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Multiple action of photoperiod on diapause
in the green lacewing *Mallada picteti* (McLachlan)
(Neuroptera Chrysopidae).*

INTRODUCTION

Mallada picteti (MacLachlan) is a west-Palaeartic green lacewing, the bionomics of which are just beginning to be investigated. Although it is a slow-growing species, it has at least two and more probably three generations a year in the field in southern France. It overwinters as a free-living larva, in accordance with the strategy built up by the (six) other Palaeartic species of the genus *Mallada* Navás known for this trait (Principi & Castellari, 1970; Principi, 1992). The morphogenetic development of *M. picteti* resumes at the end of winter or at the beginning of spring, so that the overwintering cohorts result in the first annual flight of imagos from mid-May. In this way, growing larvae of the various broods encounter all the photoperiod durations occurring during the seasons in a given place, except for the increasing daylengths in spring from March to the end of May.

Previous works recently carried out on *M. picteti* showed that under natural conditions of daylength and temperature (Canard *et al.*, 1992), the third instars are most often those which overwinter before full growth is reached. But in peculiar circumstances, second instar larvae may take up this part of the cycle, when oviposition occurs later than mid-October. This entails, in the offspring larvae, late or slow autumnal development that does not allow them to reach a more advanced instar before the arrival of short days and frost. Thus, the second instars overwinter, and do so before initiating the second ecdysis preparatory processes.

In addition, other studies in the laboratory (Canard *et al.*, 1990) led to the conclusions that: i) only the third instars exhibit an arrest of development under short photoperiods; ii) that such an arrest, similar to artificial overwintering, occurs in the shape of a diapause whose iii) induction depends on the conditions subjected to the early instars. A polymorphic diapause appears as a lengthening develop-

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ment of all larval instars, manifested slightly in the first and in the second, but strongly in the third, *i.e.* up to a temporary break of growth manifested within the stage length. Besides, a proportion of the diapausing population which depends on the acting daylength, cannot carry on morphogenesis unless there is a change in environment; these larvae die after several weeks of a true ~ and in this cases permanent ~ stopping of both growth and development. The aim of the present contribution is now to clarify the features of diapause termination and development resumption with respect to the photoperiod signal.

MATERIAL AND METHODS

The insects used were the same as those in the abovementioned experiments bearing on diapause induction. The original strain came from southwestern France. It was collected as adults in a relict spontaneous Mediterranean forest of evergreen oaks *Quercus ilex* Linnaeus and Aleppo pines *Pinus halepensis* Miller, in the "Montagne d'Alaric" (Aude). Only F₁ offspring was used for data collection.

The larvae were reared singly in 4 ml glass vials stoppered with a cotton-wool plug. They preyed on *Anagasta kuehniella* (Zeller) sterilized eggs, supplemented after the first ecdysis with the aphids *Acyrtosiphon pisum* (Harris) and *Myzus persicae* (Sulzer), all given *ad libitum*. The temperature was constantly 21 ± 1 °C, the relative humidity ranged from 60 to 80 %. Dim lighting was given by fluorescent bulbs, modulated according to an all-or-nothing type photoperiod leading to a diel cycle with an accuracy of ± 5 minutes. Three photophases were used. They tentatively simulated the long days of the summer solstice L:D 16:8 (check condition C), the equinox daylength 12:12 (condition 1), and the shortest days of the winter solstice 8:16 (condition 2). The photoperiods were either applied continuously during the lifespan (check condition, plus conditions 1 and 2), or with a returnless stepwise transition (transfer) operated at the beginning of one of the three larval stages (conditions 3 to 14), or operated during the third one (conditions 15, 16 and 17).

The time marks: hatching, ecdysis, spinning of the cocoon and adult emergence, were checked daily, at the beginning of the light phase. Every experimental batch was initiated using at least 24 individuals. The results are given as means together with standard deviations completed by ranges. Analysis of variance (ANOVA method) was used to reveal possibly significant differences when $n \geq 5$. Variations in stage length due to population polymorphism (inter-individuals) and to the rearing cabinet accuracy (inter-conditions) never reached 10 %; this is why we rejected from the duration analysis all differences lower than this discriminative value.

RESULTS AND DISCUSSION

We have already demonstrated (Canard *et al.*, 1990) that: i) the embryonic stage does not present a diapause; ii) that the two first instars exhibit a slightly lengthening which is always lower than twice the minimal stage length. Only the factors modifying the third instar development and their various effects, are analyzed in this study.

