

Life cycle characteristics in *Pseudochironomus prasinatus* (STAEGER, 1839) (Diptera : Chironomidae)

by B.R. GODDEERIS

Summary

The life cycle of *Pseudochironomus prasinatus* has been analysed by studying the larval development in two ponds in the Belgian Ardennes. The results are compared to the literature data on adult emergence.

Ps. prasinatus is a mainly univoltine summer species. The emergence is not well synchronized, but is concentrated in June - July, even in different climatic conditions. From late summer onwards, the larvae enter in diapause with a development treshold in the early fourth instar stage.

Additional key-words: *Pseudochironomus*, diapause, emergence, life cycle.

Résumé

Le cycle de vie de *Pseudochironomus prasinatus* a été examiné au moyen d'une analyse du développement des larves dans deux étangs en Ardenne belge. Ces résultats sont comparés aux données de la littérature sur l'émergence des adultes.

Ps. prasinatus est une espèce d'été, principalement univoltine. L'émergence n'est pas fort synchronisée, mais plutôt concentrée en juin - juillet, même dans des conditions climatiques différentes. A la fin de l'été, les larves entrent en diapause avec une limite de développement au début du quatrième stade larvaire.

Mots-clefs: *Pseudochironomus*, diapause, emergence, cycle de vie.

Introduction

Life cycle data on *Pseudochironomus prasinatus* in the literature mostly refer to adult emergence, which is stretched over two or more months. In spite of this long emergence period, *Ps. prasinatus* is still considered a univoltine summer species.

The only study on population dynamics of all larval stages in *Ps. prasinatus* was conducted at Mirwart in the Belgian Ardennes (GODDEERIS, 1983). This investigation was carried out by length-frequency analyses at regular sampling dates and confirmed the univoltine summer emergence of this species. The same data furthermore indicated that *Ps. prasinatus* has an overwintering diapause in the fourth instar stage (GODDEERIS, 1986). However, length-frequency analyses are not sensitive enough to accurately demonstrate a development arrest in the fourth instar (GODDEERIS, 1989). In order to determine these life cycle characteristics, the Mirwart material has been re-examined using another method: the imaginal disc development analysis.

Mirwart ponds

At Mirwart, *Ps. prasinatus* has been studied in two trout-ponds, i.e. Pond III (0.36 ha, max. depth 2.1 m), and Pond IV (0.32 ha, max. depth 1.7 m). The ponds were regularly sampled from May 1976 till May 1978.

The Mirwart ponds are extensively described in MARLIER & WATTIEZ (1977). In this context, it is worth mentioning that Pond III is rather eutrophic and Pond IV oligotrophic. Water blooms were only observed in Pond III and macrophyte growth was limited in both ponds. The sediment predominantly consisted of silt. Each pond was well mixed and the oxygen concentration always fluctuated around saturation. The surface water temperature at each sampling date is figured in Plate I.

Each year, around mid-October, the ponds were drained for a period of two months. However, a number of puddles were always present and the sediment remained wet by seepage. This drainage did not seem to influence the development of the larvae, but rather their mortality.

Methods

An extensive assessment of the methods which have been used during the Mirwart studies, is given in GODDEERIS (1989). However, a number of specific problems with regard to the present investigation on *Ps. prasinatus* need further elaboration.

The development of the imaginal discs has been described for *Chironomus*-species and the fourth instar stage could be subdivided into nine substages (WUELKER & GOETZ, 1968; INEICHEN *et al.*, 1983). However, other genera can show significantly different morphologies and development. Therefore, it was deemed necessary to re-establish the exact boundaries of the nine substages in *Ps. prasinatus*. As all substages should approximately have the same duration in undisturbed conditions, the subdivision of the fourth stage in *Ps. prasinatus* was made with reference to the one recognised in the genus *Chironomus*. For instance, the appearance of the segmentation of the tarsus is maintained as the limit between the substages 3 and 4. In contrast to *Chironomus*, however, the outgrowth of the

