Freshwater Biology (1993) **29**, 429–439

Substrate interstices as a habitat for larval *Thraulus bellus* (Ephemeroptera) in a temporary floodplain pond

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SUMMARY

1. Larvae of the ephemeropteran *Thraulus bellus* were sampled from the substrate interstices of a floodplain pond along the River Adour (south-west France). Quantitative sampling was carried out using traps arranged in five transects of four traps each, made up of five vertical compartments between +20 and −80 cm from the surface of the substrate. The 100 compartments thus obtained were each 2.86 l volume, and were sampled once a month from January 1988 to January 1989.

2. An influx of young larvae coming from the permanently flooded deep substrate invaded the upper 80 cm of the substrate on and after mid-January. An increase in larval density and frequency of occurrence in the compartments occurred until May before emergence of the adults. A second colonization phase by young larvae took place from July to September, and was followed by reductions in larval density and frequency of occurrence during the autumn/winter drop in water level.

3. Horizontal and vertical movements of the larval population within the interstitial habitat of the pond were clearly linked to the water level fluctuations. However, differences between the five transects indicated a control of these movements by factors such as slope of the substratum, macrophytic vegetation, and the influence of springs. A relationship was found between population density and probability of submergence of the compartments, indicating that the larvae avoided locations most influenced by the fluctuating water levels.

4. The temporarily flooded substrate interstices appear to be a refuge for the larvae of *T. bellus*, preventing them from overlapping with two other abundant ephemeropterans, namely *Caenis horaria* from silt habitats and *Cloeon* gr. *simile* from macrophyte beds.

Introduction

Although Ephemeroptera display a marked ability to occupy a diverse array of microhabitats they have rarely been reported from interstitial habitats. They have not been quoted as an insect order with species belonging to the Stygofauna Mundi (Botosaneanu, 1986). This distinguishes Ephemeroptera from orders such as Plecoptera, which have certain species known to dwell in the subterranean environment, at least during part of their life cycle (Stanford & Gaufin, 1974; Bretchko, 1981; Stanford & Ward, 1988).

It was therefore surprising to collect large numbers of larvae of the ephemeropteran *Thraulus bellus* Eaton (Leptophlebiidae), during a study of the fauna of interstitial habitats in a floodplain pond (Tabacchi, 1987). Species of this genus have been reported only infrequently from such habitats before (Eaton, 1881; Léger, 1927; Verrier, 1944, 1948, 1953a,b; Bishop, 1973; Gaino and Spano, 1975; Margalef *et al.*, 1977; Gallardo Mayenco & Lopez, 1981; Wendling & Erpelding, 1983).

The instability of interstitial habitats that are periodically flooded seriously restricts the fauna. This paper evaluates the colonization of substrate interstices in a floodplain pond by the ephemeropteran

T. bellus and addresses the key questions: what are its movements within the interstitial system during its larval development, which factors determine these movements, and what are the advantages for individuals of this species?

Materials and Methods

The study site

The study site is a pond located 200 m from the right bank of the River Adour downstream of the city of Tarbes in south-west France (Fig. 1). The pond was excavated 35 years ago within an alluvial deposit nearly 30 m deep, and therefore fed with groundwater. The substrate of the pond consists mainly of pebbles: 81.3% of the particles are above 10 mm in diameter, and the modal class is 100–200 mm diameter (30.4 ± 7.9%). The interstices are mainly unclogged. Thus, the effective porosity is high (45.4 ± 1.7%).

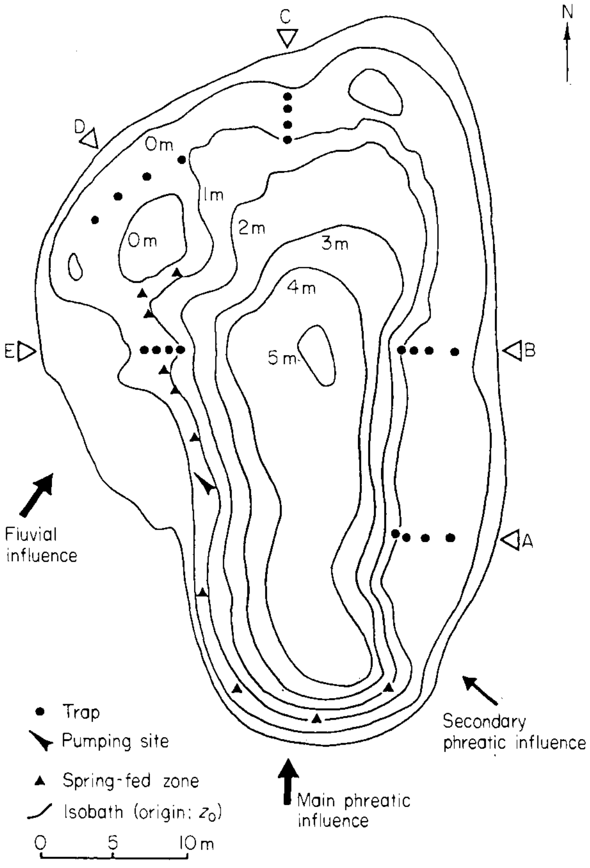

Fig. 1 Location of the five transects A to E in the temporarily flooded riparian zone of the pond. Each transect comprises four traps (dark points).

