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Life cycle characteristics in *Tanytarsus debilis* (Meigen, 1830) (Diptera, Chironomidae)

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Keywords : diapause, emergence, imaginal discs.

The life cycle of *Tanytarsus debilis* in two trout-ponds at Mirwart (Belgian Ardennes) has been investigated. The main characteristics were deduced from an analysis of the larval population dynamics. Photoperiod and temperature appear to determine the annual pattern. *T. debilis* is a spring and summer species and is trivoltine at Mirwart. Special attention is given to the synchronizing effects of diapause phenomena on the emergences and on the larval growth periods. The literature data, exclusively on adults, have been reinterpreted.

Caractéristiques du cycle de vie de *Tanytarsus debilis* (Meigen, 1830) (Diptera, Chironomidae)

Mots clés : diapause, émergence, disques imaginaux.

Le cycle de vie de *Tanytarsus debilis* a été étudié dans deux étangs à truites situés à Mirwart (Ardennes belges). Ses caractéristiques ont été déduites en analysant la dynamique de la population larvaire. La photopériode et la température semblent déterminer un schéma annuel. Cette espèce de printemps et d'été est trivoltine à Mirwart. Les effets synchronisateurs des phénomènes de diapause sur les émergences et les périodes de croissance ont été particulièrement étudiés. La littérature concernant les adultes est mieux comprise grâce aux données de Mirwart.

1. Introduction

This paper is a synthesis of investigations on *T. debilis* at Mirwart. It is the second paper in a series on the life cycle of *Tanytarsus*-species.

The chironomid fauna of two trout-ponds, i.e. Pond III and Pond IV at Mirwart (Belgian Ardennes), was sampled between May 1976 and May 1978. The ponds belong to different trophic types : Pond III was rather eutrophic and Pond IV more oligotrophic (Goddeeris 1990). Nevertheless, both ponds were dominated by the same *Tanytarsus*-species, of which *T. debilis* was the most common.

An analysis of the length frequency distributions of the larvae at regular sampling dates indicated that *T. debilis* is a trivoltine species with emergence periods in spring and summer and an overwintering diapause in the 3rd instar stage from late summer (Goddeeris 1983). Furthermore, this yearly diapause was supposed to be the synchronizing factor of the spring emergence. In order to falsify this hypothesis, the development of the overwintering larvae was re-examined by an imaginal disc analysis, a more accurate method for this purpose.

This is the very first investigation on larval population dynamics in *T. debilis* and the results are compared to the rather poor literature on adult emergence.

2. Methods

Methods used for sampling and analysing the field data are described in Goddeeris (1989). The present subdivision of the 4th instar stage of *T. debilis,* based on imaginal disc development, is similar to the one used for *T. sylvaticus* by Goddeeris (1990).

Morphology of larval stages was described by Goddeeris (1984). Unfortunately, it was impossible to distinguish between the first instars of *T. debilis* and those of other *Tanytarsus*-species at Mirwart.

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In a photoperiod experiment, *T. debilis* larvae were submitted to two different daylength programs, in order to get indications on the overwintering conditions of this species. Benthos samples were taken at Mirwart on 14.10.1980 and were kept in darkness at 6°C. Larvae of *T. debilis* were sorted the next day. As expected, all were in the 3rd instar stage, in which *T. debilis* appeared to overwinter at Mirwart (see 3.1). Eleven larvae were submitted to a short-day program (8 h 45' light per day at 17°C) and twelve larvae to a long-day programm (16 h 15' light per day at 17°C). Two Bekso-incubators were used, each equipped with three Acec LF-15W Phytor lamps at about 30 cm of the culture glass, in which the larvae were reared together on Tetramin-food. During the first month, the incubators were interchanged every week, after the adaptation of the light program, of course.

3. Results

3.1. Lenght frequency analysis

Length frequency distributions of the *T. debilis*-larvae in the Mirwart ponds are figured in Plates I to III. The abcissa is subdivided in length classes of 0.25 mm. The instar stages II to IV are indicated in these histograms by a different symbol for each stage ; prepupating larvae, recognizable by the swollen thorax and the pigmentation of the adult eyes, are also indicated.

Since *T. debilis* is a dynamic species with rapid changes in the population structure, its life history is most easily described on the results from pond IV during the 1977-season, as larval densities were very high, cohorts well separated and because sampling frequency proved to be ample. The statements given below were corroborated by comparing all data from both ponds over the two years.

First emergence period in late April - early May

T. debilis overwinters in a notably narrow cohort : in January-February, only 3rd instar larvae were present ; body length varied between 2.25 and 3,5 mm only, with a distinct peak at about 3 mm.

From early March onwards, the larvae moulted to the 4th instar, at a body length of about 3.25 mm. An important increase in length of the 3rd instars was already observed in late winter, e.g. from a mean lenght of 2.79 mm on 25.1.78 to a mean lenght of 3.17 mm on 6.3.78 in pond IV.

March-April is a period of intense growth and development. Towards mid-April, the great majority of the population had reached the 4th instar stage, but prepupation could hardly be demonstrated.

It should be noted that some differences between the population structures of early April over the two years were apparent. In pond IV, on 11.4.1978, the distribution was normal and broad, with a mean length of only 3.79 mm. In the same pond, but on 12.4.1977, the distribution was skewed to the left, with a mean length of 4.71 mm.

The emergence of the overwintering cohort occurs in mid spring. More than half of the cohort had already emerged by late April in each case, despite the differences in population structure in the first half of April. The very last emergences of this spring emergence period occured in mid-May.

Second emergence period in July

In the second half of May, with an amazing regularity, the first 2nd instar larvae of a second cohort were found in the benthos. Only in pond III-1977 was the onset of the second cohort retarded till early June, but this particular cohort appeared unsuccessful and should, therefore, be considered less representative.

The recruitment of larvae for the second cohort is limited in time, as demonstrated in pond IV-1977 where this recruitment stopped in the second half of June. Larval growth in the second cohort appeared to be continuous and the emergence occurred between the end of June and early August.

Third emergence period in August

From early July onwards, with part of the larvae of the second cohort still in full development, offspring of more advanced members of this second cohort were already observed in the sediment and constituted a third cohort.

