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CONTRIBUTIONS TO
THE BIOLOGY OF SOME DANISH FREE
LIVING FRESHWATER COPEPODS

BY

ULRIK RØEN



København 1957

i kommission hos Ejnar Munksgaard

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Synopsis.

The paper gives an outline of the biology of a number of copepods living in small lakes, ponds, and drying up pools. It contains information about the distribution of the species, the reproductive periods, the variation of the number of eggs, the number of generations during the year and the vertical distribution of the animals in the water layers. The following species have been studied: *Hetercope saliens*, *Diaptomus castor*, *Eudiaptomus vulgaris*, *Macrocyclus albidus*, *M. fuscus*, *Eucyclops serrulatus*, *E. speratus*, *Cyclops insignis*, *C. strenuus strenuus*, *C. viridis*, *C. gigas*, *C. bicuspidatus*, *C. bisetosus*, *Canthocamptus staphylinus* and *Moraria brevipes*.

Finally the author has dealt with the appearance of the species in various types of localities in relation to physico-chemical factors; and information is given about the biology of the species during unfavourable seasons and about the seasons in which reproductive periods occur.

I. Introduction.

Since the appearance of C. WESENBERG-LUND's famous work of 1904-08 on the plankton of Danish lakes, the biology of the principal Danish plankton copepods is fairly well-known, but little or no information is available concerning the species which live in small lakes, ponds, temporary pools and running water.

Most of the present work is based on collections made in 1950 and 1951; supplementary collections and counts were made in 1952 and 1953. While the work was in progress I was attached to the Freshwater Biological Laboratory of the University of Copenhagen at Hillerød. Apparatus and chemicals for chemical and physical measurements and analyses were placed at my disposal by that laboratory, and during the work I often stayed at its field laboratories, at Silkeborg in central Jutland and at the Suserup laboratory in central Sealand. For this help, without which I should not have been able to carry through the work, and for much valuable advice, my warmest thanks are due to the Director of the Laboratory, Professor KAJ BERG, Ph.D.

I beg to acknowledge with gratitude the valuable assistance given by Mr. ANKER NIELSEN, Ph.D., of the Zoological Museum, Copenhagen, at the beginning of the investigations, and I likewise thank Mr. GUNNAR NYGAARD, M.Sc., for permission to use the apparatus for plankton counts constructed by him. Mr. E.W. KAISER, M.Sc., has helped me greatly by showing me several suitable localities in central Jutland. Dr. KARL LANG, Naturhistoriska Riksmuseum, Stockholm, has identified the harpacticid *Moraria brevipes*, and Dr. KNUT LINDBERG, has indentified two *Cyclops* species for me. I further wish to express my thanks to Mr. KAJ HANSEN, Ph. D., and to Mr. K. GEMZØE for permission to use photos of Mørksø and Vildande Pond respectively. The Strødam Committee allowed me to work in the reserved area at Strødam.

I received valuable support from the Japetus Steenstrup Bequest, the Emil Herborg Bequest, the University of Copenhagen, and the Strødam Committee towards the cost of the necessary collecting journeys. To all these my warmest thanks are due.

I am indebted to the Rask-Ørsted Foundation for a grant which has enabled me to have the manuscript translated into English by Mrs. HANNE THORN and to Miss A. FAUSBØLL, M.A., and Dr. H. B. N. HYNES, Liverpool, who have revised the manuscript.

II. Review of the Danish Literature.

Danish literature on freshwater copepods is not extensive, and information about these animals is mostly to be found in papers dealing with several groups of animals. This is strange since the first systematic work on copepods is that of the Dane, O. F. MÜLLER. The first Dane who described and depicted a copepod was, however, the physician Dr. JOH. CHR. LANGE, who in his paper "Læren om de naturlige vande" (Science of natural waters) (1756) mentions some freshwater fleas found in the ordinary drinking water of Copenhagen. It is quite amazing how much LANGE was able to observe in these animals. Not only does he describe the intestine and the oviducts "in which a yellow fluid moves incessantly", but he also observed "the red and blue canal through which the eggs emerge". Furthermore his copper plates show not only the four pairs of legs but also the rudimentary fifth pair. From the description it is possible in Fig. 3 to recognize *Macrocyclops fuscus*, this being the only Danish freshwater copepod whose receptaculum seminis is coloured, while the other figures, (2 and 4), must represent a species of the *Cyclops strenuus*-group, on account of the thickened hind edges of the last thoracic somite of cephalothorax. LANGE thought that he had also found the male, but as far as can be seen from the figures his specimens seem all to have been females. LANGE also thought that he had seen "young ones emerge from the eggs", but the figures show that it was not nauplii which he observed, but more probably some species of Rotifera.

While LANGE thus contributed the first Danish figure of a *Cyclops* it was O. F. MÜLLER who really initiated the study of these animals. His first communication about them appeared in "Favna Insectorum Fridrichsdalina" (1764, p. 95) where *Monocvlvs quadricornis* is mentioned as belonging to the Danish fauna. The next communication is in "Efterretninger om ubekjendte Een-Øyer i vore ferske Vande" (Information on unknown one-eyed animals in our fresh waters) (1769). There he mentions 5 species as belonging to our fauna, assigning all of them to the genus *Cyclops*, a name used here for the first time. The next time MÜLLER refers to freshwater copepods is in "Zoologiae Danicae Prodrumus" (1776). In this 8 species of the genus *Cyclops* are mentioned, besides the genera "*Nauplius*" and "*Amyone*". Of these, however, three of the *Cyclops* species are marine and the rest correspond to the species mentioned in "Efterretninger".

In 1785, the year after MÜLLER's death, his main work on Entomostraca was published, viz.: "*Entomostraca seu insecta testacea quae in aquis Daniae et Norvegiae reperit, descripsit et inonibus illustravit.*" In this 13 *Cyclops* species, 2 *Nauplius* species, and 6 *Amyone* species are enumerated. Of these 2 *Amyone* and 6 *Cyclops* species are marine. It is impossible to correlate MÜLLER's species with those now known. *Nauplius bracteatus* is probably a juvenile stage of a water-mite, while *N. saltatorius* is the metanauplius of a *Cyclops*. All the *Amyone* species, with perhaps the exception of *A. fauna*, seem to belong to groups other than copepods. *Cyclops minutus* is undoubtedly

a *Canthocamptus* species, probably *C. staphylinus*, as this is by far our most common species. *Cyclops caeruleus*, *C. rubens*, and *C. lacinulatus* are quite obviously *Diaptomus* species, perhaps three different ones, but which cannot be decided. *Cyclops claviger* is most probably the metanauplius of a *Diaptomus* species. *Cyclops quadricornis* seems to comprise various species, all belonging to the cyclopids, as far as can be seen from Tab. XVIII. Thus Fig. 2 is probably *Macrocylops fuscus* or *albidus*, Fig. 9 a species of the *Eucyclops speratus-serrulatus* group, and Fig. 10 is a species of the *Cyclops strenuus* group, while MÜLLER's *Cyclops crassicornis* (Fig. 14) represents the copepodid stage of a species belonging to the cyclopids. From MÜLLER's biological remarks it can be seen that he noted the male fastened to the female in *Canthocamptus*, but he interprets this as the copulation proper. He has also a good figure of the copulation of *Cyclops*, but thinks that the sperm is transferred by the 1st antenna of the male. He also saw the spermatophores of *Diaptomus* but did not understand their proper function. It is strange, too, that although he knew the nauplius he does not regard this as a larval stage of the copepods, but thinks that it is the youngest larva of a copepodid stage, in spite of the fact that LEEUWENHOEK already knew the correct relationships of these stages.

Although our knowledge of Danish freshwater copepods has thus an early foundation, another century passed before these studies were resumed. About 1895 SØREN JENSEN and C. WESENBERG-LUND started to work on these animals. In 1898 SØREN JENSEN received a prize from The University of Copenhagen for an essay on a faunistic-biological investigation of freshwater ostracods and copepods. This very interesting pioneer work was, however, never published in full, because of the author's early death. The faunistic part was later published by F. MEINERT and C. WESENBERG-LUND in 1905. WESENBERG-LUND's investigations of copepods were not published in a monograph, but in a varied series of freshwater biological papers he gives information about the occurrence and biology of several species. This series began in 1896 with "Biologiske Undersøgelser over Ferskvandsorganismer" (Biological Studies on Freshwater Organisms). In this only two species are mentioned, namely *Cyclopsine castor* and *C. gracilis*. In the extensive work: "Plankton investigations of the Danish Lakes, Special Part" (1904) there is a detailed survey of the biology of our most important plankton copepods. Further information about plankton copepods is given in a series of small papers from 1904-10. In "Furesøstudier" (Studies on Fure Lake) (1917) several littoral forms are mentioned, and finally in "Ferskvandsfauna" (1937) there is a general survey of our freshwater copepods.

In recent times few studies of the Danish freshwater copepods have appeared. In a paper published in 1929 "Studies on the Plankton in the Lake of Frederiksborg Castle" by KAJ BERG and GUNNAR NYGAARD, the biology, periodicity, and vertical distribution in a shallow lake of the two planktic species, *Cyclops strenuus* and *Diaptomus graciloides*, have been described. KAJ BERG has also examined the copepod fauna in Esrom Lake (1938) and in the Susaa (1948). Finally the cyclopoid fauna of Bornholm has been examined by K. LINDBERG (1950).

III. Methods.

a. Chemical and physical analyses and measurements.

Various instruments and chemical analytical methods were employed in the examination of the localities. Usually investigations were carried out, or at any rate started in the field, but sometimes it was necessary to bring water back to the laboratory in pyrex-bottles. In such cases analyses were carried out immediately after returning.

Measurements were made of pH, temperature, colour, conductivity, iron content (both Fe^{++} and total iron content), and oxygen content.

Temperature: Temperatures were measured with small alcohol thermometers, having divisions only into whole degrees (Celsius). As these small thermometers are often not very exact, they were regularly corrected by means of a very sensitive normal thermometer with a known correction.

Colour: The colour of the water was measured in so-called "Ohle"-units, i. e. the colour which is produced by dissolving 0.01 mg. methyl-orange in 1 l. of distilled water (OHLE, 1934; BENNIKE, 1943).

pH: Most pH values were measured by means of reagent paper, manufactured by Johnson & Sons, England. By use of colour-scales, in which the values of one scale overlapped those of the following scale, the pH could be assessed with an accuracy of ± 0.1 . The reagent paper was regularly compared with measurements made with an electrical pH-meter, and this showed that the values obtained could be relied upon, as long as the paper was stored in a dry place. This method is extremely well suited to use in field studies as the paper is light and takes up little space. Besides the measurements made on each excursion, measurements of the theoretically highest and lowest values according to IVERSEN (1929) were made. These measurements were made by means of an electrical pH-meter of the brand "Radiometer pH-meter 21".

Conductivity: This was measured with a "Dionic Water Tester", whose construction, function and application has been described by WELCH (1948).

Iron content: The iron content was measured by means of α - α' -dipyridyl (MÜLLER, 1933), but MÜLLER's method was somewhat modified. A number of standard solutions with 0.02–0.06–0.1 up to 20.0 mg. Fe^{++} /l. were made up, and to 5 ml. of standard solution (taken by glass-syringe) 2 ml. of 1 % dipyridyl dissolved in n/10 HCl were added. The solution was thereby coloured more or less red according to the concentration of iron in the standard. The intensity of the colour was then measured by means of an E.E.L.-colorimeter, manufactured by Ewans Electro Selenium Ltd., both with a blue and a green filter. 5 ml. of distilled water was used to obtain the zero value. From the readings obtained a curve was drawn of the intensity of colour at various contents of Fe^{++} . For natural water the measurement was carried out as follows: The colorimeter was adjusted to zero with the water alone. Then to 5 ml. of water dipyridyl-solution was added as above, and from the intensity of the colour

the Fe^{++} -content was estimated by the aid of the curve. Next the total content of iron was found: 1 drop of concentrated HCl and 1 crystal of Na_2SO_3 were added to the sample, this reduced any Fe^{+++} present to Fe^{++} . If F^{+++} was present, the colour became a deeper red, and, after at least 10 minutes, another measurement was made with the colorimeter. For the zero-adjustment the reducing reagents were added to natural water.

Oxygen content: The oxygen determinations were made according to Winkler's method as described by BENNIKE (1943).

b. Collection and preservation of the animals.

The copepods were collected with Møller-gauze-nets of Nos. 16 and 20. When possible, the nets were mounted on a light bamboo rod, partly to ascertain in which part of the locality the animals were taken, and partly because this made it possible to let the net glide close to the bottom. The collections were taken in such a way that samples collected at various times from the same localities were as far as possible comparable. It was necessary to employ a townet in only a few localities. Immediately after collection formalin was added to the samples, the copepods being thus killed instantly and fixed in natural attitudes. On my return to the laboratory the copepods were sorted and transferred to 80 % alcohol.

Various mounting methods were employed to make microscopical preparations. Where the animals were simply to be identified I used 4 % formalin surrounded by white vaseline (NYGAARD 1951). For mounts of greater importance I used Canada Balsam or polyvinylactophenol. The latter method has two advantages; the organs of the animals are stained a handsome red when Lignin Pink (CANNON 1941) is added in very small quantities, and also animals can be transferred into polyvinylactophenol from any other medium without special treatment.

The number of copepods is indicated per litre of water at various depths. The counts were made by means of an apparatus constructed by GUNNAR NYGAARD (Fig. 1). This consists of a glass container of a capacity of 100 ml. ending in an exchangeable tube, the opening of which is adjusted according to the size of the organisms to be counted. At the top the container can be opened, and by means of a valve system water can be sucked up from the depth desired. When the container is full the outflow is started, and by means of the tap at the top the rate of the outflow of water and organisms can be regulated, so that it is possible to count the animals.

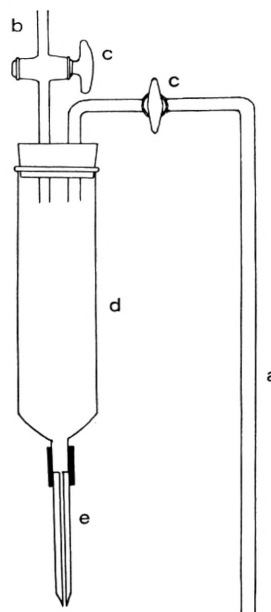


Fig. 1. The plankton counter. a: Induction-pipe. b: Drawing-pipe. c: Taps. d: Container. e: Eduction-pipe which can be replaced. Must be closed during induction.

Counts of copepods at various depths of water were made both in 1951 and in 1952. The results of the two years were quite similar. Consequently only the counts in 1952 are given below, as more were made during that year.

Counts of the number of eggs in the egg-sacs were made, the figures given are always the average of 20 egg-sacs. The egg-sacs were removed and crushed, and the eggs counted under a binocular microscope. For species with two egg-sacs the number in the two sacs were added so that the number represents the average from 20 animals.

In all cases the mean error was calculated according to the following formula $\sqrt{\frac{\Sigma d^2}{n(n-1)}}$ where d stands for the deviation of the single egg-sacs from the mean and n represents the number of observations, in this case 20. Where curves of the number of eggs have been drawn, the middle, heavy line indicates the means and the upper and lower somewhat finer lines are situated at a distance of 3 times the mean error from the latter.

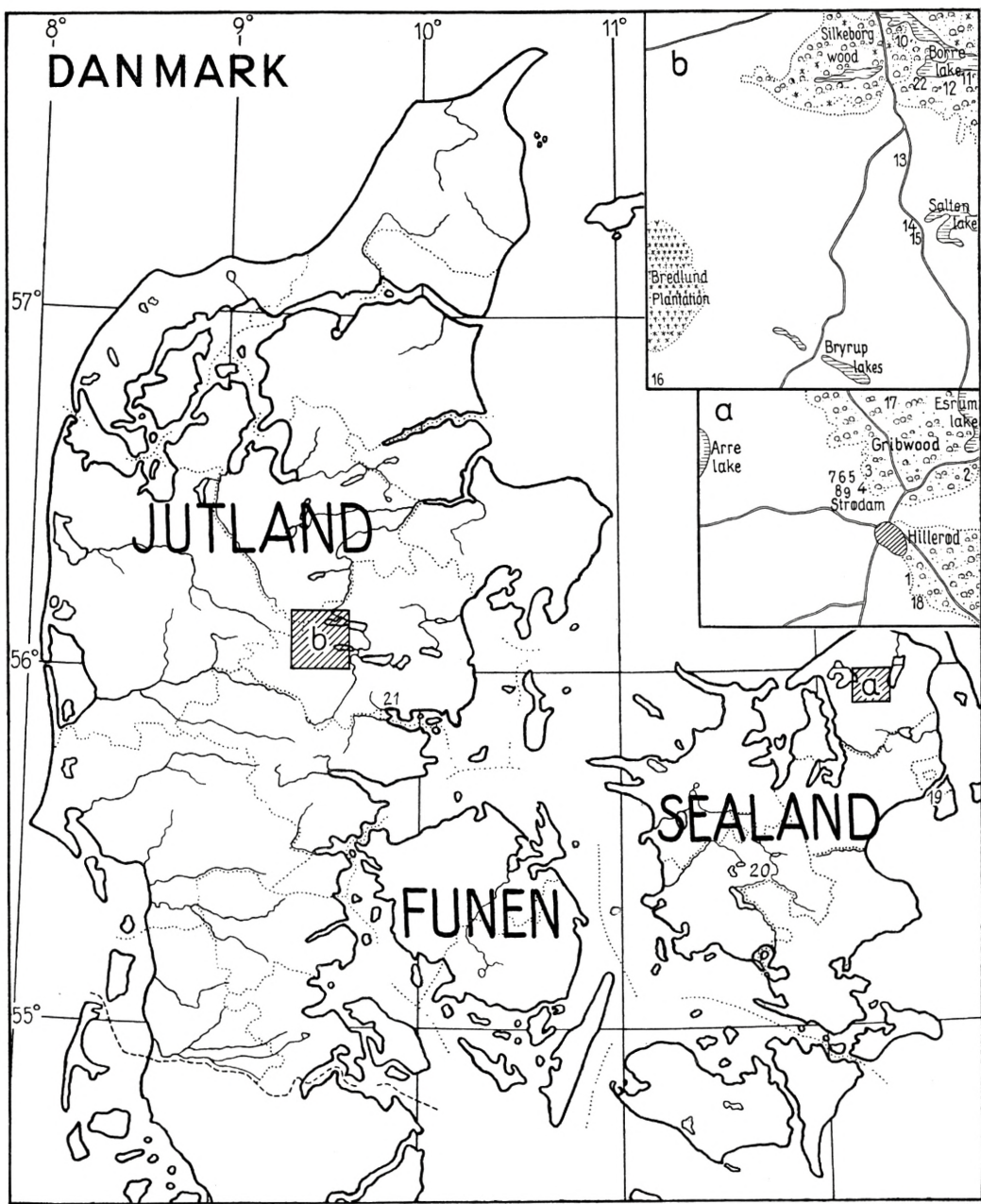
IV. List of Localities.

Most of the localities have not previously been scientifically investigated, and I have therefore considered it necessary to give detailed descriptions. Where the localities have no official name, I have put the name used by me in inverted commas. In the list of localities they are indicated by a No., corresponding to the map of Denmark (Fig. 2) and the international, geographical co-ordinates. In the description there are two numbers. The first refers to the number of the map (1:20.000) of the Danish Geodetic Institute in which the locality is situated, and the second number corresponds to the volume, map, and quadrate of the ordnance map of Denmark (1:100.000).

The collections of animals were always made on the dates when chemical and physical measurements were made, but in addition a few samples of the fauna were taken on other dates, particularly in the localities in North Sealand.

Regularly visited localities:

1. "Branchipus Pond" 55°54'44" N.L. 12°19'20" E.A.
2. "Egelund Pond" 55°57'19" N.L. 12°21'32" E.A.
3. Hjortesølen 55°57'43" N.L. 12°17'43" E.A.
4. "Triphylus Ponds" 55°57'26" N.L. 12°17'25" E.A.
5. "Vandings Pond" 55°57'29" N.L. 12°17'2" E.A.
6. "Sorte Pond" 55°57'32" N.L. 12°16'58" E.A.
7. "Brune Øje" 55°57'30" N.L. 12°16'29" E.A.
8. "Vildande Pond" 55°57'20" N.L. 12°16'28" E.A.
9. "Temporary Pond near Ullerødvej" 55°57'10" N.L. 12°16'56" E.A.
10. Mørksø 56°8'22" N.L. 9°34'22" E.A.
11. "Temporary Pond near the Saw-Mill" 56°7'34" N.L. 9°36'47" E.A.



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Fig. 2. Map of Denmark. The numbers indicate the localities investigated. a: Surroundings of Hille-rod, Sealand. b: Surroundings of Silkeborg, Jutland.

12. Rødebæk 56°7' 11" N.L. 9°36'18" E.A.
13. "Peat-digging at the 35 km. stone" 56°5'33" N.L. 9°34'30" E.A.
14. Frøsø 56°4'4" N.L. 9°34'44" E.A.
15. "Temporary Pond near Frøsø" 56°4'4" N.L. 9°34'44" E.A.
16. Troldsø 55°59'42" N.L. 9°33'56" E.A.
Localities visited on only a few occasions:
17. Gribsø 55°59'0" N.L. 12°18'24" E.A. M. 2728 Alsønderup. III, 4, C 3. Dystrophic lake in Grib forest, North Sealand. pH about 5.0. *Eudiaptomus coeruleus* and *Cyclops strenuus strenuus* dominant in the plankton.
18. "Lille Torkeri Pond" 55°54'27" N.L. 12°19'20" E.A. M. 2828 Hillerød. III, 7, C 2. Eutrophic pond in Hestehaven south of Hillerød, North Sealand. pH about 8.0, vegetation very rich. Dried up in summer. Quite dominated by *Diaptomus castor*.
19. "Brackish-water Pool in Amager Fælled" 55°38'34" N.L. 12°34'37" E.A. M. 3230, Sundbyerne, III, 13, E 2. Pool with much tall vegetation and many filamentous algae, salinity 8 ‰. Situated only 10 m. from the beach. Copepods: *Eurytemora velox*, *Cyclops bicuspidatus odessanus* and *Cyclops viridis*.
20. "Temporarily flooded meadow near Tuel Aa." 55°24'45" N.L. 11°41'49" E.A. M. 3524 Slaglille, III, 18, C 1. Very shallow flood produced by melting snow and heavy rain. Only present until the beginning of May and in late autumn. Water from this pool flowed into Tuel Aa. Contains *Cyclops bisetosus*.
21. Nørrestrand. 55°52'34" N.L. 9°51'49" E.A. M. 2912 Horsens, II, 8, B 2. Cut-off, now wholly freshwater, fiord north of Horsens, Jutland, densely overgrown with weeds. Sample taken on 22.XI. by J. DAHL, M.Sc., contained *Cyclops gigas*.
22. "Peat-digging in Rødkær" 56°7'18" N.L. 9°34'58" E.A. M. 2510. Them. I, 41, F 3. Strongly dystrophic pond in the middle of Jutland south of Silkeborg. pH about 5.0. Copepods: *Macrocyclops fuscus* and *Cyclops bicuspidatus*.

Description of Localities.

1. "Branchipus Pond". M. 2828 Hillerød; III, 7, C 3.—Situated in Lille Hestehave, south of Hillerød, about 50 m. southwest of Karlssø, on the outskirts of the wood towards the open field. Previously, 1927, examined by KAJ BERG (1931).

The surrounding area is very hilly. The ground consists of moraine deposits, partly sand and some clay. Pond very elongated, about 25 m. long and about 10 m. broad. The pond is somewhat raised above the surrounding area, and is enclosed on three sides by trees. To the north there is dense scrub, and to the west the open wood merges into a grassy meadow. There is neither inlet nor outlet. The water-level varies a good deal, and sometimes the pond dries up.

The bottom was overgrown at all seasons, mostly with grass. The vegetation was particularly rich in early summer, when the water was often completely hidden by the vegetation. Only in the north towards the scrub, was the vegetation scanty. The bottom material consisted of dark, peaty mud, with a large admixture of sand. Phyto-

plankton was usually scarce, but at times the water was completely filled with filamentous algae.

The fauna was abundant. In or on the mud or on the vegetation there were large quantities of various species of *Pisidium*, *Limnaea* and Planorbidae, as well as *Planaria* and Oligochaeta. Swimming in the water there were always various Cladocera and Ostracoda and in early spring *Lynceus brachyurus*. Once a metanauplius of *Chirocephalus grubii* was found.

Date	Temperature	pH	O ₂ (ml./l.) Surface	Notes
24.II.50	0°C	6.9	..	Greatest extent, 40 cm. deep. Thin ice.
3.III.50	0°	6.9	4.84	About 8 cm. of ice.
13.III.50, below ice .	1°	6.9	..	Old, fragile ice over greater part of pond.
melted zone	6°	7.2	..	
31.III.50	8°	7.2	..	
14.IV.50	10°	7.4	7.70	Pond somewhat smaller, about 35 cm. deep.
3.V.50	12°	7.8	..	30 cm. deep.
13.V.50	16°	8.0	6.79	Pond again somewhat smaller, 25 cm. deep.
28.V.50	20°	8.2	..	Only half the area of water, 10 cm. deep.
9.VI.50	21°	8.4	5.47	Only a puddle, 4 × 6 m., 5 cm. deep.
26.VI.50	Dried up during this period.
7.IX.50	
30.IX.50	12°	7.5	..	Puddle of 10 × 6 m., 10 cm. deep.
17.X.50	Dry.
10.XI.50	5°	7.0	..	Pond covering its full area, about 25 cm. deep.
4.XII.50	4°	6.8	5.87	About 35 cm. deep.
19.XII.50	0°	6.5	..	Thin layer of ice pond.
2.II.51	0°	6.5	2.19	About 10 cm. of ice.
4.III.51	0°	6.5	..	<i>Ibid.</i>
19.III.51				
about 6.00 a.m...	0.5°	6.5	2.85	
« 10.00 a.m...	4°	6.8	4.45	
- 2.00 p.m...	12°	7.2	7.65	Sample taken at shore.
	6°	6.8	7.39	Sample taken at centre
- 6.00 p.m...	4°	6.8	5.93	
4.IV.51	6°	7.0	..	
18.IV.51	8°	7.2	..	Pond a bit smaller.
6.V.51	14°	7.5	7.16	Still smaller, 25 cm. deep.
22.V.51	20°	8.0	..	20 cm. deep.
7.VI.51	22°	8.4	..	
19.VI.51				
about 6.00 a.m...	14°	7.3	5.12	Considerably smaller, 15 cm. deep.
- 10.00 a.m...	18°	7.9	6.54	
- 2.00 p.m...	25°	8.4	5.88	
- 6.00 p.m...	19°	8.0	5.67	
7.VII.51	22°	8.4	..	Quite small. Only 10 cm. deep. Conductivity: 285 μmho, total iron content: 0.25 mg/l, Colour: 12 Ohle-units, theoretical variation of pH 6.3-8.8.

The copepods *Diaptomus castor*, *Cyclops bicuspidatus* and *Canthocamptus staphylinus* were frequent, and occasional specimens of *Cyclops vernalis* f. *robusta* and *Ectocyclops phaleratus* were taken.

2. "Egelund Pond".

M. 2729 Fredensborg; III, 4, C 3.—Situated in the south-eastern part of the open fenced-off area which surrounds Egelund saw-mill and nursery just south of Egelund Manor. The area around the pond is moraine and the ground consists of clay. The pond is surrounded by scrub with a few large trees, its shape is oval, about 25 m. long (E-W) and about 15 m. broad. At normal water-level the depth was about 1 m., but in summer it was often considerably lower. The pond was very much polluted as a lot of rubbish was irregularly thrown into it from the saw-mill, and large quantities of leaves fall into it in autumn. In a few years it will probably be filled up.

There is no outlet or inlet.

The bottom was very soft. It consisted chiefly of decaying parts of plants and in summer contained large quantities of methane. There was never any rooted vegetation, but the surface was always covered by a thick layer of *Lemna* species. Beyond this the only plants present were filamentous algae.

The fauna was very poor. In the bottom there were a few Oligochaeta, and swimming in the water various larvae of Culicidae as well as the copepods *Cyclops viridis*, *C. gigas* and *Diaptomus castor*.

Date	Temperature	pH	O ₂ (ml./l.) Surface	Notes
17.II.50	0°C	6.5	..	Old fragile ice.
3.III.50	Ice so thick that samples could not be taken.
13.III.50	3°	6.7	..	Melting ice over most of the pond.
31.III.50	7°	6.9	..	
14.IV.50	10°	7.2	6.59	
3.V.50	12°	7.2	..	
13.V.50	15°	7.5	5.97	
28.V.50	18°	8.0	..	
9.VI.50	18°	8.0	5.42	
26.VI.50	20°	8.0	..	
19.VII.50	15°	7.8	..	
4.VIII.50	18°	8.0	5.73	
25.VIII.50	19°	8.0	..	
4.IX.50	19°	8.0	5.67	
30.IX.50	12°	7.8	..	
17.X.50	9°	7.5	5.95	
10.XI.50	6°	7.0	..	
4.XII.50	2°	6.8	4.42	
19.XII.50	0°	6.8	..	Thin layer of ice all over the pond.
2.II.51	0°	6.5	1.12	Ice about 8 cm. thick.

Date	Temperature	pH	O ₂ (ml./l.) Surface	Notes
4.III.51	0°	6.5	..	Ice about 12 cm. thick.
19.III.51				
about 7.00 a.m...	0.5°	6.5	1.78	
- 11.00 a.m...	3°	6.8	3.34	
- 3.00 p.m...	7°	7.0	5.49	
- 7.00 p.m...	2°	6.8	4.73	
4.IV.51	5°	7.0	..	
18.IV.51	7°	7.3	..	
6.V.51	12°	7.2	5.84	
22.V.51	19°	7.8	..	
7.VI.51	20°	8.0	..	
19.VI.51				
about 7.00 a.m...	8°	7.5	3.73	
- 11.00 a.m...	14°	7.8	5.73	
- 3.00 p.m...	20.5°	8.0	5.99	
- 7.00 p.m...	18°	8.0	5.47	
7.VII.51	21°	8.2	..	Iron-content: Ferro 0.3 mg./l., total 0.85 mg./l. Colour: 28 Ohle-units. Conductivity: 420 μ mho; theoretical variation of pH 6.2-8.2.