The water level of the pond fluctuates annually by 2 m, and is directly influenced by the River Adour which recharges the aquifer from January to June and drains it from July to December. This fluctuation height defines what we will call the littoral zone of the pond. The groundwater discharge is $1.5\,m^3\,s^{-1}$, the longitudinal hydraulic gradient is 7%, and permeability is $1.4 \times 10^{-3}\,m\,s^{-1}$. This results in the pond water sometimes being renewed through submersed phreatic springs. Despite their interconnections, however, the three water bodies—pond, aquifer and River Adour—all differ in their physicochemical characteristics, as shown in Table 1.

Organic matter is added to the pond as leaves from the tree canopy (*Platanus* × *acerifolia* Willd., *Populus nigra* L., *Alnus glutinosa* Gaertn., *Salix alba* L. and *Quercus pedunculata* L.), and also by macrophytes (*Myriophyllum spicatum* L., *M. brasiliense* Cambess and *Nuphar lutea* L.).

Sampling procedures

Five transects were first selected around the pond in order to cover satisfactorily the different configurations of the temporary flooded zone (Fig. 1). The main characteristics of the transects are indicated in Table 2. Each of these transects was studied using four vertical traps. The 1-m-long traps are formed by three concentric cylinders made of PCV pipes (Fig. 2). The external cylinder is perforated with 20-mm holes; it was implanted within the substrate and left permanently throughout the period of survey. The middle cylinder is perforated with 13-mm holes in 190-mm-wide bands alternating with non-perforated bands. This divides the cylinder horizontally into five compartments each 200 mm high. The inner cylinder is perforated so that its holes can be matched with those of the middle cylinder. It is divided into five superposed compartments of 2.86 l capacity each by a polyurethane bulkhead. The middle and inner cylinders (the trap itself) are filled with the substratum extracted during the implantation of the external cylinder (guide). The trap itself can be removed for sampling. The traps were removed once a month from January 1988 to January 1989, and the fauna collected and identified from 100 compartments (5 transects × 4 traps × 5 superposed compartments).

Table 1 Main physicochemical characteristics of the interconnected water bodies: pond, water table, and the River Adour. Averages and standard deviations are given for the sampling period 1986–89 (eight samples year^{-1})

	Pond (surface)	Water table (−1.05 m)	River Adour
T (average, °C)	5.8–24.2	11.8–17.8	5.0–23.0
T (daily amplitude, °C)	0.5–6.5	0.2–0.5	
% sat. oxygen	75–111	50–71	85–223
Conductance (μs. 20°C)	275.2 ± 45.7	285.1 ± 62.4	220.4 ± 64.1
PO_4^{3-} ($\mu g\,l^{-1}$)	9.5 ± 8.9	2.3 ± 1.4	5.5 ± 5.8
NO_2^- ($mg\,l^{-1}$)	14.9 ± 10.9	0.0 ± 0.0	3.3 ± 5.1
NO_3^- ($mg\,l^{-1}$)	5.2 ± 1.1	8.6 ± 0.9	7.4 ± 4.7
SiO_3^{2-} ($mg\,l^{-1}$)	20.7 ± 17.7	49.0 ± 52.4	

Table 2 Physionomic characteristics of the five transects. Averages and confidence intervals ($\alpha = 5\%$) are calculated for the twenty site samples for each transect. In addition, the percentage of *Thraulus bellus* trapped in each transect over 13 months is given

	Transect				
	A	B	C	D	E
Mean elevation (m a.s.l.)	289.55	289.64	289.44	289.72	289.55
Total length (m)	4.59	5.18	3.87	12.16	2.98
Vertical range (m)	1.59	1.67	1.54	1.36	1.53
Slope (%)	4.8 ± 4.4	15 ± 5.1	10.8 ± 11.2	3.8 ± 0.9	17.3 ± 8.9
Mean porosity (%)	45.2 ± 0.8	45.9 ± 0.4	45.6 ± 0.5	45.1 ± 1.0	44.9 ± 0.7
Probability of submergence	0.75 ± 0.17	0.69 ± 0.22	0.80 ± 0.14	0.67 ± 0.17	0.75 ± 0.18
Spring fed zones	−	−	−	−	+
Sub- and eu-aquatic vegetation	+	++	+	+++	−
Per cent of individuals	14.4	6.0	21.8	16.6	41.2

−, absent; +, present; ++, abundant; +++, very abundant.

The traps were replaced in their exact initial position after sampling. The total content of 1300 compartments (100 × 13 months) therefore was examined during the period of study.

The spatial position of each compartment was characterized by one horizontal and three vertical parameters. The horizontal position was expressed as a percentage of the total distance from the innermost (0%) to the outermost (100%) trap with respect to the centre of the pond. The vertical position was expressed with respect to: (i) the absolute altitude relative to an origin $z = 290.5$ m a.s.l.; (ii) the substrate level, ranging from +20 to −80 cm; (iii) the fluctuating water level.

