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Mortality of the terrestrial adult and aquatic nymphal life stages of *Baetis vernus* and *Baetis rhodani* in the Breitenbach, Germany (Insecta: Ephemeroptera)

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SUMMARY

1. The mortality of *Baetis vernus* Curtis and *Baetis rhodani* Pictet during the terrestrial–aerial and aquatic life stages was studied at the Breitenbach near Schlitz, Hesse, Germany. The number of females emerging from the stream was recorded with emergence traps. To estimate mortality of females of both species during terrestrial life, numbers of emerging females were compared with numbers of females returning to the stream for oviposition, as shown by numbers of egg masses found in the stream.
2. Mortality of female *B. vernus* during their terrestrial life stage was 98.8%. It was 91.2 and 96.6%, respectively, during the first and second generations of *B. rhodani*.
3. To estimate the mortality of both sexes of *B. rhodani* during the aquatic life stage, the number of eggs laid by the first generation was compared with the number of adults emerging during the second generation.
4. Mortality during the aquatic phase (both sexes combined) of *B. rhodani* was 91.1%.
5. Mortality during the terrestrial life stages was at least as high, if not higher than during the aquatic stages. Evidently, there is a considerable export of organic material into the terrestrial environment around the stream. Mortality during terrestrial life may be an important regulator of population size.

Introduction

Little is known about the mortality or other losses during the terrestrial adult life of aquatic insects (Jackson & Fisher, 1986; Gray, 1989; Gribbin & Thompson, 1990). Thus, important aspects of the interactions between limnic and adjacent terrestrial habitats as well as possibly important factors regulating population size remain poorly understood.

Baetis vernus and *B. rhodani* are very abundant in the Breitenbach near Schlitz (Hesse, Germany); they are the only members of the genus resident in the stream (Jacob, 1986; Sandrock, 1978). The present study aimed at evaluating the mortality of both species during their terrestrial life phases. *B. rhodani* is bivoltine in the Breitenbach (Jacob, 1986) and its mortality during the aquatic life stage of the second generation was also investigated.

Study area

The Breitenbach is a small first-order stream in the catchment of the Fulda River near Schlitz (Hesse, Germany) (Fig. 1). Its highest springs are near 350 m a.s.l.; it drains into the river at 220 m a.s.l., about 4.5 km, downstream. Discharge varies strongly during individual years as well as between years; in 1990, annual mean discharge was 15.39 l s^{-1}, the extremes were 1.69 and 201.25 l s^{-1}, respectively. The entire catchment of the Breitenbach is underlain by Buntsandstein, a Triassic sandstone almost free of calcium. Mean conductivity was 164.2 µS cm^{-1} (extremes: 134.5 and 197.0 µS cm^{-1}), and pH was circumneutral, usually around 7.2, short-term extremes being 6.2 and 7.6, respectively. Most of the catchment area is covered with mixed deciduous and coniferous forests. The actual bottom of the stream valley, however, is
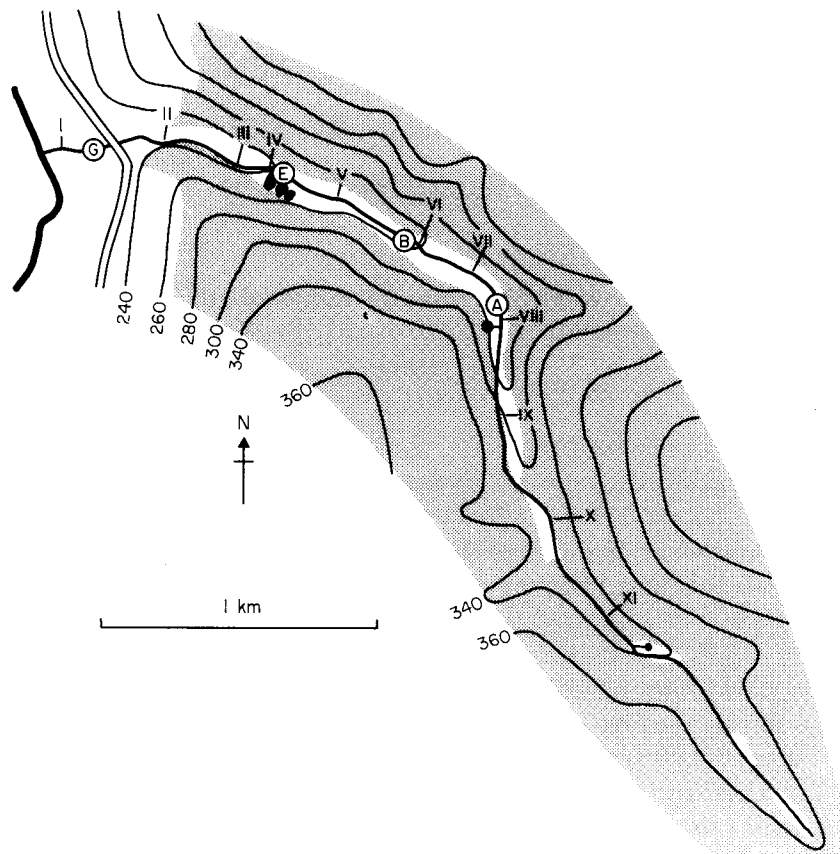
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Fig. 1 Map of the Breitenbach study area, showing the location of emergence traps A, B, E, and G (letters in circles), artificial oviposition substrata (I to XI), the major tributary spring (asterisk near Trap A), and a few ponds near Trap E. Elevations are in m a.s.l.; stippling indicates forest.

