OBSERVATIONS ON THE BIOLOGY OF THE MAYFLY, EPHEMERA DANIČA, MÜLL

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Observations on the Biology of the Mayfly, Ephemera Danica, Müll. By E. PERCIVAL, B.Sc., Lecturer in Zoology, The University, Leeds, and H. WHITEHEAD, B.Sc., Lecturer in Biology, The City Training College, Leeds.

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Introduction

The immature stages of burrowing mayflies have been studied for many years, especially by earlier naturalists, a résumé of whose work up to the middle of the ninteenth century has been given by Miall (8).

Pictet (13), who made a wider survey of mayfly nymphs, divides the immature insects into four groups—

(1) Larves fouisseuses;
(2) Larves plattes;
(3) Larves nageuses;
(4) Larves rampantes.

The genus Ephemera is included in Group 1. He states that nymphs of this genus live in large numbers in tubular galleries, straight or curved, dug horizontally just below the surface of still or slowly-flowing water. They can swim fairly rapidly by means of undulations of the body. Water rolls and carries them downstream unless they can attach themselves to a stone to resist the current.

Eaton (5) says that *E. danica,* Müll., is found in colder and swifter waters than *E. vulgata,* L.

Needham (10) states that Morgan found 30 nymphs of *E. simulans* at Ithaca in 10 square feet of mud.

Needham and Lloyd (11) describe the methods of burrowing of *Hexagenia,* which is similar in habits to *E. danica.*

Lestage (6) says that the nymphs of fossorial Ephemeroptera feed on worms and small insects, but Bengtsson (3) considered that larvæ of the genus Ephemera are detritus feeders, living on mud and argillaceous fragments. We agree with Bengtsson.

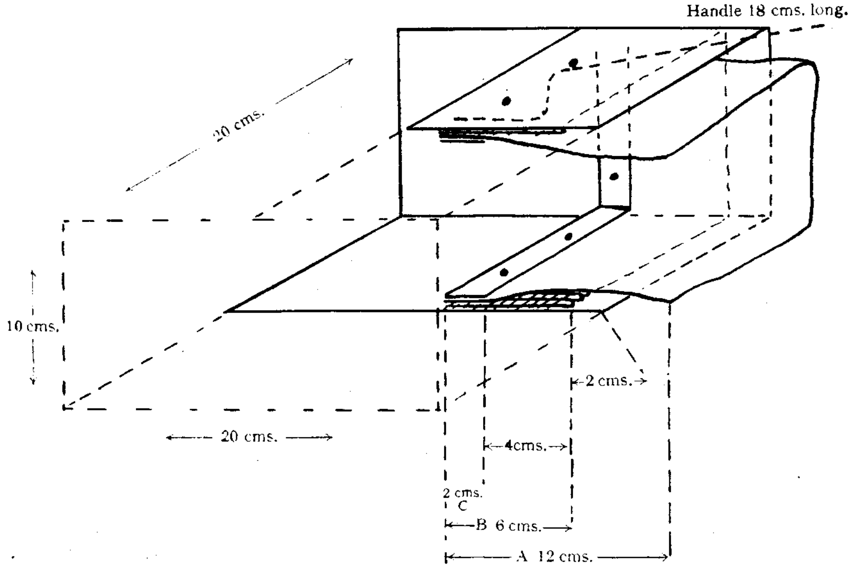
Our observations have been made with a view to ascertaining the conditions which determine the distribution in Yorkshire of *Ephemera danica.*

Our best thanks are due to the Leeds Literary and Philosophical Society, who have made grants to defray expenses.

Apparatus and Collection of Material

It soon became apparent that, in order to discover with any degree of certainty the habitat of *E. danica,* it was necessary to devise a simple means of making quantitative collections. A piece of apparatus (see Fig. 1) was made, consisting of a kind of shovel open at the back and carrying a bag into which sediment could be scooped. The bag, 2 decimetres long, made of canvas or of cellular

FIG. 1
Sectional diagram of shovel for quantitative examination of sediment (bag not shown).