When larval rearings are submitted to photoperiods of any kind, three possible fates are observed during and after the third instar development. Firstly, the lar-

vae can develop and put on weight without any arrest, in a time shorter than 10 days at 21 °C and previously considered to be diapauseless; they spin cocoons and then immediately continue their morphogenesis by preparing the pupal ecdysis which takes place within the cocoons 8.1 days later. Such a strategy represents the quickest development pattern (check time), involving the processes called “tachytelic” by Hodek (1982). Secondly, the growing larvae can stop the weight increase and manifest an arrest of development; after a delay ranging from 10 days up to sometimes more than three months, they resume growth and spin cocoons, which are heavier than before. These larvae are considered diapausing, namely with their own rhythm passing through all the physiological steps which lead to the phase often incorrectly termed “reactivation”. They proceed along the “horotelic” processes of Hodek. In the third possibility, the larvae also stop development, but they never resume it, and they die after a survival time which is often long or even very long, reaching up to five months. This situation arising from an inability to get over diapause and resulting in death is here called by us “ately” or “**atelic processes**”, deriving from Greek α = none and $\tau\epsilon\lambda\omicron\varsigma$ = end.

But, diapause in *M. picteti* cannot be manifested by a single and sharp reaction. Its polymorphic shape results in biologically mitigated responses and thus the concept of diapause intensity (see review in Danks, 1987) may here be considered. We have retained four parameters to define and quantify diapause intensity. They are: i) the proportions of larvae showing a lengthened (horotelic) third instar development: **Ho**; ii) the lengthening indices of the third instar development: **Le** = mean duration in a condition related to the duration in long daylength condition; iii) the proportions of atelic diapause: **At**; and in this last case only, iv) the survival times in days when the diapause persists: **Su** = No of days expressed by means and ranges of recorded durations.

What happened without any change in photoperiod?

When a photoperiod of long-day type 16:8, *i.e.* not diapause-inducing, was constantly provided during the whole lifespan, the tachytelic durations of the preimaginal instars were the following:

embryo 9.0 ± 0.2 days ($n = 24$)

1st instar 8.1 ± 0.4 days ($n = 23$)

2nd instar 7.5 ± 0.7 days ($n = 23$)

3rd instar 8.1 ± 1.1 days ($n = 23$ tachytelic individuals)

time within the cocoon (prepupa + pupa) 22.1 ± 0.7 days ($n = 21$)

By definition, **Le** = 1; no diapause occurred **Ho** = 0, and, of course, **At** = 0.

When photoperiods of medium- or short-day type were used to induce diapause, the changes in larval development were manifested as presented in Table 1, conditions 1 and 2. It demonstrated that medium-lengthed days started a deeper diapause in several ways. Though the two conditions triggered diapause in the two whole larval populations (**Ho** = 100), the horotelic larvae needed about 1.5 times longer to accomplish diapause under medium days than under short days. Their spontaneous termination of diapause was thus possible under medium and short days, but only in 57 and 80 % of the population, respectively. The atelic larvae were 2.3 times more numerous and their survival lasted about 1.6 times longer.

condition	photoperiod on				diapause rate (%) in 3rd instar Ho	3rd diapausing stage		ately rate (%) At	survival duration in atelic larvae Su	
	embryo	1st instar	2nd instar	3rd instar		duration	lengthening Le			
1	▨	▨	▨	▨	100	34.3±13.0 (13)[21 to 67]	4.2	43	82.2±19.0 <i>a</i> (10)[42 to 110]	
2	▨	▨	▨	▨	100	22.6±6.9 (17)[15 to 39]	2.8	19	51.8±11.4 (4)[40 to 62]	
3	▨	▨	▨	▨	20	(4)[10 to 11]	1.3	0	-	
4	▨	▨	▨	▨	83	60.6±20.1 (8)[33 to 86]	7.5	48	82.6±25.9 <i>a</i> (11)[31 to 107]	
5	▨	▨	▨	▨	100	54.6±16.5 (7)[30 to 79]	6.7	68	76.1±13.8 <i>a</i> (15)[62 to 104]	
6	▨	▨	▨	▨	100	48.4±11.2 (11)[25 to 70]	97.4±4.8 (5)[90 to 102]	6.0 12.0	30	87.1±11.2 <i>a</i> (7)[71 to 102]
7	▨	▨	▨	▨	100	44.0±11.0 (16)[25 to 58]	106.7±14.0 (3)[92 to 120]	5.4 13.2	5	(1) 116
8	▨	▨	▨	▨	100	33.1±14.6 (17)[16 to 72]	92.5±4.7 (4)[87 to 98]	4.1 11.4	12	91.7±47.2 (3)[50 to 143]

Table 1. - Diapause characteristics (see text) in the third instar of *M. picteti* under stable and decreasing (mediated by transfers) photoperiod conditions:
 □ = L:D 16:8, ▨ = 12:12, ▨ = 8:16. Durations are given in days as means ± standard deviations. In parentheses, the sample sizes; in brackets, the ranges. Survival means followed by the same letter are not significantly different according to Fisher's PLSD test ($P > 0.05$).

