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Life cycle and timing of emergence of *Oligoneuriella rhenana* (Imhoff, 1852) in the Kyll River (SW-Germany) [Ephemeroptera : Oligoneuriidae]

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Keywords : *Oligoneuriella rhenana,* life cycle, timing of emergence, egg-laying, Germany.

1) The life cycle of *Oligoneuriella rhenana* was studied by 2 mn kick samples during the period of occurrence of preimaginal stages. Six samples were carried out from May to August in the Kyll River near Trier (Rhine catchment). *O. rhenana* is a univoltine summer species with overwintering eggs and a single extremely fast growing generation that emerges in July and August. 2) Larvae larger than 8-10 mm were sexed, and the sex ratio was about 50:50. 3) Winged adults of *O. rhenana* swarming horizontally over the water surface were collected by successive random sweeps during their daily emergence period, and the changes in sex and stage composition were examined. 4) The emergence occurred mainly during a $1^1/_2$ h period beginning some time after sunset. Male subimagoes emerged synchronously and moulted to imagoes in a 30 mn period immediately prior to the emergence of female subimagoes. 5) Females were mated as subimagoes, and the imaginal moult took place during flight after mating, prior to egg-laying, which was done in about 3 batches. 6) Life span of winged stages is extremely short and lasts on average about 40 mn in males and about 50 mn in females. 7) Egg laying was observed to be completed in several batches, with the females leaving the turbulent water surface several times. As the wings of *Oligoneuriella* remain unmoulted, the hydrophobic quality of the subimaginal hairs is thought to be advantageous for this.

Cycle biologique et timing de l'émergence d'*Oligoneuriella rhenana* (Imhoff, 1852) dans la rivière Kyll (SW de l'Allemagne) [Ephemeroptera : Oligoneuriidae]

Mots-clés : *Oligoneuriella rhenana,* cycle biologique, timing d'émergence, oviposition, Allemagne.

1) Le cycle biologique d'*Oligoneuriella rhenana* a été étudié par prélèvements foulés au pied de 2 mn pendant la période d'occurrence du stade préimaginal. Six prélèvements ont été effectués de mai à août dans la rivière Kyll près de Trier (bassin-versant du Rhin). *O. rhenana* est une espèce estivale univoltine ; elle passe l'hiver à l'état d'oeufs et présente une seule génération, à croissance extrêmement rapide, qui émerge en juillet et août. 2) La détermination du sexe des larves au dessus de 8-10 mm a révélé une sex ratio voisine de 50:50. 3) Les adultes d'*O. rhenana* volant en essaims horizontalement au dessus de la surface de l'eau ont été récoltés au filet entomologique par balayages successifs au hasard durant leur période d'émergence quotidienne, et les changements dans les proportions des sexes et des stades subimaginal et imaginal ont été examinés. 4) L'émergence a lieu principalement pendant une période de $1^1/_2$ h, débutant peu après le coucher du soleil. Les subimagos mâles émergent de façon synchrone et muent en imagos sur une période de 30 minutes précédant immédiatement l'émergence des subimagos femelles. 5) Les femelles s'accouplent au stade subimaginal, et la mue imaginale a lieu durant le vol qui suit l'accouplement, avant l'oviposition, cette dernière se déroulant en trois fois environ. 6) La durée de vie des stades ailés est extrêmement brève, en moyenne d'environ 40 minutes chez les mâles et d'environ 50 minutes chez les femelles. 7) Il a été obser-

vé que l'oviposition se déroule en plusieurs fois, les femelles quittant la surface agitée de l'eau à plusieurs reprises. Du fait que les ailes d'*Oligoneuriella* ne s'exuvient pas, les caractéristiques hydrophobes des soies subimaginales apparaissent comme un avantage réel.

