The effects of a small low-head dam on benthic invertebrate communities and particulate organic matter storage in the Ilm stream (Thuringia / Germany)

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Frequently used Abbreviations

AFDM	Ash-free dry mass
ANOVA	Analysis of variance
a.s.l.	Above sea level
CA	Correspondence Analysis
CPOM	Coarse particulate organic matter
CPOM/FPOM ratio	Quotient between CPOM & FPOM
DCA	Detrended Correspondence Analysis
d.f.	Degrees of freedom
DM	Dry mass
EQ.	Equation
FFGC	Functional feeding group concept
FPOM	Fine particulate organic matter
MRPP	Multiple Response Permutation Procedure
PCA	Principal Component Analysis
PM	Particulate matter (POM + PIM)
PIM	Particulate inorganic matter
POM	Particulate organic matter
RCC	River continuum concept
S.D.	Standard deviation
S.E.	Standard error
SS1	Sample site 1 - natural stream reach (reference) upstream of the dam (≙ NR_{up})
SS2	Sample site 2 - stream reach within the impoundment of the dam (≙ Impoundment)
SS3	Sample site 3 - stream reach immediately downstream of the dam (≙ DR_{down})
SS4	Sample site 4 - natural stream reach (reference) downstream of the dam (≙ NR_{down})

Chapter 1

1. Introduction

Streams are indispensable components of the global hydrologic cycle and they are essential in global biochemical processes. It has long been recognized that streams not only serve as simple transport channels, today they are considered as complex ecosystems that intensively exchange energy and matter with the surrounding terrestrial ecosystems. The River Continuum Concept (RCC) describes stream ecosystems as a continuous series of physical gradients and associated biotic adjustments (Vannote *et al.* 1980). The concept largely focused on the interaction of stream organisms with their habitat and food resources suggesting that longitudinal changes in structural and functional characteristics of the stream community reflects longitudinal changes in the availability of habitats and of various forms of organic matter along a stream system. In many headwater streams the riparian vegetation is the primary source of organic matter and also limits the autochthonous primary production by shading. Therefore, most of the organic matter available to this stream type is of allochthonous origin. For instance, Fisher and Likens (1973) found that the input of tree leaves accounted for 99% of the energy input to a headwater stream. After entering the stream two things happen to the allochthonous material: breakdown and downstream transport. Breakdown is the result of the combined action of physical, chemical and biological processes and occurs in three phases: leaching, microbial colonization (conditioning) and fragmentation by physical forces and invertebrate feeding (Suberkropp 1998). The “shredder” invertebrates which are specialized in feeding on coarse particulate organic matter (CPOM) are a proportionally more common functional feeding group in headwater streams and play a crucial role in stream energy dynamics by converting coarse particulate organic matter (CPOM) into fine particulate organic matter (FPOM), which is then transported downstream (Winterbourn & Davis 1976, Wallace & Webster 1996, Hieber & Gessner 2002). Beside the particle size also the nutritional quality of the organic material changes during detritus processing. With increasing stream size, autochthonous primary production (aquatic macrophytes & periphyton) and fine particulate organic matter (FPOM) supplied from upstream processing of coarse particulate organic matter (CPOM) become important as energy sources for the stream communities. Therefore, the invertebrate communities in the middle reaches of a stream system will be dominated by grazers and collectors (Vannote *et al.* 1980). Further downstream in the largest reaches of a stream system planktonic algae will become the dominant primary producer and organic matter resources will be present as fine particulate organic matter (FPOM) and ultra-fine

particulate organic matter (UPOM). As a consequence filtering collectors (planktonic & benthic) will be the dominant functional feeding group in these reaches.

The unidirectional flow of water is the major physical force and the controlling ecological factor (Schönborn 1992) that causes a strong linkage of downstream reaches with the upstream reaches (Fisher & Likens 1973). Breakdown and downstream transport occur simultaneously in streams. The spiraling concept (Webster & Patten 1979, Newbold *et al.* 1982, Elwood *et al*. 1983) describes the spatio-temporal dynamics of nutrients and organic carbon. The cycles of organic matter and nutrients are stretched into spirals due to the continuous, unidirectional flow of the water. For nutrients a cycle is completed when a nutrient atom has been taken up by an organism from a dissolved available state (inorganic), passed through the food chain, and returned to a dissolved available state for reutilization (Newbold *et al.* 1982). The spiraling length and spiraling time, defined as the spatial distance and the time required for a complete cycle are used to describe the spiraling of nutrients. Because of the permanent carbon dioxide (inorganic carbon) exchange between air and water, carbon spiraling is more difficult to conceptualize. The turnover length and turnover time are used as measures for the spatio-temporal extension of carbon cycles and are defined as the distance and time traveled by a carbon atom during its residence in the stream in an organic form. But they do not refer to the complete spiral of a carbon atom. Short spiraling length and time indicate efficient recycling of resources. The spiraling of nutrients and organic matter is a function of physical and biological processes. The downstream transport and the retention of organic matter are most important in determining carbon spiraling length. Both are critical functions in stream ecosystems, because they control the loss of nutrients, particle-associated energy and connect upstream processes with downstream ones (Hall *et al.* 1996). In contrast, carbon spiraling time seems mainly determined by biological processes, such as respiration and invertebrate feeding activities. The continuous changes of many physical and biological processes along a stream continuum (Vannote *et al.* 1980) seems to cause a continuous change in the spiraling of organic matter from upstream to downstream reaches along a stream (Minshall *et al.* 1983).

Numerous anthropogenic disturbances alter stream ecosystems (Resh *et al.* 1988, Covich 1993) and impoundment is an very important one. Dams are ubiquitous structures in many stream systems throughout the world. Large storage dams alter the discharge and the temperature regimes, hydraulic characteristics, substrate composition and channel morphology and as a consequence the structure of stream communities. Many of these alterations can persist for large distances downstream. This type of dam furthermore alters the river continuum by disrupting the spiraling of

resources (nutrients and organic matter) (Ward and Stanford 1983) and disconnecting upstream and downstream reaches (Pringle 1997) resulting in declines in biodiversity and the alteration of natural stream food webs (Power *et al.* 1996, Wootton *et al.* 1996). Based on the RCC, Ward and Stanford (1983, 1995) developed the serial discontinuity concept (SDC) that considers the alterations caused by large, deep-release storage dams. The SDC describes the local effects of large storage dams, their consequences for the entire stream system and further considers the effects of multiple impoundments. Beside general impacts on physical, chemical and biological conditions, the barrier effect is a further serious one that can result from damming. Dams may reduce the hydrological connectivity by preventing or impeding the migration of organisms throughout the stream system (Pringle 2003), resulting in fragmentation of habitat and isolation of populations (Pechlaner 1986, Drinkwater & Frank 1994, Winston *et al*. 1991, Marchant & Hehir 2002). The barrier effect seems evident for migratory fish species (Lewis 1991, Mills 1989, Morita & Yamamoto 2002). However, up today most studies focused only on economically important populations of fish (migratory salmonid fishes) and comparably little is known about biota of less economic importance. The effect is especially for aquatic invertebrates by far less clear (Pringle 2003).

In contrast to large dams today there is relatively little information on the ecological impacts of smaller dams. Such small often run of river dams with a hydraulic head < 5 meters (low – head) and small impounded areas of < 20 hectare, are generally much more numerous than large storage dams in Central European stream systems. This type of dam does often not substantially alter the natural discharge regime, but influence local flow velocity patterns, sediment composition (Magilligan & Nislow 2001, Stanley *et al*. 2002), particulate organic matter (POM) budgets and CPOM/FPOM ratios (Gore 1994, Wagner 2003). Also the impoundment of these structures create distinct physical conditions in comparison to free-flowing natural reaches (Baekken *et al.* 1981b, Stanley *et al.* 2002), but chemical conditions are altered to a much lesser extent (Baekken *et al.* 1981a). The ecological consequences of small low–head dams are poorly understood (Benstead *et al.* 1999, Hart *et al.* 2002, Poff & Hart 2002) and comparably little scientific interest has been laid on this kind of human impact to stream systems. The knowledge about the ecological impacts of dams today based to a large extent on studies of large storage dams (>15 m), but most of the dams which are being removed, enclosed or reconstructed (fish passes & -ladders) by the regional stream managers in Europe at present, are small low-head dams (≤ 5 m). Underlying this fact there is a pressing need for studies about ecological responses of dam impact across a variety of dam sizes and operational types (Hart *et al.* 2002).

The aim of the present thesis is to investigate the impacts of a small low-head dam on invertebrate communities and particulate organic matter standing stocks in a headwater stream in Thuringia/Germany. It was hypothesized that invertebrate communities and POM standing stocks are altered in stream reaches close to the dam. It was furthermore assumed that the impacts of the dam are locally restricted and that the type, the magnitude and the spatial extension of the impacts are not comparable to those caused by large storage dams. Based on the facts, statements and assumptions mentioned above, the following questions arise:

- Does the dam alter the invertebrate communities and if it does, are the alterations extended downstream? The following attributes are used to investigate these questions:
  - (a) Invertebrate abundance (number of invertebrates & biomass)
  - (b) Diversity (taxon richness & evenness)
  - (c) Community composition (taxonomic & functional)

- Does the dam alter the distribution and composition of POM and if it does, are these alterations extended downstream? The investigated attributes are:
  - (d) POM standing stocks
  - (e) CPOM/FPOM ratios

- Is there a barrier effect? The investigated attributes are:
  - (f) Abundance, diversity & composition of invertebrate assemblages on stones
  - (g) Abundance, diversity & composition of drifting invertebrates

Furthermore the effects of multiple impoundments along the longitudinal profile of the regulated headwater stream Ilm on the zonational distribution of aquatic invertebrates are investigated.

In order to understand food webs and food web alterations caused by anthropogenic disturbances a detailed knowledge about the links between consumers and resources is indispensable. Therefore, an experimental laboratory study investigates the complex interaction between resources (POM) and benthic invertebrate consumers.

Thesis structure

In the first chapters the effects of a single small low-head dam on invertebrate communities and POM storage are investigated. In order to detect the impact of the dam various structural and functional attributes of the invertebrate communities (abundance, diversity, functional composition), the contents of POM in the sediment and the particle size composition of POM were measured at two dam sites and at two natural stream sites (Chapter 2). The two latter sites were selected according to structural attributes of the stream channel, indicating nearly natural conditions. The sites provide a baseline of spatial and temporal variation in invertebrate community variables and POM contents within unregulated stream reaches. Additionally in Chapter 2 the distribution of particulate organic matter (POM) is related with abundance (number & biomass) and composition of invertebrate assemblages in order to examine the spatial relation between particulate organic matter and benthic invertebrates.

The barrier effect is examined in Chapter 3. Two approaches are used to explore this effect: At first invertebrate assemblages on stone surfaces are compared between a reach immediately downstream of a dam and two natural reference sites. It was assumed that the investigated low-head dam affects invertebrate colonization by alteration of downstream drift and prevention of upstream movements. As a consequence, invertebrate assemblage composition immediately downstream of the dam should differ from those of free flowing natural reaches. In order to support the results and interpretations gained from the first study part, the downstream drift of benthic invertebrates is measured in the second part of this study. It was hypothesized that the impoundment traps invertebrates from downstream drift, resulting in differences in the invertebrate drift (density & diversity) within the impoundment, but also immediately downstream of the dam, both in comparison to free flowing natural reaches.

The longitudinal zonation of aquatic invertebrates, a gradual change of invertebrate community structure along stream systems, is a well known characteristic in undisturbed stream ecosystems. Little is known about the effects of multiple impoundments of small dams to stream systems. Therefore the effects of multiple impoundments along the longitudinal profile of a regulated headwater stream on the zonational distribution of aquatic invertebrates are investigated in Chapter 4. For this purpose the distribution of invertebrates along the stream gradient was assessed using four published data sets and compared with patterns suggested by basic concepts.

Understanding food webs and food web alterations caused by anthropogenic disturbances are central topics in ecology. To achieve this goal it is necessary (1) to

determine the sources of organic matter that provide energy and nutrients to the heterotrophs as well as their relative importance and (2) to determine the trophic pathways through which the energy of organic matter resources is transferred within food webs. Stream invertebrates are central components in stream food webs. They are essential to stream nutrient cycling by consuming and transforming organic matter and they are important in transferring energy to higher trophic levels. The functional classification of stream invertebrates has enhanced the understanding of stream nutrient cycling and trophic interactions, but the usage of functional feeding groups as trophic guilds has been criticized because they do not appropriately reflect resource utilization. The ratios of stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) are increasingly used as natural-abundance tracers to reconstruct diets and to estimate the trophic position of the animals. This method seems useful to trace the flow of energy through the ecosystem and has been used successfully to detect food web alterations caused by human disturbances. However, there have been many field studies in which it was difficult to discern the trophic structure on the basis of isotope data. Gannes *et al.* (1997) argued that a correct interpretation of stable isotope data will be achieved only if the collection of field data is accompanied by laboratory experiments. Therefore, Chapter 5 focuses on the utilization of leaf resources by two benthic invertebrate species: *Gammarus pulex* L. (Crustacea; Amphipoda) and *Baetis rhodani* Pictet (Insecta, Ephemeroptera). Laboratory experiments were designed to measure utilization of leaf resources by *Gammarus pulex* and *Baetis rhodani* and further to monitor the principal changes in chemical and isotopical composition of leaf material during breakdown.

Chapter 2

2. The effects of a small dam on invertebrate communities and particulate organic matter (POM)

2.1 Introduction

Stream regulation by damming is known to alter physical, chemical and biological conditions in streams (Ward & Stanford 1979, Ward & Stanford 1983 & 1995, Petts 1984, Gore 1994, Collier *et al.* 1996). To date there is a large body of literature documenting the profound effects of large storage dams. Such dams are essential for power supply, flood control and water storage. The regulation by these dams has substantial economic benefits, but there are the costs of fundamental alterations of stream systems. Many physical and chemical conditions are altered continuously within the storage reservoirs leading to strong response in biological communities there and in downstream sections, but depending on the position of the dam at the longitudinal stream profile (Ward & Stanford 1979). Especially the regulation of release affects the overall discharge regime of the stream (Brookes 1994, Boulton & Brock 1999).

Small run of river dams with a hydraulic head < 5 meter (low–head) and small impounded areas of < 20 hectare, are much more numerous than large storage dams in Central European streams and rivers. This type of dam does not substantially alter the natural discharge regime, but influence flow velocity patterns, sediment composition (Magilligan & Nislow 2001, Stanley *et al*. 2002), particulate organic matter budgets and the ratio between coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) (Gore 1994, Wagner 2003). Also the impoundment of these structures create distinct physical conditions in comparison to free-flowing natural reaches (Baekken *et al.* 1981b, Stanley *et al.* 2002), but chemical conditions are altered to a much lesser extent (Baekken *et al.* 1981a).

The ecological consequences of small low–head dams are poorly understood (Benstead *et al.* 1999, Hart *et al.* 2002, Poff & Hart 2002) and comparably little scientific interest has been laid on this kind of human impact to stream systems. Whereas the knowledge about the ecological impacts of dams today is based, to a great extent, on studies of large storage dams (> 15 m), most of the dams which are being removed, enclosed or reconstructed (fish passes & -ladders) by the regional stream managers in Europe at present, are small low-head dams (≤ 5 m). Underlying this fact there is a pressing need for studies about ecological responses of dam impact across a variety of dam sizes and operational types (Hart *et al.* 2002).

The objective of this study is to examine the effects of one small low-head dam on benthic invertebrate communities and particulate organic matter (POM).

Both particulate organic matter and invertebrate consumers are essential to the flow of energy in stream ecosystems. Many headwater streams are energetically dependent on the allochthonous organic matter (Fisher & Likens 1973, Cummins 1974) and POM standing stocks mostly exceed autochthonous primary production. Downstream transport and retention of particulate organic matter are critical functions in stream systems, because they control the POM standing stocks available to heterotrophs. Aquatic invertebrates contribute significantly to nutrient cycling and the turnover of organic material. Changes in detritus quality and quantity greatly influence community composition and energy budgets in streams (Vannote *et al.* 1980, Wallace *et al.* 1995 a). This study aims to describe and to compare invertebrate communities and POM standing standing stocks of stream reaches close to a dam with those of natural reference reaches upstream and downstream of a small low-head dam. The dam is considered as a man made semi-experimental system that possibly disrupts transport and storage of particulate organic matter resulting in remarkable alteration of invertebrate communities. It was hypothesized that invertebrate community attributes [abundance (number of individuals & invertebrate biomass), diversity and composition] and POM standing stocks are altered in stream reaches close to the dam. It was furthermore assumed that impacts of the dam are locally restricted and that the type, the magnitude, and the spatial extension of the impacts are not comparable to those caused by large storage dams. The following set of specific hypotheses was formulated:

(I) Invertebrate community

- Invertebrate abundance (number & biomass) is higher in stream reaches close to the dam, but there are no far reaching downstream effects:

  $\textit{Impoundment} > DR_{down} > (NR_{down} = NR_{up})$ *

- Invertebrate diversity is lower in stream reaches close to the dam, but the effect is not extended downstream:

  $(NR_{up} = NR_{down}) > DR_{down} > \textit{Impoundment}$ *

- Community composition (taxonomic & functional) is altered in stream reaches close to the dam, but the effect is not extended downstream:

  $(NR_{up} \sim NR_{down}) \sim DR_{down} \sim \textit{Impoundment}$ *

(II) Particulate organic matter

- POM standing stocks are higher in stream reaches close to the dam, but the effect is not extended downstream:

  Impoundment > DR_{down} > (NR_{up} = NR_{down}) *

- *CPOM/FPOM ratio* is lower in stream reaches close to the dam, but the effect is not extended downstream:

  (NR_{up} = NR_{down}) > Impoundment ≥ DR_{down} *

*** Abbreviations & Presuppositions:**
NR_{up} - natural reach upstream, NR_{down} - natural reach downstream, DR_{down} - dam reach immediately downstream of the dam, *Impoundment* - stream reach within the impoundment of the dam; [~ (highly similar) to ~ (least similar)]; The natural reaches are in close spatial proximity to the dam (few kilometers) and both are highly similar in their abiotic characteristics.

Most of the assumptions involved in the above hypotheses, concerning the alterations at the low-head dam, are highly similar to the patterns commonly found at large storage dams, but the hypotheses differ in that no profound and far-reaching downstream effects are assumed for the investigated small low-head dam.

Additionally particulate organic matter (POM) was related with invertebrate abundance (number & biomass) in order to examine the influence of POM on the distribution of benthic invertebrates.

2.2 Methods

Study area

The study was conducted in the 3rd order (Strahler 1957) hard water stream Ilm in Thuringia (Germany). The stream has a catchment area of approximately 1035 km^2 (Krey 1995). Average annual precipitation within this region ranges between 550 – 1200 mm m^{-2} $year^{-1}$ leading to an average annual discharge of 83 x 10^6 m^3 $year^{-1}$. The stream has an average slope of 3.16% (spring: 500 m a.s.l.; mouth: 115 m a.s.l.). Over its entire length of 137 km, 56 small low head dams are continuously distributed (average distance from another 2.30 km). All these dams are low-head, run-of- river dams with a hydraulic head < 5 meters (min. 0.70 – max. 3.10 meters) and small impounded areas of < 3 hectare. Four sampling sites were selected within a five kilometer long section located close to the town Stadtilm (11°05´ E, 50°46´ N, 360 m a.s.l.) in the metarithric zone of the stream (Figure 2.1). The four sampling sites were denoted as SS1, SS2, SS3, and SS4.

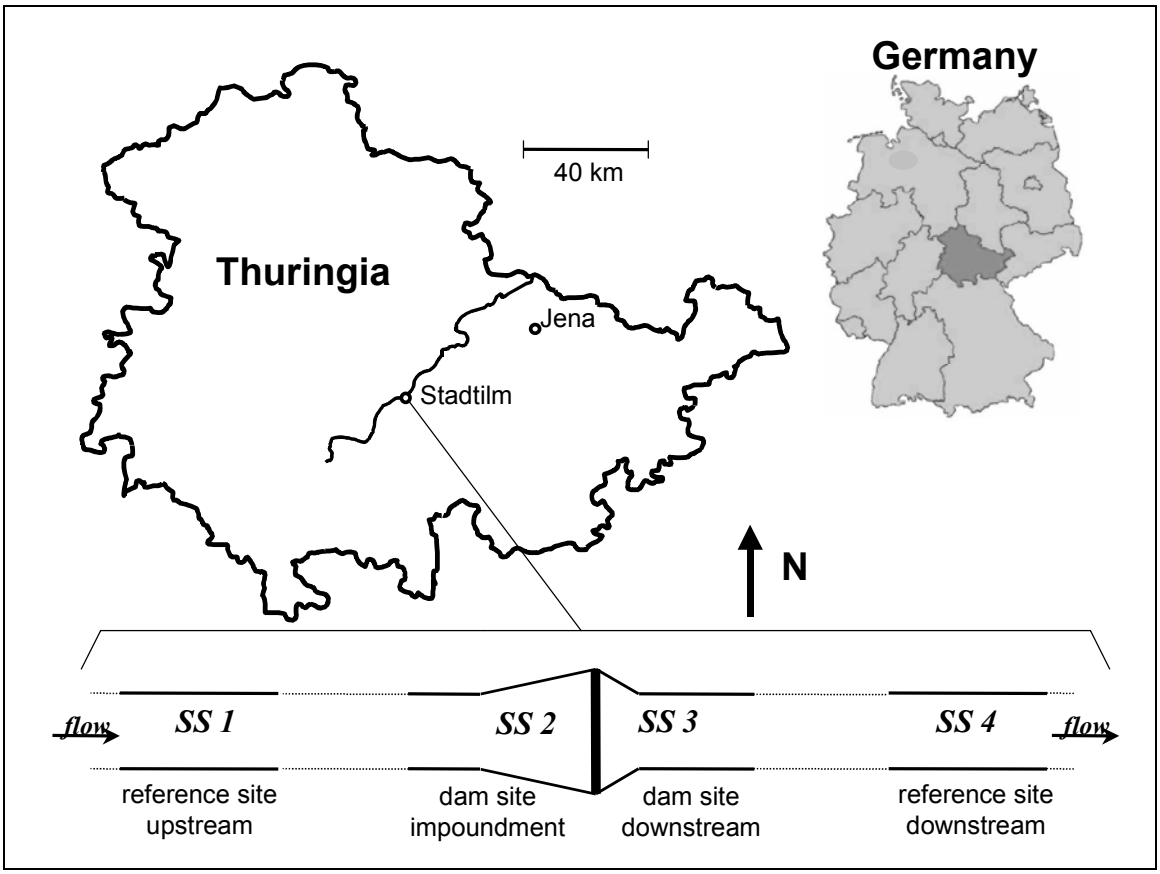

Figure 2.1: Maps of Germany, Thuringia and a schematic view to the study sites (SS1 to SS4, the dam is located within the town Stadtilm, 11°05´ E, 50°46´ N, 360 m a.s.l.).

All the sites consisted of a marked 100 meter reach. Two sites very close to a small 2.10 m high run-off-river dam and two reference sites one ~ 1.65 km downstream and the other ~ 3.28 km upstream of the dam were chosen (Figure 2.2).

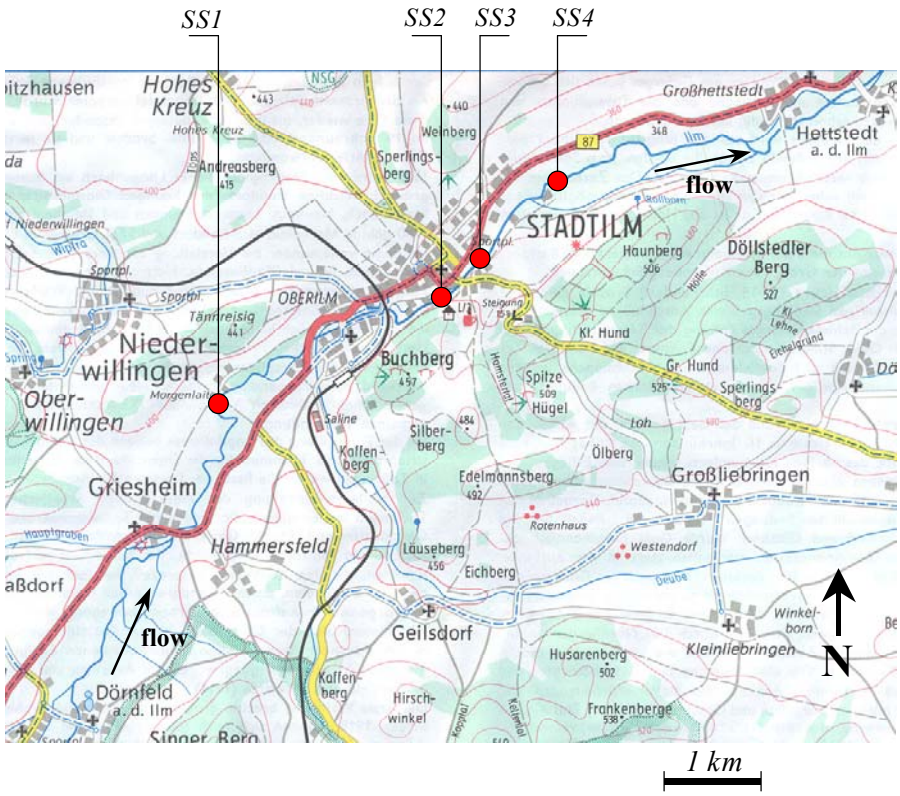

Figure 2.2: Map of the Ilm section, containing the four study sites.

The partly adjustable dam (Figure 2.3) is representative for low–head dams of the Ilm and was built more than 100 years ago. The reaches at the reference sites (upstream of the dam = SS1 & downstream of the dam = SS4) contained a typical pool-riffle sequence. The site (SS3), approximately 100 meter downstream of the dam, formed a continuos riffle. The second dam site (SS2) was 160 m upstream of the dam within the impoundment and is a pool site entirely. At all four sampling sites the vegetation on the banks was dominated by willow (*Salix sp.*), maple (*Acer platanoides* L.), ash (*Fraxinus execlsior* L.), alder (*Alnus glutinosa* L.), and poplar (*Populus tremula* L.). The site upstream of the dam (SS1) and the site close downstream of the dam (SS3) were only sparsely shaded by trees, whereas the impounded site (SS2) and the reference site downstream of the dam (SS4) were heavily shaded. The distance between the upstream and downstream reference site was chosen as small as possible to insure that at mean discharge levels a water column will pass all four sites within one day. The choice of this small spatial scale insures that longitudinal changes in most chemical

factors and hydrology were negligible between the sampling sites. Furthermore, environmental variables such as macroclimate, geology, and other catchment features can be assumed to be similar for the study reaches.

Figure 2.3: A picture of the dam investigated in this study. (View from the site immediately downstream).

Discharge was obtained from the nearest permanent hydrograph station (Gräfinau-Angstedt) located approximately 10 km upstream of the dam. At this station, the averaged annual discharge (long-term mean from 1923 to 2003) approximates 2.44 m^3 s^{-1} (Staatliches Umweltamt Erfurt, unpubl. data). The averaged annual discharge (1971-1989) measured at the investigated dam was 3.30 m^3 s^{-1}. Six small tributaries, occurring between the two locations seem to be responsible for the observed difference. The monthly mean discharges (1923-2003) at the gauge in Gräfinau-Angstedt to the monthly mean discharges at Stadtilm (1971-1989) were used in order to construct a relationship between discharges at the two points on the stream. The relationship was fitted by a regression line:

$$Q_{Stadtilm} = 1.069 \times Q_{Gräfinau\text{-}Angstedt}^{1.1697} ; R^2 = 0.983; P < 0.001; n=12$$

where $Q_{Stadtilm}$ = discharge at Stadtilm and $Q_{Gräfinau\text{-}Angstedt}$ = discharge at Gräfinau-Angstedt in m^3 s^{-1}. This equation was used to estimate the discharge regime in the study region. During the studied period (April 2001–January 2002) no large spates occur (Figure 2.4). The mean discharge during the study period measured at the

permanent gauge Gräfinau-Angstedt was 1.73 m^3 s^{-1} (1 S.D.= 1.38 m^3 s^{-1}) corresponding to a mean discharge of 2.14 m^3 s^{-1} (1 S.D.= 2.05 m^3 s^{-1}) at Stadtilm.

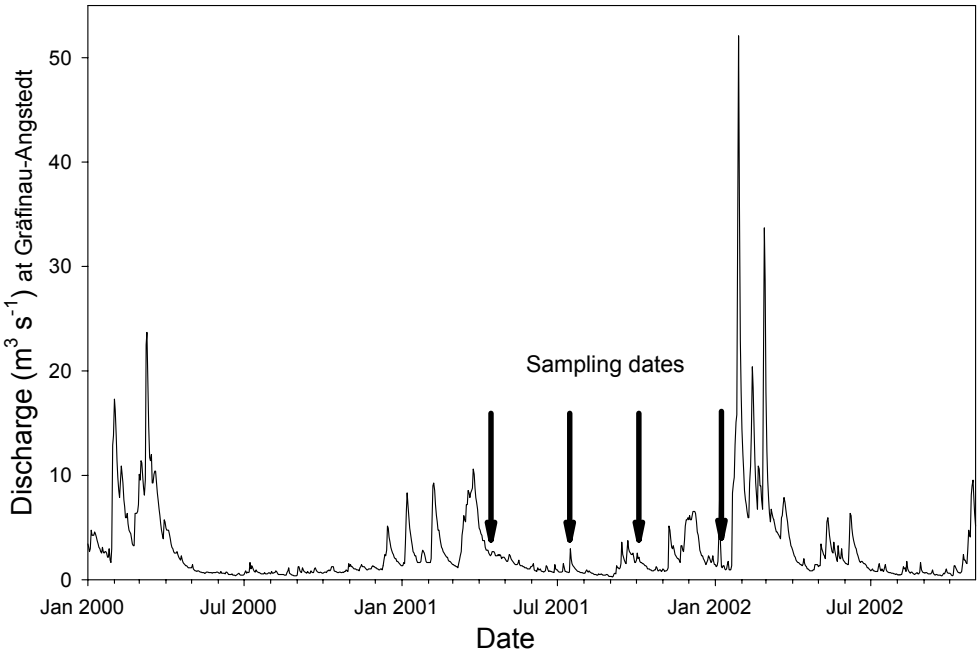

Figure 2.4: Discharge at the permanent gauge Gräfinau-Angstedt 10 km upstream from the study area from 1. January 2000 to 30. October 2002. Data provided by Staatliches Umweltamt Erfurt. Arrows indicate the dates of sampling.

Abiotic parameters of the sampling sites

At first a broad set of environmental variables was measured in order to characterize the stream reaches. These data formed a base upon it was possible to elucidate the effect of the investigated small low-head dam on invertebrate assemblage patterns and particulate organic matter (POM) budgets. During a short period pre biological sampling, the 100 m reaches at the sample sites were measured, marked, delineated, and characterized. A structural quality index (SQ-Index) (after Zumbroich & Müller 1998 and Zumbroich *et al.* 1999) basing on twenty-five visual recorded geomorphological attributes, was used to estimate the anthropogenic impact on the study reaches. The index can range between 1 indicating a natural site, to 7 corresponding to a strong anthropogenically damaged site. The distances between the study reaches and the dam were estimated from aerial photographs. Relative contribution of two macrohabitat types (pool; riffle) was estimated and expressed in percent (%) of the reach. Riparian trees and bushes at the reaches were enumerated and shading of the reaches was estimated visually in August 2001 at 12.00 hour and expressed in percent area. Flow velocity, channel width, water depth, and benthic habitat composition were assessed half way during the study at base-flow conditions in order to estimate the relative difference of these factors among the sample sites. All measurements and estimations were done during one day in order to minimize larger changes in discharge. Flow velocity was measured on 22.6.2001 (discharge at Stadtilm ~0.88 m^3 s^{-1}) using a Flo-Mate 2000 (Marsh-McBirney Inc., USA). In regular steps upstream six measurements were done starting at the downstream end of each 100 m reach. Three points were selected, two points 1 m meter from the left and the right bank each and a third in the center of the stream, while proceeding in upstream direction. Flow velocity was measured at each selected point on the surface and ~ 2 cm above the ground (n= 120). Channel width was measured on 26.6.2001 (discharge at Stadtilm ~0.75 m^3 s^{-1}) in regular steps starting the measurements at the downstream end of the reaches (n=15). Water depth and benthic habitat composition were measured on 27.7.2001 (discharge at Stadtilm ~0.75 m^3 s^{-1}) using comparable design as described for flow velocity but with a smaller sample size (n=45).

Benthic habitat composition was assessed visually using a PVC pipe (15 cm Ø) attached to one end with a transparent plexiglas pane. Estimations were made on squared patches using a metal frame (30 x 30 cm). Fourteen categories were used (boulders > 80cm, large stones 40-80 cm, pebble 20-40 cm, gravel 2-20 cm, inorganic sand 0.2-2 cm, sand & visible organic detritus 0.2-2 cm, inorganic fine sand & silt < 0.2 – 0. 002 cm, fine sand & visible organic detritus < 0.2 – 0. 002 cm, clay & loam < 0.002 cm, stream bed obstruction, dead wood, layers of fine organic detritus, tree roots and

filamentous algae (*Cladophora* sp.). The sediment categories used, followed common particle size classifications (compare Schönborn 1992). An index of habitat diversity was calculated for each sampling unit using Simpson's index of diversity (Simpson 1949):

$$1 - D = \sum_{i=1}^{C} p_i^2 \qquad \textbf{(EQ. 1)}$$

where ***D*** is Simpson's index, $\boldsymbol{p_i}$ is the proportion of each habitat category ***i*** and ***C*** the number of habitat categories (14). This index can range from 0 to ~1. In the case of habitat diversity the maximum value possible is 0.928 defined by:

$$D_{MAX} = (1 - 1/C)$$

This value is reached when all 14 categories occur in the squared sampling patch in equal proportions. The potential minimum is 0, if only one habitat category takes 100% of the sampling patch. ***D*** represents a measure of habitat heterogeneity within small squared patches (30 x 30 cm). The patch size was chosen because it is close to the area sampled during biological sampling. The averaged habitat diversity (n=45) was then compared between the sampling sites. Temperature, dissolved oxygen, conductivity, and pH-value were measured seasonally (April 2001, July 2001, October 2001, & January 2002) during biological sampling [see below; using portable, digital instruments (WTW - Weilheim, Germany)].

Sampling procedures

Benthic invertebrates and POM were sampled using a cylindrical Hess-Sampler (Hess 1941) (area 0.0707 m^2) with a 360 µm net (Figure 2.5). Hess-Sampling is known to be one of the most efficient sampling techniques for most groups of aquatic invertebrates and the method provides a semi-quantitative assessment of the benthic community (Taylor *et al.* 2001). Additionally Hess-Sampling is one of the kick-net methods that are commonly used to estimate POM standing stocks in streams. Seasonal samples were taken on four dates (in the following text the sampling campaigns are denoted as April = 17. April 2001, July = 16. July 2001, October = 2. October 2001, January = 16. January 2002). During each sampling campaign five Hess-Samples were randomly taken from each sample site, with a restriction for the two reference sites (three riffle samples and two pool samples). Sampling position was determined using random number table to select the distance from downstream end of the reach and the distance (only total numbers) from the right bank. All samples were taken within one day between the 8.00 and 18.00 hour, in order to avoid any confounding impact on invertebrate communities patterns over time or in response to changes in discharge. Note that the sampling in October took place pre autumnal fall of leaves. In winter the stream at impounded reach

(SS2) was covered with a 30 cm ice layer, this layer was opened at the randomly selected sampling positions using a large axe and then the sampling was done. The sampling procedure was standardized as far as possible: The sampler was pressed into the sediments, the substrate was disturbed three times (each 10 seconds) to a sediment-depth of 10 cm using a metal bar (length 80 cm, diameter 2 cm), after each disturbance 30 s waiting (together 120 s). The maximum water depth sampled was generally limited by the height of the sampler (0.49 m). Samples were preserved in 75% ethanol, transported to the laboratory, and stored at 10°C in the dark (refrigerator or climate chamber).

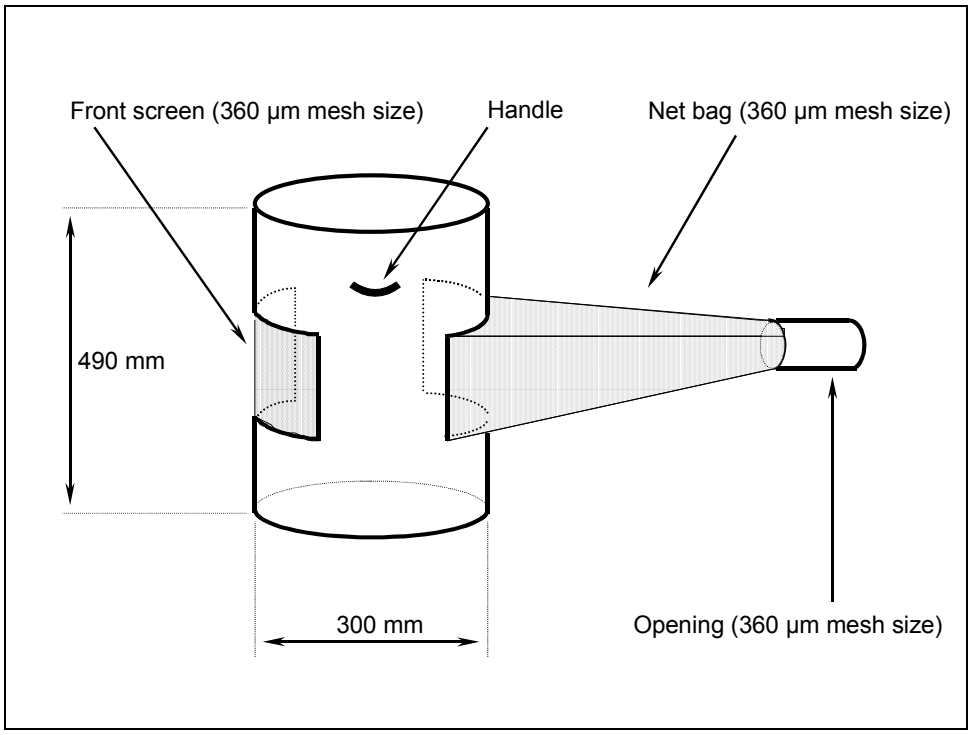

Figure 2.5: Schematic view of the Hess-Sampler used in this study.

Sample processing

In the laboratory the invertebrates were separated from the sediment–detritus-mix using a binocular microscope (Zeiss, Germany). During this separation, ethanol was removed using a 100 µm sieve and afterwards the remaining sediment – detritus-mix was again preserved in 65% ethanol and stored at 10°C in the dark. The invertebrates were counted and identified to the lowest possible taxonomic level. The literature used for identification is listed in 8.2 References - Invertebrate identification keys. In total 95679 invertebrates belonging to more than 80 invertebrate taxa were found in the samples. A summary of the invertebrate taxa found in this study is given in Appendix A (Table A.1). It was not possible to reach a constantly low level of identification for all individuals in

the samples. In particular, Chironomidae, Oligochaeta, but also large proportions of early instars and early life stages of other common groups caused this problem. For further analysis, all organisms were lumped into groups of clearly available taxonomic resolution. However, identifications were taken as far as needed to determine functional feeding group allocation following Schmedtje & Colling (1996). The taxon *Collembolla* sp. was included in further analysis, whereas a small number of aquatic and terrestrial invertebrates with visible indications of decay (death before sampling) were excluded. Disrupted body fragments mainly from Oligochaeta were also sorted out, only heads were enumerated. Invertebrate eggs, eggs clumps and cocoons, that were numerous in the samples, were also counted and identified, when practicable. Invertebrate eggs and cocoons were treated as taxon`s in the further analysis ("Oligochaeta eggs" & "Other eggs"). Furthermore, the dry mass (DM) and the ash free dry mass (AFDM) of all invertebrates of each sample was determined. For this, the invertebrates were sorted into small pre-weighed petri-dishes. Carbonate shells ($CaCo_3$), mainly from the Mollusca (*Ancylus fluviatilis*, Müller) were excluded pre determination of invertebrate dry mass. The material was dried at 80°C for 24 h and weighed. Dry invertebrate material was ground into a powder using a ball mill, sub-sampled, ashed at 600°C for 2 h and AFDM was determined. Invertebrate dry mass (DM) and biomass (based on AFDM) were positively linear related (Linear regression, R^2=0.942). Because of mass losses that occur during leaching ethanol soluble materials the dry mass and ash free dry mass presented here, may underestimate the true natural biomass (see Benke 1996), but they are applicable for comparison between the samples and sample sites in the present study (compare Kelly *et al.* 2003, Sponseller & Benfield 2001). Invertebrate abundance (number of invertebrates and biomass) were expressed as number of individuals per square meter (Inv. m^{-2}) and invertebrate biomass per square meter (mg m^{-2}) and as number of individuals per gram sediment dry mass (Inv. g^{-1}) and invertebrate biomass per gram sediment dry mass (mg g^{-1}). After removing all visible invertebrates the remaining sediment–detritus-mix was further separated in four particle size classes: coarse particulate organic matter (CPOM) >1mm, fine particulate organic matter (FPOM) 0.250 mm – 1mm, 71 µm – 250 µm, and 1.6 µm – 71 µm by wet sieving using an analysis sieving machine (AS 200, Retsch GmbH & Co KG, Haan, Germany). The fractions were dried at 105° C to constant weight, before ashing sub-samples at 600°C for 4 h to determine ash free dry mass (AFDM), to measure the organic content of the samples. The remaining inorganic sediments were used to calculate sediment composition in the samples. Some repeated spot checks (visual observation) showed, that there was no or very little reaction (bubbles) of the dry sediment-detritus mixes with 10% HCL, so that the observed mass losses by ignition were caused by losses in POM.

To estimate organic content of the smallest fraction (1.6 – 71 µm) from the remaining water- detritus – sediment mix after the sieve passages, 100 – 250 ml sub-samples of the continuously stirred mix were filtered using pre-ashed, pre-weighted Whatman GF/A filters. The volume of water- detritus – sediment mix was determined using a measuring jug. The filters were dried at 105°C to constant weight, dry material was ground into a fine powder using a ball mill, sub-sampled, ashed at 600°C for 2 h, and AFDM was determined. AFDM was corrected for small looses contributed by the glass-fiber filters and the organic content was calculated on the basis of the known volumes of filtered sub-sample and the overall volume, that resulted from the sieving procedure. Also smaller organic and inorganic fractions were quantified (see above), because a lot such particles occurred in the samples, these particles could result from blockage of the mesh (360 µm) during sampling, but also by smashing of larger labile organic particles during the sieving procedure. At least it is clear that the used method (Hess-Sampling) underestimates FPOM content in the sediments (compare Wagner 2003), but because of the standardized usage the sampled POM contents are applicable in order to address the objectives of this study. The AFDM of CPOM fraction (> 1mm), of FPOM fraction (<1mm) and of the whole sample (total POM = CPOM+FPOM fractions including of all particle fractions sampled) were used as measures of POM content within the sediments. The data were expressed as (g m^{-2}) and as (mg g^{-1}). CPOM/FPOM ratios were calculated for each sample. Additionally the Simpson's Index of diversity according to **EQ. 1** (see above) was used to estimate the heterogeneity of POM- and sediment particle size fractions in each sample. Here p_i is the proportion of each particle size fraction in relation to the total POM content or to the total sediment dry mass in a sample.

Statistical analyses

Abiotic parameters

All statistical analyses were done using the software package SPSS for Windows 11.0 and Sigma Stat 2.0 (SPSS Cooperation). Normal distribution of the data was checked by conducting Kolmogorov–Smirnov-tests and equivalency of variances using Levene–tests. Log (x+1) transformations were performed when needed to improve normality of the residual distribution and to achieve variance homogeneity before analysis. Median flow velocity, channel width and water depth at the study sites were compared using nonparametric Kruskal-Wallis analysis of variance on ranks. Substrate diversity was compared using parametric one-way analysis of variance (ANOVA). Tukey tests ($P < 0.05$) were used for multiple comparisons.

Invertebrate community variables and particulate organic matter (POM)

Invertebrate abundance (number of individuals & biomass), taxa density (number of taxa per sample), the Simpson's index of diversity (1-D) and expected taxon richness were used as variables to characterize invertebrate communities. In order to avoid the problems combined with measuring species- or taxon richness described by Gotelli & Colwell (2001), Ecosim simulation software (Gotelli & Entsminger 2001) was used to estimate the expected taxon richness for a given number of individuals drawn randomly from a sample as described by McCabe and Gotelli (2000). Ecosim performs a Monte Carlo method similar to rarefaction (Hurlbert 1971, Simberloff 1972). The smallest sample in the collection had only 83 individuals, therefore 83 individuals were randomly sampled from each sample, and the observed number of taxa was recorded, using Ecosim. The randomization was repeated 100 times for each sample and the averaged number of taxa was used as the expected taxon richness.

A two-way analysis of variance (ANOVA) was used to detect differences in POM standing stocks and invertebrate community variables (sampling season and sampling site as factors). Tukey`s test was used for multiple comparisons ($P < 0.05$). The two reference sites were independently treated in the analyses as the differences between them were also of interest. A significant site x season interaction would suggest that observed seasonal changes in the variables occur differentially among the sites. When the interaction terms in the ANOVAs were significant, multiple comparisons were made after one-way ANOVA using Fisher`s protected least significant difference (PLSD) tests. Pre analysis deviations from normality were checked by conducting Kolmogorov–Smirnov-tests and equivalency of variances using Levene–tests. Log (x+1) or double square root transformations were performed, when needed to improve normality of the residual distribution and to achieve variance homogeneity before analysis (Underwood 1997). Additionally invertebrate community variables were compared according to macrohabitat type. Samples from natural pools (SS1 & SS4; n=4) were compared to the dam pool samples (SS2; n=5) and samples from natural riffles (SS1 & SS4; n=6) were compared to the dam riffle (SS3; n=5), in both kinds separately for each season. Non-parametric Mann-Whitney U-tests ($P < 0.05$) was used for comparison among the medians, because of the unbalanced data set. Spearman rank order correlation's were used to reveal relationships of invertebrate data with POM variables and with sediment diversity separately for each season ($P < 0.05$). Ordination statistics were calculated with the program Canoco Version 4 (ter Braak & Smilauer 1998). In order to estimate the relative importance of environmental variables in influencing invertebrate community composition multivariate Redundancy Analysis (RDA) and Monte Carlo permutation procedures (Jongman *et al.* 1995) were used.

RDA as a linear ordination technique examines the variations in community composition by constraining the ordination axes as linear combinations of environmental variables. This technique allows to identify how much of the variability of invertebrate community composition was explained by particular environmental variables. A preliminary analysis (Detrended Correspondence Analysis - DCA) showed that variation in invertebrate community (abundance) data was best described by linear rather than by unimodal models (lengths of gradients was 2.14). Only invertebrate abundance data expressed per square meter (Inv. m^{-2}) were used in this analysis. For each sample the content of organic matter (total POM, CPOM, FPOM expressed as (g m^{-2}), the amount of sampled sediment (g), the CPOM/FPOM ratio, the Simpson's diversity index for POM and sediment based on their particle size distributions were used as environmental variables. Additionally the annual average values of POM standing stocks at the sample sites [total POM in (g m^{-2})], the distance from the dam (m), the structural quality index (SQ-index), the mean flow velocity (m s^{-1}) during base flow conditions, the mean benthic habitat diversity and the photoperiod (h) were used. Furthermore several variables were used to describe the discharge regime: the discharge during sampling, the mean, maximum and minimum discharge prior 30 days to sampling and the range of discharge prior 30 days to sampling. All environmental variables were standardized to zero mean and unit variance using Sigma Stat 2.03 (SPSS Co.) to remove the influence of differing scales of measurement. The invertebrate abundance data were square root transformed prior analysis. To extract a reduced variable set, co-variable environmental factors were removed if the inflation factor was greater than 20. The remaining variables were: total POM (g m^{-2}) and sediment dry mass (g) in each sample, the CPOM/FPOM ratio, the Simpson's diversity for POM, the Simpson's diversity for sediment, the distance from the dam, the SQ-index, the photoperiod and the mean discharge prior 30 days to sampling. After this a stepwise forward selection with Monte Carlo permutations (199) were done to test for significance of environmental variables and to select variables that explained most of the variability in invertebrate community composition. Monte Carlo permutations were also used to test the significance of the ordination axes.

The design of the present study took advantage of a single small low head dam on a single river. Therefore, all interpretations are limited to the investigated dam. The used design, specially the presence of more than one reference site, follows in some aspects an Beyond BACI design (Before/After and Control/Impact –Paired design) for monitoring and experimental studies (Underwood 1991, 1994 a, 1994 b). The BACI and related designs all assume that the impact study will start before the impact occurs. For the investigated dam, there are no true `before` data on invertebrate communities and

POM standing stocks available. However, in order to detect an environmental impact, the presence of two reference sites, one upstream and one downstream of the dam and both in relative close spatial relation may allow inference about the effects of the dam. The seasonal repeated measurement may also increase the probability to detect an eventual impact. The `natural reference` sites used in this study were selected according to structural attributes of the stream channel and provide a baseline of spatial and temporal variation in invertebrate community variables and POM standing stocks. A lack of differences in the investigated biotic variables among these two sites would indicate a low spatial extension of the dam impact (if present) as well as the absence of cumulative (negative) effects.

2.3 Results

2.3.1 Abiotic parameters

Table 2.1 summarizes the values of the abiotic parameters. During base-flow conditions, channel width was higher at the impounded site (SS2) and immediately downstream of the dam (SS3) in comparison to the natural references [H=49.2, 3 d.f., P < 0.001, Tukey Test: (SS2 = SS3) > (SS1 = SS4)]. Water depth was highest at the SS2 and lowest at the SS3 (H=35.0, 3 d.f., P < 0.001, Tukey Test: SS2 > SS1; SS4 > SS3). Flow velocity was significantly reduced within the impoundment [H=93.4, 3 d.f., P < 0.001, Tukey Test: (SS1= SS3 = SS4) > SS2]. Substrate diversity was lowest within the impoundment [$F_{3,176}$= 9.51, P < 0.001, Tukey Test: (SS1 = SS3 = SS4) > SS2]. There the substrate was very homogeneously structured, dominated by fine sand / silt (47%) and coarse sand (30%), both with large amounts of visible organic detritus, whereas all other sites were dominated by coarse sediments (Table 2.1). Riparian vegetation and maximum shaded area differed among the reaches. Physical and chemical conditions of the water were variable during the study period. Due to mere spot measuring and possible diurnal changes of these factors which, however, were not investigated, only the observed ranges are given in Table 2.1.

Table 2.1: Environmental characteristics of the study sites.