Each point of the littoral zone was also characterized by its probability of immersion, calculated from daily limnimetric data as:

$$\pi_z = ti/t$$

where ti is the duration of submersion during the period of study t from December 1985 to December 1990. π_z can be considered as a measure of the hydraulic instability of the interstitial system ($\pi_z = 1$ when the system is continuously submersed).

In addition to the study of the transects, pump samples of 15 l each were taken twice a month from November 1986 to January 1989 at 0.3 m deep (Bou & Rouch, 1967) in the location shown in Fig. 1. The characteristics of the life cycle of *T. bellus* were defined from these data.

Results

Annual variation in total numbers

The annual variation of total numbers of *T. bellus* is given by the variation of the number of individuals per compartment (mean and standard deviation), and by the frequency of occurrence within the 100 compartments sampled each month (Fig. 3). The system was colonized from February to May 1988 by an increasing number of old larvae (Fig. 3). The frequency of occurrence increased, together with the number of individuals per compartment, indicating

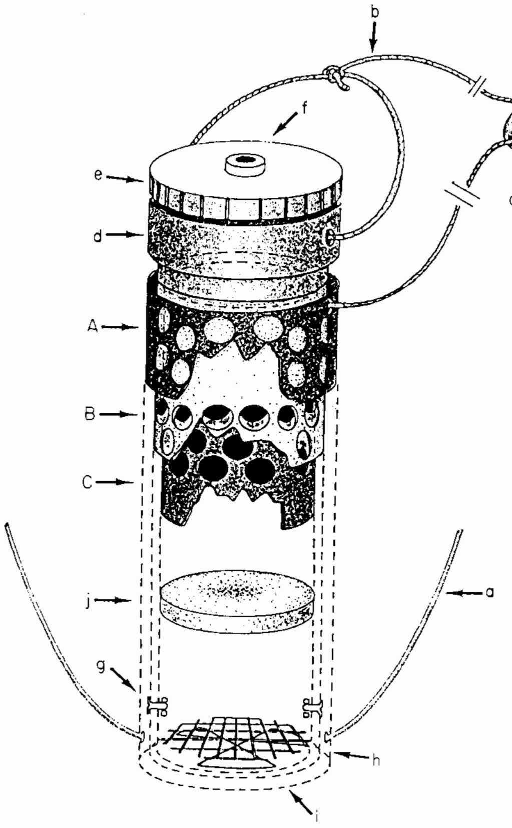

Fig. 2 Schematic view of the trap (lower part shortened). A, External cylinder; B, middle cylinder; C, inner cylinder. a, Anchor of the guide; b, halyard; c, float; d, neck; e, stopper; f, aeration hole; g, screw bolt; h, bottom mesh; i, bottom net; j, bulkhead. For explanations, see text and Tabacchi (1990).

an active dispersal of the individuals. The number of individuals per compartment decreased in May and June, due to the emergence of the adults, but this did not affect the degree of occupancy of the system, and frequency of occurrence remained stable. A new colonization phase by young larvae occurred from July to September, and was followed by a reduction in the number of individuals per compartment and of the frequency of occurrence as the water level dropped. The largest number of individuals found in any compartment was twenty-seven in September. The maximal frequency of occurrence was observed in May (fifty-seven occupied compartments out of 100).

Life cycle

A total of 1003 larvae of *T. bellus* was collected from 30 October 1986 to 15 January 1989. The length of the tibia III was measured to follow the growth of individuals. Extreme values were 63 and 2420 μm, corresponding to total body lengths (cerci excluded) of 1 and 10.5 mm, respectively.

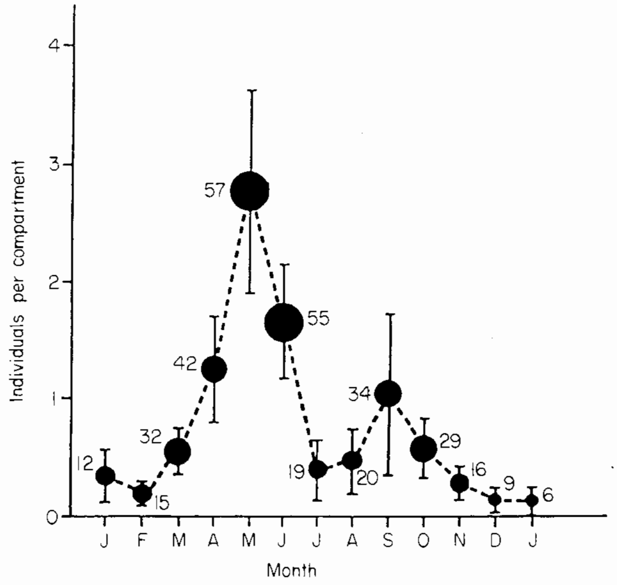

Fig. 3 Mean number of individuals per compartment from January 1988 to January 1989. The size of the dark plots is proportional to the frequency of occurrence (fraction of compartments occupied; maximum = 57% in May).