At high temperatures, development seems to be very fast. In the course of time, second and third cohorts began to overlap, as the fastest larvae of the third cohort caught up with the slowest ones of the second cohort. However, this overlap appeared limited and the two cohorts were still recognizable, even during their emergence periods, as could be demonstrated in pond IV-1977 : in early August, the emergence activity was rather low, as only the last imagines of the second cohort together with the first ones of the third cohort emerged.

From early August onwards, i.e. when the second cohort had already fully emerged, the length frequency distribution of the larvae became bimodal and even discontinuous : the third cohort gradually splitted away from a fourth cohort. At the end of August, the third cohort, now exclusively consisting of 4th instars, was completely separated from this fourth cohort, consisting of 2nd and a few 3rd instars. The larvae of the third cohort matured without any interruption, pupated and by early September the third emergence period was already over. The larvae of the fourth cohort, on the other hand, appeared retained in the 2nd and 3rd instar stage.

Overwintering in the 3rd instar stage

During late summer and autumn of the two year periods, the dynamics of the fourth cohort demonstrated an extreme similarity in both ponds. At the end of August, the fourth cohort always consisted of a large peak of 2nd and a very small minority of 3rd instars. During early autumn, the 2nd instars moulted slowly to the 3rd instar stage and, by mid-October, the proportion of the 2nd to the 3rd instar larvae was reversed, compared to late August. Furthermore, 4th instars were never observed in autumn. Unfortunately, the ponds were drained from mid-October till mid-December, but a number of puddles were still present, and the sediment remained wet by seepage. Nevertheless, the larvae appeared really blocked in the 3rd instar stage during autumn and winter, independently of this drainage : (1) Already before this drainage, in mid-October, some 3rd instar larvae reached lengths at which 4th instars may be expected (2). In late autumn and winter the mean length of the larvae had even increased, but the frequency distribution became even narrower, the 3.25 mm length class wass not passed and not a single larva was premoulting (recognizable by the eye spots, shifted to the back of the head capsule) (3). In early spring, an increase in length of the 3rd instars was observed just before moulting, the 3.25 mm limit was passed and the frequency distribution became broader again.

3.2. Photoperiod experiment

This experiment started on 16.10.1989 ; the results are represended in the figure 1. During this experiment, important differences in the development of the larvae between the two light programs became apparent.

Less than three weeks after the onset of this experiment all specimens of the long-day program emerged in a few days'time : 9 specimens emerged between 1.11 and 3.11.1980, and the 3 remaining specimens were in the pupal stage on 3.11.1980.

Compared to the long-day program, the larvae in the short-day program were significantly retarded in their development. They appeared blocked in the 3rd instar stage, at least during the first month. However, they were still active and had their gut filled with detritus. A regular increase of the mean body length was also noticed : 2.57 mm on 14.10.1980, 2.92 mm on 3.11.1980, 3.09 mm on 10.11.1980 and 3.22 mm on 20.11.1980. At this last date, a mature 3rd instar larva of 3.44 mm was recognized by the shifted eye spots. Moreover, from 20th November onwards, the third instars were bold with a swollen thorax, similar to prepupating 4th instars.

The first emergence in the short-day program was noticed on 8.12.1980 ; it was the 3rd instar with shifted eye sports at 20.11.1980. The moulting of the other short-day larvae was discontinuous, but once in the 4th instar their development appeared fast and continuous : whenever 4th instars were observed, their emergence followed within a few weeks. The last emergence in the short-day program was observed on 6.3.1981. The emergence period in the short-day program lasted three full months !

In conclusion, overwintering larvae were retained for a longer time in the third instar stage in the short day-program than in the long-day one. Furthermore, the resumption of development is characterized by a large individual variation in the short-day program.

3.3. Imaginal disc analysis

Plate IV illustrates the results of the imaginal disc analysis on the overwintering larvae at Mirwart, during spring 1977 and 1978. Moulting to the 4th instar started in early March, at water temperatures of about 6°C. At first glance, the development of the 4th instars appeared to be continuous up to

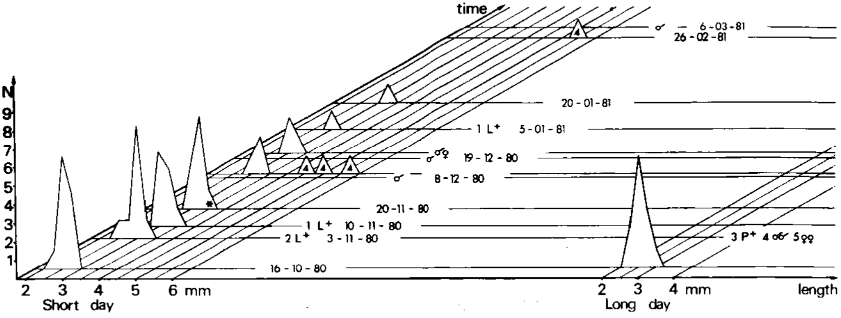

Fig. 1. *Tanytarsus debilis* : results of the photoperiod experiment on diapausing larvae. Short day program on the left, long day program on the right. Blanco = 3rd instars, asterisk = mature 3rd instar, 4 = 4th instar, p = pupa.

the point of emergence. However, there are strong arguments in favour of a developmental stop in the forward larvae in early April, just before the prepupal stage, i.a. before the limit between the substages IV7 and IV8 : (1) There is an accumulation of instars in the substages IV5-IV7 in pond III on 11.4.1978. This is indicated by a frequency distribution which is markedly skewed to the left on that date. If development was continuous, some prepupae would be expected in early April, while the frequency distribution should be far less skewed. (2) Not a single larva has passed the IV7b-IV8a limit in early April in the both ponds and in the two years studied. (3) In spite of a slower development in pond IV compared to pond III (both early April 1978), the emergences in both ponds were situated in late April-early May. The development arrearage in pond IV appeared neutralized by the developmental arrest in pond III.

This spring development arrest is not compulsory and does only occur in the most forward larvae : at Mirwart, the larvae which reached the IV5 substage only in mid-April, or later, developed without any interruption. Consequently, only a very small minority of the spring larvae demonstrated the spring development arrest in pond IV-1978, due to the developmental arrearage mentioned above.

At Mirwart, the development of the larvae in prepupating diapause restarted with the effective crossing of the IV7b-IV8a limit in mid-April at water temperatures of about 9°C. A few weeks later, the whole winter cohort had already emerged.

