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First Report on the Ecology of the Phreatic Water Beetle *Siettitia avenionensis* Guignot (Coleoptera, Dytiscidae)

by Ph. Richoux & J.L. Reygrobellet

Abstract: In the region East of Lyon (France), the discovery of a sampling site (a neglected gravel-pit) where adults and larvae of *Siettitia avenionensis* are regularly collected throughout the year, has enabled us to observe the variations of this population, in relation to the habitat and in particular to the variations of the groundwater levels. The size of the captured population has allowed us to propose a model of the life cycle of this water beetle during a mean hydrological year.

Key words: Coleoptera Dytiscidae – *Siettitia avenionensis* – ecology – groundwater.

I. Introduction

In spite of recent discoveries of subterranean Coleoptera (in particular in the New World), not many species are known at present.

In fact, apart from 10 species of *Hydradephaga* recorded by FRANCISCOLO (1983), together with the 4 species (which have not been described) of *Phreatodytes* and *Morimotoa* reported by MATSUMOTO (1976) in South-West Japan, and the species in Georgia (USSR) reported by BIRSTEIN & BOROUTZKY (1950), only 5 species of *Elmidae* have been listed, 3 of them recently (SPANGLER, 1981b) (although the status of *Zaitzevia* as a stygobiont genus should perhaps be revised), as well as one Hydrophilidae listed by SPANGLER (1981a) (Tab. 1).

The table 1 summarizes our bibliographical knowledge, except the publications of VANDEL (1964), SCHAEFLEIN (1981), SMRZ (1981, 1983), which allow to complete this literature review of the groundwater beetles; two essential points emerge from it:

- on the one hand most specimens collected come from pumping or wells; only *Trogloguignotus*, *Sanfilippodytes* and *Troglochaes* have been found in caves, mostly in very small numbers;

- on the other hand, only the larvae of 5 species (all of them *Hydradephaga*) have been described; these are *Phreatodytes relictus* and *Morimotoa phreatica* (UENO, 1957), *Phreatodessus hades* (ORDISH, 1976),

| Species | author | year | country | sampling site | described stages A=adults l=larvae |
|-----------------------------------|--------------------|------|-------------|----------------|--|
| Dytiscidae | | | | | |
| <i>Siettitia balsetensis</i> | ABEILLE DE PERRIN | 1904 | France | wells | A |
| <i>Siettitia avenionensis</i> | GUIGNOT | 1925 | France | closed well | A |
| <i>Siettitia avenionensis</i> | RICHOUX | 1980 | France | and aquifer | l |
| <i>Uvarus chappuisi</i> | PESCHET | 1932 | Haute Volta | well | A |
| <i>Phreatodytes relictus</i> | UÉNO | 1957 | Japan | wells | A+l |
| <i>Phreatodytes 2 n. sp.</i> | undescribed | | " | " | A |
| <i>Morimotoa phreatica</i> | UÉNO | 1957 | " | " | A+l |
| <i>Morimotoa 2 n. sp.</i> | undescribed | | " | " | A |
| <i>Trogloguignotus concii</i> | SANFILIPPO | 1958 | Venezuela | cave | A |
| <i>Phreatodessus hades</i> | ORDISH | 1976 | New-Zealand | aquifer | A+l |
| <i>Kuschelhydrus phreaticus</i> | ORDISH | 1976 | " | " | A |
| <i>Haideoporus texanus</i> | YOUNG & LONGLEY | 1976 | U.S.A. | artesian wells | A |
| <i>Haideoporus texanus</i> | LONGLEY & SPANGLER | 1977 | " | " | l |
| <i>Sanfilippodytes sbordonii</i> | FRANCISCOLO | 1979 | Mexico | cave | A |
| <i>n. gen. (?)</i> | undescribed | | USSR | cave | A |
| Elmidae | | | | | |
| <i>Trogloelmis leleupi</i> | JEANNEL | 1950 | Zaïre | cave | A |
| <i>Zaitzevia uenoi</i> | NOMURA | 1961 | Japan | well | A |
| <i>Anommatelmis boto-saneanui</i> | SPANGLER | 1981 | Haïti | wells | A |
| <i>Lemalelmis minyops</i> | SPANGLER | 1981 | " | " | A |
| <i>Lemalelmis fontana</i> | SPANGLER | 1981 | " | " | A |
| Hydrophilidae | | | | | |
| <i>Troglochaes ashmolei</i> | SPANGLER | 1981 | Ecuador | cave | A |

Tab. 1: Subterranean Water-beetles from the world.