Thraulus bellus was found to be univoltine (Fig. 4). Flight periods extended from May to September, with a maximum in June. The larvae hatched at the beginning of July and grew during three distinct periods: (i) summer and early autumn, following hatching, when the mean increase in length of tibia III was 6.6 μm day^{-1} between 15 July and 31 October in 1987, and 8.2 μm day^{-1} from 15 July to 2 November in 1988; (ii) late autumn and winter, when the mean increase was less: 1.2 μm day^{-1} from 31 October to 15 April in 1986–87, and 0.9 μm day^{-1} from 30 October to 15 April in 1987–88; (iii) spring when the mean increase was greatest: 14.5 μm day^{-1} from 15 April to 15 June in 1987, and 12.2 μm day^{-1} from 15 April to 15 June in 1988.

An influx of young larvae occurred each year around 15 January. This influx took place before the rise of the water table level in 1987, and after this rise in 1988 and 1989. These larvae were smaller by up to 0.5 mm (tibia III) than the smallest larvae found on 1 January. As a consequence, the mean length was reduced by 15.5%, 24.6% and 3.7%, respectively in 1987, 1988 and 1989. This confirms the role played by

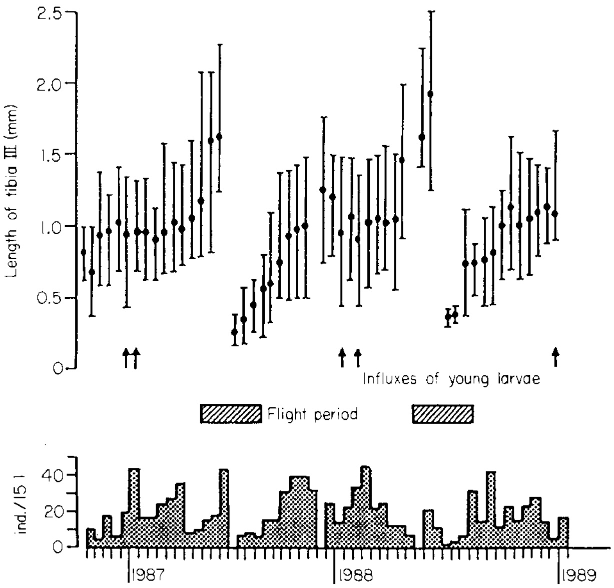

Fig. 4 Life cycle of *Thraulus bellus*. The figure indicates growth of the larvae (mean and range of the length of tibia III), influx of young larvae from the deepest zone (arrows), flight periods (grey rectangles), and numbers collected bimonthly from 15 October 1986 to 15 January 1989.

the substrate of the groundwater-saturated zone as a reservoir, where young larvae find buffered thermal conditions (Table 1).

Distribution of the larvae within the substratum

Thraulus bellus appeared clearly to be an endobenthic species during this study. Larvae were found deeper than 80 cm, as revealed by isolated pumping, with a maximum depth of −2.60 m in January 1991.

The distribution of the larvae in relation to vertical and horizontal gradients and to the emplacement of the traps around the pond (Fig. 5) was studied on a monthly basis. An important part of the population (22.6%) was present well into the substrate, at depths between −60 and −80 cm. The larvae of a first cohort moved upwards from January to May as shown in Table 3. The young larvae of a second cohort however moved downwards from September to January as seen by the numbers of individuals indicated in Table 3 (vertical distribution). Along the horizontal gradient, it appears that the innermost traps were the most frequently colonized (47.8%) and enclosed the highest population densities. The 6.04 modal class of May (old larvae) decreased gradually from the innermost to the outermost traps. The 3.08 modal class of September in the outermost traps corresponds to a new generation.

The percentage of individuals collected in the different transects is also given in Table 3. Transect E was the most populated and comprised 41.3% of the total larvae. This transect was the one most influenced by the fluvial hydraulic impulse, since it was located near the deep slow-flowing, spring-fed zones. This part of the pond was by far the most favourable for the life cycle of *T. bellus*. Transect B was the least populated and at the same time the farthest from spring-fed zones. The population reached its first modal value in May at Transects D and E, and in June at Transects A, B and C. The second modal value (new generation) was high compared to the first one at Transect C, suggesting a good ability to colonize following hatching. In contrast, this second modal value was totally absent at Transect D. The presence of larvae in late autumn indicates that this is not due to the inability of the young larvae to colonize the transect, but rather to reduced oviposition at this site. Here, the vegetative cover of macrophytes and helophytes reduces oviposition because adults are attracted to a more open water surface.

A statistical analysis of the spatial distribution was performed through ANOVA and MANOVA from the average densities of *T. bellus* in each of the 100 compartments. The effect of each strata (transect, vertical level, trap position) was measured by an F-test in MANOVA. The affinities between levels within a same strata were defined with multiple range tests (Tukey test if the F-ratio was significant, Bonferroni approximation otherwise).

