# Variations in the structure of stygobiont crustacean populations (*Niphargus rhenorhodanensis* and *Proasellus valdensis*) within the sediments of a karst outflow

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## Abstract

The interstitial fauna living within the sediments of a cave outflow situated in Verna (France) was mainly represented by two stygobiont species, the amphipod *Niphargus rhenorhodanensis* and the isopod *Proasellus valdensis*. Their population dynamics was observed by means of artificial substrates buried in the alluvia. Except for some individuals of *Niphargus* neither of these species was observed outside the cave and had low densities inside (0 to 30 individuals per species and per basket). These densities varied with time and depth within the sediment. The more superficial levels were more populated than the deeper ones. The reduction with depth was more marked for *Proasellus* than for *Niphargus*. Two distinct periods separated by a violent spate appeared during this study. The first period was characterized by high and relatively changing densities and the second by a low and constant one (except for the last sample of June 1989). Thus the recolonization of the sediment after the spate was very low. No correlations were observed between particulate organic matter ($> 150 \mu$m) and the number of individuals. The interpretation of the results took into account biological cycle features and preferential occupation of space for both species as well as the disturbance in the hydrological cycle and the phenomenon of competition.

## Introduction

A previous study carried out on the stygobiont amphipod *Niphargus rhenorhodanensis* living in the glacial sediments of a french forest canal drainage demonstrated that the structure and dynamics of populations varied mainly with water-level variations (Mathieu *et al.*, 1984; Mathieu *et al.*, 1987). Another population of the same species was more common in the river substratum, and depended not only on the water-level variations, but also on the flow velocity of the river and its disturbance spates (Marmonier & Dole, 1986). The structure of the populations of the stygobiont isopod *Proasellus valdensis*, which generally coexists with its supposed predator, *Niphargus rhenorhodanensis*, is less well known (Henry, 1976). *Proasellus valdensis* generally lives in run-

ning water but also in the interstitial milieu, as populations and not as single individuals.

The co-occurrence of *Niphargus rhenorhodanensis* and *Proasellus valdensis* in the river sediments of a cave located in the southern Jura (France) raises two questions: the influence of some factors on their distribution within this sediment and the predator/prey relations hypothesized by Henry (1976).

## Material and methods

### Study sites

The observations were carried out in a French karst area, in the transitional zone between the karst and its adjacent alluvial plain.

Verna station (département de l'Isère) (I.G.N. map 1/25 000: Montluel n° 7–8 Lambert coordinates: $x = 829.26$, $y = 91.06$, $z = 275.00$) is an outflow of a cave (grotte saint Joseph) which supplies a brook, mainly with underground water, and which is located at the geographic base-level of the karst system. The stream-bed inside the cave is composed of coarse and poorly sorted stony-sandy material plugged by decalcification clay and about 80 cm thick. The entrance of this cave presents a threshold with a low wall (20 cm high) which regulates the water-level and retains the substratum. Immediately outside the cave, the river flows over the limestone covered with only scarce alluvions (from 0 to 10 cm thick) over about 50 meters down to a break in the slope with a little cascade (80 cm high). The slope of this part of the channel is about 20° and the width from 1 to 2 meters. After the cascade the river-bed becomes larger (from 3 to 8 meters) with a slight slope. The depth of the sediment which covers the bed was about 1 meter and rests on limestone flag. Unfortunately it was not possible to record the discharge during the study. The flow velocity varied from 0.20 to 1.20 m sec$^{-1}$. Except on 12th October 1988 when a major spate oc-
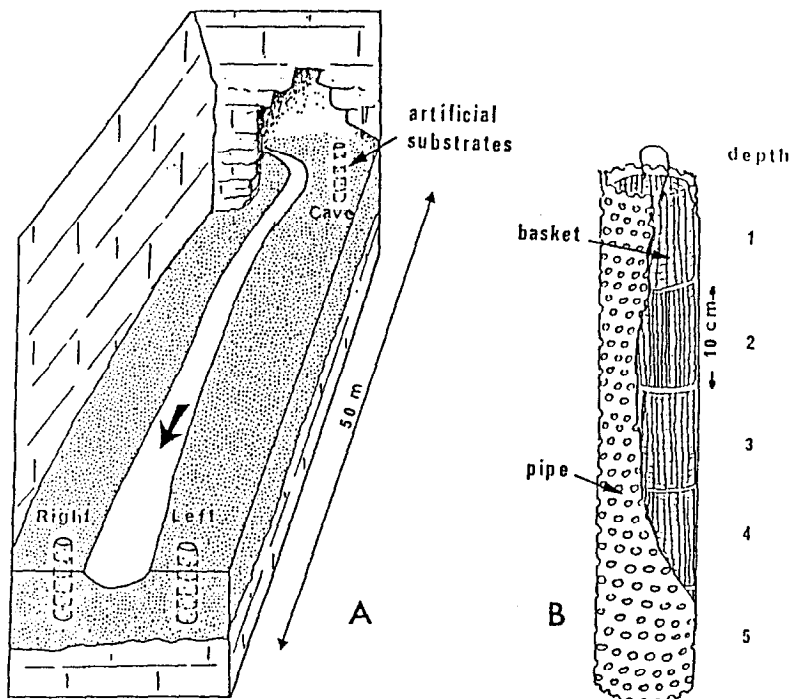