Haideoporus texanus (LONGLEY & SPANGLER, 1977) and *Siettitia avenionensis* (RICHOUX, 1980), and all of them are stygobionts. Moreover all of the larval instars have been described in only two species: *Morimotoa phreatica* and *Siettitia avenionensis*.

At present no ecological study is in existence; the literature provides information on the conditions in which these water-beetles were collected. ORDISH (1976) describes in detail the way in which the number of specimens of the 2 New-Zealand species varies according to the seasons.

As for the genus *Siettitia* the data concerning its 2 species, both of which were found in South-East France, are very different:

– *Siettitia balsetensis*, known since 1904 has been the subject of several studies, in particular its morphology (cf. bibliography in RICHOUX, 1978), and the conditions in which it has been collected by Sietti at Le Beausset (REGIMBART, 1905; ABEILLE DE PERRIN, 1906; SIETTI, 1926) or COLAS (1946) at La Seyne: unfortunately these 2 collecting sites have since been destroyed and although many wells were prospected in the region, no specimen of *Siettitia balsetensis* has been collected since (COLAS *in lit.*).

– *Siettitia avenionensis*, on the contrary, was for a long time known through a single female specimen collected by GUIGNOT (1925) in Avignon in a closed well. The male was described (RICHOUX, 1978) after it was collected from groundwater pumped East of Lyon by our Laboratory (GIBERT *et al.*, 1977). Different collecting sites in the region repeatedly yielded specimens (SEYED-REIHANI *et al.*, 1982b) and we were able to determine the 3 larval instars (RICHOUX, 1980). We would also like to point out that during studies carried out by our Laboratory on different aquatic habitats in South-East France, our colleague VERVIER (1984), found in the Ardeche Gorges a female specimen of this species, in the weeds blocking a mineral water spring; a third biogeographical site thus was discovered.

Figure 1 shows the position of the different collecting sites for *Siettitia*.

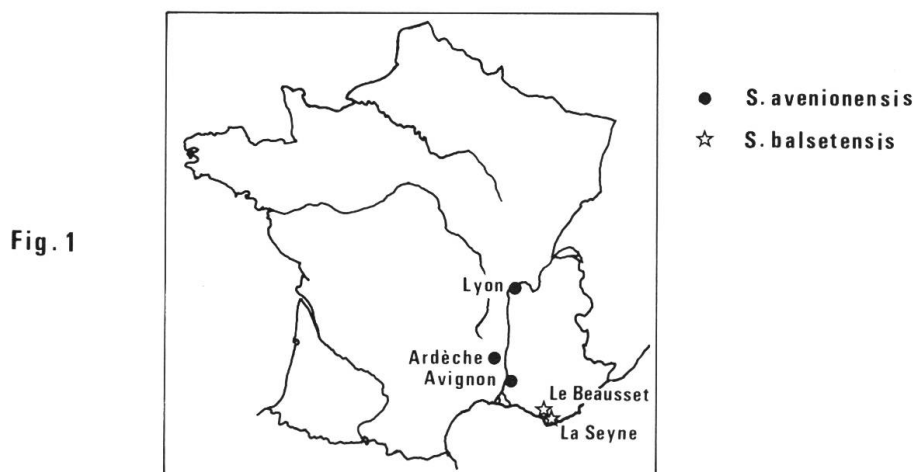


Fig. 1: Collecting sites for the genus *Siettitia* in France.

II. The plain of the region East of Lyon

This is the northernmost zone in which *Siettitia avenionensis* has been found. The alluvial plain of the region East of Lyon is situated 20 kms upstream from Lyon, just downstream from the confluence of the Ain and Rhône rivers. Ever since the last glaciation, the Rhône river has regularly shifted its position in this zone, by eroding the terraces of Wurmian moraines, and has thus created a bed of heterogeneous aquiferous alluvial deposits, varying in thickness from 15 to 30 metres. During its more recent history, the Rhône has gradually abandoned its wide meanders, the oldest of which now form a natural drainage system for the surrounding groundwater.

