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THE INFLUENCE OF PHOTOPERIODISM ON DIAPAUSE IN CHIRONOMIDS

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The influence of seasonal changes in illumination on the annual cycle of chironomids was first observed by Clever (1962) during laboratory maintenance of larvae of Camptochironomus tentans F. In these larvae, development was interrupted in the autumn under short day-length; this was accompanied by structural changes in the expanded chromosomes of the salivary glands characteristic of diapausing insects. In consequence of these observations, Engelmann and Shappirio (1965) specially investigated the role of photoperiodism in the maintenance of diapause and the reactivation of development in the same species. They confirmed that short day length preserved diapause, and then, that long day-length stimulated larval development, and interrupted diapause.

*Numbers in the right-hand margin indicate the corresponding pages in the original.

The onset of diapause under long photoperiod (at the end of May) in young (second-instar) larvae of *Parachironomus kuzini* Shilova inhabiting spring pools that dry up at the beginning of summer, was observed also by one of the authors of the present article (Shilova, 1969).

In the years 1969-70, we carried out observations on 38
some species of chironomids of which part have one generation in the local environment (their larvae emerge from hibernation fully developed, and the adults take flight at once after the melting of the snow), or two (the adults of the first generation fly from the beginning of spring to the beginning of summer). The whole investigation consisted of the elucidation of the influence of photoperiodism on maturing larvae of one or the other category in the fall-winter period.

Larvae of the 4th instar in numbers totalling more than 1800 specimens, and belonging to 10 species, were collected in the reserve zone of the Rybinsky reservoir, and in adjacent bodies of water, from Sept. 1969 to Feb. 1970. In all, 30 parallel experiments were supplied with material. Of the species used in the experiments, 4 (*Chironomus pilicornis* F., *Stictochironomus crassiforceps* Kieff., *Anatopynia plumipes* F. and *Psectrotanypus varius* F. were univoltine, flying (except *S. crassiforceps*) early in the spring, and 6 (*Chironomus plumosus* L., *Chironomus* sp., *Camptochironomus tentans* F., *Polypedilum nubeculosum* Mg., Procladius choreus Mg. and Psectrocladius ex gr. psilopterus produced two generations a year in the local environment.

Larvae were placed in Petri dishes with water and food in the form of a powder prepared from dried, ground Elodea and aquatic plants.[1] Predaceous larvae fed on tiny chironomids and enchytraeids. The experiments were carried out under temperatures of 17-19 and 20-22°; the source of light used was the common electric lamp of 25 watts. The same numbers of larvae were kept under 16- and 8-hr. exposures. During observations on development, the number of pupating larvae and flying adults was ascertained, and note was taken of the date of pupation.

It was possible to separate the species under observation into three groups according to the kind of reaction to day-length observed. To the first group belong those species the development of which is inhibited by short photoperiod and reactivated by long. The second group consists of species the development of which is reactivated not only by long photoperiod but by freezing and chilling. In the species of the third group, diapause is removed only by freezing, and photoperiodism exerts no influence on it whatever. In the first group (Table 1) one species,

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[1] Detritus feeding larvae, after the construction of shelters, never left them and fed only by means of filtration, from which it is possible to conclude that the food in the vessels was adequate (Shilova, 1955).

Table 1. Reaction to photoperiod of larvae of the first group (I, imago; P, pupa).

1. Вид	2. № опыта	3. Начало опыта	4. Фотопериод, час.	5. Начало окукливания	6. Конец окукливания	7. Количество личинок в опыте	8. Количество куколок и вылетевших имаго
Chironomus plumosus	1	19 IX	8	10 X	13 I	10	3 I, 7 P
			16	30 IX	25 X	10	1 I, 9 P
Chironomus sp.	1	17 IX	8	17 XII	17 XII	20	1 P
			16	1 X	5 X	20	4 P
Polypedilum nubeculosum	1	14 X	8	10 XI	2 XII	120	1 I, 61 P
			16	28 X	9 XI	120	17 I, 76 P
Camptochironomus tentans	1	16 IX	8	4 X	16 XI	40	1 I, 2 P
			16	2 X	4 XI	40	4 I, 20 P
	2	1 X	8	10 X	21 I	20	9 P
			16	12 X	28 X	20	11 P
	3	15 X	8	25 X	22 I	25	3 I, 18 P
			16	25 X	10 XI	25	2 I, 15 P
Stictochironomus crassiforceps	1	31 X	8	2 XII	21 I	60	11 P
			16	25 XI	11 XI	60	3 I, 35 P
	2	18 XI	8	10 XII	12 I	45	1 I, 10 P
			16	2 XII	25 XII	45	4 I, 18 P
	3	1 XII	8	19 XII	20 I	40	9 P
			16	18 XII	26 XII	40	23 P

Column headings:

1. Species
2. Experiment number
3. Date of beginning of experiment
4. Photoperiod, hours
5. Date of beginning of pupation
6. Date of end of pupation
7. No. of larvae in experiment
8. No. of pupae and flying adults

Stictochironomus crassiforceps, is univoltine, distributed in the reservoir beyond the limits of the drying and freezing shore-line and 4 (Chironomus plumosus, Chironomus sp., Camprochironomus tentans, and Polypedilum nubeculosum are bivoltine, inhabiting the freezing and non-freezing littoral zone of the reservoir, with Ch. plumosus and P. nubeculosum occurring also in the open parts. In these species, pupation takes place in a large number of larvae under long photoperiod, and begins and ends earlier than under short-day length. In Camptochironomus tentans the 39
length of photoperiod shows no or almost no influence on the date of onset of pupation. In this species, and also in Chironomus plumosus, in both situations the number of pupating larvae was almost identical, but in both species, under short day length, the period of pupation is greatly extended and becomes almost two times longer than under long photoperiod. The results of our observations on Camptochironomus tentans in general terms confirm the data of Engelmann and Shappirio. In our experiments, as in theirs, pupation began under various day lengths either simultaneously or, under long photoperiod, only two days earlier. Only in experiment No. 1 was the number of pupations 7 times greater under long photoperiod than under short. In Expt. Nos. 2 and 3 the numbers pupating in both situations was almost similar. This illustrates that in the process of hibernation the course of development of larvae is determined by the length of the photoperiod in a complicated way.

