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A STUDY ON EMBRYONIC DEVELOPMENT AND LARVAL GROWTH OF *SYMPETRUM DANAE* (SULZER) AT TWO ARTIFICIAL PONDS IN LOWER AUSTRIA (ANISOPTERA: LIBELLULIDAE)

J. WARINGER

Abteilung für Limnologie, Institut für Zoologie, Universität Wien, Biozentrum, Althanstrasse 14, A-1090 Wien, Austria

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Newly laid eggs were collected at Oberradlberg, Lower Austria (Sept. 5, 1981), and reared under natural conditions in a garden pond. The embryonic development was completed in 217-239 days, at a mean temperature of 10.8° C. The process is briefly described. A diapause stage took place immediately prior to blastokinesis. All eggs hatched within 22 days, showing a high degree of synchronisation. — The newly hatched larvae were reared in tubes in a garden pond. Ten instars were observed. The average body lenght increment per moult was proportionately constant at 27% approx. The larval growth could be well described in terms of a power law. The mean specific growth rate, which ranged from 0.8 to 1.8% lenght increment day^{-1}, is compared with the growth rates of other *Sympetrum* spp. The life cycle of *S. danae* is briefly described, and the overwintering strategies in the genus are reviewed.

INTRODUCTION

Sympetrum danae is a common and widespread cirumboreal dragonfly. Due to its wide choice of habitats it is abundant in the northern part of North America and of Europe and in higher regions of Central Europe, preferably in bogs and marshes (CORBET et al., 1960). In Austria, *S. danae* is reported from all federal states with the exception of Vorarlberg (ST. QUENTIN, 1959; LÖDL, 1976a, b). Although its biology was described in detail by GARDNER (1951c), SCHIEMENZ (1953), ROBERT (1959), CORBET et al. (1960) and AGUESSE (1968), some contradictions still remain, especially in the number and in the biometrics of larval instars. There is also a lack of information on egg development and larval growth of this species.

The aim of the present study was to obtain some quantitative information on egg development and larval growth of *S. danae* under field conditions in the Central European part of its range and to make a contribution to our present knowledge of overwintering mechanisms in Odonata.

MATERIAL AND METHODS

Eggs were obtained from a shallow, marshy pond at Oberradlberg (latitude: 48° 14'N, longitude: 15° 40'E, altitude: 249 m) in Lower Austria. The pond is a breeding locality of 15 species of Odonata.

A couple of *S. danae* was caught with a hand net during oviposition, which is of the exophytic type. Following a method described by Krull (1929), the female's wings were held together between thumb and forefinger and the tip of the abdomen was dipped into a glass tube filled with water. Egg masses were released immediately and sank to the bottom of the tube. Despite the fact that the female had started oviposition before it was caught, a total of 910 eggs was counted. All eggs for the experiments had their origin from the same female which is in the author's collection. At home, a total number of 465 eggs was distributed to five glass tubes filled with water. The tubes were closed with fine gauze (mesh size 0.2 mm) and submerged in a garden pool made of concrete. The pool was cylindrical in shape (diameter 1 m, depth 40 cm). The eggs were submerged at a water depth of approximately 30 cm. The water temperature was recorded by a minimum-maximum thermometer every time the eggs were checked; eggs were checked nearly each day by transferring egg masses into a Petri dish filled with water and examining under a binocular microscope at magnifications between 50x and 100x. The embryos were seen best by using a black background. When hatching began, the tiny larvae were gently removed with forceps. Further details of the experimental conditions are shown in Table I.

Immediately after hatching, single larvae or groups of larvae were put into glass tubes (length 8.5 cm, diameter 2.5 cm) which contained plant material as a climbing support. The tubes were closed with gauze caps and submerged at 10 cm depth in another garden pond (approx. 8 m^2, max. depth 60 cm). After each moult the mesh size of these caps was changed; the mesh size was slightly smaller than the head width of the larvae and allowed entry of a sufficient food supply from the surrounding water (c.f. WARINGER, 1982). The density of planktonic crustaceans was high, and a large number of food organisms was always found in the tubes.

