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Life history and development of *Dictyogenus fontium* (Plecoptera: Perlodidae) in two thermally contrasting streams at Lunz am See, Lower Austria¹

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A b s t r a c t : The life history of a large stonefly, *Dictyogenus fontium*, was studied over several years in two streams at Lunz, Lower Austria. Between July 2004 and July 2005, benthic samples with an 0.3 mm net were taken approximately every three months. Temperature in Springgraben fluctuated seasonally between 0 °C and 13 °C, while water temperature in the nearby Schreierbach was constantly 6 °C. Egg incubation and morphological change at larval moults were studied in the laboratory. Development of gonads and secondary sexual characters was documented by dissection, and study of vaginal scars, respectively.

Total life cycle length from oviposition to adult emergence was three years. This is the longest life cycle reported in Perlodidae. Fast summer growth in the seasonal stream lead to early adult emergence and oviposition. However, time thereby gained was lost during delayed egg development at low temperatures in autumn and winter. At constantly 6 °, adult emergence and oviposition occurred 3 months later, but first instar larvae nevertheless hatched the next spring, same as in the seasonal stream.

First rudiments of gonads were observed when specimens were about 6 mm long. At the same time, females began to show vaginal scars and the initially unimodal size distribution became bimodal. Different morphology of vaginal scars was shown to identify the last six, and different shapes of wing pads the last three larval instars. Estimated total instar number was 15 in both sexes. Smaller size of adult males probably reflected overall lower growth rates in males than in females.

K e y w o r d s : Life cycle length, egg incubation, morphology, gonad development, vaginal scars, instar number, sexual growth difference.

Introduction

The large stoneflies of genus *Dictyogenus* are endemic in the Alps. *D. alpinum* (Pictet, 1841) has an expanse of up to 44 mm and "gehört wegen seiner Häufigkeit zu den bezeichnendsten Erscheinungen unserer Bergbachfauna, zumal er sich viel mehr offen zeigt und von seiner Flugfähigkeit stärkeren Gebrauch macht als andere große Steinfliegen" (KÜHTREIBER 1934). Nevertheless, these spectacular locally abundant insects are poorly known in several respects. The identity of the two nominal species has not been definitely resolved; egg development is direct, but its dependence on temperature is undescribed; morphological change during metamorphosis is incompletely described; the number of larval instars is unknown; literature presents only doubtful estimates of life cycle length (KÜHTREIBER 1934).

¹ Prof. Dr. Hans Malicky herzlich zum 75. Geburtstag gewidmet.

At Lunz, Lower Austria, *Dictyogenus* is common in the Schreierbach; most available biological information was derived from that population (ZWICK 1982, 2003). Among streams at Lunz, the Schreierbach is distinguished by its constant 6 °C temperature regime (MALICKY 1978). The Schreierbach population flies distinctly later than one would expect from literature, and later than the one in the nearby Springgraben with a seasonal temperature regime. At the Springgraben, single late males and numerous ovipositing females were observed in late June, which agrees with various literature data on flight period elsewhere (see below).

We used the opportunity to investigate possible temperature-related differences in the life cycle, and deal with some of the before mentioned unresolved problems at the same time. Our study is based on data obtained during several field campaigns (18.06.2003; 08.07.2004; 31.10.2004; 21.04.2005; 15.07.2005; 20.01.2007). Population structure observed during occasional previous visits to the study streams agreed with present findings. Some biometric data are based in part on such earlier material. The only mid-winter sample was taken in the exceptional snow-free January 2007. In summer 2004 and January 2007 several specimens were kept in the laboratory to collect exuviae at moults.

Material and methods

Taxonomy

The distinction of the two nominal species of *Dictyogenus*, *D. alpinum* (PICHET, 1841) and *D. fontium* (RIS, 1896), was long unresolved (ZWICK 1972). The oldest available name was therefore in the past used for the populations at Lunz (ZWICK 1982). Definitive syntypes of *D. alpinum* are not available, while the type series of *D. fontium* is (ZWICK 1972). Today, males can be distinguished by characters discovered by G. VINÇON and colleagues (personal communication; paper in prep.). G. VINÇON re-examined the syntypes of *D. fontium*, specimens from Lunz actually belong to *D. fontium* whose larvae lack an erect hair fringe on the middorsal line.

Sampling sites and sampling

Both study streams are located on the outskirts of Lunz am See, Lower Austria. The Schreierbach [47°44'59"N/15°04'54"E] is a large spring run at ca 780 m a.s.l. on the steep eastern slope of Großer Hetzkogel. The streambed is dominated by large moss-covered stones, and rubble and gravel of all sizes beneath them. There is little soft detritus, but a rich growth of diatoms, including macroscopic stalked colonies. After a short course the Schreierbach flows into the main stream in the valley, Oberer Seebach. Water temperature is diurnally and seasonally around 6 °C (MALICKY 1978), as confirmed by recordings during the first part of the present study. In March 2005 an avalanche removed most of the large beech trees and small alders on the banks. The snow masses glided across the stream on top of trees that had fallen over it and protected the streambed which was not scoured. The fauna apparently remained largely unaffected, but temperature loggers were lost. Therefore, we have no temperature readings of our own during the second half of our present study.

The small stream Springgraben flows 3.8 km WNW of the Schreierbach in a forested gully along the trail Knappenweg. Samples were taken close to the spring, at ca 700 m a.s.l., at the locality Pauschenreith. The shaded streambed has many large stones on a layer of gravel and

much fine mineral and organic material. The latter is a mixture of abundant coniferous litter and fallen leaves of deciduous trees. There are no visible primary producers.

Water temperature was recorded every two hours with I-buttons (Dallas Semiconductor MAXIM), to the nearest 0.5 °C.

Specimens collected by kick-sampling with a 0.3 mm net were sorted manually. When presence of very small specimens was suspected, the sample fraction passing through a 4.0 mm sieve was preserved in ethanol and specimens picked under a dissecting microscope at 6-12x.

Biometry

Larvae with secondary sexual characters were sexed and details of vaginal scars recorded. Head capsule width across the eyes (HCW; excluding the narrow sclerite below the eyes which extends over the bases of maxillae) and several other body dimensions, especially labrum width (LW) of almost 1900 larvae and exuviae were measured to the nearest 0.1 mm with an eye-piece micrometer on a dissecting or a compound microscope, at magnifications 6x to 200x, depending on specimen size. Many small specimens and exuviae were mounted in Euparal on microscope slides.