1. Introduction

The life-cycle of *Oligoneuriella rhenana* has been described in general or in detail several times as a univoltine summer cycle by several European authors e.g. GRANDI (1947), PINET (1962), SOWA (1975), FENOGLIO et al. (2005) and others. Interestingly, little information on its life cycle in the Rhine River, after which this species was named, has been published, and there are only general descriptions on the time of occurrence of larvae and the flight period e.g. in NEERACHER (1910), SCHOENEMUND (1930) or JANSEN (2000). A full life cycle, however has never been published from this area or from any other region in Germany.

The imaginal flight of *O. rhenana* has attracted early the attention of entomologists, especially in the case of mass flights e.g. STEINMANN (1919) or BURMEISTER (1989), and there are detailed descriptions on abiotic factors influencing the emergence, as well as on flight behaviour : STEINMANN (1919), GRANDI (1947), PINET (1962, 1967), GRIMM (1988), FISCHER (1991). However, a detailed description of the timing of emergence is missing and this paper represents the first detailed description of the life cycle from Germany.

2. Materials and Methods

Study site

The study was conducted in the lower reach of the Kyll River at Kordel (long. 6°38' E, lat. 39°45' N), a 4th-order left-handed tributary of the River Mosel near the City of Trier. The Mosel River has its confluence with the Rhine River at Koblenz. At Kordel the river is about 10-15 m wide and the water flow is very rapid and turbulent. The main substratum is stones about 30-40 cm in diameter and pebbles. Larvae were collected about 100 m downstream, while imagoes were collected directly above the only bridge in Kordel.

Larvae

Larvae were sampled by 2 mn kick samples with a hand-net (mesh width 0.5 mm), monthly from January to May and from September to December, and daily from June to August 14. Specimens of *O. rhenana* were preserved in 70% ethyl alcohol solution. Their lengths without cerci were measured to the nearest 0.1 mm by use of a Wild-M3 stereo-microscope and a measuring graticule. Starting with samples from the end of June, and with an average size of about 8-10 mm, it was possible to sex the larvae using the well-known sexual dimorphism of the eyes as the main criterion (see GRANDI 1947). Simple size-frequency distribution was used to demonstrate the life-cycle.

Imagoes

On August, 4th 1994 a spectacular mass flight took place at the Kyll River. The time of appearance of the swarm was noted as well as the "behaviour" of the male swarm. The horizontal speed of the male-flight, which took place directly in front of two bridge piers, was about 2 m/s. Three years later, on August 6th, 1997 an experiment was conducted to elaborate details on the timing of emergence in the different flight stages of *Oligoneuriella,* largely following the methods introduced by WATANABE et al. (1989). Soon after sunset (~ 8.^{00} p.m.) the first male subimagoes appeared. The imagoes and subimagoes swarming over the water surface were collected by random

strokes through the air with an insect net of 40 cm diameter at a place about 3-5 m upstream of the bridge, where the water was about 30 cm deep. A ten-stroke sweep was made every 10 mn throughout the duration of the swarming, except for the last 30 mn, where 15 mn intervals were used. The specimens of *O. rhenana* were preserved in 70% ethyl alcohol solution. They were divided into their corresponding stages and sexes using GRIMM's (1988) features for separation : ♀ Subimago : tails almost as long as the body ; ♀ Imago : tails longer than the body ; ♂ Subimago : tails with distinct fringes ; ♂ Imago : tails without fringes. In addition, in female imagoes the degree of completeness of the eggs in the abdomen was noted, because several females were observed to lay some of their eggs on the water surface, drifting for several meters in the current, and then leaving the water again.

3. Results

Life cycle

The seasonal development of larvae in 1995 based on larval length without cerci is shown in Fig. 1. Nymphs were first collected on 15 May. Nymphs larger than 8-10 mm were generally sexed after 29 June to estimate larval sex-ratio. No larvae were detected on April, 13th, so that, judging from the mean size of 2.65 mm in the middle of May, egg-hatching most probably occurred between the middle and end of April in 1995. Collections on Sept. 14th were unsuccessful, so that we can conclude that the full development from hatching to emergence took place within approximately $3^1/_2$ months.