*Fig. 1.* A: sample sites in Verna station. B: artificial substrate. See text for the legend.

curred and destroyed a part of the site, there were no major variations in discharge in the course of sampling. The artificial substrate in the cave was always submerged under about 10 cm of running water. The outside artificial substrates were also always submerged but generally only by 2 or 3 of cm of running water.

Three artificial substrates were buried in the sediments (Fig. 1A). One was located in the cave entrance ('cave') the other two in the alluvial plain, one on the right bank and the other on the left bank of the stream ('right', 'left') 50 meters downstream (Fig. 1A) (Mathieu & Essafi-Chergui, 1990).



*Fig. 2.* Variations in number of individuals (N) as a function of time. The spate occurred on 12/10/88.

## Artificial substrates

The artificial substrate (Fig. 1B) consisted of a galvanized steel cylinder 10 cm in diameter and 50 cm long in which 8 mm holes had been drilled. Each cylinder was buried 50 cm deep in the stream bank. A cylinder contained five baskets (also of galvanized steel) one about the other, made of 6 mm mesh grating (diameter: 10 cm; height: 10 cm) (Mathieu & Essafi-Chergui, 1990). The baskets were filled with the stream-bed sediment, but before filling them, this sediment was carefully cleaned in the laboratory and kept dry and thus initially free of animals and organic matter. This limestone substratum was poorly sorted with fractions of both larger and smaller grains. The larger grains (about 60%) were composed of angular gravel, from about 4 mm to 4 cm wide, and fine sand ($\leq 1$ mm in diameter) (40%) which plug up spaces between gravel. Because of the cleaning, no clay was included.

## Sample collection

The artificial substrates were left in place for about one month. Their liftings occurred from 19 November 1987 to 19 January 1989 (Fig. 2 and Fig. 4).

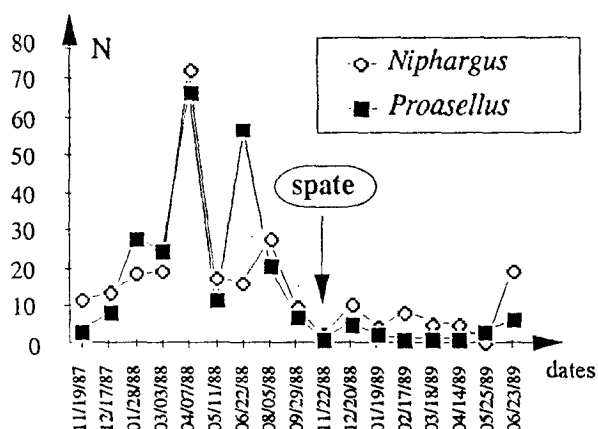In the laboratory, all the material from each basket was washed through a 150 $\mu$m mesh sieve.

