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FREEZING TOLERANCE AND DROUGHT RESISTANCE OF *SOMATOCHLORA ALPESTRIS* (SELYS) LARVAE IN BOREAL TEMPORARY POOLS (ANISOPTERA: CORDULIIDAE)

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Larval development of *S. alpestris* was studied in a semipermanent pond and 2 temporary pools in boreal Sweden. In the pond, several cohorts co-occurred with a life cycle of 3 or 4 years. The temporary pool populations were very small and included only a single larval cohort. The presence of nearly fullgrown larvae after drought periods as long as 3 months documented survival in the dry sediment. As the studied pools freeze solid during winter, the larvae must have survived for about 6 months in ice or frozen sediment. The long larval development of *S. alpestris* is unique for insects in temporary pools. It is predicted that the slow larval development characteristic for many odonates, and not the direct mortality from extreme abiotic conditions, limits their success in exploiting this environment.

INTRODUCTION

Odonate larvae occur in most kinds of freshwaters, including those of high mountains and semiarid areas (CORBET, 1962; ASKEW, 1988). Larvae of some species tolerate freezing (e.g. SAWCHYN & GILLOT, 1975, while a few others live in semiaquatic habitats (CORBET, 1980; ASKEW, 1988).

Species of many different dragonfly genera are regular inhabitants of temporary pools, and the exploitation of this environment for larval development is achieved in two major ways (WIGGINS et al., 1980): (1) oviposition in summer in dry basins followed by overwintering of eggs or larvae and larval development in spring, or (2) oviposition in water in spring followed directly by larval development and adult migration to warmer regions for overwintering. A third possibility, not mentioned by WIGGINS et al. (1980), is a prolongation of the larval development, spanning over periods of both drought and complete freezing.

Somatochlora alpestris (Sélys) is a boreo-alpine species that occurs from northern Scandinavia to Japan and in the mountains of Central Europe. *Sphagnum* bogs, tarns and small lakes are the major larval habitats (VALLE, 1938; ASKEW, 1988). Here we present life history data from one semipermanent pond and two temporary pools in northern Sweden.

STUDY AREA

The three water-bodies studied are situated in the northern Swedish province of Västerbotten, about 25 km NW of Vindeln (64°25'N, 19°30'E), at 200-220 m ASL. The area belongs to the "middle boreal" vegetation zone (AHTI et al., 1968), being covered mainly by coniferous forests dominated by pine (*Pinus sylvestris* L.). Snow covers the ground from about late October to late April.

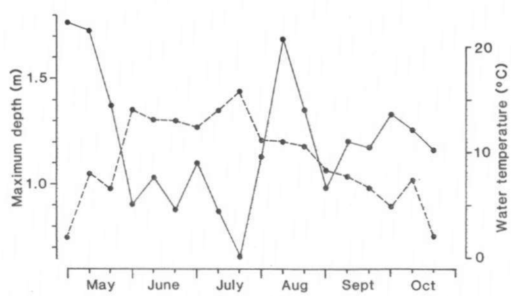

Fig. 1. Maximum depth and water temperature (broken line) in the semipermanent pond in 1987.

The semipermanent pond lies in a natural semicircular depression between the small mountain Skärtråsberget and the lake Västra Skärträsket. A small temporary stream enters this pond that has no outlet. The seasonal water level fluctuations are very pronounced. The maximum depth of the pond is about 2 m, and then the diameter reaches about 35 m. The pond freezes solid in the winter, and it is filled with snow melt in spring. In dry summers, with a low water-table, the pond may dry out completely. The pond is surrounded by willows and partially with a marginal belt of *Deschampsia* grass. Below this belt there are dense carpets of *Drepanocladus* moss with fragmented stands of *Carex vesicaria* L. and tussocks of *C. juncella* (Fr.) Th. Fr. The central part of the pond is dominated by relatively dense stands of *Sparganium* spp., *Hippuris vulgaris* L. and *Potamogeton natans* L. Water temperature and maximum depth at ten day intervals in 1987 are shown in Figure 1. During this exceptionally cold and wet summer the pond was never less than 0.7 m deep, and the maximum temperature was 15.7° C.