What happened after shortening the photoperiod?

The transfers from 16:8 to 12:12 (conditions 3, 4 and 5) and from 12:12 to 8:16 (conditions 6, 7 and 8) gave data shown in Table 1 and illustrated in Figure I. Passing from long to medium days was almost without effect if it occurred on the third instars (condition 3). However, it did act when performed after the end of the first stage (condition 4): this did not induce diapause in all the larvae (**Ho** = 83), but surprisingly, the responsive ones exhibited a mean arrest 1.8 times longer than if continuously maintained under medium-length days. When the transfer took place at hatching, all the larvae entered diapause, and later, a third of them spontaneously resumed development also after a long time. These prolonged delays were variable, ranging from one up to three months.

Transferring the larvae from medium to short days (conditions 6, 7 and 8) did not modify the full population ability to enter diapause. Once again, it was demonstrated that the transfers may substantially amplify the diapause intensity expressed by the durations which nevertheless ranged from 16 to 120 days. One may observe in Figure III that this treatment, whatever its timing, resulted in a partition in the responses of the horotelic larvae. Some individuals (about 41 %) reacted as they did under steady short or medium days (**Le** < 5), whereas the others lengthened the arrest of development. This latter part of the diapausing larval population may be seen as either moderately deepened in diapause duration if $5 < \mathbf{Le} \leq 10$ (about 38 %), or strongly deepened if **Le** > 10 (about 21 %). However, the small numbers of larvae and the large overlap in the assumed categories precludes a more precise analysis.

But, the most effective action of these transfers from medium to short days occurred when operated at the beginning of the third stage (condition 6). The dia-