The water temperature was recorded with a minimum-maximum thermometer which was read and reset each time the larvae were checked. Technical reasons limited the checks to weekly intervals. Therefore it was not possible to obtain accurate data on moult intervals. Larvae were transferred from the tube to a Petri dish filled with water. Body length and head width were measured with an ocular micrometer to the nearest 0.1 mm, and exuviae were removed from the tubes. Further details are given in Table III.

EMBRYONIC DEVELOPMENT

The embryonic development was divided into seven morphological stages which could be easily seen under the binocular microscope without preparation. The chosen stages correspond roughly with the stages described by BOEHMS (1971) for *S. vicinum*. In the following description day numbers indicate times when the described changes were observed first.

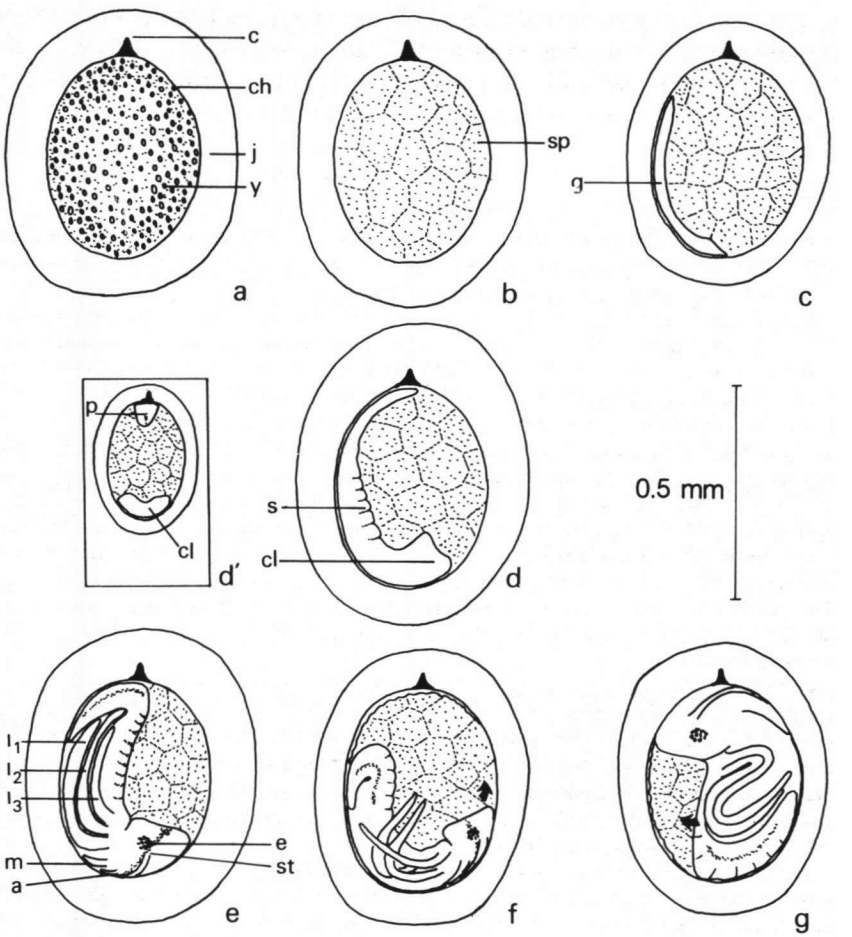

Fig. 1. Seven stages of the embryonic development of *Sympetrum danae*. Further explanation in text.