Temporary pool A lies in a shallow depression on a glade near a road about 0.5 km S of Gladaberg. The pool basin was probably formed at the time of the construction of a nearby landing strip in 1965. The maximum size of the pool is about 8x4 m, with a corresponding depth of 0.4 m. The pool normally dries out completely

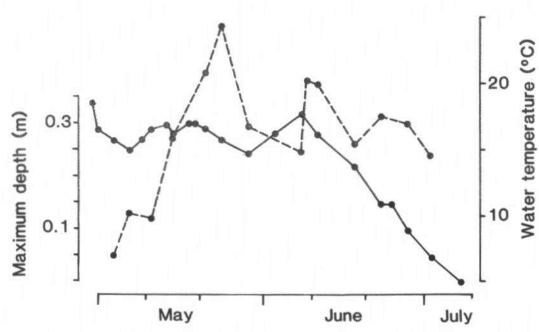

Fig. 2. Maximum depth and water temperature (broken line) in temporary pool A in 1989.

in July or August, but during wet summers like that of 1987 it is permanent. Water normally accumulates during the autumn and the pool freezes to the bottom in the winter. Maximum depth and water temperature were studied at five day intervals in 1989 (Fig. 2), and during this dry summer the pool was dry from early July to October. Occasional heavy rains during this period sometimes caused water to stay in the basin for a few days at most, and in early November water accumulated prior to freezing. The highest temperature recorded was 24.3° C. The pool bottom consists of clay covered with *Drepanocladus* moss. The macrophyte vegetation is dominated by *Equisetum palustre* L. and *Alopecurus aequalis* Sobol.

Temporary pool B lies near the small village of Gottland in a dammed up ditch along a forestry road constructed in spring 1986. The maximum size is about 40x2 m with a corresponding depth of 0.4 m. No periods of drought were observed in 1987 or 1988, but in 1989 the pool dried out completely in late July. Some water reoccurred in late September after a heavy rain, but subsequently the pool was dry until mid October. In early November, some water accumulated prior to freezing. In 1988, ice covered the pool definitively on 18 October, and on 4 March 1989 the bottom sediment was frozen under 0.2 m ice and 0.7 m snow. The highest temperature recorded in 1989 was 19.2° C. The bottom substrate is minerogenic, with scattered stones on silt, and the major part of the bottom is devoid of vegetation. In one end of the pool, however, a slightly deeper part is covered by *Sphagnum* moss. *Somatochlora* larvae were only found in this end of the pool.

MATERIAL AND METHODS

In the semipermanent pond, odonate larvae were sampled at 18 occasions at ten day intervals from 30 April to 25 October 1987. At each occasion five samples were taken with a hand-net (mesh size 0.8 mm) used intensively for one minute to cover an area of four square feet. During sampling the bottom material was stirred up with the foot. The samplings were restricted to the shallow pond margin (depth 0.3 m or less), and normally in dense vegetation. Water temperature was measured 5 cm below the water surface about 2 m from the pond margin.

The temporary A pool was observed irregularly from 1982 to 1988, and occasionally qualitative net samples were taken. Odonate larvae were found only on 27 June 1985 and on 20 May 1986. In 1989, larvae were sampled at ten occasions at five day intervals from 30 April to 28 June. Five net samples were taken at each occasion as in the semipermanent pond. However, the time was reduced to 30 s per sample and a smaller net frame was used. The samples were distributed over the entire pool. An unstandardized net sample was taken on 20 September after a thunderstorm. Water temperature was measured as above, but in the middle of the pool.

The temporary pool B was observed irregularly during 1987 and 1988. In 1989, unstandardized net samples were taken occasionally from 19 May to 14 June, and on 20 and 24 September. On 23 July and 10 August, when the pool had dried out, odonate larvae were looked for under stones.

All larvae sampled were preserved in 70% ethanol, and the material is kept in the collection of the senior author. Odonate larva identification followed SCHMIDT (1951) and SAHLÉN (1985). Larval instar determination followed THOMPSON (1975). Habitat data of *S. alpestris* from various localities in northern Sweden are also presented.

RESULTS

In total, 36 *Somatochlora alpestris* larvae were collected in the semipermanent pond. The total number of net samples was 90. Other odonate larvae recorded in this pond included *Coenagrion hastulatum* (Charp.), *Aeshna caerulea* (Ström), *A. juncea* (L.), *Leucorrhinia dubia* (Vander L.) and *L. rubicunda* (L.). The seasonal distribution of larval instars of *S. alpestris* in this pond during 1987 is shown in Figure 3. The first instar occurred on 24 July and 13 September. The final instar was present on 6 June, 24 July, 3 and 13 September. At least three larval cohorts were present in the pond this year.

