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Egg development in the mayflies of a Swiss glacial floodplain

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Abstract. The duration and timing of egg development is crucial to the survival of invertebrates in glacier-fed rivers. The relationship between egg development and environmental conditions was investigated in 3 mayfly species, *Baetis alpinus*, *Rhithrogena nivata*, and *Ecdyonurus picteti*, in an alpine glacier-fed alluvial system. Field-collected eggs were reared in the laboratory at temperatures representing field conditions (1.5, 3, 5, and 7°C). Egg-incubation period and degree-days demand (DD) were determined, and hatching in the field was predicted from field temperature records. Egg development and temperature relationships for *B. alpinus* and *R. nivata* were documented for the first time. *Baetis alpinus* had synchronous egg development and high hatching success. Faster development in warmer habitats enabled it to hatch during favorable autumnal conditions. *Ecdyonurus picteti* had a very long development time that decreased slightly at higher temperatures. However, the variation in DD was considerable. The observed long and delayed hatching would favor successful development in unpredictable habitats at the low temperatures experienced in these glacial conditions. *Rhithrogena nivata*, one of the most extreme cold-adapted mayfly species, had a long egg incubation period, and success in development largely depended on the timing of hatching and discharge conditions. This species could exploit extremely unstable and cold habitats where other species are limited by low water temperatures.

Key words: embryonic development, egg rearing, incubation period, degree-days demand, hatching, glacial streams, low temperature, Rhône, Swiss Alps, *Baetis alpinus*, *Rhithrogena nivata*, *Ecdyonurus picteti*.

A complete understanding of life histories in aquatic insects requires information on egg development because this period determines the timing and temporal extent of recruitment of new cohorts (Butler 1984). The major factor influencing egg development in aquatic insects is water temperature (e.g., Sweeney 1984, Lillehammer et al. 1989, Pritchard et al. 1996, Füreder 1999). The duration of the egg stage is considered short compared to other life stages (Butler 1984), but it is crucial in cold environments where differences in characteristics of egg development can lead to a shift in voltinism. However, studies that consider features of the egg stage (obtained from laboratory or field studies) and ecological conditions simultaneously to understand the life history of a population are sparse (Brittain 1978, Lillehammer et al. 1989).

Our study focuses on glacier-fed river systems, characterized by low water temperatures, a glacier-melt-dominated flow regime, large diel flow fluctuations, high turbidity in summer, and low channel stability (Milner and Petts 1994, Ward 1994). This system experiences substantial, but predictable, disturbances in spring and summer (Röthlisberger and Lang 1987, Poff 1992), but unpredictable large glacial or late-autumn floods that are mostly related to rain events may also occur (Collins 1998). This degree of instability and unpredictability generates spatial and temporal heterogeneity (Ward et al. 1998, Milner et al. 2001). Gradients in water temperature also are crucial in determining benthic taxonomic richness (Milner et al. 2001).

The community structure and dynamics of such environments have been well studied during the last decade (Brittain and Milner 2001, Ward and Uehlinger 2003), but few studies have been devoted to insect life histories. Egg development of the 3 most abundant mayfly species, *Baetis alpinus* (Pictet 1843), *Ecdyonurus*

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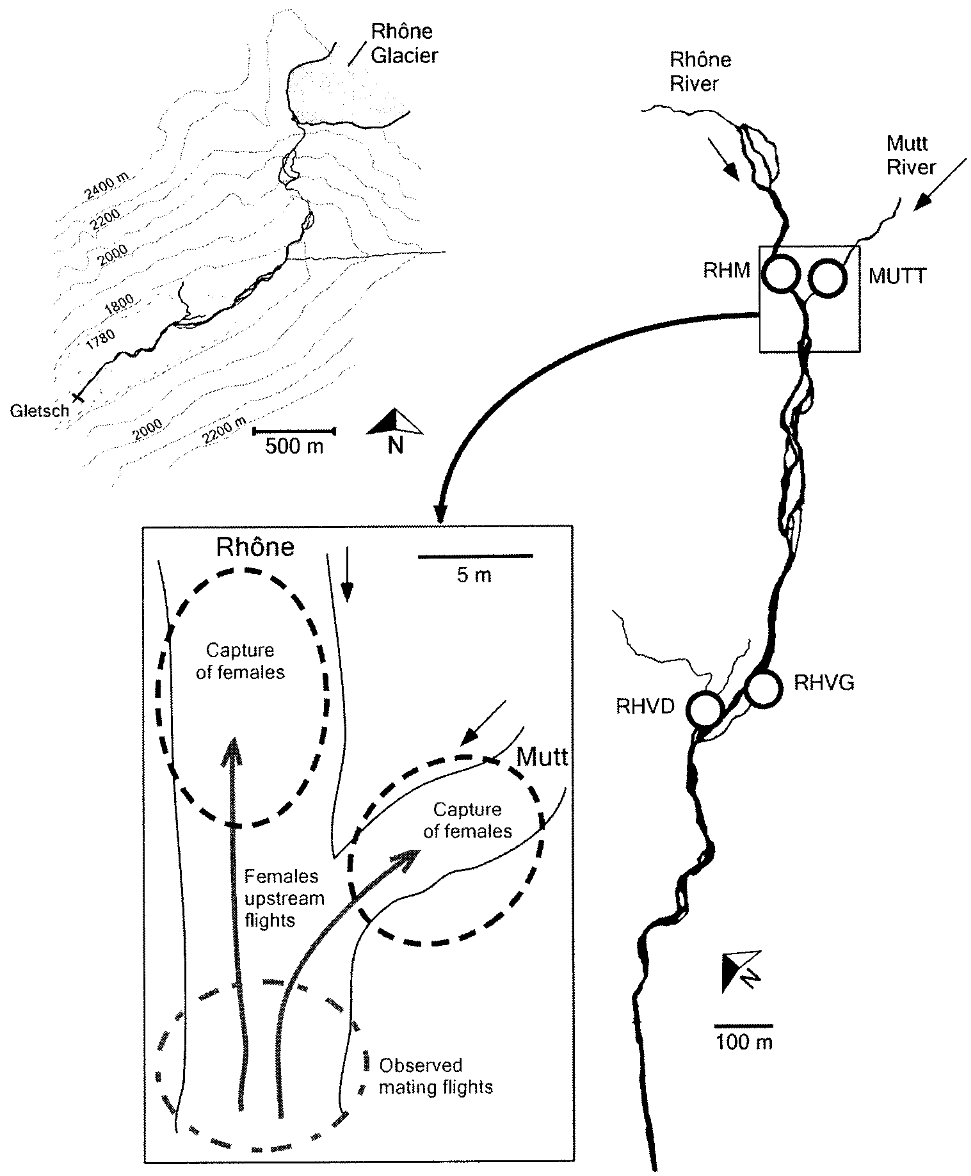

FIG. 1. Location of study sites on the Rhône and the Mutt rivers. The areas where adults were observed and captured are indicated in the detailed sketch. MUTT = the Mutt, RHM = the main channel of the Rhône above the Mutt confluence, RHVD = the right bank of the main channel of the Rhône below the confluence, RHVG = the left bank of the main channel of the Rhône below the confluence.

picteti (Meyer-Dür 1864), and *Rhithrogena nivata* (Eaton 1871), collected from the same glacier-fed river system was investigated in the laboratory at temperatures representative of field conditions. The hatching periods in the field were then predicted from field temperature records. The ultimate aim of our study was to explain possible developmental strategies enabling successful hatching in different reaches of a glacier-fed floodplain system. The following points were examined: 1) documentation of egg development in relation to water temperature under laboratory conditions, 2) prediction of hatching periods in the field in different habitats, and 3) timing and duration of egg development in relation to total life history and distribution of species.