A—Strip of leather. *B*—Strip of metal netting. *C*—Binding strip of sheet metal.

shirting material, having a mesh of about 1 mm., bears hooks outside round the mouth, and these engage with a strip of strong metal netting of $\frac{1}{4}$ in. mesh, which is attached transversely inside the posterior part of the shovel. When the bag is hooked in position its connection with the metal netting is covered on the inside by a flap of leather, which is co-extensive with the metal netting. This leather flap prevents animals from being washed out of the scoop at the junction of the bag and the metal. The leather and the metal netting are held by a strip of sheet metal 2 cm. wide, through which rivets are driven into the metal shovel. The shovel is of 22-gauge galvanised iron, 2 decimetres long, and the same broad, by 1 decimetre high. The sides are rectangular, not being shaped round at the anterior edge. The posterior half of the upper side is covered by a sheet of metal of double the thickness of the rest. To this stronger sheet is attached a handle of suitable length, say 18 cms.

With such a shovel it is easy to sample the bottom where the depth of the water is not greater than arm's length. A 2 decimetre rule is held along the stream bed immediately in front of the scoop, which is then dug into the substratum to a suitable depth and pushed horizontally up stream. In this way 4 square decimetres of deposit are obtained, and any animals which are disturbed during the process are swept into the bag along with a portion of the sediment. We have found that a depth of $2\frac{1}{2}$ to 3 inches is sufficient for the shovel to include all the nymphs present.

The catch is then sifted through sieves of desired mesh. We have used three 9 in. brass sieves, super-imposed and fitting one inside the other, having mesh of 3 mm., 1 mm., ·5 mm. The animals are picked out after the material has been thoroughly washed.

The results obtained with this scoop are quite uniform for a given type of deposit in which it is to be expected that the fauna is relatively uniformly distributed. Test counts of three neighbouring samples of the same habitat gave 83, 80, and 74 nymphs of *E. danica* per 4 square decimetres.

Another convenient sampler was made for the purpose of obtaining sediment for analysis. This consisted of a brass tube of square section, 7·5 cms. × 7·5 cms. inside measurements, and 10 cms. long. One end had a close-fitting lid, while the other end could be closed by sliding over it a brass plate about 10 cms. long. The sides and one end of this plate were turned up 1 cm. at right angles, so that there was a fair and easy fit when it was applied to the end of the brass tube.

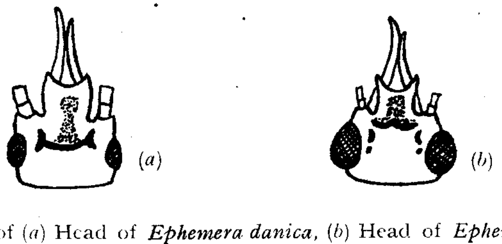
In taking a sample, the tube was pushed to a desired depth into a stream bed, the upper opening was covered by the lid, and the plate was then slid across the lower end, so as to cut off a portion of the deposit. The material was then transferred to a suitable container. After being air-dried, the samples were mechanically analysed by the method recommended by the Agricultural Education Association Sub-committee (1).

Identification of the Nymph of Ephemera danica

Lestage (*loc. cit.*) has given a description of the nymph of *E. danica* which he has later (7) confirmed. In the latter place he states that the dorso-cephalic design, given by Peterson (12) as a means of distinguishing between the nymphs of this species and those of *E. vulgata*, is not constant.

In our experience the characters given by Peterson and by Lestage, as distinguishing the head of *E. danica* nymphs, may be relied upon. These are as follows (Fig. 2A)—