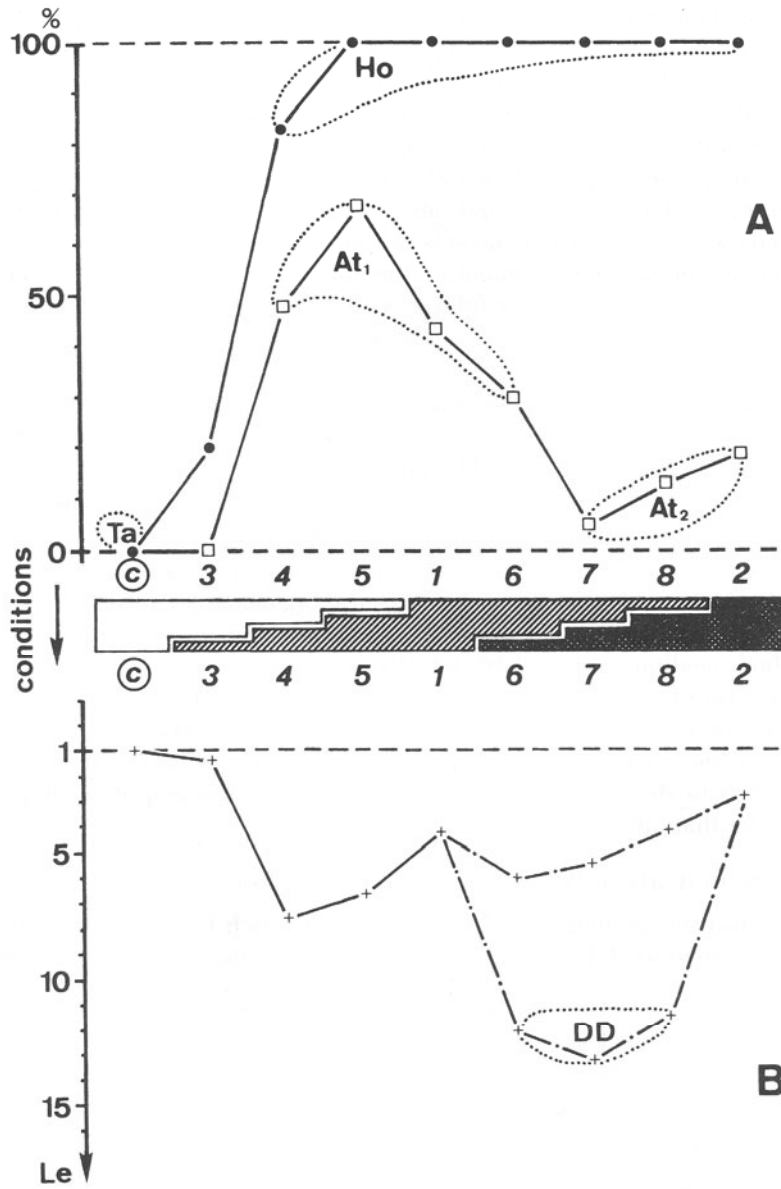


Figure I. - Schematic figures of diapause intensity effects on the third instar of *M. picteti* under the photoperiod conditions of Table 1, plus check condition (C = long days). The arrow indicates the preimaginal development march, with the same graphic convention as in Tables. A, percentages of diapausing larvae: completing diapause development ●—●— by horotely **Ho**, unachieving diapause □—□— by ately **At**; **Ta** = tachytely. B, lengthening indices **Le**, in the same conditions. **DD** = deep diapause.

pause was strengthened in several individuals, appearing as a lengthening in duration of the stage in 70 % of the sample, or as a lengthening of the survival time in the others unable to continue. This again underlines the high sensitivity of this part of life. When the transfer took place earlier, at the beginning of the second stage (condition 7) or at hatching (condition 8), almost the whole population terminated diapause. The developmental times, given by their means, indicated a lengthening in diapause; but such an average increase mainly arose from some individuals whose spinning of cocoons was greatly delayed. The conspicuous effect of a decrease in daylength simulating the autumnal state was to allow most of the larvae to overcome the strong inhibition produced by medium daylength, sometimes very late (up to 4 months after the second ecdysis). This type of photoperiod change thus lessens ately.

The stable photoperiods and the decreasing daylength transfers (Table 1) resulted in a set of close survival times, although the ranges were rather large (coefficients of variation from 0.13 to 0.33). The possible analysis of these data did not reveal any significant differences, and consequently the single computable mean is **Su** = 81.0 ± 18.3 days, n = 43, range 31 to 110 days.

To sum up, schematic graphs (Fig. I A & B) show that: i) a thorough tachytely in *M. picteti* absolutely needed long days; ii) clear diapausing responses excluded the action of long days up to and after the second moult; iii) horotely was due to the action of both medium and/or short days; iv) ately rate was mainly dependent on medium days during the full or partial development time (**At₁**), whereas short days exhibited relatively low populational effects in this way (**At₂**); v) atelic survival duration was not a good parameter to estimate the diapause intensity in many cases; vi) transfers to shortening days during larval life always amplified diapause durations more than all constant daylengths did.

What happened after lengthening photoperiod?

It is long-known that in most insects, development which has been stopped in diapause may be re-started by the action of a signal of the same kind as that

condition	photoperiod on				diapause rate (%) in 3rd instar Ho	3rd diapausing stage				ately rate (%) At	survival duration in atelic larvae Su
	embryo	1st instar	2nd instar	3rd instar		duration		lengthening Le			
9	▨	▨	▨	▨	100	17.6±3.5 (16)[13 to 25]	103.6±7.7 (5)[90 to 110]	2.2	12.8	9	
10	▨	▨	▨	▨	100	19.6±2.3 (7)[17 to 23]	102.6±17.1 (7)[67 to 118]	2.4	12.7	42	(2)[86 and 102] 99.2±17.3 a (10)[83 to 104]
11	▨	▨	▨	▨	100	100.5±22.6 (15)[45 to 151]		12.9		37	127.0±42.3 a (9)[44 to 163]
12	▨	▨	▨	▨	100	12.6±1.6 (24)[11 to 17]		1.6		0	-
13	▨	▨	▨	▨	77	11.2±1.6 (17)[10 to 16]		1.4		0	-
14	▨	▨	▨	▨	0	7.8±0.4 (10)[7 to 8]		1		0	-

Table 2. - Same legend as in Table 1, but under increasing photoperiod conditions.