Since 1975, our Laboratory has been studying the complex hydrological and biological relationships which exist in the region between the river and this group of "dead arms", both on the surface and underground (GIBERT et al., 1977; JUGET et al., 1976, 1979; JUGET & ROUX, 1982). Thus we have been able to investigate the interstitial populations as a whole, and to demonstrate their functional importance within the ecosystem (GIBERT et al., 1981; REYGOBELLET et al., 1981; REYGOBELLET & DOLE, 1982).

The sites where *Siettitia avenionensis* has been collected are shown on figure 2.

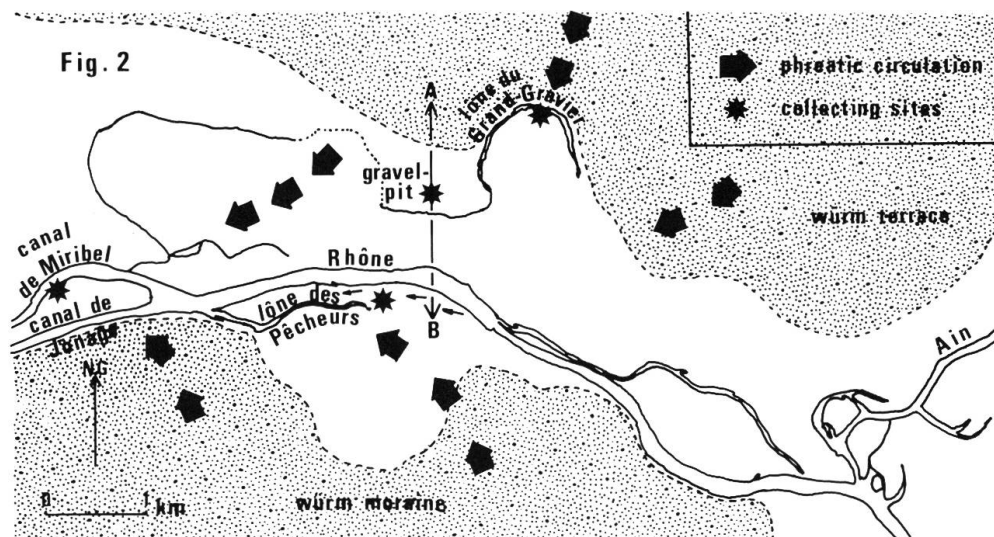


Fig. 2: Collecting sites for the species *S. avenionensis* in the plain East of Lyon (modified from REYGOBELLET & DOLE, 1982)

III. Sampling sites of *Siettitia avenionensis*

Small numbers of *Siettitia avenionensis* have been found from time to time in different sites of the region East of Lyon (Lône du Grand Gravier, Lône des Pêcheurs, Canal de Miribel; see figure 2). But the collecting site where *Siettitia avenionensis* is regularly captured in sufficient quantities for us to consider carrying out a dynamic study is a neglected gravel pit situated near the outlet of one of the oldest dead arms (Lône du Grand Gravier), which has been cut off from the main river since the end of the eighteenth century. The aquifer of the right-hand side of the Rhône meets the river in this region (see the flow directions on the figure 2) and surfaces regularly at high water levels (DAVID *et al.*, 1980). Although the sector under consideration is situated outside the present-day limits of the once-a-century floods of the river, the proximity of the latter still influences the amplitude and the rhythm of the groundwater-level variations, as we shall see later (Fig. 3). Thus in the site itself the mean amplitude, which is about one metre, is too large to enable the establishment of a permanent pool of water in the gravel pit; the likelihood of the development of surface biocenoses is thus limited.

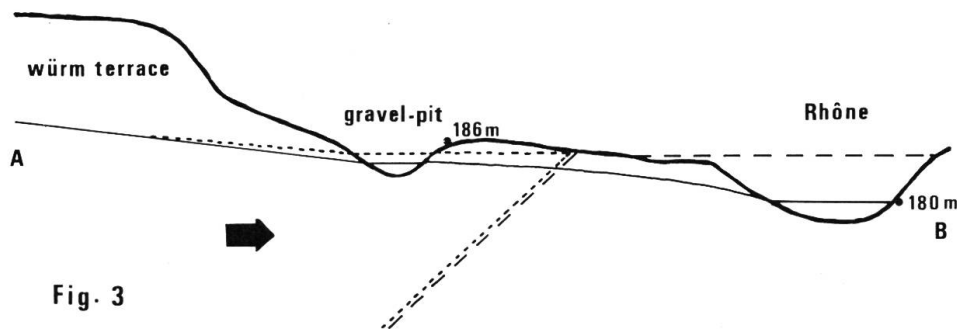


Fig. 3: Transect A. B showing the interferences between the phreatic alimentation and the Rhône levels