The growth of the larvae in this species is extraordinarily fast and impressive, as has been mentioned by several authors before. In the Kyll River *Oligoneuriella* larvae grow on average between 0.2-0.3 mm per day from mid-June to the end of July. Flexible strategies are known for *O. rhenana* with regard to thermal regimes (FENOGLIO et al. 2005). In the Kyll River increasing growth is correlated with increasing water temperature and the emergence begins at the highest water temperature (Fig. 1), but note that only single temperature values from the sampling dates are available.

Sex ratio and size

Last-instar larvae (with black wing pads) of both sexes show size differences (Table 1). Mature female larvae are approximately 3 mm larger than male larvae.

Sexing of larva was possible in 362 larvae : 180 were female, 182 male. There is therefore a strong indication that the sex-ratio in *Oligoneuriella rhenana* is about 50:50.

Date : July 29th, 1995	Size (mm) : mean ± standard deviation	Number of individuals
Sex		
♂ larvae (last instar)	14,8 ± 1,0	27
♀ larvae (last instar)	18,1 ± 0,9	19

Table 1. Mean size of full-grown larvae showing sexual dimorphism.

Tableau 1. Taille moyenne des larves en fin de développement, montrant le dimorphisme sexuel.

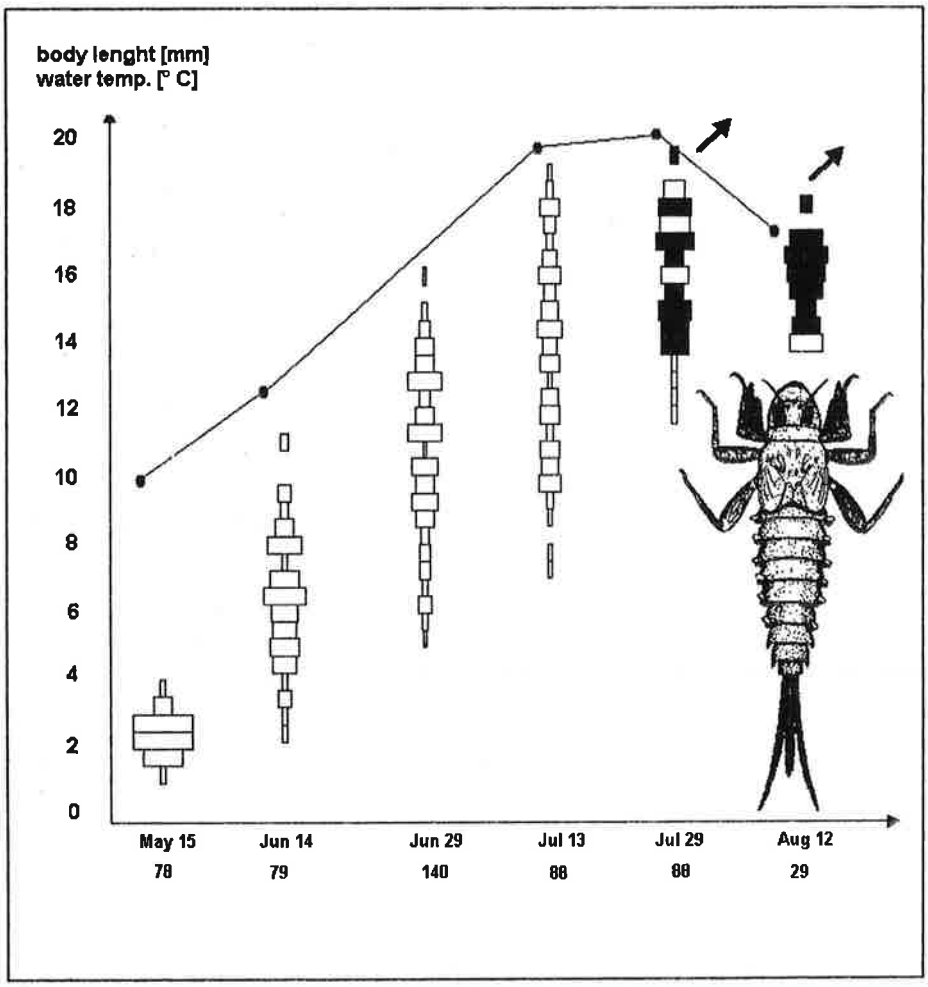

Fig. 1. Life cycle of *Oligoneuriella rhenana* (Imhoff) in the River Kyll. Boxes cover all larvae within a 0.5 mm size class. Simple size frequency is shown. Black boxes indicate the occurrence of last-instar larvae, arrows indicate time of emergence. Black spots indicate water temperature at sampling dates (~12.00 a.m.). Numbers below the dates refer to classified specimens. Figured larva from Schoenemund, 1930.

Fig. 1. Cycle biologique d'*Oligoneuriella rhenana* (Imhoff) dans la rivière Kyll. Les histogrammes rendent compte de la taille de toutes les larves par classes de 0,5 mm. Les parties foncées indiquent la présence de larves au dernier stade; les flèches indiquent la période d'émergence. Les points noirs indiquent la température de l'eau aux dates de prélèvements (~12.00 a.m.). Au-dessous des dates, les nombres correspondent aux spécimens classés. Figure de la larve empruntée à Schoenemund, 1930.

Timing of emergence

