A FLEXIBLE LARVAL DEVELOPMENT STRATEGY IN *SIPHLONURUS AESTIVALIS* EATON EXPLOITING AN UNSTABLE BIOTOPE

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ABSTRACT

The "Grüner See" near Tragöss (Styria, Austria) is one of the largest karstic waterbodies of the eastern alps. The size of the aquatic environment changes dramatically annually being completely dry and a lake with a surface area of 6.5 ha. As long as there is water in the basin – complete drying of the lake is rare – the waterbody is populated with *Siphlonurus aestivalis* without overcrowding and with emergence over the whole period suitable for adults. Based on observations from the natural population and an experimental analysis of larval development, this is achieved by a combination of delayed hatching, variable growth rates and predetermined larval development programmes.

INTRODUCTION

The "Grüner See" near Tragöss (Styria, Austria, 15°3'34" e.L., 47°32'40" n.B., 757 m a.s.l.) is one of the largest karstic water bodies of the eastern alps. A detailed description is given in Bretschko (1966). A small channel with a depth of only 3 m connects two basins, otherwise completely separated. The morphometric data are set out in Table 1. Because of the shallowness of the channel the two basins are connected by surface water for about 10 weeks per year only. Below the periodically flooded grassland the lake bottom consists of soft mud in the eastern basin (BII), densely overgrown by a moss (*Cinclodotus fontinaloides* (HEDW.) BEAUV.) and of rocks and gravel in the western basin (BI) except in the deepest parts where soft mud predominates.

The highly karstic nature of the catchment alters size and shape of the lake rapidly, frequently and dramatically: between the extremes of complete drying and total inundation of the low lying parts of the valley. In low water periods the degree of inundation differs between the basins, since basin II is shallower than basin I (Table 1). Six hydrographic stages may be defined:

1. The low lying parts of the valley are flooded.
2. The lake is filled up to its shore line as defined in Table 1. In shallow bays, grassland is inundated.
3. Both basins are filled but disconnected.
4. Both basins contain small and shallow bodies of water.
5. Basin I contains a small and shallow body of water, basin II is dry.
6. Both basins are dry.

The hydrographic cycle starts in May after the snow melt begins in the catchment and within a few days the lake is completely filled (stage 2). In most years stage 1 occurs for a few weeks. From July until late fall/early winter the water level falls. In the case of long and heavy rains (and snow in the mountains) this tendency may be

Table 1. Morphometric data

	Western Basin (BI)	Eastern Basin (BII)	Total Lake
Area (km^2)	0.046	0.019	0.065
Length (m)	349	198	547
Breadth-Max (m)	323	171	323
Breadth-Mean (m)	131.8	96.0	118.8
Depth-Max (m)	8	6.5	8
Depth-Mean (m)	4.3	4.2	4.2
Volume (10^3 m^2)	196	80	276
Shore line (m)	1380	640	2020
Development of shore line	1.815	1.309	2.234

interrupted and stage 2 recurs for short periods. For most of the time stage 3 is typical of summer and early fall. Stage 5 is normal in late fall and winter. In some years stage 4 prevails, but only rarely are both basins dry (stage 6).

Except for a few weeks in October/November the lake contains larvae and/or nymphs of *Siphlonurus aestivalis* Eaton at every time and at nearly every place, as long as there is any water in the basin. In periods with more water the slopes and littoral zones are preferred. The populations of the two basins are nearly completely separated in their larval stages. Because of their synchronous larval development, they intermingle as adults. The karstic hydrography rapidly and frequently changes the environment of the larval population in area as well as in quality: the food bearing substrate varies between newly flooded grassland or thick moss stands and bare gravel and mud. The temperature conditions experienced by a single immature individual is also variable. Larger and deeper bodies of water do not deviate greatly from the mean spring temperature of 7°C (Bretschko 1966), but shallow littoral areas vary depending on the prevailing weather. Figure 1 shows water temperatures taken during sampling at noon at a depth of about half a metre. Shallower areas are warmer, but 15°C is seldom exceeded. The highest temperature measured was 16.2°C. Close to inundated springs temperatures were always near 7°C, even in warm shallow areas. Thus, vagile littoral animals like *Siphlonurus* larvae experience daily and, because

of their movements, irregular temperature differences nearly as large as their range of tolerance for constant temperatures (Bretschko 1985).

