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Abundance and Vertical Distribution of the Phytobenthic Community within a Pool and Riffle Sequence of an Alpine Gravel Stream

key words: microphytobenthos, stream, vertical distribution, carotenoids, HPLC, algae

Abstract

In the 2nd order mountain brook “Oberer Seebach” (Austria), diatoms and cyanoprokaryotes dominate the microphytobenthos, with the diatoms forming the richest species group.

Comparative investigations of different habitats clearly show seasonal variations in algal species composition and biomass throughout the year. Pool habitats hold a higher number of taxa than riffle sites. In addition, phytobiomass is two- to nearly fourfold higher in pools. Based on investigations of the chlorophyll-*a* vertical profiles within the coarse gravel sediments, the light discontinuity layer was determined to be situated at 7–10 cm sediment depth. Vertical distribution showed a maximum of taxa a few centimeters below the sediment surface. The same diatom taxa were found throughout all sampling dates, sediment depths and sampling sites.

The results of exposed perforated metal tubes clearly indicate that the occurrence of phytobenthos in aphotic zones is primarily controlled by saltatory movements of the upper sediment layers driven by discharge.

1. Introduction

Benthic algae are a major component of aquatic food webs. They are now accepted to be the primary energy source in many medium sized (third to sixth order) streams (VANNOTE *et al.*, 1980). With increasing stream size, autotrophic production also gains in importance, but the relative contribution of periphyton declines as plant communities may shift to macrophytes (LAMBERTI, 1996) or phytoplankton (VANNOTE *et al.*, 1980). In alpine rivulets, allochthonuous material plays the most important role as an energy source, but periphyton, especially epilithic algae, must not be neglected. Frequently, the periphytic layer is visible as a typical coloured pattern within streams (GEITLER, 1927a). The coloration, indicative of the algal species composition, varies seasonally depending on environmental variables such as light and nutrient supply, water level and temperature changes (KANN, 1978).

The present investigation was designed to estimate the benthic algal biomass in the “Oberer Seebach”, a summer-cold 2nd order brook located in the Alps of Lower Austria. This location is not only well known since the intensive ecosystem investigations in its “Ritrodat-Lunz study area” (BRETSCHKO, 1981), but also because of the early work of GEITLER (1927a) on the typical coloration in alpine brooks in this area. One advantage of confining a study to a small reach of a stream like the “Ritrodat” is that the confounding effects of differing nutrient concentrations and experimental artefacts can be factored out.

Up to now only a few studies are available dealing with the horizontal and vertical distribution of microphytobenthos in alpine brooks. These investigations focused mainly on algae attached directly to the sediment surface, without consideration of the hyporheal (GEITLER,

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1927a, b; Budde, 1928; Backhaus 1968a, b, c; Kann, 1978; Rott and Pfister, 1988; Pfister, 1992a, b, 1993; Pipp and Rott, 1993, 1994). Studies dealing with the vertical distribution of attached algae and their pigments were performed mainly on lake sediments (e.g. Züllig, 1981, 1982; Steenbergen and Korthals, 1988; Yacobi *et al.*, 1991) and on marine sand and mud flats. Especially on the latter topic there exists a wide range of investigations (e.g. Pamatmat, 1968; Fenchel and Straarup, 1971; Round, 1979; Repeta and Gagosian, 1982, 1987; Skjoldal, 1982; Ridout *et al.*, 1984; Paterson, 1986; Riaux-Gobin *et al.*, 1987; Furlong and Carpenter, 1988; Happey-Wood and Jones, 1988; Delgado, 1991; Jönsson *et al.*, 1994). Poulíčková (1987) studied the phytoplankton community in the hyporheic zone respectively in the groundwater of a river. However, no previous study has analysed the phytobenthic algae within a coarse gravel brook along a vertical depth gradient. Thus, one main objective of our study was to investigate to which depth autotrophic periphyton can be found and what are the processes influencing the vertical algal distribution. For macrozoobenthos, Schwoerbel (1961, 1964) described the hyporheal as a nursery and refuge of the stream fauna. Meanwhile, the nursery role has clearly been supported by numerous studies, whereas the refuge role is still a convenient model, which has not really been proved or disproved (Palmer *et al.*, 1992). Poulíčková (1987) investigated the seasonal changes in the relative abundance of phytoplankton in the groundwater of a gravel stream compared to that in the free-flowing surface water. When the total number of algae in surface water was set to 100%, the amount of algae found in the groundwater ranged from 60 to 103% in spring and autumn, but only 2 to 36% during the main vegetation period. Similar relations were also noticed by Čistín and Himmel (1980). From that it could be hypothesized that water below the free-flowing surface represents an environment in which algae more easily survive unfavourable periods. This study addresses the question for periphyton communities.

