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KAJ BERG

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KØBENHAVN
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PREFACE

The main purpose of this paper is to elucidate the benthic distribution of the *Corethra* larvae in a Danish lake, Esrom Lake; the relation between their benthic and their limnetic behaviour; and the cause of their diurnal migration. A number of other biological particulars concerning the *Corethra* are added. These studies on the *Corethra* of Esrom Lake were carried out simultaneously with a quantitative investigation of the rest of the bottom fauna of that lake. For purposes of comparison it proved convenient to make a few observations on *Corethra* larvae in other localities as well, namely in Frederiksborg Castle Lake and in Sorte Dam near Hillerød, and to carry out some experiments on the phototaxis of the larvae. The studies on the *Corethra* having thus become comparatively comprehensive and independent, they are here published separately, while the remaining investigations from Esrom Lake will appear later.

The work was carried out at the Freshwater Biological Laboratory of the University of Copenhagen, to whose chief, Professor C. WESENBERG-LUND, I wish to express my cordial thanks for his constant interest in my work and for the helpful way in which he has sought to further it. For financial aid granted by the Carlsberg Foundation I beg to offer my respectful thanks. Finally I likewise tender respectful thanks to the Rask-Ørsted Foundation for a grant of funds which has rendered possible the translation into English of this paper by Miss ANNIE I. FAUSBØLL, whom I thank for her careful work.

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The Species in Esrom Lake.

According to EDWARDS' systematic revision of the *Culicidae* (1932) the genus *Corethra* belongs to the subfamily *Chaoborinae*, and among others comprises the following species:

Chaoborus Lichtenstein (= *Corethra* Meigen):
  Subgenus *Chaoborus* s. str.
    obscuripes van der Wulp
    crystallinus de Geer
      Syn. *fusca* Staeger
      Syn. *plumicornis* Fabricius
    flavicans Meigen
  Subgenus *Schadonophasma* Dyar & Shannon
    nyblaei Zetterstedt
  Subgenus *Sayomyia* Coquillett
    pallidus Fabricius

Of these 5 species *S. nyblaei* is Northern, whereas the other 4 are natives of Central Europe. While the imagines of these species have been determinable after MARTINI (1931) and others, it has only lately been possible, by means of a paper by FRITZ PEUS (1934), to identify the larvae belonging to them. Considering the important part played by the *Corethra* larvae in limnological literature, and not least on account of the biological difference which — as will be shown in the sequel -- exists between larvae from different localities, Peus deserves great credit for rendering possible a determination of the species of the larvae.

Already long before Peus, Wesenberg-Lund (1914, p. 13) had described morphological and ecological differences between two *Corethra* larvae, of which the one was found in ponds, the other in large lakes. Peus points out that even though it was not then possible to establish that the corresponding imagines were of different species Wesenberg-Lund's data for the two kinds of larvae are so excellent that his pond form is now seen to be *C. obscuripes* and his lake form *C. crystallinus*. These species, then, are recorded as larvae from Danish localities.

We shall now concider the morphological characters of the larvae in Esrom Lake, partly in order to determine the species, partly to ascertain whether this lake form shows deviating characters. Since the *Corethra* larvae live in localities from less than 1 to more than about 20 metres' depth and in lakes of a very different nature, it is reasonable to suppose that there may be some variation in them.

For distinguishing between the species of the *Corethra* larvae Peus (1934, p. 643) uses the mandibles and the so-called "knifeblades" ("Messerhaare"), i. e. hairshaped or flat appendages attached to the underside of the head in front of the labrum. Meinert, too, (1886, p. 401) as well as Wesenberg-Lund (1914, p. 17) has used the form of the knifeblades for the characterisation of the larvae.

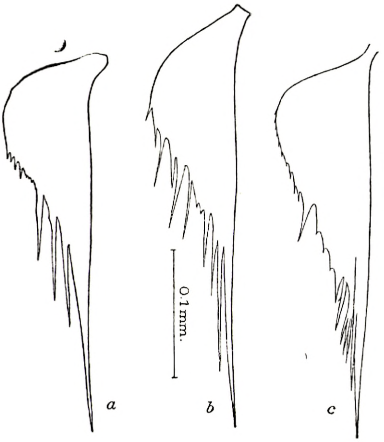
In the larvae from Esrom Lake the knifeblades are flat, leafshaped, fairly slender, and provided with teeth on the anterior side (fig. 1). Knifeblades of this shape show that the larvae belong either to *crystallinus* or to *flavicans*, in which the knifeblades, according to Peus, resemble each other both in their fundamental form and in their range of variation.

The mandibles are armed with strong teeth, 3 main teeth and 1 subordinate tooth, as also with a group of strong bristles, forming a fan, which can be unfolded or folded (fig. 2). In the larvae from Esrom Lake the subordinate tooth, which is No. 2 from behind, is placed between the 1st and 3rd main tooth, the subordinate tooth being displaced towards the 3rd tooth, though not actually issuing from it. In recently caught individuals the teeth of the mandibles are a rather deep black in their outermost third; the colour fades in preparations. The number of bristles in the fan were found to be 11 or 12; variation may occur in the same individual; the number may, for instance, be 11 on one side, 12 on the other.

Owing to the fact that the subordinate tooth is placed between the 1st and 3rd tooth, and not so much displaced as to be on the side of the 3rd tooth, the *Corethra* larva from Esrom Lake must, according to Peus' list of determinations (p. 646), be referred to *C. flavicans.* It deviates from the typical *flavicans*, which has about 15 bristles on the mandibles, in having the above-mentioned 11—12 only, and thus comes near to *crystallinus*, which has about 10. In respect of the rather dark colour of the mandibular teeth also, the Esrom Lake form occupies an intermediate position between *crystallinus*, whose teeth are very dark, and the typical *flavicans*, whose teeth are dark at the points only.

Since the *Corethra* larvae from Esrom Lake deviate somewhat from the typical *flavicans* larvae, it will be of interest to obtain confirmation of the correctness of the determination by an examination of the pupa and the imago.

The pupae of *C. crystallinus* and of *C. flavicans* have the same form of respiratory tubes. The difference between the two pupae is in the caudal swimming fan (Peus, 1934, p. 656). In the form from Esrom Lake the swimming fan



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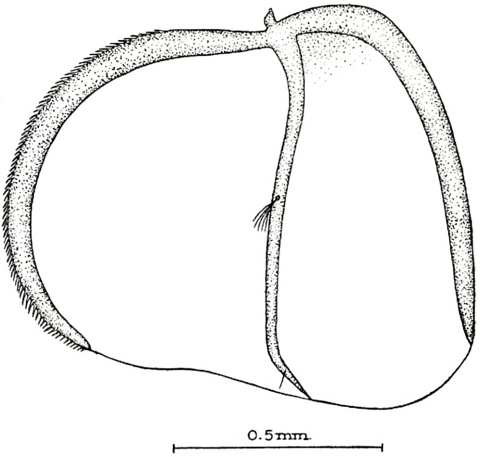

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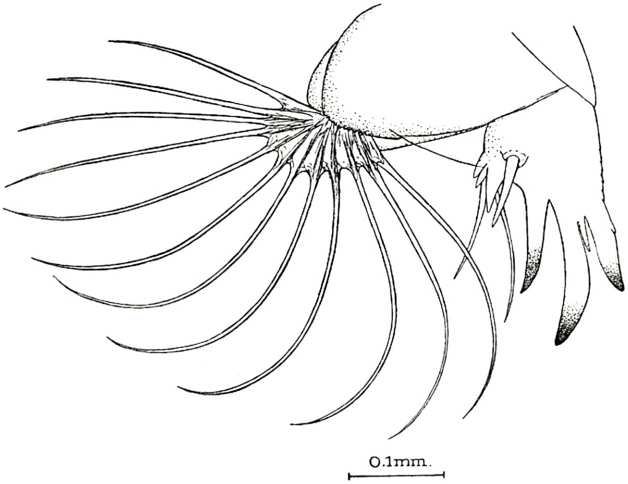

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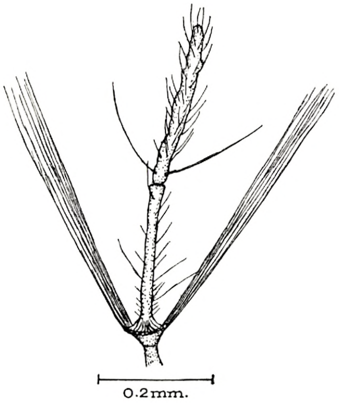
Fig. 1. Various forms of the knifeblade-shaped appendage in the larva of *Corethra flavicans* from Esrom Lake. Fig. 2. Mandible of a larva of *Corethra flavicans* from Esrom Lake. Fig. 3. Caudal leaf of pupa of *Corethra flavicans* from Esrom Lake.

has the main characters of *flavicans* (fig. 3), the outer and the inner rib being greatly thickened, and distinctly thicker than the slender median rib. The outer rib (to the right in the figure) is somewhat shortened so that the membrane belonging to it projects somewhat beyond its tip. The outer rib is always smooth at the distal end. But in a couple of less important characters the pupa from Esrom Lake deviates from the *flavicans* type: the group of bristles on the median rib seems as a rule to be placed somewhat proximally to the middle (the typical position is "medial oder etwas distal"). Further, the inner rib is provided with teeth



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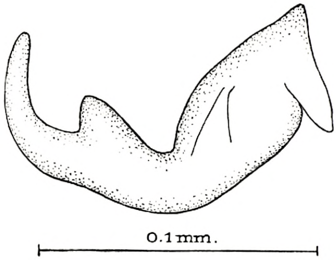

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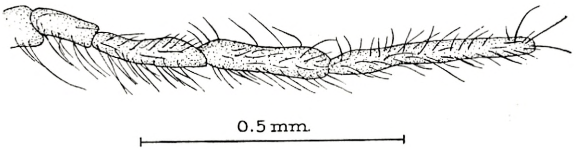

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Fig. 4. Palpus of *Corethra flavicans* from Esrom Lake. Fig. 5. The outermost joint of the antenna of *Corethra flavicans* ♂ from Esrom Lake. Fig. 6. Genital sclerite of *Corethra flavicans* ♂ from Esrom Lake.

in the outermost three-fourths of its length, whereas the typical *flavicans*, according to PEUS' figure, has teeth on the outermost half only. The principal characters in the pupae, however, show plainly enough — as in the larvae — that the species in Esrom Lake must be *flavicans*. If a great number of pupae from the large heaps washed up on shore are examined, it is seen that they all belong to this species.

If, finally, the imagines from Esrom Lake are examined, the result obtained is confirmed. The length of the last segment of the palpus is about 85 $^0/_0$ of the length of the third and fourth segments (fig. 4), a character which *C. crystallinus* and *C. flavicans* have in common. It further appears that the antenna in the male (fig. 5) has a last segment that is almost just as long as the last but one, but thicker than the latter. Further, the genital sclerite of the male is almost devoid of a head (fig. 6). These characters show conclusively that the species must be *C. flavicans*. (Compare the description in MARTINI, 1931, p. 56, and his figure 77.) The determination of the imagines was made not only on specimens taken by the lake, but also on animals hatched in aquaria from larvae taken from the lake, and Professor MARTINI and Dr. ECKSTEIN have kindly confirmed it.

Hence PEUS' view (1934, p. 642) that the lake form found by WESENBERG-LUND must be referred to *C. crystallinus* does not hold good in all cases, and at any rate not for the species in Esrom Lake.

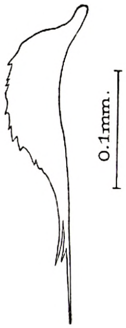
The Species in Frederiksborg Castle Lake and in Sorte Dam.

In order to throw light on the biology of the *Corethra* larvae from Esrom Lake, certain comparisons were made with the biological characters of larvae from localities with shallower water, as Frederiksborg Castle Lake and Sorte Dam near Hillerød. For the same reason morphological characters, too, were examined, and the forms of the two last-mentioned localities determined as to species with the following result:

The species from Frederiksborg Castle Lake must also be referred to *Corethra flavicans*, because the knifeblades in the larva are of the typical form; the mandibular teeth of a light colour; and especially because the subordinate mandibular tooth is placed between the first and the third tooth, and the caudal swimming fan of the pupa has the ribs typical of *flavicans*. But as in the species from Esrom Lake, so also in the species of Frederiksborg Castle Lake, there is not the typical number of mandibular bristles — about 15 (according to PEUS 1934, p. 646) — but 10—12 only. The other characters mentioned are, however, quite sufficient to show that the species from Frederiksborg Castle Lake is *C. flavicans*. An examination of the imagines confirms this.

In respect of PEUS' remark in the above-cited passage that the variability of the number of bristles seems to be very small, and that so far he has found 15 bristles only in *C. flavicans*, it must be pointed out that the observations from Esrom Lake and Frederiksborg Castle Lake render necessary a modification of both these statements. We know now that in *flavicans* the number of bristles may vary from

10—12, and according to Peus it may also be 15; the variability in this respect must therefore be said to be rather considerable. This is worth noting, because Peus thinks it possible that the number of the bristles may be of biological importance with respect to the nutrition. For the group of bristles on each mandible forms a kind of basket which prevents prey carried towards the mouth from escaping sideways. He thinks it possible that the *crystallinus* larva with 10 mandibular bristles prefers larger organisms as nourishment, and that these may be retained in the coarser meshes of the basket. The remaining species — *pallidus* with 13, *obscuripes* with 14—15, and *flavicans* with 15 bristles — should then prefer organisms of smaller average size as food. To this we must reply that since the number of bristles in *flavicans* may vary as described above, it will not be possible to point out such a nutrimental biological



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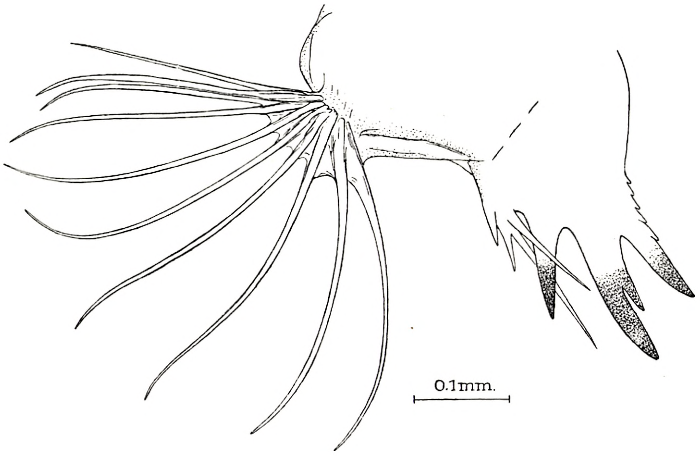

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Fig. 7. Knifeblade-shaped appendage of *Corethra crystallinus* from Sorte Dam. Fig. 8. Mandible of *Corethra crystallinus* from Sorte Dam.

difference between all populations of this species and *crystallinus*, but those that have 10—11 bristles must approximate to *crystallinus* in this respect. Within the species *C. flavicans*, on the other hand, among populations with a varying number of bristles, a biological difference may be conceived to be present similar to that which Peus thinks likely between the different species.

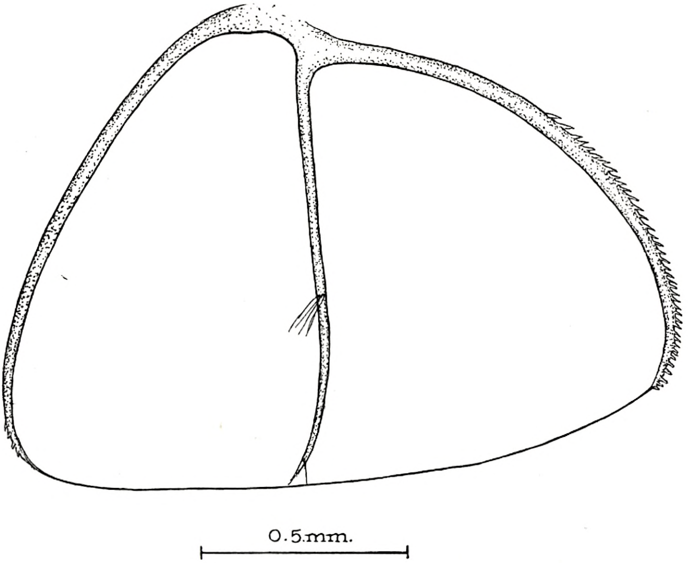
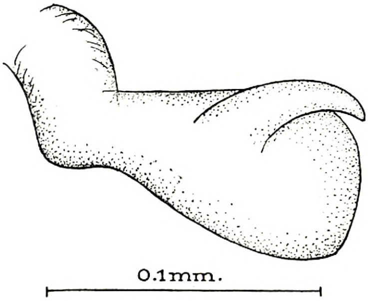


Fig. 9. Caudal leaf of pupa of *Corethra crystallinus* from Sorte Dam

In Sorte Dam the stock of *Corethra* larvae turned out to belong to 2 species. The one, which seems to be the largest and most yellowish, has knifeblades (fig. 7) which are slender, leaf-shaped and provided with teeth on the anterior side; occasionally the teeth are poorly developed. The mandibles (fig. 8) are characteristic in having the subordinate tooth placed right on the side of the largest tooth. The teeth are very dark over about two-thirds of their length. In the fan-shaped group of bristles the number of bristles is usually 10; occasionally 11 were found, and once 12 rays. After the metamorphosis, the pupa proved to have a caudal swimming fan (fig. 9) the outermost rib of which (to the left in the figure) is just as thin as the median one and almost as long; it is provided with faintly defined teeth at the distal end. The inner, strongly curved rib armed with teeth is only slightly thicker than the others. The group of bristles on the median rib is placed slightly distally to the median point. In the imagines the male has a genital sclerite (fig. 10) with a distinctly swollen head and a short hook arising far from the top of the head. The last segment of the antenna is about two-thirds of the length of the last segment but one (fig. 11). — All these characters show that this species is *C. crystallinus* (cp. Peus, 1934 and Martini 1931). Martini characterises the species as very variable. As an example we may state that the number of bristles, as mentioned above, is occasionally 11 or 12 instead of the typical 10.



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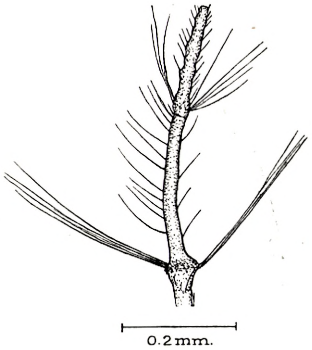

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Fig. 10. Genital sclerite of *Corethra crystallinus* ♂ from Sorte Dam.
Fig. 11. The outermost joint of the antenna of *Corethra crystallinus* ♂ from Sorte Dam.

