Life cycles of Baetidae (Insecta: Ephemeroptera) in a North Italian Prealpine stream

STEFANIA ERBA
LICIA MELISSANO
ANDREA BUFFAGNI
CNR - IRSA National Research Council, Water Research Institute (Istituto di Ricerca Sulle Acque), Via Della Mornera, 25 I-20047 Brugherio (Milano) Italy
erba@irsa.rm.cnr.it
buffagni@irsa.rm.cnr.it

Abstract

The life cycles of *Baetis alpinus*, *B. melanonyx*, *B. rhodani* and *Alainites muticus*, from the Pioverna Stream in the Italian Alps (Italy), are described over a three years period, following two main time intervals. Growth rates for the main generations identified are reported and compared.

B. alpinus exhibited two different life cycle strategies in the two periods, three and two generations per year, respectively. The development cycle of *B. melanonyx* also varied, from bivoltine to univoltine. The life cycle of *B. rhodani* was quite complex in both periods, with all life stages present simultaneously. Finally, *A. muticus* developed during a main winter-spring generation in both years, showing a secondary generation in the early summer periods. The thermal and hydrological (i.e. in terms of flow stability) characteristics of the two periods seem the major responsible for the observed differences in the life cycle patterns of *Baetis alpinus* and *B. melanonyx.* Differences in the life cycle strategies between the southern and the northern part of the Alps were apparent.

Keywords: mayfly, voltinism, temperature, growth, *Baetis*, *Alainites*.

Introduction

Detailed information on life cycles is noteworthy for many types of ecological studies on freshwater invertebrates. From an applied point of view, changes in the life history descriptors (e.g. survival or mortality, fecundity, growth rate, developmental stage, size and longevity) of various species are increasingly used in ecological assessment studies as indicator of environmental stress (e.g. Raddum and Fjellheim, 1993; see also Brittain, 1991). For example, life cycles information may be especially useful when assessing the impact of alterations to the water temperature regime (Fahy, 1973; Thibault, 1971a; Eliott, 1987). In fact the most important factors influencing life cycles are proved to be water temperature (Vannote and Sweeney, 1980), the quality of food resources (Hawkins, 1986) and photoperiod. Temperature and photoperiod can influence hatching periods, larval stages and flying period (Ward and Standford, 1982). There is a clear relationship between hatching success and water temperature. For some species, in European rivers, hatching usually remains high at intermediate temperatures and than decrease with the increasing/decreasing of temperatures, such as the duration of embryonic developement is inversely related to temperature (e.g. Humpesch, 1984). Other parameters considered important in determining life cycle strategies are dissolved oxygen, pH, current and substrate or biotic parameters involving predation or competiton (Humpesch, *op. cit.*). While the effect of water temperature on life cycles is well documented, a lower number of studies dealt with the direct or indirect effects of these other factors. For instance, the regulation of rivers for hydropower production influences the physical environment, directly acting on discharge and temperature. This also causes the modification of the bottom substrate, chemical environment and, consequently, of the biological status of a river (Armitage and Pardo, 1995). Depending on the type of river and regulation, alterations to the general pattern of the insect life cycle and/or of single parameters useful to describe its life history (e.g. voltinism, growth rate) may be expected. Life cycles descriptors, when species, cohorts or sites are compared, can themselves be useful as indicators of river functioning. Besides, the study of life cycles is of central importance in calculating secondary production, one of the best descriptors of success for any population.

In Italy, very few studies concerning the life cycles of mayfly species have been performed (Buffagni and Gomba, 1996; Ghetti *et al.*, 1979; Marchetti *et al.*, 1967). Only recently, a description of the life cycle in Northern Italy lowlands of nine common species of mayflies, including *Baetis rhodani* (PICTET, 1843) and *Alainites muticus* (LINNEUS, 1758), was pubblished (Buffagni *et al.*, 2002a).

The aim of the present work is to describe the life cycle of the four species belonging to the mayfly family Baetidae present in a prealpine river. In addition, the development patterns of the studied species will be compared between two distinct time periods.

Study area, Material and Methods

The study was carried out in the Pioverna River, which is a typical mountain stream of the Italian Alps, located in Valsassina (Pasturo, Lecco, North Italy). It flows between 2554 m a. s. l. and 418 m a.s.l. for about 20 km before running into Como Lake, near Bellano. The study site is a pristine river reach about 200 m long and, at base flow, 3 m wide. It is at 830 m a.s.l., close to the village of Pasturo. A detailed description of the study site is given in Buffagni and Comin (2000).

Benthic samples were collected monthly from April 1996 to September 1997 and from November 1998 to October 1999. A Surber sampler (mesh size 0.45 mm), covering an area of 0.8/1.2 m^2 for each date, was used to collect macroinvertebrates. For the two periods, respectively, 6 replicates (0.05x6x4 m^2) and 4 replicates (0.05x4x4 m^2) for each of four different habitat (see Buffagni and Comin, 2000) were sampled, for a total of 615 replicates over the entire study. More than 4200 larvae belonging to the family Baetidae were collected, sorted out in the field and fixed in 80% ethanol.

