universität wien

DIPLOMARBEIT

Titel der Diplomarbeit

„Hydrologic Stochasticity and Biodiversity of Biofilm Algae”

“Effects of altered flow and light conditions on community composition and algal growth within microcosms “

verfasst von

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Ich widme diese Diplomarbeit meinem Vater, Martin Adlboller,
der durch seinen plötzlichen Tod,
das Ende meines Studiums leider nicht mehr miterleben durfte.

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Abstract

Heterogeneous environmental conditions are important determinants for aquatic organisms, all algae have a species-specific optimum, where they grow and reproduce perfectly. Ecosystems recovery and resilience due to disturbances is influenced by the whole community. Flow velocity and light put a major pressure on the adaptation of algal communities. Alterations of aquatic ecosystems could lead to a shift in the community composition and biodiversity. This may modify functions and services, provided by aquatic ecosystems. The aim of this study was to gain insights into how the autotrophic biofilm community is influenced by shading and stream flow characteristics. We grew biofilms in artificial flumes, with 2 differentiating flow regimes: one was constant and one was stochastic. Filters produced a gradient in light availability over these hydrological treatments. Statistical analyses support the thesis that light had a high influence on benthic biofilms, especially under low light conditions and where flow was constant. Overall constant conditions led to higher biomass and abundance of algae. Comparison of communities did not show any clear separation. A community ordination indicates that constant flow led to a more light-driven environment and stochastic flow conditions rather to a combination of flow and light. Conditions of high light seemed to be independent of light and flow dynamic, so this habitat is probably driven by nutrient availability. Biofilms grown under low light availability were dissociated from other treatments. We suggest that, adaptation to low light availability appears to be the major driver under these conditions, although flow variability influences the community as well. Our findings brought us to the conclusion that altered light and hydrological conditions lead to modified communities and probably changes the whole ecosystem.

Introduction

Global population already reached 7 billion humans (Haub et al., 2012). Essential services delivered by ecosystems contributing to human well-being, such as water supply, water purification, fish and fiber, climate regulation, flood regulation are influenced by various drivers (Nelson, 2005; Millennium Ecosystem Assessment, 2005). Within freshwater ecosystems, depending on the region, the most important direct drivers of change include modification of hydrological regime (e.g. flood control), invasive species, eutrophication and turbidity (Nelson, 2005; Hill, 1996). Indirect drivers as changing settled ways of thinking in economics, and politics e.g. renewable power supply, have major effects on direct drivers (Nelson, 2005) and therefore shape the community as well.

Streams play a key role acting as interfaces between all aquatic habitats and terrestrial surroundings (Dodds, 2010). Lots of heterogeneous habitats due to local and seasonal variances in flow velocity, light, temperature, nutrients, and other environmental factors are provided. Flooding is an integral part of many lotic ecosystems and riparian wetlands. Recovery from spates, low flow phases (including desiccation), grazing and competition on species level are imperative necessities of stream biota to adapt to or generate other strategies (Palmer and Poff, 1997; Stanish et al., 2011). Quantity and diversity of periphyton is largely a function of time since the last disturbance occurred (Buckling et al., 2000; Tett et al., 1978). Temporal changes in flow velocity and water amount during spates or low water phases produce a stochastic sequence, characteristic for each stream, depending on seasonal variations in precipitation and snow melting, as well as on catchment characteristics (topography, land cover, geology) (Poff and Zimmermann, 2010). In intermittent streams, the importance of flow variability and its role in biodiversity and ecosystem health is evident (Poff et al., 2007). Flow stabilisation, mainly alterations in lateral and longitudinal connectivity, and constant flow, e.g. minimal residual water, leads to decreases in instream and riparian variability and flow heterogeneity. Clogging of the riverbed caused by sedimentation of fine sediments could result in a reduced diversity due to losses of sensitive and specialized species (Poff and Zimmermann, 2010; Uehlinger et al., 2003). Human alterations of dynamic hydrologic regimes effect aquatic communities depending on species composition, provided services and functions. Species are effected in a positive or negative way, but euryoecious and invasive species could be favoured (Dodds, 2010; Lytle and Poff, 2004; Poff et al, 2007).

The dominant primary producers in rivers and streams are benthic algae, providing the main energy base for higher trophic levels (Biggs et al., 2002; Lamberti, 1996). As flow is just one environmental factor for benthic algae, light is a fundamental variable too, because photosynthesis responds quantitatively and qualitatively (physiology, population growth, and community structure) to changes in light and alterations via land use are evident (Hill, 1996). As biofilm, attached algae and bacteria on substrata producing mucilage matrices, provide a three-dimensional structure filter effects through vegetation (selfshading, shading by macrophytes and/or riparian vegetation), light scattering and refraction by water molecules, and dissolved particles (turbidity) play a major role in the heterogeneity of light distribution (Hill, 1996). Within these vertical matrices the efficiency of photon use and adaptation to modified light fields (accessory pigments filter specific wavelength) alters also community composition (Hill, 2006). Adaptation and acclimation to low light levels are apparent for many species, as only some are motile or have an exposed position (Hill, 1996). High irradiations potentially have damaging effects on accessory or sheath pigments (Garcia-Pichel and Castenholz, 1991) and could inhibit photosynthesis in surface cells, a time- and wavelength-dependent effect (Hill, 1996; Smith et al., 1980).

The aim of this study was to gain insights in physical factors likely influencing algae growth and community composition in flumes. Studies on biodiversity, community composition and biovolume distribution should lead to a better understanding of the effect of light and hydrological regime on phototrophic biofilms. To check for validity of our research aim we prior specified some questions:

Is algal community composition determined by light or hydrological regime?

Which effects do we expect to detect between different flow regimes?

As in the intermediate disturbance theory, we suggest that in systems with moderate disturbances the highest biodiversity will be located, even if biomass is reduced. In constant flow regime (no high or low flow) we expect that only a few well-adapted species dominate and produce a higher biomass.

Do different light conditions select for light/shadow adapted species?

The prospect is that in flumes with low and high light transmissions only some well adapted species dominate, whereas flumes with intermediate irradiates display a variety of different species.

Do flumes with the same light conditions provide more variation between the systems?

A certain variation between the sampling points was expected caused by patchiness of the algal assembly, though we estimated that variation between the systems leads to higher variability.

Material & Methods

Experimental setup

Answering the question, if light or discharge have greater influence on algal community composition, an experiment was realized, in Cooperation with the École Polytechnique Fédérale de Lausanne (EPFL), at the "Wassercluster Lunz" (Lunz am See) in summer 2011. Simulating comparable artificial river sections with differentiating discharge conditions, 36 box-shaped flumes were separated in two different discharge regime treatments - a stochastic (S) and a constant (C) regime. The experiment consisted of 18 flumes per discharge regime, made of Plexiglas; each flume was 3 m long, 0.1 m deep and 0.05 m wide. A construction chain of a header tank (2 m long, 1 m wide, and 2.15 m deep), 2 pipes (PVC-U) and 2 smaller tanks linked the water flow from the lake to the flume panels (Picture 1).

Picture 1: Experimental setup. From right to left: header tank (A) linked by two pipes (B) with the white smaller tanks (C) and then with flume panels (D)

To keep water temperature relatively stable (10.5°C – 13.9°C) and to minimize variability in community composition, we pumped lake water from 7 m depth into the header tank. From the header tank, water entered the two pipes (one for each flow treatment, 3 m long) passing a propeller flow meter, measuring flow velocity continuously, and a ball valve before next flowing in the two smaller tanks (each 0.995 m long, 0.5 m wide and 0.7 m deep). Within the smaller tanks a vertical and a horizontal septum reduced flow velocity to continuously supply flumes with smooth water flow. Unglazed ceramic tiles covered the bottom of the flumes as substrate for biofilm growth. Flumes were divided in two longitudinally sections: an experimental part (1.75 m) and a substitutional part (located downstream the experimental section, to replace sampled tiles and to avoid lag phase induced differences). To sustain the water level in the flumes and to uniform flow, three nets were placed in the flumes; one at the flume inlet, one at 1.75 m downstream (dividing the sections) and one at the outflow. In addition to enhance friction effects sand paper was applied with glue to the last tile (Figure 1). To examine the influences of light availability, six different light filters covered the flumes randomly, leading to varying degrees of transmission.

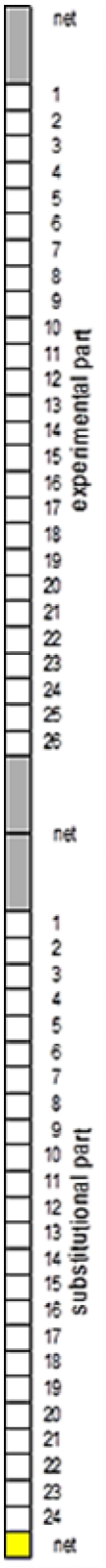


Figure 1: Flume structure. Grey tiles were not used and the yellow one represents the sandpaper.

Benthic biofilms were grown from the raw lake water over 5 weeks on ceramic tiles (22.66 cm²).

Discharge treatments

The discharge sequence of a stream is characterized by diurnal and seasonal changes, due to precipitation, snow melting, drought seasons and catchment morphology. Simulating a natural discharge means to follow a sequence of increasing-, flood, recession- and low water phases, whereas the dimensions and the frequency vary with latitude, altitude, catchment area and other stream characteristics. Reproducing the behaviour of stream flow, our colleagues from the EPFL, Switzerland, generated a stochastic model (Ceola et al., 2013). Briefly, a probability distribution function was adjusted and adapted to Oberer Seebach, the inlet to Lunzer Untersee. To reflect the typical characteristics of perennial pre-alpine streams, a time-varying discharge sequence was selected and a Monte Carlo realization was implemented to reflect the dynamics. The model was then downscaled to the flume size (Ceola et al., 2013). Two different discharge treatments, a stochastic treatment (which represents the temporal variation) and a constant treatment were performed. The regulation of flow variation within the experiment was done with a computer-controlled electric ball valve (situated in the pipe) using a LabVIEW™ (National Instruments) software in the stochastic treatment and in the constant one a manual ball valve took over this task, additionally a flow meter per pipe recorded the flow velocity every hour. The constant treatment always received the same water amount (equal the average of the stochastic regime) 0.21 L s^{-1}, whereas the stochastic variation ranges from 0.12 L s^{-1} to 0.51 L s^{-1}, leading to flow velocities between 12 and 52 cm s^{-1} (Figure 2).

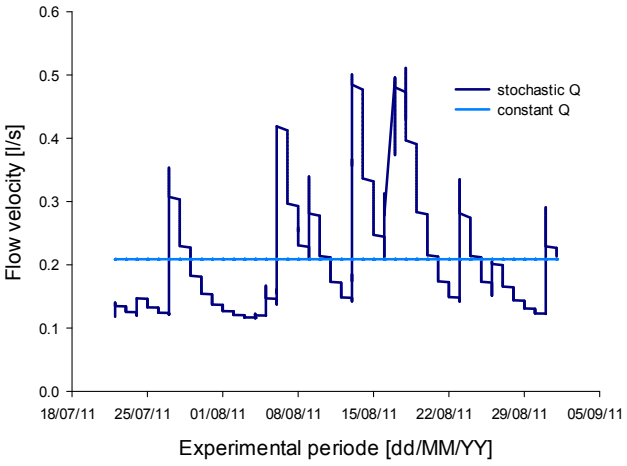


Figure 2: Discharge (Q) sequence

Light treatments

Six colour correcting Neutral Density screens foils (Table 1) were used to yield different light intensities. The different light conditions created a sequence of 100%, 77%, 55%, 32%, 15% and 8% light transmission. Creating this sequence background irradiation and irradiation beyond the filters were measured with a LiCor quantum sensor [µE m^{-2} s^{-1}] and percentage of transmission was calculated. Each flume was

covered with one lighting filter so that triplicate light treatments were achieved per discharge treatment. The series of the filter distribution was randomly selected. Flumes with 100% transmission, exposed to natural light served as control.