The other species found in Sorte Dam is *C. flavicans*; it accords with PEUS' description. However, only individuals with 13—14 mandibular bristles were observed, while PEUS states about 15 to be typical. The larvae of *C. flavicans* are more transparent than the somewhat yellowish *crystallinus* larvae present at the same time. — Since *C. flavicans*, as previously mentioned, was found both in Esrom Lake which is fairly clear and 22 m deep, in Frederiksborg Castle Lake which is $3^1/_2$ m deep, strongly eutrophic, and rich in *Cyanophyceae*, and in Sorte Dam, which is barely 1 m deep, whose bottom is covered with leaves, and whose water is, yellowish with humous substances, the species is thus able to live in highly differing environments. This is further emphasised by a comparison with the localities in which PEUS (1934, p. 663) found it. His localities for *C. flavicans* are river forests, and meadows along the Rhine, Oder, and others rivers. He states that this species has its optimum in the inundation area of large rivers and adds that it is remarkable that the larvae occur exclusively in the periodical pools found in the inundation zone proper. These waters arise from the inundation of the river, partly directly when it overflows its banks, partly because the river at high water causes a rising of the groundwater in its vicinity, which may then come to the surface as pools. The time when the pools are filled is mostly in the spring. PEUS thinks, however, that *C. flavicans*, though having its optimum in the inundation areas of rivers, is not exclusively restricted to this environment; from findings at Drewenz See (East Prussia) he supposes that it may also occur in pools at the shores of lakes with a fluctuating water level. The Danish localities and PEUS' localities in conjunction show that *C. flavicans* has a much larger power of adaptation to the different environments than Peus could know from his findings alone, and in accordance herewith its biological variation is very considerable.

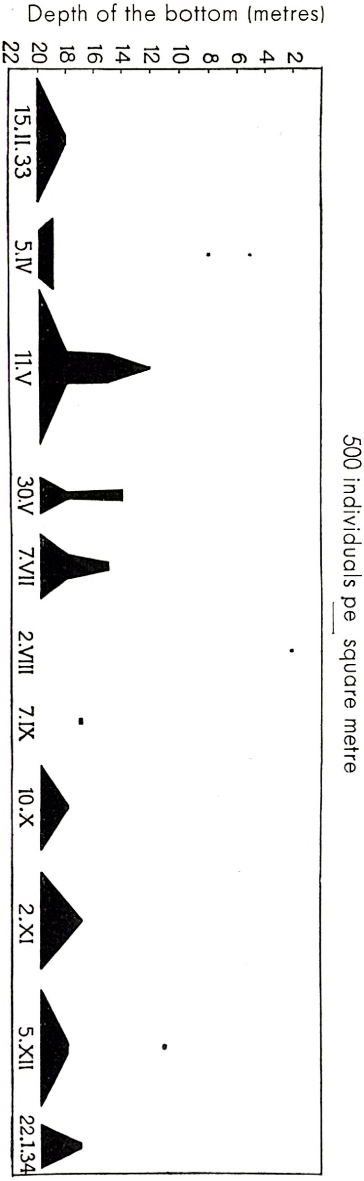

Fig. 12. Seasonal variation of the benthic distribution of *Corethra flavicans* from Esrom Lake.

Benthic Distribution in Esrom Lake.

The benthic distribution of the *Corethra* larvae was investigated by means of a Birge-Ekman bottom sampler. A series of samples was taken along a line extending into the lake in a direction approximately at right angles to the shore line. Along this line samples were taken at 7 stations, viz. at depths of about 2, 5, 8, 11, 14, 17 and 20 m; the samples from 20 m were taken in midlake. At each of the 7 stations, 2 samples were always taken. Altogether the sampling line was investigated on 12 occasions in the course of a little more than a year.

The distribution of *C. flavicans* along the sampling line is very characteristic (fig. 12). It appears that, apart from the swarming period in the middle of the summer, it always occurs in quantity at a depth of 20 m, the average number at that depth being about 1290 per sq. m. This very considerable number on the deep bottom of the lake is reduced very rapidly as we pass towards land; at the foot of the slope of the shore, in the 16—18 m zone, only few individuals are found, and at 12—15 m the species is rarely met with, or at any rate in very small numbers only. In still shallower water it is as a rule absent. On a few occasions a single individual was found in shallow water, for instance on the 5/IV 33. Since, as shown in the figure, it occurs so rarely, the animals found there have possibly been carried away by the current from their normal area of distribution.

The benthic distribution of the larvae of *Corethra flavicans* in Esrom Lake seems to be very peculiar, when considered in conjunction with the fact that the *Corethra* larvae may live even in very shallow-watered localities, and particularly when it is noted that the very same species which was found in Esrom Lake occurred in quantity in Frederiksborg Castle Lake which is fully 3 m deep, Sorte Dam which is barely 1 m deep, and in pools in the inundation area of rivers. An indication towards the explanation of the peculiar benthic distribution in Esrom Lake is afforded by some bottom samples from Møllebugt at the southern end of the lake. Here, on the 23/XI 35, at a depth of 2 m, were found 4 larvae of *C. flavicans* in a double sample, and in two double samples 3 individuals at 5 m. Even though the number of individuals was not great, yet it may be said that anything like this could hardly have been found along the sampling line. The cause of this difference is probably to be found in differences in the quality of the bottom. Along the sampling line the bottom is fairly hard in shallow water because it is sandy, and even though the content of detritus increases with the depth, it is still rather hard on most of the slope, owing to the presence of many fragments of shells. This seems to be the reason why *C. flavicans* is "uferscheu" there. In Møllebugt the bottom consists of a gyttja with coarser or finer plant remains, and in this fairly soft bottom a good deal of *Corethra* larvae can live, which is the reason why it can be found in shallow water in that part of the lake.

On the assumption that the softness of the bottom is a factor important in determining the horizontal distribution of the *Corethra* larvae, it will be more readily understood that there is such a difference in the statements regarding the depths at which the *Corethra* larvae are found. Thus Lang (1931, p. 46), in contrast with what was found along the sampling line in Esrom Lake, states that *Corethra* larvae have an extensive benthic distribution; in Lake Stråken they have been found at depths of 2,0—11,6 m. Eggleton (1931 a, p. 254) found *Corethra punctipennis* to be one of the most numerous organisms in the profundal zone, "at times in very large numbers"; frequently there is a limited number in the sublittoral zone in Douglas and Third Sister Lakes; it has not been taken in the littoral zone except when washed ashore by heavy onshore night winds. Lundbeck (1926, pp. 222 and 456) found the *Corethra* larvae in Kleiner Ukleisee at depths of from 0—4 to 12—16 m, in Ihlsee at depths of from 4—8 to over 20 m, and in Garrensee at depths of from 0—4 to over 20 m; his figures show distinctly, however, that the larvae are found in smaller numbers in shallower water where the bottom is probably harder. Lundbeck considers it probable that it is the amount of

Copepoda which determines the distribution of the *Corethra*. GUNNAR ALM (1922, p. 30) found *Corethra* larvae in the 1.5—6.0 m zone in Yxtasjön, and in the greatest quantity in the deepest places. ALM expressly emphasises this, but he likewise remarks that it is difficult to say why *Corethra* avoids the shallow-watered areas, since otherwise it often occurs in abundance in small shallow ditches. For the present no better explanation can probably be given than that the softness of the bottom at any rate has some influence on the horizontal distribution of the *Corethra* larvae in a lake. It will presumably be recognised that there is something correct in this, when the relation between the benthic and the pelagic occurrence of the *Corethra* larvae is more fully elucidated (p. 50). Probably light plays some part too. As will be shown later on, the *Corethra* larvae from Esrom Lake show a strong negative phototaxis (p. 70), and this must have the effect of making them "uferscheu".

The demonstration of negative phototaxis in the larvae of a large lake and the consequences thereof indicated above, makes it necessary to abandon LUNDBECK's view entirely (1926, p. 183). He thinks that since the *Corethra* larvae originally belong to smaller bodies of water, and thence have made their way to deep lakes, it is rather improbable that they, which previously lived in illuminated ponds, should suddenly have become photophobic. Hence he cannot explain their distribution as a flight from the light.

The average number of *Corethra* larvae found at a depth of 20 m in Esrom Lake — about 1300 per sq. m — is very considerable. Much larger numbers have, however, been found by JUDAY (1922, p. 472) in Lake Mendota. At a station with a depth of 20—23 m he found that the numbers ranged from approximately 18,000 to 30,000 individuals in the daytime from November to April. These very high figures are even surpassed by the observations of Eggleton (1931 b, p. 364), who in Douglas Lake found populations of *Corethra* larvae of nearly 4,000 per sq. m of the bottom, and in Third Sister Lake a maximum of about 71,000 per sq. m, an enormously dense population.

Periodicity.

The main features of the periodicity of *C. flavicans* in Esrom Lake in 1933 will already appear in part from fig. 12, which shows that in the spring many larvae that had wintered were found in the bottom samples. As late as the beginning of July the number is considerable, still many of the individuals have now pupated and afford evidence that the swarming period must begin at this time, that is to say, rather late. It lasts for the greater part of July and the whole of August. The bottom samples from the 2/VIII contained no *Corethra* larvae at all, but only a pupa from the littoral zone. As late as the beginning of September only some few larvae of the new generation were found, and not until October was the new stock present in quantity in the bottom ooze and henceforward was constantly to be found in the subsequent autumn and winter samples.

Confirmation of the data as regards the swarming of the imagines and a close determination of it are afforded by observations from Esrom Lake in 1934 and 35. Combined they show the following facts. At the beginning of June larvae that have wintered and are about 10.9—11.6 mm in size occur; as yet (1/VI) they show no signs of metamorphosis and are present in quantity in the bottom ooze. At the close of the month (31/VI) a couple of pupae may be found in each bottom sample, and many larvae now show signs of incipient metamorphosis. This proceeds rapidly. At the beginning of July the number of individuals in the bottom has greatly decreased, and nearly half of the individuals left are now pupae and the rest larvae which are about to pupate (2/VII); unlike what was previously the case, these individuals occur principally in the upper 5 centimetres of the mud, as shown by means of a stratification bottom sampler. Shortly after the first pupa-exuviae may be found washed up on the shores of the lake (7/VII), but the imagines do not as yet form large swarms. As early as the 13/VII, nearly all the individuals in the bottom samples have been transformed into pupae, and only a few are still in process of changing. Soon after (15/VII) large swarms may be observed on the shores of the lake, both over the water, near it, and, for instance, 1 kilometre from the shore. In damp or windy weather the bushes at the lakeside afford a shelter for thousands of animals. About at this time the first egg masses appear near the shore, floating at the surface of the water, especially where *Potamogeton* comes up to it. As yet (13/VII), however, the egg masses are not particularly numerous, but if the weather be favourable, they increase rapidly in number during the following days, and the imagines form large clouds. An examination of the population at the end of July 1934 showed that all the larvae were then (24/VII) transformed into pupae. In 1935 they had also been changed into pupae, and these, apart from some few exceptions, had ascended and been transformed into imagines (25/VII). During the time that followed *Corethra* could not be demonstrated in the bottom of the lake (9/VIII, 22/VIII), whereas the pupa-exuviae and imagines were very conspicuous on and by the shores of the lake. During the first half of August, however, the swarms rapidly decreased in numbers, and soon only some few individuals were seen. The people living near the shore know this second period with swarms of gnats very well and are aware that, even if they are conspicuous, they are scarcely as dominant as the spring swarms of *Chironomus Liebeli-bathophilus.* The ratio between the numbers of the two animals in the bottom confirms this general observation.

The above-mentioned data for the hatching of *C. flavicans* in Esrom Lake fully confirm Wesenberg-Lund's observations (1914, p. 13); he has seen the same sudden hatching, the large swarms of imagines, the large quantities of pupa-exuviae, eggs etc., as I have seen, and precisely in the same weeks. Since Wesenberg-Lund's observations have been published in Danish I have taken the liberty of describing my own observations here, but for the same reason I shall later quote several of his observations in some detail.

When the larvae of *C. flavicans* leave the bottom of Esrom Lake in the latter half of July, the oxygen conditions at the bottom of the lake are growing unfavourable. In the water over the bottom there are then about 2.5 c. c. of O_2 per litre, and the oxygen content decreases rapidly in the ensuing time. In the bottom itself it must be still less. At the same time the temperature of the bottom water has risen to about 8°, and the respiration conditions are thus very nearly the worst in the year. The large larvae escape life in this environment, being hatched at that very time. It seems natural to ask, therefore, whether the hatching precisely at this point is an ecological necessity for the species, or at any rate an advantage. It is hardly necessary for the species to leave the bottom owing to lack of oxygen, for, as will be shown later on, the young *Corethra* larvae of the next generation appear in the bottom about the 1st of September, at which time there are still poorer respiration conditions than when the former generation left the bottom. This does not seem to indicate that the *Corethra* larvae are especially susceptible to slight amounts of O_2, hence it is hardly a necessity for the large larvae to leave the bottom owing to the lack of O_2. Possibly, however, it is a biological advantage to them for the metamorphosis from larvae to pupae to take place while the amount of O_2 present in the hypolimnion is as yet not too small. — The supposition that the *Corethra* larvae are not highly susceptible to fluctuations in the amount of O_2 is also supported by observations on their vertical wanderings in Esrom Lake in the course of the twenty-four hours. It appears from these that the larvae wander from the hypoliminion poor in O_2 to the epilimnion rich in O_2 and back again. Thus the larger or smaller amount of the oxygen does not seem to be of any great importance for the *Corethra* larvae.

The literature has several statements, which do not entirely agree, about the relation of the *Corethra* larvae to the amount of O_2 in the water. FRANKENBERG (1915, p. 533) has shown that *Corethra* larvae can live for several weeks in boiled water. He states that the oxygen requirement of the *Corethra* larvae is very low compared with that of other insects, and that its metabolism is very much reduced because it so rarely moves. The extensive vertical wanderings of the *Corethra* larvae (see p. 54), however, renders this explanation improbable.

According to THIENEMANN (1920, p. 54) *Corethra* may occur in lakes with 2—3 c. c. of O_2 per litre or less, and it is absent from lakes with a comparatively high oxygen content, for instance in the *Tanytarsus* Lakes in Eifel. If, therefore, it is found in company with red *Chironomus* larvae, THIENEMANN thinks that it is a sign of a very low O_2 content in the hypolimnion of the lake in question in the summer. ALM (1923, p. 172) remarks that in many lakes *Corethra* occur exclusively in the deeper parts where there is a lack of oxygen. He thinks that this occurrence is due to the fact that elsewhere the animals are exposed to a lively competition, and that they are able to tolerate a low O_2 content. In any case, their absence from the other parts of the lake cannot be due to the fact that they cannot live in water rich in oxygen, for they may be encountered in an environment rich in O_2. Several investigators state that *Corethra* larvae may occur in bottom water entirely or almost entirely free from oxygen and containing H_2S (THIENEMANN 1913, p. 245, 1923, p. 40, BIRGE and JUDAY 1911, pp. 36, 103, JUDAY 1921, p. 272). VALLE (1927, p. 77) has investigated the occurrence of the *Corethra* larvae in relation to the oxygen content of the water in a series of Finnish lakes and arrives at the result that the larvae are not strictly limited to lakes, the oxygen content of which is low in the profundal region, nor does it occur in all the observed lakes poor in oxygen. LANG (1931, p. 49) found *Corethra* larvae in all the lakes he examined except one, in spite of the fact that the oxygen content of these was high. He does not think, therefore, that the *Corethra* larvae can be used as indicators of a low oxygen content. — The sum of these investigations would seem to show, then, that the *Corethra* larvae are fairly indifferent to the smaller or larger amount of oxygen contained in the water, and this agrees with the observations in Esrom Lake. Their absence from certain lakes must therefore be due to other causes, for instance to a lack of nourishment.

The periodicity of *Corethra flavicans* in Frederiksborg Castle Lake does not seem to follow quite the same course as in Esrom Lake, notably there does not appear to be so sudden and brief a hatching of imagines. It is possible that the imagines already appear at the Castle Lake in June; on the 7/VII, at any rate, 15—20 °/₀ of the larvae taken had been transformed into pupae. At the close of July, the swarming imagines are seen everywhere by the shore, but on the 3/VIII there were still many larvae and pupae in the lake. Throughout the month of August and as late as the 10/IX swarms of imagines may still be seen at sunset, hence the hatching seems to extend over a long period. The fairly long swarming time is perhaps connected with another phenomenon. The larvae in Frederiksborg Castle Lake vary a good deal in size in the middle of the summer, whereas those in Esrom Lake are all of the same length. On the 3/VIII larvae of *C. flavicans* measuring 11.9 mm occurred in Frederiksborg Castle Lake; they were individuals just about to pupate. But besides these there were others measuring about 7.1 mm only, and likewise intermediate sizes. Since larvae that have just been hatched grow up very quickly, there is a certain degree of probability that the small larvae which at the beginning of August are 7 mm, have been hatched from eggs laid the same year. If they had originated from eggs dating from the previous year, they would probably, in the course of the spring and the summer, have attained the full size of the species.

If larvae are about 7 mm in size at the beginning of August, it should not be excluded that they might have time to pupate and metamorphose into imagines in the same year, that is to say, in the same year in which they must be presumed to have been hatched from the first eggs produced by the species. Frankenberg (1915, p. 551) has shown that the development in aquaria with plenty of nourishment and at optimum temperatures takes two months. In order to ascertain whether the larvae measuring 7 mm could undergo their metamorphosis in the same year, a number of larvae of this size were placed in aquaria and fed plenty of *Daphnia* and plankton from Frederiksborg Castle Lake. They grew rapidly, and on the 29/VIII several pupae and a few imagines were found in the aquaria and at the surface of the water. In the course of September all the larvae had attained full size and a large number of them metamorphosed into pupae and these again into imagines; the room in which the aquaria were kept was not heated. If it is really the case that the eggs from which the animals were derived were laid in the same year, the second generation had then been hatched. And it happened at a time when imagines might still be found flying in the open in small swarms near the shores of the lake. I can only suppose, therefore, that something similar may happen in nature, at any rate in years when the late summer is mild. In the aquaria, it is true, the larvae had plenty of food, but the amount of plankton in Frederiksborg Castle Lake is also decidedly so plentiful that no difference can be supposed to occur, on that account, between the experiment and conditions in nature. However, the second generation which thus, we may suppose, could occur under favourable circumstances in nature, intermixed with the last swarms of the first generation, can hardly comprise any very large amounts of individuals.