cleared and covered by meadows, which are used to make hay or grazed by lifestock. Detailed descriptions of the stream are available (Marxsen, 1980; Schwank, 1983, unpublished data; Thomas, 1990).

The area studied was the lower 2000 m of stream, between the confluence of a major tributary spring with the upper course of the Breitenbach 105 m upstream from Trap A, and the mouth of the Breitenbach into the Fulda River, 200 m below Trap G. Emergence trap collections made further upstream in earlier years (Neumann, 1989) indicate that almost no *Baetis* occur upstream from the section considered here.

Methods

Mortality during the terrestrial life phase was determined as the difference between the number of female (sub-)imagines caught in emergence traps and the number of females returning to the stream for oviposition.

Emerging adults

The number of adults emerging is routinely determined by staff of the Limnologische Flußstation in four traps along the stream. For descriptions of the traps, see Illies (1971) and Jacob (1986); recent modifications of design (description pending) are irrelevant in the present context. Total numbers of adult mayflies emerging from the lower 2000 m of the stream were extrapolated in the following way as proposed by Jacob (1986).

Actual numbers caught in the traps were converted to numbers of specimens per metre of stream length; similar numbers were assumed to emerge in the area upstream and downstream of a given trap, until half way to the next trap. In the case of the uppermost Trap A and the lowermost Trap G, the area inhabited by uniform numbers of *Baetis* was assumed to extend to the confluence with the tributary spring, or the mouth of the Breitenbach, respectively. Because the assumed uniformity of distribution is unproven, the true number of adults emerging from the stream

may differ from our estimate. The significance of adult losses was therefore compared against arbitrarily assumed 25% lower and higher estimates, respectively.

Females returning to the stream for oviposition

The number of females returning to the stream for oviposition was equated to the number of egg masses found, on the assumption that every female lays only a single egg mass. However, Bohle (1969) does not exclude the possibility that female *Baetis* may lay several egg masses of different sizes, and distribute them in various places. Female *Baetis* are usually spent after ovipositing and perish; it appears improbable to us that they distribute egg masses on to several stones. It could at best be that a given female lays several egg masses on a single stone. Other descriptions of ovipositing behaviour of *Baetis* (Percival & Whitehead, 1928; Verrier, 1956; Harris, 1970; Elliott, 1972; Elliott & Humpesch, 1980; Humpesch & Elliott, 1984) do not address this point.

To investigate whether female *Baetis* lay one single egg mass only, thirty female *Baetis* spp. found beside a pale whitish egg mass (the colour suggesting that eggs were freshly laid) on the underside of a given stone, i.e. presumably found while ovipositing, were preserved when oviposition was completed. They were dissected for remaining eggs, to see whether enough remained to produce a second egg mass.