Radiation data over the whole experimental period were provided by the ZAMG (Zentralanstalt für Meterologie und Geodynamik).

Flume number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Light treatment [%]	100	15	77	8	32	100	15	77	15	32	55	8	77	100	55	55	8	32
Filter number	226	211	298	299	210	226	211	298	211	210	209	299	298	226	209	209	299	210

Table 1: Random distribution of the light filters for both flow panels

Experimental procedure

We monitored on a daily basis water temperature, pH, benthic chlorophyll a and in the initial phase (July 22nd to August 30th) one tile per flume was removed (replaced by uncolonized tiles) from the substitutional flume section, in intervals of 7 (at the beginning) to 2 days at end of the initial phase. These tiles were processed to get an idea of biomass accrual based on chlorophyll a (chl *a*) and ash-free dry-mass (AFDM) (Ceola et al., 2013). In the experimental phase (t_0=September 1st), in intervals of 4 days three tiles were removed from the experimental part of the flume and replaced by tiles from the substitutional part. To avoid source and time-induced gradients, the same distance between sampling sites and the same daytime (over the whole sampling period) were necessary.

Biofilm of each tile was scraped off with sterile razor blades and rinsed with filtrated water. The suspension (~20 ml) was vortexed and sonicated (10% amplitude, for about 1 minute). Afterwards 5 ml were fixed with 3.6% Formaldehyde for further diversity identification. The other 15 ml were used to measure AFDM, chl *a* and to freeze material for additional analyses in the future. Two fractions (à 3 ml) of the suspension were then filtered through glasfiber filters (Whatman™ GFC 1.2 µm) one for AFDM and one for chl *a*. AFDM samples were dried in an oven at 70°C (24h) and then rested in a desiccator for another 24 h before weighing. Afterwards the filter was muffled at 450°C for 4 h in a furnace and mass determined. The total organic matter or AFDM of the biofilm [mg/cm²] was calculated as:

$$AFDM = ((W_a - W_{ash}) * ratio_{OM}) / A_{tile}$$

W_a [mg] is the dry mass (filter plus dried biomass), W_{ash} [mg] is the ash mass (filter plus ashed biomass), $ratio_{OM}$ is the ratio between the total suspension volume (20 ml) and the filtrated volume (3 ml), and A_{tile} [cm²] is the area of the tile. For chl *a* analyses the filter was folded, wrapped in aluminium foil and frozen (-18°C) overnight. Filters were

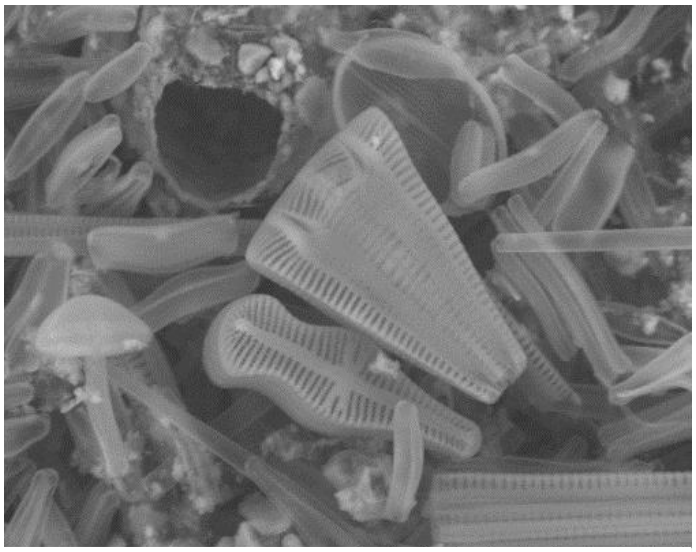
then transferred into falcon tubes with 4 ml of acetone, mechanically crushed and extracted for 24 h in the fridge (4°C). Before measuring the chl *a* the suspension was shaken and filtered (GFC filter). The absorbance at 665 nm (E_{665}) and 750 nm (E_{750}) was then measured with spectrophotometer (Shimadzu RF-5301 PC). The concentration of chl *a* [µg cm^{-2}] was calculated by the following equation

$$chl\ a = 11.41\ [((E_{665}-E_{750})(V*ratio_{chl\ a}))/A_{tile}]$$

V represents the used acetone volume [ml] and the $ratio_{chl\ a}$ is the ratio between total suspension volume and used suspension volume; A_{tile} [cm^2] is the area of the tile.

Autotrophic Community Composition [Individuals cm^{-2}]

Diatoms (Bacillariophyceae) on filters (from AFDM) were studied (Picture 2) for taxonomy using electron microscopy (Hitachi TM) and identified according to Hustedt (1930), Krammer and Lange-Berthalod (1986, 1988, 1991a,b). The quantitative measurements and classification of the algal cells (Gutowski et al., 2009; Linne von Berg et al., 2012) were done, one tile per flume, at a magnification of 400x and 1000x with an inverted microscope (Nikon) for t_0.



Picture 2: Electron microscope picture of *Gomphonema truncatum var. capitatum* (Ehrenberg)

Each sample, related to a specific aliquot of the scraped tile (5.8 cm^2), was homogenized and the equivalent amount referring to 1 cm^2 was removed and diluted with water. The dilution was individually chosen for each sample, because cell abundance differentiated and ranged between 1:50 to 1:300. All cells were identified to genus level and counted in 2 defined cross sections (Tümpling et al., 1999) in 2 to 5 Utermöhl chambers (Utermöhl, 1958) corresponding to 0.6 - 0.98 mm^2 of tile area.

To count an appropriate amount of algae species accumulation curves were constructed and at least 500 cells (per counting chamber) were classified. Then the counted individuals were extrapolated to the comparative area of 1 cm². For further analyses all specialized planktonic species were excluded (e.g. Pediastrum sp., Ceratium sp, Meridion circulare).

Biovolume [mm³ cm^{-2}]

Size measurements were done for all algal groups, except diatoms, with an ocular micrometre under the inverted microscope. Diatoms were assigned to 4 size classes and the exact size of the common diatom genera was determined from TM microscopy pictures and ®imageJ. At least 15 cells per unit were quantified and the rare taxa (less than 15 measurements) were then compared or values were directly used from literature (Tümpling et al., 1999; Hillebrand et al., 1999). The average of the measured dimensions was applied to appropriate volumetric formulas, which were also based on geometric shapes used in literature (Hillebrand et al., 1999). The contribution of each fraction was calculated by multiplying with corresponding algal cell density [Individuals cm^{-2}]. In case of diatoms the differentiation of size classes leads to varying cell distributions of volume per genera.

Species accumulation curves

Species accumulation curves (SAC) compare the diversity properties of community data sets using the number of genera for a certain number of samplings (sample based) or for a certain number of counted individuals (effort based). Random permutations of the abundance data, without replacements, lead to mean SAC and its standard deviation (Gotelli & Colwell 2001) using the vegan package in R. This was done with Gabriel Singer.

Diversity, Similarity and Evenness

To compare the diversity of each community Shannon–Weaver and Gini–Simpson indices were calculated and transformed, as these are entropies, to Shannon numbers equivalents and Simpson numbers equivalents. This gives us the ability of weighing species by their frequency without overestimating rare or common species (Jost, 2006). In case of the Shannon indices (HS) the formula was transformed to the exponential of the Shannon entropy $HS=exp(-\sum p_i * log\ p_i)$, where p_i is the relative abundance of species i (Jost, 2006). For the Simpson numbers equivalents the formula equals: $D = 1/[((\Sigma\ n_i\ (n_i - 1)))/N\ (N-1)]$; where n_i gives the number of individuals belonging to i species and N is the total number of individuals (Jost, 2006).

Pielou Evenness was calculated by the formula $J=HS/H_{max}$, HS refers to the Shannon index and H_{max} to maximum possible diversity. The evenness should be indicative of dominance structures within the biofilm community distribution. The produced results range between 0 and 1, where 1 displays a totally even species distribution.

Comparing the similarity between communities, a matrix based on presence/absence data was calculated using the Sørensen index (Sørensen, 1948). $QS=2c/(a+b)$, c is the number of shared genera between two communities, and a + b are the total number of genera found in the communities.

The Jaccard Similarity (Is_j) was applied as another similarity coefficient. $Is_j = S_{I+II}/S_I+S_{II}$, the number of genera that occurred in both sites (S_{I+II}) was divided by the total number of genera in both sites (S_I+S_{II}).

To explore similarity not only by presence/absence data, also the Horn and the Morisita-Horn, probabilistic measures, based on relative abundance data of each flume, were used to generate similarity matrices (Horn, 1966).

Results of all similarity tables are ranging between 0 and 1, 1 is representing absolute similarity.

Statistical Analyses

In all statistical analyses, measurements and graphs flume number 8 of the stochastic flow regime was excluded, due to horrific outlying data. So in the stochastic treatment at 77% light transmission only two flumes remained (n=2) and statistical analyses couldn't be performed in consequence of the small sampling number.

Testing for variances of flow and light a Kruskal-Wallis one-way analysis of variance (ANOVA) and a two-way ANOVA were performed on Shannon numbers equivalents, chl *a*, AFDM, biovolume, abundance and genus data. Biovolume and abundance data failed the Shapiro-Wilk normality test and therefore a one-way analysis of variances on ranks was progressed. The Holm-Sidak method was applied to ANOVA results producing pairwise multiple comparisons for factor light and flow. Comparing biovolume with chl *a* and Shannon numbers equivalents Pearson correlations were evaluated. To determine the differences in mean colonial size, which were effected by light and discharge, paired t-tests or if the normality failed Wilcoxon Rank Test were computed.

Illustrating the distance of flumes according to their community composition, a non-metric multidimensional scaling (NMDS) ordination was conducted by Kruskal's method, based on Bray-Curtis similarity index. Kruskal's stress formula produces stress

values between 0 and 1. When the ordination map perfectly reproduces, the data stress is zero, so the smaller the stress, the better the representation. Significances were tested by constrained analysis of principal coordinates and permutational analysis of variance using distance matrices (MANOVA). A canonical analysis of principal coordinates (CAP) was conducted on mean flume data (for abundance and for biovolume), a strictly linear and metric analysis, should further help to test effects of flow and light on the community composition. CAP (Anderson and Willis, 2003) used flow and light as additive constraints and the analysis run on semi-metric Bray-Curtis dissimilarity matrix (transformed into Euclidian distances), done by vegan package.

All analyses were performed with the software packages R 2.12.1. and Sigma Plot 12.0.

Results

Within the experimental period the photosynthetic active radiation ranged between 131 µE m^{-2} s^{-1} to 1753 µE m^{-2} s^{-1}, with an average direct sunshine of 5 h d^{-1}, a maximum duration of 11 h d^{-1} and on 4 days of the period no direct global irradiation was measured (ZAMG).

Biomass and Abundance

Comparing the polynomial curve shapes within all comparisons (Figure 3 and Figure 4), constant flow treatments yielded overall higher values of chl *a*, AFDM, total abundance and total biovolume excluding the flumes with 8% light transmission; these conditions led to a reverse trend in numbers of abundance and biovolume. Intermediate light conditions showed more or less the highest data of chl *a*, AFDM, abundance and biovolume, but aberrations were also greatest.

