Larval development and ecology of *Baetis liebenauae* Keffermüller (Ephemeroptera : Baetidae) in a north Italian lowland spring

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Keywords : Insect, Ephemeroptera, *Baetis liebenauae*, life cycle, ecology, morphological stages.

The life cycle of *Baetis liebenauae* has been investigated in a lowland spring of Northern Italy that shows a relative stability of water temperature. Nine postlarvula morphological stages of the larva were identified and a «jump development» of the wing-pads between stage pairs has been noted. *B. liebenauae* is here a typical polyvoltine species and three generations can be defined, with the late-summer/autumn generation being the main one. During this generation the species is often the dominant taxon of the benthic community and shows a high larval density. Marquet differences have been in comparison noted with the development of this species in Poland. This is probably due to the different thermal features of the two regions. A temporal shift of the main generations seems to allow the coexistence of *B. liebenauae* and other high density Baetidae species. In Southern Europe the species is typical of small lowland streams with slow flowing waters. Its larvae live on aquatic macrophytes and their presence on mineral substrata can be considered as occasional.

Développement larvaire et écologie de *Baetis liebenauae* Keffermüller (Ephemeroptera) dans l'émissaire (d'une source de l'Italie du Nord
Mots clés : Insecte, Ephemeroptera, *Baetis liebenauae*, cycle biologique, écologie, stades morphologiques.

Le cycle biologique de *Baetis liebenauae* a été étudié dans l'émissaire d'une source de plaine de l'Italie du Nord qui montre une relative stabilité de la température de l'eau. Neuf stades morphologiques postlarvules de la larve ont été identifiés par le développement des fourreaux alaires. *Baetis liebenauae* est ici une espéce typiquement polyvoltine. Trois générations peuvent se succéder dont celle de fin d'été/automne qui est la plus importante. Pendant cette géneration, l'espèce représente souvent le taxon dominant dans la communauté benthique, et montre une densité larvaire élevée. Une différence marquée comparativement au développement de l'espèce en Pologne a été mise en évidence, probablement induite par le régime thermique différent dans les deux régions. La coexistence de *B. liebenauae* avec d'autres Baetidae à haute densité semble être permise par une ségrégation temporelle des principales générations. En Europe du Sud, l'espèce est typique des petites rivières à courant lent de basse altitude. Les larves de *B. liebenauae* vivent sur les macrophytes aquatiques et leur présence sur substrat minéral peut être considérée comme occasionnelle.

1. Introduction

Baetis liebenauae Keffermüller, 1974, first recorded and described in Poland (Keffermuller 1974), has been later found in Italy (Belfiore 1983), Finland (Savolai-nen & Pulkkinen 1987), Austria (Bauernfeind 1990), Switzerland (Jann Cotti & Barbieri 1993) and Czek Republic (Soldán, pers. comm.). This species, whose real distribution probably involves a large part of Europe, has been considered as rare in Italy (Belfiore 1988) and Austria (Bauernfeind & Weichselbaumer 1991) till recent years. Successively, it appeared as one of the most common and abundant mayfly species in small water courses of the lowlands of Northern Italy (Buffagni 1992, Desio 1993). There is little data concerning its ecology and information about its life cycle have only been reported from Poland (Glazaczow 1994).

The aim of the present work is to describe the life cycle *of B. liebenauae* and to present some notes on its ecology. Furthermore, the morphological stages of the larvae are reported here.

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2. Study area, material and methods

The study has been carried out in the lotic stretch of a lowland spring (Fontanile) located near Milan: Fontanile Grande (Altitude 130 m a.s.l. ; Towns of Vittuone, Cisliano and Gaggiano - Regional Technical Map Ctr: Magenta Est sez. A6e3). The «fontanili» are artificially built springs often derived by previously existing natural springs. They are characterized by the presence of a lentic (head) and a lotic (stem) zone (Fig. 1) and show relatively constant and undisturbed chemical, physical and hydrogeological features (Cotta Ramusino, Crosa & Buffagni 1991). These springs are typical of Northern Italy and they are present, and fairly common, in the Po Valley, mainly in its Northern side, and in the Adige, Brenta, Piave and Tagliamento floodplain areas (see Buffagni 1992). The discharges of these springs have maximum values in late-spring and summer periods, owing to higher availability of ground waters and irrigative practices. Flows are, anyway, relatively constant and range from 30 to 70 l_*s^{-1} in the Fontanile Grande. Water velocity never exceeds 80 cm_*s^{-1}, and depth in the sampled areas ranged from 12 to 40 cm. Channel widths, that are uniform all over the year, range from 160 to 220 cm. These lowland springs bear a rich mayfly community and give hospitality to uncommon Ephemeroptera species (Buffagni 1994).