As controls for the above-mentioned aquarium experiments eggs of *C. flavicans* from Esrom Lake were placed in aquaria in July-August. In the course of the autumn several of them were induced to change into pupae and imagines. Hence there is no doubt that *Corethra* larvae can be brought to full metamorphosis in the same year that they are laid as eggs, if only the conditions are favourable enough. This they are certainly not in so large a lake as Esrom Lake; probably the amount of food is not so plentiful as it was in the aquaria, and at any rate the temperatures in the hypolimnion are not nearly so favourable as the room temperature of the aquaria. On the other hand, Frederiksborg Castle Lake, which is particularly rich in plankton and warm right through, provides a more favourable environment for a rapid development; since the first larvae of the year are brought into the world there somewhat earlier, there is a probability, as previously mentioned, that some of them can attain metamorphosis in the same year, the weather being favourable.

The possibility that 2 generations of *Corethra* may occur has already been discussed by MEINERT (1886, p. 406), who writes on this subject: "It (*Corethra*) winters as a half-grown or full-grown larva, and the imago most frequently appears from the close of April to June; but already in the first days of spring, after mild winters as early as before the end of March, in the captive state, imagines will appear from pupae taken as larvae in the open in the same year, before the coming of spring. From the coming of the spring proper imagines continue to appear until late in the autumn, in captivity until the last days of November, and in captivity some few winter as pupae. At the close of September and the beginning of October imagines seem to appear in larger numbers, and perhaps we may put 2 generations a year, a first or main generation from the close of April to the beginning of June, and a second or weaker generation 4 months after this, without the two generations being sharply marked off from one another, however." — As will be seen, Meinert's view of the possibility of 2 generations receives support from the observations from Frederiksborg Castle Lake that larvae of different sizes occur in the summer, and from the aquarium experiments; the main generation, however, is decidedly not as early in this locality as Meinert states.

On studying the periodicity of *Corethra* in three experimental ponds, in the forest near Frederiksdal, Wesenberg-Lund (1914, p. 8) arrived at the result that the larvae disappear from the ponds at the close of May when pupation takes place; the pupal stage lasts but a short time, only a few days; in the course of about 8 days nearly all the larvae of the ponds have been transformed into pupae. From about the 20th May to about the 15th June the ponds harboured neither pupae nor old larvae. In the first half of June the tiny larvae appear; by the end of June they have attained about half the full-grown size, and are full-grown already at the close of August. From August until May, when pupation takes place, the ponds contain full-grown larvae only; neither pupae nor small larvae were ever observed at that time; further, it must be pointed out that the larvae of the pond were at all times all of the same size, and that the pupae were never seen outside the period May 15th to June 1st. Hence Wesenberg-Lund concludes that in the case of these ponds there can be no doubt that *Corethra plumicornis* has mostly only one generation a year, the imagines of which appear at the close of May and the beginning of June. Scattered observations in numerous bogs in North Sealand also seem to show that the process of development indicated is the normal one, at any rate in certain years.

After citing the observations adduced by Meinert in support of his conjecture of 2 generations of *Corethra*, Wesenberg-Lund remarks that these, taken in conjunction with his own observations, would seem to show that the periodicity may differ; the weaker autumn generation hardly develops in all localities, and scarcely every year. Experience shows that many freshwater insects normally have only one generation in Denmark, but in warm summers they can develop one more generation. — The presumed difference between the process of development in different localities is undoubtedly correct. This is confirmed by the investigations in Esrom Lake, where it is quite certain that no autumn generation of imagines is hatched. And it is probably right, too, that the autumn generation hardly attains development every year in places where it is at all possible; or else *Corethra* larvae of mutually differing sizes as demonstrated in the Castle Lake would more often be taken in the summer. Occasionally larvae belonging to different generations may indeed be found simultaneously. In small ponds draining into Kobberdam, Hellebæk, *Corethra* larvae were thus taken on the 21/VI which were partly full-grown, partly quite small; some few animals of intermediate sizes were also found.

Frankenberg (1915, p. 508) has examined *Corethra* larvae — *C. plumicornis*, now *C. crystallinus* — from a pool near Fregeteich, Leipzig. He states that it winters in the larval stage; the larvae which have wintered under the ice pupate in March and April. Already at the beginning of May he found egg-laying females (1st generation), and the generation deriving from them emerged from the pupal stage towards the close of June and immediately laid eggs (2nd generation). But whether the larvae which appear in this pool at the beginning of July attain pupation in the same year, FRANKENBERG does not know.

MUTTKOWSKI (1918, p. 407) suggests the possibility of 3 generations of *Corethra* in one summer in Lake Mendota. RAWSON (1930, p. 50), however, points out that an exactly defined minimum abundance of the larvae was only found in August in Lake Mendota. In Lake Simcoe the minimum was found in late July. Since this minimum indicates the maximum emergence, he thinks that it is doubtful if the early and late generations are of any significant numbers.

A full understanding of how much the periodicity of *Corethra flavicans* may vary, can only be obtained, however, when the observations from the Danish localities are compared with PEUS' observations on the species from the inundation areas of German rivers (1934, p. 664). In pools along the banks of the Oder PEUS found *flavicans* larvae in enormous quantities. Adult larvae and pupae were found at the close of May in the first days of June. It may happen that the complete desiccation of some pool brings the life of the larvae and the pupae to a close before metamorphosis can take place. They may then be found as a thick gelatinous mass at the bottom of the dried up pool. Normally the imagines emerge at the close of May, and from that time to the beginning of June they attain their maximum abundance. The number then decreases rapidly, and in the beginning of July the flying animals have quite disappeared. Now PEUS, who, as was mentioned, does not know *C. flavicans* from localities such as the Danish ones, thinks that the brief space of time in which the pools are filled with water excludes the possibility that the life cycle of *C. flavicans* can take the same course as that of the other *Corethra* species. Normally the pools are dry from the early summer to the next winter or spring. But the flying period of the imagines, as far as the majority of the individuals is concerned, is over with the month of June. Hence it is impossible, Peus thinks, for oviposition to take place in the way it usually does in the rest of the *Corethra* species, viz. at the surface of the water. Further *C. flavicans* cannot winter as a larva, the hydrography of its localities simply forbidding it. Peus therefore surmises that the egg-laying takes place in a similar way to that of the *Aëdes* species occurring in company with the *Corethra* larvae in the pools. The eggs are not laid in a gelatinous mass but perhaps singly at the bottom of the desiccated pool, and there await hatching till the next spring when the water fills the pool and attains a suitable temperature. Direct observations on the oviposition are, however, not at hand yet, and the conjecture as to the special periodicity is based mainly on the hydrography of the localities where Peus found *C. flavicans.* But conditions in the localities are so well-known that of the main result that emerges in regard to the biology of *C. flavicans* Peus can write: "Nach alledem hat das Larvenstadium also eine viel kürzere Dauer als bei den anderen *Chaoborus*-Arten" (1934, p. 666).

Even though it would be particularly desirable for Peus' observations to be supplemented by direct observations on egg-laying, the hatching-time of the larvae etc., there can hardly be any doubt that his view of *C. flavicans*' biology in the inundation pools is correct. But now that we know, in addition, that *C. flavicans* lives in lakes such as Esrom Lake and Frederiksborg Castle Lake and has quite another periodicity there, we shall, on the whole, arrive at quite another idea of its biology than must be entertained by Peus. *C. flavicans* is not a species with a highly deviating and specialised biology, and with a periodicity adapted to the brief space of time in which the inundation pools are entirely filled with water. On the contrary, the species possesses an unusually large range of biological variation, which makes it possible for it to inhabit such different localities as shallow inundation pools only filled with water for a couple of months, and Esrom Lake which is 20 metres deep; and it shows a widely differing periodicity corresponding to the nature of the locality. Whether this is due solely to a great power of adaptation in *C. flavicans*, or whether this specific name possibly covers several species or subspecies is not known (compare Eckstein 1936 p. 484).

The Pupa.

If vertical hauls from the bottom to the surface are made in the daytime with coarse-meshed plankton bags in Esrom Lake at the time when the pupae are common, no animals will be taken. Hence they are not in the free water layers in the day, but can then be taken with the bottom sampler. At night, on the other hand, vertical hauls will give an abundance of pupae in the free water layers; for instance on the 22/VII at 11 o'clock p. m., vertical hauls from a depth of 1 m gave 1 pupa, from 5 m, 4 pupae, from 10 m, 50 pupae, from 15 m, 60 pupae. Thus the ascent of the pupae to the surface does not take place throughout the 24 hours, but only in the night. This being so, I suppose the ascent cannot be passive in all its phases; for then it might be expected to be evenly distributed over the 24 hours. Since the pupae are only found in the free water layers in the night, it is most reasonable to suppose that about the time the sun sets they work their way actively up through the mud, after which the ascent through the water layers takes place. At 11 p. m. only some few individuals have reached the upper water layers; the majority are standing at about 10—15 metres' depth. If the net is dragged along the surface at this juncture, half under and half over the water, no pupae or imagines are taken. It must be supposed, therefore, that the pupae about to be hatched do not reach the surface until later in the night.

Some laboratory observations on the lifespan of pupae would seem to show that they have a life-time of several, though not very many, days. It is probable, therefore, that some of the pupae which may be found in the night in the free water layers again work their way down to the bottom at daybreak. This would also seem to be indicated by the fact that only a small part of the pupae mentioned above, which had been taken at 11 o'cl., were hatched the next night in the laboratory.

The *Corethra* pupae are preyed upon by the eel. An examination of the stomach contents of some eels during the hatching period seemed to show that they constitute by far the greater part of the food of the eel during this period, which is short, it is true. Some of the eels had empty stomachs; the following examples will show the food contained in the stomachs of the others. a: 2.1 g, consisting of 1 *Chironomus bathophilus* larva, some indeterminable chitin, several hundred *Corethra* pupae. b: 2.8 g, consisting of 1 *Corethra* larva, hundreds of *Corethra* pupae; further 2—3 score *Echinorhynchus* larvae. c: 0.5 g, consisting of 3 *Chironomus bathophilus* larvae, 1 *Pisidium*, some chitinous parts of insects and hundreds of *Corethra* pupae. At this time (12/VII) *C. bathophilus*, whose larvae are indeed small just now, does not seem to play any prominent part as a food.

The *Pisidia*, too, are few in number. The *Corethra* pupae, on the other hand, had been taken in such large numbers by the eels that they must be supposed to be of some importance to these, and conversely the persecution to which *Corethra flavicans* is thus exposed probably means a perceptible loss of individuals to the species.

Since the *Corethra* larvae are so hyaline, they might be supposed not to be worth much as food after the transformation to pupae. Undoubtedly they are valuable, however, for Juday (1921, p 285) has made a chemical analysis of the larvae of *C. punctipennis*, and showed that 67 $^0/_0$ of the dry weight is crude protein and 9.5 $^0/_0$ fat. The percentage of crude protein is remarkably high, in comparison herewith the larvae of *Chironomus tentans* yielded a much smaller percentage of crude protein, namely 46 $^0/_0$. The fat percentage, too, 9.5 $^0/_0$ of the dry sample, is rather high. Together the crude protein and the fat constituted more than 76 $^0/_0$ of the dry matter. Hence Juday draws the conclusion that from the standpoint of quality this large proportion of these two excellent food materials gives the larvae of *Corethra punctipennis* a very high rank as a source of food material for other organisms. Something similar must then be supposed to apply to other species of *Corethra.*

During the metamorphosis from pupa to imago the respiratory neck-tubes of the *Corethra* pupae have a special function which Wesenberg-Lund (1914, p. 11) has pointed out. At the moment when the pupa is about to be transformed and the cephalothorax bursts in the median line, the two air-filled neck tubes are spread sideways and lie like two air-containers on the surface of the water; this stabilises the whole of the pupa-skin from which the imago emerges, and on which it usually remains for some seconds.

However rapidly the change to imago takes place, it is, none the less, a critical moment in the life of the animal; during these few seconds the neck-tubes no doubt play a certain part as floating bladders and stabilisation factors. Precisely because the *Corethra* metamorphose in the middle of lakes and ponds under rather rough conditions, the strong stabilisation of the pupa-skin is probably of more importance than in the other species.

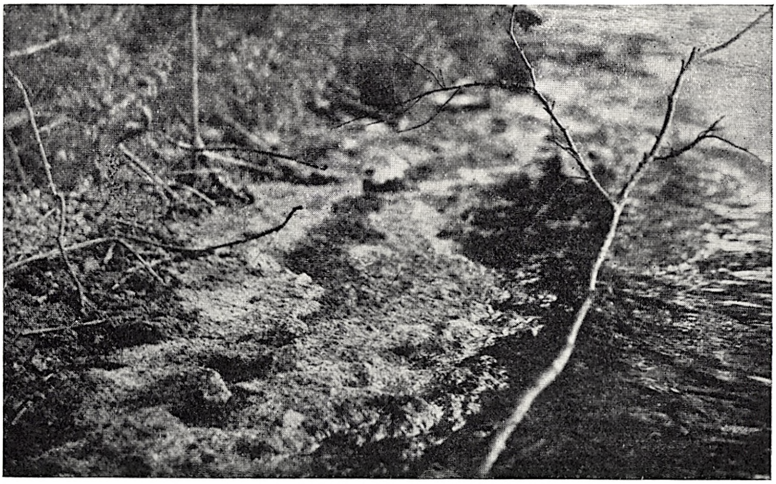

Fig. 13. From the shore of Esrom Lake in the month of July. Apparently the shore is sandy, but in reality the whole margin consists of washed up pupa-exuviae of *Corethra flavicans* with a small admixture of pupa-exuviae of *Chironomus Liebeli-bathophilus*.

On quiet mornings during the hatching periods the pupa-exuviae may be found floating in small groups dispersed over the surface of the lake. If the surface is smooth the imagines too may be seen resting there, while those which have not succeeded in emerging float about, dead, at the surface. If a strong breeze rises the whole mass is carried in to the shore, and sooner or later a margin of washed up material, 1 m wide, is formed, which in some places may be 1 decimetre deep. Over long stretches it looks as if the lake had a sandy beach (fig. 13), but there is barely one grain of sand in the margin. The pulpy mass consists chiefly of the exuviae of *Corethra* pupae (fig. 14), but thousands of dead or moribund imagines may also be found in or on it. Here and there close inspection will show that old decaying pupa-exuviae of *Chironomus bathophilus* constitute part of the mass.

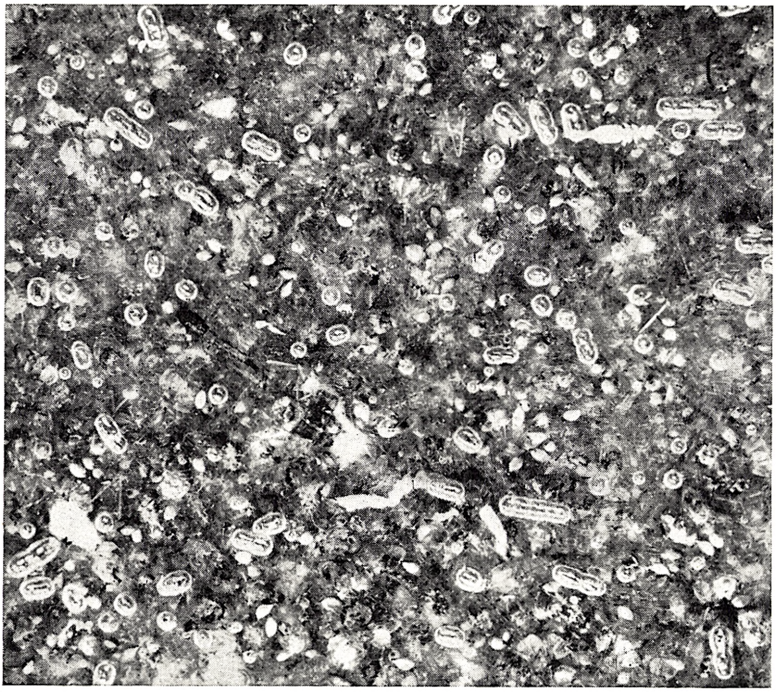

Fig. 14. The pulpy washed up mass forming the margin of Esrom Lake in July. The bulk of it consists of pupa-exuviae of *Corethra flavicans*; the small light-coloured bodies are the breathing tubes of the pupae. The pupa skins often contain one or several air-bubbles which have helped to carry the skins in to the shore.

Imagines.

The swarms of imagines are largest about the middle of July. The animals are then seen at all times of the day, but especially on quiet evenings, at sundown, when they form large clouds. In strong sunlight they often sit by myriads on the shady side of poles, on the underside of leaves etc.

Fig. 15. Bridge piles covered with a layer of the imagines of *Corethra flavicans*; from the beginning of August.

In the course of the latter half of July the swarms diminish in magnitude, but as late as the 31/VII large swarms were still observed, especially in the shady avenues along the lake. It is evident, however, that the swarming period has culminated. For dead and moribund animals form layers on the margins of washed up material along the lake, fill cobwebs by hundreds, or sit languid on the ground of garden walks. Bridge piles etc. are covered by a carpet of them (fig. 15) and among the dead animals there are many which are overgrown with fungi, which especially grow up as a fatty mass around the thorax. Mr. N. F. Buchwald has kindly informed me that among these fungi there occur *Cladosporium herbarum*, a *Penicillium*, and an *Entomophthora* species. The latter species, which is related to fly mould (*Empusa muscae*), may perhaps have helped to kill the gnats, which have then become covered with the other saprozoic fungi.

On the imagines and on the washed up accumulations of pupa-exuviae, a good many sixlegged larvae of Hydracnids may be found. They have been studied by Wesenberg-Lund (1918, p. 22), who has shown that they belong to *Diplodontus despiciens* (O. F. M.); he observed that many of the hatched gnats carried numerous larvae, usually attached to the thorax. On the walls of pupae exuviae too ran millions of small red sixlegged larvae; here and there the walls were red with larvae. Undoubtedly the larvae of *Diplodontus*, when the gnats sought the littoral region to pair, and for egg-laying, mounted onto them and were carried away with them. This took place in the first days of August. The parasitic stage can by no means have lasted more than 14 days and normally only some few days. After a thorough examination of them, Wesenberg-Lund has proved that the gnats were infested with numerous sixlegged larvae, quite similar to those which he had found upon the accumulated masses along the shore. — In 1934 and 35, I, too, saw the sixlegged, parasitic *Diplodontus* larvae on the imagines of *Corethra* at Esrom Lake and on the pupa-exuviae on the shore; though never in any great number, and at any rate not by millions. The short swarming period of *Corethra* at the close of July and in the first days of August in fact render it likely that the parasitic Hydracnid larvae are not every year fortunate enough to appear in such large numbers just at the right moment. — That *Corethra* may occur as host to larvae of *Diplodontus despiciens* has been experimentally confirmed by VIETS (1924, p. 324).