4. Discussion

The data from Mirwart are unique because they are based on the population dynamics of the larvae. The literature on the life history of *T. debilis* is poor and was thusfar based on analyses of adult emergences only. Nevertheless, reliable life cycle characteristics of *T. debilis* could be deduced, because the investigations at Mirwart were made in different conditions, i.e. in two ponds of different trophic type and this during two years. Moreover, the conclusions from Mirwart could still be compared to the literature, as far as they are linked to emergence data.

4.1. Overwintering diapause

Dormancy phenomena are well known in Chironomidae. Diapauses of the oligopause type sensu Müller (1970) have been particularly well demonstrated in the genus *Chironomus* (a.o. Fischer 1974, Ineichen et al. 1979, Bangerter & Fischer 1989). Species-specific short daylengths tend to induce a

PLATE I

Tanytarsus debilis

length-frequency distributions
at Mirwart pond III
May 1976 - May 1978

2 nd instar ● 4 th i. prepupa o
3 rd instar ★ pupa p
4 th instar ■

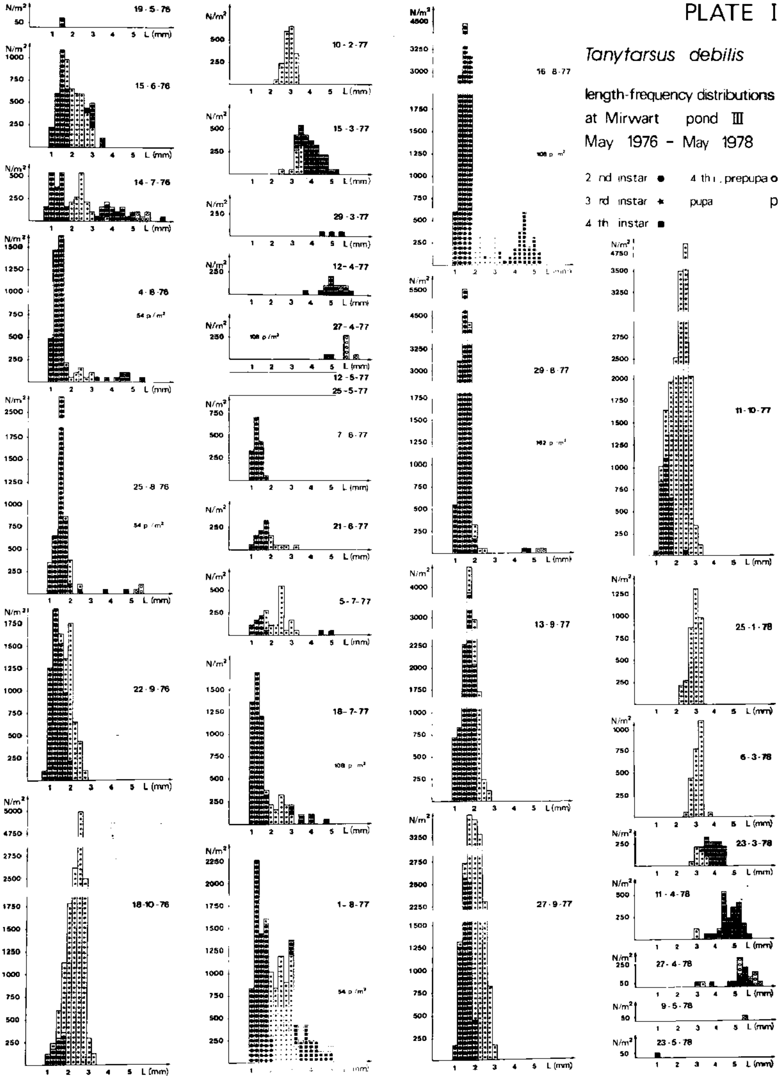

Plate I.

PLATE II

Tanytarsus debilis

length-frequency distributions
at Mirwart pond IV
19-V-1976 - 1-VIII-1977
explanations plate I

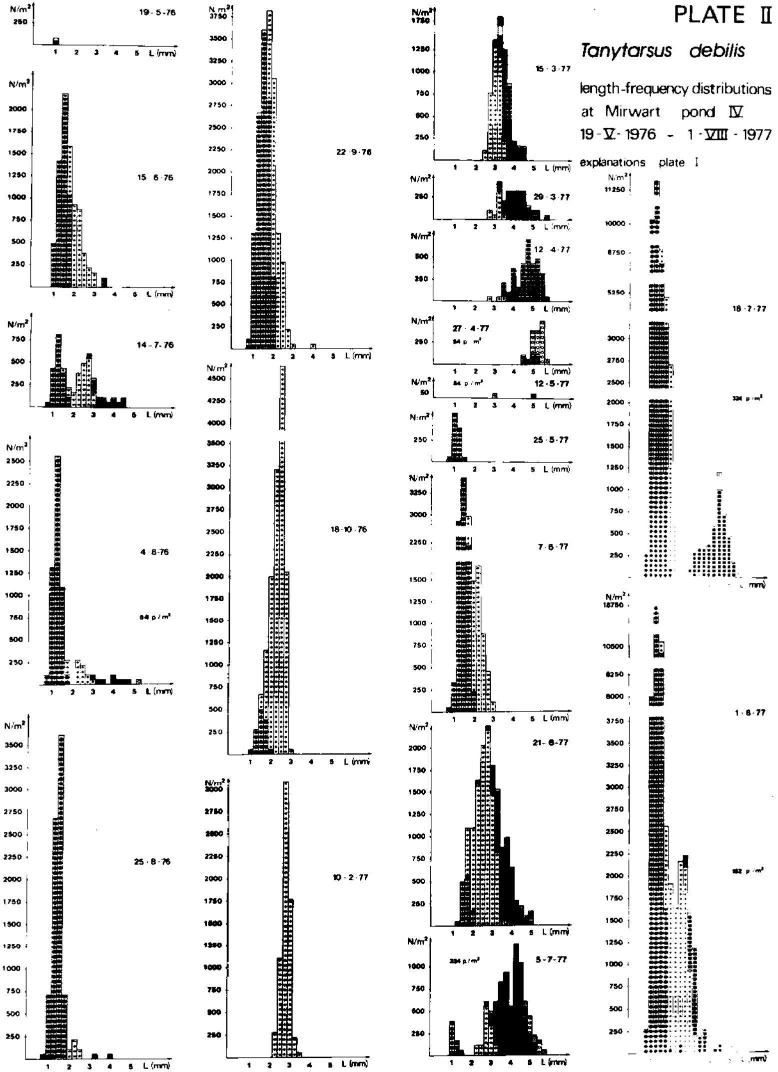

Plate II.