Numerous sized larvae of all sizes were dried to constant weight at 80 °C and dry weight (DW) determined to the nearest 0.1 mg with a Sartorius microscale.

Transport and maintenance of live larvae

In July 2004 and in January 2007 live specimens were transported to Schlitz in small mesh bags floating in aerated stream water. Each bag contained 1-3 larvae of different sizes. After about 10 hours, larvae were transferred to flowing water in 1L sprinkler boxes (ZWICK & TESLENKO 2002, ZWICK & HOHMANN 2003) with some pebbles, at temperatures between 8-12 °C. Larvae were fed with seasonally available stream fauna, mainly small mayflies, stoneflies, and blackfly larvae. Sprinkler boxes were inspected every day. Moulded specimens were allowed to harden for 2 days, then preserved with their exuviae, and labrum width (LW) measured in both.

Egg incubation

On 7 July 2004, 34 females were intercepted during oviposition flights along the Springgraben and their egg masses stored separately in 15 ml vials, in about 1 ml water. Egg incubation in the laboratory followed routine methods (ZWICK 1996). Twenty-eight egg masses were incubated in darkness in a multi-chamber water bath (MARTEN 1990), at constant temperatures between 5.5 and 18.3 °C.

Six egg masses were kept in an incubator imitating the seasonally and diurnally changing field conditions of Springgraben. A 20W light bulb signalled photoperiod, according to tables of daylength at 51°N (<http://www.frank-schlotterbeck.de/seite123.htm>). When light was on, cooling was off and the incubator slowly warmed to outside temperature of the basement where it stood. Fig. 1 illustrates samples of the resulting regime. Temperature was recorded every 10 minutes with an I-button. Overall mean incubation temperature was 13.1 °C.

Egg masses were inspected every two days, hatchlings removed and counted. Number and condition of eventually remaining unhatched eggs were recorded.

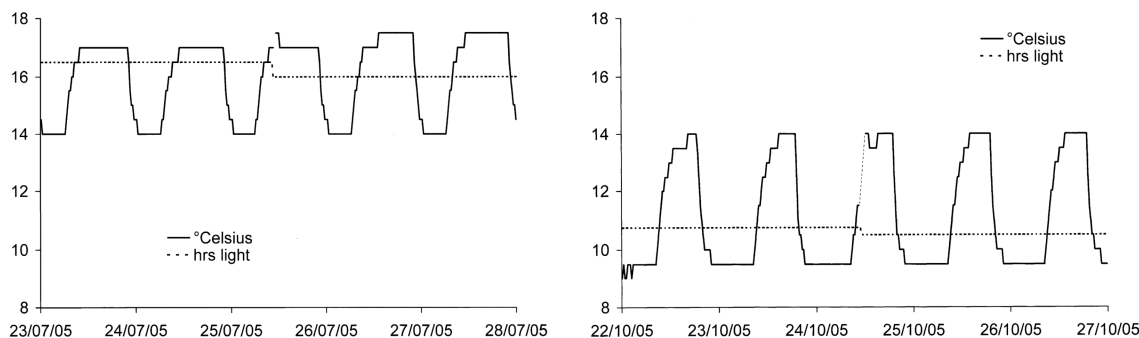


Fig. 1: *Dictyogenus fontium*, egg incubation under simulated field conditions, samples of the temperature and light regimes in summer and autumn.

Results

Stream temperatures

Springgraben exhibited pronounced annual (Fig. 2) and diurnal temperature amplitudes. The mean daily amplitude ranged from 1 degree in January to almost 3 degrees in May. Daily amplitude then declined again to little more than 1 degree in December.

Our summer and autumn measurements at the Schreierbach are more detailed than former ones but generally confirm the stable regime described by MALICKY (1978). There was some irregular variation but no regular daily pattern, mean temperatures during the day (11-17 hrs) had no consistent relation to mean nocturnal temperature (23-05 hrs) and there was no regular diurnal heat excess. These irregular variations apparently reflect temperature oscillations affecting Lunz generally because diurnal heat excess followed the same pattern at the two different streams (Fig. 3).

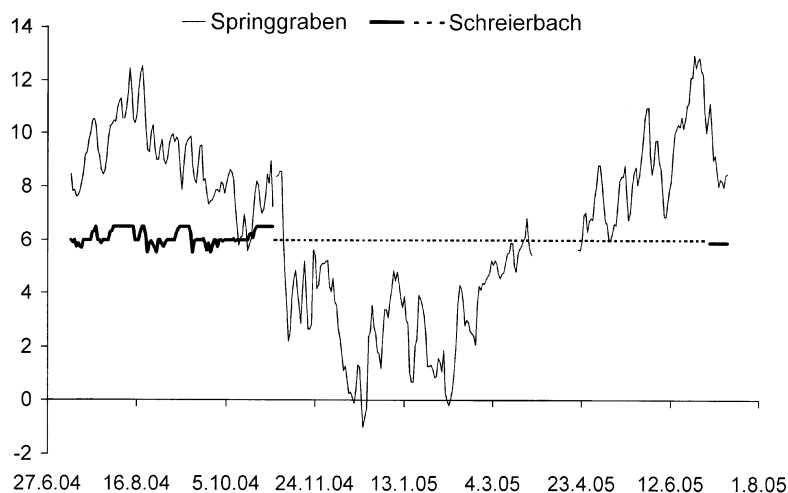


Fig. 2: Mean daily water temperature [°C] in the streams Springgraben and Schreierbach at Lunz, 2004-2005.