Parameter	Sample site			
	Reference upstream **SS1**	Dam site Impoundment **SS2**	Dam site downstream **SS3**	Reference downstream **SS4**
Structural quality index	1.7	6.4	4.7	1.5
Distance from dam (m)				
Stream line	~3280	~160	~100	~1650
Linear distance	~2900	-	-	~1400
Macro-Habitat type (%)				
Pool	~30	100	-	~30
Riffle	~70	-	100	~70
Channel width* (m) n=15	7.49 ± 1.43	15.13 ± 0.26	10.89 ± 1.09	8.00 ± 1.34
Water depth* (cm) n=45	33.5 ± 18.8	39.9 ± 14.3	22.0 ± 8.8	32.5 ± 18.4
Flow velocity* (m s^{-1})				
Surface; n=60	0.39 ± 0.27	0.11 ± 0.05	0.42 ± 0.24	0.41 ± 0.35
Ground; n=60	0.20 ± 0.22	0.07 ± 0.04	0.26 ± 0.21	0.18 ± 0.27
Total; n=120	0.29 ± 0.26	0.09 ± 0.05	0.34 ± 0.24	0.29 ± 0.33
Habitat composition (%)				
boulders	5.00	1.89	-	9.78
large stones	32.20	7.11	3.56	9.33
pebble	22.76	0.89	54.0	37.67
gravel	11.81	0	22.0	7.78
sand (inorganic)	11.33	0.89	9.11	20.67
sand (+organic detritus)	-	29.78	-	-
fine sand / silt (inorganic)	-	-	-	-
fine sand / silt (+organic detritus)	2.22	47.33	6.67	9.89
clay & loam	-	3.56	-	-
stream bed obstruction	-	5.67	3.11	-
dead wood	-	2.89	0.22	4.56
layers of fine organic detritus	4.22	-	1.22	0.33
tree roots	-	-	-	-
filamentous algae	9.89	-	0.11	-
Simpson's Habitat Diversity* n=45	0.43 ± 0.19	0.24 ± 0.21	0.39 ± 0.17	0.41 ± 0.21
Maximum shaded area (%)	~20	~80	~25	~80
Vegetation composition (%)				
Alnus glutinosa	22.8	8.9	14.2	-
Fraxinus execlsior	45.6	15.6	28.6	7.7
Acer platanoides	-	55.6	-	15.4
Salix sp.	22.8	11.1	50.0	51.9
Populus tremula	7.0	6.7	-	25.0
Corylus sp.	1.7	2.2	7.1	-
Physical and chemical conditions				
Temperature ‡ (°C)	-0.3 – 16.0	-0.2 – 16.4	-0.3 – 16.2	-0.3 – 15.8
Conductivity ‡ (µS m^{-1})	240 – 458	276 – 475	275 – 473	285 – 480
Oxygen ‡ (%)	91 – 106	88 – 99	92 – 105	89 – 98
pH ‡	7.72 – 8.10	7.76 – 8.20	7.54 – 8.16	7.73 – 8.20

SS1 = natural reference upstream, SS2 = dam site (impoundment), SS3 = dam site immediately downstream of the dam, SS4 = natural reference downstream, (* Mean ± 1 S.D.; ‡ Ranges are shown)

2.3.2 Spatial and seasonal variability of invertebrate communities

The two-way ANOVA results for invertebrate density and further community variables described below are summarized in Appendix A (Table A.2). In the two-way ANOVA`s, significant interaction between sampling site and date was observed for invertebrate density (Inv. m^{-2} and Inv. g^{-1}), for invertebrate biomass in (mg g^{-1}) and for the measures of diversity (Simpson's index of diversity, expected taxon richness and number of taxa), indicating site specific seasonal changes for these variables. No significant interaction between sampling site and date was found for invertebrate biomass in (g m^{-2}) and the number of invertebrate eggs (No. of eggs m^{-2}). Invertebrate density ranged from 1174 Inv. m^{-2} to 47770 Inv. m^{-2} and 0.22 Inv. g^{-1} to 283 Inv. g^{-1}, respectively. Invertebrate density (Inv. m^{-2}) differed significantly among the sixteen groups (four sites x four dates, One way ANOVA, $F_{15,79} = 13.31$, $P < 0.001$) and multiple comparisons (Fisher`s PLSD test) showed that the density was higher at the two dam sites in comparison to both reference sites upstream and downstream of the dam, in April and July (Figure 2.6). A different pattern was found in October [Fisher`s PLSD test, SS2 > (SS1 = SS3 = SS4)] and January [Fisher`s PLSD test, SS3 > (SS1 = SS2 = SS4)]. On the basis of the annual averages, the number of invertebrates was approximately twofold higher at the dam sites (26351 Inv. m^{-2} at SS2; 22220 Inv. m^{-2} at SS3) in comparison to both natural reference sites (9312 Inv. m^{-2} at SS1; 9805 Inv. m^{-2} at SS4). Invertebrate density expressed as (Inv. g^{-1}) showed a similar pattern as described for (Inv. m^{-2}) and although sampling date had no significant effect in the two-way ANOVA (Appendix A, Table A.2), a significant interaction between sampling site and date suggests that seasonal variation in patterns of this abundance measure differed significantly among the sampling sites. Invertebrate biomass in (g m^{-2}) was higher immediately downstream of the dam (SS3) in comparison to the impounded site and to both reference sites (Figure 2.6; see also Appendix A, Table A.2). Two-way ANOVA indicate higher invertebrate biomass in (g m^{-2}) in April and July in comparison to October and January. Summarized across the year the invertebrate biomass (AFDM) was nearly twofold higher at SS3 (3.39 g m^{-2}) in comparison to the impoundment (1.83 g m^{-2}) and to the natural reference sites (1.63 g m^{-2} at SS1; 1.97 g m^{-2} at SS4). Invertebrate biomass expressed as (mg g^{-1}) differed significantly among the sixteen groups (four sites x four dates, One way ANOVA, $F_{15,79} = 4.29$, $P < 0.001$). Multiple comparisons (Fisher`s PLSD test) indicate no difference in invertebrate biomass (mg g^{-1}) among the two reference sites and the biomass at both dam sites was in some cases higher or similar, but in no case lower than observed at the reference sites (Figure 2.6). Invertebrates (numbers and biomass) seemed spatially more homogeneously distributed at the impounded site, as indicated by lower standard deviation in relation to seasonal mean (coefficient of variation).

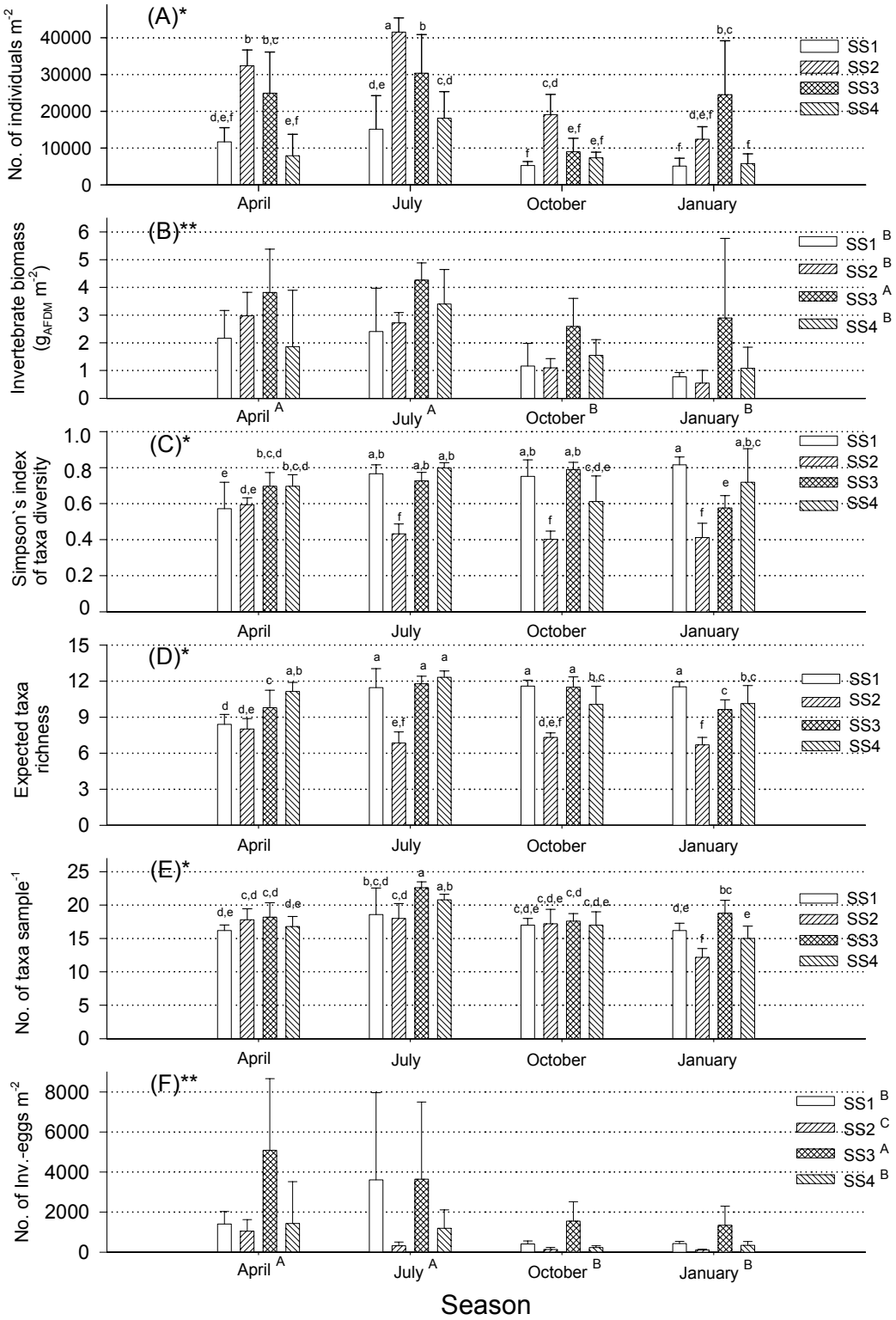

Figure 2.6: Means (± 1 S.D.) for invertebrate density (A), biomass (B), Simpson's index of diversity (C), expected taxon richness (D), number of taxa (E) and number of invertebrate eggs (F) during four seasons at the four sampling sites. *, site x season interaction was significant (one-way ANOVA and Fisher`s LSD multiple comparisons were conducted among sixteen groups; there is no significant difference between bars with the same small letter); **, site x season interaction was not significant (Tukey`s multiple comparison was conducted among sites and seasons; different capital letters indicate significant difference).

The results of the one way ANOVAs indicate a significant difference for all three diversity measures among the sixteen groups (four sites x four dates): Simpson's Index of diversity ($F_{15,79}$ = 12.79, P < 0.001), expected taxon richness ($F_{15,79}$ = 19.01, P < 0.001) and number of taxa ($F_{15,79}$ = 7.65, P < 0.001). Multiple comparisons (Fisher`s PLSD test) showed that the Simpson's Index of diversity and expected taxon richness were significantly lower at the impounded site in comparison to the SS3 and to both reference sites in July, October and January. A lower number of invertebrate taxa at the impounded site was only found in January (Figure 2.6). At the site immediately downstream of the dam (SS3) all diversity measures indicated similar conditions as observed at the natural reference sites. Only in one case (January) the Simpson's index of diversity was lower at the SS3 in comparison to the natural reference sites. The number of invertebrate eggs and cocoons ranged from 28 eggs m^{-2} to 11008 eggs m^{-2} was highest at the SS3 and the SS2 showed the lowest numbers (Tab. 4.2, Figure 2.6).

2.3.3 Functional feeding group structure and community composition

The functional feeding group structure (Figure 2.7) at the impounded site differed remarkably from all other sites investigated. More than 88% of all invertebrates belonged to the detritivorous collector - gatherer group (feeding on deposited FPOM). As observed for invertebrate abundance and diversity, the functional feeding group structure was highly comparable between the two reference reaches.

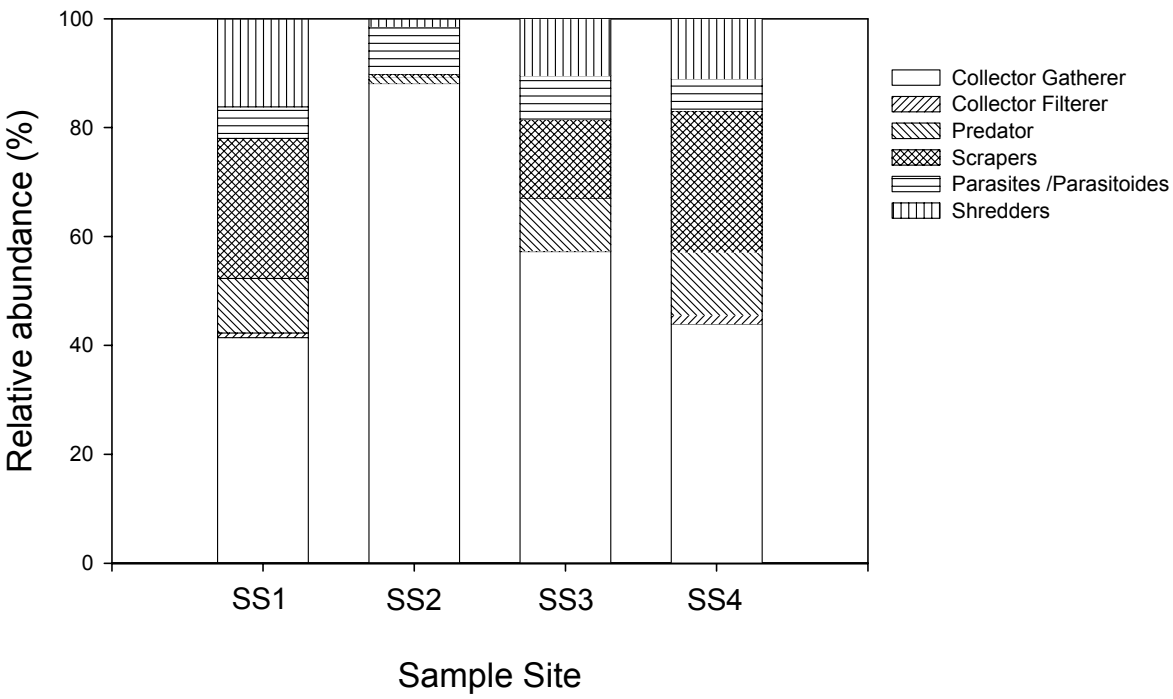

Figure 2.7: Relative abundance of functional feeding groups based on the averaged abundance from all samples.

Generally, the Chironomidae and Oligochaeta (adults & eggs) dominated the invertebrate communities representing 44.6% and 28.4% of all invertebrates.
Chironomidae (dominated by Chironominae) reached 62.4 % relative abundance within the impoundment, followed by Oligochaeta (23.9%), Ostracoda (3.96%), Nematoda (3.64%), Mites (1.83%) and Crustacea (Copepoda & Phyllopoda) (1.17%). At the downstream dam riffle (SS3) the invertebrate communities were much more heterogeneously composed: Oligochaeta (adults & eggs) were dominant 41.3 % followed by Chironomidae (37.9%), *Ancylus fluvaitilis* Müller. (3.2%), Trichoptera (3.2%), Ephemeroptera (2.6%), other invertebrate eggs (2.2%), Hirudinea (1.8%), Nematoda (1.7%), other Diptera (1.2%) and Mites (1.0%). The invertebrate communities at the natural references upstream and downstream of the dam (SS1; SS4) showed the greatest similarities and retained invertebrate communities with high proportions of typical lotic fauna elements, as also observed for the SS3. Here Oligochaeta (adults & eggs) were dominant (55.7%; 47.1 %) followed by Chironomidae (dominant were Orthocladiinae) (15.2%; 21.4%), Ephemeroptera (7.1%; 4.8%), Mollusca (*Ancylus fluviatilis*) (2.4%, 7.4%), *Gammarus pulex* (4.7%, 2.9%), other Diptera (3.2%; 4.1%), other eggs (3.3%, 1.7%), Trichoptera (1.9%, 2.3%), Crustacea (Copepoda & Phyllopoda) (2.0%, 0.8%) and Nematoda (1.1%; 1.6%)

2.3.4 Pool-Riffle comparison for invertebrate community variables

During all seasons the “dam pool” (SS2) showed significantly higher invertebrate density (Mann-Whitney U-test, $P < 0.05$), comparable invertebrate biomass and with exception in April lower taxa diversity (Mann-Whitney U-test, $P < 0.05$) in comparison to natural pools (Appendix A, Figure A.1). The riffle immediately downstream of the dam showed higher invertebrate density in April, July and January (Mann-Whitney U-test, $P < 0.05$), higher invertebrate biomass and egg - density in October and January (Mann-Whitney U-test, $P < 0.05$), but no differences for diversity measures in comparison to natural riffles. There were also significant differences for the number of taxa (Appendix A, Figure A.1).

2.3.5 Spatial and seasonal variability of particulate organic matter (POM)

Total POM standing stocks were highly variable within and among sites and seasons ranging from 7.1 g m^{-2} to 424.7 g m^{-2}. The results of the two-way ANOVAs for POM standing stocks described below are summarized in Appendix A (Table A.3). In the two-way ANOVA`s, significant interaction between sampling site and date was observed for total POM, CPOM and FPOM standing stocks expressed as (g m^{-2}) and for the CPOM/FPOM ratio (Appendix A, Table A.3), but not for POM standing stocks expressed as (mg g^{-1}).

One way ANOVAs showed significant differences in the POM (g m^{-2}) among the sixteen groups (four sites x four dates; Figure 2.8; One way ANOVA, for total POM standing stocks: $F_{15,79} = 5.58$, $P < 0.001$; for CPOM standing stocks: $F_{15,79} = 3.75$, $P < 0.001$; for FPOM standing stocks: $F_{15,79} = 14.42$, $P < 0.001$). Multiple comparisons (Fisher`s PLSD test) showed that the total POM standing stock (g m^{-2}) in the impoundment was only in January significantly higher in comparison to the natural reference sites. The CPOM (g m^{-2}) contributed the majority to the total POM standing stock and showed therefore a similar pattern (Figure 2.8). For the FPOM significant differences existed between the impoundment and the natural reference sites in July and January, but not in April and October.

When POM standing stocks were expressed as mg per sediment dry mass in the sample, two-way ANOVAs showed no significant interaction term between sampling site and date. The impounded reach (SS2) showed a higher organic matter standing stock (total POM, CPOM & FPOM) in comparison to the reaches at the reference sites (SS1 & SS4) (Figure 2.8). At the reach immediately downstream of the dam the POM standing stock differed not significantly from those observed at the reference sites. In January, the highest amount of particulate organic matter was found. On the basis of the annual averages the total POM standing stock within the impoundment (120 g m^{-2} ; 193 mg g^{-1}) was higher than at the SS3 (83 g m^{-2}; 98 mg g^{-1}) and nearly twice as high as observed for the natural reference sites (58 g m^{-2}; 70 mg g $^{-1}$ at SS1 & 64 g m^{-2}; 68 mg g $^{-1}$ at SS4). The amounts of CPOM were typically greater than the amounts of FPOM (FPOM was under-sampled with the 360 µm net) and CPOM/FPOM ratio between ranged between 0.18 – 28.82 (overall mean = 2.91, n=80). Although the two-way ANOVA indicated no significant differences among sampling sites and dates, the interaction term was significant (Tab. 4.6). Subsequent one way ANOVA also showed a significant difference among the sixteen groups (square root transformed data, $F_{15,79} = 2.06$, $P < 0.001$), but the power of this test (α=0.05: 0.61) was below the desired power of 0.80.

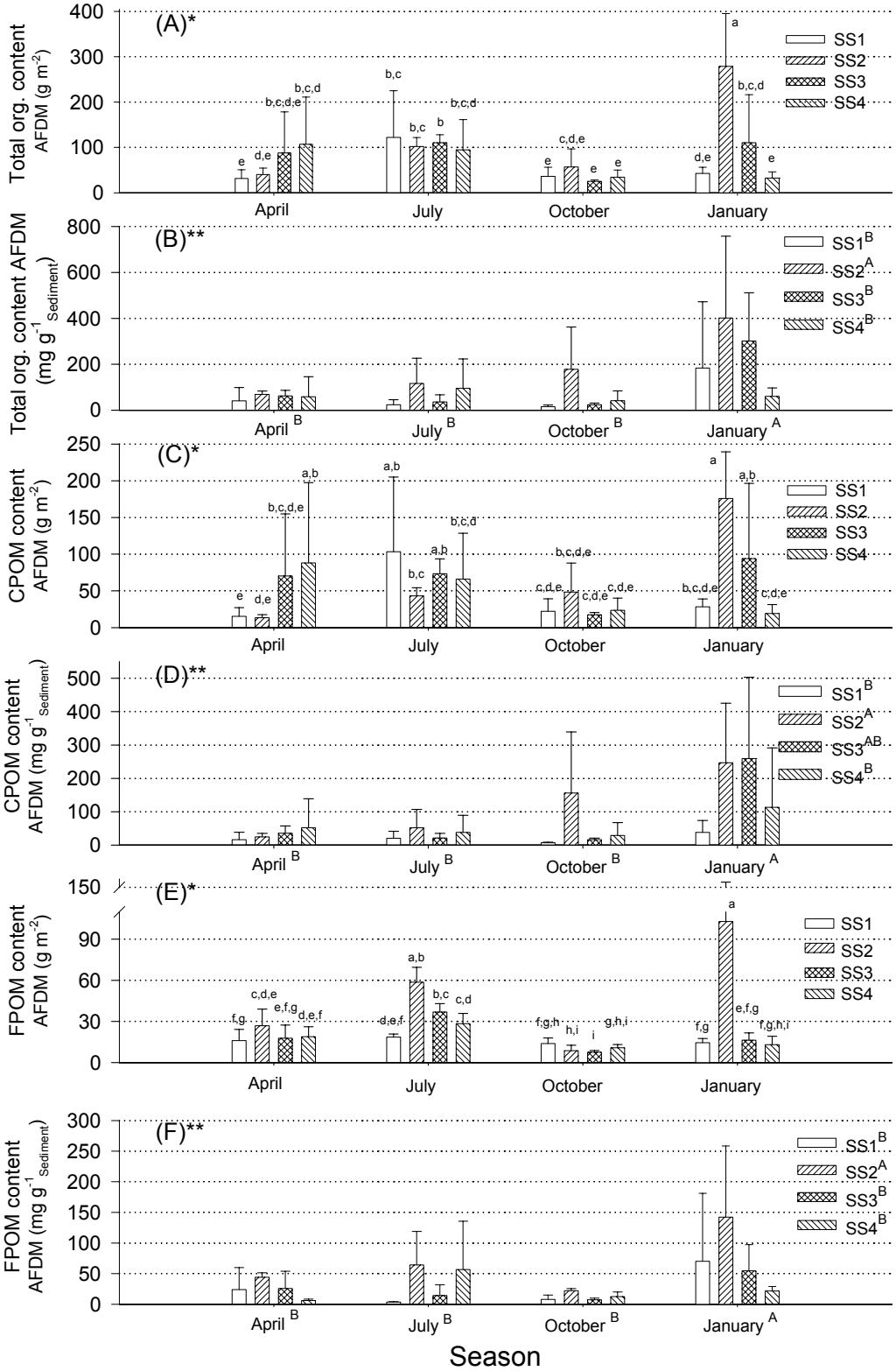

Figure 2.8: Means (±1 S.D.) for total POM - (A, B), CPOM - (C, D) and FPOM - standing stocks (E, F) expressed as (g m^{-2}) and (mg g^{-1}) during four seasons at the four sampling sites. *, site x season interaction was significant (one-way ANOVA and Fisher`s LSD multiple comparisons were conducted among sixteen groups; there is no significant difference between bars with the same small letter); **, site x season interaction was not significant (Tukey`s multiple comparison was conducted among sites and seasons; different capital letters indicate significant difference).

2.3.6 Relationship between invertebrate community variables and POM

The correlation's between POM variables and invertebrate abundance (density and biomass) referred to the area sampled and expressed as (g m^{-2}) were, in most cases, low and often not significant (Appendix A, Table A.4). In contrast, when the data were expressed as (mg g^{-1}) the correlation's were highly significant. The importance of several POM variables differed also among the seasons. During all the seasons, the FPOM standing stocks (mg g^{-1}) and the total POM standing stocks (mg g^{-1}) showed the highest correlation's to invertebrate abundance (density and biomass). Taxa diversity (Simpson's index and expected taxon richness) was in most cases negatively correlated to POM.

2.3.7 Influence of environmental factors on invertebrate community composition

In the ordination the first two axes explain 52% of the variability in community composition and the 1st axis contributed the majority (37%). Monte Carlo permutations tests showed that the ordination axes of the RDA were significant (Appendix A, Table A.5). The relationship between invertebrate community data and explaining environmental variables account for 89.9% (axis 1 and 2) indicating a strong correlation between the scores of environmental variables and invertebrate community data. The inflation factor, as an indicator for multi-colinearity (value >20) for all remaining variables was below 10.

The SQ-Index was the variable that explained the greatest percentage of variability (30 %) in the invertebrate community composition and was the environmental variable that showed the highest correlation (0.775) to the first canonical factor (Appendix A, Table A.5). The photoperiod as a measure of season explained 13% of the variability and this variable was highest correlated (-0.565) to the second canonical factor. All the remaining variables used explained less than 8% of the variability. After stepwise forward selection, only 4 variables had a significant effect on the community composition (Appendix A, Table A.6) and structural quality index (SQ-index) was by far the most important one. The above described relationships are visualized in a triplot (Figure 2.9). The relative influence of the environmental variables on invertebrate community composition is shown by arrows in the plot and the orientation of an arrow represents the direction of maximum change of a variable in the diagram. The length of an arrow is proportional to the rate of change and variables with long arrows are stronger correlated with the ordination axes than those with shorter arrows. The RDA showed that structural differences characterized by the SQ–index and seasonal changes explained most of the variability in the invertebrate community composition observed.

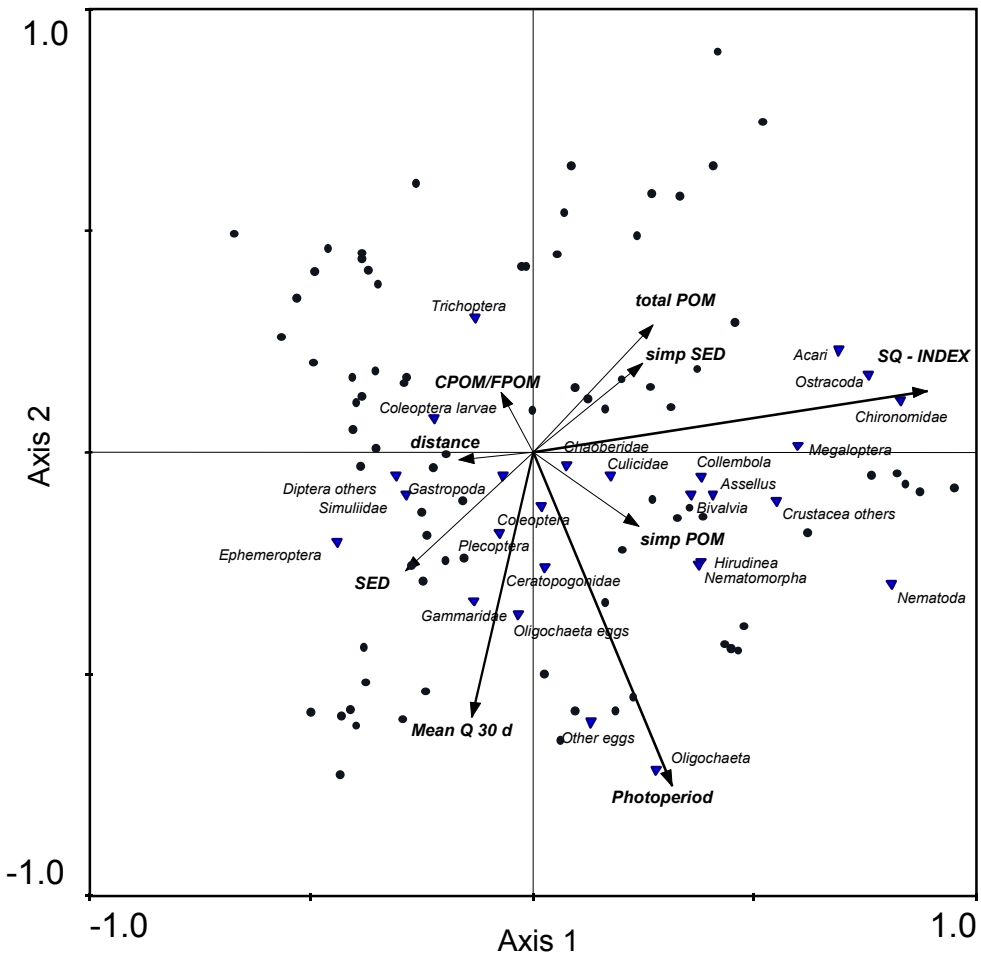

Figure 2.9: RDA triplot, showing the samples (circles), the benthic invertebrate taxa (down-triangles) and the environmental variables (arrows). Arrows refer to the direction and the relative importance of environmental variables. SQ-index, structural quality index; Photoperiod (h); Mean Q 30 d, mean discharge within 30 days prior sampling; SED, amount of particulate inorganic matter in the sample, simp POM, Simpson`s Diversity index for POM size fractions; distance, distance of the sampling reach to the dam; CPOM/FPOM, CPOM/FPOM ratio in the sample; simp SED, Simpson's Diversity index for particulate inorganic matter size fractions; total POM, POM in (g m^{-2}).

The classification of the samples according to the sample sites (Figure 2.10 A) showed a separation of sampling sites along the axis 1. Reference sites showed a high overlap indicating a comparable invertebrate community composition, whereas the impounded reach and the riffle downstream of the dam were separated away. A classification of the samples according to sampling season (Figure 2.10 B) showed a separation of all sampling seasons along axis 2, with only little overlap between the seasons. A third classification of the samples according to pool – riffle sequence (Figure 2.10 C) showed that the riffle section close downstream of the dam differed in community composition in comparison to riffles at reference sites. The community composition within the dam - pool (SS2) differed also from that of pools at reference sites. In both cases, no overlap was found.

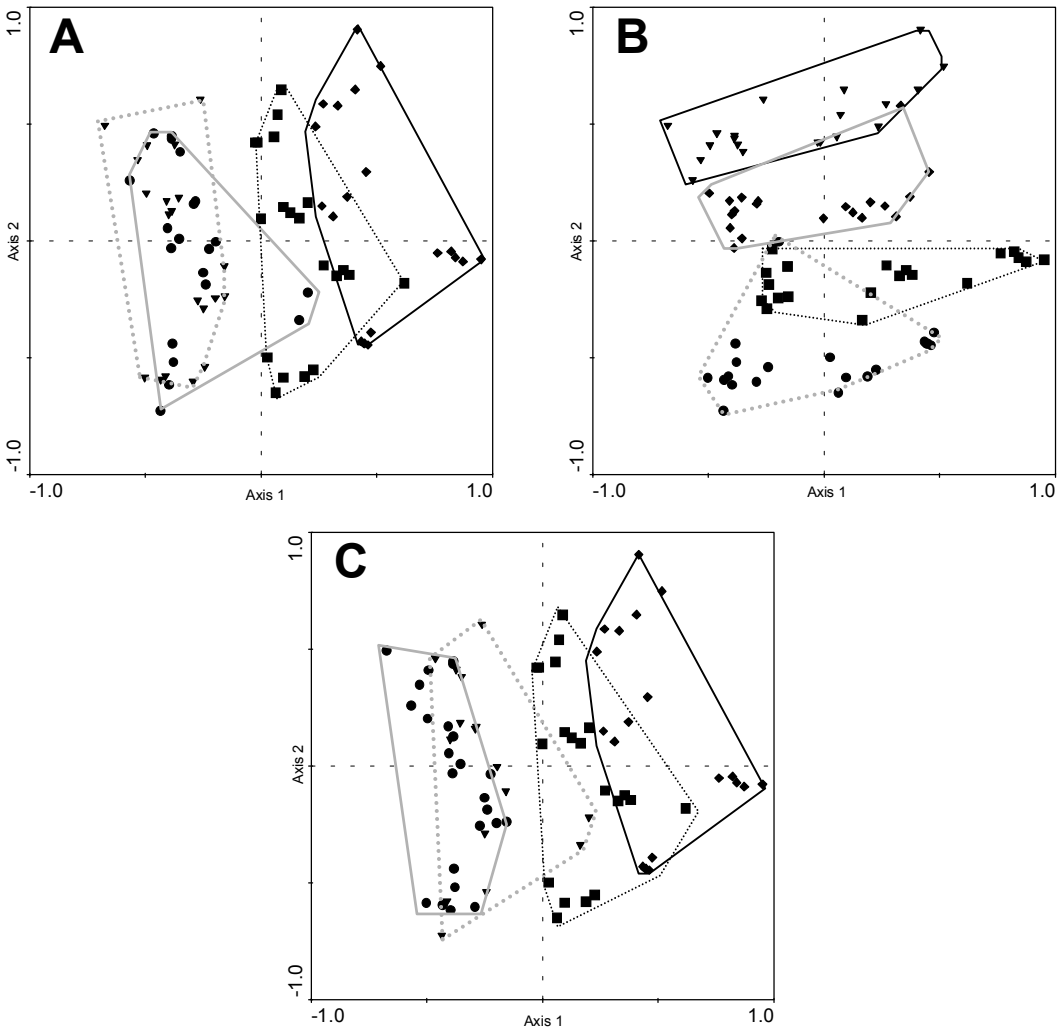

Figure 2.10: RDA plots after classification of the samples according to sample site (plot A), to sampling season (plot B) and to macrohabitat type (pool / riffle) (plot C). In plot A, the samples are shown as down-triangles (SS1), diamonds (SS2), squares (SS3) and circles (SS4). All samples of a sample site are enveloped by lines. In plot B, the samples are shown as circles (April), squares (July), diamonds (October), and down-triangles (January). All samples of a sampling season are enveloped by lines. In plot C, the samples are shown as circles (reference riffles), squares (riffle downstream of the dam = SS3), diamonds (impounded site = SS2) and down-triangles (reference pools). All samples of a specific macrohabitat type are enveloped by lines.

2.4 Discussion

Abiotic parameters

The distribution of aquatic invertebrates in streams is governed by a large number of environmental factors that typically act at different scales (Power *et al*. 1988, Malmqvist 2002), therefore a broad set of environmental factors was measured. At the reaches close to the investigated low-head dam, some environmental factors differed remarkably from those at natural references upstream and downstream of the dam. In contrast to the nearly unaltered reference sites, the structural quality index (SQ-index) indicated an anthropogenically damaged channel structure for both dam sites. The impoundment was deeper, broader and had reduced flow velocity. These factors seemed most responsible for the monotonous substrate composition dominated by fine inorganic and organic sediments. The size distinguished the impoundment clearly from naturally occurring pools in the Ilm. At the (SS3) small water depth combined with high flow velocities resulted in stronger turbulence. The natural references were highly comparable in terms of mean channel width, water depth and flow velocity, but these factors were also more variable in comparison to the dam reaches as indicated by higher coefficients of variation (standard deviation / mean). A higher variability of these factors may also be responsible for higher habitat diversity at the reference sites in comparison to the impounded site (SS2). Note that, because of the existing differences in shading, the reference sites were chosen according to this pattern, because shading influences periphyton-growth that is known to affect invertebrate community composition and diversity (Ellsworth 2000, Zimmermann & Death 2002). Physical and chemical attributes of the water at the dam were within the same ranges as observed at the reference sites. Stanley *et al.* (2002) and Baekken *et al.* (1981 a & b) also reported no remarkable changes of physical and chemical attributes at low-head dams. The absence of differences in physical and chemical attributes of the water among the sampling sites indicates that the investigated dam does not largely influence these factors. However, the measurements done were only spot checks and it is at least possible that temporary differences in physical and chemical attributes of the water occur. Especially during summer periods with minimal discharges, thermal stratification's and depressions in dissolved oxygen may occur within the impoundment, although a downstream extension of such alterations seems not likely.

The dam created distinct physical conditions at reaches close to the dam relative to free-flowing natural reaches, but the dam seemed not substantially alter the overall discharge regime and water quality factors, a result that is in agreement with other studies (Hart *et al.* 2002, Stanley *et al.* 2002). Whereas large flood control and

hydropower dams can dramatically alter discharge regimes and water quality in downstream sections of a river (Ward & Stanford 1983, Petts 1984), small low head dams seem to act more locally.

Invertebrate communities and particulate organic matter

Enhanced invertebrate abundance was found at the investigated dam. According with the initial hypothesis both reference sites showed lower invertebrate density (annual average values for Inv. m^{-2} and Inv. g^{-1}) in comparison to the dam sites, but in contrast to the assumption there was no difference between the two dam sites, leading to the following pattern: (Impoundment = DR_{down}) > (NR_{down} = NR_{up}).

Total invertebrate biomass (annual average values for g m^{-2} and mg g^{-1}) was highest immediately downstream of the dam and the impoundment differed at least not significantly from the natural references. The initial assumption must be partly rejected, because the following pattern was found: DR_{down} > (NR_{down} = Impoundment = NR_{up}) for g m^{-2} & DR_{down} > (NR_{down} = NR_{up}); Impoundment > NR_{down} for mg g^{-1}. Nevertheless noticeable deviations from the above patterns occurred seasonally. Extrapolating the annual averages of invertebrate abundance to the entire 100 m reaches result in much larger differences between the dam sites (SS3: ~24.2×10^6 Inv. ; ~3.69 kg Inv. biomass; SS2: ~39.9×10^6 Inv. ; ~2.77 kg Inv. biomass) and the natural references (SS4: ~7.84×10^6 Inv. ; ~1.58 kg Inv. biomass; SS1: ~6.97×10^6 Inv. ; ~1.22 kg Inv. biomass), because both dam sites were broader. Enhanced invertebrate abundance is commonly found at large storage dams (for review see Ward & Stanford 1979, Schönborn 1992).

Although there was a similarity in the type of the impact, the magnitude and the spatial extension (downstream) of the impact caused by the investigated small dam seems to be by far lower and therefore not comparable to the impact caused by large storage dams.

Taxa diversity (Expected taxon richness & Simpson's index of diversity) was lower at the impounded reach, but not immediately downstream of the dam. The initial assumption must be partly rejected and the following pattern can be described:

Impoundment < (NR_{down} = DR_{down} = NR_{up}) (annual average values for both measures).

For taxon richness (number of taxa per sample; annual average values) the following pattern was found: DR_{down} > (NR_{down} = NR_{up}) > Impoundment.

Reduced invertebrate diversity is often found at large storage dams (for review see Ward & Stanford 1979, Ward & Stanford 1983, Schönborn 1992, Marchant & Hehir 2002). Although invertebrate diversity was reduced within the impoundment of the investigated small dam, it was not depressed immediately downstream of the dam, as it was commonly described for large storage dams. Three different measures of taxa

diversity were used in this study. The number of taxa in a sample (taxon richness) is commonly used as a measure of richness, but it is problematic to compare this measure between samples, because of variable invertebrate abundance in the samples. The number of taxa per sample or per unit area is more a measure for taxa density (Simpson 1949). Because of this fact a method described by McCabe & Gotelli (2000) to calculate expected taxon richness was used. The method enables to compare taxa counts among samples that differ in abundance (McCabe & Gotelli 2000). Additionally the Simpson's index of diversity (1-D) as a non-parametric approach, that measures the probability that two randomly selected individuals in a sample belonging to different taxa, was used to determine sample heterogeneity. Expected taxon richness and the Simpson's index of diversity were positively related (Spearman Rank Order Correlation, $r=0.857$, $P < 0.0001$, $n=80$).

It is necessary to note that in this study the number of invertebrate taxa is only a limited measure of richness. Although a detailed list of all invertebrate taxa found was presented, it was, because of methodological constraints, not possible to reach a constantly low level of identification for all individuals in the samples (compare also methods). Incomplete taxonomy, is a common problem of studies on invertebrate communities in streams and rivers and based to major extent on the fact that the identification of many freshwater invertebrates to the species level is difficult or impossible with the present knowledge. This incompleteness in taxonomy will severely underestimate the true species richness (Harper & Cloutier 1986, Cranston 1990). In the present study, as in other monitoring studies, this is only a problem if the error is unequal between the investigated sites. The common method is to identify the organisms to the lowest practical level, resulting in a mixed taxonomy list (compare Appendix A, Table A.1). To avoid an error that is caused by mixed taxonomy, the analyses were performed on groups of clearly available taxonomic resolution (identification was done as far as possible for each individual, but for the analyses for each taxonomic group it was gone back to a clear stage of taxonomic resolution available for all individuals) and the results showed that the higher levels of taxonomy used, were sufficient to detect the impact of the investigated dam.

Invertebrate community composition differed among the sites and changed remarkably during the year. The ordination confirmed this pattern. Anthropogenic impacts on the geomorphological structure measured by the SQ-Index (as well as by flow diversity or diversity of benthic habitats) and seasonal changes (photoperiod and mean discharge within 30 d prior sampling) explained most of the variability in benthic invertebrate community composition. It is necessary to note that the SQ-Index was covariable with the measures of benthic habitat diversity, mean flow velocity, and annual average

values of POM standing stocks at the sample sites. All these four variables can be used alternatively in the ordination, leading to only small differences in the variability explained. This observation seems to reflect the fact that the four variables are hierarchically related: the dam causes differences in channel morphology, these differences are most responsible for changes in flow velocity patterns. Flow velocity affects particle size composition of the substrate and is therefore responsible for changes in benthic habitat composition and POM standing stocks in the channel. A fourth variable that showed a low, but significant influence to the observed pattern in the ordination was the sediment dry mass in the sample, indicating the existence of a sampling effect.

The invertebrate community composition was highly similar among the reference sites (Figure 2.10 A). Both sites close to the dam showed distinct separation, but at SS3, the composition was more similar to the reference sites in comparison to community composition observed within the impoundment. The composition of invertebrate communities changed continuously during the seasons (Figure 2.10 B) and the results showed that the largest shift in community structure should occur from winter to spring, probably resulting from the emergence of many aquatic insects and regular occurrence of spring floods. The reference sites were formed by the typical spatial mosaic of a pool and riffle sequence in close relation, consequently, the observed differences in invertebrate community variables and community composition will be a mixture of the major habitat types. Therefore, the data were also analyzed separately for pools and riffles, comparing samples from natural pools to the dam pool (SS2) and samples from natural riffles to the dam riffle (SS3). With respect to seasonal variability, the dam riffle (SS3) showed in no case lower invertebrate abundance, but more often significant higher invertebrate abundance in comparison to natural riffles (SS1 & SS4) and taxa diversity was comparable. The dam pool (SS2) had lower taxa diversity, higher invertebrate density and comparable community biomass in comparison to natural pools (SS1 & SS4). The ordination (Figure 2.10 C) showed that community composition differed remarkably among natural pools and the impoundment, but also among natural riffles and the dam riffle (SS3).

The spatial proximity and the smaller size of macrohabitat types in natural stream sections may be responsible for the higher similarity in the community structure.

The observed general shift in invertebrate community within the impoundment from lotic to lentic, agrees with results from other studies at low head dams (Baekken *et al*. 1981 a & b, Cortes *et al.* 1998, Stanley *et al.* 2002). In this study, the POM standing stocks were in most cases negative correlated to taxa diversity. The dominance of fine inorganic and organic materials within the impoundment favors some benthic

invertebrates. Characteristically Chironomidae, that utilize fine sediments in the construction of cases and tubes and Oligochaeta are frequently associated with fine sediments (Wood & Armitage 1997). On the other hand, the impoundment may represent an unfavorable habitat for some, but not for all lotic invertebrate species. Reduced availability of suitable habitats, due to the dominance of fine sediments, and inhibition of physiological mechanisms (oxygen uptake, feeding mechanisms) are most responsible for reduced abundance of many lotic invertebrates. The related change in functional feeding structure within the impoundment is in agreement with general observations that most functional feeding groups declined in more detritus retentive areas (Townsend & Hildrew 1984). The initial hypotheses for taxonomic and functional community composition were confirmed: (NR_{up} ~ NR_{down}) ~ DR_{down} ~ Impoundment. The high similarity in community composition at the two reference site indicate that the impact of the dam is locally restricted.

The amount of POM found in this study, was within the range reported from other streams (reviewed in Webster & Meyer 1997). Within the impoundment decreasing flow velocity causes increasing sedimentation of FPOM leading to the difference in total POM standing stocks observed in this study. The initial assumption must be partly rejected and the following pattern can be described on the basis of annual average values:

Impoundment > (NR_{down} = NR_{up}); DR_{down} = (Impoundment, NR_{down}, NR_{up}) for g m^{-2} & for mg g^{-1}. Nevertheless, noticeable deviations from the above pattern occurred seasonally. Kick net methods are commonly used to estimate POM standing stocks, but it is clear that these methods underestimated POM standing stocks. The efficiency of Hess-Sampling was recently compared to the new developed Bottom-Sampler technique. Wagner (2003) sampled POM in 2001 at the same low-head dam investigated during the present study and found that POM standing stocks estimated by Hess-Sampling were four times lower in comparison to the more quantitative Bottom-Sampler technique. Using this relation, the total POM standing stocks (annual average values, AFDM) in the present study were 480 g m^{-2} within the impoundment, 332 g m^{-2} at the SS3, 244 g m^{-2} at the SS4 and 232 g m^{-2} at the SS1. For the natural reference site downstream of the dam (SS4) there is a high correspondence to the estimations done by Wagner (2003) who reported 221 g m^{-2} total POM a natural reference reach, which was highly similar to the SS4. For the impoundment, Wagner (2003) found POM standing stocks of 721 g m^{-2} and 234 g m^{-2} for the section immediately downstream of the dam. In the present study there were no large differences in CPOM/FPOM ratios among dam sites and natural references and the initially assumed pattern was disproved. However this result must be handle with care because FPOM was under-

sampled. Wagner (2003) reported a depression of CPOM/FPOM ratio within, but not below the impoundment of the low-head dam investigated in the present study. This is in contrast to the effects of large headwater storage dams that are known to depress the CPOM/FPOM ratio in downstream sections (Ward & Stanford 1983, Gore 1994).

There was a positive relationship between total invertebrate abundance and POM in the stream sediments (compare Appendix A, Table A.4), although the relation was dependent on the scale used to express these variables. Although Hess-Sampling is a well accepted method and one of the most efficient sampling techniques (Taylor *et al.* 2001) care should be taken with the scale used to express the data, because the samples are taken from a three-dimensional structure (sediment), but the data are commonly expressed in a two-dimensional way (per unit area). When using standardized kick net methods to estimate invertebrate abundance or POM standing stocks it is, as indicated from the results of this study, necessary to express and analyze the data not only on the basis of units per unit area. To express the data per amount of sediment in the sample may partly resolve the above problem and this measure is probably more robust against a variable sampling effort caused by variability of flow velocity, water depth, substrate composition and substrate stability.

Table A.4 (Appendix A) shows that correlation's between invertebrate abundance and POM variables were higher when the variables are expressed as units per sediment dry mass in the samples. When the data expressed as units per area, low and non significant correlation's were observed more often. The strength of the relationship between invertebrate abundance and POM was variable among the seasons. So far a positive correlation between abundance of several invertebrate groups with POM contents in the streams has been found by several authors using observational and experimental approaches (Egglishaw 1964, Minshall & Minshall 1977, Hildrew *et al.* 1991, Richardson 1991, Boulton & Lake 1992, Friberg 1997). Positive correlations between POM and invertebrates at the scale of small sampling patches support the view that benthic invertebrates (dominated by detritivorous invertebrates) are aggregated on patchily distributed detrital food source (POM). Although the aggregation tendency can be a direct response to food accumulation, there are two alternative explanations: (1) the invertebrates can be controlled by the same hydraulic factors responsible for POM accumulations or (2) the invertebrate accumulation is a response to an increase in habitat diversity. Using the Spearman Rank Correlation Coefficient between the invertebrate density (Ind. g^{-1}) and the total amount of POM (mg g^{-1}) (compare Appendix A, Table A.4) as an indicator for the degree of aggregation, the coefficient tended strongly to decrease with the averaged discharge in the periods pre sampling (Figure 2.11).

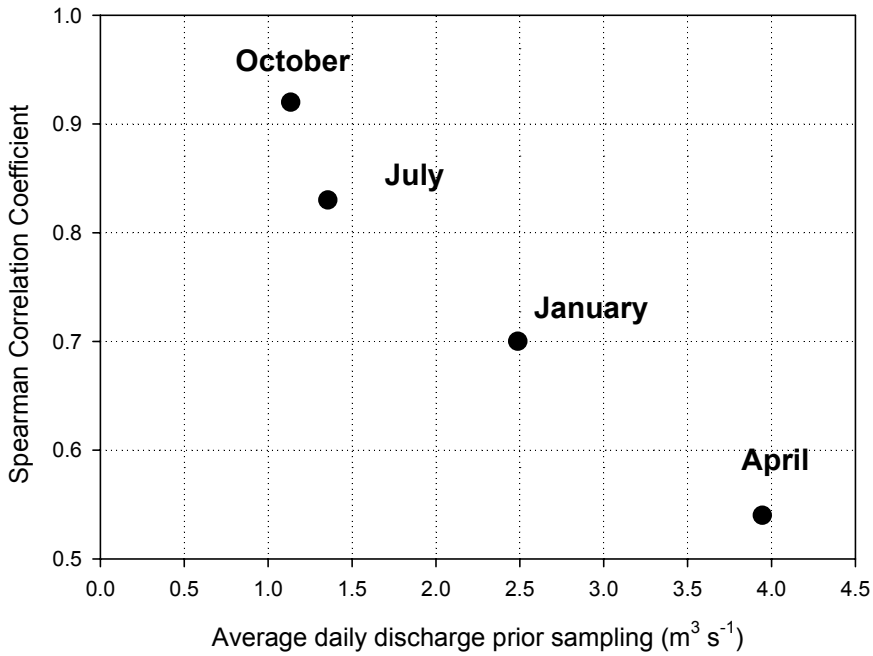

Figure 2.11: The relation observed between the averaged daily discharge prior to sampling and the Spearman Rank Correlation Coefficient between the invertebrate density (Ind. g^{-1}) and the total amount of POM (mg g^{-1}). The latter is an indicator for the degree of aggregation of invertebrates on POM. The averaged daily discharge represents the mean of daily discharge measurements in the period since last sampling (July, October, and January). For the first sampling (April), a period of 90 days prior sampling was used.

This relation may indicate that benthic invertebrates become increasingly aggregated on their patchily distributed food resource during periods with moderate discharges but were disaggregated during period with high discharges and / or during flood events. The above mechanism is supported by the results of a manipulative experimental study (Rowe & Richardson 2001). However to further support this hypothesis more data (points) are needed. Further high correlation's (not shown) between abundance of some detritivorous invertebrates and potential predator species, as observed in this study for Chironomidae and Hydracarina (data not shown), support the view that additional aggregations of predatory invertebrate species occur. Although under-sampled, FPOM contents showed highest correlation's to invertebrate abundance, probably reflecting the importance of FPOM as a resource for detritivorous invertebrate consumers. A continuous release FPOM from the impoundment and high POM standing stocks (higher than at the reference sites) are possible explanations for the higher abundance of benthic invertebrates immediately downstream of the dam observed in this study. The investigated low-head dam caused profound changes in structural and functional attributes of invertebrate communities in stream reaches close to the dam. At the references sites upstream and downstream of the investigated dam the invertebrate communities were very similar considering the attributes: invertebrate

abundance, taxa diversity, and community composition. The results indicate that the effects caused by the dam are highly restricted to stream reaches immediately upstream and downstream. The reach immediately downstream of the dam supports higher invertebrate standing crops (number of individuals & invertebrate biomass) during the year, the community structure was more comparable to natural references, and significant higher numbers of invertebrate eggs were found here. All these attributes indicate very favorable conditions for many stream invertebrates immediately downstream of the dam. Because many physical and chemical conditions were similar among the natural references and the reach immediately downstream of the dam, the quantity, the quality and the availability of food resources are probably important factors supporting a higher invertebrate standing crop (number of individuals & invertebrate biomass) immediately downstream of the dam. High density and biomass of benthic invertebrate communities is commonly observed immediately downstream of many large storage dams and is often caused by enhanced abundance of filter feeding invertebrates (Ward & Short 1978, Ward & Stanford 1979). Increased invertebrate abundance is here attributed to the release of lentic phyto- and zooplankton from the reservoirs. At the investigated low-head dam it is, because of the small size of the impoundment, not likely that plankton release alone (or only partly) causes increasing invertebrate abundance immediately downstream and in the present study no remarkable increase in the abundance of filter feeding invertebrates was observed. Future research projects should additionally focus on POM quality as well as on resource quality alterations that are likely to occur within the impoundments.

Conclusions

The investigated small low-head dam caused profound changes in structural and functional attributes of invertebrate communities in stream reaches close to the dam. But the dam seemed not to cause far-reaching downstream effects. The stream continuum (Vannote *et al.* 1980) seemed to be only locally interrupted by the impoundment of the investigated small low-head dam. Considering the serial discontinuity concept (Ward & Stanford 1983 & 1995) for the investigated small low-head dam, it seemed that the discontinuity distance, that defines the longitudinal shift by stream regulation of a given parameter, is very small (few 100 meters) for most factors and therefore no cumulative effects occur. Nutrient and carbon spiraling (Webster & Patten 1979, Webster *et al*. 1999) is probably affected by the investigated small low-head dam. Enhanced retention of POM combined with higher invertebrate standing crops (number of individuals & invertebrate biomass) at the dam indicated that spiraling length is locally tightened.

Chapter 3

3. The dam as a barrier – effects on invertebrate assemblages and downstream drift

3.1 Introduction

Various studies have been shown that large storage dams (> 15 m) can act as barriers, because these structures prevent the migration throughout the stream system, resulting in fragmentation of habitat and isolation of populations (Pechlaner 1986, Drinkwater & Frank 1994, Winston *et al*. 1991, Marchant & Hehir 2002). The barrier effect seems evident for migratory fish species (Lewis 1991, Mills 1989, Morita & Yamamoto 2002). However, up today most studies have focused only on economically important populations of fish. Migratory and resident fish species extend their movements throughout the systems after removal of the dams (see Hart *et al.* 2002).

Analyzing the barrier effect for small size aquatic invertebrates is generally much more complicated. Recently, Marchant & Hehir (2002) reported a loss in the number of invertebrate taxa immediately downstream of 19 larger dams (> 15 m) in Australia, which was probably caused by limited drift colonization. At low head dams, the barrier effect is by far less clear. Such dams may act as barriers to some invertebrates but do not affect others (Watters 1996, Cortes *et al.* 1998, Benstead *et al.* 1999, Conception & Nelson 1999, Stanley *et al*. 2002). Further, the existence of a barrier effect for benthic invertebrates probably depends on size and operational type of the dam.

In streams, the downstream drift is one of the most studied dispersal behaviors and it is generally thought to be the major path for colonization of benthic invertebrates (Townsend & Hildrew 1976, Minshall & Petersen 1985, Benson & Pearson 1987, Mackay 1992). So far comparably little information exists about dispersal in other directions (Elliott 2002 b), probably caused by methodical limitations. Single drift events of benthic invertebrates are normally short, ranging from centimeters to meters Malmquist & Sjöström 1987, Allan 1995, Elliott 2002 b), but to date little is known about total movement distances during life-time or larval life of benthic invertebrates. A better understanding of dispersal and combined compensation mechanisms is necessary to elucidate the effects of damming on invertebrate communities.

From the results presented in Chapter 2 there was no indication for a barrier effect at the investigated dam in the Ilm, because comparable number of invertebrate taxa was found immediately downstream of the dam, but at higher abundance levels. Because of the described limitations of Hess-Sampling (and other kick net methods) and the influence of abiotic conditions to the sampling effort, it was important for the present thesis, to further consider the barrier effect. Two methods were used. At first,

invertebrate assemblages on single stones were compared between the reach immediately downstream of the dam and the two natural reference sites. It was assumed that the investigated low-head dam affects invertebrate colonization by alteration of downstream drift and prevention of upstream movements. Consequently, invertebrate assemblages immediately downstream of the dam should differ from those of free flowing natural reaches. Additionally the application of an independent measure of invertebrate colonization activity in describing the successional stage of invertebrate assemblages was tested in the first part of this study.