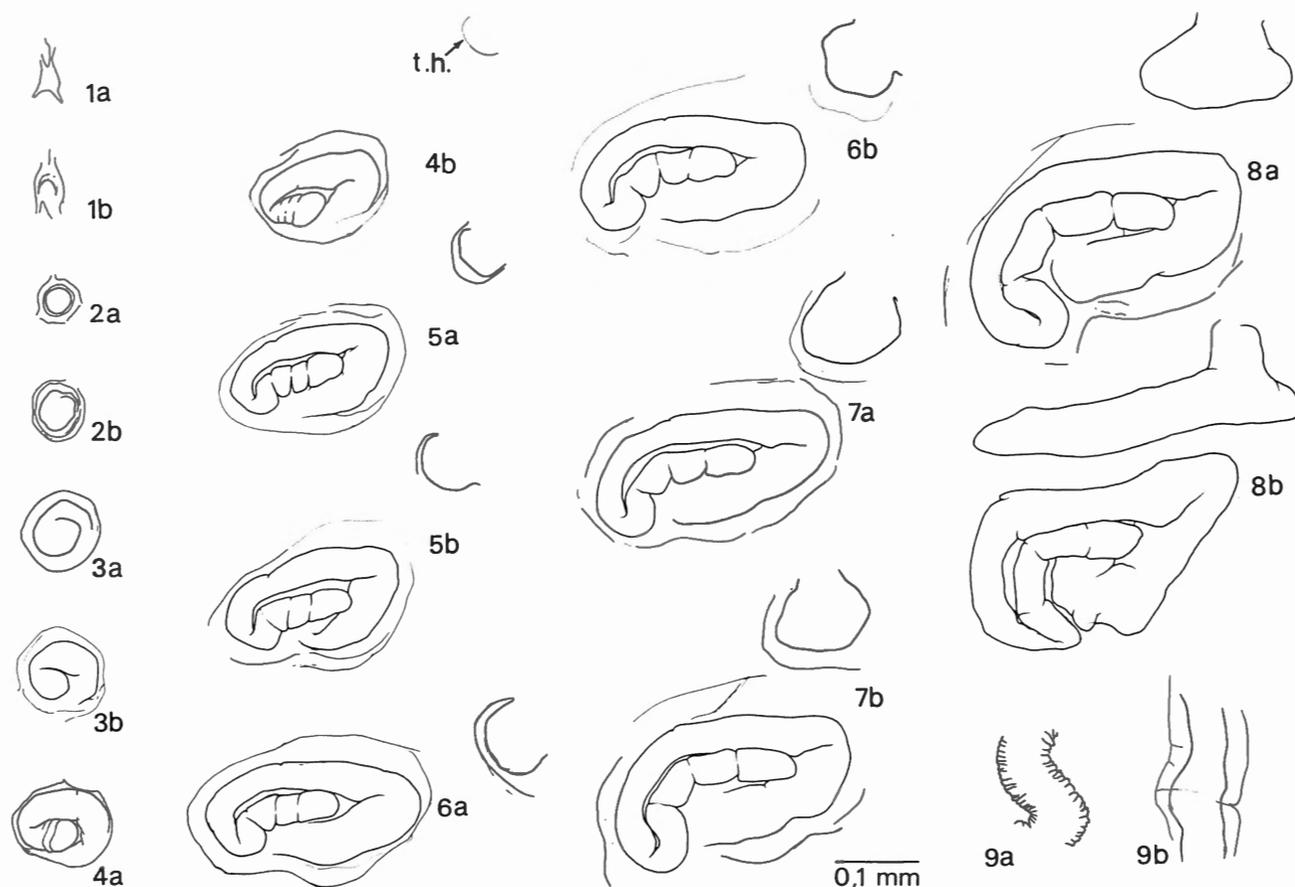


Fig. 1. – Development of the imaginal discs of the foreleg and thoracic horn (t.h.) in the fourth instar stage of *Pseudochironomus prasinatus*; the nine substages with their early (a) and late (b) phase are illustrated.

thoracic horn starts much later in *Pseudochironomus*, i.e. only at the limit of the substage 7 and 8. It was furthermore possible to distinguish an early and a late phase in each substage. The entire subdivision of the fourth instar stage in *Ps. prasinatus* is illustrated in Figure 1.

Unfortunately, it was impossible to sex all the fourth instar larvae, because they were mounted on their side in permanent euparal microscopical slides and sometimes stained too strongly with "Rose Bengale" (for sorting purposes) to allow an uninterrupted sexing.