3. Hjortesølen.

M. 2728 Alsønderup; III, 4, C 3.—Situated just south of Gadevang Huse in a coniferous woodland hollow. The bottom consists of sand.

In Hjortesølen there were two localities, the Border Pond and the Central Pond, and as they differ widely they will be treated separately.

a. Border Pond ("Lagg").

The Border Pond is a ring-shaped pond surrounding the small *Sphagnum* bog called Hjortesølen. It is 10-15 m. wide and the circumference is about 650 m. The outer shore is formed by conifer-clad slopes, while the inner one is formed by the bog. This is often covered by water, so that it is difficult to delimit the pond on the inside, while at other times there is so little water in the bog that the pond is dry. The greatest depth measured was 1¹/₄ m. There is no real inlet or outlet, as the water is surface water running down the hills and disappearing again either by evaporation or by absorption into the dome of the *Sphagnum*.

The bottom was rather firm, covered with an abundant flora, consisting especially of various species of grass. Between the grass there was a thick carpet of moss. The vegetation decreased towards the bog, being transformed into a carpet of *Sphagnum*. There was often a rich development of filamentous algae.

There were many animals in the pond, but only a few species. Culicid larvae and *Daphnia pulex* were dominant, and the following copepods were present: *Eudiaptomus vulgaris*, *Cyclops strenuus strenuus* and *C. viridis* and occasionally *Cyclops vicinus*.

Date	Temperature	pH	O ₂ (ml./l.) Surface	Notes
24.II.50	0°C	6.8	..	Bottom and surface frozen, water in between.
6.III.50	4°	6.8	..	No ice, the whole bog covered by water.
15.III.50	0°	6.8	3.33	2-3 cm. of ice.
3.IV.50	7°	7.2	..	Water a little lower, but bog still covered.
17.IV.50	5°	7.2	6.77	0.5 m. of water. Uppermost part of bog exposed.
1.V.50	6°	7.5	..	0.3m. of water. Border Pond well delimited.
20.V.50	11°	6.9	6.66	Only puddles left in bog.
9.VI.-7.IX.50	Border pond dry.
29.IX.50	11°	6.8	..	Border Pond almost filled with water.
16.X.50	10°	6.8	5.99	Bog flooded.
9.XI.50	6°	6.5	..	
3.XII.50	3°	6.3	6.38	
18.XII.50	0°	5.8	..	Thin layer of new ice.
1.II.51	0°	5.4	2.23	About 15 cm. of ice.
1.III.51	Border Pond frozen.
20.III.51	A little thin new ice in the morning.
about 6.00 a.m. .	0.5°	6.8	2.46	All the bog like one lake.
- 10.00 a.m. .	3.5°	7.0	5.62	
- 2.00 p.m. . .	10°	7.4	7.67	
- 6.00 p.m. . .	5°	7.2	6.55	
4.IV.51	6°	7.4	..	
18.IV.51	7°	7.2	..	Water somewhat lower.
5.V.51	11°	7.0	..	
22.V.51	17°	7.0	6.38	Upper part of bog exposed.
6.VI.51	20°	6.8	..	About 0.4 m. of water.
20.VI.51				
about 6.00 a.m. . .	12°	6.6	4.84	
- 10.00 a.m. . .	17°	6.8	5.39	
- 2.00 p.m. . .	21°	7.0	6.22	
- 6.00 p.m. . .	17°	6.8	5.90	
6.VII.51	21°	6.6	..	Only about 20 cm. of water. Iron-content: Ferro 0.28 mg./l., total 0.68 mg./l. Colour: 18 Ohle-units. Conductivity: 115 μmho. Theoretical variation of pH: 5.8-7.4.

b. Central Pond ("Gøl").

A small oval lake in the middle of Hjortesølen, almost where the dome of the bog is highest, about 25 m. long and about 10 m. wide. The depth was uniform and about 3¹/₂ m. The shores are very steep and they may overhang at times, they are completely surrounded by *Sphagnum* in which there are a few small conifers.

Formerly investigated by BENNIKE, 9.VIII.1940 (1943).

Unfortunately this locality could not often be visited in the winter as the water-level was too high, but it was possible when the ice was sufficiently thick.

There is neither inlet nor outlet, but water seeps in and out through the *Sphagnum*. The bottom was very soft, and it was difficult to define the borderline between

that and the water. It consisted of decayed parts of plants and there was no permanent vegetation.

The phytoplankton was scarce, but there were a large number of filamentous algae.

In the bottom there were only a few oligochaetes and chironomids, and in the water many Cladocera, Hydrachnidae and larvae of *Corethra*. The following copepods: *Cyclops viridis* and *Eudiaptomus vulgaris* were found.

Date	Temperature	pH	O ₂ (ml./m.)		Notes
			Surface	Bottom	
1.V.50.....	6° C	5.7	Could not be visited before May 1st.
20.V.50.....	10°	6.0	6.73	..	
9.VI.50.....	24°	6.4	
25.VI.50.....	22°	6.4	5.85	3.28	
17.VII.50.....	23°	6.4	
3.VIII.50.....	24°	6.6	5.88	..	
24.VIII.50.....	23°	6.6	
7.IX.50.....	17°	6.2	6.77	..	
29.IX.50.....	14°	6.0	
16.X.-18.XII.50 ...					Could not be visited because of high water.
1.II.51.....	0°	5.4	2.63	1.00	12 cm. of ice.
1.III.51.....	0°	5.4	18 cm. of ice.
20.III.51-5.V.51 ...					Could not be visited because of high water.
22.V.51.....	14°	6.2	6.91	3.84	
6.VI.51.....	18°	6.4	
20.VI.51					
about 6.30 a.m...	17°	6.0	4.80	3.38	
- 10.30 a.m...	18°	6.2	6.36	..	
- 2.30 p.m...	22°	6.4	6.22	3.08	
- 6.30 p.m...	20°	6.4	6.23	..	
6.VII.51.....	22°	6.4	Iron content: total 0.19 mg./l. Colour: 40 Ohle-units. Conductivity 110 μmho. Theoretical variation of pH: 5.2-7.0.

Comparison between the chemical and physical factors of these two localities shows that the Border Pond and the Central Pond are dependent upon each other. When there is no direct water communication between them, they are linked through the porous bog. The hydrogen-ion concentration of the Border Pond clearly indicates this connection. The greater part of its water comes from the alkaline surface of the surrounding hills, one would therefore expect that the pH would be high throughout the summer, but large quantities of acid water are introduced from the peat.

Also there is no doubt that, in the autumn, many animals are carried into the Border Pond from the Central Pond. As these animals are adapted to live in perennial waters they perish when the Border Pond dries up. They were not found in the early autumn but only when there was again free water communication over the bog.

4. "Triphylus Ponds".

M. 2728 Alsønderup; III, 4, C 3.—A series of small old peat-diggings situated in the small copse, stretching from Selskov to Ullerødvej west of and parallel to the road from Hillerød to Gadevang. There are altogether 20 small peat-diggings, but there was only water in the three northernmost ones. The underlying rock consists of moraine sand, but here it lies deep down, and the ponds have been dug in a stretch of bog. Towards the east the bog is bordered by a steep wooded hill, while towards the west it passes gradually into cultivated land.

Formerly investigated by C. WESENBERG-LUND (1930).

The physical conditions of the ponds were uniform. The lengths and widths of all the ponds were about 3 m. and the depth of the water about 75 cm. at the highest water-level. There were neither outlets nor inlets. The water was melt-water from the hills.

The bottom of the ponds consisted of very firm peat covered with a thick layer of *Fontinalis*, as did the sides. There was no other vegetation in the ponds, and phytoplankton was very scarce.

The fauna consisted of large numbers of culicid-larvae, some Rotifera, and the copepods *Cyclops strenuus strenuus* and *Canthocamptus staphylinus*.

Date	Temperature	pH	O ₂ (ml./l.) Surface	Notes
24.II.50	0°C	4.5	..	About 10 cm. of ice.
6.III.50	0°	4.5	..	<i>Ibid.</i>
15.III.50	0°	4.5	1.74	Ice melting.
3.IV.50	0°	4.5	..	Thin new ice. Water up to edge.
17.IV.50	3°	4.6	8.21	
1.V.50	5°	4.6	..	Water receded, ponds only half full.
20.V.50	14°	4.8	6.02	Only 20 cm. of water.
9.VI.50	26°	4.8	..	Only a little water left.
25.VI.—16.X.50	Ponds dried up.
9.XI.50	8°	4.6	..	Ponds a little more than half full.
3.XII.50	3°	4.5	6.84	Ponds full.
18.XII.50	0°	4.5	..	Thin new ice.
1.II. and 1.III.51	Thick layer of ice rendered sampling impossible.
20.III.51				
about 6.20 a.m. ...	0°	4.5	4.51	Thin ice in centre.
- 10.20 a.m. ...	0°	4.5	5.07	Little ice left.
- 2.20 p.m. ...	3°	4.5	5.32	
- 6.20 p.m. ...	0°	4.5	5.29	Again a little new ice.
4.IV.51	1°	4.5	..	
18.IV.51	4°	4.6	..	Water receded a little.
5.V.51	6°	4.6	..	
22.V.51	15°	4.8	6.41	Ponds scarcely half full.
6.VI.51	22°	4.8	..	Little water left.
20.VI. and 6.VII. 51	Ponds dry

Iron-content: Total 0.11 mg./l. Colour: 38 Ohle-units. Conductivity: 80 μ mho. Theoretical variation of pH: 4.2–4.8.

5. "Vandings Pond".

M. 2728 Alsønderup; III, 4, C 3.—Situated in the reserved area at Strødam, in the open fenced-in common, about 100 m. to the east of the main building, at the north-western part of a tree-clad hill. The pond is artificial, dug about 1920, and lying upon a rough moraine sand subsoil.

Previously investigated by GUNNAR NYGAARD from 1929–31 (1938, 1949).

It is irregularly oval, length about 25 m., width about 15 m. The depth does not exceed 1½ m. and in most parts of the pond is about 75 cm. There is neither inlet nor outlet. The pond is somewhat polluted as there are horses, sheep, fallow deer (*Dama dama* (L.)) and roe-deer (*Capreolus capreolus* (L.)) on the common.

Date	Temperature	pH	O ₂ (ml./l.) Surface	Notes
6.III.50	6°C	7.0	..	2–3 cm. of ice, thawed along shore.
15.III.50	0.5°	6.7	3.25	
3.IV.50	9°	7.5	..	
17.IV.50	10°	8.0	6.47	
1.V.50	11°	7.7	..	
20.V.50	18°	8.0	6.75	
9.VI.50	22°	8.6	..	
25.VI.50	23°	8.4	6.11	
17.VII.50	22°	8.4	..	
3.VIII.50	19°	9.0	6.14	
24.VIII.50	20°	8.4	..	
7.IX.50	16°	7.9	6.75	
29.IX.50	12°	8.4	..	
16.X.50	10.5°	7.5	6.95	
9.XI.50	5°	7.5	..	
3.XII.50	3°	8.0	5.46	
18.XII.50	0°	6.8	..	Thin layer of new ice.
1.II.51	0°	6.3	1.96	About 12 cm. of ice.
3.III.51	0°	6.3	..	Ice somewhat thicker.
18.III.51				
about 6.00 a.m...	1°	6.6	2.64	
- 10.00 a.m...	3°	6.8	3.15	
- 2.00 p.m...	8°	7.4	5.72	
- 6.00 p.m...	4°	7.0	5.34	
4.IV.51	5°	7.2	..	
18.IV.51	6°	7.2	..	
5.V.51	12°	7.9	6.73	
22.V.51	18.5°	8.0	..	
6.VI.51	20°	8.4	..	
18.VI.51				
about 6.00 a.m...	12°	7.5	5.27	
- 10.00 a.m...	18°	8.8	6.62	
- 2.00 p.m...	23°	9.4	6.45	
- 6.00 p.m...	20°	8.6	6.29	
6.VII.51	22°	8.8	..	

Iron-content: Total: 0.3 mg./l. Colour: 24 Ohle-units. Conductivity: 325 μ mho. Theoretical variation of pH: 6.0–9.6.



Fig. 3. Sorte Pond. 4.IV.1954.

The bottom was firm with a thin layer of mud over the shallow part in the middle of the pond, and there were only filamentous algae on stones along the shore.

The phytoplankton was very rich, particularly in summer. In July and August *Volvox* predominated. The fauna of the pond was abundant consisting especially of larvae of *Corethra*, *Daphnia pulex* and the following copepods: *Eudiaptomus vulgaris*, *Cyclops insignis* and *Cyclops viridis*.

6. "Sorte Pond".

M. 2728 Alsønderup; III, 4, C 3.—Situated in the reserved area at Strødam. The subsoil consists of moraine sand. The terrain round the pond is flat and covered with dense wood, chiefly beech, and there is much scrub. The shape of the pond is irregular, the length about 80 m., the width about 50 m., and the area about 0.25 ha. The depth probably does not exceed 75 cm. (Fig. 3).

The pond is somewhat polluted through some inlets from the farm towards the east, and there is a small outlet at the southern end.

The bottom was very soft, and consisted of decayed leaves and large quantities of *Lemna*. The surface of the pond was also covered by *Lemna*. Phytoplankton was very scarce.

The fauna consisted of Oligochaeta and larvae of Chironomidae, which were present in the upper layer of the mud, and *Corethra* and various Cladocera. There were also the copepods *Cyclops viridis* and *C. gigas*, and a few specimens of *Eudiaptomus vulgaris*.

Date	Temperature	pH	O ₂ (ml./l.) Surface	Notes
6.III.50	0°C	6.5	..	Very thin ice on pond.
15.III.50	0°	6.4	2.84	Ice somewhat thicker.
3.IV.50	7°	6.8	..	
17.IV.50	7°	6.9	5.49	
1.V.50	11°	7.0	..	
20.V.50	18°	7.2	4.77	
9.VI.50	24°	7.4	..	
25.VI.50	22°	7.4	4.16	
17.VII.50	16°	7.2	..	
3.VIII.50	19°	7.4	4.83	
24.VIII.50	20°	7.4	..	
7.IX.50	15°	7.2	5.39	
29.IX.50	11.5°	7.0	..	
16.X.50	10°	6.9	5.97	
9.XI.50	6°	6.9	..	
3.XII.50	2°	6.8	5.46	
18.XII.50	0°	6.5	..	Very thin layer of new ice.
1.II.51	0°	6.4	1.84	Ice about 10 cm. thick.
3.III.51	0°	6.4	..	Ice somewhat thicker.
18.III.51				
about 6.20 a.m...	0°	6.4	1.27	
- 10.20 a.m...	1°	6.4	2.40	
- 2.20 p.m...	4°	6.5	3.83	
- 6.20 p.m...	2°	6.5	3.05	
4.IV.51	3°	6.5	..	
18.IV.51	5°	6.9	..	
5.V.51	10°	7.0	5.29	
22.V.51	16°	7.1	..	
6.VI.51	19°	7.3	..	
18.VI.51				
about 6.20 a.m...	16°	6.9	1.73	
- 10.20 a.m...	18°	7.0	3.67	
- 2.20 p.m...	22°	7.3	4.53	
- 6.20 p.m...	19°	7.1	4.18	
6.VII.51	21°	7.2	..	

Iron-content: Ferro 0.09 mg./l., total 0.12 mg./l.

Colour: 40 Ohle-units. Conductivity: 370 μ mho.

Theoretical variation of pH: 6.3–7.4.

7. "Brune Øje".

M. 2728 Alsønderup; III, 4, B 3.—The southernmost of the two small ponds in the reserved area of Strødam at the southern end of Strødam plantation.

Formerly (1929–30) investigated by GUNNAR NYGAARD (1938).

The pond (Fig. 4) is situated on a subsoil of rough sand, and is surrounded by conifers among which are several low trees and bushes. It is nearly circular, with a radius of about 20 m. and a greatest depth of $1\frac{1}{4}$ m. It is connected by a subterranean pipe with Store Dam lying just south of "Brune Øje". The pipe functions



Fig. 4. Brune Øje. May 1954 (photo by P. WOLTERS).

both as out- and inlet, as the water level in "Brune Øje" is regulated by the level of Store Dam.

Near the shore the bottom was rather soft and muddy, while farther out it was firm. The vegetation was rich but uniform, consisting almost exclusively of *Helodea canadensis*. Among this were small accumulations of *Lemna trisulca*, and on the surface there was a good deal of *Lemna minor*.

Along the shore some *Phragmites communis* occurred. There was only a small quantity of phytoplankton, partly diatoms and partly *Volvox* species.

The fauna was abundant; on the bottom and on the plants there were *Planaria*, *Hydra*, *Pisidium*, *Limnaea* and planorbid species, and larvae of water-beetles. Swimming in the water Ephemeroptera, *Corethra* and Cladocera were abundant.

The copepods *Macrocyclus albidus*, *E. fuscus*, *Eucyclops serrulatus* and *Cyclops viridis* were particularly numerous, whereas *Cyclops vernalis* and *Eudiaptomus vulgaris* only occurred in small numbers.

Date	Temperature	pH	O ₂ (ml./l.) Surface	Notes
6.III.50	0.5° C	7.1	..	Quite thin, melting ice.
15.III.50	0.5°	7.1	4.23	Ice 5 cm. thick, melting.
3.IV.50	8°	7.4	..	
17.IV.50	9°	7.7	8.01	
1.V.50	10°	7.9	..	
20.V.50	16°	8.4	6.75	
9.VI.50	22°	8.6	..	
23.VI.50	22°	8.6	6.09	
17.VII.50	16°	8.0	..	
3.VIII.50	18°	8.2	6.47	
24.VIII.50	21°	8.0	..	
7.IX.50	17°	7.8	6.77	

Date	Temperature	pH	O ₂ (ml./l.) Surface	Notes
29.IX.50.....	14°	7.8	..	
16.X.50.....	11.5°	7.3	6.98	
9.XI.50.....	7°	7.2	..	
3.XII.50.....	3.5°	7.0	7.37	
18.XII.50.....	0.5°	7.1	..	Pond partly covered by thin ice.
1.II.51.....	0°	6.9	..	Ice about 10 cm. thick.
3.III.51.....	0°	6.9	..	Ice a little thicker.
18.III.51				Melting ice in central part.
about 6.40 a.m...	0°	7.0	2.39	
- 10.40 a.m. .	2°	7.0	4.21	
- 2.40 p.m...	6°	7.3	7.84	
- 6.40 p.m...	4°	7.1	6.53	
4.IV.51.....	4°	7.1	..	
18.IV.51.....	4.5°	7.2	..	
5.V.51.....	10°	7.4	6.94	
22.V.51.....	17°	7.8	..	
6.VI.51.....	20°	8.0	..	
18.VI.51				
about 6.40 a.m...	13°	7.4	4.93	
- 10.40 a.m...	16°	7.9	6.62	No iron. Colour: 20 Ohle-units. Conduc-
- 2.40 p.m...	22°	8.0	6.24	tivity 350 μ mho. Theoretical variation
- 6.40 p.m...	20°	7.8	6.08	of pH: 6.8-9.0 (Nygaard (1938): 6.6-9.0)
6.VII.51.....	21°	7.9	..	

8. "Vildande Pond".

M. 2728 Alsønderup; III, 4, B 3.—Situated in the reservation at Strødam, about 500 m. south-west of the main building on the southern outskirts of the park. The bottom consists of moraine sand, covered by a few metres of peat-soil.

Formerly investigated by JOHNSON (1951).

The surrounding area is flat and completely surrounded by trees or high bushes, which in autumn shed many leaves into the pond. The shape of the pond is irregular; it is about 100 m. long in the N.-S. direction, and about 50 m. in the E.-W. direction; its area is about 0.4 ha., but it appears smaller because of the abundant vegetation. The depth nowhere exceeds 1.5 m., and in several places the bottom is very near the surface.

There is no inlet, but there is a small artificial outlet on the western shore, but this usually contains little water.

The bottom was very soft, and consisted mainly of dead plant matter, and just above it there was a thick layer of *Lemna trisulca* and *Lemna minor*.

Other vegetation was extremely rich; where the water was shallow there were large growths of *Scirpus*, *Typha* and *Phragmites*, and in places these formed small islands. The water surface was covered by *Nymphaea alba* and *Lemna*, particularly *Lemna polyrrhiza*, and in the open water there were occasionally some filamentous algae and *Volvox*.

The fauna was also very rich, and almost all freshwater invertebrate-groups were present in great numbers.

Copepods present were *Eudiaptomus vulgaris*, *Macrocylops fuscus*, *M. albidus*, *Eucyclops speratus*, *Cyclops strenuus strenuus*, *C. viridis* and *Canthocamptus staphylinus*.

Date	Temperature	pH	O ₂ (ml./l.) Surface	Notes
6.III.50	4° C	6.8	..	
15.III.50	0.5°	6.8	4.54	Pond covered by thin layer of ice.
3.IV.50	5°	7.0	..	
17.IV.50	6°	7.0	7.35	
1.V.50	8°	7.2	..	
20.V.50	16°	7.8	6.74	
9.VI.50	23°	8.2	..	
25.VI.50	22°	8.4	6.31	
17.VII.50	16°	8.4	..	
3.VIII.50	19°	8.6	6.40	
24.VIII.50	20°	8.8	..	
7.IX.50	18°	8.6	6.57	
29.IX.50	13°	8.0	..	
16.X.50	10°	7.6	7.57	
9.XI.50	6°	7.2	..	
3.XII.50	2°	7.0	9.37	
18.XII.50	0°	6.8	..	Here and there thin flakes of ice.
1.II.51	0°	6.4	1.64	About 10 cm. of ice.
3.III.51	0°	6.4	..	Ice 15 cm. thick.
18.III.51				
about 7.00 a.m...	2°	6.6	2.69	
- 11.00 a.m...	4°	6.8	4.83	
- 3.00 p.m...	7°	7.0	7.94	
- 7.00 p.m...	5°	7.0	4.99	
4.IV.51	6°	7.0	..	
18.IV.51	8°	7.2	..	
5.V.51	10°	7.6	7.56	
22.V.51	12°	7.8	..	
6.VI.51	21°	8.0	..	
18.VI.51				
about 7.00 a.m...	14°	7.8	5.67	
- 11.00 a.m...	18°	8.2	6.24	
- 3.00 p.m...	20°	8.6	6.40	
- 7.00 p.m...	17°	8.4	6.27	
6.VII.51	21°	8.6	..	Iron-content: total: 0.35 mg./l. Colour: 16 Ohle-units. Conductivity: 325 μmho. Theoretical variation of pH: 6.2-9.4.

9. "Temporary Pond near Ullerødvej".

M. 2728 Alsønderup; III, 4, C 3.—Situating in an abandoned gravel-pit in the reserve at Strødam, about 1 km. to the south of the main building between a small

hill covered with conifers and the road from Gadevang to Ullerød. The subsoil consists of moraine gravel.

When quite full, the area of the pond was about 20×20 m., and the greatest depth was 25 cm.

There is neither outlet nor inlet, and the water it receives is either rain or melt water.

The bottom consisted of dark very sandy soil, covered by dense vegetation. In spring there were many algae in the water.

An immense number of culicid larvae was found in the pond, but otherwise the only animal was the copepod *Cyclops strenuus strenuus*.

Date	Temperature	pH	O ₂ (ml./l.) Surface	Notes
6.III.50	3° C	6.9	..	About 25 cm. of water.
15.III.50	Pond frozen solid.
3.IV.50	11°	7.3	..	Pond at greatest extension and depth.
17.IV.50	13°	7.3	7.47	Water receded a little, depth about 20 cm.
1.V.50	14°	7.4		Pond divided in two, each of a depth of 15 cm.
20.V.50	20°	7.8	6.27	Only 5×5 m. left, 10 cm. deep.
9.VI.50	16°	7.8	..	Only small remnants left.
25.VI.-29.IX.50	50°	Pond dried up.
16.X.50	10°	7.2	7.74	About 10 cm. of water.
9.XI.50	3°	7.0	..	About 20 cm. of water.
3.XII.50	2°	7.0	7.95	
18.XII.-3.III.51	Pond frozen solid.
18.III.41				Ice, melting in the course of the morning.
about 7.20 a.m...	0°	6.9	8.85	
- 11.20 a.m...	1°	6.9	8.44	
- 3.20 p.m...	6°	7.1	8.73	
- 7.20 p.m...	2°	7.0	8.88	
4.IV.51	7°	7.2	..	Greatest possible extension and depth.
18.IV.51	9°	7.3	..	
5.V.51	15°	7.5	6.11	Water a little lower.
22.V.51	21°	7.8	..	Water somewhat lower, only about 18 cm. deep.
6.VI.51	22°	7.8	..	Pond divided in two, depth about 15 cm.
18.VI.51				
about 7.20 a.m...	10°	7.4	7.15	Depth of water scarcely 10 cm.
- 11.20 a.m...	17°	7.8	6.76	
- 3.20 p.m...	25°	7.8	6.02	
- 7.20 p.m...	20°	7.7	6.16	
6.VII.51	24°	7.8	..	Only remnants left. Iron-content: total: 0.04 mg./l. Colour 8 Ohle-units. Conductivity: 210 μ mho. Theoretical variation of pH: 6.8-7.8.



Fig. 5. Mørksø. 21.V.1952 (photo by KAJ HANSEN).

10. Mørksø.

M. 2510 Them; I, 41, E 2.—Situated in the northern part of Silkeborg Østerskov just south of Avnsø. The lake lies on subsoil of moraine sand, and the surrounding landscape is very hilly and wooded, especially with conifers.

The lake (Fig. 5) is almost circular with a diameter of about 85 m., and an area of about $\frac{1}{2}$ ha. At the shore the depth is 2.3 m., and this increases to about 10 m. in the middle. It is surrounded by a floating mat, consisting mainly of *Sphagnum*, which is widest, about 7 m., on the northern and western sides and narrower on the other sides. There is no outlet and there are only a few inflowing ditches of which only one permanently carries water. This is, however, stagnant except in spring, when all the ditches are full of water.

The bottom consisted of loose, granular, peaty substance, which smelt rather strongly of hydrogen sulphide. A dense growth of *Fontinalis* on the bottom along the shore, and in the north of the lake there was some *Nuphar luteum*.

In spring and autumn there were many diatoms, but otherwise little phytoplankton was present. There was a rich fauna during the greater part of the year. In the surface layers of the water *Corethra* and, in the autumn, Cladocera were particularly common, and Hydrachnidae and Ephemeroptera were present. On the bottom there were only a few *Tubifex*. The copepods *Eudiaptomus graciloides*, *Macrocyclops albidus*, *M. fuscus*, and *Mesocyclops leuckarti* were found.

Date	Temperature	pH	O ₂ (ml./l.)		Notes
			Surface	Bottom	
23.III.50	7° C	6.2	
11.IV.50	9°	6.4	7.99	..	
26.V.50	19°	6.8	
5.VII.50	21°	7.0	6.25	2.12	
12.VIII.50	19°	7.0	
10.IX.50	15°	7.1	
19.X.50	10.5°	6.7	
28.XI.50	4.5°	6.4	8.77	1.73	
23.III.51	0.5°	5.8	1.75	0.58	Taken through ice, about 6 cm. thick.
	3°	6.1	3.26	0.59	Taken in open area of 8 × 25 m. towards the north.

Date	Temperature	pH	O ₂ (ml./l.)	Notes
27.IV.51	12.5°	6.4	
29.V.51	12.5°	6.8	
25.VI.51	17°	7.0	
13.VII.51	20°	7.2	
14.VIII.51	18°	6.9	6.24 ..	Iron-content: Total 0.18 mg./l. Colour 22 Ohle-units. Conductivity 120 μ mho. Theoretical variation of pH 5.9-7.1.

11. "Temporary Pond near the Saw-Mill".

M. 2510 Them; I, 41, F 3. Situated in the flat meadow west of the outflow from Slaaensø to Borresø. This is bordered by wooded hills to the south and west, by Borresø to the north, and by the outflow to the east. When the flood was at its height it covered an area of about 500 m², and the greatest depth was 15 cm. To the north and to the east foot-paths have been made between the meadow and the lake and the outflow respectively. These foot-paths are raised somewhat above the meadow, the surface of which is at the same level as Borresø. Before the foot-paths were made, the meadow was flooded each spring by the lake, but now it is a dammed up area, receiving its water from the hills, when snow melts and during heavy rain, and this water can only disappear by evaporation. No inlets or outlets are present.

The soil of the meadow was dark and peaty, and probably consisted of old lake sediments. The vegetation was very dense tall grass, and the bottom was covered by a thick carpet of moss, which was always extremely moist. The fauna was not very varied, although at times there were many individuals. Oligochaeta were abundant and there were many ostracods and culicid larvae. The copepods *Cyclops bicuspidatus*, *C. bisetosus* and *Canthocamptus staphylinus* were found.

Date	Temperature	pH	O ₂ (ml./l.) Surface	Notes
24.III.50	9° C	6.2	..	Almost all the meadow covered by water.
10.IV.50	12°	6.5	6.27	Colour: 60 Ohle-units.
27.V.50	21°	6.9	..	Only 3 cm. of water in part of the meadow.
3.VII.50-11.XI.50	During this period only damp at bottom.
19.X.50	9.5°	6.8	..	Little water over a small part of the meadow.
24.XI.50	4.5°	6.5	3.83	Somewhat more water.
24.III.51	Pond frozen.
27.IV.51	16°	6.6	..	The whole meadow covered by water, about 15 cm. deep. Conductivity 130 μ mho. Theoretical variation of pH 5.6-7.4.
29.V.51	12.5°	6.4	..	Water covering almost half of the meadow, about 10 cm. deep.
25.VI.51	22°	6.8	..	Little water in small puddles.
11.VII.-13.VIII.51	Only slightly damp at the bottom.