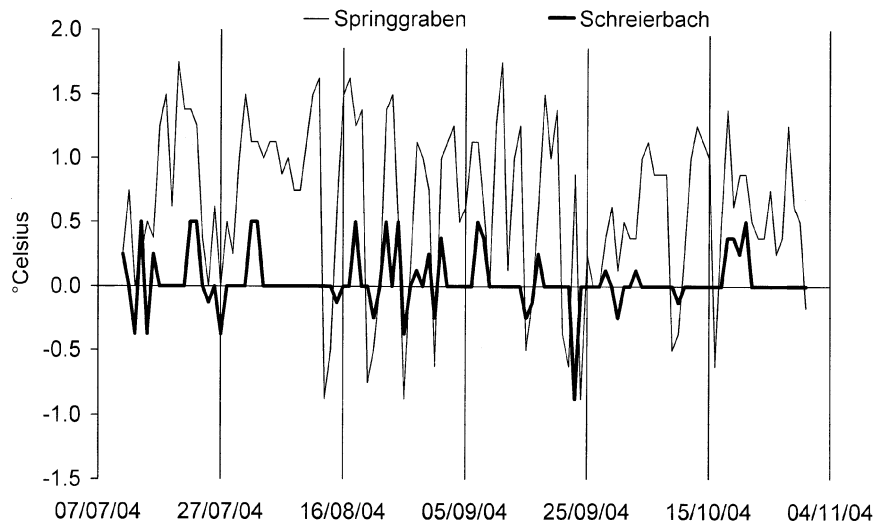


Fig. 3: Springgraben and Schreierbach at Lunz, July-Oct. 2004, diurnal heat excess (°C, the difference between diurnal (11-17 hours) and nocturnal (23-05 hours) mean temperatures).

Temperatures during periods of equipment failure were extrapolated to estimate cumulative degree-days above zero. They were 2415 °days at the Springgraben and 2234 °days at the Schreierbach, respectively, during the one-year study period.

Life history

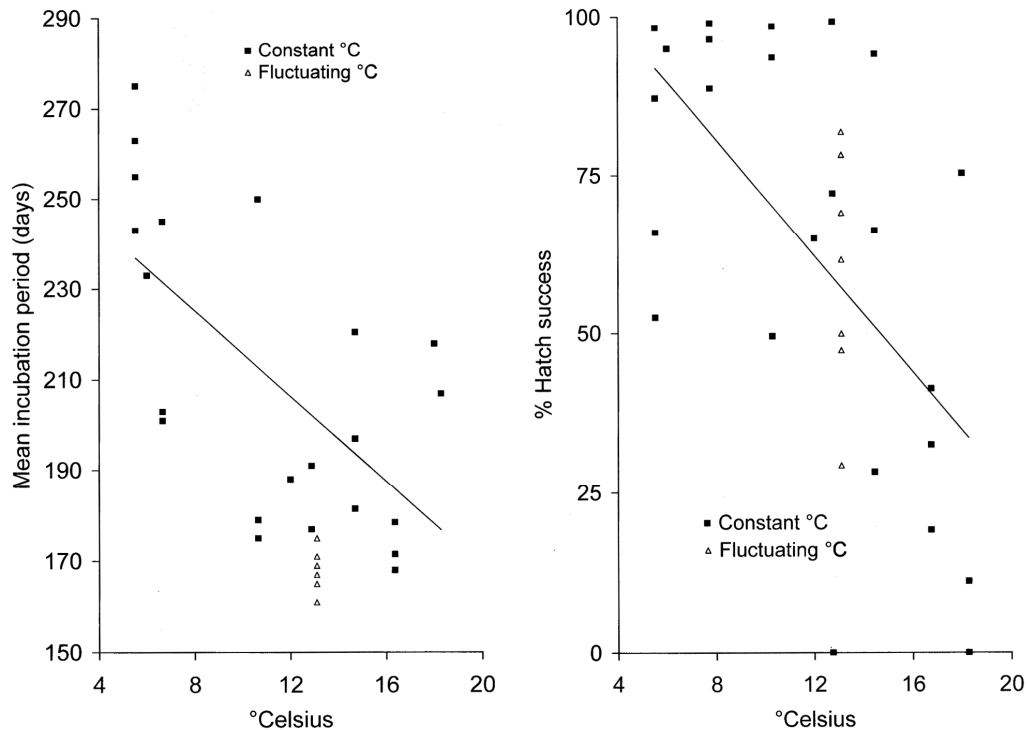
Adult flight period

In an emergence trap on the Schreierbach *D. fontium* first appeared in mid June and was present until October, occasionally December, with a distinct peak in August (ZWICK 1977). This conforms with the late appearance and presence of last-instar larvae in the benthos, see below.

Occasional field observations of adults as well as benthos samples indicate a peak flight period from late May to June at the Springgraben. Adults flying in early July were mainly females, most nearly spent, with only a small residual egg mass. At the same time, large larvae were no longer present in Springgraben.

Egg incubation

Eggs develop directly (ZWICK 1982), incubation takes long. Mean incubation period ranges from 243-275 days at 5.5 °C and drops to 160-190 days at 13 °C, most clearly under a fluctuating regime. At still higher temperatures, the incubation period is not reliably shortened further (Fig. 4). Hatch success is negatively temperature related (Fig. 5). Degree days above freezing point accumulated until mean hatch rise strongly with temperature. Relations can be described by highly significant linear correlations but low degrees of determination and high standard errors reflect the considerable variation between batches (Tab. 1).



Figs 4, 5: *Dictyogenus fontium*, mean incubation period (4, left) and hatch success (5, right) at various constant and fluctuating temperatures, respectively, with linear trend lines.

Tab. 1: *Dictyogenus fontium*, regression parameters of egg incubation.

	Incubation Period (Days)	% Hatch Success	Cumulated Degree Days
Slope	-4.89 ± 1.03	-3.78 ± 1.04	156 ± 12
Intercept	257 ± 13	111 ± 13	417 ± 146
R ²	0,41	0,33	0,85
Sign.	***	***	***
N of Observations	34	28	34

Population structure and length of life cycle

HCW size frequency distributions using 0.2 mm classes were calculated and data converted to percentages of samples (Fig. 6). In both streams, eggs laid in June and August, respectively, into the Springgraben and Schreierbach, respectively, hatched only the next spring when first-instar larvae (HCW <0.3 mm and characteristic morphology: ZWICK 1982) were found in the April 2005 samples. There were none in the January sample from Springgraben.

