

Investigations on the Influence of External Factors on the Duration of the Embryonic Development and on the Molting Rhythm of Cyclops vicinus,
by Klaus-Dieter Spindler. (*Oecologia (Berl.)* 7, 342-355, 1971).

Translated by P.L. Nacht.

Introduction.

Investigations on the control of the embryonic and post-embryonic development of arthropods have formed an intensively studied field of zoological research for a long time, Here in especially favourable cases the causal chain from the operation of external factors on the influence of physiological mechanisms, eg. of the hormone variety, is known right through to its primary influences. (Summaries on the controlled development of arthropods: Bückmann, 1962, 1970). A comparative approach to the relevant questions was in the main only made in the case of the insects.

For crustacea, investigations are available almost exclusively only for the malacostraca (Carlisle and Knowles, 1959; Waterman, 1960). The remaining (so-called lower) crabs have been experimentally investigated only incidentally with regard to embryonic and post-embryonic development and their being influenced through external conditions (eg. *Daphnia*: Stross, 1969a, b, 1971; Stross and Hill, 1968; *Artemia*: Hentschel 1967, 1968; literature on copepods is given in the corresponding chapters). This lack of comparative approaches on the one hand and the discovery of interesting seasonal cycles with intervals of quiescence for freshwater copepods on the other hand (Birge and Juday, 1908; Elgmork, 1959; Einsle, 1964a; etc.) make it appear desirable that a representative of this group could be worked on experimentally with reference to the influence of embryonic and post-embryonic development through external factors, in which especially the effect of the factors of light and temperature could be examined. As the light period has a determining influence on the entire development of *Cyclops vicinus* (Spindler, 1970), tests should be made on whether the light-darkness change serves as a regulator for a possible existing molting rhythm - a question which for the entire arthropods ~~would be~~ ^{has been} settled only very rarely (Scudamore, 1947; Rensing, 1965).

Experimental Animals and Methods

The basic material for my cultures originates from the Bodensee, and

was taken there on 14.3.68. Next Cyclops vicinus was kept under controlled conditions at $20 \pm 1^\circ\text{C}$, a photoperiod of 16 hrs. light (L) and 8 hrs. darkness (D) and a light intensity of 200 lux. Before the experiments started, two generations were reared in these conditions.

Initially 3 different media were tested as culture medium: 1) solution with earth 1:50, 2) solution with earth 1:100 and 3) a mixture of one part Brunswick mains water and nine parts of distilled water. Cyclops vicinus flourished well in all three culture media. Culture medium no. 3 was finally employed, since in both the others the growth of epizoites was in parts very strong. Up to a later time in my researches a synthetic culture medium, used by Loomis and Lenhoff (1956) for Hydra was tested, and this was revealed to be suitable for the rearing of Cyclops vicinus, but was not used for experimental purposes. The water mixture which I used in all my experiments had an overall hardness of 3.4°dH , a carbonate hardness of 1.3°dH and a pH - value of 6.45. The variations in pH-value between the changes of water were negligible.

All cultures were kept initially in glass containers. It appeared however that Cyclops vicinus is insensitive to plastic. The main cultures were therefore kept in ventilated plastic containers (20 x 20 x 6 cm). Here the water was changed at intervals of 1 - 2 weeks, and in the experiments regularly every four days. Food was given at each change of water, and at the same time exuviae and dead animals were sorted out. They were fed with the autotrophic flagellates Haematococcus spec. Also in free nature the predatory living final copepod stages and the adult animals feed on Haematococcus without disadvantageous effects. Short-term feeding experiments with nettle powder and deep-frozen spinach showed that with these culture is possible in the copepod phase, but that both means employed are not especially favourable for the culture in the nauplius phase. Haematococcus also proved to be most successful for the copepod phase, as a comparison of the mortality rates in the copepod phase with a culture of Haematococcus or nettle powder shows:

<u>Food</u>	<u>n</u>	<u>Mortality rate %</u>	<u>χ^2</u>	<u>df</u>	<u>p</u>
<u>Haematococcus</u>	1021	2.4	154.52	1	< 0.01
<u>Nettle powder</u>	167	26.4			

With Haematococcus as food and under the other culture conditions given above, I have now kept Cyclops vicinus continually in the laboratory for three years, which is equivalent to about 50 successive generations.