To estimate the total number of egg masses of *Baetis* spp. in the Breitenbach, eleven test sections were chosen. They were roughly equal distances apart within the lower 3500 m of stream, including the portion with emergence traps, and extended about 1500 m upstream from it. Sites chosen offered suitable natural oviposition substrata. Such natural substrata were removed and three particularly suitable artificial substrata that were probably 'attractive' to ovipositing female *Baetis* (Bohle, 1969; Schmidt, 1984) were exposed in each of these sections. The artificial substrata were black concrete stones, 20 × 10 × 6 cm. They were placed in the middle of the stream so that 25–50% of their upper face protruded out of the water, thereby providing *Baetis* females with possible landing sites.

The lower faces of these stones were photographed at a fixed scale at 5–14-day intervals. Stones so crowded with eggs that new egg masses would have

covered already existing ones were completely submerged to prevent the landing of additional *Baetis* females, and such stones were replaced by fresh ones.

Bohle (1969) and Schmidt (1984) gave characters permitting distinction of the egg masses of the two species. However, use of these characters in the field did not appear to be reliable; the different mode of egg development of the two species was therefore used instead to identify egg masses. According to Bohle (1969) and Schmidt (1984), *B. vernus* eggs enter diapause whereas eggs of *B. rhodani* develop directly; larvae of *B. rhodani* hatch after 10–40 days, depending on temperature (Bohle, 1969; Benech, 1972; Elliott, 1972; Brittain, 1990). Therefore, once artificial substrata had been completely submerged for 8–12 weeks, after a time span when complete hatch of *B. rhodani* could be assumed, the stones were photographed a second time. Egg massed of *B. rhodani* had either completely disappeared, or were recognized by the presence of collapsed egg shells. In contrast, egg masses of *B. vernus* were unchanged and turgid. Comparison of the two sets of photographs allowed us to safely assign each egg mass to either *B. rhodani* or *B. vernus*; they were counted on the photographic slides.

Almost all egg masses of *Baetis* spp. in the Breitenbach were laid on the artificial substrata. Very few were found during checks elsewhere, but absolute numbers could not be determined accurately. In calculations of mortality, it was assumed that 75% of all egg masses were laid and recorded on the artificial substrata.

Error of estimates

Mortality of adult *Baetis* was calculated from estimates of the number of females emerged and the number of females returning to the stream for oviposition. A 25% error was arbitrarily assumed for each estimate. To assess influence of errors on estimated mortality rates, extremely pessimistic and extremely optimistic estimates were also made by combining the highest estimate of emerging females with the lowest estimate of returning females, and vice versa.

For the second generation of *Baetis rhodani*, mortality during aquatic life was calculated as the difference between the number of eggs laid by the first generation and the number of adults emerging during the second generation.

The photographic slides of the artificial substrata were viewed at ×12 magnification under a dissecting microscope (Wild M5) and the size of every egg mass (mm^2) was measured with the aid of a digitizing tablet (Numonics 2200) attached to a computer (PDP 11, Digital) (compare Schlepper, 1989).

The number of eggs mm^{-2} was determined in thrity-one egg masses of *B. rhodani*. Egg masses were photographed with slide film at a 1.5:1 scale; photographs were viewed under the dissecting microscope at ×25 magnification, and the number of eggs mm^{-2} was counted (three replicate areas in each egg mass).

Absolute numbers of egg masses, mean area per egg mass, and mean number of eggs per unit area were used to calculate total number of eggs laid.

A problem with the first generation of *B. rhodani* was that it started emerging (and, of course, also ovipositing) before sampling of egg masses had started; only the numbers emerging from the stream were recorded for these early *B. rhodani*. Once egg mass sampling had begun, the relationship between number of adults then hatching and number of egg masses then laid was determined. The same relationship was assumed to apply to the early emerging group, and the number of egg-masses was back-calculated, accordingly. The number of eggs per unit area was also assumed to be similar.

The number of eggs was compared with the number of specimens of both sexes emerging during the second generation; this was determined as described above.

Results

Adult emergence

Numbers of *Baetis* adults (including subimagines) caught in emergence traps are listed in Table 1. The calculated total of females emerging was 206 000 *Baetis vernus*, and 11 000 and 73 000, for the first and second generations of *B. rhodani*, respectively (Table 2). A total of 175 000 specimens of both sexes emerged during the second generation of *B. rhodani* (Table 3).