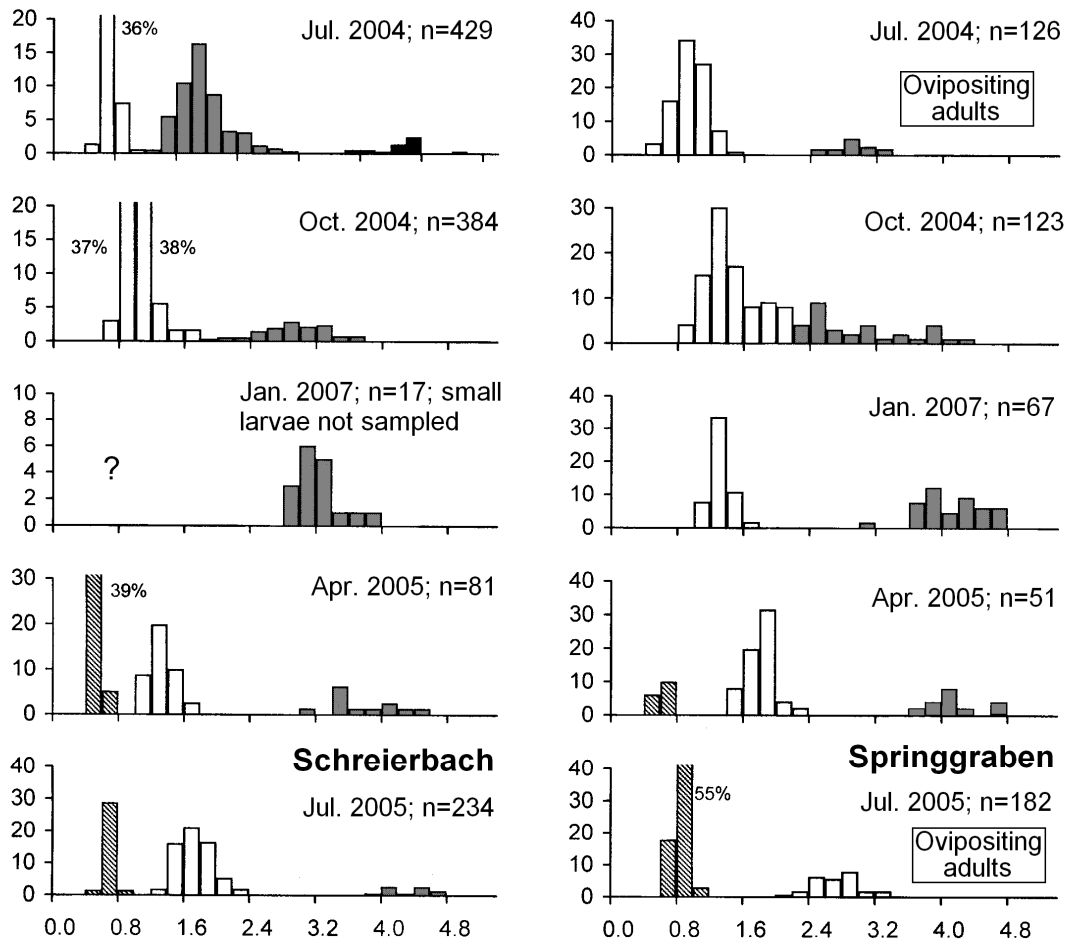


Fig. 6: *Dictyogenus fontium*, population structure in Schreierbach (left column) and Springgraben (right column) at different times. Histograms show percentage of 0.2 mm HCW size classes in each sample. Different cohorts distinguished by shading. Note that the January sample was taken in a different year than the other samples; at that occasion, high discharge in the Schreierbach prevented sampling of small specimens with a fine net.

In summer, three simultaneous generations were observed in both streams. The group of largest specimens in the Schreierbach comprised only late-instar larvae while there were already ovipositing females at the near-by Springgraben. Growth of the two cohorts of smaller larvae was clearly faster in the summer-warm Springgraben than in the Schreierbach at 6 °C. In autumn, the two larval cohorts appeared to be connected by specimens of intermediate size. In winter and spring, the size difference between the two cohorts in each stream was restored. Large larvae taken in Springgraben in January 2007 were in the penultimate instar, those in Schreierbach were 2 instars younger. A few last-instar larvae (ZWICK 1982, 2003) were taken in April in Springgraben, but only in July in the Schreierbach.

From data on egg incubation and the fate of cohorts in Fig. 6 it results that eggs laid in a given year will yield neonates in early spring the next year, in both streams. Larvae then grow for a little more than two years until they emerge as adults, in June at one stream, in August at the other. The complete life cycle, from oviposition to adult emergence, takes three years.

Larval feeding and cannibalism

For shortness of laboratory space, three larvae were kept together in each sprinkler tray. To nevertheless guarantee correct exuvial associations in case of moults, one very small, one medium sized and one large larva were kept together. Mayfly- or blackfly larvae placed in the trays were immediately attacked and devoured. However, *Gammarus* spp. and larvae of other Plecoptera (Nemouridae, *Leuctra*) were not eaten. In particular, the *Dictyogenus* larvae avoided each other completely. Larvae abruptly withdrew upon accidental contact. Even the smallest freshly moulted, completely white and soft larvae were never eaten by larger conspecifics living in the same tray.

Growth at moults, building up of biomass

Increment of linear measures of larvae at moults in the laboratory decreased linearly with absolute size, irrespective of sex. Increase of linear measures at moults ranged from 2-15%, with a mean of only 9%. This is extremely low and also in conflict with size differences between morphologically identified late instars, see below.

Biomass increase during larval growth to a size of 20 mm body length is illustrated in Fig. 7. Compare Tab. 2 for the relationship between size and dry weight.

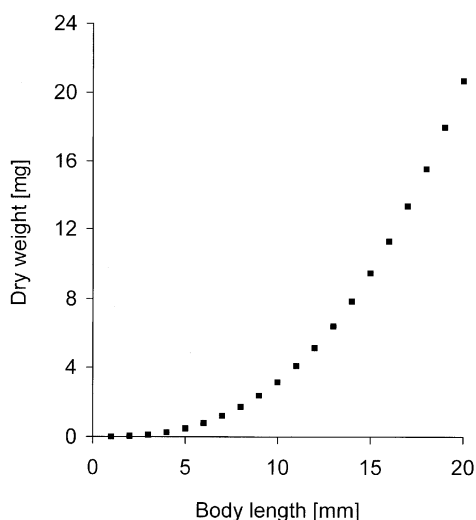


Fig. 7: *Dictyogenus fontium*, relation between body size and dry weight.

