

LIFE HISTORY PATTERNS IN THE NORTHERN EXPANSION OF DRAGONFLIES

ULF NORLING

Department of Zoology, Helgonavagen 3,
S-223 62 Lund, Sweden

As basically warm-adapted insects of tropical origin, the Odonata have evolved various life cycle patterns and cold-resistant stages in forms colonizing temperate areas. These patterns can be intricately regulated by photoperiod and temperature. To throw light on the evolution and modification of some of these patterns, my own previous work on the life cycles and photoperiodic responses of species with different seasonal patterns, growth rates and larval overwintering strategies is reviewed: *Aeshna viridis* and *A. cyanea* in S Sweden, and *Coenagrion hastulatum*, *Aeshna juncea* and *Leucorrhinia dubia* in S and N Sweden are considered.

The recorded average life history duration always exceeded one year. Although voltinism and phenology vary within and between these species, the same basic two-phase pattern of larval photoperiodic responses interacting with temperature provides the framework for seasonal regulation. A long-day diapause, often effective in several instars, prevents emergence during late summer and early autumn. A short-day diapause (hibernation) then follows, with or without a visible termination of the long-day diapause. Thereafter, long days induce rapid development, permitting emergence during spring and summer. The occurrence of these responses at different stages of development and differences in their timing and intensity were found to produce different phenological patterns and to adapt individuals to different climatic conditions.

The type of response of overwintering larvae to long days during spring is dependent on size, or developmental stage, and only larvae overwintering above a certain "winter critical size" (WCS) show rapid growth to emergence during the following season. As other, smaller larvae are prevented from emerging by the long-day diapause, a splitting of a year-class cohort is often observed early in the summer. WCS, which is genetically determined at the population level, is a key property in seasonal regulation at high latitudes, and it is instrumental in the determination of the size and location of the seasonal "gate" where emergence can take place. At least in the late-flying *Aeshna* species, WCS can also be modified in an appropriate fashion by local variation in temperature conditions. In the other, phenologically early species, overwintering close to WCS appears to be

reduced by an earlier, less understood cohort splitting, probably partly involving a different timing of the short-day diapause in different instars.

Partly speculative discussions of odonate life history changes and the evolution of larval hibernation are centred around the present results. The need for further research in some areas is indicated.

INTRODUCTION

The Odonata appear to be basically warm-adapted insects with a tropical origin. Most species occur in tropical or warm-temperate areas and, as far as is known, species which are successful at higher latitudes require comparatively high temperatures for development in all stages¹ (see PRITCHARD, 1982 for discussion and references). Development in Odonata is often relatively slow, and at temperate latitudes this often results in a two- or multi-year life history in many species. The overwintering strategy and the seasonal regulation of emergence is therefore more complicated than in most other insects, particularly because conditions for growth may vary considerably between, and even within, different water bodies (MACAN, 1964). Complex and often gradual responses to photoperiod are known to play a key role in a number of species (CORBET, 1980).

The present paper is a partly speculative attempt to discuss some of the adaptations developed by Odonata during their colonization of higher latitudes. It is focused on some traits in their life cycles, especially mechanisms of seasonal regulation of emergence, and is largely based on published and unpublished data from my own work on Swedish species. It is also an attempt to integrate a small part of the vast body of information brought to light by other workers, who like myself, have been stimulated by the thought-provoking ideas in the early papers of CORBET (see 1962).

TEMPERATURE REQUIREMENTS AND COLD SENSITIVITY IN DIFFERENT STAGES

The major problem faced by a tropical species about to colonize the temperate zone is obviously how to cope with the cold season (see PRITCHARD, 1982 for a more complete discussion). Undoubtedly, the adult is the stage least suited for surviving winter conditions. The temperature requirements for all adult activities are well known to be high (MAY, 1976, 1978), and an inactive adult would tend

1. In this paper "stage" is used to denote one of the principal forms in the life cycle (*i.e.* egg, larva, adult) and as a general term to describe any subdivision of the above that is not defined by another term. For simplicity, the stage or period between two successive ecdyses is referred to as an "instar".

to be exposed and vulnerable. Nevertheless, a few examples of winter survival of adults are known, and in some (e.g. *Sympecma*) a reproductive diapause is present (CORBET, 1962).

The egg stage seems to be intrinsically cold sensitive. Even a constant temperature as high as 15°C is lethal in at least one temperate zone species (*Enallagma boreale* Selys; RIVARD *et al.*, 1975), although 11-13°C is probably a more common threshold for survival (DEACON, 1975, 1979; MASSEAU & PILON, 1982; WARINGER, 1982). Probably the early stages of embryonic development are the most sensitive ones (WARINGER, 1982; NORLING, 1982, p. 356), and hatching may take place at otherwise lethal temperatures (DEACON, 1975). However, a cold-resistant diapause stage, be it obligatory (e.g. *Aeshna*, *Lestes*) or facultative (e.g. *Procordulia*, probably *Somatochlora*; DEACON, 1979; SCHIEMENZ, 1953), has evolved in the eggs of some genera.

The larva may be the stage intrinsically and initially best suited for the survival of an incipient winter. The lower temperature thresholds for development in some temperate-zone species (tropical ones are hardly known) have been estimated to be about 8-12°C (DEACON, 1975, 1979; PRITCHARD, 1982). This may not be very different from that of the eggs, but the larvae can still move at lower temperatures and can select suitable microhabitats. In any case, the larva, with or without diapause, is the commonest overwintering stage in Odonata.

BASIC TYPES OF LIFE CYCLE

A rough classification of odonate life cycles can be made according to the position of the possible overwintering stages in the life history (NORLING, 1975). This classification probably also reflects different initial pathways in the adaptation of the life cycle to a temperate climate.

1. A fixed univoltine life cycle with one obligatory, well-defined diapause stage for overwintering is the simplest type, in which the problems of winter survival and of seasonal regulation of reproduction are solved simultaneously. However, an additional aestivation diapause may occur in warmer areas (CORBET, 1980; UEDA, 1978). The hibernation stage is usually the egg stage, as in many *Lestes* and *Sympetrum* species, but in *Sympecma* it is the immature adult. These cold-hardy stages probably have preadaptive parallels in drought-resistant stages of tropical forms (CORBET, 1962). The rapid larval growth in this group, often associated with a colonization of temporary waters, may allow a successful colonization of areas with relatively short summers despite the obligatory univoltinism.

2. Most Odonata colonizing the temperate zone have evolved a life cycle where the winter is spent in the larval stage. Usually a wide spectrum of instars is resistant to cold (e.g. PAULSON & JENNER, 1971), sometimes all instars except perhaps the very early ones (NORLING, 1984a, b). It is possible that the first step in the colonization of the temperate zone on many occasions has been to

evolve a mechanism for seasonal regulation wherein the larval stage coincides with the adverse season. At this time the larval stage probably could survive the short and mild winter without specializations. There may be evolutionary connections with the previously mentioned type of life cycle (CORBET *et al.*, 1960), for example in genera where an egg diapause is also generally present (e.g. *Aeshna*). The ability to overwinter in a wide spectrum of larval instars, and sometimes in the egg stage as well, gives great flexibility to the life cycle, allowing a considerable variation in adult phenology. It is also a prerequisite for residence in areas where one generation can no longer be completed in one year. The complexities of this type of life cycle are discussed in the following sections.

LARVAL DORMANCY AND ITS FUNCTION IN THE WINTER SURVIVAL OF LARVAE AND IN THE SEASONAL REGULATION OF EMERGENCE

It appears that larvae of at least temperate-zone species can survive short periods (days, perhaps weeks) of low temperatures (4°C) at any interecdysis stage at any time (U. NORLING, unpublished observations). Such unspecialized and unprepared cold torpor (quiescence) may suffice for winter survival at lower latitudes. Surprisingly enough, larvae of *Lestes vigilax* Hagen and *Ischnura posita* Hagen are even reported to moult during winter as far north as North Carolina, about 35°N (PAULSON & JENNER, 1971). Observations during long-term storage (months) of Odonata larvae at 4°C suggest that the moulting cycle (the dynamic period between apolysis and ecdysis; Fig. 1a), or at least the early part of it, may be the most sensitive phase of the larval instar, and one in which a long winter cannot be survived (NORLING, 1984b). If this is true, winter survival would be expected to be greatly enhanced if the initiation of the moulting cycle late in the season could be prevented. A temperature requirement that is higher for the initiation than for the completion of the moulting cycle, or its most sensitive phase, might serve this purpose of anticipation of winter. Such a response may be present among larvae that have been reported to overwinter in a state of quiescence. A possible indication of its existence is presented by WARINGER (1982, p. 19), who found that larvae of *Coenagrion puella* (L.), which normally do not moult below 12°C, could do so if transferred from a higher temperature. However, this hypothetical response may be an incipient temperature induced diapause. Larval diapause can normally be characterized as a delay of the hormonal signal to start the moulting cycle (*cf.* Fig. 1a; CHIPPENDALE, 1977). In this paper, diapause is used in a wide sense: A reduction in development rate not directly caused by adverse conditions (as quiescence is), but which usually serves as preparation for such conditions. Diapause in Odonata larvae is sometimes not sharply delimited from normal development, and the connection with adverse conditions often seems remote.

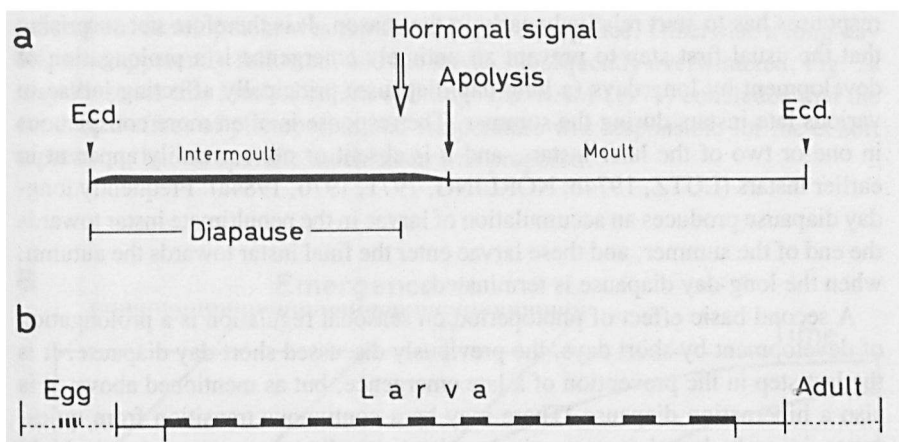


Fig. 1. Simplified presentation of probable cold-sensitive (thin lines) and cold-resistant stages (thick lines) in a larval instar (a) and in the whole life-history (b). In (a) different events in the moult/intermoult cycle and the developmental range where a diapause may be located are shown. In (b) the intermoult period of each instar, except the first (not counting the prolarva), is shown as cold-resistant, and the possible occurrence of an egg diapause is indicated.