Baetis liebenauae larvae were collected monthly during 1992 in many sites along the channel (stem) of the studied spring (Fig. 1), at a distance varying from 500 to 1000 m from the source. Samples were taken both on mineral substratum and aquatic macrophytes. Stream bottom was mainly constituted of gravels and
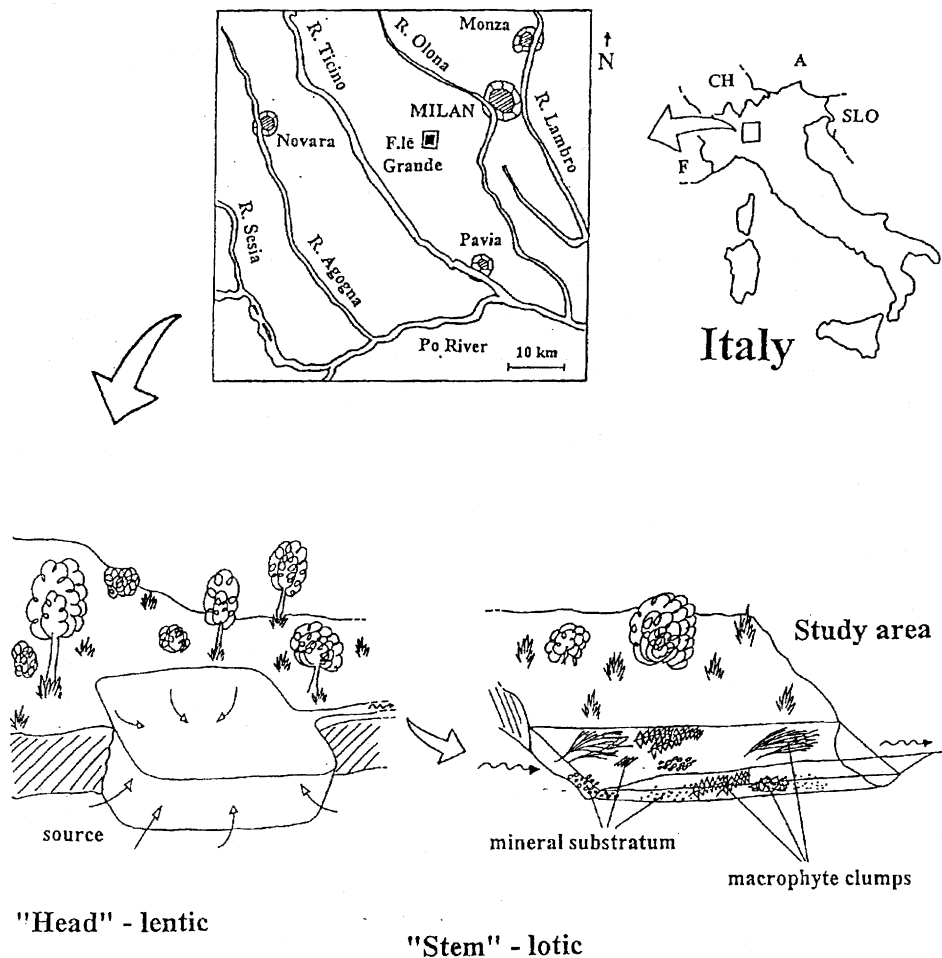