All the larvae were measured to the nearest 0.25 mm under a binocular, from the anterior edge of labrum to the posterior edge of the last abdominal segment (Welton *et al.*, 1982). Periods of adult emergence were identified on the basis of the presence of mature larvae in the samples, while the beginning of a generation was determined by the appearance of small nymphs. Maturity of the larvae was judged on the basis of body size (the largest reached per generation) and confirmed by the presence of dark wing-pads. Based on the data obtained monthly, size frequency histograms were produced. The specific

growth rates (g/day, expressed in mg d^{-1}) were calculated by the equation:

g/day = (LnW$_t$-lnW$_i$)/t

where W$_t$ is the mean dry weight after an interval t (in days) and W$_i$ is the initial dry weight. The equation utilized to convert body lenght into dry weight is lnDW = ln(a) + (b) * lnL where: DW = dry weight (mg); and L = lenght (mm). The coefficients used for the different species are reported in Meyer (1989). The growth rates reported in table 1 were calculated for the riffle habitat with the exception of *B. alpinus* autumn generation, which considers the specimens found both in the riffle and in the bedrock habitat (due to low densities in the riffle habitat). To estimate production and growth rate for the 1998/1999 winter generation of *Baetis rhodani,* the specimens collected during autumn (September/October) 1999 were integrated with those sampled in 1998 (November to March) assuming that no large variations occurred between the two periods.

During the first sampling period (1996/7), the temperature was regularly monitored every 14 days, recording the minimum, the maximum and the instantaneous values for the two weeks. Due to technical problems, for the second investigation period, only the instantaneous temperature measured when collecting samples is available.

Results and Discussion

Life cycles and growth

Baetis alpinus (PICTET, 1843)

In this study *Baetis alpinus* exhibited different strategies: a trivoltine life cycle during 1996/7 and a bivoltine life cycle during 1998/9 (Figs. 1-2). For both sampling periods two main generations were found: winter/spring and spring/summer. The timing of the duration of each generation is summarized in Table 1. In 1998/9 the winter/spring generation was made up of two cohorts. The first cohort (cohort 'a') began in November with mature nymphs ready to emerge in March. The second (cohort 'b') was found from February till July. Nymphs ready to emerge were observed in May.

During the first sampling period it was difficult to identify the beginning of the winter/spring generation, as no nymphs were found during the early winter months. This lack of nymphs in the samples, from October until January, may have been due to sampling errors whereby true riffle

habitat was not adequately sampled or to hydrological instability, which characterised the first sampling period (see Buffagni and Comin, 2000; Buffagni *et al.*, 2002b). During this period, high variability in rainfall events, expressed by high level of standard deviation, was associated to low levels of taxonomic richness in the community supporting the hypothesis of hydrological instability (Buffagni *et al.*, 2002b). More in detail, during the summer of 1996 and 1997 the highest precipitation values were reached (monthly average), corresponding to 11.5 mm in June 1996 and 1997, while the maximum level of precipitation reached in 1998/99 was 5.8 mm for September and October 1999. Due to the stress induced by flow fluctuations, the smallest nymphs may have moved into hyporheic habitats thus avoiding being sampled. The earliest individuals of this generation appeared in February, the last mature nymphs in May.
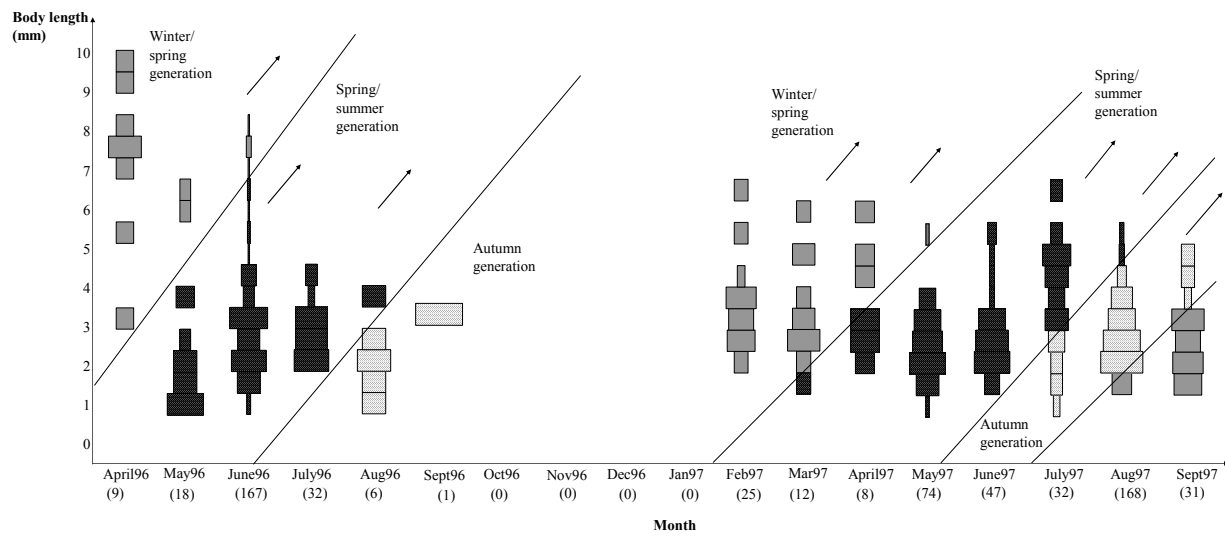