Egg masses

Altogether, 4454 egg masses of *Baetis* spp. were counted. Assuming a 75% effectiveness of the arti-

Table 1 Emergence of adult *B. vernus* and *B. rhodani* in the four traps along the Breitenbach

Emergence-trap	Metres from mouth	Numbers caught (both sexes)	
		B. vernus	*B. rhodani*
G	200	63	607
E	975	1738	659
B	1420	3151	759
A	1970	2075	178

Table 2 Calculated total number of *Baetis* females emerging from the Breitenbach, numbers of egg masses, and estimated mortality during the terrestrial life of *B. vernus* and *B. rhodani*. Bold figures are values calculated directly from collection data; above and below these, respectively, the pessimistic and optimistic estimates (see text) in normal print

	Females emerged		Number of egg masses		Mortality in %
	+25%	257 500	−25%	1836	99.3
B. vernus		**206 000**		**2449**	**98.8**
	−25%	154 500	+25%	3061	90.0
B. rhodani	+25%	13 750	−25%	728	94.7
1st generation		**11 000**		**970**	**91.2**
	−25%	8 250	+25%	1213	85.3
B. rhodani	+25%	91 250	−25%	1889	98.0
2nd generation		**73 000**		**2519**	**96.6**
	−25%	54 750	+25%	3149	94.2

Table 3 Numbers of eggs of *Baetis rhodani* laid by first generation females, numbers of adults emerging in the second generation, and calculated mortality during the aquatic larval stage; pessimistic, directly calculated (bold), and optimistic estimates shown (see Table 2)

	Number of eggs (1st generation)		Adults emerged (both sexes 2nd generation)	Mortality in %
	+25%	2 460 000	−25% 130 000	94.7
B. rhodani		**1 970 000**	**175 000**	**91.1**
	−25%	1 477 000	+25% 219 000	85.2

ficial substrates to attract ovipositing females, this corresponds to a total of 5938 egg masses in the entire stream. Of this total 2449 were of *B. vernus*, 970 and 2519 were of the first and second generations of *B. rhodani*, respectively (Table 2).

Number of egg masses per female

Of the thirty females dissected, four had the abdomen completely full of eggs. Evidently, these four individuals had not yet started oviposition and had been taken beside fresh egg masses, which were, however, not their own. In two other females, the abdomen was partly filled with eggs. However, in twenty-four of the thirty females, no eggs at all remained in the abdomen. Most females had apparently laid all their eggs at once, i.e. they had produced a single egg mass. We have assumed this to be the rule.

Total number of eggs

The mean number of eggs mm^{-2} egg mass was 59.9 for *B. rhodani*. The mean size of an individual egg mass of the first generation was 33.83 mm^2 (Table 4). A total of 1 970 000 eggs was therefore estimated to have been produced from the 970 egg masses laid by this species.

Table 4 Numbers of eggs mm^{-2} and the size [mm^2] of individual egg masses of *Baetis rhodani*

	Eggs mm^{-2}	Size of egg masses
n	31	444
Max.	74.88	82.90
Min.	50.90	3.19
Mean	59.90	33.83
SD	6.15	15.47

Mortality during the terrestrial and aquatic life stages

Calculated mortality of female *Baetis vernus* during terrestrial life was 98.8%; it was 91.2% for the first generation of *B. rhodani*, and 96.6% for the second (Table 2).

The mortality of aquatic larvae (both sexes) making up the second generation of *B. rhodani* was 91.1% (Table 3).

Discussion

The method employed here to estimate the total number of *Baetis* egg masses in a stream is new, and there is no precise test of its efficiency. However, we believe our approach is valid and accurate within

the wide error limits assumed. Very few similarly large stones suitable for oviposition remained in the stream anywhere, away from the test sections. In addition, during peak emergence most of these were covered by overhanging littoral vegetation. Previous observations at the Breitenbach (U. Werneke, unpublished data) showed that natural substrata partly hidden by vegetation as well as small stones and stones near the banks were indeed hardly used for oviposition by *Baetis*. In contrast, the concrete stones were more freely exposed and easily visible. We therefore provided artificial ovipositing substrata that were far superior to the occasional natural ovipositing substrata remaining in the stream.

Eggs on the artificial substrata were identified as *B. vernus* if they were still present at a check a few weeks after they had been laid. Eggs that had disappeared in the meantime were assumed to have developed directly, and were assigned to *B. rhodani*. Possible losses of eggs due to other causes, predation in particular, were not considered because the fauna of the Breitenbach does not include known egg predators.