One-way ANOVA of all comparisons indicated significant differences among the treatments for chl *a* (f=3.524, p=0.005) and AFDM (f=7.996, p=<0.001); multiple comparison point out that only both light treatments of 8% transmission showed significant variation. Chl *a* showed only differences between 8% and constant 15% treatment (C8 vs. C15, t=4.491, p=0.011; S8 vs. C15, t=4.425, p=0.013), whereas comparisons between AFDM produced a divergence of light treatment 8% with all other treatments except of C8 vs. S8, C15, S15, S55 and S32, and S8 vs. C8, S15 and S55. (C=constant, S=stochastic; 8-100 refers to light transmission in %). One-way ANOVA on ranks of the median values indicated no statistically significant difference (abundance p=0.066; biovolume p=0.056). Two-way ANOVA showed a significant difference for all light groups (chl *a* f=5.723 p=0.001; AFDM f=15.09 p=<0.001;

abundance f=4.122 p=0.008; biovolume f=3.66 p=0.014), but no significant interaction between light and flow was detected. A multiple comparison of light groups isolated only light treatment 8 from 32 over all data properly. Chl *a* and AFDM analysis also differentiated flow treatments by significant statistical levels (chl *a* t=2.66 p=0.014; AFDM t=3.153 p=0.004).

Highest biovolume (Figure 4) were found in the light treatment with 32% light transmission, whereas in the stochastic treatment this condition also yielded highest chl *a*. Overall highest chl *a* was found in the constant treatment at 15% light transmission (Figure 3).

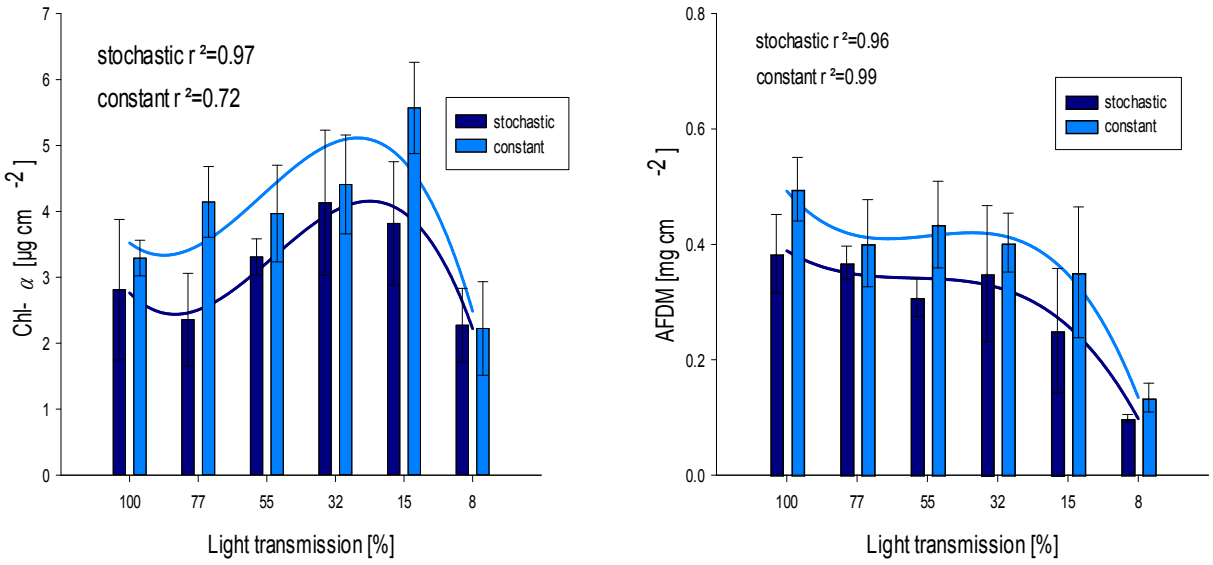


Figure 4: Comparison of chl *a* (left panel) and AFDM (right panel) values between the treatments

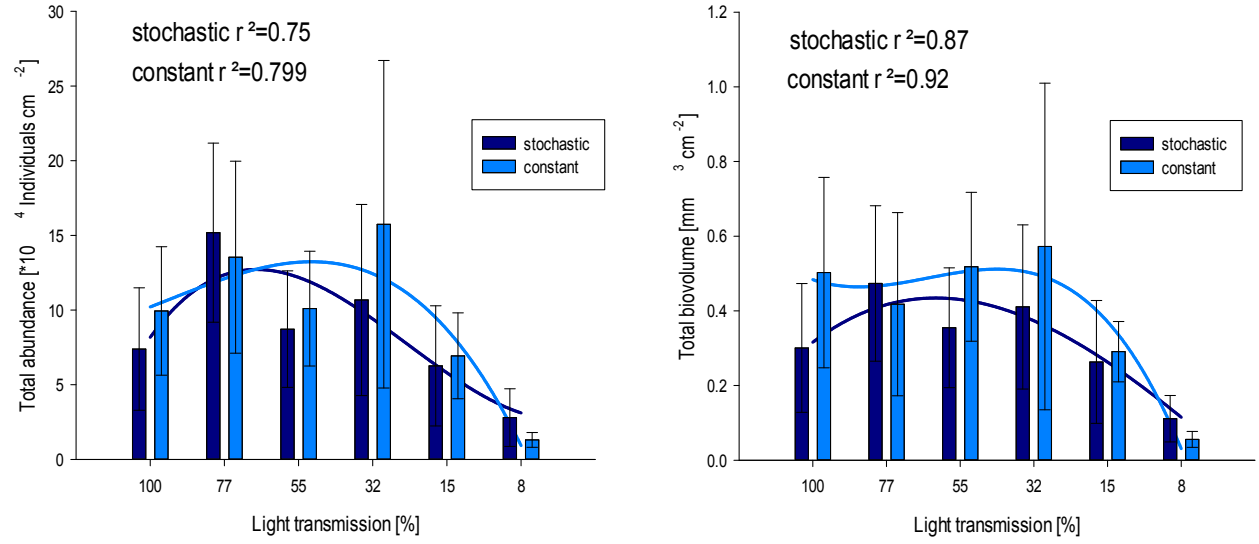


Figure 3: Total abundance (left panel) and total biovolume (right panel) in comparison with light transmission and flow treatment (stochastic vs. constant)

Correlation between Chl$_a$ and Biovolume

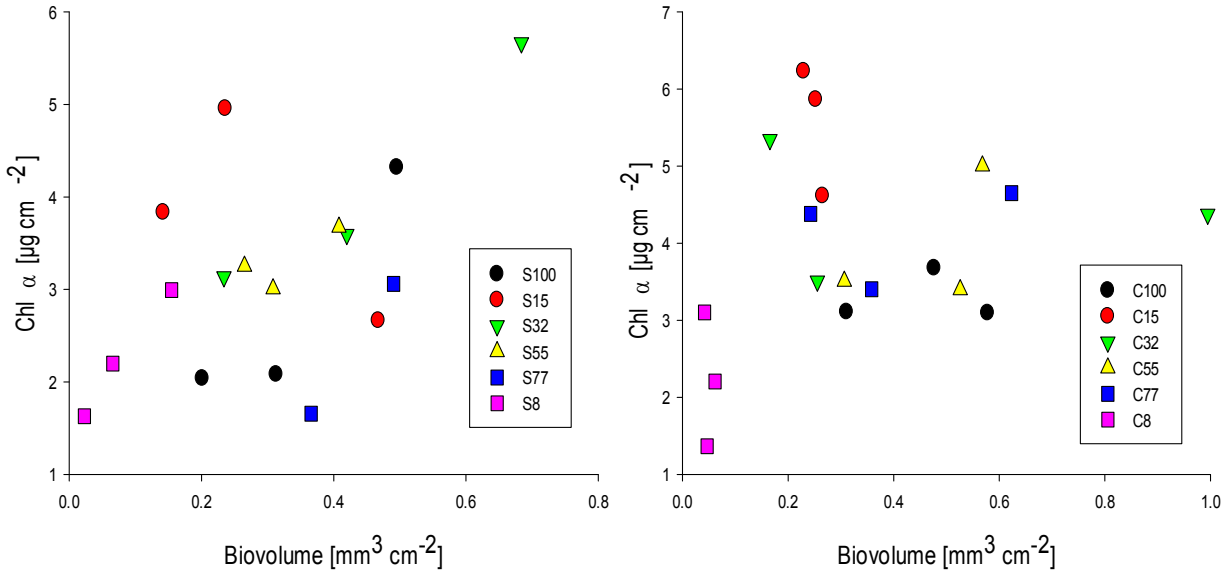


Figure 5: represents the correlation between chl *a* and biovolume. Each treatment is displayed by 3 flumes. (S=stochastic, C=constant; 8 to 100 refers to the light transmission [%] within the flumes)

Pearson Product Moment Correlations produced no significant relationships between any pair of variables in the correlation of biovolume vs. chl *a*. Although variation within the stochastic flow regime at light condition of 8% showed that increasing biovolume values led to higher chl *a* contents. A slight correlation could also be discovered in the other light treatments and chl *a* and biovolume seem related (Figure 5). Environmental conditions confined the variation, and the content of chl *a* seemed to be restricted, probably due to photosynthetic adaptation and inhibition of photosynthesis (damaged accessory pigments).

Mean colonial dimensions

Paired t-tests or if normality failed Wilcoxon Signed Rank Tests were performed, within each treatment, effected by the same light conditions and differentiate only in flow. Only light treatments of 55% within the class of Bacillariophyceae showed a significant variation (t=3.255 p=0.031) (Figure 6).

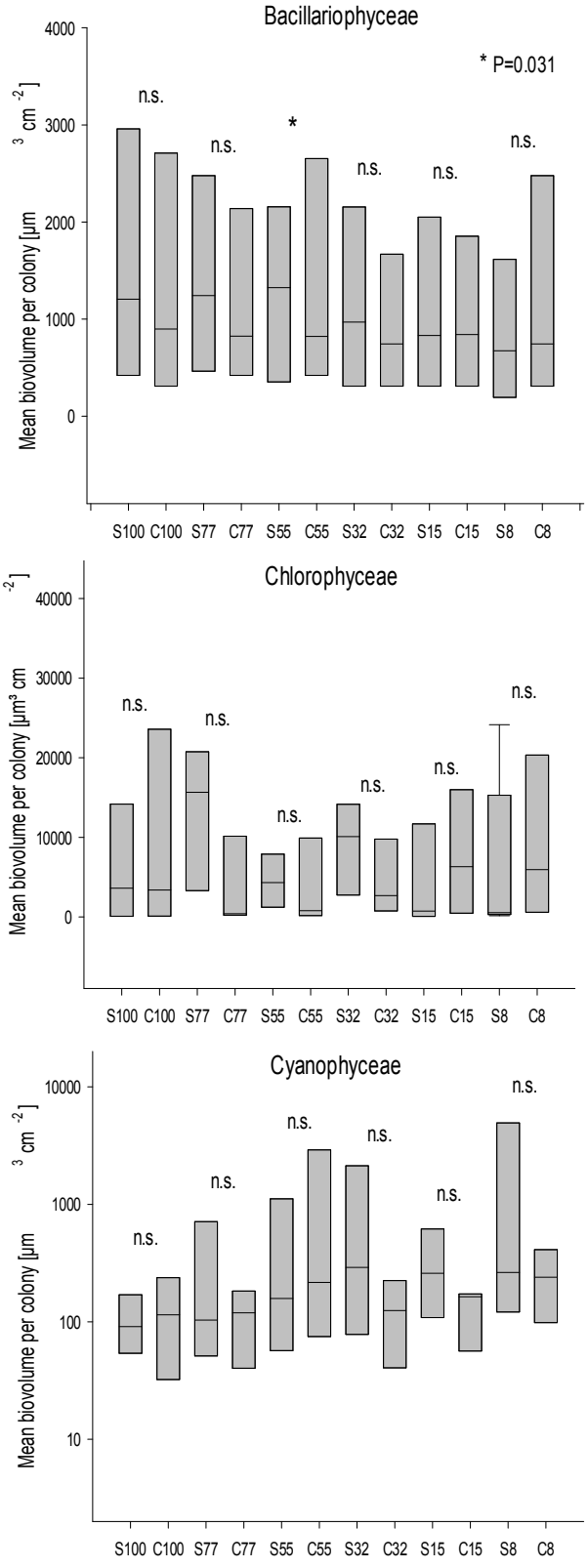


Figure 6: Mean colonial size of the algal classes Bacillariophyceae, Chlorophyceae and Cyanophyceae per treatment [C=constant, S=stochastic; 8 to 100 refer to light conditions [%]]

Quality of analyses

Species accumulation curves illustrate the quality of enumeration (counted individuals) and indicate saturation when a plateau is reached. Sample-based SAC displayed earlier saturations than effort-based did. Saturation seemed to be reached in flumes of constant flow conditions at 100%, 32% and 8% light transmission, whereas in the stochastic treatment only at 15% light a plateau was reached (Figure 7).