If the cold-sensitive period within the instar, tentatively apolysis to ecdysis (Fig. 1a), is of long duration and/or the temperature falls rapidly during the autumn, photoperiod should be preferred to temperature as the source of temporal information for a reliable timing of the induction of diapause. Thus, the next step in the evolution of winter preparations would be a short-day induced diapause, which is well known from odonate larvae (see below). For the present purposes, the diapause does not have to be any stronger than to assure that the winter is encountered in a resistant interecdysis stage. The short-day diapause may first have been realized in the late instars as part of a mechanism for seasonal regulation of emergence, maybe with the enhanced winter survival of the affected instars as a positive side-effect facilitating further extension to the north. At still higher latitudes this short-day response probably was extended to earlier instars as a pure hibernation diapause. In larvae of northern populations of *Aeshna juncea* (L.) a photoperiodically controlled diapause appears to be present in all except perhaps the first four instars, one of which is the prolarva (NORLING, unpublished, but cf. 1981). The evolution of the specific hibernation diapause has probably also been connected with an increase in resistance to oxygen-lack and subzero temperatures (SAWCHYN & GILLOTT, 1975), at least in species occupying shallow water likely to show such conditions and at very high latitudes.

The main cold-sensitive period of the life cycle is centered around reproduction and the adult, and it is considerably longer than that within each larval instar (Fig. 1b). It also includes the last phase of larval development (at least the moulting cycle of the final instar: metamorphosis) and usually the egg stage and the earliest larval instars of the next generation (Fig. 1b). In order to ensure that the completion of this long and critical developmental sequence is not curtailed by the onset of winter, the control of its initiation via the seasonal regulation

responses has to start relatively early in the season. It is therefore not surprising that the usual first step to prevent an untimely emergence is a prolongation of development by long days (a long-day diapause) principally affecting larvae in various late instars during the summer. The response is often more conspicuous in one or two of the later instars, and it is absent or not so readily apparent in earlier instars (LUTZ, 1974b; NORLING, 1971, 1976, 1984a). Frequently long-day diapause produces an accumulation of larvae in the penultimate instar towards the end of the summer, and these larvae enter the final instar towards the autumn, when the long-day diapause is terminated.

A second basic effect of photoperiod on seasonal regulation is a prolongation of development by short days, the previously discussed short-day diapause. It is the last step in the prevention of a late emergence, but as mentioned above, it is also a hibernation diapause. There may be a continuous transition from quiescence in early larval instars, via low intensity diapauses, to an increasingly intense and temporally early induced diapause in late larval instars, which is probably related to seasonal regulation (*cf.* SCHALLER, 1962; ELLER, 1963).

If both long and short days can induce diapause, when do dragonfly larvae develop rapidly? Intermediate daylengths (about late summer photoperiods) may in some species permit a more rapid development than either long or short days (NORLING, 1971, 1984a), but such conditions are transitory in the field. Short and intermediate daylengths usually appear to terminate the long-day diapause, and one or two ecdyses may take place in pre-final larval instars just before low temperatures and/or short-day photoperiods stop development in the autumn (*cf.* INGRAM, 1975; LUTZ, 1974b; NORLING, 1984a). Long days are well known to terminate the short-day diapause (*e.g.* SCHALLER, 1965; NORLING, 1984a). A diapause of the long-day type may then be induced sooner or later, or the development may become consistently rapid, leading to emergence without interruption — a definitive termination of diapause or stimulation of development (NORLING, 1971, 1975, 1976, 1981).

One of the most important questions related to seasonal regulation and phenology in Odonata at temperate latitudes is what determines whether long-day photoperiods in late instar larvae promote (1) fast development to emergence or (2) diapause.

Splitting of year-class cohorts

When different responses to long days occur simultaneously in a year-class cohort, it leads to a splitting of the cohort and a variation in voltinism.

Extremely little is known about these matters at lower temperate latitudes, where the life cycles may represent more primitive patterns than in the north. INGRAM (1971, p. 113-117; *cf.* also INGRAM & JENNER, 1976b) in North Carolina observed that a small second (bivoltine) generation of the otherwise univoltine *Enallagma aspersum* (Hagen) could occur. If a certain critical stage, the F-3 instar², was reached before a certain critical time, about 1 August,

2. Larval instars are designated in the following way: F means final, F-1 penultimate, F-2 antepenultimate, etc.

subsequent development was rapid and led to emergence. Otherwise a long-day diapause apparently followed, and the larvae subsequently overwintered. Fig. 2a may illustrate this kind of cohort splitting. INGRAM (1971) concluded that the combined effect of photoperiod and temperature was responsible for the cohort separation, but no specific mechanism was proposed.

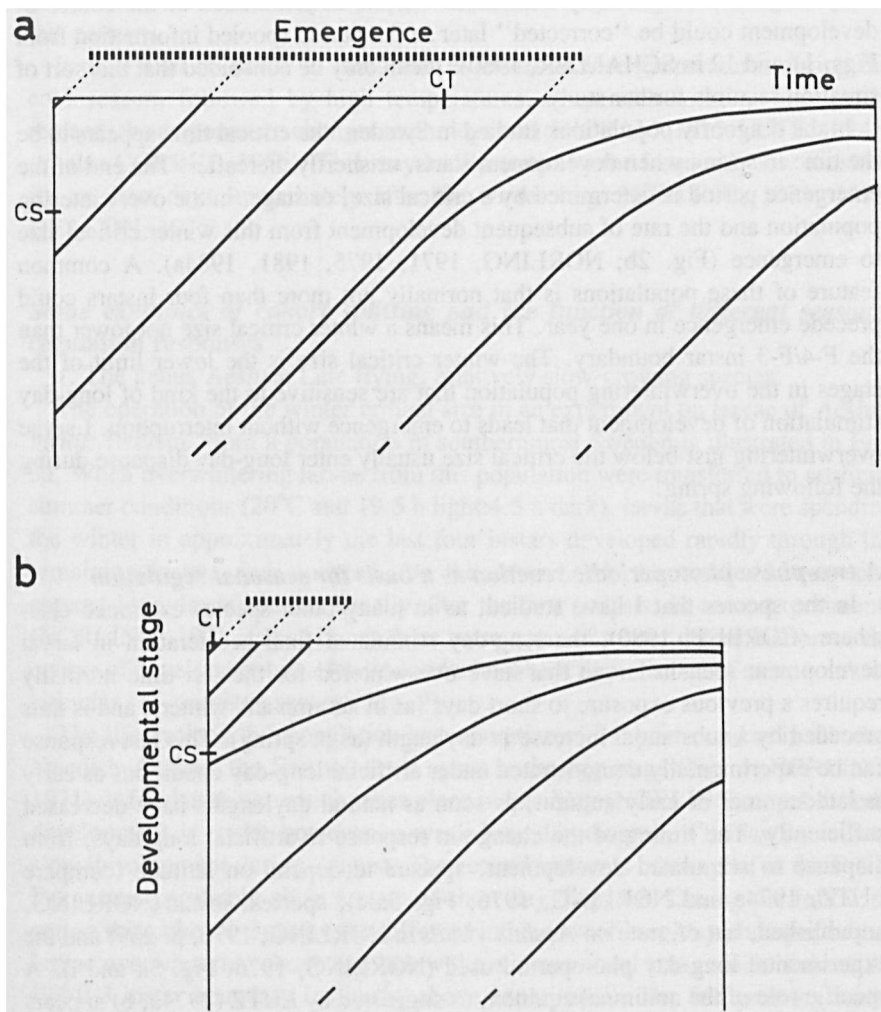


Fig. 2. Idealized presentation of the influence of seasonal regulation on larval growth pattern during one season. Development through the late non-hardy stages (at least comprising metamorphosis) is indicated by the upper broken parts of the development lines, terminating in emergence. The existence of separate instars is disregarded. (a) Late initiation of cohort splitting as perhaps occurs at lower temperate latitudes in a phenologically unspecialized or late-flying species. (b) Early cohort splitting according to the "winter critical size model", at higher temperate latitudes with shorter summers. CT: critical time; CS: critical size.

SCHALLER (1960, 1962) has described a related case in France in *Aeshna cyanea* Müll., which had a mixed 1-2 year development with one winter always being spent as eggs. He maintained that the course of development was set from the egg stage, but it appears more likely that environmental factors were operating during a critical time centred around 1 July, when a long-day diapause probably appeared in the slow-growing cohort (SCHALLER, 1960, Fig. 12). It is possible that the "critical time" was stretched out from May or early June to early August, and that early "mistakes" in the determination of the course of development could be "corrected" later in the period (pooled information from Figs. 11 and 12 in SCHALLER, 1960). It can only be concluded that this sort of situation requires further study.

In the dragonfly populations studied in Sweden, the critical time appears to be the time in spring when development starts, or shortly thereafter. The end of the emergence period is determined by a critical size, or stage, in the overwintering population and the rate of subsequent development from this winter critical size to emergence (Fig. 2b; NORLING, 1971, 1975, 1981, 1984a). A common feature of these populations is that normally not more than four instars could precede emergence in one year. This means a winter critical size not lower than the F-4/F-3 instar boundary. The winter critical size is the lower limit of the stages in the overwintering population that are sensitive to the kind of long-day stimulation of development that leads to emergence without interruption. Larvae overwintering just below the critical size usually enter long-day diapause during the following spring.

A two-phase photoperiodic reaction as a basis for seasonal regulation

In the species that I have studied, as in many other species examined elsewhere (CORBET, 1980), the long-day stimulated final acceleration in larval development seen in larvae that have overwintered for the last time normally requires a previous exposure to short days (as in autumn and winter), and is thus preceded by a substantial increase in daylength (as in spring). This fast response can be experimentally demonstrated under artificial long-day conditions as early as late summer or early autumn, as soon as natural daylengths have decreased sufficiently. The timing of the change in response to artificial long days, from diapause to stimulated development, appears to depend on latitude (compare LUTZ, 1974a and NORLING, 1976, Fig. 5a-c), species, instar (NORLING, unpublished, but *cf.* note on *Aeshna viridis* in NORLING, 1976, p. 259) and the experimental long-day photoperiod used (NORLING, 1976, Fig. 5k and l). A specific role of the autumnal equinox, as suggested by LUTZ (1974a, b) appears unlikely.

The basic framework of seasonal regulation, at least at higher latitudes, is thus a two-phase photoperiodic reaction. Untimely emergence is first prevented by restriction of development by long days. The termination of this state by shorter days may or may not be discernible. Development is then restricted by short days (hibernation diapause). After the exposure to short-days, diapause can be definitively terminated by long-days, provided the larvae are sufficiently advanced in

development. Probably no constant photoperiod is entirely favourable for growth. The above complete sequence has been experimentally confirmed for *Aeshna viridis* by manipulation of photoperiod at a constant temperature of 20°C (NORLING, unpublished). Both absolute values of photoperiod, as well as relative changes, are probably important; and the response to photoperiod is often gradual. A similar two-phase pattern of responses is known from many other, typically univoltine, insects (FURUNISHI & MASAKI, 1983, and references therein). However, the Odonata may be unparalleled in the flexibility of their utilization of this pattern.