In order to support the results and interpretations of the first study part, the downstream drift of benthic invertebrates was measured in the second part of this study. It was hypothesized that the impoundment traps invertebrates from downstream drift, resulting in differences in the invertebrate drift (density & diversity) within the impoundment, but also immediately downstream of the dam, both in comparison to free flowing natural reaches. Additionally the amount of transported particulate organic and inorganic matter was quantified in order to examine differences among the study sites.

3.2 Methods

3.2.1 Study part I - Invertebrate assemblages on stones

Sampling procedures

Individual stones were sampled, because stones are typical habitat units in streams and form clear delimited patches that were colonized by invertebrates. Generally stone sampling has become increasingly used in basic and applied stream research, because of reduced processing time, but this method is also known to overestimate invertebrate abundance and underestimate species richness of benthic communities in comparison to other common sampling techniques (Taylor *et al.* 2001).

Increasing discharge or flooding events may frequently disturb invertebrate assemblages on stones by turning and/or scraping the surfaces, removing animals and scouring epilithic layers (algae, microbes, biofilm). Generally, it seems that the intensity, frequency, and area of physical disturbances are important in determining abundance and species richness of an assemblage (Sousa 1985, Huston 1994, Townsend *et al*. 1997, McCabe & Gotelli 2000). All these three characteristics are related to the size of a stone habitat. Because of this fact, the sampling units were standardized by selection of stones with comparable sizes, in order to minimize the effects of variable disturbance regimes caused by this factor. Only stones with visible smooth and homogenous surface structure were selected.

The stones were sampled within marked 80 meter riffle-reaches at the sites described in Chapter 2. To get a continuos 80 m riffle at the references sites upstream and downstream of the dam, the original 100 m reaches were 20 m enlarged in upstream direction. The impounded reach was excluded from this study, because the sediment structure differed completely. A stratified random sampling design was used: starting at the downstream end of the riffle every five meter upstream three stones were selected along a line from the left to the right bank. One stone was taken one meter from the left and the right bank; a third stone was taken from the center of the stream.

Twenty-four stones (n = 24) were removed from three (SS1, SS3, SS4) of the four study sites, using a PVC pipe attached to one end with a transparent plexiglas pane to select the stones by their size visually (one meter radius on the sampling patch). The stones were removed by hand, using plastic bags. The bags were turned over the stones to minimize the loss of matter from the stone surfaces. All samples were taken within one day, on 02.08.2001, in order to avoid any confounding impacts on community assemblage patterns over time and in respond to changes in discharge or the impacts of events such as floods. The stones were rinsed with water, the surfaces were intensively scrubbed, and all visible materials were removed. The scrubbed

material was rinsed in a 100 µm sieve to remove the water. The samples were preserved in 60% ethanol. After scrubbing, each stone was measured for maximum length, wide, height, and wet weight, to calculate the surface area.

Estimation of the successional stage of invertebrate assemblages on stones

Succession is most simply defined as community change that occurs at a site following a disturbance (Fischer 1983 & 1990). In the concept of patch dynamics (Pickett & White 1985), ecological communities are seen as a mosaic of patches, each at a different point along the succession from open space to a climax assemblage. Succession generally involves two basic elements: colonization and subsequent changes (Fischer 1983). In streams, invertebrate assemblages on stone habitats are frequently disturbed by floods. Colonization dynamics of benthic stream invertebrates are well studied over the last decades and mostly small-scale experimental designs using artificial substrates were conducted to explore invertebrate colonization. Many studies have found that a transition in species dominance occurs during colonization (see Downes & Lake 1991). This observation suggests that succession is affected by differences in movement activity between species. The movement activity is influenced by the mode of movement (drifting, crawling, flying & egg hatching) (Mackay 1992) and by the ability or propensity to move (Turcotte & Harper 1982, Kohler 1983, Allan 1984). In streams, downstream drift is generally regarded as the most important mechanism of colonization (Townsend and Hildrew 1976, Williams and Hynes 1976, Benson & Pearson 1987). The general patterns found in experimental studies were that colonization is rapid and predictable: the number of individuals and species seemed to stabilize within short time (1-4 weeks) and possibly saturation occurs (Townsend & Hildrew 1976, Rosenberg & Resh 1982, Lake & Doeg 1985, Williams 1980, Minshall & Petersen 1985, Mackay 1992). According to colonization patterns, the first stages of invertebrate assemblage succession were often marked by high proportions of the fastest colonizers, often observed were midges (Chironomidae) (Townsend & Hildrew 1976, Mackay 1992, Winterbottom *et al.* 1997, Rosemond *et al*. 2001, Fenoglio *et al.* 2002), mayflies (Ephemeroptera especially the family Baetidae), filter feeding caddiesflies of the family Hydropsychidae and blackflies (Simuliidae) (Boulton *et al*. 1988, Robinson *et al*. 1990, Mackay 1992). Increasing development of periphyton and biofilm layers may support higher numbers of invertebrates belonging to the “Scraper” functional group, but also rising the numbers of predatory species at intermediate stages. Reduced proportions of the early colonizers and increasing numbers of late and possible slow colonizers (mollusks & sand-cased caddies-flies) will found at the latest stages (Wallace 1990, Mackay 1992). The quantification of colonization activity in form

of “activity indices” may increase the understanding of succession of invertebrate assemblages in streams. A colonization index was created for invertebrate assemblages found in this study on the basis of activity indices that based on the results from a study, which was carried out 1997 in the Ilm and during the same season by Paul Elser (1999 & 2001 a, b). In his study multidirectional movement patterns of invertebrates were investigated using artificial colonization baskets. The taxonomic composition of the benthic assemblages analyzed in this study was comparable to that observed in the present study. Estimations of relative movement activities of different invertebrates were drawn by comparing relative abundance on artificial colonization substrates with measurements of the relative abundance in adjacent benthic invertebrate assemblages. On the basis of the data set from Elser (1999 & 2001 a, b), activity indices were calculated following Panek (1991, 1992) by dividing the relative abundance of a taxon in colonization–substrate-samples by its relative abundance in benthic samples using the following equation:

$$C_i = \frac{a_i}{b_i} \qquad \textbf{(EQ. 2)}$$

where $\boldsymbol{C_i}$ is the activity index of a taxon i (without unit); $\boldsymbol{a_i}$ is the relative abundance of taxon i in colonization baskets and $\boldsymbol{b_i}$ is the relative abundance of the taxon i in natural benthos.

The activity index **(C_i)** can be regarded as an expression of the mobility of different invertebrate taxa and as a relative measure that marks the probability of colonization for a taxon or species relative to other community members. Table B.1 (Appendix B) concerns the calculated activity indices for selected taxa. There are some fast colonizers (Chironomidae), some intermediate and some slow colonizer [*Ancylus fluviatilis* (Pictet)].

The indices of activity of several taxa were combined with invertebrate abundance data from this study in order to create a colonization index (*S*) that describes the relative contribution of fast, medium and slow colonizers to the assemblage. The following equation was used:

$$S = 100 \cdot \sum_{i=1}^{N} (C_i \cdot p_i) \qquad \textbf{(EQ. 3)}$$

where $\boldsymbol{S}$ is the colonization index, $\boldsymbol{C_i}$ is the activity index of a taxon i and $\boldsymbol{p_i}$ is the relative abundance of taxon i in the community $\boldsymbol{N}$.

The colonization index (*S*) estimates the relative contribution of various invertebrate taxa, with different colonization activities to an assemblage. The index (*S*) can reach a maximum of S=164, when the fastest colonizers (Chironomidae) alone form the assemblage (100% relative abundance) and a minimum with S<4 when the

assemblage is dominated by the slowest colonizers (Mollusca: *Ancylus fluviatilis* S=3.8; Coleoptera: Elmidae S=2.4; Diptera: Limoniidae S=1.7). All species or taxa that were found in the colonization study but not on the stones investigated or vice versa were treated using a constant of C_i = 0.257 (compare Appendix B, Table B.1). As initially assumed, when upstream-downstream dispersal and / or the general colonization dynamics are modified by the dam, there should be measurable differences in the invertebrate assemblages and consequently in the calculated colonization index (*S*).

Sample processing

In the laboratory, all macro- and meiobenthic invertebrates were counted from stone samples. The invertebrates were identified to the lowest possible taxonomic level. It was not possible to identify chironomids to species level, most belonging to the families: Orthocladinae, Chironominae, Diamesinae, and Tanypodinae. Additionally it was not possible to identify some other small size invertebrates, mostly early- instar´s and life stages, to species. Therefore, all these organisms were lumped into groups of clear available taxonomic resolution. Furthermore, the dry mass and the ash free dry mass of all invertebrates of each sample was determined. Invertebrates were sorted into small pre-weighed petri-dishes, dried at 80°C for 24 h and weighed. Dry invertebrate material was ground into a fine powder using a ball mill, sub-sampled, ashed at 500°C for 2 h and ash free dry mass (AFDM) was determined.

Because of mass losses that possibly occur during leaching ethanol soluble materials the dry mass and ash free dry mass presented here, underestimated the true natural biomass (see Benke, 1996), but they are applicable for comparison between the samples and sample sites in the present study (compare Chapter 2). After separation of the invertebrates from each sample, the remaining material including filamentous algae and particulate matter was filtered using pre-ashed, pre-weighed Whatman GF/A filters and dried at 105°C to constant weight. Afterwards the dry filters were ground into a fine powder using a ball mill, sub-samples were ashed at 600°C for 5 h. Ash free dry mass (AFDM) was calculated and used as a measure for the amount of filamentous algae (organic content) on the stone surfaces. The filamentous alga *Cladophora* sp. was the dominant taxon found on stone surfaces in the Ilm stream.

Invertebrate abundance (number of individuals & invertebrate biomass), taxa density, taxa diversity and the colonization index (*S*) were used as measures to characterize the invertebrate assemblages. Diversity was measured with the Shannon index (H´) and the Simpson's index of diversity (1-D) as described in Ludwig and Reynolds (1988). Further Ecosim simulation software (Gotelli & Entsminger 2001) was used to estimate the expected taxon richness. The smallest sample in the collection had only 19 individuals. Therefore 19 individuals were sampled randomly from each sample and the

observed number of taxa was recorded, using Ecosim. The randomization was repeated 100 times for each sample and the averaged number of species was used as expected taxon richness. In a separate analysis all samples of each sample site were pooled and then Ecosim was used to create a aggregated, sample based rarefaction curve for each sample site (compare Gotelli & Colwell 2001, Gotelli & Entsminger 2001), which represents diversity measured across stone habitats of the different sample sites.

Statistical analyses

One-way ANOVA`s were used for comparing the mean of various stone size variables among the sample sites. In order to explore the influence of small variability in size of the stones sampled, Spearman Rank Order Correlation was used to compare ranking of all samples between various assemblage variables [invertebrate abundance, taxa density, taxa diversity and Colonization index (*S*)] and stone size parameters, significance of correlation was indicated at a *P*-level < 0.05. In accordance to the initial assumptions, the invertebrate assemblage variables and assemblage composition were compared among the sample sites. Normal distribution of the data was checked by conducting Kolmogorov–Smirnov-Tests and equivalency of variances using Levene–tests. Afterwards separate one-way ANOVA`s were conducted for comparing the mean of various invertebrate assemblage between the sample sites, followed by Bonferroni t-test if necessary (P < 0.05). If the data not fitted a normal distribution, the data where log (x+1) or arc sin transformed and checked again by Kolmogorov–Smirnov-Tests. If the transformation failed to normalize the data distributions, non-parametric Kruskal-Wallis analysis of variance on ranks was used for comparison among medians, followed by non-parametric Tukey`s test if necessary (P < 0.05). To assess variation in community composition among the sample sites a principal component analysis (PCA) (Jongman *et al.* 1995) was conducted on log (x+1) transformed invertebrate abundance data. Additionally a Multiple Response Permutation Procedure (MRPP) (using Sorensen`s distance measure) was performed using the software package PCORD (McCune & Mefford 1997). MRPP is multivariate analysis of variance without the requirement of multivariate normality and homogeneity of variance (Mielke 1984, Biondini *et al.* 1985). It tests the hypothesis of no difference between two or more pre-defined groups of entities with significance inferred at P < 0.05. The relations among major assemblage variables were analyzed using linear or nonlinear regressions. Additionally an agglomerative cluster analysis (Euclidean distance, WARD`s method) was conducted on invertebrate abundance data using the software package PCORD (McCune & Mefford 1997) in order to describe some major assemblage stages.

3.2.2 Study part II - Invertebrate downstream drift and seston transport

This study was a part of the Diploma – thesis of Andrea Lange (Lange 2004).

Drift - Sampling

The downstream drift of invertebrates was studied on 13.03.2003 using drift samplers (Figure 3.1). Each sampler consist of a 67 cm long and 10 cm diameter PVC pipe frame (rain pipe) and a 200 µm net attached to one end.

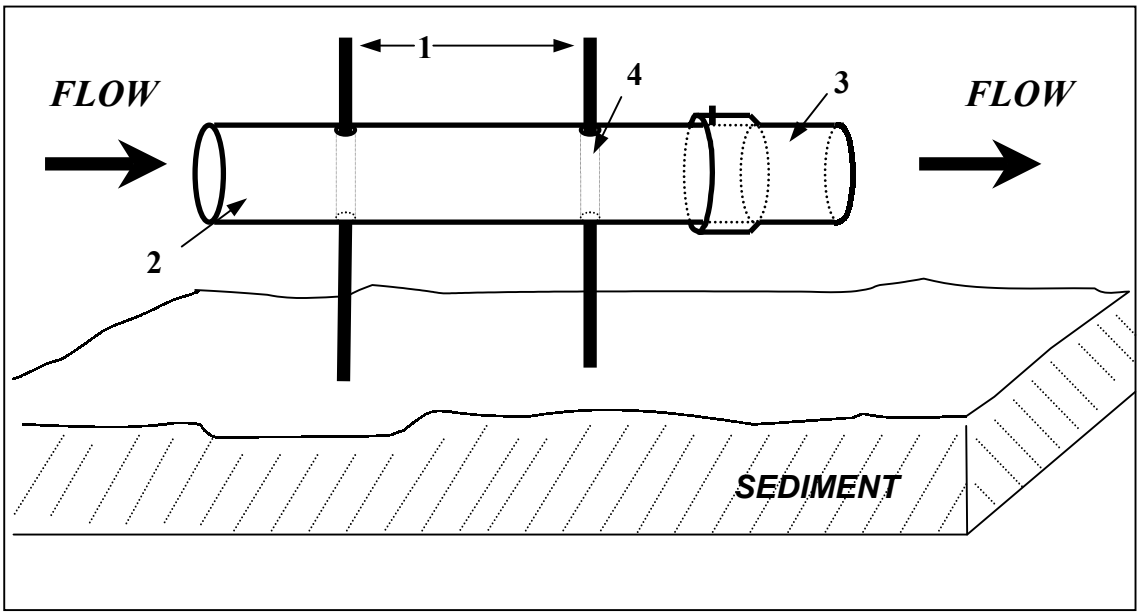

Figure 3.1: A schematic view of the Drift - Sampler. (1) metal-bar; (2) sampler part (I): a hard plastic pipe connected and adjustable by rubber stoppers; (3) sampler part (II): a short hard plastic pipe with a 200 µm net, removable to take the sample; (4) small plastic pipe welded with sampler part (I) – gateway for the bars.

The samplers were designed, mainly to quantify small vertical and horizontal differences of invertebrate drift within the streambed. A very similar sampling method was recently published by Wipfli and Gregovich (2002). This method is cost effective, easily to handle, useful to take a larger number of parallel samples and much more suitable for quantification of vertical and lateral differences of invertebrate drift within a streambed in comparison to the commonly used large drift nets. A real picture of the sampler is given in Figure 3.2. On all four sample sites, three drift samplers were used. Two metal bars that hold each sampler were placed in the stream seven days prior to drift measurements along a line from one bank to the other. The samplers were horizontally fixed at the bars using rubber stoppers. The samplers were placed 10 cm beneath the water surface, two samplers one meter from the banks and one in the center of the stream. Flow was measured on the upstream end of each sampler at the

beginning of each sampling period using a Flo-Mate 2000 (Marsh-McBirney Inc. USA), the averaged velocity was calculated for each sampler and used to determine the density of invertebrates per unit volume of water (Inv. m^{-3}).

Preliminary tests measuring the flow on the upstream and downstream end of the samplers showed that water passes continuously, but depending on detritus loads. Therefore short duration (5 minutes) sampling periods one after another were used to minimize the influence of detritus loads on the flow regime through the sampler. Water temperature, conductivity, dissolved oxygen, and pH were repeatedly measured at each site using digital instruments (WTW - Weilheim, Germany).

During sampling, the flow velocity was moderately high and ranged between 0.50 m s^{-1} and 1.52 m s^{-1}, this corresponded to a daily discharge between 4.95 m^3 s^{-1} (at $5.^{00}$ hour on 13.03.2003) and 5.75 m^3 s^{-1} (at $5.^{00}$ hour on 14.03.2003) measured at the permanent gauge Gräfinau - Angstedt 10 km upstream of the study sites. Sampling was done during one day in order to minimize larger changes in discharge. Drift samples were taken simultaneously at two sites (SS3 vs. SS4 from $11.^{00}$ - $13.^{00}$ hour and SS1 vs. SS2 from $16.^{00}$- $18.^{00}$ hour). A number of fifteen drift samples (each 5 minutes sampling & 10-15 minutes sample preservation) were taken from each sample site. Contents of each sample were preserved in 70% ethanol.

Figure 3.2: A picture of the Drift – Sampler in the stream.

Sample processing

In the laboratory, all macro- and meiobenthic invertebrates were counted from drift samples using a dissecting microscope. The invertebrates were identified to the lowest possible taxonomic level. As described above it was not possible to identify most of the very small size invertebrates to species. Therefore, all organisms were lumped into groups of clear available taxonomic resolution. The invertebrate abundance (number of individuals in each 5 minute sample & number of individuals per m^{-3}), taxon density and taxon diversity [Shannon index (H´) & Simpson's index of diversity (1-D)] were used to characterize drifting invertebrates. After separation of the invertebrates, the remaining seston material was filtered through pre-weighted, pre-ashed glass-fiber filters (Whatman GF/A), dried at 105 °C and weighed to determine total particulate matter (PM). Then the filters were ashed for 2 h at 600°C to calculate particulate organic matter (POM). Particulate inorganic matter (PIM) was calculated as the difference between PM and POM.

Statistical analyses

The drift variables were compared for differences among the sample sites. The study was designed for using comparison procedures among two groups (sample sites), but because drift variables showed no significant trend in time during the day (Kruskal-Wallis ANOVA, $P > 0.05$), therefore also multiple comparison procedures as described above to test for differences among all four sample sites were used. Only the results for multiple comparison procedures are shown (for more details see Lange 2004). Normal distribution of the data was checked by conducting Kolmogorov–Smirnov-Tests and equivalency of variances using Levene–tests. Afterwards separate one-way ANOVA`s were conducted, followed by Tukey`s-test if necessary ($P < 0.05$). If the data did not fit a normal distribution, the data were log (x-1) transformed and checked again by Kolmogorov–Smirnov-Tests. If the transformation fails to normalize the data Kruskal-Wallis ANOVA on ranks was used. If differences were significant, pair wise comparisons were made using Tukey`s tests ($P < 0.05$). Spearman Rank Order Correlation was used to compare ranking of all samples between POM and PIM contents ($P < 0.05$)

3.3 Results

3.3.1 Invertebrate assemblages on stones

In total 25233 invertebrates belonging to 32 taxa were counted from the samples. Community composition differed from that observed in the whole benthos (compare Chapter 2). Midges (Chironomidae) were the most abundant taxonomic group (69.7% relative abundance) followed by caddisflies (Trichoptera), including the families Rhyacophilidae, Glossosomatidae, Hydropsychidae, Hydroptilidae and Polycentropidae, which took 9.79%, mayflies [Ephemeroptera (*Baetis* spp., dominant were *Baetis rhodani* (Pictet), *Ephemerella ignita* (Poda) and *Ecdyonurus* spp.] with 8.55% and the Mollusca - *Ancylus fluviatilis* (Müller) took 6.67% relative abundance in all samples. These four groups account for 94.71% relative abundance in the collection.

The stones sampled varied slightly in size (average surface area: 123.70 cm^2) and no significant differences were found comparing the stones by their size among the sample sites [log (x+1) data, ANOVA, $p > 0.05$]. The stone size parameters were not significant correlated to any of the biological parameters (Spearman Rank Order Correlation, $r < 0.25$, $P > 0.05$). The mean, standard deviation, maximum, and minimum values for the measured invertebrate assemblage variables are summarized in Table 3.1.

Table 3.1: Major biotic variables (Minimum, Maximum, Mean ± 1 S.D.) for invertebrate assemblages and the organic content of the stones sampled.

Parameter	Sample site			
	Reference upstream **SS1**	Dam site Impoundment **SS2**	Dam site downstream **SS3**	Reference downstream **SS4**
Invertebrates (Ind. cm^{-2})	0.22 – 8.17 3.84 ± 2.32	n. m.	1.40 – 12.13 3.51 ± 2.26	0.23 – 2.39 1.07 ± 0.56
Inv. biomass (mg cm^{-2})	0.012 – 0.17 0.07 ± 0.05	n. m.	0.011 – 0.68 0.14 ± 0.17	0.004 – 0.33 0.08 ± 0.09
Taxa density (number of taxa)	4 – 16 9.79 ± 2.96	n. m.	6 - 18 10.71 ± 2.73	3 – 16 8.88 ± 3.40
Simpson`s index [1-D]	0.17 – 0.65 0.44 ± 0.15	n. m.	0.23 – 0.82 0.45 ± 0.16	0.35 – 0.87 0.63 ± 0.15
Shannon`s index [H`]	0.45 – 1.56 0.96 ± 0.29	n. m.	0.59 – 2.01 1.03 ± 0.34	0.84 – 2.23 1.37 ± 0.37
Expected taxon richness	2.46 – 6.12 3.95 ± 0.85	n. m.	2.85 - 7.24 4.11 ± 0.995	3.33 – 8.29 5.04 ± 1.21
Colonization index [S]	49.0 – 151.9 122.7 ± 25.4	n. m.	33.5 - 147.1 116.4 ± 33.9	15.8 – 136.3 77.2 ± 37.2
Organic content (mg cm^{-2})	0.245 - 8.738 1.644 ± 1.721	n. m.	0.269 - 2.524 0.807 ± 0.593	0.127 - 0.856 0.374 ± 0.226
Abundance of predatory & parasitical taxa (%)	0.40 – 12.5 3.38 ± 3.23	n. m.	0.32 – 34.5 5.87 ± 6.76	0.00 – 45.4 8.79 ± 12.00

n. m. – not measured; n = 24.

The total number of taxa varied slightly among the sites (SS4: 28 taxa, SS3: 27 taxa & SS1: 26 taxa). There was no significant difference for taxa density (H= 3.88, 2 d.f., P > 0.05) and invertebrate assemblage biomass based on AFDM ($F_{2,69}$ = 1.949, P > 0.05) among the sample sites. The SS3, close to the dam, and the natural reference upstream of the dam (SS1) had significant higher total invertebrate abundance (Inv. cm^{-2}) [$F_{2,69}$ = 25.3, P < 0.001, (SS1 = SS3) > SS4] and periphyton mass based on AFDM [log (x+1) transformed data, H=29.08, 2 d.f., P < 0.001, (SS1 = SS3) > SS4], but significant lower diversity in comparison to the natural reference downstream of the dam (SS4) [Simpson's index $F_{2,69}$ = 11.66, P < 0.001, SS4 > (SS1 = SS3); Shannon's index (H´) $F_{2,69}$ = 10.47, P < 0.001, SS4 > (SS1 = SS3)]. Expected taxon richness, confirmed this pattern and was significantly higher at the downstream natural reference (SS4) in comparison to the dam site (SS3) and the natural reference upstream of the dam (SS1) [$F_{2,69}$ = 7.80, P < 0.001, SS4 > (SS1 = SS3)]. The rarefaction curves for invertebrate assemblages were similar at the three sample sites for a comparison that based on corresponding numbers of randomized accumulated samples (Figure 3.3 A). However the sample-based rarefaction curves after re-scaling the x-axis from samples to the number of invertebrates showed that taxon richness was higher at the downstream reference site in comparison to the upstream reference site and the dam site (Figure 3.3 B).

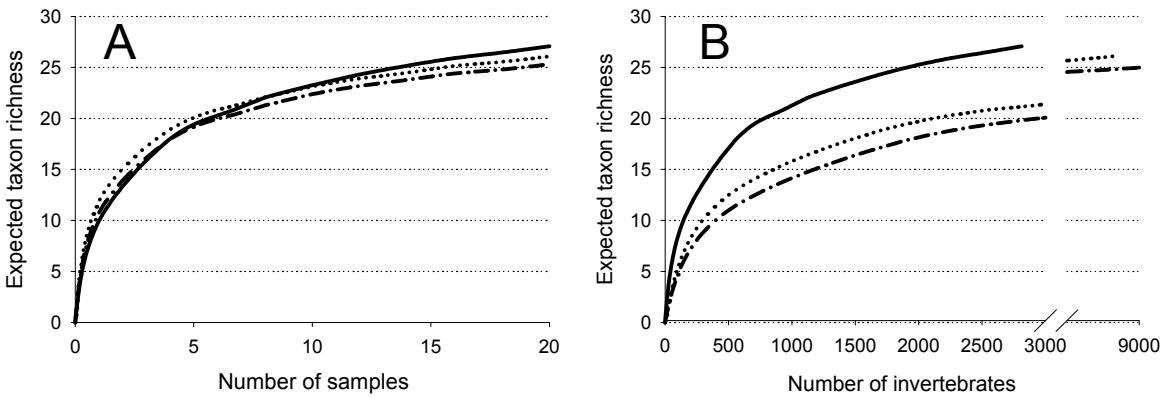

Figure 3.3: (A) Sample-based rarefaction curves of invertebrate assemblages based on corresponding numbers of randomized accumulated samples. Taxon richness appears to be similar for the three sample sites. (B) Sample-based rarefaction curves after re-scaling the x-axis from samples to invertebrates (individuals). Downstream reference site (SS4 - solid line) had higher taxon richness in comparison to the upstream reference site (SS1 - dash dotted line) and the dam site (SS3 - dotted line).

The colonization index (*S*) ranged from 15.8 to 151.9 and was higher at SS1 & SS3 in comparison to SS4 [log (x+1) transformed data, H = 20.95, 2 d.f., P < 0.001; (SS1 = SS3) > SS4]. The index (*S*) was variable within the reaches indicating the existence of

a variety of different assemblage stages. The relative contribution of predatory and parasitical taxa was variable within the sites and there was no difference among the sites (arc sin - transformed data, H = 5.21, 2 d.f., P > 0.05). The first two axes of the PCA account for 52% of the variability. Invertebrate assemblage composition was variable within the sites and there was a substantial overlap between samples of the study sites (Figure 3.4). However, MRPP showed that community composition was significantly different at SS4 in comparison to SS3 (r = 0.12, P < 0.01) and to SS1 (r = 0.08, P < 0.01). However, there was no difference among the two sparsely shaded sites SS3 and SS1 (r = 0.01, P > 0.05).

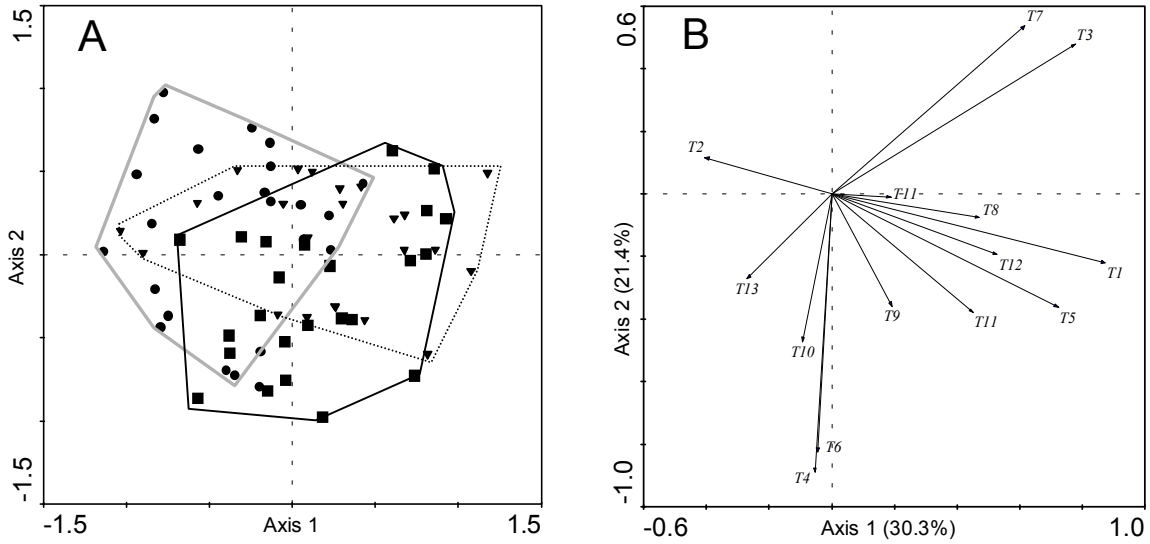

Figure 3.4: Ordination plot of a principal component analysis based on the abundance of 32 invertebrate taxa in 72 samples investigated in this study. (A) Sample scores: samples are shown as circles (SS4), squares (SS3) and down-triangles (SS1). All samples of a sample site are enveloped by dotted lines. (B) Ordination of invertebrate taxa. Only taxa with relative abundance > 0.2% in the total collection are shown. Each arrow points in the direction of steepest increase of values for the corresponding taxa. The angles between arrows indicate correlation's between the taxa. Values in parentheses along axes are the amount of variation explained by the principal component. T1=Chironomidae; T2=*Ancylus fluviatilis*; T3=*Baetis* sp.; T4=*Glossosoma* sp.; T5=Trichoptera others; T6=Limoniidae; T7=Simuliidae; T8=Rhyacophilidae; T9=Hydrachnella; T10=Oligochaeta; T11=*Hydropsyche* sp.; T12=Hydroptilidae; T13= *Erpobdella octoculata*.

Simpson's index of diversity, the Shannon index and expected taxon richness showed a hump-shaped relationship with the Colonization index (*S*) [Appendix B, Figure B.1 (A), only Colonization index (*S*) vs. Simpson's index of diversity is shown] The Simpson's index of diversity, the Shannon index and expected taxon richness tended to decrease

with increasing invertebrate abundance (Inv. cm^{-2}) [Appendix B, Figure B.1 (B), only invertebrates cm^{-2} vs. Simpson's index is shown]. The number of invertebrates (Inv. cm^{-2}) tended to increase with the Colonization index [Appendix B, Figure B.1 (C)]. There was a positive relation between organic matter content (mg cm^{-2}) and total number of invertebrates (Inv. cm^{-2}) [Appendix B, Figure B.1 (D)], but there was no significant relation to invertebrate biomass (mg cm^{-2}). Biomass showed highest variability at intermediate levels of diversity [Appendix B, Figure B.1 (E)]. Diversity tended to show higher values in assemblages with higher relative abundance of predatory and parasitical taxa [Appendix B, Figure B.1 (F), only relative abundance of predatory and parasitical taxa vs. Shannon's index is shown]. Cluster analysis divides invertebrate assemblages in five distinct groups (Appendix B, Figure B.2). Across this five groups assemblage composition changed remarkably (Appendix B, Figure B.3), the number of invertebrates, the colonization index (*S*) and the organic content (periphyton amount) tended to increased from cluster 1 to cluster 5 [Appendix B, Figures B.3 (B), (D), (F)], whereas the Shannon's index of diversity, the invertebrate biomass and the relative abundance of predatory and parasitical taxa tended to decrease [Appendix B, Figures B.3 (C), (E), (G)].

3.3.2 Invertebrate downstream drift and seston transport

Abiotic parameters

Abiotic parameters measured during drift sampling (Table 3.2) were slightly variable between the sampling sites.

Table 3.2: Physical and chemical conditions (Mean ± 1 S.D.) measured during drift sampling.

	Sample site			
Parameter	Reference upstream **SS1**	Dam site Impoundment **SS2**	Dam site downstream **SS3**	Reference downstream **SS4**
Flow velocity (m s^{-1})	1.09 ± 0.32	0.67 ± 0.19	1.40 ± 0.20	1.12 ± 0.18
Conductivity (µS cm^{-1})	213.1 ± 0.55	233.0 ± 0.00	233.6 ± 7.02	233.0 ±1.22
pH	7.26 ± 0.02	7.94 ± 0.01	7.20 ± 0.04	7.17 ± 0.00
Oxygen (mg l^{-1})	12.62 ± 0.04	13.12 ± 0.04	13.58 ± 0.04	13.28 ± 0.04
Oxygen saturation (%)	101.4 ± 0.89	105.0 ± 0.00	105.8 ± 0.45	102.6 ± 0.55
Temperature (°C)	4.17 ± 0.06	4.07 ± 0.06	4.83 ± 0.15	4.75 ± 0.00

n=6; except for temperature: n=3.

Invertebrate drift

During drift sampling a total of 2714 invertebrates were collected from 60 samples, representing 25 taxa (Appendix B, Table B.2). The mean (± 1 S.D.) for various drift variables and the drift densities for some abundant taxa are shown in Table 3.3. Aquatic (benthic and planktonic) and terrestrial invertebrates were found in downstream drift. The dominant groups were Copepoda (Cyclopoida) (52.8%), Diptera (Chironomidae) (25.9%) and Cladocera (Daphnia) (8.4%). All further taxa contributed lesser than 3% relative abundance to the collection. Drift density ranged between 5.81 Ind. m^{-3} and 33.10 Ind. m^{-3} (compare Table 3.3) and was significant higher within the impoundment [$F_{3,56}$=6.169, P = 0.001; SS2 > (SS1 = SS3 = SS4)]. The total number of taxa during 5 minute sampling ranged from 3 to 10, with lowest mean (5.53 taxa) within the impoundment and highest at the natural references [$F_{3,56}$=4.17, P = 0.01; SS2 < (SS1 = SS4); SS3 = (SS1, SS2, SS4)]. When taxon number were estimated per m^{-3} the impoundment showed higher mean (3.73 taxa m^{-3}) in comparison to the other sites [$F_{3,56}$=8.76, P < 0.001; SS2 > (SS1 = SS3 = SS4)]. Both the Simpson's index of diversity (1-D) and the Shannon's index (H`) were higher at the two reference sites (SS1 & SS4) and at the downstream dam site (SS3) in comparison to the impounded site (SS2), but difference was only significant for SS4 vs. SS2 [Simpson's index, log (x+1) transformed, $F_{3,56}$=4.84, P = 0.005; SS2 < SS4; Shannon's index, log (x+1) transformed, $F_{3,56}$=5.55, P = 0.002; SS2 < SS4]. For taxon density a small but significant difference was found between the reference sites and the impounded site [H =11.045, 3 d.f., P = 0.011; (SS1 = SS4) > SS2; SS3 = (SS1, SS2, SS4)]. Comparing the abundance of benthic invertebrates in drift, there was no difference among the sample sites ($F_{3,56}$=1.14, P = 0.343), whereas the abundance of planktonic groups in drift was significant higher within the impoundment [$F_{3,56}$=4.67, P = 0.006; SS2 > (SS1 = SS3 = SS4)]. This difference is therefore also responsible for the observed difference of total invertebrate abundance.

Table 3.3: Biotic and abiotic drift variables (Mean ± 1 S.D.) measured at the sample sites.

	Sample site			
Drift variable	Reference upstream **SS1**	Dam site Impoundment **SS2**	Dam site downstream **SS3**	Reference downstream **SS4**
Invertebrate abundance †				
Ind. m^{-3}	16.9 ± 5.37	22.9 ± 5.79	16.1 ± 4.15	18.0 ± 3.35
No. per sample	41.8 ± 12.18	34.7 ± 6.07	52.5 ± 12.78	46.7 ± 7.35
Taxon number				
No. m^{-3}	2.82 ± 0.72	3.73 ± 1.45	2.03 ± 0.55	2.71 ± 0.66
No. per sample	6.93 ± 1.03	5.53 ± 1.30	6.60 ± 1.59	6.93 ± 1.03
Simpson's index of diversity	0.62 ± 0.07	0.58 ± 0.07	0.63 ± 0.05	0.67 ± 0.06
Shannon's index	1.27 ± 0.16	1.14 ± 0.19	1.26 ± 0.15	1.38 ± 0.15
Benthic groups ‡ (Inv. m^{-3})	8.17 ± 2.73	8.24 ± 2.98	7.02 ± 2.09	7.01 ± 2.02
Planktonic groups ‡ (Inv. m^{-3})	9.86 ± 3.93	14.1 ± 4.06	10.7 ± 3.19	10.5 ± 2.09
PM (mg m^{-3})	102.3 ± 61.9	85.1 ± 7.08	75.1 ± 26.9	98.2 ± 19.2
POM (mg m^{-3})	28.1 ± 7.31	31.1 ± 4.11	23.8 ± 6.98	29.7 ± 5.78
POM (%)	31.9 ± 3.89	36.5 ± 2.81	32.6 ± 2.67	30.5 ± 2.12
PIM (mg m^{-3})	74.3 ± 60.6	54.0 ± 4.47	51.3 ± 20.1	68.4 ± 13.9
Common taxa (Ind. m^{-3})				
Cyclopoida	9.30 ± 3.76	12.66 ± 3.36	8.57 ± 2.40	8.35 ± 2.32
Chironomidae	4.39 ± 1.44	6.53 ± 2.69	3.69 ± 1.64	4.80 ± 1.64
Daphnia	0.40 ± 0.54	1.17 ± 0.99	2.18 ± 1.33	2.12 ± 1.14
Collembola	0.50 ± 0.45	0.59 ± 0.88	0.27 ± 0.33	0.46 ± 0.50
Oligochaeta	0.36 ± 0.50	0.53 ± 0.65	0.49 ± 0.52	0.67 ± 0.63
Nematoda	0.59 ± 1.01	0.40 ± 0.57	0.30 ± 0.50	0.52 ± 1.06
Tardigrada	0.63 ± 0.37	0.38 ± 0.46	0.17 ± 0.21	0.40 ± 0.52
Bosminidae	0.16 ± 0.24	0.22 ± 0.47	0.02 ± 0.07	0.06 ± 0.16
Plecoptera	0.11 ± 0.20	0.06 ± 0.22	0.04 ± 0.10	0.08 ± 0.17
Trichoptera	0.05 ± 0.14	0.07 ± 0.17	0.09 ± 0.15	0.13 ± 0.20
Simuliidae	0.11 ± 0.20	0.06 ± 0.22	0.06 ± 0.12	0.09 ± 0.16
Ostracoda	0.06 ± 0.17	0.10 ± 0.18	0.06 ± 0.13	0.06 ± 0.24
Ephemeroptera	0.06 ± 0.17	0	0.06 ± 0.13	0.12 ± 0.20

† inclusive terrestrial invertebrates; ‡ exclusive terrestrial invertebrates; n=15

Seston transport

The concentration of transported particulate matter (PM) in drift samples averaged 90 mg m^{-3}. The PM concentration tend to show higher values at both natural reference sites (compare Table 3.3), but these differences were not significant (H = 7.66, 3 d.f., P = 0.054). The drift samples contained generally more particulate inorganic matter (~61

mg PIM m^{-3}) than particulate organic matter (~28 mg POM m^{-3}) and both were positively related ($r=0.659$, $P < 0.05$, Spearman Rank Order Correlation). PIM contents were higher at the references sites (median of log (x+1) PIM at SS4 and SS1 was 1.816 and 1.810), but the difference was only significant for SS4 [$H = 11.77$, 3 d.f., $P = 0.008$, SS4 > (SS3 = SS2); SS1 = (SS2, SS3, SS4)], although slightly different from SS1. POM contents were higher at the impounded site (SS2) in comparison to the site (SS3) immediately downstream of the dam [$F_{3,56}=3.72$, $P = 0.017$, SS2 > SS3; SS1 = (SS2, SS3); SS4 = (SS2, SS3)]. The relative amount of POM (%) in seston was highest within the impoundment [$F_{3,56}=11.38$, $P < 0.001$, SS2 > (SS1 = SS3 = SS4)].

3.4 Discussion

3.4.1. Invertebrate assemblages on stones

Invertebrate density, diversity and the composition of invertebrate assemblages on stone habitats was highly variable within all sample sites. There was no consistent pattern for all measured assemblages variables comparing blocks of samples from the banks with those from the center of the stream (data not shown; compare Lange 2004). The assemblages contained various proportions of fast, intermediate and slow colonizers as indicated by the variability of the colonization index (*S*). Diversity decreased towards the two endpoints of the colonization index (*S*), due to increasing dominance of fast (Chironomidae) or slow colonizers [*Ancylus fluviatilis* (Pictet)] (Figure 3.4 A) in the assemblages. Decrease in diversity with increasing abundance (Figure 3.4 B) seemed affected by three major factors: time since the last disturbance, the intensity of last disturbance and the periphyton amount (organic content).

Physical disturbances are commonly found to reduce the total number of individuals and taxa density, but may on the other hand increase diversity measures, which are independent from abundance (McCabe & Gotelli 2000). Depending on intensity, physical disturbances may reset the colonization process. In addition, physical disturbance can reduce primary productivity or periphyton abundance (Robinson & Minshall 1986, Death 1996, Zimmermann & Death 2002). Although the overall discharge regime, and therefore the hydrological disturbance regime can assumed to be highly similar among the sample sites, it is clear, that stone movement during floods or shear stress may act individually on stones and this is one mechanism possibly responsible for the large variability of invertebrate assemblages within the sites observed in this study. The observed relation of relative abundance of predatory and parasitical taxa with measures of diversity suggest the importance of predator - prey

interactions (and parasite – host interactions) in structuring the assemblages on single stones, however among the sample sites no difference was found.

The differences in invertebrate assemblages among the sample sites, seemed to be largely influenced by shading (compare sampling site description in Chapter 2) and the related difference in the growth of filamentous algae (compare description of the sampling sites in Chapter 2). Trees and the surrounding vegetation create a mosaic of light and dark (shade) patches and influence periphyton growth. Differences in vegetation on the banks seemed most responsible for the observed higher amount of filamentous algae at open sites (SS3 & SS1) in comparison to the shaded site (SS4). This assumption agrees with patterns commonly found in other studies (Towns 1981; Hawkins *et al.* 1982, Behmer & Hawkins 1986, Quinn *et al.* 1997; Zimmermann & Death 2002). Periphyton, especially filamentous algae, affects invertebrate community composition and diversity (Ellsworth 2000, Zimmermann & Death 2002). It has been shown that the growth of filamentous algae (*Cladophora* sp.) affects invertebrate colonization in very complex ways: *Cladophora* sp. increases dramatically the space available for invertebrate colonization (Dudley *et al*. 1986), lowers light penetration to substrates (Feminella & Resh 1991) and changes flow patterns across the surfaces (Hart 1992). Although, Cladophora is largely unpalatable and resistant to grazer feeding, there is some evidence that mutualisms exist between Cladophora and invertebrate grazers that consume their epiphytes (Dodds 1991). Also Cladophora filters a lot of seston from the current water leading to accumulations of chironomid midges, which feed on this detritus and use the detritus as material for their tubes (Schönborn, 1996). Invertebrate density was found to be positively related with the amount of filamentous algae present on the stones. In particular the abundance of chironomids, mayflies and caddiesflies increase with increasing amount of filamentous algae. The investigated low-head dam seemed not to affect the growth of filamentous algae per se and this attribute is in contrast to the effect commonly observed at large deep-release storage dams, where nutrient-rich and sediment-poor waters often allow an abundant growth of dense periphyton-mats (Gore 1994). Additionally it is notable that although *Cladophora* sp. was still the dominating filamentous alga found in this study, the importance of this taxon as primary producer in the Ilm, has dramatically changed during the last nine years. In 1992, Schönborn (1996) reported for *Cladophora* sp. dry-mass densities between 207-215 g m^{-2} at open sites and 137 g m^{-2} at a shaded site (approximately 10 km upstream from the study region). In the present study in 2001, densities of *Cladophora* sp. were between 13 to 36 times lower. Vetter (2001) reported similar low values in 1997 at Stadtilm. The change seemed most likely caused by a rapid improvement of the water quality in the Ilm during the last 10 years.

Especially decreasing concentrations of inorganic nutrients (PO_4^{3-}, NO_3^-, and others) seemed to be most responsible for the reduced growth of Cladophora (Vetter 2001).

From the results of the first study part, I accord with the view that invertebrate assemblage succession is affected by both primary production (Pearson & Connolly 2000, Ellsworth 2000) and physical disturbances (Death & Winterbourn 1995, McCabe & Gotelli 2000). Lake (2000) furthermore hypothesized that both act at different scales, were physical disturbances being most important at smaller temporal and spatial scales. Some of the presented results support this view: (1) primary production seemed most important for differences among stream reaches and (2) at all levels of primary production on single stones, variable numbers of individuals occurred and may be the result of different times since last disturbance.

To date there is still only poor knowledge about the role of competitive and predator - prey interactions in structuring invertebrate assemblages of the studied habitat. The colonization index (*S*) used in this study, based on results of a short-time case study and may therefore underestimate real colonization dynamics. Winterbottom *et al*. (1997) showed that the mobility of benthic invertebrates is variable not only among species, but also among seasons and mobility was positively related to discharge and temperature. As stated above, the differences in invertebrate activity (mobility) detected by the index of activity ($\boldsymbol{C_i}$) are close to patterns commonly found in other studies.

Recently Elliott (2002 b) and Miyake *et al*. (2003) presented further evidence for existence of a dispersal continuum from rapid to very slow colonizers and they emphasized that the differences in colonization ability (& activity) among taxa must be taken in consideration when evaluating colonization dynamics of benthic invertebrates. The activity indices of benthic invertebrate taxa used in this study formed clearly a gradient from rapid to very slow colonizers and the assemblages found were composed by various proportions of these colonizers. The colonization index provides further information about the assemblage structure, but the index failed to some extent to describe the successional stage. Although it was possible to determine some major assemblage stages from the collection, which were distinct in many biological attributes, it was impossible to arrange these stages according to a successional pattern from earlier to later ones. The growth of filamentous algae affects succession and it seemed that there are two different successional directions (Figure 3.5). The two least similar groups (cluster 1 & cluster 5; Appendix B, Figure B.2 & B.3) probably represent the latest stages of the two proposed directions. One of this stages (cluster 1) was characterized by a high proportions of slow colonizers (*Ancylus fluviatilis*), combined with low total invertebrate abundance, low amounts of filamentous algae (often not visible), high assemblage diversity and large proportions of predatory and parasitical

invertebrate taxa. The other extreme (cluster 5) was characterized by large amount of filamentous algae, high proportions of early colonists (Chironomidae), low assemblage diversity, and small proportions of predatory and parasitical invertebrate taxa. Nevertheless, the quantification of invertebrate activity provides additional information that may help to understand patchy distribution of benthic invertebrates within the streambed.

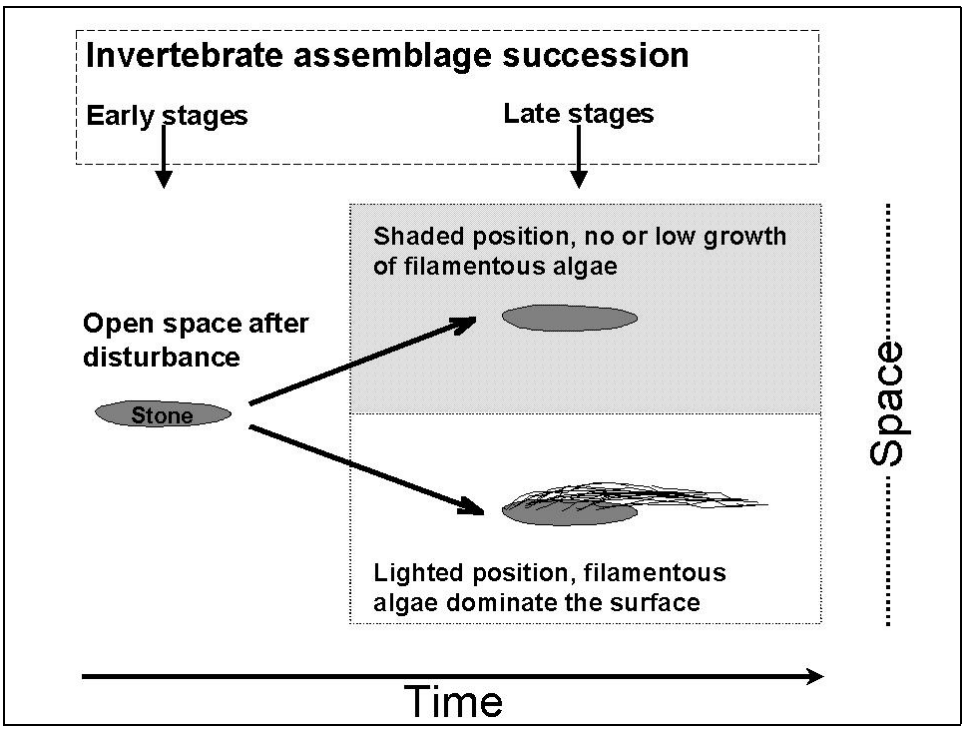

Figure 3.5: Two proposed successional directions for invertebrate assemblages on stones. The direction of assemblages succession after disturbance seems to be affected by the position of stone in the stream (light – dark mosaic) and the colonization and growth of filamentous algae (like *Cladophora* sp.).

Further, it will be necessary to conduct both, experimental and observational studies in order to understand the role of disturbance, periphyton growth, and their interplay in structuring invertebrate assemblages on the stone habitat. Additionally more knowledge about potential competitive and predator - prey interactions and their importance are needed to understand the patchy distribution of benthic invertebrates within the streambed. There was no indication that invertebrate assemblages are modified as a result of a barrier effect caused by the investigated low-head dam. The differences in invertebrate assemblages found among the sample sites seemed best explained by variable growth of filamentous algae, caused by differential degrees of canopy cover. The dam is clearly a physical barrier, but the effect as a barrier seemed unimportant for the maintenance of local invertebrate communities. This view is supported by the results of a study (Elliott 2002 a & c) at a natural barrier (small waterfall). Elliott (2002 a

& c) pointed on the importance of local reproduction of an invertebrate population (*Gammarus pulex* L.) that exceeded the continuous looses trough downstream dispersal, even in the absence of compensatory upstream movement. Also some of the results (Chapter 2 & this Chapter) may support the view that invertebrate communities in headwater streams are highly stationary and this view agrees with a growing number of dispersal studies (for a review see Malmquist 2002).

3.4.2. Invertebrate downstream drift and seston transport

The observed drift density was within the range commonly seen in other streams (<1-153 individuals m^{-3}) throughout the world (Allan 1995, Giller & Malmqvist 1998, Hieber *et al.* 2003). Downstream drift of aquatic invertebrates was modified, within the impoundment. Drift density increased, whereas diversity decreased slightly. Higher total invertebrate densities within the impoundment mainly resulted from higher numbers of planktonic crustacea, caused by locally enhanced population densities of Cyclopoida, Bosmina, and Daphnia. The densities of benthic invertebrates were similar among the sites.

The lower invertebrate diversity in drift samples within the impoundment may be a response to lower diversity of the benthic community in this reach (compare Chapter 2). The invertebrate composition in drift was very similar comparing all four sites but differed to some extent from the observed composition of the benthic communities (compare Chapter 2). The impounded reach of the dam seemed not to act as a trap for invertebrate downstream drift and immediately downstream of the dam (SS3) the invertebrate drift was comparable to that observed in natural reaches. Few drift studies at dams of various size showed that many invertebrates, which are commonly observed to avoid the impoundment, are found in the drift (Kerby *et al.* 1995, Schreiber 1995) and high numbers of lentic crustaceans are commonly observed in the drift below surface and bottom release dams (Armitage & Capper 1976, Zimmermann & Ward 1984, Layzer *et al.* 1989). So far, it seems possible that the impoundment acts temporary, for instance during summer periods with very low discharges, as a trap for drifting invertebrates.

Both the observed drift densities and the taxonomic composition are important with regard to differences in total invertebrate abundance and community composition found at the investigated sites during 2001/2002 (Chapter 2). Only ~30% of the invertebrate taxa present in the benthos were observed in the drift. The higher total invertebrate abundance in the benthos at both dam sites seems not to result in a comparable increase of invertebrate drift densities. There are many studies reporting no direct

relationship between drift rate and benthic invertebrate densities, but others support a relationship, that may depend on factors, like water velocity, type of substratum, season or the life cycle stage (for a review see Elliott 2002 b). From the results of this study, it seems further necessary to consider food availability and the nutritional status of drifting invertebrates.