The instabilities of the environment, regular on an annual basis but with irregularities between years and within a year are fully met by the *Siphlonurus* population: whenever the biotope is suitable for mature or immature stages, it is exploited. The main basis for this achievement is the combination of different developmental strategies (Bretschko 1985).

METHODS

Field samples have been taken with a hand net (mesh size: 0.25 mm) in the littoral zone in water depths of 20–100 cm. Samples were not quantita-
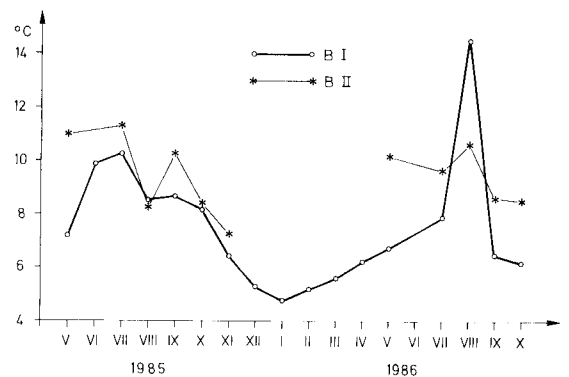

Fig. 1. Water temperatures at noon. Depth of water: 0.5 m.

tive since population size distribution is the parameter of interest rather than absolute abundance. Samples were fixed with formalin, sorted with the aid of a stereomicroscope, and preserved with 70% ethanol. Body length (to the nearest 0.25 mm in larvae < 5 mm and to the nearest 0.5 mm in larvae > 5 mm) is taken from the front edge of the head capsule to the base of the terminal filament. Maturity was assessed using wing-pad development (Bretschko 1985), with five classes being recognised (Table 1).

For laboratory studies an experimental design similar to that described by Bretschko (1985) was used. Individual larvae were kept in still water in round glass jars (diam. 40 mm) at a temperature of 7.5°C (± 0.3) with continuous light. Each jar contained a short stem of green *Cinclidotus* which served, together with its periphyton, as fresh food, but was mainly provided as a source of oxygen and a substrate for the animals. The major food was artificial pellets normally used for trout fry (org. C: 266.99 mg g^{-1}; N: 91.5 mg g^{-1}; P: 11.5 mg g^{-1}; C/N: 2.92). Every third or fourth day food and water was renewed and length and maturity of the larvae measured. For length measurements a sheet of graph paper was placed underneath the jar and length was recorded when the larva was straight. The precision of the measurement was relatively poor (precision was

5.4 ± 1.1% and 8.1 ± 2.1% for larvae smaller and larger than 5 mm, respectively) but handling was minimized. After each ecdysis the animals were placed in a new jar.

Some protozoans (*Epistylis nympharum, Vorticella convollaria*) are to be found frequently growing on larvae in nature. In the culture, the infestation was often intensified. But even when infestations were extremely dense neither mortality nor development was significantly influenced.

Because length and maturity development is synchronous only length was used for interpretation. All three characteristic phases of the sigmoid growth-curve can be approximated by a linear regression. The first, flat phase (α) may be missing, The second, steep phase (β) ends with the last larval moult (Bretschko 1985) and the third phase (γ) covers the period between the last larval moult and the emerging subimago and is not analysed here. Mean length of the natural population over time (Fig. 2) reflects the shape of the growth-curve.

RESULTS

The *Siphlonurus* population of "Grüner See" was first studied in 1960 and 1961 (Bretschko 1966). During winter basin I contained water in both years, but basin II in 1961 only. In spite of this