The Eggs.

The eggs are deposited in the well-known discs (see e. g. WESENBERG-LUND, 1914, p. 14). WESENBERG-LUND already remarks that it seems as if the egg-laying either takes place in the littoral region, or the eggs are carried in to the shore by the waves or the wind. He supposed that the first was the case, and this I can fully confirm. Oviposition takes place near the shore, with especial frequency in shallow water, where *Potamogeton pectinatus* and masses of filiform algae touch the surface. The female generally settles on these, but she may also alight directly on the water. In the course of 5—10 minutes she lays the eggs which are quite white when they are laid and only gradually assume a dark-brown colour. The eggs first deposited are pushed out towards the edge of the egg-heap by the ensuing ones. The jelly which surrounds the eggs prevents these from sinking to the bottom and likewise causes them to adhere slightly to parts of plants and to each other. They form a conspicuous dark coating on the water in those areas where the *Potamogeton* species reach the surface (fig. 16). There can be no doubt that the egg-masses are chiefly deposited in the littoral zone. Far out towards mid-lake, however, egg-heaps may also be found drifting at the surface. Some of them may possibly have been laid there. Most of them, however, have probably been carried out there from the shore by the current, for they are frequently found together with floating fragments of plants from the littoral zone. In any case, by far the greater part of the eggs are found by the shore and are hatched there.

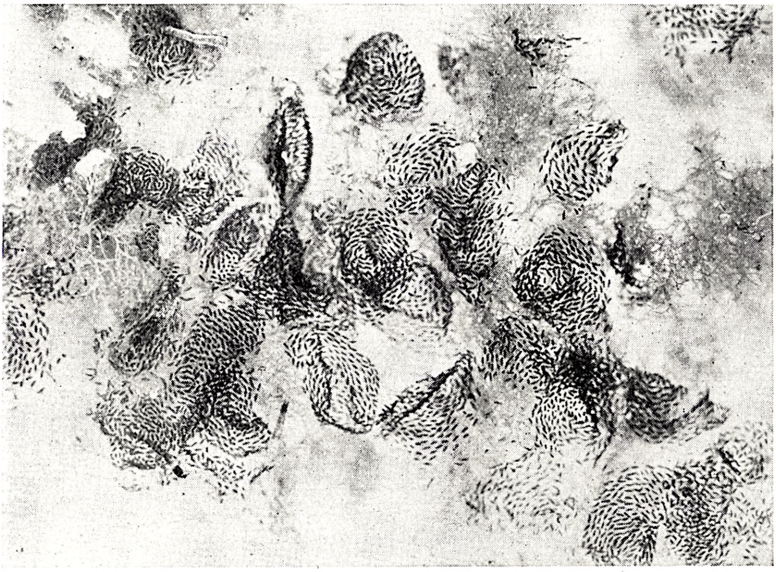

Fig. 16. Egg clumps of *Corethra flavicans* floating at the surface of the lake and adhering to algal filaments. × 2.5.

Thus the eggs of *C. flavicans* behave differently in Esrom Lake to the eggs of *C. punctipennis* which, according to Juday (1921, p. 274), sink to the bottom in aquaria, and also sink to the bottom when laid in the open, at the surface of Lake Mendota. Mud from that lake, from depths of 23 m and 18 m, was sifted through meshes fine enough to remove all larvae; the sifted mud was then placed in 2 aquaria. In the course of 5—7 days small *Corethra* larvae appeared in both aquaria, by which it was thus proved that mud from both stations contained eggs. Whether such eggs can develop in Nature in the bottom of the lake, is not known, however, for the lack of oxygen in the hypolimnion in the summer may possibly prevent or check the development. Mud from the bottom of Esrom Lake (20 m) was placed in an aquarium on the 7/VIII in order to ascertain, in a similar way, whether it contained *Corethra* eggs. It turned out not to harbour any. This further confirms the supposition that the hatching in this lake takes place at the surface only.

Oviposition probably occurs fairly soon after the emergence of the imagines, perhaps only a few hours later. In small aquaria, where isolated specimens of *Corethra* pupae are hatched, it may happen that young females, shortly after the emergence, lay eggs without having been fertilised. Since, as is well known, parthenogenesis occurs in other *Diptera* (e. g. in certain *Chironomids* and in *Miastor*) it could not at the outset be regarded as quite excluded that parthenogenetic eggs of *Corethra* might be able to develop. In the cases under observation, however, they always perished, and quite the same thing has been observed by FRANKENBERG (1915, p. 544).

The duration of the developmental period of the fertilised eggs has been investigated in the laboratory. Some females of *Corethra* were caught at Esrom Lake and kept in captivity, during which they laid eggs. Some of the egg heaps were set aside at a temperature of about 17.9—19.4° C, others at about 16.3° C. In the former case the period of development proved to be about 67 hours, in the latter about 85 hours. Since these temperatures are pretty near the temperatures in the littoral zone during the development of the eggs, we must reckon with a developmental period in nature of approximately that duration, i. e. about $2^1/_2$—$3^1/_2$ days.

The periods indicated with the temperatures belonging to them, would seem to show that small differences in temperature, in the case of temperatures of the size stated, greatly influence the duration of the developmental period; the data must therefore be said to agree very well with Juday's statements (1921, p. 274) of a developmental period of 48 hours at about 21—24° C. Frankenberg (1915, p. 544) gives a period of 3—4 days for the development of the eggs. According to Wesenberg-Lund (1914, p. 9) the egg-stage, from observations in the laboratory, hardly lasts more than 8—10 days, whereupon the young larvae appear. Compared with the periods given above, this time is very long, but since the temperature, as previously mentioned, plays a very great part, it probably applies to low temperatures of the water.

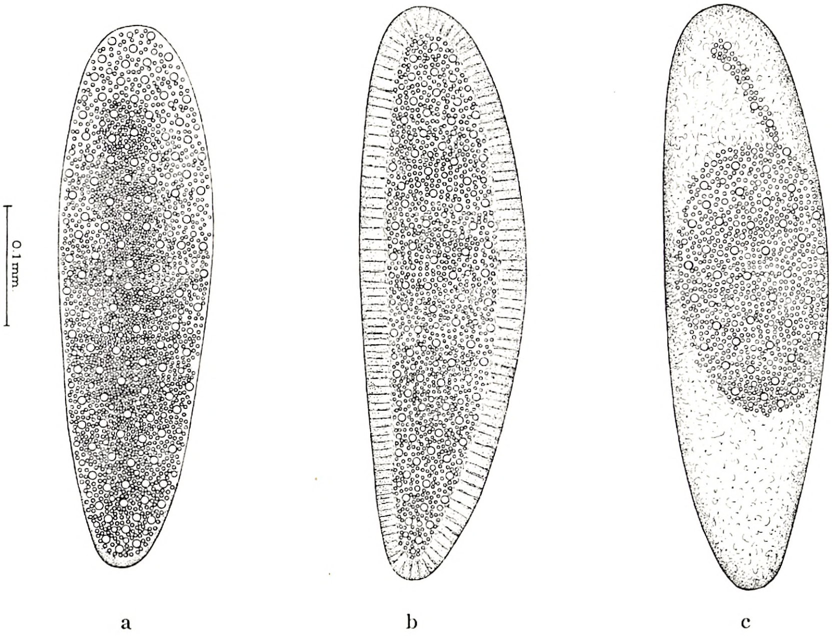

Fig. 17. Development in the egg of the larva of *Corethra flavicans*.

The newly laid, white egg (fig. 17 a) is quite filled with a uniform mass, which is drop-like; at the edges it is fairly clear and transparent. After 8 hours, a superficial cleavage has taken place, and the egg is now over the whole surface covered by high cells placed vertically to it (fig. 17 b). The inside is filled with a uniform mass of yolk. After 14 hours (fig. 17 c), the yolk is partially dissolved and absorbed in the superficial cells; these have turned greyish and their cell borders are no longer visible. The greater part of the yolk is gathered in a large dark lump in the middle of the egg. When the egg has grown 28 hours old (fig. 17 d), a faint segmentation is observable, and the yolk has grown considerably smaller. A further development of the segmentation can be observed in the egg when 34 hours old

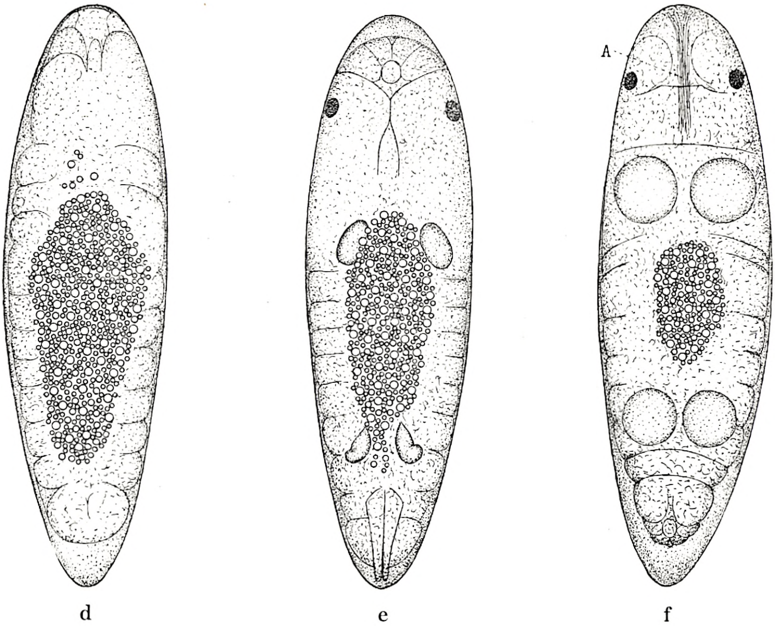

Fig. 17.

(fig. 17 e), and now different organs or incipient organs can readily be distinguished: in the head the incipient antennae and mouth parts and eyes; in the thorax and the abdomen the two pairs of tracheae, which are still small but plainly shaped as bladders, not as tubes; finally the beginnings of the segments of the swimming fan. After 57 hours (fig. 17 f) there is a larva in the shell which is almost ready to emerge. The antennae (A) are now much better developed; the tracheal bladders have grown much bigger; as far as I have been able to see, it is correct that at this time they are filled with a fluid (Meinert, 1886, p. 40). The yolk has now been reduced to a small lump in the middle of the animal;

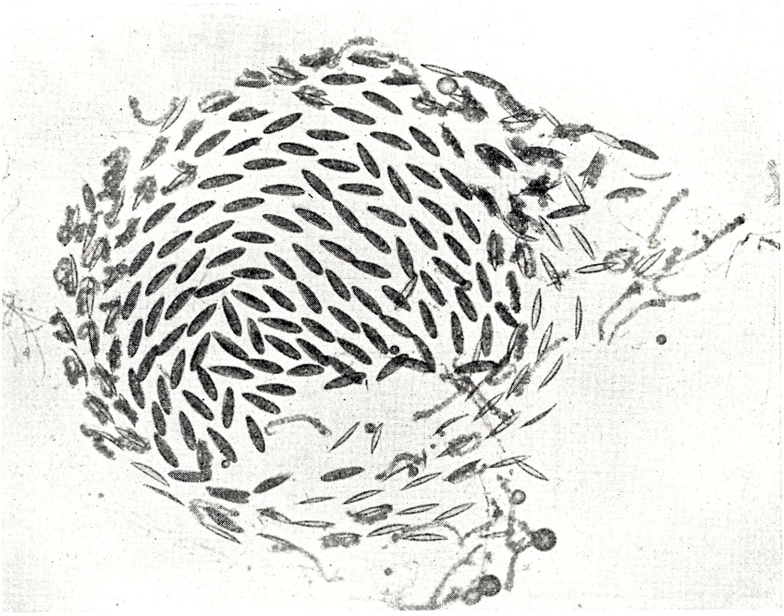

Fig. 18. Egg clumps of *Corethra flavicans*; the eggs at the edge are hatching. August 10. × 13.

in the quite young, free-swimming larva a couple of drops of it are still left. At the same time as the egg in fig. 17f was drawn, other eggs belonging to the same egg mass were hatched.

The hatching of the eggs in a heap usually first takes place in the periphery, where the oldest eggs are to be found (fig. 18). In the figure a number of larvae are seen emerging from the eggs; several of the outer eggs are already empty, while all the eggs in the centre still contain larvae. MEINERT (1886, p. 40) states that the animals come out backwards. This I have not been able to see. The egg cracks lengthwise, and then recalls a canoe in appearance. The median part of the larva is first pushed out, while it long remains attached to the egg by the head and tail. By much wriggling it tries to free itself until it at last succeeds in disengaging the ends. The development of the egg, as sketched above, took place at a temperature of about 17—19° C.

The Young Larvae.

Through the above-mentioned investigations on the place in which the eggs are chiefly deposited, and through experiments with a negative result on the hatching of larvae from mud taken from the middle of the lake, it was rendered probable that in Esrom Lake the hatching of larvae takes place exclusively at the surface of the water by the shore. An investigation of the horizontal distribution in the lake of the young larvae at the moment they emerge from the eggs confirms this. On drawing a plankton bag horizontally through the water on the 27/VII 33 over the different depths of the sampling line, in each place over a stretch of 25 m, the following numbers of larvae were found in the free water layers:

Depth	1 m (by the shore)	2 m	5 m	8 m	11 m	14 m	17 m	20 m (in mid-lake)
Number of individuals	Several hundred	2	1	1	5	5	9	4

In vertical hauls from a depth of 17 m at the foot of the slope and in mid-lake, 0—4 individuals were found per dredge haul. From these plankton samples it appears that the newly hatched larvae already at the close of July, when the swarming has culminated, were found dispersed all over the lake in the free water layers, from the shore right out into mid-lake. But it likewise appears that the number in which they occurred in mid-lake was as yet very low compared with the enormous swarms by the shore. These show that it is there that the hatching takes place. The larvae which, already at that time, were spread over the lake had probably been carried out there by the current — several times during the past 1—2 weeks a strong wind had swept over the lake. Such a transportation, in the main passive, of young larvae from the shore, can in fact readily be understood, because precisely these, as will be shown on p. 84, possess a pronounced positive phototaxis, and therefore for a time will keep above in the light and in the most agitated parts of the water masses, in the epilimnion. Hence the positive phototaxis appears to be of very considerable biological importance to the species.

It has been demonstrated by Frankenberg (1915, p. 549) that newly hatched larvae can fill their tracheal bladders with air even at an excess pressure of 56 cm Hg. He regards the demonstration of this as important and in that connection reminds the reader of WESENBERG-LUND's observation of *Corethra* larvae at a depth of 30 m in our largest lakes. Even though FRANKENBERG's demonstration is theoretically important, it must, however, be remarked that in a natural environment the young larvae cannot, on account of their being hatched by the shore, be supposed to have to fill their tracheal bladders for the first time at a excess pressure of any significance.

The larvae from the 27/VII mentioned above had just been hatched and they were only about 1.75 mm big. The growth takes place with extreme rapidity. On the 9/VIII the majority of the larvae in the lake were about 4.1 mm long, and only a small number were somewhat shorter. In the course of 13 days the size had been more than doubled. The larvae had now already left the shallow water; none at all were taken with the plankton net at the lower stations of the sampling line; only in mid-lake at about 10 metres' depth or still deeper were the larvae found swimming in the free water-layers. Bottom samples from the 20 m level showed that as yet there were no *Corethra* larvae in the mud of the bottom. The same thing is shown by fig. 12 p. 16 for the whole sampling line on the 2/VIII; the individual at the 2 m level is a pupa of the previous generation. On the 22/VIII the larvae could not be found in the bottom either. Fig. 12 shows that in 1933, as late as the 7/IX, there were only some few individuals to be found in the bottom samples, and also that the animals taken came from deep water. On the 12/IX a series of samples were taken along the whole sampling line, and now *Corethra* larvae were at last found in abundance in the bottom, even in mid-lake. Hence the animals must be assumed to make their way into the bottom about the middle of September.

The distribution over the bottom at the various depths on the 12/IX is shown in fig. 19 to the right, and for comparison the average benthic distribution is given to the left. It will be seen that as soon as the young larvae again appear in the bottom samples, they have quite the same characteristic distribution as have the larger larvae on the average at the other seasons of the year, that is to say, there is by far the greatest number of individuals at a depth of 20 m, a small number on the deepest-lying parts of the slope, and none in shallow water; only the young larvae do not as yet occur in such a large average number as is otherwise the case.

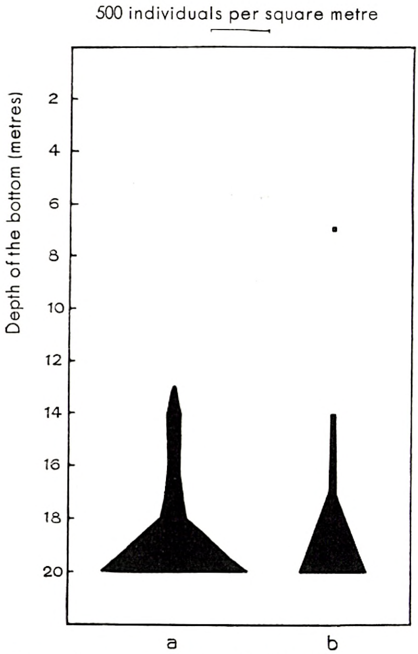

Fig. 19. Average depth distribution of *Corethra flavicans* (a) and the first depth distribution observed after the swarming period (b).