Methods

Study area

The study area, the Gletschbode floodplain, is located in the Swiss Alps (lat 46°34′N, long 8°22′E) at a mean altitude of 1790 m asl (Knispel and Castella 2003; Fig.1). The floodplain is snow-covered for 8 mo/y. The floodplain has been formed by the confluence of 2

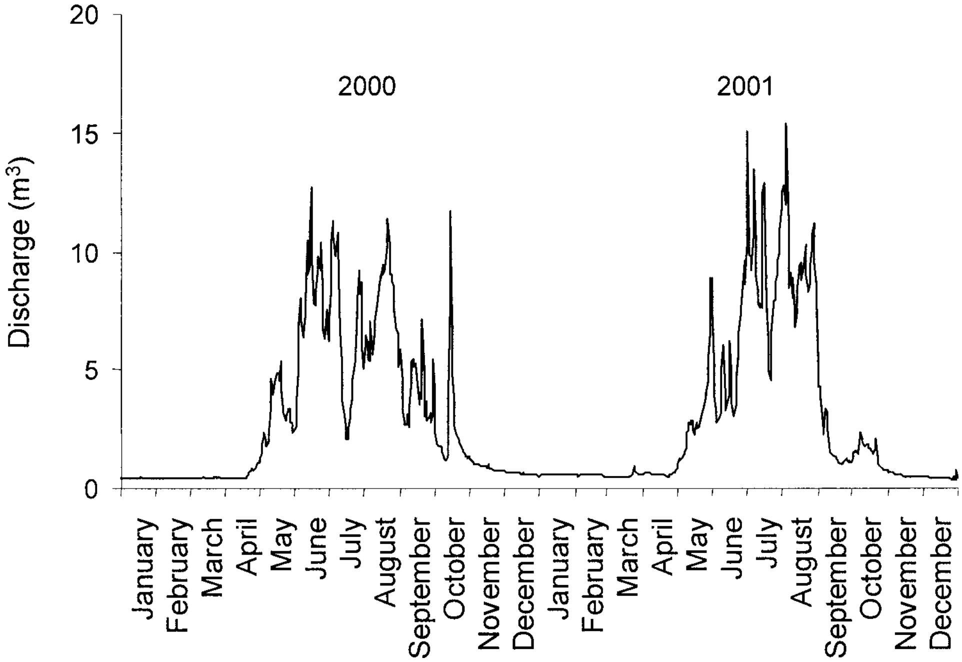

Fig. 2. Average daily discharge of the Rhône River for the study period (2000–2001). Data are from the Swiss National Hydrological and Geographical Survey.

glacial rivers, the Rhône and its tributary, the Mutt. The Rhône glacier (10.2 km^2) and the Mutt glacier (0.6 km^2) are situated 1 km and 3.5 km, respectively, from the confluence. The annual discharge pattern of the Rhône at the gauging station in Gletsch (1.5 km below the Rhône–Mutt confluence) reflects the strong glacial influence on discharge in summer and the low-flow conditions in winter (Fig. 2). The Mutt contributes 11% to the Rhône discharge on an annual basis (Bernath 1991). Mean conductivity was 10 µS/cm in the upper Rhône and 154 µS/cm in the Mutt. Suspended sediment concentrations varied more widely in the Mutt (0.5–1480 mg/L) than in the Rhône (12–913 mg/L).

Daily mean water temperature can reach 10°C during summer in the Mutt, but is $<$3.5°C in the Rhône above the confluence. Water temperatures were recorded hourly for $\geq$1 y at 4 locations: the Mutt (MUTT), the main channel of the Rhône above the Mutt confluence (RHM), the right bank of the main channel of the Rhône below the confluence (RHVD), and the left bank of the main channel of the Rhône below the confluence (RHVG; Figs 1, 3). Missing temperature data were inferred from data from the closest site for which data were available. For prediction of egg-development duration and hatching periods in the field, accumulated degree days (dd) were calculated monthly from average daily values for each of the 4 sites from the date of oviposition.

The study area is at the edge of the ranges of these mayfly species (Sartori and Landolt 1999). *Baetis alpinus* has a southern and central European distribution. *Ecdyonurus picteti* is present in central Europe as far east as the Carpathians, whereas *R. nivata* is endemic to the Alps. All 3 species have been recorded at altitudes up to the epirhithral zone.

Collection and preparation of the eggs

Larval development was followed in the field. As soon as final-instar larvae (with black wing pads) of a particular species were observed, field studies were intensified so that we would be present during mating flights. Mating flights were observed on 3 occasions in August (15–17 August 2000) and 1 occasion in September (12 September 2000). Males were observed late in the morning, mainly patrolling one reach of the Rhône River (Fig. 1). Females were observed ~1 h after the males appeared. They flew through male swarms, mated, and then flew upstream. Fertilized females were caught in defined areas (Fig. 1) using a hand net equipped with a 3-m-long pole. The females were kept in boxes with mesh to allow air to circulate, and eventually they were placed in a cooling box. Males also were caught to assist identification. Male and female *Ecdyonurus* were identified as *E. picteti* using comparative reference specimens. Females of *R. nivata* were identified by comparing their eggs with those of reared specimens of *R. nivata*, *R. loyolaea*, *R. alpestris*, *R. degrangei*, *R. endenensis*, and *R. hybrida* from alpine

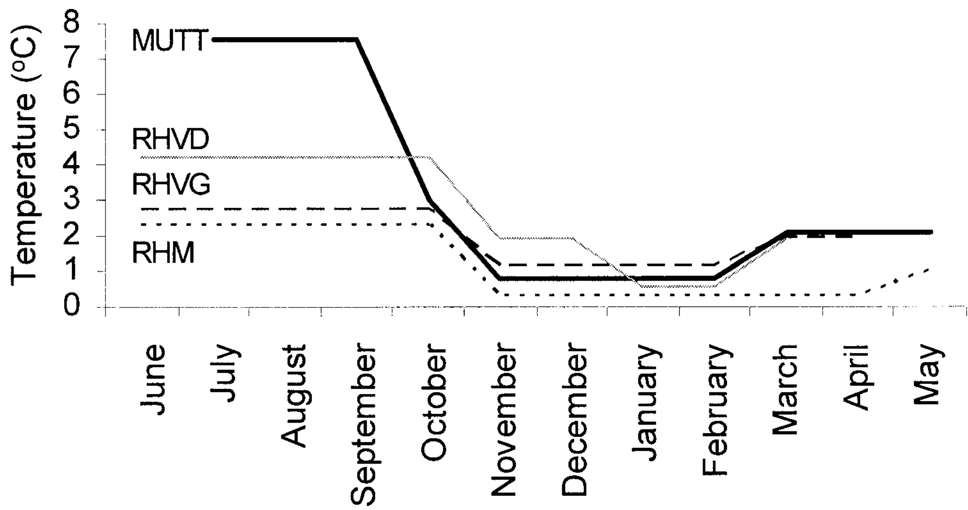

FIG. 3. Mean monthly water temperatures at the 4 study sites (1998–2000). Site abbreviations as in Fig. 1.

locations, using electronic scanning microscopy (Musée de zoologie, Lausanne, unpublished data). *Baetis alpinus* was the only *Baetis* species present in the study area.