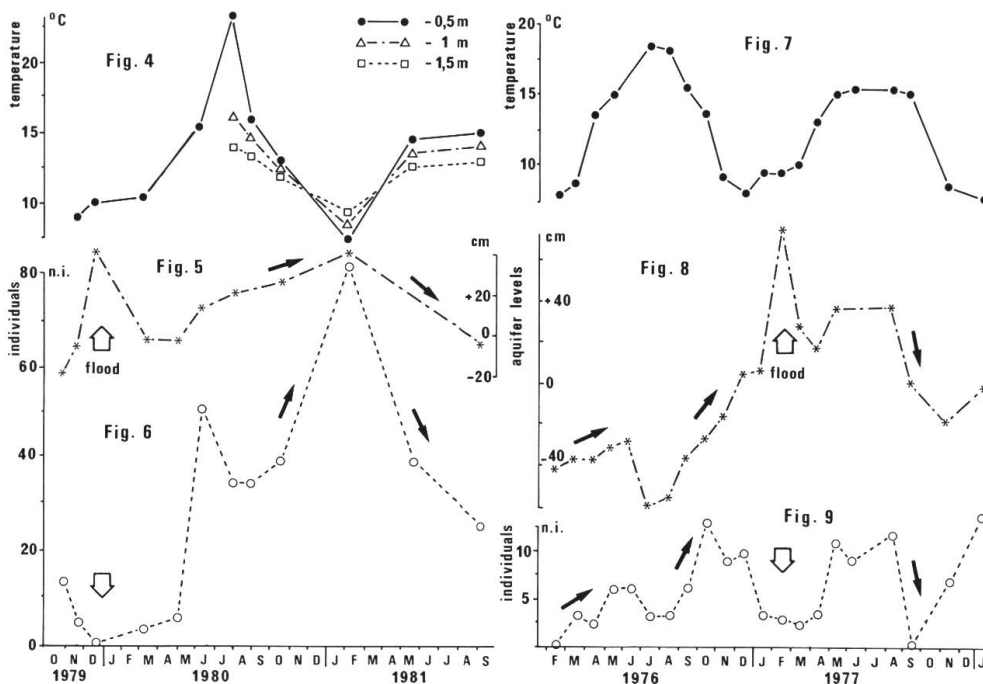
- mean level of the aquifer and the river
- flood of the river
- level of blocked aquifer during the flood

IV. Sampling methods

Sampling of interstitial populations is carried out by means of an individual, portable set of equipment which has been developed by BOU & ROUCH (1967). It consists of a perforated pipe (diameter: 35 mm). Its 5 mm holes allow even the largest animals of the alluvial habitat to be

drawn up. The pipe is sunk manually into the ground and allows sampling at depths of from 2.5 to 3 metres. A light pump (P.V.C.) draws up 60 liters of water, sediments and animals at each sampling without damaging the latter; a 160 μ mesh net is then used as a filter (for a detailed description of this equipment see BOU, 1974).

A prospective study at the collecting site enabled us to delimit an area where numbers of captured *Siettitia* were systematically larger than at other locations; this is the precise station chosen for our sampling operations. Because of environmental conditions these sampling operations are relatively irregular in time. They began in October 1979 but were gradually carried out at larger and larger intervals to ensure that the populations at the sampling station would not be exhausted. In order to take into account both the beat of the aquifer and the possibilities of behavioural movements of *Siettitia*, we pumped at 3 depths, -0.5 m, -1 m, -1.5 m. It has been shown that the interstitial biocoenoses are numerically more important near the top level of the groundwater, over a depth of approximately 1 metre (DANIELOPOL, 1976; REYGRABELLET & DOLE, 1982; DOLE, 1983), and we assumed that *Siettitia* was no exception to this rule.