Besides coarse particulate organic material (CPOM), which is the primary food source for macrozoobenthos (shredders) in small order rivers, also periphyton is of great importance. Grazers exploit this microlayer as a food source by scraping and rasping (Allan, 1995). Because water velocity and the associated physical forces represent one of the most important environmental factors affecting the organisms of running waters (Allan, 1995), the differences in algal biomass and in taxonomic composition at the class level from a pool and riffle sequence were studied in the brook "Oberer Seebach".

For studies of seasonal and vertical variability quantitative data are necessary. However, attached algae are difficult to quantify. For the most part cell counting is not possible because algae are destroyed by scraping. An estimation of different algal species on a semiquantitative scale may be used to get an impression of overall frequencies. One promising approach in solving the quantification of the relationships of taxonomic groups within the periphyton is the quantification of pigments from algal groups using class-specific pigment markers, which was done in this study. This practicable method by means of high performance liquid chromatography (HPLC) represents a powerful tool for getting information on algal class composition (Bianchi *et al.*, 1993; Downes *et al.*, 1993; Jeffrey *et al.*, 1997; Latasa *et al.*, 1992; Millie *et al.*, 1993a, b; Schagerl and Donabaum, 1998).

Main objectives of this study were to investigate the seasonal variations of A) the vertical distribution of algae within the sediments of the stream and B) the algal quantities and community composition at a pool and a riffle site with different hydraulic characteristics.

2. Materials and Methods

Phytobenthos was analyzed at a pool and a riffle site in the alpine 2nd order brook "Oberer Seebach" within the Ritrodat area, Lunz, Lower Austria (Bretschko, 1981). General characteristics of the brook are listed in Table 1; Fig. 1 shows temperature regime and water level fluctuations. The "Oberer Seebach" drains a limestone dominated, densely forested catchment. Climate and weather are consistent with

Table 1. General characteristics of the brook “Oberer Seebach”; means with ±95% confidence-limits (combined from BRETSCHKO and MOSER, 1993; BRETSCHKO, 1998; MÜLLNER, 1998).

Discharge (1980/84, $l \cdot s^{-1}$)		**Grain size frequency distribution (quartiles, mm)**	
MQ	720	Q_{25}	10.6 ± 1.2
M max. Q	2400	Median	23.1 ± 2.0
M min. Q	320	Q_{75}	47.6 ± 1.6
Max.	17500		
Min.	320	**Fractions (%) smaller than 1.0 mm**	
		LL	4.4
Water temperature (1982/86, °C)		mean	7.4
Annual mean	6.8	UL	9.3
Mean Maximum	11.1		
Mean Minimum	1.9	**porosity**:	>24%

Chemistry	**1979/82**	**March – Dec. 1997, this study**
pH	8.1 ± 0.1	8.3 ± 0.1
Conductivity ($\mu S\ cm^{-1}$)	216 ± 6	204
Alkalinity ($meq \cdot l^{-1}$)	2.18 ± 0.007	2.23 ± 0.15
Ca^{++} ($meq \cdot l^{-1}$)	2.04 ± 0.06	1.87 ± 0.12
Mg^{++} ($meq \cdot l^{-1}$)	0.52 ± 0.04	–
P_{tot} ($mg \cdot l^{-1}$)	0.01	–
N_{tot} ($mg \cdot l^{-1}$)	1.011 ± 0.238	–
$N\text{-}NO_3$ ($\mu g \cdot l^{-1}$)	–	1197 ± 261
$N\text{-}NO_2$ ($\mu g \cdot l^{-1}$)	–	0.8 ± 0.5
$N\text{-}NH_4$ ($\mu g \cdot l^{-1}$)	–	10 ± 8
O_2 ($mg \cdot l^{-1}$)	–	12.1 ± 0.8
$Si\text{-}SiO_4$ ($mg \cdot l^{-1}$)	–	0.7 ± 0.05
$P\text{-}PO_4$ ($\mu g \cdot l^{-1}$)	–	5 ± 2.5