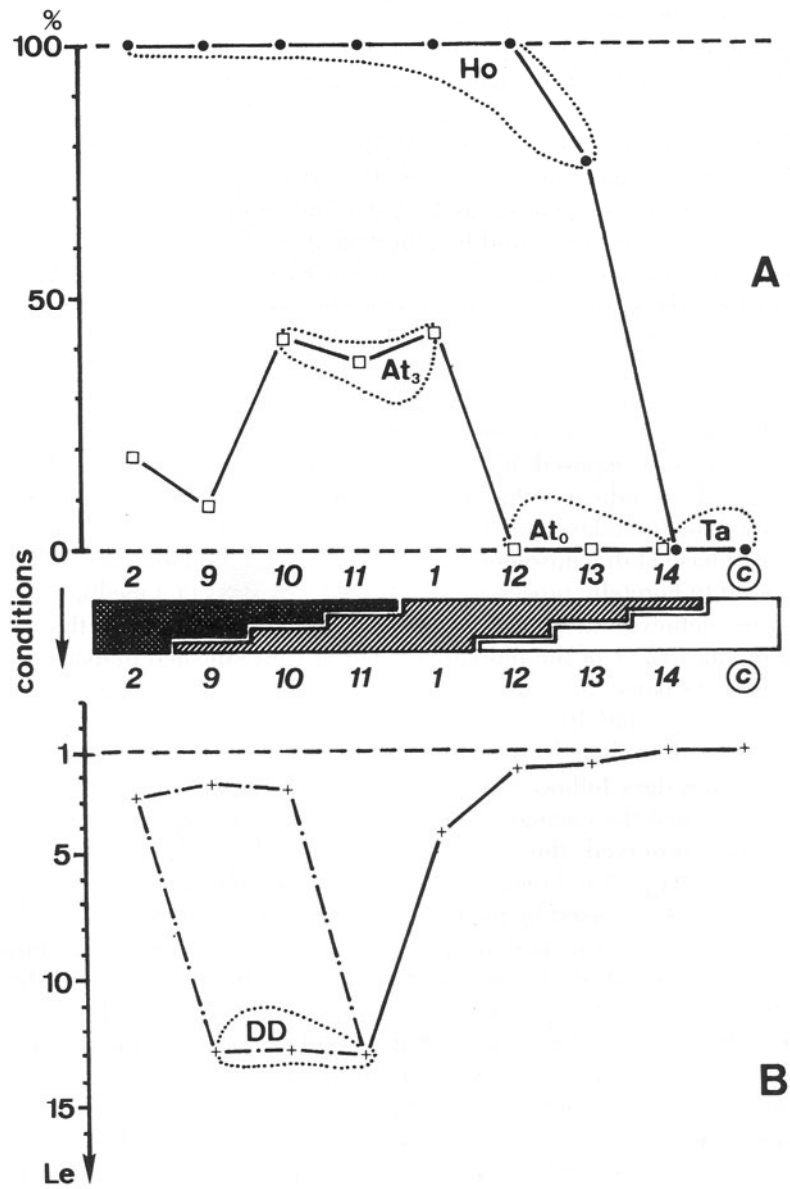


Figure II. - Same legend as in Fig. I.

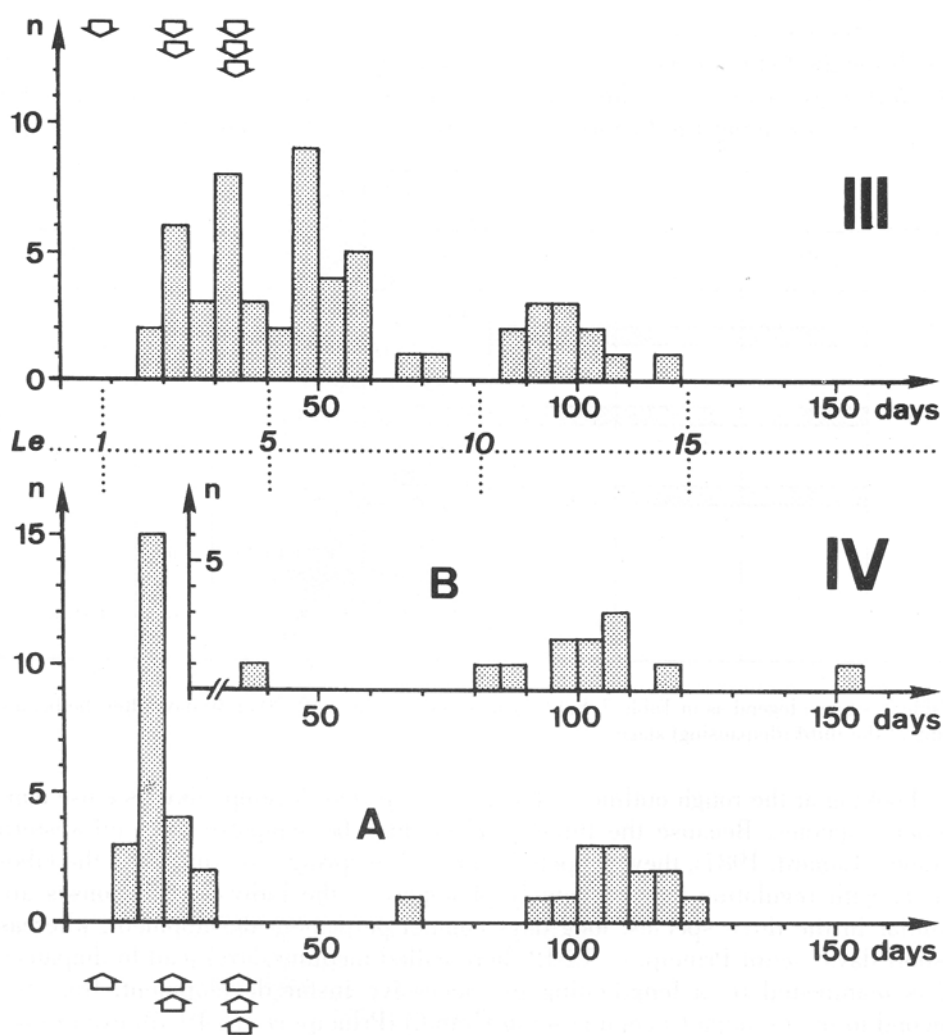
having previously induced the diapause. This is the case for numerous chrysopids (see review in Tauber & Tauber, 1976). We tested in *M. picteti* the actions of two successive photoperiods inciting the lacewing larvae by means of transfers to a longer daylength. One of these changes, short to medium days, is a practical condition the larvae encounter in the field between December and March. The other, medium to long days is not, because such solar daylength increase is not a con-