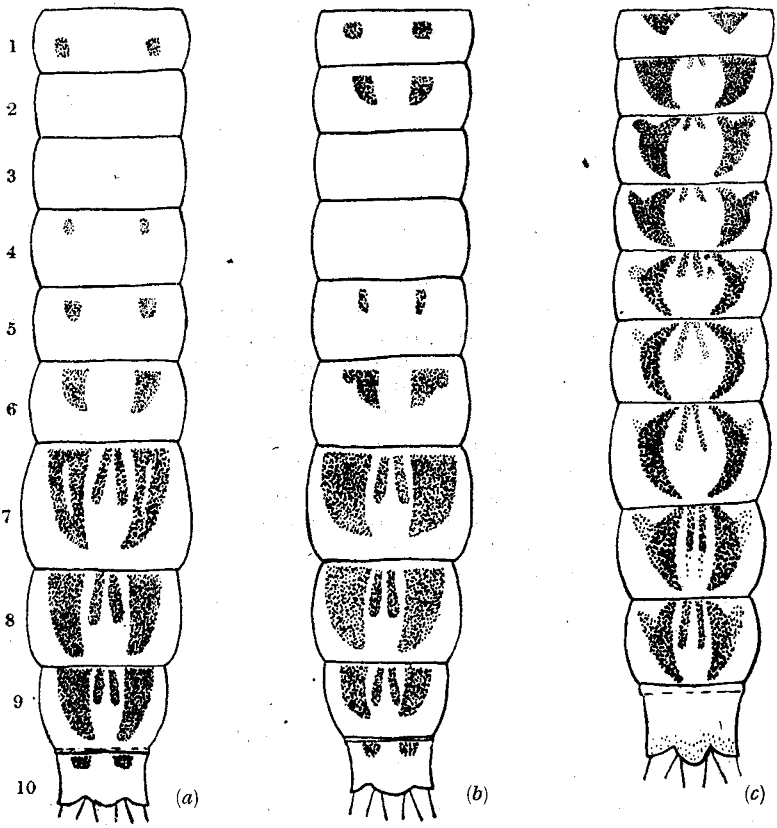
Fig. 2



Dorsal surface of (*a*) Head of ***Ephemera danica***, (*b*) Head of ***Ephemero vulgata*** (*from Lestage after Petersen*).

Head relatively small; clypeus concave, showing at the anterior border a deep indentation of which the anterior angles, prolonged forward, form two small and clear horns (Lestage, 6), in a footnote on p. 246, states that the clypeal prolongation is shorter than in *E. vulgata*, the sides are rounded, the anterior angles thicker, shorter, and the median indentation less profound).

FIG. 3



Diagrams of dorsal surfaces of abdomen of (*a*) *Ephemera danica* ♂, (*b*) *Ephemera danica* ♀, (*c*) *Ephemera vulgata* ♂ (gills omitted).

The marks on the head, which stand out well on clean specimens and which are readily seen by means of a hand-lens, are as follows (after Lestage)—"The epicranium bears a large elongated mark rising near the bottom of the clypeal indentation, and two small lateral marks connected by a thin band arched posteriorally." (The lateral ocelli lie alongside and outside the lateral marks.)

Usually the first abdominal segment of the male nymph carries dorsally a pair of spots, one each side of the middle line (Fig. 3).

The second and third abdominal segments are typically without dorsal marks. On each of segments, 4, 5 and 6, is a pair of dorsal spots becoming larger posteriorally. On each of segments, 7, 8 and 9, are two pairs of marks, an outer large triangular pair almost as long as the dorsal plate, and an inner pair, short and lying on the anterior half of the tergite. The tenth tergite bears usually a pair of spots on the anterior portion, but these, as stated by Lestage, are sometimes absent.

The female nymph has dorsal abdominal marks which, in general, are similar to those of the male, but often there is a pair on the second tergite, typically none on tergites 3 and 4, while the pair on tergite 5 is not invariably present (Fig. 3b).

It has been considered worth while to add the main features of the nymph of *E. vulgata.* The following (after Lestage) is the description of the head (Fig. 2b)—Clypeal prolongation clearly longer than in *E. danica;* sides sub-parallel, the anterior angles longer, more slender, more acute, the median indentation more profound. Lateral borders of the head more rounded. The dark marks on the clypeus and the epicranium isolated, the two small lateral spots are not fused with the anterior mark as in *E. danica.*

The dorsal surfaces of abdominal segments 2–9 have each a pair of sub-lateral, well-defined, slightly arched and posteriorally acute marks of about the length of the segment (Fig. 3c). Separating the members of each pair at their bases are two slender stripes, slightly diverging posteriorally, and of length, at the most, of half the length of the segment. On the first abdominal segment, anteriorally, is a pair of obtusely triangular sub-lateral marks.