the location, inside the northern fringe of the Eastern Alps. The Ritrodat area is a 100 m long stretch of the stream, 320 m upstream of its inflow into lake “Untersee”. The mean breadth of the channel is 14.0 ± 1.6 m at bankfull discharge, the mean slope is 0.41 ± 0.003 cm/m, averaged over the years 1980/82 (BRETSCHKO, 1983). Hydrologically, “Oberer Seebach” is a typical “flashy river”, with extremely steep discharge increases, as is to be expected from the karstic catchment. Temperatures of the surface water are always low, characterizing “Oberer Seebach” as a typical summer cold stream (Table 1, Fig. 1). The chemical composition of the water reflects the geology of the catchment: it is well buffered and without any seasonal pattern (Table 1).

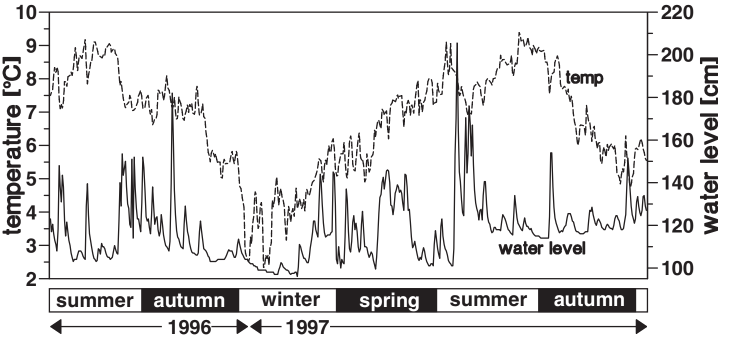

Figure 1. Water level fluctuations and temperature regime of the brook “Oberer Seebach”.

To investigate the seasonal variations of the algal quantities and community composition at a pool and a riffle site, sampling was conducted nine times during 1997 (1.3., 6.4., 4.5., 1.6., 3.7., 16.7., 10.8., 8.9., 10.12.) by scraping algae from individual sediment particles (i.e. stones). Algae were removed separately from the top, bottom and lateral surfaces of the stones. The lateral surface (flank) was sampled separately because of its special hydraulic features (AMBÜHL, 1959). A modified periphyton sampler (DOUGLAS, 1958), with its sampling area minimized down to 3.5 cm^2, was applied to also include smaller pebbles (total number of investigated stones: n = 43; scraped top, bottom and lateral areas: n = 236). Hydraulic characterization of the sampling sites (pool, riffle) was done by means of FST standard hemispheres (STATZNER and MÜLLER, 1989), which summarize key hydraulic characteristics such as shear stress, boundary Reynolds number and Froude number (FST numbers: pool always <1; riffle: mean 8.43, std dev. 1.68, n = 37).

For studying the vertical distribution of algae within the sediment, a 1 m^2 area was marked and stones cleared away in 5 cm steps down to 20 cm below surface. Each 5 cm layer was collected separately and immediately brought to the laboratory. Sampling was done by means of the same Douglas-sampler (DOUGLAS, 1958) as used for the investigations of seasonal variations of the surface algal quantities and community composition at pool and riffle site, while differentiating between top, flank and bottom surfaces of the pebbles (total number of investigated stones: n = 176; scraped top, flank and bottom areas: n = 1024; flank sampled separately from top and bottom surfaces only in the first depth layer). For data interpretation, obtained chl-*a* values (top, flank, bottom) were converted into 2 cm steps.

For investigating the processes influencing the vertical algal distribution, especially down to aphotic sediment layers, three perforated metal tubes (diameter 6 cm, length 100 cm, perforations 0.8 × 0.8 cm) filled with sterilized (180 °C, 5 h) natural substrate (grain size diameter c. 4–6 cm) where exposed in the bed sediments at a riffle site for two, three and six months, respectively.

For each sample, subsamples were created for dry and ash mass determination, pigment analysis and diatom preparation, respectively. Determination of dry mass and ash content was made by filtering homogenized and resuspended subsamples onto precombusted and preweighted Whatman GF/F filters. After drying the filtered material at 95 °C for 24 hrs, it was reweighted for dry mass determination. Then the material was combusted at 500 °C for 2 hrs for ash mass (incl. carbonate) determination.