Adults were transported to the laboratory the same day as they were captured, as soon as the mating flights were over. The abdomen of each female was dissected and the eggs were removed. Mating flights of *B. alpinus* were difficult to observe and the number of gravid females collected was insufficient to meet our study needs, so eggs were sought in the field. They were found in the form of dense masses stuck to the underside of stones (Elliott and Humpesch 1980). Light-colored egg masses were retained because they were freshly laid. Slightly orange egg masses were regarded as >1 d old, and were not used in our study.

Each egg mass was divided into 4 batches when the number of eggs/egg mass was sufficient. Each batch was placed in a separate Petri dish with stream water from a nonglacial, snowmelt-fed tributary of the River Rhône because Rhône water was highly turbid at the beginning of the experiment. Water quality does not appear to affect egg development in Ephemeroptera, and either spring water or water from the field locality has been used in other studies (Benech and Vignes 1972, Bohle 1972, Lillehammer 1975, Humpesch 1980). The Petri dishes were labelled and the corresponding female preserved in 80% ethanol. Petri dishes were placed in incubation cabinets at constant temperatures of 1.5, 3, 5, and 7°C under light conditions simulating the field photoperiod (12:12 in September–October, 11:13 in November, 10:14 in December–January, 11:13 in February, 12:12 in March–April, 14:10 in May). Batches from one female were placed in as many different temperature regimes as possible.

Observation of the egg batches

Petri dishes were checked regularly (almost daily) to follow development and count the number of hatching larvae. Once a week, batches were observed under a dissecting microscope to determine the stage of the most-developed eggs in a batch (as defined in Bohle 1968). Stages 3–4 are characterized by a retracted internal egg mass, leaving a translucent zone. Development stages 5–6 were particularly distinctive with the internal mass forming an opaque comma-shaped embryo against the eggshell. The duration of egg development until the first observation of stages 5–6 (time to stages 5–6) was noted for each batch of *E. picteti* and *R. nivata*. Egg-incubation period was defined as time (d) from the beginning of the experiment until 50% of the eggs that eventually hatched had done so (Lillehammer et al. 1989) for each batch of eggs that hatched. Hatching period was the time from when the first egg hatched to when the last egg hatched. Degree-days demand (DD) was calculated as dd required for the egg-incubation period. Hatching success was the % of eggs that hatched in each batch of eggs that hatched.

Statistical methods

Data analyses were done with S-PLUS software (version 4.5, MathSoft, Seattle, Washington). Nonparametric statistics were used to test differences in egg-incubation period, time to stages 5–6, and DD among batches at the 4 incubation temperatures. The Kruskal–Wallis rank-sum test was used to test whether egg-incubation period, time to stages 5–6, and DD were the same at all temperatures. The Wilcoxon

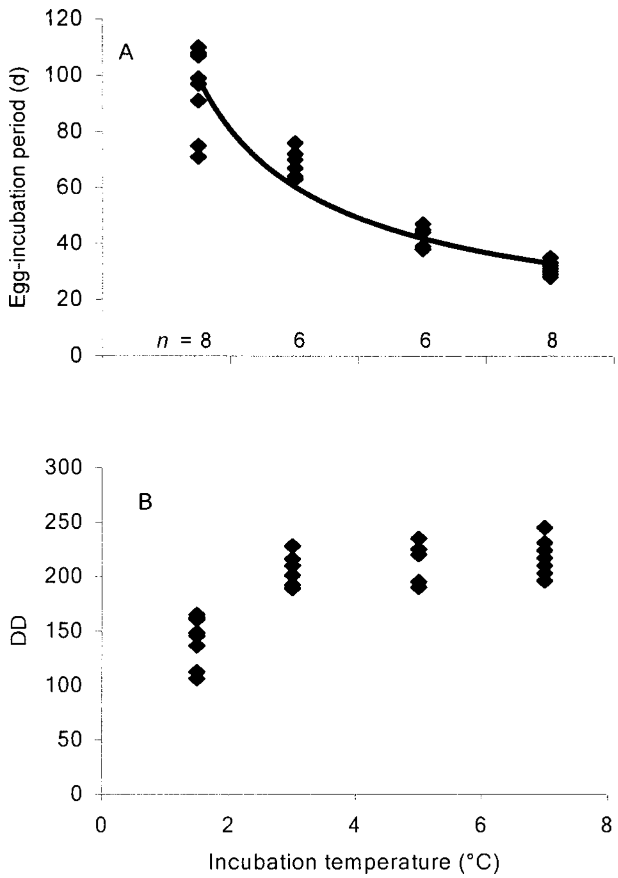

Fig. 4. Egg development in *Baetis alpinus*. A.—Relationship between egg-incubation period and incubation temperature. B.—Relationship between degree-days demand (DD) and incubation temperature. Each symbol represents an egg batch and the number of batches is given.

unilateral rank-sum test was used to identify which rank-sums were significantly different.

Results

Baetis alpinus

Baetis alpinus eggs (Appendix 1) were obtained from 14 females, 10 of which had already laid their eggs in situ. The total number of eggs/female varied from 640 to 1426 (974 ± 163, mean ± 95% confidence limit [CL]) among the 11 females for which number of eggs could be estimated, but some females may have laid >1 egg mass because several egg masses were collected from the same part of the streambed. The egg masses were separated into 35 batches, and 7 to 9 batches were incubated at each incubation temperature. All eggs in 5 batches died.

Hatching success was >95% in the remaining 30 batches. Hatching was synchronous, and 80% of the eggs hatched (10–90% interval) within a period of 5 d (4.8 ± 0.8 d; Appendix 1). The egg-incubation period decreased with increasing temperature, varying from 95 ± 10 d at 1.5°C to 31 ± 2 d at 7°C (Fig. 4A). The relationship between egg-incubation period and temperature was $y = 132.3x^{-0.715}$ ($R^2 = 0.924$, $n = 30$). DD did not differ among batches incubated at 3, 5, and 7°C (213 ± 7 dd, Kruskal–Wallis rank-sum test: $p = 0.3366$; Fig. 4B), but was significantly lower for batches incubated at 1.5°C (142 ± 15 dd, Wilcoxon unilateral rank-sum test: $p = 0$).

Ecdyonurus picteti

Sixteen fertilized *E. picteti* females were caught in the field. The mean number of eggs/female, estimated from 8 females with intact abdomens, was 1163 ± 358 eggs. The eggs were separated into 50 batches, and 11 to 15 batches were incubated at each incubation temperature. All eggs in 11 batches died. No hatching occurred in 23 batches, but development could be observed in the eggs, mostly up to stages 5–6, but sometimes only to stages 3–4.

