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Stability and changes of biomass of emerging insects and their possible causes

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With 2 figures in the text

Breitenbach near Schlitz, Hesse, Germany flows through meadows in a forested sandstone area and drops from almost 400 m a. s. l. to 220 m at its mouth into the Fulda River. The uppermost section of the 4—5 km long stream flows intermittently. It has no permanent tributaries, except a number of springs along its edge. A particularly large spring is at a sharp bend of the valley, where there are additional entries of groundwater into Breitenbach. The important influx of spring water causes a pronounced discontinuity in, e. g., the thermal gradient. This happens about 2 km before the mouth of Breitenbach and it is this lower section of stream where most studies have been done in the past. The fauna of Breitenbach is known to comprise more than 800 species of Metazoa, more than half of which are merolimnic insects. They are the dominant group in the stream also by specimen numbers. They have largely been studied with the aid of several big emergence traps (ILLIES 1971). Several regularly observed phenomena have been described (ILLIES 1982, 1983). Species composition is very stable. Abundance of every species, however, may change drastically from one year to the next, although a certain group of species forms the top group regularly. Up- and downward trends of various species tend to compensate each other largely so that despite remarkable internal shifts total biomass of emerging insects is amazingly stable. It fluctuates around a long term mean by less than 50 %. ILLIES discussed mainly predation, discharge, substrate, and temperature as causes of individual changes as well as of the overall stability of insect biomass emerging from the stream.

Temperature affects the events in Breitenbach in many ways. Here, only the effect of the thermal gradient in the lower section of Breitenbach will be considered. There is a fairly regular downstream increase of annual as well as daily temperature amplitudes (Fig. 1). When Ephemeroptera, Plecoptera and Trichoptera from five traps, nos. I—V, were analysed, ILLIES (1982) described pronounced up- or downstream trends of abundance for most species, even on the short stretch examined. The most important secondary producer, *Baetis vernus* CURTIS, was exceptional and exhibited no longitudinal zonation. The temperature gradient in the stream was and is thought to be the main reason for these clinal changes of abundance along the stream. However, it now appears that the method of analysis introduced a considerable bias.

To examine the longitudinal faunal zonation more closely, two traps were added in 1981 and 1982, respectively, downstream from the one operated by ILLIES. Another trap was installed some 80 m below the big spring in 1983, before the onset of insect emergence. Now the test stretch is almost 1700 m long and covers the entire thermal gradient. Traps presently operated are marked A—G in Fig. 1. Data from the uppermost trap, A, are presently only available for few species of Plecoptera which had ended emergence before July.

The present method of analysis differs from the one proposed by ILLIES. He had calculated total numbers of specimens caught in each of the traps I—V during the entire period 1977—1980. The picture thus obtained will largely be shaped by the year (or years) when the species was particularly abundant. Distribution in other years may have been very different but information on this is largely suppressed. For example, a downstream trend was ascribed to *Baetis rhodani* (PICTET). In fact, the species was distributed in different ways every year, but the two years when it was abundant shaped the picture. Data obtained in 1981 and 1982 also indicate that there is in fact no cline (Fig. 2 a).

In the present analysis, equal weight is given to distribution patterns every year. Data from different traps and years should be directly comparable regardless of how abundant