Fig. 1. Location in Italy of the Fontanile Grande and schematic drawing of the study area.
Fig. 1. Localisation en Italie de la Fontanile Grande et représentation schématique de la station de récolte.
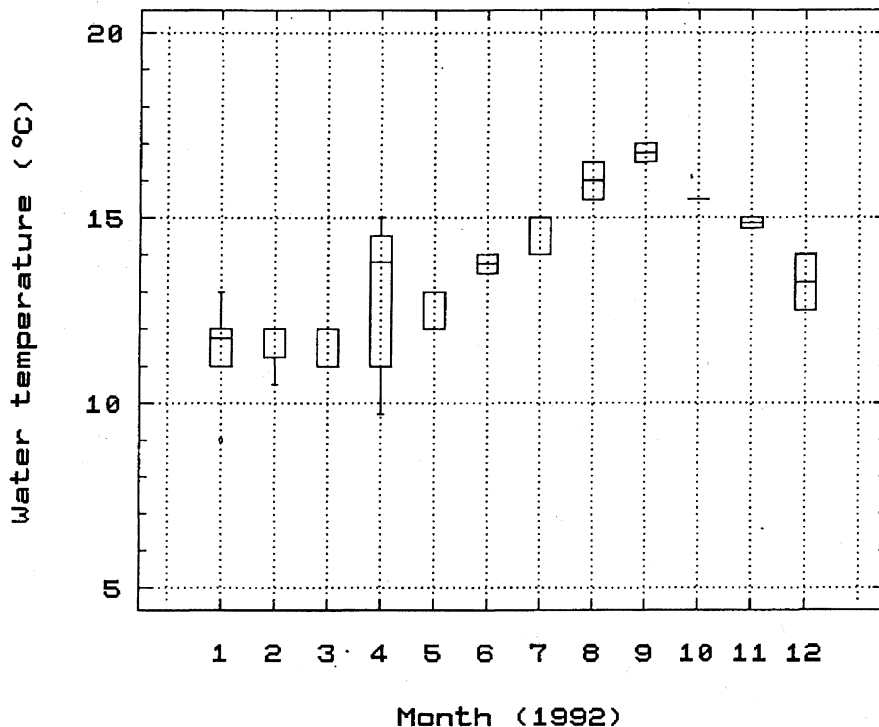
Fig. 2. Water temperature of Fontanile Grande, where the larvae of *B. liebenauae* were collected. The horizontal lines inside each box are the median values.

Fig. 2. Températures mensuelles de l'eau de Fontanile Grande. Les lignes horizontales dans chaque cadre sont les valeurs médianes.

small stones on a large-sand matrix. We used a Surber sampler (0.05m^2; mesh size 0.45 mm; 227 samples) on mineral substrata whereas collections on macrophytes were performed using a handling net (102 samples)(Table 1). Particular attention was given to select homogeneous vegetation sites of the same size and development stage in order to compare between different samples quantitatively. Instantaneous, minimum and maximum daily water temperatures were recorded in the spring channel every two weeks. In the figure 2

the annual temperature cycle of Fontanile Grande is shown. 1992 mean water temperature was 13.8°C. A narrow annual temperature range was noted: values never went below 9°C and over 17°C, mainly fluctuating between 11°C and 15°C.

Complexively, about 1200 *B. liebenauae* larvae were collected, sorted out and fixed in 75 % Ethanol. Twenty-eight imagos and subimagos were obtained by rearing mature larvae or by direct collecting. To des-

Table 1. Larval density (ind.*m^{-2}; d) of *B. liebenauae* and number of samples (n) collected on aquatic macrophytes and mineral substratum during 1992.

Tableau 1. Densité larvaire (ind*m^{-2}; d) de *B. liebenauae* et nombre d'échantillons (n) prélevés dans les macrophytes aquatiques et sur les substrats minéraux durant la période d'échantillonnage (1992).