Table 2 shows the number of male subimagoes, male imagoes, female subimagoes, and female imagoes caught by the insect net from the swarm at successive sampling times on 6 August 1997, and Fig. 2 shows the same data normalized to 100%. To estimate whether females lay their eggs in one batch, or in several, female imagoes were separated into three categories : first, females with complete egg packages in their abdomen, prior to egg laying; second, females that had partly laid their eggs; and third, females without eggs.

Central European Time p.m.	08:10	08:20	08:30	08:40	08:50	09:00	09:15	09:30
♂ Si	2	4	0	0	0	0	0	0
♂	0	14	18	14	19	1	2	0
♀ Si	0	0	0	3	0	0	0	0
♀ (full of eggs)	0	0	0	0	19	10	0	0
♀ (eggs partly missing)	0	0	0	0	0	11	0	0
♀ (without eggs)	0	0	0	0	0	0	28	12

Table 2. Timing of emergence of *O. rhenana* in the Kyll river on August, 6th, 1997.
Tableau 2. Timing de l'émergence d'*O. rhenana,* rivière Kyll, le 6 août 1997.

The large majority of *O. rhenana* emerged synchronously within 40 mn. After that time almost only egg laying female imagoes were recorded. Male emergence began abruptly at around $8.^{10}$ p.m. At first male subimagoes appeared, but the proportion of male imagoes increased rapidly and within 20 mn after detection of swarming adults, almost all males had moulted to imagoes during swarming, as is well known for this species. After this female subimagoes appeared. This stage is highly underrepresented in our data because emerging females were rapidly mated by patrolling males and then hidden away as couples high over the swarm. After a further 10 minutes the majority of specimens had been mated and fully moulted female imagoes occurred to begin egg laying. Note that in *O. rhenana* moulting occurs during flight, so that in adoption of this behaviour, the wings must remain unmoulted. Within another 10 mn at $9.^{00}$ p.m. almost only female stages were captured.

Life span of adults

Individual life span may depend largely on environmental factors during flight, especially temperature or general weather influences such as rain, storm, etc. STEINMANN (1919) reports a 2-4 hr life span for captured individuals which had no possibility for flight. Our data based on more natural conditions suggest that the life span of male adults is on average about 40 mn, and that of female adults a little longer at about 50 mn, in concordance with the field observations of FISCHER (1991). This is one of the shortest life spans of mayflies at all, and only Behningiidae are known to have as short or shorter life spans. In both families adults are rapid horizontal flyers, and females are mated as subimagoes.