Fig. 1 - Life cycle of *Baetis alpinus* during 1996/97 in the Pioverna Stream (Northern Italy, LC). Arrows indicate the emergence and numbers on the abscissa the absolute numbers of specimens measured. The width of each box represents the relative abundance of nymphs.
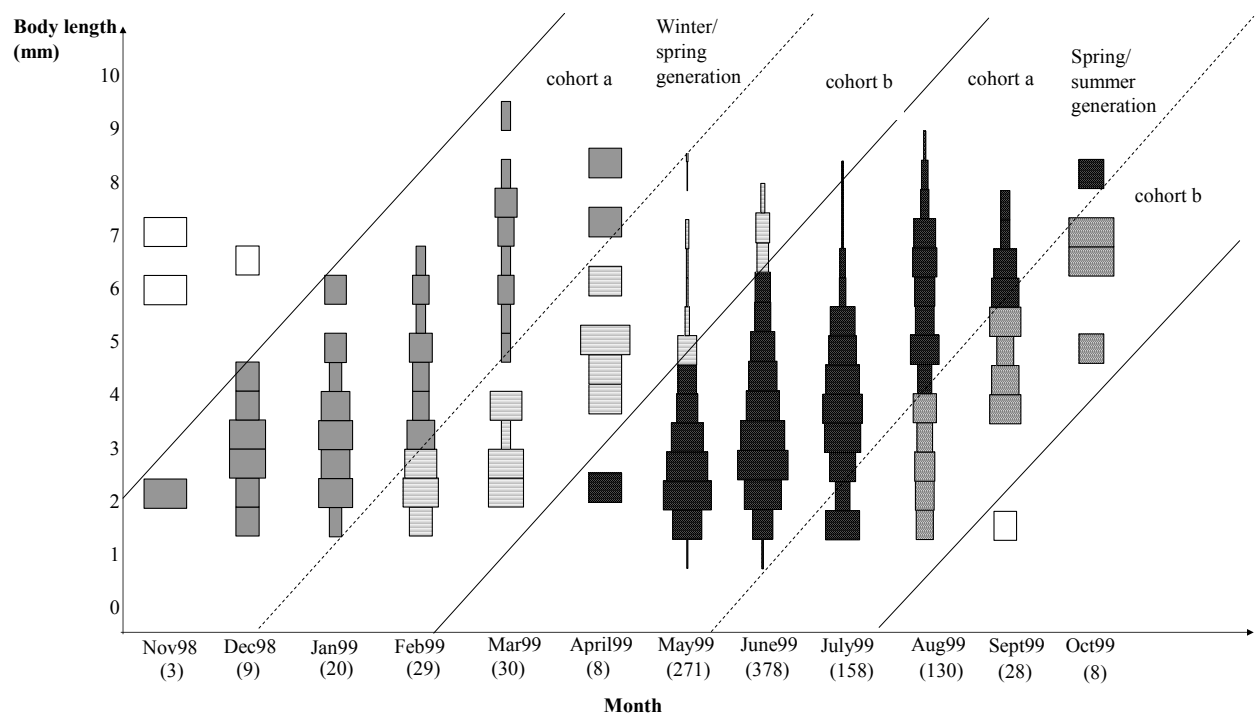

Fig. 2 - Life cycle of *Baetis alpinus* during 1998/99 in the Pioverna Stream (Northern Italy, LC). Arrows indicate the emergence and numbers on the abscissa the absolute numbers of specimens measured. The width of each box represents the relative abundance of nymphs.

LIFE HISTORY & REPRODUCTION

Table 1 - Summary of life cycle and growth strategies of the investigated species. Life cycle abbreviations as follows. M: (multivoltine) polyvoltine cycle; Bws: bivoltine winter/spring cycle; Bss: bivoltine spring/summer cycle, Us: univoltine spring cycle and Uw: univoltine winter cycle.