After removal of most sand and gravel, animals were picked from this residue and preserved in 5% Pink Bengal formalin. Particulate organic matter (POM) > 150 $\mu$m was measured by loss of mass on ignition (Golterman, 1975). After drying at 70 °C for 48 hours, the residue was ignited at 500 °C for one hour. The difference in mass represented organic matter collected on the sieve. The results were expressed in g per basket.

After the baskets were collected, water was pumped from a standpipe (Bou & Rouch, 1967) 50 cm deep in the sediment. Temperature, conductivity and pH were measured *in situ*, and the other chemical parameters in the laboratory. Temperature and conductivity were measured with a Merck CM 85 T conducti-thermometer, and pH with a Merck 85 pH meter. Alkalinity, $Ca^{2+}$ and $Mg^{2+}$ (EDTA method) were determined following methods described in Golterman (1975). Dissolved silica was measured by Heteropoly Blue, a method using Hach Co (Loveland CO) reagents.

Statistical analysis was carried out using Simple Linear Regressions, Range Correlations from Lehmann (non parametric correlation) (Chessel, 1978), ANOVA. Fig. 4 was drawn with the ADECO software from D. Chessel, J. Thioulouse, J. L. Beffy & Y. Auda (Piren-Vallées Fluviales, URA C.N.R.S. 367, Université Lyon I) (Thioulouse, 1989).
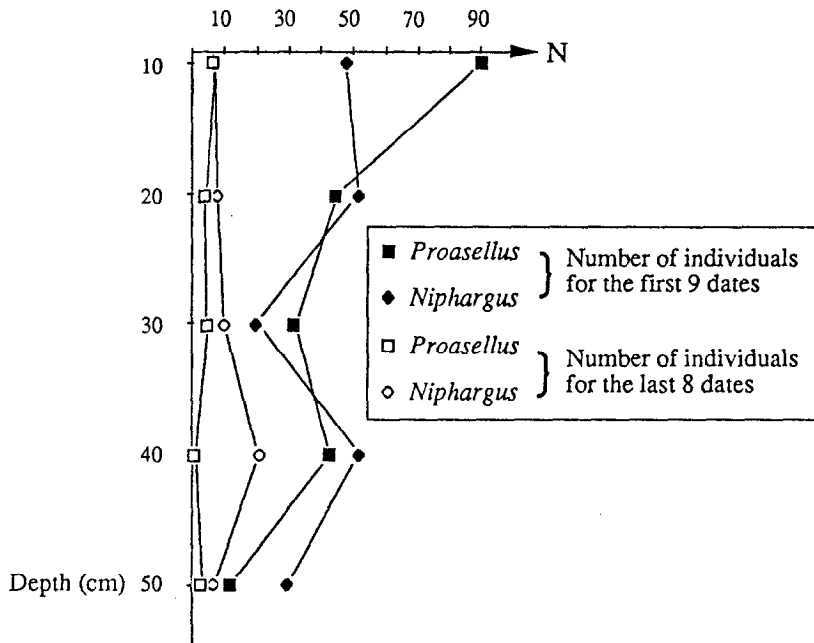
*Fig. 3.* Number of individuals (N) of *Niphargus* and *Proasellus* before the spate (12/10/88) and after, as a function of depth within the sediment.
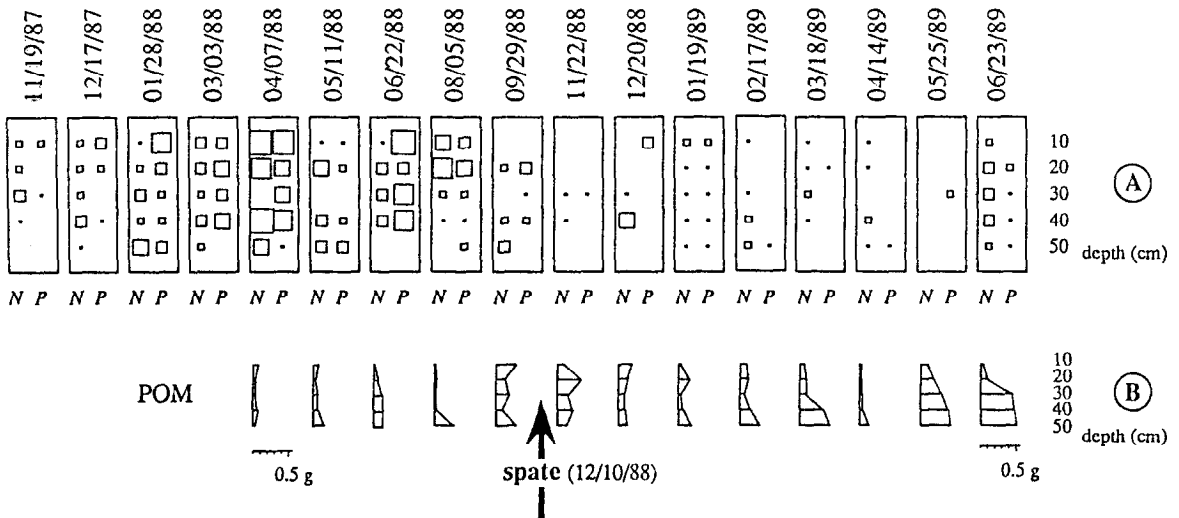