Fluorescent tubes served as light sources in all cases. For the main cultures and for the experiments on the influence of light intensity on the molting rhythm, fluorescent tubes of the type "Warmton" were used, and of the type "Tageslicht" for the other experiments. The minimum distance between fluorescent tubes and culture container amounted to 20 cm for the "Warmton" tubes, and for the other experiments a constant distance of 40 cm was given. The light intensities were measured with a milliluxmeter. Since not all experimental containers stood at precisely the same angle to the light source, and since moreover the seasoning of the fluorescent tubes has to be borne in mind, the given light intensities are to be considered with discrepancies of $\pm 20\%$.

Experiments on the influence of temperature were carried out in illuminated cryothermostats with a temperature accuracy of $\pm 0,3^{\circ}\text{C}$. All other experiments were carried out in rooms at a constant temperature of $20\pm 1^{\circ}\text{C}$.

Outline of the Development Cycle of Cyclops Vicinus

The development cycle of Cyclops vicinus is set out in Fig. 1, where the individual stages are distributed according to time around the periphery. The duration of development is valid for the following conditions: $20\pm 1^{\circ}\text{C}$, LD 16/8, 1000 Lux in the light phase, feeding with Haematococcus and change of water every four days. The entire development cycle under these conditions lasts for about 24 days. After the nauplius phase there follow five copepod stages. The differences in sex begin to appear for the first time in the fourth copepod stage, and yet clearer in the fifth copepod stage. A copepod in stage CV molts into an adult animal, and undergoes no further moltings.

Results

A. Length of the embryo development.

The influence of the factors of temperature and photoperiod on the

duration of the embryo development was tested. The experiments were carried out on isolated egg-sacs in a clean ~~medium~~ culture medium. An egg-sac appeared from time to time in a container with 8 ml culture medium. As ^A a photoperiod LD 16/8 was applied with a light intensity of 200 lux during the light phase and a value of less than 0.01 lux in the dark phase. Controls ^{were used} followed during the entire light phase at an interval of two hours. If eggs were laid, or if the nauplii hatched in the dark phase, the experiments were not counted. According to the degree of temperature, 12 to 48 egg-sacs were studied; an egg-sac consists of about 10 to a maximum of 35 eggs.

In pilot tests at 20°C it was investigated whether the isolation of the egg-sacs had an influence on the length of the embryo development. For this I removed an egg-sac from a female at the latest two hours after the egg-laying. The female with one attached egg-sac and one isolated egg-sac remained without food in the same culture medium. Hourly controls followed. The result of these pilot tests is set out in Fig. 2. Isolated egg-sacs exhibit a tendency to an insignificantly increased development. The results for the influence of temperature on the duration of the embryo development are reproduced in Fig. 3.

Exploratory experiments under short-day conditions made no difference to the experiments under LD 16/8.

B. The molting rhythm and its influencing by external and internal factors.

I. Temperature Influence.

The investigations were carried out under LD 16/8 and 200 lux, at which only the influence of temperature on the entire duration of the nauplius phase was examined. All nauplii of one generation remained in a culture container in about 25 ml of water during the experiment. Feeding and a change of water followed at an interval of four days. A control was kept on when copepods entered on the first stage; these were then isolated. Controls followed at 24°C at an interval of two hours, at 20.5°C and 13°C at an interval of four hours and at 9°C twice daily. The result of these investigations is set out in Fig. 4. Between 13°C and 24°C there appears a strong linear connection between the temperature and the duration of the

development. The Q_{10} -value for this range amounts to precisely 2.0.

II. Influence of the length of day.

In all experiments the animals were reared in single culture. I was successful in evaluating only those copepods which showed no dormancy in their development. In order to determine the length of the copepod phase, 30 to 53 animals in the male line and between 104 and 147 animals in the female line were reared in single culture according to photoperiod (with the exception of both extreme long-day conditions, for which only 30 and 57 animals respectively were available on account of the high dormancy proportion).

The results of these experiments are set out in Fig. 5. The increasing length of the day has a retarding effect on the development of both sexes in the same direction.