Table 2. Definitions of maturity-classes

| Name of maturity class	Description
Larvae sensu strictu (L)	no wing pads
Young nymphs (YN)	front wing pads are small buds or reach the end of metanotum
Halfgrown nymphs (HN)	front wing pads reach between half way along first abdominal segment and half way along second abdominal segment
Fullgrown nymphs (FN)	front wing pads reach between end of second abdominal segment and beyond
Emerging nymphs (EN)	wing pads laterally positioned and thick and black
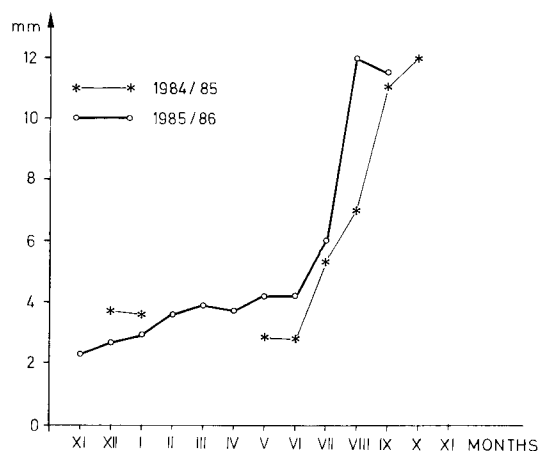
Fig. 2. Mean length of the larval population of basin I on time.
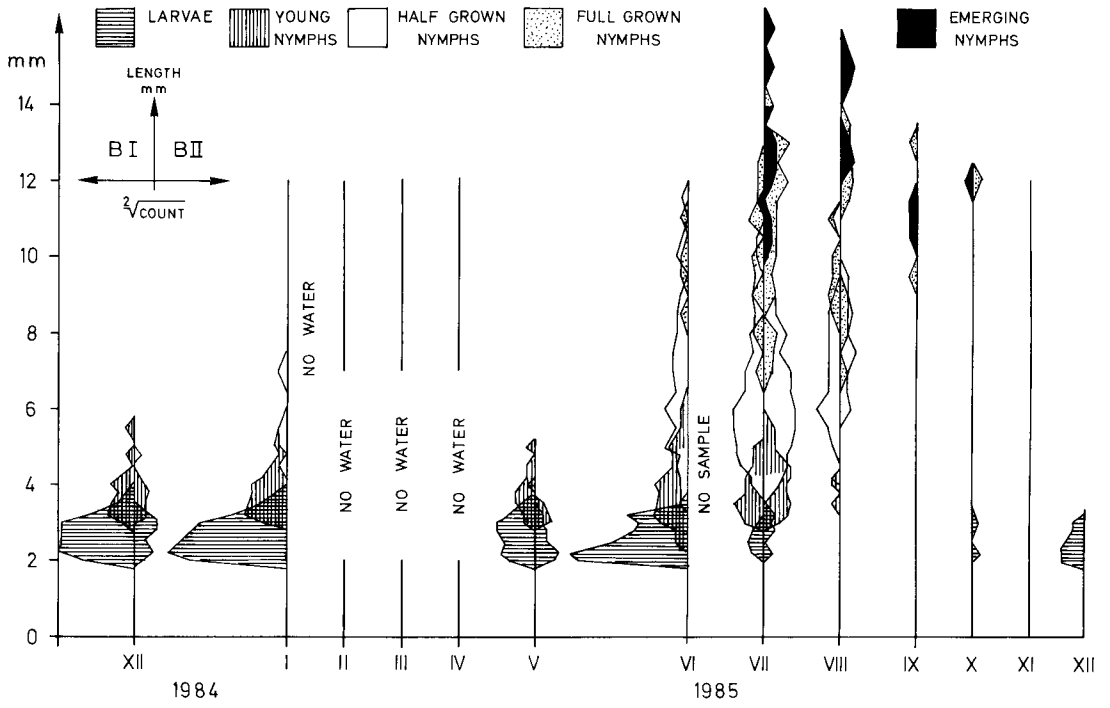
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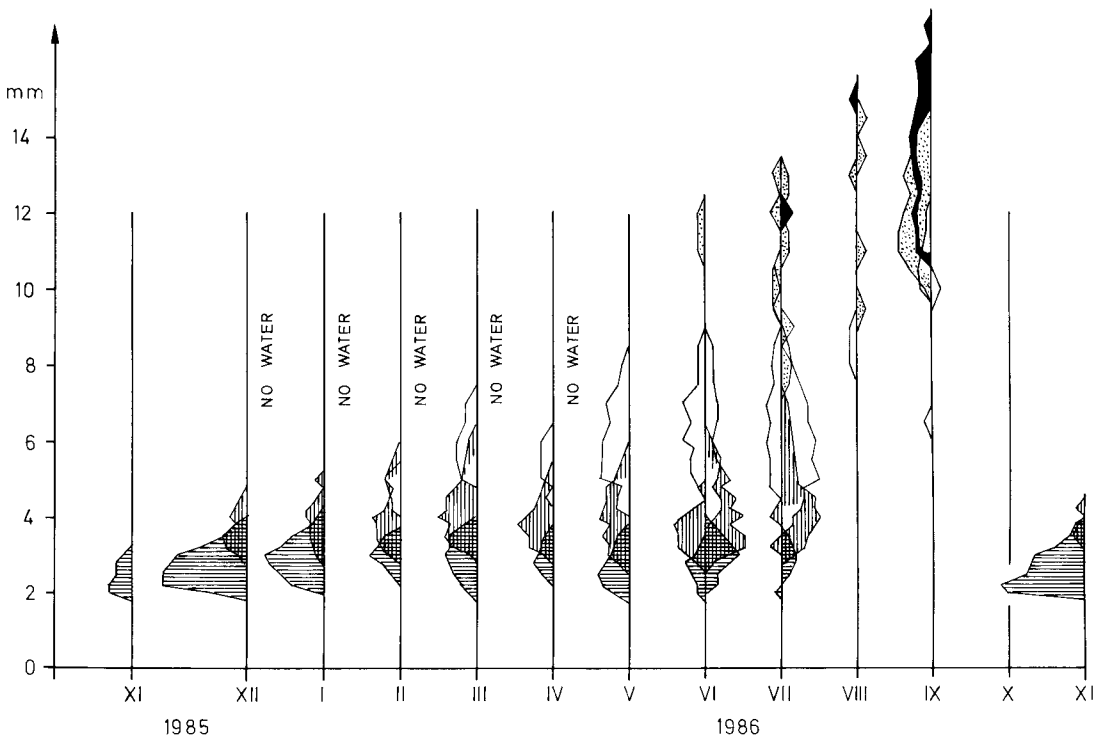
Fig. 3. The structure of the population 1984/85.