dition that larvae may endure. Spring is the time in the life cycle to spin cocoons after diapause is fulfilled, or to pupate, or at best to emerge as imagos. However artificial this lengthening of daylight hours may be, the results obtained are shown in Table 2.

Conditions 12, 13 and 14 show (Fig. II) that an exposure to long days following a beginning of development under medium days: i) was followed by a diapause rate decreasing and even disappearing as long-day influence grew; ii) the so-induced diapause was manifested by a mild lengthening of the third stage duration, always less than 2 times; iii) ately was fully eliminated by these treatments (\mathbf{At}_0). If the transfers to long days were made at various periods after the second moult had occurred, namely after the diapause had begun to extend (conditions 15, 16 and 17), the reversal of diapause was still possible, and it appeared in several aspects. Related results are shown in Table 3. Spinning the cocoons was performed by almost all the larvae, except in some rare atelic cases (12 %) where the actual diapausing pressure was imposed 30 days following the beginning of the third instar (condition 17). This indicates that ately only settled down late, and more largely if generated by medium days than by short days. Finally, the times needed to complete the last phase of diapause development decreased proportionally to the times already passed in horotelic processes. A span of thirty days of a medium-day induced diapause achieved in the following sample distribution under the new long daylength regime: 12 % of the individuals had already finished diapause because they had built cocoons from the 25th day, *i.e.* before transferring, 9 and 55 % made it within the 5 and 10 next days, respectively, and the other (horotelic) larvae did so within less than 15 days after transfer.

When medium days followed short days (Table 2, conditions 9, 10 and 11): i) diapausing remained the common fate of the whole larval population ($\mathbf{Ho} = 100$); ii) as previously observed, the medium days retained the ability to freeze development (Fig. II, \mathbf{At}_3); this breakdown involved about the same proportion of the larval population as if caused by medium days working continuously (condition 1); iii) diapause intensity estimated by the lengthening index \mathbf{Le} brings forward a paradoxal shape. Indeed, in the two conditions 9 and 10 where the transfers took place at the beginning of the second and third instars, respectively, there was a separation of the individual responses (Fig. IV): 68 % of the larvae reacted slightly by a weak decrease (22 %) of the mean durations of the diapause times, whereas the others exhibited a very strong increase (\mathbf{Le} reaching more than 12 times) for diapause completion. If the change in daylength occurred at hatching (condition 11), the effect was the highest, and thus, it planed the new developmental speed in the whole larval population (Fig. IV B). The changes from 8 to 12 hours of light a day, simulating the transition from winter to spring time may really be experienced by diapausing larvae in the field. These are the photoperiod conditions that most intensified the diapause manifestation in *M. picteti*. Such rebound effects had already been noticed long ago. For instance, the high temperatures used to reactivate the diapausing ichneumonid *Thersilochus longicornis* Thompson re-induce, in some of specimens, a diapause that is much stronger than that initially expected to be broken (Jourdheuil, 1958).