III. Influence of light intensity.

All experiments were carried out under LD 16/8. Constantly it was only those animals which ran through their development without dormancy, which succeeded for evaluation. Individual cultures were observed according to a light intensity of 79-141 for the duration of the nauplius phase; for the duration of the copepod phase the females were at 91-142, the males at 50-76.

The results of these experiments are set out in Figs. 6 and 7. As will emerge from them, the light intensity is effective during the entire development, and also on both sexes in the same way. The length of development of Cyclops vicinus between 200 and 5000 lux is a function of the logarithm of the light intensity. Between the light intensities 200, 1000 and 5000 lux there remain in all cases significant differences ($p < 0.01$) with regard to the length of the development.

In addition to retardation of development, there is also an increase in the mortality rate at higher light intensities (Fig. 8).

As the effect of light intensity on molting could only be of an indirect nature, eg. by means of the food organism (Haematococcus at higher light intensities formed haematochrome more rapidly); the experiments at 200 and 5000 lux with nettle powder as food were repeated. Nettle powder remains unchanged under the influence of different light intensities. All the exper-

imental animals were fed with Haematococcus during the nauplius phase. The newly-hatched Stage 1 copepods were still on the same day placed in a fresh culture medium and from then on fed with nettle powder (absorbed and broken up in a slight culture medium). A change of water and feeding followed at an interval of four days. Only the females passed for evaluation. The result of this experiment is set out in the following table:

<u>Light intensity</u>	<u>n</u>	<u>Average length of development in days</u>	<u>t</u>	<u>df</u>	<u>p</u>
200 lux	32	7.2 \pm 1.1	13.2	79	<0.01
5000 lux	40	8.2 \pm 1.2			

Also on feeding with nettle powder the development of Cyclops vicinus under increased light intensity significantly retarded. At any rate the difference between both light intensities which were examined is in essence less important than in the case of the experiments with Haematococcus.

IV. Molting intervals for both sexes.

The previously described experiments under different periods of daylight and light intensities show significant differences in length of development for both sexes, in which the differences are then greatest if the length of development is greatest, eg. under long-day conditions and high light intensities (V. Figs. 5 and 7). The differences here amount up to three days. The specifically sexual differences in the length of development can however only be identified for the duration of the copepod phase, and not already in the nauplius phase:

<u>Sex</u>	<u>n</u>	<u>Duration of the Nauplius phase at more than 20 hrs. of light per day</u>
Males	57	8.5 days
Females	103	8.2 days

V. The molting activity in the course of a day.

From a total of ten moltings per ontogeny, only the moltings from the last nauplius to the first copepod stage were traced. In the first experiments both photoperiods LD 8/16 and LD 16/8 were tested, with controls at

the beginning and the end of the light phase. The results are set out in the following table:

Photoperiod	n	Molting in % per hr.		χ^2	df	p
		light	dark			
LD 8/16	206	4.84	3.84	2.79	1	>0.5
LD 16/8	131	4.05	4.38	0.19	1	>0.5

In both photoperiods under investigation no significant difference in the rate of molting exists between the light and dark phase. In a following experiment there followed controls at an interval of 2 hours over the whole day. The experiments were carried out at LD 16/8, with 200 lux in the light phase and less than 0.01 in the dark phase. Here it was shown that statistically significant maxima appeared during the course of the day ($\chi^2 = 37.95$; $df = 11$; $p < 0.01$; number of observed moltings = 200). There is an overall maximum in the centre of the light phase, a second maximum at the start of the dark phase (Fig. 9). If one adds up only the moltings in the light and dark phase, as happened in the pilot tests, here also the same molting rates are arrived at in the light and dark phase ($\chi^2 = 0.06$; $df = 1$; p about 1). The following experiment was likewise undertaken at LD 16/8, however there prevailed here only a twentyfold light intensity in the light phase (light phase: 500-700 lux, "dark phase": 25-35 lux). Here the second maximum occurred two hours earlier (Fig. 10) and so still fell in the light phase, on which thereby the larger part of the molting activity drops off ($\chi^2 = 5.94$; $df = 1$; $p < 0.02$; total observed moltings = 229). A similar distribution over the whole day is not the case for this experiment ($\chi^2 = 28.42$; $df = 11$; $p < 0.01$).

