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The influence of floods on benthic insect populations in a Swiss mountain stream and their strategies of damage prevention

K.-J. Maier[1]

With 5 figures and 3 tables

Abstract: This paper describes flood induced changes of stream bed morphology and the effects of spates on the populations of dominant benthic insect taxa of a Swiss mountain stream (Kalte Sense, CH). The typical spates showed a steep increase of discharge, due to the topography of the catchment area. Within 6 hours the discharge may rise from 0.5 up to 20 m^3/s or more. During the 475 day study 45 floods were recorded of which 10 had discharges ranging from 15 to 25 m^3/s. The floods which exceeded 15 m^3/s caused large scale bed sediment movements and severe reductions in macroinvertebrate abundances. The effects of four flood situations on five insect taxa (Heptageniidae, Baetidae, Leuctridae, Chironomidae, Simuliidae) were recorded and analysed. In general, young larvae were affected much more than the older stages. Therefore, the severity of the floods and the amount of bed sediment transport correlated strongest with the reduction in abundance of young larvae. Individual severe flood events reduced the insect fauna to 60 % or even 27 % of the preflood value, a series of severe floods in November 1992 resulted in a reduction to 8 %. However, during the period from July to December, the insect populations usually recovered within 3 weeks and losses were compensated by young larvae which had just hatched.

Key words: Mountain stream, flood, aquatic insects, Switzerland.

Introduction

The concept of disturbance has long been recognized in ecology, but only during the last two decades it has gained prominence as a central theme in community organization (e.g. Ward & Stanford 1983, Resh et al. 1988). Following Pickett & White (1985), a disturbance is any relative discrete event

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[1] **Author's address:** Dr. Klaus-Jürgen Maier, Vogelsang I/I, 88437 Maselheim.

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in time that disrupts ecosystems, communities, or population structures, and changes nutrition availability, substrate composition or the physical environment. On the basis of this definition, RESH et al. (1988) pointed out that in stream ecosystems disturbance should also be characterized by the frequency, intensity, and severity of fluctuations outside of the predictable range.

In mountain streams, floods or spates are the most prominent factors which cause natural disturbance and, therefore, have enormous influence on benthic invertebrate communities (e.g. STEFAN 1965, STANFORD & WARD 1983, WARD & STANFORD 1983, PICKET & WHITE 1985, SAGAR 1986, RESH et al. 1988, TOWNSEND 1989). Floods of high intensity can cause substantial losses in benthic invertebrates (e.g. WATERS 1972, SCHWEDER & TOMSKI 1990, GILLER et al. 1991, MATTHÄI 1996), but normally the fauna recovers rather rapidly (e.g. DEBREY & LOCKWOOD 1990, LAKE & SCHREIBER 1991, UEHLINGER & MEYER 1992, MEYER 1993, MATHÄI et al. 1997). This indicates that benthic communities are well adapted to these disturbances (CUMMINS et al. 1984). However, resistance against flood-induced disturbance varies among different benthic invertebrate taxa. An example is given by HARKER (1953) who observed that among ephemerid populations *Heptagenia* sp. were most, *Ecdyonurus* sp. less and *Rhithrogena* sp. least affected by a flood.

Several authors (e.g. STEINMANN 1907, CLIFFORD 1966, WILLIAMS & HYNES 1974) described specific behaviour, phenomena during development or peculiarities in the life history of species that may function as protective strategies. However, our knowledge of the specific influence of spates on the invertebrate fauna and the species specific strategies to prevent damage is still very limited. Furthermore, little is known on the differential effects of spates on the various size classes of individual invertebrate taxa and their impact on the age structure of a population.

The objectives of this study were to determine (a) how natural spates of different intensity affect the dominant benthic insect taxa of a mountain stream, (b) the effect of floods on the different size classes of the larvae and (c) the time required by the insect populations to recover during different seasons of the year. In order to achieve these objectives, the observed changes in the benthic insect populations after flood events are placed in the context of the flood induced dynamics of the stream bed. The potential strategies to prevent damage or convey resilience to benthic insect populations are discussed.

Study site

The Kalte Sense is a mountain river in the Berner Oberland (Switzerland). It drains a catchment area of 66 km^2 at the steep north side of the Gantrisch Mountains, which are