12. Rødebæk.

M. 2510 Them; I, 41, F 3.—This rises near Christiansminde in the southern part of Silkeborg Sønderkov. It flows about 1 km. to the north, turns north-east, runs under the road Virklund-Svejbæk and then flows north-west, crossing the forest road to Slaaensø, and is finally lost in a bog. Just after passing under the forest road it forms a little pond, and from here it runs in a stony winding bed through a damp meadow. From this meadow it receives many tributaries with very brown water. The samples were taken from this part of the brook running through the meadow. The depth is about $\frac{1}{2}$ m., but the water volume varies according to the season. It was greatest just after thaw and smallest in summer. The small tributaries generally dry up in the middle of the summer. The meadow consisted almost exclusively of a thick carpet of *Sphagnum*, overgrown with grass in places. The soil is very dark peat, containing some iron. The meadow is surrounded by conifers.

There was no vegetation in the brook, but in summer it was completely hidden by plants hanging down from the shore.

Gammarus pulex was very common and there were larvae of stoneflies and Simuliidae and the copepod *Moraria brevipes*.

Date	Temperature	pH	O ₂ (ml./l.) Surface	Notes
24.III.50	9° C.	7.2	..	pH in inlet 6.3
10.IV.50	10°	7.1	7.79	pH in inlet 6.1.
27.V.50	10.5°	7.3	..	pH in inlet 6.0.
3.VII.50	12°	7.5	7.39	pH in inlet 5.3
12.VIII.50	11°	7.2	..	Inlet dried up.
11.IX.50	12.5°	7.2	..	pH in inlet 6.1. Heavy rain during preceding days.
19.X.50	9.5°	7.2	..	Inlet dried up.
24.XI.50	5.5°	7.0	8.75	pH in inlet 5.8.
22.III.51	1.9°	7.2	9.55	pH in inlet 6.8. Much melting snow round the brook.
27.IV.51	9.5°	7.5	..	pH in inlet 6.1.
29.V.51	10°	7.3	..	pH in inlet 6.0.
25.VI.51	11°	7.5	..	pH in inlet 5.7.
11.VII.51	12°	7.3	..	Inlet dried up.
13.VIII.51	10.9°	7.6	6.13	Inlet dried up.

Iron-content: Ferro 0.04 mg./l., total 0.44 mg./l. Colour: 4 Ohle-units. Conductivity: 200 μ mho.

13. "Peat-digging at the 35 km. stone."

M. 2510; II, 3, E1.—Situated in the small stretch of bog west of the road Silkeborg-Horsens, just beside the km.stone. The bog is surrounded by steep grass-clad hills.

The edges of the peat-digging (Fig. 6) were straight and sharp. It was about 30 m. long and 20 m. wide, and the banks were steep down to the greatest depth of

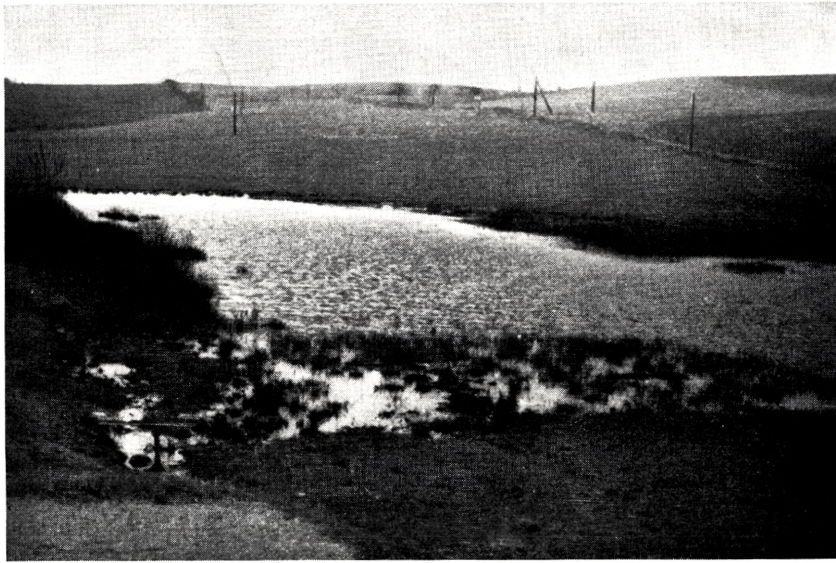


Fig. 6. Peat-digging at the 35 km. stone. 1.V.1951.

3–4 m. Sometimes the water floods the surface of the bog, which is covered by grass, but there was no vegetation on the cut surface of the peat.

There is neither inlet nor outlet, and during heavy rain or at the thaw surface water flows into the bog from the hills.

The bottom consisted of very dark peat.

Phytoplankton was almost absent, but there were often algae near the shore.

The fauna was at times very rich. *Corethra* larvae, species of *Corixa* and Hydrachnidae were always found, in the spring and autumn great quantities of *Daphnia pulex* were present, in summer the ostracod *Cypridopsis vidua* was abundant near the shore, and for short periods there were large numbers of *Acilius*- and ephemeropterid-larvae. The copepod *Cyclops bicuspidatus* was frequent, and a few specimens of *Macrocyclops fuscus* and *Cyclops strenuus strenuus* were also found.

Date	Temperature	pH	O ₂ (ml./l.) Surface	Notes
22.III.50	6° C.	6.1	..	Water a little above edge.
11.IV.50	9°	6.3	6.94	Water a little higher.
27.V.50	15°	6.8	..	Water a little below edge.
6.VII.50	18°	6.8	6.15	Water about 20 cm. below edge.
13.VIII.50	18°	6.7	..	
11.IX.50	15°	6.7	..	
21.X.50	9°	6.6	..	Water just up to the edge.
26.XI.50	2°	6.3	6.99	Thin ice covering parts of the peat-digging.
24.III.51	2°	6.0	1.95	Large part of bog submerged. Large flakes of ice.

Date	Temperature	pH	O ₂ (ml./l.)	Notes
1.V.51.....	10°	6.4	..	
30.V.51.....	14.5°	6.7	..	Water just up to the edge
26.VI.51.....	17°	6.8	..	
14.VII.51.....	18°	6.8	..	
14.VIII.51.....	20°	6.6	..	Iron-content: total 0.08 mg./l. Colour: 50 Ohle-units. Conductivity: 160 μmho. Theoretical variation of pH: 5.8–6.8.

14. Frøsø.

M. 2610 Bryrup; II, 3, F 1.—Situating on the lowest terrace in the northern part of the Salten valley, west of the 32 km. stone on the road Silkeborg–Horsens. Immediately north of the lake (Fig. 7) the land rises steeply, while to the south it slopes down towards the river Salten å. To the west there are stretches of bog, while to the east, between the lake and the road, there is a very damp meadow. The soil consists mainly of moraine sand. To the north and south there are plantations of spruce (*Picea abies* (L.)). The lake is almost circular, with a diameter of about 200 m. The area is about 3 ha. The depth, which was measured through ice, nowhere exceeds 3.5 m. Along the shores there is a 3–6 m. wide belt of reed swamp, which is widest in the north.

There is an inflow from the bog towards the west. This is a ditch 2 m. wide, which always contains water, although it is often stagnant, and the water is always brown. The lake also receives a large inflow from the land to the north during the thaw. There is an outlet to the southeast through a ditch over the meadow, which ultimately reaches the Salten å.

The water-level varied a good deal; the lowest was in August, when the colour was deepest and the hydrogen-ion concentration greatest; the highest, about 1/2 m. higher, was in April just after the thaw, when the colour and hydrogen-ion concentration were lowest.

The bed of the reed swamp and the bottom nearby consisted almost exclusively of decayed plants, while in the middle of the lake there was a poor gyttja, mixed with sand.

In spring and autumn there were many diatoms in the water, but otherwise little phytoplankton was found.

The fauna in the reed swamp was abundant. Ostracods and sometimes Cladocera were numerous and there were also small waterbeetles, Hydrachnidae and larvae of culicids. The following copepods were present: *Macrocyclops albidus*, *M. fuscus*, *Cyclops viridis* and a few *Eudiaptomus coeruleus*.

Date	Temperature	pH	O ₂ (ml./l.)		Notes
			Surface	Bottom	
22.III.50.....	6° C.	7.4	
11.IV.50.....	12°	7.2	7.43	..	Colour: 14 Ohle-units.
27.V.50.....	14°	7.0	Colour: 20 Ohle-units.
6.VII.50.....	22°	6.8	5.98	..	



Fig. 7. Frøso. 26.IV.1954.

Date	Temperature	pH	O ₂ (ml./l.)		Notes
13.VIII.50	21°	6.5	Colour: 45 Ohle-units.
11.IX.50	17.5°	6.5	Colour: 40 Ohle-units.
21.X.50	10.5°	6.4	
26.XI.50	3°	6.3	8.72	..	Colour: 35 Ohle-units. Thin ice in the middle of the lake.
24.III.51	0.5°	5.8	2.56	0.84	Colour: 55 Ohle-units. Ice about 8 cm. thick. Only a little open water at in- and outlet.
1.V.51	10.5°	7.1	Colour: 12 Ohle-units.
30.V.51	15°	7.0	
26.VI.51	18°	6.8	Colour: 16 Ohle-units.
14.VII.51	21.5°	6.8	
24.VIII.51	20°	6.3	6.68	..	Colour: 50 Ohle-units. Iron-content: total 0.08 mg./l. Conductivity: 150 μmho. Theoretical variation of pH: In the lake 6.0–6.9. In the inlet 4.2–4.7.

15. "Temporary Pond near Frøso."

M. 2610 Bryrup; II, 3, F1.—Situated in the meadow between Frøso and the road. The area of the meadow is about 300 m², but only the southern part, an area of 20–30 m², is covered by the pond, when this is largest (Fig. 8). The greatest depth was 30 cm.

There was no inflow or outlet.

The bottom of the pond consisted of very dark, peaty soil, on which there was a dense growth of grass and moss.

The fauna consisted of Dytiscidae, culicids, oligochaetes and the copepod *Cyclops bisetosus*.

In May 1951 the meadow was drained and ploughed, and consequently the locality could not be further studied that year. In the spring of 1952 it was revisited and a little water was present in which a few *Cyclops bisetosus* were found.



Fig. 8. Temporary Pond near Frøsø. 1.V.1951.

Date	Temperature	pH	O ₂ (ml./l.) Surface	Notes
22.III.50	8° C.	5.9	..	Pond at its maximum extent and depth.
11.IV.50	13°	6.2	6.76	Pond somewhat smaller. Depth 20 cm.
27.V.50	22°	6.5	..	Only remnants of pond. Depth: 8 cm.
6.VII.–22.X.50	Pond dried up.
26.XI.50	0°	6.2	4.55	Depth 20 cm. Thin new ice.
24.III.51	Pond frozen.
1.V.51	12°	6.5	..	Depth about 20 cm. Colour: 55 Ohle-units. Conductivity: 110 μmho. Theoretical variation of pH: 4.9–6.7.

16. Troldso.

M. 2609 Varde and M. 2709 Nørre Snede; II, 3, D 2.—Situated about 100 m. south of Hampen Lake in the northern part of Palsgaard Forest. The land is quite flat and the soil consists of stratified sand. The lake is surrounded by trees, particularly pine (*Pinus silvestris* L.).

Formerly investigated by IVERSEN (1929).

The lake (Fig. 9), which is almost rectangular, is about 200 m. long and about 100 m. wide and its depth is about 4 m. All round the lake there was a very broad and soft marginal mat, consisting of *Sphagnum cuspidatum*, in which at intervals there were growths of species of *Carex*, *Sparganium* and *Juncus*.

There is no permanent inflow, but a few ditches carry water to the lake in spring and autumn. There is only an outlet in years when the rainfall is abundant (as e.g. 1951) through a ditch which leads into the southern part of Hampen Lake.



Fig. 9. Trolldso. 20.VIII.1951.

The phytoplankton consisted only of diatoms, but there were many attached algae, particularly *Batrachospermum*; these were, however, only present in summer.

Bosmina longirostris was predominant in the fauna, and there were also *Corethra* larvae, Hydrachnidae and the copepods *Heterocope saliens*, *Macrocyclus fuscus*, *Macrocyclus oithonoides* and *Mesocyclus leuckarti*, the two latter being present only in small numbers.

Date	Temperature	pH	O ₂ (ml./l.)		Notes
			Surface	Bottom	
22.III.50	6° C.	4.8	
11.IV.50	11°	5.0	8.89	..	
27.V.50	15°	5.0	
6.VII.50	18°	5.2	6.25	2.05	
14.VIII.50	22°	5.4	
12.IX.50	16°	5.4	
22.X.50	6°	5.0	
27.XI.50	4.5°	4.8	8.55	2.57	
20.III.51	0.5°	4.6	2.34	1.00	Ice about 8 cm. thick.
28.IV.51	11°	4.9	
1.VI.51	17°	5.2	
27.VI.51	20°	5.2	
18.VII.51	20°	5.2	
20.VIII.51	21.3°	5.4	5.87	..	

Iron-content: total 0.21 mg./l.
 Colour: 25 Ohle-units. Conductivity: 90 μ mho. Theoretical variation of pH: 4.7–5.4.

V. Special Part. The Species Investigated.

Heterocope saliens (LILLJEBORG) 1863.

Previous investigations: Investigations on the biology of this species were made by EKMAN (1904) and GAJL (1927). EKMAN's investigations were made in North-Sweden and show that there *H. saliens* only occurs in summer, in small waters or the littoral of large lakes, and that there is only one generation per year. In agreement with ZSCHOKKE (1900) he places the species in the group of freshwater Entomostraca,

which lives in waters with constantly low temperatures, in highlands in the littoral zone, in lowlands at great depths. Where the species does occur in shallow waters in lowlands, copulation takes place in winter. GAJL's investigations were carried out in Lake Toporowy in the Polish part of the Tatra mountains, and they show that there, also, *H. saliens* only occurs in summer, the longest lived specimens disappearing at the beginning of the autumn. He found, however, that in Poland the species reappears about a month earlier than in North-Sweden. GAJL also states that *H. saliens* occurs in what he calls "inneres Litoral", i. e. a zone round the middle of the lake, below the littoral proper.

Danish literature gives no information about the biology of the species, there being only records of its occurrence.

Present investigations: I have found *H. saliens* only in Troldso (p. 30) and although I have examined the localities from which it has previously been recorded in Denmark, I have not found the species there. The life cycle in Troldso is very like that recorded by EKMAN and GAJL. The earliest adult individuals were found on 27.V.1950 and on 1.VI.1951, while nauplii were found on 11.IV.1950 and 28.IV.1951. Nauplii were found only in the spring. It must therefore be assumed that in Troldso, as elsewhere, the species has only one generation. The nauplii in Troldso were found somewhat earlier in the year than those found in Poland and Sweden, where nauplii were not found until May and June respectively. In both countries this means that nauplii were found about a fortnight after the disappearance of the ice, and this corresponds with my observations. In 1950 the ice disappeared towards the end of March in Troldso, and in 1951 probably about the middle of April, so in both years this was about a fortnight before the occurrence of nauplii.

Previous investigators (MATSCHEK 1909, and KESSLER 1913) have ascertained that the eggs of *H. saliens* are laid singly and are resting eggs with a very strong shell, the outer part of which swells to form a gelatinous capsule which presumably keeps the egg afloat in the water for a long time.

In both 1950 and 1951 the temperature of the surface water by the shore was 11°C when nauplii were first found and this suggests that this rather high temperature had influenced the hatching of the eggs. Temperature alone, however, cannot be the only factor, otherwise there would at least be one more generation during the summer, and this has not been observed by me or by other workers. The water is, however, considerably more light-absorbing in summer than in spring because of its larger content of phytoplankton. If the eggs require a good deal of light in order to develop, as well as a certain temperature, this combination of conditions will only be found in spring, because in autumn when the absorption of light is again small, the temperature will be much lower. This explanation also fits in with the fact that the eggs float. If they lay on the bottom, the bottom material would prevent fluctuations in the amount of light from affecting them. Unfortunately, the animals were so sensitive to transport that I failed to bring any back alive to the laboratory for further study of this problem.

The earliest adult individuals were found on 27.V.1950 and 1.VI.1951, so in both years the period of development must have been about five or six weeks. In both years these early females were carrying gelatinous spermatophores and about the same numbers of males and females were found, but during the summer the ratio of males to females decreased steadily. The latest date on which the species was found was 12.IX.1950, when there were only few specimens, all of which were females. It is impossible to say with certainty how long the individuals lived, since animals which were not fully developed, were found together with adults even fairly late in the summer, but presumably the adult stage lasted about 2 months.

The distribution in the lake was peculiar. All the nauplii were found less than 3 m. from the outer edge of the marginal mat, but none nearer to it than $\frac{1}{2}$ m. At the beginning of the summer adults were found only in the middle of the lake, and were never nearer than 8 m. from the shore, while young ones were usually nearer the shore. This was shown by taking samples with a tow-net, which was thrown in near the marginal mat, and at 3 m., 8 m., and 15 m. from it, and dragged to the shore. Late in the summer many females were found at the shore, while adult males remained almost exclusively in the middle of the lake. Probably copulation takes place in the open water in the middle of the lake, while the laying of eggs and development from nauplius to adult takes place in the shallow water near the shore, perhaps because the water there becomes warm more rapidly in the spring.

The following points are of interest in considering the occurrence of *Heterocope saliens* in Denmark.

The finding of this species in a shallow lake in the lowlands, with its reproduction period in summer, does not correspond with the ideas of earlier authors on its biology. According to EKMAN (1904) the reproductive period in such a locality should be the winter, and the species should be regarded as a glacial relict. As this is clearly not so in Troldso, and as the species seems to occur sparsely in Denmark, another explanation is offered.

Because it is large and strongly coloured one may assume it to be poorly adapted to competition in warm more or less neutral lakes rich in nutriment, as compared with the small, less strongly coloured species of the genus *Eudiaptomus*, especially as the latter produce more eggs. *H. saliens* because of its rather robust structure is, however, able to live under more unfavourable conditions and can tolerate scarce, non-planktonic food, a constant low pH, and low summer temperatures. It is also able to endure long periods of frost on account of its resting eggs, but it probably cannot tolerate complete dryness. The most important requirement seems to be a rich supply of oxygen, as it has never been found in lakes deficient in oxygen, and this is probably the reason why I failed to bring live specimens back to the laboratory.

Diaptomus castor (JURINE) 1820.

Previous investigations: Foreign investigations give much information about the biology of the species. Among the most important works the following may be mentioned: WOLF (1905) examined the species throughout a year, and found that when there was sufficient water it could occur at all seasons and produce several generations. The egg-sacs either sank to the bottom as resting eggs, or developed into a new generation at once. These egg-sacs contained 15–40 eggs, but were otherwise uniform, and the ability of the eggs to remain as resting eggs was due to the glutinous nature of the egg-sacs rather than to the structure of the egg-shell. The eggs do not require dryness to develop. HABERBOSCH (1920) found that in Greenland the species had only up to 30 eggs in the egg-sacs, and he found males to be much more numerous than females.

GURNEY (1931) states that the eggs can develop into nauplii in four days from the time they are laid, but that they may also function as resting eggs without any noticeable difference. On the other hand, he also found females with larger eggs than usual which were surrounded by a very strong egg-sac. These were presumably resting eggs.

For Denmark no published information about the biology of the species is available, but there are some very interesting observations in SØREN JENSEN's manuscript. Thus he shows that the eggs are only able to survive complete dryness when they are not lying freely but are covered by earth or mud, which may even be quite dry. He shows furthermore that the animals disappear towards the end of the summer, even though there is sufficient water, if this water is filled with plants so that the animals cannot swim about freely.

Present investigations: I have regularly examined *D. castor* in Branchipus Pond and in Egelund Pond, and some investigations were made in Lille Torkeri Pond and on specimens brought back to the laboratory. In Branchipus Pond (p. 10) some newly hatched nauplii were found under thin ice on 24.II.1950, but not until 13.III. did the development really begin. In the thawed zone there were then a large number of nauplii and some older juvenile stages, but no adults. On 31.III. a few individuals were fully mature but even so some females were found with attached spermatophores. In the middle of April only few immature specimens remained, and most of the females carried egg-sacs, and the number of males and females was about equal. At the same time as the water diminished the number of animals decreased, but as long as there was still some water it was possible to find both males and females, but no new broods of young ones occurred during the spring. After the drought no *D. castor* were found in the Pond and none occurred throughout the autumn, although there was sufficient water. In 1951 the beginning of the cycle was similar, but as the water level was considerably higher in that year, the pond did not dry up so early, and at the beginning of June nauplii were again found, at which time the number of adults was decreasing. By the middle of the month the number of adults had diminished considerably, but there were many specimens in the late

juvenile stages. Finally in July only adults were found, somewhat fewer in number than in mid June, and by this time there was not much water left in the pond.

In Egelund Pond (p. 12) the life cycle of *D. castor* followed the same course. In 1950 there was only one generation, and the last animals disappeared in the middle of June. In 1951 there were two generations. In both cases *D. castor* disappeared from the pond in the summer, although it did not dry up.

Because the water of both ponds was shallow and muddy no proper counts

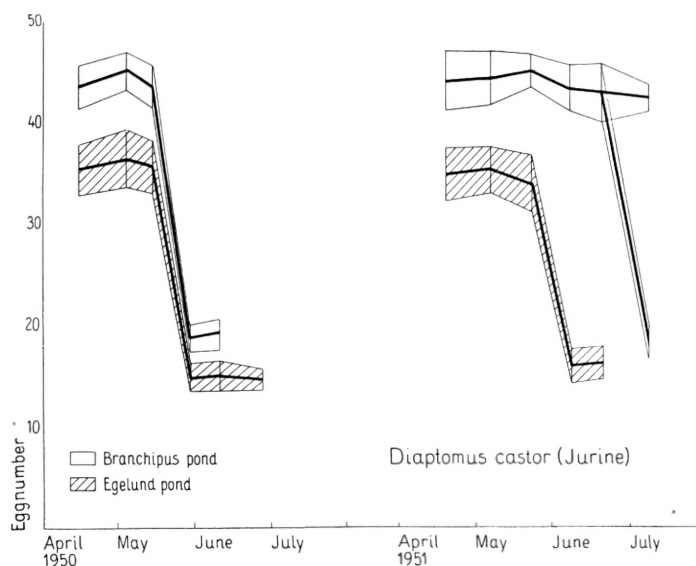


Fig. 10. *Diaptomus castor* (Jurine). The curves show the variations in the number of eggs in Branchipus pond and Egelund pond.

could be taken of the number of animals at the various depths, but in Branchipus Pond in 1951 and 1952 and in Little Torkeri Pond in 1952 samples were taken at intervals throughout the day which showed a certain daily migration. The nauplii: In the middle of March of both years these animals occurred in the vegetation at the bottom early in the morning, and most were in the deepest places, but in the course of the morning they spread all over the pond, and at noon they gathered almost exclusively along the shore where the water was warmest. In the afternoon they spread again, and in the evening they returned towards the bottom. The adults: Investigations were carried out on 9.VI.1951 and 29.IV.1952. The migration of the males and the females without egg-sacs was almost similar to that of the nauplii, but only very few females with egg-sacs occurred at any time in the open water. Most of them stayed a few cm. above or actually lay on the bottom.

My samples show that the reproductive period extends over the whole of the time when adults occur. Even in the samples containing few adults and at a time

of the year when the occurrence of the animals had almost come to an end, pairs in copulation and females with spermatophores were found.

In all the samples from Branchipus Pond and Egelund Pond in 1950 and 1951 egg counts were made when females with egg-sacs were present. The result is shown in Fig. 10. Conditions in Branchipus Pond seem to be more favourable than in Egelund Pond, the number of eggs was, in fact, always larger in the former. Probably this was chiefly due to differences in food supply, since the Egelund Pond, being covered with *Lemna*, cannot have had so high a production of plankton, and the animals there may therefore have been feeding at least partly on decomposed plant material. Examination of the intestines of some specimens from the two localities showed that those from Egelund Pond had a dark content with very few whole plankton algae, whereas those from Branchipus Pond had a greenish content consisting mostly of algae.

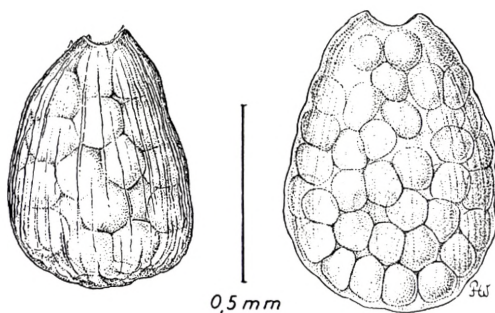


Fig. 11. *Diaptomus castor* (JURINE). Egg-sac with resting eggs (a) and subitaneous eggs (b).

During the first part of the life cycle the number of eggs was constantly high, but towards the end a sudden and marked decrease occurred. On further examination, both of the eggs and the egg-sacs, it appeared that there was a distinct difference between those produced early and late in the cycle. The

diameters of 20 eggs collected on 6.V.1950 respectively were measured and found to average: 0.117 ± 0.005 mm., whereas the average diameter of 20 eggs collected on 9.VI.1950 was: 0.138 ± 0.006 mm. While the pond was dry they were considerably larger; some dry mud which contained egg-sacs was taken to the laboratory. The average diameter of 20 of the eggs was 0.141 ± 0.005 mm., i. e. almost the same as for the eggs taken on 9.VI.1950. Furthermore there was a considerable difference between the appearance of the egg-sacs collected on 6.V.1950 and 9.VI.1950 (Fig. 11). The former were red or reddish brown, the capsule was quite thin and the surface was somewhat uneven, as the outermost eggs made it bulge a little. The eggs were closely packed and there was no glutinous substance between them. The latter were very dark brown, the capsule was strong, and over the surface there were some reinforcement lines radiating from the place where the sac was fastened to the female, there were fairly large spaces between the eggs which were filled with a brown glutinous substance.

This difference between two types of egg-sacs in *Diaptomus castor* has only been observed by GURNEY (1931), and he does not describe them. In the species *Acanthodiaptomus denticornis* (WIERZEJSKI), however, the two types are also known (HÄCHER 1901), and HÄCHER employs the name subitaneous and resting eggs (Subitaneier und Dauereier), for them. It is proposed to employ the same names for *D. castor*, but it must be emphasised that all diaptomid eggs are fertilised, and there is not the dif-

ference between subitaneous and resting eggs which occurs in Cladocera and Rotifera, where the former are parthenogenetic.

In order to ascertain whether there was any biological difference between the two types of egg-sacs, I placed several females with subitaneous egg-sacs in aquaria. As soon as the egg-sacs were shed, they were put into two open dishes containing mud and water. In one dish the mud was kept constantly moist and in the other it was left to dry up. After about 2 months the mud was placed in two aquaria, and filtered water from Lille Torkeri Pond was added. Only from the mud which had been kept moist did nauplii develop. A similar experiment was made with resting eggs, originating partly from Branchipus Pond, and partly from Lille Torkeri Pond. Here nauplii developed in both aquaria. A little mud had been retained from both experiments, and in this I found the egg sacs. The shape of the subitaneous eggs from the humid dish had not changed, whereas the egg-sacs from the dry dish had shrivelled up completely. In neither case had the resting eggs changed.

Thus, apparently, the function of the resting eggs is to prevent the species' perishing in completely dry localities. It goes without saying that in localities which are always wet it is an advantage for the species to produce subitaneous eggs, as the requirements for one egg are smaller, but they cannot secure survival during complete dryness.

It is not clear what factors make the animals produce resting eggs instead of subitaneous eggs. Drought itself cannot be the reason, as resting eggs were produced in Egelund Pond which did not dry up, nor does food shortage seem to play an important part, as there did not seem to be any difference between the contents of the intestines early and late in the life cycle. Similarly temperature cannot be a deciding factor as no resting eggs were present in Branchipus Pond in 1951 at a temperature at which only resting eggs were produced in 1950.

A possible explanation was obtained in the spring of 1952. Females with subitaneous eggs were placed singly into a series of small aquaria with slight aeration. After egg-sacs had been shed the aeration was interrupted, but the animals were left in the aquaria. A few specimens produced further subitaneous egg-sacs, but most of them produced resting egg-sacs. The oxygen content without aeration was found to be considerably below air saturation, usually about half, and shortly after the second egg-sacs were laid the animals died, probably because of lack of oxygen.

Even though these facts may be interpreted in several ways, it seems probable that the low oxygen content caused the production of resting eggs. This then may also have been the reason for the same phenomenon in the two ponds, as a marked decrease of oxygen must have occurred at the times when the resting eggs were produced, particularly towards the bottom, where the female occurred, but unfortunately no oxygen samples could be taken on account of mud.

According to WOLF (1905) nauplii of *D. castor* reach maturity in about 2 months in spring, and about 1 month in summer. My observations in Branchipus Pond seem to show that maturity was reached somewhat more quickly. At low temperatures in

spring the animals developed in about 1 month, and late in summer in about a fortnight. Some nauplii taken in Branchipus Pond in March 1952 were divided into three groups. The first group was kept at a temperature of about 4°, the second at about 10° and the third at about 20°C. The development of the first group took about 2 months, of the second group about one month and the last group were carrying egg-sacs after about a fortnight. It was therefore quite evident that a higher temperature quickens the development.

I have found that the egg-sac is produced 2 to 4 days after copulation. Some juvenile stages were isolated in small aquaria and only brought together when fully developed. After copulation the males were taken away and it was shown that at least 4 egg-sacs could be produced without further fecundation. Similar observations on cyclopoid species have been made by ERIKSEN (1951). On the average the females carried the egg-sacs for 5 days, and another was produced 2–4 days later.

Eudiaptomus vulgaris (SCHMEIL) 1898.