Fig. 4. The structure of the population 1985/86. Captions see Fig. 3.

difference, larval development was nearly the same in both basins and in both years: most eggs laid during summer did not hatch before the following spring. Only very small numbers of larvulae have been found in May, June and July and only in the open water plankton. In the present study larvulae were not collected at all. Larval development was accomplished in two to three months with imagines found from June until September. Some eggs hatched in early fall, but larval development ceased in winter and recommenced in spring. This part of the population perished if the basin dried in winter.

The studies done in 1984/85 and 1985/86 confirmed the earlier findings (Figs 3, 4). In winter 1985 both basins dried which gave the opportunity to test the described life history. The overwintering larvae perished in both basins so that the structure of the population was the same in both basins for all maturity classes (Fig. 5). In the fol-

lowing year (1985/86) only basin II dried in winter, showing the influence of the overwintering larvae for the spring population (Fig. 5). Because of the hydrographic differences the relative abundances of larvae ss differ greatly between the basins. A shift of about two months is discernable in the "young nymphs" class. No differences are to be found in half and fullgrown nymphs (Fig. 5). Although one group overwintered as eggs and the other as larvae, which lead to very different starting maturities in spring, this is compensated for by mechanisms controlling larval development. Although an interrupted flight period and adults of different sizes could be expected (e.g. group B4 in Landa 1968) this was not apparent in either the field observations (Figs 3, 4, Bretschko 1966) or the experimental cultures (Fig. 6).

Bretschko (1985) studied the suppressed growth of the overwintering larvae, at constant temperatures (2.5, 5.0, 7.5, 10.0°C) and light regimes (24/0, 16/8, 8/16, 0/24). Neither light nor temperature significantly changed the natural growth pattern, but larvae caught in November reacted differently to those caught in January. Under all conditions the phase of the growth curve was steeper in January larvae than November larvae, indicating that the natural growth pattern is programmed over the growth rate of the phase. In the natural larval winter population growth rate is increased by a parameter other than those offered in the experiment, possibly increasing day length and/or food.
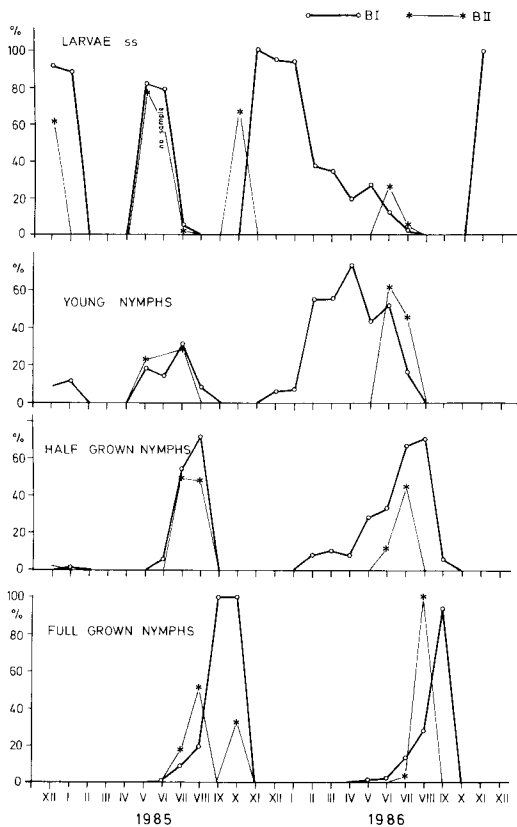