It must also be borne in mind that exposure to low temperatures during the cold season, followed by high temperatures, cooperates with, or may partly replace, the responses to changes in photoperiod (INGRAM, 1975; LUTZ, 1974b; cf. also CORBET, 1956). This may be illustrated by the frequently low sensitivity to short days immediately after the winter (e.g. NORLING, 1971, 1976; DEACON, 1975).

Some examples of cohort splitting and the function of different seasonal regulation responses

1. The genus Aeshna: Late flying, relatively slow-growing species.

The operation of the winter critical size in an experiment on larvae of *Aeshna viridis* Eversm. from a population in southernmost Sweden is illustrated in Fig. 3a. When overwintering larvae from this population were transferred to artificial summer conditions (20°C and 19.5 h light:4.5 h dark), larvae that were spending the winter in approximately the last four instars developed rapidly through the remaining instars and emerged. On the other hand, the smaller larvae soon entered long-day diapause, usually after the first ecdysis. In some experiments (NORLING, 1971, Fig. 11b, d) there were signs of a later determination of the course of development in a few individuals, which reminds one of more southern latitudes (cf. previous section; Fig. 2).

The life cycle in this population has a duration of 2-3 years, and as in all other Swedish *Aeshna*, the first winter is spent in the egg stage (Fig. 4; NORLING, 1971). After hatching, which takes place in late May (NORLING, unpublished), development is rapid; however, a weak long-day diapause (?) may sometimes slow development during August. The second winter is often spent in the F-5 to F-1 instars, probably all in a state of short-day diapause. During the following spring this cohort is split by the different influences of long-day photoperiods on larvae overwintering above and below the winter critical size, which is about the F-4/F-3 instar boundary (as in the above experiment). The fast-growing larvae emerge at a time correlated with the instar in which the winter was spent, while the slow-growing ones undergo a long-day diapause in several instars. The long-day diapause in this population is weak enough to allow the latter larvae to reach well beyond the critical size before the third winter, but sufficiently intense to prevent most of them from reaching the F instar during this time. The resulting low number of overwintering F instars reduces the number of early emergers in this basically late species, and even these few early specimens are late relative to

certain other species (see below) because of the location of the F instar diapause at an extremely early stage of interecdysis (NORLING, 1971, 1975). The emergence period lasts from mid-June to early August.

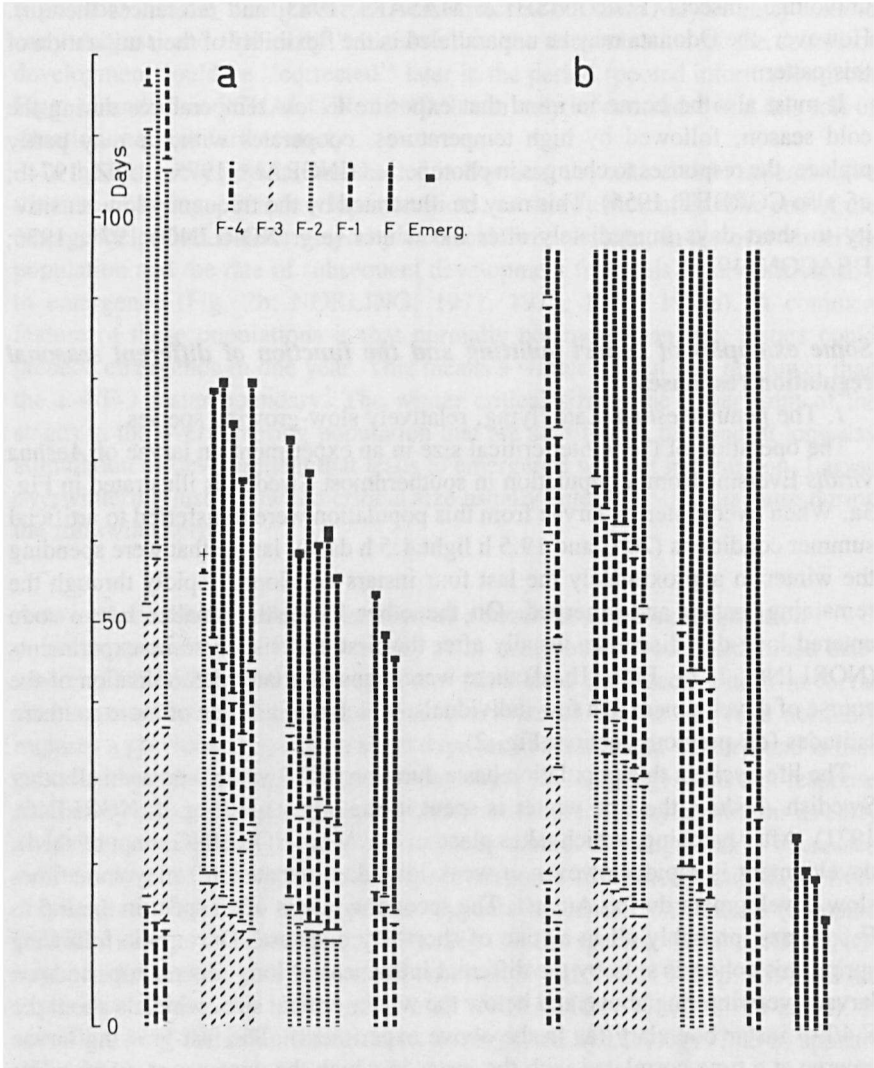


Fig. 3. (a) Individual development of overwintering *Aeshna viridis* larvae from southernmost Sweden ($55^{\circ}40'N$) after transfer to artificial summer conditions (LD 19.5:4.5 at $20^{\circ}C$). Larvae collected in the same instar are grouped together. Overwintering final instars, which were not included in this particular experiment, emerge after about 35 days under these conditions. From NORLING (1971, Fig. 9). (b) Similar presentation for *Leucorrhinia dubia* larvae from southern Sweden ($58^{\circ}42'N$) subjected to similar conditions (LD 19.3:4.7 at $20^{\circ}C$). Experiment started on 5 December 1972. (Unpublished, but cf. NORLING, 1984b).

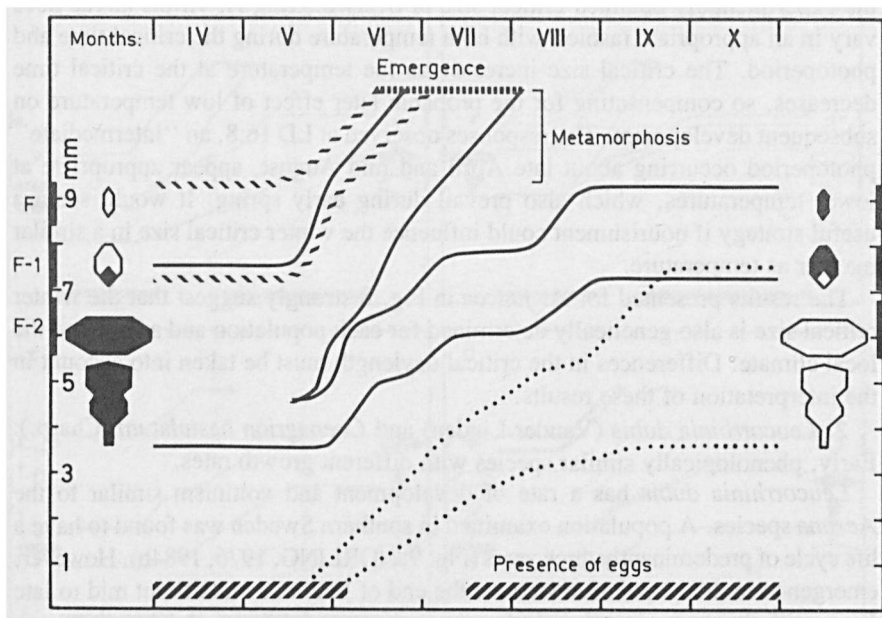


Fig. 4. Diagrammatic presentation of the usual life cycle of the *Aeshna viridis* population used for experiments (cf. Figs. 3, 7). The winter population structure before and after the growth season is shown, with successive year classes distinguished by clear and black areas. Developmental patterns are approximately delimited by lines specific for each age group. Metamorphosis (F instar development) is indicated by an extension above the maximum size. The usual size ranges of the three last instars are shown as thickenings of the vertical (head-width) axes. (From data in NORLING (1971) and unpublished).

Some of the life cycle variation of *Aeshna cyanea* observed in the field in southern Sweden is shown in Fig. 5. The duration of the life cycle varies between 2-3 (b) and 3-4 years (d), and the number of instars that can precede emergence in one year varies between approximately 4 (a) and 2 (c, d). Particularly interesting is that some of the variation occurs between different year-classes at the same locality (b-d), reflecting environmental differences between the years. Predictably, an increase in the winter critical size is correlated with an increased incidence of overwintering F instars (compare a and c).

Fig. 6 is a similar illustration for *A. juncea*, a more northern species, with (d) representing populations north of the Arctic Circle. The latter significantly extends the span of variation recorded. A life cycle duration of 2-3 (a) to 5 years (d), and about 4 (a) to 1 (d) instars preceding emergence in one year, are shown.

What are the causes of these intraspecific variations in the life cycle? The variation in voltinism can easily be explained by differences in yearly temperature sum and food availability, but the proximate causes of variation in winter critical size are not evident. The observed variation appears to be related to water temperature (Fig. 5b, d) and the length of the summer (Fig. 6). Fig. 7 shows that

the experimentally obtained critical size of overwintering *A. viridis* larvae does vary in an appropriate fashion with both temperature during the critical time and photoperiod. The critical size increases as the temperature at the critical time decreases, so compensating for the probable later effect of low temperature on subsequent development. The responses observed at LD 16:8, an "intermediate" photoperiod occurring about late April and mid August, appear appropriate at lower temperatures, which also prevail during early spring. It would seem a useful strategy if nourishment could influence the winter critical size in a similar manner as temperature.

The results presented for *A. juncea* in Fig. 8 strongly suggest that the winter critical size is also genetically determined for each population and adapted to the local climate. Differences in the critical daylength must be taken into account in the interpretation of these results.

2. *Leucorrhinia dubia* (Vander Linden) and *Coenagrion hastulatum* (Charp.): Early, phenologically similar species with different growth rates.

Leucorrhinia dubia has a rate of development and voltinism similar to the *Aeshna* species. A population examined in southern Sweden was found to have a life cycle of predominantly three years (Fig. 9; NORLING, 1976, 1984b). However, emergence in this population starts at the end of May and ends about mid to late June, with the peak occurring during the early part of the period. The winter can be spent in most larval instars, but there is no egg diapause.