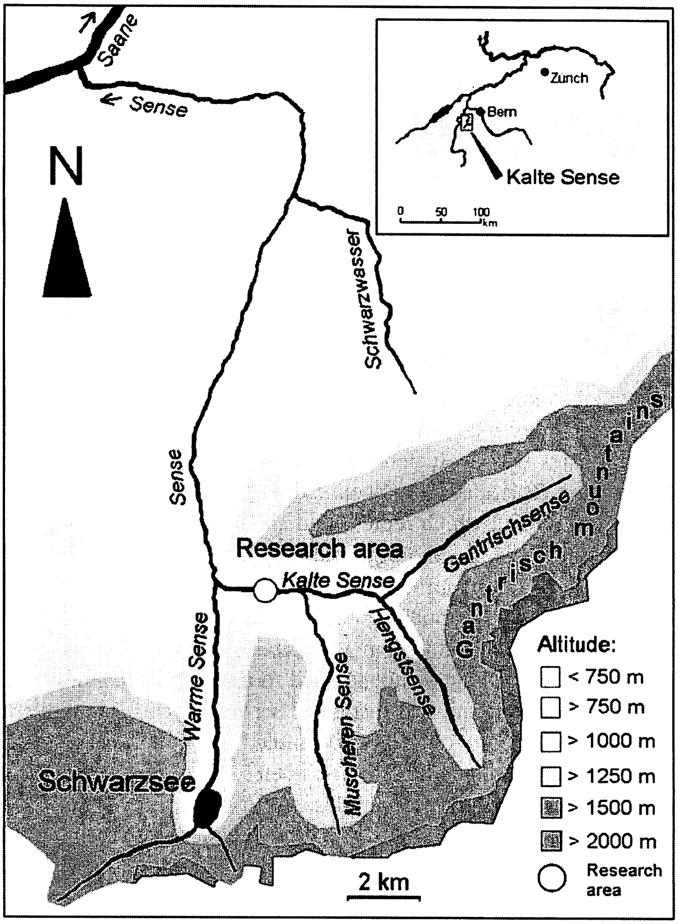


Fig. 1. Location of the Sense River with its main tributaries Warme Sense and Kalte Sense. The sampling site on the Kalte Sense (7° 20′/46° 43') is indicated by circle.

up to 2000 m a.s.l. (Fig. 1). Low flow discharges range between 0.5 to 1.5 m^3/s; the mean slope is 37‰. In its lower reaches the stream flows in a 40 to 60 m wide stony highwater bed. Spates occur with high frequency and often induce large-scale sediment transport.

The sampling site, a stream reach of 40 m in length, was in the lower part of the river (919 m a.s.l.). Here, the stream was 6 to 12 m wide and the bed sediments ranged from coarse sand to cobbles and boulders. Under low flow conditions, water current velocity ranged from 0.8 to 1.35 m/s in the midstream section. Water temperature ranged from 1 °C in winter up to a maximum of 17 °C in summer.

Material and methods

From 13/09/91 to 31/12/92 the water level was continuously measured by a water gauge 2.2 km below the sampling site. Low or intermediate discharge values were calculated from the changes in electric conductance after NaCl addition according to LUDER et al. (1988) and LUDER & FRITSCHI (1990). High discharge values were calculated with the hydraulic formula Q = v x F (Q = Discharge, v = flow speed, F = water deepness, x = width of the stream; see RÖSERT 1994).

Changes of the stream bed structure were recorded by aerial photographs which were taken periodically with a remotely controlled camera fixed to a gas balloon. In order to obtain information on the dynamics of the coarse gravel substrate, 30 color marked stones (mean diameter = 15 cm) were placed in the research area and their movements were recorded every second week for 3 months.

The effect of spates was evaluated for five dominant insect taxa belonging to the orders Ephemeroptera (Baetidae, Heptageniidae), Plecoptera (Leuctridae) and Diptera (Chironomidae, Simuliidae), which represented about 90% of the benthic macroinvertebrates and differ in body morphology, mobility and habitat preference. Reference samples were taken regularly during periods of low discharge. When a spate took place, additional sampling was conducted during the post-spate period. On every sampling date five sample units (total 0.45 m^2) were taken with a modified Surber sampler (mesh size = 100 µm). Sampling was conducted to a sediment depth of 0.15 m and restricted to 10 minutes. Every unit was evaluated separately and if the invertebrate density was high (>20,000 Ind./m^2), it was subsampled according to MEYER (1990). The effect of a spate on the benthic community was determined by comparing the reference values with those from the post-spate samples.

In order to receive information on evasive movements of the benthic insects to the stream edges, five samples from inundated areas outside the low-flow stream bed were taken with a Surber sampler during a heavy flood on 29 October 1992. The results of this survey were compared with data from pre-flood samples from the stream bottom at low-flow conditions.

The damage avoidance strategies of *Liponeura* sp. (Blepharoceridae) were examined by analyzing 2552 pupae sites with regard to water current velocity, stone size and the microstructures on the substrate surface.

For the purpose of this study the insect larvae were determined up to family or genus level. A more detailed examination of the fauna in the Kalte Sense (ZURWERRA et al., in press) shows the occurrence of the following species: 9 species of Baetidae: *Acentrella sinaicus* (BOGOESCU, 1931); *Baetis alpinus* (PICTET, 1843); *B. fuscatus* (LINNÉ, 1761); *B. lutheri* MÜLLER-LIEBENAU, 1967; *B. melanonyx* (PICTET, 1843); *B. muticus* (LINNÉ, 1758); *B. scambus* EATON, 1870; *B. rhodani* (PICTET, 1843); *Centroptilum luteolum* (MÜLLER, 1776); 10 species of Heptageniidae: *Epeorus alpicola* (EATON, 1871); *E. sylvicola* (PICTET, 1865); *Ecdyonurus helveticus* EATON, 1885; *E. picteti* (MEYER-DÜR, 1864); *E. venosus* (FABRICIUS, 1775); *Electrogena lateralis* (CURTIS, 1834); *Rhithrogena grationapolitana* SOWA, DEGRANGE & SARTORI, 1986; *R. hybrida* EATON, 1885; *R. savoiensis* ALBA-RERCEDOR & SOWA, 1987; *R. semicolorata* (CURTIS, 1834); 12 species of Leuctridae: *Leuctra albida* KEMPNY, 1899; *L. alpina*