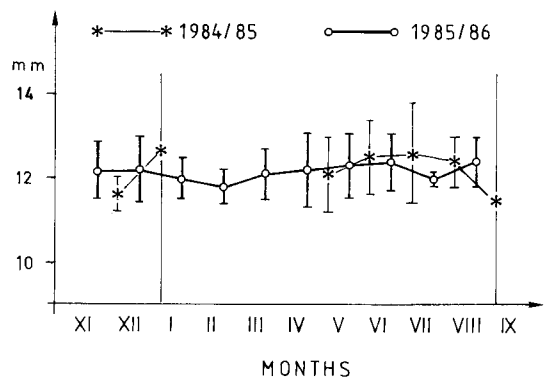Fig. 5. Relative distribution of four maturity classes for the generations 1984/85 and 1985/86.

Fig. 6. Size of emerging nymphs, collected each month as larvae-ss and developed in the laboratory. Vertical bars: 95% Confidence interval.
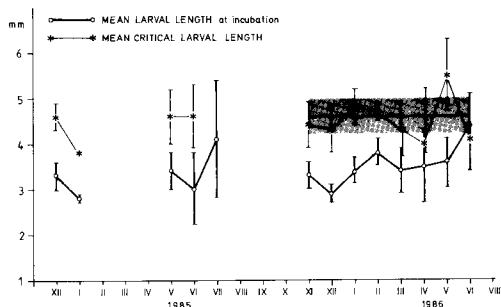
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Fig. 7. Mean larval length at time of incubation and mean critical larval length at time when phase α ends and phase β starts. Shaded area: confidence interval around the grand mean (horizontal line). Vertical bars: 95% Confidence interval.

Fig. 9. Moulting frequency in days. For captions see Fig. 7.

To test this hypothesis larvae were caught at the beginning of every month and incubated (7.5°C, continuous light). Whenever possible, ten larvae not larger than 3.5 mm were selected (Fig. 7). The growth rate was constant or at least not significantly different for all larvae in the β phase. The grand mean was 0.099 ± 0.06 (generation 1984/85) and 0.095 ± 0.007 (generation 1985/86). The difference is not significant. In the α phase growth rates increased significantly from 0.012 ± 0.007 (November larvae) to 0.045 ± 0.006 (March larvae, Fig. 8). Larvae collected in April and later originate from overwintering eggs. Besides high individual variations, the average growth rate is in the range of maximal mean growth rates found for the β phase for all larvae. The mean maximal length to be achieved in the α phase was 4.6 ± 0.4 mm (Fig. 7). At this point,

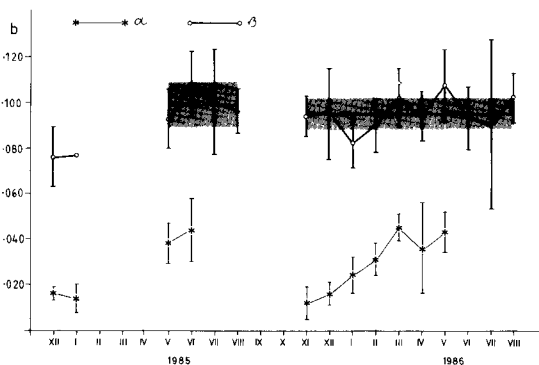*Siphlonurus* matures from larvae to young nymphs. As soon as this length and maturity is reached the α phase is terminated and the phase β commences. In larvae hatched from overwintering eggs and with sizes studied here, the α phase may be missing altogether but development is never completed in the α phase alone.