The transport of particulate matter (PM) was very similar among the sample sites. The averaged concentration of transported POM (28.2 mg m^{-3}) in drift samples was at the lower end of the magnitude reported from other streams (< 10 mg m^{-3} – 4000 mg m^{-3}) (compare Wallace *et al.* 1982, Wallace *et al.* 1991, Wallace *et al.* 1995 b, Wipfli & Gregovich 2002, Hieber *et al.* 2003, Wagner 2003). Selective sedimentation of POM and PIM caused by lower flow velocities, processing of POM and resuspension of fine particulate organic matter (FPOM) within the impounded reach may be responsible for the observed higher percentage of POM in the total seston in comparison to all other reaches. The impoundment of the dam seems to act on the one hand as a temporary sink for POM, but forms on the other hand a POM pool that may contribute FPOM continuously to the reach immediately downstream of the dam. This was indicated by higher POM contents and higher organic proportions of the seston within the impoundment and reduced POM proportions immediately downstream of the dam. Baekken *et al.* (1981 b) reported that the output of FPOM (in this case 0.45 µm – 250 µm) from a impoundment of a low-head dam in Norway was higher than the input of FPOM, leading to the view that POM processing within the impoundment can be an important process. Simple visual comparison of transported POM in the drift samples to FPOM found in benthos – samples suggested that POM in the drift differed to some extent from FPOM in the benthos. The drift – FPOM looked “softer” and contained a large proportion of round particles and algae (clumped), whereas benthos-FPOM was dominated by dark and sharp-edged particles that are probably more refractory. The validity of the results presented is restricted to moderate hydrological conditions as during sampling. Generally, the main particle transport (78% - 88% of the annual export) occurs normally during flood events (Cummins *et al.* 1983, Cuffney & Wallace 1989). It seems further clear that a single sampling date may limit the conclusions that can be drawn and the sampling represents a random spot check. Sampling was done only during daylight, in order to avoid larger drift variability in response to changes light intensity (dusk and midnight) and related drift periodicity of some invertebrate species. It seems necessary to repeat the sampling during night and in several seasons. This was not possible due to methodological and financial constraints of this study.

The small variability observed for physical and chemical parameters was probably influenced by diurnal changes. However, the low differences found, accord with the

results presented in Chapter 2. The dam seems not to affect physical and chemical conditions. Note that the small difference in conductivity between the upstream reference site and the downstream sites is not caused by the small dam and resulted from a temporary, low-concentrated release of water from a small salt-work that is situated between the two upstream sampling sites. The difference in flow velocity between the site immediately downstream of the dam (SS3) in comparison to the natural references shown in Table 3.2 reflect only differences among sampling positions, but not the differences among the sample sites (compare Chapter 2).

Summary

There was no argument that invertebrate assemblages were modified as a result of a barrier effect caused by the investigated low-head dam. The differences in invertebrate assemblages found among the sample sites seemed best explained by variable growth of filamentous algae, caused by differential degrees of canopy cover. Although, the dam is clearly a physical barrier, the effect as a barrier seemed unimportant for the maintenance of local invertebrate communities. The impoundment of the dam seemed not to act as a trap for invertebrate downstream drift. Modifications of invertebrate drift within the impoundment resulted mainly from higher number of planktonic crustacea in the samples, due to local enhanced population densities of these groups. The drift densities of benthic invertebrates were similar among the sampling sites.

Chapter 4

4. The effects of multiple impoundments on the longitudinal zonation of benthic invertebrates

4.1 Introduction

The longitudinal zonation of aquatic invertebrates, a gradual change of invertebrate community structure along stream systems, is a well-known characteristic in undisturbed stream ecosystems. Many stream systems are affected by multiple impoundments along their longitudinal profile and cumulative ecological effects are likely to be profound (Poff & Hart 2002).

Ward and Stanford (1983) developed the serial discontinuity concept (SDC) in order to describe the effects of multiple impoundments of large storage dams. The discontinuities created within the river continuum require certain recovery distances that are dependent on the position of the impoundment along the continuum, but also on the size and operational type of the dam. Generally, little is known about cumulative effects of small, low head dams on the zonational distribution of aquatic invertebrates although they represent the most abundant type of dams.

The aim of this study is to assess the longitudinal zonation of aquatic invertebrates along the Ilm stream. Beside taxonomic diversity and community composition, various biological traits (feeding modes, flow and habitat preference) were used to describe the zonational distribution of invertebrates along the stream gradient. The results were compared with longitudinal patterns of benthic community structure suggested by various basic concepts.

4.2 Methods

Four published data-sets which provide information on the longitudinal distribution of four important taxonomic groups of aquatic invertebrates were reanalyzed: Ephemeroptera (Zimmermann 1995), Trichoptera (Mey 1995), Chironomidae (Samietz 1995), and Coleoptera (Bellstedt 1995). These studies were part of a comprehensive investigation at the Ilm. Seven sampling stations that were continuously distributed along the longitudinal profile of the Ilm stream were used in these studies (Figure 4.1). The sampling stations were similar among the four base – studies. Additional details of the study region are presented in Chapter 2.

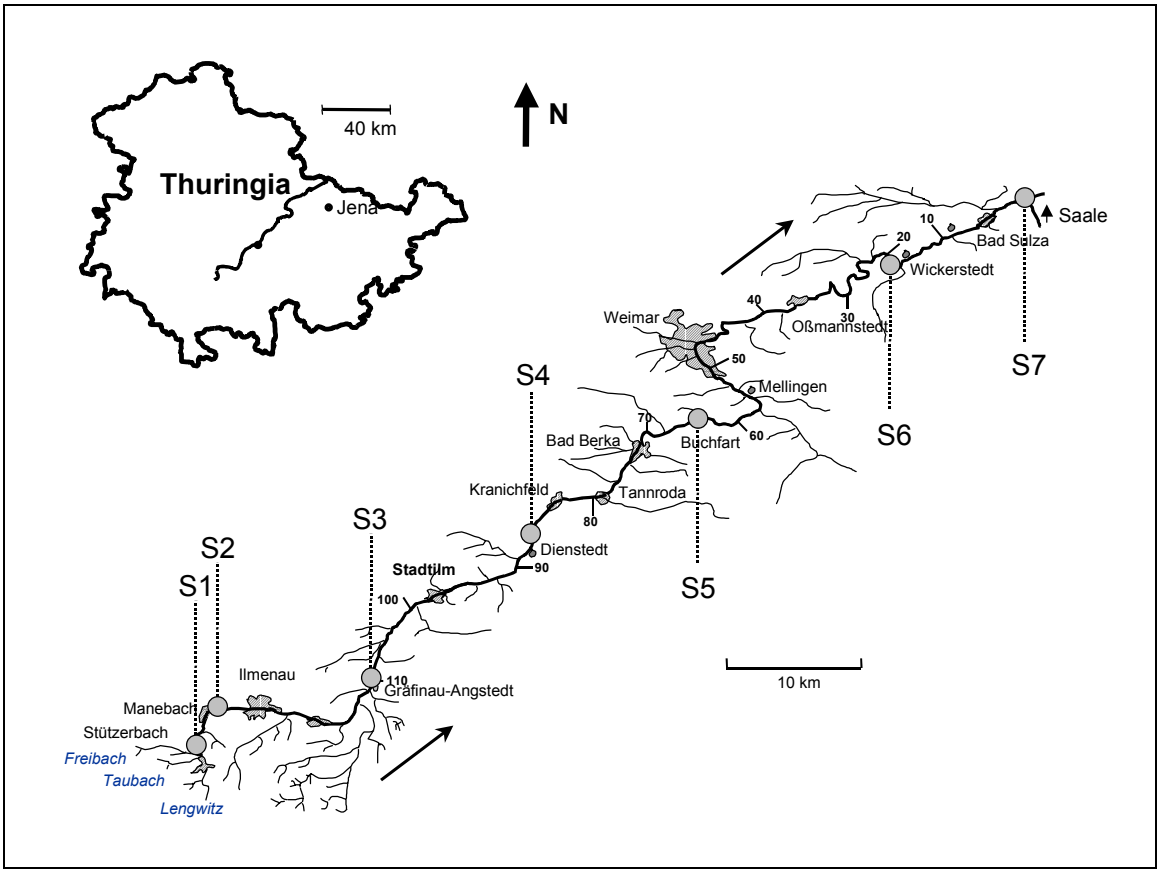

Figure 4.1: Maps of Thuringia and a detailed view of the Ilm stream. Sampling stations are denoted as S1 to S7.

Major physical and chemical characteristics of the sampling stations are given in Table 4.1. In addition to damming by many small low-head dams, the Ilm has been affected by further anthropogenic disturbances. The stream was heavily polluted in the past (~1960 to 1992). Table 4.1 summarizes long term mean values (1976 – 1992) for some chemical factors (nitrate, ammonium, nitrite, chlor, ortho-phosphate and sulfate) (after Polz unpublished data). The concentrations of most of the chemical parameters increased from upstream to downstream sections of the stream.

Table 4.1: Physical, chemical, geographical and geomorphological characteristics of the sampling stations along the Ilm profile.

	Station code						
	S1	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**
Station features							
Location name	Freibach - Stützerbach	Manebach	Gräfinau - Angstedt	Dienstedt	Buchfart	Apolda - Nauendorf	Groß-heringen
Map reference (MTBQ)	5331/3 h 5612. 700 r 4419. 870	5331/1 h 5616. 875 r 4420. 400	5332/1 h 5618. 400 r 4430. 750	5232/2 h 5629. 250 r 4440. 950	5033/4 h 5642. 800 r 4452. 550	4935/1 h 5657. 300 r 4467. 759	4835/4 h 5667. 400 r 4476. 800
Geological formation	Zechstein	Zechstein	Variegated sandstone	Limestone	Limestone	Keuper	Keuper
Elevation (m) a.s.l.	580	507	410	328	252	146	115
Distance from mouth (km)	130	122	110	85	65	18	0
Slope (%)	20	12	7	4	3	2	2
Channel width (m)	1	3	10	10	10	15	20
Number of dams (accumulated)	0	0	9	20	28	48	56
Water quality							
NO_3^- (mg l^{-1}) ‡	8.80	9.90	11.20	18.90	25.10	26.40	24.30
NH_4^+ (mg l^{-1}) ‡	0.57	0.25	1.91	1.17	1.06	1.70	2.24
NO_2^- (mg l^{-1}) ‡	0.08	0.07	0.32	0.32	0.37	0.72	0.68
Cl^- (mg l^{-1}) ‡	9.70	10.40	21.60	81.00	63.80	56.20	93.10
PO_4^{3-} (mg l^{-1}) ‡	0.39	0.33	1.86	1.99	1.84	2.35	2.52
SO_4^{2-} (mg l^{-1}) ‡	26.90	29.90	57.00	83.90	178.00	272.00	256.50

‡ long-term mean values from 1976 to 1992 (after S. Polz, FSU Jena, unpublished data).

Aquatic invertebrates were sampled using various methods: benthos collections (semi-quantitative & qualitative), net – captures (aquatic & terrestrial; qualitative), and light trappings (qualitative). Multiple sample collections were performed during 1992 and 1993, but not always simultaneously among the base studies. Therefore all data were pooled for the entire sampling period and the following analyses were performed on presence / absence data and partly on rank- abundance data (see below). The taxon richness at each sampling station was determined for the entire sampling period in order to examine trends along the stream profile. To assess variation in invertebrate community composition among the sampling stations, correspondence analyses (CA) (Jongman *et al.* 1995) were conducted. CA was performed twice, firstly on rank-abundance data and secondly on presence / absence data. In the first analysis, only the data for Ephemeroptera, Trichoptera, and Chironomidae were used, because for the Coleoptera data set only presence / absence data were available. All taxa were ranked

on the basis of their relative abundance (dominance) into four groups (Table 4.2) following Samietz (1995):

Table 4.2: The four categories used to rank the invertebrates by their abundance.

Group	Rank value	Description
1	0	The taxon was not found at the sample station
2	1	The taxon reached a relative abundance <2% (rezedent)
3	2	The taxon reached a relative abundance >2%-≤10% (subdominant)
4	3	The taxon reached a relative abundance >10% (dominant)

The rank values for each taxon at each sampling station were used in the first analysis. The second analysis was performed on presence / absence data of the full data set (Ephemeroptera, Trichoptera, Chironomidae and Coleoptera). To minimize the influence of taxa that normally do not occur in streams, in both analyses all limnobiont and limnophil taxa (occurrence restricted to stagnant waters; after Schmedtje & Colling 1996) were excluded. Limnobiont and limnophil taxa potentially occur in the data set, because of the sampling methods used. Net – captures (aquatic & terrestrial, qualitative) and light trappings (qualitative) in particular may cause this problem. In the CA on rank-abundance data only four taxa were excluded and in the CA on presence / absence data 11 taxa were excluded. In both analyses, an arch effect was present. To remove this effect detrended correspondence analyses (DCA) (Jongman *et al.* 1995, ter Braak & Smilauer 1998) were also performed. However, the interpretations on the basis of the results of CA and DCA were similar and therefore only the results of CA are presented here. The levels of identification were sufficient to allow assignment of functional-feeding group designation following Schmedtje & Colling (1996). However, from a total of 149 taxa present only 81 taxa could be classified. Especially a high number of Chironomidae with unknown or unclear modes and strategies of feeding were responsible for this reduced number. Because many aquatic invertebrates can be classified into more than one functional-feeding group the point–scores (Punktzahl) described by Schmedtje & Colling (1996) were adopted. The point–scores describe the relative proportion of a feeding mode in comparison to other feeding modes realized by a specific taxon. The point-scores can range from 0 to 10. No value (0) indicates that the taxon does not belong to the specific functional-feeding group and 10 indicate that the taxon realizes the specific feeding mode exclusively. For taxa with more than one realized feeding modes, the sum of all point–scores is always 10. The sum of all point–scores was determined for each functional-feeding group separately for each sampling station on the basis of presence / absence data for all taxa occurring at the defined sampling station. Furthermore the sum of all point-scores for each sampling station was

determined. The contribution of each functional–feeding group relative to all others was determined using the following equation:

$$a = \frac{b \cdot 100\%}{c} \qquad \textbf{(EQ. 4)}$$

where *a* is the proportion of a defined functional-feeding group at a sampling station; *b* is the sum of all point–scores for a defined functional-feeding group found at a sampling station and *c* is the sum of all point–scores for all calculated functional-feeding groups found at a sampling station.

In order to explore the zonational distribution of invertebrates along the stream profile the classification provided by Schmedtje & Colling (1996) was used. The classification describes the occurrence and preference of aquatic invertebrate taxa along a stream continuum. The categories (biocoenotic regions) are shown in Table 4.3. Occurrence and preference of aquatic invertebrates are indicated by point-scores. The point-scores provide a relative measure of preference for invertebrate taxa to occur in one of the eight biocoenotic regions. The point-scores can range from 0 to 10, no value (0) indicate that a specific taxon shows no preference for the specific stream region (does normally not occur there) and ten (10) indicates a complete preference or restriction (strong association) of a taxon to the specific biocoenotic stream region.

Table 4.3: The eight categories, their codes, and rank scores used for analysis (partly after Schmedtje & Colling 1996). The categories represent typical biocoenotic regions.

Biocoenotic region	Code	Rank - score (r)
Eukrenal	EK	1
Hypokrenal	HK	2
Epirhithral	ER	3
Metarhithral	MR	4
Hyporhithral	HR	5
Epipotamal	EP	6
Metapotamal	MP	7
Hypopotamal	HP	8

For species with preferences for more than one biocoenotic stream region, the sum of all point-scores is always 10. An indicator value (*I*) was calculated for each taxon in the data set using the following equation:

$$I_i = (r_{EK} \cdot p_{EKi} + r_{HK} \cdot p_{HKi} + ... + r_{HP} \cdot p_{HPi}) \qquad \textbf{(EQ. 5)}$$

where I_i is the indicator value for taxon *i*; r_{EK}... r_{HP} is the rank score for each biocoenotic region; p_{EKi}...p_{Hpi} is the point-score (preference) for taxon *i* for a specific biocoenotic region (*EK*..*HP*).

The indicator value (*I*) can range between 10 and 80 (without units), the minimum (10) is reached when a taxon is completely restricted in occurrence to the epikrenal zone and the maximum (80) is reached when the occurrence is completely restricted in to the hypopotamal zone. Subsequently a zonational index *(Z)* was calculated using the following equation:

$$Z = \frac{\sum_{i=1}^{N} I_i}{N} \qquad \textbf{(EQ. 6)}$$

The Index *(Z)* simply represents the mean of all indicator values (*I*) at a sample station and describes the biocoenotic region on the basis of the occurrences of invertebrates. From the total of 149 taxa present, 82 taxa were classified by their occurrence and preference for the eight biocoenotic regions: 17 taxa for Ephemeroptera, 37 taxa for Trichoptera, 13 taxa for Chironomidae and 15 taxa for Coleoptera).

In order to investigate changes in flow preference of the invertebrate community along the Ilm gradient seven preference categories were used [Table 4.4, after Schmedtje & Colling (1996)]. From the total of 149 taxa present, 79.9 % (119 taxa) were classified by their flow preference (17 taxa for Ephemeroptera, 42 taxa for Trichoptera, 35 taxa for Chironomidae and 25 taxa for Coleoptera). For each sampling station, the number of taxa belonging to one of the seven preference categories was determined and the relative contribution of flow preference was calculated for each station. In a first steps all seven categories were used. To clarify the pattern, in a second step the number of categories was reduced from seven into three categories (R, L, & IN). The category “R” includes all taxa with preference for running waters and was calculated as the sum of the percentages of rheo- / limnophil (RL), rheophil (RP) and rheobiont (RB) taxa. The category “L” includes all taxa with preference for stagnant waters and was calculated as the sum of the percentages of limno- / rheophil (LR), limnophil (LP) and limnobiont (LB) taxa. The category “IN“ is similar to the first classification.

Because longitudinal zonation of invertebrates should also reflect changes in benthic habitats and their composition, the invertebrates were classified by their preference for specific benthic habitats using Schmedtje & Colling (1996). The eight habitat categories used are summarized in Table 4.5. Because many invertebrate species have preferences for more than one habitat; a preference index (Punktzahl) described by Schmedtje & Colling (1996) was used.

Table 4.4: The seven flow preference categories, their codes, and a description of the categories used for analysis (after Schmedtje & Colling 1996).

Category	Category code	Description of the category
limnobiont	LB	Occurrence restricted to stagnant waters
limnophil	LP	Preferably occurring in stagnant waters, avoiding flow, sometimes but rarely in slow running waters
limno- / rheophil	LR	Dominant in stagnant waters, but also occurring in slow running waters
rheo- / limnophil	RL	Dominant in running waters, preferring slow flow, but also occurring in stagnant waters
rheophil	RP	Preferably occurring in running waters
rheobiont	RB	Occurrence restricted to running waters
indifferent	IN	No preference for running or stagnant waters

This index can range from 0 to 10, no value (0) indicates no preference for a specific habitat category and ten (10) indicates a complete preference or restriction (strong association) of a taxon to a specific habitat category. For species with preferences for more than one habitat category, the sum of all preference values is always 10. From the total of 148 taxa present, 66.9 % (99 taxa) were classified by their habitat preference: 16 taxa for Ephemeroptera, 32 taxa for Trichoptera, 27 taxa for Chironomidae and 24 taxa for Coleoptera. The proportion of each habitat category relative to the others was calculated according to **EQ. 4** (see above). Here *a* is the proportion of a habitat category at a sampling station, *b* is the sum of preference values for a specific habitat category at a sampling station and *c* is the sum of preference values for all habitat categories at a sampling station.

Table 4.5: The eight habitat-preference categories used in this study (after Schmedtje & Colling 1996).

Abiotic & Biotic Habitats (Habitat code)		Description of the category
Abiotic	Pelal (PEL)	mud, loose sediments with grain sizes < 0.063 mm,
	Argillal (ARG)	clay & loam, stable sediments with grain sizes < 0.063 mm,
	Psammal (PSA)	sands (grain size 0.063 – 2 mm)
	Akal (AKA)	fine and medium gravel (grain size 0.2 – 2 mm)
	Lithal (LIT)	coarse gravel, pebble, boulders (grain size > 2 mm)
Biotic	Particulate organic matter (POM)	dead wood, trees, tree roots, twigs, sticks, leaf, layers of fine organic detritus and others
	Phytal (PHY)	submerge plants, filamentous algae
	Others	Other habitats

4.3 Results

A total of 149 taxa were found along the longitudinal gradient of the Ilm. Taxon richness ranged between 31 taxa and 62 taxa (Table 4.6) and decreased continuously from upstream to downstream sampling stations. Ephemeroptera and Trichoptera richness were most responsible for this pattern. For Chironomidae, there was no distinct trend in taxon richness along the stream profile, whereas the number of taxa belonging to Coleoptera tended to increase downstream.

Table 4.6: Invertebrate taxon richness at seven sampling stations along the longitudinal profile of the Ilm during 1992-93.

	Sampling station							
Taxonomic group	***S1***	***S2***	***S3***	***S4***	***S5***	***S6***	***S7***	***Total (sum)***
Ephemeroptera	13	14	5	5	6	3	2	19
Trichoptera	23	17	10	10	6	6	4	48
Chironomidae	18	24	22	16	14	17	17	54
Coleoptera	8	5	7	7	16	14	8	28
Total (sum)	***62***	***60***	***44***	***38***	***42***	***40***	***31***	***149***

Correspondence analyses on rank-abundance data (Figure 4.2) and on presence / absence data (Appendix C, Figure C.1) obtained very similar results. In both cases, there was a clear upstream – downstream gradient for the occurrence of invertebrates. There was an arch effect (Jongman *et al.* 1995), a compression of the gradient along the first axis. The continuous distribution of invertebrates along this gradient indicated the existence of a longitudinal zonation of invertebrates along the Ilm profile. This pattern was also confirmed by detrended correspondence analyses (DCA). All taxa included in CA analyses and their codes are summarized in Table C.1 (Appendix C).

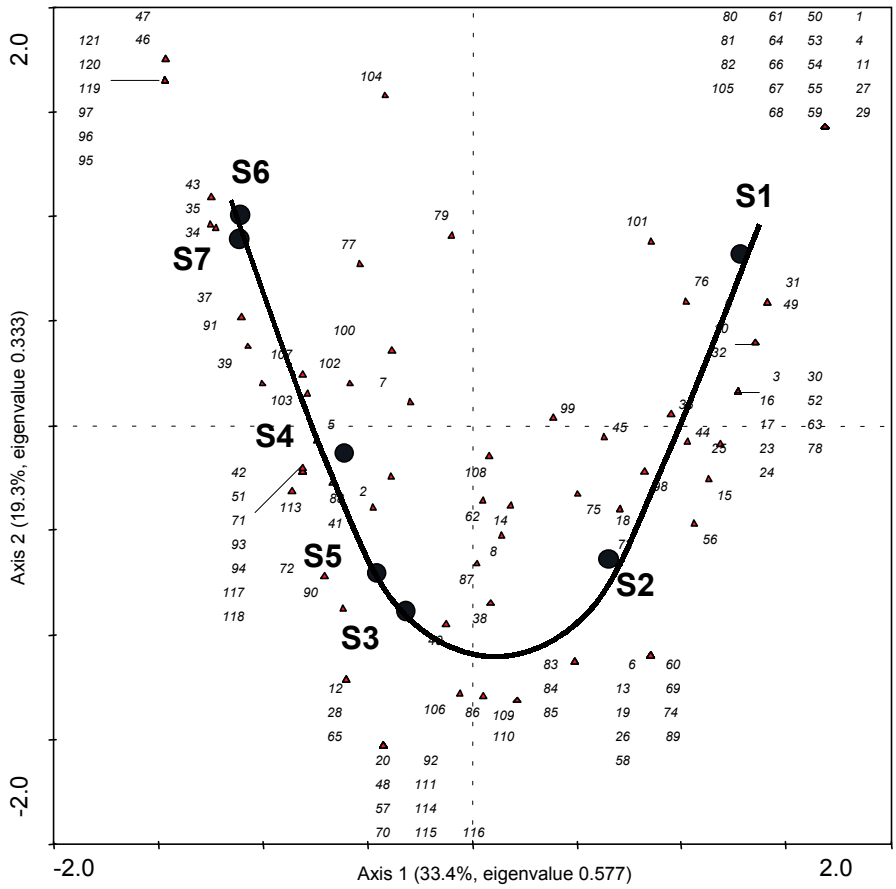

Figure 4.2: Ordination plot of a correspondence analysis based on the on rank - abundance of 117 invertebrate taxa (Ephemeroptera, Trichoptera, Chironomidae, and Coleoptera) at seven sampling stations at the longitudinal profile of the Ilm during 1992-93. Sampling stations are shown as circles (S1 to S7). Invertebrate taxa are shown as triangles and the number indicate the taxon code (see text). The curved black line describes the stream gradient.

Functional feeding group composition was influenced by the limited number of taxonomic groups analyzed. At all scraper (35.9%), collector (gatherers + filterers, 33.9%) and predatory functional traits (19.6%) were most common (Figure 4.3). Shredder and scraper contribution tended to decrease, whereas collector – filterer contribution tended to increase along the stream gradient. In addition, the proportion of taxa with “other” functional feeding traits tended to increase downstream. Especially the macrophyte piercers and wood gougers were responsible for this pattern.

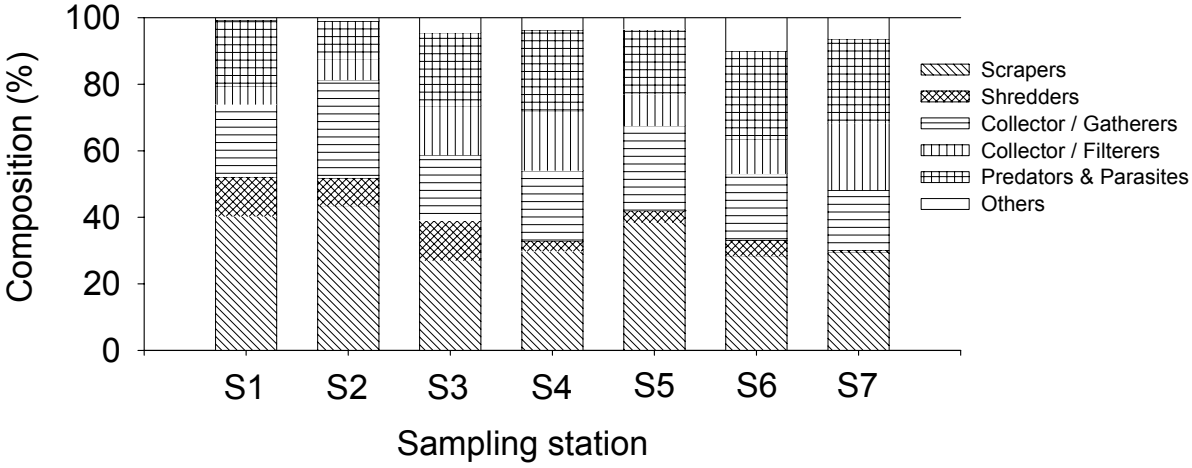

Figure 4.3: Functional feeding group composition along the stream profile of the Ilm during 1992/93.

The zonational index (*Z*) ranged from 36.3 (Epirhithral = 30; Metarhithral = 40) to 53.8 (Hyporhithral = 50) and increased continuously from upstream to downstream sampling stations (Figure 4.4). The calculated zonational index *(Z)* fits closely to the expected trend that was estimated on the basis of the zonational stream classification after Braukmann (1987), but showed a different pattern in comparison to the zonational trend published in Schönborn (1995).

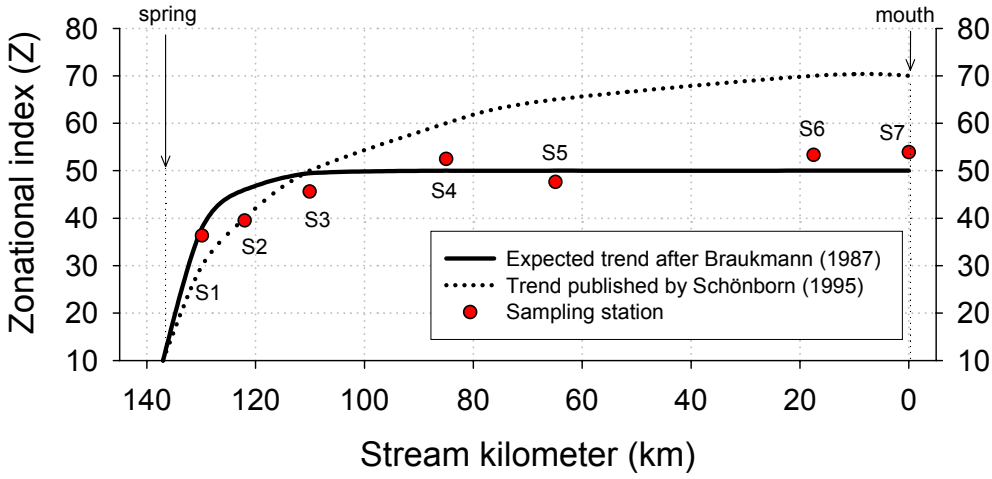

Figure 4.4: Biocoenotic zonation at the Ilm, indicated by the zonational index *(Z)*. The Index can range between 10 (Epikrenal zone) to 80 (Hypopotamal zone). spring = 137 km (stream kilometer); mouth = 0 km (stream kilometer). Circles indicate the situation at the seven sampling stations used in this study during 1992/93. Solid black line describes the expected trend, estimated on the basis of a stream classification after Braukmann (1987). Dotted black line describes a trend published in Schönborn (1995).

Flow preference composition changed continuously from upstream to downstream sampling stations. The contribution of indifferent (IN) and limno- / rheophil taxa increased, whereas the contribution of rheobiont taxa decreased along the stream gradient (Figure 4.5 A). The pattern became clearer after reducing the number of categories (Figure 4.5 B). The contribution of invertebrate taxa with preference for running waters “R” decreased and the contribution of taxa with preference for stagnant waters (L) and taxa without strong preferences to flow (IN) increased continuously along the stream gradient.

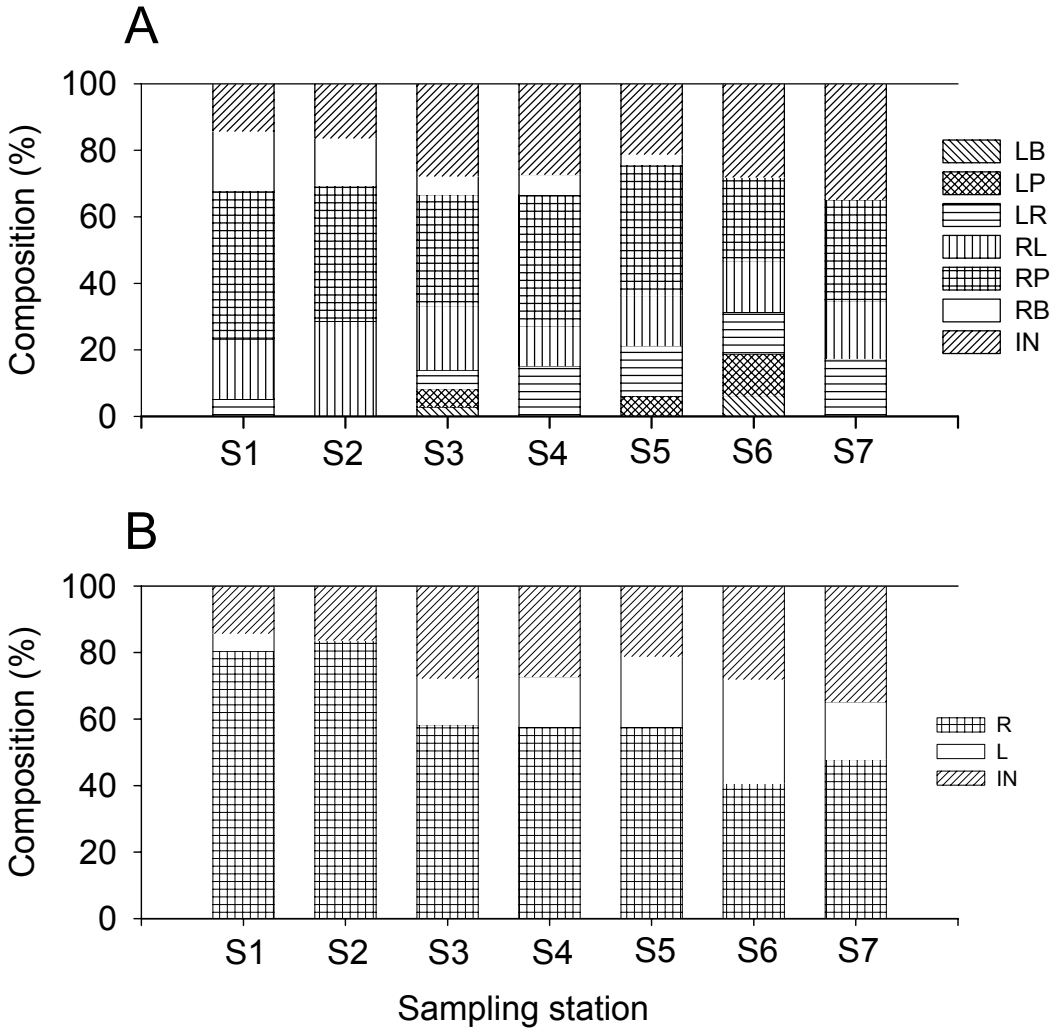

Figure 4.5: Changes in flow preference composition of invertebrate communities along the stream profile of the Ilm during 1992/93. (A) Relative contribution of seven flow preference types (LB, LP, LR, RL, RP, RB & IN) at the sampling stations (S1 –S7). LB – limnobiont, LP – limnophil, LR – limno-/ rheophil, RL – rheo- / limnophil, RP – rheophil, RB – rheobiont, IN – indifferent. (B) Relative contribution of three flow preference types (R, L, IN) at the sampling stations (S1 –S7). L is the sum of LB, LP, and LR values; R is the sum of RL, RP, and RB values.

Habitat preference composition of the invertebrate communities changed along the stream profile (Figure 4.6). Relative contribution of taxa with preference for low grain size habitats (Pelal & Argillal) increased downstream, whereas preference for habitats with large grain sizes (Akal & Lithal) decreased. No remarkable trends where observed for the preference to biotic habitats (POM & Phytal).

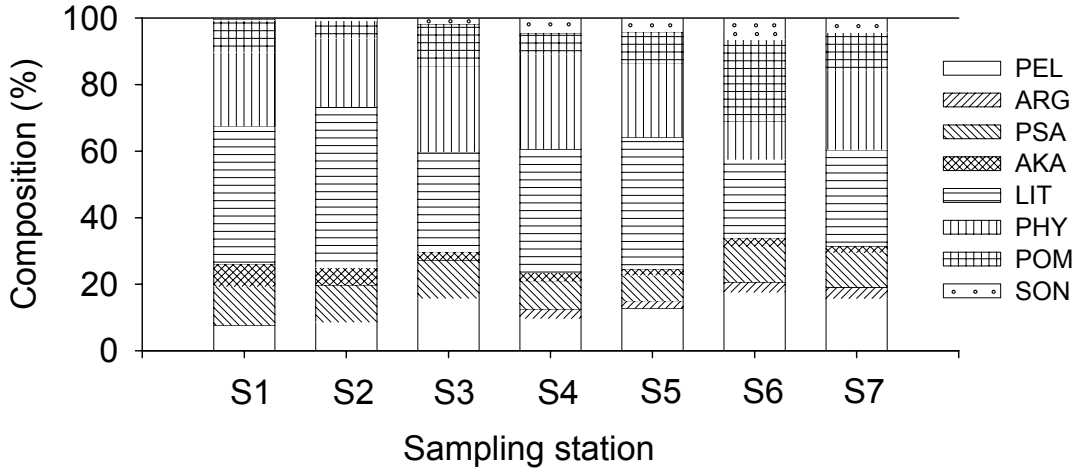

Figure 4.6: Changes in habitat preference composition of invertebrate communities along the stream profile of the Ilm during 1992/93. PEL – Pelal (mud & loose sediments; <0.063 mm); ARG – Argillal (clay & loam; <0.063 mm); PSA – Psammal (sands; 0.063-2 mm); AKA – Akal (fine & medium gravel; 0.2-2 mm), LIT – Lithal (coarse gravel, pebble, boulders; >2 mm), POM – particulate organic matter, PHY – Phytal (submerge plants, filamentous algae), SON – other habitats.

4.4 Discussion

In natural streams, the biotic diversity seems correlated with environmental variability (Vannote *et al.* 1980, Statzner & Higler 1985 & 1986). The river continuum concept (Vannote *et al.* 1980) indicates that the biological diversity (taxon richness & Shannon index) is highest in the mid-reaches of natural streams in temperate climates and the pattern is attributed to the high variability of the environmental factors within this region. An alternative pattern was described by Statzner and Higler (1986), they found a significant correlation between invertebrate diversity and the location of transitional zones between low and high hydraulic stress along longitudinal stream profiles (elevation gradients). High invertebrate diversity in these transitional zones is attributed to increased availability of substantially different hydraulic microhabitats. None of these two patterns was found at the Ilm. The authors of three of the four baseline studies (Zimmermann 1995; Mey 1995; Bellstedt 1995) used for the analyses emphasized the occurrence of a strongly modified “Species-Deficit-Concept” (Artenfehlbetrag; Kothe 1962) for the Ilm. Especially the very low taxon richness for Ephemeroptera and

Trichoptera at the downstream sampling stations seemed affected by anthropogenic disturbances, particularly from organic and inorganic pollution due to intensive agriculture and urbanization.

However, as implied by the results of correspondence analyses and the zonational index *(Z)* a longitudinal zonation of aquatic invertebrates is still present at the Ilm. The stream is a tributary of a large stream continuum (Elbe river system) and consists only of krenal and rhithral parts as indicated by the zonational index *(Z)*. The longitudinal trend described by the zonational index fits closely to a pattern predicted from a zonational classification based on stream order (Braukmann 1987).

The classification of the invertebrates by their preference to flow revealed a clear pattern. Upstream sampling stations were clearly dominated by taxa with strong preference for running waters, whereas at downstream sampling stations the proportion of taxa with a stronger preference for stagnant waters and taxa without preference to running or stagnant waters increased. The observed change in flow preference along the stream may reflect the general changes in stream geomorphology (e.g. slope). The slope is an important determinant of the types of microhabitats available and affects the hydraulic stress (thickness of the laminar layer on substrates) on the stream bottom (Statzner & Higler 1985 & 1986). Decreasing slope along the investigated stream gradient should lead to an increase of the thickness of the laminar layer on the substrate, which lowers the hydraulic stress on the stream bottom in downstream reaches. In addition, the proportion of large grain size microhabitats should decrease and the proportion of small size microhabitats should increase from upstream to downstream sampling stations. The estimations of habitat composition on the basis of the habitat preference of the invertebrates present at the sampling stations confirmed these longitudinal trends.

Longitudinal trends in functional-feeding group composition are normally analyzed on the basis of relative abundance (numbers and/or biomass). Both the number of taxonomic groups (Ephemeroptera, Trichoptera, Chironomidae & Coleoptera) used and the general data format (presence / absence), limits the conclusions that can be drawn. However, the described trends found for some functional-feeding groups are in line with the trends predicted by the RCC (Vannote *et al.* 1980).

There were no small dams within the upstream region of the stream and two uppermost stations (S1 & S2) showed highest taxon richness and the community composition differed from those observed at the other downstream stations. However care must be taken in interpreting this difference as a response to the dams, because invertebrate community structure significantly differs with altitude, especially above and below 400 a.s.l. (Schönborn 1992, Bauernfeind & Moog 2000). This difference is presumably

caused by changes in many characteristics of the surrounding terrestrial ecosystem (vegetational zonation and others) as well as in flow velocity / gradient. Furthermore, no sharp transition in functional feeding group structure, flow preference composition and habitat preference composition of the invertebrate communities between the two uppermost stations (S1 & S2) and the downstream stations were observed.

There is evidence that pollution can dramatically affect diversity leading to a disappearance of any relation to stream order (Statzner 1981, Minshall *et al*. 1982). In contrast, little is known about general effects of both single low head dams and about cumulative effects of multiple low head dams as well. The results of the intensive investigation at a single small low-head dam (Chapter 2) showed that changes in benthic communities are spatially restricted to stream reaches immediately upstream and downstream of the dam and therefore potentially little or no cumulative effects occur. This view is also supported by the observed change of the zonational index *(Z)* along the stream profile.

The changes of the invertebrate community structure that occur within the impoundments of large storage dams seemed often similar to the changes that occur from rhithral zones to potamal zones in natural streams (Schönborn 1992). On the other hand, the reaches immediately downstream of large storage dams are not only influenced by physical and chemical factors of the released water, because alterations in flow patterns affect the distribution of substrate particles and change the availability of microhabitat. As a consequence the invertebrate community structure immediately downstream of large storage dams can also be more similar to those of areas farther upstream (Stanford & Ward 1984). Today little is known about cumulative effects of multiple dams and their impoundments (small and large dams) on the remaining lotic system. In this context by Ward and Stanford (1983) hypothesized: if a factor that is modified by upstream impoundment of a large dam has not been returned to normal levels before reaching the next reservoir, the possible interaction can probably be neutral, cumulative or ameliorative. Also the extent of such interactions is unclear. If cumulative effects caused by multiple small low-head dam occur in the Ilm, the zonational distribution of invertebrates should be affected. But this was clearly not found at the Ilm. As stated above the observed change of the zonational index *(Z)* along the stream profile of the Ilm fits closely to a pattern predicted from a zonational classification based on stream order (Braukmann 1987).

Given the long history of pollution of the Ilm, it seems likely that this source of anthropogenic disturbance is most important for the observed modified “Species-Deficit-Concept” (Artenfehlbetrag, Kothe 1962). This view is further supported by changes in the invertebrates communities since 1990 – 1992. After the political reunification of

Germany in 1990, many agricultural and industrial production sites were shut down. Many waste-water treatment plants were built, resulting in a rapid improvement of the water quality in the Ilm, as in other streams. At Stadtilm, the saprobity index (Pantle & Buck 1955), decreased since 1989 from III – α-mesosaprob (heavily polluted) to II – β-mesosaprob (moderate polluted) in 2000 (TLU Jena, Germany, unpublished data) and until today the index has tended to decrease further (own calculations, not shown). The drastic change in the saprobity index clearly indicates a fast regeneration of the stream ecosystem.

However, in order to weight the various sources of anthropogenic disturbances that occur in the Ilm stream (pollution & damming by small low-head dams) by their relative importance on invertebrate communities further carefully designed, comparative studies are needed and the data presented in this study provide a broad basis for future comparisons.

5. Experiments on invertebrate feeding and detritus processing

5.1 Introduction

A central question for the understanding of ecosystems is: “What are the trophic pathways through which the energy of organic matter resources is transferred within food webs?”.

Stream invertebrates are central components in stream food webs. They are essential to stream nutrient cycling by consuming and transforming organic matter and they are important in transferring energy to higher trophic levels. The functional feeding group concept (FFGC), developed by Cummins (1973, see also Cummins and Klug 1979), has largely enhanced the understanding of stream nutrient cycling and trophic interactions. The FFGC divides stream invertebrates on the basis of autecological similarities (mouthpart specialization’s, feeding strategies) into five major groups: shredders, gathering-collectors, filtering-collectors, scrapers (grazers), and predators. In analyses of stream food webs the functional feeding groups were commonly used as trophic guilds with a primary food resource for each guild so that shredders utilize coarse particulate organic matter (CPOM), gathering-collectors utilize benthic fine particulate organic matter (FPOM), filtering-collectors utilize drift FPOM, scrapers utilize periphyton and predators derive their metabolic energy from living animal tissue. The FFGC and especially the usage of functional feeding groups as trophic guilds have been criticized because mouthpart specialization does not necessarily indicate obligate resource utilization (Minshall 1988). The revised version of the FFGC (Merritt & Cummins 1996) takes into account that many aquatic invertebrates are trophic generalists rather than obligate feeders, meaning that they are not restricted to one type of food. However, Mihuc & Minshall (1995) furthermore pointed out the importance of determining resource assimilability for consumers to establish food web links (see also Mihuc 1997).

In recent years the ratio of stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) have been increasingly used as natural-abundance tracers to reconstruct diets and to estimate the trophic position of the animals, because the $\delta^{15}N$ of a consumer is typically enriched by +3.4‰ (range 3-4‰) relative to its food (DeNiro & Epstein 1981, Minagawa & Wada 1984, Cabana & Rasmussen 1996), whereas the stable carbon isotope ratio ($\delta^{13}C$) of a consumer seems more to reflect those of its food source (±0‰ to +1‰) (DeNiro & Epstein 1978, Fry and Sherr 1984, France 1995). Therefore, stable isotope ratios of consumers and resources seem useful to trace the flow of energy through the ecosystem. Today there is a considerable number of field studies using stable isotope data of consumers and resources and the above standard trophic fractionation values in

order to determine the trophic structure of the food web. Furthermore, this method was successfully used to detect food web alterations caused by human disturbances (Thorp *et al*. 1998, Benstead & Pringle 2004). In a large number of cases, it seems very difficult to determine trophic linkages based on standard trophic fractionation values; however, this fact is not often stated. Although this complication can arise from a number of factors, the selective incorporation (assimilation) of specific components from heterogeneous detritus pools is probably one of the most important factors (Thorp *et al*. 1998). Today it seems practically impossible to isolate specific components from a pool of detritus (bacteria, fungi, algae, ciliates, flagellates, other biofilm components, allochthonous & autochthonous POM) for separate isotopic analysis (Hamilton *et al*. 1992, Ponsard & Arditi 2000). Therefore, knowledge of differences in stable isotope composition between detritus and consumers determined in quasi no choice experiments (only detritus and invertebrates present) will provide information that can increase the possibility to more properly interpret stable isotope data from the field. Recently, Gannes *et al*. (1997) pointed out the importance of laboratory experiments in order to interpret field data correctly.

Furthermore stable isotope ratios are suggested to be in-stream markers of organic matter breakdown (Wagner 2003, Guo *et al*. 2003) in the field. Breakdown is a key function in stream ecosystems and essential to the energy flow. Allochthonous organic matter, especially leaves and other components from riparian trees and vegetation are the primary energy sources in temperate headwaters (Fisher & Likens 1973, Cummins & Klug 1979, Cummins *et al*. 1989). After entering a stream this material becomes detritus, a term defined as dead particulate organic matter >0.45 µm inclusive all associated microbes (bacteria & fungi), protozoa and micro-invertebrates (Boling *et al*. 1975). The two major processes that happen with the organic matter are: breakdown and transport (Webster *et al*. 1999) and the simultaneous occurrence of these processes is commonly referred as stream spiraling (Webster & Patten 1979, Webster & Patten 1979, Newbold *et al*. 1982, Elwood *et al*. 1983). Downstream transport and retention of organic matter are critical functions in lotic ecosystems, because they control the loss of nutrients, particle-associated energy, and connect upstream processes with downstream ones (Hall *et al*. 1996). Breakdown is a result of the combined action of physical, chemical and biological processes (Webster *et al*. 1999) and occurs in three stages: leaching, microbial colonization (conditioning) and fragmentation by physical forces and invertebrate feeding (Suberkropp 1998). During these processes, the organic matter undergoes various steps of physical and biochemical transformation. As a result of breakdown, the particle size and the C/N ratio of the material decrease (Schönborn 1992). Additionally it seems that there is a regular

change in isotopic composition (Melillo *et al*. 1989, Finlay 2001). Therefore particle size, C/N ratios and isotopic composition are suggested to be in-stream markers of organic matter breakdown (Wagner 2003, Guo *et al*. 2003) in the field. By combining these measures, alterations of in-stream breakdown are possibly detectable.

The impoundments of large storage dams disrupt the detrital transport and alter the spiraling of nutrients and organic matter (Ward & Stanford 1983 & 1995). For instance, Short & Ward (1980) found that leaf breakdown was faster in a regulated river in comparison to an unregulated river. Small low-head dams also affect the downstream transport, but little is known about their effects on particulate organic matter breakdown. Although the rate of breakdown could be measured relatively easy by placing known amounts of leaf litter in packs or mesh bags in a stream and periodically determining the amount of organic matter remaining (Suberkropp 1998), little is known about the amount, the particle size structure and the chemical composition of FPOM released during breakdown and it is not easy to trace the fate of this material.

The suitability of chemical and isotopical markers was recently tested in a field study at a low-head dam in the Ilm stream (Wagner 2003). Note that this dam was the same dam investigated in Chapters 2 & 3 in the present study. Although the resolution provided by the C/N ratio was found as too low for detecting differences in the chemical composition of particulate organic matter between dam sites (impoundment & the site immediately downstream of the dam) and a natural reference site, the stable isotope composition of particulate organic matter indicated differences among the sites. However, Wagner (2003) emphasized the necessity of experimental studies on detritus processing in order to properly interpret stable isotope data from field samples.

The present study focuses on the utilization of leaf resources by two benthic macro-invertebrate species: *Gammarus pulex* L. (Crustacea; Amphipoda) and *Baetis rhodani* Pictet (Insecta; Ephemeroptera). Both species were chosen for several reasons. *G. pulex* is one of the most intensively investigated macro-invertebrate species in freshwater ecosystems, and is very abundant in small hard water streams in Thuringia, Germany. In a comprehensive study (Chapter 2) at the Ilm densities up to 2160 Ind. m^{-2} were found. Böhm *et al*. (1995) reported densities up to 8000 Ind. m^{-2} in downstream sections of this stream. This species is commonly considered as a facultative shredder as well as an omnivorous species, because *G. pulex* has the capacity to feed and grow on alternative food sources (Merritt & Cummins 1996) other than CPOM. Given the choice between different food sources, *G. pulex* exhibits a high degree of food selectivity (Arsuffi and Suberkropp 1989, Friberg & Jacobsen 1994). The mayfly, *Baetis rhodani* is the most abundant Ephemeropteran species in the Ilm stream. *B. rhodani* is

commonly considered as a scraper, feeding on epilithic biofilms and algae communities (periphyton). Although the scraper – feeding mode is dominant (~80% of feeding traits), *B. rhodani* seems also to be able to perform as a collecting gatherer (~20% of feeding traits) (Schmedtje & Colling 1996). The FFGC does not predict that this species utilizes coarse leaf materials (CPOM) as a food source.

Laboratory experiments were designed to measure utilization of leaf resources by *G. pulex* and *B. rhodani* and furthermore to monitor the principal changes in chemical and isotopical composition of leaf material during breakdown, in order to contribute to answering the following set of questions:

(A) Invertebrate consumers

- Does the macro-invertebrate species used in the experiments perform as predicted by the Functional Feeding Group Concept?
- Can they use leaf material for growth and / or survival?
- Is the growth dependent on the quality of the leaf material?
- Does the stable isotope ratios in the animal tissues after feeding leaf detritus differ from standard trophic fractionation values between a consumer and its diet?

(B) Leaf resources

- How does leaching affect the chemical and isotopical composition of the leaf material?
- Does the chemical and isotopical composition of the leaf material changes continuously and in a regular manner during breakdown?
- Does invertebrate feeding affect the physical, chemical and isotopical composition of the leaf material?

5.2 Methods

Four types of experiments were designed:

(1) leaching experiment (7 days)
(2) breakdown experiment with shredding macro – invertebrates (*Gammarus pulex*)
(3) breakdown experiment with scrapping macro – invertebrates (*Baetis rhodani*)
(4) breakdown experiment without macro – invertebrates (Control).

The experiments were conducted in an environmental container (YORK, Germany) at constant temperature (10°C) and a 12/12 h light - dark regime. Experimental units (Figure 5.1) were aerated plexiglas chambers of 40 cm x 5 cm x 10 cm (L x W x H) that contained 1.60 liters water of a defined mixture (see below). Figure 5.2 views the situation in the environmental container during the experiments. The experimental chambers were closed by a plexiglas pane. 50% of the water was replaced weekly in each chamber. During this replacement, the water was taken from the surfaces and no visible POM particles were removed. Aeration included a plastic deflector that served to create a circulating water current to simulate stream flow conditions. The water velocity (circulation) in each chamber reached 10 cm s^{-1} (± 2 cm s^{-1}) repeatedly measured by a Flo-Mate 2000 (Marsh-McBirney Inc. USA). Water temperature, oxygen saturation, conductivity and pH were measured weekly pre water replacement using portable gages (WTW) and were used for monitoring of physical and chemical changes.

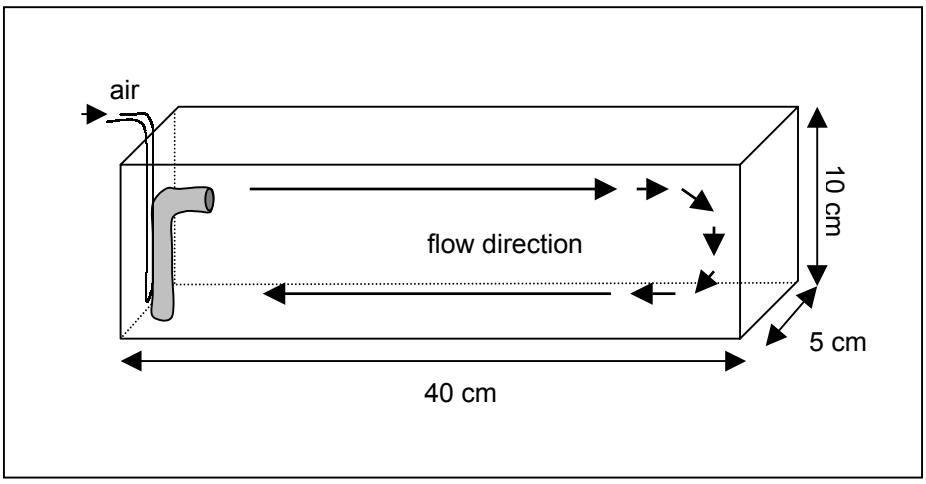

Figure 5.1: Schematic view of one experimental unit (plexiglas chamber) used in the experiments.

The resources used in the experiments were a mix of senescent, freshly abscised leaves of C_3 trees (yellow / unleached). This mix represents the natural input into the Ilm and consisted of about 40% alder (*Alnus glutinosa* L.), ~ 30% maple (*Acer platanoides* L.), ~ 20% willow (*Salix spp.*) leaves and ~ 10% ash (*Fraxinus excelsior* L.).