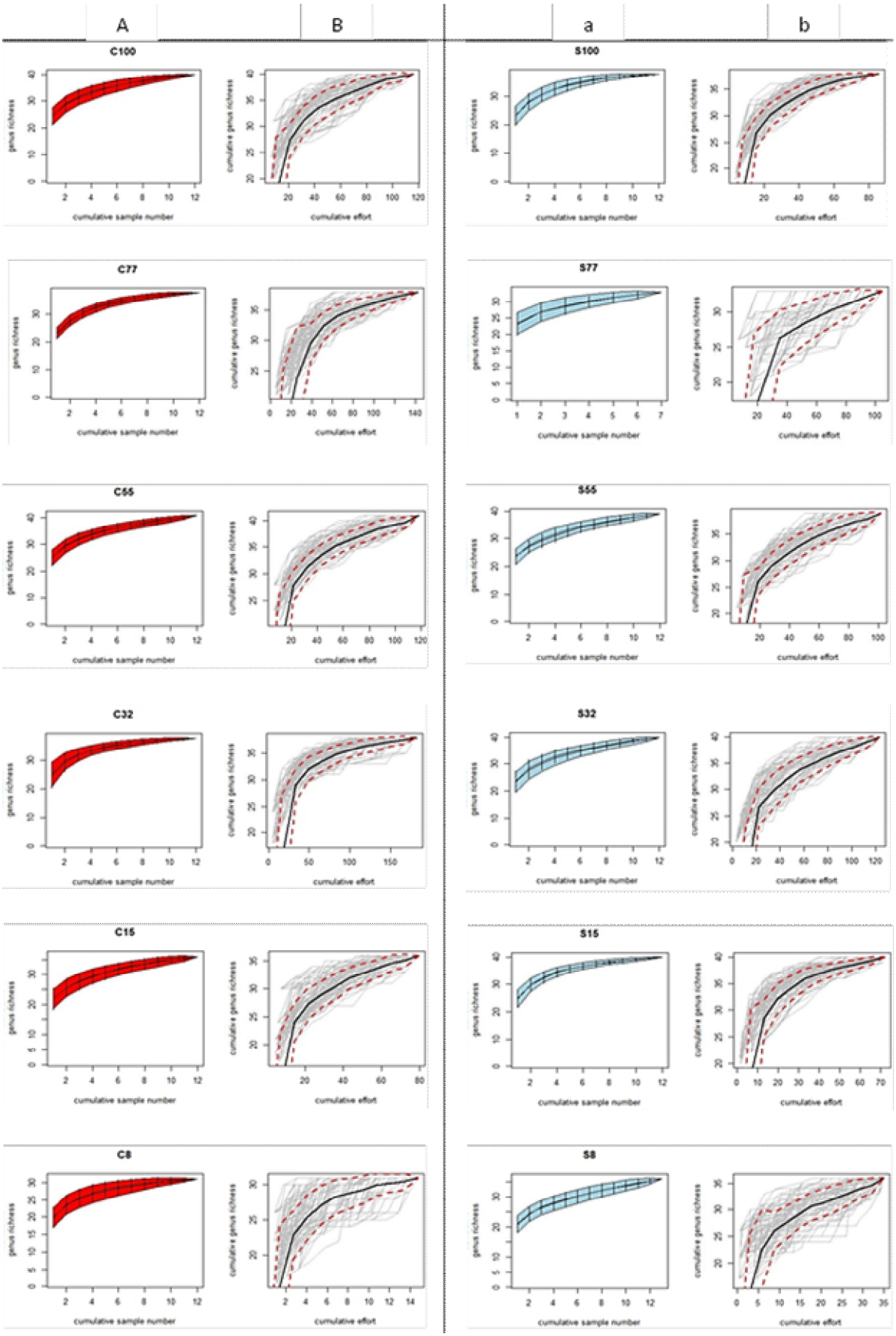


Figure 7: A, a: Sample based curve shape with 12 samples (counting chambers) per treatment, except for the stochastic treatment (a) of 77% (see methods). B, b: The cumulative effort, counting's per chamber [10^4 Individuals cm^{-2}] were compared and permutated. The black line indicates the mean and red dotted ones the standard deviation. (Side A and B = constant treatment, Side a and b = stochastic treatment)

Diversity and Evenness

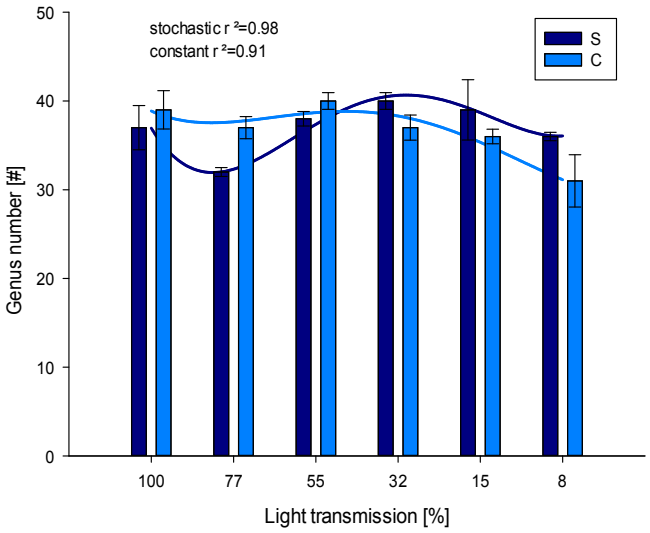


Figure 8: Counted genus number per light treatment. Colours refer to flow conditions [S=stochastic, C=constant]

The genus numbers at the end of the quantitative analysis for each flume illustrated a different curve shape than produced by abundance, biovolume, chl *a* and AFDM data. Constant flow treatment showed no more overall higher magnitude, just at higher light transmissions (100%, 77% and 55%) greater genus numbers are conducted (Figure 8). Statistical analysis point out differences in light conditions (two-way ANOVA, f=4.211 p=0.007), but neither for flow nor for interactions between light and flow.

Diversity Indices

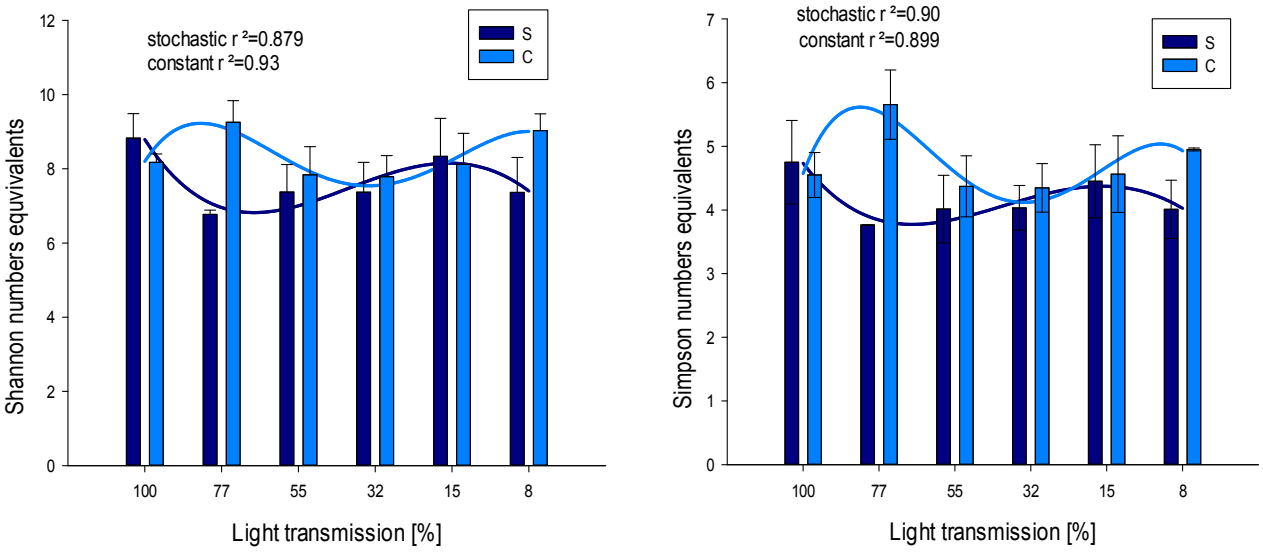


Figure 9: Shannon numbers equivalents and Simpson numbers equivalents with polynomial regressions [S=stochastic, C=constant]

At diversity level interactions of light and flow seemed to be independent and no obvious effects between treatments of light or flow were detectable (Figure 9). Highest diversities were detectable in constant flow treatments of 77%, followed by treatment of 8% light. Stochastic flow led to different patterns; the treatment of 77% light displayed lowest diversity whereas highest diversity was found in the 100% light treatments.

Correlation between Shannon diversity and Biovolume

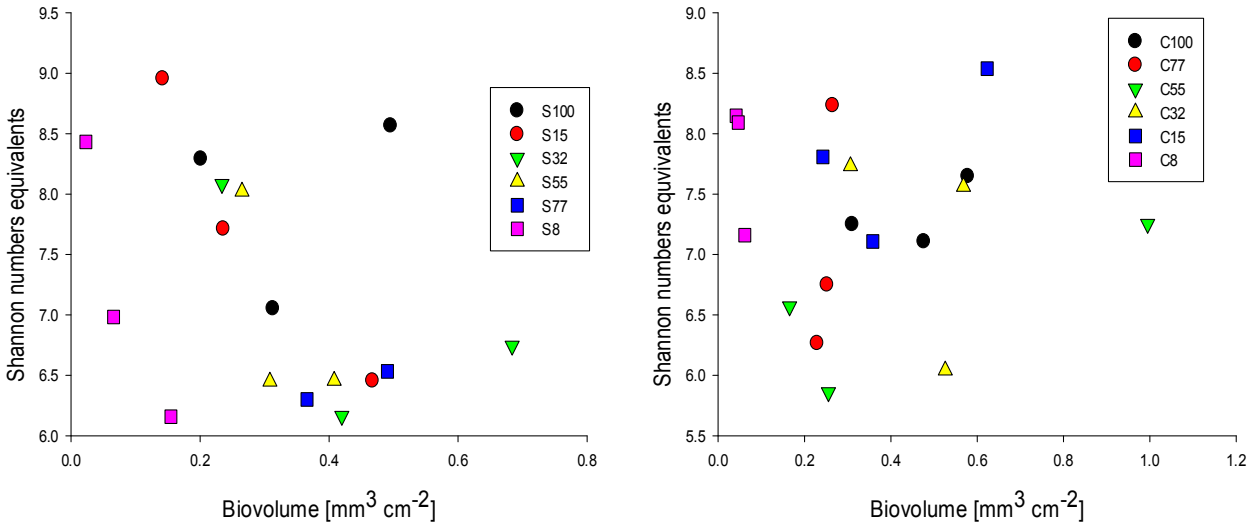


Figure 10: Correlation between biovolume and diversity [S=stochastic, C=constant, 8 t0 100 refers to light conditions in %]

Pearson correlation of biovolume vs. diversity showed no significant variance within similar light conditions nor between light treatments (Figure 10). Within the stochastic treatment, at least for treatments of 8%, 15%, 32% and 55% light, a negative correlation between diversity and biovolume is visible, reflected by the trend that in flumes with higher biomass diversity was low. In the constant treatment, it seemed that there is not such a relationship between biovolume and diversity. Highest diversity could be found in both flow treatments at 15% light transmission.