Hatching success was 0.12 to 13.2% for the remaining 16 batches and averaged 1 to 6%, depending on incubation temperature (Appendix 2). The number of batches that hatched and hatching success were higher at 5 and 7°C than at 1.5 and 3°C. The hatching period ranged from 1 to 16 wk. Time to stages 5–6 generally was <250 d and was significantly shorter at 5 and 7°C than at 1.5 and 3°C when all data were considered (Kruskal–Wallis rank-sum test: $p = 0.0008$) and when extreme values (580 d for one batch at 3°C and 500 d for one batch at 7°C) were removed ($y = -11.69x + 170.5$, $R^2 = 0.236$, $n = 36$; Kruskal–Wallis rank-sum test: $p = 0.0005$; Fig. 5A). The egg-incubation period decreased with increasing incubation temperature ($y = 486.7x^{-0.815}$, $R^2 = 0.703$, $n = 16$; Fig. 5B). DD exceeded 480 dd for all batches. The mean DD was 672 dd, but DD did not change with incubation temperature (Fig. 5C). In 3 cases, egg batches taken from the same female had constant DD, independent of incubation temperature (950 dd for one female, 550 dd for 2 females; Fig. 5C, dotted lines).

Rhithrogena nivata

Twenty-five fertilized females were caught in the field. The mean number of eggs/female, estimated from 14 females with intact abdomens, was 675 ± 100 eggs. The eggs were separated into 67 batches, and 15 to 20 batches were incubated at each incubation temperature. All eggs in 13 batches died. No hatching occurred in 17 batches, but development could be observed in the eggs, mostly up to stages 5–6 or only to stages 3–4.

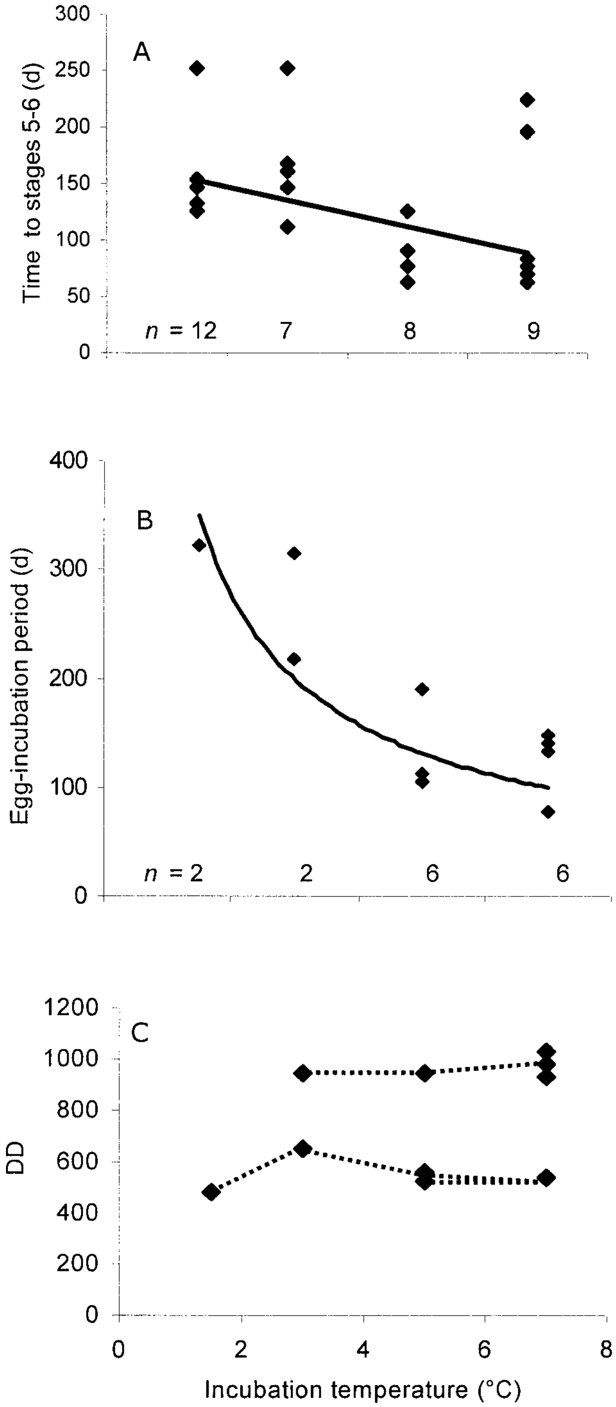

FIG. 5. Egg development in *Ecdyonurus picteti*. A.—Relationship between time to stages 5–6 and incubation temperature (2 outliers excluded). B.—Relationship between egg-incubation period and incubation temperature. C.—Relationship between degree-days demand (DD) and incubation temperature. The dotted lines connect batches of eggs from the same female. Each symbol represents an egg batch and the number of batches is given.

Hatching success was 0.4 to 15.7% in the remaining 37 batches and averaged 2 to 5% depending on incubation temperature (Appendix 3). The hatching period varied from 1 to 23 wk, with one exception (1 egg at 5°C hatched 59 wk after the 1st egg in the batch hatched). The mean time to stages 5–6 was 177 ± 14 d and was variable among batches at each temperature, but differences in time to stages 5–6 did not differ significantly among incubation temperatures (Kruskal–Wallis rank-sum test: $p = 0.8662$; Fig. 6A). Egg-incubation period varied at each temperature and did not differ significantly among incubation temperatures (Kruskal–Wallis rank-sum test: $p = 0.5736$; Fig. 6B). The mean egg-incubation period was 232 ± 14 d, and DD increased with increasing incubation temperature ($y = 233.62x^{0.978}$, $R^2 = 0.884$, $n = 37$; Fig. 6C). Mean DD (±95% CL) was 360.5 ± 43.9 dd at 1.5°C and increased to 1736 ± 167.8 dd at 7°C.

Discussion

Differentiation of egg-development characteristics

Baetis alpinus.—Larval development of *B. alpinus* has been well studied (Humpesch 1971, 1979a, b, Kukula 1997, Erba et al. 2003), even at high altitudes (Ritter 1985, Lavandier 1988), but information on the egg stage is lacking. Published data on *B. rhodani* show similar high hatching success (>90%) within a 5 to 10°C range (Bohle 1968, Benech and Vignes 1972, Elliott 1972). At 3°C, which was the lowest temperature studied (Elliott 1972), *B. rhodani* hatching success decreased to 80%, and hatching period increased to 34 d. No decrease in *B. alpinus* hatching success and no increase in hatching period were observed at the lowest temperatures. *Baetis rhodani* (DD = 340 dd at 4°C, Elliott 1972) has a higher DD than *B. alpinus* (DD = 213 ± 7 dd at 3–7°C, our study).