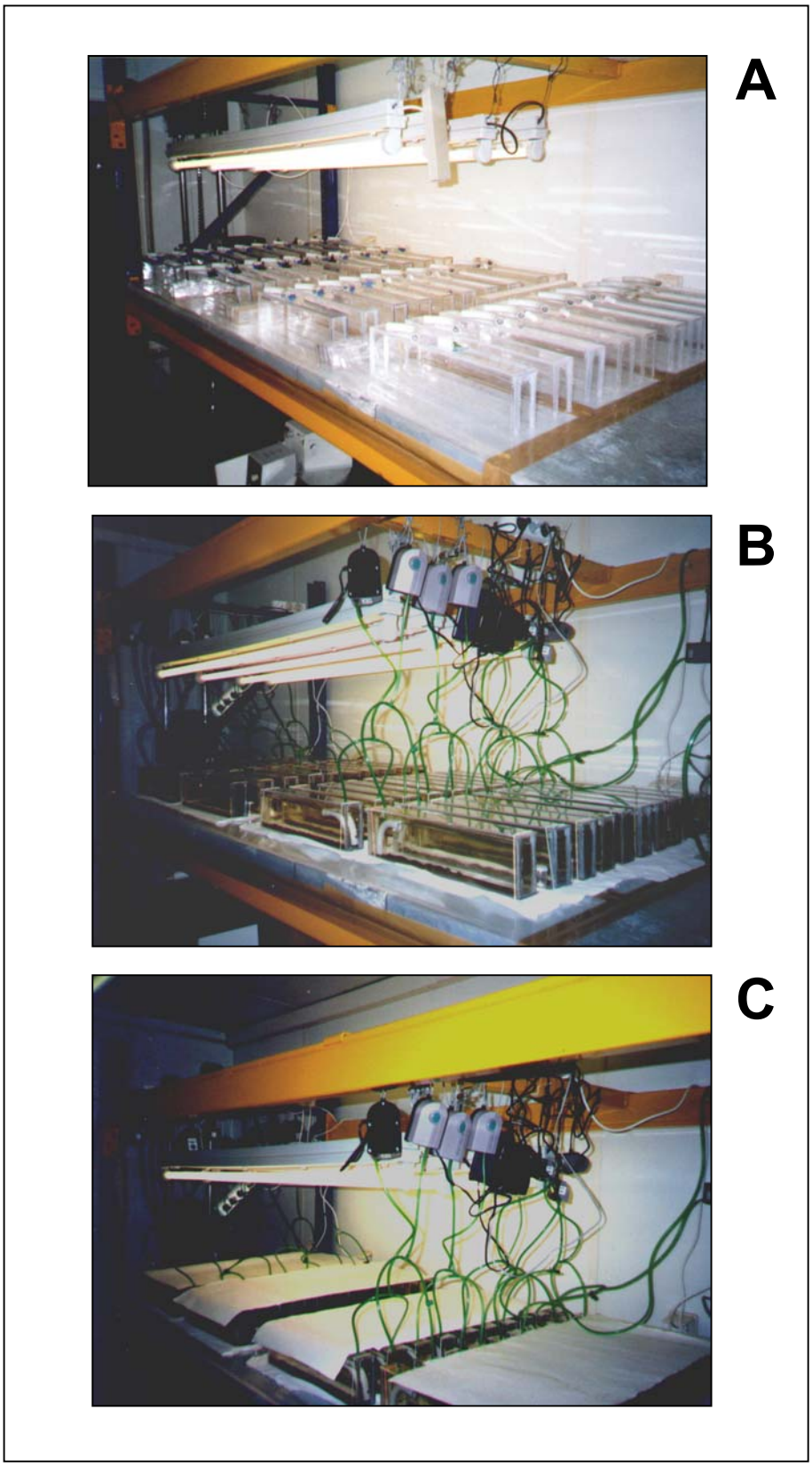

Figure 5.2: A view to the environmental container. A – pre experimentation, B – during monitoring (water replacement, measurement of physical and chemical conditions, removal of dead animals and exuviae), C – during a day cycle (all containers were covered with opaque screen (reducing light transmission) to prevent photo-autotrophic production).

Whole leaves were sampled from natural leaf packs (natural accumulations) in autumn 2000 from a metarhithric reach of the Ilm stream (Thuringia / Germany) approximately 2 km downstream of the town Stadtilm (11°05` E, 50°46` N). The material was dried at 60°C for 48 hours. Five different leaf treatments were prepared on the basis of the original material using plastic bags and a ball mill. The five leaf treatments used in the experiments were:

(L1) whole leaves and leaf fragments >2.5 mm,

(L2) leaf fragments <2.5 – >1.0 mm,

(L3) leaf fragments <1.0 mm – >250 µm,

(L4) leaf particles <250 µm - >71 µm

(L5) leaf particles <71 µm

The symbols in parenthesis (L1 to L5) are used in the following text. For preparation of larger particle size treatments dry leaves were put into plastic bags, the bags were closed up and crushed by hand. For smaller particle size treatments dry leaf material was put into a ball mill and crumbled at various time intervals (without heating). Afterwards the material was separated in different size classes by grinding and dry sieving using an analysis sieving machine (AS 200, Retsch GmbH & Co KG, Haan, Germany). The five leaf treatments used in the experiments formed a gradient of particle size and nutritional quality (for further details see below). The resource quality gradient used is artificial, but may reflect, to some extent, the natural conditions, because it resembles the commonly observed co-variation of particle size and C/N ratio of natural particulate organic matter (Findlay *et al*. 2002, Wagner 2003). Initial leaf dry mass ranged between 2.4 g in experiments with macro - invertebrate consumers and 1.3 g in experiments without consumers. The experiments consisted of four replicates for each leaf treatment during leaching experiment, five replicates for each leaf treatment with macro–invertebrate consumers (total 25 plexiglas chambers each) and 7 replicates for each leaf treatment without macro-invertebrates (Control, total 35 plexiglas chambers). Additionally, one container that contained exclusively water was used to monitor possible changes in water factors.

In the leaching experiment after seven days the leaf material was taken from the plexiglas chambers, dried at 105°C to constant weight and stored until further analysis. Duration of breakdown experiments with and without macro – invertebrates (time between adding leaf material to the chambers until removing the material) varied slightly between 36 days (*B. rhodani* experiment), 32 days (*G. pulex* experiment), and 35 days (Control experiment). Inoculation with natural microbes and protozoa was done by adding 5 ml clear stream water to each chamber and by microorganisms attached to surfaces of the leaf materials. During the experiments, all containers were covered with

opaque screens (reducing light transmission) to prevent autotrophic production, but to also allow a diurnal light pattern for the invertebrates. The leaf material was placed in each experimental chamber, 5 days (*G. pulex*) or 7 days (*B. rhodani*) prior to the addition of macro-invertebrate consumers to allow leaching and microbial colonization. The invertebrates were removed on day 29.

The individuals of the two macro-invertebrate species used in the experiments were collected from a reach (SS1; compare Chapter 2) of the Ilm stream, using a pond net. The organisms were washed in a bowl, sorted with a suction pipette, transported to the laboratory and allowed to acclimate in a large aquarium [50 cm x 30 cm x 30 cm (L x W x H)] in the environmental chamber for 7 days prior the experiments. At the beginning of the experiments a number of 5 - 6 individuals (*G. pulex*) and 4 – 5 individuals (*B. rhodani*) were put into the experimental chambers. Only early life stages of both species were used in the experiments (averaged body length: 3.9 mm for *G. pulex* & 4.4 mm for *B. rhodani*). Preliminary body size categorization and a regular distribution of the animals according to the small variability in body size allowed to monitor the animals individually. In both cases the experimental densities were well below natural abundance and used to minimize competitive interactions. Every 2-3 days throughout the experiment invertebrates were monitored and dead individuals and exuviae (molts) were removed.

Determination of survival and growth

Survival was defined as the percentage of animals alive after 24 days (*G. pulex*) and 22 days (*B. rhodani*), respectively. For *G. pulex* for each individual that survived the experiment, three growth parameters: body length (BL), body side area (BSA), and body dry mass (BDM) were measured and compared to that of a pre-experimental group of 61 individuals chosen randomly from the initial pool of animals at the beginning of the experiment. Body length (the distance from the front of the head to the tip of the longest uropod; Hoffer 1972) and body side area (the area of Cephalothorax, Peraeon and Pleon measured on individuals laying on one side of their lateral compressed body) were determined by scanning each individual using a computer scanner. Calculation of length and side area was done with the software Sigma Scan Pro (SPSS). Individual dry mass was determined to the nearest 0.01 mg after drying for 5h at 60°C and cooling to ambient room temperature in a glass desiccator with $CaSO_4$.

In the experiments with *B. rhodani*, for each individual that survived the experiment three growth parameters: body length (BL), head capsule width (HW) and body dry mass were compared to that of a pre-experimental group of 51 individuals chosen randomly from the initial pool of animals at the beginning of the experiment. Body length

(the distance from the front of the head, to the last tergit) and head capsule width (maximum width of the head) were determined visually using a graduated eyepiece. The individuals were dried for 5 h at 60°C. Because some of the individuals (*B. rhodani*) used in the experiment lost some limbs during preparation, the individual dry mass was calculated as milligrams and was determined from a length / dry mass regression equation (BDM = 0.0022 $BL^{3.19}$) of field collected individuals, instead of using the original gravimetric determinations. Relative growth rates for the animals that survived the experiments were calculated as the difference between the final body mass and initial body mass divided by the mean body mass and the experimental duration (after Waldbauer 1968):

$$RGR = \frac{m_f - m_i}{((m_i + m_f)/2) \cdot t} \qquad \textbf{(EQ. 7)}$$

RGR = relative growth rate
m_i = initial body mass
m_f = final body mass
t = duration of the experiment

The same calculations were used to measure *G. pulex* growth on the basis of body length and body side area and for *B. rhodani* growth on the basis of body length, head capsula width and body dry mass, respectively. Results are presented as relative growth rate in mm mm^{-1} d^{-1} (BL), mm^2 mm^{-2} d^{-1} (BSA) and mg mg^{-1} d^{-1} (BDM) for *G. pulex* and in mm mm^{-1} d^{-1} (BL), µm $µm^{-1}$ d^{-1} (HW) and mg mg^{-1} d^{-1} (BDM) for *B. rhodani*. For *G. pulex*, the dry mass – length relationships were analyzed using a power function, as previously described for other amphipods (Ritterhoff & Zauke 1997):

$BDM = a \cdot BL^m$, where *BDM* is body dry mass (mg), *BL* is body length (mm) and *a*; *m* are constants. For *B. rhodani*, the body length – head capsule width relationships were fitted to linear models: $BL = a \cdot HW + b$, where BL is body length (cm), HW is head capsule width (mm) and *a*; *b* are constants.

After determination of invertebrate body size the dry invertebrate material was subsequently ground using a ball mill and stored in plastic tubes until further chemical analysis.

Leaf mass loss and particle alterations

After the experimental period the leaf material was removed from the chambers and separated in particle size fractions by wet sieving in order to monitor the leaf processing. The same standard sieves as described above (preparation of leaf

treatments) were used. To get the smallest fraction (1.6 µm - 71 µm) the water – detritus mix was filtered after sieve passage, using pre-ashed, pre-weighed Whatman GF/A filters. It is necessary to note that for the L5 treatment in addition to Whatman GF/A filters also a standard sieve with a mesh size of 71µm was used to monitor processing. Particles >71 µm (larger than the original size of the L5 treatment (<71 µm) resulted from swelling of dry particles in contact with the water. Therefore, in contrast to the other leaf treatments (L1-L4) in which the amount of generated small particles was measured, for the L5 treatment the amount of particles generated was not directly evaluated. In the L5 treatment the composition of the two particle fractions (see above) were used to monitor changes in particle size caused by invertebrate feeding in comparison to the Control. The leaf detritus fractions were dried at 105°C to constant weight. Dry materials were ground to fine powders using a ball mill and sub-samples were ashed at 600°C for 3 hours. Total leaf mass loss was calculated based on the dry mass and the ash-free dry mass (AFDM) as the difference between initial leaf dry mass (or AFDM) and the final leaf dry mass (or AFDM). Total leaf mass loss was expressed in percent of the initial leaf dry mass (or AFDM) divided by the elapsed time in days [(% DM d^{-1}) & (% AFDM d^{-1})]. Note that the calculated leaf mass loss includes also generated leaf material fractions (defined by the particle size, see above). Additionally a further measure of leaf dry mass loss, in which generated particles are excluded, was calculated as the difference between initial leaf dry mass and the final leaf mass of particles that remained in original particle size. This measure of leaf mass loss (generated particles excluded) was expressed as (% DM d^{-1}). Note that in contrast to the commonly applied exponential models (Petersen & Cummins 1974), the measures used in this study to determine leaf mass loss assume a linear loss of matter during breakdown. Because of the relatively short duration of the experiments, the measures used are applicable for comparisons in the present study.

Sample processing for chemical and isotopical analysis

All chemical and isotopical analyses were performed by Heike Geilmann guided by Dr. Jan Rothe (Max Planck Institute for Biogeochemistry, Isolab, Jena, Germany). Dry animal material (pre- and post experimental groups separately for *B. rhodani* and *G. pulex*), powdered leaf detritus fractions (pre - and post - experimental material from the leaching experiment and the breakdown experiments with and without macro-invertebrates) and leaf detritus fractions that resulted from processing were pooled separately for each leaf treatment from the *G. pulex* - and the Control experiment before further analysis. The leaf detritus fractions (post - experimental material) which were taken from the *G. pulex* -, the *B. rhodani* - and the Control – experiment and then

analyzed, are given in Table 5.1. Note that for the L1, L2 and L3 treatments in the *B. rhodani* experiment only two material pools were analyzed (compare Table 5.1): (1) Leaf particle fractions, including particles that remained in original size and generated particle size classes > 71 µm (further called *Endpool L1, Endpool L2, Endpool L3*); (2) Leaf particles <71 µm. The differences in handling of the leaf detritus fractions between *B. rhodani* experiment and the two others (*G. pulex* and Control) do not create a general problem in this experimentation. In order to compare trends in chemical and isotopical composition of the leaf material between the experiments with and without macro-invertebrates two graphical methods were used:

1.) For $\delta^{13}C$, $\delta^{15}N$, C%, N% and the C/N ratio the values of the two material pools (1) materials > 71 µm and (2) materials < 71 µm from the experiments with *B. rhodani*, *G. pulex* and the Control were plotted together with initial values and leached values. The values for the pools in *G. pulex* - experiments and the Control - experiments were calculated based on known dry weights of all measured leaf detritus fractions.

2.) For *G. pulex* experiments and the Control experiments the averaged values for $\delta^{13}C$, $\delta^{15}N$, C%, N% and the C/N ratio of all leaf particle fractions were plotted together. The values represent un-weighted averages from pooled materials from 5 (*G. pulex*) or 7 (Control) replicates.

Table 5.1:The leaf material fractions analyzed in this study.

Type of experiment & leaf treatment		Particle size fraction (mm)				
G. pulex - experiment						
	L1	>2.5*	<2.5 – 1.0+	<1.0 – 0.25+	<0.25 – 0.071+	<0.071 – 0.0016+
	L2		<2.5 – 1.0*	<1.0 – 0.25+	<0.25 – 0.071+	<0.071 – 0.0016+
	L3			<1.0 – 0.25*	<0.25 – 0.071+	<0.071 – 0.0016+
	L4				<0.25 – 0.071*	<0.071 – 0.0016+
	L5				<0.25 – 0.071‡	<0.071 – 0.0016*
B. rhodani -- experiment						
	L1	>2.5†	<2.5 – 1.0†	<1.0 – 0.25†	<0.25 – 0.071†	<0.071 – 0.0016+
	L2		<2.5 – 1.0†	<1.0 – 0.25†	<0.25 – 0.071†	<0.071 – 0.0016+
	L3			<1.0 – 0.25†	<0.25 – 0.071†	<0.071 – 0.0016+
	L4				<0.25 – 0.071*	<0.071 – 0.0016+
	L5				<0.25 – 0.071‡	<0.071 – 0.0016*
Control - experiment						
	L1	>2.5*	<2.5 – 1.0+	<1.0 – 0.25+	<0.25 – 0.071+	<0.071 – 0.0016+
	L2		<2.5 – 1.0*	<1.0 – 0.25+	<0.25 – 0.071+	<0.071 – 0.0016+
	L3			<1.0 – 0.25*	<0.25 – 0.071+	<0.071 – 0.0016+
	L4				<0.25 – 0.071*	<0.071 – 0.0016+
	L5				<0.25 – 0.071‡	<0.071 – 0.0016*

∗ particle fractions that remained in original size; + particle fractions generated during the experiments; ‡ swelled particles in L5 treatments; † (Endpools) containing particle fractions that remained in original size but also some generated particle fractions in *B. rhodani* experiment, particle size classes originally added are gray-shaded.

To spot check dissolved material some water samples that were collected during water replacement from three food treatments with *G. pulex* (L1, L3 & L5) and in Control treatment (L1) 17 days after the start of the experiments, were analyzed. The water samples of each treatment were pooled. After freeze drying the samples were acidified (1M HCL) to remove carbonates, neutralized (0.1 M NaOH), rinsed (de-ionized water) and dried again. Note that the dry animal material and the leaf material does not contain significant amounts of inorganic carbon and were not acidified before further analysis.
Powdered animal tissues, leaf material fractions, and dry residuals from the water samples were weighed into tin capsules (separately for ^{15}N and ^{13}C). Finally, sample material was combusted in an EA 1110 Elemental Analyzer (ThermoQuest, 20090 Rodano, Italy). The resulting gases N_2 and CO_2 were separated by gas chromatography and analyzed for ^{15}N and ^{13}C content in a DeltaPlusXL isotope ratio mass spectrometer (Finnigan MAT, 28127 Bremen, Germany). The analytical precision was ± 0.2 ‰ for ^{15}N and ^{13}C. Working standards were acetanilide ($\delta^{15}N$ = 1.78 ‰, $\delta^{13}C$ = - 33.94 ‰) and caffeine ($\delta^{15}N$ = - 1.16 ‰, $\delta^{13}C$ = - 51.80 ‰), calibrated against international standards IAEA-N2 and NBS-22. Accuracy and repeatability of measurements were assured according to (Werner & Brand 2001). Isotopic ratios are expressed in conventional delta (δ) notation in parts per thousand: δX (‰) = ($R_{sample}/R_{standard}$ - 1) * 1000 ‰, where X = ^{15}N or ^{13}C and R = $^{15}N/^{14}N$ or $^{13}C/^{12}C$, respectively. Standard was AIR for ^{15}N and V-PDB for ^{13}C. For a number of leaf materials two samples of the same powder were analyzed separately to evaluate the homogeneity of the powders. The mean difference between duplicate measures of the same powder were $\delta^{15}N$ = 0.15 ‰ and $\delta^{13}C$ = 0.11 ‰ (n=56), showing that the samples were slightly less homogenous for nitrogen than for carbon. The number of samples and sub-samples for all materials analyzed in this study are summarized in Table D.1 (Appendix D).

Statistical analyses

Relative growth rates for the body size parameters of the invertebrates were tested against zero (0) using Mann-Whitney Rank Sum tests ($P < 0.05$) (separately for each leaf treatment). Secondly the differences in relative growth rates (log (x+1) transformed) among the leaf treatments were analyzed using One-way ANOVA followed by Tukey`s test ($P < 0.05$) if necessary.
Analysis of variance [ANOVA (General Linear Model, GLM)] was used to detect differences in leaf mass loss (leaf treatment and type of experiment as factors). Tukey`s test was used for multiple comparisons ($P < 0.05$). When the interaction terms in the ANOVAs were significant, single one-way ANOVA`s were used to test for differences

between experiments with and without macro-invertebrates separately for each leaf treatment. Tukey`s test was used for multiple comparisons ($P < 0.05$). Pre analysis deviations from normality were checked by conducting Kolmogorov–Smirnov-tests and equivalency of variances using Levene–tests. Log (x+1), arc sin square root, or double square root transformations were performed, when needed to improve normality of the residual distribution and to achieve variance homogeneity before analysis (Underwood 1997).

Particle size composition at the end of the breakdown experiments with and without macro-invertebrates were compared, using one-way ANOVA`s and Tukey`s test`s if necessary (each particle size class separately). The amount of particles generated during breakdown experiments was calculated: relative to the amount of leaf material originally added to the chambers and relative to the leaf mass loss (generated particles excluded). Both measures were expressed in (%) and (% d^{-1}).

One – way analysis of variance was used to detect differences in $\delta^{13}C$ (‰), $\delta^{15}N$ (‰), C (%), N (%), C/N ratio and (% AFDM) among the leaf treatments during leaching. Tukey-Test`s were used for multiple comparisons if necessary. Changes in isotope values (‰) and values for C (%), N (%) and C/N ratio from the beginning to the end of the breakdown experiments were calculated as $\Delta\ \delta X = \delta X_{final} - \delta X_{initial}$ and $\Delta\ X = X_{final} - X_{initial}$, respectively. To explore relations between growth / survival and isotopical and chemical changes in the invertebrates (averaged values from material pools for each treatment, n=5), but also between isotopical and chemical changes in the invertebrates and the leaf materials, regression analyses were used (averaged values from material pools for each treatment, n=5).

5.3 Results

5.3.1 Abiotic changes during the experiments

During an experimental period of 7 days intensive leaching occurred (visual indication: brown colored water). Leaching was responsible for the observed increase in conductivity. Conductivity reached the highest values in the small particle size leaf treatments (Appendix D, Table D.2). Oxygen was lower at the end of the experiment whereas pH tended to increase, both observations indicate the dominance of heterotrophic vs. photo-autotrophic processes. In the breakdown experiments conductivity after 7 days increased further until the end of the experiments. This trend was also found when the values were adjusted for changes caused by the water replacement. The slope of this trend was highest during the first 7 days and decreased afterwards. As observed during leaching, higher conductivity values in the leaf treatments with smaller particle sizes treatments (Appendix D, Table D.2) were observed until the end of the breakdown experiments. Oxygen saturation decreased during the breakdown experiments and the pH value was very constant.

5.3.2 Survival and growth

G. pulex and *B. rhodani* consumed all leaf materials offered. Filled guts (visual observations) indicated that the animals, regardless of growth or mortality, ingested the leaf material present in each treatment. During the experiments, survival of *G. pulex* was high, but lower for *B. rhodani.* Survival of *B. rhodani* decreased along the leaf treatment particle size gradient (Table 5.2).

Table 5.2: Survival (%) of *G. pulex* and *B. rhodani* in the experiments.

	Leaf treatment						
Species	L1	L2	L3	L4	L5	*n*	Duration (days)
G. pulex	84.6%	88.9%	96.0%	100%	85.2%	25-27	24 (32)
B. rhodani	77.3%	56.5%	52.2%	26.1%	20.8%	22-24	21 (36)

n = total number of individuals used per leaf treatment; duration in days = time between adding and removing of the macro-invertebrates from the chambers; values in parentheses = total duration of the experiments)

All body size – parameters indicated that *G. pulex* grew on all leaf diets (Mann-Whitney Rank Sum tests, $P < 0.05$), without significant differences in relative growth rates among the treatments (One-way ANOVA, $P > 0.05$) (Figure 5.3). For *G. pulex* the BDM-BL relationships could be appropriately expressed by power functions:

Pre-experimental group: BDM (mg) = 0.0086 BL (mm)$^{3.31}$; $r^2 = 0.914$; $P<0.0001$; n=61
Post-experimental group: BDM (mg) = 0.0041 BL (mm)$^{2.65}$; $r^2 = 0.877$; $P<0.0001$; n=116

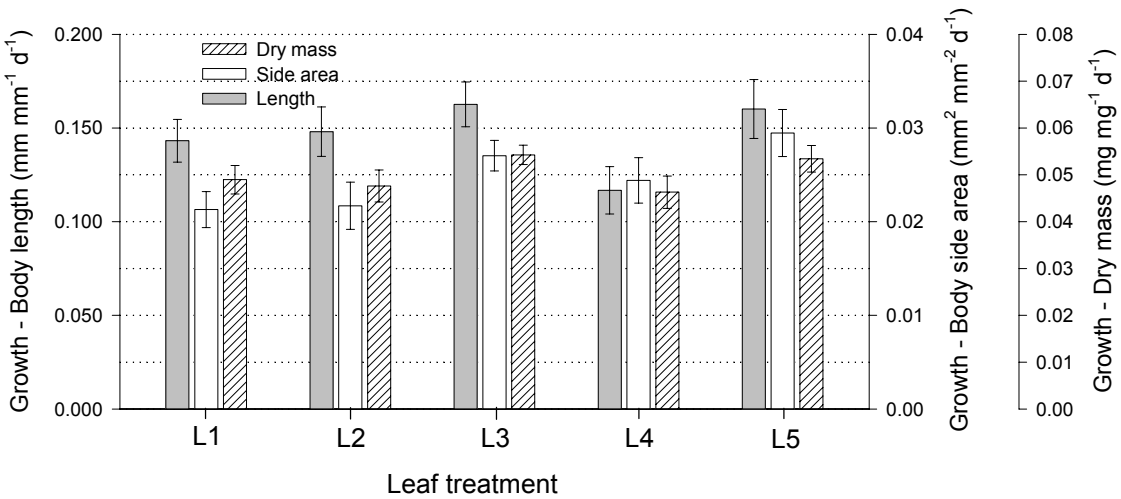

Figure 5.3: Relative growth rates (Mean ± 1 S.E.) for three body size parameters (length, side area and dry mass) of *Gammarus pulex* fed with leaf material in the experiments. All body size parameters indicated growth (Mann-Whitney Rank Sum tests, $P < 0.05$). There were no differences among the treatments (One-way ANOVA, $P > 0.05$).

For *B. rhodani* only in the L1 treatment, the growth rates for body length and head width differed significantly from zero (Mann-Whitney Rank Sum tests, $P < 0.005$), indicating growth (Figure 5.4). In all other cases growth rates differed not significantly from zero (Mann-Whitney Rank Sum tests, $P > 0.05$). The BL–HW relationships for *B. rhodani* were expressed by the following equations:

Pre-experimental group: BL (mm) = 1.351 x HW (mm) +0.09; $r^2 = 0.955$; $P<0.0001$; n=51
Post-experimental group: BL (mm) = 1.384 x HW (mm) +0.01; $r^2 = 0.910$; $P<0.0001$; n=55

Although slopes of the equations were highly similar, the individuals of the post – experimental group tend to show slightly larger head widths in comparison to the individuals of the pre-experimental group. Wing pads of larger individuals tended to increase (visual observation) and molting was observed, indicating a development for *B. rhodani,* but there was no remarkable increase in body length.

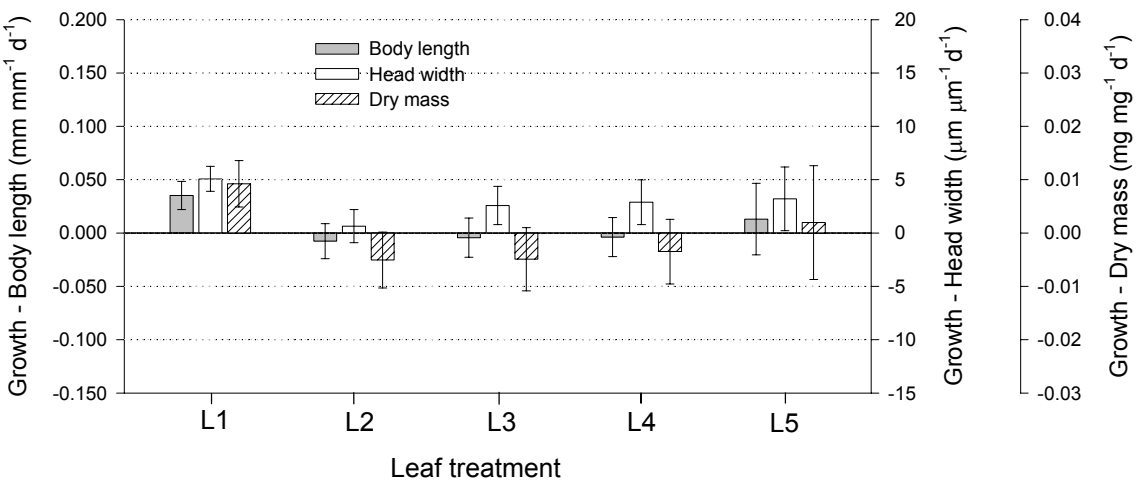

Figure 5.4: Relative growth rates (Mean ± 1 S.E.) for three body size parameters (length, head width and estimated dry mass) of *Baetis rhodani* fed with leaf material in the experiments. The relative growth rates for the body size parameters were not significantly different from zero (Mann-Whitney Rank Sum tests, P > 0.05), indicating no growth, with the exception of the relative growth rates for length and head width in L1 treatment (Mann-Whitney Rank Sum tests, P < 0.005). There were no differences among the treatments (One-way ANOVA, P > 0.05).

5.3.3 Leaf mass loss

Total leaf mass loss ranged from 0.45 % DM d^{-1} to 1.14 % DM d^{-1} and 0.57% AFDM d^{-1} to 1.26 % AFDM d^{-1}, respectively (Appendix D, Figure D.1). Total leaf mass loss as % dry mass per day, as % AFDM per day, and leaf mass loss as % dry mass per day after exclusion of generated particles differed significantly among the experiments (ANOVA (GLM), P < 0.001) and a significant interaction between the type of experiment (with and without macro - invertebrates) and leaf treatment was found. In treatments L1 to L4, all the measures used to quantify leaf mass loss indicated higher leaf mass losses in experiments with *G. pulex* in comparison to the Control and the *B. rhodani* – experiments in L1 to L4 treatments. A different pattern was found in the L5 treatment and was responsible for the significant interaction between the type of experiment and leaf treatment detected (see above). Leaf mass loss tended to increase with decreasing particle size of the leaf treatments from L1 to L4 and slightly decreased in L5. Slightly higher total leaf mass loss in % AFDM d^{-1} in comparison to mass loss in % total dry mass d^{-1} was caused by a net increase in ash content (inorganic components) in the leaf material during the experiment. This net increase in ash content was variable among the leaf treatments with the tendency to be highest in L1 to L3 and lowest in L4 and L5. The net increase occurred in a similar manner in the experiments with and without macro-invertebrates.

5.3.4 Amount and composition of particles generated during leaf breakdown

After the experiments most of the leaf material remained in original size (L1-L4 treatments). The largest proportion of the material generated in large particle size treatments (L1-L3) consisted of the smallest particles sampled (<0.071 mm – 0.0016 mm) (Figure 5.5). Differences were detected between specific particle size fractions generated during the experiments (L2; L3; L4) and in the fraction that remained in original particle size (L2 & L3) (compare Figure 5.5). In the L5 treatment the influence of invertebrate feeding was in contrast to the L1-L4 treatments, evaluated by comparing the proportion of two particle size fractions (not by the amount of particles generated, see methods). In the L5 treatment, there was no difference between experiments with and without macro-invertebrates (two separated One–way ANOVAS`s, P > 0.05).

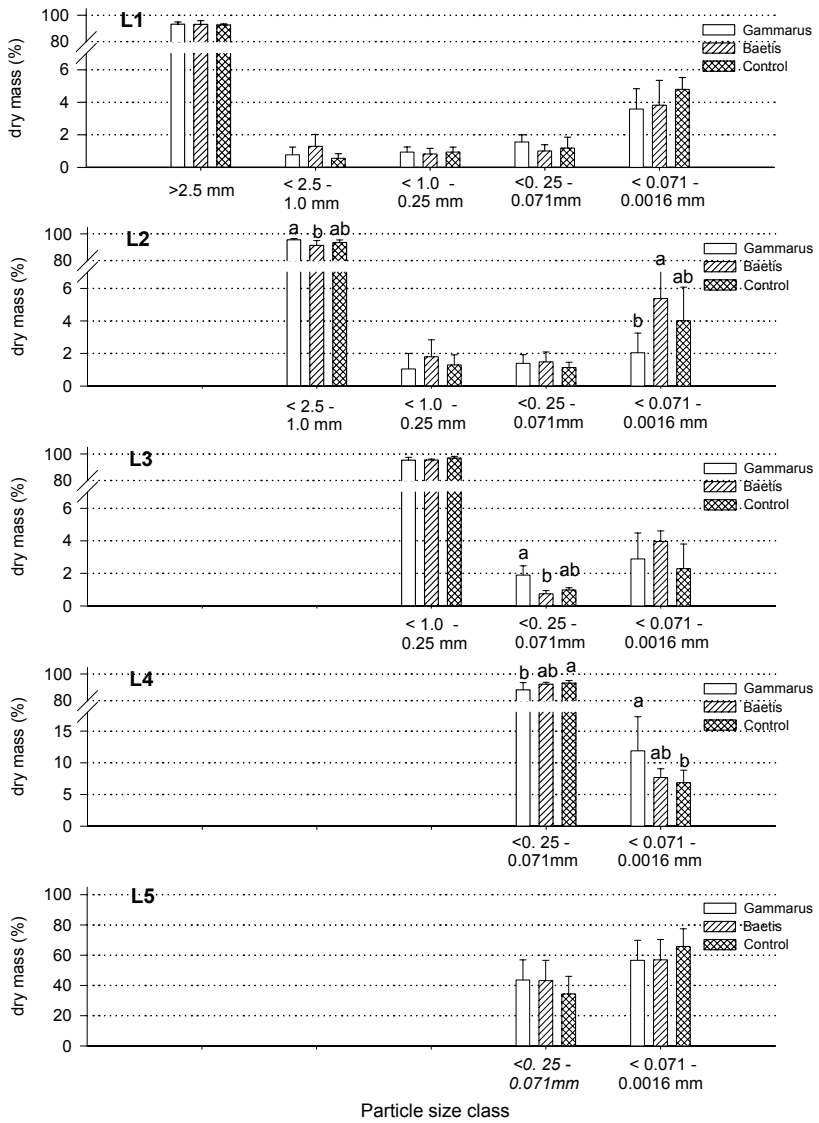

Figure 5.5: Particle size composition in the leaf treatments after the experiments. All values in (%) of remaining dry mass. Small letters indicate significant differences among experiments with and without macro-invertebrates (Tukey`s test).

The total amount of particles generated relative to the amount of material originally added to the chambers (only L1-L4 treatments) ranged from 0.99 % to 11.42 % (*G. pulex*: 2.01%-11.42%; *B. rhodani*: 2.49%-10.69%; Control: 0.99%-7.46%). Corrected by the elapsed time there were no significant differences among the experiments (L1, L2, & L3) with and without macro-invertebrates (Table 5.3). Only in the L4 treatment with *G. pulex*, the amount of particles generated was higher in comparison to the Control (Table 5.3). When calculated on the basis of the dry mass loss (original dry mass minus dry mass of particles that remained in original particle size), generated particles made between 3.54 % and 36.5 % (*G. pulex*: 5.31%-25.99%; *B. rhodani*: 9.91%-36.55%; Control: 3.54%-25.70%) of the loss. Divided by the duration of the experiment there were no significant differences among the experiments with and without macro-invertebrates (Table 5.3).

Table 5.3: The amount of particles generated during breakdown experiments relative to leaf mass initially added and relative to leaf mass loss.

Leaf treatment & type of experiment		**Generated particles**			
		(%) & (% d^{-1}) of initial leaf dry mass		(%) & (% d^{-1}) of leaf dry mass loss †	
		(%) *	(% d^{-1}) ‡	(%) *	(% d^{-1}) ‡
L1	*G. pulex*	5.1 ± 1.3	0.16 ± 0.04	16.8 ± 4.2	0.54 ± 0.13
	B. rhodani	5.6 ± 2.9	0.15 ± 0.06	21.6 ± 8.3	0.60 ± 0.23
	Control	5.9 ± 0.7	0.17 ± 0.02	22.5 ± 3.1	0.64 ± 0.09
L2	*G. pulex*	3.3 ± 0.8	0.10 ± 0.03	11.4 ± 3.0	0.35 ± 0.09
	B. rhodani	6.8 ± 3.0	0.19 ± 0.08	23.1 ± 9.7	0.64 ± 0.27
	Control	4.9 ± 1.4	0.14 ± 0.04	17.3 ± 3.8	0.49 ± 0.11
L3	*G. pulex*	3.3 ± 1.6	0.10 ± 0.05	9.6 ± 5.0	0.30 ± 0.16
	B. rhodani	3.6 ± 0.7	0.10 ± 0.02	13.6 ± 2.9	0.38 ± 0.08
	Control	2.5 ± 1.1	0.07 ± 0.03	8.9 ± 3.9	0.25 ± 0.11
L4	*G. pulex*	8.1 ± 3.6	0.25 ± 0.11[a]	19.7 ± 8.3	0.61 ± 0.26
	B. rhodani	5.7 ± 1.0	0.16 ± 0.03[ab]	18.0 ± 2.8	0.50 ± 0.08
	Control	4.9 ± 1.5	0.14 ± 0.04[b]	14.8 ± 4.6	0.42 ± 0.13
L5	*G. pulex*	n.m.	n.m.	n.m.	n.m.
	B. rhodani	n.m.	n.m.	n.m.	n.m.
	Control	n.m.	n.m.	n.m.	n.m.

n.m. = not measured; * differences not tested; ‡ treatments with and without macro-invertebrates were compared using one-way analysis of variance (small letters indicate the results of Tukey test`s, no letters & similar small letters = no differences, different letters = significant difference); † leaf mass loss calculated as the difference between initial leaf dry mass and final leaf mass of leaf particles that remained in original size.

5.3.5 Chemical and isotopical changes during the experiments

Leaching experiment

The stable isotope composition of the leaf materials changed little during initial leaching and the observed variability was high (Table 5.4). The materials tended to be enriched in ^{13}C, but the averaged difference between final and initial values and the variability tended to decrease along the leaf particle size gradient. A large variability was also observed for $\delta\ ^{15}N$ values and no clear trend occurred along the leaf particle size gradient. Leached materials showed higher AFDM (%) and higher carbon contents in comparison to the initial material. Nitrogen content increased in four of the five leaf treatments, but slightly decreased in L2 treatment. The C/N ratio therefore decreased in four of the five leaf treatments and slightly increased in the in L2 treatment (Table 5.4).

Table 5.4: Chemical and isotopical composition of the leaf materials and the changes observed during leaching experiments.

Parameter		Leaf treatment				
		L1	L2	L3	L4	L5
$\delta^{13}C$ (‰)	Initial *	-28.59	-28.42	-28.73	-28.64	-28.49
	Leached ‡	-28.27±0.18	-28.14±0.16 [a]	-28.54±0.07 [b]	-28.54±0.10 [b]	-28.51±0.10 [b]
	$\Delta\ \delta^{13}C$ †	0.32± 0.18 [a]	0.28±0.16 [a]	0.19±0.07 [ab]	0.10±0.10 [ab]	-0.02± 0.10 [b]
$\delta^{15}N$ (‰)	Initial *	1.71	1.43	1.80	2.32	2.70
	Leached ‡	1.47±0.43 [b]	1.28±0.36 [b]	1.58±0.13 [b]	2.25±0.15 [a]	2.76±0.07 [a]
	$\Delta\ \delta^{15}N$ †	-0.24± 0.43	-0.15±0.36	-0.22±0.13	-0.07±0.15	0.06± 0.07
C (%)	Initial *	40.91	42.90	44.30	40.95	38.70
	Leached ‡	43.37±0.31 [b]	43.94±0.42 [b]	45.68±1.06 [a]	44.21±0.37 [ab]	40.82±0.89 [c]
	Δ C †	2.47±0.31 [ab]	1.04±0.42 [b]	1.38±1.06 [b]	3.27±0.37 [a]	2.12±0.89 [ab]
N (%)	Initial *	1.00	1.32	1.60	1.41	1.58
	Leached ‡	1.15±0.07 [b]	1.29±0.04 [b]	1.85±0.04 [a]	1.63±0.05 [b]	1.81±0.02 [a]
	Δ N †	0.15±0.07 [b]	-0.03±0.04 [c]	0.25±0.04 [a]	0.22±0.05 [ab]	0.23±0.02 [ab]
C/N	Initial *	40.91	32.50	27.69	29.04	24.49
	Leached ‡	39.1±0.57 [a]	33.5±0.60 [b]	24.4±0.77 [d]	27.1±1.11 [c]	22.4±0.47 [e]
	Δ C/N †	-2.58±0.57 [b]	1.00±0.60 [a]	-2.72±0.77 [b]	-1.93±1.11 [b]	-2.15±0.47 [b]
AFDM (%)	initial*	90.89	93.30	93.27	88.18	81.11
	Leached ‡	93.4±1.27 [b]	93.8±0.97 [b]	96.3±0.32 [a]	95.0±1.35 [ab]	88.89±1.37 [c]
	Δ AFDM †	2.48±1.27 [bc]	0.46±0.97 [c]	3.03±0.32 [b]	6.82±1.35 [a]	7.78±1.37 [a]

*mean values from two replicate sub-samples for $\delta^{13}C$ (‰), $\delta^{15}N$ (‰), C (%), N (%), C/N ratio and mean values from three replicate sub-samples for AFDM (%); ‡ mean values from four replicate samples; † mean value for the difference between initial values and values after 7 days leaching ($\Delta\ \delta X = \delta X_{final} - \delta X_{initial}$ and $\Delta\ X = X_{final} - X_{initial}$).

Breakdown experiments

Stable isotope composition of the invertebrate consumers changed during the experiment. The $\delta^{13}C$ and the $\delta^{15}N$ signatures of the leaf materials and of the invertebrates before and after the experiments are shown in Figure 5.6. Post-experimental groups of *G. pulex* and *B. rhodani* were enriched in ^{13}C (+3.38‰ for *G. pulex* and +1.20‰ for *B. rhodani*) and depleted in ^{15}N (Ø -0.62‰ for *G. pulex* and Ø – 2.04‰ for *B. rhodani*) relative to the pre-experimental group taken from the stream. The animals were enriched in ^{13}C Ø + 4.61 ‰ (+4.50‰) for *G. pulex* and Ø + 1.39‰ (+1.42‰) for *B. rhodani* and in ^{15}N Ø + 3.31‰ (+3.36‰) for *G. pulex* and Ø + 4.28‰ (+4.53‰) for *B. rhodani* relative to the averaged values (Ø = ($\delta^{13}C_{start}$ + $\delta^{13}C_{end}$) / 2) of the leaf material during the experiments (values in parentheses refer to the enrichment relative to the values of the leaf material at the end of the experiments). Final carbon and nitrogen content (%) of the animals was higher in comparison to the pre-experimental group leading to a decrease in C/N ratios of the animals tissue. Although there were no differences in relative growth rates of *G. pulex* among the leaf treatments, the average growth rates were positive related to changes in stable carbon isotope composition ($\Delta\ \delta^{13}C$) in the animal tissue ($\Delta\ \delta^{13}C_{G.\ pluex}$ = -33492 x (RGR dry mass)^2 + 3465 x (RGR dry mass) – 85.3, R^2=0.99, n=5, P < 0.05).

The changes in stable carbon isotope composition ($\Delta\ \delta^{13}C$) of *G. pulex* were linear related to the changes in $\delta^{13}C$ observed in the leaf material during the experiments ($\Delta\ \delta^{13}C_{G.\ pluex}$ = -0.96 x $\Delta\ \delta^{13}C_{Leaf}$ + 3.60, R^2=0.84, n=5, P < 0.05). The $\Delta\ \delta^{15}N$ found in *G. pulex* was linear related ($\Delta\ \delta^{15}N_{G.\ pluex}$ = -0.41 x $\Delta\ \delta^{15}N_{Leaf}$ - 0.47, R^2=0.99, n=4, P < 0.005) only, if the values for the L5 treatment were excluded from this analysis. The $\Delta\ \delta^{15}N$ values of *G. pulex (*$\Delta\ \delta^{15}N$ = -0.72) and the leaf material ($\Delta\ \delta^{15}N$ = -0.92) in the L5 treatments were more close to the trend calculated for the observed shifts in $\Delta\ \delta^{15}N$ values of *B. rhodani (see below).*

In *B. rhodani* the changes in $\delta^{15}N$ and N (%) from the pre-experimental group to post-experimental groups were negatively linear related ($\Delta\ \delta^{15}N$ = -2.25 x Δ N – 2.07; R^2=0.98, n=5, P < 0.001). The $\Delta\ \delta^{15}N$ and Δ C/N ratio were positively linear related ($\Delta\ \delta^{15}N$ = 0.76 x Δ C/N + 0.62; R^2=0.93, n=5, P < 0.01) and were affected by the observed negative linear relation between the Δ N and the Δ C/N in the animals (Δ N = -0.34 x Δ C/N - 0.06; R^2=0.98, n=5, P < 0.01). Also there was a negative linear relation between survival (%) and the change in $\delta^{15}N$ [survival (%) = -0.023 x $\Delta\ \delta^{15}N$ – 0.97, R^2=0.99, n=5, P < 0.001] and the change in C/N ratios [survival (%) = -0.017 x Δ C/N – 0.12, R^2=0.90, n=5, P < 0.05] from the pre-experimental group to post-experimental groups. Also positive linear relation of survival to the change in N (%) from the pre-experimental group to post-experimental groups [survival (%) = 0.052 x Δ N (%) – 0.13, R^2=0.96,

n=5, P < 0.01] was observed. The changes in stable isotope composition ($\Delta\ \delta^{13}C$ & $\Delta\ \delta^{15}N$) found for *B. rhodani* were linear related to the changes in $\delta^{13}C$ and $\delta^{15}N$ observed in the leaf material during the experiments ($\Delta\ \delta^{13}C_{B.\ rhodani} = 1.72 \times \Delta\ \delta^{13}C_{Leaf} + 1.23$, $R^2=0.95$, n=5, P < 0.005; $\Delta\ \delta^{15}N_{B.\ rhodani} = -1.51 \times \Delta\ \delta^{15}N_{Leaf} - 2.04$, $R^2=0.79$, n=5, P < 0.05).

Small and variable changes in stable isotope composition were observed for leaf particle fractions that remained in original size at the end of the experiments. Greatest changes were observed for the L1 and L2 treatments. Most remarkable were the changes occurring in the generated leaf material fractions (monitored only for L1-L4). These fractions (only monitored for L1-L4) were enriched in ^{13}C in experiments with and without macro-invertebrates relative to the material at the beginning of the experiments. Generated fractions in the *G. pulex* and *B. rhodani* experiment were depleted in ^{13}C in comparison to particle fractions generated in the Control (without macro-invertebrates) (Figure 5.6). The ^{15}N values of generated particle fractions were highly variable among the treatments in all experiments.

A detailed view on the changes in $\delta\ ^{13}C$ in the leaf material fractions of the L1 treatment is given in Figure 5.7. Furthermore the changes in $\delta\ ^{13}C$ in the leaf materials of all leaf treatments are summarized in Figure D.2 [Appendix D, Left panels in Figure D.2 show the general trends in $\delta\ ^{13}C$ values in the leaf materials during breakdown experiments on the basis of material pools; Right panels show the detailed trends in $\delta\ ^{13}C$ values in the leaf materials during breakdown experiments on the basis of all particle fractions analyzed (in L1-L3 only for the *G. pulex* and the Control experiment)].

The $\delta\ ^{13}C$ values tended to increase during the experiments in L1 treatments with and without macro-invertebrates (initial < leached < final) and the highest values were observed for the smallest particle fraction analyzed (Figure 5.7 A & B). The latter observation was also made in L2 – L4 treatments (Appendix D, Figure D.2). The $\delta\ ^{13}C$ values (Figure 5.7 A & B) of the leaf material that remained in original size in the L1 treatment were similar between *G. pulex* and Control experiments and showed slightly lower values in the *B. rhodani* experiment. Larger differences were found for the leaf material fractions generated during the experiments. Particle fractions generated in the L1 treatment of the Control experiments were enriched in ^{13}C in comparison to the detritus particles generated in the *G. pulex* experiment (Figure 5.7 A & B) and in the *B. rhodani* experiment (Figure 5.7 A). A similar tendency was found for the other large particle size treatments (L2 & L3; Figure D.2, Appendix D), but the difference decreased along the leaf quality gradient leading to highly similar values (no difference) in L4 & L5 treatments.

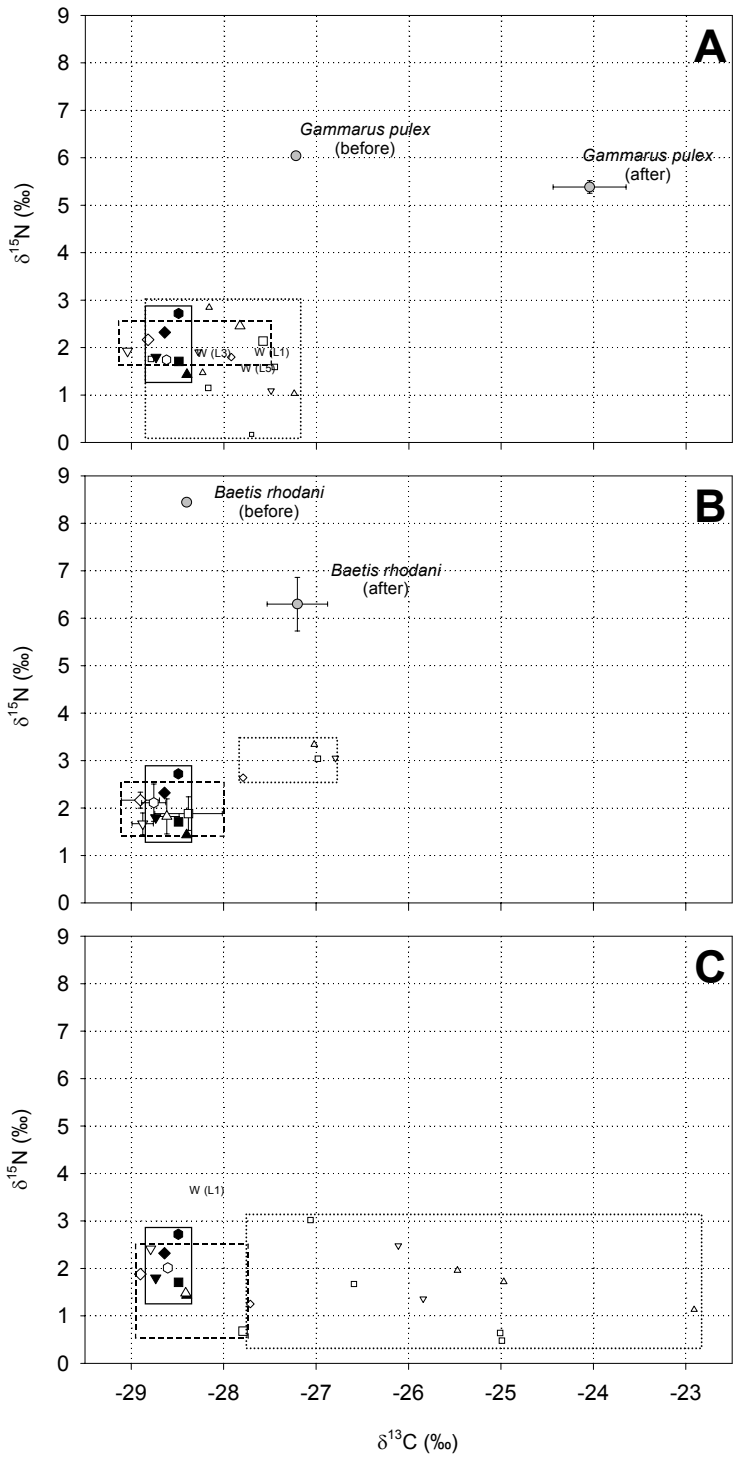

Figure 5.6: Stable carbon isotope ($\delta^{13}C$) and nitrogen isotope ($\delta^{15}N$) composition of leaf materials and invertebrates before and after breakdown experiments. A = *G. pulex* experiment, B = *B. rhodani* experiment, C = Control experiment without macro-invertebrates, solid lines envelop the isotopic signatures of the leaf materials at the beginning of the experiments [large filled symbols: square (L1), up-triangle (L2), down-triangle (L3), diamond (L4), hexagon (L5)], long dash dotted lines envelop isotopic signatures of the leaf materials that remained in original particle (L1-L4) and for L5 a pool of all particles found at the end of the experiments [large open symbols: square (L1), up-triangle (L2), down-triangle (L3), diamond (L4), hexagon (L5)], point dotted lines envelop isotopic signatures of the particle fractions generated during the experiments (only for L1-L4) [small open symbols: square (L1), up-triangle (L2), down-triangle (L3), diamond (L4)], W = water samples.

Changes in $\delta^{15}N$ during the experiments were by far more variable in comparison to $\delta^{13}C$ (Figure 5.7 C & D; Figure D.3, Appendix D). Variable differences between the experiments with and without macro-invertebrates were found. The $\delta^{15}N$ values of the final leaf materials were higher, lower, or similar in comparison to the initial values and to the values reached during leaching (Figure 5.7 C & D; Figure D.3, Appendix D). Therefore, no clear trends can be described. Ash free dry mass (%) tended to increase during leaching and further to decrease (Figure 5.7 E & F; Figure D.4, Appendix D). Particle fractions generated in L1 treatments of the Control experiments tended to show lower AFDM (%) in comparison to the detritus particles generated in the *G. pulex* experiment.

