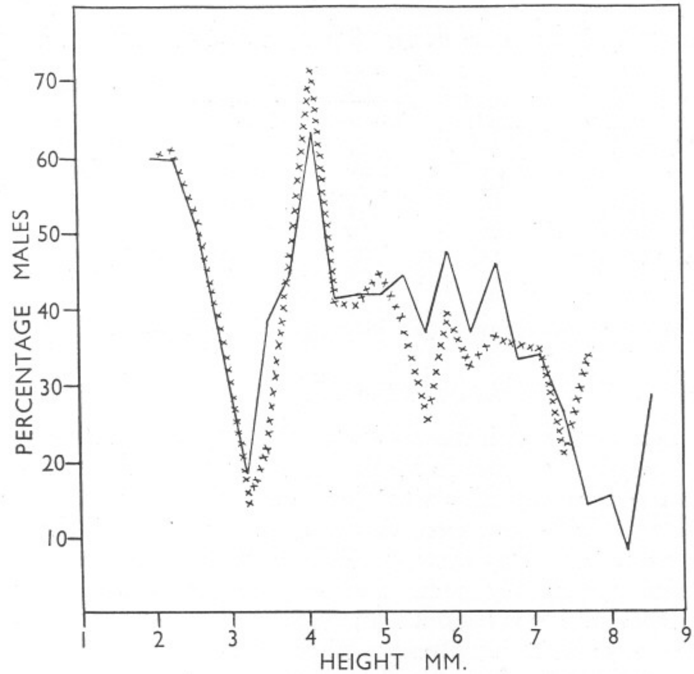

Fig. 8. Percentages of males in 0·3 mm. size groups. The continuous line shows the percentage in parasitized and unparasitized snails, and the crossed line the percentage in unparasitized snails only.

Trematode Parasites

Total Percentage Parasitism

The incidence of trematode parasites was recorded in the snails used for determining the state of the gonads at different times of the year (p. 50), comprising a total of 1270 males and 1779 females. A few samples from localities other than the Breakwater were also examined (Table VI, p. 64).

Three larval trematodes occur fairly frequently in *L. neritoides* on the Breakwater. Their systematics have not been investigated, and throughout this paper they are referred to by letters.

Infections with Metacercaria A, and Cercaria B and C occurred throughout the year, but were significantly higher in the sample examined in July 1937 (Table V) than in any other examined between April 1937 and June 1938.

The percentage of parasitism with all species rose steadily from 3·3 in snails averaging 2·0 mm. in height, to 99·8 in those of 8·8 mm. and over. The relative numbers of cercariae, both free and encysted, in the different size groups are shown in Fig. 9.

TABLE V. PARASITISM IN THE SAMPLE EXAMINED IN JULY 1938

Height mm.	No. of snails	No. parasitized: Observed	No. parasitized: Expected*	Difference
5·0	20	11	10	1
5·3	24	20	13	7
5·6	30	22	18	4
5·9	42	31	26	5
6·2	22	20	15	5
6·5	32	26	23	3
6·8	37	32	28	4
7·1	20	15	16	−1

* From the mean incidence of parasitized specimens in the material as a whole.

Incidence and Effect of Metacercaria A

This metacercaria, which was always found encysted, occurred in 3·3% of the snails averaging 2·0 mm. in height, and in 87% of those of 8·3 mm. or more. The degree of infection with this species also increased in the larger snails (Fig. 10). Infections were classed as light, medium or heavy, when 1–6, 6–25, or more than 25 cysts, respectively, were found in any one snail. These criteria were slightly modified in the largest and smallest sizes. Sometimes the whole spire was packed with cysts.

The males were more heavily parasitized than the females by this species (Fig. 11), and altogether 60·35% of the former and 52·7% of the latter were infected. Snails containing no other larval trematodes account for 47·6 and 28·7% of the total, respectively, and the remaining 12·75% of the males and 24·0% of the females were infected with Cercaria B (Fig. 9, and p. 61). There is a thus a reversal of the ratio of infection in the sexes, which may be due to some physiological disturbance caused by Cercaria B. This trematode usually causes sterility, and the sterile males are apparently less attractive to metacercariae about to encyst.