Kühtreiber, 1934; *L. aurita* Navas, 1919; *L. cingulata* Kempny, 1899; *L. handlirschi* Kempny, 1898; *L. inermis* Kempny, 1899; *L. leptogaster* Aubert, 1949; *L. moseli* Morton, 1929; *L. nigra* (Olivier, 1811); *L. pseudosignifera* Aubert, 1954; *L. rosinae* Kempny 1900; *L. teriolensis* Kempny 1900; and 4 species of Simuliidae: *Odagmia ornata* (Meigen 1818); *Prosimulium hirtipes* (Fries 1824); *Simulium monticola* Friedrichs 1920; *S. variegatum* (Meigen 1818).

Results

Frequency and characteristics of floods and their effects on stream morphology

As a consequence of its steep catchment area, the Kalte Sense reacts to rainfall with an immediate increase of discharge. During the 475 day study period 45 spates were registered (Fig. 2). Most of them were of low or medium intensity and the discharge did not exceed 10 times the low-flow value. However, 10 spates reached discharge values which were 30 to 50 times higher and caused large-scale bed sediment transport resulting in dramatic changes in the streambed.

Fig. 2 also indicates the phenotype of the typical spates in the Kalte Sense. At the 25th of October 1992, the water level increased from 0.4 to 1.74 m within 18 hours and discharge exceeded 20 m^3/s. Just three days later another spate reached a peak discharge of more than 25 m^3/s. As a consequence of the

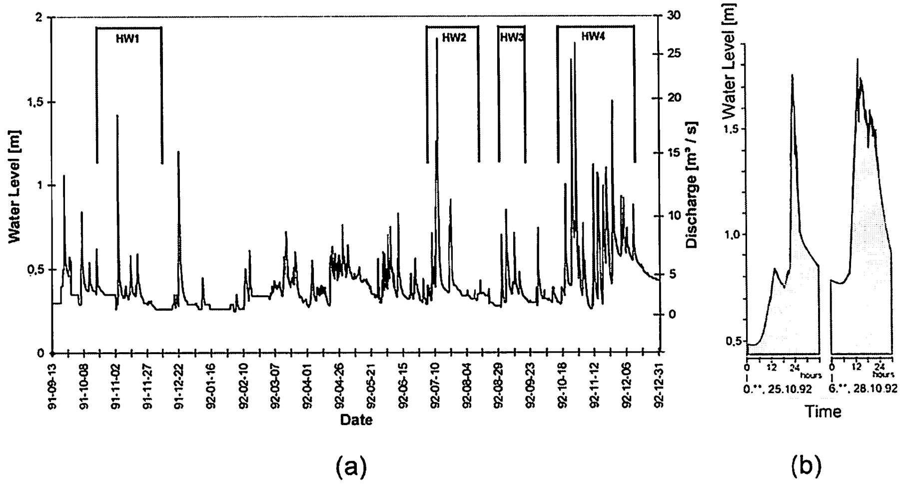


Fig. 2. **(a)** Discharge of the Kalte Sense during a 475-day period (13 September, 1991 to 31 December, 1992) at Zollhaus. The high water situations described in detail are marked as HW1, HW2, HW3 and HW4. **(b)** Water level changes during spates on 25 October 1992 and 28 October, 1992.

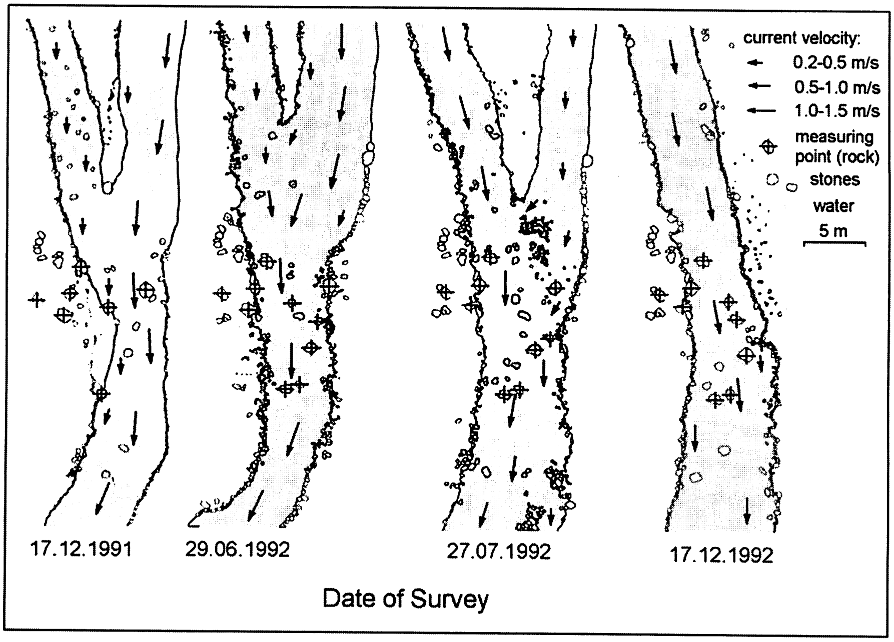


Fig. 3. Changes of stream bed morphology and flow regime (at low-flow conditions) in the sampling reach caused by floods.

steep discharge increase, within a few hours the stream changed from a clear mountain brook into a muddy roaring torrent, transporting rocks up to 0.3 m in diameter. The time period during which sediment movements took place normally lasted only a few hours. However, the changes of the stream bed were often drastic. All large scale changes in the stream bed were caused by spates which reached peak discharges of more than 15 m^3/s. The structural changes the study reach was undergoing during a 475 day study period are shown in Fig. 3.