Evenness

Pielou evenness indicated more or less equal relations of dominance across all flumes with values ranging from 0.3 to 0.35. Only in the treatment with the lowest light conditions (8%) evenness showed a slight trend towards a more competitive and dominant community (0.38 and 0.41).

Similarity

Sorensen	S100	S77	S55	S32	S15	S8	C100	C77	C55	C32	C15	C8
S100		0.841	0.827	0.909	0.947	0.849	0.921	0.865	0.857	0.865	0.904	0.853
S77			0.886	0.861	0.845	0.765	0.873	0.841	0.833	0.841	0.853	0.857
S55				0.821	0.831	0.784	0.857	0.800	0.846	0.800	0.865	0.812
S32					0.937	0.816	0.911	0.909	0.875	0.883	0.895	0.845
S15						0.880	0.949	0.895	0.886	0.868	0.907	0.857
S8							0.827	0.795	0.789	0.795	0.833	0.806
C100								0.868	0.911	0.868	0.880	0.829
C77									0.831	0.892	0.904	0.882
C55										0.857	0.842	0.845
C32											0.877	0.912
C15												0.896
C8												

Jaccard	S100	S77	S55	S32	S15	S8	C100	C77	C55	C32	C15	C8
S100		0.725	0.705	0.833	0.900	0.738	0.854	0.762	0.750	0.762	0.825	0.744
S77			0.795	0.756	0.732	0.619	0.775	0.725	0.714	0.725	0.744	0.750
S55				0.696	0.711	0.644	0.750	0.667	0.733	0.667	0.762	0.683
S32					0.881	0.689	0.837	0.833	0.778	0.791	0.810	0.732
S15						0.786	0.902	0.810	0.795	0.767	0.829	0.750
S8							0.705	0.659	0.652	0.659	0.714	0.675
C100								0.767	0.837	0.767	0.786	0.707
C77									0.711	0.805	0.825	0.789
C55										0.750	0.727	0.732
C32											0.780	0.838
C15												0.811
C8												

Table 2: Jaccard and Sørensen presence/absence based similarity in percent. S and C represent the stochastic and constant flow treatments and numbers 8 to 100 refer to the sequence of light transmission in %.

Similarity displayed in both, Jaccard and Sørensen (Table 2), matrices nearly the same patterns. Within the stochastic flow regime flumes with 15% light transmission showed the highest similarity with stochastic flumes of 100% and 32%. Communities acting as controls (100% light) demonstrated as well a high resemblance, whereas those communities affected by 8% light transmission showed the greatest dissimilarity. It should also be noticed here that stochastic flow affected by moderate (55%) and low (8%) light conditions depart from all other communities.

Horn	S100	S77	S55	S32	S15	S8	C100	C77	C55	C32	C15	C8
S100		0.973	0.975	0.972	0.975	0.962	0.988	0.927	0.978	0.975	0.974	0.972
S77			0.987	0.977	0.963	0.967	0.982	0.944	0.977	0.982	0.980	0.965
S55				0.987	0.976	0.967	0.982	0.945	0.984	0.987	0.990	0.957
S32					0.980	0.955	0.978	0.953	0.979	0.990	0.986	0.946
S15						0.968	0.971	0.924	0.976	0.977	0.975	0.946
S8							0.963	0.914	0.969	0.962	0.966	0.959
C100								0.940	0.982	0.980	0.979	0.968
C77									0.925	0.952	0.958	0.920
C55										0.983	0.979	0.968
C32											0.988	0.962
C15												0.963
C8												

Horn-Morisita	S100	S77	S55	S32	S15	S8	C100	C77	C55	C32	C15	C8
S100		0.984	0.988	0.987	0.987	0.981	0.998	0.954	0.987	0.989	0.989	0.989
S77			0.994	0.989	0.983	0.994	0.987	0.942	0.986	0.988	0.984	0.984
S55				0.998	0.996	0.994	0.990	0.952	0.997	0.998	0.995	0.982
S32					0.996	0.990	0.989	0.952	0.996	0.998	0.994	0.975
S15						0.990	0.986	0.953	0.997	0.998	0.996	0.978
S8							0.982	0.945	0.991	0.992	0.992	0.985
C100								0.957	0.989	0.990	0.990	0.990
C77									0.953	0.960	0.967	0.960
C55										0.999	0.997	0.983
C32											0.998	0.983
C15												0.987
C8												

Table 3: Horn and Horn-Morisita similarity matrices. S and C represent the stochastic and constant flow treatments and numbers 8 to 100 refer to the sequence of light transmission in %.

Similarities based on relative abundances depicted a diverse pattern as it was pointed out by presence-/absence data, even if differences were, due to the fact that 1

represents total similarity, very low. Treatment C 77 displayed the lowest consistency to all other treatments. In the table using Horn's method treatments of 8% light transmission did not seem to have much in common with higher light treatments. Within moderate shaded light transmissions (55% to 15%) differences in flow regime were minor and within treatments of 100% a compatible similarity was present (Table 3).

Community structure

Proportion of algal classes

Quantification of individuals showed an identical distribution towards dominance of Bacillariophyceae (Diatoms). In contrast, our findings indicated that most Diatoms were small. Chlorophyceae, even if the number of counted units was small, their volume component of the assembly was significant. Indeed in some flumes, Cyanophytes captured an unneglectable part too. In treatment C77, Cyanophytes showed the highest appearance due to a counted colony of Merismopedia sp. Another conspicuous finding was that within the stochastic flow regime the lowest light conditions showed the highest percentage of other algal classes than Diatoms (Figure 11).

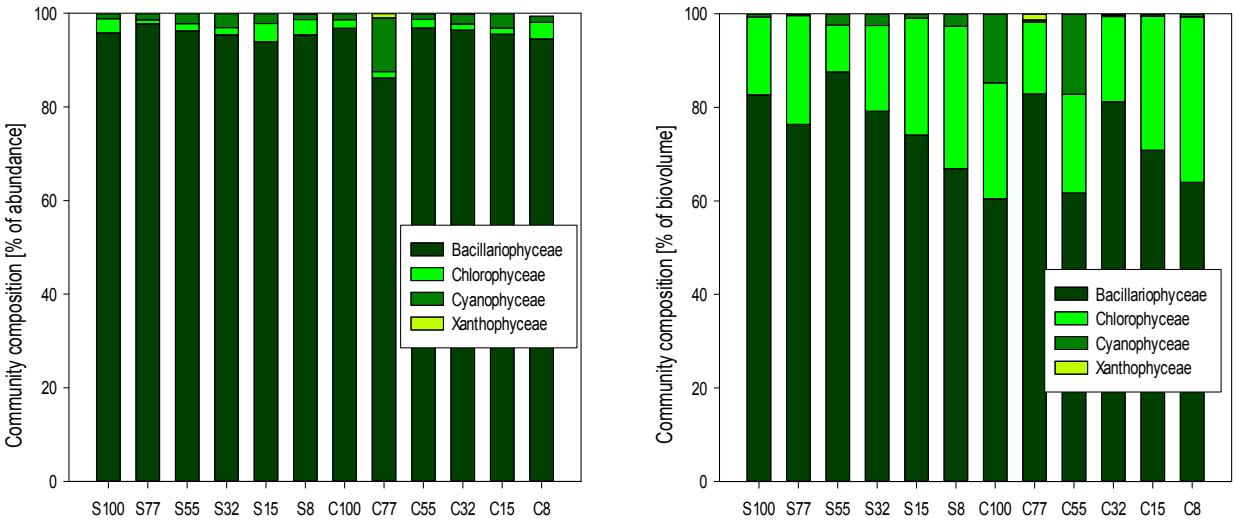


Figure 11: The percentage of each algal group within the community, producing a total of 100%, is shown for abundance (left panel) and for biovolume (right panel). (S=stochastic flow, C=constant flow; 8 to 100 refers to light conditions in %)

As Bacillariophyceae are dominating, some genera having a particular relevance for benthic biofilms in Lunz mentioned by Hustedt (1922) also appeared in our study. The algal genera are Achnanthes, Cocconeis, Cyclotella, Cymbella, Denticula, Diatoma, Diploneis, Fragilaria, Gomphonema, Navicula and Tabellaria these algae can dominate communities due to mass occurrences (Hustedt, 1922).

Individual cells

Data of abundance showed a clear dominance of the Bacillariophyta. The distribution of prostrate forms, comparing biovolumes displayed that a large share is still occupied by Bacillariophyta, but Chlorophytes had a sector in volume too (Figure 12).

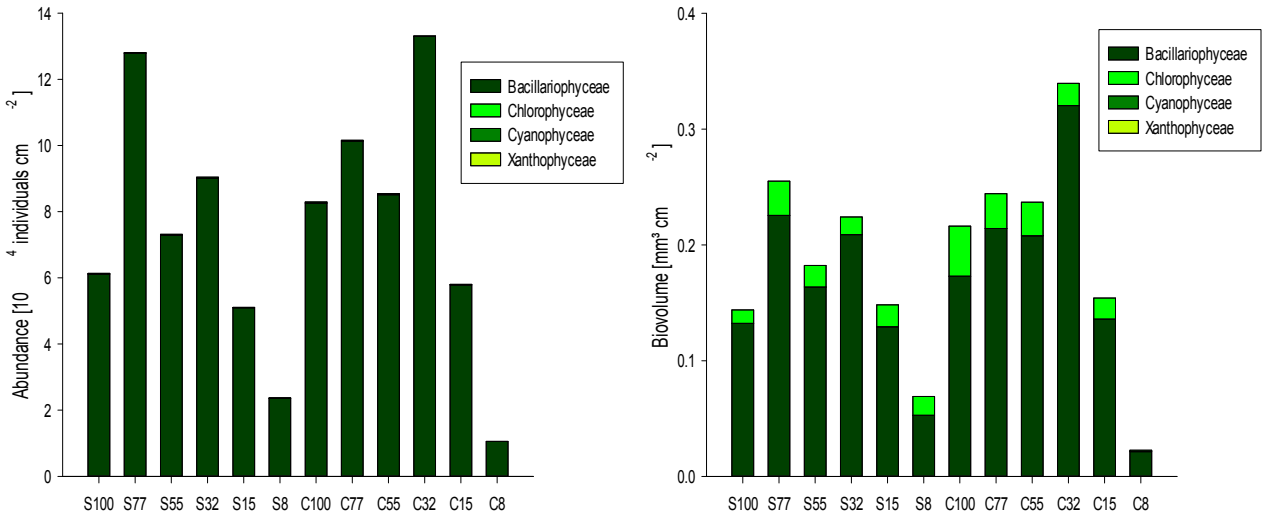


Figure 12: Unicellular living algae - A comparison of abundance (left) and biovolume (right) data [S=stochastic flow, C=constant flow; 8 to 100 refers to light conditions in %]