Discussion

A. Duration of the embryodevelopment.

There are available several investigations on the influence of the temperature on the length of embryo development of cyclopid copepods (Walter, 1922; Ziegelmayr, 1925; Taube and Nauwek, 1967; Einsle, 1968; Mittelholzer, 1970). The results obtained with Cyclops vicinus show a main correspondence

throughout the curve with the investigations of the above authors.

B. The molting rhythm and its influencing by external and internal factors.

The influence of temperature on the occurrence of molting of cyclopids has already been investigated by Walter (1922) and Ziegelmayr (1925). A basic study on the effect of constant and varying temperature on the length of development of Acanthocyclops viridis is available from Khan (1965). Lately there have also been data on the temperature dependence of the development of Cyclops vicinus (Mittelholzer, 1970). In comparison with the data communicated by Mittelholzer (1970) for the same species, the development here, so rapid as to be almost double, has been surprising; all the more so, as Mittelholzer worked under conditions of light which accelerated development and used Haematococcus as well as Scenedesmus as food. That the rearing conditions afforded in my experiments are very favourable is also apparent from the high survival rates (over 90% for the nauplii, over 95% for the copepods) in comparison with the values obtained by Mittelholzer (45% for the nauplii, 60% for the copepods).

The influence of the length of day on the molting rhythm has been studied in greater detail for malacostraca (Bliss, 1954; Stephens, 1955; Bliss and Boyer, 1964; Adelung and Bückmann, 1965; Aiken, 1966). Only isolated data are available for copepods. According to Marshall and Orr (1955) Calanus molts better in light than in darkness. Auvray and Dussart give qualitative data on the influence of the photoperiod on the development of Eucyclops serrulatus: according to them, LD 16/8 speeds up the development in comparison with LD 8/16, the duration of light taking up a middle position. Einsle (1964b) describes the effect of four different lengths of day on the duration of the nauplius phase for Cyclops vicinus at 12°C: LD 2/22 and LD 18/6 have the same indifferent effect in his experiments, with LD 6/18 in comparison to this the development is stimulated, while with LD 12/12 it is reduced. In contrast to Einsle's experiments on the same species I could not establish a minimum to the speed of development with LD 12/12; on the contrary the development under 12 hours of illumination daily signif-

icantly speeded up in comparison with the duration of light. This retardation of development with increasing length of day is also valid for the nauplius phase (Spindler, 1970) as well as for the copepod phase, and for both sexes. The mechanisms lying behind the retardation of molting are at any rate still unclear. There could be indirect causes, eg. qualitative changes of the food organism dependent on the photoperiod; the photoperiod could however also have a direct and specific influence on the Cyclops itself, as has been described by Aiken (1966) for Orconectes virilis and by Adelung and Bückmann (1965) for Carcinus maenas. In both cases the photoperiod controls the molting rhythm through regulation of the synthesis or by free-setting (?) the hormone which retards molting. An explanation of these questions is not yet possible for Cyclops on technical grounds. The increase in the duration of development with increased length of day found under experimental conditions is also confirmed through ecological findings. Mittelholzer (1970) writes, that those animals which do not fall into dormancy in the early summer have an extraordinarily long development time for the temperatures prevailing in the lake.

Investigations on the influence of the light intensity on the molting rhythm of the copepods have hitherto not been made.

The only known effects of light intensity on copepods are a decrease in the frequency of heartbeat (Harvey, 1930) as well as an increased use of oxygen with increasing light intensity (Marshall et al., 1935). The only work known to me on the question of the influencing of the molting rhythm through light intensity is an experiment by Northrop (1926) on Drosophila with contradictory results, which are to be attributed most probably to the effects of temperature. Beck (1968) states that in the case of insects, above-optimal light intensities have a restraining influence on the growth. By which mechanisms the light intensity influences the moltings is still unknown. Since there are difficulties inherent in using nettle powder as food in the control experiments (the mortality is more than ten times higher than with feeding with Haematococcus - the culture medium became partly brown-coloured, or there was a development of ciliates in the experimental vessels), the question seems to me not yet cleared up satis-

factorily, in as far as whether the light intensity effects the food for the moltings directly or indirectly and whether it is a case of both effects combined.