Ecdyonurus picteti.—The incubation period of *E. picteti* was studied by Humpesch (1980) for temperatures ranging from 3.5 to 20.4°C. We recomputed Humpesch's (1980) data for a temperature range of 3.5 to 8.2°C, which is comparable to our data range. Humpesch (1980) gave only hatching period, so egg-incubation period was calculated as the median of the hatching period. Data were then transformed to dd to obtain DD. Hatching success was higher in Humpesch's (1980) study than in our study (1.1–35.8% vs 1–6%, respectively). Hatching success in European *Ecdyonurus* species was rarely >50% (Humpesch 1980). The relationship between egg-incubation period and temperature was $y = 1263x^{-1.417}$ ($R^2 = 0.89$) for Humpesch's (1980) data, compared to $y = 486.66x^{-0.815}$ ($R^2 = 0.70$) in our study. Thus, egg-incubation period decreased faster with increasing temperature and the intercept of

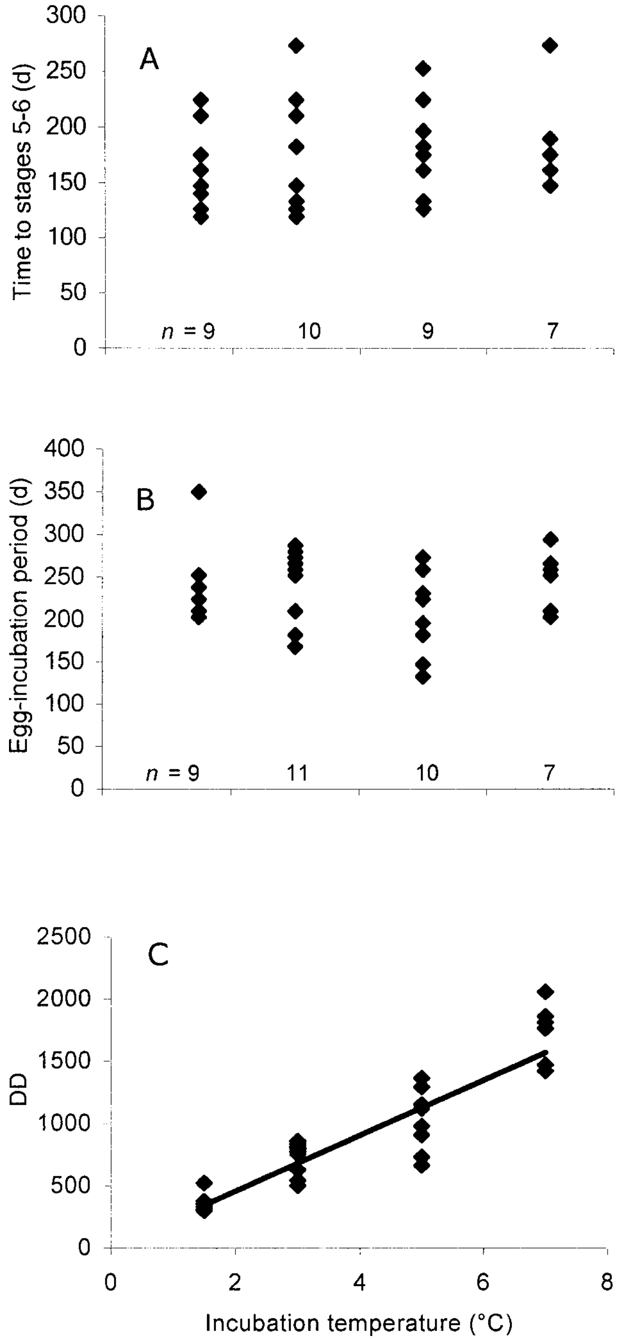

FIG. 6. Egg development in *Rhithrogena nivata*. A.—Relationship between time to stages 5–6 and incubation temperature. B.—Relationship between egg-incubation period and incubation temperature. C.—Relationship between degree-days demand (DD) and incubation temperature. Each symbol represents an egg batch and the number of batches is given.

regression line was higher in Humpesch's (1980) analyses. The absence of data for temperatures <3.5°C in Humpesch (1980) could partly explain this difference. DD in Humpesch's (1980) data had a significant negative relationship with incubation temperature, whereas no relationship was observed in our study. Pritchard et al. (1996) also recomputed Humpesch's (1980) data over a greater temperature range, separating data from the 2 study streams, but obtained similar relationships: $y = 1227x^{-0.47}$ for the Seebach and $y = 1655x^{-0.47}$ for the Herrnalmbach; $R^2 > 0.97$. Our study suggests that embryonic development in *E. picteti* shows considerable variation in duration of egg development and DD at the individual and population levels.

Rhithrogena nivata.—No data on egg development were available in the literature on *R. nivata*, but a comparison could be made with *Rhithrogena loyolaea*, another alpine species. Hatching success in *R. loyolaea* (Humpesch and Elliott 1980) was higher than in *R. nivata* and reached 33% for a similar temperature range of 1.9 to 10.2°C, and egg-incubation period and time to stages 5–6 were independent of incubation temperature. A positive linear relationship between DD and incubation temperature was described as characteristic of cold stenothermal plecopteran species by Lillehammer et al. (1989). Pritchard et al. (1996), using data from many different sources, concluded that most Ephemeroptera, with the exception of *R. loyolaea*, show a negative relationship between DD and incubation temperature. Therefore, *R. nivata* is the 2nd observation of such cold adaptation in Ephemeroptera. The slope of the relationship between DD and temperature is greater in *R. nivata* than in *R. loyolaea*, indicating a stronger cold stenothermal adaptation in *R. nivata*. A similar delay in hatching at all temperatures argues against embryonic diapause. At present, embryonic diapause is unknown in the monophyletic *hybrida* group (MS, unpublished data), to which *R. nivata* belongs.

Prediction of hatching periods in the field

The duration of egg development and timing of egg hatching are crucial elements in aquatic insect life histories. Oviposition period, water temperature, and the relationship between the duration of egg development and temperature determine the period when young larvae are present in a habitat (e.g., Sweeney 1984, Lillehammer et al. 1989, Pritchard et al. 1996, Füreder 1999). We calculated accumulated dd for each site when eggs were collected in August (Fig. 7A) and September (Fig. 7B), and predicted periods of hatching in the field from the experimentally obtained DD of each species and the calculated accumulated dd at the sites.