That heavy spates can transport course gravel over long distances was shown in July 1992, when a flash flood with a peak discharge of about 25 m^3/s moved colour marked stones (mean diameter 15 cm) up to 1025 m downstream.

The effect of spates on the benthic insect populations

To evaluate the effect of spates on benthic insects, four flood situations with differences in peak discharge, frequency of bed sediment transport, and season in which they took place were analysed in detail (Fig. 2, Table 1). In the populations of the five dominant insect taxa, Chironomidae, Simuliidae, Baetidae, Heptageniidae and Leuctridae, the following effects of the spates were detected. Here I describe the recovery of the populations after the spate. The recruitment rates of freshly hatched larvae for three time periods are listed in Table 2.

Flood situation HW1

On the 4th of November 1991 a spate with a peak discharge of about 18 m^3/s caused large scale bed sediment transport. Total insect larval density declined to 60 % of the pre-spate value (17/10/1991). This decrease resulted almost totally from losses of small larvae (<2 mm), especially in Ephemeroptera and Plecoptera. Among these taxa, larger larvae (>2 mm) and Chironomidae were only slightly affected. Eight days after the flood, the fauna had recovered completely in terms of individual numbers. Regarding total individual densities, this increase was mainly based on the appearance of very small, obviously freshly hatched insect larvae. Especially the abundance of Simuliidae, rose significantly from 33 individuals/m^2 before the flood to 481 individuals/m^2 40 days after. At this time the number of insect individuals was 127 % of the pre-flood value.

Flood situation HW2

On 12th of July 1992, heavy rainstorms caused a flood which reached a peak discharge over 25 m^3/s and caused enormous bed sediment transport. In samples taken at the 14th of July, insect densities were reduced to 27 % of the pre-flood value. Only four days after, a significant increase of their number was detected, and 21 days later their abundance exceeded the pre-flood values. After 33 days, the total abundance was 2.5 times higher than before the flood.

The spate reduced the larval densities of Baetidae, Heptageniidae and Leuctridae smaller than 2 mm to 20 % of the pre-spate value. But the losses were compensated rather quickly, obviously by freshly hatched larvae. The Chironomidae and Simuliidae also suffered reductions but both recovered within two weeks. Especially the density of Simuliidae increased rapidly during the post-spate period from 22 (14.07.) to 1237 (14.08.) individuals/m^2.

Flood situation HW3

During the period from 12th of August to 10th of September 1992, three spates of low intensity with peak discharges between 8 and 11 m^3/s caused small scale bed sediment movements. No significant reductions were found in the post-spate samples, although large numbers of young insect larvae were present. In spite of the spates, the total number of insect larvae increased almost continuously because of the hatching of young larvae. During this period, the total number of insect larvae increased from 13,965 (30.08.) to 27,134 (14.09.)

Table 1. Changes in taxa densities (individuals/m^2) from pre-flood situations to post-flood recovery periods in the Kalte Sense, Switzerland. All values are mean densities calculated from 5 samples; s indicates the standard deviation of the total densities.

Taxa		HW 1 date: 04. 11. 91 peak discharge: ≈ 15 m^3/s				HW 2 date: 12. 07. 92 peak discharge: ≈ 25 m^3/s				
	body length (mm)	pre-flood [Ind./m^2] 17. 10. 91	post-flood [Ind./m^2] 07. 11. 91	12. 11. 91	17. 12. 91	pre-flood [Ind./m^2] 26. 02. 92	post-flood [Ind./m^2] 14. 07. 92	18. 07. 92	02. 08. 92	14. 08. 92
Baetidae	<2	866	463	848	1947	87	31	297	367	652
	2–4	22	37	154	66	4	9	29	326	33
	>4	4	2	1	4	53	9	11	46	81
Heptageniidae	<2	4133	3291	5223	6090	2631	202	741	1726	5245
	2–4	220	206	235	345	162	29	68	117	92
	>4	33	22	125	55	77	53	37	57	40
Leuctridae	<2	6206	2593	5341	5557	397	73	399	1805	2389
	2–4	11	66	213	81	37	15	4	4	38
	>4	4	0	2	7	2	7	1	4	5
Chironomidae	–	327	308	573	452	406	209	300	683	848
Simuliidae	–	33	183	294	481	167	22	156	313	1237
Total density		11859 s = 5753	7171 s = 3726	13009 s = 4809	15085 s = 4458	4023 s = 1252	586 s = 218	2043 s = 880	5448 s = 1787	10660 s = 2920

Table 1. Continued.