Losses of adults from the Breitenbach populations of *Baetis* spp. are assumed to be mainly mortality but losses to other streams in the vicinity, e.g. the Fulda River, cannot be excluded. The Fulda River is regulated and slow flowing in this region and although both *B. vernus* and *B. rhodani* occur in it, they do so in low densities, especially the latter (U. Werneke, unpublished data). Therefore, immigration of adult *Baetis* from the Fulda River is assumed to be negligible. Moreover, we do not believe that significant numbers of adult *Baetis* (if any) could fly in from other streams, as has been observed elsewhere (Sutcliffe & Carrick, 1973), because the only stream in the vicinity (although in another valley, at about 1 km distance from the Breitenbach) is polluted. Other clean streams are several kilometres away from the Breitenbach, and are smaller than it.

In 1990, pre-reproductive mortality of *Baetis* spp. during terrestrial–aerial adult life was at least as high as, if not higher than that during the aquatic nymphal stage. Actual data on mortality during the adult stage concern only females. There is no known way to measure male pre-reproductive mortality. Apparently, factors acting during adult life, such as predators (at the Breitenbach, these are probably mainly spiders and birds; there are hardly any

Odonata) and weather have a strong influence on (sub-)adult mortality and thereby affect the number of egg masses and eggs (i.e. population size at the start of the next generation) to a similar extent as nymphal mortality affects population size.

Zwick (1989) has already emphasized the possible importance of the terrestrial adult life stage of aquatic insects in population dynamics. Even small changes in the percentage mortality of adults may have strong effects on the abundance of the next generation, even in *Baetis* spp., that typically occur in high densities. In fact, Brittain (1980, 1990) and Edmunds & Edmunds (1980) regard ephemeropteran life cycles with their characteristically short phase of very high adult abundance as an adaptation minimizing exposure to predators, thereby reducing mortality. Nevertheless, pre-reproductive adult mortality is very high in the case examined here.

Jackson & Fisher (1986) also describe a very high export of insect biomass from a stream into the terrestrial environment. According to their data, an average of 3% of all the emerging insects returned to the water body, corresponding to a terrestrial mortality of 97%. Their data indicate a loss of 98.7% adult *Baetis quilleri* Dodds and *B. insignificans* McDonnough in the terrestial phase but this may be an overestimate as they did perhaps not collect all (sub-)imagines returning to the stream, or falling into it.

Gray (1989) calculated an 86.7% net export of insect biomass from a prairie stream to the terrestrial environment. However, his calculation of import to the stream included not only aquatic insects returning to it, but also terrestrial insects falling into the stream.

A 28% adult mortality was calculated for the damselfly *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae) (Gribbin & Thompson, 1990); compared with data mentioned above, this is very low. Whether this relatively high return rate reflects relatively greater resistance of Odonata towards predators, and possibly also towards poor weather conditions, is unknown. Odonatan longevity allowing them several attempts in their lifetime to return to streams, or adults flying in from different water bodies may also play a role.

Finally, our findings also suggest that mortality during terrestrial life of the first generation of *B. rhodani* was possibly lower than that during the second generation. There is no obvious cause for

this but according to our observations, numbers and activities of predators (especially spiders) were considerably lower during the flight period of the first generation in April and May, than they were during the flight period of the second generation, in July to September.

Acknowledgments

References

Benech V. (1972) Etude experimentale de l'incubation des oeufs de *Baetis rhodani* (Pictet). *Freshwater Biology*, **2**, 243–252.

Bohle H.W. (1969) Untersuchungen über die Embryonalentwicklung und die embryonale Diapause bei *Baetis vernus* Curtis und *Baetis rhodani* (Pictet) (Baetidae, Ephemeroptera). *Zoologische Jahrbücher Jena, Abteilung für Anatomie*, **86**, 493–575.

Brittain J.E. (1980) Mayfly strategies in a Norwegian subalpine lake. *Advances in Ephemeroptera Biology — Proceedings of the 3rd International Conference on Ephemeroptera* (Eds J.F. Flannagan and K.E. Marshall), pp. 179–186. Plenum Press, New York.