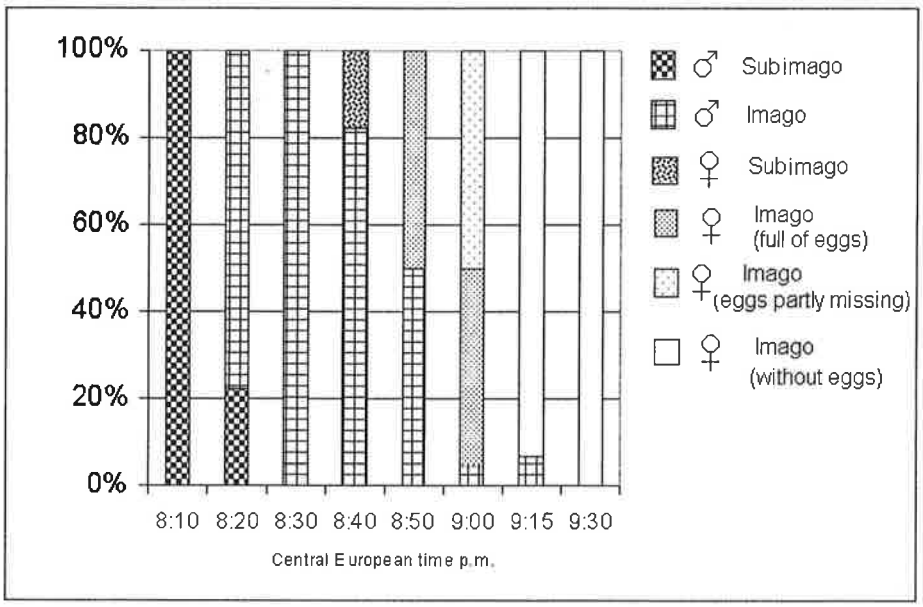

Fig. 2. Timing of emergence of *O. rhenana*. Successive appearance of male subimagoes, male imagoes, female subimagoes, female imagoes and egg laying females is figured by use of the data in Table 2.

Fig. 2. Timing de l'émergence d'*O. rhenana*. La représentation des apparitions successives des subimagos mâles, imagos mâles, subimagos femelles, imagos femelles, et des femelles en oviposition est effectuée selon les données du Tableau 2.

Egg laying

O. rhenana females were observed to lay the eggs directly on the water surface, but only in lotic areas with turbulent water and rapid flow. Females drifted 3-5 m with the current and then left the surface to fly into the swarm again. It was not possible to observe whether they were mated again, but this can't be excluded. Based on observations of the "degree of emptiness" of the abdomen in the captured female imagoes, it is suggested that females lay their eggs in at least 3 batches, and not in one large batch. There is perhaps some variability in egg-laying behaviour, dependent on the size of the females, and therefore in the temperature regime of the river in general.

4. Discussion

The current study confirmed that *O. rhenana* is a univoltine summer species with overwintering eggs and a rapid, temperature dependant growth during spring and summer. Our data also confirmed the observations and experiments of STEINMANN (1919), GRANDI (1947) and GRIMM (1988) that female subimagoes of *O. rhenana* are mated by male imagoes. The mating flight of this species is shown to be highly synchronic, and males appear very shortly before females. This kind of protandry is well known for many short living mass flyers, mainly of larger rivers, such as *Dolania americana* (Behningiidae : PETERS & PETERS 1977), *Ephoron virgo* (Polymitarcyidae : KURECK & FONTES 1996) or *Palingenia longicauda* (Palingeniidae : RUSSEV 1987), and is related to

an optimal mating strategy in males (WATANABE et al. 1989). It is important to note that females lay their eggs in batches, leaving the turbulent water surface on several occasions. For such behaviour the remaining subimaginal haired cuticle of the wings, having hydrophobic properties, is advantageous (see EDMUNDS & MCCAFFERTY 1988).

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