Taxa		HW3 date: 31. 08. – 10. 09. 92 peak discharge: ≈ 10 m^3/s				HW4 date: 20. 10. – 26. 11. 92 peak discharge: ≈ 25 m^3/s	
	body length (mm)	pre-flood [Ind./m^2] 30. 08. 92	post-flood [Ind./m^2] 03. 09. 92	06. 09. 92	14. 09. 92	pre-flood [Ind./m^2] 14. 10. 92	post-flood [Ind./m^2] 17. 12. 92
Baetidae	<2	661	643	867	966	1458	205
	2–4	189	455	354	222	57	26
	>4	88	218	44	46	37	20
Heptageniidae	<2	6375	6551	10078	13180	14390	324
	2–4	300	986	1124	1499	366	88
	>4	114	84	132	117	62	48
Leuctridae	<2	4611	4668	8871	10136	12832	427
	2–4	32	11	44	28	51	35
	>4	2	2	5	4	22	7
Chironomidae	–	1376	852	485	599	13	29
Simuliidae	–	229	144	309	337	0	1124
Total density		13965 s = 6221	14614 s = 3152	22313 s = 11746	27134 s = 16117	29288 s = 17327	2333 s = 908

individuals/m^2, an increase of 194 % for the total population and of 208 % for small larvae (<2 mm).

Flood situation HW4

From the 20th of October to the 26th of November 1992, a series of intense floods with peak discharges up to 26 m^3/s changed the stream bed completely. In the post-spate samples taken on 17th of December, the insect larval density had been reduced to 8 % of the pre-spate value. This decrease was mostly due to drastic losses in small Ephemeroptera and Plecoptera larvae. Only 3 % of the small larvae (<2 mm) survived the spate, whereas in the size classes 2–4 mm and >4 mm survivorship was 34 % and 62 %, respectively. Simuliidae, which had been absent in the pre-spate samples became the most abundant taxa (1124 individuals/m^2). Chironomidae densities were low in both pre- and post-flood samples.

Mechanisms of avoiding damage

Evasive movement to the stream margins

During a heavy flood at the 29th of October 1992, samples from inundated areas outside of the low flow streambed contained large numbers of aquatic insects (up to 4230 individuals/m^2). In contrast to the insect assemblage collected from the stream bottom before the spate, the abundance of Baetidae at the stream margins during the flood was 4 times higher, whereas abundance of Heptageniidae was the same and abundance of Leuctridae was lower. In both samples, larvae of Chironomidae were rare and larvae of Simuliidae were absent. The size distribution of larvae of Baetidae and Heptageniidae in the inundated areas showed a clear shift to larger individuals. The relative frequency of larvae larger than 4 mm was 8 times higher for Baetidae, and 33 times higher for Heptageniidae. In Leuctridae such differences were not found (Fig. 4).

Pupation site selection of *Liponeura* sp.

Liponeura sp. larvae were numerous in the research area in June and July. Most larvae entered the pupa stage in July when body length was 8–9 mm. During this time, the larvae aggregated at certain areas on the stony substrate to undergo metamorphosis. The analysis of 2552 pupae sites at the 5th of July 1992 revealed that *Liponeura* sp. prefers stones exposed to high current velocities ranging between 0.9–1.3 m/s for pupation (Fig. 5). Furthermore, most individuals (88 %) selected stones with more than 30 cm in diameter. The pupae were firmly attached to the stone surface and usually located in depressions or behind small ledges. At the 12th of July, a heavy spate destroyed many of the