Identification

Pseudochironomus prasinatus (STAEGER, 1839) is often considered the only representative of the genus *Pseudochironomus* MALLOCH, 1915 in Europe. THIENEMANN (1936) sank *Pseudochironomus nigrimanus* (KIEFFER, 1924) and *Pseudochironomus albimanus* (KIEFFER, 1924) in the synonymy of *Pseudochironomus prasinatus* (STAEGER, 1839) and this was confirmed by FITTKAU & REISS (1978).

However, SAETHER (1977) rejected this synonymy relying solely on a re-interpretation of the original, but non-illustrated descriptions (no specimens were re-examined for this analysis). According to SAETHER, *Ps. albimanus* could be close to (or even the senior synonym of) the nearctic *Pseudochironomus middlekaufi* TOWNES, 1945, which is

characterised by an apical point on the hypopygium. The gonostylus of *Ps. nigrimanus*, on the other hand, is supposed to be conspicuously large and broad, about as large as the gonocoxite.

The hypopygium of the *Pseudochironomus* males from Mirwart (Fig. 2a) indicates the affinity with *Ps. prasinatus* and completely corresponds to the figure in PINDER (1978, figure 170 B). There is no anal point, and the gonostylus is somewhat smaller than the gonocoxite. Furthermore, the pars ventralis is long, very broad and deeply divided; it is lyre-shaped as indicated by HIRVENOJA (1973, figure 17₂), but not fused with the mesal margins of the gonocoxites. The mesal volsella bears 2-4 apical setae.

Pseudochironomus-larvae are easily recognisable by their short antennal pedicels, combined with short and broad ventromental plates (Fig. 2b). The body has parallel sides with short posterior parapods and claws arranged in a horse-shoe; the anal tubules are ellipsoid shaped.

The larvae of *Pseudochironomus* were identified using a combination of the following features: antennal segments II, III and IV of about the same length; median tooth of mentum lower than the first laterals; mentum with minuscule seventh lateral teeth; ventromental plates broad and crenelated anteriorly; mandible without dorsal tooth, but with one apical and four inner teeth; posterior parapods short.

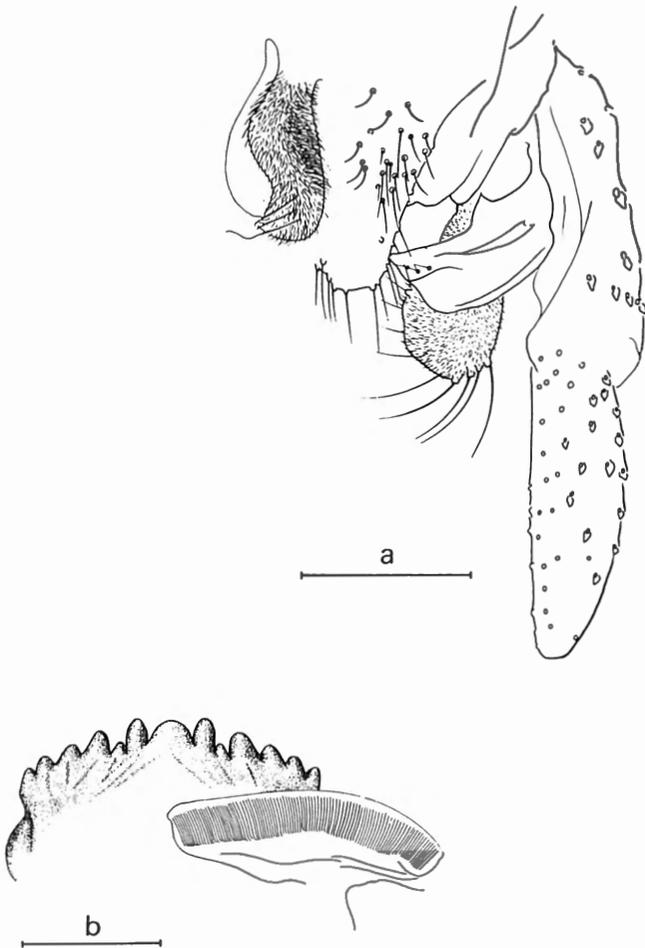


Fig. 2. – *Pseudochironomus prasinatus* from Mirwart (Belgium): (a) dorsal view of the hypopygium, the median volsella and pars ventralis figured separately; (b) mentum and ventromental plate of fourth instar larva. Scale = 0.1 mm.