Baetis alpinus.—The egg-hatching period of *B. alpinus* is strongly dependent on the in situ temperature regime. Accumulation of 213 dd (DD at 3–7°C) was used to predict the hatching period. Eggs that were laid in mid August in MUTT, where the mean

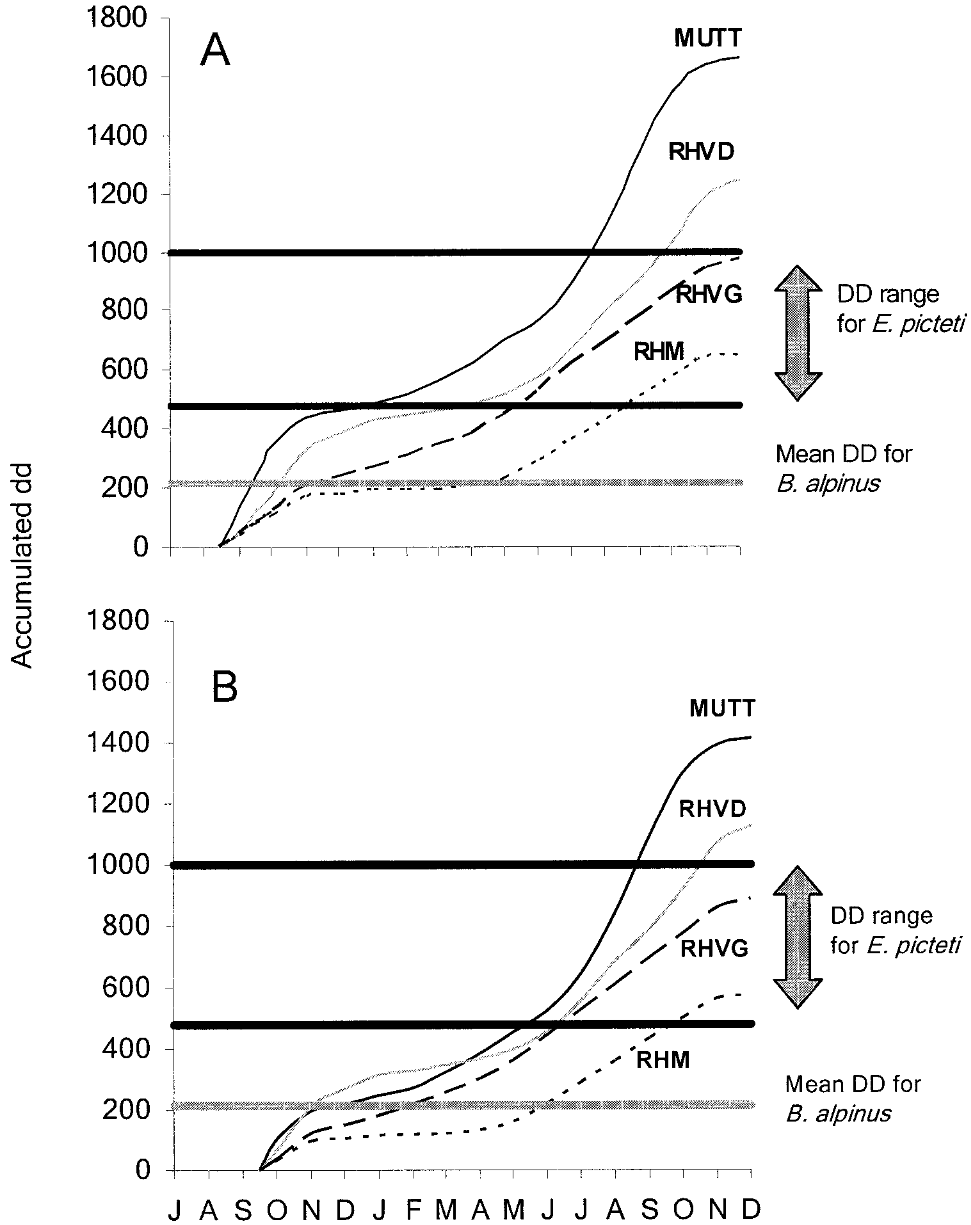

FIG. 7. Accumulated degree days (dd) at 4 sites if *Baetis alpinus* and *Ecdyonurus picteti* oviposition were to occur on 15 August (A) and 15 September (B). Degree days were calculated from daily mean water temperatures. Degree-days demand (DD) of the species are marked with horizontal lines and comments on the right. Site abbreviations as in Fig. 1.

temperature is >7°C, would hatch about mid September, before the drastic decrease in temperatures (Fig. 8). Eggs laid in other locations, where water temperatures are much lower even in summer, would require a few months to accumulate sufficient dd to complete development. Thus, hatching would be likely to take place in autumn below the confluence in RHVD and RHVG and in winter or spring in the RHM above the confluence (Fig. 8). The lower DD at 1.5°C may be an adaptation to low temperatures, whereby eggs subjected to such temperatures would hatch earlier than calculated above.

Discharge generally declines during autumn toward low winter levels, so newly hatched larvae would be able to grow in the substrate during stable winter conditions. Thus, autumn hatching should be an advantage for populations in MUTT, RHVD, and RHVG. However, a major spate in October 2000 partly rearranged the substrate and could have flushed out some freshly hatched larvae and decimated part of the population. Thus, the success of a short incubation