A recurrence of the *Corethra* larvae, in which they are first found freely in the water near the shore, then scattered over the lake and pelagically but not in the bottom and not near the shore, and finally, in the middle of September, in the bottom ooze, with quite the same benthic distribution as the older larvae, is characteristic of the species in Esrom Lake. J. Lundbeck (1926, p. 222) thinks that he has found something different; he states that the young larvae first live in the bottom in the flat zones and then, with increasing size they also go down into the deeper-lying parts of the bottom. He gives some figures from Kleiner Ukleisee, which lend support to the supposition of such a descent. He points out himself, however, that a descent in the summer of this species is in entire contrast with that ascent of many bottom animals which takes place precisely at the same time. He infers that various factors must cause this, and in the case of *Corethra* consoles himself with the conjecture that perhaps it is a nutrition-biological dependency asserting itself. It is by no means clear, however, why such a dependency should cause the animals to change their habitat from the bottom in shallow water to the bottom in deep water. The investigations in Esrom Lake show that the descent surmised by LUNDBECK at any rate does not take place everywhere, but the young larvae are dispersed pelagically over the lake, and when they recur in the bottom, they have the benthic distribution peculiar to the species. — Some observations by C. JUDAY, on the other hand, agree well with the observations from Esrom Lake. In Lake Mendota JUDAY (1921, p. 277) found that young larvae of *Corethra punctipennis* occur in the free water layers in the daytime; they occupy the lower water during the daylight hours instead of the mud, being found in the lower part of the mesolimnion and in the hypolimnion. Thus the behaviour of the young larvae is very different in the daytime from that of the fullgrown individuals, which are found in the bottom of the lake in the daytime. It appears that the young larvae inhabit the lower water in the daytime instead of the mud, until they are approximately one third grown or perhaps a little larger.

In Esrom Lake the rapid growth of the young larvae is continued in the late summer and in the autumn. On September 3rd there are already larvae about 10.5 mm in length. In October a large number having an average length of 10.8 mm were measured. This size is not very much less than that of the larvae next year immediately before pupation. The average size of the larvae well on in June and about the 1st July was thus found to be 11.2 mm. The circumstance that the *Corethra* larvae attain almost full size already in the autumn is in good agreement with the fact that in certain localities — though not in Esrom Lake — they may possibly have time to produce an autumn generation; their rapid growth to full size is essential to this.

The Relation between the Benthic and the Limnetic Behaviour of the *Corethra* Larvae.

The profusion in which the *Corethra* larvae occur in the bottom samples from Esrom Lake somewhat astonished me, since the pronounced plankton characters of the animal — its hyalinity, its tracheal bladders, and its swimming fan — combined with its well known pelagic occurrence in ponds made me regard it as a typical plankton animal which only occasionally or under certain circumstances was found in or near the bottom, besides pelagically. It was, however, well known to me that of recent years it had frequently been mentioned in bottom investigations, but the relation between its benthic and its limnetic behaviour seems not to be fully elucidated (cp. Valle 1927, p. 75, Lang 1931, p. 46), and is evidently also somewhat different from one lake to another. Therefore it was decided, at the same time as the bottom was investigated, to try to throw some light on the behaviour of the *Corethra* as a plankton animal. It then turned out that larvae of *C. flavicans* did not occupy the free water layers at all in the daytime in Esrom Lake, apart from the pelagic occurrence of the youngest stages in August-September. Since this result is rather remarkable for an organism with such pronounced plankton characters, I have assured myself of its correctness by numerous hauls with a plankton bag at different seasons of the year, at different hours of the day, and under different weather conditions. As documentary evidence I shall cite various extracts from my notes on these plankton hauls:

8/XI 33. 9—10 a. m. 8 vertical hauls with a plankton bag from the 3, 6, 10, 12, 19, and 20 m levels gave *O Corethra*. From 19 m and 20 m 2 samples were taken from each level. The one from 20 m had touched the bottom and got a couple of Chironomids but no *Corethra*.

13/XI 33. 10 a. m. 6—7 horizontal hauls with a dark plankton bag, i. e. only visible with difficulty, with lead weights attached; the plankton bag was dragged over the bottom, but took no *Corethra*. Only one haul, which touched the bottom and took up mud, contained many *Corethra* individuals. 2 vertical samples: *O Corethra*.

4/XII 33. 11 a. m. Several vertical samples from the 20 m level: *O Corethra*. Horizontal samples: *O Corethra*.

23/I. 34. 6 p. m. 3 vertical hauls from the 5 m level, and 3 from the 10 m level gave *O Corethra*. 1 vertical haul from 20 m gave 1 *Corethra*.

1/VI 34. 9—10 a. m Several vertical hauls from the 20 m level: *O Corethra*. Long horizontal hauls both at 5 m and near the bottom: *O Corethra*. Only when the net goes into the bottom and takes Chironomids etc., do the samples contain *Corethra* too.

31/VI 34. 3 p. m. Horizontal hauls with a plankton bag at 2 m, at about 10 m, and still deeper: *O Corethra*. Vertical samples from 20 m: *O Corethra*.

24/VII 34. 6 p. m. 3 vertical samples from 20 m: *O Corethra*.

12/IX 34. 10 a. m. — 1 p. m. Vertical and horizontal samples at various depths: *O Corethra*.

These as well as many other examples show that *Corethra* larvae were not found in the free water layers in the daytime. This applies to the pupae too; for in the investigation on the 24/VII the animals were practically all changed into pupae. Only when the net came too near the bottom and took up bottom material, were *Corethra* larvae or pupae taken too.

A certain possibility that the *Corethra* larvae might stand immediately above the bottom, for instance only 1—2 dm removed from it, cannot be quite excluded, despite the result of the plankton hauls described above; for the vertical hauls cannot take animals so near the bottom. And the horizontal hauls can only as a rare exception, by a lucky chance, be carried quite near the bottom without at the same time touching it. And in that case it cannot be decided whether the larvae have been in the bottom or in the water layer just above it. In order to ascertain whether the *Corethra* larvae besides being in the bottom, should also be present in the water layers 1—2 dm above it, some bottom samples were taken with a Birge-Ekman bottom sampler in such a manner that they only went a very short way into the bottom but were partly filled with water, and such bottom samples were compared with normal ones. If the *Corethra* larvae in the daytime stand just above the bottom, the less deep-going bottom samples will take more larvae than the normal samples. The less deep-going bottom samples gave the following number of *Corethra* individuals per single sample: 1 and 2 (8/XI 33), 2 (22/XI 33), 1 and 2 (5/XII 33). Since the normal bottom samples contain on an average 29 individuals per single sample, the less deep-going samples have taken much fewer animals, that is to say, the *Corethra* larvae hardly stand directly above the bottom in the daytime, but by far the greater part, at any rate, are found in the bottom.

This result is in good agreement with an observation made by K. S. Bardenfleth (Bardenfleth & Ege, 1916, p. 37), who writes on this subject that in the month of July when he made some observations in Esrom Lake with the apparatus of Dr. C. G. Johs. Petersen for quantitative examination of the bottom fauna, he always found the lake form of *Corethra* larva abundant in the bottom samples from the deeper parts of the lake (the samples were taken at depths of 20—25 m), the number of the larvae varying from 1500 to 9000 per sq. m. In order to decide whether these larvae were caught by the apparatus on its way down through the water, or if they were really living in the mud on the bottom, Bardenfleth let the apparatus go down to a depth of 1 m above the bottom, where he made the closing mechanism function. When closing, the apparatus will sink another metre, and when taken up it contained 40 larvae together with a small quantity of mud, having thus just touched the surface of the bottom. At the same station, however, when quite filled with mud, it contained 931 larvae. According to Bardenfleth, this would seem to indicate that these larvae, as distinct from the pond form, do not swim freely in the water, but live in or immediately above the muddy surface of the bottom. — The difference between the number of individuals taken when the Petersen bottom sampler only just touches the bottom, and when it is carried right down into it, is so considerable that it appears to me to show decidedly that the *Corethra* larvae are chiefly found in the bottom in the daytime; and this result quite accords with the tests with the Birge-Ekman bottom sampler. That the numbers found by Bardenfleth are greater than my average (p. 19) may be due to decrease of the population, but also to difference in the methodics.

Though Wesenberg-Lund (1908, p. 513, 1914, p. 12) accepted the view then current that the *Corethra* larva is the only insect larva so far known which has "quite emancipated itself from the bottom and the shore and found a home in the pelagic region", and found this readily understandable on account of its structural features, he had, however, already made an interesting observation on its occurrence which points in the same direction as the above. He showed that it was present in most of our large lakes (1904, p. 157), with especial frequency in Hald Lake and Esrom Lake, and expressly remarks hereof that it is only taken in large quantities when the net is drawn horizontally below a depth of 20 m.

Since *Corethra* larvae were not normally to be found in the free water layers of Esrom Lake in the daytime, a series of nightly excursions were made to the lake, in order to ascertain its presence, if possible, after dark. By means of horizontal plankton hauls its pelagic occurrence was always ascertained without exception. By means of vertical hauls from 1, 5, 10, 15, and 20 m — as a rule three hauls from each depth — with a coarse-meshed plankton bag an approximate expression for the number of individuals in the different water layers was found. Fig. 20 shows the vertical distribution ascertained in this way at various points of time after dark. The figure shows that

1) near sunset and near sunrise only few *Corethra* larvae were found in the free water layers, and none near the surface (23/I and 19/XII);

2) at certain hours well on in the night *Corethra* larvae were found in all the water layers of the lake from the surface to close to the bottom (22/XI);

3) near midnight *Corethra* larvae were found in the upper water layers, but not in water layers near the bottom. A very marked maximum was then demonstrated in the upper zone 1 m deep. There was then several times as many individuals in this water layer as were present in the corresponding deeper layers. The individuals that have wandered right up to the surface from a depth of 20 m will then, in the course of a few hours, be exposed to a considerable change of pressure — from about 3 to about 1 atmosphere (1/VI).

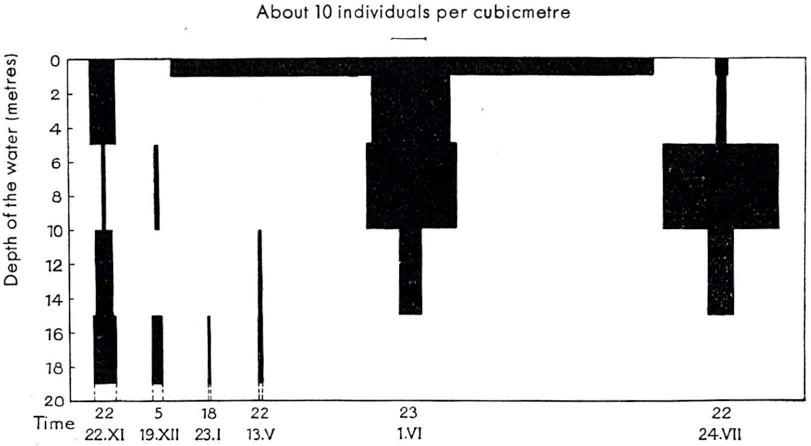

Fig. 20. Vertical distribution in the water layers of *Corethra flavicans* at night in the middle of Esrom Lake.

4) the numerous occurrence in the upper free water layers about midnight was also demonstrated, when practically all the population had been changed into pupae (this was the case on the 24/VII).

In the case where the greatest number of individuals was found to have migrated to the upper layers, viz. on the 1/VI near midnight, a calculation shows that about 400 larvae are present in the whole column of water below 1 sq. metre of the surface. But since the average number of individuals occupying 1 sq. metre of the bottom is about 1300, it is impossible that all individuals can have ascended. It is possible perhaps that they have not all contrived to do so as yet, but that it will happen later on. It is also possible that they do not all ascend every night, and that perhaps is the most probable. Or the ascent and descent might take place at slightly different times of the night and happen so quickly that all the animals are not found in the pelagic region at the same time. Bottom samples taken simultaneously with the vertical plankton hauls from the 22/XI at 10 p. m. showed that the amount of larvae which as late as this after dark were found in the bottom was approximately the normal number also found in the daytime. — In Lake Mendota where Juday (1921, p. 277) has studied the vertical migration of *C. punctipennis* in the night, he found that the bottom contained a good many larvae in the night too; it contained from one half to two thirds as many at night as were there in the daytime.

To supplement the observations on the limnetic and benthic distribution of *C. flavicans* in Esrom Lake the following observations on the corresponding distribution of the same species in Frederiksborg Castle Lake are given. On the basis of an abundance of plankton samples taken there in the daytime at different seasons of the year and for different purposes, it can be stated with certainty that in most months *Corethra flavicans* cannot be taken in the free water layers in the daytime; some few observations from midsummer only, to be dealt with below, form an exception. At night, on the other hand, it has always without exception been possible to take *Corethra* larvae limnetically. Hence there is a vertical migration of *Corethra* larvae in the lake.

In order to throw light on this migration in Frederiksborg Castle Lake plankton samples were taken at various hours of the day from the 2/VIII to the 3/VIII, 1935. The samples were taken in mid-lake with a coarse-meshed plankton bag drawn horizontally through the water over approximately 25 m at about 1 metre's depth below the surface. In each case 2 such samples were taken, in which the number of *Corethra* larvae as a rule agreed well. Only at the "critical" periods (at 9 p. m. and 4 a. m.) was there a good deal of difference between the two contemporaneous samples, the reason being probably that one sample was taken somewhat deeper down than the other; this circumstance at this time, when the upward and downward migrations are especially lively, may be of importance and seems to indicate that the larvae mostly

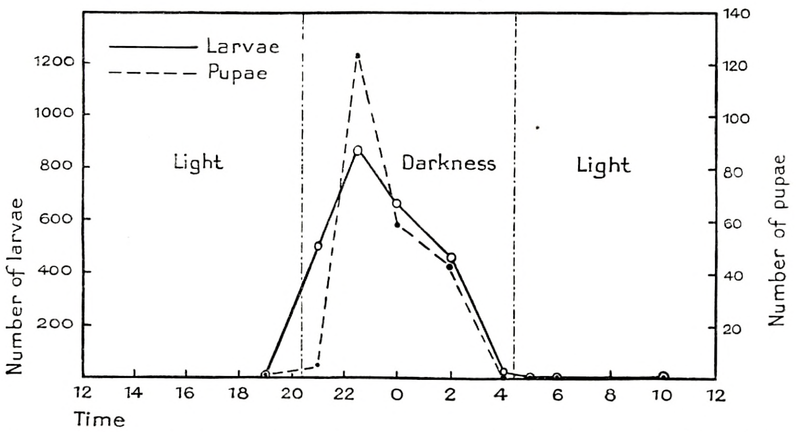

Fig. 21. Number of larvae and pupae of *Corethra flavicans* taken at the surface of Frederiksborg Castle Lake at various times of the day.

migrate in a body. — The result of the investigation, in which the larvae and pupae were counted separately, will be found in fig. 21. This shows that a migration to the upper layers only takes place at sunset. The light fades considerably earlier in the deeper layers of the lake, but as late as 7 o'clock p. m. no ascent had taken place. It did not take place until sundown. Samples taken just before, and at midnight show the largest number at the surface. After that it decreases, and already at sunrise the animals have almost entirely disappeared from the surface. In the daytime they are totally absent from the upper water layers.

The number of the pupae was counted separately and their curve has a similar form to that of the larvae. The shape of the pupa curve might perhaps be interpreted to mean that the pupae ascended from sunset to about midnight and were then gradually hatched in the course of the night, so that for that reason their number diminishes at the surface towards the morning. That probably is the case for many of the pupae. But since the life of a pupa is longer than 24 hours (see p. 33), this cannot apply to all, and some of the pupae therefore — like the larvae — probably descend when the day begins to break.

On the supposition that the larvae, when they ascended in the night, would leave few or no individuals in the bottom, but that many would be found in it in the daytime, a series of samples were taken with the bottom sampler simultaneously with the above-mentioned series of plankton samples. The result was that in 18 bottom samples distributed over various hours of the day the total of *Corethra* larvae taken was 1. This was astonishing considering the amount found in the bottom samples from other seasons of the year. The difference between such samples will appear from the following examples.

Average per double sample (500 sq. cm) of *Corethra* larvae in Frederiksborg Castle Lake.

20/III	9/VII	3/VIII	16/X
81	20	0	116

As will be seen from this, the bottom of Frederiksborg Castle Lake harbours no *Corethra* larvae in midsummer; in July already the number is small. In the spring and the autumn, on the other hand, there is a large number of animals in the bottom. The fact that there are no *Corethra* larvae in the bottom (or practically none) in August cannot, as might perhaps be supposed, be due to the hatching of the animals at that period. This must certainly be assumed to have reduced the number of animals, but as shown by the aforementioned contemporaneous plankton samples, there is still a very plentiful population left. Only this does not, when it leaves the upper water layers in the daytime, migrate right down into the bottom so that it can be taken with the bottom sampler, as is the case in the spring and the autumn. In August it is found in the daytime in the water just above the bottom. If deep plankton samples are taken from just over the bottom, larvae and pupae may be taken by hundreds, while bottom samples below and plankton samples above give no result whatever.

As to the reason why the *Corethra* larvae occupy the bottom in the daytime in the spring and the autumn, and the zone just above the bottom in the summer in Frederiksborg Castle Lake, it seems natural to put forward two possibilities, which perhaps exert a combined influence. In the summer there will probably, owing to the high temperatures prevailing in the shallow lake (Berg and Nygaard, 1929, p. 239), be a great lack of O_2 in the decidedly muddy bottom, which may possibly prevent the *Corethra* larvae from going right down into the bottom at this time. Another factor which undergoes great changes in the summer months is the intensity of the light in the lake. On account of the strongly eutrophic character of the lake an unusually marked *Cyanophyceae* maximum occurs in July-September. On calm days a strong waterbloom will be present. The transparency of the lake is then very slight; thus in August a transparency of 35 cm only was measured with a white porcelain disc. In the spring and autumn, at any rate, the transparency may be 2—3 times as great. Since now some *Corethra* larvae, as will be discussed below, are susceptible to light in rather a high degree and prove to be negatively phototactic, it is possible that it is the light which drives the larvae into the bottom at those seasons when the water is fairly transparent. But well on into the summer, when the strong *Cyanophyceae* maximum occurs, the amount of light in the water layers just above the bottom grows so slight that the *Corethra* larvae can quite well occupy this zone in the daytime (cp. Valle, 1930, p. 488). — Finally there is the possibility that the reaction of the larvae to the light differs under different conditions, for instance, different food conditions. See the later experiments p. 79.

According to the literature, the limnetic distribution of the *Corethra* larvae over different seasons of the year and different times of the day, and the relation of the larvae to the bottom, varies much from lake to lake. So far the causes of this biological variation must be said to be almost unknown, but it is, indeed, only of late years that investigators have taken an interest in these phenomena. As late as 1914

Wesenberg-Lund (p. 16) could justly say that while the plankton of clear lakes perform vertical migrations at night, and ascend to the surface, no deep-lake *Corethra* larvae have as yet ever been met with there; nor, as he points out, has any search ever been made for them at that time.