Biometry

Several most highly significant ($P \leq 0.001$) linear correlations between body dimensions of *Dictyogenus* larvae were found (means ± 1 SE). Linear dimensions (BL, body length; HCW, head capsule width; LW, labrum width) are in mm, dry weight (DW) is in mg (Tab. 2).

Tab. 2: Parameters of biometric regressions for larval *Dictyogenus fontium*.

$HCW = 1.563 (\pm 0.015) * LW + 0.207 (\pm 0.027); R^2 = 0.992; n = 91$
$BL = 4.7863 (\pm 0.0687) * HCW - 0.7346 (\pm 0.1730); R^2 = 0.980; n = 100$
$\ln DW = 2.6949 (\pm 0.0830) * \ln BL - 5.0629 (\pm 0.0830); R^2 = 0.981; n = 95$
$\ln DW = 3.0231 (\pm 0.0417) * \ln HCW - 1.3199 (\pm 0.0326); R^2 = 0.982; n = 95$

Sexual dimorphism

The HCW of neonates from a single egg mass ranged from 280-340 μm , with a distinct peak at 300 μm . The size distribution was unimodal and only slightly skewed towards smaller sizes (Fig. 8).

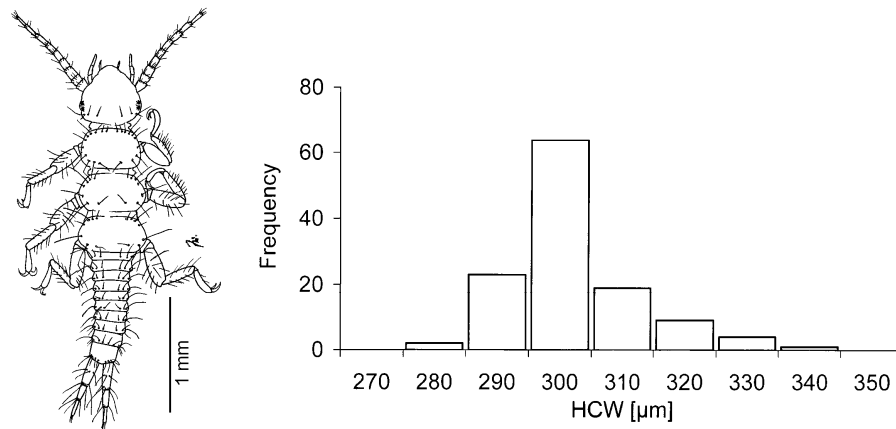


Fig. 8: *Dictyogenus fontium*, first-instar larva (from ZWICK 1982, with permission; <http://www.schweizerbart.de>) and size distribution (HCW) of first-instar larvae; siblings from Springgraben, 2004. N = 122.

Up to a HCW of about 1.4 mm or a body length of about 6 mm the size distribution was unimodal, larvae could not be sexed. When HCW attained 1.6 mm in the second year of life, female specimens could be recognized by the medially interrupted marginal setation of sternite 8. In males the setal fringe on sternite 8 was entire. Males developed no distinct additional secondary sexual characters. In fact, males were most easily recognized as "non-female". When the setal fringe of sternite 8 became divided, females developed also a vaginal scar on sternite 8. It became increasingly distinct in late instars and eventually took characteristic shapes, see below.

Once a vaginal scar first appeared the size distribution became bimodal (Fig. 9), males being smaller than females. The magnitude of the size difference could only be assessed in defined instars, i.e., in the last three instars when wings begin to develop (see below). Mean HCW of last-instar males was 3.8 mm, of females 4.5 mm. Average male and female dry weight were 15 and 22 mg, respectively. Last-instar male size resembled the size of females that were one instar younger (Fig. 10).

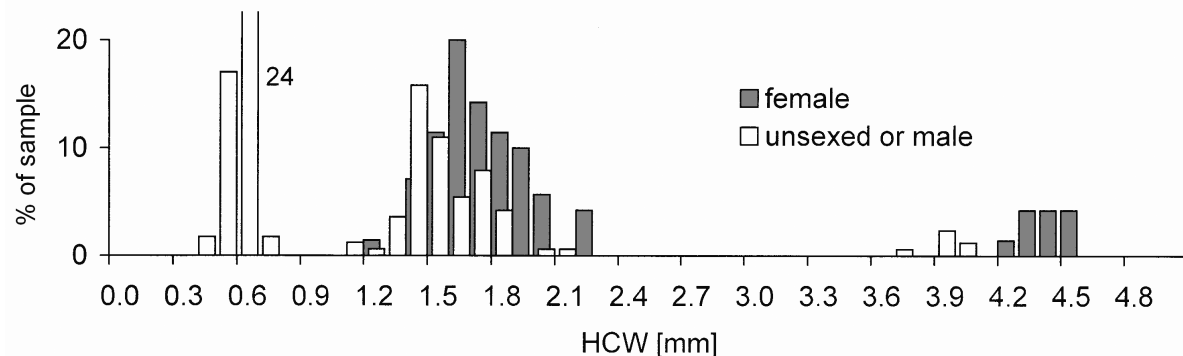


Fig. 9: *Dictyogenus fontium*, size frequency distribution of larvae in the Springgraben at Lunz, in July 2005, and sexual size difference.