Results

The raw data on the population structure of *Ps. prasinatus* on each sampling date at Mirwart are figured in Plate I. The abscissa of each figure indicates the larval developmental stages (+ pupa). In each substage of the fourth instar stage an early (a) and late (b) phase is distinguished. At Mirwart, *Ps. prasinatus* had a univoltine summer emergence in 1976-1977. In Plate I, pupae and prepupating larvae are observed only in June and July and the overwintering cohort emerges in its entirety. In Pond IV, where this species is much more common than in Pond III, the larvae of a new cohort appear in the sediment also from June onwards. This new cohort remains somewhat separated from the emerging cohort: even when the two cohorts are very close to each other as on 14.7.1976 in Pond IV, their separation is confirmed by the length-frequency distribution at that date (Fig.3). The new cohort does not emerge in the same year. The emergence of *Ps. prasinatus* starts at about the time that the water temperature rises above 15°C in June.

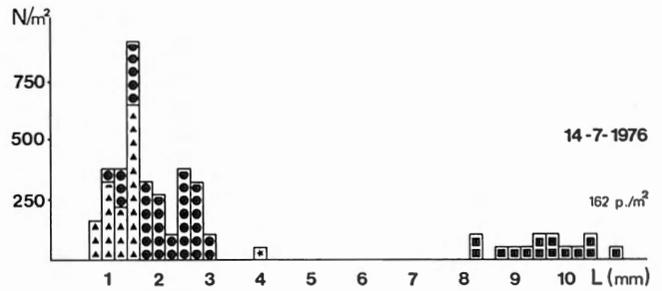


Fig. 3. – Length-frequency distribution of *Pseudochironomus prasinatus* on 14.7.1976 in Pond IV at Mirwart (Belgium): 1st instars (triangles), 2nd instars (dots), 3rd instars (asterisks) and 4th instars (squares).

However, higher water temperatures had already been reached before June without any emergence. It can be noted in the development distributions that no larvae are mature in late May, so emergence could not occur then. The main emergence is already over in late July. Nevertheless, some emergence still occurred until late August, as is indicated by the fourth instar larva in substage IV5a on 16.8.1977 in Pond IV.

From August onwards, larvae of the new cohort (the offspring of the emerging adults) moult to the fourth instar stage, but their development comes to an arrest. Indeed, not a single larva of this cohort passes the IV4 substage in spite of the rather high water temperatures in August (15°C or more). Only from the next spring onwards, this development arrest is removed at significantly lower temperatures (e.g. 12.4°C in Pond III on 9.5.1978). It is also obvious that the development threshold is somewhat higher in Pond III, i.e. substage IV4b instead of IV3b in Pond IV. In autumn, some immature fourth instar larvae of the overwintering cohort already reach body lengths at which pupation is observed in summer (Fig.4). This is the main reason why length-frequency distributions are less adequate for the analysis of development arrests in the fourth instar stage.

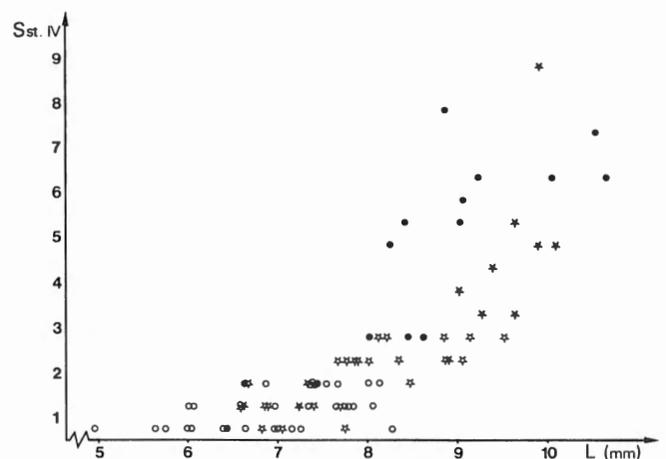


Fig. 4. – Development of the fourth instar of *Pseudochironomus prasinatus* in relation to body length of the larvae on 22.9.1976 (open dots), 18.10.1976 (open asterisks), 21.6.1977 (full dots) and 5.7.1977 (full asterisks) from Mirwart Pond IV.

Many larvae overwinter in the second or in the third instar stage. In September, the last first instars moult to the second stage, and second instars slowly moult to the third stage. In October, parallel to the temperature drop, the population structure changes much slower. Unfortunately, the sampling procedure was interrupted then by the drainage of the ponds. The population structure in mid-winter closely resembles that of mid-autumn; only the relative number of second instars has diminished. But only from early-May onwards, when temperatures reached 12° C and more, the development had undoubtedly restarted.