PLATE III

Tanytarsus debilis

length-frequency distributions
at Mirwart pond IV
16-VIII-1977 - 23-V-1978

explanations plate I

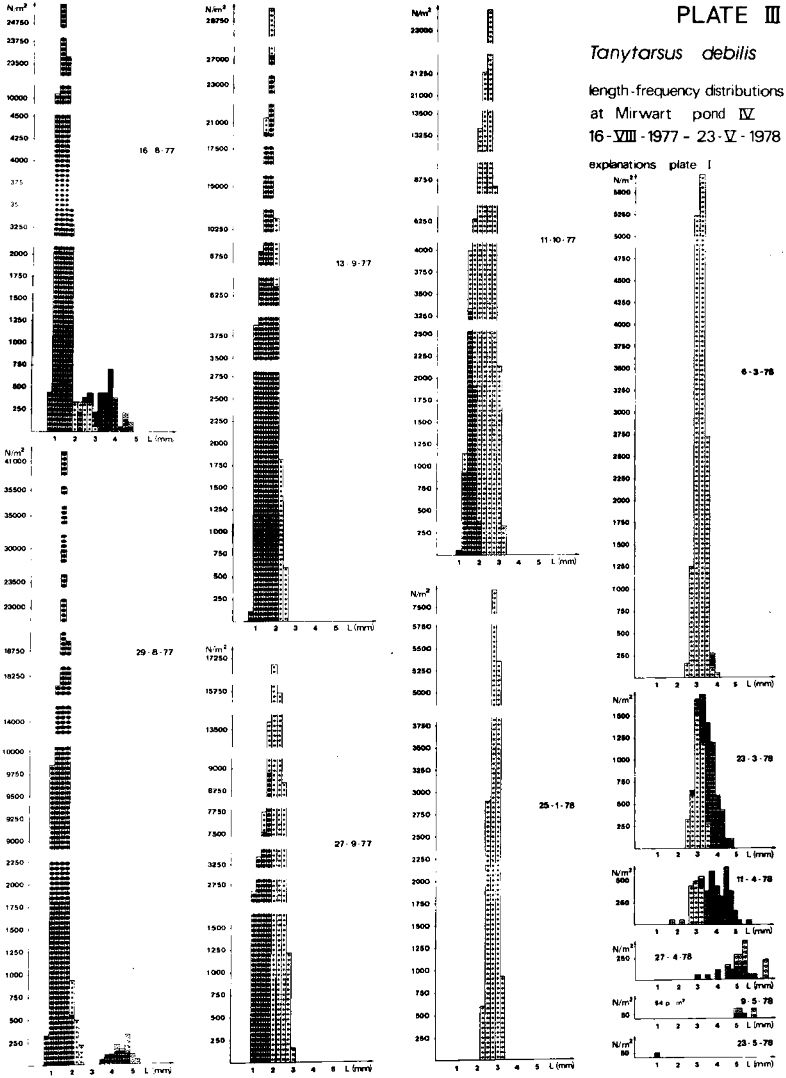

Plate III.

PLATE IV

Tanytarsus debilis

frequency distributions of the larval stages and substages in the Mirwart ponds III + IV spring 1977 + 1978

3 rd instar III * pupa p white

4 th instar substages 1 - 9 (a + b)

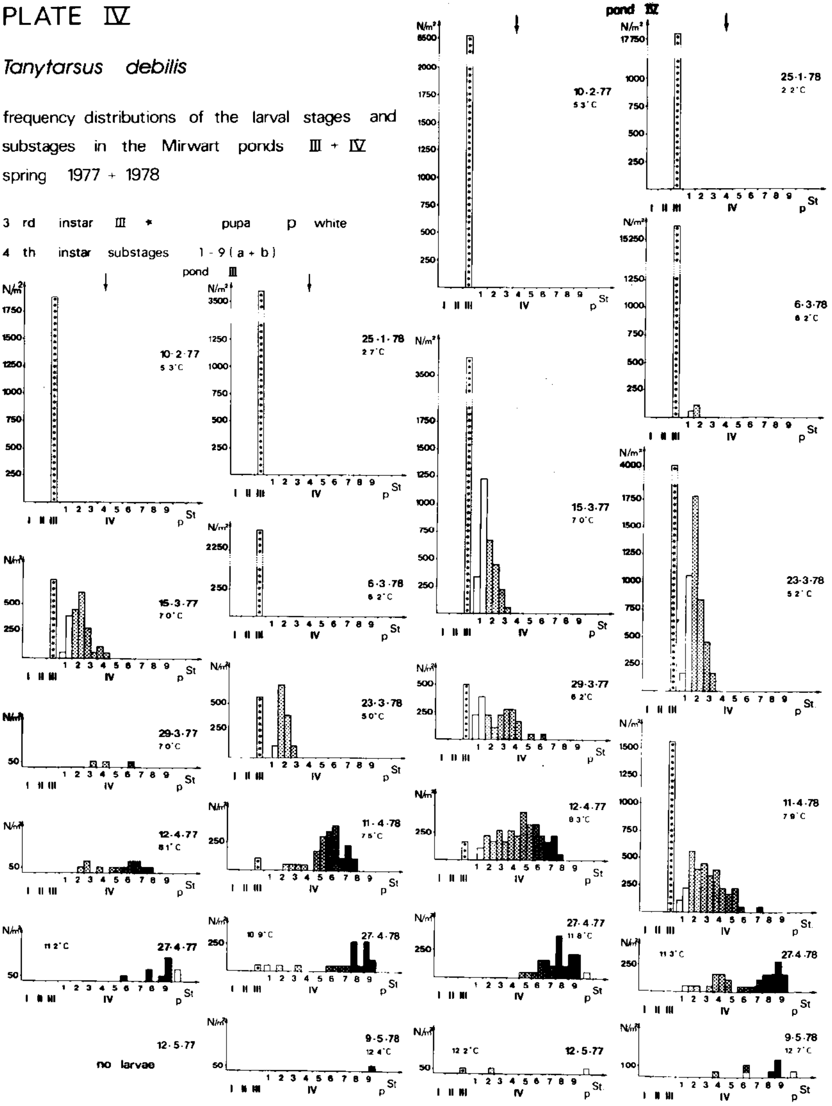

Plate IV.