As far as could be found in this population, only larvae overwintering in the F instar emerged in the following spring, although the fate of overwintering F-1 instars seems to vary in southern Sweden. The same critical size as was observed in the field was also obtained experimentally (Fig. 3b). Larvae destined not to emerge develop relatively rapidly until they reach the F instar, where they enter diapause regardless of photoperiod. The intensity of the long-day diapause in the F instar is already substantial shortly after ecdysis, and relatively little development takes place under long-day conditions. On the other hand, the short-day diapause is chiefly located at a later stage in the interecdysis period, somewhere near the start of the moulting cycle. If temperature permits, the earliest interecdysis stages are relatively rapidly completed under short-day conditions, and there is an accumulation of larvae in a fairly advanced stage during the autumn (Fig. 10 S). The latter permits an exceptionally early and also well synchronized emergence. The transition between the responses to long and short days during late summer is gradual. With the exception of a rudimentary manifestation of the long-day diapause also in the F-1 instar, the whole sequence of seasonal regulation responses appears to be confined to the F instar (NORLING, 1976, 1984b). *L. dubia* is thus an excellent example of the classical spring species of CORBET (e.g. 1962).

The material obtained from northern Sweden is not sufficient for a reliable estimate of the life history duration (NORLING, 1984b). It is only known that the first winter is spent in very early instars (probably not in the egg stage), and the last winter can be spent in an even more advanced stage than in the southern population (Fig. 10 N). From Fig. 10 it can be concluded that the northern populations could be expected to show an earlier and better synchronized emergence than the southern one if the environmental factors during the spring were

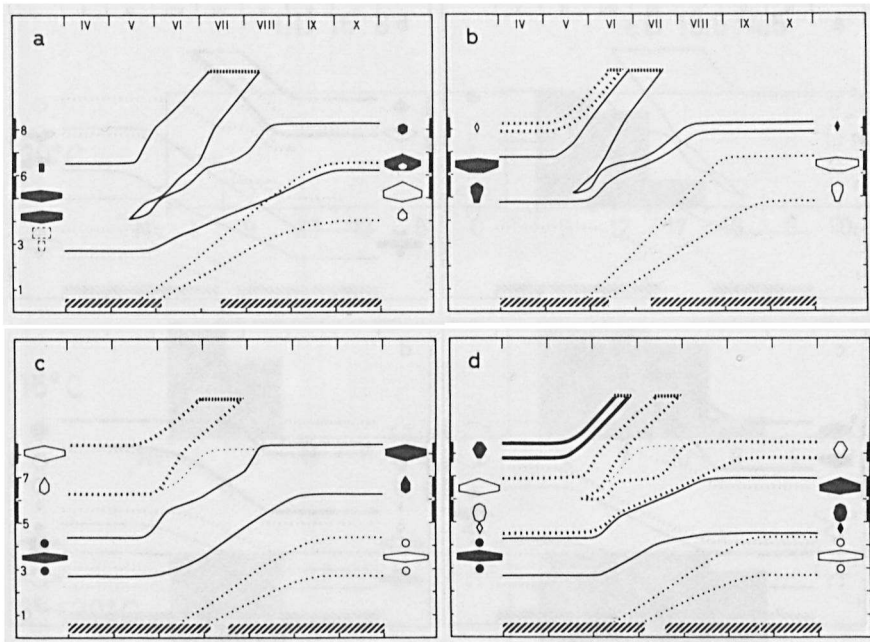


Fig. 5. Life cycle variation of *Aeshna cyanea* in southern Sweden. The graphs are built up as in Fig. 4. (a) Development during 1971 of a population at 55°40'N. The initial winter population structure was not properly recorded in the lower size range. (b-d) Development at one locality at 58°42'N, each graph showing the development of one year class throughout successive years. (b) 1971-1973. Good insolation and low population density. The fastest development recorded. (c) 1967-1969. Shaded conditions. The usual development before 1971, when the shading trees were cut. A few larvae overwintering in the F-1 instar had to overwinter also in F. (d) 1968-1971. Shaded conditions, except in 1971. The slowest development recorded.

As the size, quality and frequency of the samples varies greatly, there are some reconstructions in the graphs, usually made from other similar situations during the nine years of sampling. In particular the occurrence of eggs and small larvae shown in (a), (c) and (d) is highly tentative. The emergence periods could generally not be checked by exuvial collections. Mostly unpublished material (cf. NORLING, 1975).

equal. This probably relates to life in an area with extremely short summers, and a generally low intensity of F-instar diapause is instrumental in the achievement of the advanced overwintering stage.

There are indications of further complexity in the seasonal regulation of *L. dubia*, which may be related to another, less well-known type of cohort splitting. It is most easily observed in certain *Coenagrion* species and was first detected in *C. puella* (L.) in Britain (PARR, 1970). Therefore, before continuing with *L. dubia*, I shall discuss the life history of *C. hastulatum* as observed at the same localities (cf. NORLING, 1984a).

Coenagrion hastulatum has a winter critical size similar to that of the *Aeshna* species, but a faster development during spring (the F instar duration is 50-65% of that in *Aeshna*) makes this species phenologically more similar to *L. dubia*. In southern Sweden it has a mixed 1-2 year development without an egg diapause (Fig. 11). Emergence starts at the very end of May and lasts for about a month; in

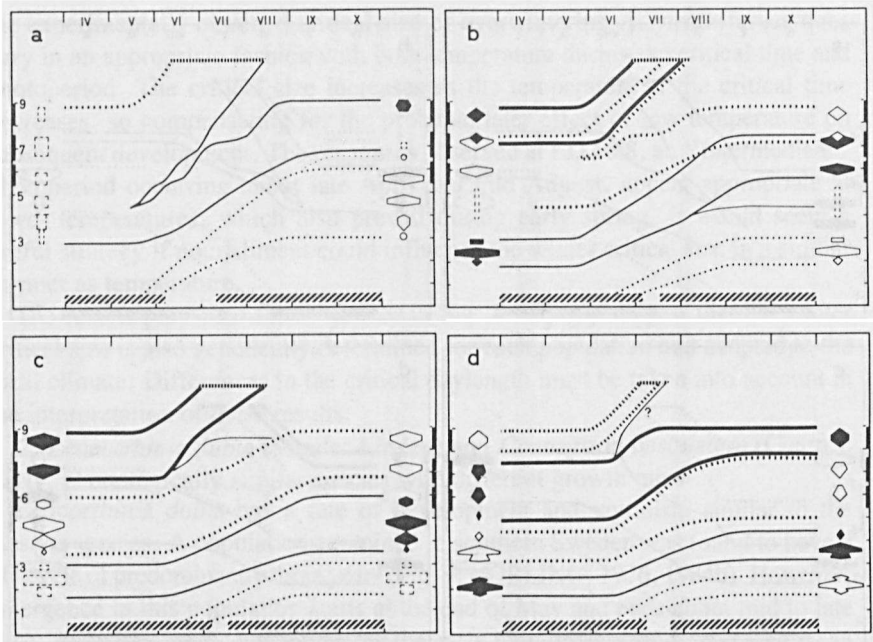


Fig. 6. Life cycle variation of *Aeshna juncea* in Sweden. The graphs are built up as in Figs. 4 and 5. (a-c) Southern Sweden, 58°42'N. (a) Development during 1971 at a locality some 20 km east of the one in Fig. 5 (b-d). The initial winter population structure was poorly recorded. (b) Development during 1967-1970 of one year-class. The most usual development before 1971 at the Fig. 5 (b-d) locality. (c) Development during 1964-1967 at the same locality as in (b). The slowest development recorded in southern Sweden. The year 1964 is reconstructed. (d) Schematic, probably common, pattern in northernmost Sweden, 67°50'N, derived from three localities sampled three times during 1972 (cf. Fig. 12). Possibly some larvae at one of the localities could overwinter the last time in the F-1 instar.

The samples are generally somewhat poorer than those of *A. cyanea*, and no conclusions other than those mentioned in the text should be drawn from the graphs. Mostly unpublished material (cf. NORLING, 1975).

experiments similar to those in Fig. 3 emergence takes place after 16-40 days.

After hatching, which mainly takes place during July, the young year-class cohort shows a successive widening of its size range until it is finally split by a distinct gap just before winter. The winter critical size is to be found somewhere in this gap (experimentally determined at LD 19.3:4.7 and 20°C to be just below the F-2 instar) and in the next spring the fast-growing cohort emerges. At the same time the slow-growing cohort continues to grow slowly, now in a state of long-day diapause effective in several instars, but most notably in the F-1 instar. The larvae in this cohort overwinter for a second time as F instars and emerge early in the following year, before the next univoltine cohort.

During the first year, cohort splitting seems to be related to: 1) difference in hatching time; 2) difference in size increase per ecdysis (ultimately leading to a difference in total number of instars); and 3) slight difference in ecdysis intervals (Fig. 11). It is possible that the cohort splitting may be a genetically predetermined condition (PARR, 1970), but it would seem a poor strategy for a species occupying a wide range of habitats to lock its life history into a completely fixed

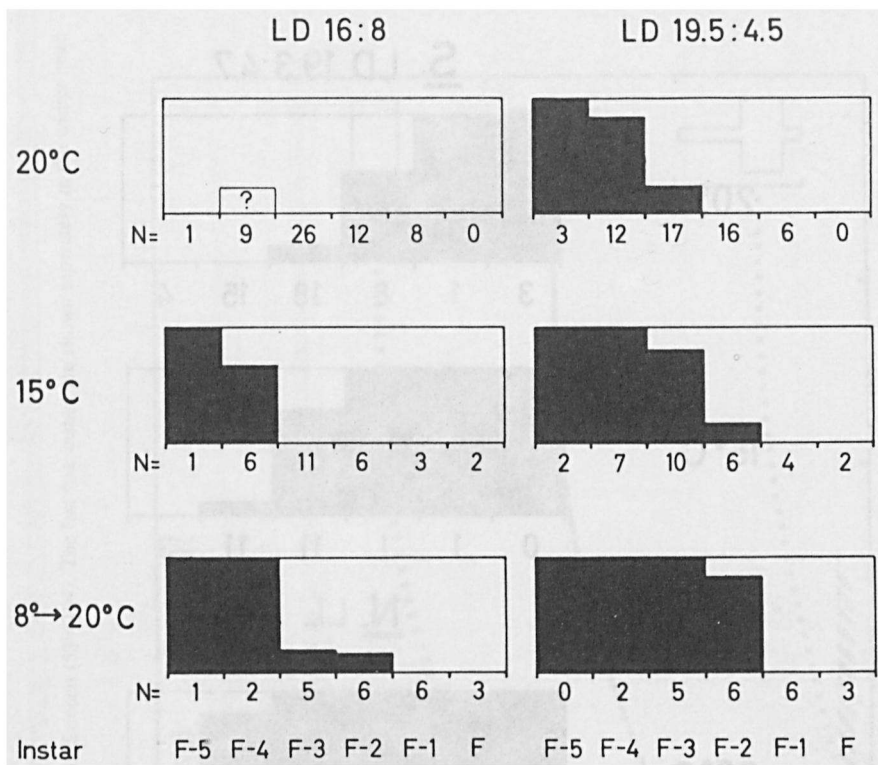


Fig. 7. Gross effect of temperature and photoperiod on subsequent development of *Aeshna viridis* larvae overwintering in different instars. Each rectangle represents the larvae examined at each photoperiod/temperature combination. The overwintering instars are distributed along the horizontal axes, as shown at the bottom of the figure. For each overwintering instar, the full length of the vertical axis represents the number of larvae examined, given below each rectangle. Larvae that died during the experiments without entering metamorphosis are excluded. The *black areas* indicate larvae with a subsequent development strongly affected by diapause, whereas the *clear areas* indicate uninterrupted development to emergence, usually somewhat slower at LD 16:8 than at LD 19.5:4.5. Intermediate responses are indicated with a question mark. Where material is missing, extrapolations are made to either end.