Frank E. Eggleton (1931 b, p. 364) found *Corethra punctipennis* limnetically in Douglas Lake in the deep water layers, but not in the upper zones. In some years no larvae were found above the 20 m level, in other years they were found higher up, and could constantly be caught at levels below 10 m. Douglas Lake has several fairly independent depressions, and the vertical distribution of the *Corethra* larvae in these depressions differs, the maximum of the larvae occurring at very different depths. In Third Sister Lake Eggleton also found *Corethra punctipennis* larvae in the free water layers and the larvae occurred at noticeably higher levels than in Douglas Lake. In Third Sister Lake the larvae were usually present up to depths of 5 metres, were frequently found 2 or 3 metres below the surface, and at times were taken even within the 0—1 metre station during the day. Eggleton also found a seasonal variation in the limnetic distribution of the *Corethra* larvae in this lake.

In Lake Mendota the vertical distribution of *Corethra punctipennis* has been studied by Juday (1921, p. 275). He found that full-grown larvae were never found in the water in the daytime; both on cloudy and on clear days the full-grown larvae left the water layers. Juday has also shown that a vertical migration of the larvae takes place at night, the ascent reaching 23.5 m. Thus the observations from Lake Mendota show great similarity to the corresponding observations from Esrom Lake. The considerable vertical migration in Lake Mendota would take place with great rapidity, viz. in the course of about an hour. The full-grown *Corethra* larvae ascended from the bottom at sunset and they entered the bottom by the end of the first half hour after sunrise. It should be noted that the downward migration was not due to direct sunlight, since it began at least half an hour before sunrise.

That the limnetic and the benthic distribution of *Corethra* larvae differ widely and are a complicated phenomenon is shown by further observations by Juday in Devils Lake, Wisconsin. He found there that the behaviour of the full-grown larvae of *C. plumicornis* Fabricius deviates in the daytime from that of *C. punctipennis* in Lake Mendota. The larvae in Devils Lake were substantially equally divided between the water and the mud on a bright morning when the water was very transparent. In other words, the day distribution of the larvae of *C. plumicornis* was practically the same in Devils Lake as the nocturnal distribution of the larvae of *C. punctipennis* in Lake Mendota.

A study of the hydrostatic mechanism of the *Corethra* larvae does not come within the scope of this work; but in connection with the extensive vertical migration shown to be peculiar to these larvae, and the consequent great variation in the pressure to which these animals are subjected, it will be natural to explain briefly how — according to the physiological works at hand — the adjustment to the varying pressures is supposed to take place. Details relating to this problem are to be found in works by Krogh (1911), Frankenberg (1915 and 1928b), Bardenfleth and Ege (1916), Akehurst (1922), Damant (1924) and Holst-Christensen (1928).

As is well known, the *Corethra* larvae are able to adjust themselves to variations in the flotation conditions. Krogh was the first to show that if the animals are subjected to increased or reduced pressure, they are at first respectively too heavy or too light, but after some time they again float quite normally. This demonstration of a power of compensation has subsequently been confirmed by others. If a floating larva is weighted down by a ring of tinfoil, it will at first be too heavy, but after 8 days it again floats normally and keeps afloat for a long time in spite of its weight (FRANKENBERG, 1928b, p. 237). Under natural conditions a quite similar adjustment takes place. After a meal of small Crustaceans the *Corethra* larvae are a little too heavy, but shortly after again float normally (FRANKENBERG 1915, p. 560).

As an explanation of the *Corethra* larvae's power of adjustment to various pressures two hypotheses have been put forward, one by KROGH (1911) and the other by FRANKENBERG (1915). KROGH has analysed the air content of the tracheal bladders and found that normally it consists of about 16 $^0/_0$ O_2 and 84 $^0/_0$ N_2. Since this composition is not altered by adaptation to increased pressure, the readjustment cannot take place by means of an O_2 secretion as in the swimming bladder of fishes. Nor would this be possible, for KROGH has further shown that a levelling by diffusion easily takes place between the content of the tracheal bladder and its surroundings. KROGH therefore supposes that the tracheal bladders act like the ballast tanks of a submarine boat. If the animal becomes too heavy, water is pumped out of it, and if it becomes too light, it is pumped in, until equilibrium with the water is restored.

FRANKENBERG arrives at another view. He points out that the tracheal bladder of the *Corethra* has a relatively rigid wall, stiffened by the chitin lists usual to tracheae.

It is not completely rigid, however, but elastic; upon change of pressure it will yield to a certain extent, but again assumes its old size when the original pressure is restored. Chiefly on the basis of this elasticity of the tracheal bladder Frankenberg put forward the following hypothesis on its regulation mechanism. Upon excess pressure the tracheal bladder is diminished in size. Its wall, on account of its elasticity, tends to increase the volume of the bladder again. This gives rise to an under-pressure in the tracheal bladder, and air must be diffused into the tracheal bladder until the tension in the tracheal wall has disappeared and the bladder has been restored to its previous volume. In under-pressure on the larva the case is reversed: the bladder expands, but owing to its elasticity it tends to contract again, its air-content being thus subjected to a certain pressure. This has the effect of diffusing air out of the bladder, until the tension in the wall has disappeared, and the bladder is restored to its previous size.

As a regulation mechanism when the *Corethra* larvae have been exposed to increase of weight owing to absorption of nourishment, there will, according to Frankenberg (1915, p. 560 and 1928b, p. 237), occur an increase in the volume of the tracheal bladders due to imbibition.

We shall not here discuss the two hypotheses, but refer the reader to the aforementioned works by Damant, Frankenberg, Holst-Christensen, and to Jacob's report (1935). From a biological point of view there will, however, be occasion to offer the following remarks: The variations in pressure to which the *Corethra* larvae have been subjected in the experiments of Krogh and Frankenberg are rather small compared with the variations in pressure to which we now know the larvae are exposed during their vertical migrations in waters of the depth of Esrom Lake. As already mentioned, the larvae in this lake migrate from a pressure of about 3 atmospheres (20 m) to about 1 atmosphere and back again, whereas in the above-mentioned experiments the animals were at most subjected to a pressure of about 2 atmospheres and usually less. On this subject KROGH (1911, p. 187) writes: "My experiments have been carried out only to pressures of + 1 atmosphere corresponding to a depth of 10 m below the surface of the water, but *Corethra* larvae, possibly belonging to other species, have been found to live near the bottom in lakes of much greater depth." KROGH realised, then, that in Nature *Corethra* larvae could be exposed to much larger pressures (cp. WESENBERG-LUND, 1914, p. 13) than employed in the experiments, but he could not at that time know that in Nature the animals are exposed to the above-mentioned great variations in pressure owing to their vertical migrations. Now that this is known, the correct explanation of the hydrostatic mechanism of the *Corethra* larvae should therefore be able to explain how the larvae can adjust themselves to variations in pressure of such a size, and likewise how such variations in pressure from 3 atmospheres to 1 atmosphere can be tolerated in the course of a very short time. The latter explanation is required on account of the rapidity with which the vertical migrations take place in Nature. JUDAY (1921, p. 275) states that a vertical migration covering 23.5 m may take place in about an hour in Lake Mendota.

Even with the relatively low pressures employed in the afore-mentioned experiments, it has been seen several times that the larvae could not tolerate the change. KROGH, for instance, states (1911, p. 187) that in experiments with larvae taken near the surface in a pond, he has found that, when the pressure is raised to + 70 to 80 cm Hg, many animals fail to react in the normal way. They remain at the bottom, and, when the pressure is again reduced to the normal, they are still too heavy. A microscopical examination then discloses the fact that the air has disappeared from the sacs and they have become filled with a fluid; the animals die in a few days. It is possible that such injuries occur because the larvae have been exposed too suddenly to the changed pressure. Possibly they are due to the fact that in these cases pond forms were used for the experiments. At any rate, lake forms, according to observations in Nature can tolerate much greater variations in pressure, when these occur in not too short a period. For that very reason it is of considerable interest to note that lake forms, unlike pond forms, in experiments by Bardenfleth and Ege, have proved able to tolerate a pressure of about 4 atmospheres; after 2—$2^1/_2$ hours such larvae can attain equilibrium again. The explanation is that the tracheal bladders of the lake form are much more thick and therefore much more resistent to pressure than those of the pond form (Bardenfleth and Ege, 1916); the observations on the different thickness I can fully confirm.

A possibility of error in the study of the *Corethra* larvae from deep lakes may in my experience lie in the fact that a large and sudden change of temperature may have a destructive effect on the regulation of their equilibrium. Upon the sudden transference from lake water with a temperature of about 4° to room temperature in the aquarium it may happen that the animals lose their equilibrium and cannot — even in the course of several weeks — regain it. The disturbance shows itself in that they become too light and so gather at the surface; only by strenuous swimming motions can they penetrate a little way downward into the water after which they are again carried passively to the surface. FRANKENBERG (1915, p. 524 and 538, 1927a, p. 133) has also observed that *Corethra* larvae which for some reason or other have been injured, become too light. He supposes that this is due to an increase in the tracheal bladders owing to an imbibition of their walls. — That it is a sudden great change in the temperature which may injure *Corethra* larvae from deep lakes, and not a great change of pressure, appears from observations on larvae likewise transferred from the lake into the laboratory but placed there at a low temperature (5—10°). They all regained their equilibrium.

Experiments on the Phototaxis of the *Corethra* Larvae.

Since, according to the observations mentioned above, the reaction of the *Corethra* larvae to light in their diurnal migrations, seems to have an important bearing on their behaviour in Nature, the following experiments were made on such reactions. These experiments, however, will not be able to furnish the final explanation of the vertical distribution of the animals but can merely yield a contribution towards it. For, as will indeed appear from the above, factors other than the light, for instance the age of the larvae and specific differences, are concurrent causes of their reactions.

If *Corethra flavicans* larvae from Esrom Lake are kept in an aquarium, the bottom of which is covered by several centimetres of soft gyttja, it will be noticed that a number of the larvae have disappeared during the daytime; they have made their way into the mud. If the aquarium is shaken, not a few come darting out of the mud, and if the larvae are now observed for some time, a number of them will again be seen to bury themselves. This is done by quick wriggling movements. First the head is pushed down, and after beating once or twice with the swimming fan, which still projects, the rest of the animal disappears. Often they burrow in a couple of jerks, pausing a moment, with the head and the anterior part of the body buried in the mud, while the rest projects obliquely into the water (fig. 22). The pause, however, merely lasts for a few seconds. In other cases they burrow without pausing, and in a very few moments the larvae have disappeared in the mud. Hence, despite their special morphologic and anatomic plankton characters, these larvae, by their inclination to seek cover under certain circumstances, show in their behaviour a biological similarity to many other diptera larvae; perhaps the *Corethra* larvae must thus be supposed to have preserved an original feature of their biology. The voluntary burrowing of the *Corethra* larvae in the bottom

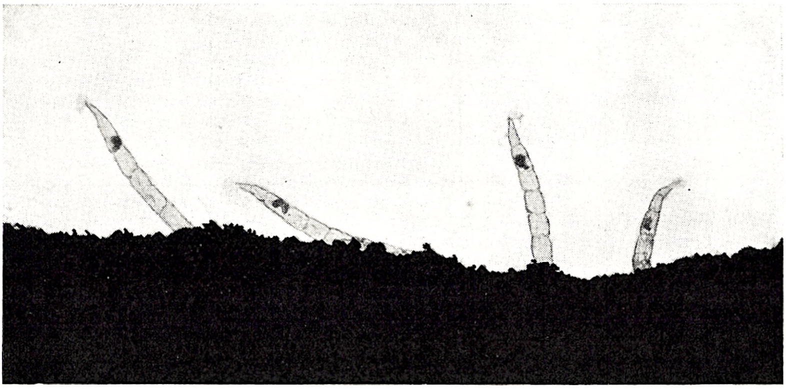

Fig. 22. *Corethra larvae* burrowing in the mud.

of aquaria was already noticed by Wesenberg-Lund (1914, p. 17).

Now and then it is stated that *Corethra* larvae "rest upon the bottom" or that "they lie upon the bottom ooze during the daytime" (Rawson, 1930, pp. 47 and 49). Observations such as the above show that they can bury themselves in the bottom ooze in the laboratory. Investigations with a stratification bottom sampler in Esrom Lake show that in Nature, too, they can bury themselves in the bottom; thus the idea that they lie on the bottom ooze is hardly correct.

The migration of *Corethra* larvae in aquaria, from the free water layers to the bottom and back again, has been utilised to study the bearing of the light on the migration under different conditions. Aquaria with a layer of gyttja at the bottom and a certain number of larvae have been set aside for several days, sometimes for some weeks, and the number of larvae in the water has been counted at various times of the day. The aquarium must be narrow so that the count can be made with sufficient certainty. The results from the days of the experiment have been summed up in a graph (e. g. fig. 23). In this the various hours of the day are plotted against the number of *Corethra* larvae observed moving freely in the water at these hours. The observations are marked by a cross. As a common expression of these a curve has been plotted which gives the average of the observations.

The curve has been constructed by means of smoothing according to the method of the successive media. By this method the mean is calculated of the 3 first observations a, b, c, in this way the first point of the smoothing curve is obtained. Then the mean of the three next observations b, c, d, is calculated and the next point of the smoothing curve is obtained, and so on. The points of the smoothing curves are given as small circles.

Experiment 1. 20/XI—1/XII 33. About 40 larvae of *Corethra flavicans* from Esrom Lake were placed in an aquarium with a mud bottom. The aquarium was put in a cellar at a temperature of about 12—14°. It was exposed to the fluctations of the daylight in the course of the 24 hours.

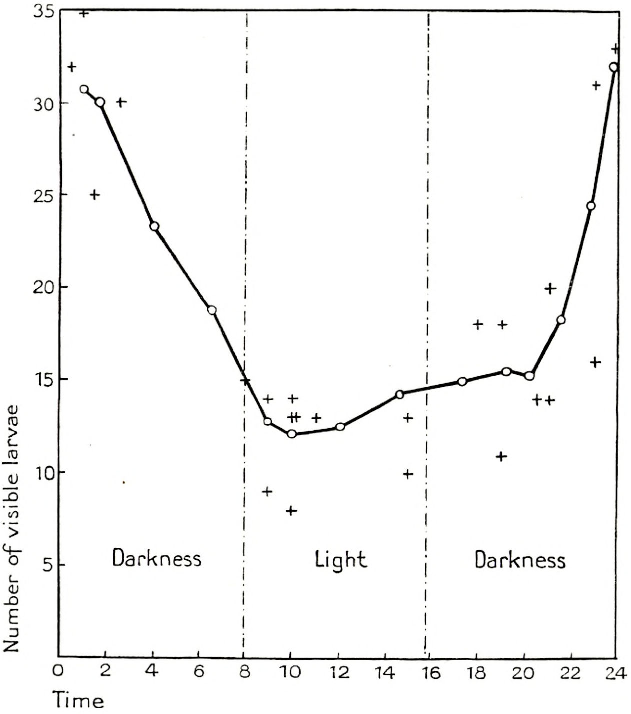

Fig. 23. Diurnal migration in an aquarium of *Corethra flavicans* from Esrom Lake. The aquarium has been exposed to the changes of the daylight in the course of the day.

The result of the experiment is shown in fig. 23, from which it appears (1) that there is at least always a small number of larvae in evidence, (2) that few larvae are out in the water in the daytime, (3) that the greatest number of larvae are to be observed about midnight (late night observations are, however, lacking), and (4) that there

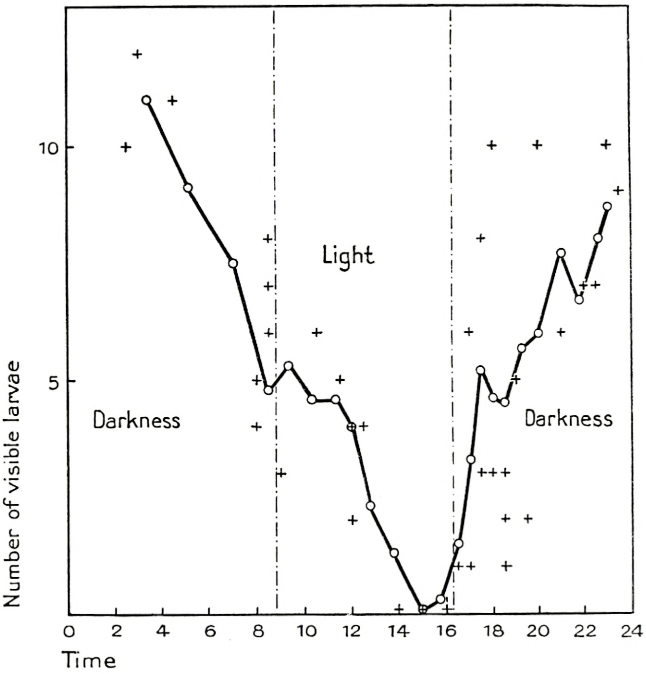

Fig. 24. Diurnal migration of *Corethra flavicans* in an aquarium. The larvae were taken at the surface of Esrom Lake.

consequently is a diurnal migration in the aquarium of *Corethra flavicans* larvae.

Experiment 2. 19/XII 33—10/I 34. In Experiment 1 the animals were not hydrostatically equilibrious, but had to prevent a slow rising by strokes of the swimming fan. Even after many days they were not equilibrious. Presumably the hydrostatic apparatus had been somewhat injured by the quick heating, when the animals were taken into the laboratory. At any rate, the diurnal migration might be supposed to be affected by the lack of hydrostatic equilibrium. The experiment was therefore repeated with *Corethra* larvae which had been brought to a hydrostatic equilibrium. After being caught at the surface of Esrom Lake in the night, they were not taken into the laboratory but placed in an aquarium out-of-doors, at a temperature of about 1—5° C. 12 larvae were lodged in the aquarium.

The result of the experiment will appear from fig. 24 which confirms the above-mentioned observations on the diurnal migrations; the latter are in this case even more conspicuous. Thus several times in the day no larvae at all were seen or only a single one was in evidence, while several times in the night nearly all the animals were observed in the water.

Experiment 3. 16/XII 33—10/I 34. After *Corethra* larvae exposed to the light of day and the darkness of night have been seen to perform diurnal migrations under these conditions, the question arises whether it is the daylight that regulates their diurnal migration. In order to obtain a reply to this question, the aquarium with the animals from Experiment 1, after this experiment was over, was covered with a black cloth, the animals being thus completely in the dark for 24 hours. Only when it was to be ascertained how many larvae were out in the water was the cloth removed, and a count taken as quickly as possible.