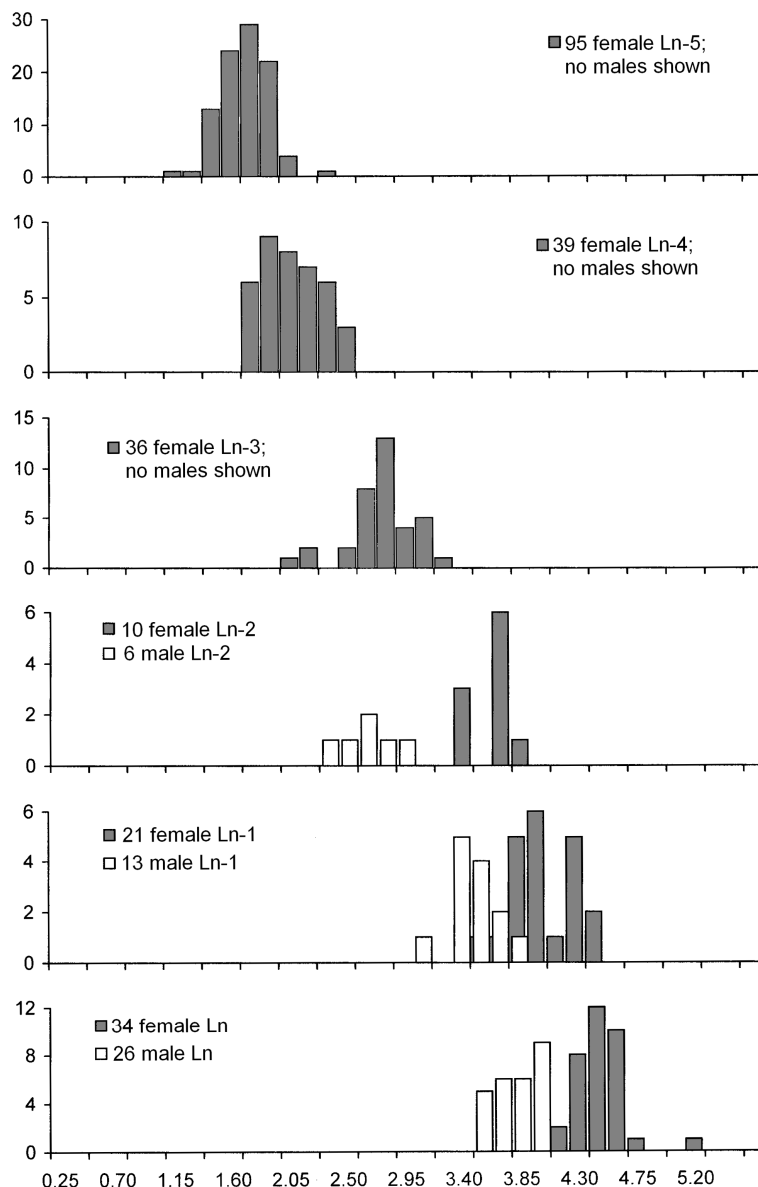


Fig. 10: *Dictyogenus fontium*, frequency (ordinate) of sizes (mm HCW, abscissa) of female and male larvae, respectively, during the last six and last three, respectively, morphologically identified instars.

Morphological change during metamorphosis

Wing development. Small larvae lacked wing pads and secondary sexual characters. The most obvious change during the stepwise metamorphosis was the appearance of wing pads which take very different shapes in the various families of Plecoptera. In most, also in Perlodidae, there are three wing-pad-bearing late larval instars which can often be identified by eye. Wing pads may first appear in very differently sized specimens. Characteristic relations between linear measures representative of body size (mainly head width, or labrum width in exuviae) and wing length (or total notum length, including wing; Fig. 11) permit reliable instar assignments (ZWICK 2003). Bimodal size frequency distributions in the last instar recorded by ZWICK (2003) were only due to mixed samples including larvae of both *Dictyogenus* species.

In *Dictyogenus*, the rear angles of meso- and metanotum became pointed in the antepenultimate instar, instead of remaining rounded as they were in younger larvae. Only in the penultimate instar distinct lengthening of the pterotheca was observed which became very pronounced in the final instar (Fig. 11).

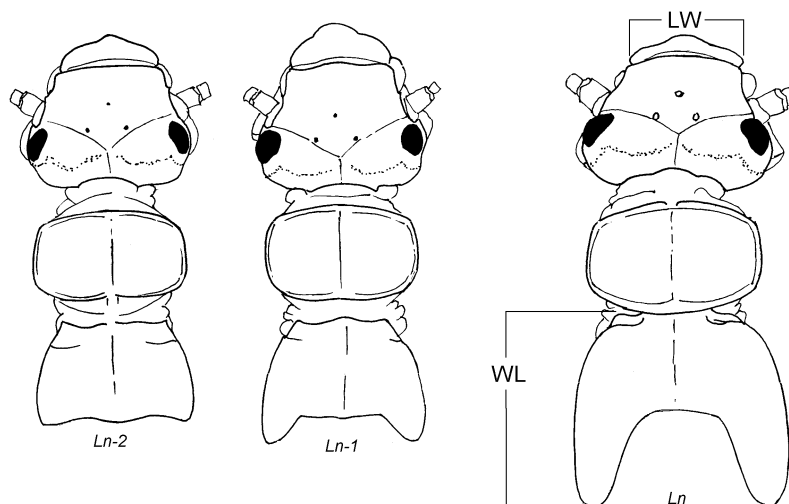


Fig. 11: *Dictyogenus fontium*, wing development during the last three larval instars. The ways in which labrum width (LW) and wing length (WL) were determined are indicated on the last instar specimen. Not to scale, distance from front edge of clypeus to rear edge of mesonotum shown to similar size.

Gonads. A vaginal scar, a secondary sexual character, first appeared in females just over 6 mm long. Some such specimens were dissected and found to possess early stages of ovaries. Similarly sized specimens without vaginal scar were indeed males with developing testes. In Plecoptera, the lateral gonads are anteriorly connected and loop-shaped (ZWICK 1973). The early rudiments of genitalia were too delicate to see any connection, if present. The early gonadal rudiments were very simple, the following successive stages were recognized in females and males, respectively:

Females:

1. Ovarioles bag-shaped, nuclei not ordered.
2. Ovarioles club-shaped, serial arrangement of nuclei.
3. ca 8 egg rudiments of similar size per ovariole.
4. ca 10 egg rudiments per ovariole, caudal ones progressively larger than anterior ones.

Males:

1. Testes a narrow band difficult to distinguish from fat body.
2. Distinct follicles, nuclei dispersed.
3. Nuclei in follicles grouped.

The six female specimens examined showed no clear correlation between body size and ovarian status. In contrast, the relation between testicular status and body size was obvious (Fig. 12).