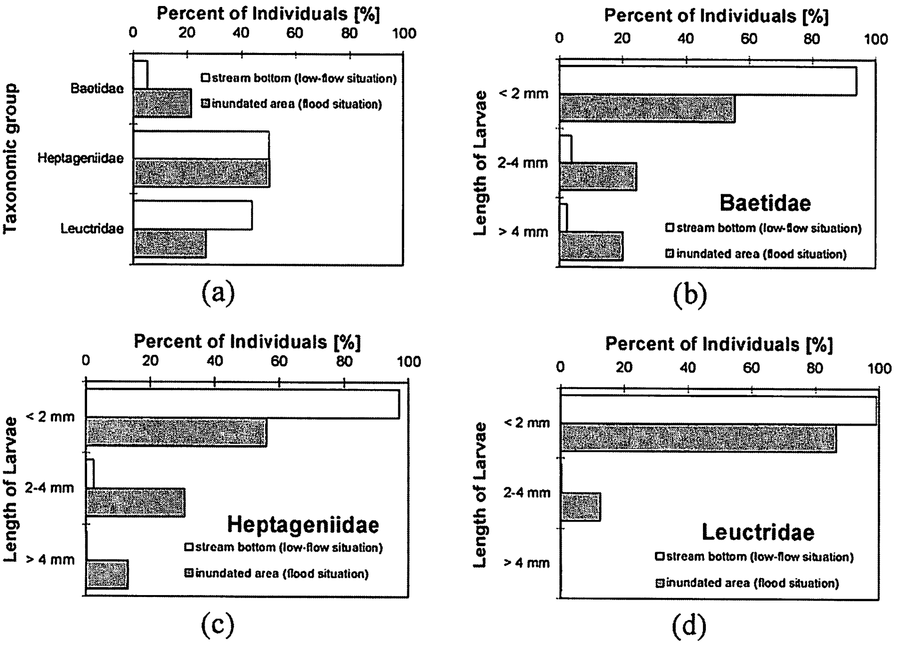


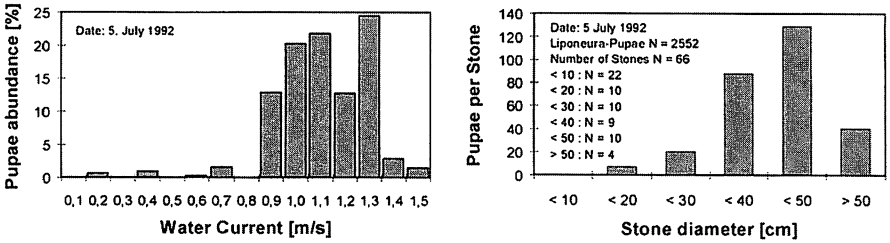
Fig. 4. Comparison of samples collected from the stream bottom at low-flow conditions (14. 10. 1992) and from marginal, inundated areas during a flood (29. 10. 1992): (**a**) relative abundance of 3 selected taxa; relative abundance of size classes of (**b**) Baetidae; (**c**) Heptageniidae; (**d**) Leuctridae.

pupae, and on 16th of July, only 502 pupae (19.7%) were counted. Almost all survivors were found on the large stones (mean diameter >30 cm) and embedded into microstructures of the stone surface which provided shelter.

Discussion

The Kalte Sense with its alluvial gravelbed and distinct riffle and pool structures represents, according to the definition of Brussock et al. (1985), a typical "gravelbed channel form". Resh et al. (1988) suggested, that in this stream type the biotic communities are generally most affected by variations in discharge. Furthermore, these authors assumed, that life history strategies vary among streams, depending on the intensity, frequency, and predictability of disturbance and that, in response to a given disturbance regime, certain reproductive, physiological, and behavioural patterns of life history may be modified or selected for.

During the 465 day study period, 45 spates were recorded (Fig. 2). Therefore, in the Kalte Sense, aquatic insect populations must survive several floods during their life cycle. Normally, these discharge events are of short duration



(a) (b)

Fig. 5. Pupation-site selection by *Liponeura:* (**a**) occurrence of pupae in relation to water current; (**b**) occurrence of pupae in relation to substrate size.

with steep discharge increases and decreases. Within a few hours, the discharge may reach the critical value when the bed sediment begins to move. In the Kalte Sense, large portions of the stream bed became mobilized when the discharge exceeded 15 m^3/s, which is about 30 times more than the low flow discharge. Ten of the recorded 45 floods surpassed this critical value and altered the streambed structure fundamentally.

Although normally the period of bed sediment transport lasted only a few hours, the stream bed underwent drastic and lasting structural changes during this period. Because stream bed morphology has strong influence on other environmental factors, for example water current and flow pattern, the environmental conditions for the benthic community in a certain stream area could change completely.

To date, our knowledge of the specific life history strategies of benthic insects to survive disturbance by floods is very limited. But there are indications that a wide range of strategies and mechanisms to prevent devastation by floods on species and on population level exist. Table 2 gives a synopsis of peculiarities in life history and behaviour, which may function as strategies of damage prevention against floods. Most of these mechanisms are poorly known and further studies are needed.

In this study, the direct influence of floods on the benthic insect populations depends on the degree of bed sediment movement. When spates cause large scale bed sediment transport they may have disastrous effects on benthic insect populations (Table 1: HW1, HW2, HW4), whereas when the transport of bed sediment is low (Table 1: HW3) the resulting effects are minor.

The function of bed sediments as resting places for the eggs seems to be of central significance. The quick replacement of the losses of young baetid, heptageniid and leuctrid larvae by freshly hatched individuals indicates that even severe spates had no serious impact on the eggs within the bed sediments. Therefore, it can be assumed that most lotic insect taxa have developed effi-

Table 2. Life history strategies and behavioural tactics of benthic invertebrates which may function as mechanisms against flood effects.

Stage of development	Characteristics		
	physiological	morphological	behavioural
Egg and Embryo	• resistance against physical stress • elongation of embryonic development • desynchronization of germination	• attachment structures on eggs • resistance against physical stress	• egg deposition in microstructures
Larva	• desynchronization of development • acceleration of larval development • desynchronization of hatching • ability to penetrate into bed sediments • resistance against physical stress • reduction of metabolism • ability to attach firmly on substrate • high mobility	• flattening or elongation of the body to reduce shear stress or to enable the animal to penetrate into the bed sediments • resistance against physical stress	• evasive movement • upstream movement • stable habitat selection • movement to stream margins
Pupa	• timing of pupation • acceleration of metamorphosis • desynchronization of pupation • resistance against physical stress	• flattening of the body to reduce shear stress • resistance against physical stress	• pupation site selection • building of protective cases
Imago	• reduction of metabolism • high fecundity • desynchronization of mating • synchronization of mating		• upstream flight • egg-laying strategy • selection of oviposition site

cient strategies of depositing their eggs in a way that minimizes the impacts of floods. Specific structures of the eggs for substrate attachment (e.g. PLESKOT 1957), varying oviposition techniques (e.g. HUMPESCH & ELLIOTT 1984) and a careful selection of the egg deposition sites by the females may work individually and together here.