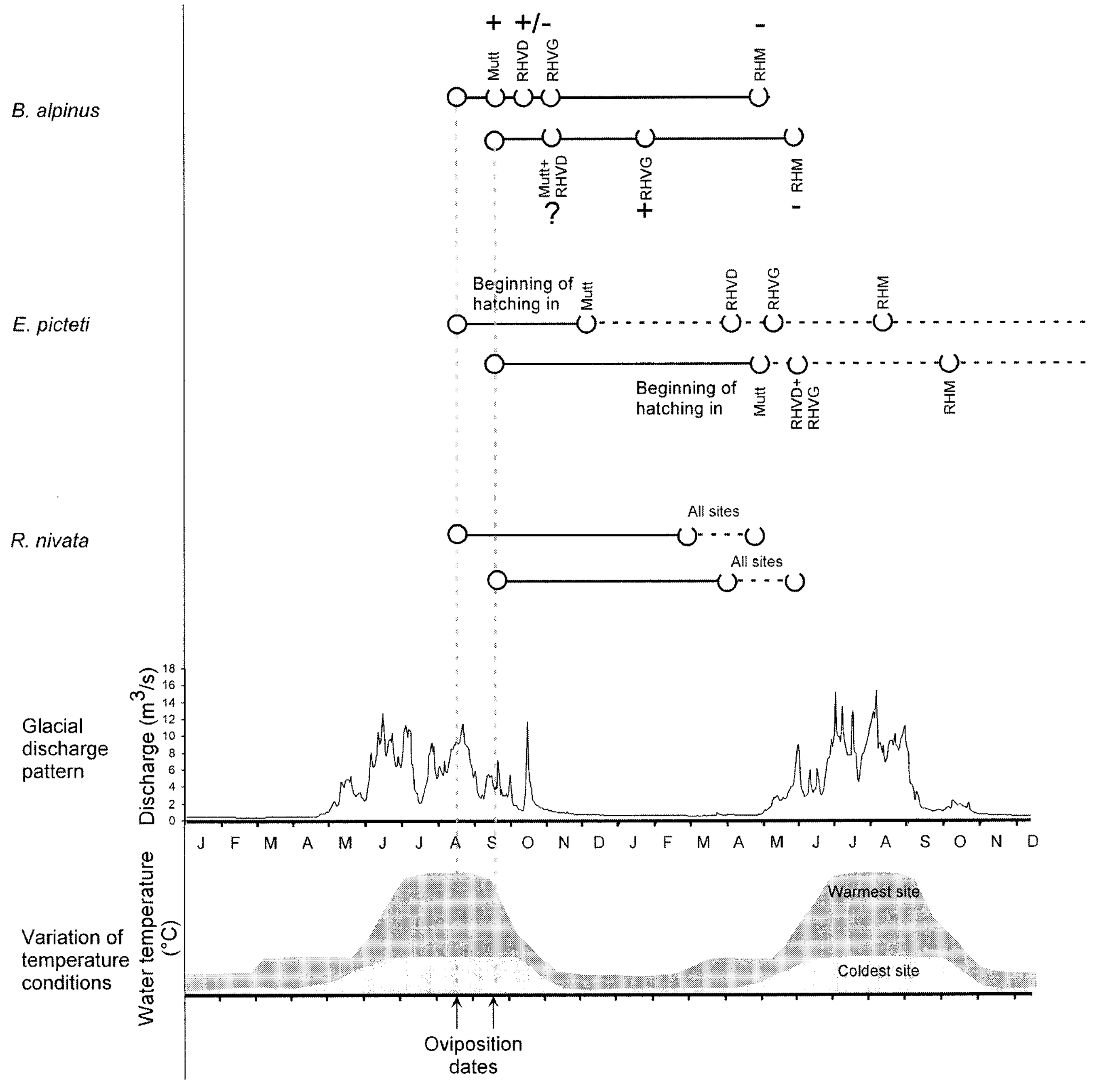

FIG. 8. Predicted duration of egg development and hatching period in the field for *Baetis alpinus*, *Ecdyonurus picteti*, and *Rhithrogena nivata* at the 4 sites and for 2 oviposition dates. Discharge and water temperature patterns are given to describe the seasonal changes in environmental conditions. The discharge data are from the gaging station in Gletsch. The temperature data are from the Mutt (warmest site) and RHM (coldest site). Site abbreviations as in Fig. 1. Circle = oviposition, incomplete circle = hatching, – – – – = delayed hatching, + = advantageous, – = disadvantageous.

strategy depends, in part, on the stability of the discharge regime and of the substrate. The slight, but significant, difference in duration of egg development at different temperatures should enable eggs laid in different habitats to withstand such autumnal spates. In fact, the attached-egg stage in *B. alpinus* may be more resistant than the young larvae, even though larvae are able to move down into the substrate or laterally into sheltered habitats. The advantageous characteristics of egg development in *B. alpinus* are its synchronicity and high hatching success. Development is faster in warmer habitats, enabling it to exploit the short period in autumn with favorable conditions when temperatures remain sufficiently high to accumulate enough dd and when the decrease in discharge begins (Milner et al. 2001), although major flood events could be limiting.

Ecdyonurus picteti.—Egg development requires a DD range of 480 to 1000 dd, and the timing of expected attainment of such accumulated values varied considerably between sites (Fig. 7). For eggs laid in mid August, hatching would begin during low-flow conditions in MUTT (December) and RHVD (beginning of April) and last until the following summer (Figs 7A, 8), giving a total duration of egg development of 4.5 to 13 mo. However, hatching would commence during the spring or summer after oviposition at RHVG and RHM and last until autumn the following year (Fig. 8), giving a duration of egg development of up to 2 y. If eggs were laid in mid September instead of mid August, hatching would be expected to begin after 7 mo of development in MUTT and after 12 mo in the coldest sites (Fig. 8). The delay in hatching would be up to 1 y, and eggs would have to survive 2 periods of glacial discharge. The likelihood of egg survival in this event seems low, particularly at RHM, given the instability of the substrate in the upper part of the Rhône (Knispel and Castella 2003). Thus, RHM and, to a lesser degree, RHVG are unsuitable habitats for egg development in *E. picteti* because of the long duration of egg development and the rigor of the glacial discharges. However, one advantage might be the ability to survive unexpected events, such as winter spates, that might flush out larvae, but leave the eggs protected in the substrate.

The hatching delay in *E. picteti* leads to asynchronous larval development with numerous cohorts overlapping throughout the year. This strategy also has been put forward for a sibling species, *E. helveticus* (Breitenmoser-Würsten and Sartori 1985), and is probably common among *Ecdyonurus* species (e.g., Sowa 1975 for *E. subalpinus*, Imhof et al. 1988 for *E. venosus*). Some preliminary results indicate that this hatching strategy is more frequent in unstable or unpredictable habitats such as those found in our study area than in stable habitats (MS, unpublished data). The only *Ecdyonurus* species known so far that exhibit a synchronous hatching and single-cohort development is *E. dispar* (Humpesch 1981), which inhabits stable lake shores and large river habitats.

Rhithrogena nivata.—On the basis of our laboratory data, eggs of *R. nivata* that were laid in situ would hatch between March and May, ~6.5 to 8.5 mo after oviposition, regardless of the water temperatures. Thus, some eggs, especially those laid in mid August, would hatch before the spring increase in discharge from snowmelt (Fig. 8). However, some of the eggs laid later in September would be affected by the spring spate. Nevertheless, hatching period may be very long in *R. nivata* and, thus, only part of the population would be negatively affected. The success of this strategy, with production of young larvae in spring, depends largely on the timing of hatching and high-discharge conditions. *Rhithrogena nivata* is well adapted to the cold, so it is able to exploit habitats, such as the extremely unstable and cold RHM, where other species would be limited by low water temperatures.

Egg-development characteristics and geographical range

The different egg-development characteristics of the 2 heptageniid species allow them to exploit different habitats in the glacial system. Our limited studies suggest that *Rhithrogena nivata* is adapted for development in the harsh habitat of RHM. This conclusion is supported by the fact that *R. nivata* females were the only ones observed ovipositing in this area during the field study. *Ecdyonurus picteti*, with its long duration of egg development and major individual variation, would require warmer conditions than *R. nivata*. However, these characteristics allow *E. picteti* to develop in extremely unpredictable habitats, such as MUTT and the alluvial section of the Rhône (RHVD and RHVG), which are subject to frequent spates. Females of *E. picteti* were caught on the opposite side of the Rhône, around the Mutt confluence, and were assumed to oviposit naturally in the Mutt.

Egg-development patterns documented in our study are consistent with the distributional ranges of the species. *Rhithrogena nivata* appears to be a specialist adapted to cold alpine environments and has the most restricted distribution among the studied species. *Ecdyonurus picteti* appears to have a flexible egg-development strategy with regard to temperature conditions. The species has a limited distribution area, but a wide altitudinal range in the Swiss Alps (400-2400 m asl). No particular adaptations to low temperatures were observed in *Baetis alpinus*, but it had the ability to develop rapidly during periods of favorable temperatures. This species occurs widely in Europe over a large altitudinal range, up to 2600 m asl. Our results suggest a possible relationship between egg-development characteristics and geographical distribution in the 3 investigated species, as seen in Ephemeroptera when compared to other aquatic insect orders, such as Plecoptera and Odonata (Brittain 1990, Pritchard et al. 1996). However, this hypothesis should be tested on a large number of populations and species over a wide geographical range.

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APPENDIX 1. Detailed results for successful batches of eggs from *Baetis alpinus*. DD = degree-days demand.