Figs 4–9: 4. Variations in temperature at the 3 sampling levels. 5–6. Aquifer levels and population of *Siettitia* during the period from October 1979 to February 1981. 7. Variations in temperature at -0.5 m. 8–9. Aquifer levels and the population of *Siettitia* during the period from March 1976 to January 1978 (results extracted of SEYED-REIHANI, 1980).

Preliminary studies had already demonstrate the stability of the physico-chemical parameters of the water of this site (SEYED-REIHANI, 1980; SEYED-REIHANI et al., 1982a) and of the whole of the aquifer of the righthand side of the Rhône (REYGROBELLET & DOLE, 1982; DOLE, 1983), and so we concentrated only on those factors likely to vary with time. Thus, only the temperature and the level of the aquifer were noted for each sampling; their variations will be discussed at the same time as the evolution of the numbers of specimens captured.

V. Changes in the global population from October 1979 to September 1981

In order to avoid any interference with the development cycle of the species, we limited our study at first to the analysis of the variations of the global size of the population (adults + larvae). The curve showing the evolution of these numbers (Fig. 6) can be divided into 3 different sequences, which seem to be totally independent of temperature (Fig. 4), but which show correlations with the major hydrological episodes influencing the level of the aquifer (Fig. 5).

a. Period from October 1979 to May 1980

A drop in populations size and the almost total disappearance of *Siettitia* at our sampling site may be linked to a sudden rise in the groundwater level. Although there is no possible interference (considering the piezometric levels) between the river water and the groundwater, every time the river floods, the groundwater flow is temporarily blocked and this leads to "groundwater flooding" around the river (see explanation Fig. 3). This phenomenon most probably has some effect on the biocoenoses and may be considered as the likely cause of the variation in numbers; not only is the discharge rate reduced to zero, the volume of sediment occupied by the groundwater increases rapidly and considerably, thus in all likelihood leading to a scattering of the population.

b. Period from May 1980 to February 1981

During this period the total size of the *Siettitia* population increased; at the same time the level of the groundwater rose steadily. This situation, linked to past precipitations over the catchment area of the righthand side of the Rhône, has no hydrological correlation with

the preceding phenomenon: this steady rise in the flow rate, usual at this period, is a result of the intrinsic cycle of the phreatic aquifer (BODELLE & MARGAT, 1980; CASTANY, 1968).

c. Period from February 1981 to September 1981

An exceptionally high number of *Siettitia* (38 larvae and 48 adults) was collected in February 1981. This was followed by a progressively diminishing yield, linked to a slow fall in the water level, which corresponds to the descending phase of the cycle of the aquifer.

VI. Comparison with previous data

We have gone over the basic or unexploited information collected in the past by SEYED-REIHANI (1980) at another station of this site (temperature, piezometric levels, *Siettitia* population) and we have expressed them in the same way in figure 7, 8 and 9.

Although the number of individuals is somewhat lower, the same general tendencies are present as during our sampling period. Thus, during an even more highly contrasted hydrological period (drought in 1976, once-a-century flood in 1977), the population seems to follow the intrinsic cycle of the phreatic aquifer itself, and almost disappears from the station when the river in flood blocks the underground flow.

VII. Development cycle

It must be remembered that the development of *Siettitia* comprises 3 larval instars (RICHOUX, 1980) and that the pupa has never been collected; this seems to confirm the supposition that this stage is located out of water as for all aquatic Coleoptera.

We have only taken into account the period between June 1980 and September 1981 for this study, as preceding numbers were too low to be significant.

First of all we worked out the ratios adults/larvae (Fig. 10), then compared the different larval instars with one another (Fig. 11). In these figures, the results are expressed by their percentage, eliminating the variations in number which are not linked to the real cycle of *Siettitia*.