Finally, the conditions leading to a very strong (magnified) diapause through



Figures III & IV. - Durations in days of diapause in horotelic larvae of *M. picteti* enduring in development a transfer between short and medium days. **Le** = lengthening indices. Single, double and triple open arrows indicate the mean durations of the third stage steadily reared under long (diapauseless), short and medium days (diapausing), respectively. III, transfers from medium to short days. IV, transfers from short to medium days. A, at the beginning of second and third stages; B, at hatching.

the action of increasing photophases from 8 to 12 hours confer upon the atelic larvae a much more delayed death when development does not resume. The earlier the transfer, the longer the survival duration (Table 2).

How do other *Mallada* differ?

Possible comparisons are limited to *M. flavifrons* (Brauer), the only species in which detailed studies have previously been carried out in Italian strains, and to *M. clathratus* (Schneider) which is considered as belonging to the same general type, with equivalent life history and ecophysiological reactions (Principi, 1992).

condition	photoperiod on				duration in days of 3rd stage	ately rate At	survival duration in atelic larvae Su (in days)
	embryo	1st instar	2nd instar	3rd instar			
15				10d	10 + 11,1 ± 1,7 (31)	0	-

16				20d	20 + 8,6 ± 1,9 (30)	0	-

17				30d	[25 to 28] (4)	0	-
	-----				30 + 8,4 ± 2,3 (25)	0	-
	-----				30 + ∞ (4)	12	(4) [42 to 55]

Table 3. - Same legend as in Table 2, but transfers were operated 10, 20 or 30 days after the beginning of the third (diapausing) stage.

Looking at the rough outline of diapause, *M. picteti* develops like its close congeneric species. Because the three *Mallada* may be sympatric in southwestern France (Canard, 1987), they compete for prey from spring. Confronted in the laboratory with regulating factors, namely photoperiod, the individual responses are similar in the three species: long days compel permanent development, whereas "short days" *sensu* Principi (= 12:12, here called medium days) lead to diapause. It is manifested by a lengthening in successive instar development, from the second to the prepupa (= eopupa *sensu* Grandi) (Principi *et al.*, 1975), even to the pupa (Principi *et al.*, 1977). Scrutinising times, *M. flavifrons* is a species basically presenting development of all instars which is slower than *M. picteti*; the related low speed of development and growth are recorded both in tachytelic and in horotelic processes, and also in all combinations used to date and quantify the reactivation of the diapausing larvae (Principi & Sgobba, 1987). But the main peculiarities featuring the bionomics of *M. picteti* were the various responses springing from the studied population. The diapause of *M. picteti* presented a noticeable polymorphism. Diversity in adaptations, partial responses and ately allowed us to state here the critical concept of diapause intensity and even to quantify it in some aspects.

KEY WORDS: photoperiod, larval diapause, diapause intensity, amplified diapause, diapause maintenance, diapause termination, Chrysopidae, *Mallada picteti*

SUMMARY

The multivoltine green lacewing *Mallada picteti* presents a general life history close to this of *M. flavifrons* and *M. clathratus*. It overwinters as free-living larvae arrested in development before being fully grown. This state of larval diapause can be induced in the laboratory by short-daylength rearing conditions. A single temperature (21 °C), and three photoperiods were used in the present experiments, namely L:D 16:8, 12:12 and 8:16, referred to as long, medium and short days, respectively. The time parameters differed from those related to *M. flavifrons* in showing all sequences shorter, especially completion of diapause. The diapause pattern manifested by *M. picteti* under short and medium days resulted in responses diversified in several ways: diapause rates, lengthening of third stage; and also, some diapausing larvae could not spontaneously *i.e.* under steady diapausing conditions resume development without any reactivating cue. Such a dead-end diapause depended on processes qualified by us "atelic" in order to complete the terminology, already using the designations tachytelic (pertaining to the quickest) and horotelic (pertaining to the diapausing standard) development to depict the completion speed.

Spontaneous resumption of development occurred more completely in the population, and earlier in individuals (ately 19 %; average lengthening 2.8 times), under short days than under medium days (ately 43 %; average lengthening 4.2 times) (Table 1, Figs I and II).

Changes in photoperiod regimes were laid out in several steps of larval development using, in each case, a single returnless transition (= transfer). Going from medium days to long days at hatching (Table 2) might resume development, eliminating diapause, either partially (low horotelically) or even totally (tachytely). In all cases, the frequency of ately was seen to fluctuate: it is considered to have a late determinism; it fully disappeared if transfers were carried out on 10- or 20-days old diapausing instars (Table 3). Going from short days to medium days (Table 2, Fig. IV) gave rise to a paradoxical separation of the population responses: some individuals reacted to this increasing daylength by shortening the diapause in all its forms; but others surprisingly reacted to the same signal by conspicuous strengthening of diapause durations which thus lasted more than 12 times longer. The earlier the shock, the deeper the diapause. Also decreasing daylengths (12 to 8 hours of light a day, Table 1, Fig. III) always induced both restrained lengthenings of diapause durations in some individuals (from 4 to 6 times), and largely maintained diapause in others (from 11 to 13 times). Transfers from long to medium days (Table 1) either lightened diapause in all aspects if occurring after the second moult, or slightly deepened it if earlier. Except for the case of amplified diapause, the survival durations belonging to atelic processes, whatever the constraining photoperiod conditions, were largely variable (from 31 to 110 days), with an average of 81 days.