The result is seen in fig. 25. This shows (1) that at all times of the day and night some individuals were out in the water, but that the number varied a great deal. More than half of the individuals were never to be seen. (2) The varying number of visible individuals shows that an upward migration and a downward migration of the *Corethra* larvae constantly takes place in the dark. (3) But the quite irregular occurrence now of many, now of few individuals,

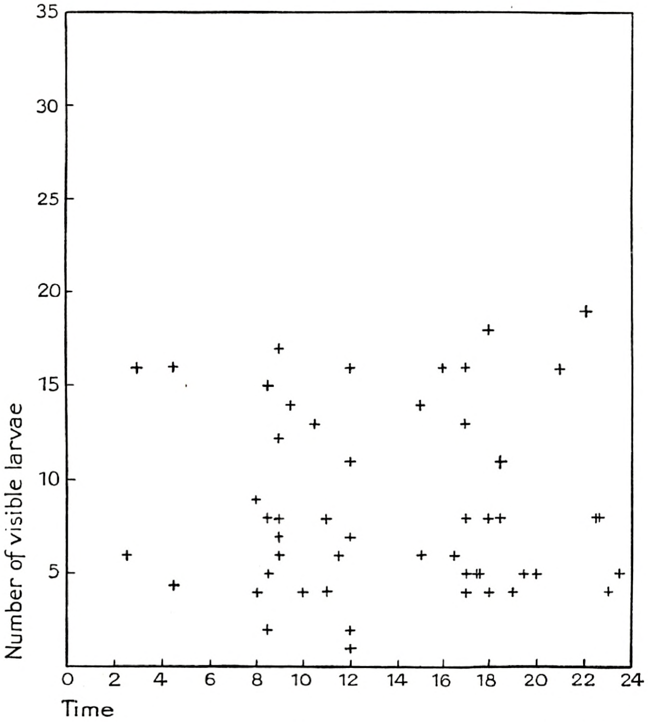

Fig. 25. The figure shows the number of larvae of *Corethra flavicans* swimming freely in the water layers of an aquarium at various times of the day. The aquarium has been covered with a black cloth. The number varies irregularly.

shows that no regular diurnal migration is observable in the dark.

It might perhaps have been expected at the outset that all the *Corethra* larvae, about 40 individuals, would have come out into the dark water when no light whatever prevented them; this they did not do. Or they might all have been expected to remain at the bottom. The fact that now many, now few, animals were in evidence in the water would seem to indicate that the *Corethra* larvae possess the tendency to migrate vertically to such a degree that they need no stimulus — changing light and darkness — for the tendency to manifest itself. But on the other hand the lack of regularity in the vertical migration in the dark with the regular migration during the change from daylight to darkness (figs. 23 and 24), shows that it is the light which is the regulating factor in the diurnal migrations of the larvae of *Corethra flavicans.*

Experiment 4. 26/I 34—13/II 34. A further demonstration of the causal significance of the light for the diurnal migrations of *Corethra* larvae from Esrom Lake was made in an experiment in which an aquarium with larvae was covered with a black cloth in the day and lighted by strong electric light at night. Thus the illumination of the animals was the opposite of what was natural. The darkness in which the larvae were left in the daytime was only interrupted for brief periods when the cloth was removed to make the count. Temperature 12—14° C.

The result of this experiment appears in fig. 26. This shows that the natural diurnal migration may be reversed, so that many larvae appear in the water in those hours of the day which have been artificially changed into "night", and conversely, few or none appear in the night which has been changed by illumination into an artificial "day". This further confirms that it is the light which determines the diurnal migration for these *Corethra* larvae.

Experiment 5. 28/XI—25/XII 33. Pond forms of *Corethra* are found in the daytime in the free water layers of the ponds. Such larvae might therefore be expected to show quite a different reaction to the influence of the light than the larvae of *C. flavicans* from Esrom Lake. In order to confirm this conjecture 35 *Corethra* larvae from Sorte Dam, Hillerød, were placed in an aquarium at a temperature of 12—14° C. and were observed as usual. The aquarium was exposed to the ordinary fluctations of the daylight.

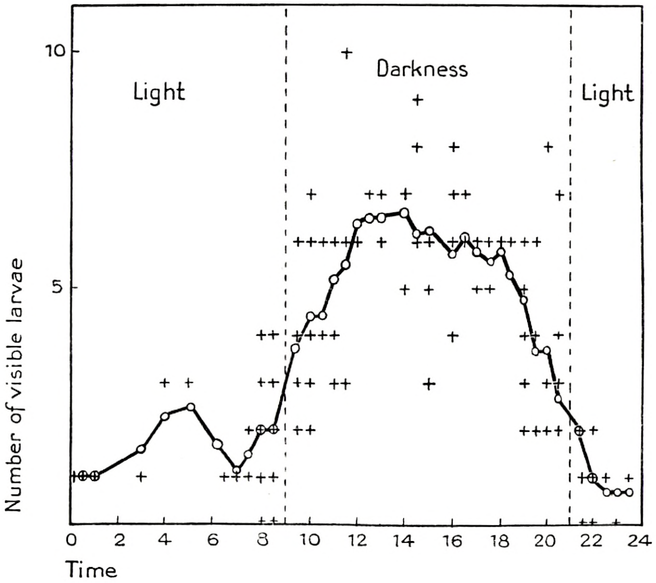

Fig. 26. Diurnal migration of *Corethra flavicans* in an aquarium placed in the dark in the daytime and in the light at night.

In Sorte Dam the larvae can always be taken in the water in the daytime with a net.

The result of the experiment is seen in fig. 27, which shows that the *Corethra* larvae from Sorte Dam performed no diurnal migrations whatever. They showed no reaction to the fluctuations in the intensity of the light. The fact that the full 35 larvae were not found in each count is due to the difficulty of carrying through the count with precision, and to the pupation of 1—2 larvae during the experiment.

At the time when this experiment was made, it was not possible to carry through a determination of the species of the larvae in the experiment. After the appearance of Peus' work (1934), the larvae could, as previously mentioned, be determined. It then turned out that Sorte Dam, as stated on p. 11, contained 2 species of *Corethra*, *C. crystallinus* and *C. flavicans.* The experiment was therefore repeated on the 15/IV—19/IV 35, in order to ascertain whether one — and which — or both species performed no diurnal migration. For the repeated experiment 22 larvae from

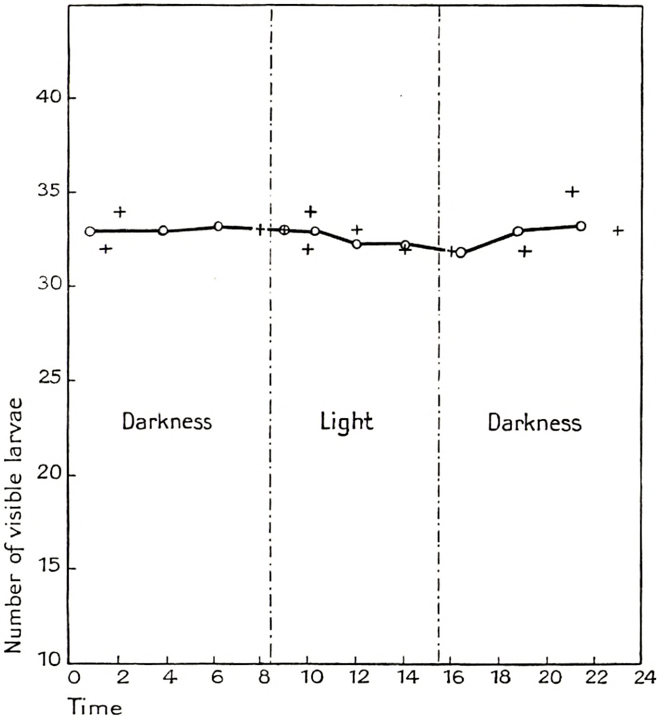

Fig. 27. The curve shows that there is no diurnal migration of larvae of *Corethra* from Sorte Dam. The aquarium has been exposed to the changes of the daylight in the course of the day.

Sorte Dam were used; the result was as shown above; they showed no reaction whatever to the change from day to night, but 20—22 individuals were always present in the water. Then the larvae were isolated, and on determining the species of the larvae, or of the pupae or imagines into which they had been metamorphosed, or of both, it was found that 17 of the larvae belonged to *flavicans* and 5 to *crystallinus*.

This result is rather remarkable and may suggest certain considerations. Thus about $^3/_4$ of the larvae in Sorte Dam were *flavicans* larvae, that is to say, they belonged to the same species which inhabits Esrom Lake. But the larvae from Sorte Dam were unaffected by the light and showed no diurnal migration in experiments, whereas the larvae from Esrom Lake were negatively phototactic and performed diurnal migrations in experiments and in Nature. The same species, *C. flavicans*, thus reacts in one way from one locality, and in another way from another. In other words, we have here come across a biologic (ecologic) variation. This phenomenon, interesting in itself, might well prompt further investigations of such problems as what is the cause of such a biological variation. Is it due to the environment which is so different in the two localities, and are the two populations of *C. flavicans* in Esrom Lake and Sorte Dam thus only phenotypically different? Or is the biological difference hereditary, and is the species divided into subspecies differing biologically? In this connection it will be worth while to recall the morphological variation of the species which was mentioned on p. 11. And is the different phototaxis of any biological importance for the 2 populations? — Such questions, which require a special investigation, it has not hitherto been possible to answer.

The experiments at hand have merely been of a preliminary character. But the questions show how little known a comparatively familiar animal such as the *Corethra* larva is in respect of causal ecological conditions.

It was found by Valle (1930, p. 488) that larvae of *Corethra* "haben sich nicht auffallend lichtscheu gezeigt" (cp. Lundbeck, 1926, p. 183, Lang, 1931, p. 49). Experiment 5 shows that such a view may be right in some cases, but the other experiments prove that it has not a general validity.

Experiment 6. 17/III—8/IV 35. By means of further experiments with *C. flavicans* larvae from Esrom Lake some more knowledge of their phototaxis was gained. When the diurnal migration of the larvae in the lake was mentioned, it was pointed out that at night only a fraction of the larvae at a time had been found to migrate upwards into the water layers; more thorough investigations by Juday (1921, p. 276) showed the same thing. Hence there might possibly be a lack of uniformity within the population, certain individuals showing a greater tendency to migrate than others. A comparison of the migrations mentioned in fig. 23, of the larvae which were caught in the bottom of the lake, with those shown in fig. 24, whose corresponding larvae had been caught at the surface of the lake, would also seem to show that the tendency to migrate is strongest in the latter. In order to try whether there was really such a difference in the susceptibility of the larvae to the influence of the light, 2 simultaneous experiments were made in the usual way, the larvae being exposed to the natural change of light from day to night. The two aquaria were treated the same in every respect, but in the one there were placed 20 larvae taken in the bottom of Esrom Lake, and in the other 20 larvae taken in the night at the surface of the lake.

The result of the experiments was that the larvae in the two aquaria showed the usual diurnal migration with quite the same degree of intensity; hence benthic and pelagic larvae must be assumed to have the same susceptibility to the influence of light. The fact that only a fraction of the larvae in Nature at a certain time take part in the great vertical migration cannot then be caused by dissimilar biological characters in the larvae, but must be due to some other cause.

Experiment 7. 27/IV—7/V 35. In experiment 1—6 the *Corethra* larvae had not as a rule been fed in the experimental period, but only afterwards. It had then occasionally been observed that the reaction of the larvae to the influence of light seemed to have changed after the consumption of food. In order to verify this conjecture an experiment was made in which the vertical migration of some larvae which had been fed very plentifully was compared with that of larvae which were not fed during the experiment. The larvae — *C. flavicans* from Esrom Lake — which were to be fed were placed in 2 aquaria, 25 in each. To the larvae in aquarium I plenty of *Crustacea* plankton was fed, consisting chiefly of *Cyclops*; those in aquarium II were fed plenty of *Diaptomus castor*. Finally 25 larvae were placed as controls in aquarium III and were not fed at all. The aquaria were alike; at the bottom they had a layer of gyttja several contimetres deep, and they stood beside each other in a window exposed to the changes of light during the day and the night.

The result of the experiment will appear from fig. 28 which shows the migration in aquarium I, and fig. 29 which shows the migration in aquarium II. In both figures the migration of the controls in aquarium III is given for comparison. From fig. 28 it appears that there are constantly about 20 larvae in the water, even in the daytime. From fig. 29 it will be seen that there are 14—18 animals in the water in the daytime and a few more at night. The controls show the usual thing: there are no animals or hardly any in evidence in the daytime, but a large number have migrated upwards in the night. In other words, the experiment shows that the catching of abundant prey may greatly affect the diurnal migration of *Corethra* larvae, either entirely stopping it (aquarium I) or much reducing it (aquarium II). And the change is evidenced by the fact

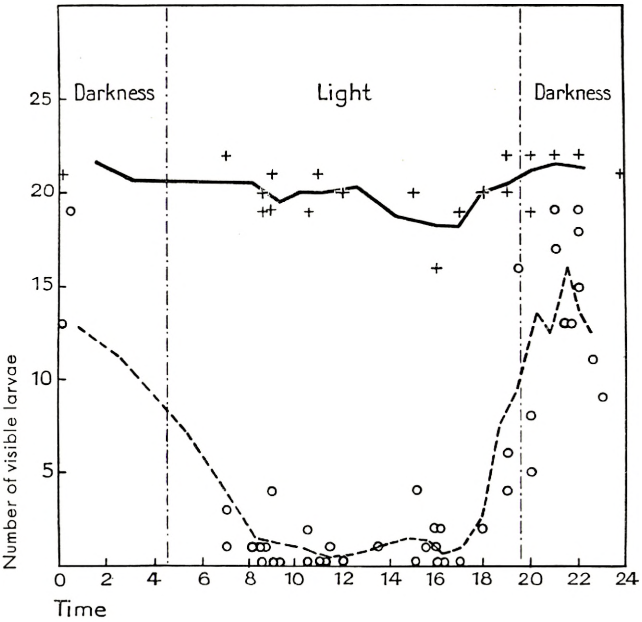

Fig. 28. The continuous curve shows the absence of a diurnal migration among larvae of *Corethra flavicans* fed on plankton (*Cyclops*). The dotted curve shows the diurnal migration of control animals not fed. The aquaria were exposed to the changes in the daylight in the course of the day.

that the larvae which have taken plenty of food are not so negatively phototactic that they bury themselves in the mud in the daytime.

Thus, according to this experiment, the importance of the amount of food consumed for the phototactic reaction of the *Corethra* larvae would seem to be very considerable. This is not without interest. It opens up a possibility of another explanation of the seasonal variation in the diurnal migrations of the *Corethra* larvae than that so far offered. As mentioned on p. 59, it has been shown that the *Corethra* larvae in Frederiksborg Castle Lake in midsummer occupy

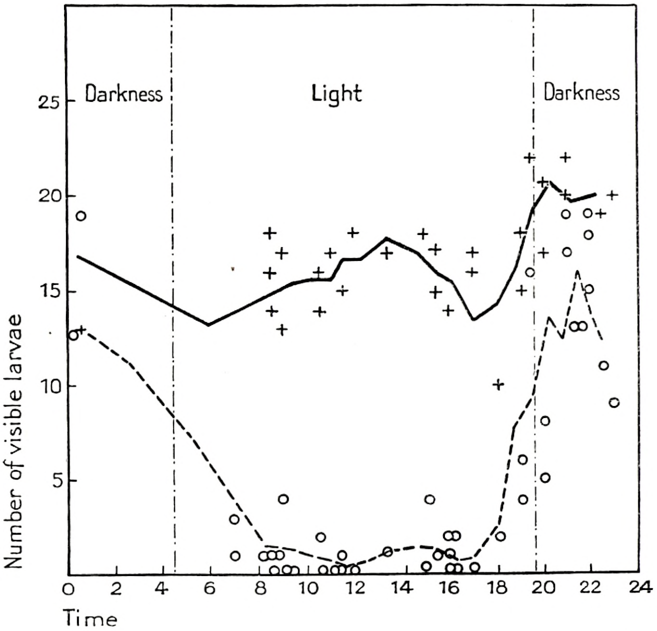

Fig. 29. The continuous curve shows the approximate absence of a diurnal migration among larvae of *Corethra flavicans* fed with *Diaptomus sp.* The dotted curve shows the diurnal migration of controls not fed. The aquaria have been exposed to the changes in the daylight in the course of the day.

the water layer immediately above the bottom in the daytime, whereas in spring and autumn they are found in large numbers in the bottom itself. Various potential causes of such a change in the vertical distribution of the larvae have previously been pointed out. To these must now be added the possibility that the reaction of the larvae to light may change under different conditions of nutrition. In the summer their negative phototaxis may, then, possibly be reduced, on account of their larger consumption of food, and consequently they remain in the daytime in the water layer near the bottom, not penetrating into it. It is clear that this explanation of the cause does not exclude the possibility of those previously given, but may quite well supplement them.

This experiment on the bearing of the amount of nourishment on the vertical migration was confirmed by several others.

Experiment 8. 18/VII—23/VII 35. Besides the amount of nourishment there seem to be other factors which affect the vertical migrations of the larvae. This applies, for instance, to the age and size of the larvae. If young, newly hatched larvae are kept in an aquarium in the usual manner, in order to find out whether they perform vertical migrations, it turns out that their reaction is quite different from that of the adult larvae. Fig. 30 shows the result of such an experiment with 25 newly hatched larvae of *C. flavicans* from Esrom Lake. At the beginning of the experiment the larvae had only a size of about 1.7 mm. The figure shows that the young larvae, unlike the majority of the adults, are in the water even in the day; no diurnal migration at all was ascertained for these young larvae in this experiment. (The fact that the full 25 larvae were not found in each observation may be due to an error of observation; it is very difficult to count the tiny hyaline larvae without overlooking some.)