Moulting frequency was constant in the β phase with grand means of 12.1 ± 1.0 days (1985) and 12.8 ± 0.3 days (1985/86, Fig. 9). In the α phase moulting frequency increased from 15.7 ± 2.6 (November larvae) to 10.2 ± 3.8 days (March larvae). In larvae caught in April or later no further increase was detected. This pattern parallels the growth pattern (Fig. 8) but is not significant because of very high individual variance.

All other parameters of development, such as moult number (Fig. 10), phase duration (Fig. 11)
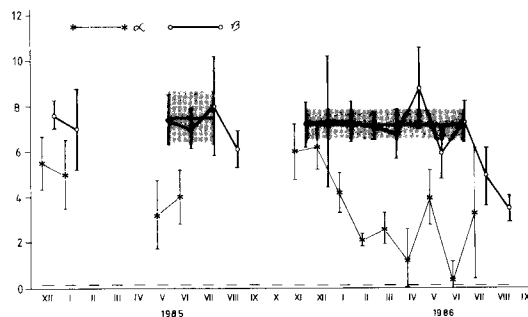

Fig. 8. Growth rates as regression coefficient "b" for phase α and β. For captions see Fig. 7.

Fig. 10. Number of moults. For captions see Fig. 7. Grand mean (Phase β): 7.5 ± 1.2 (1985) and 7.2 ± 0.7 (1985/86).
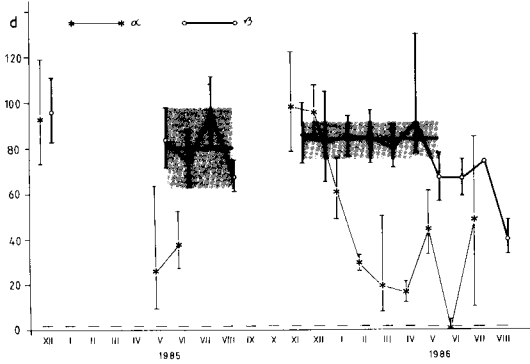
Fig. 11. Duration of phases in days. For captions see Fig. 7. Grand geometric mean (phase β): 79.3 (63.0 $\pm$ 99.6) and 83.1 (74.5 $\pm$ 92.8) for 1985 and 1985/86, respectively.

and total time for development (Fig. 12), are consequences of those discussed above. Larvae caught in late spring and summer are already larger when incubated and therefore cause deviations and irregularities (Figs 10, 11).

DISCUSSION

Although Pleskot identified the *Siphlonurus* population as *aestivalis* in 1960, Studemann (pers. comm.) has recently suggested that it might be *S. lacustris*. The life history described for the popu-
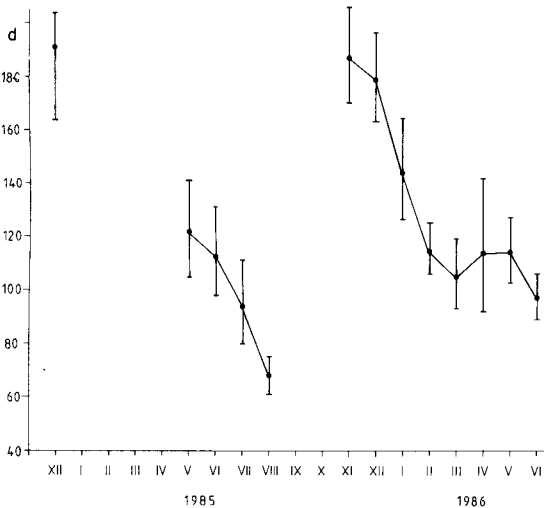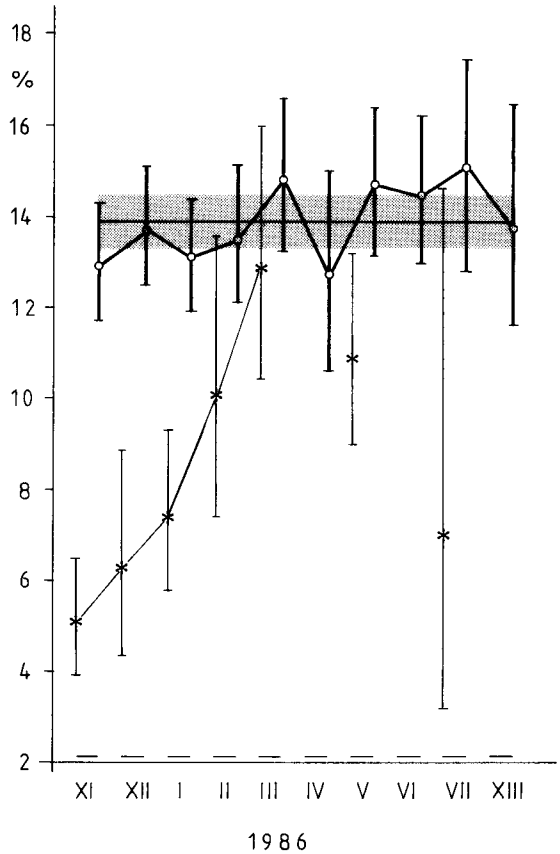