Identification number of female	Incubation temperature (°C)	Egg-incubation time (d) to:			DD to:			Total number of eggs
		10% hatching	50% hatching	90% hatching	10% hatching	50% hatching	90% hatching	
1	1.5	95	97	100	143	146	150	169
2	1.5	89	91	95	134	137	143	212
3	1.5	72	75	77	108	113	116	789
4	1.5	70	71	76	105	107	114	1421
10	1.5	101	107	109	152	161	164	31
13	1.5	108	110	116	162	165	174	96
14	1.5	98	99	107	147	149	161	137
15	1.5	107	108	114	161	162	171	48
1	3	65	67	69	195	201	207	260
2	3	61	63	68	183	189	204	140
5	3	64	64	66	192	192	198	1020
6	3	74	76	78	222	228	234	644
13	3	68	70	71	204	210	213	97
14	3	67	72	74	201	216	222	410
1	5	39	39	40	195	195	200	148
2	5	37	38	40	185	190	200	204
7	5	39	39	41	195	195	205	919
10	5	42	47	51	210	235	255	55
12	5	43	44	47	215	220	235	49
13	5	44	45	48	220	225	240	154
14	5	43	44	47	215	220	235	262
15	5	44	45	47	220	225	235	66
1	7	29	30	34	203	210	238	293
2	7	34	35	36	238	245	252	225
8	7	27	28	31	189	196	217	1195
9	7	28	29	31	196	203	217	1426
10	7	31	32	36	217	224	252	269
12	7	31	32	34	217	224	238	19
13	7	30	31	32	210	217	224	293
14	7	31	33	39	217	231	273	196

Appendix 2. Detailed results for successful batches of eggs from *Ecdyonurus picteti*. dd = degree days, DD = degree-days demand.

Identification number of female	Incubation temperature (°C)	Time to stages 5–6 (d)	dd to stages 5–6	Egg-incubation period (d)	DD	Total number of eggs	Number hatched	Hatching success (%)	Hatching period (wk)
1	1.5	252	378	–	–	150	0	–	–
2	1.5	126	189	–	–	710	0	–	–
3	1.5	133	200	322	483	801	1	0.12	1
4	1.5	154	231	–	–	100	0	–	–
5	1.5	147	221	–	–	300	0	–	–
6	1.5	133	200	–	–	240	0	–	–
7	1.5	133	200	322	483	312	12	3.85	13
8	1.5	133	200	–	–	100	0	–	–
9	1.5	147	221	–	–	260	0	–	–
10	1.5	154	231	–	–	225	0	–	–
11	1.5	154	231	–	–	390	0	–	–
12	1.5	154	231	–	–	110	0	–	–
2	3	112	336	315	945	401	1	0.25	1
3	3	112	336	217	651	285	5	1.75	5
5	3	168	504	–	–	370	0	–	–
6	3	581	1743	–	–	290	0	–	–
8	3	147	441	–	–	100	0	–	–
9	3	–	–	–	–	330	0	–	–
10	3	168	504	–	–	215	0	–	–
11	3	252	756	–	–	240	0	–	–
12	3	161	483	–	–	250	0	–	–
2	5	126	630	189	945	716	6	0.86	8
3	5	77	385	112	560	369	39	10.6	3
4	5	63	315	–	–	63	0	–	–
5	5	63	315	105	525	328	18	5.49	3
8	5	91	450	112	560	105	5	4.76	5
9	5	63	315	105	525	250	1	0.4	1
11	5	63	315	–	–	170	0	–	–
12	5	63	315	105	525	121	16	13.2	2
1	7	196	1372	–	–	230	0	–	–
2	7	77	539	140	980	753	43	5.71	12
3	7	63	441	77	539	205	15	7.32	16
4	7	84	588	–	–	120	0	–	–
5	7	70	490	77	539	133	3	2.26	1
6	7	84	588	147	1029	142	2	1.41	12
8	7	224	1568	–	–	65	0	–	–
9	7	497	3479	–	–	310	0	–	–
11	7	63	441	77	539	123	8	6.50	2
12	7	77	539	133	931	191	1	0.52	1

APPENDIX 3. Detailed results for successful batches of eggs from *Rhithrogena nivata*. dd = degree days, DD = degree-days demand.

Identification number of female	Incubation temperature (°C)	Time to stages 5–6 (d)	dd to stages 5–6	Egg-incubation period (d)	DD	Total number of eggs	Number hatched	Hatching success (%)	Hatching period (wk)
1	1.5	–	–	–	–	150	0	–	–
2	1.5	–	–	203	305	181	6	3.3	1
3	1.5	210	315	–	–	125	0	–	–
5	1.5	161	242	238	357	161	1	0.6	1
7	1.5	224	336	350	525	193	3	1.6	5
8	1.5	224	336	–	–	310	0	–	–
9	1.5	–	–	–	–	300	0	–	–
10	1.5	119	179	210	315	262	5	1.9	1
11	1.5	140	210	224	336	222	2	0.9	1
12	1.5	126	189	210	315	180	28	15.7	14
13	1.5	175	263	252	378	121	1	0.8	1
14	1.5	–	–	252	378	197	2	1.0	1
15	1.5	147	221	224	336	232	2	0.9	11
2	3	147	441	210	630	227	23	9.2	5
3	3	–	–	280	840	116	2	1.7	2
4	3	–	–	287	861	171	1	0.6	1
5	3	224	672	259	777	160	1	0.7	1
7	3	210	630	266	798	95	4	4.2	6
8	3	–	–	–	–	240	0	–	–
9	3	273	819	–	–	155	0	–	–
10	3	126	378	182	546	98	3	3.1	3
11	3	210	630	273	819	181	1	0.6	1
12	3	119	357	168	504	178	8	4.5	3
13	3	126	378	182	546	143	8	5.6	5
14	3	182	546	252	756	166	1	0.6	1
15	3	133	399	182	546	181	1	0.6	1
1	5	–	–	147	735	142	2	1.4	5
2	5	252	1260	–	–	240	0	–	–
3	5	161	805	224	1120	139	9	6.5	8
4	5	182	910	–	–	55	0	–	–
5	5	224	1120	259	1295	163	3	1.8	7
6	5	196	980	–	–	125	0	–	–
8	5	175	875	231	1155	294	4	1.4	4
9	5	–	–	133	665	158	8	5.1	21
10	5	–	–	–	–	85	0	–	–
11	5	–	–	273	1365	201	1	0.5	1
12	5	133	665	196	980	140	20	14.3	13
13	5	–	–	231	1155	108	3	2.8	59
14	5	175	875	259	1295	246	6	2.4	13
15	5	126	630	182	910	206	26	12.6	12
1	7	189	1323	–	–	160	0	–	–
2	7	–	–	–	–	260	0	–	–
3	7	–	–	–	–	85	0	–	–
4	7	–	–	–	–	140	0	–	–
5	7	–	–	252	1764	231	1	0.4	1
6	7	175	1225	294	2058	66	1	1.5	1
7	7	273	1911	–	–	55	0	–	–
8	7	175	1225	–	–	230	0	–	–
9	7	–	–	259	1813	241	1	0.4	1
10	7	–	–	266	1862	81	1	1.2	1
11	7	161	1127	203	1421	71	6	8.5	8
12	7	147	1029	210	1470	88	3	3.4	23
13	7	–	–	–	–	75	0	–	–
15	7	175	1225	252	1764	171	1	0.6	1