diapause in the 4th instar stage. In *Ch. nuditarsis,* but not in *Ch. plumosus,* this diapause only occurs in short day conditions linked to low temperatures. But diapauses have also been described from other genera. The life cycle of the univoltine *Tanytarsus sylvaticus* is even characterized by the occurence of two diapauses i.e. a summer diapause in the 3rd instar stage and a winter diapause in the 4th instar stage (Goddeeris 1990).

Also *T. debilis* displays obvious dormancy phenomena. At Mirwart, this species always overwintered in an amazingly narrow cohort, consisting exclusively of 3rd instars. The generation of this cohort already started in late summer, when the younger instars became separated from the 4th instars by growth retardation. In August, two growth rates are indeed involved under the same environmental conditions, i.e. fast growth in the 4th instar and slow growth in the younger stages with an absolute arrest in the 3rd instar. These dormancy phenomena in the younger instars may be considered as an overwintering diapause, because they are clearly limited to specific developmental stages and linked to winter. The term « overwintering » diapause is prefered to « winter » diapause since this diapause is not restricted to winter, but also covers late summer and autumn.

The very rigid population structure at the onset of the overwintering diapause is an indication of the existence of a very constant key factor in the diapause induction of *T. debilis,* and photoperiodicity is the only one known. At the end of August in the Mirwart ponds, there was always a peak of diapausing 2nd instars (and a few 3rd instars), separated from a small group of 4th instars, which continued to develop. Compared to June, when no diapause was observed at Mirwart, the daylength is not only shorter in August, but is also shortening.

But exceptionally high temperatures in late summer may postpone the onset of the overwintering diapause. Very late emergences of *T. debilis* were observed at the end of September 1959 in the littoral of Lake Erken (Sandberg 1969). This is about three weeks later than at Mirwart, where the latest emergences are limited to early September by the onset of the overwintering diapause during August. But the mean water temperature in August was 21°C in Lake Erken, i.e. about 5°C higher than in the Mirwart ponds.

The factors actually ruling the release of the overwintering diapause also remain obscure in our field data. At Mirwart, the diapause condition was always left around early March (rather short daylength) at about 5°C. However, direct comparison of these environmental factors at the onset and at the end of the diapause should be dissuaded, because the metabolic condition of the larvae probably changes during winter. Futhermore, the trend of changing daylength, i.e. shortening or prolonging, is opposite during spring and autumn. The influence of the photoperiod may become less important during the course of the overwintering diapause. In field conditions, reaching and crossing a certain temperature limit in spring could be the effective trigger to releasing the overwintering diapause in *T. debilis.*

In the photoperiod experiment (3.2.), 3rd instar larvae of October, i.e. diapausing larvae, were submitted to short days and to long days, but at 17°C. This experiment certainly does not explain the induction and release of the overwintering diapause of *T. debilis* in field conditions. Nevertheless, it confirms the expected influence of the photoperiod on this diapause short daylengths are diapause maintaining.

However, the developmental arrest in short day conditions is not absolute at 17°C : moulting of the larvae to the 4th instar is only delayed and spread over a much longer period compared to the long day program. Once the larvae reach the 4th instar stage, development is fast and continuous, even in the short day program. *Chironomus plumosus* displays a similar pattern in the release of its oligopause in the 4th instar (Ineichen et al. 1979). Other arguments also confirm the oligopause type of the overwintering diapause in *T. debilis.* In the short day program, the diapausing larvae were still active, fed and became bold for 3rd instars. Moreover, when the diapause maintaining factor was switched to long days, the larvae immediately restarted their development.

Nevertheless, the overwintering diapause of *T. debilis* is far from elucidated. The actual relationship between diapause inducing daylength and temperature is not known. Also the relative importance of these two factors during the diapause course, with changing daylenght and changing metabolic condition of the larvae remains obscure. The developmental stage, sensitive for the diapause inducing factor(s) may be different from the actually diapausing instar stage. Other factors than photoperiod and temperature may influence the overwintering diapause, too. However, relying on an analysis of the Mirwart data, food quality and/or quantity cannot be considered a diapause regulating factor in *T. debilis.* (1) The constant population structure at the end of August, described above, does not indicate the influence of a fluctuating factor such as food. (2) In spite of the different trophic types of the two Mirwart ponds, both populations exhibited an identical development of the overwintering diapause. (3) At the end of August, the 4th instar larvae grew without any interruption or indication of food shortage, while the younger instars entered into diapause. Such a sharp difference between the larval stages can hardly be attributed to the food factor. (4) When *T. debilis* entered diapause, other *Tanytarsus*-species, such as *T. holochlorus,* still developed a complete generation (Goddeeris, in prep.) (5). The diapausing 3rd instars showed no trace of food shortage. Already in autumn, several diapausing larvae became larger than the size of mature, but non diapausing larvae in summer.

4.2. Prepupating diapause

The development of the spring larvae, once they left the overwintering diapause, does not appear to be continuous, at least with regard to the forward larvae. The imaginal disc analysis of the spring larvae at Mirwart (see 3.3.) argues for a short diapause in early April, but this time limited to the substages IV5-IV7, with an absolute threshold at the IV7b-IV8a limit. As this diapause occurs just before the pupating substages IV8-IV9 (= prepupae), the name of prepupating diapause is suggested. It is worth mentioning that the prepupating diapause of *T. debilis* occurs in exactly the same substages as those of the winter diapause of *T. sylvaticus.*

It is very difficult to elucidate the causal factors of prepupating diapause of *T. debilis,* because at Mirwart it always occurred at the same time (early April = same daylength) and at about the same temperatures (circ. 9°C). A clear separation of the influences of photoperiod and temperature respectively in such circumstances as these is therefore next to impossible. However, the temperature is supposed to be more important than the photoperiod, because no developmental interruption in the 4th instar stage has been noticed in the short-day program at 17.5°C. A threshold temperature of 9°C is deduded from the field data at Mirwart : above this threshold temperature no prepupating diapause should occur in *T. debilis.* The consequent emergence at about 12°C by a slow temperature increase in spring is confirmed by the Mirwart emergence at the very and of April and the Dunmore emergence in mid-May (Morgan & Waddell 1966 a & b).