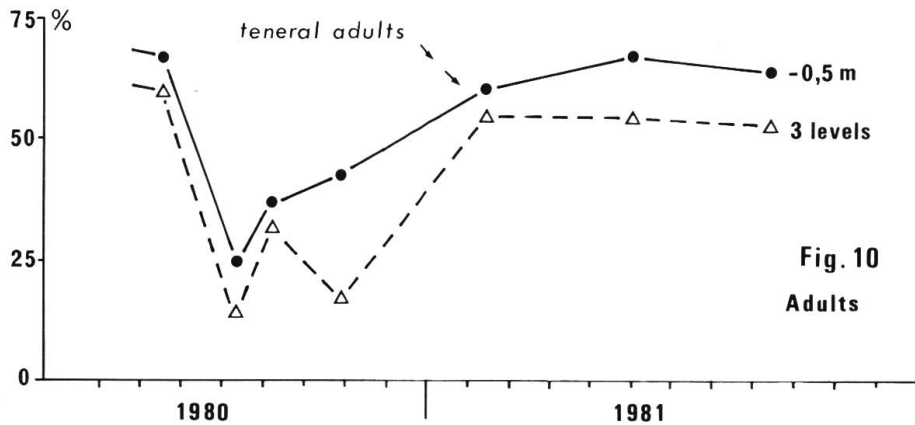


Fig. 10: Relative abundance of adults for the first sampling level (-0.5 m) and the 3 levels all together (-0.5 m; -1 m; -1.5 m)

The figure 10 (frequency of the adults expressed as a ratio of the total number of individuals on the one hand for the first sampling level (-0.5 m) and on the other hand for the three levels all together) allows us to show that the adults are systematically present in greater numbers at the top level of the aquifer, since the curve representing -0.5 m is always situated above the general curve. Moreover it seems that these adults diminish sharply in number in autumn.

The figure 11 (frequency of the three larval instars expressed as a ratio of the total number of larvae) allows us to visualize the successive maxima of stages I, II and III; this seems to indicate a smooth larval development. Although their numbers diminish sharply (see figure 10), the larvae do not disappear completely after these maxima, and the three instars remain present throughout the year, with 3rd instar being preponderant during winter and spring.

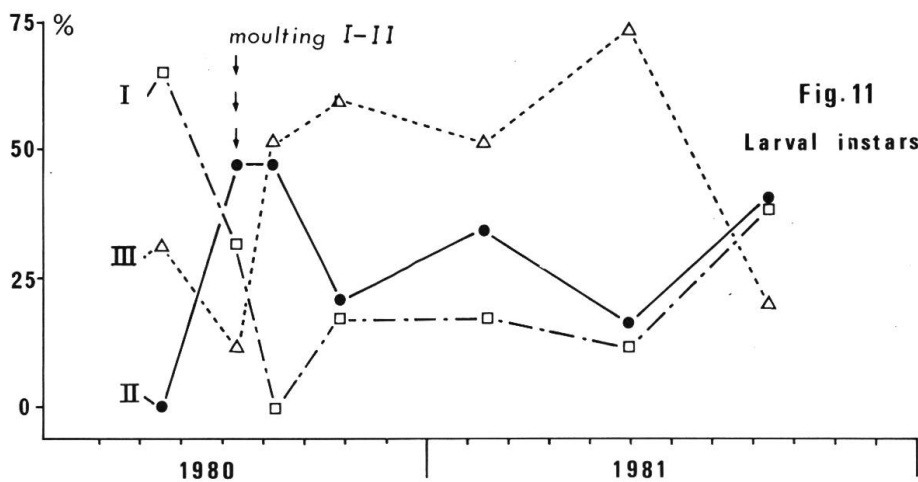


Fig. 11: Relative abundance of the 3 larval instars

Although we cannot leave out of account the likelihood that behavioural drift may be partly responsible for the numerical variations we have observed, we felt it was possible, on the basis of all the data collected so far, to construct a hypothetical model of the life cycle of *Siettitia* (see Fig. 12). It is based on our quantitative results, and furthermore it is backed up by a certain body of non-quantifiable data, which encourage us to believe that we are close to the truth (a few teneral adults collected at the end of January, moulting larvae from stage I to II in the month of August....).

Proposed model (Fig. 12)

During a mean hydrological year, egg-laying takes place in April–May, leading almost immediately to the appearance of the 1st instar (June–July). The 2nd instar appears in July–August, followed in September–October–November by the 3rd instar: during these five months, the adult mortality rate rises slightly, subsequent to egg-laying. In December–January pupation takes place, followed by the first