For pigment analysis, subsamples were filtered (Whatman GF/C) and stored at −30 °C. Pigment extraction was done by grinding the filters in 90% cold acetone following extraction in darkness at +2 °C for 12 hrs. The suspension was centrifuged and the supernatant analyzed by means of HPLC according to WRIGHT *et al.* (1991; Merck-Hitachi HPLC system; ternary low pressure gradient with distilled water, acetone and acetonitril; prederivatisation of samples with tetrabutylammoniahydroxide; column: Merck-Superspher RP-18 250/4, precolumn: Merck-Lichrospher RP-8 endcapped). Peakdetection and integration was done at 440 nm (SCHAGERL, 1993; SCHAGERL *et al.*, 1996).

Percentages of individual algal classes were determined by calculation of their respective chlorophyll-*a* (chl) part of the total chl-*a* using class-specific pigment ratios (Bacillariophyceae including Synurophyceae: fucoxanthin; Cyanobacteria: echinenone; Chlorophyta: chl-*b*; SCHAGERL and DONABAUM, 1998; WILHELM *et al.*, 1991). For microscopical work, a Reichert Polyvar supplied with differential interference contrast optics was used. For diatom determinations, combusted samples were embedded in Naphrax following the Naphrax manual.

3. Results

3.1. Seasonal Distribution – Riffle Site

The algal biomass expressed as chl-*a* (µg cm^{-1}) was low at the beginning of March and even decreased in April because of a spate, followed by only a slight increase until May due to continued changes in water discharge (Fig. 2). Subsequent constant hydrological conditions as well as the rising water temperature towards the summer season resulted in an increase of the algal biomass in June, lasting until beginning of July. A spate in July caused an almost total reduction of the phytobenthic vegetation in the whole brook. Whereas algal biomass showed only a slight increase in the first month after the flood event, a month later the phytobenthos biomass had more than doubled compared to the values at the beginning of

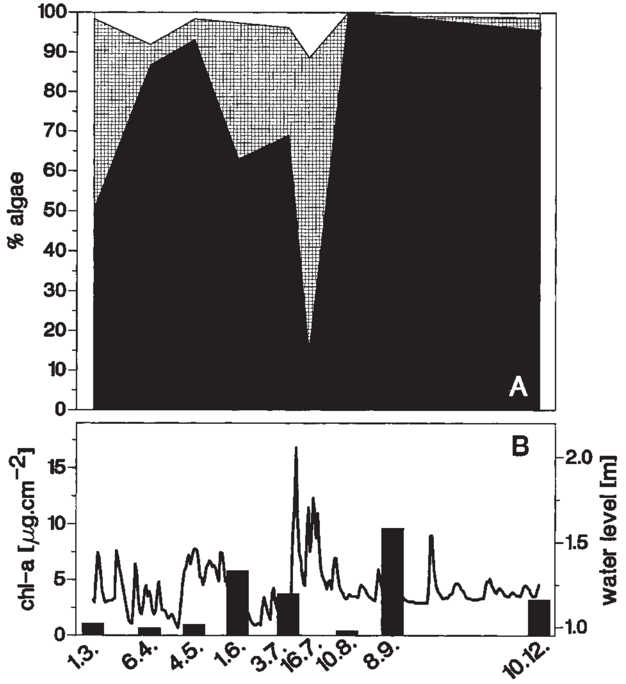

Figure 2. Seasonal changes of periphyton at the riffle site (A) class composition expressed as black – fuco-group, squared grey – greens, white – blue-greens and (B) total chlorophyll-*a* per surface area and water level fluctuations.

July. A small spate at the beginning of October, as well as the following suboptimal environmental conditions, caused a strong decrease of algal biomass in winter.

A very high abundance of the fucoxanthin containing group including the Bacillariophyceae and Synurophyceae was observed at the riffle site (Fig. 2; subsequently addressed as the fuco-group). With the exception of a single sampling date (first spate-maximum in July), this group always constituted the dominant fraction of the phytobenthos (50–100%). The most abundant species were *Phaeodermatium rivulare* HANSG. and *Hydrurus foetidus* (VILL.) TRÉV. (Synurophyceae) as well as the diatoms *Achnanthes minutissima* KÜTZ., *Cocconeis placentula* EHRENB., *Cymbella minuta* HILSE ex RABENH. and *Gomphonema angustum* AGH.

3.2. Seasonal Distribution – Pool Site

Compared to the riffle site, similar trends in whole phytobenthos biomass dynamics could be found at the pool site. A marked difference was an at least twofold higher chl-*a* value at the pool site on each sampling date with the exception of the big spate in July (Fig. 3).