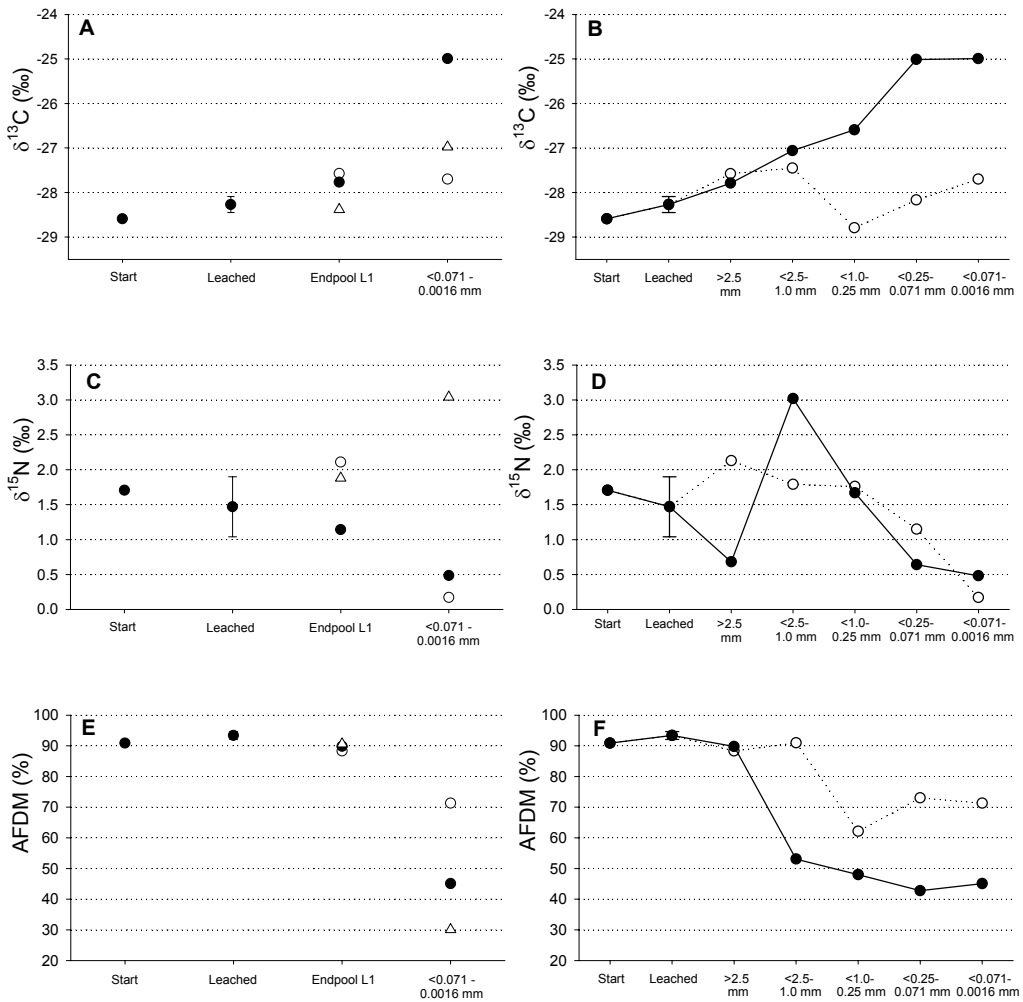

Figure 5.7: Changes in $\delta^{13}C$ (‰) (A & B), $\delta^{15}N$ (‰) (C & D) and AFDM (%) (E & F) in the leaf material of the L1 treatment during breakdown. **Left panels**: Start = initial values; Leached = values after a leaching period of 7 days (1 S.D. from 4 replicates); Endpool L1 = final $\delta^{13}C$ values of the leaf particles > 71 µm (including particles that remained in original size and generated particle size classes > 71 µm); <0.071 – 0.0016 mm = final values of the generated particles < 71 µm; *G. pulex* experiments = open circles; *B. rhodani* experiments = up – triangles; Control experiments = closed circles. **Right panels:** all leaf material fractions are separately shown, including particles that remained in original size (>2,5 mm) and all generated particle size fractions for the Control experiments (closed circles) and the *G. pulex* experiments (open circles).

A similar tendency was observed in the other large particle size treatments (L2-L3), as observed for δ ^{13}C, the difference decreased along the leaf quality gradient leading to highly similar values (no difference) in L4 and L5 treatments. In all treatments the carbon content (% of leaf dry mass) tended to increase during leaching (Figure 5.8 A & B; Figure D.5, Appendix D). In most cases carbon content increased further, reaching highest values particle fractions that remained in original size, but tended to decrease in generated particle fractions (Appendix D, Figure D.5). Nitrogen content (% of leaf dry mass) increased during the experiments reaching the highest values in generated particle fractions (Figure 5.8 C & D; Figure D.6, Appendix D).

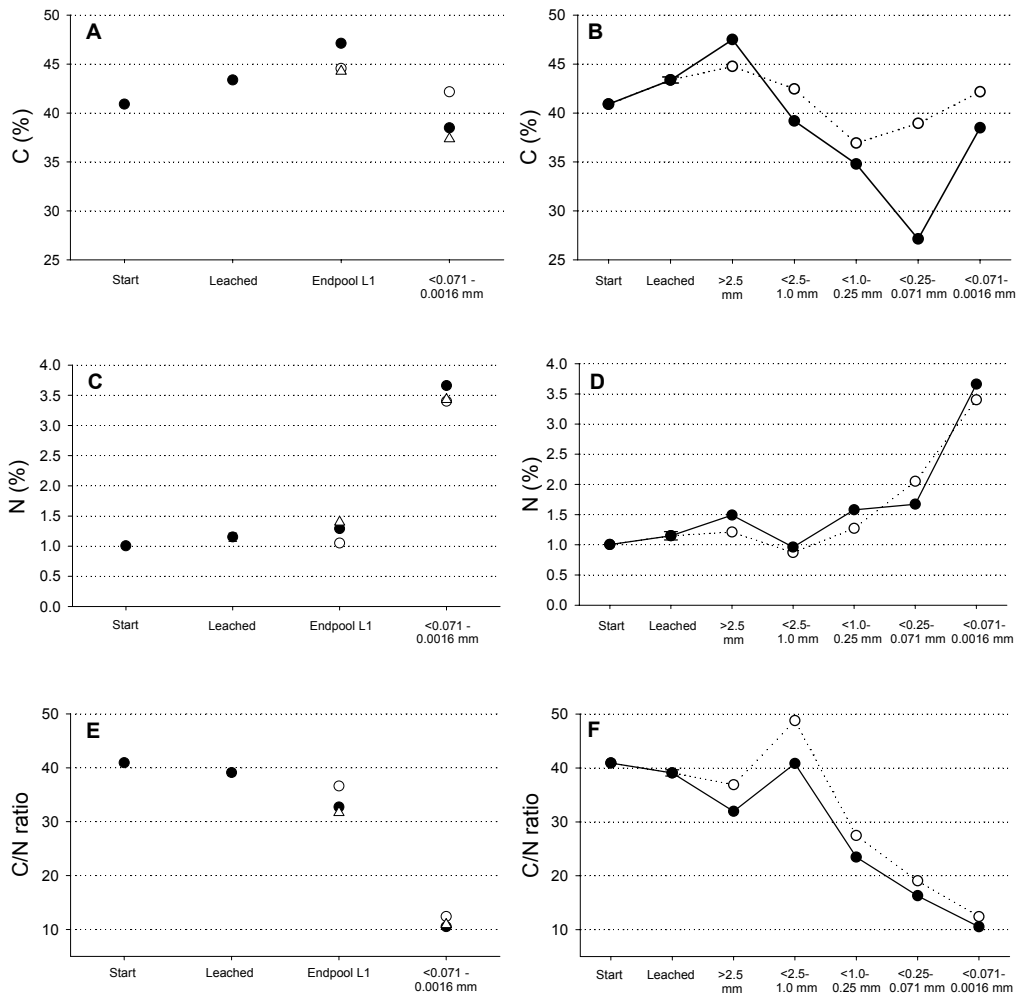

Figure 5.8: Changes in carbon contents (%) (A & B), nitrogen contents (%) (C & D) and C/N ratios (E & F) in the leaf material of the L1 treatment during breakdown. **Left panels**: Start = initial values; Leached = values after a leaching period of 7 days (1 S.D. from 4 replicates); Endpool L1 = final values of the leaf particles > 71 µm (including particles that remained in original size and generated particle size classes > 71 µm); <0.071 – 0.0016 mm = final values of the generated particles < 71 µm; *G. pulex* experiments = open circles; *B. rhodani* experiments = up – triangles; Control experiments = closed circles. **Right panels:** all leaf material fractions are separately shown, including particle that remained in original size (>2,5 mm) and all generated particles size fractions for the Control experiments (closed circles) and the *G. pulex* experiments (open circles).

Driven by the changes in nitrogen content, the C/N ratio decreased during breakdown reaching lowest values in the smallest particle fractions measured (<0.071–0.0016 mm, generated particles in L1 to L4) (Figure 5.8 E & F; Figure D.7, Appendix D).

The difference between initial C/N ratio and the C/N ratio of the smallest particle fraction analyzed decreased from L1 to L5 treatments. The largest shift was observed in the L1 treatment with and without macro-invertebrates. The C/N ratio decreased continuously (initial > leached > final). There was only one exception, particles of the 2.5-1.0 mm fraction generated in the L1 treatment showed a higher C/N ratio in comparison to the initial material, probably because this fraction consisted of broken leaf-stalk fragments (hard, structural leaf components; visual observation).

Stable isotope composition in the dry residuals from the water samples for *G. pulex* experiments were within the range observed for the generated leaf particle fractions [for L1 ($\delta^{13}C$= -27.48 ‰,$\delta^{15}N$= 1.90 ‰); for L3 ($\delta^{13}C$= -28.11 ‰,$\delta^{15}N$= 1.89 ‰) & for L3 ($\delta^{13}C$= -27.63 ‰,$\delta^{15}N$= 1.56 ‰)] (see above Figure 5.6). Dry residuals from the water samples for L1 treatment from the Control experiment were higher in $\delta^{15}N$ in comparison to the *G. pulex* experiment [L1 ($\delta^{13}C$= -28.18 ‰, $\delta^{15}N$= 3.65 ‰)]. C/N ratios of dry residuals from the water samples were high in comparison to C/N ratios of most of the generated particle fractions [for *G. pulex*: L1 (33.3), L3 (62.4) & L5 (49.73); Control: L1 (35.0)].

5.4 Discussion

Survival and growth responses of both invertebrate species used in the experiments are in line with the predictions of the FFGC (compare Merritt & Cummins 1996, Schmedtje & Colling 1996). Along the experimental food quality gradient (chemical & size), a high survival and similar high growth rates were observed for *G. pulex*. The BDM-BL relationship implies an allometric growth for *G. pulex*. The BDM-BL relationships for the pre-experimental group and post-experimental groups showed a similar form but the power function of the post-experimental animals was steeper than the one of the pre-experimental group indicating a better nutritional status of the animals after the experiment in comparison to that taken from the field. Causes for the mortality that occurred during the experiments are not quite clear, but the observed mortality rate was as comparatively low as in other experimental feeding studies (Graca *et al.* 2001). In *G. pulex*, a high growth rate was maintained along the used food quality gradient. The capacity of *G. pulex* to tolerate variable food qualities seems to be a consequence of a compensatory system in which respiration rates change to compensate for reductions in food quality (Graca *et al*. 1993). Cummins & Klug (1979) pointed out that many amphipodes, such as Gammarus, have digestive cellulases that reflect their marine phylogenetic origin. This view was recently supported. Zimmer & Bartholme (2003) found that the enzymes (cellulases & phenol oxidases) that are needed to digest major leaf litter compounds, as cellulose and lignin, seemed to be of endogenous origin in *G. pulex* and thus this species does not seem to depend on microbial activity for the degradation of the most abundant/important compounds of its food source.

In contrast to *G. pulex*, the leaf material was a poor food source for *B. rhodani* as indicated by higher mortality and low growth tendencies. The observed trend of increasing mortality along the food quality gradient (chemical & size) seems to be a result of changes in availability of surface biofilms caused by the particle size, rather than by nutritional quality of the leaf material itself. Although the surface-area to volume ratio increased with decreasing particle size, the ability of *B. rhodani* to use the surface biofilms seemed to decrease. This view is supported by visual observations that *B. rhodani* scraped intensively at the leaf surfaces of large particle size treatments, but switched gradually to a collector feeding mode in small particle size treatments. *B. rhodani* did not seem to be able to handle small particles and associated biofilms with a similar efficiency as the biofilms associated with large particles. The preferential usage of leaf associated biofilms rather than the leaf material is supported by the fact that most aquatic insects lack cellulases (Cummins & Klug 1979).

Stable carbon isotope ratios ($\delta^{13}C$) of invertebrate consumers seem to reflect those of their food source and consumers are observed to become only slightly (0‰ to +1‰) enriched in ^{13}C relative to their food (DeNiro & Epstein 1978, Fry and Sherr 1984, France 1995). The observed averaged difference in $\delta^{13}C$ (+ 4.61 ‰, relative to the leaf material, see above) in *G. pulex* which feeds on the experimental leaf treatments suggests that this species selectively incorporates specific fractions of the leaf detritus carbon into body tissue. These fractions could be of microbial origin. Especially fungi are possible candidates from which *G. pulex* assimilated most of the carbon. Other experimental laboratory studies using analysis of stable isotopes have also suggested the importance of microbes as a food source rather than POM for other aquatic invertebrates (Fantle *et al.* 1999, Hollows *et al*. 2002). To estimate the relative importance of microbes and the leaf material as food for detritivorous invertebrates, a separated analysis of these two components would be necessary, but it seems practically impossible to isolate the microbes from the litter on which they have grown (Hamilton *et al*. 1992, Ponsard & Arditi 2000). Using SEM (scanning electron micrographs) and ^{14}C labeled microbiota, Morrison and White (1980) found that estuarine amphipods unselectively ingested the microorganisms present at degrading tree leaf (*Quercus virginiana*) and they found no indication for consumption of the plant material itself.

One the other hand microbial carbon is only a small proportion of the detrital – microbe complex, comprising less than 2% of the detrital carbon (Findlay *et al*. 2002). Although the microbial contribution may be higher during early stages of decay (Gessner & Chauvet 1993) it seems questionable that microbial carbon was the most important carbon source for *G. pulex* in the experiments. In knowledge of the enzymatic equipment of *G. pulex* (see above), it seems probable that the assimilated carbon fractions were leaf components. Preferential assimilation of leaf components high in ^{13}C (cellulose, starches & sugars) will increase the proportions of slow decomposing leaf components low in ^{13}C in the material, leading to more depleted feces, that are represented by generated particle fractions in the experiments, relative to particles generated in the Control experiments.

As in *G. pulex*, the observed averaged difference in $\delta^{13}C$ (+ 1.39‰, relative to the leaf material) observed in *B. rhodani* feeding on the experimental leaf treatments was also higher than standard trophic enrichment values (± 0‰ to + 1‰). A possible explanation is that the leaf–surface-biofilms were the major carbon source for *B. rhodani*. Heterotrophic microorganisms using the leaf – detritus as their primary carbon source, become slightly enriched in ^{13}C and *B. rhodani* becomes further enriched by consuming the biofilms. But, as in *G. pulex,* it is also possible that *B. rhodani* selectively assimilates

specific fractions of the leaf detritus carbon. In contrast to *G. pulex*, the first assumption seems more likely for *B. rhodani,* because this species lacks cellulases as most aquatic insects (Cummins & Klug 1979).

The averaged difference in $\delta^{15}N$ between the macro-invertebrates (*G. pulex* & *B. rhodani*) and their leaf food source was close to the standard enrichment values (mean +3.4‰, range 3-4‰) (DeNiro & Epstein 1981, Minagawa & Wada 1984, Cabana & Rasmussen 1996). *G. pulex* seemed to be able to use the leaf nitrogen effectively. In contrast, the strong relations between $\delta^{15}N$, N (%) and C/N ratio within tissues of *B. rhodani* and the relation of these factors to the survival of *B. rhodani* indicate that the availability of leaf nitrogen was limiting for survival and possibly also growth of *B. rhodani* in the experiments. Starving animals exhibit $\delta^{15}N$ enrichment, presumably because the animals catabolize their own tissue proteins, leading to isotopic enrichment analogous to that for ingested food (Vander Zanden & Rasmussen 2001). The observed depletion in ^{15}N from pre-experimental group to the post-experimental groups indicated no complete starvation of *B. rhodani*. The used leaf particle size gradient seemed to represent a starvation gradient. The larger the changes in $\delta^{15}N$ values from the pre-experimental group to the post-experimental groups were, the higher the survival was, indicating a higher availability of nitrogen (via biofilms) in large particle size treatments.

There is hardly any knowledge on ^{15}N fractionation by microorganisms (Vanderklift & Ponsard 2003). In contrast to carbon, microbial nitrogen made between 1-20 % of the detrital – microbe complex (Findlay *et al*. 2002). If the ^{15}N fractionation between microbes and their food is assumed to be similar to that observed for macro-consumers and their food ($\Delta\ \delta^{15}N$ = +3.4‰), a consumer that uses exclusively microbial nitrogen should become enriched by +6.8 ‰ relative to the nitrogen source used by the microbes (leaf). This was clearly not the case in the presented experiments. High C/N ratios indicate that leaves are of low nutritional quality (protein), microbes and macro-invertebrates that utilize leaves probably compete indirectly for nitrogen especially when nearly no other nitrogen sources are available as in the experiments. In streams microorganisms assimilate nitrogen and other inorganic nutrients from the ambient water (Pusch *et al*. 1998, Suberkropp 1998, Sanzone *et al.* 2001). The lower nitrogen content in water samples from the experiments (water replacement) in comparison to the original mixture also indicate some uptake of nitrogen from the water during the experiments, although nitrogen concentrations in the water were generally low. However, the changes in $\delta\ ^{15}N$ signatures in the leaf material observed in the experiments are probably affected by the $\delta\ ^{15}N$ signatures of two nitrogen sources (leaf nitrogen & water nitrogen), leading partly to some of the variability observed.

All the measures used to quantify leaf mass loss (% AFDM d^{-1}) indicate higher total losses in experiments with *G. pulex* (L1-L4, except L5) in comparison to the Control and the *B. rhodani* – experiments. A similar pattern was found when leaf mass loss was calculated on the basis of the material that remained in original size (% DM d^{-1}). It is necessary to note that the differences in leaf mass loss (all used measures; L1-L4 treatments) between the *G. pulex* experiment and the Control – experiment were too high to assume that it was caused by consumption / assimilation of *G. pulex* alone. In contrast, the leaf mass loss (all used measures; L1-L4 treatments) observed in the experiments with *B. rhodani* tended to be lower than in the Control – experiments, but the difference was in most cases not statistically significant. Although *B. rhodani* clearly consumed the offered material, leaf mass loss was not affected or rather tends to be depressed. In both cases, it seems likely that feeding activities of macro-invertebrates affected the microbial communities. Microbial activity can increase in the presence of shredders (Petersen and Cummins 1974). Morrison and White (1980) found that grazing by amphipods can lead, after an initial removal of microbes, to increase of total microbial biomass and to increasing metabolic activities. Little is known about the net effects (quantitative) of such interactions on breakdown (& decomposition) rates. Alternatively, there is also the possibility that the differences in leaf mass loss between the experiments with and without macro-invertebrates were affected by general differences in microbial communities and therefore affected by used study design.

Leaf particle size composition at the end of the experiments was highly similar among the experiments with and without macro-invertebrates. Most of the generated particles in L1 and L 2 treatments were found in the smallest fraction counted (<0.071-0.0016 µm). Also in most cases there were no differences (except L4) in the amount of generated particles between the experiments with and without macro-invertebrates. In *G. pulex* - experiment (L1-L3) the higher leaf mass loss combined with a similar amount of generated particles in comparison to the Control (L1-L3), indicated an intensive reworking (recycling) of generated particle fractions. The obvious lack of larger differences in leaf particle size composition in experiments with and without macro-invertebrates is probably caused by the possibility for a re-ingestion of feces due to the lack of transportation (circulating current) of particles, the low abundance of macro-invertebrates and their small size (early life stages).

Plant litter breakdown is the result of the combined action of physical, chemical and biological processes (Suberkropp 1998). Some of the processes involved seem to have the potential to drive stable isotope signatures in opposite directions. The net effect can be enrichment, depletion, or no change, if the effects of some processes are canceled out by other processes.

Leaching seems to depend on the chemical composition of the plant material (Casas & Gessner 1999). The $^{13}C/^{12}C$ composition of different plant parts is not constant (O`Leary 1981, Farquhar *et al*. 1989). It is also known that starches and sugars tend to have $^{13}C/^{12}C$ ratios similar to that of carbon initially fixed in photosynthesis, cellulose tends to be heavier by approximately 2 ‰, but plant lipids (by up to 15‰) and lignin components (4-7‰) are depleted (Ehleringer 1991, Benner *et al*. 1987). The loss of soluble chemical components that differ in their isotopic signatures may affect the isotopical composition of the remaining material. The net effect (enrichment, depletion, or no change) depends probably on the chemical and isotopical composition of the source material (leaching rates). Leachates of C_3 plant material are observed to be depleted in ^{13}C (Coffin *et al*.1989, Hullar *et al*. 1996). As a result, the remaining material should become enriched in ^{13}C. This was confirmed in this study for the large particle size treatments. The grade of physical fragmentation of the leaf materials used in this study seemed to affect the leaching process as indicated by changes in conductivity. In the experiments higher conductivity was observed in small particle size treatments, indicating higher leaching rates in comparison to large particle size treatments, but changes in $\delta^{13}C$ of the leaf material showed an opposite trend. Although dry leaf material was used, the intactness of cell-walls seems to affect the leaching process. Leaching resulted in most cases in decreasing ash contents (except L2) and increasing carbon and nitrogen contents (%) combined with a decrease in C/N ratio (except L2). The loss of soluble components and a relative increase in structural components (Cellulose, Lignin) are probably responsible for these changes. Although the changes observed in stable isotopic composition during the short term experiment seemed to be small, leaching is clearly one of the processes that have the potential to displace the isotopic composition of the leaf detritus from the one of is parent source. Such isotopic shifts can lead to increasing uncertainty of trophic link interpretations.

Microorganisms colonizing the leaf litter preferentially use ^{12}C for their respiration (Blair *et al*. 1985, Nadelhoffer & Fry 1988). The microbial biomass becomes enriched, whereas the remaining carbon source becomes depleted in ^{13}C (Ågren *et al.* 1996, Hullar *et al.* 1996). For example, Hullar *et al.* (1996) reported that bacterial assemblages seem to reflect the stable isotope composition of their food sources and a small fractionation of + 1‰ ($\delta^{13}C$) was found. Henn *et al.* (2002) showed that a fractionation up to + 6.9‰ ($\delta^{13}C$) relative to the growth medium can occur in fungi (terrestrial), but they reported also a strong dependence of fractionation to the stage of growth. Little is known about stable carbon isotope fractionation by other biofilm components (ciliates, flagellates, and others). Because of the strong association of both components, where the microbial biomass is attached to the litter surface (biofilm) or

penetrated in the material (fungi), the relative contribution of microbial biomass may affect the stable isotope signature of whole material (detrital mixture of litter and microbes). On the other hand microbial preferences for starches and sugars (higher in ^{13}C) during first stages of litter breakdown against slow decomposing plant components lower in ^{13}C (O`Leary 1981), like lignin (Benner *et al.* 1987), lead to a more rapid loss of ^{13}C from the organic matter (Ågren *et al*. 1996) and causes ^{13}C depletion. Therefore, stable carbon isotope fractionation by microbes combined with the association with their carbon source and microbial preferences for organic matter compounds probably drive ^{13}C values in opposite directions. Their effects may partially cancel out each other. Little is known about the combined effects of microbial colonization and fragmentation by physical forces and invertebrate feeding on the stable isotope composition during litter breakdown. An enrichment in ^{13}C was observed for generated particles (especially L1 & L2 treatment), relative to the leaf material at the beginning of the experiments and relative to the material that remained in original size throughout the experiments. This result seems to be in agreement with published data on carbon isotope fractionation reported from field studies (Finlay 2001). A small but consistent ^{13}C enrichment is found during breakdown succession from live foliage to coarse particulate organic matter and further to FPOM. In field studies, the observed trend of increasing $\delta^{13}C$ values from CPOM to FPOM can be influenced by the mixing of various sources of carbon (allochthonous and autochthonous sources). The similarity to the experimental results is possibly caused by the fact that benthic POM standing stocks are dominated by terrestrial carbon sources (C_3 plants) (Webster & Meyer 1997, Finlay 2001) which are relatively constant in $\delta^{13}C$ (-28 ‰) (France 1995).

However, all these observations conflict with current theoretical frameworks describing litter decomposition (compare Wedin *et al.* 1995), because if the chemical fractions of plant tissue differ in their $\delta^{13}C$ signatures and decay at different rates the $\delta^{13}C$ signatures of the remaining material should not be constant nor should they show an enrichment in ^{13}C. In particular lignin, which decomposes slowly, is substantially depleted in ^{13}C relative to polysaccharides, which comprise the bulk of plant tissues. If lignin is preserved during litter decomposition and the relative concentration increases, the $\delta^{13}C$ signature of the remaining leaf material should decrease (lignin preservation hypothesis) (Benner *et al*. 1987). A contrary hypothesis is that a slight enrichment in ^{13}C occurs during litter decomposition in soils (Melillo *et al.* 1989). A slight enrichment in ^{13}C of the whole leaf material observed in the larger particle size treatments (L1-L2) in the experiments seems to confirm the latter hypothesis. On the other hand the $\delta^{13}C$ of leaf materials in smaller particle size treatments did not change or tend to decrease slightly. The enrichment may reflect a disproportional loss of ^{13}C depleted chemical fractions of

plant tissue and / or combined with preferential microbial use of ^{12}C during decomposition (Wedin *et al.* 1995, Nadelhoffer & Fry 1988).

In the experiments presented the FPOM fractions generated by macro-invertebrate feeding were by far less enriched in ^{13}C in comparison to the fractions generated in the Control experiments without macro-invertebrates, although the detected differences decreased along the used food quality gradient. Ash content and carbon content also differed between FPOM fractions generated by macro-invertebrate feeding in comparison to the fractions generated in the Control experiments without macro-invertebrates.

One of the mechanism responsible for the observed difference in $\delta\ ^{13}C$, that indicates differences in the chemical composition between experiments with and without macro-invertebrate, is probably that microbes selectively assimilate specific carbon components from the leaf litter leading to a typical composition of material that is generated. In quasi no-choice experiments, the macro-invertebrates are probably selective for particles size but less selective for the chemical composition of material ingested. A less selective ingestion combined with highly selective assimilation could lead to the differences in the chemical composition of the particles generated that are dominated by feces when macro-invertebrate consumers were present.

Structural leaf components like lignin may play an important role for the observed difference. Ward (1984) found that FPOM generated by microbes from leaves was lower in lignin than whole leaves and stream - collected FPOM. In small streams invertebrate feeding (generation of feces and “sloppy” feeding) is a major source of FPOM (Webster *et al*. 1999). Yoshimura *et al*. (2004) reported higher lignin content for FPOM generated by macro-invertebrate feeding (*Gammarus* spp.) in comparison to the parent CPOM. Differences in lignin content between FPOM fractions generated by microbial activities in comparison to the FPOM fractions generated by combined activities of microbes and macro-invertebrates could be (partly) responsible for the differences in $\delta\ ^{13}C$ values of FPOM fractions in the experiments with and without macro-invertebrates observed in this study, but further investigations are necessary to investigate this hypothesis.

Alternatively, it is possible that the difference in $\delta\ ^{13}C$ values of FPOM fractions between the experiments with and without macro-invertebrates were caused by differences in the microbial biomass itself. Assuming that the wet sieving procedure dislodge surface attached microbes that were then concentrated in the smallest particle size class [“generated” particles in the large particle size treatments (L1-L3)] and furthermore that macro-invertebrates were preferentially feeding on microbes leading to reduced microbial biomass, the contribution of microbial biomass in generated particle fractions

should be higher in the Controls without macro-invertebrates in comparison to experiments with *G. pulex* or *B. rhodani*. A higher microbial contribution in generated particle fractions of Control experiments should cause also higher δ ^{13}C values as observed, because microbes can be assumed to be enriched ^{13}C relative to the leaf material.

Note that the direct enumeration of microbes (data not shown) in samples of water taken at the end of the breakdown experiments did not help to support either of the two scenarios described above, probably because the enumeration's were performed on water samples but not directly on particle surface - associated biofilms. Estimated total averaged densities were: ciliates (0.64 x 10^2 cell`s $ml^{-1}$), flagellates (1.44 x $10^2$ cell`s ml^{-1}), and algae (4.6 x 10^2 cell`s $ml^{-1}$) (determined using a Sedgewick-Rafter counting cell S50; Graticules Limited, Tonbridge, England); and 1.01 x $10^8$ cell`s ml^{-1} for bacteria [determined by epifluorescence microscopy (Axioplan, Zeiss, Germany) after staining with 4', 6'-diamidino-2-phenylindole (DAPI) according to Porter & Feig (1980)].

The $\delta^{15}N$ signatures of the leaf material were by far more variable in comparison to δ ^{13}C values. During leaching there was a low tendency of decreasing $\delta^{15}N$ in all leaf treatments, this trend however was not distinct because of the high variability observed. Further, during breakdown variable changes in experiments with and without macro-invertebrates were observed.

There is a considerable number of field studies reporting δ ^{15}N signatures for coarse particulate organic matter (CPOM), fine particulate organic matter (FPOM) and seston. δ ^{15}N signatures seem generally much more variable among the studies in comparison to δ ^{13}C values. However, in many cases an enrichment in ^{15}N from CPOM to FPOM and / or seston was found (Thorp *et al*. 1998, Mulholland *et al*. 2000, Evans-White *et al*. 2001, Raikow & Hamilton 2001, Wagner 2003, Benstead & Pringle 2004). As stated above for $\delta^{13}C$, the values and the reported trend from field situations may be influenced by mixing of various sources of nitrogen (allochthonous and autochthonous sources) especially in small particle size fractions (FPOM & seston). In contrast to carbon, the nitrogen from autochthonous sources (algae) probably makes a higher proportion of the detrital mixture and therefore may largely affect the δ ^{15}N signatures of field collected FPOM. Although algae (especially diatoms) were also present in the experiments, they were found in low densities (see above) and probably had little effect on the results.

Also the immobilization of nitrogen (compare Suberkropp 1998) from the surrounding water may influence δ ^{15}N signatures in the field. In the presented experiments δ ^{15}N signatures were highly variable and it seems impossible to discern a clear pattern. In the Control experiments (L1, L4, & L5) the δ ^{15}N tended to decrease but to increase in

the L2 and L3 treatments. The δ ^{15}N of the smallest fraction analyzed (generated particles <0.071mm-0.0016mm) from the *B. rhodani* experiment were in each treatment higher than those found in the Control and the experiment with *G. pulex.* This observation is probably linked to the limited availability of leaf nitrogen for *B. rhodani,* but the underlying mechanism remains unclear.

The C/N ratio in the leaf materials clearly decreased during the breakdown experiments. This trend is commonly observed during the earlier stages of breakdown (Schönborn 1992, Pusch *et al.* 1998). In late stages of breakdown, the POM is characteristically of low size and the particles are compacted into faecal pellets that are densely colonized by microbiota (Pusch *et al.* 1998). The trend of decreasing C/N ratios probably reflects the transformation of residual structural components into plant-microbe composites by fungal and bacterial decomposers (Cloern *et al*. 2002). There is evidence for rapid colonization and growth of bacteria and fungi on decomposing leaves (Findlay & Arsuffi 1989, Suberkropp 1998). The C/N ratio of microbes (microbial biomass) is by far lower (between 5-10) (Friedel & Gabel 2001, Raubuch & Joergensen 2002, Findlay *et al*. 2002) than the C/N ratio of leaves (~ 42 in L1 treatments) and other terrestrial plant materials. The microbial biomass also contributes to contents of C and N in the detrital complex and with increasing microbial biomass the C/N ratio of the mixture (POM + microbes) will decline. Preferential assimilation of the microbial biomass by macro-invertebrates may reduce the microbial contribution to the detrital mixture, leading to higher C/N ratios in comparison to the Control experiments without macro-invertebrate feeding. This pattern was found in the large particle size treatments (L1 & L2 compare Figure) but the opposite pattern was observed in the small particle size treatments (L3-L5). The C/N ratio is commonly used as an indicator of nutritional quality, because it can reflect the amount of protein available for consumption (Shepard & Minshall 1981). For stream detritus, a covariation between C/N ratio and particle size of organic matter was observed by various authors (Cummins & Klug 1979, Thorp *et al.* 1998, Findlay *et al.* 2002, Wagner 2003). Generally, small POM fractions (FPOM) have lower C/N ratios than coarse fractions (CPOM), although FPOM is commonly seen as the refractory residue that remains from inefficient processing of allochthonous materials (Webster *et al.* 1999). Findlay *et al.* (2002) showed that microbial biofilms associated with particulate organic matter are only to a small extent responsible for the covariation between C/N ratio and particles size. Odum *et al.* (1979) pointed out that the C/N ratio can be a misleading indicator for nutritional quality of detritus because of the occurrence of resilient nitrogen. Both the microbial colonization and the relative increase of resilient nitrogen during POM breakdown may drive the C/N ratio in similar directions. When detritus quality was measured by microbial activity (respiration rates) a

comparable covariable pattern, as described above for C/N ratio, was found for lake and marine detritus (compare Webster *et al*. 1999). For stream detritus, no consistent relationship between respiration and particle size has been found, and other measures of detritus quality have been similarly inconsistent (compare Webster *et al*. 1999).

Summary

The experiments revealed that the two macro-invertebrate species performed as predicted by the FFGC. A high survival and a similar growth rate along the used food quality gradient was observed for *G. pulex*. In contrast to *G. pulex*, the leaf material was a poor food source for *B. rhodani* as indicated by high mortality and low growth tendencies. Strong relations between $\delta^{15}N$, N (%) and C/N ratio within tissues and the relation of these factors to the survival indicate that the availability of nitrogen was a limiting factor for *B. rhodani.* The observed difference in the $\delta^{15}N$ values between the consumers and the offered leaf food material was highly similar to standard trophic enrichment values, but those observed for $\delta^{13}C$ differed, indicating selective assimilation of specific carbon components. During breakdown, leaf material undergoes continuous steps of physical and biochemical transformations. Leaching affected the chemical and isotopical composition of the leaf material and is therefore clearly one of the processes that leads to increasing uncertainty of trophic link interpretations. Some of the other processes involved in breakdown seemed to have the potential to drive stable isotope signatures in opposite directions. The net effect can be enrichment, depletion, or no change, if the effects of some processes are canceled out by other processes. A large difference was found in the $\delta^{13}C$ values between organic particles generated in experiments (large particle size treatments) with and without macro-invertebrates. Macro-invertebrate feeding seems to alter the chemical composition of organic material during breakdown.

6. General Discussion

As pointed out in Chapter 2 the investigated small low-head dam caused profound changes in structural and functional attributes of invertebrate communities in stream reaches close to the dam. But the dam did not seem to cause far-reaching downstream effects. Within the impoundment the benthos clearly undergoes a succession towards lentic life forms, diversity decreased, the number of invertebrate eggs decreased and large amounts of fine sediments and POM were stored during periods of low discharges. However, major floods can reset the system (Fjellheim *et al*. 1993). Long term discharge evaluations have shown that in the Ilm five larger floods typically occur during one year (Vetter 2001). Many of these floods are intensive enough to remove most of the fine sediments and the POM stored within the small impoundments and to reset macroinvertebrate communities. After such spates the sediments are soft (making it more difficult to walk in the stream in comparison to periods with lower discharges; own observation after a major flood in spring 2002, compare Figure 2.4, Chapter 2), organic particles are nearly not visible and the surface sediments appear polished. Such observations were made close to the dam and at sites with a nearly natural channel structure. POM standing stocks at dam sites are probably reset to similar low levels as in natural reaches upstream and downstream of the dam. Apart from such clearance-effects also a filling with sediments during storm events can occur (own observations) resulting in the effect that the former impoundment looks like a stream riffle after the event (compare also Schönborn 1995). The fill up with sediments is commonly removed by dredging the impoundments. Also the waters levels during flood events are often much higher than the dams and at the same time large areas of the pastures are flooded. Such large floods are very important for the maintenance of the longitudinal connectivity (Gunkel 1996, Schönborn 1995). At the Ilm it seems that the flow regime is nearly natural (Vetter 2001, Elser 2001 b) and relatively unaffected by the small dam structures. The maintenance of the natural flow regime is possibly a function of the low size of the dams (dam height & size of the impoundments), their spatial distance from another, but may also result from specific features of the catchment area (relative high slopes, small catchment area, relative high amount of precipitation resulting from the geographical position (compare Chapter 2). High spatial and seasonal variability in POM standing stocks may also indicate the importance of smaller variations of discharge in determining POM standing stocks. Slight but frequent variations in discharge (& current velocity) can result in alternating periods of net POM fixation and net POM release (Wagner 2003).

Most streams and rivers were historically more efficient at carbon processing than they are today (Webster *et al.* 1983). The loss in processing efficiency is largely due to the extensive removal of coarse woody debris, the trapping of beaver (*Castor* sp.) (Naiman *et al*. 1987) and the removal of natural retention structures in the pastures that often are intensively used by agriculture. Debris dams (Lemly & Hildebrand 2000) and beaver dams (Naiman *et al.* 1986, Rolauffs *et al*. 2001) are very effective retention devices in natural stream channels. Although it seems unlikely that beavers were historically present in headwater streams like the Ilm, agricultural and other land-use activities have strongly reduced the size of riparian corridors. Today it is not easy to find any form of large or medium woody debris dams in the Ilm, because after major floods fallen trees were commonly removed by land owners and regional authorities (fire departments) in order to avoid backwaters and land losses. Therefore it must be hypothesized that the small dams in the Ilm partly compensate the loss in processing efficiency that is caused by the loss in natural retention devices. The small dams in the Ilm act as retentive structures, and POM as the major resource for stream biota is for a longer period retained in the system. Although invertebrate biomass does not represent a direct measure of productivity, biomass data indicate enhanced productivity at the investigated dam. This observation complies with studies where the retention efficiency was experimentally improved by other in-stream structures (log pieces, boulder clusters, artificial leaf packs) resulting in increasing productivity (Dobson *et al*. 1995, Wallace *et al*. 1995 a, Negishi & Richardson 2003). However, improved retention efficiency and detritus storage can increase invertebrate productivity, but not in each case probably depending on what factor limits the invertebrate productivity, and the consequences of in-stream structures can vary (Negishi & Richardson 2003). The consequences of small dams may also vary and more studies are needed to prove the patterns found in the present study.

There was no argument that invertebrate assemblages on stone surfaces were modified as a result of a barrier effect. The results gained from stone sampling can further be interpreted in the context of the disturbance regime (discharge). In addition to a barrier effect, the alteration of the disturbance regime (discharge) caused by dams is a common assumption and may be an alternative explanation for expected differences in assemblage composition and succession downstream of a dam. Large dams are build to regulate the flow and common downstream effects are the reduction of frequency and / or magnitude of floods (lowering flood peaks and overbank flooding events) (Petts 1984, Brookes 1994). Furthermore, increased use of water and evaporation losses from the reservoirs can reduce the downstream discharge (Nilsson & Berggren 2000). Reduced discharges and floods result in reduced intensity and

frequency of sediment disturbances, but dependent on sediment particle sizes and their composition. At the scale of stream reaches with similar sediment size composition a modified disturbance regime should cause, on average, a modified assemblage composition and / or succession. The obvious lack of large differences in invertebrate assemblage composition between upstream and downstream sites at the investigated dam supports the assumption that the dam caused no distinct downstream alterations of the disturbance regime (discharge). Because the sediment size composition was similar among the reaches studied (SS1, SS3, & SS4) and samples (stones) were chosen on the basis of their size (as similar as possible) the above assumptions seem valid. Although flow velocity during base flow conditions did not significantly differ among the site immediately downstream of the dam and the natural reference sites, the general differences in channel form (depth & width) caused a slightly higher turbulence in the reach immediately downstream of the dam, but this difference also did not cause a change in assemblage composition on stone surfaces at the sample sites. The abundance and the diversity of invertebrates, the composition and probably also the succession of invertebrates assemblages on stone surfaces seemed to be strongly influenced by the time since last disturbance, the intensity of disturbance and the variable growth of filamentous algae caused by the position of the individual stones in a stream reach (shading). Differences among the study sites seemed to result largely from the degree of canopy cover that influences the growth of algae. The differences among the sites did not seem to result from a barrier effect nor from an altered disturbance regime, neither from general differences in the form of the stream channel.

The investigated dam is clearly a physical barrier and additionally the deposition of fine sand, which represents an inherently unstable substrate, within the impoundment impedes upstream migrations of many benthic invertebrates even at low current velocities (Leudtke & Brusven 1976). But both effects seem to be unimportant for the maintenance of lotic invertebrate communities upstream and downstream of the dam. The underestimation of local invertebrate standing crops as well as of local reproduction and the overestimation of dispersal (downstream & upstream) may be most important for the common assumptions that a barrier effect at small dams is ecologically significant. As stated above, large dams can clearly alter the disturbance regime (by reduction of the frequency and /or magnitude of floods below dams) (Petts 1984, Brookes 1994). This effect, however, seems questionable for small dams. There is an increasing number of studies suggesting that this type of dam does not substantially alter the natural discharge regime (Magilligan & Nislow 2001, Stanley *et al*. 2002). Recently Downes *et al.* (2003) found “no compelling evidence” that regulated streams (regulation by low-head dams) have lower disturbance frequencies than unregulated

streams and the results of the study presented in part 1 of Chapter 3 further support this view.

The results, which were gained from part 1 of Chapter 2 provide furthermore important information about the investigated system. The filamentous alga, *Cladophora* sp., is with regard to their biomass clearly the dominant primary producer. Although, *Cladophora* sp. is largely unpalatable and resistant to grazer feeding, after dying off *Cladophora* sp. decomposes rapidly (Schönborn 1996) and becomes detritus. The relation between the averaged amounts (AFDM) of *Cladophora* sp. on stones and POM standing stocks [(annual average values; adjusted by the conversion factor (compare Chapter 2)] can be described as follows: SS1 (16.4 g m^{-2} *Cladophora* sp. to 232 g m^{-2} POM), SS3 (8.07 g m^{-2} *Cladophora* sp. to 332 g m^{-2} POM) and SS4 (3.74 g m^{-2} *Cladophora* sp. to 244 g m^{-2} POM). The above relations indicate that most of the organic matter available to the stream communities in the Ilm (at Stadtilm) must be of allochthonous origin.

Comparison of invertebrate abundance and taxon richness between stone sampling and Hess-Sampling confirmed the results recently presented by Taylor *et al.* (2001). Stone sampling overestimates invertebrate density (Ind. m^{-2}), especially when stones are covered with filamentous algae, and underestimates taxon richness of benthic communities in comparison to Hess-Sampling (Taylor *et al.* 2001). Also community composition differs among the methods, because taxa which live in the sediments interstices are not recorded (or their abundance is underestimated) by stone sampling. Interestingly invertebrate biomass (g m^{-2}) is in contrast to invertebrate density (Ind. m^{-2}) underestimated by stone sampling. Invertebrate biomass (g m^{-2}) estimations from stone samples were approximately 2.4 times lower in comparison to estimations from Hess-Sampling (Invertebrate biomass from stone samples make only 42.9 % (SS1), 41.3 % (SS3), and 40.6 % (SS4) of the biomass estimations from Hess-Sampling.). These results clearly indicate the dominance of small sized invertebrates at stone surfaces. Invertebrate biomass data from stone samples showed a similar tendency as those gained by Hess-Sampling: the site immediately downstream of the dam tended to show higher biomass in comparison to the reference sites. But in contrast to Hess-Sampling, the difference was not statistically significant due to the high variability that was observed among single stones within the reaches.

Furthermore some of the results indicate that the concept of patch dynamics (Pickett & White 1985) can be applied to stones at the upper surface of the stream sediments.

The observed modification of invertebrate downstream drift within the impoundment mainly resulted from high numbers of planktonic crustcea in the samples, caused by locally enhanced population densities. Drift densities of benthic invertebrates were similar among the study sites indicating that the impoundment did not act as a trap for drifting invertebrates. Although the results of the drift study further supported the results and assumptions, which were gained from the other study parts, they must be handled cautiously, because only ~30% of the invertebrate taxa present in the benthos were observed in the drift and no statements were possible for many other invertebrate taxa. A direct comparison between drift and benthos densities is critical because of differences in sampling time. However, it reveals an interesting view: the higher total invertebrate abundance (annual average values) at both dam sites seems not to result in a comparable increase in invertebrate drift densities. Given the averaged values for the drift densities and extrapolating them to the entire sampling reach (at base flow conditions) one can estimate that relative to the benthos densities (annual mean) only a very small proportion of animals is drifting (at the moment). Between 0.029% (SS1) and 0.023% (SS4) were estimated for the two references sites (drift density of benthic invertebrates vs. benthos densities) but at the dam sites only between 0.012 % (SS2) and 0.007 % (SS3). Note that these values represent relatively coarse estimations and the values are probably still overestimated because the drift samples mainly consists of meiobenthic invertebrates and these groups are generally under-sampled by kick-net methods like Hess–Sampling (Chapter 2). The above calculations indicate a reduced drift density at both dam sites relative to benthos densities. Downstream drift is a complex process that can be caused by various factors (Schönborn 1992) and the availability of food is probably an important one (Elliott 1967, Hildebrand 1974). POM standing stocks were higher within the impoundment and immediately downstream of the investigated dam and it can be hypothesized that enhanced invertebrate abundance in the sediments and lowered drift densities are a response to enhanced levels of food resources at the dam. Similar to the observed aggregations of invertebrates at POM at the scale of small in-stream patches it seems likely that comparable aggregations occur a the larger scale of whole stream reaches.

All the arguments collected in the first chapters indicated a low spatial extension of the dam impact. The results which were gained in Chapter 4 further support this view. Although more than 50 small dams occur in the Ilm stream, a clear longitudinal zonation of invertebrates was found . A spatially restricted impact caused by the low size of the dams and combined with relatively large spatial distances from another are probably most important for this fact. Since 1990–1992 a rapid improvement of the water quality has been documented in the Ilm, resulting in positive change in the benthic

communities that is indicated by a strong shift in the saprobity index (compare Chapter 4). Although within the same time also some of the small dams were removed, there are today still more than 50 dams present. Therefore, pollution seems most important for the modified “Species-Deficit-Concept” (Artenfehlbetrag, Kothe 1962) observed in the past. Although an impact of the dams can not completely ruled out, they seem to be by far less important than pollution. As stated in Chapter 4 carefully designed comparative studies are needed in order to get a better understanding about the relative importance various sources of anthropogenic disturbances to stream communities and in order to improve the knowledge about the consequences of multiple small dams on whole stream systems.

In the last years stable isotope analysis has become increasingly available to stream ecology. This method has the potential to trace the flow of energy through the ecosystem and was successfully used to detect food web alterations caused by human disturbances, like stream regulation and deforestation (Thorp *et al*. 1998, Benstead & Pringle 2004). Stable isotope ratios were also suggested to be in-stream markers of organic matter breakdown (Wagner 2003, Guo *et al*. 2003) in the field. Although this method can be used to describe food webs as well as food web alterations, a correct interpretation of the patterns detected (food web links) is still limited and the necessity of laboratory experiments in order to interpret field data correctly was repeatedly emphasized (Gannes *et al*. 1997, Wagner 2003). The experiments conducted during this study revealed on the one hand that the two macroinvertebrate species used performed as predicted by Functional Feeding Group Concept (Cummins 1973, Merritt & Cummins 1996). The observed enrichment in the $\delta^{15}N$ values of the consumers relative to the offered leaf food material was highly similar to standard trophic enrichment values, likely because leaves are low in nitrogen and probably can be a limiting factor for growth, especially when nearly no other nitrogen sources are available. In contrast, the observed enrichment in the $\delta^{13}C$ values of the consumers relative to the offered leaf food material was higher than standard trophic enrichment values, indicating selective assimilation of specific carbon components. Further no-choice (or quasi no-choice) and multiple choice experimentation’s are needed and will potentially increase the possibility for correct interpretation of field data.

During breakdown leaf material undergoes continuous steps of physical and biochemical transformation. Most of the processes involved have the potential to drive stable isotope signatures of the organic matter in opposite directions. The net effect can be enrichment, depletion or no change, if the effects of some processes are cancelled out by other processes. A large difference was found in the $\delta^{13}C$ values between organic particles generated in experiments (large particle size treatments) with and

without macro-invertebrates. The observation that the difference decreased from L1 (large fragments and whole leaves) to L5 (very small particles) treatments probably results probably from the sieving procedure. In the small particle size treatments the particles generated by the macro-invertebrate feeding were not (L5) or only partly (increasing tendency from L4 to L1) separated from the particles that remained in original size and from those generated by microbes alone (Control experiments). To detect a difference in small particle size treatments with and without macro-invertebrates the separation procedures must probably be refined (if possible) in order to avoid that the stable isotope signals of particles generated in experiments with and without macro-invertebrates become masked by the mixture with unaffected or less processed particles. If the difference in $\delta^{13}C$ values between organic particles generated in experiments (large particle size treatments) with and without macro-invertebrates is true it could become an indicator for the intensity of invertebrate feeding probably also in the field. But further experiments are indispensable to test these results.

The general usefulness of stable isotopes as in-stream markers for breakdown and for alterations of breakdown in the field seems questionable. Detritus pools in the field represent heterogeneous mixtures of organic materials from various sources; detritus particles come from upstream reaches and are affected by breakdown for various time intervals. Furthermore seasonal changes of isotopic signatures in plants, non-specific, overlapping of isotope ratios among primary producer groups (Lajtha & Marshall 1994, McArthur & Moorhead 1996, Chanton & Lewis 2002) as well as the selective degradation and gradual transformation of organic matter during processing, which displaces the isotopic composition of organic matter from that of its parent source, (Sherr 1982, Cloern et al. 2002, this study) are important factors that clearly lower the probability for detecting alterations (chemical) of breakdown in the field. However the combination of stable isotope analyses with other methods (more detailed chemical analyses, microbial analyses, field and laboratory breakdown experiment) needs further attention.

A brief discourse concerning fish

One of the hardest arguments against dams is the barrier effect for fish. At large storage dams this effect is evident for migratory fish species (Lewis 1991, Mills 1989; Morita & Yamamoto 2002). Small dams probably also affect the migrations but largely depending on dam size, operational type and on the migrating fish species. They may create potent barriers to small species but not for larger ones. Our knowledge is still limited because up today most studies focused only on economically important

populations and species of fish. Although dam removal studies have shown that migratory and resident fish species extend their movements throughout the systems after removal (see Hart *et al.* 2002), the extension of movements is not necessarily an indicator of populations health and / or improved ecosystem functioning. Also no changes in genetic and population structure have been observed in recent dam removal studies (Jager *et al.* 2001, Neraas & Spruell 2001).

Müller (1995) found 17 fish species in the Ilm: Brook lamprey (*Lampetra planeri* L.), Eel (*Anguilla anguilla* L.), Carp (*Cyprinus carpio* L.), Gudgeon (*Gobio gobio* L.), Chub (*Leuciscus cephalus* L.), Moderlieschen (*Leucaspius delineatus* Heckel), European minnow (*Phoxinus phoxinus* L.), Roach (*Rutilus rutilus* L.), Tench (*Tinca tinca* L.), Rainbow trout (*Oncorhynchus mykiss* Walbaum), Brown trout (*Salmo trutta* L.), Grayling (*Thymallus thymallus* L.), Bullhead (*Cottus gobio* L.), Perch (*Perca fluviatilis* L.), Loach (*Noemacheilus barbatulus* L.), Three-spined Stickleback (*Gasterosteus aculeatus* L.) and Giebel (Carassius auratus L.). Seven of them are noted in the Thuringian red-list, indicating that elsewhere rare species have still survived in the Ilm. The Eel (*Anguilla anguilla* L.) as a katadromous species is present in the Ilm and was found in upstream and downstream sections of the stream (downstream of Gräfinau-Angstedt). The community of fish in the Ilm is, as in other European streams, anthropogenically affected (by stocking) and therefore it will be not easy to separate the impacts of small dams from other anthropogenic disturbances. Already 40 years ago Hynes (1970) stated that it is extremely difficult to find any stream system that have not been affected by human activity. Since 1932 (first available data set) the number of species seems highly constant in the Ilm (Müller 1995). As stated above the flooding regime of the Ilm causes in regular intervals water levels higher than the dams potentially allowing upstream migrations by large and small fish species (compare Müller 1995). Fish ladders, fish passes and fish lifts help to lower the barrier effect of large dams. However their general effectiveness remains in many cases untested and beside the dam itself, physical and chemical conditions within large reservoirs probably create a further barrier. Also the usefulness of the above constructions at small dams and their general effectiveness is questionable. For instance Berg and Myhre (1990) investigated 372 fish ladders in Norway and found that only 37% of these constructions were functioning well (But note that an good functioning of such structures is also not easy to define!). In the Ilm populations of many resident species of fish seem relatively unaffected by multiple small dams that were built more than 100 years ago (some of them > 250 years ago). In addition to fish migrations, the dispersal of aquatic invertebrates is frequently used as an argument for the construction of fish passes and ladders even at small dams (TMLNU 2000). This argumentation based on unproved generalizations: from large

dams to small dams, as well as from migrating fish species to resident fish species and further to invertebrates. The results of the present study clearly indicate that care should be taken with such generalizations. Large dams and pollution in the main channels (higher orders), which create the link between the headwaters and the oceans are probably most important for the lack of migrating species of fish in the headwaters. Before these major dispersal paths are not adequately restored for migrating fish species all efforts to restore the headwaters for those species are questionable. However, the barrier effect for fish is probably the most serious effect caused by dams (although depending on dam size), but further investigations are indispensable in order to avoid expensive management mistakes.