Previous investigations: It is difficult to decide with certainty which papers of the old literature deal with this species and which with the closely related species *Eudiaptomus coeruleus* (FISCHER) since most authors have made no distinction between these two species. Only recently have the two species been clearly defined. As far as I can see the following authors have dealt with *E. vulgaris*: WOLF (1903, and 1905) writes of the red variety, that it lives in small bodies of water, that it only lays eggs in summer and survives through unfavourable seasons by means of resting eggs. SCHMEIL (1898) and HARTWIG (1901) find that the occurrence of the species in large lakes is quite exceptional, whereas it is common in small water bodies, even such as dry up in summer. GURNEY (1930) states that the species (or, as he says, the population with a centre in the south of France) may reproduce even in winter, and finally, HERBST (1951) has observed that in South Schleswig the species occurs both in temporary pools and in perennial waters, exclusively in summer. This latter observation is important because HERBST is the only author who has distinguished *E. vulgaris* and *E. coeruleus* as two different species.

Records from Denmark are difficult to use as they do not tell us which species is concerned. Dr. HERBST has kindly determined the species from Lake Gribso (WESENBERG-LUND 1940) as *E. coeruleus* and the biology of the Gribso population corresponds with this determination as it occurs there throughout the year.

Present investigations: In Hjortesølen, both Central Pond and Border Pond, Vandings Pond and Vildande Pond, *E. vulgaris* occurred regularly in such large quantities that it was possible to study its biology.

In Vandings Pond (p. 17) the occurrence of the animals was as follows: Towards the end of May 1950 a large number of nauplii and metanauplii was found, and only a few specimens were in more advanced stages, and none were adult. On 9.VI.

many adults, both females and males were found, and many were in copulation, most of the population was still in various juvenile stages. During June the number of adults increased rapidly and egg-sacs were found, and the number of young ones decreased. In the middle of July only adults were found, mostly females, of which most carried egg-sacs, but from this time onwards the number decreased. At the beginning of August a number of nauplii were found with the adults, and the number of these increased greatly towards the end of the month, at which time only very few adults remained. This second generation reached maturity at the beginning of September, when many adults, both males and females with egg-sacs, were found. During October the number of animals again decreased, and in the middle of November no more *E. vulgaris* were found in the pond, and none occurred there during the winter. Not until the beginning of June 1951 were specimens again found there when nauplii and metanauplii were taken. By the middle of June most of these had matured and egg-sacs were found as well as couples in copulation. Finally at the beginning of July only adults were found.

In Vildande Pond (p. 21) the cycle was essentially similar to that found in Vandings Pond.

In Hjortesølen, Central Pond (p. 14) a few adults without egg-sacs were found at the beginning of June 1950, but a few couples were in copulation, and there were a large number of juvenile stages, mostly copepodids. Later in the month most of the animals were adults and many egg-sacs and couples in copulation were found. In the middle of July only adults were present and many had egg-sacs. At the beginning of August there were still many adults, but also many newly hatched nauplii. Towards the end of the month few adults occurred, but by then the second generation had almost reached maturity, and did so during September. At the time when water conditions prevented further investigations of the locality only adults were present. No individuals of the species were found in the samples taken from the ice during the winter, and not until the beginning of June did specimens occur again. These were mostly in various copepodid stages and very few were adults. From then onward conditions developed as in 1950.

In Hjortesølen, Border Pond (p. 13) no specimens were found during the spring of 1950, and not until the middle of October, when the water covered the whole bog, was the species found there. These were few and were all adults, most of which carried egg-sacs. At the beginning of November a few animals without egg-sacs were found, and from then on and until the beginning of June 1951, when only juveniles, mostly copepodids, were found, the species was absent. Towards the end of June many adults with egg-sacs occurred, and only rather few juvenile stages, and at the beginning of July, just before the pond dried up, conditions were unchanged except that no juvenile stages were observed.

In this locality I made a few collections in the autumn of 1951, and in this year also no *E. vulgaris* were found until the water level was so high that there was free water communication over the bog.

The samples from the four localities show distinctly that here *E. vulgaris* occurs exclusively in the summer, from July until the middle of the autumn, as a dicyelic form. However, the occurrence of the species in the Border Pond is a little peculiar. The absence of specimens in the spring of 1950 was probably due to the early drying-up of the pond, before they had developed, and its occurrence so late in the autumn was no doubt merely caused by the high temperature of the upper water of the bog itself; this prevented a great decrease of temperature at night in the shallow water and so enabled the animals to survive.

Presumably the species in the Central Pond was able to survive as well, but unfortunately this could not be ascertained.

Reproduction occurred throughout the period when adults were found, and only during the last few weeks of the life cycle of the animals were no individuals in copulation or with egg-sacs found. These animals cannot have been young ones which had not yet started breeding, as no juvenile stages had been found just previously.

The following can be said about the dependence of the animals upon the temperature: In no localities were nauplii found in the spring before the water had reached a temperature of at least 16°C. In Vandings Pond in 1951 the temperature exceeded this value before any nauplii were found, but as at the same time the temperature in other localities was lower, the high temperature in Vandings Pond had probably only just been attained and the nauplii had not had time to hatch. At the next sampling the development of the animals was far advanced.

This temperature limit for the development of the eggs was not, however, quite definite in Hjortesølen, Central Pond, where the temperature suddenly increased greatly. The eggs laid at temperatures below 16°C. in the autumn did not develop into nauplii until the following year when the temperature of the water had risen above 15°C. This temperature limit, however, apparently had no influence on copulation or on the production of the eggs.

Counts of the number of animals in a litre of water were made at various times in 1952. The animals were divided into four groups: ♂♂, ♀♀ without egg-sacs, ♀♀ with egg-sacs, and juvenile stages. The counts in Vandings Pond and Vildande Pond were made on 16.VI. and in Hjortesølen 17.VI. The results of the counts were as follows:

	♂♂	♀♀ with- out eggs	♀♀ with eggs	juveniles	Total
Vildande Pond					
7.00 a.m. Surface at shore.....	17	11	2	38	68
11.00 a.m. Surface at shore.....	32	19	4	57	112
3.00 p.m. Surface at shore.....	23	21	6	49	99
7.00 p.m. Surface at shore.....	21	16	4	32	73
Vandings Pond					
6.00 a.m. Surface at shore.....	..	5	..	3	8
Surface at centre.....	17	2	..	12	41
Just over bottom	21	11	27	27	89

Vandings Pond		♂♂	♀♀ with- out eggs	♀♀ with eggs	juveniles	Total
10.00 a.m.	Surface at shore.....	12	16	3	28	59
	Surface at centre.....	13	18	7	46	84
	Just over bottom	2	6	19	14	41
2.00 p.m.	Surface at shore.....	30	35	8	48	121
	Surface at centre.....	21	26	18	36	101
	Just over bottom	8	4	26	4	42
6.00 p.m.	Surface at shore.....	32	31	3	22	88
	Surface at centre.....	28	23	4	34	89
	Just over bottom	19	17	36	28	100
Hjortesølen, Border Pond						
6.00 a.m.	Surface	21	11	4	19	55
	Just over bottom	9	12	28	18	67
10.00 a.m.	Surface.....	25	27	15	44	111
	Just over bottom	6	11	18	14	49
2.00 p.m.	Surface	27	31	11	51	120
	Just over bottom	6	10	14	23	53
6.00 p.m.	Surface	23	18	8	29	68
	Just over bottom	10	26	30	21	86
Hjortesølen, Central Pond						
6.20 a.m.	Surface	3	5	..	17	25
	1 m's depth.....	2	10	2	21	35
	2 m's depth.....	21	21	5	26	73
	3 m's depth.....	18	11	12	12	53
10.20 a.m.	Surface	16	9	2	26	53
	1 m's depth.....	19	18	8	23	68
	2 m's depth.....	24	13	18	14	69
	3 m's depth.....	4	6	10	4	24
2.20 p.m.	Surface	7	5	..	28	40
	1 m's depth.....	25	25	11	29	90
	2 m's depth.....	12	11	22	12	57
	3 m's depth.....	..	1	10	6	17
6.20 p.m.	Surface.....	19	8	4	18	49
	1 m's depth.....	26	16	14	14	70
	2 m's depth.....	30	15	15	20	80
	3 m's depth.....	17	9	17	15	68

Even though these figures are not very conclusive the following main features can, in my opinion, be noted. Apparently there is in all localities a migration during the day from the deepest parts to the upper layers, but the migration is not equally marked for the four groups, nor does it take place in the same way in the various localities.

In Vildande Pond, where observations were only made at the surface as the bottom was too soft to permit counts, the number of the animals increased considerably at the surface from morning till noon, and from then on the number of animals decreased

slowly towards evening. The adult females carrying egg-sacs differed distinctly from the other groups as only a small number reached the upper layers.

In Vandings Pond conditions were almost similar. Apparently the animals spent the night in the depths at the centre of the pond, in the morning there was a migration towards the surface and the shore and in the afternoon the migration took the opposite direction. Here, too, the animals with eggs did not follow this schedule but seemed to remain on the bottom.

In Hjortesølen, Border Pond, movements resembled those in the first two localities, but as it was so shallow the figures here are not so clear.

Hjortesølen, Central Pond, was somewhat different from the other localities. Early in the morning the animals remained in the depths, but during the morning there was a general distribution throughout the upper layers, the numbers at the surface, at 1 m and at 2 m being almost equal. Later in the day there were a great many animals at 1 m, while they were more scattered at other depths, and still later there was a movement of the animals towards the bottom. Here also ♀♀ with eggs seem to prefer the deeper parts, and the juvenile stages seem to move into layers a little above those occupied by the other groups.

Individuals with egg-sacs keep closer to the bottom than the others, and this must be due to the fact that the weight of the eggs keeps them down. Perhaps also it is necessary that their movements should not be too violent lest the egg-sacs become detached. The migration of the other groups is probably due to various conditions between which it is difficult to distinguish. The position of the food in the water layers is possibly of some importance, as well as perhaps light and temperature.

Counts of the eggs of this species were made in all localities in 1950, and the results are shown from Fig. 12.

These counts show that the populations can be divided into two groups, one including Vandings Pond and Vildande Pond, and the other Hjortesølen, Central Pond. Hjortesølen, Border Pond occupies a peculiar intermediate position.

In the first group the number of eggs was large at the beginning of the reproductive period and then decreased abruptly. In August there was a large increase in Vandings Pond, but the number of eggs in Vildande Pond remained unchanged. Finally there was an abrupt decrease in both localities towards the end of the reproduction period.

In Hjortesølen, Central Pond, the number of eggs was rather small at the beginning of the reproductive period, and it remained almost unaltered, the number being about the same as that occurring in the first group toward the end of the period.

In October 1950 the number of eggs in Hjortesølen, Border Pond, was exactly the same as in the first group, and therefore to avoid confusion this number is not marked on the curve. In the spring of 1951 counts were again made for this locality as well as for the Central Pond, as it was found that while the number in the Central Pond had remained unchanged since 1950, the number in the Border Pond had

increased considerably, even though it did not reach the high level it had had in the spring of 1950 in Vandings Pond and Vildande Pond.

Apparently these differences in the number of eggs early and late in the reproductive period were not accompanied by differences in type of egg. The eggs were all surrounded only by a thin, hyaline, gelatinous envelope. Unlike WOLF (1903, 1905) I do not think that these eggs can survive desiccation, and this is supported

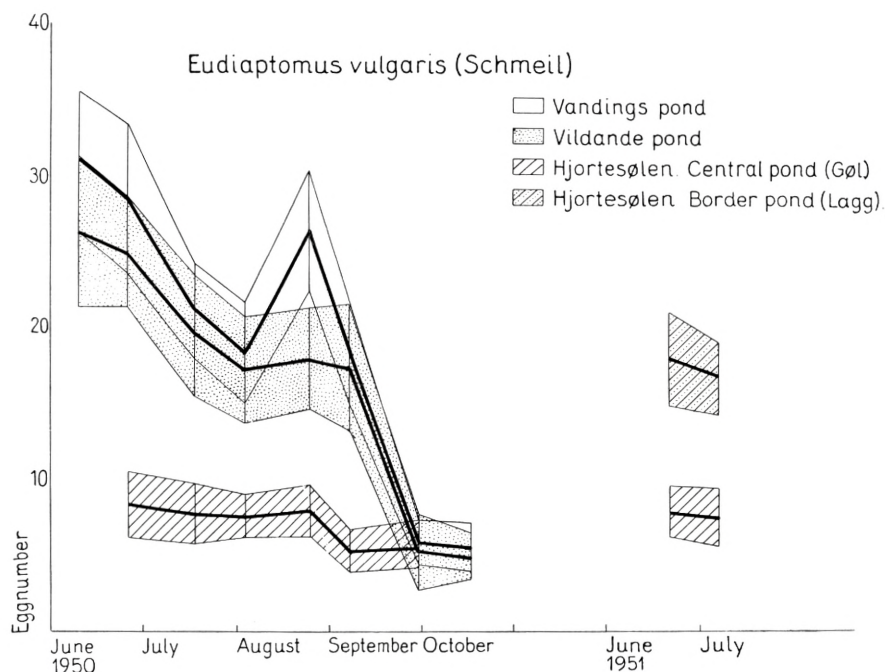


Fig. 12. *Eudiaptomus vulgaris* (SCHMEIL). The curves show the variations of the number of eggs in various localities.

by the fact that no specimens occurred in Hjortesølen, Border Pond, after it had dried up, and before there was free water communication with the Central Pond. That the species was found in the Border Pond in the spring of 1951 was because the drought occurred very late that year. In the years when the animals did not occur in spring the drying up took place so early that they had not had time to develop.

This, however, implies that the population in the Central Pond and the Border Pond are the same. If this were so one would expect the number of eggs in the two localities to be the same at all times, and it seems strange that a great difference in the number of eggs was found in the summer of 1951. It would appear that changing physico-chemical conditions brought about this difference, and that the darker and more acid water in the Central Pond does not give the same favourable life conditions as the less acid water in the Border Pond. This corresponds with the fact that the number of eggs in strongly eutrophic localities is greater than in Hjortesølen.

The occurrence of *Eudiaptomus vulgaris* in the localities examined by me does not correspond with statements in literature about the localities for the species. HARNISCH (1929) writes that centropagids cannot live at all in dystrophic localities unless they are slightly polluted, and KIEFER (1933) and HERBST (1951) support this. Hjorteløen, Central Pond, is an exception to this rule, as it is in no way polluted and is distinctly dystrophic. On the other hand, RYLOW (1935) writes that the species cannot live in strongly eutrophic waters, but Vandings Pond, and perhaps also Vildande Pond, must be described as such waters.

Macrocyclus albidus (JURINE) 1820.

Previous investigations: The literature does not contain much actual biological information about this species. SCHMEIL (1892) only states that it is very common and occurs in all types of water. WOLF (1905) also found it everywhere, but usually in small numbers. He is of the opinion that in some localities there are three reproduction periods, in January-February, June, and October, whereas in other localities there are only two, spring and autumn, but he also found egg-sacs at other times of the year. In his samples the number of eggs in each egg-sac always exceeded 25. ELTON (1929) points out that although found throughout the year the species is very much more abundant in summer. HARNISCH (1929) places the species in the group which does not occur in *Sphagnum* waters, and HERBST (1951) agrees with this.

Several Danish authors mention the species. SØREN JENSEN (1904) states that it is generally found in company with *M. fuscus* and usually in large numbers. C. WESENBERG-LUND (1917) found the species only in the profundal zone of the Lake Furesø. BERG (1938) found it in Esrom Lake, but only in small numbers, and the same author (1948) found it in the River Susaa and in Tuelaa. Here it seems to be characteristic of slowly running water with much vegetation. Finally K. LINDBERG (1950) found the species in several localities in Bornholm and also in *Sphagnum* waters.

Present investigations: I found *Macrocyclus albidus* in four localities: Brune Øje, Frøsø, Mørksø and Vildande Pond. The life cycle of the animals differed in the various localities, but in one particular they were alike: it was the fully developed animals which overwintered. Just after the thaw there was a copulation period and egg-sacs developed quickly.

In Brune Øje (p. 19) the cycle was as follows: In the middle of April 1950 hatching of some of the egg-sacs took place, and at the beginning of May young copepodid stages were found. At the same time the number of the adult overwintering animals decreased and towards the end of the month only a few were left. The next generation attained maturity at the beginning of June, at which time couples in copulation were observed. In the middle of the month females with eggs were found, and by then only a few juvenile stages remained. These conditions prevailed until the end of August the only difference being that a generation of young ones developed. At

the end of September no adults were found, and they did not reappear until November-December. No copulation or egg-sacs were observed during the winter, but reproduction began again in the spring. The cycle in 1951 then took the same course as in the previous year.

In Vildande Pond (p. 21) the overwintering generation developed egg-sacs towards the end of March 1950 and disappeared at the beginning of May. Towards the end of that month a fairly large number of adults was again found, but in this second generation no egg-sacs occurred until the beginning of June, when copepodid stages were still present. At the end of the month, when the number of adults was considerably greater, no further copepodid stages were found, but nauplii and metanauplii were present: these must represent the third generation.

In the middle of July the number of adults of the second generation decreased markedly, and at the beginning of August only a few females, all without egg-sacs, were found. At the same time the number of juvenile stages increased and some of these, belonging to the third generation, attained maturity at the end of August, when a few couples were found in copulation. At the beginning of September the number of adults had increased considerably and many egg-sacs occurred. This, however, lasted only until the end of the month. At the beginning of October only a few adults remained, and there were many juvenile stages, which became mature at the beginning of December. The next reproductive period did not occur until the following spring.

The development in Frøsø (p. 28) was apparently very like that in Vildande Pond; in that there were also three reproductive periods, in March, towards the end of May, and in August-September. Conditions are not quite clear here, as the interval in time between the samples was too great, but the development sketched above is supported by the fact that between the afore-mentioned times a decreasing number of adults and a large number of juvenile stages were found.

In Mørksø (p. 24) the reproductive period of the overwintering generation began during March 1950 and the next generation seemed to have reached maturity at the beginning of June, for at the end of March many animals in the last copepodid stages were found, but no adults, and at the beginning of July many ♀♀ with eggs were observed, but no copulation. In the middle of August adults and egg-sacs were rather scarce, but many juvenile stages occurred. In September all adults had disappeared, only young ones remaining, and adults were not found again until the middle of October. They showed no signs of copulation, they overwintered and formed the first generation of the following year.

The number of generations was therefore not the same in the different localities. Thus, in Brune Øje, in Frøsø, and in Vildande Pond, there were three generations, whereas in Mørksø only two generations occurred.

In Frøsø and in Vildande Pond each generation appeared to have a well defined reproductive period. In Brune Øje it was impossible to separate the end of the reproductive period of the second generation and the start of that of the third generation, as egg-sacs were found throughout the period from the end of June to the end of

August. This implies that a few of the overwintering animals may have belonged to the second generation. Finally there were only two reproduction periods in Mørksø, one in each generation. Apparently it was the reproductive period of autumn which had dropped out, because the second reproduction period had been delayed so much that the resulting young had not had time to develop.

The first egg-sacs in the spring were found at temperatures from about 4–12.5°. In spring the nauplii in all localities developed into adults in 1½ to 2 months, while the development in the summer was much quicker and was sometimes less than a fortnight (e. g. in Vildande Pond during the summer maximum). The development in autumn of the overwintering generation was very slow and took about 3 to 4 months. The most rapid development was in the lighter localities, Vildande Pond and Frøsø, while in the two darker localities Brune Øje and Vandings Pond it was slower. Probably it is not the greater intensity of light and the resulting higher temperature, which are the controlling factors, it is more likely the better nutritive conditions, caused by the greater production of phytoplankton in light than in dark-coloured waters.

Counts were made in Vildande Pond and in Brune Øje of the number of animals in a litre of water at various times of the day and various seasons in 1952. In Vildande Pond collections were made only at the surface, and in Brune Øje both at the surface and at the bottom. Only the adults were counted; the results were as follows:

Brune Øje, 16.III.1952		♂♂	♀♀	Total
6.40 a.m.	Surface	1	1
	Bottom	27	22	49
10.40 a.m.	Surface	6	8	14
	Bottom	23	30	53
2.40 p.m.	Surface	29	23	52
	Bottom	28	19	47
6.40 p.m.	Surface	10	8	18
	Bottom	21	24	45
16.VI.1952				
6.40 a.m.	Surface	5	7	12
	Bottom	37	46	83
10.40 a.m.	Surface	21	19	40
	Bottom	27	28	55
2.40 p.m.	Surface	22	26	48
	Bottom	14	18	32
6.40 p.m.	Surface	11	16	27
	Bottom	32	33	65
Vildande Pond 16.III.1952				
7.00 a.m.	Surface	2	2	4
11.00 a.m.	Surface	9	11	20
3.00 p.m.	Surface	25	27	52
7.00 p.m.	Surface	14	23	37

16.VI.1952		♂♂	♀♀	Total
7.00 a.m.	Surface	4	5	9
11.00 a.m.	Surface	18	20	38
3.00 p.m.	Surface	34	40	74
7.00 p.m.	Surface	19	17	36

These figures clearly show that the animals migrate throughout the day. During the dark time they stay just over the bottom, probably in the vegetation, and during the light period they ascend towards the surface. In Brune Øje there were apparently more animals in the middle of the day, as shown by the total found at the two levels; this is probably explained by the fact that all the animals which were swimming in

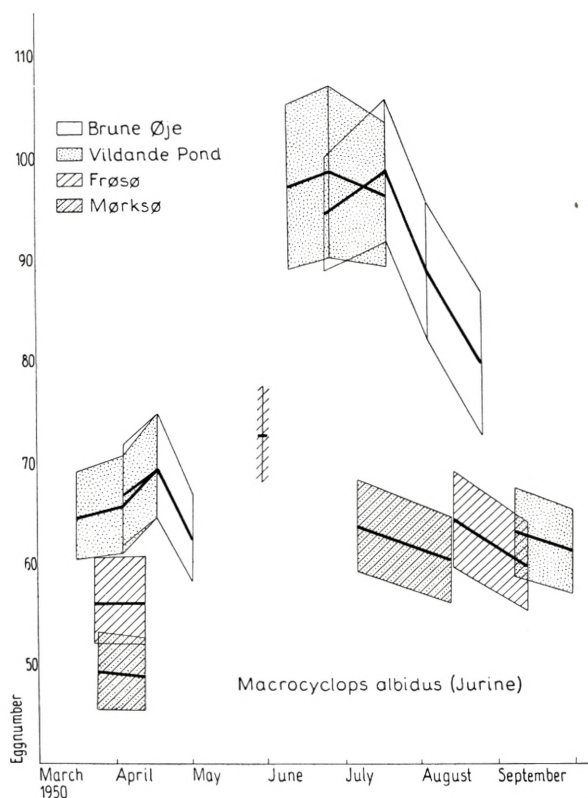


Fig. 13. *Macrocyclus albidus* (JURINE). The curves show the variations in the number of eggs in various localities.

the free water layers were caught, whereas only some of the animals in the vegetation or at the bottom were taken.

The curves show the total number of eggs in the two egg-sacs in the various localities throughout the year (Fig. 13). It can be seen that there was a considerable difference between the number of eggs in Vildande Pond and Brune Øje on the one

hand, and Frøsø and Mørksø on the other. In the two former lakes the number was considerably larger throughout the year (with the exception of Vildande Pond in late autumn). Comparisons between the chemico-physical conditions in the four localities show that the localities where the number of eggs was large were strongly eutrophic with high conductivity and a constantly high pH, whereas the localities where the number of eggs was small had low conductivity and a pH which seldom exceeded 7.0.

In each locality there are large fluctuations in the number of eggs throughout the year. In spring the number is small, in midsummer it was large, particularly in Vildande Pond and Brune Øje, less markedly in Frøsø, and during the autumn it decreased to about the same number as in the spring.

A few authors have suggested that this species is able to live in pools which dry up, e. g. ELTON (1929). It is of course possible that it may occur now and again in such localities, but the life cycle clearly shows that normally it lives in permanent waters. In such waters the species is perennial, and its development only varies with nutritive and chemico-physical conditions.

Macrocyclops fuscus (JURINE) 1820.

Previous investigations: Strangely enough biological information on this rather common species is scarce. SCHMEIL (1892) writes that it occurs in clear, stagnant water, and that it prefers ponds to large lakes. WOLF (1905) found 3 numerical maxima, in spring and autumn, and a less pronounced one in summer, and he suggests that each corresponds to one generation. HARNISCH (1929) classes the species amongst those copepods which can only live in *Sphagnum* waters when these are more or less polluted, and states that they cannot live in purely dystrophic water. KIEFER (1933) and HERBST (1951) are of the same opinion. The latter also states that the species is most common from July to November.

Some Danish authors mention the species. SØREN JENSEN (1904) found it in clear stagnant water; C. WESENBERG-LUND (1951) suggests that it prefers puddles. BERG (1948) found it in the vegetation of the River Susaa, and finally K. LINDBERG (1950) found it in some localities in Bornholm, in a *Sphagnum* moor amongst other places.

Present investigations: Regular collections of the species were made in five localities, Brune Øje, Frøsø, Mørksø, Troldso, and Vildande Pond, and a few observations were made in the following localities: Peat-digging at the 35 km. stone and Peat-digging in Rødkær.

In all the five localities which were regularly examined, the animals overwintered as adults, without any reproductive activity and without egg-sacs, but otherwise there were several differences in the annual cycles.

In Brune Øje (p. 19) one ♀ with attached spermatophores was found in March 1950, and at the beginning of April much copulation was taking place and many females were found carrying egg-sacs. Towards the end of April the number of adults

decreased greatly, and many juvenile stages appeared. At the beginning of May most of this second generation had attained maturity and were carrying egg-sacs, and few juveniles remained. At the beginning of June the adults of the second generation had already decreased in number, but the number of juvenile stages had become large. Towards the end of June and throughout most of July, the number of adults increased steadily, and the number of juvenile stages decreased. At the beginning of August a large number of nauplii, which almost certainly belonged to this species, were found, and towards the end of August few adults, but many juvenile stages were present. None of the latter, however, were in the later copepodid stages. In the middle of September very few adults were found, and none had egg-sacs, although these had been present all through the summer, but there were an immense number of young ones in all stages. During the autumn the number of adults increased considerably, and the number of young ones decreased correspondingly. At the beginning of November only adults were present, but no copulation or egg-sacs were observed. During the winter no change occurred, and not until the following March were animals again observed in copulation. After that the cycle was almost the same as in the preceding year, with the exception that the generation after the overwintering one was considerably larger than in the previous year, and there was no clear distinction between that and the following generations.

In Vildande Pond (p. 21) there were likewise only adult overwintering specimens with no reproductive activity, and not until the beginning of April 1950 were couples observed in copulation. In the middle of this month ♀♀ with egg-sacs were seen, and young ones were found at the beginning of May. From the end of May to the beginning of June the number of adults decreased considerably, and then it increased again to a high level in July, and intense reproductive activity occurred. The large number of animals persisted until the end of August, and at the same time new specimens attained maturity. At the beginning of September very few adults remained, but there were many juvenile stages. From November until the middle of March only adults were found, and there was no reproductive activity.

In 1951 the cycle was the same as in 1950.

In the Jutlandic localities Frøsø, Mørksø, Peat-digging at the 35 km stone, Peat-digging in Rødkær, and Troldsø, it was also found that no reproductive activity occurred during the winter.

In Frøsø (p. 28) animals in copulation and ♀♀ with egg-sacs were observed at the beginning of April. By the middle of May this generation had almost disappeared and many specimens in the last copepodid stages were found. During the summer both adults with egg-sacs and juvenile stages were found, but by the middle of September the number of adults had developed greatly, and the number of juvenile stages had become large. These juvenile stages attained maturity rapidly, and from the middle of October onwards only adults of the overwintering generation were found.

In Mørksø (p. 24) the species was not common and was apparently largely replaced by the closely related species *Macrocyclops albidus* (JURINE). Couples in

copulation and a few egg-sacs were found in the middle of April, and by the end of May the overwintering generation had disappeared, and only late copepodid stages were found. Otherwise the cycle was like that in Frøsø, with the exception that the overwintering generation was not fully adult until the end of November.

In Troldsø (p. 30) only one couple in copulation was found in April and no egg-sacs were seen until the end of May, by which time no juvenile stages had appeared. At the beginning of July active reproduction and many juvenile stages were observed and the same was found in the middle of August. In the middle of September, however, only late and early copepodid stages were seen (which in this locality must have belonged to this species), and the overwintering generation was not fully mature until the end of November.

Thus, apparently, there were certain differences between the cycles of the species in the five localities. The overwintering, adult generation was common to all of them, as it was to the two localities from which only a few samples were taken. Otherwise, however, considerable differences were found. The most important was that the early reproductive periods were not simultaneous. In Brune Øje breeding started in March, in Vildande Pond, Frøsø and Mørksø it did not begin until the middle of April, and in Troldsø it began even later. There is thus apparently a correlation between the chemico-physical conditions and the onset of the first reproductive period, the more eutrophic the locality is, the earlier this occurs.

It is not possible to ascertain how many generations there were in any of the localities during the year. My findings are most clear for Brune Øje and Vildande Pond where samples were taken at the shortest intervals of time. In the former the overwintering generations were, so far as I can judge, the offspring of the second and third (and perhaps even the fourth) generation, which together produced the summer maximum in July, but apparently there was one generation less in Vildande Pond. In the other localities the position is less clear, but as far as I can judge the number of generations was the same in Mørksø and Frøsø as in Vildande Pond, while there was one generation less in Troldsø, because the cycle there began later.

Correlated with the number of generations is the length of time needed for the individuals to attain maturity. This, too, seems to vary according to the seasons and to the localities. In Brune Øje the offspring of the overwintering generation developed into adults in about one month, while in Troldsø this took about $1\frac{1}{2}$ months. In summer the development in all localities was considerably more rapid, and was accomplished in a fortnight under favourable circumstances. In autumn more time was again needed, it took about $2\frac{1}{2}$ months in Brune Øje, Vildande Pond and Troldsø, and about 2 months in Frøsø and Mørksø.