	J		F		M		A		M		J		J		A		S		O		N		D		n tot.
	d	n	d	n	d	n	d	n	d	n	d	n	d	n	d	n	d	n	d	n	d	n	d	n	
Berula erecta	0	1	120	2	0	2	146	3	500	4	466	3	630	4	448	5	1160	4	1820	2	840	3	880	3	36
Callitriche obtusangola	14	3	20	2	0	2	0	1	-		-		0	1	-		-		-		-		-		9
Elodea canadensis	0	1	40	1	-	-	40	1	160	1	0	1	-		1280	1	120	1	1040	1	480	1	-	-	9
Hottonia palustris	0	1	0	1	0	1	0	1	0	1	0	1	0	1	40	1	160	1	-		-		0	1	10
Lemna trisulca	-	-	0	2	320	1	0	1	40	1	240	2	0	1	120	2	20	2	586	3	360	2	860	2	19
Nasturtium officinale	0	1	0	1	0	1	200	1	-		-		-		200	1	660	2	160	1	80	1	-		9
Ranunculus trichophyllus	40	1	0	1	0	1	0	1	-		-		0	1	460	2	160	1	1120	1	200	1	-		10
n tot.		8		10		8		9		7		7		8		12		11		8		8		6	102
Mineral substratum	21	16	14	31	2	18	1	18	1	18	0	18	0	18	0	18	3	18	3	19	9	18	2	18	227

cribe the life cycle, over 800 larvae were measured under a microscope to the nearest 0.25 mm. Emerging periods were defined on the basis of the presence of mature larvae in the samples. Because of the difficulty of keeping head capsules perfectly on line with the visual plane, body length measure (not including cerci) was preferred. Cephalic width and wing-pads length were measured for 100 specimens. The relationship between body length (bl) and cephalic width (cw) is: cw(mm)= 0.241 + 0.088 bl(mm); (r^2=0.839).

3. Results and discussion

3.1. Larval development

According to Cianciara (1980), there are two main periods of morphogenesis from the egg to the subimago in the development of mayfly nymphs: a first period of gills formation (Larvulae) and a period of wing-pads formation. During the latter, the last stage (N) is named «Nymph» and the others «Larvae» (I to VII) in *Cloeon dipterum* (Linné, 1761). In the first larval stage (L_I) the wing-pads are absent (Cianciara 1979). On the basis of a readily distinguishable morphological character - the mesothoracic wing-pads development - Cianciara could define eight post-Larvula stages. In the present work, nine post-Larvula stages have been identified for *B. liebenauae* larvae. Gaino (1987), examining the progressive organization of the wing inside the mesothoracic pad, found the same number of stages for *Habrophlebia eldae* Jacob & Sartori 1984. Glazaczow (1994) grouped *B. liebenauae* larvae in 7 classes, based on the degree of development of wing-pads. Possibly, the Class I defined by this Author included larvae with already present wing-pads. Adding the L_I stage, as previously defined, we obtain a total of 8 stages. Seven morphological stages were found in *Baetis alpinus* (Pictet, 1843) (Humpesch 1979 a), *Baetis lutheri* Müller-Liebenau 1967, and *Baetis rhodani* (Humpesch 1979 b) as well. The discrepancy with our results seems to be due to different criteria for distinguishing morphological stages (i.e. wing-pads length was not the only character in Humpesch 1979 a, 1979 b). The «exceeding» stage we found in *B. liebenauae* is possibly located between stages L_I and L_{III}. In fact, it is probably more arbitrary to define the younger larval stages than the older ones because of the smaller wing-pads. Furthermore, in the present work, morphological stages from L_{III} to N found a statistical validation through the wing-pad length measures (Lavandier 1981). In Table 2, the mean wing-pads lengths of morphological stages (L_{III} to N) for both sexes of the late-summer/autumn generation (see below) are reported. Stage N includes the mature nymphs too, that do not show an increase in wing-pads length. In Table 2 the results of a multiple range analysis for the means are also listed. Levels with asterisks in the same column form a homogeneous group of wing-pads lengths that do not show statistically significant differences. These differences are significant in all cases but the one between female larvae of stages L_{III} and L_{IV}.

In the figure 3 the mean wing-pads lengths, with 95 % confidence intervals, are plotted; it is interesting to note how, in both sexes (but mainly in males), larval stages can be grouped in pairs: L_{III}/L_{IV}, L_V/L_{VI} and L_{VII}/N. The mean distance between these three pairs is indeed higher than between single stages inside pairs so that a «jump development» of the wing-pads between stage-pairs seems to occur. In spite of this, between stages L_{VII} and N in female larvae, a strong increase in wing-pads length (25 % of the total increase between L_{III} and N) occurs.