Differences in the population structure of overwintering cohorts are illustrated in Pond IV : more than half of the larvae overwinter in the fourth instar stage in 1976-77, but only about ten percent in 1977-78. This could be caused by the much higher temperatures in June and July in 1976 compared to 1977.

Literature data

A large amount of data on the emergence of *Ps. prasinatus* has been published from different regions. However, a critical re-interpretation of these data appears necessary, as some of them are obtained from laboratory experiments. Special attention is given to the data with temperature measurements in relation to the onset of emergence.

HUMPHRIES (1938) collected exuviae of *Ps. prasinatus* in Grosser Plöner See (Northern Germany) between 10.6 and 15.8.1936, and found peak numbers on 26.6.1936. The mean temperature of the surface water in this lake was 15.7° C in the first half of June against 13.0° C in the second half of May. These data are repeated in MEUCHE (1939, table 17). HUMPHRIES (l.c.) considered *Ps. prasinatus* a summer species.

BRUNDIN (1949) observed *Ps. prasinatus* emergence in highland lakes of southern Sweden from the end of May until late July. Interesting is an early capture on 31.5.1947 in Lake Innaren (emergence trap, bottom temperature : 15° C). In Lake Skärshultsjön, emergence traps yielded a few imagines between 14.6 and 26.6.1947 at bottom temperatures between 15.5 and 21.5° C; an important water temperature increase had already been observed in May - early June (12.4° C on 7.5; 17.0° C on 11.5; 18.2° C on 28.5; 21.5° C on 1.6).

MUNDIE (1957) followed a one year cycle (21.9.1950 - 25.10.1951) in *Ps. prasinatus* by means of emergence traps in the Kempton Park East Reservoir (Southern England). Emergence started around 10.6.1951 at 16° C bottom temperature, and lasted until 6.9.1951 without a pronounced peak. However, a marked emergence regression was observed in the first three weeks of August. This long emergence period was even observed at the same depth (i.e. 2 m, when captures of three traps are lumped together). It is also worth mentioning that bottom temperatures in mid-September were still higher than 16° C and only dropped below 15° C from mid-October onwards. Despite this unusually long emergence period of three months with a regression in August, MUNDIE thought *Ps. prasinatus* to

be probably univoltine.

REISS (1968) used emergence traps in the subalpine Lake Constance in 1962 and found that *Ps. prasinatus* emerged there from early June till late July. However, the emergence pattern appeared locally more synchronized and significantly shifted in time : in the trap above 1.5 m, the imagines emerged one month earlier than in the one above 5 m. The temperature (unfortunately not measured) was supposed to be the causal factor.

SANDBERG (1969) trapped emerging imagines of *Ps. prasinatus* in Lake Erken (Southern Sweden) between 24.6 and 26.8.1959. The first emergences were observed at a bottom water temperature of about 16° C.

JØNSSON (1987) placed window traps close to Lake Esrom (Denmark) in 1980 and found *Ps. prasinatus* from early-June till mid-August, but mainly in mid-June. Only from mid-April 1980 onwards was Lake Erken ice-free and in June the temperatures rose beyond 15° C (JØNSSON, 1985). The discovery of exuviae of *Ps. prasinatus* on 7.5.1934 in the Alpine Pflögersee (THIENEMANN, 1936) is of the highest interest. This extremely early emergence could be explained by the unusually high water temperatures governing at that time. Indeed, THIENEMANN (l.c. : 243) measured surface water temperatures of 13° C on 3.5.1934 in the nearby Eibsee and 18° C on 13.5.1934 in the Riesser See. The data from EHRENBURG (1957), LENZ (1937) and MEUCHE (1939, table 16) on the emergence period of *Ps. prasinatus* are not taken into account here, as they are at least partially obtained from laboratory rearing experiments. According to EHRENBURG (l.c.) *Ps. prasinatus* should already emerge in East-Holstein at the end of March.

Discussion

In general, the summer emergence of *Ps. prasinatus* is confirmed both by the literature and the Mirwart data. The main emergence has always been observed in June and/or July, even in different climatic regions.