The analysis of variance showed that mean densities did not differ significantly (95% CI) for the vertical distribution ($F = 0.274$, $P > 0.05$). Significant evidence for differences was found for transects ($F = 11.315$, $P < 0.0001$) and the horizontal distribution ($F = 8.292$, $P = 0.0001$).

The multifactor analysis of variance confirmed that the effect due to vertical distribution did not interact significantly with other strata. However, multiple range tests discriminated the upper level (+20/0 cm) from the others ($P < 0.05$). The transects and the trap positions showed significant effects in bivariate (respectively, $F = 13.38$, and $P < 0.0001$; $F = 15.74$ and $P < 0.0001$) or full MANOVA model (respectively, $F = 15.43$ and $P < 0.001$; $F = 13.12$ and $P < 0.0001$). The innermost trap appeared to be dif-

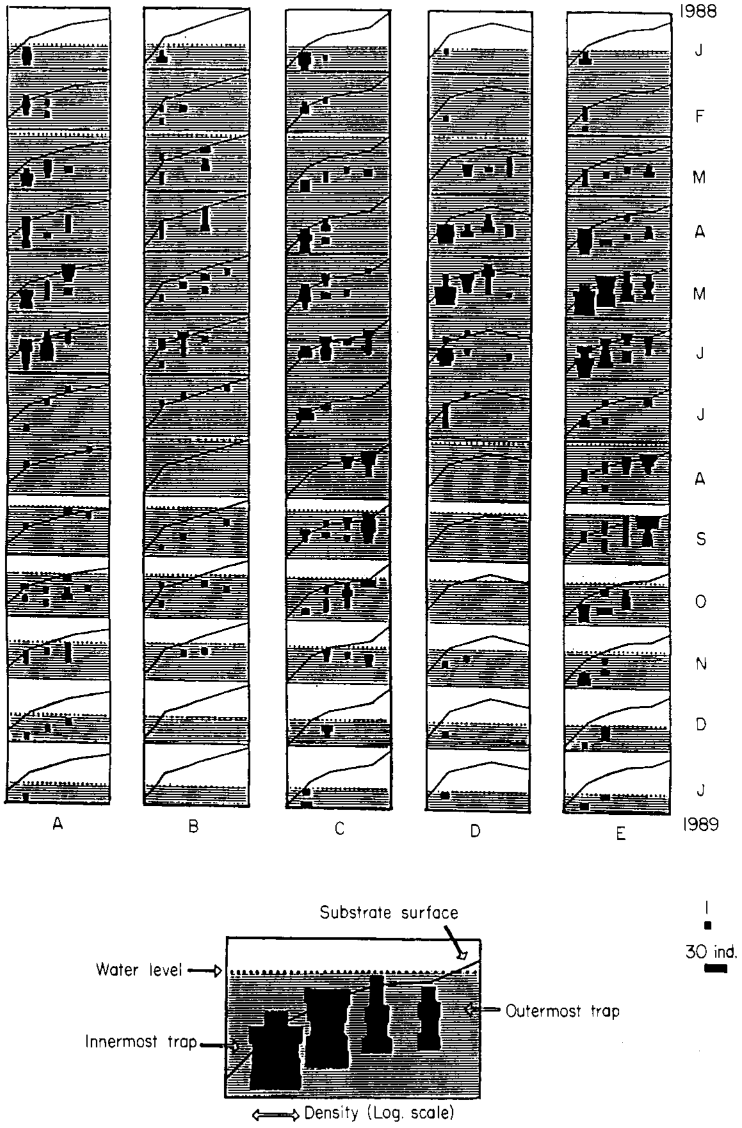

Fig. 5. Number of larvae collected from January 1988 to January 1989 per transect (A to E), per trap (from the innermost to the outermost), and per level (from the superficial compartment to the deepest). Substrate surface and fluctuating water level are also indicated.

ferent in densities to the others ($P < 0.05$), while intermediate traps could be considered as an homogeneous cluster. Transect E significantly differed from the others. The densities found in Transects A and D can be considered comparable, but densities of Transects B and C were statistically different.

Movements of the larval population

The movements of the larval population from month to month were analysed through 'barycentres' of the location of the larvae within the traps. A barycentre of the larval population of *T. bellus* for a given month is defined by:

$$B = \frac{\Sigma(n_i c_i)}{\Sigma(n_i)}$$

where i is one of the 100 compartments studied, n_i is the number of larvae in compartment i and c_i is one of the parameters characterizing the spatial position of compartment i; these parameters are: (1) the horizontal position from the innermost to the outermost trap, (2) the absolute altitude, (3) the depth from the substrate level and (4) the depth from the water level.