Colony-forming units

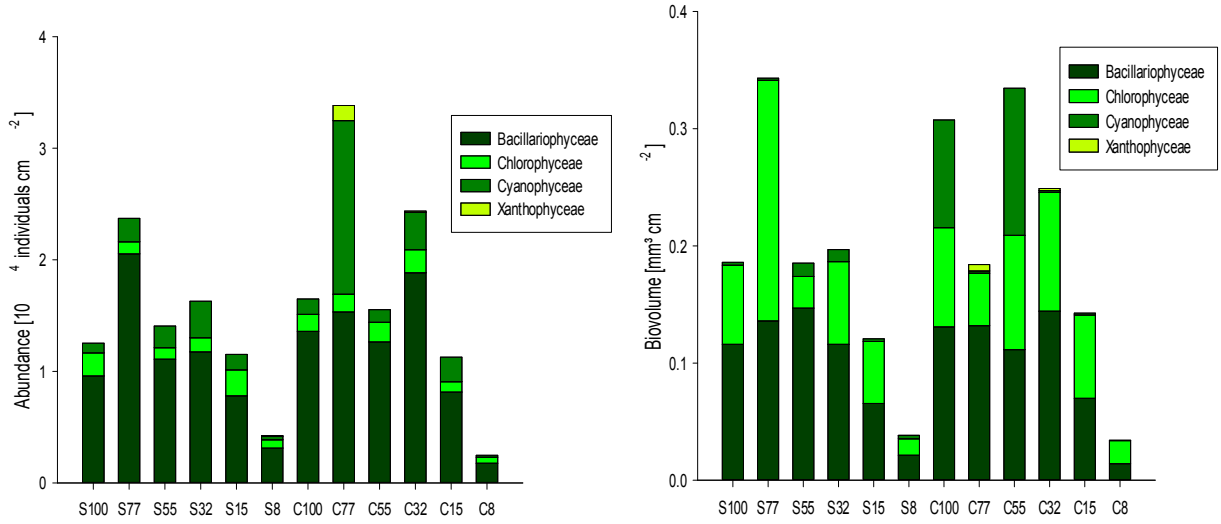


Figure 13: Colony forming algae – A comparison of abundance (left) and biovolume (right) data [S=stochastic flow, C=constant flow; 8 to 100 refers to light conditions in %]

Colony-forming cells provide a different view on the structure of the assemblage. Still diatoms (Bacillariophyceae) were dominant, except in some biovolume representing data (Figure 13). Figures illustrate that Cyanophyceae were more often colony-forming species and in some constant treatment they might even dominate the algal community. Chlorophytes demonstrated smaller counted numbers than Cyanophytes, but in case of biovolume some treatments were dominated by them.

Nonmetric dimensional scaling (NMDS) and canonical analysis of principal coordinates (CAP)

Abundance

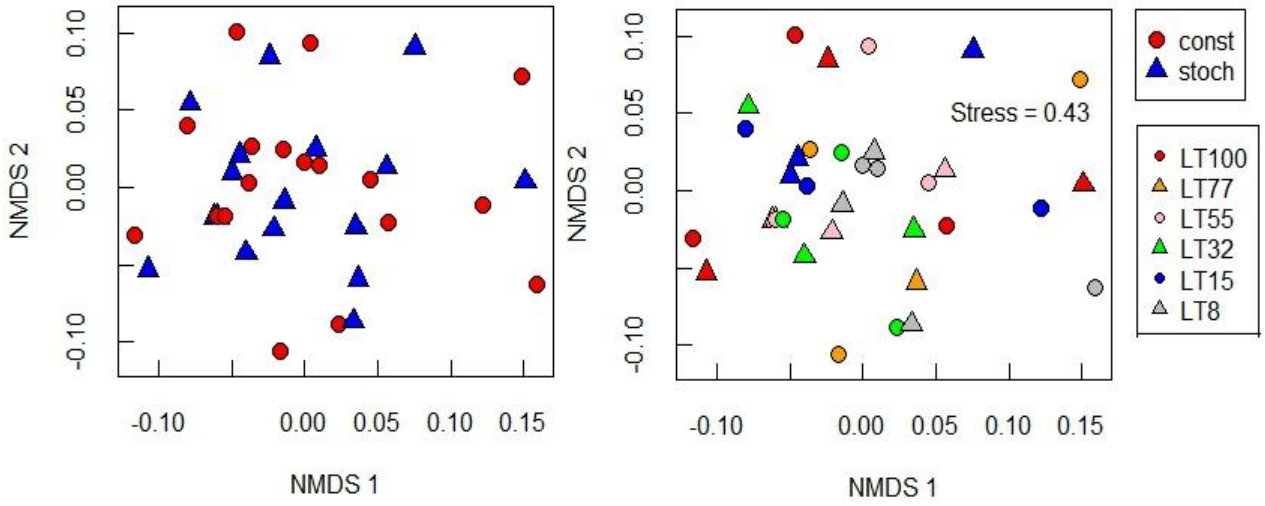


Figure 14: NMDS Ordination on abundance data of all flumes. The left and right part show the same ordination comparing flow (left part) and light-flow (right part) [const=constant, stoch=stochastic, LT=light treatment, 8 to 100 refers to light transmission in %]

Non-metric multidimensional scaling on abundance data (Figure 14) of all flumes could not separate flow treatments nor was a light-driven seperation of the treatments obvious. However, light seems to have more effect. High variances within the light treatments, between the flumes, were detectable (Figure 14: right part). Kruskal's standardized stress value indicates that the global minimum was not reached yet and optimum ordination is not represented. Permutational analysis of variance using distance matrices on mean abundance data (3 flumes represent 1 light treatment) showed significant differences in light ($F=2.046$, $p=0.005$) and also in flow ($F=2.07$, $p=0.038$) conditions.

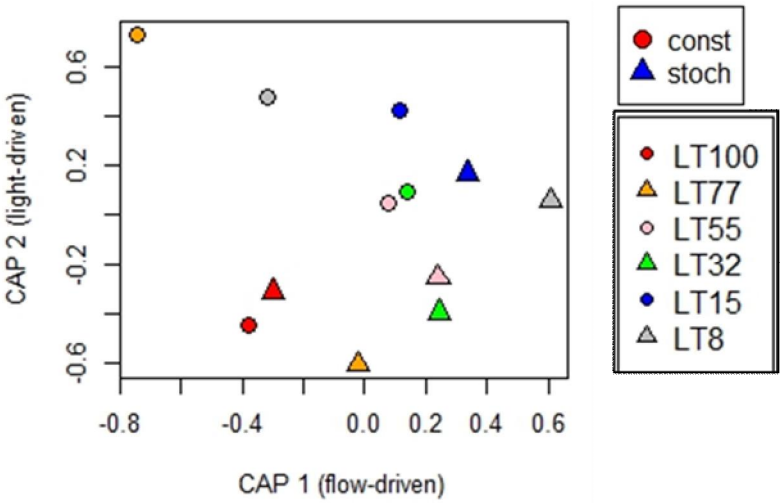


Figure 15: CAP (canonical analysis of principal coordinates) matrix on abundance data [const=constant, stoch=stochastic, LT=light treatment, 8 to 100 refers to light transmission in %]

Canonical analysis of principal coordinates (CAP) illustrated a slight diversification of constant and stochastic flow regimes (Figure 15). The only treatments dropping out of this trend were light treatments of 100%, where light and flow seemed to have no influence. The stochastic treatments indicated to be more affected by flow (except for 77% light treatment) and under constant conditions algae are more light-driven. In stochastic flow regimes at low light levels the community even seemed to be strongly driven by flow.

Biovolume

The constrained analysis of principal coordinates pointed out that light shows a significant variation (f=3.04, p= 0.0025) and permutational analysis of variance using distance matrices (MANOVA), even displayed a higher differentiation in light (F=1.97, p=0.001). But ordination matrix of biovolume data led to no significant fractionation of flow regimes. Leading to the assumption that biovolume is mainly influenced by light (Figure 16).

CAP (Figure 17) displayed that only in some constant treatments (100%, 55% and 8%) light played a major role. All other treatments (except the stochastic treatments of 100% and 77%) were effected by flow. But a few as S55, S32 and C77 were not driven by light and flow seemed to be neutral. Treatments of 15% light transmission showed high similarity and were most influenced by the flow regime.

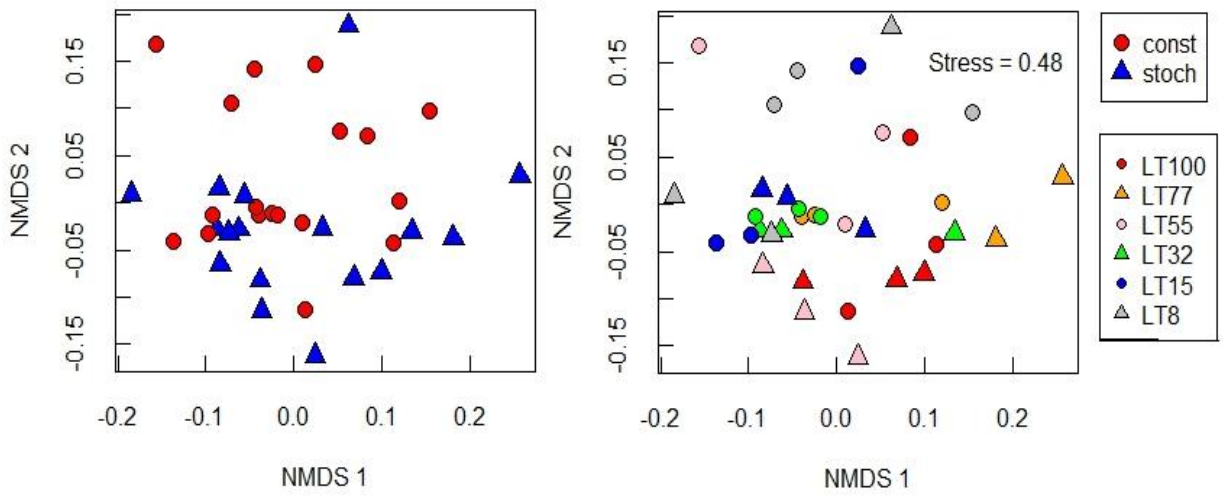


Figure 16: NMDS ordination on biovolume data of all flumes. The left and right part show the same ordination comparing flow (left part) and light-flow (right part) [const=constant, stoch=stochastic, LT=light treatment, 8 to 100 refers to light transmission in %]

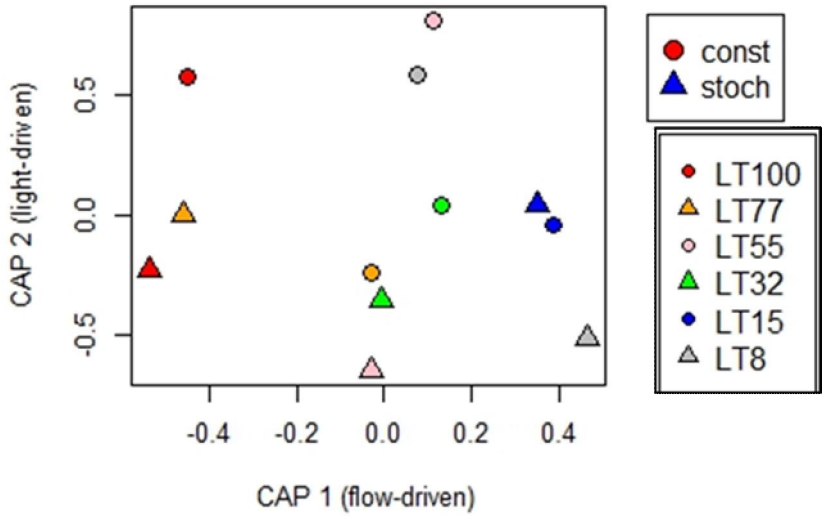


Figure 17: CAP (canonical analysis of principal coordinates) matrix on mean biovolume data [const=constant, stoch=stochastic, LT=light treatment, 8 to 100 refers to light transmission in %]