The 8°-20°C groups experienced temperatures rising from 8° to 20°C at an accelerating rate during 79 days; after 50% of this time the temperature was 11.5°C. LD 19.5:4.5 is close to the summer solstice photoperiod if the periods of Civil Twilight are included in the photophase. The 15° and 20°C graphs are prepared from data in NORLING (1971) and the 8°-20°C graphs from unpublished material. The latter experiments started on 26 March 1972.

pattern. Factors that may influence the process of cohort splitting are (NORLING, 1984a): 1) Intraspecific competition for food or feeding sites. The first larvae to hatch compete only with each other, whereas larvae hatching later also have to compete with the slightly older ones, which may have some competitive advantage over the younger larvae. This might be an important factor in the beginning of the process, perhaps reinforcing the type of development with more instars, which is shown by the semivoltine cohort, since size increase at ecdysis is known to be reduced by food shortage (LAWTON *et al.*, 1980); 2) Responses to temper-

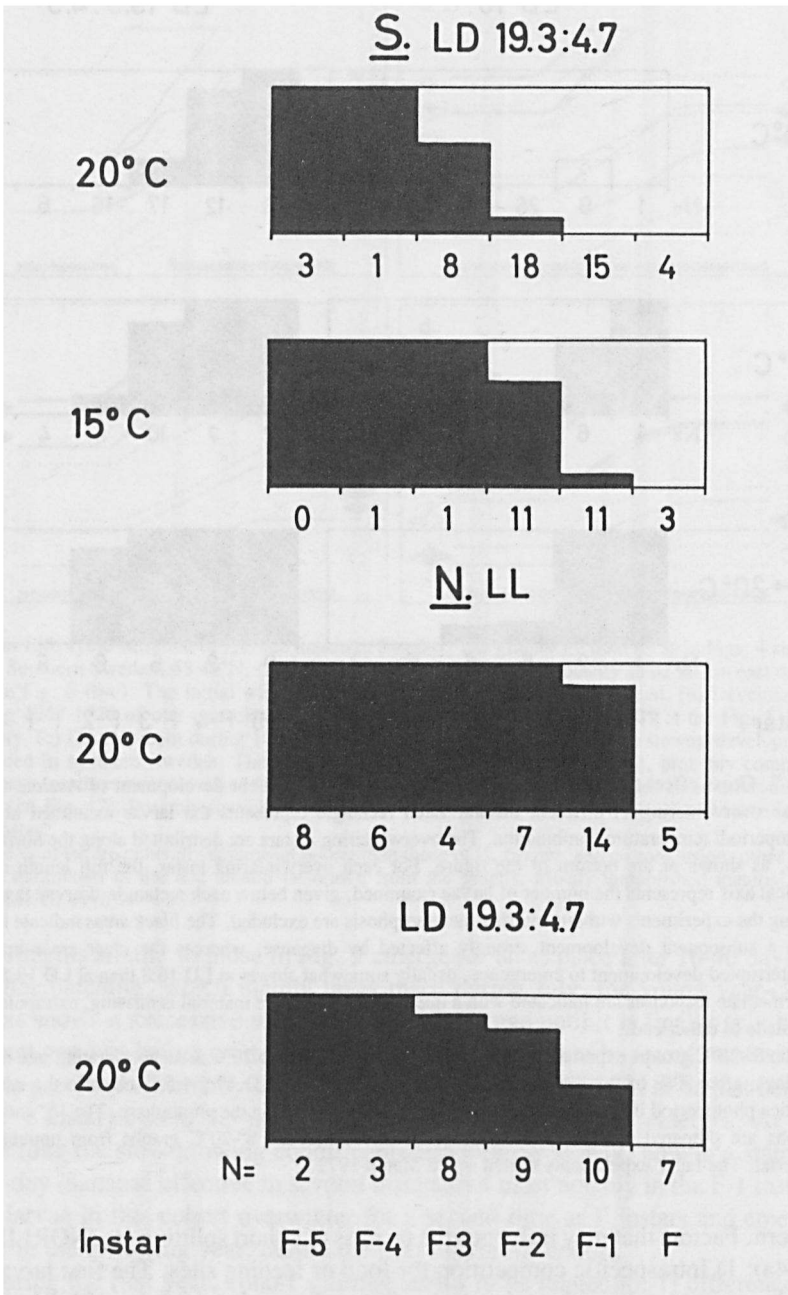
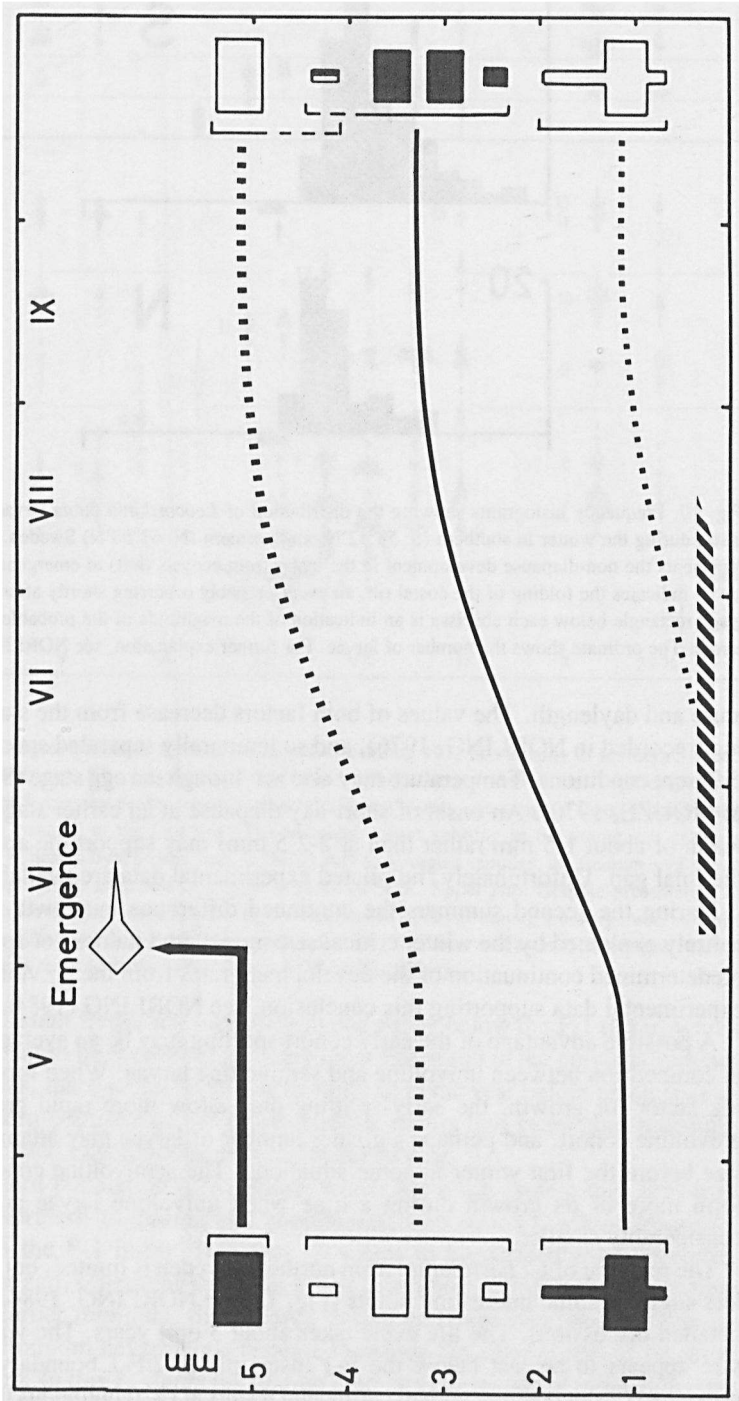


Fig. 8. Experimentally determined winter critical size in overwintering *Aeshna juncea* larvae from southern (S: 58°42', to a minor extent 55°40'N) and northern (N: 67°50' and 68°20'N) Sweden. The graphs are designed as in Fig. 7. LD 19.3:4.7 is a typical long-day summer photoperiod for the southern populations, and LL (continuous light) prevails during most of the summer in the northern areas. To the northern populations LD 19.3:4.7 is not a long-day photoperiod, but rather an intermediate one. (From unpublished data).

Fig. 9. Diagrammatic presentation of the life cycle of *Leucorhina dubia* in southern Sweden (58°42'N). The last five instars are shown separately in the winter head width-frequency graphs. (Redrawn from NORLING, 1976).



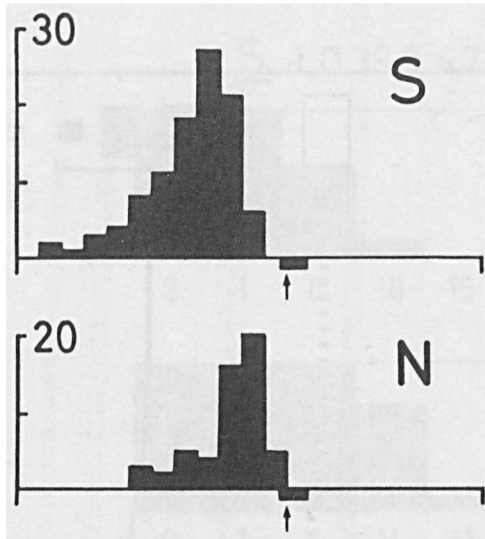


Fig. 10. Frequency histograms showing the distribution of *Leucorhina dubia* larvae within the F instar during the winter in southern (S: 58°42'N) and northern (N: 67°50'N) Sweden. The base line represents the non-diapause development in the instar from ecdysis (left) to emergence (right). The arrow indicates the folding of the costal rib, an event probably occurring shortly after apolysis. The black rectangle below each abscissa is an indication of the magnitude of the probable observational errors. The ordinate shows the number of larvae. For further explanation, see NORLING (1984b).

ature and daylength. The values of both factors decrease from the start of hatching (recorded in NORLING, 1976), and so temporally separated specimens meet different conditions. Temperature may also act through the egg stage (SCHALLER & MOUZE, 1970). An onset of short-day diapause at an earlier stage (at a head width of about 1.5 mm rather than at 2-2.5 mm) may support the appearance of the final gap. Unfortunately, no related experimental data are available.

During the second summer, the continued difference in growth rate can be entirely explained by the winter critical size model, and it does not appear to be a predetermined continuation of the development rates from the previous year. For experimental data supporting this conclusion, see NORLING (1984a).