Brittain J.E. (1990) Life history strategies in Ephemeroptera and Plecoptera. *Mayflies and Stoneflies* (Ed I.C. Campbell), pp. 1–12. Kluver Academic Press.

Edmunds G.F. & Edmunds C.H. (1980) Predation, climate, emergence and mating of Mayflies. *Advances in Ephemeroptera Biology — Proceedings of the 3rd International Conference on Ephemeroptera* (Eds J.F. Flannagan and K.E. Marshall), pp. 277–285. Plenum Press, New York.

Elliott J.M. (1972) Effect of temperature on the time of hatching in *Baetis rhodani*. *Oecologia*, **9**, 47–51.

Elliott J.M. & Humpesch U.H. (1980) Eggs of Ephemeroptera. *Annual Report of the Freshwater Biological Association*, **48**, 41–52.

Gray L. (1989) Emergence, production and export of aquatic insects from a tallgrass prairie stream. *The*

Southwestern Naturalist, **34**, 313–318.

Gribbin S.D. & Thompson D.J. (1990) A quantitative study of mortality at emergence in the damselfly *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae). *Freshwater Biology*, **24**, 295–302.

Harris J.R. (1970) *An Anglers Entomology*. Collins, London.

Humpesch U.H. & Elliott J.M. (1984) Zur Ökologie adulter Ephemeropteren Österreichs. *Archiv für Hydrobiologie*, **101**, 179–207.

Illies J. (1971) Emergenz 1969 im Breitenbach. Schlitzer Produktionsbiologische Studien (1). *Archiv für Hydrobiologie*, **69**, 14–59.

Jackson J.K. & Fisher S.G. (1986) Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. *Ecology*, **67**, 629–638.

Jacob U. (1986) Analyse der Ephemeropteren-Jahresemergenz des Breitenbaches bei Schlitz/Hessen (BRD). *Archiv für Hydrobiologie*, **107**, 215–248.

Marxsen J. (1980) Untersuchungen zur Ökologie der Bakterien in der fließenden Welle von Bächen. I. Chemismus, Primärproduktion, CO_2-Dunkelfixierung und Eintrag von partikulärem organischen Material. Schlitzer produktionsbiologische Studien (23-1). *Archiv für Hydrobiologie*, Supplement **57**, 461–533.

Neumann P. (1989) *Biozönotische Untersuchungen am Breitenbach (Hessen) unter besonderer Berücksichtigung der Eibiologie bei der Gattung Brachyptera (Plecoptera, Insecta)*. Diploma thesis, University of Kiel.

Percival E. & Whitehead B.S. (1928) Observations on the ova and oviposition of certain Ephemeroptera and Plecoptera. *Proceedings of the Leeds Philosophical and Literary Society*, **1**, 271–288.

Sandrock F. (1978) Vergleichende Emergenzmessung an zwei Bächen des Schlitzerlandes (Breitenbach und Rohrwiesenbach) 1970–1971. *Archiv für Hydrobiologie*, Supplement **54**, 328–408.

Schlepper R. (1989) Populationsökologische Untersuchungen am Eistadium von *Boophthora erythrocephala* (De Geer) (Diptera: Simuliidae). *Zeitschrift für angewandte Zoologie*, **76**, 61–83.

Schmidt H.H. (1984) Einfluß der Temperatur auf die Entwicklung von *Baetis vernus* Curtis. *Archiv für Hydrobiologie*, Supplement **69**, 364–410.

Schwank P. (1983) *Breitenbach, Grobsubstratkartierung*. Unpublished manuscript in the Limnologische Flußstation Schlitz.

Sutcliffe D.W. & Carrick T.R. (1973) Studies on mountain streams in the English Lake District I. pH, calcium and the distribution of invertebrates in the River Duddon. *Freshwater Biology*, **3**, 437–462.

Thomas J. (1990) *Räumliche und zeitliche Verteilung der β-Glucosidase-Aktivität im Sediment des Breitenbaches (Hessen)*. Diploma thesis, University of Gießen (FRG).

Verrier M.L. (1956) *Biologie des Ephémères*. Collection Armand Colin, Paris.

Zwick P. (1989) Upstream oviposition flights of Plecoptera, with notes on the adult phase as a possible control of stream insect populations. *Hydrobiologia*, **194**, 207–223.