*Fig. 4.* A: number of individuals as a function of the depth within the sediment. *N: Niphargus; P: Proasellus*. The surface of the squares is proportional to the number of individuals (from 0 to 30). B: POM: particulate organic matter distribution (g/basket).

# Results

## Physical and chemical characteristics

The surface water was well oxygenated throughout the year (> 95% saturation). However, inter-

stitial oxygen was not measured. The other physical and chemical characteristics varied little throughout the sampling period (conductivity: 535–606 $\mu$s cm$^{-1}$; temperature: 10.8–12.1 °C; alkalinity: 230–290 mg l$^{-1}$; pH: 7.1–8.1; Si: 6.2–

9.6 mg l$^{-1}$; Ca$^{2+}$: 85–120 mg l$^{-1}$; Mg$^{2+}$: 4.2–8.4 mg l$^{-1}$).

## Faunistical results

The detailed results concerning *Niphargus*, *Proasellus* and POM are given in Table 1 and Fig. 4.

The artificial substrates located in the cave were generally not densely populated (from 9 to 122 individuals/5 baskets) and only slightly diversified (only 9 taxa in 17 samples). Apart from *Niphargus rhenorhodanensis* and *Proasellus valdensis*, other taxa were rare or sporadic (Oligochaeta: 17, Gastropoda: 6, *Gammarus fossarum*: 4, Trichoptera: 4, Plecoptera: 2, Coleoptera: 1 and Cyclopoidea: 1). This is one of the reasons why only the two stygobiont species were studied here. The outside artificial substrates from the cave were more densely populated but hardly ever by hypogean taxa (from 17 to 612 individuals/5 baskets, mainly represented by *Gammarus fossarum*). The diversity also remained low (only 13 different taxa for the whole study). The results

concerning this epigean fauna have been given in another work (Essafi, 1990). Because only 10 *Niphargus* were found (5 different dates: April, July, September 1988, April and May 1989) and no *Proasellus valdensis*, the results from these two artificial substrates cannot be added to those of the cave one and will therefore not be further mentioned here.

*Effect of time.*
The data summarized in Fig. 2 represent the sum of values obtained for each of the 5 baskets for a given date, disregarding depth influence.