Thus the reaction of the newly hatched larvae is similar to that shown by larvae which have consumed a plentiful supply of food (cp. fig. 30 with figs. 28 and 29). It is therefore not without interest to recall in this connection that the young larvae, when they leave the egg, may still have inside them some drops which are the remains of the yolk mass of the egg (see p. 44). Thus it is possible that the reason why the young larvae react like the old ones which

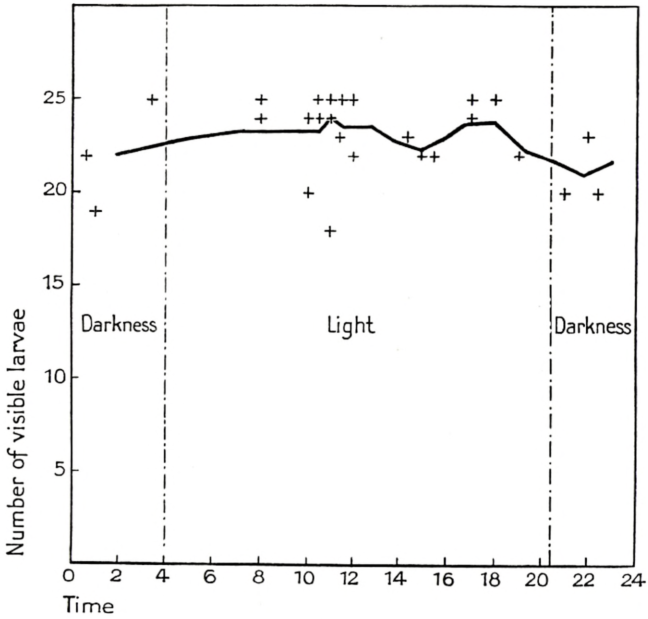

Fig. 30. The curve shows that there is no diurnal migration of newly hatched larvae of *Corethra flavicans* from Esrom Lake. The experiment was made in July. The aquarium has been exposed to the changes in the daylight in the course of the day.

have consumed a plentiful supply of nourishment is that they have a reserve stock of food, brought from the egg; the remain of the yolk mass disappears later on.

Experiment 9. 23/VII—27/VII 33. If young larvae are kept in vessels, a number of them will migrate towards the light in the vessels; this applies especially to newly hatched larvae. If half of a long aquarium, e. g. the left part, is covered with a dark cloth, and newly hatched *Corethra* larvae placed in it, the larvae will nearly all collect in the uncovered, right part of the aquarium illuminated by the daylight. Hence they are positively phototactic. The dark part of the aquarium is nearly empty, only some few of the small larvae are seen there.

At night, when the uncovered right part of such an aquarium is also in the dark, the larvae disperse evenly over the covered and uncovered parts. Thus there is a certain migration in the aquarium in the course of the 24 hours, owing to the influence of the light on the larvae. The diurnal migration in this experiment is, however, horizontal, unlike the diurnal migration of the adult larvae in Nature. And the newly hatched larvae in the experiment seek the daylight. The larvae in this experiment, like the others in experiment 8, were only about 1.7 mm.

Positive phototaxis in young larvae has previously been mentioned by Frankenberg (1915, p. 547), who, however, only observed a strong positively phototactic reaction in larvae which had not yet filled their tracheal bladders with air; larvae with the tracheae filled with air no longer showed a phototactic reaction in his experiments. Frankenberg calls these phototactic conditions strange and says that perhaps the phototaxis is intended to carry the larvae to higher water levels richer in oxygen. Since Franken-

BERG's *Corethra* larvae were derived from a small pool, it is very likely that they have soon lost their phototaxis. As we know, pond forms have no phototaxis (Experiment 5, p. 75). But the young larvae from Esrom Lake at any rate retain their positive phototaxis for some time — probably for several days — and its biological significance is no doubt another than that pointed out by FRANKENBERG, viz. that of keeping the larvae in the upper water layers, so that they may spread from the hatching zone by the shore and be carried into the deep water in midlake by the circulating currents.

For comparison with the reactions of the young larvae some adult larvae and some pupae (from Frederiksborg Castle Lake) were placed under observation in a similar aquarium half covered by a dark cloth. The result for the full-grown larvae was exactly the opposite of that for the young larvae. In the daytime the adult larvae all or nearly all migrated to the covered, dark part of the aquarium; hence they were negatively phototactic. In the night, when it was equally dark throughout the aquarium, they dispersed evenly over the whole of it. Hence there arose, in this case too, a horizontal diurnal migration, but the difference manifests itself in the fact that the adult larvae seek out the dark half of the aquarium, whereas the young larvae migrate to the illuminated part. The experiment was confirmed by repetition.

Experiments with pupae gave the same results as with full-grown larvae. The negative phototaxis of the pupae was, if possible, even more pronounced. In the daytime they went to the darkest corners of the covered half of the aquarium.

Has the Phototaxis of the *Corethra* Larvae any Bearing on their Diurnal Migrations in Nature?

On reviewing the above-mentioned experiments it appears that *Corethra* larvae which are not newly hatched have a very conspicuous negative phototaxis. It likewise appears that owing to this character diurnal migrations may occur in aquaria which bear a great resemblance to the migrations observed in Nature. It therefore seems natural to assume that it is a negative phototaxis which causes the diurnal migrations in Nature, even though certain factors (nourishment, age) may modify it or cause it to cease.

C. Juday (1921, p. 278) has, in fact, considered this idea after observing that larvae of *C. punctipennis* give a prompt negative reaction to light. But he rejects it, thinking it hardly probable that the extensive depth migration of the larvae in Lake Mendota, even including a descent into the mud, is a simple light phenomenon. The rejection of this potential explanation is motived by Juday by the following observations and conclusions.

The transparency of the water in Lake Mendota is usually low in summer; a white disc 10 centimetres in diameter generally disappears from view at a depth of two metres to about four metres at this season of the year, which indicates that the light is cut off rather rapidly by the upper strata of water. A pyrlimnimeter has been used to determine the rate at which the sun's energy is cut off by the upper strata of the lake. The results obtained with this instrument indicate that the intensity of the illumination at a depth of 23 metres on a clear day, between 11:00 a. m. and 1:00 p. m., is about equal to that produced by full moonlight at the surface of the lake. During the early forenoon and late afternoon, as well as on cloudy days, the illumination is much smaller than this. For some time before sunset, the bottom stratum must be substantially in total darkness, yet the observations show that the emergence of the larvae from the mud is very closely correlated in time with the setting of the sun.

One more objection is added by JUDAY who remarks that not only does the illumination in the bottom water become very small in the late afternoon, but there is a further protection from light afforded by the bottom ooze, in which the larvae remain concealed during the day. To what depth the larvae penetrate the loose mud is not known, but in the laboratory they readily burrow down to a depth of a centimetre or more. The dim light which reaches the bottom in the deeper portions of the lake can penetrate the ooze only to a very slight extent at most, even during the brightest part of the day, and this raises the very interesting question as to what stimulus causes the larvae and pupae to emerge from the mud so promptly and regularly about the time of sunset. No definite data bearing on this point have yet been obtained.

As to this last objection by JUDAY to the possible significance of the light for the diurnal migration it must be remarked that it is based on the quite correct fact that the *Corethra* larvae may be concealed in the mud in the daytime. JUDAY, when writting the above, was unable to know to what depths the larvae descend into the mud of the lake; but now it is shown by means of a stratification bottom sampler that they probably penetrate several centimetres into the bottom of Esrom Lake. Variations in the dim light which reaches the bottom can therefore hardly be felt by the larvae when they are buried in the mud. Hence I too think it improbable that the decreasing light should be the stimulus which makes the larvae emerge from the mud. This view receives further support from the result of Experiment 3 (p. 72); for this experiment showed that in complete darkness there were now many, now few *Corethra* larvae in the water. Hence the *Corethra* larvae possess the tendency to ascend to such a degree that it even manifests itself under these conditions, and thus it is not the varying intensity of the light that makes them come out. It must be another, unknown, stimulus which makes now a few, now many larvae emerge from the mud.

But this does not mean, of course, that the presence or absence of light cannot be a regulating factor in the migrations of the larvae which for some unknown reason have emerged from the mud in greater or less numbers. On the contrary, the above-mentioned experiments seem to me to show so plainly the regulating effect of variations in light on the diurnal migration of *Corethra* larvae in aquaria that it must be considered highly probable that something similar is the case in Nature.

However, I do not on that account deny the value of Juday's first-mentioned objection that the absorption of light in lake water is so high that the illumination near the bottom is extremely small, especially during the early forenoon and the late afternoon, and that it is therefore difficult to imagine that so slight an amount of light can make its influence felt. The facts to which Juday refers are no doubt quite correct. But it must be noted that so far nothing is known about the size of the threshold value which the light must have in order to cause a reaction in *Corethra* larvae. It is possible that this threshold value is also very low, and that the animals react vigorously to its influence. There are problems here, that call for treatment, and the solution of them might supplement the abovementioned preliminary experiments on the phototaxis of the larvae. As long as we do not know the size of the threshold value for light-intensity which may affect *Corethra* larvae, and so cannot compare this threshold value with the small light-intensity found in the water layers near the bottom of the lake, so long we cannot either reject the possibility that it may be the variations of the light which are the regulating and determining factor in the diurnal migrations of the *Corethra* larvae. And, as previously mentioned, such a possibility receives strong support from the experiments on the phototaxis of the *Corethra* larvae. —

Nourishment of the Larvae.

It is a well-known fact that *Corethra* larvae are voracious beasts of prey which especially catch and swallow small Crustaceans. Their voracity has often been mentioned by earlier authors (LEYDIG, 1851, p. 449; RYMER JONES, 1867, p. 100; WEISMANN, 1866, p. 7; POUCHET, 1872, p. 224, and MEINERT 1886, p. 409 etc.) and has subsequently been frequently confirmed. The *Corethra* larvae in Esrom Lake being benthic in the daytime and partly limnetic at night, it would seem probable at the outset that they can only during the latter time secure food amongst the plankton Crustaceans. In order to ascertain whether the *Corethra* larvae took nourishment within some limited part of the 24 hours only, the alimentary canal of the animals was examined at various hours, both in animals taken in the daytime in the bottom, and in such as had been caught in the night in the free water layers. The larvae were partly examined while alive shortly after being caught, and partly in the conserved state. Whether they were caught at one time or another, however, the numerous samples showed that in a great many of them the alimentary tract was empty, and the rest, whose intestine contained a yellowish liquid, could be taken both benthically and limnetically, and at any time within the 24 hours. Thus no definite time for the consumption of food could be established.

When a *Corethra* larva has not taken any food for some time, its empty alimentay canal is very hyaline, and the cells of its wall clear. After the consumption of food the alimentary canal is filled with a yellowish or reddish fluid (cp. Meinert, 1886, p. 409), and the walls of the intestine shortly afterwards become opaque with the nourishment absorbed.

The consumption of the food is not difficult to observe in aquaria. If some *Corethra* larvae have starved for some days, and some zoo-plankton is then put into the aquarium, larvae may shortly afterwards be seen with Daphnids or *Copepoda* in the mouth parts; some of the prey projects freely from the mouth. After a little while a great number of larvae have the anterior part of the alimentary canal (the pharynx) from the mouth to a point on a level with the anterior pair of tracheal bladders filled with prey (fig. 31). The prey as a whole passes no further. At the point on a level with the tracheal bladders there is a closing mechanism which only allows liquid nourishment to pass into the intestine. Chitinous parts are retained in the anterior part. The figure shows a larva which has swallowed two *Copepoda*. The first one has passed as far down the intestine as is possible, it is already partly dissolved. The last one has not yet passed wholly into the mouth.

That the chitinous parts do not pass right down into the intestine appears not only from the fact that the latter always only contains the yellowish liquid nourishment, but it can also be shown by isolating in small vessels *Corethra* larvae which have just swallowed some *Copepoda*. Some time after the isolation of such larvae, the chitinous skeleton of the *Copepoda* may then be found at the bottom of the vessels. After the contents of the *Copepoda* in the liquid state have passed down into the intestine of the larva, the rest, the chitinous skeleton, is brought up.

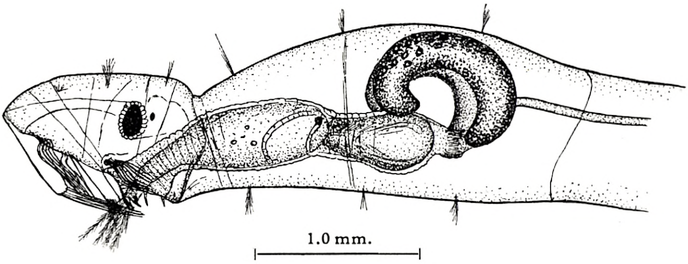

Fig. 31. *Corethra* larva which has swallowed 2 *Cyclops* for one of which there is not quite room enough in the anterior intestine.

Since the researches of Leydig (1851, p. 443) it is known that the anterior part of the intestinal canal, the pharynx, is important in a physiological respect, a partial digestion of the food taking place there. In the procedure of vomiting the pharynx may be everted, and hang out of the mouth like a long tongue (Weismann, 1866, p. 9); later it can be drawn in again. If *Corethra* larvae are exposed to pressure the pharynx is also everted. The same thing may happen if larvae are conserved in a very strong formalin. Frankenberg (1927 a, p. 127) states that it may happen that the animal is not able to draw in the pharynx again, so that it continues to hang out of the mouth. This seems especially to happen when the eversion has taken place with such violence that the thin oesophagus, the link between the pharynx and the intestine proper, is torn to pieces. But otherwise the drawing in of the pharynx occurs by the *Corethra* larva "eating" its own pharynx; for the larva conveys the pharynx into its body by exactly the same movements of the mouth parts which it uses when prey is swallowed. The normal vomiting of the chitinous remains through the pharynx takes place according to Leydig by a partial or even a complete eversion of the pharynx. According to Frankenberg (1927 b, p. 76; 1928 a, p. 58) the pharynx retains its normal position and the vomiting is due to peristaltic movements.

In addition to Daphnids and small *Copepoda* the *Corethra* larvae are also able to catch *Diaptomus*, as has previously been mentioned under Experiment 7 (p. 79). Of still larger animals I have on one occasion seen a larva catch a *Leptodora kindtii*. Meinert (1886, p. 409) gives some examples of how *Corethra* may catch rather large prey. He has, for instance, seen them swallow various larvae of *Diptera*, such as a *Dixa* larva which was nearly half the size of the *Corethra*; the *Dixa* filled the whole anterior part of the *Corethra's* alimentary canal, and partially hung out of the mouth. He has also seen a *Corethra* larva swallow another adult larva, the head of the latter being in the anterior part of the former's intestine, and in this part there were besides a *Cypris* and parts of another *Corethra* larva. — Meinert thinks that large Daphnids such as *D. pulex* and Cyprids constitute the chief food of *Corethra*. This is probably correct for *Corethra* larvae living in ponds. For larvae inhabiting such large lakes as Esrom Lake the *Copepoda* of the plankton probably form the greater part of their food (cp. LUNDBECK, 1926, p. 184; LANG, 1931, p. 50).

Summary.

It is shown that the *Corethra* species in Esrom Lake is *C. flavicans*. The same species has been found in Frederiksborg Castle Lake and Sorte Dam near Hillerød; in the latter locality *C. crystallinus* has also been found. A study of the chief characters (figs. 1—11) showed a certain morphological variation in the larvae and pupae.

The Danish localities of *C. flavicans* and the German localities (shallow inundation pools) found by PEUS (1934) together show that the species has a much larger range of biological variation than could formerly be known from the German findings alone. The larvae show a widely differing periodicity corresponding to the nature of the localities.

The benthic distribution of the *Corethra* larvae in Esrom Lake is characterised by a numerous occurrence at 20 m (about 1290 individuals per sq. m) and a rapid reduction in numbers towards land (fig. 19, p. 48).

At Esrom Lake the swarming period is in July and the beginning of August. The eggs (figs. 16—18, pp. 40—44) are deposited near the shore, especially in shallow water, where *Potamogeton pectinatus* and masses of filiform algae touch the surface. A recurrence of the *Corethra* larvae, in which they are first found freely in the water near the shore, then scattered over the lake and pelagically, but not in the bottom and not near the shore, and finally in the bottom ooze, is characteristic of the species in Esrom Lake.

The relation between the benthic and the limnetic behaviour of the *Corethra flavicans* larvae in Esrom Lake, may be described thus: The larvae do not occupy the free water layers at all in the daytime (apart from the pelagic occurrence of the youngest stages in August-September). The larvae hardly stand directly above the bottom in the daytime, but by far the greater part, at any rate, are found in the bottom.

Near sunset and near sunrise only few *Corethra* larvae were found in the free water layers, and none near the surface. At certain hours well on in the night the larvae were found in all the water layers of the lake from the surface to close to the bottom. Near midnight the larvae were found in the upper water layers, but not in the water layers near the bottom (fig. 20, p. 55).

The numerous occurrence in the upper free water layers about midnight was also demonstrated, when practically all the population had been changed into pupae.

A migration of *C. flavicans* to the upper water layers in the night has also been demonstrated in Frederiksborg Castle Lake, for larvae as well as pupae (fig. 21, pag. 57). In most months the larvae of *C. flavicans* cannot be taken in the free water layers of this lake in the daytime, but in the bottom. In midsummer, however, they are found in the daytime in the water just above the bottom.

Experiments on the phototaxis of the *Corethra* larvae yielded amongst other things the following results: There is a diurnal migration of *C. flavicans* larvae from Esrom Lake in an aquarium exposed to the fluctuations of the daylight; few larvae are out in the water in the daytime, the greatest number of larvae are to be be observed about midnight (figs. 23, 24, pp. 70—71).

In an aquarium left entirely in the dark it turned out that an uppward migration and a downward migration of the *Corethra* larvae constantly took place, but no regular diurnal migration is observable (fig. 25, p. 73).

An aquarium was covered with a black cloth in the day and lighted by strong electric light at night. Many *Corethra* larvae appeared in the water in those hours of the day which had been artificially changed into "night" and conversely, few or none appeared in the night which had been changed into an artificial day (fig. 26. p. 75). Thus the natural diurnal migration may be reversed.

The conclusion drawn from these experiments is that it is the light which determines the diurnal migration of these *Corethra* larvae; they are negatively phototactic.

In experiments pond forms of *Corethra* from Sorte Dam (*C. flavicans* and *C. crystallinus*) performed no diurnal migration whatever (fig. 27, p. 76). The same species, *C. flavicans*, thus reacts in one way from one locality (Esrom Lake) and in another way from another locality (Sorte Dam).

The fact that only a fraction of the *C. flavicans* larvae in Esrom Lake at a certain time take part in the vertical migration, cannot be caused by dissimilar biological characters in the larvae; in experiment benthic and pelagic larvae showed diurnal migration with quite the same degree of intensity.

The reaction of the *C. flavicans* larvae from Esrom Lake to the influence of light is changed after the consumption of food. The catching of abundant prey may greatly affect the diurnal migration, either entirely stopping it (fig. 28, p. 80) or much reducing it (fig. 29, p. 81).

The age or size of the *C. flavicans* larvae affects the reaction to the influence of light. Young larvae (size about 1.7 mm) showed no diurnal migration at all in the usual experiment (fig. 30, p. 83). They are positively phototactic.

On reviewing the above-mentioned experiments and the observations in Nature it seems natural to assume that the negative phototaxis is a contributory cause of the diurnal migration in Nature of the *Corethra* larvae; certain factors (nourishment, age) may modify it or cause it to cease.

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