The temperature seems to be a key factor in regulating the emergence. Indeed, the onset of the emergence frequently started when water temperatures were about 15° C. Apparently, this temperature is usually reached at the end of May or early June in a large part of Europe. In favourable years, however, emergences of *Ps. prasinatus* linked to an early temperature increase over 15° C have been observed in spring (THIENEMANN, l.c.).

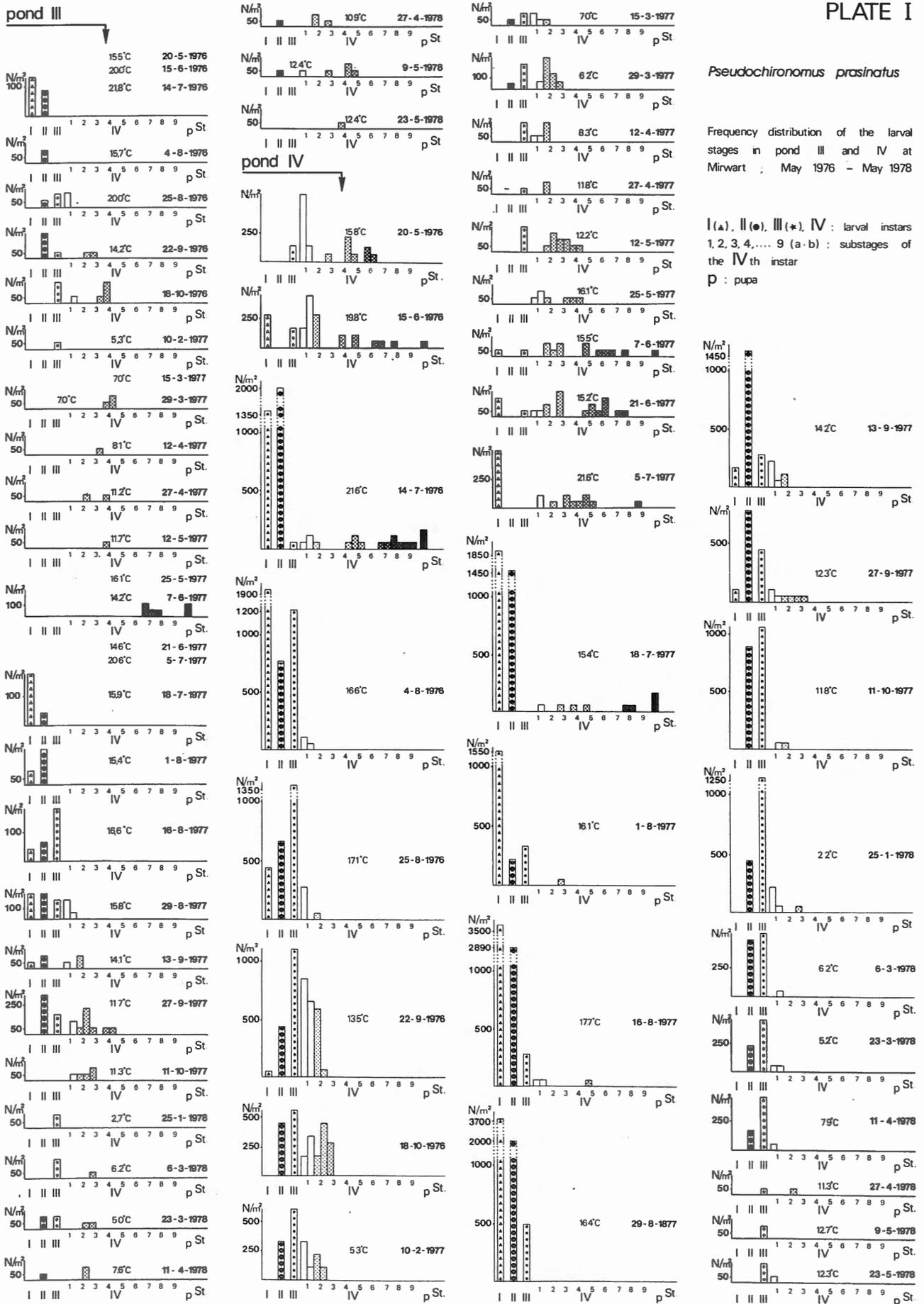
Nevertheless, the linkage of the emergence onset to water temperatures of 15° C could be indirect. BRUNDIN (l.c.) observed water temperatures over 20° C in May, but the *Ps. prasinatus* emergences only in June. Indeed, the most developed overwintering larvae of *Ps. prasinatus* are in an early fourth instar substage as demonstrated at Mirwart. The overwintering larvae are not at all ready to pupate and an important part of growth and development still has to be done in spring. At Mirwart, this further development was done within a few weeks for the first emergences at temperatures between 12° C and 16° C.