A possible advantage of the early cohort splitting may be an average reduction in competition between univoltine and semivoltine larvae. When food is a limiting factor for growth, the early splitting may allow more rapid growth in the univoltine cohort, and perhaps a greater number of larvae may attain the critical size before the first winter in some situations. The semivoltine cohort can perform more of its growth during a time when univoltine larvae are absent or considerably smaller.

The material of *C. hastulatum* from northern Sweden is limited, but it nevertheless suggests some interesting points (Fig. 12; see NORLING, 1984a for a more detailed discussion). The life cycle takes about 3 or 4 years. The winter critical size appears to be just below the F-1 instar (the F-2/F-1 boundary; Fig. 12a, upper part), which agrees with experimental results at LL (continuous illumination, the normal summer photoperiod of the area) and 20°C. During the winter, there is

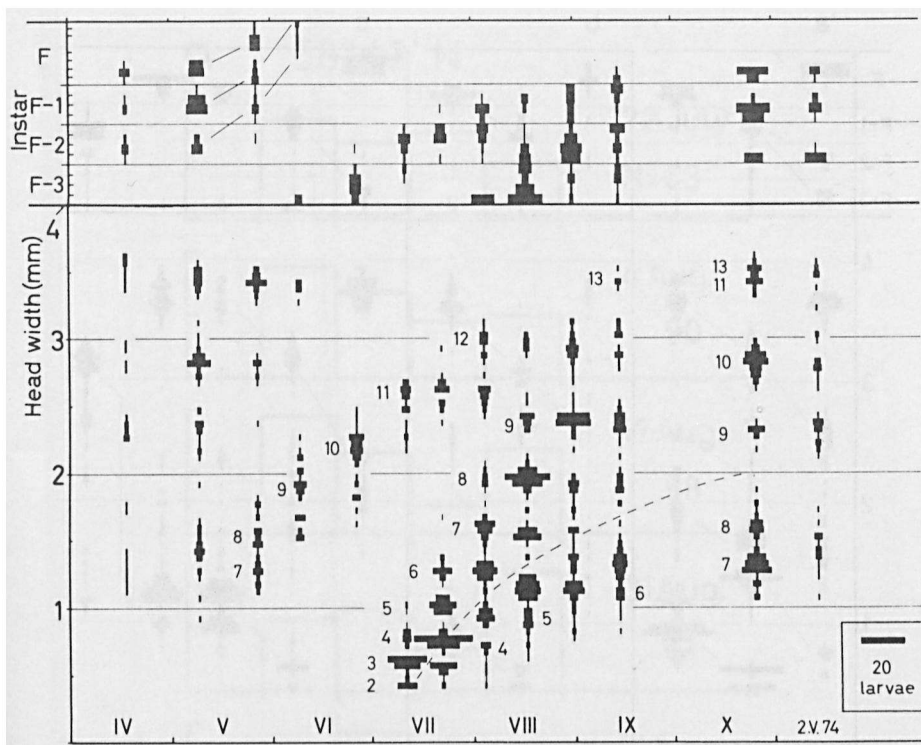


Fig. 11. Larval development of *Coenagrion hastulatum* during 1973 at a locality in southern Sweden (58°42'N). *Lower part*: Kite diagrams showing head width-frequency distributions at different times of the year. The frequency peaks, which represent different instars, are assigned instar numbers, the prolarva being counted at the first one. The incipient cohort splitting in the young age group is approximately indicated by a broken line. In the 11 July to 4 August samples, the frequency of larvae in the junior age group is shown in a scale reduced to 50%. *Upper part*: Graphic presentation of development in the last four instars, showing the distribution of larvae among arbitrary instar subunits (phases) on the different dates. Each larva is represented by the same area as in the lower part, except where the scale is reduced in the latter. (After NORLING, 1984a).

a rather consistent frequency minimum in and partly below the F-1 instar, which does not appear to be correlated with any other minimum in the previous summer samples. Thus, there seems to be cohort splitting in the year before emergence as in the southern population, but in the north it occurs two years after hatching. However, related experimental data are again lacking.

The southern population of *L. dubia*, which has a life cycle rather similar to that of the northern *C. hastulatum* populations, also shows a winter frequency minimum in the F-1 instar. However, it seems to be derived from an earlier minimum, or gap, separating different year-class cohorts (cf. Fig. 9). In one year (1973) the earlier minimum disappeared during early summer, but a F-1 instar frequency minimum nevertheless appeared towards the autumn (Fig. 13a), as in *C. hastulatum*. In this *L. dubia* population there are experimental indications that the F-1 instar less readily enters short-day diapause than do the preceding instars,

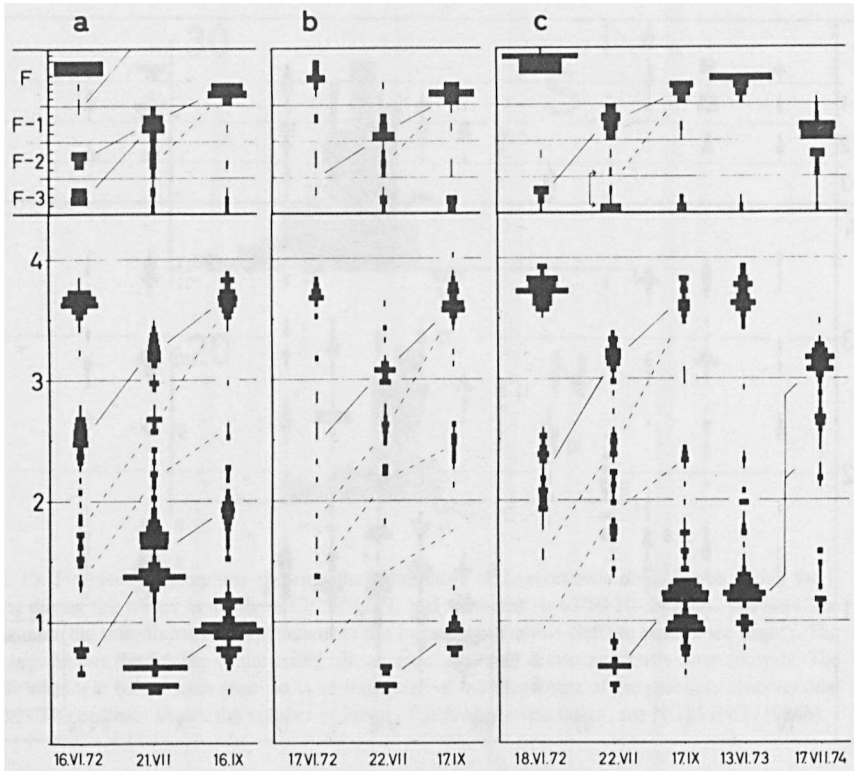


Fig. 12. Larval development of *Coenagrion hastulatum* at three northern study sites (a-c; 67°50'N). The graphs are prepared as in Fig. 11. The different sampling dates are shown at the bottom. The reasonably certain developmental pathways are indicated by solid lines, and the less certain interpretations are shown by broken lines. The instar assignment in the upper part is uncertain. (After NORLING, 1984a).

thus explaining the gap. The F-1 larvae can continue to enter the F instar while the F-2 and F-3 instars cease development (NORLING, 1976, 1984b).

In the northern populations of *L. dubia* no such winter frequency minimum was apparent (Fig. 13b). In these populations the F-1 instar is *more* prone to enter short-day diapause than are earlier instars. It even appears to be verging on an obligatory diapause, because a typical short-day diapause occurred in at least some individuals at any tested photoperiod, including LL and LD 21.5:2.5 (NORLING, 1984b). However, there is a frequency minimum close to the winter critical size in the northern populations, but it is entirely situated early within the F instar (Fig. 10 N), and it is probably assisted in its origin by an early short-day diapause in the F-1 instar.

It is probable that cohort splitting in the year before the start of emergence is a widespread phenomenon in phenologically early species with an average life cycle duration of more than one year. However, whether the examples presented in this paper truly relate to each other remains to be proven. One possible advantage of this pattern has been mentioned, viz. a reduced intraspecific

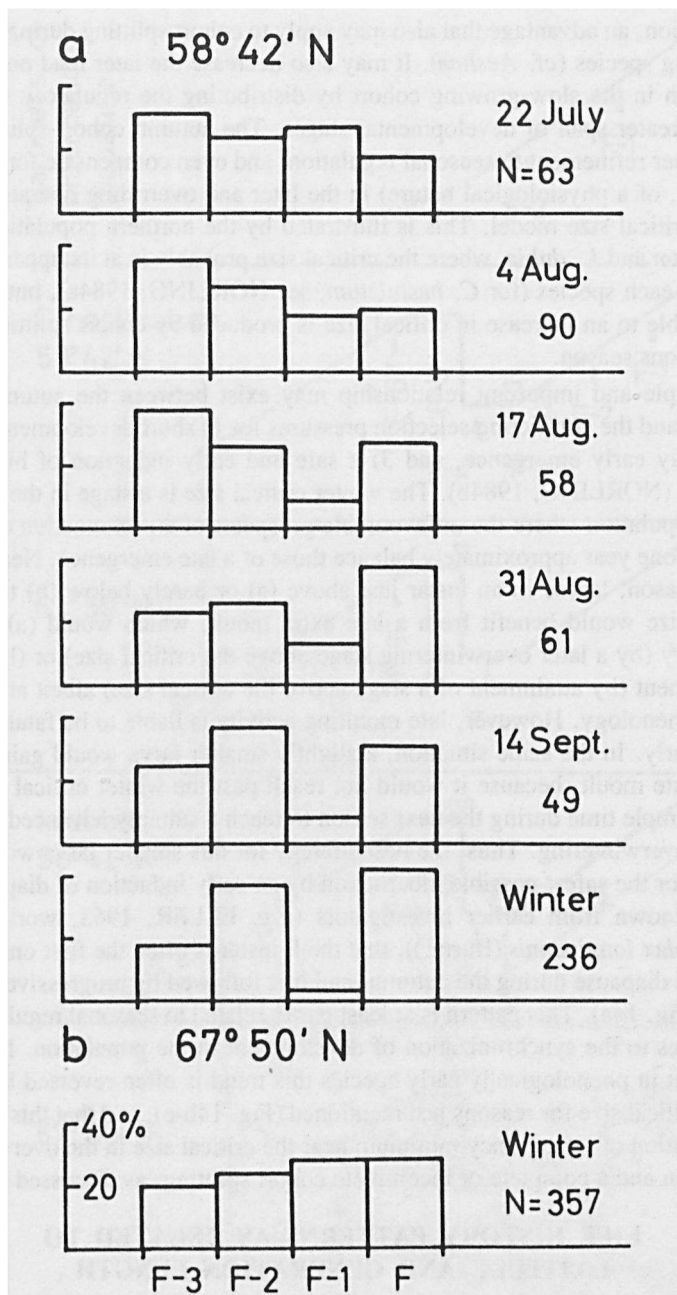


Fig. 13. Relative distribution of larvae in the last four instars of *Leucorrhinia dubia* on different occasions. (a) Material from a population in southern Sweden collected during 1973 and early 1974. The development of a winter frequency minimum in the F-1 instar is seen. (b) Material from three localities in northern Sweden, collected during the spring and autumn of 1972, and the spring of 1973, giving an average presentation of the winter situation in the area. (From data in NORLING, 1984b).

competition, an advantage that also may apply to cohort splitting during spring in late-flying species (*cf. Aeshna*). It may also decrease the later load on seasonal regulation in the slow-growing cohort by distributing the regulatory responses over a greater span of developmental stages. The autumn cohort-splitting may add further refinement to seasonal regulation, and even compensate for deficiencies (*e.g.* of a physiological nature) in the later and overriding operation of the winter critical size model. This is illustrated by the northern populations of *C. hastulatum* and *L. dubia*, where the critical size probably is at its upper practical limit for each species (for *C. hastulatum*, see NORLING, 1984a), but an effect comparable to an increase in critical size is produced by cohort splitting during the previous season.