FIRST STAGE
Figure 1 a

Newly laid eggs are whitish in colour, oval shaped (525 x 375 μm) and have a dark conical structure around the micropyle. The eggs are totally embedded in a thick jelly layer (j) (approx. 220 μm thick); in newly laid eggs, this layer is adhesive and therefore all eggs of a batch are held together and attached to the substrate. After a few hours the jelly gets more elastic and harder and loses its adhesiveness. The yolk (y) is evenly distributed and has a grainy appearance. Within 18 hours,

the colour of the chorion (ch) changes to dark brown, with the cone (c) being darkest.

SECOND STAGE
Figure 1 b

The onset of stage two occurred first four days after oviposition; it is marked by a change in the yolk structure: the grainy yolk is divided into polygonal spherules (sp) which are clearly visible at low magnification. The first steps of the formation of the germ plate remain invisible without preparation.

THIRD STAGE
Figure 1 c

Eight days after oviposition the germ plate (g) is clearly visible at the dorsal part of the egg. It is seen best by using a black background. The plasma of the germ plate appears hyaline, and no segmentation is visible. Figure 1 c shows an advanced phase of stage three.

FOURTH STAGE
Figures 1 d, 1 d'

Ten days after oviposition, the appearance of segmentation (s) marks the onset of stage four. At the aconal end of the egg, a cephalic lobe (cl) becomes visible, and the thorax and the first abdominal segments are formed. A ventral view of the egg (in respect to the situation of the fully grown embryo) shows the tip of the abdomen with first signs of the proctodaeum (p) and the medical incision of the cephalic lobe (Fig. 1 d').

FIFTH STAGE
Figure 1 e

14 days after oviposition the embryo is fully segmented. The tip of the abdomen is twisted towards the ventral side. The dark structure of the proctodaeum has become distinct; three pairs of legs (l_1 — l_3), the antennae (a), the mouthparts (m), the eyes (e) and the dark stomodaeum (st) in front of the eyes are visible.

SIXTH STAGE
Figure 1 f

The onset of stage six is characterized by the beginning of blastokinesis, observed first 189 days after oviposition. During this stage the embryo moves to

the conical end of the shell (indicated by an arrow in Fig. 1 f), undergoing a revolution of 180°. The figure shows the first step of this movement. At the end of stage 6, the head of the embryo is situated underneath the cone, and the ventral side of the embryo is at the ventral side of the egg by now.

SEVENTH STAGE
Figure 1 g

The embryo has reached its final position, first observed 197 days after oviposition. The lateral sides of the body grow dorsally (indicated by an arrow); after dorsal closure is completed, the remaining yolk is enclosed in the mid-gut.

HATCHING

The first hatching was observed 217 days after oviposition. For hatching, the conical end of the shell is broken between the eyes, and head and thorax emerge from the shell. The last abdominal segments remain within the shell. The prolarval stage lasts only c. 2 minutes, when the moult to the first larval instar occurs.

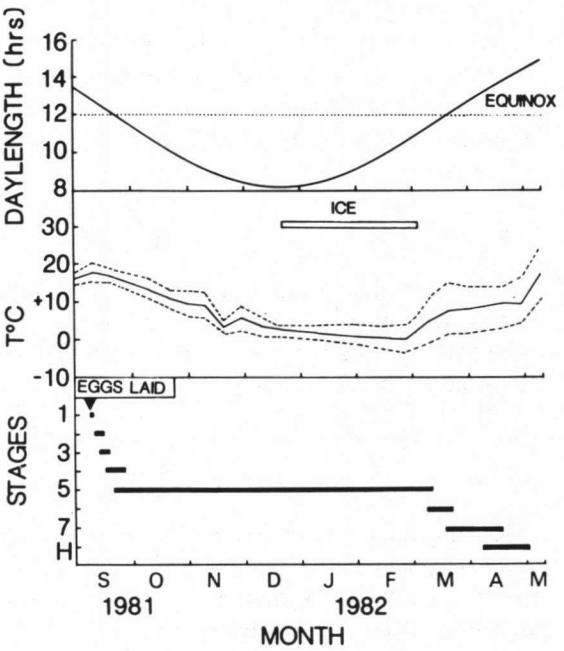

Fig. 2. Temporal distribution of the seven stages of embryonic development shown in Fig. 1 (Sept. 1981 - May 1982). The numbers, 1-7, indicate the stages, H indicates the hatching time. Values of mean water temperature (and range) are given every 10 days at the middle part of the figure, and values of day length (hours) are shown at the top.