Migrations of the animals were studied in Brune Øje and in Vildande Pond on 16.III. and 16.VI.1952 by taking counts of the number of animals in a litre of water at the surface and at the bottom at different times of the day. The results were as follows:

Brune Øje		16.III.1952			16.VI.1952		
		♂♂	♀♀	Total	♂♂	♀♀	Total
6.40 a.m.	Surface	3	1	4	13	16	29
	Bottom	47	51	98	50	49	99
10.40 a.m.	Surface	21	18	39	37	41	78
	Bottom	37	42	79	40	38	78
2.40 p.m.	Surface	35	31	66	54	49	103
	Bottom	21	26	47	19	23	42
6.40 p.m.	Surface	19	20	39	27	24	51
	Bottom	31	34	65	35	42	77
Vildande Pond							
7.00 a.m.	Surface	2	1	3	6	4	10
11.00 a.m.	Surface	17	22	39	47	40	87
3.00 p.m.	Surface	50	42	92	48	43	91
7.00 p.m.	Surface	21	19	40	31	27	58

Only fully developed animals have been included in the table, and no distinction has been made between ♀♀ with and without egg-sacs.

For this species as for the others there seems to be a daily migration, the animals remaining near the bottom throughout the night and moving into the upper water layers during the day. In June the animals ascended earlier in the day than in March. There was no difference between the daily migrations of the ♀♀ and the ♂♂.

Egg counts for this species were made in only two localities, Brune Øje and Troldso. The results are given in Fig. 14. It appears that the number of eggs was considerably larger in the eutrophic Brune Øje than in the dystrophic Troldso. It also appears that in Troldso the maximum number of eggs was found at the beginning of the reproductive period, whereas in Brune Øje the number increased from May to June and diminished during the summer.

Of the two closely related species *M. albidus* and *M. fuscus*, the latter is apparently the more common in Denmark, and where the two species are found together, *M. fuscus* is also more frequent. The only exception I have found is Mørksø. It would seem that the habitat requirements of the two species are very similar.

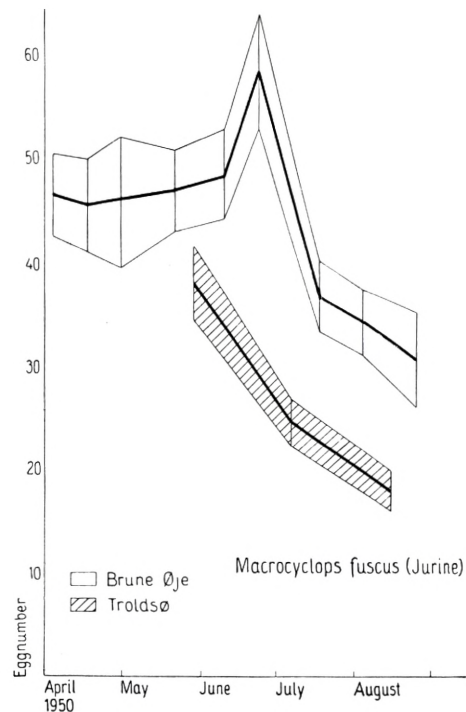


Fig. 14. *Macrocyclus fuscus* (JURINE). The curves show the variations in the number of eggs in Brune Øje and Troldso.

***Eucyclops serrulatus* (FISCHER) 1851.**

Previous investigations: All authors who have studied this species state that it is the most common cyclopid, and it is most frequent in dense vegetation and in the littoral zone of small bodies of water (SCHMEIL 1891, PESTA 1928, GAJL 1927, and HERBST 1951). The latter author found it in very large numbers in the summer, while it was rare in winter.

Previous Danish investigations: SØREN JENSEN (1904) states that it is found everywhere, but his observations probably refer to a mixture of *E. serrulatus* and the closely related *E. speratus*. C. WESEBERG-LUND (1917) states that in Furesø the species is not so common as others, and later (1937) that it is the most common species in pools. BERG (1938) found it in Esrom Lake and in the River Susaa (1948), and in the latter locality the species occurred everywhere, except in the plankton, and in all seasons. K. LINDBERG (1950) found it in Bornholm in 23 out of 30 localities examined. It was the most common species in all smaller localities, but it was rare in lakes and entirely lacking in brackish water.

Present investigations: Although most of the localities investigated were small ponds, the species was only found in sufficiently large numbers to permit biological investigations in one locality, viz. Brune Øje (p. 19).

In the middle of April 1950 many adult specimens were found, and there were also several juvenile stages. Some couples were observed in copulation, but no females with egg-sacs were found. In earlier samplings several young ones, which must have belonged to this species, had been taken. At the beginning of May females with egg-sacs occurred, there was an enormous increase in the number of adults, and almost all the juvenile stages had disappeared. At the end of May and the beginning of June the number of adults was almost the same, but new juvenile stages had appeared. By the end of June very few young ones remained and enormous numbers of adults and late juvenile stages were present; almost all adult ♀♀ carried egg-sacs. In July and August the number of adults was still large and throughout this period egg-sacs and many juvenile stages were found. At the beginning of September the number of adults had diminished considerably but it increased somewhat in October. At the same time the young ones disappeared. There was another reproductive period at the beginning of November, but no young ones were found immediately afterwards. During the winter the species became increasingly rare, most of the animals found being ♀♀ with egg-sacs, and by the beginning of March very few remained. At this time young ones were found, and these attained maturity at the beginning of April. Henceforth the cycle followed the same course as in 1950.

It is difficult to distinguish between the generations of this species. The life cycle, however, seems to be as follows: The species overwinters as fully developed animals and discarded egg-sacs, produced by a late autumn copulation. The first generation of the year attains maturity in April, and a reproductive period follows immediately afterwards. During the summer there are two or three generations, and finally there

is an autumn generation, from which the population of the following year is derived. Apparently, survival of the adults of the autumn generation does not seem to be necessary, as the number of ♀♀ with egg-sacs diminished greatly during the winter, and in the early spring of 1950 no adult animals were found at all. Probably it is only the egg-sacs shed by this generation which ensure the survival of the species.

Counts of the number of animals in a litre of water at the bottom and at the surface were made on 16.VI.1952. No counts were made in early spring, as I could not identify the juvenile stages with certainty. The results were as follows:

		16.VI.1952		
		♂♂	♀♀	Total
6.40 a.m.	Surface	8	12	20
	Just over the bottom..	26	23	49
10.40 a.m.	Surface	27	30	57
	Just over the bottom..	13	12	25
2.40 p.m.	Surface	37	36	73
	Just over the bottom..	3	4	7
6.40 p.m.	Surface	18	22	40
	Just over the bottom..	20	21	41

These figures seem to show daily migration, the animals moving into the upper water layers in the lightest hours of the day. The upper water layers were, however, never quite devoid of the species, whereas the layers near the bottom were almost deserted in the middle of the day. Apparently there was no difference between the migration of ♂♂ and ♀♀.

No egg counts were made for this species as only one locality was investigated.

From the life cycle data given above it is difficult to follow the development from nauplius to adult. In spring one month elapsed between the first occurrence of juvenile stages and that of couples in copulation, in autumn this period was about 1½ months. In the middle of the summer the development was very rapid, but as the generations overlapped it was not possible to ascertain how long each took.

***Eucyclops speratus* (LILLJEBORG) 1901.**

Previous investigations: As *Eucyclops speratus* was only fairly recently recognised as an independent species, the literature does not contain much biological information. Almost all authors agree that it occurs only in small perennial bodies of water or in the littoral zone of lakes, and that it may be found throughout the year, although in varying numbers. HERBST (1951) writes: "Zahlreicher wurde diese Art einigemale in Spätherbst (Oktober bis Dezember) einmal auch im Sommer (Juli) beobachtet."

From Denmark information is also limited. BERG (1938) has observed that the species occurs only in the shallower part of the littoral zone of Esrom Lake, and in 1948 he states that the species occurred in fairly large numbers throughout the year

in the River Susaa. It was always taken near the bottom, both in the vegetation and outside it, and only exceptionally in the plankton. LINDBERG (1950) found it in three localities in Bornholm in July, and also in running water.

Present investigations: I have only found the species in one locality, Vildande Pond (p. 21) but it was present in such large numbers that study of the biology was possible. Just after the thaw in March 1950 many individuals were caught, some were couples in copulation and some were ♀♀ with egg-sacs. The egg-sacs looked quite new, and apparently there were no immature individuals. During April and May the number of adults diminished, but at the same time young ones appeared in increasing numbers, but it was difficult to be certain of the identity of the very young stages, as only the late copepodid stages have clear characters. These young stages became mature during June and July. Immediately maturity was reached, couples in copulation were found, and somewhat later ♀♀ with egg-sacs occurred. During August and September all the adults disappeared, but at the same time a large number of juvenile stages had developed, which at the beginning of October could be certainly identified as belonging to this species. This third generation attained maturity in October and November, and although females with egg-sacs were found in November and December no juvenile stages were found during the winter. At the beginning of February 1951 many adults were taken in and just over the surface of the mud, but none were carrying egg-sacs. Such were not found again until the beginning of April, from which time the cycle took the same course as in 1950.

Thus, at any rate in Vildande Pond, *E. spératus* overwinters as adults without egg-sacs. Apparently there is a prolonged period between the mating in spring and the time when young ones are found, so the winter generation carries the egg-sacs for a long time, probably about one month. It is strange that egg-sacs were found in the late autumn but not in the winter, and that the same generation then carried egg-sacs in the spring. I think that the late autumn egg-sacs were shed and remained unhatched until the following spring since no nauplii were found during the winter. It is possible, however, that immediately after hatching the nauplii pass into a resting stage, but it would seem more likely that unhatched egg-sacs ensure the survival of the species through periods of complete freezing. The ♀♀ lost their egg-sacs as soon as ice formed on the pond, and new ones were not developed until the reproductive period in the following spring.

The distribution of the animals in the water does not vary much within the seasons. In winter all the specimens were taken on or just over the bottom and were sluggish and very disinclined to move. When taken to the laboratory and kept at room temperature for some hours they grew more active and began to swim about. On such occasions I even observed couples in copulation. The animals thus seem to be in some sort of resting state during the winter, and activity, and hence the consumption of food, are reduced. At the same time the animals are ready to profit by the first sign of improved living conditions to resume their activities. In spring presumably the higher temperatures bring about the increased activity, since neither the oxygen

conditions, nor the light were much changed in this biotope during the short period which elapsed between the thaw and the first appearance of egg-sacs. I am not sure what increase of temperature is required, but it must be small. Presumably the egg-sacs which were shed but not hatched in the autumn, hatch at similar temperatures to those at which the adults became active. No experiments were made on this point as no egg-sacs could be found in the mud.

The development of the individual seems to take a long time, as both in spring and in autumn two months elapse between the production of egg-sacs and the appearance of late copepodid stages, and another fortnight passes before the animals reach maturity.

Counts of the number of individuals per litre of water were made on 16.III. and 16.VI.1952. Only adults at the surface were counted. The results were as follows:

	16.III.1952			16.VI.1952		
	♂♂	♀♀	Total	♂♂	♀♀	Total
7.00 a.m.	2	3	5	4	5	9
11.00 a.m.	19	20	39	18	14	32
3.00 p.m.	37	42	79	41	39	80
7.00 p.m.	17	15	32	22	19	41

The table shows that this species like the others makes daily migrations. During the dark hours the animals are not so frequent in the upper layers of the water as during the light hours. There was apparently no difference between the migration in spring and in summer, nor between the behaviour of males and females.

The life cycle of *Eucyclops speratus* in this locality seems to be similar to that found by WOLF (1905) for *E. serrulatus*. I think it is possible that WOLF, in fact, studied *E. speratus*, as, since he does not cite LILLJEBORG's paper (1901), he was probably unaware of the difference between these two species.

Cyclops (Cyclops) insignis CLAUS 1857.

Previous investigations: All authors who have examined this species, SCHMEIL (1892), SARS (1918), KOZMINSKI (1927), RZOSKA (1925) and HERBST (1951) agree that it is a cold water form, and that adults occur only from December until March. HERBST (1951, p. 511) writes of the localities in which they are found: "Er tritt in grösser Häufigkeit in den kalkreichen Kleinweihern, seltener in Tümpeln auf und meidet Moorgewasser und die stark beschatteten Waldtümpel". The same author is of the opinion that the species survives the summer as resting eggs as he never found juvenile stages in that season.

In Denmark SØREN JENSEN (1904) found it at the beginning of April in a grassy pool near Aalborg, and BERG (1948) found it in April, July and December in the River Susaa, where it was always in the vegetation.

Present investigations: I have only found *Cyclops insignis* in Vandings Pond (p. 17). At the beginning of March 1950 many individuals were found, all of which were adult males and females. Some couples in copulation were observed, and several females had attached spermatophores, but no egg-sacs were seen. In the middle of the month many females carried egg-sacs, and during March the number of individuals decreased, first the males and later the females, until, at the end of April, no specimens were found. During this period no young ones were observed. Immediately after the disappearance of the adults several nauplii of cyclopids were taken to the laboratory, but all developed into other species. This was repeated until the end of September, when some of the nauplii developed into adults of *C. insignis*. In the middle of October there were two developmental stages of cyclopid species in the pond, of which the most developed forms, the 4th and 5th copepodid stages, belonged to *Cyclops viridis* while the least developed ones, the 1st and 2nd copepodid stages, were *C. insignis*. At the beginning of November a few adult males of this species occurred together with an extremely large number of animals in the latest copepodid stages. During November and December the number of adults increased steadily, but mature females did not occur until the middle of December; at the same time the number of young ones decreased. At the beginning of February only adults occurred; most of these were found just above the bottom, and very few were swimming in the water, just under the ice. The number of males and females was about equal, but neither couples in copulation nor females carrying egg-sacs were observed. At the beginning of March females with attached spermatophores occurred, but egg-sacs were still absent, and they were not found until the middle of the month. During May the species disappeared completely.

This life cycle agrees with previous observations on this species. It is clear that there is only one generation each year, and that the reproductive period starts towards the end of the winter. The exact time varies a little from year to year, but is apparently at the thaw. Probably the reproductive period is not initiated by any increase of temperature, since couples in copulation were found early in the morning under new ice caused by night frost, but by the better light conditions and the resulting enhanced biological activity.

One or two problems in the life cycle of the species deserve attention. Firstly, what factors cause the animals to disappear in the spring, secondly in what stage do the animals survive the summer, and thirdly what factors bring about a resumption of the development in the autumn?

When the animals disappeared, the temperature (at the next sampling) was 11°C (1950), 18.5°C (1951) and 14°C (1952). Oxygen and other chemico-physical conditions remained more or less unchanged, but biological conditions had altered, for just at this time there was so large a maximum of *Daphnia pulex* that the water was coloured reddish-brown. Thus there were apparently only two factors which need to be considered when seeking an explanation of the disappearance of the species, namely an increase of temperature and the appearance of a competitive species.

In the middle of February 1952 a large number of specimens was collected. They were placed in water from the locality in an icebox at 2°C, at which temperature they survived until the end of May. About once a week 25 specimens were placed five in each of 5 small aquaria. The aquaria were kept at the following temperatures: 1°, 5°, 10°, 14° and 18°C. At the beginning of May, when the last specimens were removed from the ice-box, a double set of animals was taken out and to each aquarium of one of the sets 10 *Daphnia pulex* were added. Altogether 10 series of samples were taken. The results are shown in the curves, Fig. 15. These curves are the result of adding together the number of animals surviving in aquaria kept at the same temperature and show the number of days of survival after the start of the experiment. This was permissible, since there was no difference in the mortality in May and February, nor was there any difference in the death-rate of animals in the aquaria with and without *Daphnia pulex*. The curves show that the percentage of surviving *Cyclops insignis* at 1° and at 5° was high after a period of 10 days. At 10° about 50% were still alive after 10 days, at 14° nearly all had perished, and finally all were dead after only four days at a temperature of 18°.

In other words, increase of temperature is an important factor in the disappearance in the spring, and the critical temperature seems to be about 10–14°C.

As far as can be judged from these experiments *Daphnia pulex* plays no part in the disappearance.

I should like to make the following remarks about the survival during the summer. At the time of and immediately after the disappearance of the species from Vandings Pond a number of nauplii was found, but it was shown by rearing them that they were all *Cyclops viridis*. In 1950 and 1952, immediately before young stages of *C. insignis* were recognisable a large number of nauplii and metanauplii were found, and, in aquaria, these proved to be partly *C. insignis* and partly *C. viridis*. Thus it would seem that juvenile stages of *C. insignis* are absent in the summer, and that the species survives the summer as egg-sacs.

I found loose egg-sacs in the mud of Vandings Pond several times during the summers of 1951 and 1952, and these were of such a size that they could only belong to one of the two large cyclopid species in the pond, *Cyclops viridis* or *Cyclops insignis*.

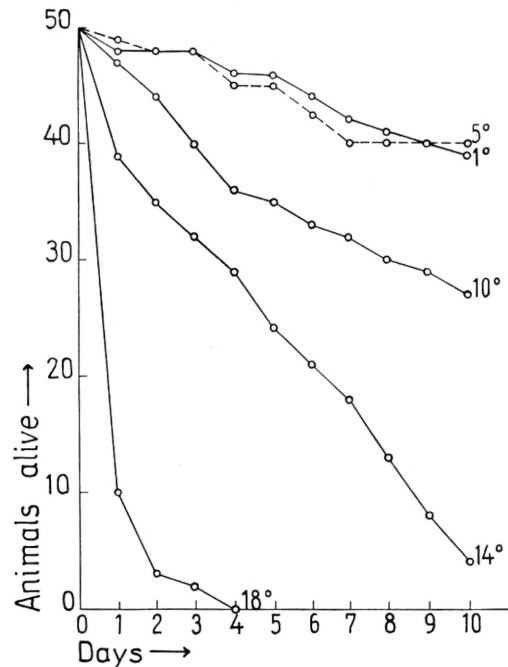


Fig. 15. *Cyclops (Cyclops) insignis* CLAUD. Curves showing the death rates of the animals at various temperatures.

Some egg-sacs were kept in the laboratory in water from the locality at about the same temperature as that prevailing in the Pond. From these egg-sacs nauplii developed which all belonged to *Cyclops virides*, but some egg-sacs did not hatch. In 1952, after nauplii had developed from *C. viridis* egg-sacs, I placed the remaining egg-sacs in aquaria at a temperature varying from 8° to 12°C. At these temperatures some more nauplii developed (the rest of the eggs had probably died), and in the course of the autumn these nauplii developed into adult *C. insignis*. This agrees well with observations made in Vandings Pond, as nauplii there occurred at a temperature of 12°. They had, however, perhaps hatched at a somewhat higher temperature.

The above shows also that the temperature at which the adults disappear is similar to the temperature at which nauplii occur, the former being somewhat higher. The egg-sacs are thus probably laid at a temperature slightly higher than that at which the eggs are able to develop, which ensures that there is no waste in spring of hatched nauplii unable to develop further during summer.

Compared with the other species the development of nauplii seems very slow, also there seems to be a difference between the rate of development of the sexes. The first newly hatched nauplii were found on 29.IX.1950 and on 9.XI. adult males occurred; the first adult females, however, were not found until 18.XII., i. e. one month later. This difference in the rate of development of the two sexes seems to persist since only females were taken on 17.IV.1951 and 5.V.1951.

The distribution of the animals in the water layers was examined on the 16.III. 1952 by counting the number present in a litre of water at various points. The results are shown below. These observations were supplemented by collections made at various depths under the ice.

		16.III.1952		
		♂♂	♀♀	Total
6.00 a.m.	Surface, shore	14	12	26
	Surface, centre	18	21	39
	Just over the bottom	31	28	59
10.00 a.m.	Surface, shore	16	19	35
	Surface, centre	10	14	24
	Just over the bottom	22	24	46
2.00 p.m.	Surface, shore	6	8	14
	Surface, centre	4	2	6
	Just over the bottom	37	29	66
6.00 p.m.	Surface, shore	13	18	31
	Surface, centre	9	8	17
	Just over the bottom	36	33	69

The investigations through the ice showed that just below the ice only males were caught, while just over the bottom specimens of both sexes occurred, but most were females. Thus it would seem that while the pond is covered with ice the sexes keep apart. The counts, however, show that this is not so later in the season, as there

were then similar numbers of the two sexes in the various water layers. The counts further show that there is a daily migration, and that during the light hours of the day the animals move from the free water layers towards the bottom.

Cyclops (Cyclops) strenuus strenuus FISCHER 1851.

Previous investigations: There are numerous published investigations on *Cyclops strenuus*, but it is difficult to see which actually deal with this subspecies. The first which certainly deals with the present subspecies were made by KOZMINSKI (1927, 1932) and RZOSKA (1931). These two authors and GURNEY (1933) and HERBST (1951) agree that it is a coldwater organism, occurring in small ponds and dried up pools, but it has also certainly been found in lakes.

The Danish investigators give little information on the biology of the subspecies concerned. It is probable that the studies of SØREN JENSEN (1905) and C. WESENBERG-LUND (1904, 1909, 1917 and 1937) did not concern this subspecies at all, but the species mentioned by BERG & NYGAARD (1929) is, however, in all likelihood *Cyclops strenuus strenuus*, which is present in Frederiksborg Castle Lake. They showed that during the night it ascends towards the surface.—BERG (1938, 1948) also records the species from Esrom Lake and the River Susaa. LINDBERG (1950) found the species only in a well in Bornholm.

Present investigations: *Cyclops strenuus strenuus* was found in large numbers in four localities, viz. Hjortesølen, Border Pond, Temporary Pond near Ullerødvej, Triphylus Ponds and Vildande Pond. The subspecies also occurred in the Peat-digging at the 35 km. stone, and a few specimens were found in Gribsø.

In Hjortesølen, Border Pond (p. 13) a large number of adult males and females were taken towards the end of February, and most of the females carried egg-sacs. The animals occurred at the surface between two layers of ice (cp. p. 14). Apparently there were no young stages, but in the middle of March many nauplii and some later stages were found, and there was an active reproduction. In the middle of April the number of adults had decreased considerably, but by then the new generation had almost reached maturity. The reproductive period of this generation must have begun shortly afterwards, for at the beginning of May many females with egg-sacs were observed. At the end of May, just before the Border Pond dried up, few individuals were left, and there were apparently no young animals.

Just after the Border Pond filled up again, in September, only very young animals were found, and not until the beginning of November did fully developed animals reappear. At this time there was a period of active reproduction and many females with egg-sacs were taken, as well as a number of nauplii, which must have belonged to this species. In the course of December these animals reached maturity, and couples in copulation and females with egg-sacs were observed under the ice at the beginning of February. Young animals were not, however, found until the beginning of March. The cycle in 1951 was very like that in 1950, except that a new

generation commenced development before the pond dried up, so that the species probably spent the summer in various juvenile stages.

Temporary Pond near Ullerødvej (p. 22). At the beginning of March 1950 a large number of adults were found, and many females had egg-sacs, but there were no young animals. At the beginning of April there were fewer adults, but many juvenile stages. These reached maturity at the beginning of May and produced egg-sacs, from which many nauplii were produced before the pond dried up. All the egg-sacs, however, had apparently not hatched by then, as a few females with egg-sacs were found in the drying mud. When the pond filled up again in the middle of October nauplii were again found, and they attained maturity very rapidly. At the beginning of December there was a reproductive period and egg-sacs were developed. It was not possible to re-examine this locality until the beginning of March, when conditions were found to be essentially the same as in December, although the pond had been frozen to the bottom most of the time.

At the beginning of April nauplii occurred again and the cycle took the same course as in 1950.

In *Triphylus* Ponds (p. 16) the annual cycle was just like that of the Temporary Pond near Ullerødvej.

Vildande Pond (p. 21). This was the only locality among those in which the subspecies was regularly examined, which did not dry up. As elsewhere, only adults, among which were many females with egg-sacs, were found in March. The eggs hatched at the beginning of April, and by the middle of May this new generation had completely replaced the overwintering one. At this time couples in copulation and females with egg-sacs were again found. At the beginning of June there were few adults but many juvenile stages. Throughout the summer no adults occurred, and the juveniles grew steadily, until at the end of September adults were again present, and several females had egg-sacs. By the middle of October fairly advanced juveniles of the next generation were found together with the adults. At the beginning of December only adults occurred, and from October until December reproductive activity continued, but apparently no nauplii developed. Both males and females with egg-sacs overwintered, and a new generation did not develop until the middle of May.

Thus apparently there is not much difference between the life cycle in localities which dry up and those which do not. The cycle in Vildande Pond and in Hjortesølen, Border Pond, was almost the same, the only difference being that in Vildande Pond development was very slow in summer, during which period the Border Pond was dry. Judging from the single observations which were made in Gribsø and in the Peat-digging near the 35 km. stone the cycle was the same as in the two localities above, with reproductive periods in spring and autumn, and only young animals throughout the summer. In *Triphylus* Ponds and the Temporary Pond near Ullerødvej the autumn breeding started so late that a new generation did not appear until the winter. The summer generation in these localities was thus the same as the overwintering one, whereas in the other localities the overwintering generation probably consisted partly of the summer generation and partly of young animals from the autumn reproductive period.

Apparently the time of development from nauplii to adults differs a good deal with the seasons. In Vildande Pond the longest uninterrupted time of development was $3\frac{1}{2}$ months, from the beginning of June until the end of September, and the shortest 1 month in spring and autumn. The same apparently applied to the localities which dried up, but here it was not so distinct because of the dry period.

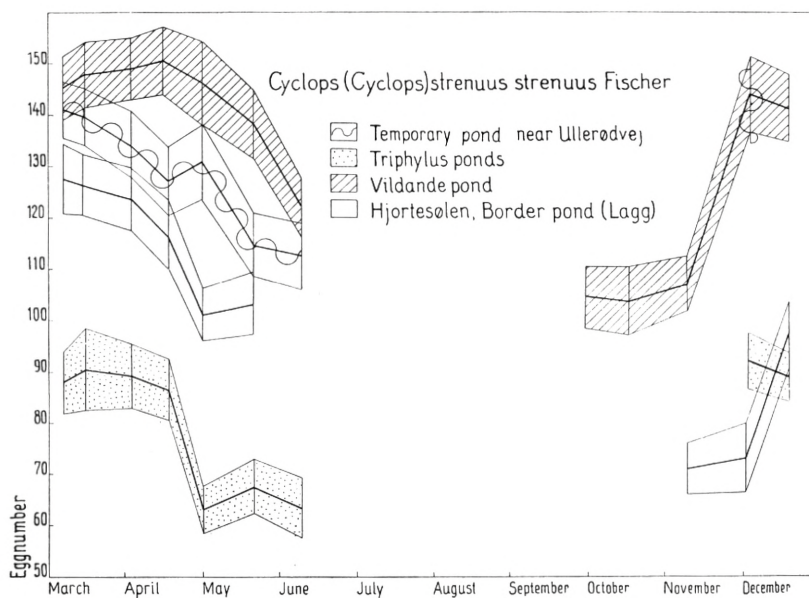


Fig. 16. *Cyclops (Cyclops) strenuus strenuus* FISCHER. The curves show the variations in the number of eggs in various localities.

Counts of the number of animals in 1000 ml. of water from different water layers were only made in Hjortesølen, Border Pond, and in Vildande Pond in 1952, and only adults were counted. The results were as follows.

Hjortesølen, Border Pond, 23.III.1952		♂♂	♀♀	Total
6.00 a.m.	Surface	19	17	36
	Bottom	24	22	46
10.00 a.m.	Surface	6	8	14
	Bottom	18	21	39
2.00 p.m.	Surface	2	3	5
	Bottom	31	35	66
6.00 p.m.	Surface	17	21	38
	Bottom	11	14	25

Vildande, Pond, 16.III.1952				
7.00 a.m.	Surface	26	23	49
11.00 a.m.	Surface	14	16	30
3.00 p.m.	Surface	4	6	10
7.00 p.m.	Surface	30	28	58

The table shows that there was a daily migration, the animals leaving the surface layers in the day time and descending towards the bottom, while in the night they occurred in the upper water layers. Apparently there was no difference between the migrations of females and males.

Egg counts were made in all localities. The results are given in Fig. 16. In the Temporary Pond near Ullerødvej and Vildande Pond, and also in the spring in Hjortesølen, Border Pond, the numbers of eggs were considerably larger than in the strongly dystrophic Triphylus Pond. In the autumn the number of eggs in the two former localities was still fairly large, while in the Border Pond it was as small as in Triphylus Ponds, probably because of the influence of the water from the Central Pond. The curves also show that in all localities the number of eggs in winter and early spring was considerably larger than it was in late spring and early autumn.

Cyclops (Megacyclops) viridis (JURINE) 1820.

Previous investigations: *Cyclops viridis* is one of the most widely distributed and commonest freshwater copepods, and one of the species whose biology has been most frequently studied. HARTWIG (1901) writes that it seems to prefer sandy bottom and that it was most frequent in spring and autumn, but also occurred throughout the year. EKMANN (1904) found it in the littoral zone of lakes and ponds in Northern Sweden. WOLF (1905) found up to 7 generations a year in several localities and observed that the period of development was longest in spring and autumn, and shortest in summer. In lakes the species seems to have one reproduction period only. The number of eggs in each egg-sac varied between 20 and 50. GRAETER (1910) found the species in caves and wells, where the average number of eggs in each egg-sac was as low as 9. WALTER (1922) states that there is constant reproduction throughout the year. She found that the eggs were not laid until 10–15 days after copulation, and that the incubation period depends upon the temperature, it being shorter at high temperatures and varying from 2 days to a fortnight. She also found that the entire development could be completed in one month at high temperatures, while at low temperatures it may take 4 months. The lifetimes of single individuals varied from 4 to 9 months, the longest living specimens being those which overwintered. KLIE (1926) records the species from springs. GURNEY (1933) writes that it is the most common copepod in England and is found in all types of water. COKER (1933) found that individuals which had been reared at low temperatures grew larger than specimens reared at high temperatures, and finally YEATMAN (1944) and HERBST (1951) have given information about the species.