Two distinct periods were distinguishable (see also ANOVA, Table 2: *periods*). The first period until 29 September 1988 (earlier to the 12 October 1988 spate), was characterized by fluctuating values for both species, in particular with one maximum for *Niphargus rhenorhodanensis* in April 1988 and two maxima for *Proasellus valdensis*, one in April and the other in June 1988. In contrast, the second period which followed the spate was marked by low values until May 1989, followed by an increase in June 1989, especially for *Niphargus rhenorhodanensis*.

*Table 1.* Abundance in *Niphargus* and *Proasellus* for each sample date and each basket. POM: weight of particulate organic matter (g/basket)

| Depths Dates | Niphargus | | | | | Proasellus | | | | | POM | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 |
| 11/19/87 | 3 | 3 | 4 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | | | | | |
| 12/17/87 | 3 | 3 | 2 | 4 | 1 | 5 | 2 | 0 | 1 | 0 | | | | | |
| 1/28/88 | 1 | 2 | 4 | 3 | 8 | 12 | 6 | 2 | 2 | 5 | | | | | |
| 3/3/88 | 5 | 4 | 3 | 4 | 3 | 5 | 7 | 5 | 7 | 0 | | | | | |
| 4/7/88 | 25 | 11 | 0 | 27 | 9 | 30 | 9 | 10 | 16 | 1 | 0.074 | 0.068 | 0.043 | 0.071 | 0.044 |
| 5/11/88 | 1 | 7 | 0 | 4 | 5 | 1 | 3 | 0 | 3 | 4 | 0.078 | 0.064 | 0.072 | 0.087 | 0.177 |
| 6/22/88 | 1 | 5 | 4 | 6 | 0 | 30 | 4 | 11 | 11 | 0 | 0.016 | 0.071 | 0.147 | 0.142 | 0.155 |
| 8/5/88 | 9 | 14 | 3 | 1 | 0 | 5 | 10 | 2 | 1 | 2 | 0.033 | 0.052 | 0.025 | 0.049 | 0.333 |
| 9/29/88 | 0 | 3 | 0 | 2 | 4 | 0 | 4 | 1 | 2 | 0 | 0.308 | 0.152 | 0.230 | 0.104 | 0.324 |
| 11/22/88 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0.128 | 0.382 | 0.199 | 0.245 | 0.170 |
| 12/20/88 | 0 | 0 | 1 | 9 | 0 | 5 | 0 | 0 | 0 | 0 | 0.228 | 0.142 | 0.120 | 0.107 | 0.168 |
| 1/19/89 | 2 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0.068 | 0.192 | 0.058 | 0.074 | 0.234 |
| 2/17/89 | 1 | 0 | 1 | 3 | 3 | 0 | 0 | 0 | 0 | 1 | 0.127 | 0.154 | 0.095 | 0.198 | 0.316 |
| 3/18/89 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0.072 | 0.103 | 0.130 | 0.386 | 0.498 |
| 4/14/89 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0.018 | 0.021 | 0.045 | 0.051 | 0.143 |
| 5/25/89 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0.126 | 0.207 | 0.343 | 0.451 | 0.495 |
| 6/23/89 | 2 | 6 | 4 | 4 | 3 | 0 | 3 | 1 | 1 | 1 | 0.044 | 0.110 | 0.547 | 0.568 | 0.601 |

*Table 2.* ANOVA on abundance of the two species as a function of *periods* (from 11/19/87 to 9/29/88 for the first and from 9/30/88 to 6/23/89 for the second) and of *depths* (calculations for global data, first and second periods of the study).