Thus the nymphs of the two species can be quite readily distinguished (see Fig. 3), even when they are no more than half an inch in length. It is to be noticed that the abdominal markings of the nymphs are practically identical with those of the winged stages

Habits and Habitat of the Nymph of Ephemera danica

In the region where our observations have been made this insect occurs occasionally in vast numbers. Usually it is found in the streams and rivers of the less hilly districts and of the plains, but adults have been taken near Pen-y-Ghent at an altitude of 1,000 ft. The aquatic stages are apparently able to adjust themselves to considerable temperature variations, as observations have shown a fall from summer temperature of 16° C. or more, to winter temperature of 5–6° C. On the other hand, they are to be found in the beds of streams issuing from cold springs where the water temperature has a variation of from 8° C. to 8·5° C.

In all cases where we have taken nymphs of *E. danica* the deposit in which they lived could be described as sandy. Table I. represents the results of the mechanical analysis of four samples of deposit taken from a single locality. No. 1 sample represents the composition at the up-stream end with relatively few nymphs per unit area (see Table II., No. 1). No. 2 was taken from that portion where the number of nymphs per unit area was greatest. No. 3 represents the down-stream limit of maximum population, while No. 4 sample was taken from the down-stream end of the particular locality where the number per unit area was very much reduced. The superficial appearance of samples 1, 2, and 3 was such as is normally described as "sandy," while that of No. 4 was dark grey, becoming black further down-stream, owing to the increase in organic matter.

It is to be noticed that corresponding with the falling off of the number of nymphs (see Table II., Nos. 3 and 4), there is a marked increase in the amount of fine deposit, especially that below 0·05 mm. in diameter.

TABLE I.

MECHANICAL ANALYSIS OF STREAM (MEANWOOD BECK, LEEDS) DEPOSITS TO A DEPTH OF 3 INCHES, CONTAINING NYMPHS OF *E. danica*.

Air-dried Material.

Samples—	1	2	3	4
	%	%	%	%
Material over 3 mm. separated from whole sample	0·94	7·58*	0·53	1·29†
Ash in same % of whole sample	0·75	5·60	0·44	0·04
Composition of remainder—				
Fine gravel <3 mm.>1 mm.	12·55	25·10	1·12	0·18
Coarse sand <1 mm.>0·25mm.	81·00	65·00	66·25	17·50
Fine sand <0·25 mm.>0·05 mm.	1·06	1·90	23·13	41·55
Silt <0·05 mm.>0·01 mm.	0·75	1·00	2·00	7·25
Fine silt <0·01...	0·25	1·00	1·00	9·50
Clay	2·75	1·00	2·50	8·50
Organic matter	1·37	2·66	2·59	12·84
Water	0·52	1·20	0·83	2·86

TABLE II.‡

NUMBER OF NYMPHS IN 4 SQUARE DECIMETRES IN REGIONS REPRESENTED BY THE ABOVE SAMPLES

May 15th, 1926	9	95	51	4
July 20th, 1926	7	54	19	5

* Ashes, pieces of bark, twigs, leaves.

† Fruits of ash, leaves.

‡ The difference in numbers between the two dates may be taken as an indication of the number of adults which emerged during that period.

TABLE III.

REACTION OF NYMPHS TO DIFFERENT TYPES OF SUBSTRATUM. EXAMINATION AFTER 24 HOURS.

Number of Nymphs and where placed at first—	Character of Substratum.				
	Mud	Sand <1 mm.> 0·25 mm.	Sand <3 mm.> 1 mm.	Sand <5 mm.> 3 mm.	Hard bottom
	Number of Nymphs recovered and where				
5 on hard bottom	2	1	0	2	0
9 on sand— <1 mm.>·25 mm.	4	1	3	1	0
11 on sand— <3 mm.>1 mm.	4	2	1	4	0

We have rarely found many nymphs in what is usually described as "mud," that is, a deposit containing abundance of fine sediment consisting of particles of below 0·05 mm. diameter and containing much organic matter. An interesting and striking example of this was seen at Collingham in a mill pond, at the end of which was a sluice controlling the flow of water to the mill wheel, while a few yards away was another sluice usually partly open and used as a means of rapidly drawing off the water. The current to the latter sluice was apparently more rapid than that to the former. Down the centre of the bed of the pond and running to the second sluice was a deep channel having a floor of sand and sides of much finer material darkened by organic matter. The latter formed the home of large numbers of *Sphærium* and the larvæ of *Sialis*, while the sand contained an abundance of the nymphs of *Ephemera danica*. There appeared to be very little migration of nymphs from sand to "mud," or reversely of *Sialis* and *Sphærium* from "mud" to sand.