The temporal distribution of stages 1 to 7 and of the hatching period is shown in Figure 2. Whilst the first stages of embryonic development are passed very quickly, stage 5 lasts for almost six months. During this time no visible changes occur in the embryo and, therefore, it seems to be a stage of delayed development where only basal physiological processes occur. Although the water temperature, which is a major factor for egg development, is still high in September the development of the eggs stops. The onset of stage 5, which is considered a diapause stage, occurs at about the autumnal equinox (Fig. 2).

During the diapause stage the eggs were very resistant to low temperatures and desiccation: the embryos survived 9 weeks enclosed in a block of ice (Fig. 2).

At the middle of March the stage of diapause was terminated, and embryonic development resumed. The hatching period lasted for 22 days, but 50% of the larvae hatched within the first 3 days (Figs 3a, b). Therefore the whole embryonic development lasted for 217 — 239 days at mean temperatures of 10.7 — 10.9° C (cf. Tab. I). Mortality was extremely low: the mean percentage (with 95% confidence limits) was 0.6 ± 1.7% (range 0 — 3%; cf. Tab. I).

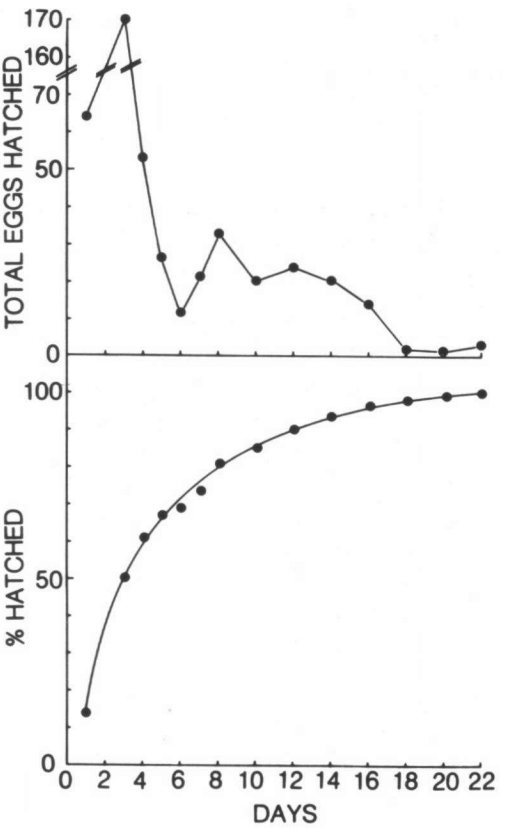

Fig. 3. Hatching in *Sympetrum danae*, using pooled data from 5 experiments cf. Tab I: (a) total number of eggs hatched; — (b) cumulative percentage of eggs hatched.

LARVAL DEVELOPMENT

Without counting the prolarva, 10 larval instars were observed. The temporal distribution of the larval instars is shown in Figure 4. The relationship between mean head width and body length, respectively, and instar number was linear on a semilog scale (Fig. 5) and is given by the regression equation

$$Y = ae^{bX} \quad [1a]$$

Converting to natural logarithms:

$$\ln Y = \ln a + bX \quad [1b]$$

where Y is the mean head width (2.34 Y = body length) and X the instar; the values for the constants a and b (with 95% confidence limits) are 0.42 ÷ 1.02 and 0.23 ± 0.01, respectively. The coefficient of determination (r^2) was 0.99; the regression was highly significant ($P < 0.01$). The average head width increment and body length increment per moult was proportionately constant at c. 27% (Tab II).