3.2. Life cycle

Hereafter Larvulae, Larvae and Nymphs are generically called larvae. The life cycle of *B. liebenauae* during the study period is shown in the figure 4. There were no difficulties in determining young larvae because of the peculiar shape of mandible outer tooth (Keffermüller 1974).

The emergence period of *B. liebenauae* is very long, as mature larvae were collected at each sampling date between March and December. A great variety of size classes were simultaneously present throughout the year. However, it is possible to identify three generations in one year (polyvoltine species). Few overwintering larvae, which get fully developed in March, yield a poor winter generation (Fig. 4). This is true at least for the winter generation ending on March 1992. In November and December of the same year, many young larvae were present, allowing us to hypothesize, for 1993, a more abundant incoming winter generation. So, it is possible that the relative importance of this generation may vary from year to year. Some of the eggs laid by the female adults of this generation may hatch in April, yielding the young larvae of the spring/summer generation. After asynchronous hatching and a fast larval growth, emergence occurs from May to July/August. Also this second generation concerns a low number of individuals.

The consequent eggs hatching leads to the development of the main *B. liebenauae* generation, the late-summer/autumn one. Hatching is strongly asynchronous, determining the presence of various cohorts, not easily distinguishable in the successive months. This generation, which regards a very high number of lar-

Table 2. Average wing-pads lengths (mm) of morphological stages L_{III} to N for both sexes.

Tableau 2. Longueurs moyennes des fourreaux alaires (mm) des stades morphologiques L_{III} à N des deux sexes.

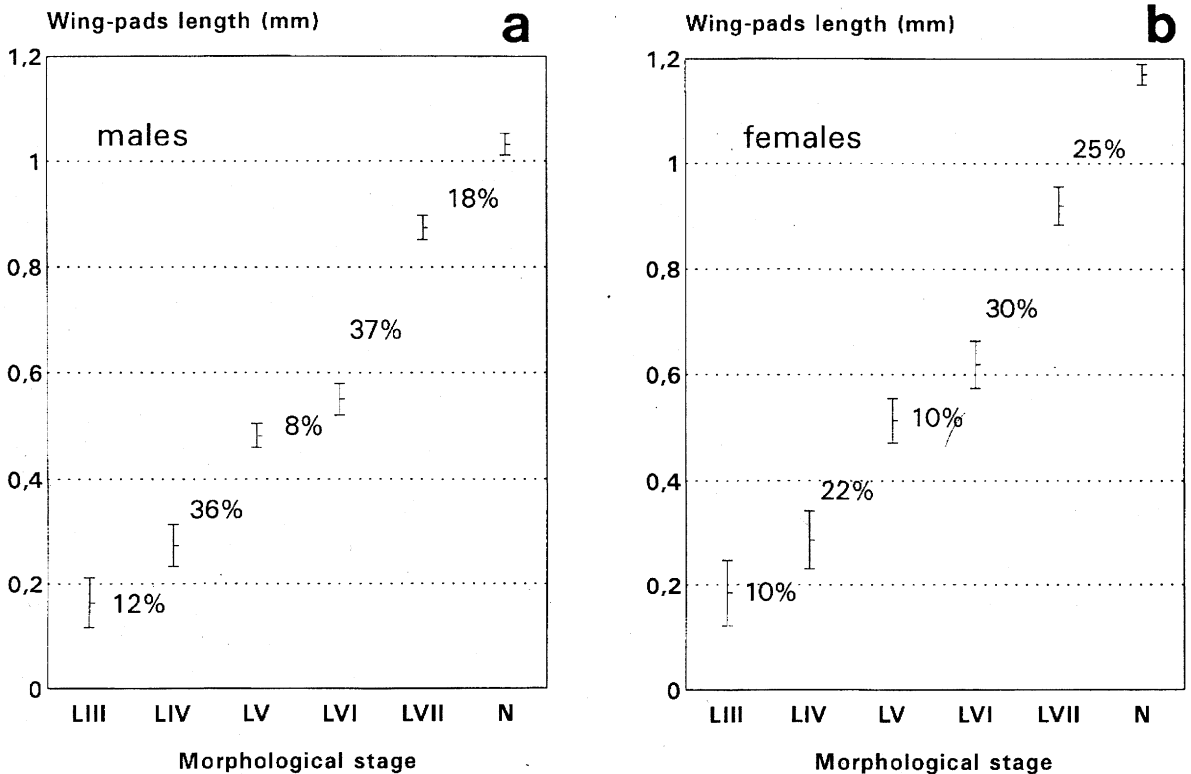| Sex	Stage	Average length	95% C.I.		Homogeneous groups						n
male	LIII	0,164	0,117	0,211	*						3
	LIV	0,273	0,233	0,314		*					4
	LV	0,48	0,458	0,503			*				13
	LVI	0,55	0,519	0,58				*			7
	LVII	0,875	0,853	0,898					*		13
	N	1,032	1,011	1,053						*	15
female	LIII	0,185	0,122	0,248	*						4
	LIV	0,287	0,231	0,343	*						5
	LV	0,511	0,471	0,555		*					9
	LVI	0,619	0,575	0,663			*				8
	LVII	0,92	0,884	0,956				*			12
	N	1,172	1,142	1,201					*		18