The mere presence of these metacercariae does not affect the seasonal development of the gonads; both males and females containing cysts produced ripe sex cells at the same time as uninfected snails. From September to April, inclusive, that is, during the breeding season, the percentages of snails with unripe, ripe and spent gonads were, respectively, 12·3, 60·0, and 27·7 in 65 snails with heavy infections, and 13·8, 77·8 and 8·2 in 152 with medium infections. The higher percentage of spent snails in those with heavy infections may include a number that were sterile, and it is quite probable that the normal development of the gonads may be inhibited through the resulting pressure when the spire is packed with cysts.

Incidence and Effect of Cercaria B

Cercaria B belongs to the *Ubiquita* Group. It was less common in the smaller size groups than Metacercaria A (Fig. 9). Infections with this species

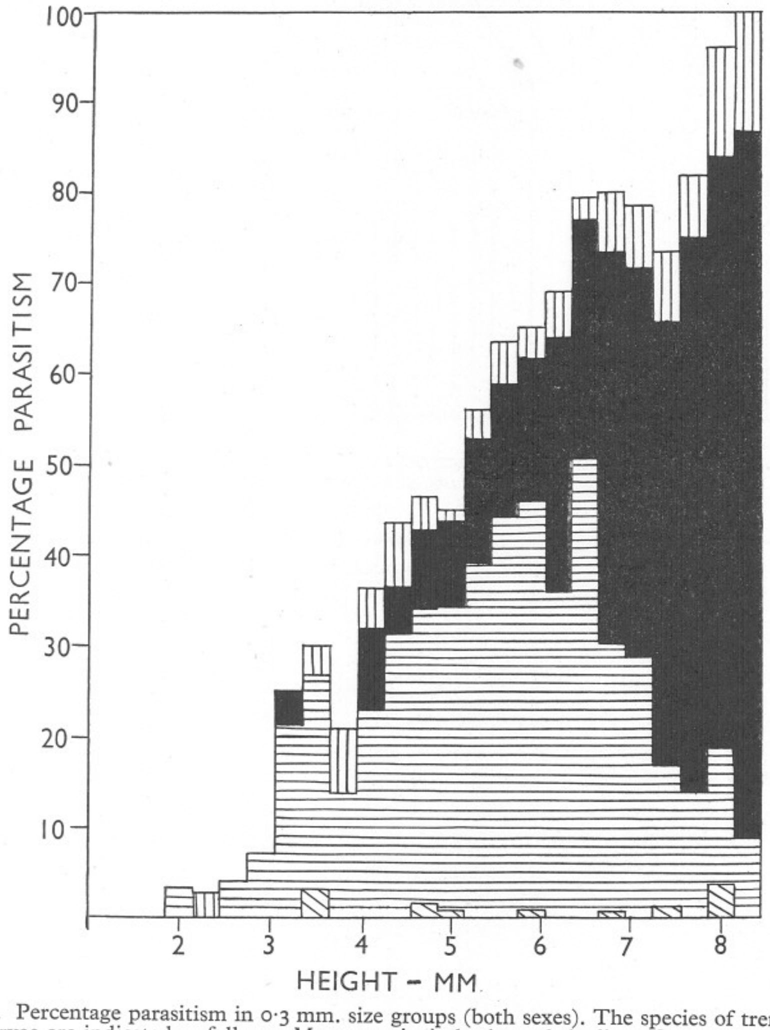

Fig. 9. Percentage parasitism in 0·3 mm. size groups (both sexes). The species of trematode larvae are indicated as follows: Metacercaria A, horizontal shading; Cercaria B, vertical shading; A plus B, solid blocking, C, diagonal shading.

were nearly always heavy, and large numbers of both sporocysts and active cercariae were usually present. Infections with this species occurred in 14·65% males, and 29·7% females, the relative difference between the sexes being much greater than in infections with Metacercaria A when total