4.3. Synchronization

The life cycle of *T. debilis* is characterized by emergence periods, which are limited in time. Especially the spring emergence is quite distinct and completely separated from the summer emergences. At Mirwart, the spring emergence of a whole population does not last more than four weeks, i.e. it is limited to mid-spring. Locally, i.e. under one trap, the emergence appears to be even more synchronized, as was demonstrated in the Massif de Néouvielle, where nearly 100 % of the individuals emerged within a few days (Laville 1971). An attempt is made to elucidate the causal factors of this yearly synchronization in this paragraph.

4.3.1. *Threshold and optimal emergence temperatures*

In the literature, threshold or optimal temperatures are suggested as key factor in synchronizing the emergence. The emergence of the overwintering cohort is supposed to occur only when this species-specific temperature is reached in spring.

At Mirwart, all spring emergence of *T. debilis* occurred at about 12°C in late April and early May. A threshold temperature of about 11°C is mentioned for *T. debilis* in Loch Dunmore (Scotland) (Morgan & Waddell 1961 a & b). *T. debilis* is very common in the Massif of Néouvielle (High Pyrenees) and is there supposed to emerge at optimal temperatures between 12.5°C and 15°C when data from all the lakes are considered together. The emergence peaks occurred in early summer (Laville 1971). In the Lac de Port Bielh (1970) the emergence peak fell just before mid-August, but the thaw was setting in markedly later that year, i.e. in the first half of July (Laville & Giani 1974).

However, in our opinion, several Néouvielle data (cf. Laville 1971) do not corroborate the optimal emergence temperatures in *T. debilis.* The range of optimal emergence temperatures, from 12.5 to 15°C, is in fact very wide. Also, in some cases water temperature had already reached the optimal temperature, before the emergence of *T. debilis* started. In the Gourg Nère Inférieur-1966, water temperature had already reached 15°C in the first half of July, but the emergence of *T. debilis* only started about two weeks later, with a peak at 13°C. In the Lake d'Anglade, *T. debilis* starded to emerge at 15°C in 1965, but at 17°C in 1967. It appears that the populations were not always ready to emerge when the so-called optimal emergence was reached. Therefore, the synchronization of the emergence can hardly be attributed to a threshold or optimal emergence temperature.

Futhermore, the summer emergences of *T. debilis* at Mirwart are not at all hampered by high temperatures, e.g. 20°C bottom water temperature. This is also an argument against the existence of a narrow temperature range for optimal emergence.

4.3.2. *Synchronization and diapause*

At Mirwart, no optimal nor threshold emergence temperatures have been observed in *T. debilis,* but there are a number of arguments in favour of the existence of a prepupating diapause in spring, as long as water temperatures do not exceed 9°C (see 4.2.). When this temperature threshold is crossed in spring, the most advanced larvae have still to pass the prepupal and pupal stages. Therefore, their emergence may only be expected a few weeks later, at temperatures higher than 9°C. Consequently, the linkage of the spring emergence to temperature appears to be indirect and not very strict.

However, since the prepupating diapause is facultative, it cannot be the main synchronizing factor at Mirwart. In some years, the prepupating diapause could not be detected, as the larvae were not yet (or hardly) prepupating when the 9°C threshold was reached (e.g. pond IV-1978), but even then the emergence remained well synchronized. In the long-day program at 17°C, the emergence was extremely well synchronized, but also these larvae did not pass through a prepupating diapause.

Nevertheless, at least a certain synchronizing effect on the spring emergence of *T. debilis* has to be attributed to the prepupating diapause. A retardation of the development of the fastest larvae, and consequently of their emergence, indeed limits the emergence period of the whole population. In the case of Mirwart pond III-1978, for example, the prepupating diapause shortened the spring emergence period by about 2 weeks. The prepupating diapause could indeed also have a desynchronizing effect in *T. debilis,* but then only when water temperatures fluctuate for a long time around 9°C, which is the presumed diapause threshold.

The synchronizing effect of the overwintering diapause appears more important, when compared to the prepupating diapause. A consequence of the overwintering diapause in *T. debilis* is indeed a drastic resettlement of the population structure every year. At Mirwart, a narrow cohort of overwintering larvae is formed from August onwards, and all larvae are synchronized into the third instar stage. This synchronization is of course reflected in the subsequent emergence period in spring, since the larvae will pass the 4th instar stage in approximately the same time.

However, the release of the overwintering diapause of a complete cohort still lasted one and a half months or more at Mirwart. Nevertheless, this is not in contradiction with the observed spring emergence which lasted only one month. There are indeed important differences between the developmental conditions of the larvae at the onset of the diapause release (6°C = slow development), and at the end of the diapause release (10-12°C = fast development). The different developmental conditions, combined with a prepupating diapause in the forward larvae, cause differences in the duration of the 4th instar stage in spring. Larvae leaving the diapause in March will grow on average slower than those which leave the diapause in April. The emergence period will consequently be shorter than the diapause releasing period.

The synchronization of the spring emergence is only partially reflected in the later emergence periods, due to the individual variation of larval growth and development. At Mirwart, the second emergence period was about twice as long as the first one and already overlapped the third. However, the third emergence period was shorter again, as it was interrupted by the onset of the overwintering diapause in August.

4.4. Lenght growth

Temperature is a well known environmental factor which greatly influence growth rate in invertebrates in general, and in chironomids in particular. At Mirwart, the mean growth rate of *T. debilis* in relation to temperature could be determined under field conditions, i.e. from the displacement of the cohorts in time in the length frequency distributions. However, it must be stressed again that this method should be applied with great care in periods of natality, emergence and developmental arrest (Goddeeris 1989).

Growth rates at different temperatures are presented in table I and in figure 2 for non-diapausing larvae, and a growth rate equation $\Delta L/\Delta t$ (in mm/day) = $-0.0215 + 0.00769\,T$ was determined.