PLATE I

Pseudochironomus prasinatus

Frequency distribution of the larval stages in pond III and IV at Mirwart; May 1976 - May 1978

I (Δ), II (●), III (*), IV: larval instars
 1, 2, 3, 4, ..., 9 (a-b): substages of the IVth instar
 p: pupa



An irregular and slow temperature increase in spring is typical of temperate lowland regions, but the low temperatures during that period do not seem to positively influence the development of *Ps. prasinatus*. This is confirmed by the Mirwart data, where the development significantly restarted only at water temperatures of about 12° C. This could be the reason why *Ps. prasinatus* emerges at approximately the same time of the year in different regions, even where spring (and the increase of the water temperature) starts later, but where water temperatures of 12° C are reached at the same time.

However, it is also possible that *Ps. prasinatus* has an absolute development zero temperature of about 12° C and a maturation or pupation temperature of about 15° C. Also this hypothesis could explain the emergence in accordance with the literature. However, the Mirwart data do not allow unequivocal conclusions about the existence of a maturation threshold in *Ps. prasinatus*.

In all the uninterrupted investigations, the emergence of *Ps. prasinatus* is spread over a long period of about two months or more. The supposed univoltine character of this unusually long emergence period is confirmed at Mirwart. *Ps. prasinatus* overwinters in a rather broad cohort of second, third and early fourth instars. Furthermore, the development seems to be restarted individually at different moments in spring and early summer. Locally, under identical environmental conditions, the emergences are better synchronised as illustrated by REISS (l.c.) on separate fractions of a *Ps. prasinatus* population.

The longest emergence period of *Ps. prasinatus* is observed in the eutrophic Kempton Park East Reservoir and is spread over the three summer months from June until the beginning of September. Moreover, the bottom water temperatures were of the highest measured in this context and still remained higher than 15° C during the whole summer. The univoltine character of such an emergence period can hardly be maintained, the more so as the animals emerging in late summer form a small, but separate cohort. A partial generation emergence at the end of the summer in the Kempton Park East Reservoir is more likely.

At Mirwart, a development arrest in a distinct development stage, i.e. the early fourth instar stage, is observed from late summer onwards. Indeed, in spite of the temperatures higher than 15° C in August, no larvae pass the IV3-4 development threshold until the next spring. These facts

point towards an overwintering diapause in *Ps. prasinatus*. Diapause phenomena are very common in chironomids (GODDEERIS, 1986). The role of photoperiod and temperature in governing the diapause have been investigated, especially in the genus *Chironomus* (a.o. RYCHEN BANGERTER & FISHER, 1989). The August daylengths in the northern hemisphere probably induce diapause in *Ps. prasinatus*. High temperatures may delay the diapause onset, but with the shortening of the daylengths in late August and September, the diapause becomes inevitable. This could explain the emergence of a partial generation in late summer in the Kempton Park East Reservoir. The environmental conditions at the diapause onset may also explain the differences in the absolute developmental threshold observed at Mirwart between Pond III (substage IV4b) and Pond IV (substage IV3b). THIENEMANN (l.c.) observed early emergences already in the beginning of May. The fact that larvae leave diapause at shorter daylengths and lower temperatures (i.e. about mid-April) is not in contradiction with the supposed diapause inducing factors. Compared to the autumn larvae, the spring larvae may be in a different metabolic condition.

Conclusions

Ps. prasinatus is a mainly univoltine summer species. The emergence is concentrated in June and July, even in different climatic regions. An additional partial generation may emerge in late summer in favourable conditions.

The life cycle of *Ps. prasinatus* is determined by growth and development at rather high temperatures and by an overwintering diapause in the early fourth instar stage from late summer onwards.

However, the exact role of the environmental factors in the life cycle still remain to be elucidated. Laboratory experiments on the influence of temperature and daylength on larval development may yield important information.

Acknowledgements

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Boudewijn R. GODDEERIS
Koninklijk Belgisch Instituut
voor Natuurwetenschappen,
Afdeling Hydrobiologie,
Vautierstraat 29,
B-1040 Brussel