RIASSUNTO

Molteplice azione del fotoperiodo sulla diapausa di *Mallada picteti* (McLachlan)
(Neuroptera Chrysopidae)

Il Crisopide polivoltino *Mallada picteti* presenta un ciclo biologico generale simile a quello di *M. flavifrons* e di *M. clathratus*. Esso sverna come larva a vita libera, il cui sviluppo si arresta prima del raggiungimento della maturità. In laboratorio si può indurre questo stato di diapausa larvale allevandolo in condizioni di giorni brevi. In questi esperimenti si impiegò una sola temperatura (21 °C) e tre fotoperiodi, cioè luce:oscurità 16:8, 12:12 e 8:16, considerati rispettivamente giorni lunghi, medi e brevi. I parametri di tempo differirono da quelli riferiti per *M. flavifrons*, perchè la durata dei vari periodi risultò più breve, specialmente di quello per il completamento della diapausa. Il comportamento della diapausa manifestato da *M. picteti* con giorni brevi e medi si risolse in reazioni che si differenziarono in varie maniere: percentuali di diapausa, prolungamento del terzo stadio; ed, inoltre, alcune larve in diapausa non poterono riprendere lo sviluppo spontaneamente (cioè rimasero in condizioni di diapausa persistente) senza un qualche stimolo di riattivazione. Una siffatta diapausa terminante con la morte dipendeva da processi che noi abbiamo definito "atelici" al fine di completare la terminologia precedentemente usata, con cui si designa tachilico lo sviluppo più veloce e orotelico quello riguardante la diapausa normale per indicare la velocità di completamento.

Nella popolazione la ripresa spontanea dello sviluppo avvenne in maniera più completa, e negli individui si verificò più precocemente (atelia 19 %; allungamento medio 2,8 volte), con esposizione a giorni brevi piuttosto che con esposizione a giorni medi (atelia 43 %; allungamento medio 4,2 volte) (Tab. 1, Figg. I e II).

I cambiamenti di regime fotoperiodico furono programmati a diversi stadi dello sviluppo larvale, impiegando in ciascun caso un unico cambiamento (= trasferimento). Il passaggio dai giorni medi a quelli lunghi dopo la schiusa (Tab. 2) permise la ripresa dello sviluppo eliminando la diapausa sia parzialmente (bassa orotelia), sia anche totalmente (tachitelia). In tutti i casi si osservò la fluttuazione delle frequenze dell'atelia. Si pensa che essa abbia un determinismo tardivo; essa spariva completamente se i trasferimenti avvenivano 10 o 20 giorni dopo l'inizio del terzo stadio diapausante (Tab. 3). Il passaggio dai giorni brevi a quelli medi (Tab. 2, Fig. IV) dette origine ad una paradossale separazione delle reazioni della popolazione: alcuni individui reagirono a questo incremento della durata del giorno abbreviando la diapausa in tutte le sue forme; ma altri, in modo sorprendente, reagirono allo stesso segnale aumentando notevolmente la durata della diapausa, la quale, pertanto, ebbe una durata più di 12 volte maggiore. Più precoce fu l'azione dello stimolo, più profonda fu la diapausa. Anche la diminuzione della lunghezza del giorno (da 12 a 8 ore di luce, Tab. 1, Fig. III) in tutti gli esperimenti produsse, in alcuni individui, la riduzione della durata della diapausa (da 4 a 6 volte) e, in altri, l'allungamento di tale durata (da 11 a 13 volte). I trasferimenti dai giorni lunghi a quelli medi (Tab. 1) resero manifesta la diapausa in tutta la sua apparenza se il trasferimento si avveniva dopo la seconda muta, mentre la resero meno vistosa, se il trasferimento si verificava più precocemente. Salvo il caso di diapausa amplificata, le durate di sopravvivenza riguardanti i processi atelici, qualsiasi fossero le condizioni fotoperiodiche limitanti, furono molto variabili (da 31 a 110 giorni) con una media di 81 giorni.

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