During the onset of the overwintering diapause in September-October, independent of the temperature, a growth rate $\Delta L/\Delta t = 0{,}018$ mm/day was deduced from the fortnightly displacement of 0.25 mm of the extremity of the autumn cohort.

4.5. Phenology

4.5.1. *Spring and summer emergence*

Both from the Mirwart data and from the literature dealing with its emergence, *T. debilis* may be considered as a spring and summer species. However, one must apply great caution when referring to ecological data from the literature. *T. debilis* (syn. *T. samboni*) belongs to the *verralli*-group and has often been confused with other species. Reiss & Fittkau (1971) have discarded the data of Humphries (1938) and Thienemann (1948), both sub *T. samboni*, as misidentifications. To avoid such erroneous identifications in future, a refined diagnose of this species was given by Goddeeris (1984). Furthermore, a new species of the *verralli*-group was found in West-Flanders (Belgium) (Goddeeris, in prep.).

Adults of *T. debilis* have been captured from mid-spring till late summer or early autumn in Europe (Armitage 1970, Birkett 1976, Brundin 1947, 1949, Morgan & Wadell 1961 a & b, Reiss & Fittkau 1971, Sandberg 1969, Thienemann 1950, sub *T. glabrescens*).

The fact that in the literature, the emergences of *T. debilis* are only observed from mid-spring onwards, and not earlier, is in complete concordance with the larval data from Mirwart. In spring, after releasing the overwintering diapause at about 5°C, the larvae have still to pass the 4th instar stage before pupation and emergence. The duration of this spring development depends on the growth rate in relation to temperature regime, but in natural conditions, emergence may only be expected several weeks after spring onset. In the Néouvielle lakes, *T. debilis* only emerged during summer (Laville 1971, Laville & Giani 1974) : the spring period (from late May or June) appears too short for the winter larvae to finish the fourth instar stage before summer.

The emergence always stops from late summer or early autumn onwards. According to the Mirwart data, later emergences appear impossible because of the onset of an overwintering diapause in August.

4.5.2. *Voltinism*

The emergence of *T. debilis* is always linked to spring and/or summer, but significant differences in the number of emergence periods are observed.

At Mirwart, *T. debilis* was always trivoltine. however, although this third emergence period was important, it is our opinion that it only consisted of a partial generation, the other part of that generation forming a fourth, overwintering cohort. The following arguments support this view : (1) The emergence period of the third cohort (early August-early September) was shorter than the emergence period of the second cohort (late June-early August). If the third cohort corresponds to a full generation, then its emergence should be longer than the second, due to the variation in growth and development of the larvae. (2) It is unlikely that the peak of the 2nd instar larvae in the beginning of August (= the onset of the fourth cohort), was already formed by offspring of the third cohort, since the third cohort only had started its emergence at about that time. Therefore, these larvae must be descendants of the second cohort, which was still emerging in late July, and consequently belong to the same generation as those of the third cohort. (3) The same pattern is observed in all length frequency distributions at the end of August, i.e. a small and well separated group of 4th instars belonging to the third cohort and a long peak of 2nd instars (and a few 3rd instars) of the fourth cohort. The separation of the third and fourth cohort larvae apparently occurred at a well-defined period, not depending on whether or not these larvae belong to the same generation.

Consequently, the fourth cohort is a mixed generation, consisting of the retarded offspring of the second cohort and the whole offspring of the third cohort. Some individuals of this fourth cohort will pass eight months as larva before pupation in the first emergence period of the following year !

Table I. *Tanytarsus debilis* : mean lengths (x) and modes in length frequency distributions at Mirwart used for the calculation of growth in relation to temperature.

pond ; dates	sizes (mm)	interval (days)	growth rate (mm/day)	mean temp. (°C)
III ; 19-5/15-6-76	1.25(e)/3.25(e)	27	0.074	15.26
IV ; 19-5/15-6-76	1.0 (e)/3.25(e)	27	0.083	16.02
III ; 10-2/15-3-77	2.88(x̄)/3.87(x̄)	33	0.030	6.15
IV ; 10-2/15-3-77	2.78(x̄)/3.32(x̄)	33	0.016	6.13
IV ; 15-3/29-3-77	3.32(x̄)/4.00(x̄)	14	0.049	6.60
III ; 15-3/12-4-77	3.87(x̄)/5.12(x̄)	28	0.045	7.37
IV ; 29-3/12-4-77	4.00(x̄)/4.63(x̄)	14	0.045	7.25
IV ; 25-5/07-6-77	1.25(e)/2.75(e)	13	0.115	15.80
III ; 07-6/21-6-77	1.5 (e)/3.0 (e)	14	0.107	14.40
IV ; 07-6/21-6-77	1.51(m)/2.71(m)	14	0.086	15.35
IV ; 21-6/05-7-77	2.71(m)/4.32(m)	14	0.115	18.40
III ; 18-7/01-8-77	1.23(m)/2.96(m)	14	0.124	16.65
III ; 01-8/16-8-77	2.96(m)/4.5 (m)	15	0.103	16.00
IV ; 01-8/16-8-77	2.65(m)/3.74(m)	15	0.073	16.90
III ; 25-1/06-3-78	2.93(x̄)/3.07(x̄)	40	0.004	4.45
IV ; 25-1/06-3-78	2.79(x̄)/3.17(x̄)	40	0.010	4.20
III ; 06-3/23-3-78	3.07(x̄)/3.73(x̄)	17	0.039	5.80
IV ; 06-3/23-3-78	3.17(x̄)/3.39(x̄)	17	0.013	6.05
III ; 23-3/11-4-78	3.73(x̄)/4.71(x̄)	19	0.052	7.15
III ; 23-3/11-4-78	3.39(x̄)/3.79(x̄)	19	0.021	7.48