Table 2. Reaction to photoperiod of larvae of the second group.

1. Вид	2. № опыта	3. Начало опыта	4. Фотопериод, час.	5. Начало окукливания	6. Конец окукливания	7. Количество личинок в опыте	8. Количество куколок и вылетевших имаго
Chironomus pilicornis	1	31 X	8	11 XI	11 XII	18	5 P
			16	9 XI	10 XI	18	2 I, 3 P
	2	17 XI	8	2 XII	31 XII	20	1 I, 4 P
			16	25 XI	29 XI	20	2 I, 13 P
	3	1 XII	8	8 XII	22 XII	10	1 I, 5 P
			16	10 XII	16 XII	10	2 I, 7 P
	4	11 II	8	17 II	25 II	25	9 I, 14 P
			16	16 II	22 II	25	18 I, 6 P
Psectrocladius ex gr. *psilopterus*	1	14 IX	8	10 XI	20 XI	40	1 I, 12 P
			16	21 X	30 X	40	3 I, 13 P
	2	31 X	8	11 XI	20 XI	40	5 I, 15 P
			16	10 XI	14 XI	40	12 I, 22 P
	3	18 XI	8	26 XI	30 XI	20	2 I, 10 P
			16	26 XI	1 XII	20	18 P
Psectrotanypus varius	1	29 IX	8	26 X	26 X	10	2 P
			16	14 X	21 X	10	3 I
	2	2 X	8	2 XI	3 XI	15	3 P
			16	15 X	21 X	15	2 P
	3	15 X	8	29 X	11 XI	40	1 I, 23 P
			16	25 X	16 XI	40	5 I, 24 P
	4	31 X	8	12 XI	29 XII	60	10 I, 20 P
			16	10 XI	21 XI	60	9 I, 18 P
	5	11 II	8	17 II	21 II	20	8 I, 6 P
			16	18 II	22 II	20	6 I, 2 P

Column headings:

1. Species
2. Experiment number
3. Date of beginning of experiment
4. Photoperiod, hours
5. Date of beginning of pupation
6. Date of end of pupation
7. No. of larvae in experiment
8. No. of pupae and flying adults

Chironomus pilicornis, *Psectrotanypus varius* (univoltine) and *Psectrocladius* ex gr. *psilopterus* (bivoltine) belong to the second group (Table 2). Long photoperiod produces reactivation and the effect of acceleration in their development only in the fall; on *Ps.* ex gr. *psilopterus* in September; on *Ch. pilicornis* in October; and on *P. varius* from September to the beginning of October. Under these conditions an almost identical number of larvae pupated (except *Ch. pilicornis* in Expt. No. 2). In an experiment begun later, after the larvae involved had already gone through natural chilling or freezing, pupation under long and short day-length began and finished almost simultaneously, and under these conditions an almost identical number of larvae pupated. 40

In the third group (Table 3) are the univoltine *Anatopynia plumipes*, living in the littoral zone of the reservoir susceptible to freezing, and the ubiquitously distributed bivoltine *Procladius choreus*. The development of their larvae proceeds independently of day-length. During the beginning of autumn they developed neither under long nor short photoperiods. From the middle of October to the beginning of November individual larvae of *A. plumipes*, collected after the first freezing, began to pupate in both series of experiments. In the experiment begun in February the number of larvae of this species beginning development was very large and pupation began and finished simultaneously

Table 3. Reaction to photoperiod of larvae of the third group.

1. Вид	2. № опыта	3. Начало опыта	4. Фотопериод, час.	5. Начало окукливания	6. Конец окукливания	7. Количество личинок в опыте	8. Количество куколок и вылетевших имаго
Procladius choreus	1	1 X	8 16	— —	— —	10 10	— —
	2	3 X	8 16	— —	— —	10 10	— —
Anatopynia plumipes	1	16 X	8 16	— —	— —	20 20	— —
	2	2 X	8 16	— —	— —	20 20	— —
	3	15 X	8 16	— 1 XI	— 1 XI	40 40	— 1 P
	4	31 X	8 16	10 XI 10 XI	2 XI 10 XI	27 27	4 P 1 P
	5	17 XI	8 16	25 XI 24 XI	1 XII 27 XI	26 26	4 P 2 P
	6	1 XII	8 16	8 XII 8 XII	10 XII 8 XII	18 18	2 P 1 P
	7	11 II	8 16	19 II 18 II	22 II 22 II	40 40	3I, 8 P 1 I, 10 P

Column headings:

1. Species
2. Experiment number
3. Date of beginning of experiment
4. Photoperiod, hours
5. Date of beginning of pupation
6. Date of end of pupation
7. No. of larvae in experiment
8. No. of pupae and flying adults

under long and short photoperiod. Thus in the species of the third group development was reactivated by freezing or by prolonged chilling. It is necessary to record however that the larvae of both species of the third group, in the course of their maintenance in the laboratory (except Expt. No. 7) were clearly sluggish and less active, and perished up to the end of the observations. This demonstrates that their life cycle is more rigid and difficult to alter under the influence of factors unusual for their natural conditions.

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