Fig. 3. Plot of mean wing-pads lengths with 95 % confidence intervals for morphological stages L_{III} to N. Percentages of length increase between stages are reported, a) Males, b) Females.

Fig. 3. Longueur moyenne des fourreaux alaires avec 95 % d'intervalle de confiance pour les stades morphologiques L_{III} a N. L'augmentation de la longueur entre les stades est rapportée en %.   a) Mâles, b) Femelles.
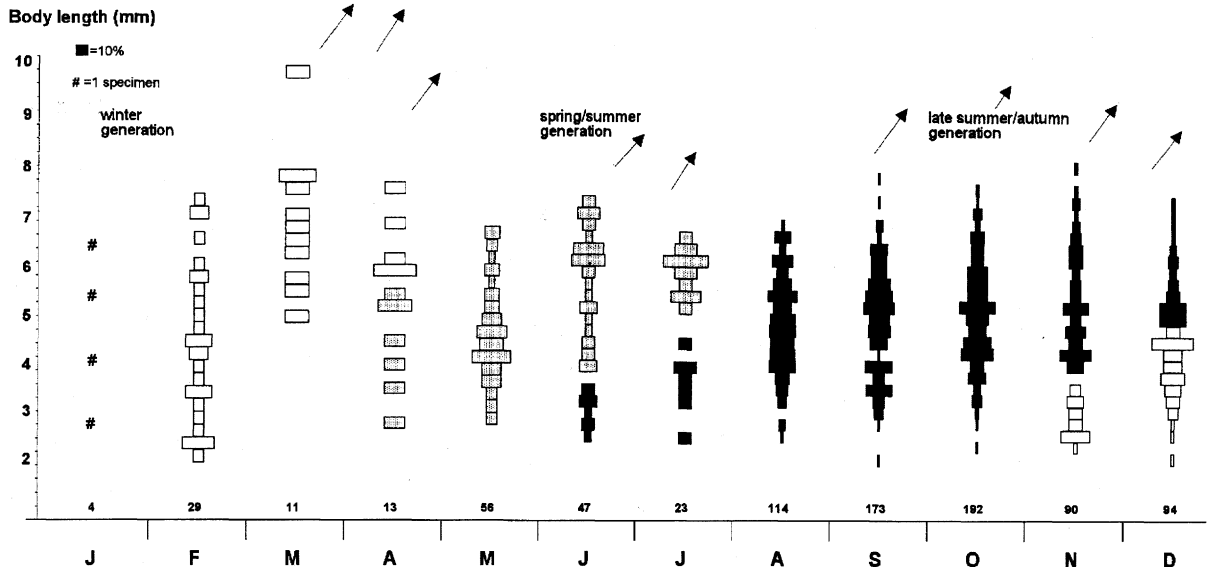
Fig. 4. Life cycle of *B. liebenauae:* Frequency distribution of body length measurements at each sampling time. Arrows indicate the emergence periods.