The main motivation for the present study was to contribute to a better understanding about the impacts of small dams on invertebrate communities and particulate organic matter dynamics in order to help to fill the gap in our knowledge about the ecological responses of small dams. The results of this study should not be interpreted in favor of small dams and / or in the sense of building more and more of them. The investigated small dam clearly alters local environmental conditions and consequently the local invertebrate communities, but the spatial extension of the impacts seems low. Both dam removal and restoration of the entire riparian zones would be the essential steps to re-establish „natural“ conditions in the Ilm. Today there are many social and economical constraints that will probably not allow to fulfill this goal completely. On the other hand small dams are today a common tool for structural restoration, especially where full restoration of the stream channel is not possible (Hey 1994). Small dams can have a positive effect on the biota (Mellquist 1985). But the size and the spacing of the dams are critical factors (Hey 1994). Investigations of dam impacts across a variety of dam sizes and operational types may also improve our general knowledge about the structure, function and processes in stream ecosystems. Such information are indispensable before we can define new and partly modified goals that will represent the best solution under existing constraints. Only if this stage is reached we can better manage stream ecosystems.

7. Summary / Zusammenfassung

7.1 Summary

Many stream ecosystems are altered by the impacts of numerous anthropogenic disturbances. Large storage dams and their impoundments are very important ones, which have profound physical, chemical, and biological effects. In contrast to large storage dams little is known about the ecological effects of small dams. The present thesis focuses on the impacts of a small low-head dam on invertebrate communities and their major energy base (particulate organic matter, POM) in the Ilm stream (Thuringia, Germany).

Invertebrate communities and particulate organic matter in the sediments were investigated seasonally at two dam sites (a site within the impoundment & a site immediately downstream of the dam) and at two stream sites with a near-natural channel structure (reference sites) using the traditional Hess-Sampling technique. Invertebrate abundance (number & biomass) and the amount of POM in the sediments were higher at both dam sites in comparison to the reference sites. Diversity was lower within the impoundment. Invertebrate community composition (taxonomic and functional) at the dam sites differed from those observed at reference sites. The dam acts as a retentive structure for POM. As expected, the investigated small low-head dam causes profound changes in structural and functional attributes of invertebrate communities in stream reaches close to the dam. But the dam dos not seem to cause far-reaching downstream effects. Furthermore positive correlation's between POM and invertebrates (abundance) support the view that benthic invertebrates are aggregated on their patchily distributed detrital food source (POM).

The investigated dam creates a physical barrier; however there was no indication that the barrier effect is of large ecological significance for benthic invertebrates. The barrier effect seems unimportant for the maintenance of invertebrate communities upstream and downstream of the dam. On individual stones the abundance, diversity and the composition of invertebrate assemblages seemed strongly influenced by the time since the last disturbance, the intensity of the disturbance and the variable growth of filamentous algae, which was caused (mainly) by the position of the individual stones to the sun. Differences in biological attributes of the invertebrate assemblages among the study sites seemed largely caused by the degree of canopy cover that influences the growth of filamentous algae. The differences among the sites did not seemed to result from a barrier effect nor from an altered disturbance regime, neither from general differences in the form of the stream channel.

Invertebrate downstream drift was slightly modified within the impoundment of the dam. The modification within the impoundment mainly resulted from high numbers of planktonic crustacea in the drift, caused by locally enhanced population densities. The impoundment of the dam did not seem to act as a trap for invertebrate downstream drift. Immediately downstream of the dam invertebrate downstream drift was highly similar to that observed at the reference sites.

Although more than 50 small dams occur in the Ilm stream, a clear longitudinal zonation of invertebrates was found. A spatially restricted impact caused by the low size of the dams and combined with relatively high spatial distances from another is probably important for this fact. Stream pollution (local & industrial wastewater's) seems most important for the modified "Species-Deficit-Concept" (reduced species richness) observed at the Ilm in the past. Although an impact of the dams cannot completely ruled out, they seem to be of minor importance.

Stable isotope analysis has the potential to trace the flow of energy through the ecosystems and this method has been increasingly used to detect food web alterations caused by human disturbances. Although this method can be used to describe food web as well as food web alterations, a correct interpretation of the detected patterns is still limited and the necessity for conducting more laboratory experiments has been emphasized repeatedly. Laboratory experiments on invertebrate feeding and leaf breakdown were conducted in this study. The experiments have revealed that two macro-invertebrate species, which were used, performed as predicted by the Functional Feeding Group Concept. The observed enrichment in the $\delta^{15}N$ values of the consumers in comparison to the offered leaf food material was highly similar to standard trophic enrichment values but those observed for $\delta^{13}C$ differed, indicating selective assimilation of specific carbon components. The exact knowledge about such deviations from standard isotopic that are caused by selective assimilation should allow better interpretations of stable isotope data from the field. During breakdown leaf material undergoes continuous steps of physical and biochemical transformations. A large difference was found in the $\delta^{13}C$ values between organic particles generated in experiments (large particle size classes) with and without macro-invertebrates. Macro-invertebrate feeding seems to alter the chemical composition of organic material during breakdown. The general usefulness of stable isotopes as in-stream markers for breakdown and for alterations of breakdown in the field remains questionable. Detritus field samples represent heterogeneous mixtures of organic materials from various sources; detritus particles come from upstream reaches and are affected by breakdown for various time intervals. Furthermore seasonal changes of isotopic signatures in

plants, non-specific overlapping of isotope ratios among primary producer groups as well as the selective degradation and gradual transformation of organic matter during processing are factors that clearly lower the probability for detecting alterations (chemical) of breakdown in the field.

The investigated small low-head dam clearly alters local environmental conditions and consequently local invertebrate communities, but the spatial extension of the impacts seems to be low. Both dam removal and the combined restoration of the entire riparian zones would be the essential steps to completely re-establish „natural“ conditions in the Ilm. Because of the existing social and economical constraints it will not be easy (if not impossible) to fulfill this goal. Considering the fact that most of the effects caused by small dams are locally restricted, as indicated by the results of the present study, and furthermore that the retentive character of the dams could (partly) compensate the loss in processing efficiency, which is caused by the loss of natural retention devices, some arguments against these structures almost disappear, making dam removal strategies without a combined restoration of the entire riparian zones questionable (but also the constructions of expensive fish ladders & passes). However, more studies about the impacts of small dams are needed before generalizations about their ecological effects are possible. The present study is among the first ones that provide a detailed and differentiated view about the effects of a small dam on benthic invertebrate communities and their major energy base (POM). The studies of that kind provide furthermore some important information that are indispensable to define new (partly modified and more realistic) restoration goals that will represent the best solution under the existing constraints. Only if this stage is reached we can manage stream ecosystems in a better way.

7.2 Zusammenfassung

Zahlreiche anthropogene Störungen haben die Fließgewässer-Ökosysteme in starkem Maße verändert. Große Staudämme sind aufgrund ihrer vielfältigen und tiefgreifenden physikalischen, chemischen und biologischen Effekte von großer Bedeutung. Im Gegensatz zu großen Staudämmen ist wenig über die ökologischen Effekte kleiner Stauanlagen bekannt. Die vorliegende Dissertation untersucht den Einfluß eines kleinen Wehres auf die Invertebraten-Gemeinschaft und das partikuläre organische Material (POM) in der Ilm, einem Mittelgebirgsbach in Thüringen (Deutschland).

Im Rahmen von saisonalen Untersuchungen wurde unter Einsatz einer traditionellen Probenahmetechnik (Hess–Sampler) die Gemeinschaft der Invertebraten und das POM im Staubereich eines Wehres, im Bereich unmittelbar unterhalb des Wehres sowie in zwei naturnahen Fließgewässerabschnitten ober- und unterhalb des Wehres erfaßt. Die Invertebraten-Abundanz (Individuendichte & Biomasse) und die Menge an POM in den Bachsedimenten waren im Bereich des Wehres erhöht im Vergleich zu den beiden naturnahen Standorten. Im Staubereich war die Diversität der Lebensgemeinschaft deutlich reduziert. Innerhalb des Staubereiches sowie im Bereich unmittelbar unterhalb des Wehres unterschied sich die taxonomische und funktionelle Zusammensetzung der Lebensgemeinschaft von der naturnaher Standorte. Das untersuchte Wehr wirkte als retentive Struktur für das partikuläre organische Material. Wie erwartet, verursachte das Wehr in wehrnahen Fließgewässerbereichen tiefgreifende Veränderungen in strukturellen und funktionellen Merkmalen der Invertebraten-Gemeinschaft. Aber das untersuchte Wehr scheint keine weitreichenden Effekte in flußabwärts gelegenen Fließgewässerabschnitten zu verursachen. Die beobachteten positiven Korrelationen zwischen den Invertebraten und dem POM unterstützen die Ansicht, daß sich benthische Invertebraten um die räumlich heterogen (fleckenhaft) verteilten Nahrungsressourcen versammeln.

Obwohl das untersuchte Wehr eine physikalische Barriere darstellt, konnten keine Anzeichen dafür gefunden werden, daß dieser Effekt von besonderer ökologischer Bedeutung für benthische Invertebraten ist. Die Wirkung des Wehres als Barriere scheint keine Bedeutung für die Aufrechterhaltung der benthischen Invertebraten-Gemeinschaften ober- und unterhalb des Wehres zu besitzen. Die Besiedlung und Vergesellschaftung (Dichte, Diversität und Zusammensetzung) von Invertebraten auf der Oberfläche einzelner Steine scheint in starkem Maße durch die Zeit seit der letzten Störung, die Intensität der letzten Störung und das Wachstum filamentöser Algen beeinflußt zu werden. Die festgestellten Unterschiede in der Besiedlung von Steinoberflächen zwischen den untersuchten Fließgewässerbereichen scheinen deshalb in

besonderem Maße durch Unterschiede in Beschattung durch die Ufervegetation verursacht zu werden, welche das Wachstum filamentöser Algen beeinflußt. Es gab keine Hinweise dafür, daß die Unterschiede zwischen den Probenahmestandorten das Ergebnis eines Barriere-Effektes oder eines veränderten Störungsregimes (Durchfluß) waren, ebenfalls sind generelle Unterschiede in der Form des Fließgewässerbettes als Ursachen nahezu auszuschließen. Innerhalb des Staubereiches war die flußabwärts gerichtete Drift der Invertebraten nur in geringem Maße modifiziert. Der beobachtete Unterschied resultierte hauptsächlich aus einer Zunahme der Driftdichte planktischer Crustacea, deren Populationsdichte innerhalb des Staues erhöht war. Das Wehr scheint nicht als Driftfalle zu fungieren. Unmittelbar unterhalb des Wehres war die flußabwärts gerichtete Drift der Invertebraten vergleichbar mit der an naturnahen Fließgewässerabschnitten ober- und unterhalb des Wehres.

Obwohl die Ilm in ihrem Verlauf mehr als 50 kleine Dämme besitzt, konnte eine klare Längszonierung aquatischer Invertebraten festgestellt werden. Ein räumlich beschränkter Einfluß, verursacht durch die geringe Größe der Wehre (geringen Höhe & Staukapazität) in Kombination mit verhältnismäßig großen Abständen voneinander, ist wahrscheinlich ein ausschlaggebender Faktor für die Aufrechterhaltung der Längszonierung. Der in der Vergangenheit an der Ilm beobachtete Artenfehlbetrag (reduzierter Artenreichtum) scheint in starkem Maße auf die Belastung mit kommunalen und industriellen Abwässern zurückzuführen zu sein. Obwohl ein Einfluß der Wehre nicht komplett ausgeschlossen werden kann, scheinen diese von geringer Bedeutung zu sein.

Die Analyse stabiler Isotope hat das Potential, den Energiefluß in Ökosystemen zu verfolgen und diese Methode wurde in zunehmendem Maße genutzt, um den Energiefluß in anthropogen veränderten Nahrungsnetzen zu untersuchen. Obwohl sich mit Hilfe dieser Methode Nahrungsnetze als auch deren Veränderungen beschreiben lassen, ist eine korrekte Interpretation häufig stark eingeschränkt und die Notwendigkeit von experimentellen Laboruntersuchungen wurde wiederholt betont. Im Rahmen der vorliegenden Dissertation wurden des weiteren Laborexperimente zur Ernährung von zwei Invertebraten-Arten und zum Abbau von Laubmaterial durchgeführt. Die untersuchten Arten verhielten sich so wie es durch das Ernährungstypenkonzept vorhergesagt wird. Die δ^{15}N-Werte beider Konsumentenarten waren erhöht im Vergleich zur angebotenen Nahrungsressource (Laubmaterial), der gemessene Unterschied lag im Bereich der in der Literatur beschriebenen Standardwerte (Erfahrungswerte). Im Gegensatz dazu fanden sich deutliche Unterschiede in der Differenz der δ^{13}C-Werte zwischen den Konsumenten und der angebotenen

Nahrungsressource. Diese Unterschiede weisen auf eine selektive Nutzung (Assimilation) spezifischer Kohlenstoff-Komponenten hin. Eine genaue Kenntnis derartiger durch selektive Assimilation bedingter Abweichungen von den in der Literatur beschriebenen Standardwerten sollte eine korrektere Interpretation von im Freiland erhobenen Daten ermöglichen. Während des Abbaus von Laub kommt es zu zahlreichen physikalischen und biochemischen Veränderungen. Die $\delta^{13}C$-Werte der während der Experimente produzierten organischen Partikel (in Ansätzen mit anfänglich grobem Laubmaterial) unterschieden sich in Ansätzen mit Makroinvertebraten deutlich von Ansätzen ohne Makroinvertebraten. Die Verwertung von Laubmaterial durch Makroinvertebraten scheint die chemische Zusammensetzung des organischen Materials während des Abbaus zu verändern. Die Verwendbarkeit stabiler Isotope zur Charakterisierung des Abbaus und der Prozessierung von organischem Material im Freiland sowie die Anwendbarkeit der Methode zur Beschreibung von Veränderungen des Abbaus im Freiland bleibt fraglich. Detritusproben aus dem Freiland repräsentieren heterogene Mischungen von organischen Materialien, die aus verschiedenen Quellen stammen. Große Mengen an Detritus stammen aus den Oberlaufbereichen und diese Partikel unterlagen dem Abbau einer unterschiedlichen Dauer. Die saisonale Variabilität der Isotopensignaturen von Pflanzen, das unspezifische Überlappen der Isotopensignaturen zwischen verschiedenen Primärproduzenten - Gruppen sowie die Veränderung der Isotopensignaturen durch den selektiven Abbau und die allmähliche Umwandlung des organischen Materials während der Prozessierung sind Faktoren, welche die Wahrscheinlichkeit, Veränderungen des Abbaus im Freiland zu detektieren, klar einschränken.

Das untersuchte Wehr verursacht räumlich beschränkte Veränderungen verschiedener Umweltfaktoren, welche zur lokalen Veränderung der Lebensgemeinschaften beitragen. Die räumliche Ausdehnung dieses Einflusses scheint gering zu sein. Die komplette Entfernung der Wehre in Kombination mit der Renaturierung der Auen wären zweifelsohne die wichtigsten Schritte, um in der Ilm komplett natürliche Bedingungen wiederherzustellen. Aufgrund der bestehenden sozialen und wirtschaftlichen Einschränkungen wird es kaum möglich sein, dieses Ziel umfassend zu erreichen. In Anbetracht dessen, daß die meisten Effekte, die durch kleine Dammstrukturen verursacht werden, lokal beschränkt sind (wie es die Ergebnisse der vorliegenden Arbeit klar zeigen) sowie die bestehende Möglichkeit, daß die Wehre den Verlust an natürlichen Retentionsstrukturen kompensieren, stellen zwei wichtige Kritikpunkte dar, welche einige Argumente gegen diese kleinen Dammstrukturen nahezu verschwinden lassen.

Ein Rückbau der Wehre ohne die kombinierte Restauration der gesamten Auenbereiche stellt deshalb eine durchaus fragliche Strategie dar. Dennoch sind weitere Untersuchungen nötig, bevor Verallgemeinerungen über die ökologischen Auswirkungen von kleinen Dammstrukturen möglich sind. Die vorliegende Untersuchung liefert als eine der ersten, ein detailliertes und differenziertes Bild über die Effekte eines kleinen Wehres auf die Invertebraten–Gemeinschaft und deren Hauptenergie–Ressource (POM). Derartige Untersuchungen liefern wichtige Informationen, die unbedingt erforderlich sind, um neue (teilweise modifizierte und realistischere) Restaurationsziele zu definieren. Diese Ziele bilden die Grundlage für ein effizientes Management unserer Fließgewässer–Ökosysteme.

8. References

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8.2 Invertebrate identification keys

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Appendix

Table A.1: A list of all invertebrate taxa found during the study.

Taxon (1)	**Taxon (2)**
Plathelminthes	
Tricladia	Trichoptera
Dugesia sp.	*Rhyacophila nubila (*Zett)
Tricladia sp.	*Rhyacophila* sp.
Nemathelminthes	*Sericostoma personatum* (Kirb & Spen.)
Nematoda	*Sericostoma* sp.
Nematomorpha	*Polycentropidae*
Mollusca	*Hydroptila sparsa* (Curt.)
Ancylus fluviatilis (Müller)	*Hydroptilidae*
Pisidium sp.	*Hydropsyche angustipennis* (Curt.)
Annelida	*Hydropsyche instabilis* (Curt.)
Oligochaeta	*Hydropsyche incognita* (Pitsch)
Tubificidae	*Hydropsyche siltala* (Döhler)
Naididae	*Hydropsyche* sp.
Chaetogaster sp.	*Limnephilidae*
Lumbricidae	*Glossosoma conformis* (Neb.)
Oligochaeta (eggs)	*Glossosoma* sp. larvae
Hirudinea	*Glossosoma* sp. pupae
Erpobdella octoculata (L.)	Diptera
Glossiphonia complanata (L.)	Tipuliidae
Glossiphonia sp.	*Tipula* sp.
Hirudinea (cocoons)	*Dicranota* sp.
Tardigrada	Limoniidae
Arthropoda	Empididae
Arachnida	*Atherix* sp.
Hydrachnella	*Chaoboridae*
Phyllopoda	*Culicidae*
Daphnia sp.	*Simuliidae* larvae
Bosmina sp.	*Simuliidae* pupae
Ostracoda	*Simulium* sp.
Copepoda	*Bezzia* sp.
Harpacticoida	*Ceratopogonidae*
Cyclopoida	*Chironomidae*
Cyclops sp.	*Diamesinae (> 3 morphospecies)*
Eucyclops sp.	*Orthocladiinae (> 6 morphospecies)*
Isopoda	*Chironominae*
Asellus aquaticus (L.)	*Polypedilum* sp.
Amphipoda	*Chironomus* sp.
Gammarus pulex (L.)	*Tanypodinae*
Insecta	Megaloptera
Collembola	*Sialis* sp.
Ephemeroptera	Coleoptera
Baetis rhodani (Pictet)	*Elmis aenea* (Müller) adults
Baetis vernus (Curtis)	*Elmis* sp. adults
Baetis fuscatus (L.)	*Elmis* sp. larvae
Baetis sp.	*Orectochilus villosus* (Müller) larvae
Ecdyonurus sp.	*Agabus paludosus* (F.)
Ephemerella ignita (Poda)	*Platambus maculatus* (L.)
(Serratella)	*Helophorus brevipalpis* (Bedel)
Plecoptera	*Helophorus* sp.
Leuctra sp.	
Isoperla sp.	

Table A.2: Summary of two-way ANOVA`s (balanced design) to test the effects of site and date, and their interactions on invertebrate community variables. Sampling sites are denoted as in the text. Sampling dates are denoted as follows: D1=April, D2=July, D3=October, D4=January.

Variable	*Effect*	*df*	*SS*	*F*	*P*	*Post hoc Tukey Test (P < 0.05)*
Inv. density (Ind. m^{-2})	Site (S)	3	4.5×10^{9}	32.64	**<0.001**	(SS2 = SS3) > (SS1 = SS4)
	Date (D)	3	3.3×10^{9}	23.63	**<0.001**	D2 > D1> (D3 = D4)
	S x D	9	1.4×10^{9}	3.43	**0.002**	
	Residual	64	2.9×10^{9}			
	Total	79	1.2×10^{10}			
Inv. density (Ind. g^{-1})	Site (S)	3	7.575	12.43	**<0.001**	(SS2 = SS3) > (SS1 = SS4)
	Date (D)	3	0.698	1.15	0.337	ns
	S x D	9	5.043	2.76	**0.009**	
	Residual	64	13.001			
	Total	79	26.317			
Inv. biomass ($g\ m^{-2}$) log (x+1) transformed	Site (S)	3	0.636	9.18	**<0.001**	SS3 > (SS1 = SS2 = SS4)
	Date (D)	3	1.037	14.96	**<0.001**	(D2 = D1) > (D3 = D4)
	S x D	9	0.222	1.07	0.398	
	Residual	64	1.479			
	Total	79	3.374			
Inv. biomass ($mg\ g^{-1}$) log (x+1) transformed	Site (S)	3	1.199	7.89	**<0.001**	SS3 > (SS1 = SS4) ; SS2 > SS1
	Date (D)	3	0.190	1.25	0.298	ns
	S x D	9	1.871	4.11	**<0.001**	
	Residual	64	3.238			
	Total	79	6.498			
Simpson`s index	Site (S)	3	0.945	41.94	**<0.001**	(SS1 = SS3 = SS4) > SS2
	Date (D)	3	0.029	1.32	0.276	ns
	S x D	9	0.466	6.89	**<0.001**	
	Residual	64	1.922			
	Total	79	7.660			
Expected taxa richness	Site (S)	3	190.5	67.87	**<0.001**	(SS1 = SS3 = SS4) > SS2
	Date (D)	3	20.33	7.24	**<0.001**	D2 > (D1 = D4)
	S x D	9	57.29	6.80	**<0.001**	
	Residual	64	59.88			
	Total	79	328.0			
Taxa number log (x+1)	Site (S)	3	0.057	9.39	**<0.001**	SS3 > (SS1 = SS2 = SS4)
	Date (D)	3	0.011	18.37	**<0.001**	D2 > D1; D3 > D4
	S x D	9	0.063	3.49	**0.001**	
	Residual	64	0.129			
	Total	79	0.360			
Inv. eggs ($eggs\ m^{-2}$) log (x+1) transformed	Site (S)	3	9.148	23.77	**<0.001**	SS3 > (SS1 = SS4) > SS2
	Date (D)	3	6.429	16.70	**<0.001**	(D1 = D2) > (D3 = D4)
	S x D	9	1.128	0.977	0.468	
	Residual	64	8.210			
	Total	79	24.92			

Table A.3: Summary of two-way ANOVA`s (balanced design) to test the effects of site and date, and their interactions on POM variables. Sampling sites are denoted as in the text. Sampling dates are denoted as follows: D1=April, D2=July, D3=October, D4=January. Double square root transformed data = dsqrt.

Variable	*Effect*	*df*	*SS*	*F*	*P*	*Post hoc Tukey Test (P < 0.05)*
Total POM	Site (S)	3	2.618	4.17	**0.009**	SS2 > (SS4 = SS1)
(g m^{-2})	Date (D)	3	6.692	10.67	**<0.001**	D2 > (D3 = D1) ; D4 > D3
dsqrt	S x D	9	8.220	4.36	**<0.001**	
	Residual	64	13.390			
	Total	79	30.910			
Total POM	Site (S)	3	13.229	9.33	**<0.001**	SS2 > (SS4 = SS3 = SS1)
(mg g^{-1})	Date (D)	3	13.986	9.86	**<0.001**	D4 > (D3 = D2 = D1)
dsqrt	S x D	9	5.514	1.30	0.257	
	Residual	64	30.263			
	Total	79	62.992			
CPOM	Site (S)	3	1.474	1.68	0.181	ns
(g m^{-2})	Date (D)	3	5.611	6.38	**<0.001**	D2 > (D3 = D1); D4 > D3
dsqrt	S x D	9	10.560	4.00	**<0.001**	
	Residual	64	18.760			
	Total	79	36.640			
CPOM	Site (S)	3	9.285	7.26	**<0.001**	SS2 > (SS4 = SS1)
(mg g^{-1})	Date (D)	3	13.961	10.92	**<0.001**	D4 > (D3 = D2 = D1)
dsqrt	S x D	9	7.349	1.92	0.065	
	Residual	64	27.282			
	Total	79	57.876			
FPOM	Site (S)	3	3.019	21.19	**<0.001**	SS2 > (SS1 = SS3 = SS4)
(g m^{-2})	Date (D)	3	4.382	30.76	**<0.001**	D2 > D1 > D3; D4 > D3
dsqrt	S x D	9	3.852	9.02	**<0.001**	
	Residual	64	3.039			
	Total	79	14.29			
FPOM	Site (S)	3	0.289	10.50	**<0.001**	SS2 > (SS1 = SS3 = SS4)
(mg g^{-1})	Date (D)	3	0.219	7.95	**<0.001**	D4 > (D3 = D2 = D1)
dsqrt	S x D	9	0.098	1.19	0.316	
	Residual	64	0.587			
	Total	79	1.194			
CPOM/	Site (S)	3	0.262	1.50	0.222	ns
FPOM	Date (D)	3	0.150	0.86	0.468	ns
ratio	S x D	9	1.775	3.39	**0.002**	
	Residual	64	3.762			
	Total	79	5.913			

Table A.4: Spearman Rank correlation coefficients between invertebrate community variables and POM variables [Total POM, CPOM, FPOM expressed as (g m^{-2}) and (mg g^{-1})], CPOM/FPOM ratio, and particle size diversity (based on Simpson index of diversity) for the POM and the sediment within the samples for each seasons (n=20). Taxon number is not shown, because it was not significant related to any of the independent variables. Significant correlation's in ranking are indicated by: **P < 0.005, *P < 0.05, ns = non-significant (P ≥ 0.05), line = not tested.

	Dependent community variable					
Independent variable	Density (Ind. m^{-2})	Biomass (g m^{-2})	Density (Ind. g^{-1})	Biomass (mg g^{-1})	Expected richness	Simpson index
Total POM (g m^{-2})						
April	ns	ns	-	-	0.77**	0.63**
July	ns	0.45*	-	-	ns	ns
October	ns	ns	-	-	ns	ns
January	0.58*	ns	-	-	-0.67**	-0.63**
Total POM (mg g^{-1})						
April	-	-	0.54*	0.46*	ns	ns
July	-	-	0.83**	0.89**	ns	ns
October	-	-	0.92**	0.78**	-0,76**	-0.77**
January	-	-	0.70**	0.48*	-0.47*	-0.60*
CPOM (g m^{-2})						
April	ns	ns	-	-	0.84**	0.72**
July	ns	0.46*	-	-	ns	ns
October	ns	ns	-	-	ns	ns
January	0.66**	ns	-	-	-0.71**	-0.71**
CPOM (mg g^{-1})						
April	-	-	ns	ns	ns	ns
July	-	-	0.67**	0.77**	ns	ns
October	-	-	0.67*	0.65**	-0.72**	-0.50*
January	-	-	0.69**	0.48*	-0.50*	-0.62*
FPOM (g m^{-2})						
April	ns	ns	-	-	ns	ns
July	0.75**	ns	-	-	-0.69**	-0.80**
October	ns	ns	-	-	ns	ns
January	ns	ns	-	-	-0.53*	ns
FPOM (mg g^{-1})						
April	-	-	0.77**	0.71*	-0.49*	ns
July	-	-	0.93**	0.96**	ns	-0.47*
October	-	-	0.91**	0.71**	-0.63**	-0.71**
January	-	-	0.72**	ns	-0.45*	-0.56*
CPOM/FPOM						
April	ns	ns	-0.60*	-0.63**	0.75**	0.62**
July	-0.70**	ns	-0.81**	-0.77**	ns	ns
October	ns	ns	ns	ns	ns	ns
January	0.59*	ns	ns	ns	ns	ns
POM diversity						
April	ns	ns	0.61**	0.62**	-0.60**	-0.52*
July	0.79**	ns	0.79**	0.73**	-0.56*	-0.52*
October	ns	ns	ns	ns	ns	ns
January	-0.65**	ns	ns	ns	ns	0.46*
Sediment diversity						
April	ns	ns	ns	ns	0.47*	0.48*
July	ns	ns	0.60**	0.64**	ns	ns
October	ns	ns	ns	ns	ns	ns
January	ns	ns	ns	ns	ns	ns

Table A.5: Summary of statistical measures of invertebrate community characteristics and environmental factors. Monte Carlo Permutation testes of significance of RDA axis 1: F=41.45, p=0.005; of the overall test: F=10.49, p=0.005).

Axes	**1**	**2**	**3**	**4**	**Total variance**
eigenvalues	0.372	0.144	0.027	0.013	1.000
Invertebrate community data – environment correlation's	0.868	0.749	0.632	0.627	
Cumulative percentage variance:					
of Invertebrate community data	37.2	51.6	54.4	55.6	
of Invertebrate community data – environment relationship	64.8	89.9	94.7	96.9	
Sum of all canonical eigenvalues					0.574

Table A.6: Ranking of 9 environmental variables by their effects on invertebrate community composition. Lambda 1 indicates the percentage of variability explained by a single variable. Lambda A indicates the percentage explained by a variable after the forward selection starting from the best variable (marginal effects). Each subsequent variable is ranked on the basis of the fit that the variables gives in conjunction with the variables already selected (conditional effects). P- and F- values indicate the level of significance of each variable obtained by Monte Carlo permutations (199 random permutations).

Variable	**Marginal Effects**	**Conditional Effects**		
	Lambda1	Lambda A	P	F
SQ –Index	0.30	0.30	**0.005**	33.71
Photoperiod	0.13	0.13	**0.005**	16.87
Mean discharge within 30 d prior sampling	0.07	0.06	**0.005**	10.19
Sediment in sample	0.06	0.03	**0.010**	3.90
Total POM	0.05	0.01	0.115	1.99
Sediment size diversity in sample	0.04	0.01	0.135	1.75
POM size diversity in sample	0.03	0.02	0.060	2.39
Distance from the dam	0.02	0.00	0.195	1.27
CPOM/FPOM ratio	0.01	0.01	0.215	1.39

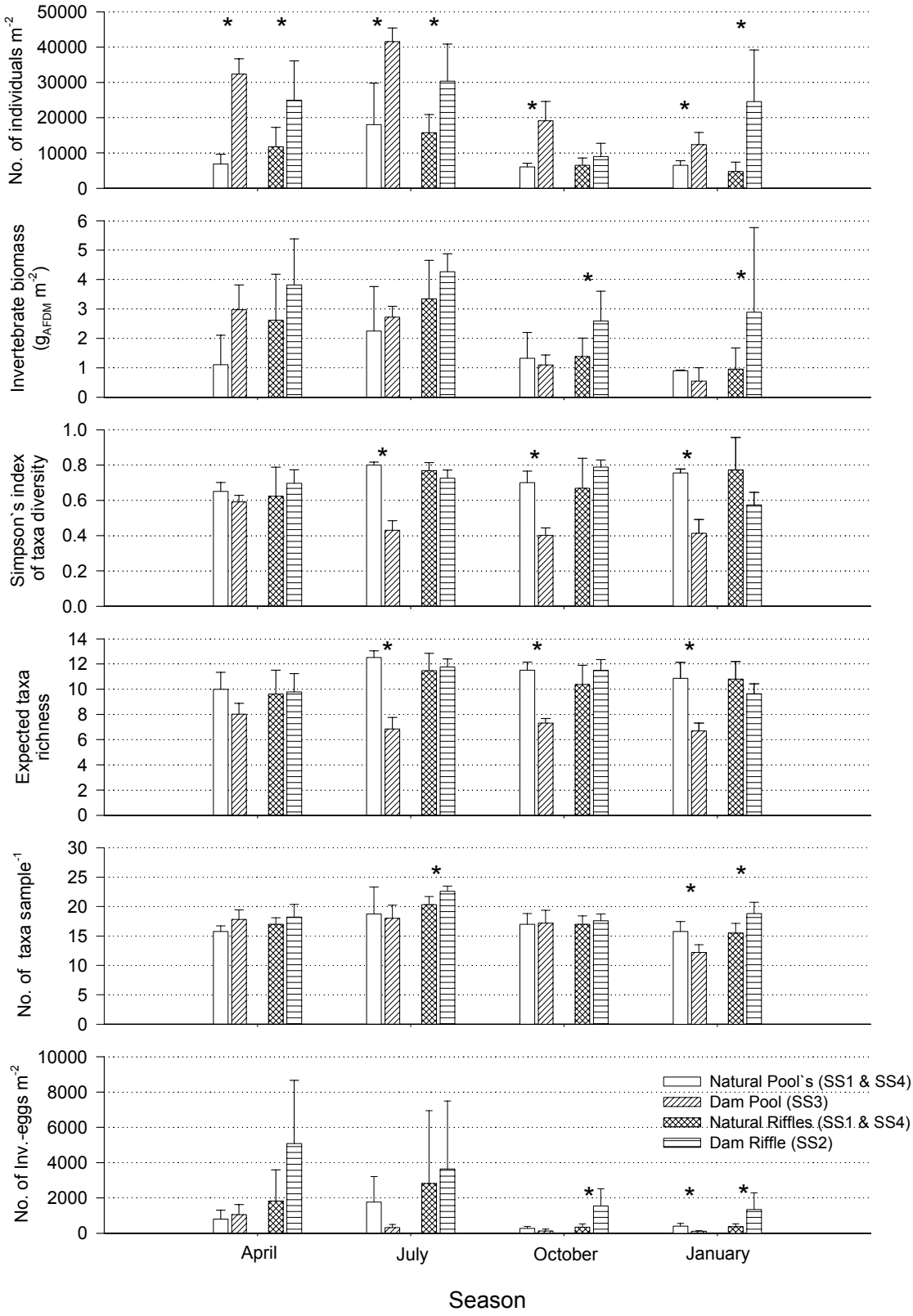

Figure A.1: Means (± 1 S.D.) for invertebrate density, biomass, Simpson`s index of diversity, expected taxon richness, number of taxa and number of invertebrate eggs in pools and riffles during four seasons. Significant differences (Mann-Whitney U-tests) among natural pools (SS1 & SS4) vs. dam pool (SS2) and natural riffles (SS1 & SS4) vs. dam riffle (SS3) are indicated by stars.

Table B.1: Relative abundance of several taxa in colonization baskets and in benthic samples based on estimations of Elser (1999 & 2001 a & b) and the calculated index of activity (C_i).

Taxon	Relative abundance (%)		Activity index
	colonization experiments	natural benthos	C_i
Arthropoda			
Insecta			
Ephemeroptera			
Baetidae			
Baetis	5.24	13.59	0.39
Serratella	0.17	1.03	0.17
Plecoptera			
Leuctridae			
Leuctra	0.10	-*	‡
Coleoptera			
Elmidae	0.02	0.82	0.02
Trichoptera			
Rhyacophilidae	0.39	3.81	0.10
Hydroptilidae	0.35	1.66	0.21
Hydropsychidae	11.42	15.23	0.75
Sericostomatidae	0.06	0.63	0.10
Diptera			
Chironomidae	76.33	46.66	1.64
Simuliidae	0.20	0.65	0.31
Limoniidae	0.02	1.18	0.02
Ceratopogonidae	-*	0.27	‡
Arachnida			
Hydracarina	0.10	0.96	0.10
Crustacea			
Ostracoda	0.06	0.36	0.17
Copepoda			
Cyclopoidae	1.79	1.19	1.50
Isopoda			
Asellus	*0.60***	*0.04***	‡
Amphipoda			
Gammarus	2.55	7.32	0.35
Annelida			
Hirudinea			
Erpobdellidae	0.39	0.41	0.95
Mollusca			
Pulmonata			
Ancylus	0.14	3.68	0.04
Turbellaria			
Dugesia	0.01	0.18	0.04
Others †	0.09	0.35	**0.257**

* not present; ** overestimation; ‡ treated as constant (0.257); † include all invertebrates that occur in very low numbers.

Table B.2: A list of all invertebrate - taxa found in drift samples and their overall composition.

Taxon				Numerical Composition (%)
Nemathelminthes				
	Nematoda			2.36
	Nematomorpha			<0.04
Annelida				
	Oligochaeta			2.80
Tardigrada				1.77
Arthropoda				
	Arachnida			
		Acari		
			Hydrachnellae	0.44
Crustacea				
	Phyllopoda			
		Cladocera		
			Bomina sp.	0.59
			Daphnia sp.	8.44
	Ostracoda			0.29
	Copepoda			
		Cyclopoida		51.8
		Harpacticoida		<0.04
	Malacostraca			
		Amphipoda		
			Gammarus pulex (L.)	0.11
		Isopoda		
			Asellus aquaticus (L.)	0.07
Insecta				
	Collembola			2.58
	Ephemeroptera			
		Baetidae		0.26
	Plecoptera			0.37
	Thysanoptera			0.07
	Coleoptera			<0.04
	Trichoptera			0.48
	Diptera			
		Limoniidae		<0.04
		Empididae		<0.04
		Psychodidae		<0.04
		Chaoboridae		<0.04
		Culicidae		<0.04
		Simuliidae		0.44
		Chironomidae		25.8

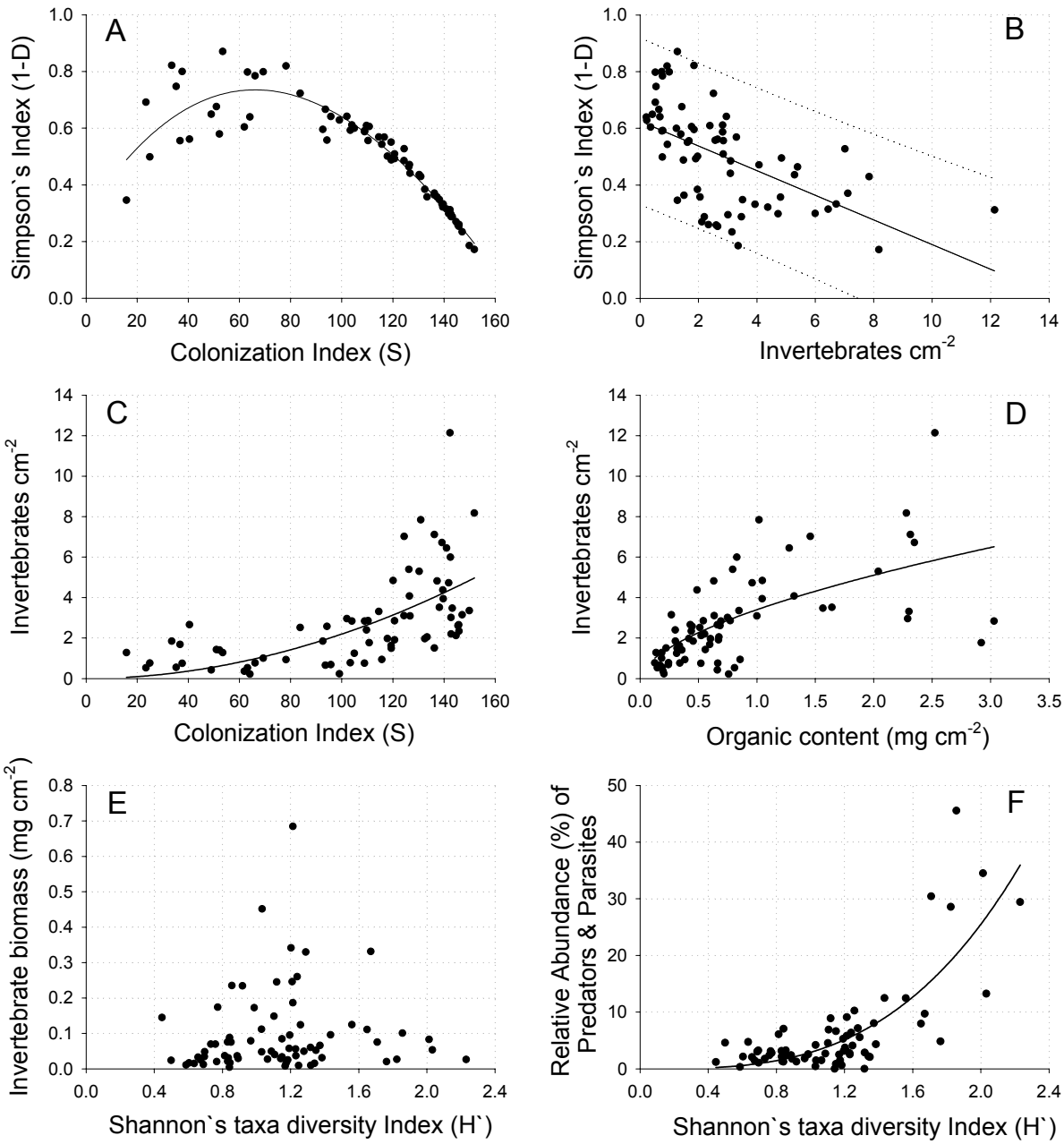

Figure B.1: Relationships between several variables measured in this study. **(A)** The relationship between Colonization Index (*S*) and Simpson`s Index of diversity (1-D). The line indicates a quadratic relationship ($y = -7.67 \cdot 10^{-5} x^2 + 0.104 x + 0.3741$, $R^2$=0.877, n=72, P<0.0001). **(B)** The number of invertebrates versus Simpson`s index of diversity. The line indicates a linear relation and dotted lines mark the prediction interval ($y = -0.0435 x + 0.625$, R^2=0.312, n=72, P<0.0001). **(C)** The Colonization Index (*S*) vs. the number of invertebrates. The relationship is described by a power function ($y= 0.0003 x^{1.95}$; R^2=0.37, n=72, P<0.0001). **(D)** The relationship between the organic matter content and the number of invertebrates. The relationship is described by a power function ($y= 3.40 x^{0.59}$, R^2=0.42, n=72, P<0.0001). **(E)** The pattern observed for Shannon`s taxa diversity index vs. assemblage biomass. **(F)** The relationship between for Shannon`s taxa diversity index and the relative abundance of predatory and parasitical taxa is described by a power function ($y= 2.89 x^{3.14}$, R^2=0.61, n=72, P<0.0001).

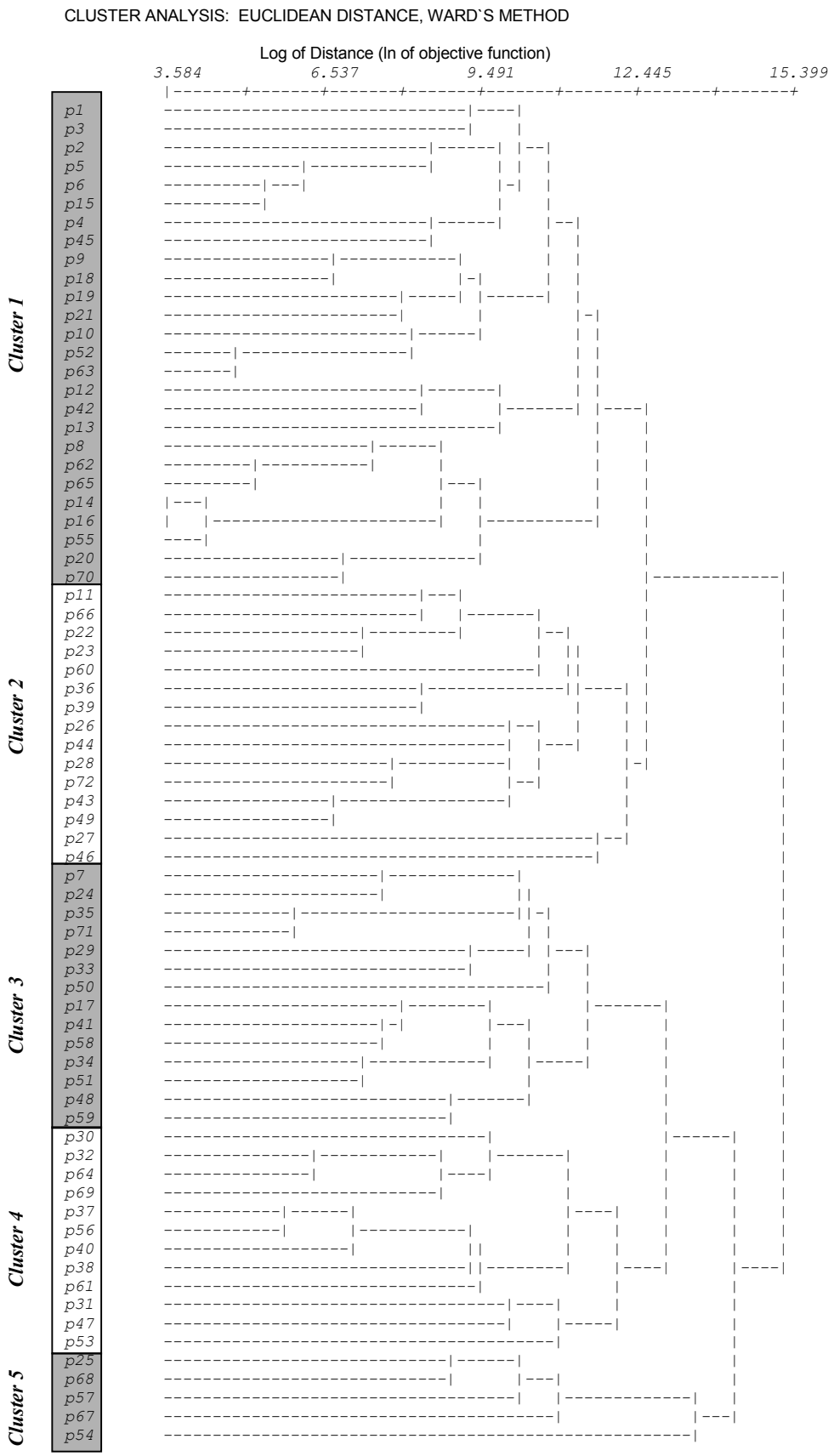

Figure B.2: Dendrogram of invertebrate assemblage similarity (based on invertebrate abundance data) among 72 samples collected from the site immediately downstream of the dam (SS3 = s25 – s48) and from the two reference sites (SS4 = s1 – s24 & SS1 = s 49 –s72). The sample codes s1 to s72 denotes the samples. The samples are divided in five groups that are denoted as cluster 1 to cluster 5.

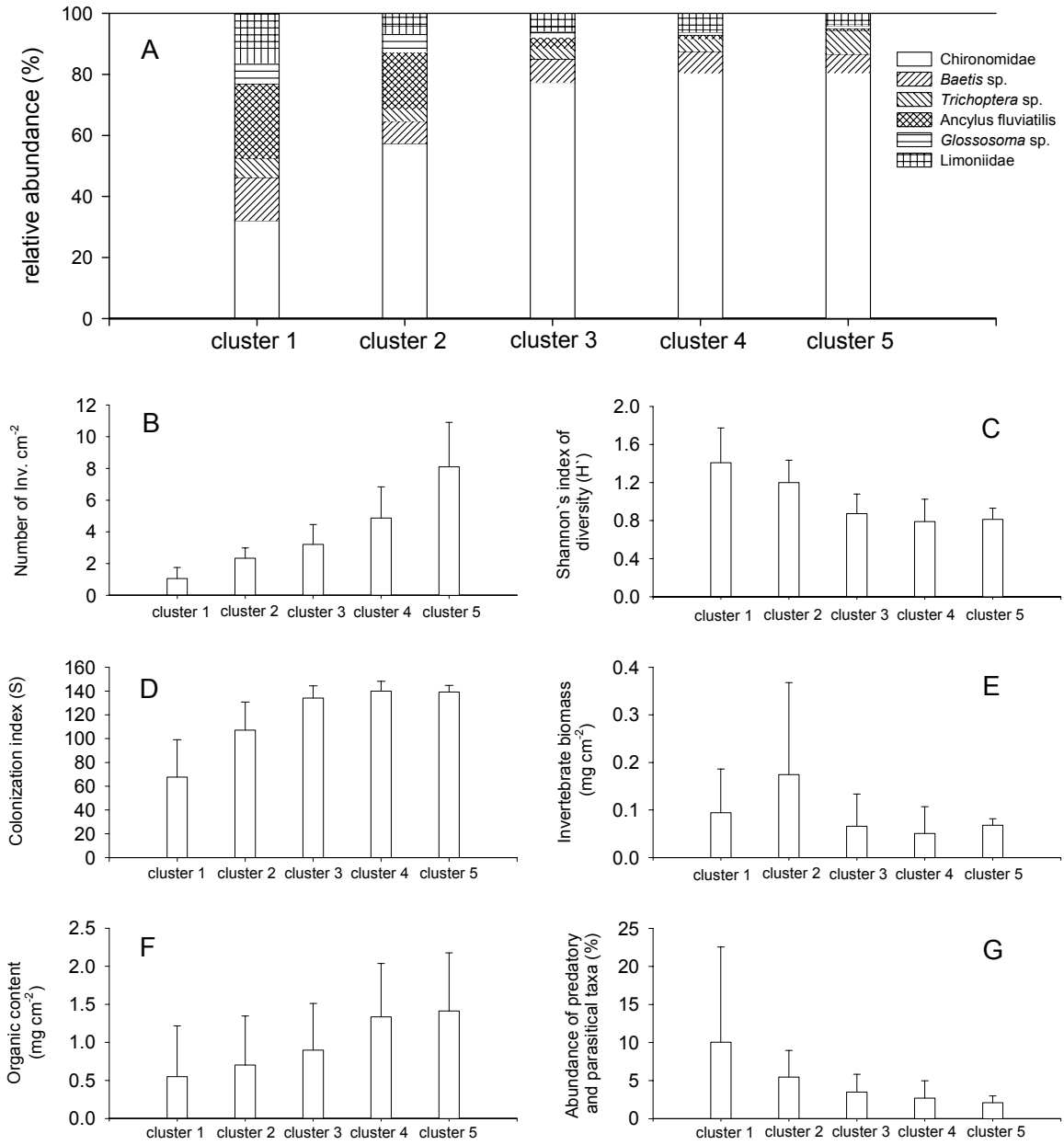

Figure B.3: Assemblage composition **(A)**, the density of invertebrates **(B)**, the Shannon`s diversity index **(C)**, the colonization index **(D)**, total Invertebrate biomass **(E)**, the organic matter content **(F)** and the relative proportion of predatory and parasitical taxa **(G)** of typical invertebrate assemblage stages found in this study. The major stages are denoted as cluster 1 to cluster 5 and were obtained from a cluster analysis (see text). Plot B – G: Mean ± 1 S.D. is shown.

Table C.1: A list and codes of all invertebrate taxa included in the ordination (CA). Code (1) terms the codes used in CA on presence / absence data. Code (2) terms the codes used in CA on rank - abundance data.