Table I
Experimental conditions for embryonic development and hatching in *Sympetrum danae* (Hatching period: days after oviposition)

Number off eggs	Mortality (%)	Water temperature (° C) *mean*	*range*	Date	Hatching period (days)
94	0	10.9 ± 0.7	0 - 28	5.IX.81 - 2.V.82	217 - 239
89	0	10.7 ± 0.8	0 - 26	5.IX.81 - 23.IV.82	217 - 230
98	0	10.8 ± 0.7	0 - 28	5.IX.81 - 29.IV.82	217 - 236
89	3	10.9 ± 0.7	0 - 28	5.IX.81 - 1.V.82	217 - 238
95	0	10.9 ± 0.7	0 - 28	5.IX.81 - 1.V.82	217 - 238

As shown in Figure 6, the relationship between body length (L, mm) and age of the larvae (t, days) is well described by the regression equation.

$L_t = ae^{bt}$ [2a]

Converting to natural logarithms:

$\ln L_t = \ln a + bt$ [2b]

where a and b are constants. The coefficient of determination (r^2) was 0.89, and the regression was highly significant ($P < 0.01$). The same relationship was applicable to the growth of single larvae.

Another expression for the growth of single larvae or of groups of larvae is the mean specific growth rate ($\bar{G}$, % length increment day^{-1}) (method given by HUMPESCH, 1979), which is given by the equation

$\bar{G} = 100b$ [3]

where b is the constant of equation [2]. The mean specific growth rates of all larvae are shown in Table III. It can be seen that $\bar{G}$ ranges from 0.79 to 1.80% with a mean value (with 95% confidence limits) of 1.40 ± 0.16% length increment day^{-1}. Unfortunately it was not possible to rear larvae until emergence took place. One larva which had swollen wing pads already and which died only a few days before emergence lived for 173 days at a mean temperature of 18.7° C.

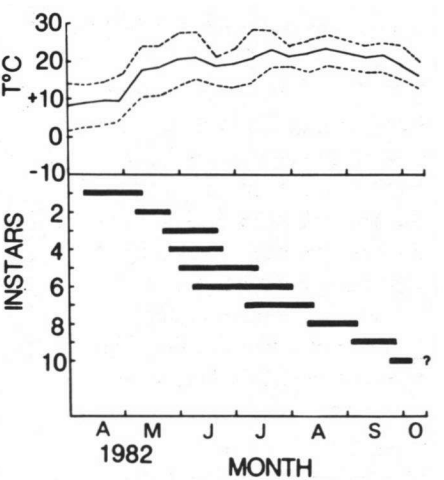

Fig. 4. Temporal distribution of the 10 larval instars of *Sympetrum danae* (Apr. - Oct. 1982). The last final instar larva died shortly before emergence. Values of mean water temperature (and range) are given every 10 days at the top of the figure.

The results have shown that *S. danae* is a univoltine species at the study area.

Table II
Biometrical data (in mm) of the 10 larval instars of *Sympetrum danae* — (Confidence limit: ± 95%)

Instar	Head width	Body length
1	0.5 ± 0.0	1.3 ± 0.0
2	0.7 ± 0.0	1.6 ± 0.1
3	0.9 ± 0.0	1.9 ± 0.1
4	1.1 ± 0.0	2.4 ± 0.2
5	1.2 ± 0.0	2.7 ± 0.1
6	1.6 ± 0.0	3.6 ± 0.1
7	2.1 ± 0.1	4.8 ± 0.7
8	2.8	6.8 ± 0.0
9	3.5	9.1 ± 2.2
10	4.1	11.6 ± 4.8

Table III
Experimental conditions and growth of single larvae of *Sympetrum danae*, showing the body length and head width (in mm) at the start and at the end of each experiment — ($\bar{G}$: mean specific growth rate = % day^{-1})