Species	Generations	Egg Hatching period	Emergence period	Life cycle	G/day in weight
Baetis alpinus	spring/summer 96	May	June - August	M	0.078
	spring/summer 97	March	July - August	M	0.034
	spring/summer 99	May	August - October	Bws	0.022
	winter/spring 96		March (?) - June	M	
	winter/spring 97	January (?)	March - May	M	0.03
	winter/spring 97/98	August - September			
	winter/spring 98/99	November - December	March - July	Bws	0.025
	autumn 96	August	----		
	autumn 97	July	September - October (?)	M	0.067
	autumn 98	----	----		
	autumn 99	----	----		
Baetis melanonyx	spring 96	May (?)	July - August	Bss	
	spring 97	April (?) - May	July	Bss	0.043
	spring 99	April (?) - May	June	Us	0.04
	summer 96	----	----		
	summer 97	June	August - September (?)	Bss	0.055
	summer 99	----	----		
Baetis rhodani	spring 96	April	July	M	0.022
	spring 97	February	May	M	0.051
	spring 99	January	May - June	M	0.028
	summer 96	July	August - September	M	0.049
	summer 97	July	August - September	M	0.024
	summer 99	May	August - October	M	0.066
	winter 96/7	October	January - March	M	0.023
	winter 98/99	September (?)	January - March	M	0.021
Alainites muticus	winter/spring 96		June	Uw	
	winter/spring 97	January	May	Uw	0.025
	winter/spring 98/99	October (?) - January	May - June	Uw	0.015

During 1999, the spring/summer generation, probably originating from eggs laid by the previous generation (the winter/spring one), developed from May until October and could be divided in two cohorts: a and b. Recruitment appeared to begin in May for the first cohort while the presence of young nymphs and the distribution of specimens between the length classes indicated the beginning of the second cohort in July. Nevertheless, a univocal interpretation of the data is very difficult. In fact, the more or less continuous hatching could be the cause of a steady presence of small individuals (e.g. Humpesch, 1984), making the division into separate cohorts questionable. However, a study performed by Humpesch and Eliott (1980) showed that this interpretation may be wrong for *Rhithrogena semicolorata* (CURTIS, 1834). For this species the presence of small nymphs all over the year seemed due to the fact that some nymphs grow very slowly after hatching (Humpesch and Eliott, 1980). While for some mayfly species a high degree of synchrony at hatching is apparent, for others there is some evidence that eggs with delayed development might be produced (Humpesch, 1984). This observation may support the existence of different cohorts. During 1999 there was a shift in the spring/summer generation compared to 1997, when this generation began earlier (March) and the emergence of adults took place one month earlier (July). In 1997, this

generation was then followed by an autumn generation, between July to September. In 1996, the spring/summer generation started in May (like in 1999) and ended in July/August (like in 1997). These data demonstrates the plasticity of *B. alpinus* with respect to life cycles. Several studies have shown that this species may exhibit different strategies, depending on environmental conditions (e.g. Breitenmoser-Wursten and Sartori, 1995). Many authors have demonstrated that its cycle may vary from univoltine, to bivoltine with a winter-summer cycle (Humpesch, 1979; Kukula, 1997; Sowa, 1975). For example Kukula (*op.cit.*) found for this species a winter cycle with one or two generations in a higher altitude site (900 m a.s.l.), and a winter/summer cycle at a lower station. This supports what we found in the Pioverna Stream when the number of generations can alter depending on environmental conditions. The present study has also demonstrated that the species can be trivoltine. Generally, the findings of Kukula (*op. cit.*) matched those of the Pioverna Stream (e.g. hatching in May, emerging in Aug-Oct). The results found in the present study for the winter-spring generation are similar to those found by others authors concerning the winter generation, which can therefore be considered as the most stable. In Switzerland, relatively close to the site investigated in the present work, Studemann *et al.* (1992) reported as a general model a univoltine winter cycle for this species

under 1500 m a.s.l. and a bivoltine winter-summer one above 1500 m a.s.l.: strong differences appear to occur between the northern (Swiss) and the southern sides of the Alps.

Temperature has been shown to be one of the major factors explaining differences in life cycle strategies in this species, determining both egg development and nymphal growth (Brittain, 1990; Humpesch, 1979; Ward and Stanford, 1982). The presence of the autumn generation in 1997 and the differing duration of the spring-summer generations between the different years, could be explained by higher temperatures during the first sampling period. Instantaneous temperatures during spring 1997 were 1-2 °C higher. Although detailed temperature records are not available for the second sampling period, the following data seem to support this hypothesis. Along the whole time period (18 +12 months), the lowest minimum temperature (1.2°C) was recorded in December 1999 and the highest (14.5°C) in September 1997. In addition, the lowest value recorded in 1997 was 3.8°C (February, 2.6°C higher than in 1999), and the maximum during 1999 (July) was 13.8°C (1.3°C lower than in 1997). The fact that mature nymphs reached a smaller individual size during the first year could indirectly confirm the overall higher water temperatures of this period (Vannote and Sweeney, 1980). The differences between the growth rates for each generation between the two periods seem to confirm this hypothesis: they go from values of 7.80% and 3.4% for the spring-summer generation in 1996 and 1997, to 2.2% for the first cohort of the same generation in 1999. It

is known that the changes in growth rates of Ephemeroptera species can be explained in terms of water temperature (Humpesch, 1981). Another factor that could have influenced the voltinism in the Pioverna Stream is the hydrological instability during the first sampling period: under these conditions, *B. alpinus* individuals may improve their chances of reproductive success by increasing numbers of generations.