Fig. 4. Cycle biologique de *B. liebenauae :* structure des populations larvaires basée sur la longueur du corps aux dates de récoltes. Les flèches indiquent les périodes d'émergence.

vae, allows emergence from September to December. Only a part of the oviposited eggs hatch immediately, starting the winter generation. For this reason, and as winged stages emerged from the spring/summer generation are probably not numerous enough to ensure large numbers in the very abundant late-summer/autumn generation, a long diapause of a part of the eggs is possible. This has been already observed for *B. liebenauae* (Glazaczow 1994) and for *Baetis vemus* Curtis, 1834 (Bohle 1969), which belongs to the same species-group.

Notable differences with the life cycle of *B. liebenauae,* as described in Poland (Glazaczow 1994), can be reported. The most interesting feature of the life cycle of *B. liebenauae* in Northern Italy is the typical highest larval abundance in late-summer/autumn, that causes the late generation to be the main one. Furthermore, larvae of the spring/summer and late summer/autumn generation showed opposite density patterns, with the first one being the main generation in Poland (Glazaczow 1994). In Italian lowland streams, the presence of overwintering larvae determines the existence of a winter generation, not present in Poland. Moreover, young larvae of the spring/summer-generation occur one month earlier in Northern Italy than in Poland. The last larvae of the late summer/autumn generation are still present in Italian lowland springs two months later than in Polish streams.

These differences could be due to the thermal regimes of the studied streams in the two regions. Glazaczow (1994) in the river where he investigated the life cycle of *B. liebenauae*, found water temperatures between 8° and 22°C, apparently not strongly different from those observed in the present study. He reported the average annual water temperature of two rivers of the same geographical region, that were 9.5° and 9.7°C, considerably lower than 13.8°C, found in the Fontanile Grande. These notable differences in the average values of water temperature and air temperature, which in Poland limits the adults' survival (Brittain 1990, Werneke & Zwick 1992), can explain the discrepancy between the life cycles of *B. liebenauae* in Italy and Poland (Vannote & Sweeney 1980, Ward & Stanford 1982, Ward 1992).

According to many previous studies on mayflies (i. e. Thibault 1971, Elliott et al. 1988), *B. liebenauae* larvae getting fully developed during the first and the last months of the year grow to larger dimensions in the Italian spring under study, than those of the late-summer/autumn period. Notwithstanding many abiotic factors that can affect the size of the final instar *of Baetis* larvae (i.e. Fahy 1973), probably mainly due to the relative stability of water temperature (Sweeney 1978, Vannote & Sweeney 1980) these body size differences are anyway not conspicuous (Vannote & Sweeney 1980).

3.3. Ecology

In Switzerland (Sartori et al. 1996) and Austria (Bauernfeind 1990), *B. liebenauae* has been collected between 300 and 350 m a.s.L, where these altitudes represent the lowest reaches of the two countries. In Poland, the species lives below 150 m (Glazaczow 1994). In Italy, *B. liebenauae* larvae had never been collected above 350 m a.s.L till recent years (Buffagni & Desio 1994). New single collections from the Italian Alps (Buffagni, unpubl. data), at about 500 m a.s.L, allow to extend the species elevation range, but *B. liebenauae* has anyway to be considered as a typical lowland taxon.

In Italy the larvae usually inhabit with large number lowland springs, small streams and artificial channels with a stream width less than 3-4 m (Buffagni 1992, 1994, Desio 1993, Buffagni & Desio 1994); in Switzerland, they were collected in a southern small tributary of Lake Lugano with a stream width less than 2 m (Sartori et al. 1996). Notwithstanding a few specimens collected in the Ticino River (Buffagni, unpubl. data), the species does not seem to be common in larger streams. On the contrary, Glazaczow (1994) found the majority of the larvae in larger rivers of Pomerania (Poland), with stream width over 12m and discharges of about 20-25 m^3*s^{-1} in their lower courses. In that region, they were nearly absent from small rivers.