The Danish literature is not very extensive. SØREN JENSEN (1904) found it everywhere in pools as well as in lakes, where it occurred on the bottom and was milk-white. C. WESENBERG-LUND (1917) recorded that it occurred in maximum numbers during the spring in Storekalv, Furesø. Later (1937) the same author states that the species is a pool organism. BERG (1938) found that it was by far the most

common copepod on the bottom of Esrom Lake, where it occurred from 0 to 17 m.'s depth. In winter it was most often taken on stones overgrown with algae, and females collected there with egg-sacs very soon produced nauplii if put into a warm aquarium. Later (1948) the same author found the species very frequently in the vegetation of the River Susaa. Finally, K. LINDBERG (1950) observed the species in many localities in Bornholm.

Present investigations: The species was regularly found in such large numbers that an investigation could be carried out in 8 localities viz. Brune Øje, Vildande Pond, Vandings Pond, Sorte Pond, Egelund Pond, Frøsø and Border Pond and Central Pond in Hjortesølen. Furthermore a single observation was also made in a Brackish Pool in Amager Fælled.

In Brune Øje (p. 19) some adults were taken in March 1950, all were females, most of which were carrying egg-sacs which appeared old and partly dissolved. The animals were covered with Vorticellidae, and no young animals were seen. No change occurred until the beginning of April, when the adults no longer had Vorticellidae, some of them carried new egg-sacs, and a number of young animals, mostly nauplii, were collected. In the middle of April no more adults were found, and only young animals occurred, a few of which were in late copepodid stages, but most of which were younger. A few of this new generation had attained maturity at the beginning of May, but most were not fully developed until the end of the month, at which time egg-sacs were found. By this time few juveniles remained, adults predominated until the end of June, after which their numbers decreased and young animals began to reappear. This change continued through the first part of July, and by the end of the month the new generation had reached maturity. At the beginning of August there was an enormous number of adults, and this declined steadily during September, until by the middle of October no adults remained. At this time, however, many specimens mostly in late copepodid stages were taken. At the beginning of November this generation had attained maturity and several couples in copulation were observed, but there were no egg-sacs. During December egg-sacs appeared and at the same time there was a change in the proportion of the sexes, many more females than males being found, whereas in November there had been equal numbers of the sexes. During the winter the only change in the population was that the number of males continued to decrease until none remained in the early spring. The females survived with their egg-sacs and became steadily more overgrown with Vorticellidae. In the middle of March 1951 the cycle recommenced and took the same course as in 1950.

In Vildande Pond (p. 21) conditions were much the same. An overwintering generation which consisted only of females with egg-sacs developed nauplii from the middle of March onwards. This generation attained maturity towards the end of May, and decreased in numbers towards the end of July. Their offspring (the third generation) were fully developed by the beginning of August and the number of adults increased until, at the end of September, it suddenly declined. At this time

there was a large number of nauplii and later juvenile stages. At the end of October and the beginning of November the number of adults was again rich and couples in copulation were observed. In the middle of November egg-sacs were found; from that time onwards the cycle took exactly the same course as that in Brune Øje.

In Vandings Pond (p. 17) the cycle did not differ much from that in the two localities described above. Three maxima of adults occurred, in May, August and November-December, of which the one in August was by far the largest. The adults of the last generation overwintered with attached egg-sacs. In this pond, as in the others, the number of males decreased rapidly, and in late winter the females were densely overgrown with Vorticellidae.

In Sorte Pond (p. 18) conditions were much as described above. The overwintering generation and the first maximum of adults were just like those in the other localities, but the summer maximum did not occur until the middle of August, and was not very marked. It was also very vaguely separated from the November-December maximum, for during the whole period from August until March females with egg-sacs occurred, although the number was relatively small in October-November.

In Egelund Pond (p. 12) conditions were somewhat different. The spring maximum was very late, occurring at the end of May and the beginning of June, and it merged into the summer maximum in August which, on the other hand, was well separated from the one in late autumn.

In the last two ponds it was sometimes difficult to be certain which of the very young animals belonged to this species and which to *C. gigas*; it was thus sometimes necessary to bring them into the laboratory and keep them in aquaria until it was possible to identify them.

The cycle in Frøsø (p. 14) was more difficult to work out as the samples were taken at fairly long intervals. Overwintering appears to have taken place in the same way as elsewhere and a large number of adult animals occurred in May, at the beginning of July and in November, but not, as in the other localities, in August, when there were not nearly so many as in July.

In Hjortesølen, Central Pond, (p. 14) the development was also difficult to follow, as the *Sphagnum* bog was at times covered by water, which prevented the taking of samples. Overwintering here took place in the same way as in the other localities, as at the beginning of May 1950 a few adults and many juvenile stages were found. These were presumably the last of the overwintering generation and the young animals hatched from their egg-sacs. The latter reached maturity at the end of May and the beginning of June, and developed egg-sacs immediately afterwards. Throughout the period from the beginning of June until the beginning of September there were many adults, though there was a slight decrease towards the end of July and at the beginning of August. Through the ice in February and March 1951 only adult females were taken, most of which were carrying egg-sacs.

Hjortesølen, Border Pond, (p. 13) is the only temporary pond where I have found *C. viridis*. In February and at the beginning of March there were, as in the

other localities, only females with egg-sacs and Vorticellidae and until the end of March conditions were similar to those elsewhere. Just before the pond dried up in the middle of June many adults and various juvenile stages were found, and immediately after the pond filled up at the end of September some metanauplii and young copepodid stages were found. These had thus been able to survive the desiccation. By the middle of October, when the whole bog was covered by water, adults occurred and many of the females carried egg-sacs. In the middle of November very few adults were taken, but there were many young ones, mostly in late stages of development. These reached maturity at the beginning of December and formed the overwintering generation.

It must be low temperatures which prevent the development of the eggs during the winter, as there were no other factors which were common to all the localities at that time of the year. The animals collected during the winter were very sluggish and always remained at or just above the bottom, even when put into collecting tubes, but when they were brought into a heated room it was not long before they started to swim about. Apparently all forms of activity decrease considerably and even moults do not take place during winter, because only then do most of the animals have Vorticellidae. Similarly it appears that no egg-sacs are produced as all those found were overgrown with epibionts.

As soon as the temperature increases a little above 0°C. development begins again, but it is slow at these low temperatures. It was, however, not possible to study the length of time required for complete individual development at very low temperatures, as the small bodies of water warmed up rapidly. Apparently, development in the spring and autumn normally takes about 2 months, it may be completed in about one month in the summer. The value, 4 months, which WALTER (1922) found experimentally in aquaria at low temperatures, is thus only of theoretical interest as regards conditions in Denmark, whereas the period 1 month at higher temperatures seems to agree with my observations on natural conditions.

Counts of the number of animals in one litre of water at various points were made in 1952 in all the localities except Egelund Pond and Frøsø. Young animals were not included and no distinction was made between females with and without egg-sacs. The results were as follows:

Brune Øje	16.III.1952			16.VI.1952		
	♂♂	♀♀	Total	♂♂	♀♀	Total
6.40 a.m. Surface	4	4	5	7	12
Bottom	2	32	34	34	29	63
10.20 a.m. Surface	1	18	19	14	18	32
Bottom	44	44	26	24	50
2.20 p.m. Surface	1	24	25	17	19	36
Bottom	2	37	39	18	20	38
6.20 p.m. Surface	11	11	10	15	25
Bottom	57	57	28	23	51
						9

Vildande Pond						
	♂♂	♀♀	Total	♂♂	♀♀	Total
7.00 a.m. Surface at shore.....	..	3	3	4	7	11
11.00 a.m. Surface at shore.....	..	12	12	18	21	39
3.00 p.m. Surface at shore.....	2	35	37	33	29	62
7.00 p.m. Surface at shore.....	..	19	19	14	15	29
Vandings Pond						
6.00 a.m. Surface at shore.....	..	18	18	16	19	35
Surface, centre	2	2	4	6	10
Bottom.....	..	38	38	32	40	72
10.00 a.m. Surface at shore.....	1	21	22	19	27	46
Surface, centre	7	7	17	14	31
Bottom.....	3	29	32	31	32	63
2.00 p.m. Surface at shore.....	..	32	32	32	29	61
Surface, centre	1	22	23	28	30	58
Bottom.....	2	30	32	6	8	14
6.00 p.m. Surface at shore.....	..	25	25	23	24	47
Surface, centre	13	13	18	14	32
Bottom.....	1	41	42	41	48	89

These counts show that there was a daily migration. During the lightest hours of the day the animals remained in the upper layers of the water, and during the night they descended towards the bottom. That the animals leave the free water in the centre of the pond during the night is suggested by the counts from Vandings Pond, where both morning and evening a considerably larger number of animals was found at the surface by the shore than at the surface in the centre of the pond. In Hjortesølen, Central Pond, a very peculiar phenomenon was noticed. While there was a distinct daily migration as described above, the animals rarely come right up to the surface, and the population was most dense at a depth of 2 m. Strangely enough *Eudiaptomus* behaved in the same way in that locality (cp. p. 41). There was apparently no difference between the behaviour of males and females.

The numbers of eggs carried by the females varied widely throughout the year and from one locality to another (Fig. 17). Egg-counts were made in four localities: Brune Øje, Frøsø, and Hjortesølen, Central Pond and Border Pond. In all localities the number was considerably larger during the winter than in the summer, and there was a decline from spring to autumn, interrupted in the perennial waters by a rise in August. In these three localities this increase coincided with the maximum of adults. In the markedly eutrophic Brune Øje the number of eggs was considerably larger almost throughout the year than in the other localities, whereas in the distinctly dystrophic locality, Hjortesølen, Central Pond, the number was constantly lower than in the other localities. The other two localities occupy intermediate positions.

In Hjortesølen, Border Pond, the number of eggs was almost as large in spring as in Brune Øje, but when the water returned in the autumn the number of eggs was considerably lower, and was indeed as low as in Central Pond. In the course of the

winter it increased again though not quite to the previous level. Here the strongly dystrophic water of the Central Pond, which fills up the Border Pond in the autumn, was probably the cause, but it may be that the specimens collected from the latter had originated in the former and travelled through the layer of water covering the moor.

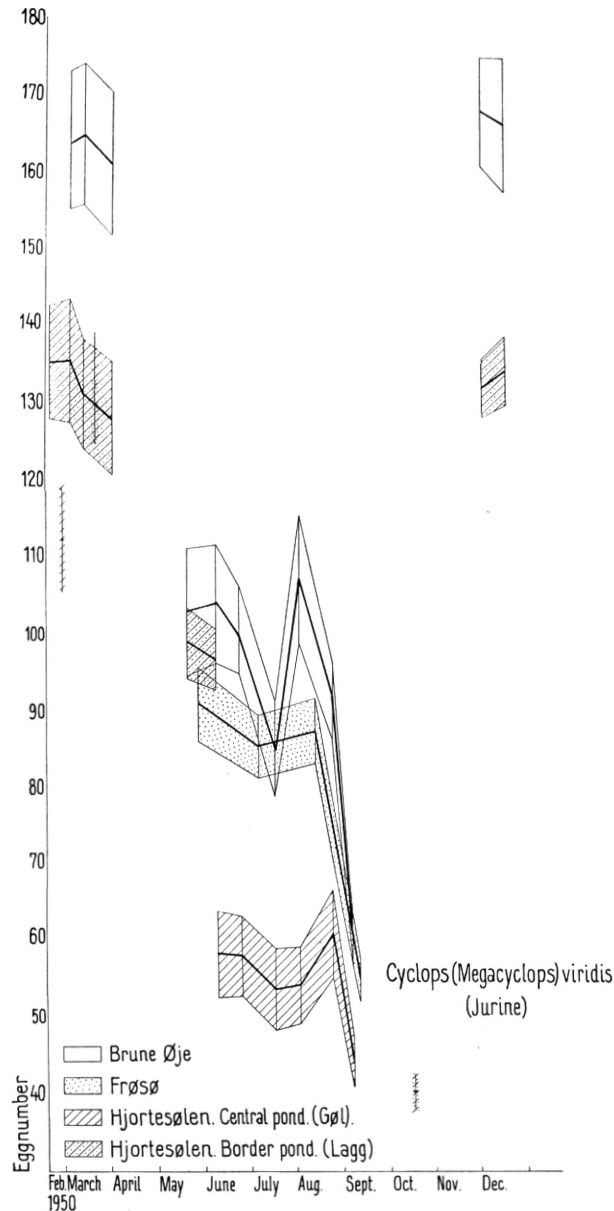


Fig. 17. *Cyclops (Megacyclops) viridis* (JURINE). The curves show the variations in the number of eggs in various localities.

In Frøsø the numbers of eggs lay, at all seasons, between those of the typically dystrophic and of the typically eutrophic localities.

No egg counts were made in the four other localities as they were all eutrophic and the results of the few counts which were made corresponded fairly well with those for Brune Øje. In Egelund Pond the maximum number of eggs for one animal was found on 13.III.1950, viz. 213 eggs, 110 in the left egg-sac and 103 in the right one. These large numbers of eggs are worthy of note, as WOLF (1905) found at most 50.

Other factors besides the eutrophic or dystrophic character of the water seem also to influence the number of eggs. Thus I found the species in a Brackish Water Pool in Amager Fælled on 26.10.1952. The salinity was 8 ‰, and the number of eggs per egg-sac was then between 11 and 15, and at the beginning of February 1953 it was between 18 and 23. Thus, apparently high salinity depresses egg-production.

Cyclops (Megacyclops) gigas CLAUS 1857.

Previous investigations: Most early authors consider this species to be a variety of *C. viridis* and so give no information of its biology. Later authors, who recognise it as an independent species, e. g. MRAZEK (1913), GURNEY (1933) and HERBST (1951) agree that adults occur only in the winter, that there is only one generation each year, and that the young ones rapidly reach the 5th copepodid stage in which they remain for some time, development not being completed until the following winter.

From Denmark the species has been recorded only by SØREN JENSEN (1904) who regarded it as a particularly robust winter variety of *C. viridis*.

Present investigation: *Cyclops gigas* was collected regularly in Egelund Pond and Sorte Pond, and one collection was made in Nørrestrand, Horsens.

In Egelund Pond (p. 68) many individuals, all of which were adults, were taken in March 1950, when the females were apparently much more abundant than the males. Almost all the females carried egg-sacs, and almost all the animals were overgrown with Vorticellidae. Most of these were at the base of the antennae, on the abdomen and egg-sac. No change occurred until the end of March, when it was found that Vorticellidae had disappeared from many of the animals, several females were without egg-sacs and some were carrying egg-sacs containing empty eggs, as the nauplii often hatch while the eggs are still fastened to the parent. Several couples were observed in copulation, and none of these animals had Vorticellidae. Several nauplii were taken, but these could not be certainly identified. Adults were taken until the middle of April. Most of them were females, almost all of them had fresh egg-sacs, and none had Vorticellidae. By the beginning of May all the adults had disappeared, but throughout the summer young animals in the 4th and 5th copepodid stage were always present. At the beginning of November adults were again found in the pond; both sexes occurred, but most of the animals were still immature, and apparently there was no reproductive activity. At the beginning of December all

animals were fully developed, copulation was occurring, and some females already had egg-sacs. This state of affairs continued until the middle of March 1951, and during the winter the animals became increasingly overgrown with epibionts. From then onward the cycle resembled that of the preceding year.

In Sorte Pond (p. 18) similar conditions prevailed, but the population of *C. gigas* was smaller and the adults remained for a longer period, being found until the end of May. During the last part of this period, however, no egg-sacs were found. A sample was taken in Nørrestrand (p. 10) on the 22.XI.1952 by JØRGEN DAHL, M.Sc., who kindly gave me the copepods. All were females of this species and were without egg-sacs.

My observations show that in Denmark, as elsewhere, this species is monocyclic, that adults and consequently reproduction occur only during the cold season. One peculiar feature should be noted. ERIKSEN (1951) showed that cyclopids are able to develop several sets of egg-sacs from a single copulation. This does not seem to be so for this species, as the egg-sacs which were laid in December were carried throughout the winter, as was shown by the large growth of Vorticellidae on them. They hatched immediately after the thaw in March. Then a moult took place resulting in the disappearance of all the epibionts, and this was followed by another copulation, after which new egg-sacs were produced.

The period between the hatching of the eggs (from the middle of March to the middle of April) and the 4th and 5th copepodid stages in which the summer is spent is rather short, being only 1-1½ months, but after that development stops and is not resumed until the beginning of November.

In order to investigate the factors which stop and restart the development I brought a large number of specimens from both localities to the laboratory towards the end of May 1951. Most of them were in the 5th copepodid stage, and a few were in the 4th. In these stages it is impossible to distinguish the present species from *C. viridis* which also occurred in both localities. 10-15 specimens were placed in each of a series of small aquaria and 8 of the aquaria were placed at room temperature (15-20°C), 8 in an ice-box at 0°C and 8 at a temperature which was a little below that at which the development of the animals stopped in the ponds, viz. 5-8°C. Of the 8 aquaria in each lot, 4 were kept in constant darkness, and 4 were left uncovered, and 2 of the dark and 2 of the light aquaria were aerated. In all aquaria at room temperature many specimens of *Cyclops viridis* remained in the copepodid stages. In the group kept at 0°C there was no development at all, but in the third series adults of both *Cyclops gigas* and *Cyclops viridis* appeared. In these aquaria the first fully developed animals appeared three days after the specimens had been taken to the laboratory. There was no difference between the rate of development in the light and the dark aquaria; but while no animals died in the aquaria which were aerated, about half the specimens died in those which were not.

The conclusion to be drawn from this experiment seems to be that the temperature is the deciding factor in the development of *C. gigas*. High temperatures

inhibit the development, the animals can complete their development at a temperature of 5–8°C, but temperatures near 0°C put them into a resting stage in which no development takes place.

I am not able to say with certainty what temperature is actually needed for growth, but, according to my observations in the field, this seems to be between 1° and 8–12°C, as development stopped at 10–12°C in the spring and started again at 8–9°C in the autumn. Light clearly does not influence development, and oxygen also seems to be without importance. I am of the opinion that the animals which died in the unaerated aquaria did not do so because of lack of oxygen, but because, as these aquaria were not stirred, insufficient food was circulated in the water. In the normal habitat of the species the oxygen conditions are not particularly good.

Counts of the number of animals in a litre of surface water were made only in Sorte Pond, on 16.III.1952, and only adults were counted. The results were as follows:

	16.III.1952		
	♂♂	♀♀	Total
6.20 a.m.	14	16	30
10.20 a.m.	11	12	23
2.20 p.m.	15	13	28
6.20 p.m.	15	17	32

The figures suggest that in this locality there was no daily migration, but as no counts could be made at greater depths it was not possible to decide how much of the population lives near the bottom and how much swims about freely.

No egg counts were made.

Cyclops (Diacyclops) biscuspidatus CLAUS 1957.

Previous investigations: WOLF (1905) records this species from a series of ponds which dry up, and he found no less than 6 generations a year. He also noticed that when the ponds were dry the animals were coated with a "crust" which disappears when the pond is filled up again. HARTWIG (1901) states that when the animals occur in temporary pools they are most frequent in the autumn. SPANDL (1926) described the formation of cysts by this species. These are egg-shaped capsules of mud, in which the animals lie with the abdomen bent up ventrally, and which are formed when the water disappears, or the temperature becomes too high. SARS (1918) states that the species was most common in spring in small bodies of water. GRAETER (1910) found it in caves in the alps, but only in small numbers, and KLIE (1926) found it in some springs in Rügen. GURNEY (1933) observed the species in small pools at all times of the year, but most often in spring and autumn, and finally HERBST (1951) combines GURNEY's observations, but notes, however, that the autumn maximum often fails to materialise because there is not sufficient water, and that then the summer resting stage may last until the middle of the winter.

In Denmark the species is known from lakes (SØREN JENSEN 1904), ponds (C. WESENBERG-LUND 1937), running water (BERG 1948) and a well (K. LINDBERG 1950).

Present investigations: The species was found in the following localities: Branchipus Pond, Temporary Pond near the Saw-Mill and Peat-digging at the 35 km. stone in numbers which rendered it possible to carry through an investigation. A few observations were also made in the Peat-digging in Rødkær.

In Branchipus Pond (p. 8) at the end of February 1950 specimens of both sexes were found under the ice. All were adults, but there were neither egg-sacs nor other signs of a reproduction. Animals in copulation were found at the end of March, as were females with egg-sacs. In the middle of April many egg-sacs were observed, and there were many nauplii and somewhat later stages, which proved to belong to this species. At the beginning of May few adults remained, and only two were found with egg-sacs, but many young animals in all stages were present. During May the number of adults steadily increased, and at the end of the month couples in copulation occurred and there were some egg-sacs. Just before the pool dried up in the middle of June many adults were taken, there were many egg-sacs but very few juvenile stages, and no nauplii were present. When the pool was partly filled again in September several adults of both sexes were found, and some of the females had egg-sacs; there were also a few juvenile stages. In the middle of November there was again sufficient water, but there were very few adults, some of which carried egg-sacs. Many juvenile stages were, however, found. At the beginning of December there were many adults and their number increased towards the end of the month, while at the same time the juvenile stages disappeared. There was no reproductive activity and no egg-sacs were found. No change occurred until the middle of March 1951, when some couples were observed in copulation, and by the beginning of April almost all the females carried egg-sacs. In that year the new generation developed very rapidly and at the end of May there were a great many adults and juvenile stages.

In Temporary Pond near the Saw-Mill (p. 25) there were many adults at the end of March 1950; copulations were observed as well as some females carrying egg-sacs, but there were no young animals. In April the condition of the adults was similar, but some juvenile stages also occurred, of which some were probably of this species. In May the number of adults had increased considerably. Many carried egg-sacs and there were many young animals. When, in the middle of October, there was again water in the pond, specimens of the species were found. Most of these were young animals, but there were also a few adults. In November also there were many animals, but by this time very few young individuals remained. No specimens with egg-sacs were taken in October and November, and no other signs of reproductive activity were observed. Both in 1951 and in 1952 the cycle took the same course as in 1950.

In the Peat-digging at the 35 km. stone (p. 26) several adults were taken in March 1950 as in the last locality. Many were females carrying egg-sacs, and there were no

juvenile stages. In the middle of April the number of adults had decreased considerably, but females with egg-sacs still occurred, and there were many young ones in all stages. In May young animals were found in smaller numbers, but the number

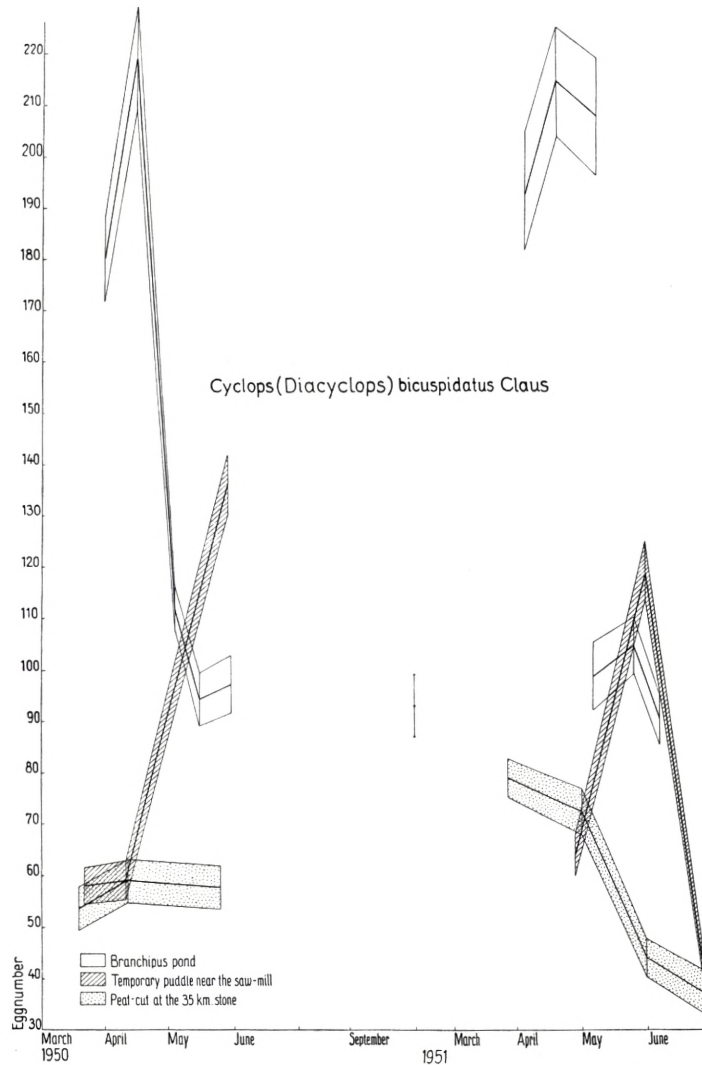


Fig. 18. *Cyclops (Diacyclops) bicuspidatus* CLAUS. The curves show the variations in the number of eggs in three localities.

of adults had become large, and there was active reproductive activity with many egg-sacs. During the summer no adults were observed, and young animals were only taken in large numbers in August. Adults were not taken again until October and then only in small numbers; none of the females carried egg-sacs. In November many adults occurred and there were some young animals in the later developmental stages.

There was no reproductive activity and there were no egg-sacs. The samples taken in 1951 showed almost the same as those taken during 1950.

It would seem that this species has two generations, the biology of which differs greatly. One generation is hatched in the early summer, develops during the summer (if the locality is not dry during this period) and the autumn, overwinters as adults, and has its reproductive period in the early spring. The other generation develops rapidly and has a reproductive period in the late spring or early summer. The two generations follow so closely upon each other that adults of the two generations may occur together.

I have not succeeded in finding the cysts mentioned by SPANDL (1926) in any of the dry localities, but during the investigation of *Cyclops bisetosus* a few specimens of *C. bicuspidatus* were found, which were lying in moss without cysts. The investigations in the Peat-digging seem to indicate that in localities which do not dry up, there is an inactive period, for in some of the summer samples there were very few animals, much fewer than were found at a later period. It was not discovered whether this was due to the formation of cysts.

Egg counts for this species are given in Fig. 18. There were great variations in the number of eggs and the curves are very irregular. Because of this irregularity, egg counts were made both in 1950 and in 1951, and in spite of the differences between the two curves, I think that the following inferences may be drawn: The number of eggs was considerably larger in the eutrophic Branchipus Pond than in the other two localities which can be classed as dystrophic. There is, however, one exception, as some of the values from Branchipus Pond were lower than the corresponding values from Temporary Pond near the Saw-Mill. In my opinion this is due to one particular factor, to which I shall revert below. It also seems that in the perennial Peat-digging at the 35 km. stone the number of eggs is more constant than in the localities which dried up. The following remarks may be made about the individual localities: In Branchipus Pond the number of eggs was fairly large at the first sampling of each year, and for a short period it increased further. Then in May of both years it declined to about half. In 1950 the early large numbers of eggs are connected in the figure with the later small numbers. This was, however, not done in 1951. Instead of one, two counts of different numbers are given for the 6.V.51. On this date the eggs were not normally distributed but divided into two groups, each of which had normal distribution. Consequently on this date eggs of 40 animals in all were counted, 20 with a large number of eggs, and 20 with a small number of eggs. I think the reason is that on this date both generations were present in the pond, the old generation having a large number of eggs, the young generation a small number. The same two generations occurred in 1950, but I did not then find them simultaneously.

In Temporary Pond near the Saw-Mill the number of eggs was rather small in March and at the beginning of April 1950, and it increased considerably towards the time when the pond dried up. This increase occurred at the same time in 1951, but in June it was interrupted by a fall, after which the number of eggs was smaller

than in the early spring. If this curve is compared with that from Branchipus Pond, there is apparently no agreement, but if the latter curve is pushed on a month, good conformity will be seen. The only thing which has happened is that the development in Temporary Pond near the Saw-Mill has been delayed a month as compared with Branchipus Pond, and that the water of the former locality disappeared so early in 1950 that the heavy fall cannot be seen from the curve.

In the Peat-digging the number of eggs was very constant in 1950 but there was a fairly considerable fall in 1951. This may be due to the fact that the spring of 1951 was very humid and cool, and it would appear that low temperature is the factor which delays the development of the animals in this locality.

Cyclops (Diacyclops) bisetosus REHBERG 1880.

Previous investigations: There is a long series of works on this species. SARS (1863) and SCHMEIL (1892) both state that the species occurs in pools which dry up in summer. RYLOV (1915), GRAETER (1910) and ROY (1932) confirm this. The latter states that the species is usually not found together with other Entomostraca, and showed that in several cases both fully developed animals and egg-sacs can survive desiccation. LILLJEBORG (1901) and KLIE (1926) found the species in springs in Skåne and in Rügen respectively. THIENEMANN (1912) found it in water with a salt content of 6 ‰, and finally GURNEY (1933) took it in tree-holes together with *Moraria arboricola*. Many authors, e. g. LILLJEBORG (1901) KREIS (1921) and GRAETER (1910), considered the species a glacial relict, but this view is contradicted by several other authors. Finally HERBST (1951) wrote that he had taken the species constantly from October till March, but generally only as single specimens. It seems to prefer *Sphagnum* waters but occurs also in other waters.

From Denmark only BERG (1948) has recorded the species in Tuel Aa, an affluent of the River Susaa. Here a few specimens of the species were found towards the end of April, and all the specimens occurred in one sample.

Present investigations: I have found the species regularly in the two temporary ponds near Frøsø (p. 28) and the Saw-Mill, and observations have also been made in a temporarily flooded meadow near Tuel Aa. In March 1950 I found many ♂♂, ♀♀, as well as juvenile stages in both the ponds. Several couples were taken in copulation, and a few ♀♀ with egg-sacs occurred. In April hardly any juvenile stages were found, but almost all ♀♀ carried egg-sacs. In May the number of adults had decreased considerably, and few were taken with egg-sacs, but there were many nauplii and somewhat later stages. When the ponds had filled up again in the autumn, a large number of young and older copepodid stages occurred in October and November, but only in the pond near the Saw-Mill were fully developed animals found in November, and two of the females were carrying egg-sacs. In 1951 the cycle took the same course. Thus, there is apparently only one generation a year in these localities, and the reproductive period is in the early spring. If, however, there is enough

water sufficiently early in the autumn for the temperature to allow the animals to develop, there may apparently be a reproductive period then.