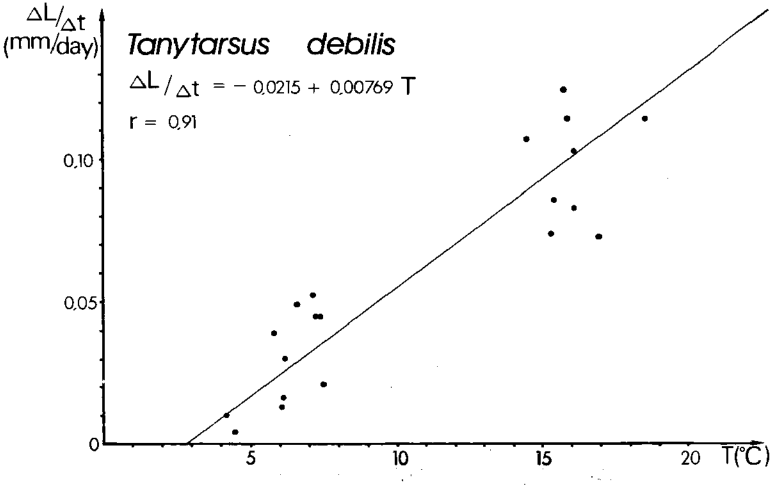

Fig. 2. *Tanytarsus debilis* : length growth (mm/day) in relation to temperature (°C).

The second cohort, on the other hand, is a genuine generation, as it comprises all the individuals born during the same reproductive period.

Morgan & Waddell (1961 a & b) consider *T. debilis* as bivoltine in Loch Dunmore (Scotland). However, no details about the second emergence period were gigen and perhaps a third, but partial, emergence was overlooked.

In the Massif de Néouvielle (High Pyrenees) *T. debilis* is a univoltine summer species, but spring starts late there and water temperature never rises above 17°C (Laville 1971). In some populations, a few adults were observed in mid-August, isolated from the emergence peak of July ; these adults may belong to a partial second emergence period.

In favourable years, with high August temperatures, the emergence stop of *T. debilis* appears postponed untill late September (cf. Sandberg 1969). High August temperatures at Mirwart should postpone the onset of the overwintering diapause and allow a complete third emergence period, and even the beginning of a fourth one.

T. debilis is potentially a multivoltine species, despite the fact that its emergence is limited from mid-spring till early autumn. The temperature regime of the habitat determines mainly the number of emergence periods. The food factor appears of secondary importance, as *T. debilis* was always trivoltine at Mirwart, despite different trophic conditions.

5. Conclusions

In the Mirwart ponds, the life cycle of *Tanytarsus debilis* follows a constant annual pattern (*fig.* 3). It is a trivoltine species with a first emergence period in mid-spring and with two emergences in

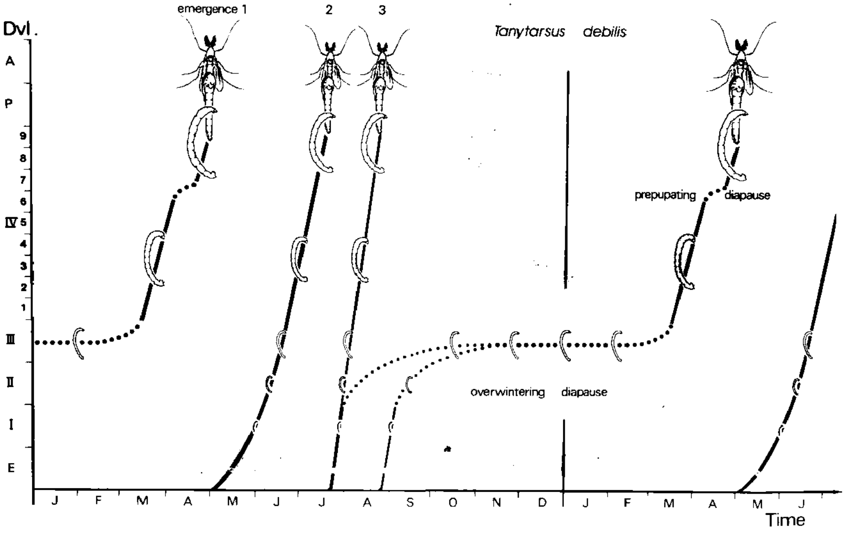

Fig. 3. The annual pattern in the life cycle of *Tanytarsus debilis* at Mirwart. The life cycle is characterized by an overwintering diapause in the 3rd instar stage from late summer onwards and by a facultative prepupating diapause in early spring. The species is trivoltine at Mirwart and the emergence periods are limited to full spring and to summer.

summer. The first emergence period consists of a mixed generation, the second of a genuine generation, and the third of a partial generation. From early August onwards, the 2nd instars enter in an overwintering diapause, but the development is completely blocked only in the 3rd instar stage, to which the 2nd instars will progressively moult in autumn.

The photoperiod and temperature are key factors in regulating diapause and growth rate in *T. debilis.* The constant annual photoperiodicity and nearly constant annual temperature cycle determine the life cycle pattern of *T. debilis* at Mirwart.

The overwintering diapause has an important synchronizing effect : each year, the whole population is resettled into the 3rd instar stage. The consequent synchronization of the spring emergence, sometimes accentuated by a facultative prepupating diapause in the fourth instar in early spring, is still reflected in the summer emergence periods. The existence of threshold or optimal emergence temperatures cannot be corroborated in *T. debilis* and availability of food does not appear to determine the life cycle.

The existing data from literature, dealing exclusively with observations on adults, are completely explained by the Mirwart data. Therefore, the occurence of an overwintering diapause in the 3rd instar from late summer onwards and a facultative prepupating diapause in the 4th instar in early spring, both limiting the emergence to full spring and to summer, are supposed to be species-specific life cycle characteristics of *T. debilis.* Geographical variation in the response to the two key factors regulating these diapauses and larval growth, i.e. photoperiodicity and temperature, appears negligible. As a consequence, the voltinism of *T. debilis*-populations becomes predictable when the local temperature regime is known. *T. debilis* is potentially a multivoltine species. In temperate climatic conditions *T. debilis* has a tendency to be bi- or trivoltine from full spring till early autumn. In extreme climatic conditions, with late springs and cold summers as in the High Pyrenees, *T. debilis* becomes a univoltine summer species.

The ecological significance of such species-specific life cycle characteristics has been demonstrated for the *Tanytarsus*-species at Mirwart (Goddeeris 1987). Growth in *T. debilis* focusses on spring and summer. Moreover, the partial alternation of the energy requirements of the cohorts of different *Tanytarsus*-species constitutes an important segregation of the specific niches in time.

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