Fig. 13. Relative moulting efficiency. 100% – size of larvae before ecdysis. For captions see Fig. 7. Grand mean: 13.9 $\pm$ 0.6.

Fig. 12. Duration of development in days from the incubated larvae-ss until emerging nymphs.

lation of "Grüner See" fits either species, although the information is not very detailed (Brittain 1980, Landa 1968, 1969, Sowa 1980).

Delayed hatching alone or combined with diapausing larvae as a developmental strategy to overcome detrimental conditions in winter is described for many mayfly species (Bretschko 1965, Flowers *et al.* 1978, Illies *et al.* 1977, Landa 1968, Macan 1978). Quality and quantity of embryonic and/or larval development achieved during winter influences emergence in many species. For example in *Stenacron interpunctatum* (Say) emergence is bimodal with adults of different sizes (Flowers *et al.* 1978) and in *Baetis vernus* Curtis emergence is uni-, bi- or trimodal according to prevailing winter temperatures (Illies *et al.* 1977). Besides the long emergence period of about four

months no consequences of differing developmental patterns are discernable in *S. aestivalis*. The great differences in overwintering strategies are fully compensated by the fast growth of the phase in spring and summer. Compensation is most likely augmented by the highly variable temperature climate to which the larvae are exposed in spring and summer.

To interpret larval development patterns it is necessary to differentiate between two possible reactions in the developing animal:

i) Development is dependent on environmental conditions (e.g.: growth rates of the β phase at different temperatures (Bretschko 1985)).

ii) Development is limited by thresholds independent of prevailing conditions. Below or above these thresholds development remains dependent on environmental conditions (e.g.: growth rates of the α phase (Bretschko 1985, Fig. 8).

Only reaction ii) could explain programmed larval development. Growth rate was measured here, but growth rate is a consequence of moulting frequency and moulting effectivity. Both vary in overwintering larvae (Figs 9 and 13). Since there are indications that extremely low moulting frequencies are avoided (Bretschko 1985), moulting effectivity alone is most likely used for programming development.

Even if development is programmed there is scope for some development of type i). Such a combination guarantees a programmed general developmental pattern with enough flexibility to react to a changing environment. This mechanism may also explain the findings of Humpesch (1979) in the larval development of *Baetis alpinus* and of Illies *et al.* (1977) in *Baetis vernus*; delayed hatching is a reaction of type two and embryonic development is a reaction of type one.

The fixation of development is terminated very gradually (Fig. 13) in all conditions offered in the experiments (Bretschko 1985). Possible causes for this termination are: a) changing temperatures, b) changing food, c) time, d) changing light regime.

Changing temperatures are most unlikely because winter temperatures are uniform and stable (Fig. 1) in the lake. Although food influences development greatly (Cianciara 1980), it is very unlikely to be the cause here, since both green growing plants and POM is offered in the experiments at any time. Elapsing time might simply elevate the threshold of moulting efficiency. Since the growth curve can be approximated by a linear regression in the phase, time cannot be the cause. Increasing day length is most probably the causative factor; mean growth rate and mean moulting efficiency are not significantly different in larvae sampled until January but both increase significantly later.

ACKNOWLEDGEMENTS

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