This relation of the nymphs of *E. danica* with sand is not readily explained. An experiment was conducted in the laboratory in which the bottom of a tank was divided transversely into five portions—four of them being covered as shown in Table III. The bottom was then kept covered with about 3 in. of standing water. The object was to determine whether the nymphs had any preference for any of the different sediments. The results are shown in Table III.

One point stands out, namely, that the nymphs will not stay exposed on a hard bottom if it is possible for them to move from it. For the rest, there is no indication of very marked preference for any particular deposit, unless it be for the mud. The higher total for the mud section may be explained by the fact that the nymphs, after being placed in the tank, usually swam away from their first position and often settled on the mud, where they often immediately proceeded to burrow.

An experiment was then made with a view to finding whether the size of particle had any effect on the ability to burrow. Three sizes of grains were used—Below 1 mm. and above 0·25 mm., below 3 mm. and above 1 mm., below 5 mm. and above 3 mm. It was found that the animals were able to burrow most readily among the coarsest and heaviest particles. After settling upon them they showed a much greater inclination to dig than when they rested on sand of 1 mm. or less. In all three deposits, however, the nymphs finally disappeared from view, whether the tank remained open to the light or was covered.

For the greater part of the nymphal life, the insects are weakly negatively phototropic in diffuse daylight. In strong sunlight the reaction is much quicker. An experiment was made with a 16 candle-power lamp, which was placed 9 in. above and slightly to one side of a glass tank of dimensions 12 in. $\times$ 12 in. $\times$ 6 in., in which nymphs in a more or less quiescent condition were scattered over the clear bottom. The depth of water was 3 in. The light produced immediately an uneasy movement among them, and very quickly a digging action similar to that described by Needham and Lloyd (11) for *Hexagenia* started, while some swam away towards the less illuminated side. Finally, the animals congregated at the darker side, remaining there for some time after the light was removed. During the whole period of disturbance there was very much in evidence the digging movement with the fore limbs, and the lifting of the abdomen so that the body inclined down towards the head and towards the darkness. In this way the body is placed in a suitable position for burrowing.

This negative phototropism would account for the fact that nymphs are not usually seen in daylight swimming over their habitat in the deposit near the banks of shallow water. We have seen them in considerable numbers swimming just above the bed at a depth of 2 feet, when the water contained a large amount of suspended matter. The transparence was very low, it being just possible to recognise the characteristic movement of the body and also to catch them in order to confirm the identification. Evidently this free movement was largely due to the very diffuse light which was able to penetrate through the silty water. The light stimulus was not sufficiently strong to produce the digging reaction. It is probable that under these conditions many nymphs fall a prey to fish, especially at night (see Southern and Gardiner (15), pp. 154–160).

As has been shown by others (e.g. Pictet, 13), the swimming power of nymphs is relatively poor. They make short and spasmodic efforts, after which they seek the bottom or cling to rough surfaces. Usually, when swimming, the insects are positively rheotropic.

It was determined by experiment* that the maximum speed of water in which nymphs of about two-thirds full growth could maintain their position by swimming was 2½ ft. per second. At this speed, however, they soon became exhausted, and either were able successfully to guide themselves to the bottom or sides, or they were swept down-stream to a less violent region, where they could control their movements.

From this we may infer that nymphs do not normally leave their shelter to swim where the current is more than 2½ ft. per second. Should they get into a stream of such speed, it is possible for them to be carried miles before reaching sufficiently calm water for them to maintain a feeble grip on the bottom. Sometimes

* A glass tube, bent unequally at right angles, with the short limb held horizontally with the opening upstream. The difference between the level of the water in the vertical limb and that of the stream is taken in inches. A calculation is made according to the formula—$V = 0{\cdot}977\sqrt{2gh}$,

where v = velocity of stream in ft. per sec.

g = gravity (32·2).

h = ht. of head of water in vertical tube. See Dodds and Hisaw (4).

nymphs of *E. danica* are found under stones which shelter species of *Perla*, *Ecdyurus*, *Bætis*, and other swift stream forms. In these cases it is probable that the *danica* nymphs have been carried down by flood water and have fortunately been swept into the shelter of such stones. It is usual to find on the down-stream side of the stone an accumulation of sand in which the nymphs live. When the stone is lifted, the sand, with its nymphs, is swept away. Instances of this kind are commonly met with in rapid streams where the accumulations of sand along the banks are disturbed during floods. In one case (Meanwood Beck, Leeds), 38 nymphs were taken from beneath a large stone lying in a torrent.