A typical dominance of the non-fuco-group was observed throughout the year (most abundant species: Chlorophyta – *Gongrosira spp.* KÜTZING, Cyanoprocaryota – *Homoeothrix varians* GEITLER, *Chamaesiphon spp.* A. BRAUN et GRUNOW, *Phormidium spp.* KÜTZING), except the sampling dates in August and September, when flood events had also removed nearly the complete algal vegetation at this site. The subsequent development of the phytobenthos vegetation was similar to that of the riffle site and therefore first of all consisted of fast growing pioneers (Synurophyceae, Bacillariophyceae).

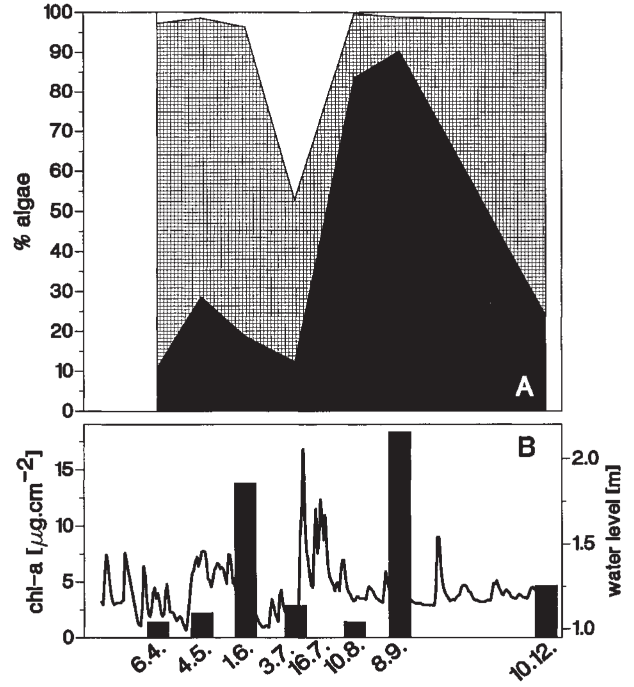

Figure 3. Seasonal changes of periphyton at the pool site (A) class composition expressed as black – fuco-group, squared grey – greens, white – blue-greens and (B) total chlorophyll-*a* per surface area and water level fluctuations.

3.3. *Vertical Distribution – Riffle Site*

Detailed analysis showed that after longer lasting stable hydrological conditions without strong saltatory sediment movements, a minimum chl-*a* amount was always found at 7–10 cm sediment depth (1.3., 1.6., 3.7., 8.9.), also referred to as the light discontinuity layer. Thus,

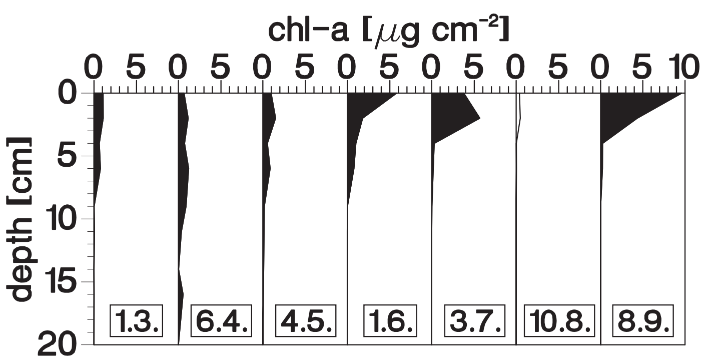

Figure 4. Vertical chlorophyll-*a* distribution within the sediment at the riffle site, 2 cm steps were obtained by conversion from the raw data set (top, flank, bottom of pebbles). Light discontinuity layer was determined at 7–10 cm sediment depth.

Table 2. Vertical distribution of total species numbers of algae within the coarse gravel sediments of the brook “Oberer Seebach” in 1997. Numbers in the top line indicate sampling depth, cm. (T = top, B = bottom, F = flank of stones; nm = not measured; in brackets number of diatom species).