A simple and important relationship may exist between the autumn cohort splitting and the conflicting selection pressures for 1) short development time, 2) reasonably early emergence, and 3) a safe and early induction of hibernation diapause (NORLING, 1984b). The winter critical size is a stage in the overwintering population where the unfavourable prospects of a prolongation of the life cycle by one year approximately balance those of a late emergence. Near the end of the season, larvae in an instar just above (a) or barely below (b) the winter critical size would benefit from a late extra moult, which would (a) improve phenology (by a later overwintering stage above the critical size) or (b) shorten development (by attainment of a stage above the critical size) albeit at a certain cost in phenology. However, late moulting activity is liable to be fatal if winter comes early. In the same situation, a slightly smaller larva would gain nothing from a late moult, because it would not reach past the winter critical size, and there is ample time during the next season to reach a suitably advanced stage for the last overwintering. Thus, the best strategy for this smaller larva would be to prepare for the safest possible hibernation by an early induction of diapause.

It is known from earlier investigators (*e.g.* ELLER, 1963, working with *Pachydiplax longipennis* (Burm.)), that the F instar is often the first one to enter short-day diapause during the autumn, and it is followed by progressively earlier instars (Fig. 14a). This pattern is at least partly related to seasonal regulation and contributes to the synchronization of development in the population. It appears likely that in phenologically early species this trend is often reversed below the winter critical size for reasons just mentioned (Fig. 14b-e), and that this assists in the formation of a frequency minimum near the critical size in the overwintering population and a complete or incomplete cohort splitting, as discussed above.

LIFE HISTORY PATTERNS AS RELATED TO LATITUDE AND GENERATION LENGTH

Excluding from consideration the intricacies and limitations of specific responses in seasonal regulation, I show the appropriate life history changes during a northern expansion of a phenologically unspecialized hypothetical species in Fig. 15. The most obvious changes are seen in voltinism (left) and in reduction of the range of stages in which the last winter before emergence can be spent, *i.e.* the stages later than "c" in Fig. 15. The latter change restricts the emergence period

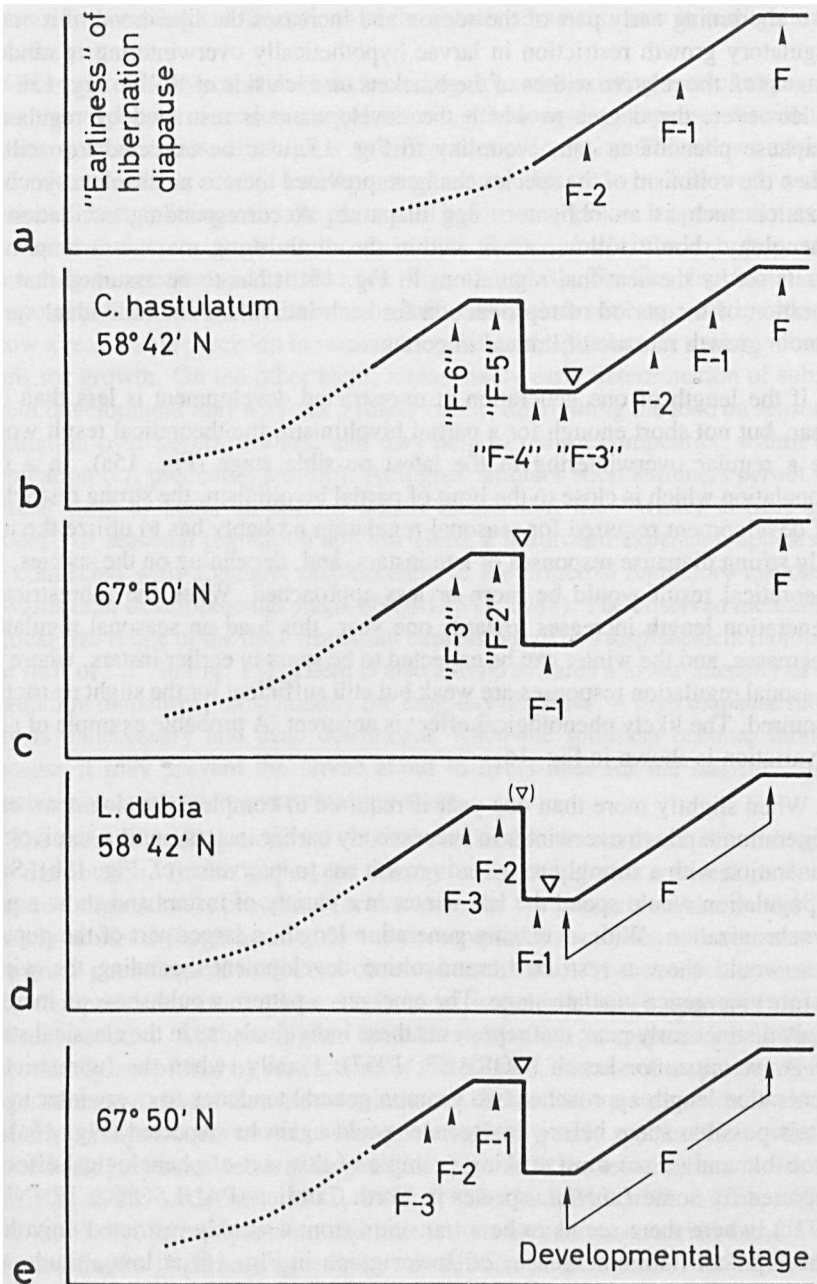


Fig. 14. Partly hypothetical relationship between the timing (intensity) of the short-day diapause and the developmental stage in some dragonfly populations. In (a) a general low-latitude or phenologically late type is illustrated, and (b) to (e) represent actual populations of early species discussed in this paper. The winter critical size, as observed in the field, is indicated with an open triangle, and each instar with a black arrow. The designation of younger instars in *Coenagrion hastulatum* (b, c) is uncertain due to supplementary moulting in diapausing individuals. In the F instar of *Leucorrhinia dubia* (d, e) different intensities of short-day diapause (=different development rates) occur in different interecydysis stages, which have an effect similar to a difference in timing in several instars.

to a shortening early part of the season and increases the likelihood of a major regulatory growth restriction in larvae hypothetically overwintering in random stages (cf. the relative widths of the brackets on each side of "c" in Fig. 15b-e).

However, the degree to which the development is restricted by regulatory diapause phenomena can, according to Fig. 15, also be expected to oscillate when the voltinism of the species changes, provided there is no absolute synchronization such as an obligatory egg diapause. A corresponding oscillation in phenology should follow, albeit within the diminishing maximum amplitude limits set by the seasonal regulation. In Fig. 15, it has to be assumed that the duration of the period of reproduction for each individual and individual variation in growth rate are of limited importance.

If the length of one generation at unrestricted development is less than one year, but not short enough for a partial bivoltinism, the theoretical result would be a regular overwintering in the latest possible stage (Fig. 15a). In a real population which is close to the limit of partial bivoltinism, the strong restriction of development required for seasonal regulation probably has to utilize the usually strong diapause responses of late instars, and, depending on the species, the theoretical result would be more or less approached. When the (unrestricted) generation length increases towards one year, this load on seasonal regulation decreases, and the winter can be expected to be spent in earlier instars, where the seasonal regulation responses are weak but still sufficient for the slight restriction required. The likely phenological effect is apparent. A probable example of such a variation is shown in Fig. 16.

When slightly more than one year is required to complete development, each generation tends to overwinter in successively earlier instars, until a semivoltine generation with a strongly restricted growth has to intervene (cf. Fig. 15b). Such a population would spend the last winter in a variety of instars and show a poor synchronization. With increasing generation length, a larger part of the population would show a restricted, semivoltine development, spending the winter before emergence in a late stage. The emergence pattern would show an increasingly distinct early peak that represents these individuals, as in the classical study of *Anax imperator* Leach (CORBET, 1957). Finally, when the (unrestricted) generation length approaches two years, a general tendency to overwinter in the latest possible stage before emergence would again be expected (Fig. 15c). A probable and (if so) most striking example of this sort of phenological effect is reported for some *Libellula* species in North Carolina (PAULSON & JENNER, 1971), where there seems to be a transition from a weakly restricted univoltine development (late emergence, cf. lower graph in Fig. 16) at low altitude to a largely semivoltine and more strongly regulated life cycle (early emergence) at higher elevations. A somewhat similar variation occurs in *C. hastulatum* in southern Sweden (NORLING, 1984a).

If the generation length is still further increased, the cycle theoretically would repeat itself (Fig. 15d, e). However, the blurring effect of individual variation in growth rate and of the duration of the reproductive period, together with the

increasing phenological limitations of the shorter summers, now in reality eliminate the pattern.

Contrary to the hypothetical species in Fig. 15, most existing species appear to have the responses of seasonal regulation (e.g. the long-day diapause) distributed among several instars, although with differences of intensity. This allows a fairly early determination of the developmental course that is to be followed, and a distinct cohort splitting can take place well before emergence. It apparently starts at a critical size, or stage, at a certain critical time, both of which may vary according to species and latitude (*cf.* Figs. 2 and 3). The developmental and temporal position of this event must be sufficiently close to emergence in order to allow a reasonable precision in seasonal regulation despite locally variable conditions for growth. On the other hand, a reasonably early determination of subsequent development may serve as a safety factor, distributing the load on seasonal regulation over several instars, and may help to reduce competition within the population (*cf.* preceding section). At higher latitudes short summers permit the critical time to occur in spring, which means that the "winter critical size model" of seasonal regulation applies. Here, a northward expansion appears to be connected with a general displacement of the principal regulatory responses towards later developmental stages (NORLING, 1981). The observed increase in critical size is one of the most important expressions of this displacement (compare the shift of "c" in Fig. 15). There is also a trend towards a lower intensity of the regulation diapauses, most notably the long-day diapause. A high diapause intensity is unnecessary and even detrimental when the summers become shorter, because it may prevent the larvae about to overwinter for the last time from reaching an appropriate overwintering stage.