Horizontal movements (Fig. 6a) towards the bank were limited to less than 50% of the distance between the innermost and the outermost traps for the old

Table 3 Occurrence of larvae of *Thraulus bellus* in the 100 2.86-l compartments of the traps at different months of the year between January 1988 and January 1989: frequency of occurrence and mean numbers according to transects, vertical gradients, horizontal gradients, and general

	Jan. 1988	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan. 1989
Frequency (%)	12	15	32	42	57	55	19	20	34	29	19	9	6
Distribution according to transects													
Transect A	0.35	0.30	0.80	0.70	1.60	1.80	0.15	0.10	0.20	0.60	0.30	0.15	0.05
Transect B	0.30	0.20	0.45	0.40	0.35	0.65	0.15	0.00	0.15	0.20	0.10	0.00	0.00
Transect C	0.70	0.25	0.55	1.20	1.00	1.55	1.00	1.00	1.70	0.90	0.35	0.25	0.30
Transect D	0.05	0.05	0.50	2.35	3.85	1.25	0.25	0.00	0.00	0.00	0.10	0.05	0.10
Transect E	0.30	0.15	0.45	1.60	7.05	3.05	0.40	1.25	3.15	1.20	0.55	0.25	0.20
Distribution according to the vertical gradient													
+20/0 cm	0.00	0.10	0.05	0.10	1.60	1.80	0.50	1.30	2.15	0.15	0.00	0.00	0.00
0/−20 cm	0.00	0.35	0.20	0.75	2.70	1.50	1.05	0.75	1.60	0.65	0.15	0.00	0.00
−20/−40 cm	0.40	0.20	0.25	1.70	3.45	1.95	0.20	0.15	0.55	0.55	0.35	0.00	0.10
−40/−60 cm	0.80	0.10	1.10	1.60	3.05	1.85	0.10	0.10	0.50	0.60	0.45	0.30	0.00
−60/−80 cm	0.50	0.20	1.15	2.10	3.05	1.20	0.10	0.05	0.40	0.95	0.45	0.40	0.55
Distribution according to the horizontal gradient													
Innermost	1.32	0.56	0.84	3.28	6.04	3.44	1.08	0.16	0.32	0.68	0.44	0.12	0.44
Inner	0.04	0.20	0.52	0.72	2.96	2.24	0.32	0.12	0.32	0.56	0.36	0.40	0.08
Outer	0.00	0.00	0.48	0.72	1.64	0.52	0.04	0.44	0.44	0.72	0.20	0.04	0.00
Outermost	0.00	0.00	0.36	0.28	0.44	0.44	0.12	1.16	3.08	0.36	0.12	0.00	0.00
General distribution (all samples)													
Total	0.34	0.19	0.55	1.25	2.77	1.66	0.39	0.47	1.04	0.58	0.28	0.14	0.13

generation (37% in April). The sudden rise in water level at the end of January was followed only in March by a lateral movement of the larval population towards the outermost trap. The barycentre of the cohort of young larvae moved towards the shore immediately after hatching, with a maximum in August at 75% of the innermost to outermost distance. The larval population then moved back towards the innermost trap as the water level dropped.

Vertical movements (Fig. 6b) appear differently depending on the parameter chosen to characterize the spatial position of the barycentre: (i) with reference to the absolute altitude (i.e. 0 reference level), the vertical amplitude was 96.5 cm, with regular ascending (January to August) and descending (August to January) movements; only the descending movement paralleled the movement of the water level; (ii) with reference to the substrate surface (i.e. to a level varying in space), the barycentre of the larval population peaked at −35 cm in February during the population growth of the larvae, and then culminated at −6 cm in August to move at −67 cm in January 1989; (iii) with reference to the water surface (i.e. to a level varying in time), the movements were inversely correlated with the piezometric level ($r = 0.62$, $P < 0.05$), and also with the photoperiod ($r = 0.70$, $P < 0.01$) independent of the irregularities in the hydrological regime, when considering mean monthly data; this seasonality is expressed in Fig. 6c as ascending and descending movements of the barycentre according to the day length.

Relation to the probability of submersion

The average value of the probability of submersion of the studied compartments was $\pi_z = 0.733 \pm 0.037$ (95% CL, $n = 100$). In other words, the midpoint of the sampling set was flooded 268 ± 14 days a year. When weighted by the population densities of *Thraulus bellus*, this average became $\pi_z = 0.795 \pm 0.007$, so significantly above the mean probability of the sampling set (previous value). Thus, *T. bellus* occurred preferentially in the more stable part of the system (complete stability is for $\pi_z = 1.000$), but could tolerate a significant degree of unstability according to the movements of the water level. The minimal stability