It would appear, from the analyses of stream deposits and the quantitative examination of the fauna, that the typical habitat of the nymphs of *E. danica* is one consisting of a considerable proportion of a mixture of sand grains varying in diameter from 1 mm. to 0·05 mm. Such deposit is found in the quieter parts of the stream, occurring naturally as small bays along the bank or along the sides of rivers. Sand-spits at the ends of islands or on the lee-side of projections of the bank usually harbour large numbers.

It sometimes happens that a sand-spit, apparently fulfilling the requirements of nymphs, will be found to be barren. We have not been able definitely to account for this. There are indications that, in such cases, the disturbance during floods is greater than is usual where nymphs are present.

As has been stated above, the occurrence of the nymph of *E. danica* among the fauna of a rapid stream may be usually regarded as accidental. An exception to this has been noticed recently in a portion of the River Nidd, where the bed consists largely of water-worn stones varying in diameter from 2 in. up to 6 in. Here, owing to the impounding of water in reservoirs higher up the river, flooding has been very much reduced. The portion of the bed examined at Ripley is described by anglers as being "dirty," owing to a considerable accumulation of fine deposit. Among the stones is found much sand of less than 1 mm. diameter, such as does not occur among stones in a typical rapid stream. Living in the sand are nymphs of *E. danica*. Although the number per unit area (about 4 per 4 sq. dec.) is not great, there is a sufficiently extensive piece of habitable river to produce a very large number of adults during emergence in June. Along the banks are long strips of sand in which the nymphs find their normal habitat and from which they can migrate owing to the slackened and fairly uniform flow of the stream. Thus, owing mainly to the absence of periodic flooding sufficient to stir up and clean the bottom, it has been possible for large numbers to exist for at least a year in a region from which, under other circumstances, they would have been swept.

Emergence of Adults

In West Yorkshire emergence takes place mainly during June. Adults have been collected on 29th May and as late as 13th July. Subimagines appear during the morning, but the numbers increase greatly after noon. Nymphs about to metamorphose come to the surface partly by their own efforts and partly by the effects of gas which accumulates between the nymphal and subimaginal skins, thus reducing the specific gravity. The moult usually takes place at the surface of the water, but occasionally after the insect has climbed up stalks of vegetation, etc., and occupies as little as 10 seconds. During emergence and the rise to the water surface, the animals may be carried some distance down-stream and many fall as prey to fish.

Eaton (*loc. cit.* p. 58) states that the subimago of *Ephemera* is quiescent for about 24–36 hours. This is undoubtedly the case in cool weather, but during warm weather, with sunshine, the subimago of *E. danica* is an active creature maintaining its heavy flight for some time. In such weather subimagines will take to the wing when disturbed, though during cool, dull periods, they are lethargic and cling to support. The final moult may take place during the morning, but it is usual to see swarms commencing after the middle of the afternoon. On one occasion, about 10 a.m., hundreds of males were seen clinging to the branches and the undersides of leaves of willow near a stream.* They had probably undergone their final moult during the previous day, since close observation failed to discover cast subimaginal skins in the immediate neighbourhood. When newly emerged imagines are found resting after emergence, it is usual to find the cast skin within a very short distance.

By about 7 p.m. (summer-time) on bright June days, adult mayflies may be seen in dense swarms along roads, over hedges and isolated trees and bushes, and near bridges. These are chiefly males flying vertically up for several feet with cerci adpressed, then with wings and cerci outspread falling vertically. This "dancing" evolution is carried out repeatedly. On one occasion a number of males was seen dancing over a tree about 20 feet high. A large female flew upwards amongst them and several males flew towards her, one successfully coupling, when the pair slowly descended. Eaton (*loc. cit.* p. 10) describes copulation in Ephemerids and has sometimes observed them coming to the ground.