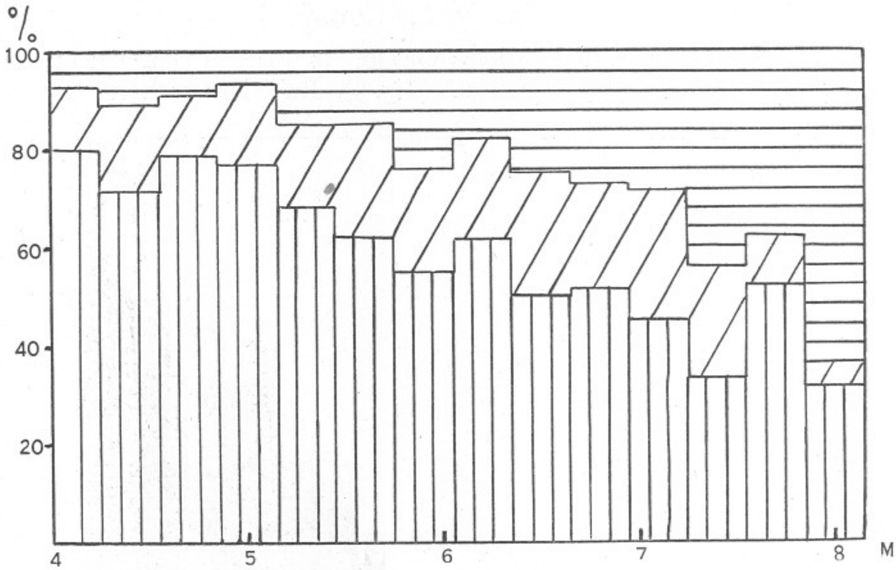

Fig. 10. Grades of infection with Metacercaria A in 0·3 mm. size groups. Vertical shading = light, diagonal = medium, and horizontal = heavy infections.

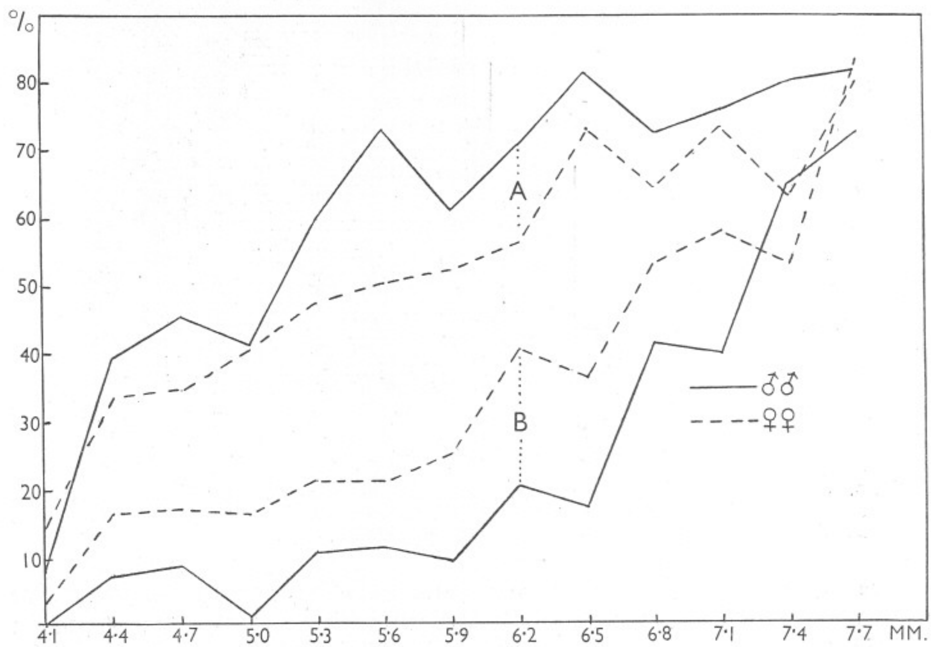

Fig. 11. Differential infections of males and females with Metacercaria A and Cercaria B.

infections are considered. The presence of Metacercaria A together with Cercaria B scarcely alters the ratio of the infections with the latter species in male and female snails, lowering it by only 1·8 % in the males and 5·7 % in the females.

During the breeding season sex cells were found in only 1 out of 86 males, and 8 out of 292 females infected with Cercaria B, so that without doubt this species usually causes sterility.

The differences in the infections of the sexes with Metacercaria A and Cercaria B are of particular interest, as male Gastropoda are usually more heavily infected than females (Pelseneer, 1928). Rothschild (1938*b*), who discusses the question in some detail, found that this was so in *Peringia ulvae*, which is a heavily infected species. Total infections have generally been considered, and it is possible that, when the incidence of separate species of trematodes has been worked out, differences such as occur in *Littorina neritoides* will prove to be common.