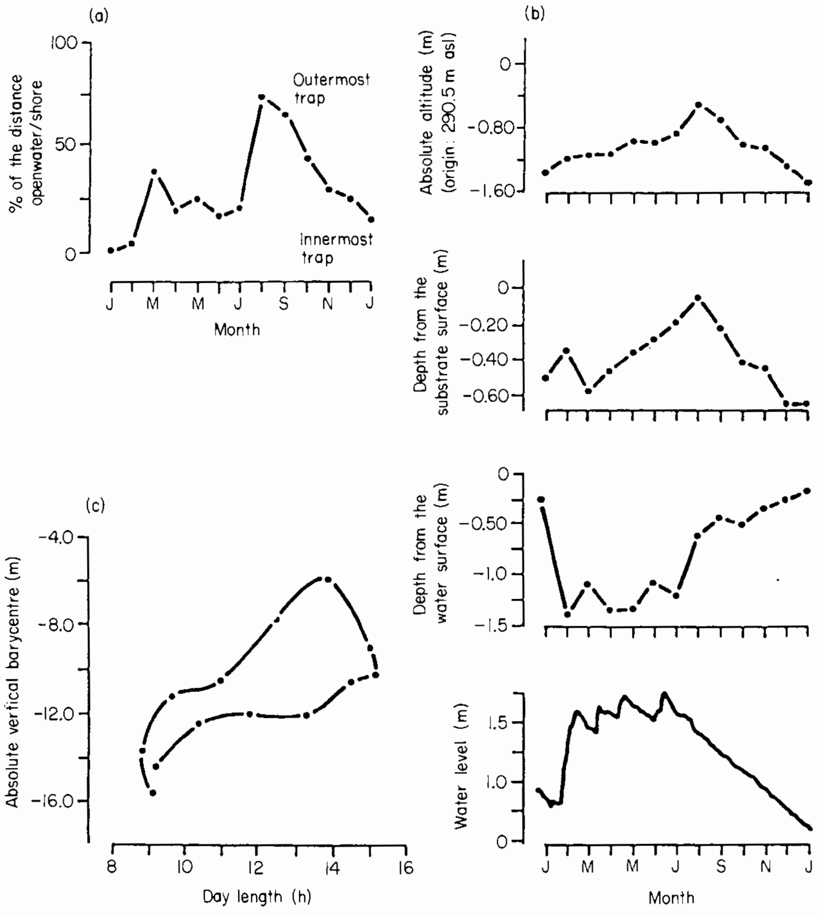

Fig. 6 Displacement of the barycentre of the population of *Thraulus bellus* from January 1988 to January 1989: (a) mean horizontal position within the fluctuating water level area, i.e. between the innermost (0%) and the outermost (100%) traps with respect to the centre of the pond; (b) mean vertical position referring to absolute altitude, substrate surface and water surface (fluctuations in water below); (c) mean vertical position (absolute altitude) *v* the length of the day (monthly average) (spline smoothing).

was reached in August ($\pi_z = 0.599$) and the maximum one in January ($\pi_z = 0.973$ in 1988, and $\pi_z = 0.993$ in 1989).

The number of individuals per compartment increased with the probability of submersion (Fig. 7). Maximum dispersion of the population occurred in May and June when the numbers collected and the variation in length of the larvae were also maximum. From July to September, the relationships between the number of larvae per compartment and the probability of submersion were lower (young cohort). During winter (i.e. December, January and February), the higher numbers of larvae per compartment were clearly located at the highest probability of submersion, indicating the refuge character of the sites permanently inundated.

Discussion

The uppermost parts of aquifers are biologically very active, and their invertebrate communities diverse (Hynes Williams & Williams, 1976; Bretchko, 1981; Dole, 1984). However, Ephemeroptera are rarely abundant in the hyporheic environment (Danielopol, 1976; Pennak & Ward, 1986), although young larvae of *Leptophlebia* and *Eurylophella* were collected by Strommer & Smock (1989) within deep sandy substrate (see also the references cited in the introduction to this paper). Ability to move gives the invertebrate fauna in general an adaptative advantage in riparian habitats (Hynes, 1974; Wiggins, Mackay & Smith, 1980; Delettre, 1986; Reygrobellet & Castella, 1987). This is the case with *T. bellus*.

Movement of *T. bellus* larvae within the littoral zone of the pond must be considered in relation to three characteristics of this unstable habitat. Firstly, two critical periods transform the system: a sudden rise of water level in February and, in complete contrast, a progressive decline in water level after August. Secondly, mainly unclogged interstices between pebbles produce a mean porosity of about 45%, facilitating the movement of the larvae within