Instars	Body lenght	Head width	Number of moultings	Date (1982)	Days	Water temperature (° C) *mean*	*range*	$\bar{G}$
1 - 10	1.2-12.0	0.5-4.1	9	10.IV- 3.X	173	18.7±0.9	3-30	1.53
1 - 7	1.2- 5.7	0.5-2.2	6	10.IV-26.VII	105	18.2±1.4	3-30	1.80
1 - 7	1.2- 4.7	0.5-2.1	6	10.IV- 4.VII	85	17.0±1.6	3-28	1.80
1 - 6	1.2- 3.5	0.5-1.5	5	10.IV-26.VI	77	16.6±1.6	3-27	1.72
1 - 6	1.2- 4.0	0.5-1.7	5	10.IV-26.VI	77	16.6±1.6	3-27	1.65
1 - 6	1.2- 3.6	0.5-1.7	5	10.IV-26.VI	77	16.6±1.6	3-27	1.52
1 - 6	1.2- 3.6	0.5-1.7	5	10.IV-20.VI	71	16.3±1.7	3-27	1.80
1 - 6	1.2- 3.4	0.5-1.6	5	10.IV-20.VI	71	16.3±1.7	3-27	1.53
1 - 5	1.2- 3.2	0.5-1.3	4	10.IV-12.VII	91	17.3±1.5	3-28	0.94
1 - 5	1.2- 3.2	0.5-1.2	4	10.IV- 4.VII	85	17.0±1.6	3-28	1.22
1 - 5	1.2- 2.9	0.5-1.2	4	10.IV- 4.VII	85	17.0±1.6	3-28	1.14
1 - 5	1.2- 2.6	0.5-1.2	4	10.IV-26.VI	77	16.6±1.6	3-27	1.13
1 - 5	1.2- 2.9	0.5-1.2	4	10.IV-26.VI	77	16.6±1.6	3-27	1.10
1 - 5	1.2- 2.4	0.5-1.2	4	10.IV-13.VI	64	16.4±1.9	3-27	1.21
1 - 5	1.2- 2.5	0.5-1.2	4	24.IV-26.VI	63	17.5±1.6	4-27	1.54
1 - 5	1.2- 2.4	0.5-1.2	4	24.IV-26.VI	63	17.5±1.6	4-27	1.43
1 - 4	1.2- 2.1	0.5-1.1	3	10.IV-20.VI	71	16.3±1.7	3-27	0.79

The flight period is reported to be from mid-July until the end of September (AGUESSE, 1968). The oviposition activity was highest during the second half of August and the first half of September. The oviposition behaviour was described in detail by SCHIEMENZ (1953) and ROBERT (1959). After the first week of April the first tiny larvae were observed and the first adults emerged in mid-July (AGUESSE, 1968).

DISCUSSION

Corbet (CORBET et al., 1960) pointed out the great influence of the annual fluctuation in temperature on the seasonal regulation of the life cycle of Odonata. The genus *Sympetrum* is of special interest, because two types of overwintering

strategies can be observed in this group: in the first type, which can be found in *S. striolatum,* eggs develop directly, and the winter is spent in the larval stage (CORBET, 1956; ROBERT, 1959), whilst the eggs of *S. vicinum* (BOEHMS, 1971, *S. depressiusculum* (ROBERT, 1959), *S. danae* (ROBERT, 1959) and *S. obtrusum* (KRULL, 1929) have a delayed egg development, and the winter is spent in the egg stage. In *S. sanguineum* both types may occur (CORBET et al., 1960). Although the water temperature in autumn may be favourable for development, the embryos of species with overwintering eggs stop the differentiation processes and enter a stage of delayed development where only physiological processes (= physiogenesis, sensu MÜLLER, 1970) take place. This form of response to environmental changes in the future was called prospective dormancy or diapause. The results in *S. danae* have shown that the onset of egg diapause occurred at photoperiods which can be observed at the autumnal equinox; although not experimentally confirmed, photoperiods of 12 hours may induce diapause development in eggs of *S. danae.*

If so, the prospective dormancy observed can be classified as eudiapause, following the terminology of MÜLLER (1970).