That the length of development for copepods is shorter for the males than for the females has already been known for a long time, and has been repeatedly confirmed. According to Augray and Dussart (1967) the differences in the length of development first appear to arise essentially in the fifth copepod stage.

Investigations on the molting activity in the course of the day are not yet available for copepods. The biological significance of the two peaks in the molting rhythm found for Cyclops vicinus under experimental conditions is still unclear. That the position of a maximum through limited amounts of light during the dark phase is susceptible, has also been described for the hatching rhythm of insects (Remmert, 1962).

Investigations on the Influence of External Factors on the Duration
of the Embryonic Development and on the Molting Rhythm
of *Cyclops vicinus*

Summary. 1. Methods are described for continuous laboratory cultivation of the pelagic freshwater copepod *Cyclops vicinus*.

2. The embryonic development is temperature dependent in a manner typical of cyclopids. Isolated egg-sacs show a slight tendency to accelerated development.

3. Increasing day length, increasing light intensity and decreasing temperature delay the process of molting throughout the whole development, in both sexes. In the copepodid-phase development is faster in males than in females.

4. Molting activity shows a maximum in the middle of the light phase and a second maximum at the beginning of the dark phase.

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Dauer der Embryonalentwicklung und Häutungsrythmus von *Cyclops* 345

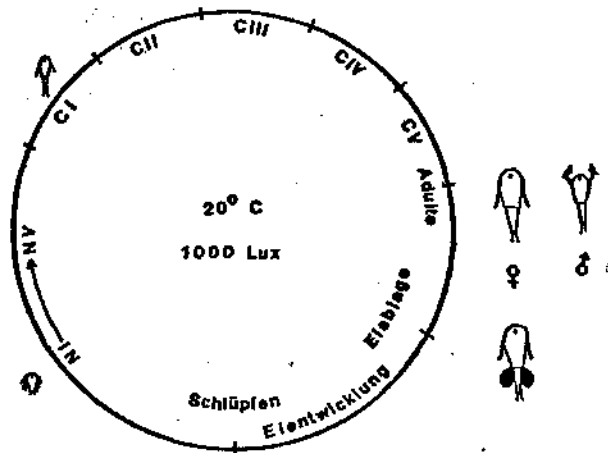
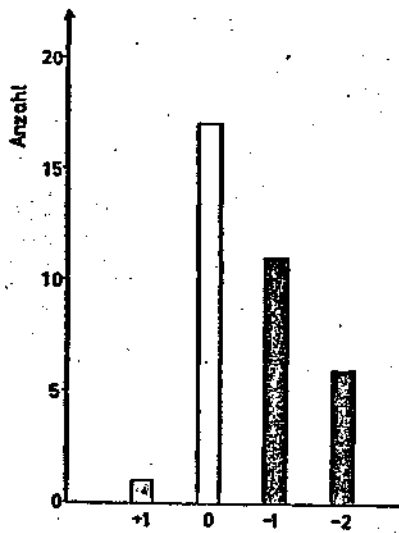
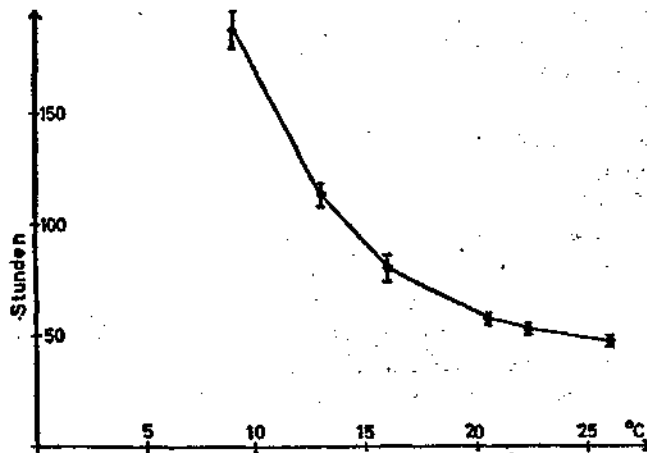


Abb. 1. Der Entwicklungszyklus von *Cyclops vicinus* in zeitgerechter Darstellung. Gesamtdauer des Zyklus: ca. 24 Tage (20°C, LD 16/8, 1000 Lux). NI — NV die 5 Naupliusstadien; CI — CV die 5 Copepodidstadien

1. The development cycle of *Cyclops vicinus* presented according to time. Total length of the cycle: c. 24 days (20°C, LD 16/8, 1000 lux. NI - NV the five nauplius stages; CI - CV the five copepod stages.