In the temporary A pool, one *S. alpestris* larva each of the instars F-5 and F-3 were found on 29 May 1986. In 1989, occasional larvae of the following instars were collected on these days only: 9 May, F-2; 8 June, F-1; 18 June, F-1; 20 September, F-0. In total, only four larvae were found in 51 net samples this year. The mature larva found on 20 September evidently had survived without access to water since early July. The larva showed normal leg movements when collected. Only a single larval cohort was seemingly present this year. Single larvae of *Coenagrion hastulatum* and *Aeshna caerulea* were found in 1986, and *A. caerulea* and *A. juncea* larvae were obtained in 1989.

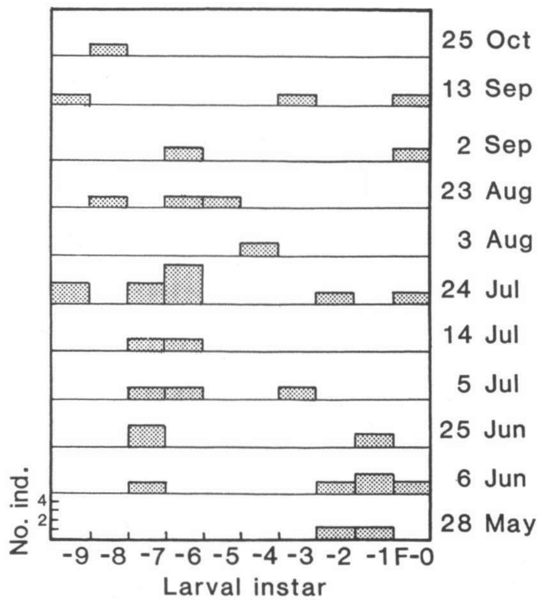

Fig. 3. The seasonal distribution of larval instars of *Somatochlora alpestris* (Sélys) in the semipermanent pond in 1987. Pooled data from five net samples at each occasion. — [F-0 = ultimate instar; — -1 = penultimate instar etc.].

In temporary pool B, a *S. alpestris* penultimate instar larva was found on May 1989. On 23 July a large larva was observed under a stone on the moist bottom of the dried out pool. The larva was covered with clay and displayed very slow leg movements when disturbed. On 10 August two large larvae were observed under identical conditions. After water had reappeared on 20 September a final instar larva was captured on 24 September. The meagre result of only one larva in spite of an intensive netting in a small area showed the very small size of this population. No other odonate larvae were found in this pool.

Out of 88 lentic and lotic waters sampled in the provice of Västerbotten *S. alpestris* was found in 13 situated from 0-780 m ASL. All these localities represented lentic waters and in nine of them *Sphagnum* moss was present. Nine of the localities had a water area not reaching one hectare, and all except the three waterbodies described above plus another semipermanent one were classified as permanent.

DISCUSSION

S. alpestris larvae seemingly have a wide tolerance to variations in abiotic factors. Drought resistance has recently been reported for Central European populations (STERNBERG, 1989), and is here documented in northern boreal habitats.

The ability to withstand drought has been noted for some species from other families. TILLYARD (1910) noted that larvae of *Synthemis eustalacta* (Burm.) could survive in dry sand for ten weeks. FISCHER (1961) found that *Coenagrion hastulatum* larvae were able to survive complete drought in a pool for four weeks and laboratory experiments showed a survival for 12 days in dry glass vessels. MONTGOMERY (1972) reported that larvae of Zygoptera, Aeshnidae and Libellulidae survived elimination of water from their habitat during the summer, and, in Japan, the larval *Lyriothemis pachygastra* was recorded to hibernate in dried up swamps (ARAI, 1983). *C. armatum* (Charp.) and *C. lunulatum* (Charp.) survived for 3-5 days in dry petri dishes (ZAIKA, 1977; as *Agrion armatum* and *A. vernale*). *Libellula quadrimaculata* L. larvae survived drought for 40 days in the laboratory under conditions simulated to be natural (ZAIKA, 1977). As *S. alpestris* has a life cycle covering three or four years at our sites (Fig. 6), and late instar larvae were found after several dry periods in the temporary pools, *S. alpestris* larvae must have a high drought resistance.