date	0–5 T	0–5 F	0–5 B	5–10 T	5–10 B	10–15 T	10–15 B	15–20 T	15–20 B
1.3.	20 (8)	22 (10)	20 (10)	23 (12)	3 (3)	21 (13)	8 (8)	2 (0)	1 (0)
6.4.	34 (27)	41 (32)	49 (43)	33 (28)	38 (32)	33 (29)	20 (20)	23 (22)	0
4.5.	29 (22)	39 (29)	28 (23)	32 (27)	5 (0)	nm	nm	nm	nm
1.6.	27 (22)	18 (12)	29 (22)	30 (22)	16 (10)	0	0	0	0
3.7.	33 (22)	37 (23)	20 (12)	31 (23)	16 (14)	0	0	0	0
16.7.	5 (0)	4 (0)	0	11 (7)	8 (6)	12 (6)	3(0)	nm	nm
10.8.	8 (6)	11 (9)	0	2 (0)	2 (0)	0	0	0	0
8.9.	29 (26)	31 (28)	20 (17)	35 (32)	18 (18)	0	0	0	0

the photic zone goes down to a depth that corresponds to SCHWOERBEL’s (1964) postulated position of about four to five times the mean grain size diameter. Only after strong flood pulses (6.4., 16.7.) was the sharpness of this boundary obscured, a fact which documents the influence of spates down to deeper regions of the sediments (Fig. 4). Two weeks after the strong summer spate which resulted in a total destruction of the phytobenthos, a thin algal pioneer biofilm had already been established, again showing the typical sharp chl-*a* decline towards the light discontinuity layer.

The investigation of the vertical distribution of diatoms showed the maximum number of taxa not at the sediment surface but always in deeper sediment layers, which was also true for the non-diatoms (Table 2). In addition, the same diatom taxa were abundant at all sampling dates, sediment depths and sampling sites. Thus, the hydraulic heterogeneity of the stream bed was not leading to a patchwork of community types.

3.4. *Sediment-Pipes*

At all sediment pipe sampling dates (10.8., 8.9., 10.12.), the exposed metal tubes were covered with a gravel layer of 8–20 cm, which impressively displays the importance of saltatory movements on the vertical distribution of algae. The surface of the sterilized stones inside the sediment pipes contained a few diatom cells at the first sampling date (10.8.: *Achnanthes minutissima, Gomphonema angustum*), but no cells could be found at the other two days (8.9., 10.9.). The pebbles stacked above the pipes by saltatoriy movements were covered by an algal vegetation resembling the one of the surrounding riverbed area.

4. Discussion

There is an increasing emphasis on the role of hydraulic features in determining the spatial distribution of organisms in streams (STATZNER *et al.*, 1988; DAVIS and BARMUTA, 1989; YOUNG, 1992; BIGGS and HICKEY, 1994; LORENZ *et al.*, 1997; BEISEL *et al.*, 1998; GIBERSON and CAISSIE, 1998; STATZNER *et al.*, 1998; FREEMAN *et al.*, 1999; LAMOUROUX *et al.*, 1999; ADAMS *et al.*, 2000). Flowing water can affect phytobenthos communities through several processes. Algal resistance to scour is strongly dependent on the stability of benthic substrata. If substrata are relocated very frequently because of spates, slow growing filamentous Cyanobacteria and Chlorophyta will not be able to establish dense layers and rapidly growing diatoms and Synurophyceae will dominate the microphytobenthos. The strong influence of dicharge pattern on the type of algal association was observed also in this study. A development from a pioneer-dominated algal vegetation (Synurophyceae, Bacillariophyceae) to a mature Chlorophyta-Cyanoprokaryota association was observed in the course of longer periods of intermediate and stable water discharge in March and June. In July there was a nearly complete removal of the epilithic algal vegetation by extreme spates; only endolithic cyanoprokaryota (e.g. *Leptolyngbya perforans* (GEITL.) ANAGN. et KOM.) and lime-incrusting green algae (e.g. *Gongrosira incrustans* (REINSCH) SCHMIDLE) survived.

Fast flowing water can also increase metabolic rates by reducing the thickness of the diffusive boundary layer, which can be seen as a barrier for metabolites to and from cells (WHITFORD and SCHUMACHER, 1961; LOCK and JOHN, 1979; RIBER and WETZEL, 1987). As water velocity increases so does skin friction and drag on the community; the shape, size and orientation of organisms to flow becomes more and more important in their bid to hold station (VOGEL, 1981). At our sampling site, diatoms, capable of high mucilage secretion and therefore being able to buffer environmental forces, dominated at the riffles together with the thin layers of the Synurophyceae *Phaeodermatium rivulare*, staying within the boundary layer of the natural substrate.