2. The effect of isolating the egg-sacs on the duration of the embryo development of Cyclops vicinus at 20°C. + 1 isolated egg-sac with an increased length of development of about 1 hr.; 0 development period of the same length; -1, -2 at 1 and 2 hrs. respectively of shortened development for isolated egg-sacs.



3. Duration of the embryo development (from egg-laying to the hatching of the nauplii) of Cyclops vicinus depending on temperature. Between 12 and 48 egg-sacs were tested per degree of temperature. I standard deviation.

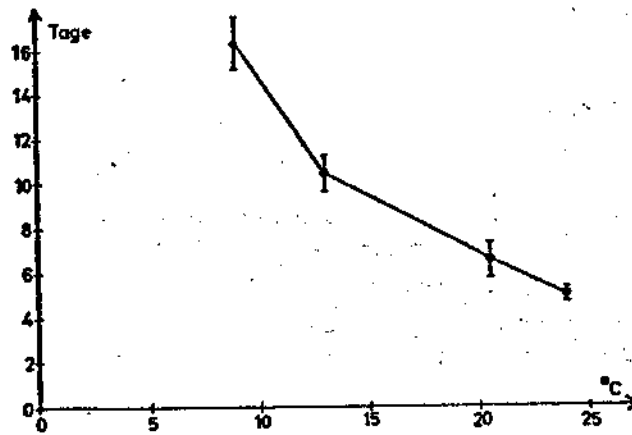


Abb. 4

4. The duration of the nauplius phase of Cyclops vicinus depending on temperature. LD 16/8, 200 lux. Total of the nauplii according to degree of temperature: 79-196. I standard deviation.

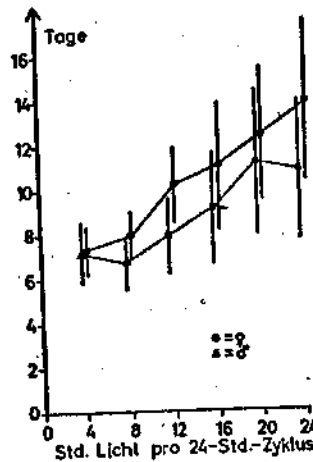
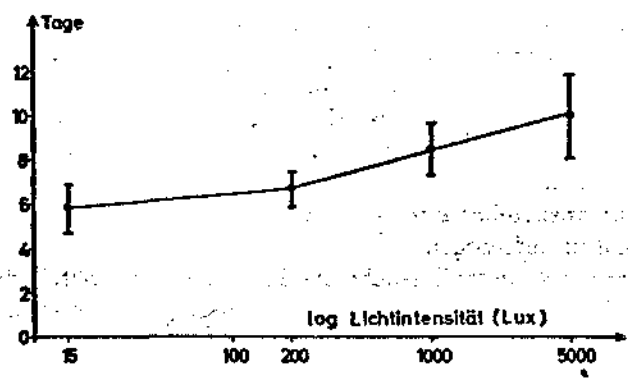
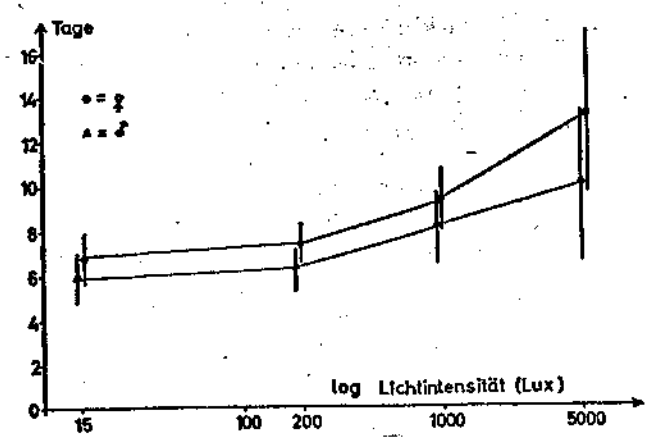