There are several reports on both Zygoptera and Anisoptera larvae surviving ice cover or freezing (CORBET et al., 1960; DABORN, 1971; MONTGOMERY, 1972; SAWCHYN & GILLOT, 1975; BEUTLER, 1989). Freezing tolerance of *S. alpestris* larvae has been inferred from studies of Central European populations (STERNBERG, 1989). In our two temporary pools, that both freeze to the bottom, the overwintering of *S. alpestris* larvae provides strong evidence for freezing tolerance. Normally, the larvae have to spend about five months in the frozen pools each winter.

The first instar larvae appeared on 24 July. Several odonates have an egg diapause (CORBET, 1980), but this is yet unknown among the *Somatochlora* species. As the flight period in northern Sweden begins in mid June (VALLE, 1938; B. Holm, pers. comm.), and eggs take 4-6 weeks to hatch (d'AGUILAR et al., 1986) it is likely that the eggs of *S. alpestris* hatch the same year as they are deposited.

We have no data on egg laying behaviour in *S. alpestris* from our sites. However, observations from Central Europe (WILDERMUTH, 1986, 1989) showed that eggs were deposited over water areas. *Sympetrum* females are known to lay eggs where no water is present (CORBET, 1962), but this behaviour has not been documented in *Somatochlora*. The temporary pools become water filled during heavy rainfalls in summer, and these short periods may be crucial for the stimulation of egg laying here. Oviposition in these pools could also be restricted to unusually wet summers without drought periods. The presence of only a single cohort in both our temporary pools supports this view. The 1987 summer was very wet (A.N. Nilsson, unpubl.) and probably the larvae collected in 1989 came from eggs laid the same year.

As the two genera, *Lestes* and *Sympetrum*, both develop in temporary pools with drought periods as long as eight months (including winter), WIGGINS et al. (1980) classified them as summer recruits ovipositing in the dry basin and overwintering as eggs or larvae. However, as both these genera overwinter as eggs and not as larvae (CORBET, 1980), the larval stage should not be included in the drought resistance of these species. The prolonged larval development, covering at least three years, including drought and freezing tolerance, here documented in *S. alpestris*, shows that odonates in temporary waters have a third strategy not mentioned by WIGGINS et al. (1980). Since boreal temporary pools normally have water in the autumn and freeze to the bottom in winter (NILSSON, 1986; p. 394, it is difficult to include the strategy of *S. alpestris* in the classification of Wiggins et al. *S. alpestris* differs from the "overwintering summer recruits" of WIGGINS et al. (1980) as the adults probably need water for oviposition, the larvae overwinter several times in the frozen bottom substrate, and an egg diapause is probably absent. Consequently, the adaptive features shown in some *Lestes* and *Sympetrum* species inhabiting temporary pools listed by WIGGINS et al. (1980, p. 145) should not be necessary for odonates exploiting this environment.

Larval development in temporary pools may be viewed as a strategy of predator avoidance. Consequently, these larvae should not need to reduce their activity as an antipredator response (SIH, 1987), and instead display fast growth in order to use the relatively short period with a high habitat favourability. Odonate larvae can be separated into two groups according to their methods of searching prey and their growth rates (JOHNSON & CROWLEY, 1980). Those with a fast life style, like *Lestes* and *Sympetrum*, show a high activity mode (PRITCHARD, 1965) and a fast growth rate (WIGGINS et al., 1980). These genera, however, are not regular inhabitants of boreal temporary pools in North Europe, in which their absence may be due to their relatively high temperature demands. Larvae with a slow life style, like those of the Corduliidae, are cryptic sit-and-wait predators (PRITCHARD, 1965), and they have a growth period covering several years (d'AGUILAR et al., 1986). This strategy makes it possible to coexist with predators because of a concealed way of living (JOHNSON & CROWLEY, 1980; SIH, 1987). We predict that the slow lifestyle of larvae of *S. alpestris* and related odonates limits the exploitation of temporary pools as the prolonged larval period may be connected with a too high mortality of this stage.

As populations here must be small, extinction rates should be high, and populations probably receive recruits from nearby populations of more permanent waters. However, our data do not show if the larval development actually was longer in the temporary pools than in the semipermanent pond.

Another important restriction for the use of temporary water may be the inability to oviposit during the dry phase, that often coincides with the flight period. This restriction may explain the presence of single cohorts in the temporary pools. Single cohorts could also result from a high mortality of young larvae during dry periods that fail to occur in some years. It is important to note that the larvae of *S. alpestris,* and maybe other species, are not excluded from temporary pools by the direct impact of abiotic factors only.

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