Because of freezing and desiccation of the biotopes the development of *C. bisetosus* must take place by fits and starts, as no complete development was observed within a single period of free water. From the occurrence of nauplii in May until fully developed animals were found in November about 6 months elapsed, and during this time there was sufficient water for the animals to develop for only about 2 months.

At this point a few remarks must be made about the species near Tuel Aa. It seemed strange to me that I had only found the species in ponds which dry up, whereas the only previous Danish record was from running water. I visited this locality in November 1951, and April and June 1952, and found there were large flooded areas on my two first visits. On my first visit I only found a few *C. bisetosus* most of which were in late copepodid stages. On my second visit I found a large number of adults of which some ♀♀ carried egg-sacs. According to BERG (1943) the water level of Tuel Aa is higher in April and the current stronger than at other times, and consequently it is possible that the specimens he found had been carried from the meadow into the river by the current. I think that previous finds of the species in springs, e. g. KLIE (1926) very likely are due to similar reasons.

The following should be noted concerning the ability of the species to survive unfavourable seasons: When the localities in which the animals live dry up in the summer, a new generation has just begun to grow up. When the water disappears, the individuals of this generation do not apparently aestivate in cysts, and as far as can be seen the animals themselves do not dry up, as stated by ROY (1932). They showed indeed no trace of such desiccation, and the places in which they occurred during the desiccation, were dense moss at the bottom of the ponds. This seemed to contain so much water, and be so well protected against evaporation, that there was always sufficient water for the animals to survive until there was again water in the ponds. The following observations seem to verify this supposition:

Part of a sample taken from the bottom of the pond near the Saw-Mill on the 11.VII.1951 was taken to the laboratory in a tightly corked bottle and another part was wrapped only in paper. In the laboratory about one week after the sample had been taken, both parts of the sample were divided into two equal portions, of which one was immediately placed in water, while the other was left unwrapped for a couple of days, exposed to the sunshine, before it was placed in water. The latter two halves were weighed before and after the drying. Before the drying they weighed 45.78 gr. and 53.39 gr. respectively and afterwards they weighed 12.48 and 18.73 gr. resp. In other words they had lost 73 % and 65 % of their original weight by evaporation.

After about a fortnight the contents of the four aquaria were examined. The two aquaria with the portions which had not been exposed to sunshine both contained live animals, but the aquaria with the portion which had been wrapped only in paper contained a smaller number. No live individuals were found in the two aquaria containing samples which had been completely dried up.

I made similar experiments with samples from the Pond near the Saw-Mill during the summer of 1952, just after the pond had dried up, as well as later in the summer, and with the same results. The animals only survived when the samples were protected against complete desiccation. I also found that the number of animals surviving seemed to decrease only slightly if the samples were taken late in the summer.

The experiments show that *C. bisetosus* can tolerate the drying out of its habitat only if the bottom is of such a kind that there are cavities which remain partly filled with water.

The overwintering of the animals must take place in a somewhat different way. The pools do not dry up in the winter, but normally they freeze to the bottom so that no water remains for the animals. Under these circumstances I could not find the animals, and so cannot state whether they hibernate in cysts, but it seems most likely that during this season also the animals do not produce cysts. They probably manage to survive in or on the bottom surrounded by ice, as the following observations would seem to indicate:

Part of the animals surviving from the experiments made in 1951 were placed in small aquaria in an ice box, while the rest were kept at room temperature as controls. At a temperature a little below 3°C the animals became inert and sank to the bottom where they remained immobile. They showed no signs of encystment in the small amount of mud at the bottom of the aquaria. The aquaria had not frozen solid and when they were again brought to room temperature, the animals began to move when the temperature rose over 3°C. I then replaced the aquaria in the ice box and allowed them to freeze solid. I left them in this state for some days before bringing them back to room temperature. Just after the ice had thawed the animals made no movement and remained at the bottom, but some began to move when the temperature had risen to about 6°C, and shortly afterwards about two thirds of them were swimming about freely; the rest appeared to have died. When the temperature was again decreased the animals stopped all activity at 3°, but recommenced it at once when this temperature was again attained; when the water was allowed to freeze it was necessary to raise the temperature a few degrees above 3°C before activity was resumed.

The whole series of experiments lasted about a fortnight and during this time the animals did not develop at all, but the animals which were kept at room temperature (16°C) underwent active development and also produced egg-sacs.

In the spring of 1952 some live animals were taken to the laboratory from the Pond near the Saw-Mill. They were placed in 15 small aquaria, 25 animals in each, and the aquaria were placed in an ice box which caused all the water to freeze solid after a few hours. They were then thawed out one by one after increasing intervals of time. Similar experiments were made with animals from the same locality in the autumn of 1952. Both experiments included animals which were still not fully developed. The results are given in the following table, where the figures indicate the number of animals which survived in each aquarium:

	Spring	Autumn
Thawed 1 day after freezing	18	16
2 days - - -	17	20
4 - - -	15	18
1 week after freezing	16	16
2 weeks after freezing	20	19
3 - - -	17	16
4 - - -	20	18
6 - - -	18	15
8 - - -	16	19
10 - - -	18	16
12 - - -	17	14
15 - - -	12	11
18 - - -	8	9
21 - - -	3	0
24 - - -	0	1

The table shows clearly that mortality was about 33 % for periods up to 12 weeks, but when the period was longer mortality increased considerably, and more than 20 weeks of freezing killed the animals. Unfortunately it was impossible to bring the temperature below about -4°C , the temperature varied about -2°C for prolonged periods. The table therefore does not show whether a harder frost is more destructive to the animals.

In both experiments the five aquaria which were first thawed out were afterwards exposed to a series of freezings and thawings in rapid succession, the animals being frozen each time for 24 hours. The freezings followed immediately upon the thawings, and were continued until all the animals in the aquaria had died. The first freezing is the one indicated in the preceding table:

	Spring					Autumn					% Loss
	1	2	3	4	5	1	2	3	4	5	
After 1st freezing	18	17	15	16	20	16	20	18	16	19	30
2nd - - -	11	12	11	9	13	10	12	13	12	10	35
3rd - - -	7	6	6	4	8	8	7	8	5	7	41.5
4th - - -	4	5	3	3	7	5	5	6	2	5	32
5th - - -	1	3	2	1	5	3	4	3	1	4	40
6th - - -	1	0	0	0	3	2	1	0	0	3	64
7th - - -	0	1	0	0	0	90
8th - - -	1
9th - - -	0

Until the 6th freezing the mortality was about 33 % on each occasion, but because of the small number remaining during the later freezings it is impossible to decide with certainty whether there is a distinct weakening of the animals or whether the increasing mortality was due to chance. Whichever is the case, it is clear that the

species can better tolerate one prolonged period of frost, if this does not exceed 12–15 weeks, than a constant variation between frost and thaw.

Light frosts which do not freeze the water to the bottom do not, apparently, have any effect on survival.

***Canthocamptus staphylinus* (JURINE) 1820.**

Previous investigations: All the authors who have discussed the biology of this species agree that it is able to survive in most types of locality, and at greatly varying temperatures. Thus LANG (1948) found it at temperatures from 0°–19°C, but apparently most frequently in the winter. WOLF (1905) found a maximum from December to February, and GURNEY (1932) observed a marked decline in summer, followed by an increase from June until December. When the number of animals is large reproductive activity is most pronounced, and sexually mature animals are very rare or absent after April–May. LAUTERBORN and WOLF (1909) and KESSLER (1913b) state that in pools which dry up the animals aestivate in cysts, but GURNEY (1932) never found these cysts and doubted if the animals always aestivate in this way.

In Denmark the species seems to be very common. SØREN JENSEN (1904) states that it occurs everywhere, particularly in small ponds, ditches and near the shores of lakes. He ascertained that it is negatively phototactic. C. WESENBERG-LUND (1917) often found it in shallow water in the lake Furesø, where it was especially numerous in the autumn. BERG (1938) found it distributed in from 1–5 m. of water with a maximum at 2 m. and single finds were made down to a depth of 12 m. He found one specimen encysted. The same author (1948) found the species in the meanders of the river Susaa in Tamose where it occurred in large numbers all through the year.

Present investigations: I have taken *Canthocamptus staphylinus* regularly in four localities: Branchipus Pond, Temporary Pond near the Saw-Mill, Triphylus Ponds and Vildande Pond.

In Branchipus Pond (p. 10) a great many specimens of the species were found under the ice in February and March 1950. Only adults, males and females, occurred; many couples were taken in copulation and nearly all the females had spermatophores attached and carried egg-sacs. Towards the end of March the number of adults had decreased somewhat and only a few ♀♀ with egg-sacs were observed, but juvenile stages were frequent. By the middle of April there was again much reproductive activity, and in May the number of young ones again increased. From that time until the pond dried up no reproductive activity was observed. Just before the pond became dry the young ones were of a conspicuous orange red colour, the body being full of oil-globules, whereas earlier in the year they had been lead-grey. During the short, wet period at the end of September 1950 only few specimens were found, but when, at the beginning of November, the pond had filled up again, many animals were present. Immediately after the water returned no egg-sacs were observed, but there were animals in copulation and females carrying spermatophores. At the beginning

of December almost all ♀♀ carried egg-sacs. Apparently these egg-sacs did not hatch until March of the following year, as no young animals were found during the intervening period. Males attached to females were observed frequently during the winter.

In Temporary Pond near the Saw-Mill (p. 25) many animals, both young and adults, were found at the end of March 1950. A few ♀♀ carried egg-sacs, and males attached to females were observed. In the middle of April copulating pairs were common and many egg-sacs occurred. At the end of May there were few adults, but

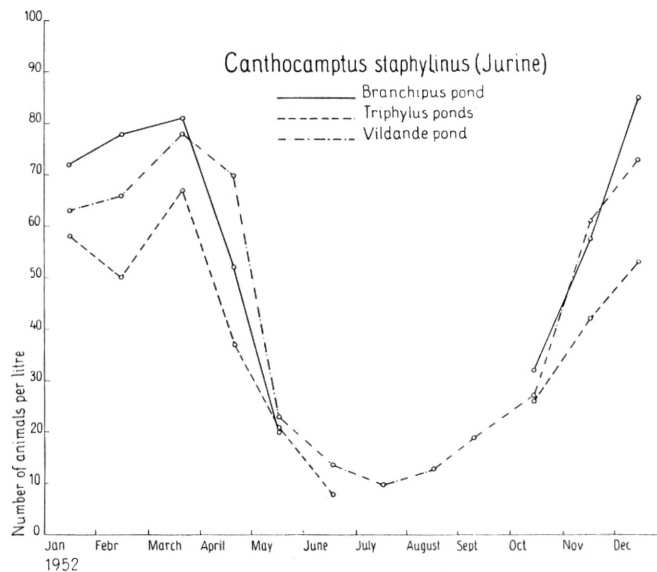


Fig. 19. *Canthocamptus staphylinus* (JURINE). The curves show the number of animals per litre of water during the year in three localities.

many juvenile stages, the colour of which, as in Branchipus Pond, was orange red. In the middle of October when the pond had filled up again, the same number of animals occurred as in May, and several couples were observed, but no ♀♀ carried egg-sacs. These were found in large numbers towards the end of November, when only adults occurred. In 1951 the cycle took almost the same course as in 1950, but as the water disappeared a little later this year, the animals had attained maturity before the desiccation of the pond. No egg-sacs or other indications of a reproductive activity were, however, observed.

In Triphylus Ponds (p. 16) the cycle was very much like that observed in Branchipus Pond. There seemed, however, to be a little delay in the hatching of the first set of egg-sacs, as large numbers of young ones were not found until the beginning of April 1950. Consequently the reproductive period of this generation did not begin until May, and the development of their offspring was not very much advanced when the pond dried up.

In Vildande Pond (p. 21) a cycle of a somewhat different character was found,

possibly because this was the only one of the localities investigated which did not dry up. During the early months of the year the cycle was the same as in the other localities; the egg-sacs of the overwintering generation were hatched and a new generation developed. But simultaneously with the development of this new generation the overwintering generation continued to develop egg-sacs, and there was apparently uninterrupted reproduction until the beginning of June. From then until the end of

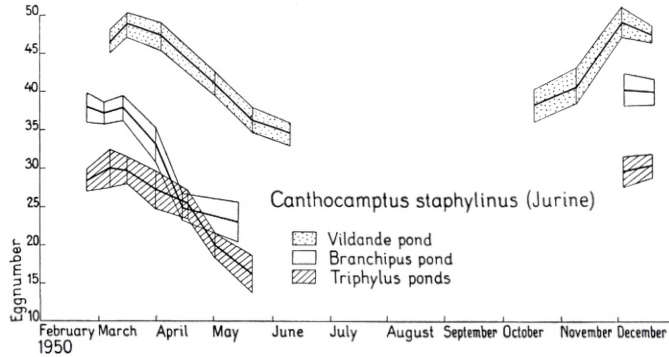


Fig. 20. *Canthocamptus staphylinus* (JURINE). The curves show the variations in the number of eggs in three localities.

September there were many individuals, both adults and young ones, but egg-sacs were rare although never completely absent. At the end of this period almost exclusively adults were found. At the beginning of October many of these were in copulation, and there were ♀♀ with spermatophores and a few egg-sacs. At the beginning of November there were many young animals, which were probably the overwintering generation.

While there were thus 2 generations in the three localities which dry up, viz. a spring generation and the summer generation which also overwintered, conditions were not so clear in Vildande Pond. Only the overwintering generation can be correlated with that of the other localities, and there was apparently one and possibly two further generations before the summer generation which here was not the same as the wintering one. Also, there was no period during the summer when no reproduction occurred. In order to investigate these differences I took, in 1952, one single sample of 1 litre of water just above the bottom of Branchipus Pond, Triphylus Ponds and Vildande Pond. The number of *C. staphylinus* was counted, but no distinction was made between ♀♀, ♂♂ and young ones. The results are given in Fig. 19. This shows that the number of individuals per litre was larger in the autumn in all three localities before the commencement of the reproductive activity than at any time in the spring when the ponds dried up (Branchipus Pond and Triphylus Ponds) or when the reproductive activity stopped (Vildande Pond). In my opinion the explanation is that during the early summer, some of the animals were encysted and hence were not included in the counts; but statistical uncertainty may also come into the question.

Unfortunately I was not able to find these cysts, but this would appear to be a reasonable explanation of the shape of the curves. If these curves, particularly that from Vildande Pond, are compared with the figures given by GURNEY (1932, p. 105), there is good agreement.

Counts of the number of eggs per egg-sac were made throughout the year of Branchipus Pond, Triphylus Ponds and Vildande Pond. The results are given in Fig. 20. For all three localities there are gaps in the curves during the summer months. In the two localities which dried up this was because no females with egg-sacs were found, and, while single finds were made in Vildande Pond, they were not nearly enough to give a statistically satisfactory result. Some of the counts were as follows: 9.VI.: 31, 34; 25.VI.: 32, 28, 26; 17.VII.: 24; 3.VIII.: 21, 18; 24.VIII.: 20; 7.IX.: 18, 17; 29.IX.: 22, 24.

It will be seen that the number of eggs in all localities was largest during the winter months and decreased towards the warmer season, and that it was smaller in the localities which dry up than in the locality where the water remains throughout the year, and smaller in the locality Triphyllus Ponds with a low pH and a low conductivity than in localities with a high pH and a high conductivity.

Moraria brevipes (G. O. Sars) 1862.

Previous investigations: Much information on the biology of *M. brevipes* is available, but mostly of a rather contradictory kind. There is, however, general agreement that the species prefers damp *Sphagnum*, although it has been found subterraneously (CHAPPUIS 1925 and HNATEWYTSCH 1929) and in open water (EKMAN 1904, KESSLER 1913 and OLOFSSON 1916). DONNER (1928) and GURNEY (1932) are of the opinion that the eggs are laid singly, but females with egg-sacs have been found by BORNER (1920) and LANG (1931). The egg-laying season was found by DONNER (1928) to be September–October, while LANG (1931) found eggs in July and September. There is only one generation yearly.

The species has not previously been found in Denmark.

Present investigations: I only found the species in Rødebæk (p. 26) and in the small meadow overgrown with *Sphagnum* through which the brook runs. The first finds of the species were made in the brook below the main affluent from the meadow, and as there were no animals in the brook above this place I followed the affluent into the meadow and found many animals. On the 14.III.1950 a number of adult males and females were found. I observed one couple in copulation and found one female with one egg-sac. In April adults were found again, among which was one female carrying eggs. During the summer a small number of young animals occurred, which must be supposed to belong to this species, and in September many copepodid stages were seen. In November several animals occurred, partly adults and partly almost fully developed copepodids. In 1951 similar observations were

made, but in June many juvenile stages occurred, partly metanauplii, partly young copepodid stages, which were undoubtedly of this species.

It was quite clear that only one annual generation developed in this locality, and this agrees with the statements of other authors. In Rødebæk, however, the reproduction period occurred in late winter or very early in the spring, and this does not agree with earlier authors, but this difference is not so great as it may seem, as all the known reproductive periods are both in the warm and the cool seasons, and, probably, investigation of other localities would show that reproduction may occur all through the year.

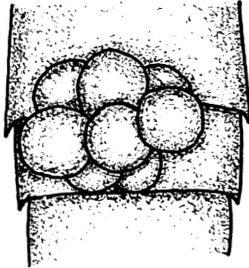


Fig. 21. *Moraria brevipes* (G. O. Sars). Genital and following segments. Female with eggs. Rødebæk, 24.III.1950.

The development is remarkably slow. The appearance of the eggs does not indicate that there is a resting stage before the nauplii are hatched, and this means that it takes 7 months before the development is completed.

As mentioned above, I found females with egg-sacs, though only a few specimens. The egg-sac is attached to the hindmost part of the genital segment and almost covers the next segment. There were 6–9 eggs in the egg-sacs, and they seemed to be kept together by a hyaline, gelatinous layer (Fig. 21). There was nothing to prevent the egg-sacs from falling off, as they were only fastened by means of this gelatinous substance. It is therefore not surprising that so few authors have found the egg-sacs, as these can easily be pushed off as the animals climb about, and perhaps the animals carry the egg-sacs for only a short time.

I did not observe the actual copulation, but I fairly often saw couples of animals, the males grasping the furca of the females with their 1st antenna.

In the autumn of 1951 and the spring of 1952 the localities were further investigated with the object of ascertaining where the natural habitat of the animals was

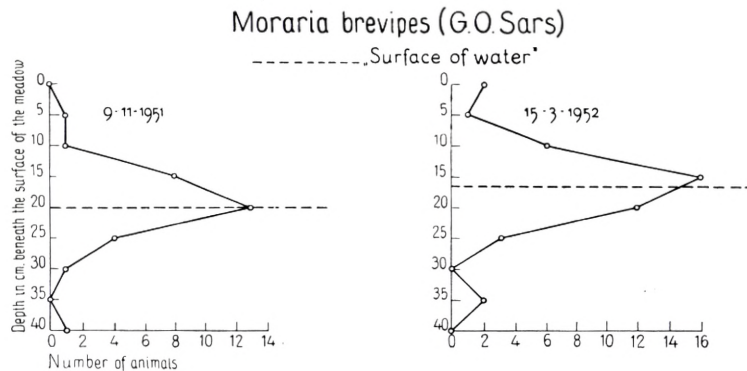


Fig. 22. *Moraria brevipes* (G. O. Sars). The curves show the distribution of the animals at various depths in the Sphagnum moss.

situated. It was clear that they could not normally live in the brook or the affluent but must be carried into the *Sphagnum* growths with the water. Near the affluent I made a vertical cut through the meadow to a depth of 40 cm. and equal samples of soil were taken at intervals of 5 cm. in this profile. The samples were carefully washed with alcohol, after which the animals were sorted out and counted. Their distribution is shown in Fig. 22. The horizontal dot-and-dash line indicates the depth below which all cavities were filled with water. The figure shows clearly that the number of animals was largest just around the surface of the ground-water. That the animals remain at exactly this depth is probably due to the fact that it is too dry higher up, and that there is a lack of oxygen lower down. The small difference between the two curves is probably due to the fact that in the spring of 1952 the surface-level of the ground water was higher than in the autumn of 1951.

Like other copepods which are found rarely *M. brevipes* has been considered to be a glacial relict. I do not think that this is justified, partly because it can be found fairly often when its ecology is known (LANG 1931), and partly because it has already been found in so many and such widely distributed localities that its occurrence must be said to show a certain continuity. Further investigations will probably show that in Denmark it is also frequent, but its small size and its hidden mode of life have caused it to be overlooked so far.

VI. General Part.

I. The occurrence of the species in various types of locality.

Table 1 shows that there is a great difference in the number of species occurring in each of the various types of locality, but it does not reveal which species occur as permanent populations and which merely by chance. By the term "population" I mean one in its natural habitat and which breeds there.

All planktonic species were found to have permanent populations in the localities where they occurred. All of these species, with the exception of *Eudiaptomus coeruleus*, *Heterocope saliens* and *Mesocyclops oithonoides*, also occurred in running, particularly slowly running water. Four of these planktonic species have been found in ponds, two in the littoral zone of lakes and one, *Cyclops strenuus strenuus*, in temporary pools. The conditions of life in the open water of large, slow-flowing streams do not differ much from those of the open water of lakes, and it is reasonable to expect that planktonic species will establish permanent populations in slow-flowing water. In the open water of ponds it is also possible for such species to maintain permanent populations, and the same seems to apply to *Cyclops strenuus strenuus* in temporary pools. The occurrence of these species in the littoral zone of lakes is, however, probably more or less accidental, and planktonic species presumably often invade the littoral zone without establishing populations.

Table 1. Occurrence of the species in relation to the various types of localities with the number of finds in each of these.

	Lakes			Ponds	Temporary pools	Damp moss	Streams		
	Planctic zone	Littoral zone	Profundal zone				Springs	Brooks	Rivers
<i>Eudiaptomus vulgaris</i> (SCHMEIL)	5	1
— <i>coeruleus</i> (FISCHER)	2
— <i>gracilis</i> (G. O. SARS)	6	3
— <i>graciloides</i> (LILLJEBORG)	7	1
<i>Diaptomus castor</i> (JURINE)	1	2
<i>Hemidiaptomus superbus</i> (SCHMEIL)	1
— <i>amblyodon</i> (MARENZELLER)	1
<i>Eurytemora velox</i> (LILLJEBORG)	2
— <i>affinis</i> (POPPE)	2
— <i>lacustris</i> (POPPE)	1
<i>Heterocope saliens</i> (LILLJEBORG)	2	1
<i>Macrocyclus albidus</i> (JURINE)	6	1	8	3
— <i>fuscus</i> (JURINE)	5	..	6	1
<i>Eucyclops macruroides</i> (LILLJEBORG)	1	..	1	2
— <i>macrurus</i> (G. O. SARS)	4	..	1	1	..	1
— <i>speratus</i> (LILLJEBORG)	3	..	1	1	1
— <i>serrulatus</i> (FISCHER)	6	..	12	1	5	2
<i>Paracyclops affinis</i> (G. O. Sars)	2	..	2	1
— <i>fimbriatus</i> (FISCHER)	3	1	1	5	3
<i>Ectocyclops phaleratus</i> (KOCH)	3	..	7	1	..	1	3	..
<i>Cyclops (Cyclops) insignis</i> CLAUS	1	1	2
— (<i>Cyclops</i>) <i>vicinus</i> Uljanin	1	..	4	1	1	1
— (<i>Cyclops</i>) <i>strenuus strenuus</i> FISCHER	10	2	..	2	3	3
— (<i>Megacyclops</i>) <i>viridis</i> (JURINE)	7	2	15	1	..	1	4	2
— (<i>Megacyclops</i>) <i>gigas</i> CLAUS	2
— (<i>Diacyclops</i>) <i>bicuspidatus</i> CLAUS	1	..	4	3	1	..
— (<i>Diacyclops</i>) <i>bicuspidatus odessanus</i> SCHMANKEWITSCH	4
— (<i>Diacyclops</i>) <i>bisetosus</i> REHBERG	3	1
— (<i>Acanthocyclops</i>) <i>vernalis</i> FISCHER	1	1	2
— (<i>Acanthocyclops</i>) <i>vernalis f. robusta</i> G. O. SARS	1	1	1	1
— (<i>Microcyclus</i>) <i>bicolor</i> G. O. SARS	1	..	6	1	..
— (<i>Mesocyclops</i>) <i>varicans</i> G. O. SARS	2	..	1
<i>Mesocyclops (Mesocyclops) leuckarli</i> (CLAUS)	11	4	..	9	1	1	2
— (<i>Thermocyclops</i>) <i>dybowski</i> (LANDE)	2	..	3
— (<i>Thermocyclops</i>) <i>oithonoides</i> G. O. SARS	10	1
<i>Nitocra hibernica</i> (BRADY)	1	..	1	..	1	..	1	2
<i>Canthocamptus staphylinus</i> (JURINE)	2	1	1	3	1
<i>Bryocamptus (Bryocamptus) minutus</i> (CLAUS)	1	..
<i>Bryocamptus (Bryocamptus) zschokkei</i> (SCHMEIL)	1
<i>Moraria brevipes</i> (G. O. SARS)	1	..	1	..
<i>Attheyella (Attheyella) crassa</i> (G. O. SARS)	4	1
— (<i>Brehmiella</i>) <i>trispinosa</i> (BRADY)	3	1

The species found in the littoral zone of lakes are mostly the same as those found in perennial ponds. It should be noted, however, that the calanids *Eudiaptomus vulgaris*, *Diaptomus castor*, *Eurytemora velox* and *Hetercope saliens* only occur in ponds and are absent from the littoral zone of lakes. This is probably due to the fact that although they are planktonic organisms they cannot survive in the disturbed water of the littoral zone of lakes. *Hetercope saliens* is actually found in the plankton of lakes, and this probably also applies to *Mesocyclops oithonoides*. Some species, however, have been found only in lakes or only in ponds, but I believe that, with the exception of *Cyclops insignis* and *Cyclops gigas* further investigations will show them to occur in both types of locality. *Cyclops insignis* and *C. gigas* have certain biological features which indicate that they may be confined to small bodies of water.

21 of the species from the littoral zone and perennial ponds have also been found in running water. Of these, however, the most have only been found there once, and only three of the species are regular inhabitants of running water. The table does not show which of the species occur as permanent populations there, but the literature gives information about the abundance of the species in the various localities, and these figures are relevant here. In the slow-flowing water *Macrocylops fuscus*, *M. albidus*, *Eucyclops macruroides*, *E. speratus*, *E. serrulatus*, *Paracyclops fimbriatus*, *Cyclops viridis* and *Cyclops vernalis* occur in such large numbers along the shores that they must be assumed to occur there as permanent populations, whereas only few specimens of the other species have been found, which indicates that their occurrence is incidental. Only *Eucyclops serrulatus*, *Paracyclops fimbriatus* and *Ectocyclops phaleratus* have been found in rapidly running water in such large numbers as to indicate that they exist there as permanent populations, and the occurrence of others is probably due to accident. These three species probably also have permanent populations in springs.

The majority of the species occurring in temporary pools may also be found in the types of locality already considered. Only *Hemidiaptomus superbis* and *H. amblydon* are apparently confined to temporary pools; *Cyclops bisetosus* which has, however, once been recorded from slowly running water, must be considered to be normally confined to temporary ponds. The other species also occur in other types of water, and according to my observations *Eudiaptomus vulgaris* (cp. p. 43) is not really an inhabitant of temporary ponds and only occur there in especial circumstances.

Only two species have been recorded from damp moss in Denmark, but this type of locality has been little studied, and probably further investigations will increase the number of species recorded. Many harpacticids, which are recorded from such places in Sweden by LANG (1931), have not yet been found in moss in Denmark.

29 species have been found in streams but a large number of these do not normally belong to the running water fauna. (a) 8 of the species have been found elsewhere only in the littoral zone of lakes, in ponds or in pools, and it must be assumed that melting snow had carried them into running water. This, at any rate, is the case with *Cyclops bisetosus* (cp. p. 75). It also seems likely that many of the species which have only been taken in running water, were probably carried out into it, particularly

the harpacticids. An exception is *Bryocamptus zschokkei* which probably is a true inhabitant of springs. The fact is that many of these species are very scarce even in running water, and so probably normally occur elsewhere. (b) Another group found in running water is composed of planktonic species which have been carried from lakes through which the streams run. *Eurytemora affinis* and *E. lacustris* probably belong to this group: They have not been found in other localities but occur in streams at the outfall from lakes. (c) Finally there is a third group which occurs both in the littoral zones of lakes and in ponds and is also frequent in running water. 10 species belong to this group and these species must be adaptable and find biotopes corresponding to the shores of lakes and ponds along the shores of slowly running water. As mentioned above, I believe that they have permanent populations in running water.

II. Occurrence of the species in relation to physico-chemical factors.

I have not been able to obtain much information from the Danish literature, as it contains little information on the physical and chemical conditions in the localities where copepods have been found. Only for Esrom Lake (BERG 1938, p. 28) is useful information given on the pH and conductivity. BERG (1943, p. 163) also gives values of the pH from the Susaa, but few of them can be used since the exact localities for the copepods are not always stated.

A. Hydrogen-ion concentration (pH).

I have divided the localities into four groups partly according to IVERSEN (1929) and NYGAARD (1938).

1. Very acid localities; pH constantly below or about 5.0.
2. Acid or neutral localities; the maximum value of pH not exceeding 7.0.
3. Weakly acid or weakly alkaline localities; the minimum value of pH not below about 6.2 and the maximum not above 9.0.
4. Alkaline localities; the minimum value of pH not much below 7.0, whereas the maximum exceeds 9.0.

In Table 2 the species have been arranged in these groups, and because most Danish fresh waters belong to group 3 the figures for this group are the highest.