Abb. 5

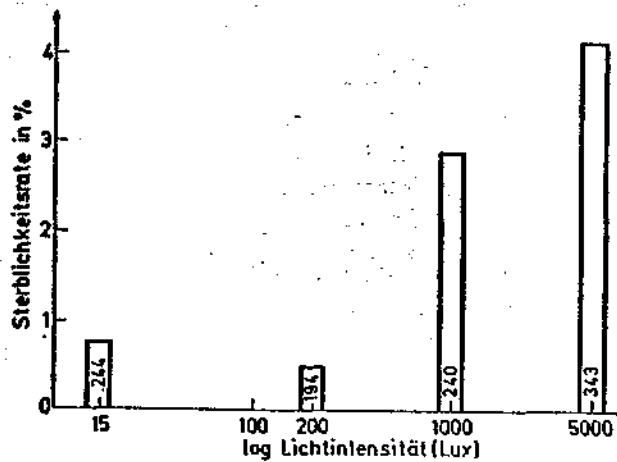
5. Duration of the copepod phase of Cyclops vicinus depending on the length of day. 20°C, 1000 lux. For the calculation of mean values and standard deviations only those animals which showed no dormancy during their development were considered. I standard deviation.



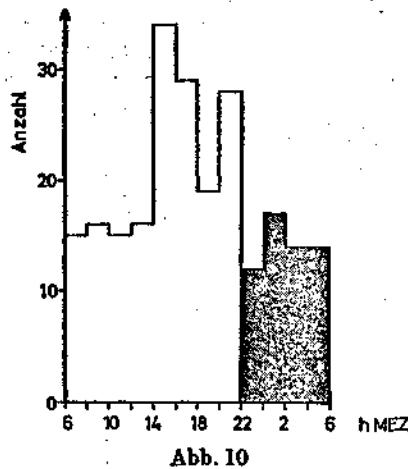
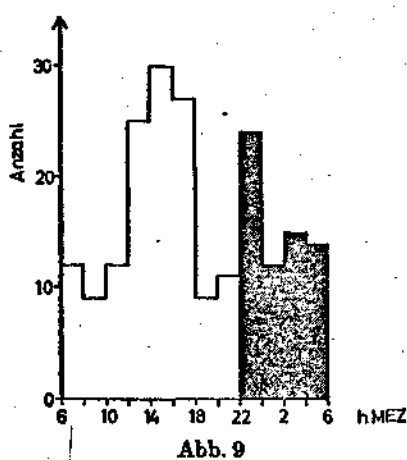
6. Influence of light intensity on the duration of the nauplius phase. Significant differences between all four points of measurement. Total of the individual cultures according to mean value: 79-141. I standard deviation.



7. Influence of the light intensity on the duration of the copepod phase, separate for males and females. Only those animals which showed no dormancy in their development were considered. Significant differences only from time to time between 200, 1000 and 5000 lux. Total of the cultures according to mean value: females 91-142, males 50-76. I standard deviation.



8. The mortality in the copepod phase of Cyclops vicinus depending on the light intensity. Between 15 (resp. 200) and 5000 lux significant differences ($\chi^2 = 5.73$ resp. 5.79; $df = 1$; $p < 0.02$). The total of the experimental animals is entered in the respective columns.



9. The molting activity of Cyclops vicinus in the course of a day at LD 16/8 (light phase: 200 lux, dark phase: less than 0.01 lux). Molting pace: transition from the last nauplius stage to the first copepod stage. Total moltings = ~~229~~ 200.
10. The molting activity of Cyclops vicinus in the course of a day at LD 16/8 (light phase: 500-700 lux, dark phase: 25-35 lux). Molting pace: transition from the last nauplius stage to the first copepod stage. Total moltings = 229.

Notice

Please note that these translations were produced to assist the scientific staff of the FBA (Freshwater Biological Association) in their research. These translations were done by scientific staff with relevant language skills and not by professional translators.