Baetis melanonyx (PICTET, 1843)

Even if based on a relatively low number of nymphs in 1999, *B. melanonyx* exhibited a univoltine cycle with larval recruitment beginning in May and only one, well defined spring generation, which lasted until June (Table 1). Due to the low numbers of specimens collected during 1999, it is only reported the life cycle during 1996/7 (Fig. 3). During 1996 and 1997 the emergence period partly shifted to July. As *B. alpinus* for the same period, in 1996 and 1997 *B. melanonyx* presented an additional generation, therefore becoming bivoltine, with a spring and a summer generation, which developed fast with a high growth rate of 5.5%. The considerations on this cycle are mainly based on the data collected during spring-summer 1997 (Fig. 3), which support the larger amount of specimens, enabling the identification of two generations. The earliest nymphs of the summer generation were found in June and reached maturity in August/September. It is likely that high temperatures, as for *B. alpinus*, explain the presence of this additional generation.
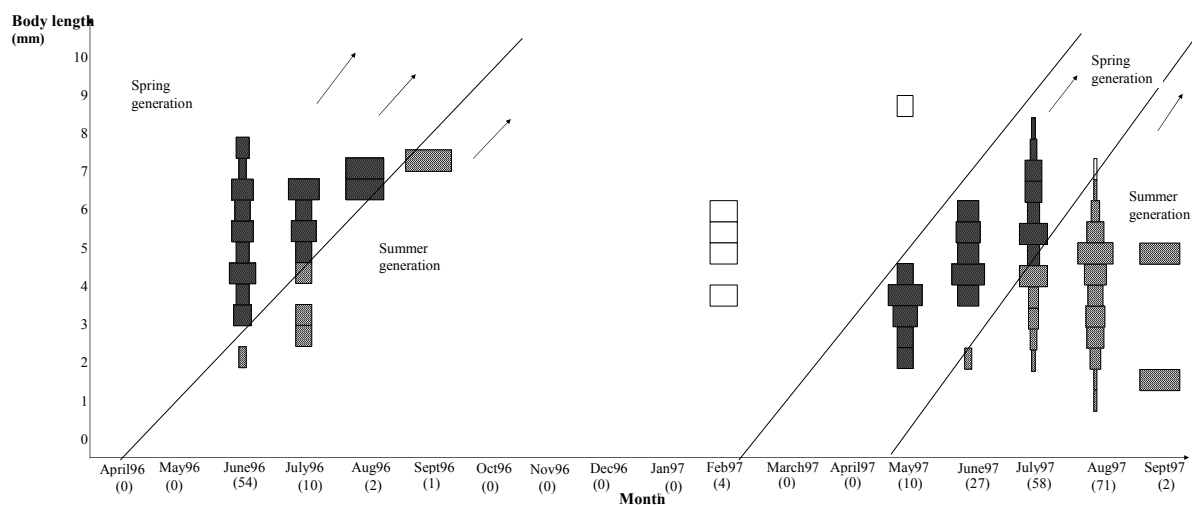

Fig. 3 - Life cycle of *Baetis melanonyx* during 1996/97 in the Pioverna Stream (Northern Italy, LC). Arrows indicate the emergence and numbers on the abscissa the absolute numbers of specimens measured. The width of each box represents the relative abundance of nymphs.

It is probable that the emergence period was followed by an egg diapause of about 7-8 months, in both sampling periods, which is in accordance with the findings of several authors (e.g. Breitenmoser-Wursten and Sartori, 1995; Kukula, 1997).

Kukula (*op.cit.*) investigated nymphs of *B. melanonyx* in the Wolosatka and Terebowiec streams (southeastern Poland). The streams were of different environmental character to Pioverna, and the species had summer cycle with one generation at both stations. Eggs, laid in July and August, underwent a long quiescence, until the following spring (Kukula, *op cit.*). A summer cycle was also found by Sowa (1975), with a single annual generation. Breitenmoiser-Wursten and Sartori (1995) during a study in two different river sites (1030 m and 1290 m in altitude) on the northwestern edge of the Bernese Alps, confirmed a univoltine summer cycle with the larval recruitment beginning in late May and June, followed by rapid growth for 3-5 months. In Studemann *et al.* (1992), for Switzerland, *B. melanonyx* is described generically as a univoltine summer species. Again, some differences can be noted between the Southern and Northern sides of the Alps, with the life cycles observed in the South being possibly more plastic and sometimes showing an additional generation.