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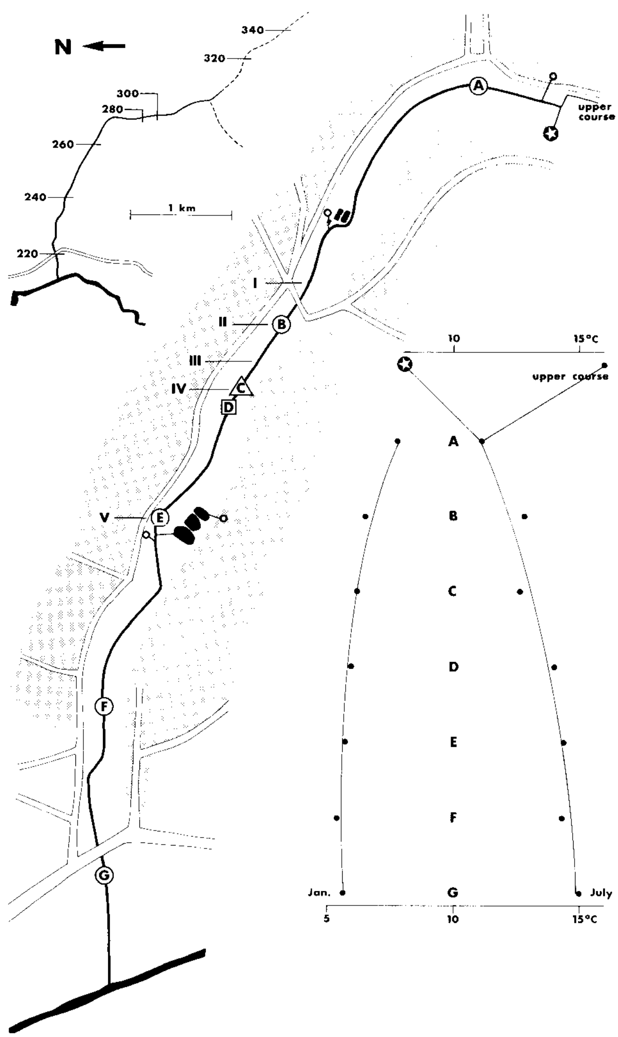

Fig. 1. Breitenbach: topography, sampling sites and thermal gradient. Top left: overview map of Breitenbach, altitudes (m above sea level) indicated. Intermittent flow indicated by interrupted line. Centre: lower section of Breitenbach between important spring (encircled asterisk; small circles: other springs) and the mouth. Black patches are fish ponds. Present trap locations marked by letters, C is the sandy, D the stony trap. Former sampling sites marked by Roman numerals, nos. I and III now abandoned.

the species was or how many traps were operated in a given year. Therefore, the total number of specimens caught in a given year is divided by the number of traps operated. This gives the number of specimens one would expect to take in every trap, provided the species had a completely uniform distribution along the stream. The number actually caught is expressed as percentage of that hypothetical mean. Data can be pooled for a vue d'ensemble of several years.

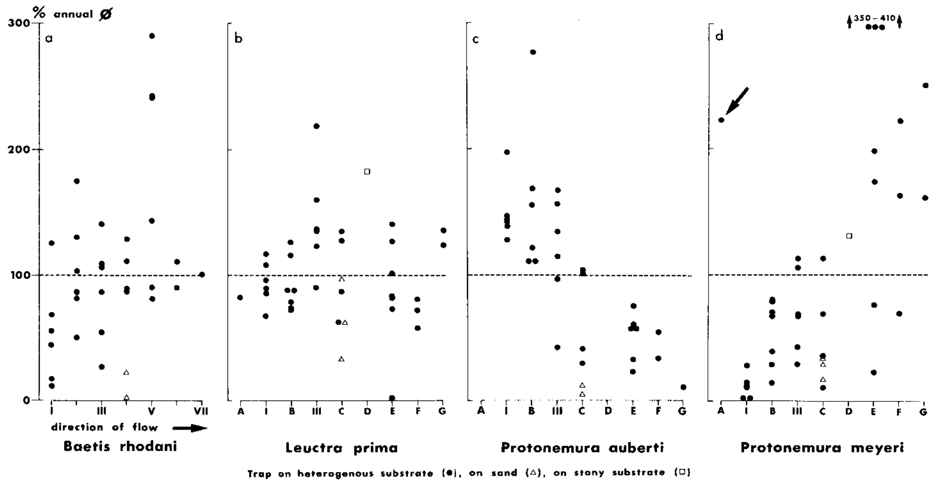

Fig. 2. Distribution of several water insects along Breitenbach. Pooled data for 1977—1982, actual catch in every trap expressed as percentage of mean annual catch/trap.

This method reveals that most species have an irregular distribution changing from year to year, and individual catches are scattered irregularly around the line of hypothetical even distribution (Fig. 2 a, b). Certainly, the temperature gradient plays at best a subordinate role in the distribution of species in this large group. Nevertheless, temperature may well be important for overall abundance in different years, etc. The distributional pattern in a given year is apparently determined by factors other than temperature. Additional experiments indicate that substrate type (which to a certain extent integrates factors like food supply, food quality, competitor pressure and so on) is particularly important. The group of irregularly or uniformly distributed species includes many that had been thought to be more abundant either up- or downstream and also all that Illies (1982) believed to be most abundant in the middle of the short stretch he studied.