The results also support the existence of a "retarded hatching" strategy as described by ILLIES (1959) for Baetidae. This phenomenon has been observed in many Ephemeroptera and Plecoptera species (ILLIES 1959, HYNES 1961, ELLIOTT 1967). It is regarded as a life cycle strategy, which leads to a desynchronization of the larval development and minimizes the effects of hydrologic disturbances on insect populations (ILLIES 1968, SCHWOERBEL 1969). The existence of retarded hatching could explain the appearance of young larvulae after sediment mobilizing flows and the rapid recovery of the larvae. However, HUMPESCH & ELLIOTT (1984) negate the existence of this mechanism and suggest that the reason for the occurrence of small larvae over long periods is due to a very slow growth rate. On the other hand, BOHLE (1969, 1972) showed that during the embryonic development some Ephemeroptera species (*Baetis vernus, B. rhodani, Ephemerella ignita*) may undergo a diapause which leads also to a prolongation of the embryonic development and, therefore, may be one reason for the appearance of young larvae long after the egg deposition period.

STEINMANN (1907) recognized already that a long embryonic development is typical for invertebrates in mountain streams. He pointed out that an extension of the embryonic stage followed by a short larval phase with accelerated larval growth and a short metamorphosis period may reduce the risk of getting damaged by floods. Rapid larval growth of mayfly species in mountain streams has been recorded also by other authors (e.g. PLESKOT 1961, HEFTI & TOMKA 1988, MAQUET & ROSILLON 1985). In this way, the life cycle characteristics of univoltine organisms, may enable them to exist in highly disturbed environments (RESH et al. 1988).

This study shows, that young insect larvae were much more affected by floods than the older stages. A reason for this difference seems to be that mobility increases with body size. Mobility is needed to move into a retreat before or during floods and to recolonize vacated areas after disturbance (TOWNSEND & HILDREW 1994). Inundated areas with low water currents at the stream margins, the deeper layers of the bed sediments, stones and rocks with high stability are regarded as such retreats (REMPEL et al. 1999).

The importance of the interstices of bed sediments as a protective area for the benthic fauna has been pointed out by several authors (e.g. WILLIAMS & HYNES 1974, RESH 1988, SCHWEDER & TOMSKI 1990, MEYER 1993). In fact, field data of CLIFFORD (1966) indicate that certain benthic invertebrates moved deeper into the substratum during a spate. But the ability to penetrate into the deeper sediment layers depends on body size, body shape and also physiological characteristics (Williams & Hynes 1974).

Even bed forming flows caused relatively little reduction in the abundance of large larvae. For example, 62 % of the Ephemeroptera and Plecoptera larvae in the size class >4 mm survived a series of heavy floods, whereas in the size class <2 mm just 3 % of larvae survived (Table 1: HW4). This leads to the conclusion that the older larvae are able to perform more effective avoiding strategies than the young ones. A reason may be, that the latter cannot escape from their substratum in time when a flood takes place. This is supported by the findings that, in contrast to small larvae, high numbers of large larvae aggregate at the stream margins with low current velocities during a flood. This aggregation is most pronounced in the largest larvae (Fig. 4). For young larvae with limited mobility, such evasive reactions are hardly possible. Hütte (1987) showed that they drift over longer distances than the larger larvae. As a consequence, their risk of getting washed out is very high if they enter the drift, especially during flood conditions. Therefore, the strategy of staying on the substrate should work well as long as the substrate stays stable. When it starts to move, the attached organisms get washed out and enter the drift. During this phase of a spate, a sharp increase in the density of drifting animals should take place, and indeed this has been recorded by several authors (Bailey 1966, Keller 1975, Hütte 1987). According to these assumptions, the insect drift during a flood should mainly consists of young larvae. Unfortunately, in most investigations this aspect of the drift has not been taken into consideration, although Hütte (1987) mentions that he collected only small-sized larvae in drift samples during a flood.

Furthermore, the analysis of the insect larval assemblage on the stream bottom at normal flow conditions or on inundated areas during a flood revealed that the relative abundance of the taxa in the latter habitat was correlated with their mobility (Fig. 4 a). The relation of abundance on stream bottom to abundance on inundated area declined according to the sequence Baetidae (1 : 4), Heptageniidae, (1 : 1) and Leuctridae (1 : 0.6). This supports the hypothesis that mobile larvae perform evasive movements to areas where current velocities are low and where no sediment movement takes place.

The ability of Leuctridae and Chironomidae to penetrate into the deeper bed sediment layers may be one reason that makes these taxa so successful in mountain streams. Due to their body shapes they are well adapted for living in the hyporheic habitat (Williams & Hynes 1974). Freeze core samples (Maier, unpubl. data) show that in bed sediments of the Kalte Sense these taxa are quite numerous down to a sediment depth of 0.7 m, whereas especially the older stages of Baetidae and Heptageniidae normally do not occur in higher densities at sediment depths below 0.2 m. Their body morphology and physiologic characteristics may limit their ability to reach or inhabit this habitat for a longer period, and therefore the bed sediments may be of less importance as flood refugia, especially for the older larvae. However, in other types of streams which have a deep hyporheos of coarse particles, like the Flathead River in Montana (STANFORD & GAUFIN 1974), bed sediments may offer protection against flood for these types of insect larvae as well.