Baetis rhodani (PICTET, 1843)

Baetis rhodani exhibited a polyvoltine cycle with three generations (Figs. 4, 5; Table 1) in both periods. The spring generation lasted from January untill May/July. The main difference regarding the two sampling periods was that in 1997 young nymphs appeared later (February) than during 1999 (January). The next generation was the summer one probably originated from eggs laid by the females of the spring generation. During 1999 larval recruitment began in May and the emergence period lasted from August until October. In 1996 and 1997 this generation is obviously shorter lasting from July until September. Overall, the summer generation appeared to be the most abundant. For the winter generation in general, nymphs developed from September to March and were ready to emerge in January. Young nymphs appeared earlier in 1999 than in 1996 (September *vs* October). Life cycles in the Pioverna Stream seem very similar for the two sampling periods, even if they are not very well synchronized. Young nymphs were found throughout the year and this together with the continuous presence of mature nymphs makes more difficult to clearly identify the beginning and the end of a generation. Anyway, it was possible to identify three periods of emergence, thus supporting Thibault's data (1971b). This is also in accordance with the data presented for some spring fed streams of the Ticino valley (Buffagni *et al.*, 2002a), where three generations were identified. However, in these small lowland streams the winter generation is the dominant one.
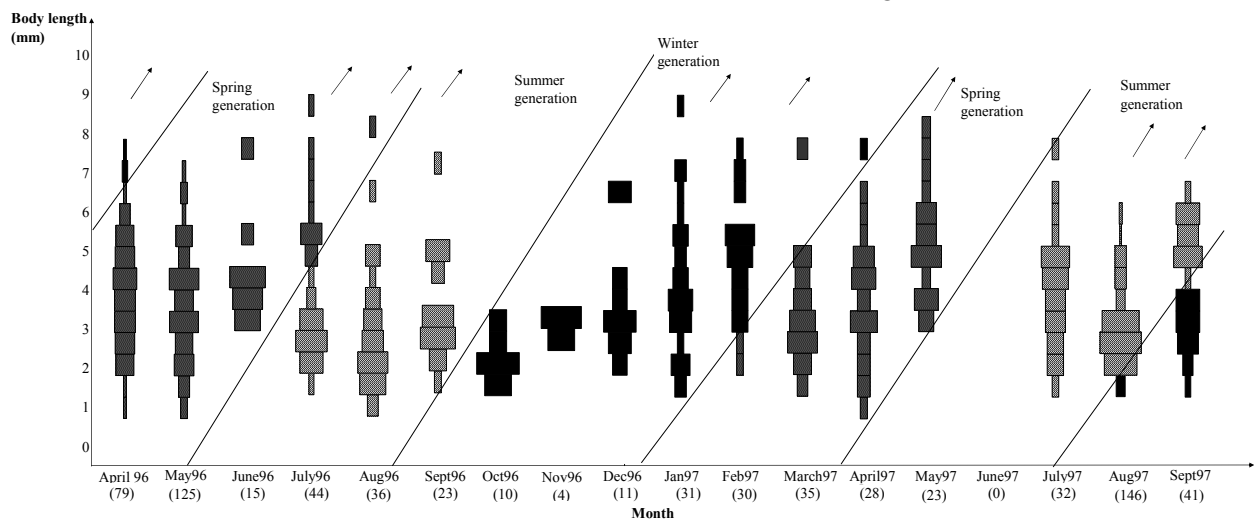

Fig. 4 - Life cycle of *Baetis rhodani* during 1996/97 in the Pioverna Stream (Northern Italy, LC). Arrows indicate the emergence and numbers on the abscissa the absolute numbers of specimens measured. The width of each box represents the relative abundance of nymphs.
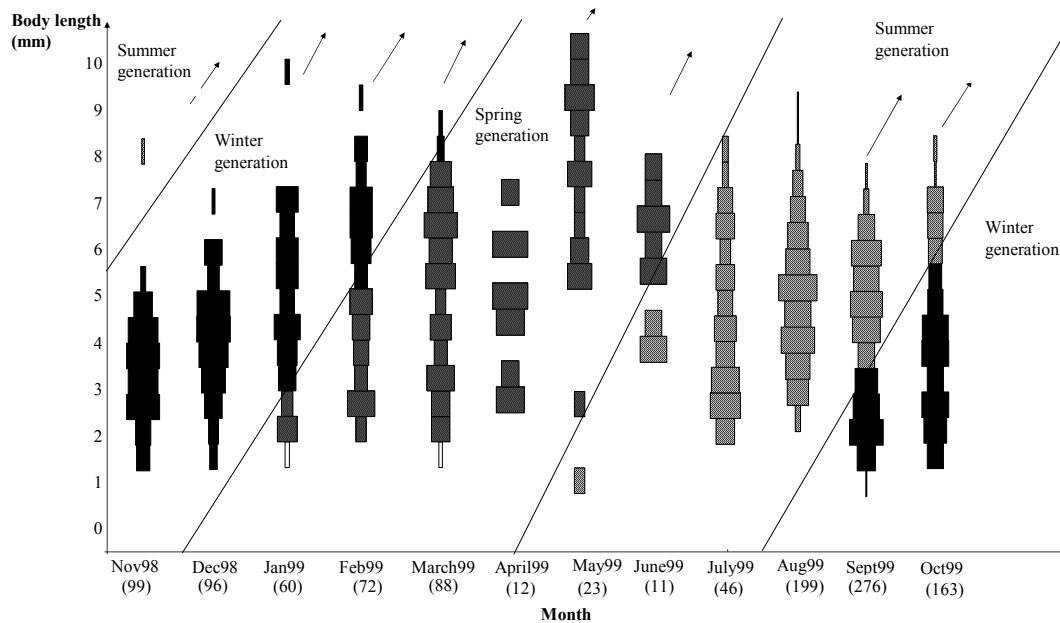
Fig. 5 - Life cycle of *Baetis rhodani* during 1998/99 in the Pioverna Stream (Northern Italy, LC). Arrows indicate the emergence and numbers on the abscissa the absolute numbers of specimens measured. The width of each box represents the relative abundance of nymphs.