The dominant Genera

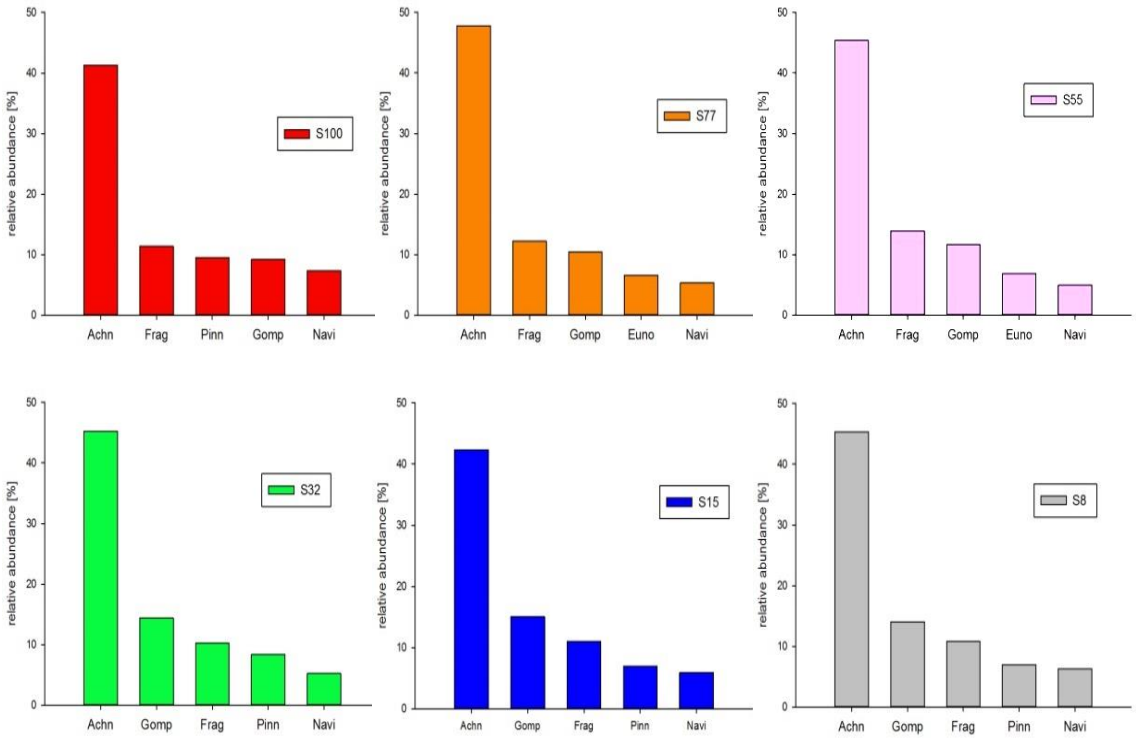


Figure 18: the 5 most abundant genera of each stochastic light treatment (S=stochastic, C=constant, 8 to 100 revers to light transmission in %) [Achn=Achnanthes sp., Chro=Chroococcopsis sp., Cosm=Cosmarium sp., Euno=Eunotia sp., Frag=Fragilaria sp., Gomp=Gomphonema sp., Meri=Merismopedia sp., Moug=Mougotia sp., Navi=Navicula sp., Pinn=Pinnularia sp., Spir=Spirogyra sp., Stau=Staurastrum sp., Tetr=Tetraspora sp., Ulot=Ulothrix sp., Zygn=Zygnema sp.]

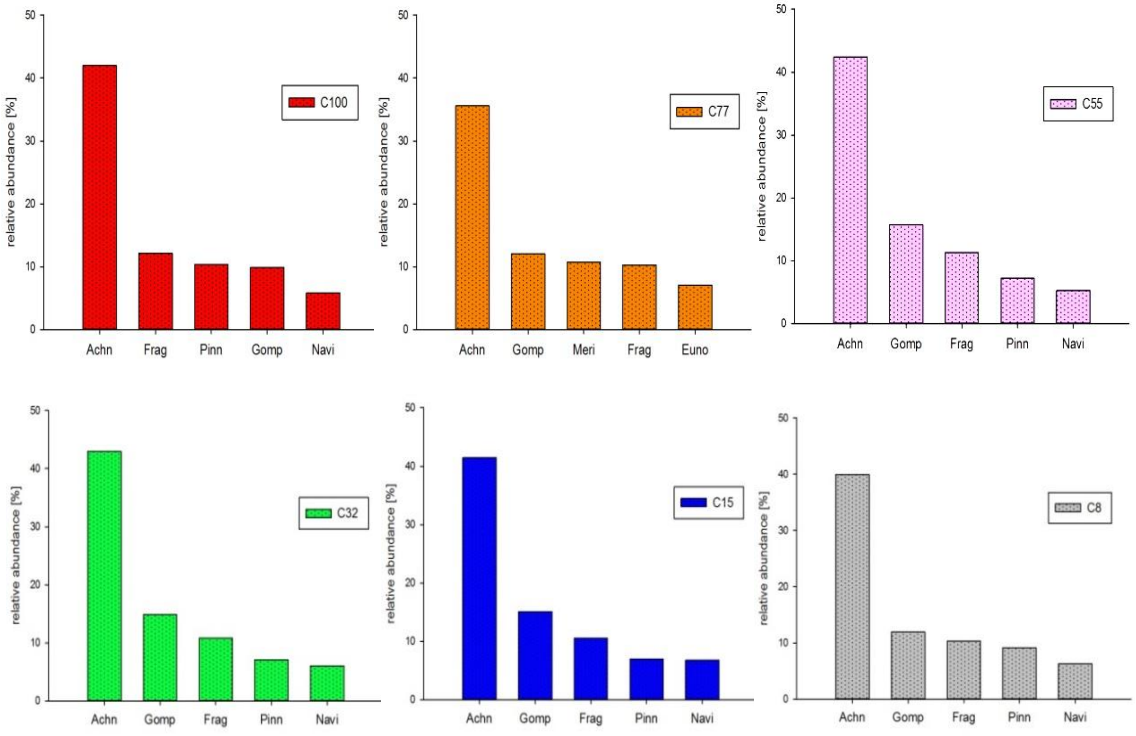


Figure 19: the 5 most abundant genera of each constant light treatment (S=stochastic, C=constant, 8 to 100 revers to light transmission in %) [Achn=Achnanthes sp., Chro=Chroococcopsis sp., Cosm=Cosmarium sp., Euno=Eunotia sp., Frag=Fragilaria sp., Gomp=Gomphonema sp., Meri=Merismopedia sp., Moug=Mougotia sp., Navi=Navicula sp., Pinn=Pinnularia sp., Spir=Spirogyra sp., Stau=Staurastrum sp., Tetr=Tetraspora sp., Ulot=Ulothrix sp., Zygn=Zygnema sp.]

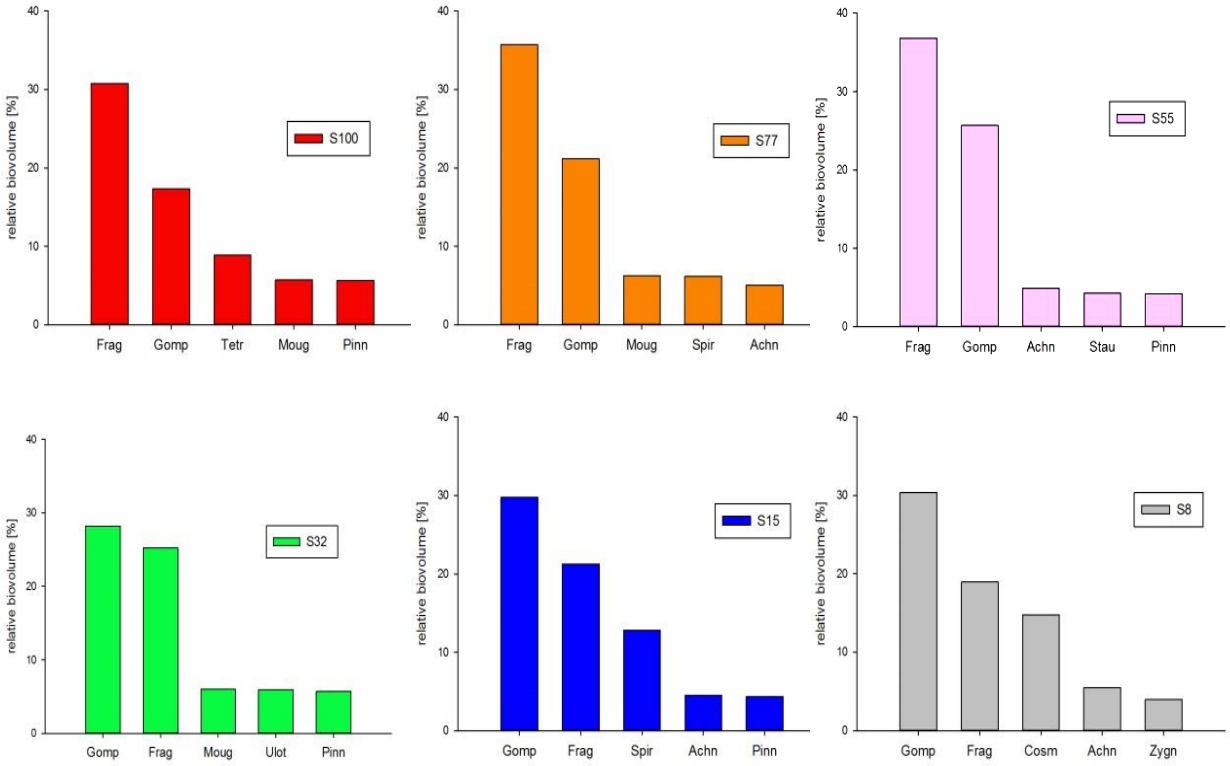


Figure 21: the 5 genera with highest biovolume of stochastic light treatments (S=stochastic, C=constant, 8 to 100 revers to light transmission in %) [Achn=Achnanthes sp., Chro=Chroococcopsis sp., Cosm=Cosmarium sp., Euno=Eunotia sp., Frag=Fragilaria sp., Gomp=Gomphonema sp., Meri=Merismopedia sp., Moug=Mougotia sp., Navi=Navicula sp., Pinn=Pinnularia sp., Spir=Spirogyra sp., Stau=Staurastrum sp., Tetr=Tetraspora sp., Ulot=Ulothrix sp., Zygn=Zygnema sp.]