The table shows that the species of the subfamily *Eucyclopinae*, with the exception of the genus *Macrocylops*, were not found in groups 1 and 2; the other great systematic units, except *Temoridae*, were found in all four groups. Some species, *Macrocylops fuscus*, *Cyclops strenuus strenuus* and *Canthocamptus staphylinus* and, to a smaller extent, *Eudiaptomus vulgaris*, *Macrocylops albidus*, *Cyclops viridis*, *C. bicuspidatus*, and *Mesocyclops leuckarti* seem to be very tolerant to variation of pH since they were found in several groups; the other species were only found in one or two groups.

The reactions of the single species to a higher or lower hydrogen-ion concentration cannot be seen from this table, but the egg counts in the Special Part (p. 31 fol.) clearly show that all the species studied produce fewer eggs at low pH values than they do at high ones. Thus apparently all these species are rather alkaliphilous, although they may occur in very acid localities, and no markedly acidophilous species have been found.

Table 2. Occurrence of the species in relation to pH showing the number of localities within each pH-group.

	Group.			
	1	2	3	4
<i>Eudiaptomus vulgaris</i> (SCHMEIL)	2	2	2
<i>Eudiaptomus coeruleus</i> (FISCHER)	1	1
<i>Eudiaptomus gracilis</i> (G. O. SARS)	3	..
<i>Eudiaptomus graciloides</i> (LILLJEBORG)	1	1	..
<i>Diaptomus castor</i> (JURINE)	3	..
<i>Heterocope saliens</i> (LILLJEBORG)	1
<i>Macrocyclus albidus</i> (JURINE)	2	5	1
— <i>juscus</i> (JURINE)	2	3	2	1
<i>Eucyclops macruroides</i> (LILLJEBORG)	3	..
— <i>macrurus</i> (G. O. SARS)	2	..
— <i>speratus</i> (LILLJEBORG)	2	1
— <i>serrulatus</i> (FISCHER)	4	..
<i>Paracyclops affinis</i> (G. O. SARS)	1	..
— <i>fimbriatus</i> (FISCHER)	3	..
<i>Ectocyclus phaleratus</i> (KOCH)	1	..
<i>Cyclops (Cyclops) insignis</i> CLAUS	2	1
— (<i>Cyclops</i>) <i>strenuus strenuus</i> FISCHER	1	2	6	1
— (<i>Cyclops</i>) <i>vicinus</i> ULJANIN	1	1	..
— (<i>Megacyclops</i>) <i>viridis</i> (JURINE)	3	7	2
— (<i>Megacyclops</i>) <i>gigas</i> CLAUS	3	..
— (<i>Diacyclops</i>) <i>bicuspidatus</i> CLAUS	1	2	2	..
— (<i>Diacyclops</i>) <i>bisetosus</i> REHBERG	2	2	..
— (<i>Acanthocyclops</i>) <i>vernalis</i> FISCHER	3	..
— (<i>Acanthocyclops</i>) <i>vernalis</i> f. <i>robusta</i> G. O. SARS	2	..
<i>Mesocyclops (Mesocyclops) leuckarti</i> (CLAUS)	1	1	3	..
— (<i>Thermocyclops</i>) <i>oithonoides</i> G. O. SARS	1	..	1	..
<i>Nitocra hibernica</i> (BRADY)	3	..
<i>Canthocamptus staphylinus</i> (JURINE)	1	1	3	1
<i>Moraria brevipes</i> (G. O. SARS)	1
<i>Attheyella (Brehmiella) trispinosa</i> (BRADY)	1	..

B. The electrical conductivity of the water.

Following OLSEN (1950, p. 336), I have, divided the localities into only two groups, in one of which the conductivity is less than or equal to 200 μ mho, and in

Table 3. Occurrence of the species in relation to conductivity of the water showing the number of localities in each conductivity-group.

	Conductivity μmho	
	≤ 200	> 200
<i>Eudiaptomus vulgaris</i> (SCHMEIL)	2	4
— <i>coeruleus</i> (FISCHER)	2	..
— <i>graciloides</i> (LILLJEBORG)	1	..
<i>Diaptomus castor</i> (JURINE)	3
<i>Heterocope saliens</i> (LILLJEBORG)	1	..
<i>Macrocyclus albidus</i> (JURINE)	2	3
— <i>fuscus</i> (JURINE)	5	2
<i>Eucyclops macruroides</i> (LILLJEBORG)	1
— <i>macrurus</i> (G. O. SARS)	1
— <i>speratus</i> (LILLJEBORG)	2
— <i>serrulatus</i> (FISCHER)	2
<i>Ectocyclops phaleratus</i> (KOCH)	1
<i>Cyclops (Cyclops) insignis</i> CLAUS	1
<i>Cyclops (Cyclops) vicinus</i> ULJANIN	1	..
— (<i>Cyclops</i>) <i>strenuus strenuus</i> FISCHER	4	3
— (<i>Megacyclops</i>) <i>viridis</i> (JURINE)	3	6
— (<i>Megacyclops</i>) <i>gigas</i> CLAUS	2
— (<i>Diacyclops</i>) <i>bicuspidatus</i> CLAUS	3	1
— (<i>Diacyclops</i>) <i>bisetosus</i> REHBERG	2	..
— (<i>Acanthocyclops</i>) <i>vernalis</i> FISCHER	1
— (<i>Acanthocyclops</i>) <i>vernalis</i> f. <i>robusta</i> G. O. SARS	1
<i>Mesocyclops (Mesocyclops) leuckarti</i> (CLAUS)	2	..
— (<i>Thermocyclops</i>) <i>oithonoides</i> G. O. SARS	1	..
<i>Nitocra hibernica</i> (BRADY)	1
<i>Canthocamptus staphylinus</i> (JURINE)	2	3
<i>Moraria brevipes</i> (G. O. SARS)	1	..

the other of which the conductivity is more than 200 μmho . Broadly this corresponds to oligotrophic and eutrophic localities.

Table 3 shows that while some species: *Eudiaptomus vulgaris*, *Macrocyclus albidus*, *M. fuscus*, *Cyclops strenuus strenuus*, *Cyclops viridis*, *Cyclops bicuspidatus*, and *Canthocamptus staphylinus* have been found in localities in both groups, the other species (which have, however, each only been taken in a few localities) have been found in one group only. The subfamily *Eucyclopinae* (with the exception of the genus *Macrocyclus*) has only been taken in localities with a high conductivity.

If the two columns are compared it will be seen that in localities with a low conductivity (altogether 12) 15 different species have been found, distributed over 32 records, while in localities with a high conductivity (9 in all) 18 different species have been found, distributed over 38 records. Even though the data are inadequate in number it would seem that in localities having a high conductivity there are both more

species altogether and more species in each locality than in localities with a low conductivity.

The egg counts (p. 35 fol.) further show that when the same species occurs in localities of both groups, the number of eggs is larger in those with a high conductivity than those with a low conductivity.

C. The NaCl content of the water.

Only a very few Danish freshwater copepods have been found in brackish water, either previously or during the present investigations. A summary of these records is given below. The first column shows records made by JENSEN (1905), the second those of LINDBERG (1950), and the third my own finds.

<i>Eurytemora velox</i> (LILLJEBORG)	1	..	1
— <i>affinis</i> (POPPE)	3
<i>Cyclops</i> (<i>Megacyclops</i>) <i>viridis</i> (JURINE).....	1
— (<i>Diacyclops</i>) <i>bicuspidatus odessanus</i> (SCHMANKEWITSCH) .	..	3	1
— (<i>Acanthocyclops</i>) <i>vernalis</i> f. <i>robusta</i> (G. O. SARS).....	..	1	..
<i>Mesocyclops</i> (<i>Mesocyclops</i>) <i>leuckarti</i> (CLAUS)	1	..

Of the six species only one, *Eurytemora affinis*, has been taken in open water, in Randers Fiord and in the Sound, while the rest have been taken only in brackish pools along the shore.

The temperature, and oxygen content of the water, have been considered in the discussions on the individual species. The iron content and colour of the water do not seem to influence the occurrence and distribution of the species studied.

If the table showing the occurrence of the species in the various types of locality (p. 84) is compared with the surveys of their occurrence in relation to pH (p. 87), conductivity (p. 88), and NaCl (p. 89), it will be seen that the species which are the most tolerant towards the various chemical factors are also those which occur in the largest number of locality types. This is particularly obvious for *Cyclops* (*Megacyclops*) *viridis* which has been found in 7 different types of localities, and *Macrocyclus albidus*, *Cyclops* (*Cyclops*) *strenuus strenuus*, *Mesocyclops* (*Mesocyclops*) *leuckarti* and *Canthocamptus staphylinus* also show the same tendency.

III. Notes on the biology of the species.

Since the ability of the species to survive unfavourable seasons, the way in which they do it, the time of their reproduction periods, and the numbers of generations per year are of importance when their occurrence and distribution are studied, I give here a brief summary of these characters as found for the species which I have studied.

A. Unfavourable seasons.

The way in which the species survive the unfavourable seasons differs for the various species. The following table shows the seasons which are unfavourable for the individual species.

- Group 1) No distinct unfavourable period.
- Group 2) Winter, low temperatures.
- Group 3) Winter, freezing of the locality.
- Group 4) Summer, high temperatures.
- Group 5) Summer, desiccation of locality.

	Group				
	1	2	3	4	5
<i>Eudiaptomus vulgaris</i> (SCHMEIL)	+	+	..	+
<i>Diaptomus castor</i> (JURINE)	+	..	+	+
<i>Heterocope saliens</i> (LILLJEBORG)	+
<i>Macrocyclops abidus</i> (JURINE)	+
— <i>fuscus</i> (JURINE)	+
<i>Eucyclops speratus</i> (LILLJEBORG)	+
— <i>serrulatus</i> (FISCHER)	+
<i>Cyclops (Cyclops) insignis</i> CLAUS	+	..
<i>Cyclops (Cyclops) strenuus strenuus</i> FISCHER	+	+
<i>Cyclops (Megacyclops) viridis</i> (JURINE)	+	+	..	+
<i>Cyclops (Megacyclops) gigas</i> CLAUS	+	..	+	..
<i>Cyclops (Diacyclops) bicuspidatus</i> CLAUS	+	+	+	+
<i>Cyclops (Diacyclops) bisetosus</i> REHBERG	+	..	+
<i>Canthocamptus staphylinus</i> (JURINE)	+	+	+	+
<i>Moraria brevipes</i> (G. O. SARS)	+

For several species it is difficult to decide whether a particular season is actually unfavourable and in the table I have included all periods in which reproductive activity did not occur, even though adults, some or all of which may have been carrying eggs, were present.

The manner in which the individual species survive these unfavourable seasons differs greatly, and unfortunately I have not always been able to ascertain with certainty how it is done, but if my observations are combined with those described in the literature the following table can be prepared.

- Group 1) Overwintering as adults with egg-sacs.
- Group 2) Overwintering as adults without egg-sacs.
- Group 3) Oversummering as juvenile stages.
- Group 4) Desiccation or freezing without development of cysts.
- Group 5) Development of cysts.
- Group 6) Egg-sacs which are not resting eggs.
- Group 7) Resting eggs.

	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7
<i>Eudiaptomus vulgaris</i> (SCHMEIL)	+	..
<i>Diaptomus castor</i> (JURINE)	+	+
<i>Heterocope saliens</i> (LILLJEBORG)	+
<i>Macrocyclus albidus</i> (JURINE)	+
<i>Macrocyclus fuscus</i> (JURINE)	+
<i>Eucyclus speratus</i> (LILLJEBORG)	+	+	..
— <i>serrulatus</i> (FISCHER)	+
<i>Cyclops (Cyclops) insignis</i> CLAUS	+	..
<i>Cyclops (Cyclops) strenuus strenuus</i> FISCHER	+	..	+	+
— (<i>Megacyclus</i>) <i>viridis</i> (JURINE)	+	+
— (<i>Megacyclus</i>) <i>gigas</i> CLAUS	+	..	+
— (<i>Diacyclus</i>) <i>bicuspidatus</i> CLAUS	+	..	+	+
— (<i>Diacyclus</i>) <i>bisetosus</i> REHBERG	+
<i>Canthocamptus staphylinus</i> (JURINE)	+	+

With the information given in the tables pp. 90 and 91 a correlation can be made between the main types of locality, i.e. those which dry up and freeze as against those which do not, and the occurrence of species with actual resting stages in the form of resting eggs and formation of cysts:

Species:	Localities without desiccation and freezing		Localities with desiccation and freezing	
	resting stages	no resting stages	resting stages	no resting stages
<i>Eudiaptomus vulgaris</i> (SCHMEIL)	+	..	+
<i>Diaptomus castor</i> (JURINE)	+	+	+	+
<i>Heterocope saliens</i> (LILLJEBORG)	+
<i>Macrocyclus albidus</i> (JURINE)	+
— <i>fuscus</i> (JURINE)	+
<i>Eucyclus speratus</i> (LILLJEBORG)	+
— <i>serrulatus</i> (FISCHER)	+
<i>Cyclops insignis</i> (CLAUS)	+
— <i>strenuus strenuus</i> FISCHER	+	..	+
— <i>viridis</i> (JURINE)	+	..	+
— <i>gigas</i> CLAUS	+
— <i>bicuspidatus</i> CLAUS	+	+	+	+
— <i>bisetosus</i> REHBERG	+
<i>Canthocamptus staphylinus</i> (JURINE)	+	+	+	+
<i>Moraria brevipes</i> (G. O. SARS)	+

From this it will be seen that 14 species occurred in localities which do not dry up or freeze totally. Of these species 4 were found to develop actual resting stages (= about 29 % of the total number of species). Against this only 7 species occurred

in localities which experience desiccation and freezing and of these 7 species 3 are able to form actual resting stages (= about 43 % of the total number of species).

Thus there seems to be some degree of correlation between the character of locality and the percentage of species developing actual resting stages. It is remarkable, however, that not a single species with the ability to form resting eggs or cysts was found to be restricted to localities which freeze and dry up. In this respect the fauna of such localities were found to be characterised only by the non-occurrence of certain of the species which are unable to form actual resting stages (*Cyclops strenuus strenuus*, *C. viridis*, and *C. bisetosus*, are all able to tolerate desiccation or freezing although they apparently develop no resting stages).

Species which survive unfavourable seasons as free-swimming individuals or by means of ordinary, but deposited egg-sacs, normally cannot tolerate desiccation or total freezing.

It is strange to find how gradual are the steps between the various kinds of egg-sacs within this small series of freshwater copepods. I presume that the original type is the egg-sac which hatches immediately after the development of the embryo, and this type is, indeed, found in the largest number of freshwater copepods. Such an egg-sac can then come to function as a resting stage, either fastened to the mother or deposited, by the structure becoming strengthened so that the eggs function as real resting eggs. The more pronounced this strengthening becomes, the smaller is the number of eggs in each egg-sac, the minimum being found in *Heterocope saliens* with only one egg per egg-sac. I have no doubt that in this species the single egg is, in fact, an egg-sac with one egg only, since KESSLER's description (1913) shows that around the egg proper there is a capsule, which must correspond to the egg-sac of the other species.

Consideration of which species have or do not have resting stages raises the problem of which of the species are perennial. The species examined can be placed in three groups, as follows:

Group 1) perennial species:

A. which normally always occur as adults.

B. which in periods only occur as young ones.

Group 2) non-perennial species.

In the table on p. 93 *Cyclops strenuus strenuus* has been included in group 1 B because it can be found in some juvenile stage throughout the summer in those localities which do not dry up (Vildande Pond and Gribsø). *Cyclops bisetosus* has been placed in the same group, since, although it has only been found in localities which dry up, it occurred from May to October in juvenile stages. These were not encysted and were ready to continue their development as soon as water appeared.

The species in group 1 A are good examples of perennial species, although all of them do reproduce for a certain period during the winter.

	Group 1		Group 2
	A	B	
<i>Eudiaptomus vulgaris</i> (SCHMEIL).....	+
<i>Diaptomus castor</i> (JURINE).....	+
<i>Heterocope saliens</i> (LILLJEBORG).....	+
<i>Macrocyclus albidus</i> (JURINE).....	+
— <i>fuscus</i> (JURINE).....	+
<i>Eucyclops speratus</i> (LILLJEBORG).....	+
— <i>serrulatus</i> (FISCHER).....	+
<i>Cyclops (Cyclops) insignis</i> CLAUS.....	+
— (<i>Cyclops</i>) <i>strenuus strenuus</i> FISCHER.....	..	+	..
— (<i>Megacyclops</i>) <i>viridis</i> (JURINE).....	+
— (<i>Megacyclops</i>) <i>gigas</i> CLAUS.....	..	+	..
— (<i>Diacyclops</i>) <i>bicuspidatus</i> CLAUS.....	+
— (<i>Diacyclops</i>) <i>bisetosus</i> REHBERG.....	..	+	..
<i>Canthocamptus staphylinus</i> (JURINE).....	+
<i>Moraria brevipes</i> (G. O. SARS).....	..	+	..

B. The number of generations per year.

Three well delimited groups may be distinguished, group (1) species which always have only one generation yearly, group (2) those which have one or two generations, group (3) those with a varying number of generations, but usually more than two. These groups are shown in the following table:

	Group 1	Group 2	Group 3
<i>Eudiaptomus vulgaris</i> (SCHMEIL).....	..	+	..
<i>Diaptomus castor</i> (JURINE).....	..	+	..
<i>Heterocope saliens</i> (LILLJEBORG).....	+
<i>Macrocyclus albidus</i> (JURINE).....	+
— <i>fuscus</i> (JURINE).....	+
<i>Eucyclops speratus</i> (LILLJEBORG).....	+
— <i>serrulatus</i> (FISCHER).....	+
<i>Cyclops (Cyclops) insignis</i> CLAUS.....	+
— (<i>Cyclops</i>) <i>strenuus strenuus</i> FISCHER.....	+
— (<i>Megacyclops</i>) <i>viridis</i> (JURINE).....	+
— (<i>Megacyclops</i>) <i>gigas</i> CLAUS.....	+
— (<i>Diacyclops</i>) <i>bicuspidatus</i> CLAUS.....	..	+	..
— (<i>Diacyclops</i>) <i>bisetosus</i> REHBERG.....	+
<i>Canthocamptus staphylinus</i> (JURINE).....	+
<i>Moraria brevipes</i> (G. O. SARS).....	+

Group 2 is the only one which is not quite homogeneous. Only *Eudiaptomus vulgaris* has two generations every year, while the other two species have one or two generations depending upon whether the year is dry or wet. Normally the number of

generations of *Diaptomus castor* is one. Most of the species in group 3 belong to the group of perennial species defined above (p. 92).

C. The season in which reproductive periods occur.

The Fig. 23 shows the reproductive periods of the species, the reproductive period being understood as the time during which animals were observed in copulation.

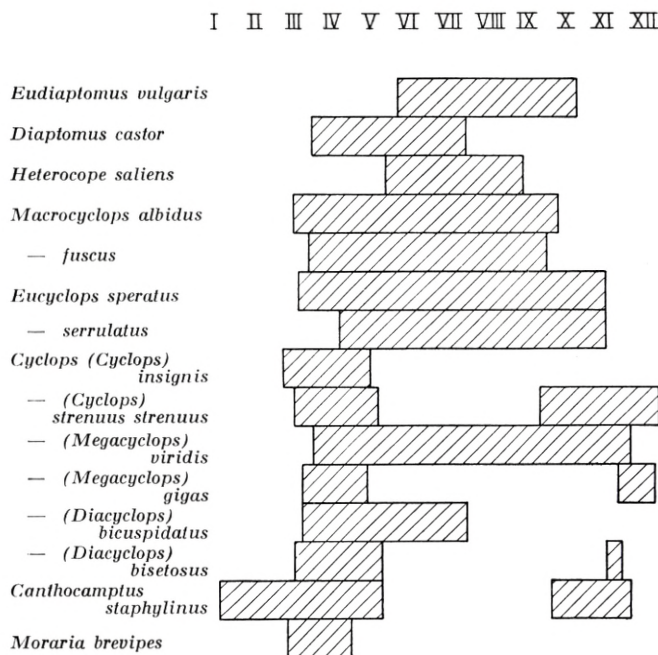


Fig. 23. Duration of the reproductive season in various copepod species.

The periods when animals were only carrying egg-sacs, are not regarded as true reproduction periods.

The figure shows that the perennial species, of which adults normally always occur (group 1 A, p. 93) have long and uninterrupted reproductive periods, and that only during the winter is the reproduction interrupted for a shorter or longer time; *Canthocamptus staphylinus* is, however, an exception as its reproductive activity is interrupted during the summer. The reproductive periods of the non-perennial species are considerably shorter.

This conclusion does not differ much from the information given in the literature. The only considerable difference is that

the reproductive period of *Moraria brevipes* may fall at other times, as has been mentioned on p. 82.

Finally if the biology of the species is compared with their distribution in the various kinds of locality, it will be seen that the species with a large number of generations and a long reproductive period belong to those which occur in most types of localities. They have also been found to be the most frequent in Denmark, whereas the species with only one or two generations, and a short reproductive period have only been found a few times and in a few types of locality.

VII. List of species recorded from Denmark quoting the literature after 1900.

Calanoida.

Diaptomidae:

Eudiaptomus vulgaris (SCHMEIL); SØREN JENSEN (1905 p. 113), C. WESENBERG-LUND (1937 p. 528 part).

Eudiaptomus coeruleus (FISCHER); C. WESENBERG-LUND (1937 p. 528 part, 1940 p. 30).

Eudiaptomus gracilis (G. O. SARS); C. WESENBERG-LUND (1904 p. 198 foll, 1937 p. 528), SØREN JENSEN (1905 p. 113 foll), BERG (1948 p. 63 foll.).

Eudiaptomus graciloides (LILLJEBORG); C. WESENBERG-LUND (1904 p. 196 foll., 1937 p. 528), SØREN JENSEN (1905 p. 114), BERG and NYGAARD (1929 p. 254 foll.), BERG (1948 p. 63).

Diaptomus castor (JURINE); SØREN JENSEN (1905 p. 112), C. WESENBERG-LUND (1937 p. 528).

Hemidiaptomus superbus (SCHMEIL); SØREN JENSEN (1905, p. 112 foll.), C. WESENBERG-LUND (1937 p. 528).

Hemidiaptomus amblyodon (MARENZELLER); C. WESENBERG-LUND (1937 p. 528).

Temoridae:

Eurytemora velox (LILLJEBORG); SØREN JENSEN (1905 p. 114 foll.).

Eurytemora affinis (POPPE); SØREN JENSEN (1905 p. 115).

Eurytemora lacustris (POPPE); SØREN JENSEN (1905 p. 115 foll.).

Heterocope saliens (LILLJEBORG); SØREN JENSEN (1905 p. 112), C. WESENBERG-LUND (1937p. 528).

Cyclopoida.

Cyclopidae.

Eucyclopinae.

Macrocylops albidus (JURINE); SØREN JENSEN (1905 p. 120), C. WESENBERG-LUND (1917 p. 159), BERG (1938 p. 66 foll., 1948 p. 63 foll.), LINDBERG (1950 p. 64 foll.).

Macrocylops fuscus (JURINE); SØREN JENSEN (1905 p. 119), C. WESENBERG-LUND (1937 p. 528), BERG (1948 p. 63 foll.), LINDBERG (1950 p. 64 foll.).

Eucylops macruroides (LILLJEBORG); BERG (1938 p. 66 foll., 1948 p. 63 foll.), LINDBERG (1950 p. 65 foll.).

Eucylops macrurus (G. O. SARS); SØREN JENSEN (1905 p. 120), C. WESENBERG-LUND (1917 p. 144, 1937 p. 528), BERG (1938 p. 66 foll., 1948 p. 63 foll.), LINDBERG (1950 p. 64 foll.).

Eucylops speratus (LILLJEBORG); BERG (1938 p. 66 foll., 1948 p. 63 foll.), LINDBERG (1950 p. 64 foll.).

Eucylops serrulatus (FISCHER); SØREN JENSEN (1905 p. 120), C. WESENBERG-LUND (1917 p. 144, 1937 p. 528), BERG (1938 p. 66, 1948 p. 63 foll.), LINDBERG (1950 p. 66 foll.).

Eucylops lilljeborgi (G. O. SARS); RØEN (1954 p. 11 foll.).

Paracyclops affinis (G. O. SARS); BERG (1948 p. 63), LINDBERG (1950 p. 64 foll.).

Paracyclops fimbriatus (FISCHER); SØREN JENSEN (1905 p. 120 foll.), C. WESENBERG-LUND (1917 p. 144, 159), BERG (1948 p. 63 foll.), LINDBERG (1950 p. 63 foll.).

Ectocyclus phaleratus (KOCH); SØREN JENSEN (1905 p. 121), C. WESENBERG-LUND (1937 p. 528), LINDBERG (1950 p. 63 foll.).

Cyclopinae:

Cyclops (Cyclops) insignis CLAUD; SØREN JENSEN (1905 p. 117), BERG (1948 p. 63 foll.).

Cyclops (Cyclops) vicinus ULJANIN; BERG (1948 p. 64), LINDBERG (1950 p. 65 foll.).

Cyclops (Cyclops) strenuus s. lat.; C. WESENBERG-LUND (1904 p. 192 foll., 1909 p. 93, 1917 p. 144, 1937 p. 528), SØREN JENSEN (1905, p. 116 foll.), BERG (1938 p. 66 foll., 1948 p. 63 foll.), LINDBERG (1950, p. 67).

Cyclops (Cyclops) strenuus strenuus (FISCHER); BERG and NYGAARD (1929 p. 252 ff), LINDBERG (1950 p. 67 foll.).

Cyclops (Megacyclops) viridis (JURINE); SØREN JENSEN (1905 p. 118 foll.), C. WESENBERG-

- LUND (1917 p. 144, 159, 1937 p. 528), BERG (1938 p. 66 foll., 1948 p. 63 foll.), LINDBERG (1950 p. 64 foll.).
- Cyclops (Megacyclops) gigas* CLAUS; SØREN JENSEN (1905 p. 119).
- Cyclops (Diacyclops) bicuspidatus* CLAUS; SØREN JENSEN (1905, p. 118), C. WESENBERG-LUND (1937 p. 528), BERG (1948 p. 63 foll.), LINDBERG (1950 p. 67 foll.).
- Cyclops (Diacyclops) bicuspidatus odessanus* SCHMANKEWITSCH; LINDBERG (1950 p. 65 foll.).
- Cyclops (Diacyclops) bisetosus* REHBERG; BERG (1948 p. 63).
- Cyclops (Diacyclops) languidus* G. O. SARS; LINDBERG (1950 p. 64 foll.).
- Cyclops (Diacyclops) nanus* G. O. SARS; LINDBERG (1950 p. 64 foll.).
- Cyclops (Acanthocyclops) vernalis* FISCHER; SØREN JENSEN (1905 p. 118), BERG (1948 p. 63 foll.), LINDBERG (1950 p. 66 foll.).
- Cyclops (Acanthocyclops) vernalis f. robusta* G. O. SARS; LINDBERG (1950 p. 66 foll.).
- Cyclops (Metacyclops) gracilis* LILLJEBORG; LINDBERG (1950 p. 64 foll.).
- Cyclops (Microcyclops) bicolor* G. O. SARS; SØREN JENSEN (1905 p. 119), LINDBERG (1950 p. 64 foll.).
- Cyclops (Microcyclops) varicans* G. O. SARS; LINDBERG (1950 p. 66 foll.).
- Cyclops (Microcyclops) rubellus* LILLJEBORG; LINDBERG (1950 p. 66 foll.).
- Mesocyclops (Mesocyclops) leuckarti* (CLAUS); C. WESENBERG-LUND (1904 p. 190, 1937 p. 528), SØREN JENSEN (1905 p. 117), BERG (1948 p. 63 foll.), LINDBERG (1950 p. 64 foll.).
- Mesocyclops (Thermocyclops) dybowskii* (LANDE); SØREN JENSEN (1905 p. 117), LINDBERG (1950 p. 66 foll.).
- Mesocyclops (Thermocyclops) oithonoides* G. O. SARS; C. WESENBERG-LUND (1904 p. 190 foll., 1937 p. 528), SØREN JENSEN (1905 p. 117), LINDBERG (1950 p. 68 foll.).
- Mesocyclops (Thermocyclops) hyalinus* (REHBERG); LINDBERG (1950 p. 66 foll.).
- Harpacticoida.
- Ectinosomidae:
- Ectinosoma (H. alectinosoma) abrau* (KRICAGIN); SØREN JENSEN (1905 p. 124).
- Canthocamptidae:
- Nitocra hibernica* (BRADY); SØREN JENSEN (1905 p. 123), BERG (1938 p. 67 foll., 1948 p. 63 foll.).
- Canthocamptus staphylinus* (JURINE); SØREN JENSEN (1905 p. 121 foll.), C. WESENBERG-LUND (1917 p. 144, 159, 1937 p. 529), BERG (1937 p. 67 foll., 1948 p. 63 foll.).
- Canthocamptus microstaphylinus* WOLF; BERG (1938 p. 67 foll.).
- Bryocamptus (Bryocamptus) vej dovskiyi* (MRÁZEK); BERG (1937 p. 67).
- Bryocamptus (Bryocamptus) minutus* (CLAUS); SØREN JENSEN (1905 p. 122).
- Bryocamptus (Bryocamptus) zschokkei* (SCHMEIL); SØREN JENSEN (1905 p. 123).
- Bryocamptus (Bryocamptus) pygmaeus* (G. O. SARS); SØREN JENSEN (1905 p. 123).
- Moraria brevipes* (G. O. SARS);
- Attheyella (Attheyella) crassa* (G. O. SARS); SØREN JENSEN (1905 p. 122), C. WESENBERG-LUND (1917 p. 159, 1937 p. 529).
- Attheyella (Brehmiella) trispinosa* (BRADY); SØREN JENSEN (1905 p. 123), BERG (1948 p. 63 foll.).
- Attheyella (Brehmiella) dentata* (POGGENPOL); SØREN JENSEN (1905 p. 123), BERG (1938 p. 67).

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