The life cycle of *B. rhodani* is frequently described as bivoltine with a slow-growing overwintering generation which emerges in the spring and a fast-growing summer generation which emerges during the late summer and autumn (e.g. Ghetti *et al.,* 1979; Elliott, 1967; Wise, 1980). According to others authors, *B. rhodani* may also exhibit additional cohorts during the year (Humpesch, 1979; Welton *et al.* 1982). According to Brittain (1991) *B. rhodani* shows a range of development models, from a fairly synchronous univoltinism in cold water habitats to a wide range of more or less synchronous multivoltine cycles. In general terms, multivoltinism enables aquatic species to cope with adverse environmental conditions (Williams and Feltmate, 1992).

In the Pioverna Stream, *B. rhodani* does not seem to exhibit embryonic diapause. Nevertheless, in the lowlands of Northern Italy a portion of *B. rhodani* eggs seemed to show locally a diapause period during summer (Buffagni *et al.*, 2002a). Fahy (1973) states that one characteristic of *B. rhodani* is its ability to complete its life cycle at a wide range of temperatures. This can explain the observed differences in the proportional weight of the distinct generations of *B. rhodani* between the two Italian areas, whose rivers show quite different thermal regimes.

Alainites muticus (LINNEUS, 1758)

Alainites muticus exhibited a life cycle with a main generation in winter/spring (Figs. 6, 7) while a few spare specimens only were collected in the summer period. The winter/spring generation started to develop in January and emerged in May/June. Smaller nymphs presumably originated from eggs that exhibited a embryonic diapause from June until (October)/December. The life cycle pattern observed in the Pioverna Stream for the winter/spring generation of *A. muticus* corresponds to that described by Wise (1980) for the north eastern England. This Author (Wise, *op. cit.*) identified a bivoltine cycle with a slow-growing winter generation and a fast-growing summer generation. Little growth occurred during winter and the summer generation was characterized by fewer individuals of smaller size. For the first generation, hatching commenced in the early autumn, but there was no noticeable growth until the following March when a rapid increase in size coincided with an increase in density. Emergence began in April and was completed by the end of May with the exception of a few final instar nymphs which delayed until June, like in the Pioverna Stream. Here, a summer generation is lacking and its absence can be due to the larger increase of temperature observed in the Pioverna Stream compared to the Coquet river in England. In fact, according to Bohle (1969), the summer egg diapause for some species of aquatic insects may be induced by a temperature increase.

Macan (1957) and Studemann *et al.* (1992), found a bivoltine winter-summer life cycle for this species. Thibault (1971b), in contrast, identified three emergence periods: one, the clearest, corresponds to the main one identified by the present study. In the Pioverna Stream, we observed the presence of young nymphs in May which could indicate the beginning of a potential summer generation. However, the specimens were too few to allow the recognition of a fully developed generation. In the other Italian area where the cycle of *A. muticus* has been investigated, the presence of a summer generation was desumed from the appearence of nymphs in June (Buffagni *et al.*, 2002a). There, accordingly with the life cycle pattern described by Thibault (1971b), two additional generations to the one

found in the Pioverna Stream were recognised, however identifying a comparable main period of flight. The environmental conditions of these small lowland rivers of the Po Valley, i.e. relatively high temperatures during winter, temperature stability all over the year, etc. (see Buffagni and Gomba, 1996), support the presence of more than one generation, differently from the Pioverna Stream. This trend seems confirmed by the anticipation of the flying period (February *vs* April) of the main generation in the lowlands and is in accordance with general developement models (e.g. Ward and Stanford, 1982), assuming that bivoltine (multivoltine) life cycles are possible when enough thermal energy exists in the system.
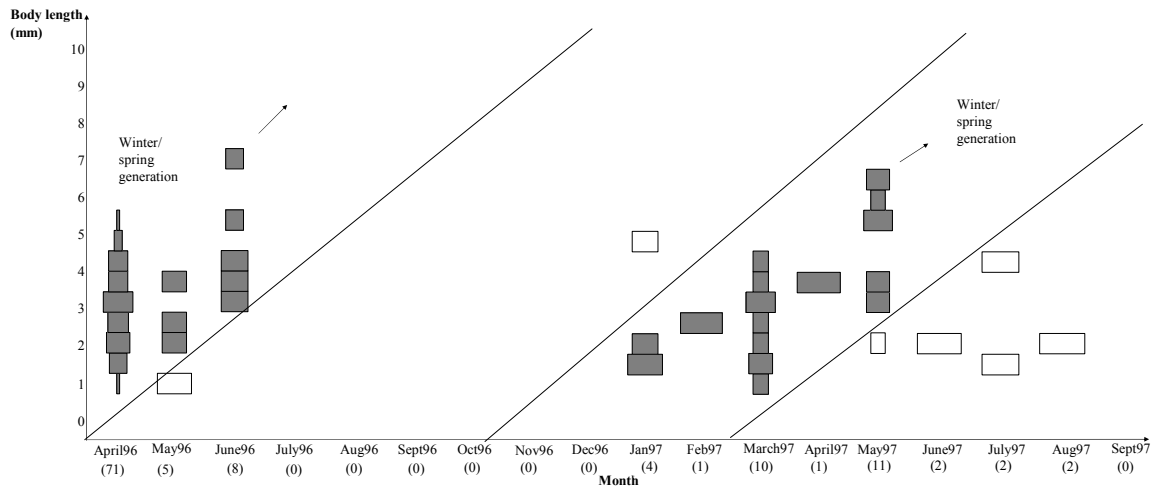