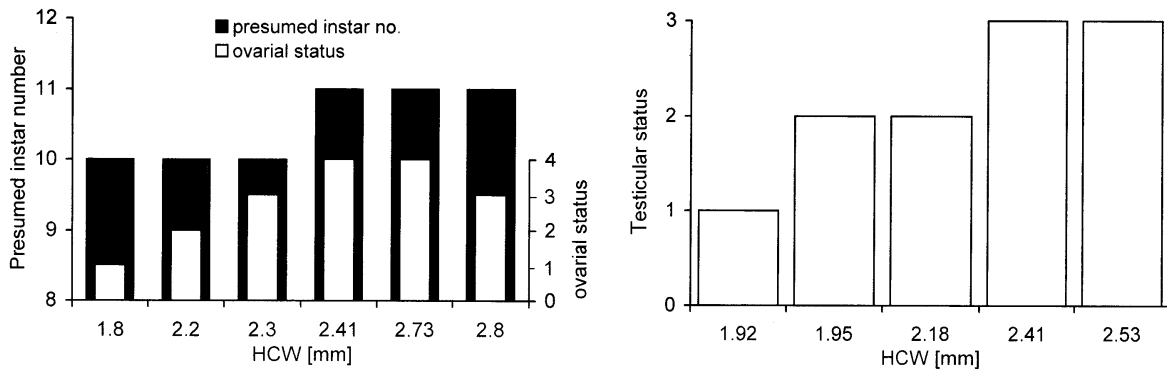


Fig. 12: *Dictyogenus fontium*, early sexual differentiation in small larvae. Left, stage of ovary and presumed instar number versus head capsule width (HCW). Right, stage of testis development versus HCW.

Secondary sexual characters. Male larvae showed no secondary sexual characters permitting instar distinctions. In contrast, in the last 6 instars female larvae showed differently shaped scars of the developing genital opening (ZWICK 1982). Comparisons of exuviae with freshly moulted captive specimens now confirmed that the illustrated shapes (Fig. 13; after ZWICK 1982) indeed represent successive instars:

Ln-5: Faint impression resembling an inverted V near middle of sternite 8, minute notch in rear margin of sternite.

Ln-4: Distinct impression with converging rounded margins in rear half of sternite 8. A faint line connecting scar to a notch in caudal margin often visible.

Ln-3: Vaginal scar wide, touching margin of sternite 8, caudal edges turn outward and merge with segment margin, dorsal wall of vaginal invagination exposed.

Ln-2: Invagination completely covered, a narrow cuticular triangle with darker lateral portions visible by transparency.

Ln-1: Invagination anteriorly rounded, about as long as its caudal width. Segmental margin contracted.

Ln (last instar): Vaginal invagination short, much wider than long, segmental margin projecting.

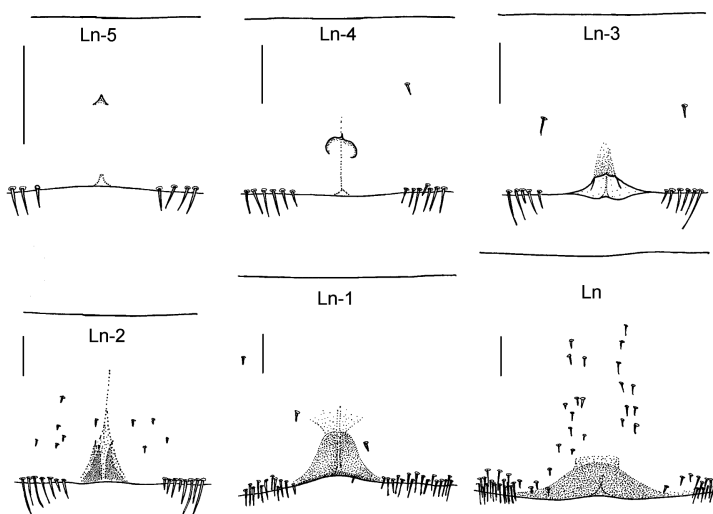


Fig. 13: *Dictyogenus fontium*, morphology of vaginal scars in the last 6 instars. Modified from ZWICK (1982; <http://www.schweizerbart.de>), with permission. Scale lines are 0.2 mm long.

Number of instars

HCW of females in each of the last 6 instars overlapped (Fig. 10), but means or modes of frequency distributions were distinct. Between instars, mean HCW increased 1.1- to 1.3-fold. The average increase of 1.22 was used to back-calculate HCW until estimates were almost identical to the known size of first-instar larvae. According to this model, female larvae grow through a total of 15 instars (Fig. 14). The last 6 instars are morphologically distinct by the vaginal scars, the last three additionally by the wing pads.

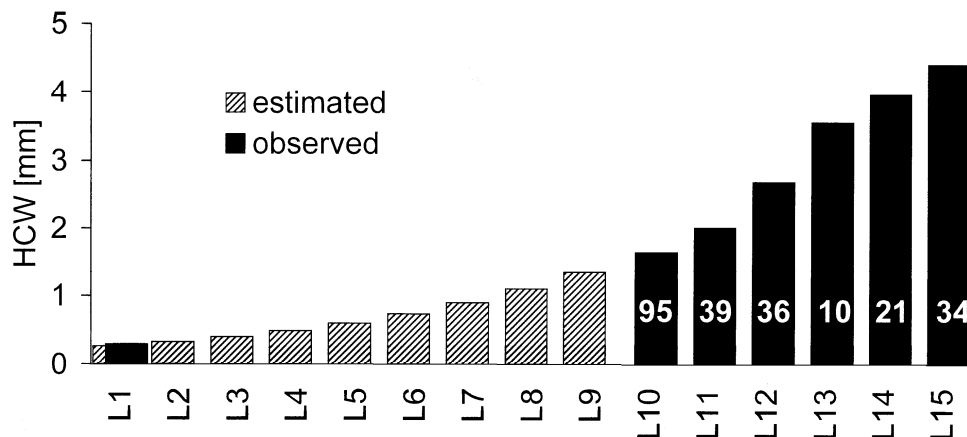


Fig. 14: *Dictyogenus fontium*, model of a female growing through 15 instars from egg to adulthood, based on extrapolation between the directly observed and morphologically identified first and the last six instars. Number of specimens examined was >100 for the first instar, and is indicated for the other.