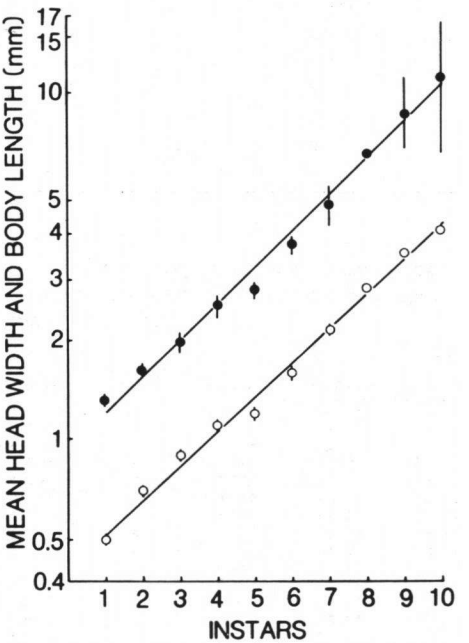

Fig. 5. Relationship between mean body length (●) and mean head width (○) and larval instar, using data from 17 animals (cf. Tab. II). Each dot is the geometric mean with 95% confidence limits.

Laboratory experiments on four species of *Lestes* (SAWCHYN & CHURCH, 1973) have shown that diapause development is completed most rapidly at 10° C. Diapause development in the field was terminated by the end of October or the end of November, but by then very low temperatures below 10° C and short day photoperiods below 12 hours inhibited subsequent embryogenesis (SAWCHYN & CHURCH, 1973). The same thermal optimum of 10° C for completing diapause development is reported by CORBET et al. (1960) for *Lestes sponsa* and by SCHALLER (1972) for *Aeshna mixta;* the thermal optimum for *S. vicinum* was 14 — 18° C (BOEHMS, 1971). Therefore temperature and photoperiod show an interaction in the regulation of diapause in these species: prediapause development is accelerated by higher temperatures and by a long day

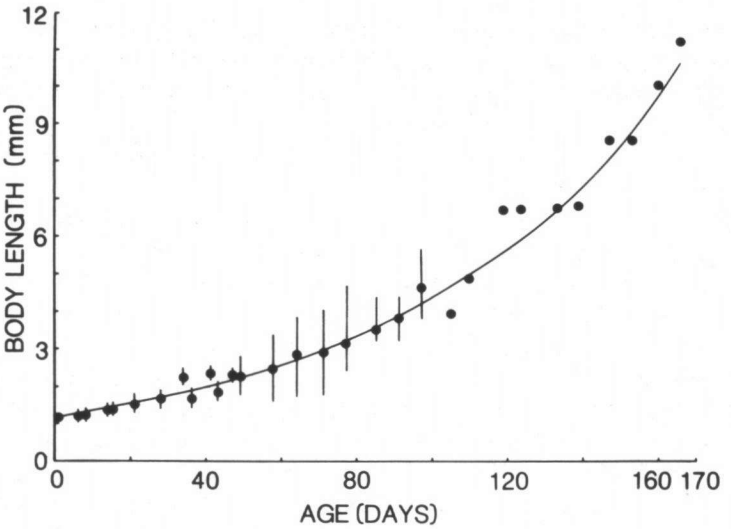

Fig. 6. Relationship between mean body length (mm) and age (days) of 17 larvae of *Sympetrum danae* in the field. The exponential curve (eqn 2) is drawn from: $1.15e^{0.013t}$. The dots are geometric means with range.

photoperiod. The diapause stage is initiated by a short day photoperiod (less than 12 hours) and is terminated most rapidly at lower temperatures; post-diapause development is induced by long day photoperiods in some species and has a positive temperature coefficient.