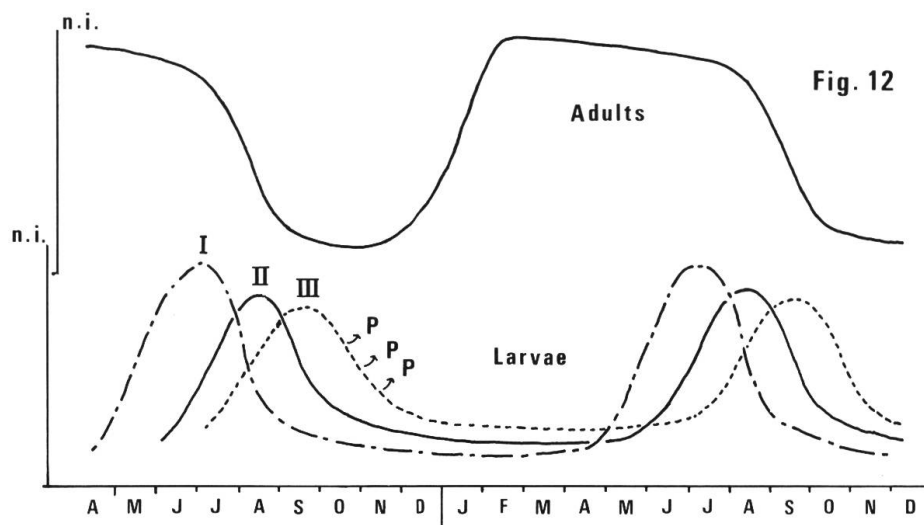


Fig. 12: Proposed model of the life cycle of *S. avenionensis* in a mean hydrological year.

imaginal moulting from January on. The number of adults thus reaches its previous level again and remains stable from March to July.

We must however return to our remark concerning the continued existence of a small number of larvae of the three instars throughout the whole period from December to May (see above). This phenomenon prevents us from determining with complete certainty the real life cycle length of these larvae and in particular of the IIIrd instar (a quiescent or

diapausal state may for example last until the December pupation and an identical phenomenon could also affect the Ist and IInd instars). We can also imagine that egg-laying and development might take place outside the essential periods. In short, the cycle may not be "exclusive" for the whole of the population.

VIII. Conclusion

In spite of population fluctuations due to certain habitat factors, the life cycle we have presented seems to be quite coherent, and to be in agreement with the results of YOUNG & LONGLEY (1976). The model must of course be tested and improved by means of a more detailed investigation, but a population numbering so many individuals (more than 550 collected since 1976) and in such a well-defined location was worth this first analysis.

On a more general ecological level, we feel that the most important argument put forward in this present study is that the distribution of *Siettitia* is above all linked to the internal pattern of the aquifer; indeed the rapid pulsations induced by the river movements seem to be experienced by the population as real "accidents" which disturb a relatively stable situation (it must be noted that the impact of level fluctuations on New-Zealand populations was not taken into account by ORDISH, 1976). This dependence on the aquifer was confirmed during an exceptional hydrological episode (the 1976 drought) when the river, its flow greatly reduced, drained the aquifer over a period of several months; it was at this moment that *Siettitia* appeared in the sites closest to the Rhône (Lône des Pêcheurs and Canal de Miribel, on figure 2) where it was to be found with other Coleoptera which are more representative of the underflow of the river: for example, g. *Esolus* (*Elmidae*). *Siettitia* has abandoned these two sites now that the river regime is more regular. This ephemeral apparition has led us to question the stability of a population at a given site: in our sampling station, the aquifer levels have remained above average over the last two years: in the "pool" which has been permanent during this period, superficial biocoenosis of stagnant type has developed with an "explosion" of algae leading to progressive silting of the bottom, which is now anoxic over a depth at least 10 cm. We are still finding all the aquatic instars of the cycle (I, II, III and adults), but it is obvious that the size of the population is at present extremely reduced at our usual collecting station; however, we have

found sporadically little groups of individuals scattered throughout the whole gravel pit. Thus we believe that we are now in the presence of a phenomenon of dispersal and we put forward the following interpretation: it is only when a rare equilibrium between a high level of oxygenation and a high trophic level appears at a given point of the aquifer (here induced by the neglect of the gravel pit), that the population concentration and “explosion” that we have observed can take place. If the situation tends to evolve toward a more important eutrophication, then this point will be more or less deserted by the population, which will enter a dispersal phase. According to the circumstances, this phase may be followed by another concentration if good conditions occur somewhere. One of these “booms” was brought to our attention quite accidentally, and has allowed to improve the knowledge of *Siettitia*; we have now to use this knowledge to investigate another site where similar “boom-conditions” could occur.

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