| | Source | Deg. of freedom | F. ratio | Prob. > F |
|---|---|---|---|---|
| *Periods* | *Niphargus* | 1 | 12.00 | 1.0 E-3 |
| | *Proasellus* | 1 | 17.00 | 8.8 E-5 |
| *Depths* | | | | |
| Global | *Niphargus* | 4 | 0.87 | 4.9 E-1 |
| | *Proasellus* | 4 | 1.90 | 1.2 E-1 |
| 1st period | *Niphargus* | 4 | 0.74 | 5.7 E-1 |
| | *Proasellus* | 4 | 2.30 | 8.1 E-2 |
| 2d period | *Niphargus* | 4 | 0.13 | 2.8 E-1 |
| | *Proasellus* | 4 | 0.53 | 7.2 E-1 |

*Effects of depth.*

Table 2 shows that there was a difference in space distribution between *Niphargus* and *Proasellus* (Table 2, *depths* global). This difference was explained for *Proasellus* which was more numerous in the highest basket and less numerous in the lowest one ($p > 0.001$) and for *Niphargus* which was less represented at 30 cm ($p > 0.05$).

Moreover, the data allow us, as previously, to separate two periods (see Table 2, *depths*, 1st and 2nd periods). The values (disregarding time influence) (Fig. 3) presented relatively homogeneous data during the second period: the number of individuals for each depth was low and almost identical (Table 2, 2nd period). Unlike this second period, the distribution of each species was different during the first period (1st period). The mean values for each depth were comparatively the same for *Niphargus rhenorhodanensis* (except for 30 cm depth where the number is lower and different from the others: $p > 0.05$). The values decreased with depth for *Proasellus valdensis*. The mean value was lowest for 50 cm depth (different from the others: $p > 0.05$). The highest data, obtained at 10 cm, was also different from the other ($p > 0.001$). Intermediate values (20, 30, 40 cm depth) were not different between them. There was a gradient with depth.

Taking all the data into account for non parametric correlation calculations between number of individuals and depth, date by date, we were able to show that the stratification of animals varied with time and that a reduction in density could exist (Fig. 4).

The number of *Niphargus* slightly increased with depth on 28th January and 22nd June 1988, the reverse occurring on 5th August 1988. The distribution was more uniform for the other dates. After the spate, the values were relatively higher in the deepest baskets than in the surface baskets. The restoration of this population was progressive and slow.

The number of *Proasellus* increased with depth on 11th May 1988. On the contrary, the values decreased for the other dates. The highest values were obtained within the 10 first cm. The effect of spate was more important for *Proasellus* than for *Niphargus*; the values remained lower and the population restoration was more difficult.

It is possible to show that there was a positive correlation between *Proasellus* and *Niphargus* numbers ($r = 0.81$ for 17 couples of values: 17 dates). The development in the number of individuals varied in the same way for both species. But this correlation appeared lower when calculations were executed on all the data ($r = 0.6$ for 85 couples of values: 17 dates × 5 depths). This interaction between the sampling dates and the depths was analysed, date by date, by calculation of correlation (non parametric correlation from Lehmann) between the number of individuals of both species at each depth. Except for the 28th January and the 22nd June 1988, where animal distribution of both species as a function of depth was reversed (cf Fig. 4), each of the other dates showed correlated values.

*Fauna and particulate organic matter*

Figure 4 shows the variations in time of the POM quantities accumulated in each basket. These quantities were generally low (from 18 to 600 mg max. by basket) and the supply generally higher in the deeper zones. The spate of 12th October

1988 did not seem to have special consequences of subsequent supplies which stayed constant and significant.

The comparison of the number of *Niphargus* and *Proasellus* with the mean quantity of POM for each date revealed no correlation ($r < 0$ and $\neq 1$, $p = 0.05$).

## Conclusion

Taking into account the observations of Coleman & Hynes (1970), Hynes (1974), Mathieu & Essafi-Chergui (1990) and Tabacchi (1990), who consider that one month is long enough for full stable occupancy of a vacant space, these results emphasize the difficulty in interpreting the distribution variations in space and time of both species studied in this work.