Unfortunately, most workers dealing with the problem of diapause in eggs of Odonata did not pay attention to the embryological changes. Therefore only a little information is available on the stages where diapause takes place. In *S. danae*, diapause occurred immediately before blastokinesis, as in *Lestes congener* (SAWCHYN & CHURCH, 1973; *L. disjunctus*, *L. unguiculatus* and *L. dryas* diapaused late in embryogenesis when the embryo was almost fully formed (SAWCHYN & CHURCH, 1973). BOEHMS (1971) reported that both types were observed in *S. vicinum*: eggs laid early in the oviposition period diapaused late in embryogenesis whilst eggs laid in autumn diapaused in a pre-revolution stage. Therefore the diapause stage seems to depend also on the date of oviposition and this may be why *L. congener* differed from the other *Lestes* species studied by SAWCHYN & CHURCH, (1973), because *L. congener* is a very late emerging species. This indicates that further work is necessary on factors affecting the diapause in Odonata and that embryonic development in *S. danae* has to be studied in eggs laid at different dates during the whole oviposition period.

The results in *S. danae* have shown that the hatching is well synchronised, and

50% of the eggs hatched within the first three days. Similar observations were made by CORBET (1962) in *L. sponsa*, by BOEHMS (1971) in *S. vicinum* and by SCHALLER (1972) in *Aeshna mixta*. It seems that eggs of all species having a diapause stage hatch in a synchronised fashion.

The number of instars observed in *S. danae* resembles the findings of GARDNER (1951). SCHIEMENZ (1953) has reported 10 instars, too, while ROBERT (1959) has observed only 8 instars in Switzerland. Other investigations in the genus *Sympetrum* show that the number of instars ranges from 8 instars in *S. sanguineum* (ROBERT, 1959) up to 12 instars in *S. striolatum* (CORBET, 1951) without counting the prolarva. CORBET (1956) has pointed out that there may be different numbers of instars within one species, especially when larvae were reared in captivity. This was also reported by other workers, e.g. KRULL (1929), SCHALLER (1972), PELLERIN & PILON (1977), RIVARD & PILON (1977) and WARINGER (1982). Until now, no sufficient explanation for this variation can be given, and further work is necessary.

In *S. danae* the average body length increment and head width increment per moult was proportionately constant at c. 27%, and therefore Dyar's rule was applicable. The percentages were also calculated from the data given by GARDNER (1951) and ROBERT (1959): the increments per moult were 35% and 40%, respectively. It seems that better climatic conditions have somewhat accelerated larval growth in both cases (Gardner, for example, kept his animals indoors). Dyar's rule is also applicable to other species of Odonata (cf. WARINGER, 1982).

There was some variation between the mean specific growth rates within one species and between different species of *Sympetrum* (Tab. IV) which may be due to variation in temperature and in food quality and quantity, as found in other freshwater animals, e.g. amphipods (SUTCLIFFE et al., 1981) and isopods (MARCUS et al., 1978). For nine European odonate species, reared under field conditions, growth rates of 0.7 to 4.1% length increment day^{-1} have been

Table IV

Mean specific growth rates ($\bar{G}$: % length increment day^{-1}) for some *Sympetrum* species, computed from literature

Species	No. annual generations	$\bar{G}$, % day^{-1}	Reference
danae	1	1.4+	GARDNER, 1951
		3.0	ROBERT, 1959
		1.4*	this paper
vicinum	1	5.6+	BOEHMS, 1971
depressiusculum	1	3.4	ROBERT, 1959
sanguineum	1	3.4	ROBERT, 1959

+ reared in the laboratory; * mean value

calculated from published data (WARINGER, 1982), and the growth rates obtained for *S. danae* are clearly well within this range. Unfortunately there is a lack of biometric data, and further investigations and the rearing of larvae are necessary to understand the growing patterns in Odonata.

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