In Italy the *B. liebenauae* larvae prefer low water velocity (Buffagni & Desio 1994). In spite of this, in relatively protected microhabitat inside macrophyte clumps, they can live in fast flowing waters, at least up to 1 m^3*s^{-1} (Bauernfeind 1990). Furthermore, Glazaczow (1994) considered the species as typical of relatively fast current habitats. Therefore, some differences occur between Poland and Italy in the type of habitat *B. liebenauae* larvae .usually inhabit, but they are possibly due to a different aquatic macrophyte colonization of rivers in these two European areas. In fact, the species seems to be exclusively present on submerged plants.

Bauernfeind (1990) reported the presence of *B. liebenauae* on *Ranunculus*, where, in the present research, larvae were also present with high number (on *R. trichophyllus* Chaix). Anyway, *B. liebenauae* can also colonize all the other sampled aquatic macrophytes (Table I): *Nasturtium officinale* R. Br. agg., *Hottonia palustris* L., *Callitriche obtusangula* Le Gall, *Elodea canadensis* Michx, *Lemna trisuica* Linne and *Berula erecta* (Hudson) Coville. On this last macrophyte, larvae can be present with high densities (up to 2300 $N*m^{-2}$) but, according to Glazaczow (1994), preferences of *B. liebenauae* for specific water plants seem not to be apparent (Table 1). In more than two hundred

samples on mineral substrata taken throughout the year, only about 50 *B. liebenauae* larvae were caught. Moreover, the bottom areas in which these specimens were collected are all located at the boundaries of sampling sites with well developed aquatic vegetation. In the studied environment, the presence of this species on mineral substrata has therefore to be considered as occasional. This confirms Desio (1993) and Glazaczow's (1994) notes about habitat requirements of the species, that lives almost exclusively on submerged macrophytes. The selection of suitable habitats (i.e. macrophytes) depends all the same on their availability in the environment. In fact, as observed for other *Baetis* species, the larval distribution in the different habitats could be linked to the aquatic plants cycle. Depending on density and vegetative stage of macrophytes, *B. rhodani* (Pictet 1843) can change its location or habitat preference, moving from plants to mineral substrata, or vice-versa, throughout the year (Ouahsine & Lavandier 1988). It is then possible that the larvae of *B. liebenauae* can live on mineral substratum when macrophytes are present in low densities. This can explain the higher larval abundances on mineral substrata observed in the present study in January and February (Table 1), when aquatic plants are scarce.

B. liebenauae larvae can tolerate a light organic pollution (Desio 1993, Jann et al. 1993).

B. liebenauae may coexist with many other mayfly species (Buffagni 1994) but it is more frequently found with the ubiquitous *Baetis rhodani* (Pictet, 1843) and *Alainites muticus* (Linné, 1758). In the autumn period, it is often the dominant species of the benthic community it belongs to (Buffagni 1992, Sartori et al. 1996).

B. liebenauae is, in the studied sites, a typical polyvoltine species. This is not surprising, as many other *Baetis* species often show two or more generations a year (Landa 1968, Thibault 1971, Sowa 1975, Elliott et al. 1988). Other numerically important Baetidae species simultaneously present — *B. rhodani* and *A. muticus* — show the same general life cycle pattern but with the winter generation as the main one and with the highest larval densities between December and April. *Centroptilum luteolum* (Miiller, 1776), sometimes present in the same microhabitat with high densities, emerges shortly before the late-summer fast increase in the population of *B. liebenauae*.

Even though in fluctuating habitats little temporal resource partitioning among mayfly taxa can occur (Benke & Jacobi 1994). Sweeney & Vannote (1981) suggested that competition between related mayfly species may be reduced by temporal segregation. Fur-

thermore, temporal shifts of emergence of high density coexisting mayfly species have been reported from many authors (i.e. Thibault 1971, Brittain 1982, Elliott & Humpesch 1983). Leading to avoidance of direct competition, a relative temporal shifting of main generations or production peaks seems then to allow the coexistence of these high-density Baetidae species.

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