However, one can consider four apparently interactive factors which control the variations in population structure: 1) the special biological cycle of each species, 2) the preferential space occupation relative to each species, 3) competition and 4) the hydrological cycle and its disturbances.

### Biological cycle

Field and laboratory observations by Ginet (1969) and then by Turquin (1975) have shown a yearly rhythm for *Niphargus rhenorhodanensis* with a greater number of ovigerous females on February, which means that laying occur in April, after about 90 days of incubation. The highest value obtained on April in this work could really be explained in accordance with the observations of these both authors. This observation is all the more probable because the individuals sampled on 7 April 88 measured from 2 to 3 mm, the size at birth.

In the same way, the field observations by Henry (1976) have shown a yearly egg-laying rhythm for *Proasellus valdensis*. This author observed higher laying values in April, as in this work. But unlike *Niphargus*, this species is able to have a second laying period, just after the first, which is separated by only one intermolt, i.e.

about 42 days. Our observations are similar in that we observed a second high value about two months after the first.

### Occupation of space

The occupation of space by interstitial fauna and migrations vary with water-level (Angelier, 1953). In the present case water level was quite constant except during the spate, and it cannot completely explain the differences in population distribution within the sediment.

The almost total absence of *Niphargus* and the total absence of *Proasellus* could be interpreted by the fact that between the upper and the lower substrates scarce sediment covers the limestone (animals cannot take refuge) and near the lower substrates live many *Gammarus* which enter into competition and eat *Niphargus*.

Previous studies (Mathieu *et al.*, 1984; Mathieu *et al.*, 1987) have demonstrated that the interstitial population of *Niphargus rhenorhodanensis* which lives in the hydromorph soil of forest drainage canals, is directly dependent on water level variations. The stratifications of values appeared comparatively homogeneous when the canals were filled with water, but very heterogeneous with lower levels. The data relative to the almost random distribution of *Niphargus rhenorhodanensis* (except at 30 cm deep) of this study are consistent with the data relative to the drainage canal sediment. *Proasellus valdensis* which lives in karstic running water can also live in sediments and more precisely prefers interstices of coarse sediments where the water flow is high (Henry, 1976). The distribution of *Proasellus* within the sediments of Verna seemed to correspond to Henry's observations. The highest number of individuals are indeed met in the upper layers of the sediment, the deepest layers being less populated.

### Competition

The differences of number of individuals between the two populations within the different baskets

could be interpreted as an interspecific competition phenomena. But statistical analysis showed nothing of the kind, and in most cases there is a positive correlation between them. These results are in contradiction with the model presented by Culver (1973) which predicts the distribution and codistribution of aquatic cave species. In the model, two species will not coexist in the same habitat unless there are large size difference between the two species. In our case, there is no large difference between the size of individuals for both species (between 2 and 4 mm difference).

*Disturbance effects*

The fourth and probably important phenomenon which can influence the distribution in time and in space of both populations could be related to disturbances.

The impact of floods or spates on invertebrates is well known (Resh *et al.*, 1988). Generally the richness and the number of individuals decrease to a large extent (Hynes, 1970; Gaschignard, 1984). This affects the rate and dynamics of recovery, particularly the mechanisms by which new colonies are derived (Minshall, 1988). Generally, both epigean and hypogean organisms are displaced vertically after each spate in interstitial layers, and the rate of recovery varies in relation to the combination of spate amplitude and duration, but this recovery is generally short (Marmonier et Dole, 1986). In this work, only one spate occurred. The recovery was very slow, over about 7 months. Indeed the reproduction period (May, June) was reduced compared with previous years. This is an example of a partial answer which can be given to the second question raised by Resh *et al.* (1988): 'will rates and sequences of recovery by a community be faster in frequently disturbed streams than in rarely disturbed streams because the community composition will have been previously influenced by disturbance events'. This situation certainly occurred rarely in large alluvial plains where supplies of individuals from the river's upper zone may be plentiful.

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