Fig. 6 - Life cycle of *Alainites muticus* during 1996/97 in the Pioverna Stream (Northern Italy, LC). Arrows indicate the emergence and numbers on the abscissa the absolute numbers of specimens measured. The width of each box represents the relative abundance of nymphs.
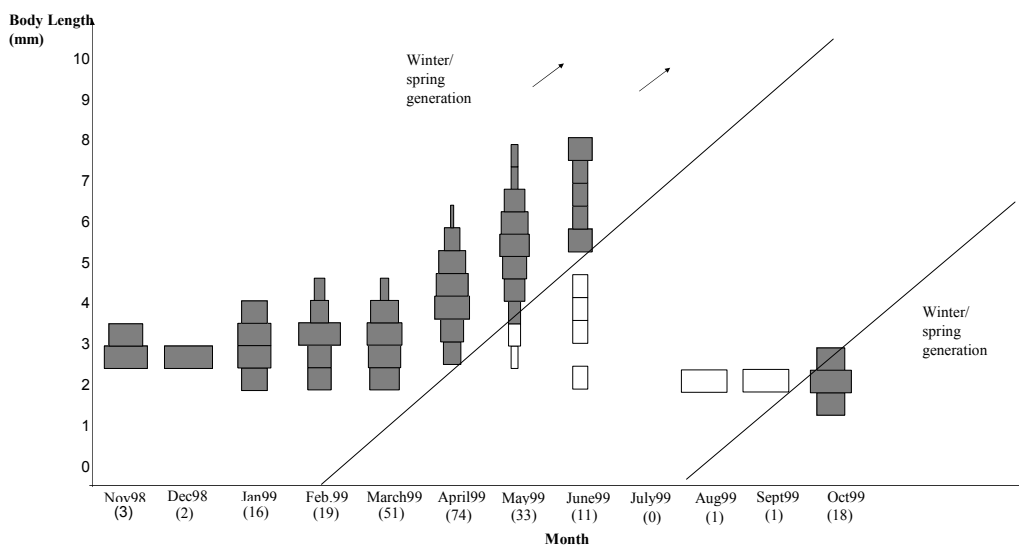

Fig. 7 - Life cycle of *Alainites muticus* during 1998/99 in the Pioverna Stream (Northern Italy, LC). Arrows indicate the emergence and numbers on the abscissa the absolute numbers of specimens measured. The width of each box represents the relative abundance of nymphs.

General remarks

In the Pioverna Stream the four Baetidae species studied showed different life cycle strategies. Two species, *B. alpinus* and *B. rhodani*, are present throughout the year with two/three and three generations, respectively. *B. melanonyx* behaves as a typical spring/summer species while *A. muticus* has a winter/spring development. *B. rhodani* showed the most complex life cycle with a egg hatching throughout the year due to delayed hatching (Elliott, 1972). The characteristics of this species' life cycle (multivoltinism and extended hatching) probably has adaptive value, especially in unpredictable environments. *B. alpinus* and *B. melanonyx,* exhibited differences between the two study periods. The plasticity of the life cycle of *B. alpinus* may also enable this species to survive adverse conditions. The hydrograph of the Pioverna river has shown over recent years a variable character, with flood events being frequent in some years (e.g. Buffagni and Comin, 2000) but quite rare in others (Buffagni *et al.*, 2002b). This may explain, together with the varying temperature pattern, the differences of the life cycles of *B. melanonyx* and *B. alpinus* among the two periods. Differences were also found comparing species life cycles in the southern and northern Alps. For *B. alpinus* and *B. melanonyx*, a higher number of generations were observed during the summer period in the Pioverna Stream (i.e. in the southern Alps) compared to other documented situations at more northern site. This study, carried out in a fairly pristine river, other than providing precious knowledge on mayfly ecology only, will also support useful comparisons when assessing the anthropogenic impacts on aquatic communities.

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