The present investigations are entirely confined to the northern part of dragonfly distribution. In this paper, an attempt at a general and coherent model of seasonal regulation is presented for this area: the "winter critical size model". It mainly works through a set of larval photoperiodic responses and accounts for the gross phenological variations observed in the area. These responses interact with temperature, which plays a role more important than it appears from the present account. At these higher latitudes the pattern of responses is probably secondarily simplified by restrictions of the climate, and therefore easier to bring together in one model than at lower latitudes. In the latter areas, a closely similar pattern perhaps occurs only in some phenologically early species. However, the same basic responses seem to be generally present at the lower latitudes also (*cf.* ELLER, 1963; INGRAM, 1971, 1975; INGRAM & JENNER, 1976a; LUTZ, 1974a, b), but their expression and interactions may be more varied and the role of temperature is perhaps greater (*cf.* discussion on p. 6 and 7; LUTZ, 1968). Were this inference to be true, it would reflect a greater variation permitted by the climate, but perhaps also the independent colonization of temperate latitudes by different taxa.

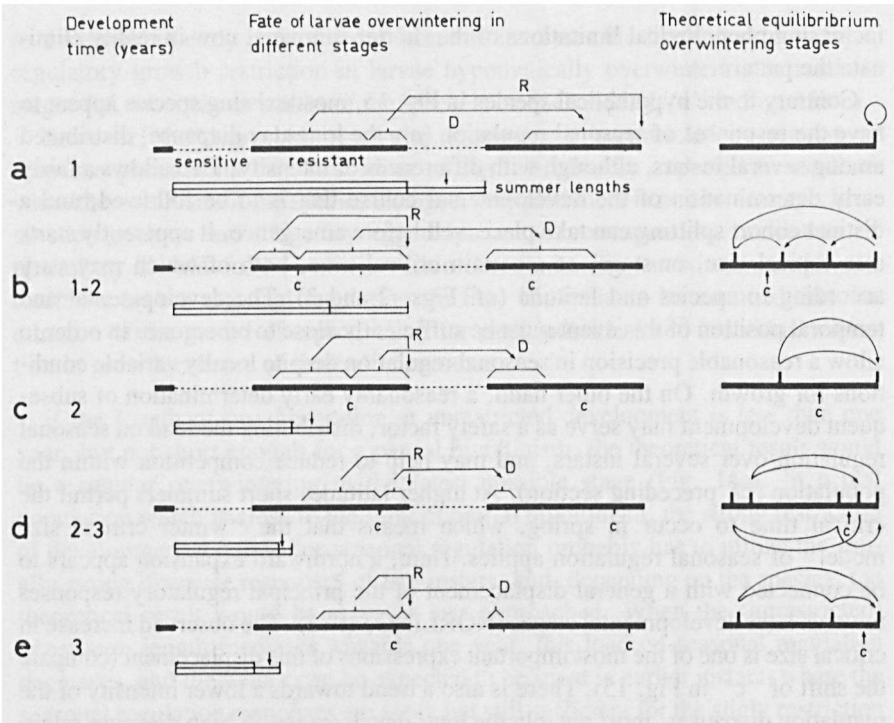


Fig. 15. Development patterns of a hypothetical, phenologically unspecialized species at different latitudes. The developmental stages of successive generations are represented by a line, showing the principal cold-resistant and cold-sensitive periods of the life cycle (cf. Fig. 1b), although separate instars and the duration of the reproductive period are disregarded, and the rate of development is supposed not to vary. Below each line, two bars show the extremes of the range of summer lengths producing each type of voltinism; these bars are drawn at the same scale as the corresponding development rate and the arrow indicates the summer length chosen for the illustration of each development pattern. The long arrows R and D in the left part show the development over one summer with and without growth restrictions, respectively. The stage "c" is comparable to the winter critical size.

In (b-e) the subsequent development of larvae overwintering in a stage larger than "c" is without growth restrictions, and they emerge during the next season. Their offspring reach the sizes shown by the brackets at the head of the arrow D. This arrow shows direct development from one generation to the next. Larvae overwintering in the size range shown by the brackets to the left of "c" can theoretically emerge during the following summer, but not sufficiently early for their offspring to reach a resistant stage before winter; therefore they have to show restricted development and overwinter as advanced resistant stages, at the head of the arrow R (meaning restricted development). The restriction is supposed to occur at this point.

In (c-e), the summers are so short that individuals in the early resistant stages (to the left of the brackets) do not have to show restricted development for seasonal regulation. The relative widths of the brackets on either side of "c" reflect the tendency of the populations to show restricted development, and hence their tendency to overwinter at R, if the overwintering stages are evenly dispersed throughout the possible resistant stages (applies also to b). However, if development proceeds for some generations in this exact, hypothetical manner, the overwintering stages are no longer random, but reach an equilibrium state, which can be predicted from the summer length. In the right-hand part of the figure, these equilibrium overwintering stages are shown as vertical bars on the span of the cold-resistant stages. Each curved arrow running between these bars indicates the development from the last overwintering stage of one generation to that of the next one. Only those arrows pointing at the "R" stage represent generations with restricted growth.

In (a), each successive generation will overwinter in progressively later stages until they reach the upper limit of the resistant stages, which is the "equilibrium" overwintering stage for the subsequent generations.

In (b-e), the offspring of the larvae overwintering at this limit (R) will at first overwinter at the right arm of the bracket at D. In (b) this stage is still to the right of "c", as also is the overwintering stage of the next (second) generation. However, the third generation at first overwinters below "c", and therefore has to overwinter once more at R, which completes an "equilibrium" cycle of 3 generations (3 arrows). In (c-e) the first generation offspring (from R) always overwinter below "c", and development always takes 2 years or more. In (c) and (e), the equilibrium state is a fixed one with restricted development always occurring (as in a), but with different voltinism. In (d), 2 generations with different voltinisms, and with or without growth restrictions, alternate for one complete cycle.

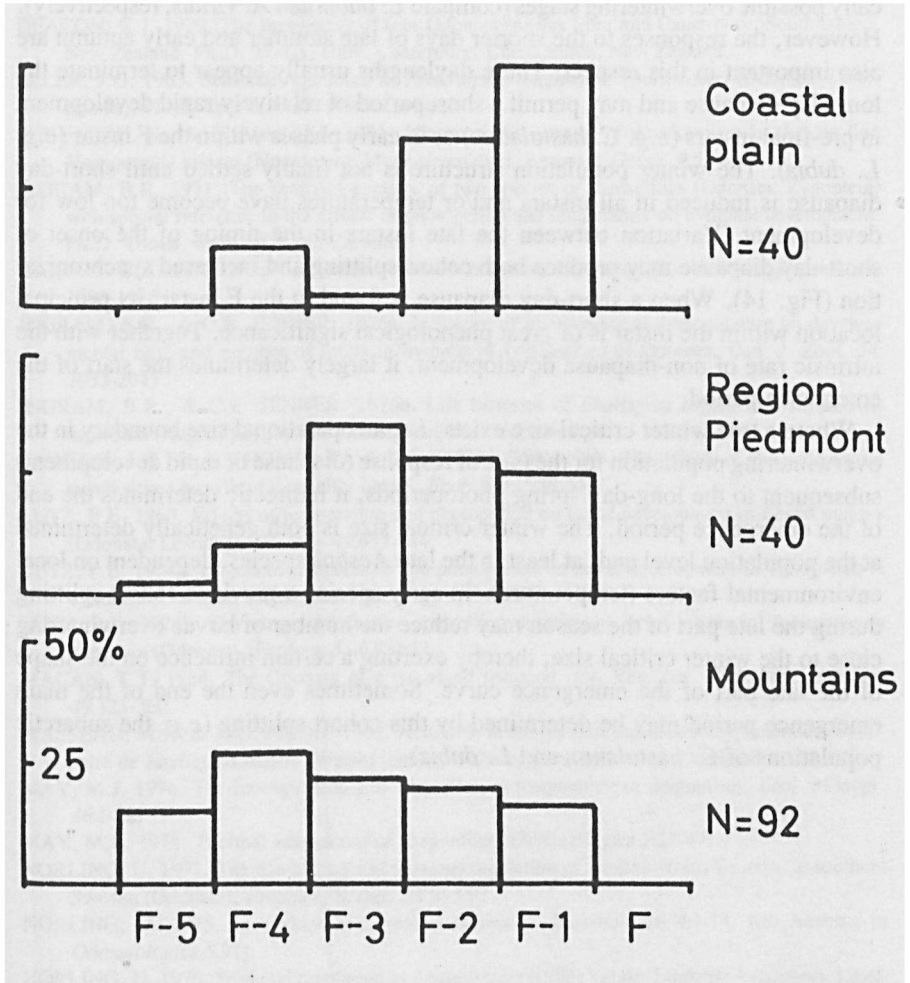


Fig. 16. Distribution of larval instars of *Enallagma aspersum* from different areas in North Carolina during early spring (10-14 March). The F instar is not an overwintering instar. At least part of the difference between these presumably mainly univoltine populations probably relates to a decreasing load on seasonal regulation with increasing altitude. (Drawn from data in PAULSON & JENNER, 1971).

SUMMARY OF THE PHENOLOGICAL EFFECT OF THE DIFFERENT RESPONSES

The phenological properties of a population are strongly dependent on the diapause characteristics in different instars. The long-day diapause is usually the first decisive step in seasonal regulation, its presence in late instars preventing metamorphosis late during the summer. Its intensity and distribution among the instars vary and can indirectly influence the shape of the early part of the emergence curve by facilitating or reducing the attainment of the latest physiologically possible overwintering stages (compare *L. dubia* and *A. viridis*, respectively). However, the responses to the shorter days of late summer and early autumn are also important in this respect. These daylengths usually appear to terminate the long-day diapause and may permit a short period of relatively rapid development in pre-final instars (e.g. *C. hastulatum*) or in early phases within the F instar (e.g. *L. dubia*). The winter population structure is not finally settled until short-day diapause is induced in all instars and/or temperatures have become too low for development. Variation between the late instars in the timing of the onset of short-day diapause may produce both cohort splitting and increased synchronization (Fig. 14). When a short-day diapause is found in the F instar, its principal location within the instar is of great phenological significance. Together with the intrinsic rate of non-diapause development, it largely determines the start of the emergence period.

Where a true winter critical size exists, *i.e.* an operational size boundary in the overwintering population for the type of response (diapause or rapid development) subsequent to the long-day spring photoperiods, it indirectly determines the end of the emergence period. The winter critical size is both genetically determined at the population level and, at least in the late *Aeshna* species, dependent on local environmental factors (temperature). In early species a previous cohort splitting during the late part of the season may reduce the number of larvae overwintering close to the winter critical size, thereby exerting a certain influence on the shape of the late part of the emergence curve. Sometimes even the end of the main emergence period may be determined by this cohort splitting (e.g. the subarctic populations of *C. hastulatum* and *L. dubia*).

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