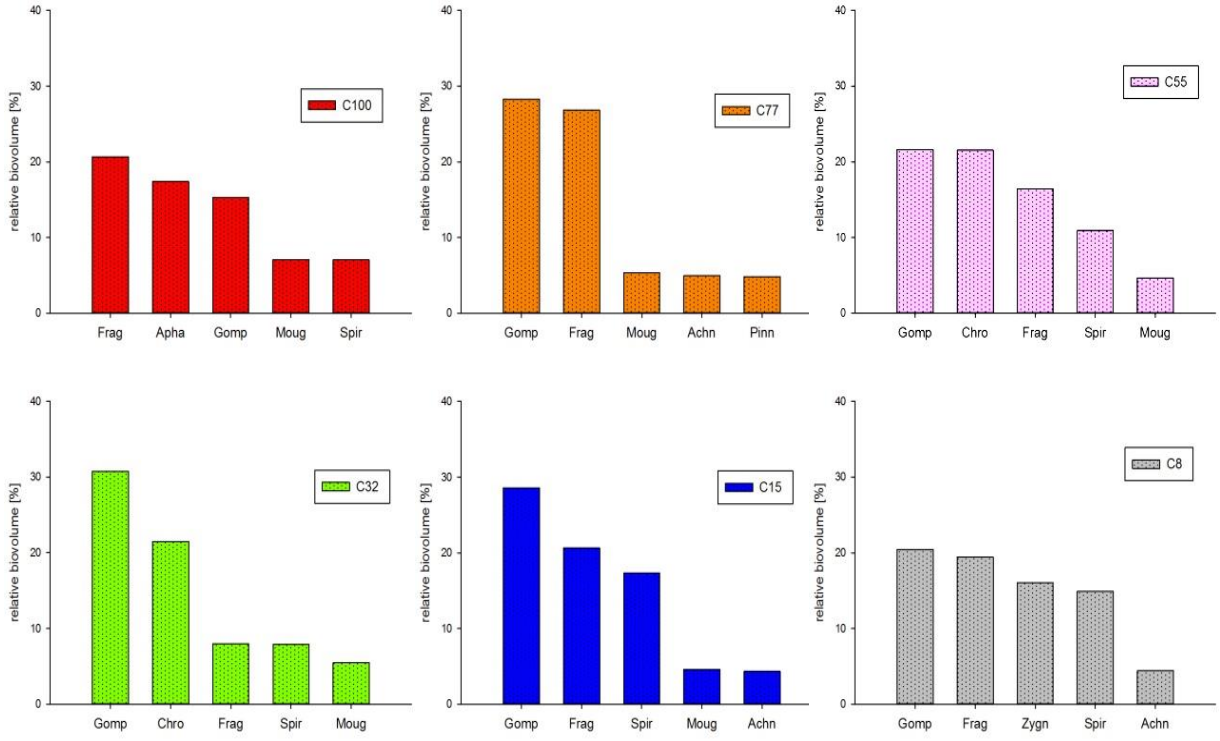


Figure 20: the 5 genera with highest biovolume of constant light treatments (S=stochastic, C=constant, 8 to 100 revers to light transmission in %) [Achn=Achnanthes sp., Chro=Chroococcopsis sp., Cosm=Cosmarium sp., Euno=Eunotia sp., Frag=Fragilaria sp., Gomp=Gomphonema sp., Meri=Merismopedia sp., Moug=Mougotia sp., Navi=Navicula sp., Pinn=Pinnularia sp., Spir=Spirogyra sp., Stau=Staurastrum sp., Tetr=Tetraspora sp., Ulot=Ulothrix sp., Zygn=Zygnema sp.]

Counted individuals of the most abundant genera were shaped in a nearly similar order; differences were more prominent in comparisons among highest biovolume. The relative distributions were also different; with high dominance by the genus *Achnanthes* sp. (dominated by *Achnanthes minutissima*) all other following genera did not even provide half of those cell numbers. Biovolume data draw a different pattern; the two genera with the highest volume did not show such a huge decline. Constant assemblies even showed nearly the same biovolume for the first and second prominent genus. It is obvious that in the stochastic treatment the genus *Fragilaria* sp., a colony forming algae, played a big role. Conspicuous was that the highest and the lowest light treatment equal there mating component of flow conditions.

Discussion

The aim of this study was to unravel the effects of flow and light regime on benthic algal communities, their biomass, composition and diversity. An unequivocal extraction of any robust statistical change in community composition of biofilm related to flow regime and light conditions was not possible, although biomass and abundance seem to be affected by flow. High light and low light availability seems to bear a challenge for algal species in benthic biofilms.

Effects of disturbances on algal communities depend on the initial algal abundance and on the intensity and frequency of disturbance, time since disturbance (community development) as well as nutrient and light supply (affecting resilience) (Stevenson, 1966).

Flow-induced influence is only visible in the magnitude of algal biomass and abundance. Uniform flow conditions lead to higher biomass and abundance. Lower biomass under variable flow regimes could be explained by the fact that impacts of disturbances are not uniform, depending on magnitude, frequency and duration, but result in a temporal biomass reduction and variability (Uehlinger et al., 2003). Benthic algae in the control flumes and in the poorly shaded treatments were not affected by the flow regime. The source of algal species an oligotrophic lake and we mimicked the dynamics of algal communities in the lake outlet. Our source of algal species may have contributed the positive effect of current because flow stochasticity is also dependent on nutrient abundance (Stevenson, 1966), even if higher discharge enhances nutrient replenishment to the benthic algae. Alterations in flow lead to a species-specific response (Poff and Zimmermann, 2010), shaping the community and further led to the fact, that matured communities withstand higher disturbances (Stevenson, 1996). Algal communities with intermediate light conditions were very similar and therefore the

influence of flow was hardly detectable, although stochastic discharges are more affected by flow. This lack of clear diversification between the flow regimes is probably caused by tight adhesions to the substrate by small adnate cells or filamentous algae (Stevenson, 1996) and by the stability of the provided sediment (Biggs and Smith, 2002). Treatments with low light and uniform flow seem to be independent of flow alteration. All these findings suggest that conditions of constant flow provide a more appropriate habitat for other algal classes, not just for Bacillariophyceae.

The three-dimensional structure of biofilms could cause elevated irradiance in the biofilm canopy and saturation to subsaturation irradiances towards the basis of the biofilm (Hill, 1996). This could explain the high biomass and lower chl *a* in high-light treatments. Interestingly, biovolume of algae growing under constant flow is more affected by light. Treatments with low light and constant flow suggest that light rather than flow drive algal biofilm structure. Hill et al. (1995) made similar observations and found that shading might select for species with a broad optimum range and that such systems may be controlled by light. Shaded algae adapt to low irradiances and require a high photosynthetic efficiency, leading to saturations at lower light intensities, but this provides only partial compensation (Hill, 1995). This may explain the low biomass and abundance in low-light treatments but also the moderate to high chl *a*. The finding that chl *a* was highest in the intermediate light treatment could be due to photosynthetic inhibition under high light irradiances. Algae in streams with little shading may have a pressure to develop mechanisms to reduce photoinhibition (Hill, 1966). Photoinhibition and chl *a* contents are also dependent on the development time and decrease with succession (Hill and Boston, 1991). Species-specific differences in light capturing pigments and membranes can lead to different light optima. Cyanophytes are better adapted to low light than Chlorophytes because Chlorophytes do not have accessory pigments (Hill, 1966). Although the results displayed that Cyanophytes played a minor part in community composition of heavy shaded habitats, this class is taking up a bigger sector just in flumes with constant flow and high to intermediate light availability.

The intermediate disturbance hypothesis suggests that in heterogeneous environments, under moderate disturbance conditions, highest diversity will be detected (Buckling et al., 2000). We failed to prove this prediction for our systems. Highest diversity was detected in the stochastic flow treatment in unshaded flumes and lowest diversity in the the treatments with moderate shading. Uniform flow conditions showed the highest diversity in shaded flumes of moderate and high-shading treatments.

Diatoms (Bacillariophyceae) comprise the richest group of autotrophic benthic species – both in our experimental setup and also in the region of Lunz (Müllner, 1999). In our experiment Chlorophytes represented a larger proportion than Cyanophyceae even though regionally seen Cyanophytes form the second largest taxonomical class. Considering the abundance data, Achnanthes sp. was the dominating group within all treatments. This genus contains many pioneering species and is generally tolerant to low light, shear stress and low nutrient conditions (Gottschalk et al., 2012). We found that Gomphonema sp. and Fragilaria sp. played a major role in the community composition, and greatly contributed abundance and biovolume. This supports our finding that diatom species with gelatinous stalks dominated the benthic communities in streams (Kann, 1933). Community composition may also be indirectly influenced by other factors like competition for space, low nutrient load, substrate affinity and species-specific optima depending on light, nutrients, substrate type and currents.

Regulations, water withdrawal and other degradations of natural streams increasingly alter the hydrological flow regime. Such changes could shift algal community composition and consequently even stream ecosystem functioning (Cardinale, 2011). As human well-being depends on the ecosystem functions and services of stream and rivers it is important to understand, which influence this alteration has on benthic autotrophic communities. The finding that uniform flow provides a different ascendency pattern as a natural variability is important and a shift in the community toward species with a broad optimum or invasive species is possible. Light availability plays a major role for phototrophic biofilms and above all influences the productivity of stream ecosystems. Increased erosion and fertilizer inputs into streams cause turbidity to increase, which may ultimately change the light regime in these systems and algal community structure as well.

We are aware that our work has some limitations. Ecological guilds are widely used in water quality assessment (Gotschalk et al., 2012). While this approach is efficient it may be too coarse, however, to detect clear effects. The fact that only fixed samples were used for identification results in uncertainty, due to degradation and changes of the cells. The same depth for all diatom volume calculation was used, which could lead to underestimations of larger diatoms and stretch the truth toward the other groups. Another limiting factor could be the experimental design, because only 3 replicates per condition were chosen and the variability between the flumes, within one light and flow treatment, was in some cases very high. For conditions of 77% light transmission and stochastic flow only two replicates were convenient and as a consequence this obliterates results. The uniform flow conditions, conducted taking the

mean of the variable flow regime, provided also a relatively high discharge and varied therefore in magnitude from alterations found in nature. Collectively, these considerations may have influenced the results of our study.

Conclusion

To conclude our findings, benthic phototrophic biofilms are influenced by a plurality of environmental factors through light and nutrient availability, natural flow disturbances and habitat characteristics. Recovery and resilience of a community and combinations of strategies to avoid pressures are important features of biofilm communities, shaping the community composition and structure. Algal growth and turnover of species are mainly influenced by light conditions, while flow variability affected biomass and community architecture.

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Zusammenfassung

Flusssysteme bieten Lebewesen sich ständig wandelnde Umweltbedingungen. Veränderungen im Abflussgeschehen über den Jahresverlauf oder wechselnde Lichtverhältnisse sind wichtige Faktoren an welche sich aquatische Organismen anpassen müssen. Zusätzliche Veränderungen durch den Menschen kann die Resistenz- und Resilienzfähigkeit des Systems und der darin vorkommenden Gemeinschaft beträchtlich verändern. Das Ziel dieser Arbeit war es, Informationen über den Einfluss von Licht und Durchfluss auf die autotrophe, benthische Gesellschaft zu generieren. Hierfür wurden 36 U-förmige Fließrinnen gebaut um zwei unterschiedliche Durchflussmodelle zu vergleichen. Ein System wurde von einem gleichbleibenden Durchfluss gespeist, während beim zweiten eine natürliche, stochastische Abfolge eines voralpinen, perennialen Baches (Oberer Seebach, Lunz) simuliert wurde. Ein Treatment umfasste je 18 Rinnen. Des Weiteren erzeugten 6 zufällig verteilte Lichtfolien artifizielle Beschattung und beeinflussten zudem Wachstum und Artgemeinschaft.

Im Allgemeinen scheint Licht eine sehr große Rolle in der Biomasseentwicklung zu spielen. Vor allem unter den erzeugten Extremen (8% und 100% Licht) und unter konstanten Fließverhältnissen dürfte Licht der entscheidende Faktor sein. Homogene Durchflussmengen führten zu höherer Individuenzahl und Biomasse, ebenso war eine Häufung von Cyanophyceen zu beobachten. Wobei die dominierende Algenklasse in den zu untersuchenden Rinnen Kieselalgen (Bacillariophyceae) waren, welche um die 80% der gezählten Individuen ausmachten. Leider konnte keine signifikante Erhöhung der Diversität bei mittleren Störungen nachgewiesen werden. Dies liegt möglicherweise an der geringen taxonomischen Auflösung (Gattungsniveau) und könnte bei verändertem Design zu anderen Resultaten führen.

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