Incidence and Effect of Cercaria C

Cercaria C, which is closely allied to *Cercaria emasculans*, was comparatively rare and was found in only 2·23 and 2·81 % respectively of the male and female snails examined. During the breeding season 3 out of 10 infected males and 8 out of 15 infected females were sterile; these numbers are obviously too small to give any indication of the effect of this trematode on the host. Cercariae and sporocysts were both abundant in the infected snails.

Double Infections. The total number of snails infected with Cercaria C was 78; 13 of these contained Cercaria C alone, 45 Cercaria C together with Metacercaria A, and 20 Cercaria C together with Cercaria B. These last 20 infected snails were all sterile. I have followed Cort *et al.* (1937) in considering these last-mentioned as true double infections and distinct from examples in which encysted metacercariae occur with active larval forms. In these double infections both types of cercaria, B and C, appeared equally active. As the total percentage infections with these trematodes were 23·3 and 2·5, respectively, the expected mean number of double infections in the 3019 snails examined is $17{\cdot}5 \pm 4{\cdot}2$. As 20 double infections were observed there does not seem to be any mutual antagonism between these trematodes, such as Sewell (1922) has postulated for some species.

Cercaria D

This larval trematode, which belongs to the *Yenchingensis* Group (Rothschild, 1938*a*) was found only once. Active cercariae and rediae, together with a fair number of cysts of Metacercaria A, were present in a female snail 5·8 mm. high, collected at the beginning of May 1938. No eggs or oocytes were present.

Sex Reversal

There is no evidence that sex reversal occurs in *Littorina neritoides*. The penis diminishes greatly in size in males infected with Cercaria B, but this reduction is no greater than the reduction in non-breeding males during the summer months, and is certainly not comparable with that found by Rothschild (1938*b*) in *Peringia ulvae*.

Incidence of Trematode Parasites in other Localities

Metacercaria A was found in snails from Kelsey Head (north Cornwall), Drake's Island, and in two localities in County Antrim, Sheep Island and the Giants' Causeway. Cercaria B was found in those from Kelsey Head and Sheep Island; and Cercaria C in those from the Giants' Causeway. Notes on the samples from these places and from others where no parasites were found are summarized in Table VI.

TABLE VI

Locality	Date	No. of snails examined	Range of heights mm.	No. of snails infected with cercariae		
				A	B	C
Crantock	30. xii. 35	7	4·3–6·0	0	0	0
,,	14. iv. 36	90	4·6–6·0	0	0	0
Kelsey Head	26. xii. 37	25	4·9–7·2	8	5	0
Rum Bay	10. xii. 35	26	1·9–5·4	0	0	0
Drake's Island	4–20. ii. 36	55	2·8–7·2	11	0	0
Tinside, Plymouth	23. i. 36	100	2·5–6·0	0	0	0
Sheep Island	26. vi. 39	60	5·5–6·9	11	2	0
Giants' Causeway	28. vi. 39	56	4·3–6·6	6	0	2
Gwbert (Cardigan)	8. viii. 39	19	3·4–5·7	0	0	0

All the snails in which parasites occurred were collected from rocks rising steeply from the sea with a high degree of exposure.

Presence of possible Alternate Hosts

Kelsey Head is opposite a small island, the Chick, frequented by gulls, shags and cormorants. Sheep Island is a breeding ground for a large colony of puffins, and numerous razorbills, guillemots and gulls. The rocks there were so bespattered with droppings that a high degree of parasitism might have been expected, but trematodes were quite scarce in the small sample of snails that was examined.

The Breakwater is a resting place for large numbers of several species of gulls (*Larus* spp.) and, less regularly, of flocks of curlew (*Numenius a. arquata*). A flock of about 30 purple sandpiper (*Calidris m. maritima*) overwinters there, and oyster catchers (*Haematopus ostralegus*) occur regularly except in the nesting season. The only invertebrate that is comparable in abundance with *Littorina neritoides* is a small harpacticid copepod which is very plentiful in the pools along the top.

Conclusions

The observations described show that in the Plymouth area *Littorina neritoides* only spawns when it is submerged. The population is concentrated about the level of extreme high water springs, and the snails do not migrate downwards, so that except in severe storms spawning can only take place at the fortnightly spring tides. Furthermore, spawning is confined to the winter months when tidal levels are likely to be raised by stormy conditions.