Taxon	Taxon code (1)	Taxon code (2)	**Taxon**	Taxon code (1)	Taxon code (2)
EPHEMEROPTERA					
Baetis alpinus	1	1	**Orthocladiinae**		
Baetis fuscatus	2	2	*Smittia aterrima*	75	75
Baetis muticus	3	3	*Brilla modesta*	76	76
Baetis niger	4	4	*Tvetenia calvescens*	77	77
Baetis vernus	5	5	*Paraphaenocladius impensus*	78	78
Baetis scambus	6	6	*Limnophyes minimus*	79	79
Baetis rhodani	7	7	*Cricotopus* sp. 3	80	80
Baetis sp.	8	8	*Metriocnemus hygropetricus*	81	81
Epeorus sylvicola	9	9	*Tvetenia* sp.	82	82
Rhithrogena picteti	10	10	*Bryophaenocladius* sp.	83	83
Ecdyonurus picteti	11	11	*Orthocladius* sp. 1	84	84
Ecdyonurus torrentis	12	12	*Orthocladius* sp. 2	85	85
Ecdyonurus venosus	13	13	*Eukiefferiella claripennis*	86	86
Ephemerella ignita	14	14	*Rheocricotopus effusus*	87	87
Ephemerella mucronata	15	15	*Cricotopus bicinctus*	88	88
Caenis beskidensis	16	16	*Rheochricotopus fuscipes*	89	89
Habroleptoides confusa	17	17	*Cricotopus sp.* 1	90	90
Habrophlebia lauta	18	18	*Brillia longifurca*	91	91
Paraleptophlebia submarginata	19	19	*Metriocnemus* sp.	92	92
TRICHOPTERA			*Orthocladius rubicundus*	93	93
Adicella reducta	20	20	*Cricotopus* sp. 2	94	94
Agraylea multipunctata			*Eukiefferiella* sp.	95	95
Agrypnia varia			*Paratrichocladius rufiventris*	96	96
Anabolia nervosa	23	23	*Rheocricotopus* sp.	97	97
Annitella thuringica	24	24	**Chironiminae**		
Anomalopterygella chauviniana	25	25	*Micropsectra notescens*	98	98
Apatania fimbriata	26	26	*Polypedilum laetum*	99	99
Brachycentrus montanus	27	27	*Micropsectra atrofasciata*	100	100
Ceraclea alboguttata	28	28	*Polypedilum apfelbecki*	101	101
Chaetopteryx villosa	29	29	*Phaenopsectra flavipes*	102	102
Drusus annulatus	30	30	*Paratanytarsus inopertus*	103	103
Ecclisopteryx dalecarlica	31	31	*Chironomus* sp.	104	104
Glossosoma conformis	32	32	*Polypedilum* sp.1	105	105
Glyphotaelius pellucidus			*Polypedilum* sp.2	106	106
Hydropsyche angustipennis	34	34	*Polypedilum* sp.3	107	107
Hydropsyche contuberalis	35	35	*Chironomus riparius*	108	108
Hydropsyche dinarica	36	36	*Paratendipes albimanus*	109	109
Hydropsyche incognita	37	37	*Polypedilum* sp.4	110	110
Hydropsyche instabilis	38	38	*Glyptotendipes gripekoveni*	111	111
Hydropsyche pellucidula	39	39	*Einfeldia longipes*		
Hydropsyche siltalai	40	40	*Microtendipes pedellus*	113	113
Hydropsyche sp.	41	41	*Chironomus annularis*	114	114
Hydrotila angulata	42	42	*Glyptotendipes pallens*	115	115
Hydrotila sparsa	43	43	*Paratanytarsus laetipes*	116	116
Limnephilidae sp.	44	44	*Dicrotendipes nervosus*	117	117
Limnephilus extricatus	45	45	*Paracladopelma camptolabis*	118	118
Limnephilus ignavus	46	46	*Polypedilum* sp.5	119	119
Limnephilus incisus	47	47	*Polypedilum* sp.6	120	120
Limnephilus rhombicus	48	48	*Stenochironomus gibbus*	121	121
Micrasema longulum	49	49	***COLEOPTERA***		
Micrasema minimum	50	50	*Brychius elevatus*	122	
Mystacides nigra	51	51	*Haliplus lineatocollis*	123	
Odontocerum albicorne	52	52	*Haliplus laminatus*	124	
Oecetis ochracea	53	53	*Haliplus fluviatilis*	125	
Philopotamus ludificatus	54	54	*Deronectus depressus elegans*	126	
Phryganea bipunctata	55	55	*Oreodytes sanmarki*	127	
Polycentropus flavomaculatus	56	56	*Platambus maculatus*	128	
Potamophylax cingulatus	57	57	*Agabus paludosus*	129	
Potamophylax latipennis	58	58	*Ilybius fuliginosus*	130	
Potamophylax luctuosus	59	59	*Hydraena gracilis*	131	
Psychomyia pusilla	60	60	*Limnebius truncatellus*	132	
Rhyacophila fasciata	61	61	*Helophorus minutus*		
Rhyacophila nubila	62	62	*Helophorus brevipalpis*		
Rhyacophila obliterata	63	63	*Cercyon ustulatus*	135	

Table C.1: extended

Taxon	Taxon code (1)	Taxon code (2)	Taxon	Taxon code (1)	Taxon code (2)
Rhyacophila tristis	64	64	*Cercyon bifenestratus*		
Sericostoma flavicorne	65	65	*Cercyon marinus*	137	
Sericostoma personatum	66	66	*Cercyon lateralis*		
Silo pallipes	67	67	*Cercyon laminatus*		
CHIRONOMIDAE			*Cercyon unipunctatus*		
Tanypodinae			*Cercyon terminatus*	141	
Procladius choreus group	68	68	*Cryptopleurum subtile*	142	
Macropelopia nebulosa	69	69	*Anacaena globulus*	143	
Tanypus punctipennis	70	70	*Enochrus bicolor*		
Ablabesmyia sp.	71	71	*Elmis aenea*	145	
Thienemannimyia sp.	72	72	*Esolus angustatus*	146	
Diamesinae			*Limnius perrisi*	147	
Diamesa tonosa	73	73	*Helodes marginata*	148	
Potthastia longimana	74	74	*Heterocerus fenestratus*	149	

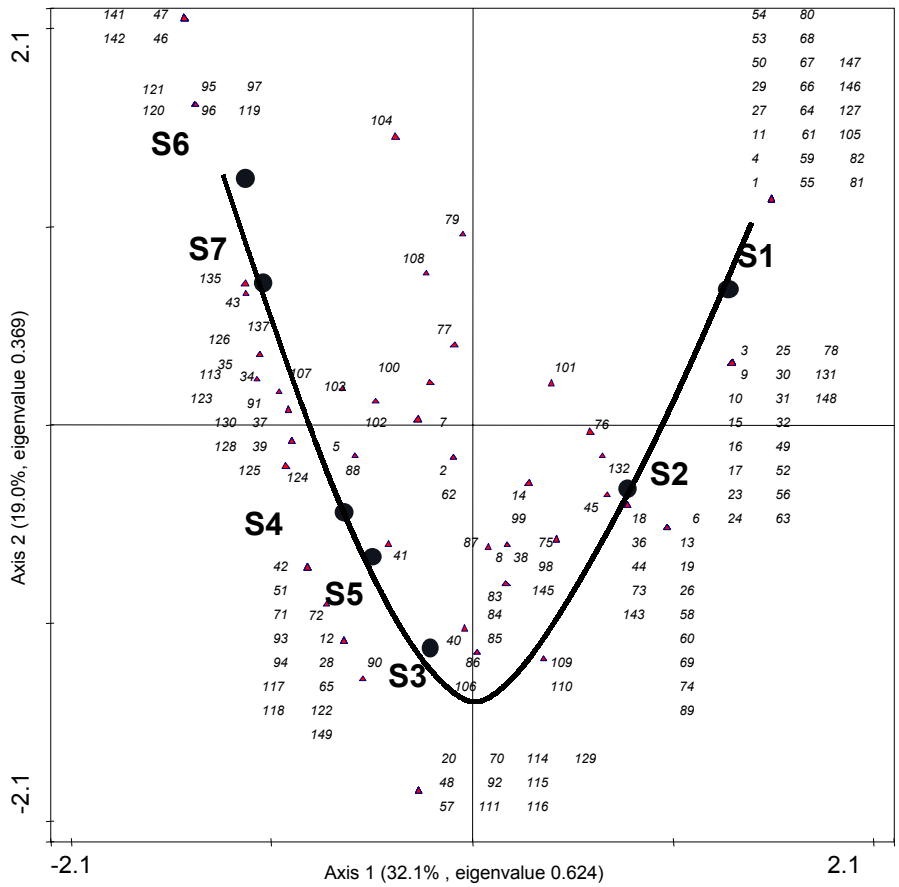

Figure C.1: Ordination plot of a correspondence analysis based on the on presence / absence data of 138 invertebrate taxa (Ephemeroptera, Trichoptera, Chironomidae and Coleoptera) at seven sampling stations at the longitudinal profile of the Ilm during 1992-93. Sampling stations are shown as circles (S1 to S7). Invertebrate taxa are shown as triangles and the number indicate the “taxon code” (see text). The curved black line describes the stream gradient.

Table D.1: The number of samples and sub-samples, which were analyzed in this study in order to determine chemical and isotopic composition. Analyses were performed twice: (1) a combined determination of $\delta^{13}C$ (‰) & C (%) and (2) a combined determination of $\delta^{15}N$ (‰) & N (%).

	Leaf treatment				
	L1	L2	L3	L4	L5
Invertebrates					
G. pulex					
Pre-treatment group			**1 (1) ***		
Post-treatment group	1 (1)	1 (1)	1 (2)	1 (1)	1 (2)
B. rhodani					
Pre-treatment group			**1 (1) ***		
Post-treatment group	1 (1)	1 (1)	1 (1)	1 (1)	1 (1)
Leaf materials					
Particle size class					
Before the experiment	1 (2)	1 (2)	1 (2)	1 (2)	1 (2)
After 7days leaching	4 (2)	4 (2)	4 (2)	4 (2)	4 (2)
After the experiment					
G. pulex experiment					
>2.5 cm	1 (2)				
2.5-1 cm	1 (1)	1 (2)			
0.25-1 cm	1 (1)	1 (1)	1 (2)		
0.071-0.25 cm	1 (1)	1 (1)	1 (1)	1 (2)	1 (2)
0.0016-0.071 cm	1 (1)	1 (1)	1 (1)	1 (1)	1 (1)
B. rhodani experiment †					
>2.5 cm	5 (2)				
2.5-1 cm		5 (2)			
0.25-1 cm			5 (2)		
0.071-0.25 cm				5 (2)	5 (2)
0.0016-0.071 cm	1 (1)	1 (1)	1 (1)	1 (1)	5 (2)
Control experiment					
>2.5 cm	1 (2)				
2.5-1 cm	1 (1)	1 (1)			
0.25-1 cm	1 (1)	1 (1)	1 (1)		
0.071-0.25 cm	1 (1)	1 (1)	1 (1)	1 (1)	1 (1)
0.0016-0.071 cm	1 (1)	1 (1)	1 (1)	1 (1)	1 (1)
Water samples					
G. pulex experiment	1 (2)	-	1 (2)	-	1 (2)
Control experiment	1 (2)	-	-	-	-

Note that the first values refer to the number of samples and values in parentheses refer to the number of sub-samples analyzed; * one sample from a pool of pre-treatment animals; † shaded boxes (L1, L2 & L3) represent material - pools including particles that remained in original size and generated particle size classes > 71 µm (compare methods – *Endpool L1, Endpool L2, Endpool L3*). Five samples (from five replicated experimental chambers) were analyzed and each sample represents the averaged value from two sub-samples.

Table D.2: Mean and 1 S.D. for oxygen (%), temperature (°C), pH values and conductivity (µS cm^{-1}) (at 20°C) measured during the experiments.

Type of experiment & leaf treatment	**Abiotic parameters**			
	Oxygen saturation (%)	Temperature (°C)	pH	Conductivity (µS cm^{-1})
Start conditions	~100	10 (air)	7.77 - 7.80	400 - 405
Leaching – experiment †				
L1	89.6 ± 8.17	9.69 ± 0.25	7.78 ± 0.06	412 ± 6.14
L2	94.0 ± 6.40	9.67 ± 0.41	7.95 ± 0.26	419 ± 11.6
L3	92.0 ± 6.96	9.66 ± 0.25	7.76 ± 0.04	418 ± 6.83
L4	94.0 ± 7.07	9.61 ± 0.37	7.99 ± 0.26	422 ± 10.2
L5	93.6 ± 5.73	9.69 ± 0.26	7.86 ± 0.27	429 ± 11.2
G. pulex – experiment ‡				
L1	91.6 ± 5.71	9.91 ± 0.95	8.01 ± 0.21	422 ± 13.0
L2	85.9 ± 6.56	9.93 ± 1.01	8.07 ± 0.23	422 ± 14.8
L3	90.6 ± 5.05	9.84 ± 0.94	8.03 ± 0.27	427 ± 5.11
L4	92.5 ± 6.02	9.83 ± 0.82	8.01 ± 0.23	428 ± 6.55
L5	86.0 ± 6.95	9.84 ± 0.82	8.02 ± 0.23	434 ± 6.95
B. rhodani – experiment ‡				
L1	87.1 ± 8.60	9.72 ± 0.23	7.81 ± 0.07	415 ± 5.79
L2	89.7 ± 6.81	9.66 ± 0.30	7.87 ± 0.17	425 ± 11.6
L3	88.7 ± 6.68	9.69 ± 0.29	7.83 ± 0.09	422 ± 8.42
L4	89.0 ± 6.92	9.68 ± 0.28	7.89 ± 0.17	429 ± 16.2
L5	92.1 ± 5.57	9.73 ± 0.27	7.84 ± 0.16	434 ± 12.2
Control – experiment ‡				
L1	90.5 ± 3.57	10.1 ± 0.41	7.67 ± 0.14	429 ± 22.3
L2	90.7 ± 5.19	10.1 ± 0.40	7.69 ± 0.14	429 ± 12.6
L3	89.9 ± 4.39	10.1 ± 0.37	7.69 ± 0.15	427 ± 12.2
L4	88.6 ± 6.09	10.0 ± 0.38	7.70 ± 0.13	431 ± 10.7
L5	90.0 ± 5.26	10.1 ± 0.37	7.68 – 0.14	438 ± 15.9

† Mean and 1 S.D. from four replicate plexiglas chambers for each leaf treatment after 7 days (n=4), **‡ M**ean and 1 S.D. from four measurements (weekly) during the experiments, each measurement represents the averaged value from 5 (*G. pulex* & *B. rhodani*) or 7 (Control) replicate plexiglas chambers).

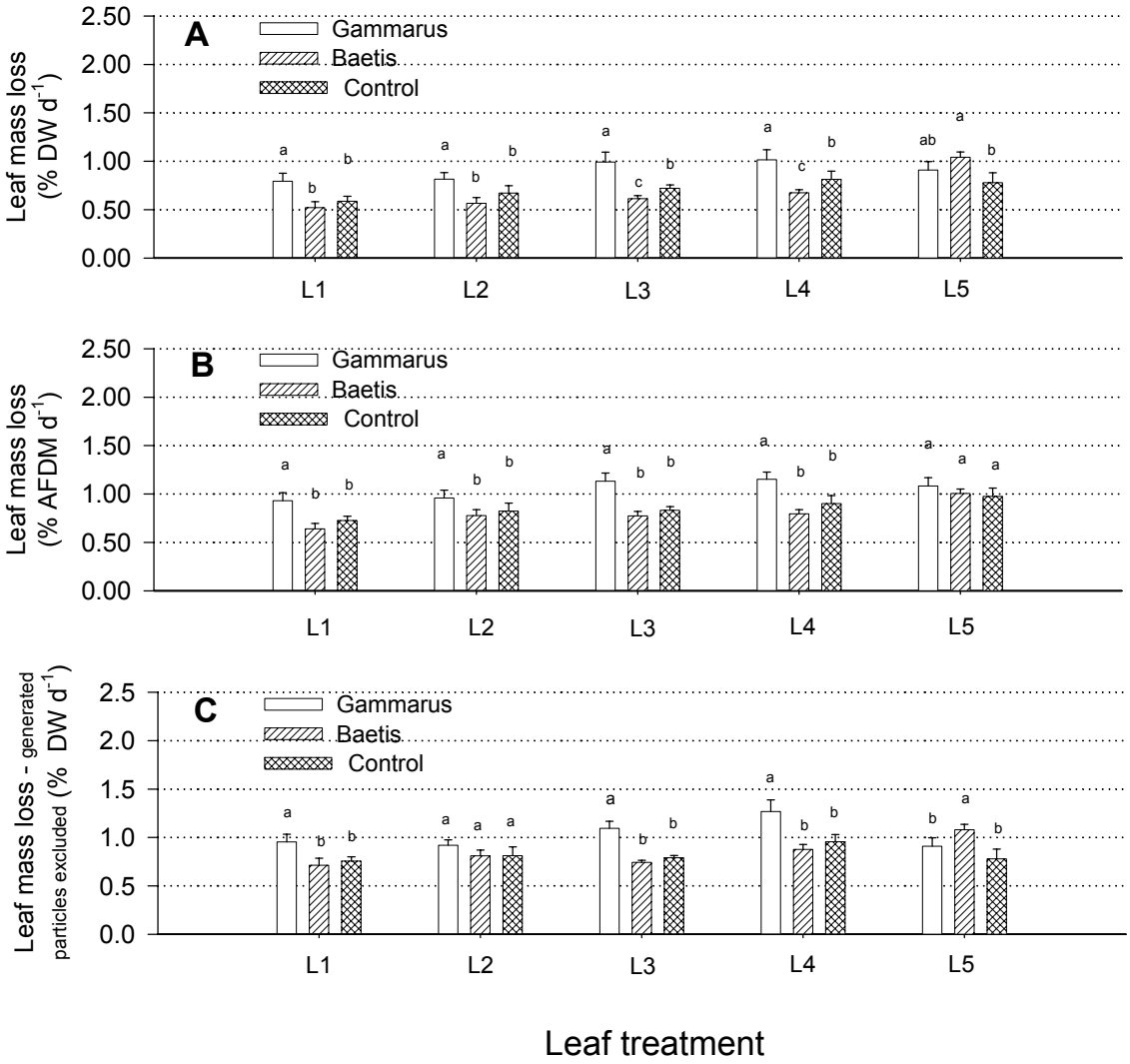

Figure D.1: Total leaf mass loss as % dry weight per day **(A)**, % AFDM per day **(B)** and leaf mass loss when generated particles were excluded as % dry weight per day **(C)**. L1- L5 = leaf treatments; For all three measures of leaf mass loss a significant interaction between the type of experiment and leaf treatment was found [ANOVA`s (GLM)]. The results of Tukey test`s following separated one-way ANOVA`s that were conducted to explore the effects of macro-invertebrate feeding (type of experiment) on leaf mass loss are indicated by small letters. Similar small letters = no difference; Different letters = significant different at P<0.05.

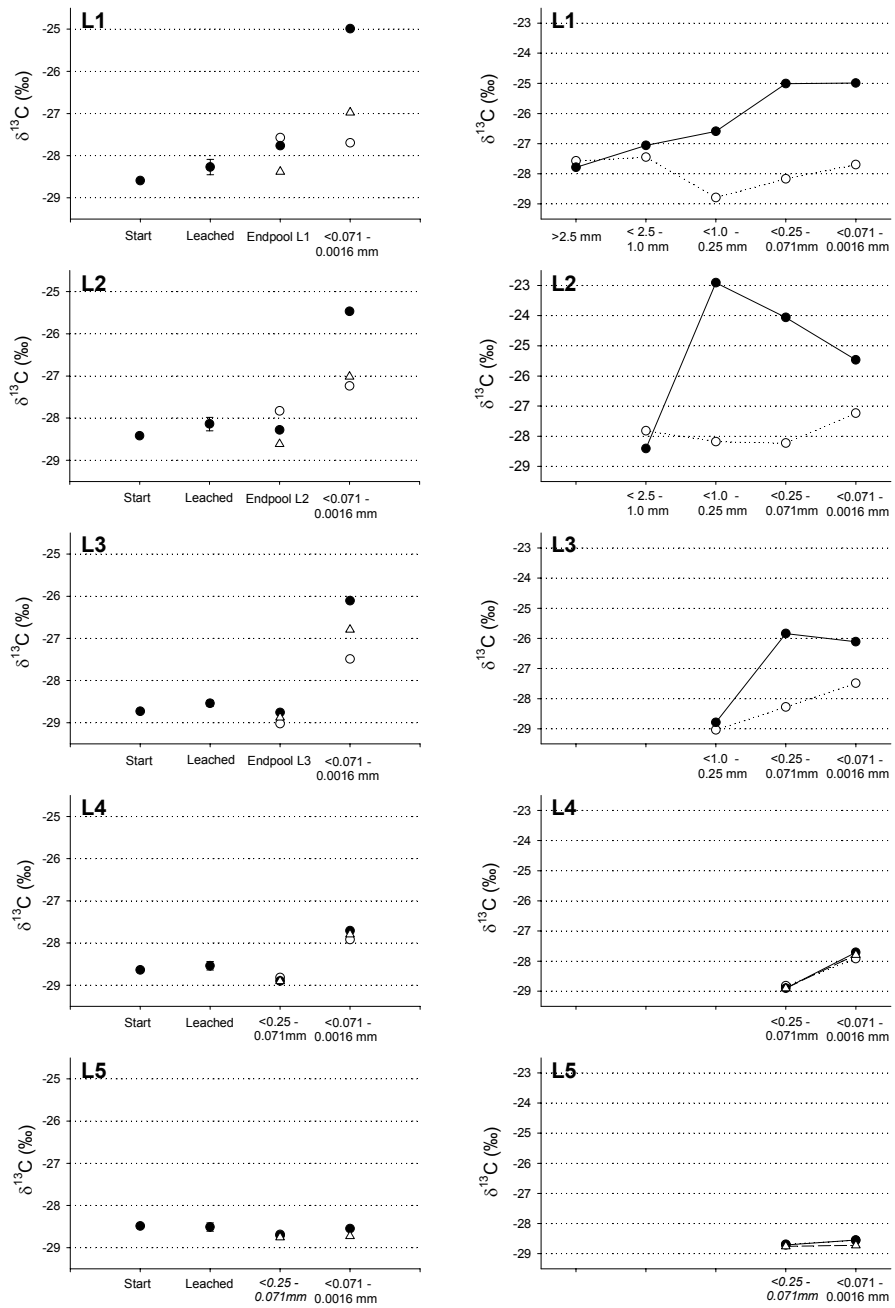

Figure D.2: Changes in $\delta^{13}C$ signatures of the leaf materials during breakdown experiments. Left panels: $\delta^{13}C$ values of the five leaf treatments (L1–L5) and the changes during breakdown. Start = initial $\delta^{13}C$ values; Leached = $\delta^{13}C$ values after a leaching period of 7 days (1 S.D. from 4 replicates); Endpools (L1-L3) = final $\delta^{13}C$ values of the leaf particles > 71 µm (including particles that remained in original size and generated particle size classes > 71 µm for L1 to L3); <0.25 – 0.071 mm = final $\delta^{13}C$ values of the leaf material (for L4 = particles that remained in original size; for L5 = swelled particles); <0.071 – 0.0016 mm = final $\delta^{13}C$ values of the leaf particles < 71 µm (generated particles < 71 µm for L1 to L4; for L5 all particles that remained in original size). *G. pulex* experiments = open circles; *B. rhodani* experiments = up – triangles; Control experiments = closed circles. **Right panels:** for L1-L3 final $\delta^{13}C$ values of all leaf material fractions (separately shown), including particles that remained in original size and all generated particles size fractions for the Control experiments (closed circles) and the *G. pulex* experiments (open circles); for L4 final $\delta^{13}C$ values of all leaf material fractions (separately shown) for the experiments with and without invertebrates; for L5 final $\delta^{13}C$ values of swelled particles (<0.25 – 0.071 mm) and particles that remained in original size (<0.071 – 0.0016 mm); *G. pulex* experiments = open circles; *B. rhodani* experiments = up- triangles; Control experiments = closed circles.

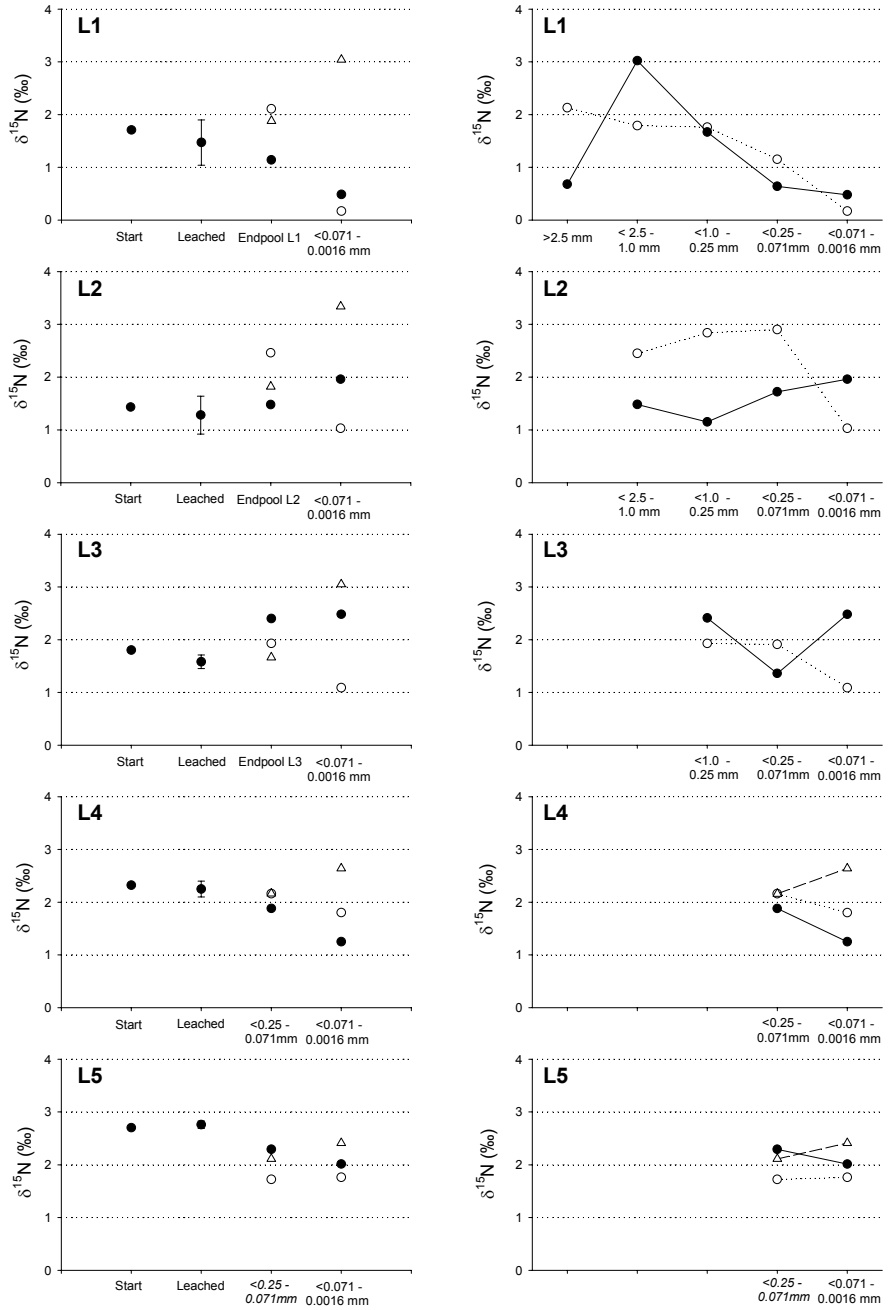

Figure D.3: **Changes in $\delta^{15}N$ signatures of the leaf materials during breakdown experiments. Left panels**: $\delta^{15}N$ values of the five leaf treatments (L1–L5) and the changes during breakdown. Start = initial $\delta^{15}N$ values; Leached = $\delta^{15}N$ values after a leaching period of 7 days (1 S.D. from 4 replicates); Endpools (L1-L3) = final $\delta^{15}N$ values of the leaf particles > 71 µm (including particles that remain in original size and generated particle size classes > 71 µm for L1 to L3); <0.25 – 0.071 mm = final $\delta^{15}N$ values of the leaf material (for L4 = particles that remained in original size; for L5 = swelled particles); <0.071 – 0.0016 mm = final $\delta^{15}N$ values of the leaf particles < 71 µm (generated particles < 71 µm for L1 to L4; for L5 all particles that remained in original size). *G. pulex* experiments = open circles; *B. rhodani* experiments = up-triangles; Control experiments = closed circles. **Right panels:** for L1-L3 final $\delta^{15}N$ values of all leaf material fractions (separately shown), including particles that remained in original size and all generated particles size fractions for the Control experiments (closed circles) and the *G. pulex* experiments (open circles); for L4 final $\delta^{15}N$ values of all leaf material fractions (separately shown) for the experiments with and without invertebrates; for L5 final $\delta^{15}N$ values of swelled particles (<0.25 – 0.071 mm) and particles that remained in original size (<0.071 – 0.0016 mm); *G. pulex* experiments = open circles; *B. rhodani* experiments = up- triangles; Control experiments = closed circles.

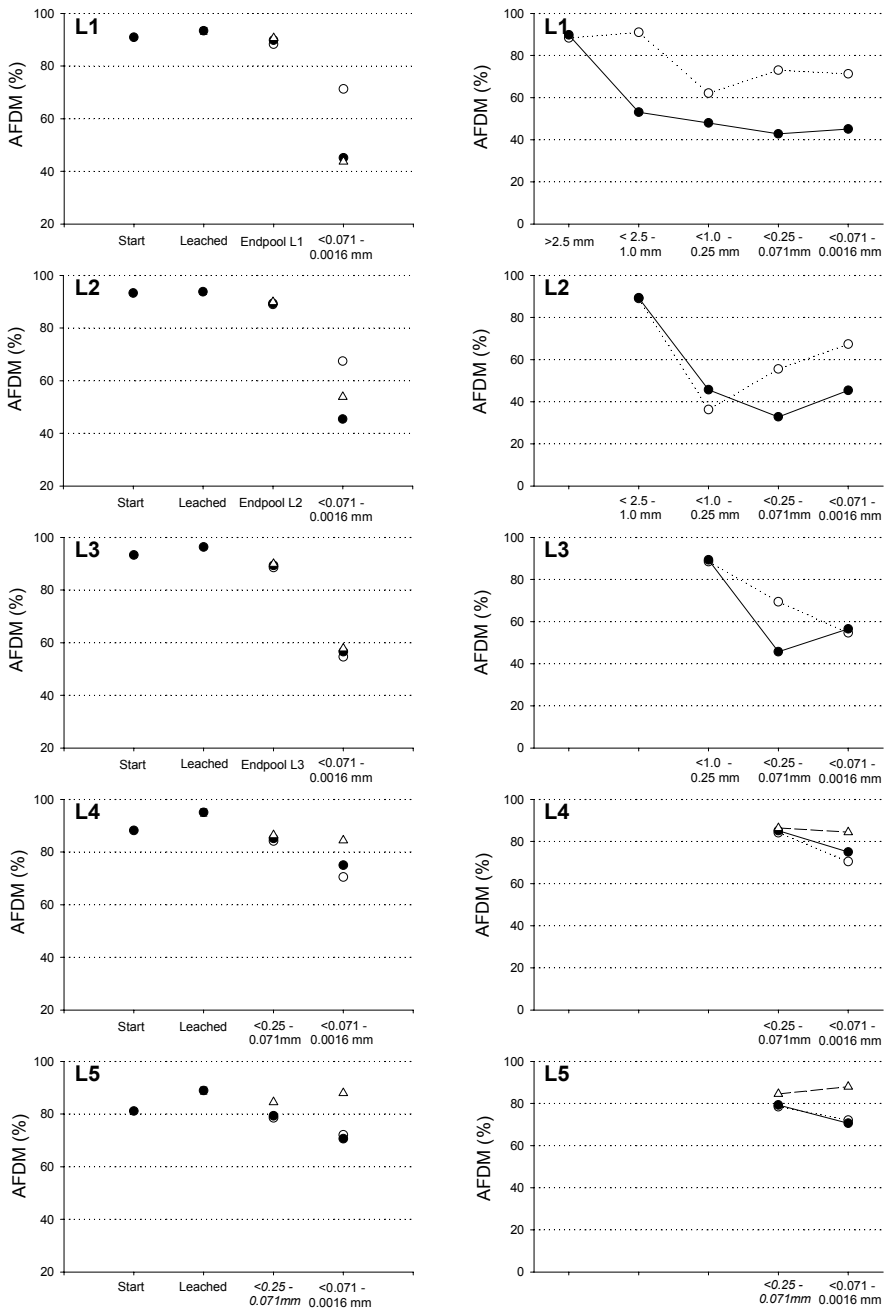

Figure D.4: Changes in ash free dry mass during breakdown of the leaf material used in this study. Left panels: AFDM (%) of the five leaf materials (L1–L5) and the changes during breakdown. Start = initial AFDM (%) of the dry leaf material; Leached = AFDM (%) of the leaf material after a leaching period of 7 days (1 S.D. from 4 replicates); Endpools (L1-L3) = final AFDM (%) of the leaf particles > 71 µm (including particles that remained in original size and generated particle size classes > 71 µm for L1 to L3); <0.25 – 0.071 mm = final AFDM (%) of the leaf material (for L4 = particles that remained in original size; for L5 = swelled particles); <0.071 – 0.0016 mm = final AFDM (%) of the leaf particles < 71 µm (generated particles < 71 µm for L1 to L4; for L5 all particles that remained in original size). *G. pulex* experiments = open circles; *B. rhodani* experiments = up- triangles; Control experiments = closed circles. **Right panels:** for L1-L3 final AFDM (%) of all leaf material fractions (separately shown), including particles that remained in original size and all generated particles size fractions for the Control experiments (closed circles) and the *G. pulex* experiments (open circles); for L4 final AFDM (%) of all leaf material fractions (separately shown) for the experiments with and without invertebrates; for L5 final C/N ratios values of swelled particles (<0.25 – 0.071 mm) and particles that remained in original size (<0.071 – 0.0016 mm); *G. pulex* experiments = open circles; *B. rhodani* experiments = up- triangles; Control experiments = closed circles.

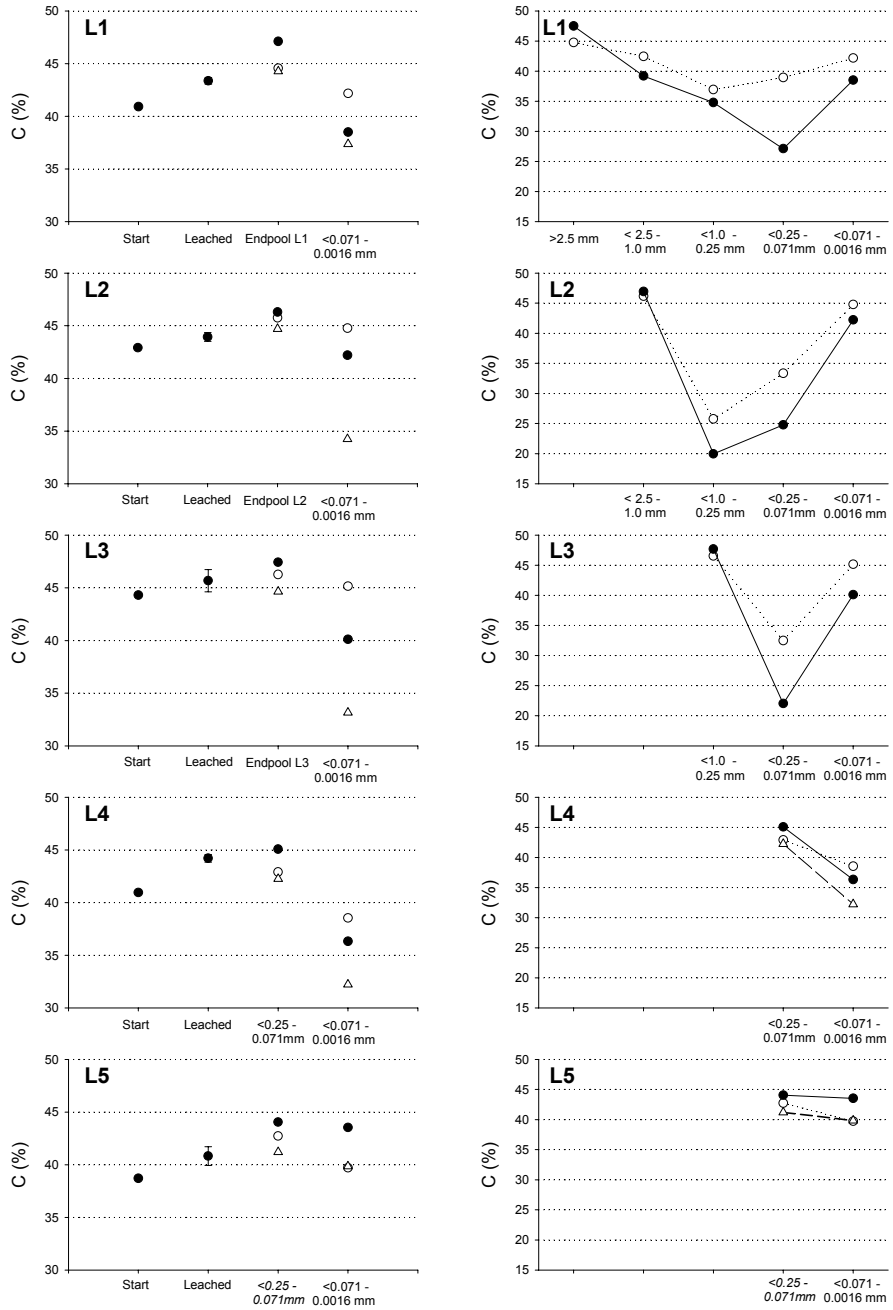

Figure D.5: Changes in carbon content during breakdown of the leaf material used in this study. Left panels: C (%) content of the five leaf treatments (L1–L5) and the changes during breakdown. Start = initial C (%) content; Leached = C (%) content after a leaching period of 7 days (1 S.D. from 4 replicates); Endpools (L1-L3) = final C (%) content of the leaf particles > 71 µm (including particles that remain in original size and generated particle size classes > 71 µm for L1 to L3); <0.25 – 0.071 mm = final C (%) content of the leaf material (for L4 = particles that remained in original size; for L5 = swelled particles); <0.071 – 0.0016 mm = final C (%) content of the leaf particles < 71 µm (generated particles < 71 µm for L1 to L4; for L5 all particles that remained in original size). *G. pulex* experiments = open circles; *B. rhodani* experiments = up-triangles; Control experiments = closed circles. **Right panels:** for L1-L3 final C (%) content of all leaf material fractions (separately shown), including particles that remained in original size and all generated particles size fractions for the Control experiments (closed circles) and the *G. pulex* experiments (open circles); for L4 final C (%) content of all leaf material fractions (separately shown) for the experiments with and without invertebrates; for L5 final C (%) content of swelled particles (<0.25 – 0.071 mm) and particles that remained in original size (<0.071 – 0.0016 mm); *G. pulex* experiments = open circles; *B. rhodani* experiments = up- triangles; Control experiments = closed circles.

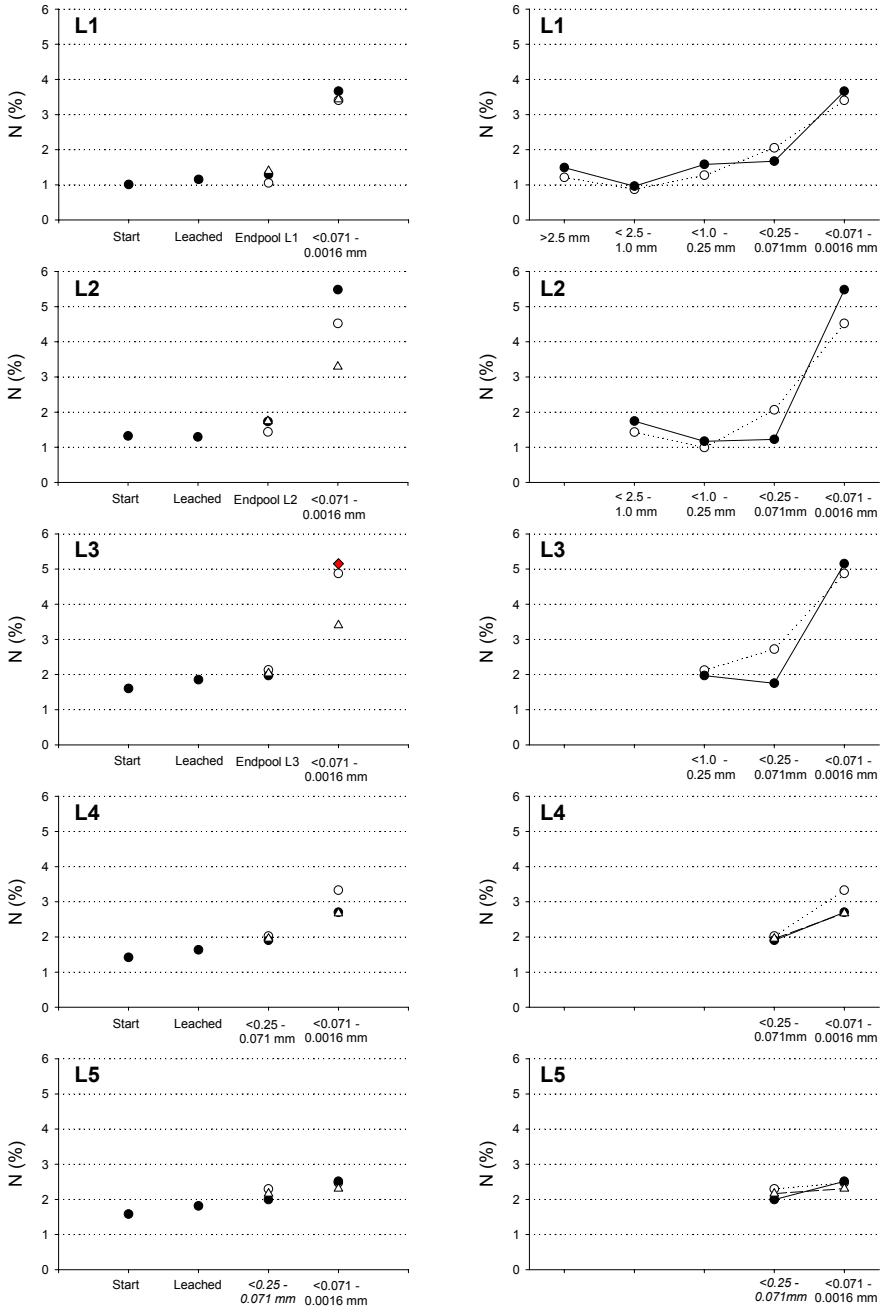

Figure D.6: Changes in nitrogen content during breakdown of the leaf material used in this study. Left panels: N (%) values of the five leaf materials (L1–L5) and the changes during breakdown. Start = initial N (%) values of the dry leaf material; Leached = N (%) values of the leaf material after a leaching period of 7 days (1 S.D. from 4 replicates); Endpools (L1-L3) = final N (%) values of the leaf particles > 71 µm (including particles that remained in original size and generated particle size classes > 71 µm for L1 to L3); <0.25 – 0.071 mm = final N (%) values of the leaf material (for L4 = particles that remained in original size; for L5 = swelled particles); <0.071 – 0.0016 mm = final N (%) values of the leaf particles < 71 µm (generated particles < 71 µm for L1 to L4; for L5 all particles that remained in original size). *G. pulex* experiments = open circles; *B. rhodani* experiments = up- triangles; Control experiments = closed circles. **Right panels:** for L1-L3 final N (%) values of all leaf material fractions (separately shown), including particles that remained in original size and all generated particles size fractions for the Control experiments (closed circles) and the *G. pulex* experiments (open circles). for L4 final N (%) values of all leaf material fractions (separately shown) for the experiments with and without invertebrates; for L5 final N (%) values of swelled particles (<0.25 – 0.071 mm) and particles that remained in original size (<0.071 – 0.0016 mm); *G. pulex* experiments = open circles; *B. rhodani* experiments = up- triangles; Control experiments =closed circles.

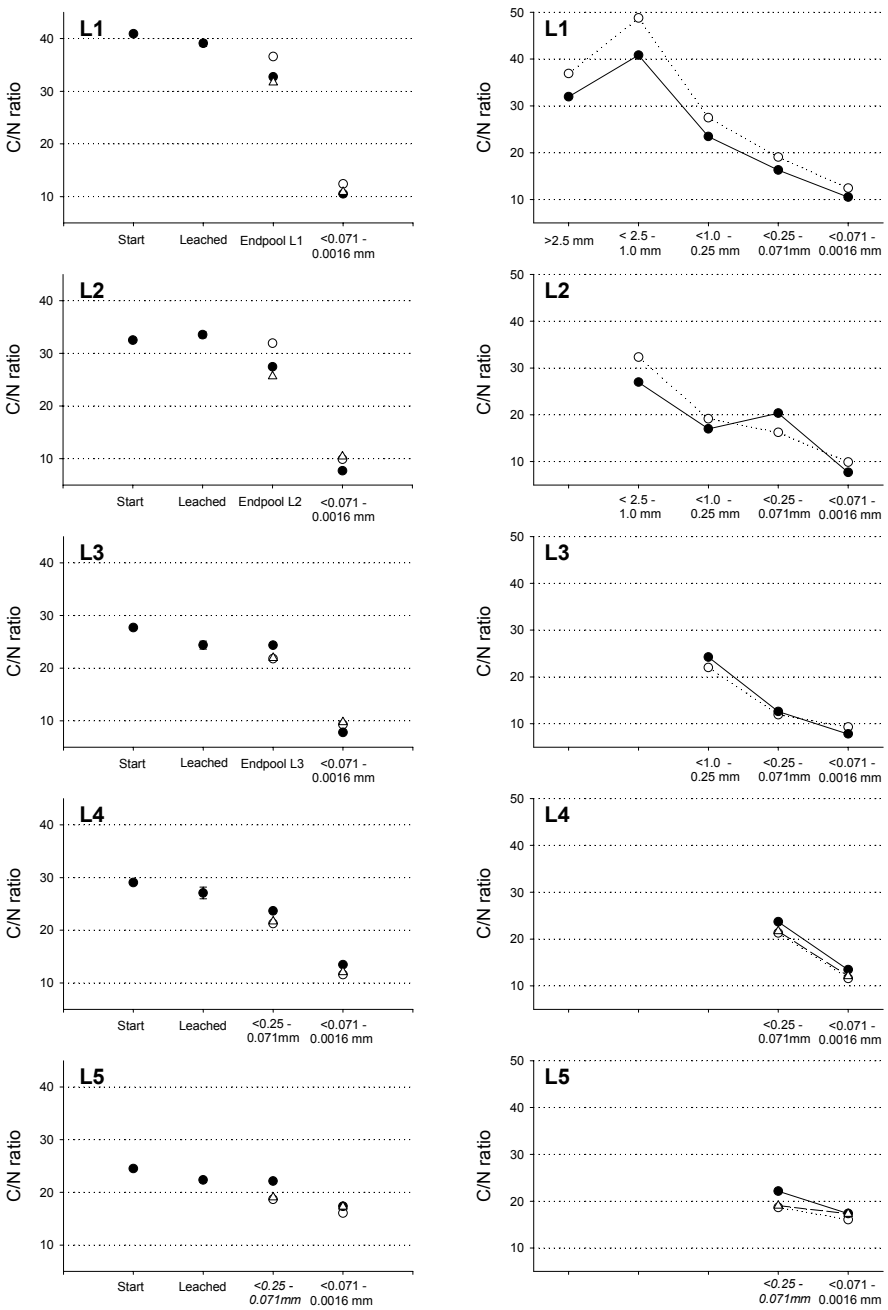

Figure D.7: Changes in C/N ratio during breakdown of the leaf material used in this study. Left panels: C/N ratios of the five leaf materials (L1–L5) and the changes during breakdown. Start = initial C/N ratios of the dry leaf material; Leached = C/N ratios of the leaf material after a leaching period of 7 days (1 S.D. from 4 replicates); Endpools (L1-L3) = final C/N ratios of the leaf particles > 71 µm (including particles that remained in original size and generated particle size classes > 71 µm for L1 to L3); <0.25 – 0.071 mm = final C/N ratios of the leaf material (for L4 = particles that remained in original size; for L5 = swelled particles); <0.071 – 0.0016 mm = final C/N ratios values of the leaf particles < 71 µm (generated particles < 71 µm for L1 to L4; for L5 all particles that remained in original size). *G. pulex* experiments = open circles; *B. rhodani* experiments = up- triangles; Control experiments = closed circles. **Right panels:** for L1-L3 final C/N ratios of all leaf material fractions (separately shown), including particles that remained in original size and all generated particles size fractions for the Control experiments (closed circles) and the *G. pulex* experiments (open circles). for L4 final C/N ratios of all leaf material fractions (separately shown) for the experiments with and without invertebrates; for L5 final C/N ratios values of swelled particles (<0.25 – 0.071 mm) and particles that remained in original size (<0.071 – 0.0016 mm); *G. pulex* experiments = open circles; *B. rhodani* experiments = up-triangles; Control experiments = closed circles.

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Aus diesem Grunde widme ich die vorliegende Arbeit meinen Eltern.

Curriculum vitae

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Education

09 / 1981 – 06 / 1990	Olga–Benario–Polytechnic Preparatory School Auma, Germany (primary school)
09 / 1990 – 06 / 1991	Erweiterte Oberschule Zeulenroda, Germany (secondary school)
09 / 1991 – 06 / 1993	Friedrich–Schiller–Gymnasium Zeulenroda, Germany (Abitur)

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07 / 1993 – 06 / 1994	6. Pionierbataillon 701 Gera, Germany

University study

10 / 1994 – 06 / 2000	Study of biology at the Friedrich–Schiller–University Jena, Germany, branch of study: biology diploma, major subject: ecology, subsidiary subjects: microbiology, zoology and geology, Diploma-thesis: „Limnologische Untersuchungen an temporären Kleingewässern im NSG Windknollen Jena (Thüringen): Dynamik der physikalisch – chemischen Parameter und der Wasserkäfergemeinschaft.“ Experts: Dr. habil. Wilfried Schönborn, Dr. PD Heike Zimmermann - Timm, Prof. Dr. Stefan Halle
since 06 / 2000	PhD student at the Friedrich–Schiller–University, Jena Topic of the PhD-thesis: „The effects of a small low-head dam on benthic invertebrate communities and particulate organic matter storage in the Ilm stream (Thuringia / Germany).“ Member of the graduate study group: „Function and regeneration analysis of disturbed ecosystems“ supported by: Deutsche Forschungsgemeinschaft (DFG) Förderkennzeichen: GRK 266/2

Jena, den

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Lebenslauf

Persönliche Angaben

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Schulausbildung

09 / 1981 – 06 / 1990	Olga–Benario–Oberschule Auma, Abschluss der 9. Klasse
09 / 1990 – 06 / 1991	Erweiterte Oberschule Zeulenroda, Abschluss: Mittlere Reife, Gesamturteil: „gut“
09 / 1991 – 06 / 1993	Friedrich–Schiller–Gymnasium Zeulenroda, Abschluss: Abitur, Gesamturteil: „gut“

Grundwehrdienst

07 / 1993 – 06 / 1994	6. Pionierbataillon 701 Gera, Entlassen als: Gefreiter

Studium

10 / 1994 – 06 / 2000	Friedrich–Schiller–Universität Jena, Fachrichtung: Biologie Diplom, Hauptfach: Ökologie, Nebenfächer: Mikrobiologie, Zoologie und Geologie, Thema der Diplomarbeit: „Limnologische Untersuchungen an temporären Kleingewässern im NSG Windknollen Jena (Thüringen): Dynamik der physikalisch – chemischen Parameter und der Wasserkäfergemeinschaft.“ Gutachter: Herr Dr. habil. Wilfried Schönborn, Frau Dr. PD Heike Zimmermann-Timm, Herr Prof. Dr. Stefan Halle Abschluß: Diplombiologe, Gesamturteil: sehr gut
06 / 2000 – bis heute	Promotionsstudent an der Biologisch-Pharmazeutischen Fakultät der Friedrich–Schiller–Universität Jena Dissertation zum Thema: „The effects of a small low-head dam on benthic invertebrate communities and particulate organic matter storage in the Ilm stream (Thuringia / Germany).“ Im Rahmen des Graduiertenkollegs: „Funktions- und Regenerationsanalyse belasteter Ökosysteme“. Gefördert durch: Deutsche Forschungsgemeinschaft (DFG) Förderkennzeichen: GRK 266/2

Lehre

06 / 2000 bis 10 /2004

Mitarbeit an der Initiierung und Betreuung folgender Diplomarbeiten:

- Seidel, D. (2002) Besiedlungsmuster von Süßwassermollusken in temporären Kleingewässern im Naturschutzgebiet Windknollen, Jena (Thüringen). Unveröffentlichte Diplomarbeit, Friedrich–Schiller-Universität, Jena.

- Schweizer, C. (2002) Herbst-/ Wintersituation an ausgewählten Kleingewässern im NSG Windknollen bei Jena. Unveröffentlichte Diplomarbeit, Friedrich-Schiller-Universität, Jena.

- Lange, A. (2004) Der Einfluss eines Wehres auf die Drift aquatischer Invertebraten. Unveröffentlichte Diplomarbeit, Friedrich–Schiller-Universität, Jena.

Betreuung von Exkursionen und Studentenpraktika an der FSU Jena:

- Geländepraktikum Ökologie 2000 & 2001, Thema: Sukzessionsstudien im limnisch – terrestrischen Bereich

- Geländepraktikum Ökologie 2002, Thema: Querbauwerke/ Wehre und ihre Bedeutung für das Fließgewässerökosystem

- „Limnologisches Grundpraktikum“ 2000

- Arthropoden – Bestimmungskurs „Artenkenntnis und Ökologie von Evertebraten“ 2000 & 2001

- Forschungspraktikum Ökologie 2002 (mehrwöchige Einzelbetreuung von Studenten)

Jena, den

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Publikationen in begutachteten internationalen Zeitschriften:

Arle J. (2002) Physical and chemical dynamics of temporary ponds on a calcareous plateau in Thuringia, Germany. Limnologica, 32, 83-101.

Symposiumsbeiträge:

Arle J. & Schönborn W. (2001) Limnologische Untersuchungen an temporären Kleingewässern im NSG „Windknollen“ Jena (Thüringen): - Posterbeitrag, Jahrestagung der Deutschen Gesellschaft für Limnologie Kiel 2001.

Arle J. & Zimmermann-Timm H. (2002) Wehre in einem Mittelgebirgsbach (Ilm / Thüringen) und ihre Konsequenzen für die Makrozoobenthos – Gemeinschaft. – Vortrag auf der Jahrestagung der Deutschen Gesellschaft für Limnologie Braunschweig 2002.

Weitere Vorträge:

Partikuläres organisches Material (POM) - Nahrung für aquatische Invertebraten, Ergebnisse eines experimentellen Ansatzes im Labor. Vortrag im Rahmen des Institutsseminar / Ökologisches Kolloquium am Institut für Ökologie der FSU Jena, November 2003.

The effects of a small, low-head dam on benthic invertebrate communities and particulate organic matter (POM) dynamics. Vortrag im Rahmen des Institutsseminar / Ökologisches Kolloquium am Institut für Ökologie der FSU Jena, April 2004.

Publikationen in Vorbereitung:

Arle J.: Diversity of aquatic beetles (Coleoptera) in temporary ponds in Thuringia (Germany).

Wagner F., Arle J. & Rothe J.: Chemical and isotopical composition of detritus as markers for organic matter processing to elucidate impacts of channel degradation on the chemical nature of benthic organic matter (BOM).

Arle J. & Zimmermann–Timm H.: The consequences of a small low-head dam for invertebrate communities in a Thuringian stream (Ilm / Germany).

Selbstständigkeitserklärung

Ich versichere an Eides statt, dass mir die geltende Promotionsordnung bekannt ist. Ich habe die vorgelegte Dissertation selbst angefertigt, sowie alle benutzten Hilfsmittel und Quellen vollständig angegeben.

Es wurde nicht die Hilfe eines Promotionsberaters in Anspruch genommen. Es haben keine Dritten geldwerte Leistungen unmittelbar oder mittelbar für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen. Es wurde weder diese noch eine andere Dissertation bei einer Fakultät der FSU Jena oder einer anderen Hochschule zur Prüfung vorgelegt.

Auma, den

Jens Arle