Examples of pronounced clinal changes of abundance along the stream are comparatively few. They are strikingly apparent in graphs of pooled data (Fig. 2 c, d) but are obvious and essentially the same every year. The only environmental factor known to change in a regular constant way along the stream is temperature. It is very likely the main cause of the abundance trends observed.

Species with clear upstream increase of abundance are only three but include the second and third species on the list of the most important secondary producers (Illies 1978). They are *Agapetus fuscipes* Curtis, *Chaetopteryx villosa* (Fabr.), and *Protonemura auberti* Illies. All were still emerging this summer and information from the new trap near the spring is therefore still incomplete or missing. *A. fuscipes* and *P. auberti* are both known to be specialists of springs and cold headwater streams (Illies 1955; Dittmar 1955; Ziemann 1967; Schumacher & Schremmer 1970). The example of *P. auberti* shows that additional factors, especially substrate, also matter because the species falls short of previous average abundance in trap C since its formerly heterogeneous substrate has intentionally been covered with a layer of sand.

A greater number of species become more abundant as one proceeds downstream. This group is formed by the mayflies *Ephemerella mucronata* BENGTSSON, *E. ignita* (PODA) and *Paraleptophlebia submarginata* (STEPHENS); the stoneflies *Nemoura flexuosa* AUBERT, *Protonemura meyeri* (PICTET) and *Nemurella pictetii* KLAPÁLEK; and the caddisflies *Adicella reducta* (MCLACHLAN), *Silo pallipes* (FABR.), *Hydropsyche saxonica* MCLACHLAN, *Limnephilus sparsus* CURTIS, plus some rare or not regularly encountered species of all groups.

None of these eurythermous, relatively thermophilous species is among the top twelve secondary producers, which is in marked contrast with the group of steno-oligothermous species listed before. This shows Breitenbach to be, on the whole, a relatively cold stream which remains so in summer. According to ILLIES (1982) the group with downstream trend would include *Tinodes rostocki* MCLACHLAN, *Protonemura intricata* (RIS), and *Leuctra nigra* (OLIV.), all three very important members of the community. However, the present analysis of old data does not confirm this, nor do the new data from the upper and lower traps support the assumption of a pronounced downstream trend. Instead, the distributions are very irregular and apparently caused by some other factor; WAGNER (in prep.) shows, that substrate is very important for all three.

The relatively high abundance of *P. meyeri* in trap A in 1983 (arrow in Fig. 2 d) appeared to upset the present interpretation that the clinal distribution is caused by the temperature gradient along the stream. At site A, annual and daily temperature amplitudes are low as could be expected for an area close to a strong spring. However, only some 80 m upward from the trap is the lower end of the upper section of Breitenbach, which, thermally, appears like a tributary of limited importance. In this tributary, temperature in summer resembles the conditions at sites F or G, and it probably does so all year round. At site F and G, *P. meyeri* is common and it is evidently so in the similar stretch above site A. *P. meyeri* collected in trap A have probably not developed at this stenothermal site, but a few meters up at the eurythermal site, and have drifted into the trap area.

It now appears that longitudinal zonation of species abundance in Breitenbach is of less general importance than appeared to former students and in our future analyses we will have to take this disturbing factor into account for less species then previously assumed, fortunately.

Summary

In Breitenbach/Germany there is a downstream increase of daily as well as annual temperature amplitudes on the 2 km stretch between a large spring entering the stream and its mouth into the Fulda River. Importance of this thermal gradient for longitudinal zonation of Ephemeroptera, Plecoptera and Trichoptera is re-evaluated. Less species than previously suggested are actually affected. A regular upstream increase of abundance is observed only in 3 species, but these include 2 of the most important secondary producers of the stream community, which is dominated by oligo-stenothermal species. More species exhibit a downstream increase of abundance, but none of these more polyeurythermal ones is among the numerically important species in the stream. Distribution and abundance of most species in the stream are irregular and apparently determined by other factors, e. g., substrate composition at the stream bottom.

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