The choice of the very dry habitat usually regarded as typical seems to be of doubtful value for a species with pelagic egg capsules. It is probable that it is primarily the need for shelter from the force of the waves that brings about the steady migration to the dry rocks at the top of the zone, and that except for the requirements of spawning the presence or absence of water is only of secondary importance for the adults.

Evidence is given which suggests that the larvae are only able to settle in the barnacle zone on exposed rock faces devoid of fucoids. The snails have very slight powers of adhesion, so that the degree of exposure that eliminates fucoids and is thus favourable to the metamorphosing larvae is unfavourable to the adults. The presence of a fortnightly spawning rhythm seems to be a secondary adaptation which is, perhaps, very deeply impressed. Thus, on the Plymouth Breakwater, where many of the snails find the maximum amount of shelter by living permanently submerged, spawning appears to be as rhythmical as when the snails are living in an excessively dry habitat.

Summary

An account is given of the distribution, life history and trematode parasites of *Littorina neritoides* on the Plymouth Breakwater; a few observations from other localities are included.

The smaller snails are most abundant on the exposed southern slopes of the Breakwater. Many of the larger ones live more or less permanently in water in small cylindrical pits on the top of the Breakwater. This habitat is apparently very similar to that described by Fischer-Piette (1932) as occupied permanently by this species at Cap Martin; Lebour (1935) has sometimes found it in water in other places in the Plymouth area.

The conditions necessary for metamorphosis of the larvae, the need of the adults for shelter from the force of the waves, and the requirements for spawning appear to be of more importance in determining the choice of habitat than the negatively geotactic and varying phototactic responses found in this species by Fränkel (1927).

The breeding season lasts from September to April. The males are ripe about two months before most of the females. Experimental evidence is given which makes it most improbable that there is any downward migration for spawning. From the examination of plankton samples it appears that there is a fortnightly spawning rhythm coincident with high tides, and that even the snails living in water discharge their eggs only at these periods.

The distribution of the size groups is discussed. The proportion of males decreases significantly in the larger size groups and it is probable that there is a difference in the growth-rate of the sexes.

Three species of cercariae and one metacercaria parasitize the snails. The total percentage parasitism increases with the size of the snail, and no kind of immunity appears to develop. Males were more heavily infected with the cysts of the metacercaria than were females, but the latter were more heavily infected with the sporocysts and cercariae of a species that caused sterility.

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APPENDIX

Notes by Dr H. B. Moore on the occurrence of Littorina neritoides *in some localities in Scotland*

9. vi. 36. Head of Loch Fyne. Very weedy shores. No *Chthamalus stellatus* or *Littorina neritoides*. Little *Balanus balanoides*.

11. vi. 36. Caolas Scalpay, Skye. Weedy shore. *Balanus balanoides* abundant in patches. No *Chthamalus stellatus* or *Littorina neritoides*.

18. vi. 36. Port na Cullaidh, Elgol, Skye. Western aspect, sheltered by Soay to the west, but otherwise 180 degrees exposure. All three species abundant on a reef of rock. Very few algae above the *Laminaria* zone.

15. vi. 36. Sgoir Beag, Vaternish, Skye. Aspect, west-north-west. Wave-beaten shore, few algae above the *Laminaria* zone. *Chthamalus stellatus* occupying a zone 50 to 100 cm. above *Balanus balanoides*. *Littorina neritoides* very abundant.

22. vi. 36. Bay of Stoer, Sutherland. Aspect, south west. Wave-beaten rocks. Little weed above the *Laminaria* zone. *Balanus balanoides* abundant. Small zone of *Chthamalus stellatus*. *Littorina neritoides* present.

24. vi. 36. Geodha chobhair, Sutherland. Aspect, west-north-west. Very wave-beaten coast. No algae except in pools and in the *Laminaria* zone. *Balanus balanoides* abundant. Few *Chthamalus stellatus*. *Littorina neritoides* present.

4. vii. 36. Bass Rock. Wave-exposed shore. Very little weed. *Balanus balanoides* abundant. No *Chthamalus stellatus*. *Littorina neritoides* very rare and scattered.