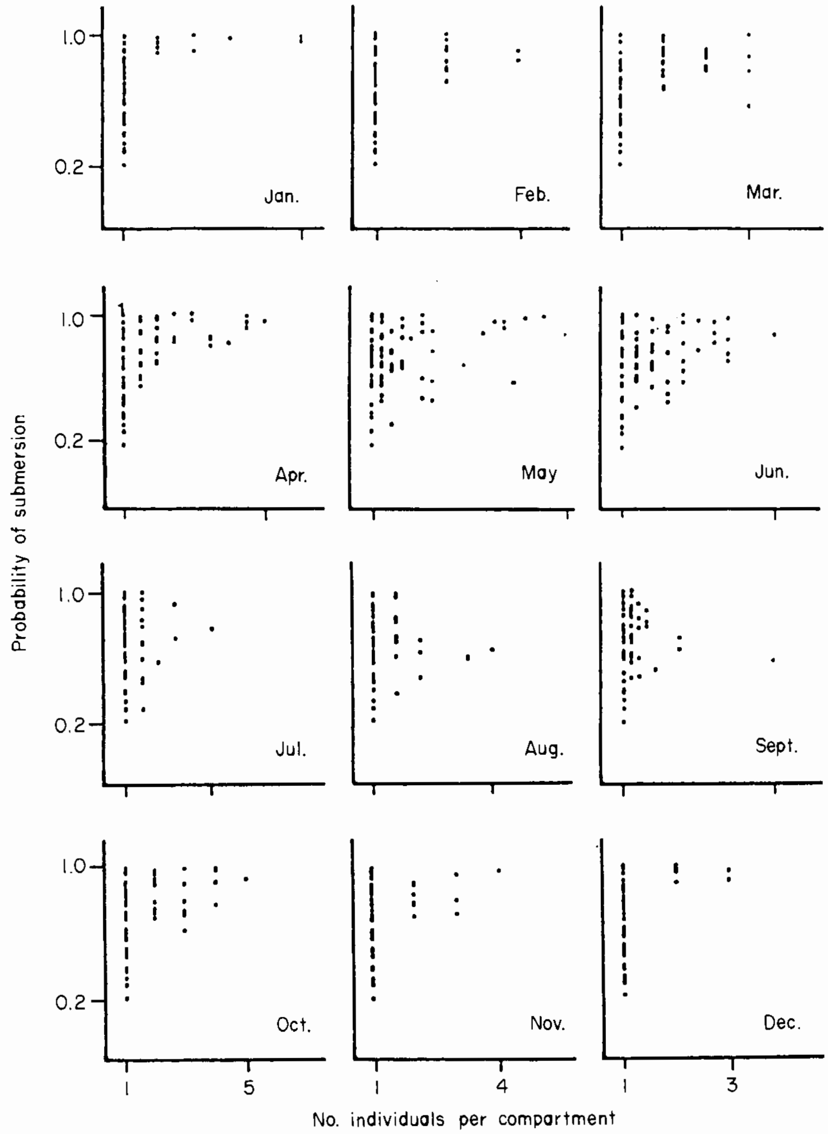

Fig. 7 Relationship between the numbers of individuals per compartment (x axis) and the probability of submersion (y axis) from January 1988 to January 1989.

the littoral zone. Thirdly, spring-fed zones allow deep groundwater to influence the upper interstitial system in some places.

Larvae of *T. bellus* rapidly colonized the temporarily inundated interstitial system after hatching. Young larvae penetrated actively into the substrate before the water level dropped, escaping possible predators and finding more stable conditions. As previously indicated, we have found young larvae at −2.60 m within the substratum. In mid-January, when the first rises in water table occurred, these young larvae left their deep reservoirs, grew within the interstitial littoral zone, and emerged as adults in July. During this second period of their life, their oblique displacement was similar to that occurring in plankton that rapidly invades the littoral zone through a passive migration during the sharp population growth of spring. However, the larvae of *T. bellus* seem to be able to control their position, probably seeking more stable conditions when population densities were high.

Due to this movement within the interstitial substratum, each cohort exploits different parts of the littoral zone along vertical and horizontal gradients. Moreover, local conditions may influence the success of different parts of the population, for example,

Table 4 Percentages of individuals (mean ± 95% CL) of the three main species of Ephemeroptera caught monthly between January and July 1987 in five habitats of the sampled system. Data from Tabacchi (1987)

	% *Thraulus bellus*	% *Cloeon* gr. *simile*	% *Caenis horaria*
Pebbles (0/−30 cm)	78.1 ± 7.8	4.5 ± 2.2	17.4 ± 6.3
Pebbles (−30/−60 cm)	90.7 ± 3.2	2.4 ± 1.0	6.8 ± 2.3
Gravel−sand (0/−30 cm)	2.4 ± 1.7	11.4 ± 8.3	86.2 ± 8.8
Silt (0/5 cm)	0.0 ± 0.0	15.7 ± 5.5	84.3 ± 5.3
Myriophyllum beds (0/+50 cm)	0.2 ± 0.2	83.5 ± 2.6	16.2 ± 2.5

the presence of a spring-fed zone as in Transect E, presence of aquatic vegetation, or slope. Some of these local conditions may permit part of the life cycle to be accomplished even when there are generally adverse conditions elsewhere. Such a heterogeneity of the interstitial littoral zone is an important factor in success: in this way the entire population is resilient towards the disturbances which characterize its habitat.

In fact, the unstable littoral system appears to be a refuge habitat for the larvae of *T. bellus*. Conditions are found to be more stable within the substratum with respect to fluctuations in water level and in temperature. At the same time, *T. bellus* may avoid competition from other ephemeropterans in the riparian system. The three most abundant species in the pond clearly preferred different habitats, as shown by Table 4. *Caenis horaria*, although eurytopic, was most abundant in silt habitats; *Cloeon* gr. *simile* preferred macrophyte beds and colonized pebbles only when the plant community had not yet grown up, or when it was invaded by periphyton during late summer. *Thraulus bellus* was more confined to the interstitial habitat where it did not overlap with other ephemeropterans.

Acknowledgments

We wish to thank Philip Say, Durham, UK, for improving the English text, and two anonymous referees, for their useful suggestions.

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(*Manuscript accepted 17 November 1992*)