The hydrological regime exerts important control over the biota of rivers. In this study, a great influence of water level stability on periphyton density was recognized. In unshaded streams, the flood disturbance regime is one of the fundamental variables determining habitat suitability and pattern for benthic algae (BIGGS, 1996), with intermediate current velocities generally leading to highest algal biomass (STEVENSON, 1996). During low water situations, there is an improvement in the light climate. At permanently submerged locations the algal vegetation is denser than in areas near the bank subjected to a fluctuating water regime. On the other hand, a decrease of the algal biomass results from the impaired light climate in deeper regions of the stream channel. Between those extremes a zone is marked, where light climate and hydrology allow an optimum development of benthic algal communities. According to SCHWOERBEL (1964), the boundary layer between benthal and hyporheal in flowing waters with relatively homogenous sediments is strongly characterized by a rapid decline of light towards the hyporheal. In this study the light discontinuity layer was determined by the coloration of the pebbles at 7–10 cm sediment depth thus confirming SCHWOERBEL'S (1964) postulated size of layer in dependence on the mean grain size diameter.

POULÍČKOVÁ (1987) compared phytoplankton from surface water with that of the interstitial of three streams in the basin of the Morava river (15, 30, 60, 100 cm below the bottom). Generally, the species composition of the sediment waters corresponded to the composition of the surface water. These results strongly indicate the dependence of the ground water phytoplankton from inoculations from the stream. The expected increase in colourless flagellates in greater depths was not observed. These facts are congruent with conclusions to be drawn from our Sediment-Pipe experiments. No confirmation could be found as to the hypothesis, that parts of algal benthic mats scraped off the surface stones are transported into the sediments and settle down. In addition to that no heterotrophic algae were found growing on the exposed stones. After intense spates, the most important pool for algal recolonization is probably surface water itself which transports algal diaspores. The occurence of phytobenthos in aphotic zones is primarily controlled by saltatory movements and other forms of displacement of stones of the upper sediment layers driven by water discharge. Concerning the diatoms, POULÍČKOVÁ (1987) found an irregular distribution in different sediment layers. She assumed that diatoms do not penetrate into the sediment evenly, some species exhibit a greater probability of intruding into deeper horizons. In this study the vertical distribution of diatoms showed the maximum number of taxa not at the sediment surface but always in the deeper sediment layers. The same three to four taxa, raphe bearing and being able to perform vertical movements, were dominant or abundant at all sampling dates, sediment depths and sampling sites: *Achnanthes minutissima, Gomphonema angustum* and *Cocconeis placentula*. Responses of phytobenthic algae to hydraulic habitat features in streams are complex and it is difficult to uncover universal hydraulic habitat preferences for this community.

By investigating the vertical distribution of chl-*a* within beach sand, SKJOLDAL (1982) found that sediment turbulences brought a part of the algal population down into layers of low or no light, thereby exerting a strong influence on the algal distribution, production and biomass. Thus, under conditions of high sediment disturbance the vertical distribution of chl-*a* was generally more uniform, with a lower content in the surface layer than in more stable sediments. This study confirmed this observation also for coarse sediments. High water events caused a more uniform distribution of chl-*a* due to strong sediment movements. In contrast to fine sediments, the movements of coarse sediments cause a much higher mortality rate of the phytobenthos community.

In addition to physical sediment mixing, also other factors influence the vertical distribution of algae and chl-*a*. These include chemical gradients, vertical distribution of grazers, the physiological and metabolic capacity of the algae for dark metabolism, and the motility of the algae (e.g. diatoms, see above). The importance of the latter has been clearly demonstrated by a broad variety of studies and experiments (e.g. FENCHEL and STRAARUP, 1971; PATERSON, 1986; HAPPEY-WOOD and JONES, 1988; JÖNSSON *et al.*, 1994). Chemical gradients and vertical distribution of grazers within the sediments of the study site "RITRODAT" have been investigated by a variety of studies (e.g. BRETSCHKO, 1981; BRETSCHKO, 1998; BRETSCHKO and KLEMENS, 1986; BRETSCHKO and LEICHTFRIED, 1988; PANEK 1991).

In this investigation HPLC pigment analysis revealed important information about the structure of benthic algal communities and the patterns of succession. However, it must be considered that algal class composition is derived from algal pigments, which are strongly influenced by the physiological state. Additionally, chl-*a* per unit biomass shows species specific as well as class specific variations. Further investigations are necessary to fully validate this method.

5. Acknowledgements

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