The Chironomidae were usually most abundant in deeper bed sediments and, thus, were less affected by a scouring flood than *Rhithrogena* and *Leuctra* (MAIER 1994). In the Surber samples from the substrate surface taken in November and December 1992 (Table 1: HW4) Chironomidae were absent, but Freeze core samples from November 1991 (MAIER, unpubl. data) revealed that they withdrew to deeper sediment layers. The maximum density of the larvae was 0.2–0.3 m below the sediment surface. This is consistent with the observation of WILLIAMS & HYNES (1974) that the Chironomidae move deeper into the substratum during autumn and winter. Therefore, late autumn and winter spates should have no serious effects on many representatives of this taxon.

Normally the recolonization of the vacated substrate was almost completed within 3 weeks. It is concluded that this took place in two ways, firstly by the return of the larvae from their retreats and secondly by enhanced hatching of larvae. Enhanced hatching of larvae in post-spate periods seems probable as the losses were quickly replaced by very small larvae of 1 to 2 mm in length which presumably had hatched recently. It is not very likely that the colonization was performed by larvae which already inhabited the deeper bed sediments. Freeze core data (MAIER, unpubl. data) showed low densities of larvae in the hyporheos of the Kalte Sense. For example, of all baetid larvae only 1.6 % and of all heptageniid larvae only 10.3 % were found in sediment layers deeper than 0.1 m on 14th of August 1992. These findings correspond well with those of EGLIN (1990) who found 94 % of the fauna in the river Thur in the upper 0.1 m of the stream bed.

MATTHÄI et al. (1996) pointed out that in the river Necker the invertebrate drift was by far the dominant pathway of colonization after a bed moving spate. But his investigations have been performed in April and May when mainly older stages of larvae are present in the river.

Simuliidae were clearly promoted by the floods. Although they were often absent or rare in the pre-spate period, the larvae regularly appeared shortly after flood events in high numbers (Table 1: HW1, HW4). High densities of them were also recorded after the spring snow melt discharges (MAIER, unpubl. data). Their rapid and highly synchronous appearance indicates that their embryonic development or the hatching of the larvae is somehow triggered by factors arising during or after a flood. The findings correspond well with those of MEYER (1993) and HEMPHILL & COOPER (1983), and the latter authors suggest that Simuliidae may act as opportunistic colonizers using the substrate vacated by a spate.

Table 3. Recruitment rates of freshly hatched larvae (Baetidae, Heptagenidae, Leuctridae).

Time period (year)	Number of days	Total increase of freshly hatched larvae	Rate of recruitment [hatched larvae $day^{-1} m^{-2}$]
18. 07. – 14. 08. (1992)	27	6849	254
14. 09. – 14. 10. (1992)	31	8765	283
12. 11. – 17. 12. (1991)	36	2182	61

The importance of pupation site selection for damage prevention was evident in *Liponeura* sp. The macro- and microstructures of the chosen site proved crucial for the survival of the individuals. For pupation, the larvae preferred stones and rocks with a mean diameter of 40 to 50 cm (Fig. 5) and sites in depressions or sheltered by ledges but exposed to a current between 0.9 to 1.3 m/s. Sometimes aggregations of hundreds of pupae were found at such locations. Other insect taxa with a pupa stage, for example Trichoptera (see HOFFMANN 1998), probably show similar preferences. As the disturbance frequency of individual rocks is negatively correlated with their size (DOWNES et al. 1998), large rocks function as disturbance refugia (LANCASTER & HILDREW 1993).

Up to now, we know little about the influence of floods on the species composition and their abundance in the following year or even longer periods. However, SEEGRIST & GARD (1972) showed that the timing of a hydrologic disturbance influences spawning success as well as abundance of brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*) in the following year. It is very probable that similar relationships exist for benthic insects. In long term studies on the emergence from the Breitenbach (Germany), ILLIES (1982, 1983) showed that the species composition of insects remains very stable over the years, but their abundance may fluctuate drastically. He suggested that discharge, predation and temperature cause these fluctuations.

The investigation in the Kalte Sense shows that the loss of individuals during floods is most drastic when mainly young larvae are present in the stream. In Switzerland, this is the case in the period from July up to December. At the beginning of this period, large numbers of insect eggs are still in the bed sediments where they constitute the recovery potential of the insect populations. If disturbances occur, the insect fauna recovers rapidly and losses of young larvae, at least in Ephemeroptera and Plecoptera, are replaced by newly hatched larvae. If heavy floods take place at the end of this period when most eggs have already developed and large numbers of young vulnerable larvae dwell on the substrate, an essential portion of these larvae may be destroyed. The number of eggs in the bed sediments may be too low to replace the losses. Therefore, it is suggested that the insect fauna is most sensitive to floods during late autumn and winter. Hence floods, which take place during this period should have the most impact on species abundance and productivity.

The data listed in Table 3 indicate that the recovery time is shortest from July to October and longest in November and December. The lower values in the winter time may be a consequence of lower temperatures, however, they may also be a consequence of a reduced "recovery potential" as most eggs have already developed.

The enormous reduction of benthic insect densities by bed forming floods indicates that floods or spates have an important influence on the productivity of the impacted species. However, the effect on total benthic insect productivity may be attenuated because some taxa, such as Simuliidae, appear to benefit from the floods and can develop large post-flood populations.

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