We have seen the extrusion of eggs from a female within two hours after copulation. The eggs are passed out from two separate oviducal openings lying between sternites 7 and 8 of the abdomen. Their number is from 2,300 to 3,750 (Rousseau, 14). They form two masses of coherent eggs. Usually, during extrusion, the female flies over water, dipping from time to time to touch the water with

* River Seven, Vale of Pickering.

the tip of the abdomen, and the egg masses, on coming into contact with the water, break up, the individual eggs falling independently.

We have measured the rate of fall of eggs through standing water at 14° C. and found it to be approximately 0·5 cm. per second. Dr. B. A. Keen, of Rothamstead Experimental Station, Harpenden, to whom we gave data, has kindly calculated the size of particles of quartz sand which would fall at the same rate through water under the same conditions. Such sand grains would have a diameter of 0·08 mm. and would be included in the fine sand fraction (see Table I).

Oviposition usually takes place during fine sunny weather with little wind. Even a very slight breeze is sufficient to make self-controlled flight difficult for females charged with eggs, they being often seen dashed on to the water and drowned. During suitable weather females can fly a considerable distance before oviposition. We have caught large numbers half a mile away from water.

The eggs have been described by Bengtsson (2), and photographs of developing eggs are given by Mosely (9). They measure about ·25 mm. long by ·14 to ·15 mm. wide, and at a magnification of 90 diameters appear to have a smooth surface.

Mosely (*loc. cit.*) describes the collection of eggs of *E. danica* for the purpose of populating fishing waters, and shows how they adhere to the substratum owing to the formation of an adhesive layer. We found that eggs so attached could not be moved, after 24 hours, by a current made with a pipette.

The physical properties of this external layer undergo interesting changes after the eggs are extruded. Thus, in air the eggs cohere; at first in water they immediately separate, then later, if kept together, they lie in a continuous jelly owing to the adsorption of water by the gel coating. This coat, during swelling, may come into contact with particles suspended in the water and these adhere so that some eggs are found practically enclosed within a shell of fine sand or other material. This may be easily observed in the laboratory.

Incubation in the laboratory occupied 15 days. Mosely (*loc. cit.* pp. 76–77) gives the period as "from 11 to 14 days, according to the temperature."

The larvæ of the first instar are quite active swimmers in still water, progressing by means of vertical undulations of the abdomen and following a spiral course. They cannot readily control their general direction in moving water. During this instar they are positively phototactic and keep very close to the surface at the side most strongly illuminated.

The Effects of the Modification of the Stream Bed

As has been shown, the nymphs of *Ephemera danica* are to be found most abundantly in a particular type of stream bed, and are present or absent in a stream in association with their special habitat. Thus, if some well-marked and comparatively permanent change be made in the structure of a stream bed, there will be a corresponding change in the fauna. Such has been noted, for instance, in the River Nidd (see above). Similar cases occur on other rivers in West Yorkshire, e.g. River Aire and River Wharfe. Dams have been erected for the purpose of obtaining water power. Many of them are found in places which, according to the contours, were previously stony with a swift flow of water. The current is now much reduced and the sand has accumulated along the banks above the dams. These sandy deposits provide suitable habitation for large numbers of nymphs of *E. danica*.

Conclusions

According to the evidence presented, it would appear that the occurrence of nymphs of *Ephemera danica* in sandy regions is largely determined as follows—The most favourable weather for emergence, copulation, and oviposition is that with sunshine, little wind, smooth water, and absence of floods. Migration of adults from the scene of emergence allows of oviposition, under the stated conditions, at places upstream and downstream where the deposition of small particles (below 0·25 mm. diameter) is commencing. Such positions vary according to the amount of water coming down and are higher up the stream during fine weather. It may be assumed that the settling of eggs through the water is regulated in a similar manner to that of other suspended particles; therefore, under the above-stated conditions, the eggs would in general be deposited higher upstream with the slacker current. This would allow of the settling of a considerable number in places having a relatively low percentage of fine sand. It has been seen that the movement of nymphs is controlled by the speed of water and the strength of light, thus too strong current and too strong light tend to limit their emergence from the stream bed and so prevent swimming. In this way they are, no doubt, usually kept from being washed away. Again, owing to their positive rheotropism, where swimming is possible, there would be a tendency to move upstream, i.e. away from the finer particles and towards the coarser. This movement would be limited by the current which would cause them to seek the bottom, and by the light which would stimulate digging.

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