Discussion

Egg development. Incubation periods tend to be proportional to egg size (GILLOOLY & DODSON 2000), *Dictyogenus* is comparable to other Plecoptera species with similarly sized eggs (MARTEN 1991, ZWICK 1982). A strong decline of hatch success with rising temperature certainly contributes to the restriction of the species to springs and epirithral mountain streams.

Larval feeding. *Dictyogenus* larvae are said to be aggressive carnivores and, at least in captivity, cannibals (KÜHTREIBER 1934: 112). FENOGLIO et al. (2007) report some cannibalism in the field, while our own observations demonstrate strict avoidance of congeners, in captivity. A similar avoidance of cannibalism was observed in otherwise highly aggressive ground beetle larvae, possibly because intra-specific recognition inhibits cannibalism (BRANDMAYR et al. 2004).

Guts of small larvae from the Schreierbach contained significant amounts of colonial diatoms (ZWICK 1982), in addition to animal prey. FENOGLIO et al. (2007) also observed important amounts of vegetal matter in the guts of some larvae, of very different sizes.

Life cycle length. The *Dictyogenus* life cycle was believed to extend over two years (KÜHTREIBER 1934: 170). Whether this included the direct but long egg development was not stated.

Population structure at Lunz clearly documents a three-year cycle of *D. fontium* in both of the thermally different streams. Fast larval summer growth leading to early adult emergence and oviposition at the Springgraben is counteracted by delayed egg development in autumn and winter. At constant 6 °C in the Schreierbach, adult emergence and oviposition are delayed but egg development continues over winter. Neonates appear in spring, in both streams.

In comparisons of the life history of *Dictyogenus fontium* with other Perlodidae, egg incubation and period of larval growth must be distinguished. Many species have semivoltine life histories mainly because of extended egg diapauses, the period of larval growth being not particularly long. In *D. fontium*, larval growth continues for more than two years which is unique among Perlodidae. Larvae of *Guadalgenus franzi*, a close relative of the present species, grow for two years in intermittent streams of Southern Spain (AGUERO-PELEGRIN & FERRERAS-ROMERO 2002). On the other hand, *Arcynopteryx compacta* and *Diura nanseni* complete larval growth within a year, at far northern latitudes (LILLEHAMMER 1988, LOSKUTOVA 2006). In the European fauna, *Perlodes* spp. hold the record, growing to a size similar to that of *Dictyogenus* in about 7 months, during the coldest part of the year (HYNES 1961, ELLIOTT 1967). The known life histories of the many North American Perlodidae (STEWART & STARK 1988) also include no examples of larval growth continuing for more than two years.

Number of instars and sexual dimorphism. We attempted to use increment at individual moults in the laboratory to analyse growth patterns and estimate instar numbers but were unsuccessful. The low increment at individual moults observed in the laboratory suggests artifacts occurred. Probable causes of failure are insufficient quality and quantity of food, and disturbance by conspecifics in the same sprinkler trays (LIESKE & ZWICK 2008).

However, the excellent visibility of female genital scars on the smooth and almost hairless yellowish cuticle of the larval abdomen allowed the distinction of the last six larval instars. This is distinctly more than in other Plecoptera where usually only the three wing-bearing instars can be identified (ZWICK 2003). The model extrapolating size between the last six and the first instar suggests a total of 15 larval instars in females. This is in keeping with several other independent estimates suggesting 9 to 16 instars for other stoneflies. The larger the species, the greater the number of instars, for example, as few as 12 in small *Leuctra* (ELLIOTT 1987a, b) but 16 in very large *Pteronarcys* species (ZWICK & TESLENKO 2002). Higher estimates (for example ŠÁMAL 1923, VAUGHT & STEWART 1974) are based on discontinuities in size-frequency-distributions which have since been shown to be unreliable (FINK 1984).

Female Plecoptera are generally larger than males, female biomass exceeds male weight twice or even three times (ZWICK 1980). Head widths of male *Dictyogenus fontium* are similar to those of females that are one instar younger (Fig. 10), same as in other Plecoptera. It has been suggested that males in fact grow through one instar less than females (ELLIOTT 1984, 1987a,b, KHOO 1964, OBERNDORFER & STEWART 1977, ZWICK & TESLENKO 2002). Alternatively, lower growth rates of males as observed in other Plecoptera (FRUTIGER 1987, TOWNSEND & PRITCHARD 1988) may apply. Our own records of growth rates at moults (which reveal no difference) seem to be affected by laboratory artifacts. However, since the sexual size difference arises early in life and increases at each moult we favour the idea of lower male growth rates.

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Zusammenfassung

Die Biologie der großen Steinfliege *Dictyogenus fontium* wurde in Lunz am See, Niederösterreich, mehrere Jahre lang in zwei Bächen untersucht. Von Juli 2004 bis Juli 2005 wurden etwa alle drei Monate Benthosproben mit einem Netz (0,3 mm Maschenweite) genommen. Die Wassertemperatur im Springgraben schwankt saisonal zwischen 0°C und 13°C, im nahen Schreierbach herrschen konstant etwa 6°C. Eientwicklung und morphologische Veränderungen bei larvalen Häutungen wurden im Labor untersucht. Der Einsatz der Gonadenentwicklung wurde durch Sektion, die Ausbildung sekundärer Geschlechtsmerkmale an den Anlagen der weiblichen Geschlechtsöffnung studiert. Von der Eiablage bis zum Schlüpfen der Imagines vergehen drei Jahre, mehr als bei anderen Perlodidae. Nach schnellem Larvenwachstum im Frühjahr schlüpfen die Imagines im Springgraben drei Monate früher als bei konstant 6°C am Schreierbach. Der Zeitgewinn am Springgraben wird aber durch verzögerte Eientwicklung im Winter kompensiert, an beiden Bächen schlüpfen die Junglarven gleichzeitig im Frühjahr. Bei 6 mm langen Larven wurden erste Gonadenanlagen festgestellt. Zugleich wird die Größenverteilung bimodal, weibliche Larven zeigen erste Anlagen der Geschlechtsöffnung, die nach sechs Stadien ausdifferenziert ist. Die drei letzten Stadien können anhand der Flügelanlagen unterschieden werden. Beide Geschlechter durchlaufen trotz ausgeprägter Größenunterschiede vermutlich 15 Häutungsstadien.

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